



A Generic Revision and Phylogenetic
Analysis of the Dendrophylliidae
(Cnidaria: Scleractinia)

STEPHEN D. CAIRNS

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ABSTRACT

Cairns, Stephen D. A Generic Revision and Phylogenetic Analysis of the Dendrophylliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*, number 615, 75 pages, 3 figures, 14 plates, 3 tables, 2001.—The Dendrophylliidae comprises 29 genera and 364 valid species, of which 20 genera and 166 species are extant. The earliest known dendrophylliid is from the Early Cretaceous (Barremian) of Serbia, but they are common throughout the fossil record since the Cretaceous and today are worldwide in distribution (except off continental Antarctica) at depths of 0–2165 m. All 29 genera are diagnosed and discussed herein, and representatives (usually the type species) of 27 of the 29 genera are also figured. For each genus, the stratigraphic range and geographic distributions are discussed, and a list of valid species is given, including junior synonyms. Bathymetric ranges are given for all Holocene species and genera. One genus is described as new: *Pourtalopsammia*. Seven genera previously considered to be in the family are removed from the Dendrophylliidae: *Petrophyllia* Conrad, 1855 (an oculinid); *Turbinacis* Gregory, 1900 (a *Stylophora*); *Rhabdopsammia* Alloiteau, 1952 (an eusmiliid?); *Kumbiopsammia* Alloiteau, 1958 (an anthemiphylliid?); *Spongiopsammia* Kuzmicheva, 1987 (a sponge); *Patelopsammia* Reig Oriol, 1988 (a fungiid?); and *Ilerdopsammia* Reig Oriol, 1992 (a caryophylliid). Four other genera, also considered to be dendrophylliids, are herein considered to be of uncertain taxonomic position and are discussed but are not included in the phylogenetic analysis of the dendrophylliid genera: *Stereopsammia* Milne Edwards and Haime, 1850; *Desmopsammia* Reis, 1889; *Aplopsammia* Alloiteau, 1958; and *Makridinophyllia* Kuzmicheva, 1987. *Ceratopsammia* Alloiteau, 1958, is newly synonymized with *Balanophyllia* (*Eupsammia*). Finally, five new names are proposed for junior homonyms within the genus *Balanophyllia*.

Phylogenetic analysis of the 29 dendrophylliid genera was done using 10 characters, comprising 41 character states. The monophyly of the Dendrophylliidae is based on its possession of a synapcticulotheca in conjunction with having septa composed of only one fan system; preliminary molecular analysis also supports its monophyly. Relationships among taxa were determined based on parsimony (PAUP* ver. 4.0) and successive weighting of characters. The early Jurassic caryophylliid genus *Discocyathus* was used as the outgroup for the analysis. Twenty-seven equally parsimonious trees of 64 steps resulted from the phylogenetic analysis, each having a tree consistency index of 0.531. Characters that contributed highly to the phylogenetic hypothesis were corallum shape, colony form, budding type, and columella type. The cladograms do not support the interpretation of two subfamilies within the Dendrophylliidae; however, all colonial genera do form a clade. In general, the consensus tree is poorly supported, leading to the conclusion that, because of the paucity of characters available from a data set consisting of both fossil and Recent taxa, phylogenetic analysis of supraspecific coral taxa based solely on corallum morphology will usually produce inconclusive and/or poorly supported results.

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A Generic Revision and Phylogenetic Analysis of the Dendrophylliidae (Cnidaria: Scleractinia)

Stephen D. Cairns

Introduction

The Dendrophylliidae ranks third among all coral families in Holocene species richness (166/1314=12.6%) and ranks fourth among all coral families in Holocene genus richness (20/221=9.0%) (see Cairns, 1999b), resulting in an average of 8.30 Holocene species per genus, which is slightly above the average (5.37) for azooxanthellate genera (Cairns, 1997). Among the 12 scleractinian families that contain azooxanthellate species, the Dendrophylliidae has the second highest number of extant azooxanthellate species and the third highest number of genera (Cairns, 1997, 1999b). Whereas most (91%) of the Holocene dendrophylliid species are azooxanthellate, three genera, comprising 14 Holocene species, are exclusively zooxanthellate, and another genus, *Heteropsammia*, contains species that are facultative, containing zooxanthellae in shallow water but lacking them in deep water. The majority of dendrophylliid species considered to be valid (198/364=54.3%) are known only from the fossil record, as early as the Early Cretaceous (Barremian) (Table 1).

Dendrophylliids occur worldwide, except off Antarctica, and live at depths from the intertidal to 2165 m; however, they seem to be most common at depths of 50–300 m (Table 1). The genera have adopted a variety of solitary and colonial growth forms, allowing them to exploit a range of ecological niches. For instance, azooxanthellate dendrophylliids range in size from small, solitary, interstitial coralla only 5 mm in diameter

(e.g., *Notophyllia*) to large colonies up to 1 m in height (e.g., *Enallopsammia*) that, together with smaller coralla, contribute to the framework of deep-water coral banks found at depths of 600–800 m worldwide (Cairns and Stanley, 1982). Some of the zooxanthellate genera (e.g., *Turbinaria*, *Duncanopsammia*), as well as one azooxanthellate genus (*Tubastraea*), form large, robust colonies, contributing to shallow-water reef structure.

Many of the dendrophylliid genera end in the suffix “-psammia,” from the Greek *psammos* (meaning sand), which alludes to the fact that the skeletal porosity of the synapticulotheca of most dendrophylliids confers a rough, sandy texture, often like fine sandpaper, to the touch.

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

Museums and Collections

BM	The Natural History Museum, London (formerly the British Museum (Natural History))
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
NMV	National Museum of Victoria, Melbourne (now the Museum of Victoria)
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMW	Naturhistorisches Museum, Wien
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NZGS	New Zealand Geological Survey, Lower Hutt
SMNH	Swedish Museum of Natural History, Stockholm
USNM	United States National Museum, Washington, D.C. (collections of which are now in the NMNH)
YPM	Yale Peabody Museum, New Haven

Expeditions and Collecting Institutions

MUSORSTOM	cruises organized jointly by the Muséum National d'Histoire Naturelle and the Institut Français de Recherche Scientifique pour le Développement en Coopération
NZOI	New Zealand Oceanographic Institute, Wellington
TU	Tulane University, New Orleans
USGS	United States Geological Survey

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Other Abbreviations

CD	Calicular diameter
CI	Consistency index
C _x , P _x , S _x	Costal, palar, or septal cycle, respectively, designated by numerical subscript
GCD	Greater calicular diameter
ICZN	International Commission on Zoological Nomenclature
PAUP	Phylogenetic Analysis Using Parsimony (see Swofford, 1998)
PD	Pedical diameter
SEM	Scanning electron microscopy

MATERIAL AND METHODS.—This study was based on the collections of the USNM and on specimens loaned from nine other museums (see “Acknowledgements”). The USNM has a particularly good representation of Holocene dendrophylliid taxa, including many types, but it is poor in fossil specimens. Of the 30 valid dendrophylliid genera and subgenera, I have examined representatives of the type species of 27; in 16 cases I examined the type material of the type species. Representatives of the type species of three genera, *Palaeopsammia*, *Reussopsammia*, and *Stichopsammia*, could not be obtained, although a congeneric was examined and illustrated of the last genus. Descriptions from the literature were used in those cases. Material of the outgroup, *Discocyathus*, was not examined, but photographs of a topotypic specimen of *D. eudesii* Michelin, 1840, were made available to me by Jarek Stolarski, Institut Paleobiologii, Polish Academy of Sciences. Although emphasis was given to the type species in defining its genus, as many species as possible were examined within each genus to fully describe its variation.

Specimens of some dendrophylliid genera are very few in number and are poor in quality. Nine nominal genera are represented by only one or two lots from one or two localities and by only one to four specimens. The genera *Lamellophyllia*, *Wadeopsammia*, *Reussopsammia*, and *Stereopsammia* are each based on only one specimen. Because the type material was either unavailable, poor, or equivocal as to family, the genera *Stereopsammia*, *Desmopsammia*, *Aplopsammia*, and *Makridi-nophyllia* were not included in the main part of the descriptive text or in the phylogenetic analysis but were treated in a separate section entitled “‘Dendrophylliid’ Genera of Uncertain Position.”

The generic synonymies include the original description, references to the standard comprehensive revisions of the order (i.e., Milne Edwards and Haime, 1848, 1850, 1851; Milne Edwards, 1860; Duncan, 1884; Vaughan and Wells, 1943; Alloiteau, 1952; Wells, 1956; and Chevalier and Beauvais, 1987), and any other significant reference that diagnosed and/or discussed the genus and its species. Generic diagnoses were written in telegraphic style to facilitate comparison, and discussions include taxonomic histories, comparisons to other genera, and a brief discussion of their phylogenetic relationships. The “distribution” sections list stratigraphic ranges and locations as well as bathymetric ranges of extant taxa (see also Table 1). The following information is provided for the type species of each genus: method of determination, type locality and broader distri-

bution, and deposition (if known). Other species in the genus are listed in stratigraphic order, oldest first. Fossil species are accompanied by their age and occurrence, extant species are accompanied by their bathymetric range and occurrence. In larger genera, the extant species are subdivided in geographic regions. When known, junior synonyms and homonyms are indicated.

To improve contrast for photography, some specimens were dyed black with a cloth dye and subsequently were recoated with a fine layer of sublimed ammonium chloride.

This is the second in a proposed series of generic revisions of the azooxanthellate coral families, the first being of the Turbinoliidae (Cairns, 1997).

ACKNOWLEDGEMENTS.—I would like to thank the following people, who loaned specimens to me used in this study or who allowed me to study the specimens housed in their institution. The publications in which these specimens were originally reported are also listed to aid future workers in locating these type depositories. R.T. Becker of the Museum für Naturkunde, Universität zu Berlin (Dietrich, 1917); J.G. Darrell of BM (Gregory, 1900; Milne Edwards and Haime, 1850); A. Johnston of the MCZ (Pourtalès, 1868, 1878); E. Lazo-Wasem of YPM (Verrill, 1870); J. Leloux and C.F. Winkler of the National Museum of Natural History, Naturalis, Leiden (Umbgrove, 1925); C. Perrin of the Paleontology Department of the MNHN (Alloiteau, 1952, 1958; Chevalier, 1961); G. Rosenberg of the Academy of Natural Sciences of Philadelphia (Conrad, 1855b); O. Schultz of the NHMW (Seguenza, 1864); and J. Vilella i Puig of the Museo Geológico del Seminario de Barcelona (Reig Oriol, 1992). I also thank Rosemarie Baron-Szabo, Hannes Löser, Vladimir Kosmynin, and Helmut Zibrowius for helping me to locate fossil type specimens. Jarek Stolarski was helpful in choosing an outgroup for the phylogenetic analysis and in providing the photographs of *Discocyathus eudesii*. Deborah Danaer assisted in the phylogenetic analyses. Figures 1–3 were drafted by NMNH staff illustrator Molly Ryan. The scanning electron photographs were taken in the SEM Laboratory of the NMNH with the assistance of Susann Braden.

Phylogenetic Analysis

OUTGROUP SELECTION

The choice of a sister group for the Dendrophylliidae that would serve as an outgroup for a phylogenetic analysis of the genera within the family is by no means clear. Essentially there are two conflicting points of view: a Late Jurassic poritoid ancestor or a Late Jurassic caryophylliid ancestor, the choice depending on the weight attributed to morphological characters of wall structure or septal structure and the molecular biology of Holocene taxa. The oldest/traditional point of view, which emphasizes septal microstructure, is that the dendrophylliids evolved from an early caryophylliid stock, such as the Theco-cyathinae. This view was advocated by Vaughan and Wells (1943:98, 233), Wells (1956), and Roniewicz and Morycowa

TABLE 1.—Summary of the distribution and the stratigraphic and depth ranges of the dendrophylliid genera and subgenera, listed from oldest to most recent origins. Number of species is presented as the total number of valid species followed by the component that are exclusively fossil and those that are known from the Holocene; the number of Holocene species with a fossil record is indicated in parentheses. († indicates an exclusively fossil genus.)

Genus	Stratigraphic range	Distribution (F = fossil; H = Holocene)	Depth range (m)	Number of species
† <i>Palaeopsammia</i>	Early Cretaceous (Barremian)—early Paleocene	F: Europe; North Africa; Madagascar; Bonaire	—	4:4/0
† <i>Calostylopsis</i>	Early Cretaceous (Albanian)	F: Madagascar	—	1:1/0
<i>Balanophyllia</i> (<i>Eupsammia</i>)	Late Cretaceous (Campanian)—Holocene	F: Europe; USA; New Zealand; Jamaica; Madagascar. H: Indo-West Pacific; West Atlantic	18–170	45:39/6(1)
† <i>Wadeopsammia</i>	Late Cretaceous (Campanian)	F: USA (Tennessee)	—	1:1/0
† <i>Areopsammia</i>	Late Cretaceous (Maastrichtian)	F: the Netherlands	—	1:1/0
<i>Dendrophyllia</i>	early Paleocene (Danian)—Holocene	F: Europe; USA; Africa; South America; Japan; Indonesia. H: cosmopolitan in tropical and temperate oceans	1–900	74:45/29(4)
<i>Balanophyllia</i> (<i>Balanophyllia</i>)	Paleocene–Holocene	F: Europe; USA; North Africa; New Zealand; Australia; Java; Peru. H: cosmopolitan except Antarctica	0–1150	129:75/54(1)
<i>Tubastraea</i>	late early Eocene–Holocene	F: Antarctica; USA. H: circumtropical	0–110	8:2/6(1)
† <i>Lobopsammia</i>	middle Eocene (Lutetian)—middle Oligocene	F: Europe	—	5:5/0
<i>Endopachys</i>	early Eocene (early Claibornian)—Holocene	F: USA; Northwest Pacific. H: Indo-Pacific	37–386	7:5/2(1)
† <i>Stichopsammia</i>	middle Eocene (Bartonian)—early Oligocene	F: Europe	—	2:2/0
<i>Enallopsammia</i>	late Eocene–Holocene	F: Europe; Tonga. H: cosmopolitan except East Pacific	110–2165	7:4/3
† <i>Reussopsammia</i>	middle Oligocene	F: Germany	—	1:1/0
<i>Turbinaria</i>	early Miocene (Aquitanian)—Holocene	F: Europe; North Africa; West Pacific. H: tropical Indo-West Pacific	reef depths	14:2/12(3)
† <i>Paleoastroides</i>	early Miocene (Aquitanian)—middle Miocene (Helvetian)	F: Europe	—	4:4/0
<i>Notophyllia</i>	middle Miocene (Balcombian)—Holocene	F: Victoria, Australia. H: southern Australia	22–458	7:4/3
† <i>Lamellophyllia</i>	middle Miocene	F: Italy	—	1:1/0
<i>Leptopsammia</i>	middle Miocene (Vindobonian)—Holocene	F: Azores. H: Atlantic; West Pacific; East Indian Ocean	3–900	11:1/10
<i>Heteropsammia</i>	late Miocene–Holocene	F: West Pacific. H: tropical Indo-West Pacific	1–622	3:0/3(1)
<i>Eguchipsammia</i>	late Miocene–Holocene	F: Dominican Republic. H: circumtropical, except East Pacific	25–988	8:0/8(1)
<i>Rhizopsammia</i>	Pliocene–Holocene	F: USA (California). H: circumtropical, except East Atlantic	0–278	11:1/10
<i>Cladopsammia</i>	late Pliocene–Holocene	F: England; Africa. H: circumtropical	0–470	6:0/6
<i>Duncanopsammia</i>	late Pliocene–Holocene	F: Papua New Guinea. H: West Pacific	6–34	1:0/1(1)
<i>Astroides</i>	late Pleistocene–Holocene	F and H: Mediterranean	0–30	1:0/1(1)
<i>Thecopsammia</i>	Holocene	West Atlantic; Southwest Pacific	214–879	3:0/3
<i>Endopsammia</i>	Holocene	tropical Indo-Pacific	0–73	3:0/3
<i>Bathypsammia</i>	Holocene	Northwest Atlantic	183–1115	3:0/3
<i>Pourtalopsammia</i>	Holocene	off South Africa	155–775	1:0/1
<i>Trochopsammia</i>	Holocene	Northwest Atlantic	532–1472	1:0/1
<i>Dichopsammia</i>	Holocene	Korea Strait	20–30	1:0/1
Total				364:198/166(15)

(1993). Although Vaughan and Wells (1943) acknowledged that dendrophylliids superficially resemble fungiids (e.g., poritoids) in having a synapticulotheca, they weighted septal microstructure (i.e., numerous simple trabecular in one fan system producing a septum with a smooth axial edge) more highly than wall structure, this concept also forming the basis for their key to the coral suborders (Vaughan and Wells, 1943: 100–101). Roniewicz and Morycowa (1993) likewise based their decision on the fact that caryophylliids and dendrophylliids have minitrabeculate septa, whereas poritoids have thick trabecular septa.

In the opposing morphological camp, Kuzmicheva (1986) included three other families in the suborder Dendrophylliina, which theretofore had contained only Dendrophylliidae. These co-subordinal families would obviously be potential candidates for the sister group to Dendrophylliidae. The additional

families were Micrabaciidae, Actinacididae, and Poritidae. These families were included in the suborder because of their similar synapticulothecate wall, which, according to Kuzmicheva (1986:8), was the viewpoint advocated by Vaughan and Wells (1943). Clearly, however, this was not the opinion of Vaughan and Wells (1943:98, 233), who advocated a caryophylliid affinity of the dendrophylliids, Kuzmicheva's misconception apparently resulting from a faulty translation or a misinterpretation of the subordinal diagnosis of Vaughan and Wells (1943:233). Nonetheless, Chevalier and Beauvais (1987), based on the synapticulothecate argument, also included three additional families in the suborder Dendrophylliina: Micrabaciidae, Actinacididae, and Astraraeidae (the family Poritidae being placed in the suborder Fungiina). As a historical footnote to the morphological evidence, Alloiteau (1952) skirted the issue by considering the Dendrophylliidae to

be a "transitional group" between the caryophylliids and the fungiids (which include the poritoids), and Veron (1995, fig. 25) implied that the Dendrophylliidae evolved from the Astraraeidae (sic) but gave no supporting evidence.

Using molecular sequencing of parts of 16S rRNA, Romano and Palumbi (1996) indicated a close affinity between the dendrophylliid genera and the poritoid genera, the caryophylliid genera being far removed; however, it should be noted that relatively few taxa were used in this analysis. Later analyses (Romano and Cairns, 2000), using more taxa and analyzing both 16S rRNA and 28S rRNA molecular segments, showed a less convincing affinity when analyzed at a bootstrap support level of 70. In another analysis by Veron et al. (1996) that sequenced part of the 28S rDNA molecule, a similar affinity was found between dendrophylliid and poritoid genera, leading them to postulate a common ancestor for these two families. It is interesting to note, however, that their analysis did not include any caryophylliid taxa.

Thus, five families may be considered as outgroups for the Dendrophylliidae: Caryophylliidae (based on septal microstructure), Micrabaciidae (based on wall microstructure), Poritidae (based on wall microstructure and molecular evidence), Actinacididae (based on wall microstructure), and Astraraeidae (based on wall microstructure). Micrabaciidae was eliminated from consideration because it does not have a Pourtalès plan arrangement of septa and because its "synapticulotheca" is not homologous to that of the dendrophylliids. If one is looking for not only an outgroup but a possible ancestor to the Dendrophylliidae, then Poritidae must be eliminated because its earliest occurrence is Middle Cretaceous, whereas the dendrophylliids are known from the Early Cretaceous. The probable ancestors to the Poritidae, however, the Actinacididae (see Vaughan and Wells, 1943:151), contain three genera that occur in the Late Jurassic: *Actinaraea*, *Dendraraea*, and *Actinaraeopsis*. These genera are all characterized by having colonial coralla (with intratentacular budding), twice the number of costae as septa, and three to five thick trabeculae per septum. All five of the earliest dendrophylliid genera (those occurring in the Cretaceous) are solitary, have a 1:1 septa:costae ratio, and have numerous minitrabeculae per septum. Furthermore, intratentacular budding did not appear in the dendrophylliids until the middle Eocene. Thus, it is difficult to believe that actinacidids were the ancestor of the dendrophylliids. Similarly, two of the three genera of Astraraeidae are intratentacular colonial forms. The third genus, *Haplaraea*, is solitary, fixed, and has an epitheca. Although it is a possible ancestor to the early dendrophylliids, *Haplaraea* has thick (compound) septal trabeculae, which is not consistent with dendrophylliid minitrabeculate septa. The caryophylliids are the most likely ancestor and outgroup for the dendrophylliids, this choice relying on the more conservative nature of septal structure compared with wall structure, as suggested by Vaughan and Wells (1943). There are only seven solitary caryophylliid genera known to exist before the origin of the dendrophylliids: *Thecocyathus* (Early Juras-

sic), *Discocyathus* (Middle Jurassic to Middle Cretaceous), *Trochocyathus* (Middle Jurassic to Holocene), *Caryophyllia* (Late Jurassic to Holocene), *Dungulia* (Late Jurassic), *Tiarasmilia* (Early Cretaceous), and *Parasmilia* (Early Cretaceous). The first two genera (*Thecocyathus* and *Discocyathus*), constituting the subfamily Thecocyathinae, are considered to be the ancestral and least derived group in the Caryophylliidae (Vaughan and Wells, 1943:201) and were thus considered to be more likely candidates for the outgroup. *Thecocyathus* was eliminated from consideration because its microstructure is unknown, and thus its inclusion in this family is somewhat doubtful (J. Stolarski, pers. comm., 1999), which, by default, left *Discocyathus* as the outgroup chosen for the analysis.

ANALYSIS OF DENDROPHYLLIID GENERA AND CHARACTERS USED

Phylogenetic trees were generated in accordance with the principle of parsimony using PAUP* 4.0 (Beta version 4.0b2) (Swofford, 1998). Characters were coded as binary variables (0, 1) or as multistate characters (0, 1, 2, etc.), the 0 state reflecting the outgroup, or presumed ancestral, condition. Multistate characters were treated as unordered except characters 2 and 4 (see discussion of characters, below). If a genus contained two states of a character, the state of the type species was used in the analysis. If the type species was polymorphic for that character, both states were included in the data matrix (see three instances in Table 3). Question marks were used in the data matrix only if the character state was unknown, not if it was inapplicable. A heuristic search was carried out using a simple stepwise addition sequence followed by branch swapping using the tree bisection-reconnection (TBR) procedure. The heuristic search, using equal character weighting, resulted in 1547 equally parsimonious trees. Other combinations of addition sequences and branch swapping produced the same number of equally parsimonious trees. The successive weighting option (Farris, 1969; Carpenter, 1988) of PAUP* 4.0 was applied to these trees, which resulted in a considerably smaller number of equally parsimonious trees through the process of a posteriori weighting of the characters based on their rescaled CI. The adjusted weights for the 10 characters in this weighted analysis are given in Table 2.

The following characters were used in the analysis:

1. CORALLUM SHAPE.—This character is primarily a descriptor of the shape of solitary dendrophylliid coralla, all colonial genera being lumped as one character state (i.e., *colonial*, state 5), the states of which are amplified in character 2. Most solitary dendrophylliids have *conical* (Plate 2a) (state 3) coralla; state 0, *discoideal* (Plate 1a), state 1, *bowl-shaped* (Plate 1d), and state 2, *globular* (Plate 2i), are autapomorphic, with the discoideal state found only in the outgroup. A *cuneiform*-shaped corallum (Plate 8a) (state 4) is associated with transverse division. The multiple states of this character were considered to be unordered in the analysis.

TABLE 2.—Characters and character states used in the phylogenetic analysis of the dendrophylliid genera and outgroup as presented in Table 3 and Figures 1, 2. Values in parentheses are the consistency indices for each character, followed by the weight of that character as determined by successive weighting.

<i>Gross Morphology of Corallum</i>	
1.	Corallum shape: 0, discoidal; 1, bowl shaped/patellate; 2, globular; 3, conical; 4, cuneiform; 5, colonial (1.0, 0.77).
2.	Colony form: 0, none (solitary); 1, stoloniferous (reptoid); 2, budding from common basal coenosteum; 3, arborescent; 4, detached buds; 5, plocoid; 6, flabellate (0.86, 1.0).
3.	Budding type: 0, none (solitary); 1, extratentacular; 2, intratentacular (1.0, 1.0).
4.	Corallum attachment: 0, free (unattached); 1, attached; 2, attached, but propagating by transverse division (0.50, 0.59).
<i>Thecal Structure</i>	
5.	Synapticulotheca: 0, granular costae; 1, hispid costae; 2, uniformly granular theca; 3, uniformly hispid theca; 4, finely serrate ridges (0.33, 0.22).
6.	Epitheca: 0, present; 1, absent (0.17, 0.14).
7.	Endotheca: 0, absent; 1, present (0.20, 0.17).
<i>Calicular Elements</i>	
8.	Septal arrangement: 0, normal; 1, Pourtales plan in adult stage; 2, reticulate (0.29, 0.23).
9.	Columella: 0, papillose; 1, spongy; 2, lamellar; 3, solid; 4, absent; 5, labyrinthiform; 6, swirled lamellae; 7, trabecular (0.67, 0.26).
<i>Zooxanthellae</i>	
10.	Zooxanthellae: 1, absent; 2, present (0.67, 0.11).

2. COLONY FORM.—The character of the corallum shape of colonial dendrophylliids was one of two multistate characters in which the character states were partially ordered based on the

TABLE 3.—Character matrix used in the phylogenetic analysis of dendrophylliid genera and outgroup, as defined in Table 2. Polymorphic conditions are indicated by "+." Questions marks were used when the character state was applicable but unknown.

Genus	Characters									
	1	2	3	4	5	6	7	8	9	10
<i>Discocyathus</i>	0	0	0	0	0	0	0	0	0	0
<i>Areopsammia</i>	1	0	0	0	?	1	0	0	0	?
<i>Palaeopsammia</i>	1+3	0	0	0	0	0	0	0	1	?
<i>Balanophyllia (Balanophyllia)</i>	3	0	0	1	1	0	0	1	1	1
<i>B. (Eupsammia)</i>	3	0	0	0	1	0	0	1	1	1
<i>Lamellophyllia</i>	3	0	0	0	0	1	0	1	2	?
<i>Heteropsammia</i>	2	0	0	0	4	1	0	1	1	1+2
<i>Wadeopsammia</i>	3	0	0	0	2	1	0	1	3	?
<i>Calostylopsis</i>	3	0	0	0	0	1	0	2	1	?
<i>Bathypsammia</i>	3	0	0	1	4	0	0	0	1	1
<i>Pourtalesopsammia</i>	3	0	0	1	3	0	0	0	4	1
<i>Trochopsammia</i>	3	0	0	1	0	0	0	0	4	1
<i>Endopsammia</i>	3	0	0	1	0	0	0	1	0	1
<i>Leptopsammia</i>	3	0	0	1	1	0	1	0	1	1
<i>Thecopsammia</i>	3	0	0	1	3	0	0	1	6	1
<i>Endopachys</i>	4	0	0	2	1	1	0	1	1	1
<i>Notophyllia</i>	4	0	0	2	1	0	0	0	1	1
<i>Eguchipsammia</i>	5	4	1	0	1	0	1	1	1	1
<i>Rhizopsammia</i>	5	1	1	1	0	0	0	1	1	1
<i>Cladopsammia</i>	5	2	1	1	0	0	1	1	0	1
<i>Paleoastroides</i>	5	5	1	1	4	0	1	1	6	?
<i>Astroides</i>	5	5	1	1	1	0	1	0	1	1
<i>Tubastraea</i>	5	5	1	1	0	1	1	0	1	1
<i>Turbinaria</i>	5	5	1	1	4	1	1	0	1	2
<i>Dendrophyllia</i>	5	3	1	1	1	1	1	1	0+1	1
<i>Enallopsammia</i>	5	3	1	1	1	1	0	0	0	1
<i>Duncanopsammia</i>	5	3	1	1	4	1	0	1	5	2
<i>Dichopsammia</i>	5	3	2	1	0	1	1	1	7	2
<i>Lobopsammia</i>	5	3	2	1	0	0	0	1	7	?
<i>Stichopsammia</i>	5	6	2	1	0	1	0	1	7	?
<i>Reusopsammia</i>	5	6	2	1	0	1	0	0	4	?

ontogenetic criterion (Figure 1A). Assuming that the outgroup, and thus the ancestral condition, of the dendrophylliids is a *solitary* corallum (state 0), it is logical to assume (Cairns, 1994) that the first stage of coloniality would be *reptoid* (Plate 8i) budding (state 1), as characterized by the genus *Rhizopsammia*. A filling in of the substrate voids created by reptoid budding may produce *budding from a common basal coenosteum* (Plate 9d,f) (state 2), from which corallites bud at random, characteristic of the genus *Cladopsammia*, or a *plocoid* (Plate 10a) corallum (state 5), if corallite integration is close and uniform, such as in *Astroides*. The other character states, *detached budding* (Plate 8c) (state 4), *arborescent* (Plate 11g) (state 3), and *flabellate* (Plate 13d) (state 6) were considered to be unordered.

3. BUDDING TYPE.—There are basically two types of budding in colonial dendrophylliids: the more common *extratentacular* (Plate 11b) (state 1) and the less common *intratentacu-*

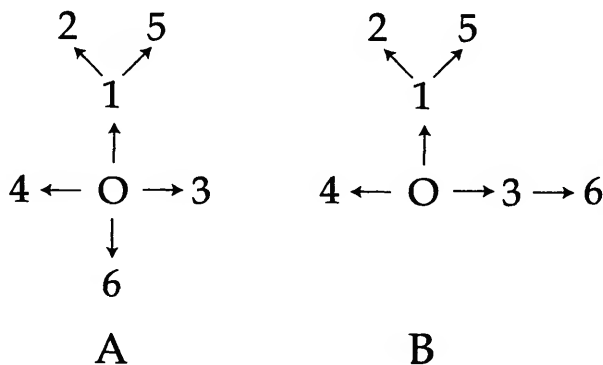


FIGURE 1.—Ordered character-state transformations for character 2 (colony form). A, original partial ordering used in phylogenetic analysis; B, ordering suggested by results of phylogenetic analysis. Character states: 0, solitary; 1, stoloniferous; 2, budding from common basal coenosteum; 3, arborescent; 4, detached buds; 5, plocoid; 6, flabellate.

lar (Plate 12j,k) (state 2), the outgroup being a noncolonial coral and thus having the 0 state (*none*) for this character. No ordering of these character states was assumed. Among the four genera that bud intratentacularly, two have distomadeal budding and two have polystomadeal budding, the latter producing flabellate coralla, a character state already included in character 2 (colony form) and thus not duplicated herein.

4. CORALLUM ATTACHMENT.—Dendrophylliid coralla occur *free* (unattached to the substrate) (Plate 2a) (state 0) or *attached* (Plate 6c) (state 1), the outgroup condition being free. A third state, *transverse division* (Plate 7b,e) (state 2), is a modification of the attached state, in that all scleractinian genera that transversely divide do so from an attached anthocaulus portion, asexually generating a proximal anthocyathus that detaches from the base. This phenomenon has been reviewed by Cairns (1989b) and is fairly widespread within various suborders and families of the Scleractinia. Ontogenetically, the transversely dividing condition thus follows the attached condition, and this three-state character is ordered as free to attached to transversely dividing.

5. SYNAPTICULOTHECA.—The synapticulotheca of dendrophylliids is an irregularly porous structure through which tissue is continuous from inside the corallum to outside. Because coenosarc covers the outside of the corallum, at least on the proximal portion, the exterior microarchitecture of the synapticulotheca is often well preserved and distinctive. This microarchitecture may be expressed in one of five ways. Longitudinal *costae*, one corresponding to each septum, may cover the exterior of the corallum, the costae covered with low, rounded *granules* (Plates 10i, 12m) (state 0) or slender, *hispid spines* (Plate 8e,f) (state 1). The corallum may also be covered *uniformly* with low rounded *granules* (Plate 3g) (state 2) or slender *hispid spines* (Plate 6f,h) (state 3), neither of which are arranged in longitudinal rows. Finally, the synapticulotheca may be covered with longitudinally arranged *finely serrate ridges* (Plate 12h,i), usually more than one corresponding to each septum (state 4). The outgroup state is costae covered with low, rounded granules, but no logical assumptions could be made about the other states, and thus they were left unordered in the analysis.

6. EPITHECA.—As the edge zone retreats up the side of the corallum, an epitheca, sometimes quite well developed, is sometimes secreted from its lower edge (Stolarski, 1996). This relatively smooth epitheca covers the underlying synapticulothecal granules or spines, sometimes rising almost to the calicular margin. The outgroup condition is to have an *epitheca present* (Plates 4b, 6f), the derived condition is assumed to be *epitheca absent*.

7. ENDOTHECA.—Within some coralla, especially elongate ones, tabular endothecal dissepiments are produced, resulting in a reduced volume of living space available to the coral and reducing the amount of calcium carbonate needed to infill the proximal corallum. The outgroup state is *endotheca absent*, the derived state is assumed to be *endotheca present* (Plates 9j, 12l).

8. SEPTAL ARRANGEMENT.—The “*normal*” arrangement of septa (Plate 4f) (state 0) in Scleractinia usually results from the septa of each successive cycle being smaller (less wide) than those of the previous cycle, having free axial edges, being relatively straight, and numbering twice the complement of the previous cycle. Most of these conditions are violated in the *Pourtalès plan* arrangement of septa (Plates 2e, 7d, 11h) (state 7), which is common to many dendrophylliid genera. The Pourtalès plan was first described by Pourtalès in 1871; it was expounded upon by Duerden (1904a, 1904b) and was named the “law of Pourtalès and Duerden” by Bourne (1905:207). Later it was simply called the Pourtalès plan. It is a form of septal substitution whereby the septa of the second and higher cycles bifurcate at their outer edges (edge adjacent to the synapticulotheca) but maintain their axial edges as one septum. The next cycle of septa forms within the space created by the bifurcated outer edge of the septa of the previous cycle and traditionally takes the number of that cycle, the bifurcated septal pair being renumbered to a higher cycle. This process may repeat for several cycles, resulting in the higher/highest cycle septa (those most recently formed) being the shortest septa and the other cycles being often curved, their axial edges joined in pairs. This process is more fully explained and illustrated by Duerden (1904a, 1904b), Bourne (1905), Wells (1956), Chevalier (1959), or Chevalier and Beauvais (1987). According to Fadlallah and Pearse (1982), the septal cavities produced as a result of the Pourtalès plan serve as brood chambers, allowing embryos to reach a large size before release as well as separating the embryos from the main digestive cavity so that feeding and brooding do not interfere with each other. The outgroup condition is the *normal* arrangement, the *Pourtalès plan* is considered derived. One genus, *Calostylopsis*, has a unique septal arrangement characterized as being *reticulate* (state 2). The three character states were left unordered in the analysis.

9. COLUMELLA.—There are seven types of columellar structures among the dendrophylliid genera: *papillose* (Plate 9e) (state 0), *spongy* (Plates 5h, 8d) (state 1), *lamellar* (Plate 2d) (state 2), *solid* (Plate 3i) (state 3), *labyrinthiform* (Plate 12g) (state 5), *swirled lamellae* (Plate 6e) (state 6), and *trabecular* (Plate 13b) (state 7). A columella may also be *absent* (Plate 4f) (state 4). For the most part, each genus has only one state. The outgroup state is *papillose*, but no logical assumptions could be made about the other states, and thus they were all considered to be unordered.

10. ZOOXANTHELLAE.—The *presence* (state 2) or *absence* (state 1) of zooxanthellae in the tissue of all Holocene genera is recorded but is scored as a question mark for all nine exclusively fossil genera, as well as for the outgroup. Because the condition of the outgroup was unknown, a zero state was not included in this character. No ordering or even polarity is assumed for this character.

RESULTS AND DISCUSSION

Numerous (1547) equally parsimonious trees were generated in the heuristic search of the 29 dendrophylliid genera. Successive weighting reduced the number of most-parsimonious reconstructions to 27 trees, each with 64 steps and a CI of 0.531. The rescaled weight of each character as used in the successive weighting algorithm is given in Table 2. Among the 27 trees, one had the precise topology of the 50% majority rule consensus tree, and thus that tree (Figure 2) was used as a basis for further discussion of genus and character evolution, with the slight modification that the two subgenera of *Balanophyllia* were forced into a monophyletic grouping at the expense of one extra step, resulting in a decreased tree CI of 0.523. Before this modification, the nominate subgenus of *Balanophyllia* was grouped in a polychotomy with *Thecopsammia* and the branch leading to *Endopachys* and *Notophyllia*. The 50% majority rule consensus of the 27 trees showed 100% support for all but six branches; those branches were all supported at the 67% level.

CHARACTER ANALYSIS.—The first four characters pertain to aspects of the gross morphology of the corallum. Character 1 (corallum shape) has a CI of 1 on the illustrated tree (Figure 2), meaning that no homoplasy is encountered in distributing its character states on this tree. This suggests that the ancestral state of a discoidal corallum evolved into the bowl-shaped form and the bowl-shaped form into the conical corallum, from which the globular, cuneiform, and colonial states evolved. The transition to state 5 (colonial) helps to unify the colonial corals as the most highly derived clade, this state being further amplified as character 2 (colony form), which also has the relatively high CI of 0.86. Character 2 was an ordered character (Figure 1A), showing little homoplasy on the tree. The only homoplasy is the reversal from state 3 to state 6 at the stem that supports *Stichopsammia* and *Reussopsammia*, which, because of the way in which these states were ordered, is a two step change. It is perhaps more logical to posit that state 6 (flabellate) evolved from state 3 (arborescent) by the acquisition of intratentacular budding from an extratentacular arborescent ancestor (see character 3), which would eliminate homoplasy from character 2 altogether (Figure 1B). The CI of character 3 (budding type) is 1.0, suggesting that the solitary state gave rise to the extratentacular state, which then gave rise to the intratentacular state, which would be consistent with the evolution of a flabellate intratentacular genus from an arborescent extratentacular ancestor. The fourth character, concerning gross morphology (character 4, corallum attachment), has a low CI of 0.50, the tree indicating that attachment evolved twice and reversed once (the reversal on the terminal branch leading to *Eguchipsammia*), whereas transverse division is suggested to have evolved only once, helping to unite *Endopachys* and *Notophyllia* in a clade.

Characters 5–7 pertain to the thecal structure of the corallum. Concerning the states of character 5 (synapticulotheca), Wells (1936a) noted that the distinctive serrate ridges (state 4, herein) of *Duncanopsammia*, *Turbinaria*, and *Heteropsammia* differed

from the wall microarchitecture of other dendrophylliids, and Vaughan and Wells (1943) used the presence or absence (replaced by spines) of costae as a character in his key to the dendrophylliid genera. Thus, the synapticulothecal microarchitecture of all dendrophylliid genera was examined and illustrated in the hope that it would support groupings of genera in a cladistic fashion. Unfortunately, the CI of this character was 0.33, requiring 12 steps to distribute the four derived character states on the illustrated tree, indicating that this character has little phylogenetic value. Character 6 (epitheca) is also a poorly supported character, having a CI of 0.17, the illustrated tree suggesting that the ancestral state of having an epitheca was independently lost five times and reacquired once (in *Lobopsammia*). The low value of this character is not surprising, as Duncan (1873) and van der Horst (1922:49) noted that the species of some genera, such as *Balanophyllia* and *Notophyllia*, may be either epithecate or nonepithecate. Nonetheless, the character is usually consistent within a genus, and Vaughan and Wells (1943) also used it to help define various dendrophylliid genera in their key to the dendrophylliid genera. But, although it may be a useful character in defining genera, it seems to have little phylogenetic value. Presence of an endotheca (character 7) is also a highly homoplastic character, having a CI of 0.20. It has never been used to key dendrophylliid genera or to suggest evolutionary relationships; it is perhaps simply a common adaptation of elongate dendrophylliid coralla.

Vaughan and Wells (1943) used the presence of the Pourtalès plan (character 8, state 1) in the adult stage of dendrophylliid genera as the primary discriminator in their key to the dendrophylliid genera, and Alloiteau (1952) used it more formally as the basis for dividing the Dendrophylliidae into two subfamilies. Kuzmicheva (1987) also adopted this character to define two evolutionary lineages among the dendrophylliid genera. On the other hand, Duncan (1884) and Wells (1933) considered the Pourtalès plan to be secondary to the character of the corallum being colonial or solitary, i.e., Wells (1933) considered the Eupsammidae to contain the solitary genera and the Dendrophylliidae to contain the colonial forms. Kuzmicheva (1987) considered the multiple origin of coloniality to be due to heterochronic parallelism, whereas the present analysis suggests one origin of coloniality in the early Paleocene (i.e., *Dendrophyllia*). Wells (1956) and Chevalier and Beauvais (1987) did not comment on the issue, uniting all dendrophylliid genera into one homogeneous family. The illustrated cladogram favors a phylogeny that emphasizes colony form in preference to septal arrangement, the CI of character 8 being only 0.29; the illustrated tree suggests the acquisition of the Pourtalès plan twice and its loss four times. It should be mentioned, however, that the aspect of coloniality in dendrophylliids may have been unintentionally weighted in this analysis in that it occurs as a character state in characters 1–3.

The CI of character 9 (columella) is relatively low (0.67), but the states of this character help support some of the internal branches of the tree as well as serve as autapomorphies for

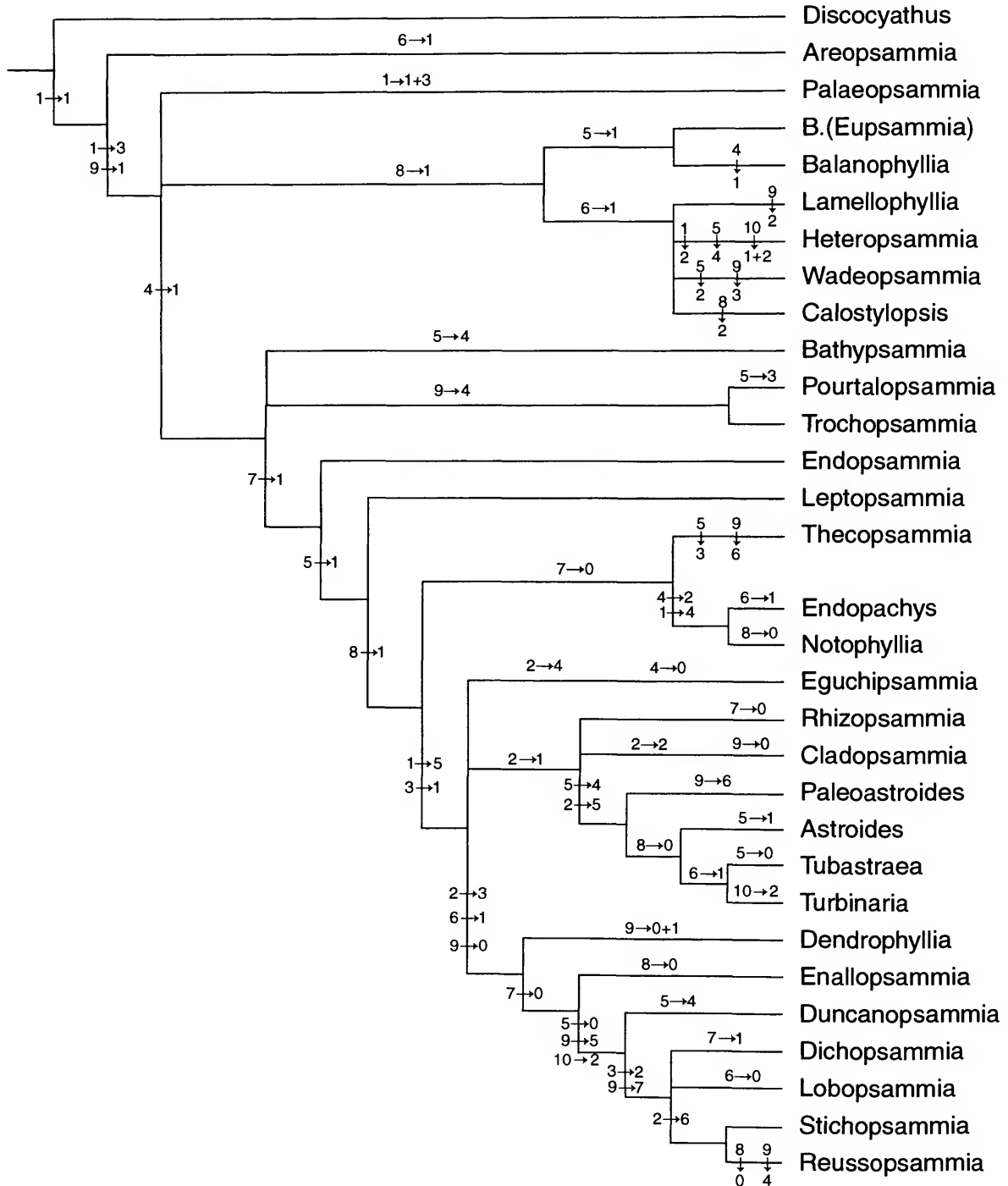


FIGURE 2.—One of 27 equally parsimonious trees of dendrophylliid genera arrived at by successive weighting (see text), modified by joining the two subgenera of *Balanophyllia*. Tree length = 64 (character 2 transforming to state 6 is a two-step change); CI = 0.523. Character-state changes indicated on every branch as coded in Tables 1, 2; character number indicated at left or at top of branch, character state indicated at right of or below branch line.

some genera. A strict interpretation of the tree would suggest that the ancestral condition of a papillose columella gave rise to both the spongy and labyrinthiform type, the former independently evolving to the lamellar, swirled lamellae, solid, and lost conditions, the latter evolving to the trabecular condition.

The presence or absence of zooxanthellae in the tissue (character 10) was not expected to be a phylogenetic character. At least one genus, *Heteropsammia*, contains species that are facultative (having zooxanthellae or not, depending on the environment), and other species in other families are also known to be facultative (Cairns, 1999b). Furthermore, corals that occur in deep water (over 200 m) are ecologically prohibited from having zooxanthellae because of a lack of light. The tree suggests that the ancestral state as well as all exclusively fossil genera before the Eocene lacked zooxanthellae but that the symbiosis was independently acquired three times, in one case helping to define the terminal clade of five colonial genera. It also suggests that *Lobopsammia*, *Stichopsammia*, and *Reussopsammia* were zooxanthellate.

TREE ANALYSIS.—The topology of the 50% majority rule tree (Figure 2) does not support the interpretation of two subfamilies within the Dendrophylliidae, as suggested by Alloiteau (1952). Instead, the top half of the tree is organized in a ladder-like arrangement including all 15 of the solitary genera. Two of the oldest known genera, *Areopsammia* and *Palaeopsammia*, diverge first, followed by a small clade consisting of five genera (*Balanophyllia* through *Calostylopsis*), which is characterized by having free coralla and the Pourtalès plan, or a derivative of the Pourtalès plan (reticulate). This clade includes the remaining three genera that are known from the Cretaceous.

The lower part of the tree (Figure 2) forms a monophyletic clade, consisting of the 14 colonial genera. This clade is divided into three monophyletic groupings, the first consisting of the single genus *Eguchipsammia*, which differs from the other colonial dendrophylliids in being free and in having a quasicolonial habit. The second grouping (*Rhizopsammia* through *Turbinaria*) consists of the six colonial genera that do not have arborescent branching. The third grouping of seven genera (*Dendrophyllia* through *Reussopsammia*) is characterized by having arborescent branching, the last four genera having intratentacular arborescent budding, and the last two of those having intratentacular arborescent budding that results in a flabellate corallum.

The low overall tree CI (0.523) does not inspire confidence, and many of the branches are supported by only one character-state change, making the trees quite labile. Obviously, more characters are needed to better resolve the phylogeny, but nine of the 29 genera are exclusively fossil, thus characteristics of the living animal, such as histology, molecular sequences, and nematocyst type, cannot be uniformly applied. Furthermore, among some of the Cretaceous genera, even some of the morphological characters are difficult to interpret. And many among the Holocene genera occur only in deep water and/or are rarely collected, making a potential analysis of soft-part

characters unfeasible. Thus the tree/cladogram in this analysis is presented not as a definitive phylogeny, but as a preliminary attempt to assess evolutionary relationships among the genera and the phylogenetic value of various characters. I think that any analysis of supraspecific coral taxa that is based solely on corallum morphology will produce inconclusive and/or poorly supported results. It is suggested that other characters, based on the soft parts (including but not necessarily exclusively based on molecular analysis), and in a stratigraphic context, are required to produce a meaningful phylogeny. Obtaining tissue from all analyzed taxa will always be a difficulty, especially for deep-water forms, but until this can be done uniformly our understanding of higher-level coral phylogeny will remain tentative.

Systematic Account

Order SCLERACTINIA

Suborder DENDROPHYLLIINA Vaughan and Wells, 1943

Family DENDROPHYLLIIDAE Gray, 1847

DIAGNOSIS.—Wall synapticulothecate, formed of irregularly arranged synapticalae, resulting in an irregularly porous theca through which extratentacular mesenterial extensions protrude. Septa consisting of one laminar fan system of simple trabeculae, but trabeculae irregularly developed and not closely united, resulting in thickened and usually perforate septa; upper and axial margins of lower-cycle septa smooth. Septa usually arranged in Pourtalès plan at some stage of skeletal ontogeny.

TAXONOMIC HISTORY.—Before the establishment of the family Dendrophylliidae, in 1847, approximately 35 dendrophylliid species (including 16 exclusively fossil species) and eight genera had been described. In describing those genera and species, most authors did not provide a higher taxonomic context for those taxa, often allying them to caryophylliid genera or placing them in the catch-all genus *Madrepora*. For instance, in Dana's (1846) "Zoophytes," all scleractinian coral genera were arranged in seven families within three tribes, with two of the three dendrophylliid genera listed in that classification placed in the family Caryophyllidae (sic) and the third genus (*Gemmipora* (= *Turbinaria*)) placed in the family Gemmiporidae. Gray's (1847) original description of the family Dendrophyllidae (sic) was quite brief and did little to differentiate it from the other seven scleractinian families in his synopsis or to place it in a higher taxonomic context, but it did include five genera: *Dendrophyllia*, *Tubastrea* (sic), *Explanaria*, *Cladocora*, and *Gemmipora*, the nominate genus defining the family. Thus, if strict priority were to be followed, Dana's (1846) Gemmiporidae, based on the type genus *Gemmipora* de Blainville, 1830 (junior synonym of *Turbinaria* Oken, 1815), was the first family-level name available for a

dendrophylliid genus, preceding Gray's (1847) Dendrophylliidae by one year.

Ironically, just a year later, Milne Edwards and Haime (1848:65) proposed yet another family-group name, the Eupsammidae, for the nominate genus *Eupsammia* (= *Balanophyllia*) and all other previously described "dendrophylliid" genera. Contrary to the interpretation of Vaughan and Wells (1943:233), Eupsammidae must be considered a junior synonym of Dendrophylliidae, not because the type genus is a junior synonym of *Balanophyllia*, but because Dendrophylliidae has priority by one year. Nonetheless, Milne Edwards and Haime (1848) provided an excellent discussion of the characteristics of the family, redescribed all 47 (26 Holocene, 21 fossil) known species and nine genera (*Stephanophyllia* not included in counts), and provided a key to the genera, in which the character of coloniality is used as the first couplet. In the first truly comprehensive and modern classification of the Anthozoa, including Scleractinia, Milne Edwards and Haime (1850) continued to place most of the dendrophylliid genera in the Eupsammidae, one of three families in the suborder Zoantharia Perforata, the other families being the Madreporidae and the Poritidae. They placed the genus *Explanaria* (= *Turbinaria*) in the tribe (=subfamily) Explanarinae of the Madreporidae. In a slightly later revision, Milne Edwards and Haime (1851), reiterated by Milne Edwards (1860), revised this classification by placing the Eupsammidae as a subfamily of the Madreporidae, and they renamed the subfamily Explanarinae as the Turbinarinae (sic), also including it as a subfamily of the Madreporidae.

Duncan's (1884) classification of the Scleractinia reverted to Milne Edwards and Haime's (1850) model, considering the Eupsammidae as a separate family, because the genera demonstrated the "variety of form" consistent with the other "great families" of Scleractinia, and it placed *Turbinaria* again as a subfamily in the Madreporidae. Duncan also divided the Eupsammidae into four "alliances" (=supergenera, not subfamilies), Stephanophyllioida, Balanophyllioida, Dendrophyllioida, and Leptopsammiioida, and four genera that he could not place in alliances. The first alliance is now considered to be the family Micrabaciidae, the second contained the solitary genera, the third contained the colonial genera, and the fourth contained the solitary genera with an incomplete fourth cycle and lacking a Pourtalès plan. The four unallied genera were those having unusual colonial form, such as irregular budding, intratentacular budding, and encrusting colonies. The alliance subdivisions were not followed by later authors.

Wells (1933) thought there were three families of "dendrophylliid" corals: Eupsammidae, which he restricted to genera with a solitary corallum; Dendrophylliidae, including genera with a colonial corallum; and Micrabaciidae, genera with solitary coralla having offset costae. He referred to the Dendrophylliidae as a new family, but it had been proposed as early as 1847 by Gray. By 1943 Vaughan and Wells had eliminated the Micrabaciidae from the family and had united all 27 dendro-

phylliid genera into the single family Dendrophylliidae, being the first authors to employ this earlier name instead of Eupsammidae. They also abolished the category of Zoantharia Perforata and created the suborder Dendrophylliida for this single family. Their key to the genera emphasized septal plan first and coloniality secondarily, although they did not divide the family into smaller taxa.

In his revision of the fossil coral genera, Alloiteau (1952) recognized two families of dendrophylliids, the Eupsammidae and Turbinariidae, a classification and nomenclature more consistent with that of the nineteenth-century authors than that of Vaughan and Wells. Alloiteau also divided the Eupsammidae into two families, although not on the basis of coloniality, as did Duncan (1884) and Wells (1933), but on the basis of septal plan, i.e., presence or absence of a Pourtalès plan. This required the establishment of a new subfamily, the Tubastraeinae, for those genera lacking the Pourtalès plan; however, the family-group name Turbinariinae Milne Edwards and Haime (1851) was already available for that group of genera. Alloiteau also proposed the "new" subfamily Eupsamminae, which in fact should have been attributed to Milne Edwards and Haime (1848), and the "new" suborder Eupsammiiida, which was a junior synonym of Dendrophylliida Vaughan and Wells (1943).

Wells's (1956) revision of the Scleractinia, which is generally accepted by most coral workers, is a reiteration of the earlier classification of Vaughan and Wells (1943). In that revision, he included 24 genera in the family Dendrophylliidae, corrected the spelling of the suborder to Dendrophylliina, and did not divide the genera into subfamilies.

In the latest classification of the Scleractinia, Chevalier and Beauvais (1987) included 20 Holocene genera in the Dendrophylliidae but also included the families Micrabaciidae, Astraraeidae, and Actiniciidae (sic) in the suborder.

REMARKS.—The familial (and subordinal) diagnosis provided above is concise, relating primarily to aspects of the microstructure of the theca and septa. Longer "diagnoses" given by other authors include characters that are variable within the family and thus do not define the family but rather distinguish genera, supergenera, or subfamilies within the family. These characters include presence or absence of coloniality, and if the former, whether achieved by intra- or extratentacular budding, and if solitary, if attached, transversely divided, or free; presence or absence of a Pourtalès septal plan in the adult stage; presence or absence of costae, thecal spinulations, or epitheca; presence or absence of endotheca, pali or paliform lobes, or columella, and if the last is present, its size and type; and presence or absence of zooxanthellae in the tissue.

The monophyly of the family Dendrophylliidae (and suborder Dendrophylliina) is based primarily on its possession of a synapticulotheca in conjunction with having septa composed of only one fan system. (The Fungiina also has a synapticulotheca but has septa composed of multiple fan systems; however, Morycowa and Roniewicz (1995) implied that the fungiine

synapticulae are not homologous with those of the dendrophylliids.) The Pourtalès plan is also unique to the Dendrophylliidae, but not all genera have this feature in the adult stage. Finally, sequence analyses of a segment of mitochondrial 16S rRNA (Romano and Palumbi, 1996) and segments of 28S rRNA (Veron et al., 1996; Romano and Cairns, 2000) in species belonging to the genera *Turbinaria*, *Tubastraea*, *Balanophyllia*, *Rhizopsammia*, and *Leptopsammia* support the monophyly of the family.

TYPE GENUS.—*Dendrophyllia* de Blainville, 1830.

SPECIES RICHNESS.—There are 364 valid species recognized in the family, of which 198 are exclusively fossil (Table 1). The remaining 166 species are known from the Holocene, 15 of which are known to have fossil records.

DISTRIBUTION.—The following stratigraphic and geographic records are a summary of what is known about the distribution of dendrophylliid corals, but it is certainly far from complete (Figure 3).

Cretaceous: Early Cretaceous: Serbia (Barremian to Early Aptian); Madagascar (Albian). Late Cretaceous: USA (Campanian); Egypt, Netherlands, Ukraine, Madagascar (Maastrichtian); Bonaire. Unspecified Cretaceous: India.

Paleocene: Early Paleocene: Egypt, Israel, Greenland, Denmark, Sweden (Danian); USA (Midwayan); France (Montian). Unspecified Paleocene: Austria.

Eocene: Early Eocene: USA (early Claibornian); Poland; England; Seymour Island, Antarctica. Middle Eocene: USA (middle Claibornian); Europe (Lutetian, Laekian, Bartonian); Belgium (Wemmelian); New Zealand (Bartonian); Jamaica. Late Eocene: Europe (Priabonian); Italy (Tongrian); USA (Jacksonian); former Czech Republic ("Tschechoslovakian"); Tonga. Unspecified Eocene: England, Spain, USA, New Zealand, Peru.

Oligocene: Early Oligocene: USA (Vicksburgian, Chickasawan); New Zealand (Duntronian); Italy ("Ligurian"); Ukraine; Germany. "Middle Oligocene": Europe, USA, Venezuela. Late Oligocene: USA. Unspecified Oligocene: Germany, Italy, Australia, Somalia.

Miocene: Early Miocene: Italy, France (Aquitainian, Burdigalian); Algeria; Burma. Middle Miocene: New Zealand (Altonian); Australia (South Australia) (Bartonian); Poland (Badenian); Italy, France ("Helvetian"); Azores, Austria ("Vinobodian"); Crete; Algeria; Bosnia; Libya. Late Miocene: Italy, France (Tortonian); Dominican Republic; Java. Unspecified Miocene: Austria, Morocco, Egypt, Java, Tasmania, Japan, Borneo.

Pliocene: Early Pliocene: Italy; Dominican Republic. Late Pliocene: England; Caribbean. Unspecified Pliocene: Italy, Taiwan, Java, Japan, Borneo, Papua New Guinea, USA (California).

Pleistocene: Late Pleistocene: Mediterranean; Vanuatu. Unspecified Pleistocene: Italy, Niger Delta, Taiwan, New Zealand, Japan.

Holocene: Cosmopolitan, except off continental Antarctica, 0–2165 m.

Areopsammia Dietrich, 1917

PLATE 1: FIGURES b–d

Areopsammia Dietrich, 1917:307, 1 fig.—Vaughan and Wells, 1943:235.—Alloiteau, 1952:680.—Wells, 1956:F433.—Alloiteau, 1957:352 [table].

Porosmilia Umbgrove, 1925:113, pl. 11: fig. 17.—[not *Porosmilia* Fromentel, 1860].

DIAGNOSIS.—Corallum solitary, bowl-shaped, probably unattached. Epitheca absent; synapticulotheca thick and porous, not costate or granular. Septa crowded, adjacent septa linked by synapticulae. Septa arranged in normal insertion pattern (not Pourtalès plan); 5 (sometimes more) cycles of septa (about 92 septa in holotype). Fossa deep; columella rudimentary (papillose).

DISCUSSION.—Vaughan and Wells (1943:235) stated that the coralla of this genus were trochoid and "probably fixed," whereas Alloiteau (1952, 1957:352) stated that they are "sub-cyclolotoid" and free. The base of the holotype, which measures 22 × 18 mm in CD, is embedded in matrix and therefore is not useful for this determination, but based on its general morphology and that of several specimens (casts) reported by Umbgrove (1925), it would seem to have a bowl-shaped corallum that was probably free.

The type specimen of *Cyclolites alacca* Morren, 1828, senior synonym of the type species *Areopsammia mastrichtensis*, was not traced; however, the specimen of *Porosmilia alacca* figured by Umbgrove (1925) to illustrate his new genus *Porosmilia* is figured herein (Plate 1c).

DISTRIBUTION.—Late Cretaceous (Maastrichtian) of the Netherlands.

TYPE SPECIES.—*Areopsammia mastrichtensis* Dietrich, 1917, by monotypy (= *Cyclolites alacca* Morren, 1828 (type species of *Porosmilia* Umbgrove, 1925, by monotypy, and senior synonym of *A. mastrichtensis*)); Late Cretaceous (Maastrichtian) of the Netherlands. Holotype (now fragmented into two pieces) deposited at Museum für Naturkunde, Berlin (MBK 1303).

OTHER SPECIES.—None, only *Areopsammia alacca* (Morren, 1828).

Palaeopsammia Wanner, 1902

Palaeopsammia Wanner, 1902:105.—Quaas, 1902:161, pl. 31: figs. 8–11.—Felix, 1914:205–206.—Oppenheim, 1930:308–315.—Wells, 1936b:122 [choice of type species].—Vaughan and Wells, 1943:235.—Alloiteau, 1952:680; 1958:203.—Wells, 1956:F433, fig. 338:3.—Hassan and Salama, 1969:92.—Kuzmicheva, 1987:146.—Abdel-Gawad and Gameil, 1995:27.

DIAGNOSIS.—Corallum solitary, conical (usually slightly curved) to patellate, unattached. Epitheca present; synapticulotheca costate, granular. Septa arranged in normal insertion pattern (not Pourtalès plan); up to 5 cycles of septa. Columella spongy (discrete).

DISCUSSION.—*Palaeopsammia* is the oldest known dendrophylliid, differing from *Areopsammia* in having an epitheca and a costate synapticulotheca.

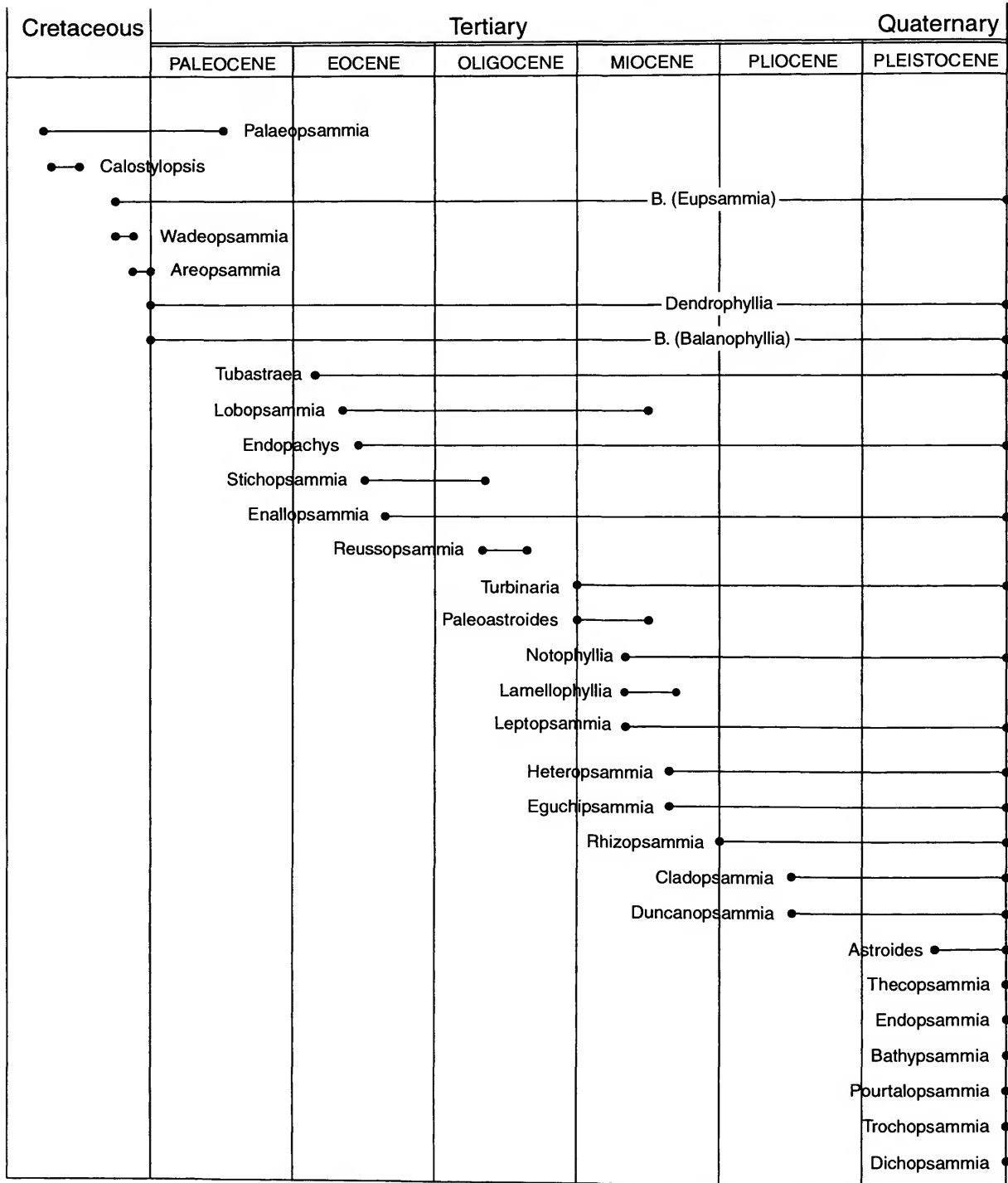


FIGURE 3.—Stratigraphic ranges of all dendrophylliid genera and subgenera, arranged according to earliest-known first occurrences.

In Alloiteau's (1958) preliminary remarks on the genus *Palaeopsammia*, he suggested that Wanner's illustrated type series of *P. multiformis* consisted of two or three species: a patellate-shaped species (Quaas, 1902, pl. 31: fig. 10) and a curved, turbinate species (Wanner, 1902, pl. 15: figs. 5–7). Alloiteau considered the latter to be typical of the species, although no lectotype was chosen. It should be noted that Alloiteau's references to pl. 31 are to Quaas (1902), not to Wanner (1902), and that his allusions to Wanner's pl. 11 are really to pl. 15. Hassan and Salama (1969) synonymized the patellate-shaped *P. zitteli* with *P. multiformis*, accepting a much greater range of variation within the species than did Alloiteau.

Representatives of this genus could not be obtained. The original description and a later description of the type species by Hassan and Salama (1969) were the basis for the diagnosis.

DISTRIBUTION.—Early Cretaceous (Barremian to Early Aptian): Serbia. Late Cretaceous (Maastrichtian): Madagascar, Tunisia, Egypt, western Turkmenistan Georgia (former USSR), Bonaire. Early Paleocene (Danian): Libya, Israel.

TYPE SPECIES.—*Palaeopsammia multiformis* Wanner, 1902, by subsequent designation (Wells, 1936b) (= *P. zitteli* Wanner, 1902; = *P. multiformis* var. *depressa* Quaas, 1902); early Paleocene (Danian: "snow white chalk") of Libya between Farāfrah and Dachel oases. Also known from the Late Cretaceous (Maastrichtian) of Madagascar, Tunisia (Alloiteau, 1958), Egypt (Hassan and Salama, 1969), and "Palestine" (Oppenheim, 1930).

Wanner (1902) stated that he investigated 170 pieces representing this species, all of which must be considered as syntypes, because he did not designate a holotype. Although the deposition of these types was not given by Wanner (1902), Wells (1936b) remarked that the types were deposited at the Paleontology Museum, Munich. Kuzmicheva (1987), however, stated that the deposition of Wanner's types was unknown and that Wanner (1902, pl. 15: fig. 9) had chosen a lectotype. In fact, no lectotype (or holotype) has been designated by Wanner or by any subsequent author. Inquiries at the Paleontology Museum in Munich failed to discover the type series.

OTHER SPECIES.—*Palaeopsammia zljebinensis* Turnšek and Mihajlović, 1981. Early Cretaceous (Barremian to Early Aptian): Serbia.

P. mitsinjoensis Alloiteau, 1958. Late Cretaceous (Maastrichtian): Madagascar.

P. sp., Pijpers, 1933. Late Cretaceous: Bonaire.

P. aegyptiaca (Wanner, 1902). Early Paleocene (Danian): Libyan desert (Egypt), "Palestine."

= *Trochocyathus epicharis* Wanner, 1902.

= *Caryophyllia jasmundi* Wanner, 1902.

***Balanophyllia* Wood, 1844**

DISCUSSION.—The genus *Balanophyllia* was described by Wood in 1844 for an attached, solitary dendrophylliid coral from the Pliocene of England; *Eupsammia* was later described by Milne Edwards and Haime (1848) for several species that

were similar to *Balanophyllia* but were unattached. Vaughan (1900) was perhaps the first to question the distinction of the two taxa, noting that some fossil species occurred in both the attached and unattached forms; nonetheless, he maintained the taxa as separate genera. Montanaro (1929) later suggested that the genera were synonymous. Vaughan and Wells (1943:236) proposed the compromise solution of regarding *Eupsammia* as a subgenus of *Balanophyllia*, stating that the differences between two taxa were "hardly even of subgeneric importance, but useful in handling collections." But, several years later, Durham (1949) determined that the species of *Balanophyllia* sensu stricto had polycyclic development (resulting in a broad, attached base), whereas species of *Eupsammia* had monocyclic development (resulting in unattached coralla or coralla with narrow bases). On this basis Durham considered the two taxa to be discrete genera, a position followed by Alloiteau (1952) and Chevalier and Beauvais (1987), whereas the subgeneric interpretation was adopted by Wells (1956) and Chevalier (1961). This distinction was primarily one concerning fossil species, as only six Holocene species belong to the unattached, or *Eupsammia*, group. Thus, most authors describing Holocene species have ignored the issue.

The rationale for considering *Eupsammia* and *Balanophyllia* as separate taxa (genera or subgenera) should rely on the monophyletic nature of each taxon, not on the convenient handling of a large collection. The meticulous work of Durham (1949) showed that there is a basis for dividing the two taxa, i.e., the monocyclic or polycyclic development of the juvenile corallum, a character that has important ramifications for the life history of a coral and one that is fairly easy to observe, even in fossil specimens. The monocyclic *Eupsammia* occur earlier in the fossil record (Late Cretaceous) and, being unattached, may have been more successful in muddy environments where hard substrates were scarce. The later (early Paleocene) evolution of a polycyclic base may have allowed for a more secure attachment to hard substrates in a higher-energy environment. A phylogenetic analysis of the species of *Balanophyllia* is beyond the scope of this paper, thus the evolutionary implications of an attached compared with an unattached mode of life are unknown. But it is easily conceivable that an adaptive radiation may have resulted from this difference, which suggests that these two taxa should be maintained at least at the subgeneric level. To that end, I have listed all species from these two taxa as subgenera of *Balanophyllia*. Some of the species, especially the Holocene ones, have never appeared before in subgeneric combinations. In the phylogenetic analysis (Figure 2), the two subgenera of *Balanophyllia* are separated by only one character (4, corallum attachment).

A similar situation occurs in the Caryophylliidae, in the genus *Caryophyllia*. Attached species were always considered to belong in the nominate subgenus, whereas unattached species were at one time placed in the genus *Ceratocyathus* Seguenza, 1864. Chevalier (1961) placed *Ceratocyathus* as a subgenus of

Caryophyllia, whereas most other authors have considered *Ceratocyathus* to be a junior synonym of *Caryophyllia*. According to Zibrowius (1980), it is premature to subdivide *Caryophyllia* until much more is known about the early skeletal ontogeny of the various species and until the evolutionary implications are known for these modifications.

One hundred seventy-four (174) species are listed for the genus *Balanophyllia*: 129 in the nominate subgenus (including 53 exclusively Holocene species) and 45 species in the subgenus *Eupsammia* (including 5 exclusively Holocene species). Undoubtedly these lists contain many junior synonyms; nonetheless, the genus is considered to be the most speciose in the family. Its 58 extant species make it the third most speciose extant genus among all scleractinian genera (see Cairns et al., 1999), exceeded in number of species only by *Acropora* and *Caryophyllia*. The subgenus *Balanophyllia* was most diverse in the Miocene and Holocene, whereas subgenus *Eupsammia* was most diverse earlier, in the Eocene, having relatively few Holocene species.

NOMENCLATURE NOTES.—Because there are so many nominal species of *Balanophyllia*, sometimes the same specific epithets have been used more than once, resulting in primary homonyms. Also, because *Eupsammia* is herein considered to be a subgenus of *Balanophyllia*, there is the potential for secondary homonyms as well. Although many of these cases of homonymy were detected and replacement names were given (e.g., Strand, 1928, and others as indicated in the species lists), some have remained undetected. Therefore, the following replacement names are herein proposed. The replacement name *B. (B.) vanderhorsti* is proposed for *Balanophyllia ponderosa* van der Horst, 1926 (Holocene, Indo-West Pacific), which is a junior primary homonym of *B. ponderosa* Vaughan, 1900 (early Paleocene, USA (Alabama)). The replacement name *B. (B.) ukrainensis* is proposed for *Balanophyllia cornu* Sokolow, 1894 (early Oligocene, Ukraine), which is a junior primary homonym of *B. cornu* Moseley, 1881 (Holocene, Western Pacific). The replacement name *B. (B.) javaensis* is proposed for *Balanophyllia variabilis* Gerth, 1921 (Miocene, Java), which is a junior primary homonym of *B. variabilis* Nomland, 1916 (Late Eocene, USA (Washington)). The replacement name *B. (B.) japonica* is proposed for *Balanophyllia teres* Cairns, 1994 (Holocene, Japan), which is a junior secondary homonym of *Eupsammia teres* Römer, 1863 (early Oligocene, Germany). The replacement name *B. (E.) sumbayaensis* is proposed for *Leptopsammia conica* van der Horst, 1922 (Holocene, Indo-West Pacific; =*Balanophyllia stimpsonii*), which is a junior secondary homonym of *Balanophyllia conica* Osasco, 1897 (middle Miocene, Italy). It should be noted that if *Eupsammia* is ultimately raised to generic status, many of the replacement names proposed for these secondary homonyms become unnecessary.

Balanophyllia (Balanophyllia) Wood, 1844

PLATE 1: FIGURES e.g–i,k

Balanophyllia Wood, 1844:11.—Milne Edwards and Haime, 1848:83; 1850:lii, 9–11; 1851:134–135.—Milne Edwards, 1860:99–100.—Duncan, 1884:175.—Durham, 1949:147.—Alloiteau, 1952:679.—Cairns, 1979:172.—Zibrowius, 1980:182; 1985:234.—Chevalier and Beauvais, 1987:691.—Zibrowius, 1991:93–94.
Clonotrochus Schaffhäutl, 1863:32.
Rhodopsammia Semper, 1872:257.
Balanophyllia (Balanophyllia).—Vaughan and Wells, 1943:236.—Wells, 1956:F434.—Chevalier, 1961:457.

DIAGNOSIS.—Corallum solitary, conical, and firmly attached through a polycyclic base; corallum usually straight. Epitheca present (e.g., type species) or absent; synapticulotheca always costate, costae irregularly porous or bearing short hispid spines (e.g., type species) or low granules. Pourtalès plan present; 5 cycles of septa often present. Columella elongate, spongy. Azooxanthellate.

DISCUSSION.—For a justification of the subgeneric classification and the position of *Balanophyllia* in the phylogenetic analysis, see discussion of the genus.

DISTRIBUTION.—Paleocene: Austria. Middle Eocene: France (Lutetian, Bartonian), New Zealand. Late Eocene: Italy (Priabonian), Germany. Eocene: Peru, Australia (Victoria). Early Oligocene: Ukraine, Germany, USA (Chickasawan), New Zealand (Duntronian). Middle Oligocene: Germany, Italy. Late Oligocene: USA. Oligocene: Australia. Early Miocene: Italy (Burdigalian). Middle Miocene: Italy (Helvetian), Poland (Badenian), Algeria, former Czechoslovakia, Australia (Victoria), Bosnia, Austria. Miocene: Java, Egypt, Morocco. Late Pliocene: Italy. Pliocene: Italy, Taiwan, Java. Pleistocene: New Zealand, Taiwan, Italy. Holocene: cosmopolitan, except for continental Antarctica, 0–1150 m.

TYPE SPECIES.—*Balanophyllia calyculus* Wood, 1844, by monotypy; late Pliocene (Red Crag) of Sutton (Norfolk), England. Known from middle Miocene to late Pliocene of England and France.

Balanophyllia calyculus was one of the earliest dendrophylliid species to be described, and as such, it was not adequately described to allow for differentiation among congeners or even other dendrophylliid genera. Indeed, in commenting on the original description, Bourne (1905:204) stated that “there is no objection to be taken to it on the score of indefiniteness.” The species was not illustrated or measured, and type specimens were not specified, although it is apparent from the description that numerous “syntypes” must have been examined in order to describe the variation discussed. This type series, stated by Wood to be deposited in his personal cabinet, cannot be located; it was not found at BM. Although little of diagnostic value is given in Wood’s description, it is apparent that he must have had at least two species in his material: the predominant one being solitary and elongate, which formed the basis of his new genus *Balanophyllia*, and a second species that was colonial, apparently plocoid, and with a broad base that “grouped together” with other corallites. The latter morphology is consis-

tent with the genus *Cladopsammia*. Indeed, specimens identified as *Balanophyllia calyculus* from the type locality deposited at both BM and the NMNH (Plate 9d) include this colonial form, as well as the solitary form (USNM 94469, Plate 1e,h). Because the type series appears to be a mixed lot that is lost, a neotype is proposed herein to typify *Balanophyllia calyculus*, the type species of the genus *Balanophyllia*. The neotype was collected from the Red Crag near Woodbridge, Suffolk, England (near the type locality), and is a solitary corallum, consistent with Wood's intention of describing this species and genus for a simple fixed coral. The neotype is cataloged as USNM 94469 and is figured herein as Plate 1e,h. It measures 32.8 mm in height, 14.5 × 12.5 mm in CD, and 9.8 mm in PD.

The fossil type species *B. calyculus* is most fully described and illustrated by Milne Edwards and Haime (1850:9–11, pl. 1: fig. 3a–d).

OTHER SPECIES (“*” indicates species with both fossil and extant occurrences).—*Paleocene*: *Balanophyllia (B.) schlosseri* Traub, 1939. Paleocene: Austria.

B. (B.) traubi Kühn and Traub, 1968. Paleocene: Austria.
Eocene:

B. (B.) alta Tenison-Woods, 1880. Early Eocene: New Zealand.
B. (B.) gravesii (Michelin, 1844). Middle Eocene (Lutetian): France.

B. (B.) geniculata (d'Archiac, 1846). Middle Eocene (Bartonian): France.

B. (B.) tenuistriata Milne Edwards and Haime, 1848. Middle Eocene (Lutetian): France.

B. (B.) vermicularis (Schafhäütl, 1863) (type species of *Clonotrochus* Schafhäütl, 1863). Middle Eocene: Germany.

B. (B.) santaelensis Frost, 1975. Middle Eocene: Mexico.

B. (B.) incerta Sismonda, 1871. Late Eocene (Priabonian): Italy.

B. (B.) fallax de Angelis, 1894. Late Eocene (Priabonian): Italy.

?*B. (B.) antiqua* (de Angelis, 1894). Late Eocene (Priabonian): Italy.

B. (B.) vagans Sismonda, 1871. Late Eocene (Priabonian) to middle Miocene: Italy.

B. (B.) vagans var. *subpraelonga* Osasco, 1897. Middle Miocene (Helvetian): Italy.

B. (B.) cylindrica (Michelotti, 1838). Late Eocene (Priabonian) to late Miocene (Tortonian): Italy.

B. (B.) cowlitzensis Durham, 1943. Late Eocene: USA (Washington).

B. (B.) haleana (Milne Edwards and Haime, 1848). Eocene: France. Early Oligocene (Chickasawan): USA (Alabama).

B. (B.) truncata Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) induta Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) fossata Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) patula Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) torta Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) cauliculata Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) basedowi Dennant, 1904. Eocene: Australia (Victoria).

B. (B.) fahringeri Kühn, 1933. Eocene: Italy.

B. (B.) piuraensis Wells, 1941. Eocene: Peru.

Oligocene:

?*B. (B.) subcylindrica* (Philippi, 1851). Early Oligocene (Ligurian): Germany.

=*B. (B.) calycina* Römer, 1863.

B. (B.) costata Keferstein, 1859. Early Oligocene: Germany.

B. (B.) granulata Duncan, 1866. Early Oligocene: England.

?*B. (B.) perlonga* (Reis, 1889). Early Oligocene (Ligurian): Italy.

B. (B.) subirregularis Sokolow, 1893. Early Oligocene: Ukraine.

B. (B.) ukrainensis, replacement name proposed herein for *B. cornu* Sokolow, 1894 (not Moseley, 1881). Early Oligocene: Ukraine.

B. (B.) salpynx Squires, 1958. Early Oligocene (Duntronian): New Zealand.

B. (B.) inaequidens Reuss, 1859. Middle Oligocene: Germany.

=*B. (B.) sinuata* Reuss, 1859.

=*B. (B.) fascicularis* Reuss, 1859.

B. (B.) mojsisovicsi Klipstein, 1879. Middle Oligocene: Germany.

B. (B.) teglandae Durham, 1942. Late Oligocene: USA (Washington).

B. (B.) campanulata Duncan, 1870. Oligocene: Australia (Victoria).

=*B. (B.) cauliculata* Dennant, 1904.

B. (B.) bellunensis Venzo, 1939. Oligocene: Italy.

B. (B.) subconica Venzo, 1945. Oligocene: Italy.

B. (B.) armata Duncan, 1870. Oligocene to Miocene: Australia (Victoria, South Australia).

B. (B.) seminuda Duncan, 1870. Oligocene to Miocene: Australia (Victoria, South Australia).

Miocene:

B. (B.) italica (Michelin, 1841). Early (Burdigalian) to middle Miocene to Pliocene: Italy, France.

=*Dendrophyllia caryophyllata* Couffon, 1905.

B. (B.) selwyni Duncan, 1870. Middle Miocene: Australia (Victoria).

B. (B.) ulrichi Duncan, 1870. Middle Miocene: Australia (South Australia).

B. (B.) stratissima Sismonda, 1871. Middle Miocene (Helvetian): Italy.

B. (B.) falcifera Sismonda, 1871. Middle Miocene (Helvetian): Italy.

B. (B.) pygmaea Reuss, 1871. Middle Miocene: “Czechoslovakia.”

[*B. (B.) cornuformis* Procházka, 1893 (nomen nudum). Middle Miocene: “Czechoslovakia.”]

[*B. (B.) bittneri* Procházka, 1893 (nomen nudum). Middle Miocene: “Czechoslovakia.”]

[*B. (B.) dichotoma* Procházka, 1893 (nomen nudum). Middle Miocene: “Czechoslovakia.”]

[*B. (B.) distans* Procházka, 1893 (nomen nudum). Middle Miocene: “Czechoslovakia.”]

[*B. (B.) falcata* Procházka, 1893 (nomen nudum). Middle Miocene: “Czechoslovakia.”]

- [*B. (B.) granulifera* Procházka, 1893 (nomen nudum). Middle Miocene: "Czechoslovakia."]
- [*B. (B.) imarginata* Procházka, 1893 (nomen nudum). Middle Miocene: "Czechoslovakia."]
- [*B. (B.) longirostris* Procházka, 1893 (nomen nudum). Middle Miocene: "Czechoslovakia."]
- [*B. (B.) morovica* Procházka, 1893 (nomen nudum). Middle Miocene: "Czechoslovakia."]
- [*B. (B.) nuda* Procházka, 1893 (nomen nudum). Middle Miocene: "Czechoslovakia."]
- B. (B.) seminudana* Strand, 1928 (replacement name for *B. seminuda* de Angelis, 1894, not Duncan, 1870). Middle Miocene (Helvetian): Italy.
- =*B. (B.) angelisi* Hegedüs, 1962 (replacement name for *B. seminuda* de Angelis, 1894, not Duncan, 1870; however, an earlier replacement name was proposed by Strand, 1928). Middle Miocene (Helvetian): Italy.
- B. (B.) cylindricella* Strand, 1928 (replacement name for *B. cylindrica* Duncan, 1870, not Michelotti, 1838). Middle Miocene: Australia (Victoria).
- B. (B.) angusticalix* Chevalier, 1961. Middle Miocene (Helvetian, Vinobodian): Touraine, Algeria.
- B. (B.) varians* Reuss, 1854. Middle Miocene to Pliocene: Europe.
- B. (B.) guidottii* Simonelli, 1896. Middle Miocene (Helvetian) to Pliocene: Italy.
- B. (B.) irregularis* Seguenza, 1864. Middle (Helvetian) to late Miocene (Tortonian) to Pliocene: Italy, Romania, Bosnia.
- B. (B.) australiensis* Duncan, 1864. Miocene (Hamilton Series): Australia (Victoria).
- B. (B.) fragilis* Duncan, 1870. Miocene (Hamilton Series): Australia (Victoria).
- B. (B.) armata* Duncan, 1870. Miocene (Hamilton Series): Australia (Victoria).
- B. (B.) complanata* Gerth, 1921. Miocene: Java.
- B. (B.) javaensis*, replacement name proposed herein for *B. variabilis* Gerth, 1921 (not Nomland, 1916). Miocene: Java.
- B. (B.) tubuliformis* Duncan, 1870. Miocene (Hamilton Group): Australia (Victoria).
- B. (B.) felixi* Strand, 1928. Miocene: Egypt.
- B. (B.) circumsulcata* Zuffardi-Comerci, 1933. Miocene: Italy.
- B. (B.) cornurupicaprae* Zuffardi-Comerci, 1933. Middle Miocene: Italy.
- B. (B.) conicocompressa* Zuffardi-Comerci, 1933. Miocene: Italy.
- B. (B.) parva* Zuffardi-Comerci, 1933. Miocene: Italy.
- B. (B.) nonaradiata* Chevalier, 1962. Miocene: Morocco.
- B. (B.) bavaria* Chevalier, 1965 (replacement name for *B. (B.) irregularis* Reuss, 1872, not Seguenza, 1864). Miocene: Italy.
- B. (B.) oppenheimi* Felix, 1913. Miocene to Pliocene: Borneo.
- Pliocene:**
- B. (B.) caryophylloides* Seguenza, 1880. Late Pliocene: Italy.
- B. (B.) circularis* Seguenza, 1880. Late Pliocene: Italy.
- B. (B.) compressa* Seguenza, 1880 (junior secondary homonym of *Eupsammia compressa* Sismonda, 1871; no replacement name suggested as yet). Late Pliocene: Italy.
- B. (B.) cornucopia* Simonelli, 1896. Pliocene: Italy.
- B. (B.) soloensis* Osberger, 1955. Pliocene: Java.
- B. (B.) formosana* Hu, 1987. Pliocene/Pleistocene: Taiwan.
- **B. (B.) elegans* Verrill, 1864. Pliocene to Holocene: eastern Pacific, 0–293 m.
- Pleistocene:**
- B. (B.) ponteni* Oppenheim, 1916. Pleistocene: Griechenland.
- B. (B.) zelandiae* Squires, 1958. Pleistocene: New Zealand.
- B. (B.) oulangiformis* Hu, 1988. Pleistocene: Taiwan.
- Exclusively Holocene (western Atlantic):**
- B. (B.) floridana* Pourtalès, 1868. (Amphi-Atlantic) 13–220 m.
- B. (B.) cyathoides* (Pourtalès, 1871). 45–494 m.
- B. (B.) palifera* Pourtalès, 1878. 53–708 m.
- B. (B.) wellsii* Cairns, 1977. 412–575 m.
- B. (B.) dineta* Cairns, 1977. 27–274 m.
- B. (B.) hadros* Cairns, 1979. 238–274 m.
- B. (B.) bayeri* Cairns, 1979. 274–311 m.
- Exclusively Holocene (eastern Atlantic):**
- B. (B.) europaea* (Risso, 1826). 0–50 m.
- = *Desmophyllum stellaria* Ehrenberg, 1834.
- B. (B.) regia* Gosse, 1853. 2–100 m.
- = *B. brevis* Duncan, 1872.
- = *B. balaerica* Lacaze-Duthiers, 1897.
- B. (B.) cellulosa* Duncan, 1873. 80–850 m.
- B. (B.) hellanae* Duncan, 1876. 18 m.
- B. (B.) striata* Duncan, 1876. 18 m.
- B. (B.) thalassae* Zibrowius, 1980. 385–1150 m.
- Exclusively Holocene (Indian Ocean/South Africa):**
- B. (B.) capensis* Verrill, 1865. 27–37 m.
- B. (B.) gemmifera* Klunzinger, 1879. 81 m.
- B. (B.) scabra* Alcock, 1893. Depth unknown.
- B. (B.) taprobanae* Bourne, 1905. Depth unknown.
- B. (B.) diffusa* Harrison and Poole, 1909. 6–274 m.
- B. (B.) vanderhorsti*, replacement name proposed herein for *B. ponderosa* van der Horst, 1926 (not Vaughan, 1900). 51–59 m.
- B. (B.) diademata* van der Horst, 1927. 165 m.
- B. (B.) bonaespei* van der Horst, 1938. Depth unknown.
- Exclusively Holocene (Australia):**
- B. (B.) bairdiana* Milne Edwards and Haime, 1848. 23–70 m.
- B. (B.) buccina* Tenison-Woods, 1878. 128 m.
- B. (B.) elliptica* (Tenison-Woods, 1878) (junior secondary homonym of *Turbinolia* (= *Balanophyllia*) *elliptica* Brongniart, 1822; no replacement name suggested as yet). 30 m.
- B. (B.) dentata* Tenison-Woods, 1879. Depth unknown.
- B. (B.) yongei* Crossland, 1952. Depth unknown.
- Exclusively Holocene (New Zealand):**
- B. (B.) chnous* Squires, 1962. 140–549 m.
- B. (B.) crassithecica* Cairns, 1995. 190–508 m.
- Exclusively Holocene (Japan):**
- B. (B.) japonica*, replacement name proposed herein for *B. teres* Cairns, 1994 (not *Eupsammia teres* Römer, 1863). 154–237 m.

Exclusively Holocene (Hawaiian Islands):

- B. (B.) diomedae* Vaughan, 1907. 110–307 m.
B. (B.) diomedae var. *mauensis* Vaughan, 1907.
B. (B.) laysanensis Vaughan, 1907. (And western Pacific) 238–400 m.
B. (B.) desmophyllioides Vaughan, 1907. (And western Pacific) 95–658 m.

Exclusively Holocene (western Pacific):

- B. (B.) scabrosa* (Dana, 1846). Depth unknown.
B. (B.) cumingii Milne Edwards and Haime, 1848. 65–307 m. = *Rhodopsammia ovalis* Semper, 1872.
B. (B.) parallela (Semper, 1872) (type species of *Rhodopsammia* Semper, 1872, by subsequent designation (Wells, 1936b)). 18 m.
B. (B.) dubia (Semper, 1872). 55 m.
B. (B.) rediviva Moseley, 1881. 90–256 m.
B. (B.) gemma (Moseley, 1881). 137–522 m.
B. (B.) cornu Moseley, 1881. 60–520 m.
B. (B.) parvula Moseley, 1881. 192–300 m.
B. (B.) gigas Moseley, 1881. (And Hawaiian Islands, New Zealand, and Indian Ocean) 90–640 m. = *B. hawaiiensis* Vaughan, 1907.
B. (B.) kalakauai Wright, 1882. Exact locality and depth unknown.
B. (B.) merguensis Duncan, 1889. Depth unknown.
B. (B.) profundicella Gardiner, 1899. 73 m.
B. (B.) corniculans Alcock, 1902. Exact locality and depth unknown.
B. (B.) tenuis van der Horst, 1922. 15 m.
B. (B.) iwayamaensis Abe, 1938. 1–3 m.
B. (B.) crassiseptum Cairns and Zibrowius, 1997. 183–250 m.
B. (B.) serrata Cairns and Zibrowius, 1997. 190–194 m.
B. (B.) generatrix Cairns and Zibrowius, 1997. 96–535 m.
- Exclusively Holocene* (eastern Pacific):
- B. (B.) galapagensis* Vaughan, 1906. 18–462 m. = *B. osburni* Durham and Barnard, 1952.
B. (B.) cedronensis Durham, 1947. 66–119 m. = *B. tiburonensis* Durham, 1947.
- Exclusively Holocene* (subantarctic):
- B. (B.) malouinensis* Squires, 1961. 75–1137 m.

Balanophyllia (Eupsammia) Milne Edwards and Haime, 1848

PLATE 1: FIGURES *fj*; PLATE 2: FIGURES *a,b,e-g*

Eupsammia Milne Edwards and Haime, 1848:77; 1850:li; 1851:133.—Milne Edwards, 1860:94.—Duncan, 1884:176.—Durham, 1949:147.—Alloiteau, 1952:679.—Chevalier and Beauvais, 1987:691.—Zibrowius, 1991:114–115.
Osteodes Conrad, 1855a:263.
Balanophyllia (Eupsammia).—Vaughan and Wells, 1943:236.—Wells, 1956:F434.—Chevalier, 1961:463.
Ceratopsammia Alloiteau, 1958:199–200, pl. 34: figs. 7–9 [new synonym].

DIAGNOSIS.—Corallum solitary, conical, and usually free, having a monocyclic base; corallum often curved or bent. Asexual budding may occur from edge zone. Epithecium present

or absent (present in type species); synapticulotheca always costate, costae of short, hispid spines. Pourtalès plan present; fifth cycle of septa often present. Columella elongate, spongy. Endotheca absent. Azooxanthellate.

DISCUSSION.—For a justification of the subgeneric classification and the position of *Eupsammia* in the phylogenetic analysis, see discussion of the genus.

Alloiteau (1958) distinguished *Ceratopsammia* (type species *C. besairiei* Alloiteau, 1958, by original designation) from other dendrophylliid genera by its possession of rows of large, regularly spaced intercostal thecal pores (like those of guyniids) and by its irregular septal insertion pattern. Examination of two poorly preserved types (see below), however, indicates that the intercostal pores of this species are not consistently present or regularly arranged and are not of particularly large size. In fact, they are consistent with the size of intercostal pores in the synapticulotheca of most dendrophylliids. Furthermore, the septal insertion pattern, although poorly defined and poorly preserved, appears to be a Pourtalès plan. Considering these changes to the generic diagnosis, *Ceratopsammia* may be synonymized with *Balanophyllia (Eupsammia)*. This species (and genus) is known only from the type series of three specimens: a holotype and two topotypes (=paratypes, ICZN, 1999, article 72.4.5) as mentioned in the original description, but the holotype is not distinguished from the paratypes in the text, figure captions, or specimen labels. But, if one assumes that the single set of measurements given by Alloiteau (1952) pertains to the holotype, then the specimen illustrated as pl. 34: fig. 7 would be the holotype. This specimen, as well as the lower part of the paratype illustrated in fig. 8, is deposited at the MNHN (Institute of Paleontology, M05028) (Plate 2*b,f*), although the upper part of that paratype (pl. 34: fig. 9) and the second paratype could not be found in 1999. The type locality of *Ceratopsammia besairiei* is the Late Cretaceous (Campanian to Maastrichtian) of Analavelona, Tulear district of Madagascar.

DISTRIBUTION.—Late Cretaceous (Campanian, Maastrichtian): Madagascar, India. Early Paleocene: USA (Midwayan), France (Montian). Early Eocene: Poland. Middle Eocene: USA (Early Claibornian), Jamaica, Belgium (Wemmelian), France (Lutetian), New Zealand (Bartonian). Late Eocene: USA (Jacksonian, Tejon), Treviso (Priabonian). Eocene: England. Early Oligocene: USA (Vicksburgian, Chickasawan), Germany. Middle Miocene: Italy (Helvetian), Libya. Late Miocene: Italy (Tortonian). Late Pliocene: Caribbean. Holocene: Indo-West Pacific, Caribbean, 18–170 m.

TYPE SPECIES.—*Madrepora trochiformis* Pallas, 1766, by subsequent designation (Milne Edwards and Haime, 1850:li) (= *Turbinolia elliptica* Brongniart, 1822); middle Eocene (Lutetian) of France. Also known from middle Eocene (Lutetian, Laekian) of France and Belgium. Deposition of type specimen unknown.

OTHER SPECIES (“*” indicates species with both fossil and extant occurrences).—Cretaceous: *Balanophyllia (E.) narin-*

densis (Alloiteau, 1936). Late Cretaceous (Late Senonian): Madagascar.

B. (E.) narindensis var. *elongata* (Alloiteau, 1951). Late Cretaceous: Madagascar.

B. (E.) collignoni (Alloiteau, 1951). Late Cretaceous: Madagascar.

B. (E.) besairiei (Alloiteau, 1958) (type species of *Ceratopsamia* Alloiteau, 1958). Late Cretaceous (Campanian, Maastriichtian): Madagascar.

B. (E.) dentata (Stoliczka, 1873). Cretaceous: India.

Paleocene:

B. (E.) ponderosa Vaughan, 1900. Early Paleocene (Midwayan): USA (Alabama).

B. (E.) ponderosa var. *texana* Vaughan and Popenoe, 1935. Early Paleocene: USA (Texas).

B. (E.) lehmani (Alloiteau, 1958). Early Paleocene (Montian): France.

Eocene:

B. (E.) pozaryskii (Rózkowska, 1955). Early Eocene: Poland.

B. (E.) inauris (Morton, 1834). Middle Eocene (Claibornian): USA (New Jersey).

B. (E.) brongniartiana (Milne Edwards and Haime, 1848). Middle Eocene (Lutetian): France.

B. (E.) bayliana (Milne Edwards and Haime, 1848). Middle Eocene (Lutetian): France.

B. (E.) burtinana (Milne Edwards and Haime, 1851). Middle Eocene (Wemmelian): Belgium.

B. (E.) hectori Tenison-Woods, 1880. Middle Eocene (Bortonian): New Zealand.

B. (E.) clarendonensis (Wells, 1934). Middle Eocene: Jamaica.

B. (E.) irrorata (Conrad, 1855a). Late Eocene (Jacksonian): USA (Louisiana, Mississippi, Alabama).

B. (E.) irrorata var. *coniformis* Vaughan, 1900. Early Eocene (early Claibornian): USA (Texas).

B. (E.) irrorata var. *dichotoma* (Gabb and Horn, 1860). Early Eocene (early Claibornian): USA (Alabama, Texas).

B. (E.) irrorata var. *mortoni* (Gabb and Horn, 1860). Early Eocene (early Claibornian): USA (Texas).

B. (E.) flabelloides (Oppenheim, 1900). Late Eocene (Priabonian): Treviso.

B. (E.) variabilis Nomland, 1916. Late Eocene (Tejon): USA (California).

B. (E.) washingtonensis (Durham, 1942). Late Eocene: USA (Washington).

B. (E.) desmophyllum Milne Edwards and Haime, 1848. Eocene (early Claibornian): England, USA (Maryland, Alabama).

B. (E.) desmophyllum var. *microcostata* Vaughan, 1900. Eocene: USA (Alabama).

B. (E.) angustinensis Vaughan, 1900. Eocene (Early Claibornian): USA (Texas).

B. (E.) annularis (Vaughan, 1900). Eocene: USA (Alabama).

B. (E.) conradi (Vaughan, 1900) (replacement name for *Turbinolia pileolus* Conrad, 1843, not Eichwald, 1829). Eocene: USA (Virginia).

Oligocene:

B. (E.) elaborata (Conrad, 1846). Early Oligocene (Chickasawan): USA (Alabama, Virginia, Maryland).

B. (E.) caulifera (Conrad, 1847) (type species of *Osteodes* Conrad, 1855a). Early Oligocene (Vicksburgian): USA (Mississippi, Louisiana).

B. (E.) caulifera var. *multigranosa* Vaughan, 1900. Eocene to early Oligocene: Patagonia, USA (Mississippi).

B. (E.) teres (Römer, 1863). Early Oligocene: Germany.

B. (E.) elongata Vaughan, 1900. Early Oligocene (Vicksburgian): USA (Mississippi).

B. (E.) fulleri Durham, 1942. Early Oligocene: USA (Washington).

B. (E.) praelonga (Michelotti, 1838). Late Oligocene (Priabonian): Italy. Middle Miocene (Helvetian): Italy, Belgium; Pliocene: Italy.

B. (E.) praelonga var. *obliqua* Zuffardi-Comerci, 1933. Middle Miocene: Italy.

B. (E.) praelonga var. *rovсандai* Zuffardi-Comerci, 1933. Middle Miocene: Italy.

Miocene:

B. (E.) sismondiana (Michelin, 1841). Middle (Langhian, Helvetian) to late Miocene: Italy, Libya.

B. (E.) sismondiana var. *albugnanensis* (Chevalier, 1966). Middle Miocene: Italy.

B. (E.) meneghinii Sismonda, 1871. Middle (Langhian, Helvetian) to late Miocene: Italy.

B. (E.) magna (Osasco, 1897). Middle Miocene (Helvetian): Italy.

B. (E.) conica Osasco, 1897. Middle Miocene (Helvetian): Italy.

B. (E.) bossolensis (Chevalier, 1961) (replacement name for *E. irregularis* de Angelis, 1894, not *B. irregularis* Seguenza, 1864). Middle Miocene: Italy.

B. (E.) pachysepta (Chevalier, 1961). Middle Miocene (Helvetian): Italy.

B. (E.) zuffardii (Chevalier, 1961) (replacement name for *E. campanulata* Zuffardi-Comerci, 1933, not *B. campanulata* Duncan, 1870). Middle Miocene: Italy.

B. (E.) zuffardiae Hegedüs, 1962 (replacement name for *B. rovсандai* Zuffardi-Comerci, 1933, not *B. praelonga* var. *rovсандai* Zuffardi-Comerci, 1933). Middle Miocene: Italy.

B. (E.) compressa (Sismonda, 1871). Middle (Helvetian, Langhian) to late Miocene (Tortonian): Italy.

=*Eupsammia sismondiana* var. *producta* Osasco, 1897.

B. (E.) patera Montanaro, 1929. Miocene: Italy.

Pliocene:

B. (E.) contorta de Angelis, 1894. Early Pliocene: Italy.

[*B. (E.) chevalieri* Fekih, 1980 (nomen nudum). Pliocene: Tunisia.]

**B. (E.) pittieri* Vaughan, 1919. Late Pliocene (Bowden) to Holocene: Caribbean, 40–96 m.

=*B. grandis* Cairns, 1977.

Exclusively Holocene:

B. (E.) caribbeana Cairns, 1977. Caribbean, 33–86 m.

- B. (E.) stimpsonii* (Verrill, 1865). Indo-West Pacific, 18–95 m.
 =*Eupsammia stimpsoniana* Verrill, 1866.
 =*Rhodopsammia affinis* Semper, 1872.
 =*Rhodopsammia incerta* Semper, 1872.
 =*Leptopsammia conica* van der Horst, 1922 (= *B. (E.) sumbayaensis*, replacement name proposed herein for *Leptopsammia conica* van der Horst, 1922, not *B. conica* Osasco, 1897).
- B. (E.) carinata* (Semper, 1872). Indo-West Pacific, 33–100 m.
 =*Rhodopsammia amoena* Semper, 1872.
- B. (E.) imperialis* Kent, 1871. Western Pacific, 18–170 m.
 = *B. malaccensis* Kent, 1871.
- B. (E.) regalis* (Alcock, 1893). Sri Lanka, 59 m.

Lamellophyllia Chevalier, 1961

PLATE 2: FIGURES *c, d*

Lamellophyllia Chevalier, 1961:491, pl. 19: figs. 8, 9.

DIAGNOSIS.—Corallum solitary, conical, free, and slightly curved. Epitheca absent; synapticulotheca costate, granular. Pourtalès plan present; 5 cycles of septa; paliform lobes present. Endotheca absent. Columella lamellar.

DISCUSSION.—Chevalier (1961) acknowledged the close resemblance of *Lamellophyllia* to *Balanophyllia* (*Eupsammia*), admitting that in the lower part of the corallum of *Lamellophyllia* there was nothing to distinguish it from *Eupsammia*, but that in the upper part, the Pourtalès plan was lost, and the columella became discretely lamellar. Chevalier further suggested that *Lamellophyllia* probably evolved from *Eupsammia*. In the context of the phylogenetic analysis (Figure 2, Table 3), *Lamellophyllia* differs from *Eupsammia* not only in having a lamellar columella but also in having granular (not hispid) costae and in lacking an epitheca.

Part of the holotype of *L. alloiteau* is now deposited at the MNHN: the lower part of the corallum illustrated by Chevalier (1961, pl. 19: fig. 9), which is broken into two pieces. The thin section presumably made from the transverse cut and the upper corallum distal to this cut (pl. 19: fig. 8) could not be found in 1999. The cut surface of the lower piece is 22.3 × 14.8 mm in CD and has 96 septa arranged in a Pourtalès plan, as shown in the illustration of the calice of the upper corallum. It is perplexing why Chevalier described this specimen as having free septa in the adult stage and thus placed it in the Tubastraeinae, a subfamily diagnosed as lacking the Pourtalès plan, when it is clear that the holotype has a well-preserved Pourtalès plan.

Lamellophyllia is one of nine dendrophylliid genera known only from the holotype or from very few specimens.

DISTRIBUTION.—Known from only one specimen from the type locality.

TYPE SPECIES.—*Lamellophyllia alloiteau* Chevalier, 1961, by monotypy; middle Miocene of Italy (Val Sanfra, Turin). Lower part of holotype deposited at MNHN (Institute of Paleontology, R10483) (see "Discussion").

OTHER SPECIES.—None.

Heteropsammia Milne Edwards and Haime, 1848

PLATE 2: FIGURES *h-j*; PLATE 3: FIGURES *a-e*

Heteropsammia Milne Edwards and Haime, 1848:89; 1850:lii; 1851:135.—Milne Edwards, 1860:105–106.—Duncan, 1884:176–177.—Vaughan and Wells, 1943:240–241, pl. 50: fig. 6.—Alloiteau, 1952:679–680.—Wells, 1956:F436.—Veron and Pichon, 1980:415–420.—Veron, 1986:576–577 [2 color figs., distribution map].—Chevalier and Beauvais, 1987:691, 693.—Hoeksema and Best, 1991:221–223, 233–240.

DIAGNOSIS.—Corallum solitary (monostomous) or colonial (polystomous), latter condition achieved by intratentacular budding and resulting in up to 40 contiguous corallites. Adult corallum free and mobile, globular in shape; juvenile coralla usually attached to small gastropod shells, these subsequently overgrown. Each specimen apparently in obligate symbiosis with a sipunculid worm, which lives in base of corallum. Epitheca absent; synapticulotheca covered with finely serrate ridges, usually 1–3 ridges per corresponding septum, not considered to be conventional costae. Pourtalès plan present; paliform lobes may be present. Columella spongy, not discrete. Endotheca absent. Zooxanthellate or azooxanthellate, depending on depth and latitude.

DISCUSSION.—*Heteropsammia* has recently been discussed and revised by Veron and Pichon (1980) and Hoeksema and Best (1991). Veron and Pichon suggested that there is only one highly variable species in the genus, with the variation in shape (and thus species names) caused by adaptation to various types of substrate (e.g., sandy, muddy, ooze) and the size and shape of the gastropod shell on which the coral larva originally settled. Hoeksema and Best cited two valid species, differentiating them based on whether they were monostomous or polystomous. I have more conservatively opted for three valid species (see "Other Species," below).

The "costae" of *Heteropsammia* have rarely been referred to as such, being more often referred to as finely serrate striae (Milne Edwards and Haime, 1848, 1850), rows of crispate granulations (Vaughan and Wells, 1943), or simply as "reduce" costae (Veron and Pichon, 1980). In fact, the synapticulotheca of the corallum edge of *Heteropsammia* is composed of finely serrate ridges (Plate 3*d, e*), one to three ridges corresponding to each underlying septum. These ridges are often discontinuous and may run obliquely instead of vertically. On and near the base of the corallum these ridges disintegrate entirely, replaced by small islands of coarsely granular "tuberculate" coenosteum (Plate 3*c*). *Heteropsammia* is part of a clade of five genera characterized by having a solitary unattached corallum and septa arranged in the Pourtalès plan (Figure 2). It is distinguished from its cohorts by having serrate costal ridges and an obligate symbiosis with a sipunculid worm that produces an irregular corallum shape.

The fascinating symbiosis between coral and sipunculid worm has been investigated in some detail (e.g., Moseley, 1881; Schindewolf, 1959; Feustel, 1966; Goreau and Yonge, 1968; Yonge, 1975; Gill and Coates, 1977; Veron and Pichon, 1980; Veron, 1986; Hoeksema and Best, 1991). To summarize,

the planula of all *Heteropsammia* must settle on a substrate, usually a dead gastropod shell (Plate 2j), that is already inhabited by a sipunculid worm (i.e., *Aspidosiphon muelleri* Diesing). A different kind of substrate, such as a scaphopod (Zibrowius, 1998) or even another coral, may also serve this function, as long as that substrate contains a viable sipunculid worm (Hoeksema and Best, 1991). The coral quickly overgrows the substrate, leaving only a basal aperture about 2 mm in diameter, which serves as an efferent pore for the worm. Concurrently, the worm outgrows the original gastropod shell but continues to grow in a circumferential/concentric (spiral) pattern around the base of the coral (Plate 3a,b). The coral coenosteum keeps pace with the worm, providing a full covering for the worm, except for the efferent pore, which is periodically reformulated at the distal end of the worm. Previous efferent pores are partially covered by coenosteum but are usually maintained at a reduced size (1/10 original diameter) along the base and edge of the corallum, often in a linear pattern. These obsolete efferent pores may serve a respiratory function for the sipunculid (Moseley, 1881). The advantage to the sipunculid in this commensal relationship is the protection afforded by the host coral. The coral benefits by being "towed" over the soft substrate by the sipunculid (Gill and Coates, 1977; Hoeksema, 1993), thus increasing its feeding range, and possibly by being uprighted after being overturned (Hoeksema and Best, 1991). Coralla of *Heteropsammia* are also commonly known to host the parasitic burrowing mussel *Lithophaga lessepsiana*.

The genus *Psammoseris* Milne Edwards and Haime, 1851 (type species: *Heterocyathus hemisphaerica* Gray, 1849, by monotypy), was originally described as a fungiid, and later it was transferred to the Dendrophylliidae by Vaughan and Wells (1943). It was considered to be a dendrophylliid until 1991, when Hoeksema and Best (1991) synonymized it with the caryophylliid genus *Heterocyathus* Milne Edwards and Haime, 1848, a view adopted and amplified by Cairns (1998). The genus *Spongiocyathus* Folkesson, 1919 (type species *S. typicus* Folkesson, 1919 (= *Heterocyathus hemisphaericus*), by monotypy), is also a junior synonym of *Heterocyathus*, as its type species is a subjective synonym of the type species of *Psammoseris*. This synonymy is mentioned here because coralla of *Heterocyathus* are similar in size and shape to those of *Heteropsammia*, and both genera have an obligate symbiosis with a sipunculid worm, but *Heterocyathus* differs in having a solid septotheca and true costae. See also "Previously Reassigned 'Dendrophylliid' Genera" for more details on *Psammoseris* and *Spongiopsammia*.

De Angelis (1894) described the fossil species *H. antiqua* from the Priabonian (late Eocene) of Italy, but its corallum shape, "subpedunculate" base, and inclusion of a gastropod shell (without mention of sipunculid) argue against this generic placement. Even de Angelis was doubtful about placing it in *Heteropsammia*. His species is probably a *Balanophyllia* and thus is not the earliest record of *Heteropsammia*.

An even earlier report of a dendrophylliid ("Dendrophylliidae, gen. et sp. inc.") exhibiting a similar symbiotic relationship was reported by Löser and Stolarski (1997) from the Early Cretaceous (Middle Albian) of France; however, these specimens have been examined and reinterpreted as a species of *Heterocyathus*.

DISTRIBUTION.—Late Miocene: Java (Gerth, 1921). Pliocene: Japan. Plio-Pleistocene: Japan, Taiwan. Holocene: tropical Indo-West Pacific (Gill and Coates, 1977, fig. 1; Veron, 1993:370, map fig. 53), 1–622 m.

TYPE SPECIES.—*Heteropsammia michelinii* Milne Edwards and Haime, 1848, by monotypy (= *Madrepora cochlea* Spengler, 1781 (senior synonym); = *H. cochlea* var. *alta* Yabe and Eguchi, 1932; = *H. rotundata* Semper, 1872; = *H. ovalis* Semper, 1872; = *Psammoseris cyliciooides* Tenison Woods, 1879; = *H. aphrodes* Alcock, 1893; = ?*H. pisum* Alcock, 1902; = *H. ovalis* var. *formosensis* Yabe and Eguchi, 1932; = *H. ovalis* var. *japonica* Yabe and Eguchi, 1932; = *H. michelini* var. *formosus* Hu, 1987); "Wanpoa, China." Known from Pliocene of Japan and the Philippines, Plio-Pleistocene of Japan and Taiwan, and Holocene of tropical Indo-West Pacific, 9–622 m (see Hoeksema and Best, 1991; Cairns, 1999a). Holotype deposited at MNHN (1080), see Hoeksema and Best (1991); figured herein (Plate 2h,i).

OTHER SPECIES.—*Heteropsammia eupsammides* (Gray, 1849). Holocene: Indo-West Pacific, 1–38 m.

= *H. geminata* Verrill, 1870.

= *H. multilobata* Moseley, 1881.

[*H. nipponica* Yabe and Eguchi, 1932 (nomen nudum). Holocene: Japan.]

H. moretonensis Wells, 1964. Holocene: Australia (Queensland), 11–48 m.

***Wadeopsammia* Wells, 1933**

PLATE 3: FIGURES f–i

Trochosmia.—Wade, 1926:26 [in part].

Wadeopsammia Wells, 1933:227–228.—Vaughan and Wells, 1943:235–236.—Wells, 1956:F433.

Heteropsammia.—Hoeksema and Best, 1991:233–234 [in part: *H. nodosa*].

DIAGNOSIS.—Corallum free, solitary, and conical, bearing circular cavity in base. Costae coarsely granular, with large rounded granules occurring unilinearly; epitheca absent. Poursalids plan present; only 36 septa occur in holotype. Columella solid, nondiscrete. Endotheca absent.

DISCUSSION.—Only two specimens of *Wadeopsammia nodosa* are known: the holotype (Plate 3f,i) (USNM I32703) and a slightly larger specimen (Plate 3g,h) from the Late Cretaceous of Texas (USNM I75183) reported by Wells (1933). The Texas specimen is very similar to the holotype in costal architecture and shape, but it differs in having a papillose columella and no indication of thecal porosity. Therefore, only the holotype was considered in the generic diagnosis.

The holotype of *W. nodosa* is a juvenile corallum only 3.3 mm in CD and 3.0 mm in height, with a basal pore 0.9 mm in diameter. Its larger costal granules are 0.12 mm in diameter, and it has 36 septa, a pair of S_4 in each system. Wells (1933) re-described the holotype adequately, noting that in the original description Wade (1926) had confused the base of the corallum with the calice and thus considered the costae to be septa and vice versa.

Hoeksema and Best (1991) synonymized *Wadeopsammia* with *Heteropsammia*, following the interpretation of Wells (1933) that the pore in the corallum base of *Wadeopsammia* was a sipunculid efferent pore, most other characters being the same. But the pore in the base of *Wadeopsammia* might equally well be interpreted as the remnants of an attachment to a cylindrical object, such as the stem of a gorgonian or antipatharian. Even at this small size, coralla of juvenile *Heteropsammia* have several smaller obsolete efferent pores in addition to the main pore, whereas no such pores are seen in the holotype of *Wadeopsammia nodosa*. Furthermore, the costae of *Wadeopsammia* are coarsely granular, whereas those of *Heteropsammia* are composed of thin serrate ridges, a character herein considered to be of generic significance. Thus, *Wadeopsammia* is removed from synonymy with *Heteropsammia* and is considered to be a separate but poorly known genus represented by only one juvenile corallum. In the phylogenetic analysis, *Wadeopsammia* is part of a clade of five genera characterized by having solitary unattached coralla and septa arranged in the Pourtalès plan (Figure 2), and it is distinguished from *Heteropsammia* by having granular costae and a solid columella.

DISTRIBUTION.—Late Cretaceous (Campanian: Ripley Formation): USA (Tennessee, ?Texas (Navarro Formation)).

TYPE SPECIES.—*Trochosmia nodosa* Wade, 1926, by original designation; Late Cretaceous (Campanian: Ripley Formation) of Tennessee. Holotype deposited at USNM (I32703) and figured herein (Plate 3*f,i*).

OTHER SPECIES.—None.

Calostylopsis Alloiteau, 1958

PLATE 3: FIGURES *j,k*; PLATE 4: FIGURE *a*

Calostylopsis Alloiteau, 1958:148, fig. 24, pl. 19: figs. 8–10.

DIAGNOSIS.—Corallum solitary, conical (ceratoid), curved, and free. Epitheca absent; synapticulotheca costate, granular, each costa (pseudocostae) corresponding to several septa. Septa sinuous, laterally joined by numerous synapticulae and “divergent sclerodermites,” together producing very reticulate and rather broad spongy zone extending to columella. Columella spongy. Endotheca absent.

DISCUSSION.—*Calostylopsis* is unique among the dendrophylliids in having broad costae that correspond to several septa and in having a thick, spongy wall composed of sinuous septa and synapticular bridges. Its name was derived from the Silurian rugosan genus *Calostylis* Lindström, 1868, which it resembles in wall structure as seen in transverse section. The wall

structure of *Calostylopsis* is also similar to the dissepimentarium of the Silurian rugosan genus *Entelophyllum* Wedekind, 1927. Although the poor preservation of the extant type series is not sufficient to verify the costal:septal ratio or even the septal pattern, a figure of a transverse section showing a reticulate septal pattern (Alloiteau, 1958, fig. 24) is sufficiently distinctive to distinguish this genus from other dendrophylliids. In the phylogenetic analysis, *Calostylopsis* groups with the clade including solitary, unattached genera that have a Pourtalès plan, but this genus differs in having a reticulate septal arrangement and in having the apparent autapomorphy of having more than one costa per septum.

Alloiteau (1958) suggested that some specimens described as *Eupsammia varians* by Stoliczka (1873) might be congeneric with *Calostylopsis*; however, the illustrations and description of *E. varians* show it to have a Pourtalès plan and to lack indication of the unique wall structure of *Calostylopsis sakalavensis*.

DISTRIBUTION.—Early Cretaceous (Albian): Madagascar. ?Cretaceous: India.

TYPE SPECIES.—*Calostylopsis sakalavensis* Alloiteau, 1958, by original designation; Early Cretaceous (Albian) of Ambaranina, Madagascar.

The holotype and three paratypes are deposited at the MNHN (Institute of Paleontology, M05021). Those specimens were illustrated by Alloiteau (1958) in his original description; however, the thin sections and apical parts of the coralla (figured as pl. 19: figs. 8a,c, 8'a, 8''a, 8'''a, 9, 10) could not be found in 1999. The deposition of the other three paratypes is also unknown.

OTHER SPECIES.—None.

Bathypsammia Marenzeller, 1907

PLATE 4: FIGURES *b–e*

Thecopsammia Pourtalès, 1868:138 [in part: *T. tintinnabulum*].

Bathypsammia Marenzeller, 1907:8.—Vaughan and Wells, 1943:240.—Wells, 1956:F436.—Squires, 1959:31–32.—Cairns, 1979:190.—Chevalier and Beauvais, 1987:691.

DIAGNOSIS.—Corallum solitary, conical, and attached by slender peduncle. Epitheca well developed, covering most of thick synapticulotheca; coenosteum distal to epitheca not costate, covered with finely hispid anastomosing ridges. Septa arranged in normal insertion pattern (not Pourtalès plan); 4 cycles of non-exsert septa. Columella variable in size, discrete, spongy. Endothecal dissepiments absent. Azooxanthellate.

DISCUSSION.—In his generic revision, Wells (1956:F436) stated that *Bathypsammia* was “like *Thecopsammia* but POURTALÈS plan apparent”; however, he undoubtedly meant to say the Pourtalès plan was not apparent. In the phylogenetic analysis (Figure 2, Table 3), *Bathypsammia* is patristically closest to *Trochopsammia*, differing from that genus in having costae composed of serrate ridges and in having a spongy columella.

DISTRIBUTION.—?Late Cretaceous (Maastrichtian) to Paleocene: Egypt. Holocene: Southeastern USA from South Carolina through Florida Keys, Cuba, 210–1115 m.

I query the Late Cretaceous occurrence of *Bathypsammia* reported by Hassan and Salama (1969) because they did not describe the nature of the synapticulotheca beneath the epitheca (costate or not) of *B. cleopatrae* and because of the great similarity of this species to *Palaeopsammia multiformis*, which they reported from the same region. *Bathypsammia cleopatrae* is described as being "wholly epithecate," whereas Holocene species of *Bathypsammia* may have 90%–95% of the wall covered with epitheca, but distal to the epitheca the synapticulotheca is not costate. If, in fact, the underlying synapticulotheca of *B. cleopatrae* is costate, it would fall to *Palaeopsammia* and would probably be synonymous with *P. multiformis*.

TYPE SPECIES.—*Thecopsammia tintinnabulum* (Pourtalès, 1868), by original designation; USA off Florida reefs, 183–549 m. Also known from southeastern USA from South Carolina through Florida Keys, 210–1115 m (Cairns, 1979).

The lectotype, MCZ 2768 (designated by Cairns and figured as pl. 38: figs. 1–3 (Cairns, 1979); figured herein as Plate 4*b,c*), and 260 paralectotypes are deposited at the MCZ. Eleven more paralectotypes are deposited at BM, and one is deposited at the YPM (see Cairns, 1979).

OTHER SPECIES.—?*Bathypsammia cleopatrae* Hassan and Salama, 1969. Late Cretaceous (Maastrichtian) to Paleocene: Egypt (Tarawak Chalk).

B. fallosocialis Squires, 1959. Holocene: southeastern USA from Georgia through Florida Keys and Cuba, 213–805 m.

Portalopsammia new genus

PLATE 4: FIGURES *f–i*; PLATE 5: FIGURE *a*

Balanophyllia.—van der Horst, 1927:5–6 [in part: *B. togata*].

Thecopsammia.—Wells, 1935:531 [in part: *T. togata*].

Trochopsammia.—Cairns and Keller, 1993:275–276 [in part: *T. togata*].

DIAGNOSIS.—Corallum solitary, conical to subcylindrical (sometimes scolecooid), and attached. Epitheca well developed, covering basal synapticulotheca; coenosteum distal to epitheca covered with thin, hispid ridges. Septa arranged in normal insertion pattern (not Portalès plan); 3 cycles of septa; inner edges of S_1 highly sinuous. Columella absent. Endothecal dissepiments absent. Azooxanthellate.

DISCUSSION.—*Portalopsammia* is similar to *Bathypsammia* and *Trochopsammia* but differs from *Trochopsammia* in having a noncostate, hispid theca, as noted by Cairns and Keller (1993). It differs from *Bathypsammia* in lacking a columella (Figure 2).

DISTRIBUTION.—As for the type species.

TYPE SPECIES.—*Balanophyllia togata* van der Horst, 1927:5; Holocene of "Buffalo River, N 15 miles, 310 fms [=567 m]," South Africa. Known from Agulhas Bank to Durban, South Africa, 155–775 m (Cairns and Keller, 1993). Deposition of holotype not traced, but probably in BM (fide H. Zibrowius).

OTHER SPECIES.—None.

ETYMOLOGY.—Named in honor of Count Louis François de Portalès (1824–1880).

Trochopsammia Portalès, 1878

PLATE 5: FIGURES *b–e*

Trochopsammia Portalès, 1878:208.—Vaughan and Wells, 1943:239–240, pl. 50: fig. 7.—Wells, 1956:F436, fig. 339:5a–b.—Cairns, 1979:194–195, pl. 40: figs. 1–3.—Chevalier and Beauvais, 1987:694, fig. 401:4.—Cairns and Keller, 1993:275.

DIAGNOSIS.—Corallum solitary, conical, firmly attached. Epitheca covering lower theca. Synapticulotheca thick (i.e., as wide as septal thickness at calicular edge), costate; costae wide (i.e., over 5 times width of intercostal striae) and finely granular. Septa arranged in normal insertion pattern (not Portalès plan); 3 cycles of septa, all septa about same size. Columella rudimentary or absent. Endotheca present. Azooxanthellate.

DISCUSSION.—*Trochopsammia* appears to be most closely related to *Portalopsammia*, as discussed in the account of that genus (see also Figure 2). It has the deepest-known occurrence among the solitary dendrophylliids.

DISTRIBUTION.—Holocene: off northwestern Cuba and Lesser Antilles (St. Vincent and Grenada), 532–1472 m.

TYPE SPECIES.—*Trochopsammia infundibulum* Portalès, 1878, by monotypy; off northwestern Cuba, 1161–1472 m. Also known from throughout Lesser Antilles, 532–1472 m.

Two syntypes are deposited at the MCZ (5607, one is illustrated herein as Plate 5*b,c*), and two more are deposited at BM (1939.7.20.430–431).

OTHER SPECIES.—None.

Endopsammia Milne Edwards and Haime, 1848

PLATE 5: FIGURES *f–i*

Endopsammia Milne Edwards and Haime, 1848:91; 1850:lii; 1851: 135–136.—

Milne Edwards, 1860:107–108.—Duncan, 1884:181.—Vaughan and Wells, 1943:238 [not pl. 50: fig. 12].—Wells, 1956:F435 [not fig. 339:2]; 1964:117, 118, pl. 2: figs. 12, 13.—Cairns and Zibrowius, 1997:188, pl. 28: figs. c–e.

Leptopsammia.—van der Horst, 1922:48 [in part].

Leptopsammia (*Endopsammia*).—Chevalier and Beauvais, 1987:691.

DIAGNOSIS.—Corallum solitary, conical to cylindrical, and firmly attached. Epitheca thin, covering most of synapticulotheca; coenosteum distal to and underlying epitheca weakly costate, covered with low granules. Septa arranged in normal insertion pattern (not Portalès plan); up to 4 cycles of septa; axial edges of all septa coarsely dentate to lacinate. Columella spongy, nondiscrete. Tabular endothecal dissepiments present in elongate coralla. Azooxanthellate.

DISCUSSION.—Whereas most authors have distinguished *Endopsammia* from *Leptopsammia* based on their difference in axial septal dentition, van der Horst (1922) considered them to be synonymous and Chevalier and Beauvais (1987) placed *Endopsammia* as a subgenus of *Leptopsammia*. Herein, *Endopsammia* is distinguished from *Leptopsammia* by having coarser, dentate axial septal edges of the S_1 ; a noncostate theca (character 5); a nondiscrete columella; and a shallower fossa. In the phylogenetic analysis, only one character (5, synapticulotheca) separates the two genera (Figure 2).

Whereas Cairns and Zibrowius (1997) placed *Thecopsammia regularis* Gardiner, 1899, in synonymy with *Endopsammia philippensis*, I have subsequently examined the types series and conclude they are different, *E. regularis* differing in having a smaller corallum and a much smaller columella.

DISTRIBUTION.—Holocene: tropical regions of Indo-Pacific from the Maldive Islands to the Galápagos, 0–73 m.

TYPE SPECIES.—*Endopsammia philippensis* Milne Edwards and Haime, 1848, by monotypy; Philippines. Also known from throughout Indo-West Pacific, 0–62 m (Cairns and Zibrowius, 1997).

Cairns and Zibrowius (1997) stated that the holotype, a specimen from the historic Stokes collection, was deposited at BM (1855.12.77.25); however, in 1999 another specimen was found at the MNHN (1076) of precisely the same dimensions of the holotype (7.4 × 6.6 mm in CD, 7.5 mm in height) and bearing the label “p. 91, pl. 1, fig 5, Philippines,” the original pagination and type locality of the holotype. Both specimens appear to be conspecific and both are illustrated herein.

OTHER SPECIES.—*Endopsammia regularis* (Gardiner, 1899). Loyalty Islands, 73 m.

E. pourtalesi (Durham and Barnard, 1952). Galápagos, depth unknown.

Leptopsammia Milne Edwards and Haime, 1848

PLATE 5: FIGURES j–l; PLATE 6: FIGURES a,d

Leptopsammia Milne Edwards and Haime, 1848:90; 1850:lii; 1851:135.—Milne Edwards, 1860:106–107.—Duncan, 1884:181.—van der Horst, 1922:68.—Wells, 1964:117.—Zibrowius, 1980:191.—Chevalier and Beauvais, 1987:691.—Cairns and Zibrowius, 1997:186.—Cairns, 2000:167.
Balanophyllia.—Vaughan and Wells, 1943:236 [in part].—Wells, 1956:F433 [in part].

DIAGNOSIS.—Corallum solitary, conical to subcylindrical, and firmly attached. Synapticulotheca epithecate basally, costate proximally; costae covered with short spines. Septa arranged in normal insertion pattern (not Pourtalès plan); 4 to 5 cycles of septa; axial edges of S₁–S₂ smooth, those of higher-cycle septa dentate to lacinate. Columella spongy, usually discrete. Tabular endothecal dissepiments sometimes present. Azooxanthellate.

DISCUSSION.—In the middle of the twentieth century, *Leptopsammia* was considered to be synonymous with *Balanophyllia* (Vaughan and Wells, 1943; Wells, 1956); however, Wells (1964) resurrected *Leptopsammia* for *Balanophyllia*-like species that did not display a Pourtalès plan, which was considered to be its original distinction from *Balanophyllia*. It is interesting to note, however, that one species, *L. formosa*, has coralla containing a normal arrangement of septa as well as those showing a poorly developed Pourtalès plan. Another point of variation among the species of this genus is the costae, which are well defined in most species but are obsolete in *L. queenslandiae*. A final point of variation concerns the columella, most species having a discrete, well-developed col-

umella, but two species (*L. queenslandiae*, *L. trinitatis*) have a rudimentary, nondiscrete one.

As Zibrowius (1980) and Cairns and Zibrowius (1997) have noted, whereas the Atlantic species of this genus are fairly well represented and characterized, the Indo-Pacific species are known from very few specimens, thus their range of variation and taxonomy is unclear.

DISTRIBUTION.—Middle Miocene (Vindobonian): Azores. Holocene: tropical regions of the Atlantic, eastern Indian Ocean (off Western Australia), and western Pacific (Philippines, Indonesia, Malacca, and Queensland), 3–900 m.

TYPE SPECIES.—*Leptopsammia stokesiana* Milne Edwards and Haime, 1848, by monotypy; Holocene of Philippines. Also known from Indonesia and Malacca, 46–69 m (Cairns and Zibrowius, 1997). Holotype deposited at BM (1855.12.27.1).

OTHER SPECIES.—*Leptopsammia zbyzsewskii* Chevalier, 1965. Middle Miocene (Vindobonian): Azores.

L. britannica (Duncan, 1870). Holocene: off Great Britain, 160–665 m (Zibrowius, 1980).

=*Balanophyllia* (*Thecopsammia*) *socialis* var. *costata* Duncan, 1870.

=*Balanophyllia* (*Thecopsammia*) *socialis* var. *jeffreysia* Duncan, 1870.

L. pruvoti Lacaze Duthiers, 1897. Holocene: northeastern Atlantic, 3–150 m (Zibrowius, 1980).

=*L. microcardia* Döderlein, 1913.

L. poculum (Alcock, 1902). Holocene: Indonesia, 90 m (see van der Horst, 1922).

=*L. poculum* van der Horst, 1922.

L. formosa (Gravier, 1915). Holocene: northwestern Atlantic, 400–900 m (Zibrowius, 1980).

=*Thecopsammia imperfecta* Gravier, 1915.

L. columna Folkeson, 1919. Holocene: Australia (Western Australia), 20 m.

L. crassa van der Horst, 1922. Holocene: Philippines, Indonesia, 22–187 m.

L. queenslandiae Wells, 1964. Holocene: Australia (Queensland), 87 m.

L. chevalieri Zibrowius, 1980. Holocene: off northwestern Africa, 70–500 m.

L. trinitatis Hubbard and Wells, 1986. Holocene: Caribbean, 15–40 m (Cairns, 2000).

Thecopsammia Pourtalès, 1868

PLATE 6: FIGURES b,c,e–h

Thecopsammia Pourtalès, 1868:138 [in part: *T. socialis*].—Moseley, 1881:195 [in part: *T. elongata*].—Marenzeller, 1907:8.—Vaughan and Wells, 1943:240.—Wells, 1956:F436.—Cairns, 1979:188.—Chevalier and Beauvais, 1987:691.

Balanophyllia (*Thecopsammia*) Duncan, 1870:296; 1884:175 [in part: specimens from Florida].—[not Alcock, 1902:42 (= *Balanophyllia*)].

Balanophyllia.—Duncan, 1873:333–334 [in part: *B. socialis*].—van der Horst, 1922:49 [in part: *B. socialis*].

DIAGNOSIS.—Corallum solitary, conical, and firmly attached. Epithecata always present, covering basal 20%–95% of

synapticulotheca; synapticulotheca thick (3–4 mm) and hispid, not costate. Pourtalès plan present; paliform lobes present or absent. Columella small (less than 20% GCD) to moderate in size; discrete; composed of several discrete lamellae that are often slightly twisted, swirled, or fused together. Endotheca absent. Azooxanthellate.

DISCUSSION.—*Thecopsammia* was considered to be so similar to *Balanophyllia* that between 1870 and 1922 some authors (see synonymy) placed *Thecopsammia* as a subgenus of *Balanophyllia*, and others (e.g., Duncan, 1873; van der Horst, 1922) considered it to be completely synonymous. Later, Vaughan and Wells (1943) and Wells (1956) considered *Thecopsammia* to be a separate genus based on its lacking a Pourtalès plan in the ephebic (adult) stage; however, Cairns (1979) and Zibrowius (1980) showed conclusively that *Thecopsammia socialis* has a distinct Pourtalès plan in the adult stage. If one considers *Thecopsammia* to have a Pourtalès plan, it would, in fact, key to the genus *Balanophyllia* in Vaughan and Wells's (1943) key to the genera of the Dendrophyllidae. There is one significant difference, however, that separates these two genera: *Thecopsammia* has no costae, whereas *Balanophyllia* does. Zibrowius doubted whether this criterion was sufficient to distinguish between genera but did not synonymize them. In this paper, thecal architecture is considered a significant character, thus *Thecopsammia* is considered a distinct genus. Although *Thecopsammia* and *Balanophyllia* are not closely adjacent on the cladogram (Figure 2), there are only two characters that separate them: synapticulotheca (character 5), as discussed above, and a minor difference in columellar type (character 9).

A second species in this genus, *T. elongata* Moseley, 1881, was previously known only from the worn holotype from *Challenger* station 219 (1°54'S, 146°39'40"E, 274 m, Nares Bay, Admiralty Islands; BM 1880.11.25.148). Two additional, well-preserved (live-when-collected) coralla are reported herein from *Nimbus* station 55 (26°27'S, 153°50'E, 271–273 m, off southeastern Queensland, Australia; USNM 78560). The larger corallum (Plate 6*b,e*) is 15.5 × 13.5 mm in CD, 30 mm in height, and 3.9 mm in PD. The theca is covered by thin bands of epitheca to within 1–5 mm of the calice, and there clearly are no costae anterior to or beneath the epitheca. The corallum contains 58 septa ($S_1-S_2>S_4>S_3$), having several additional incompletely filled half-systems. A crown of 16 prominent paliform lobes (P_3), each two to three times the width of an S_3 , encircles a spongy columella. The smaller corallum is 12.2 mm in GCD, its theca is completely covered with epitheca, and it contains 48 septa and 12 paliform lobes. Both coralla are pedicellate, slightly bent, and detached from the substrate. These specimens were collected from virtually the same depth as the holotype, also from the southwestern Pacific. *Thecopsammia elongata* differs from *T. socialis* by having prominent paliform lobes.

A third species, *T. cylindrica* Kuzmicheva, 1987, was described from the late Eocene of Ukraine, Russia, but the types could not be obtained on loan, and based on the illustrations of the types, it is considered highly unlikely that this species is congeneric.

REMARKS.—The columella of *T. socialis* does not increase in size as the corallum grows. Thus, a large corallum will appear to have a relatively small columella, and occasionally a corallum may have no columella. Large coralla typically have 72 septa, consisting of a pair of S_5 in every half-system adjacent to an S_1 ; at most, 80 septa were found in any corallum.

DISTRIBUTION.—Holocene: western Atlantic off USA from Georgia to Florida Keys, 214–878 m (Cairns, 1979); southwestern Pacific (Admiralty Islands; off Queensland, Australia), 271–274 m.

Duncan's (1884) record of the Pliocene of England is unsubstantiated, and Kuzmicheva's (1987) record from the late Eocene is also questioned.

TYPE SPECIES.—*Thecopsammia socialis* Pourtalès, 1868, by subsequent designation (choice following elimination) (Vaughan and Wells, 1943); Holocene of USA (Florida Keys), 183–549 m (see Cairns, 1979), but species ranges from Georgia to Florida Keys, 214–879 m. Thirty-nine syntypes deposited at MCZ (5601, 2773), 1 syntype at YPM (4764), and 5 syntypes at BM (see Cairns, 1979). Syntype from MCZ (5601) figured herein (Plate 6*g*).

Portalès (1868) included two species in the genus *Thecopsammia* but did not designate a type species. Marenzeller (1907) later made one of these species the type of a new genus, *Bathypsammia tintinnabulum*, logically making the other species, *T. socialis*, the type species by fixation by elimination. The passive process of the elimination of all but one of the originally included nominal species from a genus, however, does not in itself constitute type fixation (ICZN, 1999, article 69.4). Instead, fixation of the type species must be attributed to Vaughan and Wells (1943), who specifically listed *T. socialis* as the type species "by elimination," in accordance with recommendation 69A.3.

OTHER SPECIES.—? *Thecopsammia cylindrica* Kuzmicheva, 1987. Late Eocene: Ukraine, Russia.

T. elongata Moseley, 1881. Holocene: southwestern Pacific, 271–274 m.

Other species have been attributed to *Thecopsammia* (e.g., as many as six by Chevalier and Beauvais, 1987), but all but two have been transferred to other genera, including *Balanophyllia*, *Bathypsammia*, *Leptopsammia*, and *Eguchipsammia*.

Endopachys Lonsdale, 1845

PLATE 7: FIGURES a–e,g

Endopachys Lonsdale, 1845:514–516 [in part: fig. a, *E. alatum*].—Milne Edwards and Haime, 1848:81–82; 1850:iii; 1851:133–134.—Milne Edwards, 1860:97–98.—Duncan, 1884:176.—Yabe and Eguchi, 1932a:11–14.—Vaughan and Wells, 1943:236, pl. 50: fig. 4.—Umbgrove, 1950:648–650, fig. 2, pl. 82: figs. 1–10, pl. 83: fig. 7.—Alloiteau, 1952:679.—Wells, 1956:F434, fig. 338:5; 1975:173.—Chevalier and Beauvais, 1987:693, fig. 401:8.—Cairns, 1995:121, pl. 41: figs. c–h; 1999a:132, pl. 22: fig. f.
Rhectopsammia Vaughan, 1900:183–184.

DIAGNOSIS.—Corallum (anthocyathus) solitary and free, resulting from transverse division or budding from corallum edge; corallum straight. Shape of corallum variable, including cuneiform, compressed-cylindrical, and flabellate. Some spe-

cies with 6 or 12 robust ridges or flanges (paracostal ridges of Wells, 1975) aligned with C_1 and C_2 . Epitheca absent; base of corallum covered with spines arranged in no order; toward calice spines usually aligned into narrow costae. Pourtalès plan present; up to 5 cycles of septa; paliform lobes (P_3 or P_4) usually present. Columella elongate, discrete, and spongy. Azooxanthellate.

DISCUSSION.—*Endopachys* has always been considered to be very similar to *Balanophyllia*, especially species of the unattached subgenus *Eupsammia*, but has been purported to differ by its cuneiform corallum shape and its propensity to have paracostal ridges. Some species of *Endopachys* (e.g., *E. minutum*, *E. tampae*), however, are not cuneiform but rather are compressed-cylindrical or flabellate, and some species of *Eupsammia* (e.g., *B. (E.) carinata*) are somewhat compressed and have edge crests. Furthermore, not all species of *Endopachys* have paracostal ridges. Therefore, although corallum shape is helpful in distinguishing the two genera, it is not diagnostic.

Endopachys differs consistently from *B. (Eupsammia)* in asexually reproducing by transverse division, a phenomenon described and illustrated for extant *E. grayi* by Cairns (1999a:132, pl. 22f). The characteristic basal scar that results from transverse division is often seen on small fossil coralla (anthocyathi) of *E. maclurii* (Plate 7e) and on Holocene *E. grayi*, and it is easily seen on the fossil species *E. minutum*, the coralla of which resemble those of *Notocyathus*. Basal scars can be seen only on relatively small (less than 6 mm GCD) coralla (anthocyathi) because the base rapidly heals and becomes covered with costal granules. Although thousands of anthocyathi of Eocene *E. maclurii* have been examined, no corallum in the process of division has been discovered, and only seven attached anthocauli have been found, four of which comprise the type series of *Rhectopsammia claibornensis* (=anthocaulus stage of *Endopachys maclurii*, Plate 7c). It is herein suggested that transverse division is found in all species of *Endopachys* and that this character, along with corallum shape and lack of epitheca, may serve to distinguish the genus from *Eupsammia*. Transverse division in *Endopachys* was noted by Vaughan (1907) and Cairns (1989b) and was advocated by the latter as a potential genus-level discriminator.

Endopachys australiae Tenison-Woods, 1878, reported from off Port Jackson, New South Wales, Australia, is believed to be a turbinoliid, probably of the genus *Platytrachus*. Yabe and Eguchi (1932a), Umbgrove (1950), Wells (1975), and Cairns (1999a) provide informative taxonomic and morphological observations about the genus.

DISTRIBUTION.—Early Eocene (early Claibornian) to early Oligocene (Vicksburgian): southeastern USA from Texas to North Carolina. Early Miocene: Florida. Plio-Pleistocene: tropical northwestern Pacific. Holocene: Indo-Pacific from western Indian Ocean to Gulf of California, 37–386 m (Cairns, 1994).

TYPE SPECIES.—*Endopachys alatum* Lonsdale, 1845, by subsequent designation (Wells, 1975) (= *E. maclurii* (Lea, 1833)); middle to late Eocene of USA (Alabama). Deposition of holotype unknown (not at BM).

Virtually all authors (e.g., Milne Edwards and Haime, 1850; Vaughan and Wells, 1943; Wells, 1956; Cairns, 1994) have designated *Turbinolia maclurii* Lea, 1833, as the type species of *Endopachys*; however, that species was not one of the three originally attributed to the genus by Lonsdale and thus cannot be the type species (ICZN, 1999, articles 67.2, 69.1). Of the three species mentioned by Lonsdale as belonging to *Endopachys*, one is a turbinoliid (i.e., *Sphenotrochus semigranosa* Michelin, 1845); another is *Balanophyllia (Eupsammia) elliptica* Brongniart, 1822; and the third is the dendrophylliid *Endopachys alatum* Lonsdale, 1845. Lonsdale (1845, figs. b,c) also figured a specimen as belonging to *Endopachys*, which is certainly the turbinoliid *Platytrachus stokesii*. Subsequently, Wells (1975) appears to have been the first reviser to designate correctly a type species for the genus. Coincidentally, the type species *E. alatum* is considered to be a junior synonym of *E. maclurii* (= *Turbinolia maclurii* Lea, 1833, middle to late Eocene (early Claibornian to Jacksonian) of southern USA (Texas, Louisiana, Mississippi, Alabama, Georgia, South Carolina, North Carolina) (senior synonym of *E. alatum*); = *E. alticostatum* Lonsdale, 1855; = *Rhectopsammia claibornensis* Vaughan, 1900; = *E. maclurii* var. *tenuis* Vaughan, 1900, early Eocene (early Claibornian) of southern USA (Texas, Louisiana); = *E. maclurii* var. *triangulare* Conrad, 1855, late Eocene to early Oligocene (Jacksonian to Vicksburgian) of southern USA (Louisiana, Mississippi)).

OTHER SPECIES.—*Endopachys lonsdalei* Vaughan, 1900. Early Eocene (early Claibornian): USA (Mississippi, Alabama). *E. minutum* Vaughan, 1900. Late Eocene (Jacksonian): USA (Louisiana, Mississippi). *E. schaleri* Vaughan, 1900. Eocene: USA (Alabama). *E. tampae* Wells, 1975. Early Miocene (Tampa Formation, Silex Bed): USA (Florida). *E. grayi* Milne Edwards and Haime, 1848. Pliocene: Taiwan. Plio-Pleistocene: Java, Japan. Holocene: Indo-Pacific, 37–386 m. = *E. weberi* Alcock, 1902. = *E. oahense* Vaughan, 1907. = *E. japonicum* Yabe and Eguchi, 1932a. = *E. vughani* Durham, 1947. *E. bulbosa* Cairns and Zibrowius, 1997. Holocene: Indonesia, 233–251 m.

Notophyllia Dennant, 1899

PLATE 7: FIGURES *f,h,i*; PLATE 8: FIGURES *a,b*

Sphenotrochus.—Tenison-Woods, 1878:189–190 [in part: *Sphenotrochus variolaris*].

Notophyllia Dennant, 1899b:285.—Vaughan and Wells, 1943:237, pl. 50: figs. 9, 9a.—Alloiteau, 1952:680.—Boschma, 1952:238–247.—Wells, 1956: F434, fig. 339:8, 8a.—Chevalier and Beauvais, 1987:693–694, fig. 401:6.—Cairns and Parker, 1992:51–52.—Cairns, 1998:405–406.

DIAGNOSIS.—Corallum solitary, cuneiform to compressed-cylindrical. Transverse division occurring in all species, although attached anthocyathus-stage not observed; antho-

cyathus free, usually with remnant of basal scar. Epithelial bands present (e.g., type species) or absent; costae present in some species (e.g., type species), replaced by small spines in others. Septa arranged in normal insertion pattern (not Pourtalès plan) in hexamer (e.g., type species) or decamer symmetry. Columella spongy (e.g., type species) or lamellar (most other species). Endotheca absent. Azooxanthellate.

DISCUSSION.—The similarity of *Notophyllia* to *Endopachys* has been noted by many authors, both genera having cuneiform anthocyathi that result from transverse division; however, *Endopachys* differs in having a well-developed Pourtalès plan. The phylogenetic analysis (Figure 2) unites *Notophyllia* and *Endopachys* in a small clade of two genera based on the synapomorphy of transverse division (character 1, cuneiform).

DISTRIBUTION.—Middle Miocene (Balcombian: Fyansford Formation): Australia (Victoria). Holocene: Australia (South Australia, New South Wales, Western Australia), 22–458 m (Cairns, 1998).

TYPE SPECIES.—*Notophyllia semivestita* Dennant, 1899b, by original designation; middle Miocene (Balcombian) of Australia (Victoria). Holotype deposited at NMV (P27078).

OTHER SPECIES.—*Notophyllia variolaris* (Tenison-Woods, 1878). Middle Miocene (Balcombian): Australia (Victoria).

N. gracilis Dennant, 1899b. Middle Miocene (Balcombian): Australia (Victoria).

N. aperta Dennant, 1899b. Middle Miocene (Balcombian): Australia (Victoria).

N. recta Dennant, 1906. Holocene: Australia (New South Wales, South Australia, southern Western Australia), 40–458 m.

N. etheridgi Hoffmeister, 1933. Holocene: Australia (South Australia, New South Wales), 37–238 m.

N. piscacauda Cairns, 1998. Holocene: Australia (Western Australia), 22–51 m.

Eguchipsammia Cairns, 1994

PLATE 8: FIGURES c–f

Dendrophyllia (*Alcockia*) Eguchi, 1968:C63 [junior homonym of *Alcockia* Goode and Beane, 1896].

Eguchipsammia Cairns, 1994:85; 1995:122; 2000:168.

DIAGNOSIS.—Colony commonly unattached (recumbent), resulting from sparse, irregular, extratentacular budding from parent corallum; third generation buds rare. Intratentacular budding also occurs infrequently. Theca costate and hispid, usually partially covered with epitheca. Pourtalès plan present; paliform lobes may be present. Columella spongy. Endothecal dissepiments present. Azooxanthellate.

DISCUSSION.—Except for the differences in corallite integration, *Eguchipsammia* is very similar to *Balanophyllia* (*Eupsammia*), especially to those species that are known to propagate by asexual budding. Nonetheless, because the phylogenetic analysis weights coloniality rather heavily, *Eguchipsammia* is included as an outlier in the clade of colonial

genera. According to the tree (Figure 2), *Eguchipsammia* is the only representative with the condition detached budding, one of three directions taken by colonial dendrophylliids, the second direction being reptoid budding, and the third direction being budding leading to an arborescent colony.

DISTRIBUTION.—Late Miocene to early Pliocene: Dominican Republic. Holocene: circumtropical to warm temperate in all oceans except eastern Pacific, (18?)25–988 m.

TYPE SPECIES.—*Dendrophyllia cornucopia* Pourtalès, 1871, by original designation; Holocene of USA off Key West, Florida, 220–229 m. Also known from late Miocene to early Pliocene of Dominican Republic; ampho-Atlantic in Holocene, 91–960 m. Nine syntypes deposited at MCZ, 1 deposited at BM (see Cairns, 1979).

OTHER SPECIES (all Holocene).—?*Eguchipsammia socialis* (Semper, 1872). Philippines, 18 m.

E. gaditana (Duncan, 1873). Widespread in tropical and temperate oceans except eastern Pacific, 30–988 m.

=*Balanophyllia praecipua* Gardiner and Waugh, 1939.

E. japonica (Rehberg, 1892) (senior homonym of *Dendrophyllia japonica* van der Horst, 1922). Western Pacific, 114–785 m.

E. fistula (Alcock, 1902). Indo-West Pacific, Kermadecs, 210–900 m (see Cairns, 1995).

=*Dendrophyllia oahensis* Vaughan, 1907.

E. serpentina (Vaughan, 1907). Hawaiian Islands, 200–362 m.

E. wellsii (Eguchi, 1968). Western Pacific, 32–196 m.

E. strigosa Cairns, 2000. Southeastern Caribbean, USA (North Carolina), 25–77 m.

Rhizopsammia Verrill, 1870

PLATE 8: FIGURES g–i; PLATE 9: FIGURES a, b

Rhizopsammia Verrill, 1870:510.—Duncan, 1884:182–183.—van der Horst, 1922:64.—Vaughan and Wells, 1943:237.—Wells, 1956:F434–435.—Zibrowius, 1980:181.—Wells, 1982:213.—Chevalier and Beauvais, 1987:694.—Cairns, 1994:87.—Cairns and Zibrowius, 1997:188–190.

DIAGNOSIS.—Corallum of small reptoid colonies produced by extratentacular stoloniferous budding. Synapticulotheca of finely granular costae, often covered with epitheca. Pourtalès plan present; pali absent. Columella spongy, usually small. Endotheca absent. Azooxanthellate.

DISCUSSION.—As suggested by Cairns (1994), except for *Eguchipsammia*, *Rhizopsammia* represents the most elementary level of corallite organization among the colonial dendrophylliids.

DISTRIBUTION.—Pliocene: USA (California). Holocene: cosmopolitan (except for eastern Atlantic) in tropical and warm temperate oceans, 0–278 m.

TYPE SPECIES.—*Rhizopsammia pulchra* Verrill, 1870, by monotypy; Holocene of Pearl Islands, Gulf of Panama. Holotypic colony deposited at YPM (5375) and figured herein (Plate 8g, h).

OTHER SPECIES.—*Rhizopsammia arnoldi* Durham, 1941. Pliocene: California.

R. goesi (Lindström, 1877). Holocene: western Atlantic, 5–119 m (see Cairns, 2000).

R. verrilli van der Horst, 1922. Holocene: western and eastern Pacific (Galápagos and Cocos Islands), 6–278 m.

=?*R. chamissoi* Wells, 1954.

=*Balanophyllia scheeri* Durham, 1966.

R. minuta van der Horst, 1922. Holocene: western Pacific; 0–176 m.

R. minuta mutsuensis Yabe and Eguchi, 1932.

R. minuta bikiniensis Wells, 1954.

R. nuda van der Horst, 1926. Holocene: Indo-West Pacific, 9–220 m (see Cairns and Zibrowius, 1997).

R. annae (van der Horst, 1933). Holocene: South Africa, 0–80 m.

R. bermudensis Wells, 1972. Holocene: Bermuda, 8–12 m.

R. wellingtoni Wells, 1982. Holocene: Galápagos, 2–43 m.

R. wettsteini Scheer and Pillai, 1983. Holocene: Red Sea, 4 m.

R. compacta Sheppard and Sheppard, 1991. Holocene: Gulf of Oman, southwestern Indian Ocean, 35–110 m.

Cladopsammia Lacaze-Duthiers, 1897

PLATE 9: FIGURES c–f

Cladopsammia Lacaze-Duthiers, 1897:208.—Vaughan and Wells, 1943: 237.—Wells, 1956:F435.—Zibrowius, 1980:179.—Cairns, 1994:87; 1995: 125; 2000:177.

"*Rhizopsammia*."—Cairns, 1979:193–194.

Rhizopsammia.—Chevalier, 1966:1382.—Zibrowius, 1980: 181 [in part: *R. manuelensis*].

DIAGNOSIS.—Small bushy colonies formed by extratentacular budding from common basal coenosteum and occasionally from edge zone of larger corallites. Costae well developed, granular; epitheca may be present. Pourtalès plan well developed; pali usually absent. Columella small, papillose. Endothecal dissepiments present. Azooxanthellate.

DISCUSSION.—As previously noted (Cairns, 1994), the coralite integration of *Cladopsammia* is intermediate between the stoloniferous/reptoid budding of *Rhizopsammia* and the upright branching of *Dendrophyllia*. Although new coralites may originate by stoloniferous budding, the coenosteum is quickly filled in between all coralites, resulting in a continuous, common coenosteum. Furthermore, coralites occasionally bud from the theca of larger coralites. Thus *Cladopsammia* falls within the clade (Figure 2) characterized by colonial corals that pass through a stage of reptoid budding.

The inclusion of *C. manuelensis* in this genus is problematic. Chevalier (1966) and Zibrowius (1980) considered it to belong to *Rhizopsammia*, primarily because it has prominent paliform lobes (P_3) and a swirled trabecular columella. I (Cairns, 1979) considered it to be transitional between *Rhizopsammia* and *Cladopsammia*, implying that it might even be a new genus or subgenus of *Cladopsammia*, but later (Cairns,

2000) I placed it in *Cladopsammia* based on its level of coralite integration being similar to other species in the genus. Its distinctive paliform lobes are thus considered to be intragenetic variation.

As discussed in the account of *Balanophyllia*, some specimens identified as *Balanophyllia calyculus* Wood, 1844, from its type locality of late Pliocene, England, are in fact not solitary coralla but colonial (Plate 9d), as in *Cladopsammia*. Although this species is probably unnamed, these specimens indicate the occurrence of *Cladopsammia* in the late Pliocene.

DISTRIBUTION.—Late Pliocene (Red Crag), Norfolk, England. Pleistocene: Niger Delta. Holocene: circumtropical and warm temperate, 0–470 m.

TYPE SPECIES.—*Cladopsammia rolandi* Lacaze-Duthiers, 1897, by monotypy; Holocene of La Calle (Constantine), Algeria. Also known from western Mediterranean, 12–50 m (Zibrowius, 1980). Type material deposited at MNHN (see Zibrowius, 1980).

OTHER SPECIES.—*Cladopsammia manuelensis* (Chevalier, 1966). Pleistocene: Niger Delta. Holocene: tropical amphiatlantic, 55–366 m (see Cairns, 2000).

C. gracilis (Milne Edwards and Haime, 1848). Holocene: Indo-West Pacific, 0–95 m (see Cairns, 1994).

=?*Dendrophyllia conferta* Quelch, 1886.

=?*Dendrophyllia coarctata* Duncan, 1889.

=?*Dendrophyllia elegans* van der Horst, 1922 (not Duncan, 1866).

=*Tubastraea coccinea tijimaensis* Eguchi, 1968.

C. willeyi (Gardiner, 1900). Holocene: Loyalty Islands, Japan, shallow water.

C. eguchii (Wells, 1982). Holocene: tropical and warm temperate eastern and western Pacific; 1–85 m.

=*Dendrophyllia arbuscula* var. *compressa* Eguchi and Sasaki, 1973.

C. echinata Cairns, 1984. Holocene: Hawaiian Islands, Indonesia, 222–470 m.

Paleoastroides Chevalier, 1961

PLATE 9: FIGURES g–j

Paleoastroides Chevalier, 1961:487, figs. 189, 190, pl. 22: fig. 8.

DIAGNOSIS.—Massive, plocoid coralla formed primarily by extratentacular budding (occasionally intratentacular budding). Synapticulotheca costate (finely serrate ridges) and sometimes weakly epithecate. Pourtalès plan present; 4–5 cycles of septa present, however, higher-order septa often irregular in anastomosis. Columella well developed, ribboned, composed of elongate paliform lobes (P_1 – P_3). Exothecal and endothecal dissepiments both present, but rare.

DISCUSSION.—Although consisting of three or four species, the genus *Paleoastroides* is known from very few specimens, perhaps fewer than 12. Chevalier (1961) compared *Paleoastroides* to *Dendrophyllia*, differentiating it by its plocoid

growth form (not dendroid), its irregular Pourtalès plan, and its lesser-developed coenosteum. It differs from *Astroïdes* in having a Pourtalès plan and better-developed costae. Chevalier (1961) suggested that *Paleoastroïdes* may have been the ancestor of *Astroïdes*, even though the latter genus lacks the Pourtalès plan. Indeed, in the phylogenetic analysis, *Paleoastroïdes* belongs to a clade of four genera characterized by having a plocoid colony, differing from *Astroïdes* primarily in having finely serrate costae (compared with hispid costae) and in having a Pourtalès plan.

DISTRIBUTION.—Early (Aquitanian, Burdigalian) to middle Miocene (Helvetian): France, Italy.

TYPE SPECIES.—*Paleoastroïdes michelini* Chevalier, 1961, by original designation; middle Miocene (Helvetian) shell marl of Touraine, France. Holotype (only known specimen of species) deposited at MNHN (Institute of Paleontology, R8466).

OTHER SPECIES.—*Paleoastroïdes provincialis* Chevalier, 1961. Early Miocene (Aquitanian): Provence, France.

P. subirregularis (Osasco, 1897). Early (Burdigalian) to middle Miocene: Italy.

?*P. theolvoltensis* (Michelin, 1842). Middle Miocene (Helvetian): France.

Astroïdes Quoy and Gaimard, 1827

PLATE 10: FIGURES a–h

Astroïdes Quoy and Gaimard, 1827:187.

Astreïdes de Blainville, 1830:332 [misspelling].

Astroïtis Dana, 1846:405–406 [unjustifiable emendation].

Astroïdes.—Milne Edwards and Haime, 1850:xli; 1851:139.—Milne Edwards, 1860:131.—Duncan, 1884:181–182.—Vaughan and Wells, 1943:239, pl. 50: fig. 11.—Alloiteau, 1952:681.—Wells, 1956:F436, fig. 338:9.—Zibrowius, 1980:198–201.—Chevalier and Beauvais, 1987:694, fig. 401:9.—Zibrowius, 1991:92–93; 1995:9–16.

DIAGNOSIS.—Corallum colonial, small to medium-sized, produced by extratentacular budding from edge zone or from discrete stolons. Corallites closely spaced (polygonal and cerioid, or plocoid) to widely spaced (phaceloid); in former case, holotheca surrounds perimeter of colony; in latter case, epitheca surrounds individual corallites. Costae present (e.g., type species) or absent; when present, costae usually finely hispid. In coralla with cerioid-arranged corallites, low coenosteal ridge sometimes encircles each corallite, appearing to be continuous with epitheca of holotheca. Four cycles of normally arranged septa (no Pourtalès plan); axial edges of septa coarsely dentate. Fossa shallow; columella massive, discrete, spongy, and free-standing, sometimes composed of swirled elements. Tabular endothelial dissepiments present. Azooxanthellate.

DISCUSSION.—Zibrowius (1980) has thoroughly monographed this monotypic genus, including aspects of its morphology, distribution, ecology, and taxonomic history. Later (Zibrowius, 1995), he discussed its Pleistocene distribution, transplantation experiments, and its value as an indicator of paleotemperatures and climatic change. According to Zibrowius,

coralla with closely spaced, cerioid corallites occur in shallow water regions of high water turbulence, whereas the branching forms are characteristic of deeper waters.

Astroïdes is part of a clade of three genera characterized by having plocoid or arborescent branching and having a normal insertion pattern (Figure 2). It is distinguished from the other two genera in this clade by having hispid costae and an epitheca (Table 3).

DISTRIBUTION.—As for the type species (see Zibrowius, 1980, 1995).

TYPE SPECIES.—*Astroïdes luteus* Quoy and Gaimard, 1827, by monotypy (= *Astroïdes calycularis* (Pallas, 1766)); Holocene of southwestern Spain, Guettare anchorage in Bay of Algeciras, near Strait of Gibraltar, ~1 m. Also known from late Pleistocene of northwestern Mediterranean (Zibrowius, 1991, 1995) and Holocene of western (primarily southwestern) Mediterranean (see Zibrowius, 1980, 1995), 0–30 m.

Although it is logical to assume that the type of *A. luteus* would be in the Quoy and Gaimard collection at the MNHN (Zibrowius, 1980), it could not be found there in 1999.

OTHER SPECIES.—None.

Tubastraea Lesson, 1829

PLATE 10: FIGURES i–l

Tubastraea Lesson, 1829:93.—Wells, 1936b:132 [nomenclatural note].—Vaughan and Wells, 1943:238–239.—Alloiteau, 1952:681.—Boschma, 1953:109–118.—Wells, 1956:F436; 1982:216; 1983:243 [nomenclatural note].—Ogawa and Takahashi, 1993:95–109.—Cairns, 1994:93.

Coenopsammia Milne Edwards and Haime, 1848:106–107; 1850:liii [type species designated]; 1851:138–139.—Milne Edwards, 1860:125.—Chevalier and Beauvais, 1987:694.

Astropsammia Verrill, 1869:392.—Duncan, 1884:179.—Vaughan and Wells, 1943:239.—Chevalier and Beauvais, 1987:694.

Pachypsammia Verrill, 1866:30.—Duncan, 1884:179.

Dendrophyllia (*Coenopsammia*).—Duncan, 1884:178.

DIAGNOSIS.—Budding extratentacular, corallum of most species plocoid (including type species) with corallites originating from thick, common basal coenosteum, but *T. micranthus* with large, erect, dendroid colonies. Intratentacular budding occurring rarely (Boschma, 1953). Synapticulotheca thin and highly porous; granular costae usually present; epitheca absent. Corallites of plocoid forms flush with coenosteum or highly exsert; corallites invariably over 4 mm in CD. Septa normally arranged, higher-cycle septa often having dentate or lacinate axial edges fused to lower-cycle septa (but not in Pourtalès plan arrangement). Fossa relatively deep, containing spongy to trabecular (e.g., type species) columella ranging from rudimentary to moderate in size. Endothelial dissepiments common. Azooxanthellate.

DISCUSSION.—According to the phylogenetic analysis, *Tubastraea* is very similar to *Turbinaria*, differing only by having granular costae (compared with serrate ridges) and in being azooxanthellate (Figure 2, Table 3), the latter character considered to be of low weight; however, *Turbinaria* also has the un-

scored autapomorphy of having elongate, uniaxially oriented corallites. *Tubastraea* is also similar to *Enallopsammia*, and, if one admits that the dendroid *Tubastraea micranthus* is in this genus, Vaughan and Wells's (1943) key does not distinguish the two genera. Nonetheless, *Tubastraea* has granular (not hispid) costae and has an endotheca (absent in *Enallopsammia*). It also has a more highly porous corallum and a deeper fossa, and it occurs in considerably shallower water than does *Enallopsammia*. Furthermore, some species of *Enallopsammia* are uniaxial and have rostrate corallites, characters that do not occur in *Tubastraea*, and all species of *Enallopsammia* are dendroid, whereas most species of *Tubastraea* are plocoid, only one being dendroid. *Tubastraea* is also quite similar to *Stereopsammia*, but not enough is known about the latter genus to make adequate comparisons (see "'Dendrophylliid' Genera of Uncertain Position," below).

Because all species of *Tubastraea* occur in relatively shallow water and have brightly colored tissue, they are often collected, which in turn has led to an excessive description of new species. Boschma (1953) synonymized many of the nominal species and provided a very useful discussion of the variation within and among species. Wells (1983) finished the process of synonymization by reducing all described species to three but ironically added another three species to the list (Wells, 1982, 1983), all from the Galápagos! Several more fossil species are now considered to be congeneric, although the Oligocene *T. nomlandi* Durham, 1942, is not a convincing representative of the genus.

DISTRIBUTION.—Late early Eocene (La Meseta Formation): Seymour Island, Antarctica. ?Early Oligocene: USA (Washington). Late Miocene (Tortonian): France. Pleistocene: Cape Verde. Holocene: circumtropical, 0–110 m.

TYPE SPECIES.—*Tubastraea coccinea* Lesson, 1829, by monotypy (also type species of *Coenopsammia* Milne Edwards and Haime, 1848, by subsequent designation (Milne Edwards and Haime, 1850:liii)) (= *Lobopsammia aurea* Quoy and Gaimard, 1833; = *Dendrophyllia aurantiaca* Dana, 1846; = *Coenopsammia ehrenbergiana* Milne Edwards and Haime, 1848; = *C. gaimardi* Milne Edwards and Haime, 1848; = *C. tenuilamellosa* Milne Edwards and Haime, 1848; = *C. urvillii* Milne Edwards and Haime, 1848; = *C. radiata* Verrill, 1864; = *C. manni* Verrill, 1866; = *Astropsammia pedersenii* Verrill, 1869 (type species of *Astropsammia* Verrill, 1869, by monotypy); = *Dendrophyllia surcularis* Verrill, 1869; = *Pachypsammia valida* Verrill, 1869 (type species of *Pachypsammia* Verrill, 1869, by monotypy); = ? *Placopsammia darwini* Duncan, 1876; = *Dendrophyllia (Coenopsammia) affinis* Duncan, 1889; = *Coenopsammia willeyi* Gardiner, 1899; = ? *Dendrophyllia turbinata* Nemenzo, 1960; Holocene of Bora Bora, Society Islands, but range circumtropical, 0–110 m (Cairns, 1994). Also known from Pleistocene of Cape Verde (Boeckschoten and Best, 1988). Holotype deposited at MNHN (see Wells, 1936b:132) but not retrievable in 1999.

OTHER SPECIES.—*Tubastraea* sp. sensu Stolarski, 1996. Late early Eocene: Antarctica.

- ?*T. nomlandi* Durham, 1942. Early Oligocene: USA (Washington).
T. puyricardensis (Chevalier, 1961). Late Miocene (Tortonian): France.
T. puyricardensis var. *grandiflora* Chevalier and Demarcq, 1964. Late Miocene (Tortonian): France.
T. micranthus (Ehrenberg, 1834). Holocene: Indo-West Pacific, 0–50 m.
 = *Dendrophyllia nigrescens* Dana, 1846.
 = *Coenopsammia viridis* Milne Edwards and Haime, 1848.
 = *Dendrophyllia aequiserialis* Milne Edwards and Haime, 1848.
 = *Dendrophyllia micranthus* var. *grandis* Crossland, 1952.
T. diaphana (Dana, 1846). Holocene: Indo-West Pacific, 1–15 m.
 = *Dendrophyllia micranthus* var. *fruticosa* Nemenzo, 1960.
 = *Dendrophyllia sibogae* van der Horst, 1922.
T. faulkneri Wells, 1982. Holocene: Galápagos, western Pacific, 3–5 m.
T. tagusensis Wells, 1982. Holocene: Galápagos, western Pacific, 1–43 m.
T. floreana Wells, 1982. Holocene: Galápagos, 2–5 m.

Turbinaria Oken, 1815

PLATE 11: FIGURES a–f

Turbinaria Oken, 1815:67.—Milne Edwards and Haime, 1851:141.—Milne Edwards, 1860:164.—Duncan, 1884:184.—Bernard, 1896:1–22 [monograph].—Vaughan, 1918:147–148.—Yabe and Sugiyama, 1941:85.—Vaughan and Wells, 1943:241, pl. 51: fig. 4.—Alloiteau, 1952:682.—Crossland, 1952:174.—Wells, 1954:471; 1956:F436.—Nemenzo, 1960:3–4.—Chevalier, 1961:494–495.—Veron and Pichon, 1980:371–374.—Zou, 1980:127–133.—Veron, 1986:562.—Chevalier and Beauvais, 1987:695, fig. 401:10.—Veron, 1993:331, fig. 111; 1995:263–264.—Latypov, 1996:146–150.
Explanaria Lamarck, 1816:254 [in part: *E. crater* and *E. mesenterina*].—Milne Edwards and Haime, 1850:liv.
Gemmipora de Blainville, 1830:352.—Dana, 1846:408–409.
Turbinacis Quenstedt, 1880.—[not *Turbinacis* Gregory, 1900:38–39 (= ? *Stylophora*)].

DIAGNOSIS.—Founder corallite usually produces stalk; addition corallites budd extratentacularly, resulting in wide variety of corallum shapes, including crateriform (vasiform) (e.g., the type species), explanate, foliate, mesenteriform (inrolled tubes of coenosteum on corallum edge), tabulate (layered), encrusting, flabellate, and hemispherical (massive). Coralla large, up to 1 m in diameter. Corallites often elongate, extending for a significant distance below coenosteum oriented in direction of corallum growth (away from edge), then bending upward, terminating on face of corallum. Corallites uniaxial, plocoid to phaceloid in exsertness. Epitheca absent. Coenosteum abundant, covered with discontinuous, hispid ridges. Septa usually arranged normally in larger corallites, but occasionally some systems show remnant of Pourtalès plan arrangement (more common in small corallites, but occasionally also occurring in

large corallites). Columella usually well developed, solid, spongy (e.g., type species), or labyrinthiform, occupying large percentage of relatively shallow fossa. Endothecal dissepiements sparse. Zooxanthellate.

DISCUSSION.—Bernard's (1896) monograph of *Turbinaria* was a watershed event in the study of this genus, even though it was highly criticized by Vaughan (1918), Wells (1954), Veron and Pichon (1980), and others for recognizing far too many species that were based on intraspecific environmental variation. Indeed, most contemporary authors (e.g., Veron and Pichon, 1980; Veron, 1995; Cairns et al., 1999) recognize only 13 to 15 valid species of *Turbinaria* compared to the 58 listed by Bernard (1896), many of which are now considered to be either junior synonyms or species of uncertain status (see below). But, in all fairness to Bernard, he was well aware of the "species problem" as it pertained to *Turbinaria* and the of difficulty of distinguishing species based on extremely variable morphological characters from a limited suite of museum specimens. Bernard (1896:19) agonized: "Are these local forms of growth of any value? ... Are all these to be classed as new species? ... If we classify strictly according to growth-forms, we should have to answer in the affirmative. But this would lead to needless splitting of specimens, closely united by other characters." Nonetheless, Barnard did use growth form to distinguish species, stating that it was "because there really appeared no choice. No other characters presented themselves with sufficient certainty or constancy to be made use of." Bernard (1896:20) went on to apologetically conclude, "All that I can actually affirm is, that the position assigned to them appears to me to be the best," and finally he implied that binomial nomenclature was inadequate to the task of naming these kind of variable colonial organisms. This statement of frustration presaged his eventual abandonment of binomial nomenclature in his later monographs published in the *Catalogue of the Madreporarian Corals* (Bernard, 1903, 1905, 1906). Only recently, a century later, are we beginning to look at corals from new perspectives (Lang, 1984; Veron, 1995; Latypov, 1996), with a legitimate hope of determining true species boundaries.

The earliest known *Turbinaria*, *T. alabamensis* Vaughan, 1900, was described from the Oligocene of Alabama, and this age has generally been cited by all subsequent revisers as the earliest-known date for this genus. Vaughan (1900), however, only questioningly placed this species in *Turbinaria*, suggesting that it might belong to *Actinacis* (family Actinacididae). Reexamination of the syntype series of *T. alabamensis* (USNM M158479-81) shows it to be a very poorly preserved specimen, having a styliform columella and a method of budding inconsistent with that of *Turbinaria*, but both characters are consistent with a placement in *Actinacis*. Accordingly, this species is not considered to be a *Turbinaria* or a dendrophylliid, and thus the earliest geologic age for the genus is early Miocene.

Gregory (1900) described the genus *Turbinacis* (a junior homonym of *Turbinacis* Quenstedt, 1880) for a species collected from the Pleistocene of Berbera, British Somaliland, stating that it had similarities to *Stylophora*, *Actinacis*, and *Turbinaria*. Vaughan and Wells (1943:245) considered it to be a genus of uncertain position but questioningly attributed it to *Turbinaria*. No other monographers appear to have considered this genus. Examination of the holotype (including two thin sections) of *T. erythraeensis* Gregory, 1900 (BM R5026) (type species of *Turbinacis*), shows it to have a solid, but pitted, non-perforate coenosteum; three cycles of septa, the first being by far the most prominent; and a styliform columella (Plate 14d,e). It is not dendrophylliid in nature but is probably allied to *Stylophora* or *Palauastrea*, one of the options suggested by Gregory.

NOMENCLATURE NOTES.—All of the new names published in Oken's (1815) *Lehrbuch der Naturgeschichte*, including the genus *Turbinaria*, were considered invalid and unavailable for nomenclature purposes by the ICZN because Oken did not consistently use binomial nomenclature in that work (Opinion 417, Sep 1956, see Melville and Smith, 1987:319; see also Potts, 1995). Nonetheless, some generic names have been conserved from the Oken (1815) publication by special application to the ICZN, including the coral genus *Acropora* (China, 1963) and at least nine other nonanthozoan genera (Gentry, 1994). Another application is pending (Potts, 1995) that proposes to conserve another two coral genera (*Galaxea* Oken, 1815, and *Mussa* Oken, 1815). No formal application, however, has ever been made to conserve the name *Turbinaria*, and thus despite its widespread usage, this name officially remains nomenclaturally invalid.

The phylogenetic affinities of *Turbinaria* are discussed in the genus *Tubastraea*.

DISTRIBUTION.—Early Miocene (Aquitanian, Burdigalian): France, Algeria. Middle Miocene (Helvetian, Vinobodian, Altonian): Italy, France, Austria, Hungary, New Zealand. Miocene: Borneo (Gerth, 1923). Late Pliocene (Era Beds): Papua New Guinea (Veron and Kelley, 1988). Pleistocene: Japan (Yabe and Sugiyama, 1935). Holocene: Indo-West Pacific, reef depths (Veron, 1993, fig. 111).

TYPE SPECIES.—*Madrepora crater* Pallas, 1766, by subsequent designation (Vaughan, 1918) (= *Explanaria infundibulum* Lamarck, 1816); Holocene of "East Indies," but now known to occur throughout Indo-West Pacific reefs.

Vaughan and Wells (1943) stated that the type species was fixed by monotypy, but this cannot be the case, because Oken included four species in his original description of the genus *Turbinaria*. Oddly, Milne Edwards and Haime (1850), a source that designated type species for most of the coral genera up to that date, does not even include *Turbinaria*, and, although Bernard (1896) listed *T. crater* first among the 58 species he discussed, he did not refer to a type species for the genus. Subsequently, Vaughan (1918:147) appears to be the first author to designate the type species *M. crater* for *Turbinaria*. His logic

may have been one of "position priority" (ICZN, 1999, recommendation 69A.10). The type of *M. crater* is lost, according to Veron and Pichon (1980:374).

Madrepora crater is also the type species of *Gemmipora* de Blainville, 1830, by subsequent designation (Wells, 1986).

OTHER SPECIES.—*Turbinaria cyathiformis* (de Blainville, 1830). Early Miocene (Aquitainian, Burdigalian): France, Algeria. Middle Miocene: Italy.

T. cyathiformis var. *lamelliformis* Chevalier, 1961. Early Miocene (Burdigalian): France.

T. cyathiformis var. *turonensis* (d'Orbigny, 1850). Middle Miocene (Helvetian): France.

T. cyathiformis var. *reussi* Chevalier, 1961. Middle Miocene (Vinobodian): Austria, Hungary.

T. grandis Chevalier, 1961. Early Miocene (Burdigalian): France.

T. peltata (Esper, 1794). Late Pliocene: Papua New Guinea. Pleistocene: Japan. Holocene: Indo-West Pacific; shallow reef slope.

=*T. dichotoma* Verrill, 1871.

=*T. maxima* Ortmann, 1888.

=*T. marima* Ortmann, 1888.

=*T. peltata* var. *gibiari* Crossland, 1952.

T. mesenterina (Lamarck, 1816) (type species of *Explanaria*, by subsequent designation (Milne Edwards and Haime, 1850) and *Turbinacis* Quenstedt, 1880, type fixation unknown). Late Pliocene: Papua New Guinea. Holocene: Indo-West Pacific; shallow reefs.

=*T. tubifera* Bernard, 1896.

=*T. venusta* Bernard, 1896.

=*T. speciosa* Bernard, 1896.

=?*T. crassa* Bernard, 1896.

T. frondens (Dana, 1846). Late Pliocene: Papua New Guinea. Pleistocene: Japan. Holocene: Indo-West Pacific; shallow reefs.

=*T. frondescens* Milne Edwards, 1860.

=?*T. danae* Bernard, 1896.

=?*T. contorta* Bernard, 1896.

=?*T. rugosa* Bernard, 1896.

=*T. foliosa* Bernard, 1896.

=*T. pustulosa* Bernard, 1896.

=*T. magna* Bernard, 1896.

=*T. edwardsi* Bernard, 1896.

=*T. abnormalis* Bernard, 1896.

=*T. aurantiaca* Bernard, 1896.

=?*T. ramosa* Yabe and Sugiyama, 1941.

T. stellulata (Lamarck, 1816). Holocene: Indo-West Pacific; upper reef slope.

=*T. hemisphaerica* Rehberg, 1892.

=*T. globularis* Bernard, 1896.

=*T. subversa* Bernard, 1896.

=?*T. elegans* Bernard, 1896.

=*T. titizimaensis* Yabe and Sugiyama, 1941.

=*T. stephensoni* Crossland, 1952.

=?*T. mantonae* Crossland, 1952.

T. patula (Dana, 1846). Holocene: Indo-West Pacific; inshore reefs.

=?*T. cupula* Ehrenberg, 1834.

=*T. robusta* Bernard, 1896.

=*T. fungiformis* Michelin, 1841.

=*T. bankae* Giebel, 1861.

T. bifrons Brueggemann, 1877. Holocene: Indo-West Pacific; shallow reefs.

=*T. aequalis* Quelch, 1886.

=*T. dendrophyllia* Bernard, 1896.

=*T. gracilis* Bernard, 1896.

=?*T. conspicua* Bernard, 1896.

=?*T. nidifera* Bernard, 1896.

T. conspicua Bernard, 1896. Holocene: Northern Australia; shallow reefs.

T. irregularis Bernard, 1896. Holocene: Indo-West Pacific; shallow reefs.

T. radicalis Bernard, 1896. Holocene: Indo-West Pacific; shallow reefs.

T. reniformis Bernard, 1896. Holocene: Indo-West Pacific; fringing reefs.

=?*T. reptans* Bernard, 1896.

=?*T. lichenoides* Bernard, 1896.

=?*T. veluta* Bernard, 1896.

T. heronensis Wells, 1959. Holocene: Indonesia; northeastern Australia; upper reef slope.

SPECIES OF UNKNOWN VALIDITY.—*Turbinaria cinerascens* (Ellis and Solander, 1786).

T. patifera (Lamarck, 1816).

T. brassica (Dana, 1846).

T. sinensis Verrill, 1866.

T. parvistella Saville Kent, 1871.

T. gemmulata Verrill, 1875.

T. conica Klunzinger, 1879.

T. quincuncialis Ortmann, 1889.

T. crispa Rehberg, 1892.

T. marmorea Rehberg, 1892.

T. mollis Bernard, 1896.

T. laminata Bernard, 1896.

T. plicata Bernard, 1896.

T. undata Bernard, 1896.

T. pocilliformis Bernard, 1896.

T. orbicularis Bernard, 1896.

T. agaricia Bernard, 1896.

T. auricularis Bernard, 1896.

T. calicularis Bernard, 1896.

T. porcellanea Bernard, 1896.

T. pulcherrima Bernard, 1896.

T. aspera Bernard, 1896.

T. brueggemanni Bernard, 1896.

T. tayamai Yabe and Sugiyama, 1941.

T. immersa Yabe and Sugiyama, 1941.

T. carinata Nemenzo, 1971.

T. yaelae Nemenzo, 1976.

***Dendrophyllia* de Blainville, 1830**PLATE 11: FIGURES *g-j*

Dendrophyllia de Blainville, 1830:319–320.—Dana, 1846:384–385 [in part: *D. ramea*].—Milne Edwards and Haime, 1848:95–96; 1850:liii [type species designated]; 1851:136–137.—Milne Edwards, 1860:112–115.—Vaughan and Wells, 1943:237.—Alloiteau, 1952:680.—Wells, 1956:F435.—Chevalier, 1961:476–477.—Cairns, 1979:179.—Zibrowius, 1980:169.—Cairns, 1994:34, 89.—Ogawa and Takahashi, 1995:15–19 [in part: species 1–8].—Potts, 1995:143.

Brasseya Wright, 1882:77–78.

Dendrophyllia (*Dendrophyllia*).—Duncan, 1884:117.—Eguchi, 1968:C63.

DIAGNOSIS.—Extratentacular budding forms colonies of three general forms: arborescent colonies with axial corallites (e.g., type species) (group 1); small, bushy colonies with sparse branching from main stem (group 2); and dendroid colonies with sympodial branching (group 3). All three forms originate from single basal stem. Epitheca absent. Costae usually well defined, covered with small hispid granules. Septa arranged in Pourtalès plan; pali present or absent (absent in type species). Columella spongy or papillose, type species having both states. Tabular endothelial dissepiments may be present (absent in type species). Azooxanthellate.

DISCUSSION.—Milne Edwards (1860) divided the 16 species of *Dendrophyllia* into three sections, based on their budding pattern and resultant growth form. Section 1, the arborescent *Dendrophyllia*, contained only the type species *D. ramea* and was characterized by a corallum that branched in a regular, alternating manner. Section 2, the branching *Dendrophyllia*, consisting of eight species, contained species with coralla that budded in a more irregular fashion. Section 3, the encrusting or massive *Dendrophyllia*, including seven species, consisted of species with irregular budding and an encrusting, nonbranching corallum. Duncan (1884) followed this subdivision of the genus, but no subsequent authors until Cairns (1994) employed a subdivision of *Dendrophyllia*. Now, most, if not all, of the species in Milne Edwards' third section are considered to belong to the genus *Tubastraea*, and the single species he placed in section 1, *D. ramea*, does not have regular, alternating branching but rather has axial corallites from which other corallites bud in a random manner. My (Cairns, 1994) subdivision of the genus into three groups followed slightly different criteria than those of Milne Edwards (1860): Group 1 (axial group) consists of species with tall arborescent colonies, often flabellate, having several larger axial corallites from which shorter corallites budded in an irregular manner. This group includes the type species, *D. ramea*. Group 2 (bushy group) consists of species with small, bushy colonies that also have axial corallites, but the corallites are fewer and larger. Group 3 (sympodial group) consists of species with large dendroid coralla with fairly regular sympodial budding, the terminal corallite of each branch being replaced by each successive corallite. But all species of *Dendrophyllia* are characterized as having a single basal branch from which all sub-

sequent branching occurs. The group designations for all Holocene species are indicated in the listing below.

Dendrophyllia is part of a clade of seven genera (Figure 2) characterized by having arborescent branching. It is stratigraphically the oldest of the seven genera and is the least derived in this clade. According to the cladogram (Figure 2), it has no unique characters that distinguish it from other genera but is distinguished by a combination of characters.

NOMENCLATURE NOTES.—As of the publication of this work, the nomenclatural stability of the genus *Dendrophyllia*, and thus of the family Dendrophylliidae and suborder Dendrophylliina, is potentially threatened, as fully explained by Potts (1995). To briefly summarize, the common cosmopolitan reef genus *Porites* Link, 1807, is known to have a senior homonym *Porites* Cuvier, 1798. Cuvier's genus was based on three species: *Madrepora* (= *Galaxea*) *fascicularis*, *Madrepora* (= *Mussa*) *angulosa*, and *Madrepora* (= *Dendrophyllia*) *ramea*, none of which were ever designated as the type species of Cuvier's genus. In order to preserve the validity of *Porites* Link, 1807, and to protect the availability of the generic names *Galaxea*, *Mussa*, and *Dendrophyllia*, Potts (1995) appealed to the ICZN to suppress the generic name *Porites* Cuvier, 1798, for the purposes of both the principle of priority and the principle of homonymy. Although this suggestion is quite reasonable (Rosen, 1995), as of the publication of this work the Commission has not yet ruled on the proposal.

DISTRIBUTION.—Early Paleocene (Danian): Greenland, Denmark, Sweden. Early Eocene (early Claibornian): USA (Louisiana). Middle Eocene (Claibornian): USA (Alabama), England. Late Eocene (Tongrian): Italy, USA (Washington). "Eocene": USA (South Carolina, California), Peru, New Zealand, Spain. Early Oligocene (Ligurian): Italy. Middle Oligocene: Venezuela, USA (Washington), Austria. "Oligocene": Somalia. Early Miocene (Burdigalian): France, Italy, Burma. Middle Miocene (Helvetian): Italy, France, former Czechoslovakia, Poland, Crete. Late Miocene (Tortonian): Italy, France. "Miocene": Tasmania, Japan, Egypt, Java. Pliocene: Italy, USA (California), Java, Borneo. Pleistocene: Japan. Late Pleistocene: Vanuatu. Holocene: worldwide in tropical and temperate oceans, 1–900 m.

TYPE SPECIES.—*Madrepora ramea* Linnaeus, 1758, by subsequent designation (Milne Edwards and Haime, 1850:liii); Holocene of southwestern Mediterranean (see Zibrowius, 1980). Also known from Holocene of northeastern Atlantic; 40–150 m. Miocene and Pliocene records doubted by Zibrowius (1980) (group 1).

Linnaeus based his description of *M. ramea* on the figures of several specimens in Petiver (1711, pl. 76: fig. 7) and Marsilli (1725, pl. 30: fig. 136, pl. 31: fig. 144). Zibrowius (1980) chose the latter of the Marsilli (1725) figures as the lectotype, the specimen of which, according to him, should be deposited at the University of Bologna (see Potts, 1995).

OTHER SPECIES ("*" indicates species having fossil and Holocene occurrences).—*Paleocene*: *Dendrophyllia candela-*

brum Hennig, 1899. Early Paleocene (early, middle and late Danian): Greenland, Denmark, Sweden (see Floris, 1972).

Eocene:

D. striata Vaughan, 1900. Early Eocene (early Claibornian): USA (Louisiana).

D. dendrophyloides Milne Edwards and Haime, 1848. Middle Eocene: England.

D. lisbonensis Vaughan, 1900. Middle Eocene (Claibornian): USA (Alabama).

D. elegans Duncan, 1866. Middle Eocene to Oligocene: England.

D. abnormis Michelotti in Sismonda and Michelotti, 1871. Late Eocene (Tongrian): Italy.

D. cowlitzensis Durham, 1942. Late Eocene: USA (Washington).

D. laevis Lonsdale, 1845. Eocene: USA (South Carolina).

?*D. italica* Schauroth, 1865. Eocene: Italy.

D. tetonensis Nomland, 1916. Eocene (Tejon Group): USA (California).

D. peruviana Vaughan, 1922. Eocene: Peru.

D. pahiensis Squires, 1962. Eocene: New Zealand.

D. reguanti Alvarez et al., 1993. Eocene: Spain.

Oligocene:

D. rugosa (Gümbel, 1861). Early Oligocene (Ligurian): Italy. =?*D. vincentina* Canestrelli, 1908.

D. nodosa Reuss, 1864. Middle Oligocene: Austria.

D. hannibali Nomland, 1916. Middle Oligocene: USA (Washington).

D. araguensis Wells, 1944. Middle Oligocene to Middle Miocene: Venezuela.

D. californica Nomland, 1917. Oligocene: USA (California).

D. inaequalis Zuffardi-Comerci, 1937. Oligocene: Somalia.

Miocene:

D. irregularis de Blainville, 1830. Early Miocene (Burdigalian) to middle Miocene (Helvetian): France, Italy. =?*D. theotvoldensis* Michelin, 1847

D. sp. U Ba Maw, 1975. Early Miocene: Burma.

D. taurinensis Milne Edwards and Haime, 1848. Middle Miocene (Badenian): Italy, Bosnia, Poland, Austria, former Czechoslovakia.

=*Balanophyllia concinna* Reuss, 1871.

=*D. prismatica* Reuss, 1871.

D. taurinensis var. *subramosa* Osasco, 1897. Middle Miocene (Helvetian): Italy.

D. taurinensis var. *triserialis* Osasco, 1897. Middle Miocene (Helvetian): Italy.

D. cladocoracea Michelotti in Sismonda and Michelotti, 1871. Middle Miocene (Helvetian): Italy.

D. globulina Michelotti in Sismonda and Michelotti, 1871. Middle Miocene (Helvetian): Italy.

=?*D. microstellata* Zuffardi-Comerci, 1933.

D. longaeva Michelotti in Sismonda and Michelotti, 1871. Middle Miocene (Helvetian): Italy.

D. michelini Michelotti in Sismonda and Michelotti, 1871. Middle Miocene (Helvetian): Italy, France.

D. orthoclada Reuss, 1871. Middle Miocene: former Czechoslovakia.

[*D. ramosa* Procházka, 1893 (nomen nudum). Middle Miocene: former Czechoslovakia.]

D. deformis de Angelis, 1894. Middle Miocene (Helvetian): Italy.

D. humilis de Angelis, 1894. Middle Miocene (Helvetian): Italy.

D. subirregularis Osasco, 1897. Middle Miocene (Helvetian): Italy.

D. multigemmata Zuffardi-Comerci, 1933. Middle Miocene: Italy.

D. multigemmata var. *subplana* Kühn, 1965. Middle Miocene: Germany.

D. paroniana Zuffardi-Comerci, 1933. Middle Miocene: Italy.

D. alternaticosta Chevalier, 1961. Middle Miocene (Helvetian): France.

D. incerta Osasco, 1897. Middle Miocene (Helvetian) to late Miocene (Tortonian): Italy.

D. amica (Michelotti, 1838). Middle Miocene (Helvetian) to early Pliocene: Italy.

D. clavigera (Lamarck, 1816). Middle Miocene (Helvetian) to Pliocene: Italy.

**D. cornigera* (Lamarck, 1816) (not *D. cornigera* Michelin, 1842). ?Middle Miocene (Helvetian), ?late Miocene (Tortonian), Pliocene, Pleistocene: Italy (see Zibrowius, 1980). Holocene: northeastern Atlantic, 80–600 m (group 2).

D. cornigera var. *michelotti* Kühn, 1936. Crete.

D. digitalis Michelin, 1842. Middle Miocene (Helvetian) to Pliocene: Italy, France.

D. digitalis var. *elongata* Michelin, 1842.

D. digitalis var. *minor* Osasco, 1897. Middle Miocene (Helvetian): Italy.

D. digitalis var. *subtaurinensis* Osasco, 1897. Middle Miocene (Helvetian): Italy.

D. trifurcata Michelotti in Sismonda and Michelotti, 1871. Middle Miocene (Helvetian) to early Pliocene: Italy.

D. collonjoni Thiollère, 1866. Late Miocene (Tortonian): France.

D. crassa Osasco, 1895. Late Miocene (Tortonian) to Pliocene: Italy.

D. epithecata Duncan, 1875. Miocene: Tasmania.

D. duncani Tenison-Woods, 1876. Miocene: Tasmania.

D. sp. Felix, 1903. Miocene: Egypt.

D. sp. Gerth, 1921. Miocene: Java.

D. koiwaii Yabe and Eguchi, 1944. Miocene: Japan.

Pliocene:

D. guidotti Dieni and Omenetto, 1960. Early Pliocene: Italy.

**D. oldroydae* Oldroyd, 1924. Middle Pliocene and Pleistocene: USA (California). Holocene: eastern Pacific, 40–576 m (group 3).

=*D. cortezi* Durham and Barnard, 1952.

- D. rutteni* Gerth, 1921. Pliocene: Java.
D. sp. Gerth, 1923. Pliocene: Borneo.
D. oroseinsis Chevalier, 1962. Pliocene: Italy.

Pleistocene:

- **D. cribrosa* Milne Edwards and Haime, 1851. Pleistocene: Japan. Holocene: Indo-West Pacific, 7–40 m (group 1).
 =[**Dentipora anastomozans* de Blainville, 1830 (nomen nudum).]
 **D. ijimai* Yabe and Eguchi, 1934. Late Pleistocene: Vanuatu. Holocene: Indo-West Pacific; 10–366 m [group 1].
 =?*D. subcornigera cylindrica* Eguchi, 1968.

Holocene (group 1):

- D. granosa* Studer, 1878. Australia, 91 m.
D. minuscula Bourne, 1905. Sri Lanka, depth unknown.
D. velata Crossland, 1952. Eastern Australia, depth unknown.
D. indica Pillai, 1969 ("1967"). Indian Ocean off southern India, 5 m.
D. carleenae Nemenzo, 1983. Philippines, depth unknown.

Holocene (group 2):

- D. radians* (Wright, 1882) (type species of *Brasseya* Wright, 1882). "Southern Seas," depth unknown.
D. robusta (Bourne, 1905). Sri Lanka, depth unknown.
D. arbuscula van der Horst, 1922. Indo-West Pacific, 2–353 m.
 =*D. nouhuysi* Gardiner and Waugh, 1939.
 =*D. horsti* Gardiner and Waugh, 1939.
 =?*D. erecta* Nemenzo, 1960.
 =?*D. subcornigera* Eguchi, 1968, sensu stricto.
D. cladonia van der Horst, 1927. Southwestern Indian Ocean, 49–457 m.
D. incisa (Crossland, 1952). Eastern Australia, depth unknown.
D. laboreli Zibrowius and Brito, 1984. Northeastern Atlantic, 1–70 m.
D. aculeata Latypov, 1990. South China Sea, 11–21 m.
D. suprarbuscula Ogawa and Takahari, 2000. Japan, 90 m.
D. paragracilis Ogawa and Takahari, 2000. Japan, 1–10 m.
D. futojiko Ogawa and Takahari, 2000. Japan, 2 m.
D. minima Ogawa and Takahari, 2000. Japan, 2 m.

Holocene (group 3):

- [*D. semiramosa* de Blainville, 1834 (nomen nudum).]
D. alternata Pourtalès, 1880. North Atlantic, 276–900 m.
D. florulenta Alcock, 1902. Western Pacific, 69–243 m.
 =*D. florentula* (sic) Wells, 1954 (misspelling).
D. boschmai van der Horst, 1926 (replacement name for *D. japonica* van der Horst, 1922, not Rehberg, 1892, the latter now considered to be *Eguchipsammia japonica*). Japan, 40–165 m.
D. dilatata van der Horst, 1927. Southwestern Indian Ocean, 97–132 m.
D. californica Durham, 1947. Eastern Pacific, 42–93 m.
D. alcocki (Wells, 1954). Indo-West Pacific, 118–616 m.
 =*D. palita* Squires and Keyes, 1967.
D. johnsoni Cairns, 1991. Galápagos, 373–462 m.

Holocene (group unknown):

- D. cecilliana* Milne Edwards and Haime, 1848. "Liewkiew Islands," China, depth unknown.

***Enallopsammia* Michelotti, 1871**

PLATE 11: FIGURES *k,l*; PLATE 12: FIGURES *a–e*

Enallopsammia Michelotti in Sismonda and Michelotti, 1871:285.—Vaughan and Wells, 1943:240, pl. 50: figs. 13, 14.—Alloiteau, 1952:681.—Wells, 1956:F436, fig. 339:1a,b.—Chevalier, 1961:492.—Zibrowius, 1973:37–41 [revision].—Wells, 1977:G11–12.—Cairns, 1979:184.—Zibrowius, 1980:201.—Cairns, 1982:57.—Chevalier and Beauvais, 1987:695, fig. 401:14.—Zibrowius, 1991:113–114.—Cairns, 1994:92.—Cairns and Zibrowius, 1997:194.
Anisopsammia Marenzeller, 1904:314.

DIAGNOSIS.—Corallum in form of arborescent colonies produced by extratentacular budding. Distinct costae covered with hispid granules (e.g., type species) may be present, or coenosteum may be uniformly covered with small spines. Epithecium absent; synapticulotheca porous only near calicular edge. Corallites sympodially or unifacially arranged, resulting in bushy or planar coralla, respectively; costoseptal rostra sometimes strongly expressed. Septa normally arranged (no Pourtalès plan, although S_3 often fused to common S_2); usually only three cycles of septa. P_2 (paliform lobes) sometimes present. Columella papillose and small. Endotheca absent. Azooxanthellate.

DISCUSSION.—Zibrowius (1973) revised the species of *Enallopsammia*, but much new information has emerged since then. Nonetheless, this revision serves as a valuable iconography of the Holocene species.

Both Alcock (1902) and Zibrowius (1973, 1991) strongly implied that the Neogene *E. scillae* is conspecific with the Holocene *E. rostrata* (as *E. amphelioides*), both species noted for having coralla with or without rostrate corallites, other characters being similar. Indeed, some of the syntypes of *E. scillae* have well-developed costoseptal rostra (Plate 12a) whereas others do not (perhaps worn off), and they are extremely similar to Holocene specimens. Nonetheless, I prefer to delay the synonymy of the Neogene species with the Holocene species until more well-preserved Pliocene specimens are compared to extant forms.

Wells (1977) suggested that *E. puyricardensis* Chevalier, 1961 (late Miocene (Tortonian): France), belonged to the genus *Tubastraea*, a view I endorse having examined the types of that species (MNHN, Institute of Paleontology: R10712 (holotype) R10713 (2 paratypes)).

The middle Miocene New Zealand records of *Enallopsammia* sp. reported by Squires (1958) were examined (NZGS GS 3159) and determined not to be dendrophylliid. Finally, the specimens reported by Chevalier (1966) as *E. micranthus* (Ehrenberg) from shallow water of Cape Verde were reassigned to *Tubastraea* by Laborel (1974:435).

Enallopsammia is most similar to *Dendrophyllia*, differing from that genus (Figure 2) in having regularly arranged septa (not a Pourtalès plan) and in lacking endotheca. It also has the unscored autapomorphy of having unifacial, often rostrate corallites. Stratigraphically, its first occurrence was in the Eocene, shortly after that of *Dendrophyllia*.

DISTRIBUTION.—Late Eocene: Tonga. Middle Miocene: Italy. Late Miocene (Tortonian): Italy, Czech Republic, France.

Pliocene to Pleistocene: Italy. Holocene: cosmopolitan except for eastern Pacific and off continental Antarctica, 110–2165 m.

TYPE SPECIES.—*Coenopsammia scillae* Seguenza, 1864, by monotypy; Pliocene of Italy (Sicily). Also known from middle Miocene of Italy (Chevalier, 1961).

Seven coralla, consisting of five branches and two colonies, are deposited at the NHMW (catalog number 1864-XXI-240). Although they are not the specimens figured by Seguenza (1864, pl. 14: figs. 2a–f), they are from the type locality and from the Seguenza collection and are herein considered to be syntypes (Plate 12a,b).

OTHER SPECIES.—*Enalopsammia laddi* Wells, 1977. Late Eocene: Tonga.

E. poppelacki (Reuss, 1847). Middle Miocene: Italy. Late Miocene (Tortonian): Italy, Czech Republic, Austria (reported herein: USNM M155295).

E. puyricardensis Chevalier, 1961. Late Miocene (Tortonian): Provence, France.

E. puyricardensis var. *grandiflora* Chevalier and Demarcq, 1964. Late Miocene (Tortonian): Rhone valley.

E. profunda (Pourtalès, 1867). Holocene: western Atlantic, 403–1748 m.

E. rostrata (Pourtalès, 1878) (type species of *Anisopsammia* Marenzeller, 1904, by monotypy). Holocene: cosmopolitan, except for eastern Pacific and off continental Antarctica, 110–2165 m.

=*Amphihelia adminicularis* Rehberg, 1892.

=*Coenopsammia amphelioides* Alcock, 1902.

=*Dendrophyllia amphelioides* var. *cucullata* Vaughan, 1907.

=*E. amphelioides disticha* Eguchi, 1968.

E. pusilla (Alcock, 1902). Holocene: Indo-West Pacific, 371–805 m.

=*E. marenzelleri* Zibrowius, 1973.

Duncanopsammia Wells, 1936a

PLATE 12: FIGURES f–i

Dendrophyllia.—Milne Edwards and Haime, 1848:101 [in part: *D. axifuga*].—van der Horst, 1922:53–54 [in part: *D. axifuga*].—Gardiner and Waugh, 1939:235–236 [in part: *D. axifuga*].

Duncanopsammia Wells, 1936a:547–548.—Vaughan and Wells, 1943:241.—Wells, 1956:F436.—Veron and Pichon, 1980:412–415.—Veron, 1986:574–575 [color figures and distribution map].—Chevalier and Beauvais, 1987:694–695.—Veron, 1993:339, fig. 35 [distribution map].

DIAGNOSIS.—Flat-topped, arborescent colonies formed by unifacial (upward), extratentacular budding from lower, outer margins of parent corallites. Coenosteum thick and not costate, instead covered with short (discontinuous) thin, parallel, finely serrate ridges (Plate 12h,i) not corresponding in number or position to septa. Epithecium absent; septa arranged in Pourtalès plan; septa not exsert. Pali and paliform lobes absent. Columella robust and discrete, composed of numerous finely serrated ridges linked together in labyrinthiform structure. Endotheca absent. Zooxanthellate.

DISCUSSION.—*Duncanopsammia* is part of a clade of seven dendrophylliid genera characterized by having arborescent budding (Figure 2). It is distinguished from the other six genera by having serrate costal ridges and a labyrinthiform columella. It also has the unscored autapomorphy of having uniaxially arranged corallites. The type species is well described and figured by Veron and Pichon (1980).

According to Veron and Pichon (1980), the polyps of this species are extended both day and night, the color of the coenosarc being green to a blue grey. Although zooxanthellate, it is not often found on reefs but prefers a horizontal sand or rubble substrate.

DISTRIBUTION.—Late Pliocene (Era Beds): Papua New Guinea. Holocene: tropical northern Australia (including Queensland, Northern Territory, and Western Australia), southern Indonesia, and South China Sea (see Veron, 1993, map 35), 6–34 m (zooxanthellate). Not known from Miocene, contrary to suggestion by Wells (1956) (see Veron and Kelley, 1988:60).

TYPE SPECIES.—*Dendrophyllia axifuga* Milne Edwards and Haime, 1848, by original designation; Holocene of Port Essington, Cobourg Peninsula, Northern Territory, Australia. Complete distribution of species listed as that for genus. Syntypes deposited at BM (46.7.30.38–39).

OTHER SPECIES.—None.

Dichopsammia Song, 1994

PLATE 12: FIGURES j–m

Dichopsammia Song, 1994 (April):213–214.

Schizopsammia Cairns, 1994 (October):94.

DIAGNOSIS.—Corallum arborescent, colonies produced exclusively by distomadeal intratentacular budding. Epithecium absent; synapticulotheca costate near calices, uniformly granular on branches; costae covered with fine rounded granules. Septa arranged in weak Pourtalès plan. Pali and paliform lobes absent. Columella feeble, trabecular. Endothecal dissepiments common. Zooxanthellate.

DISCUSSION.—Song (1994) compared *Dichopsammia* most closely to *Duncanopsammia*, but there are significant differences between these genera (Table 3, Figure 2), not least of which are the differences in budding type and costal morphology. *Dichopsammia* appears to be more closely related to the Eocene-Oligocene European genus *Lobopsammia* Milne Edwards and Haime, 1848, differing from that fossil genus in having exclusively distomadeal budding (no tristomadeal budding), lacking epithecium, and in having endotheca. All of these differences are minor, and it may later be decided that the genera are synonymous. *Dichopsammia* is the only extant dendrophylliid genus known to have intratentacular budding.

DISTRIBUTION.—Holocene: known only from Korea Strait, 20–30 m.

TYPE SPECIES.—*Dichopsammia granulosa* Song, 1994, by original designation (= *Schizopsammia songae* Cairns, 1994 (type species of *Schizopsammia* Cairns, 1994, by original des-

ignation)); Holocene of Mip'o, Korea Strait (35°09'N, 129°11' E), 20–30 m. Holotype (Ant. 800515) and most paratypes (Ant. 740713, 831127) deposited at the Department of Biology, College of Natural Sciences, Ewha Womans University, Seoul; some paratypes also deposited at the Natural History Museum, Ewha Womans University, Seoul, Republic of Korea.

OTHER SPECIES.—None.

Lobopsammia Milne Edwards and Haime, 1848

PLATE 13: FIGURES a–c

Lobopsammia Milne Edwards and Haime, 1848:105; 1850:liii [type species designated]; 1851:138.—Milne Edwards, 1860:123–124.—Duncan, 1884:182.—Vaughan and Wells, 1943:237.—Alloiteau, 1952:680.—Wells, 1956:F435.
Placopsammia Reuss, 1859:486–487.—Duncan, 1884:179.

DIAGNOSIS.—Corallum consisting of small arborescent colonies produced by di- or tristemadeal intratentacular budding. Calices often irregular or elongate in shape. Epithea present at base; entire synapticulotheca costate, costae granular and separated by deep intercostal furrows. Septa arranged in Pourtalès plan; full fifth cycle never attained. Columella trabecular. Endotheca absent.

DISCUSSION.—Vaughan and Wells (1943) and Wells (1956) diagnosed this genus as having mono- or distomadeal intratentacular budding, the permanent condition being monocentric, but “monostomadeal budding” is a contradiction in terms, even though the monocentric condition might eventually result from distomadeal budding. In fact, the budding in *Lobopsammia* is distomadeal (two serially linked centers) and tristemadeal (three linked centers), and occasionally with even a fourth serially linked center. Usually each budded corallite becomes individualized (monocentric), but *L. parisiensis* is distinguished by maintaining its linkage between budded corallites (di- and tricentric).

Lobopsammia is one of four dendrophylliid genera constituting a clade characterized by having intratentacular budding (Figure 2), and it is probably most closely related to *Dichopsammia*, as discussed in the account of that genus.

DISTRIBUTION.—Middle Eocene (Lutetian, Bartonian): France, Italy. Late Eocene (“Tschechoslovakian”): Czech Republic. Early Oligocene: England, Germany, Italy. Middle Oligocene: Germany.

TYPE SPECIES.—*Lithodendron cariosum* Goldfuss, 1826, by subsequent designation (Milne Edwards and Haime, 1850) (= *Dendrophyllia variabilis* de Blainville, 1830; = *L. dilatata* Römer, 1863. Early Oligocene: Germany); middle Eocene (Lutetian) of Meudon (Seine). Also known from middle Eocene (Lutetian, Bartonian) of France, late Eocene (“Tschechoslovakian”) of Czech Republic, and early Oligocene of England and Germany. Deposition of type specimens not traced.

OTHER SPECIES.—*Lobopsammia parisiensis* (Michelini, 1844). Middle Eocene (Lutetian): France.

L. multilamellosa d'Archiardi, 1875. Middle Eocene: Italy.

[*L. cylindrica* de Angelis, 1894 (nomen nudum). Italy.]

L. arbuscula Felix, 1885. Early Oligocene: Italy.

L. dichotoma (Reuss, 1859) (type species of *Placopsammia*). Middle Oligocene: Germany.

Stichopsammia Felix, 1885

PLATE 13: FIGURES d,e

Stichopsammia Felix, 1885:417; 1925:165 [type species selected].—Vaughan and Wells, 1943:238.—Wells, 1956:F435.

DIAGNOSIS.—Corallum consisting of small colonies, produced by polystomadeal intratentacular budding, corallites linked in linear series (polycyclic condition), resulting in flabellate branches. Epithea absent; synapticulotheca costate, finely granular. Septa arranged in Pourtalès plan. Columella trabecular. Endotheca absent.

DISCUSSION.—*Stichopsammia* is generally described as being like *Lobopsammia* but having polystomadeal intratentacular budding, resulting in a permanent linear series of linked corallites (the polycentric condition) and thus flabellate branches. On this basis it is hard to justify the separation of this genus from *Lobopsammia*.

The dendrophylliid genus *Cahuzacopsammia* Chaix, 1999, which consists of one species known only from the late Oligocene (Chattian) of Aquitaine, France, was described too late to be included in the phylogenetic analysis of this paper. It is characterized by having intratentacular budding leading to a meandroid corallum, disassociated costae, a Pourtalès plan septal arrangement, a trabecular columella, and sparse endotheca. As Chaix (1999) suggested, it is probably closely related to *Lobopsammia* or *Stichopsammia*, differing from these genera in having a meandroid corallum. Stratigraphically it may be a descendant of either of these two genera.

DISTRIBUTION.—Middle Eocene (Bartonian): France (reported herein). Late Eocene (Priabonian): Italy. Early Oligocene (“Ligurian”): Italy.

TYPE SPECIES.—*Stichopsammia gyrosa* Felix, 1885, by subsequent designation (Felix, 1925); early Oligocene (“Ligurian”) of Crosara (Venezia), Italy.

The holotypes, stated to be deposited at the Paleontology Museum in Berlin (Felix, 1885), could not be located despite requests to the Museum für Naturkunde, Humboldt-Universität, Berlin, and the Bundesanstalt für Geowissenschaft und Rohstoffe, Berlin.

OTHER SPECIES.—*Stichopsammia miocaenica* (Michelotti in Sismonda and Michelotti, 1871). Late Eocene (Priabonian): Italy.

Reussopsammia Wells, 1937

Stereopsammia.—Reuss, 1864:204, pl. 1: figs. 1, 2 [in part: *S. granulosa*].—Felix, 1925:166 [in part: *S. granulosa*].

Reussopsammia Wells, 1937:75.—Vaughan and Wells, 1943:238, pl. 50: figs. 1a–d.—Alloiteau, 1952:681.—Wells, 1956:F435, fig. 339:3a–c.

DIAGNOSIS.—Corallum consisting of small colonies produced by intratentacular polystomadeal budding, resulting in mono- and polystomadeal corallites arranged in flabello-den-

droid pattern. Costae well defined, granular, bifurcating and rejoining one another on coenosteum. Epitheca absent. Septa normally arranged (no Pourtalès plan); up to 60 septa. Columella absent. Endotheca presumed to be absent.

DISCUSSION.—*Reussopsammia* is generally compared to *Lobopsammia* (and *Stichopsammia*), differing from those genera in having a normal arrangement of septa and no columella. It is known only from the type series.

DISTRIBUTION.—Middle Oligocene: Rheinland, Germany.

TYPE SPECIES.—*Stereopsammia granulosa* Reuss, 1864, by original designation; middle Oligocene of Welshberge, near Waldböckelheim (Rheinland), Germany.

According to Ortwin Schultz (pers. comm., 1999), the type specimen should be deposited at the State Paleontology Museum in Munich; however, it could not be located through a request made of that museum.

OTHER SPECIES.—None.

“DENDROPHYLLIID” GENERA OF UNCERTAIN POSITION

Stereopsammia Milne Edwards and Haime, 1850

PLATE 13: FIGURE g

Milne Edwards and Haime (1850) described the genus *Stereopsammia* from a single specimen from the middle Eocene (Bartonian) of Bracklesham Bay, Isle of Wight, England (type species: *S. humilis* Milne Edwards and Haime, 1850, by original designation). The holotype, which is deposited at BM (Paleontology 49580), is so badly damaged that it is difficult to truly assess the characterization and systematic position of this taxon. Only about one-fifth of the original corallum survives (Plate 13g). Because the type cannot provide the necessary characters, *Stereopsammia* is considered to be of uncertain position and is not included in the phylogenetic analysis. The holotype is plocoid, having extratentacularly budded corallites projecting up to 3 mm above the coenosteum. Corallites are cylindrical and quite small, only about 1.4 mm in diameter. Costae consist of thin, nongranular ridges; there is no epitheca. Three cycles of normally arranged septa are present; $S_1 \gg S_2 - S_3$, the axial edges of the S_1 being smooth and sinuous. The columella is rudimentary. *Stereopsammia* has been recognized by most monographers as a valid dendrophylliid genus, similar to *Tubastraea* but having smaller corallites and only a rudimentary columella. Reuss (1864) added another species to the genus, *S. granulosa*, but Wells (1937) later made this the type species of *Reussopsammia*. Wells (1956) also questioningly included *Bosnopsammia* Oppenheim, 1908 (type species: *B. katzeri* Oppenheim, 1908, by monotypy), from the Eocene of Yugoslavia as a junior synonym.

Desmopsammia Reis, 1889

Reis (1889) established the genus *Desmopsammia* for two species from the early Oligocene (Ligurian) of northern Italy

and Germany: *Desmophyllum subcylindricum* Philippi, 1851 (type species of *Desmopsammia* by subsequent designation (Felix, 1925)), and *Desmopsammia perlonga* Reis, 1889. Reis characterized the genus as colonial, having corallites budding from a common basal coenosteum similar to that of *Cladopsammia*. However, the type species, *Desmopsammia subcylindrica* (Philippi, 1851), was based on two solitary corallites that Keferstein (1859) and Römer (1863) interpreted as belonging to the genus *Balanophyllia*. Vaughan and Wells (1943) placed the genus close to *Cladopsammia* but admitted that the original diagnosis was unsatisfactory. The genus has been ignored by other monographers. Even if Reis had intended the genus to be characterized by having extratentacular budding from a common basal coenosteum, the characteristics of the type species are equivocal, underlining the need to have a complete corallum of a dendrophylliid specimen before even a reliable generic identification can be made (Cairns, 1999a:129). *Desmopsammia subcylindrica* may be a simple corallum (e.g., *Balanophyllia*) or a single broken corallite from a larger colony (e.g., *Rhizopsammia*, *Eguchipsammia*, *Cladopsammia*, or even a *Dendrophyllia*). The deposition of *Desmophyllum subcylindricum* is unknown. Because the salient characteristics of the type species cannot be determined, this genus is considered to be of uncertain position and is not included in the phylogenetic analysis.

Aplopsammia Alloiteau, 1958

PLATE 13: FIGURES f,h

Alloiteau (1958) described the genus *Aplopsammia* (based on the type species *A. collignoni* Alloiteau, 1958, type by original designation) for two specimens from the Early Cretaceous (Albian) of Ambaramaninga, Madagascar. It has not been reported subsequent to its original description. It is diagnosed as having a corallum that is solitary, elongate-conical (ceratoid), and free. Synapticulotheca are finely granular over the entire surface (no costae or epitheca). Septa are arranged normally (no Pourtalès plan) in four cycles, the columella is spongy, and sparse endothecal dissepiments are present. The lower part of the paratype (illustrated by Alloiteau, 1958, pl. 2: fig. 11, pl. 23: fig. 6), but not the thin section or upper corallum (pl. 2: fig. 10), is deposited at the MNHN (Institute of Paleontology, M05014). The holotype could not be found at the MNHN in 1999; its deposition is unknown. *Aplopsammia* is reputed to differ from all other dendrophylliid genera in having no costae or epitheca, being otherwise similar to *Palaeopsammia*. Unfortunately, the only specimen available for study (Plate 13: figures f,h), the paratype, is so poorly preserved that its lack of costae and epitheca might well be due to erosion, and the septal plan cannot be determined. Based on such poor and lost material, the genus cannot be confidently diagnosed and thus it is considered to be of uncertain position and is not included in the phylogenetic analysis.

***Makridinophyllia* Kuzmicheva, 1987**

Kuzmicheva (1987) described the genus *Makridinophyllia* (type species: *M. makridini* Kuzmicheva, 1987, type by original designation) for four specimens (holotype (MGU185/880) and three paratypes) from the late Eocene of southern Ukraine. It has not been subsequently reported. A translation of Kuzmicheva's (1987:152) original Russian genus diagnosis follows: "Corallites are solitary; mushroom-like in form; attached to the ground by a stem, which is widened at the attachment; in adult forms there is observed more growth outward [girth] than upward. Outer surface of corallites covered with uniform relatively thin ridges. The formation of septocostae during early and young stages of ontogeny is according to the Pourtalès plan, although larger individuals have some deviation from this plan. Septocostae are numerous. During the mature stage adjacent septocostae of the first order fuse by their distal edges and form thick spongy septocostae. Columella elliptical in shape and well developed." The species description goes on to add that the holotype is 75 × 57 mm in CD and 50 mm in height, the surface of the calice is dome shaped, and the edge of the calice is thin and flat. Up to 350 septa are present in large coralla, but the Pourtalès plan is present only in smaller coralla. Distinct costae are present; both theca and septa are porous. Although Kuzmicheva described this species as solitary and with a Pourtalès plan, her illustrations of the holotype (pl. 27: figs. 1a,b) show a polycentric condition with normally arranged septa, whereas the smaller paratype illustrated in pl. 27, fig. 2a,b, does indeed appear to be solitary and to have a Pourtalès plan. The type series could not be obtained from Kuzmicheva at Moscow State University. It is possible that the type series may constitute two species, the illustrated paratype being a species of *Balanophyllia* and the holotype representing a new genus, as suggested by Kuzmicheva. The holotype may well represent a distinct dendrophylliid genus characterized by intratentacular budding, a normal septal insertion pattern consisting of numerous (almost 7 cycles) septa, costae, a columella, and a mushroom-shaped corallum, which would place it closest to *Reussopsammia* in characteristics. But, without access to the type series, it is difficult to resolve the inconsistencies in the original description and illustrations. The genus is thus considered to be of uncertain position and is not included in the phylogenetic analysis.

PREVIOUSLY REASSIGNED "DENDROPHYLLIID" GENERA

Unlike the genera of uncertain position discussed above, some of which may in fact be dendrophylliids, a number of genera have been incorrectly assigned to this family. Some of these misassignments have long been known, others are suggested here for the first time. Those genera previously reassigned include the following.

***Stephanophyllia* Michelin, 1841, *Leptopenus* Moseley, 1881, *Discopsammia* d'Orbigny, 1849**

The genus *Stephanophyllia* (type species *Fungia elegans* Bronn, 1837, by original designation), was considered to belong to the "Eupsammidae" by all late nineteenth and early twentieth-century authors (e.g., Milne Edwards and Haime, 1848, 1850; Milne Edwards, 1860; Duncan, 1884; Felix, 1925, 1927; Yabe and Eguchi, 1932b). Duncan (1884) even established an alliance named the Stephanophyllioida, one of four such alliances within the family Eupsammidae, which contained the genus *Stephanophyllia*, as well as *Leptopenus* (type species: *L. discus* Moseley, 1881, by subsequent designation, Wells, 1936b) and *Discopsammia* (type species: *Stephanophyllia bowerbankii* Milne Edwards and Haime, 1848) (the latter a junior synonym of *Micrabacia*). The genera of this alliance were distinguished as having a discoidal, horizontal wall. Yabe and Eguchi (1932b) described the new subgenus *Stephanophyllia* (*Stephanopsammia*) (type species: *S. discoides* Milne Edwards and Haime, 1848, by original designation), which they also placed in the family Eupsammidae, although they were the last authors to consider *Stephanophyllia* to be a dendrophylliid. Meanwhile, Vaughan (1905) established the family Micrabaciidae, placing it within the suborder Fungiina and including in it *Micrabacia*, but he did not include the closely related genus *Stephanophyllia*. It was not until 1933 that Wells finally attributed both *Stephanophyllia* and *Leptopenus* to the fungiine family Micrabaciidae, explaining that although both families had a perforate theca, the perforations occur in a very different manner. Furthermore, all micrabaciids have an alternation in position of costae and septa, an autapomorphy for that family. And finally, the septal insertion pattern of micrabaciids, usually assumed to be a variation of the Pourtalès plan, is not at all similar in ontogeny or final result to the dendrophylliid Pourtalès plan (see Cairns, 1989a:13) but is another autapomorphy of that family. Thus the genus *Stephanophyllia* and its related genera are now classified in the family Micrabaciidae, superfamily Fungiioidea, suborder Fungiina. Holocene accounts of this genus include Owens (1986) and Cairns (1989a). It is of interest to note, however, that Chevalier and Beauvais (1987) placed the family Micrabaciidae as a sister family to the Dendrophylliidae in the suborder Dendrophylliina.

***Dactylosmilia* d'Orbigny 1849**

D'Orbigny (1849:6) described the genus *Dactylosmilia* (based on the type species *D. carantonensis*, type by monotypy) for two specimens (syntypes) from the Late Cretaceous (Cenomanian) of Aix, France. Few subsequent references have been made to this genus, Vaughan and Wells (1943:242) eventually considering it to be a genus of uncertain position, but "possibly a dendrophylliid." It is apparently a colonial coral that buds intratentacularly, the permanent condition being monocentric. D'Orbigny stated that it had pali and a thin epitheca, but Vaughan and Wells (1943) characterized it as nonepi-

thecate and as having costae. All three authors describe it as having a columella, and Vaughan and Wells (1943) go on to say that it has a perforated wall, laminar (probably nondentate) septa, and thin and sparse dissepiments, these observations apparently being made from the type specimens deposited in the d'Orbigny Collection of the MNHN (6701). Neither author commented on the septal insertion pattern. Unfortunately these type specimens could not be located at the MNHN in 1999. Roniewicz and Morycowa (1993) considered this genus to belong to the family Meandrinidae. Because of the contradictions in previous descriptions of the type series, the lack of availability of the types, and the opinion of Roniewicz and Morycowa, *Dactylosmia* is not considered to be a dendrophylliid.

***Psammoseris* Milne Edwards and Haime, 1851**

Psammoseris (type species: *Heterocyathus hemisphaericus* Gray, 1849, by monotypy) was originally described as a lophoserine fungiid and was considered as such by Duncan (1884) and Vaughan (1905); however, some authors considered it to be a dendrophylliid (e.g., Moseley, 1881; Marenzeller, 1888), similar to if not a junior synonym of *Heteropsammia*. Whereas Gardiner (1905) was equivocal about the issue, Bourne (1905) and Folkson (1919) emphatically disagreed with the dendrophylliid placement, considering *Psammoseris* to be a junior synonym of *Heterocyathus* Milne Edwards and Haime, 1848. *Heteropsammia* and *Heterocyathus*, in addition to having similar names, have a very similar (convergent) growth form and an obligate symbiosis with a sipunculid worm. Nonetheless, they belong to different suborders, the former a dendrophylliid, the later a caryophylliid. For unexplained reasons, Vaughan and Wells (1943), Wells (1956), and Chevalier and Beauvais (1987) considered *Psammoseris* to be a valid dendrophylliid genus. More recently, Hoeksema and Best (1991) and Cairns (1998), after examining the type specimen of *Heterocyathus hemisphaericus* (deposited at BM), concluded that although it had spongy septa, its theca was septothecate and thus it should be considered a caryophylliid. They both considered it a junior synonym of *Heterocyathus*, the genus in which Gray (1849) originally placed it! The syntypes of *Spongiocyathus typicus* (type species of *Spongiocyathus* Folkson, 1919, by monotypy), deposited at the SMNH (4753-56), are conspecific with *Heterocyathus hemisphaericus* (see Cairns, 1988), and thus *Spongiocyathus* was also placed as a junior synonym of *Heterocyathus* by Hoeksema and Best (1991) and Cairns (1998).

***Trematotrochus* Tenison-Woods, 1879**

Trematotrochus (type species: *Conocyathus fenestratus* Tenison-Woods, 1878, by monotypy) was originally and correctly placed in the family Turbinoliidae by Tenison-Woods (1879). Even though all species of this genus have a perforate theca, this character was judged to be a convergent, genus-level char-

acter by Tenison-Woods (1879) and most later authors. Denant (1899a), however, transferred the genus into the Eupsammidae, a decision followed by Filliozat (1911) and by Felix (1927) in the *Fossilium Catalogus*. Despite its perforate theca, Vaughan and Wells (1943) and all subsequent authors (see Cairns, 1997) have considered *Trematotrochus* to be an aberrant turbinoliid, not a dendrophylliid.

***Gravieropsammia* Filliozat, 1910, *Felixopsammia* Filliozat, 1910**

Filliozat (1910) described two "dendrophylliid" genera from the middle Eocene (Lutetian) of the Paris Basin: *Gravieropsammia* (type species: *G. cornucopiae*, by monotypy) and *Felixopsammia* (type species: *F. arcuata*, by monotypy), both names ending with the characteristic dendrophylliid suffix "-psammia." The former genus was stated to have affinities with *Astroides*, the latter with *Thecopsammia*. Felix (1925) dutifully reported both genera as dendrophylliids in the *Fossilium Catalogus*, but Vaughan and Wells (1943) and later Wells (1956:F374) transferred *Gravieropsammia* to the Acroporidae, diagnosing it as "a solitary *Astreopora*." The same authors considered *Felixopsammia* a junior synonym of the mussid genus *Circophyllia* Milne Edwards and Haime, 1848. The French monographers (Alloiteau, 1952; Chevalier and Beauvais, 1987) ignored these two genera.

NEWLY REASSIGNED "DENDROPHYLLIID" GENERA

***Petrophyllia* Conrad, 1855**

PLATE 14: FIGURES a,b

Dendrophyllia ? (*Petrophyllia*) Conrad, 1855b:266.—Vaughan, 1900:200–201.—[not *Petrophyllia* Felix, 1885:397 (junior homonym, renamed *Petrophylliella* by Felix, 1925)].

Archohelia Vaughan, 1919:352–353.—Wells, 1956:F411.

Petrophyllia.—Vaughan and Wells, 1943:243.—Wells, 1956:F437.

Dendrophyllia ? Richards, 1968:12.

DIAGNOSIS.—See "Discussion."

DISCUSSION.—Conrad (1855b) described the subgenus *Dendrophyllia* (*Petrophyllia*) for a single specimen collected in the United States from the Eocene of White River, Arkansas, although he expressed some doubt that the type species *P. arkansensis* (established by monotypy) actually belonged to that genus. Part of his hesitation was probably because the type specimen, although well preserved, was covered with muddy sediment that obscured the fossa of all corallites. The original description was short and not very diagnostic, as well as being unillustrated. Because Vaughan (1900) could not find Conrad's type specimen and because the original description was ambiguous, he (Vaughan and Wells, 1943:243) considered *Petrophyllia* to be a "genus of uncertain position" but suggested that it was "an indeterminate dendrophylliid." Wells (1956) also considered it to be a genus of uncertain position and noted that it was the senior homonym of the faviid genus

Petrophyllia Felix, 1885 (Oligocene, Italy), later named *Petrophylliella* by Felix (1925) to avoid homonymy. Richards (1968) noted that the holotype of *Petrophyllia arkansensis* was deposited at the Philadelphia Academy of Natural Sciences (ANSP 30718). My examination of the cleaned specimen showed it to be a typical oculinid, having P_1 – P_2 and typically larger axial corallites, which places it in the genus *Archohelia* Vaughan, 1919, several species of which have been described from the Paleogene of the United States Gulf Coast (e.g., Vaughan, 1900, as *Oculina* and *Astrohelia*; Vaughan, 1919:195, 199, 352; and Vaughan, 1941). Thus, Conrad's (1855b) *Petrophyllia* is a valid oculinid name and has nomenclatural priority over *Archohelia* Vaughan, 1919.

There is a slight doubt that the specimen figured herein is the holotype of *P. arkansensis*, as one of the labels written by "E.J.T." in 1958 explains that this corallum was separated from a larger "mixed lot" containing several labels, but this specimen does match Conrad's brief description and is thus considered to be the holotypic specimen.

Rhabdopsammia Alloiteau, 1952

PLATE 13: FIGURES *i*–*k*

Rhabdopsammia Alloiteau, 1952:680; 1957, pl. 4: figs. 5a,b.—Baron-Szabo, 1999:8.

DIAGNOSIS.—See "Discussion."

DISCUSSION.—The history of this genus is rather confused. In 1952 Alloiteau briefly diagnosed the genus and the type species (*R. lunquinei*, by monotypy) in two lines, attributing the description of the genus to himself, but in 1951. There is no record of this genus or species having been described in 1951, thus the brief unfigured 1952 diagnosis must serve as the original description for both genus and species, as allowed by the ICZN (1999, Article 13.4). Several years later Alloiteau (1957, pl. 4: fig. 5) figured the holotype of the species, and in the caption he noted that it was a "nov. gen. nov. sp.," which would not be the case at that time, especially because there is no text or even index reference to this species or genus in the main body of the 1957 publication. Wells (1956) apparently overlooked *Rhabdopsammia* in his revision of the scleractinian genera, and it has only been noted once more quite recently by Baron-Szabo (1999).

The genus is known from only two specimens: the holotype and the specimen reported by Baron-Szabo. The holotype, deposited at the MNHN (Institute of Paleontology, R10960), consists of one primary corallite 14.0 mm in CD and about 50 mm in height, from which two smaller corallites (CD=9.3 and 9.5 mm) have intratentacularly budded and remain near the calicular margin. Costae appear to be present as distinct ridges. Septa (approximately 32) are thick and arranged normally (not according to a Pourtalès plan). A columella is absent. According to Baron-Szabo (1999), there are vesicular endothecal dissepiments in the Austrian specimen. The type locality of *R. lunquinei* is the Late Cretaceous (Santonian) of Provence, France,

whereas Baron-Szabo (1999) has reported a species of this genus from the Late Cretaceous of Austria.

Alloiteau (1952) originally diagnosed *Rhabdopsammia* as a simple coral, but he described it as having intratentacular budding, a seeming contradiction. He also placed it in the subfamily Tubastraeinae, characterized by having normally arranged septa; however, Baron-Szabo (1999) indicated an irregular Pourtalès plan for her specimen, another seeming contradiction. Examination of the holotype shows it to have a nonperforate theca, thick solid septa, and a dense corallum, character states more suggestive of a faviid or eusmiliid genus than of a dendrophylliid. Consequently, *Rhabdopsammia* is not considered further in the context of this revision.

Kumbiopsammia Alloiteau, 1958

PLATE 14: FIGURES *g*–*i*

Kumbiopsammia Alloiteau, 1958:201–202, pl. 24: figs. 1–4.—Hassan and Salama, 1969:94.

DIAGNOSIS.—Corallum solitary, patellate, free. Costae poorly developed but represented by linear arrangement of coarse granules. Epitheca absent. Septa not arranged in Pourtalès plan, but higher cycle septa (S_4) anastomose with those of lower cycle (S_3); usually 40 septa. Columella well developed, parietal. Endotheca consisting of thick but relatively rare dissepiments.

DISCUSSION.—Alloiteau (1958) compared *Kumbiopsammia* to *Palaeopsammia* but distinguished it by its patellate corallum shape, lack of epitheca (instead having coarse, aligned costal granules), and its better-developed columella. After examining the type series, however, I question whether *Kumbiopsammia* is a dendrophylliid at all. The axial edges of the septa of the holotype are thickened and coarsely dentate, in the manner of a faviid or even an anthemiphylliid. Furthermore, the structure of the wall, stated to be thin and synapticulothecate by Alloiteau (1958), could not be verified from the type series. Until more and better-preserved specimens can be examined by thin section, I do not consider this genus to be a dendrophylliid. The holotype measures 7.4 mm in CD and 3.7 mm in height.

DISTRIBUTION.—Late Cretaceous (Maastrichtian): Madagascar, paper shales of southwestern Egypt.

TYPE SPECIES.—*Kumbiopsammia besairiei* Alloiteau, 1958, by original designation; Late Cretaceous (Maastrichtian) of Ampasindava, Madagascar. Holotype (Plate 14*g*–*i*) and 8 paratypes, including those illustrated in original description, deposited at MNHN (Institute of Paleontology, M05080). Ninth paratype could not be located in 1999.

OTHER SPECIES.—None.

Spongiopsammia Kuzmicheva, 1987

Spongiopsammia Kuzmicheva, 1987:153.

DIAGNOSIS (translated from original Russian).—"Small solitary coralla of conical shape. Septocostae arranged in a Pour-

talès plan during whole ontogeny. Septocostae not numerous. They are thin, with large, round pores distributed all over the surface. Synapticulae not numerous. Columella parietal. The thinness and crookedness of the septocostae, as well as their porosity and synapticular bars, give the corallum a spongy structure. The wall is synapticulothecate. It is very thin. Coralla are covered outside by a wrinkled epitheca.”

DISCUSSION.—Very little is known about this genus, which is known only from the types series of four specimens. Although Kuzmicheva (1987) stated that the septa were arranged in a Pourtalès plan for its whole ontogeny, the calicular view of the holotype (Kuzmicheva, 1987, pl. 27: fig. 3b) shows a decidedly different arrangement: septa anastomosing in a reticulate manner, as in a labyrinthiform columella. Indeed, the figured holotype looks more like a “sclerosponge” than a coral. Vacelet (pers. comm, 1999) suggested that it is very similar to the coralline demosponge *Astrosclera willeyana* Lister, 1900 (order Agelasida, family Astroscleridae) (see Wörheide, 1998). Unfortunately, the type specimens could not be obtained from Kuzmicheva at the Moscow State University for confirmation. Based on the illustration of the holotype, *Spongiopsammia* is tentatively considered to be a sponge and thus is not considered in the phylogenetic analysis.

DISTRIBUTION.—Known only from four specimens from the type locality.

TYPE SPECIES.—*Spongiopsammia amitrovi* Kuzmicheva, 1987, by original designation; late Eocene of South Ukraine. Holotype deposited at MGU (N185/885).

OTHER SPECIES.—None.

Patelopsammia Reig Oriol, 1988

PLATE 14: FIGURES c,f

Patelopsammia Reig Oriol, 1988:3.

DIAGNOSIS (fide Reig Oriol).—Corallum solitary, patellate, free. Theca covered by smooth epitheca (no costae). Septa arranged according to Pourtalès plan; 6 cycles; upper edges of septa coarsely dentate. Columella absent; center of calice depressed.

DISCUSSION.—Although this genus is listed in the 1988/89 Zoological Record (vol. 125:17), it has never been cited again, and its method of publication is unclear. The paper appears to have had a limited distribution as a reprint but was not published in a journal or in a book. Furthermore, the type specimen is said to be deposited at the Museo Geológico del Seminario de Barcelona, but Calzada and Urquiola (1992), who listed the types of all other coral species described by Reig Oriol up to that time, did not list it among the type specimens held by that museum. A request was made to the Barcelona Museum to borrow the type specimen of *P. gurraei*, but instead, two topotypic specimens were sent, which appear to be conspecific with the holotype as judged from the illustrations of Reig Oriol. Examination of these specimens, however, revealed that they have

solid theca and septa, a costate outer calicular edge, septa arranged normally (not in a Pourtalès plan), and strongly beaded/dentate upper septal edges. Thus, even if the genus and species is legitimately described, these characters are not consistent with a placement in the Dendrophylliidae, but rather, they have a faviid or even fungiid affinity.

DISTRIBUTION.—Known only from the two types and two additional specimens (USNM 100169) from the type locality.

TYPE SPECIES.—*Patelopsammia gurraei* Reig Oriol, 1988, by monotypy; middle Eocene (Lutetian) of Puebla de Fontora (Huerco), northeastern Spain. Type (holotype and 1 paratype) said to be deposited at Museo Geológico del Seminario de Barcelona but not listed in catalog of types contained at that museum (Calzada and Urquiola, 1992) and not found there in 1999.

OTHER SPECIES.—None.

Ilerdopsammia Reig Oriol, 1992

PLATE 14: FIGURES j-l

Ilerdopsammia Reig Oriol, 1992:28.

DIAGNOSIS.—Corallum solitary, cylindrical, and presumed to be free. Theca bearing prominent, granular costae longitudinally arranged on vertical face. Epitheca absent. Septa hexamerally arranged in 4 cycles, with axial edges of S_4 bending toward their adjacent S_3 , but septa not arranged in Pourtalès plan. P_1 – P_2 present. Columella lamellar. Sparse endothecal dissepiments present.

DISCUSSION.—Reig Oriol (1992) described this genus as having a porous synapticulotheca and porous septa arranged in a Pourtalès plan, which would place it in the Dendrophylliidae. Examination of the holotype, which is the only known specimen of this species and genus, however, shows it to have a nonperforate theca (probably a septotheca) and nonperforate septa in a regular arrangement (not a Pourtalès plan), with the fourth cycle septa bending toward those of the third cycle. Also, because the base of the corallum is sheared off, it is impossible to tell if the corallum was attached or free. The holotype measures 11.1×10.1 mm in CD and 5.4 mm in height. *Ilerdopsammia* clearly does not have the characteristics of the Dendrophylliidae but rather has those of the Caryophylliidae or the Turbinoliidae. For instance, it is similar to the turbinoliid genus *Peponocyathus*, especially the Miocene species *P. duncani* (Reuss, 1871), both species having the same corallum shape, prominent costae and deep intercostal grooves, similar septal and costal arrangement, P_1 – P_2 , and a similar columella.

DISTRIBUTION.—Known only from one specimen from the type locality.

TYPE SPECIES.—*Ilerdopsammia eduardi* Reig Oriol, 1992, by original designation; Late Cretaceous (Campanian) of Torallola (Lleida), northeast Spain. Holotype deposited at Museo Geológico del Seminario de Barcelona (uncataloged).

OTHER SPECIES.—None.

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PLATE 1

- a. Discocyathus eudesii* from Croisille, Calvados (near Bayeux), France, Middle Jurassic (Bojajian), MNHN M00086, calicular and basal views of same specimen, $\times 2.7$ (courtesy J. Stolarski).
- b–d. Areopsammia mastrichtensis*, holotype, Netherlands, Late Cretaceous (Maastrichtian), Museum für Naturkunde, Berlin, MBK 1303: *b*, oblique view of two reconstructed fragments, $\times 2.7$; *d*, stereo view of calice, $\times 2.4$. *c. Porosmia alacca* as figured by Umbgrove (1925), National Museum of Natural History (Naturalis), Leiden, 76599, cast of lower corallum, $\times 2.7$.
- e.g.h. Balanophyllia (B.) calyculus*: *e,h*, neotype, Red Crag, Suffolk, England, late Pliocene, USNM 94469, calicular and side views, $\times 3.2$, $\times 1.8$, respectively; *g*, Red Crag, England, late Pliocene, USNM M156433, polycyclic base, $\times 5$.
- f.j. Balanophyllia (E.) caribbeana* from Oregon station 5696, $12^{\circ}05'N$, $72^{\circ}13'W$, 33 m, USNM 62612: *f*, detail of axial edges of several septa showing both minute serration of septal edge resulting from closely spaced, small-diameter trabeculae and fenestration on face of septum, $\times 28$; *j*, hispid costae covered with diaphanous epitheca, $\times 18$.
- i,k. Balanophyllia (B.) floridana*: *i*, Dry Tortugas, Florida, 71 m, USNM 81003, side view of largest known specimen, $\times 2.5$; *k*, Fish Hawk station 7516, off Fowey Rocks, Florida, 82 m, USNM 22037, detail of hispid costae, $\times 95$.

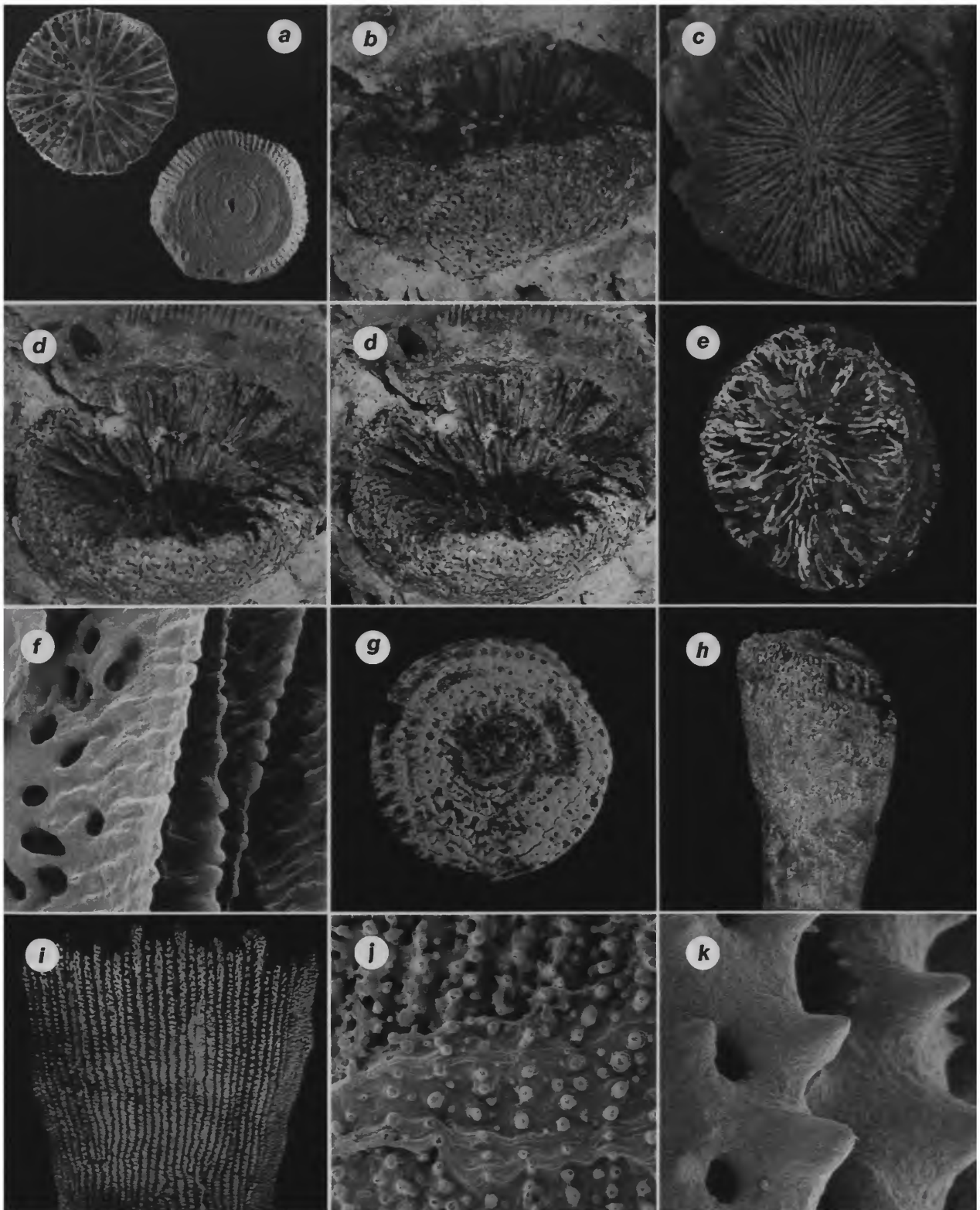


PLATE 2

- a.e. Balanophyllia (E.) trochiformis* from Le Vivray (Oire), France, middle Eocene (Lutetian), USNM M369877, side and calicular views of same specimen, $\times 2.6$, $\times 3.7$, respectively.
- b.f. Ceratopsammia (=Eupsammia) besairiei*, Late Cretaceous (Campanian) of Analavelona, Madagascar: *b.* side view of presumed holotype, MNHN M05028, $\times 5.1$; *f.* holotype (left) and paratype, $\times 3.6$.
- c.d. Lamellophyllia alloiteaui*, holotype, Turin, Italy, middle Miocene, MNHN R10483: *c.* side view of broken holotype, $\times 1.9$; *d.* calicular view of upper corallum, $\times 3$.
- g. Balanophyllia (E.) elongata* from USGS 5263, late Oligocene, Mississippi, USNM 66419, monocyclic base showing original 12 septa, $\times 20$.
- h-j. Heteropsammia cochlea*: *h.i.* holotype of *H. michelinii*, Wanpoa, China, MNHN 1080, side and calicular views, both $\times 3.8$; *j.* USNM 90137, Albatross station 5146, $5^{\circ}46'40''\text{N}$, $120^{\circ}48'50''\text{E}$, 44 m, damaged juvenile specimen showing whorls of gastropod shell on which the coral settled, $\times 16$.

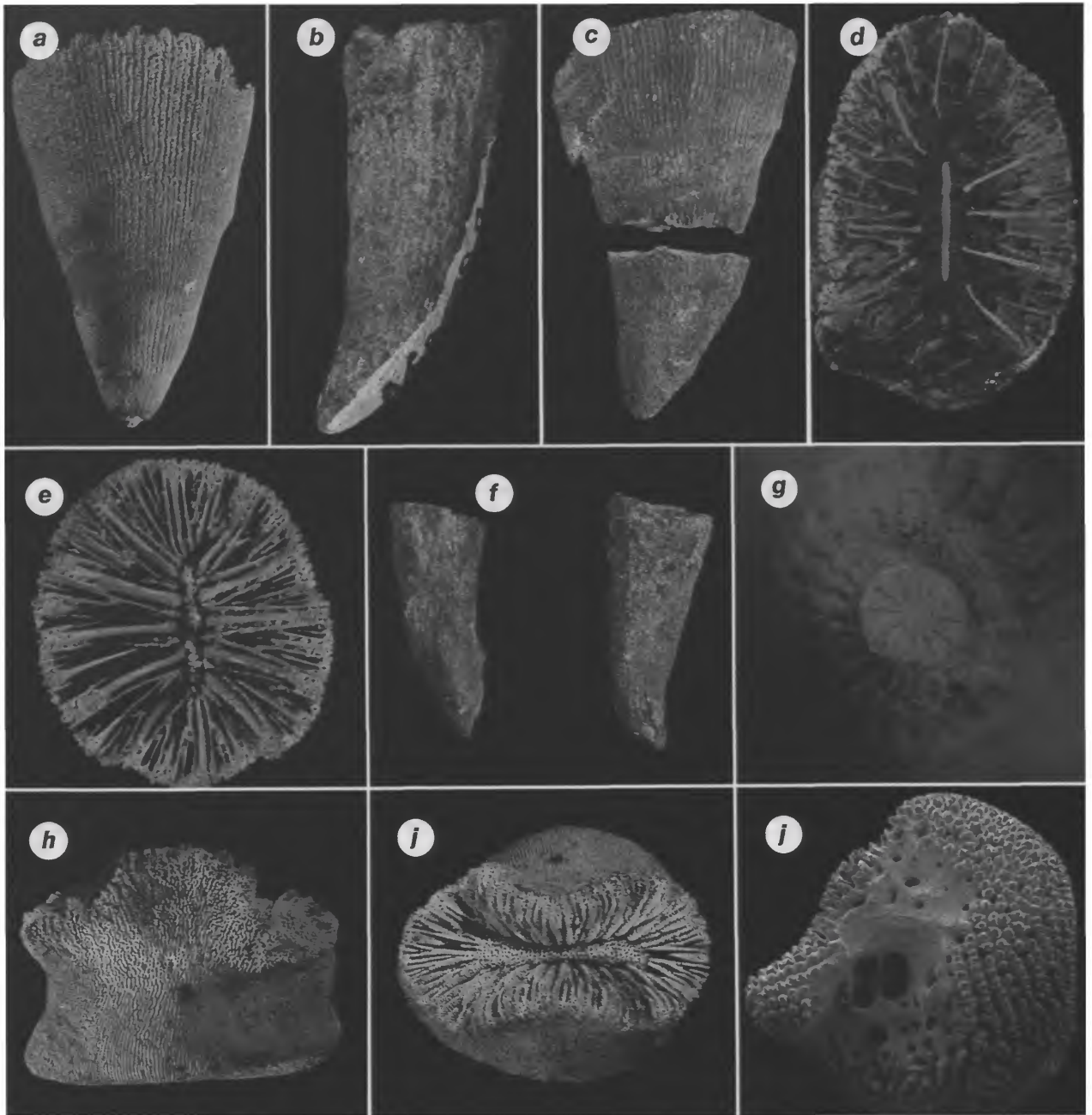


PLATE 3

- a–e. Heteropsammia cochlea*: *a,d,e*, Ile Oueri, New Caledonia, 8 m, USNM 73772: *a*, longitudinal cut revealing sipunculid chamber and part of dried sipunculid, $\times 4.5$; *d,e*, detail of serrate costal ridges, $\times 29$, $\times 200$, respectively. *b,c*, MUSORSTOM 3-140, $11^{\circ}42.6'N$, $122^{\circ}34.5'E$, 93–99 m, USNM 97652: *b*, transverse section of corallum showing concentric sipunculid chamber, $\times 3.2$; *c*, base of same specimen, showing main efferent pore of sipunculid, $\times 3.2$.
- f,i. Trochosmilia (=Wadeopsammia) nodosa*, holotype, Coon Creek, Tennessee, Late Cretaceous (Campanian), USNM 132703, side and calicular views, respectively, both $\times 14.5$.
- g,h. Wadeopsammia nodosa* sensu Wells (1933): USGS 15537, Mustang Creek, Texas, Late Cretaceous, USNM 175183, side and calicular views, respectively, both $\times 8.1$.
- j,k. Calostylopsis sakalavensis* from Ambaraminga, Madagascar, Early Cretaceous (Albian), MNHN M05021: *j*, side view of holotype, $\times 3.5$; *k*, holotype (bottom left) and three paratypes, $\times 2.2$.

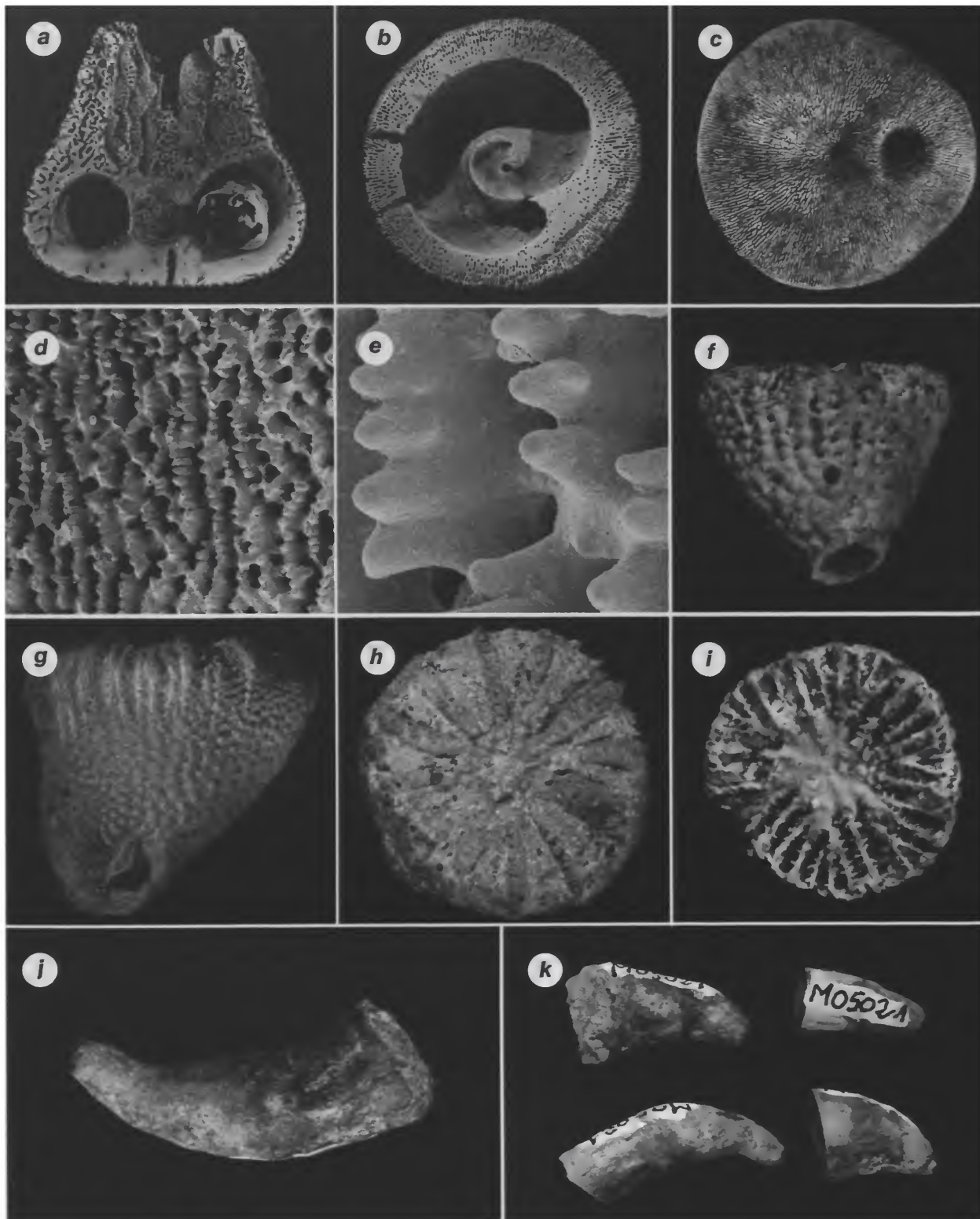


PLATE 4

- a. Calostylopsis sakalavensis* from Ambaraminga, Madagascar, Early Cretaceous (Albian), MNHN M05021, calicular view, $\times 6.8$.
- b-e. Bathypsammia tintinnabulum*: *b,c*, lectotype, off Florida, 183–549 m, MCZ 2768, side and calicular views, $\times 6.8$, $\times 3.5$, respectively. *d,e*, Albatross station 2676, $32^{\circ}30'N$, $77^{\circ}01'W$, 745 m, USNM 14569, two views showing uniformly hispid theca at border with epitheca, $\times 27$, $\times 10$, respectively.
- f-i. Pourtalopsammia togata*: *f*, Meiring Naude station SM-226, $32^{\circ}28.6'S$, $28^{\circ}58.8'E$, 710–775 m, USNM 91792, calicular view, $\times 7.9$. *g,i*, Meiring Naude station SM-232, $32^{\circ}14.9'S$, $29^{\circ}10.4'E$, 620–650 m, USNM 91791: *g,h*, two views showing uniformly hispid theca at border with epitheca, $\times 11$, $\times 25$, respectively; *i*, an elongate, vermiform corallum, $\times 2.3$.

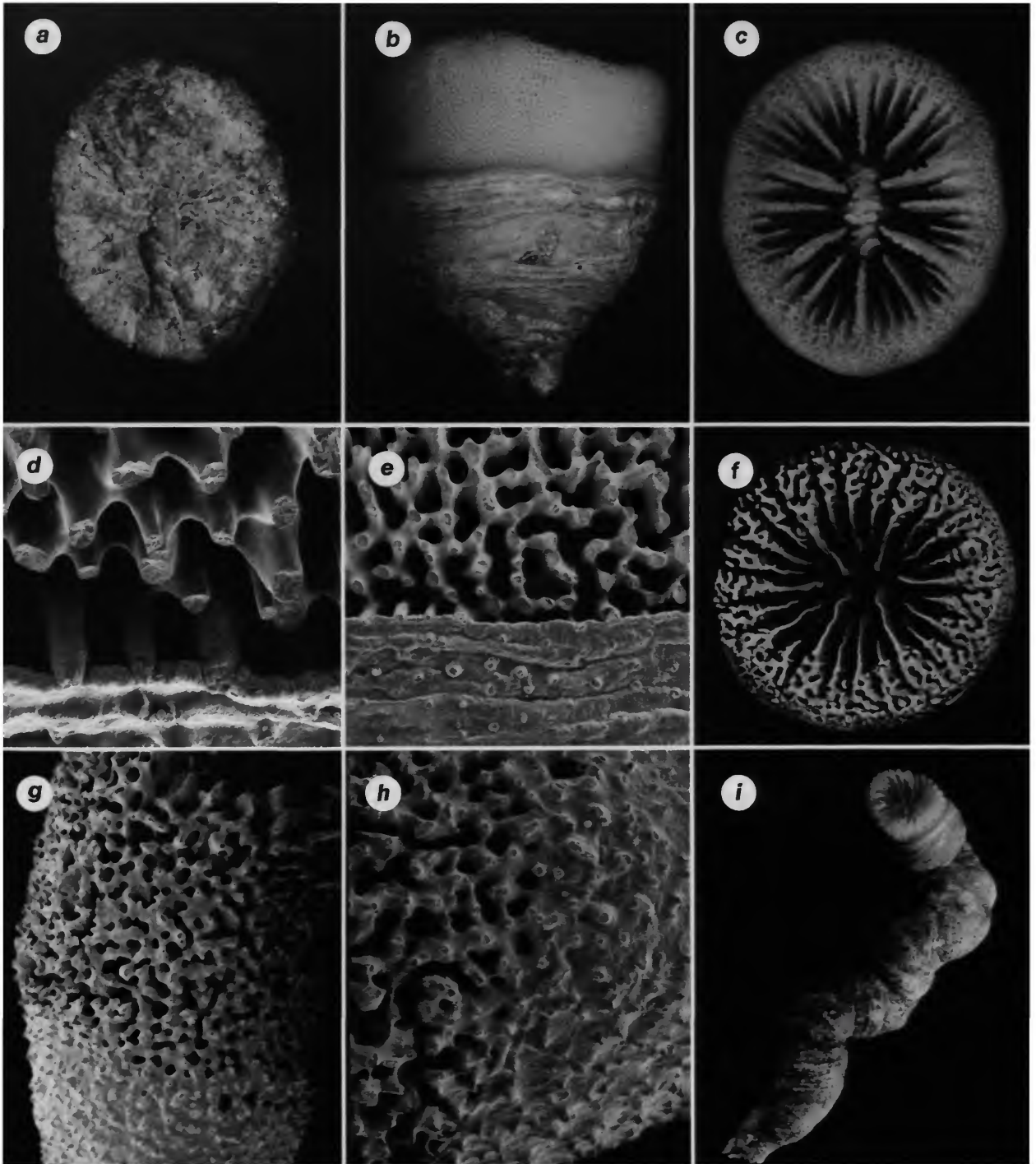


PLATE 5

- a. *Pourtalopsammia togata* from Meiring Naude station SM-226, 32°28.6'S, 28°58.8'E, 710–775 m, USNM 91792, side view showing synapcticulotheca and epitheca, $\times 6.6$.
- b–e. *Trochopsammia infundibulum*: b,c, syntype, Blake station 25, off northwestern Cuba, 1161–1472 m, MCZ 5607, side and calicular views, respectively, both $\times 5$. d,e, Gerda station 114, 24°02'N, 83°02'W, 759–869 m, USNM 46722, side and calicular views, $\times 4.5$, $\times 5.1$, respectively.
- f–i. *Endopsammia philippensis*: f, ?holotype, Philippines, BM 1855.12.77.25, calice, $\times 6.7$; g, ?holotype, Philippines, MNHN 1076, calice, $\times 7.4$. h,i, Heron Island, Queensland, 1 m, USNM 83006: h, detail of columnella and axial septal edges, $\times 15$; i, granular theca at border with epitheca, $\times 43$.
- j,k. *Leptopsammia stokesiana* from near Singapore, South China Sea (specimen figured by Searles, 1956), USNM 78603, calicular and side views of elongate corallum, $\times 4.5$, $\times 1.8$, respectively.
- l. *Leptopsammia pruvoti* from Cassis (near Marseille), France, 10 m, USNM 48414, hispid costae, $\times 36$.

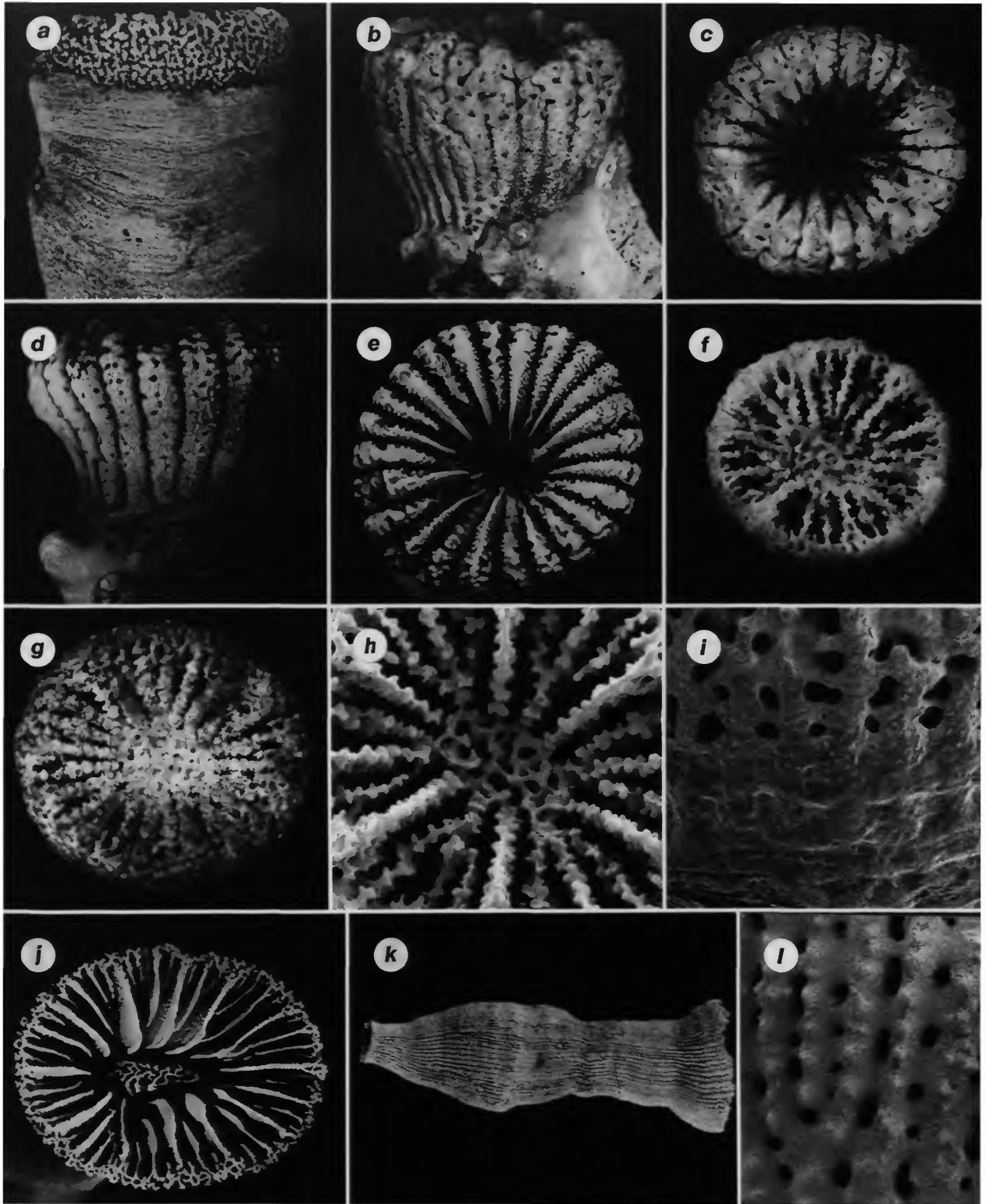


PLATE 6

- a, d.* *Leptosammia stokesiana*, holotype, Philippines, BM 1855.12.27.1, side and calicular views, $\times 3$, $\times 4.8$, respectively.
- b, e.* *Thecopsammia elongata* from *Nimbus* station 55, $26^{\circ}27'S$, $153^{\circ}50'E$, 271–273 m, USNM 78560, side and calicular views, $\times 2.5$, $\times 3.5$, respectively.
- c, f–h.* *Thecopsammia socialis*: *c.* *Eastward* station 34952, $30^{\circ}12'N$, $79^{\circ}50.1'W$, 610 m, USNM 61828, side view showing synapticulotheca and epitheca, $\times 3.2$; *f, h.* *Albatross* station 2662, $29^{\circ}25'N$, $79^{\circ}43'W$, 793 m, USNM 61832, uniformly hispid theca at border with epitheca, $\times 20$, $\times 70$, respectively; *g.* syntype, off Florida, 183–549 m, MCZ 5601, stereo calicular view, $\times 3.3$.

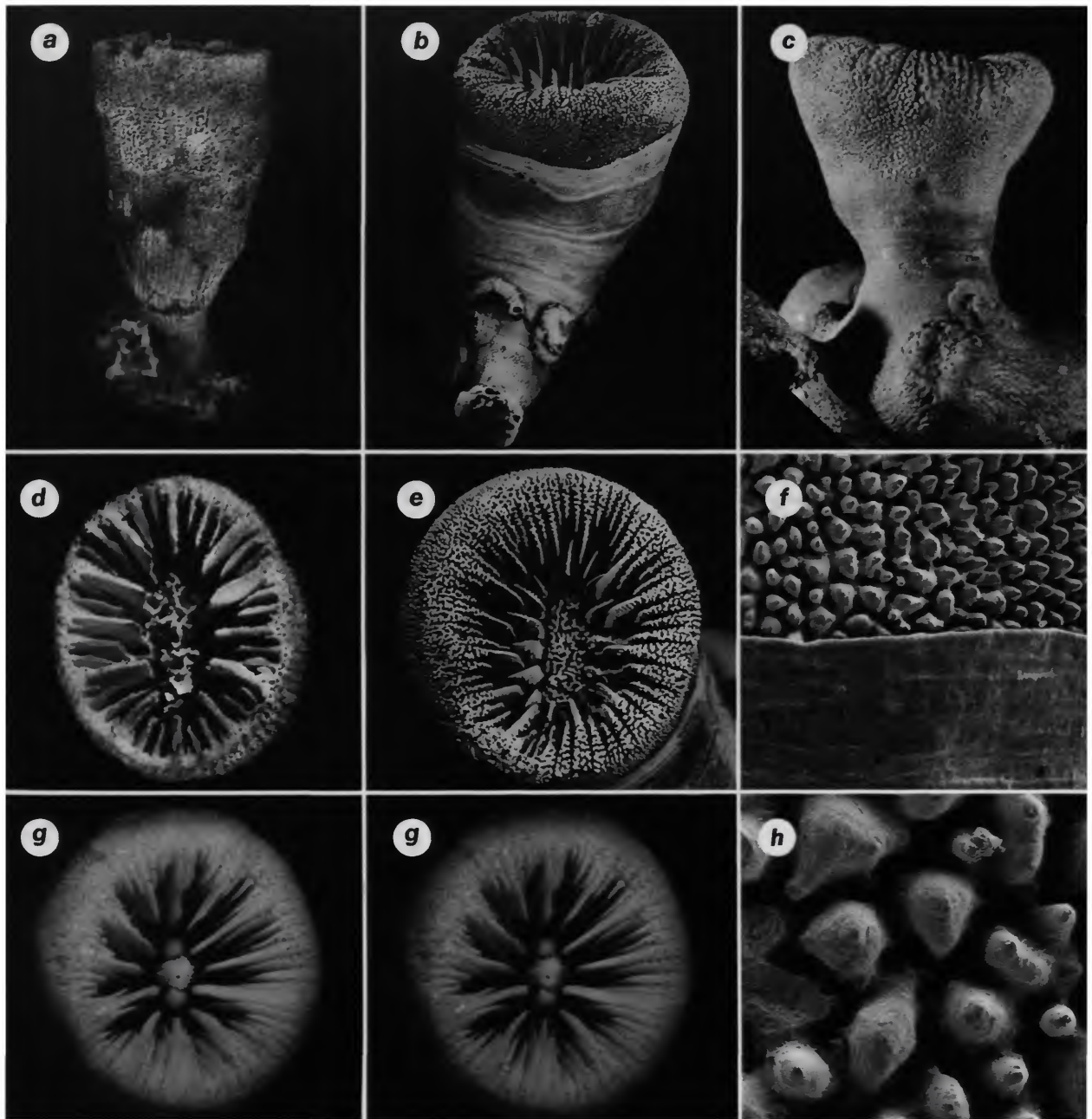


PLATE 7

- a-e. Endopachys maclurii: a,b*, USGS 2391, Claiborne, Alabama, Eocene, USNM M158412, calicular and oblique basal views of same corallum showing pronounced costal spurs, $\times 2.7$, $\times 2.5$, respectively; *c*, syntypes of *Rhectopsammia claibornensis* Vaughan, 1900, #263, Claiborne, Alabama, Eocene, USNM M158401, anthocaulus stages, $\times 5.5$; *d*, TU 923, Newton, Mississippi, Eocene (illustrated by Wells, 1975), USNM M647320, calice of extremely well-preserved corallum showing Pourtalès plan, $\times 3.2$; *e*, USGS 6087, Alabama, Eocene, USNM 66277, series of 6 coralla (anthocyathi) showing repair of basal scar, $\times 1.9$.
- f.i. Notophyllia semivestita*, holotype, Gellibrand River, Victoria, Australia, middle Miocene, NMV P27078, calicular and side views, $\times 6$, $\times 4.5$, respectively.
- g. Endopachys grayi* from Anton Bruun station 7-372L, 25°07'S, 34°34'E, 112 m, USNM 77245, hispid costae, $\times 21$.
- h. Notophyllia aperta* from Balcombe Bay, Victoria, Australia, middle Miocene (Balcombian), USNM M353586, hispid costae, $\times 48$.

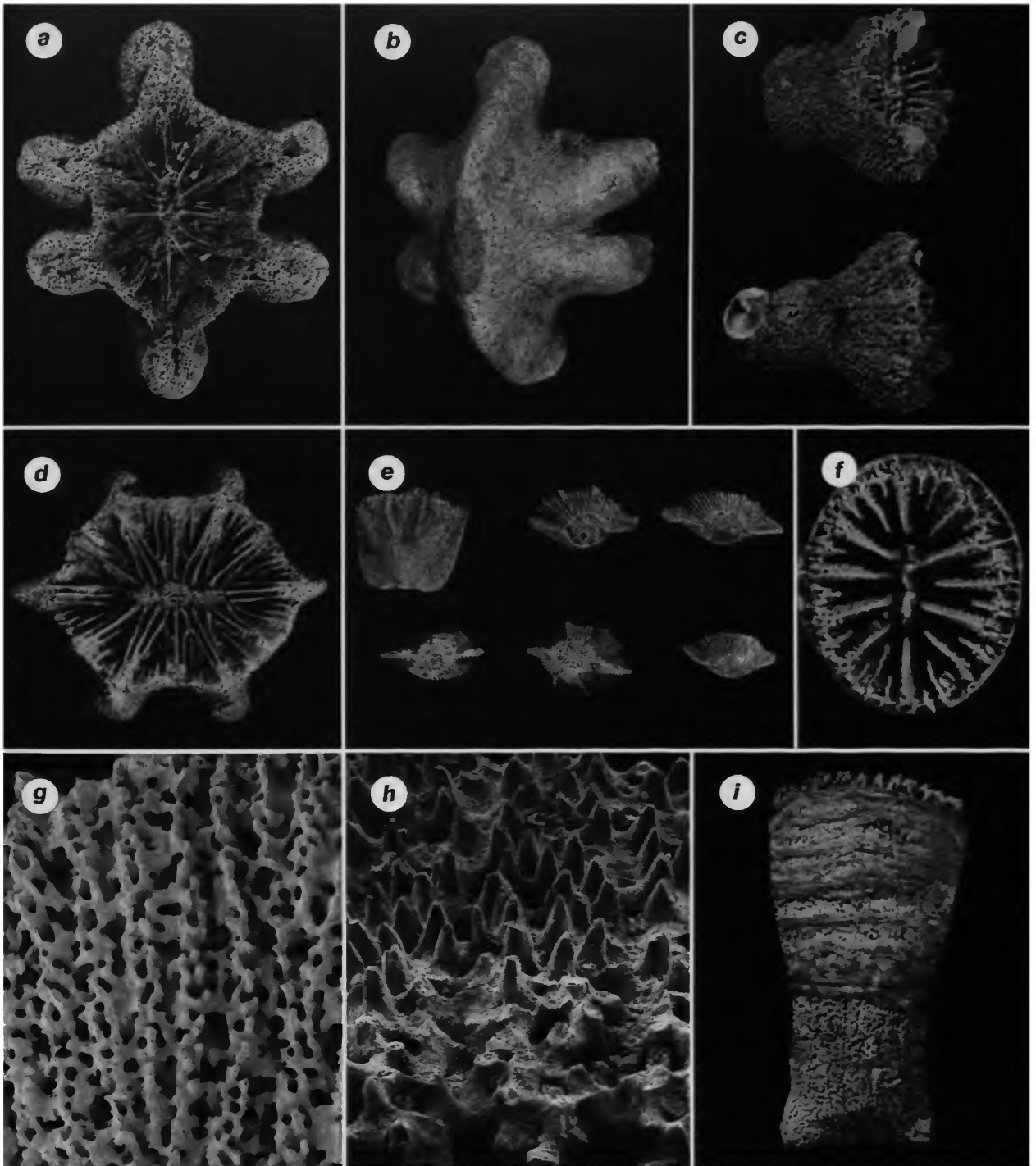


PLATE 8

- a, b.* *Notophyllia semivestita* from Grice's Creek, Victoria, Australia, middle Miocene (Balcombian), USNM M353587, side and calicular views, $\times 5.5$, $\times 6.2$, respectively.
- c-f.* *Eguchipsammia cornucopia*: *c, d*, syntype, Bibb station 173, $24^{\circ}24'N$, $81^{\circ}52'W$, 220 m, MCZ 2752, side and calicular views of same corallum, $\times 0.9$, $\times 2.7$, respectively; *e, f*, off Western Dry Rocks, Florida Keys, 263 m, USNM 62318, enlargements of hispid costae, $\times 60$, $\times 90$, respectively.
- g, h.* *Rhizopsammia pulchra*, holotypic colony from Pearl Islands, Gulf of Panama, YPM 5375, two views of reptoid colonies, $\times 2.8$, $\times 3.1$, respectively.
- i.* *Rhizopsammia annae* from Anton Bruun station 7-391J, $29^{\circ}21'S$, $31^{\circ}35'E$, 57 m, USNM 91790, small reptoid colony, $\times 3.3$.

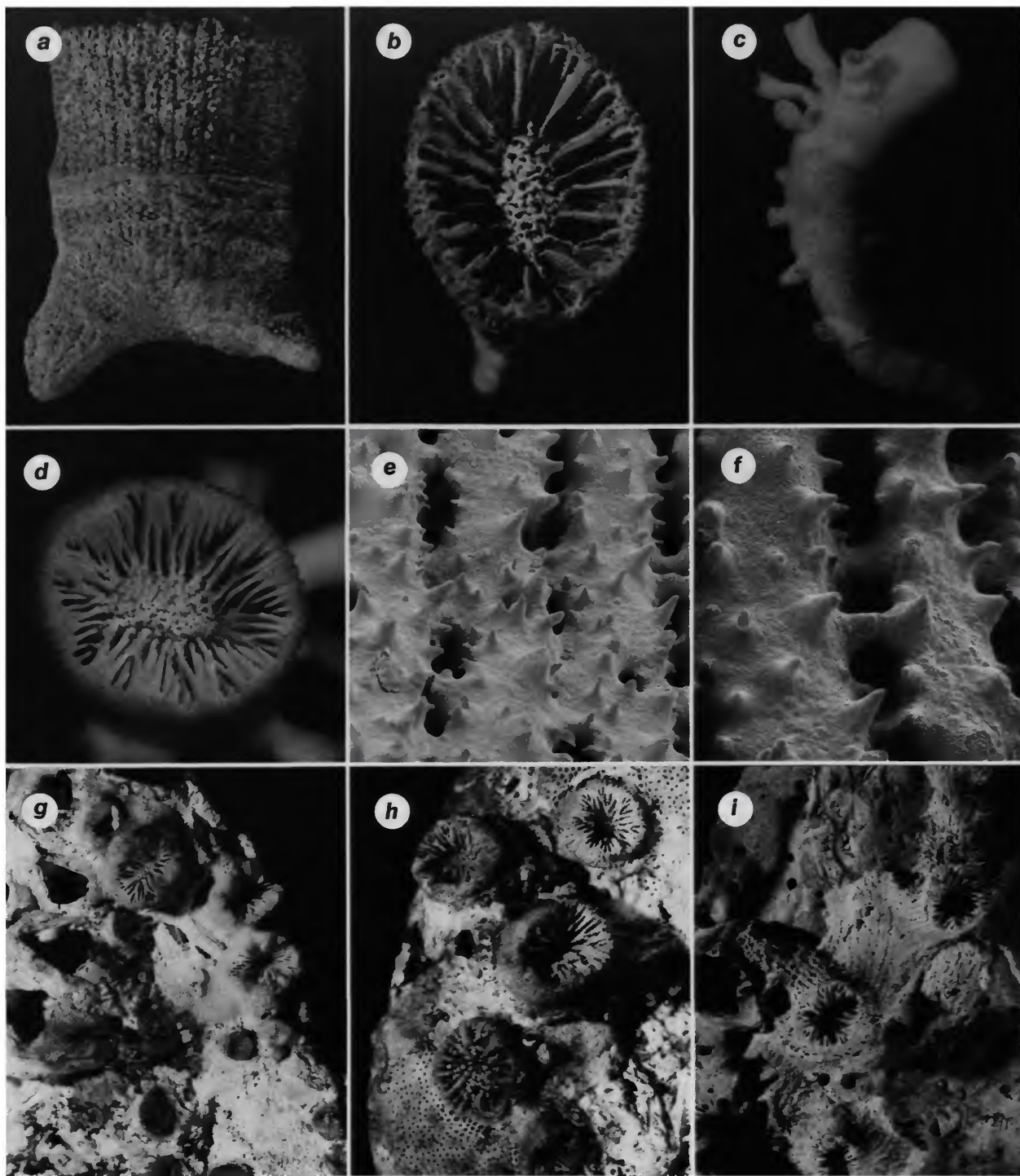


PLATE 9

- a, b.* *Rhizopsammia compacta*, Meiring Naude station ZA-49, 25°54.3'S, 32°55.5'E, 45 m, USNM 91799, views of granular costae, $\times 39$, $\times 150$, respectively.
- c, e, f.* *Cladopsammia rolandi*: *c, f.* 37°19.2'N, 11°02.5'E, 30 m, USNM 48468: *c.* granular costae, $\times 28$; *f.* small colony, $\times 1.1$. *e.* Zembra Island, Tunisia, 15 m, USNM 78764, calicular view, $\times 7.5$.
- d.* *Cladopsammia* sp. from Red Crag, Suffolk, England, late Pliocene, BM (Paleontology) 55642, small colony, $\times 1.7$.
- g-j.* *Paleoastroides michelini*, holotype, Touraine, France, middle Miocene (Helvetian), MNHN R8466: *g.* entire corallum, $\times 0.85$; *h.* two corallites, $\times 2.5$; *i.* intratentacular budding, $\times 3.3$; *j.* tabular endothecal dissepiments, $\times 2.5$.

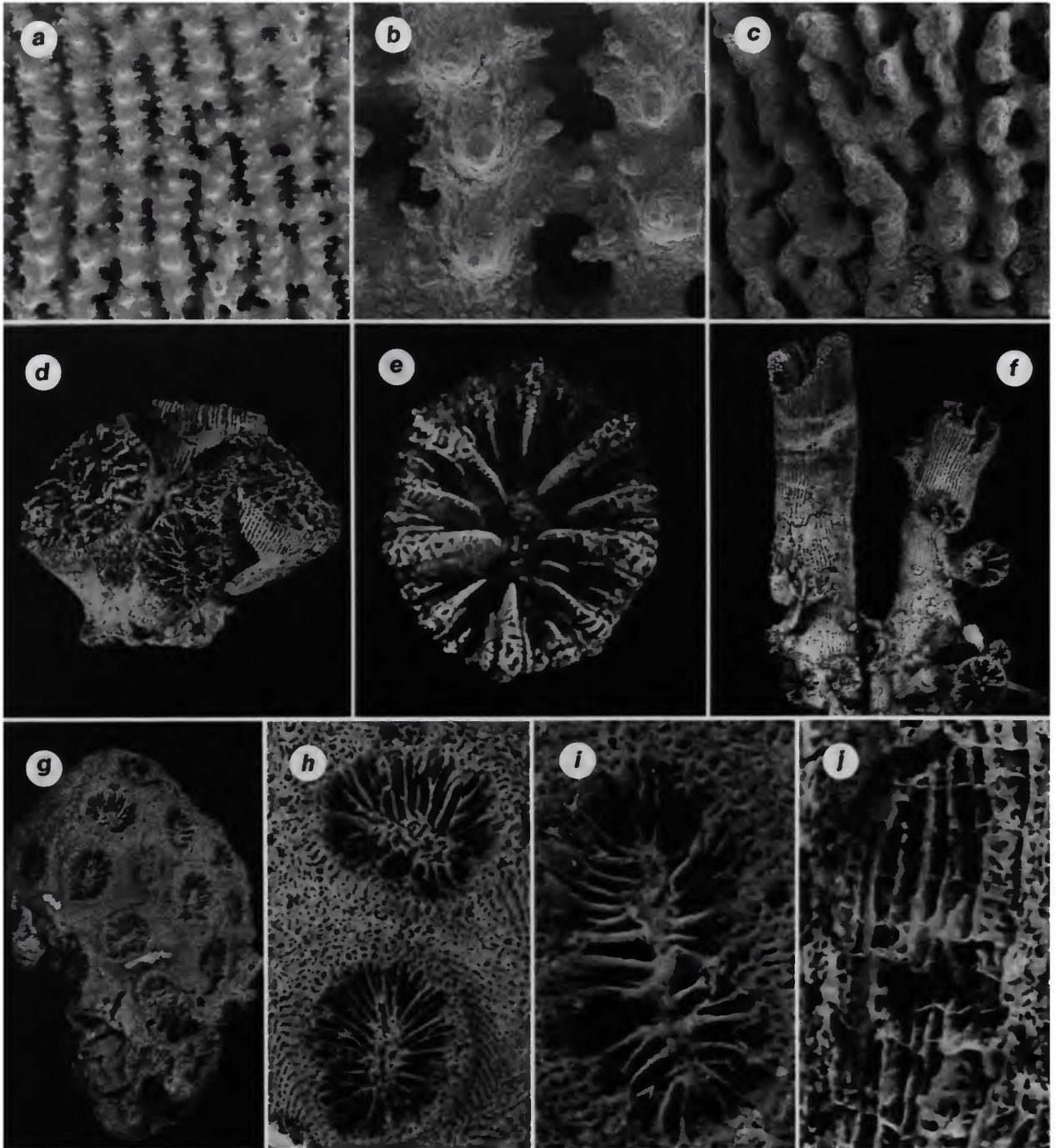


PLATE 10

- a-h. Astroides calycularis*: *a-e*, off Zembra Island, Tunisia, 3 m: *a*, USNM 78767, cerioid corallum, $\times 1.5$; *b*, USNM 78765, longitudinal section through colony revealing tabular endothecal dissepiments, $\times 2.3$; *c*, USNM 48459, calicular view, $\times 11$; *d,e*, USNM 48459, two views of hispid costae, $\times 12$, $\times 48$, respectively. *f-h*, Tabarka, Tunisia, 14 m, USNM 48460: *f*, juvenile corallite showing Pourtalès plan, $\times 15$; *g*, corallite with well-developed epitheca, $\times 13$; *h*, border of epitheca and synapticulotheca, $\times 70$.
- i-l. Tubastraea coccinea*: *i,j*, Atimaono Bay, Tahiti (topotypic), 7 m, USNM 83660: *i*, granular costae, $\times 37$; *j*, small colony, $\times 1$. *k*, Bartolomé, Galápagos, 20–27 m, USNM 46973, several corallites, $\times 2.9$. *l*, holotype of *Tubastraea tenuilamellosa*, Panama, MNHN 1062, several corallites, $\times 2.2$.

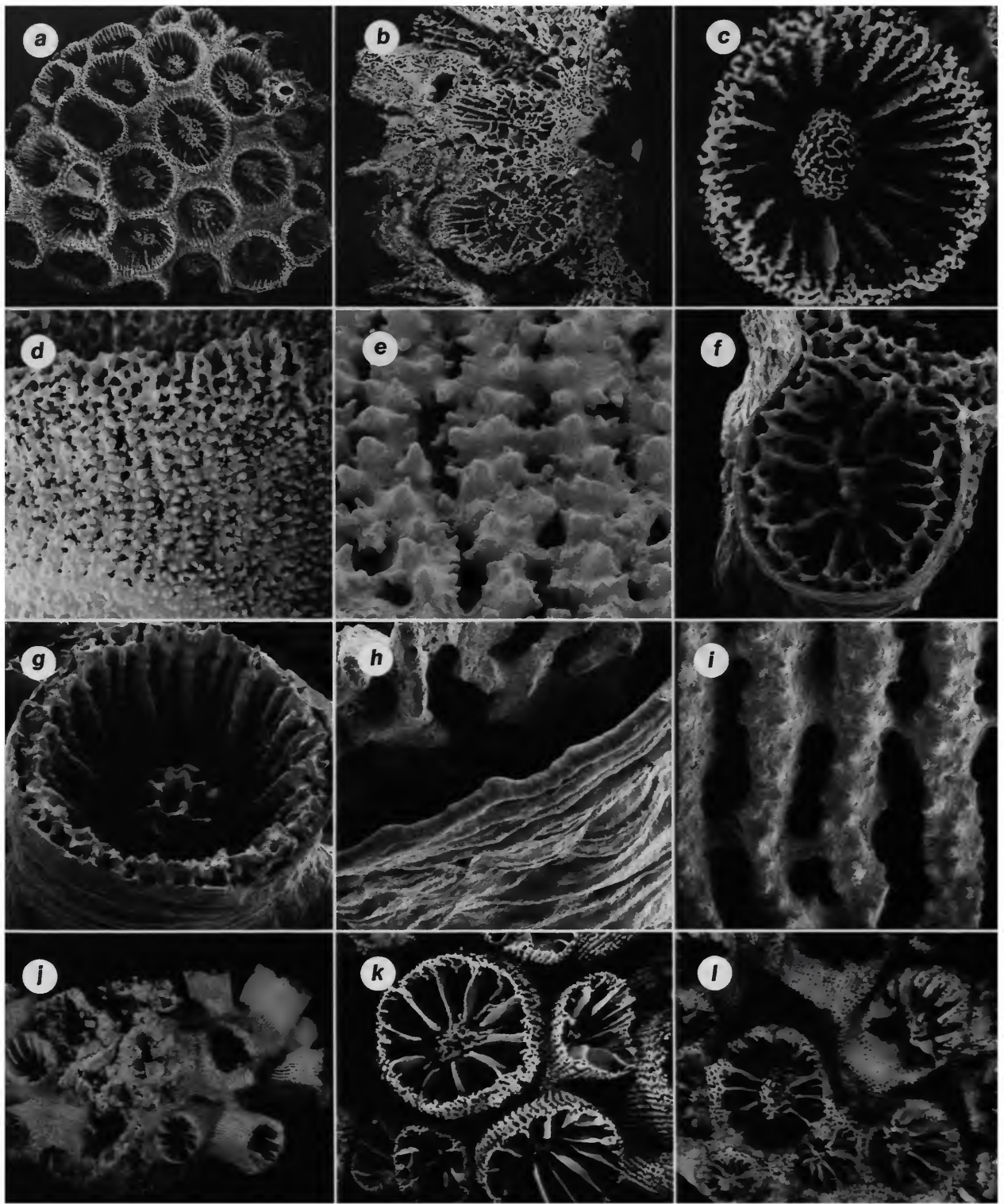


PLATE 11

- a-c, e, f.* *Turbinaria* sp. cf. *T. crater*: *a, b*, Palau Perhentians, Malaysia, 15 m, USNM 83733, side and top view of small colony, respectively, both $\times 1.0$. *c, e, f*, Heron Island, Queensland, Australia, USNM 83627: *c*, general aspect of coenosteum and two corallites, $\times 13$; *e*, longitudinal fracture through colony showing orientation of corallites, $\times 3.2$; *f*, detailed view of hispid ridges, $\times 71$.
- d.* *Turbinaria peltata* from Eil Malk, Palau, 6 m, USNM 47144, two corallites with well-developed columellas, $\times 4.7$.
- g-j.* *Dendrophyllia ramea*, Pillsbury station 30, $4^{\circ}45'N$, $2^{\circ}33'W$, 61–64 m, USNM 48497: *g*, small colony, $\times 0.7$; *h*, calice showing Pourtalès plan, $\times 4$; *i, j*, two views of hispid costae, $\times 22$, $\times 77$, respectively.
- k.* *Enallopsammia laddi*, USGS 24686, Tonga, Eocene (topotypic), USNM 1251796, best preserved corallite from type locality, showing slightly enlarged septocosta, $\times 16$.
- l.* *Enallopsammia rostrata*, Albatross station 3827, off Molokai, Hawaiian Islands, 583–679 m, USNM 60600, corallite with distinctly enlarged septocosta, $\times 15$.

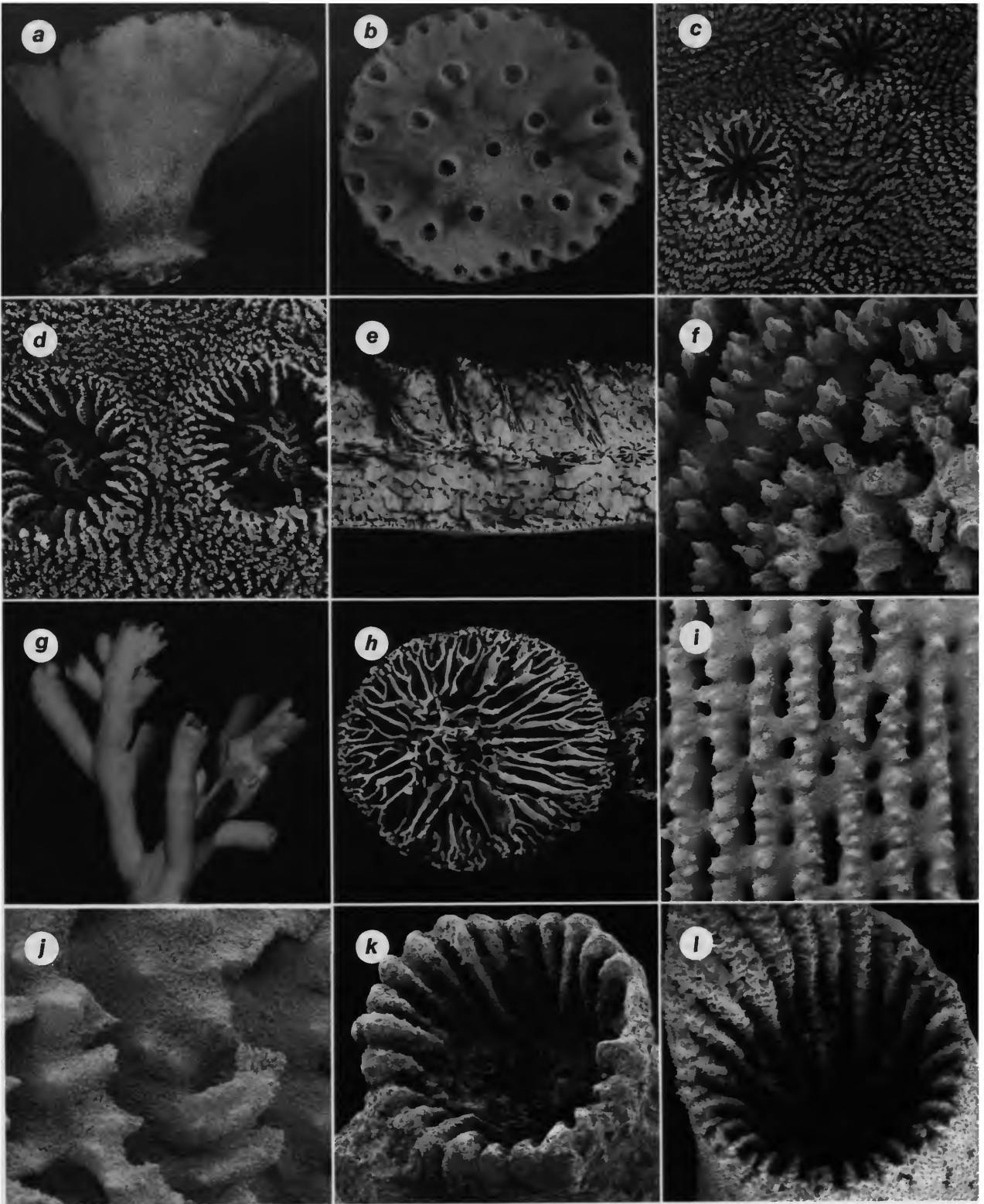


PLATE 12

- a, b. Enallopsammia scillae*, syntypes from Rometto, Messina, Italy, Miocene, NHMW 1864-XXI-240: *a*, two corallites with rostra, $\times 3.2$; *b*, costae on posterior side of branch, $\times 2.5$.
- c. Enallopsammia laddi*, USGS 24686, Tonga, Eocene (topotypic), USNM 1251796, well-developed costae on posterior (acalicular) side, $\times 6$.
- d, e. Enallopsammia rostrata*, NZOI P-8, $32^{\circ}40.8'S$, $167^{\circ}26.8'E$, 757–660 m, USNM 94206, two views of hispid costae, $\times 200$, $\times 80$, respectively.
- f–i. Duncanopsammia axifuga*, Port Newry, Queensland, Australia: *f*, USNM 83501, apical view of part of small colony, $\times 0.45$; *g*, USNM 85997, corallite with well-developed columella, $\times 5$; *h, i*, USNM 85997, serrate costal ridges, $\times 30$, $\times 115$, respectively.
- j–m. Dichopsammia granulosa*, Pusan, Korea, depth unknown: *j*, holotype of *Schizopsammia songae*, USNM 15847, part of corallum showing two examples of intratentacular budding, $\times 2.4$. *k–m*, paratype of *S. songae*, Pusan, Korea, depth unknown, USNM 92910: *k*, intratentacular budding, $\times 4.6$; *l*, longitudinal fracture revealing endothecal dissepiments, $\times 3.7$; *m*, granular costae, $\times 30$.

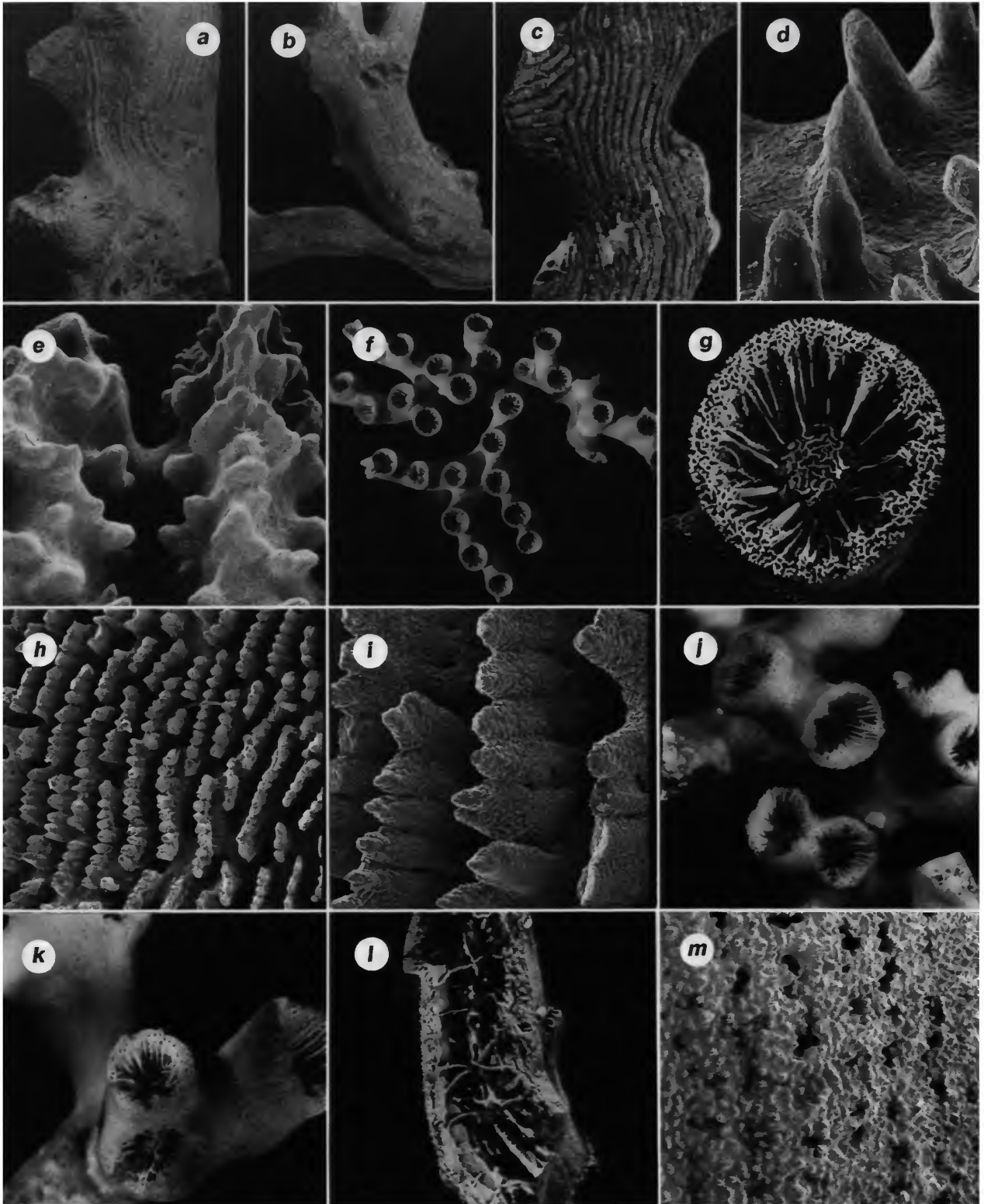


PLATE 13

- a-c. Lobopsammia cariosa*: *a*, Le Fayal (Seine-et-Oise), France, Eocene, USNM 64630, colony, $\times 1.6$. *b,c*, Auvers-sur-Oise (Seine-et-Oise), France, middle Eocene (Bartonian), USNM 180277: *b*, intratentacular budding, $\times 8.4$; *c*, costae, $\times 7.3$.
- d,e. Stichopsammia* sp., Legoufre, Seine-et-Mame, France, middle Eocene (Bartonian), USNM 93199, calicular view and costae of same specimen, $\times 5.4$, $\times 6.2$, respectively.
- f,h. Aplopsammia collignoni*, paratype, Ambaramanina, Madagascar, Early Cretaceous (Albian), MNHN M05014, side and calicular views of same corallum, $\times 4.2$, $\times 8$, respectively.
- g. Stereopsammia humilis*, holotype, Bracklesham Bay, England, middle Eocene (Bartonian), BM (Paleontology) 49580, stereo view of remnant of holotype, $\times 5.3$.
- i-k. Rhabdopsammia lunquinei*, holotype, Provence, France, Late Cretaceous, MNHN R10960: *i*, calicular view, $\times 2.0$; *j,k*, side views, both $\times 2.3$.

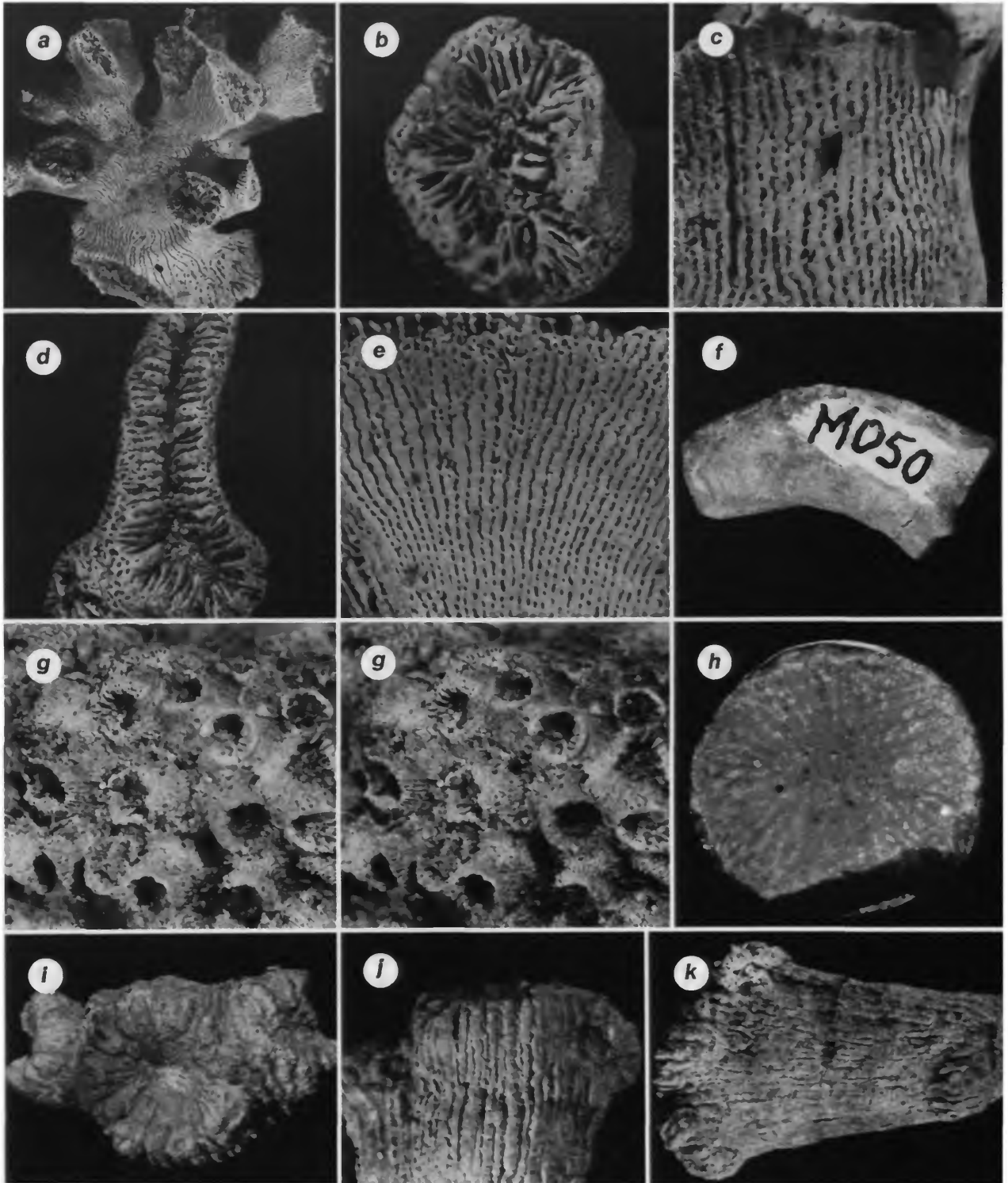
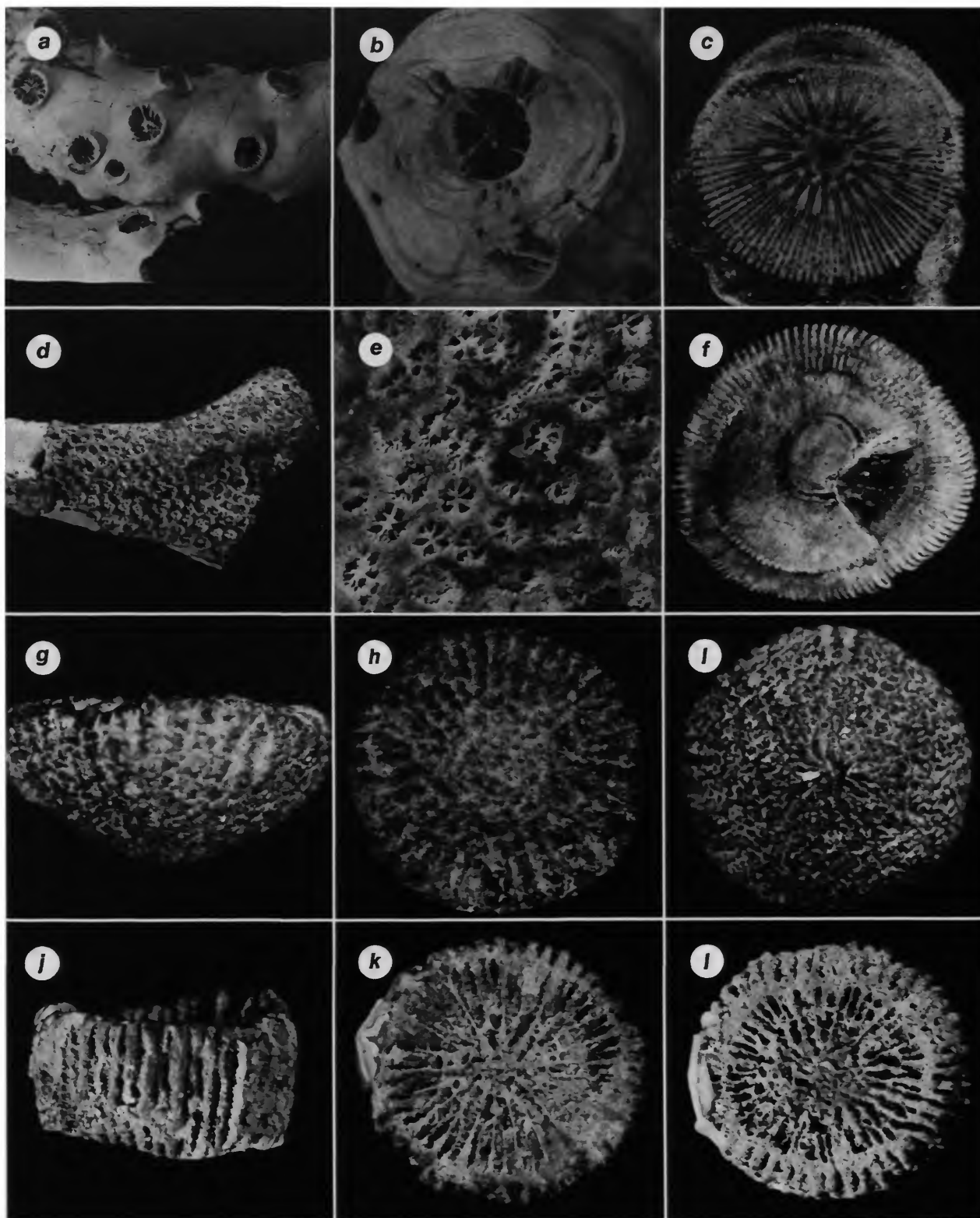


PLATE 14

- a, b.* *Petrophyllia arkansensis*, holotype, White River, Arkansas, Eocene, Academy of Natural Sciences, Philadelphia, 30718: *a*, branch, $\times 1.9$; *b*, cross-section of axial corallite, $\times 3.7$.
- c, f.* *Patelopsammia gurraui*, Puebla de Fontora, northeastern Spain (topotypic), middle Eocene (Lutetian), USNM 100169: *c*, transverse section, $\times 2.8$; *f*, base, $\times 3$.
- d, e.* *Turbinacis erythraeensis*, holotype, Somaliland, Pleistocene, BM (Paleontology) R5026: *d*, whole corallum, $\times 2.1$; *e*, enlargement of corallites, $\times 9.5$.
- g-i.* *Kumbiopsammia besairiei*, holotype, Ampasindava, Madagascar, Late Cretaceous (Maastrichtian), MNHN M05080: side, calicular, and basal views, $\times 8.5$, $\times 7.4$, $\times 7.4$, respectively.
- j-l.* *Ilerdopsammia eduardi*, holotype, Torallola (Lleida), northeastern Spain, Late Cretaceous (Campanian), Museo Geológico del Seminario de Barcelona (uncataloged): side, calicular, and basal views, $\times 4.2$, $\times 4.8$, $\times 4.8$, respectively.



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