

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

STEPHEN D. CAIRNS

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A B S T R A C T

Cairns, Stephen D. A Generic Revision and Phylogenetic Analysis of the Turbinoliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*, number 591, 55 pages, 5 figures, 10 plates, 6 tables, 1997.—The monophyly of the Turbinoliidae is based on the unique (within the Caryophylliina) character of having its entire corallum invested with tissue, which is reflected in its well-formed costae from base to calice and its characteristically deep intercostal regions. All turbinoliids are solitary and free-living, and thus the complete investiture of its corallum might facilitate movement through or across a sandy substrate.

The Turbinoliidae consists of 28 genera and 163 valid species, of which 22 genera and 49 species are extant. The earliest known turbinoliid is from the Late Cretaceous (Campanian) of Antarctica. All 28 genera are diagnosed and figured herein. The stratigraphic and geographic distributions are discussed for each genus, and a list of species known for each genus, including junior synonyms, is given. Two genera and two species are described as new: *Pleotrochus*, *P. zibrowii*, *Foveolocyathus*, and *Sphenotrochus wellsi*. *Peponocyathus* is restricted to those species having transverse division, which requires the resurrection of *Deltocyathoides* Yabe and Eguchi, 1932, for those species that do not reproduce by transverse division, and it also requires the synonymy of *Truncatocyathus* Stolarski, 1992. *Tropidocyathus* is divided into two genera, allowing the resurrection of *Cyathotrochus* Bourne, 1905. *Oryzotrochus stephensi* Wells, 1959, is identified as a *Turbinolia*, which synonymizes *Oryzotrochus* and extends the stratigraphic range of *Turbinolia* from the Oligocene to Recent.

Phylogenetic analysis of the 28 turbinoliid genera was carried out using 16 characters, comprising 49 character states. Relationships among taxa were determined based on parsimony and successive weighting of characters. Subfamilies of the Caryophylliidae were used as outgroups. Characters that contributed highly to the phylogenetic hypothesis were costal ornamentation, costal origination, and septal number. Characteristics of thecal structure (i.e., imperforate, externally pitted, perforate) were re-examined in all genera. The resulting phylogenetic hypothesis (Figure 2) suggests that the turbinoliids are divided into two major clades. One (clade 2) contains 12 genera including all six Late Cretaceous Antarctic genera, as well as genera first recorded from the Eocene of New Zealand and Oligocene of South Australia. Coralla of this clade are characterized by having trifurcate costal origination and serrate costal ornamentation. The other major clade (clade 3) contains 14 genera, including one from the Late Cretaceous of New Zealand, five with first occurrences in the Paleocene to Miocene of Europe and North America, and three from the Eocene to Oligocene of South Australia. These are genera characterized by coralla with less than 48 septa and granular or smooth costae. It is cautioned that the results of this analysis are considered preliminary, as it is based exclusively on skeletal characters. Consequently, clades are not highly supported, nonetheless, this analysis suggests which skeletal characters should be examined more carefully in the future, and it serves as a comparison for future analyses that might include tissue and/or molecular characters. The status of the Early Cretaceous genus *Platytrochopsis* Sikharulidze, 1975, is also discussed.

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Introduction

The Turbinoliidae is one of twelve scleractinian families that includes azooxanthellate species, and one of seven that exclusively contains azooxanthellate species (Table 1). Among the twelve families, it ranks fourth in Recent species richness (49 species, or 7.9% of the Recent azooxanthellate species) and second in genus richness (22 genera, or 19.1% of the Recent azooxanthellate genera), resulting in an average of 2.2 species per genus, which is relatively low compared to the overall azooxanthellate average of 5.37. However, the known geologic range of Turbinoliidae begins in the Cretaceous, and at least an additional 114 species and 6 genera are known from the fossil record, resulting in a total of 163 valid species and 28 genera within the family, and an average of 5.82 species per genus.

Their small size and apparent interstitial habit within sandy substrates at lower shelf to upper slope depths have resulted in the collection of relatively few turbinoliid specimens. However, more recent, exhaustive deep-water collections (e.g., MUSORSTOM, KARUBAR, NZOI, ORI) have shown that turbinoliids are common in the upper slope environment, sometimes occurring in high numbers and diversity, especially in regions such as the Banda Sea (Cairns and Zibrowius, 1997) and the Philippines (Cairns, 1989a).

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

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Museums, Collecting Institutions, Expeditions

BMNH	The Natural History Museum, London (formerly the British Museum (Natural History))
DEKI	Danish Expedition to the Kei Islands
KARUBAR	A French expedition (1991) that collected in the southeastern Banda Sea, specifically the Kei, Aru, and Tanimbar islands.
MNHN	Muséum National d'Histoire Naturelle, Paris
MUSORSTOM	Muséum National d'Histoire Naturelle and Office de la Recherche Scientifique et Technique d'Outre-Mer
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NZOI	New Zealand Oceanographic Institute, Wellington
ORI	Ocean Research Institute, University of Tokyo, Tokyo
TIUS	Institute of Geology and Paleontology, Tōhoku (Imperial) University, Japan
USNM	United States National Museum, Washington, D.C. (now the National Museum of Natural History)
ZMA	Zoölogisch Museum, Amsterdam
ZMK	Zoologisk Museum, Kobenhavn

Morphological Terms

c:s	Ratio of number of costae to septa
CD	Calicular diameter
GCD	Greater calicular diameter
GCD:LCD	Ratio of greater calicular diameter to lesser calicular diameter
Sx, Cx, Px	Septa, costae, or pali/paliform lobes (respectively) of cycle designated by numerical subscript
Sx > Sy	Septa of cycle x broader than those of cycle y

Other Abbreviations

CI	Consistency index
DPE	The subfamilies Desmophyllinae, Parasmiliinae, and Eusmiliinae
PAUP	Phylogenetic Analysis Using Parsimony (see Swofford, 1991)
RCI	Rescaled consistency index
SEM	Scanning electron microscopy
WA	Western Australia

TABLE 1.—Number of Recent azooxanthellate species and genera by family. An asterisk indicates that the family is composed of exclusively azooxanthellate species. A complete list of species names is on file with the UNESCO-IOC Register of Marine Organisms and is available on request from the author.

Families	Number of Recent species	Number of Recent genera	Average number species/genus
Caryophyllidae	238	38	6.3
Dendrophylliidae	136	18	7.6
*Flabellidae	91	11	8.3
*Turbinoliidae	49	22	2.2
*Rhizangiidae	31	4	7.8
*Fungiacyathidae	18	1	18.0
Oculinidae	14	7	2.0
*Micrabaciidae	14	4	3.5
Pocilloporidae	11	1	11.0
*Guynidae	7	7	1.0
*Anthemiphylliidae	5	1	5.0
Faviidae	2	1	2.0
Incertae Sedis	1	-	-
TOTAL	617	115	5.37

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Phylogenetic Analysis

METHODS

Although several phylogenetic analyses have been performed on groups of Scleractinia (Cairns, 1984; Hoeksema, 1989, 1991, 1993a; Wallace et al., 1991; Pandolfi, 1992), none have been performed on groups within the Caryophyllidae or even the suborder Caryophyllina. Therefore, to determine appropriate outgroups for the Turbinoliidae, a preliminary phylogenetic analysis was first performed on the higher level taxa within the superfamily Caryophylloidea, i.e., the five subfamilies of the Caryophyllidae (the colonial rhipidogyrids were not considered to be a likely sister group). The second analysis included all 28 genera of the Turbinoliidae. The two analyses used different characters and data sets (see Tables 2–5) and are discussed separately below. Phylogenetic trees were generated based on the principle of parsimony using PAUP (Swofford, 1991), and character evolution of these phylogenetic trees was further analyzed using MacClade (Maddison and Maddison, 1992). Characters were coded as binary variables (0, 1) or as multistate characters (0, 1, 2, ...), the 0 state reflecting the presumed ancestral condition. All

multistate characters were treated as unordered unless otherwise stated in the character discussions (e.g., character 15, edge zone).

ANALYSIS OF OUTGROUPS.—The five caryophylliid subfamilies that could be considered as a possible sister group and successive outgroups to the Turbinoliidae are the Thecocyathinae, Caryophyllinae, Desmophyllinae, Parasmiliinae, and the Eusmiliinae. Although there has been no phylogenetic analysis of the higher taxa of the Caryophylloidea, there is general agreement (Vaughan and Wells, 1943; Chevalier, 1987) that the Thecocyathinae is the ancestral group from which the other caryophylliid lines evolved. This interpretation is consistent with the geologic ranges of the groups, the Thecocyathinae first occurring in the Early Jurassic, whereas the first occurrences of the other higher taxa are progressively later: Caryophyllinae and Desmophyllinae (Late Jurassic), Parasmiliinae (Early Cretaceous), Turbinoliidae (Late Cretaceous), and Eusmiliinae (Oligocene). Thus, by the criterion of geological character precedence (Wiley, 1981), the character states found in the Thecocyathinae were considered to be ancestral (Tables 2, 3). Furthermore, the three character states of character 2 (endotheca) were ordered based on the ontogenetic argument that endotheca must have proceeded from an ancestral state of being absent through an intermediate state of being weakly developed to the fully derived state of being well developed. The same

TABLE 2.—Characters used in the phylogenetic analysis of the caryophylliid subfamilies (outgroups) and Turbinoliidae as presented in Table 3 and Figure 1. Values in parentheses are the consistency indices for the characters.

Character	Character states
1. Theca (1.0)	0, epithecate 1, septothecate
2. Endotheca (1.0)	0, absent 1, weakly developed 2, well developed (character states ordered)
3. Edge Zone (0.75)	0, narrow 1, moderate 2, well developed 3, complete investiture (character states ordered)
4. Coloniality (1.0)	0, solitary 1, colonial
5. Budding (1.0)	0, budding does not occur 1, extratentacular 2, intratentacular
6. Corallum Attachment (1.0)	0, attached 1, unattached
7. Pali (1.0)	0, present 1, absent
8. Transverse Division (1.0)	0, absent 1, present

TABLE 3.—Character matrix used for phylogenetic analysis of caryophylliid subfamilies and Turbinoliidae, as illustrated in Figure 1. Character numbers refer to those described in Table 2. Polymorphic states are symbolized accordingly: $0+1 = a$; $1+2 = b$.

Taxa	Characters							
	1	2	3	4	5	6	7	8
Thecocystiniae	0	0	0	0	0	0	0	0
Caryophylliinae	1	0	1	0	0	a	a	a
Desmophylliinae	1	1	1	a	b	0	1	0
Parasmiliinae	1	2	1	a	b	0	1	0
Eusmiliinae	1	2	2	1	2	0	1	0
Turbinoliidae	1	0	3	0	0	1	a	a

logic was applied to order the multiple states of character 3 (edge zone).

The phylogenetic analysis performed at the family to subfamily levels scored eight characters consisting of 11 character states (Tables 2, 3) and was run using the exhaustive search algorithm of PAUP. It resulted in three equally parsimonious trees, each tree having 18 steps and a CI of 0.944. However, the sister-group relationship of the Turbinoliidae is different in each alternative; in one tree it is the Caryophylliinae; in another tree, the Turbinoliidae diverge from the stem that leads to the Desmophylliinae, Parasmiliinae, and Eusmiliinae; and in the third tree the Turbinoliidae is the sister group to the stem that leads to the Caryophylliinae, Desmophylliinae, Parasmiliinae, and Eusmiliinae. The strict consensus of the three alternative trees is illustrated as Figure 1. Although this analysis did not lead to an unequivocal sister group for the Turbinoliidae, all three trees did unite Desmophylliinae, Parasmiliinae, and Eusmiliinae (abbreviated DPE) in a monophyletic unit, with the Caryophylliinae in a variable position. Therefore, DPE was subsequently treated as one group whereas the diverse Caryophylliinae was "decomposed" into five subgroups (Caryophylliinae A-E), such that each group of genera would have monomorphic character states for the eight characters used in the analysis. For example, Caryophylliinae A includes genera that are attached, have pali, and do not have transverse division (Table 1: characters 6:0, 7:0, 8:0), e.g., *Trochocystus* and *Vaughanella*. Then all seven of these groups (i.e., the Thecocystiniae, Caryophylliinae A-E, and the stem leading to subfamilies DPE) were included in the phylogenetic analysis of the turbinoliid genera. The inclusion of these outgroups in the turbinoliid generic analysis required the addition of five character states not found in the Turbinoliidae (noted in Table 3) and resulted in outgroups that were highly polymorphic for several characters that were only meant to be used to distinguish turbinoliid genera.

ANALYSIS OF THE TURBINOLIID GENERA.—Sixteen characters, consisting of 49 character states, were scored for the phylogenetic analysis of the 28 turbinoliid genera (Tables 4, 5). Thirteen of the 16 characters used in the analysis were qualitative, only three (characters 12, 14, and 15) being

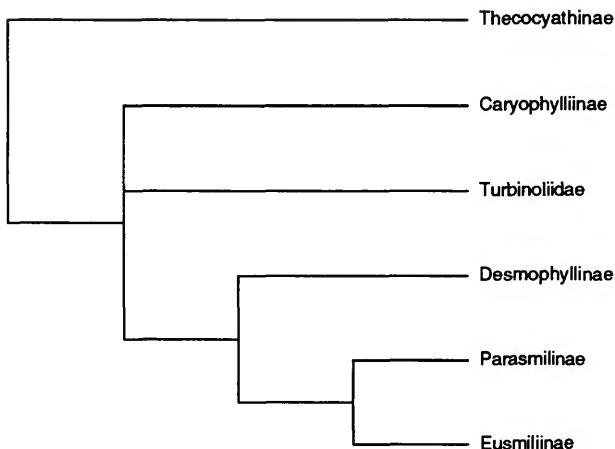


FIGURE 1.—Strict consensus cladogram of caryophylliid outgroups and the Turbinoliidae.

quantitative. All characters used related to the corallum, because six of the 28 genera are known only as fossils. Furthermore, living turbinoliids are rarely collected, and alcohol-preserved specimens are even rarer, making histology, molecular, and nematocyst analyses impractical to impossible at this time.

A phylogenetic hypothesis about relationships within the group was generated using PAUP. A heuristic search was carried out using a simple stepwise addition sequence followed by branch swapping using the tree bisection-reconnection procedure (TBR). The heuristic search without character weighting resulted in 5876 equally parsimonious trees. To reduce that number, successive weighting (Farris, 1969; Carpenter, 1988) was employed. This procedure reduced the number of trees for consideration by an a posteriori weighting of characters based on the rescaled consistency indices of each character. The adjusted weights for all 16 characters are given in Table 4.

The following characters were used in the analysis.

Character 1: Exterior Thecal Pits. Because the theca of all turbinoliids is completely invested with tissue, costae are well developed from the base to the calice, and the intercostal regions are usually quite deeply recessed. In most turbinoliids this deep intercostal region is relatively flat or smooth, as in most other scleractinians, but in several genera there is an alignment of regularly spaced shallow, circular pits in each intercostal furrow. The pits do not penetrate the theca and are usually easily visible with a stereomicroscope (Plate 8b). In the genus *Turbinolia* a double series of alternating pits occurs in each intercostal region (Plate 8c). The ancestral condition of this character is considered to be the absence of pits; this condition is found in all seven outgroups. The states of having one row or two rows of pits are considered derived but are not ordered. Two other thecal modifications occur in the turbino-

TABLE 4.—Characters used in the phylogenetic analysis of the turbinoliid genera and outgroups, as presented in Table 5 and Figures 2–4. Values in parentheses are the consistency indices for each character as expressed for the tree illustrated in Figure 3, followed by the weight of that character as determined by successive weighting.

Character	Character states
1. Exterior Thecal Pits (0.400, 0.160)	0, absent 1, one row in each intercostal furrow 2, two rows in each intercostal furrow
2. Pali (0.588, 0.294)	0, present before all but last cycle of septa 1, P2 only 2, P2-3 3, absent 4, present before all but last cycle: P1-2 vestigial, P3 fused in V-shaped structures 5, before penultimate cycle of septa (occurs only in outgroups) 6, before antepenultimate septal cycle (occurs only in outgroups) 7, P1-2 (occurs only in outgroups)
3. Paliform Lobes (0.889, 0.444)	0, absent 1, P2 2, multiple lobes on S1-3 3, P3 (occurs only in outgroups)
4. Columella (0.722, 0.120)	0, papillose 1, styliform 2, absent or rudimentary fusion 3, lamellar or labyrinthiform 4, fascicular 5, trabecular (occurs only in outgroups)
5. Transverse Division (0.200, 0.040)	0, absent 1, present
6. Costal/Septal Correspondence (1.000, 1.000)	0, correspond 1, offset
7. Corallum Shape (0.500, 0.000)	0, cylindrical 1, bowl-shaped 2, conical 3, labyrinthiform (occurs only in outgroup)
8. Thecal Edge Costae (0.500, 0.000)	0, normal 1, alate
9. Costal Ornamentation (0.857, 0.750)	0, granular 1, smooth 2, serrate
10. Costal Origination (higher cycle) (0.333, 0.292)	0, independent 1, bi- or trifurcate
11. Septal Independence (0.500, 0.266)	0, independent 1, higher cycle septa fuse to next lower cycle septa
12. Septal Cycles (1.0, 1.0)	0, $\geq S4$ (≥ 48 septa) 1, $< S4$ (10–46 septa)
13. Costae: Septa (0.750, 0.563)	0, 1:1 1, 2:1
14. Corallum Size (0.667, 0.611)	0, large (GCD over 1 cm) 1, small (GCD less than 1 cm)
15. Edge Zone (1.0, 1.0)	0, narrow (occurs only in outgroups) 1, moderate to well developed (occurs only in outgroups) 2, corallum completely invested (ordered character states)
16. Corallum Attachment (1.0, 1.0)	0, attached (occurs only in outgroups) 1, unattached

TABLE 5.—Character matrix used in the phylogenetic analysis of the turbinoliid genera and outgroups, as illustrated in Figures 2–4. Character numbers refer to those described in Table 4. Polymorphic states are symbolized accordingly: 0 + 1 = a; 0 + 2 = b; 0 + 3 = c; 0 + 6 = d; 0 + 2 + 3 = e; 0 + 3 + 4 = f; 0 + 5 + 7 = g; 0 + 3 + 5 + 7 = h; 1 + 3 = i; 2 + 3 = j; 2 + 3 + 5 = k (only a–c, and i found in turbinoliid genera, the other permutations found only in the outgroups). DPE = Desmophyllinae + Parasmiliinae + Eusmiliinae.

Taxa	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Thecocystathinae	0	d	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caryophyllinae A	0	a	b	f	0	0	2	0	0	0	0	0	0	0	0	1
Caryophyllinae B	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0
Caryophyllinae C	0	h	b	e	0	0	b	0	0	0	0	0	0	0	0	1
Caryophyllinae D	0	3	b	f	0	0	2	0	0	0	0	0	0	0	0	0
Caryophyllinae E	0	3	c	0	0	0	2	0	0	0	0	0	0	0	0	1
DPE	0	3	e	k	0	0	j	0	0	0	0	0	0	0	0	0
Alatotrochus	0	3	0	0	0	0	2	1	0	0	0	0	1	0	2	1
Pleotrochus	0	1	0	0	0	0	2	0	b	0	a	0	1	0	2	1
Australocyathus	0	3	2	2	1	0	0	0	0	1	1	0	0	0	2	1
Tropidocyathus	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	2
Cyathotrochus	0	0	0	0	0	0	2	0	2	0	1	0	0	0	0	2
Deltocyathoides	0	0	0	0	0	0	1	0	2	1	1	0	0	a	2	1
Notocyathus	0	4	0	0	0	0	2	0	2	1	0	0	0	1	2	1
Palocyathus	1	2	0	0	0	0	2	0	2	1	0	0	0	1	2	1
Bothrophoria	1	0	0	0	0	0	2	0	2	1	0	0	0	1	2	1
Levicyathus	0	3	0	1	0	0	2	0	2	1	0	0	0	1	2	1
Thrypticotrochus	0	3	2	0	0	0	2	0	2	1	0	0	0	1	2	1
Cryptotrochus	0	1	0	0	0	0	2	0	b	1	a	0	0	1	2	1
Laminocyathus	1	1	0	2	0	0	2	0	?	1	0	0	0	1	2	1
Alveolocyathus	1	1	0	0	0	0	2	0	2	1	0	0	0	1	2	1
Pseudocyathoceras	0	3	0	4	0	0	2	0	0	0	0	1	0	0	2	1
Idiotrochus	0	0	0	0	1	1	2	0	1	0	0	1	0	1	2	1
Dunocyathus	0	0	0	0	1	1	0	0	0	0	0	1	0	1	2	1
Wellsotrochus	0	3	0	1	0	0	1	0	?	0	0	a	1	1	2	1
Holcotrochus	0	3	0	2	0	0	2	0	0	0	0	1	1	1	2	1
Conocyathus	1	1	0	2	0	0	2	0	0	0	1	1	1	1	2	1
Turbinolia	2	3	0	i	0	0	2	0	1	0	1	a	a	1	2	1
Sphenotrochus	0	3	0	c	0	0	2	0	a	0	1	1	a	1	2	1
Foveolocyathus	1	3	0	0	0	0	2	0	0	1	0	a	0	1	2	1
Endocyathopora	0	1	0	0	0	0	2	0	0	1	0	1	0	1	2	1
Trematotrochus	0	3	1	0	0	0	2	0	0	1	0	1	0	1	2	1
Kionotrochus	0	3	1	0	1	0	2	0	0	1	0	1	0	1	2	1
Platytrochus	0	3	0	0	0	0	2	a	a	1	1	a	0	1	2	1
Peponocyathus	0	0	0	0	1	0	0	0	0	1	1	a	0	1	2	1

liids: species of *Trematotrochus* possess intercostal pores that penetrate the theca (Plate 10a–c), and *Endocyathopora* possesses pits on the interior of its theca (Plate 9h). Because both of these states are unique (autapomorphic) and would therefore not contribute to tree structure, they are not listed in the suite of character states for this character, and these two taxa are coded as lacking external thecal pits.

Character 2: Pali. Within the Turbinoliidae, there are five character states (0–4) pertaining to the number and placement of pali within the calice of a turbinoliid. Character states 5–7 are included only to fully resolve the various outgroups. The outgroups are highly polymorphic for this character, whereas polymorphism of this character does not occur within any

turbinoliid genus, probably because it has been strictly interpreted as a genus-level discriminator. The ancestral character state is considered to be pali occurring before all but the last cycle of septa, a state that exists in the Thecocystathinae and several of the other outgroups, either exclusively or as part of a polymorphism. However, this character changes to state 3 (pali lacking) ancestral to the turbinoliid divergence. No ordering of character states was assumed; however, Cairns (1989a) noted that state 4 (i.e., pali before all but last cycle of septa, pairs of P3 fused in V-shaped structures, P1–2 vestigial), which occurs only in *Notocyathus*, ontogenetically recapitulates state 0 (pali before all but last cycle of septa) and probably evolved from state 0. A juvenile *Notocyathus* is illustrated in

Plate 4*j*, showing an early stage with well-developed P1–2. This possibility is revisited in the discussion of the phylogenetic trees.

Character 3: Paliform Lobes. Of the turbinoliid genera that do not have pali, some have paliform lobes arranged before their S2 (state 1) or multiple lobes occurring before their S1–3 (state 2); other genera lack both pali and paliform lobes (state 0). A fourth character state (3) of having P3 was included to properly score the outgroup taxa. The ancestral character is considered to be a lack of paliform lobes, which is characteristic of the Thecoccyathinae and all of the other outgroups, even if only as part of a polymorphic condition, and is characteristic of all six of the earliest known turbinoliid genera from the Late Cretaceous. No ordering of character states was assumed.

Character 4: Columella. Five columellar character states occur in the turbinoliids, including the absence of a columella; a sixth state, numbered 5 (trabecular), is also included to properly score the outgroups. Whereas the outgroups are usually highly polymorphic regarding this character, only two of the 28 turbinoliid genera have the polymorphic condition (Table 5). The ancestral state is considered to be papillose, a condition present in the Thecoccyathinae and present uniquely or as part of a polymorphic condition in all but one of the other outgroups. No ordering of character states was assumed.

Character 5: Transverse Division. A number of coral species that routinely asexually reproduce by transverse division has been discovered over the last decade (Cairns, 1989a,b; Stolarski, 1992), and, based on this mode of reproduction, they have been referred to other genera separate from the otherwise similar species that do not divide. The ancestral state of this binary character is assumed to be the lack of transverse division, which is shared with Thecoccyathinae and all but one of the other outgroups and all six Late Cretaceous turbinoliid genera. There is no polymorphism expressed in this distinctive character.

Character 6: Costal/Septal Correspondence. In most Scleractinia, including most turbinoliids, there is a direct physical correspondence between each septum within the calice and a costa on the exterior of the theca. In fact, the combined structure is sometimes called a septocosta. However, in two turbinoliid genera the costae are offset from their septa, such that a smooth thecal region corresponds to the position aligned with the septa, the costae being located where the intercostal furrows normally would be (Plates 2*i*, 5*h*, 7*l*, 8*a*). The ancestral state is assumed to be that of costoseptal correspondence, this state occurring in all outgroups and the six Late Cretaceous turbinoliid genera. Another example within the Scleractinia in which costae and septa alternate in position occurs in the Micrabaciidae, in which this character serves as a synapomorphy for the family.

Character 7: Corallum Shape. Turbinoliid coralla may be cylindrical (often the result of transverse division), bowl-shaped, or conical; a fourth shape, labyrinthiform, is included to score the outgroups. Conical coralla may be compressed (cuneiform), elliptical, or circular in cross section, but the

transition between these grades of circularity is so gradual that no distinction was made. The ancestral state is considered to be cylindrical, the state present in the Thecoccyathinae.

Character 8: Thecal Edge Costae. In some species that have an elliptical calice and thus a somewhat laterally flattened corallum, the two thecal edges are well defined and sometimes produced into a thickened alate ridge (Plate 1*a,e*). The ancestral condition is assumed to be the normal, non-alate morphology of the end costae, which is present in Thecoccyathinae and all but one of the other outgroups.

Character 9: Costal Ornamentation. The costal surface of turbinoliids has three basic types of textures: smooth, granular, or serrate. The smooth condition is self explanatory (Plates 2*i*, 8*e,f*). The granular state consists of numerous low, rounded, closely packed granules uniformly arranged over the costal surface (Plates 7*b*, 8*a*, 9*g*). The serrate state, which may be unique to the Turbinoliidae, consists of a unilinear row of massive outward-projecting conical spines on each costa, flanked on either side by smaller spinules that project into the intercostal space at right angles to the larger spines (Plate 7*g,i*). The ancestral state is considered to be granular, the state shared by all the outgroups. In some Late Cretaceous genera, the preservation of the corallum was not adequate to determine this character state and thus it was coded with a question mark. Four turbinoliid genera were polymorphic for the character.

Character 10: Costal Origination (higher cycle). Whereas the first 12 costae (C1–2) of turbinoliids are invariably independent (straight and not fused to adjacent costae), higher-cycle costae (C3–5) may be independent (Plates 2*i*, 3*a,b*) or may originate from bi- or trifurcations of a lower-cycle costa (Plate 7*a,e,j*). The ancestral state is assumed to be the independent morphology, found among all the outgroups.

Character 11: Septal Independence. Similar to the previous character, the first 12 septa (S1–2) of most turbinoliids are straight with free inner edges that border the axial fossa; however, in some genera the inner edges of the higher-cycle septa (S3–5) bend toward and fuse with their adjacent lower-cycle septa or pali. For instance, the inner edges of a pair of S4 will bend toward and fuse to the S3 they flank, or the inner edges of a pair of S3 will fuse to their common S2. The independent septal state, shared by all outgroups, is considered ancestral. There appears to be no correlation between this character and costal origination, contrary to expectation.

Character 12: Septal Cycles. In most solitary Scleractinia, the number of septa and septal cycles increases as the coral increases in size; 12 septa (two cycles), 24 (three cycles), 48 (four cycles); however, adult coralla usually have a predetermined number of septa regardless of the ultimate corallum size (Mori and Minoura, 1983), such that one would not necessarily expect a good correlation between character state 12:0 (high number of septa) and character state 14:0 (large size). Among the turbinoliids there seems to be a dichotomy between those genera that have ≥ 48 septa ($\geq S4$) and those that have less than a full fourth cycle (≤ 48 septa, usually 24). A third state of having only 10 septa could be added for *Holcotrochus*, but,

being autapomorphic for this genus, it would not contribute to tree structure and thus was scored as simply having less than 48 septa. The ancestral state is considered to be ≥ 48 septa ($\geq S4$), shared by all outgroups. This is one of three qualitative characters used in the analysis but one based on stepwise, discontinuous values, i.e., 10, 24, 36, 48, or 72 septa.

Character 13: Costae: Septa (c:s). As discussed for character 6, there is a 1:1 correspondence of septa to costae in most Scleractinia, even when they alternate in position, which results in an equal number of septa and costae for a corallum. However, in some turbinoliids, there are twice as many costae as septa, the supernumerary costae (herein named intercostae) forming between the normal costae (Plates 1a, 9c) and resulting in a 2:1 ratio of costae to septa. The ancestral condition of 1:1 is found in all outgroups.

Character 14: Corallum Size. Although adult corallum size might seem to be an arbitrary quantitative character, among the turbinoliids there seems to be a dichotomy between those genera having adult coralla over 1 cm in GCD and those that are smaller. In only one genus, *Deltocyathoides*, was it necessary to code this character as polymorphic. All outgroups have large coralla, which is considered to be ancestral.

Character 15: Edge Zone. The fold of the polyp's body wall that extends over the edge of the calice is called the edge zone. The cell layer on the inner corallum side of the edge-zone forms the costae and its ornamentation. If the distal margin of this cell layer does not extend very far beyond the calicular margin (i.e., restricted to the upper several mm of the theca) it is termed a narrow edge zone. Conversely, if the edge zone fully encapsulates the corallum, the character state is termed entire. Intermediate edge-zone coverage, scored as moderate or well developed in the subfamily analysis (Table 2), was scored as one state in the generic analysis (Table 4). This is the only ordered multistate character used in the generic analysis, the ancestral state being narrow, found in the Thecoccyathinae, the other two states showing an ontogenetic progression of increasing edge-zone development.

Character 16: Corallum Attachment: Turbinoliid coralla are not cemented to a hard substrate and thus the genera are scored as unattached. The only reason the character state of attached was included in the analysis was to help resolve outgroup relationships. The ancestral state for this character is considered to be attached (found in Thecoccyathinae), changing to the unattached state at the stem leading to the turbinoliids and their sister taxa.

Characters 1 (theca), 2 (endotheca), 4 (coloniality), and 5 (budding) of the subfamilial analysis (Table 2) were not used in the turbinoliid generic analysis because their derived states were autapomorphic for the DPE outgroup and thus would not lend structure to a generic phylogenetic tree.

RESULTS

Numerous (5876) equally parsimonious trees were generated in the heuristic search of the 28 turbinoliid genera. Successive

weighting reduced the number of most-parsimonious reconstructions to 82 trees with 99 steps each and a consistency index of 0.657 (RCI = 0.442). The strict consensus of these 82 trees is presented as Figure 2.

In order to further reduce the number of trees under consideration, certain logical assumptions or guesses were made. For instance, if for character 2 (pali), it is assumed that character state 4 (pali before all but last cycle, P3 V-shaped, P1-2 vestigial) evolved from state 0 (pali before all but last cycle of septa), as suggested in the character descriptions, the 82 trees may be reduced to 20. Among those 20 trees there are two regions of topological variation. One concerns whether *Wellsotrochus* and *Holcotrochus* are fully resolved (Figure 3) or form a trichotomy with a group of three other genera (Figure 2), and is dependent on how the states of character 4 (columella) are distributed. The larger region of topological variation involves the eight genera of clade 2 that are grouped as an unresolved polytomy in the consensus tree (Figure 2) but in more resolved fashions in Figures 3 and 4. Ten topologies are produced in this group of genera, all contingent on the distribution of the states of character 2 (pali), the five more-resolved topologies illustrated in Figures 3 and 4A-D. The topologies of Figure 4A,C are considered less likely than the three others because they imply the unlikely character-state

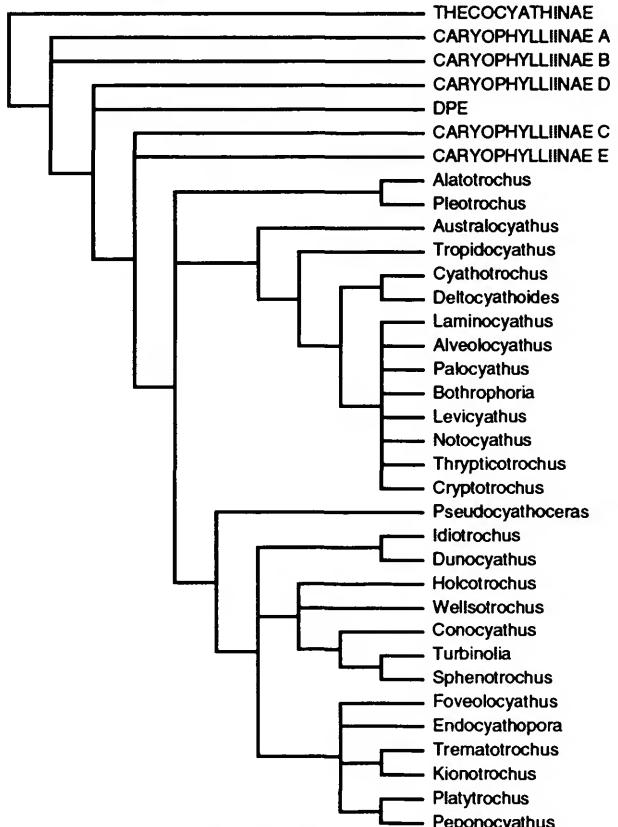


FIGURE 2.—Strict consensus cladogram of turbinoliid generic analysis.

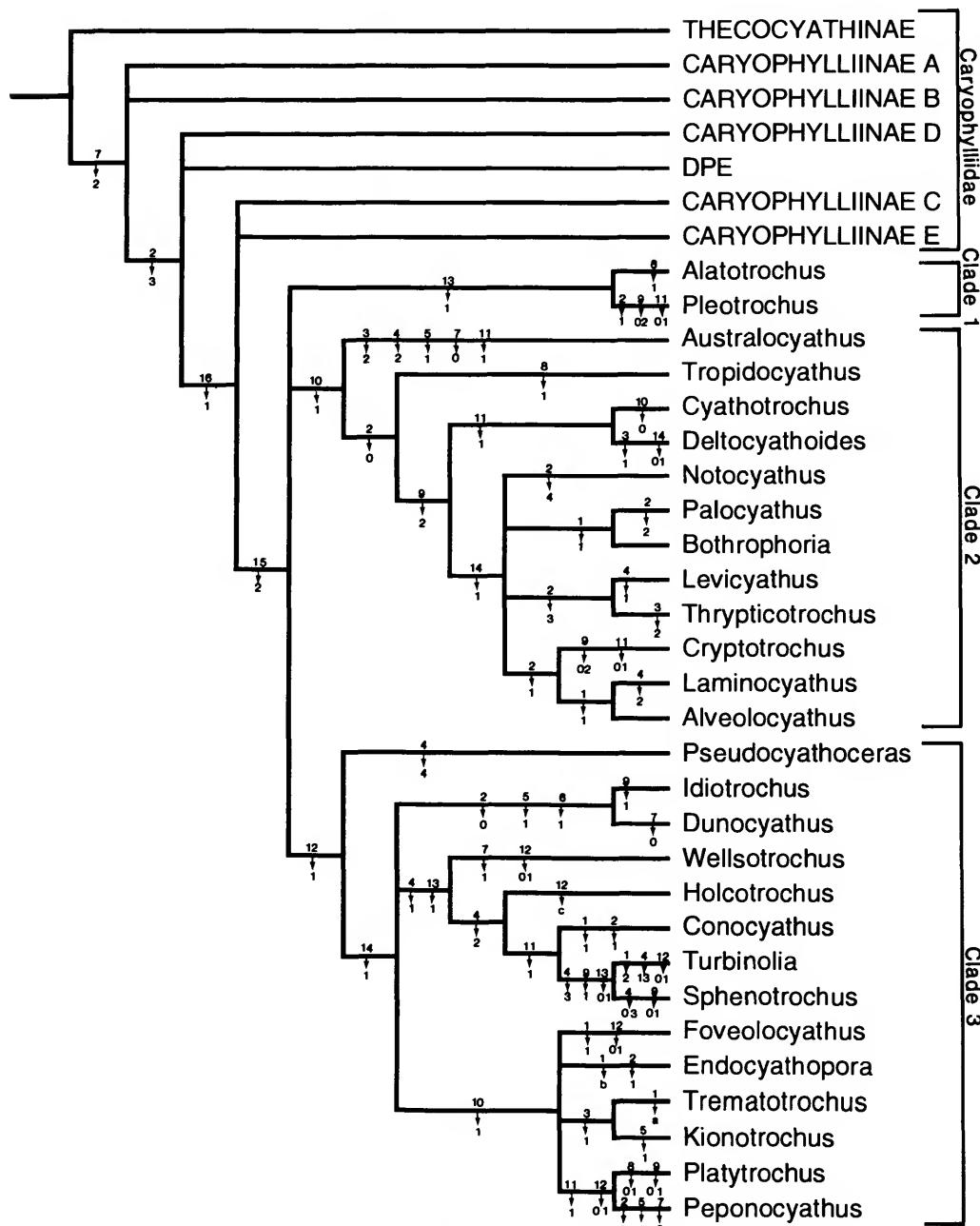


FIGURE 3.—One of the equally parsimonious cladograms of turbinoliid genera arrived at by successive weighting (see text), indicating the three clades discussed in the text. Tree length = 99, CI = 0.66, RCI = 0.44. Character-state changes indicated on every branch as coded in Tables 4, 5, character number on top, character state on bottom of horizontal stem line. Character-state changes not shown for outgroups. Additional autapomorphic character states not coded in analysis: a, perforate theca; b, interior thecal pits; and c, corallum with only 10 septa.

transition of $0 \rightarrow 3 \rightarrow 1$ or $0 \rightarrow 1 \rightarrow 2$, respectively for character 2, which is considered less likely to occur than $0 \rightarrow 1 \rightarrow 3$ (Figures 4B,D) or $3 \leftarrow 0 \rightarrow 1$ (Figure 3). Although there is progressively

less justification for choosing one tree from among the last 20, for the sake of discussion and ordering of taxa, the more resolved topology of the *Wellsotrochus/Holcotrochus* region

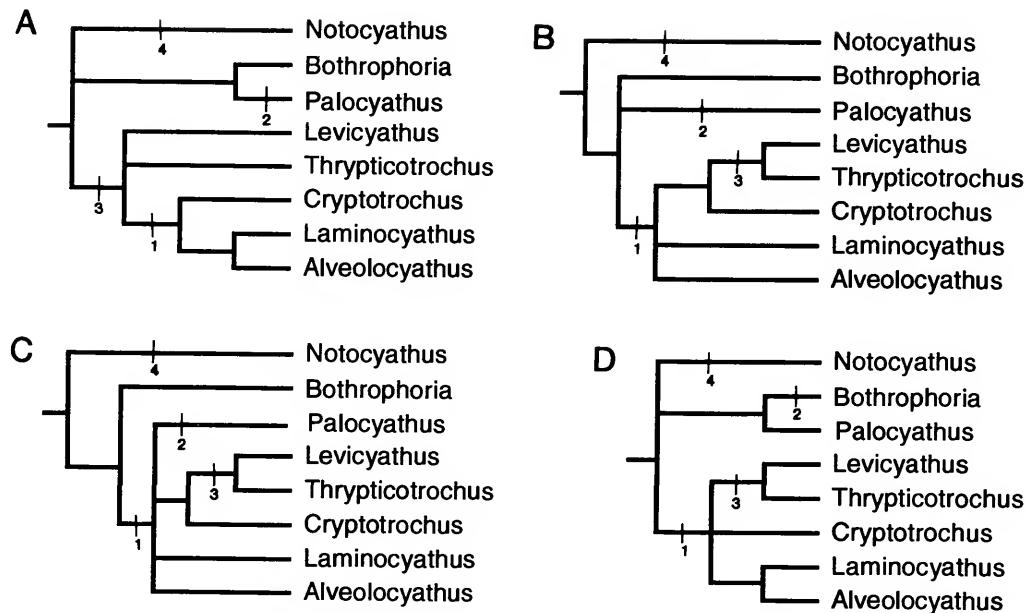


FIGURE 4.—Four variations of highly variable region of clade 2 illustrating equally parsimonious distribution of states of character 2 (pali). Fifth topology illustrated in Figure 3.

and the topology resulting from an interpretation of $4:3 \leftarrow 0 \rightarrow 1$ results in the tree of Figure 3.

The phylogenetic analysis (Figures 2, 3) shows the Turbinoliidae to be monophyletic, characterized by having a completely invested corallum (character 15:2). The outgroups used in the analysis, the subfamilies of Caryophylliidae, are shown to be paraphyletic, with most outgroup taxa being highly polymorphic in several characters. The sister group to the Turbinoliidae is Caryophylliinae C and E, the groups composed of unattached solitary corals that may or may not have pali, e.g., *Deltocyathus*, *Aulocyathus*. The Turbinoliidae is divided into three clades, the stems of which meet in a polychotomy, and thus a most derived or most ancestral taxon cannot be inferred. Clade 1 (Figure 3) contains only two Indo-West Pacific Pleistocene–Recent genera united by character state 13:1 (i.e., a costoseptal ratio of 2), a state that also occurs in clade 3. The validity of clade 1 is doubted. Clade 2 contains 12 genera including all six Lower Cretaceous Antarctic genera, as well as genera first recorded from the New Zealand Eocene, South Australian Oligocene, and four known only from the Recent of the Indo-West Pacific and Atlantic. No genera are included in this clade from the Tertiary of Europe or North America. Clade 2 is characterized by having trifurcate costal origination and serrate costal ornamentation and differs from those genera in clade 3 that also have trifurcate costae by having ≥ 48 septa. Clade 3 contains 14 genera including one Late Cretaceous New Zealand genus, five genera with first occurrences in the Paleocene to Miocene of Europe and North America, three with earliest occurrences in the Eocene to

Oligocene of South Australia, and four known only from the Indo-Pacific Recent. Clade 3 is characterized by having coralla with ≤ 48 septa and granular or smooth costae. More specific relationships within the three clades are discussed in the generic discussions.

DISCUSSION

In my key to the turbinoliid genera (Cairns, 1989a), I used the perforate (pitted) nature of the theca as the first discriminator among genera, followed by characteristics of pali and columella. In a similar key, Filkorn (1994) emphasized the presence or absence of pali as the first discriminator, followed by characteristics of the columella and theca. The turbinoliid generic key of Vaughan and Wells (1943) employed characteristics of the columella, pali, theca, and costae, in that order. The results of the phylogenetic analysis give lesser weight to any of these characters but instead base its higher cladistic structure primarily on characters 9, 10, and 12: costal ornamentation, costal origination, and septal number. Interestingly, Filkorn (1994:41) noted that costal ornamentation and origin might be useful discriminators among turbinoliid species, but he did not expand upon that idea. Characters 13 and 6 (c:s ratio and costal/septal correspondence) also provide cladistic structure at a lower level; and characters 15 and 16 (edge zone, corallum attachment), as expected, give structure only at the level of the outgroups and are noninformative among the turbinoliid genera.

It is acknowledged that the cladogram of suggested

TABLE 6.—Occurrence, distribution, and number of species of the turbinoliid genera. Number of species presented as the total number of valid species followed by the component that are exclusively fossil and those that are known in the Recent, the number of those Recent species with a fossil record indicated in parentheses.

Genus	Stratigraphic range	Depth range	Distribution	Number of species
<i>Alatotrochus</i>	Pleistocene–Recent	193–751	western Pacific	1:0/1(1)
<i>Pleotrochus</i>	Recent	200–1137	western Pacific	2:0/2
<i>Australocyathus</i>	Recent	16–148	Australia	1:0/1
<i>Tropidocyathus</i>	?Late Cretaceous (Maastrichtian)–Pleistocene–Recent	50–421	?Antarctic Peninsula, Indo-West Pacific	?3: ?2/1(1)
<i>Cyathotrochus</i>	?Miocene–Pleistocene–Recent	123–522	Indo-West Pacific	5:2/3(1)
<i>Deltocyathoides</i>	?M. Eocene–Late Eocene–Recent	44–635	widespread marine, New Zealand, Europe	6:4/2
<i>Notocyathus</i>	?Eocene–Late Oligocene (Duntronian)–Recent	34–1110	western Pacific	5:3/2(2)
<i>Palocyathus</i>	Late Cretaceous (Maastrichtian)	—	Antarctic Peninsula	1:1/0
<i>Bothrophoria</i>	Late Cretaceous (Campanian, Maastrichtian)	—	Antarctic Peninsula	1:1/0
<i>Levicyathus</i>	Late Cretaceous (Maastrichtian)	—	Antarctic Peninsula	1:1/0
<i>Thrypticotrochus</i>	Recent	95–925	Indo-West Pacific	2:0/2
<i>Cryptotrochus</i>	Recent	320–675	Atlantic and western Pacific	2:0/2
<i>Laminocyathus</i>	Late Cretaceous (Maastrichtian)	—	Antarctic Peninsula	1:1/0
<i>Alveocyathus</i>	Late Cretaceous (Maastrichtian)	—	Antarctic Peninsula	1:1/0
<i>Pseudocyathoceras</i>	Recent	91–183	Galápagos Islands	1:0/1
<i>Idiotrochus</i>	Early Oligocene (Janjukian)–Recent	82–645	western Pacific	4:1/3(2)
<i>Dunocyathus</i>	Recent	64–549	South Australia, Tasmania	1:0/1
<i>Wellsotrochus</i>	Late Cretaceous (Haumurian)	—	New Zealand	3:3/0
<i>Holcotrochus</i>	Early Oligocene (Janjukian)–Recent	9–185	S. Australia, Victoria, Torres Straits	2:0/2(1)
<i>Conocyathus</i>	Paleocene–Recent	6–130	w. Africa, Europe, South Australia, Indo-West Pacific	8:7/1(1)
<i>Turbinolia</i>	Early Paleocene (Midwayan)–Recent	9–24	w. Africa, Europe, U.S., Peru, Great Barrier Reef	44:43/1
<i>Sphenotrochus</i>	M. Eocene–Recent	7–403	Europe, U.S., W. Indies, New Zealand, widespread marine	35:24/11(1)
<i>Foveolocyathus</i>	Eocene–Recent	27–238	South Australia, New South Wales	4:2/2
<i>Endocyathopora</i>	Recent	46–100	western Pacific	1:0/1
<i>Trematotrochus</i>	?Eocene–Late Oligocene–Recent	365–576	South Australia, New South Wales, Cuba	7:5/2
<i>Kionotrochus</i>	Recent	44–622	New Zealand	1:0/1
<i>Platytrochus</i>	Early Paleocene (Midwayan)–Recent	22–201	U.S., S. Australia, ?Dominican Republic, W. Australia	14:10/4(1)
<i>Peponocyathus</i>	Early Miocene (Waitakian)–Recent	30–1110	Europe, New Zealand, Japan, wide-spread marine	5:2/3(1)
TOTAL				162:113/49(12)

phylogenetic relationships (Figure 3) is one of many equally parsimonious trees and that the principle of successive weighting, which significantly reduced the number of possible trees, is not acceptable to some. Also, the tree is quite labile, many branch stems being supported by only one character-state change. Furthermore, the polymorphism attributed to various genera and outgroups also tends to compound the lability and number of possible trees. However, in partial defense of this exercise, I must reiterate that about one-fifth of the turbinoliid genera are exclusively fossil (Late Cretaceous) and extant turbinoliids are rarely collected and virtually never seen alive, making histological, molecular and nematocyst analyses impractical to impossible at this time. The cladogram as presented is not implied to be a definitive phylogeny, but a preliminary attempt at elucidating the evolutionary relationships among the turbinoliid genera, with a suggestion that characters previously thought to be phylogenetically important may, in fact, be highly homoplastic and that other characters (e.g., costal origination and ornamentation) should be examined more carefully.

A possible 29th turbinoliid genus was rediscovered after the cladistic analysis was completed: *Platytrochopsis* Sikharulidze,

1975, represented by its type species *P. lashensis*. It is known only from the Lower Albian (late Early Cretaceous) of western Georgia (Gruzinskaya S.S.R.), Russia, and Mexico (Turnek, LeMone, and Scott, 1984), making it potentially the geologically oldest turbinoliid genus. From a translation by Mark J. Grygier of the Russian, this genus can be diagnosed as follows: Corallum conical, slightly compressed, with a rounded base; thecal edge crests present; calice elliptical in cross section. Corallum up to 12 mm in GCD. Costae number twice as many as septa (c:s = 2), granular, alternating in size; theca imperforate. Costae independent in origin. Septa hexamerally arranged in 4 cycles (S1–2>S3>S4). Pali or paliform lobes present before all but last septal cycle (P1–3), their inner edges contributing to a spongy columella. The character coding for this genus, as described in Tables 4, 5, is 0006002100001021, the sixth state of character 4 being an autapomorphy for this genus: a spongy columella.

Sikharulidze (1975) suggested a similarity of *Platytrochopsis* with *Platytrochus* and *Cyathotrochus*, but it differs from the latter genus in having a spongy columella, alate edge costae, granular costae, independent septa, and a c:s of 2. It differs from *Platytrochus* in even more characters (Table 5). However,

Platytrochopsis is quite similar to *Alatotrochus*, differing only in two characters used in the phylogenetic analysis, i.e., having a spongy columella, not papillose, and having pali (P1-3). A phylogenetic analysis including *Platytrochopsis* places it in clade 1 as a sister genus to *Alatotrochus* in 60% of the trees, the synapomorphy of alate edge costae (character 8:1) separating them from *Pleotrochus*.

However, two aspects of Sikkharulidze's description are somewhat confusing. He stated that the septa were porous on their inner margins, which would suggest a dendrophylliid affinity, although the wall was clearly stated to be septothecate. Secondly, the columella was stated to consist of "interlaced pali positioned in prolongations of the septa of the first three orders," which could be interpreted as true pali, paliform lobes, or simply the inner edges of the S1-3. Because no specimens were available for examination, this point was not resolved. If the prolongations of the septa are not pali or paliform lobes, the resemblance of *Platytrochopsis* to *Alatotrochus* would be almost total.

Generic Revision

MATERIAL AND METHODS

This study was based primarily on the collections of the USNM, but also on observations of other specimens from various museums over the last two decades. Of the 163 valid turbinoliid species (Table 6), 101 (62%) are represented at the USNM, and I have seen examples of two additional species, for a total of 103 species. The USNM holds representatives of 25 of the 28 type species of the genera, and I have seen one more (*Wellsotrochus cyathiformis*) on loan (26/28 = 93%), only the type species *Conocyathus sulcatus* and *Cyathotrochus herdmani* having not been examined by the author. Of the 28 holotypes or syntype series of the turbinoliid genera, nine are deposited at the USNM, six are lost or of unknown deposition, three are at the BMNH, and the remaining ten are deposited at ten other institutions (see "Type Species" accounts of respective genera). Although emphasis was given to the type species in defining the genus, as many species as possible were examined within each genus to fully describe the character range of the genus and to properly code it for the phylogenetic analysis.

Generic synonymies include the original description, reference to the standard revisions of the order (i.e., Milne Edwards and Haime, 1848, 1850, 1857; Vaughan and Wells, 1943; Alloiteau, 1952; Wells, 1956; and Chevalier, 1987), and any significant reference that diagnosed or discussed the genus and its species. Generic diagnoses were written in consistent telegraphic style to facilitate comparison, and discussions include taxonomic histories, comparison of 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 6). The following information is provided for the type species of each

genus: method of determination, distribution, and, if known, museum of deposition. Other species are listed in stratigraphic order, oldest first. Illustrations of the genera are grouped by aspect, not taxonomy, to facilitate comparison of features. Plates 1-3 present calicular side views of all the genera, Plates 4-6 present calicular views, and Plates 7-10 present details of various features.

Systematic Account

Order SCLERACTINIA

Suborder CARYOPHYLLIINA

Superfamily CARYOPHYLLIOIDEA Vaughan and Wells, 1943

Family TURBINOLIIDAE Milne Edwards and Haime, 1848

DIAGNOSIS.—Corallum small (usually less than 10 mm in CD), solitary, and free (completely invested by polyp), except for species having transverse division, in which case anthocaulus stage is attached and thus not completely invested by polyp. Corallum conical, bowl-shaped, or cylindrical. Costae originate independently or by trifurcation; surfaces granular, serrate, or smooth in texture; intercostae present in some genera, and an alternation of septa and costae present in others. Intercostal regions solid, pitted, or, in one case, perforate; epitheca absent. Septa usually exsert and hexamerally arranged in 3 to 4 cycles (24-48 septa); however, range of septal number is 10 to 72, including decameral symmetry. Pali and paliform lobes in various arrangements or absent altogether. Likewise, columella papillose, styliform, lamellar, fascicular, or absent. Endotheca absent.

Ecologically, turbinoliids are azooxanthellate, nonconstructional, and ahermatypic.

TAXONOMIC HISTORY.—Milne Edwards and Haime (1848:234) established the family Turbinoliidae and included in it two "tribes" or subfamilies, the Turbinoliinae and Cyathiae, the former containing 10 genera that were devoid of pali, the latter comprised of 14 genera characterized by having pali. The 10 genera placed in the Turbinoliinae consist of a polyphyletic assemblage, three of which (*Turbinolia*, *Sphenotrochus*, *Platytrochus*) are still recognized as turbinoliids, the other seven genera subsequently have been reassigned to the Caryophylliidae and Flabellidae. The other subfamily, the Cyathiae, based on the genus *Cyathina* (= *Caryophyllia*), also included a polyphyletic assemblage, including genera now assigned primarily to the Caryophylliidae, but also including one genus now in the Flabellidae, and one turbinoliid (i.e., *Tropidocyathus*). However, because Dana (1846:364) established the family Caryophylliidae (type genus *Caryophyllia* = *Cyathina*) two years before Milne Edwards and Haime's (1848) Turbinoliinae and Cyathiae, Caryophylliidae has priority for the family name of those genera typified by *Caryophyllia*, and Turbinoliidae is thus the earliest available name for the

family that includes the genus *Turbinolia*. Nonetheless, the family name Turbinoliidae (sensu Milne Edwards and Haime, 1848) was used by many (e.g., Pourtalès, 1871; Duncan, 1885; Alcock, 1902b,c; Dennant, 1906; Gardiner and Waugh, 1938; Yabe and Eguchi, 1942; and Alloiteau, 1952) to refer to the caryophylliids and turbinoliids in ignorance of the earlier name of Caryophylliidae Dana, 1846.

In Duncan's (1885) classification, the Turbinoliidae sensu lato was divided into three subfamilies based on whether they were solitary (*simplices*) or colonial (*reptantes* or *gemmantae*). The turbinoliids fell into three "alliances" (supergenera) of subfamily 1, the *Turbinolidae simplices*: Placotrochoida (in part), Turbinoloida (in part), and Trochocyathoida (in small part). These divisions, as with most of Duncan's reorganization of the Scleractinia, were not adopted by later workers.

In the first modern revision of the Scleractinia, Vaughan and Wells (1943) placed 15 genera in the subfamily Turbinoliinae of the family Caryophylliidae. They did not further subdivide the subfamily but their key to the genera stressed columellar type, followed by palar arrangement, thecal integrity, and costal structure.

Alloiteau (1952) considered the turbinoliids to comprise a family with two subfamilies: the Turbinoliinae, which lacked pali, and a newly named subfamily Conocyathinae, which had pali, once again dividing the turbinoliids by the same criterion used by Milne Edwards and Haime a century before. However, like Duncan (1885), who ignored the subfamilial divisions of Milne Edwards and Haime (1848) that were based on presence or absence of pali, Wells (1956) ignored Alloiteau's similar subfamilial divisions, presenting 16 turbinoliid genera in the unified subfamily Turbinoliinae.

After 1956, new turbinoliid genera were described by Squires (1958, 1960b), Wells (1959), Cairns (1988, 1989a, 1991, 1994), Cairns and Parker (1992), and Filkorn (1994). Alloiteau and Tissier (1958) also described three turbinoliid genera from the late Early Paleocene of the Pyrenees, France, but because all three were characterised by having an epitheca, they are not considered to be true turbinoliids (Filkorn, 1994:39). Cairns (1989a) gave a brief history of the subfamily and a key to all genera, which emphasized the presence or absence of thecal perforations as the first couplet, followed by characteristics of pali and the columella. However, in his review of the Late Cretaceous Antarctic Scleractinia, Filkorn (1994, table 5) correctly noted that only one turbinoliid genus has a truly perforate theca, the other genera previously placed in this category actually having an exteriorly pitted, not perforate, theca. His key to the turbinoliid genera (1994, table 6) emphasized the presence or absence of pali, followed by characteristics of columellar and thecal structure.

Although the recognition of the turbinoliids has vacillated since 1848 from the family to subfamily rank, most recent treatments of the group (e.g., Chevalier, 1987; Cairns, 1994; Filkorn, 1994) consider them as a discrete family: the

Turbinoliidae, the sister family to the Caryophylliidae in the superfamily Caryophylloidea.

REMARKS.—The monophyly of the Turbinoliidae is based on the unique (within the Caryophylliina) character of having its entire corallum invested with its polyp. This complete investiture is reflected in the corallum by having well-formed costae from base to calice and deep intercostal regions, because costae continue to accrete over the entire thecal surface throughout the life of the coral. Even the anthocyathus stage of those species that asexually reproduce by transverse division quickly cover their basal scar with the edge zone, and subsequently form costae, such that it is often difficult to assess whether or not the coral was the result of transverse division (e.g., *Peponocyathus*, *Australocyathus*) unless a corallum in the process of division is collected. The anthocaulus of a transversely dividing species is the only exception to the rule of complete investiture by the polyp, as the anthocaulus is sometimes attached, or in the case of *Kionotrochus*, embedded in a small bryozoan colony.

ECOLOGY.—One might ask what adaptive value the complete investiture of a corallum confers to the turbinoliids. Because the coralla are so small and are rarely collected, knowledge of living turbinoliids is extremely limited. With the exception of *Sphenotrochus* (see Rossi, 1961), it is doubtful if any turbinoliids have been observed alive. Writing of *Tropidocyathus*, Gardiner (1939a:249) stated that "how they lived at all is a mystery"; Vaughan and Wells (1943) stated that the attitude of the conical forms was unknown; and Filkorn (1994), in his review of the ecology and paleoecology of the Turbinoliidae, limited his comments primarily to compilations of bathymetric and geographic occurrences and water temperature. However, all three authors agreed that the turbinoliids are usually found on fine sandy substrates; Vaughan and Wells (1943) suggested that some might be sand-burrowing; and Rossi (1961) and Clausen (1971) reported *Sphenotrochus* to be an interstitial dweller.

Whereas most Scleractinia require a hard substrate not only for original attachment but also for subsequent support, the propensity of a turbinoliid to incorporate the substrate into its base limits it to environments in which the substrate is composed of small objects, such as sand and small pieces of shell. Such an environment probably would not be conducive to the settlement and growth of most other larger solitary or colonial corals due to lack of support. All turbinoliids are free-living, not attached to a substrate. If all or most turbinoliids are semi-burrowers or interstitial, then complete investiture of the corallum could facilitate movement through and across a sandy medium, as in the case of certain fungiids (Hoeksema, 1993b). Thus, the complete investiture of the conical to cuneiform turbinoliid corallum might be interpreted as an adaptation to a semi-burrowing habit in sandy substrates at lower shelf to upper slope depths—a niche exploited by few other azooxanthellate Scleractinia. One exception is *En-*

Cretaceous	Tertiary					Recent
	PALEOCENE	EOCENE	OLIGOCENE	MIocene	PLIOCENE	PLEISTOCENE
<i>Bothphoria</i>						
<i>Wellstrochus</i>						
<i>Palocyathus</i>						
<i>Laminocyathus</i>						
<i>Levicyathus</i>						
<i>Alveolocyathus</i>						
<i>Tropidocyathus</i> ?	—	—	—	—	—	—
<i>Turbinolia</i>						
<i>Platytrochus</i>						
<i>Conocyathus</i> ?	—	—				
	<i>Foveolocyathus</i> ?	—				
	<i>Trematotrochus</i> ?	—				
	<i>Notocyathus</i> ?	—				
	<i>Sphenotrochus</i>	—				
	<i>Deltocyathoides</i> ?	—				
		<i>Holcotrochus</i> ?	—			
		<i>Idiotrochus</i> ?	—			
			<i>Peponocyathus</i>	—		
			<i>Cyathotrochus</i>	—		
				<i>Alatotrochus</i>	—	
					<i>Pseudocyathoceras</i>	—
					<i>Endocyathopora</i>	—
					<i>Kionotrochus</i>	—
					<i>Australocyathus</i>	—
					<i>Dunocyathus</i>	—
					<i>Thrypticotrochus</i>	—
					<i>Cryptotrochus</i>	—
					<i>Pleotrochus</i>	—

FIGURE 5.—Stratigraphic ranges of all turbinoliid genera, arranged according to earliest known first occurrences. Dashed lines indicate uncertainty regarding age of origin. Question mark indicates uncertainty about assignation of species of that age to that genus.

dopachys, a solitary dendrophylliid that has a completely invested cuneiform corallum very similar in shape to *Tropidocyathus*, as well as occurring in the same sandy environments and often being collected with other turbinoliids. Because it is in a different suborder, the growth form and investiture of *Endopachys* is interpreted as a convergent adaptation. Two other azooxanthellate families, Fungiacyathidae and Micrabaciidae (in suborders other than the Caryophyllina), and several species of *Deltocyathus* (within the Caryophyllina) also have completely invested coralla, but those taxa usually have small to large discoidal coralla and are characteristic of deeper water and finer substrate (silt-mud) environments.

TYPE GENUS.—*Turbinolia* Lamarck, 1816.

SPECIES RICHNESS.—One hundred sixty-three valid species are recognized in the family, of which 114 are exclusively fossil (Figure 5, Table 6). The remaining 49 species are known

from the Recent, 12 of which also have fossil records.

DISTRIBUTION.—Late Cretaceous: Antarctic Peninsula (Campanian, Maastrichtian); New Zealand (Haumurian).

Paleocene: North America (Midwayan); Tonga; Nigeria.

Eocene: North America (Midwayan, Claiornian); Europe (Ypresien, Bruxellien, Lutetian, Auversian, Bartonian, Latortrian); Barbados; ?Victoria, Australia.

Oligocene: North America (Vicksburgian); Victoria (Janjukian); New Zealand (Duntronian); Peru.

Miocene: Victoria (Balcombian); New Zealand (Waitakian, Otaian, Altonian, Clifdenian); Europe (Burdigalian, Badenian, Vinobadian, Tortonian); West Indies (Langhian); Java.

Pliocene: New Zealand; Europe.

Pleistocene: Japan; Ryukyu Islands.

Recent: Widespread in world oceans, but not known from off continental Antarctica, the eastern Pacific (except for off Lower

California and the Galápagos), and the cold temperate northwest Atlantic. Turbinoliids are most diverse in the Indo-West Pacific region, especially off Australia, New Zealand, and Indonesia. Bathymetrically they are known from 6 to 1137 m, but are most common from 50 to 650 m.

Alatotrochus Cairns, 1994

PLATES 1a, 4a

Platytrochus.—Moseley, 1876:552 [in part].

Sphenotrochus.—Moseley, 1881:157 [in part].

Alatotrochus Cairns, 1994:68; 1995:84.

DIAGNOSIS.—Corallum conical, with rounded base; thick, prominent thecal edge crests; calice elliptical in cross section. Corallum relatively large: up to 20 mm in GCD. Costae number twice as many as septa (c:s = 2) and granular; intercostal region relatively shallow, smooth, and not pitted. Edge crests transversely ridged. Costae independent in origin. Septa highly exsert and hexamerally arranged in 4 complete cycles (48 septa). Pali and paliform lobes absent. Columella papillose, consisting of 4–12 discrete pillars, each circular to lamellar in cross section.

DISCUSSION.—Nothing is added herein to the original and subsequent descriptions and comparisons (Cairns, 1994, 1995) of this recently described monotypic genus. The type species was well described and illustrated by Moseley (1881) and Cairns (1994).

The phylogenetic analysis places *Alatotrochus* in the smallest of the three turbinoliid clades (Figures 2, 3), composed of only two relatively underived genera: *Alatotrochus* and *Pleotrochus*. *Alatotrochus* differs from its sister genus in having alate edge crests, lacking pali, and in consistently having granular costae and independent septa. *Alatotrochus* is also very similar to *Platytrochopsis* Sikharulidze, 1975, as noted in the discussion of the “Phylogenetic Analysis” section.

DISTRIBUTION.—Pleistocene: Okinawa, Ryukyu Islands (Cairns, 1994). Recent: Kyushu and Ryukyu Islands, Japan; Banda Sea; southern Norfolk Ridge; 193–751 m (Cairns, 1995).

TYPE SPECIES.—*Platytrochus rubescens* Moseley, 1876, by original designation. Distribution as for genus. Four syntypes are deposited at the BMNH, one numbered: 1880.11.25.163.

OTHER SPECIES.—None.

Pleotrochus, new genus

PLATES 1b,c, 4b,c

Ceratotrochus.—Alcock, 1902a:92; 1902c:10 [in part: *C. venustus*].

Cryptotrochus.—Cairns, 1995:88 [in part: *C. venustus*].

DIAGNOSIS.—Corallum conical, with pointed base and calice circular to elliptical in cross section; GCD up to 13.3 mm. Costae narrow ridges, serrate (type species) to finely granular (*P. zibrowii*) in ornamentation; intercostal regions relatively shallow, equal in width to costae, and not pitted. Costae

independent in origin, those on lower half of corallum often having brief discontinuities; c:s = 2. Septa exsert and hexamerally arranged in 4 complete cycles (48 septa). Papillose columella encircled by crown of 6 prominent lamellar P2.

DISCUSSION.—As in *Cryptotrochus*, *Pleotrochus* is polymorphic in the same two characters used in the phylogenetic analysis: *P. venustus* has serrate costae and completely independent septa, whereas *P. zibrowii* has finely granular costae and pairs of S3 that often fuse to their common P2. I recently (Cairns, 1995) placed *P. venustus* in the genus *Cryptotrochus*, but in the course of this revision I realized that the two species now placed in *Pleotrochus* differ from *Cryptotrochus* in having costae independent in origin and often discontinuous near the base, a c:s of 2, much wider intercostal regions, and a larger corallum. As inferred from the phylogenetic analysis (Figures 2, 3), *Pleotrochus* is more closely related to *Alatotrochus* than *Cryptotrochus*, as more fully discussed in the account of *Alatotrochus*. That both genera are polymorphic for the same characters is interpreted as a parallel adaptive radiation.

The type species, *P. venustus*, is diagnosed (Cairns and Zibrowius, 1997) and illustrated (Cairns, 1995, pl. 27a,b) based on the holotype and topotypic specimens from the Kei Islands, Banda Sea.

ETYMOLOGY.—The genus name *Pleotrochus* (Greek *pleos*, full + *trochus*, wheel, a common coral suffix), refers to the fullness of the trochoid to campanulate corallum. The gender is masculine.

DISTRIBUTION.—Recent: Banda Sea; Three Kings Ridge, New Zealand; 200–1137 m (Cairns, 1995).

TYPE SPECIES.—*Ceratotrochus venustus* Alcock, 1902a, new combination, herein designated. Recent: Banda Sea; 200–397 m. Holotype deposited at the ZMA (Coel. 1184).

OTHER SPECIES.—*Pleotrochus zibrowii*, new species. Recent: Three Kings Ridge; 1137 m.

Pleotrochus zibrowii, new species

PLATES 1c, 4c

Cryptotrochus venustus.—Cairns, 1995:88–89 [in part; pl. 26g–i, not pl. 27a,b].

DESCRIPTION.—Calice circular to slightly elliptical in cross section (GCD:LCD = 1.01–1.05). Largest specimen (holotype) 13.3 × 13.2 mm in CD and 14.9 mm in height. Costae ridged, 0.15–0.25 mm wide, and finely spinose, the granules only about 23 µm in diameter. Intercostae equally broad as normal costae but terminate at calicular edge. Costae on lower third of corallum often discontinuous and sometimes slightly sinuous. Intercostal regions relatively shallow. Septa of most specimens hexamerally arranged in 4 cycles: S1>S2>S3>S4, one paratype having a pair of S5 resulting in 50 septa. S1 highly exsert (up to 3 mm) and independent; S2 only slightly less exsert and about four-fifths width of the S1, each bearing a tall, slender (lanceolate) palus that rises well above the columella and even

slightly above the calicular edge. S3 about three-quarters width of the S2, their lower inner edges often fused to their adjacent P2 through an irregular paliform process. S4 only about 1 mm exsert, one-third width of the S3, and independent. Columella papillose, composed of 2–7 granular pillars, encircled by and fused to inner edges of the 6 P2.

DISCUSSION.—Although similar, *P. zibrowii* differs from *P. venustus* in having a calice more circular in cross section (GCD:LCD = 1.01–1.05 versus 1.10–1.20, respectively); granular, not serrate, costae; much more prominent P2, those of *P. venustus* rising not much above its columella; nonexsert intercostae; a larger corallum; and S3 that often fuse to adjacent P2 (all septa of *P. venustus* are independent). *Pleotrochus zibrowii* was more fully described and illustrated by Cairns (1995) as *Cryptotrochus venustus*.

ETYMOLOGY.—The species is named for Helmut Zibrowius (Station Marine d'Endoume, Marseille), who first pointed out to me its distinction from *P. venustus*.

DISTRIBUTION.—Known only from the type locality.

MATERIAL EXAMINED/TYPES.—Holotype: NZOI Stn U584, NZOI H.656 (Cairns, 1995, pl. 26g,h). The holotype was previously cataloged as USNM 94178 but was subsequently transferred to the NZOI. Paratypes: NZOI Stn U584, 4 (USNM 94178, Cairns, 1995, pl. 26i), 16 (NZOI P.1085).

TYPE LOCALITY.—31°26.3'S, 172°35.6'E (Three Kings Ridge, New Zealand), 1137–1150 m.

Australocyathus Cairns and Parker, 1992

PLATES 1d, 4d, 7a–c

Deltocyathus.—Dennant, 1904:6 [in part].
Australocyathus Cairns and Parker, 1992:38–39.

DIAGNOSIS (emended).—Corallum asexually reproduces by transverse division, resultant anthocyathus a low cylinder, circular in cross section with flat to slightly concave base; anthocaulus as yet unknown. Anthocyathus up to 11 mm in CD. Costae finely granular (Plate 7b), rounded, delimited by deep, nonpitted intercostal regions. Higher cycle costae (C3–4) originate by trifurcation (Plate 7a). Septa hexamerally arranged in 4 complete cycles. Small paliform lobes on lower inner edges of S1–3, multiple lobes on S2–3 (Plate 7c). Columella a low granular mass.

DISCUSSION.—No additional specimens of this genus have been reported since its original description, but reanalysis of previously reported specimens (Cairns and Parker, 1992) provides two corrections to the original generic diagnosis. Small specimens of *A. vincentinus* have poorly formed costae and a basal structure consistent with a recent transverse division. Although no coralla are known that are in the process of transverse division, the basal costal morphology of small coralla strongly suggest this ontogeny. Specimens collected in the future should be closely examined for such “unseparated stages,” which, in the case of *Peponocyathus duncani*, occurred in only 3% of the specimens examined by Stolarski (1992).

Secondly, the original generic diagnosis stated that the columella was papillose, but it is actually a low, granular mass that was classified as rudimentary in the phylogenetic analysis. The type species, *A. vincentinus*, is more fully described and illustrated by Cairns and Parker (1992).

Although the discovery of transverse division in *Australocyathus* increases its resemblance to *Peponocyathus*, an affinity suggested by Cairns and Parker (1992), *Australocyathus* differs from that genus in having a rudimentary, nonpapillose columella; multiple paliform lobes per septum (not discrete pali); a larger corallum with more septa; and a short, cylindrical corallum (versus a tall, narrow, cylindrical corallum). Because of these differences and the way in which the characters were weighted in the phylogenetic analysis, *Australocyathus* is placed as the sister taxon to the remainder of clade 2, whereas *Peponocyathus* is grouped within clade 3 (Figures 2, 3).

DISTRIBUTION.—Recent: Western and South Australia; 16–148 m (Cairns and Parker, 1992).

TYPE SPECIES.—*Deltocyathus vincentinus* Dennant, 1904, by original designation. Distribution as for genus. Paratypes are deposited at the South Australian Museum and the USNM (Cairns and Parker, 1992) and possibly at the National Museum of Victoria, Melbourne (Stranks, 1993).

OTHER SPECIES.—None.

Tropidocyathus Milne Edwards and Haime, 1848

PLATES 1e, 4e, 7d

Tropidocyathus Milne Edwards and Haime, 1848:326–327; 1850:xv.—Vaughan and Wells, 1943:213.—Wells, 1956:F426 [in part].—Chevalier, 1987:749.—Cairns, 1989a:33 [in part]; 1994:67 [in part].—Filkorn, 1994:51 [in part].

Tropidocyathus (*Tropidocyathus*).—Duncan, 1885:22.

DIAGNOSIS.—Corallum cuneiform, with rounded base and calice elliptical in cross section; GCD up to 16 mm. Costae low, flat, and covered with small granules (Plate 7d); edge costae expanded into alate edge crests and also uniformly granulated; intercostal regions shallow, narrow, and not pitted. Higher cycle costae originate by trifurcation. Septa highly exsert and hexamerally arranged in 4 complete cycles. Lamellar pali in 3 crowns before all but last septal cycle (P1–3), each pair of P3 and single P2 in system forming a chevron arrangement, but not fused. Columella papillose.

DISCUSSION.—Several species previously considered as *Tropidocyathus* have been transferred to *Cyathotrochus*, as discussed in the account of that genus. *Tropidocyathus* differs from *Cyathotrochus* in having low, granular costae that originate by trifurcation; shallow, narrow intercostal regions; an exclusively papillose columella; and alate or well-developed edge crests. The two Late Cretaceous species of *Tropidocyathus* described by Filkorn (1994) are only tentatively assigned to this genus because the calicular morphology of all coralla he reported is not preserved well enough to verify the palar structure, if any. Nonetheless, their compressed shape,

granular costae, and well-developed edge crests place them closer to *Tropidocyathus* than to *Cyathotrochus*.

The taxonomic history of *Tropidocyathus* was discussed by Cairns (1989a), who also provided a description and illustrations of the type species. The phylogenetic analysis (Figures 2, 3) places *Tropidocyathus* as the sister taxon to the larger part of clade 2, which includes the genus *Cyathotrochus*.

DISTRIBUTION.—?Late Cretaceous: Antarctic Peninsula (Filkorn, 1994). Pleistocene: Ryukyu Islands. Recent: Indo-West Pacific; 50–421 m (Cairns, 1994).

TYPE SPECIES.—*Flabellum lessonii* Michelin, 1842 (= *T. wellsi* Yabe and Eguchi, 1942), by monotypy. Distribution as for genus with exception of Late Cretaceous Antarctica. The syntypes of *F. lessonii* are considered to be lost because they could not be found at the MNHNP in 1995 (M. Guillaume, pers. comm.).

OTHER SPECIES.—?*Tropidocyathus seymourensis* Filkorn, 1994. Late Cretaceous (Maastrichtian), Seymour Island, Antarctic Peninsula.

?*T. minimus* Filkorn, 1994. Late Cretaceous (Maastrichtian), Seymour Island, Antarctic Peninsula.

Cyathotrochus Bourne, 1905

PLATES 1f,g, 4f

Trochocyathus.—Alcock, 1902a:96 [in part; *T. pileus*].

Cyathotrochus Bourne, 1905:192; 1906:450.—Vaughan and Wells, 1943:213.—Chevalier, 1987:749.

Tropidocyathus.—Wells, 1956:F426 [in part].—Cairns, 1989a:33 [in part]; 1994:67 [in part]; 1995:91 [in part].—Filkorn, 1994:51 [in part].

DIAGNOSIS.—Corallum cuneiform, with rounded base and calice elliptical in cross section; GCD up to 25 mm. Costae highly ridged, independent in origin, and serrate in ornamentation; intercostal region equal to costae in width, not pitted, and quite deep. Septa highly exsert and hexamerally arranged in 4 to 5 cycles (48–96 septa). Lamellar pali in 3 crowns before all but last septal cycle (P1–3 or P1–4), higher-cycle pali arranged in chevrons. Columella papillose to sublamellar.

DISCUSSION.—Wells (1956) synonymized *Cyathotrochus* with *Tropidocyathus*, the two genera similar in having relatively large, cuneiform coralla; lamellar pali before all but the last cycle; and a papillose columella. However, in reviewing the species characteristics for scoring of the genus *Tropidocyathus* for the phylogenetic analysis, several characters otherwise conservative at the generic level were required to be coded as polymorphisms in order to include both *T. pileus* and *T. lessonii* in the same genus. Therefore *Cyathotrochus* was resurrected for those species that differ from *Tropidocyathus lessonii* in having ridge-like, serrate costae of independent origin; deep intercostal regions; a papillose to sublamellar columella; and in lacking alate thecal edge crests. Although the types of the Miocene Javanese species *T. nudus* and *T. affinis* (Martin, 1880) have not been examined, they are tentatively included in this genus based on their similarity to *C. pileus*.

In the phylogenetic analysis, *Cyathotrochus* is part of the sister group to *Tropidocyathus* and forms a monophyletic group with *Deltocyathoides*, differing from that genus only in having a conical (not bowl-shaped) corallum and independent costal origination.

DISTRIBUTION.—?Miocene: Java. Pleistocene: Ryukyu Islands. Recent: Indo-West Pacific, including Norfolk Ridge and off Queensland; 123–522 m (Cairns, 1995).

TYPE SPECIES.—*Cyathotrochus herdmani* Bourne, 1905 (= *C. pileus*), by monotypy. Recent: off Ceylon; depth not recorded. Deposition of types not traced.

OTHER SPECIES.—?*Cyathotrochus nudus* (Martin, 1880), new combination, Miocene: Java.

?*C. affinis* (Martin, 1880), new combination. Miocene: Java. *C. pileus* (Alcock, 1902a), new combination (= *T. bouganvillei* Milne Edwards and Haime, 1857; *T. intermedius* Yabe and Eguchi, 1932b). Pleistocene: Ryukyu Islands; Recent: Indo-West Pacific; 123–522 m.

?*C. nascornatus* (Gardiner and Waugh, 1938), new combination. Recent: southwestern Indian Ocean; 183–457 m.

Deltocyathoides Yabe and Eguchi, 1932

PLATES 1h, 4g, 7e,f

Deltocyathoides Yabe and Eguchi, 1932a:389.—Vaughan and Wells, 1943:207.—Wells, 1956:F424.—Zibrowius, 1980:112.—Chevalier, 1987:740–741.

Deltocyathus (*Paradeltocyathus*) Yabe and Eguchi, 1937:130.

Citharocyathus (*Paradeltocyathus*).—Vaughan and Wells, 1943:211.—Alloiteau, 1952:646.

Notocyathus (*Paradeltocyathus*).—Wells, 1956:F425.—Squires, 1958:55.

Peponocyathus.—Cairns, 1979:113 [in part]; 1989a:28–30 [in part]; 1995:89–90 [in part].—Zibrowius, 1980:111–113 [in part].

DIAGNOSIS.—Corallum bowl-shaped, with rounded base, and calice circular in cross section; transverse division not present. Coralla up to 17 mm in CD, but most Recent specimens less than 10 mm in diameter. Costae ridged and serrate (Plate 7f); intercostal regions deep, narrow, and not pitted. Higher cycle costae (C3–4) originate by bi- or trifurcation (Plate 7e). Septa hexamerally arranged in 4 complete cycles. Sublamellar to styliform pali before all but last cycle of septa (P1–3). Columella papillose.

DISCUSSION.—The history of the genus was given by Cairns (1989a) as part of his discussion of *Peponocyathus*, and the type species was described and illustrated by Cairns (1994). The synonymies for *Peponocyathus* and *Deltocyathoides* provided herein now reflect those groups of species that undergo transverse division and those that do not, respectively.

I (Cairns, 1989a, 1994, 1995; Cairns and Parker, 1992) had previously synonymized the type species *Deltocyathoides japonicus* (= *D. orientalis*, *D. lens*, *D. minutus*), common to the Indo-West Pacific, with *Peponocyathus stimpsonii* (exclusively Atlantic) and *P. australiensis* (Eocene to Pliocene, Indo-West Pacific), the earliest name being *Peponocyathus australiensis*. Although all three species are remarkably similar, it is unlikely that one species would have persisted from the Late Eocene to

Recent and would now be worldwide in distribution (H. Zibrowius, pers. comm., 1994). Therefore, among the species listed below, the Tertiary species, as well as the Atlantic populations, are listed as separate species.

As discussed in the account of *Peponocyathus*, *Deltocyathoides* is reserved for those species previously placed in *Peponocyathus* that do not undergo transverse division. *Deltocyathoides* is further distinguished by having a bowl-shaped (versus cylindrical) corallum and serrate (not granular) costae. *Deltocyathoides* is similar to *Notocyathus*, but differs from that genus in corallum shape and in having independent P3. *Wellsotrochus*, the only other turbinoliid genus with a bowl-shaped corallum, differs in having independent costae, no pali, a c:s of 2, and a styliform columella. The similarities of *Deltocyathoides* to *Cyathotrochus* are discussed in the account of the latter.

DISTRIBUTION.—?Middle Eocene (Bartonian): New Zealand. Late Eocene: Tonga. Oligocene (Duntronian): New Zealand. Miocene (Otaian, Clifdenian, Altonian): New Zealand; South Australia, Italy. Pliocene: Japan. Recent: Indo-West Pacific and Atlantic; 44–635 m.

TYPE SPECIES.—*Deltocyathoides japonicus* Yabe and Eguchi, 1932a (junior synonym of *Deltocyathus orientalis* Duncan, 1876, which is the type of *Paradeltocyathus* by original designation; = *Deltocyathus lens* Alcock, 1902a; = *Deltocyathus minutus* Gardiner and Waugh, 1938; not *Peponocyathus orientalis* Yabe and Eguchi, 1932b). Recent: southwestern Indian Ocean to Japan; 44–635 m. Holotype deposited at the TIUS (50091).

OTHER SPECIES.—*Deltocyathoides pedicellatus* (Tenison-Woods, 1880). Middle Eocene (Bartonian) to Middle Miocene (Clifdenian): New Zealand.

D. australiensis (Duncan, 1870). Late Eocene: Tonga. Oligocene (Duntronian): New Zealand. Early Miocene (Altonian): New Zealand. Miocene: Australia. ?Pliocene: Japan.

?*D. cuspidatus* (Squires, 1958) (= ?*Sphenotrochus huttonianus* Tenison-Woods, 1880). Early Miocene (Otaian-Altonian): New Zealand.

D. cylindricus (Sismonda, 1871). Middle Miocene: Italy.

D. stimpsonii (Pourtales, 1871). Recent: amphi-Atlantic; 110–600 m.

Notocyathus Tenison-Woods, 1880

Plates 1*i,j*, 4*h-j*, 7*g*

Notocyathus Tenison-Woods, 1880:9 [in part; *N. viola*].—Vaughan and Wells, 1943:214.—Squires, 1962:147.—Chevalier, 1987:748.—Cairns, 1989a:26–27; 1994:64; 1995:91.

Nototrochus Duncan, 1885:16–17.

Citharocyathus Alcock, 1902b:118; 1902c:21.

Citharocyathus (*Citharocyathus*).—Vaughan and Wells, 1943:210–211.

Notocyathus (*Notocyathus*).—Wells, 1956:F425.

Citharocyathus [sic].—Alloiteau, 1952:646.

DIAGNOSIS.—Corallum conical, with pointed base and calice circular to slightly elliptical in cross section; GCD up to 7.4 mm. Costae ridge-like and serrate (Plate 7*g*) in ornamentation;

intercostal regions deep, narrow, and not pitted; higher cycle costae originate by bi- or trifurcation. Septa exsert and hexamerally arranged in 4 complete cycles. Pali before all but last cycle of septa (P1–3); however, P1–2 often fused to columella in larger specimens, and inner edges of each pair of P3 within a system fuse together in a V-shaped structure (Plate 4*i*). Columella papillose.

DISCUSSION.—*Notocyathus* is unique among the turbinoliids in having fused pairs of P3 and a suppression of the P1–2 stage in the adult corallum. It is one of eight genera in clade 2 to form an unresolved polychotomy in the strict consensus tree (Figure 2); however, if two of the eight character states of character 2 are considered to be ordered (2:0→4, see “Phylogenetic Discussion”), the position of *Notocyathus* will always be as a sister taxon to the other seven genera (Figure 4B,C) or as part of a polychotomy, which leads to various combinations of the other seven genera (Figures 3, 4A,D). The genus has remained relatively static from Late Oligocene to Recent, specimens of Late Oligocene *N. euconicus* being quite similar to Recent *N. venustus*, although the P1 of the Middle Miocene *N. viola* (Plate 4*h*) are better developed than in Recent specimens.

The taxonomic history of the genus was reviewed by Cairns (1989a), who also included illustrations of the holotype of the type species.

DISTRIBUTION.—?Eocene (possibly Late Oligocene): Victoria. Late Oligocene: Victoria (Janjukian); New Zealand (Dantronian). Middle Miocene: Victoria (Balcombian); New Zealand, Java (Waianan). Pleistocene: Ryukyu Islands. Recent: western Pacific (Japan to Norfolk Islands); 34–1110 m.

TYPE SPECIES.—*Caryophyllia viola* Duncan, 1864, by subsequent designation (Felix, 1927). Early Oligocene (Janjukian) to Middle Miocene (Balcombian), Victoria. Holotype deposited at the BMNH (R29281).

OTHER SPECIES.—*Notocyathus euconicus* Squires, 1962. Late Oligocene (Duntronian) to Middle Miocene (Waianan): New Zealand.

N. subviola (Dennant, 1902a). “Eocene” (age uncertain, possibly as young as Late Oligocene): Spring Creek, Victoria.

N. conicus (Alcock, 1902b). Miocene: Java. Pleistocene: Ryukyu Islands. Recent: north of New Zealand, Indo-West Pacific; 34–1110 m (type species of *Citharocyathus*, designated by Faustino, 1927).

N. venustus (Alcock, 1902b). ?Pleistocene: Japan, Vanuatu. Recent: Philippines, Indonesia, Japan; 70–555 m.

Palocyathus Filkorn, 1994

PLATES 1*k*, 4*k*

Palocyathus Filkorn, 1994:57.

DIAGNOSIS.—Corallum conical, with pointed base and calice circular in cross section; holotype 7.2 mm in CD. Costae narrow, beaded (serrate) ridges; intercostal regions greater than width of costae and exteriorly pitted. Higher cycle costae (C3–4) originate by trifurcation near corallum base. Septa

exsert and hexamerally arranged in 4 complete cycles. Small P2 and P3, the pairs of P3 usually fused to their common S2 within each system. Columella papillose.

DISCUSSION.—Among the seven turbinoliid genera having an exteriorly pitted theca (Table 5), *Palocyathus* is unique in having pali before the S2 and S3. Unfortunately, the genus is based on only one specimen, the holotype of *P. seymourensis*, and nine “questionable” specimens (Filkorn, 1994); the palar configuration of all 10 specimens is difficult to interpret due to poor preservation. Although possible, it is not considered unequivocal that *P. seymourensis* is characterized as having P2–3; additional, better-preserved specimens are required to confirm the generic diagnosis.

Filkorn (1994) compared *Palocyathus* to the nonpitted genus *Notocyathus* because of the latter’s fusion of pairs of P3 before their common S2. It is of interest to note that in the phylogenetic analysis *Palocyathus* is usually placed as a sister taxon to *Notocyathus*. *Palocyathus* is one of eight genera in clade 2 that forms an unresolved polychotomy in the strict consensus tree, but in the more resolved topologies that result from successive weighting (Figures 3, 4A,D) *Palocyathus* is often paired with *Bothrophoria*, both genera having exterior thecal pits; but *Palocyathus* differs in having P2–3, whereas *Bothrophoria* has P1–3.

DISTRIBUTION.—Late Cretaceous (Maastrichtian): López de Bertodano Formation, Seymour Island, Antarctic Peninsula.

TYPE SPECIES.—*Palocyathus seymourensis* Filkorn, 1994, by original designation. Distribution as for genus. Holotype deposited at the USNM (93050).

OTHER SPECIES.—None.

Bothrophoria Felix, 1909

PLATES 11, 41

Bothrophoria Felix, 1909:9–11.—Vaughan and Wells, 1943:210.—Alloiteau, 1952:645.—Wells, 1956:F425.—Chevalier, 1987:749.—Filkorn, 1994:42.

DIAGNOSIS (emended).—Corallum conical, with rounded base and calice elliptical in cross section (GCD:LCD = 1.12–1.49 (Filkorn, 1994)); specimens up to 11.0 mm in GCD but most less than 10 mm in diameter. Costae serrate in ornamentation; intercostal regions equal to or wider than costae and exteriorly pitted. Higher cycle costae (C3–5) originate by trifurcation. Septa hexamerally arranged in 4 cycles, some specimens with additional pairs of S5 in end half-systems resulting in 48–58 septa. Pali present before all but last septal cycle, the P3 and P4 lamellar and broad, the P1–2 rudimentary. Columella papillose to spongy.

DISCUSSION.—Having examined the type material of *B. ornata*, Filkorn (1994) emended the generic diagnosis to include P3 and to clarify that the theca was exteriorly pitted, not perforate. Although not apparent in most of the additional specimens reported by Filkorn, the best preserved specimen (Plate 41) also has small P1–2 in addition to the broad P3.

Bothrophoria is distinguished from other exteriorly pitted Cretaceous Antarctic genera by having an elliptical calice (compressed corallum) and is unique among the exteriorly pitted turbinoliids in having pali before all but the last septal cycle. Its similarity to *Palocyathus* is discussed in the account of that genus and illustrated by the tress shown in Figures 3 and 4.

DISTRIBUTION.—Late Cretaceous (Campanian and Maastrichtian): Seymour Island and Snow Hill Island, Antarctic Peninsula.

TYPE SPECIES.—*Bothrophoria ornata* Felix, 1909, by monotypy. Distribution as for the genus. Two syntypes are deposited at the Naturhistoriska Riksmuseet, Sektionen för Paleozoologi, Stockholm, Sweden (Cn87b, 88).

OTHER SPECIES.—None.

Levicyathus Filkorn, 1994

PLATES 2d, 5a

Levicyathus Filkorn, 1994:59.

DIAGNOSIS.—Corallum conical, with pointed base and calice circular in cross section; holotype 5.2 mm in CD. Costae tall thin ridges, bordered by deep, equally wide, nonpitted intercostal regions; costal ornamentation beaded, interpreted as abraded serrate morphology. Higher cycle costae (C3–4) originate by trifurcation. Septa hexamerally arranged in 4 complete cycles. Pali and paliform lobes absent. Sublamellar/styliform columella present in holotype.

DISCUSSION.—Filkorn (1994) compared *Levicyathus* to *Turbinolia*, even suggesting that it might be a “potential likely candidate” for the ancestral genus to *Turbinolia*. Characters in common between the two genera include: corallum shape, similar columella, and absence of pali; however, *Levicyathus* differs in having a nonpitted theca, serrate costal ornamentation, and trifurcate higher cycle costae. The phylogenetic analysis does not suggest a close relationship to *Turbinolia*, but rather to several other Late Cretaceous Antarctic genera and to *Thrypticotrochus*, being paired with the latter genus in 68% of all trees generated (e.g., Figures 3, 4B–D). *Levicyathus* differs from *Thrypticotrochus* only in having a styliform (not papillose) columella and in lacking paliform lobes, whereas *Thrypticotrochus* has multiple paliform lobes.

Levicyathus is known only from two specimens, and one of these, the paratype, is useless for calicular detail. As with most of the species described from the Late Cretaceous Antarctic Peninsula, more specimens are required to better characterize them and to properly place them into a phylogeny.

DISTRIBUTION.—Late Cretaceous (Maastrichtian): López de Bertodano Formation, Seymour Island, Antarctic Peninsula.

TYPE SPECIES.—*Levicyathus cairnsi* Filkorn, 1994, by original designation. Distribution as for genus. Types deposited at the USNM (93038, 93039).

OTHER SPECIES.—None.

***Thrypticotrochus* Cairns, 1989**PLATES 2*h*, 5*b*, 7*i**Thrypticotrochus* Cairns, 1989a:37; 1995:92.

DIAGNOSIS.—Corallum conical, with pointed, but often irregularly shaped base—latter characteristic of asexual reproduction by regeneration from parent fragment. Calice circular in cross section; largest specimen 6.1 mm in CD. Costae serrate in ornamentation (Plate 7*i*); intercostal regions narrow, deep, and not pitted. Higher cycle costae (C3–5) originate by bi- or trifurcation. Septa hexamerally arranged in 4 or more cycles (48–72 septa). Multiple paliform lobes (Plate 7*h*) on all but last septal cycle (P1–3, or P1–4). Columella papillose.

DISCUSSION.—Only one other turbinoliid genus, *Australocyathus*, has multiple paliform lobes on all but its last cycle of septa, but it differs from *Thrypticotrochus* in many other characters (Table 5). *Thrypticotrochus* is unique in the family for having a seemingly consistent mode of asexual reproduction by regeneration from parent fragments. The phylogenetic position of *Thrypticotrochus* and its relation to *Levicyathus* are discussed in the account of the latter. The type species is described and figured by Cairns (1989a, 1995).

DISTRIBUTION.—Recent: Indo-West Pacific, including off Queensland, New South Wales, and the Norfolk Ridge; 95–925 m.

TYPE SPECIES.—*Thrypticotrochus multilobatus* Cairns, 1989, by original designation. Distribution as for genus except for off New South Wales. Holotype and most paratypes deposited at the USNM; one paratype at the MNHNP; one paratype at the Australian Museum (see Cairns, 1989a).

OTHER SPECIES.—*Thrypticotrochus petterdi* (Dennant, 1906). Recent: off New South Wales; 457 m.

***Cryptotrochus* Cairns, 1988**PLATES 2*a*, 5*c*, 7*j,k**Cryptotrochus* Cairns, 1988:709–710; 1995:88 [in part; not *C. venustus*].

DIAGNOSIS.—Corallum conical, with pointed base and calice circular in cross section; coralla less than 10 mm in CD. Costae highly ridged and serrate (Plate 7*k*) or granular in ornamentation; intercostal regions deep, relatively narrow, and not pitted. Higher cycle costae (C3–4) originate by trifurcation (Plate 7*j*). Costae continuous from point of origin to calice, showing no evidence of fragmentation; c:s = 1. Septa hexamerally arranged in 4 complete cycles. Six P2 encircle a papillose columella.

DISCUSSION.—*Cryptotrochus* is polymorphic in two of the characters used in the phylogenetic analysis. The type species *C. carolinensis* has serrate costae (character 9) and fused higher cycle (S3–4) septa (character 11), whereas *C. javanus* has granular costae and independent septa. A third species, *C. venustus*, was included in the genus by Cairns (1995) but was transferred to *Pleotrochus* for reasons discussed in the account of that genus. *Cryptotrochus* is one of eight genera in clade 2 that constitute an unresolved polychotomy in the strict

consensus tree (Figure 2), and its position is variable in the five more resolved topologies illustrated in Figures 3, 4A–D. Based on the characters used in the phylogenetic analysis, *Cryptotrochus* is most similar to *Alveolocyathus* (see Filkorn, 1994), differing only in having a nonpitted theca and in having species that are polymorphic for characters 9 and 11 (i.e., costal ornamentation and septal independence).

DISTRIBUTION.—Recent: western Atlantic (off North Carolina); Java Sea; 320–585 m.

TYPE SPECIES.—*Cryptotrochus carolinensis* Cairns, 1988, by original designation. Recent: off North Carolina; 320–338 m. Types deposited at the USNM (46914–15).

OTHER SPECIES.—*Cryptotrochus javanus* Cairns, 1988. Recent: Java Sea; 585 m.

***Laminocyathus* Filkorn, 1994**PLATES 2*b*, 5*d**Laminocyathus* Filkorn, 1994:63–64.

DIAGNOSIS.—Corallum conical, with pointed base and calice circular in cross section; holotype 7.5 mm in CD. Costae beaded (?abraded serrate); intercostal regions equal in width to costae and exteriorly pitted. Higher cycle costae (C3–4) originate by trifurcation near corallum base. Septa hexamerally arranged in 4 cycles. Six P2 lamellar and prominent. Columella rudimentary, expressed only as a horizontal fusion of lower inner edges of P2.

DISCUSSION.—This genus, which is based on only the holotype of *L. wellsi*, is more fully described by Filkorn (1994). Although it appears to differ from all other turbinoliid genera, additional specimens are required to better define the genus. The most logical assumption for the state of costal ornamentation, which was indicated by a question mark in the data matrix (Table 5), is serrate.

Laminocyathus differs from the other Late Cretaceous turbinoliid genera by lacking a columella. Like *Conocyathus*, it has P2 and lacks a columella, but *Conocyathus* differs in having costae of independent origin, fused higher cycle septa, less than 48 septa, and a c:s of 2. The similarity of *Laminocyathus* to *Alveolocyathus* is discussed in the account of the latter.

DISTRIBUTION.—Late Cretaceous (Maastrichtian): López de Bertodano Formation, Seymour Island, Antarctic Peninsula.

TYPE SPECIES.—*Laminocyathus wellsi* Filkorn, 1994, by original designation. Distribution as for genus. Holotype deposited at the USNM (93035).

OTHER SPECIES.—None.

***Alveolocyathus* Filkorn, 1994**PLATES 2*c*, 5*e**Alveolocyathus* Filkorn, 1994:60–62.

DIAGNOSIS.—Corallum conical, with pointed base and calice

circular in cross section; holotype 8.3 mm in CD. Costae serrate; intercostal regions equal in width to costae and exteriorly pitted. Higher cycle costae (C3–4) originate by trifurcation on lower third of corallum. Septa hexamerally arranged in 4 cycles. Six lamellar P2 encircle papillose columella.

DISCUSSION.—*Conocyathus felixi* is considered to be a junior synonym of *A. nordenskjöeldi* because of its similarity to the holotype of that species. *Conocyathus*, as defined in this revision, differs from *Alveolocyathus* in having independent costal origins, fused higher cycle septa, only three cycles of septa, a c:s of 2, and granular costae. *Conocyathus felixi* has none of the previously listed characters.

Although not noted by Filkorn (1994), *Alveolocyathus* is quite similar to *Laminocyathus*, differing only in having a papillose columella instead of a rudimentary horizontal axial plate. *Alveolocyathus* is one of eight genera in clade 2 that constitute an unresolved polychotomy in the consensus tree; however, consistent with their morphological similarities, *Alveolocyathus* and *Laminocyathus* are paired as a monophyletic unit (Figures 3, 4A,D) or in a unresolved polychotomy (Figure 4B,C).

DISTRIBUTION.—Late Cretaceous (Maastrichtian): López de Bertodano Formation, Seymour Island, Antarctic Peninsula.

TYPE SPECIES.—*Alveolocyathus nordenskjöeldi* Filkorn, 1994 (= *Conocyathus felixi* Filkorn, 1994), by original designation. Distribution as for genus. Holotype deposited at the USNM (92997).

OTHER SPECIES.—None.

Pseudocyathoceras Cairns, 1991

PLATES 2e, 5f

Kionotrochus.—Durham and Barnard, 1952:88 [in part].

Cyathoceras.—Cairns, 1982:22 [in part].

Pseudocyathoceras Cairns, 1991:20.

DIAGNOSIS.—Corallum conical, with calice circular to slightly elliptical in cross section and narrow base in which 6 protosepta of basal disc often apparent. Largest corallum 10.3 mm in GCD. Costae independent in origin, finely granular, and separated by relatively shallow intercostal regions. Septa highly exsert and decamerally arranged in 3 cycles (i.e., 10:10:20 = 40 septa). Pali and paliform lobes absent. Columella fascicular.

DISCUSSION.—The planular larvae of all Scleractinia settle on and subsequently attach to a hard substratum after which they either remain attached by consolidating their base, detach from the substratum, or incorporate the substratum into their base, the last two conditions resulting in unattached (free) coralla. Most turbinoliids follow the third mode described above, usually overgrowing the small sand grain or shell fragment on which it settled by incorporating it into the base of its corallum, leaving little or no evidence of its original attachment. *Pseudocyathoceras* is known from very few

specimens (about 16, see Cairns, 1991) but is distinct among the turbinoliids in that its corallum appears to detach from the substratum at a later ontogenetic stage, temporarily revealing the six protosepta of the basal disc, which it later covers with edge zone and costae. This temporary pedicellate pseudoattachment, a growth mode alluded to by Durham and Barnard (1952) for *P. hoodensis*, as well as its fascicular columella and shallow intercostal regions, are all character states more characteristic of the various caryophylliid subfamilies and thus suggestive of an ancestral placement of *Pseudocyathoceras* within clade 3 and perhaps even an implied ancestral morphology for the family. The type species is more fully described and illustrated by Cairns (1991).

DISTRIBUTION.—Recent: Galápagos; 91–183 m.

TYPE SPECIES.—*Kionotrochus avis* Durham and Barnard, 1952 (= *Kionotrochus hoodensis* Durham and Barnard, 1952), by original designation. Distribution as for genus. Types transferred from Allan Hancock Foundation to the Santa Barbara Museum of Natural History in 1991.

OTHER SPECIES.—None.

Idiotrochus Wells, 1935

PLATES 2f,i, 5g, 7l

Sphenotrochus (*Idiotrochus*) Wells, 1935:532–533.

Idiotrochus.—Vaughan and Wells, 1943:212.—Wells, 1956:F425.—Chevalier, 1987:746.—Cairns, 1989a:35–35; 1994:69.

DIAGNOSIS.—Corallum commonly results from transverse division; anthocyathus cuneiform in shape (elliptical in cross section), with planar thecal faces, rounded edges, and wedge-shaped base that may bear 2 short downward- or outward-projecting costal spurs; anthocaulus conical. Anthocyathus up to 6.6 mm in GCD. Costae broad, smooth, alternating in position with septa (Plate 7l). Intercostal spaces narrow, relatively shallow, and not pitted; costae independent in origin. Septa hexamerally arranged in 3 cycles (24 septa). Crown of 10 or 12 pali before S1–2, the 2 principal P1 often absent or rudimentary. Columella linear-papillose.

DISCUSSION.—*Idiotrochus emarginatus* and *I. australis* are very similar to *Sphenotrochus wellsi* in gross morphology, all three species having the “fishtail” basal costal spurs (Plate 9d). Furthermore, all three species occur together in the Balcombe stage (Middle Miocene) of Victoria. If the same range of variation of corallum shape was allowed for *Idiotrochus* as occurs in *Sphenotrochus wellsi*, then *I. australis* and *I. emarginatus* would be considered conspecific. *Idiotrochus* differs from *Sphenotrochus* in having a papillose columella, P1–2, and independent costae that alternate with their septa.

Idiotrochus and *Dunocyathus* form a small, but well-supported unit within clade 3 (Figures 2, 3), characterized by having pali before all but the last cycle, transverse division, and alternating costae and septa. *Idiotrochus* is distinguished from *Dunocyathus* by having smooth (not granular) costae and narrower intercostal regions; a compressed, conical (not short

and cylindrical) corallum; and monomorphic pali.

DISTRIBUTION.—Early Oligocene (Janjukian) to Middle Miocene (Balcombian); Victoria, Australia. Recent: western Pacific, including South Australia, Queensland, Indonesia, and Japan; 82–645 m.

TYPE SPECIES.—*Sphenotrochus emaciatus* Duncan, 1865 (= *Sphenotrochus excisus* Duncan, 1870; = *Sphenotrochus emaciatus* var. *peregrinus* Dennant, 1906), by original designation. Early Oligocene to Middle Miocene of Victoria; Recent of South Australia; 82–238 m. Holotype deposited at the BMNH (R29276).

OTHER SPECIES.—*Idiotrochus australis* (Duncan, 1865). Middle Miocene (Balcombian): Victoria.

I. kikutii (Yabe and Eguchi, 1941). Recent: Indonesia and Japan; 97–645 m.

Idiotrochus new species, sensu Cairns and Parker, 1992. Recent: off Queensland; 150 m.

Dunocyathus Tenison-Woods, 1878

PLATES 2*k,l*, 5*h*, 8*a*

Dunocyathus Tenison-Woods, 1878b:305.—Vaughan and Wells, 1943:177.—Wells, 1956:F425–F426; 1958:266.—Chevalier, 1987:728.—Cairns and Parker, 1992:41–42.

DIAGNOSIS.—Corallum commonly asexually reproduced by transverse division; anthocyathus discoidal in shape, circular in cross section, with flat to slightly concave base; coralla up to 6.3 mm in CD. Anthocaulus conical, rarely more than 3 mm in diameter, base invariably immersed in cone-shaped bryozoan colony (Plate 2*k*). Costae broad, flat, and covered with numerous small granules; costae alternate in position with septa (Plate 8*a*); intercostal spaces broad, relatively shallow, and not pitted. Costae independent in origin. Septa hexamerally arranged in 3 cycles. Crown of 12 pali before first 2 cycles, P2 being taller and wider than P1. Columella papillose.

DISCUSSION.—Although a specimen in the process of transverse division has not been collected, there is little doubt (Wells, 1958) that the species asexually reproduces in this manner, anthocyathus and anthocaulus stages often being found at the same station. Both stages were described independently by Tenison-Woods (1878b), the small, more rarely collected anthocaulus stage as *Dunocyathus parasiticus*, and the larger, more common anthocyathus stage as *Deltocyathus rotaeformis*.

Vaughan and Wells (1943) and Chevalier (1987) placed *Dunocyathus* in the Rhizangiidae, probably because Tenison-Woods described *Dunocyathus* as having denticulate inner septal edges. Tenison-Woods may have been referring to denticulate palar edges, because the inner septal edges of *Dunocyathus* are smooth, as in all turbinoliids and caryophyllidiids. Wells (1958) correctly placed the genus in the Turbinoliidae. The type species was recently described and figured by Cairns and Parker (1992).

Using the characters in the data matrix (Table 5), *Duno-*

cyathus is most similar to *Idiotrochus* (Figure 3), as discussed in the account of that genus.

DISTRIBUTION.—Recent: South Australia to New South Wales, including Tasmania; 64–549 m (Cairns and Parker, 1992).

TYPE SPECIES.—*Dunocyathus parasiticus* Tenison-Woods, 1878b (= *Deltocyathus rotaeformis* Tenison-Woods, 1878b), by monotypy. Distribution as for genus. Deposition of type material unknown.

OTHER SPECIES.—None.

Wellsotrochus Squires, 1960

PLATE 2*j*

Wellsia Squires, 1958:57 [not Imlay, 1957].

Wellsotrochus Squires, 1960b:1053 [new name]; 1962:145.

DIAGNOSIS.—Corallum bowl-shaped, with flat to rounded base, and calice circular in cross section; CD up to 8 mm. Costae presumed to be granular; c:s = 2, interseptal costae being quite narrow; intercostal regions also narrow and not pitted. Costae independent in origin. Septa hexamerally arranged in 3 to 4 cycles (24–48 septa). Pali and paliform lobes absent. Columella styliform.

DISCUSSION.—*Wellsotrochus* is the most poorly known of the turbinoliid genera. The nine specimen type-series of *W. cyathiformis*, as well as three additional topotypic specimens (AU H325–327), were examined on loan from Auckland University. The holotype is 6.75 mm in diameter and has costae 0.5 mm in width, the presumed interseptal costae only 0.2 mm wide. The reason for the lack of knowledge about this genus is that all 12 known specimens of the type species are embedded, calice down, in a hard, sandy matrix, not allowing a proper determination of columella, septal, or palar structure. For those character states, the original description (Squires, 1958) was used, which must have been based on a polished cross section of one paratype (Squires, 1958, pl. 10: fig. 16), not seen by the author.

According to the phylogenetic analysis, *Wellsotrochus* is most closely related to *Holcotrochus*, either as a sister taxon to the group that includes *Holcotrochus* (Figure 3) or in a trichotomy with *Holcotrochus* and three other genera (Figure 2). *Wellsotrochus* differs from *Holcotrochus* in having a styliform columella and a bowl-shaped (versus conical) corallum. The most logical assumption for its state of costal ornamentation, which was indicated as a question in the data matrix, is granular.

DISTRIBUTION.—Late Cretaceous (Haumurian (= Maastrichtian)): North Island, New Zealand. Squires' (1958) first indication of an earlier Piripauan stage (= Campanian) was subsequently corrected by him (Squires, 1962) to the later Haumurian stage.

TYPE SPECIES.—*Wellsia cyathiformis* Squires, 1958, by original designation. Late Cretaceous (Haumurian), New Zealand. Type material deposited at the Auckland University,

Department of Geology (AUC 9a-i).

OTHER SPECIES.—*Wellsotrochus conicus* Squires, 1962. Late Cretaceous (Haumurian): New Zealand.

W. discus Squires, 1962. Late Cretaceous (Haumurian): New Zealand.

Holcotrochus Dennant, 1902

PLATE 2g

Holcotrochus Dennant, 1902a:1.—Vaughan and Wells, 1943:214.—Wells, 1956:F426.—Chevalier, 1987:747.

DIAGNOSIS.—Corallum elliptical in cross section, with rounded base and inflated or planar thecal faces. Corallum small, largest known only 3.5 mm in GCD. Costae corresponding to septa independent, quite wide, and coarsely granular; additional cycle of much smaller intercostae occur between major costae, these smaller costae originating by bifurcation and not corresponding to septa. Septa highly exsert and hexamerally arranged in two cycles, second cycle always incomplete, with only 4 of 6 S2 developed ($6 + 4 = 10$ septa). Pali and paliform lobes absent. Columella rudimentary, composed of a fusion of inner septal edges.

DISCUSSION.—*Holcotrochus* is a distinctive genus, differing from other turbinoliid genera by having only 10 septa and much smaller intercostae, some of which originate by bifurcation. The type species, *H. scriptus*, differs from *H. crenulatus* by having narrower intercostae that are continuous from calice to base, lacking a thecal edge sulcus, and in having convex thecal faces. Both species were described and figured by Cairns and Parker (1992).

The phylogenetic analysis places *Holcotrochus* either as the sister taxon of *Conocyathus* and two other genera (Figure 3) or in a trichotomy with *Wellsotrochus* and three other genera, one of which is *Conocyathus* (Figure 2). The similarities between *Holcotrochus* and *Wellsotrochus* are discussed in the account of the latter genus. *Holcotrochus* differs from *Conocyathus* by having independent septa, a nonpitted theca, and lacking pali.

DISTRIBUTION.—Early Oligocene (Janjukian): Torquay, near Geelong, Victoria. Middle Miocene (Balcombian): Muddy Creek, Victoria. Recent: off South Australia; off Murray Island, eastern Torres Strait; 9–185 m.

TYPE SPECIES.—*Holcotrochus scriptus* Dennant, 1902a, by monotypy. Early Oligocene to Middle Miocene: Victoria; Recent: South Australia and Torres Strait; 9–185 m. Holotype deposited at the National Museum of Victoria, Melbourne (P27086).

OTHER SPECIES.—*Holcotrochus crenulatus* Dennant, 1904. Recent: off South Australia; 40–101 m.

Conocyathus d'Orbigny, 1849

PLATES 3a, 5j, 8b

Conocyathus d'Orbigny, 1849:5.—Milne Edwards and Haime, 1851:20.—Vaughan and Wells, 1943:210.—Alloiteau, 1952:646.—Wells,

1956:F425.—Chevalier, 1987:747–748.—Filkorn, 1994:49–50.

Sylocyathus Reuss, 1856:266.—Not d'Orbigny, 1849:4.

Pleurocyathus Kefferstein, 1859:364.

Not *Madrepora* (*Conocyathus*) Brook, 1893:160 [= *Acropora*].

?*Conocyathus* (*Chingchingocyathus*) Ogbe, 1976:2.

DIAGNOSIS.—Corallum conical, with rounded base and calice circular to slightly elliptical in cross section; coralla small, largest known specimen only 3.4 mm in CD. Costae corresponding to septa independent in origin and very finely granular, giving the appearance of being smooth. Additional cycle of equal-sized intercostae also present (c:s = 2). Unilinear series of deep thecal pits in each costal/intercostal region (Plate 8b), but only in worn specimens do these pits completely penetrate theca. Septa hexamerally arranged in 3 cycles. One crown of 6 styliform or lamellar pali (P2) occurs before S2. Columella rudimentary to absent.

DISCUSSION.—The genus and type species of *Conocyathus*, *C. sulcatus*, were described in four short lines without a figure (d'Orbigny, 1849). It is the only genus in this revision for which a representative of the type species was not examined. Most of the species in this genus are also poorly known or are of doubtful status. The generic diagnosis given above was based on several Recent specimens of *C. zelandiae* (see Cairns, 1995) and the syntype of *C. cyclocostatus* Tenison-Woods, 1878.

Filkorn (1994) has given a comprehensive account of the various species previously assigned to *Conocyathus*, concluding that there are six valid species, including his new species *C. felixi*. In re-examining the type of *C. felixi*, I have reassigned it to the genus *Alveolocyathus*, but added *C. cyclocostatus* and two other species described from the Paleocene of Nigeria (Ogbe, 1976). The latter two species are strongly queried as belonging to this genus, both species stated as having dissepiments, which is inconsistent with a placement in the Turbinoliidae.

Conocyathus is quite similar to *Turbinolia*, a similarity noted by most authors who have studied the two genera, including d'Orbigny (1849), who described *Conocyathus* in comparison to *Turbinolia*. Tenison-Woods (1878b:302) summed up their similarities, when, in writing of *C. zelandiae*, stated: "It is in all respects a *Turbinolia* with pali, instead of a columella." This similarity is increased in those species of *Turbinolia* (e.g., *T. pharetra*, *T. wautubbeensis*) that have a stellate columella that is composed of six lamellar plates aligned with the six S2, their inner edges strongly fused into a central columella. This stellate structure is considered to be analogous rather than homologous to the six P2 of *Conocyathus*, the inner edges of which are free, not fused into a central structure. It should also be noted that *Conocyathus* also differs from *Turbinolia* in having only one row of exterior pits between each costa, and in having finely granular, not smooth, costae. Nonetheless, the morphological similarity of these two genera is reflected in the phylogenetic analysis by having *Conocyathus* as the sister taxon to *Turbinolia* and *Sphenotrochus* (Figures 2, 3).

DISTRIBUTION.—Paleocene: Tonga; Nigeria; Togo. Early Oligocene (Rupelian): Europe. Eocene to Middle Miocene (Balcombian): South Australia and Victoria. Recent: Indo-West Pacific; 6–130 m.

TYPE SPECIES.—*Conocyathus sulcatus* d'Orbigny, 1949, by monotypy. Early Oligocene (Rupelian): Mayence (= Mainz), Germany. Deposition of types unknown (probably lost).

OTHER SPECIES.—*Conocyathus togoensis* Oppenheim, 1915. Paleocene: Togo and Nigeria.

?*C. danae* Ogbe, 1976. Paleocene: Togo and Nigeria.

?*C. ireneae* Ogbe, 1976. Paleocene: Nigeria.

C. turbinoloides (Reuss, 1856). Oligocene: Cassel, northern Germany (type species of *Stylocyathus*).

C. dilatatus (Roemer, 1863). Late Oligocene: Cassel, northern Germany (type species of *Pleurocyathus*).

C. zelandiae Duncan, 1876 (= *C. scrobiculatus* Dennant, 1902b; = *C. australiensis* (Gardiner, 1939b)). Oligocene: New Zealand. Eocene to Miocene: South Australia. Recent: Persian Gulf to New Zealand; 6–130 m.

C. cyclocostatus Tenison-Woods, 1878a. Middle Miocene (Balcombian): Muddy Creek, Victoria.

Turbinolia Lamarck, 1816

PLATES 3b-d, 5i,k,l, 8c-g

Turbinolia Lamarck, 1816:229 [in part].—Milne Edwards and Haime, 1850:xvi; 1857:60.—Quayle, 1932:94–95.—Vaughan and Wells, 1943:211 [in part; not *Batotrochus*].—Alloiteau, 1952:645.—Wells, 1956:F425 [in part; not *Batotrochus*].

Oryzotrochus Wells, 1959:286–287 [new synonym].

DIAGNOSIS.—Corallum conical, circular in cross section and small, rarely exceeding 3.5 mm in CD. Costae independent in origin, usually well-developed, smooth ridges, and C1–2 sometimes thickened basally. Intercostae present or absent, depending on species; in type species, present as alignment of low mounds, becoming low ridges only near the calice. Series of circular pits up to 70 µm in diameter flank each costa, each bordered on distal and proximal edges by small thecal buttresses oriented perpendicular to the costa and often fused to the intercostae, if present (Plate 8c,f). Thecal pits thus appear to form a double column, often in alternating arrangement. Septa exsert, hexamerally arranged in 2–4 cycles (12–48 septa). Pali and paliform lobes absent. Columella quite variable, including styliform, stellate, hexameral, and lamellar (see Quayle, 1932).

DISCUSSION.—When Wells (1937a) established the subgenus *Turbinolia* (*Batotrochus*) for the modern species *T. corbicula* Pourtales, 1878, he effectively extended the latest known geologic occurrence of the genus from Oligocene to Recent. However, when Cairns (1979) subsequently transferred *T. corbicula* to *Trematotrochus*, a genus characterized by having complete thecal perforations and paliform lobes (P2), the stratigraphic range of *Turbinolia* once again reverted to Paleocene to Oligocene. However, in reanalyzing coralla of *Oryzotrochus stephensi* by SEM, it was noted that they

possess thecal pits identical in construction to those of *Turbinolia*, as well as all other characters consistent with that genus. Wells (1959) had noted the close resemblance between *Oryzotrochus* and *Turbinolia* but distinguished the former by not having thecal pits; well-preserved specimens of *Oryzotrochus* clearly have these pits, albeit smaller ones (Plate 8d,g). *Oryzotrochus* differs from other species of *Turbinolia* in having a very small corallum, perhaps the smallest of any scleractinian (CD max. = 1.7 mm) and only two cycles of septa (12 septa). In his generic diagnosis of *Turbinolia*, Quayle (1932:94) allowed for species with two, three, and four cycles of septa (12, 24, 48 septa, respectively), although I could find no description of a species with only 12 septa. Nonetheless, in examining some unidentified *Turbinolia* in the USNM collections from the Middle Eocene (Lutetian) of France (Grignon, Ferme de l'Orme, Seine et Oise), several specimens were found that were virtually identical to modern *Oryzotrochus*, including having only 12 septa (Plates 3d, 5l, 8e). The cryptic *Oryzotrochus stephensi* is thus reinterpreted to be the only known Recent representative of *Turbinolia*, distinguished from other species in the genus by having only two cycles of septa and a very small corallum.

Because of the species richness of this genus (45 species) and numerical abundance in some sediments, *Turbinolia* has received considerable attention. Some noteworthy publications include the following: a fine description of the type species, *T. sulcata*, by Milne Edwards and Haime (1850:13–15); a review of the California Eocene species and an evaluation of columellar variation (Quayle, 1932); a review of the American Gulf Coast species (Monsour, 1944); a redescription of 14 species (Glibert, 1974); and a discussion of ontogenetic development in several European species (Chaix, 1980). Nonetheless, little revisionary work has been done on the species of this genus, and the list of 45 species below is undoubtedly incomplete as well as including possible synonyms.

The phylogenetic analysis (Figures 2, 3) groups *Turbinolia* and *Sphenotrochus* as a well-supported unit, *Turbinolia* differing primarily in having an exteriorly pitted theca and a corallum circular (not elliptical) in cross section. Three of the characters are expressed in an overlapping polymorphic fashion, i.e., *Turbinolia* has species with lamellar or styliform columellas, whereas *Sphenotrochus* has species with lamellar or papillose columellas; *Turbinolia* has smooth costae, whereas *Sphenotrochus* has smooth or granular costae; and *Turbinolia* has species with 12 to 48 septa, whereas *Sphenotrochus* species have fewer than 48 septa.

DISTRIBUTION.—Paleocene: southeastern U.S. (Midwayan); west Africa. Early Eocene: southeastern U.S. (Midwayan); Belgium (Ypresien); Barbados. Middle Eocene: North America (Claibornian); Europe (Lutetian, Bruxellien). Late Eocene: North America, Europe (Auversian, Bartonian, Lattorfian); west Africa. Early Oligocene: southeastern U.S. (Vicksburgian); Peru. Recent: Great Barrier Reef; 9–24 m.

TYPE SPECIES.—*Turbinolia sulcata* Lamarck, 1816, by subsequent designation (Milne Edwards and Haime, 1850:xiv). Middle Eocene (Lutetian) England, France, Belgium. Deposition of type material unknown.

OTHER SPECIES.—*Turbinola midwayensis* Monsour, 1944. Paleocene (Midwayan): U.S. (Mississippi).

?*T. rosetta* Howe, 1960. Paleocene (Midwayan): U.S. (Alabama).

T. frescoensis Barta-Calmas, 1969. Middle Paleocene: Côte d'Ivoire, West Africa.

T. acuticostata Vaughan, 1895. Early Eocene: U.S. (Virginia, Maryland).

T. barbadensis Wells, 1945. Early Eocene: Barbados.

T. barbadensis crassicostata Wells, 1945. Early Eocene: Barbados.

T. pusillanima Nomland, 1916 (= *T. jollaensis* Hanna, 1927). Early Eocene: U.S. (California).

T. dickersoni Nomland, 1916. Early Eocene: U.S. (California).

T. panisellensis Glibert, 1974. Early Eocene (Ypresien) to Middle Eocene (Bruxellien): Belgium.

T. clarki Quayle, 1932. Middle Eocene: U.S. (California).

T. dispar de France, 1828. Middle Eocene (Lutetian): France.

T. dixoni Milne Edwards and Haime, 1848. Middle Eocene: France, England.

T. imbulata (Hanna, 1927). Middle Eocene: U.S. (California).

T. subtercisa Monsour, 1944. Middle Eocene (Claibornian): U.S. (Texas, Alabama, Louisiana).

T. subtercisa var. *lisbonensis* Monsour, 1944. Middle Eocene (Claibornian): U.S. (Alabama).

T. subtercisa var. *mauricensis* Monsour, 1944. Middle Eocene (Claibornian): U.S. (Louisiana).

T. tenuis Monsour, 1944. Middle Eocene (Claibornian): U.S. (Alabama).

T. tenuis var. *conica* Monsour, 1944. Middle Eocene (Claibornian): U.S. (Alabama).

T. gigantissima Monsour, 1944. Middle Eocene (Claibornian): U.S. (Alabama).

T. pharetra Lea, 1833. Middle Eocene (Claibornian): U.S. (Texas, Alabama, Louisiana).

T. wautubbeensis Vaughan, 1900. Middle Eocene (Claibornian): U.S. (Mississippi, Alabama, Louisiana).

T. costata Milne Edwards and Haime, 1848. Middle Eocene (Lutetian): France.

T. vincenti Glibert, 1930. Middle Eocene (Lutetian): Belgium.

T. nilensis Gilbert, 1930. Middle Eocene (Lutetian): Belgium.

T. bowerbanki Milne Edwards and Haime, 1850. Middle Eocene: England.

T. exarata Duncan, 1866. Middle Eocene: England.

T. claibornensis Vaughan, 1900. Late Eocene (Claibornian): U.S. (Alabama).

T. vaughani Filliozat, 1914. Late Eocene (Auversian): France.

T. forbsi Duncan, 1866. Late Eocene (Bartonian): England.

T. humilis Milne Edwards and Haime, 1850. Late Eocene (Bartonian): England.

T. nystiana Milne Edwards and Haime, 1850. Late Eocene (Bartonian): Belgium.

T. gerardi Vincent, 1921. Late Eocene (Bartonian): Belgium.

T. frederickiana Milne Edwards and Haime, 1850. Late Eocene (Bartonian): England.

T. firma Milne Edwards and Haime, 1850. Late Eocene (Bartonian): England.

T. prestwichii Milne Edwards and Haime, 1850. Late Eocene (Bartonian): England.

T. minor Milne Edwards and Haime, 1850. Late Eocene (Bartonian): England.

T. attenuata Kefferstein, 1859. Late Eocene (Lattorfian): Germany.

T. lamellifera Kefferstein, 1859. Late Eocene (Lattorfian): Germany.

T. pygmaea Roemer, 1863. Late Eocene (Lattorfian): Germany.

T. affinis Duncan, 1866. Late Eocene: England.

T. sp. sensu Wells, 1937a. Late Eocene: Nigeria.

T. weaveri Durham, 1942. Eocene: U.S. (Washington).

T. quaylei Durham, 1942. Eocene: U.S. (Washington).

T. insignifica Vaughan, 1900. Early Oligocene: U.S. (Mississippi).

T. vicksburgensis Monsour, 1944. Early Oligocene (Vicksburgian): U.S. (Alabama, Mississippi, Louisiana).

T. olssonii Wells, 1937a. Oligocene: Peru.

T. octoscissa Quenstedt, 1881. Oligocene: Germany.

T. stephensonii (Wells, 1959), new combination. Recent: Great Barrier Reef; 9–24 m (type species of *Oryzotrochus*, original designation).

Sphenotrochus Milne Edwards and Haime, 1848

PLATES 3j, 6a, 8h,i, 9a–e

Sphenotrochus Milne Edwards and Haime, 1848:240–241; 1850:xvi.—Vaughan and Wells, 1943:211–212.—Alloiteau, 1952:645.—Wells, 1956:F425.—Chevalier, 1987:746.—Cairns, 1989a:37–38.

Sphenotrochus (*Eusthenotrochus*) Wells, 1935:530; 1956:F425.—Vaughan and Wells, 1943:212.—Alloiteau, 1952:645.—Chevalier, 1987:746.

DIAGNOSIS.—Corallum cuneiform, with rounded base and calice invariably elliptical in cross section; coralla rarely exceed 10 mm in GCD. Costal ornamentation variable, including smooth and finely granular. Costae continuous from base to calice (Plate 9a); fragmented into short, parallel lamellae; meandering (Plate 8h); or occurring in combinations

of the former (Plate 9e). Costae independent in origin; thecal pits not present. Septa exert, hexamerally arranged in 3 and sometimes partial fourth cycle (24–44 septa). Pali and paliform lobes absent. Columella lamellar to sublamellar, latter characterized by series of short, aligned lamellae or elongate labyrinthiform arrangement of interconnected lamellae (Plate 8i).

DISCUSSION.—Wells (1935) established the subgenus *S. (Eusthenotrochus)* for those species having costae composed of short segments (sometimes three or four elongate granules across a costa), instead of the more typical single costal ridge that extends from its origination to the calice. Those seven species having the *Eusthenotrochus*-type costal morphology are marked with an asterisk in the list below. However, in some species the lower one-third to one-half of the thecal faces has linear costae, whereas the upper portion has discontinuous costae. Even the type species, *S. crispus*, has a unique transitional morphology: the costae near the base are linear, but away from the base they become quite sinuous (convoluted) and occasionally disjunct (Plate 9e). It is not difficult to imagine a transition to a *Eusthenotrochus*-type costal morphology if the distalmost section of each costal convolution were to become disjunct. Because the *Eusthenotrochus*-type costal morphology is sometimes difficult to interpret (especially in juveniles), and may occur mixed with the linear type (e.g., in *S. senni*, *S. clairbornensis*), I suggest abandoning this subgeneric differentiation. A more meaningful subgeneric division might be to group the two species having a c:s of 2 and a fishtail basal corallum shape, e.g., *S. wellsi* and *S. trinitatis* (see below).

The similarities between *Sphenotrochus* and *Turbinolia* are discussed in the account of the latter. Both genera are rich in species and abundance, but neither has been recently revised at the species level. The list of 35 nominal species below is probably incomplete and may contain junior synonyms, but it gives an approximation of the distribution of this genus over time.

DISTRIBUTION.—Middle Eocene: Europe (Bruxellian, Lutetian); North America (Clairbornian); Barbados. Late Eocene: England (Auversian); Alps; Java. Oligocene: Europe. Early Miocene: France (Burdigalian). Middle Miocene: West Indies (Langhian); South Australia (Balcombian). Late Miocene: West Indies; Canary Islands. Pliocene: England; New Zealand. Recent: widespread, including the following: tropical eastern Pacific (Lower California and Galápagos); Indo-West Pacific; western Atlantic from Caribbean to Patagonia; eastern Atlantic from South Africa to North Sea; 7–403 m.

TYPE SPECIES.—*Turbinolia crispata* Lamarck, 1816, by subsequent designation (Milne Edwards and Haime, 1850:xvi). Middle Eocene of France (Lutetian) and Belgium (Bruxellian). Deposition of type specimens unknown.

OTHER SPECIES.—*Sphenotrochus dumasi* Filliozat, 1914. Middle Eocene: France.

**S. granulosus* (de France, 1828). Middle Eocene (Lutetian): Europe.

S. milletianus (de France, 1828) (= *S. cuneolus* Couffon, 1903; = *S. cicatricosus* Couffon, 1903; = *S. bouveti* Couffon, 1903; = *S. tonsurratus* Couffon, 1903). Middle Eocene: France.

S. mixtus (de France, 1828). Middle Eocene (Lutetian): France.

S. pulchellus (Lea, 1833). Middle Eocene (Lutetian): France.

**S. fragariooides* Wells, 1945. Middle Eocene: Barbados.

**S. clairbornensis* Vaughan, 1900. Middle Eocene (Clairbornian): U.S. (Alabama).

S. nanus (Lea, 1833). Middle Eocene (Clairbornian): U.S. (Alabama).

S. davisi Thomas, 1942. Late Eocene (Auversian): England.

S. javanus Gerth, 1933. Late Eocene: Java.

S. faudonensis Barta-Calmas, 1973. Late Eocene: Alps.

**S. semigranulosus* (Michelin, 1844). Eocene: France.

S. laculatus Squires, 1962. Tertiary: New Zealand.

S. n. sp. A sensu Squires, 1962. Tertiary: New Zealand.

S. intermedius (Goldfuss, 1827) (= *S. roemerii* Milne Edwards and Haime, 1850). Oligocene to Pliocene: Germany, England, Belgium.

S. cestasensis Chevalier, 1961. Early Miocene (Burdigalian): France.

S. trinitatis Vaughan in Vaughan and Hoffmeister, 1926. Middle Miocene (Langhian): Trinidad.

S. wellsi, new species. Middle Miocene (Balcombian): Victoria, Australia.

**S. senni* Wells, 1945. Middle Miocene to Late Pliocene: Caribbean.

S. pharetra Rothpletz and Simonelli, 1890. Late Miocene: Canary Islands.

S. brassensis Vaughan in Vaughan and Hoffmeister, 1926. Late Miocene to Early Pliocene: Trinidad.

S. aschistus Squires, 1958. Pliocene: New Zealand.

S. boytonensis Tomes, 1888. Pliocene: England.

S. hancocki Durham and Barnard, 1952. Late Pliocene to Recent: western Pacific and tropical eastern Pacific; 18–274 m.

S. excavatus Tenison-Woods, 1878b. Recent: New South Wales; depth unknown.

S. ralphae Squires, 1964. Recent: New Zealand; 7–104 m.

S. squiresi Cairns, 1995. Recent: New Zealand; 66–318 m.

S. aurantiacus Marenzeller, 1904. Recent: southwestern Indian Ocean; 155–366 m.

**S. gilchristi* Gardiner, 1904 (= *S. moseri* Wells, 1935, type of *Eusthenotrochus*, by original designation; = *S. dentosus* Boshoff, 1981, new name). Recent: off South Africa; 24–165 m.

S. evicostatus Cairns in Cairns and Keller, 1993. Recent: southwestern Indian Ocean; 12–73 m.

S. imbricatocostatus Cairns in Cairns and Keller, 1993. Recent: southwestern Indian Ocean; 37–347 m.

S. gardineri Squires, 1961. Recent: southern South America; 9–403 m.

**S. auritus* Pourtalès, 1874. Recent: western Atlantic; 70 m.

S. andrewianus Milne Edwards and Haime, 1848 (= *S. wrighti* Gosse, 1859). Recent: northeastern Atlantic; 12–105 m.

Sphenotrochus wellsi, new species

PLATE 9a,b,d

DIAGNOSIS.—Corallum cuneiform, with planar thecal faces meeting in rounded thecal edges. Holotype 7.7×4.6 mm in CD and 8.9 mm in height; however, largest paratype 9.7×6.0 mm in CD. Calice regularly elliptical ($GCD:LCD = 1.48:1.57$ –1.67), but corallum narrows aborally to thin, wedge-shaped base that usually possesses 2 downward-projecting, triangular (“fishtail” morphology) costal spurs; or, in some specimens fishtail triangles project outward in plane of GCD. In the former, more common case (Plate 9a), an indentation is produced between the 2 triangles, the apex of which is at midpoint of corallum base. In the latter case, the base is nearly linear (Plate 9d). Costae of well-preserved coralla granular, rounded, about 0.20 mm wide, and relatively low in profile. Additional cycle of intercostae of equal width to normal costae occur in all specimens: c:s = 2, total number of costae usually 80. Costae originate independently and continuous from their origin to calice. In specimens in which fishtail spurs project downward, costae confluent on basal spurs, but in outward-projection form, basal spurs ornamented with additional short, discontinuous costae oriented perpendicular to those of the thecal faces.

Septa hexamerally arranged in 4 cycles, last cycle always incomplete, the most common septal complement being 40 (6:6:12:16, S1–2>S3>S4) and highest number of septa being 44. Corallum with 40 septa usually lacks pairs of S4 in 4 specific half systems, such that if the 12 half-systems are numbered in clockwise direction starting with one adjacent to one of the 2 principal septa, half-systems 3 and 5 and their mirror images 10 and 8 would lack S4. (If the corallum is rotated 180°, half-system numbers become 2, 4, 11, 9, but their relation to one another is obviously the same.) Holotype with only 36 septa, also lacking pairs of S4 in half-systems 4 and 9 (or 3 and 10). S1–2 highly exsert (up to 2.5 mm), with slightly sinuous inner edges that fuse to columella low in fossa. Two principal S1 slightly wider than other 10 S1–2. S3 one-half width of S1–2 and about two-thirds as exsert. S4 about one-half width of S3 and two-thirds as exsert. Columella lamellar in large coralla, aligned with the 2 principal S1 and equally as thick. In young coralla, columella formed by line of closely spaced papillae that later fuse into a solid lamella, but, even in large coralla, upper edge of lamellar columella often uneven, reflecting an earlier fusion of separate elements.

DISCUSSION.—Among the 35 species of *Sphenotrochus*, *S. wellsi* is most similar to *S. trinitatis* Vaughan, 1926, also known from the Middle Miocene (Langhian), but of Trinidad.

Both species have the characteristic fishtail basal spur morphology, the same shape and size, and appear to have a c:s of 2. Although Vaughan (in Vaughan and Hoffmeister, 1926) stated that the holotype of *S. trinitatis* (USNM M353645) had 24 large and 24 small costae and that S4 were quite short, the holotype and only known specimen of this species actually has 27 large and 27 smaller ridges, the larger being 0.6 mm in width, the smaller 0.2 mm and much less exsert. The preservation of the calice does not allow a direct view of any S4, and it is possible that they could be missing. If S4 are indeed absent, the 27 smaller ridges' costae may be interpreted as intercostae, as in *S. wellsi*. *Sphenotrochus wellsi* differs from *S. trinitatis* by having costae and intercostae of equal width, and more septa (40–44 versus 27). Another species with a fishtail basal morphology is *S. auritus* Pourtalès, 1874 (Recent, Brazil); however, that species has multiple, discontinuous costal striae (a *Eusthenotrochus*-type costal morphology), no intercostae, and only 24 septa.

Four specimens from Spring Creek, Bird Rock, near Torquay Cliffs, Victoria (Janjukian, Early Oligocene) (USNM 77077) are identical to *S. wellsi* except that their intercostae are only half the width and height as normal costae (Plate 9c). Given the earlier age of these specimens, they might be interpreted as a possible ancestor to *S. wellsi*.

A similarly shaped species, *Idiotrochus australis* (Duncan, 1865), also occurs in the Balcombian of South Australia and Victoria; however, *Idiotrochus* is easily distinguished by having costae that alternate in position with its septa, a c:s of 1, P1–2, and a papillose columella.

ETYMOLOGY.—This species is named in honor of John W. Wells (1907–1994), who diagnosed the species as new in 1954 but never published an account.

DISTRIBUTION.—Middle Miocene (Balcombian): Muddy Creek, Comb Bay, and Altona Bay, Victoria, Australia.

MATERIAL EXAMINED/TYPES.—Holotype: Muddy Creek (Balcombian), Victoria, Australia, USNM 82090. Paratypes: USGS 10817, Muddy Creek (Balcombian), 8, USNM M353593; USGS 10674, Muddy Creek, 10, USNM 77068; USGS 10820, Muddy Creek, 4, USNM 77057; Muddy Creek, 18, USNM 67969; USGS 10809, Comb Bay, Mornington, Victoria, 1, USNM 77070; Altona Bay, Port Phillip, 1, USNM 68009.

TYPE LOCALITY.—Middle Miocene (Balcombian): Muddy Creek, Victoria, Australia.

Foveolocyathus, new genus

PLATES 3e, 6b,c, 9f

Trematotrochus Dennant, 1901:50–51 [in part]; 1904:1, 5–6 [in part].—Cairns and Parker, 1992:30–32 [in part].

DIAGNOSIS.—Corallum conical, calicular margin typically elliptical in cross section, but circular in one species (*F. declivis*); GCD up to 9.3 mm. Costae covered by fine granulation (Plate 9f). Intercostal spaces bridged with transverse bars, as in *Trematotrochus*, but space between successive

bars only a pit that does not fully penetrate the theca (Plate 9f). Higher-cycle costae originate by trifurcation. Septa hexamerally arranged, 40–72 in number; pairs of higher-cycle (S3–5) septa not developed in some end half-systems. Pali and paliform lobes absent. Columella elongate parallel to GCD; papillose.

DISCUSSION.—*Foveolocyathus* is similar to *Trematotrochus*, differing by lacking paliform lobes and having an imperforate, though exteriorly pitted, theca. Dennant (1901, 1904) was well aware that he included species with perforate and pitted theca in the same genus (i.e., *Trematotrochus*), but he considered these character states to represent subgeneric differences. In fact, Dennant (1901) implied that species with the perforate state may have evolved from those with the pitted state based on the consistent stratigraphic relationships between the two groups. Cairns and Parker (1992) divided the species of *Trematotrochus* into two groups: one group of seven species having a perforate theca, and the other group of four species having an exteriorly pitted theca, and suggested a generic or subgeneric differentiation but did not give names to the groups. More recently, Filkorn (1994:39–41) discussed the various kinds of turbinoliid thecal structures, including a key to five types. He distinguished the perforate state from the exteriorly pitted state and interpreted this character to be a “taxonomic discriminator at the generic level.” In the original description of *Trematotrochus*, Tenison-Woods (1879) suggested that the complete perforation of the thecal wall was a generic, if not familial, level character. I concur with Tenison-Woods (1879), Dennant (1901), and Filkorn (1994) that, even if a pitted theca is considered to be an intermediate evolutionary stage between imperforate and perforate, a perforate theca is morphologically and potentially physiologically different from those having an imperforate, pitted theca, and thus should be considered as a separate genus.

The phylogenetic analysis (Figures 2, 3) places *Foveolocyathus* in a polychotomy with *Endocyathopora* and two other pairs of genera. Based on characters used in the analysis, three states separate *Foveolocyathus* from *Trematotrochus*, as previously discussed, but three characters also separate it from *Endocyathopora*. Among the turbinoliid genera that do not have a pitted or perforate theca, *Foveolocyathus* is most similar to *Platytrochus*, sharing with that genus almost all character states except that of an exteriorly pitted theca and independent septa. Clearly, additional characters are needed to clarify the relationships among the six genera in this clade.

ETYMOLOGY.—The generic name *Foveolocyathus* (Latin *foveola*, small pit + *cyathus*, cup) refers to the exteriorly pitted theca of the species in this genus. Gender: masculine.

DISTRIBUTION.—Eocene: Adelaide and Victoria, Australia. Recent: Western Australia to New South Wales; 27–238 m.

TYPE SPECIES.—*Trematotrochus verconis* Dennant, 1904, here designated. Recent: South Australia; 73–101 m. Neotype designated by Cairns and Parker (1992) and deposited at the South Australian Museum (H542). Possible paratypes are also listed by Stranks (1993).

OTHER SPECIES.—*Foveolocyathus kitsoni* (Dennant, 1901), new combination. Eocene: Adelaide bore; Cape Otway; Wilkinson’s Aire Coastal Section 4; Gellibrand River.

F. declivis (Dennant, 1901), new combination. Eocene: Brown’s Creek, Victoria.

F. alternans (Cairns and Parker, 1992), new combination. Recent: Western Australia to New South Wales; 27–238 m.

Endocyathopora Cairns, 1989

PLATES 3*i*, 6*d*, 9*g–i*

Endocyathopora Cairns, 1989a:39.

DIAGNOSIS.—Corallum conical, with blunt, rounded base and circular calice up to 4.0 mm in CD. Costae broad and flat, covered with fine granulation (Plate 9*g*); intercostal regions deep and narrow, but wider near theca, undercutting adjacent costae (Plate 9*h*). Interseptal region on inside of corallum aligned with each intercostal region possess single row of small, shallow depressions (interior pits). Higher-cycle costae (C2–3) originate by bi- and trifurcation. Septa hexamerally arranged in 3 cycles. Six pali (P2). Columella papillose, but usually formed by only 1 or 2 elements.

DISCUSSION.—In the intercostal regions the theca of *Endocyathopora* is quite thin (about 75 µm) and even thinner in those regions that overlie an interior depression. It is conjectured that soon after death the theca begins to dissolve, which, if dissolution occurs homogeneously, would result in thecal perforations in the regions of lesser calcification, i.e., over the interior pits. Thus, the coralla of some recently dead individuals bear some irregularly shaped perforations in their intercostal regions (Plate 9*i*), but these pores are not interpreted as homologous with those of *Trematotrochus*, which are structurally and ontogenetically different.

Endocyathopora differs from all other turbinoliid genera by having an interiorly pitted theca and broad, flat-topped costae that overhang adjacent intercostal regions. The phylogenetic analysis (Figures 2, 3) places this genus in a polychotomy as one of three sister groups to *Trematotrochus* and *Kionotrochus*. Morphologically most similar to *Trematotrochus*, *Endocyathopora* differs by having pali (P2) versus paliform lobes (P2) and interiorly pitted theca versus complete thecal perforations.

DISTRIBUTION.—Recent: Philippines, Indonesia; 46–100 m (Cairns and Zibrowius, 1997).

TYPE SPECIES.—*Endocyathopora laticostata* Cairns, 1989a, by original designation. Distribution as for genus. Types deposited at the USNM (holotype, USNM 81984).

OTHER SPECIES.—None.

Trematotrochus Tenison-Woods, 1879

PLATES 3*h*, 6*g*, 10*a–c*

Trematotrochus Tenison-Woods, 1879:59.—Dennant, 1899a:121.—Vaughan and Wells, 1943:210.—Alloiteau, 1952:646.—Wells, 1956:F425.—Cairns, 1979:111–112.—Chevalier, 1987:748.

Turbinolia (*Batotrochus*) Wells, 1937a:239; 1956:F425.

DIAGNOSIS (emended).—Corallum conical, with pointed base and calice circular to slightly elliptical in cross section; coralla small, not exceeding 4.5 mm in CD. Costae coarsely granular (hispid) in ornamentation. Intercostal spaces porous (Plate 10a), adjacent costae united by ladder-like series of obliquely oriented lamellae 40–60 µm in thickness (Plate 10b, c), which define thecal perforations 90–140 µm in diameter. Higher-cycle costae (C3–4) originate by bi- or trifurcation. Three and sometimes partial fourth cycle of hexamerally arranged septa present, highest cycle septa often rudimentary. Six small paliform lobes (P2) present. Columella rudimentary to papillose.

DISCUSSION.—The generic diagnosis of *Trematotrochus* is emended to include only those species having a perforate theca. Several species previously included in *Trematotrochus* that possess an externally pitted theca are transferred to *Foveolocyathus* (see “Discussion” of *Foveolocyathus*). *Trematotrochus* is the only turbinoliid genus that is characterized by having a truly perforate theca.

Owing to its small size and the relatively deep bathymetric range of living species, coralla of *Trematotrochus* rarely have been collected. Additional specimens of both living and fossil species are needed to better characterize polar and columellar variation and to better understand its stratigraphic distribution. Characters that can be used to distinguish the seven species of *Trematotrochus* include corallum shape (circular vs elliptical in cross section), number of septa (24 or 40), and the relative width of costae. The type species has a small (up to 3 mm GCD) corallum that is characterized by having a circular cross section, 24 septa, with the S3 being rudimentary, and equal-sized costae.

The phylogenetic analysis (Figures 2, 3) places *Trematotrochus* and *Kionotrochus* together based on their shared possession of paliform lobes (P2). *Trematotrochus* differs from *Kionotrochus* only by having a perforate theca and lacking transverse division.

DISTRIBUTION.—?Eocene: Victoria, Australia. Middle Miocene (Balcombian): Victoria. Recent: New South Wales; Cuba; 365–576 m.

The Eocene attribution of two species given by Dennant (1899b, 1901) from Maude and Spring Creek, Victoria, are probably not accurate. Wells (1956) gave the earliest age for this genus as Late Oligocene, whereas Chevalier (1987) gave a Miocene to Recent range.

TYPE SPECIES.—*Conocyathus fenestratus* Tenison-Woods, 1978a, by monotypy. Middle Miocene (Balcombian) of Muddy Creek, Victoria. Syntypes deposited at the Macleay Museum, Sydney (F430, F1698).

OTHER SPECIES.—*Trematotrochus mulderi* Dennant, 1901. Eocene: Maude, Victoria.

T. complanatus Dennant, 1899b. Late Eocene to Middle Miocene: Spring and Muddy Creeks, Victoria.

T. lateroplenus Dennant, 1899b. Late Eocene to Middle Miocene: Spring and Muddy Creeks, Victoria.

T. clarkii Dennant, 1899a. Miocene: Gippsland Lakes, Victoria.

T. hedleyi Dennant, 1906. Recent: New South Wales; 365–457 m.

T. corbicula (Pourtales, 1878). Recent: Cuba; 400–576 m (type species of *Batotrochus*, by original designation).

Kionotrochus Dennant, 1906

PLATES 3f, g, 6e, 10d, e

Kionotrochus Dennant, 1906:154–155.—Vaughan and Wells, 1943:213.—

Wells, 1956:F426.—Chevalier, 1987:748.—Cairns, 1989a:29–30; 1995:87.

Kionotrochus (*Kionotrochus*).—Squires, 1960a:287.

DIAGNOSIS.—Corallum (anthocyathus) the result of asexual reproduction by transverse division. Attached anthocaulus stage cylindrical (Plate 3g) with polycyclic base; free-living anthocyathus stage conical with rounded base (Plate 3f), or, if recently budded, slightly convex base (Plate 10e). Anthocyathus up to 7 mm in CD. Costae finely granular (Plate 10d); intercostal regions deep and not pitted; higher-cycle costae (C3–4) originate by trifurcation. Septa hexamerally arranged in 3 and sometimes incomplete fourth cycle (24–36 septa). Poorly formed crown of 6 styliform paliform lobes (P2) closely encircles papillose columella, paliform and columellar elements sometimes indistinguishable.

DISCUSSION.—Although *Kionotrochus* is endemic to a relatively small region off northern New Zealand, it frequently has been collected there between 100–200 m and thus has been described and illustrated several times (see Cairns, 1995, for a complete synonymy). As many as 10 species have been placed in the genus, but all but one have been reassigned to other genera (Cairns, 1989a:29–30). The phylogenetic relationships of *Kionotrochus* are illustrated in Figures 2, 3 and discussed briefly in the discussion of *Trematotrochus*.

Alloiteau and Tissier (1958) ascribed four new species from the Early Paleocene of the Pyrenees, France, to *Kionotrochus*; however, all four species have an epitheca, a spongy columella, an apparently attached corallum, and lack pali. It is doubtful if these species are turbinoliids.

DISTRIBUTION.—Recent: endemic to northern New Zealand, including Three Kings Islands; 44–622 m (Cairns, 1995, map 8).

TYPE SPECIES.—*Kionotrochus suteri* Dennant, 1906, by monotypy. Distribution as for genus. The syntypes are deposited at the National Museum of Victoria, Melbourne, and the USNM (see Cairns, 1995, and Stranks, 1993).

OTHER SPECIES.—None.

Platytrochus Milne Edwards and Haime, 1848

PLATES 3i, 6f, 10f

Platytrochus Milne Edwards and Haime, 1848:246–247; 1850:xvii; 1857:71.—Vaughan, 1900:73–74.—Vaughan and Wells, 1943:212.—

Alloiteau, 1952:645.—Wells, 1956:F426.—Chevalier, 1987:749.

Koilotrochus Tenison-Woods, 1878b:313.—Wells, 1956:F426.

Aldrichia Vaughan, 1900:70–71 [junior homonym of *Aldrichia* Coquillet, 1894].

Aldrichiella Vaughan, 1903:101 [new name].—Vaughan and Wells, 1943: 212–213.

?*Dominicotrochus* Wells, 1937b:248; 1956:F426.—Vaughan and Wells, 1943:213.—Cairns and Wells, 1987:36.

DIAGNOSIS (emended).—Corallum laterally compressed, often cuneiform, with calice elliptical in cross section and rarely more than 10 mm in GCD. Alate thecal edge costae may be present or absent. Costae smooth or granular, type species having coarsely granular costae (Plate 10f). Intercostae and thecal pits absent. Higher-cycle costae originate by trifurcation. Septa exsert, hexamerally arranged in 3–4 cycles, and in some cases (i.e., *P. stokesii*) separated from their corresponding costae by notch at calicular edge (Plates 6f, 10f). Pali and paliform lobes absent. Columella papillose, consisting of 2 or more irregular rows of papillae.

DISCUSSION.—*Koilotrochus* Tenison-Woods, 1878b, was first synonymized with *Platytrochus* by Dennant (1902b) when he placed the type species of *Koilotrochus*, *K. vacuus* (Tenison-Woods, 1878a), in *Platytrochus*. This equivalence was maintained until Wells (1956) resurrected *Koilotrochus* (with *Aldrichiella* as a junior synonym) for two *Platytrochus*-like species that lacked alate thecal edges. The expression of alate edge costae is not considered to be a generic-level character herein. In retrospect, this character (Table 4: number 8) should not have been used in a generic-level revision of this family. Therefore, both *Koilotrochus* and *Aldrichiella* are considered junior synonyms of *Platytrochus*. Re-examination of the type series of *Aldrichiella elegans* (USNM 66601 and M158010) reveals that the purported attachment of this species occurs in only one very small specimen, which, as in *Pseudocyathoceras*, is probably a vestigial scar left from the original planular settlement. All other specimens are typically free-living and *Platytrochus*-like in character.

Dominicotrochus is a very poorly known genus, the type species, *D. dominicensis*, based on one small, poorly preserved specimen that has been lost or misplaced (Cairns and Wells, 1987). The two subsequent reports of the species (Wells, 1945; Frost and Langenheim, 1974) are not reliable. Because of its poor preservation, the purported lack of a columella in this species cannot be considered reliable. The shape of its corallum (cuneiform with alate edge costae) suggests a *Platytrochus* affinity, which is tentatively adopted herein.

As emended, *Platytrochus* is a variable genus polymorphic in three characters used in the phylogenetic analysis: thecal edge crests, costal ornamentation, and number of septa. It is grossly similar to *Sphenotrochus*, but it differs by having a trifurcate origin of higher-cycle costae and a papillose, not lamellar, columella. However, there are some species of *Sphenotrochus* that appear to have a papillose columella, e.g., *S. ralphae*, *S. squiresi*, *S. claibornensis*, *S. pulchellus*, but in these species the papillae are usually closely spaced and linear, often simply projecting from an underlying lamellar founda-

tion, in contrast to the papillae of *Platytrochus*, which are clustered along the calicular midline and not underlain with a lamellar foundation. In fact, the lamellar columella of *Sphenotrochus* may ontogenetically originate from a series of aligned papillae that only later fuse into a lamellar structure.

The phylogenetic analysis (Figures 2, 3) places *Platytrochus* in monophly with *Peponocyathus* but separated from it by five character-state changes; however, five character-state changes also separate it from both *Trematotrochus* and *Endocyathopora*. The relationships among the six genera in this part of clade 3 are highly problematic and suggest the need for more study of this group of genera.

DISTRIBUTION.—Paleocene (Midwayan): U.S. (Texas). Middle Eocene (Claibornian): U.S. (Alabama, Mississippi, Texas, ?California). Late Eocene (Jacksonian): U.S. (Alabama, Mississippi). Eocene: Victoria, Australia. Middle Miocene (Balcombian): Victoria, Australia; ?Dominican Republic; ?Martinique. Recent: Western Australia to New South Wales; 22–201 m.

Re-examination of the holotype of *Platytrochus vaughani* (Stephenson, 1916) (USNM I147655) from the Late Cretaceous of Maryland does not allow an accurate diagnosis of its columella, but its costae are arranged in a *Sphenotrochus*-like morphology. Removal of this species from *Platytrochus* changes the earliest occurrence of this genus from Late Cretaceous to the Paleocene.

TYPE SPECIES.—*Turbinolia stokesii* Lea, 1833, by subsequent designation (Milne Edwards and Haime, 1850:xvii). Middle Eocene (Claibornian) of Alabama, Texas, and Mississippi. Deposition of type specimens unknown.

OTHER SPECIES.—*Platytrochus primaevus* Vaughan and Popoe, 1935. Paleocene (Midway Group): U.S. (Texas).

P. goldfussi (Lea, 1833). Middle Eocene (Upper Claibornian): U.S. (Alabama).

P. claibornensis (de Gregorio, 1890). Middle Eocene (Upper Claibornian): U.S. (Alabama).

P. elegans (Vaughan, 1900). Late Eocene (Jacksonian): U.S. (Alabama, Mississippi) (type of *Aldrichiella*, by monotypy).

P. airensis Dennant, 1902b. “Eocene”: Victoria, Australia.

?*P. merriami* (Nomland, 1916). Eocene (Tejon Group): U.S. (California).

P. vacuus (Tenison-Woods, 1878a). Middle Miocene (Balcombian): Victoria, Australia (type species of *Koilotrochus*, by monotypy).

P. curvatus Dennant, 1902b. Middle Miocene (Balcombian): Victoria, Australia.

?*P. dominicensis* (Vaughan in Vaughan and Hoffmeister, 1925): Middle Miocene: Dominican Republic, Martinique (type species of *Dominicotrochus*, by original designation).

P. hastatus Dennant, 1902b. Middle Miocene (Balcombian) to Recent: Western Australia to Victoria; 27–148 m.

P. compressus (Tenison-Woods, 1878b). Recent: New South Wales; 64 m.

P. laevigatus Cairns and Parker, 1992. Recent: South

Australia; 22–165 m.

P. parisepta Cairns and Parker, 1992. Recent: South Australia; 40–201 m.

Peponocyathus Gravier, 1915

PLATES 3k, 6h–j, 10g–i

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

Peponocyathus Gravier, 1915:5.—Wells, 1956:F426.—Cairns, 1979:113 [in part]; 1989a:28–30 [in part]; 1995:89–90.—Zibrowius, 1980:111–113 [in part].

Trochocyathus (*Peponocyathus*).—Vaughan and Wells, 1943:205.

Discotrochus (*Cylindrophyllia*) Yabe and Eguchi, 1937:142.

Kionotrochus.—Vaughan and Wells, 1943:213 [in part; *Cylindrophyllia*].

Cylindrophyllia.—Wells, 1956:F426.

Kionotrochus (*Cylindrophyllia*).—Squires, 1960a:287.

Truncatocyathus Stolarski, 1992:423–424.

DIAGNOSIS.—Corallum may asexually reproduce by transverse division; shape of corallum variable, but usually both anthocaulus and anthocyathus stages cylindrical (circular in cross section), the latter with flat to gently rounded base. Rejuvenation of daughter coralla also occurs (Plate 6*i*). Corallum small, 8 mm or less in CD. Costae finely granular (Plate 10*g*), delimiting deep, narrow intercostal regions that lack pits (Plate 10*i*). Higher-cycle costae originate by trifurcation. Septa hexamerally arranged in 3–4 cycles (24–48 septa). Small pali before all but last septal cycle, the P1 often indistinguishably fused with papillose columella.

DISCUSSION.—Species assigned to *Peponocyathus* have traditionally included those that are now known to undergo transverse division as well as those that do not. Because Stolarski (1992) considered that character state to have generic value, he divided the genus accordingly and established the name *Truncatocyathus* for those species that transversely divide, while reserving *Peponocyathus* for those that do not. I (Cairns, 1995) later asserted that the type species of *Peponocyathus*, *P. variabilis* (= *P. folliculus*) is, in fact, a transversely dividing species, which implies that *Truncatocyathus* is a junior synonym of *Peponocyathus* and that *Deltocyathoides* Yabe and Eguchi, 1932, should be resurrected for those species that do not transversely divide, which is the view adopted herein. Further evidence is provided below to illustrate that *P. folliculus* (= *P. variabilis*, type species of *Peponocyathus*) is indeed a transversely dividing species.

In his excellent redescription of *Peponocyathus duncani*, Stolarski (1992) concluded that transverse division results in (1) anthocyathi that become free of the parent anthocaulus, (2) young anthocyathi that have no basal skeleton or that exhibit horizontal basal scars with poorly formed costae, (3) daughter coralla of the same corallum diameter and with the same number of septa as the parent, and, (4) in those rare cases in

which the anthocyathus is still attached to the anthocaulus (unseparated coralla), costae that are continuous from parent to daughter (Stolarski, 1992, fig. 1A,B) and irregular intercostal perforations visible at the incipient point of dehiscence. In contrast, the process Stolarski referred to as “total rejuvenescence,” sometimes results in multiple coralla that remain attached to one another, daughter coralla that are often smaller and have fewer septa than the parent, and daughter costae that are not necessarily continuous with those of the parent. Although the two processes are quite different, it is often difficult to determine which of the two process occurred in many coralla. Stolarski considered *P. folliculus* to display total rejuvenescence, not transverse division. However, one population of *P. folliculus* from off Madeira (USNM 48764) contains coralla that display rejuvenescence (Plate 6*i*) and coralla that exhibit evidence of transverse division, as shown in an unseparated specimen (Plate 6*j*), and a base of an anthocyathus (Plate 10*h*), thereby fulfilling all of Stolarski’s criteria for transverse division. Plate 6*j*, in fact, is extremely similar to Stolarski’s (1992, fig. 1B) illustrated specimen of *P. duncani*, which exemplifies a corallum in the process of transverse division, including the characteristic intercostal perforations that facilitate the later dehiscence of the distal anthocyathus. If *P. folliculus* (= *P. variabilis*) is accepted as having true transverse division, then *Truncatocyathus* must be considered as a junior synonym of *Peponocyathus*, and *Deltocyathoides* becomes available as the earliest name for the genus of those species that do not asexually reproduce by transverse division.

DISTRIBUTION.—Early Miocene (Waitakian): New Zealand. Middle Miocene (Badenian/Vindobonian): Europe. Late Miocene (Tortonian): central Europe. Pleistocene: Japan. Recent: tropical amphi-Atlantic; western Pacific; 30–1110 m.

TYPE SPECIES.—*Peponocyathus variabilis* Gravier, 1915 (= *P. folliculus* (Pourtalès, 1868); = *P. orientalis* Yabe and Eguchi, 1932b), by monotypy. Recent: Atlantic; western Pacific from Banda Sea to off Japan; 30–582 m. Fourteen syntypes of *P. variabilis* are deposited at the Musée océanographique de Monaco (Zibrowius, 1980:113).

OTHER SPECIES.—*Peponocyathus minimus* (Yabe and Eguchi, 1937). Early Miocene (Waitakian to Otaian) to Recent: Indonesia to Japan; 30–903 m (type species of *Cylindrophyllia* by original designation).

P. duncani (Reuss, 1871) (type species of *Truncatocyathus*, by original designation) (= *Discotrochus pseudoduncani* Vášíček, 1946; = *Discotrochus minutus* Vášíček, 1946). Middle Miocene (Badenian/Vindobonian): Austria, Poland. Late Miocene (Tortonian): Czechoslovakia.

P. lecomptei (Wells, 1937a). Miocene (“Bolderian”): Belgium, Germany.

P. dawsoni Cairns, 1995. Recent: New Zealand; 87–988 m.

Appendix

Station Data Pertaining to Specimens Figured in Plates 1–10.

Station	Latitude	Longitude	Depth (m)	Date
<i>Albatross</i> 5178	12°43'N	122°06'05"E	134–143	25 III 1908
<i>Albatross</i> 5217	13°20'N	123°14'15"E	192	22 IV 1908
<i>Albatross</i> 5506	8°40'N	124°31'45"E	479	5 VIII 1909
<i>Albatross</i> 5508	8°17'24"N	124°11'42"E	494	5 VIII 1909
<i>Albatross</i> 5576	5°25'56"N	120°03'39"E	507	23 IX 1909
<i>Alpha Helix</i> M15	11°31'30"S	135°48'48"E	24	2 VI 1979
<i>Anton Bruun</i> 365D	23°20'S	43°32'E	475–695	12 VIII 1964
<i>Anton Bruun</i> CH5	2°38'30"S	40°43'E	155	18 VI 1971
BS 438	3.9 km off Nugent, Kermadecs		146–165	28 X 1975
<i>Gosnold</i> 1811	33°00.5'N	77°16.2'W	320	22 VI 1964
<i>Jean Charcot</i> 49	32°27.5'N	16°32.0'W	450–500	18 VII 1966
KARUBAR 7	5°47'35"S	132°20'39"E	282–287	22 X 1991
KT9015-B52	32°43.38'N	132°06.52'E	193–199	3 XI 1990
KT9015-HK5	34°55.07'N	131°18.74'E	97	1 XI 1990
MUSORSTOM 2-33	13°23.3'N	121°07.5'E	130–137	24 XI 1980
NZOI C793	36°39.9'S	175°02.2'E	132	23 II 1962
NZOI F915	34°58.7'S	174°18.0'E	251–265	11 X 1968
NZOI K818	29°13.3'S	177°56.4'W	95–116	24 VII 1974
NZOI U584	31°26.3'S	172°35.6'E	1137–1150	6 II 1988
<i>Oregon</i> 4226	0°18'N	44°17'W	274	9 II 1963
Siboga 95	5°43.5'N	119°40'E	522	26 VI 1900
Siboga 256	5°26.6'S	132°32.5'E	397	11 XII 1900

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PLATE 1

Side views of the turbinoliid genera

- a. *Alatotrochus rubescens*, KT9015-BS2, USNM 92776, $\times 3.2$.
- b. *Pleotrochus venustus*, KARUBAR 7, USNM 94785, $\times 4.3$.
- c. *Pleotrochus zibrowii*, paratype, NZOI Sta U584, USNM 94784, $\times 3.6$.
- d. *Australocyathus vincentinus*, Gulf of St. Vincent, USNM 85699, oblique basal view, $\times 7.4$.
- e. *Tropidocyathus lessonii*, Albatross-5178, USNM 81845, $\times 3.8$.
- f.g. *Cyathotrochus pileus*: f, syntype, Siboga-95, ZMA 7352, $\times 3.9$; g, *C. pileus*, Albatross-5508, USNM 81854, $\times 2.5$.
- h. *Deltocyathoides orientalis*, MUSORSTOM 2-33, USNM 81836, $\times 13.3$.
- i. *Notocyathus venustus*, Albatross-5576, USNM 81785, $\times 8.9$.
- j. *Notocyathus viola*, Muddy Creek, Victoria (Balcombian), USNM 77067, $\times 5.8$.
- k. *Palocyathus seymourensis*, holotype, USNM 93050, $\times 7.4$.
- l. *Bothrophoria ornata*, Seymour I. (Maastrichtian), USNM 92999, $\times 4.8$.

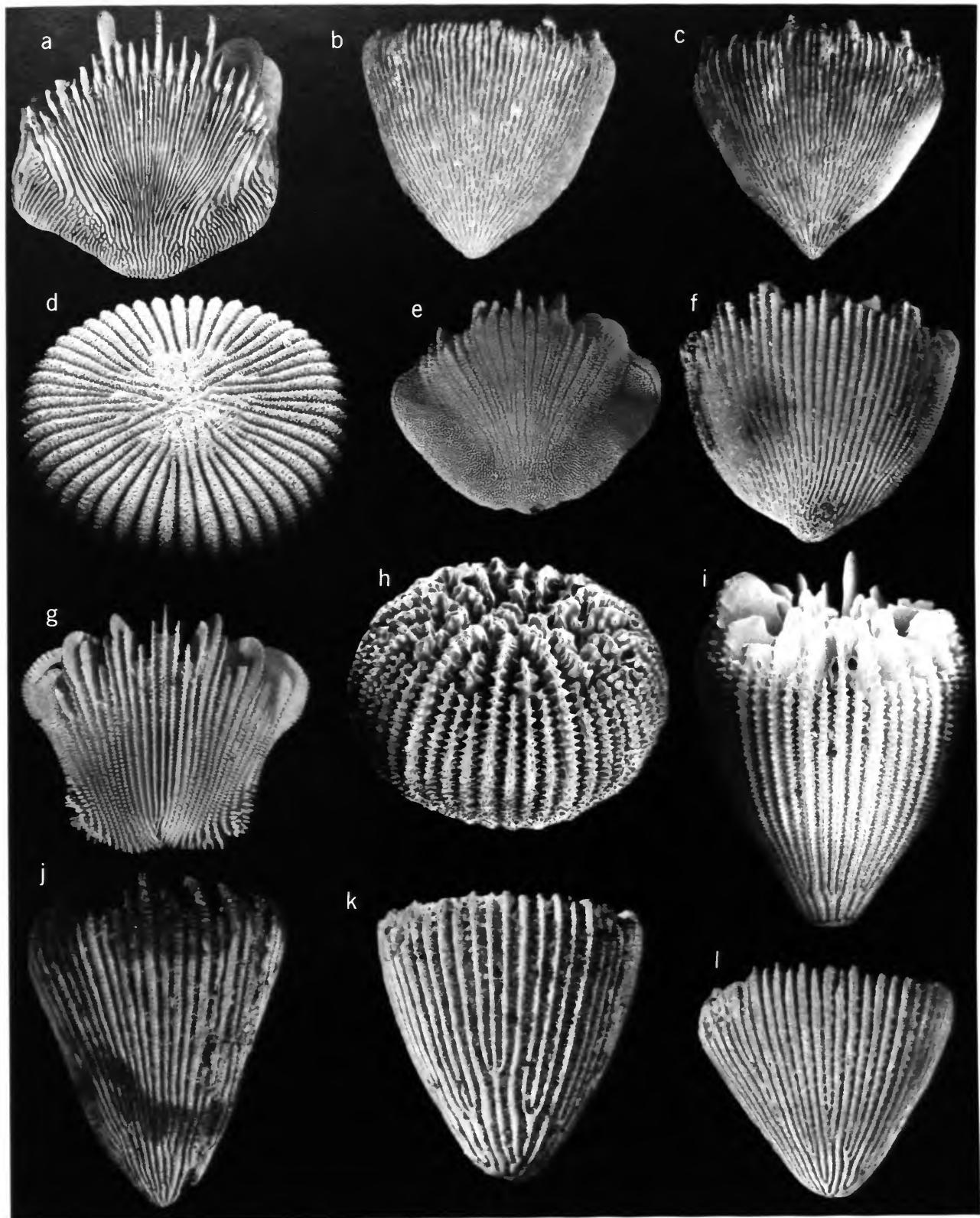


PLATE 2

Side views of the turbinoliid genera (continued)

- a. *Cryptotrochus carolinensis*, holotype, USNM 46914, $\times 7.7$.
- b. *Laminocyathus wellsi*, holotype, USNM 93035, $\times 7.7$.
- c. *Alveolocyathus nordenskjoeldi*, holotype, USNM 92996, $\times 7.1$.
- d. *Levicyathus cairnsi*, holotype, USNM 93038, $\times 9.3$.
- e. *Pseudocyathoceras avis*, Galápagos, USNM 46962, $\times 5.6$.
- f. *Idiotrochus emaciatus*, syntype showing anthocyathus and remnant anthocaulus, Neptune I., USNM 85701, $\times 20.1$.
- g. *Holcotrochus scriptus*, Kangaroo I., USNM 85687, $\times 29.7$.
- h. *Thrypticotrochus multilobatus*, BS438, USNM 94179, $\times 11.4$.
- i. *Idiotrochus emaciatus*, Muddy Creek, Victoria (Balcombian), USNM 77060, $\times 7.7$.
- j. *Wellsotrochus cyathiformis*, base of holotype, Auckland University H574, $\times 6.5$.
- k,l. *Dunocyathus parasiticus*: k. anthocaulus encrusted by bryozoan colony, Cape Jaffa, USNM 85698, $\times 14.6$; l, USNM 85697, $\times 16.6$.

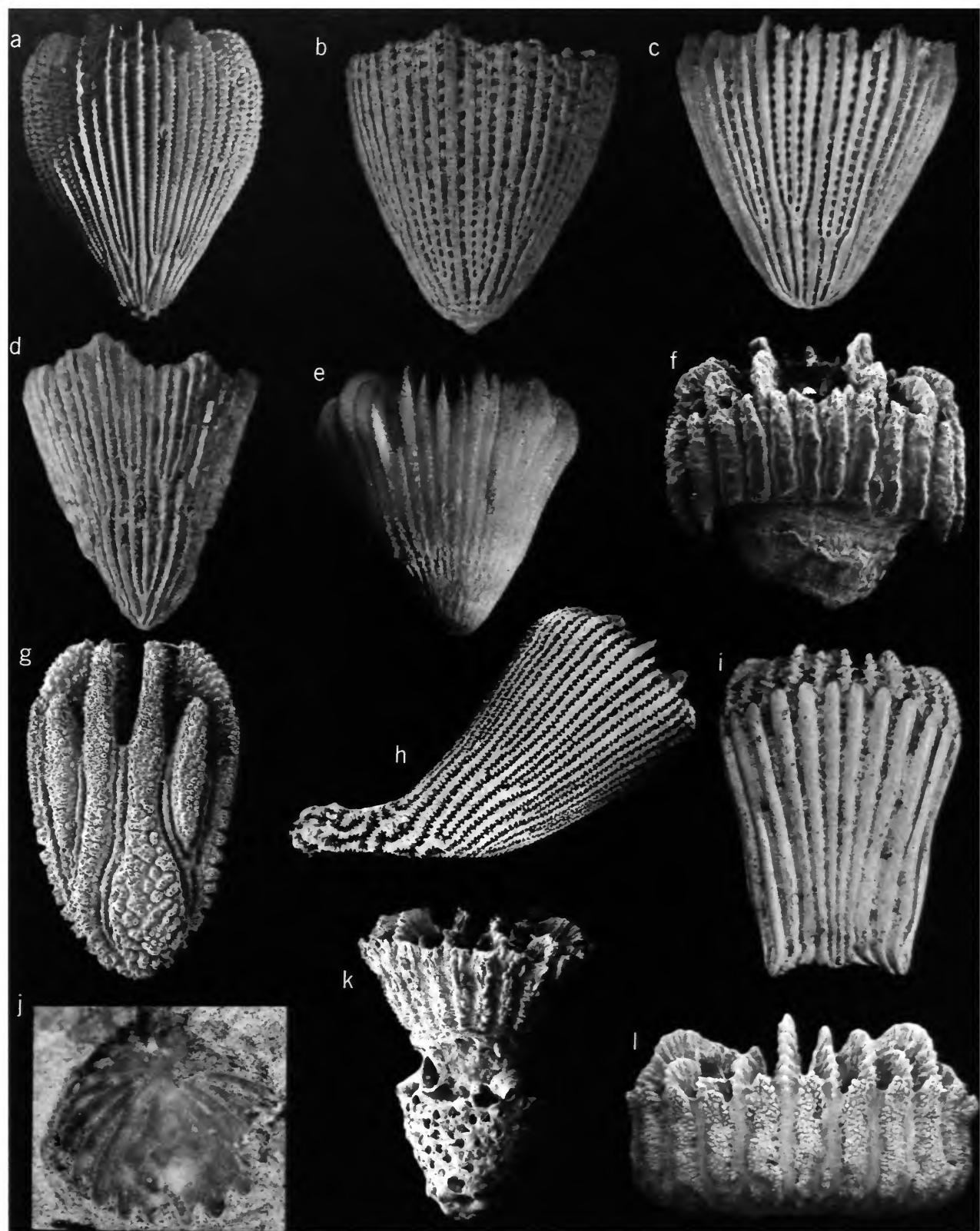


PLATE 3

Side views of the turbinoliid genera (continued)

- a. *Conocyathus zelandiae*, King George Sound, WA, USNM 85713, $\times 14.3$.
- b. *Turbinolia sulcata*, Parnes, France (Middle Eocene), USNM 64511, $\times 8.5$.
- c. *Turbinolia stephensi*, Alpha Helix M-15, USNM 80014, $\times 30.7$.
- d. *Turbinolia* sp., Orme, France (Middle Eocene), USNM 94783, $\times 17$.
- e. *Foveolocyathus verconis*, Beachport, S. Australia, USNM 85684, $\times 13.8$.
- f.g. *Kionotrochus suteri*: f, anthocyathus, NZOI Stn F915, USNM 94200, $\times 10.6$; g, anthocaulus, NZOI Stn C793, USNM 94195, $\times 19.8$.
- h. *Trematotrochus fenestratus*, Muddy Creek (Balcombian), USNM 67970, $\times 15.2$.
- i. *Platytrochus stokesii*, Claiborne, Alabama (Eocene), USNM M158019, $\times 8.0$.
- j. *Sphenotrochus crispus*, Grignon, France (Middle Eocene), USNM M327604, $\times 7.1$.
- k. *Peponocyathus folliculus*, Albatross-5217, USNM 81839, $\times 15.3$.
- l. *Endocyathopora laticostata*, holotype, USNM 81894, $\times 17.0$.

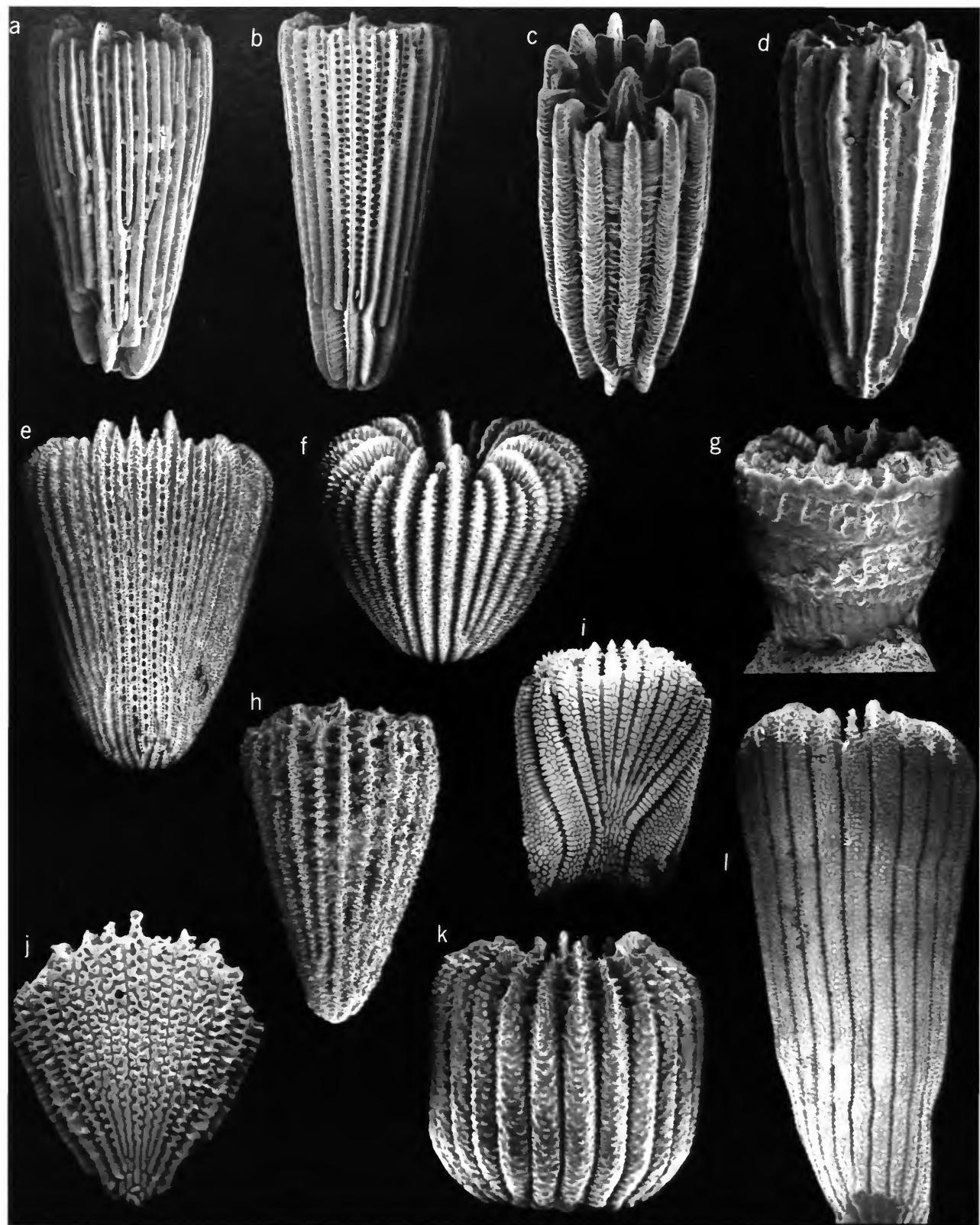


PLATE 4

Calicular views of the turbinoliid genera

- a. *Alatotrochus rubescens*, KT9015-BS2, USNM 92776, $\times 3.6$.
- b. *Pleotrochus venustus*, holotype, Siboga-256, ZMA Coel. 1186, $\times 5.4$.
- c. *P. zibrowii*, holotype, NZOI Stn U584, USNM 94178, $\times 3.6$.
- d. *Australocyathus vincentinus*, Gulf of St. Vincent, USNM 85699, $\times 7.2$.
- e. *Tropidocyathus lessonii*, Albatross-5178, USNM 81845, $\times 4.3$.
- f. *Cyathotrochus pileus*, Albatross-5506, USNM 81848, $\times 2.3$.
- g. *Deltocyathoides stimpsonii*, Oregon-4226, USNM 61852, $\times 9.6$.
- h. *Notocyathus viola*, Muddy Creek (Balcombian), USNM 77067, $\times 8.6$.
- i. *N. venustus*, Albatross-5576, USNM 81785, $\times 9.3$.
- j. *N. conicus*, juvenile with P1-2, MUSORSTOM 2-33, USNM 81801, $\times 19.6$.
- k. *Palocyathus seymourensis*, holotype, USNM 93050, $\times 7.3$.
- l. *Bothrophoria ornata*, Seymour I. (Maastrichtian), USNM 92999, $\times 4.9$.

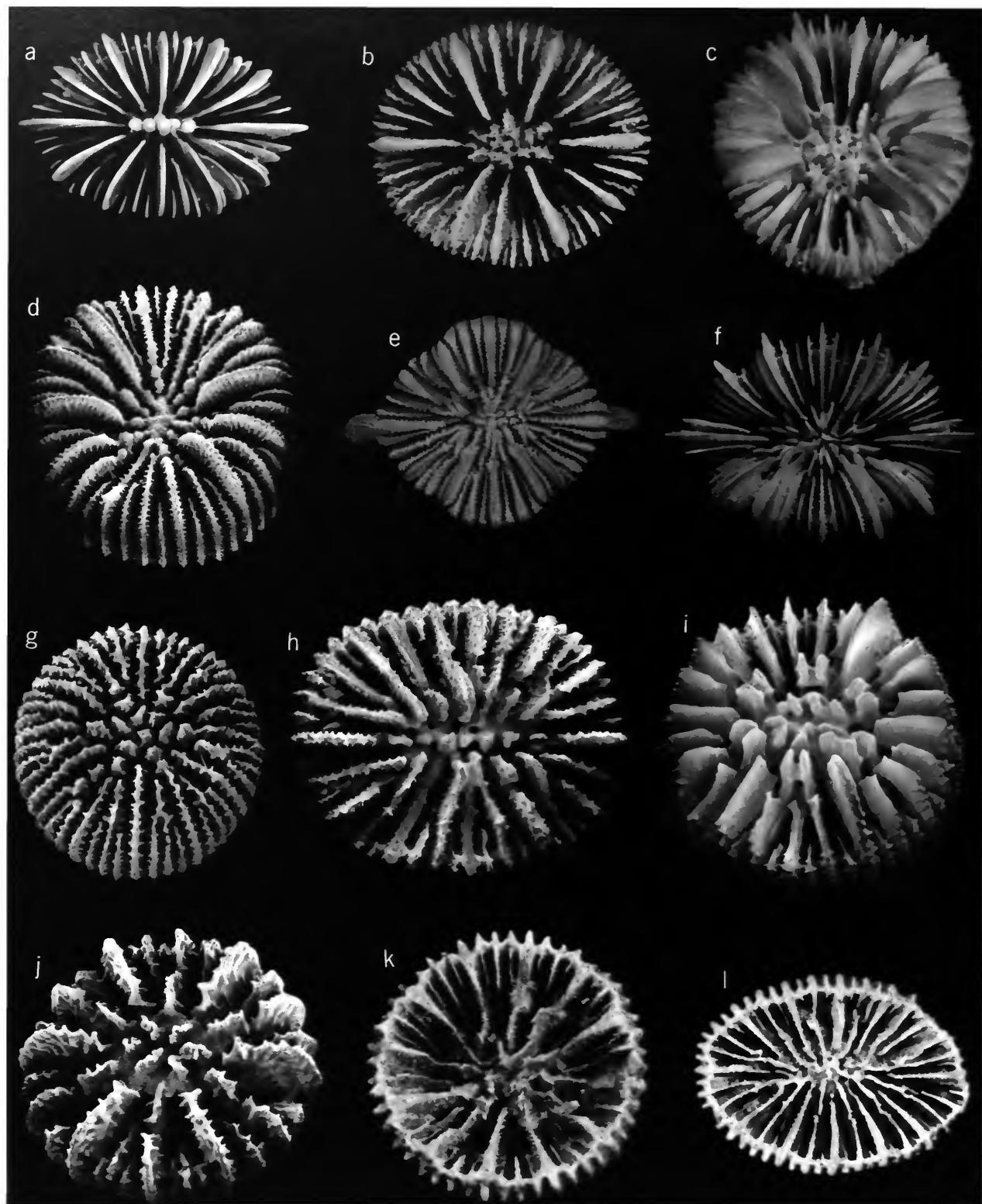


PLATE 5

Calicular views of the turbinoliid genera (continued)

- a. *Levicyathus cairnsi*, holotype, USNM 93038, $\times 10.0$.
- b. *Thrypticotrochus multilobatus*, BS438, USNM 94179, $\times 12.8$.
- c. *Cryptotrochus carolinensis*, holotype, USNM 46914, $\times 8.6$.
- d. *Laminocyathus wellsi*, holotype, USNM 93035, $\times 7.0$.
- e. *Alveolocyathus nordenskjöeldi*, holotype, USNM 92996, $\times 7.1$.
- f. *Pseudocyathoceras avis*, Galápagos, USNM 46962, $\times 5.9$.
- g. *Idiotrochus kikutii*, MUSORSTOM 2-33, USNM 81911, $\times 14.1$.
- h. *Dunocyathus parasiticus*, Cape Jaffa, USNM 85697, $\times 13.6$.
- i. *Turbinolia sulcata*, Parnes, France (Middle Eocene), USNM 64511, $\times 16.2$.
- j. *Conocyathus zelandiae*, King George Sound, WA, USNM 85713, $\times 22.3$.
- k. *Turbinolia stephsoni*, Alpha Helix M-15, USNM 80014, $\times 33.9$.
- l. *Turbinolia* sp., Orme, France (Middle Eocene), USNM 94783, $\times 19.6$.

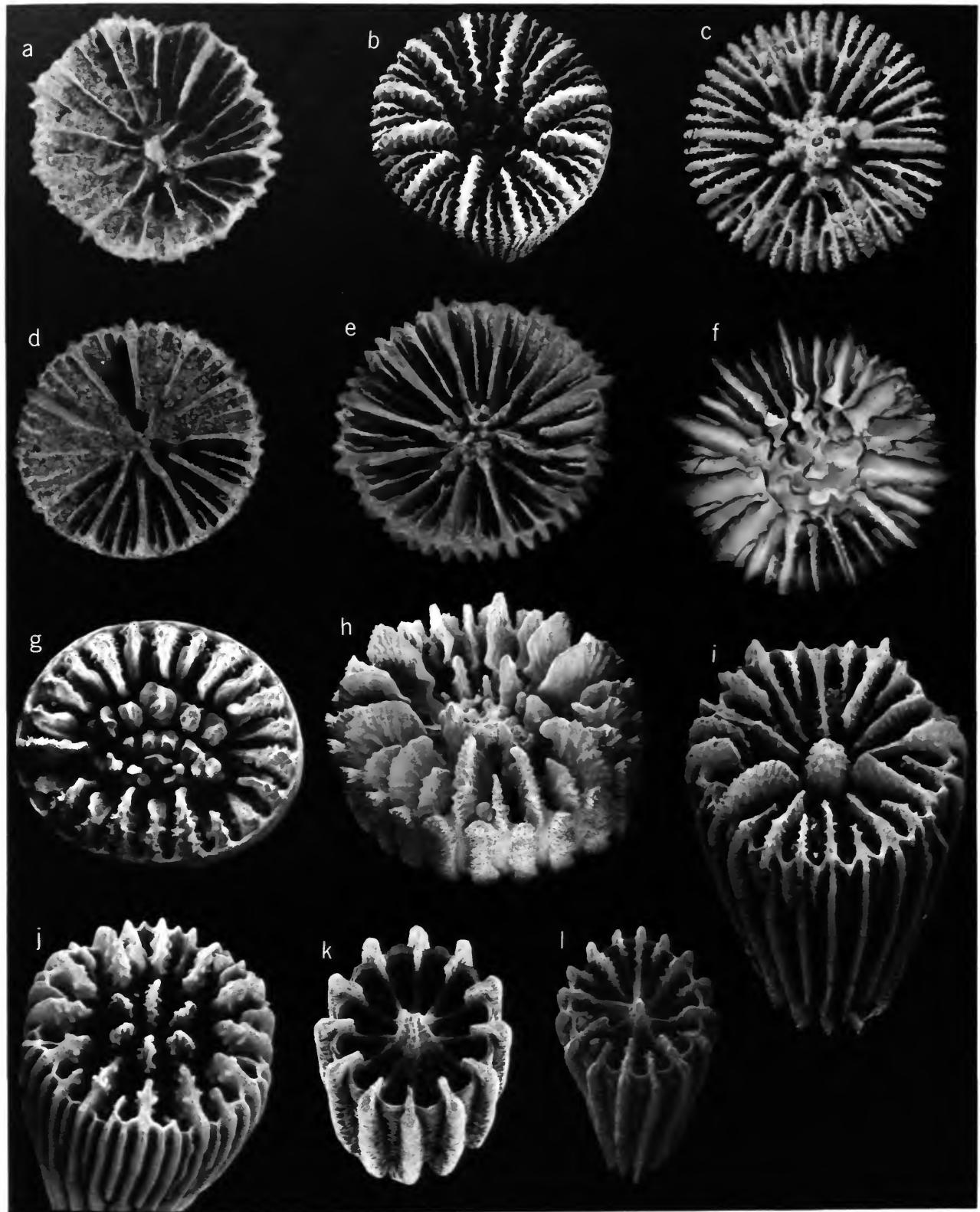


PLATE 6

Calicular views of the turbinoliid genera (continued)

- a. *Sphenotrochus crispus*, Grignon, France (Middle Eocene), USNM M327604, $\times 11.7$.
- b. *Foveolocyathus verconis*, Beachport, S. Australia, USNM 85684, $\times 16.6$.
- c. *F. alternans*, paratype, Gulf of St. Vincent, USNM 85688, $\times 17.4$.
- d. *Endocyathopora laticostata*, holotype, USNM 81894, $\times 19.7$.
- e. *Kionotrochus suteri*, NZOI Stn F915, USNM 94200, $\times 8.6$.
- f. *Platytrochus stokesii*, Claiborne, Alabama (Eocene), USNM M158019, $\times 10.6$.
- g. *Trematotrochus fenestratus*, Muddy Creek, Victoria (Balcombian), USNM 67970, $\times 20.7$.
- h-j. *Peponocyathus folliculus*: h, Albatross-5217, USNM 81839, $\times 15.4$; i, Jean Charcot-49, USNM 48764, corallum displaying rejuvenescence, $\times 23.3$; j, corallum displaying incipient transverse division, $\times 23.3$.

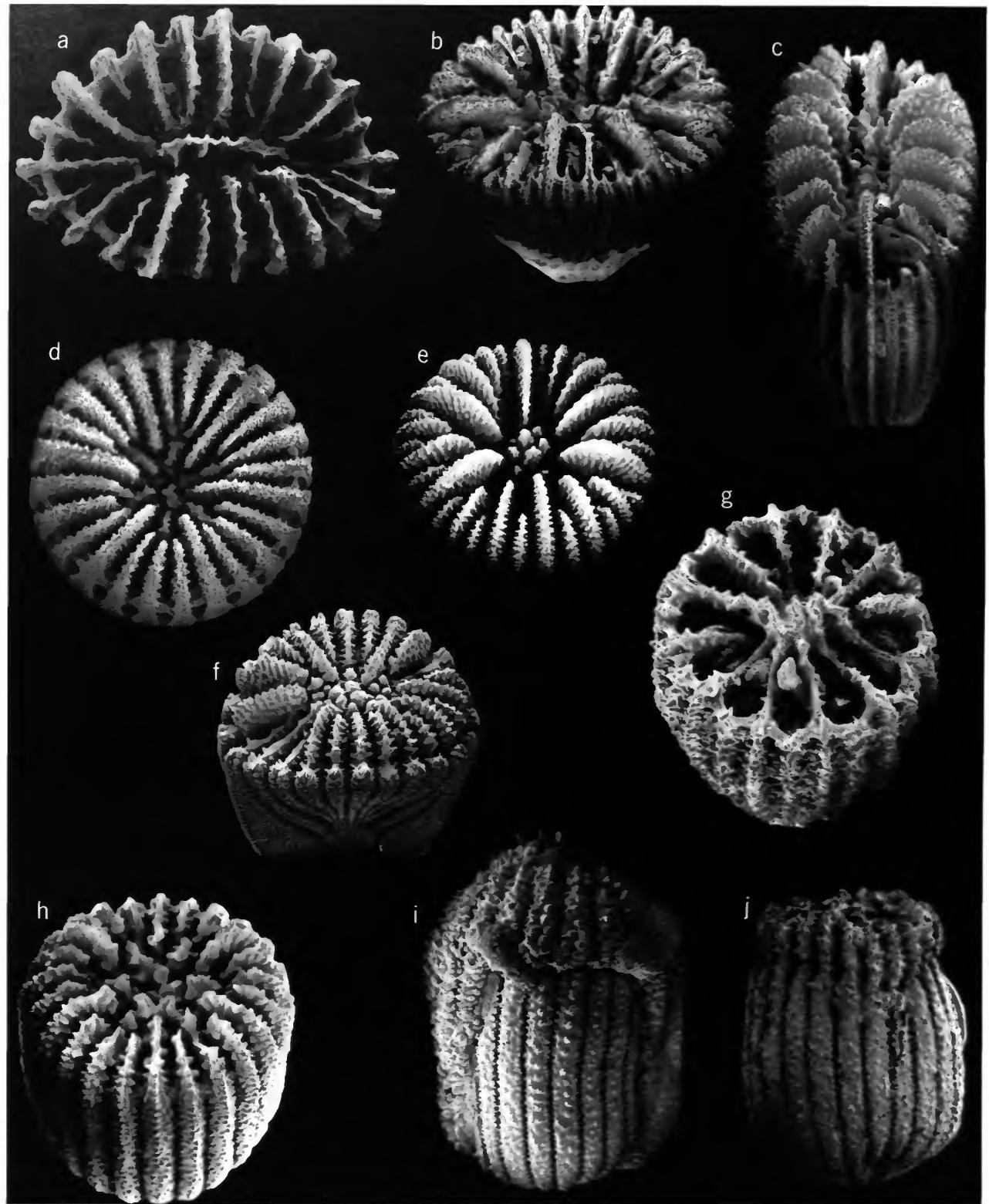


PLATE 7

- a–c.* *Australocyathus vincentinus*, from Gulf of St. Vincent, USNM 85699: *a*, trifurcation of S3, and S4, $\times 10.6$; *b*, costal granulation, $\times 57.4$; *c*, rudimentary columella and multiple paliform lobes, $\times 22.3$.
- d.* *Tropidocyathus lessonii*, Anton Bruun CH-5, USNM 78582, costal granulation, $\times 35.0$.
- e.* *Deltocyathoides stimpsonii*, Oregon-4226, USNM 61852, costal trifurcations, $\times 63.6$.
- f.* *D. orientalis*, KT9015-HK5, USNM 92766, serrate costal ornamentation, $\times 70.0$.
- g.* *Notocyathus venustus*, Albatross-5576, USNM 81785, serrate costal ornamentation, $\times 62.5$.
- h.i.* *Thrypticotrochus multilobatus*: *h*, NZOI Stn K818, NZOI, multiple paliform lobes, $\times 33.9$; *i*, Anton Bruun 365D, USNM 91709, serrate costal ornamentation, $\times 44.5$.
- j.k.* *Cryptotrochus carolinensis*, paratype from Gosnold-1811, USNM 46915: *j*, costal trifurcation, $\times 13.3$; *k*, serrate costal ornamentation, $\times 206.7$.
- l.* *Idiotrochus kikutii*, MUSORSTOM 2-33, USNM 81911, calicular edge showing intercalation of a septum between 2 costae, $\times 132.5$.

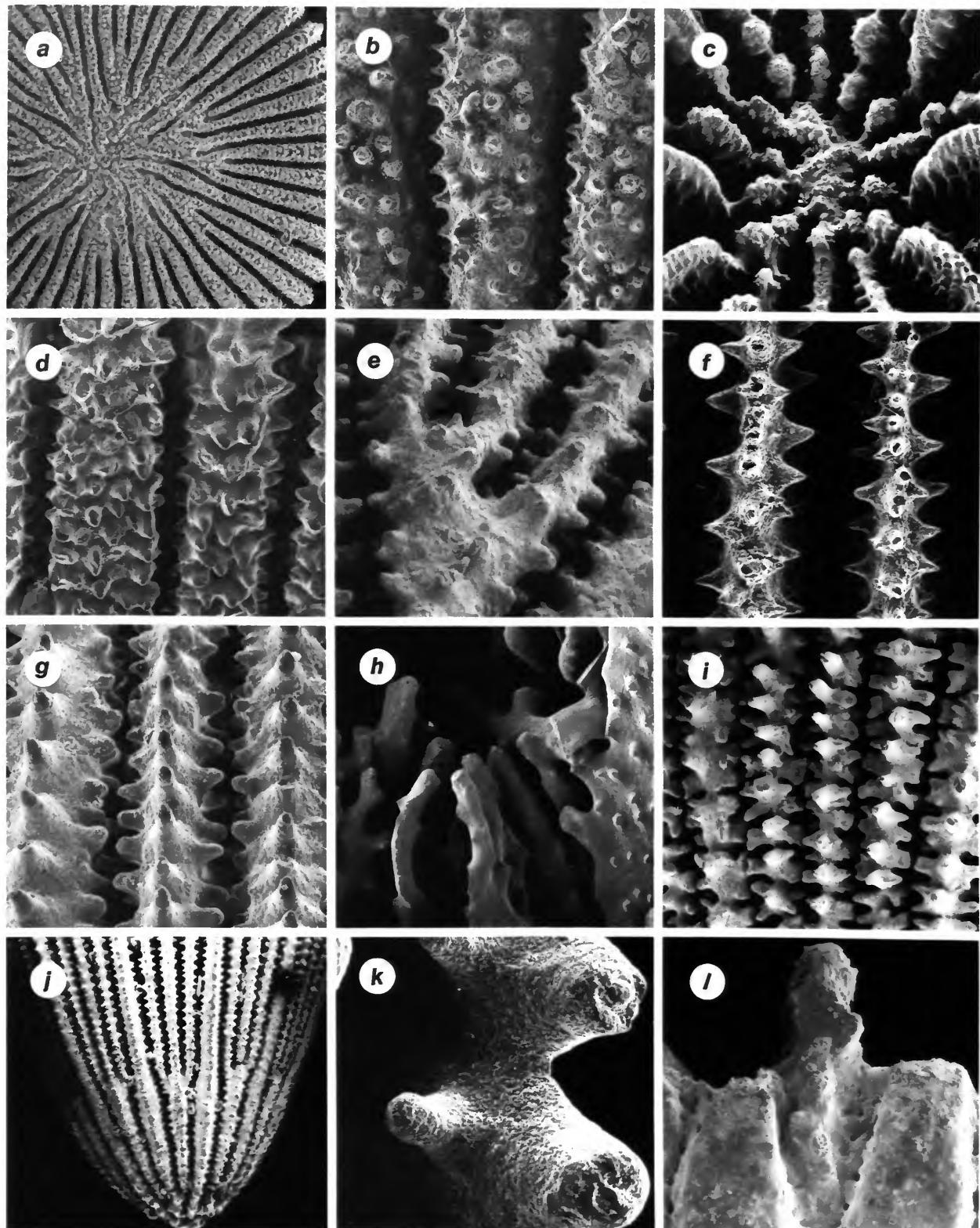


PLATE 8

- a. *Dunocyathus parasiticus*, Cape Jaffa, USNM 85697, granular costae alternating with a septum, $\times 76.3$.
- b. *Conocyathus zelandiae*, King George's Sound, Western Australia, USNM 85713, costae and pitted intercostal regions, $\times 116.6$.
- c,f. *Turbinolia sulcata*, Parnes, France (Middle Eocene), USNM 64511: direct and oblique views of pitted theca, $\times 84.8$, $\times 90.1$, respectively
- d,g. *T. stephensi*, Alpha Helix M-15, USNM 80014: two views of shallow-pitted intercostal region, $\times 169.6$, $\times 127.2$, respectively
- e. *Turbinolia* sp., Orme, France (Middle Eocene), USNM 94783, costae and pitted intercostal region of specimen with only 12 septa, $\times 174.9$.
- h,i. *Sphenotrochus crispus*, Grignon, France (Middle Eocene), USNM M327604: h, convoluted costae in upper half of corallum, $\times 65.7$; i, labyrinthiform-lamellar columella, $\times 13.6$.

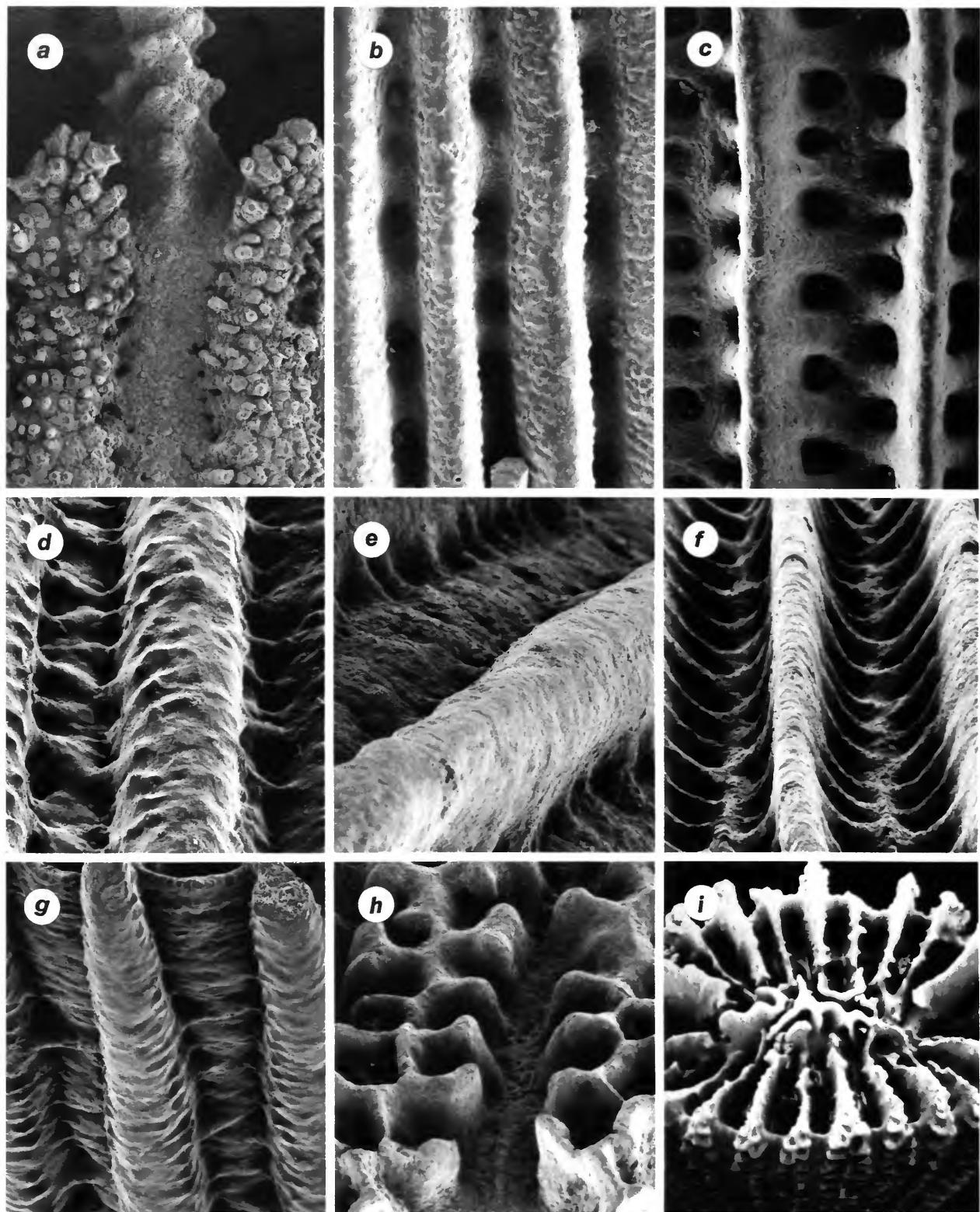


PLATE 9

- a,b,d.* *Sphenotrochus wellsi:* *a,b*, lateral and calicular views of holotype, USNM 82090, $\times 7.4$, $\times 9.4$, respectively; *d*, paratype, USNM 77057, fishtail morphology, $\times 6.5$.
- c.* *Sphenotrochus* sp. cf. *S. wellsi*, Spring Creek, Victoria (Balcombian), USNM 77077, illustrating unequal-sized costae and intercostae, $\times 7.4$.
- e.* *S. crispus*, Grignon, France (Middle Eocene), USNM M327604, basal costal region, $\times 11.1$.
- f.* *Foveolocyathus verconis*, Beachport, S. Australia, USNM 85684, pitted theca between costae, $\times 129.3$.
- g-i.* *Endocyathopora laticostata*, holotype, USNM 81894: *g*, broad granular costa, $\times 180.2$; *h*, portion of calice and costae, $\times 60.4$; *i*, DEKI, Amboina, ZMK, weathered costae revealing irregular dissolution of intercostal regions, $\times 51.9$.

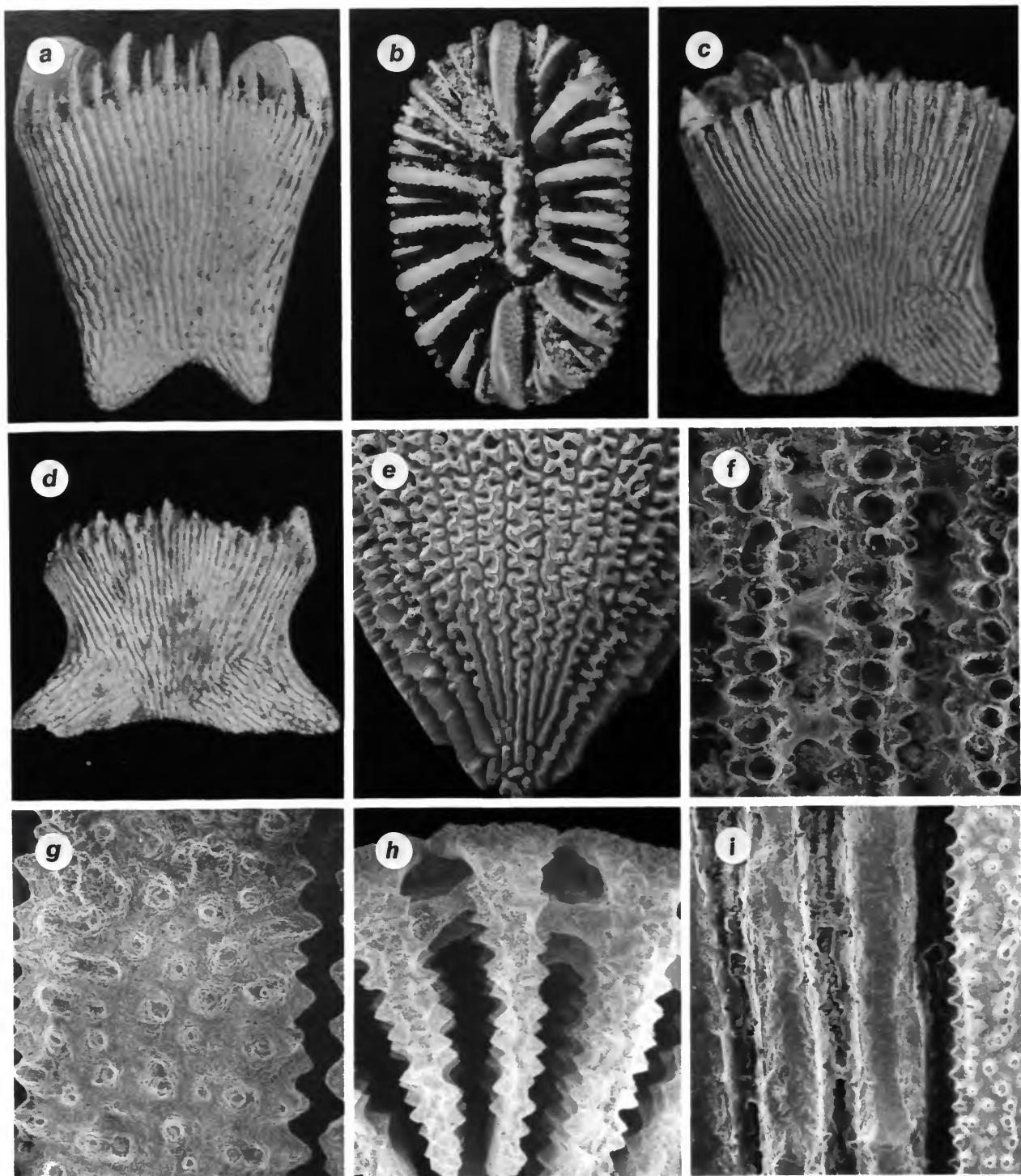
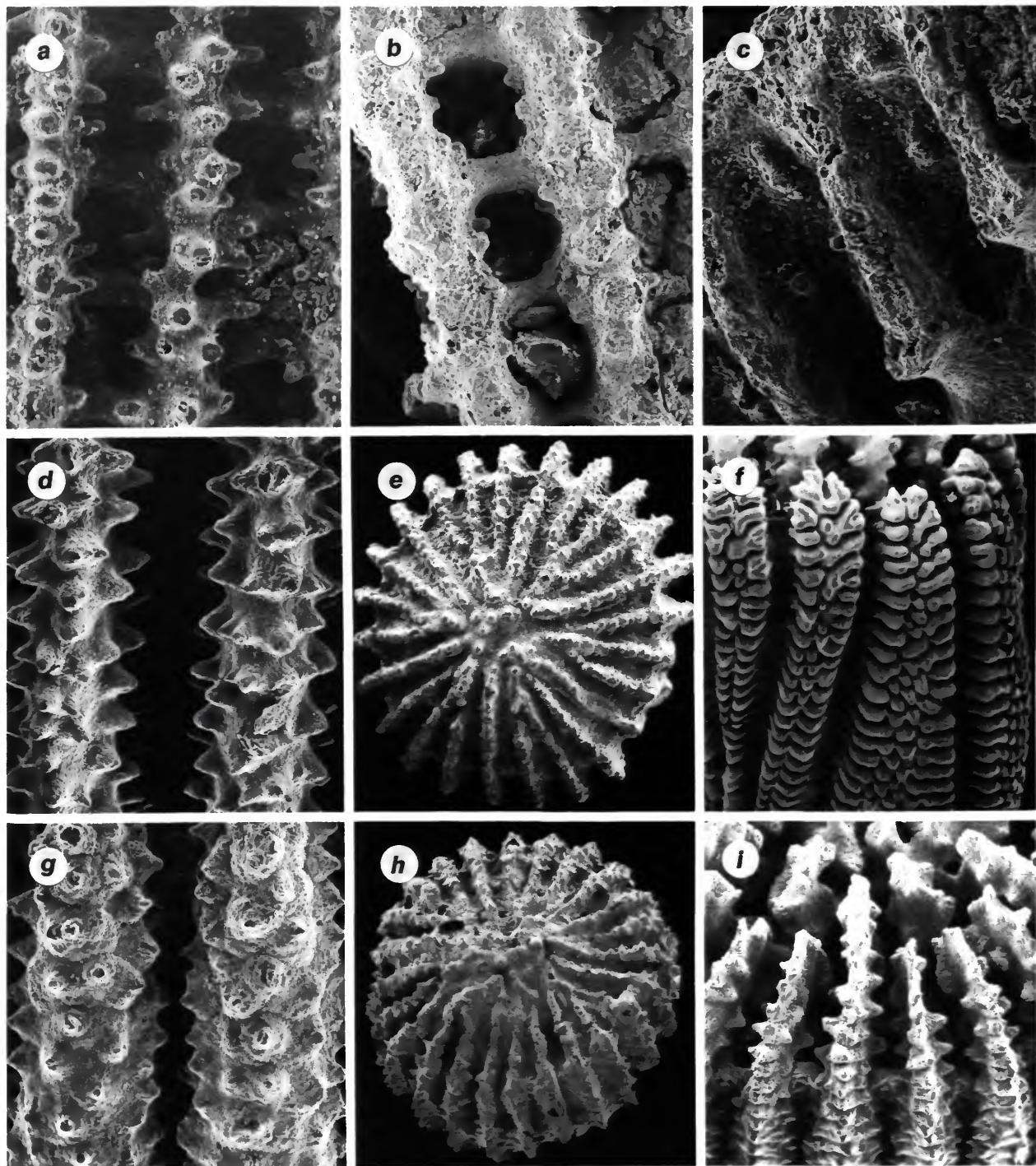


PLATE 10

- a–c.* *Trematotrochus fenestratus* from Muddy Creek, Victoria (Balcombian), USNM 67970: *a,b*, porous theca, $\times 84.8$, $\times 111.3$, respectively; *c*, longitudinal fracture through theca revealing three broken intercostal lamellar like those shown intact in *b*, $\times 169.6$.
- d,e.* *Kionotrochus suteri*: *d*, NZOI Stn F915, USNM 94200, granular costa, $\times 72.1$; *e*, Cuvier I., USNM 78586, base of recently budded anthocyathus, $\times 21.2$.
- f.* *Platytrochus stokesii*, Claiborne, Alabama (Eocene), USNM M158019, coarsely granular costae, $\times 31.8$.
- g,i.* *Peponocyathus orientalis*, Albatross-5217, USNM 48764: *g*, granular costae, $\times 72.1$; *i*, calicular edge, $\times 35.5$.
- h.* *P. folliculus*, Jean Charcot-49, USNM 48764, base of juvenile specimen, $\times 23.3$.



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