

Living and Fossil Genera of the
Clypeasteroidea (Echinoidea:
Echinodermata): An Illustrated
Key and Annotated Checklist

RICH MOOI

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 488

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ABSTRACT

Mooi, Rich. Living and Fossil Genera of the Clypeasteroidea (Echinoidea: Echinodermata): An Illustrated Key and Annotated Checklist. *Smithsonian Contributions to Zoology*, number 488, 51 pages, 34 figures, 1989.—The illustrated key allows identification of 26 living and 49 fossil clypeasteroid genera, plus the tiny fossil, *Togocyamus*. It incorporates internal and external characteristics of the test, Aristotle's lantern, spines, pedicellariae, and podia. Figures depict features used in the key, and provide an illustrated glossary of clypeasteroid terminology. A checklist groups the genera into three suborders (the Clypeasterina, Laganina, and Scutellina) and summarizes, for each genus, information on authorities, type species, number of included species, distribution, and stratigraphic occurrence.

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Contents

	<i>Page</i>
Introduction	1
Conventions Used in the Key	1
Note on Taxa and Classification Used in the Key and Checklist	2
Acknowledgments	2
An Illustrated Key to the Living and Fossil Genera of the Clypeasteroidea	3
Order CLYPEASTEROIDA A. Agassiz, 1872	4
Suborder CLYPEASTERINA A. Agassiz, 1872	5
Suborder LAGANINA Mortensen, 1948	13
Suborder SCUTELLINA Haeckel, 1896	23
Annotated Checklist of the Clypeasteroid Genera	34
Sister Group to the Clypeasteroidea	34
Order CLYPEASTEROIDA A. Agassiz, 1872	34
Suborder CLYPEASTERINA A. Agassiz, 1872	34
Suborder LAGANINA Mortensen, 1948	35
Suborder SCUTELLINA Haeckel, 1896	38
Illustrated Glossary	44
Literature Cited	50

Living and Fossil Genera of the Clypeasteroidea (Echinoidea: Echinodermata): An Illustrated Key and Annotated Checklist

Rich Mooi

Introduction

The order Clypeasteroidea A. Agassiz, 1872 is composed of some 150 living and 750 fossil species of irregular echinoids commonly known as the sand dollars, keyhole urchins, and sea biscuits. There have been no comprehensive keys to the genera of this order since Mortensen's (1948) great monograph. Since the publication of that work, several workers (for example, Nisiyama, 1963; Philip and Foster, 1971; and especially Durham, 1954, 1955; and Durham et al., 1966) have described new genera and redescribed some of the lesser known fossil taxa covered by Mortensen. Therefore, there is need for a revised key that draws upon this new information, and allows identification of specimens without resorting to the out-dated generic keys scattered throughout Mortensen's large monograph. The new checklist provides brief notes on authorities, type species, number of species, geographic range, stratigraphic occurrence, and selected representative figures gleaned from the literature and personal observations. The key and checklist represent an uncritical tabulation of the known clypeasteroid genera, and are merely intended to allow identification, and to summarize current knowledge of these genera. Although the key is, of course, artificial, it relies on many characters used in studies like that of Mooi (1987; in press), which provide phylogenetic classifications above the subordinal level as well as generic and familial revisions of each suborder.

The specimens used in the formulation of this key (and the pending phylogenetic analyses) were provided in part by the following institutions: National Museum of Natural History, Smithsonian Institution (NMNH), Washington, D.C., which

houses the collections of the former United States National Museum (USNM); the British Museum (Natural History) (BMNH), London; the Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts; the American Museum of Natural History (AMNH), New York; the Muséum National d'Histoire Naturelle (MNHN), Paris; the Western Australia Museum (WAM), Perth; the Royal Ontario Museum (ROM), Toronto; and the Florida Department of Natural Resources (FDNR), St. Petersburg. Additional specimens were examined from the collections in the laboratory of Malcolm Telford, University of Toronto (UT).

CONVENTIONS USED IN THE KEY.—The new key relies on characteristics of both the test (apical system, peristome and periproct position, gonopores, hydropores, internal buttresses, Aristotle's lantern, lantern supports, and plate patterns) and external structures (pedicellariae, spines, podia) to provide as complete characterizations of adult morphology of both fossil and living genera as possible. Ambulacra and interambulacra are numbered according to Lovén's system (See Illustrated Glossary, Figure 31). Fossil genera in the key are marked with a dagger (†). A brief comment on the range ("*terra typica*") of both living and fossil genera is provided to aid in identifying specimens for which collection data are available.

Unfortunately, it was necessary to resort to characteristics of internal structure in some cases in order to make the couplets unambiguous. With the increasing use of radiography in taxonomic work, it is hoped that dissection of specimens will not always be necessary to reveal useful characters in these couplets. As many opposing characters as possible are used in each couplet to maximize the possibility for accurate identification of incomplete specimens and poorly preserved fossil material. Because fossil material seldom displays the

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podial, pedicellarial and spine features sometimes given in the couplets, an attempt has been made to provide alternatives to these types of characters whenever fossils are involved.

The terminology associated with echinoid morphology can be complex. To aid the reader in the interpretation of these terms, an Illustrated Glossary is provided at the end of the paper. This type of glossary is provided instead of a written glossary because (1) an image is more useful to someone trying to interpret the key, (2) images tend to remain in the mind of the reader, and (3) verbal descriptions can often become jargon-laden themselves, leading the reader on a potentially circular chase for definitions. The first time a term occurs in the key, it is accompanied by a reference to the figure(s) in the Illustrated Glossary (denoted in the text by "I.G." and a figure number) that explicates that term. If the reader prefers, a written glossary can be found in Durham et al. (1966:U253-U256) and Davies (1971:161-165), and a general guide to echinoid morphology can be found in Smith (1984:1-6).

NOTE ON TAXA AND CLASSIFICATION USED IN THE KEY AND CHECKLIST.—The present key incorporates a total of 75 clypeasteroid genera (26 living, 49 fossil), plus *Togocyamus*, which has here been tentatively recognized as lying outside the order Clypeasteroida. *Togocyamus* occupies this special position partly because of a lack of certain features generally felt to be diagnostic of the Clypeasteroida, most notably the greater width of ambulacra relative to interambulacra, the distribution of accessory podia in fields, and the enclosure of the sphaeridia within the test (Kier, 1982; Mooi, in press). Eight fossil genera (*Fibulina*, *Peronellites*, *Tetradiella*, *Scutulum*, *Samlandaster*, *Proescutella*, *Kieria*, and *Mennerella*), and one living genus (*Marginoproctus*) are omitted from the key (but included in the checklist) because their characteristics are too poorly known to allow placement. Stephenson (1968:136) synonymized *Fibulina* Tornquist, 1904, with *Fibularia* Lamarck, 1816 and *Peronellites* Hayasaka and Morishita, 1947 has recently been synonymized with *Peronella* Gray, 1855 by Wang (1982b:143). *Runa* L. Agassiz, 1841 and *Tournoueraster* Lambert, 1914 are not considered in either key or checklist, as they are probably internal casts of previously described forms (Durham, 1955:187). The living genus *Taiwanaster* Wang, 1984 is, as far as can be determined, identical with *Sinaechinocyamus* Liao, 1979, and is listed with *Sinaechinoc-*

yamus in the key. Because type material from these genera has not yet been examined in order to make a decision regarding synonymy, these two genera are listed separately in the checklist.

Three of the four suborders recognized by Durham et al. (1966) are employed as major subsections of the key: the Clypeasterina, Laganina, and Scutellina. For the purposes of the key, the suborder Rotulina has been incorporated into the Laganina, as many rotuline characters are shared with the Laganina. One other modification has been introduced to the basic scheme of Durham et al. (1966). Four of the fossil genera (*Scutellina* L. Agassiz, 1841; *Porpitella* Pomel, 1883; *Lenita* Desor, 1847; *Eoscutum* Lambert, 1914) that have long been considered members of the family of tiny laganines, the Fibulariidae, have little in common with this family, apart from small size. This is reflected by their position in the key, as they do not even fall within the suborder Laganina. They have here been referred to the suborder Scutellina, in both the key and the annotated checklist. Apart from this relatively minor provisional change, no attempt has been made to formally revise clypeasteroid classification, or group genera into families.

ACKNOWLEDGMENTS.—I would like to thank Malcolm Telford, who provided encouragement and advice during the formative years of a project that laid the groundwork for this key—truly a man in an iconoclass of his own. David Pawson and Cindy Ahearn, of the NMNH, facilitated access to specimens and information, and helped convince me that this undertaking was indeed necessary. I thank Steve Beadle for valuable new information on stratigraphic occurrences of western American clypeasteroids. I am also grateful to the following for hospitality extended during pillaging raids: Frederick Collier and Jann Thompson (Paleobiology, NMNH); Ailsa Clark, Gordon Paterson, Andrew Smith, David Lewis, and Richard Jefferies (BMNH); Robert Woollacott and R.C. Eng (MCZ); Catherine Vadon, Jean Roman, and Y. Gayraud (MNHN); Loiset Marsh and Kenneth McNamara (WAM); Harold Feinberg (AMNH); Janet Waddington (ROM); Sandra Farrington and David Camp (FDNR). Personal support was provided by a Natural Sciences and Engineering Research Council of Canada Post-doctoral Fellowship held while I was a Post-doctoral Fellow at the NMNH.

An Illustrated Key to the Living and Fossil Genera of the Clypeasteroidea

(† = fossil taxa)

1. Ambulacra [I.G., Figure 31] narrower than interambulacra [I.G., Figure 31] at ambitus [I.G., Figure 31]; single "open" (not enclosed within test) sphaeridium [Figure 1a; I.G., Figure 32b] in each ambulacrum near peristome [I.G., Figure 31]; non-respiratory podia in lines [Figure 1a] along adradial sutures [I.G., Figure 31] *Togocyamus*† (West Africa)

Ambulacra as wide as or wider than interambulacra at ambitus; one or two sphaeridia [Figure 1b,c] enclosed within test in sphaeridial chamber [I.G., Figure 32b] in each ambulacrum near peristome; many non-respiratory podia per plate, distributed in patches, or fields [Figure 1b,c], not in radiating lines (Order Clypeasteroidea). 2

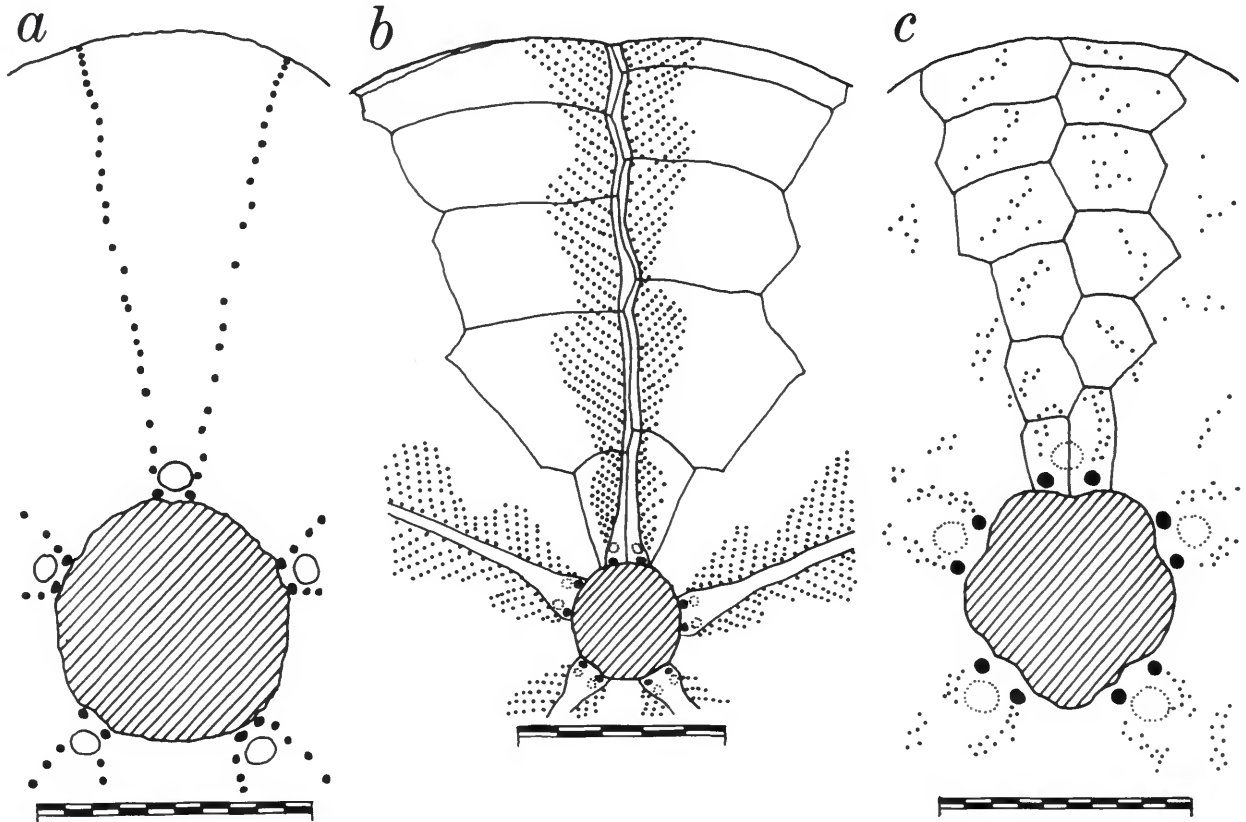


FIGURE 1.—Sphaeridia and podial distribution in ambulacrum III: a, *Togocyamus seefriedi* Oppenheim, USNM, no number (plate pattern not known); b, *Monostychia australis* Laube, USNM 96251; c, *Fibularia ovulum* Lamarck, UT, Enewetak. (Buccal and accessory podial pores indicated by solid dots; "open" sphaeridia indicated by solid circle, sphaeridia enclosed within test by dotted circle; plate pattern shown for ambulacrum III only, pattern unknown in a; peristome cross-hatched; scale bars: a and c = 1 mm; b = 5 mm.)

Order CLYPEASTEROIDA A. Agassiz, 1872

- 2. Two enclosed sphaeridia in each ambulacrum near peristome [Figure 1b]; Aristotle's lantern [I.G., Figure 34a] with small internal wings [Figure 2a; I.G., Figure 34a]; supra-alveolar processes [I.G., Figure 34a] form ring at highest part of lantern [Figure 2a]; lantern supports [I.G., Figure 34b] paired as auricles [Figure 3a; I.G., Figure 34b], one on each ambulacral basicoronal plate [Figure 3a; I.G., Figure 31] (Suborder Clypeasterina) 3
- Single enclosed sphaeridium in each ambulacrum near peristome [Figure 1c]; Aristotle's lantern with well developed internal wings [Figure 2b-d]; supra-alveolar processes do not form ring at highest part of lantern [Figure 2b-d]; lantern supports single, one on each interambulacral basicoronal plate [Figure 3b] 10

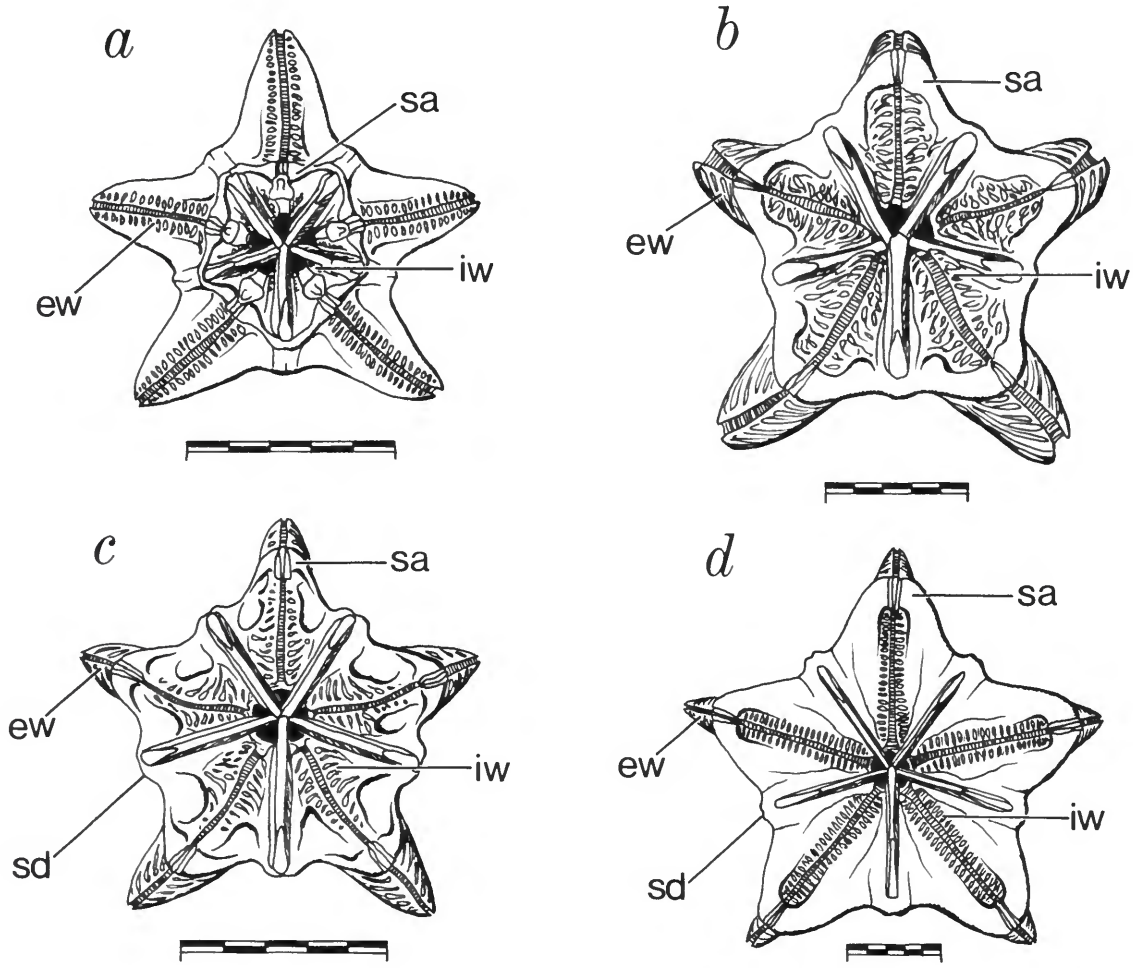


FIGURE 2.—Top (aboral) view of Aristotle's lantern in clypeasteroids: a, *Arachnoides placenta* (Linné), WAM 271.77; b, *Laganum laganum* (Leske), WAM 2082.25; c, *Encope emarginata* (Leske), UT, Belize; d, *Echinodiscus bisperforatus* (Leske), UT, New Guinea. (Anterior towards top of page; scale bars = 5 mm; abbreviations: ew = external wing; iw = internal wing; sa = supra-alveolar process; sd = subdental process.)

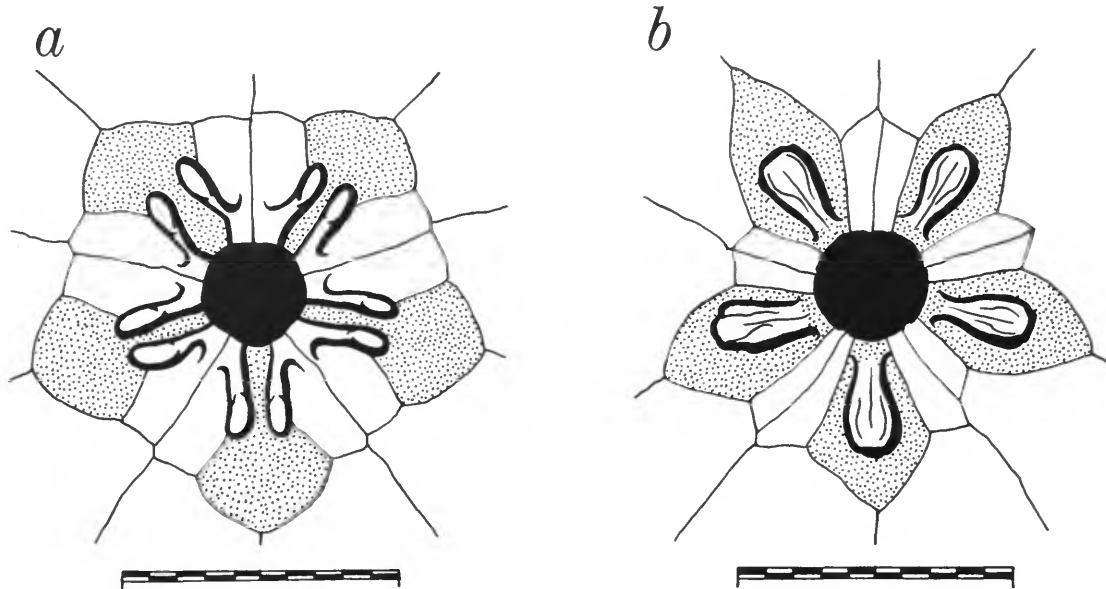


FIGURE 3.—Internal view of lantern supports and basicoronal plate patterns in clypeasteroids: *a*, *Fellaster zelandiae* (Gray), adapted from Kier (1970, pl. 23); *b*, *Echinarachnius parma* (Lamarck), adapted from Kier (1970, pl. 23). (Peristome in solid black, interambulacra stippled, lantern supports in heavy outline; anterior towards top of page; scale bars = 10 mm.)

Suborder CLYPEASTERINA A. Agassiz, 1872

- 3. Periproct [I.G., Figure 31] submarginal or distinctly on oral surface [I.G., Figure 31], never on aboral surface [I.G., Figure 31] 4
- Periproct supramarginal or distinctly on aboral surface, never on oral surface 6
- 4. Food grooves [I.G., Figures 32*b*, 33*b*] not reaching the ambitus [Figure 4*a*], not continuing onto aboral surface towards apical system [I.G., Figure 32*a*]; no “combed” rows of spines and podia in ambulacra adjacent to food grooves; five gonopores [I.G., Figure 32*a*; note that this figure is generalized, and actually shows only four gonopores] *Clypeaster* (Circumtropical)
- Food grooves continuing from peristome around ambitus onto aboral surface towards apical system (similar to situation shown in Figure 4*b,c*); “combed” rows of spines and podia in ambulacra adjacent to food grooves [Figure 1*b*]; four gonopores 5

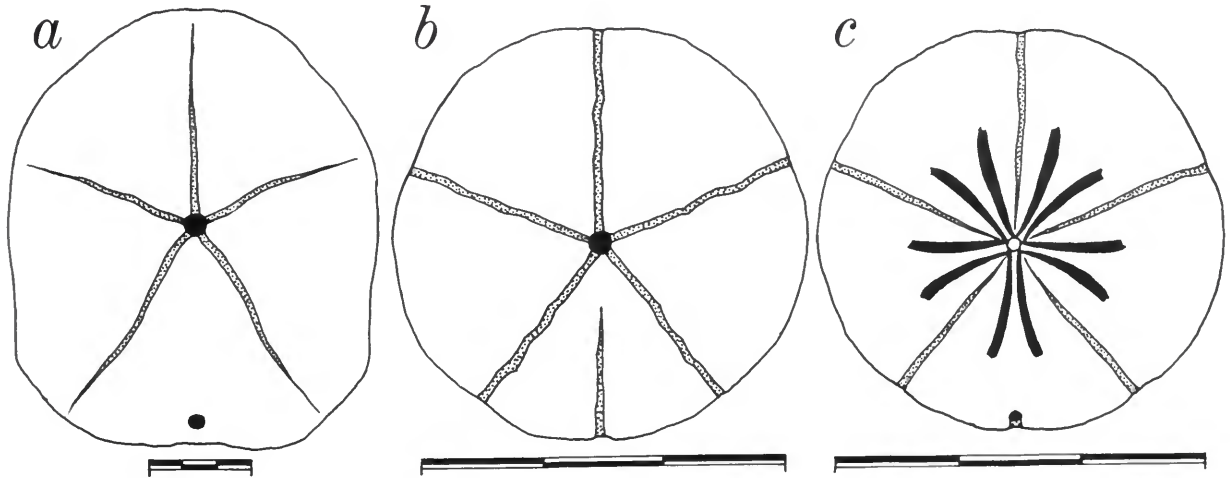


FIGURE 4.—Food grooves of clypeasterines: *a*, Oral surface of *Clypeaster subdepressus* (Gray), UT, Florida Keys; *b*, oral surface of *Arachnoides placenta* (Linné), UT, New Guinea; *c*, aboral surface of *Arachnoides placenta* (Linné), UT, New Guinea. (Respiratory podial rows, peristomes, and periprocts in solid black; food grooves and periproctal grooves stippled; anterior towards top of page; scale bars = 30 mm.)

5. At least seven plates in each paired interambulacrum [interambulacra 1, 2, 3, 4] on oral surface [Figure 5*a*]; periproct distinctly on oral surface, approximately one third distance from ambitus to edge of peristome [Figure 5*a*] *Ammotrophus* (South and West Australia)
- Six plates in each paired interambulacrum on oral surface [Figure 5*b*]; periproct on oral surface, but close to ambitus (submarginal) [Figure 5*b*] *Monostychia*† (South Australia)

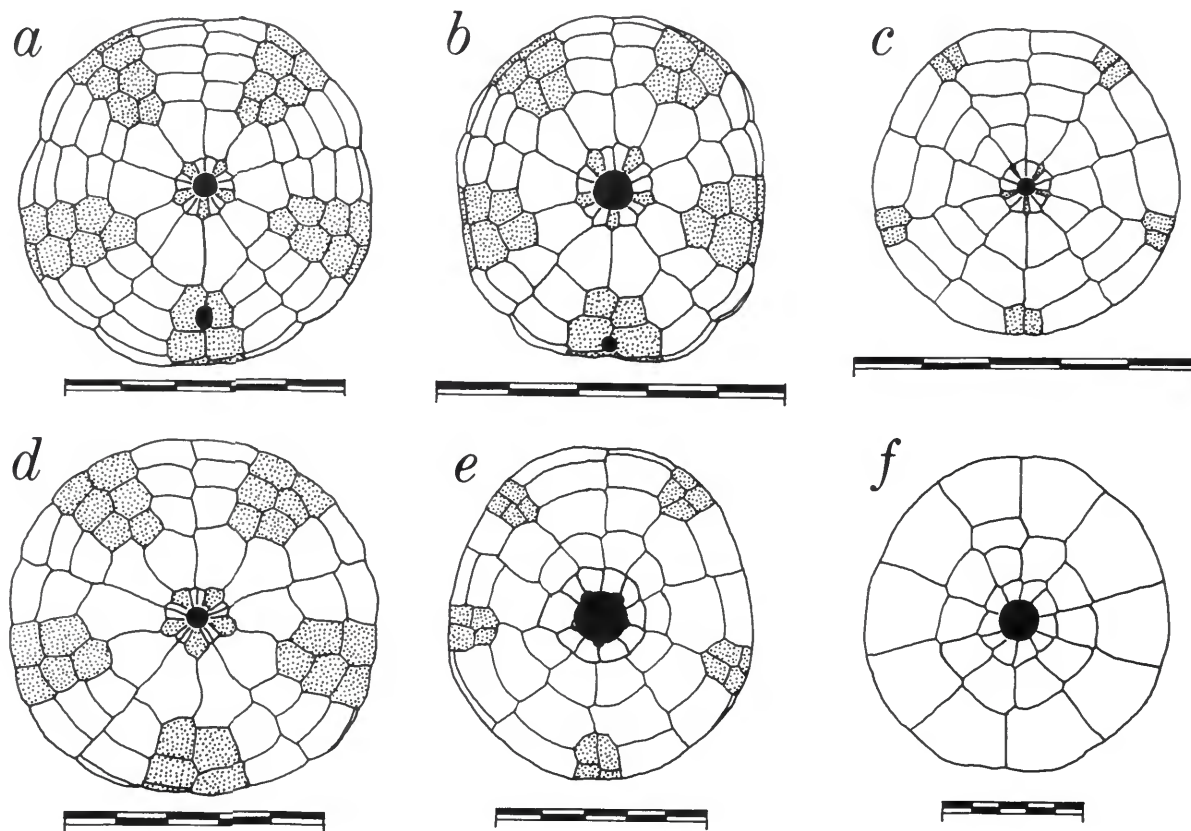


FIGURE 5.—Plate patterns on the oral surface of clypeasterines: *a*, *Ammotrophus cyclius* H.L. Clark, Paratype, MCZ 3352; *b*, *Monostychia australis* Laube, after Durham (1955:126); *c*, *Arachnoides placenta* (Linné), UT, New Guinea; *d*, *Fellaster zelandiae* (Gray), AMNH 2302; *e*, *Scutellinoides patella* Tate, USNM 96254; *f*, *Willungaster scutellaris* Philip and Foster, after Philip and Foster (1971:689). (Interambulacra shaded; anterior towards top of page; scale bars: *a-d* = 50 mm; *e-f* = 5 mm.)

6. Petaloids [I.G., Figures 31, 32a] well developed, distinct conjugation groove [I.G., Figure 32a] between pores in pore pairs; regularly arranged demiplates [I.G., Figure 32a] in petaloids present [Figure 6a], alternating with primary plates; prominent "combed" rows of spines and podia adjacent to food grooves [similar to that in Figure 1b]; food grooves continue from edge of peristome around ambitus onto aboral surface towards apical system [Figure 4b,c]; interambulacral basicoronral plates clearly visible externally next to peristome [Figure 5c,d]; test of adults large (greater than 40 mm in length), very flat, discoidal, with sharp edge (ambitus) 7
- Petaloids poorly developed or absent, conjugation groove between pores in pore pairs indistinct; demiplates in petaloids absent; "combed" rows of spines and podia absent; when present, food grooves restricted to oral surface, not reaching ambitus; interambulacral basicoronral plates barely visible or not visible externally next to peristome [Figure 5e, f]; test of adults small (less than 20 mm in length), high, slightly elongate, with rounded ambitus 8

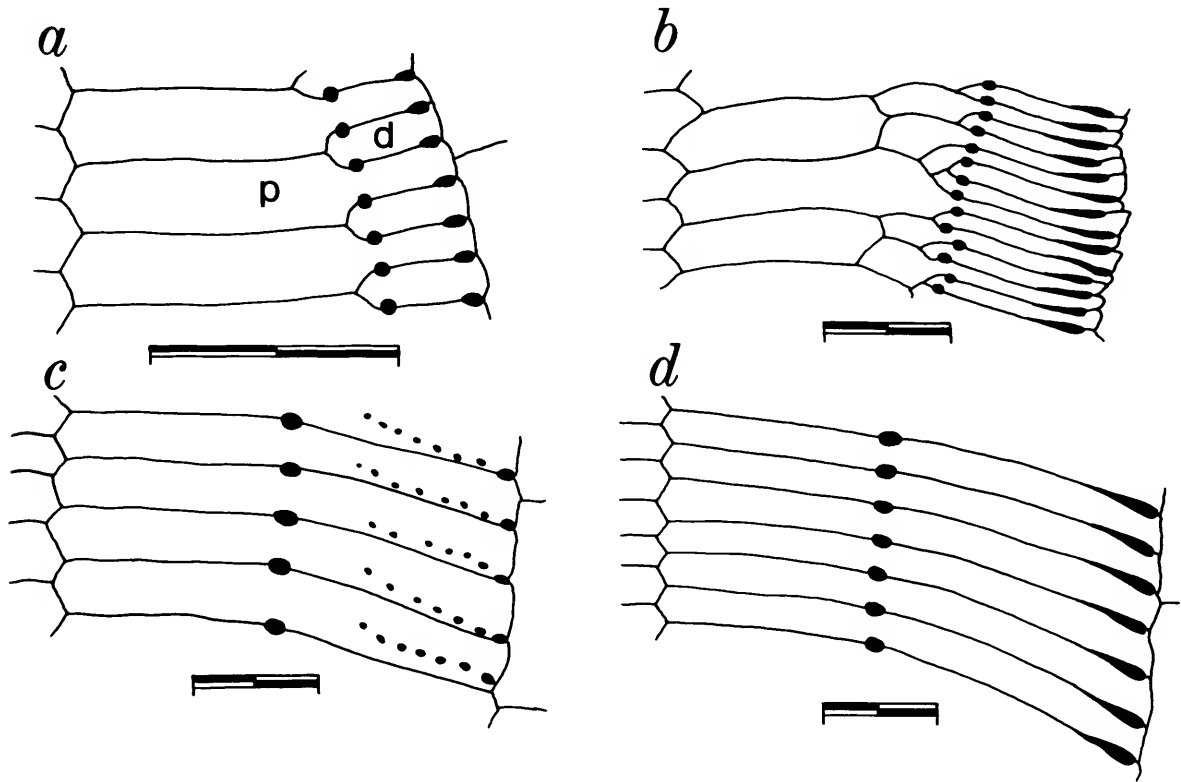


FIGURE 6.—Demiplates and primary plates in the petaloids of clypeasteroids: a, *Arachnoides placenta* (Linné), UT, New Guinea; b, *Neorumphia elegans* (Sánchez Roig), after Durham (1954:683); c, *Rotula deciesdigitata* (Leske), USNM 6991; d, *Monophoraster darwini* (Desor), ROM 5578. (All figures show a portion of a petaloid in a half ambulacrum; ambitus towards bottom of page; respiratory podial pores in solid black; scale bars = 20 mm; abbreviations: d = demiplate; p = primary plate.)

7. Single plate in each column of oral interambulacra [Figure 5c]; individual interambulacral basicoronal plates smaller than individual ambulacral basicoronal plates [Figure 5c]; usually with conspicuous narrow groove from periproct around ambitus towards peristome [Figure 4b]; pedicellariae with three jaws, present as tridentate [I.G., Figure 33c] and triphyllous [I.G., Figure 33c] forms *Arachnoides*
(Indo-Pacific)
- Two or three plates in each column of oral interambulacra [Figure 5d]; individual interambulacral basicoronal plates larger than individual ambulacral basicoronal plates [Figure 5d]; no groove associated with periproct; pedicellariae with two jaws, present as bidentate [I.G., Figure 33c] and biphyllous [I.G., Figure 33c] forms *Fellaster*
(New Zealand, Australia)
8. Food grooves short, but distinct; interambulacral basicoronal plates barely visible externally next to peristome [Figure 5e], each plate with a single spine tubercle [I.G., Figure 33a]; females without marsupium in anterior oral ambulacrum *Scutellinoides*†
(South Australia)
- Food grooves lacking; interambulacral basicoronal plates not visible externally [Figure 5f], without tubercles; females with marsupium, a deep, often divided depression in anterior oral ambulacrum 9
9. Aboral interambulacra continue around ambitus, with one or two small plates just submarginal on oral surface; tuberculation coarse, spine tubercles widely spaced *Fossilaster*†
(Australia)
- Post-basicoronal interambulacral plates restricted to aboral surface [Figure 5f], stopping short of ambitus about two thirds of the way down from the apical system; tuberculation fine, spine tubercles closely spaced *Willungaster*†
(Australia)

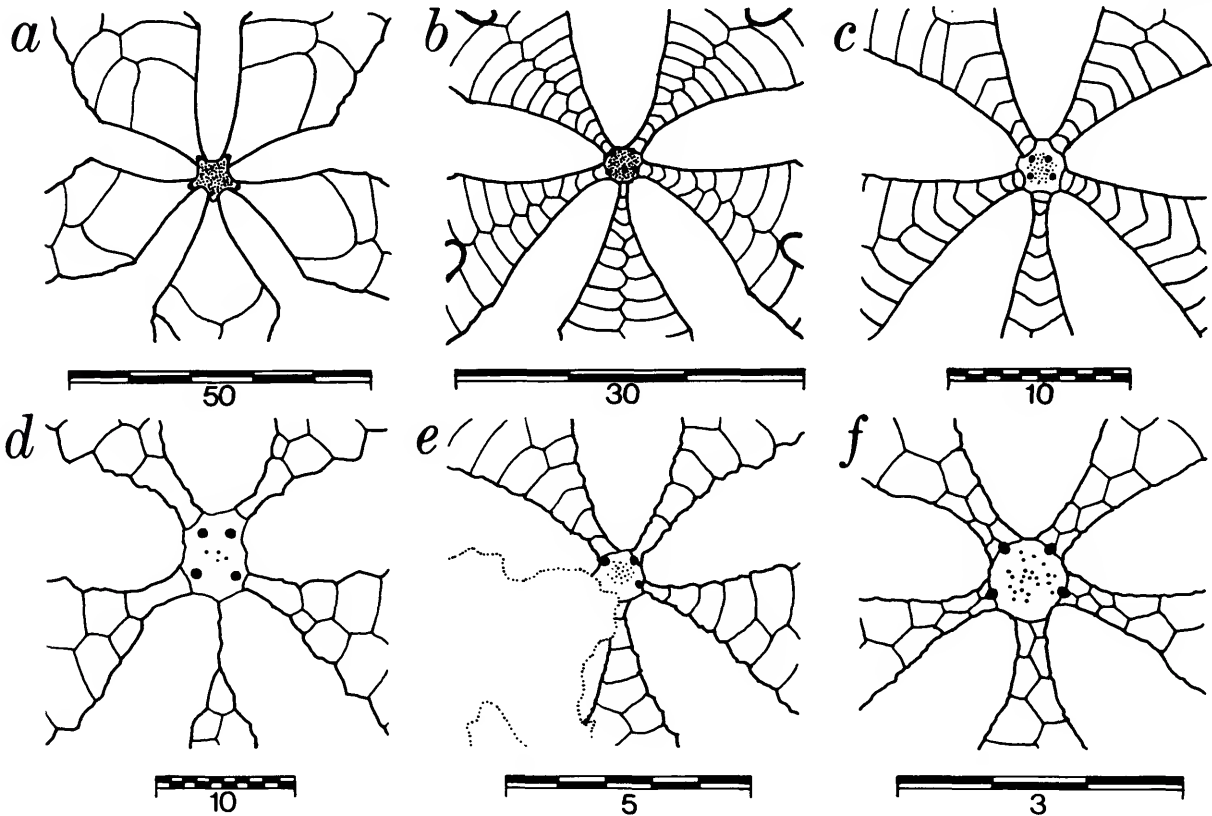


FIGURE 7.—Interambulacral plate pattern adjacent to the apical system of clypeasteroids: a, *Peronella lesueuri* (Valenciennes), BMNH 1981.2.6.86; b, *Rotula deciesdigitata* (Leske), USNM 2307; c, *Tarphygygus clarki* (Lambert), USNM 2522; d, *Fibulariella oblonga* (Gray), MCZ 7565; e, *Thagastea wetterlei* Pomei, ROM 4100 (ambulacrum V obscured by matrix); f, *Scutellina lenticularis* (Lamarck), BMNH 31187. (Details of ambulacral plating and petaloids omitted; anterior towards top of page; scale bars in mm.)

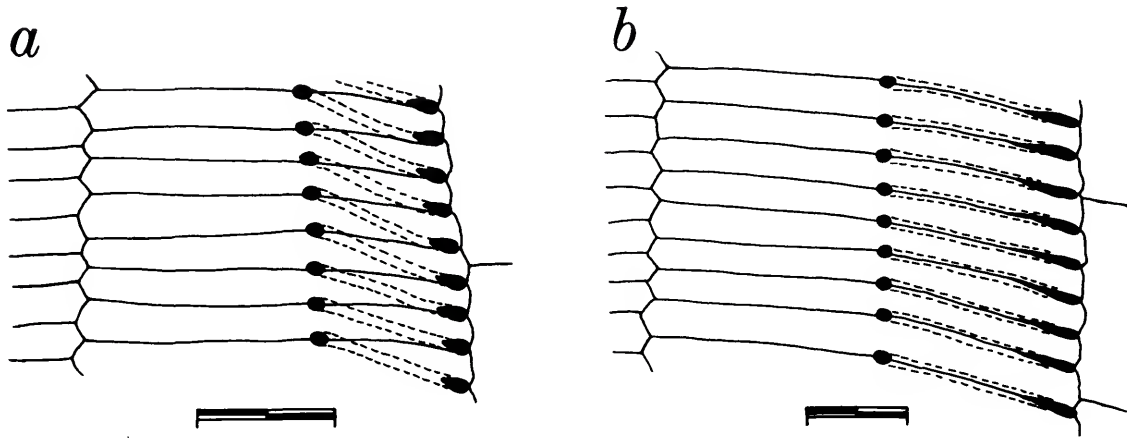


FIGURE 8.—Arrangement of respiratory podia in petaloids of clypeasteroids: *a*, Condition typical of laganines, *Laganum laganum* (Leske), UT, New Guinea; *b*, condition typical of clypeasterines and scutellines, *Echinodiscus bisperforatus* (Leske), UT, New Guinea. (Both figures show portion of a petaloid in a half ambulacrum; pore pairs solid black, conjugation groove indicated by dashed lines, plate sutures by solid lines; ambitus towards bottom of page; scale bars = 20 mm.)

10. Single plate [Figure 7*a,d*], or monoserial column of plates [Figure 7*b,c,e*] in interambulacra adjacent to apical system; respiratory podia [I.G., Figure 33*a*] crossing petaloid sutures, not aligned with circumferential sutures [I.G., Figure 31] of petaloid plates [Figure 8*a*]; ambulacral basicoronal plates longer than [Figure 9*a*], or equal in length to interambulacral basicoronal plates [Figure 9*b*], when equal in length, ambulacral basicoronal plates do not form point [Figure 9*b*]; keel [I.G., Figure 32*b*] in food grooves near peristome not well developed, never terminating in calcite peristomial point [I.G., Figure 32*b*] that projects into peristome [Figure 10*a*]; miliary spines [I.G., Figure 33*a*] with crown-shaped tips [Figure 11*a*], never with epithelial sac; accessory podia (sensu Mooi, 1986a:86) only, barrel-tipped podia [I.G., Figure 33*b*] absent; sub-dental process of Aristotle's lantern lacking [Figure 2*b*]; rotules [I.G., Figure 34*a*] of lantern reduced to sliver of calcite [Figure 12*a,b*], or lacking (Suborder Laganina) 11
- Double column of alternating plates in interambulacra adjacent to apical system [Figure 7*f*]; respiratory podia not crossing petaloid sutures, aligned with circumferential sutures of petaloid plates [Figure 8*b*]; interambulacral basicoronal plates usually longer than ambulacral basicoronal plates [Figure 9*d,e*], ambulacral basicoronal plates form point even when equal in length to interambulacral basicoronal plates [Figure 9*f*]; keel in food grooves near peristome well developed, terminating in calcite peristomial point projecting into peristome [Figure 10*b, c*]; miliary spines with slightly expanded tip usually ornamented with teeth and distal pin-like structures, never crown-shaped in adults [Figure 11*b,c*], tip with [Figure 11*c*] or without epithelial sac [Figure 11*b*] (see Mooi, 1986b); barrel-tipped podia in fields adjacent to food grooves; sub-dental process [Figure 2*c,d*] of Aristotle's lantern extending from supra-alveolar process under distal portion of tooth [I.G., Figure 34*a*]; rotules of lantern well developed [Figure 12*c,d*], usually with adoral, pointed expansion [Figure 12*c*] (Suborder Scutellina) 38

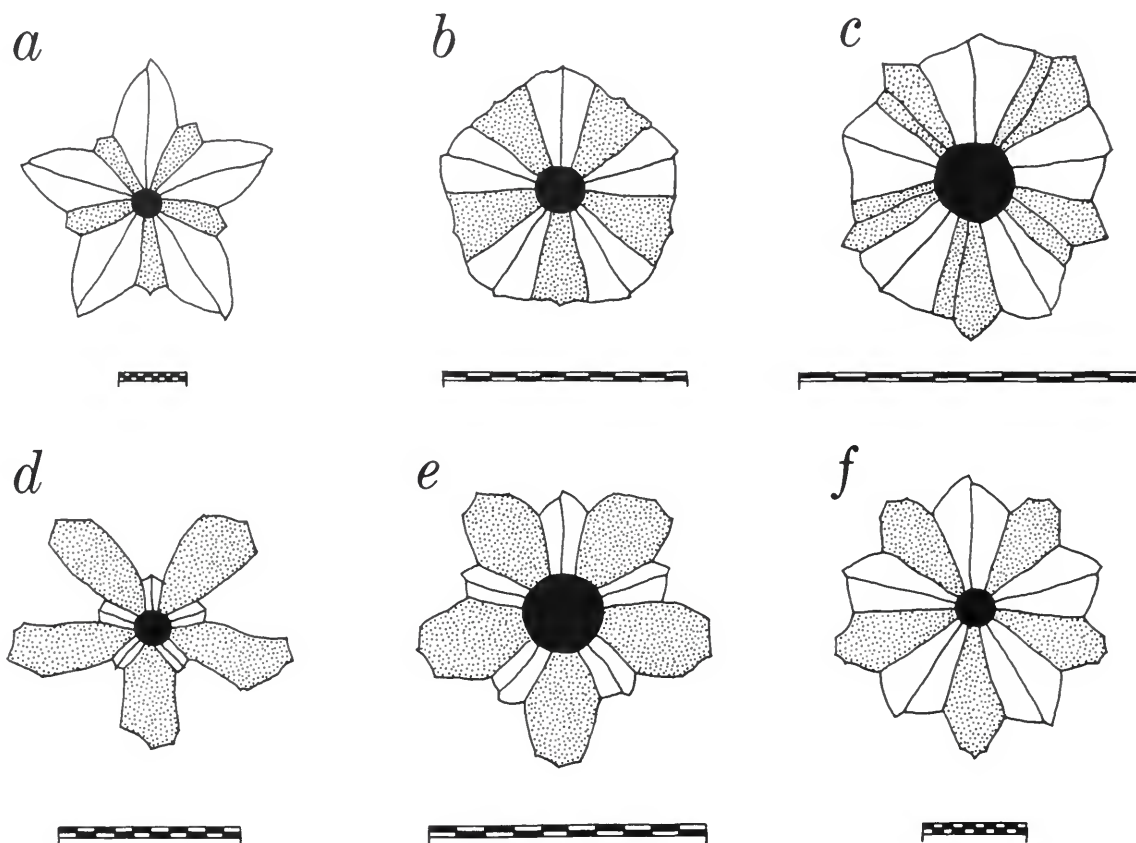


FIGURE 9.—Basicoronal plate patterns of clypeasteroids: *a*, *Peronella lesuewi* (Valenciennes), BMNH 1981.2.6.86; *b*, *Neolaganum archerensis* (Twitchell), after Durham (1954:679); *c*, *Rotula deciesdigitata* (Leske), MCZ 2551 (note that paired plates adjacent to peristome are not basicoronals, but first post-basicoronals); *d*, *Eoscutella coosensis* (Kew), after Durham (1955:98); *e*, *Iheringiella patagonensis* (Desor), after Durham (1955:126); *f*, *Scutella subrotunda* (Leske), after Durham (1955:98). (Interambulacral plates shaded, peristomes in solid black; anterior towards top of page; scale bars = 10 mm.)

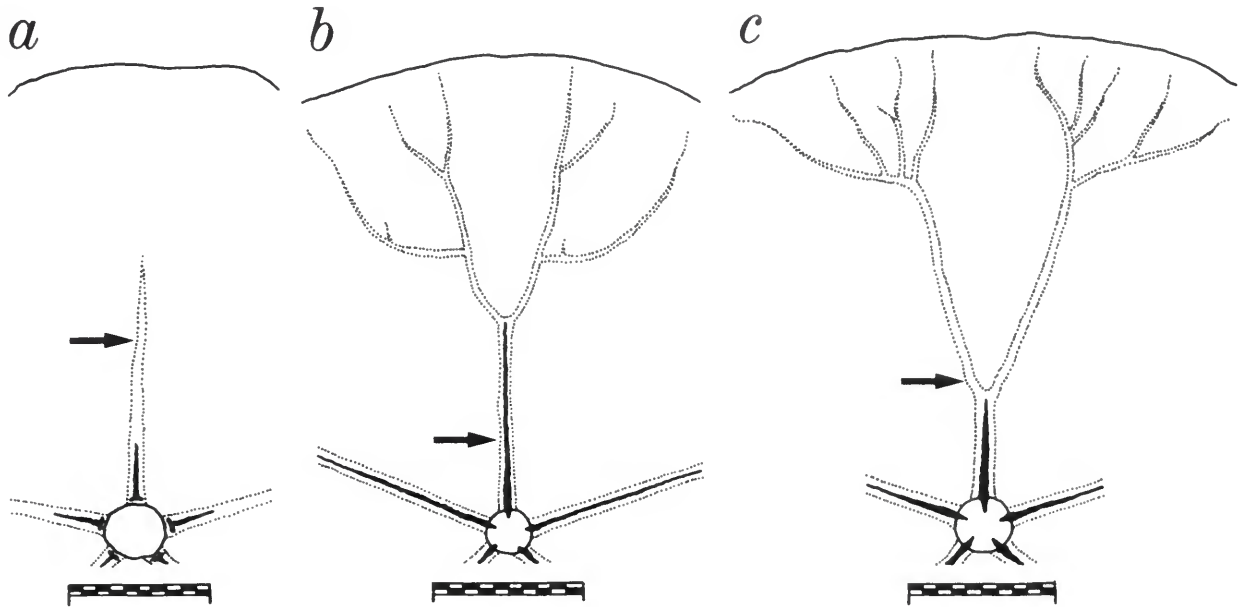


FIGURE 10.—Keels and peristomial points in the food groove of oral ambulacrum III in clypeasteroids: *a*, *Wythella eldridgei* (Twitchell), USNM Acc. 268937; *b*, *Periarachus lyelli* (Conrad), USNM 312506; *c*, *Scaphechinus mirabilis* A. Agassiz, UT, Vostok Bay. (Ends of ambulacral basicoronal plates indicated by arrows; Food grooves represented by dotted lines, keels and peristomial points in solid black; anterior towards top of page; scale bars = 10 mm.)

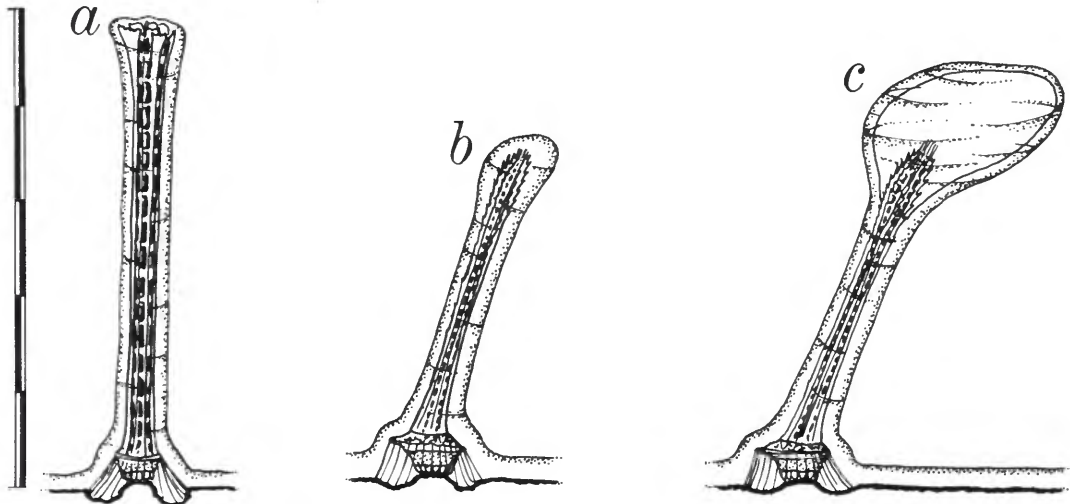


FIGURE 11.—Miliary spines of clypeasteroids: *a*, *Heliophora orbiculus* (Linné), BMNH 1953.1.29.197; *b*, *Echinarachnius parma* (Lamarck), UT, New Brunswick; *c*, *Leodia sexiesperforata* (Leske), UT, Florida Keys. (Semitransparent views showing epidermis, basal musculature, and internal calcite skeleton. Heavy line at base of spine represents surface of test; scale bar = 500 μ m.)

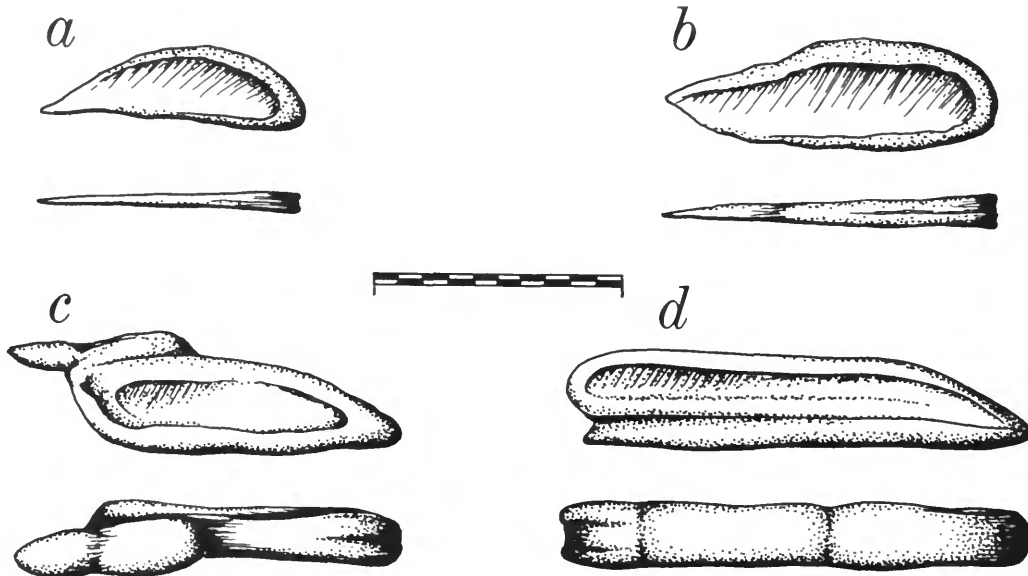


FIGURE 12.—Rotules from the Aristotle's lanterns of clypeasteroids: *a*, *Echinocyamus pusillus* (O.F. Müller), UT, Scotland; *b*, *Heliophora orbiculus* (Linné), BMNH 1904.10.28.5-8); *c*, *Mellita quinquesperforata*, UT, North Carolina; *d*, *Echinodiscus bisperforatus* (Leske), UT, New Guinea. (In each of *a* to *d*, center of lantern is to left; upper figure shows side, and lower figures top of a single rotule; scale bar = 1 mm.)

Suborder LAGANINA Mortensen, 1948

- 11. Food grooves well developed, extending almost to ambitus [Figure 13*a*]; each food groove bifurcated twice, once near peristome, with each branch then bifurcating near ambitus [Figure 13*a*]; posterior edge of test with shallow or deep notches [Figure 14*a-c*]; interambulacral basicoronal plates not visible externally [Figure 9*c*] 12
- Food grooves poorly developed or absent, stopping well short of ambitus [Figure 13*b*]; when present, food grooves straight, unbranched [Figure 13*b*]; posterior edge of test without notches [Figure 16*a-i*]; interambulacral basicoronal plates visible externally [Figure 9*a-b*] 14

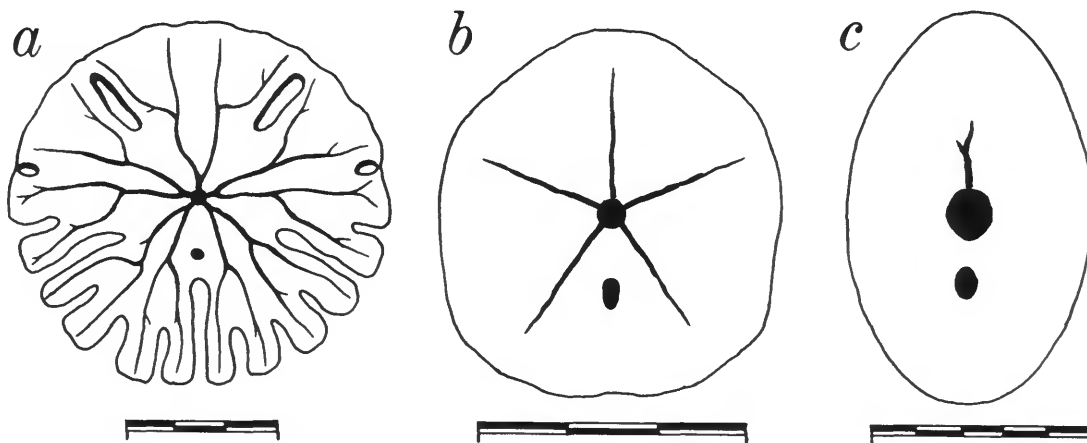


FIGURE 13.—Food grooves of laganines: *a*, *Rotula deciesdigitata* (Leske), USNM 2307; *b*, *Laganum laganum* (Leske), UT, New Guinea; *c*, *Fibulariella oblonga* (Gray), MCZ 4094. (Food grooves, peristome, and periproct in solid black; scale bars: *a* and *b* = 30 mm; *c* = 5 mm.)

12. Posterior edge of test with shallow notches in ambitus at each radial suture, creating lobe at end of each posterior plate column [Figure 14a]; all oral interambulacra continuous [Figure 14a]; test relatively thick, slightly elongate [Figure 14a] *Rotuloidea*† (West Africa)
- Posterior edge of test with deep notches in ambitus at each radial suture, creating long finger-like process at end of each posterior plate column [Figure 14b, c]; at least one paired oral interambulacrum discontinuous [I.G., Figure 31] between first and second pairs of post-basicoronal plates [Figure 14b, c]; test relatively thin, discoidal [Figure 14b,c] 13

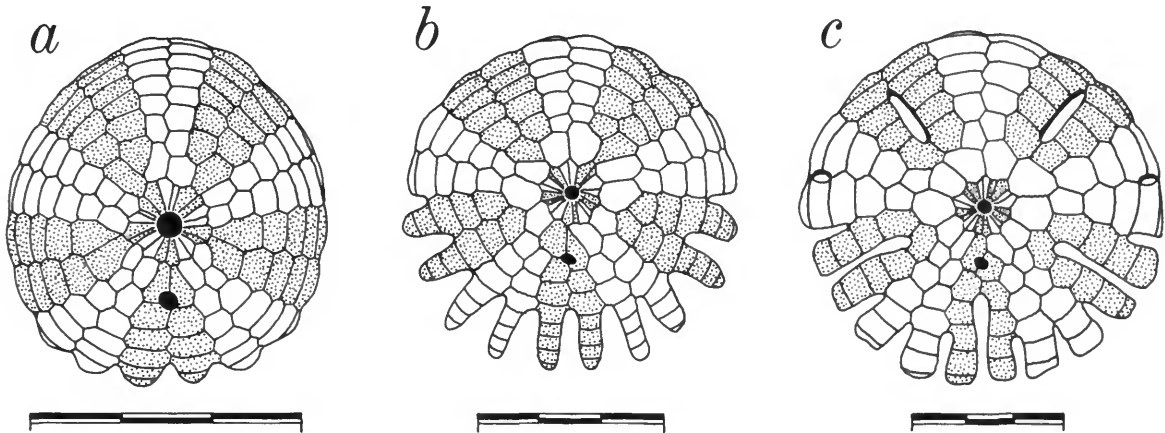


FIGURE 14.—Plate patterns on the oral surface of rotulid laganines: a, *Rotuloidea fimbriata* Etheridge, after Durham (1955:99); b, *Heliophora orbiculus* (Linné), USNM 32900; c, *Rotula deciesdigitata* (Leske), USNM 2307. (Interambulacra shaded; anterior towards top of page; scale bars = 30 mm.)

13. Without lunules [I.G., Figure 32b] in anterior part of test [Figure 14b]; outer pore [I.G., Figure 32a] of respiratory podia single [Figure 15a]; aboral primary spines [I.G., Figure 33a] sensu Mooi (1986b:213) only slightly club-shaped [Figure 15c] *Heliophora* (West Africa)
- Two to six lunules in anterior portion of test [Figure 14c]; outer pore of respiratory podia subdivided into several small pores [Figure 15b]; aboral primary spines strongly club-shaped [Figure 15d] *Rotula* (West Africa)

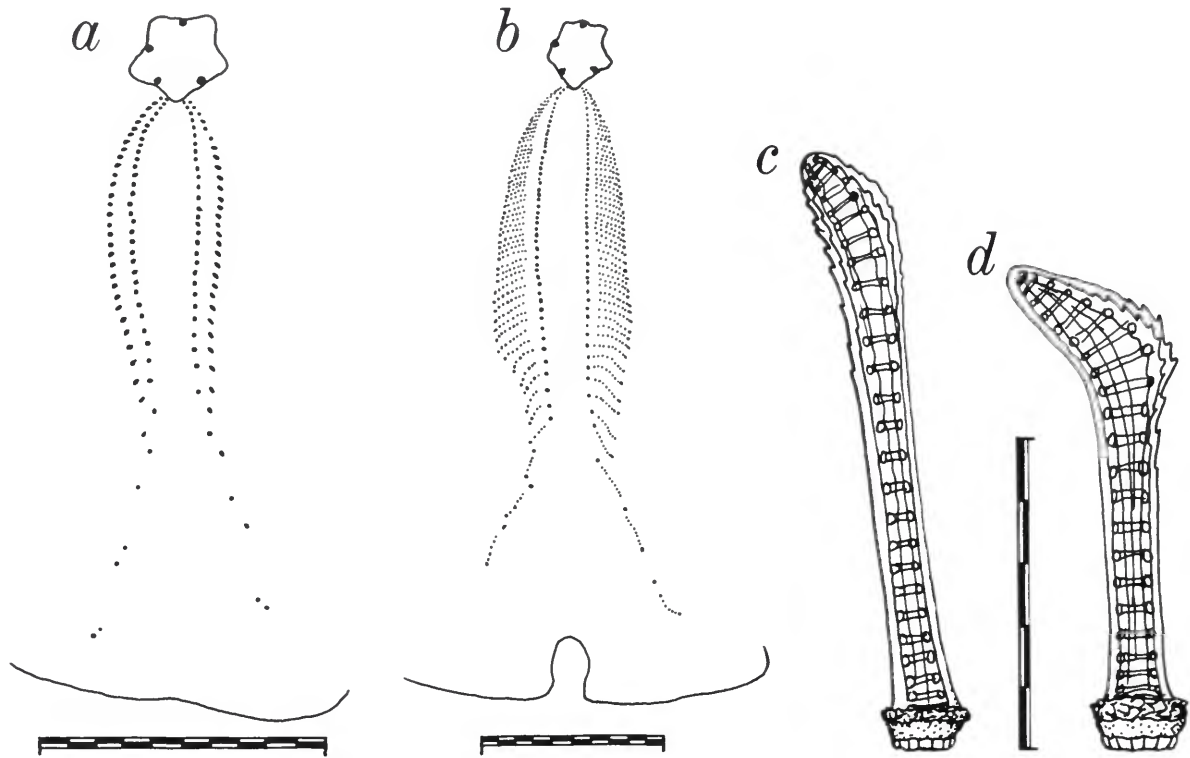


FIGURE 15.—Respiratory podial pores and spines of rotulids: *a*, Petaloid in ambulacrum IV of *Heliophora orbiculus* (Linné), AMNH 2298; *b*, petaloid in ambulacrum IV of *Rotula deciesdigitata* (Leske), USNM 2307; *c*, aboral primary spine of *Heliophora orbiculus* (Linné), BMNH 1953.1.29.197; *d*, aboral primary spine of *Rotula deciesdigitata* (Leske), MNHN EcEn997. In *a* and *b*, ambitus is shown at bottom of drawing, and scale bars = 10 mm; in *c* and *d*, scale bar = 500 μ m.)

14. Ambulacral and interambulacral basicoronal plates approximately same length, so that basicoronal rosette appears pentagonal in outline [Figure 9*b*]; irregularly arranged demiplates in petaloid ambulacra [Figure 6*b*]; first post-basicoronal plates in paired interambulacra much larger than others in oral post-basicoronal series [Figure 16*a-d*] 15
- Interambulacral basicoronal plates longer than ambulacral basicoronal plates, so that basicoronal rosette appears star-shaped in outline [Figure 9*a*]; no demiplates in petaloid ambulacra [condition similar to Figure 6*c,d*]; first post-basicoronal plates in paired interambulacra not conspicuously larger than others in oral post-basicoronal series [Figure 16*e-i*] 22

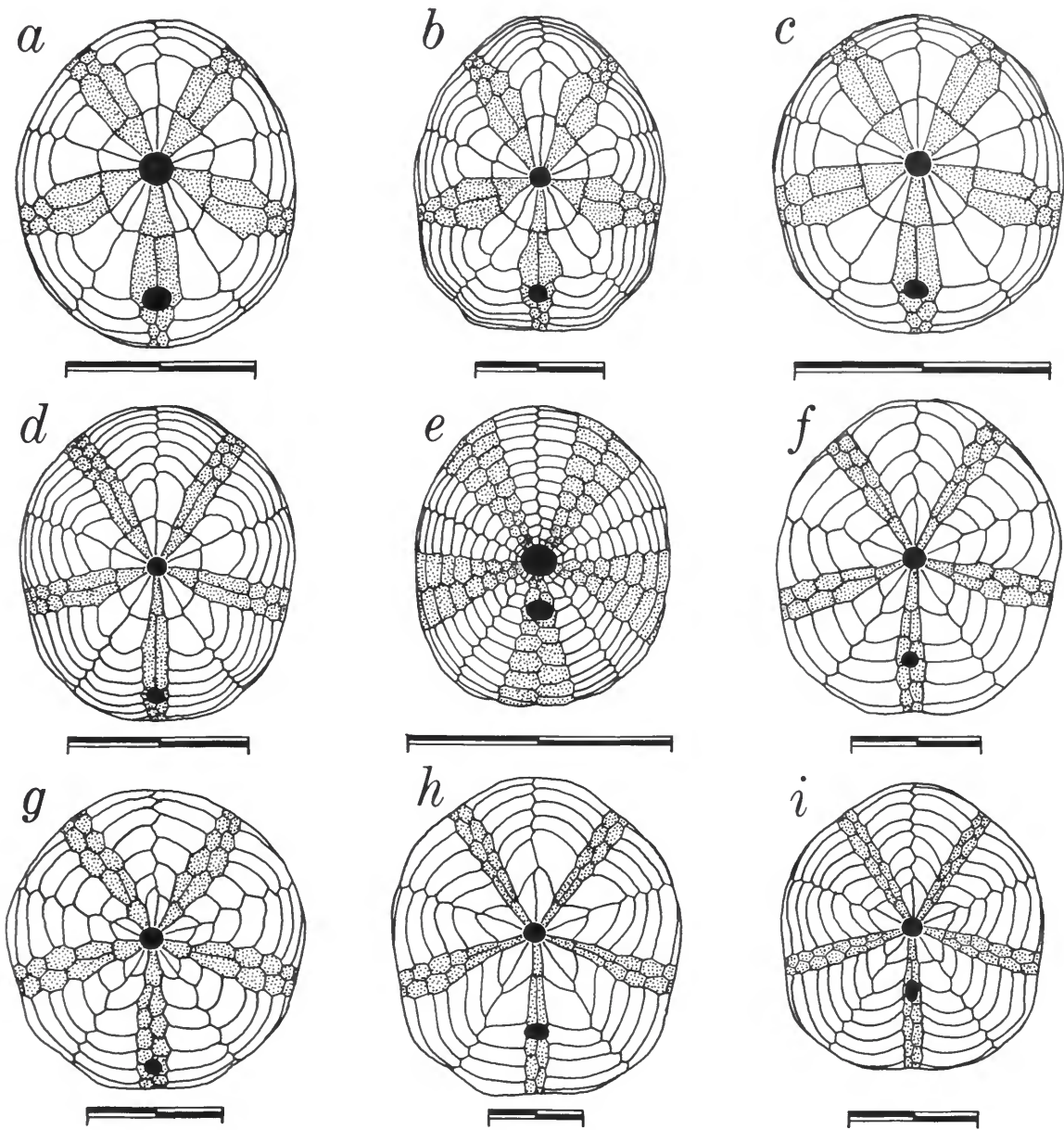


FIGURE 16.—Plate patterns on the oral surface of laganid and neolaganid laganines: *a*, *Weisbordella caribbeana* (Weisbord), after Durham (1954:678); *b*, *Wythella eldridgei* (Twitchell), after Durham (1954:683); *c*, *Neolaganum archerensis* (Twitchell), after Durham (1954:678); *d*, *Cubanaster torrei* (Lambert), after Durham (1954:678); *e*, *Tarphygyus clarki* (Lambert), USNM 2522; *f*, *Peronella peronii* (L. Agassiz), BMNH 48.5.8.2-7; *g*, *Hupea decagonale* (Lesson), after Durham (1955:140); *h*, *Jacksonaster conchatus* (McClelland), USNM E6999; *i*, *Laganum laganum* (Leske), UT, New Guinea. (Interambulacra shaded; anterior towards top of page; scale bars = 20 mm.)

- 15. Five gonopores 16
- Four gonopores 17
- 16. Petaloids reduced to four or five pore pairs in each respiratory podial row [Figure 17a]; single hydropore, not in groove [Figure 17a]; test of adults less than 5 mm in length; females with aboral marsupia around apical system [Figure 17a] *Pentedium*†
(Southeast North America)
- Petaloids not reduced, with more than 15 pore pairs in each respiratory podial row [Figure 17b]; hydropores in short, unbranched groove in madreporite [Figure 17b]; test of adults more than 20 mm in length; females without marsupia [Figure 17b] *Durhamella*†
(Southeast North America)

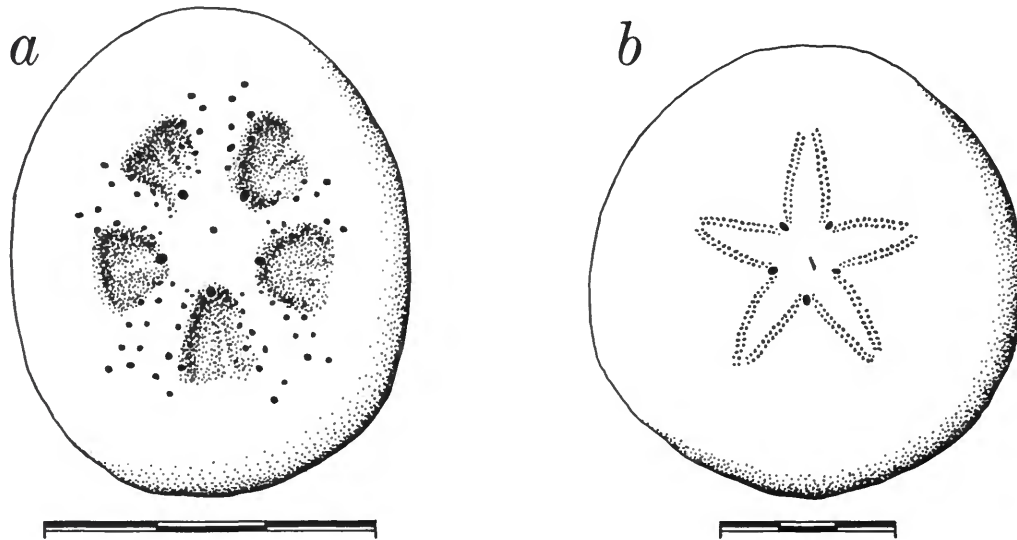


FIGURE 17.—Aboral surfaces of neolanigans: a, Female *Pentedium curator* Kier, after Kier (1967:Plate 129); b, *Durhamella floridana* (Twitchell), after Kier (1968:34). (Anterior towards top of page; scale bars = 3 mm.)

- 17. Hydropores in simple, unbranched groove [Figure 18a] 18
- Hydropores in branched groove [Figure 18b] 19
- 18. Four plates in each post-basicoronal column of oral ambulacrum III [Figure 16a]; oral surface deeply concave; ambitus relatively thick, rounded *Weisbordella*†
(Southeast North America, West Indies)
- Six or seven plates in each post-basicoronal column of oral ambulacrum III [Figure 16b]; oral surface flat; ambitus not thickened, sharp *Wythella*†
(Southeast North America, West Indies)

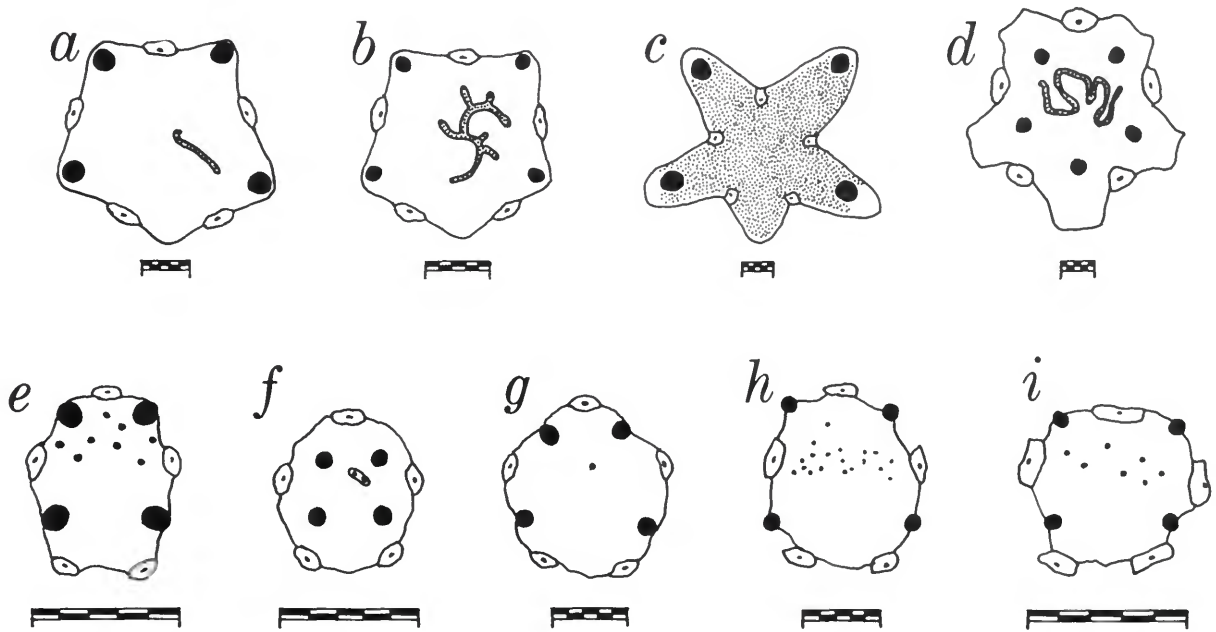


FIGURE 18.—Madreporic plate, ocular plates, hydroids, and gonopores of laganines and scutellines: *a*, *Wythella eldridgei* (Twitshell), USNM Acc. 268937; *b*, *Neolaganum durhami* Cooke, Holotype, USNM 562290a; *c*, *Peronella pellucida* Döderlein, USNM 34258; *d*, *Laganum laganum* (Leske), WAM 2082.75; *e*, *Fibulariella oblonga* (Gray), MCZ 4590; *f*, *Fibularia ovulum* Lamarck, UT, Eniwetok; *g*, *Echinocyamus pusillus* (O.F. Müller), UT, Scotland; *h*, *Porpitella hayesiana* (Desmoulins), MNHN, no number; *i*, *Eoscutum doncieuxi* (Lambert), MNHN. (Anterior towards top of page; scale bars = 500 μ m.)

19. Fewer than six plates in each post-basicoronal column of oral ambulacrum III [Figure 16c]; fewer than four plates in each post-basicoronal column of oral interambulacra 2 and 3 [Figure 16c]; oral surface flat or concave, never convex . . . 20
 More than six plates in each post-basicoronal column of oral ambulacrum III [Figure 16d]; five or six plates in each post-basicoronal column of oral interambulacra 2 and 3 [Figure 16d]; oral surface slightly or markedly convex [Figure 19a,b] . . . 21

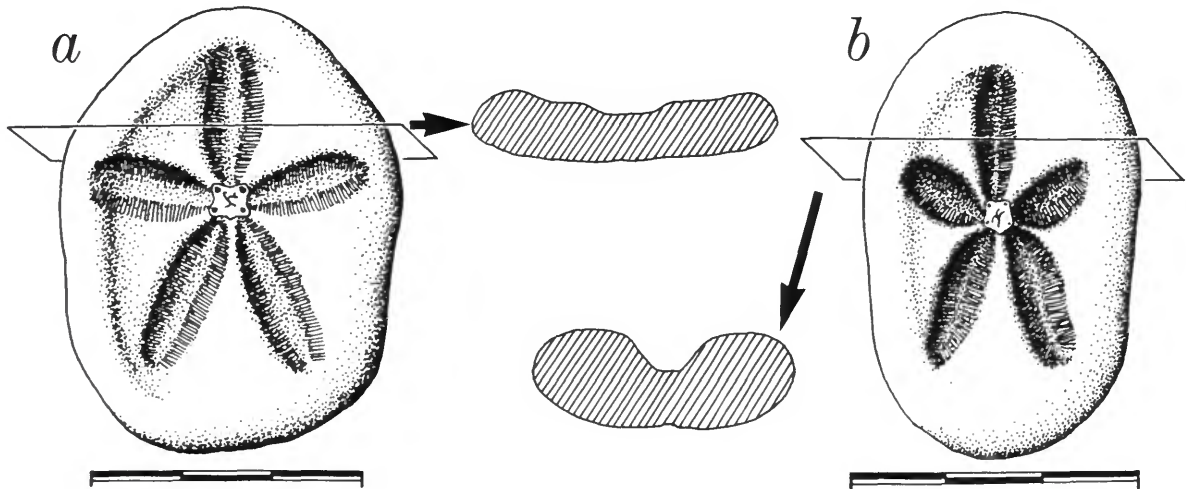


FIGURE 19.—Aboral surface and transverse profiles of neolaganids: *a*, *Cubanaster acunai* (Sánchez Roig), after Durham et al. (1966:U474); *b*, *Sanchezella sanchezi* (Lambert), USNM, no number. (Anterior towards top of page; scale bars = 30 mm.)

20. Oral surface flat; ratio of total width of interporiferous zone [I.G., Figure 32a] to width of individual respiratory podial row approximately 1:1 [Figure 20a]; petaloids widened, distally closed and rounded [Figure 20a]; test of adults small, less than 30 mm in length *Neolaganum*†
 (Southeast North America, West Indies)
- Oral surface slightly concave; ratio of total width of interporiferous zone to width of individual respiratory podial row approximately 3:1 [Figure 20b]; petaloids long, narrow, distally closed and somewhat pointed [Figure 20b]; test of adults large, greater than 40 mm in length *Neorumphia*†
 (Cuba)

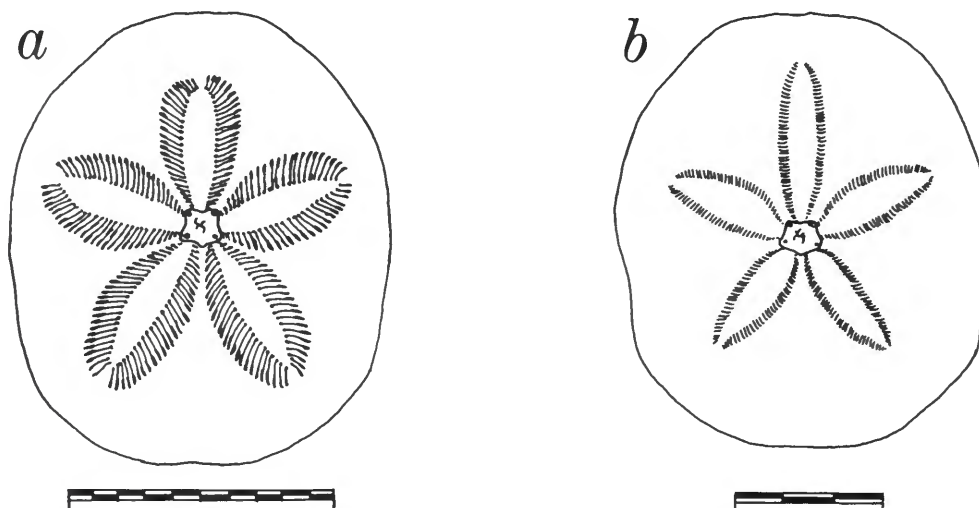


FIGURE 20.—Petaloids of neolaganids: a, *Neolaganum dalli* (Twitchell), BMNH E75279; b, *Neorumphia elegans* (Sánchez Roig), after Durham et al. (1966:U474). (Anterior towards top of page; scale bars; a = 10 mm; b = 30 mm.)

21. Petaloids slightly sunken [Figure 19a]; test roughly pentagonal, not greatly elongate [Figure 19a] *Cubanaster*†
 (West Indies, Panama)
- Petaloids deeply sunken [Figure 19b]; test greatly elongate [Figure 19b] *Sanchezella*†
 (West Indies)
22. Test of adults large, greater than 30 mm in length; petaloids well developed, with more than 30 pore pairs in each respiratory podial row; more than 30 hydropores; food grooves present in all oral ambulacra [Figure 13b] (indistinct grooves in *Tarphypygus*) 23
- Test of adults small, less than 20 mm in length; petaloids somewhat reduced, with fewer than 30 pore pairs in each respiratory podial row; fewer than 30 hydropores, typically only one or two (up to 30 in *Thagastea* and 20 in *Fibulariella*); food grooves always lacking in paired oral ambulacra [Figure 13c] (present in oral ambulacrum III only in *Thagastea* and *Fibulariella*) 28
23. Test high, globose; at least four plates in monoserial column in interambulacra adjacent to apical system [Figure 7c]; nine or more plates in each column of oral interambulacra 2 and 3 [Figure 16e]; more than ten plates in each column of oral ambulacrum III [Figure 16e]; internal circumferential ambulacral [I.G., Figure 34b] and radiating interambulacral buttresses [I.G., Figure 34b] absent *Tarphypygus*†
 (Jamaica, Cuba)
- Test typically low, never globose; never more than three plates in monoserial column in interambulacra adjacent to apical system [Figure 7a]; six or fewer plates in each column of oral interambulacra 2 and 3 [Figure 16f-i]; seven or fewer plates in each column of oral ambulacrum III [Figure 16f-i]; internal circumferential and radiating interambulacral buttresses well developed [Figure 21a] 24

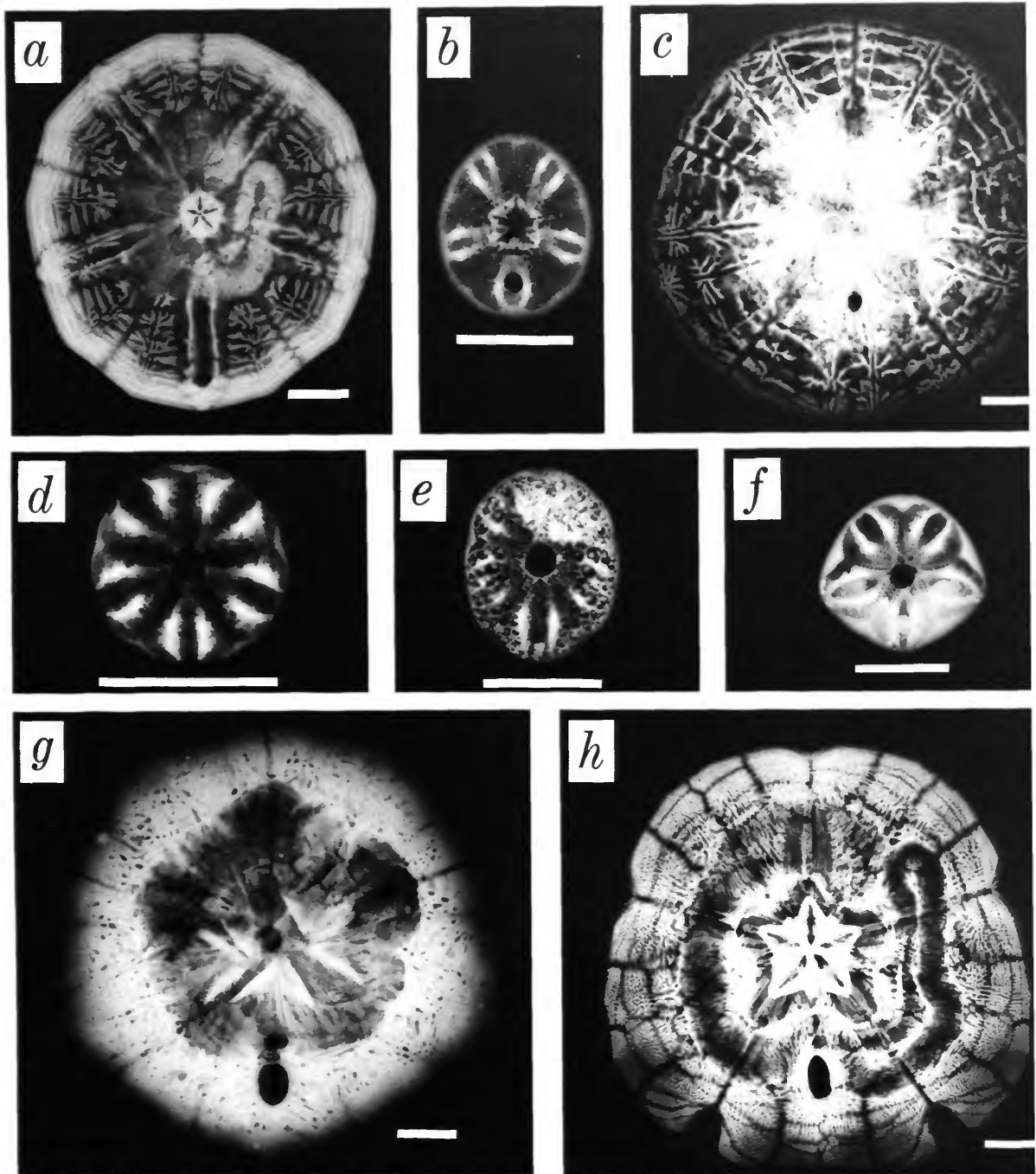


FIGURE 21.—Radiographs showing internal buttress systems of clypeasteroids: *a*, *Peronella lesueurii* (Valenciennes), BMNH 1981.2.6.86; *b*, *Echinocyamus pusillus* (O.F. Müller), UT, Scotland; *c*, *Periarchus lyelli* (Conrad), USNM; *d*, *Scutellina lenticularis* (Lamarck), BMNH 31187; *e*, *Lenia patellaris* (Leske), MNHN, no number; *f*, *Taiwanaster mai* Wang, paratype, USNM E32412; *g*, *Monophoraster darwini* (Desor), USNM Acc. 339378; *h*, *Encope aberrans* Martens, FDNR I18975. (Anterior towards top of page; scale bars: *a, c, d, g*, and *h* = 10 mm; *b, e*, and *f* = 5 mm.)

- 24. Four gonopores [Figure 18c] 25
- Five gonopores [Figure 18d] 26
- 25. Test width less than 77% test length; periproct less than twice its own length from ambitus *Rumphia*
(Indo-Pacific)
- Test width greater than 77% test length; periproct more than twice its own length from ambitus [Figure 16f] *Peronella*
(Indo-Pacific)
- 26. Hydropores distributed evenly throughout madreporite, not in groove; periproct near ambitus, between third and fourth, or fourth and fifth pairs of oral post-basicoronal plates [Figure 16g] *Hupea*
(Malaysia, Polynesia)
- Hydropores in long, sinuous, and sometimes branched groove in madreporite [Figure 18d]; periproct not near ambitus, between first and second, or second and third pairs of oral post-basicoronal plates [Figure 16h,i] 27
- 27. First pair of oral post-basicoronal plates in interambulacrum 5 greatly elongate [Figure 16h] *Jacksonaster*
(Indo-Pacific)
- First pair of oral post-basicoronal plates in interambulacrum 5 not greatly elongate [Figure 16i] *Laganus*
(Indo-Pacific)
- 28. Median area of oral surface with tuberculation greatly reduced to form "naked zone" [Figure 22a,b]; greatly enlarged tubercles with sunken areoles in lateral areas on oral surface [Figure 22a,b] 29
- No "naked zone" on oral surface; greatly enlarged oral tubercles lacking 30
- 29. Test almost as wide as it is long [Figure 22a]; anterior end rounded, or slightly truncated [Figure 22a] *Lenicyamidia*†
(Australia)
- Test elongate, width less than 63% of length [Figure 22b]; anterior end pointed [Figure 22b] *Leniechinus*†
(Southeast North America)

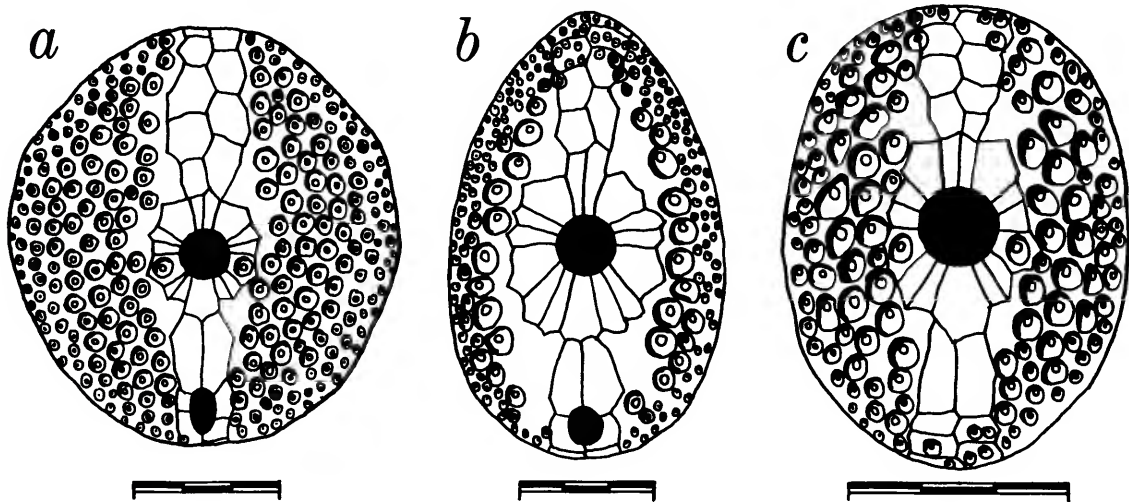


FIGURE 22.—Tuberculation on oral surface of laganines and a scutelline: a, *Lenicyamidia compta* Brunnschweiler, after Durham et al. (1966:U470); b, *Leniechinus herricki* Kier, after Kier (1968:6, pl. 1, fig. 4); c, *Lenia patellaris* (Leske), MNHN, no number. (Peristome and periproct in solid black; anterior towards top of page; plate pattern shown only in naked zone (ambulacrum III and interambulacrum 5); scale bars = 3 mm.)

30. At least five hydropores in anterior part of madreporite, never in groove [Figure 18e]; small food groove in oral ambulacrum III [Figure 13c]; non-globiferous pedicellariae with two valves [I.G., Figure 33c]; ophicephalous pedicellariae [I.G., Figure 33c] absent; aboral primary spines slightly club-shaped [Figure 23b]; globiferous pedicellariae [I.G., Figure 33c] present [Figure 23c]; spicules in peristomial membrane [I.G., Figure 32b]; six podial spicules in sucking disk of podia [Figure 23d]; internal circumferential ambulacral and radiating interambulacral buttresses absent 31
 Fewer than five hydropores (typically one or two), sometimes in short groove [Figure 18f,g]; food grooves completely absent; all pedicellariae with three valves; ophicephalous pedicellariae present; globiferous pedicellariae absent; no spicules in peristomial membrane; aboral primary spines never club-shaped [Figure 23a]; podial spicules absent; internal circumferential ambulacral and radiating interambulacral buttresses present or absent 32

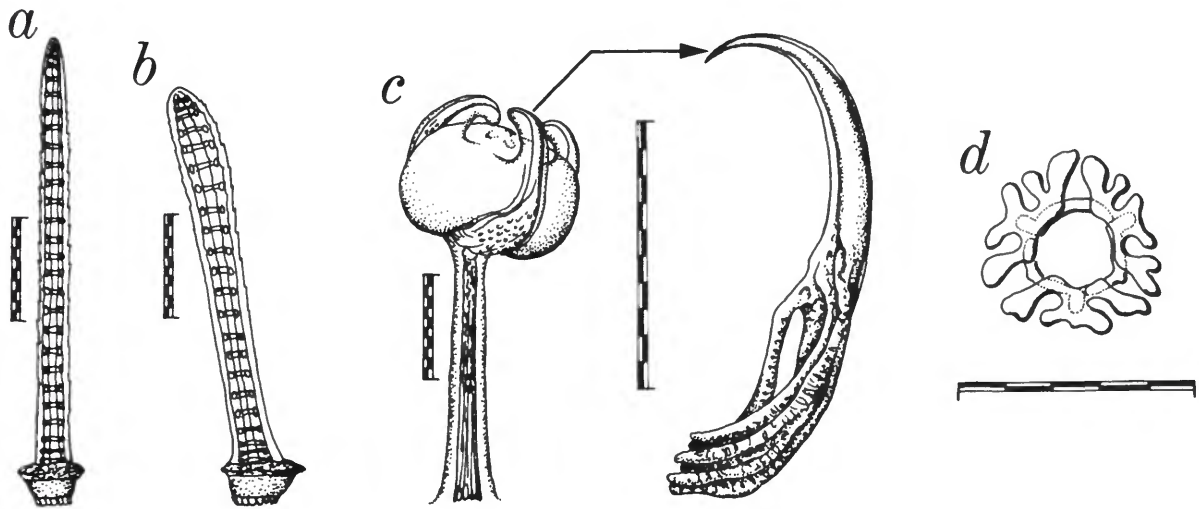


FIGURE 23.—Spines, pedicellariae, and podial spicules of laganines: a, Aboral primary spine of *Fibularia ovulum* Lamarck, MNHN EcEk131; b, aboral primary spine of *Fibulariella oblonga* (Gray), MCZ 7565; c, intact globiferous pedicellaria with poison glands (left), and single, cleaned valve (right) of *Fibulariella oblonga* (Gray), MCZ 7565; podial spicules of *Fibulariella oblonga* (Gray), after Mortensen (1948:219). (Scale bars: a to c = 100 μ m; d = 50 μ m.)

31. Single plate in monoserial column in interambulacra adjacent to apical system [Figure 7d]; fewer than 20 hydropores [Figure 7d]; six to ten pore pairs in each respiratory podial row *Fibulariella* (Indo-Pacific)
 Three or four plates in monoserial column in interambulacra adjacent to apical system [Figure 7e]; more than 20 hydropores [Figure 7e]; more than 15 pore pairs in each respiratory podial row *Thagastea*† (West Africa)
32. Periproct between sixth and seventh pairs of oral post-basicoronal plates; periproct just submarginal *Fibulaster*† (Europe)
33. Periproct between first and second pairs of oral post-basicoronal plates; periproct close to peristome, not submarginal . 33
 Petaloids large, extending to ambitus, more than 20 pore pairs in each respiratory podial row; circumferential ambulacral elements of internal buttress system reduced, but present; one or two hydropores in groove in madreporite *Sismondia*† (Europe, Africa, Indo-Pacific, Australia)
 Petaloids usually small, not extending to ambitus, fewer than 20 pore pairs in each respiratory podial row; circumferential ambulacral elements of internal buttress system completely lacking [Figure 21b]; hydropores in groove or not in groove 34
34. Both circumferential ambulacral and radiating interambulacral elements of internal buttress system completely absent; five

- relatively large, radiating plates in periproct [Figure 24a]; no spine tubercles on plates in periproctal membrane [I.G., Figure 32b] 35
- Internal buttress system present as a pair of radiating partitions in each interambulacrum [Figure 21b], or in interambulacrum 5 only; at least six, usually relatively small plates in periproct [Figure 24b,c]; plates in periproctal membrane with or without spine tubercles 37
35. Three gonopores *Tridium*†
(India)
- Four gonopores 36
36. One or two hydropores in short groove in madreporite [Figure 18f]; fewer than seven pore pairs in each respiratory podial row; area around peristome flat or convex; test typically globose *Fibularia*
(Indo-Pacific, worldwide as fossil)
- Single hydropore, not in groove [similar to that shown in Figure 18g]; more than seven pore pairs in each respiratory podial row; area around peristome slightly concave; test somewhat flattened *Cyamidia*†
(Indo-Pacific, Australia)
37. Internal buttresses present as a pair of radiating partitions in each interambulacrum [Figure 21b]; few small plates in periproctal membrane [Figure 24b]; plates in periproctal membrane without spine tubercles [Figure 24b]; periproct round [Figure 24b], or slightly elongate *Echinocyamus*
(Europe, Caribbean, Indo-Pacific, Australia, worldwide as fossil)
- Internal buttresses present as a pair of radiating partitions in interambulacrum 5 only [one partition on each side of periproct]; many small plates in periproctal membrane [Figure 24c]; plates in periproctal membrane with spine tubercles [Figure 24c]; periproct wider than long [Figure 24c] *Mortonia*
(Indo-Pacific)

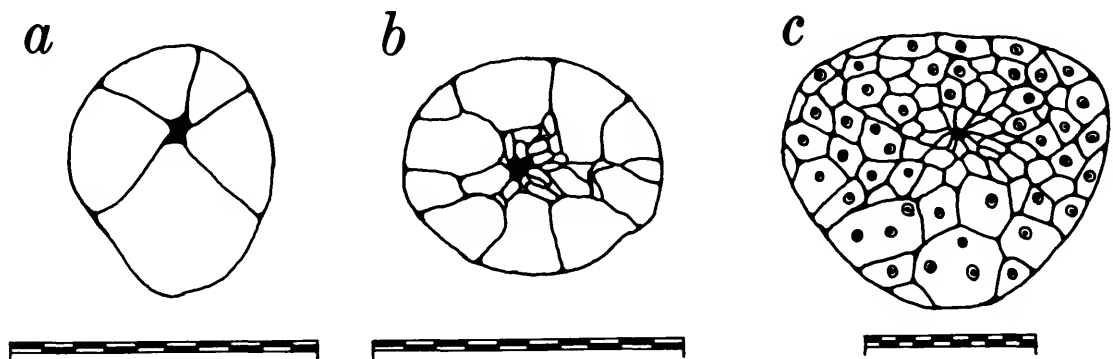


FIGURE 24.—Plate patterns and tuberculation of periproctal membrane of laganines: a, *Fibularia ovulum* Lamarck, MNHN EcEs5756; b, *Echinocyamus pusillus* (O.F. Müller), UT, Scotland; c, *Mortonia australis* (Desmoulins), after Mortensen (1949:160). (Anterior towards top of page; scale bars = 1 mm.)

Suborder SCUTELLINA Haeckel, 1896

38. No lunules [I.G., Figure 32b] or notches [Figures 25a-j, 26a-l, 27a-h]; pressure drainage channels [I.G., Figure 33b] absent [Figure 25a-j]; circumferential ambulacral and radiating interambulacral elements of internal buttress system discrete [Figure 21c] (reduced or absent in some forms), not sponge-like, macrocanal system poorly developed [Figure 21c] (incipiently developed in *Dendraster* and *Abertella*) 39
- At least one notch or lunule present, either in interambulacrum 5, and/or in at least two of the ambulacra [Figures 26m-p, 27i-p]; pressure drainage channels present, one in each oral ambulacrum, leading to a lunule, notch, or ambitus [Figure 25k, l]; circumferential ambulacral and radiating interambulacral elements of internal buttress system densely packed (never reduced or absent), sponge-like, forming well developed "macrocanal" system [Figure 21g,h] 65

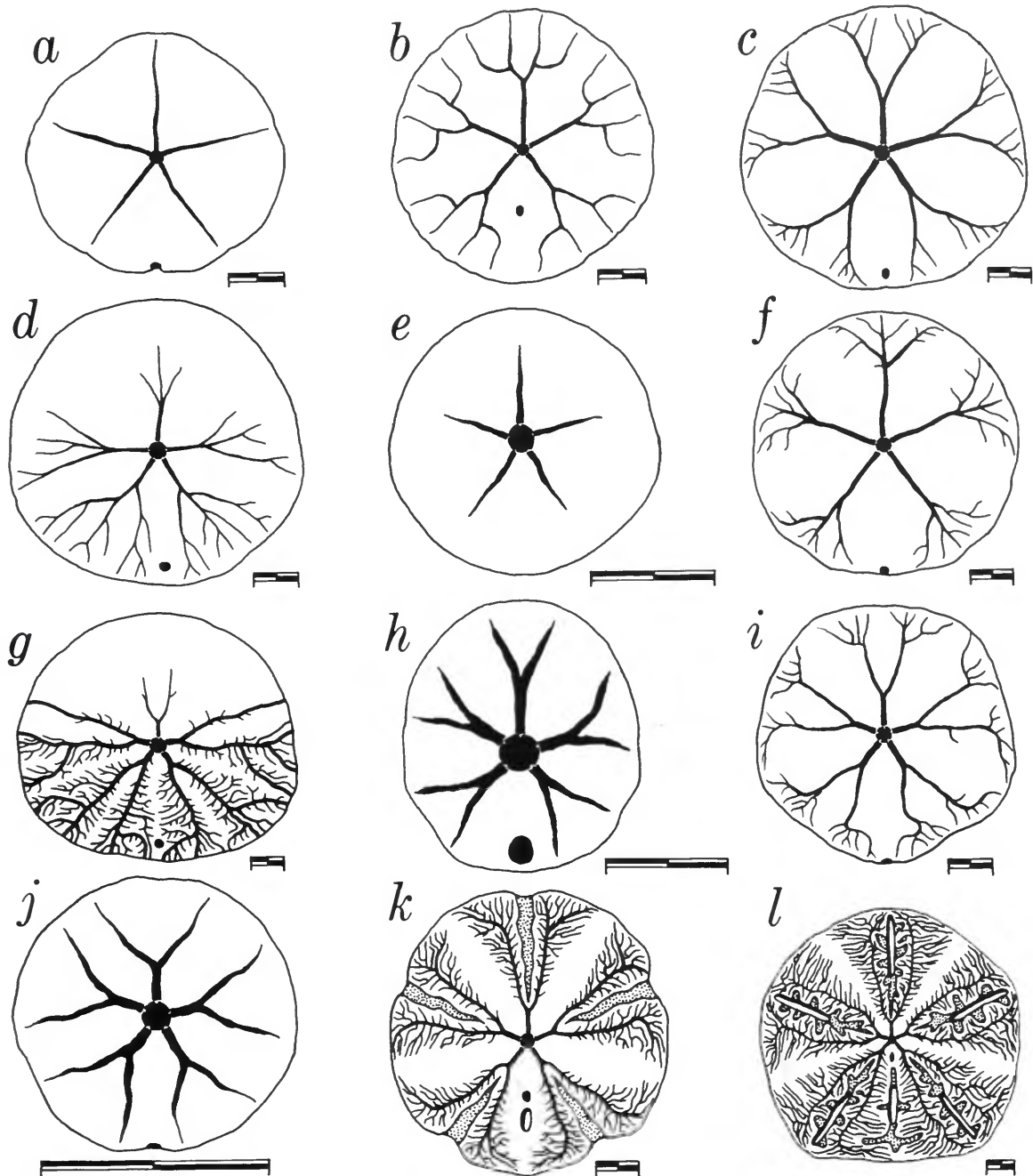


FIGURE 25.—Pressure drainage channels and food grooves of scutellines: *a*, *Protoscutella mississippiensis* (Twitchell), USNM, no number; *b*, *Periarchus lyelli* (Conrad), USNM 264066; *c*, *Iheringiella patagonensis* (Desor), BMNH E43225; *d*, *Scutellaster oregonensis major* (Kew), after Durham (1955:79); *e*, *Kewia blancoensis* (Kew), USNM 264125 (partially reconstructed); *f*, *Echinarachnius parma* (Lamarck), UT, New Brunswick; *g*, *Dendraster excentricus* (Eschscholtz), UT, Alaska; *h*, *Merriamaster perrini* (Weaver), BMNH E39170; *i*, *Scaphechinus mirabilis* A. Agassiz, UT, Vostok Bay; *j*, *Remondella waldroni* Wagner, USNM 181153; *k*, *Monophoraster darwini* (Desor), MCZ 3369; *l*, *Leodia sexiesperforata* (Leske), UT, Florida. (Pressure drainage channels stippled; peristomes and periprocts in solid black; anterior towards top of page; scale bars = 10 mm.)

- 39. Five gonopores; circumferential ambulacral and radiating interambulacral elements of internal buttress system very thin (circumferential ambulacral elements never absent), widely spaced so that coelomic spaces between elements are wider than calcite elements comprising buttress system [Figure 21c]; very long, prominent keel [Figure 10b] that extends well beyond ambulacral basicoronal plates in that part of food groove along perradial suture [I.G., Figure 31] 40
- Four gonopores; circumferential ambulacral and radiating interambulacral elements of internal buttress system thickened (circumferential ambulacral elements absent in some forms), more or less densely packed so that coelomic spaces between elements are narrower than calcite elements comprising buttress system; keel in that part of food groove along perradial suture does not extend much beyond ambulacral basicoronal plates [Figure 10c] 42
- 40. Posterior oral interambulacrum usually discontinuous, paired oral interambulacra continuous [Figure 26a]; food grooves straight, unbranched [Figure 25a]; periproct just submarginal, between third and fourth pairs of post-basicoronal plates [Figure 26a] *Protoscutella*†
(Southeast USA)
- All oral interambulacra always continuous [Figure 26b]; food grooves bifurcated beyond ends of ambulacral basicoronal plates, highly branched beyond this bifurcation [Figure 25b]; periproct approximately half way between peristome and ambitus, between first pair of post-basicoronal plates [Figure 26b] 41

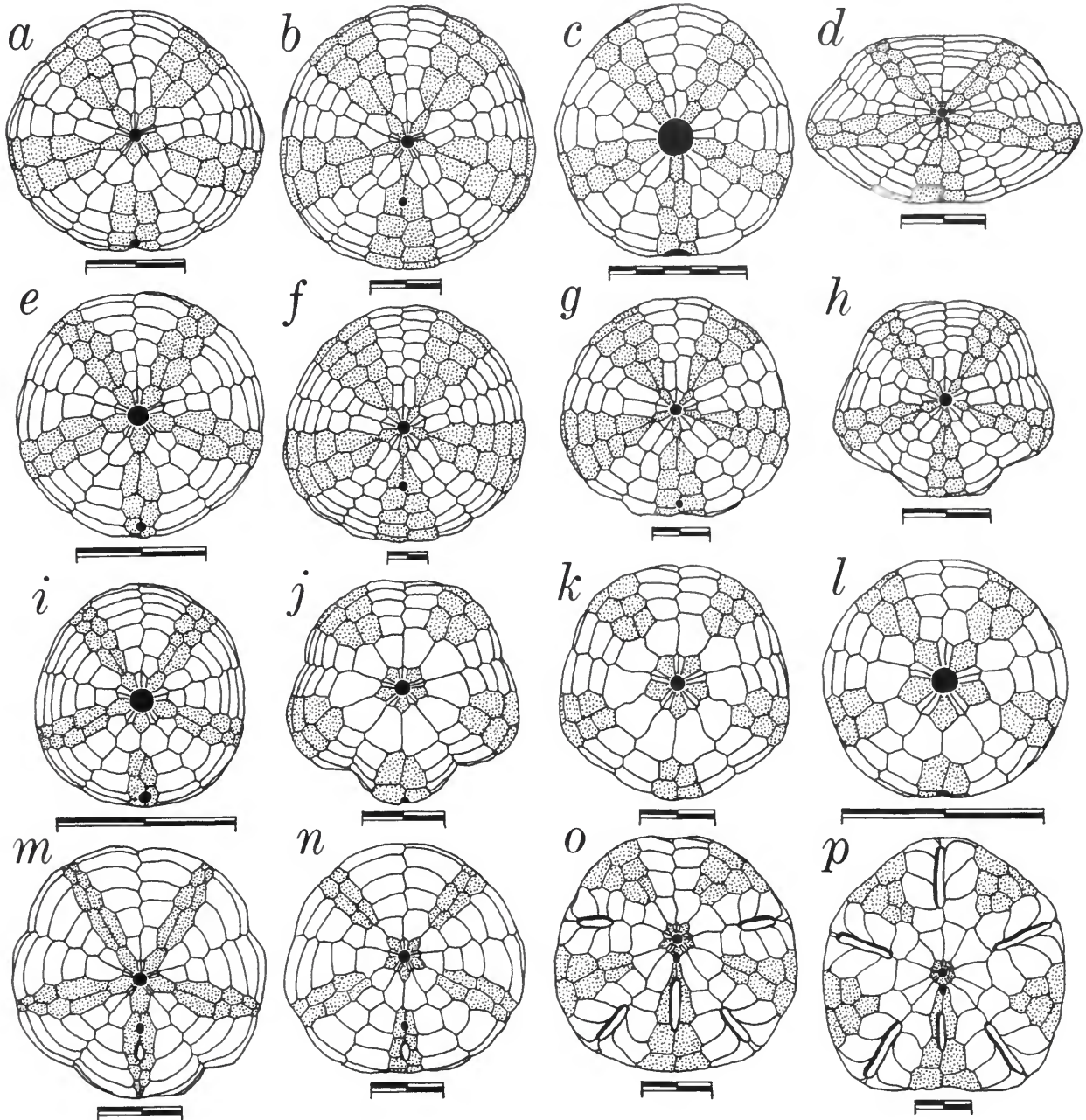


FIGURE 26.—Plate patterns on the oral surface of scutellines: *a*, *Protoscutella mississippiensis* (Twitchell), after Durham (1955:154); *b*, *Periarchus tyelli* (Conrad), USNM Acc. 326367; *c*, *Scutellina obovata* L. Agassiz, MNHN, no number; *d*, *Eoscutella coosensis* (Kew), after Durham (1955:98); *e*, *Iheringiella patagonensis* (Desor), after Durham (1955:126); *f*, *Scutella subrotunda* (Leske), after Durham (1955:98); *g*, *Parascutella bonali* (Tourmouer), MNHN, no number; *h*, *Parmulechinus subtetragona* (Grateloup), after Durham (1955:98); *i*, *Nipponaster nipponicus* (Nisiyama), after Durham (1955:154); *j*, *Vaquerosella norrisi* (Pack), after Durham (1955:103); *k*, *Scaphechinus mirabilis* A. Agassiz, UT, Vostok Bay; *l*, *Remondella waldroni* Wagner, USNM 181153; *m*, *Monophoraster darwini* (Desor), MCZ 3369; *n*, *Karlaster pirabensis* Marchesini Santos, adapted from Durham et al. (1966:U484); *o*, *Mellita quinquiesperforata* (Leske), UT, North Carolina; *p*, *Leodia sexiesperforata* (Leske), UT, Florida. (Interambulacra shaded; anterior towards top of page; scale bars: *a*, *b* and *d*-*p* = 20 mm; *c* = 5 mm.)

- 41. Test relatively thick, with rounded ambitus; respiratory podial rows widened, ratio of total width of interporiferous zone to width of individual respiratory podial rows approximately 1:1 [Figure 27a] *Mortonella*†
(Southeast USA, Cuba)
Test relatively thin, especially at sharp ambitus; respiratory podial rows narrow, ratio of total width of interporiferous zone to width of individual respiratory podial rows approximately 2:1 [Figure 27b] *Periarachus*†
(Southeast USA, Cuba)
- 42. All oral interambulacra continuous [Figure 26c-h] 43
At least one or two, and sometimes all oral interambulacra discontinuous [Figure 26i-l] 51
- 43. Small forms, test of adults less than 20 mm in length; food grooves reduced or absent, never bifurcated; fewer than 20 pore pairs in each respiratory podial row; circumferential ambulacral elements of internal buttress system poorly developed or absent [Figure 21d,e] 44
Large forms, test of adults greater than 30 mm in length; food grooves well developed, bifurcated; more than 40 pore pairs in each respiratory podial row; circumferential ambulacral elements of internal buttress system well developed 47
- 44. Periproct marginal, never distinctly on aboral surface [Figure 26c]; small circumferential ambulacral elements present in internal buttress system [Figure 21d] *Scutellina*†
(Europe)
Periproct distinctly on aboral surface; circumferential ambulacral elements of internal buttress system entirely absent [Figure 21e] 45
- 45. Median area of oral surface with tuberculation greatly reduced to form “naked” zone [Figure 22c]; greatly enlarged tubercles with sunken areoles in lateral areas on oral surface [Figure 22c]; small supernumerary radiating buttresses between each pair of radiating interambulacral internal buttresses [Figure 21e] *Lenita*†
(Europe)
No naked zone on oral surface; greatly enlarged tubercles lacking; no supernumerary buttresses between radiating interambulacral buttresses 46
- 46. Test of adults greater than 10 mm in length; more than 15 pore pairs in each respiratory podial row; more than ten hydropores in madreporite [Figure 18h] *Porpitella*†
(Europe, Southeastern USA?)
Test of adults less than 6 mm in length; fewer than 10 pore pairs in each respiratory podial row; fewer than 10 hydropores in madreporite [Figure 18i] *Eoscutum*†
(Europe)
- 47. Test much wider than long, test length only approximately 65% test width [Figure 26d]; ambulacral basicoronal plates very small, interambulacral basicoronal plates greatly enlarged, more than 2.5 times the length of ambulacral basicoronal plates [Figure 9d] *Eoscutella*†
(Southwestern USA, Argentina)
Test approximately as long as wide [Figure 26e-h]; interambulacral basicoronal plates less than 2.5 times the length of ambulacral basicoronal plates [Figure 9e, f] 48

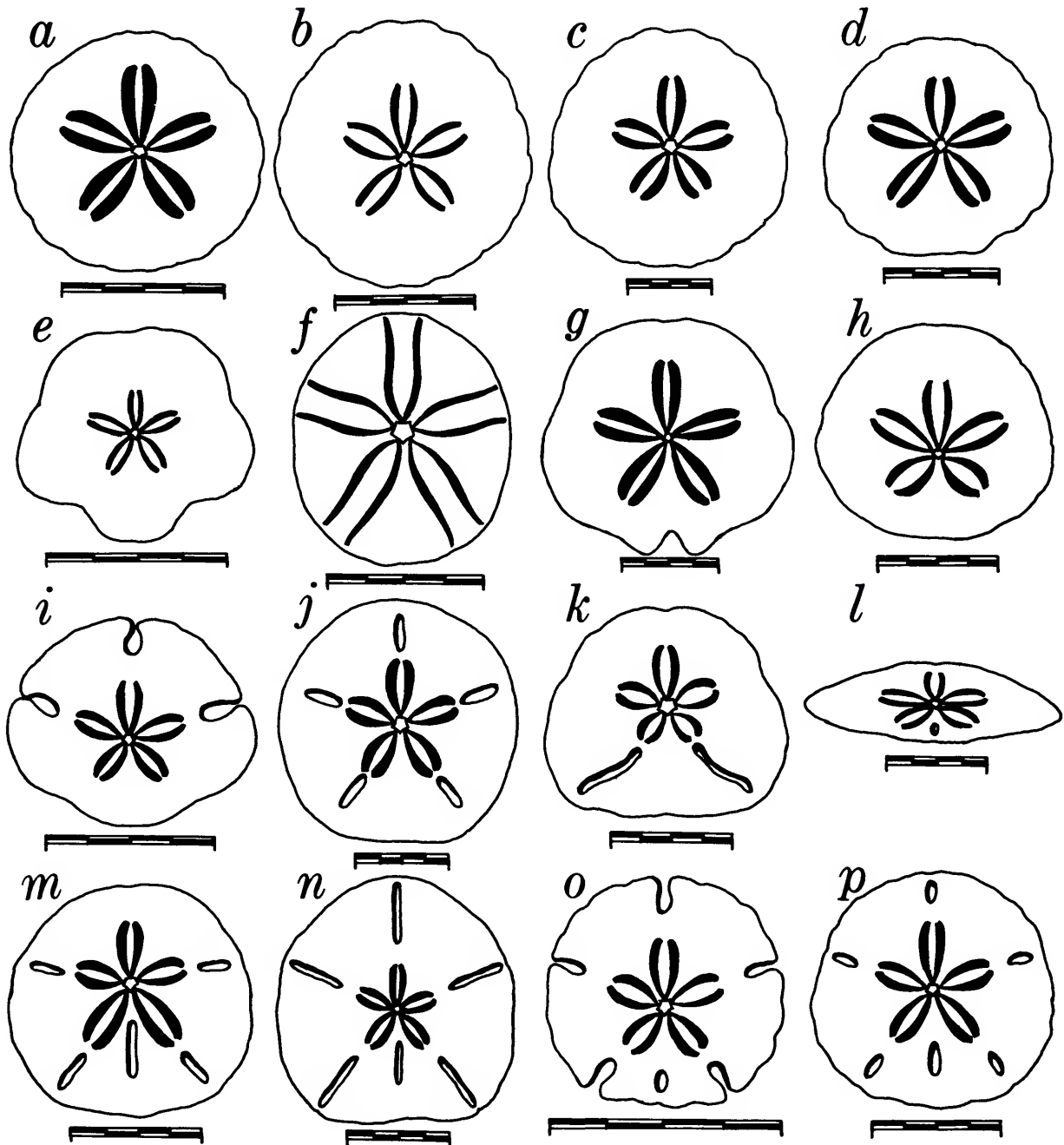


FIGURE 27.—Aboral surface of scutellines showing test shape and petaloids: *a*, *Mortonella quinquefaria* (Say), adapted from Durham et al. (1966:U479); *b*, *Periarachus lyelli* (Conrad), USNM 312506; *c*, *Scutella subrotunda* (Leske), adapted from Durham (1953a:352); *d*, *Parascutella bonali* (Tourmouer), MNHN, no number; *e*, *Parmulechinus subtetragona* (Grateloup), ROM 4122; *f*, *Astrodapis spatiosus* Kew, USNM 15575; *g*, *Abertella aberti* (Conrad), USNM, no number; *h*, *Dendraster excentricus* (Eschscholtz), UT, Alaska; *i*, *Scutaster andersoni* Pack, USNM 371777; *j*, *Astriclypeus manni* Verrill, BMNH 81.8.2.3; *k*, *Echinodiscus bisperforatus* Leske, BMNH 97.6.10.1-7; *l*, *Amplaster coloniensis* Martínez, adapted from Martínez (1985:506); *m*, *Mellia quinquesperforata* (Leske), UT, North Carolina; *n*, *Leodia sexiesperforata* (Leske), UT, Florida; *o*, *Mellitella stokesii* (L. Agassiz), USNM E15164; *p*, *Encope micropora* L. Agassiz, UT, Panama. (Petaloids in solid black; anterior towards top of page; scale bars = 40 mm.)

48. Interambulacra slightly "pinched" towards ambitus [Figure 26e], narrower at ambitus than at a point midway down aboral surface; four or five "trailing" podia at end of each respiratory podial row [Figure 28a]; food grooves bifurcate well beyond ends of ambulacral basicoronal plates; main branches of food grooves continuously divergent in arcs distal to bifurcation [Figure 25c] *Iheringiella*†
(Argentina, Chile)
- Interambulacra not "pinched" towards ambitus [Figure 26f-h], about same width at ambitus as at a point midway down aboral surface; "trailing" podia at end of each respiratory podial row lacking [Figure 28b]; food grooves bifurcate on, or just distal to ends of ambulacral basicoronal plates; main branches of food grooves more or less parallel distal to bifurcation, not continuously divergent in arcs 49

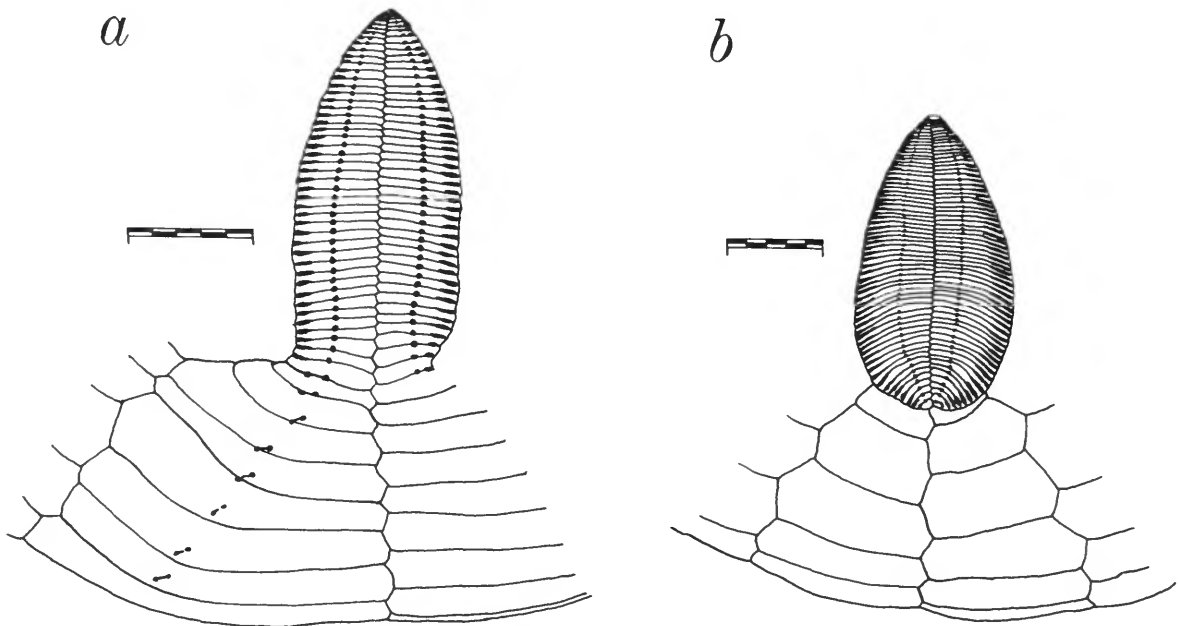


FIGURE 28.—Trailing podia and plate patterns of petaloids in scutellines: a, Aboral ambulacrum IV of *Iheringiella patagonensis* (Desor), ROM 5433M (plate pattern partially obscured); b, aboral ambulacrum II of *Parascutella* sp., UT, France. (Ambitus towards bottom of page; scale bars = 5 mm.)

49. Periproct about midway between peristome and ambitus, between first and second pairs of post-basicoronal plates [Figure 26f]; anterior petaloid (in ambulacrum III) longer than paired petaloids [Figure 27c] *Scutella*†
(Europe)
- Periproct just submarginal or marginal, between third and fourth, or fourth and fifth pairs of post-basicoronal plates [Figure 26g, h]; anterior petaloid (in ambulacrum III) shortest of petaloids [Figure 27d, e] 50
50. Periproct just submarginal, between third and fourth pairs of post-basicoronal plates [Figure 26g]; interambulacra as wide as ambulacra at ambitus; petaloids large, more than half as long as corresponding aboral ambulacra [Figure 27d]; ambitus not broadly indented at perradial sutures [Figure 26g] *Parascutella*†
(Europe)
- Periproct marginal, between fourth and fifth pairs of post-basicoronal plates [Figure 26h]; interambulacra approximately half as wide as ambulacra at ambitus; petaloids small, less than half as long as corresponding aboral ambulacra [Figure 27e]; ambitus broadly indented at perradial sutures, especially in ambulacra I and V [Figures 26h, 27e] *Parmulechinus*†
(Europe)
51. Periproct distinctly on aboral surface 52
- Periproct distinctly on oral surface, submarginal, or marginal, never distinctly on aboral surface 54

52. Large forms, test of adults usually greater than 50 mm in length; food grooves well developed, highly branched, trifurcated [Figure 25d]; apical system slightly displaced posteriorly; circumferential ambulacral elements of internal buttress system well developed, comprised of numerous, complicated pillars *Scutellaster*†
(Western USA, Alaska)
Small forms, test of adults usually less than 30 mm in length; food grooves usually reduced, never trifurcated [Figure 25e]; apical system approximately central; circumferential ambulacral elements of internal buttress system lacking [Figure 21f] 53
53. Test of adults greater than 20 mm in length; petaloids with more than 20 pore pairs in each respiratory podial row *Kewia*†
(Northwestern North America, Japan)
Test of adults less than 15 mm in length; petaloids with fewer than 15 pore pairs in each respiratory podial row *Sinaechinocyamus*, *Taiwanaster*
(Yellow Sea, Taiwan)
54. Food grooves straight and unbranched, or trifurcated [Figure 25f]; no sac on tip of miliary spines [Figure 11b] 55
Food grooves always bifurcated [Figures 25g–j], usually highly branched [Figure 25g,i]; tip of miliary spines enveloped by epithelial sac filled with fluid and collagen fibres [Figure 11c] 61
55. Test of adults relatively small, less than 20 mm in length; circumferential ambulacral elements of internal buttress system lacking *Allaster*†
(Japan)
Test of adults more than 20 mm in length; circumferential radiating elements of internal buttress system fairly well developed 56
56. Petaloids continuing to ambitus, open distally [Figure 27f]; petaloids typically inflated, aboral interambulacra more or less sunken (this condition is variable, but diagnostic when present), apical system usually depressed *Astrodapsis*†
(Southwestern USA)
Petaloids stopping short of ambitus, tending to close distally; petaloids not inflated, aboral interambulacra not sunken, apical system not depressed 57
57. Food grooves trifurcated near ambitus [Figure 25f] 58
Food grooves simple, unbranched. (Unfortunately, this character is very difficult to determine on fossil forms. Further study of *Tenuiarachnius* and *Vaquerosella* might show that trifurcated food grooves occur in these taxa as well. For the purposes of this key, if the grooves are unambiguously trifurcated, then advancement to couplet 58 is advocated, if there is doubt concerning trifurcation, then examination of couplets 59 and/or 60 is recommended.) 59
58. Periproct marginal *Echinarachnius*
(Northwestern North American, Japan
Northeastern North America)
Periproct distinctly on oral surface *Faassia*†
(Kamchatka)
59. Periproct distinctly on oral surface; all paired oral interambulacra broadly continuous [Figure 26i]; test slightly elongate *Nipponaster*†
(Japan, Kamchatka)
Periproct marginal or slightly supramarginal; at least one or two of paired oral interambulacra discontinuous [Figure 26j]; test not elongate 60
60. Periproct just supramarginal; test not broadly indented at perradial sutures *Tenuiarachnius*†
(Southwestern USA)
Periproct marginal; test typically broadly indented at perradial sutures [Figure 26j] *Vaquerosella*†
(Southwestern USA)
61. Deep notch in ambitus in posterior interambulacrum [Figure 27g] at interradian suture [I.G., Figure 31]; test of adults very large, frequently exceeding 100 mm in length *Abertella*†
(Eastern USA)
No notch in ambitus in posterior interambulacrum [Figure 27h]; test of adults seldom exceeding 80 mm in length 62
62. Apical system displaced posteriorly [Figure 27h]; periproct distinctly on oral surface; geniculate spines [I.G., Figure 33b] in very narrow geniculate fields [I.G., Figure 33b] on oral surface adjacent to food grooves; locomotory spines [I.G., Figure 33b] in locomotory fields [I.G., Figure 33b] much longer than oral spines in ambulacra (geniculates) [Figure 29a]; on oral surface, long barrel-tipped podia occur at perimeter of geniculate spine areas, short barrel-tipped podia occur within geniculate spine fields 63

Apical system approximately central; periproct marginal or just submarginal; geniculate spines absent; locomotory spines in locomotory fields only slightly longer than oral spines [Figure 29b] in ambulacra; barrel-tipped podia not differentiated into long and short varieties 64

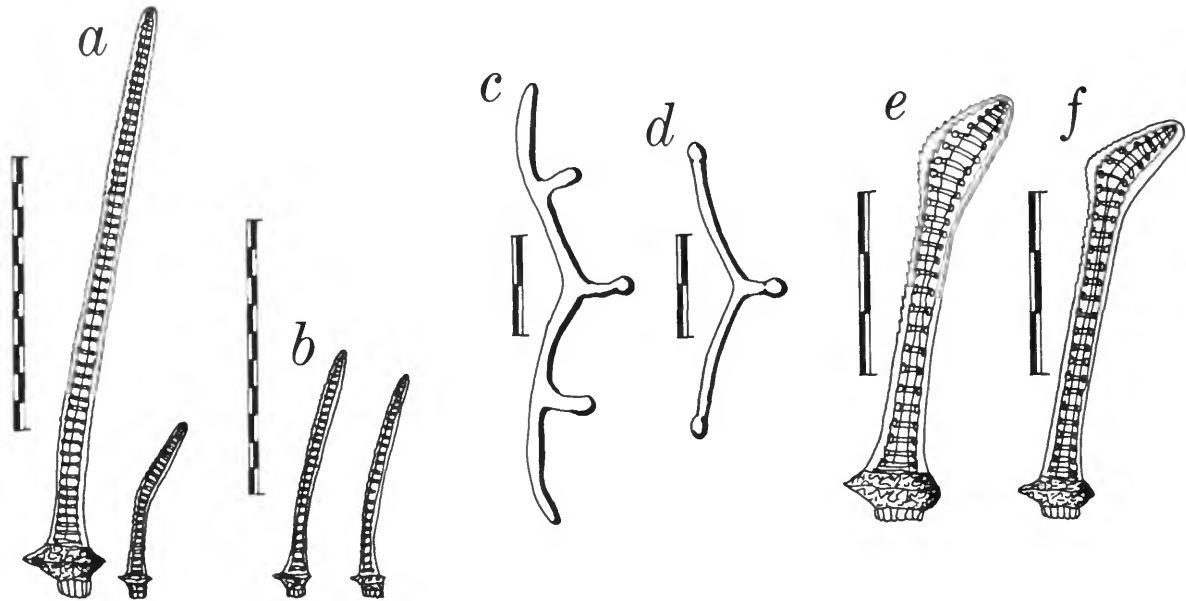


FIGURE 29.—Spines and podial spicules of scutellines: a, Locomotory spine (left) and geniculate spine (right) from the oral surface of *Dendraster excentricus* (Eschscholtz), UT, Alaska; b, locomotory spine (left) and ambulacral spine (right) from the oral surface of *Scaphechinus mirabilis* A. Agassiz, BMNH 1902.12.4.1-5; c, single spicule from tip of an accessory podium of *Astriclypeus manni* Verrill, MCZ 262A; d, single spicule from the tip of an accessory podium of *Mellita quinquesperforata* (Leske), UT, North Carolina; e, aboral primary spine of *Mellita quinquesperforata* (Leske), UT, North Carolina; f, aboral primary spine of *Leodia sexiesperforata* (Leske), UT, Florida. (Scale bars: a and b = 1 mm; c and d = 30 μ m; and e and f = 300 μ m.)

- 63. Test of adults greater than 50 mm in length; circumferential elements of internal buttress system well developed, highly complicate; food grooves highly branched beyond bifurcation [Figure 25g], continue onto aboral surface; test thin, with sharp margins; tuberculation relatively fine *Dendraster*
(Southeastern Alaska to Baja California)
- Test of adults less than 30 mm in length; circumferential ambulacral elements of internal buttress system reduced to simple pillars; food grooves seldom branched beyond bifurcation [Figure 25h], restricted to oral surface; test thick, with rounded margins; tuberculation relatively coarse *Merriamaster*†
(Southwestern USA)
- 64. All oral interambulacra discontinuous in adults [Figure 26k]; food grooves highly branched beyond bifurcation [Figure 25i]; circumferential ambulacral elements of internal buttress system well developed, highly complicated *Scaphechinus*
(Japan, western USSR)
- Anteriormost pair of oral interambulacra continuous [Figure 26l]; food grooves not highly branched beyond bifurcation [Figure 25j]; circumferential ambulacral elements of internal buttress system reduced to simple pillars . . . *Remondella*†
(Southwestern USA, Alaska)
- 65. Lunule or deep notch in ambulacra II, III, and IV only [Figure 27i]; periproct near ambitus, between second pair of post-basicoronal plates *Scutaster*†
(Southwestern USA)
- When ambulacral lunules or notches present, they never occur solely in ambulacra II, III, and IV [Figure 27j-p]; periproct not near ambitus, usually between first pair of post-basicoronal plates, never in contact with second pair of post-basicoronal plates [Figure 26m-p] 66

66. No lunule in posterior interambulacrum (i.e., there is no "anal" lunule), ambulacral lunules always present, at least in ambulacra I and V [Figure 27j,k]; lunule walls with vertical sutures ("cross-linked") [Figure 30a]; Aristotle's lantern extremely flattened, external wing [I.G., Figure 34a] barely visible in top view of pyramid [I.G., Figure 34a] due to great expansion of internal wings [Figure 2d]; pedicellariae with three valves; podial spicules E-shaped [Figure 29c]; accessory podia [I.G., Figure 33a] present in interperiferous zone of petaloids 67
- Lunule in posterior interambulacrum (i.e., there is an "anal" lunule), ambulacral lunules or notches present or absent [Figure 27l-p]; when present, walls of ambulacral lunules with horizontal sutures running along long axis of lunule ("festooned") [Figure 30b]; Aristotle's lantern moderately flattened, external wing clearly visible in top view of pyramid, internal wings moderately developed [Figure 2c]; pedicellariae with two valves; podial spicules not E-shaped, lacking upper and lower branches of "E" [Figure 29d]; accessory podia absent from interperiferous zone of petaloids 69

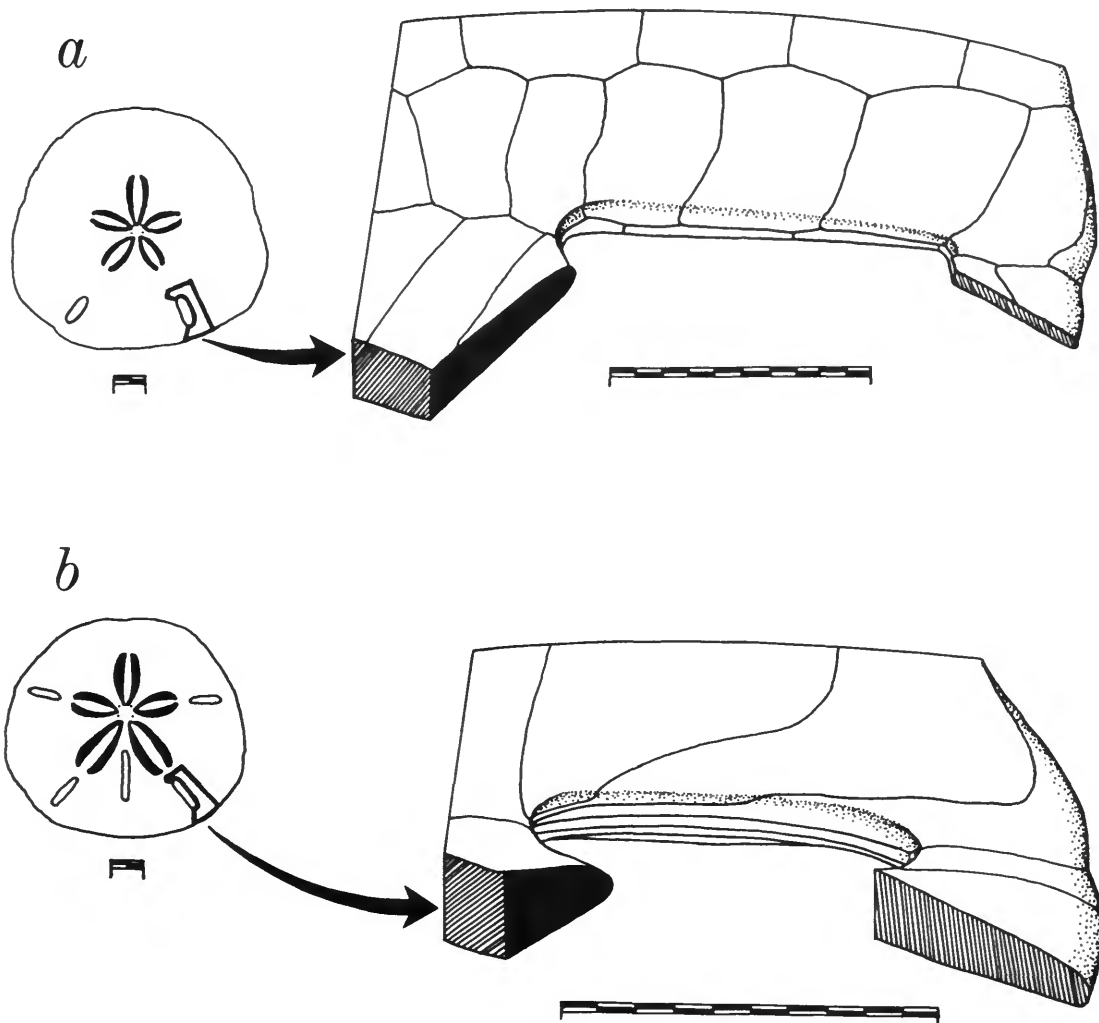


FIGURE 30.—Lunule structure in scutellines: *a*, Oblique aboral view of cross-linked lunule wall from ambulacrum I of *Echinodiscus bisperforatus* (Leske), UT, New Guinea (entire specimen at left); *b*, oblique aboral view of festooned lunule wall from ambulacrum I of *Mellita quinquiesperforata* (Leske), UT, North Carolina (entire specimen at left). (Scale bars = 10 mm.)

- 67. Lunule in each ambulacrum [Figure 27j]; test roughly circular [Figure 27j]; all petaloids approximately the same length [Figure 27j]; ophicephalous pedicellariae absent in adults *Astriclypeus*
(Cambodia, Southern Japan)
- Lunules in ambulacra I and V only [Figure 27k]; test broadly truncated posteriorly [Figure 27k]; petaloids in aboral ambulacra I and V shorter than those in ambulacra II, III, and IV [Figure 27k]; ophicephalous pedicellariae typically found near ambitus on aboral surface 68
- 68. Lunules or notches elongate, slit-like [Figure 27k] *Echinodiscus*
(Indo-Pacific)
- Lunules oval, usually wider than long, never occur as notches *Amphiope*†
(Europe, Africa, India)
- 69. No ambulacral lunules or notches, ambitus sometimes broadly indented at perradial sutures [Figure 26m]; lunule in posterior interambulacrum (“anal” lunule) very small [Figure 26m,n], with prominent ridge around aboral opening; intestine not lying in channel through macrocanal system [Figure 21g] 70
- Ambulacral lunules or notches always present, at least in ambulacra I, II, IV, and V [Figure 26o,p]; lunule in posterior interambulacrum (“anal” lunule) typically large [Figure 26o, p], without prominent ridge around aboral opening; intestine typically lying in channel through macrocanal system [Figure 21h], or at least with pillars between intestine and Aristotle’s lantern 72
- 70. All oral interambulacra continuous [Figure 26m]; interambulacra very narrow at ambitus [Figure 26m], often with only single column of very small plates traversing ambitus; interambulacral basicoronal plates greatly enlarged, at least twice length of ambulacral basicoronal plates [Figure 26m] *Monophoraster*†
(Argentina, Chile)
- Posterior oral interambulacra discontinuous, paired oral interambulacra variably so [Figure 26n]; interambulacra not very narrow at ambitus, with paired plates traversing ambitus [Figure 26n]; interambulacral basicoronal plates not enlarged, less than twice length of ambulacral basicoronal plates [Figure 26n] 71
- 71. Test greatly widened, approximately twice as wide as long [Figure 27l] *Amplaster*†
(Uruguay)
- Test about as long as wide *Karlaster*†
(Brazil)
- 72. Four gonopores; periproct slightly or deeply indenting basicoronal in interambulacrum 5 [Figure 26o] 73
- Five gonopores; periproct not indenting basicoronal in interambulacrum 5 (periproct may touch basicoronal, but not indent it, in some species of *Encope*) 74
- 73. Single ambulacral plate between each pair of first interambulacral post-basicoronal plates and corresponding basicoronal plate in paired oral interambulacra [Figure 26o]; petaloids approximately half length of corresponding aboral ambulacrum [Figure 27m]; lunule in ambulacrum III usually lacking [Figures 26o, 27m] (present as a complete lunule only in some fossil forms, and some aberrant living populations); aboral spines club-shaped, but not strongly so [Figure 29e]; found only on terrigenous (siliceous) sands *Mellita*
(Southeastern USA, east and west coasts of Mexico, West Indies, northern South America)
- Two ambulacral plates between each pair of first interambulacral post-basicoronal plates and corresponding basicoronal plate in paired oral interambulacra; petaloids much less than half length of corresponding aboral ambulacrum [Figure 27n]; long, slit-like lunule in every ambulacrum [Figures 26p, 27n]; aboral spines strongly club-shaped [Figure 29f]; found only on biogenic (carbonate) sands *Leodia*
(West Indies, Florida Keys to North Carolina)
- 74. Apical system and peristome slightly posterior of midpoint; petaloids in ambulacra I and V shortest [Figure 27o]; lunule in posterior interambulacrum (“anal” lunule) not lying between posterior petaloids for any part of its length [Figure 27p] *Mellitella*
(Northwestern South and Central America, Caribbean and northern South America as fossil)
- Apical system and peristome at, or slightly anterior of midpoint; petaloids in aboral ambulacra I and V as long as other petaloids, or longer [Figure 27p]; anal lunule lying between posterior petaloids for at least part of its length [Figure 27p] *Encope*
(Southeastern USA, South America, West Indies, Galápagos)

Annotated Checklist of the Clypeasteroid Genera

The following is a checklist of all the known genera currently placed in the order Clypeasteroida, plus *Togocyamus*, which represents an entirely extinct sister group to that order (Mooi, in press). Although the generic synonymies of Mortensen (1948), Durham (1955), Durham et al. (1966), Philip and Foster (1971), and Kier and Lawson (1978) are adhered to in this list (interested readers are referred to these works for that information, it is not reiterated here), no attempt has been made to follow any particular family level classification, pending phylogenetic revision of the group. For that reason, the clypeasteroid genera are grouped into three major suborders, the Clypeasterina, Laganina, and Scutellina, and listed alphabetically in those suborders. Authorities for the genera, the type species, approximate number of species (because of the uncertain status of some taxa, this is not intended to be an exhaustively accurate estimate, but is merely intended to suggest the size, and to a certain extent, the relative taxonomic importance of the genus), distribution, stratigraphic range, and selected sources of figures (in the present, and other works) that illustrate general morphology are given for each entry.

Sister Group to the Clypeasteroida

Togocyamus Oppenheim, 1915

TYPE SPECIES.—*Echinocyamus (Togocyamus) seefriedi* Oppenheim, 1915.

NUMBER OF SPECIES.—Two (Kier, 1982:6).

DISTRIBUTION.—Known only from French West Africa, Togo, Senegal, and the "Gold Coast."

STRATIGRAPHIC OCCURRENCE.—Paleocene.

FIGURES.—Figure 1a, ambulacrum; Kier (1982, pl. 1), podial pores, aboral and oral surfaces.

Order CLYPEASTEROIDA A. Agassiz, 1872

Suborder CLYPEASTERINA A. Agassiz, 1872

Ammotrophus H.L. Clark, 1928

TYPE SPECIES.—*Ammotrophus cyclus* H.L. Clark, 1928.

NUMBER OF SPECIES.—Two or three known living species, with at least one fossil species (Durham, 1955:127–128).

DISTRIBUTION.—Southern and Western Australia; Tasmania.

STRATIGRAPHIC OCCURRENCE.—Pleistocene to Recent.

FIGURES.—Figure 5a, oral surface plate pattern; Durham et al. (1966:U468), aboral and oral surfaces.

Arachnoides Leske, 1778

TYPE SPECIES.—*Echinus placenta* Linné, 1758.

NUMBER OF SPECIES.—Mortensen (1948:144) lists two

living species, but no species are known only as fossils.

DISTRIBUTION.—Andaman Islands to Queensland, Western Australia; Java; Sumatra; New Guinea; Philippines.

STRATIGRAPHIC OCCURRENCE.—Pliocene to Recent.

FIGURES.—Figure 4b, oral surface; Figure 4c, aboral surface; Figure 5c, oral surface plate pattern; Figure 6a, petaloid plate pattern; Durham et al. (1966:U467), aboral and oral surfaces.

Clypeaster Lamarck, 1801

TYPE SPECIES.—*Echinus rosaceus* Linné, 1758.

NUMBER OF SPECIES.—Including fossil taxa, about 400 species names have been used for members of this genus (Mortensen, 1948:19). Approximately 40 living species are known.

DISTRIBUTION.—Living forms are common from the Caribbean, tropical Atlantic, Indian, eastern and western Pacific Oceans, especially the East Indies, Australia, and Hawaii, but not from the Mediterranean, where it is known only as a fossil.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene (Auversian) to Recent.

FIGURES.—Figure 4a, oral surface with food grooves; Durham et al. (1966:U466), oral surface plate patterns, profiles, internal view of test, aboral surface.

Fellaster Durham, 1955

TYPE SPECIES.—*Arachnoides zelandiae* Gray, 1855.

NUMBER OF SPECIES.—The type, and a fossil species have been described.

DISTRIBUTION.—Once thought endemic to New Zealand, a fossil species has been described from southeastern Australia (Foster and Philip, 1980:155–156; Sadler and Pledge, 1985:175–176).

STRATIGRAPHIC OCCURRENCE.—Durham (1955:127) listed it from the Pliocene, but later (Durham et al., 1966:464) suggested that *Arachnoides* occurs from the Oligocene to Recent.

FIGURES.—Figure 3a, lantern supports, basicoronal plates; Figure 5d, oral surface plate pattern; Durham et al. (1966:U467), aboral and oral surfaces.

Fossilaster Lambert and Thiéry, 1925

TYPE SPECIES.—*Fossilaster halli* Lambert and Thiéry, 1925.

NUMBER OF SPECIES.—Philip and Foster (1971:682–687) list two.

DISTRIBUTION.—South Australia.

STRATIGRAPHIC OCCURRENCE.—Upper Oligocene or Lower Miocene (Janjukian or Longfordian).

FIGURES.—Philip and Foster (1971, figs. 5, 7, pls. 125, 127, 128, 130–132), aboral and oral surface plate patterns, internal

view of test, aboral and oral surfaces, side views.

Monostychia Laube, 1869

TYPE SPECIES.—*Monostychia australis* Laube, 1869.

NUMBER OF SPECIES.—Two or three (Durham, 1955:128).

DISTRIBUTION.—Southern Australia; Tasmania.

STRATIGRAPHIC OCCURRENCE.—Miocene.

FIGURES.—Figure 1*b*, ambulacrum; Figure 5*b*, oral surface plate pattern; Durham et al. (1966:U468), aboral and oral surfaces.

Scutellinoides Durham, 1955

TYPE SPECIES.—*Scutellina patella* Tate, 1891.

NUMBER OF SPECIES.—Probably only one (Philip and Foster, 1971:682).

DISTRIBUTION.—South Australia.

STRATIGRAPHIC OCCURRENCE.—Miocene.

FIGURES.—Figure 5*e*, oral surface plate pattern; Durham et al. (1966:U468), aboral and oral surfaces.

Willungaster Philip and Foster, 1971

TYPE SPECIES.—*Willungaster scutellaris* Philip and Foster, 1971.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—South Australia.

STRATIGRAPHIC OCCURRENCE.—Upper Oligocene or Lower Miocene (Janjukian or Longfordian).

FIGURES.—Figure 5*f*, oral surface plate pattern; Philip and Foster (1971, fig. 8, pls. 127, 131, 133), aboral and oral surface plate patterns, aboral and oral surfaces, side views, internal view of test.

Suborder LAGANINA Mortensen, 1948

Cubanaster Sánchez Roig, 1952

TYPE SPECIES.—*Jacksonaster torrei* Lambert in Sánchez Roig, 1962.

NUMBER OF SPECIES.—Approximately ten (Durham, 1954:681; Kier and Lawson, 1978:66).

DISTRIBUTION.—Cuba.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 16*d*, oral surface plate pattern; Figure 19*a*, aboral surface and transverse profile; Durham et al. (1966:U474), madreporite, aboral and oral surfaces.

Cyamidia Lambert and Thiéry, 1914

TYPE SPECIES.—*Echinocyamus nummulitica* Duncan and Sladen, 1884.

NUMBER OF SPECIES.—Mortensen (1948:227) suggests that there are two or three.

DISTRIBUTION.—India; Pakistan; Australia.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Durham et al. (1966:U469), madreporite, aboral and oral surfaces.

Durhamella Kier, 1968

TYPE SPECIES.—*Laganum ocalanum* Cooke, 1942.

NUMBER OF SPECIES.—Two (Kier, 1968:23–38).

DISTRIBUTION.—Georgia, Florida, USA.

STRATIGRAPHIC OCCURRENCE.—Middle Eocene.

FIGURES.—Figure 17*b*, aboral surface; Cooke (1959, pl. 20), aboral and oral surfaces, side view; Kier (1968, figs. 31–33, 37–39, 40–42, pls. 6–10), aboral and oral surfaces, apical system, internal view of test, lantern supports, aboral and oral surface plate patterns.

Echinocyamus van Phelsum, 1774

TYPE SPECIES.—*Echinocyamus pusillus* O.F. Müller, 1776.

NUMBER OF SPECIES.—Approximately 50, including fossil forms. Mortensen (1948:176–177) lists 16 living species, not counting members of his subgenus *Mortonia*, herein considered a separate genus.

DISTRIBUTION.—Caribbean; eastern Atlantic; northwestern Europe; Mediterranean; Indian Ocean; Australia; East Indies; Philippines; Malaysia; Hawaii; worldwide as a fossil.

STRATIGRAPHIC OCCURRENCE.—Durham et al. (1966:U469) say Upper Cretaceous (Senonian) to Recent, but Kier (1982:4) was apparently unable to find any clypeasteroids in strata before the Paleocene.

FIGURES.—Figure 18*g*, apical system; Figure 21*b*, internal buttress system; Figure 24*b*, periproctal membrane; Durham et al. (1966:U469), aboral and oral surfaces, internal view of test.

Fibularia Lamarck, 1816

TYPE SPECIES.—*Fibularia ovulum* Lamarck, 1816 (subsequent designation by the International Commission of Zoological Nomenclature [ICZN], 1950).

NUMBER OF SPECIES.—Probably at least 20, including fossils. Mortensen (1948:207) lists four living species, not counting members of his subgenus *Fibulariella*, herein considered a separate genus.

DISTRIBUTION.—Australia; East Indies; Indian Ocean; Red Sea; worldwide as a fossil.

STRATIGRAPHIC OCCURRENCE.—Upper Cretaceous (Senonian?) to Recent (See *Echinocyamus*).

FIGURES.—Figure 1*c*, ambulacrum; Figure 23*a*, aboral primary spine; Figure 24*a*, periproctal membrane; Durham et al. (1966:U469), aboral and oral surfaces.

Fibulariella Mortensen, 1948

TYPE SPECIES.—*Fibularia acuta* Yoshiwara, 1898.

NUMBER OF SPECIES.—Four or five, all living (Mortensen, 1948:207).

DISTRIBUTION.—Malaysia; south, west, and north Australia.
STRATIGRAPHIC OCCURRENCE.—Recent.

FIGURES.—Figure 7*d*, plate pattern adjacent to apical system; Figure 13*c*, food grooves; Figure 18*e*, apical system; Figure 23*b*, aboral primary spine; Figure 23*c*, globiferous pedicellaria; Figure 23*d*, podial spicules.

Fibulaster Lambert and Thiéry, 1914

TYPE SPECIES.—*Sismondia michelini* Cotteau, 1861.

NUMBER OF SPECIES.—Apparently only the type species has been ascribed to this poorly known genus.

DISTRIBUTION.—Europe, France.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Durham et al. (1966:UU469), aboral and oral surfaces, internal view of test.

Fibulina Tornquist, 1904

TYPE SPECIES.—*Fibulina gracilis* Tornquist, 1904.

NUMBER OF SPECIES.—Only the type species has been described. Stephenson (1968) synonymized *Fibulina gracilis* with *Fibularia voeltzkowi* Tornquist, 1904.

DISTRIBUTION.—Madagascar.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Durham et al. (1966:U472), aboral surface. Not in key.

Heliophora L. Agassiz, 1840

TYPE SPECIES.—*Echinus orbiculus* Linné, 1758.

NUMBER OF SPECIES.—Two (Durham, 1955:186), with one known living species.

DISTRIBUTION.—Tropical west coast of Africa; Cape Verde Islands; Ascension Island.

STRATIGRAPHIC OCCURRENCE.—Miocene to Recent.

FIGURES.—Figure 11*a*, miliary spine; Figure 12*b*, rotule; Figure 14*b*, oral surface plate pattern; Figure 15*a*, petaloid; Figure 15*c*, aboral primary spine; Durham et al. (1966:U490), aboral and oral surfaces, oral surface plate pattern.

Hupea Pomel, 1883

TYPE SPECIES.—*Laganum decagonalis* Lesson, 1883.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Malaysia; Polynesia.

STRATIGRAPHIC OCCURRENCE.—Pliocene to Recent.

FIGURES.—Figure 16*g*, oral surface plate pattern; Durham et al. (1966:U472), aboral and oral surfaces.

Jacksonaster Lambert and Thiéry, 1914

TYPE SPECIES.—*Echinarachnius conchatus* M'Clelland, 1840.

NUMBER OF SPECIES.—Kier and Lawson (1978:64–65) list two or three species that are probably attributable to this genus,

with one known living species. New world species are not attributable to this genus.

DISTRIBUTION.—Java; Indonesia; Red Sea.

STRATIGRAPHIC OCCURRENCE.—Miocene to Recent.

FIGURES.—Figure 16*h*, oral surface plate pattern; Durham et al. (1966:U473), aboral and oral surfaces.

Laganum Link, 1807

TYPE SPECIES.—*Echinodiscus laganum* Leske, 1778.

NUMBER OF SPECIES.—At least 30 species have been named, including fossils. Mortensen (1948:307–308) lists about 11 living species.

DISTRIBUTION.—Philippines; New Guinea; Malaysia; Polynesia; north Australia; Japan; Indian Ocean; Red Sea; eastern Africa; Madagascar.

STRATIGRAPHIC OCCURRENCE.—Oligocene to Recent.

FIGURES.—Figure 2*b*, Aristotle's lantern; Figure 8*a*, respiratory podial pores; Figure 13*b*, food grooves; Figure 16*i*, oral surface plate pattern; Figure 18*d*, apical system; Durham et al. (1966:U472), madreporite, aboral and oral surfaces.

Lenicyamidia Brunnschweiler, 1962

TYPE SPECIES.—*Lenicyamidia compta* Brunnschweiler, 1962.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Western Australia.

STRATIGRAPHIC OCCURRENCE.—Lower Eocene (Cuisian or Lutetian).

FIGURES.—Figure 22*a*, oral surface tuberculation; Durham et al. (1966:U470), aboral and oral surfaces.

Leniechinus Kier, 1968

TYPE SPECIES.—*Leniechinus herricki* Kier, 1968.

NUMBER OF SPECIES.—Only the type species is known (Kier, 1968:5–12).

DISTRIBUTION.—Georgia, USA.

STRATIGRAPHIC OCCURRENCE.—Lower Middle Miocene.

FIGURES.—Figure 22*b*, oral surface tuberculation; Kier (1968, figs. 1–4, pls. 1, 2), aboral and oral surface plate patterns, peristome, aboral and oral surfaces, side view, internal view of test.

Marginoproctus Budin, 1980

TYPE SPECIES.—*Marginoproctus djakonovi* Budin, 1980.

NUMBER OF SPECIES.—Only the type species has been described. Although Budin (1980:305) placed this genus in the laganine family Fibulariidae, he was correct in noting affinities to *Scuellina*, which has here been listed in the suborder Scutellina.

DISTRIBUTION.—East Kamchatka, Commander and Kurile Islands, Sea of Okhotsk "to depths of 60 to 800 m" (Budin, 1980:308).

STRATIGRAPHIC OCCURRENCE.—Recent.

FIGURES.—Budin (1980, figs. 1–8), aboral and oral surfaces, side view, spines, and pedicellariae. Not in key.

Mortonia Gray, 1852

TYPE SPECIES.—*Fibularia australis* Desmoulin, 1837.

NUMBER OF SPECIES.—Mortensen (1948:197) lists two species, both living.

DISTRIBUTION.—Hawaii; Eniwetok; central Pacific.

STRATIGRAPHIC OCCURRENCE.—Recent.

FIGURES.—Figure 24c, periproctal membrane; Durham et al. (1966:U470), aboral and oral surfaces, internal view of test.

Neolaganum Durham, 1954

TYPE SPECIES.—*Laganum archerensis* Twitchell, 1915.

NUMBER OF SPECIES.—At least two (Durham, 1954:680–681).

DISTRIBUTION.—Gulf of Mexico, Florida.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 9b, basicoronal plates; Figure 16c, oral surface plate pattern; Figure 18b, apical system; Figure 20a, aboral surface; Cooke (1959, pl. 21), aboral and oral surfaces, side view; Durham et al. (1966:U474), aboral and oral surfaces, side view.

Neorumphia Durham, 1954

TYPE SPECIES.—*Rumphia elegans* Sánchez Roig, 1949.

NUMBER OF SPECIES.—Three (Durham, 1954:681–682).

DISTRIBUTION.—Cuba.

STRATIGRAPHIC OCCURRENCE.—Upper Oligocene.

FIGURES.—Figure 6b, petaloid plate pattern; Figure 20b, aboral surface; Durham et al. (1966:U474), petaloid plate pattern, aboral and oral surfaces.

Pentedium Kier, 1967

TYPE SPECIES.—*Pentedium curator* Kier, 1967.

NUMBER OF SPECIES.—Kier (1967) described only the type species.

DISTRIBUTION.—Georgia, USA.

STRATIGRAPHIC OCCURRENCE.—Lower Middle Miocene.

FIGURES.—Figure 17a, aboral surface; Kier (1967, figs. 2, 3, pls. 129, 130), juveniles, aboral and oral surfaces, oral surface plate pattern, internal view of test; Kier (1968, pl. 4) aboral surface.

Peronella Gray, 1855

TYPE SPECIES.—*Laganum peronii* L. Agassiz, 1841.

NUMBER OF SPECIES.—At least 30 species are known, including fossils. Mortensen (1948:258–259) lists about 15 living species.

DISTRIBUTION.—Indian Ocean; Australia; Japan; Taiwan; Malaysia; Philippines; Polynesia; East Indies.

STRATIGRAPHIC OCCURRENCE.—Upper Miocene to Recent.

FIGURES.—Figure 7a, plate pattern adjacent to apical system; Figure 9a, basicoronal plates; Figure 16f, oral surface plate pattern; Figure 18c, apical system; Figure 21a, internal buttress system; Durham et al. (1966:U473), aboral and oral surfaces.

Peronellites Hayasaka and Morishita, 1947

TYPE SPECIES.—*Peronellites ovalis* Hayasaka and Morishita, 1947.

NUMBER OF SPECIES.—Only the type species is known. Wang (1982b:143, 144) synonymized *Peronellites* with *Peronella*.

DISTRIBUTION.—Taiwan.

STRATIGRAPHIC OCCURRENCE.—Miocene.

FIGURES.—Not in key, but see *Peronella* (sensu Wang, 1982b:144).

Proescutella Pomel, 1883

TYPE SPECIES.—*Scutella cailliaudi* Cotteau, 1861.

NUMBER OF SPECIES.—Two or three.

DISTRIBUTION.—France.

STRATIGRAPHIC OCCURRENCE.—Middle Miocene.

FIGURES.—Durham et al. (1966:U490), aboral and oral surfaces, side view. Not in key.

Rotula Schumacher, 1817

TYPE SPECIES.—*Echinodiscus octiesdigitatus* Leske, 1778 (= *Echinodiscus deciesdigitatus* Leske, 1778).

NUMBER OF SPECIES.—Only the type is known.

DISTRIBUTION.—West Africa, Angola.

STRATIGRAPHIC OCCURRENCE.—Miocene to Recent.

FIGURES.—Figure 6c, petaloid plate pattern; Figure 7b, plate pattern adjacent to the apical system; Figure 9c, basicoronal plates; Figure 13a, food grooves; Figure 14c, oral surface plate pattern; Figure 15b, petaloid; Figure 15d, aboral primary spine; Durham et al. (1966:U490), aboral and oral surfaces.

Rotuloidea Etheridge, 1872

TYPE SPECIES.—*Rotuloidea fimbriata* Etheridge, 1872.

NUMBER OF SPECIES.—Two other known fossil species, besides the type.

DISTRIBUTION.—West Africa, Morocco.

STRATIGRAPHIC OCCURRENCE.—Miocene to Pliocene.

FIGURES.—Figure 14a, oral surface plate pattern; Durham et al. (1966:U490), oral surface plate pattern.

Rumphia Desor, 1858

TYPE SPECIES.—*Laganum rostratum* L. Agassiz, 1841.

NUMBER OF SPECIES.—Only the type is known.

DISTRIBUTION.—East Indies; Australia.

STRATIGRAPHIC OCCURRENCE.—Miocene to Recent.

FIGURES.—Durham et al. (1966:U473), aboral and oral surfaces.

Sanchezella Durham, 1954

TYPE SPECIES.—*Jacksonaster sanchezi* Lambert, 1926.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Cuba.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 19*b*, aboral surface and transverse profile; Durham et al. (1966:U474), oral surface plate pattern, aboral and oral surfaces.

Sismondia Desor, 1858

TYPE SPECIES.—*Scutella occitana* DeFrance, 1827.

NUMBER OF SPECIES.—Mortensen (1948:234) claims that some 30 species have been ascribed to this genus.

DISTRIBUTION.—Europe; Africa; East Indies; Australia; Japan.

STRATIGRAPHIC OCCURRENCE.—Eocene to Miocene.

FIGURES.—Durham et al. (1966:U473), aboral and oral surfaces, side view; Kier (1982, pl. 2), aboral and oral surfaces, side view.

Tarphypygus Arnold and Clark, 1927

TYPE SPECIES.—*Tarphypygus ellipticus* Arnold and Clark, 1927.

NUMBER OF SPECIES.—At least five (Kier and Lawson, 1978:63).

DISTRIBUTION.—Cuba; Jamaica.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Figure 7*c*, plate pattern adjacent to apical system; Figure 16*e*, oral surface plate pattern; Durham et al. (1966:U471), aboral and oral surfaces, side view.

Tetradiaella Liao and Lin, 1981

TYPE SPECIES.—*Tetradiaella sinica* Liao and Lin, 1981.

NUMBER OF SPECIES.—One.

DISTRIBUTION.—China, Guangxi.

STRATIGRAPHIC OCCURRENCE.—Late Tertiary, probably Pliocene.

FIGURES.—Liao and Lin (1981, figs. 1–2, pl. 1), aboral and oral surfaces, side view, internal buttress system. Not in key.

Thagastea Pomel, 1888

TYPE SPECIES.—*Thagastea wetterlei* Pomel, 1888.

NUMBER OF SPECIES.—One or two.

DISTRIBUTION.—Europe; northern Africa, Tunisia.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Figure 7*e*, plate pattern adjacent to apical

system; Durham et al. (1966:U471), aboral and oral surfaces, side view.

Tridium Tandon and Srivastava, 1980

TYPE SPECIES.—*Tridium kieri* Tandon and Srivastava, 1980.

NUMBER OF SPECIES.—Only the type species has been described.

DISTRIBUTION.—Known only from Kutch, India.

STRATIGRAPHIC OCCURRENCE.—Middle Eocene.

FIGURES.—Tandon and Srivastava (1980, figs. 1–2, pl. 1), apical system, basicoronal plates, aboral and oral surfaces, petaloids, internal structure, periproct and peristome.

Weisbordella Durham, 1954

TYPE SPECIES.—*Peronella caribbeana* Weisbord, 1934.

NUMBER OF SPECIES.—Probably at least three (Durham, 1954:682).

DISTRIBUTION.—Gulf of Mexico; West Indies.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 16*a*, oral surface plate pattern; Cooke (1959, pl. 20), aboral and oral surfaces, side views.

Wythella Durham, 1954

TYPE SPECIES.—*Laganum eldridgei* Twitchell, 1915.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Gulf of Mexico, Georgia.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 10*a*, keel in food groove; Figure 16*b*, oral surface plate pattern; Figure 18*a*, apical system; Cooke (1959, pl. 21), aboral and oral surfaces, side view; Durham et al. (1966:U474), aboral and oral surfaces.

Suborder SCUTELLINA Haeckel, 1896

Abertella Durham, 1955

TYPE SPECIES.—*Scutella aberti* Conrad, 1842.

NUMBER OF SPECIES.—Durham (1953b:351; 1955:178) suggested that four species belong to this genus, including the type. He later added two more species (Durham, 1957:627).

DISTRIBUTION.—Eastern USA, Maryland; Guatemala; Mexico.

STRATIGRAPHIC OCCURRENCE.—Middle Miocene (Steven C. Beadle, pers. comm.).

FIGURES.—Figure 27*g*, aboral surface; Cooke (1959, pl. 16), aboral and oral surfaces, side view; Durham et al. (1966:U488), aboral and oral surfaces, side view.

Allaster Nisiyama, 1968

TYPE SPECIES.—*Allaster rotundatus* Nisiyama, 1968.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Hokkaido, Japan.

STRATIGRAPHIC OCCURRENCE.—Oligocene or Miocene.

FIGURES.—Nisiyama (1968, pls. 17, 18), aboral and oral surfaces.

Amphiope L. Agassiz, 1840

TYPE SPECIES.—*Scutella bioculata* Desmoulins, 1835.

NUMBER OF SPECIES.—At least six (Mortensen, 1948:413–414; Kier and Lawson, 1978:73).

DISTRIBUTION.—Europe; western Africa; India.

STRATIGRAPHIC OCCURRENCE.—Late Eocene or Oligocene to Miocene.

FIGURES.—Durham et al. (1966:U487), aboral and oral surfaces.

Amplaster Martínez, 1985

TYPE SPECIES.—*Amplaster coloniensis* Martínez, 1985.

NUMBER OF SPECIES.—Only the type species is known (Martínez, 1985).

DISTRIBUTION.—Known only from Uruguay.

STRATIGRAPHIC OCCURRENCE.—Upper Miocene.

FIGURES.—Figure 27l, aboral surface; Martínez (1985, figs. 1, 2), aboral and oral surfaces.

Astriclypeus Verrill, 1867

TYPE SPECIES.—*Astriclypeus manni* Verrill, 1867.

NUMBER OF SPECIES.—The type is the only living species. Wang (1983:116–117) recently added a new fossil species to the 3 fossil species already known from Japan.

DISTRIBUTION.—Cambodia to southern Japan.

STRATIGRAPHIC OCCURRENCE.—Durham et al. (1966:U489) give the range as Miocene to Recent, but Wang (1983:118) reports an *Astriclypeus* from the Late Oligocene.

FIGURES.—Figure 27j, aboral surface; Figure 29c, podial spicule; Durham et al. (1966:U487), aboral and oral surfaces.

Astrodapsis Conrad, 1856

TYPE SPECIES.—*Astrodapsis antiselli* Conrad, 1856.

NUMBER OF SPECIES.—Grant and Hertlein (1938:68–78) list over 25 species from the middle Tertiary of California alone. Durham (1952) suggested that none of the species from Kamchatka or Sakhalin were true *Astrodapsis*, and relegated them to *Nipponaster*. With these accounted for, there are probably still in excess of 40 species ascribed to the genus *Astrodapsis*. Hall (1962:48) reduced the 59 named species, subspecies, and varieties to twelve.

DISTRIBUTION.—Western USA, California.

STRATIGRAPHIC OCCURRENCE.—Middle Miocene to Upper Miocene (Steven C. Beadle, pers. comm.).

FIGURES.—Figure 27f, aboral surface; Durham et al. (1966:U483), aboral and oral surfaces, side view.

Dendraster L. Agassiz, 1847

TYPE SPECIES.—*Scutella excentricus* Eschscholtz, 1831.

NUMBER OF SPECIES.—Raup (1956:685) reports that over 25 species and subspecies have been placed in the genus *Dendraster*. Mortensen (1948:381) lists four living species.

DISTRIBUTION.—Western North America, Pacific coast of Baja, Gulf of California (only as fossil?) north to southeastern Alaska.

STRATIGRAPHIC OCCURRENCE.—Latest Upper Miocene, or Pliocene to Recent (Steven C. Beadle, pers. comm.).

FIGURES.—Figure 25g, food grooves; Figure 27h, aboral surface; Durham et al. (1966:U480), aboral and oral surfaces plate patterns, food grooves.

Echinarachnius Gray, 1825

TYPE SPECIES.—*Scutella parma* Lamarck, 1816.

NUMBER OF SPECIES.—Grant and Hertlein (1938:56–64) list about five species that could still be referable to *Echinarachnius*, once those taxa now recognized as belonging to other genera such as *Kewia* and *Vaquerosella* are accounted for. Nisiyama (1968:95–104) lists seven fossil species from Japan, and Wagner (1974:109–116) three from Alaska. There are probably more than 15 fossil species attributable to this genus, as well as two known living species.

DISTRIBUTION.—Eastern North America from Labrador at least as far south as Chesapeake Bay and perhaps northern North Carolina; western North America from the Bering and Chukchi Seas along the Aleutian Islands north to Point Barrow and south to southeastern Alaska; northeast Asia, Kamchatka, Sakhalin, northern Japan.

STRATIGRAPHIC OCCURRENCE.—Upper or Middle Miocene to Recent.

FIGURES.—Figure 3b, lantern supports; Figure 11b, miliary spine; Figure 25f, food grooves; Durham et al. (1966:U483), aboral and oral surfaces.

Echinodiscus Leske, 1778

TYPE SPECIES.—*Echinoglycus irregularis* Leske, 1778 (= *Echinodiscus bisperforatus* Leske, 1778 by action of the ICZN, 1950).

NUMBER OF SPECIES.—Nisiyama (1968:132–134) lists two fossil species from Japan, but Wang (1982a:150) lists three fossil species, and adds two more (Wang, 1982a:150, 1984a:107). Kier (1972a:91–92) described two species from Saudi Arabia, so there are probably about nine known fossil species. Mortensen (1948:400) lists three living species.

DISTRIBUTION.—Red Sea; Madagascar and southeastern Africa; northern Indian Ocean; Philippines; Australia; New Caledonia; southern Japan.

STRATIGRAPHIC OCCURRENCE.—Wang (1984a:109) records a single specimen of a new species, *Echinodiscus tiliensis*, that he found “in the collection of the Museum of the Department

of Geology, National Taiwan University ... Probably the holotype of this new species comes from the middle or upper part of the Tachien Sandstone ... as judged from the feature [sic] of the sandstone matrix (C.H. Chen, CGS, 1982, personal communication) although no calcareous nannofossils are found in the matrix" (Wang, 1984a:109). The Tachien Sandstone is "considered Eocene in age by Chen" (Wang, 1984a:109), but the "Chiayang Formation which overlies the Tachien Sandstone is Early to Middle Eocene... in age ... then the Tachien Sandstone should be either Early Eocene or Late Paleocene in age" (Wang, 1984a:109). At present it would appear to be more profitable to investigate further and ascertain the suggested locality and age of strata in which the single specimen of *E. tiliensis* Wang was found than to revise present views (for example Durham et al., 1966; Kier, 1982) of the origins, not only of the Scutellina, but of the entire Clypeasteroidea. Until corroboration is available, the attribution of *Echinodiscus* to the Late Paleocene or Early Eocene cannot be accepted without reservation, and the stratigraphic range of *Echinodiscus* is here regarded as Late Oligocene or Early Miocene to Recent.

FIGURES.—Figure 2*d*, Aristotle's lantern; Figure 8*b*, respiratory podial pores; Figure 12*d*, rotule; Figure 27*k*, aboral surface; Figure 30*a*, lunule; Durham et al. (1966:U487), aboral and oral surfaces, side view.

Encope L. Agassiz, 1840

TYPE SPECIES.—*Encope grandis* L. Agassiz, 1840.

NUMBER OF SPECIES.—From papers by Mortensen (1948:436), A.H. Clark (1946), H.L. Clark (1948), and others, a list of fifteen living species can be compiled. Approximately 25 fossil species have been described by workers such as Durham (1950), Jeannot (1928a,b) and Cooke (1961).

DISTRIBUTION.—Eastern North America as far north as North Carolina; Caribbean; Gulf of Mexico; northern and eastern South America to Rio de la Plata; western North America, Gulf of California south to Peru; Galápagos and Cocos Islands.

STRATIGRAPHIC OCCURRENCE.—Pliocene (perhaps Upper Miocene) to Recent.

FIGURES.—Figure 2*c*, Aristotle's lantern; Figure 21*h*, internal buttress system; Figure 27*p*, aboral surface; Durham et al. (1966:U468), aboral and oral surfaces.

Eoscutella Grant and Hertlein, 1938

TYPE SPECIES.—*Scutella coosensis* Kew, 1920.

NUMBER OF SPECIES.—Grant and Hertlein (1938:54–55) listed only the type species, and Mortensen (1948:386) suggested the existence of a second fossil species. Parma (1985:37–39) described one, and possibly a second new species of *Eoscutella* from Argentina.

DISTRIBUTION.—Western USA, California and Oregon; Patagonia, Argentina.

STRATIGRAPHIC OCCURRENCE.—Middle to Upper Eocene.

FIGURES.—Figure 9*d*, basicoronal plates; Figure 26*d*, oral surface plate pattern; Durham et al. (1966:U479), aboral and oral surfaces; Parma (1985, figs. 3, 4, pl. 1), adapical plate pattern, basicoronal plates, aboral and oral surfaces, side views.

Eoscutum Lambert, 1914

TYPE SPECIES.—*Porpitella doncieuxi* Lambert, 1905.

NUMBER OF SPECIES.—Mortensen (1948:231) suggests that five or six have been described.

DISTRIBUTION.—Europe, France.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Figure 18*i*, apical system; Mortensen (1948:230), aboral and oral surfaces, side view; Durham et al. (1966:U469), aboral and oral surfaces.

Faassia Schmidt, 1971

TYPE SPECIES.—*Faassia globosa* Schmidt, 1971 (in Schmidt and Sinel'nikova, 1971).

NUMBER OF SPECIES.—Only the type species has been described.

DISTRIBUTION.—Known only from western Kamchatka.

STRATIGRAPHIC OCCURRENCE.—Upper Miocene.

FIGURES.—Schmidt and Sinel'nikova (1971, fig. 1), aboral and oral surfaces, side view; Budin (1977, figs. 1, 2), growth rings, food grooves, oral surface plate pattern.

Iheringiella Berg, 1898

TYPE SPECIES.—*Scutella patagoniensis* Desor, 1847.

NUMBER OF SPECIES.—Apparently only the type species has been referred to this genus.

DISTRIBUTION.—Eastern South America, Argentina, Tierra del Fuego; Chile. Hotchkiss and Fell (1972:371) report the discovery of a fossil petaloid from Antarctica that might be referable to this genus.

STRATIGRAPHIC OCCURRENCE.—Durham (1955:171) records that the type species is from the Lower Miocene. Larrain (1984:30) extends this stratigraphic range from the Lower (Middle[?]) Eocene to the Miocene(?).

FIGURES.—Figure 9*e*, basicoronal plates; Figure 25*c*, food grooves; Figure 26*e*, oral surface plate pattern; Figure 28*a*, petaloid; Durham et al. (1966:U484), aboral surface.

Karlaster Marchesini Santos, 1958

TYPE SPECIES.—*Karlaster pirabensis* Marchesini Santos, 1958.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Brazil.

STRATIGRAPHIC OCCURRENCE.—Miocene.

FIGURES.—Figure 26*n*, oral surface plate pattern; Durham et al. (1966:U484), oral surface.

Kewia Nisiyama, 1935

TYPE SPECIES.—*Scutella blancoensis* Kew, 1920.

NUMBER OF SPECIES.—Wagner (1974:116–119) added four new Alaskan species to the six known Japanese species, and there are six more described from western North America in deposits south of Alaska, for a total of 16 named species (Linder et al., 1988).

DISTRIBUTION.—Western North America, Oregon, Washington, Alaska, California; Japan.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene to Pliocene.

FIGURES.—Figure 25e, food grooves; Durham et al. (1966:U483), aboral and oral surfaces, side view.

Kieria Mihály, 1985

TYPE SPECIES.—*Kieria semseyana* Mihály, 1985.

NUMBER OF SPECIES.—Only the type species has been described. It is not clear whether the specimens upon which the description is based represent adult echinoids. Their small size suggests that they are juvenile astriclypeids, possibly *Amphiope*, but the presence or absence of gonopores cannot be ascertained from the plates or description in Mihály (1985:255, 261).

DISTRIBUTION.—Known only from a locality near Budapest, Hungary.

STRATIGRAPHIC OCCURRENCE.—Upper Badenian, Middle Miocene.

FIGURES.—Mihály (1985, pl. 4), aboral and oral surfaces.

Lenita Desor, 1847

TYPE SPECIES.—*Echinites patellaris* Leske, 1778.

NUMBER OF SPECIES.—One, or possibly two species can be referred to this genus.

DISTRIBUTION.—Europe, France, Belgium, Germany.

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Figure 21e, internal buttress system; Figure 22c, oral surface tuberculation; Durham et al. (1966:U470), aboral and oral surfaces; Kier (1968, pl. 1), aboral and oral surfaces.

Leodia Gray, 1852

TYPE SPECIES.—*Echinodiscus sexiesperforatus* Leske, 1778.

NUMBER OF SPECIES.—Only the type species can legitimately be referred to this genus.

DISTRIBUTION.—Restricted to biogenic (carbonate) substrates of Florida Keys; Central and South America; some Caribbean Islands.

STRATIGRAPHIC OCCURRENCE.—Pliocene to Recent. A recently discovered specimen in the NMNH suggests that this genus occurs in the Pleistocene of Florida. Previous references to fossil *Leodia* are actually attributable to *Mellita caroliniana* (Ravenel).

FIGURES.—Figure 11c, miliary spine; Figure 25l, pressure

drainage channels and food grooves; Figure 26p, oral surface plate pattern; Figure 27n, aboral surface; Figure 29f, aboral primary spine; Durham et al. (1966:U486), oral surface plate pattern.

Mellita L. Agassiz, 1841

TYPE SPECIES.—*Echinodiscus quinquesperforatus* Leske, 1778.

NUMBER OF SPECIES.—Four living species were recognized by Mortensen (1948:422). Workers such as Durham (1961) and Kier (1963; 1972b) recognized five or six fossil species. The genus is currently being revised by Harold and Telford (in prep.).

DISTRIBUTION.—Restricted to terrigenous (siliceous) substrates of eastern North America as far north as Virginia; Caribbean; Gulf of Mexico; northern South America to Sao Paulo, Brazil; Gulf of California; west side of Isthmus of Panama.

STRATIGRAPHIC OCCURRENCE.—Pliocene (perhaps Upper Miocene) to Recent.

FIGURES.—Figure 12c, rotule; Figure 26o, oral surface plate pattern; Figure 27m, aboral surface; Figure 29d, podial spicule; Figure 29e, aboral primary spine; Figure 30b, lunule; Durham et al. (1966:U486), aboral and oral surfaces, side view.

Mellitella Duncan, 1889

TYPE SPECIES.—*Encope stokesii* L. Agassiz, 1841.

NUMBER OF SPECIES.—The type is the only living species recognized to date. One or two fossils are known (Durham, 1950; Cooke, 1961).

DISTRIBUTION.—Gulf of California; west side of Isthmus of Panama; northern South America.

STRATIGRAPHIC OCCURRENCE.—Pliocene (perhaps Upper Miocene) to Recent.

FIGURES.—Figure 27o, aboral surface; Durham et al. (1966:U486), aboral and oral surfaces.

Mennerella Schmidt, 1971

TYPE SPECIES.—*Mennerella ovata* Schmidt, 1971 (in Schmidt and Sinel'nikova, 1971).

NUMBER OF SPECIES.—Only the type species has been described.

DISTRIBUTION.—Known only from Kavran-Utkholok Bay, western Kamchatka.

STRATIGRAPHIC OCCURRENCE.—Upper Miocene.

FIGURES.—Schmidt and Sinel'nikova (1971, fig. 1), aboral and oral surfaces, side view. Not in key.

Merriamaster Lambert, 1911

TYPE SPECIES.—*Scutella perrini* Weaver, 1908.

NUMBER OF SPECIES.—At least three species are known

(Durham, 1978; Durham and Morgan, 1978:301-303).

DISTRIBUTION.—Central and southern California; Baja California.

STRATIGRAPHIC OCCURRENCE.—Upper Miocene to Upper Pliocene.

FIGURES.—Figure 25*h*, food grooves; Durham et al. (1966:U480), aboral and oral surfaces, side view, food grooves.

Monophoraster Lambert and Thiéry, 1921

TYPE SPECIES.—*Monophora darwini* Desor, 1847.

NUMBER OF SPECIES.—Three species have been described (Mortensen, 1948:419).

DISTRIBUTION.—South America, Argentina. Although Durham (1955:169) was probably in error in recording this genus from Chile, Larrain provides "the first documented record of *M. darwini* in the Chilean Tertiary" (1984:27).

STRATIGRAPHIC OCCURRENCE.—Miocene, possibly Upper Eocene (Larrain, 1984).

FIGURES.—Figure 6*d*, petaloid plate pattern; Figure 21*g*, internal buttress system; Figure 25*k*, pressure drainage channels and food grooves; Figure 26*m*, oral surface plate pattern; Durham et al. (1966:U484), aboral and oral surfaces.

Mortonella Pomel, 1883

TYPE SPECIES.—*Scutella quinquefaria* Say, 1825.

NUMBER OF SPECIES.—Probably at least two.

DISTRIBUTION.—Southeastern United States; Cuba; Gulf of Mexico.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 27*a*, aboral surface; Durham et al. (1966:U479), aboral and oral surfaces, side view.

Nipponaster Durham, 1952

TYPE SPECIES.—*Astrodapsis nipponicus* Nisiyama, 1934.

NUMBER OF SPECIES.—Probably three or four species can be ascribed to this genus, following Durham's (1955) revision, plus two or three species originally described as members of the genus *Pseudoastrodapsis*, herein considered synonymized with *Nipponaster* following Durham et al. (1966:U482).

DISTRIBUTION.—Japan; Sakhalin(?) and Kamchatka(?).

STRATIGRAPHIC OCCURRENCE.—Miocene to Pliocene(?).

FIGURES.—Durham et al. (1966:U483), aboral and oral surfaces, oral surface plate pattern.

Parascutella Durham, 1953

TYPE SPECIES.—*Scutella leognanensis* Lambert, 1903.

NUMBER OF SPECIES.—Probably about ten (Durham, 1953b: 349-350; Kier and Lawson, 1978:66-67).

DISTRIBUTION.—Europe, France.

STRATIGRAPHIC OCCURRENCE.—Miocene.

FIGURES.—Figure 26*g*, oral surface plate pattern; Figure 27*d*, aboral surface; Figure 28*b*, petaloid; Durham et al.

(1966:U478), aboral and oral surfaces.

Parmulechinus Lambert, 1910

TYPE SPECIES.—*Scutella agassizi* Oppenheim, 1902.

NUMBER OF SPECIES.—Five or six known (Durham, 1953b:349).

DISTRIBUTION.—Europe, northern Africa, Malta.

STRATIGRAPHIC OCCURRENCE.—Lower Miocene.

FIGURES.—Figure 26*h*, oral surface plate pattern; Figure 27*e*, aboral surface; Durham et al. (1966:U478), aboral and oral surfaces.

Periarchus Conrad, 1866

TYPE SPECIES.—*Sismondia alta* Conrad, 1865.

NUMBER OF SPECIES.—At least three (Durham, 1955:155; Kier, 1980:40-43).

DISTRIBUTION.—Southeastern and eastern USA as far north as North Carolina; Cuba; Gulf of Mexico.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Figure 10*b*, keel and peristomial point in food groove; Figure 21*c*, internal buttress system; Figure 5*b*, food grooves; Figure 26*b*, oral surface plate pattern; Figure 27*b*, aboral surface; Cooke (1959, pls. 12-14), aboral and oral surfaces, side view; Durham et al. (1966:U479), aboral and oral surfaces, side view.

Porpitella Pomel, 1883

TYPE SPECIES.—*Cassidulus Hayesianus* Desmoulins, 1837.

NUMBER OF SPECIES.—At least three species have been ascribed to this genus (H.L. Clark, 1937; Mortensen, 1948:232-233).

DISTRIBUTION.—Europe, France, Alabama(?).

STRATIGRAPHIC OCCURRENCE.—Eocene.

FIGURES.—Figure 18*h*, apical system; Mortensen (1948:231), aboral and oral surfaces, side and rear views; Durham et al. (1966:U470), aboral surface.

Protoscutella Stefanini, 1924

TYPE SPECIES.—*Scutella mississippiensis* Twitchell, 1915.

NUMBER OF SPECIES.—Mortensen (1948:390) lists five fossil species.

DISTRIBUTION.—Southeastern and eastern USA as far north as North Carolina; Gulf of Mexico.

STRATIGRAPHIC OCCURRENCE.—Middle to Upper Eocene.

FIGURES.—Figure 25*a*, food grooves; Figure 26*a*, oral surface plate pattern; Cooke (1959, pl. 15), aboral and oral surfaces, side view; Durham et al. (1966:U479), aboral and oral surfaces.

Remondella Durham, 1955

TYPE SPECIES.—*Clypeaster gabbi* Rémond, 1863.

NUMBER OF SPECIES.—Three (Wagner, 1974:120–121; Budin, 1977:446).

DISTRIBUTION.—Western USA, California and Alaska. There are reports that *Remondella* is also found in Kamchatka (Budin, 1977:446).

STRATIGRAPHIC OCCURRENCE.—Upper Miocene in California to Lower Pliocene in Alaska (the Alaskan deposits might also be Upper Miocene, according to Steven C. Beadle, pers. comm.). It is found in the Upper Miocene in Kamchatka (Budin, 1977:446).

FIGURES.—Figure 25j, food grooves; Figure 26l, oral surface plate pattern; Durham et al. (1966:U484), oral surface plate pattern; Wagner (1974, pl. 3), aboral and oral surfaces, side view.

Samlandaster Lambert and Thiéry, 1914

TYPE SPECIES.—*Scutella germanica* von Beyrich, 1847.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Europe, Poland.

STRATIGRAPHIC OCCURRENCE.—Upper Eocene.

FIGURES.—Durham et al. (1966:U489), oral surface, internal view of test. Not in key.

Scaphechinus A. Agassiz, 1863

TYPE SPECIES.—*Scaphechinus mirabilis* A. Agassiz, 1863.

NUMBER OF SPECIES.—Nisiyama (1968:110–111) lists two fossil species, and Mortensen (1948:374) lists three living species.

DISTRIBUTION.—Northeastern Asia, Vostok Bay; Japan; Taiwan (as a fossil only?).

STRATIGRAPHIC OCCURRENCE.—Pliocene to Recent.

FIGURES.—Figure 10c, keel and peristomial point in food groove; Figure 25i, food grooves; Figure 26k, oral surface plate pattern; Figure 29b, spines from oral surface; Durham et al. (1966:U480), aboral and oral surfaces.

Scutaster Pack, 1909

TYPE SPECIES.—*Scutaster andersoni* Pack, 1909.

NUMBER OF SPECIES.—Two or three (Durham, 1955:180).

DISTRIBUTION.—Western USA, California.

STRATIGRAPHIC OCCURRENCE.—Lower Oligocene to Lower or Middle Miocene (Steven C. Beadle, pers. comm.).

FIGURES.—Durham et al. (1966:U488), aboral surface, oral surface plate pattern, food grooves.

Scutella Lamarck, 1816

TYPE SPECIES.—*Echinodiscus subrotundus* Leske, 1778.

NUMBER OF SPECIES.—Durham (1953b:349) feels that only the type species can be referred to this genus with any certainty. Kier and Lawson (1971:66–67) list more than 20 species of *Scutella*, some of which are probably not true *Scutella* (sensu Durham, 1953b). The New World species are unlikely to be

Scutella, and some of the European taxa will undoubtedly turn out to be *Parascutella* or *Parmulechinus* (sensu Durham, 1953b). Of the “*Scutella*” listed by Kier and Lawson (1971:66–67), seven were described after Durham’s (1953b) attempt to unravel the complicated taxonomy of this group. The placement of these taxa may or may not reflect Durham’s recommendations.

DISTRIBUTION.—Malta, Austria, Italy, Hungary.

STRATIGRAPHIC OCCURRENCE.—Upper Oligocene or Lower Miocene.

FIGURES.—Figure 9f, basicoronal plates; Figure 26f, oral surface plate pattern; Figure 27c, aboral surface; Durham et al. (1966:U476), aboral and oral surfaces, food grooves, side view.

Scutellaster Cragin, 1895

TYPE SPECIES.—*Scutella interlineata* Stimpson, 1856.

NUMBER OF SPECIES.—Approximately ten (Wagner, 1974:118).

DISTRIBUTION.—Western North America, central California to Oregon; Alaska; Sakhalin(?).

STRATIGRAPHIC OCCURRENCE.—Upper Miocene to Pleistocene (Steven C. Beadle, pers. comm.)

FIGURES.—Figure 25d, food grooves; Durham et al. (1966:U481), aboral surface, oral surface plate pattern, food grooves.

Scutellina L. Agassiz, 1841

TYPE SPECIES.—*Scutella lenticularis* Lamarck, 1816.

NUMBER OF SPECIES.—Mortensen (1948:229) suggests that there are at least twelve species of *Scutellina*, all fossil.

DISTRIBUTION.—Europe, northern Africa.

STRATIGRAPHIC OCCURRENCE.—Middle Eocene. Engel’s (1976:55–56) intimation that his new species of *Scutellina* is from the Cretaceous is suspect, and he himself suggests that the specimens “may belong to remaniated Eocene material.”

FIGURES.—Figure 7f, plate pattern adjacent to apical system; Figure 21d, internal buttress system; Figure 26c, oral surface plate pattern; Durham et al. (1966:U470), aboral and oral surfaces.

Scutulium Tournouer, 1869

TYPE SPECIES.—*Scutulium parisiense* Tournouer, 1869.

NUMBER OF SPECIES.—Only the type species is known.

DISTRIBUTION.—Europe, France.

STRATIGRAPHIC OCCURRENCE.—Oligocene.

FIGURES.—Durham et al. (1966:U489), aboral surface. Not in key.

Sinaechinocyamus Liao, 1979

TYPE SPECIES.—*Sinaechinocyamus planus* Liao, 1979.

NUMBER OF SPECIES.—Only the type species is presently contained in this genus.

DISTRIBUTION.—Yellow Sea.

STRATIGRAPHIC OCCURRENCE.—Recent.

FIGURES.—Liao (1979, figs. 1–4, pl. 1), periproct, peristome, spines, aboral and oral surfaces.

Taiwanaster Wang, 1984

TYPE SPECIES.—*Taiwanaster mai* Wang, 1984.

NUMBER OF SPECIES.—Three. The type is the only living species (Wang, 1984b:134–151).

DISTRIBUTION.—Taiwan.

STRATIGRAPHIC OCCURRENCE.—Early Pliocene to Recent.

FIGURES.—Figure 21f, internal buttress system; Wang (1984b, figs. 4–9, pls. 1–8), aboral and oral surfaces, spination, aboral and oral surface plate patterns, internal views of test, lantern supports, apical system, tubercles, podial pores.

Tenuiarachnius Durham, 1955

TYPE SPECIES.—*Echinarachnius gabbii kleinPELLI* Grant and

Hertlein, 1938.

NUMBER OF SPECIES.—Apparently only the type species is known.

DISTRIBUTION.—Western USA, California.

STRATIGRAPHIC OCCURRENCE.—Upper Miocene.

FIGURES.—Durham et al. (1966:U484), aboral surface, oral surface plate pattern.

Vaquerosella Durham, 1955

TYPE SPECIES.—*Scutella andersoni* Twitchell, 1915.

NUMBER OF SPECIES.—Four or five (Durham, 1955:166–167; 1957:630–631).

DISTRIBUTION.—Western USA, California, Oregon; Mexico; Baja California.

STRATIGRAPHIC OCCURRENCE.—Middle Miocene.

FIGURES.—Figure 26j, oral surface plate pattern; Durham et al. (1966:U484), aboral surface, oral surface plate pattern.

Illustrated Glossary

To find a diagram that illustrates a given term, look up that term on the alphabetical list below. The figure(s) indicated show(s) the structure referred to by the term. Although not all of the terms in the following list occur in the text of the key, they are illustrated in the glossary (Figures 31–34) for general reference. In Figure 31, comparisons are made between the general test morphology of a typical clypeasteroid, and that of a related form, an echinolampadid cassiduloid.

- | | |
|---|--|
| Aboral surface (Figure 31) | Interambulacral buttress (Figure 34b) |
| Accessory podium (Figure 33a) | Interambulacrum (Figure 31) |
| Adradial suture (Figure 31) | Internal wing (Figure 34a) |
| Ambitus (Figure 31) | Interporiferous zone (Figure 32a) |
| Ambulacral buttress (Figure 34b) | Interpyramidal muscle (Figure 34a) |
| Ambulacral pillar (Figure 34b) | Interradial suture (Figure 31) |
| Ambulacrum (Figure 31) | Keel (Figure 32b) |
| Anus (Figure 32b) | Labial process (Figure 34a) |
| Apex (Figure 31) | Lantern supports (Figure 34b) |
| Apical system (Figure 32a) | Large food groove podium (Figure 32b) |
| Aristotle's lantern (Figure 34a) | Locomotory field (Figure 33b) |
| Auricles (Figure 34b) | Long barrel-tipped podium (Figure 33b) |
| Basiconal plates (Figure 31) | Lovén's system (Figure 31) |
| Bourrelet (Figure 31) | Lumule (Figure 32b) |
| Buccal podium (Figure 32b) | Mouth (Figure 32b) |
| Circumferential suture (Figure 31) | Neck of pedicellaria (Figure 33c) |
| Conjugation groove (Figure 32a) | Ocular plate (Figure 32a) |
| Demiplate (Figure 32a) | Oral surface (Figure 31) |
| Discontinuous interambulacrum (Figure 31) | Outer pore (Figure 32a) |
| Epiphysis (Figure 34a) | Pedicellariae: |
| External wing (Figure 34a) | Bidentate (Figure 33c) |
| Food groove (Figures 32b, 33b) | Biphylloous (Figure 33c) |
| Food groove podium (Figure 32b) | Globiferous (Figure 33c) |
| Geniculate field (Figure 33b) | Ophicephalous (Figure 33c) |
| Gonopore (Figure 32a) | Tridentate (Figure 33c) |
| Hinge of pedicellaria (Figure 33c) | Triphylloous (Figure 33c) |
| Inner pore (Figure 32a) | |

Periproct (Figure 31)
Periproctal membrane (Figure 32b)
Peristome (Figure 31)
Peristomial membrane (Figure 32b)
Peristomial point (Figure 32b)
Perradial suture (Figure 31)
Petaloid (Figures 31, 32a)
Phyllode (Figure 31)
Pressure drainage channel (Figure 33b)
Pyramid (Figure 34a)
Respiratory podium (Figure 33a)
Rotule (Figure 34a)
Short barrel-tipped podium (Figure 33b)
Sphaeridial chamber (Figure 32b)

Sphaeridium (Figure 32b)
Spines:
 Aboral primary (Figure 33a)
 Geniculate (Figure 33b)
 Locomotory (Figure 33b)
 Miliary (Figure 33a)
 Stem of pedicellaria (Figure 33c)
Stereom (Figure 33a)
Supra-alveolar process (Figure 34a)
Test (Figure 33a)
Tooth (Figure 34a)
Tooth slide (Figure 34a)
Tubercle (Figure 33a)
Valve of pedicellaria (Figure 33c)

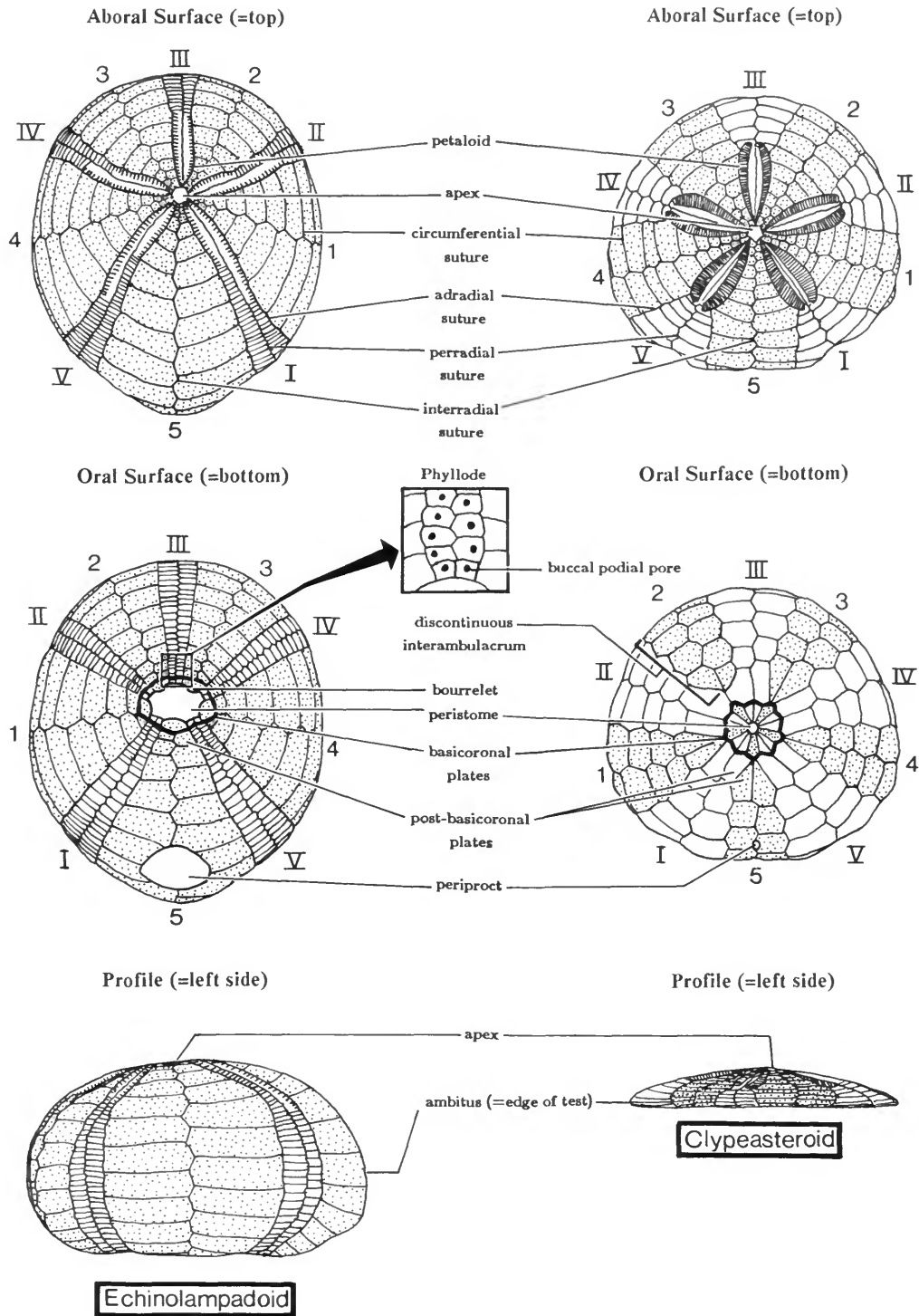


FIGURE 31.—Terminology associated with plate patterns on aboral and oral surfaces of an echinolampadoid, *Echinolampas depressa* Gray, and a generalized clypeasteroid. (Paired interambulacral plate columns stippled; paired ambulacral plate columns unshaded; perradial and interradial sutures numbered according to Lovén's system; ambulacra in Roman numerals, interambulacra in Arabic. (In all cases except for profiles, anterior is towards top of page.)

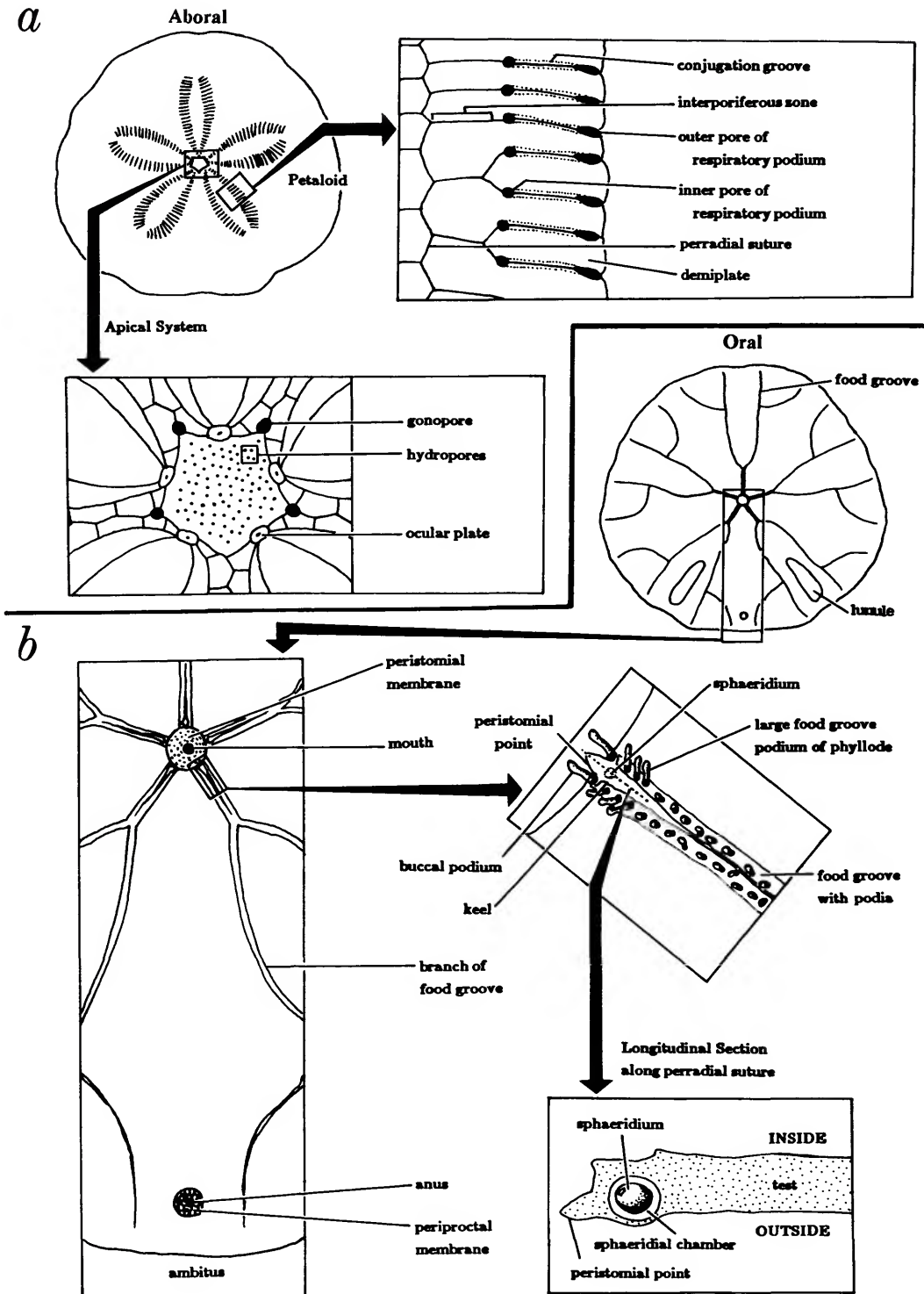


FIGURE 32.—Terminology associated with (a), petaloids and apical systems of a generalized clypeasteroid; and (b), peristomes, periprocts, food grooves, and sphaeria of a generalized clypeasteroid.

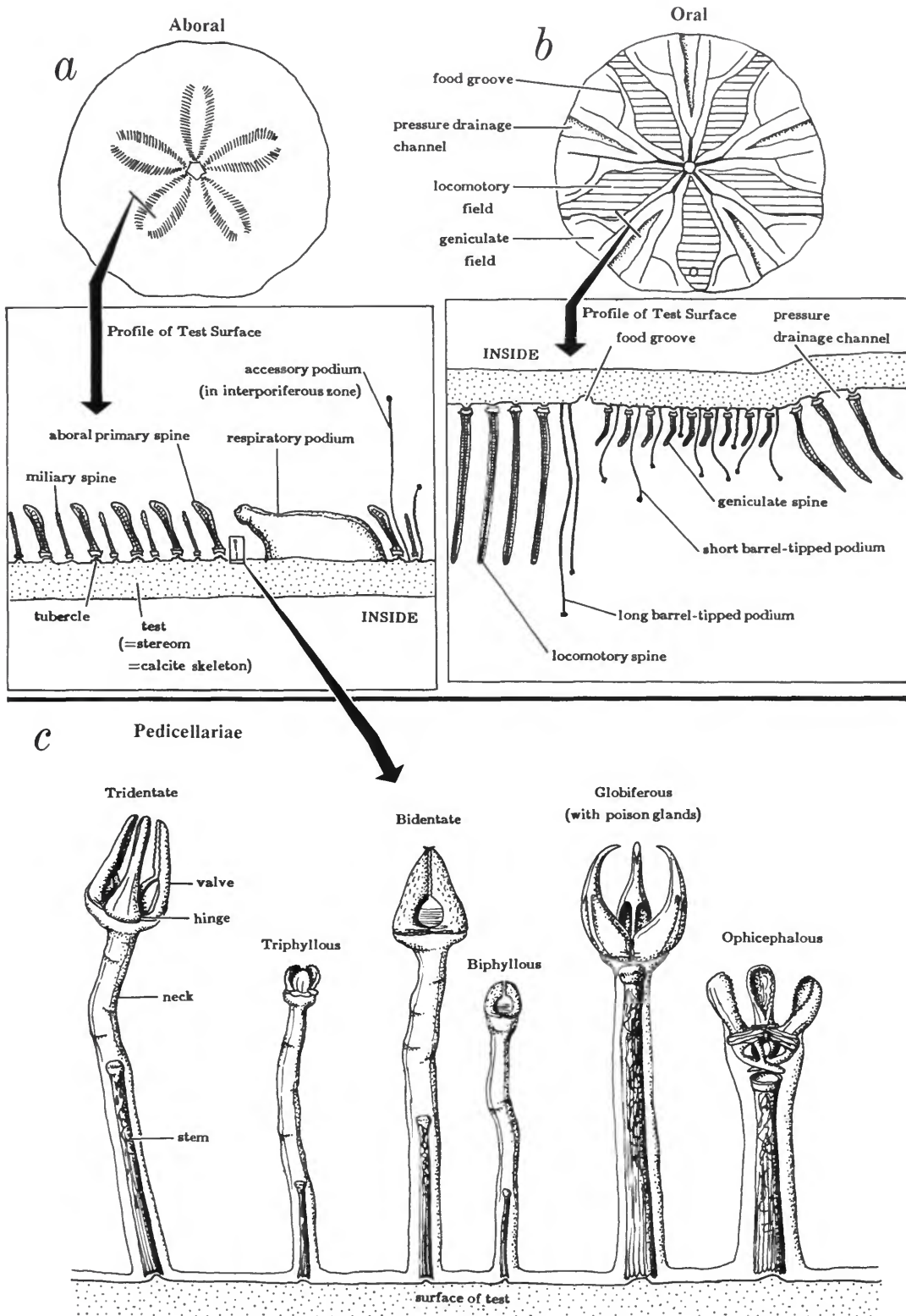
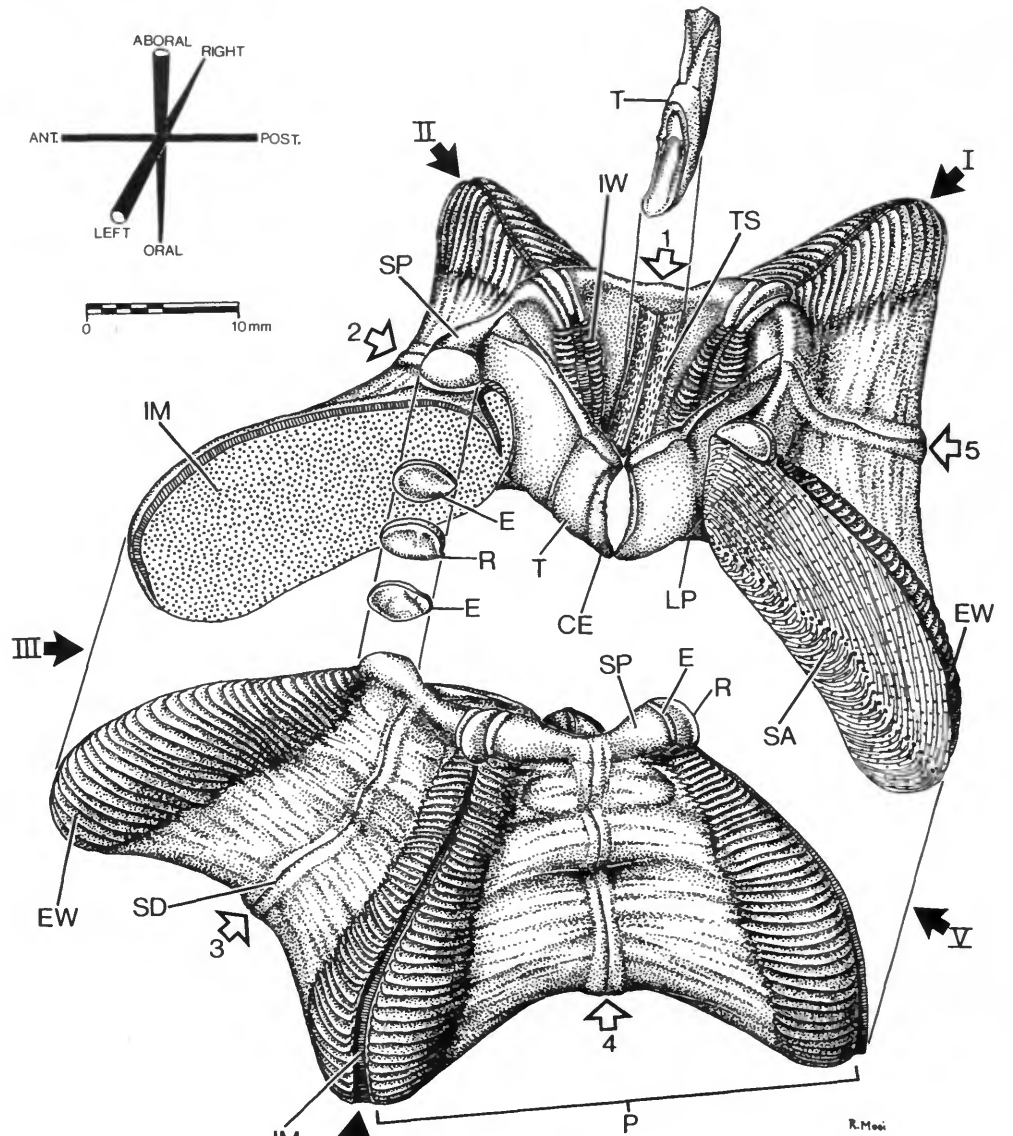


FIGURE 33.—Terminology associated with *a*), external features on aboral surface of a generalized clypeasteroid; *(b)*), external features on the oral surface of a generalized clypeasteroid; and *(c)*), pedicellariae of a generalized clypeasteroid.

a Aristotle's Lantern



LEGEND

- CE—Chewing Edge
- E—Epiphysis
- EW—External Wing
- IW—Internal Wing
- IM—Interpyramidal Muscle
- LP—Labial Process
- P—Pyramid
- R—Rotule
- SA—Smooth Area
(Interpyramidal muscle attachment)
- SP—Supra-alveolar Process
- SD—Symphysis Between Demipyramids
- T—Tooth
- TS—Tooth Slide

b

Internal View of Test

(Generalized clypeasteroid)

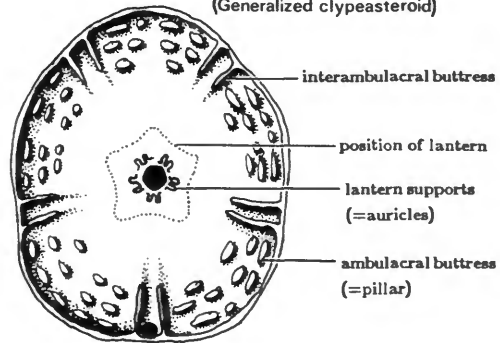


FIGURE 34.—Terminology associated with (a), the Aristotle's lantern of a clypeasteroid, *Clypeaster rosaceus* Linné, legend at lower left, numbered according to Lovén's system; and (b) lantern supports and internal buttress systems of a generalized clypeasteroid.

Literature Cited

- Budin, I.N.
 1977. [Miocene Sand Dollars of Kamchatka Peninsula.] *Biologiya Morya*, 3(6):443-447, figures 1-3. [In Russian.]
 1980. [A New Genus of Sand Dollars of the Family Fibulariidae (Echinoidea).] *Zoologicheskii Zhurnal*, 59(2):305-308, figures 1-6. [In Russian.]
- Clark, A.H.
 1946. Echinoderms from the Pearl Islands, Bay of Panama, with a Revision of the Pacific Species of the Genus *Encope*. *Smithsonian Miscellaneous Collections*, 106(5):1-11, plates 1-4.
- Clark, H.L.
 1937. A New Eocene Sea Urchin (*Porpütella micra*) from Alabama. *Journal of Paleontology*, 11(3):248-249, figures 1-3.
 1948. Report on the Echini of the Warmer Eastern Pacific, Based on the Collections of the *Velero III*. *Allan Hancock Pacific Expeditions*, 8(5):225-352, figures 1-3, plates 35-71.
- Cooke, C.W.
 1959. Cenozoic Echinoids of the Eastern United States. *United States Geological Survey Professional Paper*, 321:1-106, plates 1-43.
 1961. Cenozoic and Cretaceous Echinoids from Trinidad and Venezuela. *Smithsonian Miscellaneous Collections*, 142(4):1-35, plates 1-14.
- Davies, A.M.
 1971. *Tertiary Faunas, I: The Composition of Tertiary Faunas*. Second edition, 571 pages. London: Allen and Unwin.
- Durham, J.W.
 1950. 1940 E.W. Scripps Cruise to the Gulf of California, Part 2: Megascopic Paleontology and Marine Stratigraphy. *The Geological Society of America Memoir*, 43:1-216, plates 1-48.
 1952. Not *Astrodapsis* in Japan. *Journal of Paleontology*, 26(5):844-846, figure 1.
 1953a. *Scutellaster* and *Anorthoscutum*. *Journal of Paleontology*, 27(1):147-149, figure 1.
 1953b. Type-Species of *Scutella*. *Journal of Paleontology*, 27(3):347-352, figure 1, plate 47.
 1954. A New Family of Clypeasteroid Echinoids. *Journal of Paleontology*, 28(5):677-684, figures 1-3.
 1955. Classification of Clypeasteroid Echinoids. *University of California Publications in Geological Sciences*, 31(4):73-198, figures 1-38, plates 3-4.
 1957. Notes on Echinoids. *Journal of Paleontology*, 31(3):625-631, figures 1-2, plate 72.
 1961. The Echinoid *Mellita* in the Pacific Coast Cenozoic. *Contributions in Science, Los Angeles County Museum*, 48:1-12, figure 1, plates 1-2.
 1978. Polymorphism in the Pliocene Sand Dollar *Merriamaster* (Echinoidea). *Journal of Paleontology*, 52(2):275-286, figures 1-3, plates 1-3.
- Durham, J.W., and S.R. Morgan
 1978. New Sand Dollars (Echinoidea) of the Genera *Merriamaster* and *Dendroaster* from Purisima Formation, California. *Proceedings of the California Academy of Sciences*, 41(11):297-305, figures 1-5.
- Durham, J.W., H.B. Fell, A.G. Fischer, P.M. Kier, and C.D. Wagner
 1966. *Treatise on Invertebrate Paleontology, Part U: Echinodermata 3*. Volumes 1 and 2, 695 pages, 534 figures. Geological Society of America, Inc. and the University of Kansas Press.
- Engel, H.
 1976. On a New Echinid from the Cretaceous of Maastricht: *Scutellina supramarginalis* (Echinoidea, Gnathostomata, Clypeasteroidea, Lagamina, Fibulariidae). *Bulletin Zoologisch Museum Universiteit van Amsterdam*, 5(7):55-57, figure 1.
- Foster, R.J., and G.M. Philip
 1980. Some Australian Late Cainozoic Echinoids. *Proceedings of the Royal Society of Victoria*, 91(2):155-160, figure 1, plates 19-20.
- Grant, U.S., and L.G. Hertlein
 1938. The West American Cenozoic Echinoidea. *Publications of the University of California at Los Angeles in Mathematics and Physical Sciences*, 2:1-225, figures 1-17, plates 1-30.
- Hall, C.A., Jr.
 1962. Evolution of the Echinoid Genus *Astrodapsis*. *University of California Publications in Geological Sciences*, 40(2):47-180, figures 1-4, plates 1-44, 4 figures and 1 map in pocket.
- Harold, A.S., and M. Telford
 In prep. Systematics, Phylogeny and Biogeography of the Species of *Mellita* (Echinodermata: Echinoidea).
- Hotchkiss, F.H.C., and H.B. Fell
 1972. Zoogeographical Implications of a Paleogene Echinoid from East Antarctica. *Journal of the Royal Society of New Zealand*, 2(3):369-372, figure 1.
- Jeannet, A.
 1928a. Contribution à l'étude des échinides Tertiaires de la Trinité et du Venezuela. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft*, 41(1):1-49, figures 1-12, plates 1-6.
 1928b. Sur les échinides Tertiaires du Venezuela et de la Trinité conservés au Musée d'Histoire Naturelle de Bâle. *Verhandlungen Schweizerische Naturforschende Gesellschaft*, 109:220-221.
- Kier, P.M.
 1963. Tertiary Echinoids from the Caloosahatchee and Tamiami Formations of Florida. *Smithsonian Miscellaneous Collections*, 145(5):1-63, figures 1-58, plates 1-18.
 1967. Sexual Dimorphism in an Eocene Echinoid. *Journal of Paleontology*, 41(4):988-993, figures 1-3, plates 129-130.
 1968. Echinoids from the Middle Eocene Lake City Formation of Georgia. *Smithsonian Miscellaneous Collections*, 153(2):1-45, figures 1-44, plates 1-10.
 1970. Lantern Support Structures in the Clypeasteroid Echinoids. *Journal of Paleontology*, 44(1):98-109, figures 1-8, plates 23-24.
 1972a. Tertiary and Mesozoic Echinoids of Saudi Arabia. *Smithsonian Contributions to Paleobiology*, 10:1-242, figures 1-50, plates 1-67.
 1972b. Upper Miocene Echinoids from the Yorktown Formation of Virginia and Their Environmental Significance. *Smithsonian Contributions to Paleobiology*, 13:1-41, figures 1-7, plates 1-10.
 1980. The Echinoids of the Middle Eocene Warley Hill Formation, Santee Limestone, and Castle Hayne Limestone of North and South Carolina. *Smithsonian Contributions to Paleobiology*, 39:1-102, figures 1-26, plates 1-22.
 1982. Rapid Evolution in Echinoids. *Palaeontology*, 25(1):1-9, figures 1-3, plates 1-2.
- Kier, P.M., and M.H. Lawson
 1978. Index of Living and Fossil Echinoids 1924-1970. *Smithsonian Contributions to Paleobiology*, 43:1-182.
- Larrain, A.P.
 1984. The Fossil and Recent Shallow Water Irregular Echinoids from Chile. 235 pages. Doctoral dissertation, University of Southern

- California, Los Angeles, California.
- Liao, Y.
1979. A New Genus of Clypeasteroid Sea-urchin from Huang Hai. *Oceanologia et Limnologia Sinica*, 10(1):67-72, figures 1-4, plate 1.
- Liao, Y., and C. Lin
1981. [A New Echinoid with Sexual Dimorphism from the Late Tertiary Deposits of Beibuwan, Guangxi.] *Acta Palaeontologica Sinica*, 20(5):482-484, figures 1-2, plate 1. [In Chinese.]
- Linder, R.A., J.W. Durham, and W.N. Orr
1988. New Late Oligocene Echinoids from the Central Western Cascades of Oregon. *Journal of Paleontology*, 62(6):945-958, figures 1-6.
- Martínez, S.
1985. [*Amplaster coloniensis* n.g. n.sp. (Echinoidea: Monophorasteridae) from the Miocene of Uruguay.] *Memoria Congreso Latinoamericano de Paleontología*, 3:505-508, figures 1-4. [In Spanish.]
- Mihály, S.
1983. Late Badenian Echinoidea from New Exposures in Budapest. *Magyar Állami Földtani Intézet Évi Jelentése*, 1983:235-262, figures 1-3, plates 1-5.
- Mooi, R.
1986a. Non-respiratory Podia of Clypeasteroids (Echinodermata, Echinoidea), II: Diversity. *Zoomorphology*, 106(2):75-80, figures 1-28.
1986b. Structure and Function of Clypeasteroid Miliary Spines (Echinodermata, Echinoidea). *Zoomorphology*, 106(4):212-223, figures 1-20.
1987. A Cladistic Analysis of the Sand Dollars (Clypeasteroidea: Scutellina) and the Interpretation of Heterochronic Phenomena. 208 pages. Doctoral dissertation, Department of Zoology, University of Toronto, Toronto, Ontario.
In press. Paedomorphosis, Aristotle's Lantern, and the Origin of the Sand Dollars (Echinodermata: Clypeasteroidea). *Paleobiology*.
- Mortensen, T.
1948. Clypeasteroidea, Clypeasteridae, Arachnoididae, Fibulariidae, Laganidae, and Scutellidae. In Mortensen, A *Monograph of the Echinoidea*, 2(4): 471 pages, 258 figures, 72 plates. Copenhagen: C.A. Reitzel.
- Nisiyama, S.
1968. The Echinoid Fauna from Japan and Adjacent Regions, Part 2. *Paleontological Society of Japan Special Papers*, 13:1-491, figures 26-77, plates 19-30.
- Parma, S.G.
1985. [*Eoscutella* Grant and Hertlein (Echinodermata: Clypeasteroidea) in the Patagoniano (Early Tertiary) of the Province of Santa Cruz, República Argentina.] *Ameghiniana*, 22(1-2):35-41, figures 1-4, plate 1. [In Spanish.]
- Philip, G.M. and R.J. Foster
1971. Marsupiate Tertiary Echinoids from South-eastern Australia and their Zoogeographic Significance. *Paleontology*, 14(4):666-695, figures 1-9, plates 124-134.
- Raup, D.M.
1956. *Dendroaster*: A Problem in Echinoid Taxonomy. *Journal of Paleontology*, 30(3):685-694, figures 1-4.
- Sadler, T., and N.S. Pledge
1985. The Fossil Sea Urchin *Fellaster incisa*—An Extension of Range. *Transactions of the Royal Society of South Australia*, 109(4):175-176, figures 1-2.
- Schmidt, O.I., and V.N. Sinelnikova
1971. [Echinoids of the Kavran Series, Western Kamchatka.] *Doklady Akademii Nauk SSSR*, 199(4):909-912, figure 1. [In Russian; English translation, 1972, American Geological Institute.]
- Smith, A.B.
1984. *Echinoid Palaeobiology*. 190 pages. London: Allen & Unwin.
- Stephenson, D.G.
1968. An Aberrant Species of *Fibularia* from Kenya and Madagascar. *Geological Magazine*, 105(2):136-139, figure 1.
- Tandon, K.K., and D.K. Srivastava
1980. A New Genus and Species of the Clypeasteroid Echinoid from the Middle Eocene Rocks of Kutch, India. *Journal of the Palaeontological Society of India*, 23-24:1-3, figures 1-2, plate 1.
- Wagner, C.D.
1974. Fossil and Recent Sand Dollar Echinoids of Alaska. *Journal of Paleontology*, 48(1):105-123, figures 1-2, plates 1-3.
- Wang, C.-C.
1982a. On the Early Miocene Sand Dollar *Echinodiscus yeliuensis* n.sp. from the Taliuo Formation of Yeliu, Northern Taiwan. *Proceedings of the Geological Society of China*, 25:150-157, figures 1-4, plates 1-4.
1982b. On the Fossil Laganid Echinoids from Taiwan, with a Discussion of the "Genus" *Peronellites* Hayasaka & Morishita. *Acta Geologica Taiwanica*, 21:140-156, plates 1-4.
1983. A New Species of *Astriclypeus* from the Wuchihshan Formation Near Chilung, Taiwan. *Bulletin of the Central Geological Survey of Taiwan*, 2:113-120, figure 1, plates 1-2.
1984a. Fossil *Echinodiscus* from Taiwan. *Bulletin of the Central Geological Survey of Taiwan*, 3:107-115, figure 1, plate 1.
1984b. New Classification of Clypeasteroid Echinoids. *Proceedings of the Geological Society of China*, 27:119-152, figures 1-10, plates 1-8.

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