PHYLOGENETIC SYSTEMATICS OF TERTIARY MONOPHORASTERID SAND DOLLARS (CLYPEASTEROIDA: ECHINOIDEA) FROM SOUTH AMERICA

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ABSTRACT—Sand dollars in the Monophorasteridae Lahille, 1896, form an important part of the South American Cenozoic echinoid fauna. Re-examination of type and other material adds significantly to our knowledge of the morphology and taxonomy of the family, and shows that besides *Monophoraster darwini* (Desor, 1847), *M. duboisi* (Cotteau, 1884), *Amplaster coloniensis* Martínez, 1984, and *A. alatus* Rossi de Garcia and Levy, 1989, there is a new species, *A. ellipticus*. We also show that *Karlaster* Marchesini Santos, 1958, is not a monophorasterid as once thought. A phylogenetic analysis of 24 characters assessed from all species of *Monophoraster* Lambert and Thiéry, 1921, and *Amplaster* Martínez, 1984, along with genera of the Mellitidae Stefanini, 1912, produced a single most parsimonious tree. The analysis demonstrates monophyly of mellitids and monophorasterids, and that *Iheringiella* Berg, 1898, should be excluded from the latter. Although both *Monophoraster* Lambert and Thiéry, 1921, and *Amplaster* Martínez, 1984, retain many features of an ancestor in common with the Mellitidae Stefanini, 1912, they also exhibit bizarre morphologies quite different from those of mellitids. The study has also resulted in a clearer picture of the biogeography and biostratigraphy of the Monophorasteridae, and their great significance in the evolution of lunulate sand dollars in the Americas.

INTRODUCTION

SCUTELLINE CLYPEASTEROIDS known as sand dollars are conspicuous and common fossils in many of the Cenozoic rocks of the Americas. For example, the Tertiary deposits that crop out along the Patagonian Atlantic and Uruguayan coasts have abundant and diverse scutelline faunas (Figs. 1, 2). In spite of this, and although the first descriptions of these faunas date from as early as the mid-19th century (d'Orbigny, 1842), published studies of eastern South American echinoids have been infrequent and many are outdated (Desor, 1847; Lahille, 1896, 1898; Ortmann, 1902; de Loriol, 1901, 1902; Boehm, 1903; Lambert, 1903; Bernasconi, 1959; Rossi de Garcia and Levy, 1989; Parma, 1985, 1988, 1989, 1996a, 1996b; Parma and Martínez, 1994; Chiesa et al., 1995).

Some of the most important fossil sand dollars from South America are found in the entirely extinct group of New World lunulates (sand dollars bearing holes, or lunules through the test) known as monophorasterids. Based on the presence of an unpaired lunule in the posterior interambulacrum (the anal lunule), Lahille (1896) proposed a scutellid subfamily, Monophorinae, to contain species in a genus known then as *Monophora* Desor, 1847 (=*Monophoraster* Lambert and Thiéry, 1921). This proposal was followed by Mortensen (1948) in his great monograph of the echinoids. Durham (1955) not only elevated the group to family, he added the non-lunulate genus *Iheringiella* Berg, 1898, based on features that he felt diagnosed the family better than the anal lunule. Durham (1966) also placed an extremely poorly known supposed lunulate, *Karlaster* Marchesini Santos, 1958, in the Monophorasteridae.

Durham's (1966, p. U485) diagnosis included widespread, plesiomorphic clypeasteroid features such as size and overall shape, petal morphology, plate pattern, periproct position, gonopore number, and food groove bifurcation. In fact, only a single character listed in this diagnosis, "interambulacra . . . narrower at ambitus than midway on oral surface" could be construed as unique to the family Monophorasteridae, although the question of whether even this character was to be found among all its members was not well established. Durham's diagnosis is therefore difficult to apply, particularly given the fact that oral plate patterns of the genera he included were poorly or erroneously

depicted in previous literature. Durham's inclusion of a non-lunulate, *Iheringiella*, in the family also meant that Lahille's (1896) and Mortensen's (1948) most conspicuous diagnostic character, the anal lunule, no longer formed part of the diagnosis.

Amplaster coloniensis was later added to the family by Martínez (1984). *Amplaster* contains among the most bizarre of all sand dollar taxa. One of the species has a test as much as three times wider than it is long. In spite of this odd attribute, members of *Amplaster* resemble *Monophoraster* in possessing an anal, but no other lunules. In spite of some work attempting to depict the oral plate patterns in *Amplaster* (Martínez and Durham, 1988), the characters listed by Durham (1966) in the familial diagnosis remain problematic.

Recently, renewed interest in the family has prompted additional work (Mooi et al., 1998). Rossi de Garcia and Levy (1989) described *Amplaster alatus* from the Tertiary of Chubut Province, Argentina. This species was proposed in a short paper not widely available. *Amplaster alatus* was recently made the sole member of a new genus, *Lunulaster*, in an abstract (Parma and Martínez, 1994). Because of this, a complete revision of *Amplaster* is appropriate to determine the validity of this new genus.

Although some monophorasterid species, notably in the genus *Monophoraster*, are very well known and widely distributed (Fig. 1), others are remarkably poorly known and usually given only cursory treatment in overviews (e.g., Durham, 1966; Mooi, 1989). There has been considerable confusion concerning taxonomic placement of some species, and new information is starting to highlight problems with even the most basic of morphological data (Martínez and Mooi, 1997). For example, *Karlaster* was originally known from only a few broken specimens, and the features that have been used to diagnose the Monophorasteridae are virtually impossible to discern in this material. Details of the oral plate pattern of *Karlaster* are also inconsistent with the type genus of the monophorasterids. As noted by Durham (1966), *Karlaster* has discontinuous paired oral interambulacra, whereas all the other monophorasterids known at the time had continuous interambulacra. Another example of the difficult systematics of the group is that *M. caldensis* Gigoux, 1916, listed by Durham (1955) as a *Monophoraster* was found to be a member of the Mellitidae Stefanini, 1912 (Covacevich and Frassinetti, 1977).

FIGURE 1—Maps of monophorasterid collecting localities. Localities listed below names of *Amplaster* species correspond to labels of stratigraphic columns in Fig. 2 (the Arroyo Limetas locality, marked by "*", is not depicted in these columns).

In summary, the Monophorasteridae has been poorly diagnosed, and some members actually lack the most conspicuous features first used to erect the family itself. To add to the systematic difficulties, monophorasterid genera are inadequately described, with many of the diagnostic features of the family remaining unknown in taxa such as *Karlaster, Amplaster,* and *Lunulaster.* In addition, analysis of width to length ratios of all known material of *Amplaster* indicates the existence of an unnamed form that does not fit the diagnoses of either of the described species of *Amplaster.* Therefore, a taxonomic revision of all the taxa listed at one time as members of the Monophorasteridae is warranted: *Monophoraster, Iheringiella, Karlaster, Amplaster,* and *Lunulaster.*

Monophorasterids are gaining prominence as stratigraphic markers in South American deposits (Fig. 2). They also have important biogeographic implications, given that lunulate sand dollars are today rather rare in the regions in which monophorasterids were once common. They have also figured in analyses of intraspecific variation (Lahille, 1896; Martínez, 1985) and

predation patterns in the Cenozoic (Zinsmeister, 1980). Monophorasterids are also pivotal to our understanding of the evolution of the extremely diverse lunulates in the Mellitidae. Postulated as basal lunulate taxa (Smith and Ghiold, 1982; Mooi, 1987), the monophorasterids are very important to our understanding of major events in the origins of the New World sand dollar faunas. Studies on *Monophoraster* and its relatives can provide data concerning basic ontogenetic mechanisms that produce prominent modern features such as the anal lunule (Telford, 1988). Monophorasterids can also increase our comprehension of the appearance of radical new morphologies represented by ambulacral lunules, pressure drainage channels, highly complicated peripheral ballast systems, and specialized spine and podial types.

Phylogenetic analysis is central to understanding the systematics and biological significance of the Monophorasteridae. Although Smith and Ghiold (1982), Mooi (1987), and Telford (1988) all suggested that the monophorasterids were the sister group to the mellitids, detailed character descriptions and rigorous phylogenetic analyses are still lacking. It is only in the
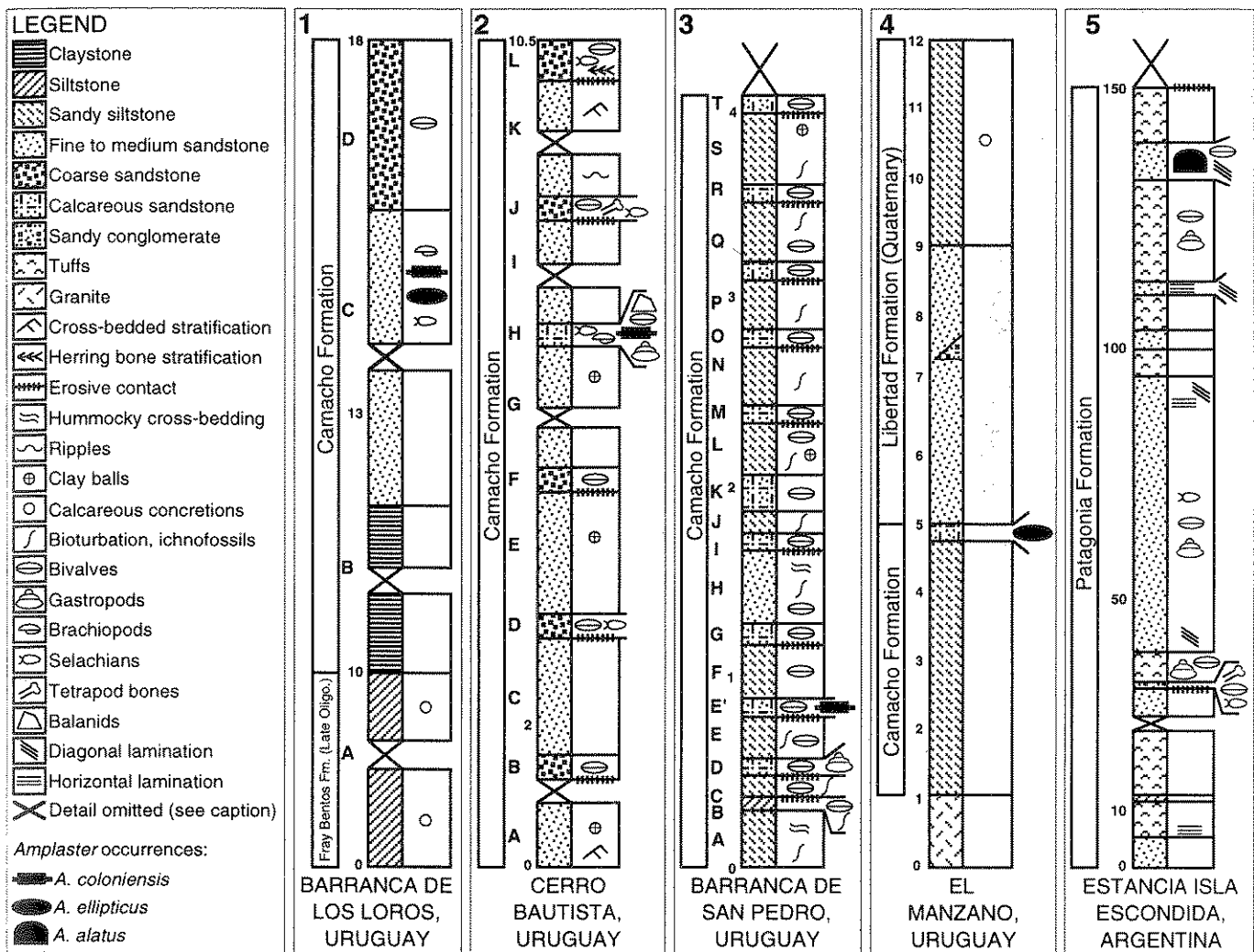
FIGURE 2—Stratigraphic columns for sections at *Amplaster* localities. Arroyo Limetas, at which *A. coloniensis* MMNP 507 and *A. alatus* FCDP 2831 were collected, is not represented due to a lack of precise data concerning the horizons there. Parts of the section represented by a large "X" are obscured by vegetation, or indicate uniform expanses of strata omitted to preserve space in the figure. *1*, Barranca de Los Loros locality for *A. coloniensis* holotype MNA-CPO 3426 and *A. ellipticus* n. sp. paratype MNA-CPO 3425 (formerly a paratype of *A. coloniensis*); *2*, Cerro Bautista locality for *A. coloniensis* MMNP 321; *3*, Barranca de San Pedro locality for *A. coloniensis* paratype MMC 1516; *4*, El Manzano locality for *A. ellipticus* n. sp. holotype FCDP 2205 (adapted from Serra, 1943); *5*, Estancia Isla Escondida locality for *A. alatus* holotype SEGEMAR 15527 and paratypes SEGEMAR 15526, 15528, 15529 (adapted from Franchi, 1983).

context of a complete phylogeny that the preceding species-level revision can have any relevance to our understanding of the evolution of this important group of sand dollars.

TAXA USED IN SYSTEMATIC REVISION
AND PHYLOGENETIC ANALYSIS

Abbreviations.—BMNH = Natural History Museum, London, U.K.; CASG = California Academy of Sciences Geology collection, San Francisco, U.S.A.; CASIZ = California Academy of Sciences Invertebrate Zoology collection, San Francisco, U.S.A.; CPBA = Catedra de Paleontología de la Universidad de Buenos Aires, Argentina; DNPM = Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil; FCDP = Facultad de Ciencias, Departamento de Paleontología, Montevideo, Uruguay; MCZ = Museum of Comparative Zoology, Harvard, U.S.A.; MMC = Museo Municipal de Colonia, Uruguay;

MMNP = Museo Municipal de Nueva Palmira, Uruguay; MNA-CPO = Museo nacional de Antropología, Collección Paleontológica F. Oliveras, Uruguay; MNRJ = Museu Nacional, Rio de Janeiro, Brazil; NMNH = National Museum of Natural History, Washington, U.S.A.; ROM = Royal Ontario Museum, Toronto, Canada; SEGEMAR = Servicio Geológico Minero Argentino, Buenos Aires, Argentina.

Outgroups.—Because of previously suggested relationships between the Monophorasteridae and the Mellitidae (Smith and Ghiold, 1982; Mooi, 1987; Telford, 1988), it was necessary to include representatives of the latter family in the overall analysis. To develop characters for the analysis, we focused on the type species of each of the three mellitid genera, and examined the following material specifically: *Mellita quinquiesperforata* (Leske, 1778), material listed in Mooi and Harold (1994); *Encope grandis* L. Agassiz, 1841, numerous specimens at the NMNH and CASIZ; *Leodia sexiesperforata* (Leske, 1778),

NMNH E36424 and numerous specimens in CASIZ. However, enough is understood about the phylogenetics of each of the representative genera that characters assessed in type species are also known to occur in the basal members the clades to which they belong. To root the overall tree, we relied on information concerning a wide variety of taxa believed representative of basal scutellines as suggested by Mooi (1987). However, we ultimately chose to represent basal scutellines with *Proescutella cailliaudi* (Cotteau, 1861), by examining specimens in lot NMNH 438178. Data from the literature and from unpublished observations of the first author concerning other taxa such as the Protoscutellidae Durham, 1955, and Eoscutellidae Durham, 1955, near the base of the scutelline clade helped inform coding and rooting decisions. Examination of all these outgroup taxa was necessary in order to test membership of *Iheringiella* in the Monophorasteridae.

Status of Karlaster.—Durham (1966) considered *Karlaster* Marchesini Santos, 1958, from the Pirabas Formation of the Miocene of Brazil to be a member of the Monophorasteridae, primarily on the supposed presence of a small anal lunule. Without seeing actual material of *Karlaster,* Mooi (1987) used cladistic arguments to remove it from the monophorasterids, and left *Karlaster* as a genus level plesion in a sister group relationship with a clade containing monophorasterids and mellitids. Martínez and Mooi (1997) examined the two known specimens of *Karlaster pirabensis* Marchesini Santos, 1958: the holotype (DNPM 4493) and another (MNRJ 5245-I) described in Brito (1979) and Brito and Ramires (1974). Martínez and Mooi (1997) showed conclusively that these specimens cannot be referred to the Monophorasteridae. As Mooi (1987) discussed, the disjunct interambulacra of the holotype are not characteristic of monophorasterids. In addition, the supposed anal lunule of *K. pirabensis* is a broken posterior notch (Martínez and Mooi, 1997). Such a notch is diagnostic of *Abertella* Durham, 1953 (Abertellidae Durham, 1955). The second specimen of *"K. pirabensis"* (MNRJ 5245-I) is undoubtedly a young *Abertella complanata* Brito, 1981, which is well known from the Pirabas Formation (Brito, 1981, 1986). Comparison with several specimens of *A. complanata* in the lots MNRJ 5460-I (the holotype of *A. complanata*) and MNRJ 5536-I adds to our suspicions that the holotype of *K. pirabensis* is also conspecific with *A. complanata.* Therefore, we hereby remove *"Karlaster" pirabensis* from the Monophorasteridae, and place it in the genus *Abertella.* The Abertellidae is sufficiently basal in the phylogeny of the Scutellina (Mooi, 1987) that it is appropriate to exclude both *Abertella* and *"Karlaster"* from our present consideration of more crownward lunulates represented by the monophorasterids and mellitids.

Ingroups.—Present information on the genus *Monophoraster* Lambert and Thiéry, 1921, leads us to recognize two valid taxa, *M. darwini* (Desor, 1847) and *M. duboisi* (Cotteau, 1884), for the purposes of the phylogenetic analysis. Examination of all known material of *Amplaster* Martínez, 1984, and the recently suggested genus *Lunulaster* Parma and Martínez, 1994, meant to contain the single species, *L. alatus,* strongly supports the need to include three additional lunulate taxa in our analysis of the monophorasterids. Apart from *L. alatus*, these include *Amplaster coloniensis* Martínez, 1984, and a new species of *Amplaster* named herein. The present analysis will re-examine the status of *Lunulaster.* The material examined for each of the monophorasterid taxa in the analysis is listed below under Systematic Paleontology.

Durham (1966) and Larrain (1984) included the non-lunulate *Iheringiella* with the lunulate monophorasterids, largely on the basis of the common possession of continuous interambulacra that become markedly narrow as they approach the ambitus, and

the elongation of the first post-basicoronal plates (Fig. 3). These are prominent characters in the description of the Monophorasteridae, and the narrowing of the interambulacra appears to be evidence for inclusion of *Iheringiella* with the other members of the family. Therefore, it was necessary to keep *Iheringiella* as part of the analysis of the monophorasterids to determine whether it belongs in this family, or whether it falls outside the family. Mooi (1987) suggested that *Iheringiella* fell below the clade containing mellitids and monophorasterids, and the present analysis is intended specifically to address this assertion. We examined the following material attributed to *Iheringiella patagoniensis* (Desor, 1847): CPBA 18477–18728, 18744–18844; ROM 19, 5433M, 5468, 5469.

Mooi (1987) also established that other lunulate taxa such as the Astriclypeidae Stefanini, 1912, were not more closely related to the mellitids than monophorasterids. Although they share some of the apomorphies that distinguish mellitids and monophorasterids from more basal scutellines such as Protoscutellidae Durham, 1955, and *Proescutella* Pomel, 1885, astriclypeids are omitted from the analysis because they are beyond the scope of this paper, and in need of revision themselves. We feel that astriclypeids do not bear directly on the question of monophyly of mellitids and monophorasterids, nor the relationships within these groups.

SYSTEMATIC PALEONTOLOGY

Class ECHINOIDEA Leske, 1778
Order CLYPEASTEROIDA A. Agassiz, 1872
Suborder SCUTELLINA Haeckel, 1896
Family MONOPHORASTERID Lahille, 1896

Type genus.—Monophoraster Lambert and Thiéry, 1921.

Diagnosis.—Sand dollars with only a single lunule located in the posterior interambulacrum (interambulacrum 5); strongly developed ridge around lunule on aboral surface; no pressure drainage channels leading to anal lunule on oral surface; ambulacral basicoronal plates long and extremely narrow; interambulacral basicoronal plates greatly enlarged; first post-basicoronal plates in interambulacra elongated (a condition also found in Iheringiella); interambulacra narrowing towards ambitus (a condition also found in *Iheringiella*).

Description.—Test of medium to large size (but seldom greater than 60 mm in test length). Aboral surface slightly domed, oral surface flat, highest point of test at apical system or slightly anterior to it. Apical system monobasal, central or slightly anterior, with numerous hydropores scattered over the madreporic plate. Four gonopores, one in each of the paired interambulacra, on the suture between the madreporic plate and the first adapical plates of the interambulacral column. Petaloids almost closed, relatively large, with two to four trailing podia (sensu Mooi, 1987) at the distal end of each column of respiratory podia. Respiratory podial pairs strongly conjugated, pores aligned along circumferential sutures of ambulacral plates, inner pore circular, outer pore somewhat elongate. Peristome circular, midway along anterior-posterior axis. Periproct small, about two-thirds of the distance from the peristome to the lunule, between the first pair of post-basicoronals and not in contact with the basicoronal plate in interambulacrum 5. Food grooves bifurcating near the distal ends of the ambulacral basicoronal plates, becoming highly branched near the ambitus (Mooi, 1989). Accessory podial pores absent from interporiferous zone of petaloids. On oral surface, podial pores (presumably once supporting barrel-tipped podia sensu Mooi, 1986) densely packed throughout ambulacra except in pressure drainage channels (as in mellitids, see Telford et al., 1985). Interambulacral basicoronal
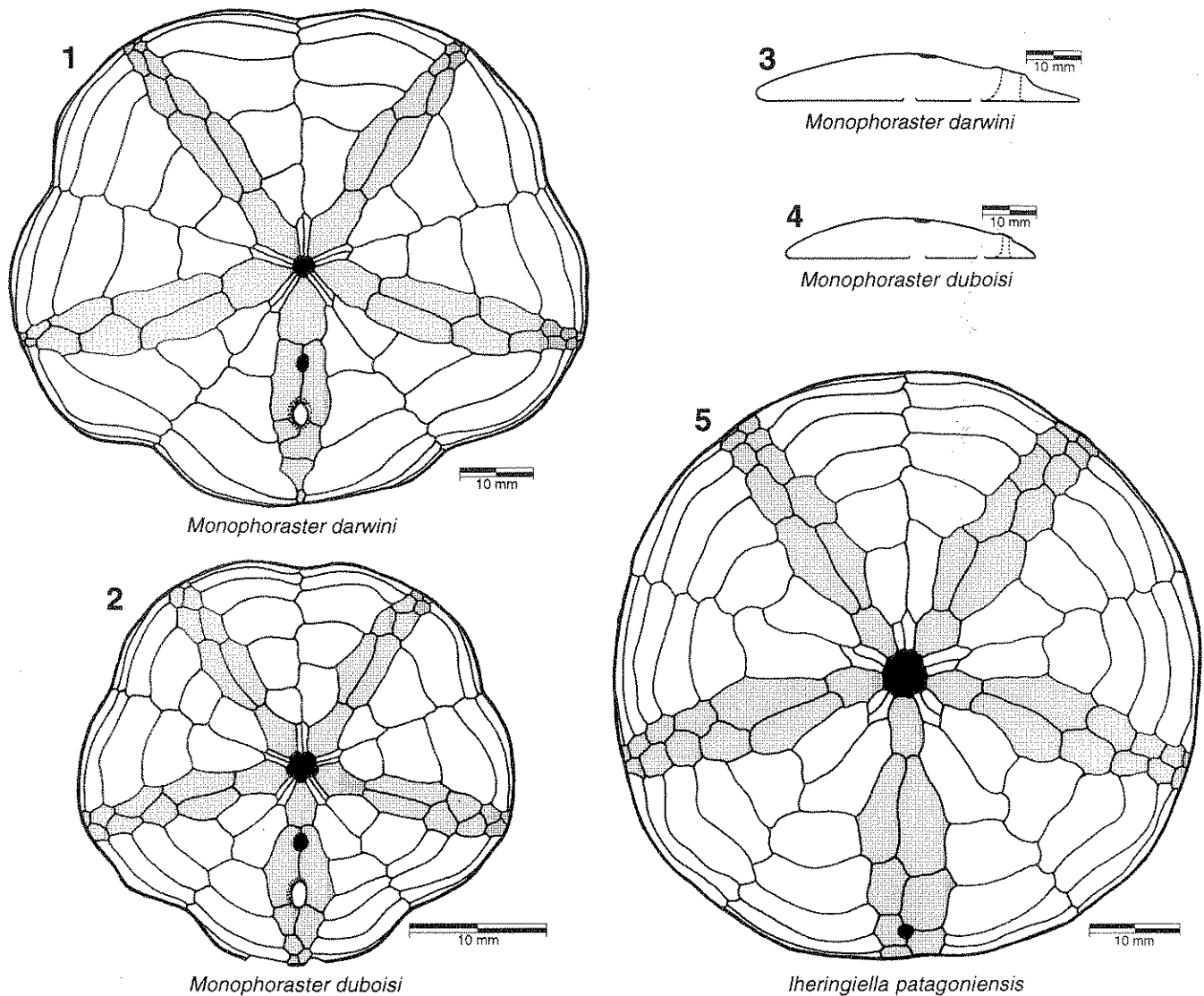
FIGURE 3—*Monophoraster* and *Iheringiella*. For *1*, *2*, and *5*, interambulacral plates shaded, peristome and periproct in solid black, anterior is at top, for *3* and *4*, anterior is to the left, apical system is in solid black, left aperture on oral surface marks position of peristome, right aperture marks position of periproct, passage of lunule from aboral to oral surface indicated by dotted lines. *1*, Plate architecture on oral surface of *M. darwini* (Desor, 1847), CASG 67875.01; *2*, plate architecture on oral surface of *M. duboisi* (Cotteau, 1884), CASG 68036.01; *3*, profile of *M. darwini* (Desor, 1847), ROM5578; *4*, profile of *M. duboisi* Cotteau, 1884, after Cotteau (1884); *5*, plate architecture on oral surface of *I. patagoniensis* (Desor, 1847), ROM 5433M.

plates very large, broadly in contact with both of the first post-basicoronal plates in all interambulacra. Ambulacral basicoronal plates only about half the length of the interambulacrals, and extremely narrow. At their adoral ends, each member of a pair of ambulacral basicoronals contributes half of a prominent projection into the peristome. Single, completely enclosed sphaeridium on the perradial suture separating ambulacral basicoronal plates. Ambulacra with the most distal plates much wider than high so that they form striplike ambital plates. Interambulacra relatively narrow and straight. The first post-basicoronal interambulacral plates are the largest of the series, approaching twice the length of the next largest plates in the series, the second post-basicoronals. Pressure drainage channels in the oral ambulacra not very deep, without conspicuous side branches. No ambulacral lunules. Anal lunule present, with an elevated ridge around aboral opening. Peripheral ballast system strongly developed, but without elements between intestine and Aristotle's

lantern. Microcanal system well-developed. Lantern extremely flattened, like that of mellitids (Mooi, 1989), teeth almost horizontal in tooth slide, lantern supports on interambulacral basicoronal plates only. Spine tubercles supporting club-shaped and miliary spines aborally, and pressure drainage channel, locomotory, miliary, and geniculate spines orally (spine types according to Telford et al., 1985).

Genus MONOPHORASTER Lambert and Thiéry, 1921

Type species.—*Monophora darwini* Desor, 1847, by monotypy of original description.

Diagnosis.—Monophorasterid sand dollars with extreme narrowing of the interambulacra at the ambitus, the interambulacra frequently becoming monoserial as they pass around the ambitus, especially in the posterior interambulacrum (interambulacrum 5); ambulacra with very shallow but distinct indentations at the point where the perradial suture meets the ambitus.

TABLE 1—Calculable lengths, widths, and width to length ratios of all known material of the three species of Amplaster, and representative specimens of Monophoraster. Chubut Province is in Argentina, all other localities are in Uruguay (see Fig. 1). Widths in italics are estimates made by doubling the distance from the center of the peristome to an undamaged lateral edge.

Species/specimen	Locality	Width (mm)	Length (mm)	Width/Length
A. coloniensis Holotype, MNA-CPO 3426	Barranca de los Loros	125	38	3.3
A. coloniensis Paratype, MMC 1516	Barranca de San Pedro	161	51	3.2
A. coloniensis MMNP 321	Cerro Bautista	137	41	3.3
A. coloniensis MMNP 507	Arroyo de las Limetas	—	—	—
A. ellipticus Holotype, FCDP 2205	El Manzeno	62	28	2.2
A. ellipticus Paratype, MNA-CPO 3425	Barranca de los Loros	90	41	2.2
A. alatus Holotype, SEGEMAR 15527	Chubut Province	—	73	—
A. alatus Paratype, SEGEMAR 15526	Chubut Province	102	69	1.5
A. alatus Paratype, SEGEMAR 15528	Chubut Province	104	69	1.5
A. alatus Paratype, SEGEMAR 15529	Chubut Province	—	—	—
A. alatus FCDP 2831	Depto. de Colonia	—	36	—
M. darwini CASG 67875.01	Chubut Province	77	66	1.2
M. darwini CASG 67875.03	Chubut Province	56	50	1.1
M. darwini CASG 67876.01	Chubut Province	70	61	1.1
M. darwini CASG 67876.02	Chubut Province	45	39	1.2
M. darwini CASG 67876.03	Chubut Province	44	38	1.2
M. duboisi CASG 68036.01	Depto. de Colonia	32	30	1.1
M. duboisi CASG 68036.02	Depto. de Colonia	24	21	1.1
M. duboisi CASG 68036.03	Depto. de Colonia	40	37	1.1

Description.—Test of medium to large size (but seldom greater than 60 mm in test length), subcircular, with shallow, smooth ambulacral indentations. Ambulacra with four or five post-basicoronal plates per column on the oral surface. Almost straight interambulacra with four or five plates per column on the oral surface. Interambulacra become very narrow as they approach the ambitus on both surfaces. In some specimens, the normally paired columns of interambulacral plates can become monoserial near the ambitus, with a single plate spanning the entire interambulacral region. Anal lunule subcircular to elongated along anterior-posterior axis, usually very small. Other characters as for the family.

MONOPHORASTER DARWINI (Desor, 1847)
Figure 3.1, 3.3

Monophora Darwini DESOR, 1847, p. 287; LAHILLE, 1896, p. 411, pls. 1–4.
Monophoraster darwini LAMBERT AND THIÉRY, 1921, p. 324; MORTENSEN, 1948, p. 419; DURHAM, 1955, p. 170, fig. 29e; DURHAM, 1966, p. U485, fig. 6a–c.

Diagnosis.—Typical *Monophoraster* in which the aboral side is relatively low, not domed, with slightly concave or straight rising slopes anterior and posterior to the apex.

Description.—Test large. Length and width measures for selected specimens in this study given in Table 1. Other features as for the family and genus.

Material examined.—BMNH E79279–84, Punta Piramides, Argentina; CASG 67876.01, Peninsula Valdés, Argentina (figured herein); CPBA 6726, 6747, 6684, 7843, 8623, 13623, 12199–12205, 13424–13432, 13434–13437, 13472–13476, 13629–13638, 13650–13655, 17910–17932, from various localities in Argentina; MCZ 3369, San Matías Bay, Argentina; ROM 5578, Puerto Pirámides, Argentina (figured herein).

Occurrence.—As in Figure 1.

Discussion.—In museum collections, *M. darwini* is the most commonly encountered of all the monophorasterids. In many of the deposits in which it is found, both juvenile and adult specimens are preserved in such excellent condition that almost all of the features known from extant lunulates can also be assessed for *M. darwini*, including minute unipores in the interporiferous zones of the petaloids.

MONOPHORASTER DUBOISI (Cotteau, 1884)
Figure 3.2, 3.4

Monophora duboisi COTTEAU, 1884, p. 341, pl. 6, figs. 9–12.
Monophora Darwini BORCHERT, 1901, p. 229, pl. 10, figs. 28–30.
Monophoraster duboisi MORTENSEN, 1948, p. 419; DURHAM, 1955, p. 170.

Diagnosis.—*Monophoraster* in which the aboral surface is convex along the entire camber.

Description.—Test of medium size (the holotype is 32.9 mm in test length and 35.4 mm in test length), seldom attaining the size of *M. darwini*. Length and width measures for selected specimens in this study given in Table 1. Other features as for the family and genus.

Material examined.—FCDP 2112, 2114, 2115, 2185, 2186, 2649, San Pedro, Departamento de Colonia, Uruguay.

Occurrence.—As in Figure 1.

Discussion.—Lambert and Thiéry (1921) thought that *M. duboisi* Cotteau, 1884, was merely a variety of *M. darwini* Desor, 1847. However, in Cotteau's (1884, pl. 6, fig. 9) figure, *M. duboisi* is high and continuously convex from anterior to posterior (Fig. 3.4). *M. darwini* has straight or even slightly concave rising slopes anterior and posterior to the apex (Fig. 3.3). In addition, the interambulacra on the oral surface are narrower at the ambitus in *M. darwini* than in *M. duboisi* (Fig. 3.1 vs. 3.2). Other characters mentioned by Cotteau (1884) and Bernasconi (1959) as differentiating these species, such as marginal thickness, peripheral lobes, and the relative dimensions of the poriferous and interporiferous zones of the petaloids, are size-dependent and not very reliable. Lunule shape distinguishes the species only at a statistical level (Martínez, 1985). Because of common usage of the name *M. darwini*, and confusion in the previous literature, all previous authors studying the Camacho Formation (e.g., Goso and Bossi, 1966; Figueiras and Broggi, 1971) mentioned the presence of *M. darwini*. However, this species is not present in the Miocene of Uruguay (see Stratigraphic Occurrence and Age of Monophorasterids, below) and all the known specimens from the Camacho Formation are in fact referable to *M. duboisi*.

Genus AMPLASTER Martínez, 1984

Type species.—*Amplaster coloniensis* Martínez, 1984, by original designation.

Diagnosis.—Monophorasterids in which the test is greatly widened, the test width always at least 1.5 times the test length.

Description.—Medium to large, flattened test (but seldom greater than 65 mm in test length), with alate (winglike) or almost knifelike outline (test width to length ratio varying from 1.5 to 3.3), indentations that correspond to ends of the ambulacra shallow or absent. Anterior paired petaloids (in ambulacra II and IV) longer than the others. Paired ambulacral plates becoming extremely elongated circumferentially as they approach the ambitus, especially in posterior paired ambulacra (ambulacra I and V). Interambulacral columns narrow, constricting slightly at the contact between basicoronal and post-basicoronal plates, except in interambulacrum 5 where the contact is usually wide. Posterior paired interambulacral columns (interambulacra 1 and 4) markedly longer than the others. Other features as for the family.

AMPLASTER COLONIENSIS Martínez, 1984
Figure 4.3–4.7

Amplaster coloniensis MARTÍNEZ, 1984, p. 506, figs. 1–2; MARTÍNEZ AND DURHAM, 1988, p. 185, fig. 1.

Diagnosis.—*Amplaster* in which the test is more than three times wider than long; petaloids in anterior paired ambulacra (ambulacra II and IV) at right angles to anterior unpaired ambulacrum (ambulacrum III); aboral ridge around anal lunule thickened; anal lunule closer to posterior edge than to apical system; peristome relatively large (feature shared with *A. ellipticus* n. sp.); interambulacral columns narrow over their entire length (character shared with *A. ellipticus* n. sp.).

Description.—Test not very long, but greatly widened and spindle- or knife-shaped. Length and width measures given in Table 1. Other features as for the family and genus.

Material examined.—Holotype MNA-CPO 3426, Barranca de los Loros, Uruguay. Paratype MMC 1516, Barranca de San Pedro, Uruguay. Additional material, MMNP 507, Arroyo de las Limetas, Uruguay (specimen figured herein, but not the stratigraphic column from which it was collected); MMNP 321, Cerro Bautista, Uruguay (figured herein).

Occurrence.—As in Figures 1 and 2.

Discussion.—Martínez and Durham (1988, fig. 2) were the first to draw the plate architecture of any member of the genus *Amplaster.* They described and illustrated supernumerary plates in an anterior paired oral interambulacrum, wide disjunctions in a posterior interambulacrum, and a single plate reaching the anterior paired interambulacral basicoronal. If accurate, these would be unique features of *A. coloniensis,* if not of clypeasteroids in general. However, re-examination of the specimen used to make the drawing in Martínez and Durham (1988), along with complete mapping of plate architectures in other specimens of *A. coloniensis,* show these details to be inaccurate due to misinterpretation of cracks in the specimen. Once the sutures are distinguished from taphonomic effects, the plate architecture is much the same as in other species of *Amplaster.*

AMPLASTER ALATUS (Rossi de Garcia and Levy, 1989)
Figures 4.1, 5.1–5.5, 6.1–6.3

Amplaster alatus ROSSI DE GARCIA AND LEVY, 1989, p. 89–92, text-fig. 1, pl. 1, figs. 1–4.
Lunulaster alatus PARMA AND MARTÍNEZ, 1994, p. 65–66.

Diagnosis.—*Amplaster* with the test width approximately 1.5 times the test length; anal lunule extremely widened and almost circular.

Description.—Test large, with prominent "winglike" extensions of the paired posterior interambulacra. Length and width measures given in Table 1. Other features as for the family and genus.

Material examined.—Five almost complete specimens: holotype SEGEMAR 15527 (figured herein); paratypes SEGEMAR 15526 (figured herein), 15528 (figured herein), 15529, all from Chubut Province, Argentina; and an additional specimen, FCDP 2831, Departmento de Colonia, Uruguay.

Occurrence.—As in Figures 1 and 2.

Discussion.—In terms of surface area, *A. alatus* is the largest of the monophorasterids. The wide lunule is clearly independent of the extreme widening of the test, because in *A. coloniensis,* the test is much wider than in *A. alatus,* but without concomitant widening of the lunule.

There is little or no support in the diagnosis or description of *A. alatus* for the erection of the new genus *Lunulaster* Parma and Martínez, 1994, to house this one species. Even the genus *Amplaster* itself is not well distinguished from *Monophoraster,* because the only unequivocal difference between the two genera rests on relative test widths. However, there is some phylogenetic significance in distinguishing *Amplaster* from *Monophoraster* (see below), and these names have also been more prominent in the literature than *Lunulaster.* There are fewer differences between *A. alatus* and the other *Amplaster* than are found among species in other clypeasteroid genera, such as *Mellita* L. Agassiz, 1841. The creation of a separate genus for *A. alatus* does nothing to improve our understanding of the phylogenetic relationships of this species to the other taxa in the Monophorasteridae. Although the phylogeny (see below) suggests that *A. alatus* is basal to the other two species in *Amplaster,* a new monotypic genus would fail to recognize this important relationship.

The discovery of a single, small specimen of *A. alatus* from Uruguayan deposits suggests that this species had a much greater geographic range than the previously known material indicated. No other monophorasterid has a greater range (Fig. 1). *Monophoraster darwini* is much better represented by material collected from a wider range of localities, but even its known range is smaller than that of *A. alatus.*

AMPLASTER ELLIPTICUS new species
Figure 4.2

Amplaster coloniensis MARTÍNEZ, 1984, p. 506, fig. 2.

Diagnosis.—*Amplaster* with the test width just over twice the test length; test outline elliptical with slight perradial indentations; aboral ridge around anal lunule not very prominent; peristome relatively large (character shared with *A. coloniensis*); interambulacral columns narrow over their entire length (character shared with *A. coloniensis*).

Description.—Test not very long, but widened and almost elliptical. Length and width measures given in Table 1. Other features as for the family and genus.

Etymology.—The species name is in reference to the elliptical outline of the ambitus.

Types.—Holotype, FCDP 2205, El Manzano, Uruguay (figured herein); paratype, MNA-CPO 3425, formerly a paratype of *A. coloniensis,* see Martínez (1984, fig. 2).

Occurrence.—As in Figures 1 and 2.

Discussion.—This species was only discovered after width to length ratios were found to fall into three well-delimited ranges, one for each of the two previously recognized species of *Amplaster,* and a third for the new taxon. Admittedly, the material is sparse. The collection of additional specimens may fill the gap in ratios between *A. ellipticus* and *A. coloniensis,* which the new species most resembles, and validity of the new taxon might then require reassessment. This similarity is great enough that
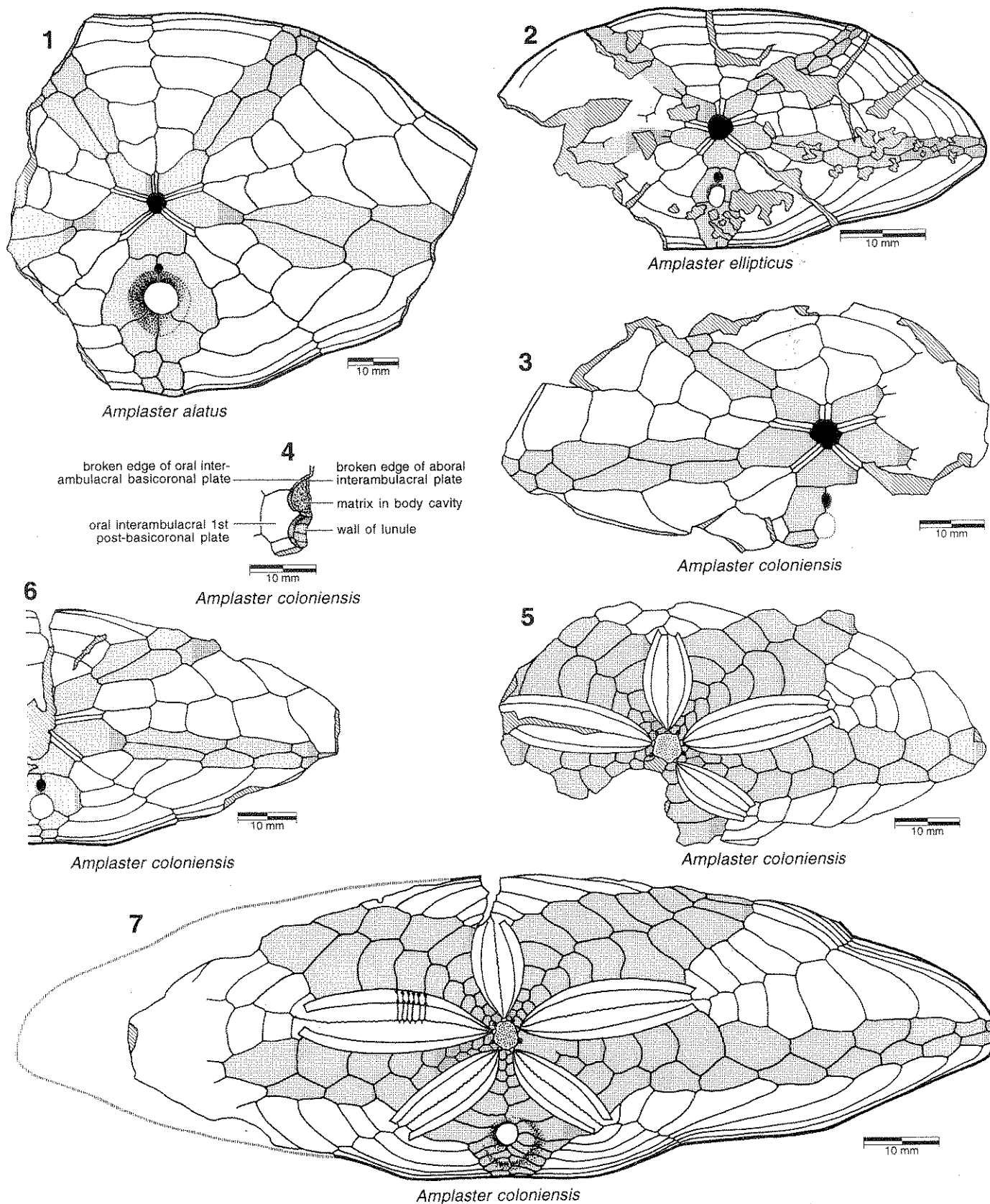
FIGURE 4—Plate architecture of *Amplaster*. Interambulacral plates shaded, broken edges and damaged regions indicated by diagonal hatching, peristome and periproct in solid black, heavier lines indicate unbroken ambitus, anterior is at top. *1*, Oral surface of *A. alatus* Rossi de Garcia and Levy, 1989, holotype SEGEMAR 15527; *2*, oral surface of *A. ellipticus* n. sp., FCDP 2205; *3*, oral surface of *A. coloniensis* Martínez, 1984, MMNP 507, corrected
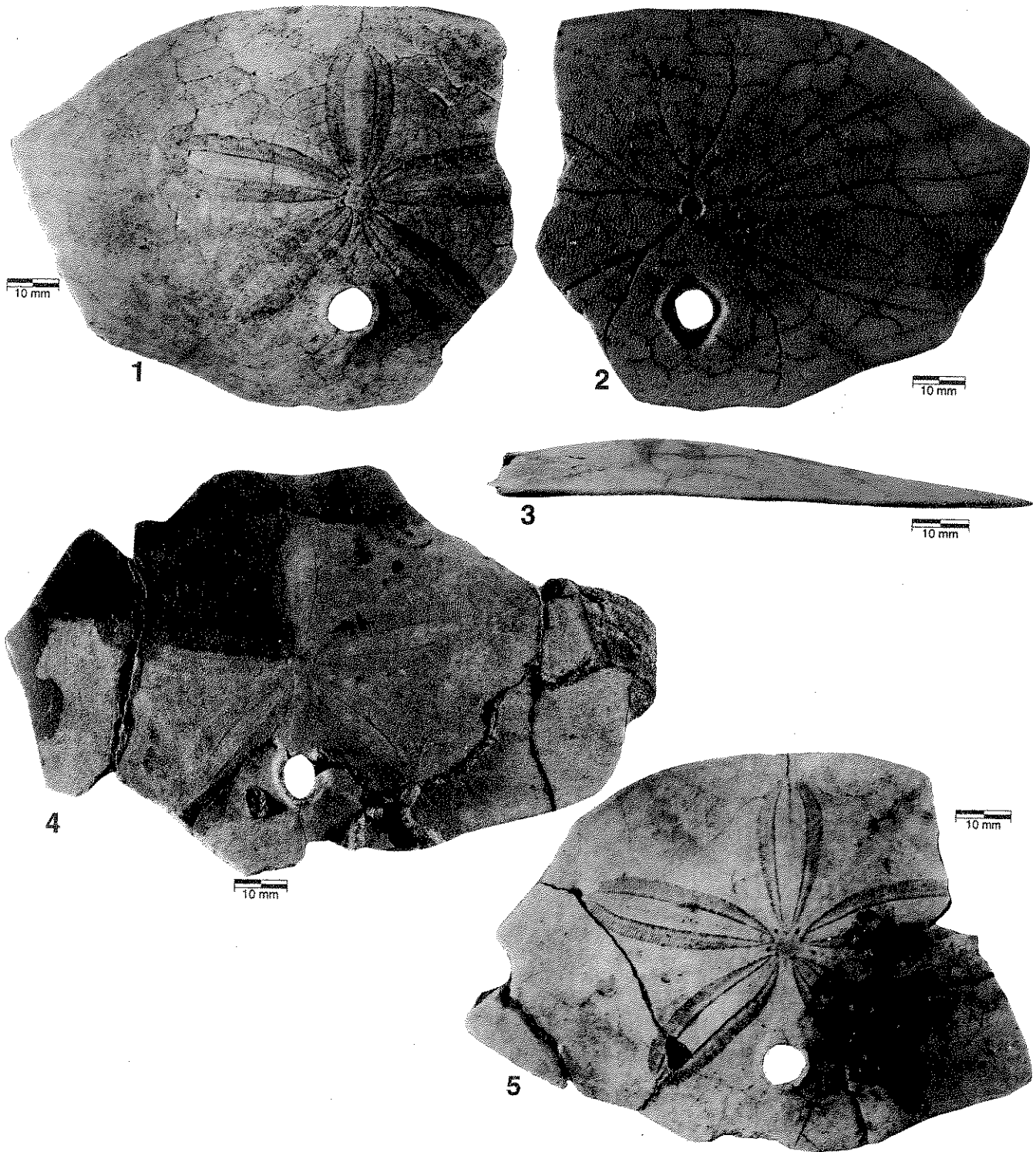
FIGURE 5—*Amplaster alatus* Rossi de Garcia and Levy, 1989. *1–3,* Holotype SEGEMAR 15527; *1,* aboral surface; *2,* oral surface; *3,* ambital view of anterior end; *4, 5,* paratypes; *4,* aboral view of SEGEMAR 15528; *5,* aboral view of SEGEMAR 15526.

plate map for specimen originally figured in Martínez and Durham (1988); *4,* oblique view of lunule wall of *A. coloniensis* Martínez, 1984, same specimen as shown in *3; 5,* aboral surface of *A. coloniensis* Martínez, 1984, MMNP 321, shaded line at left indicates reconstructed outline, details of petaloid plating indiscernible except for part of petaloid in ambulacrum IV, same specimen as shown in *3; 6,* oral surface of *A. coloniensis* Martínez, 1984, MMNP 321; *7,* aboral surface of *A. coloniensis* Martínez, 1984, MMNP 321, same specimen as shown in *6.*
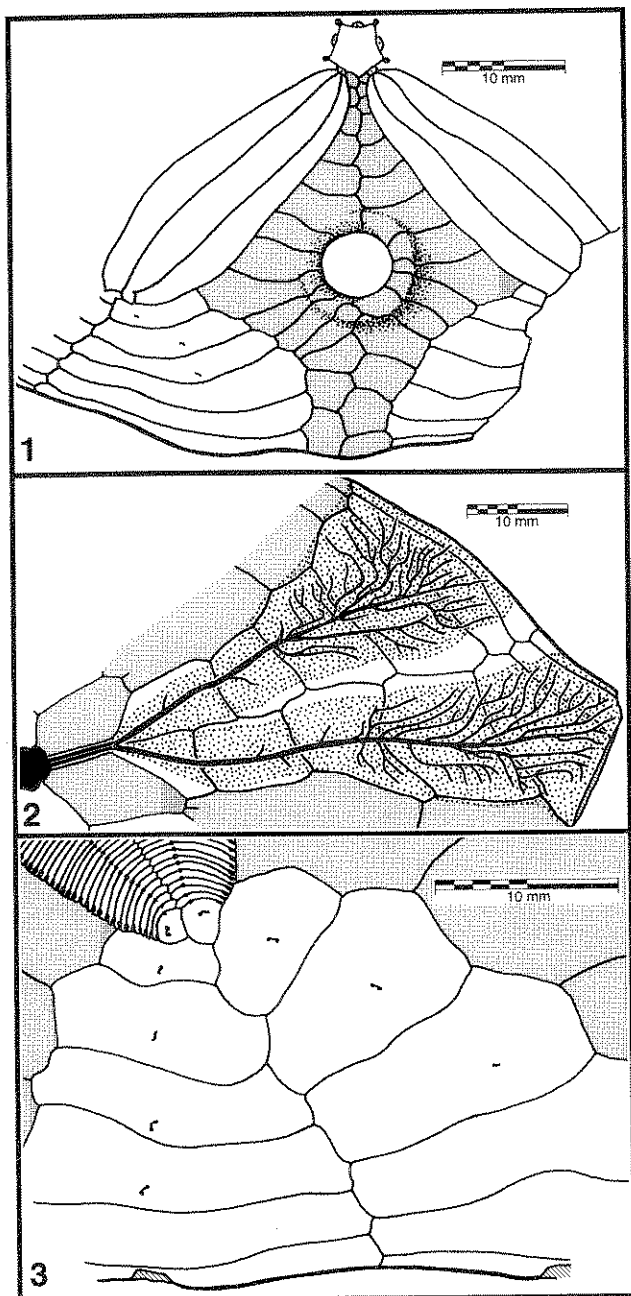
FIGURE 6—*Amplaster alatus* Rossi de Garcia and Levy, 1989, holotype SEGEMAR 15527. Interambulacral plates shaded, broken edges and damaged regions indicated by diagonal hatching, heavier lines indicate unbroken ambitus. *1*, Plate architecture on aboral surface around the anal lunule, apical system at top; *2*, food groove pattern and plate architecture in ambulacrum IV, distribution of food-gathering tube feet indicated by stippling, food grooves by heavy lines, mouth in black; *3*, trailing podia and plate architecture at end of petaloid in ambulacrum IV.

the paratype of *A. ellipticus* was previously recognized as a paratype of *A. coloniensis* (Martínez, 1984). Breakage around the ambitus could greatly alter the width to length ratio, particularly as the flaring, lateral extensions on *A. coloniensis* are thin and more fragile than the more central parts of the test. However, careful examination of both specimens shows that no significant breakage has occurred, and that the ratios are accurate for the

material attributed to the new species. Unfortunately, only the oral surface of the holotype is exposed, and the specimen was deemed too friable to prepare the aboral surface. The plate patterns were only visible after careful polishing of most of the oral surface on the specimen.

The lithology of the matrix in the two specimens of *A. ellipticus* is different. The paratype is in a gray, angular sandstone and exhibits considerable recrystallization, much like most of the material of *A. coloniensis*. The holotype of *A. ellipticus* is in a finer, beige, friable matrix with better preservation of trabecular detail in some areas because of a lower amount of recrystallization on the surface of the specimen itself. The difference in lithology also made it more difficult to recognize that the two specimens should be placed in the same species. It is impossible to say whether the differences in matrix indicate variation in habitat preference.

Apart from the width to length ratio, the paratype of the new species seems to have a less prominent ridge around the anal lunule, and slightly narrower interambulacra on the oral surface than *A. coloniensis*.

STRATIGRAPHIC OCCURRENCE AND AGE OF MONOPHORASTERIDS

Monophorasterids occur in rocks in both northern (Uruguay, northernmost Argentina) and southern (Patagonian region of Argentina) stratigraphic assemblages, as well as a locality on the Pacific coast of Chile (Fig. 1). Much of the work that has been done on these South American Tertiary strata is not well known in other parts of the world, so we have made an effort to provide comprehensive citations of this research.

Northern material from the Camacho Formation.—The Camacho Formation is one of the most highly fossiliferous units of Uruguay, and has drawn the attention of several authors since the middle of last century when Darwin (1839, 1846) and d'Orbigny (1842) made the first mention of these strata. The Camacho Formation crops out at the littoral of the Colonia and San José Departments in Uruguay. It underlies the Uruguayan coastline, reaching the western region of the Pelotas Basin, near the Uruguay–Brazil border. *Amplaster coloniensis*, a new species of *Amplaster* (described below), and *Monophoraster duboisi* are found in the Camacho Formation (Fig. 2).

The Camacho is largely made up of fine to coarse sandstones, sandy siltstones, and siltstones with the occasional thin bed of claystones (Fig. 2). Caorsi and Goñi (1958) named the unit the "Camacho Sandstones." Later, Bossi (1966) recognized it as a Formation. The Camacho Formation usually overlies the lower Oligocene?-lower Miocene? Fray Bentos Formation (Preciozzi et al., 1985; Ubilla et al., 1994), and is overlain by the Pliocene Raigon Formation or by the Pleistocene Libertad Formation (Preciozzi et al., 1985). Paleoecology and paleoenvironments of the Camacho Formation have been discussed by Sprechmann (1978), Sprechmann et al. (1994), and Martínez (1994), who suggested shallow marginal-marine deposition conditions for that unit and also identified some facies that characterized it. The monophorasterids occur in either very bioturbated sandy siltstones, interpreted as background sedimentation disturbed by bioturbating organisms that also taphonomically rearranged some of the echinoid tests, or in very fossiliferous sandstones with carbonate cement, interpreted as tempestites. The fauna of these two facies is considered parautochtonous and have the same taxonomic composition. Martínez (1994) included them in the *Chionopsis-Mactra* association that lived in and on a soft subtidal substrates. *Monophoraster duboisi* specimens are usually found in patches that might reflect original populations, although isolated specimens also occur. The specimens are found in a variety of positions, but there is some tendency for them to

be horizontal. The *Amplaster* specimens are too rarely encountered to make useful inferences about their circumstances of deposition or life habits.

Research on foraminifers (Sprechmann, 1978; Bertels, 1979; Boltovskoy, 1979), brachiopods (Manceñido and Griffin, 1988; Figueiras and Martínez, 1995), and mollusks (Martínez, 1990), indicated subtropical conditions when the Camacho Formation was deposited. The Miocene marine depositional event in Uruguay is considered a widespread transgressive-regressive cycle, known in older literature as the "transgresión entrerriana." Argentinean strata recognized as the Puerto Madryn Formation in Chubut Province (Haller, 1978; Spiegelman and Busteros, 1979), the Paraná Formation in Entre Ríos Province (Herbst and Zabert, 1987), and the subsurface Brazilian horizon described by Closs (1970) were all deposited by this "entrerriense" sea, which seems to have extended from southernmost Brazil to northern Patagonia (Camacho, 1967; Martínez, 1988, 1990). For many years, strong faunal similarities were noted between the Paraná Formation and Camacho Formation, and these data influenced the age determination of the Camacho Formation. The Uruguayan unit has been placed in the Pliocene (Kraglievich, 1928; Teisseire, 1928; Walther, 1931; Lambert, 1940; Serra, 1943; Caorsi and Goñi, 1958; Pereira de Medina, 1962; Goñi and Hoffstetter, 1964; Goso and Bossi, 1966; Francis, 1975) or in the Miocene (Closs and Madeira, 1968; Sprechmann, 1978, 1980).

Figueiras and Broggi (1971) compared the mollusks contained in the Camacho Formation with those from the Argentinean Paraná and Puerto Madryn Formations. Using the age then accepted for the latter units, they considered the Camacho Formation to be of upper Miocene age. Herbst and Zabert (1979, 1987) arrived at similar conclusions when comparing the foraminifers and ostracods of the Camacho Formation with those of the Paraná Formation. Mones (1979), Figueiras and Broggi (1985), and Martínez (1988, 1990) agreed with an upper Miocene age for this unit, but recent studies made by del Río (1988, 1989, 1991) placed the Argentinean molluskan fauna in the middle Miocene. Recent studies on mammal content from the top of the Camacho Formation at the Arazati area (Perea et al., 1985, 1989) showed that the assemblage must be placed in the Huayquerian South American land-mammal age, from the upper Miocene (L. G. Marshall et al., 1983, 1986). We continue to consider the Camacho Formation to be upper Miocene, or perhaps middle to upper Miocene.

Southern material from the Patagonia Formation.—*Amplaster alatus* was collected from the Tertiary marine sequence of the Patagonia Formation along the Atlantic central coastal area of Chubut Province, Argentina (Figs. 1, 2). The geology of this area was mapped by Franchi (1983). The marine platform sediments of the Patagonia (or "Patagoniense" or "Patagoniano") Formation (Camacho, 1979a; Stipanicic and Methol, 1972) lie above a disconformity atop the tuffs and rhyolitic tuffaceous breccias of the Sarmiento Formation (Yrigoyen, 1969), which are of an Eocene-Oligocene age (L. G. Marshall et al., 1977), and below the middle Miocene (del Río, 1988, 1992) marine sandstones of the Puerto Madryn Formation (Haller, 1978). An upper Eocene age has been suggested by the presence of species belonging to the *Venericardia* (*Venericor*) group and correlations with other molluskan faunas (Camacho, 1974, 1979b). Rossi de Garcia et al. (1980) used the presence of *Neovenericor*, a junior synonym of *Venericardia* (*Venericor*) according to Camacho (1981), to argue for an upper Oligocene age. Based on palynomorph data, Barreda (1993) favored an age of upper Oligocene to lower Miocene in the "Patagoniense" of Comodoro Rivadavia ("*Monophoraster* and *Venericor* strata" or Chenque Formation, in part), and the vertebrate fauna has been used to

TABLE 2—Matrix used in phylogenetic analysis.

Taxon	Character				
	12345	1 11111 67890	11112 12345	11112 67890	2222 1234
Basal Scutellines	00000	00000	10000	0?0?0	0000
Iheringiella patagoniensis	00000	00100	10100	0?0?0	0000
Leodia sexiesperforata	01111	00001	00001	20111	1111
Mellita quinquiesperforata	01111	00001	00001	20111	1111
Encope grandis	01011	00001	00001	10111	1011
Monophoraster darwini	01101	11100	10210	11101	1011
Monophoraster duboisi	01101	11100	10210	11101	?011
Amplaster coloniensis	111?1	11110	11100	11101	?011
Amplaster alatus	11101	11100	10100	11101	1011
Amplaster ellipticus	111?1	11110	11100	11101	?011

suggest a Miocene age (Pascual and Odreman Rivas, 1973). The *A. alatus* specimens were collected from tuffaceous fine-grained sandstones that overlay the very fossiliferous yellowish tuffs containing abundant remains of bivalves, echinoids, whale vertebrae, and selachian teeth (Fig. 2). These outcrops occur at Cañadón Isla Escondida and in the proximity of the homonymous Estancia, 5 km north of Punta Lobos (inset, Fig. 1).

Monophoraster darwini is unknown in Uruguay and northern Argentina, where *M. duboisi* is the only *Monophoraster* found (Fig. 1). However, *M. darwini* is frequently collected, sometimes in large numbers, from Argentinian sites in Patagonia. It is perhaps best known from coastal localities in Chubut Province such as Península Valdés, where it occurs in the Puerto Madryn Formation, considered to be middle Miocene on the basis of bivalve faunas (del Río, 1992). Another form of *Monophoraster* presently identified as *M. darwini* but possibly representing a new species (at the time of writing, too little is known of this form to name a new taxon), is also known from the Chenque Formation in the "Lower Section" of the "*Monophoraster* and *Venericor* strata," considered Oligocene to Miocene (Barreda, 1993; Palamarczuk and Barreda, 1992; Bellosi, 1990), or perhaps upper Eocene by mollusk taxa such as *Venericardia* (*Venericor*) (Camacho, 1974).

Monophoraster darwini is also found in the Gran Bajo del Gualicho Formation in the Río Negro Province of Argentina, suggested to be Oligocene to Miocene in age (Lizuain Fuentes and Sepúlveda, 1979) and in the Chenque Formation near Comodoro Rivadavia, also in Chubut Province. The latter occurrence appears to represent the known southern limit of *M. darwini* (Fig. 1). The "Upper Section" of the "*Monophoraster* and *Venericor* strata" in which the monophorasterids are found in the Chenque Formation appear to be upper Oligocene to Miocene or perhaps even upper Eocene according to the presence of the bivalve *Venericardia* (*Venericor*) (Barreda, 1993; Bellosi, 1990; Palamarczuk and Barreda, 1992).

Western material from Chile.—Larrain (1984) recorded *Monophoraster darwini* from the Eocene of coastal Chile (Fig. 1). The stratigraphy and correlation of the rocks in which these specimens were found is imperfectly known, but Larrain (1984) suggests that they might be as old as the Eocene.

CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

Character analysis is pivotal to any phylogenetic analysis. Therefore, we provide below a list of the characters numbered to correspond with the matrix in Table 2. The list includes a description of the feature with figure references, and the states (in square brackets) recognized for the purposes of the analysis of the Monophorasteridae. When the state of the character was not discernible in any of the material examined, it was coded with a question mark in the matrix.

1) Test outline.—Almost all clypeasteroids are discoidal (as wide as long), or slightly elongate. Some specimens of *Monophoraster* can be slightly wider than long, but are generally closer to being discoidal (Fig. 3). All species of *Amplaster* are extremely widened, and the test width can be more than three times the length (Figs. 4, 5). In some scutelline taxa, such as those in the genus Eoscutellidae Durham, 1955, the test can be significantly wider than it is long. These taxa never attain the extreme condition seen in *Amplaster.* The eoscutellids in particular are so different in plate architecture and other features from all members of the mellitid plus monophorasterid clade that it is untenable to suggest that the widened test in eoscutellids is homologous to that in *Amplaster.* [0 = discoidal or elongate; 1 = widened]

2) Test camber.—Relative to their overall size, most basal scutellines tend to be quite high and continuously arched from anterior to posterior edge. Mellitids and monophorasterids are very low domed relative to their test length. Although there are some non-lunulate (such as abertellids) and unrelated lunulate (such as the astriclypeids) scutellines with fairly low tests, the most basal forms of these clades do not exhibit the extreme flattening of the mellitids and monophorasterids. There appears to be a distinctly higher camber in *Iheringiella* that sets it apart from the lunulate forms. [0 = high-domed, 1 = very flat]

3) Ambitus.—Mellitids and monophorasterids have sharply defined, thin edges, particularly along the posterior part of the ambitus (Fig. 3.3, 3.4). *Iheringiella* is thick-edged, much like early scutelline taxa. [0 = thick and rounded, 1 = thin and sharp]

4) Intestine position.—In all scutellines, with the exception of the Mellitidae, the intestine loops anteriorly on the right side of the test, and turns back posteriorly, all within a cavity completely contiguous with the rest of the coelom (Mooi, 1989, fig. 21g). In mellitids, the intestine is separated from the rest of the coelom by a well-defined wall of the peripheral ballast system (see Character 5, below). Therefore, the intestine lies in a channel through the peripheral ballast system (Mooi, 1989, fig. 21h). [0 = not within peripheral pillars, 1 = within peripheral pillar system]

5) Peripheral ballast system.—In virtually all clypeasteroids, there is an internal series of calcite pillars or vertical sheets that extend from the "ceiling" to the "floor" of the coelom between the aboral and oral surfaces. These constitute the peripheral ballast system (sensu Mooi, 1987, 1989). In basal scutellines, this system is relatively diffuse and coarsely expressed as distinct cylindrical pillars and walls. In mellitids and monophorasterids, the peripheral ballast system is extremely dense, and not easily subdivided into pillars and walls. It has a spongy appearance, and is penetrated by an anastomosing network of microcanals (Mooi, 1989, fig. 21g, 21h). [0 = simple and without microcanals, 1 = with complex microcanal system]

6) Ambulacral basicoronal plates.—Ambulacral basicoronal plates are not extremely variable in shape and size throughout the clypeasteroids. They are always shorter than the interambulacral basicoronals, and usually trapezoidally or rectangularly blocklike (Fig. 3.5). In the monophorasterids, they are elongated and very narrow (Figs. 3, 4). [0 = short and rectilinear, 1 = long and narrow]

7) Interambulacral basicoronal plates.—These plates are always larger than, but seldom exceed twice the length of individual ambulacral basicoronals. In *Iheringiella*, notable for the size of its interambulacral basicoronals, they are still less than twice the length of the longest ambulacral basicoronals (Fig. 3.5). However, in *Monophoraster* and *Amplaster,* the interambulacral basicoronals are greatly enlarged. They can be twice the length of the ambulacral basicoronals, and many times their surface area (Figs. 3, 4). [0 = small, 1 = enlarged]

8) Interambulacral first post-basicoronal plates.—In most clypeasteroids, the first post-basicoronal interambulacral plates (immediately distal to the basicoronals) are about the same dimensions as the plates more distal to them. In *Iheringiella, Amplaster* and *Monophoraster,* the first post-basicoronal plates are greatly elongated, and much longer than any other plates in the entire interambulacral column (Figs. 3, 4). [0 = not longer than others in series, 1 = longer than others in series]

9) Peristome size.—Relative to basicoronal size, the peristome can seem quite large in taxa such as *Iheringiella* (Fig. 3.5) and a few other clypeasteroids, notably laganines. However, in the vast majority of clypeasteroids, particularly scutellines, the peristome is relatively small. Neither these taxa nor *Iheringiella* have as large a peristome as *Amplaster coloniensis* or *A. ellipticus.* The size of the basicoronals in these taxa tends to minimize the impression of a large peristome (Fig. 4.2, 4.3). However, further investigation and the collection of appropriate quantitative data unavailable at this time might undermine the unique homology implied between *A. coloniensis* and *A. ellipticus.* [0 = relatively small, 1 = relatively large]

10) Periproct position.—The position of the periproct is usually stated as supra-, infra-, or submarginal (Durham, 1955, 1966). Because of the amount of variation within taxa, this terminology is inadequate for evaluating putative homologies. Few works have concentrated on the position of the periproct with respect to the plate architecture of the test, but accurate maps showing the plates in which the periproct is in contact reveal useful homologies. Although the periproct can occur in between the first pair of posterior post-basicoronals (for example, in protoscutellids and the monophorasterids), it has long been recognized that only in the mellitids is the periproct in contact with the basicoronal plate (Kier 1963, 1972). In some members of the genus *Encope* L. Agassiz, 1841, the periproct has moved slightly posteriorly, and is not always in contact with the basicoronal. However, the basal members of the *Encope* clade have the periproct in contact with the basicoronal, so this posterior movement of the periproct away from the basicoronal is a secondarily derived condition. [0 = not in contact with basicoronal, 1 = just touching or indenting basicoronal]

11) Continuity of paired oral interambulacral columns.—The interambulacra on the oral surface are continuous in the earliest of the scutellines and *Iheringiella* (Fig. 3.5). In later taxa, such as the lunulates considered here, there is a separation between the basicoronal and the first pair of post-basicoronals in the paired interambulacra 1, 2, 3, and 4 (Figs. 3, 4). [0 = discontinuous, 1 = continuous, 2 = partially]

12) Shape of paired oral interambulacral columns.—In almost all scutellines, the interambulacra on the oral surface are narrower than the ambulacra, even at their widest point. In monophorasterids, the interambulacra tend to narrow somewhat near the ambitus (see Character 13, below). However, the condition seen in *A. coloniensis* and *A. ellipticus* is extreme, in which the interambulacra on the oral surface are very narrow for their entire length (Fig. 4.2, 4.3–4.6). [0 = not narrow, 1 = very narrow]

13) Interambulacral columns at ambitus.—In virtually all scutellines, the interambulacra widen just distal to the basicoronal plate, and then maintain their width or continue to widen as they approach the ambitus. However, in certain taxa, such as the monophorasterids and *Iheringiella,* the interambulacra narrow to varying degrees at the ambitus (Figs. 3.5, 4). In the genus *Monophoraster,* the interambulacral columns are extremely attenuated, particularly the posteriormost interambulacral column (Fig. 3.1, 3.2). In some specimens, the posterior interambulacrum can be represented right at the ambitus by only a single, tiny plate,

or very narrow monoserial column (Fig. 3.1). [0 = wide, 1 = attenuated, 2 = extremely attenuated]

14) Ambulacral indentation at ambitus.—In the genus *Monophoraster*, there are conspicuous indentations marking the point at which the perradial sutures intersect the ambitus (Fig. 3.1, 3.2). These are broad concavities in the ambitus that could be considered precursors to the ambulacral notches of certain mellitids. Mellitid notches could be considered plesiomorphically open versions of the completely closed ambulacral lunules found in other mellitids (see Character 15, below). However, there is ontogenetic and phylogenetic evidence to suggest that the open notch at the ambitus found in certain adult mellitids in the genus *Encope* is actually a derived condition, and not an intermediate condition between the indentations found in *Monophoraster* and the complete lunules of crownward mellitids. In addition, the fact that not all members of the Monophorasteridae have these indentations strongly suggests that the indentations are unique to the genus *Monophoraster*, and have therefore been scored accordingly. [0 = absent, 1 = present]

15) Festooned ambulacral lunules.—Only among the mellitids do we find festooned ambulacral lunules or notches (sensu Mooi, 1987). Ambulacral lunules are known in certain other scutellines, such as *Scutaster* and the astriclypeids. The phylogenetic position, and therefore the homologies of the lunules of *Scutaster*, a poorly known fossil taxon, is difficult to assess and is beyond the scope of the present analysis. The cross-linked ambulacral lunules of the astriclypeids are not homologous with the festooned lunules of mellitids (Mooi, 1987). Notches ("open" lunules) are ambulacral lunules that form close enough to the ambitus that the ambitus is unable to close over the distal part of the notch to form a closed lunule. Notches, known in certain members of the genus *Encope*, and a single, unnamed fossil species of *Mellita* are derived from festooned lunules, and are not scored separately in this analysis. [0 = no lunules or notches, 1 = lunules or notches present, at least in paired ambulacra]

16) Anal lunule.—All mellitids, *Monophoraster* and *Amplaster* have a distinct anal lunule in the posterior interambulacrum. This type of lunule is completely unknown in any other echinoid. The monophorasterid lunule is constructed of cross-linked sutures (Fig. 4.4), just as it is in mellitids. The anal lunule can be short (Figs. 3.1, 3.2, 4.1–4.3, 4.6, 4.7, 5, 6.1, 8.6–8.10), or long and slotlike (Fig. 8.3–8.5). [0 = absent, 1 = present but short, 2 = present and slotlike]

17) Ridge around anal lunule.—In *Monophoraster* and *Amplaster*, there is a conspicuous, sharply-defined ridge around the aboral edge of the anal lunule (Figs. 4.7, 5.1, 5.4. 5.5, 6.1). In some mellitids, notably in the genus *Encope*, there is occasionally a ridge around the anal lunule, but it is never as well developed as in monophorasterids. This character cannot be assessed in the forms which lack the lunule entirely (*Iheringiella* and basal scutellines). [0 = absent, 1 = present]

18) Ambulacral pressure drainage channels.—Pressure drainage channels (see Telford et al., 1985) are strongly developed in mellitids. They are also surprisingly well developed in *Monophoraster* and *Amplaster* (Fig. 7.2, 7.3), in spite of the absence of ambulacral lunules with which the channels are associated in mellitids. However, they are completely absent in basal scutellines and *Iheringiella* (Fig. 7.1). Pressure drainage channels are also prominent in many species of astriclypeid (not represented in the matrix), and it is unknown whether these channels are homologous with those of mellitids and monophorasterids. Present phylogenetic evidence suggests that they are not, but there are no morphological or developmental data to support this. [0 = absent, 1 = present]

19) Anal lunule pressure drainage channel.—In spite of its overall similarity to the pressure drainage channels found in the paired ambulacra, the pressure drainage channel in the posterior interambulacrum associated with the anal lunule appears to be independently derived. This is to be expected, given that the anal lunule also exhibits a separate evolutionary history from other types of lunules. The pressure drainage channel around the anal lunule is well developed in mellitids. It does not occur in monophorasterids, although they have well-developed ambulacral pressure drainage channels (see Character 18, above). [0 = absent, 1 = present]

20) Food groove branching.—With only a few demonstrably derived exceptions, food grooves of scutellines bifurcate adjacent to the distal portion of the ambulacral basicoronals. However, there is considerable variation in the degree to which the secondary branching is developed. In mellitids, *Monophoraster*, and *Amplaster*, the food groove branches are complex, reaching virtually every part of the field of food-gathering, barrel-tipped podia (Fig. 6.2). In spite of superficially similar primary branching of the food grooves figured for *Iheringiella* by workers such as Durham (1955, fig. 2D), the secondary branching is not as complex as in monophorasterids. [0 = simple, 1 = complex]

21) Petaloid non-respiratory podia.—The assessment of this character can be extremely difficult in most fossils, particularly as it relies on the ability to demonstrate the absence of minute non-respiratory podial unipores. However, successful searches on exceptional specimens of *Iheringiella* have shown how easy it is to detect these unipores even in fossils. Similar searches on even better preserved material of *Monophoraster darwini* and *Amplaster alatus* have failed to turn up unipores in the petaloids, suggesting that these taxa have lost the non-respiratory podia in the petaloids, as have the mellitids (Mooi, 1986, 1989). Material of other *Monophoraster* and *Amplaster* species was not adequate to assess this character. [0 = present, 1 = absent]

22) Number of trailing podia.—Trailing podia (sensu Mooi, 1987, 1989, fig. 28) are very well developed and numerous in virtually all scutellines, including monophorasterids (Fig. 6.3). They are reduced to only one or two at the end of each respiratory pore pair column in *Leodia* Gray, 1851, and *Mellita*. [0 = many, 1 = few]

23) Geniculate spine fields.—Geniculate spines are associated with fields of barrel-tipped podia (sensu Mooi, 1986), and it would appear that these two features are tightly correlated. Because of lack of independence from the expression of barrel-tipped podia, only the presence or absence of geniculate spine fields is coded. In addition, the spine fields are easier to assess in fossils (see analysis in Fig. 7). In some specimens of *Monophoraster darwini*, patches of spines on both oral and aboral surfaces are preserved in situ. Sand dollar spines that are well enough preserved to provide useful phylogenetic information are extremely rare, but in the case of *M. darwini*, enough is known about these spines (Fig. 7.5) to say with confidence that there are strongly developed geniculate and locomotory spine fields. Geniculate spines (sensu Mooi, 1987, 1989, fig. 33b) are extremely prominent on the oral surfaces of living mellitids. Analysis of spine tubercle size distribution shows that geniculate spine fields were also present in monophorasterids, but not *Iheringiella* (Fig. 7). [0 = absent or poorly developed, 1 = greatly expanded]

24) Locomotory spine fields.—In spite of an identical coding pattern, this character is known to be independent from Character 23 because locomotory spines can be well developed in taxa that lack prominent fields of geniculate spines. Analyses of spine size distributions on the oral surface of fossil taxa, as well as direct observation of preserved spines (Fig. 7.5) show that *Monophoraster* and *Amplaster* had the mellitid condition of well-differentiated locomotory spine fields (Figs. 7.2, 7.3), but
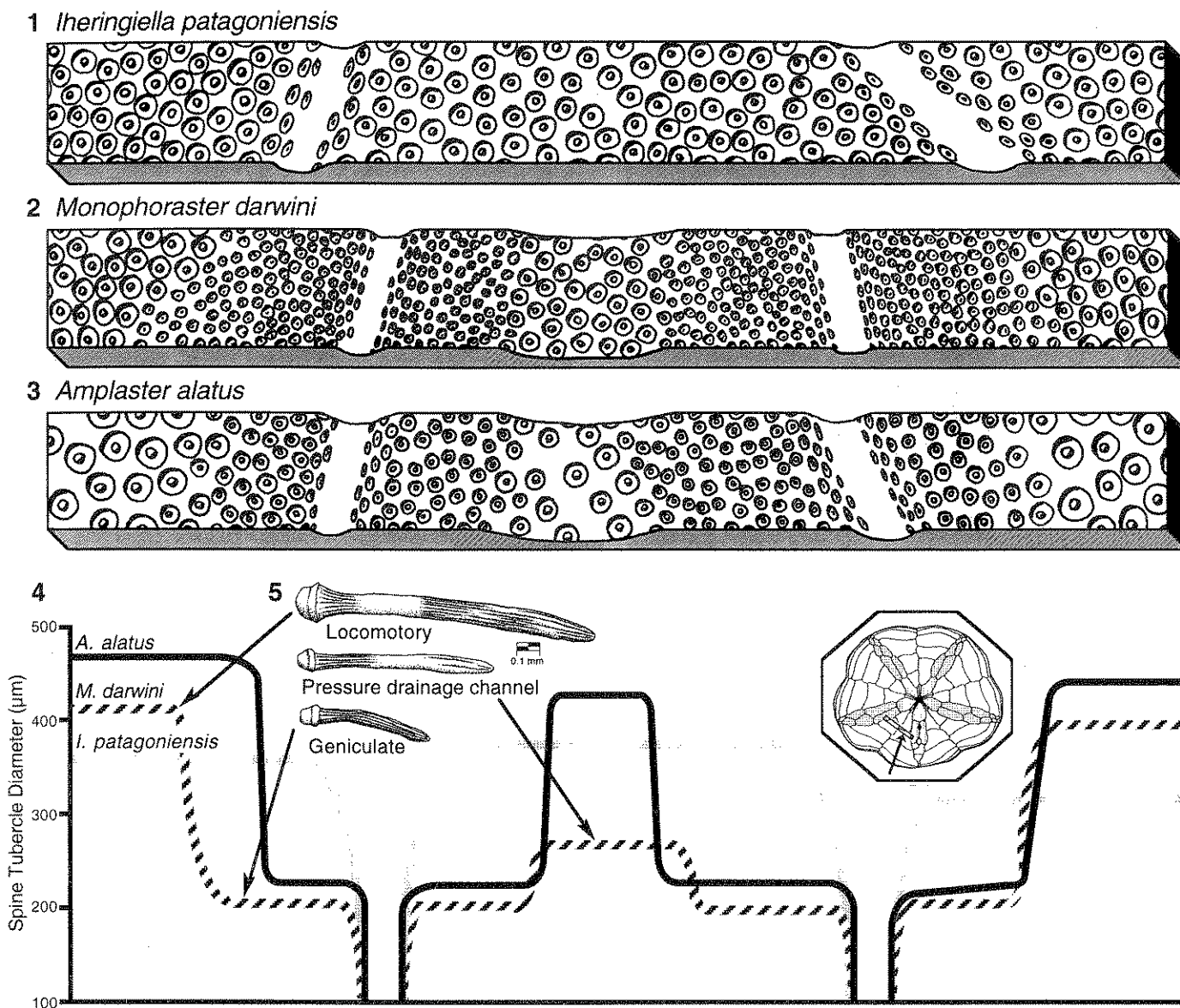
1 *Iheringiella patagoniensis*

2 *Monophoraster darwini*

3 *Amplaster alatus*

FIGURE *7*—Tubercle size distributions and spines across ambulacrum I in *Monophoraster, Amplaster,* and *Iheringiella. 1–3,* Tuberculation patterns from 20 × 2 mm region indicated in boxed area (arrow) of octagonal inset; *1, I. patagoniensis* (Desor, 1847), ROM 5469M; *2, M. darwini* (Desor, 1847), CASG 67876.01; *3, A. alatus* Rossi de Garcia and Levy, 1989, holotype SEGEMAR 15527; *4,* schematic graphs of tubercle size changes from left to right for the specimens illustrated in *1–3; 5,* examples of three spine types drawn by camera lucida (some surface details lacking due to preservation) from the oral surface of *M. darwini,* BMNH E79279–84, with arrows indicating tubercle regions in which they were found.

that *Iheringiella* did not (Fig. 7.1). [0 = not well-differentiated, 1 = in distinct fields]

RESULTS OF PHYLOGENETIC ANALYSIS

The phylogeny was produced with the aid of the computer package Phylogenetic Analysis Using Parsimony (PAUP*), version 4.0b1 (Swofford, 1998) performed on the matrix given in Table 2. Because only ten taxa were included in the analysis, we were able to run an exhaustive search (DELTRAN optimization) on a Macintosh equipped with a PowerPC chip in approximately 0.05 seconds. This produced a single shortest tree 29 steps in length, with a consistency index of 0.897, retention index of 0.932, and rescaled consistency index of 0.835. A bootstrap search using 100,000 iterations was run, yielding the bootstrap percentages given in Figure 8. We include bootstrap values

only to provide a rough indication of the relative robustness of the different nodes without implying statistical significance. The analysis reveals that the matrix contains little homoplasy, and there is sufficiently little congruence among homoplastic characters that a relatively strong phylogenetic signal remains even when the actual number of characters supporting a node is low.

The analysis unequivocally demonstrates the monophyly of the Monophorasteridae when the non-lunulate, *Iheringiella,* is excluded from the family. Attaching *Iheringiella* to the base of the Monophorasteridae adds at least six steps to the tree. Only two characters, the elongate first post-basicoronal plates in the interambulacra, and the narrowing of the interambulacra at the ambitus, can be used to place *Iheringiella* in the Monophorasteridae. The phylogeny also supports the monophyly of the Mellitidae proposed by workers such as Mooi (1987) and Telford
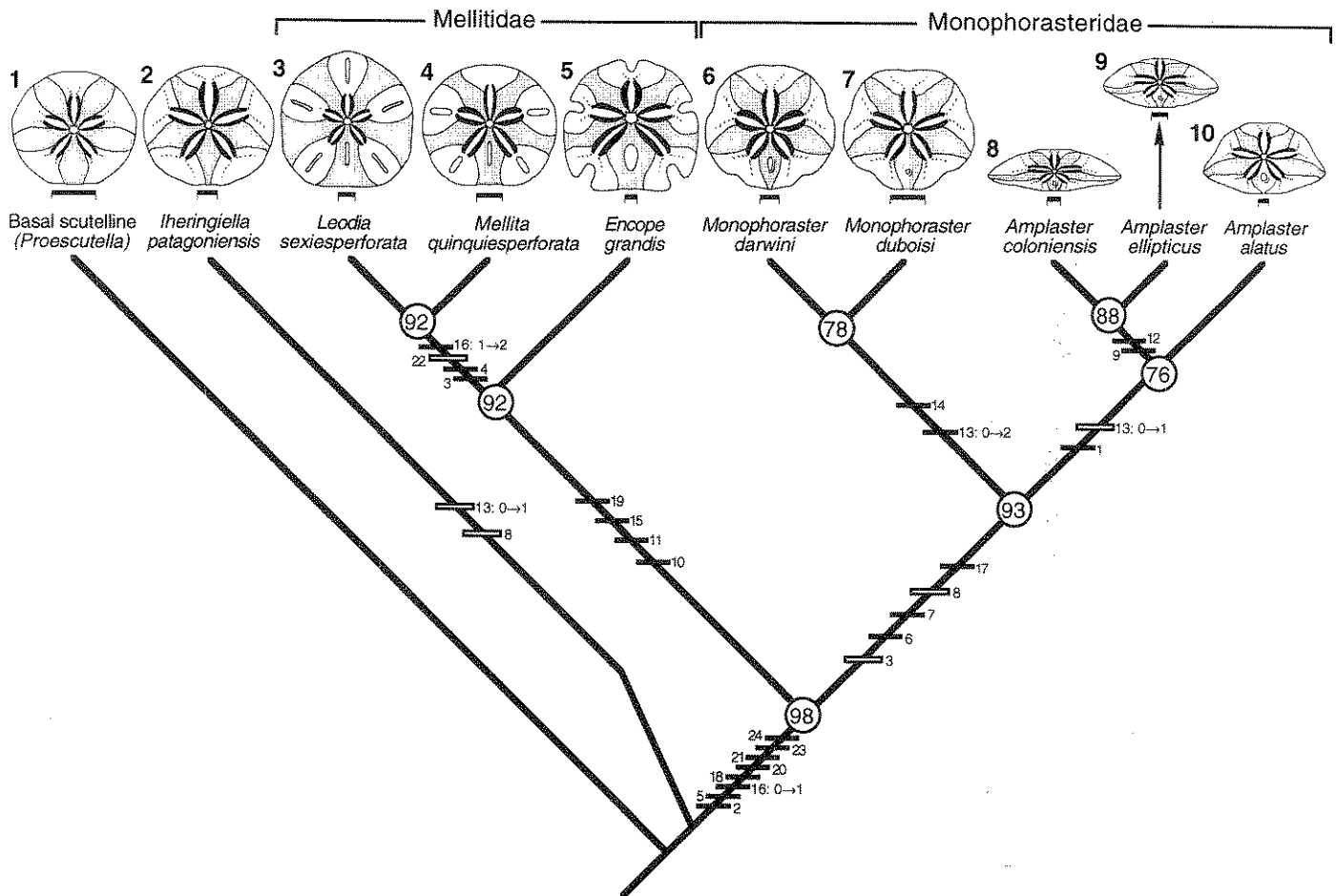
FIGURE 8—Phylogeny of the Monophorasteridae and its immediate outgroups, with figures of terminal taxa. Interambulacra are shaded, petaloids are in black, and scale bars are 10 mm long. Circled numbers at nodes are bootstrap percentages for 10,000 replicates. Solid bars indicate non-homoplastic character changes, open bars indicate homoplastic character changes. Character numbers correspond to those used in the text. All changes are from 0 to 1 unless otherwise noted. See text for description of tree and parameters. *1–10*, Aboral surfaces of representatives of terminal taxa; *1, Proescutella cailliaudi* (Cotteau, 1861), NMNH 438178, representing basal scutellines (see text); *2, Iheringiella patagoniensis* (Desor, 1847), MCZ 2496; *3, Leodia sexiesperforata* (Leske, 1778), NMNH E36424; *4, Mellita quinquiesperforata* (Leske, 1778), after Mooi and Harold (1995); *5, Encope grandis* L. Agassiz, 1841, after Durham (1966); *6, Monophoraster darwini* (Desor, 1847), ROM 5578; *7, M. duboisi* Cotteau, 1884, after Bernasconi (1959); *8, Amplaster coloniensis* Martínez, 1984, after Martínez (1984); *9, A. ellipticus* n. sp., after Martínez (1984); *10, A. alatus* Rossi de Garcia and Levy, 1989, reconstructed from type material as redescribed herein.

(1988). Many features found in monophorasterids and mellitids, including the greatly flattened test, complex peripheral ballast system, anal lunule, pressure drainage channels, periproct between the first pair of post-basicoronal plates in interambulacrum 5, highly branched food grooves, absence of accessory podia in the interporiferous zone of the petaloids, and strongly developed geniculate and locomotory spine fields (Fig. 7) exclude *Iheringiella* from this clade of lunulate sand dollars. The relationship of *Iheringiella* to other, more basal sand dollars awaits further phylogenetic analysis of the entire suborder Scutellina. At this point we can, with some confidence, reject Durham's (1955, 1966) placement of *Iheringiella* within the Monophorasteridae and hereby remove it from this family.

Amplaster and *Monophoraster* are both monophyletic (Fig. 8), although one of the characters supporting the latter, the presence of ambulacral indentations, could be subject to some reinterpretation in further analyses (see Discussion, below). However, the second character, the extreme attenuation of the interambulacra at the ambitus, is unique to this genus. *Amplaster* is monophyletic and instantly recognizable on the basis of the extreme widening of the test.

DISCUSSION

The strangeness of Amplaster.—There are several scutelline taxa in which the test width exceeds test length. These include the eoscutellids. However, members of the genus *Amplaster* (*A. ellipticus* and *A. coloniensis* in particular) have the greatest width to length ratios of any known echinoids. The functional significance of this morphology is poorly known. Given that it is only fossil groups in which the extreme widening is manifested, experimental approaches will probably have to be restricted to some forms of *Mellita*, in which the test is only slightly wider than it is long.

However, studies on the "podial particle picking" mechanism described for sand dollars (Telford et al., 1985) suggest that extreme widening of the test is related to feeding. Sand dollars crawl slowly on the sandy bottom, gathering food by picking up particles from the substrate over which they pass using their fields of barrel-tipped podia (Mooi, 1986). Organisms in and on the sand grains are manipulated towards the mouth along the food grooves, and then exposed and/or macerated by the crushing action of the Aristotle's lantern. Fresh food materials are

encountered as the sand dollar moves forward. The number of fresh grains encountered by the barrel-tipped podia can be dramatically increased by increasing the width of the test, relative to the overall size of the sand dollar. By doing so, *Amplaster* might have enhanced the rate at which new particles were encountered per unit surface area of the podial field. This in turn increased the ratio of newly encountered, and presumably higher-quality food particles to those that had already been picked over by podia on more posterior parts of the test.

Phylogeny and first appearance of monophorasterids.—The many works dealing with South American stratigraphy cited above reveal some difficulties in developing definitive data on times of origin for the various species in the Monophorasteridae. However, the general suggestion from the literature is that monophorasterids originated in epeiric seas of South America perhaps as early as the upper Eocene or lower Oligocene, and diversified until the upper Miocene, when they became extinct. Because sister taxa are of equal ages, the phylogeny suggests that the divergence time of *Monophoraster* and *Amplaster* must be at least as early as the earliest taxon, likely *M. darwini.* Estimates place *M. darwini* in strata as old as the upper Eocene and as young as the Miocene. It is difficult to believe that *M. darwini* existed unchanged from the Eocene to the Miocene (Mooi, 1989), and more information is required on some of the formations from which *M. darwini* has been recorded to resolve this problem. If monophorasterids originated in the upper Eocene, it is to be expected that mellitids also had their origins at this time, although the fossil record has yet to support this conclusion. Interestingly, the most "extreme" members of *Amplaster, A. ellipticus* and *A. coloniensis,* are the most recently diverged taxa in the phylogenetic analysis. This corresponds well with the overall impression from the fossil record, because *A. alatus* is known from strata that appear to be upper Oligocene or lower Miocene at the latest, whereas *A. ellipticus* and *A. coloniensis* occur in middle to upper Miocene rocks of the Camacho Formation.

Phylogeny and scenarios for the evolution of New World lunulates.—The monophorasterids have usually been considered closely related to the Mellitidae (Durham, 1955, 1966; Smith and Ghiold, 1982; Mooi, 1987; Telford, 1988). The present work represents strong cladistic support for this supposition because there is clear evidence that the Monophorasteridae is the sister group of the Mellitidae. Monophorasterids can therefore be used to root trees that explore the relationships among taxa within the Mellitidae. The monophorasterids, although possessing a number of synapomorphies suggesting a significant amount of evolution within the clade, also illustrate a variety of characteristics that one would predict to exist in forms basal to the large and highly diverse clade of mellitids. These include the absence of ambulacral lunules, lack of a wall between the intestine and the Aristotle's lantern, a periproct that never contacts the interambulacral basicoronal, continuous interambulacra, and lack of a pressure drainage channel around the anal lunule. Therefore, although they possess conspicuous specializations of their own, monophorasterids display morphologies intermediate between the highly specialized mellitids and more basal scutellines. The presence of ambulacral indentations in *Monophoraster* could be a precursor to the ambulacral notches that characterize some of the earliest mellitids, instead of an apomorphy of *Monophoraster.* In this scenario, their apparent lack in *Amplaster* could be product of the extreme widening of the test, which could make the indentations harder to detect.

These and other attributes have been used to develop scenarios for the origin and evolution of New World sand dollar clades (Seilacher, 1979), notably the lunulate forms. Unfortunately, these scenarios also lacked a cladistic basis, and some of the conclusions overreached the available data. Seilacher (1979, p. 219) concluded that the scutellines "originated in the Caribbean," and that "a southeastern branch expanded to Argentina, where the first immigration wave (Monophorasteridae with only one lunule) later was replaced by, or evolved into, the Mellitidae with multiple lunules," Durham (1955) felt that *Monophoraster* could be derived from *Iheringiella,* and later (Durham, 1966) derived mellitids directly from the Protoscutellidae, with the monophorasterids only distantly related to mellitids.

In showing the most recent common ancestry of monophorasterids and mellitids, the present work is widely divergent from the phylogenetic hypothesis of Durham (1966, fig. 356). Although monophorasterids and mellitids are sister groups, there are no known synapomorphies that would put protoscutellids in a sister group to this clade to the exclusion of other scutellines. Therefore, we cannot support Durham's (1966) derivation of New World lunulate clades from an ancestor in common with protoscutellids, either. In fact, Mooi (1987) and Telford (1988) showed that several major clades exist in the Scutellina that share more recent common ancestry with mellitids and monophorasterids than do protoscutellids. We cannot find any evidence to support Seilacher's (1979) contention that the scutellines themselves originated in the Caribbean. Basal scutellines, which include forms such as *Proescutella,* occur in the Eocene of Europe. Detailed analysis of basal scutellines and their sister taxa is needed before much can be said concerning the origins and diversification of this group.

The relationships of mellitids and monophorasterids to other scutelline clades also await more detailed phylogenetic analysis of the deeper scutelline nodes. The poorly understood abertellids could figure in the resolution of this problem. Evidence is beginning to suggest that abertellids ranged widely throughout the Caribbean and along the eastern coasts of North and South America (Durham, 1957; Britö, 1981, 1986). At the moment, it is difficult if not impossible to identify synapomorphies between abertellids and members of the monophorasterid plus mellitid clade, so this requires further study. Much of the known abertellid material is at least as well preserved as that for monophorasterids, including spination, so the prospects are good for finding additional information on this interesting and largely overlooked group of non-lunulate scutellines.

Astriclypeids possess geniculate spines, locomotory fields, and pressure drainage channels. In many ways, they are more like mellitids than any other known sand dollar group. However, the relationships of astriclypeids to the other sand dollars remain very poorly known. Extant astriclypeids are distributed throughout the Indo-Pacific, and inhabited the Tethyan regions of Europe during the Miocene. Seilacher (1979) suggested that they descended from non-lunulate forms that also lacked the pressure drainage channels and differentiated locomotory and geniculate spine fields that are characteristic of both astriclypeids and the New World lunulates. If this is true, then astriclypeids evolved these remarkably convergent features independently from monophorasterids and mellitids. It has already been established (Mooi, 1987, 1989) that the ambulacral lunules of astriclypeids and mellitids are formed in very different ways, and unlikely to be homologous. Could this not also be true for other features shared by astriclypeids and New World lunulates, such as spination? C. R. Marshall (1992) also discussed the possibility that external features closely linked to specific adaptive functions common to these major scutelline clades could lead to convergences of this type. Further work based on sound phylogenetic and character analysis will be necessary to determine if astriclypeids are members of the same, or very different clades as the mellitids and monophorasterids.

The present study supports the idea that several monophorasterid features are precursors to those seen in *Mellita, Leodia,* and *Encope.* With a reasonably stable phylogeny in place, it should be possible to delve deeper into the evolution of the mellitids themselves. Identification of the earliest members of each of the genera, and provision of a basis for the timing and adaptive significance of their most conspicuous features such as lunules and the peripheral ballast system will be feasible. By recognizing the phylogenetic significance of the monophorasterids, and the sequence of events in the evolution of New World lunulate sand dollars in general, it will also be possible to develop new, cladistically-based evolutionary scenarios for diversification of even these most highly derived and bizarre of the scutellines.

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