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The phylogeny and classification of post-Palaeozoic echinoids

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The relationships of post-Palaeozoic echinoids at family level are established through phylogenetic analysis of 169 taxa and 306 skeletal characters (excluding pedicellariae). Previous phylogenetic analyses of echinoids have either examined specific subgroups in detail or have looked at a relatively small number of taxa selected from across the class, with sparse sampling potentially affecting the reliability of results adversely. Our new analyses represent a compromise between encompassing the diversity of form that exists, while keeping the number of taxa to a level that does not make rigorous analysis impossibly time-consuming. In constructing the taxon-character data matrix we have encountered a surprising lack of primary data on plating pattern, lantern, and girdle structure for many supposedly "well-known" taxa. A well-resolved phylogenetic hypothesis was obtained and is used as the basis for a formal classification. Characters generally have a high retention index (>0.7) but low consistency index (<0.25) suggesting that, although characters are largely retained after they first evolve, most also undergo occasional reversal or convergence. Although parts of the resulting trees are only weakly supported (e.g. the precise sister group of the Irregularia), other parts are unambiguously resolved. Not unexpectedly, deep nodes are often not supported by unique apomorphies and higher taxa acquire their characteristic set of features over time. Diagnoses based on crown group taxa thus often fail to encompass fossil stem-group members adequately. Establishing the relationships of taxa at the root of large groups is hampered by limited character resolution. The influence of fossil taxa on the topology was explored by comparing the tree topologies obtained with and without their inclusion. We show that removal of fossils from stem groups makes no difference where their crown group is morphologically conservative, but has a major influence where extant sister groups are separated by large morphological gaps. Completeness of the echinoid record and its match to the stratigraphical record of first occurrences is tested using various metrics and found to be highly congruent, with irregular echinoids showing a higher congruence than regular ones.

Keywords: Echinoids; phylogeny; cladistics; evolution; classification

Introduction

Echinoids today form a conspicuous and important element of many marine benthic communities (e.g. Kier & Grant 1965; Nebelsick 1996; Barnes & Brockington 2003; David *et al.* 2005). They exploit a wide array of marine habitats, from the poles to the equator and from the intertidal zone to the deep sea, although they achieve greatest levels of diversity and abundance in shallow shelf areas (Smith *et al.* 2001; Linse *et al.* 2008). Regular echinoids, as one of the dominant algal grazers in shallow marine communities, are important ecologically and include a number of keystone taxa that can impact the health of the wider community (e.g. Scheibling 1984; Edmunds & Carpenter 2001). They can also be major bioeroders in shallow marine environments (Bak 1990). Irregular echinoids are important as bioturbators and through their deposit-feeding activities, which modifies the structure of the sediment (Hammond 1981).

Currently there are some 850 living species of echinoids, allocated to approximately 70 families, and this diversity has all arisen since the late Permian, approximately 265 Mya (Kier 1984a; Smith & Hollingworth 1990; Smith *et al.* 2006). Echinoids have a multiplated skeleton or test composed of high-magnesium calcite. Although this is constructed of many individual elements, test plates usually interlock to a greater or lesser extent creating a relatively robust structure in almost all post-Palaeozoic echinoids. As a consequence echinoids have left a rich fossil record: in total there are about 1200 named genera and 174 families. However, it seems likely that current diversity is greater than at any time in the geological past.

Since the start of the Triassic echinoids have evolved to encompass a wide diversity of morphologies and modes of life. Furthermore, because they have left a relatively good fossil record, they have figured prominently in evolutionary and palaeobiological studies for over 100 years. The complexity of the echinoid skeleton, composed as it is of a large number of individual elements with complex microarchitecture, has another advantage – it provides a large number of phylogenetically informative characters. This

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is important because groups with a well-founded phylogenetic framework are now seen as the key for addressing many current palaeobiological problems (e.g. Sumrall & Brochu 2008).

Previous work on the systematics of echinoids

The early history of research into echinoid systematics and phylogeny has been summarized by Durham (1966). The study and classification of echinoids began in earnest with the various works of Louis Agassiz and Edouard Desor from the 1830s to 1850s (Agassiz 1835; Agassiz & Desor 1846-47; Desor 1855-58). However, it was Mortensen (1928a, 1935, 1940, 1943a, b, 1948a, b, 1950a, 1951) who really established the foundation of our modern taxonomy of echinoids in his *Monograph of the Echinoidea,* by providing an authoritative overview of the group at species level for the Recent and at genus level for the fossil ones. The detailed classification that he developed drew heavily from Jackson (1912) and was based primarily on skeletal features and thus is equally applicable to Recent and fossil taxa, with the exception of few groups based mainly on pedicellarial characters.

Subsequently there have been three substantive revisions of echinoid classification and phylogeny, all of them predating the advent of numerical cladistics. Durham & Melville (1957) in preparation for the publication of the *Treatise on Invertebrate Paleontology* volume on the Echinoidea, developed a detailed classification that departed somewhat from the structure outlined by Mortensen. Like that of Mortensen, groupings were based on a mixture of primitive and derived characters. Because it formed the underpinning structure for the *Treatise* (Durham 1966), it became widely adopted, although not without detractors (e.g. Philip 1965). The advent of cladistic methods in the 1960s was slow to make inroads into echinoderm classification. Jensen (1982) developed a 'cladistic' classification in which autapomorphies of terminal branches were identified, but not synapomorphies supporting any of the larger groupings. The first true cladistic analysis of echinoids was by Smith (1981), and was directly translated into a formal classification, later amplified in Smith (1984). Although the cladogram was justified in that all nodes had supporting synapomorphies, it had been 'hand-crafted' and was not based on rigorous analysis of a taxon-character data matrix.

With the advent of molecular gene-sequence data in the 1990s a new era of rigorous phylogenetic approaches began. Littlewood & Smith (1995) provided the first numerical cladistic analysis across the class based on a combination of morphological and molecular data. Although this provided a robust basis for understanding phylogenetic relationships, it was constructed for only a small number of taxa for which gene data were available and no attempt was made to turn this into a formal classification. While larger databases of taxa have now been assembled and analyzed (e.g. Smith *et al*. 2006), there has still been no formal attempt to take this new molecular perspective and integrate it into a formal classification.

While there have been relatively few analyses that cover the entire group, there have been a relatively large number of cladistic analyses that have focussed on individual groups within the Echinoidea aimed at understanding detailed relationships: cidaroids (Smith & Wright 1989; Matsuoka & Inamori 1999), echinothurioids (Smith & Wright 1990; Mooi *et al*. 2004), diadematoids (Smith & Wright 1990; Lessios 2001), stirodonts (Smith & Wright 1990), camarodonts (Smith 1988; McCartney *et al*. 2000; Jeffery *et al*. 2003; Lee 2003; Lee *et al*. 2004), primitive irregulars (Smith & Anzalone 2000; Solovjev & Markov 2004; Barras 2006, 2007; Saucède *et al*. 2007), cassiduloids (Suter 1994; Smith 2001; Saucède & Néraudeau 2006), clypeasteroids (Marshall 1992; Mooi 1987; Wang 1994; Mooi & Peterson 2000; Mooi *et al.* 2000), holasteroids (David 1988; Mooi & David 1996; Smith 2004) and spatangoids (Markov & Solovjev 2001; Villier *et al*. 2004; Stockley *et al*. 2005; Kroh 2007). All provide detailed snapshots of parts of the phylogenetic tree of echinoids. What we intend doing in this paper is to establish an overarching phylogenetic framework for these and future studies. We undertake the first comprehensive numerical cladistic analysis of the group which attempts to sample the diversity of post-Palaeozoic echinoids by including all named families both extant and extinct, and constructing a set of characters that captures the variable features used previously by taxonomists.

Methods and materials

Sampling considerations

A robust and accurate phylogeny is of course the ultimate goal of all phylogenetic studies. However, phylogenetic trees can be sensitive to sampling issues, with the position of weakly supported branches prone to change with the addition or removal of either taxa or characters from an analysis (e.g. Carlson & Fitzgerald 2008). This problem has spawned considerable debate concerning the best strategy to adopt: whether it is better to add more characters or to add more taxa given limited resources. This debate has mostly focused on phylogenies constructed from molecular data, but the problem is more general.

When it comes to outgroup selection, careful selection of additional outgroup taxa, aimed at breaking up long branches, may be the more beneficial (Smith 1994a; Rannala *et al*. 1998). Increased sampling of taxa from within a monophyletic group increases the average accuracy of reconstructed phylogenies because it decreases the average lengths of external (tip) branches. But adding new characters has also been demonstrated to be highly beneficial, at least in molecular studies (e.g. Mitchell *et al.* 2000; Rosenberg & Kumar 2001) On the other hand, sparse sampling also has its problems and the dangers of focusing on just a small number of 'model' organisms to derive phylogenetic hypotheses have been highlighted by Zwickl & Hillis (2002) and Hillis *et al*. (2003). Poe (1998) showed that the sensitivity of a tree was directly related to the number of taxa subsampled – the smaller the number of taxa sampled the more variable the resultant tree.

In reality then both denser taxon sampling and more comprehensive character sampling are of benefit when it comes to phylogenetic estimation (Delsuc *et al*. 2002; Yoder & Jodi 2005). It is now clear that improved character and taxon sampling in phylogenetic analysis helps to pick up homoplasy and improves the robustness and accuracy of the resultant tree. Of course adding new suites of characters is considerably easier in molecular studies compared to classical morphological studies, where unused suites of attributes are rarely available. In this study we have tried to increase sampling significantly both across the taxonomic spectrum and by including as diverse and complete a spectrum of morphological characters as is feasible. Because we are integrating Recent and fossil taxa, however, we have omitted certain categories of characters. No pedicellarial characters are included as these are almost exclusively known from extant taxa. A parallel study is currently underway examining the phylogenetic significance of pedicellarial morphology. We have also omitted all soft-tissue characters relating to internal organs, as these again are known only from extant taxa. Again work is currently underway to utilize this as an additional source of phylogenetic information (A. Ziegler pers. comm. 2009).

Choice of taxa

We confine our study to crown-group echinoids. With over 1200 post-Palaeozoic nominal genera to select from, our choice of taxa for inclusion in this analysis represents a compromise between capturing sufficient diversity of form and keeping the analysis to a reasonable number of taxa. Traditionally taxa at family/subfamily-level have been established for groups of morphologically related genera. There are 174 named families/subfamilies of post-Palaeozoic echinoid and these therefore form the basis of our analyses (Table 1). Three taxa were omitted from further consideration immediately either because they were spine-based taxa (Braunechinidae Vadet, 1999b) or were based on such poor material that much of their morphology is simply unknown (Kieritiaridae Vadet, 1999b; Thielicidaridae Vadet, 1999b). For the remaining 171 we selected the type genus for scoring, wherever possible making direct observations on specimens in the Natural History Museum, Vienna (NHMW), or the Natural History Museum, London (NHM).

After character scoring a further three taxa were removed from our analysis as follows:

1. Circopeltinae Smith & Jeffery, 2000. The type species of *Circopeltis* is *Leiosoma meridanense* Cotteau, 1866, p. 765, by subsequent designation of Lambert & Thiéry, 1914, p. 254. However, the morphological attributes of this species are currently uncertain. Material in Lambert's Collection in the Muséum National d'Histoire Naturelle, Paris, labelled *Leiosoma meridanense* does not conform to the original species description and illustrations of Cotteau in important ways. However, Cotteau's illustrations are notorious for being untrustworthy in the details they show, and we have not been able to trace Cotteau's original material of this species. Until we do, it seems unwise to create any higher taxonomic group on the basis of such conflicting information.
2. Tiarechinidae Gregory, 1897. This is based on a well-preserved, but highly aberrant, small (5–6 mm) echinoid from the Carnian of northern Italy. Its test structure is unique in having just four plates in each interambulacrum, with a single adoral element and three upper elements. It has been described by both Lovén (1883) and Kier (1977b) but its strange morphology provides little clue as to what its closest relatives might be.
3. Triadocidaridae Smith, 1994c. Again this is based on a type species that is very incompletely known. It is a cidaroid-like echinoid from the Middle Triassic of Europe without lantern supports and possibly not part of the crown group.

This left us with a total of 168 ingroup taxa (listed in Appendix 2) for inclusion in our phylogenetic analyses. Over half of these (57%) are fossil. As outgroup we used the Carboniferous genus *Archaeocidaris* (Archaeocidaridae). This is an unambiguous late stem-group member, and its morphology is well documented thanks to two recent studies of spectacularly well-preserved individuals (Lewis & Ensom 1982; Schneider *et al*. 2005).

Character scoring

We have tried to identify and score all skeletal-based characters that have been used previously by taxonomists as diagnostic at family/subfamily level or higher. Soft-tissue characters were excluded because they are very sporadically known amongst extant taxa and impossible to score in fossil taxa. We also exclude all characters associated with pedicellariae, as these are almost never preserved in fossils. Initially we scored for 325 characters of which we subsequently rejected 21 as being either dependent of other characters scored, or for being too trivial for the level of analysis being undertaken, and changed one character into three independent characters bringing the total to 306. Of

Table 1. List of taxa and sources for scorings. Supplementary information on lantern and girdle were taken from Hawkins (1934). Additionally, data obtained from specimens were cross-checked for consistency with the descriptions published in the monographs of Mortensen (1903b, 1907, 1928, 1935, 1940, 1943a, b, 1948a, b, 1950a, 1951), Kier (1962, 1967a, 1977b, 1984a, b), Mooi (1989), Jagt (2000), Smith & Jeffery (2000), Radwańska (2003). Crystallographic data were taken from Raup (1959, 1960, 1962, 1965).

Family	Author	Species scored (* = type species)	Source of data
Abertellidae	Durham, 1955	*_Abertella aberti_ Conrad, 1842	Specimens
Acrolusiidae	Mintz, 1968	*_Acrolusia gauthieri_ Lambert, 1920b	Specimens
Acropeltinae	Lambert & Thiéry, 1914	*_Acropeltis aequituberculata_ L. Agassiz, in L. Agassiz & Desor, 1846	Specimens
Acrosaleniidae	Gregory, 1900	*_Acrosalenia spinosa_ L. Agassiz, 1840	Specimens
Aeropsidae [Aeropidae]	Lambert, 1896	*_Aeropsis rostrata_ Thomson, 1877	Specimens
Ammotrophinae	Durham, 1955	*_Ammotrophus cyclius_ H. L. Clark, 1928	Specimens
Anorthopygidae	Wagner & Durham, 1966b	*_Anorthopygus orbicularis_ (Grateloup, 1836)	Specimens
Antillasterinae	Lambert, in Lambert & Thiéry, 1924	*_Antillaster cubensis_ (Cotteau, 1871)	Kier (1984b)
Apatopygidae	Kier, 1962	*_Apatopygus recens_ (Milne Edwards, in Cuvier, 1836)	Specimens and Mortensen (1921) for lantern
Arachnoididae	Duncan, 1889	*_Arachnoides placenta_ (Linnaeus, 1758) & _Fellaster zealandiae_ (Gray, 1855)	Specimens
Arbaciidae	Gray, 1855	*_Arbacia lixula_ (Linnaeus, 1758)	Specimens and Gordon (1929)
Archaeocidaridae	McCoy, 1844	_Archaeocidaris whatleyensis_ Lewis & Ensom, 1982 and _A. brownwoodensis_ Schneider _et al._ 2005	Specimens and Schneider _et al._ (2005)
Archiaciidae [Archiacidées]	Cotteau & Triger, 1869	*_Archiacia sandalina_ Agassiz & Desor, 1847	Specimens
Aspidodiadematidae	Duncan, 1889	_Aspidodiadema jacobi_ A. Agassiz, 1880	Specimens
Asterostomatidae	Pictet, 1857	_Asterostoma pawsoni_ Kier, 1984b	Specimens
Astriclypeidae	Stefanini, 1912	*_Astriclypeus mannii_ Verrill, 1867	Specimens
Breyninae	Lambert, 1905	*_Breynia australasiae_ (Leach, 1815)	Specimens
Brisasterinae	Markov, 1994	*_Brisaster fragilis_ (von Düben & Koren, 1846)	Specimens
Brissidae [Brissina]	Gray, 1855	*_Brissus unicolor_ (Leske, 1778)	Specimens
Brissopsidae	Lambert, 1905	*_Brissopsis lyrifera_ (Forbes, 1841) and _B. alta_ Mortensen, 1907	Specimens
Calymnidae	Mortensen, 1907	*_Calymne relicta_ Thomson, 1877	Specimens
Cardiasteridae	Lambert, 1917	*_Cardiaster granulosus_ (Goldfuss, 1829)	Specimens
Cardiotaxinae	Smith & Jeffery, 2000	*_Sternotaxis plana_ (Mantell, 1822)	Specimens
Carnarechininae	Mironov, 1993	*_Carnarechinus clypeatus_ (L. Agassiz, 1879)	Mironov (1978, 1993)
Cassidulidae	L. Agassiz & Desor, 1847	*_Cassidulus caribaearum_ Lamarck, 1801	Specimens and A. Agassiz (1904)
Cidaridae	Gray, 1825	*_Cidaris cidaris_ (Linnaeus, 1758)	Specimens
Circopeltinae	Smith & Jeffery, 2000	*_Circopeltis meridianense_ (Cotteau, 1867)	No reliable data
Claviasteridae	Ali, 1992	_Claviaster libycus_ Gauthier, 1889	Specimens and Zaghbib-Turki (1981)
Clypeasteridae	L. Agassiz, 1835	*_Clypeaster rosaceus_ (Linnaeus, 1758)	Specimens
Clypeidae	Lambert, 1898	*_Clypeus plotii_ Leske, 1778	Specimens
Clypeolampadidae	Kier, 1962	*_Clypeolampas ovatus_ (Lamarck, 1816)	Specimens
Coelopleuridae	Märkel, 1969	*_Coelopleurus equis_ Agassiz, 1840 and _Coelopleurus maillardi_ (Michelin, 1862)	Specimens
Coenholectypinae	Smith & Wright, 1999	*_Coenholectypus macropygus_ (L. Agassiz, 1837)	Specimens and Jagt (2002)
Collyritidae	d'Orbigny, 1853	*_Collyrites ellipticus_ (Lamarck, 1816)	Specimens
Conoclypidae	von Zittel, 1879	*_Conoclypus conoideus_ (Leske, 1778)	Specimens
Conulidae	Lambert, 1911a	*_Conulus albogalerus_ Leske, 1778	Specimens
Corasterinae	Lambert & Thiéry, 1924	*_Coraster vilanovae_ Cotteau, 1886	Specimens
Corystidae	Foster & Philip, 1978	*_Corystus dysasteroides_ (Duncan, 1877) and _C. relictus_ (de Meijere, 1902)	Specimens
Ctenocidarinae	Mortensen, 1928	*_Ctenocidaris speciosa_ Mortensen, 1910b	Specimens
Cyclasterinae	Poslavskaya, 1964	_Cyclaster regalis_ Baker, 1969	Specimens
Dendrasteridae	Lambert, 1900	*_Dendraster excentricus_ (Eschscholtz, 1831)	Specimens
Desorellidae	Lambert, 1911a	*_Desorella elatus_ (L. Agassiz & Desor, 1847)	Specimens
Diadematidae	Gray, 1855	_Diadema antillarum_ Philippi, 1845	Specimens
Diplocidaridae	Gregory, 1900	*_Diplocidaris gigantea_ (Agassiz, 1840)	Specimens
Diplopodiidae	Smith & Wright, 1993	*_Diplopodia pentagona_ McCoy, 1848	Specimens
Disasteridae	Gras, 1848	*_Disaster granulosus_ (Goldfuss, 1829)	Specimens

Table 1. *(Continued)*.

Family	Author	Species scored (* = type species)	Source of data
Discoidinae	Lambert, 1900	**Discoides subuculus* (Leske, 1778)	Specimens
Echinarachniidae	Lambert in Lambert & Thiéry, 1914	**Echinarachnius parma* (Lamarck, 1816)	Specimens
Echinidae	Gray, 1825	**Echinus esculentus* Linnaeus, 1758	Specimens
Echinocardiidae	Cooke, 1942	**Echinocardium cordatum* (Pennant, 1777)	Specimens
Echinocorythidae	Wright, 1857	**Echinocorys scutata* Leske, 1778	Specimens
Echinocyamidae	Lambert & Thiéry, 1914	**Echinocyamus pusillus* Müller, 1776	Specimens
Echinolampadidae	Gray, 1851a	**Echinolampas ovata* (Leske, 1778)	Specimens and Märkel (1978) for lantern
Echinometridae	Gray, 1855	**Echinometra lucunter* (Linnaeus, 1758)	Specimens
Echinoneidae	Agassiz & Desor, 1847	**Echinoneus cyclostomus* Leske, 1778	Specimens
Echinothuriidae	Thomson, 1872a	*Araeosoma fenestratum* (Thomson, 1872b)	Specimens
Emiratiidae	Ali, 1990	**Emiratia raskhaimahensis* Ali, 1990	Specimens
Enichasterinae	Lambert, 1920a	**Enichaster oblongus* de Loriol 1882	Specimens
Eodiadematidae	Smith, 1984	**Eodiadema granulatum* Wilson in Wilson & Crick, 1889	Specimens
Eoscutellidae	Durham, 1955	**Eoscutella coosensis* Kew, 1920	Durham (1955), Parma (1985)
Eupatangidae	Lambert, 1905	**Eupatagus valenciennesi* Agassiz & Desor, 1847 and *E. lymani* (Lambert & Thiéry, 1924)	Specimens
Eurypataginae	Kroh, 2007	**Eurypatagus ovalis* Mortensen, 1948c	Specimens
Faujasiidae	Lambert, 1905	**Faujasia apicalis* (Agassiz & Desor, 1847) and *F. eccentripora* Lees, 1928	Specimens
Fibulariidae	Duncan, 1889	**Fibularia ovulum* Lamarck, 1816	Specimens
Fossulasteridae	Philip & Foster, 1971	**Fossulaster halli* Lambert & Thiéry, 1925	Specimens
Galeritidae	Gray, 1825	**Galerites vulgaris* (Leske, 1778)	Specimens
Galeropygidae	Lambert, 1911a	**Galeropygus sublaevis* (McCoy, 1848)	Specimens
Glyphocyphidae	Duncan, 1889	**Glyphocyphus radiatus* (Goldfuss, 1829)	Specimens
Glyphopneustidae	Smith & Wright, 1993	*Glyphopneustes hattaensis* Ali, 1992	Specimens
Glypticidae	Lambert & Thiéry, 1914	**Glypticus heiroglyphicus* (Goldfuss, 1829)	Specimens and Vadet *et al.* (2002) for spines
Glyptocidaridae	Jensen, 1982	**Glyptocidaris crenularis* A. Agassiz, 1864	Mortensen (1935)
Goniocidarinae	Mortensen, 1928	**Goniocidaris tubaria* (Lamarck, 1816)	Specimens
Goniophorini	Smith & Wright, 1990	**Goniophorus lunulatus* L. Agassiz, 1838	Specimens
Hemiasteridae	Clark, 1917	**Hemiaster bufo* (Brongniart, 1822)	Specimens
Hemicidaridae	Wright, 1857	**Hemicidaris intermedia* (Fleming, 1828)	Specimens
Hemipneustidae	Lambert, 1917	**Hemipneustes striatoradiatus* (Leske, 1778)	Specimens
Heterodiadematidae	Smith & Wright, 1993	**Heterodiadema lybica* (L. Agassiz & Desor, 1846)	Specimens
Histocidaridae	Lambert, 1900	**Histocidaris elegans* (A. Agassiz, 1879)	Specimens
Holasteridae	Pictet, 1857	**Holaster nodulosus* (Goldfuss, 1829)	Specimens
Holectypoidae	Lambert, 1900	**Holectypus depressus* (Leske, 1778)	Specimens
Holosaleniini	Smith & Wright, 1990	**Holosalenia batnensis* (Cotteau, Peron & Gauthier, 1879)	Specimens
'Hyboclypids'	Barras, 2007	*Hyboclypus gibberulus* L. Agassiz, 1839 and *H. sandalinus* Merian in Desor, 1857	Specimens
Hygrosomatinae	Smith & Wright, 1990	**Hygrosoma petersii* (A. Agassiz, 1880)	Specimens
Hyposaleniinae	Mortensen, 1934	**Hyposalenia stellulata* (L. Agassiz, 1838)	Specimens
Kamptosomatidae	Mortensen, 1934	**Kamptosoma asterias* A. Agassiz, 1881	Specimens
Laganidae	A. Agassiz, 1873	**Laganum laganum* (Leske 1778)	Specimens
Loveniidae	Lambert, 1905	**Lovenia elongata* (Gray, 1845)	Specimens
Macropneustidae	Lambert, 1895	**Macropneustes deshayesi* Agassiz & Desor; 1847 & *M. mortoni* (Conrad, 1850)	Specimens
Maretiidae	Lambert, 1905	**Maretia planulata* (Lamarck, 1816)	Specimens
Megapneustinae	Fourtau, 1905	*Megapneustes grandis* Gauthier in Fourtau, 1900	Specimens
Mellitidae	Stefanini, 1912	**Mellita quinquesperforata* (Leske, 1778)	Specimens
Micrasteridae	Lambert, 1920a	**Micraster coranguinum* (Leske, 1778)	Specimens
Micropygidae	Duncan, 1889	**Micropyga tuberculata* Agassiz, 1879	Specimens
Miocidaridae	Durham & Melville, 1957	*Eotiaris verneuiliana* (King, 1850)	Specimens
Monophorasteridae	Lahille, 1896	**Monophoraster darwini* (Desor, 1847)	Specimens

(Continued)

Table 1. *(Continued)*.

Family	Author	Species scored (* = type species)	Source of data
Neoglobatoridae	Endelman, 1980	**Adelopneustes montainvillensis* (Sorignet, 1850)	Specimens
Neolaganidae	Durham, 1954	*Neolaganum durhami* Cooke, 1959 and **N. archerensis* (Twitchell in Clark & Twitchell, 1915)	Specimens and Durham (1954, 1955)
Neolampadidae	Lambert, 1918a	**Neolampas rostellata* A. Agassiz, 1869	Mortensen (1948a)
Nucleolitidae [Nucléolides]	L. Agassiz & Desor, 1847	**Nucleolites scutatus* Lamarck, 1801	Specimens
Oligopygidae	Duncan, 1889	**Oligopygus wetherbyi* de Loriol, 1887; *O. haldemai* (Conrad, 1850) and *Haimea rutteni* (Pijpers, 1933)	Specimens and Kier (1967a, 1974)
Orthopsidae	Duncan, 1889	**Orthopsis miliaris* (d'Archiac, 1837)	Specimens
Ovulasteridae	Lambert, 1896	**Ovulaster gauthieri* Cotteau, 1884 & *O. protodecimae* Giusberti *et al.*, 2005	Specimens and Giusberti *et al.* (2005)
Palaeostomatidae	Lovén, 1868	**Palaeostoma mirabilis* (Gray, 1851b)	Specimens
Palaeotropidae	Lambert, 1896	**Palaeotropus josephinae* Lovén, 1874	Mortensen (1950a), Mironov (2006)
Paleopneustidae	A. Agassiz, 1904	**Paleopneustes cristatus* A. Agassiz, 1873	Specimens
Paraphormosomatinae	Smith & Wright, 1990	**Paraphormosoma alternans* de Meijere, 1902	Mortensen (1935)
Parasaleniidae	Mortensen, 1903b	**Parasalenia gratiosa* A. Agassiz, 1864	Specimens
Parechinidae	Mortensen, 1903b	**Parechinus angulosa* (Leske, 1778)	Specimens
Paurocidaridae	Vadet, 1999a	**Paurocidaris rinbianchi* Zardini, 1973	Kier (1977b)
Pedinidae	Pomel, 1883	*Caenopedina cubensis* A. Agassiz, 1869	Specimens
Pelanechinidae	Groom, 1887	**Pelanechinus corallina* (Wright, 1858)	Specimens
Pelanodiademinae	Hess, 1972	**Pelanodiadema oolithicum* Hess, 1972	Specimens and Hess (1972)
Periasteridae	Lambert, 1920a	**Periaster elatus* d'Orbigny, 1853	Specimens
Pericosmidae	Lambert, 1905	**Pericosmus latus* Agassiz & Desor, 1847 and *P. cordatus* Mortensen, 1950a	Specimens
Phormosomatidae	Mortensen, 1934	**Phormosoma placenta* Thomson, 1872b	Specimens
Phymosomatidae	Pomel, 1883	**Phymosoma koenigi* (Mantell, 1822) and *Gauthieria radiata* (Sorignet, 1850)	Specimens
Plesiasteridae	Lambert, 1920a	**Plesiaster peini* (Coquand, 1862)	Specimens
Plesiolampadidae	Lambert, 1905	*Plesiolampas placenta* Duncan & Sladen, 1882b	Specimens
Plexechinidae	Mooi & David, 1996	**Plexechinus cinctus* A. Agassiz, 1898 and *Antrechinus nordenskjoeldi* (Mortensen, 1905)	Specimens and Mooi & David (1996)
Pliolampadidae	Kier, 1962	*Pliolampas vassalli* (Wright, 1855)	Specimens
Polycidaridae	Vadet, 1988	*Polycidaris legayi* (Sauvage & Rigaux, 1873) and **P. spinosa* (L. Agassiz, 1840)	Specimens
Polydiadematinae	Hess, 1972	**Polydiadema mammillanum* (Roemer, 1836)	Specimens
Poriocidarini	Smith & Wright, 1989	**Poriocidaris purpurata* (Thomson, 1872b)	Specimens
Pourtalesiidae	A. Agassiz, 1881	*Pourtalesia jeffreysi* Thomson, 1872b	Specimens
Prenasteridae	Lambert, 1905	**Prenaster alpinus* Desor, 1853	Specimens
Protoscutellidae	Durham, 1955	*Protoscutella plana* (Conrad, 1865)	Specimens
Pseudholasterinae	Smith & Jeffery, 2000	**Pseudholaster bicarinatus* (L. Agassiz in L. Agassiz & Desor, 1847)	Specimens
Pseudocidaridae	Smith & Wright, 1993	**Pseudocidaris thurmanni* (Agassiz, 1840)	Specimens
Pseudodiadematidae	Pomel, 1883	**Pseudodiadema pseudodiadema* (Lamarck, 1816)	Specimens
Pseudosaleniidae	Vadet, 1999b	**Pseudosalenia aspera* (L. Agassiz, 1838)	Specimens
Psychocidaridae	Ikeda, 1936	**Psychocidaris ohshimai* Ikeda, 1935	Specimens
Pygasteridae	Lambert, 1900	**Pygaster semisulcatus* (Phillips, 1829)	Specimens and Melville (1961)
Pygaulidae	Lambert, 1905	*Pygaulus desmoulinsii* L. Agassiz in L. Agassiz & Desor, 1847	Specimens
Pygorhytidae	Lambert, 1909b	**Pygorhytis ringens* (L. Agassiz, 1839)	Specimens
Rhabdocidaridae	Lambert, 1900	**Rhabdocidaris orbignyana* (L. Agassiz in L. Agassiz & Desor, 1847)	Specimens
Roseicidaridae	Vadet, 1991	**Roseicidaris morieri* (Cotteau, 1875)	Specimens
Rotulidae	Gray, 1855	**Rotula deciesdigitatus* (Leske, 1778)	Specimens and Kier (1970)
Saleniidae	Agassiz, 1838	*Salenia petalifera* (Defrance, 1825)	Specimens
Salenocidarini	Smith & Wright, 1990	**Salenocidaris varispina* A. Agassiz, 1869	Specimens

Table 1. *(Continued).*

Family	Author	Species scored (* = type species)	Source of data
Schizasteridae	Lambert, 1905	*Schizaster* (*Ova*) *canaliferus* Lamarck, 1816	Specimens
Scutasteridae	Durham, 1955	**Scutaster andersoni* Pack, 1909	Durham (1955)
Scutellidae	Gray, 1825	**Scutella subrotunda* Lamarck, 1816	Specimens
Scutellinidae [Scutelliniens]	Pomel, 1883	**Scutellina lenticularis* (Lamarck, 1816)	Specimens
Scutellinoididae	Irwin, 1995	**Scutellinoides patella* (Tate, 1891)	Specimens
Serpianotiaridae	Hagdorn, 1995	**Serpianotiaris coaeva* (Quenstedt, 1873)	Hagdorn (1995)
Somaliasteridae	Wagner & Durham, 1966a	**Somaliaster magniventer* Hawkins, 1935	Specimens
Spatangidae	Gray, 1825	**Spatangus purpureus* Müller, 1776	Specimens
Sperosomatinae	Smith & Wright, 1990	**Sperosoma grimaldii* Koehler, 1897	Specimens
Stegasteridae	Duncan, 1889	**Stegaster gillieroni (*de Loriol, 1873)	Specimens
Stenonasteridae	Lambert, 1922	**Stenonaster tuberculata* (Desor, 1858)	Specimens
Stereocidaridae	Lambert, 1900	**Stereocidaris sceptrifera* (Mantell, 1822)	Specimens
Stigmatopyginae	Smith & Wright, 2000	*Stigmatopygus pulchellus* Smith, 1995	Specimens
Stomechinidae	Pomel, 1883	**Stomechinus bigranularis* (Lamarck, 1816)	Specimens
Stomopneustidae	Mortensen, 1903b	*Stomopneustes variolaris* (Lamarck, 1816)	Specimens
Strongylocentrotidae	Gregory, 1900	**Strongylocentrotus droebachiensis* (Müller, 1776)	Specimens
Taiwanasteridae	Wang, 1984	**Taiwanaster mai* Wang, 1984	Wang (1984)
Temnopleuridae	Agassiz, 1872	**Temnopleurus toreumatica* (Leske, 1778)	Specimens
Tiarechinidae	Gregory, 1897	**Tiarechinus princes* Neumayr, 1881a	Neumayr (1881a), Kier (1977b)
Tithoniidae	Mintz, 1968	**Tithonia convexa* (Catullo, 1827)	Specimens
Toxasteridae	Lambert, 1920a	**Toxaster retusus* (Lamarck, 1816)	Specimens
Toxopneustidae	Troschel, 1872	**Toxopneustes pileolus* (Lamarck, 1816)	Specimens
Triadocidaridae	Smith, 1994c	**Triadocidaris subsimilis* (Münster in Wissmann & Münster, 1841)	Specimens
Triadotiaridae	Hagdorn, 1995	**Triadotiaris grandaevus* (Goldfuss, 1829)	Hagdorn (1995)
Trigonocidaridae	Mortensen, 1903b	**Trigonocidaris albida* A. Agassiz, 1869	Specimens
Typocidaridae	Vadet, 1988	**Typocidaris malum* (Gras, 1848)	Specimens
Unifasciidae	Cooke, 1959	**Unifascia carolinensis* (Clark in Clark & Twitchell, 1915)	Cooke (1959)
Urechinidae	Duncan, 1889	**Urechinus naresianus* A. Agassiz, 1879	Mooi & David (1996)
Zeuglopleuridae	Lewis, 1986	**Zeuglopleurus costulatus* Gregory, 1889	Specimens

these, 18 characters turned out to be parsimony uninformative (single-taxon autapomorphies).

Scoring was carried out independently by each of us and then compared and checked for consistency. This resulted in a number of initial character definitions being refined to remove potential ambiguity. Wherever possible we verified character scorings using actual specimens in the NHM or the NHMW. In a small number of cases, material that had been studied at first hand in other museums by one or other of us formed the basis for some character scores. For a few rare taxa we had to rely on original published descriptions supplemented by statements and illustrations from reliable authorities such as Mortensen (1928a, 1935, 1940, 1943a, b, 1948a, b, 1950a, 1951), or Lovén (1874, 1883). Appendix 1 provides a full listing of character states and their descriptions, provides source data and illustrations of key character states for clarification.

Characters were drawn from all aspects of the skeleton. Thirty-six characters (11.8%) relate to general aspects of the test, such as test shape, plate-plate boundaries, plate sculpture, internal buttressing and lunule development, 47 (15.4%) relate to apical disc and periproct plating, 71 (23.2%) to ambulacral plates, 67 (21.9%) to interambulacral plates and tuberculation, 24 (7.8%) to the peristome and peristome plating, 16 (5.2%) to the lantern and perignathic girdle, and 45 (14.7%) to the spines, fascioles and sphaeridia. Where character states could not be scored for a particular taxon because of poor preservation or lack of data, the character was scored with a '?'. If on the other hand the character state was inapplicable in a taxon (i.e. logically impossible, as with characters that describe different states affecting a structure that is not present), we scored with a '-'. Polymorphic taxa were scored as having both states occurring (e.g. as 1&2). Where we could not decide (due to lack of appropriate material) which of two or more states were present, but could rule out certain other states we scored as '0/1' indicating state 0 or state 1 might be potentially developed.

For our initial analyses all characters were treated as of equal weight. For 16 of the characters there was a clear ontogenetic or size progression between character states, and these were treated as ordered (see Appendix 1). All other characters were treated as unordered. Three of the ordered characters (characters 80, 81 and 183) are positional characters relating to plate pattern and had large numbers of states. In order not to give these undue weight, states were downweighted in each character so that their combined weight summed to 1.

Not unexpectedly, the fossil taxa that we include have a larger portion of unknown character states. The proportion of missing information for the fossil taxa ranges from 2.6 to 40.5% (mean 14.0%), whereas in extant taxa it ranges from 0.0 to 31.4% (mean 2.2%). Inapplicable characters are approximately similar (at 14.5 to 15%) in the two groups. Lantern characters are the poorest known, followed by spine and sphaeridial features.

Phylogenetic analysis

Our data matrix (Appendix 2) was compiled in the program MacClade (Maddison & Maddison 2005) and analysed using the parsimony programs TNT (Goloboff *et al.* 2003) and PAUP* (Swofford 2005). Because of the large number of taxa (169), searching was only possible using the heuristic algorithm and proved to be both extremely slow and ineffective. We therefore adopted the following strategies to try to find the shortest trees.

We first undertook a single heuristic search of the full data matrix using PAUP*, with stepwise addition of taxa and TBR branch swapping. Hoswever, memory limitations meant that the analysis could not be completed and the search aborted after finding 590,000 equally parsimonious trees. We then ran a Parsimony Ratchet analysis using TNT, with 20 drift cycles, 400 ratchet iterations and 10 rounds of tree fusion. PAUPRat (Sikes & Lewis 2001) and PRAP2 (Müller 2004, 2007) with 200 iterations produced similar results. The Parsimony Ratchet is a method invented by Nixon (1999), which is very fast and effective at searching across tree space for the shortest tree. In a standard heuristic search with random addition replicates in PAUP*, a starting tree is constructed by stepwise addition drawing taxa at random from the pool. After constructing this starting tree, a process of branch swapping then takes place which searches very thoroughly for topologies within that island of similar or shorter tree length. Only once this has been completed is a new starting tree built and the process repeated, usually several hundred times. Heuristic searches thus search very thoroughly randomly selected local regions of a complex landscape. However, rather than undertaking a large number of thorough, independent heuristic searches the Parsimony Ratchet approach uses a method of searching widely and rapidly across tree space by slightly perturbating the original data (by reweighting a small proportion of characters at random) to hop between tree islands, then calculating the unweighted tree length. It too goes through a number of iterations, but each iteration is not independent of the previous search: the best tree is passed on to the next iteration. Only one tree is saved at each iteration.

Our second approach was to construct a single concatenated tree from two independent heuristic searches of partitions of the full data set. Exploratory heuristic searches consistently identified Irregularia as a monophyletic group. We therefore carried out standard heuristic searches after having partitioned the data into two subgroups of approximately equal size: one containing all regular echinoids and the basal representatives of the irregulars (68 taxa), the other containing all the irregulars and their immediate outgroup regular taxa (103 taxa). In this way we had an overlap of 4 species that appeared in both analyses. For each we carried out 500 random addition heuristic searches with TBR branch swapping. From each analysis a strict consensus of the most parsimonious trees was constructed and the two consensus trees were concatenated to form a single composite tree for all 169 taxa. This composite tree was then used as a starting input tree for a full heuristic search using TBR branch swapping in PAUP*.

In both these approaches characters were treated initially as being of equal weight. However, we also ran further analyses after reweighting characters once by their retention index based on the trees found from our unweighted analyses. Our reweighted matrix was subjected to a standard heuristic search with 100 random addition replicates.

Finally we removed all fossil taxa from the data matrix and carried out a heuristic search with 100 random additions using PAUP*. Again the initial results were used to reweigh characters by their retention index and the parsimony analysis repeated under the new weighting scheme.

Bootstrap percentages are based on 100,000 fast (simple addition without branch swapping) heuristic searches in PAUP*.

Results

Our PAUP* heuristic analysis on the full matrix with equal weights ran out of memory after having identified some 590,000 equally parsimonious trees, all 1,709 steps in length. A Parsimony Ratchet analysis of the same matrix found just 13 trees, also 1,709 steps long. However, when three characters (80, 81, 183) were weighted proportionally our PAUP* heuristic search completed returning almost 520,000 trees of 1,643.53 steps, very slightly shorter than one of the Parsimony Ratchet trees at 1,643.875. Despite these large numbers of equally parsimonious solutions, a strict consensus reveals a great deal of structure to the data with only a small number of local polytomies (Fig. 1). Importantly, there were no taxa whose position on the tree was so unstable that they were able to shift position drastically. Our heuristic searches of partitioned data confirmed that only a few taxa were causing problems. To achieve effective heuristic searches within a reasonable time we therefore pruned five taxa from the tree whose general position was clear but which were causing local instability (polytomies): the cidaroids *Anisocidaris* and *Paurocidaris*, the stirodonts *Pseudocidaris* and *Glyphopneustes*, and the

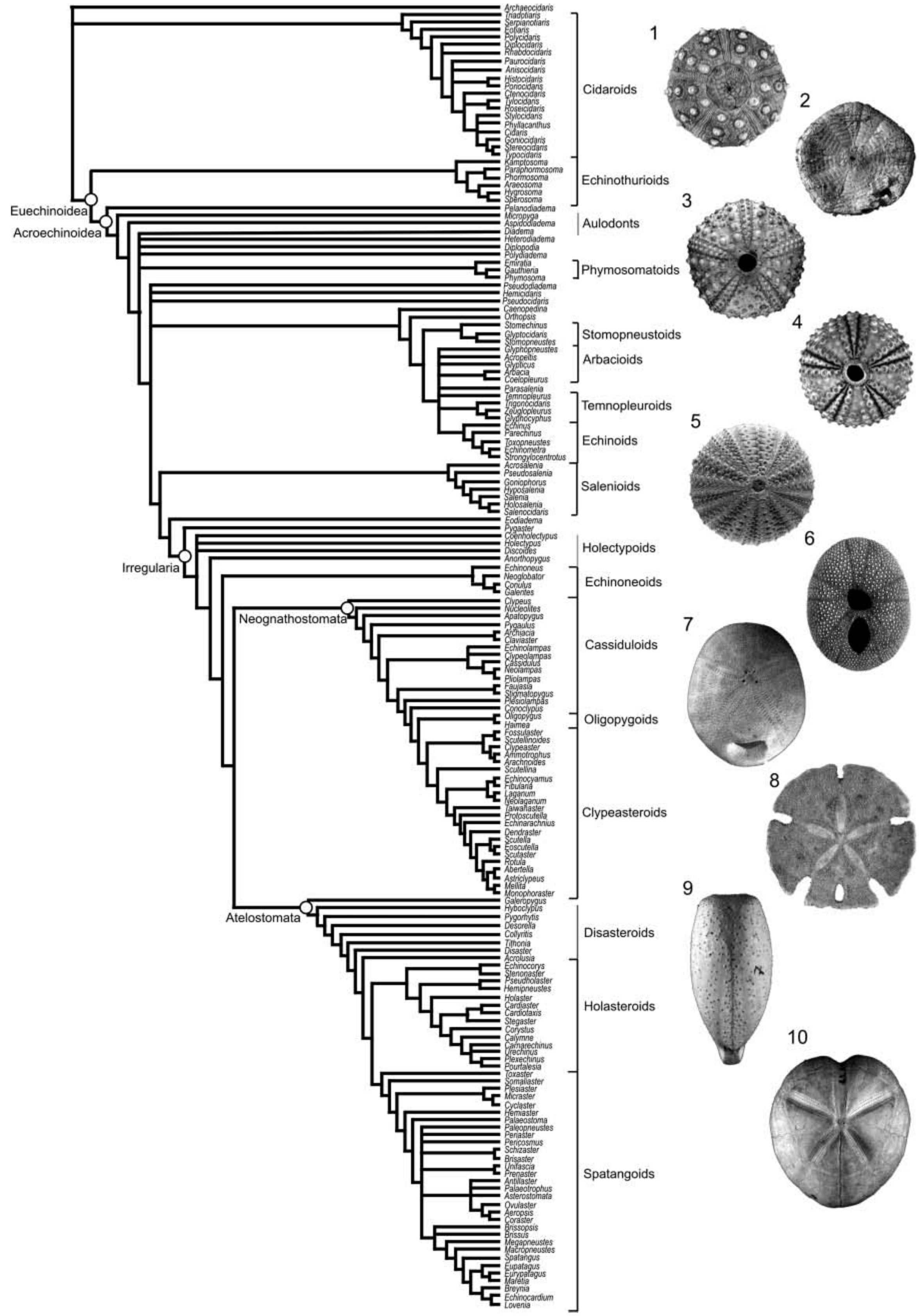

Figure 1. Strict consensus of 520,000 trees found from a parsimony analysis of the data matrix in Appendix 1. All characters are treated as of equal weight with three ordered characters proportionally scaled to 1. Tree length is 1,643.53 steps. Major traditional taxonomic groups are indicated. 1, Cidaroid (*Eucidaris*); 2, Echinothurioid (*Hapalosoma*); 3, Aulodont (*Diadema*); 4, Arbacioid (*Arbacia*); 5, Temnopleuroid (*Temnopleurus*); 6, Echinoneoid (*Echinoneus*); 7, Cassiduloid (*Cassidulus*); 8, Clypeasteroid (*Mellitella)*; 9, Holasteroid (*Pourtalesia*); 10, Spatangoid (*Faorina*).

spatangoid *Enichaster*. These taxa are all fossil, and their instability partially reflects the larger proportion of missing data each shows.

Removing these five taxa and rerunning a heuristic search with a starting tree constructed by stepwise addition and 10 random-addition replicates, resulted in 9,323 equally parsimonious trees 1,624.57 steps in length with a Consistency Index (CI) of 0.277 and a Retention Index (RI) of 0.800. The high RI shows that characters, once evolved, are usually retained within subsequent members of a clade, but the low CI shows that most characters show ocassional reversals. Our concatenated starting tree built from analysis of the two partitions was two steps longer, but a heuristic search very quickly found the same 9,323 trees of 1,624.57 steps in length.

Reweighing characters by their maximum RI in the 9,323 trees above and then carrying out a heuristic search with 10 random addition replicates generated 135 equally parsimonious trees of length 1,156.66, CI 0.284, RI 0.833. A strict consensus of these trees is shown in Fig. 2.

A heuristic search with 100 random addition replicates of just the 75 Recent taxa found 10,660 trees of 974.83 steps, with a CI of 0.423 and a RI of 0.813. Reweighting the data matrix by the retention index from this analysis generated 27 trees 715.89 steps in length, (hit in 74% of replicates), shown in Fig. 3.

Discussion

Finding the best-supported trees is a particularly difficult task when dealing with large databases such as these. Standard heuristic searches with random addition replicates simply require too much computing time to be a viable alternative, since random addition replicates often end up searching through and saving many thousands of suboptimal trees. We have used two alternative approaches to speed up the efficiency of this process, the Parsimony Ratchet and building a concatenated starting tree based on thoroughly searched data partitions. Whereas the parsimony ratchet is fast and effective at searching across a complex topology for islands of trees, it may greatly underestimate the number of equally parsimonious solutions that exist. On the other hand, a thorough search of subsets of taxa can find optimal solutions quickly and efficiently. By concatenating the results together to generate a composite starting tree we gained confidence that our less thorough search of the full data matrix had been effective.

We undertook a number of different analyses to explore the sensitivity of our results. All trees, whether with equal weights or reweighted, show a very similar core structure, summarized in Fig. 4. All show an initial dichotomy between cidaroids and euechinoids, followed by a dichotomy between the echinothurioids and acroechinoids as found in previous analyses (Durham & Melville 1957; Durham 1966; Smith 1981, 1984; Littlewood & Smith 1995). Relationships amongst basal acroechinoids remain less clear-cut. All four of the aulodont taxa (i.e. those with grooved teeth—diadematids, aspidodiadematids, micropygids and pedinoids) consistently fall at the base. The precise order of these four taxa is, however, sensitive to sampling and analytical method. Whereas the micropygids are always the most basal, pedinoids come out as either the sister group to all irregular, echinacean and calycinid taxa or as sister group to just the Echinacea + Calycina. With weighting aspidodiadematoids shift to become sister group to the Irregularia. The Irregularia form a large monophyletic clade in all analyses, with a small basal array of primitive irregulars, including *Echinoneus*, and two major groups—the atelostomates (spatangoids and holasteroids) and the neognathostomates (cassiduloids and clypeasteroids). Amongst the regular echinoids there is a consistent clade formed of camarodonts, arbacioids and stomopneustids, and another of salenioids and phymosomatoids. However, depending upon the analysis, the saleniids plus phymosomatoids either come out as sister group to the enlarged camarodont clade or as sister group to the irregular echinoid clade.

For our working topology we have selected the analysis of 164 taxa, Recent and fossil, after a single *a posteriori* reweighting (Fig. 2). This is because we feel that some relative weighting of characters is appropriate in order to emphasize those that have greater phylogenetic stability, and this can be achieved most objectively by including as many taxa as possible in the first equal weights analysis. Work by Goloboff *et al.* (2008) has demonstrated that there are distinct advantages to weighting against homoplasy in cladistic analysis. The more taxa included the better the chances of discovering true levels of homoplasy and convergence. We therefore use this as the basis for all subsequent discussion.

Comparison with existing molecular-based phylogenies

Our resultant phylogeny compares favourably with previous morphology and gene-based estimates. The most comprehensive study of echinoid phylogenetic relationships prior to this is that of Smith *et al*. (2006). In that study 49 extant species covering ca 30 of the 50 extant families and 13 of the 14 extant orders were sampled for morphological and genetic characters. In their analysis a morphological data matrix of 119 characters was compiled, and sequences from three nuclear genes totalling almost 4,000 base pairs were assembled. The morphological tree was almost identical to that obtained here, except that arbacioids and *Stomopneustes* formed a clade distinct from camarodonts, and diadematids and aspidodiadematids also formed a clade. The comparison with the molecular data throws up two major differences, however (Fig. 5). Firstly molecular data (with low support) suggests that echinothurioids lie in a clade with diadematids, aspidodiadematids and pedinoids. This arrangement contrasts with the relatively strong morphological support we find for placing echinothurioids as sister group to all other acroechinoids. More worryingly, however, is the very strong support from molecular data for a paraphyletic Clypeasteroida, with extant cassiduloids forming a clade that is sister group to just the scutelline clypeasteroids, and with clypeasterine clypeasteroids as sister group to a combined scutellines plus

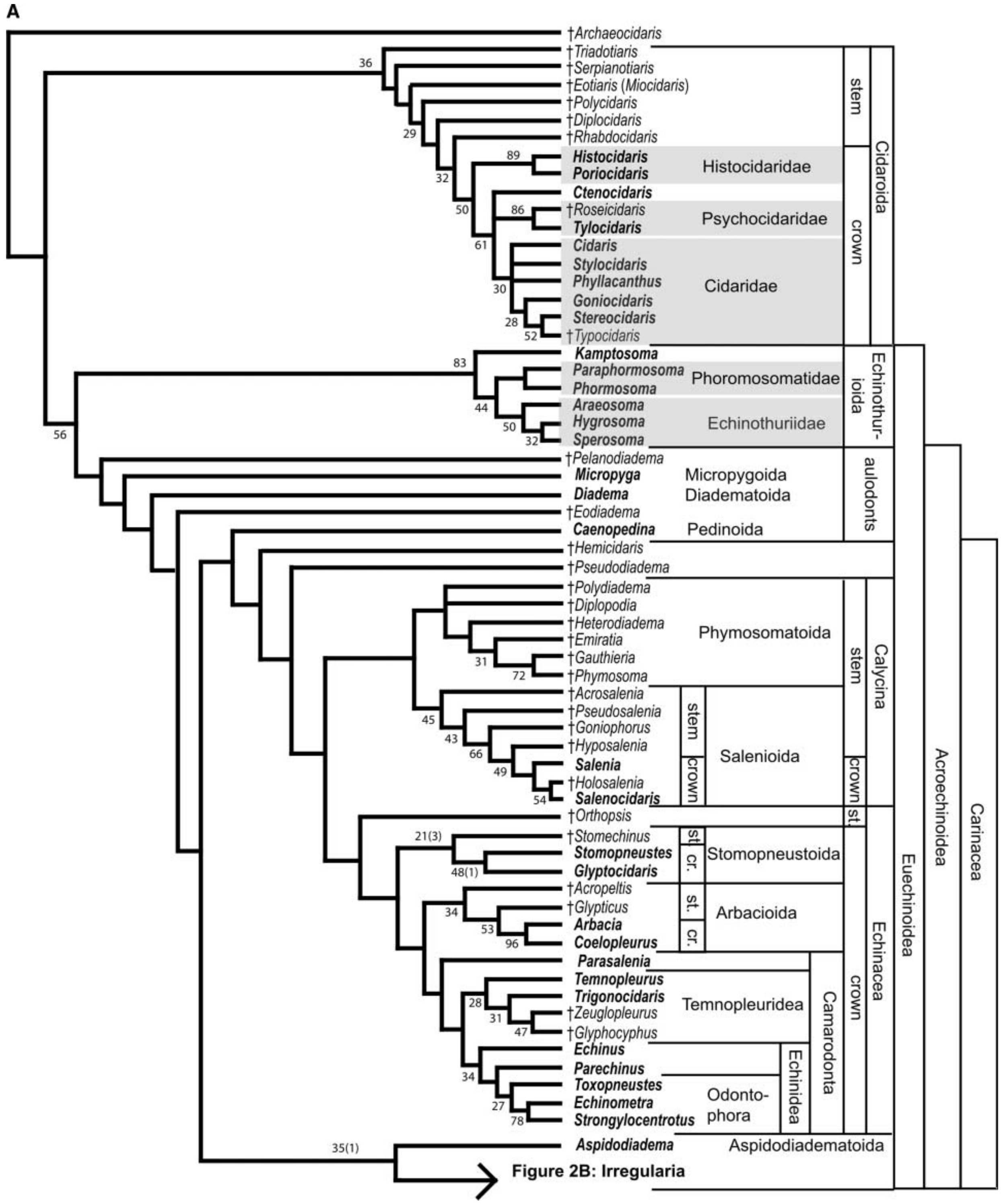

Figure 2. Strict consensus of 135 trees found after a single reweighting of characters based on their maximum Retention Index from the tree in Fig. 1. Tree length is 1,156.66 steps. A revised classification scheme is shown on the right-hand side. **A,** regular echinoids. (*Continued*)

Figure 2. *(Continued).* **B,** irregular echinoids. Numbers next to the nodes are bootstrap support values (based on 100,000 fast heuristic searches); values less than 20% are not shown.

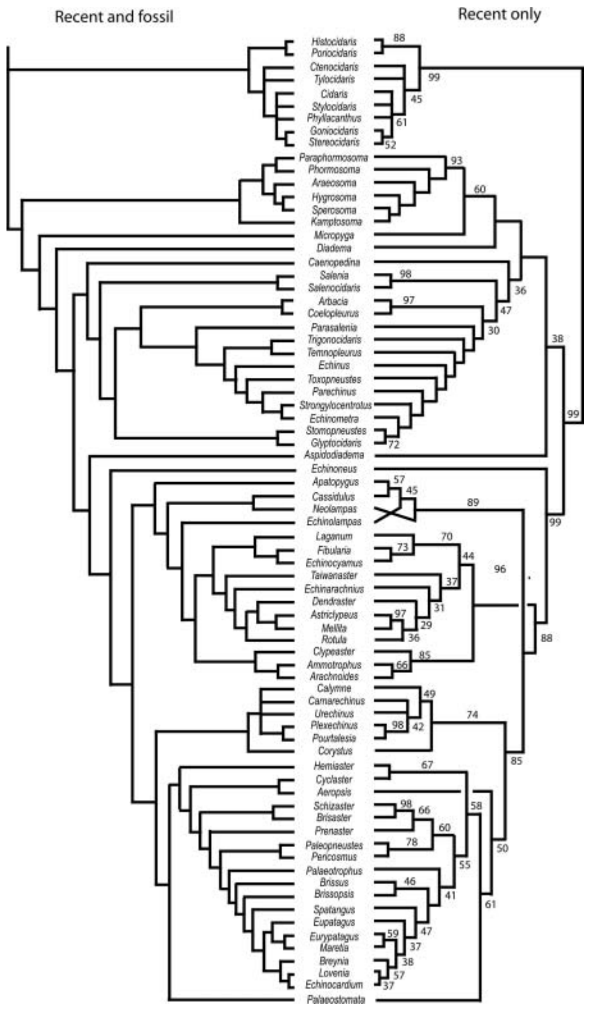

Figure 3. Trees derived for just the taxa with living representatives. The left hand cladogram was constructed by simply removing all fossil taxa from the tree shown in Fig. 2 generated from analysing the data matrix of Recent and fossil taxa. The right-hand cladogram is derived from a comparable analysis of only the extant taxa. It is a strict consensus tree of 27 most parsimonious trees found after a single reweighting of characters based on their maximum Retention Index. Tree length is 715.89 steps. Numbers next to the nodes are bootstrap support values (based on 100,000 fast heuristic searches).

cassiduloids. There is no morphological support for this, and morphological analyses consistently identify cassiduloids as a grade taxon comprising a series of branches leading up to a monophyletic clypeasteroid clade. At present, this mismatch remains inexplicable and represents a serious obstacle to generating a reliable, corroborated phylogenetic hypothesis. Additional molecular analyses including different gene loci and a wider taxon selection are needed to clarify these contrasting results.

Phylogenies with and without fossils

The addition or subtraction of any taxa from a phylogenetic analysis has the potential to alter the resultant topology and, although early work suggested that fossils might have a more significant role to play in phylogenetic reconstruction (Donoghue *et al.* 1989), more recent reviews have found that fossil taxa are no more important than extant ones in affecting tree outcome (Cobbett *et al.* 2007). In our analysis fossil taxa make up slightly more than half of the taxa we use and are, on average, approximately 10% less completely known than their extant counterparts. However, fossil taxa also fill in some critical gaps in coverage, especially at the base of the irregular echinoids where major extant clades are highly differentiated morphologically. It is in these regions that fossil taxa might be expected to play a critical role in improving the accuracy of the trees.

Focusing first on the irregular echinoids, there is a clear difference in the overall structure (Fig. 3). When analysis is based on just the extant taxa the clypeasteroids are identified as sister group to atelostomates and the cassiduloids. By contrast molecular data and the analysis of the full complement of Recent and fossil taxa consistently finds a clade comprising cassiduloids plus clypeasteroids and a clade of atelostomates. In this case, the lack of early primitive irregular echinoids has severely hampered the correct polarization of characters. A similar situation seems to pertain with regard to the relationships of the various stirodont and camarodont groups.

On the other hand the pruning of a large number of stem group cidaroid taxa or holasteroid taxa from the analysis has made no difference to the overall topology within either clade. In both of these cases it is a single relatively derived clade that has survived. The difference is evident in the mean number of character differences (Table 2). The crown group cidaroids show a paltry 3.6% mean character differences, whereas crown group holasteroids show 9.5% mean character difference. Both are strongly cohesive groups morphologically. By contrast crown group cassiduloids, spatangoids and clypeasteroids shown mean character differences of 7.7%, 12.7% and 14.0% and differences between these three groups range from 20.9% to 26.8%. Fossil taxa have more impact on phylogenetic reconstruction when they are added to groups where there are significant morphological gaps to be filled.

Phylogenetic relationships within orders

Cidaroids. In all analyses cidaroids emerge as a well-supported clade and as primitive sister group to all other echinoids (Fig. 2A). They differ from all other echinoids in a number of important features, including the structure of their perignathic girdle (which has only apophyses), their lack of sphaeridia, and their simple ambulacral plating. These long-established differences justify retaining Cidaroidea and Euechinoidea as subclasses.

Mortensen (1928a) placed all living cidaroids in one subfamily, the Stereocidarinae, with seven divisions. Subsequently these divisions were elevated to subfamily level by Durham & Melville (1957), who also added a new family,

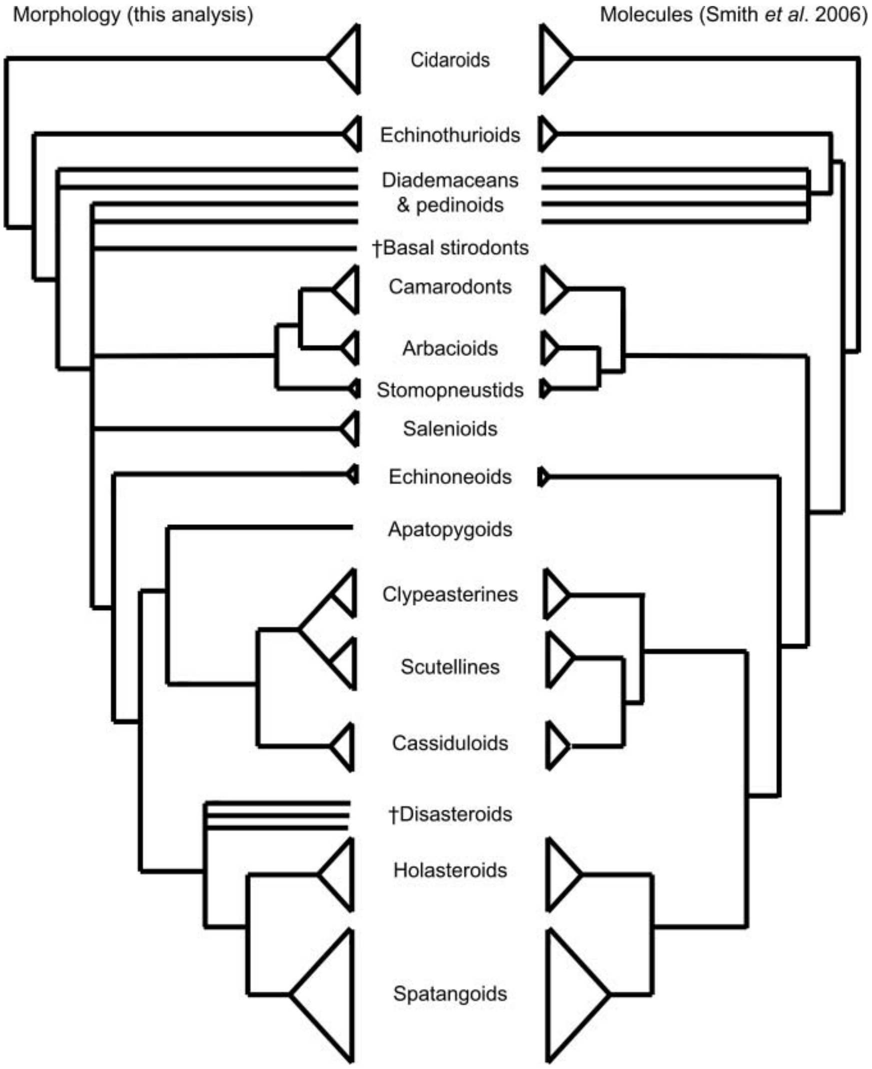

Figure 4. Simplified phylogenetic trees based on morphological data (left-hand side; this paper) and gene sequence data (right-hand side) (from Smith *et al.* 2006).

the Psychocidaridae. Smith & Wright (1989) provided the first and only comprehensive cladistic analysis to date for the group, which closely resembles our results. In our analyses Histocidaridae are always placed as sister group to other cidaroids with 50% bootstrap support (Fig. 2A). Histocidaridae lack complete scrobicular circles, cortical hairs on their spines and retain obviously crenulated tubercles. Their sister group, what Smith & Wright (1989) referred to as Cidaridae, contains three fairly well-defined groups: Psychocidaridae with their club-shaped spines and lack of non-ambulacral plates in the peristome, Ctenocidaridae, with their very poorly differentiated scrobicular tubercles and spines, and the Cidaridae, which includes Goniocidarinae, Cidarinae, Stereocidarinae, Typocidarinae and Phyllacanthinae (Fig. 2A), all of which have highly, flattened secondary spines developed outside the scrobicular ring of interambulacral plates. Test characters offer little help in differentiating amongst these last forms, and our analysis does not provide any firm resolution of this part of the tree. However, it does associate the fossil taxon Typocidarinae with the Stereocidarinae with 52% bootstrap support, and the fossil Tylocidaridae with Psychocidaridae, with 86% bootstrap support (Fig. 2A).

The stem group of the Cidaroida is extensive and includes, in order of branching, Triadotiaridae, Miocidaridae and Serpianotiaridae, Polycidaridae, Diplopodidae and Rhabdocidaridae (Fig. 2A). Of these only the phylogenetic position of Serpianotiaridae had previously been in doubt. In more comprehensive cladistic analyses of Triassic genera Smith (1994c, 2007) found *Serpianotiaris* to be a primitive euechinoid representative. Its perignathic girdle comprises small adradially-positioned

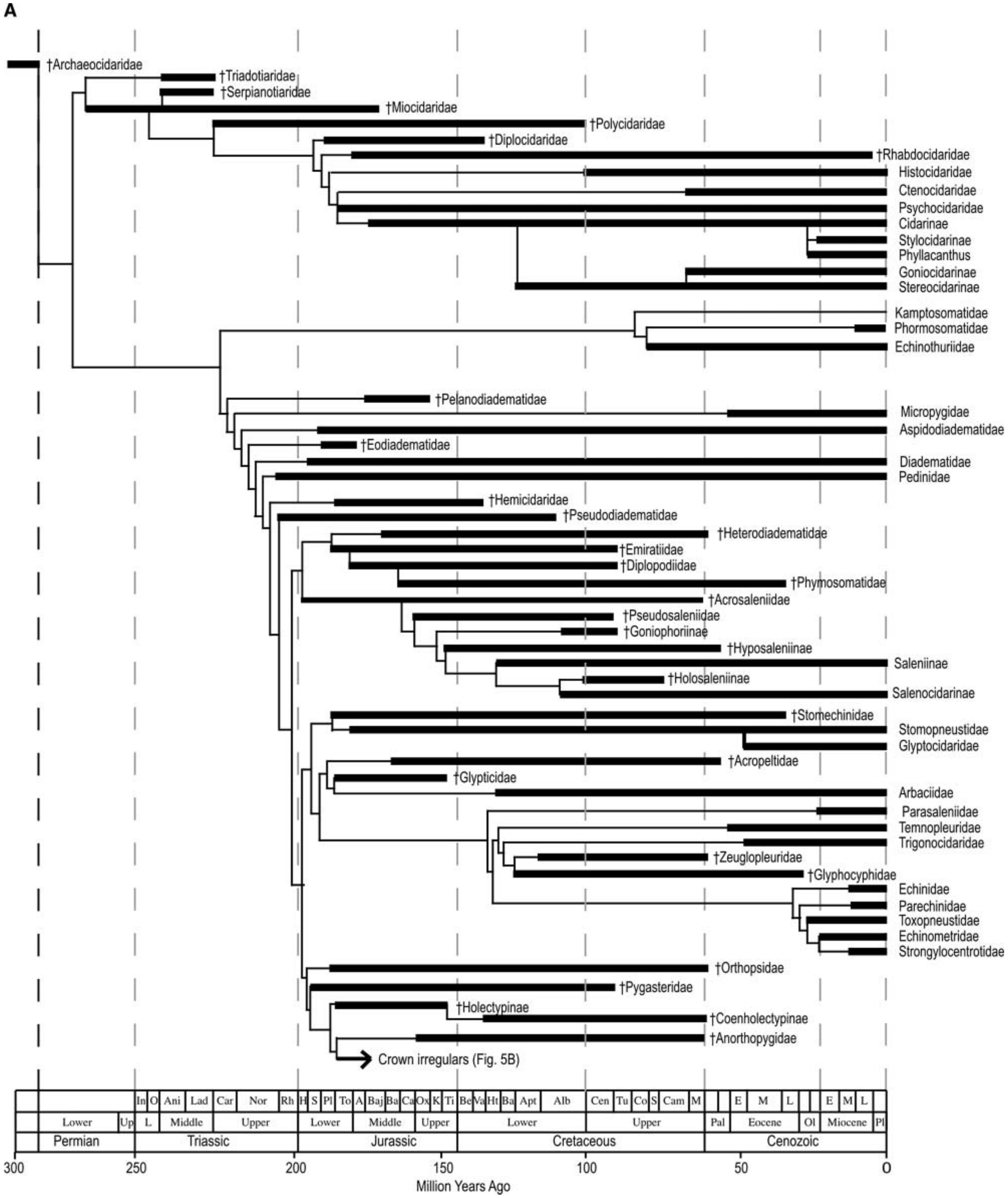

Figure 5. Evolutionary tree for the Echinoidea constructed by calibrating the cladogram shown in Fig. 2 against the observed fossil record (Appendix 3). Heavy lines = observed fossil record; thin lines = inferred missing fossil record. **A,** regular echinoids plus stem group Irregularia. (*Continued*)

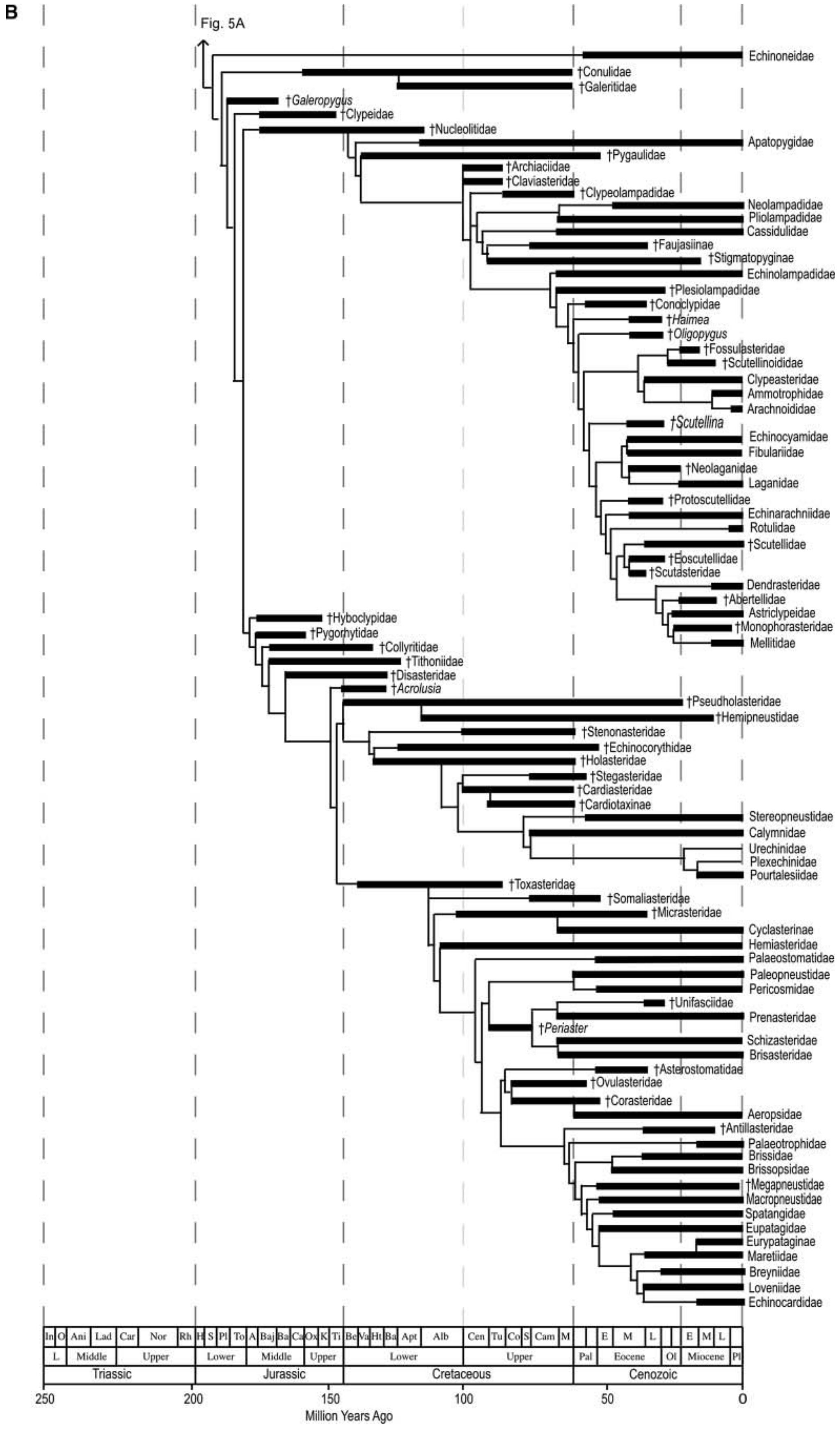

Figure 5. *(Continued).* **B,** crown group Irregularia.

Table 2. Mean cladistic character differences between major groups of extant echinoids. These figures were derived by optimizing characters onto the tree shown in Figure 2 and finding the average number of character step changes between members of each group.

	Outgroup	Cidaroids	E'thurioids	Aulodonts	Salenioids	Stomopn.	arbacioids	Camaro.	Echinone.	Cassids	Clypeast.	Holast.	Spatang.
Outgroup	–												
Cidaroids	0,1184	0,0360											
Echinothurioids	0,1518	0,1814	0,0674										
Aulodonts	0,1557	0,1551	0,1201	0,0838									
Salenioids	0,1832	0,1439	0,2083	0,1314	0,0240								
Stomopneustoids	0,1956	0,1698	0,1564	0,1042	0,1089	0,0397							
Arbacioids	0,2098	0,1824	0,1892	0,1203	0,1328	0,1040	0,0348						
Camarodonts	0,2027	0,1682	0,1755	0,1266	0,1223	0,0744	0,1044	0,0485					
Echinoneoids	0,2242	0,2243	0,2325	0,1890	0,2021	0,1670	0,1833	0,1722	–				
Cassiduloids	0,2989	0,2890	0,3005	0,2582	0,2797	0,2562	0,2650	0,2622	0,1758	0,0767			
Clypeasteroids	0,3343	0,3340	0,3400	0,3100	0,3322	0,3233	0,3294	0,3257	0,2448	0,2162	0,1402		
Holasteroids	0,2925	0,2885	0,2955	0,2616	0,2867	0,2830	0,2974	0,2808	0,2199	0,2229	0,2682	0,0955	
Spatangoids	0,3429	0,3457	0,3502	0,3143	0,3402	0,3300	0,3309	0,3374	0,2580	0,2353	0,3037	0,2088	0,1270

flanges that also cause slight swellings in the ambulacral zone, rather than the broad flanges that extend across the interambulacral zone in other cidaroids. Its position is clearly sensitive to sampling and *Serpianotiaris* may be wrongly positioned in our less comprehensively sampled analysis.

The two poorly known cidaroid taxa that were omitted from the analysis, *Paurocidaris* and *Anisocidaris*, both fall inside the crown group Cidaroida, but cannot be placed with any more precision at present.

Echinothurioids. The most detailed and thorough analysis of echinothurioids to date is that of Mooi *et al.* (2004). They provided a rigorous phylogenetic analysis covering all extant species. Our results differ from those presented by Mooi *et al*. (2004) in two areas, the position of *Sperosoma* and the position of the root, specifically whether Kamptosomidae is primitive or derived. In our analysis we obtained the same ingroup topology whether characters were equal weighted or not. *Sperosoma* is nested high within the group as sister taxon to Hygrosomatinae (Fig. 2A), whereas in the analysis of Mooi *et al*. it remains unresolved forming a trichotomy at the base of the tree. Grouping in the present analysis is based on the expanded hyaline hoofs in *Sperosoma*, *Araeosoma* and *Hygrosoma*, a feature that is unique to that group and for us a convincing synapomorphy. However, bootstrap support for this grouping is only 50%.

The second major difference concerns the placement of *Kamptosoma*, which comes out as a sister group to *Phormosoma* in Mooi *et al*. (2004), but is here resolved as basal member of the Echinothurioida (Fig. 2A). We are completely in agreement with Mooi *et al.* (2004, p. 1917), that *Kamptosoma* is highly derived in its ambulacral structure, its apical disc, its single primary interambulacral tubercles, its crenulated tuberculation and its arrangement of buccal plates. However, Mooi *et al.* made no clear case for why *Kamptosoma* is resolved as sister group to *Phormosoma* and identified no synapomorphies. Furthermore, the topology of the Mooi *et al.* tree is compatible with our analysis when re-rooted on *Kamptosoma.* This suggests that the discrepancy between our two results may relate to choice of outgroup. In Mooi *et al.* the outgroup chosen was *Acrosalenia,* a relatively derived acroechinoid (see Fig. 2A). Our analysis uses a much more extensive selection of potential outgroups and suggests that *Kamptosoma* is primitive compared to the remaining echinothurioids based on the following characters: uniserial arrangement of ambulacral pores and single interambulacral tubercles.

The extremely poor fossil record of the echinothurioids (Kroh 2004) probably accounts for the lack of stem-group members of this group. Pelanodiadematidae share with echinothurioids their primitive peristomial plating (they have a biserial row of ambulacral plates rather than a pair of buccal plates associated with each ambulacrum), but in this analysis *Pelanodiadema* comes out as more derived and sister group to all other euechinoids excluding the echinothurioids (but with less than 25% bootstrap support), based on the shared presence of large, open buccal notches and differentiated phyllodes. A similar position for this taxon was suggested by Smith & Wright (1990).

Diadematoids and pedinoids. All regular echinoids above the echinothurioids have two features in common: their ambulacral plating involves elements which are fused together by the overgrowth of a primary tubercle, and the ambulacral plating on the peristomial membrane is reduced to just a pair of large buccal plates. This clade, the Acroechinoidea, appears in all of our analyses.

Mortensen (1940) and Durham & Melville (1957) grouped together all primitive regular echinoids with grooved teeth, ‘simple’ ambulacral plate compounding and semi-rigid coronas. These comprise the Aulodonta of Mortensen and the Diadematacea of Durham & Melville. Smith (1981) recognized the paraphyletic nature of this grouping and separated pedinoids from diadematoids. However, the diadematoids have continued to be treated as a natural group despite growing evidence that they may not be (e.g. Emlet 1988). There are three groups that have traditionally been united in the diadematoids as separate families, the Aspidodiadematidae, Diadematidae and Micropygidae. Our analyses could not find any convincing synapomorphy to unite the Diadematidae, Micropygidae and Aspidodiadematidae and in all analyses they appeared as separate successive lineages (Fig. 2A). They are therefore best considered as separate clades, each with a long independent history. The term “diademataceans” is here used as an informal name when referring to these three groups in combination.

While our analyses showed no support for a monophyletic Diadematacea, neither did it provide a robust solution to how these three clades are related. After reweighting, the Micropygidae were sister group to all other acroechinoids, but without significant bootstrap support. *Micropyga* has a highly distinctive ambulacral arrangement with biserial plating from apex to peristome, and its aboral tube feet are umbrella-like and completely different in structure from those seen in any other echinoid (Mortensen 1940). Its fossil record is extremely sparse, however, with just *Kierechinus* (Early Eocene) and possibly *Pedinothuria* (Middle Jurassic) as fossil representatives.

Aspidodiadematids have a unique apical disc with membrane-embedded ocular and genital plates of the same size that are not attached to the corona, and has the most simple ambulacral plate compounding of any regular echinoid. In the unweighted tree (Fig. 1) they fall between micropygids and diadematids, but in the reweighted tree (Fig. 2A) they come out as sister group to the Irregularia: in both cases with little bootstrap support. Their fossil record extends back to the Early Jurassic (*Gymnotiara*). Molecular data (Smith *et al.* 2006) confirm a deep divergence between aspidodiadematoids and diadematoids such as *Diadema* and *Centrostephanus*. *Eodiadema*, an Early Jurassic diadematacean with a hemicyclic disc, rather simple ambulacral plate compounding, and either grooved or wedge-shaped teeth, depending upon species, shows a similar ambivalent position, either situated between the Diadematidae and Pedinidae (in the weighted trees – Fig. 2A) or as sister group to the Irregularia (in the unweighted trees – Fig. 1). This interesting paraphyletic or polyphyletic taxon apparently comprises a number of primitive species that are badly in need of restudy.

The Diadematoida is here restricted to the family Diadematidae. These have a hemicyclic apical disc with plates firmly attached to the corona, and their ambulacral plate compounding is more developed than that of aspidodiadematids.

With only one representative of the Pedinoida in our phylogenetic analysis (*Caenopedina*) we cannot comment on whether this is a monophyletic grouping. However, in all of our analyses *Caenopedina* usually emerges as sister group to the Echinacea+Calycina or to the larger group comprising Irregularia, Calycina and Echinacea. It has a long fossil record extending back to the Late Triassic (Kier 1977b).

Stirodonts. Our analyses clearly suggest that the order Stirodonta is not a monophyletic group, but is paraphyletic, by exclusion of the Camarodonta. Furthermore we recognize that there are two major clades differing in apical disc construction. One clade (the phymosomatoids plus salenioids) comprises those forms with a large apical disc that incorporates angular suranal plates, the other (uniting arbacioids, stomopneustids, stomechinids and the camarodonts), all have a small, compact apical disc with a smooth periproctal rim. In the former group the Salenioida and the Phymosomatoida are both monophyletic (Fig. 2A). Acrosaleniids are sister group to the pseudosaleniids and saleniids, while in the Phymosomatoida we have heterodiadematids and polydiadematids with their perforate tuberculation, as sister group to the Phymosomatidae with imperforate tubercles.

The second group, the Echinacea, includes the Stomopneustoida, Arbacioida and Camarodonta but is not well supported by unique synapomorphies. One of the uniting characters is the similarity in size between ambulacral and interambulacral tubercles, but his has evolved parallel in the phymosomatoids as well. In all these analyses we have a basal group of stomechinids, stomopneustids and *Glyptocidaris* (Fig. 2A), all of which have a similar ambulacral plate compounding style. *Glyptocidaris* was previously classified as the only living representative of the Phymosomatoida by Mortensen (1943a) and Durham (1966) on account of its imperforate, crenulated tubercles. Its ambulacral plate compounding, however, resembles that of stomopneustids rather than that of phymosomatoids, and it lacks the characteristic large, monocyclic apical disc of phymosomatoids, having instead a small hemicyclic disc firmly attached to the corona. Arbacioids also share a distinctive style of ambulacral compounding that differs from that of stomopneustids and are consistently identified as a clade. Arbacioids consistently come out as sister group to the Camarodonta (Fig. 2A). Molecular data by contrast (Smith *et al.* 2006) identify arbacioids and stomopneustids as a clade, with camarodonts as their joint sister group.

While there are two well-defined clades (phymosomatoids+salenioids and arbacioids+stomopneustids+camarodonts) it is not yet clear how these relate to a third major clade, the Irregularia. When characters are reweighted by their maximum RI, the two clades group together and are sister group to the Irregularia (Fig. 2A). However, when characters are weighted by their maximum RC the two clades branch successively and the phymosomatoid+salenioid clade alone forms the sister group to the Irregularia. In the unweighted analysis (Fig. 1) the salenioid clade alone is resolved as sister group to the Irregularia. In terms of apical disc structure the most primitive irregular echinoids more closely resemble the phymosomatoid+salenioid clade. However, they have a very similar tubercle structure to orthopsids, which have a more compact apical disc firmly bound to the corona. A more detailed analysis, which includes a wider representation of the basal primitive members of each clade, is required to resolve this trichotomy.

Camarodonts. The largest clade of extant regular echinoids is the Camarodonta. Camarodonts have long been recognized as a natural group sharing a distinctive and derived lantern structure (epiphyses are united above the pyramids to form a strengthening brace) and, in all but a few primitive taxa, echinoid-style ambulacral plate compounding. Traditionally there have been two major groups, the Echinoida, with unornamented tests, generally hemicyclic apical discs and broad ambulacral pore zones that do not form phyllodes, and the Temnopleuroida, with pitted or granular test ornament, dicyclic apical discs and uniserial pore zones. This basic dichotomy is also recognized in our analyses (Echinidea vs Temnopleuridea, Fig. 2A).

Toxopneustids, which were placed within the temnopleuroids by Mortensen (1943a), Durham & Melville (1957) and Durham (1966), are here grouped within the Echinoida, as first suggested by Smith (1988). Toxopneustids uniquely share with echinometrids and strongylocentrotids the derived presence of tooth supports on their epiphyses and we here name this previously unrecognized group the Odontophora. There are, however, two surprising outcomes.

In all analyses that were run *Parasalenia* was consistently resolved as the basal member of the Camarodonta (Fig. 2A).

This is in stark contrast to its overall resemblance to *Echinometra*, in possessing an ovate corona elongated along axis III-5 and massive tubercles with their highly developed mamelon. Additionally, it shares with *Echinometra* the central periproct position within the periproctal membrane. As noted by Mortensen (1943b) and confirmed by our own observations, however, *Parasalenia* lacks tooth supports on its epiphyses, a derived characteristic that unites the echinometrids, strongylocentrotids and toxopneustids. The only other features setting *Parasalenia* apart from that group are the presence of an anal cone (4 valves covering periproct similar to arbaciids) and the lack of broad, multiserial pore bands on the oral surface. Nevertheless, forcing *Parasalenia* to be resolved as sister group to *Echinometra* results in a tree nine steps longer.

A second unexpected outcome is the position of the two fossil families, Zeugopleuridae and Glyphocyphidae. These taxa lack echinoid-style plate compounding and Glyphocyphidae also has a monocyclic apical disc and lacks imperforate tubercles, yet they are identified as derived temnopleuroids rather than basal camarodonts where they have more usually been placed (e.g. Smith & Wright 1996). Here again it is rooting on *Parasalenia* that is causing this anomaly. If the camarodonts were rooted on Glyphocyphidae then a more conventional tree would result, with Zeugopleuridae as sister group to temnopleurids and with a monophyletic Echinoida with parasaleniids as their most primitive member. Unfortunately there are currently no molecular data on *Parasalenia* to provide an independent assessment of camarodont rooting. Incomplete knowledge of the lantern structure of zeuglopleurids and glyphocyphids is also a hindrance and we strongly suspect that the camarodonts are wrongly rooted in this analysis due to our poor knowledge of primitive camarodonts.

Primitive Irregularia. The Irregularia come out as a strongly supported monophyletic group in both unweighted (Fig. 1) and weighted analyses (Fig. 2). At the base come a number of primitive extinct groups. Pygasteridae, with their primitive apical disc and periproct position, are basal, as has long been argued (e.g. Smith 1981; Barras 2006; Saucède *et al.* 2007). Slightly higher come the Holectypidae, then Anorthopygidae and finally the most primitive extant clade of irregular echinoids, the echinoneoids. These basal branches of the Irregularia are, however, poorly supported and sensitive to sampling. For example, Barras (2006), using a different set of outgroup taxa, found *Holectypus* and *Pygaster* to pair together. Also, including the holectypoid *Discoides* destabilizes this region of the tree in certain analyses, breaking up the holectypoid clade and creating a pectinate series with *Discoides* basal, *Coenholectypus* next and *Holectypus* as the most derived, in direct contradiction to their stratigraphic order. In this case the characters pulling *Discoides* down to the base of the holectypoid clade all appear to relate to its small size and presumed retention of juvenile features. Here we favour treating *Holectypus*, *Discoides* and *Coenholectypus* as a clade, and await a more detailed phylogenetic analysis to resolve the position of other holectypoids.

Anorthopygids come out as the next most basal branch of the Irregularia (Fig. 2B). They have traditionally been placed within the Holectypoida (Mortensen 1948a; Smith & Wright 1999), but lack the characteristic large peristome with well-developed buccal notches of that group. Their apical disc is also different, being ethmolytic. They should therefore be removed and treated as a distinct plesion of early primitive irregular echinoid.

Echinoneus has long been recognized as the most primitive of living irregular echinoids (Mortensen 1948a; Durham & Melville 1957; Smith 1981). *Echinoneus* is resolved as sister group to *Conulus, Neoglobator* and *Galerites*, and all four share the following derived characters: presence of glassy tubercles on the oral side, ocular plates I and V separated by interambulacral plates and the presence of pyrinoid plating (demiplates reaching the adradial suture only).

Atelostomates. As has long been recognized, spatangoids and holasteroids together form a monophyletic group (the Atelostomata), with a long stem of primitive extinct forms largely comprising the disasteroids. At the base of the holasteroids comes the taxon *Stenonaster* (Fig. 2B). *Stenonaster* has a compact apical disc like that of spatangoids, but a primitive holasteroid style plastron, and its position has long been uncertain (e.g. David 1988). However, in the unweighted tree (Fig. 1) it is sister group to *Echinocorys,* raising the possibility that it might be a derived echinocorythid. In fact, we have observed that occasionally *Echinocorys* develops an apical disc approaching that of *Stenonaster* in form, by the insertion of ocular plate IV. Next come the pseudholasterids and hemipneustids (Fig. 2B), both of which retain a primitive style of plastron plating with a small labral plate that abuts both sternal plates. The remaining holasteroids all have a meridosternous arrangement of plastron plating and form a monophyletic clade. Within the meridosternous holasteroids there is a crown group of extant forms, all with a very characteristic plastron structure in which plates 3b and 2a are paired and opposite. *Plexechinus* is identified as sister group to the pourtalesiids largely on the basis of similarities of fasciole and apical disc structure, and Urechinidae is identified as their sister group. *Corystus* is placed as the most basal of the living holasteroids on account of its amphisternous plating in the lateral interambulacra.

Relationships of the modern holasteroid taxa are as found in the detailed analysis of Mooi & David (1996), except for the position of *Calymne*, which does not form a clade with *Pourtalesia* here but lies more basal (Fig. 2B). A broadly similar topology resulted in the analysis of holasteroid relationships by Smith (2004) again with the exception of the position of *Calymne*. In Smith's (2004) analysis *Calymne* grouped with stegasterids on the basis that both shared a lateral fasciole.

There have been two detailed phylogenetic analyses of spatangoids recently (Villier *et al*. 2004; Stockley *et al*. 2005). Our analysis identifies basically the same pattern, with toxasterids as the most primitive member and hemiasterids, aeropsids and micrasterids as relatively deep branches that just survive to the present. In the Stockley *et al.* (2005) analysis the bulk of living forms, fell into one of two monophyletic clades, the Paleopneustina and Brissina. These differ in their fasciole arrangement, the Paleopneustina having a lateral or latero-anal fasciole and the Brissina having a subanal fasciole (Smith & Stockley 2005). We found the same arrangement when Atelostomata alone were analysed. However, in our full analysis of all taxa the paleopneustinids form a paraphyletic grade of three taxa; schizasterids, paleopneustids plus pericosmids, and prenasterids plus unifasciids (Fig. 2B). Characters supporting each of these steps all show a large amount of homoplasy (26 characters with mean CI of 0.31, only one character with a CI of 0.5 or greater), whereas the opposing smaller number of characters supporting a monophyletic Paleopneustina have a higher consistency index (6 characters mean CI = 0.53, 5 characters with a CI of 0.5 or greater). Here a large number of weak characters appear to be swamping the signal from a few strong fasciole-based characters.

The stem group of the atelostomates comprises a pectinate series of branches, previously grouped together as disasteroids. In our unweighted analyses (Fig. 1) all the disasteroid taxa form this stem group, with *Hyboclypus* resolved as the most primitive and *Acrolusia* as the most derived, in agreement with Mintz (1968). However, after reweighting *Hyboclypus*, *Pygorhytis* and *Desorella* switch to the base of the Neognathostomata (Fig. 2B). The position of these three taxa is clearly unstable, and sensitive to how characters are weighted. In the detailed genus-level analysis by Barras (2007), some disasteroids (disasterids) were found to be more closely-related to spatangoids and others (collyritids, tithoniids) to holasteroids. We were unable to confirm this but none of the branches in this part of the tree are well supported.

Neognathostomates. The sister group to the Atelostomata is the Neognathostomata. This comprises the traditional groups of Cassiduloida and Clypeasteroida. As in all analyses from Smith (1981) onwards, the Clypeasteroida are identified as a monophyletic clade and the Cassiduloida as a paraphyletic grade (Fig. 2B). Within the paraphyletic cassiduloids a series of extinct and extant clades branch off on the line leading up to the Clypeasteroida. At the base clypeids and nucleolitids represent extinct groups that belong to the stem group of the entire neognathostomate clade. Apatopygidae are the first extant sister group to branch off, followed by a larger clade comprising the modern Cassidulidae, Neolampadidae and Pliolampadidae amongst others. In our equal-weights analysis the Echinolampadidae also fall into this clade (Fig. 1), but after weighting characters *a posteriori* echinolampadids move crownward to become the closest extant cassiduloid group to the clypeasteroids (Fig. 2B). The detailed branching order of these various extant and extinct groups is, however, poorly supported and sensitive to taxon sampling. Furthermore, previous workers have not agreed upon the identity of the extant sister group of the clypeasteroids with neolampadids (Suter 1994), echinolampadids (Mooi 1987, 1990a) and apatopygids (Smith 2001) all being suggested. What is, however, very clear now is that some extinct taxa traditionally grouped as cassiduloids or oligopygoids now fall into the stem group of the clypeasteroids. The most basal of these is the clade Faujasiidae, which pulls the stem group deep into the Cretaceous. Although faujasiids hold this position in both the unweighted and unweighted trees (Figs 1, 2) there are no unique synapomorphies supporting this placement and bootstrap support at this node is negligible. Higher groupings, however, are better supported and more securely tied to the Clypeasteroida. *Plesiolampas*, *Conoclypus* and the oligopygoids *Oligopygus* and *Haimea* are extinct taxa that form the immediate outgroups to crown group clypeasteroids. *Conoclypeus* and the oligopygoids share with clypeasteroids the presence of a well-developed and morphologically very similar perignatic girdle and lantern as adults, and multiple ambulacral pores piercing ambulacral plates. *Plesiolampas* shares with *Conoclypus* and the oligopygoids a similar ambulacral structure, with small demiplates running along the adradial suture. In oligopygoids these demiplates are excluded from the interior and the larger ambulacral plates are thus pierced by multiple pores, as in clypeasteroids. From our analysis it is not clear whether *Oligopygus* and *Haimea* form a clade or not. In our equal-weights analysis these two taxa pair together (Fig. 1), but in some less inclusive analyses and after weighting *Oligopygus* is placed closer to the crown clypeasteroids than *Haimea.* Within crown group clypeasteroids the arrangement of taxa is stable with and without reweighting. There is a basal dichotomy between clypeasterines and the rest, followed by a second dichotomy separating the fibulariids plus laganines from scutellines (*Scutellina* being sister group to both). Lunulate forms are apparently not monophyletic as was already suggested by Seilacher (1979). However, anal lunules are confined to the mellitid+monophorasterid clade and appear to have evolved just once (Mooi *et al.* 2000).

There are, however, a couple of unexpected results. Firstly rotulids, which were treated as a separate group from scutellines by Mortensen (1948b) and as a member of the Laganina by Durham (1955), nest within the Scutellina in our analyses (Figs 1, 2B). Durham (1955) identified rotulids as laganines because both develop uniserial interambulacral plating close to the apical disc. Nevertheless, although clearly very derived, there are several characters that unit rotulids with more advanced scutellines, including the branched food grooves and a characteristic asymmetry of adoral interambulacral plates. In the laganids, fibulariids and echinocyamids the posterior suture of interambulacral plate 4.b.2 lies aborally of the posterior suture of plate 4.a.2, whereas in *Rotula* and the scutellines it lies adorally. Forcing rotulids to group with laganines results in significantly longer trees. However, their precise position within the scutellines is sensitive to weighting. Under equal weights (Fig. 1) rotulids are identified as a derived clade, sister group to the lunulate group of *Abertella* and all the lunulate forms except *Scutaster*. In the reweighted analysis (Fig. 2B) it resolves as an early offshoot more derived than Dendrasteridae, but prior to any other lunulate forms. However, when just Recent taxa are analysed rotulids shift to become the immediate sister group to the mellitids, monophorasterids and astriclypeids. More work is required to resolve their precise sister group relationships amongst scutellines.

The other somewhat anomalous finding is the position of *Taiwanaster* at the base of the scutelline tree (Figs 1, 2B). *Taiwanaster* Wang, 1984 is a taxon based on tiny forms exhibiting only juvenile features. As shown by Mooi (1990b) *Taiwanaster* is probably not primitive, but a neotenous form closely related to the Pacific genus *Scaphechinus.* We therefore place no weight on the fact that this taxon roots at the bottom of the tree and accept Mooi's arguments that *Taiwanaster* is a neotenously derived scutelline.

Comparing cladogram structure with the fossil record of first occurrences

If the structure of the tree we have found is approximately correct and the fossil record reasonably complete we would expect to see a good correspondence between the order in which clades branch and the temporal order in which they appear in the fossil record (Norell & Novacek 1992; Benton & Hitchin 1997; Benton *et al*. 1999). Alternately, the mismatch in the observed versus the inferred stratigraphical ranges can provide a measure of the quality of the fossil record. Although these comparisons are best done with a phylogenetic tree that has been independently corroborated through morphological and molecular data, insights into the nature of the fossil record are still possible if we can assume that our tree is reasonably accurate. Here we quantify the match between cladogram and stratigraphy using Huelsenbeck's (1994) stratigraphical consistency index (SCI), Benton's (1995) relative completeness index (RCI) and Wills' (1999) Gap Excess Ratio (GER). SCI looks at the relative ages of sister taxa in every three-taxon statement in the cladogram. In each three-taxon statement, there is a pair of taxa that are more closely related to each other than either is to the third. If both are of similar age or younger than their presumed outgroup then the node is said to be consistent. If, on the other hand, the outgroup taxon only appears in the fossil record sometime after the first appearance of either of the more derived pair then that node is said to be inconsistent. The SCI is then simply the proportion of consistent nodes found. The RCI measures the inferred completeness of the fossil record rather than the match in branching order *per se*. It does this by looking at the ratio of known ranges to the inferred ranges (i.e. it measures the amount of ghost lineage that must be inferred for any phylogenetic hypothesis when calibrated against known stratigraphic ranges. The Gap Excess Ratio (GER: Wills 1999) measures the relative amount of implied gap when a cladogram is calibrated against stratigraphy and is the best measure for comparing amongst different datasets. It scales the minimum implied gap (MIG) (measured in absolute time) between the sum of ghost ranges obtained for the best (Gmin) and worst (Gmax) fits of a given set of stratigraphic data onto any tree topology. The GER is widely used and behaves well in simulations (Finarelli & Clyde 2002).

Appendix 3 lists the genera we currently assign to each family listed here, and their stratigraphic age, while Fig. 5 shows the cladogram of Fig. 2 calibrated against the observed fossil record. Using these data all three measures of fit were implemented using the computer program Ghosts (Wills 1999) with 500 random resampling analyses to determine the significance of fit. Because this program limits tree size to 65 taxa, we split the tree into four non-overlapping partitions and ran analyses on each separately. Our four groups were: (1) total group Atelostomata, (2) total group Neognathostomata, (3) cidaroids+aulodonts, and (4) Echinacea+Calycina plus basal Irregularia. From these individual results it is possible to derive an overall score for the whole tree. Results are shown in Table 3.

Overall the fit of cladogram to stratigraphy was extremely good and significantly better than random. With a GER at 0.8 echinoids show a much better correspondence than do the majority of dinosaur phylogenies investigated by Wills *et al*. (2008). The neognathostomes have the highest GER (0.93) while Echinacea+Calycina have the lowest (0.6) supporting the idea that Echinacea+Calycina have a relatively poor fossil record because they have adapted for life in hard bottoms where preservation potential is considerably reduced (Kier 1977a; Greenstein 1991).

Classification

Here we present a primary framework for the classification of the group based on extant taxa into which fossil taxa have then be incorporated. The reasons for adopting this approach are straightforward. Extant taxa are not only

Table 3. Summary of the Stratigraphic Consistency Index (SCI), Relative Consistency Index (RCI), Minimum Implied Gap (MIG), and Gap Excess Ratio (GER) results. See text for explanation.

	Min. gap	Max. gap	Total ranges*	MIG	GER	RCI	Total nodes	Consit. nodes	SCI	RCI uncertainty	SCI uncertainty
Cidaroids+aulodonts	365	7442	2234	1739	0,81	22,2	30	12	0,4	0,20%	12,20%
Echinacea+Calycina +basal irregulars	202	3954	2855	1714	0,6	40	42	18	0,43	0,50%	26,00%
Atelostomata	187	5492	2232	1026	0,84	54	48	23	0,48	1,00%	1,00%
Neognathostomes	169	4529	1256	473	0,925	62,3	36	23	0,64	0,50%	0,50%
all taxa	923	21417	8577	4952	0,8	42,3	156	76	0,49		

Note: *Total observed ranges.

more completely documented in terms of their morphology, but are also more completely known (the rate at which new species are being discovered is much higher in the fossil record compared to the extant fauna). Furthermore, we are not reliant on just one source of data for constructing phylogenies: all phylogenetic hypotheses are open to independent testing using both morphological and molecular data. Finally, basing our classification on the hierarchical arrangement of extant taxa thus has the distinct advantage of allowing new fossil finds to be incorporated without disrupting the structure of the classification (Forey 1992).

For incorporating fossil taxa the concepts of stem-group and crown group are extremely important (Jefferies 1979; Smith 1994b; Donoghue 2005). A crown group is a clade defined by reference to two extant taxa and comprises their latest common ancestor and all its descendants. A total group is a crown group plus all the fossil taxa more basal back to the latest common ancestor of the crown-group's immediate extant sister taxon. Fossil taxa belong to only one stem group and can be ordered according to their position relative to the crown group. In most cases we prefer to base formal taxonomic names on total groups with fossils assigned to stem group. We use formal Linnaean categories for family level and ordinal level only, leaving names without category at intermediate levels. Fossil taxa are indicated by the symbol † in front of their name. We largely follow the structure of the cladogram shown in Fig. 2, based on our reweighted analysis, unless otherwise discussed in the text.

Class **Echinoidea** Leske, 1778

Stem group **Echinoidea**
† Family **Archaeocidaridae** McCoy, 1844

Crown group **Echinoidea**

Subclass **Cidaroidea** Smith, 1984
  Order **Cidaroida** Claus, 1880
  Stem group **Cidaroida**
    † Family **Triadotiaridae** Hagdorn, 1995
    † Family **Serpianotiaridae** Hagdorn, 1995
    † Family **Miocidaridae** Durham & Melville, 1957
    † Family **Polycidaridae** Vadet, 1988
    † Family **Diplocidaridae** Gregory, 1900
    † Family **Rhabdocidaridae** Lambert, 1900
  Crown group **Cidaroida**
    Superfamily **Histocidaridea** nov.
      Family **Histocidaridae** Lambert, 1900

Superfamily **Cidaridea** [possibly includes *Paurocidaris* Kier, 1977b]
  Family **Ctenocidaridae** Mortensen, 1928a [incertae sedis]
  Family **Psychocidaridae** Ikeda, 1936 [includes † **Roseicidaridae** Vadet, 1991]
  Family **Cidaridae** Gray, 1825 [includes **Cidarinae** Mortensen, 1928a; †**Stereocidarinae** Lambert, 1900; †**Typocidaridae** Vadet, 1988; **Phyllacanthina** Smith & Wright, 1989; **Goniocidaridae** Mortensen, 1928a]

Subclass **Euechinoidea** Bronn, 1860

Order **Echinothurioida** Claus, 1880

Family **Kamptosomatidae** Mortensen, 1934
Family **Phormosomatidae** Mortensen, 1934 [includes **Paraphormosomatinae** Smith & Wright, 1990]
Family **Echinothuriidae** Thomson, 1872a [includes **Hygrosomatinae** Smith & Wright, 1990 and **Sperosomatinae** Smith & Wright, 1990]

Infraclass **Acroechinoidea** Smith, 1981
† Family **Pelanechinidae** Groom, 1887 [includes **Pelanodiademidae** Hess, 1972]
Order **Micropygoida** nov.
  Family **Micropygidae** Mortensen, 1903b
Order **Diadematoida** Duncan, 1889 [restricted usage]
  Family **Diadematidae** Gray, 1855
Order **Aspidodiatematoida** nov.
  Family **Aspidodiadematidae** Duncan, 1889
Order **Pedinoida** Mortensen, 1939
  Family **Pedinidae** Pomel, 1883

Carinacea nov. [refers to shared presence of keeled teeth]
[incertae sedis]
† Family **Hemicidaridae** Wright, 1857 [includes **Pseudocidarinae** Smith & Wright, 1993]
† Family **Pseudodiadematidae** Pomel, 1883
† Family **Orthopsidae** Duncan, 1889

Crown group **Carinacea**
Calycina Gregory, 1900
  Stem group **Calycina**
  Order **Phymosomatoida** Mortensen, 1904
    † Family **Polydiadematidae** Hess, 1972
    † Family **Diplopodiidae** Smith & Wright, 1993
    † Family **Heterodiadematidae** Smith & Wright, 1993
    † Family **Emiratiidae** Ali, 1990
    Family **Phymosomatidae** Pomel, 1883
  Order **Salenioida** Delage & Hérouard, 1903
    † Family **Acrosaleniidae** Gregory, 1900
    † Family **Pseudosaleniidae** Vadet, 1999b
    † Family **Goniophoridae** Smith & Wright, 1990
    † Family **Hyposaleniinae** Mortensen, 1934
  Crown group **Calycina**
    Family **Saleniidae** L. Agassiz, 1838 [includes **Salenocidarini** Smith & Wright, 1990 and † **Holosaleniini** Smith & Wright, 1990]

Echinacea Claus, 1876
Order **Stomopneustoida** nov.
  † Family **Stomechinidae** Pomel, 1883
  Family **Stomopneustidae** Mortensen, 1903b
  Family **Glyptocidaridae** Jensen, 1982
Unnamed clade [Arbacioida + Camarodonta]
  † Family **Glyphopneustidae** Smith & Wright, 1993 [incertae sedis]

Order **Arbacioida** Gregory, 1900
 † Family **Acropeltidae** Lambert & Thiéry, 1914
 † Family **Glypticidae** Lambert & Thiéry, 1914
  Family **Arbaciidae** Gray, 1855 [includes **Coelopleuridae** Märkel, 1969]
Order **Camarodonta** Jackson, 1912
  Family **Parasaleniidae** Mortensen, 1903b [possibly grouping low because of rooting problems]
Infraorder **Temnopleuridea** nov.
  Family **Temnopleuridae** A. Agassiz, 1872
  Family **Trigonocidaridae** Mortensen, 1903b
 † Family **Zeuglopleuridae** Lewis, 1986
 † Family **Glyphocyphidae** Duncan, 1889
Infraorder **Echinidea** nov.
  Family **Echinidae** Gray, 1825
  Family **Parechinidae** Mortensen, 1903b
Superfamily **Odontophora** nov.
  Family **Toxopneustidae** Troschel, 1872
  Family **Strongylocentrotidae** Gregory, 1900
  Family **Echinometridae** Gray, 1855

Irregularia Latreille, 1825
Stem group **Irregularia**
 † Family **Pygasteridae** Lambert, 1900
Order **Holectypoida** Duncan, 1889
 † Family **Discoididae** Lambert, 1900
 † Family **Coenholectypidae** Smith & Wright, 1999
 † Family **Holectypidae** Lambert, 1900
 † Family **Anorthopygidae** Wagner & Durham, 1966b

Crown group **Irregularia**
Order **Echinoneoida** H. L. Clark, 1925
  Family **Echinoneidae** L. Agassiz & Desor, 1847
Superfamily **Conulidea** nov.
 † Family **Conulidae** Lambert, 1911a
 [† Family **Neoglobatoridae** Endelman, 1980]
 † Family **Galeritidae** Gray, 1825

Microstomata Smith, 1984
Microstomata *incertae sedis*
 † Family **Desorellidae** Lambert, 1911a
 † Genus *Hyboclypus* L. Agassiz, 1839 [‘hyboclypids’ of Barras, 2007]
 † Genus *Pygorhytis* Pomel, 1883 [Family † **Pygorhytidae** Lambert, 1909b]
 † Family **Galeropygidae** Lambert, 1911a

Crown group **Microstomata**
Neognathostomata Smith, 1981
Stem group **Neognathostomata**
 † Family **Clypeidae** Lambert, 1898
 † Family **Nucleolitidae** L. Agassiz & Desor, 1847
Crown group **Neognathostomata**
  Family **Apatopygidae** Kier, 1962
 † Family **Pygaulidae** Lambert, 1905
 † Family **Archiaciidae** Cotteau & Triger, 1869 [includes † **Claviasteridae** Ali, 1992]
 † Family **Clypeolampadidae** Kier, 1962
Order **Cassiduloida** L. Agassiz & Desor, 1847
Superfamily **Cassidulina** Philip, 1963b

Family **Cassidulidae** L. Agassiz & Desor, 1847
Superfamily **Neolampadina** Philip, 1963b [ex. Neolampadoida]
Family **Neolampadidae** Lambert, 1918a [includes † **Pliolampadidae** Kier, 1962]
Order **Echinolampadoida** nov.
Family **Echinolampadidae** Gray, 1851a
Order **Clypeasteroida** L. Agassiz, 1835
Stem group **Clypeasteroida**
† Family **Faujasiidae** Lambert, 1905 [includes † **Stigmatopyginae** Smith & Wright, 2000]
† Family **Plesiolampadidae** Lambert, 1905
† Family **Conoclypeidae** von Zittel, 1879
† Family **Oligopygidae** Duncan, 1889
Crown group **Clypeasteroida**
Suborder **Clypeasterina** L. Agassiz, 1835
Family **Clypeasteridae** L. Agassiz, 1835 [includes **Clypeasterinae** L. Agassiz, 1835; **Ammotrophinae** Durham, 1955; **Arachnoidinae** Duncan, 1889]
† Family **Fossulasterinae** Philip & Foster, 1971 [includes † **Scutellinoididae** Irwin, 1995]
Suborder **Scutellina** Haeckel, 1896
Stem group **Scutellina**
† Family **Scutellinidae** Pomel, 1888a
Infraorder **Laganiformes** Desor, 1847
Family **Fibulariidae** Gray, 1855 [includes **Echinocyamidae** Lambert & Thiéry, 1914]
Family **Laganidae** A. Agassiz, 1873 [includes **Laganinae** A. Agassiz, 1873; † **Neolaganinae** Durham, 1954]
Infraorder **Scutelliformes** Haeckel, 1896
Family **Taiwanasteridae** Wang, 1984 [incertae sedis, juvenile features]
Stem group **Scutelliformes**
† Family **Protoscutellidae** Durham, 1955
Crown group **Scutelliformes**
Family **Echinarachniidae** Lambert in Lambert & Thiéry, 1914
Family **Dendrasteridae** Lambert, 1900
Family **Rotulidae** Gray, 1855
† Family **Scutellidae** Gray, 1825
† Family **Eoscutellidae** Durham, 1955
† Family **Scutasteridae** Durham, 1955
† Family **Abertellidae** Durham, 1955
Family **Astriclypeidae** Stefanini, 1912
† Family **Monophorasteridae** Lahille, 1896
Family **Mellitidae** Stefanini, 1912

Atelostomata von Zittel, 1879
Stem group **Atelostomata** [‘disasteroids’]
† Family **Collyritidae** d’Orbigny, 1853
† Family **Tithoniidae** Solovjev, 1966
† Family **Disasteridae** Gras, 1848
† Family **Acrolusiidae** Mintz, 1968
Crown group **Atelostomata**
Order **Holasteroida** Durham & Melville, 1957
Stem group **Holasteroida**
† Family **Stenonasteridae** Lambert, 1922
† Family **Hemipneustidae** Lambert, 1917
† Family **Pseudholasteridae** Smith & Jeffery, 2000
Meridosternata Lovén, 1883
† Family **Echinocorythidae** Wright, 1857
† Family **Holasteridae** Pictet, 1857
Infraorder **Cardiasterina** Pomel, 1883 [includes **Stegasterina** Lambert, 1917]
† Family **Stegasteridae** Lambert, 1917

- † Family **Cardiasteridae** Lambert, 1917 [includes **Cardiotaxinae** Smith & Jeffery, 2000]
- Crown Group Holasteroida
  - Family **Corystidae** Foster & Philip, 1978 [incertae sedis; Boyko (2008) proposed an emendation of spelling to **Corystusidae** to remove homonymy with a crab family, decision pending]
  - Family **Calymnidae** Mortensen, 1907
- Infraorder **Urechinina** H.L. Clark, 1946
  - Family **Carnarechinidae** Mironov, 1993
  - Family **Urechinidae** Duncan, 1889
  - Family **Plexechinidae** Mooi & David, 1996
  - Family **Pourtalesiidae** A. Agassiz, 1881

Order **Spatangoida** L. Agassiz, 1840a

Stem group **Spatangoida**

- † Family **Toxasteridae** Lambert, 1920a
- † Family **Somaliasteridae** Wagner & Durham, 1966a
- Crown group **Spatangoida**
  - Family **Palaeostomidae** Lovén, 1868
  - Family **Hemiasteridae** H. L. Clark, 1917
- Suborder **Micrasterina** Fischer, 1966
  - † Family **Plesiasteridae** Lambert, 1920a
  - Family **Micrasteridae** Lambert, 1920a [includes **Cyclasterinae** Poslavskaya, 1964]
  - Family **Aeropsidae** Lambert, 1896 [includes † **Corasterinae** Lambert & Thiéry, 1924]
  - † Family **Ovulasteridae** Lambert, 1896
- Suborder **Paleopneustina** [possibly paraphyletic]
  - † Family **Periasteridae** Lambert, 1920a
  - Family **Schizasteridae** Lambert, 1905 [includes **Brisasterinae** Markov, 1994]
  - Family **Prenasteridae** Lambert, 1905 [includes † **Unifasciidae** Cooke, 1959]
- Superfamily **Paleopneustidea** A. Agassiz, 1904
  - Family **Pericosmidae** Lambert, 1905
  - Family **Paleopneustidae** A. Agassiz, 1904
- Suborder **Brissidina** Stockley *et al.*, 2005
  - † Family **Antillasteridae** Lambert, in Lambert & Thiéry, 1924
  - † Family **Asterostomatidae** Pictet, 1857
  - Family **Palaeotropidae** Lambert, 1896
  - Family **Brissidae** Gray, 1855 [including **Brissopsidae** Lambert, 1905]
- Superfamily **Spatangidea** Fischer, 1966
- Stem group **Spatangidea**
  - † Family **Megapneustinae** Fourtau, 1905
  - † Family **Macropneustidae** Lambert, 1905
- Crown group **Spatangidea**
  - Family **Spatangidae** Gray, 1825
  - Family **Eupatangidae** Lambert, 1905
  - Family **Maretiidae** Lambert, 1905
  - Family **Eurypataginae** Kroh, 2007
  - Family **Loveniidae** Lambert, 1905 [includes **Breyninae** Lambert, 1905; **Echinocardiidae** Cooke, 1942]

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Note

Appendices 2 and 3 can be viewed online.

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Appendix 1: Morphological characters scored for echinoid taxa

A. Shape and general features

Test shape

A1. *Symmetry of test outline in plan view: basically circular and pentaradial (0); test with evident bilateral symmetry passing along plane III-5 (1); test ovate with bilateral symmetry passing through plane I-3 (2).* Bilateral symmetry has evolved at least twice in echinoids, with the axis of symmetry either passing through the plane defined by ambulacrum III, interambulacrum 5 (many irregular echinoids), or through ambulacrum I—interambulacrum 3 (some camarodonts). We refer here only to the outline shape and ignore any bilateral symmetry defined by periproct position or the presence of an anal sulcus.

A2. *Corona dorso-ventrally flattened: no (0); yes, with tumid margin (1); yes, with sharp margin (2).* This character refers to discoidal tests such as those of laganids (Fig. 6K with a thickened rounded margin, or mellitids (Fig. 6J) with thin, sharp margins.

A3. *Corona high, hemispherical to dome-shaped, with flattened oral surface: no (0); yes (1).* (Fig. 6D)

A4. *Test profile in lateral profile: distinctly taller in posterior third of test (0); tallest in central third of test (1); tallest in anterior third of test (2).* In most echinoids the test is domed and the tallest point on the test coincides with the central portion of the test. However, there are some taxa that are distinctly wedge-shaped, with the test sloping from the posterior to the anterior (schizasterids and *Aceste* for example: Fig. 6A) and whose tallest point lies close to the posterior border. Similarly there are a few taxa such as Archiaciidae (Fig. 6B) in which the test slopes in the opposite direction and whose tallest point lies close to the anterior border. [ordered]

A5. *Apical region of test elongated as a rostrum: no (0); yes (1).* A very few echinoids such as *Hagenowia* have the anterior portion of the test pinched and extended to form a rostrum (Fig. 6C).

A6. *Anterior margin in plan view: convex anterior (0); flattened (1); distinct notch/indentation (2).* The outline of the test usually forms an unbroken curve around the anterior or at most becomes flattened. However in many spatangoids and holasteroids the frontal region is depressed with ambulacrum III sunken and the walls of the adjacent interambulacra sloping inwards. This character can be polarized as juveniles always lack an indentation We score an anterior sulcus as present if, in the adult, the anterior border is concave in plan view. We draw a distinction between a sulcus, which is a broad, depressed zone affecting both ambulacral

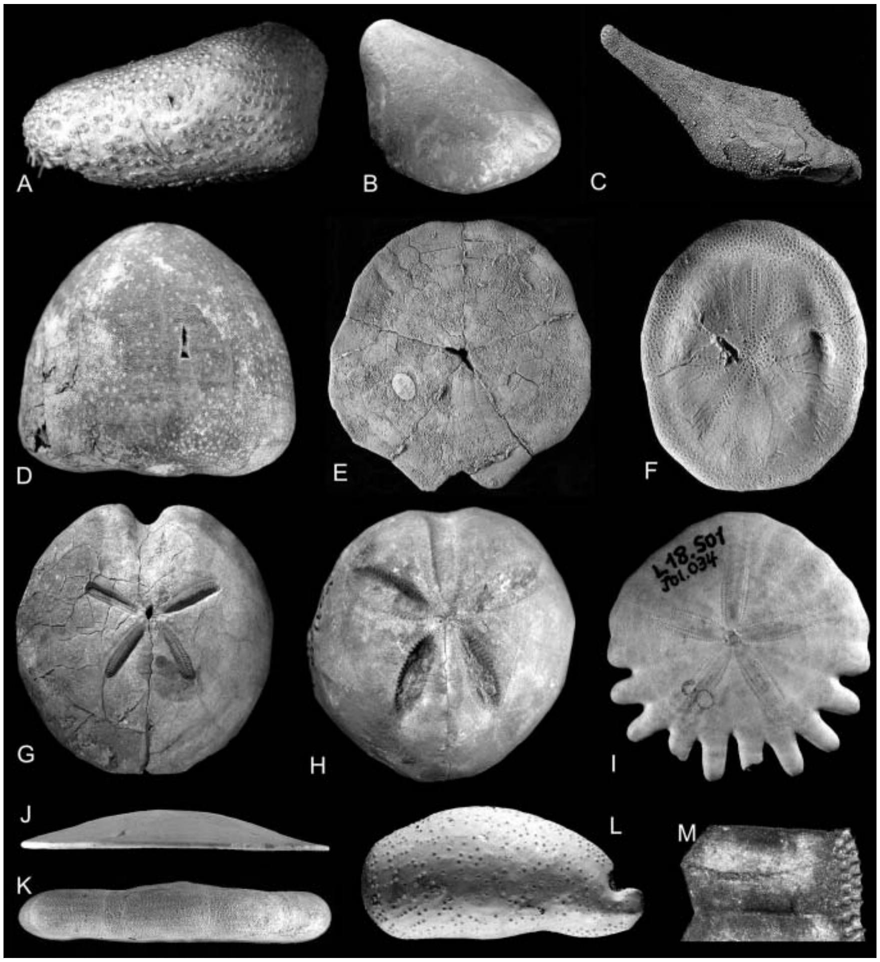

Figure 6. Shape and general features of the test. **A**, *Aceste* (spatangoid) in lateral profile, anterior to the left. **B**, *Claviaster* (stem neognathostomate) in lateral profile, anterior to the left. **C**, *Hagenowia* (stem holasteroid) in lateral profile, anterior to the left. **D**, *Echinocorys* (stem holasteroid) in posterior profile. **E**, *Abertella* (scutelline clypeasteroid) in oral view, showing posterior notch. **F**, *Cubanaster* (clypeasteroid) in apical view, showing thickened rim. **G**, *Pericosmus* (spatangoid) in apical view with deep anterior sulcus; **H**, *Trachyaster* (spatangoid), in apical view with shallow anterior sulcus. **I**, *Rotuloidea* (clypeasteroid) in apical view with perradial, adradial and interradial notches around the posterior. **J**, *Mellita* (clypeasteroid) in lateral profile. **K**, *Laganum* (clypeasteroid) in lateral profile. **L**, *Pourtalesia* (holasteroid) in lateral profile, anterior to the left. **M**, *Miocidaris* (stem cidaroid); internal surface of two interambulacral plates showing denticulate adradial margin. Not to scale.

and adjacent interambulacral columns (Fig. 6H), and a notch, which is a sharply defined indentation (Fig. 6G). [ordered]

A7. *Subanal portion of test projecting as a distinct protuberance: no (0); yes (Fig. 6L) (1).*

A8. *Lunules: in posterior paired ambulacra (I and V); no (0); yes (1).*

A9. *Lunules: in anterior paired ambulacra (II and IV); no (0); yes (1).*

A10. *Lunules: in anterior ambulacrum (III); no (0); yes (1).*

A11. *Lunules: in anterior paired interambulacra (2 and 3); no (0); yes (1).*

A12. *Perradial notches or lunules: no (0); yes, constructed from cross-linked plating (1); yes, constructed from festooned plating (2).* Seilacher (1979) drew the distinction between lunules formed by resorption, where plate sutures run vertically between apical and oral surfaces within the lunules opening (cross-linked), and those formed by closure of an original notch, where plate boundaries curve obliquely inwards (festooned).

A13. *Anal lunule: absent (0); present (1).* Only certain scutellines have a lunule in the posterior interambulacral mid-line into which the periproct opens.

A14. *Edge of test raised around anal lunule on aboral surface forming distinct rim: no (0); yes (1).* In *Monophoraster* there is a distinct rim around the anal lunule whereas in mellitids the anal lunule lies flush with the test.

A15. *Ambital notches in posterior interambulacra: absent (0); distinct indentation in posterior*

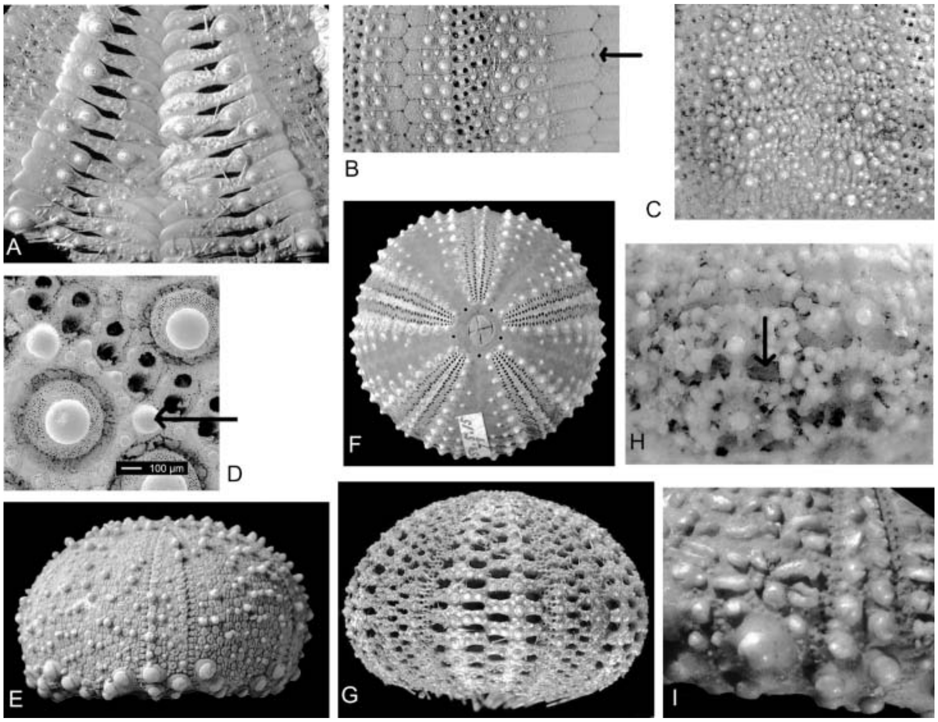

Figure 7. Test plating and ornamentation. **A**, *Araeosoma* (echinothurioid), detail of aboral interambulacral plating showing the large gaps between plates. **B**, *Mespilia* (temnopleurid), detail of ambital plating showing small pin-prick depressions at triple suture junctions in ambulacral and interambulacral (arrowed) zones. **C**, *Ortholophus* (temnopleuroid), detail of lateral interambulacral plating showing raised reticulate ornamentation in between the tubercles. **D**, *Echinoneus* (echinoneoid). SEM image of plate surface showing glassy tubercles (arrow) scattered amongst the larger tubercles. **E**, *Codiopsis* (stem arbacioid) in lateral profile showing aboral surface covered in well-developed glassy tubercles. **F**, *Arbacia* (arbacioid), in lateral profile showing adapical interradial naked zones. **G**, *Temnotrema* (temnopleuroid) in lateral view, showing well-developed sutural pits. **H**, *Zeuglopleurus* (temnopleuroid), detail of ambital interambulacral plates showing large pits (arrow) developed beneath and to either side of the primary tubercle. **I**, *Glypticus* (stem arbacioid), detail of lateral plating showing coarse epistromal ornament on upper plates. Not to scale.

interambulacrum (1). Most echinoids have a rounded or flattened posterior face in plan view, but a few scutellines have a distinct indentation to the test at the midline of the posterior interambulacrum (e.g. abertellids Fig. 6E).

A16. *Notches developed at adradial sutures around the posterior of the test as well as at perradial and interradial sutures: no (0); yes (1)*. In rotulids all three posterior interambulacra are indented which, together with the ambulacral lunules, creates a digitate posterior margin (Fig. 6I).

Plate-plate characteristics

A17. *Test coronal plates: interambulacral plating imbricate (0); weakly imbricate (interior view) adapically but firmly sutured adorally (1); interambulacral plates firmly sutured together throughout (2)*. [ordered]

A18. *Ambulacral plates: imbricate beneath adradial edge of interambulacral plates (0); vertically abut against interambulacral plates (1)*.

A19. *Adradial internal edge of interambulacral plates smooth (0); denticulate to accommodate ambulacral plates (1)*. In certain primitive cidaroid groups the interior adradial suture of the interambulacral zones is grooved and ridged, usually with a small raised tubercle that articulates with a shallow socket in the overlapping ambulacral plate (Fig. 6M). In echinothurioids the interambulacral plates overlap ambulacral plates without such articulation facets.

A20. Marginal of test raised as a thickened rim: no (0); yes (1) (e.g. *Cubanaster* Fig. 6F).

A21. Membranous gaps present between interambulacral plates: no (0); yes (1) (Fig. 7A).

A22. Membranous gaps present between ambulacral plates: no (0); yes (1).

Test ornamentation

A23. *Coronal plates: smooth and unornamented (0); with sutural pits at triple points (1)*. Note that sutural pits are depressions of the plate surface

(Fig. 7G) and are distinct from gaps left between raised external ornament of the plate.

A24. *Apical disc plates: smooth and unornamented (except for tubercles) (0); with deep and obvious sutural pits (1); with plate surface covered in small pits or furrows (2); raised ridges giving geometric pattern (e.g.* Goniophorus*) (3)*. This character is largely confined to salenioids.

A25. *Pits on coronal plates: minute pin-pricks hardly developed in adults (Fig. 7B: arrow) (0); small rounded pits on either side below primary tubercle (Fig. 7H: arrow) (1); large ovate grooves extending along sutures from triple points (Fig. 7G) (2)*.

A26. *Raised ornament of ridges linking secondary tubercles and forming a radiating network: absent (0); present (1*). (e.g. *Ortholophus*, Fig. 7C)

A27. *Glassy tubercles developed on the aboral surface: no (0); yes (1)*. Glassy tubercles are so named from their appearance under the light microscope. They are microscopic knobs of solid calcite that grow out from the plate and which are scattered amongst the secondary tubercles in certain irregular echinoids (Fig. 7D, E)

A28. *Glassy tubercles developed on the oral surface: no (0); yes (1)*.

A29. *Epistromal ornament of raised ridges and/or nodes: absent (0); present (1)*. Epistromal ornament takes the form of irregular raised calcitic ridges and is developed on plates surfaces in between any tuberculation that is present (Fig. 7I)

Internal buttressing

Internal buttressing is confined to clypeasteroids and one small group of holectypoids. The structural arrangement is studied either by sectioning or grinding the test, or by X-ray. Radial bars are straight partitions that are developed from the adradial margins of interambulacral zones. They usually connect lower and upper surfaces only towards the periphery of the test. Pillars are vertical partitions of calcite that run between the oral and aboral surface and which have limited lateral extent. Partitions are wall-like structures again connecting lower to upper surface. These are arranged either parallel to the circumference of the test (circumferential) or as an irregular, stellate mesh centred on each plate (stellate). In certain clypeasteroids the partitions become extremely dense so that only small, interconnected porespaces are left (microperforate system). The latter has sometimes been referred to as a microcanal system. Because the arrangement of partitions can differ in ambulacral and interambulacral zones, we score the two regions separately.

A30. *Internal radial bars at adradial edge of interambulacral zones: absent (0); present (Fig. 8A, C) (1)*.

A31. *Internal buttresses in ambulacral zones: absent (0); circumferential partitions [e.g. "double" or multiple wall in* Clypeaster*] (Fig. 8F) (1); irregular mesh (Fig. 8D) (2); radiating mesh from the centre of each plate (Fig. 8E) (3)*.

A32. *Internal buttresses in interambulacral zones: absent (0); circumferential partitions (Fig. 8C) (1); irregular mesh (2); radiating mesh from the centre of each plate (Fig. 8E) (3)*.

A33. *Lantern and/or pharynx and gut: lie within a single continuous cavity within the test, not separated by internal calcified pillars or meshwork (0); separated by internal pillars (Fig. 8F) (1); gut enclosed with microperforate mesh, so that the course of the gut is picked out as a sinuous cavity (Fig. 8D) (2)*.

A34. *Dense microcanal (microperforate) system present within coronal plates: no (0); yes (Fig. 8G) (1)*.

Crystallographic axes of coronal plates (data taken from Raup 1959, 1966)

A35. *Interambulacral plate crystallographic axis: tangential (0); perpendicular (1)*.

A36. *Ambulacral plate crystallographic axis: tangential (0); perpendicular (1)*.

B. Apical disc

Position, structure and general organization

B1. *Position of apical disc: central or subcentral (0); less than 30% test length from the anterior border in adults (1); posterior—more than 60% distance from anterior border (2)*. The position of the apical disc has been measured from the anterior margin to the posterior edge of genital plate 2.

B2. *Periproct position: enclosed by apical disc (0); to posterior of apical disc but remaining in contact with posterior oculars (1); fully outside apical disc and opening bounded by plates of interambulacrum 5 (2)*. [ordered]

B3. *Apical disc structure in adult is a circlet of plates: yes (Fig. 9B) (0); no, is a cluster of plates (Fig. 9P) (1); no, is an elongate array (genital and ocular plates forming a biseries (Fig. 9J) (2)*.

B4. *Apical disc plating: adjunct, with genital and ocular plates forming single contiguous area (0); disjunct, with the posterior oculars separated from the rest of the apical disc (Fig. 9M) (1); disjunct ring with periproctal plates lying between genital and ocular plates in the ring (e.g. echinothurioids) (Fig. 9D) (2)*.

B5. B5 *Apical disc plating: monocyclic (Fig. 9G) (0); hemicyclic (Fig. 9F) (1); dicyclic (Fig. 9E) (2);*

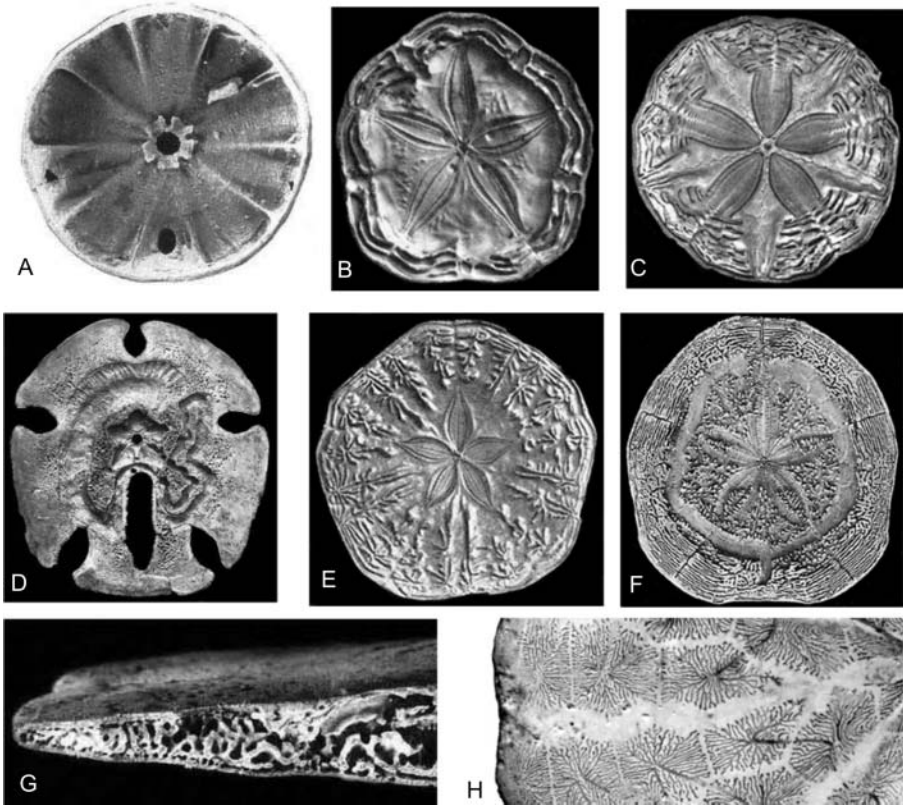

Figure 8. Internal buttressing. **A**, *Camerogalerus* (holectypoid), internal view of oral surface showing radial bars. **B**, *Laganum* (clypeasteroid), internal view of apical surface showing circumferential partitions. **C**, *Echinarachnius* (clypeasteroid) internal view of apical surface. **D**, *Encope* (clypeasteroid), internal view of oral surface. **E**, *Hupeia* (clypeasteroid), internal view of apical surface. **F**, *Clypeaster* (Clypeasteroid), internal view of apical surface. **G**, *Mellita* (clypeasteroid), test in section. The layer of small pores just above the base of the test marks the microcanal system. **H**, *Parascutella*, artificially exposed microcanal system. Not to scale. Figs B-F from Mortensen (1948b).

cidarid-style with ocular plates either just insert or just exsert (Fig. 9A) (3). Where this character is scored as 3, characters B6–10 are scored as inapplicable.

B6. *Ocular plate I: in contact with periproct—yes (0); no (1)*.

B7. *Ocular plate II: in contact with periproct—yes (0); no (1)*.

B8. *Ocular plate III: in contact with periproct—yes (0); no (1)*.

B9. *Ocular plate IV: in contact with periproct—yes (0); no (1)*.

B10. *Ocular plate V: in contact with periproct—yes (0); no (1)*.

B11. *Oculars II and IV in contact at midline: no, separated (Fig. 4K) (0); yes (Fig. 9J) (2)*.

B12. Genital plates 1 and 4 in contact at midline: no, separated by genital plate 2 (Fig. 9O) (0); no, separated by periproctal/complemental plates (Fig. 9G, K) (1) yes (Fig. 9J) (2).

B13. Ocular plates I and V in contact: no, separated by genital plate 2 (Fig. 9T) (0); no, separated by periproctal/complemental plates (Fig. 9I) (1) no, separated by genital plate 5 (Fig. 9C) (2); no, separated by interambulacral plates (3); yes, in contact (Fig. 9R) (4).

B14. *Genital plate 4 in contact with genital plate 2: no (Fig. 9B) (0); yes (Fig. 9Q) (1)*.

B15. *Apical disc plates connect to the corona: almost always preserved attached to coronal plates: not prone to loss (0); caducous—very rarely preserved attached to corona (1)*.

B16. *Periproct: opening flush with test (Fig. 10C) (0); opening into an anal sulcus (Fig. 10A, B) (1); invaginated opening with well-like entrance (Fig. 10D) (2)*.

B17. *Anal sulcus: forming a well-developed groove on test (Fig. 10B) (0); a shallow subanal ledge (Fig. 10A) (1)*.

B18. *Shape of periproct: longitudinally elongate (0); circular to subcircular or pentagonal (1); transversely elongate (2)*.

B19. *Periproctal plates integrated into apical disc: no (0); yes (Fig. 9A, C, K) (1)*.

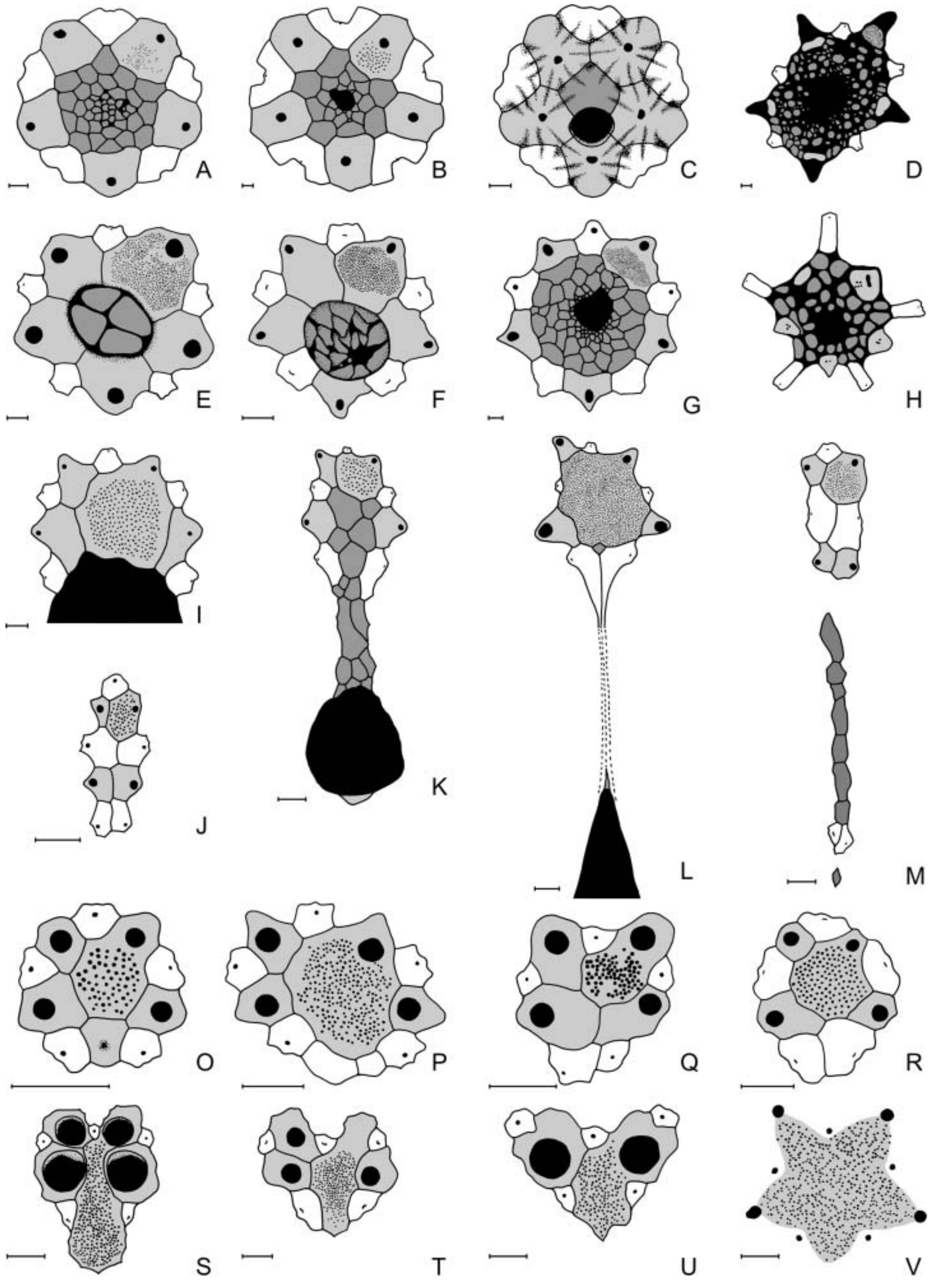

Figure 9. Apical disc plating. **A**, *Prionocidaris* (cidaroid), cidaroid-type disc. **B**, *Goniocidaris* (cidaroid), cidaroid-type disc with Y-shaped ocular plates. **C**, *Hyposalenia* (salenioid), salenioid disc with suranal plate (dicyclic). **D**, *Phormosoma* (echinothurioid), monocyclic echinothurioid disc in form of a disjunct ring. **E**, *Arbacia* (arbacioid), dicyclic disc with periproctal plates forming an anal valve. **F**, *Toxopneustes* (echinoid), hemicyclic disc. **G**, *Micropyga* ('diadematoid'), monocyclic disc. **H**, *Kamptosoma* (echinothurioid), disjunct ring with strongly projecting ocular plates (redrawn from A. Agassiz & Clark 1909). **I**, *Pygaster* (basal irregular), cluster of plates in contact with the periproct (from Barras 2006: figure 21b). **J**, *Holaster* (holasteroid), elongate apical disc. **K**, *Pronucleolites* (stem-neognathostome), disjunct cluster of plates with complemental plates, genital plat 5 remaining in contact with the periproct. **L**, *Clypeus* (stem neognathostomate), cluster of plates, posterior genitals elongated, remaining in contact with periproct. **M**, *Collyrites* ('disasteroid'), disjunct disc. **O**, *Holectypus* (holectypoid), compact disc retaining genital plate 5. **P**, *Anorthopygus* (stem irregular), tetrabasal disc. **Q**, *Toxaster* (stem spatangoid), ethmophract disc. **R**, *Micraster* (spatangoid), hemilytic [semi-ethmolytic] disc. **S**, *Brissus* (spatangoid), ethmolytic disc. **T**, *Pericosmus* (spatangoid), ethmolytic disc with reduced number of gonopores. **U**, *Schizaster* (*Ova*) (spatangoid), ethmolytic disc with reduced plating. **V**, *Mellita* (clypeasteroid), monobasal disc. Ocular plates: white, genital plates: light grey, periproctal/complemental plates: dark grey, periproct and pores: black. Scale bars = 1 mm.

B20. *Apical disc as raised cap: no (0); yes (1).* Only salenioids and goniopygids have a thickened, raised apical disc.

Genital plates

B21. *Number of genital plates: more than 5 (6); 5 (5); 4 (4); 3—single anterior genital plate (3); 2 genital plates (Fig. 9U) (2); 1 (monobasal: Fig. 9V) (1).*

B22. *Gonopores on genital plates: each plate with multiple gonopores arranged in an arc (0); each plate with a single gonopore (1); multiple gonopores moved onto genital plate 2 (2).* In forms where the apical disc is monobasal, the gonopores have moved to open through the single remaining plate (genital plate 2).

B23. *Number of gonopores: 2 gonopores only, positioned in anterior genital plates (Fig. 9U) (1)*; *2 gonopores only, positioned in posterior genital plates (2); 3 gonopores, no gonopore on G2 (Fig. 9T) (3); 4 gonopores, no gonopore in posterior zone (Fig. 9P) (4); 5 gonopores (5); more than 5 gonopores (6); 3 gonopores, no gonopore on G3 (7).*

B24. *Gonopores opening fully within genital plate (0); marginal, bounded externally by interambulacral plates (1); outside in interambulacra (2); open through large membranous gap (3).* The gonopores in some cassiduloids such as *Faujasia* open far outside the apical disc plates. In some echinothurioids they open through a large membranous opening. In monobasal discs of cassiduloids and clypeasteroids the gonopore openings are often partially bounded by the large madreporic plate and partially bounded by the surrounding interambulacral plates.

B25. *Sexual dimorphism in size of gonopores: not developed (0); present (1).*

B26. *Madreporite more than 1.5 times larger than the other genital plates: no (0); yes (1).* (e.g. Fig. 9L, P)

B27. *Genital plates strongly pointed and projecting significantly further than adjacent ocular plates forming pentagonal outline: no (0); yes (Fig. 9D) (1).*

B28. *Posterior gonopores opening through ocular plates II and IV: no (0); yes (1).* In certain disasteroids and holasteroids the posterior pair of genital pores, instead of opening through genital plates 1 and 4, have shifted position to open through ocular plates II and IV (see Smith 2004; Saucède *et al.* 2004)

B29. *Hydropore openings: confined to genital 2 (0); spread over all anterior genital and ocular plates (1); spread over periproctal plates also (2).*

B30. *Hydropores: opening in groove: no (0); yes (1).*

B31. *Hydropores: opening in pit: no (0); yes (1).*

B32. *Genital plates with sunken groove facing into periproct: no (0); yes (1).* This is found in certain arbacioids.

B33. *Periproctal tubercles on genital plates: none (0); a distinct ring surrounding periproct on top of plates (Fig. 10E) (1); single large perianal tubercle on genital plates (Fig. 10F) (2).*

B34. *Genital plates with raised periproctal rim: no (0) yes (1).*

Ocular plates

B35. *Ocular plates II and IV as large (wide) as genital plates: no* (Fig. 9E) *(0); yes* (Fig. 9G) *(1).* In scoring this character we ignore the madreporite and compare the relative widths of the other genital plates at their outer edge.

B36. *Ocular plates rectangular and projecting: no (0); yes (1).* Strongly projecting ocular plates are found only in *Kamptosoma* (Fig. 9H) and some arbacioids.

B37. *Ocular plates Y-shaped: no (0); yes (1).* Y-shaped ocular plates (Fig. 9B) are found only in a small number of cidaroids.

B38. *Ocular plates with single pore (0); with double (bridged) pore (1).* In some arbacioids the gonopore opening is bridged by an arch of calcite which makes the pore appear double. This bridge of calcite is superficial, however, and only a single pore passes through the genital plate.

Periproct (position and organization)

B39. *Single enlarged periproctal plate (suranal plate): absent (0); present at least in juveniles but not sutured to or indenting apical disc ring (1); present in adults and firmly sutured to apical disc (Fig. 9C) (2)* [ordered]. In certain camarodonts there is a distinctly enlarged periproctal plate that is obvious in juveniles but which becomes progressively less obvious as growth proceeds. In zeuglopleurids this plate physically indents the apical disc ring at the anterior, but in other camarodonts the periproctal opening remains smoothly rounded and the enlarged plate lies entirely within the periproctal membrane (e.g. *Genocidaris*).

B40. *Periproct margin: angular with or without wedge-shaped plates indenting between genital plates forming a pentagonal central zone (Fig. 9A, B) (0); smooth and rounded (Fig. 9E, F) (1); smooth and rounded except for suranal(s) (Fig. 9C) (2).*

B41. *Within periproctal membrane; anal opening: central (Fig. 9G) (0); displaced adorally (in the*

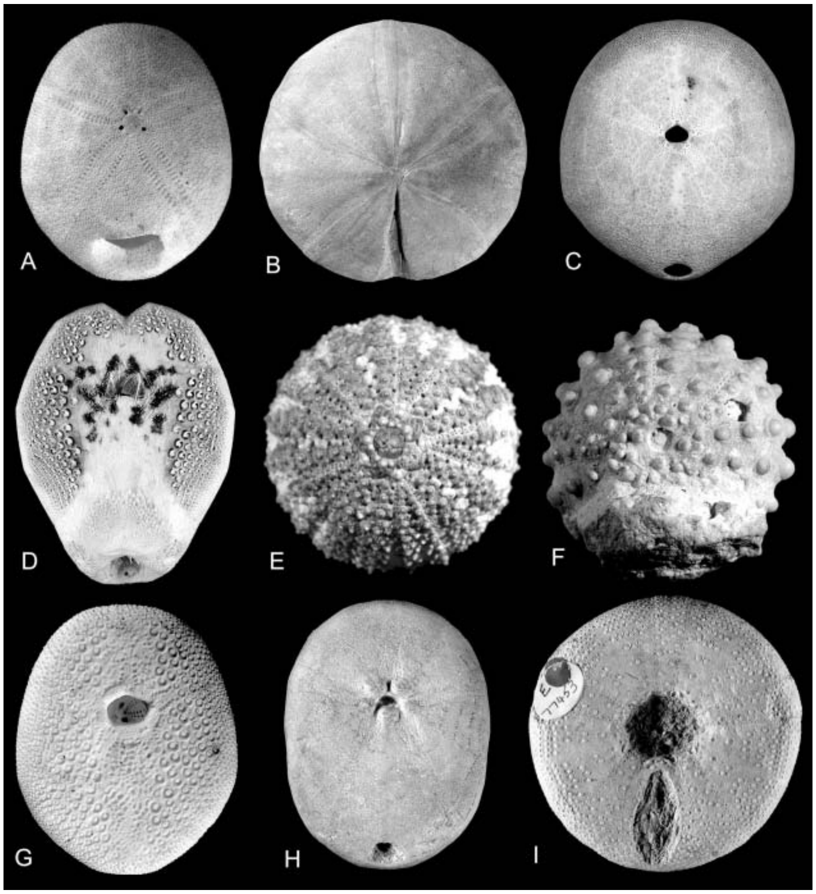

Figure 10. Peristome and periproct. **A**, *Cassidulus* (cassiduloid), apical view. **B**, *Clypeus* (stem neognathostomate), apical view. **C**, *Echinolampas* (cassiduloid), oral view. **D**, *Lovenia* (spatangoid), oral view. **E**, *Temnotrema* (temnopleuroid), apical view. **F**, *Acropeltis* (stem arbacioid), apical view. **G**, *Cassidulus* (cassiduloid), oral view. **H**, *Conoclypeus* (cassiduloid), oral view. **I**, *Holectypus* (stem irregular), oral view. Not to scale.

direction of interambulacrum 5) (Fig. 9H) (1); displaced towards ocular I (Fig. 9F) (2); displaced towards adapical edge (3).

B42. *Periproctal plates forming a single valve-like ring structure (anal cone): no (0); yes (1)*. Valve-like periproctal plating is seen in arbacioids (Figs 7F, 9E) and *Parasalenia*.

B43. *Periproctal membrane: a series of thick, tessellated plates (Fig. 9B, C) (0); a dense series of thin, membrane embedded, platelets (1); small spicules in membrane; appearing largely naked (2); a few large plates in a largely naked membrane (3)*.

B44. *Periproct position in adult: apical (0); supramarginal (1); marginal (2); inframarginal (3); oral (4)* [ordered, fractional weighting].

B45. *Position of base of periproct in adult*. We scored this as the number of the lowest plate in interambulacrum 5 to touch the base of the periproct opening, counting from the peristome. Scored as 9 in all cases where it is plate 9 or above. [ordered, fractional weighting]

B46. *Internal calcitic wall projecting down from apical disc: no (0); yes (1)*. This structure surrounds the hydropore and axial organ in irregular echinoids.

B47. *Number of interambulacral plates separated by the periproctal opening*. We score the lower number of plates if the two sides of the periproct have different plate counts. Scored as 7 in forms with seven or more plates separated by the periproct. Not applicable in regular echinoids.

C. Ambulacra

Structure of ambulacra

C1. *Different zones of plates can be distinguished around the test (differing in the shape and size of the plates found within each zone): no (0); yes (1)*. In this character we looked for discrete regions of different shaped-plating, (e.g. petals vs. episternal zones in spatangoids). We do not count differences caused by pore crushing in phyllodes.

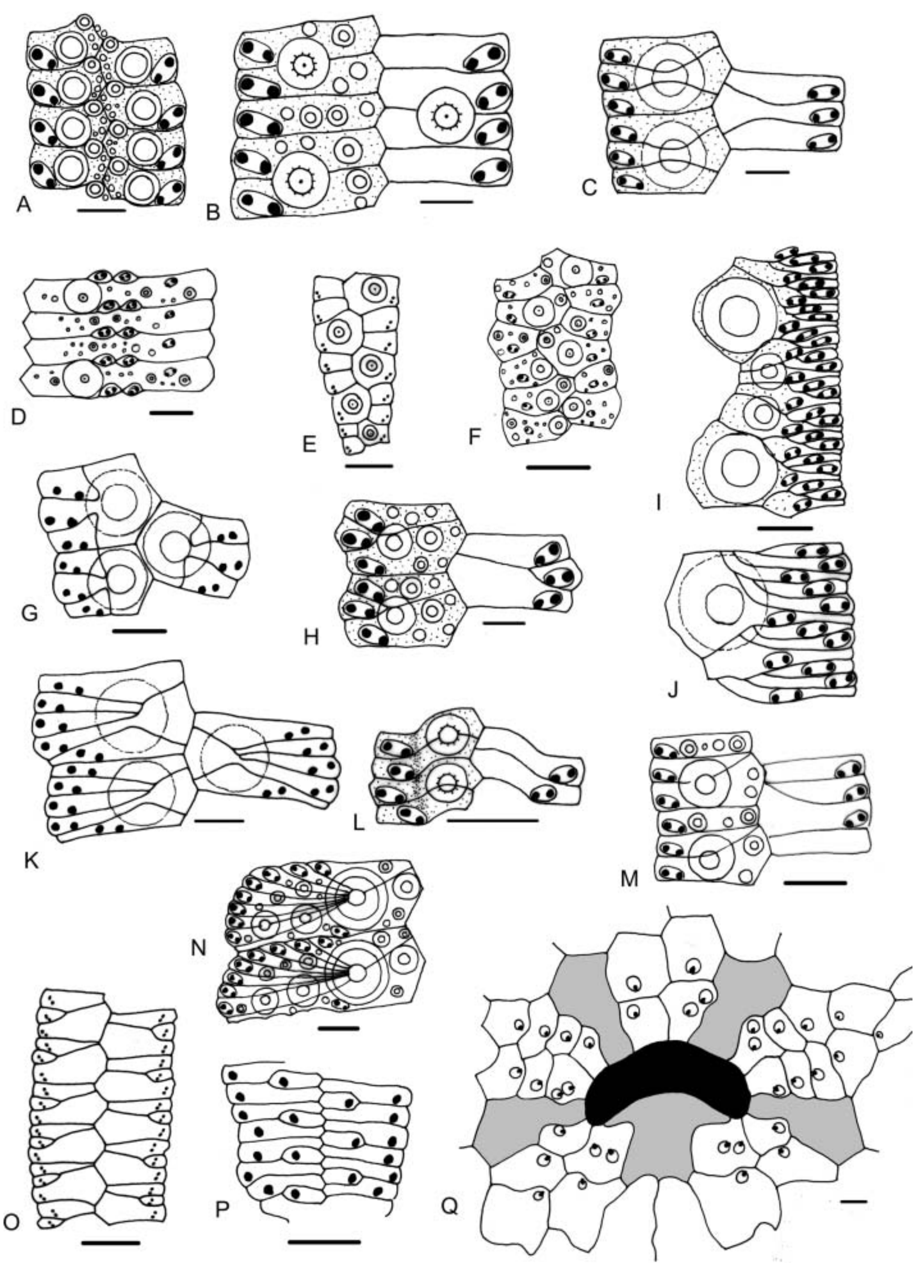

Figure 11. Ambulacral plate compounding. **A**, *Salenia* (*Pleurosalenia*) (salenioid), simple ambulacral plating. **B**, *Acrosalenia* (stem salenioid), acrosalenioid plating. **C**, *Caenopedina* (pedinoid), diadematoid plating. **D**, *Araeosoma* (echinothurioid), echinothurioid plating. **E**, *Aspidodiadema* (aulodont). **F**, *Chaetodiadema* (diadematoid). **G**, *Coelopleurus* (arbacioid), arbacioid plating. **H**, *Ortholophus* (temnopleuroid), trigeminate echinoid plating. **I**, *Glyptocidaris* (stomopneustid), stomopneustid plating. **J**, *Leiosoma* (stomopneustid), stomopneustid plating. **K**, *Actinophyma* (phymosomatoid), phymosomatoid plating. **L**, *Salenia* (*Salenia*) (salenioid), bigeminate plating. **M**, *Echinopsis* (temnopleuroid), echinoid plating. **N**, *Strongylocentrotus* (echinoid), polygeminate echinoid plating. **O**, *Neoglobator* (stem echinoneoid), pyrinid plating. **P**, *Conoclypus* (cassiduloid), phyllode plating. **Q**, *Echinocardium* (spatangoid), perioral plating (peristome in black). Scale bars 1 mm.

C2. *Ambulacral plating: successive elements within zone similar (in size and shape—simple) and equally developed (Fig. 11A) (0); development of a repeated structural unit composed of multiple elements (compound plate: Fig. 11B-P) on ambital and oral surface only (1); development of a repeated structural unit composed of multiple elements (compound plate) throughout (2); development of a repeated structural unit composed of multiple elements (compound plate) on aboral surface only [viz. the petals] (3); development of a repeated structural unit composed of multiple elements (compound plate) close to the mouth only (4)*. This character scores for the presence of compound plating and its development around the corona.

C3. *Ambulacral plates: unfused by overgrowth of primary tubercle (Fig. 11D, F) (0); coalesced elements united by overgrowth of primary tubercle (Fig. 11B, C) present adorally (1); coalesced elements united by overgrowth of primary tubercle present throughout (2)* [ordered].

C4. *Number of elements overgrown by primary tubercle: 2 (Fig. 11B, L) (0); 3 (Fig. 11C) (1); >3 (Fig. 11K) (2).*

C5. *Primary tubercle on each element: no (0); yes (Fig. 11A) (1).* When scoring this character we ignored multiple small tubercles of irregulars.

C6. *Each compound plate bears a primary tubercle: yes (Fig. 11N) (0); no, primary tubercles only on every second or third compound plate in a column, or more irregular (Fig. 11G) (1).*

C7. *In compound plates, all elements reach the perradial suture in mature plates: yes (Fig. 11B, C) (0); no, there are demiplates which reach the adradial suture only (Fig. 11I) (1); no, there are occluded plates which end before reaching both the perradial and adradial sutures (Fig. 11D) (2); no, there are occluded plates which reach the perradial suture and form an inner series down the perradius (Fig. 11P) (3); one primary, one adradial demiplate and one occluded plate (e.g.* Paraphormosoma*) on ambital plates (4); Separate adradial and perradial series of occluded plates forming multiple columns (e.g.* Triadotiaris*) (5).* This character was scored for the most developed state that was seen in adults. This is because there can be a marked change in development from juvenile to adult, with smaller plates initially occupying the full column width and becoming progressively occluded as growth proceeds.

C8. *Number of elements involved in compound plate: none (Fig. 11A) (0) 2 (Fig. 11L) (2); 3 (Fig. 11B, C) (3); 4 or more (Fig. 11H, K) (4).*

C9. *Maximum number of demiplates or occluded plates in a compound: 0 (0); 1 (Fig. 11J) (1); 2 (Fig. 11K) (2); 3 or more (Fig. 11O) (3).*

C10. *Position of largest element in compound plate: lowest (echinoid: Fig. 11J) (0); middle (arbacioid/stomopneustid: Fig. 11C, I, H) (1); second of multiple elements (not middle element—e.g. phymosomatid: Fig. 11K) (2).*

C11. *Complex compound plates constructed from two or more trigeminate units present: no (0); yes (1).* Complex plating, in which compound units of different sizes together make up a supercompound plate, is seen a number of stirodont taxa (Fig. 11G, H).

C12. *Triad present with lower element reduced to a small occluded plate not reaching either suture: no (0); yes (Fig. 11D) (1).*

C13. *Triad present with upper element reduced to a small occluded plate not reaching either suture: no (0); yes (Fig. 11D) (1).*

C14. *Elements grouped to form a single compound plate with a common straight-edged and unbroken perradial wedge: no (Fig. 11B) (0); yes (Fig. 11J), on oral surface only (1); yes, throughout (2).* This character was treated as not applicable in forms such as echinothurioids (Fig. 11D) and arbaciids (Fig. 11I) where only a single element in a compound plate forms the entire perradius.

C15. *First ambulacral plates morphologically differentiated from succeeding plates: no (0); yes (1).* This character was scored for irregular echinoids, primarily cassiduloids, where the first ambulacral plates are distinctly enlarged and of very different shape to the succeeding ambulacral plates

C16. *Ambulacral width at ambitus: narrower than interambulacra (<90%) (0) approximately as wide (1); distinctly wider than interambulacral zones (2); significantly wider than interambulacral zones (>150%) (3).*

C17. *Ambulacral plating becomes uniserial adapically: no (0); yes (1).* This character applies to a small number of spatangoids.

C18. *First pair of ambulacral plates in basicoronal ring paired: no (0), yes (1).* We scored plates as paired where they were more or less symmetrical in size and shape (e.g. as in *Scutella*).

C19. *Second pair of ambulacral plates distinctly enlarged: no (0); yes (1).* In certain clypeasteroids (e.g. *Arachnoides*) the second pair of ambulacral plates are considerably larger than the succeeding ambulacral plates.

C20. *Oral surface almost exclusively composed of ambulacral plates: no (0); yes (1).* This is true of the clypeasteroids *Fossulaster* and *Scutelloides*.

C21. *Ambulacral projection into peristome at perradius: no (0); yes (1).* In almost all scutelline clypeasteroids the small circular mouth is indented by five short ambulacral projections that form as perradial ridges on the most adoral plates.

C22. *Presence of superficial plates down adradius: no (0); yes (1).* In oligopygids and *Conoclypus* the small demiplates that run down the adradial margin of the ambulacra do not penetrate the full thickness of the test but lie on top of the larger ambulacral plates. These superficial plates are often lost in weathered specimens, leaving a series of shallow adradial pits.

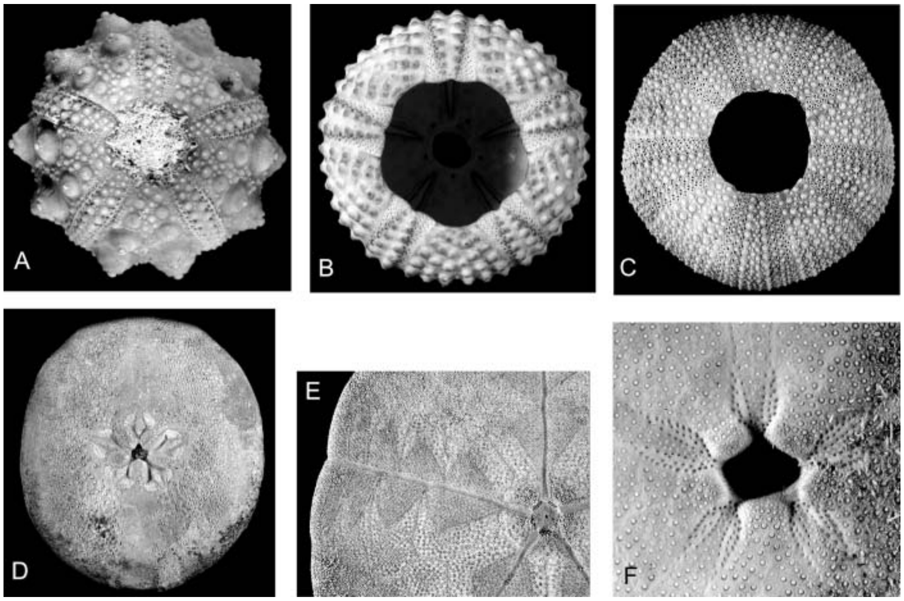

Figure 12. Phyllodes. **A**, *Goniophorus* (salenioid), oral view. **B**, *Arbacia* (arbacioid), oral view. **C**, *Parechinus* (echinoid), oral view. **D**, *Gongrochanus* (cassiduloid), oral view—note the pointed bourrelets surrounding the peristome. **E**, *Ammotrophus* (clypeasteroid), detail of oral surface showing combed areas of aligned pores and tubercles. **F**, *Echinolampas* (cassiduloid), detail of oral area showing phyllodes and well-like entrance to the peristome. Not to scale.

Ambulacral pores/tube-feet in ambulacra II/IV

(Where the pores and tube-feet in ambulacrum III are differentiated from the other ambulacra these are scored separately below).

C23. *Aboral pores or pore-pairs: pore-pairs with narrow interporal partition (0); pore-pairs widened and conjugate or subconjugate (1); widened pore-pairs with elongate raised interporal partition (2); rudimentary pores only (3); well-developed single pores (4).*

C24. *Elongate pore-pairs present in which the outer pore is subdivided by calcite septa: no (0); yes (1).* This is true of certain clypeasteroid petal pore-pairs (e.g. *Parascutella*).

C25. *Oral pores single (1); double (0).* We score the nature of the ambulacral pores adoral to any petal development.

C26. *Pores or pore-pairs; aboral arrangement— uniserial column (0); biserial column (1); multiserial band (offset arcs) (2).*

C27. *Pores or pore-pairs; ambital arrangement— uniserial column (Fig. 1B) (0); biserial column (1); multiserial band (offset arcs: Fig. 11H) (2).*

C28. *Pores or pore-pairs; position of pore-pair band on ambital plates: adradial (0); central (1).*

C29. *Pores or pore-pairs; organization at ambitus— widely spaced from each other (Fig. 11F) (0); forming a single dense contiguous band (Fig. 11G) (1): forming discrete arcs (Fig. 11N) (2); forming multiple discrete columns (Fig. 11D) (3).*

C30. *Pores or pore-pairs; organization adorally— widely spaced from each other (0); forming single dense contiguous band (1): forming discrete arcs (2); forming multiple discrete columns (3).*

C31. *Pores or pore-pairs; forming a distinct phyllode close to the peristome: no (Fig. 12A, C) (0); yes, by pore-crowding and column multiplication, as in regular echinoids (Fig. 12B) (1); yes, as V-shaped zone of differentiated pores, as in cassiduloids (Fig. 12D, F) (2).*

C32. *Adoral ambulacral pores (tube-feet) differentiated in size and structure from those at the ambitus and above adorally (large, suckered tube feet present): no (0); yes (Fig. 12F) (1).* To score as present there needed to be a significant difference in the shape and structure of the pore-pairs around the corona, not just a small change in relative size. Not scored for any taxon where aboral tube-feet are rudimentary.

C33. *Tube-foot or pore-pair on primary element of compound plate reduced and rudimentary: no (0); yes (1).* This is a feature seen in some echinothurioid genera only.

C34. *More than one tube foot and microscopic pore present on ambulacral plates at ambitus: no (0); yes (1).* We scored oligopygids as having multiple tube-feet because the ambulacral plates that lie beneath the superficial demi-plates are pierced by more than one tube-foot canal.

C35. *Multiple microscopic tube feet/pores present within the adapical region (within the petals where present): no (0) yes (1).*

C36. *Microscopic pores arranged: as combs forming discrete oblique rows between rows of tubercles (Fig. 12E) (0); irregularly scattered in fields over plate (1); aligned along plate sutures only (2).* In many clypeasterines the pores are aligned forming combed fields, while in some primitive clypeasteroids such as *Scutellina* the pores are confined to the sutures only.

C37. *Pores and tube-feet fields extend beyond ambulacral zones and onto interambulacral plates: no (0); yes (1).*

C38. *Outer pore in petal pore-pairs pierce or notch interambulacral plates not ambulacral plates: no (0); yes (1).*

C39. *Penicillate perioral tube-feet present on adoralmost plates: no (0); yes (1).* Penicillate tube-feet have a large disc covered in small finger-like projections. Their associated pore-pairs are also distinctive, with a large circular base and relatively small perforation and allow the presence of this type of tube-foot to be recognized in fossils.

C40. *In adult, one of each pair of peribuccal ambulacral plates bearing two tube-feet (basicoronal plates retained in corona): no (0); yes, distinct enlarged plate with two pores present (Fig. 11Q) (1).* This is the typical pattern found in atelostomates.

C41. *Three pores passing through first ambulacral plates: no (0); yes (1).* This is best observed from the interior of the test and seems to be true for most cassiduloids, oligopygids and *Conoclypus.*

C42. *In the subanal region of the test, penicillate tube feet and their associated enlarged pore-pairs: absent (0); present (1).*

C43. *Ambulacral plates in subanal region project into interambulacrum 5 to indent the plastron behind plates 5.a.3, 5.b.3: no (0); yes (Fig. 23B) (1).* This is a characteristic found only in some spatangoids.

C44. *Single large pore differentiated at base of phyllode on adoral plate (buccal pore); no (0); yes (1).*

C45. *Ambulacra constricted to less than half-width between phyllodes and margin on oral surface: no (0); yes (1).* This arrangement is seen in certain spatangoids, notably in *Lovenia* and its relatives.

C46. *Phyllode development in lateral paired ambulacra: phyllode pores/tube feet no more than 1 or 2 in a column (0); 4–7 in each column (1); 8–12 in each column (2); 13+ in each column (3).*

C47. *Skeletal supports at tip of suckered tube-feet: absent (0); a ring of small spicules (1); a solid ring (2); a rosette structure of (usually) 5 elements (3); a pair of spicules only (4); a ring of rather irregular-shaped plates (5).*

Ambulacrum III where differentiated

C48. *Aboral tube feet in ambulacrum III differentiated from those in other ambulacra: no (0); yes: small sensory tube-feet (1); yes: large and suckered funnel-building tube-feet (2); yes: large and penicillate funnel building tube feet (3).* Where tube-feet are not preserved we can often identify their structure from the shape of the associated pore-pairs.

C49. *Ambulacrum III sunken adapically: no (0); yes, becoming increasingly depressed from apex to ambitus (1); yes, deeply depressed from apex (2).*

C50. *Ambulacral sunken adorally: no (0); yes, forming a funnel-like entrance to the peristome (1); yes, forming obvious grooves over oral surface (2).*

Petal arrangement

C51. *Petaloid regions differentiated aborally: no (0); yes (1).* Petals are specialized aboral zones of tube-feet and pore-pairs used for gaseous exchange.

C52. *Ambulacral pore series more or less parallel or diverge towards ambitus (Fig. 13E) (0); inner pore series bowed so that petals contract distally (Fig. 13B) (1); pore-pairs in lateral ambulacra appear to from continuous arc (Fig. 13C) (2).*

C53. *Perradial zone equal or narrower than width of a single pore-pair aborally (maximum width) (Fig. 9A) (0); more than 1 times width of pore-pair (Fig. 13B-I) (1).* Measured at the widest point in the petals.

C54. *Posterior paired petal length compared to anterior paired petals: similar in length (Fig. 13B) (0); much shorter—less than 70% the length of anterior (Fig. 13D) (1); much longer, more than 125% as long (Fig. 13I) (2).*

C55. *Ambulacral symmetrically arranged (pentaradiate) (0); ambulacra with II and IV more or less at 180 degrees (e.g.* Brissus*) (1); anterior petals flexed forwards so as to become subparallel to anterior ambulacrum (Fig. 13D) (2); posterior petals flex outwards larger than 100 degrees (e.g.* Dendraster *Fig. 13G) (3); posterior petals subparallel (e.g.* Stigmatogpygus*) (4).* In scoring this character in disasteroids we ignored any separation between the bivium and trivium.

C56. *Occluded plates present at ends of petals: no (0); yes* (Fig. 18A) *(1).* In some petals the lowest few plates do not reach the adradial suture.

C57. *Enlarged pore-pairs present adapically which extend adorally to different extents in the two columns of an ambulacral zone: no (0); yes (1).* This character is developed primarily in echinolampadid cassiduloids (Fig. 13F).

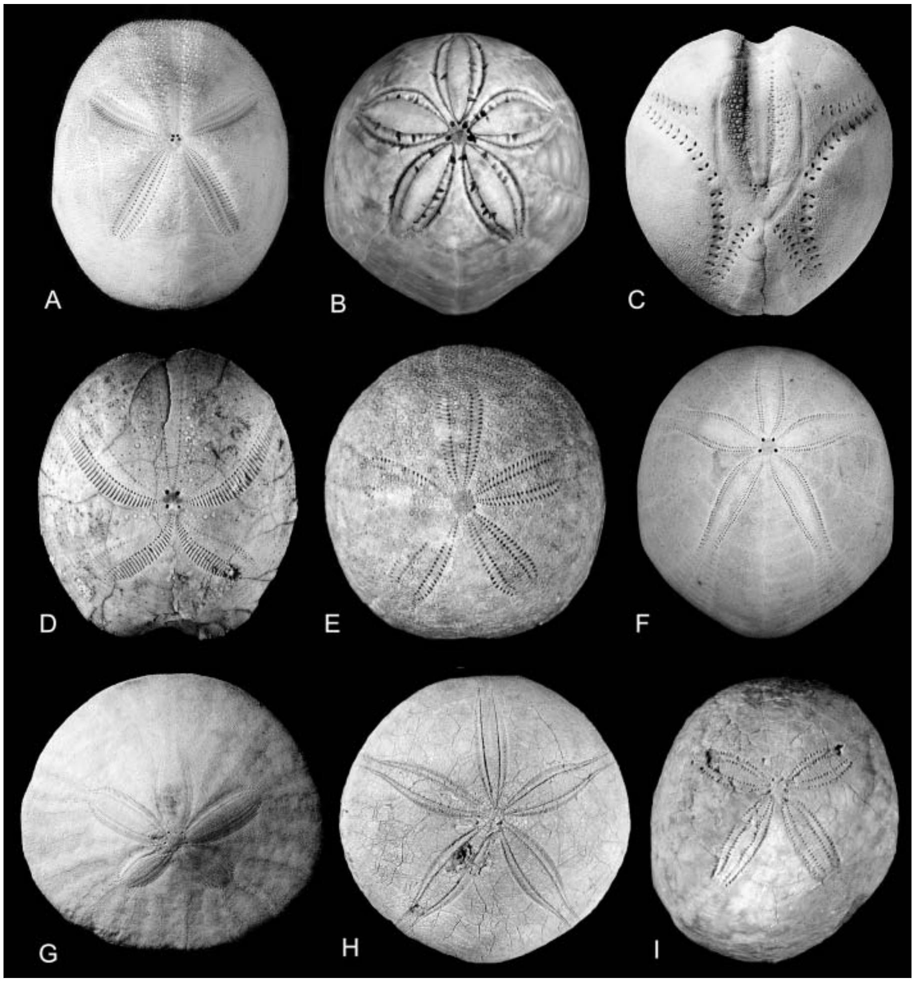

Figure 13. Petals. **A**, *Metalia* (spatangoid). **B**, *Domechinus* (cassiduloid). **C**, *Echinocardium* (spatangoid). **D**, *Opissaster* (holasteroid). **E**, *Haimea* (stem clypeasteroid). **F**, *Echinolampas* (cassiduloid). **G**, *Dendraster* (clypeasteroid). **H**, *Astrolampas* (stem neognathostomate). **I**, *Eolampas* (stem clypeasteroid). All in apical view. Not to scale.

C58. *Ambulacral zones sunken adapically: Paired ambulacra (I,V and II,IV): no (0); yes, weakly to moderately depressed (Fig. 13A) (1); deeply invaginated (2)*. Petals are scored as deeply invaginated when their depth is more than their width.

C59. *Termination of petals; gradual decrease in size of pores and increase in spacing* (Fig. 13H) *(0); abrupt termination of petals* (Fig. 13A, B) *(1)*. Clypeasteroids such as *Dendraster* (Fig. 13G), where there are a small number of trailing podia beyond the ends of the petals, are scored as state 0.

C60. *In anterior paired petals (or ambulacra II, IV where no petals are developed), pore-pairs reduce in size adapically equally in the two columns (0); anterior column of pore-pairs reduced more rapidly in anterior column adapically (1); large pore-pairs developed in lower part only changing abruptly to microscopic pore-pairs adapically (2); no large pore-pairs present in anterior column (Fig. 13D) (3)*.

C61. *Aboral pore-pairs of adult: the two pores not markedly different in size (outer pore no more than twice the width of the inner pore) (Fig. 13E) (0); outer pore significantly wider and more slit-like than inner pore (more than 3 times the diameter) (Fig. 13D) (1)*.

Food grooves (Fig. 14)

C62. *Food grooves in ambulacra: absent (0); present (1)*.

C63. *Branching style: no branches (Fig. 14E) (0); food groove branches (Fig. 14B, C, F) (1)*.

C64. *Branching pattern: primary trunk gives off side branches (Fig. 14B) (0); primary trunk branches dichotomously just once (Fig. 14A, C) (1); food groove branches more than once dichotomously (Fig. 14F) (2)*.

C65. *Multiple side branches to secondary branches: no (Fig. 14F) (0); yes, close to periphery (1); yes, along entire length (Fig. 14C) (2)*.

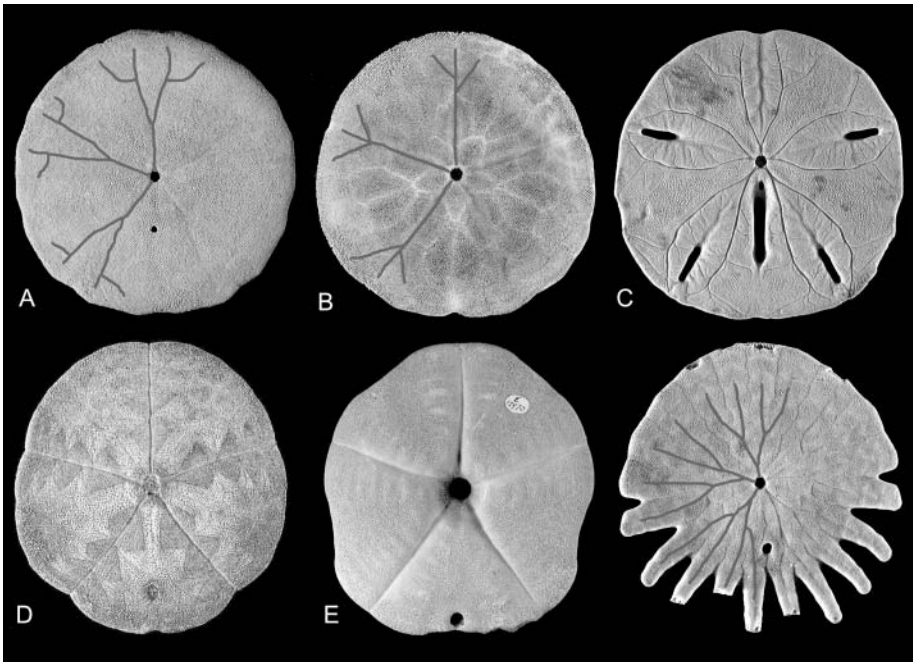

Figure 14. Food grooves in clypeasteroids. **A**, *Periarchus* (clypeasteroid). **B**, *Echinarachnius* (clypeasteroid). **C**, *Mellita* (clypeasteroid). **D**, *Ammotrophus* (clypeasteroid). **E**, *Clypeaster* (clypeasteroid). **F**, *Heliophora* (clypeasteroid). All in oral view. Track of food grooves is marked on left hand side of test in A, B and F. Not to scale.

C66. *Side branches arise on one side only (internal) (0); arise from external side only (1) arise from both sides (2).*

C67. *Food groove arrangement: pentaradiate (Fig. 14B, C) (0); with obvious anterior-posterior asymmetry (Fig. 14F) (1).*

C68. *Position of bifurcation: at end of first ambulacral plate (Fig. 14C) (0); towards the end of plate 2 (Fig. 14A) (1); more distal than plate 2 (2).*

C69. *Primary food grooves extend aborally: no (0); yes (1).* True of some clypeasterines.

C70. *Secondary food grooves extend aborally: no (0); yes (1).*

C71. *On oral surface, posterior ambulacral zones (episternal zones bordering the plastron) largely free of tubercles: no (0); yes (1).*

Interambulacra

Plate arrangement: general (Fig. 15)

D1. *Interambulacral zones composed of: four columns of plates (0); just two columns of plates (1); three columns of plates (2).* All crown-group echinoids have a test constructed of just 20 columns of plates, but archaeocidarids have tests with 30 columns of plates. *Tiarocidaris* is unique in its plate organization, having a single adoral plate followed by a row of three adapical plates.

D2. *A pair of interambulacral plates (second interambulacral plates) borders the peristome: no, first (basicoronal) plate retained as part of corona and visible externally in adult (0); yes (1).* In echinoid development the first-formed interambulacral plate is often not retained into adulthood and the peristome is bordered by a pair of plates. However, in irregular echinoids (Fig. 15) and some regular echinoid groups also, this plate is retained and forms the margin to the peristome.

D3. *Basicoronal plate internal and not visible externally—in external view basicoronal ring with plates 2a, 2b reaching peristome edge: no (0); yes (1). Rotula* is unusual amongst clypeasteroids in having a pair of interambulacral plates bordering the peristomial opening. As shown by Kier (1970) the basicoronal plate is present but only visible internally.

D4. *Interambulacra 1 and 4 on oral surface: plate columns contiguous (0); columns disjunct, separated by one pair of ambulacral plates behind basicoronal plate (1); columns disjunct, separated by two or more pairs of ambulacral plates behind basicoronal plate (2).*

D5. *Interambulacra 2 and 3 plating on oral surface: contiguous (0); columns disjunct, separated by one pair of ambulacral plates behind basicoronal plate (1); columns disjunct, separated by two or more pairs of ambulacral plates behind basicoronal plate (2).*

D6. *Interambulacra 5 plating on oral surface: contiguous (Fig. 15A-C) (0); columns disjunct, separated*

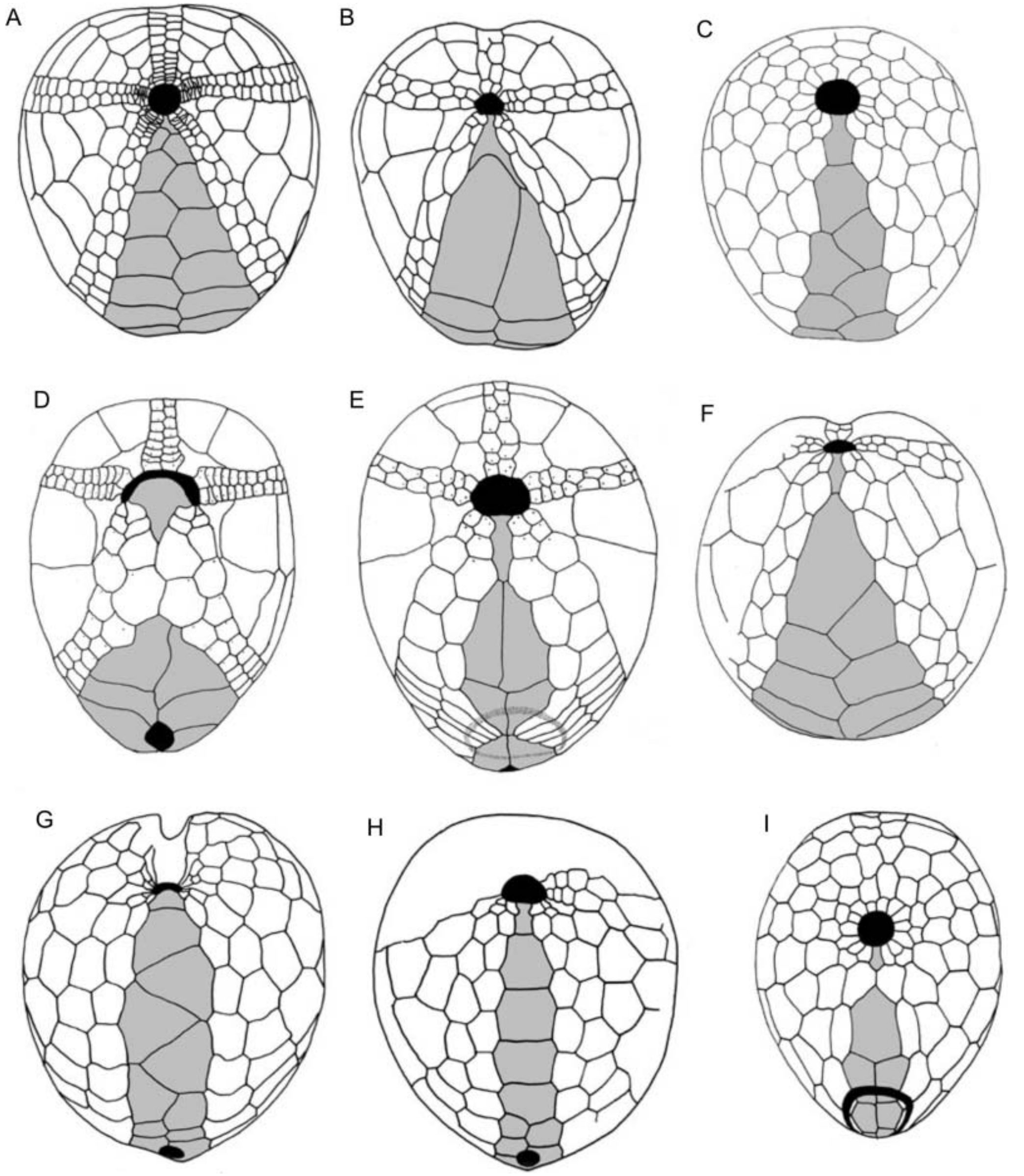

Figure 15. Oral plating in atelostomates (plastron shaded). **A**, *Pygomalus* (stem atelostomate). **B**, *Toxaster* (stem spatangoid). **C**, *Offaster* (stem holasteroid). **D**, *Brachysternaster* (spatangoid). **E**, *Pycnolampas* (spatangoid). **F**, *Somaliaster* (stem spatangoid). **G**, *Cardiaster* (stem holasteroid). **H**, *Sternotaxis* (stem holasteroid). **I**, *Plexechinus* (holasteroid). I redrawn from Mooi & David (1996). Not to scale.

by one pair of ambulacral plates behind basicoronal plate (1); columns disjunct, separated by two or more pairs of ambulacral plates behind basicoronal plate (Fig. 15D) (2).

D7. *Adoral plating in interambulacral 1: both post-basicoronal plates contact basicoronal plate (amphisternous, e.g. Fig. 15B) (0); single post-basicoronal plate in contact with basicoronal plate (meridosternous, e.g. Fig. 15G, H) (1).*

D8. *Adoral plating in interambulacral 4: both post-basicoronal plates follow basicoronal plate (amphisternous, e.g. Fig. 15B) (0); single post-basicoronal plate follows the basicoronal plate (meridosternous, e.g. Fig. 15G, H) (1).*

D9. *Adoral plating in interambulacral 2 and 3: both post-basicoronal plates contact the basicoronal plate (amphisternous, e.g. Fig. 11E) (0); single post-basicoronal plate follows the basicoronal plate (meridosternous, e.g. Fig. 15I) (1).*

D10. *Adoral plating in interambulacral 5: both post-basicoronal plates contact the basicoronal plate (amphisternous, e.g. Fig. 11E) (0); single post-basicoronal plate follows the basicoronal plate (meridosternous, e.g. Fig. 15F) (1).*

D11. *In interambulacrum 5, a single more or less bilaterally symmetrical plate follows the labral plate: no (0); yes (1).* In some cases although there is only a single interambulacral plate following the labral plate, this is rather asymmetrial and is clearly still forming part of a biseries (e.g. Fig. 15F, G). In other taxa the plate that follows the labral plate is more or less bilaterally symmetrial (e.g. Fig. 15H, I).

D12. *In interambulacrum 5, more than two plates are uniserially arranged behind the peristome: no (0); yes, alternating left and right (Fig. 11G) (1); yes, forming a uniserial column (Fig. 15H) (2).*

D13. *In interambulacrum 5, plates 2a and 2b separated by: an oblique suture (Fig. 15B) (0); a vertical median suture (Fig. 11E) (1) a more or less horizontal suture (Fig. 15H) (2).*

D14. *In interambulacrum 5, plates 2a and 2b paired and of similar size: no (e.g. Fig. 15B, F) (0); yes (Fig. 15E) (1).*

D15. *In interambulacrum 5, basicoronal (labrum) plate shape: very small and undifferentiated (Fig. 15A) (0); stout and subquadrate (Fig. 15C) (1); at least twice wider than long (2); elongate and wedge-shaped, twice as long as wide (Fig. 15E) (3); triangular, expanding to rear (Fig. 15B) (4).*

D16. *Suture at rear of labral plate (boundary between labral and sternal plates): straight (Fig. 15C, G) (0); strongly concave to anterior (Fig. 15B) (1); oblique (Fig. 15A) (2).* Not scored where the labral and sternal plates are separated.

D17. *In interambulacrum 5, episternal plates (5.a.3, 5.b.3) paired and opposite: no (0); yes (Fig. 15E) (1).*

D18. *In interambulacrum 5, plate 3b fills the entire width of interambulacrum 5—contacting left and right adradial sutures: no (0); yes (1).* A single large plate forms the rear of the plastron in both the holasteroid *Corystus* and the spatangoid *Palaeostoma*.

D19. *In interambulacrum 5, plates 2b and 3a paired and opposite: no (0); yes (Fig. 15I) (1).*

D20. *In interambulacra 1 and 4, plates 2a, 2b distinctly elongate compared to succeeding plates in interambulacral zone on oral surface, and separated by a near vertical suture so that they are paired and opposite: no (0); yes (1).* This is a feature of some clypeasteroids.

D21. *Interambulacrum 1: number of plates below ambitus and seen in oral view: 3 plates (0); 4–6- plates (1) 7 or more plates (2).*

D22. *Interambulacra end adapically in a single plate: no, continue as a biseries to the apical disc (0); yes, end with a single enlarged adapical plate (1); yes, end with one or more small subequal plates forming a series of plates leading to the apex (2).* A single plate or row of uniserially arranged plates are found in some clypeasteroids only.

D23. *Posterior suture of interambulacral plate 4.b.2 lies aborally of the posterior suture of plate 4.a.2: no (0); yes (1).* Where a single uniserial plate follows the basicoronal plate this character was scored as not applicable. Regular echinoids and primitive irregular echinoids where no clear basicoronal plate is present were scored as unknown.

D24. *Posterior suture of interambulacral plate 1.b.2 lies aborally of the posterior suture of plate 1.a.2: no (0); yes (1).* Where a single uniserial plate follows the basicoronal plate this character was scored as not applicable. Regular echinoids and primitive irregular echinoids where no clear basicoronal plate is present were scored as unknown.

D25. *Interambulacral basicoronal plates distinctly swollen forming bulge adjacent to the peristome (bourrelets): no (0); yes (1); yes, pseudobourrelets (2).* The difference between a bourrelet and a pseudobourrelet is that a bourrelet arises from a single basicoronal interambulacral plate that becomes swollen and projects, whereas a pseudobourrelet is composed of a large number of small interambulacral plates which together form a projecting region of the test.

D26. *In interambulacrum 1: aboral edge of basicoronal plate lies against the first adjacent ambulacral plate in ambulacra II: yes (0) : no—extends to ambulacral plate 2 (1); no—extends to ambulacral plate 3 or beyond (2).*

D27. *In interambulacrum 2: aboral edge of basicoronal plates lies against the first adjacent ambulacral plate in ambulacrum III: yes (0); no—extends to ambulacral plate 2 (1); no—extends beyond ambulacral plate 2 (2).*

D28. *In interambulacrum 5: aboral edge of basicoronal plates: does not extend beyond the first ambulacral plate: (0); lies against the second adjacent ambulacral plate (Figs 11Q, 15C, F) (1); reaches to plate 3 or beyond (Fig. 15D, E) (2).*

D29. *Number of ambulacral plate abutting rear suture of plate 5.b.2 in ambulacrum I: 1(1); 2 (2); 3 (3); 4 (4); 5 (5); 6 (6), 9+ (9).* (ordered, fractional weighting)

D30. *Interambulacra with a zone of much narrower plates at the ambitus: no (0); yes (Fig. 16H) (1).*

D31. *Length of labral plate (basicoronal plate in interambulacrum 5): much smaller than succeeding sternal plates (0); 20–50% of sternal plate length (1); more than 50% of sternal plate length (2).*

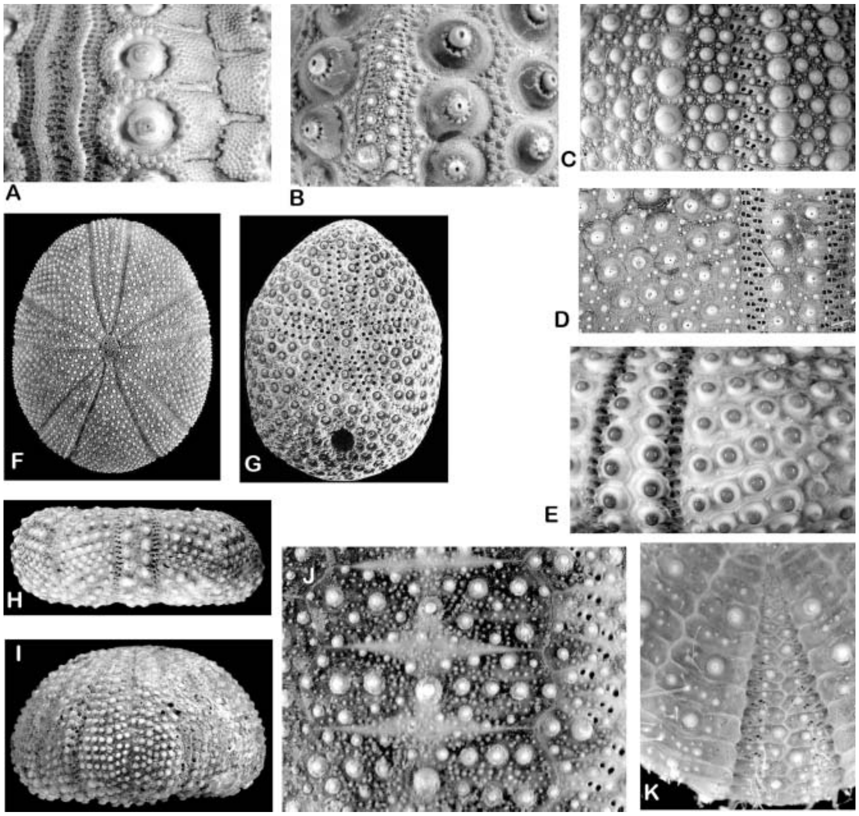

Figure 16. Tuberculation patterns. **A**, *Goniocidaris tubaria* (cidaroid), ambital plating showing well developed extrascrobicular granulation. **B**, *Hemicidaris* (stirodont), detail of ambital plating showing ambulacral (left) and interambulacral (right) zones. **C**, *Psammechinus* (echinoid), detail of lateral interambulacral (left) and ambulacral (right) plating. **D**, *Micropyga* (aulodont), interambulacral (left) and ambulacrtal (right) plating in subambital region. **E**, *Arbacia* (arbacioid) in lateral profile showing ambulacral (left and interambulacral (right) zones. **F**, *Echinoneus* (echinoneoid), in aboral view. **G**, *Togocyamus* (stem group clypeasteroid) in aboral view, showing sunken tuberculation. **H**, *Plistophyma* (phymosomatoid), test in lateral view with ambulacral zone central. **I**, *Polycyphus* (stem stomopneustid), test in lateral view with interambulacral zone central. **J**, *Gillechinus* (echinoid), detail of lateral interambulacral plates. **K**, *Calveriosoma* (echinothurioid), detail of adapical plating, ambulacral zone central. Not to scale.

Tuberculation style

D32. *Naked, tubercle-free zone developed adapically down middle (interradius) of interambulacral zones: no (0); yes (Fig. 7F) (1).*

D33. *Naked, tubercle-free zone running along midline of posterior interambulacrum on oral surface: absent (0); present* (*Fig. 10G, H*) *(1).* This character applies mostly to cassiduloids, but we also scored it as present in certain spatangoids where the labral plate is entirely or partially tubercle-free (e.g. Fig. 10D).

D34. *Interradial naked zone on oral surface pitted: no* (*Fig. 10H*) *(0); yes* (*Fig. 10G*) *(1).* The naked interradial zone is either smooth or slightly granular, or has a characteristic coarse reticulate ornament of pits.

D35. *In interambulacrum 5, basicoronal plates with tuberculation continuing from plates 2a/b: no (0); yes (1).*

D36. *In interambulacrum 5 plates 2a,b (sternal plates): fully tuberculate (0); anterior part of plates naked (1); almost entirely without tubercles (Fig. 10D) (2).*

D37. *Interambulacral zones with more than 10 small sub-equal tubercles/spines to each plate: no (0); yes (1).* In almost all irregular echinoids a large number of subequal tubercles cover each interambulacral plate at the ambitus.

D38. *Dense equal-sized tubercles sunken below surface of test over aboral surface so that only their mamelons protrude: no (0); yes (Fig. 16G) (1).* This style of tuberculation is widely developed in cassiduloids and clypeasteroids and is also seen in some holectypoids and spatangoids.

D39. *Interambulacral plates with primary tubercles: no (0); yes (1).*

D40. *Single primary tubercle differentiated on an ambital interambulacral plate: no (0); yes (Fig. 16A, B) (1).*

D41. *Two or more subequal primary tubercles present on an ambital interambulacral plate, usually forming a row: no (0); yes (Fig. 16D, E) (1).*

D42. *Primary tubercle flanked by smaller (secondary) tubercles on ambital plates; no (0); yes (Fig. 16C, J) (1).*

D43. *Primary tubercle surrounded by an incised (sunken) areole (muscle attachment area): no (Fig. 16E) (0); yes (Fig. 16A) (1).*

D44. *Primary interambulacral tubercle with surrounding ring of differentiated scrobicular tubercles and spines: no (0); yes, a scrobicular ring is present (Fig. 16A, B) (1).*

D45. *Scrobicular ring: present and forming a complete ring surrounding the primary tubercle (Fig. 16A) (0); confined to adradial and interradial sides of primary tubercle in ambital region and not forming a complete circle (Fig. 16B) (1).*

D46. *On ambital plates primary tubercle(s) dominate, occupying more or less the full height of the interambulacral plate (Fig. 16B) (0); tubercle(s) small compared to plate height; with a band of secondary tubercles or granules intervening between successive tubercles (Fig. 16J) (1).*

D47. *Densely packed field of small, identical granules cover outer margins of plate outside scrobicular circle: no (0); yes* (Fig. 16A) *(1).* This character refers to the small dense fields of granules that cover the interambulacral plates beyond the scrobicular circle of certain cidaroids, such as *Goniocidaris*.

D48. *Interambulacral tubercles: imperforate (0); perforate adapically, imperforate adorally (1); perforate throughout (2).* (ordered). Scored for primary tubercles where present, or for the largest of tubercles developed in irregular echinoids.

D49. *Interambulacral tubercles: smooth (0); weakly crenulate (1); strongly crenulate (2).* (ordered)

D50. *Size of interambulacral tubercles compared to adjacent ambulacral tubercles at ambitus: much smaller than ambulacral tubercles (0): approximately the same size (Fig. 16E) (1); yes, at least 1.5 times larger (2); yes, at least 3 times larger (Fig. 16B) (3).*

D51. *Mamelon on primary tubercles: massive without obvious surrounding platform: no* (Fig. 16B) *(0); yes* (Fig. 16E) *(1).* In many regular echinoids the mamelon is surrounded by a small platform at the top of the boss. However, in certain camarodonts and stirodonts the mamelon is relatively large and fills the entire upper surface of the boss.

D52. *Mamelon on tubercles largest adapically: no (0); yes (1).* In some regular echinoids mamelons on tubercles progressively increase towards the apex, whereas in most the largest mamelons are found on ambital primary tubercles.

D53. *Pattern of radial indentations at base of boss of primary tubercles: no (0); yes (1).* In a small number of regular echinoids, such as *Gauthieria*, the areole of primary tubercles is indented by a series of radial ridges and grooves imparting a distinctive pattern.

D54. *Oral tubercles with distinct radial symmetry to areoles: no (0); yes (1).* In holectypoids and pygasterids oral tubercles show a very strong radial symmetry with areoles much enlarged on their adambital side. It is this feature that is being scored for here.

D55. *Distinct zone of small densely packed tubercles surrounding the mouth—associated spines forming a grill across the opening to the mouth: no (0); yes (Fig. 12F) (1).* These zones of spines are used for manipulating food particles in clypeasteroids and cassiduloids.

D56. *Long backward-curving primary spines present aborally: no (0); yes (1).* This refers to the large primary spines that are scattered over the upper surface of certain spatangoids, such as *Lovenia*.

D57. *These long backward-curving primary spines attached to tubercles that are: superficial on plate (0); sunken (1).*

D58. *These primary aboral tubercles: crenulated (0); non-crenulate (1).*

D59. *Aboral tubercles lie scattered in a dense groundmass of fine granules: no (0); yes (1).* We score tubercles as scattered in a groundmass when they are separated by at least the diameter of 1 tubercle with smaller secondaries in between. This is a feature appearing in certain atelostomates.

D60. *Oral surface with 5 identical fields of differentiated locomotory spines: no (0); yes (1).* This character refers to the distinctive spine arrangement seen in certain sand dollars.

D61. *Posterior interambulacral zone (plastron) differentiated and bearing locomotory spines: no (0); yes (1).* Only Atelostomata have a differentiated plastron bearing specialized locomotory spines.

D62. *Subanal zone of enlarged tubercles and spines: absent (0); present forming a single cone (1); present forming a double cone (2*). This subanal cone of spines is used in certain burrowing spatangoids to maintain a drainage channel to the rear. It is either a single or double cone.

D63. *Tubercles present in aboral perradial zone of paired ambulacra between columns of pore-pairs: no (0); yes, a few scattered secondary spines (1); tuberculation as in interradial zones (2); small primary tubercles (cidaroid style) (3).* In most echinoids the adapical ambulacra remain tuberculate.

However, in some spatangoids the zone between pore-pair columns in the petals becomes naked and devoid of tubercles. Because the tuberculation in the ambulacra of cidaroids differs from that of the interambulacra these are scored separately.

D64. *Distinct fields of obliquely aligned tubercles aborally in interambulacra 2 and 3 bordering the anterior ambulacrum: no (0); yes (1).* Certain spatangoids (e.g. *Echinocardium*, *Lovenia*) have fields of aligned tubercles bordering the anterior ambulacrum. These support spines that arch across the frontal groove.

D65. *Lateral tubercles on the oral surface with areoles enlarged postero-laterally and with spiral parapet: no (0); yes (1).* This pattern of tuberculation is found in certain spatangoids such as *Lovenia* (Fig. 10D).

D66. *Aboral tubercles with strongly asymmetric mamelon and close-packed: no (0); yes (1).* Many spatangoids have densely-packed aboral tubercles with a distinctive morphology. These support strongly curved and overlapping spines that are used in maintaining the cohesion of the burrow walls in these infaunal taxa.

D67. *Pressure drainage channels present: no (0); yes (1).* Pressure drainage channels are weakly depressed, radially directed channels on the oral surface in clypeasteroids. They run to lunules or notches.

Peristome and girdle

E1. *Peristomal opening sunken below the general oral surface: no (0); yes (1).*

E2. *Peristomal margin in interambulacrum 5: flush with oral side (e.g. spatangoids) (0); narrow, down-turned (incurving) lip (e.g.* Arachnoides*) (1); large, concave depression that flattens out at the peristome (e.g.* Clypeaster*) (2); deep well-like entrance (e.g.* Echinolampas*) (3); inward-sloping zone forming a funnel-like entrance (e.g.* Nucleolites*) (4).*

E3. *Peristome outline: circular (0); bilaterally symmetrical wider than long (1); oblique and trigonal: axis 2-V (2); oblique and trigonal: axis 3-I (3) bilaterally symmetrical longer than wide (4); biconvex (5).*

E4. *Presence of labrum indenting posterior edge of peristome: no (0); yes (1).*

E5. *Presence of swollen interambulacra indenting all five faces of the peristome: no (0); yes (1).*

E6. *Peristome central (0); strongly displaced anteriorly (1); distinctly posterior of centre (2).*

E7. *Peristome orientation: downward-facing (0); obliquely facing forwards with posterior edge distinctly lower than anterior edge (1); peristome vertical and almost entirely hidden in plan view (2).*

E8. *Buccal notches: absent (0); present (1).*

E9. *Buccal notches: feeble (0); large, and U-shaped (1); deep, narrow and sharp (2).*

E10. *Distinct, smooth tag on interambulacral plates developed immediately behind the buccal notches: absent (0); present (Fig. 12B) (1).*

E11. *Ambulacral plates continue over the peristomial membrane: no ambulacral plates on peristomial membrane: no (0); yes (1).*

E12. *Ambulacral plate arrangement on peristome: rows of ambulacral plates and tube-feet continue as a series across the peristome (cidaroid pattern) (0); a short row of ambulacral plates extends across the peristome, with the most adoral pair clearly differentiated as buccal plates bearing specialized tube-feet (Kamptosoma) (1); only a pair of strongly differentiated buccal tube-feet and plates in each ambulacral segment of the peristome* (acroechinoid pattern, see David et al. 1995 for a definition) *(2).* (ordered)

E13. Five valve-like plates without associated tube-feet cover the peristome *(e.g. Palaeostoma, Conulus): no (0); yes (1).*

E14. *Columns of interradial plates over the peristomial membrane separating adjacent ambulacral zones: no (0); yes (1).*

E15. *Peristomial membrane: more or less densely plated (0); with only spicules present (1); completely naked (2).*

E16. *Peristomial ambulacral plates bear a prominent internal prong: no (0); yes (1).*

E17. *Perignathic girdle includes apophyses developed from the pair of perioral interambulacral plates: no (0); yes, as raised rim (1); yes, as upright flange-like apophyses (Fig. 17A) (2).*

E18. *Apophyses: separate adradial flanges widely separated and not connected interradially (0); Discrete adradial lobes that meet interradially—developed from continuous wall (cidaroid) (1); Single raised wall without adradial flanges—forming a single continuous wall across both plates (2).*

E19. *Perignathic girdle comprises 5 perradial spoon-shaped flanges, one from each basicoronal interambulacral plate: no (0); yes (Fig. 17C) (1).*

E20. *Perignathic girdle includes auricles developed from ambulacral plates: no (0); yes, from basicoronal plates (Fig. 17B) (1); yes, from second or subsequent ambulacral plates (excluding buccal plates) (2).*

E21. *Presence of auricles that meet and are fused above ambulacrum: no (0); yes (Fig. 17B) (1).*

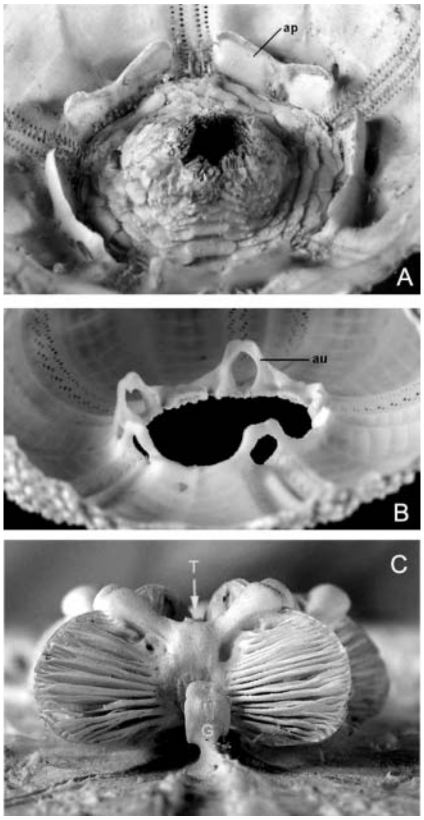

Figure 17. Perignathic girdle. **A**, *Prionocidaris* (cidarid), interior of oral surface showing apophyses (ap). **B**, *Paracentrotus* (echinoid), interior of oral surface showing auricles (au). **C**, *Hupea* (clypeasteroid) interior of oral surface in oblique view showing lantern and interradial element of periganthic girdle (G). Not to scale.

E22. *Perignathic girdle includes adradial prongs arising from two basicoronal interambulacral plates (those in interambulaca 1 and 4): no (0); yes (1).*

E23. *Internal muscle attachment pits in interambulacral zones bordering peristome: no (0); yes (1).* This character is developed only in *Conulus* and conulids.

E24. *Wing-like calcitic extension present internally in adoral interambulacrum 4 immediately inside the peristome: no (0); yes (Fig. 18B) (1).* An internal structure seen only in certain spatangoid echinoids, which supports the lower gut.

Lantern (Fig. 19)

F1. *Lantern apparatus present in adults: no (0); yes (1).*

F2. *Lantern present at some time during development: no (0); yes (1).* In some extant cassiduloids a lantern is present in post-metamorphic juveniles but is later resorbed.

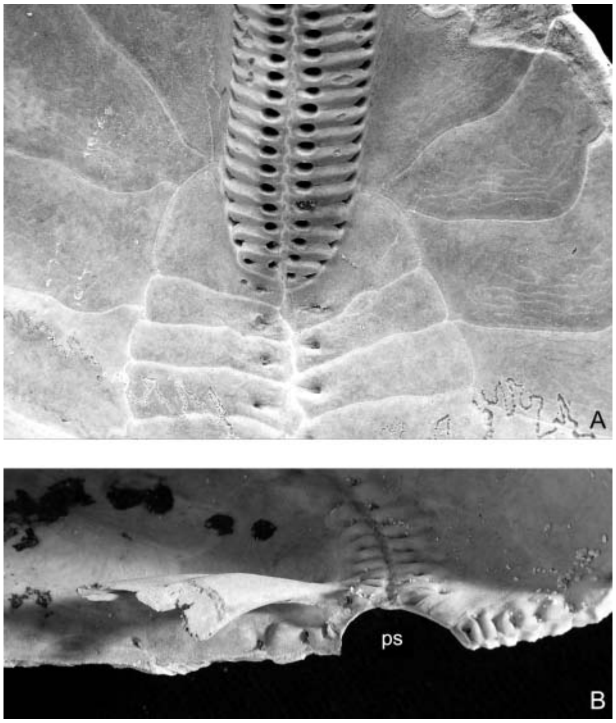

Figure 18. Internal features. **A**, *Meoma* (spatangoid), occluded plates at the end of the petals. **B**, *Meoma* (spatangoid), internal calcitic wing besides the peristome. ps = peristome. Not to scale.

F3. *Lantern in plan view: pentaradially symmetric (0); shows a strong antero-posterior bilateral symmetry (1).* A bilaterally symmetrical lantern is seen in many clypeasteroids and in juvenile cassiduloids.

F4. *Lantern with a deep foramen magnum: no (0); yes (1).* The lantern pyramid elements have a variably developed aboral notch, the foramen magnum. This is scored as deep where it forms at least one-third the height of the pyramids.

F5. *Top of hemipyramid with long inward-directed process supporting epiphysis: no (0); yes (1).*

F6. *Lantern with compasses: no (0); yes (1).*

F7. *Tooth shape in cross-section: U-shaped (0); keeled (1); wedge-shaped (2).* The shape of the tooth is dictated by the relative development of secondary tooth-plates. Keeled and wedge-shaped teeth have well-developed secondary plates while grooved teeth have poorly developed secondary tooth plates. In keeled teeth the secondary tooth plates bear a long projection, the lappet.

F8. *Epiphyses fused above foramen magnum: no (0); yes (1).* This is the characteristic arrangement seen in camarodonts.

F9. *Epiphyses with a prominent finger-like projection that support the tooth: no* (Fig. 19B) *(0); yes* (Fig. 19C) *(1).* This epiphysis projection is developed only in toxopneustids, strongylocentrotids and echinometrids.

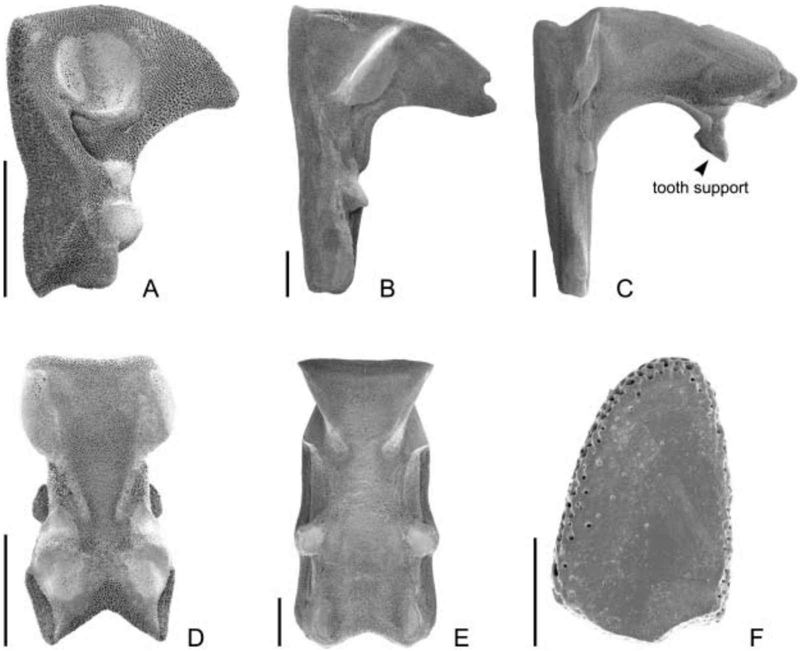

Figure 19. Lantern. **A**, *Stylocidaris* (cidaroid), cidaroid-type epiphysis. **B**, *Arbacia* (arbacioid), echinacean-type epiphysis. **C**, *Tripneustes* (echinoid), echinacean-type epiphysis with tooth support. **D**, *Stylocidaris* (cidaroid), rotula with ball-and-socket joint. **E**, *Arbacia* (arbacioid), rotula with hinge-type joint. **F**. *Echinocyamus* (fibulariid), rotula reduced to small, plate-like element. Scale bars A-E = 1 mm, F = 0.1 mm.

F10. *Articulation between the rotula and epiphyses: a ball-and-socket joint (Fig. 19D) (0); a hinge-type joint (Fig. 19E) (1); a flat planar surface (Fig. 19F) (2).*

F11. *Rotula: reduced to a small plate-like element: no (0); yes* (Fig. 19F) *(1)*. Rotulas are reduced to very small plates in clypeasteroids.

F12. *Shape of epiphysis: large and hatchet-shaped (Fig. 19A-C) (0); small and ear-shaped (1); large and subquadrate (e.g.* Triadotiaris*) (2).*

F13. *Hemipyramids with external wing-like extensions buttressed by flanges: no (0); present but poorly developed (1); present and strongly developed (Fig. 17C) (2).*

F14. *Hemipyramids with internal wing-like extensions buttressed by flanges: no (0); present but poorly developed so that the internal wings are much shorter than the exterior wings (1); present and strongly developed, equalling in size the external wings (2).*

F15. *Lantern projects through peristome: no (0); yes (1)*. The lantern of clypeasteroids never projects out of the peristome as it does in regular echinoids.

F16. *Tooth tip: serrated (0); with single terminal point (1)*. Archaeocidarids have multiple points whereas the teeth of all crown-group echinoids have only a single point.

External appendages

Spines (Fig. 20)

G1. *Central part of shaft of primary spine: a hollow lumen (Fig. 20H, I, L) (0); filled with a labyrinthic stereom mesh (Fig. 20G) (1); with dissepiments linked by thin pillars (Fig. 20K) (2); a lumen crossed by occasional trabeculae (Fig. 20J) (3).*

G2. *In cross-section the shaft of a primary spine is differentiated into medulla and lamellae: no (0); yes (Fig. 20G) (1).*

G3. *In cross-section radiating calcitic wedges originate from a well-defined basal plate: no (0); yes (Fig. 20I, J, L) (1).*

G4. *Spines covered in a cortex: no (0); yes (Fig. 20G) (1).*

G5. *Spine shaft with long neck before cortex starts: no, cortex commences within the first 10% of the spine's length (0); yes, a cortex is absent from the lower part of the spine (1).*

G6. *Spine ornament along shaft: appearing smooth to the eye, with only microscopic granulation (Fig. 20A) (0); scattered thorns along the shaft (Fig. 20B) (1); beaded or serrated ribs parallel to the shaft (Fig. 20D) (2); rows of thorns (Fig. 20C) (3); a dense pustular rugosity (4); whorls of thorns around the shaft (5).*

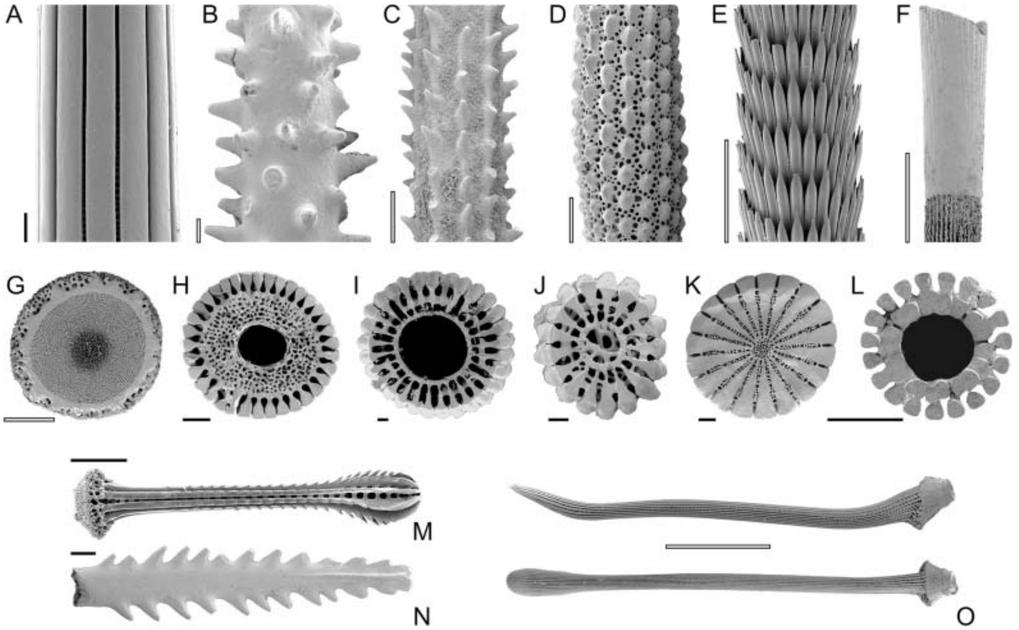

Figure 20. Spines. External ornament: **A**, *Paracentrotus* (echinoid), "smooth". **B**, *Prionocidaris* (cidaroid), scattered, coarse thorns. **C**, *Stylocidaris* (cidaroid), row of thorns. **D**, *Eucidaris* (cidaroid), beaded ribs. **E**, *Diadema* (diadematoid), verticillate. **F**, *Asthenosoma* (echinothurioid), hyaline hoof. Cross sections: **G**, *Eucidaris* (cidaroid), differentiation in central medulla, lamellae and cortex. **H**, *Asthenosoma* (echinothurioid), hollow spine with labyrinthic mesh. **I**, *Diadema* (diadematoid), hollow spine with well-defined basal plate. **J**, diadematoid with occasional trabeculae crossing central lumen. **K**, *Paracentrotus* (echinoid), dissepiments linked by thin pillars. **L**, *Brissopsis* (spatangoid), hollow spine with well-defined basal plate. General appearance: **M**, *Echinodiscus* (scutelline), aboral spine with swollen, bent head. **N**, Histocidarid, specialized adoral primary spine with saw-tooth edges. **O**, *Brissopsis* (spatangoid), spatulate-tipped spine in two views. Black scale bars equal 100 μm, white scale bars 1 mm. (B, C, J and N from Kroh 2005).

G7. *Spines: non-verticillate (0); verticillate (Fig. 20E) (1).*

G8. *Adoral primary spines flattened with saw-tooth edges; no (0); yes (Fig. 20N) (1).*

G9. *Secondary spines small, paddle-shaped and adpressed: no (0); yes (1).* In cidaroids the small secondary spines outside the scrobicular circles may be simple and cylindrical or more flattened, paddle-shaped and overlapping forming a protective coat.

G10. *Secondary spines: end in blunt rounded point without gland (0); end in an open crown (1); end in a glandular sac (2).* This character has been used as a key character in the classification of clypeasteroids.

G11. *Spine expanded distally as a crown-like tip: no (0); yes (1).*

G12. *Spines end in a hyaline hoof: no (0); yes (Fig. 20F) (1).*

G13. *Spine tip encased within a large bulbous gland: no (0); yes (1).*

G14. *Spines massive and club-like in shape: no (0); yes (1).*

G15. *Curved, overlapping spines developed over the aboral surface forming a hair-like coating: no (0); yes (1).* In fossils this arrangement of overlapping spines can be recognized from the presence of distinctive close-packed asymmetric tubercles.

G16. *Aboral spines spatulate-tipped: no (0); yes (Fig. 20O) (1).*

G17. *Spines with swollen and bent head present: no (0); yes* (Fig. 20M) *(1).* These distinctive spines are found in certain clypeasteroids only.

G18. *Aboral spine canopy dense, spines short, vertical and uniform in height forming a felt-like coating: no; (0); yes (1*). In cassiduloids and clypeasteroids the short dense spines form a very uniform felt-like coating. In fossils this pattern is evident from the dense arrangement of small, uniform tubercles.

Sphaeridia (Fig. 21)

G19. *Sphaeridia: absent (0); present (1).*

G20. *Sphaeridia: superficial on plate surface (Fig. 21A, F) (0); set in shallow pits (Fig. 21E) (1); fully enclosed within plate (Fig. 21G, I-M) (2); in open grooves (Fig. 21H) (e.g. as in* Eupatagus*) (3).*

G21. *Sphaeridia: one per ambulacrum (Fig. 21B, L) (0); a pair close to the peristome (Fig. 21I, M)*

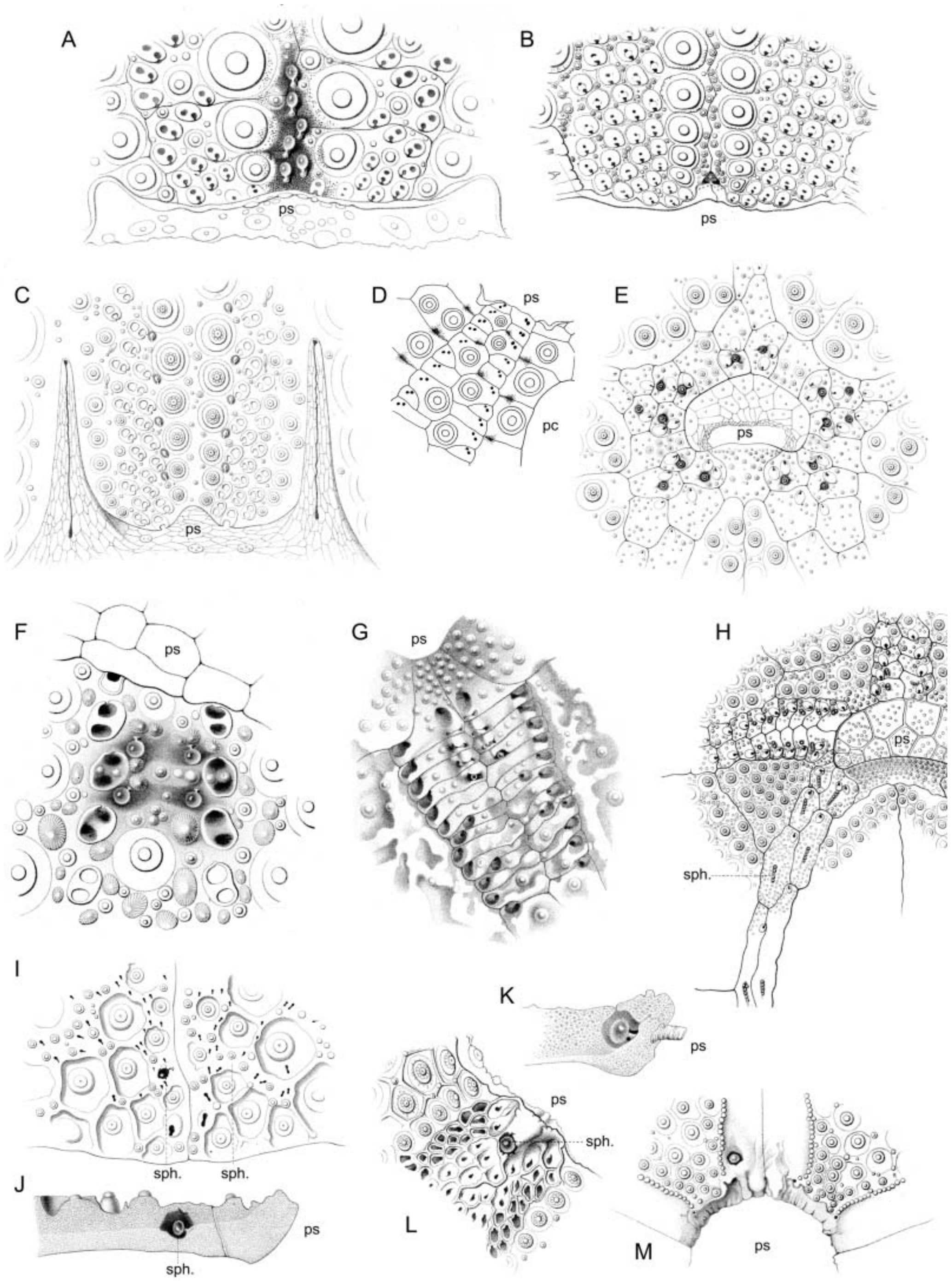

Figure 21. Sphaeridia. **A**, *Strongylocentrotus*, a short adoral row of superficial sphaeridia (one per compound plate, perradial position). **B**, *Arbacia*, a single adoral, perradial sphaeridium. **C**, *Astropyga*, adradial sphaeridia in shallow pits. **D**, *Discoides*, possible sphaeridial pits. **E**, *Echinocardium*, adradial sphaeridia in pits. **F**, *Echinoneus*, superficial sphaeridia. **G**, *Cassidulus*, a short adoral row of sunken sphaeridia along the perradial suture of the phyllodes. **H**, *Brissus*, multiple sphaeridia per plate in shallow grooves. **I-J**, *Clypeaster*, a pair of fully enclosed, adoral sphaeridia. **K**, *Echinarachnius*, cross section, single, perradial, fully enclosed sphaeridium characteristic for scutelline taxa. **L**, *Encope*, cross section, see K. **M**, *Arachnoides*, see I. In I, L and M, the sphaeridia are artificially exposed to show their position. 'ps' indicates the peristome, 'pc' the periproct. Not to scale. A-C, E-M from (Lovén 1874).

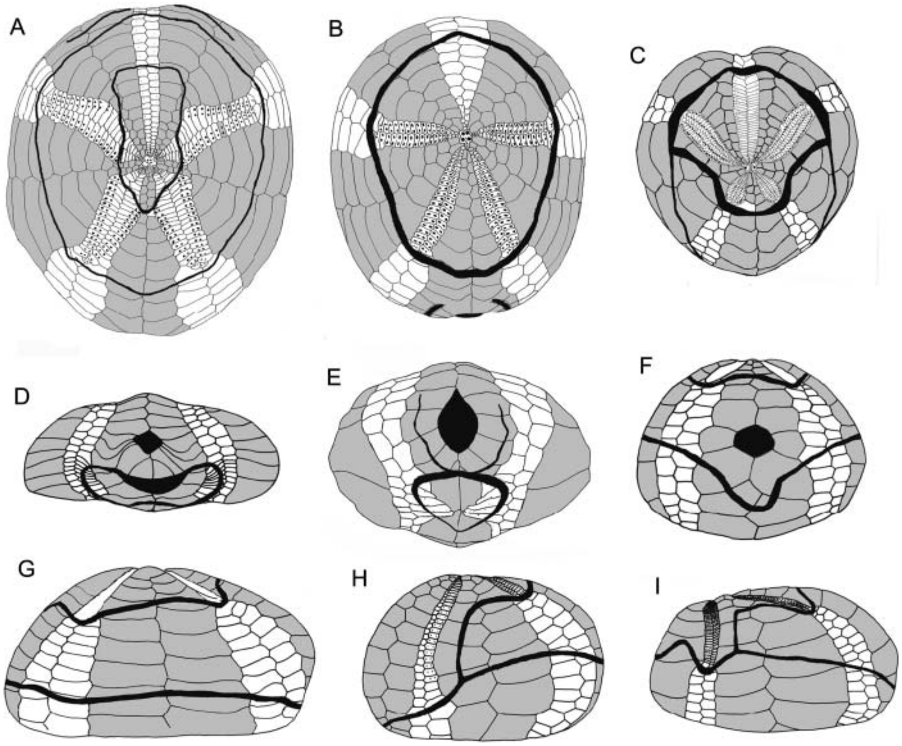

Figure 22. Fasciole patterns in spatangoids. **A**, *Breynia*, in apical view showing inner and peripetalous fascioles. **B**, *Rhynobrissus*, in apical view, showing peripetalous fasciole. **C**, *Schizaster* (*Ova*), in apical view showing peripetalous and lateroanal fascioles. **D**, *Lovenia*, in posterior view showing subanal fasciole. **E**, *Rhynobrissus*, in posterior view showing subanal and anal fascioles. **F**, *Schizaster* (*Ova*), in posterior view showing lateroanal fasciole. **G**, *Pericosmus*, in lateral view (anterior to the left), showing peripetalous and marginal fascioles. **H**, *Agassizia*, in lateral view (anterior to the left), showing peripetalous and lateroanal fascioles. **I**, *Brissus*, in lateral view (anterior to the left) showing peripetalous and lateroanal fascioles. Not to scale.

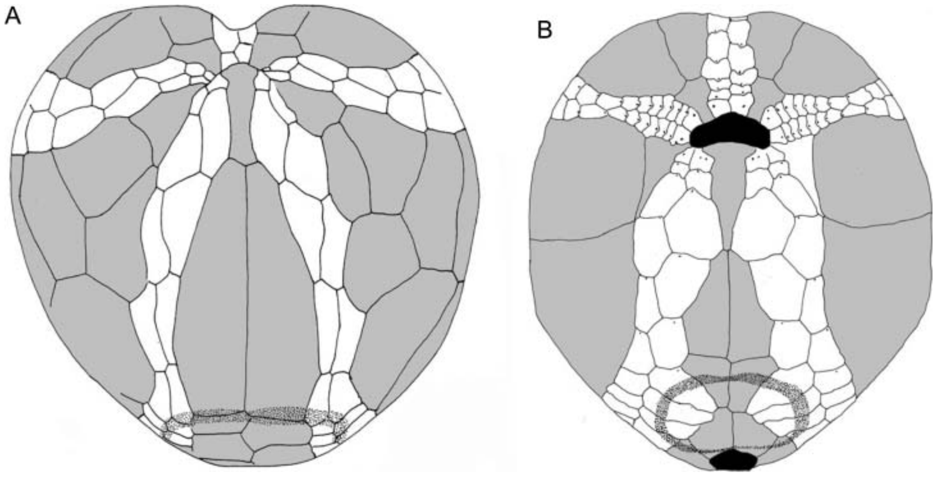

Figure 23. Oral plating and fascioles in spatangoids. **A**, *Micraster*, adoral branch of the subanal fasciole crossing plates 2a, 2b. **B**, *Lovenia*, adoral branch of the subanal fasciole restricted to plates 3a, 3b.

(1); a short row restricted to the adoral region (Fig. 21A, G) (2); multiple extending above ambitus (3).

G22. *Sphaeridia restricted to a short row at the ambitus: no (0); yes (1).*

G23. *Sphaeridia position: adradial (beside pore-pairs) (Fig. 21C, E, F, H) (0); perradial (Fig. 21A, B, G, L) (1).*

G24. *Number of sphaeridia: one per compound plate (Fig. 21A, C) (0); one each on upper and* *lower elements of a compound plate (1); one on each element (2); two or more per plate/element (Fig. 21H) (3).*

G25. *Shallow pits in adradial position on adoral interambulacral plates: no (0); yes* (Fig. 21D) *(1).* These shallow pits are found in holectypoids and are of unknown purpose.

Fascioles (Figs 22, 23)

G26. *Clavullae present and clustered into distinct zones/bands over the test to form fascioles or parafascioles (sensu Néraudeau et al. 1998): no (0); yes (1).*

G27. *Presence of a peripetalous fasciole band in posterior interambulacrum crossing in region of plates 8–14, passing above periproct: no (0); yes, enclosing only part of the posterior petals (1); yes, fully enclosing petals (Fig. 22B, C) (2).* This character scores for the presence of a peripetalous fasciole.

G28. *Fasciole bends sharply adapically in interambulacral columns 4a, 1b crossing two or three plates (Fig. 22C, H, I): no (0); yes (1).*

G29. *A peripetalous fasciole crosses interambulacral columns 4a, 1b on plate 6 or above (Fig. 22B): no (0); yes (1).*

G30. *A peripetalous fasciole crosses plate 5 in interambulacral columns 4a, 1b (Fig. 22C): no (0); yes (1).*

G31. *A peripetalous fasciole crosses plate 4 in interambulacral columns 4a, 1b (Fig. 22H): no (0); yes (1).*

G32. *A marginal fasciole crosses plate 4 in interambulacral columns 4a, 1b (Fig. 22G): no (0); yes (1).*

G33. *A marginal fasciole crosses plate 5 or higher in interambulacral columns 4a, 1b: no (0); yes (1).* This is the pattern seen in holasteroids.

G34. *Peripetalous and marginal fascioles merge in columns 4a, 1b: no (Fig. 22G) (0); yes (Fig. 22C, H) (1).*

G35. *Fasciole band running across interambulacral 4b, 1a crossing on or beneath plate 6 (Fig. 22G-I): no (0); yes (1).* This scores for the presence of a latero-anal or marginal fasciole.

G36. *Fasciole band beneath the anterior paired petals: crosses plates immediately underneath the end of petals (Fig. 22C, I) (0); passes across ambulacra II and IV two or three plates below the end of the petal (Fig. 22H) (1).* Where there are multiple fasciole bands we score for the one closest to the petal ends.

G37. *Fasciole crossing ambulacrum III below ambitus on plate 3/4 (Fig. 22H): no (0); yes (1).*

G38. *Fasciole crossing ambulacrum III above ambitus above plate 5 (Fig. 22I): no (0); yes (1).*

G39. *Internal fasciole passing across most adapical plates in posterior ambulacra and interambulacrum 5 immediately behind apical disc (Fig. 22A): no (0); yes (1).*

G40. *In interambulacrum 5, a single fasciole band crosses ambitally beneath periproct (Fig. 22F): no (0); yes (1).*

G41. *In interambulacrum 5, a subanal ring fasciole (Fig. 22D, E): absent (0); present (1).*

G42. *Adapical path of subanal fasciole: crosses no lower than plate 5 or 6 (0); crosses plate 4 (Fig. 22E) (1); crosses plate 4 but lost in adults (2).*

G43. *Adoral path of subanal fasciole passes: across plate 2b (Fig. 23A) (0); through centre of plate 3b (Fig. 23B) (1).*

G44. *Shape of subanal fasciole: distinctly oval with major axis horizontal (Fig. 23A) (0); distinctly bilobed (Fig. 22D) (1); semi-circular to oval with major axis vertical (Fig. 22B) (2); triangular (Fig. 22E) (3).*

G45. *Additional fasciole band present above subanal fasciole (Fig. 22E): no (0); yes (1).*