Article

The test architecture of *Clypeaster* (Echinoidea, Clypeasteroida) and its phylogenetic significance

MORANA MIHALJEVIĆ[1], IWAN JERJEN[2] & ANDREW B. SMITH[3]

[1]*Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland.*
E-mail: morana.miha@gmail.com

[2]*Empa - Swiss Federal Laboratories for Materials Testing and Research, Überlandstrasse 129, 8600 Dübendorf, Switzerland.*
E-mail: Iwan.Jerjen@empa.ch

[3]*Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW75BD, UK. E-mail: a.smith@nhm.ac.uk*

Abstract

Clypeaster is a speciose echinoid genus with almost 50 extant and approximately 350 extinct species, encompassing a great heterogeneity of form. While some attempts to subdivide this genus have been made, none has gained widespread support, and all recent taxonomic treatments have left the genus intact. Here we report new data on internal buttress arrangement, determined from X-Ray tomography, and plate architecture, and use this to establish relationships amongst 19 extant species encompassing 8 of the 10 nominal subgenera that have been proposed. A cladistic analysis of these characters allows us to test the validity of previously suggested subgenera of *Clypeaster*. Our analysis confirms that *Clypeaster* is monophyletic with the clypeasteroid family Arachnoididae (as represented by *Arachnoides* and *Ammotrophus*) as its immediate sister-group. It also identifies *Orthanthus* as the most primitive subgenus in the family *Clypeaster*. However, none of the previously proposed subdivisions of *Clypeaster* were recovered as clades and test architecture proves too homoplasous to allow a confident basis on which to subdivide the genus.

Key words: Echinoidea, *Clypeaster*, test structure, buttressing, phylogeny

Introduction

Clypeaster is the type genus of the Clypeasteroida, an order of irregular echinoids that includes the sand dollars and sea biscuits. It is a common shallow-water echinoid that is to be found in all of the world's tropical and subtropical seas and lives in or on soft sediments from the littoral zone down to ca. 500 m, although most species are confined to the shallow continental shelf (Mortensen 1948b). There are some 49 currently available species names for living *Clypeaster*, making it the most speciose extant genus of echinoid. The fossil record of *Clypeaster*, extending back to the Middle Eocene, encompasses yet another 350 nominal species (Durham 1955; Mortensen 1948b; Poddubiuk & Rose 1984; Rose & Poddubiuk 1987; Smith 2005; Kier & Lawson 1978; Kroh 2010). Due to its rather sturdy test it is one of the commonest fossil echinoids in the Tertiary (Michelin 1855). Yet subdividing *Clypeaster* taxonomically has proved to be difficult, largely because its various species show extensive gradation in test shape (Figs. 1–3). Gradation of features can be observed in traits such as test size, ambital outline, test profile, petal shape, periproct position and tuberculation (Hopkins 1988; Rose & Poddubiuk 1987). A difficult situation has been made much worse by palaeontologists establishing new fossil species based on minor shape differences in poorly preserved specimens and without reference to taxa described in other regions, which has undoubtedly led to the inflation of the number of nominal species (Poddubiuk 1985).

There have been several attempts to divide this diverse genus, starting with Agassiz (1863) and culminating in Mortensen (1948b), who reviewed and summarized all previous subdivision attempts (Pomel 1887; Lambert 1912; Lambert & Thiéry 1909–1925). Mortensen accepted 10 subgenera of *Clypeaster* (Table 1) based on a range of test characters including test shape, thickness of the test's edge, petal form and internal structure, but his definitions and diagnoses were rather vague and there is inconsistency in how individual traits are reported (Table 1). Probably as

TABLE 1. Mortensen's (1948b) ten subgenera of *Clypeaster* and the characters he used to distinguish them. Taxa that we have included in this study are in bold; dagger after species name indicates it is fossil.

Subgenus	Type species	Other species	Main characters
C. (**Clypeaster**) Lamarck 1801	**C. rosaceus**	C. pallidus, C. eurypetalus	Double wall
C. (**Orthanthus**) H. L. Clark, 1941	**C. euclastus**	C. cyclopilus, **C. ravenelii**	Flat test, broadly opened and straight pore pairs, strongly developed marginal buttressing
C. (**Alexandria**) Pfeffer, 1881	**C. europacificus**		Flat test, opened petals and straight pore pairs, well developed internal structure with several marginal lamellae
C. tumidus	C. tumidus		Ovoid test outline, very wide opened petals, pore pairs reaching almost the edge of the test
C. (**Leptoclypus**) Koehler, 1922	**C. annandalei**	**C. rarispinus**	Anterior petal widely opened, paired petals closed, internal structure moderately developed
C. (**Coronanthus**) Lambert, 1913	**C. microstomus†**	C. amplificatus, **C. latissimus**, C. pateriformis, **C. telurus**	Large and flat test: broad, ovoid and nearly closed petals
C. (**Rhaphidoclypus**) Agassiz, 1863	**C. reticulatus**	C. lytopetalus, **C. australasiae**, **C. fervens**	Absence of marginal internal lamellae
C. (**Stolonclypus**) Agassiz, 1863	**C. humilis**	**C. eurychorius**, C. virescens, **C. japonicus**, C. speciosus, **C. ochrus**, **C. rotundus**, **C. subdepressus**, C. lamprus, C. prostratus, C. lutkeni, **C. miniaceus**, C. leptostracon, C. nummus	Test with flattened margin and raised central part, well developed marginal buttressing
C. (*Bunactis*) Pomel, , 1887	C. scille†	**C. rangianus**	Flat test, elevated petals (more or less closed distally)
C. (*Pavaya*) Pomel, 1887	C. corvini†	C. ohshimensis	Ovoid test outline, widely opened petals, adoral bourrelets

a result, Durham (1955, 1966) and subsequent authors (e.g. Serafy 1970, 1971; Hopkins 1988; Mooi 1989; Schultz 2006) have all chosen not to use any of Mortensen's groupings, instead leaving all species within the single 'umbrella' genus *Clypeaster* while acknowledging that there is considerable heterogeneity amongst species.

The wide geographical distribution, high taxonomic diversity, excellent preservation potential and rich fossil record make *Clypeaster* a prime subject for biogeographical and palaeobiological studies. However, the taxonomy and phylogeny within the genus has to be resolved before this potential can begin to be exploited. Here we revise the taxonomy of *Clypeaster* based on new analyses of the test architecture of extant taxa drawn from 8 of the 10 subgenera accepted by Mortensen (1948b). We compile data on internal buttress architecture using X-Ray tomography, and combine this with character analysis of plating pattern and test morphometrics to construct a phylogenetic framework that we hope provides a more secure basis for the subdivision of this speciose taxon.

Material and methods

Taxa. We selected 19 species of *Clypeaster*, representing 8 of 10 subgenera defined by Mortensen (1948b), for detailed analysis (Table 1, bold; Figs. 1–3). Wherever possible we included the type species of the nominal subgenera, but where this was a fossil taxon we chose one or more of the included extant species in preference. Three species (*C. reticulatus*, *C. humilis* and *C. ravenelii*) were each represented by two specimens of different size, which were scored independently to check whether internal buttressing characters showed ontogenetic consistency. As scoring for each pair was virtually identical and the two conspecifics grouped together in the phylogenetic analyses we omit the duplicates from all further mention. Two of Mortensen's (1948b) subgenera could not be included in this study, *Clypeaster* (*Pavaya*) Pomel, 1887 and *C.* (*Anomalanthus*) Bell, 1884. The type species of *Pavaya* is a fossil and Mortensen only tentatively placed one modern species, *C. ohshimensis* in this subgenus. *Clypeaster ohshimensis* is extremely rare and Mortensen (1948b) was only able to find one possible example, an encrusted dead test, to illustrate. Its plating and internal construction remain unknown and it has never been refigured. *Anomalanthus* is based on a single species, *A. tumidus* Bell, which was also very poorly known until Endean & Pope (1964) rediscovered a population living in the vicinity of Lord Howe Island. While Endean & Pope provide important new information on the pedicellariae and external shape of this species, there is no mention of test plating or internal buttressing. With so much unknown about these taxa we omitted them from our analyses.

We include eight other taxa in our analysis to act as an outgroup for establishing character polarity. *Arachnoides* (Figs. 3C, D) and *Ammotrophus* (Figs. 3E, F) are members of the Arachnoididae and, along with *Fellaster*, the only other living genera that belong to the suborder Clypeasterina. They are thus the closest living relatives to *Clypeaster* (Mortensen 1948b; Durham 1966; Smith 2005). Three fossil Arachnoididae, *Philipaster*, *Scutellinoides* and *Monostychia*, were added to increase our representation of this family. We also included two primitive stem group Scutellina from the Eocene, *Scutellina*, one of the most primitive representatives of the sister group to the Clypeasterina and approximately contemporary with the oldest known fossil *Clypeaster* (Kroh & Smith 2010), and *Sismondia* (Figs. 3G, H). Finally to root all these crown-group clypeasteroids we added *Oligopygus*, which is widely accepted to be a late stem-group Clypeasteroida (Smith 1981; Mooi 1990; Kroh & Smith 2010).

Morphological characters used in analysis. To construct our character data matrix we assembled 28 phylogenetically informative morphological characters, drawn from internal buttress organization, plate architecture and a select number of morphometric features from the test (listed and described in the Appendix 1). Basic test measurements were made using digital callipers and a curve-measuring tool used to construct profiles and measure the degree of sunkenness of the peristome, sharpness of the ambitus and flatness of the oral surface (Fig. 4). The ratio of distance from apical disc to peristome edge versus apical disc to baseline gave a measure of the degree to which the peristome was sunken. The flatness of the oral surface was measured by the angle at which the test sloped inwards from the baseline from the lowest point. We also scored for the relative position of the periproct and its proximity to the margin, and for the shape of the petals. As the anterior petal often have a different morphology to the paired petals, measurements were made on both the anterior petal and one of the paired lateral petals. Histograms of continuously variable characters were plotted to determine the most appropriate break points when defining character states (Fig. 5). In all cases, however, there was a considerable degree of gradation.

Specimens of approximately comparable size were chosen for X-Ray imaging and placed in an X-ray micro tomography cone beam instrument to generate radiographs and stacked computer tomography images of the test

samples' internal structures. Radiograph images and mechanically sectioned tests from Mortensen (1948b), when available, were also consulted, to check for consistency of character states and for deriving the scores of taxa not accessible to us. Plating diagrams of the oral surface and of the petals were made using a camera lucida attachment to a binocular microscope. This proved difficult for some thick-tested species and complete plating diagrams could not always be developed. However, only in the case of *Clypeaster rosaceus* was it impossible to work out plating pattern, and for that species we used the plating diagram in Durham (1955, fig. 25a).

Phylogenetic methods. A parsimony analysis of the taxon-character data matrix set out in the Appendix 1 was carried out using the program PAUP* (Swofford 2002). Multistate characters that were based on linear or continuous characters were treated as ordered (these are identified as such in the Appendix 1) and all characters were initially given equal weight. The most parsimonious trees were found using a heuristic search algorithm with 1000 random addition replicates to ensure the most parsimonious trees were found. After this initial run characters were reweighed by their rescaled consistency index and the analysis repeated. One thousand random addition replicate analyses were done to calculate bootstrap support values and Bremer support values were calculated by relaxing the parsimony criterion by one step at a time and calculating the strict consensus of the resulting trees.

Results

Plating architecture. The construction of the test in *Clypeaster* is highly conserved, as noted previously by Durham (1955) based on a much smaller sampling, with all species showing very similar plating arrangements (Fig. 6). In all cases all five interambulacral zones are disjunct with the basicoronal plate separated from other plates in the zone by a single pair of ambulacral plates. There are, however, two previously overlooked aspects of plating that may be phylogenetically significant: petal plate organization and position of the periproct.

The shape of the petals varies in *Clypeaster* from being divergent and widely open distally (Fig. 2G) to being strongly bowed and effectively closed distally (Fig. 2E). This difference correlates with the extent to which occluded plates are developed in ambulacral zones at the ends of the petals. Petals that are widely opened distally lack or have very few occluded plates while strongly bowed petals have many occluded plates (Fig. 7). The degree to which plate occlusion is developed is clearly linked to petal shape.

The periproct always opens on the oral surface close to the posterior margin (Figs. 1–3), but the precise interambulacral plates that bound this opening varies from species to species. In most species the periproct is bounded at its anterior by plates 5.b.4 and 5.a.3 or by plates 5.b.4 and 5.a.4 (Fig. 6), but in *C. rosaceus* it is bounded by plates 5.b.5 and 5.a.5.

Oral tuberculation. While tuberculation pattern within *Clypeaster* is rather uniform, that of *Arachnoides, Ammotrophus* and *Monostychia* is strikingly different. In these latter species there are triangular-shaped patches in ambulacral plates where tubercles are arranged into oblique rows, each separated by a row of pores, forming what are termed 'combed areas' (Figs. 3C, F). In all *Clypeaster* species and in the other Arachnoididae taxa tubercles in the ambulacral zones are unorganized, though with a tendency to become smaller approaching the food groove, and pores lie scattered across the plate. Notably, however, a few species of *Clypeaster* such as *C. rarispinus* (Fig. 3A), *C. euclastus* and *C. subdepressus* do develop distinct triangular zones where tuberculation is finer and a dense array of pores is to be found.

Internal buttressing (Appendix 1, characters 1–8). Radiographs showing the arrangement of internal buttressing in *Clypeaster* species are given in Figures 8 and 9. Buttresses connect the lower and upper plated surfaces of the test and we use the term pillar for a calcite connection that is rounded to oval in cross-section, bar for a calcite connection that is obviously flattened and elongate. Bars can be circumferentially or radially aligned (Fig. 10). In ambulacral zones they are usually circumferentially arranged to accommodate the lateral lobes of the water vascular system, whereas in interambulacral zones they are more often arranged radially from the growth centre of each plate. In most species there is a clear distinction between a marginal zone of buttressing, composed of relatively stout bars and walls, and a central zone of buttressing that usually comprises a series of fine pillars sometimes bounded by a rim of curtain-like bars and with adradial bars bounding the petals. The main coils of the gut lie between these two zones of buttressing. The gut runs anteriorly from the central mouth along the left side of ambulacrum III, and its tract is evident by an absence of pillars and a break in the rim. *C. reticulatus,* however, differs from all other clypeasteroid species examined in having its gut directly against the tests margin. Here the outer buttressing is absent (Fig. 8A).
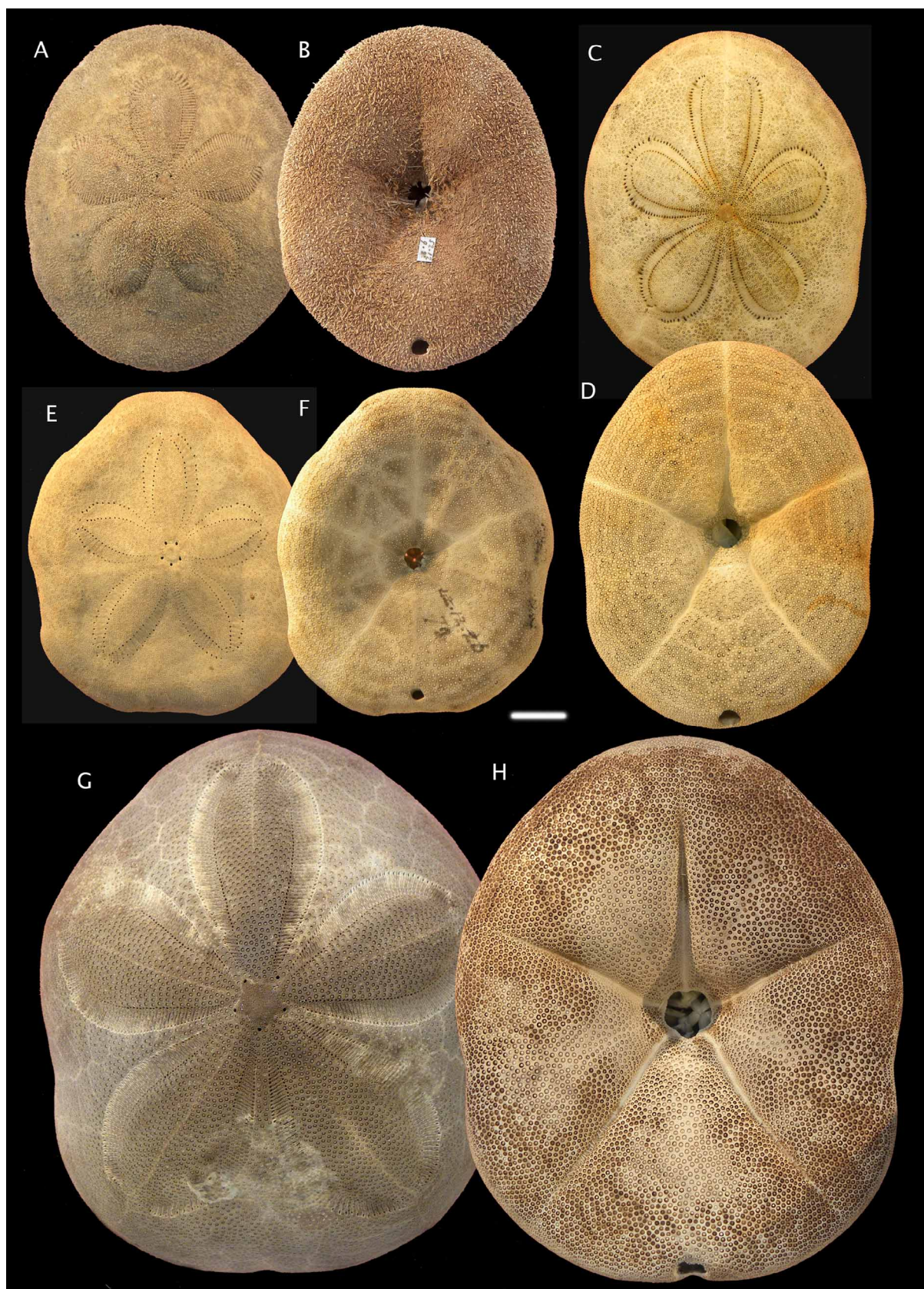
FIGURE 1. A, B, NHM 1952.12.9.8, *Clypeaster australasiae* (Gray, 1851), Australia (no detailed location); A, apical, B, oral. C, D, NHM EE140012, *Clypeaster japonicus* Döderlein, 1885, Miyake-jima, Izu Island, Japan: C, apical, D, oral. E, F, NHM 1942.12.26.72, *Clypeaster reticulatus* Agassiz, 1863, Mauritius; E, apical, F, oral. G, H, NHM EE14011, *Clypeaster rosaceus* Linnaeus, 1758, Carrie Bow Cay, Belize; G, apical, H, oral. Scale bar = 10 mm.
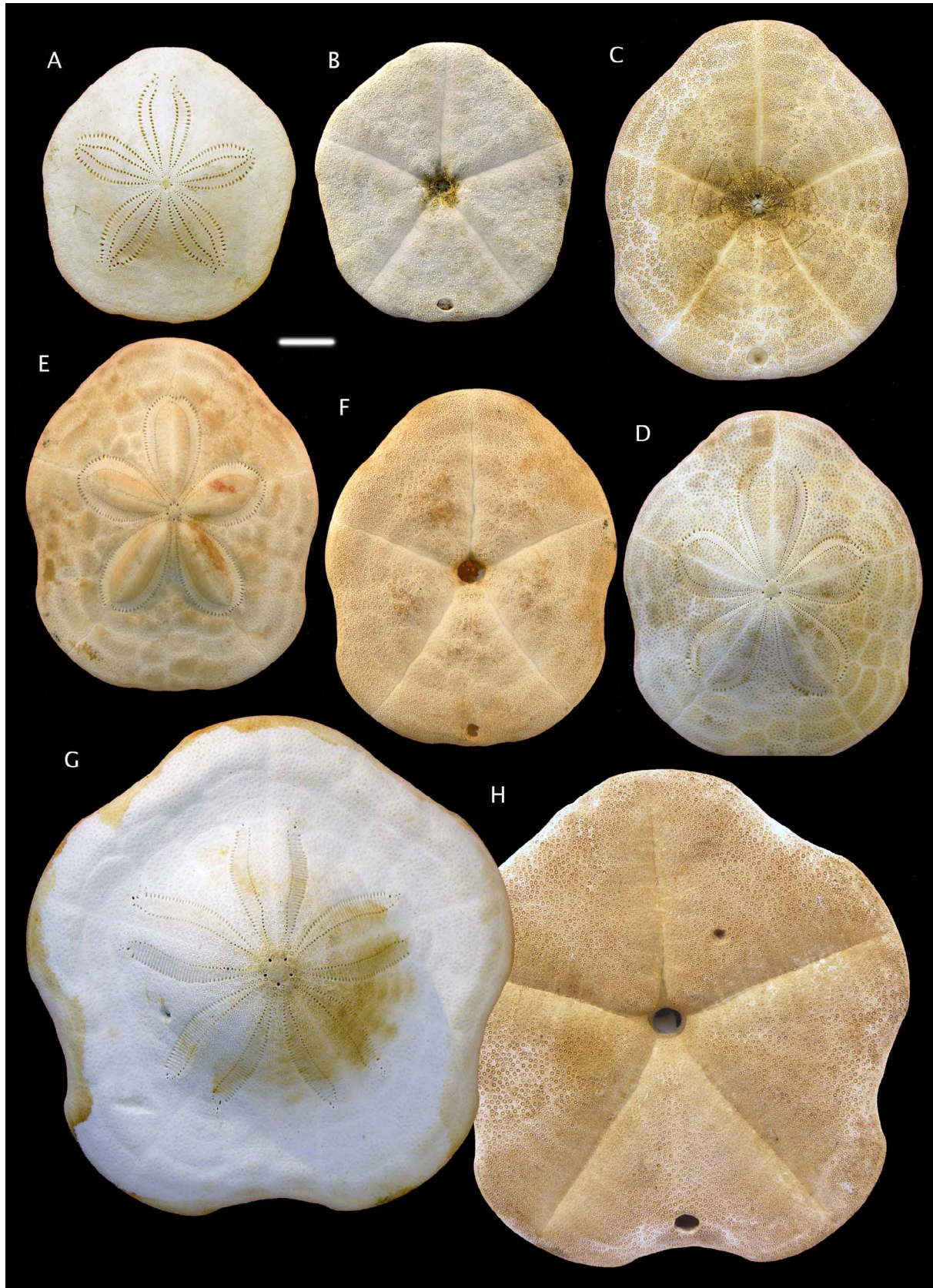
FIGURE 2. A, B, NHM 1948.12.9.122, *Clypeaster annandalei* Koehler, 1922, Station 194, John Murray Expedition; A, apical, B, oral. C, D, NHM 1948.12.9.17, *Clypeaster fervens* Koehler, 1922, station 53, John Murray Expedition; C, oral, D, apical. E, F, NHM EE14009 *Clypeaster humilis* Leske, 1778, from Western Australia; E, apical, F, oral. G, H, NHM 1937.5.9.18, *Clypeaster ravenelii* (Agassiz, 1869), off Tortingas, Gulf of Mexico; G, apical, H, oral. Scale bar = 10 mm.
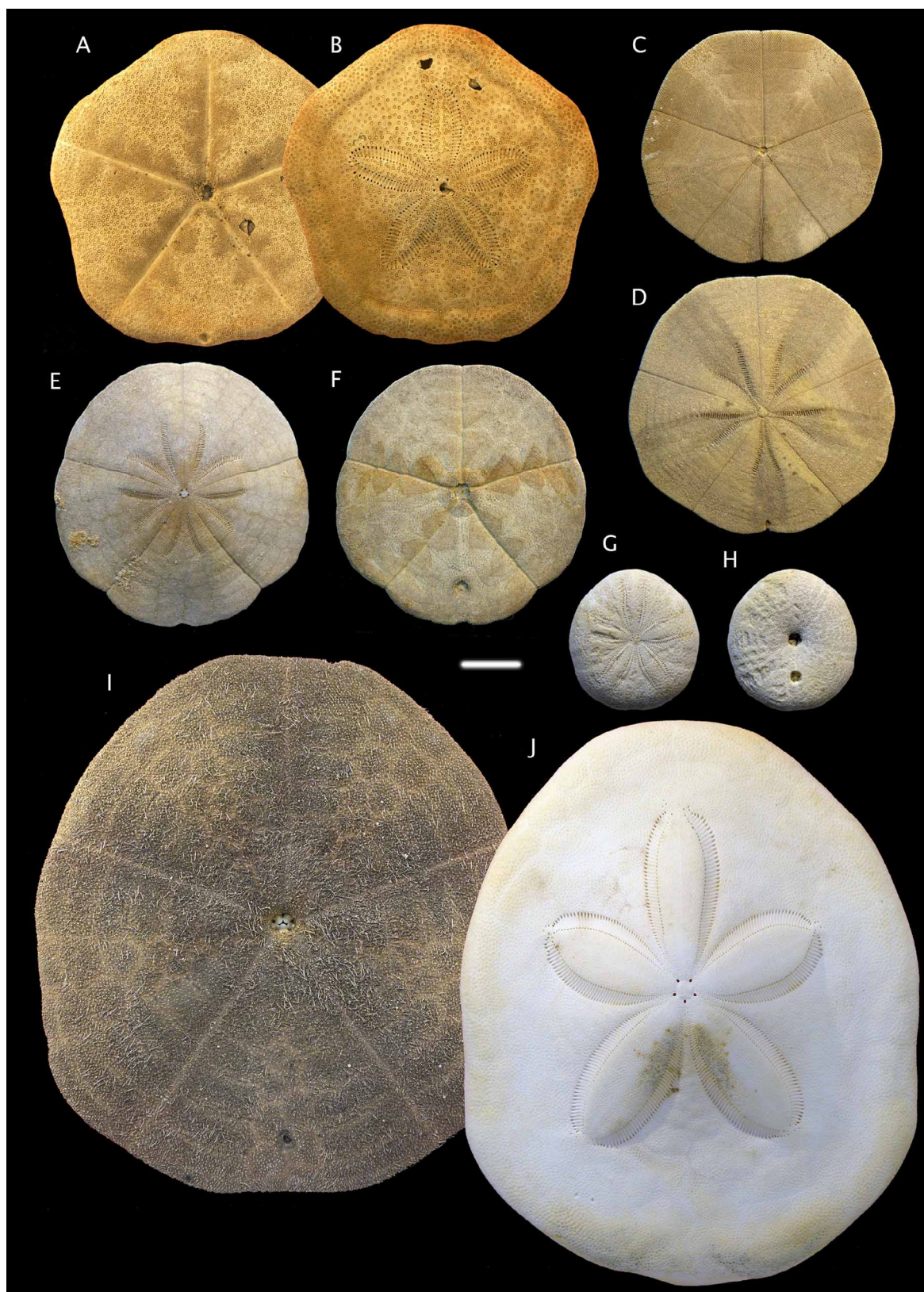
FIGURE 3. A, B, NHM 1968.12.6.69, *Clypeaster rarispinus* de Meijere, 1902, Eritrea coast; A, oral, B, apical. C, D, NHM EE14008, *Arachnoides placenta* Linnaeus 1758, Cairns, Australia; C, oral, D, apical. E, F, NHM 1939.6.15.44, *Ammotrophus cyclius* Clark, 1938, Encounter Bay, Australia; E, apical, F, oral. G, H, NHM 57883, *Sismondia occitana* (Defrance, 1827), Eocene (Priabonian) of St Colombe, Manche, France; G, apical, H, oral. I, NHM 1953.1.24.34, *Clypeaster telurus* Clark, 1914, Monte Bello Island, Australia; oral side. J, NHM EE14010, *Clypeaster subdepressus* (Gray, 1825), Carrie Bow Cay, Belize; apical. Scale bar = 10 mm.
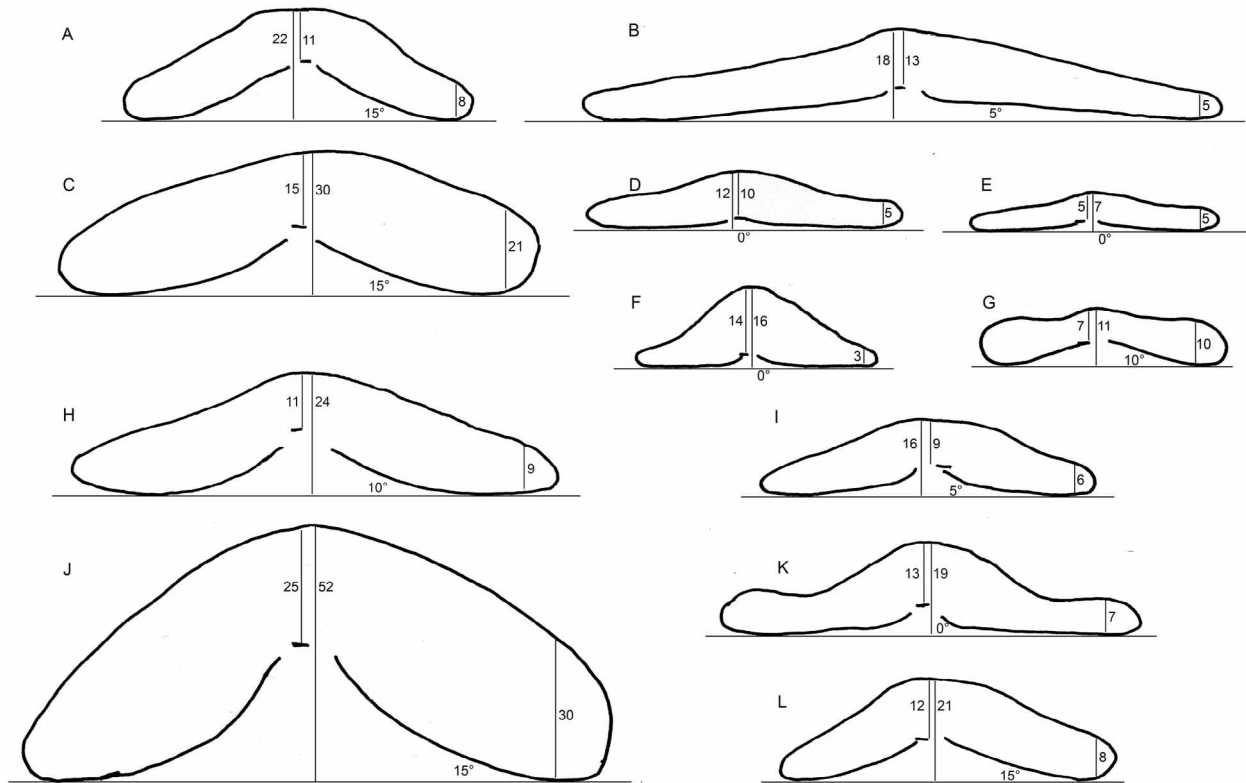
FIGURE 4. Test profile outlines showing position of measurements taken. A. *Clypeaster ravenelii*, B. *Clypeaster australasiae*, C. *Clypeaster fervens*, D. *Clypeaster subdepressus*, E. *Clypeaster humilis*, F. *Clypeaster rangianus*, G. *Clypeaster rarispinus*, H. *Clypeaster japonicus*, I. *Clypeaster reticulatus*, J. *Clypeaster rosaceus*, K. *Clypeaster annandalei*, L. *Clypeaster telurus*.

In some species marginal buttressing is well developed, comprising an extensive zone of walls, bars and pillars (e.g. Fig. 8E, 9E) but in other species it is reduced to a single ring of bars and/or walls that are intermittently developed around the periphery (e.g. Figs. 8A–D). A third arrangement is found in *C. rosaceus* where a single buttress wall is not just confined to the periphery, but extends orally and aborally forming what Mortensen (1948b) referred to as a 'double wall' (Fig. 8F). A microcanal system is formed between the inner and outer wall that houses branches of the water vascular system and these are circumferentially aligned. In species with well-developed marginal zones, some are constructed from a series of discrete circumferential walls (e.g. Fig. 9E) while others are formed of rows of aligned bars and pillars (e.g. Fig. 9A). While no *Clypeaster* species has well developed radial bars positioned along the adradial margins of the anterior and lateral interambulacra, in a few species the periproct is bounded laterally by two radial bars along adradial sutures (e.g. Fig. 8C). In species with a well-developed marginal buttress zone discrete radial bars are absent and instead a clear channel is developed through buttressing which tends to coalesce at the edges (e.g. Fig. 9D).

Buttressing in the central zone is generally much finer and sparser than in the marginal zone and in *C. annandalei* (Fig. 9F) is reduced to just a few isolated adradial pillars. In many species there is a distinct ring of bars that bound the ends of the petals and which extend adradially towards the apex (Figs. 9D, E). In *C. rangianus* (Fig. 8E) this ring is extremely well developed, forming an almost continuous bounding wall, whereas in others, such as *C. telurus, C. subdepressus* and *C. rarispinus* (Figs. 9A–C) it is effectively absent. Scattered pillars are usually developed in the interambulacral zones between the petals (Figs. 9A–C) but are only rarely encountered in ambulacral zones within the petals (e.g. Fig. 9A).

One final character that is easily observed from radiographs is the degree to which the loop of the gut extends around the anterior (Appendix 1, character 26). The digestive system runs from the mouth towards the anterior along ambulacrum III where it coils anticlockwise for about 360 degrees. It then loops back on itself and returns clockwise along the right-hand side until it reaches the periproct. In some species the gut loops back on itself before it reaches the midline of ambulacrum III (Figs. 9A, B) whereas in others it extends almost to interambulacrum 3 and thus overlaps the early part of the gut (Figs. 8B, 9C). The boundary between the two is often marked by a row of pillars (Fig.8E).
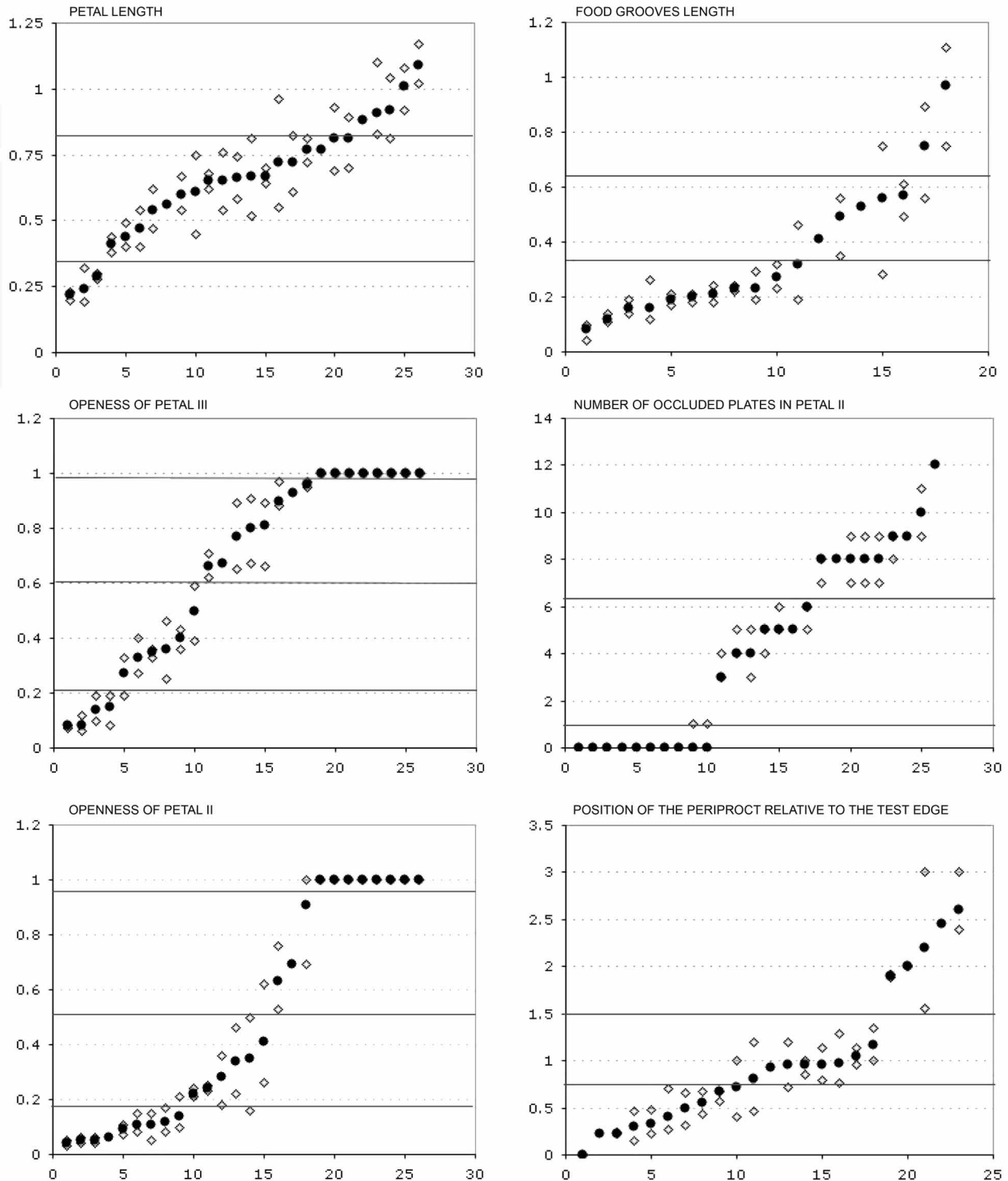
FIGURE 5. Histograms of continuously variable characters with break points used for defining character states marked. Circle = mean; diamonds = minimum and maximum.

Phylogenetic results. Parsimony analysis of the assembled data matrix (Appendix 1) generated 2028 equally parsimonious solutions with best tree score of 129 steps, a consistency index of 0.38, and a retention index of 0.69. These 2028 trees were found in 99% of the replicates run. After reweighting characters based on their rescaled consistency index and rerunning the analysis just three trees were found (recovered in 73% of the replicate searches). These trees have a length of 42.253 steps, with a consistency index of 0.53 and a retention index of 0.80. A strict

consensus of these three trees (Fig. 11) is taken as our best-supported hypothesis. However, few nodes are supported by more than 70% bootstrap support, so the topology is not robust. Nevertheless, a number of tentative conclusions can be drawn from this tree.
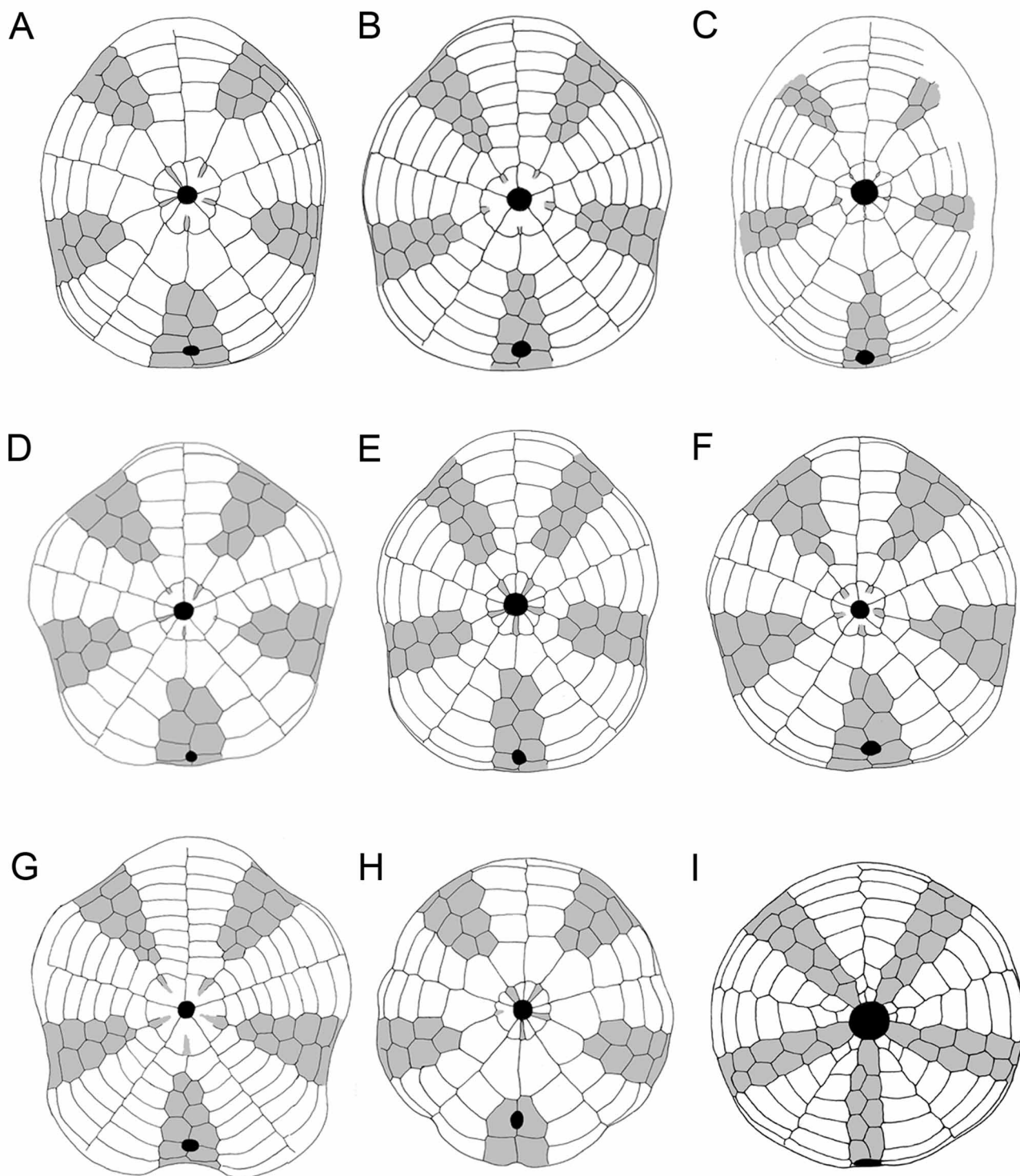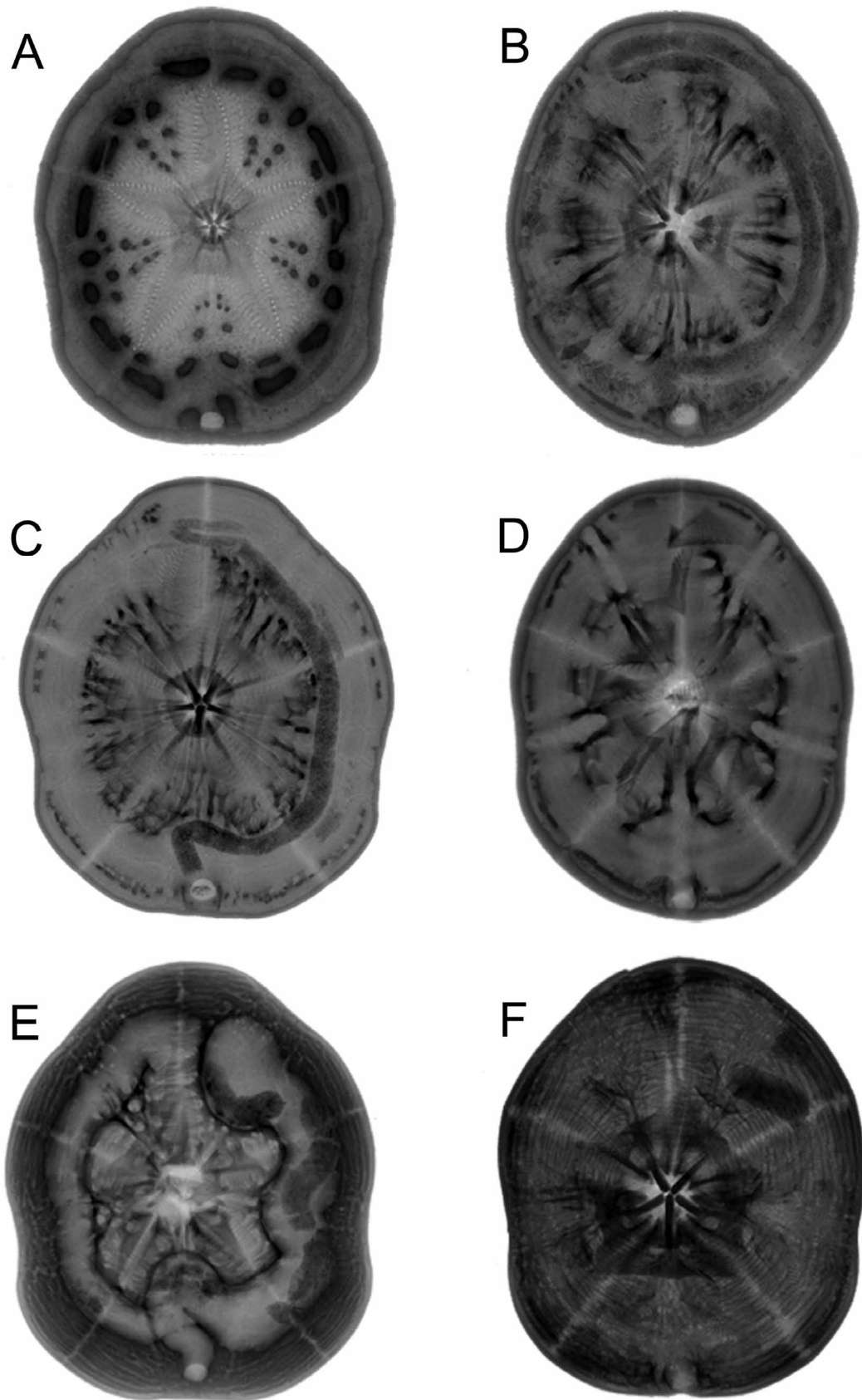

FIGURE 6. Camera lucida drawings of oral surface plating. A, *Clypeaster reticulatus* Agassiz, 1863; NHM 1938.1.6.15. B, *Clypeaster fervens* Koehler, 1922; NHM 1948.12.9.17. C, *Clypeaster japonicus* Döderlein, 1885; NHM EE140012. D, *Clypeaster rarispinus* de Meijere, 1902; NHM 1968.12.6.69. E, *Clypeaster humilis* Leske, 1778; NHM EE14009. F, *Clypeaster annandalei* Koehler, 1922; NHM 1948.12.9.122. G, *Clypeaster ravenelii* (Agassiz, 1869); NHM 1937.5.9.18. H, *Ammotrophus cyclius* Clark, 1938; NHM 1939.6.15.44. I, *Sismondia occitana* (Defrance, 1827); NHM 57883. Not to scale.

MIHALJEVIĆ *ET AL.*
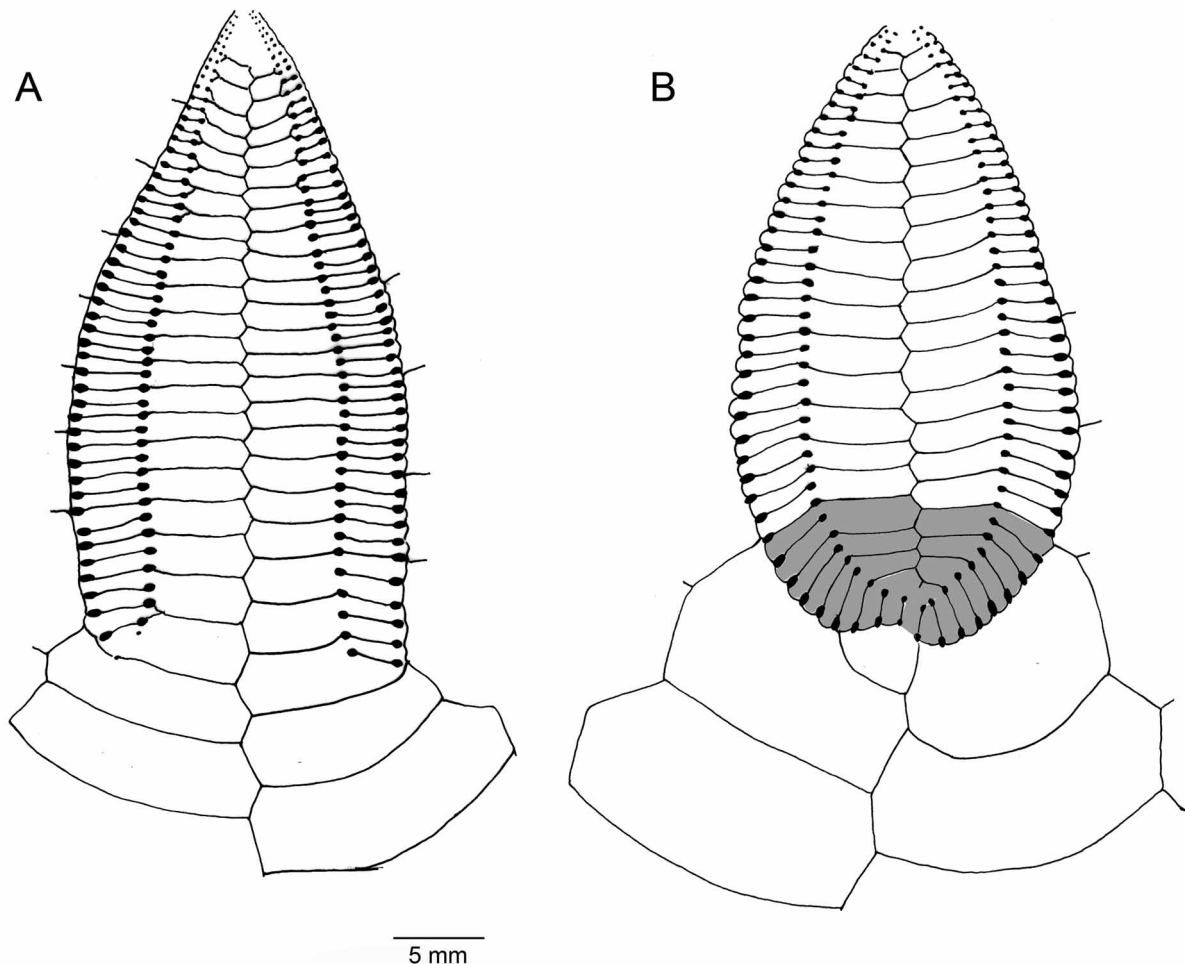
FIGURE 7. Camera lucida drawings of petal plating on the aboral side showing the correlation between number of occluded plates (grey) and degree of closure of petals. A. *Clypeaster annandalei* Koehler, 1922; NHM 1948.12.9.122 ; open petals. B. *Clypeaster ravenelii* (Agassiz, 1869); NHM 1937.5.9.18; closed petals. Scale bar 5 mm; apical plates at top.

First, the monophyly of *Clypeaster* is strongly supported, whereas the Arachnoididae, as currently defined, is paraphyletic. Amongst Arachnoididae, the Arachnoidinae and Ammotrophinae together form the sister taxon to *Clypeaster* while the two Fossulasteridae (*Scutellinoides* and *Philipaster*) are more distantly related. Arachnoidinae and Ammotrophinae share with all *Clypeaster* species the derived character of having demiplates in their petals, and share with more basal *Clypeaster* a complex marginal buttress zone comprising circumferential ambulacral walls and radially arranged interambulacral bars, and demarcated triangular areas of tube-feet. *Clypeaster* differs from all outgroup taxa in having five not four gonopores while Arachnoidinae and Ammotrophinae both have combed areas in their oral ambulacra and food grooves that extend from the oral surface to the apex. The Arachnoididae are a Southern Hemisphere clade confined to Australia and New Zealand with a fossil record that extends back only to the Oligocene whereas the fossil record of *Clypeaster* extends back to the late Eocene (Smith 2005; Kroh & Smith 2010). Our tree implies that the earliest fossil record of arachnoidids must be missing.

Of the *Clypeaster* species included in our analysis the most primitive is *C. euclastus*. *C. euclastus* shares with Arachnoidinae and Ammotrophinae petals that expand distally to remain wide open distally and so lack occluded plates. While a few other *Clypeaster* species have broadly open petals none are open quite to this degree. Other characters that are primitive within *Clypeaster* include having a sharp margin and broad flattened edge to the test supported internally by a well-developed marginal buttress zone. The periproct opens close to the ambitus between plates 3a and 3b whereas in more advanced *Clypeaster* it is displaced to plate 4 or even 5. *C. euclastus* is the type species of *Orthanthus* Clark, 1941, which is thus an available name for this basal form.

FIGURE 8. X-ray images showing internal structures. A, *Clypeaster reticulatus* Agassiz, 1863*;* NHM 1942.12.26.72. B, *Clypeaster australasiae* (Gray, 1851); NHM 1952.12.9.8. C, *Clypeaster fervens* Koehler, 1922; NHM 1948.12.9.17. D, *Clypeaster japonicus* Döderlein, 1885; NHM EE140012. E, *Clypeaster rangianus* Desmoulins, 1835; NHM 1957.7.2.48. F, *Clypeaster rosaceus* Linnaeus, 1758; NHM EE14011.
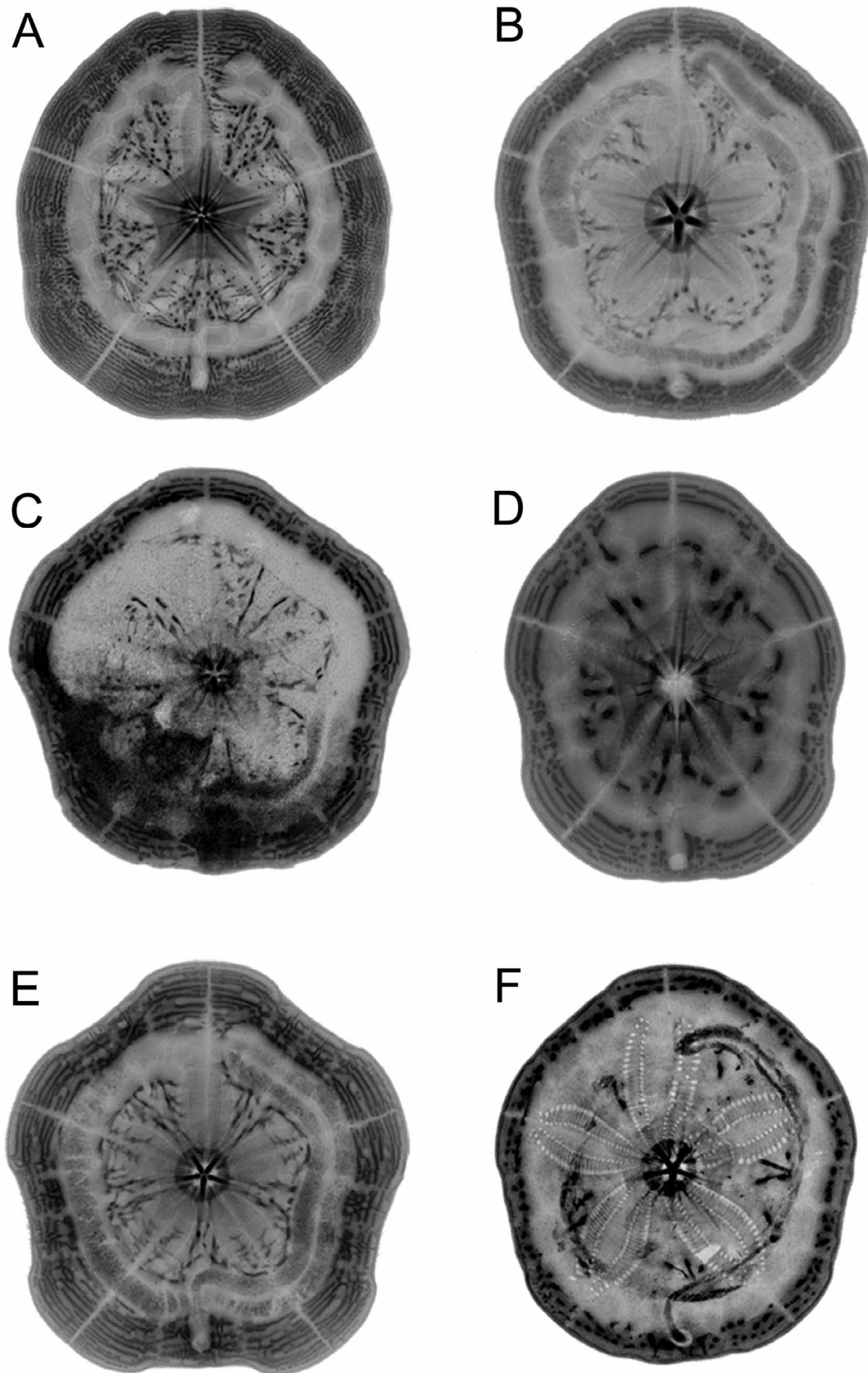
FIGURE 9. X-ray images showing internal structures. A, *Clypeaster telurus* Clark, 1914; NHM 1953.1.24.34. B, *Clypeaster subdepressus* (Gray, 1825); NHM 1962.7.2.11. C, *Clypeaster rarispinus* de Meijere, 1902; NHM 1968.12.6.69. D, *Clypeaster humilis* Leske, 1778; NHM EE14009. E, *Clypeaster ravenelii* (Agassiz, 1869); NHM 1937.5.9.18. F, *Clypeaster annandalei* Koehler, 1922; NHM 1948.12.9.122. Not to scale.
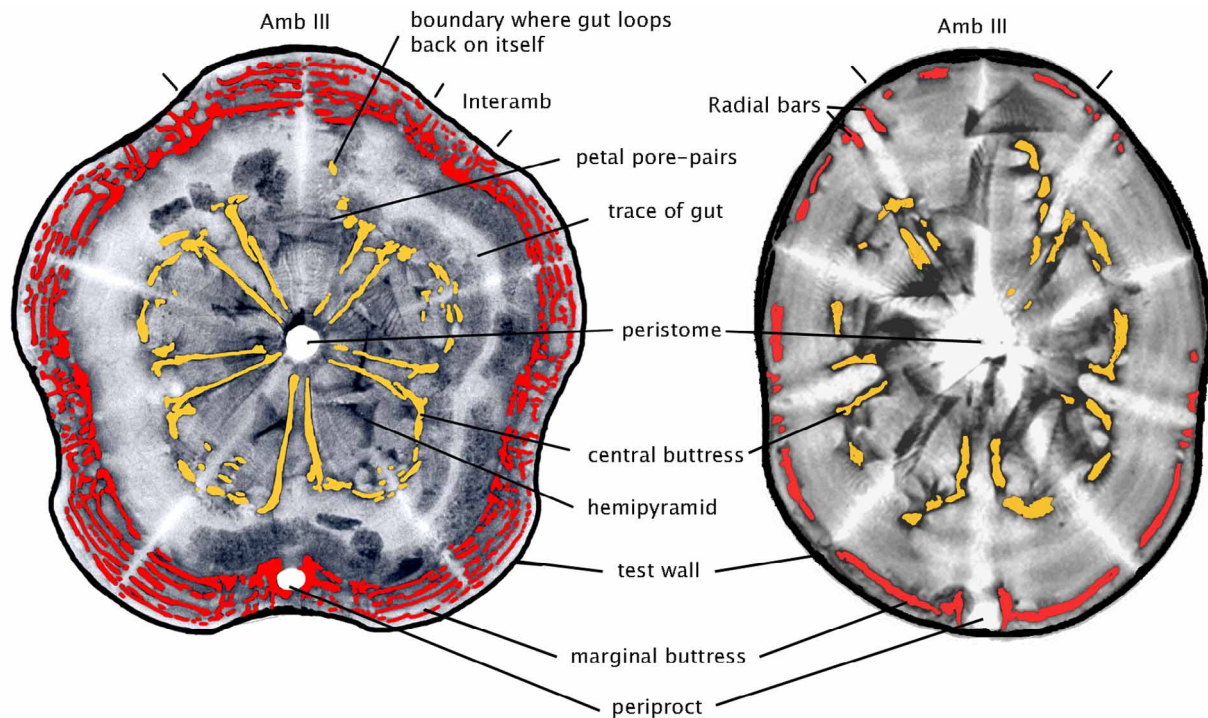
FIGURE 10. Summary diagram explaining expressions used in description of internal buttressing.

The next most basal clade unites the taxa *C. europacificus, C. eurychorius* and *C. ravenelii* though without strong character support. These share plesiomorphic characters with *C. euclastus* including having a sharp ambitus, widely open petals with few occluded plates and well developed marginal zones of buttressing. The internal buttressing is typically fine and dense in this group, as it is in *C. euclastus*.

The more derived *Clypeaster* species fall into two groups: one characterized by simple marginal buttressing with absent or single internal wall, a well developed inner partition of radial bars along adradial sutures, short food grooves, and a distinctly sunken oral surface, the other characterized by primitively retaining complex multipartitioned marginal buttressing, long food grooves and usually numerous median pillars between and sometimes within the petals. Both have bowed petals that converge distally to a greater or lesser extent and incorporate significant numbers of occluded plates. The first comprises a core grouping of *C. reticulatus, C. australasiae, C. fervens, C. japonicus, C. ochrus* and *C. rosaceus* that forms a well-defined clade. *Clypeaster rosaceus*, as type species of the genus *Clypeaster*, confers its name to this clade. *Clypeaster rosaceus* is unique in having a double wall and microcanal system. This unusual test structure was the basis for Mortensen's (1948b) subgenus *C. (Clypeaster)*. However, this structure is present at the ambitus in several of these taxa, and *C. ochrus* and *C. rosaceous* uniquely have their periproct opening at plates 5a/5b. *C. ochrus* and *C. rosaceous* are identified as sister taxa with strong support.

Clypeaster reticulatus, the type species of the subgenus *Rhaphidoclypus,* is unique in having no buttressing outside the loop of the gut (Fig. 8A). This marginal position of the gut distinguishes *Rhaphidoclypus reticulatus* from all other species we have examined. Mortensen (1948b) assigned two other species to his subgenus *Rhaphidoclypus, Clypeaster (Rhaphidoclypus) australasiae* and *Clypeaster (Rhaphidoclypus) fervens*. However, in our analysis (Fig. 11) these two species form a clade with *Clypeaster japonicus* all three having a single of incomplete internal wall separated from the test edge. *Clypeaster japonicus* was previously assigned by Mortensen (1948b) to his subgenus *Stolonoclypus,* despite lacking the well developed internal marginal buttressing that characterizes the type species of that genus.

The other major group in our phylogenetic tree is more weakly supported and combines forms with a flat base, thin test margin and moderately to well developed peripheral buttressing zones, and medium to long, closed petals with many occluded plates at their tips. This includes many species that Mortensen assigned to his subgenera *Stolonoclypus* and *Coronanthus*, the former having a more domed central zone than the latter. This group includes the type species of *Stolonoclypus* Agassiz, 1863, *Clypeaster humilis*, which is therefore the oldest available name for the clade.
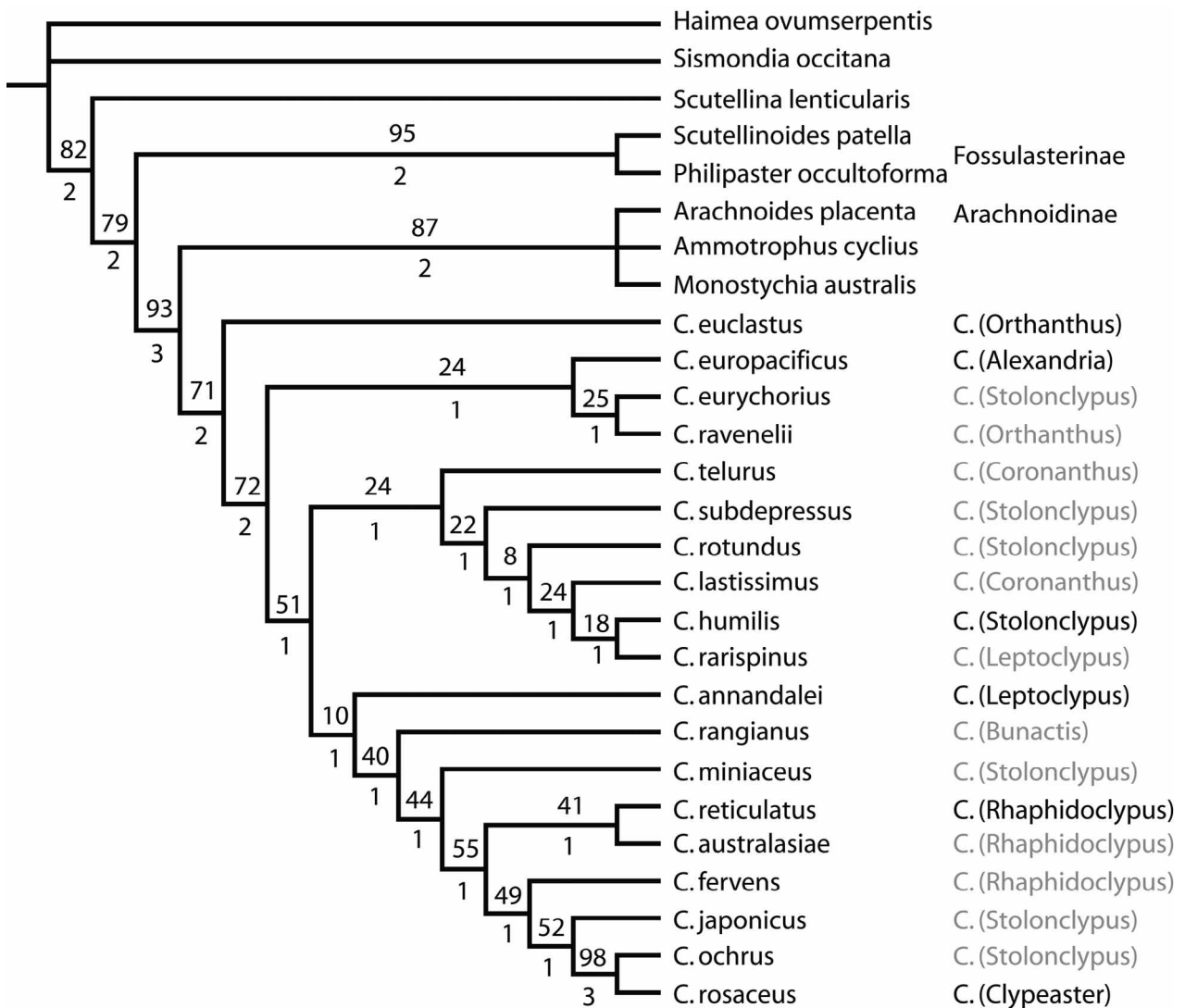
FIGURE 11. Strict consensus tree that was found from parsimony analysis of the data matrix in the Appendix. Trees have a length of 42.25 steps, a consistency index of 0.53 and a retention index of 0.80. Mortensen's (1943) original supraspecific classification of *Clypeaster* species is indicated on the right.

There is one remaining taxon, *Clypeaster annandalei* which, while falling within the clade characterized by having a distinct zone of marginal buttressing, lies outside *Stolonoclypus* and *Orthanthus*. *Clypeaster annandalei* is a type species of the subgenus *Leptoclypus* Koehler, 1922. It is unusual in having relatively poorly developed marginal and central buttressing and shows a strong difference in the degree of closure between the anterior (widely opened) and paired petals (closed).

Conclusions

We have tested the basis of Mortensen's (1948b) subdivision of the genus *Clypeaster* and found little support for his species groupings. In all cases where we have included two or more species from one of his subgenera these have not clustered together in our phylogenetic tree. However, although internal buttressing and ambulacral plate organization at the petal ends do provide characters that are phylogenetically informative, homoplasy within this group is rife and unambiguous apomorphies are wanting for most nodes. While the most basal (*Orthanthus*) and most derived (*Clypeaster*) clades are well supported there is only very weak support for other groupings. We therefore refrain from establishing a formal taxonomy for the genus a phylogenetic analysis based on gene sequence data that can confirm or refute our morphology-based relationships.

Acknowledgements

Literature

Agassiz, A. (1863) List of the Echinoderms. *Bulletin of the Museum of Comparative Zoology, Harvard,* 1, 17–28.

Agassiz, A. (1869) Preliminary report on the echini and starfishes dredged in deep water between Cuba and the Florida reef. *Bulletin of the Museum of Comparative Zoology, Harvard,* 1, 253–308.

Bell, F.J. (1884) On the generic position and relations of *Echinanthus* (*Anomalanthus* n. g.) *tumidus. Proceedings of the Zoological Society, London,* 1884, 40–44, pls 2–3.

Clark, H.L. (1914) The echinoderms of the Western Australian Museum. *Records of the Western Australia Museum,* 1, 132–173, pls17–26.

Clark, H.L. (1938) Echinoderms from Australia. *Memoirs of the Museum of Comparative Zoology, Harvard,* 55, 1–597, pls 1–28.

Clark, H.L. (1941) Reports on the Scientific Results of the Atlantis Expeditions to the West Indies under the Joint Auspices of the University of Havana and Harvard University: The Echinoderms (Other Than Holothurians). *Memorias de la Sociedad Cubana de Historia Natural*, 15, 1–154.

de Meijere, J.C.H. (1902) Vorläufige Beschreibung der neuen, durch die Siboga-Expedition gesammelten Echiniden. *Tijdschrift van de Nederlansche Dierkundige Vereeniging Leiden* (2), 8, 1–16.

Desmoulins, C. (1835) Premier mémoire sur les Échinides. Prodrome d'une nouvelle classification des ces animaux. *Actes de la Société Linnéenne de Bordeaux*, **7**, 167–245.

Döderlein, L. (1885) Seeigel von Japan und den Liu-Kiu-Inseln. *Archiv der Naturgeschichte*, 51, 73–112.

Durham, J.W. (1955) Classification of Clypeasteroid echinoids. *University of California Publications in Geological Sciences*, 31, 73–198.

Durham, J.W. (1966) Clypeasteroids. *In*: Moore, R.C. (Ed.) *Treatise on Invertebrate Paleontology.* University of Kansas and Geological Society of America Press, Boulder, Co., pp. U450–491.

Endean, R., and E.C. Pope, 1964. Rediscovery of the echinoid *Clypeaster tumidus* (Tenison-Woods) and an emended description. *Records of the Australian Museum,* 26(9), 275–281, pls 29–30.

Gray, J.E. (1825) An attempt to divide the Echinida, or sea eggs, into natural families. *Annales of Philosophy*, 26, 423–431.

Gray, J.E. (1851) New genera and species of Scutellidae and Echinolampidae. *Proceedings of the Zoological Society London*, 19, 34–38.

Hopkins, T.S. (1988) A review of the distribution and proposed morphological groupings of extant species of genus Clypeaster in the Caribbean Sea and Gulf of Mexico. *In*: Burke R.D. et al. (Eds) *Echinoderm Biology*, Balkema, Rotterdam, pp. 337–345.

Kier & Lawson (1978) *Index of living and fossil Echinoids 1924–1970*. Smithsonian Contributions to Paleobiology, 34, 182 pp.

Koehler, R. (1922) Echinides du musée indien à Calcutta. 11. Clypeastridés et Cassidulidés. *Echinoderma of the Indian Museum*, part IX, Echinoidea (II). Calcutta, 161 pp.

Kroh, A. (2010) Index of living and fossil Echinoids 1971–2008. *Annalen des Naturhistorischen Museums in Wien, Serie A,* 112, 195–470.

Kroh, A. & Smith, A. B. (2010). The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology,* 8, 147–212.

Lamarck, J.B. (1801). *Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux*. Déterville, Paris.

Lamarck, J.B. (1816) *Histoire naturelle des animaux sans vertèbres*, *volume 3. Echinides*. Paris, pp. 1–59.

Lambert, J. (1912) Description des échinides des terrains Néogènes du bassin du Rhone. *Mémoires de la Société Paléontologique Suisse*, 38, 51–102, pls 4–7.

Lambert, J. (1913) Description des échinides des terrains Néogènes du bassin du Rhone. *Mémoires de la Société Paléontologique Suisse*, 39, 105–151, pls 8–12.

Lambert, J. & Thiéry, P. (1909–1925) *Essai de nomenclature raisonnée des échinides*. Chaumont, Librairie Ferrière, 607 pp.

Leske, N.G. (1778) *Iacobi Theodori Klein Naturalis dispositio Echinodermatum*. Leipzig, Germany.

Linnaeus, C. (1758) *Systema naturae per regna tria naturae :secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Laurentii Salvii, Stockholm.

Michelin, H. (1855) Notice sur un genre nouveau a établir dans la famille des Spatangoides sous le nom de Maera. *Revue et Magazine de Zoologie*, 2e serie, 7, 245–248.

Mooi, R. (1989) Living and Fossil Genera of the Clypeasteroida (Echinoidea: Echinodermata): An Illustrated Key and Annotated Checklist. *Smithsonian Contributions to Zoology*, 488, 1–51.

Mooi, R. (1990) Paedomorphosis, Aristotle's lantern, and the origin of the sand dollars (Echinodermata: Clypeasteroida). *Paleobiology,* 16, 25–48.

Mortensen, T. (1948a). New Echinoidea (Cassiduloida, Clypeasteroida): preliminary notice. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 111, 67–72.

Mortensen, T. (1948b) *A monograph of the Echinoidea. Volume 4, part 2, Clypeastroida.* Copenhagen: C.A. Reitzel. 471 pp. 72 pls.

Pfeffer, G. (1881) Die Clypeasteriden des Hamburger Museums. *Verhandlungen für naturwissenschaften vereins Hamburg-Altona,* 5, 56–70.

Poddubiuk, R.H. (1985) Evolution and adaptation in some Caribbean Oligo-miocene Clypeasters. *In*: Keegan, B.F. & O'Connor, B.D.S. (Eds) *Proceedings of 5th International Echinoderm Conference*. Rotterdam, Balkema, pp. 75–80.

Poddubiuk, R.H. & Rose, E.P.F. (1984) Relationships between Mid-Tertiary echinoids faunas from the central Mediterranean and eastern Caribbean and their palaeobiographic significance. *Annales Géolgiques des Pays Helleniques*, 32, 115–128.

Pomel, A. (1887) Classification méthodique et généra des échinides vivants et fossiles. Alger, Typ. Adolphe, Jordan, 132 pp.

Rasband, W.S. (1997–2009) ImageJ, U.S. National Institutes of Health, Bethesda, ?Maryland, USA, http://rsb.info.nih.gov/ij/.

Rose, E.P.F. & Poddubiuk, R.H. (1987) Morphological variations in the Cenozoic echinoid Clypeaster and its ecological and stratigraphic significance. *Annales de l'Institute geologique de Hongrie*, 70, 463–469.

Schultz, H. (2006) *Sea Urchins, a guide to worldwide shallow water species*. Hemdingen: Heike & Peter Schultz Scientific Publications

Serafy, D.K. (1970) A new species of *Clypeaster* from the Gulf of Mexico and Caribbean and a key to the species in the tropical Northwestern Atlantic. *Bulletin of Marine Science,* 20, 662–677.

Serafy, D.K. (1971) A New Species of *Clypeaster* (Echinodermata, Echinoidea) from San Felix Island, with a Key to the Recent Species of the Eastern Pacific Ocean. *Pacific science*, 25, 165–170.

Smith, A.B. (1981) Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology*, 24, 779–801.

Smith, A.B. (2005) The Echinoid Directory. World Wide Web electronic publication. http://www.nhm.ac.uk/research-curation/projects/echinoid-directory/index [06.07.2010].

Swofford, D.L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

APPENDIX 1. List of characters scored and data matrix used in our phylogenetic analysis. [O] = ordered character state.

Marginal buttressing:
1. Extent of marginal buttressing: absent (0); single internal wall around part or all of test (1); series of walls forming a wide buttressed zone (2). [O]
2. Ambulacral buttress organization: bar(s) (0); aligned pillars (1).
3. Internal wall effectively forming a double wall with microcanal system: no (0); yes (1).
4. Radial bars projecting in from test margin along adradial sutures: absent (0); along just posterior interambulacrum (periproctal) (1); along all adradial sutures (2). [O]

Central buttressing:
5. Central buttressing structures: absent (0); present (1).
6. Central buttressing of interambulacral zones: dominated by large adradial bars/pillars bounding lower ends of petals (e.g. *C. humilis*) (0); infill of relatively fine pillars + bars in interradial zone (e.g. *C. ravenelii C. subdepressus*) (1).
7. Central buttressing fused to form an almost continuous curtain enclosing petaloid area: no (0); yes (e.g. *C. rangianus*, Fig. 5E) (1).
8. Central ambulacral zones within petals: no buttressing (0); fine pillars only (1); thick transverse bars (2).

Petals
9. Distance from distal end of petal III to ambitus vs. length of petal III: <0.25—petals almost reach ambitus (0); 0.35–0.65 (1); >0.7—petals end far from ambitus (2). [O]
10. Petal III opened or closed - distance between inner pore-pairs vs. max broadness of inner 1-petals: <0.15—almost closed (0); 0.15–0.75 (1); 0.76–0.95—widely open (2); 1.00—diverging distally. [O]
11. Petal II opened or closed - distance between inner pore-pairs vs. max broadness of inner petals: <0.15 (0); 0.15–0.75 (1); >0.75 (2); 1.00—diverging distally. [O]
12. Number of occluded plates in petal II: <1 (0); 1–6 (1); >6 (2). [O]
13. Demi-plates in petals: absent (0); present (1).

Test shape
14. Sunkeness of oral surface: rounded oral surface (e.g. *Haimea*) (0); flat outer region with inturned test close to the peristome (e.g. *C. euclastus*) (1); test with broad adoral concavity (e.g. *C. rosaceus*) (2).

15. Angle of peristome to point of contact: 0° (0); 5°–10° (1); >10°(2). [O]
16. Peripheral swollen rim: absent (0); present (1).
17. Thickness of the test edge: no edge (0); rounded (1); thin/sharp (2). [O]

Food grooves
18. Food grooves absent (0); present on oral surface only (1); present and extending from peristome to apical disc (2). [O]
19. S/T ratio (distance of distal end of the food groove to ambitus vs. distance of peristome to ambitus): 0- food grooves extend aborally (0); <0.35—food groove extends almost to ambitus (1); 0.4–0.7 (2); >0.7—food groove confined to adoral region (3). [O]
20. Combed area: absent (0); present (1).
21. Tubercle differentiation along ambulacra: absent; pores scattered across plates (0); present, pores in distinct V-shaped region on each plate (1).

Periproct
22. Distance to ambitus from periproct /periproct length: <0.8 (0); 0.8–1.5 (1); >1.5 (2). [O]
23. Situated between plates: 2b and 2a (0); 3b and 3a (1); 4b and 3a (2); 4b and 4a (3); 5b and 4a (4) 5b and 5a (5). [O]
24. Situated: on oral surface (0); at ambitus (1); on adapical surface (2). [O]

Tract of digestive system
25. Gut coiling: comes out slightly left of centre and loops around front (crosses perradius of ambulacrum III) (0); runs anteriorly and loops back before reaching perradius of ambulacrum III (1).

Apical disc
26. Number of gonopores: 4 (0); 5 (1).

Lantern support structures
27. Lantern supports: paired (0); single (1).

Interambulacral plates
28. Aboral surface composed of: ambulacral and interambulacral columns of plates (0); large paired ambulacral plates, interambulacral plates reduced or absent: (1).

Data matrix: a= 0&1; b=1&2; c=3&4; inapplicable=-

Haimea ovumserpentis	0-000 -0003 30001 000-0 0250? 000
Sismondia occitana	0-020 -0003 30001 000-0 0200? 010
Scutellina lenticularis	0-020 -0013 30010 020-0 0051? 010
Arachnoides placenta	21000 -0023 30110 02201 1-121 000
Ammotrophus cyclius	21001 00123 30110 02201 12001 000
Monostychia australis	21001 001b3 30110 02201 1010? 000
Scutellinoides patella	10001 000-- -0020 020-0 0-12? 001
Philipaster occultof.	11001 00023 30020 020-0 0-12? 001
C. annandalei	21001 00012 11110 02110 11201 100
C. australasiae	10011 10112 11122 01130 01c00 100
C. euclastus	21001 10123 30110 02110 10201 100
C. europacificus	20001 10112 21110 02110 10411 100
C. eurychorius	20001 10122 21110 01110 10400 100
C. fervens	11011 10112 02122 01120 00300 100
C. humilis	20001 00010 02111 02110 1a300 100
C. japonicus	10011 00012 02122 00120 00400 100
C. latissimus	20001 101b0 02110 02110 12301 100
C. miniaceus	20011 00022 01111 01120 11401 100
C. ochrus	10111 00211 12122 00120 00501 100
C. rangianus	20001 01011 11121 01110 01401 100
C. rarispinus	20001 10120 01110 11110 10200 100
C. ravenelii	20001 10122 20110 11110 1ac01 100
C. reticulatus	0-011 00010 01121 11130 01200 100
C. rosaceus	10111 00201 12122 00120 00501 100
C. rotundus	20001 10111 02110 02110 11301 100
C. subdepressus	21001 10111 02110 02110 11301 100
C. telurus	21001 10121 12111 02110 12201 100