

PHYLOGENY AND SYSTEMATICS OF HOLASTEROID ECHINOIDS AND THEIR MIGRATION INTO THE DEEP-SEA

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ABSTRACT. Holasteroids are a major clade of irregular echinoids that today is confined to the deep-sea, but which has a rich fossil record extending back to the start of the Cretaceous Period. A cladistic analysis of this clade, encompassing the great majority of living and fossil genera, is undertaken based on new data on test architecture. The classification of the group is reviewed and a new hierarchical scheme is proposed. The highly atypical apical disc structure of pourtalesiid holasteroids is discussed and critical data for understanding its plate homologies are provided by the most primitive pourtalesiid, the Late Cretaceous *Galeaster*. This supports the idea that plates previously identified as posterior genital plates in pourtalesiids are in fact ocular plates II and IV. An evolutionary tree for holasteroids is constructed by calibrating the cladogram against the stratigraphic record. This is then used to examine how holasteroid diversity and ecology have changed through time. Holasteroids have migrated into the deep-sea at least four times independently. Three of these lineages can be traced back to sister taxa living in deep-water continental shelf environments in the Late Cretaceous–early Tertiary, while a fourth represents a very much younger migration event, possibly Late Miocene in age.

KEY WORDS: cladistic analysis, diversity, deep-sea, test architecture, palaeoecology.

SEA urchins that are obviously bilaterally symmetrical in shape and have an anterior mouth are informally termed ‘heart urchins’ and they comprise one of the most easily recognisable groups within the class Echinoidea. Because they live in or on unconsolidated sediments, they have left a comparatively good fossil record (Kier 1977; Greenstein 1993). They first appear at the base of the Cretaceous and, from the start, can easily be separated into two well-defined clades, the holasteroids and spatangoids. These clades are distinguished principally on the arrangement of plates in the apical disc and plastron. In holasteroids the apical disc is almost always elongated with the anterior and posterior pairs of genital plates separated by a pair of ocular plates (Text-fig. 1B). In spatangoids the four genital plates meet to form a compact disc (Text-fig. 1A). Initially holasteroids and spatangoids coexisted in very similar palaeoenvironmental settings. However, today holasteroids are confined to deep-sea environments whereas spatangoids remain most diverse in continental shelf settings. Furthermore, although today there are relatively few species of holasteroids, they may have developed a greater morphological diversity (disparity) than spatangoids (e.g. David 1988). Indeed, of all the echinoids, holasteroids arguably display the most extreme morphological body-forms (Mooi and David 1996).

Because of their peculiar morphologies holasteroids have attracted the interest of evolutionary biologists. For example, Eble (1998, 2000) undertook a comparative analysis of the evolution of morphological disparity in holasteroids and spatangoids using landmark-based morphometrics. He found that a pronounced loss in disparity occurred amongst holasteroids at the Cretaceous/Tertiary extinction, which was not mirrored in spatangoids. Eble’s approach required no detailed phylogenetic hypotheses, since he was documenting overall disparity in the two sister clades through time. However, a more detailed understanding of the evolution of morphological disparity requires phylogenetic hypotheses with greater resolution. For spatangoids, these are just beginning to appear (e.g. Villier *et al.* in press, who provide an excellent analysis of the initial diversification of the Spatangoida). Holasteroid phylogeny is

somewhat better established, thanks to the detailed work of Mooi and David (1996). They generated a phylogenetic hypothesis for the majority of extant holasteroids. However, the extant fauna comprises only a small portion of holasteroid diversity, and if we are to understand the evolutionary history of holasteroids, phylogenetic hypotheses that encompass fossil taxa are essential.

One outstanding question concerning holasteroid evolution relates to when holasteroids moved into the deep-sea environment and what factors might have been involved in driving this ecological change. David (1988) first broached this question and used a cladistic approach to analyse the relationships of Recent and fossil holasteroids. However, he was not able to resolve the question because his data were consistent with a number of alternative phylogenies. One of the major stumbling blocks for David was that the plate architecture of fossil holasteroids was poorly known at that time.

Fossil holasteroids, and especially Cretaceous holasteroids, are now very much better known. Several monographic works in which holasteroid taxa are revised and documented in detail have recently been published (Smith *et al.* 1988, 1999; Jeffery 1997; Smith and Jeffery 2000; Jagt 2001; Kroh 2001). Furthermore, detailed analysis of all British holasteroid species has been undertaken as part of the revision of the British Cretaceous echinoid fauna (Smith and Wright 2003). Consequently, accurate plating diagrams for many taxa are available for the first time, providing a number of potentially informative characters for phylogenetic analysis. This new information is brought together here and used to construct a cladistic hypothesis for the group. The phylogeny is then used to explore certain aspects of the evolutionary history of holasteroids.

HISTORY OF CLASSIFICATION

The division of echinoids into two broad groups according to whether their periproct opens at the apex of the test inside the apical disc ('regular' echinoids) or is displaced towards the mouth and opens within an interambulacral zone ('irregular' echinoids) has been established for almost 200 years (Latreille 1825). Amongst the irregular echinoids, those with a strongly marked bilateral symmetry and the mouth displaced towards the anterior have long been recognised as a natural group, variously termed heart urchins, spatangoids or atelostomates (e.g. Agassiz 1839; see also Mortensen 1950; Durham and Melville 1957). The Atelostomata (*sensu* Durham and Melville 1957) is one of the most diverse of modern echinoid taxa, both in terms of numbers of species and breadth of habitats occupied.

Early workers did not distinguish between spatangoids and holasteroids; prior to 1883 the many species of *Holaster* and *Cardiaster* were placed in a single family 'holasteriens'. Pomel (1883) recognised two groups of atelostomate echinoids having elongate or disjunct apical discs, 'les Phyalides ou Pourtalesides' and 'les Holasteriens'. Within the former he included the Recent genera *Pourtalesia*, *Ceratophysa*, *Calymne*, *Spatagocystis*, *Cystechinus* and *Urechinus*. Within 'les Holasteriens' he had two fossil groups, 'les Cardiastéridés' and 'les Ananchytidés'. Lambert (1917) dealt more thoroughly with the family. He divided the Ananchytidae into two subfamilies, Holasteridae and Urechinidae, the former with ambulacral plates pierced by a double pore, the latter with ambulacral plates bearing a single pore. He further divided his Holasteridae into five tribes: (1) Hemipneustinae (with no fascioles, posterior periproct, plates of the test low and petals heterogeneous); (2) Cardiasterinae (with marginal or submarginal fasciole, posterior periproct, test with low plates, petals heterogeneous); (3) Lampadocorinae (with posterior periproct, test with low plates, petals homogeneous); (4) Stegasterinae (with posterior periproct and test with high plates); (5) Echinocorinae (with inframarginal periproct).

Clark (1946) recognised the importance of plastron plating for the classification of heart urchins and proposed the suborder Urechinina for all heart urchins in which a single sternal plate follows the labral plate. Mortensen (1950) provided an authoritative review of the group, in which he separated the Spatangoida into three groups according to plastron structure. His Protosternata comprised forms in which the labral plate is small and undifferentiated and makes contact with two succeeding plates (5.b.2 and 5.a.2). He included disasterids and asterostomatids, the latter wrongly attributed here on the basis of an incorrect plating diagram in the *Paléontologie Française* (d'Orbigny 1853–60). His Amphisternata corresponds to the Spatangoida of Durham and Melville (1957) and includes all spatangoids with paired sternal plates. Mortensen's (1950) Meridosternata included all spatangoids whose labral plate

was enlarged and in contact with just a single interambulacral plate to the posterior (plate 5.b.2). Five families were recognised within the Meridosternata: Holasteridae, Stenonasteridae, Pourtalesiidae, Urechinidae and Calymnidae. These families were differentiated on apical disc structure, presence or absence of a frontal groove, whether ambulacral pores were single or double, and on oral plating architecture. Mortensen further attempted to subdivide holasterids and recognized five 'tribes' as follows: (1) Cardiasterinae (*Holaster*, *Taphraster*, *Pseudholaster*, *Sternotaxis*, *Aureliaster*, *Cardiaster*, *Cardiotaxis*); (2) Offasterinae (*Paronaster*, *Zumoffenia*, *Cibaster*, *Duncaniaster*, *Messaoudia*, *Stereopneustes*, *Offaster*, *Ganbirretia*, *Garumnaster*); (3) Hemipneustinae (*Hemipneustes*, *Toxopatus*, *Opisopneustes*); (4) Stegasterinae (*Lampadocorys*, *Rispolia*, *Pseudoffaster*, *Stegaster*, *Seunaster*, *Galeaster*, *Tholaster*, *Guetaria*, *Sanchezaster*, *Infulaster*, with *Hagenowia* as a synonym, *Lampadaster*); (5) Echinocorinae (*Pseudananchys*, *Echinocorys*, *Scagliaster*, *Galeola*, *Jeronia*). Mortensen (1950), however, added that only the Stegasterinae was well enough characterised (by the oral groove and vertical peristome) to be distinguished as a subfamily; the rest were too poorly limited.

Durham and Melville (1957) erected the order Holasteroida as a group uniting Mortensen's Protosternata and Meridosternata, and this classification was followed in the Treatise on Invertebrate Paleontology (Wagner and Durham 1966). In addition to the five meridosternous families recognised by Mortensen, Wagner and Durham (1966) added a sixth, the Somaliasteridae, for forms with a meridosternous plastron but a compact apical disc. Philip (1965), however, objected to Durham and Melville's scheme and reverted to Mortensen's tripartite division of spatangoids. A seventh family, Corystidae, was later added by Foster and Philip (1978) for Tertiary forms with a rostral plate in their plastron.

David (1988) was the first to attempt a cladistic analysis of the group and he recognised six groupings, as follows: Group A, *Basseaster*, *Cardiaster*, *Echinocorys*, *Galeola*, *Ganbirretia*, *Holaster*, *Ismidaster*, *Labrotaxis*, *Messaoudia*, *Offaster*, *Opisopneustes*, *Paronaster*, *Pseudholaster*, *Scagliaster*, *Taphraster*, *Toxopatus*, *Zumoffenia* plus possibly *Hemipneustes*, *Entomaster* and *Pseudananchys*; Group B, *Lampadaster*, *Lampadocorys*, *Pseudoffaster*; Group C, *Aureliaster*, *Cardiotaxis*, *Sternotaxis*, possibly *Hemipneustes* and *Pseudananchys*; Group D, *Hagenowia*, *Infulaster*; Group E, *Jeronia*, *Rispolia*, *Tholaster* and possibly *Entomaster*; Group H, *Guetaria*, *Galeaster*, *Stegaster*. None of these groups was formally named or diagnosed by David.

Mooi and David (1996) undertook a formal cladistic analysis of the Recent genera of Urechinidae and proposed a further family, Plexechinidae, for the species of *Plexechinus*. Finally, the Somaliasteridae Wagner and Durham, 1966, have been formally recognised as derived amphisternate spatangoids (Jeffery 1999).

Only those irregular heart-urchins with a non-amphisternous plastron and an elongate apical disc in which the anterior and posterior paired genital plates are separated by intercalated ocular plates II and IV are considered here as true Holasteroida. This broadly corresponds to Mortensen's (1950) and Philip's (1965) Meridosternata, but differs from Durham and Melville's (1957) and Wagner and Durham's (1966) order Holasteroida by exclusion of the protosternous families Disasteridae and Collyritidae. In addition, the Somaliasteridae Wagner and Durham, 1966, are clearly derived amphisternate spatangoids (Jeffery 1999) and have nothing to do with Holasteroida. Thus, the Holasteridae Pictet, 1857, Pourtalesiidae Loven, 1883, Urechinidae Duncan, 1889, and the monospecific Calymnidae Mortensen, 1907, are the only families listed by Wagner and Durham (1966) that remain included.

CLADISTIC ANALYSIS OF THE HOLASTEROIDA

Taxonomic coverage

To establish a working phylogeny of holasteroid taxa, a cladistic analysis of 43 Cretaceous to Recent genera (Table 1) has been undertaken. All genera whose plating was sufficiently well known were included. However, the Pourtalesiidae, comprising seven extant genera, form a well-defined clade with a very characteristic and highly derived apical disc structure (see below). Their monophyly is in no doubt and so only a single representative (*Pourtalesia*) is included in the analysis.

TABLE 1. Genera and species used in scoring characters for the phylogenetic analysis (* indicates type species of genus). Illustrations and diagnoses for all genera can be found at www.nhm.ac.uk/palaeontology/echinoids.

Genus	Species included
<i>Antrechinus</i> Mooi and David, 1996	* <i>A. mortenseni</i> (David and Mooi, 1990)
<i>Basseaster</i> Lambert, 1936	* <i>B. rostratus</i> Lambert, 1936
<i>Calymne</i> Wyville Thomson, 1877	* <i>C. relict</i> a Wyville Thomson, 1877
<i>Cardabia</i> Foster and Philip, 1978	* <i>C. bullarensis</i> Foster and Philip, 1978
<i>Cardiaster</i> Forbes, 1850	* <i>C. granul</i> osus Goldfuss, 1829
<i>Chelonechinus</i> Bather, 1934	* <i>C. suvae</i> Bather, 1934
<i>Cibaster</i> Pomel, 1883	* <i>C. bourgeois</i> anus (d'Orbigny, 1853)
<i>Corystus</i> Pomel, 1883	* <i>C. dysasteroides</i> (Duncan, 1877)
<i>Crassiholaster</i> Smith and Wright, 2003	* <i>C. subglobosus</i> (Leske, 1778)
<i>Cystechinus</i> Agassiz, 1879	* <i>C. wyvillei</i> Agassiz, 1879
<i>Echinocorys</i> Leske, 1778	* <i>E. scutatus</i> Leske, 1778
<i>Entomaster</i> Gauthier, 1888	* <i>E. rousseli</i> Gauthier, 1888
<i>Eoholaster</i> Solovjev, 1989	* <i>P. poslavskae</i> Solovjev, 1989
	<i>P. lafattei</i> (Devries, 1960)
<i>Galeaster</i> Seunes, 1889	* <i>G. bertrandi</i> Seunes, 1889
<i>Galeola</i> Quenstedt, 1874	* <i>G. papillosa</i> Quenstedt, 1874
<i>Garumnaster</i> Lambert, 1907	* <i>G. michaleti</i> Lambert, 1907
<i>Giraliaster</i> Foster and Philip, 1978	* <i>G. jubileensis</i> Foster and Philip, 1978
<i>Guettaria</i> Gauthier, 1888	<i>G. roccardi</i> (Cotteau, 1889)
<i>Hagenowia</i> Duncan, 1889	* <i>H. rostrata</i> (Forbes, 1852)
<i>Hemipneustes</i> Agassiz, 1836	* <i>H. striatoradiatus</i> (Leske, 1778)
	<i>H. persicus</i> Cotteau & Gauthier, 1895
<i>Holaster</i> Agassiz, 1836	* <i>H. nodulosus</i> (Goldfuss, 1829)
<i>Huttonechinus</i> Foster and Philip, 1978	* <i>H. spatangiformis</i> (Hutton, 1873)
<i>Infulaster</i> Desor, 1858	* <i>I. excentricus</i> (Woodward, 1833)
<i>Jeronia</i> Seunes, 1888	* <i>J. pyrenaica</i> Seunes, 1888
<i>Lampadocorys</i> Pomel, 1883	<i>L. enni</i> si Smith and Wright, 2003
<i>Offaster</i> Desor, 1858	* <i>O. pillula</i> (Lamarck, 1816)
<i>Plesiocorys</i> Pomel, 1883	* <i>P. plana</i> (Mantell, 1822)
<i>Plexechinus</i> Agassiz, 1898	* <i>P. cinctus</i> A. Agassiz, 1898
	<i>P. spectabilis</i> Mortensen, 1948
	<i>P. sulcatus</i> David and Mooi, 2000
<i>Pourtalesia</i> Agassiz, 1869	* <i>P. jeffreysi</i> Thomson, 1873
<i>Pseudananchys</i> Pomel, 1883	<i>P. completa</i> (Cragin, 1893)
<i>Pseudholaster</i> Pomel, 1883	* <i>P. bicarinatus</i> (Agassiz, 1847)
<i>Pseudocardiaster</i> Smith and Wright, 2003	* <i>P. truncatus</i> (Goldfuss, 1829)
<i>Pseudoffaster</i> Lambert, 1924	* <i>P. caucasicus</i> (Dru, 1884)
<i>Rispolia</i> Lambert, 1917	* <i>R. subtrigonata</i> (Catullo, 1827)
<i>Sanchezaster</i> Lambert, 1924	* <i>S. habanensis</i> Lambert, 1924
<i>Seunaster</i> Lambert, 1912	* <i>S. bouillei</i> (Cotteau, 1873)
' <i>Stegaster</i> ' <i>sensu lato</i>	<i>S. cotteau</i> i (Seunes, 1889)
<i>Sternopatagus</i> de Mejeire, 1902	* <i>S. sibogae</i> de Mejeire, 1902
<i>Toxopatagus</i> Pomel, 1883	* <i>T. italicus</i> Manzoni and Mazzetti, 1878
<i>Tholaster</i> Seunes, 1891	* <i>T. munieri</i> (Seunes, 1889)
<i>Urechinus</i> Agassiz, 1879	* <i>U. naresianus</i> A. Agassiz, 1879

The family Calymnidae Mortensen (1907) contains a single species, *Calymne relict*a Wyville Thomson, that has never been adequately described. In the original description of *C. relict*a (Wyville Thomson, 1877) the figures are rather sketchy, and the importance of plate architecture was not appreciated and thus ignored. By the time Agassiz (1881) came to redescribe the material the type specimens were already

broken and he was only able to add details about spines and pedicellariae. I have therefore redescribed the apical disc and plastron plating in the type material (see below).

Another problematic deep water taxon is *Pilematechinus* A. Agassiz. *Pilematechinus* was restudied by Mooi and David (1996) based on new collections in the Smithsonian Institute, Washington, DC. It has a very unusual plastron in which the labral and first sternal plates are greatly reduced. Nevertheless, it is clearly a holasteroid since it has the elongate apical disc characteristic of that group and its plastron plating is meridosternous. Although originally scored, this taxon was omitted from the final analysis as it introduced too much instability to the cladogram. Mooi and David (1996) considered it to be a derived urchinid, which seems highly likely.

Two species of *Holaster sensu lato* were included; *Holaster nodulosus* (Goldfuss), the type species of the genus, and *Crassiholaster subglobosus* (Leske), a much more rounded and thick-tested form with affinities to *Lampadocorys*. Two species of *Cardiaster sensu lato* were also included; the type species *Cardiaster granulatus* (Goldfuss) from the Maastrichtian, which has typical metasternal plastron plating, and *Pseudocardiaster truncatus* (Goldfuss) from the Turonian, which has a protosternous plastron (see Smith and Wright 2003). In addition, one well-known deep-water taxon of late Cretaceous age, '*Stegaster*' *cotteaui*, was included. Details of all these genera can be found at the Echinoid Directory (www.nhm.ac.uk/palaeontology/echinoids).

Thirty-four characters relating to the structure of the test were eventually scored, and are listed and discussed below.

Characters and character definitions

Test shape. Holasteroids include some of the most bizarrely shaped echinoids that have evolved (Pls 1–2). Early holasteroids were ovate without a frontal groove and had a gently domed aboral surface. However, diversification led to strongly domed forms, subconical forms and to forms with an elongate apical snout (Pl. 2, fig. 12). Shape differences are, however, hard to quantify without rigorous morphometric analysis, and small differences in the curvature of lower or upper surface, or in the position of the ambitus, seem highly homoplasious. Consequently no descriptive shape characters are deemed to be worth including in this high-level analysis, other than those dealing with the development of the frontal groove.

In holasteroids the form taken by the frontal ambulacrum is quite varied. In members of the immediate outgroup, such as *Proholaster*, there is no frontal groove and the anterior ambulacrum is flush with adjacent interambulacral zones. This condition is also found in some of the stratigraphically earliest holasteroids. However, in many Cretaceous forms, including *Holaster* itself, the anterior ambulacrum is feebly depressed. In many stegasterines a pronounced groove is present from the ambitus adorally but rapidly diminishes and is lost above the ambitus. In cardiasterines the groove is clearly defined from apex to peristome. Here the form taken by the frontal ambulacrum is captured by two characters, one relating to the oral surface, the other to the aboral surface. In each case a three-state character is used, with the groove either absent, weakly depressed (without clearly defined margins), or well-defined (where there is a distinct change in angle of the plates bordering the groove so as to form a clearly-marked edge). Because these characters relate to the same feature, each was scaled for equal character weight (i.e. each character state change carried a weighting of 0.5). In effect, the two characters combined have the same weight as any other structural character in the cladistic analysis.

Test thickness shows marked variation both between and within genera but has not been scored because there is clearly some environmental signal, with deep-water modern forms having exceptionally thin tests.

1. Frontal groove aboral to ambitus: absent (0); shallow indentation at ambitus, weakly defined aborally (1); deep groove on aboral surface, with lateral carina (2).
2. Frontal groove on oral surface: absent (0); present as shallow, poorly-defined depression (1); distinct channel leading to the peristome (2).

Apical disc (Text-fig. 1). Most holasteroids share a very characteristic apical disc structure; one that is longitudinally elongate with plates arranged in pairs along the anterior-posterior axis. Ocular plates II

and IV abut behind the anterior genital plates, and, behind these, genital plates 1 and 4 are in contact (Text-fig. 1B). The apical disc in their immediate sister group, the collyritid *Proholaster*, has a similar elongate apical disc plating arrangement. However, in *Proholaster* the posterior ocular plates (Oc I and Oc V) are separated from the posterior genital plates by intercalated interambulacral plates of interambulacral zones 1 and 4 (Text-fig. 1J). A similar disjunct apical disc system recurs in some extant deep-sea forms, as well as in the Cretaceous *Hagenowia* (Text-fig. 1D).

The arrangement of plates in the apical disc provides a number of important structural characters. There may be only a single anterior genital plate, bearing both gonopores (Text-fig. 1I), in place of the usual two. Although this condition is often referred to as 'fused' (e.g. Mooi and David 1996), it seems much more likely that this condition arises through the reduction and loss of genital plate 3 (a view now supported by ontogenetic data; Mooi, pers. comm. 8/2002). There are several taxa in which genital plate 3 is reduced to a tiny element not much larger than the gonopore that it houses (e.g. Text-fig. 1C). A second character is afforded by the distribution of hydropores. The hydropores are primitively confined to genital plate 2, giving that plate a pepper-pot appearance. However, in a few taxa hydropores have expanded onto the adjacent genital and ocular plates (Text-fig. 1F), which is clearly a derived condition. Thirdly there is variation in the number of gonopore openings that are developed. The primitive condition in irregular echinoids is to have one gonopore opening to each genital plate and this is the most common arrangement seen in holasteroids. In a few cases, however, there are only three gonopores, and in every case it is the opening through genital plate 2 that is absent. In one case gonopores are reduced to two in number with only the anterior pair of genital plates pierced by gonopores. Two taxa expand the number of gonopores, by having either ancillary genital plates (*Lampadaster*) or additional gonopores piercing the lateral ocular plates (*Guettaria*; Text-fig. 1E).

Pourtalesiids have a highly derived apical disc structure (Text-fig. 1H) very different from that of other holasteroids. How this has arisen is discussed below, but for the present it is sufficient to know that in this group the two posterior gonopores open through ocular plates II and IV and the posterior genital plates are imperforate.

Finally, although there is variation in the actual position of the apical disc in plan view, ranging from slightly posterior to slightly anterior of centre, a few taxa have their apical disc placed significantly to the anterior.

3. Posterior ocular plates: disjunct from remainder of apical disc (0); only one of the posterior ocular plates in contact with the posterior genital plates (1); both posterior ocular plates in firm contact with the posterior genital plates (2).
4. Anterior genital plates: separate (0); reduced to a single plate by loss or fusion (1).
5. Hydropore openings: confined to genital plate 2 (0); scattered over all anterior ocular and genital plates (1).
6. Number of gonopores (genital plates only): 4, one to each genital plate (0); 3 (no gonopore in genital plate 2) (1); 2 (no gonopores in posterior genital plates) (2).
7. Gonopores in ocular plates II and IV: no (0); yes, single (1); yes, multiple (2).
8. Position of apical disc: subcentral (0); closer than 20 per cent test length to anterior (1).

EXPLANATION OF PLATE 1

Figs 1–2. *Holaster nodulosus* (Goldfuss, 1829), NHM E77879. Cenomanian, Upper Cretaceous, Wendover, Buckinghamshire, UK. 1, oral; 2, lateral; length of test 50 mm.

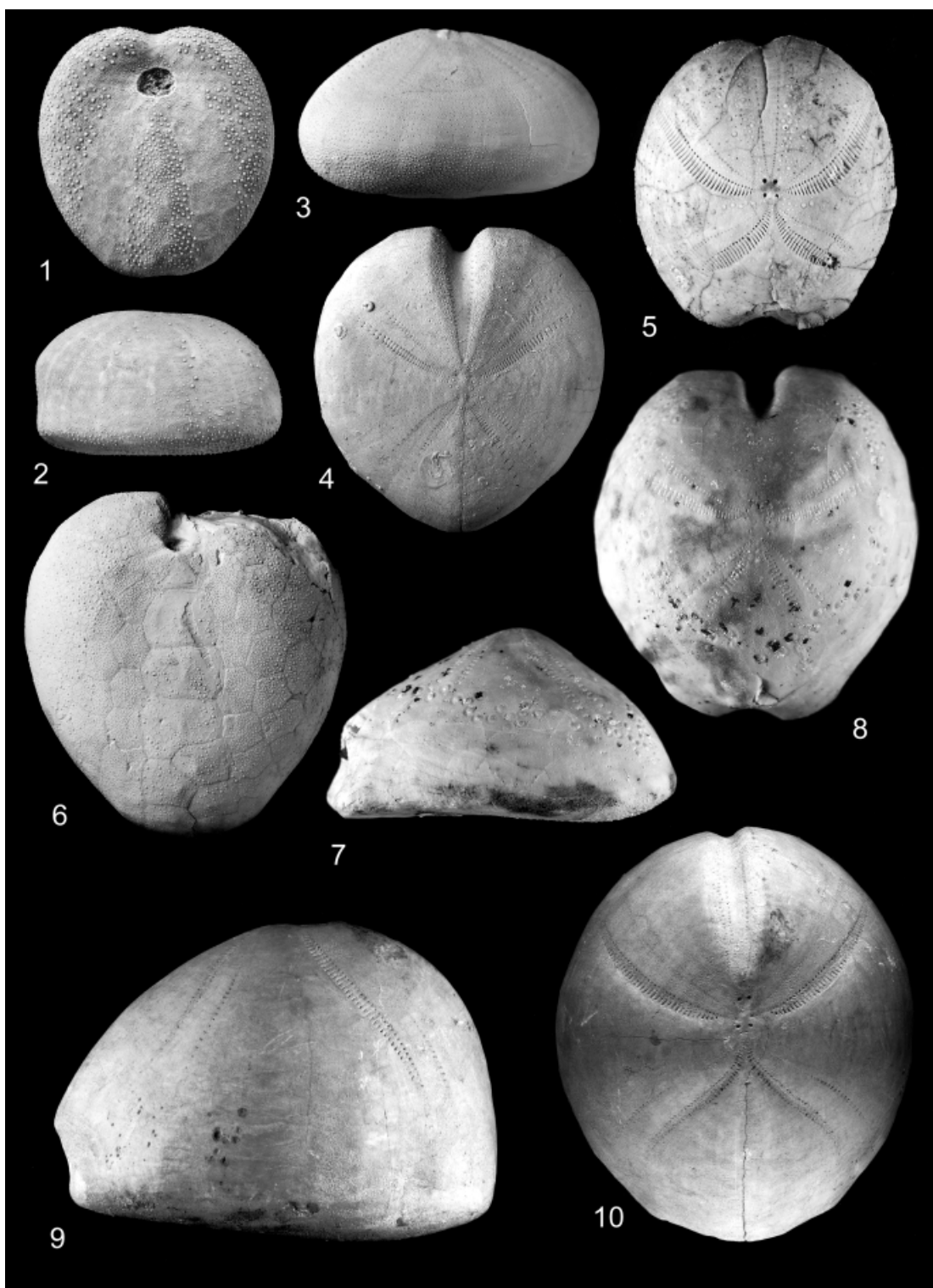
Figs 3–4. *Cardiaster granulatus* (Goldfuss, 1829), NHM 24891. Late Campanian, *B. mucronata* Zone, Norwich, Norfolk, UK. 3, lateral; 4, apical; length of test 63 mm.

Fig. 5. *Opisopneustes cosoni* Gauthier, 1889; NHM E42107. Senonian (?Campanian), coast of Sirte, Libya; apical view; length of test 40 mm.

Fig. 6. *Plesiocorys heberti* (Cotteau, in Cotteau and Triger 1860), NHM EE6097. Campanian, *B. mucronata* Zone, Hartford Bridge, Norfolk, UK; oral view; length of test 76 mm.

Figs 7–8. *Guettaria roccardi* (Cotteau, 1889), NHM E18706. Late Campanian or early Maastrichtian, Montagnes des Français, Madagascar. 7, oral; 8, lateral; length of test 58 mm.

Figs 9–10. *Hemipneustes striatoradiatus* (Leske, 1778), NHM E2837. Upper Maastrichtian, Maastricht district, The Netherlands. 9, lateral; 10, apical; length of test 101 mm.



SMITH, holasteroid echinoids

Plastron plating (Text-fig. 2). All previous workers (Lambert and Thiéry 1924; Clark 1946; Mortensen 1950; Wagner and Durham 1966; David 1988) have recognised the importance of plastron architecture for the classification of holasteroids. The primitive arrangement, seen in the collyritid *Proholaster* and in early holasteroids such as *Eoholaster* and *Pseudoholaster* (Text-fig. 2B, H), is for the labral plate to be wide and asymmetrically crescentic, with a horn extending laterally and downwards on the left-hand side to reach the second sternal plate (plate 2a). The labral plate thus contacts both sternal plates and subsequent plating is biserial. This arrangement is termed 'protosternous'. A number of more derived patterns developed from this.

With narrowing and elongation of the plastron the labral plate can lose contact with sternal plate 2a. In the cardiasterids and hemipneustids the original protosternous architecture is evident in juveniles. In these groups the labral plate remains rather broad and squat, while sternal plates are broad and wedge-shaped, only just extending the full width of interambulacral zone 5. Plate 2b is typically slightly less developed than plate 2a. Such plastrons are termed 'metasternous'. In primitive forms the uniserially arranged plates clearly alternate to left and right (Text-fig. 2D, I). However, in more derived members the plastron plates are arranged as a single column of polygonal and bilaterally symmetrical plates extending posteriorly from the peristome (Text-fig. 2E, K).

The most common form of plastron plating in holasteroids is termed 'meridosternous' (Text-fig. 2C). In this arrangement the labral plate is sagittally elongate and abuts only sternal plate 2b. In primitive meridosternous forms plates 2a and 2b are similar in size and shape (Text-fig. 2J), and plates to the posterior of plate 2b are biserially arranged and alternate. In more derived plastrons the two plates following plate 2b (termed 'episternals'; plates 2a and 3b) are more or less paired and opposite, and the plastron is then said to be 'orthosternous' (Text-fig. 2F, L). Posterior to the episternals, plating may be alternately biserial (Text-fig. 2F), paired and opposite, or there may be only a single lozenge-shaped plate termed the 'rostral plate' (Text-fig. 2L). The rostral plate is interpreted as representing plate 4a, plate 3a having been lost.

Any of the above forms of plastron may become interrupted by intercalation of ambulacral plates between the labral plate and the first sternal plate (Text-fig. 2G, K). This tends to occur whenever the test becomes particularly elongate and narrow.

In primitive holasteroids a large number of plates form the flat to weakly keeled oral surface of the plastron, but this number becomes reduced in more derived members. The posterior of the plastron in these derived forms may be formed of paired post-episternal plates, or even by paired episternal plates.

Finally, the arrangement of plates in the paired interambulacra also provides characters of taxonomic importance. There is always a single interambulacral plate bordering the peristome, but this can be

EXPLANATION OF PLATE 2

Figs 1–2. *Pourtalesia jeffreysi* Thomson, 1873, NHM EE8525. Recent, North Atlantic. 1, lateral; 2, oral; length of test 38 mm.

Figs 3–4. *Galeaster bertrandi* Seunes, 1889, NHM EE5614. Danian of Koshak, Mangyshlak, Kazakhstan. 3, oral; 4, lateral; length of test 21 mm.

Figs 5–6. *Urechinus naresianus* A. Agassiz, 1879, NHM 81.11.22.51. Recent, South Indian Ocean. 5, apical; 6, oral; length of test 28 mm.

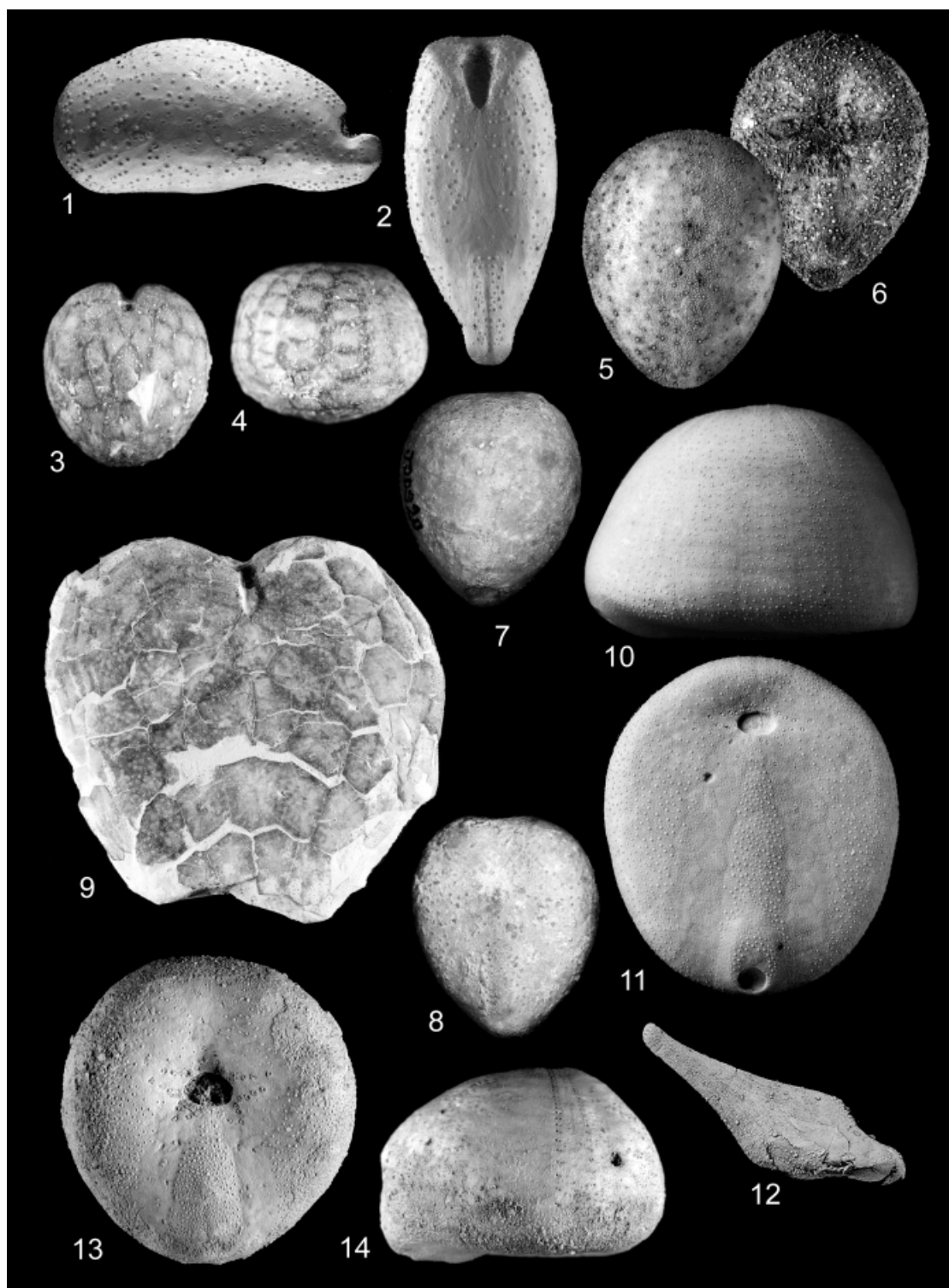
Figs 7–8. *Basseaster rostratus* Lambert, 1936, Muséum National d'Histoire Naturelle, Paris, J00920. Maastrichtian of Madagascar. Apical; length of test 18 mm.

Fig. 9. *Sanchezaster habanensis* Lambert, in Sánchez Roig, 1924, NHM E17204. Middle Oligocene, Canteras Tejar Consuelo Cerro, Cuba. Oral view; length of test 110 mm.

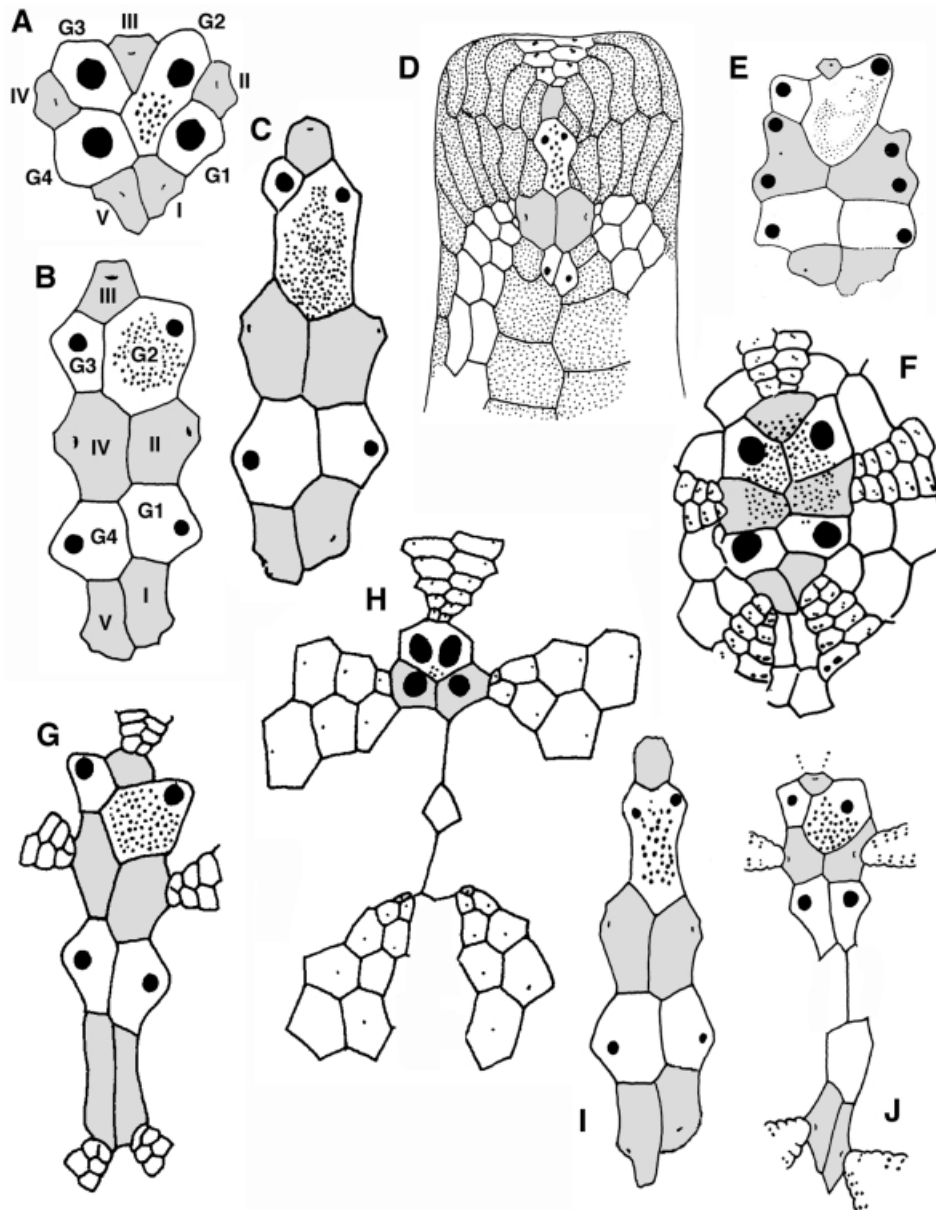
Figs 10–11. *Echinocorys scutata* Leske, 1778, NHM E32224. Lower Campanian, *G. quadrata* Zone, Portsdown Hills, Hampshire, UK. 10, lateral; 11, oral; length of test 83 mm.

Fig. 12. *Hagenowia rostrata* (Forbes, 1852), NHM E76838. Santonian, *M. coranguinum* Zone, Broadstairs, Kent, UK. Lateral view; length of test 29 mm.

Figs 13–14. *Corystus dysasteroides* (Duncan, 1877), NHM EE330. Early Miocene Mannum Formation, Younghusband, near Mannum, South Australia. 13, oral; 14, lateral; length of test 57 mm.



SMITH, holasteroid echinoids



TEXT-FIG. 1. Apical disc plating in spatangoids (A), collyritids (J) and holasteroids (B-I). Ocular plates are shaded grey and numbered I-V in A and B, genital plates are white and numbered G1 to G4. A, *Washitaster* sp., NHM E31472, Albian, Lower Cretaceous, Fort Worth, Texas, USA. B, *Holaster subglobosus* (Leske), NHM E8584, Cenomanian, Upper Cretaceous, Burham, Sussex, UK. C, *Infulaster* sp. nov., NHM EE6771, Upper Turonian, Upper Cretaceous, Kiplingcotes, Yorkshire, UK. D, *Hagenowia rostrata* (Forbes), NHM E76838, Lower Santonian, Upper Cretaceous, Broadstairs, Kent, UK (interambulacral zones stippled). E, *Guettaria grandidieri* (Cotteau), Late Campanian or early Maastrichtian, Upper Cretaceous, Montagnes des Français, Madagascar (from Lambert 1896). F, *Hemipneustes arabicus* Ali, NHM EE5027, Maastrichtian, Upper Cretaceous, Jebel Rawdah, Oman. G, *Eoholaster laffittei* (Devries, 1960), Berriasian, Lower Cretaceous, Bel Kheir, Algeria (from Devries, 1960, pl. 5, fig. 14). H, *Pourtalesia tanneri* Agassiz, Recent, East Pacific (from Agassiz, 1904, pl. 56, fig. 5). I, *Infulaster excentricus* (Woodward), NHM EE6797, Turonian, Upper Cretaceous, Elloughton, Yorkshire, UK. J, *Proholaster auberti* Gauthier, 1896 (from Devries, 1958).

followed either by a pair of plates (amphiplacous condition) or a single plate (meridoplacous condition). As in the posterior interambulacrum plating may be continuous or disjunct, with adjacent ambulacral columns separating the basicoronal plate from those following.

9. Labral plate followed by a single plate posteriorly; no (0); yes (1).
10. First sternal plate largest (plastron meridosternous); no (0); yes (1).
11. Sternal plates 5.a.2, 5.b.3 uniserial (plastron metasternous); no (0); yes (1).
12. Sternal plates 5.a.2 to 5.a.3 forming a straight line and effectively symmetric; no (0); yes (1).
13. Episternals (5.a.2, 5.b.3) effectively paired and opposite, with suture to rear almost straight (less than 10 per cent offset relative to plate height) (plastron orthosternous); no (0); yes (1).
14. Plates forming rear of plastron: biserial, 4a/5b or greater (0); paired post-episternals (1) paired episternals (2).
15. Rostral plate: absent (0); present (1).
16. Plastron disjunct: no (0); yes (1).
17. Anterior interambulacral plating: amphiplacous (0); meridoplacous (1).
18. Lateral interambulacral plating: amphiplacous (0); meridoplacous (1).
19. Lateral interambulacra disjunct adorally; no (0); yes (1).

Ambulacral structure. Mooi and David (1996) used the number of ambulacral plates to the rear of the labral plate and first sternal plate in their phylogenetic analysis. Here I score for the ambulacral plate in zone I that abuts the posterior suture of the labral plate, and which abuts the suture between 5.b.3 and 5.b.4 (the rear of the left episternal in oral view). The two, though to some degree linked, are sufficiently independent to merit scoring separately.

Whether pore-pairs in ambulacral plates are single or double was a character stressed by Mortensen (1950) and David (1988). Although there is clearly a strong environmental signature to the nature of ambulacral pores, the character is nevertheless included. Taxa that have pore-pairs in the posterior column well developed but those in the anterior column highly reduced (Pl. 1, fig. 5) are scored separately. Among forms with reduced or rudimentary pores, some have their ambulacra composed of tall, hexagonal plates aborally, while in others the plates remain low and more densely packed compared to those in adjacent interambulacral zones. This character has also been included.

Another character that appears independent of how well developed the petals are is the degree to which the posterior ambulacra are flexed. In hemipneustids the posterior petals are strongly flexed (Pl. 1, figs 5, 10), whereas in all other taxa the petals are more or less straight. Finally, a small number of taxa are characterised by having pore-pairs in the frontal ambulacrum subpetaloid and identical to those in the paired ambulacra.

20. Plate (numbered from the peristome) that lies adjacent to rear of labral plate in ambulacrum I: 1 (1); 2 (2); 3 (3).
21. Plate (numbered from the peristome) at rear suture of plastron plate 5.b.3 (left episternal in oral view) in ambulacrum I: 6 or 7 (0); 5(2); 4 (3).
22. Aboral ambulacral plates: narrow and crowded (0); large and hexagonal, approximately the same height as interambulacral plates (1).
23. Aboral ambulacral pores: single and rudimentary (0); double, with the two columns equal (1); double with a strong inequality in the size of pore-pairs in the anterior and posterior columns (2).
24. Aboral pores in frontal ambulacrum well developed and identical to those in paired ambulacra: no (0); yes (1).
25. Posterior ambulacra strongly flexed on aboral surface: no (0); yes (1).

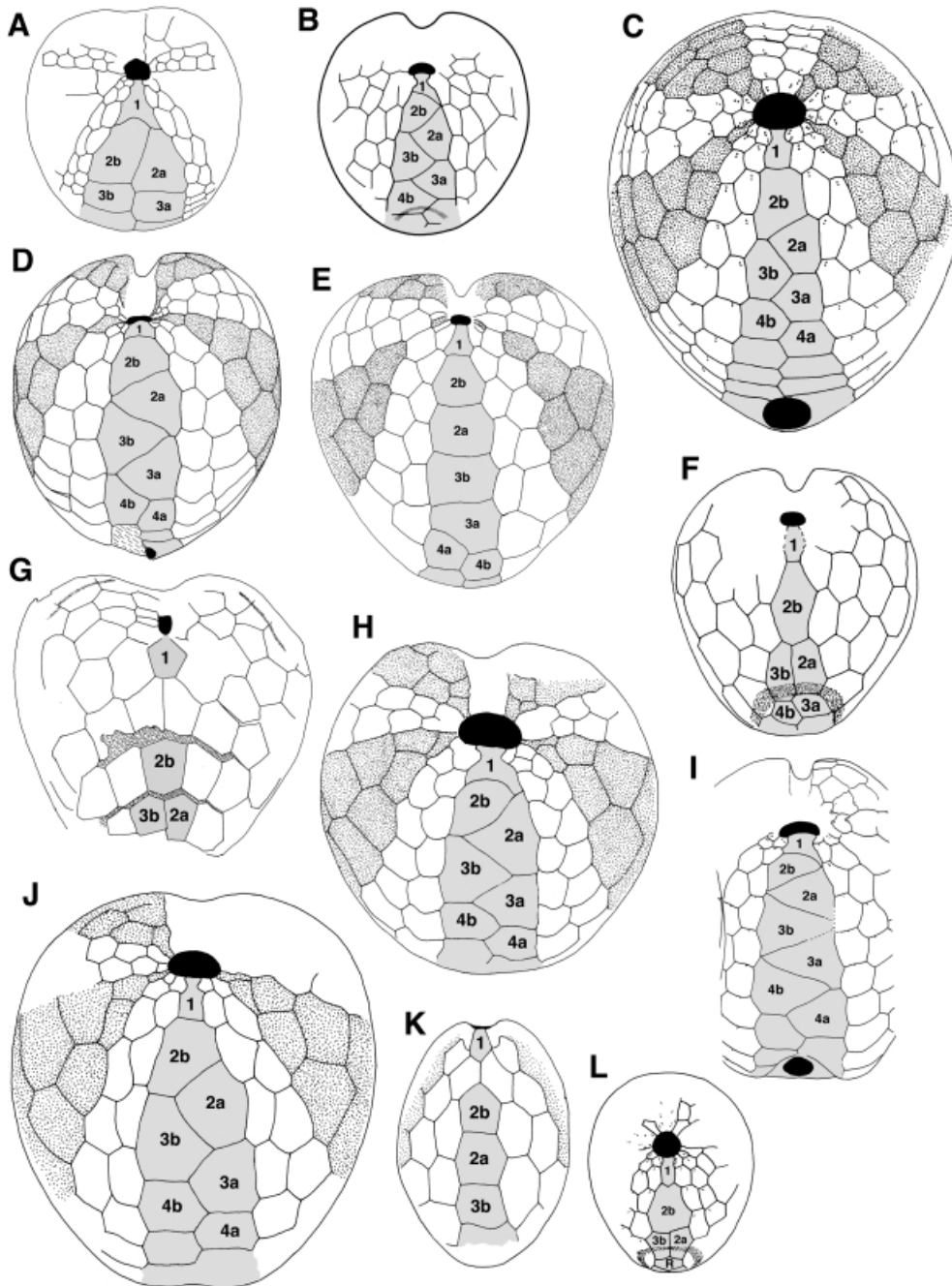
Peristome and periproct. The position and orientation of the peristome have been used as higher-level characters by various workers (e.g. Lambert and Thiery 1924; David 1988). However, shape and orientation are difficult to quantify objectively, and few characters provide clear-cut boundaries. One important structural character is provided by which interambulacral plates bound the adoral edge of the periproct, as this marks the stage in development at which the periproct starts to migrate away from the apical disc. In holasteroids, like all irregular echinoids, the periproct is initially aboral and migrates to the final adult position as development proceeds.

26. Labral plate curves out to form a prominent lip: no (0); yes (1).

27. Peristome orientation: approximately horizontal or gently inclined to lower surface (0); steeply inclined or vertical (1).

28. Periproct opening framed on oral side by interambulacral plates 5.a/4/5.b.5 (0); 5.a.5/5.b.6 (1); 5.a.6/5.b.7 or above (2).

29. Periproct in adult: supramarginal, with distinct subanal shelf (0); marginal, on vertically truncate face (1); inframarginal (2); on oral surface (3).



Tuberculation. The presence of fascioles has long been considered of great importance in holasteroid taxonomy. However, as Mooi and David (1996) pointed out, fascioles should only be considered homologous if they are developed across the same series of plates. Thus, for example, a subanal fasciole is developed in both urechinids and in the fossil *Giraliaster*. However, in *Giraliaster* the fasciole crosses interambulacral plates 5.b.4, 5.b.5 /5.a.4 on its adoral side, whereas in urechinids it is invariably found crossing plates 5.a.2/5.b.3. This strongly suggests that the two fasciole bands are not homologous. Similarly, the marginal fasciole passes either across plates 5.a.5/5.b.6 or 5.a.4/5.b.5 in the posterior interambulacrum beneath the periproct. A further complication with fascioles is that they may be present only in juveniles and lost in adults. Where preservation is poor, or where only adults are known, an absence of fascioles is scored as unknown rather than absent.

The presence or absence of large aboral tubercles in holasteroids is often highly variable amongst species of the same genus but their pattern of distribution has been used as a character.

30. Subanal fasciole: absent (0); present, crossing plates 5.a.2/5.b.3 on its adoral side (1); present crossing plates 5.b.4/5 and 5.a.4 on its adoral side (2).
31. Subanal fasciole on periproctal side passes over: plates 5.a.5/5.b.6 (1); plates 5.a.4/5.b.5 (2).
32. Marginal fasciole: absent (0); present around posterior only (1); present around entire test margin (2).
33. Beneath the periproct the marginal fasciole passes over: plates 5.a.5/5.b.6 (1); 5.a.4/5.b.5 (2).
34. Tuberculation style: no primary tubercles (0); primary tubercles present along anterior groove and adapical zone only (1); primary tubercles scattered over aboral interambulacral plates (2); primary tubercles confined to supra-ambital band (3).

Analytical method

The resulting data matrix (Table 2) was analysed using the computer program PAUP* (Swofford 2001). All characters were treated as unordered and of equal weight, except for characters 1 and 2 which were given half-weighting (see above). Because of the large number of taxa involved, the heuristic search option was employed. However, 100 replicate searches using random taxon addition were run to increase the chances of finding multiple islands of trees. Trees were rooted on *Eoholaster* and 100,000 'fast' bootstrap replicates were carried out in order to test the robustness of the groupings.

RESULTS

The analysis found 1601 equally parsimonious trees, tree length 122, and with a Consistency Index of 0.41 and Retention Index of 0.72. The semistrict consensus and 50 per cent majority rule consensus of these is shown in Text-figure 3. Despite the large number of trees there is excellent structure in the cladogram, and it is really just a small number of basal taxa with few derived characters that are causing problems. With

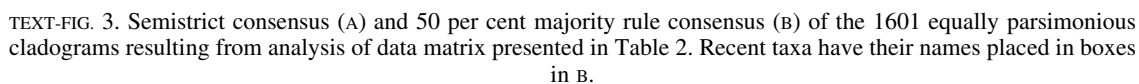
TEXT-FIG. 2. Plastron plating in spatangoids (A) and holasteroids (B–K). A, *Miotoxaster seynensis* (Lambert), BMNH EE8127, Lower Barremian, Lower Cretaceous, Lussan, Gard, France. B, *Giraliaster jubileensis* Foster and Philip, Cardabia Formation, Middle Palaeocene, north end of the Giralia Range, Western Australia (from Foster and Philip 1978). C, *Galeola papillosa* Quenstedt, NHM EE6733, Campanian, Upper Cretaceous, Hover, Hannover, Germany. D, *Cardiaster granulosus* (Goldfuss), NHM E41288, Campanian, Upper Cretaceous, Norwich, Norfolk, UK. E, *Sternotaxis heberti* (Cotteau, in Cotteau and Triger), NHM E8725, locality and age uncertain, but probably Campanian, B. mucronata Zone, Upper Cretaceous, Norfolk, UK. F, *Galeaster bertrandi* Seunes, NHM EE5595, Danian, Palaeocene, Koshak, Mangyshlak, Kazakstan. G, *Sanchezaster habanensis* Lambert, in Sánchez Roig, NHM E17204, Middle Oligocene, Canteras Tejar Consuelo Cerro, Cuba. H, *Pseudholaster wrighti* (Lambert), NHM E1551, Aptian, Lower Cretaceous, Atherfield, Isle of Wight, UK. I, *Hemipneustes pyrenaicus* Hebert, NHM EE3745, Maastrichtian, Upper Cretaceous, Jebel Rawdah, Oman. J, *Holaster bischoffi* (Renevier), NHM E80259, Cenomanian, Upper Cretaceous, Wilmington, Devon, UK. K, *Hagenowia blackmorei* Wright and Wright, NHM E8404, Campanian, Upper Cretaceous, Haldon, Devon, UK. L, *Cardabia bullarensis* Foster and Philip, NHM EE7721, Middle Palaeocene, Cardabia Formation, Giralia Range, Western Australia; R, rostral plate.

TABLE 2. Character matrix used in the phylogenetic analysis. Characters 1–34 are described in the text.

	1	6	11	16	21	26	30
	/	/	/	/	/	/	/
Eoholaster	00100	00000	00000	00003	10100	00210	0000
Pseudoholaster	21200	00000	00000	00003	10100	00210	0000
Giraliaster	21200	00000	00000	00002	10100	00212	1000
Pseudocardiaster	21200	00000	00000	01102	10100	00210	0100
Cardiaster	21200	00010	10000	01102	10100	00210	0101
Sternotaxis	11200	00010	11000	01102	10100	00210	0100
Infulaster	22210	00110	11000	0?1?2	20100	01210	0101
Hagenowia	22010	00110	11000	1???2	20000	01210	0101
Hemipneustes	21201	00000	00000	00002	10201	10220	0000
Toxopatus	2120?	000??	00???	0????	?0201	10?20	0000
Echinocorys	00200	00011	00000	00003	00110	00220	0000
Pseudananchys	00201	00011	00000	00003	00110	00220	0000
Holaster	11200	00011	00000	01103	00100	00210	0002
Jeronia	00200	10011	00000	01102	21100	00030	0003
Cibaster	11200	00011	00000	01102	20100	00210	0200
Offaster	01200	00011	00000	01102	21100	00210	0200
Galeola	01200	00011	00000	01102	21100	00220	0000
Crassiholaster	11200	00011	00000	00002	20100	01210	0000
Lampadocorys	02200	00011	00000	00?02	20100	00220	0??0
Pseudoffaster	11200	00011	00110	00112	31100	01210	0210
Calymne	01100	20011	00110	00102	31000	00210	0210
Sanchezaster	02200	00011	00110	10?12	31000	01?10	0210
Sternopneustes	02200	00011	00110	1???2	?1000	01120	0210
Chelonechinus	00200	00011	00110	10?12	31000	0012?	???0
'Stegaster'	22200	00011	00000	10112	211?0	00200	0?00
Rispolia	22200	00011	00000	0???2	20100	00200	0?00
Entomaster	22200	00011	00110	0????	?0100	01200	0202
Guettaria	22200	01011	00110	00112	20100	01200	0203
Seunaster	22200	00011	00110	??112	20100	01200	0?03
Tholaster	22200	00011	00000	0?1??	?0100	0?200	0?02
Garrumnaster	00200	10011	00120	01102	20100	00?0?	0000
Huttonechinus	01200	00011	00121	00002	20100	00221	2000
Corystus	00200	00011	00121	00002	20100	00201	2000
Cardabia	00200	10011	00121	00002	20100	00211	2000
Antrechinus	00200	00011	00100	01102	21000	00111	2000
Cystechinus	00210	00011	00100	01103	21000	0012?	?000
Urechinus	00200	10011	00100	01102	31000	00121	2000
Plex-cinctus	00010	20011	00120	11102	31000	00201	1000
Plex-spect	00210	00011	00120	11102	31000	00201	1000
Plex-sulcatus	12010	20011	00120	1?102	31000	00211	10?0
Galeaster	22010	02011	00120	00112	21100	01211	10?0
Pourtalesia	12010	02111	00120	11112	31000	01201	20?0
Basseaster	02000	00011	00120	01102	31100	00?1?	?0?0

such a low character to taxon ratio it is not surprising that the statistical support for the most parsimonious tree is extremely low, with few nodes even reaching 50 per cent. Nevertheless, the groupings that are recognised are founded for the most part on major structural characters of test plating, and most are intuitively sound and justifiable.

The stratigraphic range of these taxa is shown in Text-figure 6. An evolutionary tree has been constructed by selecting one of the equally most parsimonious cladograms that minimises gaps in the stratigraphic record and calibrating it against the record of first and last appearances (Text-fig. 6).



DISCUSSION

Classification

The Holasteroida *sensu* Durham and Melville (1957) and Wagner and Durham (1966) is a blatantly paraphyletic grouping that encompasses the stem group and part of the crown group (all atelostomate echinoids without amphisternous plastron plating). This unsatisfactory situation is, however, easily rectified by restricting the order Holasteroida to coincide precisely to the sister group of the Spatangoida. Holasteroida would then be the total group defined as having the stretched holasterid-style apical disc (or derivatives thereof), while Spatangoida would be defined as having amphisternous plastron plating (or derivatives thereof). The Collyritidae and Disasteridae, which Durham and Melville (1957) included in their Holasteroida, are grade taxa that constitute a large part of the stem group of the Atelostomata. These primarily Jurassic forms need revising before any progress can be made in unravelling the early evolution of atelostomate echinoids.

Within the Holasteroida, meridosternous plastron plating characterises all living holasteroids and many of the mid to late Cretaceous and Tertiary taxa. By contrast, most of the early Cretaceous taxa have the more primitive protosternous plastron plating. Thus, in keeping with Mortensen's (1950) and Loven's (1883) use of the term, Meridosternata can be used to designate the clade of holasteroids that have meridosternous plastron plating. This includes all living representatives. Those with protosternous plating form a grade consisting of the early members of the holasteroid stem group. This stem group includes one major clade that extends from the Early Cretaceous through to the Miocene, and includes *Pseudholaster*, *Cardiaster*, *Infulaster*, *Hagenowia*, *Sternotaxis*, *Hemipneustes* and *Giraliaster*. The oldest available name for this group is *Cardiasterina* Pomel, 1883.

Cardiasterina. Within the *Cardiasterina*, *Pseudholaster* Pomel occupies the most basal position and is plesiomorphic with respect to other members of this clade. *Pseudholaster* has a protosternous plastron, no fascioles and has hydropores confined to genital plate 2. *Giraliaster* Foster and Philip has an identical test architecture and tuberculation, and differs from *Pseudholaster* only in having a subanal fasciole. Clearly then *Pseudholaster* is a plesiomorphic grade taxon and will include the likely ancestors of *Giraliaster*. Preservation in specimens of late Cretaceous–early Tertiary cardiasterines such as '*Holaster*' *faxensis* Hennig from the Danian of Denmark, and '*Cardiaster*' *indicus* Forbes, from the Maastrichtian of India, that have been examined is too poor to tell whether a subanal fasciole is present or not. No subanal fasciole is ever present in Early and early Late Cretaceous species of *Pseudholaster*.

Cardiaster Forbes resembles *Pseudholaster* in test shape but has metasternal plastron plating, meridosternous lateral interambulacra and a partial marginal fasciole. In the type species the labral plate remains broad and subsequent plating is clearly biserial, although the first two or three plates reach the opposite adradial suture. Intermediate forms exist between *Cardiaster* and *Pseudholaster* [e.g. *Pseudocardiaster truncatus* (Goldfuss)] having protosternous plating but a marginal fasciole. Three other genera have metasternous plastron plating and group with *Cardiaster*, namely *Sternotaxis*, *Hagenowia* and *Infulaster*. In these forms the peristome is small, circular and faces forward into the frontal groove, and their plastron plates are more symmetrical and strictly uniserially arranged. *Hagenowia* and *Infulaster* are clearly closely related, as both display the derived condition of having a single anterior genital plate instead of the usual two. All of these metasternal taxa constitute a well-defined clade and constitute the family Cardiasteridae Lambert, 1917.

Hemipneustes Agassiz seems to be closely related to three other less well-documented taxa, *Opisopneustes* Gauthier, *Medjesia* Jeffery and *Toxopatagus* Pomel. All four share two distinctive synapomorphies; the hydropores are densely scattered over all three anterior ocular plates and genital plates 2 and 3, and the posterior petals are strongly flexed away from the midline before curving backwards. In all three the labral plate is tongue-like and projects strongly over the peristomial opening. Plastron plating is protosternous, although occasional adoral plates can extend across the full width of the plastron. These three genera differ in small details only. *Opisopneustes* has coarse aboral tubercles, while *Toxopatagus* is rather depressed with a sharper ambitus and more widely open frontal sulcus than *Hemipneustes*. This clade was first recognised and named Hemipneustinae by Lambert, 1917. Its sister

group is the plesiomorphic *Pseudoholaster*. The oldest taxon that shows the hemipneustid characteristic of having hydropores scattered widely over apical disc plates is *Plesiohemipneustes revestensis* Lambert, from the Lower Cenomanian of western Europe.

Stegasterina. Amongst the extant taxa, *Sternopatagus* was recognised as being far removed from other holasteroids by Mortensen (1950), and this is confirmed by my cladistic analysis. *Sternopatagus* differs from most other extant holasteroids in having a marginal fasciole rather than a subanal fasciole. In *Sternopatagus* the marginal fasciole crosses plates 5.a.4/5.b.5 beneath the periproct, post-episternal plates are large and paired and form the posterior of the plastron, and ambulacral plate 4 lies adjacent to the rear of the episternal plates. These derived characters are also present in *Calymne* and in the fossil taxa *Pseudoffaster* and *Sanchezaster*. The oldest available name for this clade is Calymnidae Mortensen, 1907.

The Late Miocene–Pliocene *Chelonechinus* has been somewhat difficult to place phylogenetically. Bather (1934) proposed that *Chelonechinus* shared closest affinities with *Sanchezaster*, whereas Mooi and David (1996) placed *Chelonechinus* within the Urechinina, close to *Urechinus* and *Cystechinus*. This cladistic analysis confirms that *Chelonechinus* belongs to the Calymnidae, as it shares at least two of the three synapomorphies of that clade (inadequate preservation prevents us knowing whether this taxon has a marginal fasciole).

Forming a sister group to the Calymnidae is a fossil clade of unusually thick-tested holasteroids comprising *Rispolia*, *Guettaria*, *Entomaster* and *Seunaster*. These taxa have a supramarginal periproct with a distinct subanal shelf, and a very strongly developed adoral sulcus. A marginal fasciole is known to occur in three of these, and it passes over plates 5.a.5/5.b.6 beneath the periproct. *Rispolia* is the most primitive, lacking the paired episternal plates of the other three taxa. The oldest available name for this clade is Stegasteridae Lambert, 1917. Unfortunately, the type species of *Stegaster*, *S. guilleroni* de Loriol, is very poorly known and both its plastron plating and apical disc plating remain undescribed. From the sketchy figure and description given of this species it would appear to be identical to the much better known type species of *Rispolia* Lambert.

Together these two families comprise the Stegasterina Lambert, 1917, a name that is employed here to designate the sister group to the extant Urechinina. Detailed relationships within the basal Stegasterina remain poorly resolved, but may include *Lampadocorys* and *Crassiholaster subglobosus* (Leske). *C. subglobosus* differs from the type species of *Holaster* in having the rounded form, thick-shelled test and the small forward-facing peristome characteristic of many Stegasterina, but lacks the pronounced adoral groove found in later members of this clade, has biserially offset episternal plates and no trace of a marginal fasciole.

Urechinina. All the extant holasteroids, with the exception of *Sternopatagus* and *Calymne*, fall into a second major clade, the Urechinina H. L. Clark, 1946. This group is characterised by having an oval subanal fasciole that crosses on its oral side interambulacral plates 5.a.2/5.b.3. The classification of the recent members of this group has been discussed in admirable detail by Mooi and David (1996) and is largely confirmed by this analysis. However, they did not have the data to take into account fossil representatives of this group. Of the four readily recognisable clades within the Urechinina three have a fossil record.

The Corystidae, with three genera, is an Indo-Pacific taxon distinguished by the presence of a rostral plate immediately posterior to the paired episternals. The oldest species to possess a rostral plate, *Cardabia bullarensis* Foster and Philip, comes from deposits of late Palaeocene age in Australia (Foster and Philip 1978), and the lineage survives to the present day with one living deep water species, *Corystus relictus* (de Meijere). The Palaeocene genus *Garumnaster*, although lacking a rostral plate, is identified as the immediate sister group to the Corystidae.

The Pourtalesiidae are an equally distinctive clade, on account of their apical disc structure, in which the posterior gonopores open through ocular plates II and IV. Poslavskaya and Moskvina (1960) first suggested that the Maastrichtian to Palaeocene *Galeaster* should be classified as a pourtalesiid, and this is now confirmed. *Galeaster* shares with pourtalesiids the highly characteristic apical disc structure in which the posterior gonopores have shifted onto ocular plates II and IV.

Plexechinids have few defining test characters although they have lost genital plate 3, and have a disjunct plastron and subanal heel, all characters shared with *Pourtalesia*. However, the aboral portion of the subanal fasciole passes across plates 5a/6b as it does in *Galeaster*, rather than plates 4a/5b as in *Pourtalesia*. *Basseaster* is more primitive still and may be part of the common stem group of plexechinids and pourtalesiids.

The fourth group, Urechinidae, has no definite fossil record. Basal to the crown group Urechinina lie *Jeronia* and *Galeola*, two Upper Cretaceous genera that have meridosternous plating in all interambulacral zones, lack a frontal groove and have their periproct inframarginal. This is also where the enigmatic *Pilematechinus* A. Agassiz usually falls when included in the cladistic analysis. Other possible members of the Urechinine stem group include *Offaster* and *Cibaster*, but both lack convincing synapomorphies.

Basal Meridosternata. The least well resolved (and most unstable) part of the cladogram is made up of the basal members of the Meridosternata. The type species of *Holaster*, *H. nodulosus* (Goldfuss) comes out as having the most advanced test architecture since all of its interambulacral zones are meridoplacous. However, in contrast to *Cibaster* and higher groups, it has no fascioles and its labrum extends to reach the third ambulacral plate. Closely related to *Holaster* is *Scagliaster* Munier Chalmas (= *Holasteropsis* Elbert), a form with a lower periproct and coarse tuberculation confined to a supramarginal band. *Echinocorys* and *Pseudananchys* form a clade that may be more basal. In these taxa the labrum also extends to reach the third ambulacral plate, but they lack an anterior sulcus and share the derived condition of having pore-pairs in all five ambulara identical in appearance. Furthermore they retain the primitive condition of amphiplacous plating in their lateral and anterior interambulacra. The split between the Echinocorythidae and Holasteridae can be traced back to the Aptian, when *Pseudananchys* first appears.

There are insufficient data to resolve which of these taxa belongs to the crown group and which to the stem group. Given that all have meridosternous rather than protosternous or metasternous plastron plating, all are treated as basal members of the Meridosternata.

In summary, the diverse fossil genera included in the family Holasteridae by Wagner and Durham (1966) can be partitioned into stem-group Stegasterina (*Entomaster*, *Guettaria*, *Rispolia*, *Seunaster*, *Tholaster*, *Pseudoffaster*), extinct crown-group members of the Urechinina (*Basseaster*, *Garumnaster*, *Galeaster*, fossil Corystidae), stem-group Urechinina (*Galeola*, *Jeronia*), basal Meridosternata (*Echinocorys*, *Holaster*) and stem group Meridosternata (e.g. *Pseudholaster*, *Hemipneustes*, *Cardiaster*).

A revised classification is presented in Table 3 and is mapped onto the cladogram in Text-figure 3B.

Key morphological transformations in the evolution in holasteroids

Three aspects of holasteroid morphological evolution are worth considering in a little more detail; plating of the apical disc and the plastron, and the development of fascioles.

Apical disc evolution. Amongst holasteroids the most unusual apical disc structure is that seen in *Pourtalesia* and the Pourtalesiidae. At first sight their disc appears to be compact, like that of spatangoids, with the four gonopores close together on adjacent plates (Text-fig. 4C). Closer inspection shows that the anterior plate is single and houses the hydropores as well as the anterior two gonopores. One peculiar aspect of the pourtalesiid disc is the absence of an obvious ocular plate at the apex of ambulacra II and IV. Previous workers such as Loven (1883) have interpreted the smallest plate at the apex of ambulacra II and IV as the ocular plate. However, this is an abnormal position, for in other atelostomates the ocular plates nestle at the junction between the anterior and posterior genital plates (Text-fig. 1A–B). The fact that the lateral ambulacra abut squarely against the centre of the posterior gonopore-bearing plates is most peculiar. A second peculiarity of the pourtalesiid disc is that one or two supplementary enclosed plates are found along the mid-line behind the apical disc within interambulacra 1 and 4. These are imperforate. The disc is always disjunct with the posterior oculars separated from the remainder of the disc.

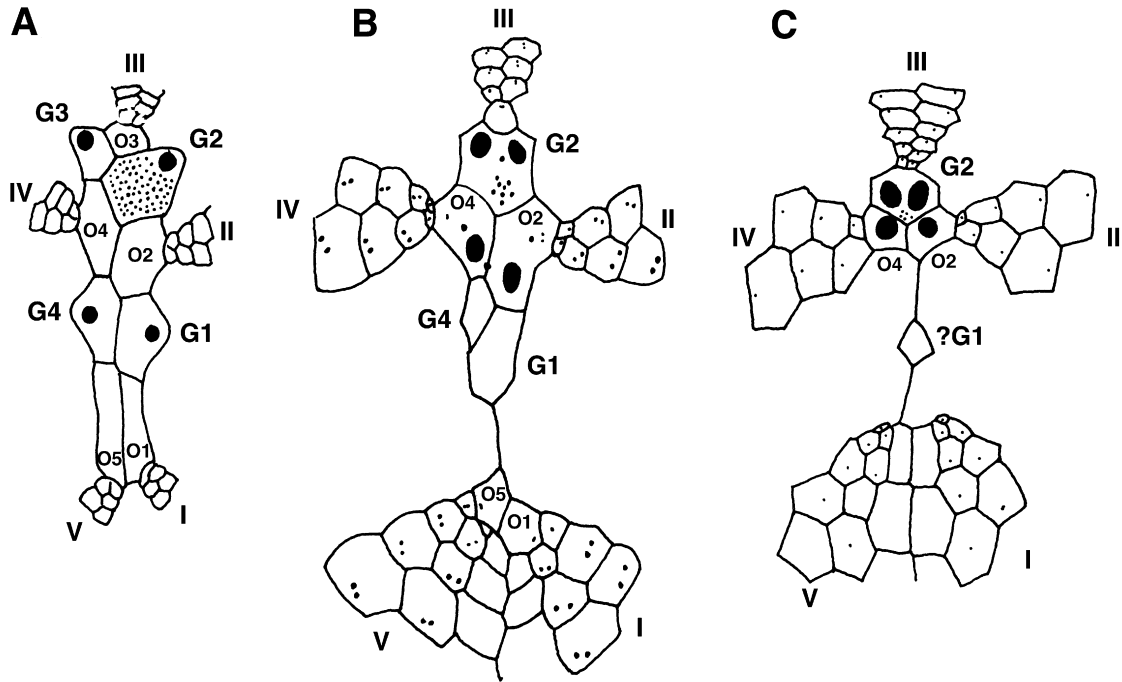
The pourtalesiid disc, as conventionally interpreted, thus presents several puzzling features and appears very different from the elongate holasterid-style apical disc that characterises all other meridosternous

TABLE 3. Revised classification for the clade Holasteroida.

Holasteroida Durham and Melville, 1957 [= Total Group]	Calymnidae Mortensen, 1907
'Basal holasteroids'	<i>Pseudoffaster</i> Lambert, 1924
<i>Eoholaster</i> Solovjev, 1989	<i>Sternopatus</i> de Meijere, 1902
<i>Taphraster</i> Pomel, 1883	<i>Sanchezaster</i> Lambert, 1924
Cardiasterina Pomel, 1883	<i>Chelonechinus</i> Bather, 1934
<i>Pseudholaster</i> Pomel, 1883	Urechinina H. L. Clark, 1946
<i>Giraliaster</i> Forster and Philip, 1974	<i>Pilematehinus</i> A. Agassiz, 1904 (<i>incertae sedis</i>)
Hemipneustidae Lambert, 1917	Stem group Urechinina
<i>Hemipneustes</i> Agassiz, 1836	<i>Galeola</i> Quenstedt, 1874
<i>Opisopneustes</i> Gauthier, 1889	<i>Jeronia</i> Seunes, 1888
<i>Toxopatus</i> Pomel, 1883	Urechinidae Duncan, 1889
<i>Medjesia</i> Jeffery, 1998	<i>Antrechinus</i> Mooi and David, 1990
Cardiasteridae Lambert, 1917	<i>Cystechinus</i> A. Agassiz, 1879
<i>Cardiaster</i> Forbes, 1850	<i>Urechinus</i> A. Agassiz, 1879
<i>Infulaster</i> Desor, 1858	Corystidae Foster and Philip, 1978
<i>Hagenowia</i> Duncan, 1889	<i>Garumnaster</i> Lambert, 1907
<i>Sternotaxis</i> Lambert, 1893 (= <i>Cardiotaxis</i>	<i>Cardabia</i> Foster and Philip, 1978
Lambert, 1917)	<i>Corystus</i> Pomel, 1883
Meridosternata Loven, 1883 [= Crown Group]	<i>Huttonechinus</i> Foster and Philip, 1978
'Basal Meridosternata'	Unnamed clade
Echinocorythidae Wright, 1857	<i>Basseaster</i> Lambert, 1936
<i>Echinocorys</i> Leske, 1778	Plexechinidae Mooi and David, 1996
<i>Pseudananchys</i> Pomel, 1883	<i>Plexechinus</i> A. Agassiz, 1896
<i>Lampadocorys</i> Pomel, 1883	Pourtalesiid A. Agassiz, 1881
Holasteridae Pictet, 1857	<i>Galeaster</i> Seunes, 1889
<i>Holaster</i> Agassiz, 1836	<i>Pourtalesia</i> A. Agassiz, 1869
<i>Scagliaster</i> Munier-Chalmas, 1891	<i>Ceratophysa</i> Pomel, 1883
<i>Offaster</i> Desor, 1858	<i>Cystocrepis</i> Mortensen, 1907
<i>Cibaster</i> Pomel, 1883	<i>Echinocrepis</i> A. Agassiz, 1879
Stegasterina Lambert, 1917	<i>Echinosisgra</i> Mortensen, 1907
Stegasteridae Lambert, 1917	<i>Helgocystis</i> Mortensen, 1907
<i>Rispolia</i> Lambert, 1917 [? = <i>Stegaster</i> Pomel,	<i>Spatangocystis</i> A. Agassiz, 1879
1883]	
<i>Tholaster</i> Seunes, 1890	
<i>Entomaster</i> Gauthier, 1888	The following are currently too poorly known for
<i>Guettaria</i> Gauthier, 1888	placement:
<i>Lampadaster</i> Cotteau, 1889	<i>Ganbirretia</i> Gauthier, 1903
<i>Seunaster</i> Lambert, 1912	<i>Paronaster</i> Airaghi, 1906 (possibly a spatangoid)

holasteroids. Recently, however, Saucedo *et al.* (in press) have presented an alternative interpretation of the pourtalesiid disc, in which the posterior genital pores open not through genital plates 1 and 4 but through ocular plates II and IV. The correctness of this interpretation becomes immediately clear when the structure of the apical disc of *Galeaster*, the oldest pourtalesiid, is examined (Text-fig. 4B). This shows clearly that the posterior gonopores open on ocular plates II and IV. These plates have both small ocular pores and large gonopores. Immediately to their rear come two imperforate plates that I interpret as genital plates 1 and 4. These in turn are separated from the paired posterior ocular plates. Thus, in this primitive pourtalesiid the apical disc plates remain paired and opposite, alternating between genital and ocular plates, but the posterior gonopores have shifted from the genital to the ocular plates.

Other aspects of the apical disc have also changed over time. The disjunction between posterior ocular plates and the rest of the apical disc occurred at least twice independently, once in the *Hagenowia* lineage and once or more in *Basseaster* and its descendants. In the case of *Hagenowia* this is clearly associated with a narrowing and elongation of the apical region of the test, and the same is certainly true of some



TEXT-FIG. 4. Apical disc structure in holasteroids. A, standard holasteroid disc plating. B, disc plating in *Galeaster bertrandi* Seunes, 1889, based on NMH EE5588 from the lower Danian of Mangyshlak, Kazakhstan. C, disc plating in *Pourtalesia tanneri* Agassiz, taken from Agassiz, 1904, plate 56, figure 5. G1–G4, genital plates; O1–O5, ocular plates; ambulacra numbered I–V.

pourtalesiids. Similarly the loss of genital plate 3 has occurred at least three times independently, once in the *Infulaster*–*Hagenowia* lineage, a second time at the base of the *Plexechinus* – pourtalesiid clade, and once in *Cystechinus*. There is no obvious functional explanation for this trend. The spread of hydropores over all of the anterior plates of the apical disc has occurred in the Hemipneustidae and forms a characteristic feature of all members of that clade. However, a similar condition has evolved at least twice independently, in *Pseudananchys* and in *Pilematechinus*. In hemipneustids the spread of hydropores is almost certainly associated with the extensive development of respiratory tube-feet in these taxa.

Plastron evolution. In primitive holasteroids, plastron plates are arranged as a simple alternating double column of undifferentiated plates behind the first interambulacral plate. Over time, the trend has been for these plates to become more symmetrical and opposite, and for proximal plates to become differentiated. The first plate in interambulacrum 5 (the labrum) is primitively crescentic, with a strongly convex posterior plate boundary. The plate extends to abut both interambulacral columns. The shift to a more symmetrical labrum that is in contact with just a single posterior plate appears to have occurred twice, once in the Meridosternata and at least once in the metasternous Cardiastrina, where the resulting pattern of plating is rather different. In Cardiastridae the development of a narrow plastron composed of uniserial plates is associated with test elongation and the shifting of the peristome closer to the anterior border.

Other groups also became elongate with an anterior peristome, but accommodated these changes in a different way, by disconnecting the labral plate from the following plates thereby allowing adjacent ambulacral columns to meet interradially. Such disjunct plastrons have evolved extensively in pourtalesiids, in *Hagenowia*, and in the Calymnidae. The geometric problems for plate accommodation were even more extreme in the lateral interambulacra and even more groups display a loss of contact between the basicoronal plates and the peristomial edge.

The second interambulacral plate (5.b.2) becomes highly symmetrical and is followed by paired episternal plates in at least two lineages, once in the Urechinata and one or more times in the Stegasterina, with both Calymnidae and advanced Stegasterina having highly symmetrical plastronal plating. However, only in one clade, the Corystidae, does posterior narrowing result in a single rostral plate.

Fasciole evolution. Fascioles are notoriously unstable characters, yet the two major groups of Meridosternata each have a distinctive fasciole pattern. Most Stegasterina have a marginal fasciole that passes around the ambitus and beneath the periproct, whereas in the Urechinata the fasciole is a subanal ring. In both cases there is evidence for parallel evolution. A partial marginal fasciole characterises the Cardiasteridae (*Cardiaster*, *Infulaster*, *Hagenowia*) and was independently derived from the complete marginal fasciole that characterises most Stegasterina. Furthermore, in the two families of Stegasterina the marginal fasciole follows a slightly different path. A subanal fasciole is present in the cardiasterine genus *Giraliaster*, as well as in most members of the Urechinata. However, the subanal fasciole crosses a different set of plates in these two groups. It is not surprising that fascioles show some degree of convergence, given their great functional significance in maintaining water circulation around the test.

HOLASTEROID DIVERSITY AND MIGRATION INTO THE DEEP-SEA

Changes in diversity over time

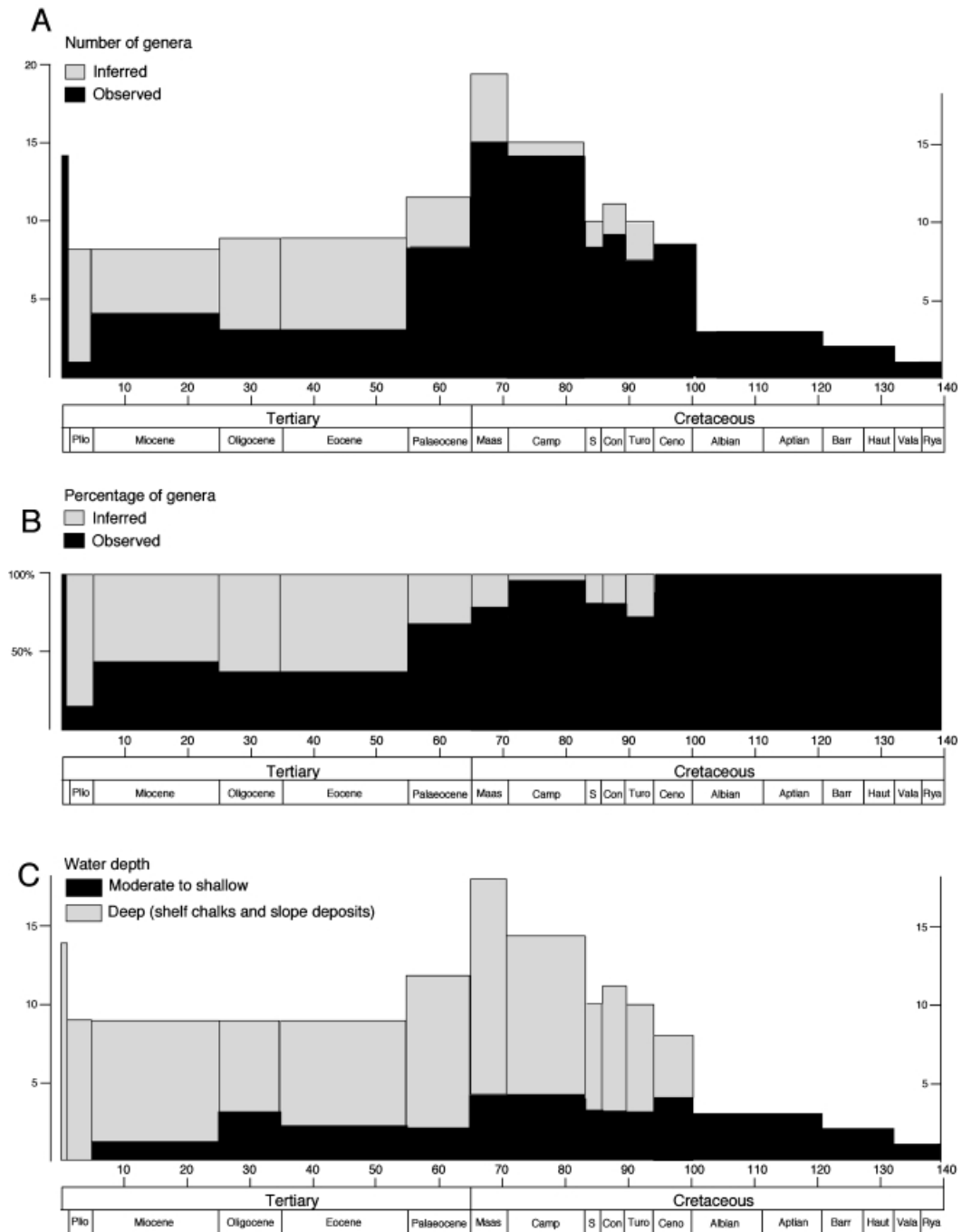
It has long been known that holasteroids reached their peak of taxonomic diversity in the Late Cretaceous (e.g. Eble 2000). From a small number of lineages in the Early Cretaceous, holasteroids expanded markedly in the Cenomanian and reached peak diversity in the Maastrichtian (Text-fig. 5A). For all of this time interval, sampling at generic level is efficient, with few Lazarus-effect gaps in the record. (A Lazarus-effect gap is where a taxon has been sampled from the time interval above and below, but has yet to be sampled from the intermediate time interval.) After the Maastrichtian there was a major drop in total diversity, and a marked increase in the proportion of lineages unsampled in the fossil record. Sampled diversity shows a further major fall between the Palaeocene and Eocene with the proportion of Lazarus gaps again increasing markedly. However, when Lazarus taxa are taken into consideration, there is little overall loss in taxonomic diversity at this time. Sampled diversity remains low throughout the remainder of the Tertiary and declines even further in the Pliocene.

If diversity is plotted as the proportion of sampled to inferred lineages through time (Text-fig. 5B) an apparent decline in the quality of the fossil record of holasteroids is evident. This is at least partially due to the pull of the Recent, since several extant lineages are inferred to have a long Tertiary record. However, it is also clear that this coincides with a major change in the nature of oceanographic conditions in the North Atlantic and western Tethyan regions during the late Cretaceous–early Tertiary and a move of holasteroids off the continental shelf and into slope and basin settings.

Migration into the deep-sea

The early diversification of holasteroids is recorded from sediments laid down in the relatively shallow water environments that predominated on the continental shelves in the Early Cretaceous. Yet today they are confined to continental slope and abyssal settings in water depths of greater than 400 m. To understand how this transition took place, taxa have been scored as to whether they were living in mid-shelf to inner shelf environments (clastic and bioclastic sediments with diverse benthic fauna), or in deep water chalks and continental slope turbiditic successions. The former are likely to have been in less than 100–150 m water depth and the latter considerably deeper and in more oligotrophic settings. Text-figure 6 maps the distribution of these two categories of taxa onto the phylogenetic tree, and Text-figure 5C shows the relative proportion of the two over geological time.

The marked expansion in generic diversity that took place in the mid Cretaceous was predominantly driven by the expansion of holasteroids into deeper-water shelf environments characterised by chalk deposition (Text-fig. 5C). Chalk deposition became widespread in the mid Cretaceous (Cenomanian onwards) and marked the onset of more oligotrophic oceanographic regimes and a switch from



TEXT-FIG. 5. Holasteroid diversity through time. A, generic diversity; black bars, number of observed genera in each time interval; stippled bars, number of additional genera inferred to have been present from phylogenetic tree (Text-fig. 6). B, proportion of total generic diversity inferred from sampled taxa (black) and Lazarus gaps (stippled). C, number of genera inferred to have been living in shallow to moderate water depths in mesotrophic settings (black), and in deeper-water shelf chalks and continental slope turbiditic settings (stippled).

predominantly mixed to stratified conditions across wide stretches of the deeply flooded cratonic blocks of Europe and central Asia (see Gale *et al.* 2000). It was for these relatively organic-poor habitats that many holasteroids became morphologically specialised. In today's deep-sea environments organic input is typically pulsed and deposit feeders are heavily dependent on 'organic snow' episodically accumulating at the sediment-water interface (e.g. Graf 1992). Modern pourtalesiids have evolved funnelling systems whereby flocculated surface organics can be skimmed off and channelled into the peristome via an anterior funnel. Such modifications contrast with the infaunal sediment feeding techniques of spatangoids whereby particulate material is picked by perioral tube-feet. Cretaceous holasteroids such as *Cardiotaxis*, *Hagenowia*, *Infulaster*, *Galeaster* and the stegasterids have all independently evolved test morphologies similar to those of modern pourtalesiids and presumably fed in a similar way.

The general global sea-level fall that started in the late Cretaceous and continued through the Tertiary (Haq *et al.* 1988) brought an end to deep-water stratified conditions in the shelf areas bordering the North Atlantic and western Tethys. Chalk deposition, which was so widespread in the mid Late Cretaceous, became more and more restricted in area, finally disappearing in the Late Palaeocene. By the late Cretaceous holasteroids were already to be found inhabiting continental slope habitats (e.g. in the Bay of Biscay; Smith *et al.* 1999). Several of the now exclusively deep-sea lineages have their immediate sister taxon in deep-water shelf and upper continental slope chalks and marls of the Maastrichtian and Palaeocene (*Galeaster* for the Pourtalesiids, *Basseaster* for Plexechinidae, *Pseudoffaster* for Calymnidae). These successful specialists appear to have moved downslope and off-shelf as global sea levels fell in the North Atlantic and western Tethyan region. Thus the marked drop in the quality of the holasteroid record after the early Palaeocene probably indicates a shift in the nature of the rock record that is preserved on continental shelves. Prior to the Eocene there were widespread chalks representing deep-water, stratified conditions and these contain a diverse holasteroid fauna. By contrast, deep-water deposits are much more restricted in occurrence from the Eocene onwards, and are largely confined to tectonically emplaced slope deposits at convergent plate boundaries.

There appear to have been at least four independent migrations into the deep-sea by holasteroids.

1. The urechinines (plexechinids and pourtalesiids) represent the most successful of these and had already expanded into deep-water shelf settings by the Maastrichtian, as evidenced by *Galeaster*. Furthermore, the occurrence of a deep-water *Pourtalesia* in the Middle Miocene Tatsukuroiso mudstone (a slope setting) in Ibaraki Prefecture, north-eastern Honshu, Japan (Kikuchi and Nikaido 1985) shows that much of the diversification within the Pourtalesiidae must have occurred prior to then.
2. The Calymnidae and Stegasteridae were very successful in the late Cretaceous in deep-water shelf settings and had expanded to slope settings by the Maastrichtian. The Oligocene *Sanchezaster* and Miocene–Pliocene *Chelonechinus* give rare glimpses of this lineage in slope environments.
3. The mid Miocene *Toxopatus* is found associated with a number of apparently deep-sea spatangoids such as *Linopneustes* and *Heterobrissus* in a molasse deposit from Italy (Stefanini 1908). Its sister taxon is the widespread shallow-water *Hemipneustes* of the Cretaceous. No record of this lineage exists between the Maastrichtian and mid Miocene, and so the precise time of migration remains poorly bounded, but is likely to have been late Cretaceous–early Tertiary.
4. The modern *Stereopneustes relictus* is found today at depths of 400 m or more in slope environments. *Stereopneustes* is here treated as a junior synonym of *Corystus*, since only a slight difference in the positioning of the periproct separates the modern species from its Miocene sister taxon. *Corystus* is found in relatively shallow water deposits up to the early Mid Miocene, after which it disappears from the rock record. It seems likely, therefore, that this lineage is the most recent to have shifted into the deep-sea environment, sometime during the Mid to Late Miocene.

By contrast there has only been one apparent shift from deeper-water settings to shallow-water settings. That occurred in the Corystidae. Corystidae nest within an exclusively mid- to deep-water shelf clade of Cretaceous age. The precise sister group of corystids is not clear, but all of its potential close relatives were living in deeper-water conditions than, for example, *Corystus* from the Murrey River Formation of South Australia.

It is important to realise that members of the Cardiasterina continued to thrive within shallow-water clastic environments throughout the Cretaceous and Palaeogene (Text-figs 5c, 6). For example,

Hemipneustes and *Opisopneustes* were prominent and diverse members of the benthic fauna in shallow-water carbonate platform settings (e.g. Smith 1995) and successfully competed for resources alongside the more numerous spatangoids. Also, like spatangoids, they relied on penicillate tube-feet around the mouth for selecting organic material from the sediment in which they lived. During the latest Cretaceous these shallow-water lineages were extremely widespread, being found in North America, Europe, North Africa, the Middle East, India and south-western China (Smith and Jeffery 2000). However, in the Tertiary the only shallow water representatives are found in the Southern Hemisphere, specifically in Australia and New Zealand. Clearly, events at the end of the Cretaceous had a major impact in reshaping the ecological and biogeographical distribution of holasteroids.

Holasteroids and the K/T event

Both Eble (2000) and Jeffery (2001) have pointed out that holasteroids and spatangoids differed in their pattern of survivorship across the Cretaceous/Tertiary boundary, with holasteroids suffering much greater loss than spatangoids. Jeffery made a convincing case that this differential survival is related to the more specialised feeding mode of most holasteroids, while Eble noted that disparity amongst holasteroids greatly diminished. Yet, when losses are placed in a phylogenetic context (Text-fig. 6) it is evident that at least ten and possibly as many as 12 separate lineages of holasteroid crossed the K/T boundary. As pointed out by Jeffery (2001) it is mainly the specialist deep-water clades (*Hagenowia*, Cardiasteridae, Stegasteridae) that suffered most extinction. As discussed above, these lineages evolved many of the same structural adaptations for surface grazing 'organic snow' that are seen in the deep-water pourtalesiids. For example, there is striking convergence in body form of the Cretaceous *Hagenowia* and the modern *Echinosigra*, although a detailed examination of test architecture shows that these two taxa are not closely related. Specialist deep-sea feeders such as *Hagenowia* and *Cardiotaxis* were largely lost at the K/T event, and it is a different clade that has given rise to the vast majority of deep-water holasteroids that are living today.

In conclusion, irregular echinoids that have become morphologically specialised for harvesting the episodic supply of flocculated organic detritus from the sediment-water interface have evolved twice, once in the Late Cretaceous and once during the Tertiary. This double radiation lends further support to the view that the crash in primary productivity in ocean settings was a crucial event in the history of holasteroids. It presumably eradicated the majority of specialist deep-sea forms. Only as surface water productivity returned in the late Palaeocene and Eocene did favourable conditions return allowing expansion and diversification off-shelf.

SYSTEMATIC DESCRIPTION OF *CALYMNE*

Family CALYMNIDAE Mortensen, 1907

Genus CALYMNE Wyville Thomson, 1877

*Calymne relict*a Wyville Thomson, 1877

Text-figure 7A–C

1877 *Calymne relict*a Wyville Thomson, 1877, p. 397.

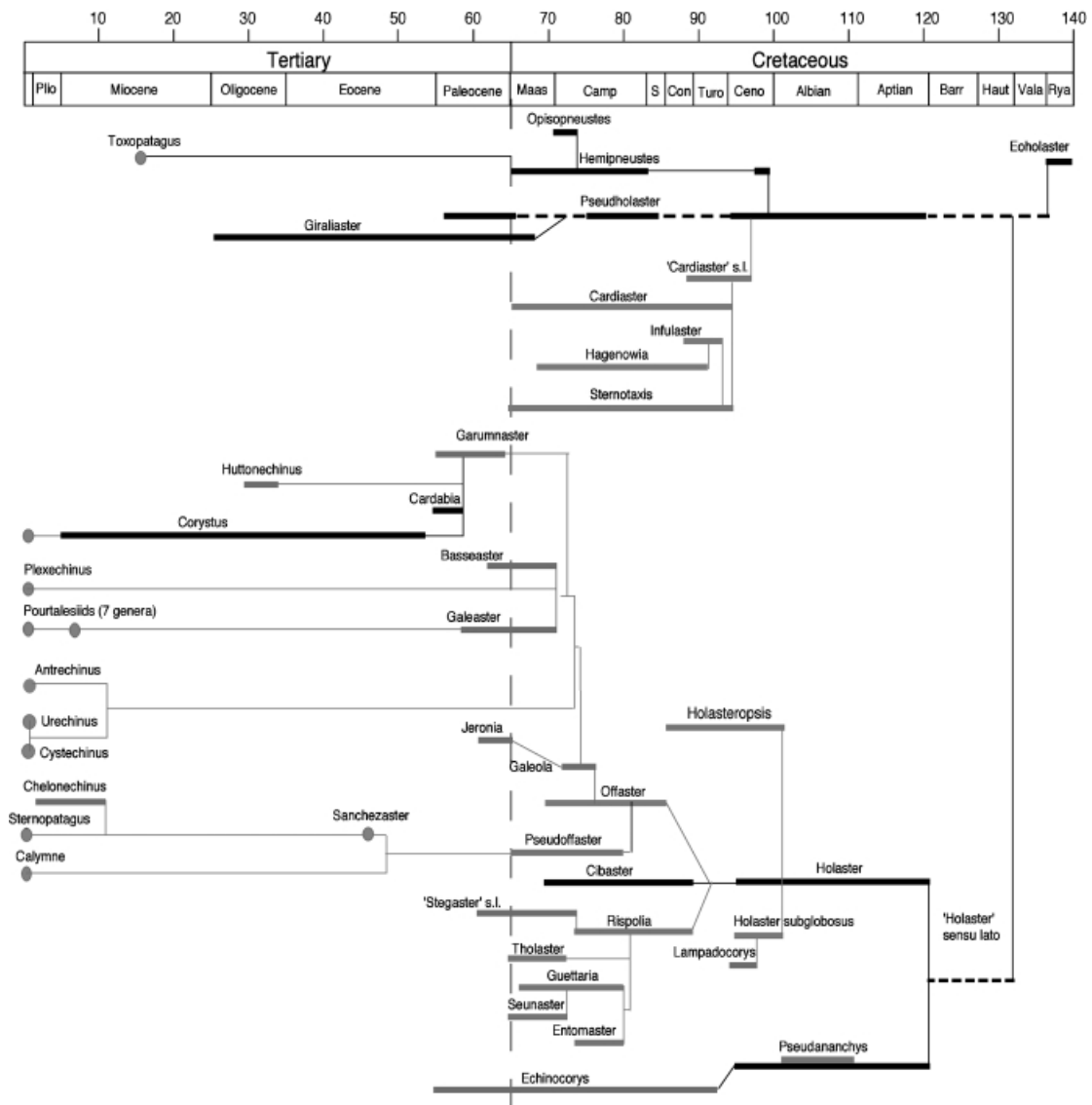
1881 *Calymne relict*a Wyville Thomson; Agassiz, p. 155, pls 34, 39, figs 24–26, 40, figs 63–65, 43, fig. 24, 44, figs 47–48.

1925 *Calymne relict*a Wyville Thomson; Clark, p. 188.

Types. Two fragmentary specimens, BMNH 81.11.22.46.

Occurrence. Challenger station 54, north of the Bermudas, 2650 fathoms (4844 m).

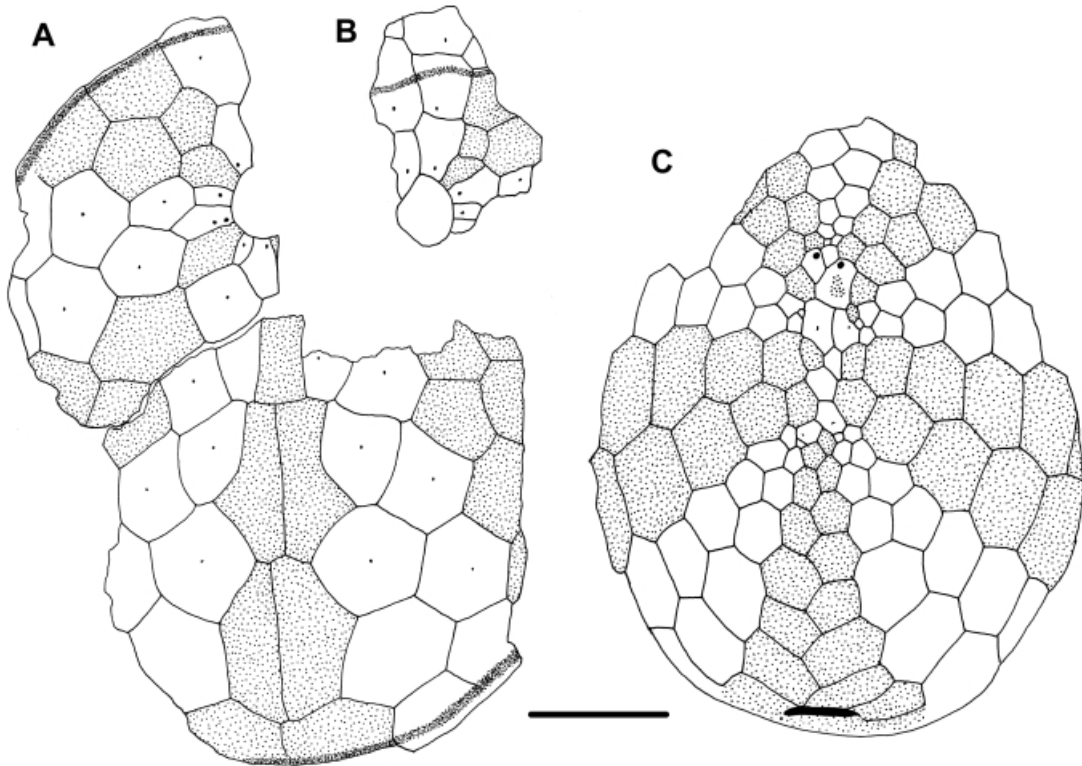
Description. Test broadly similar to *Pseuoffaster* in shape. It has a relatively flat base that is raised slightly along the midline of the plastron. The aboral surface is domed with a sagittal keel, steeply sloping flanks and low ambitus. There



TEXT-FIG. 6. Evolutionary tree for holasteroids derived from calibrating the cladogram against the stratigraphic record. Dashed lines indicate that species attributed to *Holaster sensu lato* have been recorded at this horizon which may turn out to belong to the genus indicated when test architectural characters are analysed. Black lines, lineages occurring in mid- to shallow-water shelf or carbonate platform settings; grey lines, lineages found in deep-water shelf chalks or slope deposits.

is a vertically truncate posterior face, and the anterior slopes steeply to the ambitus without a sulcus aborally. A shallow but distinct sulcus is found adorally.

The apical disc is elongate with the posterior ocular plates and posterior genital plates uniserially arranged (Text-fig. 7c). Both anterior genital plates are present and each bears a gonopore. Genital plate 2 is the larger and is perforated centrally by a small number of hydropores. Genital plate 3 is separated from ocular plate IV. Ocular plate III is small and triangular, ocular plates II and IV are much larger and opposite one another, meeting behind genital plate 2. Genital plates 1 and 4 are presumably represented by imperforate plates connecting the posterior oculars to ocular plates II and IV. They are uniserially arranged.



TEXT-FIG. 7. Camera lucida drawings of plating of the two syntypes of *Calymene relictæ* Wyville Thomson, 1877, NHM 81.11.22.46. A, oral plating of two fragments of the lower surface. B, oral plating of the second specimen showing the amphiplacous arrangement of plates in interambulacrum 3. C, aboral plating, including apical disc. Interambulacral zones are stippled; marginal fasciole is shown in dense stippling. Scale bar represents 5 mm.

Aboral pores are microscopic and single throughout in all ambulacra. They are situated centrally on all but those plates closest to the peristome. Aboral ambulacral plates are large and polygonal, and are similar in size to the interambulacral plates.

The peristome is small and subcircular, being slightly longer than wide. The mouth opening is central and plating on the peristomial membrane comprises small undifferentiated platelets. The periproct is circular and opens high on the posterior face. Its lower half is bounded by interambulacral plates 5.a.7/5.b.8 and its upper half by plates 5.a.8/ 5.b.9.

Aboral interambulacral plates are large and polygonal. On the oral surface the posterior interambulacrum is orthosternous, with a small labral plate followed by a larger sternal plate (5.b.2). The remaining fragments do not preserve the labral plate intact, but it is clearly shown in Wyville Thomson's original description as abutting the first sternal plate. The episternal plates (5.a.2, 5.b.3) are elongate and paired with quite marked angular projections laterally. They are followed by a further pair of elongate post-episternal plates (5.a.3, 5.b.4) that are opposite rather than alternate. Subsequent plating becomes distinctly offset and biserial, especially above the periproct. Plating adjacent to the peristome in interambulacra 1–4 is amphiplacous.

A complete marginal fasciole is present. It passes over the second pair of ambulacral plates in the frontal ambulacrum, and over interambulacral plates 5.a.4, 5.b.5 at the posterior beneath the periproct. The plastron is tuberculate and the wide periplastral areas naked of tubercles, having only a sparse covering of small granules supporting miliary spines. There is a very marked naked band from just above the marginal fasciole to a level where the periproct starts.

Remarks. The types were already fragmented by the time Agassiz (1881) came to redescribe the type material and he therefore concentrated on providing details of spines and pedicellariae only. No details of

the apical disc were given and the fasciole was wrongly stated to pass over the periproct (which would have made it a peripetalous fasciole).

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REFERENCES

- AGASSIZ, A. 1904. The Panamic deep sea Echini. *Memoirs of the Museum of Comparative Zoology, Harvard University*, **31**, i–x, 1–243, pls 1–112.
- AGASSIZ, L. 1839. Description des Echinodermes fossiles de la Suisse, 1. Spatangoides et Clypeasteroides. *Mémoires de la Société Helvétique des Sciences Naturelles*, **3**, 1–110, pls 1–13.
- 1881. Report on the Echinoidea dredged by H.M.S. Challenger during the years 1873–76. *Reports of the Challenger Expedition, Zoology*, **3** (9), 1–321, pls 1–45.
- BATHER, F. A. 1934. *Chelonechinus* N. G., a Neogene urchinid. *Bulletin of the Geological Society of America*, **45**, 799–876.
- CLARK, H. L. 1925. A catalogue of the Recent sea-urchins (Echinoidea) in the collections of the British Museum (Natural History). The Trustees of the British Museum (Natural History), London, 250 pp., 12 pls.
- 1946. The echinoderm fauna of Australia; its composition and its origin. *Publications of the Carnegie Institute, Washington*, **566**, 1–567.
- DAVID, B. 1988. Origins of the deep-sea holasteroid fauna. 331–346. In PAUL, C. R. C. and SMITH, A. B. (eds). *Echinoderm phylogeny and evolutionary biology*. Clarendon Press, Oxford, 373 pp.
- DEVRIES, A. 1958. Note sur le genre *Proholaster* Gauthier. *Bulletin de la Société d'Histoire Naturelle, Afrique Nord*, **49**, 245–253.
- 1960. Contribution à l'étude de quelques groupes d'échinides fossiles d'Algérie. *Publications du Service de la Carte Géologique de l'Algérie. Paléontologie Mémoire*, **3**, 1–278.
- D'ORBIGNY, A. 1853–60. *Paléontologie française. Terrain Crétacé. Tome VI. Echinoides irréguliers*. G. Masson, Paris, 596 pp., pls 801–1006.
- DURHAM, J. W. and MELVILLE, R. V. 1957. A classification of echinoids. *Journal of Paleontology*, **31**, 242–272.
- EBLE, G. J. 1998. Diversification of disasteroids, holasteroids and spatangoids in the Mesozoic. 629–638. In MOOI, R. and TELFORD, M. (eds). *Echinoderms: San Francisco*. A. A. Balkema, Rotterdam, 923 pp.
- 2000. Contrasting evolutionary flexibility in sister groups: disparity and diversity in Mesozoic atelostomate echinoids. *Paleobiology*, **26**, 56–79.
- FOSTER, R. J. and PHILIP, G. M. 1978. Tertiary holasteroid echinoids from Australia and New Zealand. *Palaeontology*, **21**, 791–822.
- GALE, A. S., SMITH, A. B., MONKS, N. E. A., YOUNG, J. A., HOWARD, A., WRAY, D. S. and HUGGETT, J. M. 2000. Marine biodiversity through the late Cenomanian–Early Turonian: palaeoceanographic controls and sequence stratigraphic biases. *Journal of the Geological Society, London*, **157**, 745–757.
- GRAF, G. 1992. Benthic-pelagic coupling: a benthic view. *Oceanography and Marine Biology Annual Reviews*, **30**, 149–190.
- GREENSTEIN, B. J. 1993. Is the fossil record of regular echinoids really so poor? A comparison of living and subfossil assemblages. *Palaios*, **8**, 587–601.
- HAQ, B. U., HARDENBOL, J. and VAIL, P. R. 1988. Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. *SEPM (Society for Sedimentary Geology) Special Publication*, **42**, 71–108.
- JAGT, J. W. J. 2001. Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium. Part 4: Echinoids. *Scripta Geologica*, **121**, 181–375.
- JEFFERY, C. H. 1997. All change at the Cretaceous–Tertiary boundary? Echinoids from the Maastrichtian and Danian of the Mangyshlak Peninsula, Kazakhstan. *Palaeontology*, **40**, 659–712.
- 1999. A reappraisal of the phylogenetic relationships of somaliasterid echinoids. *Palaeontology*, **42**, 1027–1041.
- 2001. Heart urchins at the Cretaceous/Tertiary boundary: a tale of two clades. *Paleobiology*, **27**, 140–158.
- KIER, P. M. 1977. The poor fossil record of regular echinoids. *Paleobiology*, **3**, 168–174.
- KIKUCHI, Y. and NIKAI, A. 1985. The first occurrence of abyssal echinoid *Pourtalesia* from the Middle Miocene Tatsukuroiso Mudstone in Ibaraki Prefecture, northeastern Honshu, Japan. *Annual Report, Geosciences, University of Tsukuba*, **11**, 32–34.

- KROH, A. 2001. Echinoids from the Danian (Lower Paleocene) Bruderndorf Formation of Austria. *Osterreichische Akademie der Wissenschaften Schriftenreihe der Erdwissenschaftlichen Kommissionen*, **14**, 377–435, pls 1–14.
- LAMBERT, J. 1896. Note sur quelques échinides Cretacés de Madagascar. *Bulletin de la Société Géologique de France, Série 3*, **24**, 313–332.
- 1917. Notes sur quelques Holasteridae. *Bulletin de la Société des Sciences Historique et Naturelles de Yonne*, **70**, 101–133.
- 1936. Nouveaux échinides fossiles de Madagascar. *Annales Géologiques du Service des Mines*, **6**, 9–32, pls 1–4.
- and THIERY, P. 1924. *Essai de nomenclature raisonnée des Echinides*. Fasc. 6–7. Librairie Septime Ferrière, Chaumont, 384–512, pls 10, 11, 14.
- LATREILLE, P. A. 1825. *Familles naturelles du Règne animal exposées succinctement et dans un Ordre analytique, avec l'indication de leurs genres*. Paris, 570 pp.
- LOVEN, S. 1883. On *Pourtalesia*, a genus of Echinoidea. *Kongelige Svenska Vetenskaps-Akademiens Handlingar*, **19** (7), 1–95, pls 1–21.
- MOOI, R. and DAVID, B. 1996. Phylogenetic analysis of extreme morphologies: deep-sea holasteroid echinoids. *Journal of Natural History*, **30**, 913–953.
- MORTENSEN, T. 1907. Echinoidea. *The Danish Ingolf-Expedition*, **4** (2), 1–200.
- 1950. *A monograph of the Echinoidea. V.I. Spatangoida 1*. C. A. Reitzel, Copenhagen, 432 pp., 25 pls.
- PHILIP, G. M. 1965. Classification of echinoids. *Journal of Paleontology*, **39**, 45–62.
- POMEL, N. A. 1883. *Classification méthodique et Genera des Echinides vivants et fossiles. Thèses présentées à la Faculté des Sciences de Paris*. Alger, Paris, 132 pp.
- POSLAVSKAYA, N. A. and MOSKVIN, M. M. 1960. Echinoids of the order Spatangoida in Danian and adjacent deposits of Crimea, Caucasus and the Transcaspiian Region. 47–82, pls 1–8. *International Geological Congress, 21st session: Reports of Soviet Geologists Problem 5: The Cretaceous-Tertiary Boundary*. Publishing House of the Academy of Sciences of the USSR, Moscow. [In Russian].
- SAUCEDE, T., DAVID, B. and MOOI, R. in press. The strange apical system of the genus *Pourtalesia* (Holasteroida, Echinoidea). In FERAL, J.-P. (ed.). *Proceedings of the European Conference on Echinoderms, Banyuls-sur-mer, 2001*. A. A. Balkema, Rotterdam.
- SMITH, A. B. 1995. Late Campanian–Maastrichtian echinoids from the United Arab Emirates – Oman Borders Region. *Bulletin of the Natural History Museum, London (Geology Series)*, **51**, 121–240.
- and JEFFERY, C. H. 2000. Maastrichtian and Palaeocene echinoids: a key to world faunas. *Special Papers in Palaeontology*, **63**, 1–406.
- and WRIGHT, C. W. 2003. British Cretaceous echinoids. Part 7, *Atelostomata*, 1. Holasteroida. *Monograph of the Palaeontographical Society*, **156** (619) (for 2002), 440–568, pls 139–182.
- PAUL, C. R. C., GALE, A. S. and DONOVAN, S. K. 1988. Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England. *Bulletin of the British Museum (Natural History), Geology Series*, **42**, 1–245.
- GALLEMI, J., JEFFERY, C. H., ERNST, G. and WARD, P. D. 1999. Late Cretaceous – early Tertiary echinoids from northern Spain: implications for the Cretaceous-Tertiary extinction event. *Bulletin of the Natural History Museum, London (Geology)*, **55**, 81–137.
- STEFANINI, G. 1908. Echinidi del Miocene Medio dell'Emilia. *Palaeontographica Italica*, **14**, 65–119, pls 13–16.
- SWOFFORD, D. L. 2001. PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods) Version 4. Sinauer Associates, Sunderland, Mass.
- VILLIER, L., NÉRAUDEAU, D., CLAVEL, B., NEUMANN, C. and DAVID, B. in press. Phylogeny of Early Cretaceous spatangoids (Echinodermata: Echinoidea) and taxonomic implications. *Palaeontology*, **47**.
- WAGNER, C. D. and DURHAM, J. W. 1966. Holasteroids. U523–543. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part U, Echinodermata 3*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 695 pp.
- WYVILLE THOMSON, C. 1877. The voyage of the Challenger. The Atlantic. A preliminary account of the general results of the exploring voyage of H. M. S. Challenger during the year 1873 and the early part of the year 1876. *Reports of the Challenger Expedition*, **1**, 396 pp.

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