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PHYLOGENY OF THE JURASSIC TO EARLY CRETACEOUS 'DISASTEROID' ECHINOIDS (ECHINOIDEA; ECHINODERMATA) AND THE ORIGINS OF SPATANGOIDS AND HOLASTEROIDS

Colin G. Barras

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PHYLOGENY OF THE JURASSIC TO EARLY CRETACEOUS ‘DISASTEROID’ ECHINOIDS (ECHINOIDEA; ECHINODERMATA) AND THE ORIGINS OF SPATANGOIDS AND HOLASTEROIDS

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SYNOPSIS The ‘disasteroids’ are a morphologically unusual group of echinoids characterised by having a disjunct, or divided, apical disc. The group is now recognised as being basal to the two extant orders of irregular echinoid, the Holasteroida and Spatangoida. There are a number of theories that detail the pathway leading from the ‘disasteroids’ to the holasteroids and spatangoids, but all lack a rigorous phylogenetic hypothesis. Following a re-examination of ‘disasteroid’ material, the number of valid ‘disasteroid’ genera is here reduced to 16, including the new genus *Smithiaster*. New plating diagrams of the majority of these taxa are presented and form the basis of an analysis of ‘disasteroid’ phylogenetic relationships. The new analysis provides a phylogenetic hypothesis linking the ‘disasteroids’ to the basal Atelostomata (*Hyboclypus* and *Aulacopygus*) and also to the Holasteroida and Spatangoida. The phylogeny also confirms that the problematic genera *Desorella*, *Infraclypeus* and *Menopygus*, together with the ‘disasteroid’ *Grasia*, form a monophyletic group the Desorellidae, in the stem group Atelostomata.

KEYWORDS Systematic revision, Evolution, Morphology, Atelostomata, Desorellidae, *Smithiaster*

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INTRODUCTION

Only twice in the long history of the echinoids have taxa with divided (disjunct) apical discs (Fig. 1B) evolved. The most recent of these evolutionary events led to the appearance of the Late Cretaceous to Recent Pourtalesiidae, a highly modified group within the Holasteroida. The origins of this group are reasonably clear and they form a well-defined clade (e.g. Mooi & David 1996; Smith 2004a). An earlier evolutionary event, sometime in the late Early Jurassic to early Middle Jurassic, gave rise to a small, morphologically diverse group of echinoids placed in the plesion (order) 'Disasteroida' Mintz 1968. Although this short-lived group went extinct early in the Cretaceous, the 'disasteroids' are of fundamental importance in the evolutionary history of the irregular echinoids. They form the most primitive order within the Atelostomata *sensu* Smith 1981, the most diverse of extant echinoid lineages. However, the pathways leading from the 'disasteroids' to the two extant orders of Atelostomata (Spatangoida and Holasteroida) remain unclear, largely because of the unusually specialised 'disasteroid' apical disc (e.g. Eble 2000). The most recent attempts to address the evolutionary history of the 'disasteroids' have done so in a purely qualitative manner (e.g. Mintz 1966, 1968; Solovjev 1971; Vadet 1997). The work presented in this paper follows a fresh examination of 'disasteroid' material in a number of key museum collections in France, Switzerland and England, encompassing the vast majority of previously named genera. New plating diagrams of many of these genera are presented and form the basis of a re-evaluation of 'disasteroid' generic taxonomy. Of the previously named genera, only 15 are recognised as valid, while a sixteenth, previously unrecognised, genus is described. The data gathered during this re-evaluation has

been used in a cladistic analysis, from which a new 'disasteroid' phylogeny has been produced. While this new phylogeny confirms some of the groupings previously identified, some revision of known 'disasteroid' taxonomy is necessary. The new phylogeny also provides the first well-resolved phylogenetic hypothesis for the origin of both the Spatangoida and Holasteroida from within the 'disasteroids'.

HISTORY OF CLASSIFICATION

The 'disasteroids' are a morphologically varied group and include taxa with a morphology reminiscent of the Cassiduloida *sensu* Kier (1962), together with taxa that are morphologically very similar to the crown group Atelostomata *sensu* Smith (1981). These features, together with the unusual disc condition, have led to considerable confusion throughout the history of 'disasteroid' classification.

Initially, two independent 'disasteroid' classification schemes developed in parallel, based on the perceived importance, or unimportance, of the disjunct apical disc. Desmoulins (1835) erected the first 'disasteroid' genus, *Collyrites*. While today *Collyrites* contains only species with a disjunct disc, under its original definition the genus also included a number of taxa in which the apical disc was a single unit (an 'adjunct' apical disc: Fig. 1A). Desmoulins attributed no special taxonomic importance to the disjunct disc. It was, rather, the strongly anterior position of the disc by which he defined his genus. *Collyrites* was later incorporated into the family Collyritidae by d'Orbigny (1854) who, following Desmoulins, also regarded the disjunct disc as of only minor importance. The family Collyritidae was originally

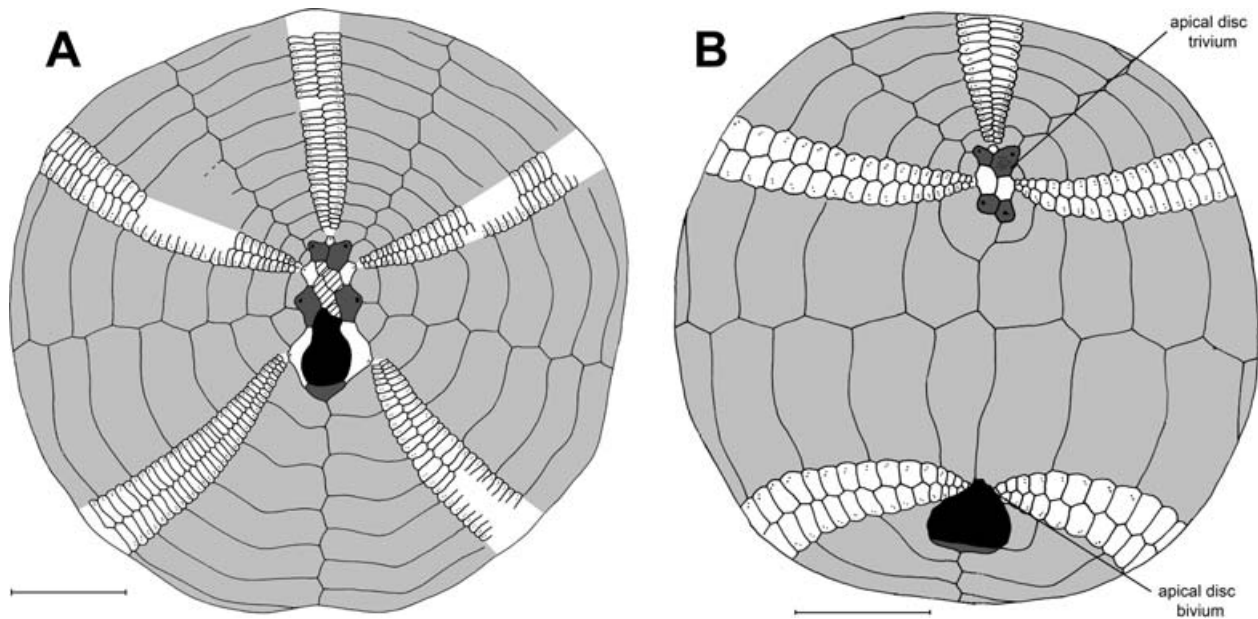


Figure 1 Plating diagrams. **A**, aboral surface of *Aulacopygus caudatus* (NHM E11904). **B**, aboral surface of *Pygomalus ovalis* (NHM E11837). Interambulacral zones are shaded pale grey; genital plates are shaded dark grey; ambulacra and ocular plates are unshaded; complemental plates hatched. Scale bars = 5 mm.

defined on the separation of the anterior and posterior genital plate pairs by ocular plates II and IV. Thus the Collyritidae initially included, together with *Collyrites*, the typical holasteroid genera *Echinocorys*, *Holaster* and *Cardiaster*. According to Desmoulins, the structure of the mouth suggested similarities between *Collyrites* and the 'Spatangues', corresponding roughly with the Atelostomata.

Almost exactly contemporary with the Desmoulins-d'Orbigny taxonomic scheme, another was being formulated in which the disjunct disc was regarded as of primary importance. In the year following Desmoulins' paper, Agassiz (1836) erected the genus *Disaster* to incorporate only those taxa in which the disc was disjunct. Although *Disaster* was, therefore, less inclusive than *Collyrites*, it still necessarily included many, and morphologically varied, taxa. In recognition of this, Agassiz himself subsequently subdivided the genus, placing those forms with an elongate rostral process into the genus *Metaporinus* Agassiz, 1844. The definition of this genus was soon refined to include only those species in which the test was especially tall (Michelin in Agassiz & Desor 1847). Gras (1848) suggested that the disjunct apical disc of *Disaster* and *Metaporinus* was unusual enough to place both in a new family, the 'Dysastéridées'. Unlike the Collyritidae, the 'Dysastéridées' was defined primarily on the disjunct nature of the apical disc.

The strong bilateral symmetry displayed by *Disaster*, in which the test is elongate, the peristome positioned towards the anterior and the periproct towards the posterior (see Pl. 2, figs 2a & 2b), led Agassiz (1836, 1839) to place his genus within the 'Spatangues', roughly equivalent to the Atelostomata. Evidently Agassiz quickly came to regard this classification as unsatisfactory, placing *Disaster* instead within the 'Clypeastroidea', a group containing all irregular echinoids other than the Atelostomata (Agassiz 1840). Unfortunately,

this latter short publication is little more than a taxonomic list and Agassiz gave no explanation for moving *Disaster*. However, Desor (1842) also placed *Disaster* within the 'Clypeastroides' and he cited shared similarities in the structure of the peristome as the reasoning behind this. He did, though, admit to general morphological similarities with the spatangoids. Shortly afterwards, both of these authors revised their opinion, Agassiz for the second time. *Disaster* was placed once more within the spatangoids (Agassiz & Desor 1847). As is apparent, the morphology of *Disaster* did not fit comfortably into any of the taxonomic groups as defined in the mid-Nineteenth Century.

There was a clear and obvious taxonomic overlap between the Collyritidae and 'Dysastéridées' and so, in an important contribution to the taxonomic history of the group, Desor (1857) married the two taxonomic schemes. He regarded the Collyritidae as synonymous with the 'Dysastéridées', but recognised a taxonomic distinction between *Collyrites* and *Disaster*. Thus the family Dysastéridées *sensu* Desor (1857) contained the genera *Disaster*, *Metaporinus*, *Collyrites* and a fourth genus, *Grasia* Michelin, 1854. Following Gras, Desor defined the 'Dysastéridées' primarily on the presence of a disjunct apical disc. This necessitated a revised definition of *Collyrites*. For the first time, this genus included only those forms with a disjunct disc. This revised definition remains in common usage. While *Metaporinus* and *Grasia* were defined largely on their unusual test shape, *Metaporinus* being exceptionally tall, *Grasia* being exceptionally elongate, Desor distinguished *Disaster* and *Collyrites* on differences in the apical disc structure. While the disc is disjunct in both *Collyrites* and *Disaster*, Desor noted that the anterior portion of the disc, the disc trivium (Fig. 1B), is elongate in *Collyrites*, but compact in *Disaster*. This difference in the shape of the

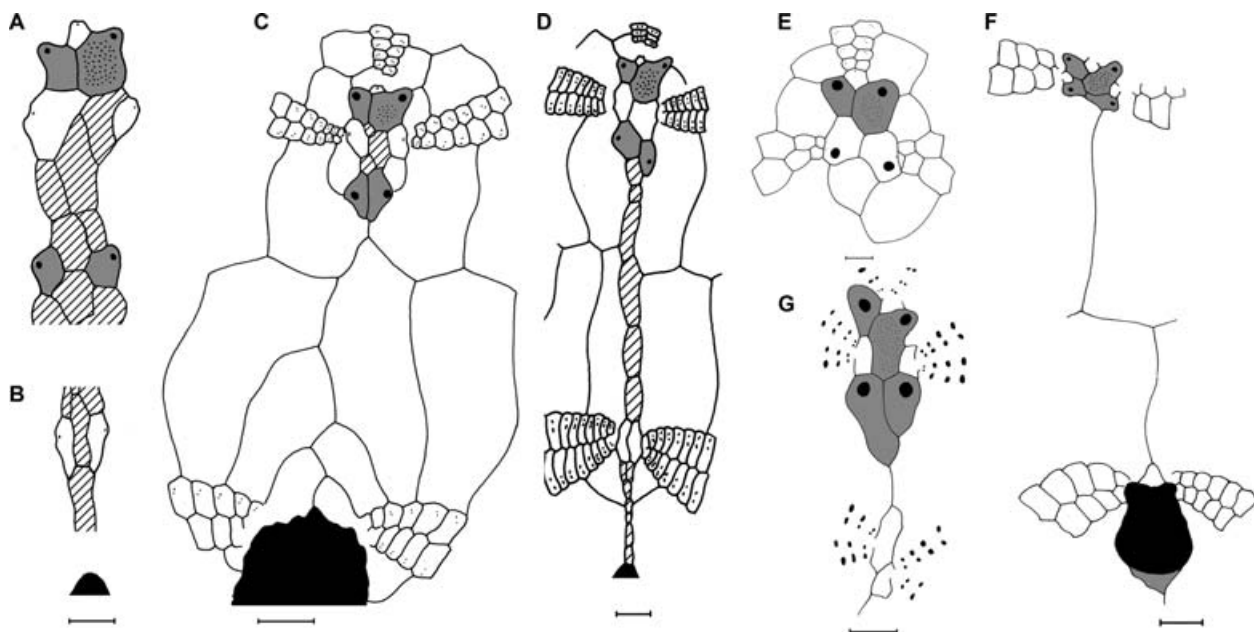


Figure 2 Variation in apical disc structure. **A**, disc trivium of *Cyclolampas voltzii* (MNHN L20.067); **B**, disc bivium of *Cyclolampas voltzii* (MNHN L20.069); **C**, *Pygorhytis ringens* (NHM 26493); **D**, *Collyrites elliptica* (MNHN B49317); **E**, disc trivium of *Tithonia convexa* (MNHN L20.157); **F**, *Disaster granulosus* (NHM E83558); **G**, *Acrolusia gauthieri* (MNHN Jo1258). Genital plates are shaded grey; ocular plates are unshaded; complemental and catenal plates are hatched; periproct is shown in black. Scale bars = 1 mm.

apical disc trivium would remain of fundamental importance in many subsequent 'disasteroid' taxonomic schemes.

Shortly after Desor's work, Wright (1859) resurrected the family Collyritidae. Wright also limited his definition to include only those forms with a disjunct apical disc, revising d'Orbigny's family accordingly. Thus Collyritidae *sensu* Wright (1859) was essentially identical to 'Dysastéridées' *sensu* Desor (1857). Indeed, Wright included the same four genera, *Disaster*, *Collyrites*, *Metaporinus* and *Grasia*, within the Collyritidae. Elsewhere in the same publication, however, Wright made it clear that he saw no taxonomic distinction between *Collyrites* and *Disaster*, regarding the latter as synonymous with the former (Wright 1859: 307).

By 1860, the number of recognised 'disasteroid' genera stood at five, following the identification of *Orbigniana* Ébray, 1860. While *Orbigniana* has a clearly disjunct apical disc, Ébray noted close morphological similarities with *Hyboclypus*. For instance, both possess a prominent periproct groove stretching from the posterior of the disc to the ambitus (see Pl. 1, figs 4a & 6a). This was the first clear evidence for the point of origin of the 'disasteroids', as both *Hyboclypus*, and the morphologically very similar *Galeropygus*, are often placed within the Cassiduloida (e.g. Kier 1962).

With Pomel's (1883) revision of echinoid taxonomy, the number of 'disasteroid' taxa rose to 14. Pomel's newly recognised genera, *Tithonia*, *Perioxus*, *Cardiopelta*, *Cardiolampas*, *Pygorhytis*, *Pygomalus*, *Cyclolampas*, *Corthya* and *Spatoclypus* were placed, together with *Metaporinus*, *Disaster*, *Collyrites* and *Grasia*, within the Echinoneidae, on the basis of their simple ambulacra. The fourteenth genus, *Dialyster*, was placed in the 'Progonastérides' together with taxa typical of the crown group Atelostomata, seemingly because of the presence of sub-petaloid ambulacra.

Gauthier (1896) added two further 'disasteroid' genera, *Collyropsis* and *Proholaster*. While the former is syn-

onymous with *Cardiopelta* (see below), the latter genus is noteworthy for its morphological similarity to the holasteroids. Indeed, the disjunct apical disc aside, Gauthier found the morphology of *Proholaster* consistent in every way with that of the holasteroids. Just as the discovery of *Orbigniana* had explained some of the similarities between the 'disasteroids' and the cassiduloids, so the discovery of *Proholaster* offered an explanation for the shared similarities with the crown group atelostomates.

The Twentieth Century history of 'disasteroid' taxonomy began with a re-appraisal of 'disasteroid' internal classification. Following Pomel (1883), Lambert (1909) suggested similarities between the 'disasteroids' and the Echinoneidae. Lambert recognised that the 'disasteroid' genera appeared to fall into one of the two categories originally used by Desor (1857) to distinguish *Disaster* and *Collyrites*. Choosing to place all of the taxa within the family Collyritidae, Lambert consigned those taxa with an elongate apical disc to the tribe Pygorhytinae, including *Pygorhytis*, *Collyrites*, *Cardiopelta* and *Grasia*. Those with a compact disc he placed in the tribe Disasterinae, including the genera *Disaster* and *Metaporinus*. Lambert & Thiéry (1924) revised this taxonomic classification, raising the Pygorhytinae and Disasterinae to subfamilies. The subfamily Pygorhytidae (*sic* Lambert & Thiéry, 1924) now incorporated 'Orbigniana' (misspelled by Lambert & Thiéry and virtually all subsequent authors), *Pygorhytis*, *Pygomalus*, *Collyrites*, *Cyclolampas*, *Cardiopelta* (including the subgenera *Collyropsis* and *Cardiolampas*), *Grasia* and *Proholaster*. The subfamily Disasteridae (*sic* Lambert & Thiéry, 1924) included *Disaster*, *Tithonia*, *Corthya*, *Metaporinus* and a recently described genus, *Acrolusia* Lambert, 1920. The discovery of *Acrolusia* was as important as that of *Proholaster*, in that *Acrolusia* possesses the ethmophract apical disc of an early spatangoid, but the disjunct disc of a 'disasteroid' (Fig. 2G). Its discovery

suggested a close relationship between the spatangoids and 'disasteroids'. Despite this evidence, Lambert & Thiéry (1924) placed all 'disasteroid' genera within Lambert's sub-order Procassiduloida rather than within the Spatangoida, because of the presence of phyllodes in some early forms and the absence of a well-developed plastron or labrum. Beurlen (1934) and, later, Mortensen (1950) disagreed with this view. As Mortensen pointed out, derivation from the Galeropygidae *sensu* Lambert, 1911 (= *Galeropygus*, *Aulacopygus* and *Hyboclypus*) is not sufficient to regard the 'disasteroids' as cassiduloids.

Prior to 1934, there was no attempt to produce a 'disasteroid' phylogeny. Beurlen, publishing in that year, was the first to place the 'disasteroid' genera in phylogenetic context (Fig. 3A). Beurlen's phylogeny was based on a detailed revision of 'disasteroid' taxonomy, incorporating some characters relating to the oral surface as well as those relating to the apical disc. All taxa were placed in the family Collyritidae. The Pygorhytidae *sensu* Lambert & Thiéry, 1924 was divided into the Pygorhytinae *sensu stricto* and the Collyritinae. Beurlen defined the former by the sunken nature of the peristome and oral ambulacra, with a rudimentary floscelle. In the Collyritinae, the sister group to the Pygorhytinae, the peristome is not sunken and there is no floscelle. The Disasterinae *sensu* Beurlen, 1934 was defined primarily on the compact apical disc structure. Beurlen noted that the compact apical disc structure differed in detail to the disc structure in the Pygorhytinae and Collyritinae. While in the latter two, ocular plates II and IV are large and separate the anterior and posterior genital plate pairs, in the Disasterinae, ocular plates II and IV are much reduced in size and the anterior and posterior genital plates juxtapose (cf. Figs 2D & 2F). Beurlen's phylogeny showed the Disasterinae evolving from *Galeropygus* and ultimately giving rise to the Spatangoida. The roots of the Pygorhytinae and Collyritinae are unknown, but the Collyritinae are suggested to be ancestral to the Holasteroida.

Mortensen (1950) followed Beurlen's preferred taxonomy, although he chose to place all taxa within the family Disasteridae, regarding Collyritidae as a junior synonym. He also added the genera *Acrolusia*, *Dialyaster* and *Oustechinus* Lambert, 1931 to the Disasterinae.

Beurlen's (1934) suggestion that the 'disasteroids' be placed in the lineage leading to spatangoids and holasteroids became widely accepted (e.g. Mortensen 1950; Devriès 1960), although the details differed (e.g. Devriès 1960; cf. Figs 3A & 3B). However, some regarded Beurlen's theory as problematic. The apical disc is less specialised in both the spatangoids and holasteroids than in the 'disasteroids', suggesting evolution away from specialisation (e.g. Mortensen 1950: 12). Specifically, Durham & Melville (1957) refused to accept that the Disasterinae *sensu* Beurlen, 1934 could give rise to the 'amphisternous spatangoids' (= Spatangoida). Durham & Melville argued that this implied an evolutionary transition from an adjunct to a disjunct apical disc to produce the 'disasteroids' and a later transition from a disjunct to an adjunct disc to produce the spatangoids from the 'disasteroids'. Such an apparent evolutionary reversal was thought highly unlikely. Durham & Melville instead thought the origins of the early spatangoids (toxasterids) unclear, but tentatively traced them to the Galeropygidae, a hypothesis that implied a stratigraphical gap of some 50 Myr (Villier *et al.* 2004; Fig. 3C). Curiously, Durham & Melville accepted Collyritinae *sensu* Beurlen, 1934 as basal to the holaster-

oids, although a similar 'reversal of evolution' is required to produce the adjunct holasteroid disc from the disjunct collyritid condition (e.g. Mintz 1968). They placed almost all known 'disasteroid' taxa in the family Collyritidae, placing the family Disasteridae (containing just *Disaster*) between the Collyritidae and Holasteroida.

It had previously been noted that the distance between the disc trivium and bivium was much reduced in many of the stratigraphically youngest 'disasteroids' (e.g. Mortensen 1950: 12). In all such taxa, the periproct was clearly removed from the bivium and remained in a near ambital position. Beurlen (1934: 161) suggested the logical continuation of this process would be the eventual reunification of the disc. The influential work of Jesionek Szymanska (1959) provided a solution for the apparently paradoxical position of the disjunct 'disasteroids' as transitional between the adjunct galeropygids (*Galeropygus*) and hyboclypids (*Hyboclypus* and *Aulacopygus*) and the adjunct holasteroids and spatangoids. Jesionek Szymanska recognised that the periproct still lay within the apical disc in many early irregular echinoids, a condition termed endocyclic. The galeropygids and hyboclypids always have an adjunct endocyclic disc (e.g. Fig. 4A). While the stratigraphically earliest 'disasteroids' have a disjunct disc, the periproct is still surrounded by apical disc plates and so is demonstrably endocyclic (Jesionek Szymanska 1963: text-pl. 7, fig. 2; Fig. 4E). In fact, the migration of the periproct out of the apical disc (the exocyclic condition: Fig. 4F) occurs separately and subsequently, to the origin of the disjunct disc. The exocyclic disc is most clear in those 'disasteroids' in which the bivium and periproct are separated. As previously noted by Beurlen (1934), such taxa are often characterised by a reduced degree of disjunction. The hypothesised continuation of this process produces a re-unified, adjunct apical disc, but one that is not directly comparable with the adjunct galeropygid disc. For, while the adjunct galeropygid disc is endocyclic, the adjunct spatangoid and holasteroid disc is exocyclic (Mintz 1966, 1968).

While the details were still unresolved, it was clear by the mid- to late-1960s that the 'disasteroids' evolved from somewhere within the galeropygids and hyboclypids and that both the spatangoids and holasteroids evolved from the 'disasteroids'. It was, therefore, unfortunate that in the 1966 *Treatise on Invertebrate Paleontology* (edited by Moore) the 'disasteroid' taxonomy follows that of Durham & Melville (1957; cf. Fig. 3C). Wagner & Durham (1966a) placed the 'disasteroids' within the order Holasteroida, but refused to accept a link with the spatangoids (although elsewhere in the *Treatise*, Fischer (1966) does suggest a link between the collyritids and spatangoids, via *Toxaster laffittei* from the Berriasian of North Africa). Wagner & Durham's (1966a) 'disasteroid' taxonomy is somewhat simplistic in comparison to that of Beurlen. They recognised just two subdivisions, the families Disasteridae and Collyritidae, distinguishing them only on the structure of the apical disc trivium (cf. Figs 2D & 2F). The Collyritidae, corresponding roughly to Pygorhytinae *sensu* Lambert & Thiéry, 1924, included *Collyrites*, *Cardiopelta*, *Cyclolampas*, *Grasia*, *Orbigniana*, *Proholaster*, *Pygomalus* and *Pygorhytis*. The Disasteridae roughly corresponds to Disasterinae *sensu* Lambert & Thiéry, 1924. This family included *Disaster*, *Acrolusia*, *Cardiolampas*, *Collyropsis*, *Corthya*, *Dialyaster*, *Metaporinus*, *Oustechinus* and *Tithonia*.

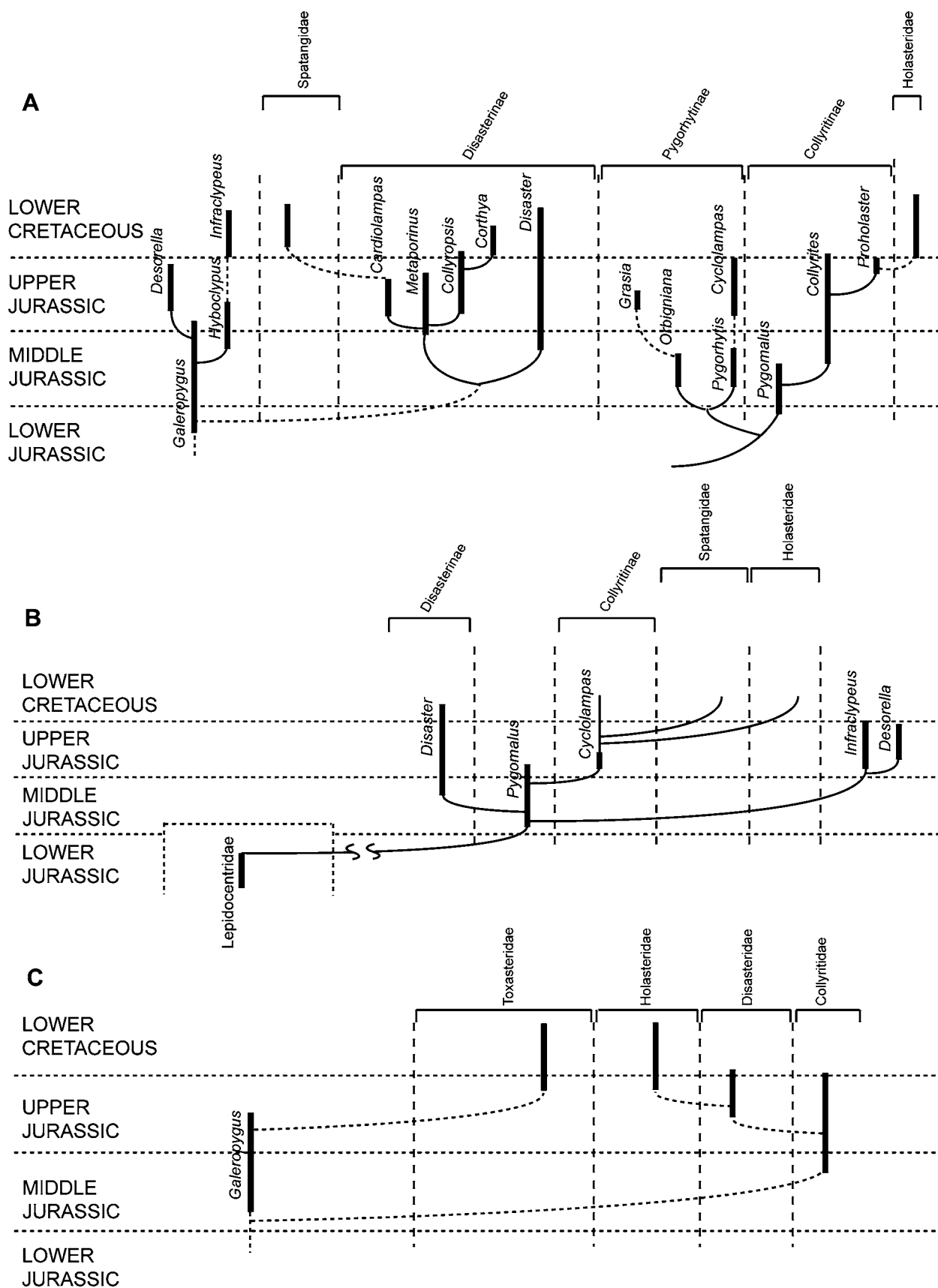


Figure 3 For legend see facing page.

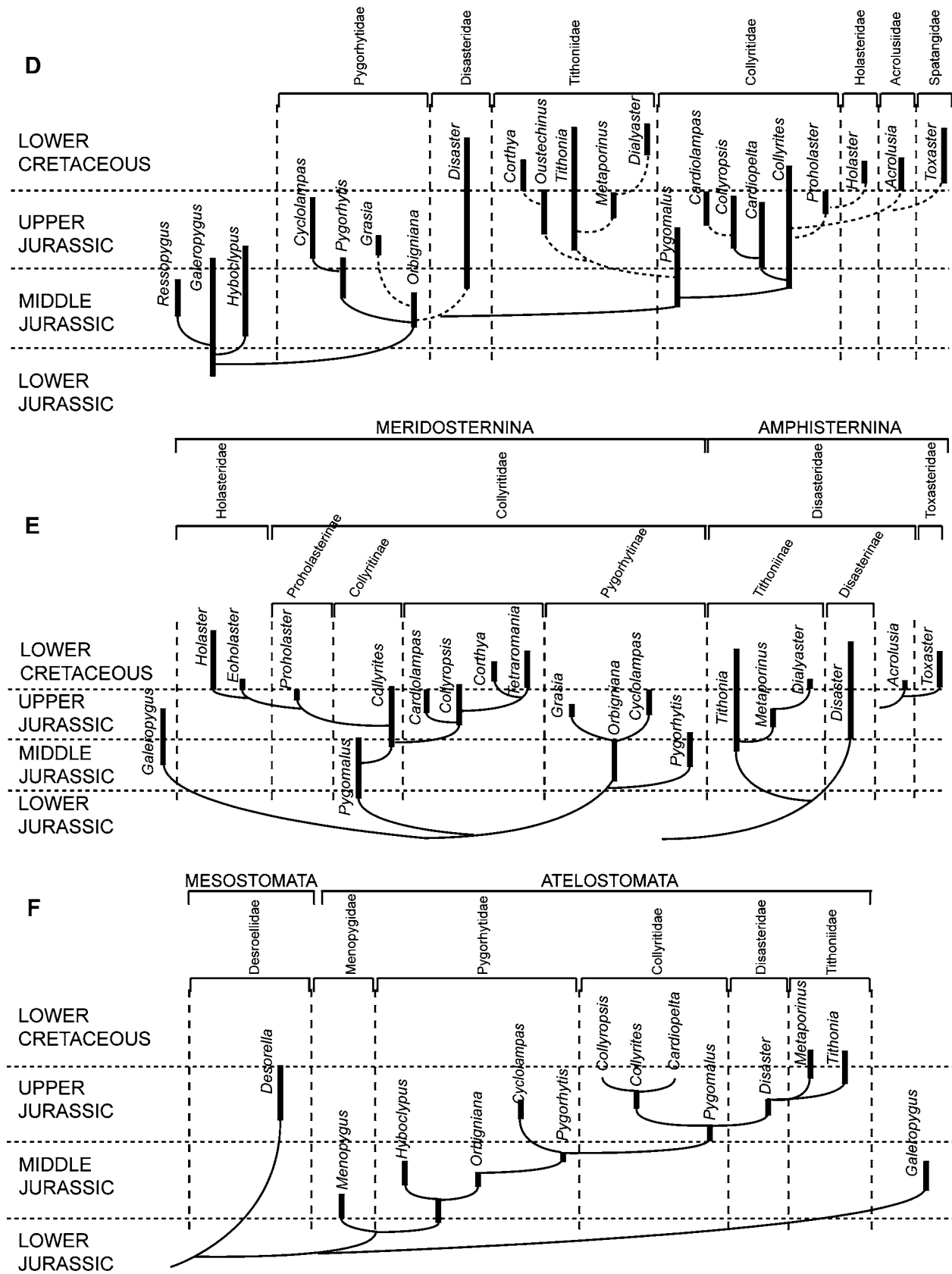


Figure 3 Previously suggested 'disasteroid' phylogenies. **A**, Beurlen (1934); **B**, Devriès (1960); **C**, Durham & Melville (1957); **D**, Mintz (1968); **E**, Solovjev (1971); **F**, Vadet (1997).

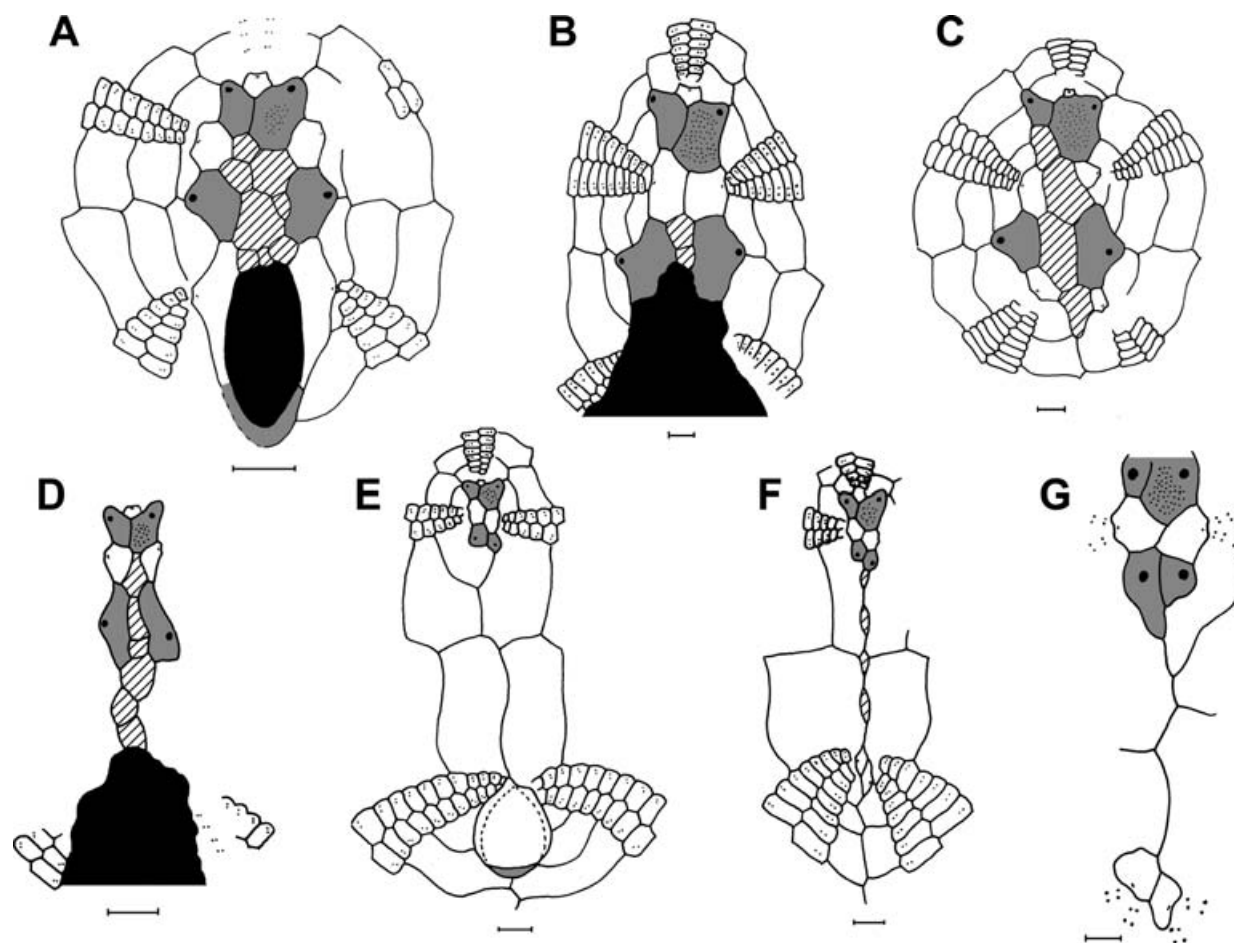


Figure 4 Variation in apical disc structure. **A**, *Aulacopygus caudatus* (NHM E1505); **B**, *Hyboclypus gibberulus* (NHM E1571); **C**, *Desorella elata* (SM J864); **D**, *Orbigniana ebrayi* (MNHN L20.071); **E**, *Pygomalus ovalis* (NHM E11837) posterior oculars reconstructed with reference to Jesionek Szymanska 1963, text-pl. 7, fig. 2; **F**, *Cardiopelta trigonalis* (MNHN L20.061); **G**, *Proholaster auberti* (MNHN Jo1430). Genital plates are shaded grey; ocular plates are unshaded; complemental and catenal plates are hatched; periproct is shown in black. Scale bars = 1 mm.

Following a detailed study of the group, Mintz (1968) produced a new taxonomy that he felt better reflected the evolutionary history of the 'disasteroids' (Fig. 3D). He suggested that the compact disc trivium, so long used as an important defining character, had at least four independent origins. As such, Mintz rejected the family Disasteridae *sensu* Wagner & Durham (1966a). His new taxonomic scheme included many elements from Beurlen's (1934) taxonomy, in conjunction with observations first made by Jesionek Szymanska (1963). Mintz divided the 'disasteroids' into five families: Pygorhytidae, Collyritidae, Disasteridae, Tithoniidae and Acrolusiidae. The Pygorhytidae *sensu* Mintz, 1968, defined on the presence of a disc trivium in which ocular plates II and IV are juxtaposed (a condition Mintz termed 'intercalary'; e.g. Fig. 2D) and on the depression of the ambulacra around the peristome, are basal to the 'disasteroids'. They give rise to the Collyritidae and Disasteridae. In neither the Collyritidae nor the Disasteridae are the ambulacra depressed around the peristome. The Collyritidae *sensu* Mintz, 1968 retains the ancestral 'intercalary' state, while the disc of the Disasteridae *sensu* Mintz, 1968 is defined on the reduced size of ocular plates II and IV and the large size of the madreporite (Mintz's 'non-intercalary'

disc; Fig. 2F). The Collyritidae give rise independently to the Tithoniidae Mintz, 1968 and to the Holasteroidea and Spatangoida, arriving at the latter through the Acrolusiidae Mintz, 1968. Jesionek Szymanska (1963) had first noted that the trivium in many 'disasteroid' taxa contained only five, rather than the usual seven, plates (cf. Figs 2D & 2E). Mintz suggested that this reflected the fusing of genital 1 with ocular II and of genital 4 with ocular IV, an unusual character that Mintz used to define the Tithoniidae. The Acrolusiidae were defined on the presence of an ethmophract, or 'semi-intercalary' disc (Fig. 2G). Both the Holasteroidea and Spatangoida were presumably defined on the re-unification of the disc trivium and bivium, an independent process in the two groups.

Solovjev (1971) produced a phylogeny of the 'disasteroids' in which, uniquely, the plastron was used to define the higher taxonomy (Fig. 3E). Recognising that the holasteroid plastron is often meridosternous (e.g. see Fig. 12C), while the spatangoid plastron is amphisternous (see Fig. 12B), Solovjev divided the Spatangoida (equating to the Atelostomata *sensu* Smith, 1981) into the suborders Meridosternina and Amphisternina. Solovjev suggested that the Meridosternina and the 'galeropygids' shared a common, unknown ancestor.

But, following Durham & Melville (1957), Solovjev was uncertain of the ultimate origin of the Amphisternina, and suggested only a tentative link between the Amphisternina and the Toxasteridae (early spatangoids).

The most recently published phylogenetic interpretation of the 'disasteroids' is that of Vadet (1997). Vadet recognised five 'disasteroid' families: Menopygidae, Pygorhytidae, Collyritidae, Disasteridae and Tithoniidae (Fig. 3F), although he did not formally define these families. There is an initial divide between the Menopygidae and the Pygorhytidae. The Pygorhytidae then give rise to the Collyritidae that, in turn, give rise to the Disasteridae. The Disasteridae are the sister group to the Tithoniidae. Vadet did not discuss the relationship of the 'disasteroids' to the spatangoids and holasteroids.

Smith (2004b) tentatively adopted the taxonomy of Mintz (1968), while acknowledging that Mintz's taxonomy lacked a rigorous phylogenetic hypothesis.

MATERIAL AND METHODS

Museum abbreviations

All of the material studied is housed in major museum collections, abbreviated as follows: **NHM**, Natural History Museum, London; **SM**, Sedgwick Museum of Earth Sciences, University of Cambridge; **MNHN**, Muséum National d'Histoire de la Terre, collection du Domaine des Sciences de la Terre, Paris; **EM**, Collections de l'École Nationale Supérieure des Mines de Paris, Université Claude Bernard Lyon 1; **MHNN**, Musée d'Histoire Naturelle de Neuchâtel; **NMBA**, Naturhistorisches Museum Basel; **NMBE**, Naturhistorisches Museum Bern; **MHNG**, Muséum d'Histoire Naturelle de la Ville de Genève.

Included taxa

More than 70 species of 'disasteroid' have been named, spread among 21 genera. Following a re-appraisal of 'disasteroid' taxonomy, the number of valid genera has been reduced to 16, all of which were coded in the analysis. A thorough revision of 'disasteroid'-specific taxonomy was beyond the scope of this study and so it was necessary to assume monophyly of the 16 'disasteroid' genera. This is arguably a valid assumption, because the specific taxonomy of the 'disasteroids' is highly subjective. While the genera are defined on clear differences in plate architecture (see 'systematic descriptions' below), species are generally defined on arbitrary differences in test shape, characters suggested to carry little phylogenetic meaning (e.g. David 1988; Mooi & David 1996). The type species of each valid 'disasteroid' genus was coded. Where only poorly preserved specimens of type species were available, additional information was added from other species. Table 1 lists the taxa included in the analysis and the sources of the data.

The strong morphological similarities between the hyboclypids (*Hyboclypus* and *Aulacopygus*) and the 'disasteroids', have long suggested that the 'disasteroids' are derived hyboclypids. Both genera of hyboclypid were coded into the analysis. These two genera, together with *Galeropygus*, form the outgroup to the analysis.

To examine the relationship between the 'disasteroids' and the holasteroids and spatangoids, primitive members of the latter two were included. *Eoholaster* and *Pseudholaster* represented the basal holasteroids. *Eoholaster* has an elongate, exocyclic disc, in which ocular V is attached to genital 1, but in which ocular I still does not share a contact with a genital plate (Solovjev 1989: fig. 1c). The 'semi-disjunct' condition shown by *Eoholaster* appears to represent an intermediate stage in the move towards re-unification of the apical disc. The position of *Eoholaster* as a very early holasteroid is generally accepted (e.g. Smith 2004a). *Pseudholaster* is one step further into the basal holasteroids. The disc is fully adjunct and of the elongate holasteroid type, with oculars II and IV separating the posterior and anterior genital plate pair (Smith & Wright 2003: fig. 184a).

Devriès (1960: 22) suggested that *Toxaster laffittei*, from the Berriasian should be placed somewhere at the point of divergence of holasteroids, disasterids *sensu stricto* and toxasterids (early spatangoids). Fischer (1966) thought that the species linked the collyritids and spatangoids. The species was used to root a recent cladistic analysis of the spatangoids (Villier *et al.* 2004), although following Clavel (*in* Jablonski & Bottjer 1990) these authors regarded the species as synonymous with the holasteroid *Holaster cordatus*. The spatangoids were represented in the current analysis by two species of *Toxaster sensu stricto*; the Hauterivian *Toxaster africanus*, and the type species of *Toxaster*, *Toxaster retusus*. Also included was the *Toxaster*-like *Heteraster inflatus*.

The Middle Jurassic echinoid fauna contains a small number of problematic taxa of uncertain origins, sometimes placed within the family Menopygidae Lambert, 1911 (e.g. Mintz 1966; Rose & Olver 1988). Of these, it has previously been suggested that *Desorella* shares affinities with the 'disasteroids' (e.g. Mortensen 1948). Indeed Devriès (1960: 176) suggested that both *Desorella* and a second menopygid, *Infraclypeus*, evolved from *Pygomalus* (Fig. 3B). In contrast, Mintz (1966) suggested that the menopygid morphology was so unusual that these taxa had origins independent from all other irregular echinoids. Similarly, Vadet (1997) could find no place for *Desorella* in the Atelostomata, erecting a new superorder Mesostomata to incorporate the Desorellidae (*Desorella* and *Pachyclypus*; Fig. 3F). *Desorella*, *Infraclypeus* and *Menopygus* were also included in the current analysis.

Character definitions

Characters based on differences in test structure are generally less variable, and carry more phylogenetic meaning, than do characters such as general test size or shape (David 1988; Mooi & David 1996) and were preferentially chosen in the analysis.

Apical disc

1. *The disc is: disjunct between the posterior oculars and posterior genitals (0); semi disjunct (1); adjunct (2).* Desmoulins (1835) and d'Orbigny (1854) aside, all echinoid workers have united the 'disasteroid' taxa on the presence of a disjunct apical disc. In detail, the posterior genital plate pair and the posterior ocular plate pair never lie in direct contact (e.g. Fig. 2C). These plates do share a contact in the three outgroup taxa (e.g. Fig. 4A) and in *Desorella*, *Infraclypeus* and the holasteroids and spatangoids. The disc may also be disjunct in *Desorella*, a taxon

Table 1 Analysed taxa.

Coded genera	Species examined (** denotes type species)	Material examined (** denotes type specimen)
'Disasteroids'		
<i>Acrolusia</i>	* <i>Acrolusia gauthieri</i>	* MNHN J01258
<i>Cardiolampas</i>	* <i>Cardiolampas friburgensis</i>	* NMBE 8/7,9,10 MNHN J01431
<i>Cardiopelta</i>	* <i>Cardiopelta trigonalis</i>	* NMBA M9866 MNHN L20.061 NMBE J12 A5123 5000528 MNHN L20.133, L20.134 NHM E12583-12613
<i>Collyrites</i>	<i>Cardiopelta carinata</i> <i>Collyrites bicordata</i> * <i>Collyrites elliptica</i>	* MNHN B49317 MNHN R62445
<i>Corthya</i>	* <i>Corthya hemisphaerica</i> <i>Corthya ambigua</i>	Solovjev 1971, figs 32, 33 MNHN L 20.067, L20.069
<i>Cyclolampas</i>	* <i>Cyclolampas voltzii</i>	Solovjev: 1971: fig. 18 NHM E83558 and E83563 MNHN L20.107, L20.110, L20.119 Jesionek Szymanska 1963: text-pl. 12 Mintz 1966: text-fig. 38-40 Mintz 1968: text-fig. 4
<i>Disaster</i>	* <i>Disaster granulosus</i>	* MHNN V66 Smith 2004b
<i>Grasia</i>	* <i>Grasia elongata</i>	* MHNN V31 MHNG 59-27234 Jesionek Szymanska 1963: text-pl. 13
<i>Metaporinus</i>	* <i>Metaporinus michelini</i>	MHNG 58-27141 MNHN L20.071
<i>Orbigniana</i>	<i>Metaporinus convexus</i> * <i>Orbigniana ebrayi</i>	* MNHN J01430 NHM E11832-41, E42968-71
<i>Proholaster</i>	* <i>Proholaster auberti</i>	* MHNN 16, 20 NHM E11849-61
<i>Pygomalus</i>	* <i>Pygomalus ovalis</i>	MNHN A24446
<i>Pygorhytis</i>	* <i>Pygorhytis ringens</i>	* MNHN J01258 Solovjev 1971: fig. 30 MHNG 60-27238-44 MNHN L20.157: J00924 Solovjev 1971: figs 38-39
<i>Smithiaster</i>	* <i>Smithiaster loryi</i>	
<i>Tetraromania</i>	* <i>Tetraromania ovulum</i>	
<i>Tithonia</i>	* <i>Tithonia convexa</i> <i>Tithonia praeconvexa</i>	
Holasteroids		
<i>Eoholaster</i>	* <i>Eoholaster poslavskae</i>	Solovjev 1989: fig. 1
<i>Pseudholaster</i>	* <i>Pseudholaster bicarinatus</i> <i>Pseudholaster benstedii</i>	Smith & Wright 2003: text-fig. 184. NHM E1550, E1551
Spatangoids		
<i>Toxaster</i>	<i>Toxaster africanus</i>	Devriès 1960: pl. 1
Galeropygids		
<i>Galeropygus</i>	* <i>Galeropygus sublaevis</i>	* SM J34963 and J34964 NHM E11892, E11894-9, E76044, E77494
Hyboclypids		
<i>Aulacopygus</i>	* <i>Aulacopygus caudatus</i>	* NHM E1579 E12028-33
<i>Hyboclypus</i>	* <i>Hyboclypus gibberulus</i>	* MHNN 75, 76 NHM E12034, E78974, E79072, EE2515, E3434, E1987a, E1987b
Problematica		
<i>Desorella</i>	* <i>Desorella elata</i>	SM J864, Solovjev & Markov 2004: fig. 1
<i>Infraclypeus</i>	* <i>Infraclypeus thalabensis</i>	NHM E3652, Rose & Olver 1988: fig. 3f
<i>Menopygus</i>	* <i>Menopygus nodoti</i>	* EM40070, MHNG 58-27141, Rose & Olver 1988: fig. 3b

not traditionally included within the 'disasteroids'. However, the anterior portion of the *Desorella* disjunct disc contains only genital plates 2 and 3 and ocular plates II

and III. The posterior portion of the disc contains oculars I, IV and V and genitals 1 and 4 (Fig. 4C). This is clearly distinct from the typical 'disasteroid' condition, in

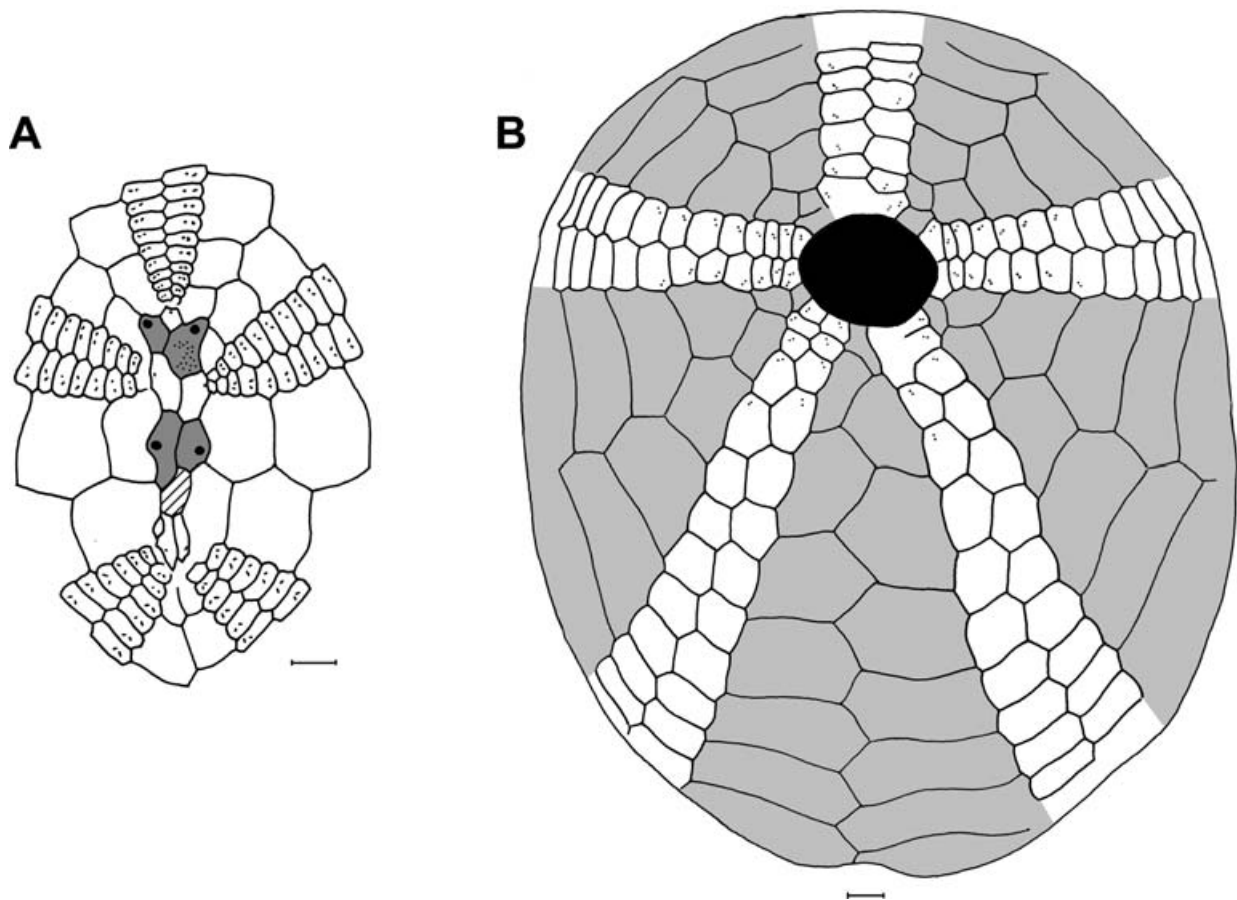


Figure 5 Test architecture of *Smithiaster loryi* (MNHN Az4446). **A**, apical disc. Genital plates are shaded grey; ocular plates are unshaded; complementary plate is hatched; **B**, oral surface. Interambulacra are shaded grey; ambulacra are unshaded; peristome is shown in black. Scale bars = 1 mm.

which disjunction is always between the posterior paired genitals and posterior paired oculars. Given that this character is variable within *Desorella* (many examples show a clearly adjunct disc, e.g. Solovjev & Markov 2004: fig. 1), only the typical 'disasteroid' disjunction is coded in the analysis.

The disjunct disc is coded as a three-state character, to draw the distinction between the semi-disjunct disc of *Eoholaster*, in which only one of the posterior ocular plates is separated from genital plates 1 and 4 (Solovjev 1989: fig. 1c) and the truly disjunct disc of the 'disasteroid' taxa. Although the semi-disjunct disc is known in one taxon only and so is phylogenetically uninformative, it is coded separately because of the potential importance of *Eoholaster* to the accepted hypothesis of evolution within the atelostomates. To derive the adjunct holasteroids and spatangoids from the disjunct disasteroids implies the existence of intermediate semi-disjunct forms such as *Eoholaster*. Because the semi-disjunct *Eoholaster* disc is clearly an intermediate condition between the disjunct 'disasteroid' disc and the adjunct holasteroid disc, this character was treated as ordered.

2. *The posterior ocular plate pair and posterior genital plate pair are: not joined by complementary plates (0); joined by at least five large complementary plates of comparable size to genitals 1–4 (1); joined by only one large complementary*

plate of comparable size to genitals 1–4 (2). While the disc of *Orbigniana* is clearly disjunct, this condition has been achieved simply through the addition of complementary plates within the disc (Fig. 4D), such complementary plates being characteristic of the three outgroup taxa (e.g. Fig. 4A). This is quite distinct from the disjunct disc condition shown by the majority of other 'disasteroid' taxa, in which the bivium is completely isolated from the trivium, and the lateral interambulacra meet along the test midline (e.g. Fig. 2C). *Cyclolampas*, *Collyrites* and *Cardiopelta* show a similar condition. *Smithiaster* displays a third condition. The disc is almost adjunct and just one complementary plate separates the trivium and bivium (see Fig. 5A). Although not phylogenetically informative, the condition shown by *Smithiaster* is coded separately because the reduced degree of disjunction in this taxon suggests that it is closely related to the adjunct holasteroids. The single complementary plate aside, the disc of *Smithiaster* is very similar to that of the holasteroid *Pseudholaster*.

3. *The periproct is contiguous with bivium (the apical disc is endocyclic): no (0); yes (1)*. The periproct lies far to the posterior of the apical disc in all extant irregular echinoids (e.g. Smith & Wright 1999). But following the work of Jesionek Szymanska (1959), it was realised that the periproct is completely surrounded by apical disc plates in a large number of early irregular echinoids (the endocyclic

condition). All three outgroup taxa possess an endocyclic disc (e.g. Fig. 4A), and this is clearly the primitive condition. Although the 'disasteroid' disc is disjunct, in many of these taxa the periproct is still closely associated with the bivium and is indeed surrounded by the bivium plates (Jesionek Szymanska 1963: text-pl. 7, fig. 2) and, therefore, endocyclic. The periproct only moves outside the ring of disc plates (becoming exocyclic) subsequent to the origin of a disjunct disc (e.g. Fig. 4F). Unfortunately, the bivium plates surrounding the periproct in the endocyclic 'disasteroids' are fragile and often missing (e.g. Fig. 4D). In those taxa missing the posterior ocular plates, it is difficult to determine whether or not the disc was truly endocyclic. However, all demonstrably endocyclic 'disasteroid' taxa are characterised by the close association of the bivium and periproct. Those with a clearly exocyclic disc have the periproct far removed from the bivium (cf. Figs 4E & 4F). Therefore, the relative position of the periproct to the bivium is used as a proxy for the presence of exocyclism.

4. *Large complemental plates are incorporated into the apical disc trivium: no (0); yes (1).* There is considerable variation in the composition of the disc trivium in the taxa included in the analysis (cf. Figs 2 & 4). The disc contains a large number of complemental plates in each of the three outgroup taxa (e.g. Fig. 4A) and also in many ingroup taxa (Figs 2A & 2C). Because large complemental plates are incorporated into the disc of *Desorella* (Fig. 4C), *Menopygus* and *Infraclypeus* (Rose & Olver 1988: figs 3b & 3f), these taxa are clearly very similar to the outgroup taxa. While the 'disasteroid' disc is disjunct, it often contains a large number of complemental plates clearly similar to those of the outgroup (e.g. Figs 2A & 2C). The disc trivium of stratigraphically higher 'disasteroids' and the disc of the holasteroids and spatangoids never contains complemental plates, a derived condition (e.g. Figs 2E–G).
5. *There are: no complemental plates separating ocular plates II and IV or genital plates 1 and 4 (0); complemental plates separating ocular plates II and IV (1); complemental plates separating genital plates 1 and 4 (2); complemental plates separating ocular plates II and IV and genital plates 1 and 4 (3).* A consequence of the presence of complemental plates in the anterior portion of the disc is that ocular plates II and IV and genital plates 1 and 4, are often precluded from direct contact. This condition is seen in the outgroup taxa *Galeropygus* and *Aulacopygus* and also in *Desorella* (Fig. 4C), *Infraclypeus* (Rose & Olver 1988: fig. 3f), *Orbigniana* (Fig. 4D) and *Cyclolampas* (Fig. 2A). The later 'disasteroids' possess no complemental plates within the disc trivium and both oculars II and IV and genitals 1 and 4 lie in direct contact. In *Hyboclypeus* the complemental plates only preclude the direct contact of genital plates 1 and 4; oculars II and IV share a contact (Fig. 4B). There are also fewer complemental plates in the apical disc of *Pygorhynchus* and these preclude the direct contact of oculars II and IV but not genitals 1 and 4. Because these two latter character states are each known in only one taxon, neither is phylogenetically informative. However, both are potentially important in order to test the hypothesis that there is an evolutionary trend towards a reduced number of complemental plates within the atelostomate disc.

Therefore, both of these character states are coded in the analysis.

6. *The apical disc is: intercalary (0); ethmophract (1).* The majority of 'disasteroids' have an intercalary disc, in which oculars II and IV preclude direct contact of the anterior and posterior genital plate pairs (e.g. Fig. 2D). In only four of the analysed taxa (*Disaster*, *Acrolusia*, *Toxaster* and *Heteraster*) is the disc modified. Mintz (1968) drew a distinction between the 'non-intercalary' disc of *Disaster* and the 'semi-intercalary' disc of *Acrolusia*. A 'non-intercalary' disc is one in which the anterior and posterior genital plate pairs share a direct contact and preclude the direct contact of oculars II and IV (Fig. 2F). A 'semi-intercalary' disc is one in which only the madreporite extends to the posterior, precluding the direct contact of oculars II and IV. Genitals 3 and 4 do not share a direct contact (Fig. 2G). Mintz saw similarities between the 'semi-intercalary' disc of *Acrolusia* and the disc of the early spatangoids (toxasterids). However, the 'non-intercalary' disc of *Disaster* is also clearly very similar to the disc of many spatangoids (e.g. the hemiassterids). As such, it is clear that the differences between the 'non-intercalary' and 'semi-intercalary' discs are superficial. Indeed, the disc of *Disaster*, *Acrolusia*, *Toxaster* and *Heteraster* is better described as 'ethmophract', a disc in which the madreporite separates oculars II and IV.
 7. *The apical disc trivium contains only four plates to the posterior of ocular III, rather than six (tithoniid condition): no (0); yes (1).* In a small number of taxa, four disc plates rather than the usual six lie in the disc trivium to the posterior of ocular plate III. Each of these four plates carries a large gonopore. This condition was first noted by Jesionek Szymanska (1963) and is characteristic of *Tithonia*, *Metaporinus*, *Tetraromania* and *Corthya* (e.g. Fig. 2E). A superficially similar disc trivium is seen in the extant pourtalesiid echinoids. Information from studies of the water vascular system and ontogenetic development has been used to demonstrate that, in the case of the pourtalesiids, this architecture has been achieved by the migration of the posterior gonopores to ocular plates II and IV (Saucède *et al.* 2004). The imperforate posterior genital plates lie removed from the anterior portion of the disc (Saucède *et al.* 2004: fig. 2c). The water vascular system is unknown in the 'disasteroid' taxa that possess a reduced number of disc plates and specimens are too few in number for detailed ontogenetic series to be constructed. Therefore the exact nature of the disc construction in these taxa is unknown.
- A clue to the origin of this 'disasteroid' disc condition is shown in a specimen of *Tithonia praeconvexa* figured by Jesionek Szymanska (1963: text-pl. 13, fig. 5). The disc of this specimen contains five disc plates to the posterior of ocular III, one of the posterior gonopores opening onto a small plate that is clearly the remnant of genital plate 1. The other gonopore opens onto a plate in the ocular IV position. It appears that the reduction in the number of disc plates in these taxa follows the reduction in size of the posterior genitals. Subsequently, the gonopores presumably migrated forward to occupy positions on oculars II and IV and the posterior genitals continue to reduce in size and disappear.
8. *The apical disc is elongate (apical disc width, measured between the apices of ambulacra II and IV, is under 60%*

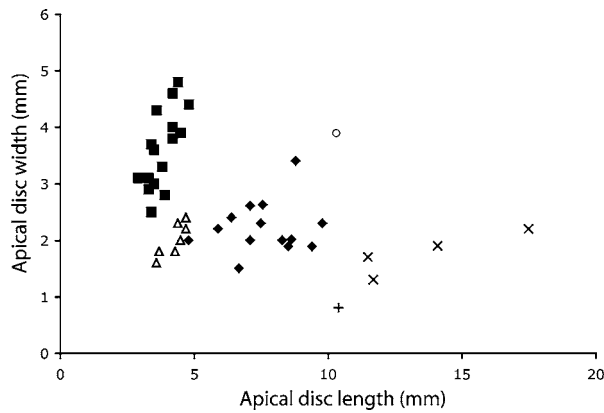


Figure 6 Biometric comparison of apical disc elongation in the Jurassic irregular echinoids. ■, *Galeropygus*; △, *Aulacopygus*; ◆, *Hyboclypus*; ○, *Desorella*; x, *Pygorhytis*; +, *Disaster*.

of disc length, measured between the apex of ambulacrum III and the midpoint of a line joining the apices of ambulacra I and V): no (0); yes (1). *Galeropygus* and all of the cassiduloids *sensu* Kier (1962) possess a compact apical disc, in which the area of the disc enclosed by the five ambulacra is roughly equidimensional. Among the early atelostomates, this area is much more elongate. This is most striking in taxa with a disjunct disc. However, even in *Hyboclypus* and *Aulacopygus*, the area enclosed by the five ambulacra has a maximum width under 60% of its maximum length (Fig. 6). The apical disc is also elongate in the holasteroids, but reverts to a more compact form in the spatangoids. Of the taxa included in the analysis, only *Galeropygus* and *Toxaster* possess a compact disc. Durham & Melville (1957) suggested that the origin of the toxasterids lay in the galeropygids. The inclusion of this character in the analysis will assess whether the apparent similarities between *Galeropygus* and *Toxaster* are homologous or arose independently.

Ambulacra

9. The ambulacra are: subpetaloid with oblique pore pairs (0); subpetaloid with circumflexed pore pairs (1); petaloid to an equal extent in both columns of each ambulacrum (2); petaloid to a greater extent in the posterior column of each ambulacrum (3); apetaloid with microscopic pore pairs (4). There is considerable variation in the nature of the petals in the included taxa. All members of the outgroup and a number of ingroup taxa share a clearly primitive condition in which there is no pore pair differentiation aborally. Each aboral ambulacral plate carries a modestly sized pore pair, both pores in the pair being simple and ovoid. The two pores lie obliquely on the plate (Fig. 7A). A number of the ingroup taxa have subtly modified pore pairs. Although still small and of similar size, the two pores in each pair are slightly elongate and circumflexed rather than oblique (Fig. 7B). More obvious are the taxa with clear petals. In the four taxa possessing clear petals (*Acrolusia*, *Toxaster*, *Heteraster* and *Pseudholaster*), both pores within the pore pair are elongate, the outer pore being slightly more elongate than the inner pore (Fig. 7C). The pore pairs are circumflexed or linear in all three taxa. *Heteraster* and

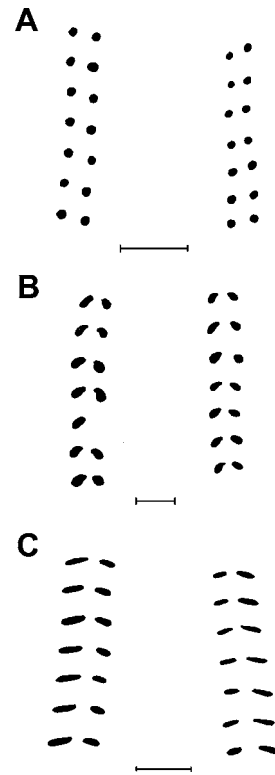


Figure 7 Variation in pore pair structure within the petals. **A**, simple oval pore pairs of *Hyboclypus* (NHM E43789); **B**, circumflex pore pairs of *Collyrites* (NHM E3287); **C**, elongate pore pairs of *Pseudholaster* (NHM EE6660). Scale bars = 1 mm.

Pseudholaster differ in that, in each of the paired ambulacra, the pore pairs of the posterior column are roughly twice as elongate as the pore pairs of the anterior column. No such differentiation is seen in *Acrolusia* or *Toxaster*. Finally, a small number of taxa are characterised by microscopic pore pairs of uncertain structure. These are, again, coded separately.

10. The anterior ambulacrum is clearly differentiated: no (0); yes (1). In *Pseudholaster* and a small number of 'disasteroid' taxa, the pore pairs of the anterior ambulacrum are clearly smaller and simple in comparison to those of the paired ambulacra (e.g. Smith & Wright 2003: pl. 146, fig. 6). The primitive condition, shown by the outgroup taxa and the majority of included taxa, is for no obvious differentiation of pore pairs. The pore pairs are microscopic in *Corthya*, *Tetraromania* and *Tithonia*. The pore pairs may be undifferentiated in these taxa, but it was not possible to demonstrate this.
11. The anterior ambulacrum: is flush with the test surface (0); lies in a distinct groove orally (1); lies in a distinct groove along its entire length (2). The anterior ambulacrum is sunken in a very distinct ambulacral groove along its entire length in *Pseudholaster*. A similarly prominent groove is seen in *Proholaster*, *Cardiolampas* and *Heteraster* (see Pl. 2, figs 5a & 7a). While no other taxon possesses such a prominent groove along the entire length of the ambulacrum, the anterior ambulacrum is often distinctly sunken orally and, consequently, the peristome is often angled towards the anterior of the test rather than facing downwards. This is coded as a separate

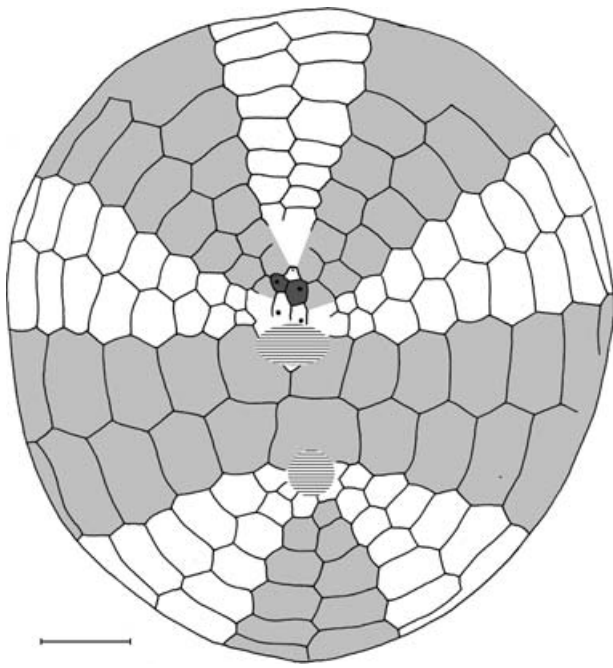


Figure 8 Aboral surface of *Corthya hemispherica* (MNHN R62445). Interambulacral plates are shaded pale grey; ambulacral plates are unshaded; horizontal lines represent areas where plating is obscured. Scale bar = 5 mm.

character state. The primitive condition, in which ambulacrum III is flush with the test surface along its entire length, is shown by all three outgroup taxa together with the majority of ingroup taxa.

12. *Ambulacral width is: under 50% of interambulacral width (0); over 80% of interambulacral width (1).* The ambulacra in the basal atelostomates are generally much narrower than the interambulacra. This is true of all three outgroup taxa and of the majority of ingroup taxa (e.g.

Fig. 1). In all, the ambital width of the ambulacra is under 50% of the ambital width of the interambulacra. A derived condition is seen in *Corthya* and *Tetraromania*, taxa in which the ambulacra have an ambital width comparable to interambulacral ambital width (cf. Figs 1 & 8). Similarly broad ambulacra are seen in *Pseudholaster*.

13. *Oral ambulacral plate height beyond the phyllodes is: under 90% of plate width ('short') (0); over 90% of plate width ('tall') (1).* Beyond the phyllodes on the oral surface, the ambulacral plates are much wider than they are tall in *Galeropygus* (plate height is under 90% of plate width) while in the 'disasteroid' taxa, they are generally taller than they are wide (plate height is at least 90% of plate width; Fig. 9). The transition to taller ambulacral plates begins in the hyboclypids, falling in the outgroup to the analysis. In these taxa, plate height is roughly equivalent to plate width (Figs 10B & 10C). Plate height is over 90% of plate width in all 'disasteroid' taxa with the exception of *Cyclolampas*, an unusual 'disasteroid' with the well-developed phyllodes of *Galeropygus* (cf. Figs 10A & 10D). Ambulacral plates beyond the phyllodes are wider than they are tall in *Cyclolampas*, as in *Galeropygus*.
14. *One basicoronal plate in each ambulacrum tall (plate height over 90% of plate width), carrying two rather than one pore pair: no (0); yes (1).* Characteristic of the microstomates is that five of the ten ambulacral plates lying in direct contact with the peristome carry two rather than one pore pair. These early-formed plates are evidently commonly resorbed later in ontogeny, as the majority of basal microstomates possess only one pore pair on each plate lying in direct contact with the peristome (Fig. 10). However, in a small number of the analysed taxa, these basicoronal plates are still present. These plates are enlarged and one in each ambulacrum has a height at least 90% of plate width and carries a second pore pair (e.g. *Disaster*: Fig. 11B).

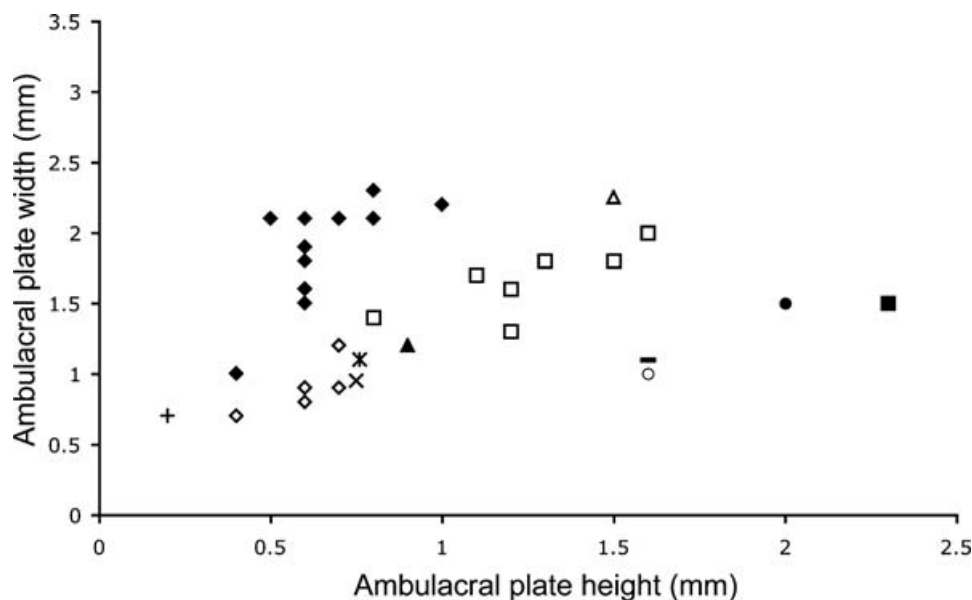


Figure 9 Biometric comparison of oral ambulacral plate size beyond the phyllodes. ◆, *Galeropygus*; ▲, *Orbigniana*; ◇, *Aulacopygus*; □, *Hyboclypus*; △, *Desorella*; ×, *Menopygus*; ×, *Pygorhytis*; -, *Pygomalus*; +, *Cyclolampas*; ■, *Collyrites*; ●, *Smithiaster*; ○, *Disaster*.

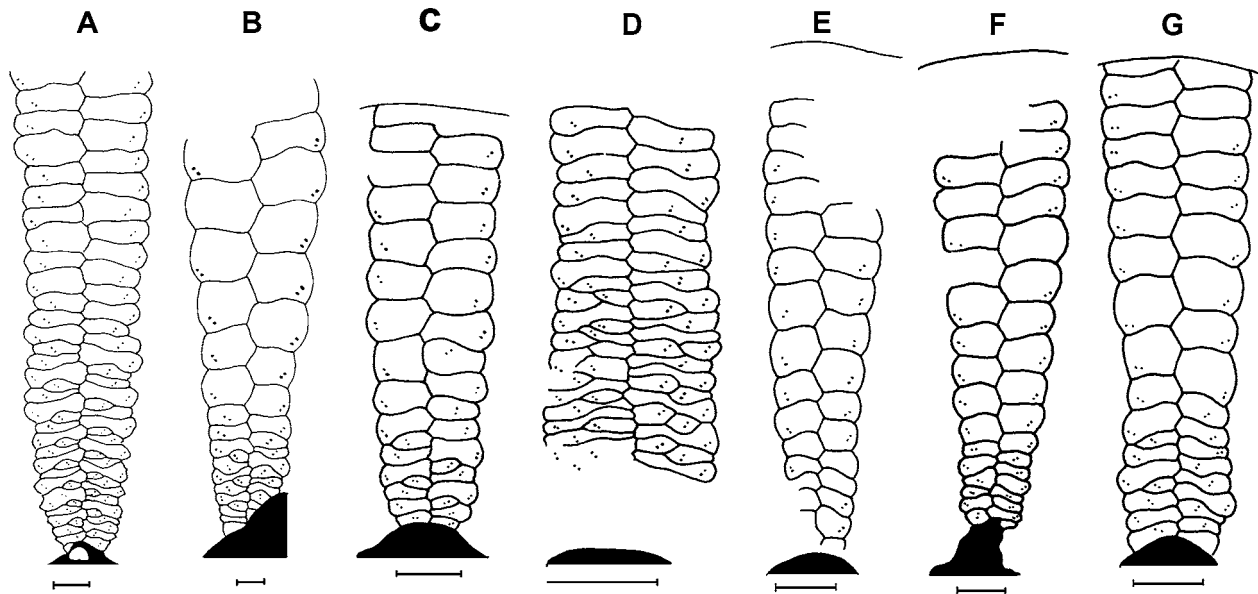


Figure 10 Variation in phyllode structure. **A**, *Galeropygus sublaevis* (NHM E11894); **B**, *Hyboclypus gibberulus* (NHM E75834); **C**, *Aulacopygus caudatus* (NHM E1579); **D**, *Cyclolampas voltzii* (MNHN L20.069); **E**, *Menopygus nodoti* (MHNG 58-27141); **F**, *Orbigniana ebrayi* (MNHN L20.071); **G**, *Pygorhytis ringens* (NHM E42478). Peristome is shown in black. Scale bars = 1 mm.

Phyllodes

15. Approaching the peristome: the pore pairs are not crowded into triads within the phyllodes (0); pore pairs are crowded into triads within the phyllodes that account for under 50% of oral ambulacral length (1); pore pairs are crowded into triads within the phyllodes that account for over 50% of oral ambulacral length (2). Phyllodes in which the pore pairs are crowded into triads approaching

the peristome are characteristic of all basal cassiduloids and are prominent in *Galeropygus* (Fig. 10A). Phyllodes with pore pair triads are also present in the hyboclypids (Figs 10B & 10C) and in a small number of 'disasteroid' taxa (e.g. Fig. 10D). The phyllodes of these taxa are distinguished from those of *Galeropygus* by their length. The phyllodes of *Galeropygus* extend almost to the ambitus and always over at least half the oral ambulacral

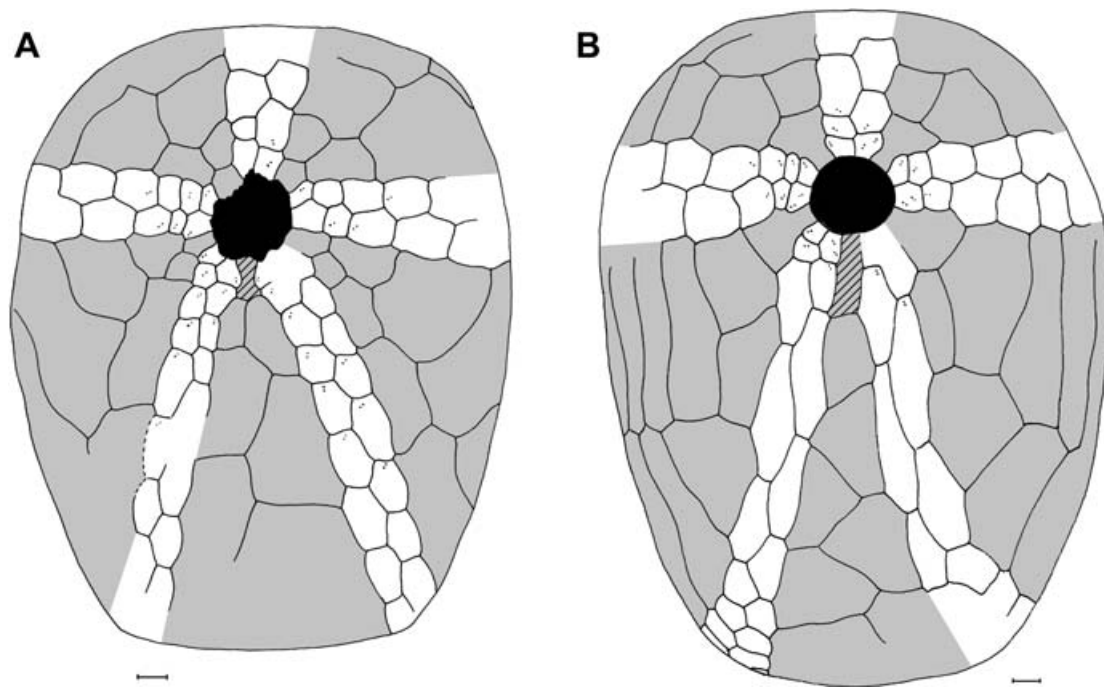


Figure 11 Variation in plastron structure within *Disaster*. **A**, protosternous plastron (NHM E83558); **B**, meridosternous plastron (MNHN L20.110). Interambulacra are shaded grey; ambulacra are unshaded; basicoronal plate of plastron is hatched; peristome is shown in black. Scale bars = 1 mm.

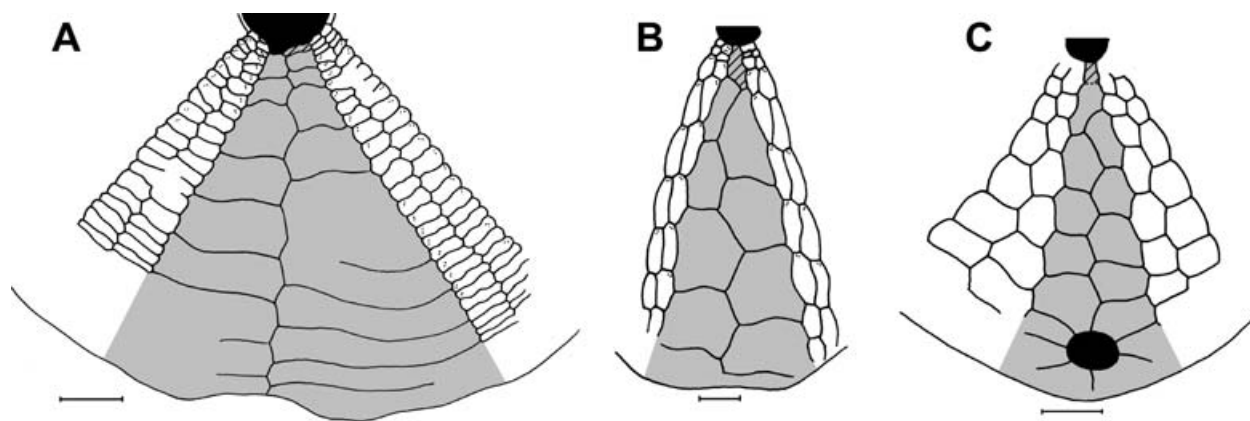


Figure 12 Variation in plastron structure. **A**, protosternous plastron of *Desorella elata* (SM J864); **B**, amphisternous plastron of *Tithonia convexa* (MHNG 60–27238); **C**, meridosternous plastron of *Corthya hemispherica* (MNHN R62445). Interambulacra are shaded grey; ambulacra are unshaded; basicoronal plate of plastron is hatched; peristome and periproct are shown in black. Scale bars = 5 mm.

length. The phyllodes of all other included taxa, even the prominent phyllodes of *Cyclolampas* (Fig. 10D), are always much shorter, accounting for under 50% of oral ambulacral length. The majority of ‘disasteroid’ taxa possess very weak crowding of pore pairs within the phyllodes (e.g. Fig. 10G).

Periproct

16. A deep periproctal groove is developed between the test apex and the ambitus: no (0); yes (1). In the three outgroup taxa, the periproct lies supra-ambitally in a deep periproctal groove (e.g. see Pl. 1, figs 1a & 4a). This primitive feature is lost within the ‘disasteroids’ as the periproct moves to the ambitus. However, the periproctal groove is maintained in *Orbigniana* and *Menopygus* (see Pl. 1, figs 3a & 6a) and to a lesser degree in *Grasia* (Smith 2004b).

Peristome

17. A vertically sided peristomial well is: absent (0); present (1). *Galeropygus* and all cassiduloids possess a prominent, vertically sided peristomial well, the peristome being clearly sunken below the test surface. In later cassiduloids, a ring of small differentiated tubercles is associated with the peristomial well, although there is little tubercle differentiation seen around the peristome in *Galeropygus*. Just as phyllodes are developed in the hybocypids and a small number of ‘disasteroids’, so a vertically sided peristomial well is present in many of these taxa. The majority of ‘disasteroids’ show a derived condition, in which the peristome is flush with the test surface. This is modified again in those taxa possessing an anterior ambulacral groove, the peristome generally being slightly sunken to the anterior and, therefore, facing slightly towards the anterior in these taxa. However, a deep, vertically sided peristomial well never re-appears among the atelostomates.
18. The peristome is ‘oblique’, with the axis of obliquity running from ambulacrum 1 to interambulacrum 3: no (0); yes (1). Although derived spatangoids and holasteroids both possess a modified peristome (e.g. Smith & Wright

2003: pl. 147, fig. 1), the peristome is roughly circular in most taxa examined here (e.g. see Pl. 2, figs 1b & 6b). However, in *Desorella*, *Infraclypeus*, *Menopygus* and *Grasia*, the peristome is slightly oblique (see Pl. 1, figs 2b & 3b). That is, the axis of peristome elongation lies slightly oblique to the plane of antero-posterior symmetry. This unusual character is not seen in the other included taxa.

Plastron

19. Plastron plating is: protosternous (0); meridosternous (1); amphisternous (2). The plastron becomes highly modified in the crown group atelostomates. Its detailed structure is one of the clearest means of differentiating the holasteroids and spatangoids, the holasteroids often possessing a meridosternous plastron but never an amphisternous one (e.g. Smith 2003), while the spatangoids possess an amphisternous plastron but only rarely a meridosternous one (the aberrant Somasteridae possess a meridosternous plastron, e.g. Smith & Stockley 2003). The plastron is poorly differentiated within the outgroup to the analysis and in the majority of ‘disasteroids’. All tend to show the primitive protosternous plastron of the outgroup (e.g. Fig. 12A). However, a small number of ‘disasteroids’ possess an amphisternous plastron (Fig. 12B) and a second small group possess meridosternous plating (Figs 11B, 12C). *Disaster* uniquely shows a great deal of plastron variation, with examples of protosternous (Fig. 11A), amphisternous (Solovjev 1971: fig. 35a) and meridosternous plating (Fig. 11B).

Phylogenetic analysis

A data matrix was constructed within the computer programme MacClade 4.0 (Maddison & Maddison 2000), containing 26 taxa coded for the 19 characters described above (Table 2). This was then imported into the computer programme PAUP* 4.0b10 (Swofford 2002). Other than for character number 1, all characters were treated as unordered. All characters were weighted equally. A branch and bound search

Table 2 Data matrix.

	5	10	15	19
<i>Acrolusia</i>	00000	10120	?0???	??0?
<i>Cardiolampas</i>	0?000	001?0	20???	000?
<i>Cardiopelta</i>	02000	00110	101??	0000
<i>Collyrites</i>	02000	00110	00110	0000
<i>Corthya</i>	00000	0114?	01110	0001
<i>Cyclolampas</i>	02012	00100	00??1	0000
<i>Disaster</i>	00100	10100	00110	000?
<i>Grasia</i>	0?0??	? ? 1 ? ?	00??0	111?
<i>Metaporinus</i>	00000	01111	10???	000?
<i>Orbigniana</i>	02112	00100	00101	1100
<i>Proholaster</i>	00000	00111	201??	000?
<i>Pygomalus</i>	00100	00100	001?1	0000
<i>Pygorhytis</i>	00111	00100	00101	0100
<i>Smithiaster</i>	01000	00110	00110	0000
<i>Tetraromania</i>	00000	0114?	111??	0001
<i>Tithonia</i>	00100	0114?	101??	0002
<i>Eoholaster</i>	10000	001??	?01??	0?00
<i>Pseudholaster</i>	20000	00131	21110	0000
<i>Toxaster</i>	20000	10020	00110	0002
<i>Heteraster</i>	20000	10030	20110	0002
<i>Galeropygus</i>	20112	00000	00002	1100
<i>Aulacopygus</i>	20112	00100	00101	1100
<i>Hyboclypus</i>	20110	00100	00101	1100
<i>Desorella</i>	20012	00100	00000	0110
<i>Infraclypeus</i>	20012	00100	00100	011?
<i>Menopygus</i>	201??	? ? 1 0 0	00000	1110

was executed. The robustness of the resultant phylogeny was assessed by running 100,000 'fast' step-wise addition bootstrap replicates and also through calculating the Bremer support for each internal node. It was clear that a number of the characters had low levels of consistency across the phylogeny. Consequently the characters were re-weighted according to their Rescaled Consistency Index, obtained in the original analysis, and the analysis was re-run.

RESULTS

The initial analysis returned 192 equally parsimonious trees, of tree length 51 with a Consistency Index (CI) of 0.55 and a Retention Index (RI) of 0.77. The strict consensus is relatively well resolved, although the relationships among the crown group atelostomates are not clear (Fig. 13A). There is a clade containing *Menopygus*, *Grasia*, *Desorella* and *Infraclypeus* (the Desorellidae) at the base of the phylogeny. The other stem group atelostomates form a paraphyletic grade to the crown group. Within the crown group, there is a clade containing *Metaporinus*, *Tithonia*, *Tetraromania* and *Corthya* (the Tithoniidae). There is also a clade containing *Toxaster* and *Heteraster*.

Bootstrap values are predictably low given the extremely low character:taxon ratio. Bremer support values are low across the phylogeny. This reflects the almost chaotic relationships among a number of both the stem group and crown group atelostomates. Nevertheless, the important clades on the phylogeny, the desorellids, the tithoniids and the crown group atelostomates, are all founded on characters with a high CI value across the phylogeny. The phylogeny

provides a credible explanation of character evolution among the 'disasteroids'.

Re-weighting the characters and re-running the analysis returns just six equally parsimonious trees. The strict consensus of this gives better resolution among the crown group atelostomates (Fig. 13B). The crown group atelostomates are now clearly divisible into stem group holasteroids and stem group spatangoids. The latter group is the smaller, containing just *Disaster*, *Acrolusia*, *Toxaster* and *Heteraster*. Among the stem group holasteroids, there is an initial polytomy containing *Cardiopelta*, *Collyrites*, *Smithiaster* and a clade containing all other stem group holasteroids. Of these, *Cardiolampas* is the most basal and the other taxa form a polytomy containing the tithoniids, *Proholaster* and a group containing *Pseudholaster* and *Eoholaster*.

DISCUSSION

There are comparatively few previously published phylogenetic interpretations of the 'disasteroids' (e.g. Beurlen 1934; Devriès 1960; Mintz 1968; Solovjev 1971; Vadet 1997; cf. Fig. 3). The new phylogeny produced above includes elements of all of these, together with some new groupings.

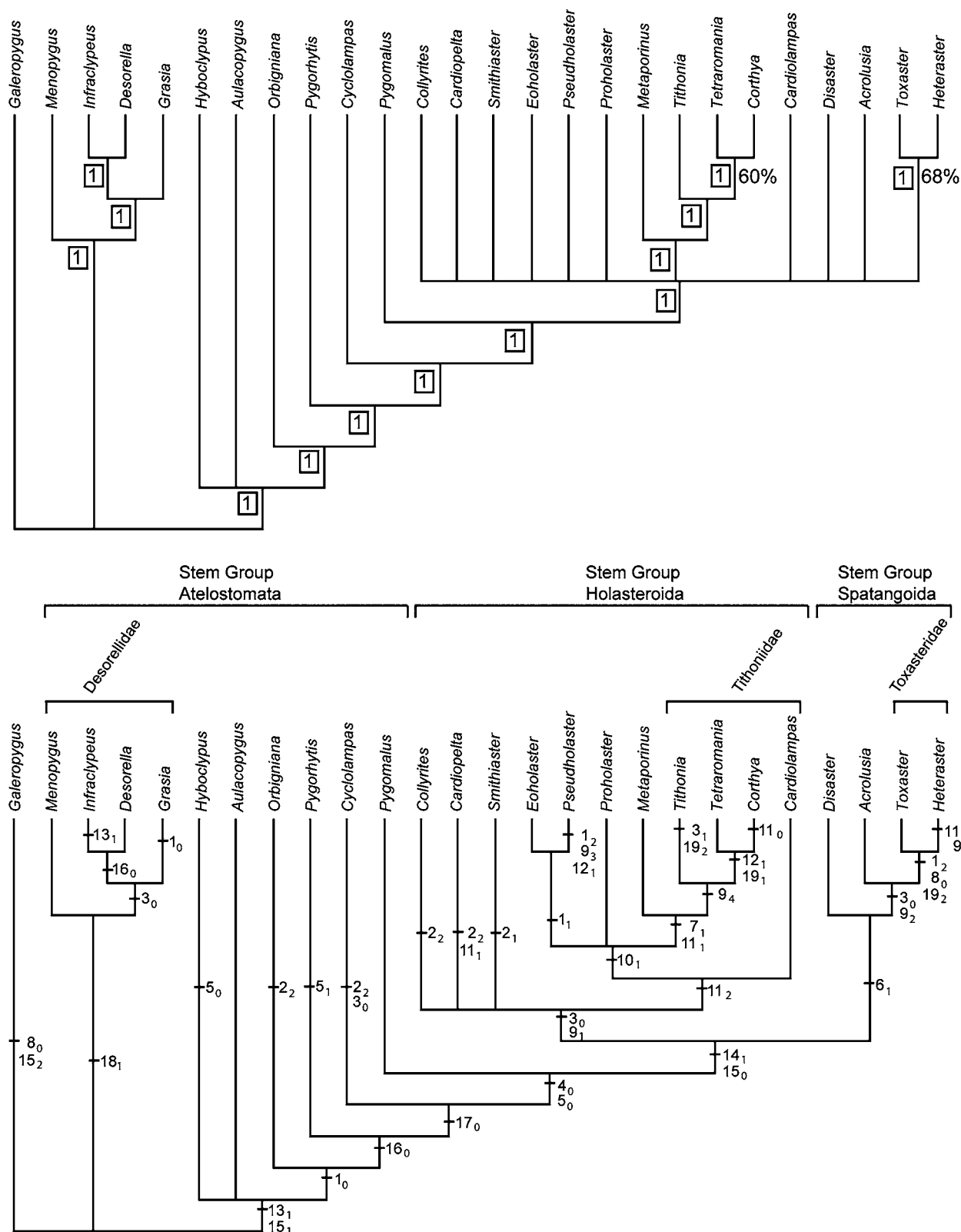
Hyboclypids

The Galeropygidae *sensu* Lambert (1911) is no more than a plesiomorphic grade at the base of the Microstomata *sensu* Smith (1984). It traditionally incorporates *Galeropygus*, *Aulacopygus* and *Hyboclypus*. The 'Galeropygidae' supposedly share an equally close relationship with both the Atelostomata and the Cassiduloida. However, following a re-examination of these taxa, it is clear that *Hyboclypus* and *Aulacopygus* belong within the Atelostomata, while *Galeropygus* shares a closer relationship with the Cassiduloida (Barras 2006). In recognition of this, *Hyboclypus* and *Aulacopygus* have been incorporated into a hyboclypid grade at the base of the Atelostomata. In common with the other stem group atelostomates, the hyboclypid apical disc is elongate, with a maximum width under 60% of disc length (Fig. 6). A new phylogenetic analysis (Barras 2006) suggests that this is a synapomorphy of the stem group atelostomates. There is no such elongation in the *Galeropygus* or cassiduloid disc. These taxa group together on the basis of plesiomorphic features (Barras 2006).

The hyboclypids, here incorporating *Hyboclypus*, *Aulacopygus* and *Orbigniana*, are simply a poorly resolved grade at the base of the stem group Atelostomata. They possess no unique apomorphies. Rather they share in common with the galeropygids a primitive endocyclic disc, a supra-ambital periproct and a deep periproctal groove extending towards the ambitus. In common with the other stem group Atelostomata, the hyboclypids possess only short phylloides and generally tall oral ambulacral plates (Fig. 9), as well as the pore pair specialisation and elongate disc detailed above.

Desorellidae

One unusual finding of the current analysis is the position of *Grasia*. This has traditionally been placed within the 'disasteroids', as a member of the Pygorhytinae *sensu* Beurlen



(1934) and Solovjev (1971), or the Pygorhytidae *sensu* Mintz (1968). Here, *Grasia* shares a sister group relationship with *Desorella* and *Infraclypeus* and lies apart from the other

'disasteroids'. The apical disc in *Desorella* and *Infraclypeus* is elongate and contains a number of complementary plates but is generally adjunct (e.g. Solovjev & Markov 2004: fig. 1),

while that of *Grasia* is clearly disjunct (Smith 2004b). Nevertheless, the taxa do share apomorphies, principally in the possession of a weakly oblique peristome, a character also seen in *Menopygus*. It has previously been noted that *Desorella*, *Infraclypeus* and *Menopygus* lack phyllodes (e.g. Rose & Olver 1988; Figs 10E & 12A). While specimens of *Grasia* are extremely rare and generally poorly preserved, it too appears to have possessed, at best, poorly developed phyllodes (Smith 2004b). The four are grouped in the family Desorellidae Lambert, 1911. Although a close relationship between *Menopygus*, *Desorella* and *Infraclypeus* has previously been suggested (e.g. Mintz 1966; Rose & Olver 1988), this is the first time that *Grasia* has been included within this group.

Pygorhytids

Pygorhytis, *Cyclolampas* and *Pygomalus* lie in a second paraphyletic grade. The disc in all three is distinctly disjunct and the bivium lies at the posterior margin of the test. There is no periproctal groove, as displayed by the hyboclypids.

Cyclolampas in particular shares few characters in common with the other two pygorhytids. While *Pygorhytis* and *Pygomalus* both possess an endocyclic apical disc, the disc is exocyclic in *Cyclolampas* (Figs 2A & 2B). While all three genera have phyllodes, these are very weakly developed in *Pygorhytis* and *Pygomalus* (e.g. Fig. 10G) but almost cassiduloid-like in *Cyclolampas* (Fig. 10D).

Stem group spatangoids

Four of the analysed taxa fall within the stem group spatangoids, *Disaster*, *Acrolusia*, *Toxaster* and *Heteraster*. The stem group spatangoids are defined on the presence of an ethmophract apical disc (e.g. Figs 2F & 2G). While this is disjunct in *Disaster* and *Acrolusia*, it is adjunct in *Toxaster* and *Heteraster*. Thus the origins of the compact spatangoid apical disc can be seen in the disjunct ancestors to all later spatangoids.

Stem group holasteroids

The Holasteroida *sensu stricto* are defined on the presence of an adjunct, elongate apical disc and, of the taxa analysed, includes only *Eoholaster* and *Pseudholaster*. However, because the stem group spatangoids form a well-defined clade in the analysis, the Tithoniidae, *Collyrites*, *Cardiopelta*, *Smithiaster*, *Cardiolampas* and *Proholaster* become, by default, stem group holasteroids. Because this clade lacks any distinctive apomorphies, these taxa are only tentatively referred to the stem group holasteroids. The clade is defined only on the presence of an exocyclic disc and circumflexed pore pairs adapically. However, exocyclic disc is similarly common within the spatangoids, while the circumflexed pore pairs are modified within both the tithoniids and *Pseudholaster*. The absence of any apomorphies in the early stem group holasteroids offers an explanation for the poor resolution among the crown group atelostomates in the initial analysis described above and for the traditionally poorly resolved relationships among these taxa. For instance, while Mortensen (1950) was convinced that *Proholaster* was basal to the holasteroids, Villier *et al.* (2004) suggested that *Proholaster* might, in fact, be ancestral to the spatangoids. The

analysis outlined above confirms that *Proholaster* is not a stem group spatangoid, but its position within the stem group holasteroids is unclear. Until such time as clear apomorphies are found that unite all of the basal holasteroids, the exact relationships among these taxa must remain unresolved.

Tithoniidae

The Tithoniidae was first recognised by Mintz (1968) and his definition remains virtually unchanged here. The family is defined primarily on the presence of an unusual disc trivium, containing just four disc plates to the posterior of ocular III (Fig. 2E). The likely origins of this disc condition are discussed above (character number 8). The majority of tithoniids also possess a distinct oral ambulacral III groove and a forward facing peristome (see Pl. 2, fig. 9b). *Tithonia* itself often possesses an endocyclic apical disc (e.g. Jesionek Szymanska 1963: text-pl. 13, fig. 9).

Metaporinus has previously been assumed ancestral to the spatangoids (e.g. Beurlen 1934; Mortensen 1950). This relationship, implying the re-appearance of a seven-plate disc trivium following its disappearance in *Metaporinus*, is not supported in the current analysis. Instead, the tithoniids form a monophyletic group within the stem group holasteroids.

Morphological transformations in the early evolution of the Atelostomata

Phyllodes and peristome

There is a gradual reduction in the extent of phyllode development through the stem group Atelostomata (cf. Fig. 13B, character 15). The one exception to this rule is *Cyclolampas*, a pygorhytid with well-developed, although short, phyllodes (Fig. 10D). Crowded pore pair triads are not seen in the Desorellidae. The pore pair triads are also absent in the crown group Atelostomata. However, while the pore pairs are therefore uniseriably arranged throughout in both the Desorellidae and crown group Atelostomata, the latter are distinguished by the enlargement of the basicoronal ambulacral plates. Within the crown group atelostomates, one basicoronal plate in each ambulacrum has a height at least 90% of plate width and carries two pore pairs (Fig. 13B, character 14). Coincident with this loss of the pore pair triads is the loss of the peristomial well (character 17).

Apical disc and periproct

The apical disc is clearly endocyclic in the early Atelostomata. It becomes exocyclic independently four times across the phylogeny, in the Desorellidae, *Cyclolampas*, the stem group Holasteroida and the stem group Spatangoida (Fig. 13B, character 3). Endocyclism is secondarily developed in *Tithonia*. Although the periproct may be completely surrounded by disc plates in this taxon, it is also commonly only partially enclosed, or not at all enclosed (cf. Jesionek Szymanska 1963: text-pl. 13, figs 3 & 9).

The hyboclypid apical disc is very similar to that of *Galeropygus*. Namely it is adjunct, endocyclic and contains a large number of complemental plates. Its only derived feature is that the area between the apices of the five ambulacra is decidedly more elongate than in *Galeropygus* (Fig. 13B, character 8). This represents the first stage in the gradual posterior-ward shift of the apices of ambulacra I and V. As the paired posterior ambulacra continue to shift towards the

posterior, the apical disc is apparently stretched to breaking point and becomes disjunct. The disc becomes disjunct independently in the desorellids (*Grasia*) and in the other stem group atelostomates (character 1).

At this stage, the disc still contains a number of complementary plates (e.g. *Orbigniana* (Fig. 4D), *Pygorhytis* (Fig. 2C), *Desorella* (Fig. 4C)), but these are gradually reduced in both size and number, such that in the later stem group atelostomates, there are no such plates in the disc (e.g. Fig. 4G). With the loss of the complementary plates, the apical disc trivium becomes relatively stable, with large ocular plates II and IV separating the paired anterior genitals from the paired posterior genitals. This condition, first seen in the pygorhytids, is retained into the crown group Atelostomata and is characteristic of the stem group holasteroids. Among the stem group holasteroids, the disc is only modified among the tithoniids, through a reduction in the number of plates in the trivium (e.g. Fig. 2E). The disc is also modified in the stem group spatangoids, through the posterior elongation of the madreporite and the consequent separation of oculars II and IV (Fig. 13B, character 6).

Finally, the bivium and trivium are re-united to create an adjunct apical disc independently in the stem group spatangoids and in the stem group holasteroids (Fig. 13B, character 1).

Petals

The stem group atelostomates are all characterised by primitive, undifferentiated aboral pore pairs, both pores of each pore pair being identical and with each pore pair lying obliquely on the plate (e.g. Fig. 7A). Pore pairs are modified in the crown group atelostomates, although *Disaster* retains the primitive condition (Fig. 13B, character 9). In the other stem group spatangoids, both pores become elongate and are circumflex or linearly arranged on the plate (e.g. Fig. 7C). The stem group holasteroids are characterised by small, circumflexed pores in the petals (e.g. Fig. 7B). Within the more advanced tithoniids, the pore pairs are microscopic and of uncertain structure. The pore pairs are also modified in *Pseudholaster*, in which the pores are elongate and linear in the paired ambulacra (cf. Fig. 7C). In the basal tithoniids (*Metaporinus*) and in *Proholaster* and *Pseudholaster*, the anterior ambulacrum is modified and does not carry a petal, although the paired ambulacra are petaliferous.

Plastron

The plastron is protosternous in all stem group atelostomates (e.g. Fig. 12A) and in the majority of crown group atelostomates included in the analysis. Among the stem group spatangoids, the plastron is modified in *Disaster*. This taxon generally possesses a protosternous or amphisternous plastron. However, at least one specimen of *D. granulatus* (MNHN L20.110; Fig. 11B) possesses a meridosternous plastron. The plastron structure is unknown in *Acrolusia*, but in *Toxaster* and *Heteraster* it is amphisternous (e.g. Smith & Stockley 2003). The plastron is protosternous in all stem group holasteroids analysed other than the tithoniids. The plastron is variable in the tithoniids, being amphisternous in *Tithonia* (Fig. 12B), but meridosternous in *Corthya* and *Tetraromania* (e.g. Fig. 12C).

SYSTEMATIC DESCRIPTIONS

Stem Group ATELOSTOMATA Zittel, 1879

DIAGNOSIS. Microstomates with an elongate apical disc (the area of the disc enclosed by the apices of the ambulacra has a maximum width under 60% of its maximum length).

Genus HYBOCLYPUS Agassiz, 1839 (Figs 4B, 7A, 10B, Pl. 1, figs 4a–c)

[= *Hyboclybus* Agassiz, 1840: 6 (*nomen vanum*); *Hyboclipus* Desor, 1842: 7 (*nomen vanum*); *Hyboclypeus* Cotteau, 1873a: 364 (*nomen vanum*); *Hybodyhus* Ébray, 1859: 761 (*nomen vanum*)]

TYPE SPECIES. *Hyboclypus gibberulus* Agassiz, 1839: 75, by original designation.

DIAGNOSIS. Stem group Atelostomata with an adjunct apical disc. The disc contains no more than six complementary plates and oculars II and IV always share a direct contact. The genus retains the primitive characters of a vertically sided periproctal groove (Pl. 1, fig. 4a), oral pore pairs crowded into phyllodes (Fig. 10B) and a peristomial well (Pl. 1, fig. 4c).

OCCURRENCE. Bajocian to Oxfordian, Europe.

REMARKS. Very similar to *Aulacopygus*, but the disc of *Hyboclypus* is more elongate and compact than that of *Aulacopygus*, reflecting the smaller number of complementary plates present (cf. Figs 4A & 4B). The complementary plates preclude oculars II and IV from a direct contact in *Aulacopygus* but not in *Hyboclypus*. This character is the only clear difference between the two genera.

Genus AULACOPYGUS Pomel, 1883 (Figs 1A, 4A, 10C, Pl. 1, figs 1a–c)

TYPE SPECIES. *Hyboclypus caudatus* Wright, 1852: 100, by monotypy.

DIAGNOSIS. Stem group Atelostomata with an elongate adjunct apical disc. The disc contains a large number of complementary plates and these separate oculars II and IV. The primitive periproctal groove is retained (Pl. 1, figs 1a, c), together with pore pairs crowded into phyllodes (Fig. 10C) and a peristomial well (Pl. 1, fig. 1b).

OCCURRENCE. Aalenian to Bathonian, Europe.

REMARKS. The apical disc, although elongate and clearly that of an atelostomate, is similar to that of the stem group cassiduloid *Galeropygus*, in that the central portion of the disc contains a large number of complementary plates (Fig. 4A). These preclude the direct contact of ocular plates II and IV. *Aulacopygus* is possibly the most primitive of all atelostomates.

Genus ORBIGNIANA Ébray, 1860 (Figs 4D, 10F, Pl. 1, figs 6a, b)

[= *Spatoclypus* Pomel, 1883: 51 (objective); = *Orbignyana* Lambert & Thiéry, 1924: 389 (*nomen vanum*)]

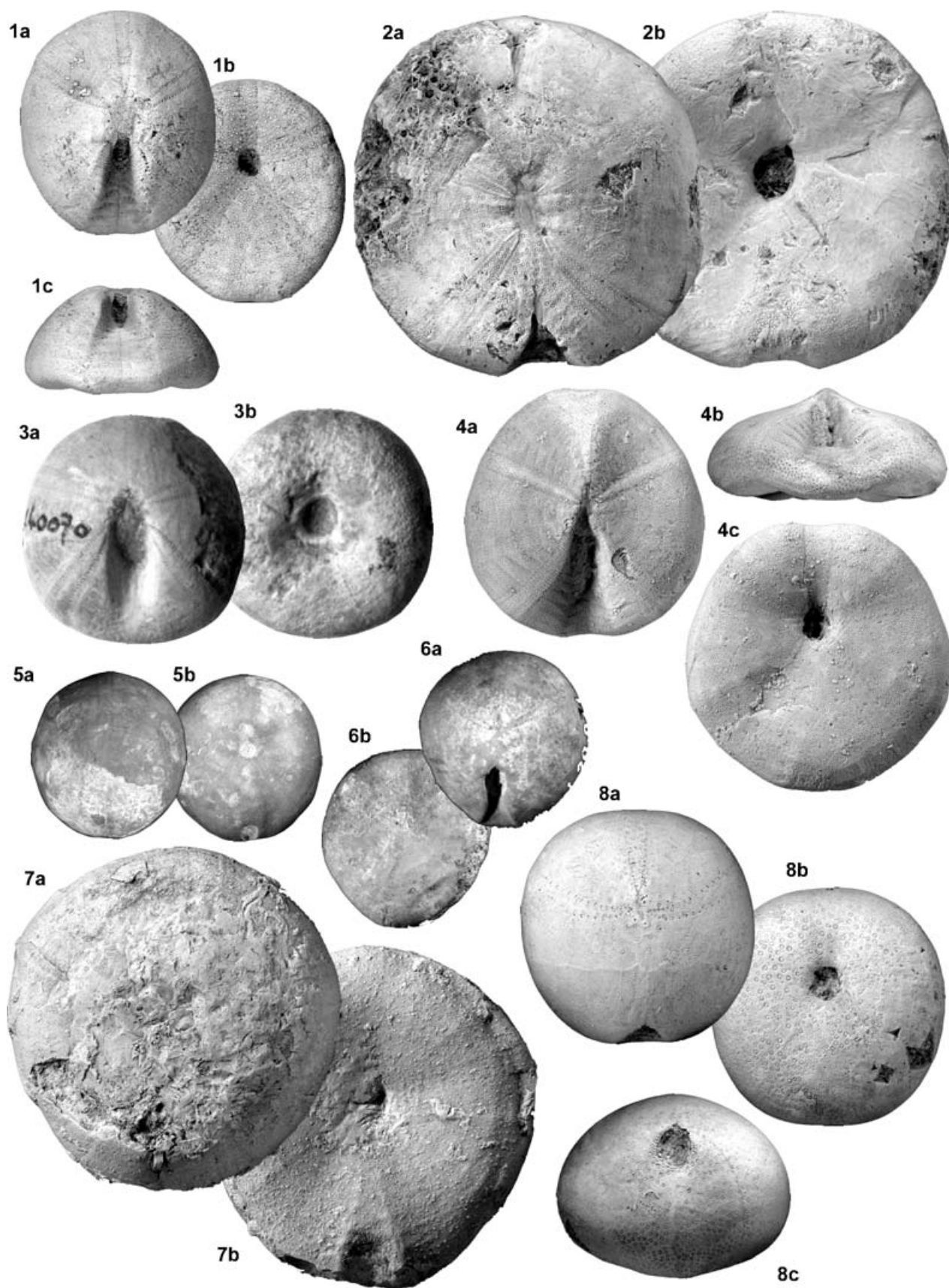


Plate 1 1. *Aulacopygus caudatus* (NHM E1505); **a**, aboral surface; **b**, oral surface; **c**, posterior profile: x2. 2. *Desorella elata* (SM J864); **a**, aboral surface; **b**, oral surface; x1. 3. *Menopygus nodoti* (EM 40070); **a**, aboral surface; **b**, oral surface: x2. 4. *Hyboclypus gibberulus* (NHM E78974); **a**, aboral surface; **b**, posterior profile: x1. 5. *Cyclolampas voltzii* (MNHN L20.069); **a**, aboral surface; **b**, oral surface: x1. 6. *Orbigniana ebrayi* (MNHN L20.071); **a**, aboral surface; **b**, oral surface: x2. 7. *Infraclypeus thalebensis* (NHM E3652); **a**, aboral surface; **b**, oral surface: x1. 8. *Pygomalus ovalis* (NHM E11837); **a**, aboral surface; **b**, oral surface, **c**, posterior profile: x2.

TYPE SPECIES. *Collyrites ebrayi* Cotteau, 1869: 168, by subsequent designation Lambert & Thiéry, 1924: 390. Type species of *Spatoclypus* = *Collyrites ebrayi*, by original designation.

DIAGNOSIS. Stem group Atelostomata with an elongate disjunct apical disc. The disc contains a number of complemental plates that preclude the direct contact of oculars II and IV and also of genitals 1 and 4 (Fig. 4D). The disc trivium and bivium are joined by a short string of complemental plates, similar in size to the genitals. The genus retains the primitive periproctal groove (Pl. 1, fig. 6a) and also phyllodes (Fig. 10F) and a peristomial well (Pl. 1, fig. 6b).

OCCURRENCE. Bajocian, France.

REMARKS. When originally naming *Orbigniana*, Ébray (1860: 56) noted the superficial similarities with *Hyboclypus*. The similarity is based on plesiomorphic characters such as the presence of a deep periproctal groove (Pl. 1, figs 4a, 6a). The slightly disjunct disc apart, *Orbigniana* is, in fact, indistinguishable from *Aulacopygus*. Pomel distinguished *Spatoclypus* from *Hyboclypus* on the presence of a disjunct disc. The original definition is, therefore, the same as that given for *Orbigniana*. Pomel was evidently unaware of Ébray's genus when naming *Spatoclypus*. The two now share the same type species and are objective synonyms.

Genus **PYGORHYTIS** Pomel, 1883 (Figs 2C, 10G, Pl. 2, figs 1a–c)

TYPE SPECIES. *Disaster ringens* Agassiz, 1836: 183, by subsequent designation Lambert & Thiéry, 1924: 390.

DIAGNOSIS. Stem group Atelostomata with a clearly disjunct apical disc containing a small number of complemental plates (Fig. 2C). The complemental plates preclude the direct contact of oculars II and IV. The periproct lies at the posterior of the test in a slight depression, the remnant of a periproctal groove (Pl. 2, fig. 1c). The genus retains the primitive short phyllodes (Fig. 10G) and the peristome lies in a slight depression (Pl. 2, fig. 1b).

OCCURRENCE. Bajocian to Callovian, Europe.

REMARKS. Superficially very similar to *Pygomalus*, following Beurlen (1934) *Pygorhytis* is distinguished principally on the presence of slightly better developed phyllodes and the sunken nature of the peristome. *Pygorhytis* possesses a periproctal depression at the ambitus, there is no depression in *Pygomalus* (cf. Pl. 1, fig. 8c, Pl. 2, fig. 1c). While the disc of *Pygorhytis* always contains a small number of complemental plates, such plates are rare to absent in *Pygomalus* (cf. Figs 2C, 4E).

Genus **CYCLOLAMPAS** Pomel, 1883 (Figs 2A, B, 10D, Pl. 1, figs 5a, b)

TYPE SPECIES. *Disaster voltzii* Agassiz, 1839: 8, by subsequent designation Lambert & Thiéry, 1924: 391.

DIAGNOSIS. Stem group Atelostomata with prominent phyllodes, with three columns of pore pairs per half ambulacrum (Fig. 10D). The apical disc is exocyclic and contains a number of complemental plates (Fig. 2A & 2B). The complemental plates generally preclude the direct contact of ocular

plates II and IV, the posterior paired genitals are also precluded from direct contact. The periproct lies subambitally (Pl. 1, fig. 5b).

OCCURRENCE. Callovian to Tithonian, Europe.

REMARKS. The well-developed phyllodes in *Cyclolampas* are quite unlike those of any other atelostomate. This feature fits uncomfortably with the other atelostomates. Although so far unique, *Cyclolampas* is so unlike any other atelostomate that it is impossible not to view it as the only known representative of a distinct group within the Atelostomata that evolved broad phyllodes and a distinctive, cassiduloid-like feeding strategy.

Genus **PYGOMALUS** Pomel, 1883 (Figs 1B, 4E, Pl. 1, figs 8a–c)

TYPE SPECIES. *Spatangites ovalis* Leske, 1778: 253, by subsequent designation Beurlen, 1934: 65.

DIAGNOSIS. Stem group Atelostomata with a clearly disjunct apical disc containing few or no complemental plates (Fig. 4E). Ocular plates II and IV share a direct contact. The periproct lies at the posterior of the test, flush with the test surface (Pl. 1, fig. 8c). The peristome is also flush with the test surface. Phyllodes are poorly developed.

OCCURRENCE. Bajocian to Bathonian, Europe.

REMARKS. Very similar to *Pygorhytis*, but the two can be relatively easily distinguished, as described above.

Family **DESORELLIDAE** Lambert, 1911

[= Dysastéridées Desor, 1857: 198 (*pars*); = Collyritidae Wright, 1859: 304 (*pars*); = Menopyginae Lambert, 1911: 30 (objective)]

TYPE GENUS. *Desorella* Cotteau, 1855b: 713.

OTHER GENERA INCLUDED. *Grasia* Michelin, 1854: 439, *Infraclypeus* Gauthier, in Cotteau *et al.*, 1884: 24 and *Menopygus* Pomel, 1883: 52.

DIAGNOSIS. Stem group atelostomates with an adjunct to disjunct apical disc. Orally, there is no crowding of pore pairs into phyllodes. The peristome is oblique and lies in a peristomial well.

REMARKS. Early irregular echinoids with an oblique peristome were placed in the family Desorellidae by Lambert (1911: 30). Lambert subdivided the Desorellidae, defining the tribe Menopyginae within the Desorellidae by the absence of phyllodes. In this original publication, the Menopyginae contained *Menopygus*, *Desorella* and *Infraclypeus*. The grouping was a contentious one; while maintained by Lambert & Thiéry (1921: 326), Mortensen (1948) instead grouped all of these taxa within the Galeropygidae. While these three genera, together with *Galeroclypeus* and *Loriolella*, were dealt with together in the *Treatise of Invertebrate Paleontology* (Wagner & Durham 1966b: U631), they were not formally placed within the family Desorellidae or within the tribe Menopyginae. Mintz (1966: 29) resurrected the tribe Menopyginae to encompass those genera lacking phyllodes, raising it to familial level under the name Menopygidae.

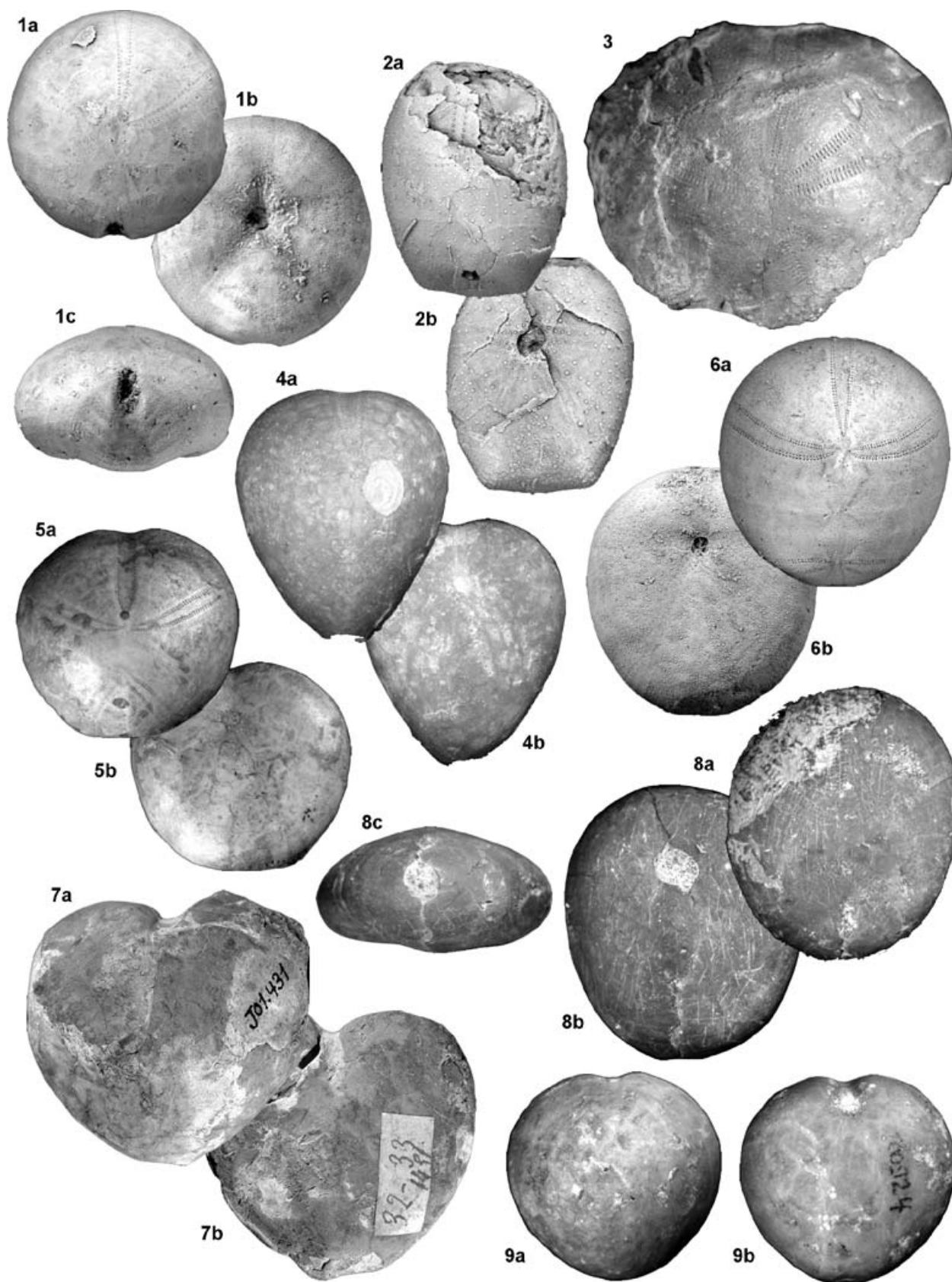


Plate 2 1. *Pygorhytis ringens* (NHM E11860); **a**, aboral surface; **b**, oral surface; **c**, posterior profile: x2. 2. *Disaster granulosus* (NHM E83558); **a**, aboral surface; **b**, oral surface: x2. 3. *Acrolusia gauthieri* (MNHN J01258) aboral surface: x2. 4. *Cardiopelta trigonalis* (MNHN L20.061); **a**, aboral surface; **b**, oral surface: x1.5. 5. *Proholaster auberti* (MNHN J01430); **a**, aboral surface; **b**, oral surface: x1. 6. *Collyrites bicordata* (NHM E3287); **a**, aboral surface; **b**, oral surface: x1. 7. *Cardiolampas friburgensis* (MNHN J01.431); **a**, aboral surface; **b**, oral surface: x1. 8. *Smithiaster loryi* (MNHN A24446); **a**, aboral surface; **b**, oral surface, **c**, posterior profile: x2. 9. *Tithonia convexa* (MNHN J00924); **a**, aboral surface; **b**, oral surface: x1.

Indeed, Mintz thought the Menopygidae so unique that he speculated its origins lay independent from the Gnathostomata and Atelostomata. Consequently, he suggested, the Menopygidae may represent a unique order or even super-order. Rose & Olver (1988) disagreed with this view, seeing the menopygids as the outgroup to the Microstomata *sensu* Smith, 1984.

With the recognition here that *Grasia*, previously considered a typical 'disasteroid' genus, possesses the longitudinally elongate and weakly oblique peristome of *Desorella* and *Infraclypeus* and also appears to lack phyllodes, the position of these problematic taxa becomes clearer. They form a small monophyletic group in the stem group Atelostomata. Desorellidae is the senior synonym for this group and is here resurrected. The Desorellidae, as here defined, differs from the original definition given by Lambert (1911) through the removal of the caratomins (*Echinogalerus*, *Galeraster*) and globatorins (*Globator*, *Echinoneus*, *Pseudohaimea*).

Genus **DESORELLA** Cotteau, 1855b (Figs 4C, 12A, Pl. 1, figs 2a, b)

[= *Desoria* Cotteau, 1855a: 11 *non* Nicolet, 1841: 384 (*nomen vetitum*); = *Pachyclypus* Desor, 1857: 195; = *Pachyclypeus* Cotteau, 1873b: 389 (*nomen vanum*)]

TYPE SPECIES. *Hyboclypus elatus* Desor in Agassiz & Desor, 1847: 152, by subsequent designation Cotteau, 1873a: 333. Type species, by monotypy, of *Pachyclypus* = *Dysaster semi-globus* Desor, 1842: 18 [= *Nucleolites semiglobus* Münster in Goldfuss, 1829: 139, pl. 49, fig. 6 (*sic* Desor 1842: 18)].

DIAGNOSIS. Desorellids with an adjunct to slightly disjunct apical disc. Disjunction is in the anterior portion of the disc. The apical disc is exocyclic and the periproct is marginal.

OCCURRENCE. Bathonian to Oxfordian, England and France.

REMARKS. Elements of the morphology of *Desorella* have been touched upon elsewhere in this paper. While the disc is not disjunct between the posterior paired genitals and posterior paired oculars, it may be disjunct in the anterior portion of the disc (Fig. 4C). However, the disc always forms a single unit because of the presence of numerous large complemental plates. Although phyllodes are absent, the oral ambulacral plates are arranged in a trigeminate fashion (Fig. 12A). *Desorella* is distinguished from the similar *Infraclypeus* on the presence of an ambital, rather than subambital, periproct which lies in a slight vertical groove (cf. Pl. 1, figs 2 & 7). The periproct of *Infraclypeus* lies in a shallow depression.

Genus **GRASIA** Michelin, 1854

TYPE SPECIES. *Hyboclypus elongatus* Gras, 1852: 49, by monotypy.

DIAGNOSIS. Desorellids with a clearly disjunct, exocyclic apical disc. The periproct lies supra-ambitally, in a deep periproctal groove.

OCCURRENCE. Oxfordian, France.

REMARKS. *Grasia* is known from only a small number of poorly preserved internal moulds and the test structure is

unclear. The internal moulds do suggest, however, that the genus had no phyllodes and an oblique peristome (Smith 2004b). The taxon has always previously been considered a 'disasteroid', but in the analysis detailed above lies within the desorellids. However, because of the poor nature of preservation, in the new analysis described above many character states were coded as unknown in *Grasia* (Table 2). With better-preserved specimens and more character information, the position of *Grasia* as a desorellid may be overturned.

Genus **INFRACLYPEUS** Gauthier in Cotteau *et al.*, 1884 (Pl. 1, figs 7a, b)

TYPE SPECIES. *Infraclypeus thalebensis* Gauthier in Cotteau *et al.*, 1884: 24, by monotypy.

DIAGNOSIS. Desorellids with an adjunct, exocyclic apical disc. The peristome lies sub-ambitally, in a shallow depression.

OCCURRENCE. Tithonian, Algeria.

REMARKS. Very similar to *Desorella*, the two are distinguished on the position of the periproct (Pl. 1, figs 2 & 7).

Genus **MENOPYGUS** Pomel, 1883 (Fig. 10E, Pl. 1, figs 3a, b)

TYPE SPECIES. *Galeropygus nodoti* Cotteau, 1859: 294.

DIAGNOSIS. Desorellids in which the periproct lies in direct contact with the apical disc. There is a wide and deep periproctal groove stretching to the posterior, from the test apex to the ambitus.

OCCURRENCE. Bajocian to Oxfordian, Europe.

REMARKS. This taxon is superficially very similar to *Galeropygus*, but the area of the apical disc bound by the apices of the ambulacra is elongate and not compact (Rose & Olver 1988: fig. 3b). Orally, the peristome is relatively much larger than it is in *Galeropygus* and it is oblique (Pl. 1, fig. 3b). The periproct lies in contact with the apical disc at the anterior end of a periproctal groove (Pl. 1, fig. 3a) and the disc is presumably endocyclic, in common with the majority of early microstomates in which the periproct lies in contact with the disc. *Menopygus* is, therefore, the most primitive of desorellids, as all of the other taxa possess a clearly exocyclic disc.

Crown group **ATELOSTOMATA** Zittel, 1879

DIAGNOSIS. Atelostomata with enlargement of the basicoronal ambulacral plates (one basicoronal plate in each ambulacrum has a plate height equal to, or exceeding, plate width). Five of the ten basicoronal ambulacral plates carry two, rather than one, pore pairs. The phyllodes are narrow, with a single series of pore pairs.

Stem group **SPATANGOIDA** Claus, 1876

DIAGNOSIS. Crown group atelostomates with a disjunct or adjunct, compact ethmophract apical disc (i.e. one in which the madreporite extends to the posterior and precludes the direct contact of oculars II and IV).

Genus **DISASTER** Agassiz, 1836 (Figs 2F, 11A, B, Pl. 2, figs 2a, b)

[= *Dysaster* Agassiz, 1839: 95 (*nomen vanum*)]

TYPE SPECIES. *Nucleolites granulatus* Goldfuss, 1829: 138, by subsequent designation of Desor, 1857: 201.

DIAGNOSIS. Stem group Spatangoida with a disjunct, endocyclic apical disc (Fig. 2F). Plastron plating is highly variable, variously showing protosternous, amphisternous, and meridosternous plating (Figs 11A & 11B).

OCCURRENCE. Callovian to Hauterivian, Europe.

REMARKS. This genus has always been placed in the family Disasteridae Gras, 1848. This family, initially defined on a compact apical disc (e.g. Desor 1857), was later revised to contain only those taxa with a 'non-intercalary' apical disc (Mintz 1968). Because both the 'non-intercalary' apical disc of *Disaster* and the 'semi-intercalary' disc of *Acrolusia* are formally defined as ethmophract, the apical disc of *Disaster* is no longer unique. Consequently, the family Disasteridae is abandoned. *Disaster* is, however, unique among crown group atelostomate taxa in showing extremely variable plastron plating. Otherwise identical specimens are known that show protosternous, meridosternous and amphisternous plating (see above). *Disaster* is easily distinguished from *Acrolusia* in possessing an endocyclic disc. The disc of *Acrolusia* is exocyclic.

Genus **ACROLUSIA** Lambert, 1920 (Fig. 2G, Pl. 2, fig. 3)

TYPE SPECIES. *Acrolusia gauthieri* Lambert, 1920: 158, by original designation.

DIAGNOSIS. Stem group Spatangoida with a slightly disjunct, exocyclic apical disc (Fig. 2G) and well developed aboral petals (Pl. 2, fig. 3). Ambulacrum III lies in a slight groove aborally.

OCCURRENCE. Neocomian, Algeria.

REMARKS. The only known specimen of this genus is incomplete and the oral surface is unknown. However, the preserved fragment of the aboral surface is well preserved and shows the ethmophract apical disc of a spatangoid. The disc of both *Acrolusia* and *Disaster* is disjunct and shows that the characteristic spatangoid apical disc began to evolve in the stem group spatangoids before final reunification of the disc.

Stem group **HOLASTEROIDA** Durham & Melville, 1957

REMARKS. By virtue of the ethmophract apical disc, *Disaster*, *Acrolusia*, *Toxaster* and *Heteraster* fall in the stem group Spatangoida. Consequently, all of the other crown group atelostomates analysed are here placed within the stem group Holasteroida. Phylogenetically, the stem group holasteroids are supported by the possession of an exocyclic disc and circumflexed pore pairs within the phylloides. Both characters are variable within the stem group holasteroids and exocyclic disc is common within the stem group atelostomates and the stem group spatangoids. There are no unique apomorphies with which to define the stem group holasteroids.

Genus **COLLYRITES** Desmoulins, 1835 (Figs 2D, 7B, Pl. 2, figs 6a, b)

TYPE SPECIES. *Ananchytes elliptica* Lamarck, 1816: 318, by original designation.

DIAGNOSIS. Crown group Atelostomata with a disjunct apical disc. A string of catenal plates links the trivium and bivium. An additional string of catenal plates links the bivium and periproct (Fig. 2D).

OCCURRENCE. Callovian to Tithonian, Europe.

REMARKS. *Collyrites* and *Cardiopelta* are extremely similar, being differentiated only on the presence in *Collyrites* of a string of catenal plates between the bivium and periproct (cf. Figs 2D & 4F). They have previously been considered synonymous (Thierry 1984), but are treated separately here.

Genus **CARDIOPELTA** Pomel, 1883 (Fig. 4F, Pl. 2, figs 4a, b)

[= *Collyropsis* Gauthier, 1896: 22; = *Procollyropsis* Beurlen, 1934: 129]

TYPE SPECIES. *Collyrites trigonalis* Desor in Desor & De Loriol, 1872: 371, pl. 59, by subsequent designation of Savin, 1905: 144. Type species of *Collyropsis* = *Spatangites carinatus* Leske, 1778: 245, by subsequent designation of Lambert & Thiéry, 1924: 392. Type species of *Procollyropsis* = *Dysaster platypygus* Quenstedt, 1874: 565, pl. 83, figs 31–34, by original designation.

DIAGNOSIS. Crown group Atelostomata with a disjunct apical disc. A string of catenal plates links the trivium and bivium, but there are no catenal plates between the bivium and periproct (Fig. 4F).

OCCURRENCE. Oxfordian to Berriasian, Europe.

REMARKS. Gauthier (1896) identified *Collyropsis* as ancestral to the 'Ananchytidae', characterised by simple ambulacra and no anterior ambulacral groove. While this definition varies slightly with that given by Pomel (1883) for *Cardiopelta* (an anterior ambulacral groove is present), the type species later selected for these two genera are very similar. Savin (1905: 144) designated *Collyrites trigonalis* Desor the type of *Cardiopelta*, while Lambert & Thiéry (1924: 392) designated *Spatangites carinatus* Leske the type species of *Collyropsis*. The types of neither *Spatangites carinatus* nor *Collyrites trigonalis* have here been examined, but specimens of the two species in the Muséum National d'Histoire Naturelle, Paris are indistinguishable (Smith 2004b). It is likely that the two are in fact synonymous. Consequently, *Collyropsis* and *Cardiopelta* may share the same type species and become objective synonyms. They are certainly subjective synonyms. Beurlen (1934) subdivided *Collyropsis*, placing those taxa in which the periproct is visible when viewed from above under the subgenus *Procollyropsis*. This small distinction is regarded as of only minor importance and *Procollyropsis* is treated as a subjective synonym of *Cardiopelta*.

Genus **CARDIOLAMPAS** Pomel, 1883 (Pl. 2, figs 7a, b)

TYPE SPECIES. *Collyrites friburgensis* Ooster, 1865: 55, by subsequent designation Gauthier, 1896: 21.

DIAGNOSIS. Crown group Atelostomata with a disjunct apical disc. Ambulacrum III lies in a prominent groove along its entire length, giving the test a distinctly heart-shaped outline (Pl. 2, fig. 7a).

OCCURRENCE. Tithonian, Europe.

REMARKS. The genus is poorly known because of the poor state of preservation of all examined specimens. The genus is similar to *Proholaster*, but does not appear to possess the petals of that genus.

Genus **PROHOLASTER** Gauthier, 1896 (Fig. 4G, Pl. 2, figs 5a, b)

TYPE SPECIES. *Proholaster auberti* Gauthier, 1896: 18, by monotypy.

DIAGNOSIS. Crown group Atelostomata with a disjunct apical disc (Fig. 4G). There is only a limited degree of apical disc disjunction. Ambulacrum III lies in an ambital groove along its entire length (Pl. 2, fig. 5a). The paired ambulacra are modestly petaloid, ambulacrum III is subpetaloid (Pl. 2, fig. 5a).

OCCURRENCE. Berriasian, North Africa.

REMARKS. As discussed above, this genus has variously been considered as a stem group spatangoid (Villier *et al.* 2004) and a stem group holasteroid (Mortensen 1950). While it does not fall among the stem group spatangoids as here defined, its final position in the stem group holasteroids is not clear.

Genus **SMITHIASTER** nov. (Figs 5A, B, Pl. 2, figs 8a–c)

TYPE SPECIES. *Dysaster loryi* Gras, 1852: 49, by monotypy. The type of *Dysaster loryi* was not found in the current study. It may be in Gras's collections in the Muséum d'Histoire Naturelle, Grenoble.

OTHER SPECIES INCLUDED. Monospecific genus.

MATERIAL STUDIED. MNHN A24446.

DIAGNOSIS. Crown group Atelostomata with a disjunct apical disc. The two portions of the apical disc are linked by a single, large complemental plate (Fig. 5A). The ambulacra are petaliferous with slightly elongate, circumflexed pore pairs aborally. Ambulacrum III is flush with the test surface along its entire length.

OCCURRENCE. Oxfordian to Kimmeridgian, France and North Africa.

DESCRIPTION. The test is elongate, with test length 25 mm and test width 21 mm. The test is relatively tumid, with a maximum test height 44% of test length.

The apical disc is elongate and approximately central. Its anterior margin lies 43% of the test's length from the test's anterior margin. The disc is intercalary, ocular plates II and IV separating the anterior and posterior genital plate pair (Fig. 5A). There is a large complemental plate between the posterior genital plate pair and posterior ocular plate pair and so the disc is disjunct. Other than for this plate, there are no other complementals incorporated into the disc.

The periproct lies at the posterior margin of the test, far removed from the apical disc. The disc is therefore exocyclic. The periproct is roughly ovoid, with a length 15% of test length and a maximum width 75% of periproctal length.

Orally, the peristome is in an anterior position, its anterior margin lying only 22% of the test's length from the test's anterior margin. The peristome is large and circular, with a maximum length 15% of test length. It is flush with the test surface. The plastron is protosternous and simple (Fig. 5B). Five of the ten ambulacral plates lying in direct contact with the peristome carry two, rather than one, pore pair. Details of the tuberculation are unknown from the single worn specimen examined.

REMARKS. *Disaster loryi* is clearly distinct from any other species of *Disaster*. In recognition of this, it was moved into the genus *Cardiopelta* by Lambert & Thiéry (1924: 392). However, it fits little better in this genus. The near-adjunct apical disc is quite unlike any other species of *Cardiopelta* and very reminiscent of the typical holasteroid disc (cf. Fig. 5A; Smith & Wright 2003: text-fig. 184a). Indeed, other than for the complemental plate separating the bivium and trivium, the species would fit among the conventional holasteroids. Smith (2004b) first recognised that Gras' species fits into no previously recognised 'disasteroid' genus. In recognition of this, the genus is named *Smithiaster*.

Family TITHONIIDAE Mintz, 1968

[= *Dysasteridées* Gras, 1848: 65 (*pars*); *Collyritidae* Wright, 1859: 304 (*pars*); = *Cardiasteridés* Pomel, 1883: 45 (*pars*)]

TYPE GENUS. *Tithonia* Pomel, 1883: 49.

OTHER GENERA INCLUDED. *Corthya* Pomel, 1883: 51; *Tetraromania* Solovjev, 1971: 64; *Metaporinus* Agassiz, 1844: 730.

DIAGNOSIS. Crown group Atelostomata with a disjunct disc containing a reduced number of plates (e.g. Fig. 2E). The posterior genital plates are lost, the posterior gonopores opening instead on ocular plates II and IV.

REMARKS. The unusual apical disc condition uniting the tithoniids is unlike that seen in any other atelostomate, except for the pourtalesiids (see above for discussion). A tithoniid disc illustrated by Jesionek Szymanska (1963: text-pl. 13, fig. 5) demonstrates that, prior to their loss, the posterior genitals occupied a position immediately to the posterior of oculars II and IV. This is the elongate, intercalary disc of the holasteroids. The unique disc condition immediately distinguishes members of this family, which otherwise show a relatively high degree of variation: the disc may be endocyclic or exocyclic, petals may or may not be developed, and plastron plating may be amphiosternous or meridosternous.

Genus **TITHONIA** Pomel, 1883 (Figs 2E, 12B, Pl. 2, figs 9a, b)

[? = *Oustechinus* Lambert, 1931: 92 (*nomen dubium*)]

TYPE SPECIES. *Nucleolites convexus* Catullo, 1827: 28, by monotypy. Type species of *Oustechinus* = *Oustechinus basae* Lambert, 1931: 92, by original designation.

DIAGNOSIS. Tithoniids with an endocyclic apical disc (cf. Jesionek Szymanska 1963: text-pl. 13, fig. 9). The peristome is angled to face towards the anterior. Plastron plating is amphisternous (Fig. 12B). The pore pairs are microscopic.

OCCURRENCE. Callovian to Tithonian.

REMARKS. *Oustechinus*, named by Lambert (1931: 92) is known from a single, very poorly preserved specimen (Lambert 1931: 3, figs 31–32), found in association with two species of *Tithonia*. The specimen is almost certainly a misidentified specimen of one of the *Tithonia* species. It is, however, missing from the Lambert collection (Smith 2004b) and so must be regarded as a *nomen dubium*. Phylogenetically, *Tithonia* possesses a secondarily endocyclic disc. It is the only tithoniid with an endocyclic apical disc and so is readily identified.

Genus **CORTHYA** Pomel, 1883 (Figs 8, 12C)

TYPE SPECIES. *Dysaster hemisphaericus* Gras, 1848: 66, by original designation.

DIAGNOSIS. Tithoniids with ambulacral zones as wide as the interambulacral zones at the ambitus (Fig. 8). The pore pairs are microscopic and the ambulacra are apetaliferous. Ambulacrum III is flush with the test surface along its entire length and the peristome faces directly downwards. Plastron plating is meridosternous (Fig. 12C). The apical disc is exocyclic and the periproct is sub-ambital. A small number of catenal plates may be present between the trivium and bivium.

OCCURRENCE. Berriasian to Albian, Europe and Russia.

REMARKS. *Corthya* is easily recognisable by its large hexagonal aboral ambulacral plates, which are similar in size to interambulacral plates (Fig. 8).

Genus **TETRAROMANIA** Solovjev, 1971

TYPE SPECIES. *Dysaster ovulum* Desor, 1842: 22, by original designation.

DIAGNOSIS. Tithoniids with ambulacral zones as wide as the interambulacral zones at the ambitus. The ambulacra are apetaloid, with microscopic pore pairs. Ambulacrum III lies in a shallow groove sub-ambitally and the peristome faces slightly towards the anterior. Plastron plating is meridosternous (cf. Solovjev 1971: fig. 30a). The apical disc is exocyclic and the periproct marginal (Solovjev 1971: fig. 30a). A small number of catenal plates may occur between the trivium and bivium.

OCCURRENCE. Berriasian to Barremian, Europe and Russia.

REMARKS. *Tetraromania* is superficially similar to *Tithonia*, but the two are easily distinguished on the disc structure, which is endocyclic in *Tithonia* but exocyclic in *Tetraromania*. Plastron plating is amphisternous in *Tithonia*, but meridosternous in *Tetraromania*. The ambulacra are relatively much wider in *Tetraromania* than in *Tithonia* and are similar in width to the ambulacra of *Corthya*.

Genus **METAPORINUS** Agassiz, 1844

[= *Metaporhinus* Michelin in Agassiz & Desor, 1847: 33 (*nomen vanum*); = *Thesaporhinus* Ébray, 1859: 761 (*nomen vanum*); = *Thecaporhinus* Ébray, 1859: 1159 (*nomen vanum*); = *Perioxus* Pomel, 1883: 49; = *Dialyaster* Pomel, 1883: 46]

TYPE SPECIES. *Metaporinus michelini* Agassiz, 1844: 270, by monotypy. Type species, by monotypy, of *Perioxus* = *Collyrites censoriensis* Cotteau, 1855a: 302. Type species of *Dialyaster* = *Metaporhinus gueymardi* Gras, 1848: 69, by monotypy.

DIAGNOSIS. Tithoniids in which the paired ambulacra are petaliferous (Smith 2004b). The anterior ambulacrum is only sub-petaloid. The anterior ambulacrum is generally flush aborally, but lies in a distinct groove orally. The periproct generally faces slightly towards the anterior.

OCCURRENCE. Callovian to Oxfordian, Europe.

REMARKS. Pomel (1883) erected the genus *Perioxus* for those species of *Metaporinus* with a strongly sloping posterior, the test apex lying to the anterior of the apical disc. He also mentioned alterations to the ambitus of *Perioxus*, where it intersects the ambulacra. Beurlen (1934) examined Pomel's specimen and claimed that it was fragmentary. This offers an explanation for the alterations to the ambitus noted by Pomel. Pomel's specimen has not been examined in the current study, but following Beurlen's observations on the fragmentary nature of the specimen, *Perioxus* is regarded as a subjective synonym of *Metaporinus*. *Dialyaster* is apparently very similar to *Metaporinus*. In both, the paired ambulacra are petaloid, although in *Dialyaster* ambulacrum III lies in an ambital groove along its entire length and the periproct lies in a shallow depression that continues orally. These features are only known through examination of figures given by d'Orbigny (1854: pl. 833), as the single specimen of the genus is now missing. *Dialyaster* is, at best, a dubious genus. It is provisionally regarded as a subjective synonym of *Metaporinus*.

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