

Probing the cassiduloid origins of clypeasteroid echinoids using stratigraphically restricted parsimony analysis

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Abstract.—Clypeasteroid echinoids are a familiar and easily defined clade with a cryptic origin. They first appear in the late Paleocene and are believed to have arisen from cassiduloid ancestry, but identifying sister-group relationships more precisely has proved difficult. Two factors are responsible for this problem, the extreme morphological conservatism of cassiduloids, which has given rise to high levels of character exhaustion, and the origin of crown-group clypeasteroids through paedomorphosis. Previous analyses, based on extant representatives alone or including all Mesozoic to Recent genera, have proved unsatisfactory.

Here a parsimony analysis is undertaken using a restricted set of all stem-group clypeasteroids and cassiduloid taxa that existed immediately prior to the appearance of crown-group clypeasteroids. Inclusion of *Togocyamus*, the fossil taxon lying closest to the origin of crown-group clypeasteroids, is phylogenetically uninformative because that taxon is highly paedomorphic and has only generalized juvenile characteristics. However, earlier stem-group plesions provide critical data that identify Apatopygidae as extant sister group to the Clypeasteroidea. Stratigraphically restricted analyses cannot eradicate the problems that arise from character exhaustion, but can minimize these with respect to specific phylogenetic questions.

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Accepted: 18 August 2000

Introduction

Ever since systematists started to subdivide Latreille's family Irregularia, more than 150 years ago, four major groups of irregular echinoid have been consistently distinguished. By the time of Mortensen's monumental monograph of the Echinoidea (1928–1951), these four groups had become standardized as the orders Holoctypoida, Clypeasteroidea, Cassiduloida, and Spatangoida. Three of these have long pedigrees, with representatives of the Spatangoida, Cassiduloida, and Holoctypoida extending back 175 million years to the early Middle Jurassic (Smith and Anzalone 2000). The Clypeasteroidea, by contrast, appears to be of comparatively recent origin, first appearing just 55 million years ago (Kier 1982).

Members of the Clypeasteroidea are very easy to recognize. They are the only sea urchins to have more than one tube foot associated with each ambulacral plate, and are the only extant irregular echinoids to have a lantern and perignathic girdle as adults. They are today a highly successful and morphologically diverse group that includes such well known forms as the sand dollars, sea biscuits,

and pea urchins. Indeed, *Clypeaster* is so common in the fossil record that there are approximately 400 nominal species. Surprisingly, however, the origins of this distinctive group have remained largely cryptic.

Two aspects make the origin of clypeasteroids a particularly difficult phylogenetic problem to solve. First, the earliest generally acknowledged member of the clade has clearly undergone drastic developmental curtailment and its morphology is predominantly juvenile in character (Kier 1982; Mooi 1990a). Subsequent evolution in the Tertiary has added a large number of new and complex morphological features to the clade, but no obvious synapomorphies remain to link the group back to a specific cassiduloid clade.

Second, the cassiduloids are a morphologically highly conservative grade and no significant skeletal novelties have arisen in any of its constituent clades since the late Cretaceous. Cassiduloids thus show distinct signs of character exhaustion (Wagner 2000a and personal communication 2000), and throughout much of their later history evolution has involved skeletal characters being shuffled rather than

added to. Kier (1962) noted many examples of parallel evolution among late Cretaceous cassiduloids. To add to the problems there is at least one extant cassiduloid clade, the neolampadids, that also appears to have had paedomorphic origins and is thus convergent on early clypeasteroids.

The only serious attempt to resolve how clypeasteroids nest within cassiduloids is the work of Suter (1994a,b). Suter performed two cladistic analyses. In one he included extant taxa only and was thus able to include information on pedicellariae, tube feet, and other soft-tissue structures. The second analysis was restricted to hard skeletal characters commonly preserved in fossils, but he expanded the number of taxa to include almost all genera of cassiduloid that are currently recognized, from the Middle Jurassic to Recent. In both cases large numbers of equally most parsimonious cladograms were found and resolution was poor. Whether based on just living groups or on all genera of cassiduloid, the cladograms offered weak support for placing neolampadids as sister group to clypeasteroids. However, this pairing was based entirely on character reversals to juvenile states.

Here a different approach is adopted. Problems of homoplasy that arise from character exhaustion are likely to be minimized if representatives of clades that lie as close as possible to the inferred divergence time are selected. It was for this reason that Ausich (1998a,b) developed a stepwise approach to reconstructing phylogenetic relationships of early Paleozoic crinoids. It is also possible that basal representatives of clades can reveal morphologies that have been subsequently lost through curtailed development. The oldest generally accepted clypeasteroid is *Togocyanus* from the late Paleocene (Kier 1982; Mooi 1990a). Only cassiduloids have been recorded from the Maastrichtian and so, by inference, clypeasteroids probably evolved from cassiduloids sometime around the end of the Cretaceous or early part of the Paleocene. Furthermore, undoubted members of almost all extant cassiduloid lineages are present by the middle Eocene. The cladistic analysis therefore was designed to include only taxa living close to the time of clypeasteroid origination.

This of course does not entirely remove the problem of character exhaustion, since many of cassiduloid taxa present in the Maastrichtian may themselves have diverged back in the Early Cretaceous or Late Jurassic. However, it does provide the minimal feasible distance between stem-group clypeasteroids and a range of potential ancestral groups.

Materials and Methods

A total of 41 skeletal characters were scored for 48 species of cassiduloid and clypeasteroid (Appendix 1). Representatives of all Maastrichtian and Paleocene genera of cassiduloid were included, together with Eocene representatives of extant families. All characters were treated as unordered and of equal weight and subjected to a parsimony analysis using PAUP* 4.0b3a (Swofford 2000). Because of the size of the data matrix, parsimony analysis was carried out using a heuristic search, with 100 random-addition replicates to check for the existence of multiple tree islands. Bootstrap support for individual nodes was determined by running 1000 bootstrap replicates, with maxtrees set at 100, and Bremer support was determined using Autodecay, Version 3.0 (Eriksson and Wikström 1998). Trees were rooted on the cassiduloid *Nucleolites*, a primitive and early member of the stem-group neognathostomates.

For comparison the same characters were scored for modern representatives of all major cassiduloid clades and a modern clypeasteroid. The analysis was rooted by reference to *Echinoneus*, phylogenetically the most basal living irregular echinoid known. Searches were undertaken as above, but using the "Exhaustive Search" option. Trees were rooted on *Echinoneus*, the most primitive of extant irregular echinoids.

In considering the origins of clypeasteroids, I have included the following groups:

Clypeasteroids.—Living clypeasteroids are classified into some 150 species in 26 genera, many of which are prominent members of shallow-marine benthic communities. The details of their classification are largely irrelevant to this paper and have been treated in depth by Mooi (1989, 1990a). Mooi used a crown-group definition for the Clypeastero-

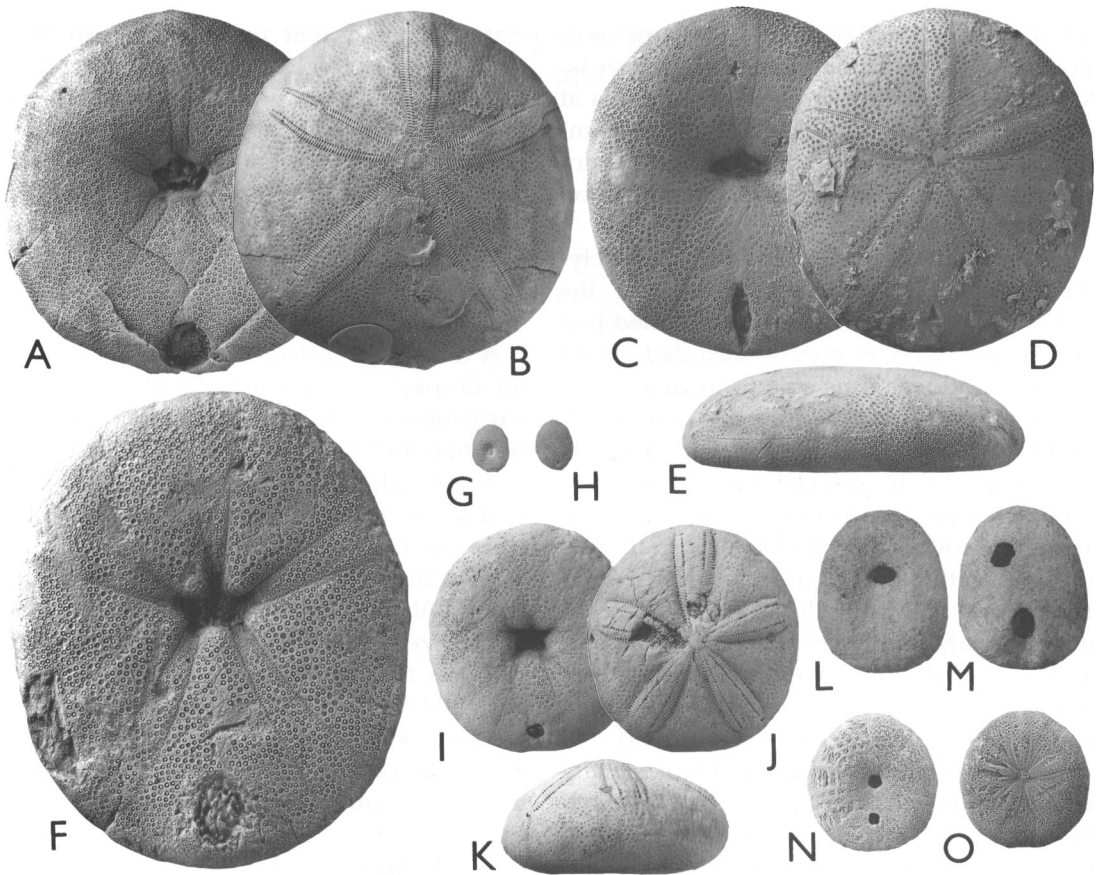


FIGURE 1. Key taxa in understanding the origin of clypeasteroid echinoids. A, B, *Oriolampas saharae* (Bather), NHM EE2257; a late Paleocene stem-group Clypeasteroidea. C–E, *Plesiolampas placenta* d’Archiac and Haime, NHM E729; a late stem-group Clypeasteroidea from the late Paleocene of Pakistan. F, *Conoclypus sindensis* Duncan and Sladen, NHM EE5291; a stem-group clypeasteroid from the late Paleocene of Oman. G, H, *Togocyamus seegfriedi* (Oppenheim), NHM E37649; the most crownward stem-group plesion of the Clypeasteroidea from the late Paleocene of Ghana. I–K, *Haimea ovumserpentis* (Guppy), NHM E17713; a stem-group clypeasteroid from the late Eocene of Jamaica. L, M, *Apatopygus mannumensis* Holmes, NHM EE637; an apatopygid “cassiduloid” from the late Miocene of Australia. N, O, *Sismondia occitana* Defrance, NHM 57883; a primitive crown-group clypeasteroid from the Eocene of France. All specimens $\times 1$, except G, H, L, M, which are $\times 2$.

ida and recognized three suborders, with Clypeasterina as sister taxon to the Laganina plus Scutellina, as previously argued by Philip (1965), Kier (1970), and Smith (1981). However, unlike previous workers, he left the Laganine-Scutelline clade unnamed.

The oldest and also the least specialized taxon that can be confidently assigned to the clypeasteroids is *Togocyamus* from the late Paleocene of West Africa (Kier 1982; Mooi 1990a; Mooi and Chen 1996) (Fig. 1). *Togocyamus* was originally described as a fibulariid clypeasteroid and treated as such by Mortensen (1948) and Durham (1955, 1966b). Kier (1982) provided excellent SEM micrographs of the type

species, *T. seegfriedi* (Oppenheim), and provided new information on its lantern supports. He argued for its being ancestral to all other clypeasteroids. Mooi (1990a) reinterpreted the lantern supports in *Togocyamus* and removed it from the Fibulariidae, placing it as the most advanced plesion prior to the divergence of crown-group clypeasteroids.

Unfortunately, the ambulacral plating in *Togocyamus* remains ambiguous. Mooi (1990a: Fig. 3) illustrated simple plating in the interior oral surface of *Togocyamus*. However, at the ambitus there are definitely three or more pores to a single primary ambulacral plate externally. In oligopygids and *Conoclypus* there

are also multiple pores to every primary plate, but accessory pores occur on minute demiplates that are restricted to the outer surface (Kier 1967). In weathered specimens of oligopygids the demiplates are often lost, but their position is marked by small, shallow pits along the adradial margins of the primary plates. Because no such pitting is ever seen in weathered specimens of *Togocyamus*, it seems unlikely that it possessed demiplates. *Togocyamus* is therefore scored as having multiple pores along the adradial margin of ambulacral plates.

Cassiduloids.—Cassiduloids today are a very minor group with just 30 living species (Mooi 1990b). These are currently placed into four families: the Echinolampadidae, comprising *Echinolampas* and *Conolampas*; the Apatopygidae, comprising *Apatopygus* and *Porteropygus*; the Cassidulidae, comprising *Cassidulus*, *Rhyncholampas*, *Eurhodia*, *Oligopodia*, and *Studeria*; and the Neolampadidae, comprising *Neolampas*, *Anochanus*, *Aphanopora*, *Nannolampas*, and *Tropholampas*. Suter (1994b) found support for most of these groupings, but had *Studeria* as closer to the neolampadids rather than grouping with other cassidulids. The Neolampadidae are an exclusively deep-water group that have been difficult to classify. Stefanini (1913) and later Philip (1963) both argued for their being neotenuously derived from more-standard cassiduloids because of their extremely simple ambulacral structure. Philip (1963) placed them in their own suborder within the Cassiduloidea, whereas Durham and Wagner (1966) removed them completely from the Cassiduloidea, placing them in their own order, Neolampadoidea.

Representatives from each of the four extant groups have been included, on the basis of study of museum material. As representative of Cassidulidae I included *Rhyncholampas conradi* (Conrad) from the late Eocene of Florida and the Recent *Cassidulus cariboeorum* Lamarck. Two Echinolampadidae were included, *Echinolampas alta* Duncan and Sladen, from the middle Eocene of India, and *E. leymeriei* Cotteau, from the middle Eocene of France, representing morphological extremes. The genus *Studeria* is represented by *Studeria elegans* (Laube) from the Miocene of Australia and *S.*

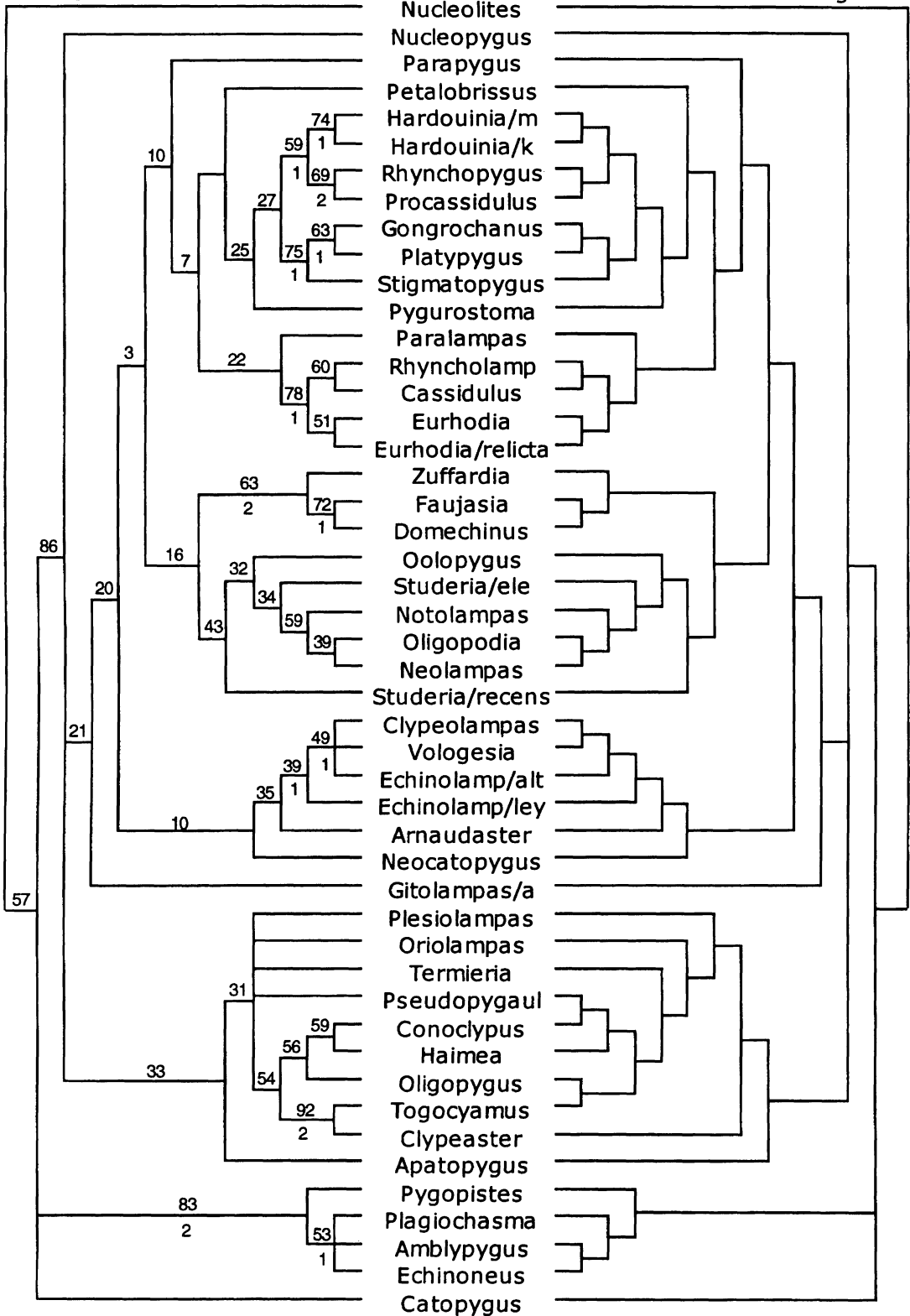
recens (Agassiz). Among neolampadids, *Neolampas*, from the upper Miocene of Australia, is the least derived and is scored on the basis of the description given by Philip (1963). *Neolampas rostellata* Agassiz is included as an extant representative of that clade. The Recent *Oligopygus epigonus* (van Martens) was scored on the basis of museum specimens and data on *Eurhodia relictata* Mooi are taken from the detailed description given by Mooi (1992). Finally, I included *Apatopygus recens* (Milne Edwards) as the best known representative of the Apatopygidae, on the basis of museum specimens and the excellent description given by Baker (1983). *A. mannumensis* Holmes (1999) (Fig. 1), from the Miocene of Australia, is undoubtedly congeneric and was used as the fossil representative.

In the Late Cretaceous cassiduloids were much more diverse. Twenty-three genera are recognized in the Maastrichtian and a further four appear in the Paleocene (Smith and Jeffery 2000). Using data presented by Smith and Jeffery (2000), I included the following Maastrichtian–Paleocene taxa: *Nucleopygus*, *Pygopistes*, *Plagiopasma*, *Amblypygus*, *Catopygus*, *Parapygus*, *Zuffardia*, *Faujasia*, *Domechinus*, *Oolopygus*, *Petalobrissus*, *Paralampas*, *Harduinia mortonis*, *Harduinia kellumi*, *Gongrochanus*, *Platypygus*, *Stigmatopygus*, *Rhynchopygus*, *Procassidulus*, *Eurhodia*, *Pygurostoma*, *Clypeolampas*, *Vologesia*, *Gitolampas abiadensis*, *Neocatopygus*, *Arnaudaster*, *Plesiolampas* (Fig. 1), *Oriolampas*, *Termieria*, and *Pseudopygaulus*.

Oligopygoids.—The oligopygoids include just two genera, *Haimea* and *Oligopygus*. These were first described by Michelin (1851) as cassiduloids, and were treated as such by most nineteenth- and twentieth-century taxonomists, including Mortensen (1948). However, Durham and Melville (1957) recognized that both included genera had lanterns as adults, and they placed them, together with a third genus, *Conoclypus*, in a suborder of the Holecypoida, the Conoclypina. Kier (1967) undertook a magnificent study of the two genera and provided a wealth of new data, including information on their lanterns and perignathic girdles. Kier found a very close resemblance between oligopygids and clypeasteroids, especially in lantern form, and argued that the

unweighted

weighted



two were close relatives. However, the presence of demiplates and the absence of multiple ambulacral pores in oligopygoids served to keep them separate from clypeasteroids.

Two oligopygid taxa were included, *Haimea ovumserpentis* (Guppy), from the middle Eocene of Jamaica (Fig. 1), and *Oligopygus wetherbyi* de Loriol, from the late Eocene of Florida.

Conoclypids.—*Conoclypus* is another exclusively fossil taxon that was initially placed in the Cassiduloida. However, Loriol (1880, 1881) described a lantern from this genus, and there is also a large and well-developed perignathic girdle. These features distinguish *Conoclypus* from other cassiduloids and caused Mortensen (1948) to remove this genus into its own suborder, Conoclypina. Furthermore, it has a distinctive ambulacral plating with extensive development of pyrinoid plates below the petals (Fig. 4E). Durham and Melville (1957) transferred the Conoclypina to the Holoctypoida and added the oligopygids, on account of the similarity of their lanterns. However, both Philip (1963, 1965) and Kier (1967) continued to treat *Conoclypus* as a cassiduloid that had retained its lantern into adulthood. "*Clypeolampas*" *helios* Noetling, from the Maastriichtian of Baluchistan, may represent the oldest conoclypeid, but internal structures in this species remain unknown.

Conoclypus sindensis Duncan and Sladen, from the latest Paleocene, and *C. alveolatus* Duncan and Sladen, from the Eocene of the Middle East and India (Fig. 1), formed the basis for scoring this taxon.

Echinoneidae.—The extant *Echinoneus cyclostomus* Leske was included as the most primitive known extant irregular echinoid. Although it was held to be a cassiduloid when first described, Mortensen (1948) transferred it to the Holoctypoida because of its lack of petals and retention of a lantern into adulthood.

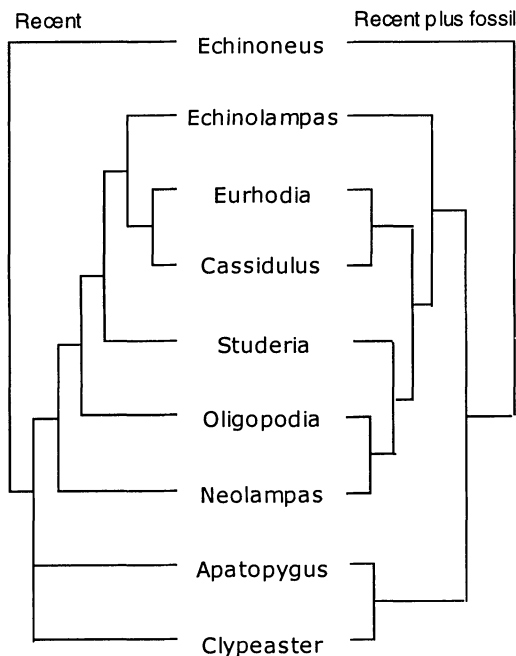


FIGURE 3. Strict consensus of the two equally most parsimonious trees derived when only extant cassiduloid genera are included (left-hand side) compared against a pruned version of the results from the full analysis using Recent and fossil taxa (Fig. 2)

Results

An initial parsimony analysis with all characters treated as of equal weight produced a total of 48 equally parsimonious solutions in a single tree-island cluster (Fig. 2). Tree length was 179 steps, with a Consistency Index (CI) of 0.33 and a Retention Index (RI) of 0.73. In order to select a working hypothesis, characters were then reweighted according to maximum values of rescaled consistency index (which down-weights characters that show greater degrees of homoplasy) and a second analysis carried out. This resulted in just six equally parsimonious solutions, a subset of the original 48, and a strict consensus of these requires just two trichotomies (Fig. 2). Bootstrap and Bremer Support values are, howev-

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FIGURE 2. Semistrict consensus tree from the 48 equally parsimonious cladograms derived from treating all characters as of equal weight (left-hand side: unweighted), and semistrict consensus of the six equally most parsimonious trees found after reweighting characters according to their rescaled consistency index (right-hand side: weighted). Numbers above branches are bootstrap values, those below the line are Bremer support values for unweighted analysis.

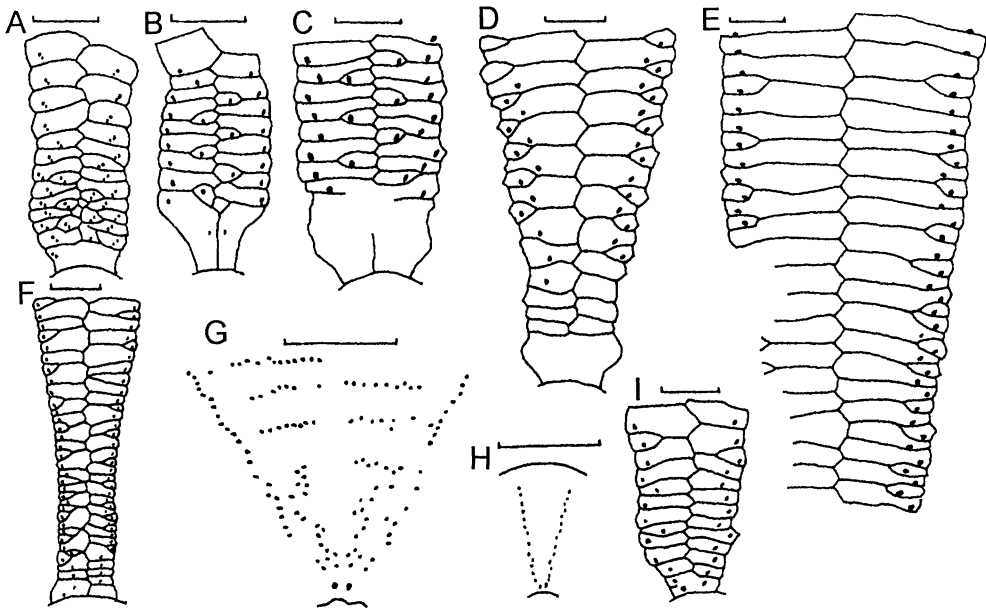


FIGURE 4. Adoral ambulacral plating in cassiduloids and clypeasteroids. A, *Nucleolites crepidula* Desor, in Agassiz and Desor; Bathonian of Yonne, France, NHM E11249. B, *Petalobrius* (*Paralampus*) *platisternus* Smith; Maastrichtian of Oman, NHM EE3535. C, *Oriolampus saharae* (Bather); late Paleocene of Mali, NHM E9326. D, *Haimea ovumserpentis* (Guppy); middle Eocene of Jamaica, NHM E75919. E, *Conoclypus alveolatus* Duncan and Sladen; Eocene of Pakistan, NHM E699. F, *Apatopygus recens* (Milne Edwards); Recent of New Zealand (from Hawkins 1920: Plate 7, Fig. 1). G, *Eoscutum concava*; middle Eocene of Libya (primitive crown-group clypeasteroid), NHM E79768 (pores follow transverse and adradial plate sutures). H, *Togocyamus seegfriedi* (Oppenheim); late Paleocene of Gold Coast, NHM E37649 (pores follow adradial plate sutures with three pores to a primary plate). I, *Plesiolumpas placenta* Duncan and Sladen; late Paleocene of Pakistan, NHM E78090. Scale bars, 1 mm.

er, disappointingly low for most branches. The analysis including just extant taxa identified two equally parsimonious trees with length of 59 steps, differing in basal branch order (Fig. 3). This topology is very different from that identified when fossil taxa are included, although only an additional two steps are required to derive the topology of modern taxa inferred from the full analysis.

Discussion

The Sister Group of Clypeasteroids.—During the nineteenth and early part of the twentieth centuries it was almost universally held that clypeasteroids arose from among Mesozoic holectypoids (e.g., Hawkins 1912). This view was based on the fact that both groups had a lantern as adults, a feature observed in no other irregular echinoid group. Mortensen (1921, 1948) was the first to cast doubt on this simple dichotomy of irregular echinoids into those with lanterns and those without. He found that fully formed lanterns developed in juve-

nile cassiduloids but that these were resorbed during ontogeny. This observation led him to conclude that cassiduloids must themselves have evolved from jawed ancestors, and he considered that four separate lines of irregular echinoid—holectypoid, cassiduloid, clypeasteroid, and spatangoid—evolved independently from regular echinoids. Nevertheless, the association of clypeasteroids and holectypoids (Gnathostomata) as distinct from cassiduloids and spatangoids (Atelostomata) continued to be popular and was the classification adopted by Durham (1966a) in the *Treatise on Invertebrate Paleontology*.

Kier (1967) made a major advance when he identified the extinct oligopygoids as the closest fossil group to clypeasteroids, on the basis of the detailed similarity of their lanterns and perignathic girdles. This led him a few years later to remark that "the resemblance between the oligopygoid-clypeasteroid lantern and the cassiduloid lantern suggests that the oligopygoids and clypeasteroids evolved from a

cassiduloid ancestor" (Kier 1974: p. 55). Mooi (1990a) subsequently identified *Togocyamus* as a late stem-group member positioned between oligopygids and crown-group clypeasteroids.

Morphological analysis of Recent taxa alone fails to resolve the sister-group relationships of clypeasteroids to cassiduloids. However, when fossil taxa close to the inferred time of divergence are included, *Apatopygus* is identified as the extant sister group to Clypeasteroids. No synapomorphies exist linking the extant members of these two clades, and it is key fossil taxa displaying intermediate character combinations that provide critical data. This is almost certainly because paedomorphosis played a major part in the origin of this clade.

Phelan (1977) first noted that fibulariid clypeasteroids showed many simple test characters, such as a single-pored madreporite, poorly defined petals, and lack of food grooves, which suggested that they may have evolved from the juvenile stage of their ancestor. He also noted that cassiduloids by the end of the Cretaceous had evolved a monobasal apical disk, single ambulacral pores below the petals, respiratory tube feet between plates rather than within plates, and distinctive buccal pores, all of which were also present in the earliest clypeasteroids. Finally, he noted that the lack of compasses in clypeasteroid lanterns also pointed to their origin through neoteny, since compasses are the last elements to form in the ontogeny of a regular echinoid lantern. All of these observations suggested to him that clypeasteroids had evolved from the juvenile stage of a cassiduloid through curtailed development. Phelan's basic premise has subsequently been accepted by almost all workers (Jensen 1981; Smith 1981; Mooi 1990a; Suter 1994a,b). The same point was emphasized by Kier (1982) for *Togocyamus*, a taxon that never gets larger than 5 mm. *Togocyamus*, as the immediate sister group to crown-group clypeasteroids, lies very close to the latest common ancestor of all modern clypeasteroids. This paedomorphic phase in the evolution of clypeasteroids had two effects: it resulted in the simplification of body form and the loss of many of the derived adult morphologies of immediate predecessors, and it

provided a clean slate on which to build the adult clypeasteroid bodyplan.

Togocyamus is, however, not key to this phylogenetic analysis. Adding *Togocyamus* to the data matrix of extant genera did not help to resolve the phylogenetic relationships of clypeasteroids and cassiduloids (analysis not shown). This is because *Togocyamus* is so juvenile and generalized in much of its morphology that it groups with the most paedomorphic of the cassiduloid clades, the neolampadids. The key taxon is the plesion that immediately preceded the paedomorphic event, namely the oligopygids.

The importance of oligopygids from a phylogenetic perspective is that they have not undergone such a drastic juvenilization of their morphology as *Togocyamus*. In particular, they retain a unique and characteristic ambulacral plating style that is otherwise seen in only two clades of cassiduloid, the Pygaulidae and Apatopygidae. Hawkins (1920) first pointed out the very unusual natural of ambulacral plating in *Apatopygus* when erecting this genus. In *Apatopygus* every third ambulacral plate is reduced to a small demiplate restricted to the adradial boundary, a pattern that persists from the base of the petals to the peristome (Fig. 4F). This so-called 'pyrinoïd' plating style is seen also in the phylloides of *Plesiolumpas* and is more extensively developed in *Conoclypus* and the oligopygoid genera (Fig. 4) but is absent from all subsequent clypeasteroids. Pyrinoïd plating is present in the echinoneïds and pygaulids but in no other Cretaceous cassiduloid clade. When other characters such as peristome morphology and phylloïde structure are taken into account, it is clear that only *Apatopygus* and its relatives could be close relatives of clypeasteroids. Thus the crucial data are provided by identifying a fossil taxon that is immediate sister group to the highly paedomorphic precursor to crown-group clypeasteroids.

The Dismemberment of the Cassiduloïda.—Although the Cassiduloïda has long been treated as a taxonomic grouping on a par with Clypeasteroïda and Atelostomata, they are clearly a grade, not a clade. Some cassiduloïds belong to the stem group of the cassiduloïds plus clypeasteroids, others fall clearly within stem or

crown groups of the four major existing cassiduloid clades, while a few turn out to be stem-group clypeasteroids. Although the analysis fails to identify robust sister-group pairings, an initial attempt at defining clades can be made.

Most Jurassic taxa, along with the Cretaceous Nucleolitidae and Clypeidae belong to the stem lineage of cassiduloids and clypeasteroids combined. They are thus stem-group Neognathostomata. Future research needs to be directed toward determining the branching order of the various plesions leading up to the crown group.

Among crown-group neognathostomates the earliest dichotomy is between echinoneids and other neognathostomates. Echinoneids have a very characteristic asymmetrical peristome and the oldest undoubted member of this clade is Late Jurassic. They have long been recognized as the most primitive extant irregular echinoid. Durham (1966a) placed them within the Holoctypoida on the basis of shared plesiomorphic conditions, but they have recently been separated off into their own order, the Echinoneoida Clark 1925 (Smith and Wright 1999).

The next split separates the majority of Cretaceous and Tertiary cassiduloids from a line leading to the extant *Apatopygus* and clypeasteroids. As the former contains *Cassidulus*, it would seem sensible to restrict the name Cassiduloida to this clade. Three extant clades comprise the Cassiduloida sensu stricto, the Echinolampadidae, Neolampadidae, and Cassidulidae, with the latter two identified as sister groups, although on very weak support.

Three extant genera, *Rhyncholampas*, *Cassidulus*, and *Eurhodia*, form a clade and share, among other features, the posterior, transverse periproct, broad, tubercle-free, pitted zones on the oral surface, and transverse and weakly swollen basicornal plates that form a vertical-walled entrance to the peristome. The Late Cretaceous *Paralampas* is identified as their immediate sister taxon, with the Late Cretaceous Faujasiidae as a more basal plesion. The oldest available name for this clade is Cassidulidae Agassiz and Desor 1847.

The Neolampadidae, rather than representing a distinct order, are simply a specialized

paedomorphic offshoot that has moved into the deep-sea environment. Most show distinct sexual dimorphism of gonopore size and the majority have just three gonopores, there being no gonopore in genital plate 3. The clade can be traced back to the Cenomanian *Penesticta* and the oldest available name for this clade is Neolampadidae Stefanini 1913.

Echinolampas is the most diverse of the Recent genera of cassiduloid and it belongs to a clade that includes the Late Cretaceous *Arnau-daster* and Clypeolampadidae.

The apatopygid-clypeasteroid clade is sister group to the Cassiduloida sensu stricto, with *Togocyamus*, Oligopygidae (including *Conoclypus*), and *Plesiolampas* as successively more basal plesions of the Clypeasteroida.

Critical Data from Fossils.—Despite the relative paucity of characters provided by fossils, paleontological data are often seen as pivotal when trying to reconstruct phylogenetic relationships of extant taxa (Donoghue et al. 1989; Smith 1994; Wills et al. 1995; Brochu 1997; Sumrall 1997; Lee 1998). Furthermore, computer simulation experiments suggest that more accurate estimates of phylogenetic relationships may be achieved if fossil taxa are included (Huelsenbeck 1991). Homoplasy is the primary source of error for phylogenetic reconstruction methods, and homoplasy levels tend to increase over time as clades evolve (Wagner 2000a,b).

As homoplasy builds up along long branches in a phylogeny, it becomes progressively more likely that parsimony and other methods will reconstruct false relationships, sometimes with high support (Felsenstein 1978; Huelsenbeck and Hillis 1993; Lecointre et al. 1993). This well-known "long branch attraction" syndrome has long been established as a problem for molecular data and has now also been shown to affect morphological data (Wagner 2000a). Wagner examined 56 cladistic analyses involving fossil taxa and found that in most there was evidence that new character states were distinctly limited in number and non-uniformly distributed through time. In general he found that there was a reduction in the appearance of new character states in clades over time and a corresponding increase in levels of homoplasy. This phenomenon

Wagner referred to as "character exhaustion." Thus, not only do homoplasy levels rise through chance convergence as branch lengths get longer in phylogenetic trees, but innovation in morphological design also supposedly becomes less common in the latter part of a clade's history. Both effects act to decrease the chances of capturing the correct phylogenetic relationships of deep branches.

In the case of Neognathostomata (i.e., cassiduloids plus clypeasteroids), character exhaustion does occur, but it is decidedly skewed over the phylogenetic tree. New character suites continued to evolve in the more crownward parts as clypeasteroids diverged and specialized. Thus over the past 55 Myr clypeasteroid morphology has increased significantly in complexity with the evolution of complex patterns of radial water-vessel lobes and associated accessory tube feet, origin and increase in complexity of internal buttressing, extreme modification in the design of their lantern elements, and origin and morphological differentiation of a complex food-groove system. All represent morphological novelties that greatly increase the number of character states that can be scored. By contrast, the more basal clades of neognathostomate that continue through the Tertiary are morphologically highly conservative. Among cassiduloids, the most recent innovation in test morphology that created a new suite of scorable characters was the development of a naked interradial zone on the oral surface, a Late Cretaceous innovation. So effectively, from the Late Cretaceous onwards cassiduloid evolution has involved the "shuffling" of a limited suite of test characters without innovation. Character exhaustion is thus not uniformly distributed across the Neognathostomata.

Curtailed development, in the form of evolution through neoteny or progenesis, is another major source of error. It effectively removes many if not all of the derived character traits that characterize the ancestral adult. Lineages that originate through curtailed development are often particularly difficult to place phylogenetically. Thus the analysis of Recent neognathostomates failed to give satisfactory results because taxa with shared ju-

venile features were paired together and placed basally.

Access to fossil data might be expected to alleviate problems of character exhaustion through shortening the lengths of internal branches and to reveal morphologies that existed before paedomorphic bottlenecks. However, adding all available fossil data seems to make the problem worse. Suter (1994a) included all cassiduloid genera from the Middle Jurassic onwards but found many thousands of equally parsimonious solutions. Suter's data matrix not only had a very low character-to-taxon ratio (71 taxa and 40 characters) but was one of those analyzed by Wagner (2000a) and found to show high levels of character exhaustion. The total-evidence approach failed here because there were simply too few characters available and character states were being endlessly recycled. It would therefore appear that if too many fossil taxa are added that span a long interval of geological time then character exhaustion among the longer, more basal branches starts to become a major problem.

The alternative is to make a much more focused selection that includes only those taxa relevant to the question in hand, as carried out above. Ausich (1998a,b) came to a similar conclusion when trying to unravel early crinoid phylogeny. He made separate cladistic analyses of Arenig, Llanvirn, and Caradoc crinoids in an attempt to reduce problems of homoplasy. However, although this approach resulted in a highly resolved hypothesis in comparison to that of Suter (1994b), it has not been entirely successful. Specifically, it has failed to generate reliable support for any of the higher groupings. Relationships still remain tentative despite careful pruning of taxa. Nevertheless, sometimes careful selection of taxa from key time intervals may be better than a total evidence approach.

Acknowledgments

I am grateful for the perceptive reviews of an earlier draft by R. Mooi and P. Wagner. Their constructive criticism has helped improve this paper.

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Appendix 1

Characters Scored in the Cladistic Analysis

1. Apical disk plating: 0 = tetrabasal, with genital plates subequal; 1 = tetrabasal, with all but genital plate 2 reduced to small elements; 2 = monobasal.
2. Gonopore number: 0 = 4; 1 = 3 (G3 missing); 2 = 3 (G2 missing).
3. Sexual dimorphism in gonopore size: 0 = no; 1 = yes.
4. Gonopore opening: 0 = within genital plate; 1 = within interambulacra.
5. Shape of petals: 0 = bowed with convergent columns distally; 1 = approximately parallel.
6. Petal length: 0 = anterior petal longer than other petals; 1 = subequal, anterior petal 80–100% length of other petals; 2 = anterior petal significantly shorter than other petals or absent.
7. Columns in each petal: 0 = of equal length; 1 = unequal in length.
8. Petal termination: 0 = grading gradually into ambital pore-pairs, with no clearly defined end-point 1 = sharply defined termination.
9. Shape of periproct: 0 = transverse (width > 1.2 length); 1 = subcircular (width 0.8–1.2 length); 2 = longitudinal (width < 0.8 length).
10. Position of periproct: 0 = supramarginal; 1 = marginal; 2 = inframarginal; 3 = oral.
11. Subanal region: 0 = flush; 1 = invaginated opening or anal sulcus.
12. Periproct opening forming tubelike invagination: 0 = no; 1 = yes.
13. Roof of periproct distinctly notched: 0 = no; 1 = yes.
14. Periproct with wide subanal depression forming platform: 0 = no; 1 = yes.
15. Shape of peristome: 0 = bilaterally symmetric; 1 = oblique along axis II-5.
16. Shape of peristome: 0 = transverse (width > twice length); 1 = weakly transverse (width = 1.2–1.75 length); 2 = equant (width = 1.2–1.0 length); 3 = longitudinal (width < length).
17. Shape of peristome: 0 = circular; 1 = subpentagonal; 2 = trigonal; 3 = biconvex.
18. Position of peristome: 0 = subcentral (43–50% test-length from the anterior; 1 = weakly anterior (35–42% test-length from anterior); 2 = strongly anterior (<35% test-length from anterior).
19. Perioral area: 0 = undifferentiated; 1 = test curved inwards with simple perioral ring of fine tuberculation; 2 = with vertical-walled vestibule leading into the peristome formed of interambulacral elements.
20. Basicoronal interambulacral plates: 0 = short and transversely wide to squarish; 1 = distinctly longer than wide.
21. Interambulacra adjacent to peristome: 0 = flush and undifferentiated; 1 = weakly tumid and moundlike; 2 = developed as distinct peglike projections.
22. Pseudobourrelets (projections formed of multiple interambulacral plates): 0 = absent; 1 = present.
23. Liplike rim to peristome: 0 = no; 1 = yes.
24. Dense peribuccal granulation around the peristome: 0 = absent; 1 = peribuccal granulation restricted to peristomal walls; 2 = extending radially along the proximal margins of the phyllodes as radial bands.
25. Ambulacral pores beneath petals: 0 = double; 1 = single.
26. Pyrinoid ambulacral plating present adorally: 0 = no; 1 = yes.
27. Ambulacra with small superficial demiplates that do not extend to the interior but are floored by other ambulacral plates: 0 = no; 1 = yes.
28. Buccal pores: 0 = undifferentiated; 1 = differentiated.
29. Position of buccal pores: 0 = immediately adjacent to the edge of the peristome; 1 = at the outer edge of the peristome vestibule; 2 = separated from the peristome by an obvious gap.
30. Buccal pores: 0 = contiguous with phyllodes; 1 = separated by a distinct gap from other phyllode pores.
31. Buccal pores: 0 = similar in size to other phyllode pores; 1 = much smaller than other pores.
32. Phyllodes: 0 = single straight to weakly offset column of pores; 1 = distinct outer and inner columns of pores; 2 = outer series and irregular inner band of pores.
33. Phyllodes: 0 = intermediary pores (between inner and outer series) absent; 1 = present.
34. Phyllode shape: 0 = parallel or tapering adorally; 1 = weakly to strongly bowed; 2 = broad fan-shaped arrangement widening toward the peristome.
35. Inner series of pores in phyllode rudimentary, confined to small arc at adambital end of phyllode: 0 = no; 1 = yes.
36. Sphaerial pits: 0 = absent; 1 = one pair only; 2 = two to many pairs in a column.
37. Lantern muscle attachment structures developed as peglike outgrowths on interior of test in adult: 0 = no; 1 = yes.
38. Internal radial buttressing developed: 0 = no; 1 = yes.
39. Oral surface to rear of peristome: 0 = uniformly covered in tubercles; 1 = narrow interradial band lacking tubercles; 2 = broad tubercle-free zone developed.
40. Oral surface in front of peristome: 0 = uniformly covered in tubercles; 1 = lacking tubercles.
41. Oral surface with ornament of dense pits in tubercle-free zones: 0 = no; 1 = yes.

Appendix 2

Data matrix.

| | | | | | | | | | |
|-------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|---|
| <i>Nucleolites</i> | 00001 | 10020 | 10000 | 11100 | 00000 | 0000? | ?1010 | 20000 | 0 |
| <i>Nucleopygus</i> | 10001 | 10120 | 10000 | 11110 | 00011 | 00110 | 01010 | 20000 | 0 |
| <i>Pygopistes</i> | 10001 | 20022 | 00001 | 12100 | 00000 | 0000? | ?1010 | 00000 | ? |
| <i>Plagiochasma</i> | 10001 | 20020 | 00001 | 12100 | 00000 | 0000? | ?0000 | 00000 | ? |
| <i>Amblypygus</i> | 10001 | 20023 | 00001 | 12100 | 00000 | 0000? | ?0010 | 00000 | ? |
| <i>Catopygus</i> | 10001 | 10011 | 00000 | 21100 | 11010 | 0001? | ?1010 | 20000 | 0 |
| <i>Parapygus</i> | 10000 | 10121 | 00000 | 11101 | 10011 | 00110 | 01010 | 20020 | 0 |
| <i>Zuffardia</i> | 20000 | 10121 | 00000 | 31121 | 20021 | 00111 | 01010 | 20010 | 0 |
| <i>Faujasia</i> | 20010 | 10113 | 00000 | 31121 | 20021 | 00121 | 11010 | 20010 | 0 |
| <i>Domechinus</i> | 20000 | 10113 | 00000 | 31121 | 20021 | 00121 | 01010 | 20010 | 0 |
| <i>Oolopygus</i> | 11101 | 00111 | 11000 | 31121 | 10011 | 00121 | 11010 | 20011 | 0 |
| <i>Studeria elegans</i> | 21101 | 10111 | 11000 | 31121 | 10011 | 00110 | 01010 | 20000 | 0 |
| <i>Notolampas</i> | 21101 | ?0?12 | 11000 | 30121 | 00011 | 00110 | 0100? | 20000 | 0 |
| <i>Petalobrissus</i> | 10000 | 10120 | 10000 | 11121 | 10011 | 00110 | 01010 | 20021 | 0 |
| <i>Paralampas</i> | 20000 | 10121 | 10000 | 11121 | 10011 | 00110 | 11010 | 20021 | 0 |
| <i>Hardouinia mortonis</i> | 10000 | 10110 | 11000 | 21021 | 20021 | 00121 | 01021 | 20021 | 0 |
| <i>Hardouinia kellumi</i> | 10000 | 10120 | 11000 | 21021 | 20021 | 00121 | 01021 | 20021 | 0 |
| <i>Gongrochanus</i> | 12000 | 00120 | 10110 | 11021 | 20021 | 00121 | 12120 | 20021 | 0 |
| <i>Platypygus</i> | 10000 | 00120 | 10110 | 11121 | 20021 | 00121 | 11010 | 20021 | 0 |
| <i>Stigmatopygus</i> | 10000 | 00120 | 10100 | 21121 | 20021 | 00121 | 11010 | 20021 | 0 |
| <i>Rhynchopygus</i> | 10101 | 10110 | 11010 | 21121 | 20021 | 00121 | 10011 | 20021 | 1 |
| <i>Procassidulus</i> | 10000 | 00110 | 11000 | 21121 | 20011 | 00121 | 10011 | 20021 | 1 |
| <i>Rhyncholampas</i> | 20000 | 11101 | 10000 | 11120 | 10011 | 00110 | 01010 | 20021 | 1 |
| <i>Eurhodia</i> | 20000 | 10101 | 10000 | 31220 | 10011 | 00110 | 01010 | 20021 | 1 |
| <i>Cassidulus</i> | 20000 | 11101 | 10000 | 11120 | 10011 | 00110 | 00000 | 20021 | 1 |
| <i>Pygurostoma</i> | 10000 | 10123 | 10000 | 11121 | 20021 | 00120 | 02120 | 20021 | 0 |
| <i>Clypeolampas</i> | 10001 | 10103 | 00000 | 01120 | 11021 | 00120 | 01120 | 20020 | 0 |
| <i>Vologesia</i> | 10001 | 10103 | 00000 | 01220 | 00011 | 00110 | 01110 | 20020 | 0 |
| <i>Gitolampas</i> | 10001 | 20121 | 00000 | 11120 | 00011 | 00110 | 00010 | 200?0 | ? |
| <i>Neocatopygus</i> | 10000 | 10122 | 00000 | 11120 | 00111 | 00110 | 01110 | 20000 | ? |
| <i>Arnaudaster</i> | 10000 | 11122 | 00000 | 11120 | 00011 | 00110 | 01100 | 20010 | 0 |
| <i>Plesiolampas</i> | 20001 | 10123 | 00000 | 03010 | 00001 | 10100 | 01000 | 20010 | 0 |
| <i>Apatopygus</i> | 10001 | 10120 | 10000 | 13110 | 00001 | 10100 | 01000 | 20000 | 0 |
| <i>Oriolampas</i> | 20001 | 10113 | 00000 | 11010 | 00001 | 00100 | 01000 | 20010 | 0 |
| <i>Termieria</i> | 20000 | 20113 | 00000 | 20110 | 00001 | 00100 | 00000 | 20010 | 0 |
| <i>Pseudopygaulus</i> | 20000 | 20123 | 00000 | 13110 | 00001 | 00100 | 01000 | 20010 | 0 |
| <i>Conoclypus</i> | 20001 | 10123 | 00000 | 11010 | 01001 | 11100 | 00000 | 21000 | ? |
| <i>Oligopygus</i> | 20001 | 10113 | 00000 | 10010 | 00001 | 11100 | 00000 | 21000 | ? |
| <i>Haimea</i> | 20001 | 10113 | 00000 | 21010 | 01001 | 11100 | 00000 | 21000 | ? |
| <i>Togocyamus</i> | 20001 | 10110 | 00000 | 2000? | 00001 | ??100 | 00000 | 11100 | ? |
| <i>Echinolampas alta</i> | 20001 | 10103 | 00000 | 01120 | 01011 | 00110 | 01100 | 20010 | 0 |
| <i>Echinolampas leymeriei</i> | 20000 | 11103 | 00000 | 11020 | 00011 | 00110 | 01000 | 20010 | 0 |
| <i>Oligopodia</i> | 20101 | 10121 | 11000 | 30120 | 00011 | 00110 | 00000 | 20000 | 0 |
| <i>Eurhodia relicta</i> | 20000 | 10101 | 10000 | 31120 | 10011 | 00110 | 01010 | 20021 | 1 |
| <i>Studeria recens</i> | 21101 | 10111 | 10000 | 31121 | 10021 | 00011 | 01011 | 20000 | 0 |
| <i>Echinoneus</i> | 2000? | ??023 | 00001 | 22000 | 00000 | 100?? | ?000? | 00000 | 0 |
| <i>Clypeaster</i> | 20000 | 10113 | 00000 | 20000 | 00001 | 00100 | 0???? | 11100 | 0 |
| <i>Neolampas</i> | 21101 | ??11 | 11000 | 20121 | 00011 | 00100 | 00000 | 20000 | 0 |