



Molecular phylogeny of the Valvatacea (Asteroidea: Echinodermata)

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The Valvatacea is one of the most ecologically important, taxonomically diverse, and widespread groups of post-Palaeozoic (i.e. modern) Asteroidea. Classification within the group has been historically problematic. We present a comprehensively sampled, three-gene (12S, 16S, early-stage histone H3) molecular phylogenetic analysis of the Valvatacea. We include five of the six families within the Paxillosida, the monotypic Notomyotida, and 13 of the 16 families of the living Valvatida. The Solasteridae is removed from the Velatida (Spinulosacea) and joins the Ganeriidae and the Leilasteridae as members of the clade containing the Asterinidae. The Poraniidae is supported as the sister group to the large cluster of Valvatacea. Asteropseids and poraniids are phylogenetically distant, contrary to morphological evidence. Several goniasterid-like ophiasterids, such as *Fromia* and *Neoferdina* are supported as derived goniasterids rather than as Ophiasteridae. The Benthoplectinidae (Notomyotida) are supported as members of the Paxillosida as are two members of the Pseudarchasterinae that have traditionally been considered members of the Goniasteridae. Our data suggest that Antarctic valvataceans may be derived from sister taxa in adjacent regions.

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INTRODUCTION

The Valvatacea (*sensu* Blake, 1987) is one of three superorders, in addition to the Forcipulatacea and the Spinulosacea, within the post-Palaeozoic Asteroidea. Valvataceans occur worldwide, especially in the tropical Indo-Pacific region (A.M. Clark & Rowe, 1971; Blake, 1990) where they are amongst the most frequently encountered and taxonomically diverse Asteroidea known.

The Valvatacea includes some of the most widely studied and ecologically important families of asteroids, including the Asterinidae, the Oreasteridae, the Goniasteridae, and the Ophiasteridae (all in the Valvatida) as well as the Astropectinidae and the

Luidiidae (in the Paxillosida). The Asterinidae (popularly known as bat stars or cushion stars) are studied in multiple fields, including developmental biology and larval biology (e.g. Byrne *et al.*, 2005; Byrne, 2006). Other families, such as the Oreasteridae and the Ophiasteridae, are commonly taken as tourist trinkets. These exploited species, especially oreasterids such as *Protoreaster*, have become a subject of concern by conservation biologists (e.g. Bos *et al.*, 2008; Scheibling & Metaxas, 2008). The Goniasteridae includes many taxa that have not been studied since their original description, but is the largest and most diverse family of living asteroids. However, some goniasterids, such as the cold-water *Hippasteria*, are known to be ecologically important as predators of cnidarians, including sea pens (Birke-land, 1974) and deep-sea corals (Krieger & Wing, 2002; Mah, Nizinski & Lundsten, 2010). Other

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members of the Valvatacea, such as the astropectinids and luidiids, are ecologically important members of benthic communities living in sandy and/or unconsolidated sediment habitats (e.g. McClintock & Lawrence, 1985; Hart, 2006), where they prey upon bivalves and other molluscs. Astropectinids and luidiids, along with other members of the Paxillosida, have also played an important role in the understanding of asteroid evolution (e.g. Wada, Komatsu & Satoh, 1996).

BACKGROUND: CLASSIFICATION OF THE ASTEROIDEA

Concepts of modern higher classification amongst living Asteroidea, particularly for nonforcipulate Asteroidea, began with Perrier (1884, 1894) and were later summarized and modified by Sladen (1889) and Fisher (1911). Perrier (1884) heavily emphasized pedicellariae as the diagnostic features for his four groups, the Forcipulatae, Spinulosae, Valvatae, and Paxillosae. Sladen (1889) developed a different classification that largely emphasized marginal plates and regrouped the higher classification into the Phanerozonia, which included several groups displaying prominent marginal plate series versus those in the Cryptozonia, which included those groups that displayed more inconspicuous marginal plate series. Sladen's perspectives were significantly modified by Fisher (1911) who established a broad division into three groups that is still largely used today in asteroid classifications. It was during this period that the discussions between Mortensen (1922, 1923) and MacBride (1921, 1923) took place, focusing on ancestral forms in asteroids, an issue that we will re-visit in our Discussion section. Spencer & Wright (1966) modified Fisher's (1911) classification by placing fossils alongside modern asteroid taxa. Their treatment was heavily influenced by the work of Fell (1962a, b) and his interpretation of the Luidiidae as recent survivors of the Palaeozoic, a perspective that was later contested by Blake (1972). Blake (1972) dismantled the Platyasterida and placed the Luidiidae in the Paxillosida.

Gale (1987b) and Blake (1987) both undertook extensive morphological cladistic analyses addressing higher-level classification of the Asteroidea. Both studies supported a post-Palaeozoic crown group clade of asteroids (Gale's Neoasteroidea), in spite of having substantial fundamental differences in tree topology, primarily regarding basal relationships amongst the Neoasteroidea. Several molecular analyses of asteroids have since been undertaken, including Lafay, Smith & Christen (1995), Wada *et al.* (1996), Knott & Wray (2000), Janies (2001), Matsubara, Komatsu & Wada (2004), and Matsubara *et al.* (2005). Tree topologies vary, but practically all of

these efforts reconstructed phylogenetic history from relatively few specimens as exemplars of the major lineages present within the Asteroidea.

Here, we present the most comprehensively sampled molecular phylogeny yet produced for the Valvatacea. Our goal is not to determine basal asteroid relationships, for which the presently available molecular data are probably inadequate (e.g. Smith *et al.*, 2004; Foltz *et al.*, 2007). Instead, we address the classification of prominent familial groups within this superorder (such as the Asterinidae and the Goniasteridae). These groups have particular importance to diverse fields in biology but are taxonomically complicated and have historically been difficult to classify.

MATERIAL AND METHODS

MOLECULAR METHODS

For the main analysis of Valvatacea shown in Figure 1, DNA extraction, PCR and sequencing were carried out as in Foltz *et al.* (2007) and Foltz & Mah (2009). Sequences (~355 bp of the mitochondrial 12S rDNA gene, ~625 bp of the 16S rDNA gene, and 327 bp of the nuclear early-stage histone H3 gene) were assembled and reconciled in SEQUENCHER 4.0. Each gene region was aligned separately in ClustalX (Thompson *et al.*, 1997). Conserved regions within each rDNA alignment were identified with the program GBlocks v. 0.91b (Castresana, 2000), using the following options: (1) minimum length of a conserved block was set to five nucleotides and (2) gaps were allowed provided they constituted less than half of the data per site, with further editing to remove priming sites and several poorly aligned regions. The data as analysed had 254 bp for the 12S gene, 503 bp for the 16S gene, and 327 bp for the histone H3 gene (1084 bp total). Concatenated sequences were submitted as a sequential PHYLIP file to the www.phylo.org server for analysis by RAxML (Stamatakis, 2006), with the following options specified: (1) bootstrapping with the number of replicates (150) determined automatically; (2) a mixed/partitioned model with each gene region treated separately; (3) per gene branch length optimization; and (4) the GTR + G substitution model, which is a general time-reversible nucleotide substitution model with gamma-distributed rate heterogeneity among sites. To permit our results to be compared with those of Waters, O'Loughlin & Roy (2004a, b) on the Asterinidae, we also amplified larger regions of the 12S and 16S rDNA genes in selected taxa. As this work relied mostly on extracting, amplifying, and sequencing mitochondrial DNA from preserved museum specimens (for technical details, see Foltz *et al.*, 2008), we used a combination of existing PCR primers and their complements (Wada *et al.*,

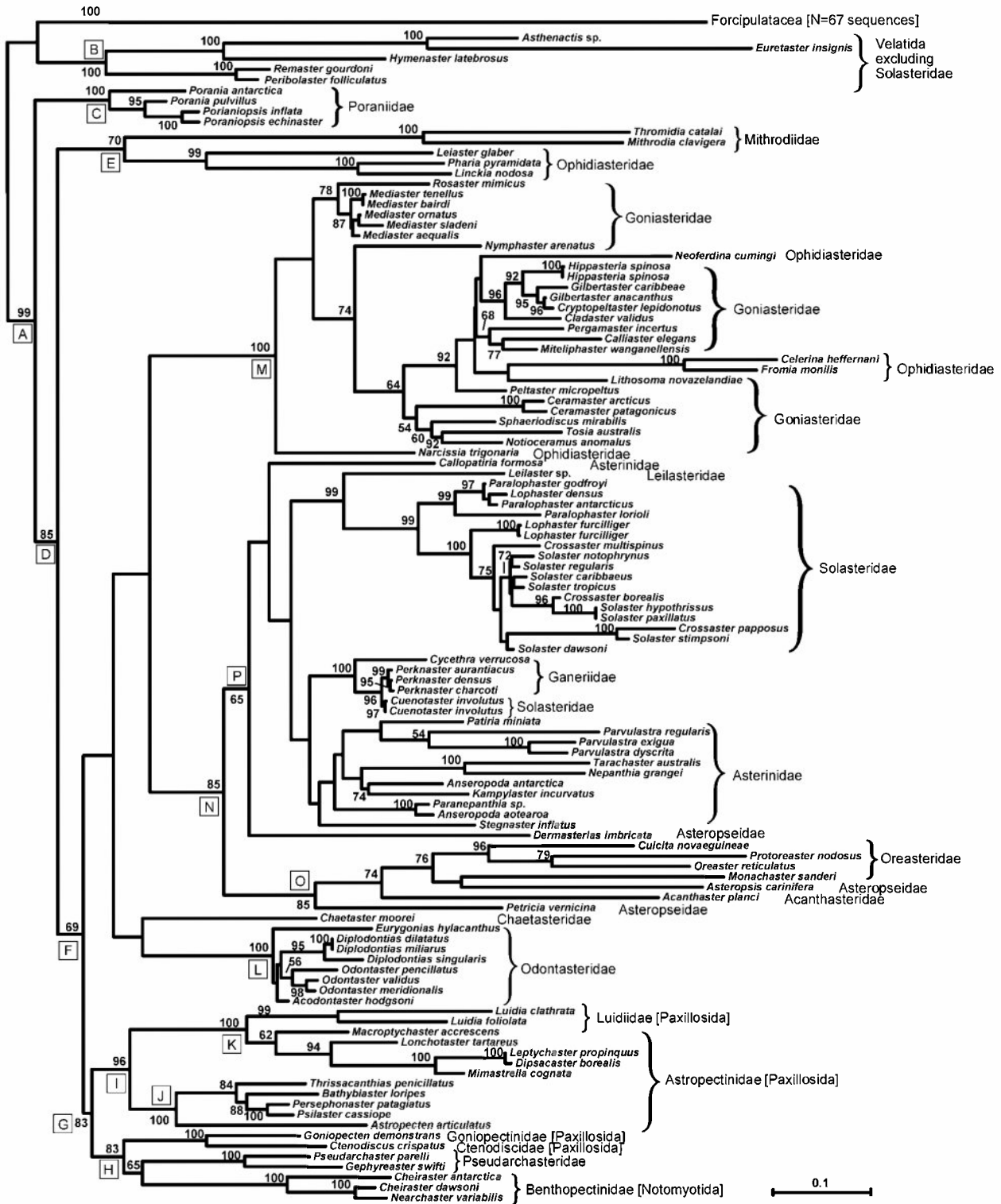


Figure 1. Maximum likelihood tree of valvatacean sea stars rooted against forcipulatacean + velatid sea stars. The analysis is based on 1084 bp of concatenated sequence data from two mitochondrial rDNA genes and one nuclear protein-coding gene, early-stage histone H3. As discussed in the text, solasterids are treated as part of the ingroup. The analysis was carried out in RAxML with bootstrap percentages indicated for nodes that had > 50% support. Boxed letters A–P are referred to in the text. Traditional family names are shown at the right; all families are in the Valvatida except as noted. The scale bar shows the expected number of substitutions.

1996; Waters *et al.*, 2004a,b, Foltz *et al.*, 2007) and two novel primers (see Appendix 2) that amplified the two rDNA genes in abutting pieces that ranged in size from 250–600 bp.

TAXON SELECTION

Difficulties in determining the root of the asteroid tree via outgroup rooting have been discussed and summarized by Foltz *et al.* (2007). Previous phylogenetic studies have variously put the Paxillosida, Valvatida, Spinulosida, or Forcipulatida closest to the root, when the tree was rooted against other echinoderm sequences. These varying results could be because of rate heterogeneity amongst genes or lineages, combined with differences amongst studies in taxon selection and the absence of a close sister group to the Asteroidea. In the present study, inclusion of sequences from some representative pterasterids (*Pteraster* and *Diplopteraster*) and echinasterids (e.g. *Henricia*) produced long terminal or subterminal branch lengths in preliminary analyses, and were excluded from the definitive analyses reported here. These long branches could reflect rate heterogeneity or (in the case of the histone H3 gene) possible gene conversion or amplification of a paralogous gene copy (Foltz & Mah, 2010). The most taxon-rich of earlier molecular phylogenetic analyses (Foltz *et al.*, 2007; C. Mah & D. Foltz, unpubl. data) have suggested that forcipulatacean sea stars (Forcipulatida + Brisingida), or possibly Forcipulatacea + Pterasteridae, are a monophyletic assemblage. A close relationship between the Forcipulatacea and Pterasteridae is also supported by presence/absence data for two ancient repeats in the ATP synthase, β subunit gene (Foltz, 2007). Additionally, phylogenetic analysis of a more slowly evolving paralogous copy of the histone H3 gene suggests a basal split between forcipulates and valvatids, when rooted on sea urchin sequences (no spinulosids, velatids, brisingids, paxillosids, or notomyotids were included in this analysis: Foltz & Mah, 2010). Therefore, in the present study valvatacean sequences ($N = 89$ sequences representing 88 nominal species in the Notomyotida, Paxillosida, and Valvatida) were rooted on forcipulataceans ($N = 67$ sequences) plus five velatidan sequences (from the Korethasteridae, Myxasteridae, and Pterasteridae). Matsubara *et al.* (2004) had previously suggested a close relationship between the Asterinidae and the Solasteridae, so we also included solasterid sequences ($N = 19$ sequences representing 17 species) as part of the ingroup, even though solasterids are traditionally assigned to the Velatida. Details on all nonforcipulatacean taxa included in the analysis, such as GenBank accession numbers and specimen voucher numbers (where available), are in Appendix 1. Approximately

80% of the sequences in Appendix 1 were collected as part of the present study and are analysed here for the first time. Nearly all families traditionally assigned to the Valvatida, the Paxillosida, and the Notomyotida were sampled. This included, for the Valvatida, the Asterinidae, Asteropseidae, Chaetasteridae, Ganeridae, Goniasteridae (including the Pseudarchasterinae), Mithrodiidae, Odontasteridae, Ophidiasteridae, Oreasteridae, and the Poraniidae; for the Paxillosida, the Astropectinidae, Ctenodiscidae, and the Luidiidae; and for the Notomyotida, the Benthoplectinidae (all taxa follow the nominal classification of A.M. Clark, 1989, 1993, 1996). Higher level classification used herein is summarized in Table 1. Multiple genera were sampled from each family in order to represent better the morphological diversity of each group. Subfamily groupings, where present (e.g. the Hippasterinae in the Goniasteridae), were sampled to test their monophyly. We were able to comprehensively sample several families, including the monotypic Chaetasteridae and Ctenodiscidae plus both genera in the Mithrodiidae, and we were able to sample nearly completely the Odontasteridae and the Solasteridae. Some families, such as the Goniasteridae and the Asterinidae have a large number of genera and although sampling was adequate to test monophyly and show diversity, further in-depth sampling is needed.

Preliminary analyses with the three-gene data set suggested that taxa closely related to the asterinids included *Leilaster*, several solasterid genera (*Crossaster*, *Lophaster*, *Paralophaster*, and *Solaster*) traditionally included amongst the Velatida, *Acanthaster*, several oreasterids (*Culcita*, *Monachaster*, *Oreaster*, *Pentacaster*, and *Protoreaster*), and several asteropseids (*Asteropsis*, *Dermasterias*, and *Petricia*). Therefore, our analysis of the Asterinidae using an expanded rDNA sequence data set included one or more representatives of each of the above genera, as well as available asterinid sequences from GenBank (see Appendix 1 for details). The mitochondrial-only rDNA data set was also curated with the program GBlocks and analysed by RAxML, using the same settings as for the three-gene data set. The mitochondrial-only analysis included 732 bp of the 12S rDNA gene and 685 bp of the 16S rDNA gene.

RESULTS

CLADE GROUPINGS AND SUPPORT

Basal support for the three-gene tree (Fig. 1) rooted against forcipulatacean + velatidan sea stars is strong (node A, bootstrap support = 99%) and upholds a dichotomy between velatidan taxa minus the Solasteridae (i.e. *Hymenaster*; *Euretaster*; *Asthenactis*,

Table 1. Existing classification of Valvatacea *sensu* Blake (1987) and A.M. Clark (1993)

Valvatacea
Notomyotida
Benthopectinidae: <i>Cheiraster</i> ; <i>Nearchaster</i>
Paxillosida
Astropectinidae: <i>Astropecten</i> , <i>Bathybiaster</i> , <i>Dipsacaster</i> , <i>Leptychaster</i> , <i>Lonchotaster</i> , <i>Macroptychaster</i> , <i>Mimastrella</i> , <i>Persephonaster</i> , <i>Psilaster</i> , <i>Thrissacanthias</i>
Ctenodiscidae: <i>Ctenodiscus</i>
Goniopectinidae: <i>Goniopecten</i>
Luidiidae: <i>Luidia</i>
Porcellanasteridae (NS)
Radiasteridae (NS)
Valvatida
Incertae sedis- <i>Leilaster</i> (Leilasteridae)
Archasteridae (NS)
Asterinidae: <i>Anseropoda</i> , <i>Aquilonastra</i> , <i>Asterina</i> , <i>Callopatiria</i> , <i>Kampylaster</i> , <i>Meridiastra</i> , <i>Nepanthia</i> , <i>Paranepanthia</i> , <i>Parvulastra</i> , <i>Patiria</i> , <i>Patiriella</i> , <i>Stegnaster</i> , <i>Tremaster</i>
Acanthasteridae: <i>Acanthaster</i>
Asterodiscididae (NS)
Astropseidae: <i>Asteropsis</i> , <i>Dermasterias</i> , <i>Petricia</i>
Chaetasteridae: <i>Chaetaster</i>
Ganeriidae: <i>Cycethra</i> , <i>Perknaster</i> , <i>Tarachaster</i>
Goniasteridae: <i>Calliaster</i> , <i>Ceramaster</i> , <i>Cladaster</i> , <i>Cryptopeltaster</i> , <i>Gephyreaster</i> , <i>Hippasteria</i> , <i>Lithosoma</i> , <i>Mediaster</i> , <i>Mitteliphaster</i> , <i>Notioceramus</i> , <i>Nymphaster</i> , <i>Peltaster</i> , <i>Pergamaster</i> , <i>Pseudarchaster</i> , <i>Rosaster</i> , <i>Sphaeriodiscus</i> , <i>Tobia</i>
Mithrodiidae: <i>Mithrodia</i> , <i>Thromidia</i>
Odontasteridae: <i>Acodontaster</i> , <i>Diplodontias</i> , <i>Eurygonias</i> , <i>Odontaster</i>
Ophidiasteridae: <i>Celerina</i> , <i>Fromia</i> , <i>Leiaster</i> , <i>Linckia</i> , <i>Narcissia</i> , <i>Neoferdina</i> , <i>Pharia</i>
Oreasteridae: <i>Culcita</i> , <i>Monachaster</i> , <i>Oreaster</i> , <i>Pentacaster</i> , <i>Protoreaster</i>
Podosphaerasteridae: <i>Podosphaeraster</i>
Poraniidae: <i>Porania</i> , <i>Poraniopsis</i>
Spinulosacea
Velatida
Korethrasteridae: <i>Peribolaster</i> ; <i>Remaster</i>
Myxasteridae: <i>Asthenactis</i>
Pterasteridae: <i>Euretaster</i> ; <i>Hymenaster</i>
Solasteridae: <i>Crossaster</i> ; <i>Cuenotaster</i> ; <i>Lophaster</i> ; <i>Paralophaster</i> ; <i>Solaster</i>

NS, not sampled.

Remaster; *Peribolaster*; node B, bootstrap support = 100%) + Forcipulatacea as the sister clade to the larger ingroup Valvatacea + Solasteridae. Basal dichotomy for the Valvatacea + Solasteridae supports a separation between poraniid genera (*Porania*, *Poraniopsis*; node C, with bootstrap support = 100%) and the remaining valvatacean taxa (node D, bootstrap support = 85%). The nonporaniid valvatacean clade includes members of the Paxillosida, the Notomyotida, the Valvatida, and the Solasteridae and is split basally into a smaller clade (node E, bootstrap support = 70%) and a more taxon-rich clade (node F, bootstrap support = 69%). The clade subtended by node E includes several ophiasterids (*Leilaster*, *Linckia*, and *Pharia*; bootstrap support = 99–100%) as sister taxa to the Mithrodiidae (*Mithrodia* and *Thro-*

midia; bootstrap support = 100%). The clade subtended by node F includes taxa that closely correspond to the historical Valvatida + Paxillosida + Notomyotida, as well as several members of the order Velatida (Solasteridae). This clade is separated into two clusters. The smaller clade (node G, bootstrap support = 83%) is further split into (1) a clade composed of representatives of three orders (the Benthopectinidae, Goniopectinidae, and Pseudarchasterinae; node H, bootstrap support = 83%) that are reciprocally monophyletic with 100% bootstrap support and (2) a larger, primary 'Paxillosida' clade (node I, bootstrap support = 96%) that includes genera which have all been previously assigned to the Paxillosida. This larger 'Paxillosida' clade contains multiple taxa from the Astropectinidae and the Luidiidae.

Astropecten is supported as the sister clade to *Thrissacanthias* + [*Bathybiaster* + (*Persephonaster* + *Psilaster*)] with 100% bootstrap support (node J). The latter four genera are also highly supported by 84–100% bootstrap values. The remaining ‘Paxillosida’ clade (node K, bootstrap support = 100%) has a basal dichotomy with *Luidia* (bootstrap support = 99%) as the sister clade to a lineage that has *Macroptychaster* (bootstrap support = 62%) as sister to a clade containing *Lonchotaster*, *Mimastrella*, *Dipsacaster*, and *Leptychaster* (all supported with bootstrap values between 94 and 100%).

Figure 1 shows the remaining ‘Valvatida’ clade including (1) the Odontasteridae (node L, bootstrap support = 100%); (2) *Chaetaster* (Chaetasteridae); (3) a smaller cluster that is largely consistent with the Goniasteridae + some Ophidiasteridae (node M, bootstrap support = 100%); and (4) a larger cluster (node N, bootstrap support = 85%) that includes members from the Acanthasteridae, Asterinidae, Asteropseidae, Ganeriidae, Oreasteridae, and the Solasteridae. A well-supported subclade (node O, bootstrap support = 85%) includes several oreasterid genera (*Culcita*, *Protoreaster*, *Oreaster*, *Monachaster*) and two asteropseids (*Petricia* and *Asteropsis*). A moderately supported subclade (node P, bootstrap support = 65%) is composed primarily of solasterids + asterinids along with two ganeriid genera, the enigmatic *Leilaster* (Leilasteridae) and the asteropseid *Dermasterias*.

The mitochondrial-only tree (Fig. 2) included more taxa and more total sequence length (1417 vs. 1084) than the three-gene tree. Unlike the three-gene tree, the two-gene tree recovered a monophyletic Asterinidae + Solasteridae + Ganeriidae + Leilasteridae with moderate support (bootstrap support = 70%, node 1 in Fig. 2). Basal relationships within the Asterinidae were mostly unresolved, but some taxon-rich clades were well supported (bootstrap support = 100%), including the Solasteridae (exclusive of *Cuenotaster*), the Ganeriidae (including *Cuenotaster*) and *Paranepanthia* + *Anseropoda aotearoa*. Three genera (*Anseropoda*, *Crossaster*, and *Lophaster*) were each reconstructed as polyphyletic.

DISCUSSION

COMPARISONS: HIGHER LEVEL CLASSIFICATION, PHYLOGENY, AND FOSSILS

Our results, when considered in conjunction with the known fossil record for valvatacean asteroids, support a hypothesis of early, rapid diversification within the Asterozoa. Both mid-point rooting and molecular clock analyses (details not shown) support the root at node A in our main tree (Fig. 1). Alternative rootings at nodes C–G would not change the conclusions below

about the relationships amongst valvatidan families or amongst paxillosidan families. Alternative rootings would, however, give a different picture of basal differentiation amongst the extant Asterozoa. Figure 1 suggests an early and fairly rapid diversification of forcipulatacean, velatid, poraniid, mithrodiid, and valvatacean lineages. The short internodes separating these groups, plus the relatively long terminal and subterminal branches in some clades (e.g. Mithrodiidae), emphasize again the need for additional taxon sampling of problematic groups and for more slowly evolving nuclear protein-coding sequences, to resolve basal asteroid relationships (Smith *et al.*, 2004). Although the histone H3 gene is a classic example of amino acid sequence conservation at deep phylogenetic levels (e.g. Malik & Henikoff, 2003), it actually shows a rate of substitution at synonymous sites that is roughly comparable to the more conserved and readily alignable regions of the mitochondrial 12S and 16S rDNA genes (D. Foltz, unpubl. data). As shown in Figure 1, these relatively fast-evolving sequences (H3, 12S, and 16S) can usually resolve relationships at the genus and family level, but do not always resolve relationships amongst families and orders. Given the proposed root in Figure 1, the taxonomic composition and relationships amongst taxa are similar to the phylogenetic concept and classification of the Valvatacea as proposed by Blake (1987). Blake’s (1987) Valvatacea included the Paxillosida + Notomyotida as part of a sister clade to the Valvatida. However, the Solasteridae – which was included in the Velatida (Spinulosacea) in Blake’s (1987) tree and in the Spinulosa by Fisher’s (1911) classification – is included as part of the Valvatacea in Figure 1. The tree also shows similarities to the phylogenetic affinities proposed by Blake, Tintori & Hagdorn (2000) who supported *Solaster* as a sister clade to *Asterina* (Asterinidae) and *Cycethra* (Ganeriidae) as well as a Paxillosida + Notomyotida relationship.

The earliest molecular phylogenetic treatment for valvatacean taxa was that of Lafay *et al.* (1995). Although their study had limited molecular data (400 bp of 28S ribosomal sequence) and taxon sampling, their maximum-likelihood topology did show some similarities to relationships in Figure 1 (e.g. *Asterina* as the sister group to *Crossaster* plus *Henricia* and *Echinaster*). Wada *et al.*’s (1996) topology also recovered asterinids as the sister group to *Crossaster*, but otherwise had little similarity to the tree in Figure 1. Knott & Wray (2000) used cytochrome *c* oxidase subunit 1 (COI) and tRNA sequences and included a more diverse taxon sampling for the Valvatida and the broader Valvatacea. Although taxonomic sampling was incomplete, and monophyly/phylogenetic placement of several taxa was inconsistent, Knott and Wray also showed support for the

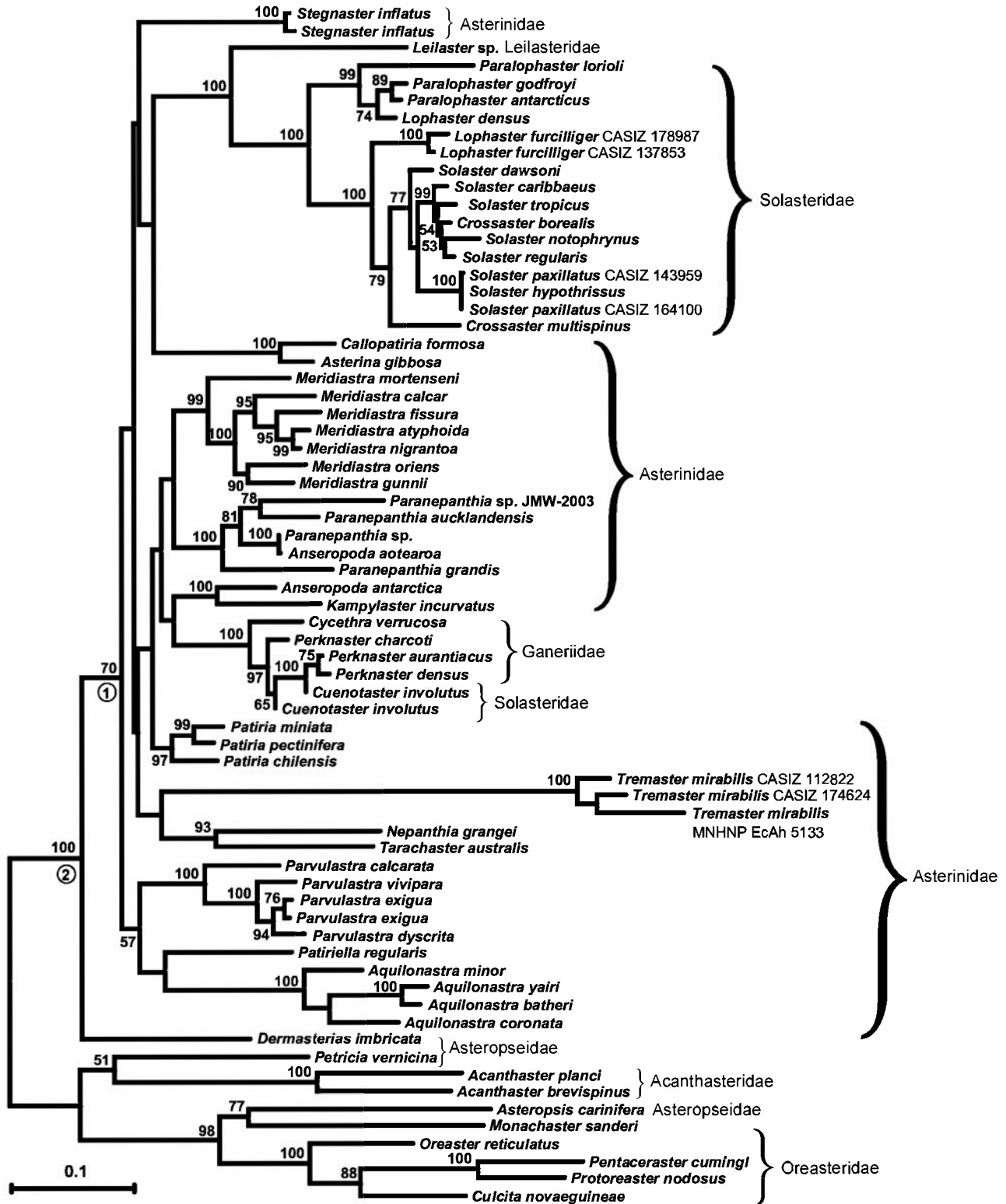


Figure 2. Maximum likelihood tree of asterinid + solasterid sea stars rooted against closely related valvatid sea stars. The analysis is based on 1417 bp of concatenated sequence data from two mitochondrial rDNA genes. Circled numbers 1 and 2 are referred to in the text. Other details as in Figure 1.

Paxillosida + Valvatida (Valvatacea) grouping. The total evidence tree of Janies (2001) included several putative valvatidan taxa but included no consistently monophyletic groupings within the Asteroidea. Matsubara *et al.* (2004) showed a sister group relationship between asterinid and solasterid taxa based on nuclear 18S rDNA plus mitochondrial 12S and 16S rDNA data. Their trees included several valvatidan taxa, but aside from the asterinid + solasterid clade and other secondary sister-taxon relationships, basal relationships were poorly resolved. Matsubara *et al.* (2005) analysed complete mtDNA nucleotide sequences for two paxillosidans (*Luidia* and *Astropecten*), a valvatidan (*Asterina*), and two forcipulatidans (*Asterias* and *Pisaster*). Based on their tree, they concluded that paxillosidan characters were secondarily derived, but their tree showed different relationships to those in Figure 1 (e.g. asterinids and paxillosidans do not share a similarly close relationship in our analysis). A recent COI molecular phylogeny of the Asteroidea (Yasuda *et al.*, 2006) rooted against two sea urchins showed a tree topology composed almost entirely of valvataceans that was consistent with relationships presented in Figure 1.

Valvatacean fossil occurrences are consistent with the phylogenetic trees presented herein (Figs 1, 2) and are further suggestive of (or at least do not contradict) a hypothesis for early Mesozoic diversification in asteroids. Phylogenetic hypotheses developed by Blake (1987) and Gale (1987b) suggest post-Palaeozoic asteroid lineages and imply early Mesozoic diversification. Where fossils were known to occur, they were compared with ingroup taxa that had similar or shared morphological synapomorphies. Groups that are not discussed below either lack information on fossil occurrence or have uncertain or unhelpful fossil occurrence (e.g. the Ophidiasteridae or the Leilasteridae).

THE VELATIDA (REVISED)

Although a survey of the outgroup was not a primary objective of this study and taxon sampling for the group is incomplete, our data did present some insight into the relationships amongst velatidan taxa, which were distanced from the other large nominal velatidan group, the Solasteridae. *Remaster* and *Peribolaster* were supported as sister taxa, which is consistent with their placement within the Korethasteridae. The placement of *Asthenactis* (Myxasteridae) and the two pterasterids, *Euretaster* and *Hymenaster* on the same clade, is broadly consistent with relationships outlined by Blake (1987) but disagrees with the phylogeny of Villier *et al.* (2004).

Villier *et al.* (2009) characterized several Jurassic members of the Velatida, including the Paleobentho-

pectininae and described a Jurassic multi-armed velatidan, *Deacuminaster*, which suggested relationship with the Myxasteridae. Villier *et al.* (2004) established pterasterid fossils remains from the Late Cretaceous and placed them within a morphology-based phylogeny for the Pterasteridae. Consideration of the Velatida as sister group to the Valvatida is not contradicted by fossil occurrence.

THE PORANIIDAE

The basal phylogenetic position of the Poraniidae relative to the larger cluster of valvataceans is consistent with Blake (1987), who separated the Poraniidae from the Asteropseidae. This is a position contrary to the perspective of traditional revisions, which have often treated the two families as closely linked to one another (e.g. Hotchkiss & Clark, 1976, A.M. Clark, 1984; Gale, 1987a). The thickened dermal tissue present on members from both groups has led to several studies supporting the two groups as closely related (e.g. A.M. Clark, 1984; Gale, 1987b; Blake *et al.*, 2000). Our results are consistent with the notion of Blake *et al.* (2000), who discussed the possibility that the thickened dermal tissue in the Poraniidae and the Asteropseidae were subject to homeomorphy, which would explain the difficulty in correctly placing these taxa within a classification.

The Poraniidae is represented by two early Mesozoic fossils, the Triassic *Noriaster barberoi*, described from northern Italy by Blake *et al.* (2000) and the Middle Jurassic *Sphaeraster jurassicus*, described by Hess (1972). *Noriaster* is supported in Blake *et al.* (2000) as phylogenetically similar to *Porania*, suggesting a possible time frame for diversification of the Valvatacea on the tree. The Triassic represents a potentially important period for recognizing diversification in the Asteroidea early in the Mesozoic and the basal location of the Poraniidae does not disagree with Triassic fossil occurrence for the group.

THE ODONTASTERIDAE AND THE CHAETASTERIDAE

Prior treatments (e.g. Fisher, 1911) have supported the Odontasteridae as having close affinities with the Goniasteridae. This notion has been supported by morphology-based phylogenies (Blake, 1987; Gale, 1987b) and by our molecular data (Fig. 1). The position of the monotypic Chaetasteridae in Blake's (1987) phylogeny is also consistent with the relatively stemward position of this taxon relative to the Odontasteridae and other valvatidans in Figure 1.

Fell (1954) described a Jurassic occurrence of *Odontaster* from South Auckland, New Zealand, which would be consistent with its relatively stemward phylogenetic position. The fossil shares recognizable

features (e.g. Fell's first ambulacral) with other odontasterids. Fell (1954) was confident in assigning the specimen to *Odontaster* but pending a full assessment of the Odontasteridae, it is unclear how reliable this character is for correct taxonomic assignment.

A single early Cretaceous member of the Chaetasteridae, *Chaetasterina gracilis*, was described by Hess (1970), which he postulated was intermediate between the Radiasteridae and the Ganeriidae (as represented by *Hyalinothrix*). However, *Chaetaster* was supported as sister taxon to *Odontaster* and was not supported on either of the clades containing radiasterid or ganeriid taxa (Fig. 1).

THE ASTERINIDAE, GANERIIDAE, AND SOLASTERIDAE

The Asterinidae has occupied a controversial position in the history of asteroid classification, having been placed in Spinulosida in Fisher (1911) and others (e.g. Sladen, 1889) but later independently reassigned to the Valvatida by Blake (1987) and Gale (1987b). Classification and revision within the Asterinidae has been a constant source of activity (e.g. A.M. Clark, 1983; O'Loughlin & Waters, 2004), but the distinctive morphology of asterinids has generally suggested a derived and potentially monophyletic assemblage with only limited subdivision (e.g. the Tremasterinae Sladen, 1889; Anseropodinae Fisher, 1906; summary in Spencer & Wright, 1966). Waters *et al.* (2004a) provided the first molecular phylogenetic treatment of the Asterinidae that included taxa beyond *Asterina + Patiriella*, using mitochondrial COI, 12S, and 16S rRNA data, primarily from Australasian taxa. Their phylogenetic tree did not support monophyly for the Asterinidae, but was the basis for subsequent far-reaching taxonomic revisions (O'Loughlin & Waters, 2004).

Basal relationships in the large clade subtended by node P in Figure 1 were mostly unresolved. Somewhat better resolution was obtained in the two-gene tree (Fig. 2) for some groups, such as *Parvulastra* and *Kampylaster + Anseropoda antarctica*. However, support for all basal nodes in the asterinid clade of our two-gene tree (i.e. those subtended by node 1 in Figure 2) was also relatively poor (< 50%), suggesting that basal relationships within this group will require further study. However, when placed into the context of greater taxonomic sampling, our phylogenetic results mirror the results of Waters *et al.* (2004a) and cast substantial doubt on the monophyly of the Asterinidae. This strongly suggests that the Asterinidae, as traditionally defined, is a paraphyletic assemblage. The stemward positions on node P of all the asterinid taxa suggest that they occupy a relatively plesiomorphic condition, forming more of a grade relative to more derived taxa, such as the solasterids and the

ganeriids. This represents a significant shift in perception of the Asterinidae, which has historically been supported by distinct morphological autapomorphies and has been perceived more as a derived, terminal branch (e.g. Blake, 1987; Gale, 1987b) rather than as an ancestral grouping.

Several of the other phylogenetic and taxonomic results produced by Waters, O'Loughlin & Roy (2004a) and O'Loughlin & Waters (2004), especially the monophyly of the higher branches, such as *Meridiastra*, *Patiria*, *Paranepanthia*, *Aquilonastra*, and *Parvulastra*, are upheld by our results. The basal branches in Waters, O'Loughlin & Roy (2004a) are clarified in our results. *Dermasterias*, which was shown embedded within the ingroup Asterinidae, is clearly removed from the Asterinidae by our trees. Our exemplar species of *Nepanthia*, *Nepanthia grangei*, differs from that of Waters, O'Loughlin & Roy (2004a) who used *Nepanthiaroughtoni* but our result shows *Nepanthia* as the sister to the ganeriid *Tarachaster australis*.

Tremaster has traditionally been placed in the Asterinidae but has been separated by some workers (e.g. Sladen, 1889; Smith & Tranter, 1985) into the Tremasterinae, which included *Tremaster*, *Stegnaster*, and two fossil tremasterines (Spencer & Wright, 1966). Jangoux (1982) disagreed with this classification and removed *Stegnaster* from the Tremasterinae, a conclusion that is consistent with our mitochondrial-only tree (Fig. 2). Available data support *Tremaster* as a divergent lineage within the Asterinidae with uncertain affinities.

Derived members of the 'asterinid' clade include primarily former members of the Solasteridae and the Ganeriidae, plus the Leilasteridae. The solasterid + asterinid relationship, as supported by molecular data, was first observed by Wada, Komatsu & Satoh (1996) and later developed by Matsubara *et al.* (2004). The presence of ganeriid taxa, such as *Cycethra* and *Perknaster*, within the asterinid clade is consistent with historical classifications that have demonstrated affinities between asterinids and ganeriids. The Ganeriidae have always been supported as similar to or morphologically close to the Asterinidae. Early classifications (e.g. Sladen, 1889) included *Cycethra* and *Ganeria* as members of the Ganeriinae, part of a subfamily within the Asterinidae. This affinity has been further supported by contemporary morphology-based phylogenies (Blake, 1987; Gale, 1987b). Further sampling will be necessary to test the monophyly and affinities of the Ganeriidae.

The Solasteridae, *sensu* A. M. Clark (1996) was largely supported as monophyletic with the sole exception of the Antarctic *Cuenotaster involutus*, which was included as the sister clade to the ganeriid *Perknaster*. Although much work remains to be completed regarding this question, some morphological

characters are consistent with *Cuenotaster* as a member of the Ganeriidae.

Jurassic fossils are known for taxa within the clade subtended by node P (Solasteridae + Asterinidae + Ganeriidae + Leilasteridae) but are limited to the Asterinidae and the Solasteridae. Asterinid fossils are limited to those showing affinities with *Tremaster* in the subfamily Tremasterinae.

Tremaster is supported on a long branch as sister group to a clade containing *Nepanthia* and *Tar-chaster* (Fig. 2). Tremasterine fossils, such as *Mesotremaster felli* Hess, 1972 and *Mesotremaster zbindeni* Hess, 1981 from Germany and *Protremaster uniserialis* Smith & Tranter, 1985 from Antarctica have been collected from Jurassic strata. Nontremasterine asterinid fossils are unknown.

Plesiosolaster (described as *Brachisolaster*) *moretonis* was re-described and discussed by Blake (1993) and further discussed by Villier, Charbonnier & Bernard (2009) from the Jurassic of England and is the only well-preserved fossil solasterid known. Although a full phylogenetic analysis was not undertaken, Blake hypothesized that the multiarmed condition for solasterids was derived relative to a more ancestral *Lophaster* or *Rhipidaster*-like morphology. Blake's hypothesis is consistent with our phylogenetic tree (Figure 1). This may imply that the lineage containing multiarmed taxa (*Solaster* and *Crossaster*) may be closely associated with the Jurassic occurrence of multiple arms in the Solasteridae.

THE OREASTERIDAE, ACANTHASTERIDAE, AND ASTEROPSEIDAE

Although still supported as a member of the Valvatida and/or Valvatacea in Figure 1, the oreasterid/asteropseid lineage has historically been considered as most closely related to either the Goniasteridae and/or the Ophidiasteridae. The close relationship between the oreasterids and asteropseids (node O in Fig. 1) agrees with Blake (1987) and Gale (1987b), but our topology agrees more closely with the tree of Blake (1987) in that it supports poraniids as a lineage separate from asteropseids. Gale (1987b) considered asteropseids as members of the same lineage as poraniids.

The Asteropseidae was not supported as monophyletic, supporting *Asteropsis*, *Dermasterias*, and *Petricia* on different lineages. *Asteropsis* most closely resembles the tree topology presented by Blake (1987) in that it is supported as sister taxon to the goniasterid-like oreasterid *Monachaster* on the sister clade to the large primary Oreasteridae (*Culcita*, *Oreaster*, etc.). *Petricia* was supported as the sister taxon to *Acanthaster*. *Dermasterias* was supported as the sister taxon to the Asterinidae + Solasteridae +

Ganeriidae + Leilasteridae in the three-gene tree (node P in Fig. 1) with moderate bootstrap support (65%). Although we used the relationships in Figure 1 as the basis of rooting the asterinid tree in Figure 2, placing the root at the branch subtending node 2 rather than at node 1 would still leave the asterinid tree monophyletic and would group *Dermasterias* with the remaining members of the asteropseid/oreasterid clade, which is more consistent with prior classifications (e.g. Hotchkiss & Clark, 1976).

Acanthaster is supported as the sister group to the included oreasterids, which is consistent with the close relationship between the Acanthasteridae and the Oreasteridae as supported by Blake (1979, 1987) based on skeletal evidence. In our tree, the (Oreasteridae + Asteropseidae) + Acanthasteridae/Asteropseidae clade is supported (node N in Fig. 1) as the sister clade to the large Asterinidae + Ganeriidae + Leilasteridae + Solasteridae + *Dermasterias* clade, which is a substantial departure from prior phylogenetic hypotheses.

The presence of *Acanthaster* as the sister taxon to the Oreasteridae + *Asteropsis* is consistent with the morphological evidence and phylogenetic hypothesis of Blake (1979, 1987). He documented an Eocene oreasterid (Blake, 1979) that was close to *Anthenea* or *Gonioidiscaster* and showed a morphology demonstrating characters consistent with *Acanthaster* and other Oreasteridae. Thus, oreasterid fossil occurrence can be shown to be present in the Eocene. Otherwise, there are relatively few oreasterid fossils known and most are either too poorly known or too incomplete to be useful here.

THE GONIASTERIDAE

The Goniasteridae + four ophidiasterid genera are supported as monophyletic (node M in Fig. 1), consistent with historical definitions such as those outlined in A.M. Clark (1993) and Mah (2009). Several affinities between goniasterid genera are supported by our data, including between *Calliaster* and *Milteliphaster*, as suspected by Aziz & Jangoux (1985), and between *Mediaster* and *Rosaster*, as suggested by Fisher (1919).

Our data also support the monophyly of the cold-water corallivorous Hippasterinae as reviewed by Fisher (1911) and later by Mah *et al.* (2010). Fisher (1906) perceived affinities between *Gilbertaster* and the Hippasterinae, which were later confirmed by Mah *et al.* (2010). This subfamily originally included *Hippasteria*, *Cryptopeltaster*, and the distantly related *Cladaster*. *Cladaster* forms the sister group to the Hippasterinae in Figure 1, which may or may not agree with the relationship hypothesized by Mah (2006) and Mah *et al.* (2010) depending on subsequent taxonomic sampling.

The most substantial difference from previous definitions in the Goniasteridae in Figure 1 is the inclusion of several goniasterid-like ophidiasterids, including *Fromia* + *Celerina* (which may be synonyms), and *Neoferdina*. This result supports a nonmonophyletic Ophidiasteridae and suggests that other unsampled goniasterid-like taxa, such as *Dissogenes*, *Paraferdina*, *Ferdina*, and *Bunaster* may also be correctly placed within the Goniasteridae. The particularly goniasterid-like appearance of *Dissogenes* has been discussed by Fisher (1919) and Jangoux (1981) as intermediate between ophidiasterids and goniasterids. *Narcissia trigonaria* is supported in an unusual position as the sister clade to the larger, diverse members of clade M, which removes it from both the historical Ophidiasteridae, as well as the 'ophidiasterid-like goniasterid' condition observed in *Fromia* and *Neoferdina*. However, the 100% bootstrap support for clade M, which includes *Narcissia*, strongly implies that it is not supported with the traditional Ophidiasteridae.

Our results show asterinids in a phylogenetic position that is similar to prior groupings established by morphological phylogenies. Blake (1987) showed asterinids, ganeriids, and poraniids as sister taxa to a large and diverse clade including goniasterids, ophidiasterids, and oreasterids, amongst others. Gale (1987b) included the asterinids (and ganeriids) as part of a polytomy with goniasterids and odontasterids. Aside from *Pseudarchaster* (which is discussed below) only one molecular phylogeny has included goniasterids in their taxonomic coverage. Knott & Wray (2000) included *Mediaster*, *Hippasteria*, and *Ceramaster* and although they were supported on a clade with other valvataceans, they did not cluster together.

Amongst modern Asteroidea, the Goniasteridae are perhaps the best observed in the fossil record, having a particularly rich diversity of fossil taxa in the Cretaceous of northern Europe (e.g. Breton, 1992). Jurassic Goniasteridae do occur (e.g. Breton, 1992) but several taxa are based on incomplete material and/or are similar to pseudarchasterines, which are supported with the Paxillosida in our treatment. *Nymphaster*, which occurs close to the basal dichotomy of the goniasterid lineage, occurs primarily in Cretaceous strata (Gale, 1987a; Breton, 1992). Stemward amongst the Goniasteridae is *Mediaster*, which is represented by *Mediaster hayi* Blake 1986 from the Cretaceous of California. Other included genera with Cretaceous fossil occurrence include *Hippasteria* (Fell, 1956) and *Cladaster* (Medina & Del-Valle, 1983).

Although *Tosia* was not explicitly dated, the pentagonasterine phylogeny presented by Mah (2007) suggested that phylogenetic events in the

Tosia + *Pentagonaster* lineage were probably close to the Eocene/Oligocene climate shift associated with the isolation of Antarctica from Australia. This relatively younger *Tosia* + *Pentagonaster* lineage would be consistent with its relatively derived phylogenetic position and its relatively close relationship with the Antarctic *Notioceramus*. Molecular data supporting the presence of several goniasterid-like ophidiasterids amongst the Goniasteridae also shift the interpretation of goniasterid-like ophidiasterid fossils. Blake & Reid (1998) described two such taxa, *Denebia* and *Altairia*, from the Cretaceous of Texas.

THE OPHIDIASTERIDAE AND MITHRODIIDAE

The sister group relationship between several ophidiasterids and the Mithrodiidae, as supported by Blake (1987), is confirmed by our data. The nonmonophyly of the Ophidiasteridae is consistent with morphological breaks in identification keys and classifications (e.g. H.L. Clark, 1946) that separate the goniasterid-like ophidiasterids (e.g. *Fromia*) from those with more cylindrical arms and small disks (e.g. *Linckia*).

No unambiguous ophidiasterid fossils exist that are comparable in morphology to those sampled for our tree. Identified ophidiasterid fossils demonstrate closer affinities with 'goniasterid-like' ophidiasterids (e.g. Blake & Reid, 1998) rather than those with small disks and long arms (e.g. *Linckia*). Further associations between molecular data and fossil occurrence will await additional clarification of ophidiasterid fossils.

THE PAXILLOSIDA, NOTOMYOTIDA, AND THE PSEUDARCHASTERINAE

The sister clade to the large, primary grouping of Valvatacea (node F in Fig. 1) includes a well-supported clade (node G) with taxa that have been previously included in the Paxillosida (Astropectinidae, Ctenodiscidae, Gonioplectinidae, Luidiidae), the monotypic Notomyotida (Benthopectinidae), and genera that have been included in the Pseudarchasterinae, a group that has historically been placed with the Goniasteridae (Valvatida). The overall taxonomic composition of this clade is very similar to the composition and subgroupings of the Archasteridae *sensu* Sladen (1889), which included primarily members of the Benthopectinidae and the Astropectinidae. The Pseudarchasterinae was recently reviewed by Blake & Jagt (2005) and included several fossil taxa in addition to *Pseudarchaster*, *Paragonaster*, *Perissogonaster*, and *Gephyreaster*. Pseudarchasterines were separated from other goniasterids by Blake (1987) but have been retained in the Goniasteridae, without distinction, in several recent accounts (e.g. Clark &

Downey, 1992; A.M. Clark, 1993). *Pseudarchaster* has been interpreted as being similar to certain goniasterid-like astropectinids, such as *Plutonaster* with which it shares several skeletal character similarities but differs in that most species of *Pseudarchaster* have nonpointed tube feet. Rowe & Gates (1995: 68) stopped short of moving *Pseudarchaster jordanii* to the Paxillosida based on this single character. The addition of *Pseudarchaster* to this clade effectively isolates this body form to the Paxillosida. *Pseudarchaster* has been included in several other molecular phylogenies that have either (1) loosely supported affinities with other valvatidan taxa (e.g. Knott & Wray, 2000) or (2) been ambiguous (e.g. Janies, 2001).

The position of the Notomyotida (Benthopectinidae) as members of the same clade as the Paxillosida (node G in Fig. 1) is consistent with the phylogenies of Blake (1987) and Gale (1987b). Both supported the Notomyotida as the sister group to the larger, primary Valvatida clade. The remaining genera in the primary 'Paxillosida' clade (node I in Fig. 1) formed two subclades, one of which (node J) included several taxa with a marginal plate series that forms a distinctive periphery frequently with acute triangular arms bearing prominent spines (*Astropecten*, *Thrissacanthias*, *Bathybiaster*, *Persephonaster*, and *Psilaster*) versus those with more nondescript marginal plate series with smaller to absent spines (*Dipsacaster*, *Leptychaster*, *Mimasterella*, *Macroptychaster*, and *Luidia*). These morphological distinctions are reflected in several traditional identification keys and classifications (e.g. Fisher, 1911; Clark & Downey, 1992). The primary 'Paxillosida' clade includes *Luidia* supported as a derived lineage amongst the astropectinids (node K).

Historically, the Paxillosida has included a diverse assemblage of asteroids that occur on bottoms with unconsolidated sandy or muddy sediment. Because of this environmental constraint, this body form may be predisposed to being buried rapidly and is relatively well represented in the fossil record. Amongst the several 'paxillosid-like' forms observed in the fossil record are the Pseudarchasterinae, the Astropectinidae, the Luidiidae, the Ctenodiscidae, and the Radiasteridae. The Pseudarchasterinae has traditionally been classified as a subfamily of the Goniasteridae (in the Valvatida), but is here supported as a member of the Paxillosida.

Pseudarchaster portlandicus was described from the Jurassic of England by Blake (1986) and showed close affinities with living *Pseudarchaster*. Breton (1992) summarized and figured several *Pseudarchaster*-like Jurassic and Cretaceous taxa in the genus *Comptoniaster*. Based on our results, this suggests that these taxa maybe properly placed

within the Pseudarchasterinae in the Paxillosida rather than the Goniasteridae in the Valvatida. *Tethyaster* is living today (e.g. Clark & Clark, 1954) and is known from Jurassic fossils (Blake, 1986).

Cretaceous paxillosidans are relatively well represented in the fossil record. Fossil taxa close to *Mimastrella* include the Cretaceous *Betelgeusia* in the Radiasteridae, which was described by Blake & Reid (1998). Blake (1988a) described a Cretaceous ctenodiscid, *Paleoctenodiscus*, and identified the presence of cribiform organs in the fossil record. Gale (2005) described the Cretaceous *Chrispaulia* as the first fossil record of the Gonioplectinidae, represented in Figure 1 by *Goniopecten*. Villier, Breton & Atrops (2007) described *Prothrissacanthias* from the Cretaceous of Algeria, which they described as morphologically close to *Thrissacanthias* and *Persephonaster*, which are both included in Figure 1. Breton, Bilotte & Sigro (1995) described *Dipsacaster jadeti* from the Cretaceous of France. *Luidia* has been documented with a Miocene to Recent fossil occurrence (e.g. Blake, 1982) and it is likely to have diversified relatively recently. Its phylogenetic position does not disagree with the relative timing of its fossil occurrence.

Fossil material tentatively identified as *Cheiraster* has been identified from the Cretaceous by Blake & Jagt (2005) in addition to other fossils that have been described from the Cretaceous (Blake & Reid, 1998; Jagt, 2000). The Jurassic Paleobenthopectininae as described by Blake (1984) were reassigned by Villier *et al.* (2009) to the Velatida and are discussed elsewhere.

THE PAXILLOSIDA: PHYLOGENETIC PERSPECTIVES AND INSIGHT ON THE 'GREAT DEBATE'

The Paxillosida have occupied a prominent position in the discussions surrounding asteroid evolution and the early studies seeking out the 'primitive' asteroid ancestor. This discussion began with discussions between Mortensen (1922, 1923) and MacBride (1921, 1923) regarding the 'primitive' status of the Astropectinidae (Paxillosida) because of a number of morphological specializations, including, but not limited to pointed tube feet and the absence of a brachiolaria larvae. Mortensen argued for the primitiveness of the Astropectinidae whereas MacBride argued the opposite. Morphology-based phylogenies continued this discussion. Gale (1987b), following Mortensen, supported the Paxillosida as the basal sister taxon to the other living Asteroidea, whereas Blake (1987, 1988b) echoed MacBride, and supported the Paxillosida as having derived adaptations to living on a soft-bottom or unconsolidated, sediment type setting. Because of the focus on this argument, all subsequent phylogenetic studies have included paxillosidans, but most

have given ambiguous results. Many of these studies have not supported a monophyletic Paxillosida (e.g. Wada *et al.*, 1996; Knott & Wray, 2000; Matsubara *et al.*, 2004) and those that have, include relatively limited taxon sampling (e.g. Lafay *et al.*, 1995; Matsubara *et al.*, 2005; Yasuda *et al.*, 2006).

Although we do not have a definitive result supporting a basal lineage within the Asteroidea, our results do not place the Paxillosida as basal amongst the Valvatacea (following Mortensen, 1922, 123; Gale, 1987b) relative to our outgroup choice. The Paxillosida occur as derived relative to the Poraniidae and the clade containing the Ophidiasteridae + Mithrodiidae.

All of the included taxa on node G possess a 'Paxillosida' type morphology, which is associated with unconsolidated, soft-bottom substrate settings. All included taxa possess characters, such as the presence of paxillar abactinal and marginal plates, pointed tube feet and well-developed fasciolar grooves between the abactinal, marginal, and actinal plates, which imply a derived morphology (*sensu* MacBride, 1921, 1923 and later Blake, 1987, 1988b). It should be noted that our tree includes not only the Paxillosida *sensu* Blake (1987) but also the Notomyotida and the Pseudarchasterinae.

Archaster closely resembles *Astropecten* and possesses several similar morphological characteristics. *Archaster* was not included in our analysis because of a lack of histone H3 sequence data, but all prior studies from morphology (e.g. Blake, 1987) and molecules (Knott & Wray, 2000; Matsubara *et al.*, 2004) do not suggest that it shows any close relationship with the Paxillosida, suggesting that its *Astropecten*-like appearance is a result of convergence.

ANTARCTIC AND SUB-ANTARCTIC VALVATIDA

Two of the ingroup taxa, the Odontasteridae and the Ganeriidae, occur only in cold-water habitats, but occur primarily at high-latitudes in the Southern Hemisphere. Although isolated members occur in the deep-sea and the Arctic/boreal regions, both families demonstrate the greatest biodiversity and abundance in the Southern Ocean and adjacent regions.

Although sampling remains incomplete, taxa included in the analysis suggest possible patterns of diversification for these groups into Antarctic regions from the adjacent sub-Antarctic regions. We sampled a majority of the genera within the Odontasteridae (four out of six) and show (Fig. 1) that the New Zealand *Eurygonias* is the sister clade to a larger clade containing the Antarctic *Acodontaster*, the Antarctic (some deep-sea species) *Odontaster*, and the sub-Antarctic *Diplodontias* (southern tips of South Africa, South America, and New Zealand). Similarly,

the Antarctic *Perknaster* and *Cuenotaster* are supported on a single clade, which forms the sister to the sub-Antarctic *Cycethra*. Several other, more poorly sampled, clades, such as *Pergamaster* (Antarctic) and *Calliaster* (South-Central Pacific) plus *Mitteliphastrer* (South Pacific) and *Tosia* (temperate water Australia) and *Notioceramus* (Antarctic) place Antarctic lineages as the sister group to taxa occurring in adjacent regions. Additional specific sampling of these lineages is needed to test these relationships.

CONCLUSIONS

We present a comprehensively sampled, three-gene molecular phylogenetic review of the Valvatacea. Our tree has substantial implications for the classification of the most diverse group of modern Asteroidea, and suggests possible ancestry for Antarctic taxa. A full summary of differences between the historical classification and our results is shown in Table 2. Major conclusions include

1. The Solasteridae is removed from the Velatida and is supported within the Valvatida, which contains the Asterinidae, the Ganeriidae, and the Leilasteridae. *Cuenotaster*, which has historically been included in the Solasteridae, is supported herein with the Ganeriidae.
2. The Poraniidae is supported as sister taxa to the majority of valvataceans and is separated from prior hypotheses of close relationship with the Asteropseidae.
3. The Benthoplectinidae (Notomyotida) and the Pseudarchasterinae are supported as sister taxa in a clade that includes the Gonioplectinidae, the Ctenodiscidae, the Luidiidae, and the Astropectinidae, all within the Paxillosida.
4. Although traditional long-arm and small disk type Ophidiasteridae are supported, some goniasterid-like ophidiasterid forms are supported as members of the Goniasteridae. The traditional Ophidiasteridae is not supported as monophyletic.
5. Lineages with predominantly Antarctic members, such as the Odontasteridae and the Ganeriidae, are supported as having sister taxa that occur in adjacent regions, suggesting possible ancestry for these faunas.

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Table 2. Revised list of valvatacean clades analysed in this study. Shaded lines indicate changes from historical classification. Family names are used here out of convenience. Bold face indicates those genera which are included with new families. A fully revised classification is in preparation.

Valvatacea

Poraniidae: *Porania*, *Poraniopsis*

'Ophidiasteridae' clade:

Mithrodiidae: *Mithrodia*, *Thromidia*

Ophidiasteridae: *Leiaster*, *Linckia*, *Pharia*

Paxillosida

Astropectinidae: *Astropecten*, *Bathybiaster*, *Dipsacaster*, *Leptychaster*, *Lonchotaster*, *Macroptychaster*, *Mimastrella*, *Persephonaster*, *Psilaster*, *Thrissacanthias*

Benthopectinidae: *Cheiraster*, *Nearchaster*

Ctenodiscidae: *Ctenodiscus*

Goniopectinidae: *Goniopecten*

Luidiidae: *Luidia*

Pseudarchasterinae: *Gephyreaster*, *Pseudarchaster* (from Goniasteridae)

Valvatida

Asterinidae: NOT MONOPHYLETIC. *Anseropoda*, *Aquilonastra*, *Asterina*, *Callopatiria*, ***Dermasterias***, *Kampylaster*, ***Leilasteridae*** (*Leilaster*), *Meridiastra*, *Nepanthia*, *Paranepanthia*, *Parvulastra*, *Patiria*, *Patiriella*, ***Solasteridae***, *Stegnaster*, *Tremaster*

Ganeriidae: ***Cuenotaster*** (from Solasteridae), *Cycethra*, *Perknaster*, *Tarachaster*

Goniasteridae: (all bold from Ophidiasteridae) *Calliaster*, ***Celerina***, *Ceramaster*, *Cladaster*, *Cryptopeltaster*, ***Fromia***, *Hippasteria*, *Lithosoma*, *Mediaster*, *Milteliphaster*, ***Narcissia***, ***Neoferdina***, *Notioceramus*, *Nymphaster*, *Peltaster*, *Pergamaster*, *Rosaster*, *Sphaeriodiscus*, *Tosia*

Odontasteridae + Chaetasteridae clade: *Acodontaster*, *Chaetaster*, *Diplodontias*, *Eurygonias*, *Odontaster*

Oreasteridae clade: ***Acanthasteridae*** (*Acanthaster*), ***Asteropseidae*** (not monophyletic), ***Asteropsis***, *Culcita*, *Monachaster*, *Oreaster*, *Pentaceraster*, ***Petricia***, *Protoreaster*

Solasteridae: *Crossaster*, *Leilaster*, *Lophaster*, *Paralophaster*, *Solaster*

Spinulosacea

Velatida

Korethrasteridae: *Peribolaster*, *Remaster*

Myxasteridae: *Asthenactis*

Pterasteridae: *Euretaster*, *Hymenaster*

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Appendix 1

Species	12S	16S	H3-early stage	Voucher
<i>Acanthaster brevispinus</i> #	AB231476	AB231476	–	–
<i>Acanthaster planci</i>	AB084569	AB231475	–	–
<i>Acanthaster planci</i>	–	–	GQ288607	CASIZ 113560
<i>Acodontaster hodgsoni</i>	EU072963	EU072933	EU707685	CASIZ 174598
<i>Anseropoda antarctica</i>	EU723018	EU722940	EU707722	CASIZ 175766
<i>Anseropoda aotearoa</i>	EU723078	EU722997	EU707755	NIWA 15416
<i>Aquilonastra batheri</i> #	AY370698	AY370725	–	MV-MOL 247
<i>Aquilonastra coronata</i> #	AY370697	AY370724	–	MV-MOL 246
<i>Aquilonastra minor</i> #	AY370696	AY370723	–	MV-MOL 243
<i>Aquilonastra yairi</i> #	AY370709	AY370737	–	–
<i>Asterina gibbosa</i> #	AY370700	AY370726	–	MV-MOL 242
<i>Asteropsis carinifera</i>	EU072964	EU072935	EU707689	CASIZ 117863
<i>Asthenactis</i> sp.	EU723034	EU722957	EU707746	CASIZ 157505
<i>Astropecten articulatus</i>	DQ273741	DQ297079	DQ676901	AMCC 113394
<i>Bathybiaster loripes</i>	EU072966	EU072937	EU707657	CASIZ 162501
<i>Calliaster elegans</i>	EU723050	EU722973	EU707726	MNHNP EcAh 4845
<i>Callopatiria formosa</i>	GQ288476	GQ288521	GQ288581	CASIZ 102191
<i>Celerina heffernani</i>	EU723020	EU722942	EU707730	CASIZ 113789
<i>Ceramaster arcticus</i>	EU723021	EU722943	EU707731	CASIZ 143443
<i>Ceramaster patagonicus</i>	EU723035	EU722958	EU707732	CASIZ 174590
<i>Chaetaster moorei</i>	EU072967	EU072938	EU707672	CASIZ 118047
<i>Cheiraster antarctica</i>	EU072981	EU072951	EU707641	CASIZ 169932
<i>Cheiraster dawsoni</i>	EU723028	EU722950	EU707736	CASIZ 143965
<i>Cladaster validus</i>	EF624432	EF624400	EU707669	CASIZ 158252
<i>Crossaster borealis</i>	GQ288502	GQ288543	GQ288589	CASIZ 179002
<i>Crossaster multispinus</i>	GQ288468	GQ288513	GQ288567	NIWA 27595
<i>Crossaster papposus</i>	DQ273725	DQ297084	DQ676904	AMCC 113349
<i>Cryptopeltaster lepidonotus</i>	GQ288486	GQ288531	GQ288580	CASIZ 111828
<i>Ctenodiscus crispatus</i>	EU072969	EU072940	EU707696	CASIZ 173281
<i>Cuenotaster involutus</i>	EU072970	EU072941	EU707671	CASIZ 163086

Appendix 1 *Continued*

Species	12S	16S	H3-early stage	Voucher
<i>Cuenotaster involutus</i>	GQ288492	GQ288553	GQ288582	CASIZ 176010
<i>Culcita novaeguineae</i>	EU072971	EU072942	EU0707688	CASIZ 113508
<i>Cycethra verrucosa</i>	EU723017	EU722939	EU707654	–
<i>Dermasterias imbricata</i>	–	–	DQ676906	AMCC 113399
<i>Dermasterias imbricata</i>	AY370691	AY370718	–	–
<i>Diplodontias dilatatus</i>	DQ273732	DQ297075	DQ676898	AMCC 113383
<i>Diplodontias miliaris</i>	DQ377827	DQ297078	DQ676900	AMCC113392
<i>Diplodontias singularis</i>	EU723016	EU722938	EU707653	–
<i>Dipsacaster borealis</i>	EU723037	EU722960	EU707738	CASIZ 143420
<i>Euretaster insignis</i>	EU072974	EU072944	EU707691	CASIZ 104210
<i>Eurygonias hylacanthus</i>	DQ273739	DQ297089	DQ676908	AMCC 114324
<i>Fromia monilis</i>	EU072975	EU072945	EU707692	CASIZ 107520
<i>Gephyreaster swifti</i>	EU072976	EU072946	EU707690	CASIZ 158251
<i>Gilbertaster anacanthus</i>	GQ288478	GQ288523	GQ288568	CASIZ 159080
<i>Gilbertaster caribbeae</i>	GQ288485	GQ288530	GQ288604	USNM 1126238
<i>Goniopecten demonstrans</i>	GQ288507	GQ288539	GQ288605	–
<i>Hippasteria spinosa</i>	EU723022	EU722944	EU707728	CASIZ 163253
<i>Hippasteria spinosa</i>	GQ288482	GQ288525	GQ288576	CASIZ 163250
<i>Hymenaster latebrosus</i>	EU072978	EU072948	EU707670	CASIZ 163076
<i>Kampylaster incurvatus</i>	GQ288477	GQ288522	GQ288571	CASIZ 167617
<i>Leiaster glaber</i>	EU723023	EU722945	EU707748	CASIZ 104486
<i>Leilaster</i> sp.	GQ288469	GQ288514	GQ288565	MNHNP EcAs 12610
<i>Leptychaster propinquus</i>	EU723039	EU722962	EU707739	CASIZ 158249
<i>Linckia nodosa</i>	EU723024	EU722946	EU707734	CASIZ 112840
<i>Lithosoma novazelandiae</i>	EU723068	EU722989	EU707749	NIWA 15423
<i>Lonchotaster tartareus</i>	EU072979	EU072949	EU707660	CASIZ 163084
<i>Lophaster densus</i>	EU072980	EU072950	EU707665	CASIZ 163121
<i>Lophaster furcilliger</i>	GQ288475	GQ288520	GQ288572	CASIZ 137853
<i>Lophaster furcilliger</i>	GQ288504	GQ288550	GQ288592	CASIZ 178987
<i>Luidia clathrata</i>	DQ273743	DQ297096	DQ676913	AMCC 113393
<i>Luidia foliolata</i>	EU072982	EU072952	EU707697	CASIZ 105625
<i>Macrotychaster accrescens</i>	DQ273742	DQ297098	DQ676915	AMCC 113410
<i>Mediaster aequalis</i>	EU723013	EU072953	EU707662	CASIZ 120090
<i>Mediaster bairdi</i>	GQ288489	GQ288535	GQ288601	USNM 1127106
<i>Mediaster ornatus</i>	EU723047	EU722970	GQ288562	CASIZ 157499
<i>Mediaster sladeni</i>	EU723069	EU722990	EU707751	NIWA 27627
<i>Mediaster tenellus</i>	GQ288488	GQ288534	GQ288594	CASIZ 178975
<i>Meridiastra atyphoida</i> #	AY370716	AY370742	–	MV-MOL 185
<i>Meridiastra calcar</i>	AY370702	AY370728	–	Australian Mus. J21954
<i>Meridiastra fissura</i> #	AY370714	AY370740	–	MV-MOL 187
<i>Meridiastra gunnii</i> #	AY370701	AY370727	–	MV-MOL 54
<i>Meridiastra mortenseni</i> #	AY370707	AY370735	–	MV-F89163
<i>Meridiastra nigranota</i> #	AY370715	AY370741	–	MV-MOL 8
<i>Meridiastra oriens</i> #	AY370704	AY370730	–	MV-MOL 175
<i>Miteliphaster wanganellensis</i>	EU723025	EU722947	EU707725	CASIZ 108646
<i>Mimastrella cognata</i>	EU723005	EU722928	EU707655	–
<i>Mithrodia clavigera</i>	EU072983	EU072954	EU707699	CASIZ 115525
<i>Monachaster sanderi</i>	EU723026	EU722948	EU707733	CASIZ 173553
<i>Narcissia trigonaria</i>	GQ288490	GQ288537	GQ288603	USNM 1127111
<i>Nearchaster variabilis</i>	GQ288495	GQ288538	GQ288595	CASIZ 178988
<i>Neoferdina cumingi</i>	EU723029	EU722951	EU707729	CASIZ 113512
<i>Nepanthia grangei</i>	EU723079	EU722998	EU707753	NIWA 15417
<i>Notioceramus anomalus</i>	GQ288481	GQ288527	GQ288577	CASIZ 176007
<i>Nymphaster arenatus</i>	GQ288484	GQ288526	GQ288579	CASIZ 112827

Appendix 1 *Continued*

Species	12S	16S	H3-early stage	Voucher
<i>Odontaster meridionalis</i>	DQ273730	DQ297100	DQ676917	AMCC 113406
<i>Odontaster penicillatus</i>	EU723001	EU722926	EU707656	–
<i>Odontaster validus</i>	EF624444	EF624414	EU707663	CASIZ 169926
<i>Oreaster reticulatus</i>	GQ288470	GQ288515	GQ288570	USNM 1135008
<i>Paralophaster antarcticus</i>	GQ288506	GQ288552	GQ288588	CASIZ 174645
<i>Paralophaster godfroyi</i>	GQ288505	GQ288551	GQ288587	CASIZ 176011
<i>Paralophaster lorioli</i>	EU723058	EU722979	GQ288563	CASIZ 167622
<i>Paranepanthis aucklandensis</i> #	AY370708	AY370736	–	–
<i>Paranepanthis grandis</i> #	AY370713	AY370739	–	MV-MOL 178
<i>Paranepanthis</i> sp.	GQ288471	GQ288516	GQ288566	MNHNP EcAs 12508
<i>Paranepanthis</i> sp. JMW-2003#	AY370693	AY370720	–	–
<i>Parvulastra calcarata</i> #	AY370712	AY370738	–	MV-MOL 249
<i>Parvulastra exigua</i> #	AY370703	AY370729	–	–
<i>Parvulastra vivipara</i> #	AY370705	AY370733	–	–
<i>Patiria chilensis</i> #	AY370694	AY370721	–	MV-MOL 240
<i>Patiria miniata</i>	–	DQ297074	DQ676897	AMCC 113402
<i>Patiria miniata</i>	DQ273727	–	–	AMCC 113382
<i>Patiria miniata</i> #	AY370695	AY370722	–	–
<i>Patiria pectinifera</i> #	D16387	D16387	–	–
<i>Patiriella dyscrita</i>	GQ288473	GQ288518	GQ288574	CASIZ 118456
<i>Patiriella exigua</i>	EU723040	EU722963	EU707724	CASIZ 117900
<i>Patiriella regularis</i>	DQ273733	–	DQ676925	AMCC 113390
<i>Patiriella regularis</i>	–	AY370734	–	–
<i>Patiriella regularis</i> #	AY370706	AY370734	–	–
<i>Peltaster micropeltus</i>	EU723030	EU722953	EU707727	CASIZ 171710
<i>Pentacerastraster cumingi</i> #	EU723031	EU722954	–	CASIZ 109407
<i>Pergamaster incertus</i>	GQ288483	GQ288529	GQ288578	CASIZ 163059
<i>Peribolaster folliculatus</i>	EU072984	EU072955	EU707668	CASIZ 163123
<i>Perknaster aurantiacus</i>	GQ288493	GQ288554	GQ288585	CASIZ 174670
<i>Perknaster charcoti</i>	EU072985	EU072956	EU707686	CASIZ 163085
<i>Perknaster densus</i>	GQ288494	GQ288555	GQ288586	CASIZ 174651
<i>Persephonaster patagiatus</i>	EU723006	EU722937	EU707650	CASIZ 116778
<i>Petricia vernicina</i>	EU723077	EU722996	EU707757	NIWA 2768
<i>Pharia pyramidata</i>	EU723033	EU722956	EU707759	CASIZ 163788
<i>Porania antarctica</i>	EU072986	EF624418	EU707663	CASIZ 167616
<i>Porania pulvillus</i>	EU722999	EU722924	EU707658	USNM 1127105
<i>Poraniopsis echinaster</i>	EU723000	EU722923	EU707652	–
<i>Poraniopsis inflata</i>	EU723041	EU722964	EU707741	CASIZ 120150
<i>Protoreaster nodosus</i>	GQ288472	GQ288517	GQ288569	USNM1135007
<i>Pseudarchaster parelli</i>	EU723042	EU722965	EU707737	CASIZ 120380
<i>Psilaster cassiope</i>	GQ288511	GQ288540	GQ288600	CASIZ 178991
<i>Remaster gourdoni</i>	EU072987	EU072957	EU707667	CASIZ 167615
<i>Rosaster mimicus</i>	EU723059	EU722980	EU707750	NIWA 15432
<i>Solaster caribbaeus</i>	GQ288501	GQ288549	GQ288602	USNM 1127108
<i>Solaster dawsoni</i>	GQ288474	GQ288519	GQ288573	CASIZ 119165
<i>Solaster hypothrissus</i>	GQ288496	GQ288546	GQ288584	CASIZ 163958
<i>Solaster notophrynus</i>	GQ288499	GQ288545	GQ288583	CASIZ 163147
<i>Solaster paxillatus</i>	GQ288497	GQ288547	GQ288590	CASIZ 164100
<i>Solaster paxillatus</i> #	GQ288498	GQ288548	–	CASIZ 143959
<i>Solaster regularis</i>	GQ288503	GQ288544	GQ288591	CASIZ 174602
<i>Solaster stimpsoni</i>	DQ273726	DQ297113	DQ676930	AMCC 113400
<i>Solaster tropicus</i>	GQ288500	GQ288542	GQ288593	CASIZ 104211
<i>Sphaeriodiscus mirabilis</i>	GQ288487	GQ288533	GQ288606	CASIZ 174584
<i>Stegnaster inflatus</i>	EU723076	EU722995	EU707756	–

Appendix 1 *Continued*

Species	12S	16S	H3-early stage	Voucher
<i>Stegnaster inflatus</i> #	AY370692	AY370719	–	MV-MOL 241
<i>Tarachaster australis</i>	EU723061	EU722983	EU707754	NIWA 15419
<i>Thrissacanthias penicillatus</i>	EU723045	EU722968	EU707740	CASIZ 115075
<i>Thromidia catalai</i>	EU072989	EU072959	EU707698	CASIZ 107266
<i>Tosia australis</i>	EU072990	EU072960	EU707693	USNM 1135012
<i>Tremaster mirabilis</i> #	EU723046	EU722969	–	CASIZ 174624
<i>Tremaster mirabilis</i> #	EU723049	EU722972	–	MNHNP EcAh 5133
<i>Tremaster mirabilis</i> #	GQ288479	GQ288524	–	CASIZ 112822

#These sequences were analyzed only in Fig. 2.

Appendix 2 PCR and sequencing primers used in the present study

Primer	Sequence (5'→3')	Location*	Reference¶
AST-12SL	CTTAATTGACAAAGCAAAGCACTGA	5940-5964	Waters <i>et al.</i> (2004a)
12SF#	GGTHAATTATGTGCCAGCCACCG	6232-6254	this study
12SN#	TTAAAACTCAAAGRACCTGGCGGT	6484-6507	Foltz <i>et al.</i> (2007)
A12S#	CARCNTGTATACCATCRTCCTCAG	6581-6604	Foltz <i>et al.</i> (2007)
12SA#	ACACATCGCCCGTCACTCTC	6818-6837	Smith <i>et al.</i> (1993)
AST-12SR	AACCTCCTTCCTTTAATTTACAAGA	7025-7001	Waters <i>et al.</i> (2004a)
WadaB	CCGGTITGAACTCAGATCAIGT	7637-7658	Wada <i>et al.</i> (1996, modified)
AST16SL2	CGTAGGATTTTAATGGTTCGAACAGA	7656-7680	Waters <i>et al.</i> (2004b)
Alt16S#	AAARGAAIAAGTTACCRYAGGGATAA	7804-7779	Foltz <i>et al.</i> (2007)
16SB#	ACGAGAAGACCCTITIGAGCTT	8047-8026	Smith <i>et al.</i> (1993, modified)
WadaA#	CGCCTGTTTTIICAAAAACAT	8275-8256	Wada <i>et al.</i> (1996, modified)
16SF#	AAAAAGTAGGATTAATAGCATC	8437-8415	this study
AST16SR2	TGTGAAGGAAAGTTGAAATAATGTG	8879-8858	Waters <i>et al.</i> (2004b)

*In the *Patiria pectinifera* complete mtDNA sequence (D16387).

#These were generally used as both forward and reverse (complementary) primers.

¶See article for references, except Smith *et al.* (1993) is from *J. Mol. Evol.* **36**: 545–554.