



Molecular phylogeny of the Forcipulatacea (Asteroidea: Echinodermata): systematics and biogeography

CHRISTOPHER MAH^{1*} and DAVID FOLTZ²

¹Smithsonian Institution, PO Box 37012, MRC 163, Washington, DC 20013-7012, USA

²Louisiana State University – Biological Sciences, Baton Rouge, LA 70803, USA

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We present a comprehensively sampled three-gene phylogeny of the monophyletic Forcipulatacea, one of three major lineages within the crown-group Asteroidea. We present substantially more Southern Hemisphere and deep-sea taxa than were sampled in previous molecular studies of this group. Morphologically distinct groups, such as the Brisingida and the Zoroasteridae, are upheld as monophyletic. Brisingida is supported as the derived sister group to the Asteroiidae (restricted), rather than as a basal taxon. The Asteroiidae is paraphyletic, and is broken up into the Stichasteridae and four primary asteroiid clades: (1) a highly diverse boreal clade, containing members from the Arctic and sub-Arctic in the Northern Hemisphere; (2) the genus *Sclerasterias*; (3) and (4) two sister clades that contain asteroiids from the Antarctic and pantropical regions. The Stichasteridae, which was regarded as a synonym of the Asteroiidae, is resurrected by our results, and represents the most diverse Southern Hemisphere forcipulatacean clade (although two deep-sea stichasterid genera occur in the Northern Hemisphere). The Labidiasteridae is artificial, and should be synonymized into the Heliasteridae. The Pedicellasteridae is paraphyletic, with three separate clades containing pedicellasterid taxa emerging among the basal Forcipulatacea. Fossils and timing estimates from species-level phylogeographic studies are consistent with prior phylogenetic hypotheses for the Forcipulatacea, suggesting diversification of basal taxa in the early Mesozoic, with some evidence for more widely distributed ranges from Cretaceous taxa. Our analysis suggests a hypothesis of an older fauna present in the Antarctic during the Eocene, which was succeeded by a modern Antarctic fauna that is represented by the recently derived Antarctic Asteroiidae and other forcipulatacean lineages.

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INTRODUCTION

The Forcipulatacea represent one of the three major superorders, in addition to the Valvatacea and Spinulosacea, within the modern Asteroidea (Blake, 1987). Several morphologically diverse groups exist within the Forcipulatacea (Heliasteridae, Zoroasteridae, and Brisingida) (Fig. 1), but taxonomic diversity has historically been dominated by the Asteroiidae and related families, including the Labidiasteridae, Pedicellasteridae, Pycnopodiidae,

and Neomorphasteridae (e.g. Clark & Downey, 1992; Clark & Mah, 2001). Although forcipulatacean monophyly has been relatively uncontroversial (e.g. Blake, 1987; Gale, 1987; Foltz *et al.*, 2007), taxonomic groupings within the Forcipulatacea have been regarded as artificial since the early 20th century (e.g. Fisher, 1928, 1930). Previous molecular phylogenetic studies of the Forcipulatacea were summarized in Foltz *et al.* (2007).

Relative to Northern Hemisphere taxa, the systematics for asteroiid taxa from the Southern Hemisphere has received a disproportionately small focus of attention. Fisher (1930) artificially separated Southern from Northern Hemisphere Asteroiidae

*Corresponding author. E-mail: mahch@si.edu

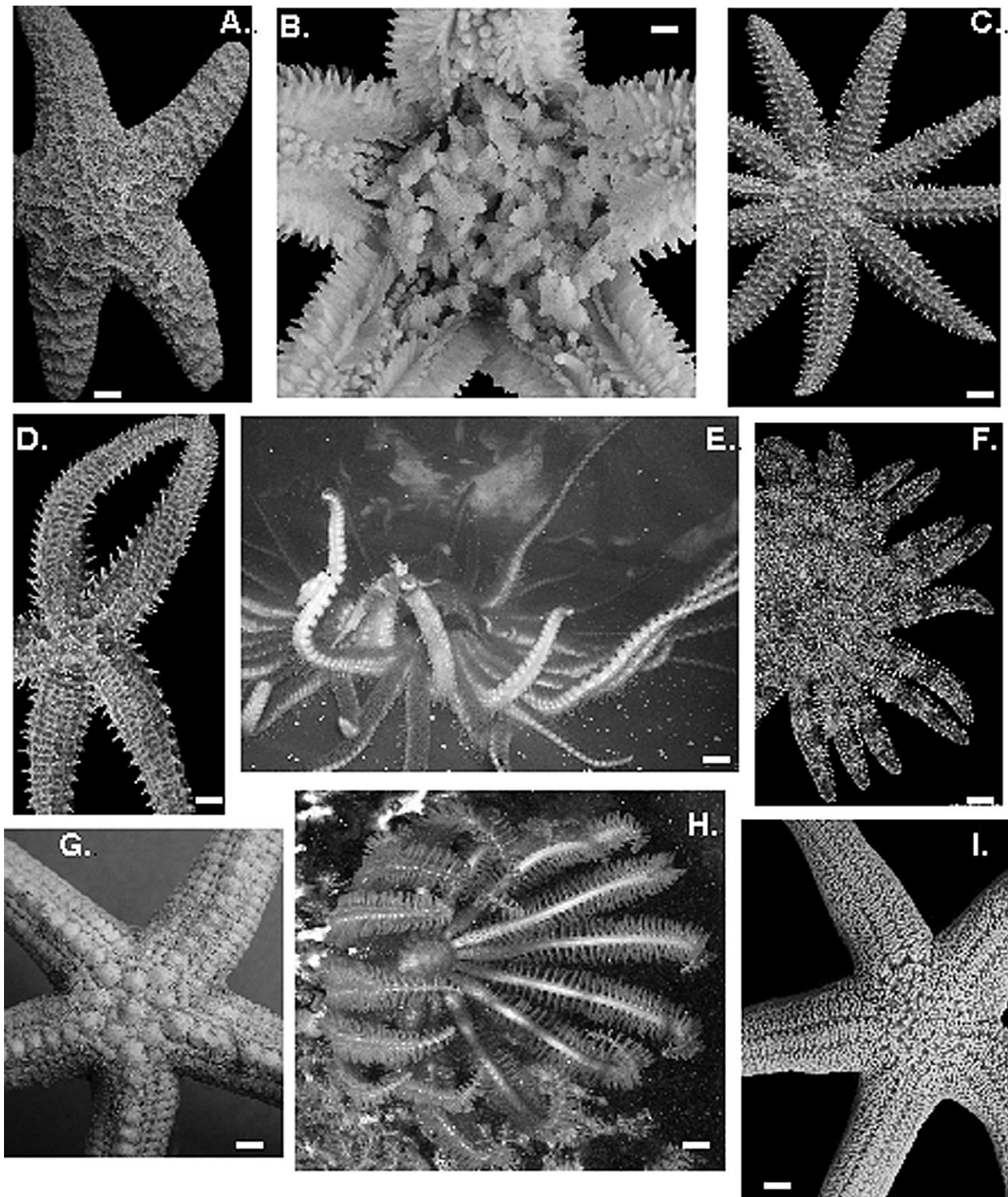


Figure 1. Forcipulatacean diversity. Preserved specimens from the USNM collections; images by C. Mah, unless otherwise noted. A, *Pisaster ochraceus* E01663 (boreal-clade Asteroidea) B, *Diplasterias brandti* 1121889, showing brooded juveniles (Antarctic-clade Asteroidea), image courtesy of Adrian Testa, USARP. C, *Coscinasterias tenuispina* E10146 (pantropical-clade Asteroidea). D, *Sclerasterias mollis* E09987 (*Sclerasterias*-clade Asteroidea). E, *Labidaster annulatus* (Heliasterid/Labidiasteridae). F, *Heliaster multispinus* E45326 (Heliasteridae). G, *Zoroaster fulgens* USNM 1017683 (Zoroasteridae). H, *Novodinia antillensis* (Brisingiida), image courtesy of Sandra Brooke, MCBI. I, *Stichaster striatus* 1082892 (Stichasterid clade). Scale bar: 1.0 cm.

with a taxonomic key and a comprehensive, if brief, summary of the genera and species. This taxonomic arrangement followed his apparent dismissal of the Stichasteridae (Mortensen, 1927), one of the few morphologically well-defined groups, during his revision of the Forcipulatacea and his subsequent review of Antarctic Asteriidae (Fisher, 1940). Fisher's apparent synonymy of the Stichasteridae with the Asteriidae, and his creation of the seemingly redundant Neomorphasteridae, have led to the large current aggregation of unclassified genera that composes the Asteriidae (*sensu* Clark & Mah, 2001).

This study expands on the data and analysis of Foltz *et al.* (2007), who sampled primarily from the Northern Hemisphere. Our objective was to comprehensively sample the Forcipulatacea, with the Asteriidae as the key target taxon. Extensive sampling of Southern Hemisphere and deep-sea taxa was undertaken in order to obtain a more representative sample of the entire group. Our results were considered in the context of the known literature on fossil forcipulataceans and previously published phylogenetic hypotheses.

MATERIAL AND METHODS

MOLECULAR METHODS

DNA extraction, polymerase chain reactions (PCRs), and sequencing were performed as described in Foltz & Mah (2009) and Mah & Foltz (2011). Opposite strands were assembled, edited, and aligned as described in Mah & Foltz (2011). Conserved regions within each alignment (12S rDNA, 16S rDNA, and early-stage histone *H3* genes) were identified with the program GBLOCKS v0.91b (Castresana, 2000), using the following options: (1) the minimum length of a conserved block was set to five nucleotides; (2) a data column in which one or more sequences had a gap was allowed to remain in the curated alignment, provided that such sequences constituted less than half of the total number of sequences. GBLOCKS-curated files were further edited to remove several AT-rich and poorly aligned regions (totaling 56 bp) of the 16S gene.

PHYLOGENETIC METHODS

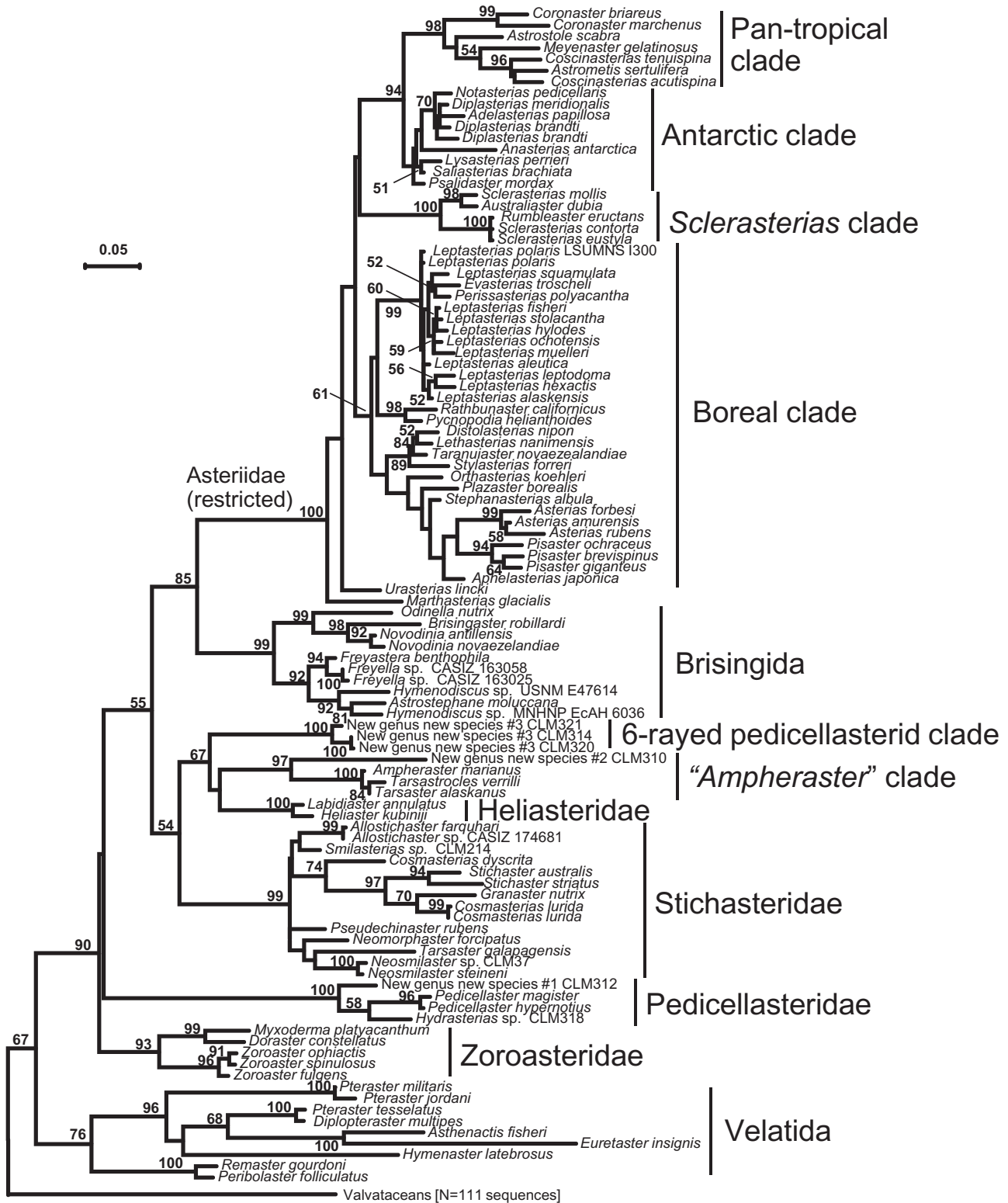
The curated files were concatenated as an interleaved PHYLIP file, converted to sequential format, and submitted to RAXML v7.0.4 (Stamatakis, 2006) on the <http://www.phylo.org> server, with the following options specified: (1) bootstrapping with the number of replicates determined automatically; (2) a mixed/partitioned model with each gene region treated separately; (3) per gene branch length optimization; and (4) the GTR + G substitution model.

Further details are included in the legends to Figures 2 and 3. Analysis of the concatenated three-gene data set in MRBAYES, with the same substitution model and gene partitions as used in the RAXML analysis, resulted in a consensus tree topology that was not appreciably different from the maximum-likelihood tree presented in Figure 3. Similar results were also obtained when each gene region was analysed separately in RAXML (details not shown).

SELECTION OF TAXA

All forcipulatacean families were sampled, but taxonomic sampling was more complete for the 12S plus 16S data set (two-gene data set, $N = 95$ concatenated sequences) relative to the histone *H3* plus 12S plus 16S data set (three-gene data set, $N = 78$). Complete genus-level sampling was accomplished for the Labidiasteridae and the Heliasteridae. All historically recognized morphological groupings of Asteriidae plus Pycnopodiidae (*sensu* Clark & Mah, 2001) were sampled for the two-gene data sets, except for *Caimanaster*, *Calasterias*, *Icasterias*, *Kenrickaster*, *Lysastrosoma*, *Aphanasterias*, *Stichasterella*, and *Uniophora*. However, none of these genera has occupied controversial taxonomic positions, and the first five genera listed above (*Caimanaster*–*Lysastrosoma*) are either seldom encountered or problematic (i.e. known only from single specimens, etc.). Complete sampling of genera was not possible for three deep-sea families: the Pedicellasteridae, the Zoroasteridae, and the Brisingida. However, we attempted to survey the morphological diversity within these three groups, and several key taxa were included in the analysis (e.g. *Novodinia*, *Odinella*, and *Brisingaster* for the Brisingida, and *Myxoderma* in the Zoroasteridae; see Mah, 1998, 2007a). New nominal genera and species of deep-sea pedicellasterids collected recently by Mah from the North-Central Pacific (Gorda Ridge and adjacent areas) were also sampled. In a few instances (such as for *Leptasterias polaris*, *Cosmasterias lurida*, and *Diplasterias brandti*), two or more exemplars of a nominally conspecific taxon were included in the analysis, to provide phylogenetic evidence for or against conspecificity. Details on all taxa included in the in-group, such as GenBank accession numbers and specimen voucher numbers (where available), are listed in Appendix S1.

As the immediate sister taxon to the Forcipulatacea is unknown, sequences from the Velatida and the Valvatacea were used as out-groups. GenBank accession numbers and specimen voucher numbers for all out-group taxa can be found either in Appendix S1 or in Mah & Foltz (2011).



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Figure 2. Maximum-likelihood tree for 95 forcipulate taxa and nine velatidan taxa, rooted on 111 taxa belonging to the Valvatida, Paxillosida, and Notomyotida (these taxa have been omitted for clarity), and based on 261 bp of sequence data for the 12S rDNA gene and 437 bp for the 16S rDNA gene. Bootstrap support values are based on 250 pseudoreplicates and are shown as percentages when $\geq 50\%$. Named clades correspond either to traditional taxonomic groups or to geographically restricted lineages.

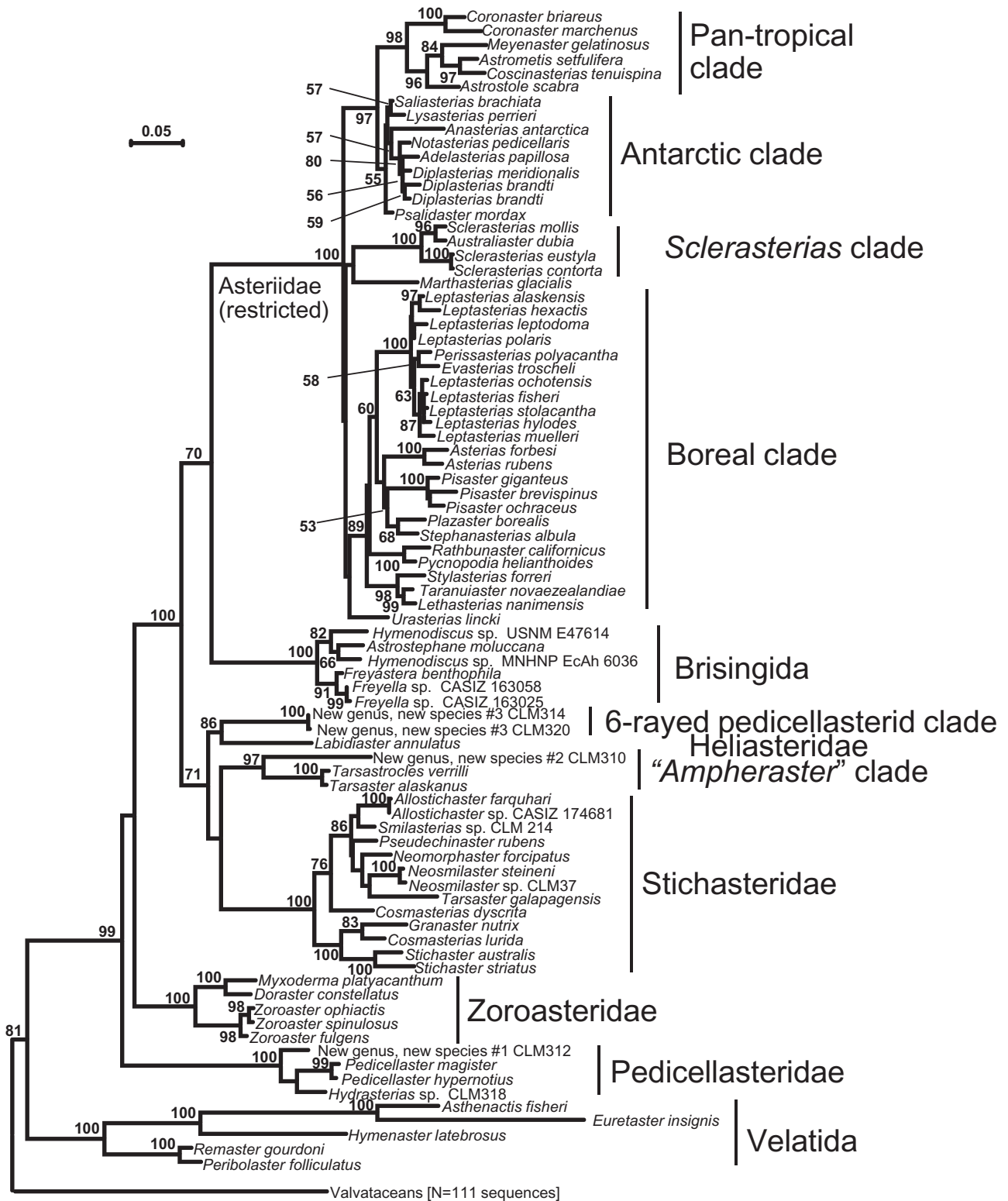


Figure 3. Maximum-likelihood tree for 78 forcipulate taxa and five velatidan taxa, based on 327 bp for the early-stage histone H3 gene plus the same rDNA sequences that were used in Figure 2. Bootstrap support values are based on 200 pseudoreplicates. Other details are as described in Figure 2.

RESULTS & DISCUSSION

PHYLOGENETIC OVERVIEW

Monophyly for the Forcipulatacea is recovered with strong support (90% for the two-gene data set; 99% for the three-gene data set), with several primary clades recovered in both data sets (Figs 2, 3, respectively), which in some cases are historically recognized forcipulatacean groupings with distinctive diagnostic features, such as the Brisingida or the Zoroasteridae. Forcipulatacean monophyly has been uncontroversial, and the present analysis agrees with results from prior phylogenetic studies using morphological (e.g. Blake, 1987) and molecular (e.g. Foltz *et al.*, 2007) data.

Strongly upheld clades included the Zoroasteridae (93% in the two-gene data set; 100% in the three-gene data set), the basal pedicellasterid clade (100% for both), the Brisingida (99% in the two-gene data set; 100% in the three-gene data set), the Stichasteridae (99% in the two-gene data set; 100% in the three-gene data set), the large and restricted Asteroiidae clade (100% in both) with the Asteroiidae + Brisingida clade (85% in the two-gene data set; 70% in the three-gene data set) receiving moderate support.

Several clades within the Asteroiidae are also well-supported, including the *Sclerasterias* clade (100% in both), the *Leptasterias* clade (99% in the two-gene data set; 100% in the three-gene data set), the pantropical clade (98% in both), and the Antarctic plus the pantropical clade (94% in the two-gene data set; 97% in the three-gene data set).

Although the Zoroasteridae and Pedicellasteridae are recovered among the basal Forcipulatacea, there is poor bootstrap support for relationships between the two relative to the remaining Forcipulatacea. Placement of these two taxa is consistent with relationships derived by Gale (1987), Blake (1990), and Blake & Hagdorn (2003), who also show the Zoroasteridae and/or the Pedicellasteridae as basal, relative to the Asteroiidae.

In terms of the number of sampled genera, the largest clade within the Forcipulatacea is formed by the Brisingida + Asteroiidae, which forms the sister group to a clade of largely Southern Hemisphere and deep-sea taxa. Included in this latter sister clade are several new genera of pedicellasterids collected from Gorda Ridge in the Central Pacific, the pedicellasterid *Tarsaster alakanus*, the unusual deep-sea asteroiid *Tarsastrocles*, *Heliaster* (representing the monotypic Heliasteridae), *Labidiaster*, which bears the name for the artificial grouping, the Labidiasteridae (as discussed below), and the newly reinstated Stichasteridae (see details below).

Our trees support a large clade containing traditional members of the Asteroiidae as the sister taxon to

a monophyletic Brisingida, a group that previously has not found consistent placement within the Forcipulatacea (Figs 2, 3). Blake (1987) recovered brisingidans as the sister group to the Forcipulatida. The morphological tree of Mah (2000) established brisingidans as highly derived relative to the other Asteroiidae. Our tree is similar to the morphology and fossil-based tree of Gale (1987), who placed the Brisingida as the sister clade to the Asteroiidae and the Devonian Helianthasteridae. Prior molecular accounts, such as those of Knott & Wray (2000) and Janies (2001), have included brisingidans that were not recovered within a monophyletic Forcipulatacea. Foltz *et al.* (2007) recovered *Brisingaster* + *Odinella* as part of a basal polytomy within the Forcipulatacea.

With the exception of stichasterid taxa, the huge diversity of taxa within the Asteroiidae has defied stable classification. Subfamilies such as the Coscinasterinae and/or the Notasteriinae have historically been relegated to synonymy within the Asteroiidae. Our results show four primary clades within the Asteroiidae that correspond to specific biogeographic regions. These clades have not been previously recognized by prior studies (e.g. Fisher, 1928, 1930), which have largely emphasized morphological characters among the Asteroiidae. These clades are outlined and discussed below.

THE PEDICELLASTERIDAE

The family Pedicellasteridae was established based on a number of reduced skeletal characters, including the lack of fused proximal adambulacral plates (i.e. an adoral carina), a more decalcified body wall, and several other characters interpreted as intermediate between the derived Asteroiidae and non-forcipulate asterooids (Fisher, 1928; Blake, 1990). For example, most pedicellasterids possess only two rows of tube feet versus four in the Asteroiidae. Two rows of tube feet are considered plesiomorphic for most other living Asterozoa (e.g. Blake, 1987). Four of the six genera of nominal Pedicellasteridae – *Ampheraster*, *Hydrasterias*, *Pedicellaster*, and *Tarsaster* – were included in the analysis, as well as three pedicellasterid genera that are new to science and are currently being described (C. Mah, unpubl. data).

Our trees recover a non-monophyletic Pedicellasteridae, which places putative pedicellasterids on three different clades: the Pedicellasteridae; the *Ampheraster* clade, including new genus 2; and the six-rayed pedicellasterid clade (new genus 3). The Pedicellasteridae clade includes the name-bearing *Pedicellaster*, *Hydrasterias*, and a new genus and species of pedicellasterid (new genus 1). The second 'pedicellasterid' clade contains the pedicellasterids *Tarsaster alakanus*, *Ampheraster marianus*, the

Hawaiian asteriid *Tarsastrocles*, and a new pedicellasterid genus and species 2. Finally, the third clade includes the six-rayed new genus/species 3, which was collected from the Gorda Ridge region and adjacent areas in the North Pacific.

The genus *Tarsaster* is not supported as monophyletic, with *Tarsaster galapagensis* recovered among the Stichasteridae and *Tarsaster alaskanus* placed with *Ampheraster*, *Tarsastrocles*, and new genus/species 1. Although *Tarsaster* has historical seniority over *Ampheraster*, the lack of monophyly in *Tarsaster* has dictated that for the time being, *Ampheraster* be used to describe the non-Stichasteridae clade, which includes *Tarsaster alaskanus*, until taxonomic issues in *Tarsaster* can be fully resolved. Depending on whether the type species for *Tarsaster*, *Tarsaster stichodes* is placed among the Stichasteridae or among the members of the 'Ampheraster' clade, assignments to new genera will probably be necessary.

Although not recovered as monophyletic, pedicellasterids were never recovered as part of the restricted Asteroiidae or any of the more recently derived forcipulatacean lineages, supporting the interpretation of at least some pedicellasterids as basal or stemward forcipulataceans. Although the multiple pedicellasterid lineages suggest that the characters associated with pedicellasterids are independently derived, it seems more likely, especially based on phylogenetic hypotheses based on fossils (e.g. Blake & Hagdorn, 2003), that these characters are plesiomorphic for the Forcipulatacea.

THE ZOROASTERIDAE

Monophyly of the Zoroasteridae was shown by Blake (1990) and reviewed by Mah (2007a), who tested relationships among the genera within the family. Our results (Figs 2, 3) show *Zoroaster* as the monophyletic sister clade to a lineage that supports *Myxoderma* and *Doraster* as sister taxa. This differs from the zoroasterid relationships outlined by Mah (2007a), which support *Doraster* + *Zoroaster* as a sister taxon to *Myxoderma*, but three nominal zoroasterid genera are absent from our trees. Further taxon sampling is needed for a complete test of intrafamilial relationships.

THE STICHASTERIDAE AND SYNONYMY OF THE NEOMORPHASTERIDAE

Among the most diverse stemward clades is a lineage (99% bootstrap support on the two-gene tree; 100% bootstrap support on the 3-gene tree) that includes nearly all members of the Stichasteridae, as designated by Perrier (1885) and Sladen (1889). Perrier's (1885) Stichasteridae included *Stichaster*, *Neomor-*

phaster, and *Granaster*. Sladen (1889) modified the Stichasteridae to include *Stichaster*, *Neomorpha-*
staster, as well as *Stichaster* (= *Allostichaster*) *polyplax* and *Stichaster* (= *Cosmasterias*) *felipes*. Our results also show *Neosmilaster*, *Pseudechinaster*, and *Smilasterias* as members of the Stichasteridae.

Our results uphold *Stichaster* as monophyletic, but not *Cosmasterias*. *Cosmasterias dyscrita* was separated from a larger clade of Stichasteridae in both trees. In the three-gene tree, *Cosmasterias lurida* is a member of the sister group to the large clade containing *C. dyscrita*. In the two-gene tree, *C. lurida* is supported as part of the same clade as *C. dyscrita*.

Based on the position of *Neomorpha-*
staster within the stichasterid clade, the monotypic Neomorphasteridae Fisher, 1923 should be synonymized with the Stichasteridae Perrier, 1885. Our results do not support *Neomorpha-*
staster as the sister taxon to *Zoroaster*, as indicated by Mah (2000). However, the shared morphological similarities may be indicative of plesiomorphic character states between zoroasterids and stichasterids.

Sampled members of the Stichasteridae lineage are limited to temperate waters in the Southern Hemisphere, with two exceptions: the deep-water *Neomorpha-*
staster occurring in the Northern Hemisphere in the North Atlantic (none have been reported from the South Atlantic), and *Neosmilaster* sp. nov. (supported as the sister to *Neosmilaster steineni*) from the North Pacific. The unsampled North Atlantic *Stichasterella* was placed within the Stichasteridae by Mortensen (1927), based on several shared morphological characters. If *Stichasterella* is upheld as a member of this clade, it would also be included among the Northern Hemisphere Stichasteridae. There is evidence that the stichasterid lineage has experienced some extinction and range restriction. Blake & Peterson (1993) described the *Neomorpha-*
staster-like *Pegaster* from the Cretaceous of California. A significant level of forcipulatacean diversity that is restricted to the Australia/New Zealand/South Pacific region includes members of the stichasterid clade, including *Stichaster*, *Pseudechinaster*, *Allostichaster*, *Smilasterias*, and 'Cosmasterias' *dyscrita* (a separate lineage from *C. lurida*). Only the shallow-water South Australian *Uniophora* was absent from our sampling. However, *Uniophora* shares several morphological characters with other stichasterids, and therefore we suggest it will probably be included as a member of the Stichasteridae in future molecular phylogenetic studies.

THE HELIASTERIDAE AND THE SYNONYMY OF THE LABIDIASTERIDAE

The monotypic Heliasteridae includes the sole genus *Heliaster*, which comprises a species complex in the

tropical East Pacific from Baja California, west to the Galapagos, and south to Chile (H. L. Clark, 1907).

In our two-gene tree (Fig. 2) the monotypic Heliasteridae, represented by the Eastern Pacific species *Heliaster kubiniji*, is supported (100% bootstrap) as the sister taxon to the Southern Ocean/sub-Antarctic *Labidiaster*. The three-gene tree, which lacks *Heliaster*, shows *Labidiaster* as sister taxa to a new genus and species of deep-sea six-rayed pedicellasterid from the Central Pacific (86% bootstrap support), but with much longer branch lengths, suggesting greater divergence between the two taxa. If *Labidiaster* and *Heliaster* are sister taxa, this would further suggest a close biogeographic relationship between the South American and Antarctic/sub-Antarctic asteroid faunas. Janosik *et al.* (2008) have shown pelagic larvae for *Labidiaster annulatus* present in the Drake Passage, suggesting gene flow between South American and Antarctic populations.

Support for *Labidiaster* as the sister taxon to *Heliaster* is consistent with the assertion that the Labidiasteridae (*sensu* Spencer & Wright, 1966) is a purely artificial grouping (e.g. Mah, 2000; Foltz *et al.*, 2007). *Labidiaster* is a phylogenetically separate taxon from the other labidiasterids (*sensu* Clark & Mah, 2001), including *Plazaster*, *Coronaster*, and *Rathbunaster*. Because *Labidiaster* is the type genus for the Labidiasteridae, this places synonymy of the Labidiasteridae into the Heliasteridae rather than the Asteroiidae, as has been implied by earlier studies (e.g. Mah, 2000). The other genera within the Labidiasteridae have emerged with phylogenetically distinct clades: *Plazaster* and *Rathbunaster* on separate clades within the boreal Asteroiidae, and *Coronaster* with the pantropical Asteroiidae. All members of the polyphyletic Labidiasteridae were characterized by large numbers of elongate arms (up to 50 in *Labidiaster*), biserial tube foot rows, and prominent pedicellariae. Based on our phylogenetic trees, these characters may be independently derived adaptations for benthopelagic predation, which has been observed in *Labidiaster* (Dearborn, Edwards & Fratt, 1991) and *Rathbunaster* (Lauerman, 1998).

THE BRISINGIDA

Our results (Figs 2, 3) recover the Freyellidae (*Freyella* and *Freyastera*) as the sister group to more archetypical brisingidans, such as *Hymenodiscus* and *Astrostephane*. The greater taxon sampling in Figure 2 supports the former Freyellidae and Brisingidae as the sister group to *Odinella*, *Brisingaster*, and *Novodinia*. The latter two genera emerge as the sister group to *Odinella*. This result is similar to the morphology-based phylogenetic trees developed by Mah (1998, 1999), who supported those brisingidans,

occurring in shallower depths, with widely abundant papulae present on the abactinal surface (*Odinella*, *Novodinia*, and *Brisingaster*), as the sister group to the other, more derived brisingidans.

Mah (1998, 1999) considered *Odinella*, *Novodinia*, and *Brisingaster* as having an intermediate brisingid morphology relative to an asteroiid or labidiasterid sister taxon. This was especially the case for *Odinella*, which has the distinct, wing-like ambulacral ossicles present in asteroiids rather than the vertebrae-like ambulacrals present in other brisingidan genera. This perspective is consistent with Mah's (1998) hypothesis of a bathymetric shift between the shallower-water members of this clade and the deeper-water Freyellidae and Brisingidae.

It should be noted that, although a new classification has not been finalized, our placement of the brisingidans as a derived sister branch to the Asteroiidae disagrees with the ordinal-level ranking that places it on a parallel with the Forcipulatida.

THE ASTEROIIDAE: OVERVIEW

The restricted Asteroiidae contains four primary clades, representing the most recent and diverse radiation of taxa within the Forcipulatacea. Three are associated with discrete biogeographic regions, whereas the fourth (*Sclerasterias*) is widely distributed in the Atlantic, Pacific, and Indian oceans. These clades include: (1) the boreal clade, which includes primarily genera from the Northern Hemisphere, although one or two exceptional Southern Hemisphere genera are also included; (2) the *Sclerasterias* clade, including ~14 globally distributed species; and (3) and (4), the Antarctic and pantropical clades, which are strongly supported (94% on the two-gene tree; 97% on the three-gene tree) as sister taxa in both of our trees (Figs 2, 3). The Antarctic clade includes nominal Asteroiidae, which are present only in the Southern Ocean and adjacent regions. The pantropical clade includes several asteroiid genera that occur primarily at low latitudes, often in shallow-water, tropical settings.

THE ASTEROIIDAE: BOREAL CLADE

Among the most diverse of the asteroiid lineages is a boreal clade that includes primarily shallow-water, continental-shelf genera from the Arctic, temperate to high-latitude North Atlantic, and North Pacific, inclusive of cold and temperate waters in Asia (Japan and Taiwan) and Russia. Several familiar genera of Asteroiidae, including the intertidal *Asterias* and *Pisaster*, are supported as monophyletic. These two genera show a sister-group relationship in the two-gene tree (Fig. 2), but a more distant relationship in

the three-gene tree. *Stephanasterias* and *Plazaster* are united as sister taxa on the three-gene tree (Fig. 3) with 68% bootstrap support, and are shown as closely related on the two-gene tree, which further suggests close affinities between the two genera.

The largest clade, containing the greatest number of species within the holarctic Asteriidae, is the one upholding the genus *Leptasterias*, a highly diverse lineage that has shown extensive diversification across the Arctic and temperate to high-latitude North Atlantic and North Pacific.

All included species of *Leptasterias* were recovered on a single clade, which also included the North Pacific *Evasterias* and the Southern Hemisphere *Perissasterias* as sister taxa within the *Leptasterias* lineage. Previous phylogenetic studies of the genus *Leptasterias* employing more taxa and longer sequence reads than those analyzed here (Hrincevich, Rocha-Olivares & Foltz, 2000; Foltz *et al.*, 2008) have reported somewhat different results from those in Figures 2 and 3: (1) *Evasterias* was strongly supported as the sister group to *Leptasterias*; (2) *Leptasterias fisheri* + *Leptasterias stolacantha* + *Leptasterias muelleri* was strongly supported as the sister group to the six-armed subgenus *Hexasterias*; (3) *Leptasterias polaris* (Polaris section of Fisher, 1930) was strongly supported as the sister group to the remaining *Hexasterias* (i.e. Fisher's *Camtschatica* section); (4) *Leptasterias leptodoma* was supported as the sister group to the remaining members of the *Camtschatica* section. *Leptasterias hylodes*, *Leptasterias ochotensis*, *Leptasterias squamulata* were not sampled in the earlier studies. These differing results probably reflect the difficulty of inferring phylogenetic relationships within a recent, rapid radiation (Foltz *et al.*, 2008).

Two Southern Hemisphere genera, *Perissasterias* and *Taranuiaster*, were present among the predominantly Northern Hemisphere boreal Asteriidae. Further data are needed to make any definitive conclusions, but if the results are taken at face value, then two interpretations are possible for one or both of these genera. *Perissasterias* and *Taranuiaster* may belong to mostly extinct lineages of Asteriidae, which suggests a greater number of taxa with a more widespread distribution in the past, especially into the Southern Hemisphere. Alternatively, larval or adult dispersal may have transported ancestors of these taxa to the Southern Hemisphere, providing suitable environmental conditions to settle, thrive, and establish an adult population. Fisher (1930) noted that *Perissasterias* was one of the few Southern Hemisphere genera to share characters with Northern Hemisphere Asteriidae. Also, *Perissasterias* and *Taranuiaster* are deep-sea taxa, and live in environments that may parallel cold-water settings similar to those of *Leptasterias* and other boreal Asteriidae.

Pycnopodia was supported as the sister taxon to *Rathbunaster*. *Pycnopodia* has been classified as one of two genera (the other being *Lysastroma*) within the Pycnopodiidae (see Clark & Mah, 2001). However, *Lysastroma* was not included in our treatment, which for the moment, prevents us from completely testing the monophyly and validity of the Pycnopodiidae.

THE ASTERIIDAE: ANTARCTIC AND PANTROPICAL CLADES

The pantropical asteriid clade was supported as the sister taxon to the Antarctic asteriid clade in Figures 2 and 3, with 94% bootstrap support on the two-gene tree and 97% bootstrap support on the three-gene tree. There is a similar pattern observed in between the Antarctic urchin *Sterechinus* and its tropical South American sister taxa, *Loxechinus* and *Pseudechinus* (Lee *et al.*, 2004). This is consistent with a relationship between asteriid taxa from the Antarctic/sub-Antarctic and adjacent tropical regions. Several non-asteriid Forcipulatacea show relationships between tropical and Antarctic/sub-Antarctic taxa. For example, the tropical shallow-water *Heliaster* is supported as the sister taxon to the Antarctic/sub-Antarctic *Labidiaster*. The Antarctic brisingidan *Odinella* is supported as sister taxon to a clade containing basal brisingidans *Brisingaster* and *Novodinia*. Although *Novodinia* is widely distributed, *Brisingaster* is known only from the Indian Ocean and New Caledonia (Mah, 1999). A more complete species-level data set, for both the Antarctic and the pantropical clade, will be needed to discover the closest sister taxon to the Antarctic fauna.

The pantropical Asteriidae is well-supported as the sister group to the diverse Antarctic Asteriidae. The pantropical Asteriidae is composed of *Coronaster*, members of which occur mostly in the deep sea, as the sister clade to four shallow-water tropical genera: *Astrostole*, *Astrometis*, *Coscinasterias*, and *Meyenaster*. *Astrostole*, *Astrometis*, and *Meyenaster* are known only from the shallow-water settings from the Eastern Tropical Pacific, whereas *Coronaster* and *Coscinasterias* occur widely in the Atlantic and the Indo-Pacific. *Coronaster* occurs primarily in the deep sea (> 200 m), although some species (e.g. *Coronaster marchenus*) do occur in shallow waters (< 10 m).

Nearly every known genus of nominal Antarctic Asteriidae was supported as part of a single lineage, occurring only at high latitudes in the Southern Hemisphere. Relative to more stemward Antarctic/sub-Antarctic forcipulataceans, such as *Granaster*, *Neosmilaster*, or *Labidiaster*, the Antarctic Asteriidae clade evolved more recently and as a single event. Our trees did not support *Diplasterias* as monophyletic, but *Diplasterias* forms a species complex in the

Southern Ocean region similar to the one formed by *Leptasterias* in the boreal north. This suggests that further taxonomic sampling and additional genes with longer reads are likely to contribute to a better understanding of *Diplasterias*, similar to the prior studies of *Leptasterias* discussed above.

The diversification of the Antarctic Asteroiidae may be associated with the isolation of the Southern Ocean fauna and the formation of the Antarctic Counter Current at the end of the Eocene/early Oligocene (25 Ma), as outlined by Clarke & Crame (1992) and Aronson *et al.* (2009).

Distribution data for several of the genera included in the Antarctic asteriid clade (Fisher, 1940; Bernasconi, 1973, C. Mah, unpubl. data) show that *Anasterias*, *Diplasterias*, *Lysasterias*, and *Psalidaster* occur well into the South Atlantic as well as the Southern Ocean, with *Adelasterias*, *Notasterias*, and *Saliasterias* apparently limited to the Southern Ocean. We suggest that the ancestors to the Antarctic asteriid lineage occupied a much broader distribution from the Southern Ocean and the adjacent sub-Antarctic region, including the South Atlantic and South Pacific, prior to the formation of the Antarctic Circumpolar Current (ACC). The ACC would have isolated the Southern Ocean fauna from the adjoining population, leaving the adjoining population 'outside' the ACC boundary in the South Atlantic/sub-Antarctic region. Several accounts have documented other invertebrate species that have a similar distribution, but which demonstrate either limited or no gene flow across the ACC (e.g. Hunter & Halanych, 2008; Thornhill *et al.*, 2008). This suggests that nominal Antarctic asteriid species, with identical morphology on either side of the ACC, could be genetically distinct, cryptic species complexes.

The presence of Southern Ocean and sub-Antarctic populations separated by the ACC would also be consistent with widespread circumpolar distribution of so many of the Antarctic asteriids, which lack planktonic larvae. The sub-Antarctic populations would conceivably be ancestral relative to those in the Southern Ocean. This notion would also be consistent with the seeming plesiomorphic morphology shared by *Psalidaster*, *Saliasterias*, and several multi-armed and widespread members of the pantropical Asteroiidae, such as *Coronaster* and *Astrostole*. However, further comprehensive biogeographic analyses of the clade members would be necessary to test this hypothesis.

THE ASTEROIIDAE: *SCLERASTERIAS* CLADE AND *MARTHASTERIAS*

The New Zealand species *Sclerasterias mollis* and the South Australian/South Pacific *Australiaster* were

supported on both the two-gene and three-gene trees with 100% bootstrap support. The sister clade to the *Sclerasterias mollis* + *Australiaster* lineage included *Rumbleaster* and two Atlantic *Sclerasterias* species, *Sclerasterias contorta* and *Sclerasterias eustyla*. In both trees, all members of the *Sclerasterias* clade are strongly supported with 100% bootstrap support.

Australiaster and *Rumbleaster* possess few morphological distinctions from *Sclerasterias*, which compels us to conclude that they are synonyms of *Sclerasterias*. *Sclerasterias* (including *Rumbleaster* and *Australiaster*) includes 14 species (Clark & Mah, 2001), which are present in the Atlantic, Pacific, and Indian Oceans, occurring at continental shelf, upper bathyal depths of approximately 20–700 m. The genus *Sclerasterias* is unusual as a primary clade within the Asteroiidae in that it shows relatively conservative morphology (i.e. all members of the genus *Sclerasterias* are recognizable), but includes species from a widespread distribution.

Sclerasterias has been collected in shallow-water (i.e. littoral) sediments from the Eocene of Seymour Island (Blake & Zinsmeister, 1979, 1988), but has not been recorded from the modern Antarctic fauna, although some species are recorded from the South Atlantic and sub-Antarctic regions (e.g. Bernasconi, 1979). *Sclerasterias* species are not known from the Arctic.

The phylogenetic placement of *Rumbleaster* within the *Sclerasterias* clade adds an unusual environmental association to the phylogeny. This lineage includes two of the few asteroid species known to occur in association with cold seep-type chemosynthetic communities in two different oceanic regions. *Sclerasterias tanneri* in the Gulf of Mexico has been described as a 'colonist'-type member of a chemosynthetic system (Carney, 1994), with species obtaining 50–100% of their nutrition from cold-seep production (MacAvoy *et al.*, 2002). More recently '*Rumbleaster*' (= *Sclerasterias*) *eructans* was described from the Rumble submarine volcanoes in the Bay of Plenty, New Zealand (McKnight, 2006), where it was observed feeding on the *Bathymodiulus*-like mytilid mussel *Gigantidas gladius* (vonCosel & Marshall, 2003). Feeding habits for other species of *Sclerasterias* have not been reported, but only one species (*Sclerasterias mollis*) occurs in relatively shallow water (Clark & Mah, 2001), with the remaining species known to occur as deep as 700 m. The phylogenetic significance of this association is unclear, but is presented here as an encouragement towards further study.

The widely distributed Atlantic asteriid *Marthasterias* occurs as the sister group to the *Sclerasterias* lineage in our three-gene tree, but not in our two-gene tree. Our two-gene tree places *Marthasterias* as the

sister lineage to the entire Asteroidea clade. Neither of these relationships was well-supported (if at all) by bootstrap values.

PHYLOGENY AND FOSSIL FORCIPULATACEA:
TIMING AND HISTORICAL RANGE

Evidence outlined below suggests that several of the more stemward lineages, including the Zoroasteridae, the Pedicellasteridae, and the Stichasteridae, formerly possessed a greater distribution relative to the more derived Asteroidea clade. This, in addition to fossils and molecular dates for derived taxa, suggests that members of the Asteroidea clade may have only recently come to occupy their current range, as older forcipulatacean lineages shifted to more restricted distributions.

Our phylogenetic evidence, when compared with the available fossils, is consistent with diversification in the early Mesozoic/late Paleozoic, as summarized by Twitchett & Oji (2005), and suggested by the phylogenies of Blake (1987, 1990), Blake & Hagdorn (2003), and Gale (1987). The fossil evidence includes *Trichasteropsis* and the Trichasteropsida, as the fossil sister branch to the modern Forcipulatacea, as supported by Blake & Hagdorn (2003). Pedicellasterids possess characters intermediate between forcipulataceans and non-forcipulataceans, including biserial tube foot rows and the absence of an adoral carina (i.e. abutted oral adambulacral ossicles), which places them as the sister group to the other forcipulataceans in morphology-based trees such as those of Blake & Hagdorn (2003) and Villier, Charbonnier & Riou (2009). Our results also reconstruct pedicellasterids, along with zoroasterids, on basal phylogenetic positions within the Forcipulatacea. Phylogenetic hypotheses of Blake (1990) and Blake & Hagdorn (2003) suggest that pedicellasterids were present early in the diversification of the Forcipulatacea, but they are not observed in the fossil record until the Cretaceous (Blake, Breton & Gofas, 1996).

The phylogenetic position of *Trichasteropsis* as basal within the Forcipulatacea (Blake, 1987; Blake & Hagdorn, 2003) is consistent with the similar phylogenetic positions of the Zoroasteridae and the pedicellasterids in our molecular tree (Figs 2, 3). Also, modern zoroasterids and the Mesozoic Trichasteropsida (Blake & Hagdorn, 2003) both share characters, such as a single series of marginal plates, which are distinctive for some basal crown-group asteroids. This suggests that our data remain consistent with the basal position of *Trichasteropsis*, as outlined by Blake & Hagdorn (2003) and Blake (1987, 1990).

Morphology of several Jurassic taxa, such as *Germanasterias* and *Hystrixasterias* (see Blake, 1990) is similar to that of basal forcipulataceans, such as

pedicellasterids and some zoroasterids. This pattern suggests that some characters (such as the open, reticulate skeleton) may be plesiomorphic among basal forcipulataceans. Villier *et al.* (2009) re-analysed several Jurassic taxa and supported *Terminaster*, which had previously been considered a zoroasterid (Hess, 1974), as sister group to the Forcipulatacea.

Subsequent lineages included the Stichasteridae + Heliasteridae and a second clade of pedicellasterids as sister clade to the Asteroidea + Brisingida. A fossil stichasterid, *Pegaster stichos*, was described by Blake & Peterson (1993) from the Cretaceous of California. This Northern Hemisphere presence of *Pegaster* suggests that stichasterids have been more widely distributed before their current restriction to the Southern Hemisphere. Today, the North Atlantic *Neomorphaster*, and probably *Stichasterella*, are the only known living stichasterids in the Northern Hemisphere.

A Cretaceous pedicellasterid, *Afraster scalariformis*, was described from Angola, Africa (Blake *et al.*, 1996), and was morphologically similar to *Pedicellaster*. Cruciform ossicles, which could be asteroid or pedicellasterid-like, have also been recovered from the Cretaceous of the Paris Basin in France (Breton & Ferre, 1995), suggesting that pedicellasterids were once more widespread.

Jones & Portell (1988) described a Pliocene *Heliaster microbrachius*, which extended the occurrence of living *Heliaster* in the East Pacific to the Pliocene of Florida. Figure 2 supports *Heliaster* as the sister taxon to the Magellanic/Antarctic *Labidiaster*, suggesting that the historical range for the heliasterid lineage was much more extensive than its current distribution. Extrapolating from biogeographic relationships between the Neogene mollusc fauna of Florida and the modern fauna of the Eastern Tropical Pacific, Jones & Portell (1988) speculated that heliasterids originated in the Atlantic and migrated to the Eastern Tropical Pacific. Although our taxon sampling is incomplete, we are unable to support this hypothesis based on the Pacific-only taxa, which have been supported as sister taxa to the *Heliaster* clade.

Following the diversification of the Stichasteridae and its sister taxa, such as the Heliasteridae, we observe the most recent radiation within the Forcipulatacea, the Asteroidea + Brisingida. Brisingidan fossils are rarely encountered, but a fossil of the brisingidan *Hymenodiscus* (described as *Brisingella*) has been described from the Miocene of the Morozaki group (Yamaoka, 1987). The Antarctic *Odinella* shows characters intermediate between asterooids and brisingidans, and suggests that ancestry for this group may be from the Southern Hemisphere.

The restricted Asteroiidae is inferred to be the most recently derived and most diverse of the primary clades within the Forcipulatacea. Fossils associated with this lineage are consistent in geologic age with the relative age implied by the tree. For example, fossils from the Eocene of Seymour Island (Blake & Zinsmeister, 1988; Blake & Aronson, 1998) show the presence of *Sclerasterias* (Pantropical clade) and *Zoroaster* (Zoroasteridae) in the Antarctic region. Both genera are currently widely distributed in the Atlantic, Pacific, and Indian oceans, but are absent from the living Southern Ocean fauna (Mah, 2007a). Younger fossils for living taxa exist, but largely serve mainly to reinforce the known distributions of those taxa. For example, *Asterias forbesi* (boreal clade) fossils occur in the Pleistocene of North Carolina, which is consistent with the distribution of the living species (Barker & Zullo, 1980).

The timing of lineage-splitting events for derived taxa based on molecular data is also consistent with the geological evidence. The relatively derived positions of *Coscinasterias* and *Astrostole* among the pantropical Asteroiidae are consistent with the Pliocene/Pleistocene divergence dates estimated for global *Coscinasterias* species by Waters & Roy (2003). Similarly, the timing estimates of *Asterias* and *Leptasterias* with Pliocene (3.5 Ma) divergence dates, as estimated by Wares (2001) and Foltz *et al.* (2008), respectively, is consistent with their position on the tree as recently derived.

TREE TOPOLOGY AND ANTARCTIC EVENTS

In the context of fossil occurrence and other data for the relative timing on the forcipulatacean tree, diversification of Antarctic clades appears to be consistent with events associated with the middle Eocene formation of the ACC, and the subsequent cooling of Antarctic waters (as outlined by Clarke & Crame, 1992). This includes diversification within the more recently derived Antarctic Asteroiidae clade, and older forcipulatacean lineages such as *Odinella* (Brisingida), *Labidiaster* (Heliasteridae), *Granaster* (Stichasteridae), and *Neosmilaster* (Stichasteridae). If these diversification events are considered in conjunction with the forcipulatacean fossils from the Eocene of Seymour Island, and the timing of the extinction of the fauna of Seymour Island, they imply a succession of forcipulatacean taxa in the Southern Ocean.

Zoroaster and *Sclerasterias* both occur as fossils from Eocene rocks on Seymour Island, but are absent from the modern asteroid faunas in the Southern Ocean (Mah, 2007a). The Antarctic asteroiid clade, as well as the other stemward, modern forcipulatacean Antarctic taxa (e.g. *Granaster*, *Labidiaster*, etc.), may have diversified into niches left absent following the

extinction of the pre-glaciation, Eocene fauna. Cooling trends, which eliminated durophagous predators (Aronson *et al.*, 2009), may have also created a more favourable ecological setting for these taxa, such as the long-armed suspension feeding *Labidiaster*, to diversify.

CONCLUSION

A phylogenetic analysis of forcipulatacean taxa (as summarized by Clark & Mah, 2001; see Table 1) using *12S*, *16S*, and early-stage histone *H3* genes adds multiple Southern Hemisphere and deep-sea taxa to the phylogeny of Foltz *et al.* (2007). These results can be summarized as follows (see also Table 2).

1. The Zoroasteridae and the Brisingsida are recovered as monophyletic based on prior morphological definitions, as outlined in Blake (1987) and Clark & Downey (1992). Our data set shows the Brisingsida as derived rather than basal, as indicated by Blake (1987), suggesting that ordinal status is not warranted.
2. The Labidiasteridae is not upheld as monophyletic. Based on the sister-group relationship between *Labidiaster* and *Heliaster*, the Labidiasteridae is not upheld as monophyletic.

Table 1. Classification of groups tested and included genera, following the classification outlined by Clark & Mah (2001)

Forcipulatacea
Forcipulatida
Asteroiidae: <i>Adelasterias</i> , <i>Allostichaster</i> , <i>Anasterias</i> , <i>Asterias</i> , <i>Astrometis</i> , <i>Astrostole</i> , <i>Australiaster</i> , <i>Coscinasterias</i> , <i>Cosmasterias</i> , <i>Diplasterias</i> , <i>Evasterias</i> , <i>Granaster</i> , <i>Leptasterias</i> , <i>Lethasterias</i> , <i>Lysasterias</i> , <i>Marthasterias</i> , <i>Meyenaster</i> , <i>Neosmilaster</i> , <i>Notasterias</i> , <i>Orthasterias</i> , <i>Perissasterias</i> , <i>Pisaster</i> , <i>Psalidaster</i> , <i>Pseudechinaster</i> , <i>Rumbleaster</i> , <i>Saliasterias</i> , <i>Sclerasterias</i> , <i>Smilasterias</i> , <i>Stephanasterias</i> , <i>Stichaster</i> , <i>Stylasterias</i> , <i>Taranuiaster</i> , <i>Tarsastrocles</i> , <i>Urasterias</i>
Heliasteridae: <i>Heliaster</i>
Labidiasteridae: <i>Coronaster</i> , <i>Labidiaster</i> , <i>Plazaster</i> , <i>Rathbunaster</i>
Neomorphasteridae: <i>Neomorphaster</i>
Pedicellasteridae: <i>Ampheraster</i> , <i>Hydrasterias</i> , <i>Pedicellaster</i> , <i>Tarsaster</i>
Pycnopodiidae: <i>Pycnopodia</i>
Zoroasteridae: <i>Doraster</i> , <i>Myxoderma</i> , <i>Zoroaster</i>
Brisingsida
Brisingidae: <i>Astrostephane</i>
Freyellidae: <i>Freyastera</i> , <i>Freyella</i>
Novodiniidae: <i>Novodinia</i> , <i>Odinella</i>

Table 2. Classification suggested by new molecular phylogenetic results, summarized in Figures 2 and 3

Forcipulatacea

Asteriidae

Antarctic Clade: *Adelasterias*, *Anasterias*, *Diplasterias*, *Lysasterias*, *Notasterias*, *Psalidaster*, *Saliasterias*

Boreal Clade: *Asterias*, *Distolasterias*, *Evasterias*, *Leptasterias*, *Perissasterias*, *Pisaster*, *Plazaster*, 'Pycnopodiidae' (status uncertain), *Pycnopodia*, *Rathbunaster*, *Stephanasterias*, *Stylasterias*, *Taranuiaster*

PanTropical Clade: *Astrometis*, *Astrostole*, *Coronaster*, *Coscinasterias*, *Meyenaster*

Sclerasterias: *Australiaster* (synonym), *Rumbleaster* (synonym), *Sclerasterias*

'Brisingida': *Astrostephane*, *Brisingaster*, *Freyella*, *Freyastera*, FREYELLIDAE, *Hymenodiscus*, *Novodinia*, NOVODINIIDAE, *Odinella*

Ampheraster Clade: *Ampheraster*, New genus 2, *Tarsaster alaskanus*, *Tarastrocles*,

Heliasteridae: *Heliaster*, *Labidiaster*, LABIDIASTERIDAE (synonym)

Six-rayed Pedicellasteridae Clade: New genus 3.

Pedicellasteridae Clade 1: *Hydrasterias*, *Pedicellaster*, New genus 1.

Stichasteridae: *Allostichaster*, *Cosmasterias*, *Granaster*, *Neomorphaster*, NEOMORPHASTERIDAE (synonym), *Neosmilaster*, *Notasterias*, *Pseudechinaster*, *Smilasterias*, *Stichaster*, '*Tarsaster galapagensis*'

Zoroasteridae: *Doraster*, *Myxoderma*, *Zoroaster*

Modified from Table 1. A formal taxonomic classification is in preparation. Out-groups are absent from this table.

teridae should be considered as a synonym of the Heliasteridae. Because most members of the Labidiasteridae have been observed as benthopelagic predators in geographically disparate localities, morphological characters used to justify the Labidiasteridae are attributed to convergent evolution.

- The Pedicellasteridae, including several newly collected deep-sea taxa from the central North Pacific, are reconciled as two distinct clades: one is basal within the Forcipulatacea and the other is supported within the Stichasteridae.
- The large family Asteriidae is separated into four well-supported clades. The largest of the four lineages supports diversification into the Arctic and sub-Arctic regions of the Northern Hemisphere. Two of those lineages show a sister-group relationship between pantropical and Southern Ocean/Antarctic asteriids. Finally, the globally distributed *Sclerasterias* (with probable synonyms

Rumbleaster and *Australiaster*) is also upheld as a discrete lineage.

- The Stichasteridae, as described by Perrier (1885), and further defined by Sladen (1889), is well supported by our results, contrary to Fisher's apparent synonymy of the family into the Asteriidae (Mortensen, 1927). Neomorphasteridae should be synonymized into the Stichasteridae. The Stichasteridae represents a major diversification of forcipulataceans, which occurs primarily in the Southern Hemisphere, although two genera are known from the Northern Hemisphere. The occurrence of a Cretaceous stichasterid implies that the historical range of the Stichasteridae may have once been more widespread.
- Shared characters such as the single marginal plate series shared between the Trichasteropsida and the Zoroasteridae, or the reticulated skeleton in Jurassic asteriids and some pedicellasterids, permit us to link Mesozoic and modern basal forcipulates. Our trees are consistent with prior phylogenetic hypotheses that have incorporated these fossils within the Forcipulatacea.
- Eocene fossil taxa, including *Sclerasterias* and *Zoroaster*, from Seymour Island, Antarctica, are unknown from the modern Southern Ocean fauna. This suggests the possibility of an extinction event of an older fauna, followed by the diversification of the Antarctic asteriid clade and other modern Antarctic forcipulataceans.

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