

Preliminary Phylogeny of the Forcipulatacean Asteroidea¹

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SYNOPSIS. The superorder Forcipulatacea (Asteroidea, Echinodermata) includes two orders, the Brisingida and the Forcipulatida. The Forcipulatida is diverse, including the Asteroiidae, Coscinasteriinae, Pedicellasteridae, Labidiasteridae, Neomorphasteridae, Pycnopodiinae (Asteroiidae), Heliasteridae, and the Zoroasteridae, whereas the Brisingida is limited to the Brisingasteridae, Brisingidae, Freyellidae, Hymenodiscidae, and Odinelidae. A phylogenetic analysis of forcipulataceans using morphological characters resulted in 12 most parsimonious trees at a tree length of 68 steps.

The Brisingida, recognized as basal in one early analysis and derived in another, is here considered to be derived. Two genera of pedicellasterids emerged as the sister group to the remaining Forcipulatida.

Bremer and bootstrap measures show strong support for the brisingidan and zoroasterid plus neomorphasterid clades. Certain other traditional taxonomic groupings, including the Pedicellasteridae, Labidiasteridae, Asteroiidae, and Pycnopodiinae, are not supported as monophyletic. Support for the pedicellasterids as a sister group to the remainder of the Forcipulatida is not robust.

Morphological data suggest widespread homoplasy and therefore comprehensive generic or even species-level analyses are required to further evaluate questions of derivation and relationships among these taxa.

INTRODUCTION

The Forcipulatacea comprises one of three superorders within the post-Paleozoic Asteroidea (*sensu* Blake, 1987). Forcipulataceans include approximately 90 genera, and they range from the Triassic Period (Blake, 1999) to the present. Forcipulataceans are important in many marine communities (*e.g.*, Paine *et al.*, 1985), from rocky intertidal zones [*e.g.*, *Pisaster ochraceus* (Asteroiidae)] abyssal plains [*e.g.*, *Freyella elegans* (Freyellidae)]. Forcipulataceans are morphologically diverse, ranging from very delicate to very robust in skeletal development, and possessing from five to 50 rays (Clark and Downey, 1992). Most forcipulataceans inhabit cold to temperate waters. They are a minor component of

tropical settings such as the Indo-West Pacific (Blake, 1990).

Blake (1987) recognized two orders, the Brisingida and the Forcipulatida, within the Forcipulatacea. Forcipulatidans (*sensu* Blake, 1987) included the Zoroasteridae, the Heliasteridae, and the Asteroiidae. The Brisingida includes five families and 17 genera with nearly 70 species. Mah (1997, 1998) and Downey (1986) provided recent re-evaluations of the order. The Zoroasteridae includes 7 genera and approximately 40 species. Downey (1970) proposed ordinal rank for the group. Phylogenetic analysis of the Zoroasteridae has never been undertaken. The Heliasteridae contains about 10 species, all assigned to *Heliaster* (H. L. Clark, 1907). It is known today exclusively from the tropical shallow-water shelf of Mexico and South America, although a Pliocene occurrence from Florida has been recorded (Jones and Portell, 1988).

A number of familial and subfamilial taxon concepts have been used for the Asteroiidae *sensu lato*, including the Asteroiinae, Labidiasterinae, Neomorphasterinae, Pedicellasterinae, and Pycnopodiinae. The most

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important taxonomic treatments of this group are those of Fisher (1923, 1928, 1930) and more recently Clark and Downey (1992), who elevated all but the Pycnoperidiinae (Asteriidae) from subfamilial to familial rank. Rankings of Clark and Downey (1992) are used here. The Coscinasteriinae, synonymized with the Asteriinae (Spencer and Wright, 1966), is separated here based on the data of Matsuoka *et al.* (1994).

MATERIALS AND METHODS

Twenty-five forcipulatacean taxa were selected to broadly sample the morphology of the group and to encompass all earlier taxon concepts at the subfamilial level and above (see Appendix 3). Twenty-five characters (summarized in Appendix 1) were included in the data matrix (Appendix 2). Exemplars are from all oceans and a broad range of depths. For each higher taxon, the name-bearing genus was utilized if possible. Wet and dry specimens were examined.

Where necessary, specimens were partially denuded using a 5% solution of sodium hypochlorite. Characters derived from endoskeletal morphology stress the ambulacral, adambulacral, abactinal, and actinal ossicular series. Soft-part characters are based on tube foot row number and papular and ampullar morphology. Aspects of overall body morphology, such as arm length and general disk morphology, were also used. Multiple rays (>5) have arisen many times (Hotchkiss, 2000) and therefore ray number was omitted, although more comprehensive research will certainly yield useful characters.

Henricia leviuscula (Echinasteridae, Spinulosida), a partial homeomorph of many asteriids, was chosen as the outgroup. Its usage does not imply direct sister group relationship.

RESULTS

Cladistic analysis

A branch and bound search using PAUP 4.0* was run using unpolarized and unweighted character options. Uninformative characters (*e.g.*, autapomorphies) were omitted from the matrix. The search yielded 12 most parsimonious trees each of 68 steps with a consistency index of 0.53 and a re-

scaled consistency index of 0.39. Figure 1 shows the 50% majority rule consensus tree.

Relaxation from strict consensus permits the recognition of support for some signal in branch arrangement. Node 9 shows relatively strong support (83%) between labidiasterids and brisingidans. Clades above node 12 show only modest support (50%).

Bremer-support values were calculated using methods outlined by Bremer (1988) and defined by Källersjö *et al.* (1992) using the branch and bound search algorithm. Support was also derived from 100 bootstrap replicates using the heuristic search option. Bremer and bootstrap support measures are shown in Fig. 2. Bremer support shows overall collapse above node 1 after one step (Fig. 2b). However, the brisingidan and zoroasterid clades show Bremer support values of at least 3 (Fig. 2b).

Bootstrap analysis (Fig. 2a) does not support the tree topology summarized by the 50% consensus tree in Fig. 1. Nodes 1 and 2 are relatively well supported by the bootstrap analysis. Four clades, the Brisingida (99%), the Coscinasteriinae (65%), the Zoroasteridae plus Neomorphasteridae (98%), and the Asteriidae (62%) are also relatively strong branches.

DISCUSSION

Previous phylogenetic hypotheses

Blake (1987) separated post-Paleozoic asteroids into two branches, the Forcipulatacea and the Spinulosacea plus Valvatatacea; this interpretation was consistent with that of Fisher (1923, 1928). Gale (1987) in contrast, recognized the Paxillosida as the sister group to the remaining living orders, the Forcipulatida, Valvatida and, Notomyotida, in his terminology. Gale's positioning of the Paxillosida is in keeping with views of Mortensen (1922). Both of these studies generalized approximately at the familial level.

Based on combined morphological and molecular data, the reconstruction of Lafay *et al.* (1995) is in general agreement with the tree topology of Gale (1987), whereas the molecular phylogeny by Wada *et al.*, (1996) places the forcipulataceans high in the asteroid tree as the sister group to the Asteriidae. Littlewood *et al.*, (1997) pre-

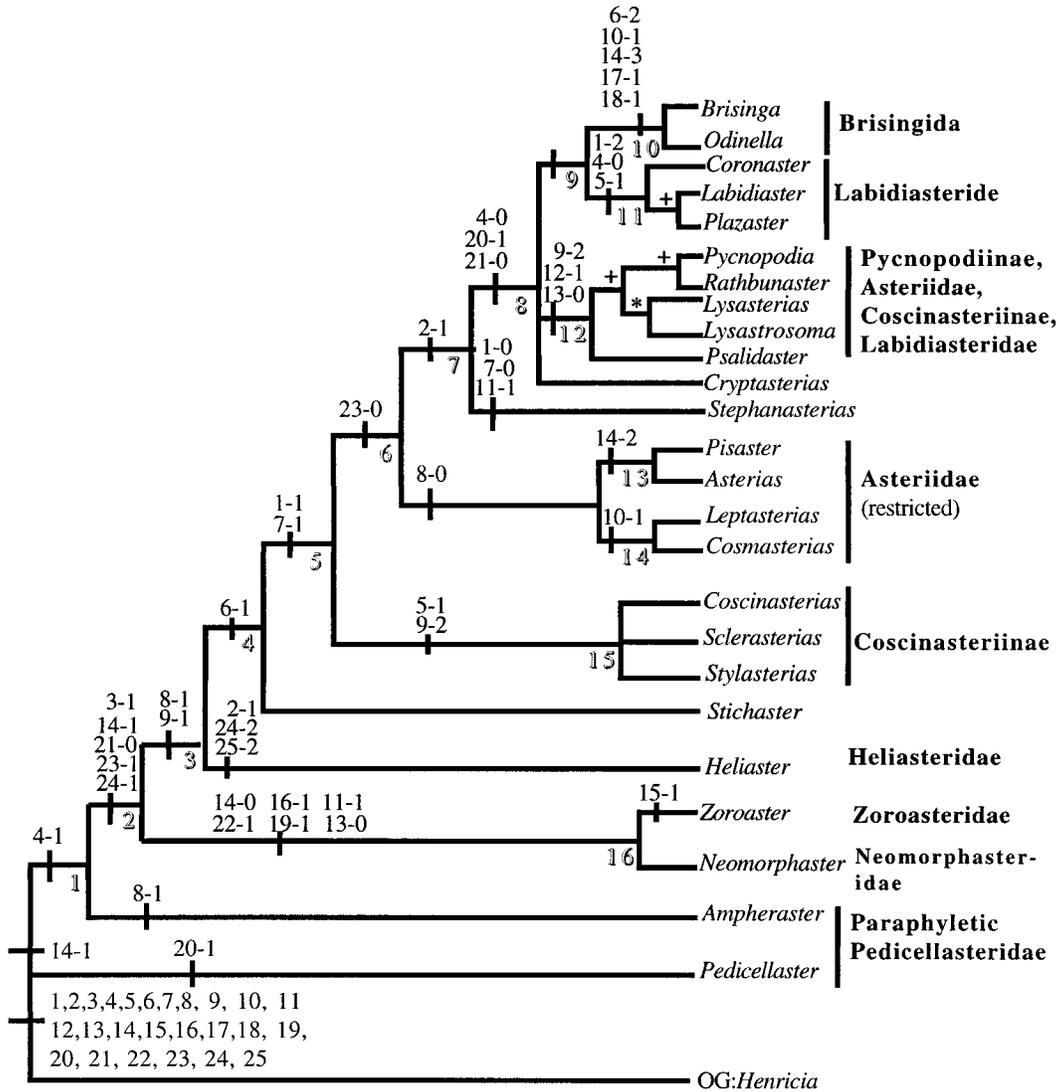


FIG. 1. 50% Majority rule consensus tree showing distribution of characters mapped onto branches. Numbers in shadow represent nodes. Plesiomorphic state (= 0) represented by plain numbers on branches. Apomorphies and reversals are followed by dash and character state, for example 6-2 represents character six, state two. Percentage values represent >50% support. Asterisk (*) represents 58% support. Plus (+) represents 50% support. Values represent support from consensus tree values.

sented two most parsimonious total-evidence trees. The first tree, including SSU rRNA data, showed a paxillosidan (*Astropecten*) as the sister to a branch containing a forcipulatacean (*Asterias*) and a valvatidan (*Porania*). The second tree included LSU rRNA data, and it showed a forcipulatacean (*Asterias*) as the sister taxon to a valvatidan

(*Asterina*) (*sensu* Blake, 1987) and a velatidan (*Crossaster*).

Matsuoka *et al.*, (1994) examined genetic distance among five species of Japanese forcipulataceans. They generated a distance tree showing *Asterias amurensis* (Asteriidae) and *Plazaster borealis* (Labidiasteridae) on one branch and *Aphelasterias japonica* (Cosci-

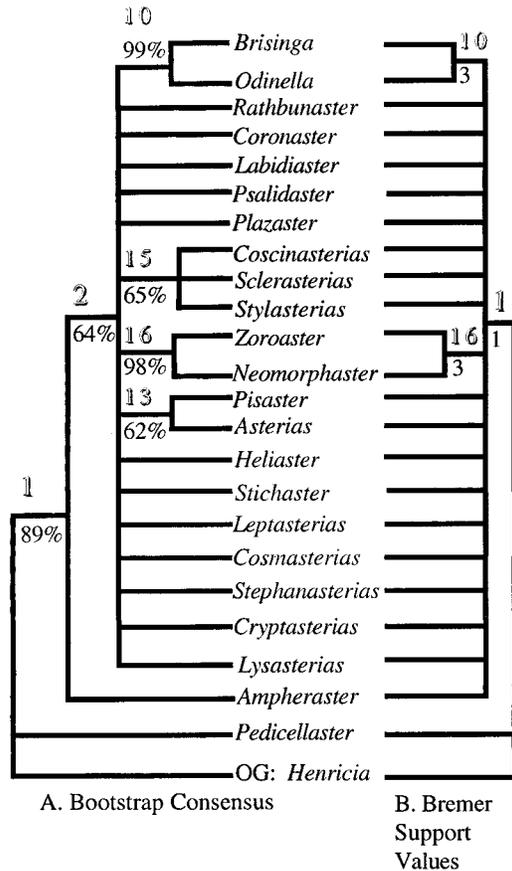


FIG. 2. Strict consensus trees expressing support values. In a, only bootstrap values >50% are shown. Numbers in shadow represent corresponding nodes from Figure 1.

nasteriinae) and *Distolasterias nipon* (Coscinasteriinae) on its sister branch. *Coscinasterias acutispina* (Coscinasteriinae) was most distant from all four species. Wada *et al.*, (1996) showed a coscinasterine (*Coscinasterias*) as the sister branch to a branch including an asteriid (*Asterias*) and a coscinasterine (*Distolasterias*).

The molecular phylogeny of Knott and Wray (2000) includes exemplars from the Asteriidae, Brisingida, Coscinasteriinae, Heliasteridae, Labidiasteridae, Pycnopodiinae, and Zoroasteridae. Their preliminary reconstruction supports the Forcipulatacea as monophyletic but suggests that many subfamilial and familial groupings are paraphyletic.

The inconsistencies probably reflect both incomplete taxon sampling and morpholog-

ical homoplasy derived from separate lineages adapting to broadly similar habitats over long periods of geologic time.

Higher versus intermediate level taxon sampling

Results obtained from generic level sampling differ in important ways from earlier morphological treatments of Blake (1987) and Gale (1987). Brisingidans, rooted at or near the base of the tree in both Blake (1987) and Gale (1987), are here nested high in the tree, above node 10, and they are therefore considered derived. For comparative purposes, the Brisingida were placed at the base of the tree using MacClade, which added 7 steps and changed the tree topology from 69 to 76 steps. Brisingidans resemble labidiasterids, and the two were placed together by Perrier (1885). Ten of 12 most parsimonious trees show the labidiasterid clade (Fig. 1: node 11) as sister group to the Brisingida (Fig. 1: node 10), but support for this arrangement from Bremer and bootstrap measures was absent.

Figure 1 shows the pedicellasterid genera *Ampheraster* and *Pedicellaster* as the sister branches to the other extant forcipulataceans. Figure 2 does not show much support from either Bremer or bootstrap measures for *Ampheraster* or *Pedicellaster* as the sister clade to the Forcipulatida. However, pedicellasterids were not included in earlier more broadly sampled studies (*e.g.*, Blake, 1987; Gale, 1987), and it is important to note their inclusion in a tree topology that significantly differs from those of Blake (1987) or Gale (1987).

Paraphyly within the forcipulatacea

The Forcipulatacea is monophyletic (Fig. 1), a conclusion consistent with perspectives extending back to Fisher (1923, 1928, 1930). Many of the historical subgroupings (*e.g.*, the Pedicellasteridae, the Asteriidae) within the Forcipulatacea show varying degrees of paraphyly. However, the present study, although more detailed in generic sampling than those of earlier cladistic morphological studies, only reaffirms rather than resolves the perplexing picture of relationships among the Forcipulatida.

For example, at node 11 (Fig. 1) *Coron-*

aster, *Labidiaster*, and *Plazaster* (Labidiasteridae) consistently group together whereas *Rathbunaster* (Labidiasteridae) emerges at node 12 on a branch with the Pycnopodiinae (*Pycnopodia*), Coscinasteriinae (*Psalidaster*), and Asteriidae (*Lysasterias*). The weakness of the groupings as tested using Bremer support and bootstrap analysis suggest widespread homoplasy, a hypothesis not contradicted by the relatively low CI.

CONCLUSION

The Brisingida is a monophyletic, derived forcipulatacean branch. Subfamilial and familial grouping within the Forcipulatida are paraphyletic. The apparent paraphyly of many groups within the Forcipulatacea suggests widespread homoplasy. Furthermore, our level of knowledge regarding basic homologies in forcipulates is relatively poor, ontogenetic information is not well known, and an extensive, generic-level revision of the group has not been attempted since Fisher (1923). Results of this study suggest that many historical forcipulatacean groupings are phylogenetically weak. Incomplete knowledge of the characters probably is significant.

The very differing tree topologies of this study compared to previous studies illustrates the need for greater sampling at lower taxonomic levels. Development of a phylogeny calls for enlarged taxon samples in both morphological and molecular work and further research on a poorly understood but significant fossil record.

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APPENDIX 3

EXEMPLARS USED FOR ANALYSIS

(Taxonomy follows Clark and Downey, 1992)

BRISINGIDA:

Brisinga synaptoma NMNHIZ E09296;
Novodinia antillensis NMNHIZ E12913;
Astrolirus panamensis CASIZ 108121;
Odinella nutrix CASIZ 103266.

FORCIPULATIDA: ASTERIIDAE:

Asterias forbesi CASIZ 108851; *Cosmas-
terias lurida* CASIZ 102715; *Cryptasterias*
sp. UCB no number; *Leptasterias hexactis*
CASIZ 8612; *Lysasterias* sp. UCB RCI.3;
Pisaster brevispinus CASIZ no number; *Pi-
saster ochraceus* CASIZ 112049; *Stephan-
asterias albula* CASIZ 34622, 112417; *Sti-
chaster striatus* CASIZ 111937.

ASTERIIDAE: COSCINASTERIINAE:

Coscinasterias acutispina CASIZ 108865;
Psalidaster mordax, holotype BMNH,
Sclerasterias heteropaes, CASIZ 111722;
Stylasterias forreri CASIZ 111935.

HELIASTERIDAE: *Heliaster kubiniji*
CASIZ 75598.

LABIDIASTERIDAE: *Coronaster halice-
pus* CASIZ 108860; *Labidiaster annulatus*
CASIZ 113228; *Plazaster borealis* CASIZ
113229; *Rathbunaster californicus* CASIZ
103200, 106655.

NEOMORPHASTERIDAE: *Neomorphas-
ter margaritaceus* CASIZ 116534.

PEDICELLASTERIDAE: *Ampheraster*
marianus CASIZ 112096; *Pedicellaster*
magister CASIZ 111713.

PYCNOPODIINAE: *Lysastroma* sp. CAS-
IZ no number; *Pycnopodia helianthoides*
CASIZ 102818.

ZOROASTERIDAE: *Zoroaster fulgens*
CASIZ 113326; *Zoroaster evermanni* CAS-
IZ 769.

Bold represents specific taxon represented
in phylogenetic analysis. Groupings shown
are in alphabetical order. Abbreviations are
as follow: CASIZ = California Academy of
Sciences, NMNHIZ = Natural History Mu-
seum, Smithsonian Institution, UCB = Uni-
versity of California, Berkeley, and BMNH
= British Museum of Natural History.