

Xyloplax is an asteroid

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ABSTRACT: Concentricycloids are small disk-shaped echinoderms recently discovered on sunken wood from the abyssal seas off New Zealand and the Bahamas. Their water-vascular system is circular rather than pentaradial as is characteristic of echinoderms. As a result of this remarkable body plan, a new class (the sixth extant) of the Phylum Echinodermata, Concentricycloidea, was erected to accommodate two species of genus *Xyloplax*. This classification remains controversial because it implies that *Xyloplax* is an ancient group that is a sister taxon to all asteroids and ophiuroids. We tested the validity of the 'class Concentricycloidea' with cladistic analyses of nucleotide sequences and morphology from exemplars of most echinoderm orders. *Xyloplax* is nested within a monophyletic Asterozoa in the most congruent total evidence tree. Thus the rank of class is an inappropriate representation of the evolutionary history of the concentricycloids and should be suppressed. Moreover, these results suggest that fundamental features of body organization were labile late in the diversification of the asteroids.

1 INTRODUCTION

In 1986, Baker et al. reported the discovery of an unusual echinoderm on sunken wood from the South Pacific Ocean and Tasman Sea (1057-1208 m) off the North and South Islands of New Zealand. This animal, *Xyloplax medusiformis*, was classified in the subphylum Asterozoa [*sensu* Ubaghs (1966) = class

Asterozoa, Ophiurozoa, and the extinct class Somasteroidea] but was considered sufficiently distinct to warrant exclusion from these classes. A second species, *Xyloplax turnerae*, was later recognized from collections of fauna associated with sunken wood from the Tongue of the Ocean (2066 m) off Andros Island, Bahamas (Rowe et al. 1988).

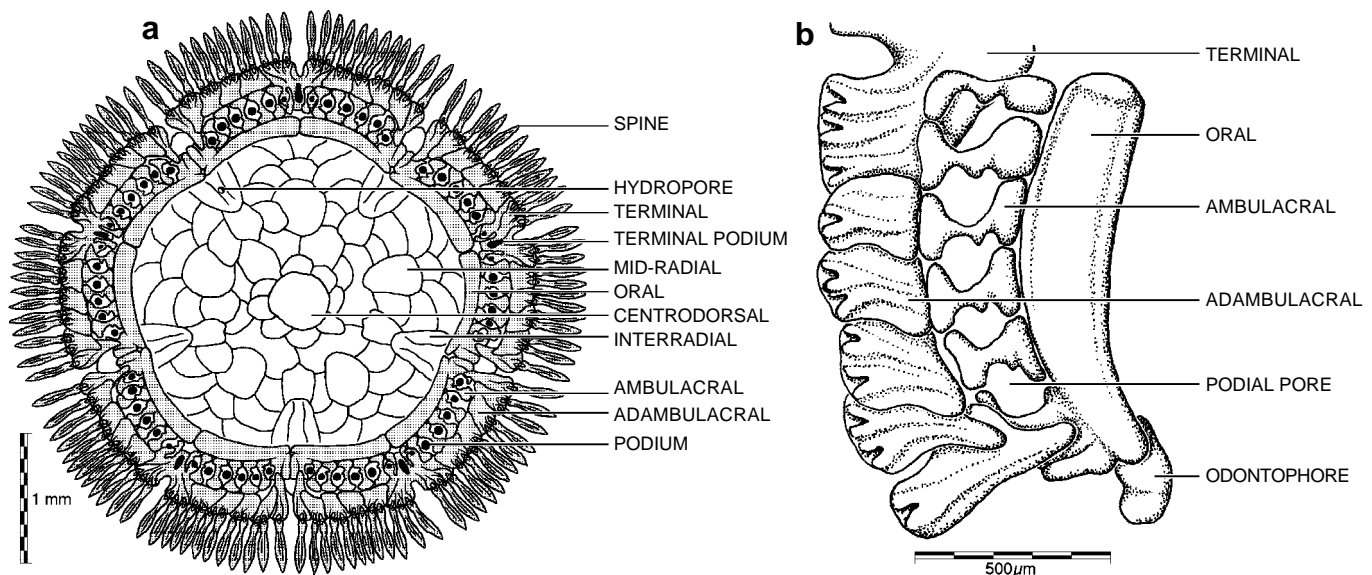


Figure 1. Morphology of adult *Xyloplax turnerae*. a: Oral surface, axial elements shaded. b: Oral view of skeletal elements from a single half-ambulacrum of a specimen in MCZ 12013, spines omitted.

Both species of *Xyloplax* are small (2-13 mm diameter) for sexually mature echinoderms (Fig. 1). Growth of the axial portions of the water-vascular system and associated skeleton from the tips of the ambulacra and the emergence of podia between plates clearly places *Xyloplax* within the subphylum Asterozoa (Baker et al. 1986; Rowe et al. 1988; Mooi et al. 1998). However, *Xyloplax* lacks radiating arms and water-vascular canals typical of adult asteroids and ophiuroids (Fig. 2a). Diagnostic features of the 'class Concentricycloidea' included the arrangement of the skeletal plates and the water-vascular system. As originally described, the water-vascular system of *Xyloplax* consists of *two* circumoral ring canals supposedly joined by five short inter-ring canals. The podia of adult *Xyloplax* branch from the outer circumoral ring canal in a single series that circumscribes the periphery of the oral surface. In *Xyloplax* a simple hydropore (a structure typical of larvae) connects the inner circumoral ring canal to external sea water (Fig. 2a).

The water-vascular system of asterozoans consists of a *single* circumoral ring canal with an axial complex including an axocoel (an adult derivative of the larval hydropore) that connects the water-vascular system to external sea water. In asterozoans the water-vascular system consists of five (or more in species with supernumerary arms) radial canals that extend from the circumoral canal into the arms. In each arm, lateral canals connect a biserial row of podia to the radial canals (Fig. 2b).

X. medusififormis lacks a stomach, intestine, and anus. As described, there is a thin layer of coelomic tissue attached to the ossicles of the mouth frame. This tissue is termed a velum, yet its role in feeding and/or locomotion is unknown. *X. turnerae* lacks an intestine and anus yet has a stomach that appears to be capable of eversible feeding (Baker et al. 1986; Rowe et al. 1988). Eversible feeding is common among asteroids and lack of an anus occurs in the order Paxillosida. The taxonomic position of *Xyloplax* has been extremely controversial in the few years since

discovery. Various hypotheses are summarized below:

1) A new class: The discoverers of *Xyloplax* argued that features such as: two circumoral canals, inter-ring canals, uniserial peripheral ring of podia, modified mouth-frame skeleton, and modified digestive and feeding structures warrant taxonomic distinction between *Xyloplax* and asterozoans. Thus *Xyloplax* should be set apart as a new (the sixth extant) echinoderm class - the Concentricycloidea (Baker et al. 1986; Rowe et al. 1988; Rowe 1989; Pearse & Pearse 1994). This view has pervaded textbooks (e.g. Brusca & Brusca 1990; Harrison & Chia 1994).

2) Aberrant asteroids: A morphological cladistic analysis of limited context (only the asteroid order Velatida) placed *Xyloplax* as sister group to the Caymanostellidae (Smith 1988). The unique body plan of *Xyloplax* is likely the result of paedomorphosis (Smith 1988) in velatids which exhibit extreme direct development (Janies & McEdward 1994).

3) A new asteroid order: Belyaev (1990) suggested that wood-dwelling, deep-sea asteroid families, Xyloplacidae and Caymanostellidae, should be separated into a new order, Peripoidoidea, within the class Asteroidea.

The identification of morphological characters that may be informative of the history of *Xyloplax* is difficult because its morphology is enigmatic.

The original descriptions of the internal structure of *Xyloplax* have not been confirmed by our own recent observations. The outer circumoral ring is clearly a water-vascular ring that produces lateral canals, ampullae, and podia. However, the inner ring is not unequivocally hydrocoel. Further work is warranted to explore the possibility that the inner ring is part of a haemal system, which has yet to be found in *Xyloplax*. The need for this work is underscored by our inability to positively identify the inter-ring canals. Studies are under way (Mooi, David, and Rowe in prep.) that will expand upon the earlier

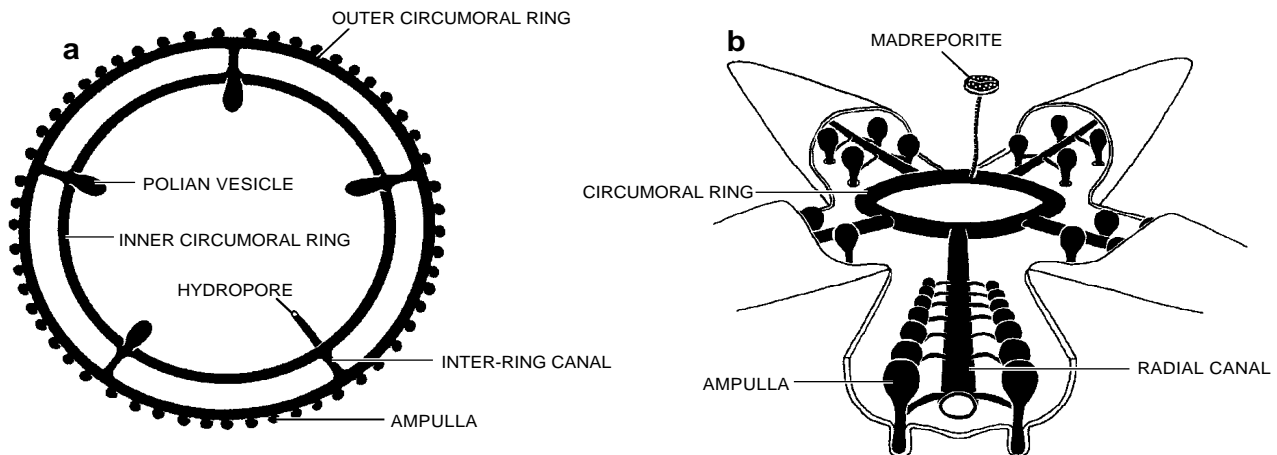


Figure 2. Comparison of adult water-vascular morphology. a: Concentricycloids (based on original descriptions of *Xyloplax turnerae* (Rowe et al. 1988). b: Other asterozoans (based on asteroids).

descriptions of Baker et al. (1986); Rowe et al. (1988); and Mooi et al. (1988).

The class level cladistic analysis of Pearse & Pearse (1994) placed *Xyloplax* in a trichotomy with asteroids and ophiuroids due to lack of resolution in the consensus of their equally parsimonious trees rather than unambiguous character support.

The adult skeletal morphology of *Xyloplax turnerae* has been recently redescribed (Mooi et al. 1998). Important changes in the description of the axial skeleton include: 1) plates that bear the podia are ambulacrals, 2) the outermost ring of plates are adambulacrals, 3) the innermost, large ossicles are oral plates and are derived from the adambulacral series. The first two characters add to the list of asterozoan features for *Xyloplax* but do not place it within either the class Asterozoa or Ophiurozoa. Although Mooi et al. (1998) make no argument for the taxonomic revision of *Xyloplax*, the third suggestion that the large plates they term 'oral plates' of *Xyloplax* are modified adambulacral plates has important ramifications for the inclusion of *Xyloplax* within Asterozoa. Several authors contend that the oral plates of asteroids are derived from the adambulacral series whereas the oral plates of ophiuroids are derived from the ambulacral series (Spencer & Wright 1966; Blake 1998). However, the mouth frame of Asterozoa is poorly understood as a character system and merits complete revision.

2 METHODS

2.1 DNA Sequencing

DNA was extracted from aldehyde/ethanol preserved fragments of the ambulacra of the concentricycloid,

Xyloplax turnerae (MCZ lot 12007). Partial gene regions corresponding to positions 140-250 and 1139-1394 of the 18S rDNA sequence of *Amphipholis squamata* (Genbank accession X97156) and positions 807 and 1125 of the 28S rDNA sequence of *Encope aberrans* (Genbank accession Z37117) were amplified with PCR and sequenced on an ABI 373 automated DNA sequencer using the methods described in manufacturer's protocols (Perkin-Elmer/Applied Biosystems Prism kit). After sequences were obtained from *Xyloplax turnerae*, DNA was extracted with the same protocol and 18S and or 28S rDNA was sequenced for the following species: *Amphipholis squamata*, *Gorgonocephalus eucnemis*, *Cucumaria pseudocurata*, *Brisingaster robillardii*, *Asterias forbesi*, *Pteraster obscurus*, *Pseudarchaster parelli*, *Rathbunaster californicus*, *Dermasterias imbricata*, *Echinaster sepositus*, *Solaster dawsonii*, *Astropecten articulatus*, *Asterina gibbosa*, *Luidia foliolata*, *Heliaster helianthoides*, *Dorometra aegyptica*, *Capillaster multiradiatus*, and *Antedon mediterranea*. Unpublished 18S rDNA *Glossobalanus minutus* sequence was provided by Gonzalo Giribet (AMNH).

2.2 Morphology and non-sequence character data

A total of 62 non-sequence characters (hereafter referred to as 'characters') for echinoderms were drawn largely from literature sources but several (especially larval characters) are original. Eight characters are unordered multistate and 54 are binary. Morphological characters were coded or recoded for each terminal taxon represented by DNA sequences. Mitochondrial gene order characters are provided only in those taxa in which the observation was made (except for crinoids).

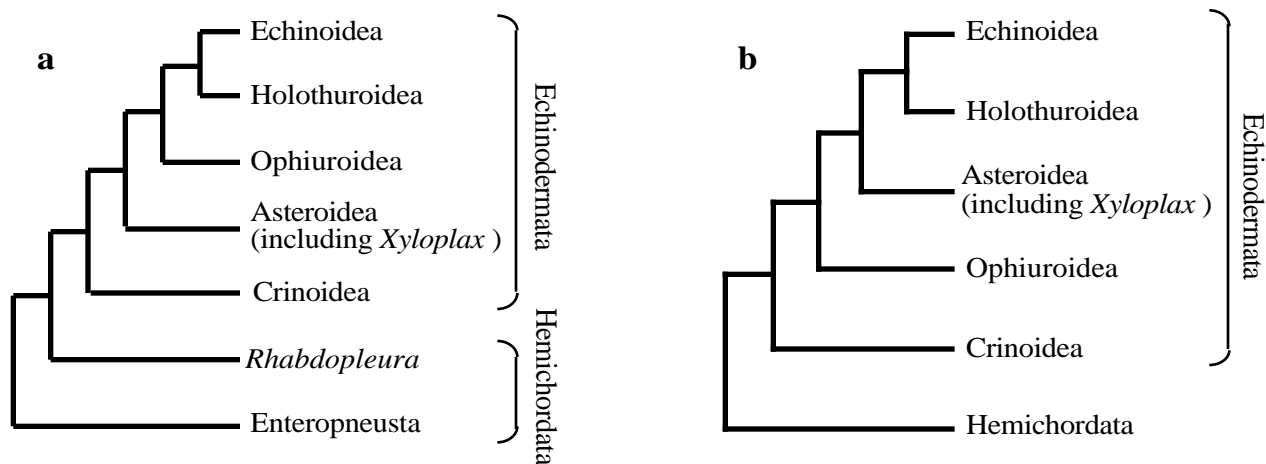


Figure 3. Results of analyses of various data types. a. Summary of most parsimonious topology supported by nonsequence character data (92 steps). b. Summary of most congruent topology supported by 18S and 28S rDNA data (MFES = 0.0174). In both analyses *Xyloplax* is nested within the class Asterozoa.

2.3 Taxonomic sampling

A thorough investigation of the evolutionary history of *Xyloplax* among Echinodermata required sampling many lineages. 44 partial and complete 18S rDNA sequences and 30 partial 28S rDNA sequences were analyzed. These sequences exemplify: 10 of 12 orders of the class Echinoidea, 7 of 17 families of the class Ophiuroidea, 6 of 7 orders of the class Asteroidea, 3 of 6 orders of Holothuroidea, and 2 of 4 orders of the class Crinoidea. Hemichordates are represented by three full 18S rDNA sequences from the class Enteropneusta and one partial sequence of 18S rDNA for the class Pterobranchia, *Rhabdopleura normani*. Hemichordates were chosen as the outgroup to echinoderms because this relationship occurs in recent molecular phylogeny (Giribet & Ribera, 1998) and in molecular and morphological studies (Zrzavy et al. 1998) with well sampled metazoan exemplars.

2.4 Analyses

Analysis of the character data in NONA (Goloboff 1993) yielded 5041 equally parsimonious topologies at 92 steps. A strict consensus of these topologies is summarized in Figure 3a. These topologies lack resolution within classes. The presence of the odontophore, an interradial mouth frame ossicle, supports the monophyly of the Asteroidea. This clade includes *Xyloplax*, as it has a prominent odontophore in the interradial position, precisely as in asteroids (Fig. 1a). One synapomorphy, the absence of an anus in adults, supports the clade (*Xyloplax* (*Astropecten Luidia*)). Genbank/Embl/DDJB accession numbers for each region sequenced and analyzed are provided in a table of supplementary information available from the authors. Unaligned sequence data were subjected to direct optimization analysis in POY on a cluster of 23 UNIX-based workstations of heterogeneous architectures integrated into a parallel virtual machine (Geist et al. 1993). A total of 20 parameter sets were explored. The ratio of weights among indels and the greater of transversion or transition weights ranged from 1 to 8. The transversion: transition ratios ranged between 0.5 and 4. Some parameter sets were set to examine transversion parsimony (i.e. transitions were set at 0 cost yielding a transversion: transition ratio of 0.5). Character data weights ranged from 1 to a variable cost pegged to the cost of indels. Sequence data were also analyzed without character data as the following data partitions 18S + 28S, 18S only, and 28S only. Character data were analyzed as a single partition. The addition of taxa (including putative outgroups) was randomized during the build and swapping

processes for molecular data and during swapping for molecular and morphological data. Tree searches included TBR and SPR swapping.

Character congruence, an extension of parsimony, was used as the optimality criterion for choosing among various topologies that are produced. The Mickevitch - Farris extra steps index (MFES) measures the number of extra steps that occur in an analysis of combined data versus separate analysis of individual partitions (Mickevitch & Farris 1981). As character incongruence among data partitions increases, MFES increases. The number of extra steps is normalized by the length of the combined analysis. Therefore when parameter sensitivity analyses are conducted on the same data partitions, MFES scores are comparable despite different weighting schemes. In this study the test was conducted for morphological and sequence data as follows (Equation 1):

3 Results

Combined analyses of the 18S and 28S rDNA sequences across 20 parameter sets (graded variations of cost ratios i.e. indels: transversion: transition) in POY (Gladstein & Wheeler 1996) yielded a single most congruent topology (MFES = 0.0174) when indels, transversions, and transitions were weighted at 1. This topology is summarized in Figure 3b. Combined analyses of the 18S and 28S rDNA sequences character data weighted at 1 across 20 parameter sets in POY yielded 6 most congruent topologies (MFES = 1.86) when insertion-deletion events and transversions were weighted at 2 and transitions were weighted at 1. A strict consensus of these topologies with branch decay values (Bremer 1988) at nodes is presented in Figure 4.

Heuristic branch decay values were calculated for the most congruent trees based on a TBR search in POY rather than via collapsing equivocal nodes from evermore inclusive branch and bound searches. As a result these values may overestimate group support.

4 Conclusions

Xyloplax is an asteroid in the shortest tree and the result is not the consequence of an arbitrary choice of evolutionary model (in this case the parameter sets included weights of insertion-deletion events, nucleotide transformations, and changes in morphological and other character data). In the most congruent total evidence tree *Xyloplax* is sister taxon to *Rathbunaster*, an exemplar of the order Forcipulatida (Fig. 4). The clade, Asteroidea including *Xyloplax*, is recovered under almost all analysis parameters that recover asteroid monophyly (fig. 5).

$$\text{MFES} = \frac{(\text{treelength combined data}) - (\text{treelength 18S}) - (\text{treelength 28S}) - (\text{treelength nonsequence characters})}{(\text{treelength combined data})} \quad (1)$$

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Appendix 1

Genbank accession numbers

AF088801
AF088802
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AF088807
AF088808
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Appendix 2

Nonsequence character matrix; electronic versions in HENNIG86 and NEXUS formats available on request.

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