

A new species of *Xyloplax* (Echinodermata: Asteroidea: Concentricycloidea) from the northeast Pacific: comparative morphology and a reassessment of phylogeny

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Abstract. *Xyloplax janetae* n. sp. is described from the northeast Pacific Ocean. This is the third species recognized for the monogeneric Concentricycloidea. Skeletal structures are elaborated by scanning electron microscopy and compared with those of *Xyloplax medusiformis* from New Zealand and *Xyloplax turnerae* from the Bahamas. Critical-point-dried specimens show fibrous connective tissue emerging from openings on the abactinal surface, on the abactinal spine bases, and at broken cross sections of the adambulacral spines. Knob-like structures emerging through the stereom openings of the abactinal spine base are also observed. Tube feet have round, swollen knobs and show few striations relative to other asteroidea. Cosmopolitan bathyal–abyssal echinoderm species tend to exhibit few morphological differences over broad geographic ranges; this generalization is true of *Xyloplax*. The Concentricycloidea is proposed as an infraclass within the Asteroidea, as the sister branch to the Neoasteroidea (the crown-group asteroidea) within the subclass Ambuloasteroidea. The hypothesis presented is compatible with recent phylogenetic data supporting affinities between *Xyloplax* and the Asteroidea. Characters plesiomorphic in basal neoasteroidea are consistent with a sister-group relationship to concentricycloids. Actinal plate presence, an important synapomorphy for the Neoasteroidea, is absent from concentricycloids. The substantial morphological departure of *Xyloplax* is considered to be associated with the post-Paleozoic diversification of crown-group asteroidea rather than from modification of an established and conservative morphology.

Additional key words: neoasteroidea, evolution, extraxial–axial theory

The study of environments in the bathyal and abyssal zones has presented unique opportunities to document morphological novelty in the evolution of marine biodiversity (Gage & Tyler 1991; Mooi & David 1996). Significant new perspectives on existing paradigms in invertebrate evolution and systematics have resulted from observations of novel morphologies and body plans in select deep-sea taxa. One such taxon is the genus *Xyloplax*, a tiny (~1–8 mm diameter) discoidal echinoderm living at abyssal depths on sunken wood. When originally described, *Xyloplax* displayed sufficient morphological disparity relative to other echinoderms that it was considered a sixth extant class of Echinodermata, the Concentricycloidea (Baker et al. 1986). *Xyloplax* has inspired discussions and alternative phylogenetic hy-

potheses (summarized below), including discussions of homology and the definition of class-level relationships within the Echinodermata.

Xyloplax janetae n. sp. MAH 2006 is described from specimens collected in the north Pacific at 2675 m (Voight 2005). This is the third described species of *Xyloplax* and the second from the Pacific Ocean. *Xyloplax medusiformis* BAKER et al. 1986, the type species, was collected 1057–1208 m off the New Zealand coast. This was followed by the description of *Xyloplax turnerae* ROWE et al. 1988 collected at 2066 m from the Tongue of the Ocean, Bahamas.

Baker et al. (1986) and Rowe et al. (1988) referred *Xyloplax* to a new class, the Concentricycloidea, parallel to the Asteroidea and the Ophiuroidea, based on unique characters such as the development of the tube feet and mouth frame into a uniserial ring. Smith (1988) and Belyaev (1990) argued placement of *Xyloplax* within the Caymanostellidae (Velatida, Asteroidea; see Table 1 for asteroid classification),

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Table 1. Classification of the Asterozoa *sensu* Blake (1987) and Blake & Hagdorn (2003) featuring taxa mentioned in the text.

Class Asterozoa	
Subclass Ambuloasteroidea	
<i>Incertae sedis</i>	
Family Calliasterellidae: genus <i>Calliasterella</i>	
Family Compsasteridae: genus <i>Compsaster</i>	
Infraclass Neoasteroidea	Infraclass Concentricycloidea
Superorder Forcipulatacea	Superorder Peripodacea
Order Trichasteropsida	Order Peripodida
Family Trichasteropsidae	Family Xyloplacidae
Genus <i>Trichasteropsis</i>	Genus <i>Xyloplax</i>
Genus <i>Berkhemeraster</i>	<i>X. janetae</i> n. sp.
Order Brisingida	<i>X. medusiformis</i>
Family Brisingasteridae	<i>X. turnerae</i>
Genus <i>Brisingaster</i>	
Order Forcipulatida	
Family Zoroasteridae	
Family Asteroidea	
Genus <i>Asterias</i>	
Genus <i>Rathbunaster</i>	
Superorder Spinulosacea	
Order Velatida	
Family Caymanostellidae	
Family Pterasteridae	
Order Spinulosida	
Superorder Valvatacea	
Order Notomyotida	
Order Paxillosida	
Family Porcellanasteridae	
Other pertinent echinoderm classes	
Class Ophiuroidea	
The brittle stars—sister group to the asteroids	
Class Somasteroidea	
Paleozoic-only grouping of taxa considered ancestral to asteroids and ophiuroids.	

challenging the distinctiveness of the Concentricycloidea as a separate class. Janies & McEdward (1994a,b) derived *Xyloplax* from the velatid asteroid body plan and argued that concentricycloids were progenetic velatidan asteroids.

Pearse & Pearse (1994) presented a cladistic analysis of morphological characters comparing *Xyloplax* with other echinoderm taxa, including ophiuroids and all orders of crown-group asteroids. They argued that phylogenetic affinity with caymanostellids or ophiuroids of similar appearance (e.g., *Astrophiura*) could alternatively be explained through convergence. They emphasized that available evidence was insufficient to clearly identify affinities and retained *Xyloplax* as a separate class. Mooi et al. (1998) applied their extraxial-axial theory (EAT) to inferred homologies in *Xyloplax*, questioning proposed affinities with the caymanostellids, and pointed out that unequivocal synapomorphies be-

tween concentricycloids and the Asterozoa had not yet been found. However, Janies & Mooi (1999) presented a tree that combined morphological and molecular data (rDNA) that placed *Xyloplax* on distal branches within the Asterozoa. Further elaboration of these data was presented by Janies (2001).

Structural and population studies of *Xyloplax* include those of Rowe (1988), who presented additional morphological data on *X. turnerae* and reinterpreted the Paleozoic cyclocystoids (class Cyclocystoidea) based on observed features in *Xyloplax*. Healy et al. (1988) and Rowe et al. (1994) reported on spermiogenesis, and spermatozoon and body microstructure, respectively.

A new collection of 103 specimens initially reported by Voight (2005) is described herein. These specimens represent the first concentricycloids collected since those included in Rowe et al. (1988). The previous absence of fresh material limited opportunities

for DNA extraction and sequence analysis, and precluded additional morphological studies involving destructive or otherwise restrictive methods, such as sputter coating for scanning electron microscopy (SEM). Morphological variation within *X. janetae* n. sp. is examined with SEM, allowing visualization of structures previously only documented with diagrams and histological cross sections, and compared with that of currently known species. *Xyloplax* is also considered within relatively recent phylogenetic contexts and homologies established by the EAT established by Mooi & David (2000).

Methods

Specimens (n = 103) were recovered from wood experimentally deployed by the Monterey Bay Aquarium Research Institute's remotely operated vehicle *Tiburon* on July 28, 2002 and recovered by the deep submergence vehicle *Alvin* on August 31, 2004. Additional collection details, including growth patterns, gender, and other aspects of population structure, were summarized by Voight (2005). Material was collected via a submersible, and specimens were in excellent condition, retaining delicate morphological structures, such as spinelets on parent plates. Approximately 60 of the collected specimens were made available for this study, but all were examined. All specimens were fixed and preserved in 95% ethanol and were deposited at the Field Museum of Natural History (FMNH), Chicago, USA. Determination of males and females for this study was based on the kidney-shaped gonads as outlined by Voight (2005:78). Measurements for disk diameter in *Xyloplax janetae* n. sp. and *Xyloplax turnerae* were taken from the disk itself and did not include the length of the adambulacral spines.

The holotype of *Xyloplax medusiformis* is missing and assumed to either have disintegrated or be lost (R. Webber, TePapa Museum [=the NMNZ, National Museum of New Zealand in Baker et al. 1986], unpubl. data). However, the paratypes remain available from the TePapa Museum and high-resolution images of three paratype specimens (NMNHZ EC 4239, 4241, 4242) were provided by Rick Webber, TePapa Museum. Additional morphological data for *X. medusiformis* and *X. turnerae* were obtained from Baker et al. (1986), Rowe (1988), and Rowe et al. (1988).

The large number of specimens available here permitted detailed imaging of morphological features using SEM with an environmental scanning electron microscope (ESEM). Six specimens from FMNH lot 12458 were sputter coated with gold/palladium and

studied using a Philips XL30 SEM (FEI Company, Hillsboro, OR). Two were dried using a critical-point dryer (CPD). The remaining four specimens were air dried before sputter coating. Two specimens, including a female with embryos, were studied using the ESEM, which does not require sputter coating of the subject (Valdecasas & Camacho 2005). The remaining images were obtained using a Nikon 990 (Chiyoda-ku, Tokyo, Japan) with dissection microscope attachments.

Terminology

Morphological terminology for *Xyloplax* follows Mooi et al. (1998), inferring homologies between *Xyloplax* and other echinoderms based on the EAT (David & Mooi 1996). The terms adambulacral, ambulacral, inferomarginal, and oral plates as used by Baker et al. (1986) and Rowe et al. (1988) were reinterpreted by Mooi et al. (1998) as ambulacrals, oral plates, adambulacrals, and oldest ambulacral plates, respectively. The "marginal spine" of Baker et al. (1986), Rowe et al. (1988), and Voight (2005) is now termed "adambulacral spine" as interpretation of the basal plate for these spines has changed from inferomarginal to adambulacral. The term "segment" refers to each subdivided region flanked on either side by a terminal plate and the oldest ambulacral.

Other descriptive terms follow Rowe et al. (1988). Abactinal and actinal are applied to the aboral and oral surfaces. Radii and radial refer to axes from the center of the body extending to the terminal plates whereas interradii and interradiial are midway between the radii. These terms refer to geographic locations and not to regions with implied homology (i.e., actinal interradius). The terminology applied to tube feet follows that of Flammang et al. (1994) and Santos et al. (2005), who have presented a recent comprehensive account of tube foot morphologies.

Results

Taxonomic account

Class Asterozoa DE BLAINVILLE 1830
 Subclass Ambuloasteroidea BLAKE & HAGDORN 2003
 Infraclass Concentricycloidea BAKER et al. 1986
 Order Peripodida BAKER et al. 1986
 Family Xyloplacidae BAKER et al. 1986
 Genus *Xyloplax* BAKER et al. 1986
Xyloplax janetae nov. sp. (Figs. 1–8).

Synonymy. Voight (2005:77).

Material. Full collection and locality information was provided in Voight (2005).

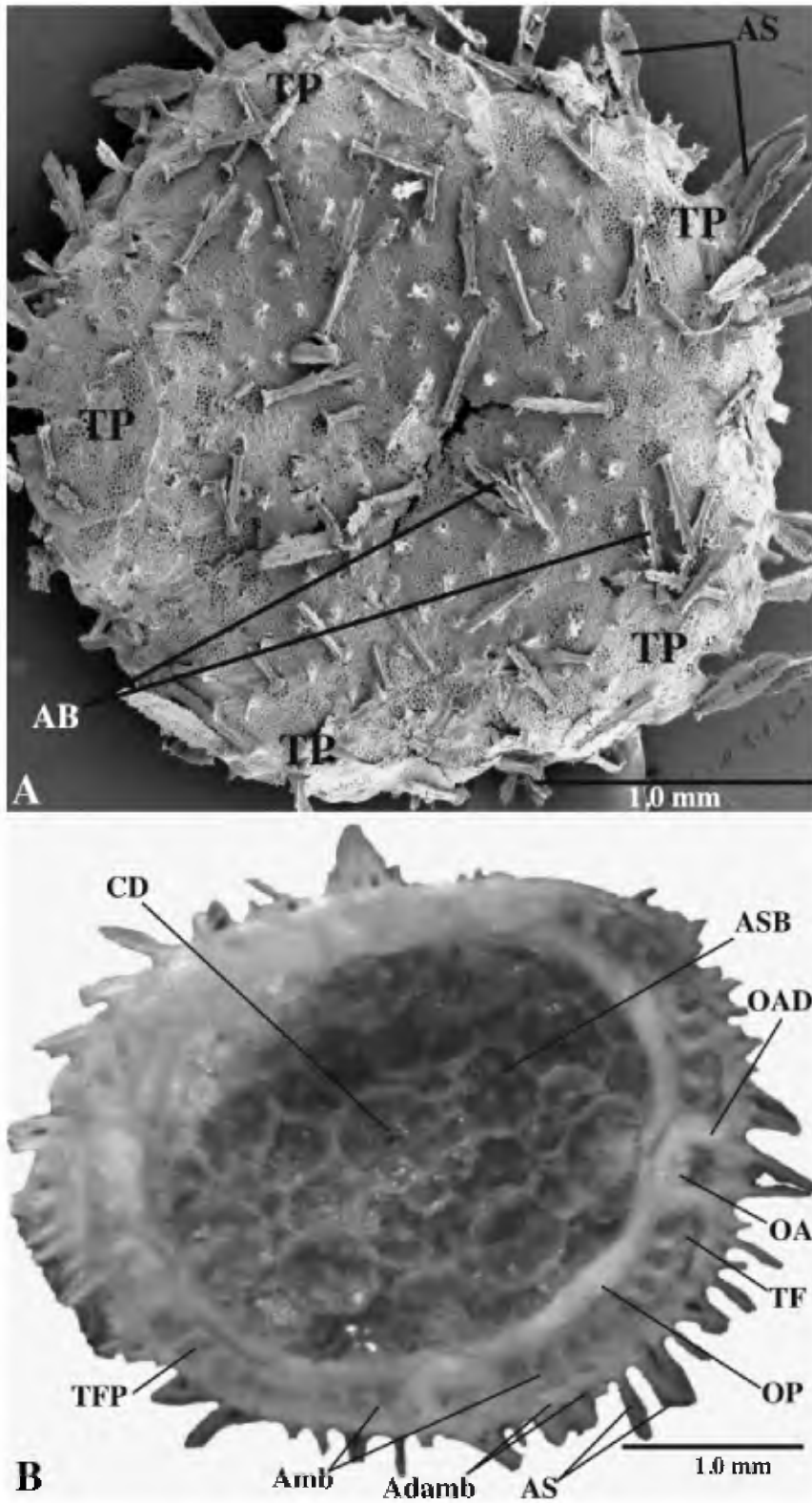


Fig. 1. *Xyloplax janetae* n. sp. Male (air-dried specimens). **A.** SEM of abactinal surface. **B.** Actinal surface. AB, abactinal spines; Adamb, adambulacral plate; Amb, ambulacral plates; AS, adambulacral spine; ASB, abactinal spine base; CD, centrodorsal plate; OA, oldest ambulacral; OAd, oldest adambulacral plate; OP, oral plate; TF, tube foot; TFP, tube foot pore; TP, terminal plate.

Holotype. FMNH 12541. Gorda Ridge, GR-14 on margin of hydrothermal vent field in basalt talus with sediment, sieved from water in recovery box of oak

and fir wood blocks that were deployed July 28, 2002. 42°45.258'N, 126°42.572'W, 2701 m. Coll. M. Daly, ALVIN et al., August 31, 2004.

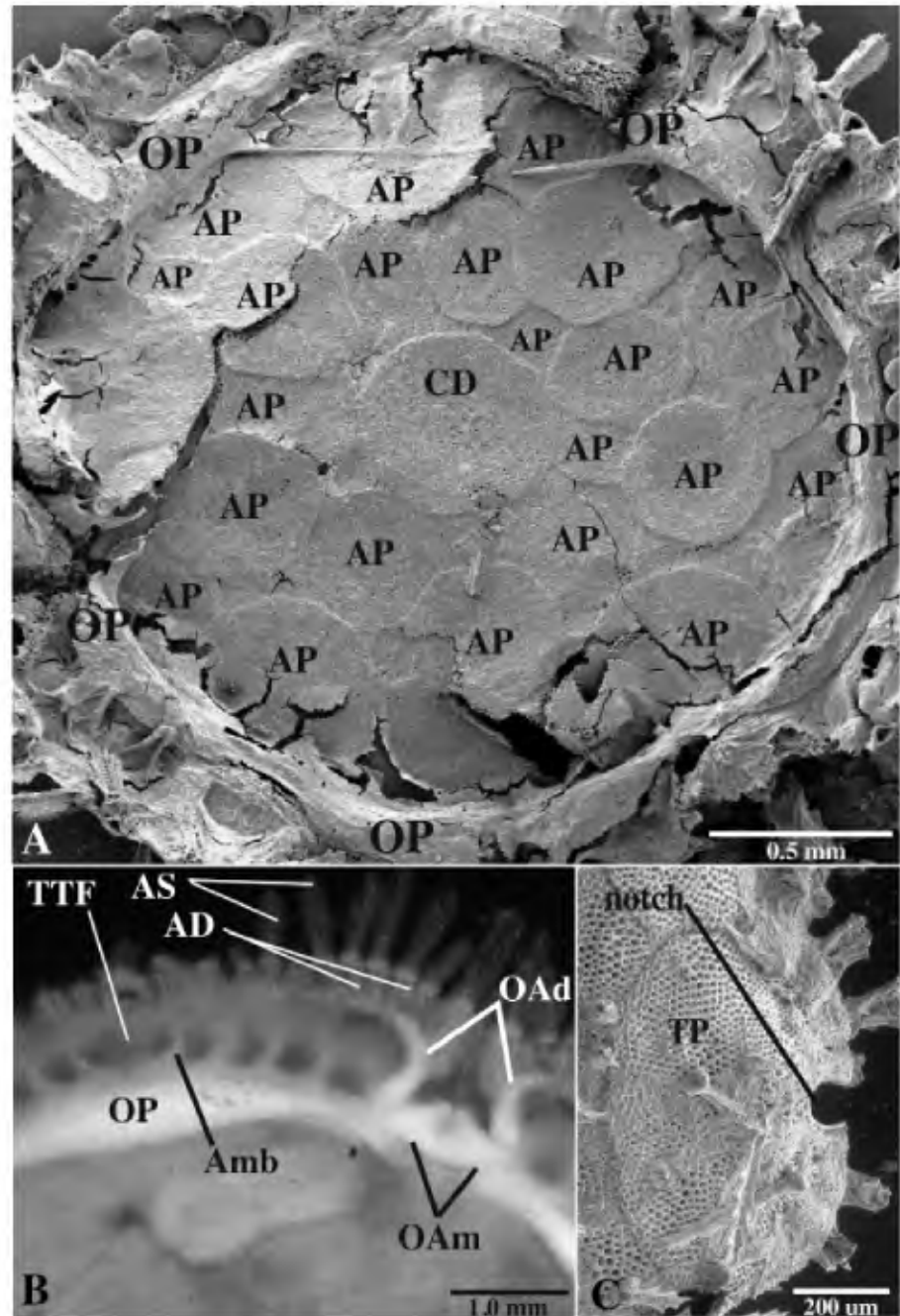


Fig. 2. Miscellaneous plates (air dried). **A.** Abactinal plates viewed from actinal surface. **B.** Oldest ambulacral. **C.** Terminal plate. AD, adambulacral plate; Amb, ambulacral plates; AP, abactinal plate; AS, adambulacral spine; CD, centrodorsal plate; OAd, oldest (first) adambulacral plate; OAm, oldest (first) ambulacral plate; OP, oral plate; TP, terminal plate; TTF, terminal tube foot (on TP).

Paratypes. FMNH 12458. Gorda Ridge, GR-14 on margin of hydrothermal vent field in basalt talus with sediment, sieved from water in recovery box of oak and fir wood blocks that were deployed July 28, 2002. 42°45.258'N, 126°42.572'W, 2701 m. Coll. M. Daly, ALVIN et al., August 31, 2004. FMNH 12459. Gorda Ridge, GR-14 on margin of hydrothermal vent field in basalt talus with sediment, sieved from water in recovery box of oak and fir wood blocks that were deployed July 28, 2002. 42°45.258'N,

126°42.572'W, 2701.0 m. Coll. M. Daly, ALVIN et al., August 31, 2004.

Other material. FMNH 12460, Gorda Ridge, GR-14 on margin of hydrothermal vent field in basalt talus with sediment, sieved from water in recovery box of oak and fir wood blocks that were deployed July 28, 2002. 42°45.258'N, 126°42.572'W, 2701 m. Coll. M. Daly, ALVIN et al., August 31, 2004. FMNH 12461, Gorda Ridge, GR-14 on margin of hydrothermal vent field in basalt talus with sediment,

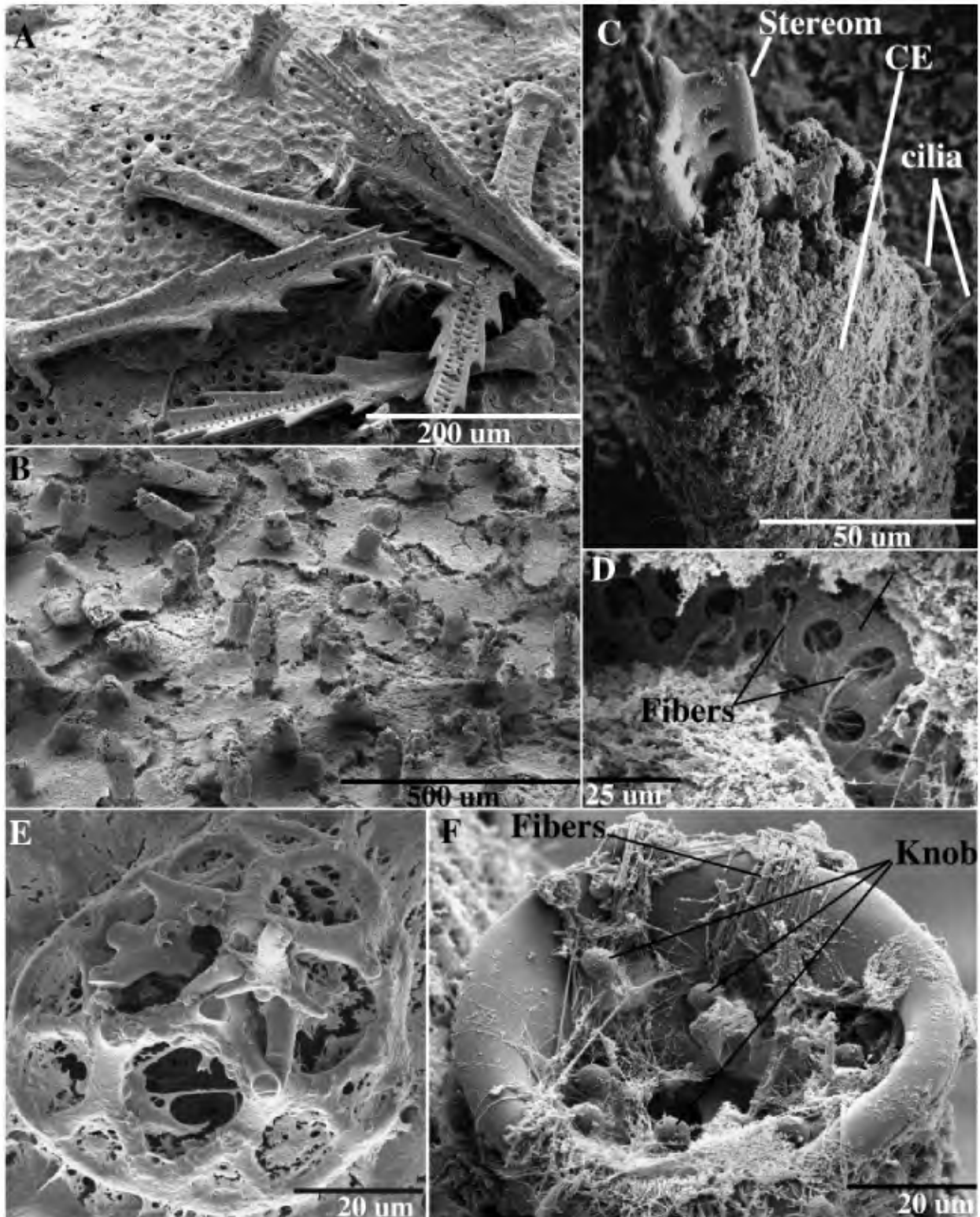


Fig. 3. Abactinal spines. **A.** Spine endoskeleton (air dried). **B.** Abactinal surface with epidermis showing spines (critical point dried). **C.** Damaged spine showing endoskeleton and ciliated epidermis (CE) and cilia (critical point dried). **D.** Torn epidermis showing connective tissue fibers through stereom (critical point dried). **E.** Spine base (air dried). **F.** Actinal view of spine base showing fibers and knob-like structures (see text) present in spine base openings (critical point dried).

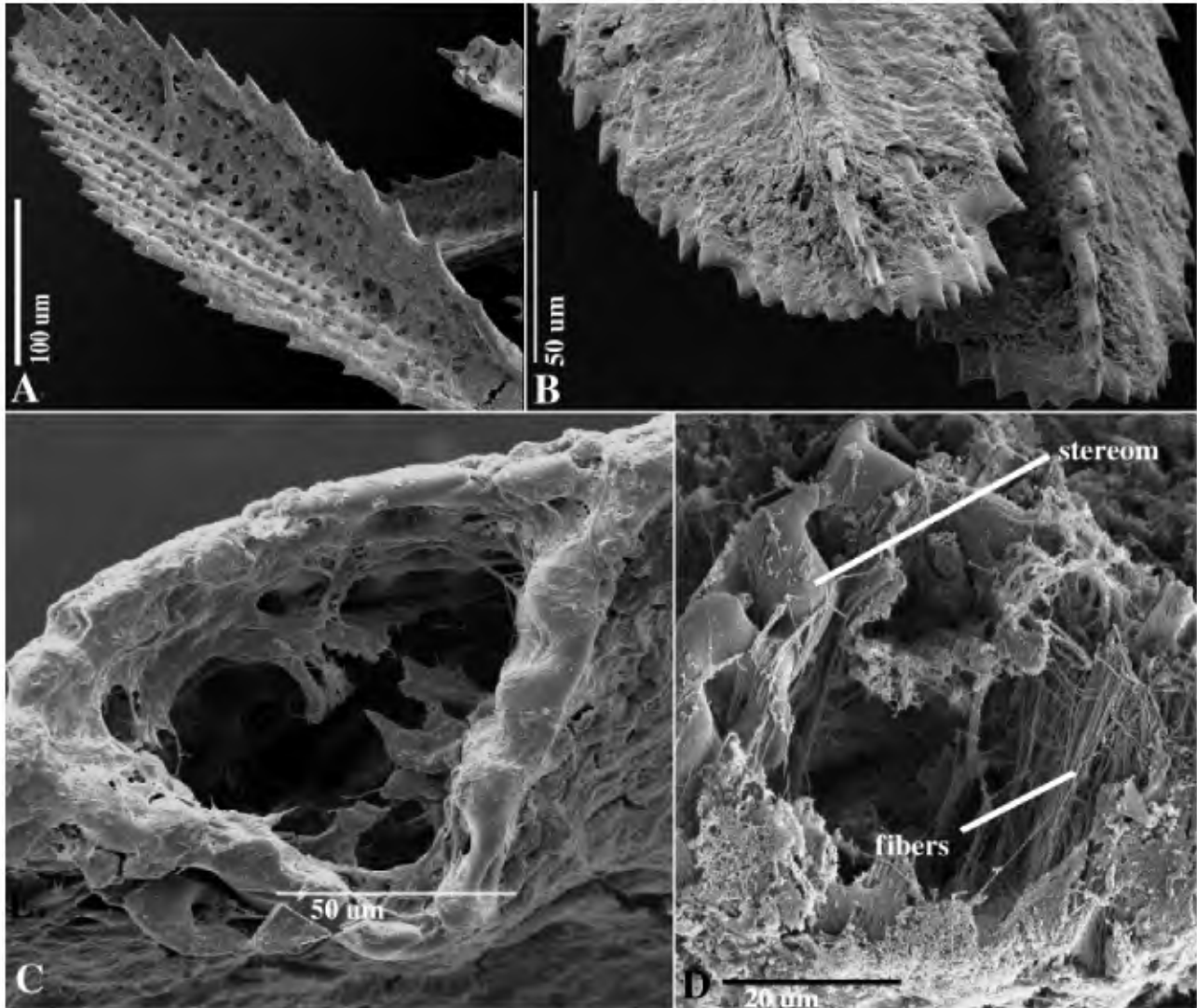


Fig. 4. Adambulacral spines (all but D air dried) **A.** Spines observed from concave surface. **B.** Spine tips, surface in closer detail. **C.** Broken adambulacral spine showing fibrous connective tissue and epidermis (from a critical-point-dried specimen). **D.** Close-up of broken spine base in cross section.

sieved from water in recovery box of oak and fir wood blocks that were deployed July 28, 2002. 42°45.258'N, 126°42.572'W, 2701 m. Coll. M. Daly, ALVIN et al., August 31, 2004.

Other material examined. *Xyloplax medusiformis*-AM J19660. Paratype. East off Castle Point, New Zealand. 41°24'S, 176°08'E, 1103–1071 m, on water-logged wood. October 16, 1984. *Xyloplax turnerae*-NMNH E350709. Atlantic Ocean, Bahamas; Tongue of the Ocean. 12°077'N, 40°12'W, 2066 m. Coll. R. Turner, November 9, 1978. R/V *Alvin*.

Etymology. This species is named for Dr. Janet Voight, curator of invertebrates in the Department of Zoology at the Field Museum of Natural History.

Revised diagnosis for *Xyloplax*. Overall body dorsoventrally flattened. Body discoidal, but subdivided into five discrete regions, each in turn subdivided interradially. Each segment with identical number of tube feet, adambulacral spines. *R/r* ratio is ~1:1.

Abactinal disk plates flattened, irregularly round, overlapping, varied in size (Figs. 1, 2A). Larger plates ≤ 5 times the size of smaller plates on any single specimen. Centrodorsal plate overlapped by five to seven smaller plates (Figs. 1B, 2A). Abactinal spines present (Fig. 1A).

Terminal plates present at terminus of body radius (Fig. 1A), flattened, rounded, with pronounced,

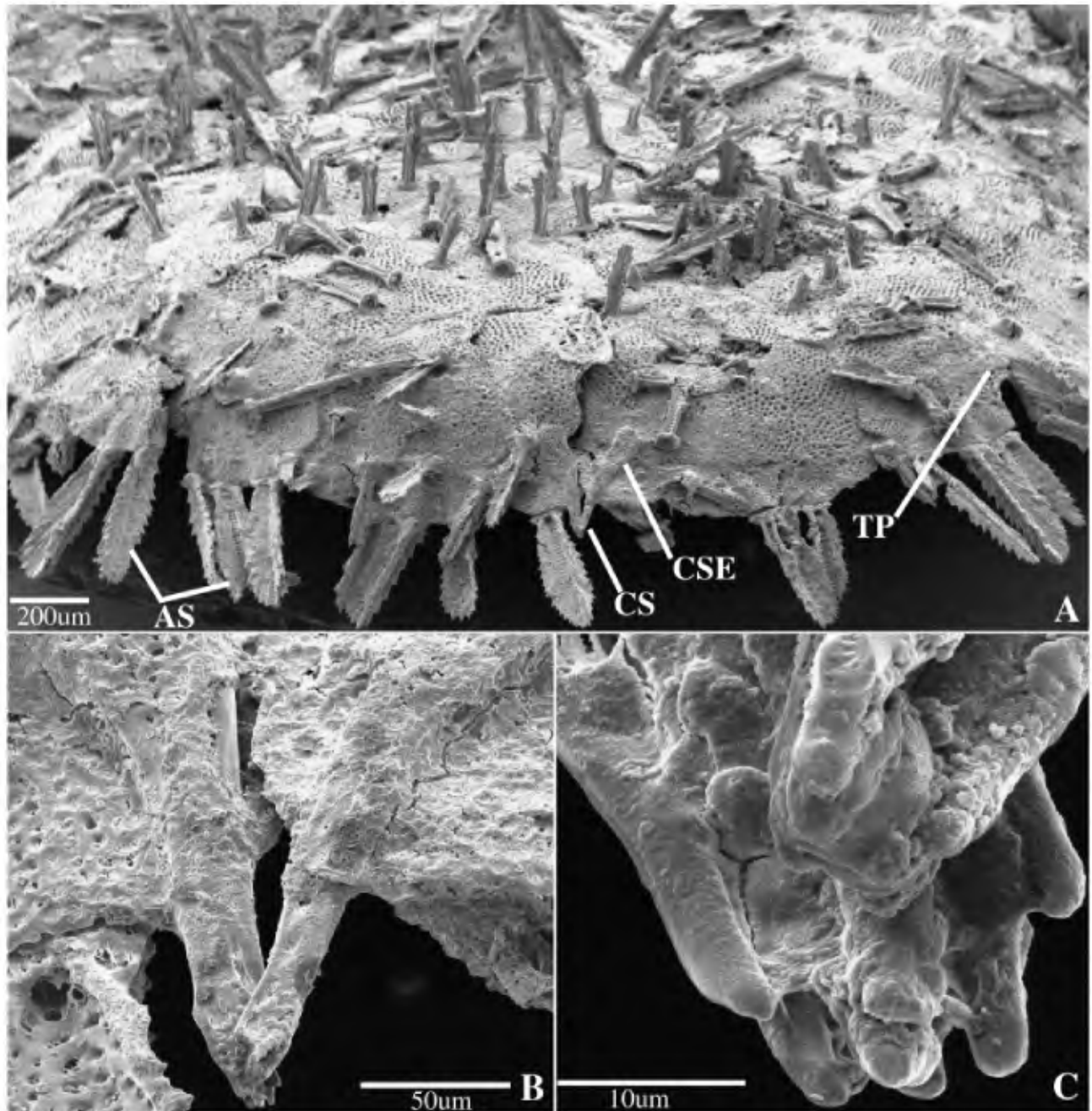


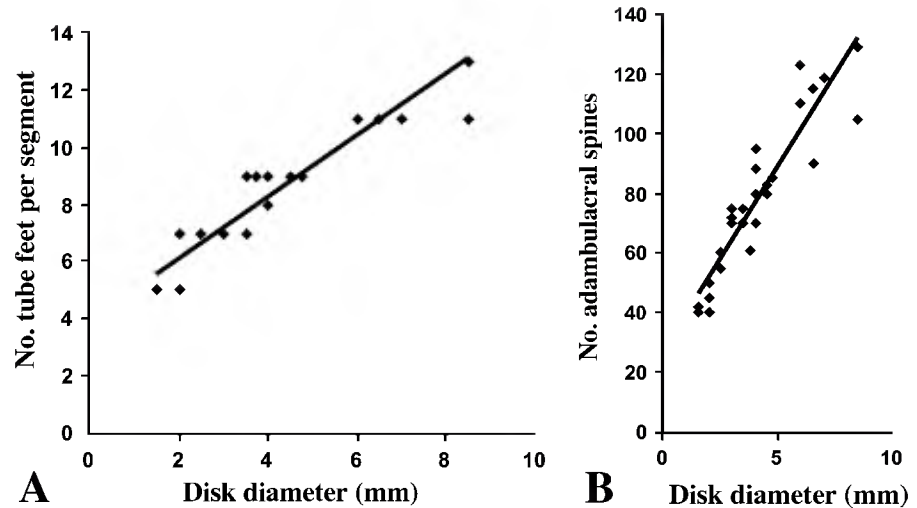
Fig. 5. Cygnoid spinelets (air-dried specimens). **A.** Lateral body view showing cygnoid spinelets relative to adambulacral spines. Note the flattened extension of cygnoid spinelet sitting on adjoining adambulacral plates and three adambulacral spines per plate. **B.** Paired cygnoid spinelets. **C.** Cygnoid spinelet tip. AS, adambulacral spines; CS, cygnoid spinelet; CSE, cygnoid spinelet extension, flattened basal extension of cygnoid spinelet; TP, terminal plate.

distally facing medial cleft corresponding to terminal tube foot (Fig. 2B,C). Terminal plates enlarged relative to adjacent adambulacral and disk plates (Fig. 2C), ~5 times the size of smaller plates.

Adambulacral flattened (*sensu* Mooi et al. 1998), overlapping, forming periphery of body (Figs. 1, 2B), oblique and adjacent to ambulacral plates and

podial pores. Terminal tube foot flanked by equal number of podial pores on either side (Fig. 2B). Ambulacral in individual series not paired (Figs. 1B, 2B), arranged around periphery of body between adambulacral and oral plates. Oldest (or first) ambulacral and adambulacral adjacent interradially (Fig. 2B). Adambulacral spines present, forming

Fig. 6. *Xyloplax janetae* n. sp. **A.** Size in disk diameter (mm) versus number of tube feet per segment. **B.** Size in disk diameter (mm) versus total adambulacral spine number.



continuous series around periphery of body (Figs. 1, 2A,B).

Oral plates curved, tusk shaped (Figs. 1B, 2A,B). Narrow tips of adjacent oral plates abut interradially. Odontophore present between narrow tips of adjacent oral plates interradially, but otherwise oral plates form innermost series of plates as observed actually (the adambulacrals, the ambulacrals, and the orals from distalmost to proximalmost, respectively) (Fig. 2A,B).

Male and female dimorphism present: paired cygnoid spinelets present interradially in males, absent from females (as shown in Rowe et al. 1988). Maximum size for adult females (diameter = 8.5) greater than maximum known size for adult males (diameter = 4.0).

Description and comparative morphology

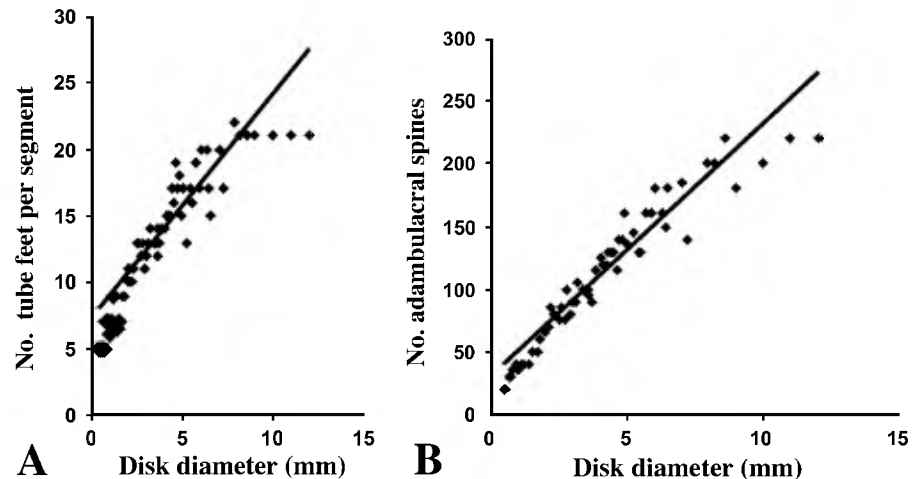
Xyloplax janetae n. sp. is described and compared with the two other known species of *Xyloplax*.

A summary of diagnostic characters for the three species is presented (Table 2). Earlier species were distinguished primarily on degree of difference (Rowe et al. 1988) rather than discrete characters.

SEM images differ significantly between air-dried and critical-point-dried specimens. More complete soft-tissue detail is evident on specimens prepared using the latter method. Tissue and tissue-related features, such as the ciliated epidermis, connective fibers, and tube foot surface, are preserved on critical-point-dried specimens but largely lost from air-dried specimens. Similar imaging artifacts were observed in air-dried versus critical-point-dried post-metamorphic asteroid specimens (Sumida et al. 2001).

Although ciliation is absent from air-dried specimens, it is observed on all plate and spine surfaces of critical-point-dried specimens (e.g., Fig. 3B,C). Ciliation is not apparent on tube-foot surfaces or on the tissue present in the mouth. Several broken abactinal spines (Fig. 3C) display the epidermal tissue layers

Fig. 7. *Xyloplax turnerae*. **A.** Size in disk diameter (mm) versus number of tube feet per segment. **B.** Size in disk diameter (mm) versus total adambulacral spine number.



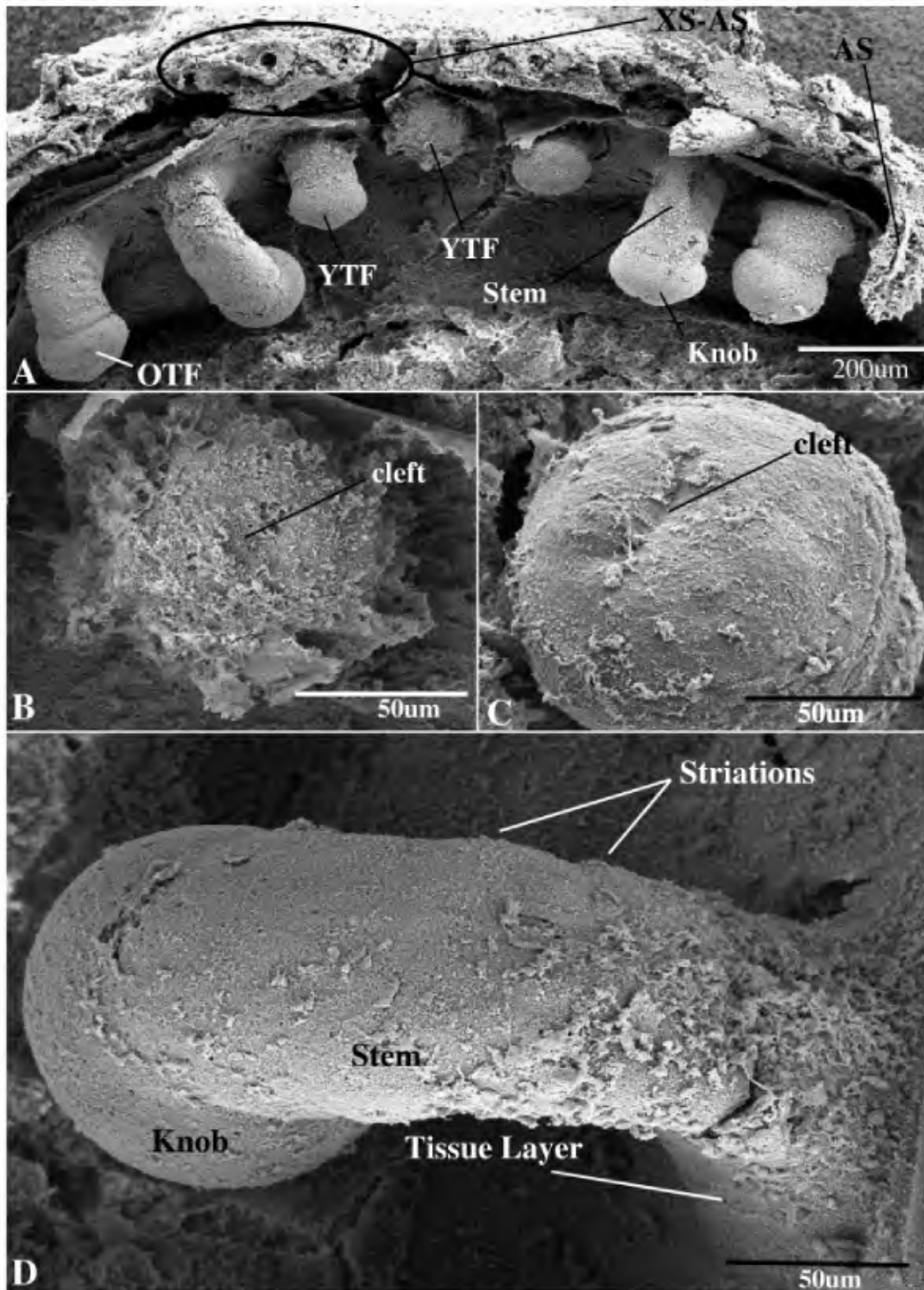


Fig. 8. Tube feet (critical point dried). **A.** Terminal and adjacent tube feet. **B.** Single tube foot. **C.** Tube foot knob. **D.** Terminal tube foot. AS, adambulacral spine; OTF, oldest tube feet; TTF, terminal tube foot; XS-AD, cross sections of adambulacral spines; YTF, youngest tube feet of series shown.

Table 2. Tabular key to *Xyloplax* species.

	<i>Xyloplax janetae</i> n. sp.	<i>Xyloplax medusiformis</i>	<i>Xyloplax turnerae</i>
Cygnoid spinelet	Smooth, elongate, only mildly curved	Upwardly curved, jagged with hook-like protrusions	Smooth, elongate, only mildly curved
Abactinal spine base	Rounded to polygonal	Stellate with jagged edges	Stellate with jagged edges
Abactinal spine size range	Uniform size distribution	Uniform size distribution	Bimodal size distribution
Adambulacral spine number per plate	Three spines	Two spines	Three spines
Total number of adambulacral spines	70 (at 3.0 mm diameter)	50 (at 3.1 mm diameter)	80–100 (at 3.0 mm diameter)
Tube feet per segment	Seven (at 3.0 mm diameter)	Nine (at 3.1 mm diameter)	11–13 (at 3.0 mm diameter)
Tube foot shape	Round-bulbous	Papillate	Round-bulbous
Gut expression	Gut absent	Gut absent	Residual gut present
Developmental mode	Intraovarian embryonic development	Nonplacental, viviparous with intraovarian embryonic development	Oviparous with only oocytes in the ovaries
Occurrence	Northeastern Pacific	South Pacific (New Zealand)	Atlantic (Bahamas)
Depth (m)	2675	1057–1208	2066

(=25–30 μm), which comprise ~50% of the total spine thickness (=50–60 μm). The epidermis forms a complete, continuous sheath between the abactinal surface (Fig. 3B) and the abactinal spines (Fig. 3C). The jagged edges observed on air-dried spines (e.g., Fig. 1A) are obscured by the epidermis in critical-point-dried specimens.

Xyloplax janetae n. sp. possesses abactinal spinelets that are ~300–350 μm in length (Fig. 3A,B) and are most similar to abactinal spines (300–400 μm) in *X. turnerae*. *Xyloplax turnerae* was described as having spines of two distinct lengths (=“spinelet height” in Rowe et al. 1988), including the 300–400 μm length spines and spines with a shorter length (90–150 μm). Abactinal spinelets in *X. medusiformis* are shorter (height = 40–75.0 μm) and more uniform than those in *X. turnerae* (Rowe et al. 1988:438). Shorter spinelets are absent from *X. janetae* n. sp. However, the shorter spinelets indicated for *X. medusiformis* (Rowe et al. 1988:pl. 3, figs. 26–28) and *X. turnerae* (Rowe et al. 1988:pl. 3, figs. 47–49) resemble broken spinelets in *X. janetae* n. sp.; breakage is at oblique angles to form jagged tips (Fig. 3C) and suggests that size differences might be artifactual.

Abactinal spinelet bases (Fig. 3E,F) in *X. janetae* also differ from those shown by Rowe et al. (1988:pl. 3, figs. 26–28, pl. 4, figs. 47–51) for *X. medusiformis* and *X. turnerae*, in that bases in *X. janetae* n. sp. are round (Fig. 3E,F) to polygonal in outlines whereas the outlines in both other *Xyloplax* spp. are more jagged.

Connective tissue fibers are observed on the abactinal surface extending longitudinally between the pores of the stereom of the abactinal plates and the

openings of the abactinal spine bases (Fig. 3D,F). The large openings (Fig. 3E) are occupied by multiple plug-like structures bearing a round, bulb-like protrusion extending toward the parent plate (Fig. 3F).

There are denuded adambulacral spine edges with numerous sharp ridges; spines are triangular in cross section, convex, or scoop-like (Fig. 4A,B). Adambulacral spines are ~150–250 μm in length. In air-dried specimens, the adambulacral spine stereom is covered with linear channels present at oblique angles along the convexity of the spine. Approximately 13–15 serrations are present along each lateral edge of the adambulacral spines (Fig. 4A,B). Adambulacral spines are sheathed by the epidermis, which obscures their serrated edges. The convex surface of the adambulacrals possesses an additional serrated ridge along the radii of the spine with ~13–15 serrations present (Fig. 4B). Cross sections through broken adambulacral spines (Fig. 4C,D) show fibrous, possibly connective tissue oriented longitudinally along the surface grooves on the convex surface.

The number of adambulacral spines per adambulacral plate varies among species. The number of adambulacral spines on either side of the terminal plate, that is, those on either side of the medial notch (Rowe et al. 1988:440), is identical to the number present on the other adambulacral plates (Fig. 2C). *Xyloplax medusiformis* has two per plate whereas *X. turnerae* and *X. janetae* n. sp. have three (Figs. 2C, 5A,B).

Images of three paratype specimens and direct examination of AM paratype J19660 of

X. medusiformis reveal inconsistencies with the diagrams shown in Baker et al. (1986) and Rowe et al. (1988). Diagrams of *X. turnerae* are closer to their descriptions, showing similar numbers of adambulacral spines per plate (but with some showing only two spines per plate). *Xyloplax medusiformis* was shown in Rowe et al. (1988: figs. 3, 5) with only one adambulacral spine per plate, whereas two are present in the paratype specimens.

The cygnoid spinelet in *X. janetae* n. sp. (Fig. 5B,C) is smooth, weakly concave with several blunt extensions at the tip (Fig. 5C), and ~100 µm in length. Cygnoid spinelets shown by Rowe et al. (1988: figs. 38, 63) were extensions of a broader, flatter plate, which was paired and articulated with a larger, more spatulate plate (Rowe et al. 1988: figs. 60, 61) present on the periphery of the body. Observations here show the flattened part of the cygnoid spinelet plate articulated on or adjacent to the adambulacral or possibly the abactinal plates (Fig. 5A).

The cygnoid spinelet present in *X. janetae* n. sp. (Fig. 5A–C) is more similar to the smooth, upturned spine shape of *X. turnerae* than to the cygnoid spinelet in *X. medusiformis*. The cygnoid spinelet present in *X. turnerae* was straight and elongate, with a smooth surface. This contrasted with the illustrated cygnoid spinelet for *X. medusiformis*, which was upwardly curved and jagged with several hook-like protrusions. The cygnoid spinelet morphology for *Xyloplax* described by Rowe et al. (1988:440) was generalized as “upwardly curved and smooth with a trifold tip.” Although *X. turnerae*’s cygnoid spinelet (Rowe et al. 1988:pl. 4, fig. 63) was broadly consistent with this description, that of *X. medusiformis* (Rowe et al. 1988:pl. 3, fig. 38) was not.

Rowe et al. (1988) noted that the gonopore in *Xyloplax* is flanked on either side by cygnoid spinelets and suggested that male *Xyloplax* were capable of depositing sperm by inserting the tip of their penial projection into the vestibular antechamber of the paired ovaries.

On the basis of body diameter, tube foot, and adambulacral spine counts (Figs. 6, 7), tube feet and adambulacral spine number were related to specimen diameter and gender (females are larger). Distinct ranges were present in each species. At 3.0 mm, *X. janetae* n. sp. males had seven tube feet per segment and ~70 adambulacral spines around the body periphery (Fig. 6). At ~3.0 mm, males of *X. turnerae* possess 11–13 tube feet per segment and 80–100 adambulacral spines around the body periphery (Fig. 7). Data for *X. medusiformis* showed nine tube feet per segment and ~50 adambulacral spines at 3.1 mm (Baker et al. 1986:fig. 1).

Tube feet of *X. janetae* n. sp. have stems that appear to be continuous with a layer of tissue that obscures the outlines of the podial basins (Fig. 8A,D). This tissue layer appears to be an extension of the velum encompassing the basal tube foot regions (Fig. 8D). Relatively few weakly developed striations occur on the stem of the tube feet and the disk and stem are poorly demarcated from one another (Fig. 8B).

The color of fresh specimens was white (J. Voight, unpubl. data).

Embryos observed in *X. janetae* n. sp.

A female specimen is shown with 13 embryos (Fig. 9A) located within the oral region associated with tissue present within the mouth. Seven to eight of the embryos are oriented actinally (i.e., mouth facing downward, away from the disk). The remaining are either obscured by tissue or oriented abactinally (i.e., mouth facing the disk). Embryos in *X. janetae* n. sp. were imaged using ESEM. Adambulacral (Fig. 9B) and abactinal spines (Fig. 9C) are present in individuals with diameters as small as ~600 µm. Only specimens with a diameter of 1.5 mm (=1500 µm) or greater were studied in detail. Embryos showed no apparent regular actinal or abactinal orientation. The adambulacral spines of one embryo (Fig. 9B) are tucked inward toward the mouth, contrary to the orientation in adults, which show the adambulacral spines directed outward. Adambulacral spines observed in the embryo are ~150–200 µm in length and show the grooves present on adambulacral spines of air-dried specimens. The other embryo figured (Fig. 9C) is present within folds of tissue showing the abactinal surface directed outward with abactinal spine lengths of ~100 µm.

Discussion

Interpretations from morphology

Mobile spines in echinoids, ophiuroids, and asteroids are articulated at ball-and-socket joints (Byrne 1994; Cavey & Märkel 1994; Chia & Koss 1994). The flat basal disks on the abactinal spines (Fig. 3A,E,F) of *Xyloplax* suggest little if any motion. Articulation between adambulacral spines and plates (Fig. 4C) suggests a broader range of movement than those on the abactinal surface. Adambulacral spines tucked under the surface of the disk of an embryo suggest flexibility (Fig. 9B).

Tube feet in *Xyloplax janetae* n. sp. are similar to those in *Xyloplax turnerae*, which Rowe et al. (1988:440, 443) described as having a bulbous or

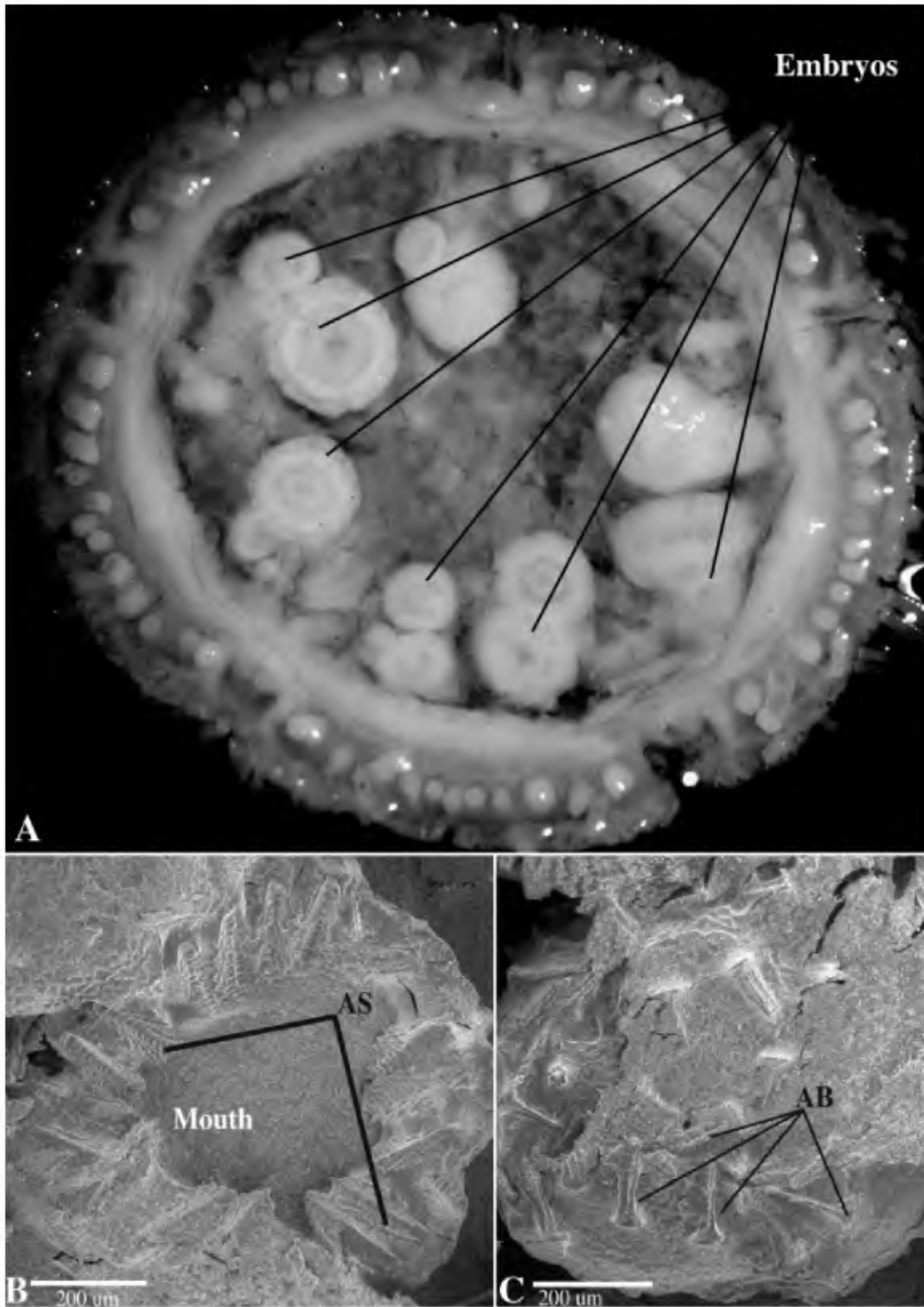


Fig. 9. *Xyloplax janetae* n. sp. **A.** Actinal surface of adult female showing 13 embryos. **B.** Environmental scanning electron microscopy (ESEM) of embryo showing peripheral spines. **C.** ESEM of embryo showing abactinal surface with spines. AB, abactinal spines; AS, adambulacral spines.

swollen tip. Tube foot morphology observed in *X. janetae* n. sp. (Fig. 8A) is most similar to those taxa with either simple disk-ending tube feet, including most species within the Valvatida, or those that end in reinforced disks, including forcipulatidans, spinulosidans, and velatidans. Tube feet in *Xyloplax medusiformis* (Rowe et al. 1988:440) were described as papillate. Comparisons with SEM images of tube feet in other asteroids (e.g., Flammang et al. 1994; Vickery & McClintock 2000) show that those in *X. janetae* n. sp. are less striated (i.e., show fewer muscular bands on the tube foot stem).

Systematics

Differences between species in *Xyloplax* are based on numerical variation between characters (e.g., number of spines); relatively few characters, such as the cygnoid spinelet or the abactinal spine bases, show discrete disparity. Conservative morphology observed in *Xyloplax* is similar to that of other widely distributed, frequently cosmopolitan, lower bathyal to abyssal echinoderms. For example, the Porcellanasteridae (order Paxilloidea; Asterozoa) includes genera such as *Erenicaster* and *Hyphalaster* from the Atlantic, Pacific, and Indian Ocean basins (Madsen 1961; Clark & Downey 1992) that show variation between species primarily based on numerical variation between number of spines and arm ratio (R/r) differences.

Different cygnoid spinelet morphologies could reproductively isolate species in *Xyloplax*. *Xyloplax turnerae* and *X. janetae* n. sp. share similar cygnoid spinelet morphologies, which suggest they could be more closely related than either is to *X. medusiformis*.

Phylogenetic perspectives on *Xyloplax*

The morphological disparity observed in *Xyloplax* relative to other echinoderms has inspired hypotheses regarding its evolution since it was first described (Baker et al. 1986; Rowe et al. 1988; see Fig. 10B,C). Morphological (Smith 1988) and combined evidence (Janies 2001) approaches have been used in attempts to understand evolutionary relationships between *Xyloplax* and other echinoderm classes. The earliest cladistic treatment of *Xyloplax* was that of Smith (1988), who challenged recognition of a new, separate class (Baker et al. 1986; Rowe et al. 1988). He proposed that *Xyloplax* was the sister branch to *Caymanostella* (Caymanostellidae), a derived velatidan asteroid. Pearse & Pearse (1994) concluded that class-level affinities of *Xyloplax* were ambiguous. Subsequent phylogenetic studies (e.g.,

Janies & Mooi 1999; Janies 2001) further supported *Xyloplax* as a derived branch within the Asterozoa. However, placement of many taxa within the Asterozoa by Janies & Mooi (1999) and Janies (2001) is inconsistent with current classifications of post-Paleozoic Asterozoa (e.g., Blake 1987; Clark 1989, 1993, 1996; Clark & Downey 1992; Clark & Mah 2001). Nevertheless, the consensus tree (from two trees with 5265 steps) shown in Janies & Mooi (1999) and Janies (2001) shows consistent clustering of echinoderm taxa at the class level, supporting *Xyloplax* as a member of the asteroid lineage. With the exception of Baker et al. (1986) and Rowe et al. (1988), other studies have consistently assigned *Xyloplax* to positions within the Asterozoa. Pearse & Pearse (1994) retained *Xyloplax* within the Concentricyclozoa because class-level phylogenetic affinities were considered ambiguous.

Relationships between *Xyloplax* and other asteroids are considered within the context of more recent paleontological data (e.g., Blake 1998; Blake & Hagdorn 2003) and the application of the EAT (Mooi & David 1996). The EAT seeks to explain homologies based on ontogenetic development of the skeletal systems within the Echinodermata. It permits recognition of basic ontogenetic differences in two main types of echinoderm skeleton—axial and extraxial (David & Mooi 1996)—and provides a rigorous basis for character analysis. An important aspect of the EAT is the manner in which plates and tube feet are laid down in accord with the ocular plate rule (OPR). In asteroids, the terminal plate is laid down first, followed by subsequent ambulacral and tube foot growth. The first and oldest plate is formed adjacent to the terminal plate, with subsequent plates being laid down as the terminal plate (the arm tip) grows away from the disk. The oldest and most developed ambulacral plates and tube feet are located closest to the mouth, whereas the youngest are located adjacent to the terminal plate (Mooi & David 1996).

Observed characters in *X. janetae* n. sp. are in agreement with the OPR, including the orientation of the tube feet relative to the terminal tube foot. The terminal tube foot sits centrally with tube feet on either side (Fig. 8A–C), changing from smallest adjacent to the terminal and becoming larger farther away from the terminal.

The impact of the EAT on homologies between *Xyloplax* and caymanostellids was addressed by Mooi et al. (1998), who underscored the need for caution in interpreting *Xyloplax* and caymanostellids as sister taxa. Mooi & David (1996) presented EAT-based homologies and a character distribution for somasteroids, asteroids, and ophiuroids (see Table 1

for a taxonomic summary). Interpretations from the EAT were not directly applied toward the phylogenetic tree presented in Janies & Mooi (1999) and Janies (2001). The morphological data supporting *Xyloplax* as a highly derived asteroid (Janies 2001) were developed primarily from morphological data presented by Littlewood et al. (1997). The morphological data included in Blake (1998) and Blake & Hagdorn (2003) further elaborated apomorphies and classification for post-Paleozoic asteroids. Blake & Hagdorn (2003) established the subclass Ambuloasteroidea to include Paleozoic and post-Paleozoic asteroid taxa with modern (i.e., crown-group type) ambulacral construction. Their study also further redefined the infraclass Neoasteroidea, which includes all known post-Paleozoic asteroids, primarily based on the expression of actinal plates (Blake & Hotchkiss 2004).

Characters plesiomorphic to asteroids, ophiuroids, and concentricycloids include planar body form and the presence of adambulacrals with accessory elements. Synapomorphies for ophiuroids, such as an enclosed radial canal, semi-internal podial basins, laterals (=adambulacrals) present under proximal ambulacrals, and the presence of proximal ambulacral plates forming the buccal opening, are absent in *Xyloplax*. Characters supporting the inclusion of *Xyloplax* within the asteroid lineage (Fig. 10A) include the presence of an odontophore, a radial water canal nested in a groove, and differentiated adambulacrals. Rowe et al. (1988) identified the odontophore in *Xyloplax*. McKnight (1975) identified the absence of the odontophore from somasteroids, which he recognized only in the Asteroidea. The odontophore was the only unique character supporting the Asteroidea in the phylogeny presented by Janies (2001). The position of the odontophore in *Xyloplax* relative to the ambulacrals and the oral plates, as established by Rowe et al. (1988), was consistent with homologies outlined by Mooi et al. (1998) and Janies & Mooi (1999: fig. 1b). Baker et al. (1986:862) described the presence of a groove for the water vascular canals.

Within the Asteroidea, *Xyloplax* is included within the Ambuloasteroidea based on possession of offset ambulacral and adambulacrals plates and presence of ambulacral plates with a broadly inverted J-shape and well-developed abactinally facing podial pores (Fig. 10A). The Ambuloasteroidea includes the crown-group Neoasteroidea, the Concentricycloidea, and two Paleozoic genera, *Compsaster* and *Calliasterella* (Table 1, Blake & Hagdorn 2003).

The Neoasteroidea, designated by Gale (1987), are exclusively post-Paleozoic starfish. They form a mon-

ophyletic clade including all modern asteroids. Neoasteroids are supported primarily by the expression of numerous actinal plates (Blake & Hotchkiss 2004).

Among the most significant of features in *Xyloplax* is the apparent absence of the actinal plate surface. Other characters in *Xyloplax* that differ from those in neoasteroids (Fig. 10A) include the presence of ambulacrals typically larger than adambulacrals plates (ambulacral plates smaller in *Xyloplax*), adambulacrals plates wider than that of ambulacral articular flanges (adambulacrals much wider in *Xyloplax*), and the overlapping of ambulacral plates with other ambulacral plates (no overlap in *Xyloplax*).

Concentricycloids are proposed as the sister group to the Neoasteroidea (Fig. 10A) and are included within the subclass Ambuloasteroidea. They are considered as a second infraclass in addition to the infraclass Neoasteroidea as designated by Blake & Hagdorn (2003). Many of the putative apomorphies recognized for *Xyloplax* are based on axial components, which show conservative evolution (David & Mooi 1996; Mooi & David 1996). These include the mouth frame and ambulacral plates that demonstrate limited change across taxa (e.g., Blake 1981). This suggests radical changes in these structures to produce the highly modified morphology observed in *Xyloplax* from the conservative ambulacral architecture established within derived, crown-group asteroids. Implicit in this reconstruction is the fact that the substantial morphological departure of *Xyloplax* was associated with the post-Paleozoic diversification of crown-group asteroids rather than from a modification of established and conservative morphology, such as those in derived asteroids.

Characters in basal neoasteroids are consistent with a sister-group relationship to concentricycloids. The fossil genera indicated below and asteroids within the Zoroasteridae (see Table 1 for asteroid classification) are classified within the Forcipulatacea, which have been considered basal by Blake (1987, 1990). Rowe et al. (1988) discussed and rejected the possibility that *Xyloplax* was derived from forcipulate asteroids based on the absence of shared characters between the two taxa. However, characters considered here are considered plesiomorphic for the class Asteroidea. This is also consistent with taxa emerging adjacent to *Xyloplax* on the tree (*Rathbunaster*, *Asterias*, *Brisingaster*) presented by Janies & Mooi (1999) and Janies (2001), although *Xyloplax* itself does not occur at the base of their tree.

Although EAT-based homologies in concentricycloids were indicated as preliminary, only a single row of marginals was illustrated by Mooi et al. (1998). If an additional series of marginal ossicles is

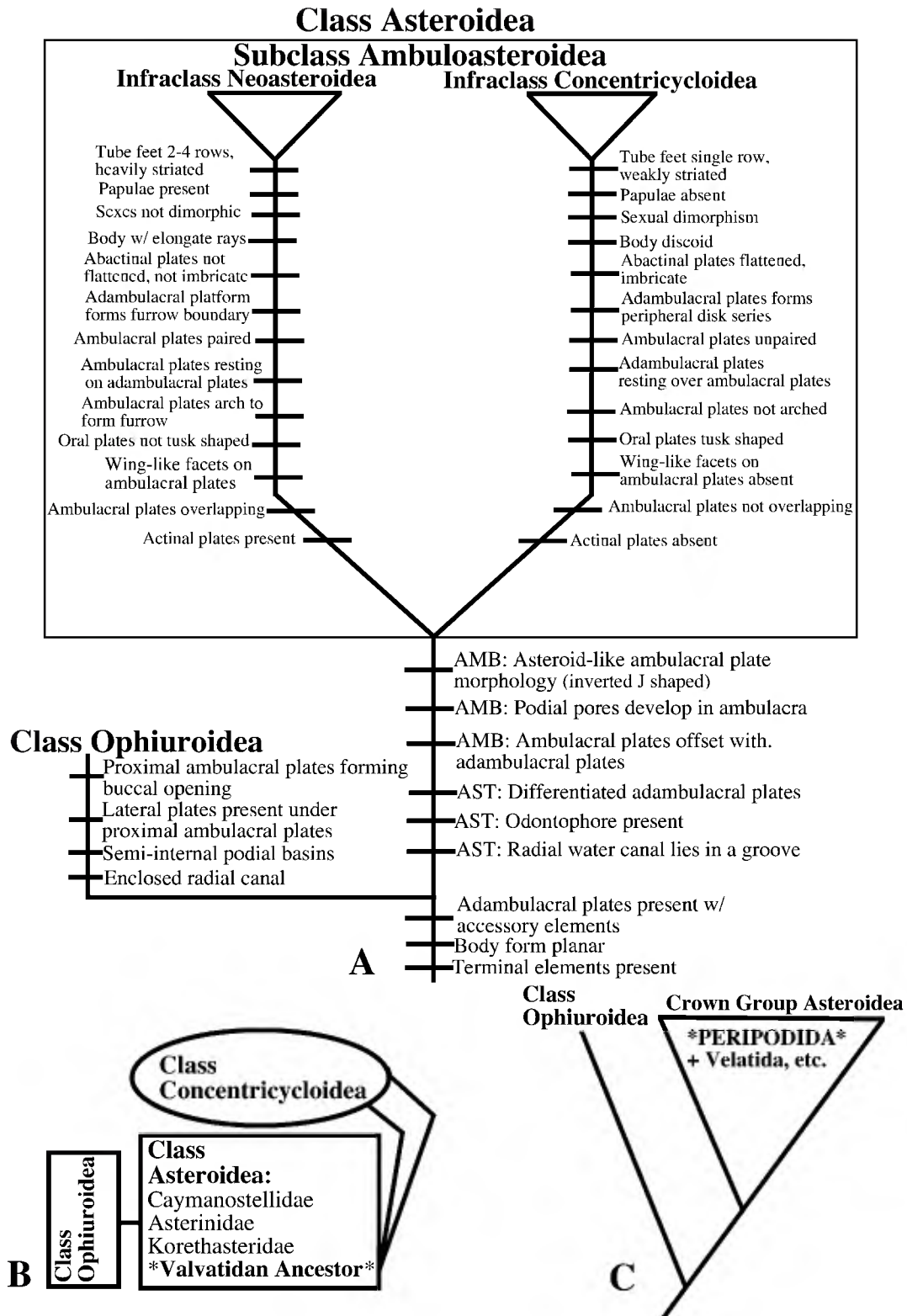


Fig. 10. **A.** Character distribution applied to crown-group asteroids and concentricycloids (ophiuroids included for reference). Characters from Blake (1998) and Mooi & David (1996). **AMB,** character defining Ambuloasteroidea; **AST,** character defining Asteroidea. **B.** Phylogenetic hypothesis showing *Xyloplax* as a separate class (Baker et al. 1986; Rowe et al. 1988). **C.** Phylogenetic hypothesis showing *Xyloplax* as a crown-group asteroid (Smith 1988; Belyaev 1990).

not confirmed, this would be consistent with the presence of this character in basal crown-group asteroids (Blake & Hagdorn 2003), including the Triassic genera *Trichasteropsis* and *Berckhemeraster* as well as that of the extant Zoroasteridae (Blake 1987, 1990).

Odontophore morphologies from several major asteroid lineages (summarized in Table 1), including velatidans, paxillosidans, spinulosidans, valvatidans, and forcipulatidans, were surveyed from several sources (Viguier 1879; Fisher 1928; Turner & Dearborn 1972). Comparison with the odontophore morphology present in *Xyloplax* (Rowe et al. 1988:55) suggests that it is most similar to odontophores in forcipulate asteroids (e.g., Fisher 1928: pl. 39, figs. 2, 43).

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