AMER. ZOOL., 40:355–364 (2000)

Comparative Morphology of Tube Feet Among the Asteroidea: Phylogenetic Implications[1]

MINAKO S. VICKERY[2] AND JAMES B. MCCLINTOCK

Department of Biology,
University of Alabama at Birmingham,
Birmingham, AL 35294-1170

SYNOPSIS. **Tube-foot morphology has been included among a variety of taxonomic criteria for the Asteroidea over the past twenty-five years. Other than a few families belonging to the order Paxillosida, which are thought to have pointed, non-suckered tube feet that are used for digging and burial in soft sediments, the presumption has been that asteroids have flat-tipped, suckered tube feet. This has become an accepted model despite the fact that the comparative morphology of asteroid tube feet has not been considered. In the present study we examine tube-foot morphology of 45 species of Asteroidea representing 19 families. Our analysis confirms that members of the Luidiidae and Astropectinidae (order Paxillosida) lack suckers on the tips of their pointed tube feet. We demonstrate that there is considerable variation in tube-foot morphology among members of the Asteroidea including an entirely new type of flat-tipped, non-suckered tube foot in species belonging to the order Valvatida. The external morphology of tube feet in species belonging to the order Velatida could not be distinguished from ''typical'' flat-tipped, suckered tube feet; nonetheless, histological sections revealed a distinctive internal morphology. Finally, we report the first observations of the tube-foot morphology of representatives of deep-sea asteroids belonging to the orders Notomyotida and Brisingida, a group that also lacks the typical flat-tipped, suckered tube-foot morphology. The results of our study demonstrate that the current tube-foot morphology model needs to be reconsidered, as there is considerably greater variation than was previously believed to be the case. Moreover, we conclude that while tube-foot morphologies show consistent similarities within orders, tube-foot morphology is less appropriate as a taxonomic character below this level.**

INTRODUCTION

Extant asteroids currently number approximately 1,600 species, occurring from the intertidal to the abyssal and from tropical to polar seas (Blake, 1989). Classifications of asteroids have been based primarily upon skeletal morphologies of adults (Spencer and Wright, 1966; Downey, 1973; Hayashi, 1973; Blake, 1987; Gale, 1987; Clark and Downey, 1992). Morphological differences or similarities of adult skeletons have been used to group asteroids into species, genera, families, and orders. Nonetheless, asteroid classifications have not gone without considerable debate among taxonomists. Species belonging to the families Astropectinidae and Luidiidae are a classic example of such a debate.

Both families were initially separated into two entirely different orders (Spencer and Wright, 1966; Downey, 1973; Hayashi 1973), only to be re-classified within Paxillosida (Blake, 1987; Gale; 1987; Clark and Downey, 1992). The question of whether paxillosidans are ''primitive'' or ''advanced'' members of the Asteroidea has been a matter of considerable discussion (Fell, 1963; Blake, 1987, 1988; Gale, 1987; Lafay *et al.*, 1995; Wada *et al.*, 1996; and Knott and Wray, 2000). Paxillosidans were originally positioned as a primitive group based upon a skeletal morphology that appeared to be similar to early fossil asteroid species (Blake, 1987). Moreover, *Luidia* spp. display similarities to the somasteroid *Platasterias latiradiata*, considered by Fell

---

[1] From the Symposium *Evolution of Starfishes: Morphology, Molecules, Development, and Paleobiology* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 6–10 January 1999, at Denver, Colorado.

[2] E-mail: vickerym@uab.edu

(1963) to be a ''living fossil.'' Blake (1972, 1982) re-examined the skeleton of *P. latiladiata* and concluded it was an advanced asteroid belonging to the Luidiidae. This reclassification of the Paxillosida was based upon various characteristics including not only adult skeletal morphologies, but functional considerations such as developmental mode and, importantly, tube-foot morphology of both juveniles and adults (Blake, 1987). Oguro *et al.* (1976) reported that newly metamorphosed juveniles of the paxillosidan *Astropecten scoparius* possessed suckered tube feet, while adults lacked suckered tube feet.

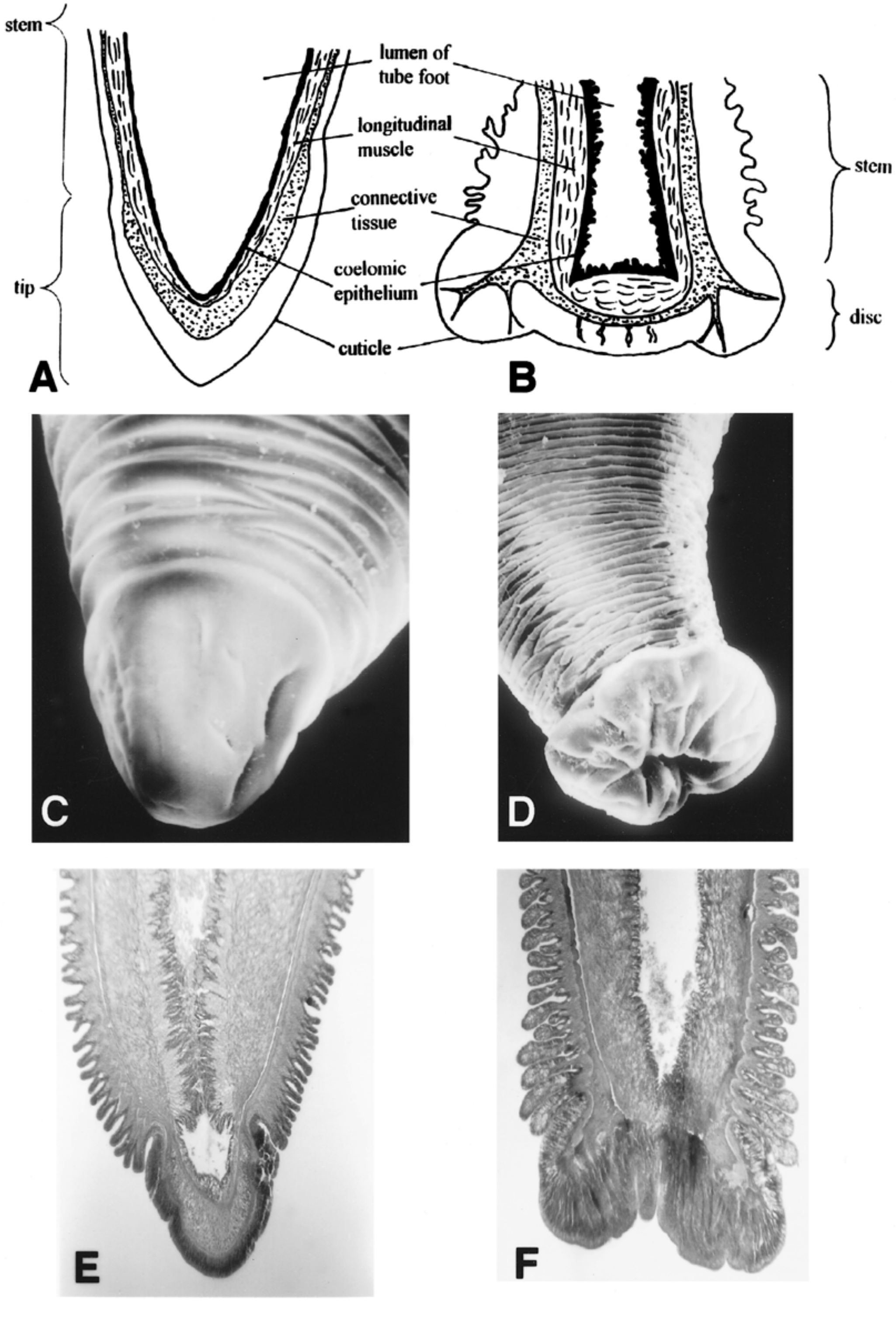
Both histological and ultrastructural studies of asteroid tube feet have been conducted (Paine, 1926, 1929; Smith, 1937, 1947; Hyman, 1955; Souza Santos, 1966; Souza Santos and Silva Sasso, 1968, 1970, 1974; Engster and Brown, 1972; Hermans, 1983; Thomas and Hermans, 1985; Flammang *et al.*, 1994; Flammang, 1995*a*, 1995*b*; McCurley and Kier, 1995). Nonetheless, none of these morphological studies have taken a broad comparative approach. Engster and Brown (1972) examined the (typical) pointed, non-suckered tube feet of *Astropecten* sp. (Fig. 1A). The tube foot was divided into a stem and a tip instead of a stem and a distal disc. The tip of the tube foot was tapered, the lumen was elongated into the tip, there was a thin layer of longitudinal muscle and an accumulation of mucopolysaccharide granules in the epithelial layer (providing capacity for adhesion), and there was no branching of connective tissue. Suckered tube feet (Fig. 1B) were carefully examined in *Asterias vulgaris* by Paine (1929) who described the basic internal morphology. A longitudinal section of the tube foot revealed a distinct stem and a flat distal disc with an outer cuticle, underlaid by an epithelium, nervous and connective tissues, longitudinal muscle, endothelium (coelomic lining), and lumen. The connective tissues were branched in the disc area and extended toward the distal end of the tube foot. The basic internal morphology of the (typical) suckered tube feet described by Paine is similar to the internal morphology of the pointed, non-suckered tube feet described above.

The adhesive properties of the tube foot of *Asterias vulgaris* were shown to involve a combination of mechanical suction and secretion of mucus (Paine, 1926), and a simple suction cup model of the tube foot was proposed by Smith (1937, 1947). More recently, the morphologies and adhesive properties of tube feet from various species were examined in detail (Hermans, 1983; Thomas and Hermans, 1985; Flammang *et al.,* 1994; Flammang, 1995*a, b*). These studies suggested that tube-foot morphologies might be more diverse than previously thought, which emphasizes the need for the examination of tube-foot morphology on a broad scale, with possible phylogenetic implications. To date, no such broad scale comparative analysis of asteroid tube-foot morphology has been conducted, thus the general concept has been that asteroids have only one of two tube-foot types, a pointed, non-suckered tube foot in members of the Paxillosida and a flat-tipped, suckered tube foot in all other orders (Spencer and Wright, 1966; Downey, 1973; Hayashi, 1973; Blake, 1987; Gale, 1987; Clark and Downey, 1992).

In the present study we examine the adult tube-foot morphology of 45 species of asteroids representing 19 families and 7 orders (Clark and Downey, 1992) to determine whether the flat-tipped, suckered versus pointed, non-suckered tube-foot model can be used to accurately generalize asteroid tube-foot morphology. Moreover, in order to evaluate whether there is an ontogenetic component to tube-foot morpholo-

→

FIG. 1. A. Schematic diagram of the pointed, non-suckered tube foot of *Astropecten* sp. (modified after Engster and Brown, 1972). B. Schematic diagram of the flat-tipped, suckered tube foot of *Asterias vulgaris* (modified after Paine, 1929). C. Scanning electron micrograph of the pointed, non-suckered tube foot of *Psilaster charcoti*. D. Scanning electron micrograph of the flat-tipped, suckered tube foot of *Diplasterias brucei*. E. Paraffin section of the pointed, non-suckered tube foot of *Luidia foliolata*. F. Paraffin section of the flat-tipped, suckered tube foot of *Pycnopodia helianthoides*. Scale bars: C–F, 200 μm.


stem
tip
lumen of tube foot
longitudinal muscle
connective tissue
coelomic epithelium
cuticle
stem
disc
A
B
C
D
E
F

gy, the external morphology of the tube feet from recently-metamorphosed juveniles of three species representing the families Luidiidae, Pterasteridae, and Asteriidae were examined. We interpret our findings in a phylogenetic context by examining patterns of species-specific tube-foot morphology with respect to current classification schemes for the Asteroidea and evaluate the use of tube-foot morphology as a taxonomic character.

MATERIALS AND METHODS

Asteroids were collected from a variety of geographical regions (Table 1). Representatives included species from six orders (Paxillosida, Valvatida, Velatida, Spinulosida, Forcipulatida, Brisingida) from the Pacific Northwest, five orders (Paxillosida, Notomyotida, Valvatida, Velatida, Forciupulatida) from Antarctica, two species of brisingids from the Pacific, and two species of paxillosids from the Gulf of Mexico. Tube feet of each species collected from the Pacific Northwest and the Gulf of Mexico were surgically removed and immediately preserved in 70% ethanol after being relaxed in 5% $MgCl_2$ in filtered sea water. Two preserved samples of brisingids were obtained from the California Academy of Sciences. Tube feet from specimens obtained from the Antarctic Invertebrate Collections at the Smithsonian Institution had been fixed in formalin and then transferred into 70% ethanol.

The external morphology of tube feet of all species was observed under a dissecting microscope. Representative species from each family were chosen for further examination using scanning electron and light microscopy. Tube feet were re-fixed with 1% osmium (Sigma) in 0.1 M cacodylate buffer (pH 7) after being submerged in distilled water for 24 hr (modified after Amemiya and Emlet, 1992). After a one-hour fixation period, tube feet were dehydrated using a graded ethanol series (50%, 70%, 80%, 90%, and 100%, 5 min each). The samples were subsequently mounted on aluminum specimen mounts (SPI Supplies) with carbon conducting tabs (Ted Pella, Inc.) following critical-point drying. A single layer of gold-palladium was applied by sputter coating, and samples were examined and photographed with a Philips 515 scanning electron microscope.

For light microscopical examination of histological sections, tube feet were re-fixed with Bouin's fixative after being held in distilled water for 24 hours. Standard paraffin (melting point 52–55°C, Fisher Scientific) embedding methods were applied after dehydrating the samples in a graded ethanol series (70%, 80%, 90%, and 100%, 5 min each) and treatment with toluene as a clearing agent (5 min) (Humason, 1997). Seven-micrometer thick longitudinal, serial sections of tube feet were stained with Harris's hematoxylin and eosin and then permanently mounted with ParaMount (Sigma). The sections were examined under a Leitz Diaplan versatile microscope and photographed with an Olympus C-35 camera.

Juveniles of *Luidia foliolata* and *Pisaster ochraceus* (adults are believed to have pointed, non-suckered tube feet and flat-tipped, suckered tube feet, respectively) and *Pteraster tesselatus* (adults are believed to have flat-tipped, suckered tube feet) were obtained by standard larval culture techniques (Strathmann, 1987). After the bipinnaria larvae of *L. foliolata* and the brachiolaria larvae of *P. ochraceus* completed metamorphosis, juveniles were immediately fixed in 70% ethanol. As *P. tesselatus* has lecithotrophic development (McEdward, 1992), larvae (mesogens) were kept in small containers without food until they completed metamorphosis, after which juveniles were fixed in 70% ethanol. The external morphologies of juvenile tube feet were examined using dissecting and compound light microscopy.

RESULTS

Tube feet of members of the order Paxillosida had pointed tips. *Psilaster charcoti* provided a representative example of the paxillosidan tube-foot design with a sharply-tapered tip lacking a distal depression (Fig. 1C). At the tip, dense mucus secretory granules were observed in the epidermal layer. One of the four species of astropectinids examined by scanning electron microscope, *Macroptychaster accrescens*, had pointed tube feet with slightly rounded tips.

Nonetheless, histological sections of tube feet of *M. accrescens* revealed an internal morphology similar to those of *P. charcoti, L. clathrata,* and *L. foliolata,* and therefore, must be considered pointed, non-suckered just as in other members of the Luidiidae and Astropectinidae.

Representatives of the orders Forcipulatida (*Diplasterias brucei, Pycnopodia helianthoides, Labidiaster annulatus*) and Spinulosida (*Henricia* sp.) displayed external and internal tube-foot morphologies consistent with the typical flat-tipped, suckered tube foot (Fig. 1B, D, F). Eleven representative species from five families of the order Valvatida were examined to determine whether tube feet were suckered. Scanning electron microscopy revealed that the tube feet of *Acodontaster conspicuus* lacked suckers (Fig. 2A), with no distinct concavity in the center of the disc, as seen in a typical flat-tipped suckered tube foot. Histology further revealed an unusually-thin longitudinal muscle layer and an extension of the lumen into the distal disc. Scanning electron micrographs of the discs of the tube feet of *Odontaster validus* revealed varying degrees of concavity. Nonetheless, histology confirmed a non-suckered tube-foot design similar to *A. conspicuus.* Histological observations of additional representatives from the five valvatid families revealed that they all lacked typical flat-tipped, suckered tube feet, possessing instead a more intermediate morphology. For example, the lumen was broadly expanded into the disc area and quite distinct from either the classic pointed, non-suckered or flat-tipped, suckered tube feet (Fig. 2B). Although divided into stem and disc, tube-foot epithelial, longitudinal muscle and connective tissues were thinner than those found in the typical pointed, non-suckered tube foot. In the central disc area, the epidermis was much thinner than in other portions of the disc. A slight concavity was observed in the disc. The longitudinal muscle layer was thinner than that observed for any other tube feet, and the connective tissue layer was branched in the disc area and surrounded by lumen. This branching may provide support for the disc. As this type of tube foot has not been described previously, and was observed in all eleven representative members of the order Valvatida examined (see Table 1), we broadly classified this novel tube foot type as ‘‘flat-tipped, non-suckered.’’

The two representatives of the order Velatida that were examined histologically, *Pteraster tesselatus* (Pterasteridae) and *Solaster stimpsoni* (Solasteridae), were observed to have tube feet that differed from the typical flat-tipped, suckered tube foot. Sections revealed that the connective tissue was not branched within the disc, and very thin connective tissue and muscle layers were evident (Fig. 2C). We considered such morphological differences to be a variation of the typical flat-tipped, suckered tube foot and classified the tube feet of *P. tesselatus* and *S. stimpsoni* as ‘‘semi-flat-tipped, suckered.’’

We examined tube feet from seven species representing four families of deep-sea asteroids from the orders Notomyotida and Brisingida. In contrast to the classic tube-foot model, we found that *Cheriaster gerlachei* (Notomyotida) lacked a typical flat-tipped, suckered tube foot. Instead, the tip of the tube foot was a rounded point. Histological sections revealed that *C. gerlachei* lacked the typical internal anatomy of a flat-tipped, suckered tube foot (Fig. 2D). Specifically, while the tube foot was distinguished clearly into a stem and a tip, the lumen did not extend into the distal tip area as seen in *Luidia foliolata* (Fig. 1E). Moreover, connective tissue branched at the tube-foot tip, perhaps explaining the rounded shape. The epithelial and longitudinal muscle layers were thinner than the ‘‘typical’’ flat-tipped, suckered tube foot described by Paine (1929) for *Asterias vulgaris.* Accordingly, we classified the tube foot of *C. gerlachei* as ‘‘semi-pointed, non-suckered.’’

Among four species of the deep-sea order Brisingida examined, *Novodinia pacifica* possessed a rounded, knob-like, tube-foot tip. Histological examination of the internal tube-foot structure revealed that the central portion of the disc had a very thin epidermal layer, making the tube foot appear similar to the flat-tipped, non-suckered tube feet described in the order Valvatida

Table 1. *Taxonomic classification, tube-foot morphology, methodological approach taken to examine tube-foot morphology, and geographical location of asteroids examined.**

	Tube-foot morphology	Methods	Geographical location
PAXILLOSIDA			
Luidiidae			
Luidia clathrata	PNS	H	Gulf of Mexico
Luidia foliolata	PNS	H	Pacific N. W.
Astropectinidae			
Astropecten articulatus	PNS	DM	Gulf of Mexico
Bathybiaster loripes	PNS	DM	Antarctica
Leptychaster flexuosus	PNS	DM	Antarctica
Psilaster charcoti	PNS	H/SEM	Antarctica
Macroptychaster accrescens	PNS	H/SEM	Antarctica
Porcellanasteridae			
Eremicaster vicinus	PNS	DM	Antarctica
Goniopectinidae			
Ctenodiscus procurator	PNS	DM	Antarctica
NOTOMYOTIDA			
Benthopectinidae			
Cheriaster gerlachei	SPNS	H	Antarctica
VALVATIDA			
Odontasteridae			
Acodontaster conspicuus	FNS	H/SEM	Antarctica
Odontaster validus	FNS	H/SEM	Antarctica
Odontaster meridionalis	FNS	DM	Antarctica
Ganeridae			
Perknaster fuscus antarctica	FNS	H/SEM	Antarctica
Perknaster sp.	FNS	DM	Antarctica
Asterinidae			
Asterina miniata	FNS	H	Pacific N. W.
Tremaster mirabilis	FNS	DM	Antarctica
Goniasteridae			
Mediaster aequalis	FNS	H	Pacific N. W.
Pergamaster synaptorus	FNS	DM	Antarctica
Poranidae			
Dermasterias imbricata	FNS	H	Pacific N. W.
Porania antarctica	FNS	H	Antarctica
VELATIDA			
Solasteridae			
Cuenotaster involutus	SFS	DM	Antarctica
Lophaster stellans	SFS	DM	Antarctica
Solaster regularis	SFS	DM	Antarctica
Solaster stimpsoni	SFS	H	Pacific N. W.
Pterasteridae			
Pteraster affinis	SFS	DM	Antarctica
Pteraster tesselatus	SFS	H	Pacific N. W.
Koremasteridae			
Remaster gourdoni	SFS	DM	Antarctica
SPINULOSIDA			
Echinasteridae			
Henricia sp.	FS	H	Pacific N. W.
FORCIPULATIDA			
Zoroasteridae			
Myxoderma platyacanthum	FS	DM	Monterey Bay
Asteriidae			
Cosmasterias lurida	FS	DM	Antarctica
Diplasterias brucei	FS	H/SEM	Antarctica
Evasterias troschelii	FS	H	Pacific N. W.
Leptasterias hexactis	FS	DM	Pacific N. W.
Notasterias stolophora	FS	DM	Antarctica
Orthasterias koehleri	FS	DM	Pacific N. W.
Pisaster ochraceus	FS	H	Pacific N. W.
Pycnopodia helianthoides	FS	H	Pacific N. W.

TABLE 1. *Continued.*

	Tube-foot morphology	Methods	Geographical location
Labidiasteridae			
Labidiaster annulatus	FS	H	Antarctica
BRISINGIDA			
Brisingidae			
Brisingidensis auchista	SFNS	H	Celebes
Hymenodiscus sp.	SFNS	H	Monterey Bay
Novodiniidae			
Novodinia pacifica	SFNS	H/SEM	Hawaii
Novodinia magister	SFNS	SEM	Indo-Pacific
Novodinia sp.	SFNS	DM	Monterey Bay
Freyellidae			
Freyella insignis	SFNS	H	Monterey Bay

* Species are classified according to Clark and Downey (1992). Key to abbreviations of tube-foot morphology: pointed, non-suckered (PNS), semi-pointed, non-suckered (SPNS), flat-tipped non-suckered (FNS), semi-flat-tipped, suckered (SFS), flat-tipped, suckered (FS), semi-flat-tipped, non-suckered (SFNS). Key to abbreviations of methodology to examine tube-foot morphology: histological sections (H), scanning electron microscopy (SEM), histological sections and scanning electron microscopy (H/SEM), examination using dissecting microscope (DM).

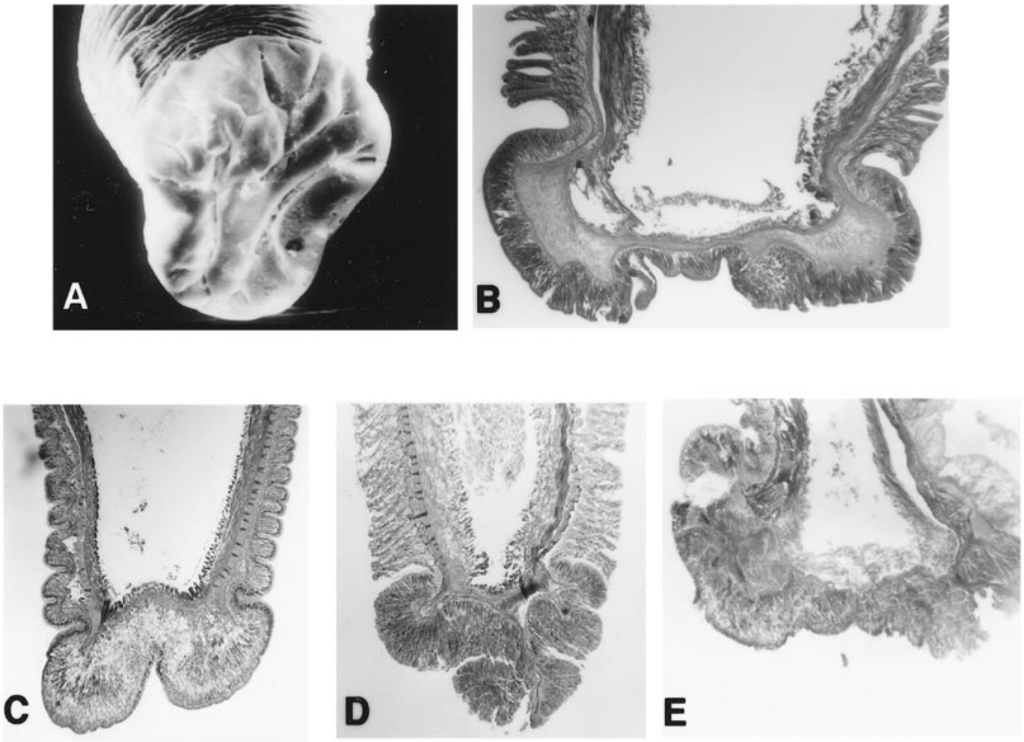


FIG. 2. A. Scanning electron micrograph of the flat-tipped, non-suckered tube foot of *Acodontaster conspicuus.* B. Paraffin section of the flat-tipped, non-suckered tube foot of *Dermasterias imbricata.* C. Paraffin section of the semi-flat-tipped, suckered tube foot of *Pteraster tesselatus.* D. Paraffin section of the semi-pointed, non-suckered tube foot of the deep-sea species *Cheriaster gerlachei.* E. Paraffin section of the semi-flat-tipped, non-suckered tube foot of the deep-sea species *Novodinia pacifica.* Scale bars: A–D, 200 μm; E, 300 μm.

(Fig. 2E). Examinations of the internal morphology of two additional brisingid species revealed that they also lacked a typical flat-tipped, suckered tube foot. Histological sections of the tube feet of *Brisingidensis auchista* and *Freyella insignis* revealed a thin epidermal layer in the central disc and a semi-flat-tipped, non-suckered tube-foot morphology, similar to *N. pacifica.*

By dissecting and compound light microscopy, it was determined that the tube feet of recently metamorphosed juveniles of *Luidia foliolata, Pteraster tesselatus,* and *Pisaster ochraceus* lacked suckers. Juvenile tube feet of all three species were similar in shape and design, with rounded tips, indicating that considerable modification in tube-foot design occurs between the juvenile and adult phases.

DISCUSSION

The current flat-tipped, suckered *versus* pointed, non-suckered model for asteroid tube feet is inadequate. We found three distinct types of tube feet among the representative species examined: flat-tipped suckered, flat-tipped non-suckered, and pointed non-suckered. Each of these three types is further distinguished by variations on the general theme. Among those species with flat-tipped, suckered tube feet, some possessed thin connective and muscular tissues suggesting a weakened ability to grasp the substrate; we classified these as semi-flat-tipped, suckered tube feet. Flat-tipped, non-suckered tube feet were further distinguished in deep-sea species by the lack of branched connective tissues and a flattened tip with a slightly-rounded shape (semi-flat-tipped, non-suckered). This is the first examination of tube-foot morphology among any members of the deep-sea asteroids. Finally, species with pointed, non-suckered tube feet could be divided into those that had tube feet with or without branched connective tissues (Fig. 1A; Paine, 1929). It can be expected that these variations upon tube-foot morphology will have functional consequences.

As described earlier, there has been an on going debate among asteroid phylogeneticists about whether Luidiidae and Astropectinidae (both members of the Order Paxillosida) should be considered ‘‘primitive’’ or ‘‘advanced’’, and this has been based, in part, on differences in tube-foot morphology (Blake, 1987). Our analysis of the tube feet of 45 species of asteroids sheds some light on the question of whether pointed, non-suckered tube feet can be considered ‘‘primitive’’, while flat-tipped, suckered tube feet should be considered ‘‘advanced’’ (Gale, 1987). It is clear from our analysis that it is not possible to simply categorize asteroid tube feet as pointed, non-suckered (primitive) or flat-tipped, suckered (advanced) because of the diversity of tube-foot morphologies that characterize the Asteroidea. The varied tube-foot morphologies that we detected suggest that there has been considerable evolutionary adaptation to a wide variety of substrates and/or feeding habits. While we found pointed, non-suckered tube feet across all representatives we examined from the Paxillosida, we also detected semi-pointed, non-suckered tube feet among representatives of the deep-sea order Notomyotida. This suggests that tube-foot morphology should be viewed with caution when used as a measure of which asteroid taxa should be considered ‘‘primitive’’ or ‘‘advanced.’’

In a further analysis of the question of whether paxillosids are primitive, Blake (1988) argues that pointed, non-suckered tube feet are, in fact, advanced rather than primitive. This was based on a study of juvenile tube-foot morphology in *Astropecten scoparius* (Oguro *et al.,* 1976) which ‘‘suggested’’ that newly-metamorphosed juveniles possessed suckers on their tube feet while adults lacked suckered tube feet. Blake (1988) surmised that this example of potential phylogenetic recapitulation in the ontogeny of the morphology of juvenile tube feet supported his argument that the paxillosidans were indeed an advanced group. In contrast, our evaluation of the tube feet of newly-metamorphosed juveniles from three species representative of three orders, revealed an absence of suckers on juvenile tube feet. Our findings, in addition to other studies showing scanning electron micrographs of juveniles of *Asterina pseudoexigua pacifica, Patiriella exigua, Patiriella regularis, Patiriella vivipa-*

ra, *Pseudarchaster pareli*, and *Pteraster tesselatus* (Komatsu *et al.*, 1990; Chia *et al.*, 1993; Byrne, 1995; Byrne and Barker, 1991; Byrne and Cerra, 1996), clearly indicate that juveniles do not possess suckers on their tube feet. It is significant that the tube-foot morphology of all of the juvenile species examined to date, including those in the present study, are similar in design, with non-suckered, rounded, knob-like tips. This indicates that considerable morphological change occurs in the post-juvenile tube foot. Particularly-dramatic changes occur in those species whose tube feet ultimately possess suckers as adults, where the central portion of the adult tube-foot disc becomes markedly concave (M. S. Vickery, unpublished observations).

An examination of the major classification schemes (excluding more recent phylogenetic trees based on molecular data) for the Asteroidea reveals a consistent progression from the primitive paxillosids to the more advanced forcipulatids (Spencer and Wright, 1966; Downey, 1973; Hayashi, 1973; Gale, 1987; Clark and Downey, 1992). If one accepts this as dogma, then it follows that pointed, non-suckered tube feet might be considered by association to be ''primitive,'' while flat-tipped, suckered tube feet might be construed as ''advanced.'' This theme has been perpetuated in the literature and contested by Blake (1987, 1990) who argued that morphological diversity in the Asteroidea is a result of adaptation to habitat and that, specifically, tube-foot morphology is an adaptation to varying types of substrata. Our study demonstrates that a consistent relationship exists between tube-foot morphotype and taxonomic order (see Table 1), however, the variety of tube-foot morphologies observed suggests plasticity in tube-foot design that might reflect adaptations to variable environments. Further, more detailed, biomechanical and histological studies using additional species from each order and diverse habitats may shed more light on this issue. The present study suggests that tube-foot morphology may be useful as a taxonomic character at the ordinal level.

ACKNOWLEDGMENTS

We would like to thank Dan Blake and Dan Janies for inviting us to participate in this symposium. We especially thank Dan Blake for his generous assistance and encouragement. Valuable specimens were provided to us by Cynthia Ahearn of the Smithsonian Institution, Chris Mah of the California Academy of Sciences, and Richard Strathmann of Friday Harbor Laboratories. We also thank Robert Angus, Asim Bej, Thane Wibbels, and Michael Vickery for their support. Daniel Jones, Chair of the Department of Biology at The University of Alabama at Birmingham, kindly provided facilities and funding for this research. Several Antarctic specimens were collected with support provided by NSF grants #OPP-9530753 to J. B. McClintock and C. D. Amsler and #OPP-9526610 to B. J. Baker.

REFERENCES

Amemiya, S. and R. B. Emlet. 1992. The development and larval form of an echinothurioid echinoid, *Asthenosoma ijimai*, revised. Biol. Bull., 182:15–30.

Blake, D. B. 1972. Sea star Platasterias: Ossicle morphology and taxonomic position. Science 176: 306–307.

Blake, D. B. 1982. Somasteroidea, Asteroidea, and the affinities of *Luidia* (*Platasteridas*) *latiradiata*. Palaeontology 25:167–191.

Blake, D. B. 1987. A classification and phylogeny of post-Paleozoic sea stars (Asteroidea: Echinodermata). J. Nat. Hist. 21:481–528.

Blake, D. B. 1988. Paxillosidans are not primitive asteroids; a hypothesis based on functional considerations. *In* R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley (eds.), *Echinoderm biology*, pp. 309–314. A. A. Balkema, Rotterdam.

Blake, D. B. 1989. Asteroidea: Functional morphology, classification and phylogeny. *In* M. Jangoux and J. M. Lawrence (eds.), *Echinoderm studies*, pp. 170–223. A. A. Balkema, Rotterdam.

Blake, D. B. 1990. Adaptive zones of the class Asteroidea (Echinodermata). Bull. Mar. Sci. 46:701–718.

Byrne, M. 1995. Changes in larval morphology in the evolution of benthic development by *Patiriella exigua* (Asteroidea: Asterinidae), a comparison with the larvae of *Patiriella* species with planktonic development. Biol. Bull. 188:293–305.

Byrne, M. and M. F. Barker. 1991. Embryogenesis and larval development of the asteroid *Patiriella regularis* viewed by light and scanning electron microscopy. Biol. Bull., 180:332–345.

Byrne, M. and A. Cerra. 1996. Evolution of intragonadal development in the diminutive asterinid sea stars *Patiriella vivipara* and *P. parvivipara* with an overview of development in the Asterinidae. Biol. Bull. 191:17–26.

Chia, F. S., C. Oguro and M. Komatsu. 1993. Sea-star (asteroid) development. Oceanogr. Mar. Biol. Annu. Rev. 31:223–257.

Clark, A. M. and M. E. Downey. 1992. *Starfishes of the Atlantic.* Chapman and Hall, New York.

Downey, M. E. 1973. Starfishes from the Caribbean and the Gulf of Mexico. Smithsonian Contr. Zool. 126:1–158.

Engster, M. S. and S. C. Brown. 1972. Histology and ultrastructure of the tube foot epithelium in the phanerozonian starfish, *Astropecten.* Tissue & Cell 4:503–518.

Fell, H. B. 1963. The phylogeny of sea-stars. Phil. Trans. R. Soc. (B) 246:381–435.

Flammang, P. 1995*a.* Fine structure of the podia in three species of paxillosid asteroids of the genus *Luidia* (Echinodermata). Belg. J. Zool. 125:125–134.

Flammang, P. 1995*b.* Adhesion in echinoderms. *In* M. Jangoux and J. M. Lawrence (eds.), *Echinoderm studies* 5:1–60. A. A. Balkema, Rotterdam.

Flammang, P., S. Demeulenaere. and M. Jangoux. 1994. The role of podial secretions in adhesion in two species of sea stars (Echinodermata). Biol. Bull. 187:35–47.

Gale, A. S. 1987. Phylogeny and classification of the Asteroidea (Echinodermata). Zool. J. Linn. Soc. 89:107–132.

Hayashi, R. 1973. *Asteroids-Sagami Bay.* Hoikusha, Japan.

Hermans, C. O. 1983. The duo-gland adhesive system. Oceanogr. Mar. Biol. Annu. Rev. 21:283–339.

Hyman, L. H. 1955. *The Invertebrates,* Vol. 5, *Echinodermata.* McGraw-Hill Book Company, New York.

Humason, G. L. 1997. *Animal tissue techniques.* W. H. Freeman, San Francisco.

Komatsu, M., Y. T. Kano, and C. Oguro. 1990. Development of a true ovoviviparous sea star, *Asterina pseudoexigua pacifica* Hayashi. Biol. Bull. 179:254–263.

Knott, K. E. and G. A. Wray. 2000. Controversy and consensus in asteroid systematics: New insights to ordinal. Amer. Zool. 40:382–392.

Lafay, B., A. B. Smith and R. Christen. 1995. A combined morphological and molecular approach to the phylogeny of asteroids (Asteroidea: Echinodermata). Syst. Biol. 44:190–208.

McCurley, R. S. and W. M. Kier. 1995. The functional morphology of starfish tube feet: The role of a crossed-fiber helical array in movement. Biol. Bull. 188:197–209.

McEdward, L. R. 1992. Morphology and development of a unique type of pelagic larva in the starfish *Pteraster tesselatus* (Echinodermata: Asteroidea). Biol. Bull. 182:177–187.

Oguro, C., M. Komatsu, and Y. T. Kano. 1976. Development and metamorphosis of the sea-star *Astropecten scoparius* Valenciennes. Biol. Bull. 151: 560–573.

Paine, V. L. 1926. Adhesion of the tube feet in starfishes. J. Exp. Zool. 45: 361–366.

Paine, V. L. 1929. The tube feet of starfishes as autonomous organs. Am. Nat. 689:517–529.

Smith, J. E. 1937. The structure and function of the tube feet in certain echinoderms. J. Mar. Biol. Ass. U.K. 22:345–357.

Smith, J. E. 1947. The activities of tube feet of *Asterias rubens* L. I. The mechanics of movement and of posture. Quart. J. Microsc. Sci. 88:1–14.

Souza Santos, H. 1966. Ultrastructure of a mucous gland cell found in the tube feet of the starfish *Asterina stellifera.* Experientia 22:812–814.

Souza Santos, H. and W. Silva Sasso. 1968. Morphological and histochemical studies on the secretory glands of starfish tube feet. Acta Anat. 69:41–51.

Souza Santos, H. and W. Silva Sasso. 1970. Ultrastructural and histochemical studies on the epithelium revestment layer in the tube feet of the starfish *Asterina stellifera.* J. Morphol. 130:287–296.

Souza Santos, H. and W. Silva Sasso. 1974. Ultrastructural and histochemical observations of the external epithelium of echinoderm tube feet. Acta. Anat. 88:22–33.

Spencer, W. K. and C. W. Wright. 1966. Asterozoans. *In* R. C. Moore (ed.), *Treatise on Invertebrate Paleontology,* part U, Vol. 1, *Echinodermata,* pp. 4–107. Geol. Soc. of American, Kansas University Press, Lawrence.

Strathmann, M. F. 1987. *Reproduction and development of marine invertebrates of the Northern Pacific coast.* University of Washington Press, Seattle.

Thomas, L. A. and C. O. Hermans. 1985. Adhesive interactions between the tube feet of a starfish, *Leptasterias hexactis,* and substrata. Biol. Bull. 169:675–688.

Wada, H., M. Komatsu, and N. Satoh. 1996. Mitochondrial rDNA phylogeny of the Asteroidea suggests the primitiveness of the Paxillosida. Mol. Phylog. Evol. 6:97–106.