



Detecting invasions of marine organisms: kamptozoan case histories

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Abstract

Detecting marine invasions can be challenging, especially for lesser-known taxa, and requires (a) thorough field surveys of the region of interest for members of the taxon, (b) systematic analyses to identify all species found, (c) literature searches for the worldwide distribution of these species and for previous records of the taxon in this region, and (d) application of rigorous criteria to assess whether each species found is native or introduced. We carried out these steps in order to detect and document kamptozoan (entoproct) invasions on the American mid-Atlantic coast. We report on the occurrence of two colonial kamptozoans (*Barentsia benedeni*, *Loxosomatoides laevis*) in Chesapeake Bay (Maryland and Virginia, USA). On the American Atlantic coast, *B. benedeni* had previously only been reported from Massachusetts, although this species has a worldwide distribution in bays and harbors. The genus *Loxosomatoides* had not previously been reported from North America and *L. laevis* was known only from India. Since the genus *Loxosomatoides* was very poorly characterized, we briefly review all four of its species, which differ only slightly from each other. We have also synonymized *L. japonicum* with *L. laevis*. We did not find any of the kamptozoan species previously recorded in surveys of Chesapeake Bay and the American Atlantic coast. This is the first detailed consideration of anthropogenic influences on kamptozoan distributions, and we emphasize that most kamptozoan species are cryptogenic pending further investigation.

Introduction

Detection of recent invasions of new regions by species from elsewhere is straightforward only for taxa for which there are accurate systematic descriptions and extensive and reliable historical records of distributions. Among marine invertebrates, such groups (e.g., large crabs, snails, and sea stars) are in the minority – most species of marine animals are small and inconspicuous, and have been largely overlooked. However, knowledge of the diversity and distribution of this overlooked majority is essential for detecting community changes over time. Moreover, even tiny and obscure organisms may nonetheless be abundant,

and have large impacts on their physical environments and biological communities.

How can we detect invasions by lesser-known groups of tiny marine organisms? Collection of these organisms often takes special care and methods. Identification of the species located usually requires thorough taxonomic analyses (with the incidental benefit of increasing our understanding of the systematics of the group). Historical records are limited, and not necessarily reliable. To determine whether the distribution of the species has been affected by anthropogenic influences, knowledge of its ecology (e.g., microhabitat, association with known introductions, salinity tolerances) and life history (especially duration of the larval

period and natural dispersal mechanisms) is required, but such information is not usually available in the literature.

Despite these challenges, detection of marine invasions can be readily accomplished. By carefully attending to the ecology and systematics of the species involved, we were able to document the recent invasion of Chesapeake Bay by two species of kamptozoans (entoprocts). The approach we took is applicable to other poorly known taxa of marine organisms.

Kamptozoans constitute a phylum of aquatic, sessile, suspension-feeding invertebrates. Due to their small size (zooids range from less than a millimeter to a few centimeters in height), they are easily overlooked in general surveys. Kamptozoan species are found in all the world's oceans, as well as in estuarine and freshwater habitats, and are sometimes extremely abundant members of the fouling community.

Colonial kamptozoans have only rarely been reported from the Atlantic coast of North America (Table 1). One member of the family Pedicellinidae

(*Pedicellina cernua*) and six members of the Barentsiidae (all in the genus *Barentsia*) are known from this coast. In Chesapeake Bay, previous records (Osburn 1944; Wass 1972) document the occurrence of *P. cernua*, *B. discreta*, *B. gracilis*, and *B. laxa*. Based on our survey of the kamptozoan fauna of Chesapeake Bay, we have added a new barentsiid, *Barentsia benedeni*, to this list. Along the American Atlantic coast, this species was previously known only from Massachusetts. We also found a second kamptozoan species, the pedicellinid *Loxosomatoides laevis*, in Chesapeake Bay. The genus *Loxosomatoides* was not previously known to occur in North America.

In the fouling community that included these kamptozoans, the dominant species occupying primary substrate were apparently introduced to this area by anthropogenic means (Von Holle and Ruiz, in prep.). We hypothesize that *B. benedeni* and *L. laevis* are also exotic invaders, and test this hypothesis (vs. the null hypothesis that they are native) using a rigorous set of criteria (Chapman and Carlton 1994). Lindroth

Table 1. Records of colonial kamptozoans on the Atlantic Coast of North America.

| | | |
|------------------------------|------------------------------|---|
| Pedicellinidae | | |
| <i>Loxosomatoides laevis</i> | Wasson et al. (this paper) | Chesapeake Bay, MD & VA |
| <i>Pedicellina cernua</i> | Dublin (1905) | Cold Spring Harbor, Long Island, NY |
| | Osburn (1912) | Beaufort, NC; Tortugas, FL |
| | Osburn (1944) | Chesapeake Bay, VA; Chincoteague Bay, VA |
| | Maturo (1957, 1959) | Beaufort, NC |
| | Wass (1972) | Chesapeake Bay, VA |
| | Calder and Maturo (1978) | Various sites, SC |
| Barentsiidae | | |
| <i>Barentsia benedeni</i> | Jebram and Everitt (1982) | Lagoon Pond, Martha's Vineyard, MA |
| | Nielsen (1989) | Cape Cod, MA |
| | Wasson et al. (this paper) | Chesapeake Bay, MD & VA |
| <i>B. discreta</i> | Osburn (1912) | Woods Hole, MA; Beaufort, NC; Tortugas, FL |
| | Osburn (1944) | Chesapeake Bay, MD |
| | Maturo (1957) | Beaufort, NC |
| | Calder and Maturo (1978) | Charleston Harbor, SC |
| <i>B. gracilis</i> | Osburn (1944) | Chesapeake Bay, VA |
| <i>B. laxa</i> ^a | Osburn (1944) | Chesapeake Bay, VA; Chincoteague Bay, MD & VA; Nantucket Island, MA |
| | Rogick (1948) | Woods Hole, MA |
| | Maturo (1957, 1959) | Beaufort, NC |
| | Calder and Maturo (1978) | Various sites, SC |
| | Osburn (1912) | Woods Hole, MA |
| <i>B. major</i> ^b | Osburn (1912) | Woods Hole, MA |
| <i>B. minuta</i> | Winston and Håkansson (1986) | Capron Shoal, FL |

^aThe material identified as *B. laxa* Kirkpatrick, 1890 probably consists of *B. elongata* Jullien & Calvet 1903. *B. laxa* appears to be native to Indopacific, from which it was first described.

^bThe status of *B. major* Hincks, 1888 is very uncertain. Osburn's identification may refer to *B. elongata* Jullien & Calvet 1903.

(1957) was one of the first to propose general criteria for the recognition of introduced species. He focused on terrestrial species, and presented five criteria. Carlton (1979a) expanded these criteria into six sets, divided into 13 categories. Chapman (1988) and Chapman and Carlton (1991, 1994) further developed these criteria, and applied them to some temperate amphipod and isopod crustaceans. To our knowledge, our use of these criteria represents their first application to colonial taxa.

Materials and methods

Field surveys

Our characterization of Chesapeake Bay kamptozoans was part of a larger investigation of the Chesapeake Bay fouling community (G. Ruiz et al., unpublished data). Data from two separate studies were used to identify and quantify the distribution of Chesapeake Bay kamptozoans. The first was a study of the fouling community composition of Chesapeake Bay, designed to identify and track the introduction of fouling organisms (G. Ruiz et al., unpublished data). There were 10 study areas, five clustered in northern Chesapeake Bay around the port of Baltimore, MD and five clustered in southern Chesapeake Bay around the port of Norfolk, VA. Five sites at approximately 2 km intervals were sampled within each area. (The exact location of these sites is available upon request from the authors.) At each site, four settlement plates (10 × 10 cm) were hung about 1 m below mean low water. Plates were set out in March and June 1995, and in June 1996 and 1997. They were collected in July and October–November of 1995, August–September 1996, and October 1997. All foulers that had settled on the plates were identified with light microscopy. Number of individuals (zooids, for colonial species) per species were estimated on the lower surface of one plate from each site.

The second study from which we obtained data on kamptozoans was a quantitative investigation of the effect of an introduced hydrozoan, *Cordylophora caspia*, on the community structure of the Chesapeake Bay fouling community (Von Holle and Ruiz, in prep.). Twenty-four wooden plates (25 × 25 cm) were immersed 2 m below mean low tide at three sites near Baltimore Harbor. The plates were deployed in June 1995 and collected twice, in July and August 1995. All

foulers that had settled on the plates were identified with light microscopy. Percent cover by each species was estimated on the lower surface of each plate.

Systematics

Vouchers were taken from settlement plates from both studies described above, and the specimens preserved in 4% buffered formalin solution. We carefully examined and photographed these specimens using light microscopy. For 20 zooids of each species, measurements were taken with an ocular micrometer; the average and standard deviation for each measured parameter was calculated. Colonies from Chesapeake Bay were also cultured in the laboratory; they grew well at 18 °C, salinity approximately 20 parts per thousand, fed twice weekly about 10 cells/μl of a mixture of phytoplankton (*Dunaliella*, *Rhodomonas*, and *Isochrysis*) cultures.

Since the genus *Barentsia* has been fairly well characterized in the literature, identification of one kamptozoan species as *B. benedeni* was straightforward. However, the genus *Loxosomatoides* is poorly known, and identification was more difficult. To correctly identify the *Loxosomatoides* species, we requested type material of all previously described species in the genus.

Criteria for introduced species

To test the hypothesis that the kamptozoans were introduced to Chesapeake Bay rather than native, we assessed how well they met nine criteria presented by Chapman and Carlton (1994): (1) appearance in local regions where not found previously; (2) expansion of local range subsequent to first appearance; (3) access to human mechanism(s) of dispersal; (4) association with known introductions; (5) prevalence in or restriction to artificial or altered environments; (6) discontinuous or restricted regional distribution; (7) disjunct global distribution; (8) insufficient life history adaptations for global dispersal, and (9) exotic evolutionary origin.

Results

The four kamptozoan species reported by Osburn (1944) from the mouth of Chesapeake Bay were not found despite our extensive three-year survey in many

regions, including higher salinity sites near the mouth of the Bay. However, two previously unreported kamptozoan species were common on our settlement plates.

Barentsia benedeni (Foettinger, 1887)

One of the kamptozoan species collected in Chesapeake Bay was readily identified as *Barentsia benedeni*. The Chesapeake zooids (Figure 1) closely match a recent re-description (Wasson 1997) of *B. benedeni*, in quantitative measurements and qualitative traits, and so a detailed description is not given here. The zooids have a characteristic segmented appearance, consisting of



Figure 1. *Barentsia benedeni* zooids from Chesapeake Bay. Scale bar = 150 μ m.

many nodes and rods. The upper nodes are sometimes urn-shaped, tapering basally. The basal nodes are packed with conspicuous storage cells. The rods lack pores, and are often extremely short, such that nodes directly abut each other like beads on a string. There is a thick cuticular septum at the stalk–calyx junction. The calyx is oriented slightly obliquely, tilted towards the oral side. This suite of traits exhibited by the Chesapeake zooids is unique to *B. benedeni*; there is no other species with which the zooids could be confused.

The Chesapeake *B. benedeni* zooids consisted of large, well-developed zooids in lush colonies. No hibernacula were visible in the colonies collected; hibernaculum production may not occur during spring and summer in this population. We have deposited a voucher of this species from Chesapeake Bay in the British Natural History Museum (1998.1.14.1).

B. benedeni was found on settlement plates at six sites and during four collection periods in the first study. In northern Chesapeake Bay, it was collected at one site near the Severn River in summer 1995, and at two sites near Baltimore Harbor in fall 1997. In the southern Bay, it was collected at two sites in Mobjack Bay in spring 1995 and at one site near Norfolk Harbor in summer 1996. *B. benedeni* was not found on any of the 24 plates deployed near Baltimore Harbor during the second study. Salinity ranged from 14 to 21 parts per thousand and temperature ranged 13 °C to 30 °C at these sites when kamptozoans were present. Three of the settlement plates on which *B. benedeni* was found had high (51–100) numbers of zooids, while the fourth had a moderate (11–50) number. *B. benedeni* was found intertwined in the fouling matrix provided by other abundant fouling organisms, including the barnacle *Balanus improvisus*, the bryozoan *Conopeum* sp., the scyphozoan *Chrysaora quinquecirrha*, the polychaetes *Demonax* sp., *Hydroides* sp., *Polydora cornuta*, *Sabella macrophthalma* and their associated tubes, and the tunicate *Molgula manhattensis*. The protozoan *Metafolliculina* sp. was found on top of many species listed above as well as on the primary substrate. Common mobile species on the plates included the amphipod *Corophium* sp., various harpacticoid copepods including *Parategastes sphaericus*, and the flatworm *Stylochus ellipticus*.

Loxosomatoides laevis Annandale, 1915

The second kamptozoan species collected in Chesapeake Bay was identified as *L. laevis* Annandale,

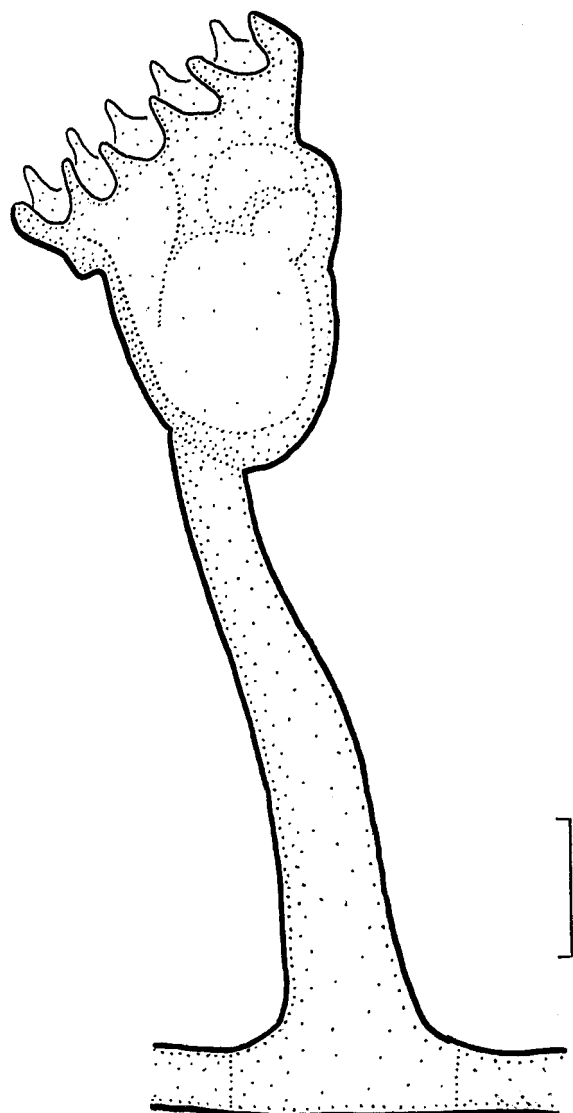


Figure 2. *Loxosomatoides laevis*. Diagram based on camera lucida drawing of a live, semi-contracted zooid from Chesapeake Bay. Scale bar = 100 μm .

1915. Our specimens (Figures 2 and 3) match the original species description, except that our zooids were smaller, and had less pronounced cuticular shields. In order to provide a thorough justification of our identification of this poorly known species, a taxonomic description of material from Chesapeake Bay and a systematic review of the genus is provided in Appendix 1.

L. laevis was detected at 11 different sites, and during all five collection periods in the first study. In northern

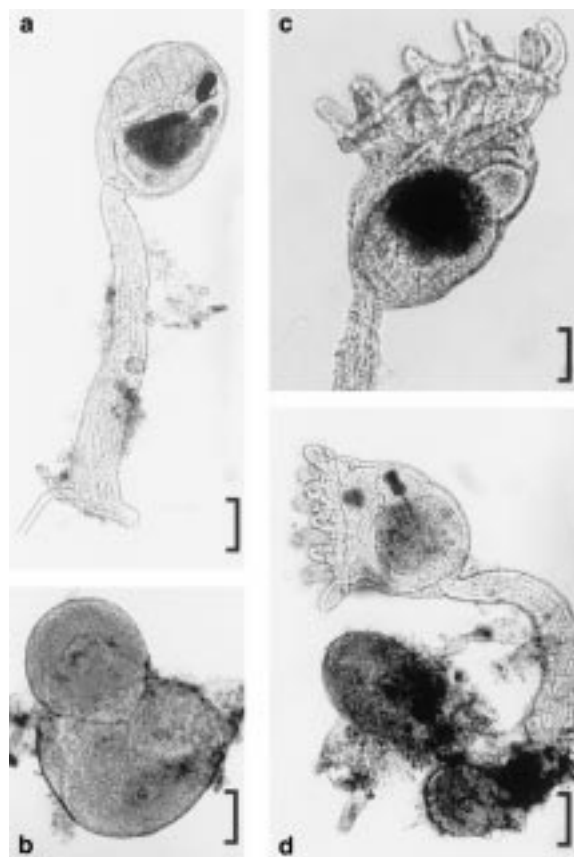


Figure 3. *Loxosomatoides laevis* from Chesapeake Bay. a: Contracted zooid, scale bar = 100 μm ; b: two hibernacula, scale bar = 50 μm ; c: semi-contracted calyx, scale bar = 50 μm ; d: semi-contracted zooid, scale bar = 100 μm .

Chesapeake Bay, it was found at two sites near the Rhode River in spring 1995 and fall 1997, at two sites near the Chester River in spring 1995, and at five sites near Baltimore Harbor in summer 1995, fall 1995, summer 1996, and fall 1997. In the southern Bay, it was found at two sites near Norfolk Harbor in summer 1996 and fall 1997. At sites and times of collection, the salinity ranged from 4.7 to 14.8 parts per thousand, and temperature ranged from 23 °C to 28.1 °C. Zooid numbers ranged from moderate (11–50) to very high (> 1000) on the settlement plates. *L. laevis* occurred on 22 of the 24 plates deployed near Baltimore Harbor in the second study, and increased in abundance in the four weeks between sampling intervals. The average \pm standard deviation of percent cover of the species on the plates was 0.03 ± 0.03 in July, but had increased to 2.54 ± 0.25 in August. This species was

found in the fouling matrix of primary space occupiers, including the hydroid *Cordylophora caspia*, various bivalves, and the bryozoan *Victorella pavidata*. The protozoans *Metafolliculina* sp., *Stentor* sp., *Vorticella* sp., and *Zoothamnium* sp. were found growing on these organisms as well as on the primary substrate. Common mobile species included various flatworms, harpacticoid copepods, and the nudibranch *Tenellia adspersa*.

Discussion

Predicted attributes of anthropogenically introduced species

Both *B. benedeni* and *L. laevis* from Chesapeake Bay display many of the nine predicted attributes (Chapman and Carlton 1991, 1994) of anthropogenically introduced species.

Attribute 1: Appearance in local regions where not found previously. This attribute could be readily assessed because there are reliable historical surveys of the regional fauna; both kamptozoans met this criterion. Osburn (1944) did not find either *B. benedeni* or *L. laevis* in his survey of kamptozoans of Chesapeake Bay (Table 1); he found various kamptozoans near the mouth of the bay, but found none in the upper, more brackish regions. Other surveys of Atlantic coast kamptozoans (Table 1) did not document the presence of these two species, either (Osburn 1912; Mauro 1957, 1959; Calder and Mauro 1978). Jebram and Everitt (1982) and Nielsen (1989) reported the presence of *B. benedeni* in Massachusetts; theirs are the only other report of this species on the Atlantic coast of North America (Table 2). No species in the genus *Loxosomatoides* was reported from this continent before our study (Table 3).

Attribute 2: Expansion of local range subsequent to first appearance. This criterion could not be adequately assessed because ours is the first report of these two species in Chesapeake Bay; we have no information on the exact location at which they first appeared nor any subsequent expansions of their local ranges.

Attribute 3: Access to human mechanism(s) of dispersal. Both of these kamptozoan species have access to human mechanisms of dispersal, locally in Chesapeake Bay and in other parts of their global distributions. We found both species in major ports in Chesapeake Bay.

B. benedeni is known exclusively from bays and harbors around the world (Carlton 1979a; Emschermann 1994; Wasson 1997). *L. laevis* (and its congeners) is also known only from bays and harbors. Both species thus are found currently and historically in close association with ship traffic, one major human mechanism of dispersal for marine species. Their ability to settle and grow rapidly on panels (Rao et al. 1988; this study) would allow both species to attach to vessels in the short amount of time that the ships are in port. The capacity of both species to form hibernacula would enable them to withstand the stresses of long oceanic voyages. Ship-fouling (externally on the hull or internally in the sea chest and pipes) has been the most ubiquitous human mechanism of transoceanic and intercontinental dispersal of marine organisms during the last several centuries (Scheltema and Carlton 1984; Carlton 1985). Ballast water dumping by large international vessels is another possible vector for these kamptozoans. Fragments of adult colonies could be transported in ballast water from one port to another. Larval transport in ballast tanks is less plausible, since colonial kamptozoans have short-lived larvae. In an intensive sampling of ballast water of ships travelling from Japan to Oregon, Carlton and Geller (1993) did not positively identify any kamptozoan larvae or adults, but larvae may be difficult to recognize, and adults may be transported only occasionally during seasonal peaks in density when fragments are likely to be floating in harbor waters.

Transport and culturing of exotic oysters is another major human dispersal mechanism (Carlton 1992a,b). Both of these kamptozoan species are known to grow in oyster beds. The type colony of *B. benedeni* was collected in 1885 on a Belgian oyster bed (Foettinger 1887) and other *Barentsia* species are often reported on oysters (e.g., Korryng 1951). *L. laevis* was collected growing with oysters in Visakhapatnam harbor, India (Rao et al. 1988).

Attribute 4: Association with known introductions. Both locally in Chesapeake Bay and elsewhere in the world, *B. benedeni* and *L. laevis* grow in a community of introduced fouling organisms. As described above, we found them in Chesapeake Bay with non-native species, especially the bryozoan *V. pavidata* and the hydroid *C. caspia*. The first record of *B. benedeni* on the Atlantic coast (Jebram and Everitt 1982) lists this species as part of the community of what we here recognize as introduced victorellids. In Lake

Table 2. The distribution of *Barentsia benedeni*.

| | |
|--|--|
| <i>Northern Eurasia (North Atlantic and Baltic Coasts)</i> | |
| Oostende, Belgium | Foettinger (1887) |
| Osterschelde & Westerschelde, The Netherlands | Emschermann (1994) |
| Rendsburg (Nord-Ostsee Kanal), Germany | Emschermann (1994) |
| Western Baltic Sea | Nielsen (1989) |
| Hull, England | Ritchie (1911) |
| Port Erin, Isle of Man, Great Britain | Emschermann (1994) |
| Tynemouth, England | Emschermann (1994) |
| <i>Southern Eurasia (Black, Caspian, Adriatic, and Mediterranean Seas)</i> | |
| Sebastopol Bay (Black Sea), Crimean Peninsula, Ukraine | Nasanov (1926); Zernov (1913) |
| Varna (Black Sea), Bulgaria | Valkanov (1951) |
| Istanbul Bogazi (off Black Sea), Turkey | Valkanov (1951) |
| Krasnovodsk Bay (Caspian Sea), Turkmenistan | Zevina and Kuznetsova (1965) |
| Po River Delta (Adriatic Sea), Italy | Pisano (1980) |
| Rovinj (Adriatic Sea), Croatia | Emschermann (1994) |
| Banyuls-sur-Mer (Mediterranean Sea), France | Emschermann (1994) |
| <i>Western North America (Pacific Coast)</i> | |
| San Francisco Bay, CA | Craig (1929); Mariscal (1965); Carlton (1979a,b); Cohen and Carlton (1995); Wasson (1997) |
| Salton Sea, CA | Jebram and Everitt (1982) |
| Coos Bay, OR | Hewitt (1993); Wasson (1997) |
| Puget Sound, WA | Mills et al. (2000) |
| <i>Eastern North America (Atlantic Coast)</i> | |
| Martha's Vineyard, MA | Jebram and Everitt (1982) |
| Cape Cod, MA | Nielsen (1989) |
| Chesapeake Bay, MD & VA | Wasson et al. (this paper) |
| <i>Japan (Pacific Coast)</i> | |
| Matsushima Bay, Honshu | Toriumi (1944, 1951) |
| <i>Australia (Pacific Coast)</i> | |
| Port Adelaide, South Australia | Wasson and Shepherd (1997) |
| Port Kembla, New South Wales | |

Merritt, Oakland (San Francisco Bay) California, *B. benedeni* was found with introduced bryozoans in the genera *Conopeum* and *Victorella* (Carlton 1979b). *L. laevis* was collected in Visakhapatnam harbor, India, with potentially introduced fouling species including the bryozoan *Bowerbankia gracilis*, the hydroid *Obelia* sp., and the worm-snail *Serpula vermicularis* (Rao et al. 1988).

Attribute 5: Prevalence in or restriction to artificial or altered environment(s). Both species were collected in Chesapeake Bay on artificial settlement panels in an otherwise mostly soft-bottom habitat, and both were abundant around the two largest ports in the bay. *B. benedeni* occurs on harbor piers, pilings, and floats around the world (Carlton 1979a; Emschermann 1994;

Wasson 1997). Rao et al. (1988) found *L. laevis* on glass panels and harbor structures in India.

Attribute 6: Discontinuous or restricted regional distribution. Too little is known about the regional distribution of either species on the Atlantic coast (Tables 2 and 3) to make a satisfactory assessment. Their known distributions on this coast are disjunct, with known occurrences only in bays associated with ports, but no thorough surveys have been carried out at sites between known occurrences.

Attribute 7: Disjunct global distribution. Both species occur in multiple regions of the world (Tables 2 and 3). It seems unlikely that the distribution of these species is continuous; this would require extension into polar seas

mechanisms and is not associated with other invaders. *B. hildegardae* is sometimes encountered on floats, and thus tenuously meets the criteria for attributes 3, 4, and 5. The two northeastern Pacific species have short-lived larvae and thus meet the criterion for attribute 8; this attribute is not meaningful for determining whether a particular kamptozoan is invasive, since most kamptozoans have very limited dispersal. The evolutionary origins of the species are unknown, so attribute 9 could not be assessed.

B. benedeni and *L. laevis* in Chesapeake Bay thus display generalized attributes of invasive species, and differ in significant ways, mostly regarding their distribution, from kamptozoans presumed to be native. We therefore conclude that both of these species represent anthropogenic introductions to Chesapeake Bay.

Biogeography of B. benedeni and L. laevis

B. benedeni has been reported from selected bays and harbors in Europe, Japan, Australia, and North America (Table 2). Since its colonies are small and inconspicuous, the species has almost certainly been overlooked in many other bays and harbors within its known continental range; it may also be present but as yet unnoticed in other areas, such as South America, Africa, and Asia. Furthermore, it will probably continue to spread to new areas in the future. This species' tolerance of a wide range of salinity and temperature conditions has apparently enabled it to survive in many novel regions to which it has been transported. However, the species seems to be found almost exclusively in disturbed habitats, often in brackish water. Currently we have no evidence whether pre- or post-settlement factors limit its distribution to such habitats.

While *B. benedeni* was probably introduced to most parts of its current distribution by anthropogenic means, namely ship-fouling and oyster-culturing (Carlton 1975, 1979a,b; Cohen and Carlton 1995), it must be native somewhere in the world. Where did this species occur naturally, centuries ago? This question cannot be answered given our very limited knowledge about the past and present distribution of this species. It was first reported from northern Europe, then from southern Europe, western North America, Japan, eastern North America, and Australia, in turn (Table 2). Based on this pattern, Carlton (1979a) suggested that the species was native to Europe. However, except for the American Atlantic coast none of the regions in which *B. benedeni* is now

known to be present were thoroughly surveyed prior to the first report of the species. Its apparent spread from Europe may simply represent the order in which the kamptozoan fauna of the regions was studied.

We do have evidence that *B. benedeni* was introduced fairly recently to eastern North America, since the kamptozoan fauna of the Atlantic coast, including Chesapeake Bay, had been surveyed by Osburn (1912, 1944) and others (Table 1) and this species was not found until 1982 (Jebram and Everitt, 1982). By far the most common anthropogenic transport mechanism for invertebrates into Chesapeake Bay is international shipping, and the majority of current ship traffic entering Chesapeake Bay is from Europe (Carlton et al. 1995). Therefore, it is likely the Chesapeake populations of *B. benedeni* are derived from European populations transported via ship-fouling. However, other vectors and other source populations cannot be excluded. Ships arrive from other destinations, and oysters have been brought into Chesapeake Bay from the American Pacific coast and from elsewhere (Mann 1979; Mann et al. 1991; Carlton 1992a,b; Lipton et al. 1992). Since *B. benedeni* is known to grow on them, planting of imported oysters is a plausible mechanism of introduction, through a much less frequent event than arrival of ships from distant waters.

L. laevis is known only from India, Japan, and Chesapeake Bay (Table 3). The closely related species *L. athleticus* and *L. colonialis* are known from Thailand and India, respectively (Table 3). The kamptozoan fauna of Asia (except for Japan) has never been thoroughly surveyed, so it is difficult to determine the nature of the regional distribution of these species. They were collected from brackish bays and harbors, and may be limited by pre- or post-settlement factors to such environments.

Given the current distribution of these *Loxosomatoides* species (Table 3), it seems likely that they are native to Asia, and that *L. laevis* was introduced from somewhere in Asia to Chesapeake Bay sometime after 1944, when Osburn carried out his survey of the region. As discussed in Appendix 1, Chesapeake Bay *Loxosomatoides* zooids are morphologically more similar to Japanese than to Indian material. We therefore suggest that *Loxosomatoides* arrived in Chesapeake Bay on ships travelling from Japan.

If *L. laevis* has been transported from Asia to eastern North America, why has this species not also been introduced to other regions around the world? Of course, it may occur unrecorded in regions that

have not been surveyed for kamptozoans. However, the species was not detected in recent surveys of northern Europe (Nielsen 1989; Emschermann 1994), eastern and southern Australia (Wasson and Shepherd 1997), and western North America (Wasson 1997). Members of the genus *Loxosomatoides* are rather distinctive, and not easily confused with other pedicellinids, so the absence of reports probably reflects a real absence from these regions. This absence remains, for now, a mystery, and we will be curious to observe whether *Loxosomatoides* appears in bays and harbors of other regions in coming years. With our current knowledge about its distribution as a baseline, we will be able to document the spread of this species if it invades regions that continue to be regularly surveyed, such as western North America and northern Europe.

Environmental physiology of Chesapeake Bay kamptozoans

B. benedeni and *L. laevis* are the only kamptozoans that we found in the disturbed regions of Chesapeake Bay, and they thrive near the two major ports (Table 1). What enables these species to survive in such disturbed habitats? Both species have wide temperature and salinity tolerances, and both species form hibernacula that enable them to resist extreme environmental fluctuations. *B. benedeni* zooids have been reported to survive temperatures from 5 °C to 30 °C (Wasson 1997; this study) and salinities from 7 to 35 parts per thousand (Emschermann 1994; Wasson 1997; this study). Moreover, new zooids can be regenerated from stalk nodes and hibernacula after months of immersion in pure fresh water (Nasanov 1926). Hibernacula also are resistant to cold temperatures and even freezing, as well as to low oxygen levels and brief periods of desiccation (Emschermann 1994). The multiple stalk nodes of this species may represent an adaptation to sedimentation; new stolons form from upper stalk nodes and allow colony growth to continue when colonies are buried in sediment (Emschermann 1994). *L. laevis* zooids have been found at water temperatures of 23–32 °C (Rao et al. 1988; this study) and salinities of 4.7–28 parts per thousand (Rao et al. 1988; this study). Annandale (1915) collected colonies at salinities of 9–14 parts per thousand, but found colonies could withstand brief immersion in pure fresh water and also survived in very saline (35 parts per thousand) water. Such broad tolerances and the formation of hibernacula are unusual

traits for kamptozoans, and are surely related to the brackish water habitats of these species.

Kamptozoans: native, introduced, or cryptogenic?

Many kamptozoans have broad, ‘cosmopolitan’ distributions. For instance, three of the four colonial kamptozoans previously reported from Chesapeake Bay – *Barentsia discreta*, *B. gracilis*, and *Pedicalina cernua* – have been reported from numerous sites around the world (Nielsen 1989; Wasson 1997). Many of these reports may represent misidentifications; non-experts often gave European names to specimens from distant localities without a sufficiently thorough taxonomic investigation to justify doing so. For instance, Wasson (1997) found that all reports of *B. gracilis* and *P. cernua* from the northeastern Pacific were in error, and referred to undescribed endemic species. However, even if literature by non-experts is disregarded, it is clear that some kamptozoan species are currently broadly distributed in bays and harbors around the world.

Are ‘cosmopolitan’ distributions the result of natural processes, or should they be attributed to anthropogenic influences? One way to answer this question is to rigorously compare observed attributes of the species to predicted attributes of introduced species. This method was developed for amphipod and isopod crustaceans (Chapman 1988; Chapman and Carlton 1991, 1994) and was used in this study for kamptozoans, but could be applied to any taxon. Such an analysis can be used to determine whether the hypothesis that a given population of a species is native, or the alternative hypothesis that it has been anthropogenically introduced, is better supported by the available evidence. In the absence of such a test of hypotheses, no assumptions should be made about whether a species is native or introduced. We therefore recognize that most kamptozoan species, especially those with widespread distributions, should be classified as cryptogenic (Carlton 1996). Only further investigations can reveal whether their distributions are the result of natural processes or human influences.

The challenge of detecting marine invasions

We took four steps to detect whether there were any invasive kamptozoans in Chesapeake Bay: (a) thorough field surveys of the region for members of the taxon,

(b) systematic analyses to identify all species found, (c) literature searches for the worldwide distribution of these species and for previous records of the taxon in this region, and (d) application of rigorous criteria to assess whether each species found was native or introduced. These steps are generally applicable to the detection of invasions by any taxon in any region. Based on this study of kamptozoans, we have a few cautionary notes for each of these steps, relevant in particular to other neglected marine organisms.

a) To locate tiny marine organisms, a casual search of substrata will likely not suffice; specialized searching methods may be required. We were able to locate the kamptozoans only through extensive deployment of settlement plates at many sites over multiple seasons.

b) Identification of the species found may not be straightforward for many marine taxa. The taxonomy of tiny organisms, in particular, is often difficult, since described species are not well-characterized in the literature, and many species remain undescribed. Identification therefore often involves far more than simply using an existing key – type specimens must be requested from museums and the original species descriptions obtained. After doing the systematic work necessary for identifying the species, it may be useful to characterize the systematics of the species or genera in question, as we have done here, since this may require little extra effort and provide a critical resource for future investigators.

c) To determine the worldwide distribution of species found in the field, and, for suspected invaders, to investigate their route of spread, it is necessary to search taxonomic papers from around the world. An additional literature search must be carried out for all members of the taxon in the region of interest, to allow for comparison between previous records and the current study. For many marine taxa, there will be few records of the species in question. Those papers that are located often are not straightforward to interpret. The species identifications cannot necessarily be relied upon, since (i) they may have been carried out by non-experts, and (ii) experts may have worked under the assumption that most species have cosmopolitan distributions, and put European names on species found elsewhere despite consistent differences with their name-sakes. If possible, it is best to augment the literature search with an examination of vouchers from the authors of each record.

d) The application of rigorous criteria to determine whether species found in a region are native or

introduced requires knowledge of ecological and life history attributes of the species, as well as of their systematics and distribution. This information is often not available in the literature, and must be determined firsthand. We also found it useful to compare closely related species that are presumed to be native to potential invaders (Table 4); this required additional knowledge about the traits of the native species.

Despite these cautionary notes, we strongly advocate taking this type of a thorough approach to the detection of marine invasions. Only through a combination of extensive field surveys, systematic analyses and examination of historical records can we understand the dynamics of invasion for any particular taxon or region, and only by combining knowledge from many taxa and regions can we discover broad-scale patterns of distribution and abundance of invasive species.

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Appendix 1. Systematic review of the genus *Loxosomatoides*

Overview

The genus *Loxosomatoides* was erected in 1908 by Annandale, for *L. colonialis*. He later described *L. laevis* and *Chitaspis athleticus*, both of which were quite similar to *L. colonialis*. Because of this similarity, we hereby synonymize the genus *Chitaspis* Annandale, 1916

with *Loxosomatoides*. In 1939, Marcus described another species in the genus *Loxosomatoides*, *L. evelinae*; this species seems very similar to *Myosoma spinosa* Robertson, 1900. In 1951, Toriumi described *Loxosomatoides japonicum*. This species is here synonymized with *L. laevis* Annandale, 1915.

Loxosomatoides and related genera

Loxosomatoides species display all the characteristic traits of the Family Pedicellinidae (*sensu* Emschermann, 1972), to which they belong; they form stolonate colonies of zooids whose stalks are not differentiated into nodes and rods. They differ from *Pedicellina* species in having stronger oral calyx musculature, an obliquely tilted calyx, an aboral shield of thickened cuticle on the calyx, and in general, less laterally compressed calyces (Appendix 2). The genus *Loxosomatoides* differs from *Myosoma* in having somewhat less muscular stalks, in occurring in brackish water, and in sometimes forming hibernacula. Nevertheless, the two genera are rather similar, and could be synonymized.

The four *Loxosomatoides* and two *Myosoma* species can each be differentiated by the attributes presented in the tabular key (Appendix 2). The differences between them may be due to genetic isolation and differentiation; i.e., they actually may represent six distinct biological species. Alternatively, the differences between them may represent environmentally-induced plasticity, or local adaptation; some of these species may turn out to be populations of the same species. All six species are certainly quite similar to each other, and thus are probably very closely related. Their exact status cannot be determined without further material.

We converted the information in Appendix 2 into binary characters, (0 = no, 1 = yes), and analyzed this data matrix of unordered and unpolarized characters using PAUP (Phylogenetic Analysis Using Parsimony) version 3.1.1 (Swofford 1993). An exhaustive search yielded the tree shown in Appendix 3, with length 11, consistency index of 0.82, and retention index of 0.78. A bootstrap analysis with 1000 replicates and a branch-and-bound search with a 50% majority were carried out; the resulting bootstrap values are shown on the nodes in Appendix 3. This tree must be considered a preliminary hypothesis of the relationships between these six species, since it is based on only nine characters and since none of the nodes are very well supported. Nevertheless, this cladogram summarizes our current state of knowledge about the relationship of these taxa, suggesting that (1) *L. colonialis* and *L. laevis* are closely related; (2) the genus *Myosoma* is paraphyletic; (3) *L. evelinae* is not closely allied to the other species in the genus *Loxosomatoides*.

The four *Loxosomatoides* species are briefly discussed below. For a review of *Myosoma*, see Wasson (1997).

Loxosomatoides colonialis Annandale, 1908

Synonymy. *L. colonialis* Annandale, 1908: 14–19, Figures 2–7; Annandale, 1915: 129.

Type locality. Brackish ponds at Port Canning, Bay of Bengal, India.

Types. Holotype deposited in the Indian Museum (specimen number unknown); 'cotype' in British museum (BMNH 1908.9.14.3-4).

Material examined. The specimen sent by the Indian Museum consists of two twigs covered by lush growth of a number of different colonies; this specimen bears no number or collection information, but presumably comprises the material deposited by Annandale as the holotype. The British Museum has a 'cotype' (BMNH 1908.9.14.3-4) and two supplementary slides (BMNH 1912.1.1.144, BMNH 1917.1.1.176); we examined the 'cotype' and the former slide.

Brief description and discussion. Zooids of this species are characterized by spines on the aboral side of the calyx, but not on the stalk (Appendix 2). Our examination of the material from India generally matches Annandale's description. Measurements given below (as averages \pm standard deviations) are based on our observations. A photomicrograph of this material is available from K. Wasson on request.

The stolon is fairly narrow ($63 \pm 23 \mu\text{m}$), divided regularly into fertile and sterile segments. We observed occasional golden-brown, generally two chambered hibernacula (about $200 \mu\text{m}$ in diameter) among the stolons; Annandale had not reported hibernacula for this species. The stalk is long ($1253 \pm 297 \mu\text{m}$), tapering slightly from base to apex; it is wider in the middle ($183 \pm 34 \mu\text{m}$) than at the calyx ($138 \pm 24 \mu\text{m}$). The layer of longitudinal muscles in the stalk is somewhat thicker on the oral than the aboral side. There are no stalk spines. The stalk – calyx attachment occurs on the oral side of the calyx, and the calyx is tilted obliquely. The calyx is large ($493 \pm 72 \mu\text{m}$), a bit narrower in lateral view ($341 \pm 45 \mu\text{m}$) than in oral view ($365 \pm 35 \mu\text{m}$); it is not laterally compressed. Within the oral hemisphere of the calyx, there are multiple muscle strands running from the base of the calyx to the esophagus; Annandale did not note this calyx musculature. There are 12–14 tentacles, which are oriented obliquely to the stalk. Calycal spines are invariably present, but differ greatly in length from zooid to zooid; they range from short ($5 \mu\text{m}$) nubbins to long ($20 \mu\text{m}$) protuberances. The aboral shield varies from a delicate, pale yellow shell to a thick, dark brown covering, with polygonal cuticular ridges. The whole aboral side of the calyx is generally obscured by adhering debris. The ornamentation pattern we observed on the aboral shield was less conspicuous than Annandale illustrated, perhaps due to the extended period of fixation. Calyces appear to be gonochoric. Female and male calyces seem to occur in separate regions of the substrate, so perhaps the colonies are gonochoric as well.

As the first member of the genus, this species is in no danger of being synonymized with another *Loxosomatoides* species. It does resemble *Myosoma spinosa*, but can be distinguished by its consistent lack of stalk spines and its brackish water habitat.

Loxosomatoides laevis Annandale, 1915

Synonymy. *L. laevis* Annandale, 1915: 129–132, Figures 1–3; Rao et al. (1988): 66–67, Figures 12, 13 and 18; *L. japonicum* Toriumi, 1951: 17, Figures 5–8.

Type locality. Chilka Lake, Bay of Bengal, India.

Types. The type (ZEV 6211/7, Indian Museum) is damaged and unavailable for study (12 May 1997, P. Mukhopadhyay, Zoological Survey of India, pers. comm.).

Material examined. Many colonies from Chesapeake Bay.

Description of Chesapeake Bay material. Our specimens (Figures 2 and 3) match the original species description, except that our zooids were smaller, and had less pronounced cuticular shields. A voucher has been deposited in the British Natural History Museum (BMNH 1998.1.14.2). Colonies cultured in the laboratory did not differ from field-collected material. Most of the colonies collected were very small, and contained mostly small zooids close to a growing stolon tip. The measurements given (as averages \pm standard deviations) therefore may not encompass the upper limits for many of the parameters.

The stolon is pale and fairly narrow ($48 \pm 12 \mu\text{m}$), divided into fertile (zooid-bearing) and sterile segments, as in most other colonial species. No hibernacula were present in our spring and summer collections, but many hibernacula formed in colonies collected in October and cultured in the laboratory. The hibernacula are dark brown chambers about the size of calyces ($192 \pm 48 \mu\text{m}$), covered with a thick cuticle and filled with granular material. New zooids were observed germinating from hibernacula in lab cultured material in November (one month after collection).

The stalk is fairly wide ($73 \pm 16 \mu\text{m}$ in the middle), tapering at the apex just beneath the calyx ($46 \pm 6 \mu\text{m}$ at the apex). It is about two times as long ($552 \pm 153 \mu\text{m}$) as the calyx is high. The layer of longitudinal muscles in the stalk is somewhat thicker on the oral than the aboral side. There are no stalk spines. The stalk–calyx attachment occurs on the oral side of the calyx (rather than at the base, as in *Pedicellina*); as a result, the junction is sloped, and the calyx is tilted obliquely. There are about 5–8 star cells bridging the junction.

Most calyces examined were quite small ($235 \pm 36 \mu\text{m}$). They are only slightly wider in side view ($166 \pm 35 \mu\text{m}$) than in aboral or oral view ($160 \pm 31 \mu\text{m}$); calyces are very slightly compressed laterally. There are 12–14 tentacles, which extend obliquely, rather than vertically, due to the orientation of the calyx. Strong muscle fibers prominently run from the base of the calyx to the atrium in the oral half of the calyx. In the smallest calyces, the cuticle of the oral and aboral sides is similar in appearance. In larger calyces, the aboral side of the calyx is covered with debris, apparently adhering to glandular secretions of large, lumpy cells visible in the body wall. In the largest calyces examined, the cuticle on the aboral side was thick and shield-like, and cracked into a reticulated pattern of closely meshed polygons on the calycal surface. No deep depressions or more conspicuous ornamentation was present in any calyces, and spines were always absent.

The larger calyces from all collection dates were sexually mature. They appear to be single-sexed, but calyces of both sexes were sometimes found together in the same clump, suggesting that colonies may be hermaphroditic. The brood chamber is large and thick-walled. Only small embryos were observed in the brood chamber; the larval form is not known. The presence of many tiny colonies on settlement plates during spring and summer suggests that larval recruitment was occurring during this period.

Discussion. The key trait distinguishing *L. laevis* from *L. colonialis* is the consistent absence of calycal spines in the former (Appendix 2). In *L. colonialis*, spine length can vary greatly; it seems possible that spines might be entirely absent under some environmental conditions, in which case *L. laevis* should be

synonymized with *L. colonialis*. However, colonies of *L. laevis* cultured in the laboratory under varying conditions never developed spines.

L. laevis also resembles *Myosoma hancocki* Soule, 1955, but can be distinguished by its lack of oblique stalk musculature, by its brackish water habitat, and by the ability to form hibernacula.

Our material from Chesapeake Bay contained mostly small calyces with thin aboral shields, but the larger calyces we observed had thicker, more ornamented calycal shields. Toriumi (1951) erected *L. japonicum* for a species that resembled *L. laevis* except for the smaller size and less developed aboral shields. The type material for *L. japonicum* does not exist anymore; the jar originally containing the specimen only has a few tiny pieces of an ascidian in it (25 April 1996, P. Emschermann, University of Freiburg, pers. comm.). We find it very likely that Toriumi's material consisted of some young *L. laevis* colonies, and have therefore synonymized *L. japonicum* with *L. laevis*.

Rao et al. (1988) found *L. laevis* in Visakhapatnam harbor, India. Their description matches that of Annandale, so we have confidently included their identification in the synonymy for this species.

Loxosomatoides athleticus Annandale, 1916

Synonymy. *Chitaspis athleticus* Annandale, 1916: 17–19, Figure 1 and pl. 1.

Type locality. Thale Sap, Gulf of Thailand.

Types. The type (ZEV 7157/7, Indian Museum) is damaged and unavailable for study (12 May 1997, P. Mukhopadhyay, Zoological Survey of India, pers. comm.).

Material examined. None.

Brief description and discussion. This species strongly resembles *L. laevis*. However, *L. athleticus* has oblique stalk musculature that is apparently absent in the other *Loxosomatoides* species; in this regard, the species resembles *Myosoma*. However, it bears an even greater resemblance to *Loxosomatoides*, especially in terms of the ornamentation of the aboral shield, and its brackish water habitat. Annandale believed that this species differed from *Loxosomatoides* species in having conspicuous calyx muscles; we have found that *L. laevis* and *L. colonialis* have conspicuous calyx musculature as well. The differences between this species and *L. laevis* seem too slight to justify its being in a separate genus, and we therefore have synonymized the genus *Chitaspis* with *Loxosomatoides*.

Loxosomatoides evelinae Marcus, 1939

Synonymy. *L. evelinae* Marcus, 1939: 121–122, Pl. 5, Figure 2a–c.

Type locality. Bahia de Santos, Brazil.

Types. The British Museum has the only known specimen (1948.2.16.77) of this species, but it is currently lost (21 April 1997, M.E. Spencer Jones, British Museum, pers. comm.). There is apparently no type material in the Zoology department of the University

of São Paulo, where Marcus worked (4 June 1997, C.E.F. da Rocha, pers. comm.).

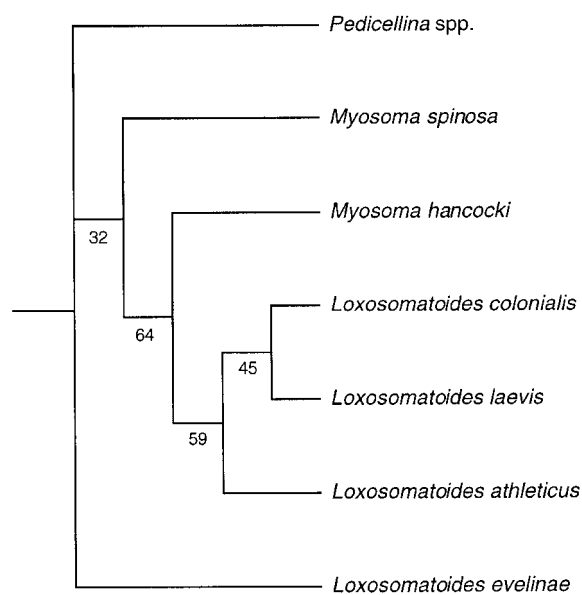
Material examined. None.

Brief description and discussion. This species appears to be very similar to *Myosoma spinosa* Robertson, 1900. It differs only in

lacking oblique stalk musculature (Appendix 2), but oblique muscles are not always readily visible, even in *Myosoma* (Wasson, pers. obs.). This species differs from the other *Loxosomatoides* species in having a spiny stalk and in lacking ornamentation of the aboral shield.

Appendix 2. Tabular key comparing the four *Loxosomatoides* species, the two *Myosoma* species, and generalized *Pedicellina* species.

| Trait | <i>Loxosomatoides</i> | | | | <i>Myosoma</i> | | <i>Pedicellina</i> spp. |
|---|-----------------------|---------------|-------------------|-----------------|----------------|-----------------|-------------------------|
| | <i>colonialis</i> | <i>laevis</i> | <i>athleticus</i> | <i>evelinae</i> | <i>spinosa</i> | <i>hancocki</i> | |
| Oblique stalk musculature | No | No | Yes | No | Yes | Yes | No |
| Stalk spines | No | No | No | Yes | Yes | No | Varies with sp. |
| Calycal spines | Yes | No | No | Yes | Yes | No | Varies with sp. |
| Aboral shield present | Yes | Yes | Yes | Yes | Yes | Yes | No |
| Polygonal ornamentation on aboral region of calyx | Yes | Yes | Yes | No | No | No | No |
| Calyx oblique; tilted orally | Yes | Yes | Yes | Yes | Yes | Yes | No |
| Strong calyx musculature | Yes | Yes | Yes | Yes | Yes | Yes | No |
| Hibernacula | Yes | Yes | ? | ? | No | ? | No |
| Brackish habitat typical | Yes | Yes | Yes | No? | No | No | No |



Appendix 3. Cladogram of the relationships between *Loxosomatoides*, *Myosoma*, and *Pedicellina* species, based on a phylogenetic analysis of the characters shown in Appendix 2. An exhaustive search using PAUP (Swofford, 1993) yielded this single tree, with length 11, consistency index of 0.82, and retention index of 0.78. A bootstrap analysis with 1000 replicates and a branch-and-bound search with a 50% majority were carried out; the resulting bootstrap values are shown on the nodes.

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