

Review Article

Macrofauna Associated with Echiuran Burrows: A Review with New Observations of the Innkeeper Worm, *Ochetostoma erythrogrammon* Leuckart and Rüppel, in Venezuela

Arthur Anker^{1,*}, Galena-Vantsetti Murina², Carlos Lira³, Jonathan A. Vera Caripe³,
A. Richard Palmer¹, and Ming-Shiou Jeng⁴

¹Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada
E-mail: aanker@ualberta.ca, rich.palmer@ualberta.ca

²Department of Mariculture and Applied Oceanology, Institute of the Biology of the Southern Seas N.A.S. Ukraine, 2, Nakhimov Avenue, 99011, Sevastopol, Ukraine. E-mail: murina@ibss.iuf.net

³Universidad de Oriente, Boca del Río, Isla Margarita, Estado Nueva Esparta, Venezuela
E-mail: c_lira_g@hotmail.com, clira@ne.udo.edu.ve, j_vera_a_c@yahoo.com

⁴Research Center for Biodiversity, Academia Sinica, Taipei, Taiwan 115, R.O.C. E-mail: jengms@gate.sinica.edu.tw

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ABSTRACT

Arthur Anker, Galena-Vantsetti Murina, Carlos Lira, Jonathan A. Vera Caripe, A. Richard Palmer, and Ming-Shiou Jeng (2005) Macrofauna Associated with Echiuran burrows: a review with new observations of the innkeeper worm, *Ochetostoma erythrogrammon* Leuckart and Rüppel, in Venezuela. *Zoological Studies* 44(2): 157-190. Because of their size and semipermanent nature, burrows of larger echiuran worms (phylum Echiura: Urechidae, Echiuridae, Bonelliidae, and Thalamematidae) host a remarkable variety of symbionts. Most symbionts appear to be commensals (occasionally with tendencies to kleptoparasitism), although at least 1 echiuran, *Bonellia viridis*, may in turn be a commensal of the soft rock-burrowing mudshrimp, *Upogebia mediterranea*. Commensal animals most frequently observed in echiuran burrows are bivalves (11 species in 8 hosts), polychaetes (mostly polynoids; 14 species in 8 hosts), brachyuran crabs (mostly pinnotherids and varunids; 16 species in 8 hosts), alpheid shrimps (6 species in 6 hosts), and copepods (3 species in 3 hosts). Some are facultative commensals (e.g., many polynoids and pinnotherids), but obligate and host-specific associations also occur, particularly among copepods and the loxosomatid entoprocts, *Loxosomella* spp. (with their associated gastropod predator, *Sigaretornus planus*). An alpheid shrimp, *Alpheus barbatus*, may also live in association with non-burrowing, crevice-dwelling echiurans. Other, less-frequent, echiuran commensals include polyclad flatworms (1 species), nemertean (1 species), nematodes (2 species), entoprocts (2 species),

* To whom correspondence and reprint requests should be addressed.

gastropods (2 species), and fishes (2 species). Most echiuran-associated bivalves, entoprocts, and some polychaetes are so-called burrow energy users. The most-diversified communities of commensal animals are found in U-shaped burrows of larger species, such as *Urechis* spp. and *Ochetostoma* spp., but also in some relatively small echiurans, e.g., *Lissomyema exilii*, which builds U-shaped chambers in discarded mollusc shells. Finally, the cosmopolitan echiuran species or species complex, *Ochetostoma erythrogrammon* Leuckart and Rüppel, 1828 (Echiura: Thalassematidae), is reported here for the 1st time from Venezuelan waters. At least 2 species of pinnotherid crabs, *Pinnixa* spp., and an unidentified sportellid bivalve were collected from the burrows, together with the echiurans and the upogebiid mudshrimp, *Upogebia omissa*, suggesting that the crabs and the bivalve may be commensally associated with 1 or both of these burrowing animals.

<http://www.sinica.edu.tw/zool/zoolstud/44.2/157.pdf>

Key words: Echiura, Burrows, Infauna, Commensalism, *Ochetostoma*.

INTRODUCTION

The echiurans (phylum Echiura), popularly known as “spoon worms” or “innkeeper worms”, occur in shallow-water habitats throughout the world’s oceans, from tropical seas to subpolar regions (e.g., Fischer 1926, Sato 1939, Wesenberg-Lund 1939, Murina 1981, Saiz-Salinas 1996). These animals have a peculiar non-segmented, sausage- or sac-shaped body with a highly extensible proboscis that cannot be retracted into the body. Although relatively common, echiurans are rarely collected, mainly because of their cryptic, mostly burrowing life styles. Most species excavate deep tunnels or burrows in fine sediments (see Ikeda 1904, Fisher and MacGinitie 1928b, Stephen and Edmonds 1972, Morton and Morton 1983, Ricketts et al. 1985, Biseswar 1991, Arp et al. 1992, Nickell and Atkinson 1994, Rogers and Nash 1996).

The burrows of some echiurans are large enough to harbor smaller infaunal animals collectively called “commensals” (Fisher and MacGinitie 1928b, Rachor and Bartel 1981, Ditadi 1982, Morton and Morton 1983, Ricketts et al. 1985, Morton 1988, Nickell et al. 1995). These commensals belong to many animal groups, and each may have a very different association with its echiuran host. Some are facultative symbionts also found free-living in the background sediments or associated with other burrowing animals, such as mud and ghost shrimp (Thalassinidea). While some echiuran burrows host only 1 or 2 symbiont species, others may contain a diverse symbiont complex. Unfortunately, most biological aspects of these symbiotic communities, including trophic relations with the host and interactions between the symbionts, largely remain unknown.

Remarkably, although echiuran burrows are widely recognized as home to many symbionts, we are unaware of any systematic survey of echiuran symbionts. The finding by the 1st author of a new

commensal complex associated with the large innkeeper worm, *Ochetostoma erythrogrammon* - reported here for the 1st time from Venezuela - prompted a more-extensive review of the animals associated with echiuran burrows. We paid particular attention to the following questions. (1) How common are associations between echiurans and other animals? (2) What is the nature of these associations? (3) What animal groups participate in these associations? (4) Do the shape and volume of the burrow or feeding mode influence the diversity of the associated infauna?

An exhaustive literature survey revealed surprisingly few studies dealing specifically with echiuran symbionts. What information exists is rather scarce and scattered among taxonomic studies and investigations of echiuran burrow morphology. However, these studies provide sufficient data for the 1st worldwide review of macro-symbionts of the Echiura (parasites, mainly endosymbiotic Protozoa and Platyhelminthes, excluded). This review is followed by a more-detailed description of the newly collected Venezuelan material of *O. erythrogrammon*, with remarks on the ecology and taxonomy of this species.

Biology of the Echiura

Stephen and Edmonds (1972) first reviewed the general biology of the Echiura, but condensed summaries occur in major treatises (e.g., Dawydoff 1959, Kästner 1993, Brusca and Brusca 2003) and regional overviews (e.g., Sterrer 1986, Edmonds 2000). Until relatively recently, the phylogenetic placement of the phylum within the Metazoa was enigmatic (Purschke et al. 2000). The exquisite photomicrographs of Hessling and Westheide (2002) document an unambiguously segmental nervous system in echiuran larvae that extends by terminal addition during ontogeny just as in annelids. Molecular evidence also suggests that echiurans (together with pogonophorans) are

derived annelids (McHugh 1997, Bleidon et al. 2003). Edmonds (2000) and Nishikawa (2002) discussed the most-recent classification. Classically, 3 orders are recognized: Echiuroinea or Echiuroidea (with Echiuridae, Bonelliidae, and Thalassematidae), Xenopneusta (with Urechidae) and Heteromyota (with Ikedidae). The echiuroid family, the Thalassematidae, is also treated as a subfamily of the Echiuridae (Nishikawa 2002). Two aspects of echiuran biology, the feeding modes and burrow morphology, are particularly relevant to this review of symbionts.

Two modes of feeding exist among echiurans: surface deposit feeding (in the majority of species) and filter feeders (among members of 1 genus only). The deposit feeders (Bonelliidae, Echiuridae, Thalassematidae, and possibly Ikedidae) keep their trunk inside the burrow and extend their sometimes extraordinarily long proboscis – up to 300 or more times the trunk length (e.g., to 1.5 m in some species, Herring 2003) – out of the burrow to collect surficial sediment and organic particles near the burrow opening. Dorsal cilia transport the collected particles along the proboscis to the mouth. The organic components are digested, and the remaining sediments are deposited as small fecal pellets near the burrow opening (Sluiter 1884, Wilson 1900, Chuang 1962a, Stephen and Edmonds 1972, Hughes and Crisp 1976, Jaccarini and Schembri 1977a b, Schembri and Jaccarini 1977, Sterrer 1986, Hughes et al. 1993, Nickell and Atkinson 1994, Brusca and Brusca 2003).

Filter feeders (members of the monogeneric family Urechidae) have a relatively short proboscis poorly adapted for surface deposit feeding. Instead these echiurans secrete a mucus net from a circle of glands around the base of the proboscis. This funnel-shaped net is attached at its wider end to the burrow wall, and at its narrower end to the circle of glands. Retrograde peristaltic contractions of the body pump water through the burrow and mucous net, which can filter out particles as small as 40 Å (0.04 mm). When loaded with food, the worm loosens the net from its attachments and swallows it whole (Fisher and MacGinitie 1928b, MacGinitie and MacGinitie 1968, Stephen and Edmonds 1972, Morris et al. 1980, Ricketts et al. 1985, Julian et al. 2001). Both deposit and filter feeders can turn around in their burrow and feed from either aperture, and coprophagy is not uncommon (Fisher and MacGinitie 1928b, Gislén 1940, Morris et al. 1980, Ditadi 1982, Sterrer 1986).

Burrow morphology has been studied in echiuran species from 4 families (Fisher and MacGinitie 1928b, Gislén 1940, Schembri and Jaccarini 1978, Morris et al. 1980, Rachor and Bartel 1981, Ricketts et al. 1985, Morton and Morton 1983, Nickell et al. 1995, Hughes et al. 1996, Rogers and Nash 1996), and burrowing behavior has been described in detail for *Ochetostoma caudex* (Biseswar 1991). Most species, including *Echiurus echiurus*, *Urechis caupo*, and *Ochetostoma bombayense* (Prasad and Awati, 1929) (originally described as *Thalassema bombayensis*), construct U-shaped burrows in fine sand or mud (Fisher and MacGinitie 1928b, Awati and Deshpande 1935, Gislén 1940, Ditadi 1982). In burrows of large *U. caupo*, for instance, the 2 openings are 40–100 cm apart, and the depth may reach 50 cm. The burrow walls are usually lined with mucus, except for burrows made in coarse clear sand (Ditadi 1982), and burrow openings usually resemble large flattened mounds. Most species of *Ochetostoma* and *Lisriolobus* make either U-shaped burrows with 2 openings or oblique L-shaped burrows with 1 opening (Jones and Stephen 1955, Ditadi 1982, Rogers and Nash 1996). In some species (e.g., some *Thalassema* spp.), the burrows are simple, sac-shaped, and vertical, and also have only 1 opening (Morton and Morton 1983). Other species of *Thalassema* build their galleries among branches of scleractinian corals (*Mussismilia*, *Madracis*) and ramifications of giant bryozoans (*Schizoporella*) (Ditadi 1982). Species of the genus *Lissomyema* live in dead, silt-filled mollusc shells, in empty barnacle shells, and tests of irregular urchins (Ditadi 1982). Finally, some species excavate short burrows under rocks and dead corals (Wesenberg-Lund 1939 1954, Stephen 1952, Sterrer 1986) and others, including species of *Bonellia* and some *Ochetostoma*, inhabit coral rock crevices, bivalve-excavated rock galleries, or the multibranched system of galleries perforated by some mudshrimps (Wharton 1913, Schembri and Jaccarini 1978, Ditadi 1982). Occasionally echiurans are found in abandoned galleries of teredinid bivalves, empty polychaete tubes, and under algal roots (Ditadi 1982).

Echiuran parasites include gregarinid sporozoans, ciliates, trematodes, nematodes, polychaetes, and cestodes (Stephen and Edmonds 1972, Lauckner 1980). Among the latter are larvae of a tetraphyllidean tapeworm that infests *U. caupo*. The echiuran apparently acts as an intermediate host for the tapeworm, the definitive host

being the bat eagle ray *Myliobatis californica* Gill, 1865, which preys upon *U. caupo*. Another parasite worth mentioning is the polychaete, *Oligognathus bonelliae* Spengel, 1882 (Oeonidae), which specifically infests the gut and body cavity of *Bonellia viridis* (Pettibone 1957, Stephen and Edmonds 1972, Martin and Britayev 1998). Singhal and Datta Gupta (1980) briefly mentioned that "a few protozoans" were found in the "coelomic fluids" of 3 Indian echiuran species.

Review of Symbiotic Animals Associated with Echiurans

Burrows of at least 17 echiuran species may contain associated commensal macrofauna (Appendix I). However, rather few of these commensals are obligate echiuran symbionts. Most are general burrow dwellers (facultative symbionts) and occur in burrows of mudshrimps, polychaetes, sipunculids, and other burrowing animals. Several "commensals" are free-living species and occur only occasionally in echiuran or other burrows (guests).

Most commensals and inquilines associated with echiuran burrows are "energy commensals" (coined by Nielsen 1964, see Ditadi 1982): they benefit from rich food- and oxygen-containing water pumped through the tunnel by the host. The burrow also offers shelter from epibenthic predators. Some of the more-agile commensals, such as crabs and polychaetes, are at least occasional kleptoparasites, and may steal appreciable quantities of food from the host. The following account is, to our knowledge, the most complete review of echiuran associates since Ditadi (1982). Taxonomic authorities and comments on nomenclatural name changes of hosts and commensals are listed in Appendix I.

1. *Urechis caupo* (Urechidae)

The large (average 20 cm, up to 50 cm in full extension), filter-feeding Californian "fat innkeeper worm" *Urechis caupo* (Figs. 1, 2a) is one of the best-studied echiurans. Its discovery and description (Fisher and MacGinitie 1928a) practically coincided with a detailed study of its ecology and the associated fauna (Fisher and MacGinitie 1928b). More recently, its burrowing ecology and physiology were investigated by Arp et al. (1992 1995), Julian and Arp (1992), Julian et al. (1996 1998 1999 2001), and Osovitz and Julian (2002).

Because *U. caupo* may live up to 25 years

(MacGinitie and MacGinitie 1968), which is unusually long for an invertebrate, its U-shaped burrows, if undisturbed, constitute stable and long-lasting microhabitats that often harbor an impressive array of commensals. These include the scale worm, *Hesperonoe adventor* (Polynoidae); the arrow goby, *Clevelandia ios* (Gobiidae); the hooded shrimp, *Betaeus longidactylus* (Alpheidae); and the pea crabs *Scleroplax granulata*, *Pinnixa fransiscana*, *P. longipes*, and *P. schmitti* (Pinnotheridae) (Fisher and MacGinitie 1928a b, MacGinitie 1934, Fisher 1946, Dales 1957, Hart 1964, MacGinitie and MacGinitie 1968, Butler 1980, Morris et al. 1980, Ricketts et al. 1985, Jensen 1995, Ruff 1995, Martin and Britayev 1998). Figure 1 illustrates a stereotypical view of the innkeeper worm and three of its commensals (*H. adventor*, *S. granulata*, and *C. ios*). Nybakken (2000) provided a photograph of *U. caupo*, *H. adventor*, *S. granulata*, and *B. longidactylus* in a transparent artificial burrow.

The polynoid, *H. adventor* (Fig. 3a), is the most-tightly associated with *U. caupo* burrows, at least in California. This agile worm is rarely, if ever, found outside the innkeeper's burrows, and often dwells in the immediate proximity of the host (Fig. 1). Usually only 1 worm inhabits a burrow, since it immediately and forcibly drives any other individuals out. The scale worm feeds mainly on detritus trapped in the innkeeper's mucous net. As soon as *U. caupo* starts to devour the net, the worm nervously grasps the food particles with its eversible pharynx (Fisher and MacGinitie 1928b, Ricketts et al. 1985). In Alaska, *H. adventor* inhabits burrows of another echiuran, *Echiurus echiurus alaskensis* Fisher, 1946 (Fisher 1946; see below). Yet another *Hesperonoe* species, the bright yellow-orange *H. complanata* (Johnson, 1901), lives associated with the blue mudshrimp, *Upogebia pugettensis* (Dana, 1852), and the ghost shrimp, *Neotrypaea californiensis* (Dana, 1854) (MacGinitie and MacGinitie 1968, Morris et al. 1980, Ricketts et al. 1985, Ruff 1995, Martin and Britayev 1998, Sato et al. 2001). All *Hesperonoe* species are commensals or inclined to dwell in the burrows of other animals (see also below).

The pinnotherid crab, *S. granulata* (Figs. 1, 2b), occurs in burrows of *U. caupo* either as a single individual or in (possibly male-female) pairs. This crab also feeds primarily on particles trapped by the innkeeper's mucous net and, as the crab is very agile and more aggressive, it often snatches the best parts away from the scale worm. The competition for food between the 2 "commensals"

probably has negative effects on the host. First, the innkeeper may lose part of its food to the scale worm and to the crab, and second, these 2 “commensals” often interfere with the regular activities of the innkeeper, for example during the feeding. In their attempts to reach the chemically sensed, larger food particles trapped in the mucous net, the polynoid and the crab often cause *U. caupo* to retract the net prematurely, and then simply steal the food (Fisher and MacGinitie 1928b, Ricketts et al. 1985). *Scleroplax granulata* is not confined to burrows of *Urechis*, and also inhabits burrows of *U. pugettensis* and *N. californiensis* (MacGinitie 1934, MacGinitie and MacGinitie 1968, Jensen 1995).

Other pinnotherid crabs, e.g., *Pinnixa franciscana* (Fig. 2c) and *P. schmitti* (Fig. 2e) also occur in burrows of *U. caupo*, but are encountered much less commonly. *Pinnixa franciscana* usually inhabits burrows of *U. pugettensis* and *N. californiensis*, while *P. schmitti* frequents the burrows of another spoon worm, *Echiurus echiurus alaskensis* Fisher, 1946 (see below), and rarely those of *U. pugetten-*

sis and *N. californiensis* (Ricketts et al. 1985). *Pinnixa longipes* (Fig. 2d) was reported to be mostly a commensal of tubes of various polychaetes, including *Axiiothella* (Schmitt et al. 1973, see also fig. 288 in Ricketts et al. 1985).

Interactions between the alpheid shrimp, *Betaeus longidactylus* (Fig. 2f), and *U. caupo*, and between the shrimp and all the other inhabitants of the innkeeper’s burrows are unknown. *Betaeus longidactylus* is known mostly as a free-living species or to be facultatively associated with burrows of *U. pugettensis* or *U. caupo* (MacGinitie 1935 1937, Hart 1964, Jensen 1995). Within the burrow, the shrimps may occasionally feed on detritus or ingest food particles discarded or lost by the innkeeper or the other inhabitants, and thus act as a burrow cleaner. The arrow goby, *Clevelandia ios*, is another transient guest in the innkeeper’s burrows. From 1 to 5 individuals may simultaneously inhabit a burrow. The gobies forage outside much of the time and use the innkeeper’s burrow mainly as shelter (Ricketts et al. 1985). They may also seek shelter in burrows of other animals,

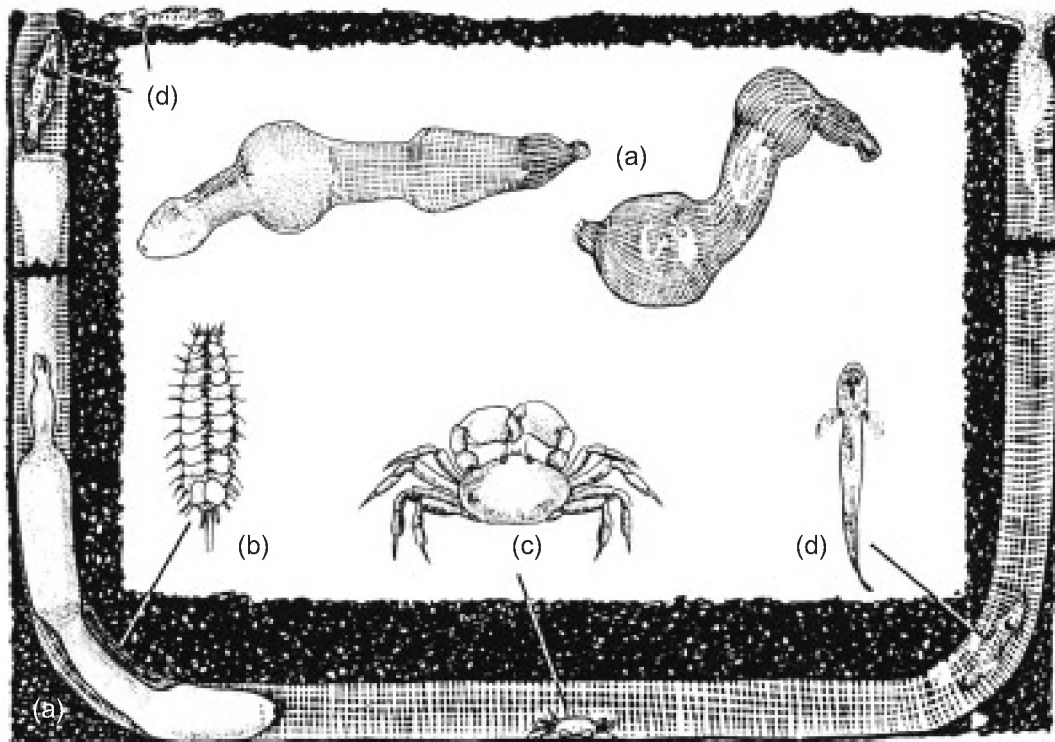


Fig. 1. Typical U-shaped burrow of the Californian innkeeper worm, *Urechis caupo*, with commensals. (a) Host, TL ~10 cm; (b) scale worm *Hesperonoe adventor* (Polynoidae), TL ~5 cm; (c) pea crab, *Scleroplax granulata* (Pinnotheridae), CW ~12 mm; (d) arrow goby, *Clevelandia ios* (Gobiidae), TL ~4~5 cm (adapted from EF Ricketts, J Calvin, JW Hedgpeth. 1985. Between Pacific tides. 5th ed. Copyright 1948, 1952, 1962, 1968, 1985 by the Board of Trustees of the Leland Stanford Jr. University. All rights reserved, used with permission of Stanford Univ. Press). TL, total length; CW, carapace width.



Fig. 2. Inhabitants of *Urechis caupo* burrows. (a) *Urechis caupo* in the vertical portion of the burrow; (b-e) commensal pea crabs (Pinnotheridae), usually (b) or occasionally (c-e) associated with *U. caupo*: (b) *Scleroplax granulata*, CW ~12 mm; (c) *Pinnixa franciscana*, CW 10~22 mm; (d) *P. longipes*, CW ~6 mm; (e) *P. schmitti*, CW ~10 mm; (f) alpheid shrimp, *Betaeus longidactylus*, TL ~3 cm, occasionally associated with *U. caupo* (a, photograph courtesy of Phillip Colla, Oceanlight.com, b-f, photographs courtesy of Greg Jensen).

including *U. pugettensis* and *N. californiensis* (MacGinitie 1934).

A more-distinctive member of the *U. caupo* burrow community is the myid clam, *Cryptomya californica* (Conrad, 1837). This clam, characterized by very short siphons, often lies in the sediment close to the burrows of *U. caupo*, but also those of *U. pugettensis* and *N. californiensis*, and extends its siphons into the burrows to take advantage of the feeding currents maintained by the host (MacGinitie 1934, Morris et al. 1980).

Typically for mudflat environments, sulfide levels drastically increase, while oxygen levels decrease, during the low tide. Because sulfide is toxic to most aerobic organisms, questions arise about how all the *U. caupo* commensals survive

such highly hypoxic conditions during low tide. *Urechis* itself is able to detoxify the sulfide in several ways (Arp et al. 1995). The coelomic fluid is rich in hemoglobin and hematin, which bind sulfide and may also catalyze the oxidation of sulfide to thiosulfate. The abundantly secreted mucus protects the aerobic epithelium from sulfide poisoning, while symbiotic bacteria and specialized organelles (SOBs) also help transform the sulfide into thiosulfate (Arp et al. 1995), which is eliminated by passive diffusion across the hindgut (Julian et al. 1999). So, commensals of *Urechis* are exposed to particularly high concentrations of both sulfide and thiosulfate during low tides, especially in deeper parts of the burrow. Some of these commensals, particularly those living more permanently in *Urechis* burrows, may also be physiologically adapted to tolerate high sulfide concentrations. Nonetheless, although the burrow may represent an extreme environment, it may be less extreme than the surrounding sediment and thus extends the niche for these associated fauna (D. Felder, pers. comm.).

2. *Urechis unicinctus* (Urechidae)

Preliminary investigations of *Urechis unicinctus* burrows in south-central Japan (Itani, in prep.) revealed presence of several commensals, including crabs (Itani et al. 2005) and copepods (Itani, in prep.). Three species of crabs were collected just beneath the echiuran hosts in their burrows. These included 2 varunid crabs, *Acmaeopleura toriumii* (Fig. 3b) and *A. balssi* (Varunidae), and the pinnotherid crab, *Pseudopinnixa carinata*. *Acmaeopleura toriumii* and *P. carinata* also live commensally in thalassinidean burrows (Davie 1992, Itani 2002, Itani et al. 2002), while the larger *A. balssi* Shen, 1932, may associate with polychaete worms (Sakai 1965). However, given its relatively large body size, *A. balssi* may also be free-living, at least locally (Itani et al. 2002). Furthermore, Sakai's (1965) "annelid" might have been an echiuran (G. Itani, pers. comm.). *Acmaeopleura* species are unusual among varunid crabs in having a "pinnotherid" body form (Fig. 3b), a striking example of morphological convergence as a result of similar lifestyles.

The poecilostomatoid copepod, *Goidelia japonica*, was originally described from the rectum of *Urechis* in Japan (Kim 2000). On the mudflats of the Korean Yellow Sea, Kim (2000) collected *G. japonica* from the alimentary canal of *U. unicinctus*. Interestingly, not a single ovigerous

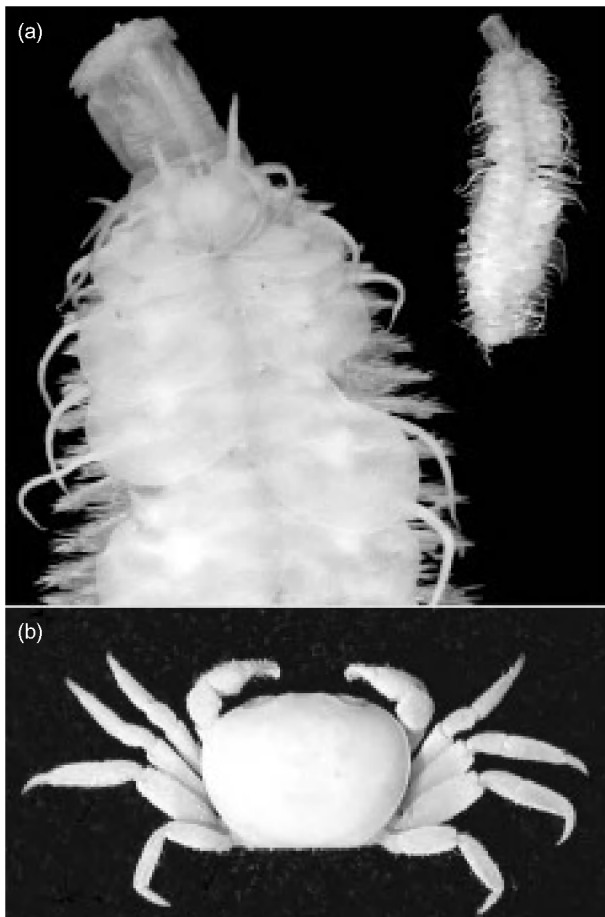


Fig. 3. Echiuran commensals. (a) *Hesperonoe adventor* (Polynoidae), TL ~5 cm, obligate associate of *Urechis caupo*, entire animal and head and anterior segments enlarged; (b) *Acmaeopleura toriumii* (Varunidae), CW ~4.5 mm, occasionally found in burrows of *Urechis unicinctus* and *Ochetostoma erythrogrammon* (a, photograph courtesy of Leslie Harris; b, photograph of holotype courtesy of Ngan-Kee Ng).

female of *G. japonica* was discovered, despite examination of hundreds of specimens of these copepods. In south-central Japan, G. Itani (pers. comm.) found *G. japonica* attached to the body wall of the host. The biology and the taxonomic identity of this *Goidelia* population are currently under study (G. Itani, in prep.). A closely related species, *G. pelliviva* Kim, 2000, lives associated with the echiuran, *Thalassema* sp. (Kim 2000; see below).

The alpheid shrimp, *Athanopsis dentipes* (Fig. 7a), occasionally inhabits burrows of *U. uncinatus* (Miya 1995), although originally this species was described from burrows of another Japanese echiuran, *Anelassorhynchus mucosus* (Miya 1980; see below).

3. *Echiurus echiurus echiurus* (Echiuridae)

The common spoon worm, *Echiurus echiurus*, builds U-shaped burrows in muddy sand or mud, attaining 10~50 cm at the deepest point (Gislén 1940, Rachor and Bartel 1982). The biology of *E. echiurus*, including burrow morphology, feeding, locomotion, and associated fauna was studied by Gislén (1940), Nyholm and Bornö (1969), and Rachor and Bartel (1981). Rachor and Bartel found a surprisingly diverse macrofauna associated with its burrows in the German Bight of the North Sea, including 3 polychaetes, viz., 2 scale worms, *Harmothoe sarsi* and *Gattyana cirrhosa* (Polynoidae), and *Pholoe minuta* (Pholoidae), and 3 bivalves, viz., *Mysella bidentata* (Montaculidae), *Abra alba* (Semelidae), and *Nucula nitidosa* (Nuculidae). Furthermore, resin casts of sediment cores always contained burrows of the polychaetes, *Notomastus latericeus* (Capitellidae) and *Scalibregma inflatum* (Scalibregmatidae), which in most cases had tapped into the *E. echiurus* burrows (Reineck et al. 1967, Rachor and Bartel 1981). When *E. echiurus* and *N. latericeus* were maintained together in the same aquarium, Rachor and Bartel (1981) consistently found communicating burrows of both species within a few weeks.

The polychaetes, especially the agile polynoids, are likely to directly steal some food particles from the extended proboscis. The wall linings of inhabited burrows are always well oxygenated because of the spoon worm's pumping activity, assured by regular peristaltic movements of the body (Rachor and Bartel 1981). In aquarium observations, the polychaete, *G. cirrhosa*, preferred the ventilated tubes of *Echiurus* over other tubes and burrows. In most cases, *Echiurus*

seemed undisturbed by the polychaete's activities, and both animals moved in close contact, with the polychaete sometimes creeping underneath its host. However, in 1 case, the spoon worm drove a *G. cirrhosa* out of its burrow several times (Rachor and Bartel 1981). Preference for a particular burrow or close alliance with a particular host individual does not appear to exist, as *G. cirrhosa* often changes its shelter and may stay on the sediment surface for short periods of time (Rachor and Bartel 1981).

Like other echiurans, *E. echiurus* produces immense quantities of feces (Rachor and Bartel 1981), that are still rich in organic material and can be used as nutrients by the spoon worms themselves or by some burrow commensals, e.g., the clam, *Abra alba*. The siphons of this clam were often seen near the defecation openings of *Echiurus*, and the clams moved actively during and after feces expulsion by the echiuran (Rachor and Bartel 1981). The polychaete, *Notomastus latericeus*, probably feeds on feces as well, and connects to the *Echiurus* burrows for a consistent source of food (capitellids, including *Notomastus*, frequently occur in large numbers around sewage outfalls and other such areas with high organics and hydrogen sulfide, L. Harris, pers. comm.). *Scalibregma inflatum* is presumably a sediment feeder, and may also feed on feces (L. Harris, pers. comm.).

Thus, associates of *Echiurus* clearly "derive manifold profits from all these activities of *Echiurus* as long as density is not too high so that settling larvae are devoured and competition prevails" (Rachor and Bartel 1981). These benefits influence local species diversity: as a rule, when *Echiurus* was found in a bottom sample, the total species number of the macrofauna increased (Rachor and Bartel 1981).

4. *Echiurus echiurus alaskensis* (Echiuridae)

The Alaskan spoon worm, *Echiurus echiurus alaskensis* (also known as *E. e. alaskanus* or *E. pallasii*), is exceedingly abundant in southeastern Alaska, where it occurs embedded in gravely substrates with a clay component, as well as in mudflats. It is a typical deposit feeder, with a long scoop-shovel-shaped proboscis (Ricketts et al. 1985). The pinnotherid crab, *Pinnixa schmitti*, often occurs in burrows of *E. e. alaskensis* (Schmitt et al. 1973, Ricketts et al. 1985) and occasionally in burrows of *Urechis* sp. (Schmitt et al. 1973) and the thalassinideans, *Upogebia*

pugettensis and *Neotrypaea californiensis* (see above). Relationships between the crab and the echiuran remain to be studied. The polynoid worm, *Hesperonoe adventor*, also occurs in *E. e. alaskensis* burrows (Fisher 1946), and further south, it associates with *Urechis caupo* (see above). Another northeastern Pacific pea crab, *Pinnixa occidentalis* Rathbun, 1893 (synonym: *P. californiensis*), was reported from burrows of *Echiurus* sp. (possibly *E. e. alaskensis*) in Alaska (Rathbun 1904, Schmitt et al. 1973).

5. *Ikedosoma* sp. (Echiuridae)

The snapping shrimp, *Alpheus barbatus*, associates with the deposit-feeding echiuran, *Ikedosoma* sp., in Taiwan (Tzeng and Chen 1992) (Fig. 4a). The same alpheid species also associates with *Ochetostoma erythrogrammon* in southern Japan (Nomura 2000; but see below). *Alpheus barbatus* belongs to the diversified *A. brevirostris* (Olivier, 1811) species group. Most species of this group burrow in fine and coarse sediments, and many associate with gobiid fishes (e.g., Karplus 1987). *Alpheus barbatus* is unique within this species group in having a relatively short, stout major chela and rows of thickened setae on the fingers of the minor chela, forming a dense brush (Fig. 4b; see also Banner and Banner 1982). Although the function of this brush is unknown, it may collect food particles and/or help clean the burrow. Unlike most species of the *A. brevirostris* group, *A. barbatus* does not excavate deep burrows and instead lives in deep coral and rock crevices or under coral rubble (Nomura 2000). The shrimp uses echiuran dwellings as shelter and may occasionally directly profit from the echiuran's feeding activities, e.g., by picking up sediment particles from the echiuran's proboscis or collecting small animals disturbed and exposed by echiuran movements. So the relationship between the echiuran and the shrimp can be described as facultative commensalism. The commensals (mostly copepods) of *Ikedosoma gogoshimense* (Ikeda, 1904) are currently being investigated (G. Itani, pers. comm.).

6. *Lissomyema exilii* (Echiuridae)

In southern Brazil, the relatively small-sized (3~4 cm) echiuran, *L. exilii*, builds U-shaped galleries inside silt-filled shells of various bivalves (*Phacoides*, *Anomalocardia*, *Trachycardium*, *Chione*, and *Dosinia*) or tests of sand dollars

(*Mellita*), embedded 15~22 cm deep in muddy sand (Ditadi 1982). The echiurans communicate with the surface through a pair of narrow channels connecting the burrow to the surface sediment; these channels are usually separated by 4~10 cm (Fig. 5a). Both the channels and the main burrow tunnel ("inhabiting chamber") are lined with hardened mucus (Ditadi 1982). Each channel may be used either as an exit or entrance. The population density at Araçá Flat, São Paulo, was 11 animals/m² (Ditadi 1982).

Burrows of *L. exilii* harbor many taxa, including 5 polychaete worms, viz., *Harmothoe imbricata* (Polynoidae), *Bhawania goodei* (Chrysopetalidae), *Nainereis setosa* (Orbinidae), *Ophiodromus pallidus* (Hesionidae), and *Nematonereis unicornis* (Eunicidae); 2 entoprocts, viz., *Loxosomella zima* and *L. ditadii*; the nudibranch, *Lophodoris scala* (Goniodorididae); the pea crab, *Pinnixa* sp. (Pinnotheridae); and 2 free-living nematodes (Marcus and Marcus 1968 1970, Ditadi 1969 1975 1982).

Ditadi (1982) grouped the associates of *L. exilii* into 3 categories depending on their location in the burrow. In the 1st category are the eunicid polychaete, *N. unicornis*, and 2 unidentified nema-

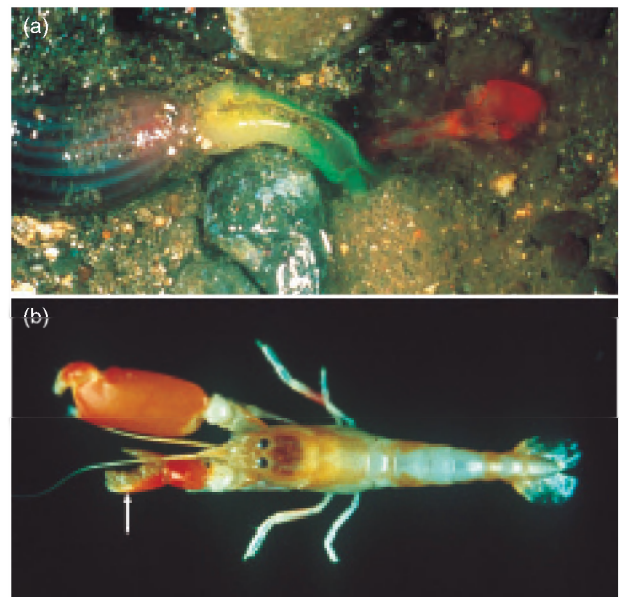


Fig. 4. Association between a rock-dwelling echiuran, *Ikedosoma* sp., and the alpheid shrimp, *Alpheus barbatus*. (a) The echiuran and the shrimp in situ on a rocky intertidal in southern Taiwan; (b) *A. barbatus*, dorsal view of a male specimen (TL ~23 mm) from Taiwan; the arrow shows dense rows of setae on the fingers of the minor chela (a, photograph courtesy of Tai-Taiung Chen; b, photograph by Ming-Shiou Jeng).

todes, which build their own burrows into the walls of the echiuran burrow and maintain only a small communication with it. These animals do not move into the lumen of the echiuran burrow and likely profit only from the host's water current (Ditadi 1982), and therefore, can be qualified as "energy commensals".

In the 2nd category are 2 sessile entoprocts, *Loxosomella* spp. (Fig. 5d-g), which have part of their bodies embedded into the burrow walls, and the major part hanging free in the burrow lumen. *Loxosomella ditadii* (Fig. 5d, e) differs from *L. zima* (Fig. 5f, g) by the presence of an opalescent dorsal shield, which is usually covered with sediment. The entoprocts are typical "energy commensals" (Nielsen 1964, Ditadi 1982), filtering food particles out of the host's water current, although some polychaete-associated loxosomatids attached to the host cuticle may have a negative effect on the host (Williams 2000). The entoprocts associated with *L. exilii* settle along the entire extension of the inhabiting chamber and on the lower 3/4 of both channels. The absence of the entoprocts on the upper 1/4 of the channels is explained by the poorly compacted muddy sand in this portion and maybe also by the absence of the mucus sheath. The settlement of entoprocts in galleries of *L. exilii* suggests that these constructions are indeed relatively stable (Ditadi 1982). Nielsen (1964) noted that entoprocts require a long time to reach sexual maturity, which likely explains why they associate only with long-lived hosts, such as echiurans. Individuals of *L. exilii* survived in aerated aquaria for over 2 yrs.

The 3rd category of *L. exili* symbionts includes all the remaining animals that move freely inside the burrow. The goniodorid nudibranch, *L. scala* (Fig. 5b), feeds, possibly exclusively, on the entoprocts, *Loxosomella* spp., which colonize the burrow walls (Marcus and Marcus 1970, Ditadi 1982). This nudibranch is the only commensal to have been observed to creep on the host's trunk (Ditadi 1982). The polychaetes, *H. imbricata* and *B. goodei* (Fig. 5c), generally prefer other animals' burrows and burrow-like structures (Pettibone 1964, Morris et al. 1980, Martin and Brityaev 1998), and so are not obligate commensals. A burrow of *L. exilii* usually contains only 1 polychaete, although some burrows may contain 2 or 3 different polychaetes of different species (Ditadi 1982). When disturbed, the polychaetes try to hide under the host (Ditadi 1982). Among the 4 polychaete species, the scale worm, *H. imbricata*, appears to be the most "loyal" to echiuran bur-

rows, and its biology is probably similar to that of *Hesperonoe adventor* which is associated with *Urechis caupo* and *Echiurus echiurus alaskensis* (see above). However, the identification of Brazilian specimens as "*H. imbricata*" by Ditadi (1982) needs confirmation. Given its reported "loyalty" to echiuran burrows, these animals may not be *H. imbricata* at all. This species is problematic taxonomically as several morphologically similar species commonly go by this name (L. Harris, pers. comm.). In California, *H. imbricata* (sensu lato) is common in local dock fouling communities, as well as in subtidal habitats, and prefers hard substrates, although occasionally it is also found in soft sediments, where it may live commensally in tubes of terebellid and other polychaete worms (L. Harris, pers. comm.). *Bhawania goodei* is also primarily a free-living worm and only occasionally associates with echiuran (Ditadi 1982) or sipunculid (Gibbs 1969) burrows. In the British Virgin Islands, *B. goodei* was collected from algal washes, coral rubble, and soft sediment around algae or coral, never from another organism's burrows (L. Harris, pers. comm.), while in Bermuda, it is known from "rocks and cobbles" (Sterrer 1986).

The pea crab, *Pinnixa* sp., was considered a "fortuitous commensal" (i.e., an occasional guest) of *L. exilii* (Ditadi 1982). Only 2 young individuals were found in more than 200 investigated burrows. On the other hand, this crab is a common commensal in burrows of the parchment worm, *Chaetopterus variopedatus* Cuvier, 1827 (Chaetopteridae), which is very common at Araçá's sandy mudflats. Therefore, these 2 individuals may have accidentally entered the gallery of *L. exilii* as larvae, and been unable to escape the narrow burrow channels after reaching a certain size (Ditadi 1982).

7. *Bonellia viridis* (Bonelliidae)

The green spoon worm, *Bonellia viridis*, is perhaps the best-known and best-studied echiuran (e.g., Stephen and Edmonds 1972). This large spoon worm (trunk, 8~15 cm, to 1.5 m with proboscis fully extended) lives in burrows made in crevices of rocks, at depths of about 1~30 m, sometimes to 100 m (Schembri and Jaccarini 1978, Riedl 1986). For example, in Malta, *B. viridis* inhabits burrows with multiple exits (never in blind burrows) in calcareous rocks (Schembri and Jaccarini 1978). The substrate may vary from relatively soft globigerinal limestone to relatively hard coralline limestone. Jaccarini and Schembri

(1977a b), and Schembri and Jaccarini (1977) described the feeding behavior and locomotion of the trunk and distally bifurcated proboscis. *Bonellia* is famous for its most-peculiar method of sex determination. The sex of each individual depends on where a larva settles. If it settles alone, it becomes a female, but if it settles on a female it becomes a minute male (Fig. 6b, right) that lives as a degenerate parasite in the uterus and pharynx of the much-larger female (Fig. 6b,

left) (see also Berec et al. 2005).

The infaunal community associated with *B. viridis* was described by Schembri and Jaccarini (1978). By far, the most-frequently observed commensals are the mudshrimp, *Upogebia mediterranea* (Upogebiidae) (Fig. 6c); the snapping shrimp, *Alpheus dentipes* (Alpheidae) (Fig. 6d); the crab, *Xantho hydrophilus granulicarpus* (Xanthidae); and the chiton, *Lepidopleurus cajetanus* (Leptochitonidae) (Fig. 6f). Also often

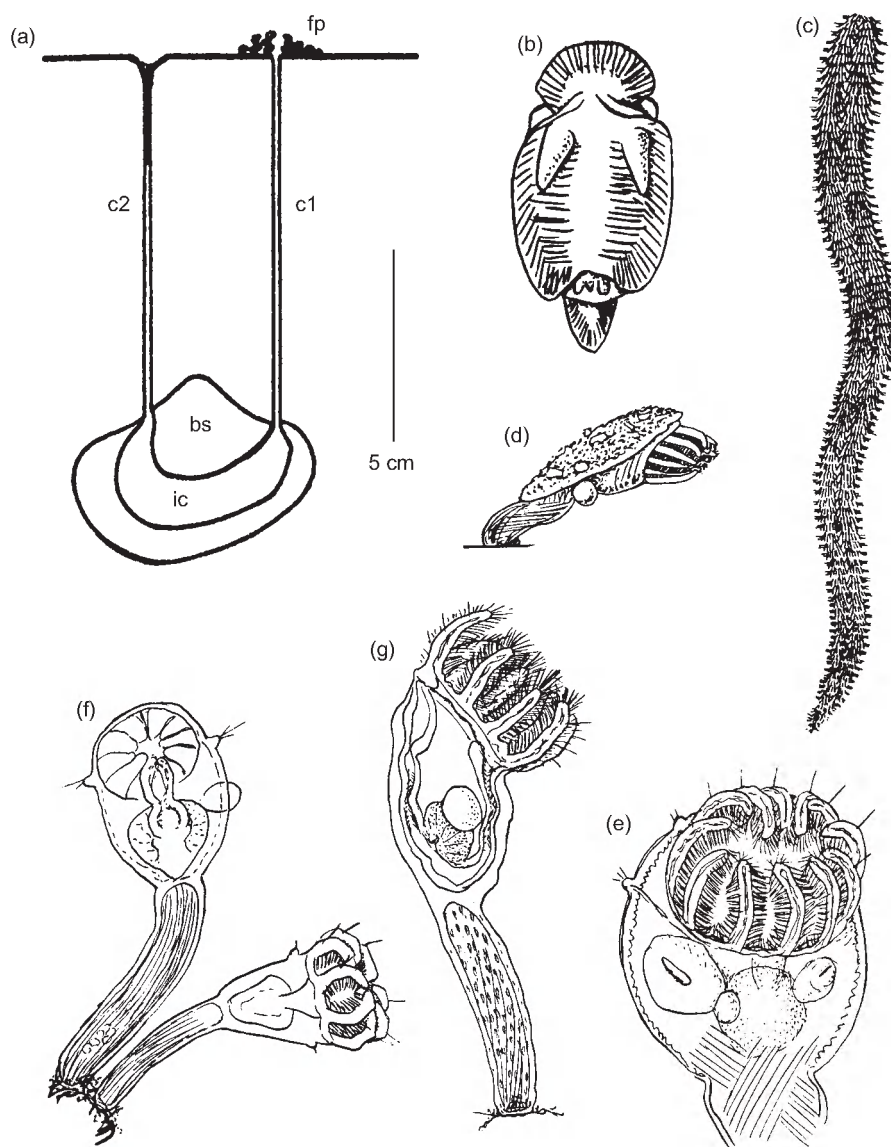


Fig. 5. Commensal community associated with burrows of the echiuran, *Lissomyema exilii*. (a) Typical U-shaped burrow of *L. exilii*. bs, bivalve shell; c1, c2, channels; fp, fecal pellets; ic, inhabiting chamber; (b–d) some animals associated with burrows of *L. exilii*: (b) sea slug, *Lophodoris scala* (Goniadoridae), TL 10 mm; (c) scale worm, *Bhawania goodei* (Polynoidae), TL ~20 mm; (d, e) sessile entoproct, *Loxosomella ditadii* (Loxosomatidae), TL ~0.5 mm, (d) lateral view showing peduncle, trunk, and dorsal shield (s), (e) anteroventral view of trunk, showing extended tentacles; (f, g) sessile entoproct, *Loxosomella zima* (Loxosomatidae), TL ~0.4 mm; (f) general view showing peduncle and trunk; (g) lateral view showing extended tentacles and internal structure (a, from Ditadi 1982; b, from Marcus and Marcus 1970; c, from Sterrer 1986, with permission from W. Sterrer; d–g, from Marcus and Marcus 1968).

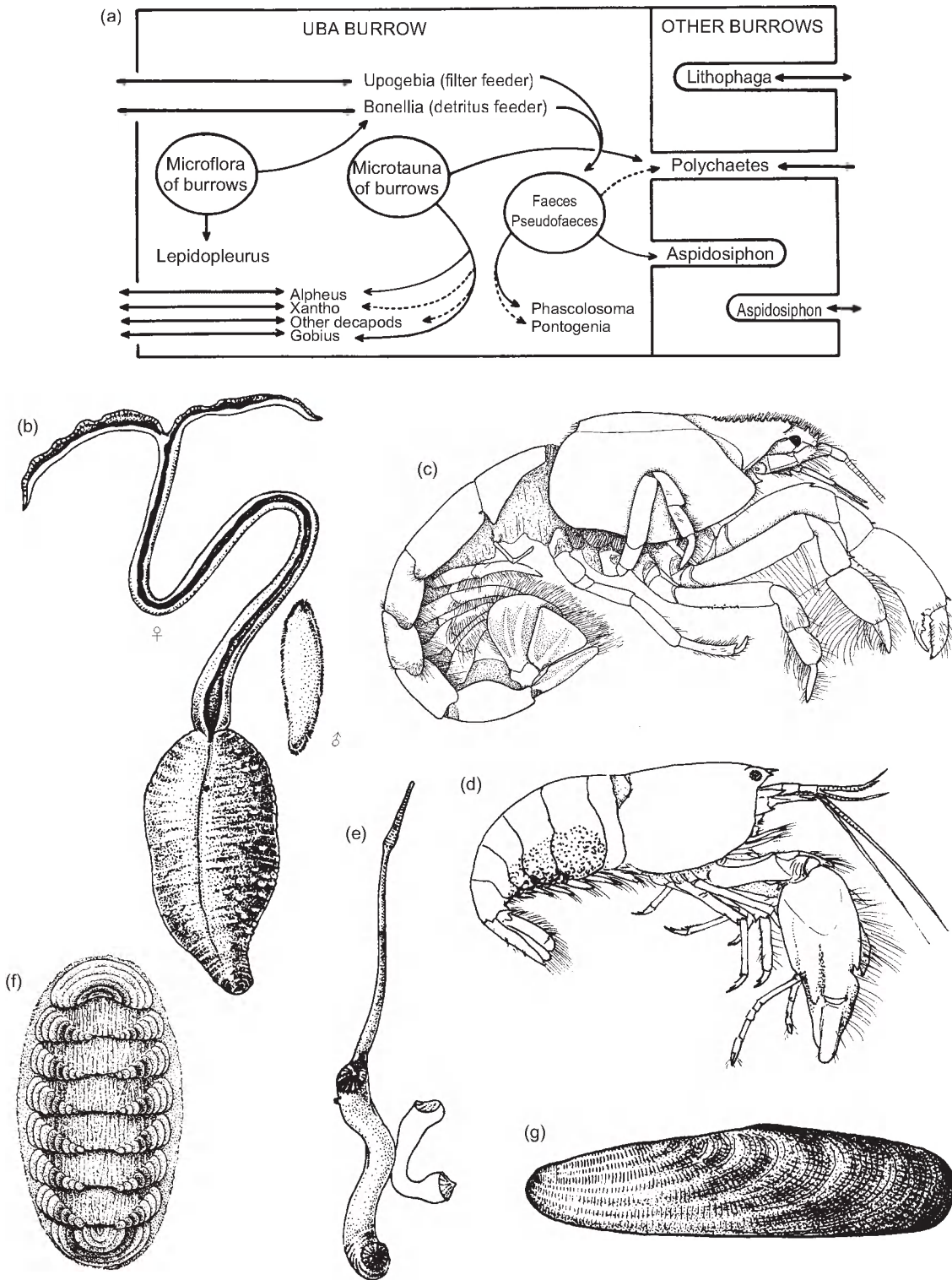


Fig. 6. Commensal macrofauna associated with the rock-burrowing mudshrimp, *Upogebia mediterranea*, and the echiuran, *Bonellia viridis*, in Malta. (a) Diagram of trophic relationships within the *B. viridis*-*U. mediterranea* community; (b) *Bonellia viridis*, female (TL 10 cm) and male (TL 2 mm); (c) *Upogebia mediterranea* (Upogebiidae), TL ~5 cm; (d) *Alpheus dentipes* (Alpheidae), ovigerous female, TL ~3 cm; (e) *Aspidosiphon muelleri* (Sipunculida), TL 2 cm; (f) *Lepidopleurus cajetanus* (Polyplacophora), TL 3 cm; (g) *Lithophaga lithophaga* (Bivalvia), TL 5 cm (a, from Schembri and Jaccarini 1978; b, e-g, adapted from Riedl 1986, copyright Paul Parey Verlag, Berlin; c,d, original drawings by Nguyen. Ngoc-Ho and Arthur Anker, respectively).

encountered were several species of polychaetes, e.g., *Pontogenia chrysocoma* (Aphroditidae). Less-abundant or occasional associates included the sponge, *Cliona* sp.; a non-identified nemertean worm; the sipunculids, *Phascolosoma granulatum* and *Aspidosiphon muelleri* (Fig. 6e); the rock-boring bivalve, *Lithophaga lithophaga* (Lithophagidae) (Fig. 6g); the goby, *Gobius geniporus* (Gobiidae); the shrimps, *Athanas nitescens* (Alpheidae), *Periclimenes* cf. *scriptus* (Palaemonidae), and *Lysmata seticaudata* (Hippolytidae); the ghost shrimp, *Pestarella candida* (Callianassidae); and the squat-lobster, *Galathea intermedia* (Galatheidae). Most of these animals are primarily free-living. For instance, *A. dentipes* lives in many habitats, including rock crevices, coralline algae, polychaete tubes, and sponges (e.g., Coutière 1899, Lewinsohn and Galil 1982, Garcia Raso and Fernandez Muñoz 1988).

Schembri and Jaccarini (1978) found 4 types of burrows. Larger burrows were inhabited mainly by *U. mediterranea*, *B. viridis*, and *A. dentipes*, and therefore, were called “UBA burrows”. Based on experimental evidence, Schembri and Jaccarini (1978) suggested that *U. mediterranea* mechanically excavated the UBA burrows (Aasgaard et al. (1997) argued that the substrate in Malta is soft enough to use the term burrows instead of boreholes, as the latter is usually used when hard ground is involved.), and *B. viridis* eventually secondarily modified them “by secretion of an acidic mucus and gentle mechanical action”. Therefore, the echiuran, in this case *B. viridis*, actually lives as a commensal in the burrows of a mudshrimp host.

UBA burrows were described by Schembri and Jaccarini (1978) as an “interconnecting and apparently randomly oriented system of winding tunnels with many openings to the outside”. These burrows included 2 types of tunnels: main tunnels and blind tunnels. The walls of main tunnels were covered with coarse scratches, occasionally obscured by a green-tinted paste of silt, and were free of encrusting organisms, except for areas around the tunnel opening and a short distance from the opening inside the tunnel. Blind tunnels appeared to be unfinished tunnels under construction, and some contained small rock fragments, plant material, other debris, and a black, hydrogen sulfide-smelling mud (Schembri and Jaccarini 1978). All specimens of *B. viridis* and *A. dentipes*, and most specimens of *U. mediterranea* were found inside the main tunnels, with *B. viridis* and *U. mediterranea* occupying the deepest parts,

and *A. dentipes* occurring in all regions of the burrow system. The stone crab, *X. granulicarpus*, also occurs throughout the burrow system, while the sipunculid, *P. granulatum*, and the polychaete, *P. chrysocoma*, mostly inhabit the deeper portions. An unidentified nemertean worm usually occupies areas close to the openings. However, no other animals were found in those stretches of the burrow occupied by this nemertean, possibly because of its sticky and slightly toxic mucus (Schembri and Jaccarini 1978). Most other organisms associated with the UBA burrows, e.g., the chiton, *L. cajetanus*; the shrimp, *A. nitescens*, *L. seticaudata*, and *P. cf. scriptus*; and the squat-lobster, *G. intermedia*, were extracted from the 1st 10 cm of the main tunnels. These animals obviously use only the superficial portions of the burrow system as a shelter, and were guests rather than permanent commensals.

Like all species of *Alpheus*, the snapping shrimp, *A. dentipes*, is armed with a massive snapping claw used both offensively and defensively and which can supply supplementary protection to other burrow inhabitants. The shrimp would likely react aggressively to all burrow intruders. Schembri and Jaccarini (1978) did not specify whether the shrimp occurred in groups, as single individuals, or in pairs, although this latter possibility is most likely, as most *Alpheus* spp. are usually quite intolerant to conspecifics of the same sex (*A.* Anker, pers. obs.). Additional chemical protection to the community associated with *U. mediterranea* and *B. viridis* may come from *B. viridis* itself, which releases a green-tinted mucus in abundance when molested. This mucus and the body fluids contain the pigment, bonellin, which is known to be toxic to other animals, making *Bonellia* unpalatable to many potential predators (Schembri and Jaccarini 1979).

Three other burrow types were also found in these rocks. The rock-boring sipunculid, *A. muelleri*, inhabits long, blindly ending tunnels of 3–6 mm in diameter, which occasionally open into UBA burrows (Schembri and Jaccarini 1978). The sea date, *L. lithophaga*, also excavates blind, smooth-walled tunnels. However, these tunnels always open to the exterior and never into UBA burrows or tunnels of *A. muelleri*. The 4th category of burrows consists of tunnels inhabited by polychaetes. These are actually cracks in the rocks that are occupied and eventually enlarged by various errant polychaetes (Schembri and Jaccarini 1978). Most of the tunnels inhabited by polychaete were only a few millimeters in width and many opened

into UBA burrows. Figure 6a illustrates possible trophic relations within the animal community associated with *B. viridis* and *U. mediterranea*.

8. *Maxmuelleria lankesteri* (Bonelliidae)

Most aspects of the biology of the northeastern Atlantic spoon worm, *Maxmuelleria lankesteri*, including burrow morphology, burrowing, feeding, and surface activity, were investigated in heavily bioturbated sediments off Scotland (Hughes et al. 1993 1996, Nickell et al. 1995). Burrows made by this species are U-shaped (Hughes et al. 1996), contrary to an earlier suggestion that they were L-shaped (Nickell et al. 1995: fig. 2; however, these authors suggested that the casts could have been incomplete because of the lateral extent of the burrow, and because the presence of the worm may have blocked passage of the resin).

Several polychaetes and 2 bivalves, *Mysella bidentata* (Montacutidae) and *Saxicavella jeffresii* (Hiatellidae), were found to colonize the burrow walls of *M. lankesteri* (Nickell et al. 1995). The colorful polychaete, *Ophiodromus flexuosus* (Hesionidae), occasionally enters the burrow of *M. lankesteri*. The laomediid mudshrimp, *Jaxea nocturna*, may modify the borrows by forming side branches near the tunnel end (Nickell et al. 1995: fig. 2c), while the large black goby, *Gobius niger* (Linnaeus, 1758), sometimes alters the upper burrow around the opening (Nickell et al. 1995).

Most animals residing within the burrows of *M. lankesteri* also occur in the background sediment and thus are not obligate commensals. For instance, the bivalve, *Mysella bidentata*, normally lives in muddy sand or fine gravel and in crevices of dead oyster valves, and is occasionally found associated with the brittlestar, *Amphiura brachiata* (Montagu, 1804), or in burrows of the sipunculid, *Golfingia* sp. (Ockelmann and Muus 1978). Similarly, the polychaete, *O. flexuosus*, also lives freely on the sediment surface, often foraging among sea pens, *Virgularia mirabilis* (Müller, 1776), or near the spread arms of feeding brittle stars, *Amphiura filiformis* (Müller, 1776) (photographs by B. Picton). Within the echiuran burrow, the bivalve and polychaete benefit from the host's irrigation activities, which supply both oxygenated water and food, and they may also gain some refuge from predators. Some facultative commensals may be on an evolutionary route towards more-stable and species-specific associations, because they belong to genera containing obligate commensals of other organisms. For

instance, the bivalve, *Mysella cuneata* (Verrill and Bush, 1898), closely related to *M. bidentata*, associates with burrows of the subtidal sipunculid, *Phascolion strombi* Montagu, 1804, which builds galleries in discarded gastropod shells (Hampson 1964, Gage 1968b). The hesionid genus *Ophiodromus* contains several other obligate or facultative commensals, such as *O. pugettensis* (Johnson, 1901), which frequently associates with the bat sea star *Asterina miniata* (Brandt, 1835) (Morris et al. 1980, Ricketts et al. 1985, Martin and Britaeyev 1998), although it also lives freely in soft sediments and hard substrates (L. Harris, pers. comm.).

9. *Anelassorhynchus* spp. (Thalassematidae)

In Japan, a small galeommatid bivalve, *Scintilla thalassemicola*, and a similarly small alpheid shrimp, *Athanopsis dentipes* (Fig. 7a), appear to be associated with the thalassematid echiuran, *Anelassorhynchus mucosus* (Habe 1962, Miya 1980, Morton and Scott 1989). The bivalves usually attach themselves to the proboscis and body of the echiuran, while the alpheids live in the burrows. These 2 associations and the burrows of *A. mucosus* remain to be studied. Miya (1995) reported *A. dentipes* from burrows of "yumushi", which is the Japanese name for another echiuran species, *Urechis unicinctus* (G. Itani, pers. comm.) (see above). Therefore, Miya (1995) may have corrected the name of the host, so the actual host of *A. dentipes* may be *U. unicinctus*, not *A. mucosus* (G. Itani, pers. comm.). The copepod, *Echiurophilus fizei*, was collected from burrows of the closely related *Anelassorhynchus inansensis* (Boxshall and Halsey 2004, as *Thalassema inansense*).

10. *Thalassema* spp. (Thalassematidae)

Some species of the genus *Thalassema*, e.g., *T. fuscum* Ikeda, 1904 from eastern Asia, build simple burrows with 1 opening (Morton and Morton 1983), while others, such as the European *T. thalassema* (Pallas, 1776), build U-shaped burrows with 2 openings (Nickell and Atkinson 1994). *Thalassema fuscum* basically makes a short, vertical, blindly ending shaft (Morton and Morton 1983: fig. 9.14.B). Such simple burrows, being almost entirely occupied by the host, are apparently unsuitable for commensals, which may explain why no commensals were found in burrows of *T. fuscum* in Hong Kong (Morton and Morton 1983).

The pinnotherid crab, *Pinnixa lunzi* (Fig. 7c), was found in burrows of *Thalassema harmani* (also known as *T. hartmani*) in the southeastern United States. Like many other *Pinnixa* species, *P. lunzi* is a facultative commensal of *T. harmani*; it also inhabits burrows of polychaetes, sipunculids, holothurians, cerianthid tubes, and tubes of tubicolous amphipods (Williams 1984) and can survive extended periods of time without a host (Boesch 1971). The copepod, *Goidelia pelliviva*, was collected from the body surface of a non-identified species of *Thalassema* on the mudflats of the Korean Yellow Sea (Kim 2000). According to Boxshall and Halsey (2004), both *Goidelia* and *Echiurophilus* (see above) belong to the cyclopoid family Echiurophilidae, although Kim (2000) treated *Goidelia* as a poecilostomatoid.

11. *Listriolobus sorbillans* (Thalassematidae)

The small bivalve, *Pseudopythina ochetostomae* (Fig. 8b, c) (erratically assigned to the families Lasaeidae, Kelliidae, or Galeommatidae), lives commensally in burrows of the echiurans, *Listriolobus sorbillans* (formerly *L. riukiensis* Sato, 1939, cf. Nishikawa 2004) and *Ochetostoma erythrogrammon*, on tidal flats of the Ryukyu Is. (Kosuge et al. 2003) (see below). These clams usually attach to the burrow wall, and rarely directly on the host itself (Fig. 8a). Each burrow is typically inhabited by a single bivalve, but some may contain up to 5 individuals. *Pseudopythina ochetostomae* occurs most commonly with *O. erythrogrammon* (92% of the likely U-shaped burrows), but also occurs in 67%~78% of the smaller, blindly ending (Fig. 8a) burrows of *L. sorbillans* (Kosuge et al. 2003). Clearly this bivalve associates with multiple hosts.

12. *Listriolobus pelodes* (Thalassematidae)

The echiuran, *Listriolobus pelodes*, does not excavate permanent burrows, but lives in open exposed pits, sweeping its proboscis across the sediment (D. Cadien, pers. comm.; L. Harris, pers. comm.); the echiurans can afford to live in such a partially exposed way possibly because they appear to be distasteful to fish predators (L. Harris, pers. comm.). Pilger (1980) and Stull et al. (1986) give the most-detailed reports of its biology and ecology off the Californian coast.

The scale worm, *Hesperonoe laevis* (Polynoidae), associates with *L. pelodes* communities (Hartman 1961 1968, Ruff 1995, Sato et al.

2001). Although from the same genus as *H. adventor*, which associates with burrows of *Urechis caupo* (see above), *H. laevis* appears to have a different lifestyle. *Hesperonoe laevis* was initially found in areas with abundant *L. pelodes*. In these areas *L. pelodes* sporadically occurs in extremely high numbers, then virtually disappears, while the density of *H. laevis* does not change significantly (D. Cadien, pers. comm., C. Brantley, pers. comm.). In most recent samples, *H. laevis* is rarely found without *L. pelodes* (C. Brantley, pers. comm.). Unfortunately, because these communities are sampled by grab or trawl, direct evidence of a close association of *H. laevis* with *L. pelodes* is lacking; *H. laevis* may just live in the same general area (L. Harris, pers. comm.).

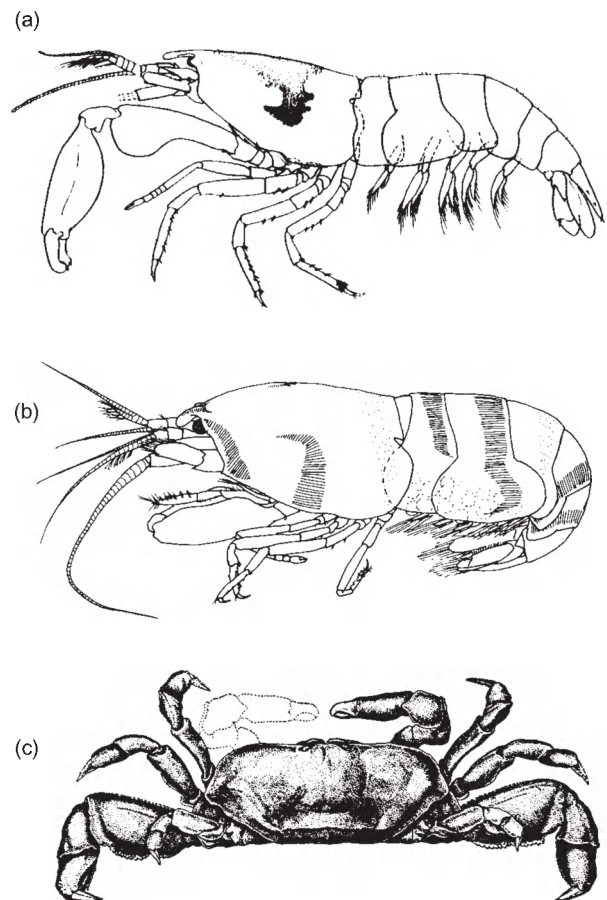


Fig. 7. Crustacean commensals of echiuran burrows. (a) *Athanopsis dentipes* (Alpheidae), TL 14 mm; (b) *Athanopsis rubricinctata* (Alpheidae), TL 12 mm; both described from burrows of thalassematid echiurans; (c) *Pinnixa lunzi* (Pinnotheridae), CW 21 mm, occasionally found in burrows of the echiuran, *Thalassema harmani* (a, from Miya, 1980; b, from Berggren 1991, copyright by The Crustacean Society; c, from Glassell 1937 in Williams 1984).

13. Ochetostomatinae, gen. et sp. indet. (Thalassematidae)

A small alpheid shrimp, *Athanopsis rubricincta* (Fig. 7b), was collected from burrows of a non-identified echiuran from the thalassematid subfamily Ochetostomatinae in Mozambique (Berggren 1991). The closely related *A. dentipes* associates with either *Anelassorhynchus mucosus* or *Urechis unicinctus* in Japan (Miya 1980 1995; see also above).

14. *Ochetostoma azoricum* (Thalassematidae)

The deep burrows of the Azorean innkeeper worm, *Ochetostoma azoricum*, are L-shaped, i.e., vertical or oblique and with only 1 opening, although some U-shaped burrows are known (Rogers and Nash 1996: fig. 7). Only 1 species of bivalve was recovered from these burrows; however, it has not yet been identified to family level.

15. *Ochetostoma erythrogrammon* (Thalassematidae)

A. Indo-West Pacific

Ochetostoma erythrogrammon is probably the best-studied echiuran in the tropical Indo-West Pacific. Its burrow morphology and feeding behavior were studied on intertidal sandy mud of Pulau Hantu, Singapore (Chuang 1962a). Here, its burrows are U-shaped with 2 vertical or oblique tunnels, each 20 cm long, connected by a horizontal tunnel of 24~45 cm, although Stephen and Robertson (1952) noted that in eastern and southern Africa, its horizontal tunnel may reach 90 cm. At low tide, the proboscis is extruded to collect sand grains and detritus from the surface. The fully extended proboscis, exceeding 25 cm in some individuals, becomes thin and narrow, and its entire ventral surface accumulates sand grains, detritus, and extruded mucus. When fully loaded (or when disturbed) the proboscis is withdrawn,

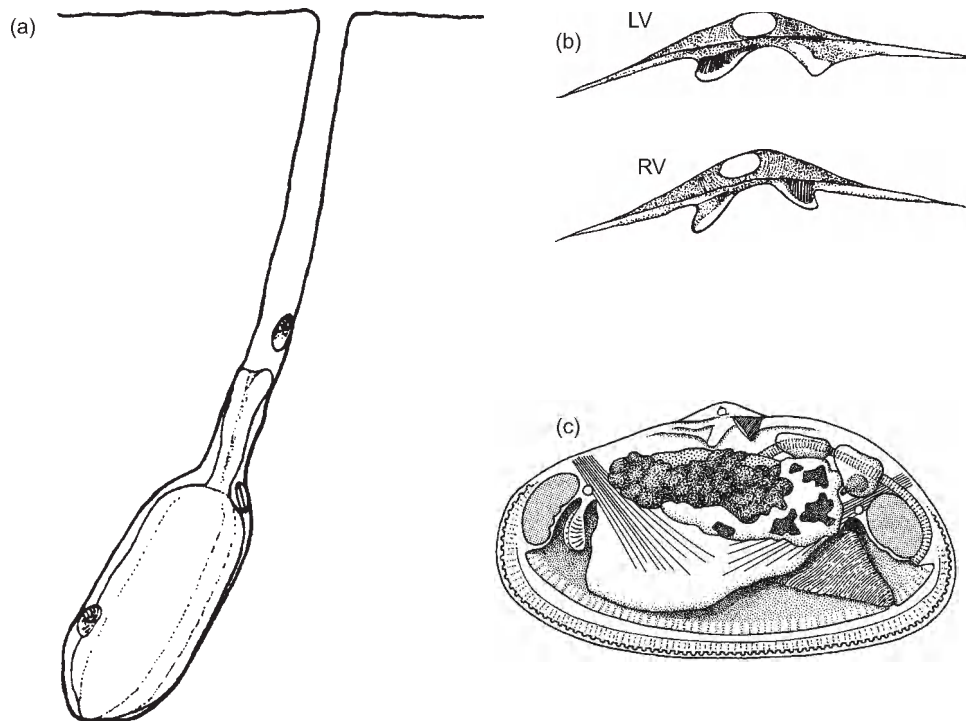


Fig. 8. Commensal bivalve *Pseudopythina ochetostomae* (Lasaeidae), TL ~7 mm, associated with echiuran burrows. (a) Blind burrow of the echiuran, *Listriolobus sorbillans*, showing the host and 3 individuals of *P. ochetostomae*; (b) *P. ochetostomae*, valves in dorsal view (LV and RV, left and right valves, respectively); (c) same, internal anatomy (for abbreviations see Jespersen et al. 2002) (a, b, adapted from Kosuge et al. 2003; c, adapted from Jespersen et al. 2002, with permission from Åse Jespersen and Springer Verlag, Heidelberg).

leaving a narrow track on the wet muddy sand. At the end of a period of low tide these tracks radiate in different directions from the burrow opening (see Chuang 1962a: fig. 1). Chuang described in detail the ciliary currents on the proboscis, the course of the accepted and rejected particles (Chuang 1962a), and the respiratory physiology (Chuang 1962b), but neither study mentioned any associated fauna.

The U-shaped burrows of *O. erythrogrammon* from the muddy shores of Hong Kong contain a diverse community of associates (Fig. 9) (Morton and Morton 1983). This community includes a non-identified red polyclad flatworm; the bivalve, *Pseudopythina ochetostomae* (see above); a non-identified polynoid worm; the small, dark brown risoid snail, *Sigaretornus planus* (Tornidae); the pinnotherid crab, *Mortensenella forceps*; and the tiny purplish poecilostomatoid copepod, *Hemicyclops mortoni*, from the family Clausidiidae (Morton and Morton 1983, Morton 1988; for descriptions of commensals see Rathbun 1909, Boxhall and Humes 1987, Manning and Morton 1987, Morton and Scott 1989).

At least two of these associates can occur together in the same burrow but they are usually spatially separated from each other (Morton and

Morton 1983, Morton 1988). The red flatworm (Fig. 10c) and groups of 3 or 4 copepods (*Hemicyclops mortoni*, Fig. 10b) occur just inside the burrow entrance. The copepods swim around when the burrow is filled with water at high tide, and skitter over the surface of the burrow walls when the tide is out (Morton 1988). Noteworthy, a closely related copepod species, *Hemicyclops ventriplanus* Kim, 2000, occurs in burrows of the mudshrimp, *Upogebia major* (De Haan, 1849), in Korea (Kim 2000). The presence of 2 closely related copepods in burrows of *O. erythrogrammon* and *U. major* may indicate once more that echiurans and upogebiids frequently share the same or closely related associates. However, *Hemicyclops* spp. live symbiotically with many other hosts, such as corals, polychaetes, ocypodid crabs, and upogebiid mudshrimps (e.g., Humes, 1984 1995, Ho and Kim 1990 1991, Itoh and Nishida 1998 2002, Kim 2000).

The snail, *Sigaretornus plana* (Fig. 10d), occurs in deeper parts of the burrow, where it crawls around and feeds by rasping away the mucous-bound material, with which the echiuran lines its burrow. At rest, it flattens itself against the burrow wall. Usually 3 or 4 snails occupy each burrow (Morton 1988). The small, darkly stained

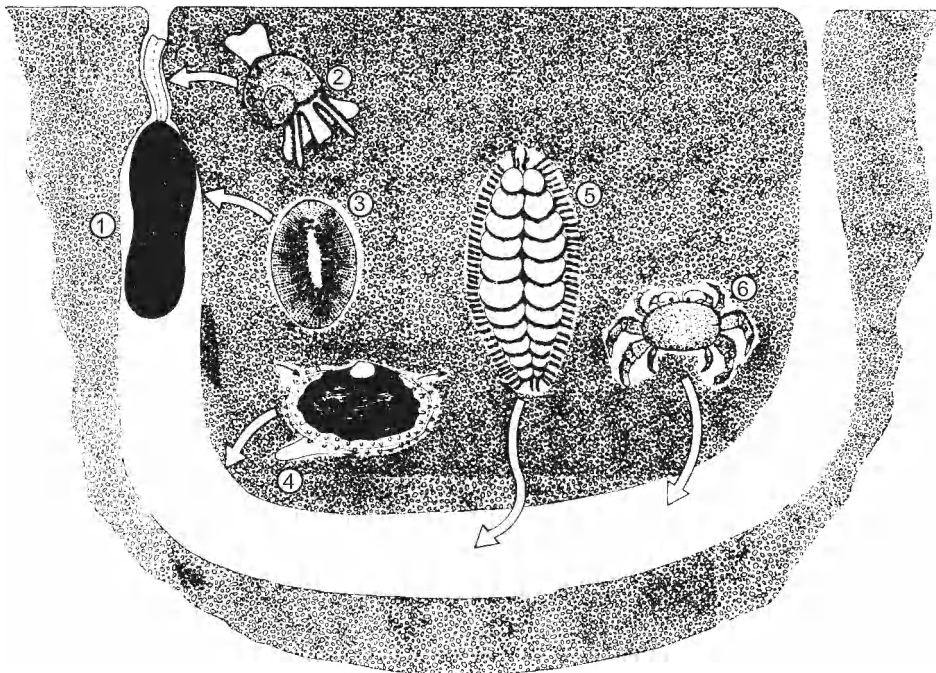


Fig. 9. Diagram showing commensal community associated with large U-shaped burrows of the echiuran, *Ochetostoma erythrogrammon*, in Hong Kong (figures of animals not to scale). (1) Host; (2) the gastropod, *Sigaretornus plana*; (3) unidentified flatworm; (4) the bivalve, *Pseudopythina ochetostomae* (as "cf. *Achasmea* sp." in Morton and Morton 1983: 176); (5) unidentified polynoid worm; (6) pinnotherid crab, *Mortensenella forceps* (from Morton and Morton 1983, with permission from Hong Kong Univ. Press).

bivalve, *Pseudopythina ochetostomae* (Figs. 8b, c, 10e), also occurs deep inside the burrow, where it flattens itself against the burrow wall to avoid being dislodged by activities of the echiuran, and feeds by filtering small organic particles out of the passing water (Morton 1988, Morton and Scott 1989). This species is hermaphroditic, although males and females may occur (Jespersen et al. 2002). Kosuge et al. (2003) also found *P. ochetostomae* in burrows of another echiuran, *L. sorbillans* (see above).

The pea crab, *Mortensenella forceps*, possesses tiny sharp-pointed claws (Fig. 10a) used to collect fragments of material from the burrow wall. The body is flattened and setose, as in most burrow-dwelling pinnotherids; however, the eyes are not reduced. This crab also occurs in burrows of the sipunculid, *Siphonosoma cumanense* (Keferstein, 1867) (Manning and Morton 1987, Morton 1988).

A small varunid crab, *Acmaeopleura toriumii* (Fig. 3b), inhabits burrows of the echiuran, *O. erythrogrammon*, or mudshrimp, *Upogebia major*, in Hong Kong (Davie 1992). When living with *U. major*, these crabs are commensal omnivores that never cling onto their hosts or feed on their tissues (Itani 2002). The association between *A. toriumii* and *O. erythrogrammon* may be similar, but remains to be investigated.

The snapping shrimp, *Alpheus barbatus* (Fig.

4b), is also a commensal of the echiurans, *O. erythrogrammon* and *Ikedosoma* sp., in Japan (Nomura 2000) and Taiwan (Tzeng and Chen 1992; see above), respectively. The shrimp's biology is discussed under *Ikedosoma* sp. (above).

Nomura (2000) reported *O. erythrogrammon* from crevices or spaces beneath stones on reef flats, while Morton and Morton (1983) found it in mudflats, where it makes deep, U-shaped burrows. Do these echiurans with such radically different biological characteristics and habitats belong to the same species? According to T. Nishikawa (pers. comm.), *O. erythrogrammon* does indeed occur in burrows on sandy substrata and also in crevices and under stones or coral boulders. In addition, Nishikawa et al. (1995) reported *O. erythrogrammon* from a small amount of sand in crevices of stones or under *Hormomya* beds. Nomura's (2000) color photograph of *O. erythrogrammon* shows an echiuran very similar in external appearance to the echiuran identified as *Ikedosoma* sp. in Tzeng and Chen (1992) (Fig. 4a) or as *Listriolobus riukiensis* (Bonelliidae) in Chen (2001). All these echiurans are also similar in color, occur in the same habitat (gravel with rocks and rubble) and are associated with the same shrimp, *A. barbatus*. Therefore, the question of whether both Nomura's (2000) and Tzeng and Chen's (1992) echiurans belong to the same species, either *Ikedosoma* sp. or *O. erythrogram-*

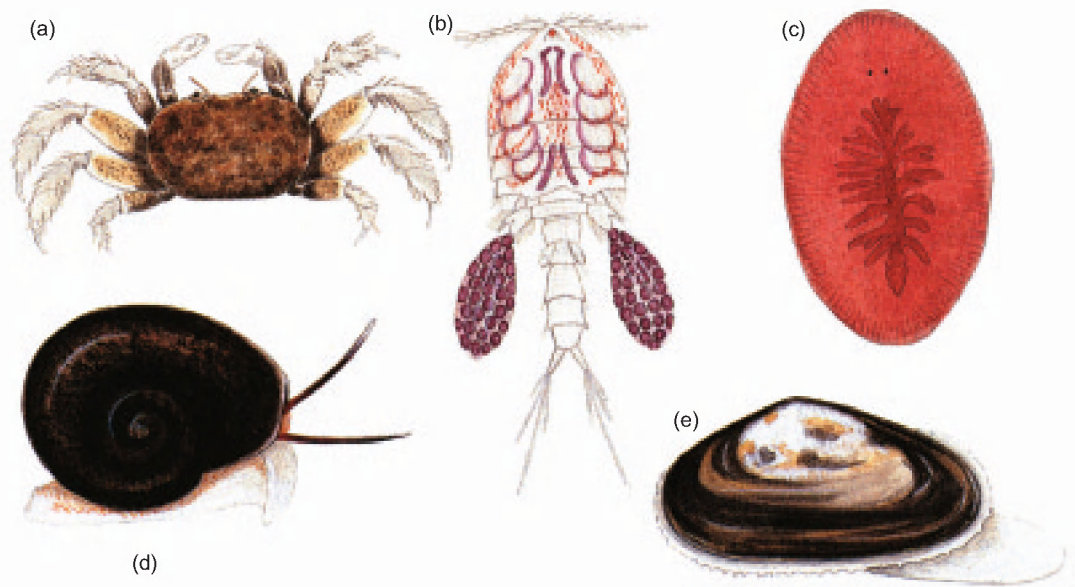


Fig. 10. Some commensals of the echiuran, *Ochetostoma erythrogrammon*, in Hong Kong (not to scale). (a) The pinnotherid crab, *Mortensenella forceps*; (b) the copepod, *Hemicyclops mortoni*; (c) an unidentified red polyclad flatworm; (d) the gastropod, *Sigaretornus plana*; (e) the bivalve, *Pseudopythina ochetostomae* (from Morton 1988, with permission from Hong Kong Univ. Press).

mon, remains open.

B. Western Atlantic

Burrows of *O. erythrogrammon* at Araçá, São Paulo, southern Brazil, like those of the closely related *O. azoricum* from the Azores (Rogers and Nash 1996; see above), were irregularly L-shaped, not U-shaped, and so appeared to have only 1 entrance (Ditadi 1982). The tunnels appeared to end blindly (the end of the burrow could not be reached by polyethylene injections), and Ditadi could find no obvious exit opening onto the beach. More interesting, however, each burrow of *O. erythrogrammon* at Araçá had an oblique side arm connecting to the surface close to the main opening, thus creating an entrance opening with 2 holes, separated by 5 cm from each other and connecting about 5 cm under the surface (see Ditadi 1982: figs. 1C, 2). Ditadi found no commensals with this species in southern Brazil. Sterrer (1986) stated that in Bermuda *O. erythrogrammon* “forms deep burrows in intertidal muds”, but did not mention the shape of the burrows or the presence of any commensal animals.

In Venezuela, the burrows of *O. erythrogrammon* were sampled from a shallow water bank (maximum depth at low tide about 1 m), between the beach and a mangrove “island”, and close to extensive sea grass beds and mangroves of the Parque Nacional La Restinga. This site was about 100 m from the docks and the marine laboratory of the Universidad de Oriente in Boca del Río on the southern shore of Peninsula Macanao, Isla Margarita, off the northeastern coast of Venezuela. Animals were collected using 2 bait pumps (“yabby pumps”) and a sieve with about a 2 mm mesh size.

Burrows of *O. erythrogrammon* were found in fine but relatively firm sand mixed with mud, gravel, shell, wood debris, etc. The main burrow openings were recognizable as large, flat mounds with a relatively small (usually not exceeding 0.5 cm in diameter) hole on the top. The burrow form remains to be studied, but they may be either U-shaped or L-shaped (see above). Both the water and the sand extracted from the burrow were dark gray to black, indicating the anoxic conditions of the deeper sediment. The other burrowing fauna consisted mainly of the mudshrimp, *Upogebia omissa* (Fig. 11c) (for description see Gomez Corrêa 1968, Williams 1993). Two species of the pinnotherid genus *Pinnixa* White, 1846 (*sensu lato*) were collected from the burrows. The smaller brown-marbled species, of which 5 specimens

were collected, has an oval-shaped, rugose (sculptured) carapace (Fig. 11d, e) and was identified as *Pinnixa* sp. aff. *chaetoptera*. The males of this species are slightly smaller sized, and the carapace in males is also more angular compared to the rounded carapace in females (cf. Figs. 11d, e); the females also have more-weakly developed cardiac ridges (D. Felder, pers. comm.). The larger, orange-colored species, of which only 1 specimen was obtained, has a smooth, suboval-triangular carapace and was tentatively identified as *Pinnixa* sp. aff. *monodactyla* (Fig. 11f) (D. Felder, pers. comm.). One of the samples also contained a single specimen of a yet unidentified small bivalve (Fig. 11g) from the family Sportellidae, possibly close to the genus *Basterotia* Mayer, 1859 (P. Valentich-Scott, pers. comm.). The life history of these small bivalves is very poorly known (see Coan 1999 for most recent review), but some species are commensals (Coan 1999, P. Valentich-Scott, pers. comm.). This bivalve may just occur in the background sediments and not, or only occasionally, in *O. erythrogrammon* burrows.

The large echiurans (with a maximum length at full extension of about 15 cm) were not easy to extract from their deep burrows, and the proboscis was often lost. The smaller upogebiids (with a maximum total length of about 4 cm) were more easily collected. On several occasions, *Pinnixa* spp. were collected together along with the detached proboscis of the echiuran. At least the 2 pea crabs may be associated with either *O. erythrogrammon* (more likely) or *U. omissa*, or perhaps with both hosts. The burrow openings of *O. erythrogrammon* and *U. omissa* were sometimes as close as 5–10 cm, and may have interconnected under the sediment surface, allowing commensals to pass from one burrow to another. Echiuran burrows may also have collapsed more easily so that water entered from neighboring mudshrimp burrows (G. Itani, pers. comm.). This water may have contained mudshrimp and their commensals, pumped by the suction pump, together with the water containing the echiurans. Since burrow morphology, stability of the burrow walls, and interconnections with other burrows have not been determined, the actual host of the aforementioned pinnotherids and bivalve remains unknown. Therefore, more work is needed to determine the hosts and host specificity of these commensals.

The finding of *O. erythrogrammon* in Isla Margarita constitutes the 1st report of an echiuran from Venezuelan waters (G. Pereira, pers. comm.) and only the 3rd confirmed record of *O. erythro-*

grammon in the Western Atlantic. Except for 2 figures (habitus and nephridia) provided by Sterrer (1986), no published illustrations exist of the Western Atlantic specimens. Therefore, we provide a short taxonomic description and figures of the newly collected Venezuelan material deposited at the Zoological Museum, Moscow State University (ZMMU).

Description of *Ochetostoma erythrogrammon* from Venezuela

Genus *Ochetostoma* Leuckart and Rüppell, 1828
***Ochetostoma erythrogrammon* Leuckart and Rüppell, 1828 [sensu lato]**

Figs. 8a, b, 9a-d

Material examined: Three specimens, ZMMU,

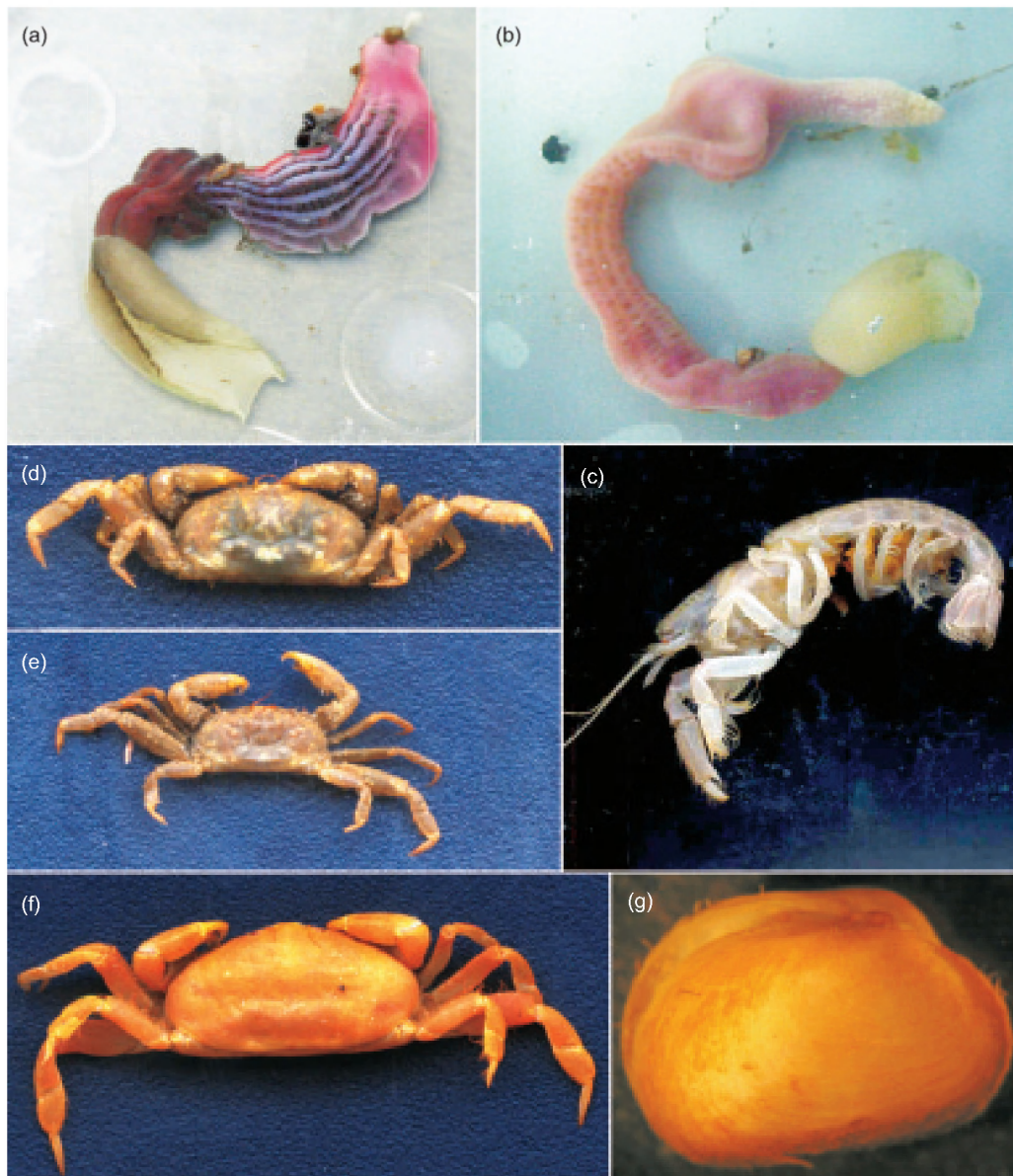


Fig. 11. Infaunal animals collected from burrows in Bocal del Río, Isla Margarita, Venezuela. (a, b) The echiuran, *Ochetostoma* cf. *erythrogrammon*, TL 10~15 cm; (c) the mudshrimp, *Upogebia omissa* (Upogebiidae), TL 4~5 cm; (d, e) the pea crab, *Pinnixa* sp. aff. *chaetoptera* (Pinnotheridae), female (d), CW ~10 mm and male (e), CW ~7 mm; (f) the pea crab, *Pinnixa* sp. aff. *monodactyla*, female, CW ~15 mm; (g) unidentified sportellid bivalve, possibly *Basterotia* sp., TL 12.1 mm.

Venezuela, Estado Nueva Esparta, Isla Margarita, Peninsula Macanao, Boca del Rio, in front of marine laboratory, depth 0.5~0.6 m, sand and sandy mud close to sea grass beds and mangroves, yabby pump, A. Anker and J. A. Vera Caripe colls., 13~14 Dec. 2003.

Diagnosis: Proboscis 1/3~3/4 length of body (Fig. 12a); dorsal surface bright green, ventral side yellow with a mauve line on each side. Body up to 80~160 mm in length; posterior region violet and marked with light- to dark-red longitudinal grooves (Fig. 12a, c). Longitudinal muscles assembled into 14 bundles (14~18 according to Fischer 1926: 115). Transverse fascicles of oblique muscles situated between longitudinal muscles. Three pairs of nephridia (Fig. 12d), 1st pair opening in front of setae; nephrostome with spirally coiled lips. Rectal cecum present. Anal vesicles developed as very thin brown tubes (Fig. 12b).

Color: Dark reddish-purple to reddish-brown, proboscis pale yellow (Fig. 11a, b), blood dark red.

This color generally agrees with the color pattern of specimens from Bermuda (Sterrer 1986) and the Indo-West Pacific (Morton and Morton 1983, Morton 1988).

Distribution: Indo-West Pacific: Red Sea (Stephen 1952, Wesenberg-Lund 1957); Indian Ocean, e.g., Somalia, Zanzibar, Mauritius (Shiple 1899 1902, Stephen and Robertson 1952, Wesenberg-Lund 1959, Murina 1981); Malaysia, Indonesia (Sluiter 1884, 1902); Annam (Vietnam) (Wesenberg-Lund 1959); Hong Kong (Morton and Morton 1983); Japan (Sato 1935, Nishikawa et al. 1995); and tropical Pacific Ocean (Wesenberg-Lund 1954); Eastern Atlantic: Mediterranean Sea (Herubel 1904), Cape Province of South Africa (Wesenberg-Lund 1959); and Western Atlantic: Bermuda (Sterrer 1986), Bahamas (Wesenberg-Lund 1959), Venezuela (present study), and Brazil (Ditadi 1982).

Ecology: This species was reported to occur in a variety of habitats, including crevices under-

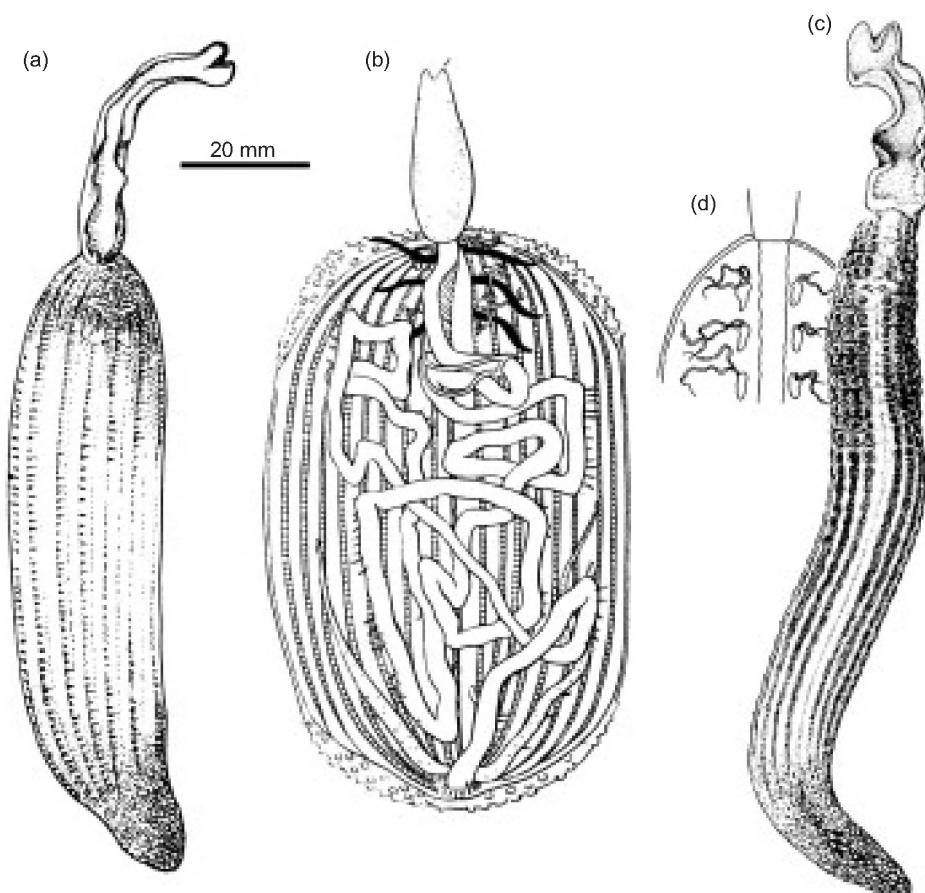


Fig. 12. (a, b) Morphology and anatomy of the echiuran, *Ochetostoma cf. erythrogrammon*. (a) Specimen from Boca del Río, Isla Margarita, Venezuela, TL ~14 cm (body + proboscis moderately extended), general view; (b) same specimen, dissected; (c) specimen from Bermuda, TL 15 cm, habitus; (d) same, detail of nephridia (a, b, original drawings by Galena-Vantsetti Murina; c, d, adapted from Sterrer 1986, with permission from Wolfgang Sterrer).

neath rocks and coral (Wesenberg-Lund 1939 1954, Stephen 1952, Nomura 2000), rocky galleries excavated by the bivalve, *Gastrochaena* sp. (Wharton 1913), muddy sand shores and mudflats (Chuang 1962a, Morton and Morton 1983, Sterrer 1986, Morton 1988), fine sand bottom near mangroves and sea grass (present study), and clean sandy beaches (Ditadi 1982). For the general biology and ecology of this species see Chuang (1962a b). As already noted, the burrow shape varies from the typical U-shaped tunnels (Chuang 1962a, Morton and Morton 1983) to L-shaped blind tubes with a side arm and 2 holes at the entrance (Ditadi 1982). Ditadi (1982) suggested that these differences are related to substrate variations and noted similar observations for the lugworm, *Abarenicola pacifica* (Healy and Wells, 1959). The echiuran, *Thalassema thalasseum*, exhibits similar ecological plasticity: this species was found in galleries and crevices in rocks by Cuénot (1922) in France, while 2 individuals of apparently the same species were collected while digging for sand-dwelling tube anemones (cerianthids) in Scotland, and they later constructed U-shaped burrows in an aquarium (Nickell and Atkinson 1994). Like Ditadi (1982), Nickell and Atkinson (1994) suggested that differences among populations of *T. thalasseum* are due to the variable responses of the worms to environmental factors, in this case substratum types. Nevertheless, the considerable ecological differences among different populations and the vast distribution range of *O. erythrogrammon* suggest that this species may be either a species with a high ecological plasticity or a complex of several geographically and/or ecologically isolated cryptic species. Cutler (1994: p. 320) did not exclude this possibility for some cosmopolitan species of sipunculids. However, in view of small morphological variability of *O. erythrogrammon* (and echiurans in general), genetic studies are required to clear up this problem.

Taxonomic remarks: *Ochetostoma erythrogrammon*, the type species of the genus, was originally described from the Red Sea and subsequently reported from numerous localities in the Indo-West Pacific. At least 30 species have been described in the genus *Ochetostoma* from various parts of the Indo-Pacific and Atlantic, including the Western Atlantic *O. baronii* (Greeff, 1872) and the Eastern Atlantic *O. azoricum*. Stephen and Edmonds (1972: p. 427) provided a key to all species of *Ochetostoma*, with the exception of *O. punicea* Dartnall, 1976 and *O. azoricum* which were described after 1972. Most of these species

have similar internal anatomies, differing mainly in the number of longitudinal muscle bands, usually from 13 to 18, and the taxonomic identity of some of these species remains uncertain. Some (Wesenberg-Lund 1939) or perhaps many (Sato 1939) could be identical with *O. erythrogrammon*. Furthermore, some species have been transferred to other genera, e.g., *Listriolobus* Spengel, 1912 (Biseswar and Moodley 1989, Nishikawa 2004), and at least some specimens from the tropical Western Atlantic once referred to as "*Thalassema erythrogrammon*" are now included in *Listriolobus* (Nishikawa 2004). This genus is represented in the Atlantic by several species, including the Caribbean *L. bahamensis* Fischer, 1926. *Listriolobus* appears to differ from *Ochetostoma* by the disposition of the oblique muscles between the longitudinal bands (in *Ochetostoma* these muscles are grouped into fascicles), but a discussion on the validity and taxonomy of *Ochetostoma* species would be beyond the scope of the present study.

DISCUSSION

Among the many symbiont taxa found cohabiting echiuran worm burrows, 4 deserve further comment because of their frequent symbioses with other host taxa. Because their biology is better known, knowledge of their activities with other hosts may provide some clues about the adaptive significance of their association with echiurans.

1. Bivalve associates. Bivalves from different families (particularly the Galeommatoidea) are frequent commensals or ectoparasites in burrows of various animals, including echinoderms, mostly sea cucumbers and sea urchins (e.g., Dales 1957, Ponder 1968), polychaetes (e.g., Gage 1968a, Martin and Britayev 1998), stomatopods (e.g., Mikkelsen and Bieler 1989), thalassinideans (e.g., Kato and Itani 1995 2000, Kerr and Corfield 1998, Lützen et al. 2001b, Itani and Kato 2002, Itani 2004), albuneid crabs (Boyko and Mikkelsen 2002), alpheid shrimps (Taylor 1968), crabs (e.g., Jepsersen et al. 2001, Lützen and Takahashi 2003), sipunculids (Gage 1968b 1979, Jepsersen and Lützen 2000, Lützen et al. 2001a), and echiurans (Habe 1962, Ockelmann and Muus 1978, Rachor and Bartel 1981, Jepsersen et al. 2002, Nickell et al. 1995, Rogers and Nash 1996, Kosuge et al. 2003). The biology of most bivalves associated with echiuran burrows remains to be studied, but most species are likely facultative commensals that seek protection and food in oxy-

genated tunnels of their hosts.

2. Polychaete associates. Hundreds of species of the large polychaete family, the Polynoidae, are obligate or facultative symbionts of other animals, such as sponges (including hexactinellids), gastropods, bivalves, sea cucumbers, sea stars, and various crustaceans (e.g., Martin et al. 1992, Martin and Britayev 1998, Sato et al. 2001, Britayev et al. 2003). In fact, more than 1/2 of all known commensal polychaetes are polynoids (Martin and Britayev 1998), so it is no surprise that nearly 1/4 of all echiuran symbionts are polynoids (Table 1). Most polynoid associates qualify as commensals, but some, e.g., *Hesperonoe adventor* associated with *Urechis caupo*, show strong tendencies to kleptoparasitism. Some may also live as ectosymbionts on their hosts, at least temporarily. Sato et al. (2001) found juveniles of the bright red *Hesperonoe hwanghaiensis* Uschakov and Wu, 1959, closely related to *H. adventor*, attached to the ventral surface of the host, the mudshrimp, *Upogebia major*. The adults of *H. hwanghaiensis* were obtained only from sediment samples, suggesting that at some point, they detach from the host and move freely within the burrow. Some polynoids, e.g., *Gastrolepidia clavigera* Schmarda, 1861, associated with holothurians, are commensals that may occasionally shift from parasitism (feeding on the host's tissue) to mutualism (feeding on the host's parasites) (Britayev and Lyskin 2002).

3. Crab associates. Most species of the diverse crab family, the Pinnotheridae, are symbiotic with a wide range of marine animals, including molluscs (bivalves and gastropods), sipunculids, polychaetes, thalassinideans, echinoderms (sea cucumbers and sea urchins), enteropneusts, tunicates, and echiurans (e.g., Berner 1952, McDermott 1962, Pearce, 1966, Schmitt et al. 1973, Telford 1978 1982, Manning and Holthuis 1981, McDermott 1981, Morton and Morton 1983, Bell 1984, Williams 1984, Manning and Morton 1987, Manning and Felder 1989, Campos 1990, Vassilenko, 1990, Geiger and Martin 1999, Hamel et al. 1999). Members of several genera, particularly *Pinnixa* (sensu lato), a large genus, but also several smaller genera (*Parapinnixa*, *Scleroplax*, *Mortensenella*, etc.), seem to be confined to burrow habitats. These crabs are particularly well adapted to a commensal lifestyle in burrows: they are small bodied (with a carapace width usually less than 1 cm) and their body and legs are strongly flattened, while their chelipeds are relatively

small, squat, and carried folded proximal to the body (see Figs. 2b-e, 7c, 10a, 11d, f). Most pinnotherids reported from echiuran burrows are facultative commensals that also occur in burrows of thalassinideans and burrowing polychaetes. On the other hand, increasing sampling effort means that more pea crab species will likely be found in echiuran burrows in the future, especially in the Indo-West Pacific.

Several species of the varunid crab genus, *Acmaeopleura*, appear to be commensals or semi-parasites of polychaete worms, mudshrimps, and echiurans (Sakai 1965, Itani 2002, Itani et al. 2002). Some of them, e.g., *A. toriumii*, are omnivorous feeders, using the burrows only for shelter and foraging, occasionally stealing food from the host, but never damaging the host. However, 1 undescribed species (*Acmaeopleura* sp.) associated with *Upogebia major* is clearly a parasite; it usually clings to the ventral side of the anterior segments of the abdomen, where it pierces the integument and feeds on the host's tissues, creating deep wounds (Itani 2002). Relationships between the *Acmaeopleura* crabs and the echiuran, *Urechis unicinctus*, are currently under study (G. Itani, pers. comm.). Due to similar commensal lifestyles in burrows, *Acmaeopleura* crabs are remarkably similar in external appearance to pinnotherid crabs (Fig. 3b).

4. Shrimp associates. Within the highly diverse shrimp family, the Alpheidae, echiuran associations evolved independently in 3 not closely related genera *Alpheus*, *Athanopsis*, and *Betaeus* (Anker, pers. obs.). In most cases, alpheid-echiuran associations are clearly facultative (*Alpheus barbatus*, *A. dentipes*, and *B. longidactylus*), although in some instances, these associations appear to be more echiuran-specific (*Athanopsis dentipes* and *A. rubricinctuta*). All alpheid shrimp have very cryptic lifestyles and many could have been "pre-adapted" to live in echiuran burrows or in crevices close to their dwelling places. At least 20 species of alpheids are known as infaunal symbionts of burrows of other burrowing animals, including stomatopods, thalassinideans, larger alpheids (*Alpheus* spp.), and fishes (e.g., Coutière 1899, Hart 1964, Williams 1984 1988, Felder and Manning 1986 1997, Karplus 1987, Froggia and Atkinson 1998, Dworschak and Coelho 1999, De Grave and Anker 2000, Dworschak et al. 2000, Anker et al. 2001 2004, Hayashi 2002, Anker, 2003).

CONCLUSIONS

This first systematic survey of associations between macrofaunal animals and echiuran worms (Appendix 1; Table 1) is undoubtedly incomplete, and more associates will likely be discovered in the future. Nonetheless, 2 important generalizations emerge.

First, the diversity of higher taxa associated with echiuran burrows is comparable to that of other fossorial groups that build permanent or semipermanent burrows, like thalassinideans (Dworschak 2000, Itani 2004), stomatopods (Holthuis 1951, Felder and Manning 1986, Manning and Rieka-Kudla 1990, Froglija and Atkinson 1998, Hayashi 2002), chaetopterid polychaetes (Enders 1905, Pearse 1913, Ng and Sasekumar 1993, Grove and Woodin 1996, Criales and Lemaitre 1997, Martin and Britayevs 1998), and sipunculid worms (Manning and Morton 1987, Cutler 1994). Animals from at least 8 phyla associate with echiuran burrows or rock-inhabiting echiurans (Appendix 1; Table 1). The most-frequent commensals of echiurans are bivalves (about 10 species from 7 families), polychaetes (14 species from 9 families; most commonly polynoids or scale worms), crabs (at least 15 species from 3 families, most commonly pinnotherids and varunids), and alpheid shrimps (6 species). Other major taxa with associates of echiuran worms include flatworms (1 species), nemerteans (1 species), nematodes (2 species, family unknown), gastropods (2 species from 2 families), copepods (3 species from 2 families), loxosomatid entoprocts (2 species from 1 family), and gobiid fishes (1 species). Occasionally, echiurans themselves are found as commensals in burrows of other animals, as in the case of *Bonellia viridis* inhabiting burrows of the rock-burrowing mudshrimp, *Upogebia mediterranea*.

In its general composition, the commensal fauna of echiurans appears similar to that of sipunculid worms (Sipuncula). For instance, hydroids, bryozoans (ectoprocs), entoprocts (including Loxosomatidae), bivalves, a pyramidellid gastropod, and various polychaetes are commensals or ectosymbionts of burrowing or boring sipunculids (Cutler 1994 and references therein), while several pinnotherid crabs and leptonacean bivalves associate with sipunculids in Hong Kong (Manning and Morton 1987, see also Morton 1988).

The burrowing echiuran infauna is also similar, although to a lesser degree, to the thalassinidean infauna, which at a worldwide scale

appears to be by far the most diverse among burrowing animals. This fauna consists mostly of alpheid shrimps (e.g., Hart 1964, Dworschak and Coelho 1999, Dworschak et al. 2000, Anker et al. 2001); pinnotherid and varunid crabs (e.g., MacGinitie and MacGinitie 1968, Schmitt et al. 1973, Manning and Felder 1989, Itani 2004); bivalves (e.g., Kato and Itani 1995 2000, Kerr and Corfield 1998, Lützen et al. 2001b, Itani and Kato 2002, Itani 2004); polynoid worms (MacGinitie and MacGinitie 1968, Morris et al. 1980, Martin and Britayev 1998, Sato et al. 2001); and gobiid fishes, including a peculiar blind goby (MacGinitie 1939, MacGinitie and MacGinitie 1968).

Second, the species richness of echiuran symbionts for individual host species is also comparable to that observed in thalassinideans (Itani 2004, although this study is limited to bivalves, crabs, and parasitic bopyrids), chaetopterid worms (Martin and Britayev 1998), and sipunculid worms (Cutler 1994). Most echiuran species host fewer than 5 symbiont species, but some host an impressive diversity (Table 1). *Lissomyema exilii* holds the current record with 3 obligate and 8 presumably facultative commensals from a total of 5 different phyla. Three other species (*Urechis caupo*, *Echiurus echiurus echiurus*, and *Ochetostoma erythrogrammon*) host at least 8 associates from 3~5 phyla.

Third, although the ecology and biology of most echiuran commensals remain to be studied in detail, most appear to be facultative (Table 1). Nonetheless, obligate associates occur among most symbiont taxa. Facultative symbionts also associate with other burrowing taxa, suggesting that the burrow, rather than the particular burrow maker, attracts them (see "Discussion"). Some obligate commensals, however, appear to have a more evolved association with the echiuran host. This is particularly true for the loxosomatid entoprocts, and the predatory opisthobranch that appears to specialize on them, which to our knowledge are known exclusively from burrows of the echiuran, *Lissomyema exilii* (Ditadi 1982). Some copepods may also be highly host-specific (species- or genus-specific) (G. Itani, pers. comm.).

Burrow shape and size (the latter often directly related to the host size) may possibly influence the diversity of commensals, but this remains to be clearly demonstrated. Nonetheless, current observations do suggest that larger U-shaped echiuran burrows contain more commensal species than smaller, simple, blind burrows. Itani (2004) com-

pared the diversity of commensals among 3 families of mudshrimps, the Callianassidae, the Upogebiidae, and the Laomedidae, and found that upogebiids serve as hosts for more commensals and ectosymbionts than do callianassids and especially laomedids (in *Laomedea astacina* De Haan, 1849, the only symbiont found was a branchial bopyrid). Itani (2004) suggested that these differences in commensal diversity could be related to the feeding mode of the host, the availability of oxygen in the burrow, or to some other factors, such as burrowing activity or the suitability of the host's surface for ectosymbionts. Some of these factors may also explain differences in diversity and composition of commensal faunas in echiuran burrows, but more-detailed field observations and experiments are needed.

The location of symbionts inside echiuran burrows remains to be studied for most species. Although direct evidence is lacking, one would expect sedentary commensals (e.g., some polychaetes or entoprocts) or slow-moving commensals (e.g., bivalves) to associate with the burrow roof, reflecting the position and disturbance caused by the echiuran in its burrow. Some commensals (e.g., bivalves and copepods) appear to be directly associated with the host surface, since they were found attached to the echiurans. Highly mobile commensals, such as scale worms, shrimp, and crabs, move freely within the burrow, and their location most likely depends on their own and the host's activities. For example, when the host is feeding, these commensals may move closer to the burrow entrance and/or to the host's proboscis, as in the case of the innkeeper, *U. caupo*. Similarly, the location of the nudibranch, *Lophodoris scala*, in burrows of the echiuran, *Lophodoris exilii*, depends on the location of its prey, the entoprocts, *Loxosomella* spp. However, in most cases, the interactions between the commensals and their preferred location in the burrow remain to be studied.

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APPENDIX I : Preliminary checklist of echiuran symbionts

Order Xenopneusta**Family Urechidae*****Urechis caupo* Fisher and MacGinitie, 1928 [California]****Facultative commensals***Hesperonoe adventor* (Skogsberg, 1928) (Polychaeta: Polynoidae)*Scleroplax granulata* (Rathbun, 1893) (Brachyura: Pinnotheridae)*Pinnixa franciscana* Rathbun, 1918 (Brachyura: Pinnotheridae)*Pinnixa longipes* (Lockington, 1877) (Brachyura: Pinnotheridae)*Pinnixa schmitti* Rathbun, 1918 (Brachyura: Pinnotheridae)*Clevelandia ios* (Jordan and Gilbert, 1882) (Teleostei: Gobiidae)*Betaeus longidactylus* Lockington, 1877 (Caridea: Alpheidae)*Cryptomya californica* (Conrad, 1837) (Bivalvia: Myidae)**References:** Fisher and MacGinitie 1928a b, MacGinitie 1934, Dales 1957, Hart 1964, MacGinitie and MacGinitie 1968, Butler 1980, Morris et al. 1980, Ricketts et al. 1985, Jensen 1995, Ruff 1995.***Urechis unicinctus* von Drasche, 1881 [Japan, Korea]****Obligate commensals***Goidelia japonica* Embleton, 1901 (Copepoda: Poecilostomatoidea: Catinidae)**Facultative commensals**? *Athanopsis dentipes* Miya, 1980 (Caridea: Alpheidae)*Acmaeopleura balssi* Shen, 1932 (Brachyura, Varunidae)*Acmaeopleura toriumii* Takeda, 1974 (Brachyura: Varunidae)*Pseudopinnixa carinata* Ortmann, 1894 (Brachyura: Pinnotheridae)**References:** Miya 1995, Kim 2000, Itani et al. 2002, G. Itani (pers. comm.)**Order Echiuroidea (Echiuroinea)****Family Echiuridae*****Echiurus echiurus echiurus* (Pallas, 1767) [NE Europe]****Facultative commensals***Harmothoe sarsi* (Kinberg, 1865) (Polychaeta: Polynoidae)*Gattyana cirrhosa* (Pallas, 1776) (Polychaeta: Polynoidae)*Pholoe minuta* (Fabricius, 1780) (Polychaeta: Pholoidae)*Notomastus latericeus* Sars, 1851 (Polychaeta: Capitellidae)*Scalibregma inflatum* Rathke, 1843 (Polychaeta: Scalibregmatidae)*Mysella bidentata* (Montagu, 1803) (Bivalvia: Montaculidae)*Abra alba* (Wood, 1802) (Bivalvia: Semelidae)*Nucula nitidosa* Winckworth, 1930 (Bivalvia: Nuculidae)**References:** Gislén 1940, Reineck et al. 1967, Rachor and Bartel 1981.***Echiurus echiurus alaskensis* Fisher, 1946 [Alaska]****Facultative commensals***Hesperonoe adventor* (Skogsberg, 1928) (Polychaeta: Polynoidae)*Pinnixa schmitti* Rathbun, 1918 (Brachyura: Pinnotheridae)*Pinnixa occidentalis* Rathbun, 1893 (Brachyura: Pinnotheridae)** Reported from burrows of *Echiurus* sp., possibly *E. e. alskanus*.

APPENDIX I : (Cont.)

References: Rathbun 1904, Schmitt et al. 1973, Ricketts et al. 1985.

Ikedosoma* sp. (identification needs verification) [Taiwan]*Facultative commensal**

Alpheus barbatus Coutière, 1897 (Caridea: Alpheidae)

References: Tzeng and Chen 1992.

Lissomyema exilii* Müller, 1883*Obligate commensals**

Loxosomella zima Marcus and Marcus, 1968 (Entoprocta)

Loxosomella ditadii Marcus and Marcus, 1968 (Entoprocta)

Lophodoris scala Marcus and Marcus, 1970 (Opisthobranchia: Goniodorididae)

Facultative/occasional commensals

Harmothoe imbricata (Linnaeus, 1767) (Polychaeta: Polynoidae)

Bhawania goodei Webster, 1884 (Polychaeta: Chrysopetalidae)

Nainereis setosa (Verrill, 1900) (Polychaeta: Orbiniidae)

Ophiodromus pallidus (Claparede, 1864) (Polychaeta: Hesionidae) (formerly *Podarke pallida*)

Nematonereis unicornis (Grube, 1840) (Polychaeta: Eunicidae)

2 species of unidentified free-living nematodes

Pinnixa sp. (Brachyura: Pinnotheridae)

References: Marcus and Marcus 1968 1970, Ditadi 1969 1975 1982.

Family Bonelliidae***Bonellia viridis* Rolando, 1821 [Mediterranean Sea]****Facultative "host"**

Upogebia mediterranea Noël, 1992 (Thalassinidea: Upogebiidae) (originally reported as *U. deltaura* (Leach, 1815); for reidentification of Schembri and Jaccarini's material see Asgaard et al. 1997)

Facultative commensals

Pontogenia chrysocoma (Baird, 1865) (Polychaeta: Aphroditidae)

Lepidopleurus cajetanus (Poli, 1791) (Polyplocophora: Leptochitonidae)

Alpheus dentipes Guérin, 1832 (Caridea: Alpheidae)

Xantho hydrophilus granulicarpus Forest in Drach and Forest 1953 (Brachyura: Xanthidae)

Occasional commensals and guests

Cliona sp. (Porifera)

Unidentified nemertean worm (Nemertea)

Phascolosoma granulatum Leuckart, 1828 (Sipunculida)

Aspidosiphon muelleri Diesing, 1851 (Sipunculida)

Athanas nitescens Leach, 1814 (Caridea, Alpheidae)

Periclimenes cf. *scriptus* (Risso, 1822) (Caridea: Palaemonidae)

Lysmata seticaudata (Risso, 1816) (Caridea: Hippolytidae)

Pestarella candida (Olivi, 1792) (Thalassinidea: Callianassidae) (originally reported as *Callianassa (Callichirus) pestae* De Man, 1928)

Galathea intermedia Lilljeborg, 1851 (Anomura: Galatheididae)

Gobius geniporus Valenciennes, 1837 (Teleostei: Gobiidae)

Sharing same micro-biotope, but not found in burrows

Lithophaga lithophaga (Linnaeus, 1758) (Bivalvia: Lithophagidae)

References: Schembri and Jaccarini 1978 (see also Asgaard et al. 1997).

***Maxmuelleria lankesteri* (Herdman, 1898) = *Thalassema lankesteri* [Scotland]**

APPENDIX I : (Cont.)

Facultative commensals

Ophiodromus flexuosus (Chiaje, 1827) (Polychaeta: Hesionidae)

Mysella bidentata (Montagu, 1803) (Bivalvia: Montacutidae)

Saxicavella jeffresii Winckworth, 1930 (Bivalvia: Hiatellidae)

Gobius niger (Linnaeus, 1758) (Telestei: Gobiidae)

Syntopic, possibly interconnecting burrows

Jaxea nocturna Nardo, 1847 (Thalassinidea: Laomeidiidae)

References: Nickell et al. 1995.

***Achaetobonellia maculata* Fisher, 1953 [India]**

Acanthobonellia vulgaris* Menon, DattaGupta and Johnson, 1964 (possibly junior synonym of *A. pirotanensis

Jose, 1964, see Stephen and Edmonds (1972: 363-364) [India]

Facultative commensals

Unidentified helminth worms, crabs, and molluscs

References: Singhal and Datta Gupta 1980.

Family Thalassematidae

***Anelassorhynchus mucosus* (Ikeda, 1904) = *Thalassema mucosum* [Japan]**

Obligate commensals?

Scintilla thalassemicola (Habe, 1962) (Bivalvia: Galeommatidae) (junior synonyms: *Achasmea thalassemicola*, *Scintillorbis thalassemicola*, and *Sagamiscintilla thalassemicola*, K. S. Tan, pers. comm., see also Morton and Scott 1989)

? *Athanopsis dentipes* Miya, 1980 (Caridea: Alpheidae)

References: Habe 1962, Miya 1980, Morton and Scott 1989.

Anelassorhynchus inansensis* (Ikeda, 1904) [Vietnam]*Obligate commensal**

Echiurophilus fizei Delamare-Deboutteville and Nunes-Ruivo, 1955 (Copepoda: Cyclopoidea; Poecilostomatoidea according to Kim 2000)

References: Kim 2000, Boxshall and Halsey 2004.

Anelassorhynchus branchiorhynchus* (Annandale and Kemp, 1915) [India]*Facultative commensals**

Unidentified helminths, crabs, and molluscs

References: Singhal and Datta Gupta 1980.

Thalassema harmani* Fisher, 1947 [SE USA]*Facultative commensal**

Pinnixa lunzi Glassell, 1937 (Brachyura: Pinnotheridae)

References: Boesch 1971, Williams 1984.

Thalassema* sp. [Korea]*Obligate commensal**

Goidelia pelliviva Kim, 2000 (Copepoda: Poecilostomatoidea: Catinidae)

References: Kim 2000.

Listriolobus sorbillans* (Lampert, 1883) = *L. riukiensis* Sato, 1939 [Japan, Taiwan]*Obligate commensal**

Pseudopythina ochetostomae Morton and Scott, 1989 (Bivalvia: Lasaeidae; sometimes placed in Kelliidae and Galeommatidae)

APPENDIX I : (Cont.)

Facultative commensal

? *Alpheus barbatus* (Caridea: Alpheidae)

References: Chen 2001, Kosuge et al. 2003.

Listriolobus pelodes* Fisher, 1946 [W USA]*Facultative commensal?**

Hesperonoe laevis Hartman, 1961 (Polychaeta: Polynoidae)

References: Hartman 1961 1968, Sato et al. 2001.

Ochetostomatinae, gen. et sp. indet. [Mozambique]**Obligate commensal?**

Athanopsis rubricinctata Berggren, 1991 (Caridea: Alpheidae)

References: Berggren 1991.

Ochetostoma azoricum* Rogers and Nash, 1996 [Azores]*Facultative commensal?**

Unidentified bivalve (Bivalvia, fam. et gen. indet.)

References: Rogers and Nash 1996.

Ochetostoma erythrogrammon* Leuckart and Rüppel, 1828 [1. Hong Kong, Japan]*Obligate commensals?**

Unidentified polyclad flatworm (Plathyhelimithes: Turbellaria)

Unidentified scale worm (Polychaeta: Polynoidae)

Sigaretornus planus (Adams, 1850) (Gastropoda: Rissoidea: Tornidae)

Pseudopythina ochetostomae Morton and Scott, 1989 (Bivalvia: Lasaeidae; also placed in Kelliidae or Galeommatidae)

Hemicyclops mortoni Boxshall and Humes, 1987 (Copepoda: Poecilostomatoidea: Clausidiidae)

Facultative commensals?

Mortensenella forceps Rathbun, 1909 (Brachyura: Pinnotheridae)

Acmaeopleura toriumii Takeda, 1974 (Brachyura: Varunidae)

References: Morton and Morton 1983, Boxshall and Humes 1987, Manning and Morton 1987, Morton 1988, Morton and Scott 1989, Davie 1992, Itani et al. 2002, Jespersen et al. 2002, Kosuge et al. 2003.

Ochetostoma cf. erythrogrammon* Leuckart and Rüppel, 1828 [2. Ryukyu Islands]*Facultative commensal?**

Alpheus barbatus Coutière, 1897 (Caridea: Alpheidae)

References: Nomura 2000.

Ochetostoma cf. erythrogrammon* Leuckart and Rüppel, 1828 [3. Venezuela]*Facultative commensals?**

Pinnixa sp. aff. *chaetoptera* Stimpson, 1860

Pinnixa sp. aff. *monodactyla* (Say, 1818)

Commensal or in background sediment

? *Basterotia* sp. (Bivalvia: Sportellidae)

Syntopic, possibly interconnecting burrows

Upogebia omissa Gomez Corrêa, 1968 (Thalassinidea: Upogebiidae)

References: Present study.
