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James Darwin Thomas
Newfound Harbor Marine Institute, thomasjd@nova.edu

George W. Taylor
Florida International University

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MOUTHPART MORPHOLOGY AND FEEDING STRATEGIES OF THE COMMENSAL AMPHIPOD, *ANAMIXIS HANSENI* STEBBING

James Darwin Thomas and George W. Taylor

ABSTRACT—The lack of the information on the biology of the commensal amphipod family Anamixidae prompted investigations into mouthpart ultrastructure, feeding biology, and host specificity of *Anamixis hanseni* Stebbing, 1897. Earlier investigators presented conflicting reports on the structural composition of the buccal region and feeding modes in anamixids. Scanning electron microscope analysis of *A. hanseni* showed a complete set of mouthparts to be present, although much modified and reduced, except for the well-developed maxilliped palps. Feeding is not parasitic (piercing and sucking host tissue) as previously believed but is accomplished while *A. hanseni* rests inside its host. Minute food particles are trapped on a filter net of setal tufts located on the medial carpal lobes of the enlarged second gnathopods. Both pairs of antennae and maxilliped palps are employed in maneuvering the food mass to the mouth. Mucus secretions by the host may aid in agglutination of food particles and could itself be a food source.

Findings show that *A. hanseni* is a highly specialized commensal with closest affinities to the genus *Leucothoides* of the Leucothoidae. *A. hanseni* inhabits compound tunicates and small solitary calcareous sponges.

The fleshy, transparent nature of the mouthpart structures in the Anamixidae make them difficult to observe using standard light microscopic techniques. In an attempt to interpret the mouthpart structure of *Anamixis hanseni* Stebbing, 1897, specimens were submitted to scanning electron microscope techniques for analysis. In addition, observations of live *A. hanseni* inside an ascidian host, *Ecteinascidia turbinata* Herdman, 1888, were initiated to elucidate feeding methods, host selection, and reproduction in *A. hanseni*.

The family Anamixidae is currently composed of eight species in two genera, with most species being found in shallow water (1–60 m) as commensals in sponges and ascidians in tropical and warm-temperate seas. Comprising the species in the genus *Anamixis* are *A. hanseni* (West Indies); *A. stebbingi* Walker, 1904 (Ceylon); *A. linsleyi* Barnard, 1955 (California); *A. falarikia* Barnard, 1965 (Caroline Islands); and *A. grossimana* Ledoyer, 1978 (Indian Ocean). *Paranamixis,* which differs from *Anamixis* in lacking the first gnathopods, contains *P. bocki* Schellenberg, 1938 (Gilbert Islands); *P. indicus* Sivaprakasm, 1968 (Gulf of Manaar, India); and *P. excavatus* Ledoyer, 1978 (Indian Ocean).

Conflicting reports on the presence or absence of various mouthparts appear throughout the literature on anamixids. Stebbing (1906) noted in *A. hanseni* the presence of microscopic teeth on the anterior edge of the ventral keel which he believed represented the coalescence of the mandibles. Stebbing also recorded the absence of maxillae 1 and 2. Schellenberg (1938) attempted to illustrate the mouthparts of *P. bocki,* but the figures presented were unclear and confusing. In his 1969 guidebook, J. L. Barnard noted the absence of mandibles, lower lip, and maxillae. Later, working with better material of *A. stebbingi,* he noted (1970) three pairs of tiny vestiges, possibly representing the mandibles and maxillae. The mandible appeared as a tiny palp with a long terminal seta, while maxilla 1 appeared as a small lobe dorsolateral to a larger lobe presumed to be maxilla 2. Sivaprakasam (1968) also believed the mandibles and maxillae to be absent in *P.*

indicus. Results of this study show that *A. hanseni* has a full complement of mouthparts.

The role of anamixids within their hosts has been assumed to be of a parasitic nature, the ventral keel being used to pierce the host tissues. *In situ* studies of *A. hanseni* revealed passive filtration as the only feeding type observed within the host. These observations do not exclude the possibility of other feeding patterns, and additional work is needed to further clarify feeding behavior.

The lack of data relating to specificity of habitat of anamixids for their hosts has caused investigators to lump hosts as "sponges and ascidians" with no further qualification. The variety of microhabitats available in these organisms is great and more detailed data are needed to clarify specific host-commensal relationships. Of possible importance also are other amphipods co-occurring with anamixids. In the Caribbean (Bahamas, Florida Keys, Tortugas, and Belize) *A. hanseni* is commonly found with *Leucothoides pottsi* Shoemaker, 1933, (Thomas, 1979). Occasional pinnotherid crabs and other species of *Leucothoe* may be taken, but the *Anamixis-Leucothoides* pairing is encountered over 90% of the time. It is not known whether this co-occurrence represents a dependency of one species on the other, or reflects selection for similar habitat. It seems the amphipods prefer constancy of microhabitat rather than a specific host species as a major criterion for host selection. Most specimens of *A. hanseni* are taken from either compound tunicates or small, calcareous, ascenoid sponges with the internal cavities of both having the same approximate size (12–25 mm × 2–7 mm).

Methods of reproduction in the Anamixidae are unknown and primary sexual characters appear lacking, making sexual determinations speculative. Barnard (1955) noted what were possibly two or three shrunken embryos in *A. linsleyi,* but found no brood plates or evidence of sexual dimorphism. Observations of *A. hanseni* have failed to reveal any ovigerous specimens, discernible reproductive structures, or other obvious sexual differences.

METHODS

Specimens for this study were taken from shallow (1–2 m) rocky bottoms in Coupon Bight (Big Pine Key, FL) and Carrie Bow Cay, Belize. Amphipods were collected with their ascidian host and kept in covered culture dishes for observations. The transparent nature of the host ascidian allowed extended, undisturbed observations of *A. hanseni* within the tunicate. After observation, specimens were then preserved and stored in 2% formalin until analysis. During preparation, the amphipods were first put in shell vials (9 × 25 mm) and placed in an ultrasonic cleaner for 10–20 sec depending on the amount of debris clinging to the amphipod. Specimens were then dehydrated through a graded alcohol series. Following dehydration to absolute ethyl alcohol, specimens were transferred to a Ladd Critical Point Dryer (Ladd Research Industries, Inc.) and dried using liquid carbon dioxide as the exchange medium. After mounting on stubbs with silver paint, the specimens were coated with gold-palladium (60/40) in a DESK-1 Sputter-Coater (Denton Vacuum, Inc.). Observations were made with an ISI-A scanning electron microscope operated at 30 KV. Photographs were made with Polaroid Type 55 P/N film.

RESULTS

Figure 1 shows the antero-ventral one-third of *A. hanseni* as it appears before dissection of the second antennae (1a), the maxilliped palps (1b), and the chelate first gnathopods (1c). The buccal mass (1d) is reduced in size and located between the bases of the enlarged maxilliped palps and the second antennae. Figure 2 shows this same region after the removal of the above-mentioned structures. Prominent in this view is the large ventral keel (epistome) 2a. The reduction in the relative size of the mouthparts and their fleshy nature is apparent. In Figure 3 the second maxilla is represented by a large, soft lobe (3a). Anterior to this is
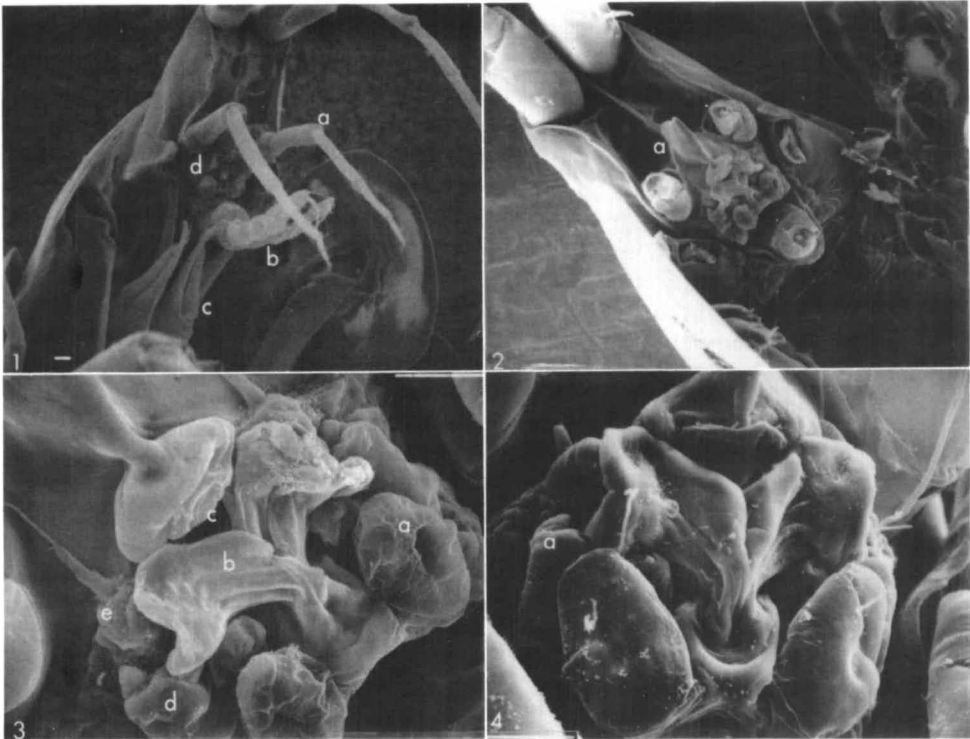
Figure 1. *Anamixis hanseni* Stebbing, ventral, 30×: a, antenna 2; b, maxilliped palps; c, gnathopod 1; d, buccal mass.

Figure 2. *Anamixis hanseni* Stebbing, ventral, 2nd antennae, maxilliped palps, and gnathopod 1 removed, 50×: a, ventral keel.

Figure 3. *Anamixis hanseni* Stebbing, buccal mass, 500×: a, 2nd maxilla; b, lower lip; c, upper lip; d, 1st maxilla; e, mandible.

Figure 4. *Anamixis hanseni* Stebbing, 750×: a, 1st maxilla with palp.

the lower lip (3b) and the upper lip (3c), located at the base of the ventral keel. The first maxilla (3d) is represented by two lobes, the inner and outer plates. The outer plate bears a small stub of a palp; the inner plate is located between the second maxilla and the lower lip. The mandible (3e) has a large base and a one-segmented palp bearing a long terminal seta. Figure 4 is another preparation showing the first maxilla and palp from a different perspective. Figure 5 shows a stalked choanoflagellate attached to the base of article 2 of the first gnathopod which is in close proximity to the buccal region.

Feeding observations of *A. hanseni* within its host revealed passive filtering and entrapment of food particles to be the only method of feeding. *A. hanseni* rests in the branchial basket of the tunicate, facing the buccal siphon, and traps particulate material on tufts of setae located medially on the carpal lobes of the second gnathopods. Periodically the second gnathopods are flexed posteriorly, drawn through the abdominal appendages, and then are moved forward where the antennae and maxilliped palps remove trapped material. The antennae and maxilliped palps are then used in opposition to handle the food mass, which is pushed into the mouth by the antennae.
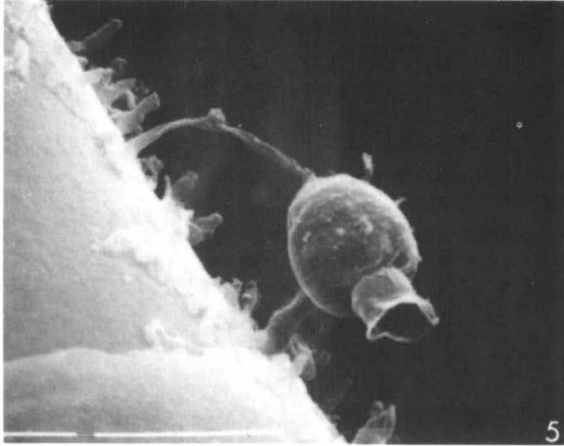
Figure 5. *Anamixis hanseni* Stebbing, article 2 of gnathopod 1 with choanoflagellate, 7000×.

DISCUSSION

The results indicate an even closer relationship of the Anamixidae with the Leucothoidae than previously believed, due to the presence of mandibles and maxillae in *A. hanseni*. Similarities in mouthpart morphology indicate that the anamixids represent buccal degeneration derived from further reduction and modification of the basic leucothoid mouthparts. Similarities are especially evident in the first and second maxillae, mandibles, and maxillipeds. The second maxillae in leucothoids generally have the outer plates much reduced in size while they have been lost in anamixids. The first maxillae in leucothoids have short, stubby palps; a similar though reduced condition seen in anamixids. The mandibular morphology of *A. hanseni* is closest to that of *Leucothoides,* which has a small one-segmented palp bearing two terminal setae. While the maxilliped palps are well developed in both leucothoids and anamixids, the inner and outer plates show stages of fusion and reduction. The outer plates are absent in anamixids, much reduced in leucothoids. The inner plates are small and completely fused in anamixids, reduced and partially fused in leucothoids. Other characteristics (little or no sexual dimorphism, commensal habitat, similar gnathopod configuration) indicate that the anamixids have evolved as a specialized extension of the Leucothoidae. With the exception of the maxilliped palps, the total loss of spines and setae on movable mouthparts, and their soft, fleshy nature indicate a food source that requires no processing prior to ingestion.

Structurally, the sharp marginal ridges on the head, the central keel, the large coxae and second gnathopods, all suggest the animal can fold up its appendages and effect a type of lateral shield, somewhat like an ostracod. This "shield" could enable *A. hanseni* to direct and concentrate pleopod and/or host-generated feeding currents into a filter net or screen for feeding purposes.

Swallowing is probably accomplished by sucking actions of the upper and lower lips. Presumably, the remaining mouthparts and the first gnathopods assist in feeding by helping to manipulate the food mass. The use of the second antennae as food-handling structures may explain their extreme posterior location. The presence of what seem to be grooves on either side of the ventral keel would receive the peduncular segments of the first antennae. The peduncles could fold

back into these grooves, leaving the flagellum of antenna 1 closely approximated to antenna 2, where it could assist in food-handling. It is possible that the secretion of mucus by the host during feeding (produced by the endostyle in ascidians) may be a secondary food source for *A. hanseni*. The specific role of the first gnathopod is unresolved at present.

The presence of many broken choanoflagellate stalks (Fig. 5) suggest these organisms were numerous and probably removed during ultrasonic cleaning. Their occurrence indicates current flow, such as that produced by the host tunicates and sponges, or in the generation of a pleopodal feeding current that *A. hanseni* has been observed to produce. Choanoflagellates feed on finely suspended material and could be expected to occur in areas of favorable attachment sites and food supplies.

The question of parasitic feeding by *A. hanseni* can all but be ruled out in light of the present observations and the nature of the mouthparts. Most families of amphipods known to be parasitic have piercing mouthparts arranged in a large conical bundle (Acanthonotozomatidae, some Lysianassidae, Ochlesidae). In addition, the piercing and sucking of tissue in the small calcareous sponges *A. hanseni* inhabits would be hampered by the dense layer of interlacing spicules present in these thin-walled sponges. Also, such epizoants as the choanoflagellates (Fig. 5) would be rasped off as *A. hanseni* routinely attempted to penetrate the spicule layer.

Another interesting, though unsubstantiated, theory is that of egg parasitism by anamixids. An egg (amphipod or ascidian) could be readily grasped by the opposing antennae and maxilliped palps, pierced by the ventral keel and the contents sucked out by the soft mouthparts.

In summary, *A. hanseni* has been shown to possess a full complement of mouthparts, though much reduced. The habitats of *A. hanseni* are small, tubular sponges and certain compound ascidians, in which the amphipod can passively filter small particulate material from currents produced by the host and enhanced by the pleopod-generated feeding currents. The mouthparts of *A. hanseni* represent specialization and reduction in complexity from the leucothoid line, as a result of the passive feeding mode of *A. hanseni* in which the second antennae and maxilliped palps have become the primary food handling structures, while the mouthparts only assist in manipulation and swallowing of food materials. The nature of the ingested material is not resolvable under high magnification (900×) but is assumed to be suspended inorganic material, phytoplankton, and small zooplankton.

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ADDRESSES: *(JDT) Newfound Harbor Marine Institute, Rt. 3, Box 170, Big Pine Key, Florida 33043;
(GWT) Department of Biological Sciences, Florida International University, Tamiami Campus,
Miami, Florida 33199.*

ANOMALOUS AERIAL ROOTS IN *AVICENNIA GERMINANS* (L.) L. IN FLORIDA AND COSTA RICA

Samuel C. Snedaker, Jorge A. Jimenez and Melvin S. Brown

Avicennia (Avicenniaceae) represents one of the dominant genera in the world-wide mangrove flora and the species are characterized by ascending, pencil-shaped aerial pneumatophores (=pneumorhiza) which project vertically from the sediment surface. Pneumatophores are negatively geotropic and develop as first-order laterals (along with positively-geotropic descending anchoring roots) of shallow, radiating horizontal roots (Jenik, 1978), also referred to as cable roots in Chapman (1976). The pneumatophores have a nominal diameter of 8–10 mm and a variable height ranging from a few centimeters to a reported maximum of 35 cm. They are further characterized by the presence of short absorbing rootlets within the surface sediments and hydrophobic lenticels on the above-ground segment (see Chapman, 1976). Pneumatophores are the only form of aerial roots known to be produced by *Avicennia*.

As a specific class of morphological adaptations, pneumatophores (also called peg roots, knee roots, and root spines, depending on morphological variation) occur among both halophytes and glycophytes in such diverse plant families as the Palmae, Taxodiaceae, Meliaceae, Rhizophoraceae, Combretaceae and Son-neratiaceae. It is generally agreed that pneumatophores are structural adaptations which facilitate exchange of gases (oxygen and carbon dioxide) in anaerobic re-ducing environments typical of swamp habitats, and thus represent an example of convergent evolution. For the halophytic mangroves, Chapman (1944) and Scholander et al. (1955) provide experimental evidence for gas exchange which occurs primarily through the lenticels but also via diffusion through the phello-derm. The related respiratory function of pneumatophores was experimentally demonstrated by Chapman (1944) and more recently, demonstrated under field conditions by Lugo et al (1975). Aerial prop or stilt roots in species of *Rhizophora* (and *Acanthus*) have the same aerating function (see Scholander et al., 1955; Lugo et al., 1975; and Gill and Tomlinson, 1977) but are distinguished from pneu-