Mechanoreceptors in Early Developmental Stages of the Pycnogonida

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ABSTRACT Members of the phylum Arthropoda detect fluid flow and sound/particle vibrations using sensory organs called sensilla. These sensilla detect sound/particle vibrations in the boundary layer. In the present study, archived specimens from the United States National Museum of Natural History were examined in an effort to extend our knowledge of the presence of sensilla on the early post hatching developmental stages, first and second instars, of pycnogonids. In the work presented here we look at three families, four genera and ten species of early post hatching developmental stages of sea spiders. They are Family Ammotheidae, *Achelia cuneatis* Child, 1999, *Ammothea allopodes* Fry and Hedgpeth, 1969, Ammothea carolinensis Leach 1814, *Ammothea clausi* Pfeffer, 1889, *Ammothea striata* (Möbius, 1902), Family Nymphonidae, *Nymphon grossipes* (Fabricius, 1780), *N. australe* Hodgson, 1902, *N. charcoti* Bouvier, 1911, *N. Tenellum* (Sars, 1888) and Pycnogonidae, *Pentapycnon charcoti* Bouvier, 1910. Electron micrograph images of these species were used to identify and describe the sensilla present.

Most body organs such as mouthparts, the eye tubercle, appendages and spines are proportionally much smaller in the early post hatching developmental stages compared to their size in the adults, while the sensilla are comparable in size and shape to those found on the adults. In the first instar of *Pentapycnon charcoti* sensilla are present, but not in the adult. The sensilla have an external morphology homologous to the sensilla found on adult pycnogonids. The sensilla shaft lengths are tens of microns and two to seven in number. It is only possible to establish the presence of sound detecting sensilla. Their functionality remains to be established in future experimental work. Theoretical detection ranges of 1 to 100 m and 10 to 1 kHz are possible.

Key Words: mechanoreceptors, Pycnogonida, Protonymphon, Sensilla

Introduction

Members of the phylum Arthropoda detect sound energy using sense organs classed as mechanoreceptors on the surface cuticle of the animal. These same sense organs may also detect tactile signals and particle motion, fluid flow patterns and sound energy. The sensory inputs from these mechanoreceptors assist the animals in the detection of prey organisms, potential predators and mates [1-7]. Chemical sensory organs have also been described from the cuticle of arthropods [4 & 8]. These sensory sensilla termed filiform hairs in insects, trichobrothria in

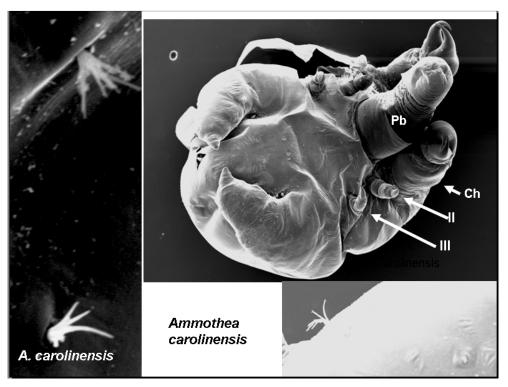


Fig. 1. The large image in the upper right is the 550 µm long second post hatching stage of *Ammothea carolinensis* Leach 1814 as seen in a ventral view. Pb= the proboscis; Ch= the cheliphore(s); II= the second larval appendage or larval palps; III= the third larval appendage or larval ovigerous appendage. The image on the left side shows two five (5) branched sensilla found on the cheliphores. The bottom right image is the same sensilla as seen from a side view.

arachnids and peg sensilla in crustaceans have been described in the scientific literature for over 130 years [8-12]. Sensory sensilla have been reported for the early developmental stages of two genera and four species of sea spiders [13 & 14].

Sea spider reproductive biology is unique among the invertebrates in several ways. Sexually mature male and female spiders release their gametes into the aquatic environment where

external fertilization occurs. The males then use special appendages called ovigerous appendages to collect the fertilized eggs, which are carried by the male until they hatch. If the newly hatched sea spiders receive any post hatching care it is provided by the male [15, 16 & 17]. There are six developmental patterns observed in the Pycnogonida [17 & 18]

Methodology

Archived specimens of pycnogonid early developmental stages from the collections of the National Museum of Natural History, Smithsonian Institution were used in this study. Larvae were recovered from the ovigers of adult male specimens. The specimens were critical point dried and coated with gold alloy for the scanning electron micrographs. A Phillips Electron

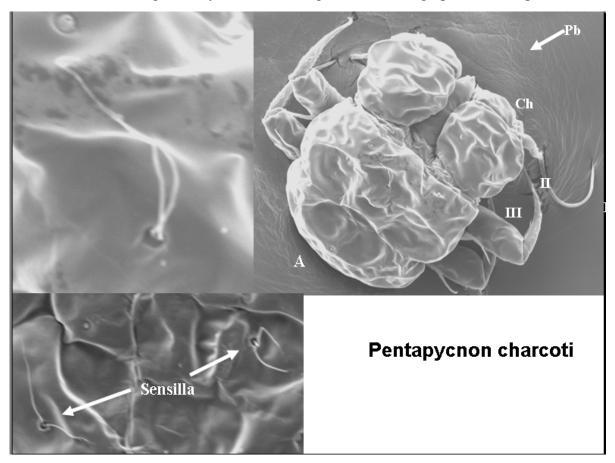


Fig. 2. Images A shows a dorsal view of the 141 μ m long the first post hatching stage of *Pentapycnon charcoti*. Pb= the proboscis; Ch= cheliphore(s); II = Second larval appendages or larval palps; III= the third larval appendages or larval ovigerous appendages. The sensilla are found on the dorsal side of the body.

Microscope was used in this study. The length of the sensilla and diameter of the socket was measured on the electron micrographs. A total of 48 images of 25 specimens were analyzed in this study [18 & 19].

Results

The mechanoreceptors found on the early post hatching developmental stages of 10 species representing four genera and three families of sea spiders had socket diameters ranging from 1 µm to 8 µm; with shaft lengths ranging from 5 µm to 39 µm and 2 to 6 shafts (See Table 1).

Mechanoreceptors called sensilla were found on the cuticle of Family Ammotheidae, *Achelia cuneatis* Child, 1999, *Ammothea allopodes* Fry and Hedgpeth, 1969, *Ammothea carolinensis* Leach, 1814 (See Fig. 1), *Ammothea clausi* Pfeffer, 1889, *Ammothea striata* (Möbius, 1902), Family Nymphonidae, *Nymphon grossipes* (Fabricius, 1780), *N. australe* Hodgson, 1902, *N. charcoti* Bouvier, 1911 (See Fig. 3), *N. Tenellum* (Sars, 1888) and Pycnogonidae, *Pentapycnon charcoti* Bouvier, 1910 (See Fig. 2). The sensilla were located on the cheliphores (See Fig. 1-3) and dorsal surface) of the early post hatching stages of members of these three families, four genera and eight species.

The external form of the mechanoreceptors is the same as those described in adult sea spiders other chelicerates, crustaceans and insects [1-4, 8-13 & 22]. Electron micrographs showing the morphology of the early post hatching stages of sea spiders and their mechanoreceptors are provided in Figures 1-3.

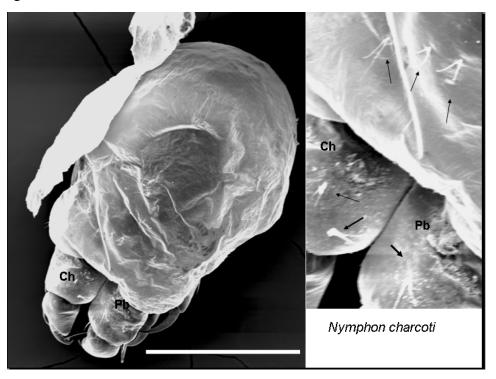


Fig. 3. Nymphon charcoti First post hatching stage on the left. Ch= cheliphore(s); Pb= proboscis. The scale bar is $200 \,\mu\text{m}$. The arrows show the bifurcated sensilla on the dorsal side of the animal on the cheliphores and proboscis.

Discussion

The sensory organs on the early post hatching stages of sea spiders described in this study are of the fluid flow type described in the literature. They are composed of hair-like projections extending from a socket in the cuticle [9 & 10]. The hair-like shaft functions as a leaver responding to viscous forces in the water. The movements of the base end of the shaft stimulates

one or more neurons which, signals indicating the velocity, direction and acceleration of the water particles [7]. The sensing of fluid particle motion, that is, acoustic vibrations occurs in the boundary layer. The boundary layer in aquatic organisms is thinner than in air, on the order of 100 µm resulting in sensilla 10s of µm in length [20]. Homologous organs in crustaceans have been shown to detect sound frequencies between 10 Hz and 1 kHz. The detection ranges vary from approximately 1 m to 100 m [2 & 7]. Sea spiders have mechanoreceptors like those described above with sensilla attached to bi-polar neurons [10, 12 & 21]. The size and form of these sensilla are comparable to those found in adult specimens of sea spiders. Alexeeva et al. [14] have shown that the bifurcated sensilla of *Nymphon brevirostre* early post hatching stages have a bipolar neuron linked to the central nervous system. From this it may be inferred that at the time of hatching these sensory organs are in fact functional [21]. The functionality of these sensilla as mechanoreceptors is somewhat problematical due to the fact that at the time of hatching embryonic development is still incomplete [22].

Species	Socket	Number of shafts	Shaft length
Achelia cuneatis	$3 \mu m$	4	16 µm
Ammothea allopodes	1.0 µm	6	9 µm
Ammothea carolinensis	1.0 µm	5	8 µm
Ammothea clausi	$4.0~\mu m$	2	39 µm
Ammothea glacialis	$8.0 \mu m$	5	5.0 µm
Ammothea striata	3.6 µm	4	10 µm
Nymphon australe	5.0 µm	2	16 µm
Nymphon charcoti	$4.0~\mu m$	2	36 µm
Nymphon grossipes	2.6 µm	2	39 µm
Pentapycnon charcoti	2.0 µm	2	16 µm

Table 1. Showing the socket diameter, number of shafts and shaft length of mechanoreceptors found on early post hatching developmental stages of pycnogonids.

The developing body structures such as appendages and the other sense organs like the eyes are proportionally small in the early developing stages. The mechanoreceptors, by comparison, are formed in the size and shape found in the adults [20]. Whether such sensory sensilla are functional in detecting sound energy in the form of particle vibrations is not yet established.

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References

[1] **Trauntz, J., & Sandeman, D. C.** The detection of water born vibrations by sensory hairs On the chelae of the crayfish. Journal of Experimental Biology, **88**: 351-356, 1980.

- [2] **Derby, C. D.** Structure and function of cuticular sensilla of the lobster *Homarus Americanus*. Journal of Crustacean Biology, **2** (1): 1-21, 1982.
- [3] **Kiel, T. A.** Functional morphology of insect mechanoreceptors. Microscopy Research And Technique, **39** (6): 506-531, 1997.
- [4] Iwasaaki, M., Itoh, T. & Tominaga, Y. VI Mechano-and Phonoreceptors. In: Atlas of Arthropod Sensory Receptors. Springer Press, 1999.
- [5] **Barth, G. G.** Spider mechanoreceptors. Current Opinion in Neurobiology, **14**: 415-422, 2004.
- [6] **Popper, A. R., Salmon, M. & Horch, K. W.** Acoustic detection and communication by Decapod crustaceans. Journal of Comparative Physiology, **187**: 83-89, 2001.
- [7] Casas, J. & Dangles, O. Physical ecology of fluid flow sensing in arthropods. Annual Review of Entomology, 505-520, 2010.
- [8] **Stock, J. H.** Experiments on food preference and chemical sense in Pycnogonida. In "Sea Spiders (Pycnogonida)". Zoological Journal of the Linnean Society of London, 63: 59 -74, 1978.
- [9] **Dohrn, A.** Die Pantapoden des Golfes von Naples und der angrenzen Meeresabachunitte. In: Monographis der fauna und flora des Golfes von Naples, **Vol.** 3, pp.1-252. Wilhelm Englemann, Liepzig 1881.
- [10] Helfer, H. & Schlottke, E. Pantapoda. In: Klassen und ordnungen des tierreichs (H. G. Bronns, ed.), Vol. 5 Abteilung 1 Buch 2, pp.1-314. Akademische Verlagsgesellschaft, Leipzig, 1935.
- [11] **Brenneis, G.** Pycnogonida (Pantapoda). In: Structure and evolution of invertebrate nervous systems (A. Schmidt-Racsa, S. N. Harzsch, & G. Purschke, eds.) pp. 419-427, 2016.
- [12] **Lehmannm, Heβ. M. & Meizer, R.** Sense organs in Pycnogonida: A review. Acta Zoologica, **Vol.** 98: 1-2, 2017.
- [13] **Bogomolova, E. V.** Larvae of three sea spiders of the genus *Nymphon* (Arthropoda: Pycnogonida) from the White Sea. Invertebrate Zoology, **Vol.**33: 145-160, 2007.
- [14] **Alexeeva, N., Bogomolova, E., Tamburg, Y. & Shunatova, N.** Oligomeric larvae of the pycnogonids revisited. Journal of Morphology, 278(9):1284-1304 (Arthropoda: Pycnogonida) from the White Sea. Invertebrate Zoology, 33 (3): 145-160, 2017.
- [15] King, P. E. Pycnogonids. St Martens Press, 1973
- [16] **Bain B. A.** Larval types and a summary of postembryonic development within the pycnogonids. Invertebrate Reproduction and Development, 43, 193-222, 2003.
- [17] **Brenneis, G., Bogomolova E. V., Arango, C. P. & Krapp F.** From egg to "no-body": an overview and revision of developmental pathways in the ancient arthropod lineage Pycnogonida. Frontiers in Zoology, 14, 1-22, 2017.
- [18] **Fornshell, J. A.** Larval stages of two deep-sea pycnogonids. Invertebrate Zoology, 12, 197–205, 2015.
- [19] **Fornshell, J. A.** Larval stages *Nymphon charcoti* Bouvier 1911. Arthropods. (ISSN 2224-4255), 6, 1-7, 2017.
- [20] **Rienstra, S.W. & Hirschberg, A.** An Introduction to Acoustics. Eindhoven University of Technology, 2016.
- [21] **Fornshell, J. A. & Harlow, A. P.** Mechanoreceptors in pycnogonids (Arthropoda: Pycnogonida). Journal of Crustacean Biology, **Vol. 38** (3); 385-387, 2018.
- [22] **Fornshell, J. A.** Early post hatching stages of *Nymphon australe*. Arthropods. (ISSN 2224-4255), In Press.