Article

The morphology and potential function of mechanoreceptors found on members of the family Coenobitidae

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Received 12 September 2023; *Accepted 20 October 2023*; *Published online 16 November 2023*; *Published 1 March 2024*

Abstract
The mechanoreceptors of land-dwelling juveniles of the family Coenobitidae were studied using scanning electron microscopy to determine how their morphology varied from the mechanoreceptors of the marine dwelling zoea stage. Archived specimens of *Birgus latro* Leach, 1816 and *Coenobita clypeatus* Latreille,1829 from the collections maintained in the National Museum of Natural History, Smithsonian Institution were examined. The mechanoreceptors on the antennules of the planktonic marine larval stage, zoea, are potentially capable of detecting near field sound energy at frequencies two orders of magnitude lower than those of the antennules of the land-dwelling juveniles in both genera. This sensitivity to lower frequencies potentially enables the larval stages to detect sound energy sources at much greater distances.

Keywords bioacoustics; *Birgus latro*; *Coenobita clypeatus*; Glaucothoë; land hermit crabs; zoea.

Arthropods
ISSN 2224-4255
URL: http://www.iaees.org/publications/journals/arthropods/online-version.asp
RSS: http://www.iaees.org/publications/journals/arthropods/rss.xml
E-mail: arthropods@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

The members of the family Coenobitidae inhabit the nearshore tropical marine environment as larva, zoea and Glaucothoë stages (Burggern and McMahon, 1988). They may in the case of *Birgus latro* Leach, 1816 come ashore in the Glaucothoë stage (Wang et al., 2007). *Birgus latro* is the largest land-dwelling arthropod, reaching 1 meter in length and 4 kg in mass. The members of this family as juveniles and sexually mature adults are land animals inhabiting tropical islands in the Indian Ocean, Pacific Ocean, Caribbean Sea, Central American countries as well as the northern coast of the continent of Australia (Burggern and McMahon, 1988; Wang et al., 2007; Drewa et al., 2010). There are two genera in this family, the *Coenobita* comprising 17 species and *Birgus* with one species. When on land the adult form of *B. latro* produces and responds to environmental acoustic signals both the near field and far field (Shintia et al., 2021). Species of the genus *Coenobita* have also been shown to produce and to respond to sounds when on land in their juvenile and adult stages (Imafuku and Ikeda, 1990; Aaden et al., 2010, 2011; Stahlmana et al., 2011; Rayna et al., 2012; Tuchina et al., 2015).

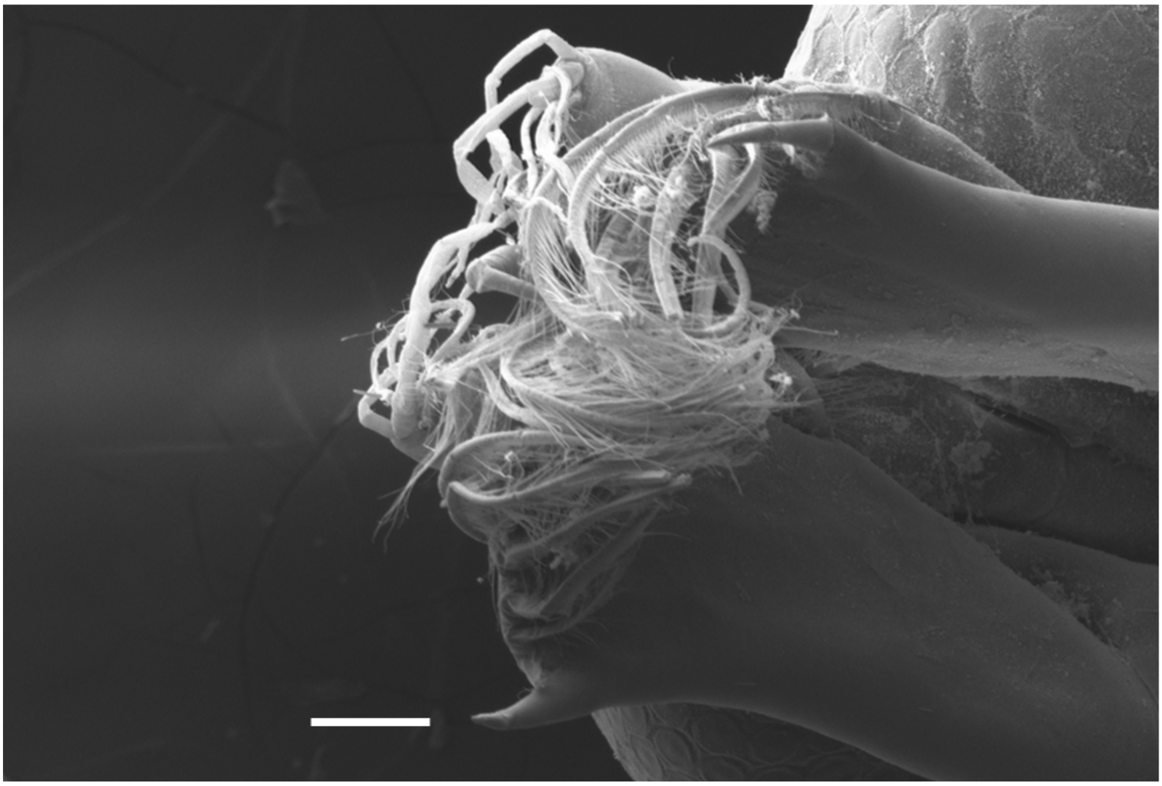


Fig. 1 The sensilla on the antennules of *Birgus latro* zoea. The scale bar is 40 μm.

Sound energy exists in two forms, particle motion, and pressure waves. The former, near field sound, dominates the sound energy at distances less than one wavelength from the source. The latter, pressure waves, called far field sound, dominates the sound energy at greater distances from the source (Nedelec et al., 2016). Many members of the class Crustacea are known to be able to detect near field sound energy (Breithaupt and Tautz, 1990; Senter, 2000; Popper et al., 2001; Fields and Weissburg, 2005; Boon et al., 2009; Stanley et al., 2011; Kavlie and Albert, 2013; Nedelec et al., 2016; Montgomery and Radford, 2017). Also, chelicerates are capable of detecting near field sound (Barth, 2004; Fornshell and Harlow, 2018; Fornshell, 2021, 2022).

Peg Sensilla are potentially sensitive to near field sound energy as well as water currents (Breithaupt and Tautz, 1990). Chordontal Organs which are also found in hermit crabs are sensitive to far field sound, sound pressure waves (Taylor, 1966, 1967a, 1967b; Kavlie and Albert, 2013). The frequencies, ω, to which peg sensilla respond are related to the length of the sensilla (Popper et al., 2001). Two different models for the response of peg sensilla to near field sound frequencies have been proposed. The first, by Barth (2004), holds that the sensilla must extend out of the boundary layer of the frequency being detected. This boundary thickness layer, δ, is defined by the equation $[\text{kinematic viscosity}/\ \omega]^{1/2}$ (see Graph 1) (Barth, 2004). This was derived for near field sound energy detection by spiders (Barth, 2004). Using this model δ is more than twice as thick in air than in water for any given frequency (Barth, 2004). A second model derived by Fields, & Weissburg (2005) for copepod sensilla defines the sensitivity of the sensilla with the equation $\omega \sim L^{-3}$, where L is the length of the sensilla in millimeters. In both models longer sensilla detects lower frequencies and shorter sensilla detects higher frequencies. These theoretical models may be used to make inferences as to the potential response of mechanoreceptors, sensilla, to different frequencies of sound, both which frequencies and at what distances from the source.

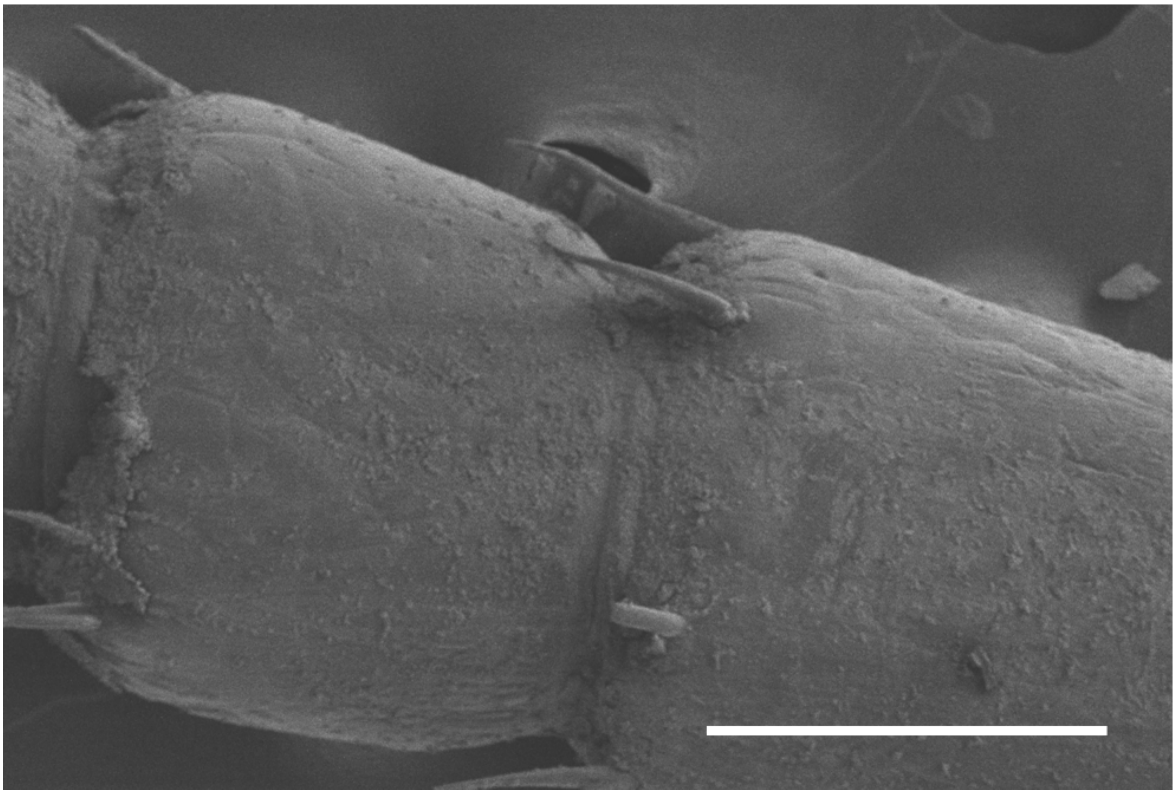


Fig. 2 The sensilla on the antennules of juvenile *Birgus latro*. The scale bar is 200 µm.

In this study we will attempt to primarily identify and describe the morphology of mechanoreceptors potentially capable of detecting near field sound energy in larval and juvenile stages of hermit crabs of the family Coenobitidae.

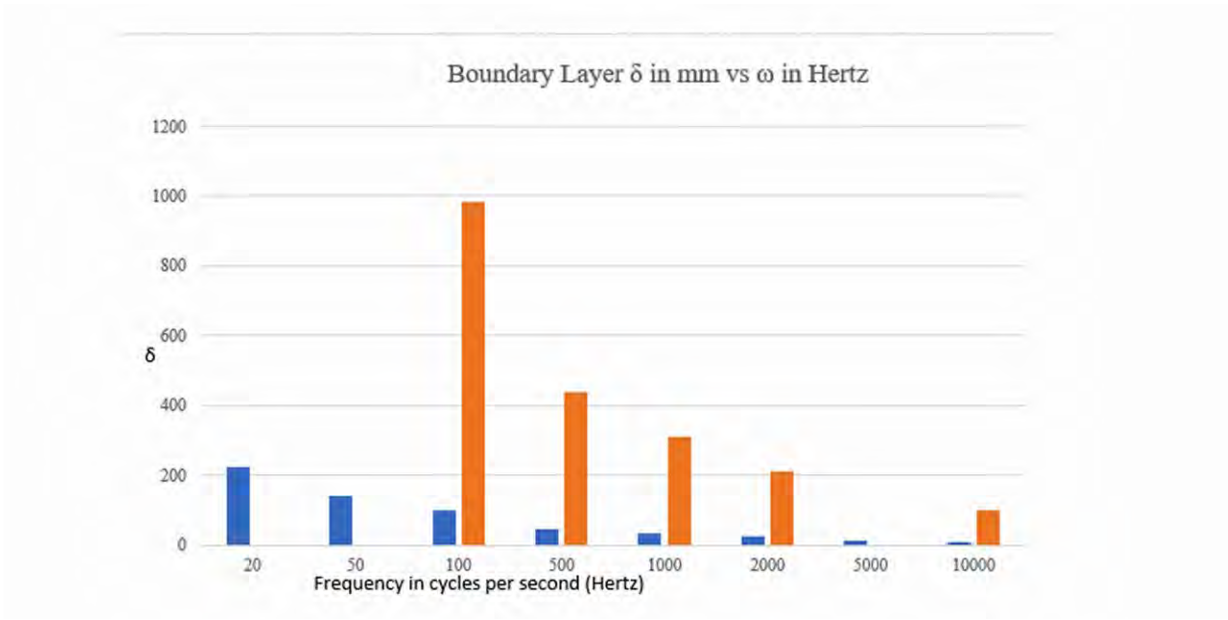
2 Materials and Methods

Zoea of *B. latro* from the collections of the U. S. National Museum of Natural History archived in 70% ethyl alcohol were progressively dehydrated in 75%, 90%, and 100% ethyl alcohol solutions. Antennules removed from the whole specimens of juvenile *B. latro*, body length 15 cm, and *C. clypeatus*, body length 2 cm, also stored in 70% ethyl alcohol were similarly prepared to make the electron micrographs of the antennules. After critical point drying, the specimens were coated with gold palladium alloy before making scanning electron micrographs. The images were produced using a Zeiss EVO MA15 Electron Microscope (Zeiss, Tokyo, Japan). All size measurements were made from the electron micrographs.

3 Results

Multiple 200 µm long plumose sensilla are found on the terminal segment of the antennules of *B. latro* zoea. Similar plumose sensilla 160 µm in length were observed on the antenna of the zoea. These sensilla are potentially capable of detecting near field sounds as low as 0.050 kHz (Barth, 2004; Fornshell, 2022).

The antennules of juvenile *B. latro* also have nonplumose sensilla. There are three or four sensilla 120 µm to 250 µm in length on each annulus of the antennules. On the base of the antennule of *B. latro* there are numerous 125 µm long sensilla. These sensilla are potentially capable of detecting near field sound energy above 2 kHz to 10 kHz (Fig. 2, Graph 1, and Table 1) (Barth, 2004; Nedelec et al., 2016; Fornshell, 2022).



Graph 1 This graph depicts the boundary layer, δ, in μm thickness for particle motion boundary layer in air (Orange) and in Water (Blue) as a function of frequency, ω, in Hertz following Barth (2004).

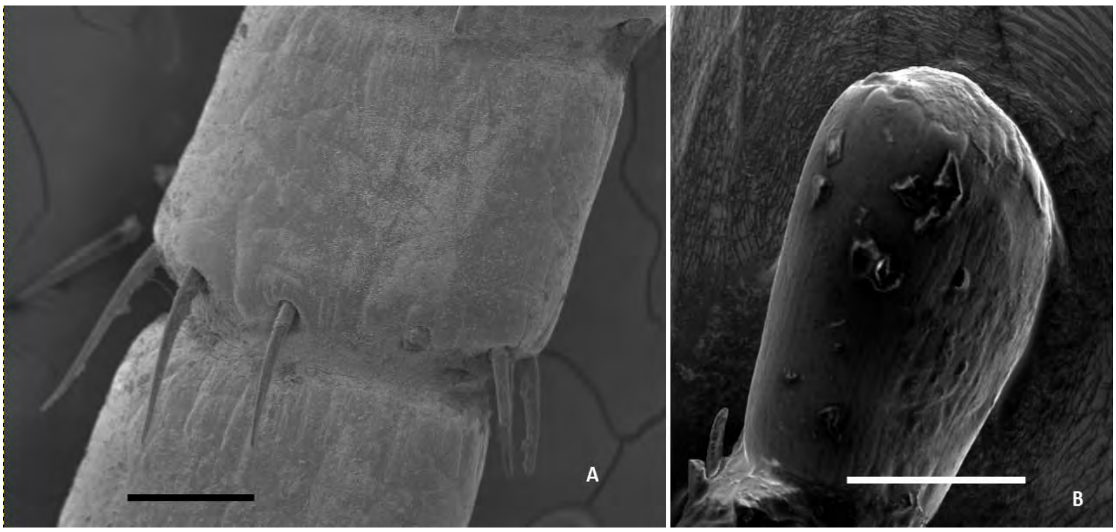


Fig. 3 The sensilla on the antennules of juvenile *Coenobita clypeatus.* Image A is an annulus mid-way along the antennule; Image B is the terminal annulus of the antennule. The scale bars are 100 μm in both image A and B.

The antennules of juvenile *C. clypeatus* typically have six simple sensilla @ 125 μm to 170 μm long on each annulus (Fig. 3 and Table 1). There are several sensilla of the same size on the first segment of the antennule. These sensilla are potentially capable of detecting near field sound energy in the range of 6 kHz to 10 kHz (Fig. 2, Table 1 and Graph 1) (Barth, 2004; Fornshell, 2022). There no sensilla found on the terminal annulus of the antennule of *C. clypeatus* (Fig. 4 and Table 1). The chela and walking legs, of juvenile *C. clypeatus* have sensilla 200 μm to 2000 μm long. These sensilla are potentially capable of detecting near field sound energy above 1 kHz in the case of the shorter sensilla and as low as 0.10 kHz in the case of the longer sensilla (Table 1 and Graph 1) (Barth, 2004; Fornshell, 2022). On the abdomen of *C. clypeatus* there are sensilla 85 µm long to 300 µm long (Fig. 5). The sound energy sensitivity of these sensilla is problematical. The members of the genus *C. clypeatus* maintain a supply of water in the gastropod shell. If immersed in water, these sensilla could detect near field sound energy in the 0.02 kHz to 0.5 kHz range. If functioning in air, then only frequencies above 10 kHz would be detected (Table1 and Graph 1) (Barth, 2004; Fornshell, 2022).

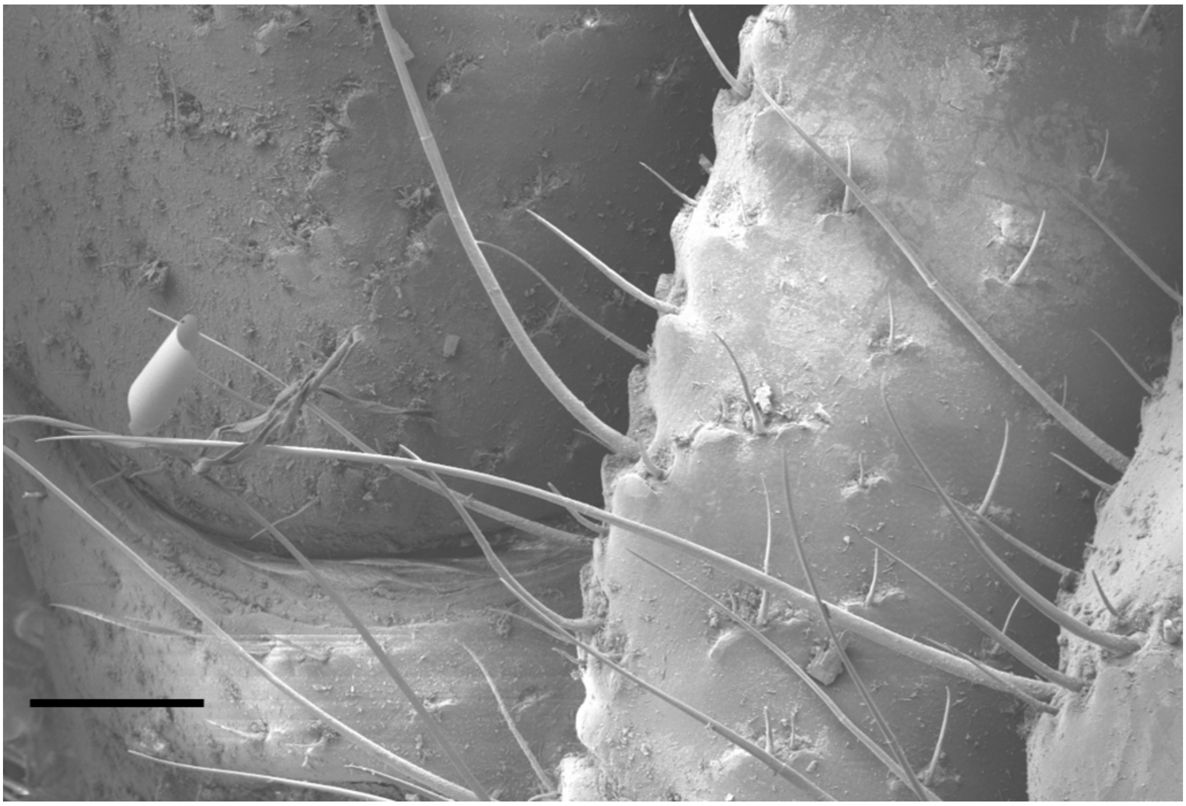


Fig. 4 The sensilla on the walking legs of *Coenobita clypeatus*.The scale bar is 200 µm**.**

4 Discussion

The members of the Coenobitidae juveniles have mechanoreceptors potentially well suited to detecting sound in the near field at higher frequencies than reported as being produced by hermit crabs themselves (Imafuku, 1990; Aaden et al., 2010, 2011; Ryana et al., 2012; Stahlmana et al., 2012; Shintia et al., 2021). The sounds produced by juvenile and adult *B. latro* are most intense at 0.05 kHz to 0.1 kHz and 0.35 kHz to 0.45 kHz (Shintia et al., 2021). The near field would be 1.5 to 2.5 m for the lower frequencies and 0.35 m to 0.75 m from the crab producing the sound. The results of Shintia et al. (2021) do not show any results of higher harmonics, although, the equipment used in their study had a frequency range of 0.005 kHz to 20 kHz (Shintia et al., 2021). The coconut crab may be responding to higher harmonics of the observed frequencies.

The Coenobitidae have been shown to respond to the lower frequencies produced by conspecific sources (Imafuku, 1990; Aaden et al., 2010, 2011; Ryana et al., 2012; Stahlmana et al., 2012). The marine hermit crab *Petrochirus californiensis* Bouvier, 1895, in the family Diogenidae has been shown to have a chordontal organ at the base of the antenna capable of detecting sound pressure waves (Taylor, 1966, 1967a, 1967b). This type of organ has not been reported for the members of the family Coenobitidae. It would be good to look for chordontal organs like those described for the marine hermit crab *P. californiensis*.

Table 1 Length of sensilla capable of detecting near field sound energy found on members of the family Coenobitidae. The frequency sensitivities are calculated based on the equations given in Barth (2004).

Organ	Sensilla length	Frequency sensitivity
Antennules of *B. latro* zoea	200 µm	≤ 0.02 kHz
Antennae of *B. latro* zoea	160 µm	≤ 0.05 kHz
Antennules of *B. latro* juveniles	120 µm to 250 µm	≥ 2.0 kHz
First segment of the antennule of juvenile *B. Latro*	125 µm	≥ 2.0 kHz
First segment of the antennule of juvenile *C. clypeatus*	125 µm to 170 µm	≥ 2.0 kHz
Juvenile *C. clypeatus* chela and walking legs	200 µm to 2000 µm	0.1 kHz to 2.0 kHz
Abdomen of *C. clypeatus*	85 µm to 300 µm	1.0 kHz to 2.0 kHz in air 0.02 kHz to 0.5 kHz in Water

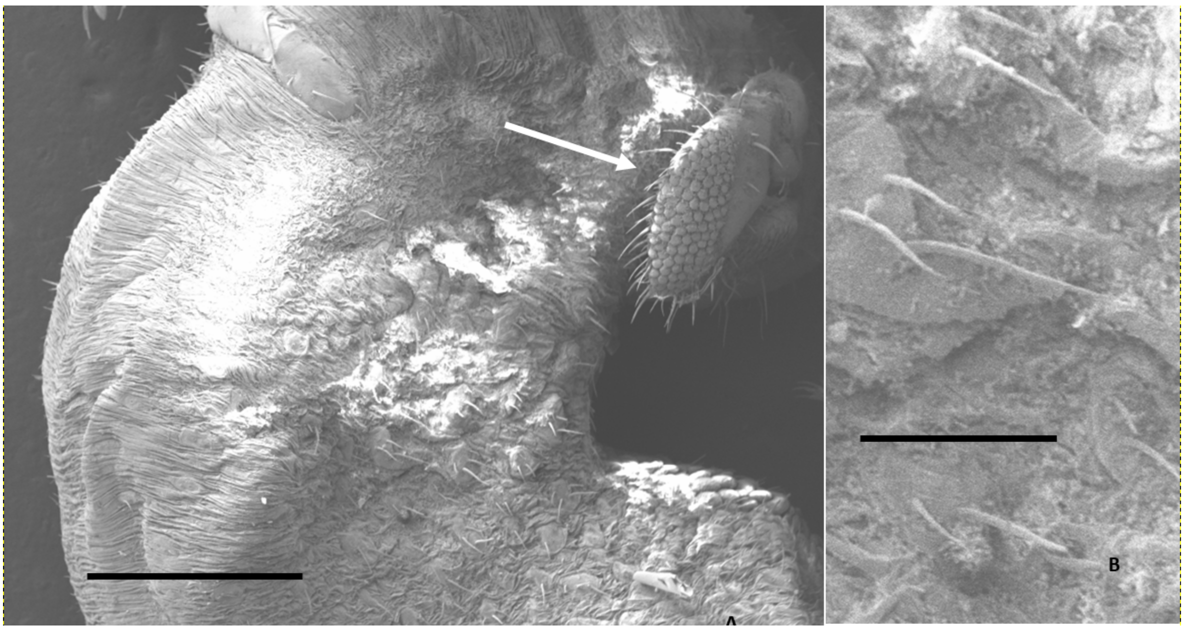


Fig. 5 The sensilla on the abdomen of *Coenobita clypeatus*. The arrow is the greatly reduced fifth walking leg. The scale bar in A is 1 mm and in image B 300 µm.

The mechanoreceptors on the larval stage antennules are potentially capable of detecting near field sound energy at frequencies two orders of magnitude lower than those on the antennules of the land-dwelling juveniles in both genera. This may facilitate the orientation of the swimming motion of the larval stage when seeking a suitable habitat, the shore (Radford et al., 2010; Stanley et al., 2011).

The work of Stanley et al., (2011) has shown that the larvae of marine decapods can use sound as a cue to find a suitable habitat for metamorphosis into the adult stage. The Coenobitidae larvae potentially have this capability also and may use it to orient their movements to shore. The size and potential sensitivity of juvenile and adult mechanosensory sensilla are independent of the size of the land-dwelling animals, less than 2 centimeters long *C. clypeatus*, to 15 centimeters, *B. latro*, in the case of the specimens used in this study.

Acknowledgements

Thanks for assistance with the electron microscope work are due to Scott Whittaker of the Imaging Laboratory, National Museum of Natural History.

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