Article

Sound producing stridulitrum in mantis shrimp

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Abstract
There are three sound producing mechanisms employed in the Order Stomatopoda: (1) Sounds generated by raptorial appendages, the second maxillipeds used to attack prey organisms as described by Tirmizi and Kazmi (1984), Vetter and Caldwell (2015); (2) The “Stomatopod Rumble” in the family Gonodactyloidea involving the vibrations of the carapace by the posterior remoter muscle of the mandible (Patek and Caldwell, 2006); and (3) Stridulating structures (Stridulitrum) on the uropods and telson as described in *Squilla empusa* Say 1818 and in *S. mantis* (Linnaeus, 1758) by Brooks (1886a) and Giesbrecht (1910). The presence of stridulating structures has been used as a morphological character in defining, the Squillidea. The stridulating structures are on the back side of the endopod of the uropods and on the ventral surface of the telson. Little attention, however, has been paid to the detailed morphology of these stridulating structures. Members of the Family Squillidea use a stridulitrum to produce sounds. Electron micrographs of this structure in the Squillidea and were produced in this study. Images showing the detailed structure of four species of the genus *Squilla* and one from the genus *Oratosquilla* were analyzed. The clicking sound produced by the raptorial appendages of *Squilla empusa* Say 1818 was also studied (Say, 1818). Spectral analysis of these clicking sounds are presented.

Keywords bioacoustics; Squillidea; Stomatopoda; stridulitrum; clicking sound.

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1 Introduction

The ability of mantis shrimp to produce sounds was first documented in the late nineteenth century (Brooks, 1886a). “*Squilla* [*empusa*] stridulates by rubbing the serrated spine of the swimmeret across the serrated ridge of the ventral surface of the telson. The noise which is thus made underwater can be clearly heard above the surface.” (Brooks, 1886a). *Squilla mantis* (Linnaeus, 1758) has been reported to produce similar sounds “when it grasped with a pair of forceps” (Giesbrecht, 1910). The structures used to produce the sounds, stridulating structures, on the uropods have been used as taxonomic defining traits of the family Squillidea (Brooks, 1886a;

Giesbrecht, 1910; Kemp, 1913; Ahyong, 1997). While all these researchers provided verbal references to the stridulitrum, detailed descriptions and or illustrations were not provided apart from the highly detailed drawings included in the Challenger Reports (Brooks, 1886b). In this study electron micrographs of the stridulitrum in the Squillidea are presented. The stridulitrum is on the posterior side of the endopod in Squillidea. The second mechanism has been documented in the twenty-first century in the family Gonodactyloidea and involves the vibrations of the carapace by the posterior remoter muscle of the mandible (Patek and Caldwell, 2006). The stridulitrum structure is lacking in the Gonodactyloidea (Vetter and Caldwell,2015).

The raptorial appendages, second maxillipeds, used for prey capture, have been found to produce a sharp clicking sound resulting from the rapid extension of the raptorial appendages, second maxillipeds. The sounds may result from cavitation, the impact on another animal, a solid substrate or “striking a spine on the penultimate segment of the maxilliped itself” (Tirmizi and Kazmi, 1984). These clicks have been interpreted as having a conspecific communication function (Vetter and Caldwell, 2015). These sounds were recorded in *S. empusa*, and a spectral analysis is presented as part of this research work.

2 Materials and Methods

At the time of collection, the specimens were fixed in a formaldehyde solution and, after species determination stored in a 70% ethyl alcohol solution. In preparing the specimens for examination with the electron microscope, the uropods and telson were dehydrated in progressively more concentrated solutions to 100% ethyl alcohol and critical point dried and coated with gold palladium alloy. The images were produced using a Zeiss EVO MA15 Electron Microscope. All measurements were made from the electron micrographs. Images showing the detailed structure of stridulitrum_on the uropods of five species of Squillidea, *Squilla deceptrix* Manning 1969, *Squilla empusa* Say 1818, *Oratosquilla inornata* Tate 1883, *Squilla mantis* (Linnaeus, 1758), *Squilla mantoidea* Bigelow 1893 are presented (Linnaeus, 1758; Say, 1818; Manning, 1969; Bigelow, 1893)

In this study clicking sounds produced by *S. empusa* were recorded using a Cermic ER-M3 omnidirectional microphone placed directly over the 15 L aquarium tank in which a single 4 cm long male specimen was maintained. The microphone was less than five centimeters above the surface of the water. The sound recordings were stored on the hard drive of a Dell laptop computer for further processing. The sensitivity of the microphone was -58 dB to + 3 dB, and the signal to noise ratio was 60 dB.

3 Results

***Oratosquilla inornata*:** The stridulitrumis on the posterior edge of the endopod of the uropod with teeth present in pairs. The average separation between members of the pairs is 167 μm and the average separation between the pairs is 400 μm. The individual stridulitrum ridges are 33 μm to 100 μm high (Fig. 1). A scraping structure on the lateral margin of the ventral side of the Telson is 109 μm wide and 2,182 μm long. The telson is 12,000 μm long (Fig. 2). The ratio of scraping structure length to telson length is 0.18183:1.

***Squilla deceptrix*:** The stridulitrumis located on the posterior edge of the endopod of the uropods and made up of teeth 18 μm to 54 μm high and spaced at intervals of 145 μm to 454 μm. No scraping structure was observed on the ventral surface of the Telson.

***Squilla empusa*:** The stridulitrumis located on the posterior edge of the endopod of the uropods and made up of teeth 40 μm to 100 μm high and spaced at intervals of 160 μm to 400 μm. A scraping structure on the lateral margin of the ventral side of the Telson is 220 μm wide and 3,000 μm long. The telson was 11,000 μm long. The ratio of scraping structure length to telson length is 0.27273:1.

***Squilla mantis*:** The stridulitrumis located on the posterior edge of the endopod of the uropods and made up of teeth 45 µm high and spaced at intervals of 136 µm. A scraping structure on the lateral margin of the ventral side of the Telson is 125 µm wide and 3,375 µm long. The telson is 8,000 µm long. The ratio of file length to telson length is 0.421875:1.

***Squilla mantoidea*:** The stridulitrumis located on the posterior edge of the endopod of the uropods and made up of teeth 65 µm high and spaced at intervals of 217 µm. A scraping structure on the lateral margin of the ventral side of the Telson is 2,500 µm long. The telson was 12,000 µm long. The ratio of scraping structureto telson length 0.2083:1.

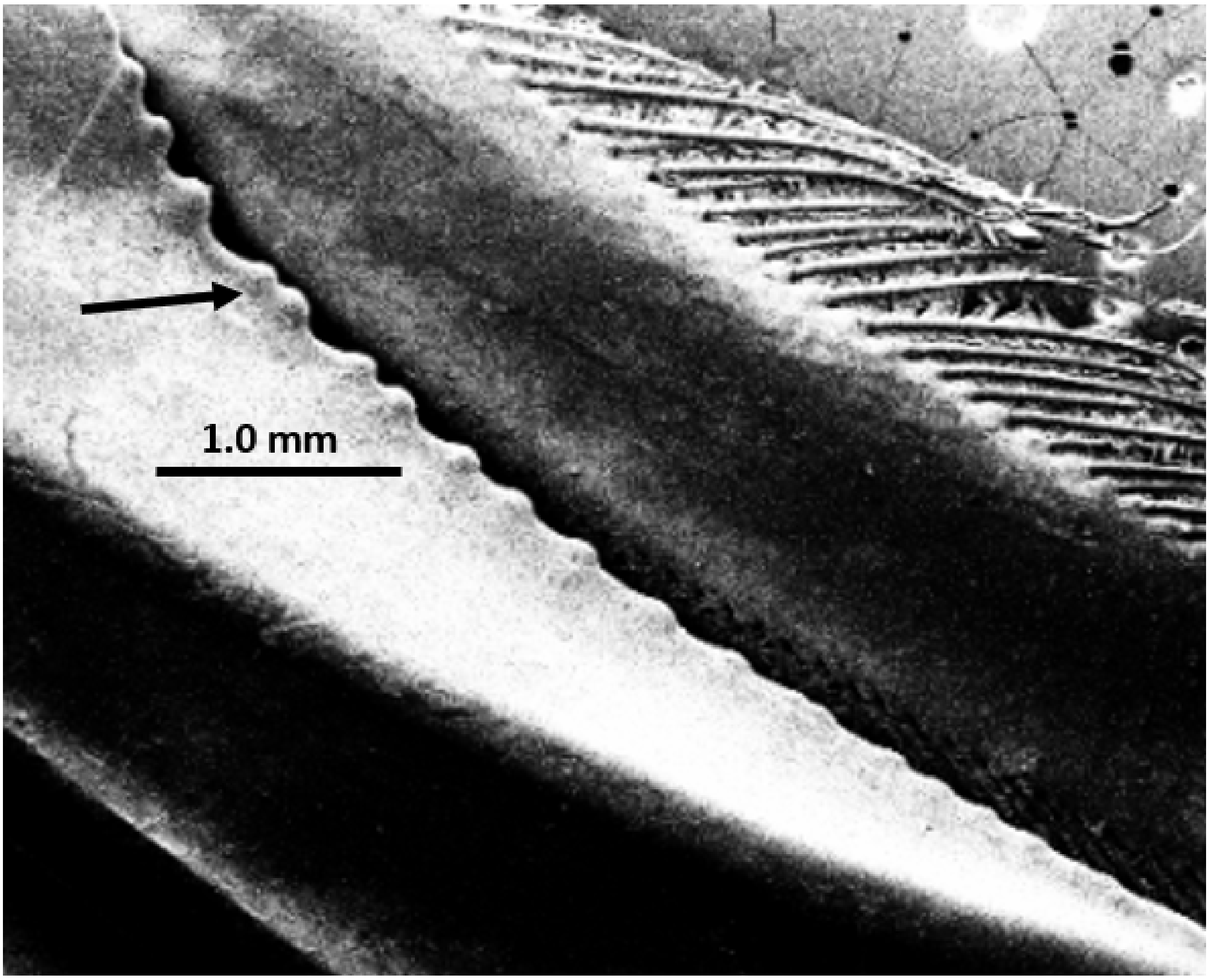

Fig. 1 The stridulitrum (arrow) on the back side of the endopod of the uropods of *Squilla inornata.* The arrow indicates the paired teeth of the stridulitrum.

Two different sounds were heard from the tank holding *S. empusa,* a sharp clicking sound and a rasping sound. Recordings of a clicking sound were made. A spectrogram of the clicking sounds is presented in Fig. 3. The peak sound intensities were at 2 kHz and 14 kHz. The range is 0.04 kHz to 22 kHz. These sounds are believed to result from rapid motions of the raptorial feeding appendages (Tirmizi and Kazmi, 1984; Vetter and Caldwell, 2015). When swimming *S. empusa* was heard to produce a sharp rasping sound. This rasping sound is distinctly different from the clicking sound produced by the extension of the maxillipeds. It has not proven possible to record this very intermittent sound.

Table 1 Summary of observations of the sound producing structures.

Species	Spacing of stridulitrum ridges	Height of stridulitrum ridges	Length of the scraping structure	Ratio of scraping structure: Telson length
S. deceptrix	145-454 µm	18-54 µm	Not present	-
S .empusa	160-400 µm	40-100 µm	3,000 µm	0.27273:1
O. inornata	167-400 µm	33-100 µm	2,182 µm	0.18183:1
S. mantis	136 µm	45 µm	3,375 µm	0.421875:1
S. mantoidea	217 µm	65 µm	2,500 µm	0.2083:1

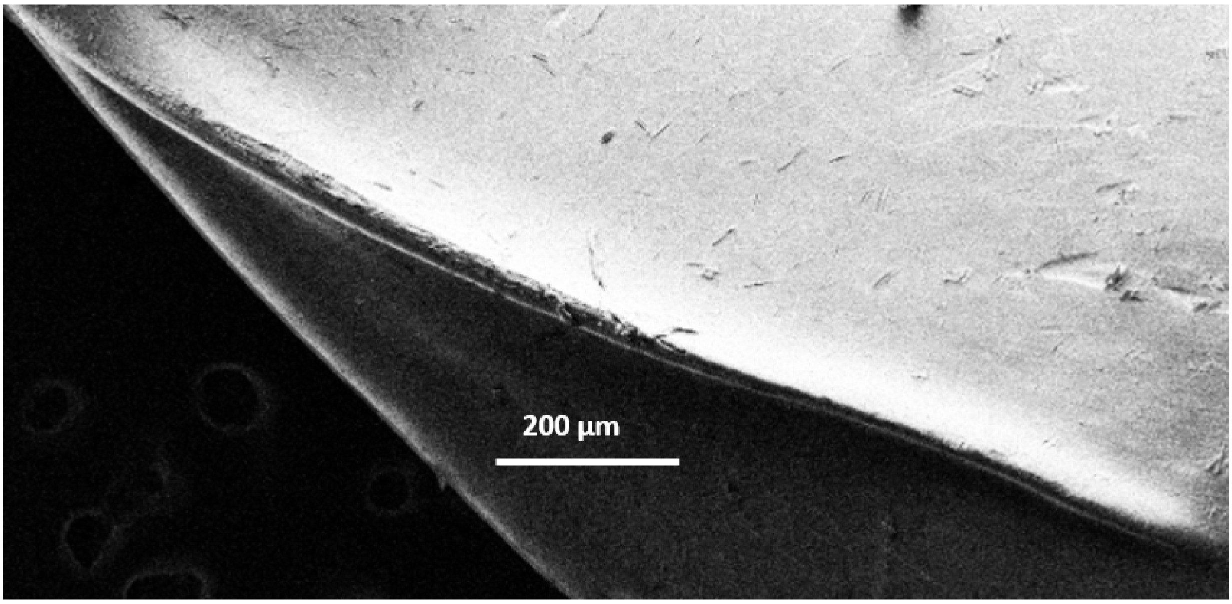

Fig. 2 The scraping structure on the ventral side of the telson of *Oratosquilla inornata.*

4 Discussion

The ability of stomatopods to detect sounds is not fully resolved at this time. Tirmizi and Kazmi (1984) state that stomatopods have pressure sensing organs, chordontal organs, at the base of their antennae allowing them to detect sound energy in the far field. Popper et al. (2001) however, report that most crustaceans are said to lack pressure sensing organs and are therefore unable to detect the far field, that is, the pressure component of sound. This issue needs further research to resolve the question of the ability of the Stomatopoda to detect sound in the far field. Stomatopoda do, however, have mechanoreceptors on their cuticle and can detect particle motion or the near field component of sound (Breithaupt and Tautz, 1990; Popper et al., 2001). The setae found on the cuticle of stomatopods are of the appropriate range of sizes to detect the far field component of sound (Breithaupt and Tautz, 1990; Popper et al., 2001). The setae found on the cuticle of stomatopods are of the appropriate range of sizes to detect or near field environmental and conspecific acoustic signals in the form of particle motions (Schram et al., 2013).

The clicking sounds were recorded when the animal was swimming or walking on the soft sand bottom in this study are believed to be the same sounds referred to by Vetter and Caldwell (2015). These same authors attribute the clicking sounds to have meaning during conspecific interactions as in territorial disputes (Vetter and Caldwell (2015). Hazlett and Winn (1962) recorded the clicking sound produced by *Gonodactylus oerstedii* which they attributed to a byproduct of the movement of the maxillipeds during feeding activities.

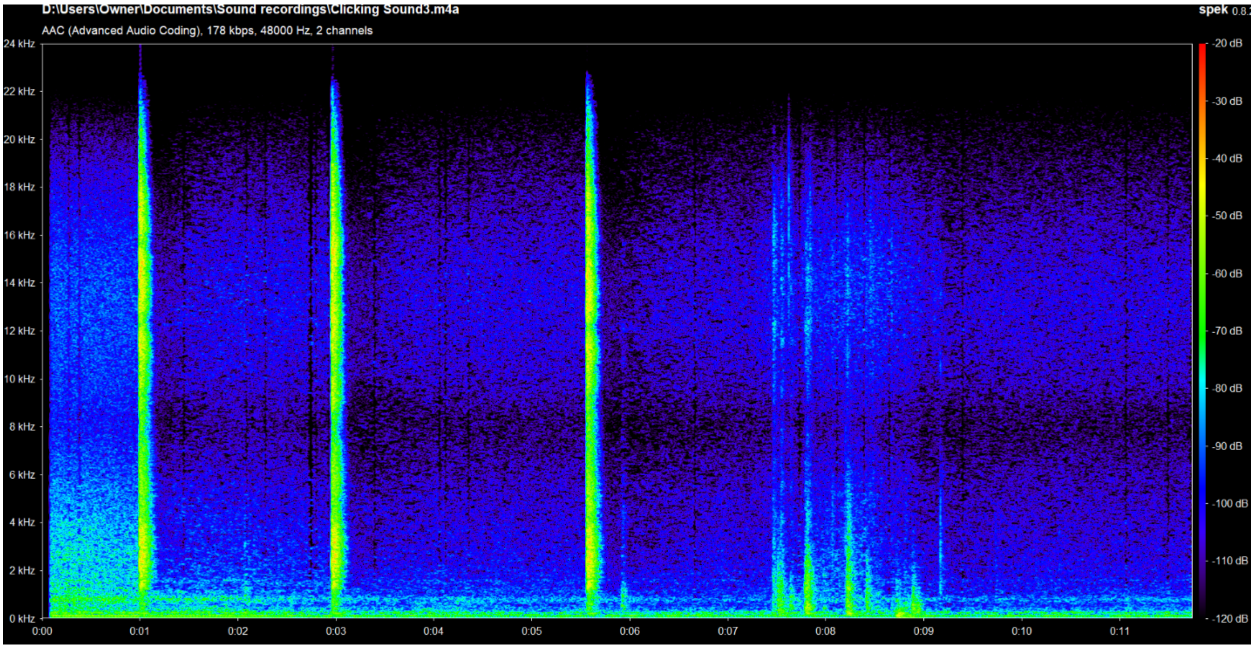

Fig. 3 A spectrogram of the clicking sound produced by *Squilla empusa* while swimming. The highest intensity of the recorded sound was observed at 2 kHz and 14 kHz.

The ability of the Stomatopoda to both detect sounds and the presence of the stridulating organs is indicative of the potential to communicate acoustically. Members of the Stomatopoda display behavior patterns indicating that they interact with one another acoustically (Vetter and Caldwell, 2015). Mantis shrimp respond to sounds in their environment, as recorded by Heitler et al. (2000) in their study of the escape response of *S. mantis* (Heitler et al., 2000).

The ability to produce sounds via stridulating mechanisms has evolved multiple times in the crustaceans dating back to the Mesozoic (Senter, 2000). The parallel evolution of this capacity to produce sounds is a strong indication of a definite survival benefit.

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