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OBSERVATIONS ON SOUND PRODUCTION BY TWO SPECIES OF CRABS FROM PANAMA (DECAPODA, GECARCINIDAE AND PSEUDOTHELPHUSIDAE) [1]

BY

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INTRODUCTION

Stridulation by crabs has been reviewed by Guinot-Dumortier & Dumortier (1960, 1961) and Dumortier (1963). Neither of these authors report any examples of sound production by crabs of the families Gecarcinidae or Pseudothelphusidae. No mention is made of sound production in recent works on the biology of gecarcinids (Bliss, 1963, 1968; Wright, 1968) or in works dealing with pseudothelphusids (Bott, 1968; Chace & Hobbs, 1969). However, an investigation of the defensive adaptations of some Panamanian crabs (Robinson, Abele & Robinson, 1970) led to the discovery that both *Gecarcinus quadratus* de Saussure, 1853, and *Potamocarcinus richmondi* (Rathbun, 1893) produce sounds. In this report we describe the sound producing apparatus of both species and discuss its possible adaptive significance.

Gecarcinus quadratus is a terrestrial species living high above the tide line and often at considerable distance (more than 100 m) from any water. It occurs on the west coast of Central America from Mexico to Ecuador. It is active nocturnally and retires by day beneath rocks and logs. In the laboratory the crab can be maintained on a diet of fruit.

Potamocarcinus richmondi inhabits freshwater streams and wet areas in the forest. It is known from Nicaragua to Panama and subspecies have been described from both Atlantic and Pacific drainages (Bott, 1968). It often constructs shallow burrows beneath rocks in stream beds. Crabs have been observed feeding on earthworms, fruit and insects. They seem to be more active nocturnally although they have been observed during the day in shaded areas of the forest.

METHODS AND MATERIALS

All observations were carried out during June 1969. *Gecarcinus quadratus* was studied on Naos Island on the Pacific coast of the Panama Canal Zone adjacent to the Smithsonian Tropical Research Institute Marine Laboratory. A total of 30

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specimens was observed ranging in size (carapace width) from 27 to 50 mm. Forty-one specimens of *Potamocarcinus richmondi* ranging in size (carapace width) from 20 to 75 mm were studied on Barro Colorado Island in the Panama Canal. Field and laboratory observations were carried out both during the day and night. The observations consisted of searching for the crabs and, when found, attempting to stimulate sound production by attacking the crabs with a dummy predator (see Robinson, Abele & Robinson, 1970). Recordings were attempted using a Uher 4000-L recorder and a Uher 512 microphone at 7½ cps. Unfortunately, our efforts to record the sounds in the field proved largely unsuccessful because of background noise. The crabs could be maintained in the laboratory but their observed behavior in the laboratory differed from that observed in the field. The crabs became lethargic and would not respond to most stimuli. No recordings of sounds were obtained in the laboratory. The sonographs from our poor quality field recordings (through the kind cooperation of Dr. A. S. Rand) only allowed us to establish the frequency range and duration of the bursts of stridulatory sound of *Gecarcinus quadratus*. We were unable to obtain even poor recordings of the sound produced by *Potamocarcinus richmondi*.

RESULTS

Seventeen of 30 specimens of *G. quadratus* produced sounds during our observations. The crabs produced sounds when disturbed in their retreats by day, when attacked with a dummy predator after such disturbance and also at night. At night stridulation occurred during dummy attacks and whenever the experimenters approached the crabs. This latter stridulation, which occurred when we were still several meters away, is most interesting and we are uncertain about the nature of the stimulus involved.

The sounds produced by *P. richmondi* were not noted until after we had observed over 30 specimens. However, five additional specimens examined in an open area all produced sounds when attacked by a dummy predator. The sounds produced were such that they could have easily gone unheard during our earlier observations which took place in areas where the background noise was at a high level, e.g., areas adjacent to running streams.

Gecarcinus quadratus produces two types of sounds. The first is caused by friction of the merus of the cheliped against the subhepatic region of the carapace. There are a number of oblique rows of forwardly directed tubercles present on the subhepatic region which may be considered the pars stridens (figs. 1A, 1B). These tubercles begin on the subhepatic region just posterior to the orbit and continue ventrally to the pterygostomial region just above the base of the cheliped. The tubercles continue posteriorly to the posterior border of the carapace. The merus of the cheliped (figs. 1C, 1D) rubs against this area. The interior area of the merus is concave medially but becomes straight to convex distally. It is the distal portion of the merus which may be considered the plectron as it is the area which actually rubs against the carapace. The lateral margins of this portion of the

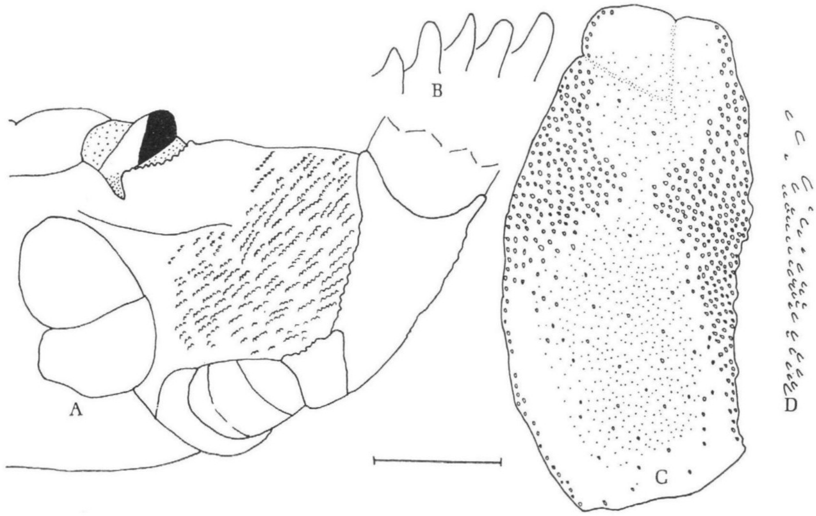

Fig. 1. *Gecarcinus quadratus* de Saussure, adult male. A, frontal view; B, row of tubercles from the subhepatic region shown in A; C, inner surface of merus of A; D, granules on lateral margins of C. Scale = 13 mm for A, 1 mm for B, 7 mm for C, D.

merus are armed with small tubercles (fig. 1D). As the cheliped moves back and forth across the carapace it is at a slight angle and the sound produced is similar to that produced by rapidly running an object over the teeth of a stiff comb. In large male specimens, small, blunt granules may be present on the distal portion of the merus but they are not necessary for sound production. Each burst of sound was distinct, lasting about 0.109 second. The frequency rose from 0 to 16 KHz over this period of time.

The second type of sound, produced by almost all crabs, is a bubbling sound caused by fluid being forced out and over the third maxillipeds. This occurred whenever the crab was grasped. The fluid was brown in color and had a bitter taste that is possibly unpleasant to a predator. A similar bubbling sound produced by *Ocypode* has been analysed by Horch & Salmon (1969).

Two types of sounds were also produced by *Potamocarcinus richmondi*. The first was a low pitched whirling sound. It was produced by friction of the merus of the third maxilliped against the propodus (penultimate segment) of the second maxilliped (figs. 2A, 2B, 2C). The inner surface of the merus of the third maxilliped is divided into two unequal concave areas. The areas are separated by a raised ridge lined proximally-distally with strong, long black setae (fig. 2C). On the inner surface of the larger area, in the upper interior corner, there is a subcircular raised area which is covered by very strong, short black setae which have their extreme tips slightly bent. This raised setaceous region may be considered the pars stridens. The propodus (penultimate segment) of the second maxilliped is expanded laterally. It is pitted on the expanded portion and may be considered

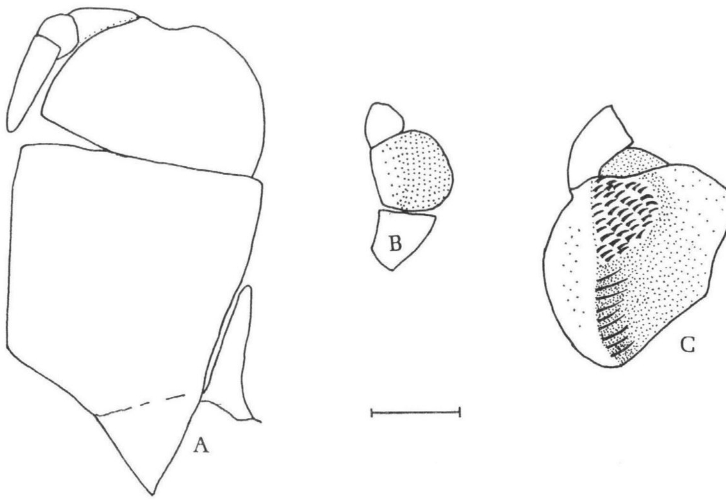

Fig. 2. *Potamocarcinus richmondi* (Rathbun), adult male. A, outside surface of third maxilliped; B, distal three segments of second maxilliped; C, inner surface of merus of third maxilliped. Scale = 5 mm.

the plectron. This expanded region of the second maxilliped fits against the raised setaceous region of the merus of the third maxilliped. The merus of the third maxilliped rotates circularly against the propodus of the second maxilliped. The proximal exterior angle of the merus of the third maxilliped serves as the pivot when the merus rotates. The sound was of variable duration, occasionally lasting one full second but we have no other data on the characteristics of this sound.

The second type of sound is the bubbling sound similar to that produced by other crabs. The fluid was clear and tasteless and was produced when the crab was attacked as well as when the crab was grasped.

DISCUSSION

The mechanism of sound production of *Gecarcinus quadratus* allows it to be grouped with some species in the families Grapsidae and Ocypodidae following the scheme of Guinot-Dumortier & Dumortier (1960). The apparatus is present in other species of *Gecarcinus* although none has been reported to produce sound. The apparatus is perhaps the least specialized morphologically and is not strikingly obvious when compared to that of other species in the same group or even to the apparatus of other crabs known to stridulate (see examples in Guinot-Dumortier & Dumortier, 1960). The movements of the cheliped against the subhepatic regions of the carapace in *G. quadratus* could be "derived" from the movements involved in the transition from an attitude of repose to that of either threat or flight. When the crab is under a stone by day the chelipeds are pressed against the ventral surface of the carapace. When moving slowly or feeding the chelipeds are largely held anteriorly or in a ventral position. However, when the crab is disturbed, either by being exposed in its diurnal retreat or by being attacked in its active phase, the crab raises its body into a display or running position, and rapidly raises the chelipeds. These arousal movements may predispose the crab to rub the cheliped against the carapace, a situation potentially favorable to the evolution of an acoustic anti-predator display and the specialization of a stridulatory device.

The mechanism of sound production of *Potamocarcinus richmondi* seems to be unique among the Decapoda in that no other apparatus involving the second and third maxillipeds has, to our knowledge, been described. A few species of African freshwater crabs in the same superfamily (Potamidae) produce sound by friction of the ambulatory legs against the carapace. We have observed the mouthpart modification, described for *P. richmondi,* present in other species of *Potamocarcinus* and in species of the related genus *Pseudothelphusa.* In the case of *P. richmondi* the movements resulting in stridulatory sound production may have been "derived" from a pre-existing preening behavior. The crabs were often observed using the palp of the third maxillipeds to clean the antennae, antennulae and eyestalks. The palp was pulled across them removing bits of debris in the process. The movement of the third maxillipeds during this behavior was very similar to that involved in the production of sound, the main difference being that during cleaning the movements were quite slow and no apparent sound was produced. However, if the crabs were disturbed by attack or startled while they were involved in this preening behavior the movements of the third maxillipeds would increase rapidly and the stridulatory sound would be produced. From this apparently pre-existing preening behavior the movements necessary for sound production would be present. Again a situation potentially favorable to the evolution of an acoustic anti-predator display and the specialization of a stridulatory device would exist.

Sound production by brachyuran crabs has been related to sexual behavior, defense of territory, social interaction and "intimidation" (Guinot-Dumortier & Dumortier, 1960). Sound production in the present species may also be used as a form of interspecific communication. In both species, sound production preceded attack autotomy and occurred when the crabs were attacked with a dummy predator (see Robinson, Abele & Robinson, 1970). It seems possible that the stridulation of both species could be associated with defense against predators. It could work in at least two ways. The sound could have a startle effect that could temporarily disorient an attacking predator or, if the sound were produced in close temporal proximity with pain inflicted by chelipedal biting (or attack autotomy) the predator might learn to associate the sound with the pain and exhibit avoidance behavior.

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ZUSAMMENFASSUNG

Gecarcinus quadratus Saussure, 1853 (Gecarcinidae) und *Potamocarcinus richmondi* (Rathbun 1893) (Pseudothelphusidae) produzieren jeweils zwei verschiedene Typen von Geräuschen. Der erste Geräuschtyp ist ein sprudelnder („bubbling") Ton, der hervorgerufen wird durch Flüssigkeit, welche aus und über den 3. Maxillipeden hervorgebracht wird; der zweite Geräuschtyp ist ein zirpender Ton. Der zirpende Ton von *G. quadratus* wird ausgelöst durch Friktionen von Merus und Cheliped gegen die subhepatische Region des Karapax. Das zirpende Geräusch von *P. richmondi* entsteht durch Friktionen zwischen dem Propodus des zweiten Maxillipeden und dem Merus des dritten Maxillipeden.

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NOTE ADDED IN PROOF

This manuscript was accepted for publication 20 November 1970, but was unfortunately misplaced by the editor for two years. Recently Klaassen (1973, J. comp. Physiol., **83**: 73-79) has described stridulation in *Gecarcinus lateralis*. He has described the mechanism of sound production as friction between the subhepatic region of the carapace and the inner side of the hand. This mechanism differs from that of *G. quadratus*. In the latter, sound is produced by friction between the subhepatic region of the carapace and the merus of the cheliped rather than the hand.

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