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Short communications

Acoustic concomitants of the defensive discharges of a primitive bombardier beetle (*Metrius contractus*)*

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Summary. *Metrius contractus*, a primitive paussoid bombardier beetle, emits its defensive quinonoid froth with accompanying sound (a faint "hiss"), but the sound is not pulsed, indicating that the secretory emission itself is not pulsed. Pulsed secretory delivery in bombardier beetles appears to occur in Brachinini only.

Key words. Defensive glands – discharge mechanism – quinones – bioacoustics – Carabidae

Arthropods that discharge defensive secretions usually do so inaudibly. The exceptions include a number of insects that discharge froths. The grasshopper, *Romalea guttata*, for instance, emits a bubbling foam when disturbed, a mixture of secretion and tracheal air that it ejects with a hissing sound from the mesothoracic spiracles (Fig. 1A) (Alsop 1970). Defensive froth emission also occurs in many arctiid moths, which discharge the foam from the anterolateral corners of the thorax (Fig. 1B), and may do so with accompanying sound (Carpenter 1938). But sound producers also include insects that eject jets of fluid rather than froth. Loudest, perhaps, are the familiar bombardier beetles of the genus *Brachinus*, which emit a distinct "pop" when they discharge their hot quinonoid spray (Schildknecht 1957; Aneshansley *et al.* 1969). Naturalists early on called attention to the detonations. In what is probably one of the first accounts of *Brachinus*, a Swedish student, Daniel Rolander, reports encountering a remarkable insect, which upon being seized, gave off a "kleinen Knalle" (a little crack) and a puff of "Rauch" (smoke). He called the insect a "Schussfliege" (or shooting fly; the term bombardiers was not coined until later), told Linnaeus about it, and published a description of it in 1750, in the Proceedings of the Royal Swedish Academy of Sciences [available to us in the German translation (Rolander 1754)].

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Bombardier beetles comprise two evolutionary branches (see Fig. 1 in Eisner *et al.* 2001) within the family Carabidae (references in Eisner *et al.* 2001). One branch, the brachinoid branch, includes the "advanced" bombardiers of the tribe Barachinini (comprising the genera *Brachinus* and *Stenaptinus*, among others) and the primitive species of the tribe Crepidogastrini. The other branch, the paussoid branch, features a number of tribes judged to be more or less advanced (Mystropomini, Ozaenini, Paussini), and one tribe, the Metriini, generally considered to be the most primitive of the paussoids. There is uncertainty whether the two branches are linked at their base (in other words, whether the two lineages have a common bombarding ancestor) or whether they represent parallel lineages in which the ability to bombard evolved independently (references in Eisner *et al.* 2001).

To help settle the question it becomes useful to learn as much as possible about the two groups that are the most primitive within each branch, the Crepidogastrini and the Metriini. Beetles of both these tribes are relatively hard to come by, but thanks to helpful collectors we have been able to obtain live individuals of each, and have published descriptions of their defenses (Eisner *et al.* 2000, 2001).

One finding of interest concerned the evolution of an important feature of the discharge mechanism, namely the pulsed nature of the secretory expulsion. The Brachinini typically show such pulsed emission (Fig. 8 in Eisner *et al.* 2001), which represents an adaptive refinement of the delivery system (Dean *et al.* 1990). The crepidogastrines, we have now shown, do not pulse their emissions (Eisner *et al.* 2001), indicating that the ability to pulse did not evolve in brachinoids until *after* the appearance of the brachinine stock. The absence of pulsation in crepidogastrines was detected acoustically, from the absence of temporal discontinuity in the sound oscillograms of these beetles.

When we published on *Metrius* (Eisner *et al.* 2000), we had not recorded its discharge sounds, and were therefore unable to determine whether this beetle pulses its discharges. Given the primitive phyletic status of *Metrius*, and the fact that in other paussoids (Ozaenini) the discharge sounds failed to reveal pulsation (T.

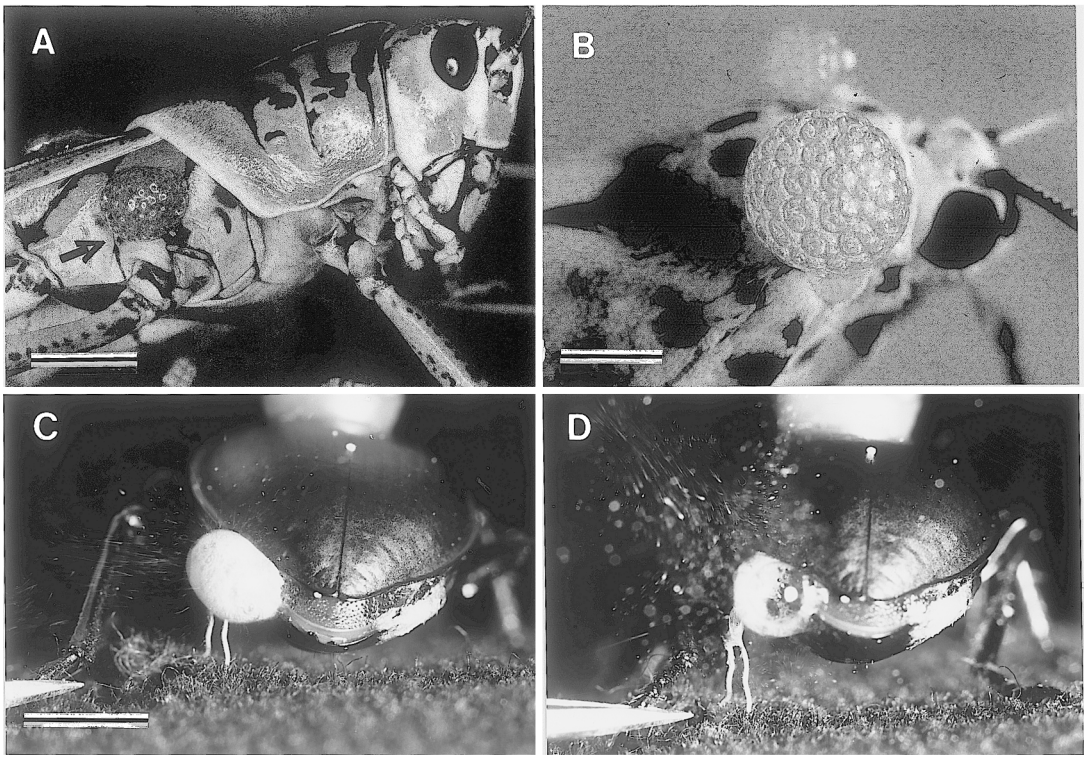

Fig. 1 **A**. *Romalea guttata*, discharging defensive froth (arrow) from the mesothoracic spiracle. **B**. The arctiid moth, *Utetheisa ornatrix*, discharging froth from the cervical region. Many arctiids emit such froth with accompanying sound. *U. ornatrix* does so inaudibly. **C, D**. Tethered *Metrius contractus*, in rear end view, discharging from the same gland on two separate occasions. In (**C**) the photo caught the emission early on, after onset of the discharge, and the froth has just formed; in (**D**) the picture is of the discharge at a later stage, when many tiny droplets, engendered by the bursting bubbles of the froth, are spewed into the air. Bars (**A**) 5 mm; (**B, C**) 2 mm

Eisner & D. J. Aneshansley, unpublished recordings of *Goniotropis nicaraguensis*), we thought it unlikely that *Metrius* would pulse. However, without evidence we could not be certain. We have now made recordings with *Metrius* and here report that its discharges, like that of crepidogastrines and probably paussoids generally, is non-pulsed. We are thus led to the conclusion that pulsation evolved in the brachinoid branch only, and that within the brachinoids it is an exclusive feature of the Brachinini.

Our sound recordings were done with *Metrius contractus*, using the same apparatus and techniques we used in recording the discharge sounds of crepidogastrines (Eisner *et al*. 2001). We had four live *M. contractus* available and made sound recordings with each. It was clear just from listening to the discharge sounds of *Metrius* that these were more faint and of different quality than the ones typical of *Brachinus*. The *Metrius* sound, unlike the sharp ''pop'' emitted by *Brachinus*, is in the nature of a hiss. The difference is doubtless a consequence of the different ways in which the two beetles effect their discharges. While *Brachinus* emits its secretion as discrete forcible jets (Eisner and Aneshansley 1999), *Metrius* discharges a froth that bubbles away on the surface of its body (Eisner *et al*. 2000) (Fig. 1C, D). To the ear, in fact, a *Metrius* discharge has very much the attributes of a faint *Romalea* emission.

We recorded several discharges from each of the four *M. contractus*. The beetles were tethered as described for other bombardiers (Eisner *et al*. 2001) and they were caused to discharge by pinching their legs with forceps. The periods over which they were subjected to stimulation ranged from 1.5 to 3 minutes. The interval between consecutive discharges was therefore in the range of seconds to over a minute. *M. contractus* discharges from one gland at a time, restricting its emission to the gland of the body side stimulated (Eisner *et al*. 2000). Since we usually pinched the legs of a beetle in no particular order, we had no way of

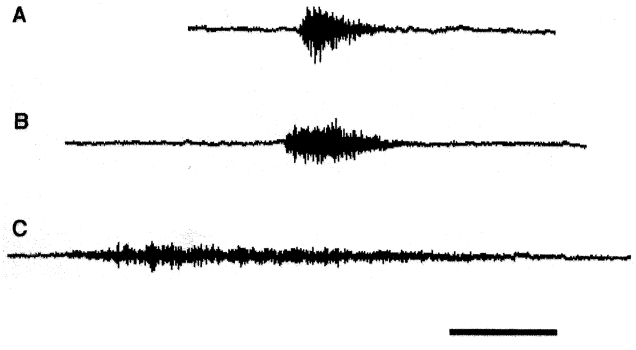

Fig. 2 Oscillograms of sound accompanying discharges from a single *Metrius contractus*. **A, B,** and **C** represent the first, third, and fifth discharges from a single gland over a period of 40 seconds. The relative sound amplitudes decrease, while the durations increase, with successive discharges. Bar 50 ms

determining the sequence of alternation of the discharges in the oscillograms or whether any one discharge stemmed from the right or left gland. It was impossible therefore to determine in most cases how the acoustical properties of the discharges of any one gland changed as a function of the progressive depletion of that gland, although we could tell that toward the end of the sound tracts, when both glands must have been approaching depletion, the discharges tended to become longer and of decreased intensity, as if the glands were then "fizzing out." This was clearly evident from the oscillogram of the one beetle in which we did record 5 consecutive discharges from one gland. Three of the discharge sounds of that beetle are depicted in Fig. 2. At any rate, the tracts left no doubt as regards pulsation, for which there was no evidence in any of the 13 discharges that we recorded.

A question that has never been answered is whether the accompanying sound contributes to the defensive effectiveness of a bombardier's ejections. While one can easily imagine the relatively loud detonations of a *Brachinus* having a startling effect on a predator, one is hard put envisioning the soft hiss of a *Metrius* having an impact on any but the smallest of enemies.

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