SOME NOTES ON LARVAL STRIDULATION IN NEOTROPICAL PASSALIDAE (COLEOPTERA: LAMELLICORNIA)[1]

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RESUMEN

El aparato estridulador de la larva de los Passalidae está compuesto por el reducido par de patas metatorácicas que actuan como escraper (*pars stridens)* y el par de coxas mesotorácicas que funcionan como fila (*plectrum).* En *Odontotaenius zodiacus* (Truqui), las estrias de la fila están separadas por una distancia del orden de las 8 a 11 micras. Tres oscilogramas del sonido emitido por esta especie fueron analizados en detalle. El sonido producido consiste de una serie de pulsos, cada pulso es el resultado del impacto de una parte del escraper contra una estría de la fila. En cada impacto del escraper, hacia abajo y hacia arriba, se produce un número de pulsos sonoros, cerca de 20. El ciclo completo de impactos hacia abajo y arriba puede ser repetido varias veces por segundo. Existe una considerable variación entre golpes sucesivos y entre los diferentes períodos de estridulación.

ABSTRACT

The stridulatory apparatus of passalid larvae consists of the much-reduced metathoracic leg acting as a scraper and the mesothoracic coxa acting as a file. In *Odontotaenius zodiacus* the ridges on the file are about 8 to 11 microns apart. Three oscillograms of the sound emitted were examined in detail. The sound consists of series of pulses, each pulse arising from the impact of a part of the scraper on a file ridge. In each downstroke and in each upstroke of the scraper a number, of the order of 20, of sound pulses were emitted. The complete cycle of upstroke and downstroke could be repeated several times per second. There was considerable variation between successive strokes and between different periods of stridulation.

The most striking characteristic of passalid larvae is the obvious reduction of the metathoracic legs which, together with the coxae of the mesothoracic legs, make up a typical stridulatory apparatus, a fact which has been widely commented upon in the entomological literature.

This type of stridulatory apparatus is known in about 20% of species of passalid larvae and is probably universally present in this group (Schuster and Reyes-Castillo 1979).

The stridulatory apparatus of the larvae of several passalid species has been described or illustrated in detail. That of *Odontotaenius disjunctus* (Il-

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liger) was described by Sharp (1899), of *Passalus* sp. by Wheeler and Bailey (1920), of *P. punctiger* Lepeletier et Serville by Bruch (1942), of *Ptichopus angulatus* (Percheron) by Hendrichs and Reyes-Castillo (1963) and of *Odontotaenius zodiacus* (Truqui) by Schuster and Reyes-Castillo (1979).

Candeze (1861) said that the atrophied third pair of legs in passalid larvae was completely useless. Baker (1967) observed that the larvae of the 3 species of *Pentalobus* did not produce any audible sound. Sharp (1899) was the first to demonstrate that the reduced third pair of legs in passalid larvae were sound-producing organs. Ohaus (1900) ascribed to the sounds the role of intraspecific communication, a view which was supported by Wheeler and Bailey (1920) and by Wheeler (1923). However, Heymons (1929) denied that the sound emitted by the larva of *Passalus interstitialis* Eschscholtz could serve as a means of communication, since it was produced only when the larva was disturbed.

The sound made by the larva is normally weaker than that made by the adult (Ohaus 1900, Heymons 1929, Bruch 1942, Schuster and Schuster 1971, Schuster 1975). Nevertheless, in *O. disjunctus*, the larva does have the ability to produce a sound of intensity similar to that of the adult (Alexander *et al.* 1963).

The disturbance sound of *O. disjunctus* was studied by Alexander *et al.* (1963) who pointed out the possibility of the existence of "a special adult sound resulting from contact with the larvae". Schuster (1975) described this sound for *O. disjunctus* and *Passalus affinis* Percheron, noting also the sounds resulting from larva-larva contact.

There is now no doubt that sound signals play an important part in the social behaviour of Passalidae. Schuster (1975) has discovered 17 different types of sound signal in the adults and larvae of *O. disjunctus*, which represents the most elaborate system of sound communication known for any arthropod.

In the present work, we present numerical data on the disturbance sound produced by larvae of *O. zodiacus*, together with brief descriptions of the mechanism of sound production and of the stridulatory apparatus, which is illustrated by scanning electron micrographs. Observations on larvae of *Proculejus brevis* (Truqui) are also recorded.

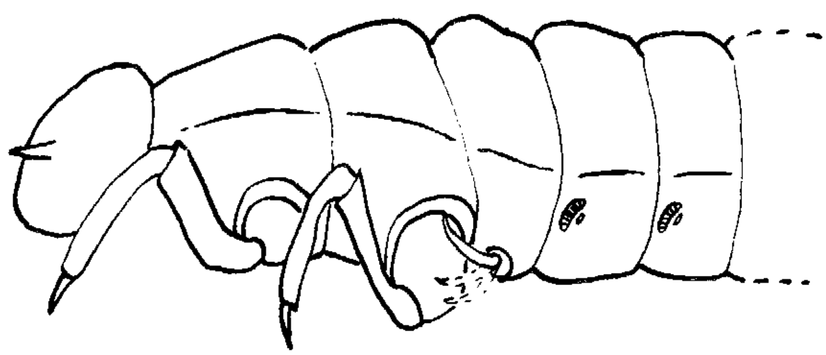


Fig. 1, Diagram of a passalid larva showing the movement of a metathoracic leg during stridulation.

Materials and Methods

The *O. zodiacus* larvae used in this study were collected from rotting tree trunks in a humid mixed forest near Acaxochitlan, state of Hidalgo, Mexico, and were subsequently kept at room temperature in Petri dishes containing rotting wood and fibres chewed off by adults of the same species. Some larvae were kept in a dish with an adult, others in a dish containing only larvae. Most larvae died within a week or two of capture, but two survived for periods of several months; sound recordings were made from these two, 1-2 months after collection.

The sound recording apparatus consisted of a B. & K. Laboratories microphone type 4145 feeding a sound level meter type 2204 which was used as a preamplifier. The output of this was connected to an Ampex FR 1100 instrumentation tape recorder using ¼ inch tape running at 60 inches per second (152 cm sec^{-1}). In normal usage, the frequency response of this equipment would have been only a few dB down at 75 kHz, but in the present work the ultrasonic response would have been severely restricted by the need to work with the larva as close as possible to the microphone diaphragm, because the sound was so weak.

Scanning electron micrographs were made using a Cambridge Stereoscan instrument.

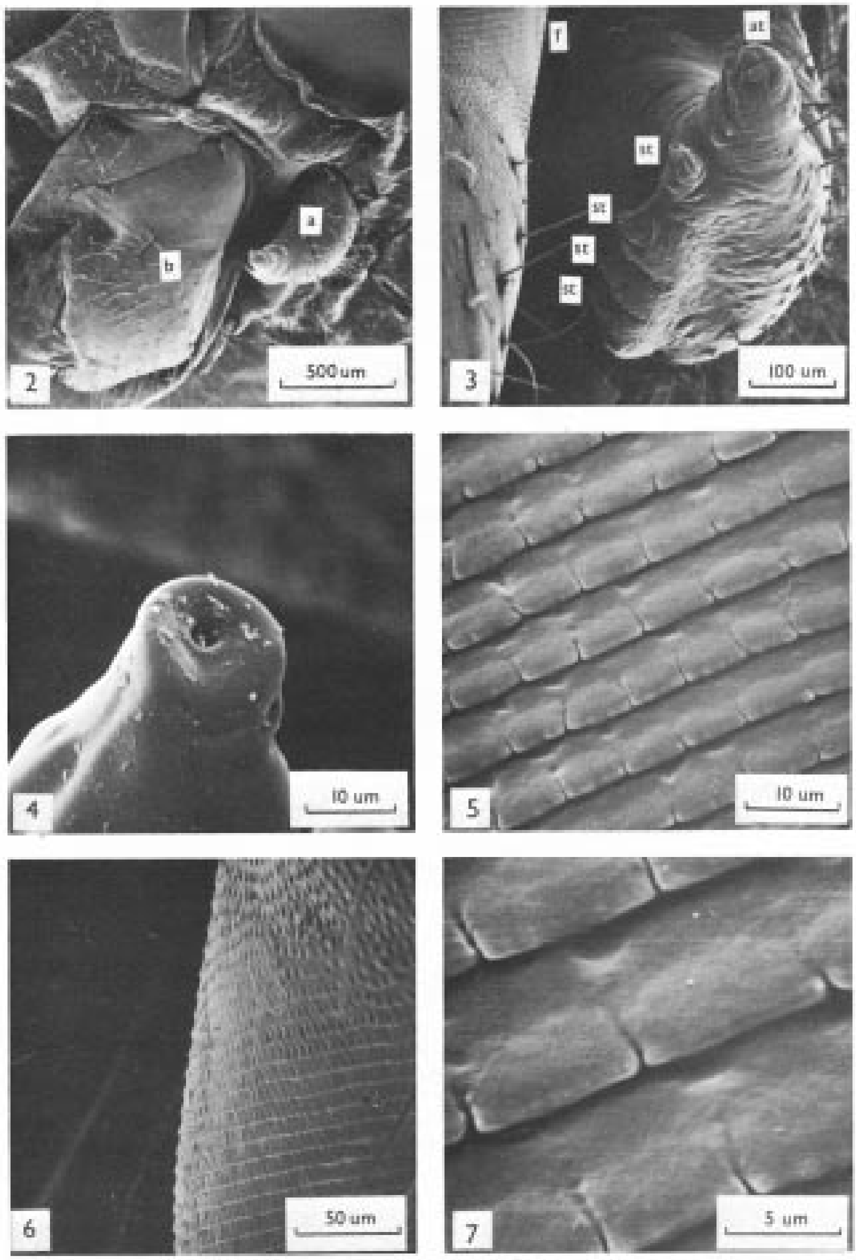
Stridulatory Apparatus

The stridulatory apparatus of passalid larvae (Figs. 1 and 2) is made up of the metathoracic legs which act as scraper, or *plectrum*, and small areas situated on the lateroposterior parts of the mesothoracic legs, acting as the file, or *pars stridens*.

The scraper (Figs. 3 and 4) consists of a series of teeth at the distal extremity of the metathoracic leg. There is one apical tooth, which is the largest one, and a variable number of subapical teeth (Schuster and Reyes-Castillo 1979). There are 5 subapical teeth in the majority of species for which this number is known. Exceptions are *Proculus goryi* (Melly), in which there are 6, *Undulifer incisus* (Truqui), *Heliscus* and *Publius*, which have 4, and *Proculus opacipennis* (Thompson), which can have either 4 or 5. It is also possible for there to be, on one and the same specimen, (*O. zodiacus)* 4 subapical teeth on one leg and 5 on the other. On each tooth of the scraper there is a sensory hair (Fig. 3), located in an obvious depression at the extremity, whose function has not yet been determined. In the rest position, the metathoracic leg lies on the basal part of the mesothoracic coxa with the teeth pointing forwards and upwards (like the leg) at an angle of 30° with the long axis of the body. This position has been observed in living larvae of *O. zodiacus, P. brevis, Heliscus tropicus* (Perch.) and *Spurius halffteri* Reyes-Castillo.

The files, located on the mesothoracic coxae, consist of parallel striations (Figs. 5, 6 and 7) lying in the direction of the long axis of the body. The separation of the striations, measured in 2 fixed and 1 living larvae of *O. zodiacus*, varied from 8.8 to 10.8 μm.

Each striation consists of a series of cuticular excrescences. These structures are formed by the epidermal cells which secrete the cuticle (Hinton *et al.* 1969), as can be seen clearly at the borders of the file (Fig. 6).



Figs. 2-7, Scanning electron micrographs of *Odontotaenius zodiacus* (Truqui): Fig. 2: Stridulatory apparatus showing (a) metathoracic leg, (b) mesothoracic coxa. Fig. 3: Metathoracic leg showing (at) apical tooth, (st) 4 subapical teeth and (f) file on the nearby mesothoracic coxa. Fig. 4: Subapical tooth of a metathoracic leg, showing sensory hair in apical depression. Fig. 5: File on mesothoracic coxa. Fig. 6: File on a mesothoracic coxa in lateral view, showing its profile. Fig. 7: File on a mesothoracic coxa at high magnification.

Stridulatory Movements

At rest, the metathoracic leg points anteriorly upwards at an angle of approximately 30° to the long axis of the body. The 'direction' of the leg is taken as the direction of the line joining the apical tooth to the point about which the leg rotates. This is depicted in Fig. 1, the solid line showing the rest position of the third leg. To make a sound, this leg rotates through an angle of very roughly 80° to a position about 50° below the long axis of the larva. This movement may be called the 'downstroke'. After a slight pause, the leg returns rapidly (the 'upstroke') to an intermediate position approximately 30° below the long axis. Subsequent slow downstrokes and fast upstrokes take place between this intermediate position and the lowest, 50°, position. Fig. 1 shows these positions as dashed lines. Stroke length varies, even between successive strokes; it appears to the visual observer that this variation results from variability of the intermediate position rather than that of the lowest position. The upstroke is noticeably more audible to the human ear than is the downstroke, though oscillograms do not usually show a great difference in amplitude between the two phases. Frequently the stridulation is continuous for as long as the larva is being disturbed. When the disturbance ceases, the metathoracic leg returns from the intermediate to the uppermost, rest, position. Very occasionally the legs of only one side of the larva stridulate, but more often both are involved. If the legs of both sides rub, they do so with about the same frequency, but there is no fixed relationship between their phases; certainly they do not, for instance, always perform their upstrokes synchronously.

As an order-of-magnitude calculation, it may be noted that a metathoracic leg of length 1 mm, rotating through an angle of 20°, would cross about 35 ridges of the mesothoracic coxa if it travelled perpendicular to them, and somewhat fewer otherwise.

It is important to note that the description given here applies only to the two individual 3rd. stage larvae of *O. zodiacus* from which sound recordings were made. Additional visual observations were made on larvae of all 3 stages of *O. zodiacus* and on 3rd. stage larvae of *P. brevis*. These confirmed that there were large individual variations in the habit of stridulation in response to handling by the experimenter. Differences between the behaviour of these larvae and that of the two reported in detail were as follows. Many individuals appear not to display the 'intermediate position' of the 3rd. leg as described above, but, instead, every downstroke starts and every upstroke finishes at the 'rest position'. Some individuals stridulate with only a single down-and-up stroke of the third leg followed by a long pause. In such cases visual observation appeared to show near synchrony between the movements of the legs on the two sides of the larva.

Sound Records

Both the larvae used produced very weak sounds, the pressure level of which could not be measured reliably. The larvae were placed as close as possible to the recording microphone and even so the records suffered from both acoustic and electrical noise. The recorded sound is made up of a series of pulses, each pulse resulting from the impact of a part of the 3rd. leg on a ridge of the coxal file on the 2nd. leg. At times, the sound pulses are regularly-spaced, which would be the case if only a single tooth on the 3rd.

leg were striking the regularly-spaced ridges on the 2nd. coxa. On the oscillograms, of which Fig. 8 is an example, it is possible to time and count the pulses in the up- and down-strokes.

Oscillograms of 3 periods of stridulation were studied in detail. In the first, the microphone picked up sound from the legs on both sides of the larva. In the other two, the recording was deliberately done with the right legs much closer than the left legs to the microphone, so as to avoid the complication inherent in interpreting an oscillogram containing equally intense sounds from both organs. The measurements made from the 3 oscillograms are summarised in Table 1.

In the circumstances of the experiment, an accurate frequency analysis of the sound would have been impossible. In particular, the question of whether ultrasound is produced at a significant level must remain open, though clearly the audible sound is not overwhelmed by ultrasound, or some of the latter would have shown on the oscillograms despite the technical shortcomings mentioned earlier.

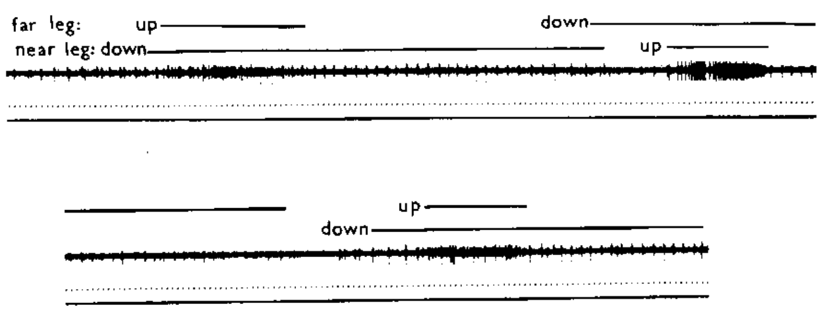


Fig. 8, Oscillogram of the disturbance sound produced by a larva of *Odontotaenius zodiacus* (Truqui). The upper two lines give the authors' interpretation of the leg movements which produce the sound, solid lines indicating periods of movement and gaps the periods when the leg is presumed to be stationary. The third line is the trace of sound pressure level, as recorded, but heavily filtered at both ends of the audio spectrum for display purposes. The leg nearer the microphone gives rise to the larger pulses. The fourth line is a time marker, the dots indicating milliseconds. The lower sequence follows the upper without a break.

Acknowledgments

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TABLE 1. Measurements related to sounds of *O. zodiacus* larvae. Figures following the measurements are standard deviations of several consecutive measurements in the same recording.

	1st. recording			
	leg 1	leg 2	2nd. recording	3rd. recording
Length of larva mm	37	37	31	37
Length of metathoracic leg mm	1.0	1.0	1.3	1.0
Duration of downstroke msec	86±41%	72±22%	102±15%	57±18%
Number of pulses in downstroke	25±31%	19±54%	30±22%	24±16%
Silence preceding upstroke msec	21±59%	25±16%	23±35%	38±19%
Duration of upstroke msec	26±16%	10±29%	25±18%	12±23%
Number of pulses in upstroke	37±13%	14±32%	11±29%	20±16%
Silence following upstroke msec	124±27%	156±7%	349±82%	83±21%
Duration of complete cycle msec	257±5%	263±8%	500±57%	191±11%

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