

STRIDULATION BY WORKERS OF THE ANT,
LEPTOTHORAX MUSCORUM (NYLANDER)
(HYMENOPTERA: FORMICIDAE).*

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INTRODUCTION

Many ponerine, myrmicine and pseudomyrmecine ants possess an abdominal stridulatory apparatus (Markl, 1973) of the type first described by Landois in 1874. The file (*pars stridens*) consists of a series of fine, regular, transverse striations, and is located medially on the anterior portion of the fourth abdominal tergite. The posterior edge of the preceding tergite serves as the scraper (*plectrum*), and stridulation is effected by dorso-ventral movements of the gaster which telescope the *pars stridens* beneath the *plectrum*. Exceptions to this typical arrangement have been documented by Sharp (1893), Marcus and Marcus (1951) and Taylor (1978).

Ant stridulation produces a substrate-borne vibratory signal, which is accompanied by an acoustic component in larger species (Dumortier, 1963). However, ants are not known to hear airborne sound, and it is the substrate-borne component of this signal which is thought to function in communication (Haskins and Enzmann, 1938; Markl, 1968, 1970). In *Atta cephalotes*, three groups of campaniform sensilla at the joint between the trochanter and femur are apparently responsible for vibration reception (Markl, 1970).

Ant stridulation occurs in a variety of contexts and, although various effects have been attributed to this signal (see review in Dumortier, 1963), few have been demonstrated (Markl, 1965, 1967; Markl et al., 1977; Markl and Holldobler, 1978). Furthermore, most previous authors have investigated stridulation in a particular context, in one or a few species, and there is little appreciation of how species specific some of the documented contexts may be, or in

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how many contexts single species may utilize stridulation. One exception is the work of Zhantiev and Sulkanov (1977), who found that certain *Myrmica* species would stridulate during immobilization, trophallaxis, fighting and eating insects. Nevertheless, the stridulatory signal itself is relatively simplistic and, according to Markl and Holldobler (1978), is probably not capable of containing more than one type of message. They have suggested that ant stridulation is a form of modulatory communication, and that the signal does not release any specific response, but merely modulates the responses of ants to other stimuli.

In their work with *Novomessor*, Markl and Holldobler (1978) found that a stridulating worker did not transmit any detectable signal to the substrate through its legs. Apparently, other portions of the ant's body had to be in contact with the substrate for effective transmission to occur. This discovery, if generally applicable to other ants, could be an important restriction on communication by stridulation.

Leptothorax muscorum (Nylander) is a small (length = 2.1–3.8 mm), common, circumboreal myrmicine ant (Brown, 1955; Bernard, 1968). In North America, *L. muscorum* colonies normally consist of one or more queens, and less than 100 workers, and can be found nesting in rotting wood, under rocks and in other similar cavities (Stuart, 1978). Haskins and Enzmann (1938) reported that *L. acervorum canadensis* var. *yankee* (= *L. muscorum*, Brown, 1955) workers stridulated when licking their larvae. Stridulation has also been noted among other Leptothoracine ants (Adlerz, 1896; Wheeler, 1903; Wilson and Fagan, 1974).

This study is a preliminary investigation of stridulation in *L. muscorum* workers. The purpose is to observe the stridulatory apparatus of *L. muscorum* workers; to monitor the substrate-borne and airborne components of their stridulatory signal; to discover if the signal can be transmitted through the ant's legs; and to enumerate the contexts in which *L. muscorum* workers stridulate both inside and outside their nests.

METHODS AND MATERIALS

L. muscorum colonies were collected from rotting wood near Rouyn, Quebec, and maintained in the laboratory using techniques described by Alloway (1980). The ants were fed three times a week

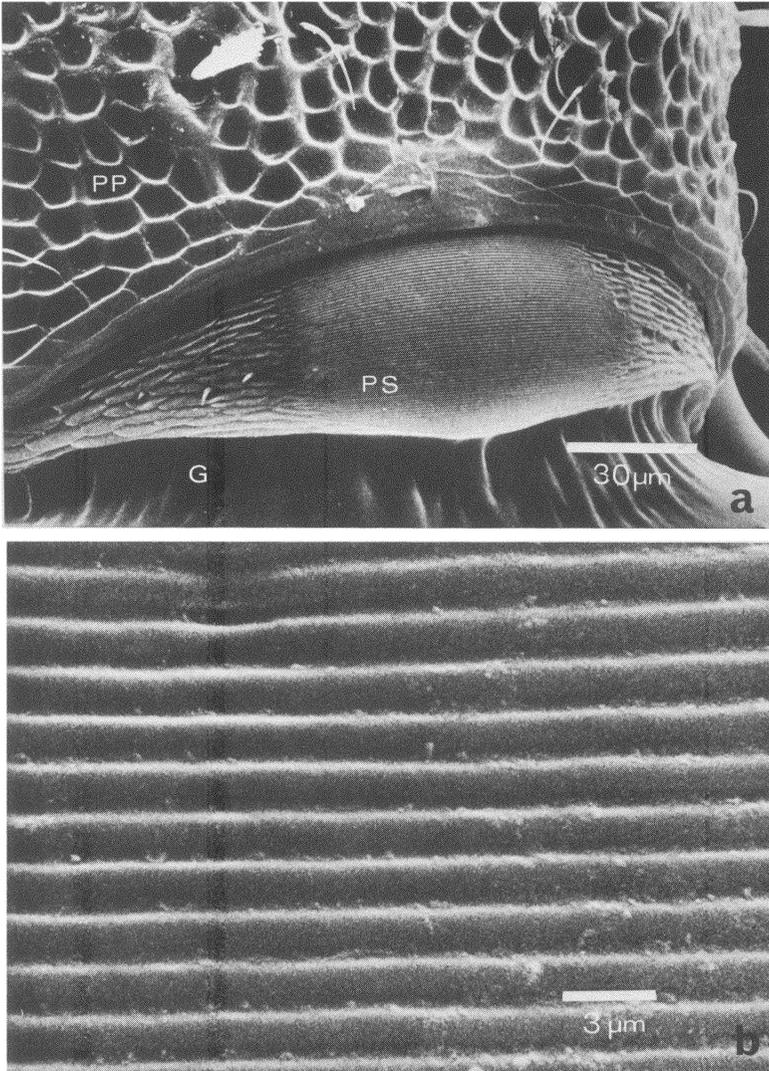


Fig. 1. Scanning electron micrographs of the stridulatory apparatus of an *L. muscorum* worker: a, general view; PP, post-petiole, PS, pars stridens, G, gaster. b, detail in central region of pars stridens.

on a liquefied diet of the type described by Bhatkar and Whitcomb (1970), and water was available ad libitum in their foraging dishes by way of bottles, stoppered with cotton.

Substrate vibrations were detected using a Bruel and Kjaer 4344 accelerometer, and amplified by a B & K 2304 impulse sound level meter on linear response. The vibrations were recorded on a Uher 4000 Report IC tape recorder. Oscillograms were produced on a Tektronix 455 oscilloscope, and recorded with a Nihon Kodon continuous photographic recorder. Attempts to record the airborne component of the stridulatory signal utilized a B & K 4133, $\frac{1}{2}$ " (1.25 cm) microphone in conjunction with the above mentioned sound level meter and tape recorder. The stridulatory apparatus was photographed with a Cambridge S 180 scanning electron microscope.

Ants normally stridulate when they are restrained (Markl et al., 1977) and, therefore, in our initial attempts to record the stridulatory vibrations produced by a *L. muscorum* worker, we glued the ventral portion of its head to the base of the accelerometer with contact rubber cement. To test for the transmission of stridulatory

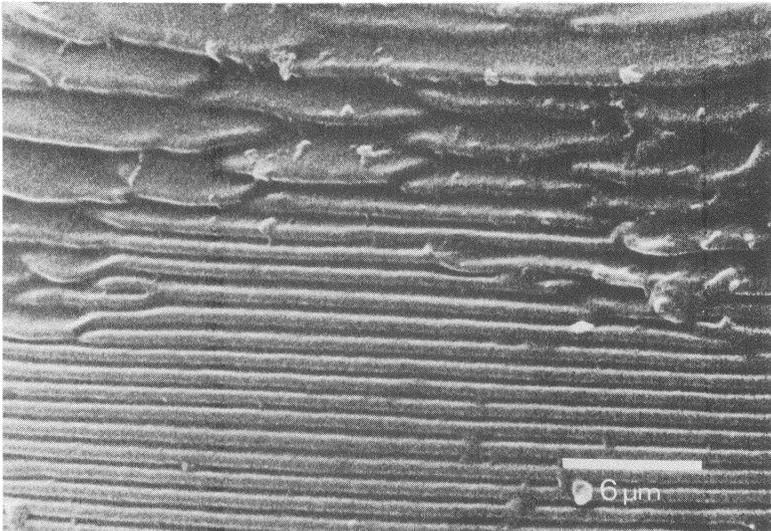


Fig. 2. Same as figure 1: leading edge of the pars stridens, after removing the post-petiole, showing the interface between the fine structure of the file and the sculpturing of the adjoining region.

vibrations through the legs, a worker's antenna was clamped in forceps secured above the accelerometer, such that only the ant's legs rested upon the base. Attempts to monitor the airborne component of stridulation were made using the initial procedure, and by holding the microphone to within 1 cm of the ant. All recordings were conducted in a sound attenuating room which floats on a concrete, vibration-dampening pad.

During recording sessions, the ants were observed through a dissecting microscope, and were occasionally stimulated with a camel's hair brush, or with air blown through a tygon hose (diam = 0.5 cm). Stridulatory contexts were determined visually through observation of laboratory colonies through a dissecting microscope, and under varying conditions as described in the results. Voucher specimens have been deposited in the Museum of Comparative Zoology, Harvard University.

RESULTS

1. Structure

The stridulatory apparatus of a *L. muscorum* worker occurs on the dorsal surface of the third and fourth abdominal tergites. The pars stridens is located in the mid-dorsal region of the anterior portion of the first gastric segment, and the plectrum apparently consists of the trailing edge of the post-petiole (Figs. 1 and 2). Other portions of the worker's body were examined with the electron microscope in an attempt to locate other possible stridulatory structures, but none were found.

2. Signal

Workers glued to the accelerometer surface responded by persistently pulling and struggling to free themselves. This activity was accompanied on an intermittent basis by very characteristic and regular dorsoventral movements of the gaster, which occurred in short bursts and in more prolonged sequences. During these movements a distinct vibratory signal was detected by the accelerometer (Fig. 3). The highly characteristic stridulatory movements of this species make visual observation through a dissecting microscope a reliable means of determining the occurrence of stridulation. The acceleration of the vibratory signal was measured as 1.4×10^{-4} m/sec² RMS (= 1.95×10^{-4} m/sec² p-p). However, no further

analysis of the signal was attempted due to the high signal-to-noise ratio. We were unable to detect any airborne component to this stridulatory vibration. Workers restrained by having an antenna clamped in forceps responded in the same manner as those restrained with glue. Similarly, when a worker was engaged in apparent stridulatory movements, a vibratory signal of the type described above was recorded from the substrate. Thus, the vibratory signal produced by a *L. muscorum* worker is readily transmitted to the substrate through its legs.



Fig. 3. Sonogram of the substrate-borne vibratory signal produced by a stridulating *L. muscorum* worker.

3. Context

A. Restrained

L. muscorum workers will stridulate when they are restrained. Such restraint can be imposed by glue or forceps, and occasionally occurred in laboratory colonies when an ant became trapped under the lid of its nest or foraging dish. It has been suggested that similar situations might arise in nature as the result of nest cave-ins, or fighting (Markl, 1965; Spangler, 1967).

B. Fighting

L. muscorum workers are often aggressive to alien conspecifics, and will bite, pull and dismember such aliens during prolonged fights (Stuart, 1978). Stridulation is characteristic of these fights and is displayed not only by workers which are being held or pinioned by their opponents, but also by those workers which are holding or pinioning their opponents. Stridulation in the former situation may be analogous to that displayed by restrained ants, but in the latter situation occurs in quite a different behavioral context. Adult alien conspecifics are dismembered and killed but are not eaten (Stuart, 1978), and therefore this context differs from feeding.

C. Feeding

L. muscorum workers stridulate intermittently as they bite, pull and tear apart solid food such as insect fragments, both outside and inside their nests. Stridulation is seen among groups of workers biting on a common food item, and is also displayed by workers biting on tissue individually. In culture, workers do not normally stridulate when consuming liquids. However, if a colony has been deprived of food and water for 5–7 days, workers will frequently stridulate when consuming honey, Bhatkar and Whitcomb diet, or even water.

D. Trophallaxis

When foragers return to the nest after having consumed liquid food, they engage in oral trophallaxis with adult members of their colony. Recipients hold their mandibles closed during trophallaxis and frequently stridulate; while donors hold their mandibles open and occasionally stridulate. In one study, 20 bouts of trophallaxis, lasting longer than 10 sec, were observed in each of three colonies. Thirty-eight bouts had a single recipient, eleven had two, seven had three, three had four, and one had five. Forty-seven of the 98 recipients stridulated at least briefly during trophallaxis; while only 4 donors did so. At least one recipient stridulated in each of 38 bouts, and both donor and at least one recipient stridulated during two bouts. Stridulation occurred in short bursts and prolonged sequences, and appeared to occur more often near the end of bouts, or when additional workers joined groups already engaged in trophallaxis.

L. muscorum workers also stridulate during certain bouts of oral trophallaxis with larvae. During the feeding session described above, five incidents of trophallaxis between workers and larvae were recorded. They lasted 5, 6, 10, 20, and 25 sec respectively. In each case the worker stridulated for nearly the entire bout. However, on other occasions workers have been observed engaging in apparently similar bouts of trophallaxis, but with no stridulation whatsoever. In either case, it is unknown whether the workers involved were actually giving liquids to the larvae, or receiving them.

E. Allogrooming

In laboratory colonies, *L. muscorum* workers often lick the body surfaces of their nest-mates. This grooming is directed to adults and

to brood, and under normal conditions, is not accompanied by stridulation. However, if colonies are deprived of food and water for 5-7 days, workers grooming other adults and larvae will frequently stridulate. It is possible that secretions are being obtained from the body surfaces, and that under such stressful conditions provide sufficient stimuli to induce stridulation.

F. Brood Manipulation

In attempting to manipulate or move larvae, workers occasionally encounter a larva which has become securely stuck to the floor of the nest. Workers respond to this resistance by pulling on the larvae, and frequently stridulate as they do so. In this context stridulation is associated with pulling, as it is when fighting or feeding. Nevertheless, all of these situations represent different behavioral contexts, and have therefore been considered separately.

DISCUSSION

L. muscorum workers possess a well defined stridulatory apparatus, similar to that of certain other ponerine, myrmicine and pseudomyrmecine ants (Markl, 1973). When restrained, *L. muscorum* workers display characteristic dorsoventral movements of the gaster which are associated with, and apparently induce, weak vibrations in the substrate, but no detectable airborne sound. This vibratory signal is transmitted to the substrate through the ant's legs. Similar stridulatory movements are observed when workers are fighting, dissecting insects, engaging in trophallaxis with adults and larvae, and when attempting to move larvae that adhere to the substrate. Furthermore, in food and water deprived colonies, stridulation occurs when workers groom other adults or larvae, or consume liquid food or water. Although the function of stridulation during the above contexts remains unknown, the intermittent nature of this behavior during all of these activities indicates that it is not an essential component of any of them.

Markl (1970) found that small workers of *Atta cephalotes* were more sensitive to stridulatory vibration than large workers. The minimum threshold for vibration reception in these small workers was 2.5 cm/sec^2 (p-p) (sic) acceleration. In this study, the acceleration of the *L. muscorum* stridulatory vibrations was $1.95 \times 10^{-6} \text{ cm/sec}^2$ (p-p). The small size of *L. muscorum* workers probably

accounts for the weak stridulatory signal, and for the apparent absence of any airborne signal (see discussion in Dumortier, 1963).

Markl and Holldobler (1978) reported that *Novomessor* workers did not transmit any detectable vibratory signal to the substrate through their legs. We found this not to be true with *L. muscorum* workers. However, the necessity of having some part of the ant's body, other than its legs, in contact with the substrate, or some other object or individual, to facilitate transmission of the signal, could be an important communicative constraint in some species.

Wilson and Fagen (1974) included stridulation in their ethogram of *L. curvispinosus* workers, and apparently observed it as a mutually exclusive behavior pattern. In the present study, *L. muscorum* workers only stridulated in association with some other behavior. However, in *L. curvispinosus* colonies cultured under similar conditions we have observed workers exhibiting such mutually exclusive stridulation in apparent response to a mild disturbance, such as moving the culture dish across the stage of a dissecting microscope. In addition, *L. curvispinosus* workers will stridulate in many of the contexts outlined in this paper for *L. muscorum*, but only in this 'mild alarm' context is this behavior mutually exclusive. *L. muscorum* workers begin to run about their nests, even upon a slight disturbance, and we have never observed stridulation in a similar context for this species. Free-standing stridulation of this type underlines the potential importance of the transmission of a stridulatory signal through an ant's legs to the substrate.

Our behavioral observations of *L. muscorum* workers confirm and extend previous accounts of stridulation in Leptothoracine ants. Adlerz (1896) noted that workers stridulated during trophallaxis, when feeding or licking their nest-mates, and when feeding their larvae. Wheeler (1903) observed workers stridulating while feeding on insect fragments, and Haskins and Enzmann (1938) reported workers stridulating when licking their larvae.

The occurrence of stridulation in such a wide variety of contexts within a single species, such as *L. muscorum*, argues against the possibility that this signal might release a specific response, and supports Markl and Holldobler's (1978) suggestion that ant stridulation serves a modulatory function. The fact that stridulation is observed in additional contexts when colonies have been deprived of food and water, suggests that the motivational state of the ants may be a factor in stridulation. Zhantiev and Sulkanov (1977)

report variations in the stridulatory signal of *Myrmica* which they suggest could reflect the relative motivation of the signalling worker. If so, stridulation could constitute a finely graded signal which serves as a sensitive indicator of the relative motivational state of workers engaged in various social interactions with nest-mates. In this manner, stridulation would be an important contribution to the efficiency of these interactions and of the colony as a whole. Stridulation could simultaneously serve as an effective short-range recruitment signal or orientation cue, especially within the nest. Outside the nest, *L. muscorum* workers recruit nest-mates by tandem running to food (Moglich et al., 1974) and to fighting (Stuart, 1978). The occurrence of stridulation at the scene of either of these activities could serve to facilitate such chemical recruitment, as it has been shown to do for food recruitment in *Novomessor* (Markl and Holldobler, 1978). However, these suggested functions for stridulation in *L. muscorum* remain speculative, and the precise determination of the effects of this signal, in the various contexts described in this study, await further research.

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SUMMARY

L. muscorum workers possess a stridulatory apparatus on the dorsal surface of the third and fourth abdominal tergites. Stridulation is readily induced by gluing the ventral portion of a worker's head directly to the accelerometer. Under these conditions, a vibratory signal with an acceleration of 1.4×10^{-4} m/sec² RMS is recorded from the substrate. However, no sound is detected by a microphone held to within 1 cm of the stridulating ant. A similar vibratory signal is recorded from the substrate when a worker is restrained by having an antenna clamped in forceps such that the ant is free-standing on the accelerometer surface. This proves that

the vibratory signal can be transmitted through the ant's legs to the substrate. *L. muscorum* workers will stridulate when restrained, fighting, dissecting insect fragments, engaging in trophallaxis with adults and larvae, and when attempting to move a larva adhering to the substrate. In addition, in food and water deprived colonies, workers will also stridulate when grooming other adults and larvae, and when consuming liquid food or water. The significance of these findings is discussed in terms of the possible function of stridulation in the above contexts.

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