

DISTURBANCE STRIDULATION AND CHEMICAL DEFENCE IN NYMPHS OF THE TROPICAL COCKROACH *MEGALOBLATTA BLABEROIDES*

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Abstract—(1) *Megaloblatta blaberoides* nymphs stridulate in response to disturbance. Sounds are produced by rubbing a pair of bilateral ventral files on the sixth sternum across opposing stationary scrapers located laterodorsally on the fifth sternum. The forward-moving file on one side and the backward-moving contralateral file generate sound simultaneously.

(2) Intact nymphs produce a broad frequency band noise (5–35 kHz). Due to superposition of signals and silent pauses produced by the bilateral organs, no regular pattern of amplitude modulation is measurable. The sound produced by unilaterally muted nymphs contains regular pulse-train groups (forward and back cycle) each of which is divided into a short forward motion and a longer backward motion. These are interrupted by a short pause. A longer pause occurs prior to the anteriorly directed motion of the intact file.

(3) *Megaloblatta's* proteinaceous tergal secretion is chemically and physically similar to that of *Blatta orientalis*. Coupling of acoustic warning, bright colour patterns, and chemical defence constitutes a multi-modal aposematic display which may be effective both nocturnally and diurnally against potential predators.

Key Word Index: Disturbance stridulation, cockroaches, sound production, tergal and cercal secretion

INTRODUCTION

DISTURBANCE or anti-predator stridulation in insects may have several roles. Vibrations transmitted through the cuticle may increase the predator's handling time and allow the prey to escape. Intense airborne sound may startle and repel a predator if the sound is associated with a prior negative experience. Acoustic signals as well as visual, olfactory, and gustatory cues may function in a multi-modal aposematic or mimetic system. Thus, a brightly coloured insect or one capable of producing a noxious secretion may couple an acoustic signal to this warning system. As in visual aposematism, such disturbance signals are expected to be similar in unrelated species, and sufficiently broad to cover the range of receptor systems of potential predators (MASTERS, 1980). That is, the signal is not limited to the auditory perception of a given predator, but rather has a broad frequency spectrum.

ROTH and HARTMAN (1967) list five mechanisms for sound production in cockroaches. However, only NELSON and FRASER (1980), using muting and play-back techniques, report experimental determinations of the adaptive role of sound production. In this paper we report a new, sixth mechanism of sound production in cockroaches and describe its morphology, characterize the sound acoustically, and discuss its expected role in an aposematic system involving sound, visual, and chemical defence. It is the first

reported case of stridulation in cockroach nymphs (Blattaria) or in juveniles of related groups (Orthoptera).

MATERIALS AND METHODS

Insects

Megaloblatta blaberoides Walker is a large tropical cockroach (7–9 cm head to wing tip). The wings of the adults are reddish brown; the abdominal terga and sterna orange with black margins. The nymphs are black with orange head and legs. An orange spot is conspicuous on each side of the first five terga (Fig. 1). Ventrally, the nymphs resemble the adults.

Nymphs and adults were collected between April 1979 and May 1980 at Finca La Selva, an Organization for Tropical Studies field station in a lowland Caribbean rain-forest in Costa Rica (see HOLDRIDGE *et al.*, 1971 for site description). The 6 nymphs examined ranged between 2.5 and 5.5 cm in body length. Earlier juvenile stages have not been seen. We also examined congeneric nymphs and adults (*insignis*, *longipennis*, *regina*) and specimens of the related genera *Nyctibora* and *Paratropes*.

Morphology

The sterna bearing the files and scrapers were removed from pinned specimens relaxed in Barber's fluid. They were cleaned ultrasonically in 10% KOH, sputter-coated with gold-palladium (200 Å), and

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examined with a Phillips 501 Scanning Electron Microscope.

Intertooth distances (crest to crest) were obtained from photographic enlargements of files and scrapers. The data were digitized with a GTCO digitizer and stored in a DEC11/03 minicomputer which was programmed to calculate distances and their means and standard deviations from XY coordinates.

Acoustical analyses

We follow the terminology of MORRIS and WALKER (1976). *Pulse*: The interaction of one tooth of the file with the scraper. *Pulse train*: Produced by the movement of the file over the scraper in one direction. Movement in the opposite direction may produce a second pulse train that may be different from the first (same as ELSNER's (1974) "syllable"). *Pulse train group*: Produced by the movement of the file across the scraper in one direction and its return in the opposite direction (Elsner's "chirp"). *Mode*: A series of pulse train groups separated by a long pause from a second mode (Elsner's "sequence").

Most of the cockroach sounds were recorded with a Uher 4400 Report Stereo IC tape recorder at 19 cm/sec and a Uher M517 microphone with an upper frequency limit of 15 kHz; some were recorded with a Sennheiser 805 shotgun microphone and a Kudelski Nagra 3 tape recorder at 38.1 cm/sec. All tape recordings were made at night in an outdoor insectary in Costa Rica. Sonograms were obtained with a Kay 6061B Sonograph from tape recordings, and spectral analysis was done indoors with a live nymph (no tape recording) using a Gen Rad model 2512 Spectrum analyzer with a Bruel and Kjaer $\frac{1}{2}$ -in. microphone Type 4136. The Fourier analysis was done within the 0-100 kHz range. We used representative oscillograms from two nymphs to determine durations of pulse trains, pulse train groups, and pauses.

To correlate the sounds produced at the different phases of stridulation with the movement of the file across the scraper, we analyzed the sounds produced by intact nymphs ($n = 4$) and nymphs unilaterally muted ($n = 2$) by removing teeth from the scraper with an insect pin. Initially, the temporal characteristics of the stridulation were examined with a Tektronix 7313 storage oscilloscope and a Tektronix C-50 camera. Later, an opto-electronic movement detector (HELVERSEN and ELSNER, 1977) and a Uher M517 microphone were coupled to the oscilloscope and a dual trace of the sound and movements was obtained.

Chemical analysis of the defensive secretion

Like nymphs of other members of the subfamily Nyctiborinae, and other juvenile and adult cockroaches (e.g. *Blatta orientalis*—PLATTNER *et al.*, 1972 and ROTH and STAHL, 1956; *Eurycotis floridana*—ROTH and ALSOP, 1978; *Pseudoderopeltis bicolor*—NAYLER, 1964; *Xestoblatta hamata*—SCHAL, unpublished), nymphs of *Megaloblatta* produce a gray, sticky secretion on the dorsal surface of the last two visible abdominal segments. This material is effective against ants (see Figs. 42 and 43 in PLATTNER *et al.*, 1972). We analyzed the tergal secretions of *Megalob-*

latta, *Nyctibora* (2 species), and *Blatta* for amino acid composition and compared our results with those reported by Plattner *et al.* for *B. orientalis*.

The material was collected with a glass rod and hydrolyzed in 6 N HCl in a sealed ampoule. Amino acid composition was determined with a Beckman 120C Amino Acid Analyzer adapted to use a Durrum Single Column with a Resin DC 6A Lithium buffer system.

RESULTS

In *Megaloblatta blaberoides*, the sound-producing mechanism was found to be of the file and scraper type. The scraper and file were paired on either side of the fifth and sixth abdominal sterna, respectively. The file is lateroventral on the sixth sternum; the scraper is dorsolateral on the fifth (Fig. 2A). The nymphal structures differed from those of adults in size, general morphology of the stridulatory fields, and the shape and spacing of the teeth. Members of related genera do not possess these structures.

The following analysis is of a 3.2 cm long *M. blaberoides* nymph:

File. The file (Figs. 3A and B) was 1.68 mm long and 1.18 mm wide. In the view of Fig. 3(A) two distinct fields were apparent. A medial region that was 0.41 mm wide contained approx. 250 irregularly spaced small ($\sim 25 \mu\text{m}$ long) teeth. The more lateral, adjacent region contained about 430 teeth. The teeth in the anterior and posterior sections were small; the central region contained longer teeth (up to $80 \mu\text{m}$). The average spacing between teeth in a 3.2 cm long nymph was $36.9 \pm 13.8 \mu\text{m}$ (mean \pm S.D.). At rest, the long axes of the teeth of the files are approximately perpendicular to the body long axis.

Scraper. The scraper on the fifth sternum (Figs 3C and D) was 0.95 mm long and 0.48 mm wide. The medial section consisted of linearly arranged large teeth ($\sim 74 \mu\text{m}$ long), whereas the lateral region contained smaller, more irregularly arranged teeth which

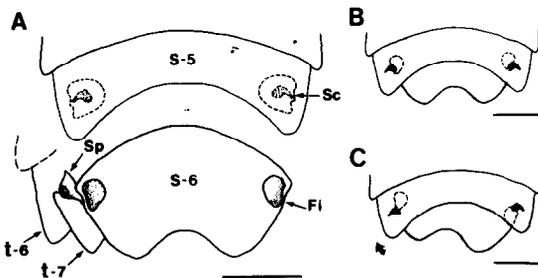


Fig. 2. Ventral views of the anatomy of the stridulatory structures of *Megaloblatta blaberoides*. (A) The fifth (S-5) and sixth (S-6) sterna are separated to show the files (Fi) and spiracles (Sp). The scrapers (Sc) are on the dorsal surface of sternum 5. (B) Normal positions of the files and scrapers. (C) Following the completion of one pulse train. The pause between the forward and backward file movement (left structure viewed ventrally) is shorter than the pause between the backward and forward file movement (right file viewed ventrally). Calibration bar is 0.5 cm on all drawings.



Fig. 1. Leaf litter habit photograph of a *Megaloblatta blaesoides* nymph showing the gray tergal secretion and orange spots on its dorsum. The calibration bar is 1 cm.

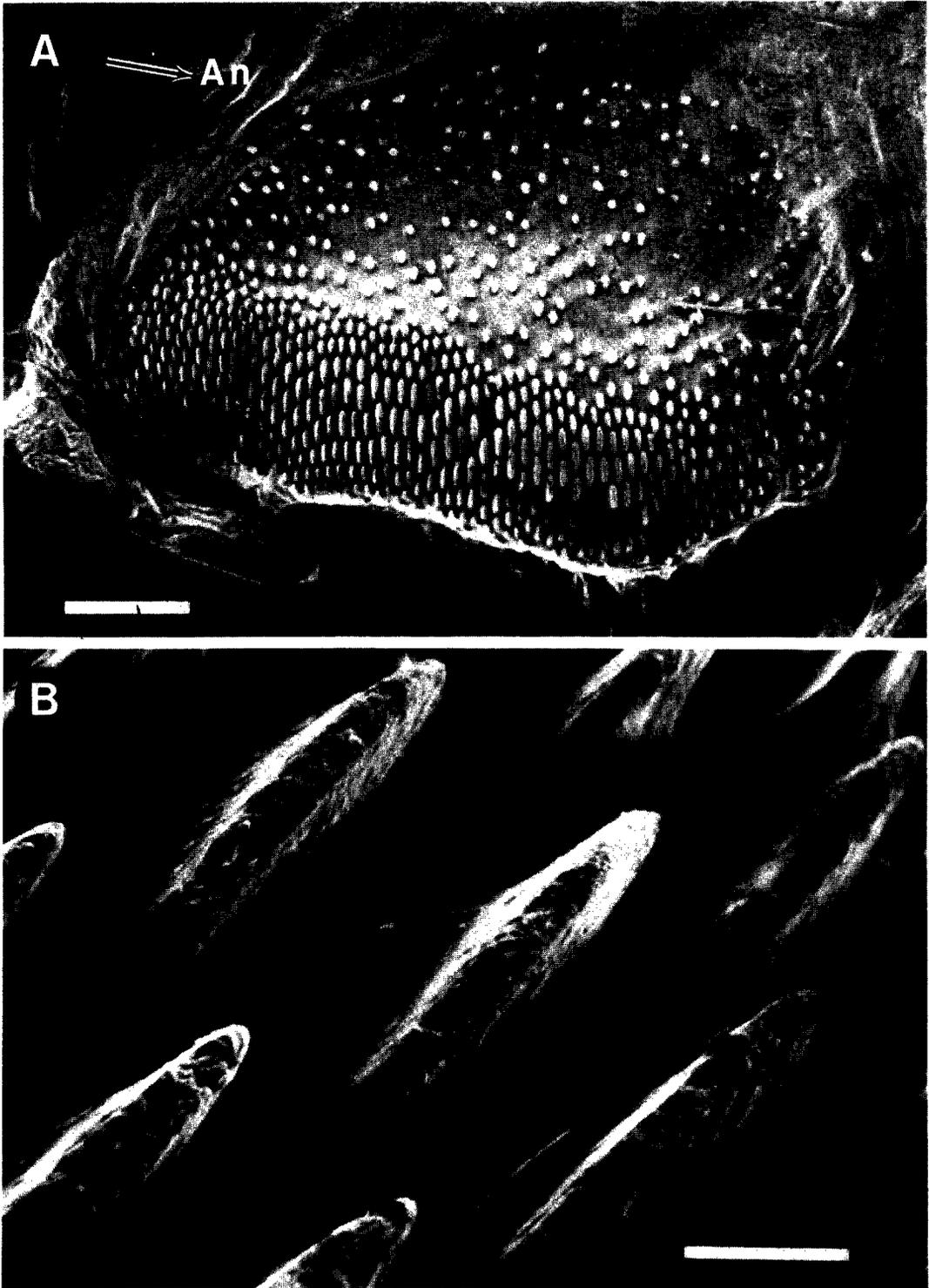


Fig. 3(A-B).

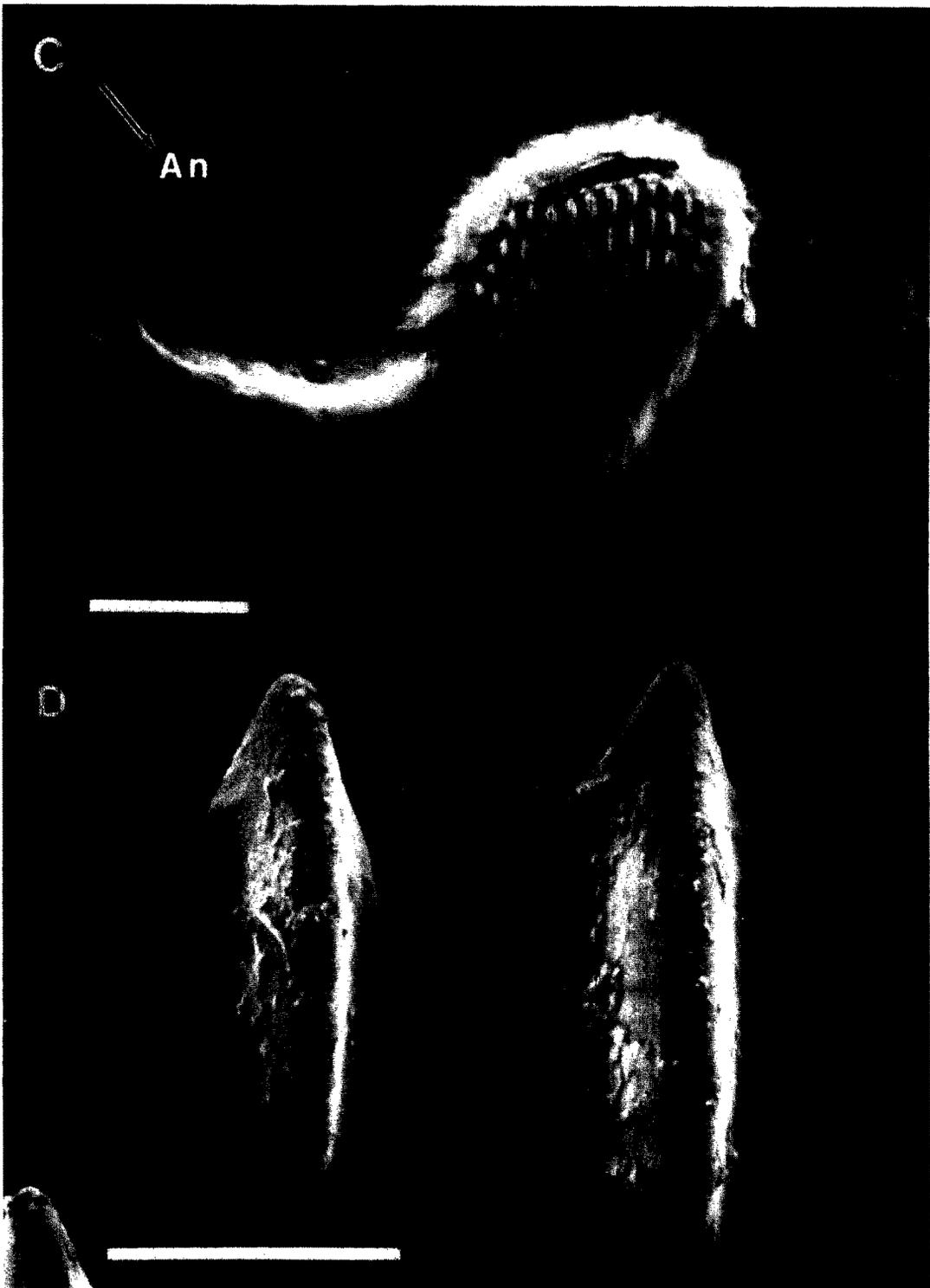


Fig. 3. Scanning electron micrographs of a right file (A and B, ventral view) and a right scraper (C and D, dorsal view). Arrows in (A) and (C) are parallel to the longitudinal body axis and point anteriorly. Lower photographs are close-ups of the respective upper photographs. Calibration bars on the upper photographs represent 300 μm ; on the lower photographs, 30 μm .

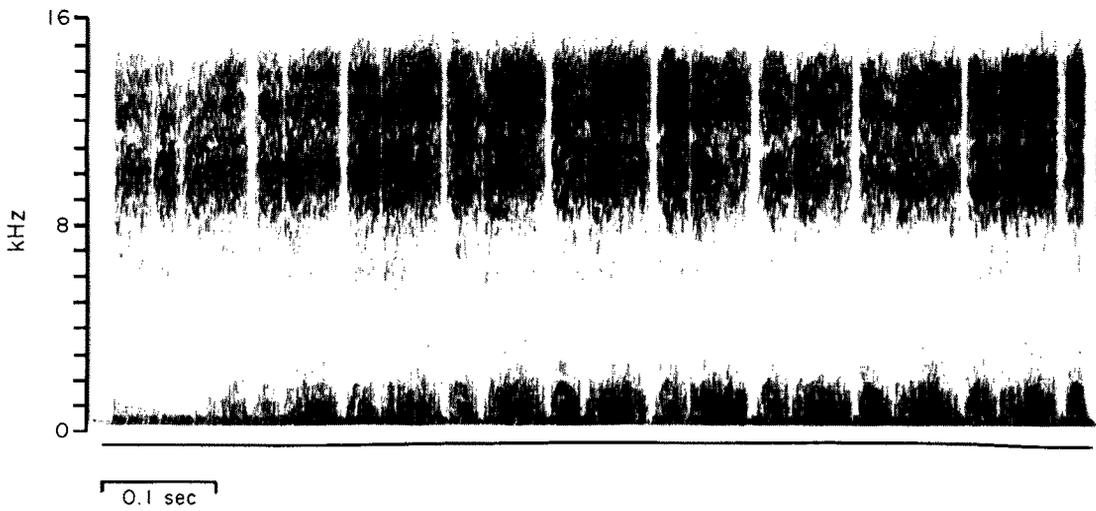


Fig. 4. Sonogram of disturbance sound of an intact *M. blaberoides* nymph stridulating unilaterally. Direct behavioural observations corroborate that unilateral rather than synchronous bilateral stridulation is represented. When both organs are used the silent pauses are masked. Use of a Uher M517 microphone set 15 kHz as the upper limit of this analysis.

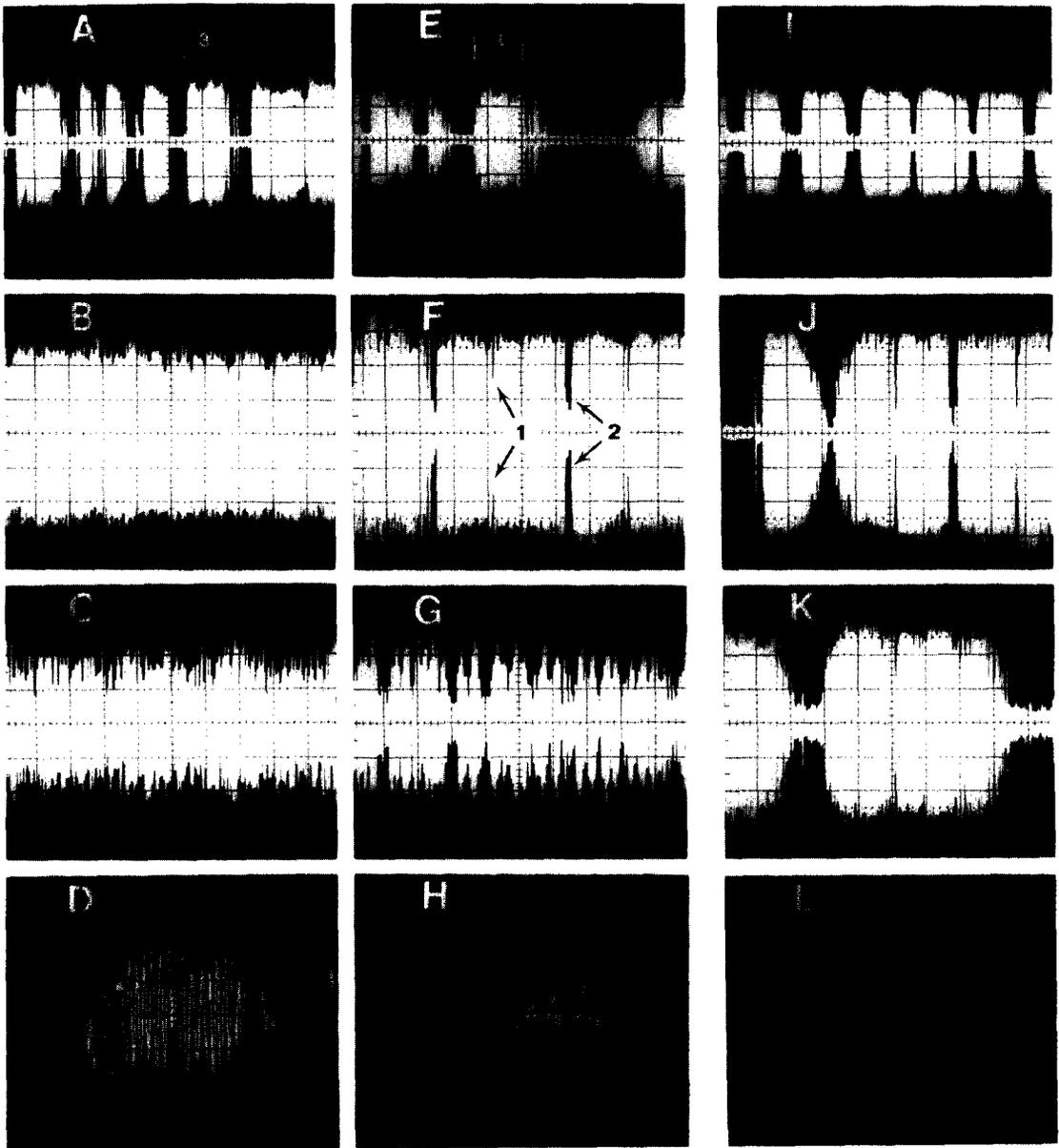


Fig. 6. Oscillograms of stridulatory sound of intact (A-D) and unilaterally muted (E-L) *M. blaberooides* nymphs. Adjacent traces in the two columns on the left have equal time scales. The right column resolves the traces of unilaterally muted nymphs at intermediate time scales. (3) in A and E represent rapid repetition of pulse train groups. (1) in F is a short pause prior to backward movement of the file. (2) in F is a longer pause prior to forward movement of the file. The horizontal divisions of the oscilloscope screen represent the following time scales: A and E, 1 div = 1 msec; B, F, and J = 25 msec; C and G = 1.25 msec; D and H = 0.25 msec; I = 50 msec; K = 12.5 msec; L = 0.0625 msec.

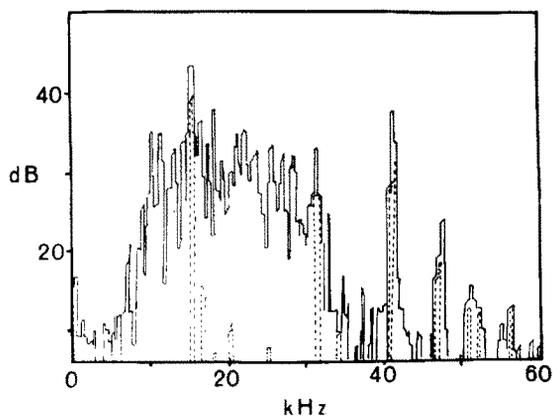


Fig. 5. Power spectrum for disturbance stridulation of a *M. blaberoides* nymph recorded at a distance of 3 cm. The time window is 4 msec. Frequency resolution in Hz is 250. Dotted lines represent background noise.

trailed off posterolaterally. The average distance between the 72 teeth was $54.0 \pm 31.0 \mu\text{m}$. The scraper is positioned with the long axis of its teeth forming a 60° angle with the body long axis. Hence, at rest, the long axis of the file and scraper teeth meet at a 30° angle (Fig. 2A). Upon disturbance, *Megaloblatta* nymphs produce a loud stridulatory sound by rotation of the sixth abdominal segment. The lateral regions bearing the files translate (slide) back and forth against the stationary scrapers (Figs 2B and C). Thus, anteriorly directed movement of one file is simultaneous with posteriorly directed motion of the contralateral file.

Acoustical analysis

Sonograms reveal that up to 15 kHz, the upper limit of the analysis, the frequency spectrum remains the same throughout the pulse train (Fig. 4). Fourier analysis (Fig. 5) shows *Megaloblatta* stridulation to be a broad-band noise characteristic of the disturbance sounds produced by other insects (MASTERS, 1980). The bandwidth is about 30 kHz with most of the energy between 5 and 35 kHz.

Sounds made by intact nymphs using both stridulatory structures are difficult to analyze temporally because the sound produced by the forward moving right file is simultaneous with that produced by the backward-moving left file. Since the duration of the sound produced by a single contraction on one side is not equal to the duration of sound produced by the simultaneous motion of the opposite side, pauses which occur when the files change directions are masked (Fig. 6B).

On the other hand, the sound produced by unilaterally muted nymphs and intact nymphs using only one set of stridulatory structures contains pauses which are resolved by the human ear (Figs. 4 and 6F). The length of a complete train group is 75–100 msec (83.35 ± 10.92 ; $\bar{x} \pm \text{S.D.}$, $n = 40$ from 2 nymphs). Two types of pauses occur between pulse trains (Fig. 6F). The long pause (12.46 ± 2.94 msec, $n = 20$) corresponds to the most posterior position of the file (right file in Fig. 2C) prior to its anteriorly directed motion. The shorter pause (4.19 ± 1.28 msec, $n = 20$)

corresponds to the most anterior position of the file (left file in Fig. 2C). The backward stroke is longer (44.43 ± 4.95 msec, $n = 40$) than the forward stroke (35.92 ± 5.16 msec, $n = 40$) when stridulation is rapid (Figs 6F and K). Both pulse trains have similar amplitude characteristics with sudden onsets to peak amplitude and fast declines followed by a pause (Figs 6F and K). At slower repetition rates ("tick" sequence, MORRIS and WALKER, 1976) the forward stroke may be longer than the return stroke and the amplitude of the sound produced by the anteriorly directed motion may increase slowly and monotonically; the decline in intensity is rapid (Fig. 6J).

In unilaterally muted nymphs individual tooth impacts are resolved (Figs 6H and L). The intervals between pulses vary, probably because of variations in both the speed of stridulation and in tooth spacing.

Ninety four days following unilateral muting, two nymphs decreased the rate of repetition of pulse train groups and showed a marked drop in the amplitude of the backward stroke. In 16 sequences with silent backward motion the forward stroke was 26.75 ± 4.23 msec ($\bar{x} \pm \text{S.D.}$) and the interval between successive pulse trains (forward strokes) was 107.3 ± 41.70 msec. This change may have occurred sooner after muting but we did not monitor the sound between the 14th and 94th day. Two intact nymphs, in captivity for 65 and 87 days, did not alter their stridulation.

Chemical analysis

Table 1 compares the amino acid composition of the tergal secretion of *M. blaberoides*, *Nyctibora lutzi*, and *N. noctivaga* nymphs to that of *B. orientalis* (PLATTNER *et al.*, 1972). All are whitish-gray viscous secretions which assume the consistency of a rubbery glue upon removal from the nymph. With the exception of glutamic acid, lysine and arginine, the amino acids in our and Plattner *et al.*'s *Blatta* samples are represented similarly. *Megaloblatta* has a higher proline and a lower glutamic acid content. We present results for *N. lutzi* and *N. noctivaga* (Table 1) mainly to suggest that although the tergal and cercal secretions are physically (mechanically) similar in all the species thus far examined, phylogenetic relations may determine the degree of similarity in their microchemical composition. In addition, differences in diets and life stages (PLATTNER *et al.*, 1972) may account for variations in the amino acid content of the secretion.

Megaloblatta adults, unlike adult females of *B. orientalis*, do not produce this secretion.

Behavioural responses to disturbance

Megaloblatta's response to disturbance depended on the intensity of the stimulus. In the field, the nymph assumed a posture with the tip of its abdomen pointing toward the ground (Fig. 1). When a hind leg was touched with forceps the nymph responded by raising the end of the abdomen and tilting it towards the stimulus so that the secretion and orange colouration were conspicuous.

Pinching the leg momentarily with forceps resulted in a faster response which usually included stridulation. When the insect was grasped, an escape response was always accompanied by intense stridulation which usually continued after the stimulus was with-

Table 1. A comparison of the amino acid composition of the tergal secretions of *Blatta orientalis*, *Megaloblatta blaberoides*, *Nyctibora lutzi* and *Nyctobora noctivaga*

Amino acid	<i>B. orientalis</i> * (%)	<i>B. orientalis</i> (%)	<i>M. blaberoides</i> (%)	<i>N. lutzi</i> (%)	<i>N. noctivaga</i> (%)
Cysteic acid	†	0	0.97	0	0
Aspartic acid	8.83	9.82	10.31	9.11	9.44
Threonine	1.76	2.36	2.62	4.42	4.13
Serine	3.07	3.66	5.08	3.44	3.33
Glutamic acid	7.81	27.44	11.24	11.15	14.22
Proline	7.24	4.53	18.25	6.87	7.73
Glycine	17.80	19.36	22.70	19.10	19.64
Alanine	2.49	4.16	1.33	3.95	3.44
Valine	3.34	4.21	2.70	6.44	5.50
Cystine	†	0	0.22	0	0
Methionine	†	0	0.03	0.65	0.11
Isoleucine	5.27	2.30	1.71	3.70	2.94
Leucine	5.27	4.65	3.73	4.70	3.96
Tyrosine	3.25	3.06	1.92	4.25	4.49
Phenylalanine	†	0.98	1.78	2.20	1.66
Lysine	11.22	5.36	6.48	11.57	11.21
Histidine	†	2.62	1.44	3.78	3.82
Arginine	27.91	5.47	7.46	4.65	4.37

* From PLATTNER *et al.*, 1972.

† Not reported.

drawn. Other stimuli such as substrate vibration, sudden bright light, and in one case, intense air-borne sound elicited the stilt posture and stridulation. *Megaloblatta* is not a common species, so quantitative behavioural analyses involving experimental manipulations with potential predators were precluded. Nevertheless, we were able to establish that this sequence of defensive behaviour occurred in semi-natural contexts when army ants (*Eciton burchelli*) and large ponerine ants (*Paraponera clavata*) were placed in the cage.

DISCUSSION

To the best of our knowledge, this is the first analysis of stridulatory sound production in cockroach nymphs. ROTH and HARTMAN (1967) describe stridulation in cockroaches as "scraping the pronotum over the costal veins," a mechanism which necessarily excludes juveniles. Whereas pronotal files in adult cockroaches consist of extremely small striae (*Nauphoeta cinerea* = 4 μ m, *Leucophaea maderae* = 4 μ m, *Panchlora nivea* = 3 μ m, *Henshouedenia flexivitta* = 4.7 μ m, ROTH and HARTMAN, 1967; *Henshouedenia epilamproides* = 5 μ m, GUTHRIE, 1966), the stridulatory teeth of *Megaloblatta* are separated by an average distance of 37 and 54 μ m in the file and scraper, respectively.

Nymphs and adults of four *Megaloblatta* species possess specialized scrapers and files. Other genera in the subfamily Nyctiborinae (Family Blattellidae) have no stridulatory mechanisms or remnants thereof. Moreover, stridulation has not been shown outside the subfamily Oxyhaloinae (Family Blaberidae), though some members of the closely related subfamily Panchlorinae possess pronotal-tegmina cuticular specializations (ROTH and HARTMAN, 1967). The Nyctiborinae are phyletically far removed from these groups (MCKITTRICK, 1964). We infer that the stridulatory structures in *Megaloblatta* are of monophyletic

evolutionary origin explainable on the basis of morphological homology, and are not a result of convergent evolution within the genus. Interestingly, though adults of both sexes of *M. blaberoides* possess sound production structures, thus far we have not been able to elicit disturbance or courtship sounds from any of four adults.

In *Megaloblatta* both anteriorly and posteriorly directed strokes are sonorous. ELSNER (1974) describes mechanisms in which the bilaterally symmetrical and mechanically independent stridulatory organs produce different sounds. This is the result of either (a) inherently different motions or (b) temporal shifts in phases between the two moving parts. The latter is true for *Megaloblatta*. By definition, one pulse train group consists of two pulse trains, one due to the forward and one due to the backward movement of the file. The stridulatory motion is such that one organ is one pulse train (180°) out of phase with the contralateral structure. If the durations of both pulse trains were equal, the sounds and pauses produced synchronously by both sides would add and produce pauses of equal duration following each pulse train. Structural rigidity (the bilateral organs are on the same sterna) would synchronize the acoustic and silent components. However, in unilaterally muted nymphs the two pulse trains have unequal durations. The lack of a pause in stridulation of intact nymphs may result from either (1) elasticity of the sternum, or (2) circular motion of the sternum bearing the file. In the latter case, at some point in the forward stroke the scraper and file disengage (probably by the action of tergal-sternal and intersegmental tergo-sternal muscles—FORD, 1923), producing a longer pause and a short forward pulse train. Elasticity of the sixth sternum may account for both the different durations of the forward and backward pulse trains and the masking of pauses in intact nymphs.

Occasionally, when stimulation is applied unilaterally

ally, the nymphs produce sound with only one file and scraper (Fig. 4). From this it follows that the two sound producing organs are not obligatorily coupled. Whether they are under independent motor control is not yet known. Perhaps when the cockroach tilts in response to unilateral stimulation, the sterna on the contralateral side separate, disengaging the file and scraper on that side.

Direct motor control (rather than separation of the sterna due to tilting) of one-sided stridulation is implied by the long-term effects of unilateral muting. Bilateral stridulation is probably generated by antagonistic longitudinal muscles (e.g. inner and outer sternal muscles—FORD, 1923) in such a way that contraction of a muscle results in an ipsilateral forward stroke and a simultaneous contralateral backward stroke. In freshly muted nymphs contralateral muscles operate in opposition with similar contraction intensities, hence producing similar sounds in both pulse trains of a stridulatory cycle. After some time, lack of proprioceptive or auditory input from the mute side may cause a decrease in the intensity of the ipsilateral contraction. This would result in a slower return stroke of lower amplitude at the intact side. At slow repetition rates the backward stroke may be silent.

Several physical and morphological factors could contribute to the wide frequency spectrum of the airborne sound in *Megaloblatta*. Both the file and the scraper are composed of distinct densely and sparsely distributed fields with many teeth arranged in several rows (Fig. 3). Several file teeth impact upon several scraper teeth within a short time. Moreover, the paired files and scrapers produce sound simultaneously but not synchronously on both sides of the insect. Hence, the resultant sound is an interaction of the impacts of many unevenly spaced teeth on each side. Short damped oscillations result from the impacts of file and scraper teeth; the resulting carrier frequency in this "non-resonant" mechanism is higher than the rate of tooth impacts (ELSNER and POPOV, 1978). This is unlike the situation in crickets where a hardened wing edge strikes a row of evenly spaced teeth. Since the tooth impact rate corresponds to the natural frequency of the elytral resonator, a relatively narrow frequency band sound is produced (see KOCH, 1980). In *Gromphadorhina portentosa* the fourth spiracle acts as a resonator during hissing (NELSON, 1979). In *M. blaberoides* a spiracle which is adjacent to the file (Fig. 2A) may be used for this purpose. If the resonant frequency does not correspond to an energetic frequency component of the vibration, and/or if the resonator is heavily damped, a sound of broad frequency bandwidth will be produced (MICHELSEN and NÖCKE, 1974). Similarly, the abdominal surface may act as such a damped (low Q) resonator (MASTERS, 1980).

We consider *Megaloblatta*'s sound to be disturbance stridulation. Evidence for this classification include the acoustic characteristics of the sound and the behavioural context in which it is elicited. Disturbance sounds are usually temporally "unpatterned" (HASKELL, 1974), they span a broad-frequency bandwidth (MASTERS, 1979, 1980), and the amplitude envelope shows rapid rises and falls in energy (NELSON and FRASER, 1980). The sound produced by *Megalob-*

latta fits all of these criteria. Sexual display is not considered a possible function of this sound in nymphs. The solitary habit of nymphs suggests that the sound does not function in intraspecific communication.

PLATTNER *et al.* (1972) and ROTH and STAHL (1956) analyzed the tergal secretions of *Blatta orientalis*. With the exception of 3 amino acids, our results (Table 1) agree with theirs regarding amino acids in the material. Little may be deduced from all three studies beyond the fact that the secretions are similar in amino acid composition. The macromolecular composition remains unknown. Nevertheless, their sticky nature, chemical similarities, and the area of accumulation of the materials suggest that they serve similar functions in *B. orientalis*, *M. blaberoides*, and probably in many other species. Moreover, the behavioural coupling of sounds with exposure of the secretion suggests that it may function in chemical defence. NAYLER (1964) has shown that a similar secretion in the cockroach *Pseudoderopeltis bicolor* protects the insect against carabid beetles, ants, and centipedes. Of course, this does not preclude a possible role in trophallaxis, as speculated by ROTH and STAHL (1956).

Megaloblatta's display of bright colour patterns ("deimatic response" MALDONADO, 1970) coupled with an acoustic signal may startle potential predators. Since the duration of the predator-prey encounter is critical (SANDOW and BAILEY, 1978) and the latency of the defensive reaction in most insects is similar to or smaller than the duration of the attack (ROEDER, 1967), prolonging the prey catching phase of the attack (startle reaction) confers some protection on the prey.

The context in which the sound is produced, the nature of the sound, the proximity of its generators to chemical defences, and the behavioural responses suggest that *Megaloblatta* may be part of a complex acoustic Mullerian or Batesian mimicry system consisting of unrelated animals which may or may not couple a defensive secretion or sting with the disturbance sounds (MASTERS, 1980).

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