SOUND-PRODUCING MECHANISMS OF
BUENOA MACROTIBIALIS HUNGERFORD
(HEMIPTERA: NOTONECTIDAE)

R. Stimson Wilcox*

Department of Zoology, The University of Michigan, Ann Arbor, Michigan 48107, U.S.A.

Abstract—In *Buenoa macrotibialis*, experimental results indicate that the stridulatory mechanism composed of the tibial combs and rostral prongs is involved in producing trills, chirps, and dart-chirps; the femoral ridges and coxal peg mechanism is involved in producing grasping-chirps and cleaning-chirps; and the forelegs probably stridulate in unison. Either half of the tibial comb can produce trills, chirps and dart-chirps, though these signals are usually altered from normal. Both combs are normally involved in signal production, but one tibial comb can produce these signals with only slight alterations. The frequency spectrum of acoustic signals of *macrotibialis* is generated by resonation, not by rate of stridulation. The body proper, or some part(s) thereof, apparently functions as the resonator. Vibrations created by stridulation of the tibial comb-rostral prong and femoral ridge-coxal peg mechanisms probably are transmitted to the resonator by the rostrum and/or coxae.

Index descriptors (in addition to those in title): Acoustic signals, mating behavior, rostral prongs, tibial combs, coxal pegs, femoral ridges, frequency-generator, resonator.

INTRODUCTION

WHILE sound-producing structures have been described in many orders of arthropods (Dumortier, 1963a), the ease of describing structures has usually been counterbalanced by the difficulty of demonstrating that the structures actually do produce sound, how the structures are manipulated during sound production, and what the spectral characteristics of the sounds are due to. In most cases, experimentation is necessary to elucidate these factors. For example, it has taken several years of discussion and research by various workers to reach the conclusion that the cohesive forces of water play a major role in the dactyl-snapping of snapping shrimp (*Alpheus californiensis*) (Ritzmann, 1973), or to demonstrate the role of sound-radiating parts of the tegmina in the production of calling songs in cricket and katydid species (Nocke, 1971).

In the family Notonectidae (backswimmers), the males of all species of the genera *Buenoa* and *Anisops* possess stridulatory structures, as do females of a few species of *Buenoa*. Acoustic behavior has been described briefly in one *Buenoa* species (Hungerford, 1924), and two *Anisops* species (Hale, 1923; Poisson, 1926). However, no work has been published examining whether and how the structures described for any species actually are involved in sound production, nor what produces the spectral characteristics of the sounds.

* Present Address: Division of Biological Sciences, Kansas State University, Manhattan, Kansas 66506, U.S.A.

Three stridulatory mechanisms have been proposed for males of most species of *Buenoa* (Bare, 1928):

(1) *Tibial comb-rostral prong mechanism.* Each foretibia possesses an elongate elevation of its inner proximal face, with a longitudinal trough in the elevation. A comb of flattened setae is firmly seated in the trough. The forelegs could scrape these combs against striated, sword-like projections (the rostral prongs) located on both sides of the third rostral segment (Fig. 1, (A) and (B) line 2).

(2) *Femoral ridge-coxal peg mechanism.* The inner face of each fore-femur possesses an area of more or less parallel sclerotized ridges which could be scraped against a short heavy seta (the coxal peg) located on the lateral face of the coxa of the same leg (Fig. 1, (A) and (B) line 3.).

(3) *Femoral apex-base of beak mechanism.* The inner distal ends of the femora are sclerotized and possess several stout hairs. Either or both the femoral ends or stout hairs could pluck against the base of the beak (Fig. 1, (A) and (B) line 1).
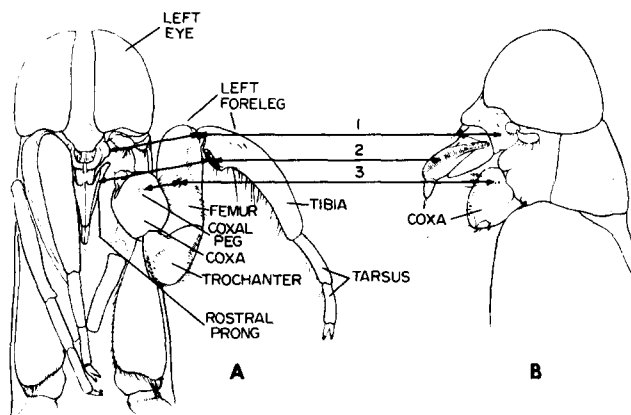

FIG. 1. Stridulatory structures of *B. macrotibialis* (A) and (B) Ventral and lateral view, respectively, showing stridulatory structures. Left foreleg pulled out sideways in (A) and removed in (B). Line 1 connects femoral apex-base of beak stridulatory mechanism. Line 2 connects tibial comb-rostral prong mechanism. Line 3 connects femoral ridge-coxal peg mechanism. Coxal pegs are drawn disproportionately large. Scale = 34×.

Males of *Buenoa macrotibialis* possess all 3 above mechanisms, all of which, from anatomical appearence, could produce sounds with similar anterior and/or posterior rocking movements of the forelegs. Such movements can easily be observed during the production of some signals. However, the forelegs partially or wholly obscure all 3 mechanisms during stridulation. Observation alone cannot resolve whether the mechanisms are actually involved in sound production, much less resolve which one or more mechanisms produce which sounds, thus making experimentation on the structures necessary.

In this study I concentrated on *B. macrotibialis*, and attempted first to determine whether the proposed tibial comb-rostral prong and femoral ridge-coxal peg mechanisms actually are involved in sound production; second, to determine the respective signals the structures produce; and third, to locate the factor or factors responsible for the frequency spectra of the signals i.e., to locate the frequency-generator. The femoral apex-base of beak mechanism was not examined because the structures involved do not appear to be specialized to the

degree that the other 2 mechanisms are, and because it became apparent that the mechanism is rarely used by *macrotibialis* males.

MATERIALS AND METHODS

The insects were observed and recorded in a 22 long × 15 wide × 12·5 cm deep aquarium which had a 2-cm layer of Styrafoam in the bottom. The microphone rested in a corner of the aquarium at about a 45° angle from vertical, with the front end submerged. All recordings were made when the insects were between 2 and 12 cm from the microphone [one exception, Fig. 5(E)] and within a 45° angle originating from the front outer edge of the microphone. Recordings were made with a Uher 4000 Report-L tape recorder and a Uher M514 microphone, with the windscreen removed and a prophylactic placed over the end and body of the microphone, thus making it partially submersible. Signals were recorded at a tape speed of 7½ inches per second and analyzed audio-spectographically with a Kay Vibralyzer. Vibralyzer settings were: Mark Level Gain 7·0–7·5, Bandwidth Wide, Pattern Normal, and Shape Flat. The filter bandwidth was 800 Hz. Analyses of the same recorded signals on different days showed that signal frequency varied as much as 1800 Hz from one day to the next, probably due to differences in tape-recorder and/or Vibralyzer recording-drum speed.

As described more fully elsewhere (Wilcox, 1969), *macrotibialis* males produce at least 4 acoustic signals during courtship behavior: trills [Fig. 2(A) and (B)] and chirps [Fig. 2(E)], produced prior to and during early courtship stages, with chirps also being produced during later courtship stages; dart-chirps [Fig. 2(C) and (D)], produced during a late courtship stage; and grasping-chirps [Fig. 2(G) and (H)], produced during the last courtship stage, when the male grasps the female. Other chirps are produced during non-courtship behavior: disturbance-chirps [Fig. 2(F)], sometimes produced in response to sharp, intense noises (such as a sharp rap on the side of the aquarium); cleaning-chirps [Fig. 2(I)], sometimes produced when the forelegs are rocked anteriorly over the eyes in an apparent cleaning function; and capture-chirps [Fig. 2(J)], sometimes produced during the capture of prey. In keeping with acoustic terminology in current usage, as reviewed by Alexander (1967), I have defined the word impact as the basic "building block" of a pulse, a pulse corresponding to the passage of the scraper over the file in one direction. A chirp is composed of one to a few pulses. A trill is a succession of chirps that is too long to be sensibly called a chirp. The word signal denotes a communicative function, determined herein primarily through context.
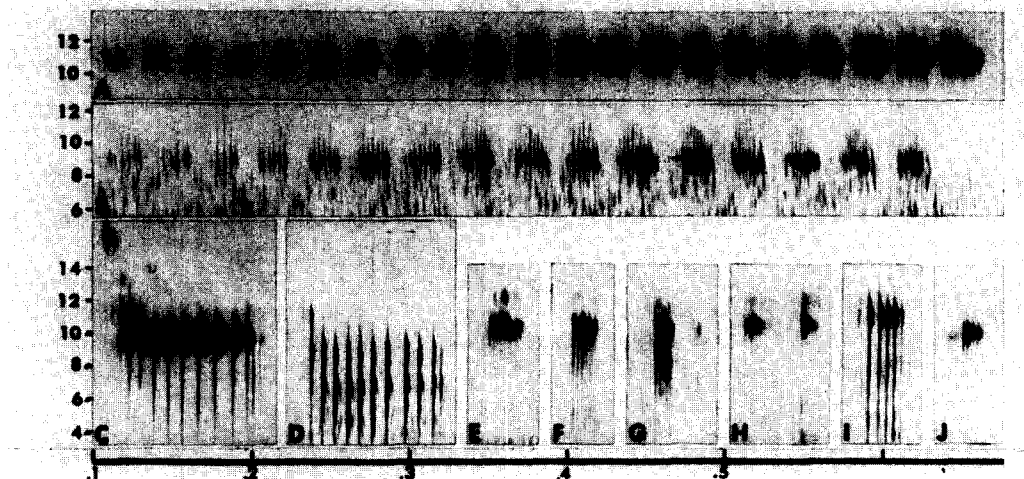

Fɪɢ. 2. Acoustic signals produced by *Buenoa macrotibialis*. All recordings made in the laboratory except where noted. (A) Complete trill. 24·4 (B) Trill (field recording). 23·9 (C) Dart-chirp. 20·6 (D) Dart-chirp (field recording). 23·9 (E) Chirp. 22·2 (F) Disturbance-chirp. 22·2 (G) Grasping-chirp followed by soft, click-like pulse. 21·1 (H) Grasping-chirp followed by an intense click-like pulse. Pulse is variable in intensity and is sometimes absent. 21·1 (I) Cleaning-chirp. 22·8 (J) Capture-chirp, produced during the capture of a *Daphnia*. 21·7 Ordinate: frequency in kHz Abscissa: time in tenths of a second.

E

By operating underwater on chloroform-anesthetized insects, I altered stridulatory structures in the following ways: (1) The tibial combs were covered with fingernail polish applied underwater with a stiff bristle. The polish formed a low, smooth mound, and could be removed by popping it off with a pin. (2) The tibial combs were partially or wholly removed by tearing out the comb hairs with a fine-tipped, pick. (3) One tibia was amputated by clipping it off at the joint between tibia and femur. (4) The coxal pegs were removed by pushing them out of their sockets with a pin. (5) The femoral ridges were removed by grinding them off with a fine-tipped dental drill, thus removing the sclerotized ridges without rupturing the integument. (6) The free-projecting lengths of the rostral prongs were shortened by clipping off thier apices with iridectomy scissors. (7) Various parts of the legs, rostrum and body of a live male, restrained in the rubber operating platform, were plucked with an insect pin, and the resulting sounds recorded. The pin's vibrations were damped by passing it through a section of rubber tubing. (8) The joint between the second and third rostral segments, and perhaps also the position of the rostral prongs, was altered by positioning a rubber band (i.d. about 0·20 mm, o.d. about 0·26 mm) around the rostrum at the joint the band lying underneath the ends of the rostral prongs. The signals of each individual were recorded before and after structural alterations, so each individual served as its own control. Each alteration was examined under the microscope after recording post-operative signals.

In addition, the trills and dart-chirps of a male were recorded while the water temperature was slowly raised from 14·4 to 25·0°, the water being stirred at frequent intervals and temperatures taken within 2·5 cm of the male after each recorded signal; and the volume of the ventral air bubble of a male was altered rapidly by placing a male in a sealed 1-pint jar filled ¾ full of water, and compressing or decompressing the air over the water during trills, by quickly pushing in or withdrawing the plunger of a 50-cc syringe connected to the jar cap. Each plunger stroke began after a trill began, ended before the trill ended, and took approximately 0·3 seconds. The pressure changes, and the percent change in the insect's bubble volume, were estimated by attaching a glass tube vertically to the jar cap, thus making a manometer, and placing a segment of pipette containing an air bubble in the jar, then compressing the system with the plunger and noting the difference in height of the water in the tube and in the volume of the pipette's air bubble. The change in pressure was about 1·9 psi and the volume change about 21%.

Five sham operations were performed on 5 individuals, respectively. (1) The tibial combs were scraped with the pick. (2) The coxa was scraped near the coxal peg. (3) The dental drill was held against the forefemora near the area of ridges, but no integument removed. (4) The integument was ruptured at the distal base of the tibial comb elevation on both forelegs, the area ruptured being approximately equal to that resulting from removal of an entire tibial comb. (5) The rostral prongs were scraped and gently moved about with a pin.

In experiments designed to alter the characteristics of signals, rather than eliminate the signals entirely, I analyzed trills and dart-chirps and ignored chirps because chirps are less structured and more variable in frequency than trills and dart-chirps, and seemed less likely to show clear differences resulting from alterations.

Buenoa macrotibialis was chosen for intensive study because the species courts readily in the laboratory and was available in quantity. All temperatures are degrees celsius.

RESULTS AND DISCUSSION

Sham Operations

Since all individuals produced normal signals soon after sham operations, operative procedures themselves had no significant effect on signal characteristics.

Stridulatory Mechanisms

Tibial-combs covered with fingernail polish (3 *individuals*). The insects produced normal grasping-chirps and cleaning-chirps, but no trills, chirps or dart-chirps, although they

Fig. 3. Acoustic experiments on *macrotibialis* males. (A–D) (E–I) (J–M) represent 3 different individuals expectively. (See text for further explanation.) (A–M) Partial Tibial Combs Removed (A) Preoperative trill. 22·2° (B) Postoperative trill: proximal ½ combs removed. 22·2° (C) Preoperative dart-chirp. 22·2° (D) Postoperative dart-chirp: proximal ½ combs removed. 22·2° (E) Preoperative dart-chirp. 21·1° (F) Postoperative dart-chirp: proximal ½ combs removed. (G) Preoperative trill. 21·1° (H) Postoperative trill: proximal ½ combs removed. 21·1° (I) Postoperative trill: proximal ½ combs removed. 21·1° (J) Preoperative trill. 21·1° (K) Postoperative trill: proximal ½ combs removed. 20·6° (L) Preoperative dart-chirp. 21·1° (M) Postoperative dart-chirp: proximal ½ combs removed. 20·6° Ordinate: frequency in kHz Abscissa: time in tenths of a second.
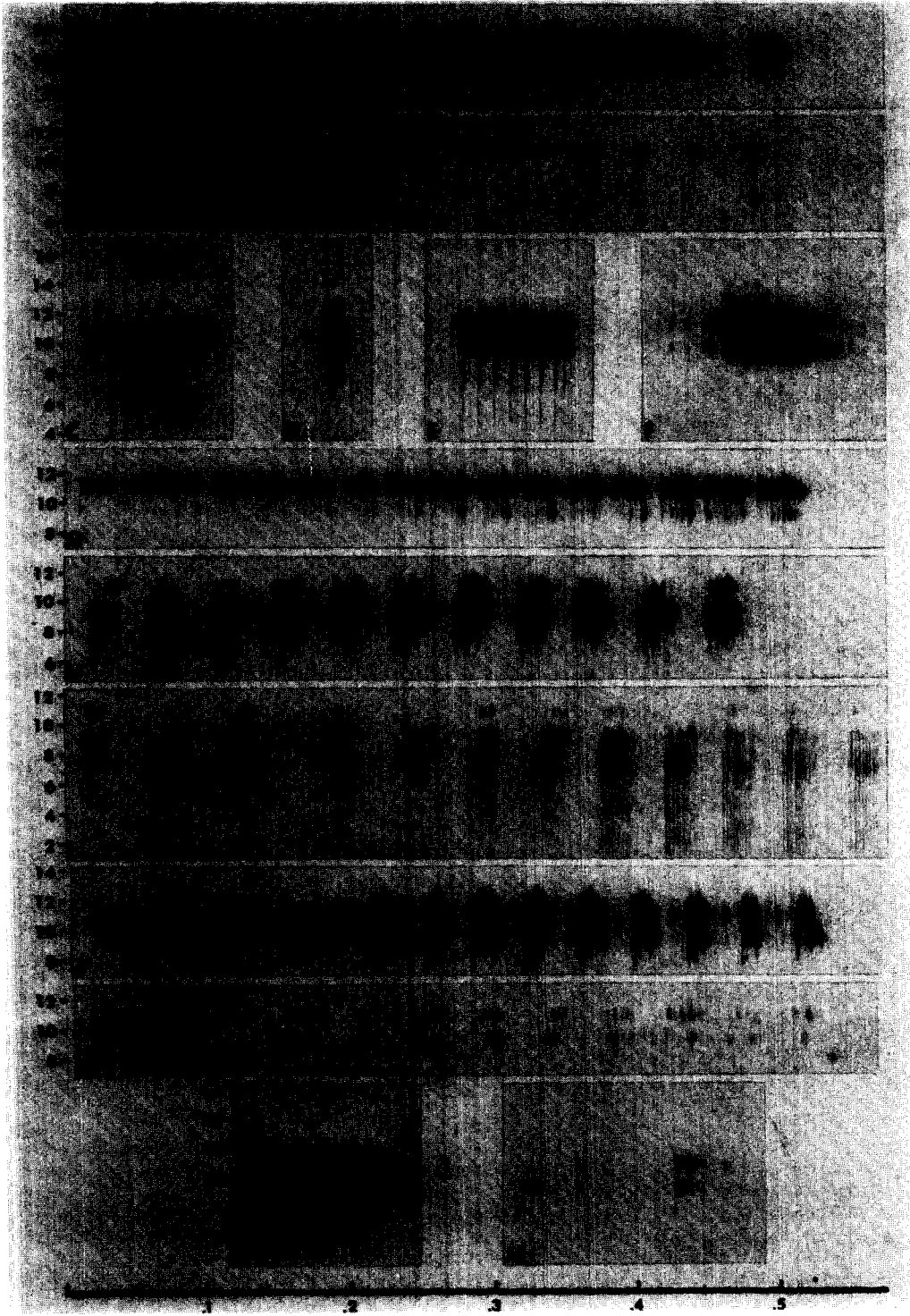
Fɪɢ. 3.

performed the leg-motions of the last 3 signals. After removal of the polish from one insect, it again produced normal trills, chirps and dart-chirps.

These results suggested that the tibial combs were involved in producing trills, chirps and dart-chirps and not in producing grasping-chirps and cleaning-chirps. But because the polish might have altered normal stridulatory positions and/or motions, I operated on the tibial combs themselves.

Entire tibial combs removed (2 *individuals*). The same results were obtained as covering the combs with fingernail polish, suggesting the same conclusions.

Coxal pegs removed (6 *individuals*). Normal trills, chirps and dart-chirps were produced, but no grasping-chirps and cleaning chirps. These results suggested that the coxal pegs were involved in producing grasping-chirps and cleaning-chirps.

Femoral ridges removed (3 *individuals*). As in removal of the coxal pegs, no grasping-chirps or cleaning-chirps were produced, so it appeared that the femoral ridge-coxal peg mechanism is involved in producing only these signals. Furthermore, cleaning-chirps are usually produced while the forelegs are rotated dorsally in a movement which apparently cleans the eyes, during which the tibial combs are clearly not in contact with the rostral prongs.

Both coxal pegs and tibial combs removed (1 *individual*). No signals were produced, although the insect performed the entire courtship sequence several times, with apparently normal stridulatory motions clearly visible. This experiment suggested that in *macrotibialis* all signals investigated are produced by the tibial comb-rostral prong and femoral ridge-coxal peg mechanisms.

The preceeding experiments relied on signal presence or absence for evidence. The following experiments were designed to alter structures to produce alterations in signals, rather than to eliminate signals.

Partial tibial combs removed (10 *individuals*). In 6 individuals I removed the proximal third of both tibial combs (= proximal 1/3 combs); in 2 more individuals the proximal half of the combs (= proximal 1/2 combs); and in 2 further individuals the distal half of the combs (= distal 1/2 combs). All 10 of these operations resulted in a distinct decrease in trill and dart-chirp intensity and a tendency toward loss of impact definition in audiospectrographs (Figs. 3 and 4). All dart-chirps also showed a decrease in impact interval to produce a scrape-like sound [Fig. 3, (D)]. The dart-chirps in 4 of the 6 proximal 1/3 combs individuals showed a decrease in dart-chirps length [Fig. 3, (D)]. In the 2 distal 1/2 comb operations the dart-chirps possessed an intensified band of frequencies between 14 and 16 kHz, as well as the usual intense band of frequencies between 8 and 11 kHz [Fig. 4, (F) and especially (L)].

The results of the operations on trills involved in all cases a longer chirp interval and shortened chirps [Fig. 3, (B)]; chirps either shortened or not but with the frequency span

Fig. 4. Acoustic experiments on *macrotibialis* males. (A–D) (E–H) (I–L) represent 3 different individuals respectively. (See text for further explanation.) (A–L) Partial Tibial Combs Removed (A) Preoperative trill. 22·2° (B) Postoperative trill: proximal ½ combs removed. 22·2° (C) Preoperative dart-chirp. 22·2° (D) Postoperative dart-chirp: proximal ½ combs removed. 22·2° (E) Preoperative dart-chirp. 21·7° (F) Postoperative dart-chirp: distal ½ combs removed. 22·2° (G) Preoperative trill. 21·7° (H) Postoperative trill: distal ½ combs removed. 22·2° (I) Preoperativetrill. 22·2° (J) Postoperative trill: distal ½ combs removed. 22·2° (K) Preoperative dart-chirp. 22·2° (L) Postoperative dart-chirp: distal ½ combs removed. 22·2° Ordinate: frequency in kHz Abscissa: time in tenths of a second.
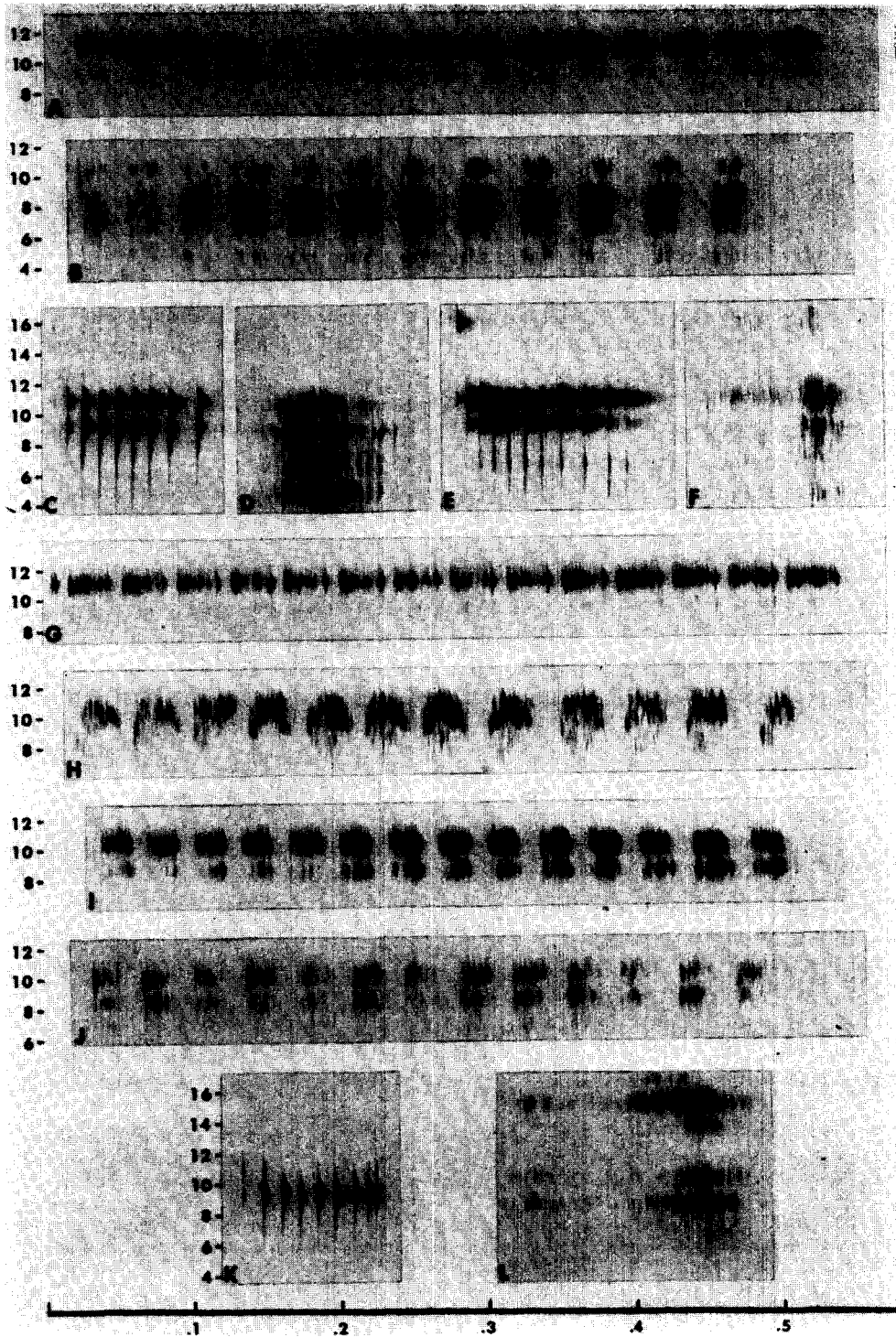
Fig. 4.

slightly to strongly lowered [Fig. 3, (I)]; and essentially no other change not within the range of variation of *macrotibialis* (4 of the 10 individuals).

The strong lowering of the frequency span in Fig. 3, I is similar in appearance to the signals of males newly molted to adulthood. Recent molting cannot be invoked as an explanation for the results of any of the experiments, however, for the preoperative signals show that all males in the experiments reported herein were capable of producing normal-appearing (mature) signals. Nor can the effects of rupture of the body wall be used as a likely explanation (see Sham Operations above). Thus it seems likely that the changes in trills and dart-chirps resulted primarily from changes in the tibial combs. Also, it appears that *macrotibialis* can produce sounds with either half of the combs.

Right tibial comb removed or covered (3 *individuals*). Removal of the right tibial combs of 2 individuals resulted in the trills and dart-chirps of both individuals being less intense than the control signals and having slightly longer chirp intervals. Both kinds of signal of one individual showed no other alteration except a slight decrease in impact interval and an increase in number of impacts in the dart-chirp. The trills of the other individual showed a strong downward increase in frequency span.

Covering the left tibial comb of one individual with fingernail polish caused no change except a slight loss of impact definition in the trill and a slight loss of intensity. After removal of the polish the signals of this individual appeared normal again.

Right tibia amputated (2 *individuals*). The results showed diminished intensity of trills and dart-chirps, with dart-chirps showing a decrease in impact interval compared to normal. The trills showed a strong downward extension of the frequency span, an increase of chirp interval and, in one individual, a decrease in chirp-length.

The results of this and the preceding 2 experiments show that *macrotibialis* males can produce trills and dart-chirps with only one tibial comb, but indicate that both combs are normally involved. Also, since the signal structure was reasonably similar to normal in some cases, it seems likely that the forelegs stridulate in unison.

Rostral prongs shortened (3 *individuals*). Removal of about 1/4 of each rostral prong in 2 individuals produced no significant change in trills or dart-chirps [Fig. 5, (A–D)]. Removal of 1/2 of each rostral prong in another individual produced no change in the trill, but a slight decrease in impact length in the dart-chirp [Fig. 5 (E–H)]. Removal of 1/2 the right prong in another individual resulted in the dart-chirp appearing to be unaltered by the operation [Fig. 5, (M) and (N)]. However, 25 of 26 trills recorded were composed either of trills with a chirp-structure bordering on the range of variation normal to *macrotibialis* trills [Fig. 5, (J)], or of trills composed of abnormally short chirps, with a downward increase in frequency span [Fig. 5, (K)]. The one exception was a short trill which began with 3 rather atypical chirps, then abruptly altered to an apparently normal

Fig. 5. Acoustic experiments on *macrotibialis* males. (A–D) (E–H) (I–N) represent 3 different individuals respectively. (See text for further explanation.) (A–N) Rostral Prongs Shortened at Apex (A) Preoperative trill. 21·7° (B) Postoperative trill: both rostral prongs ¼ shortened. 23·9° (C) Preoperative dart-chirp. 21·7° (D) Postoperative dart-chirp: both rostral prongs ¼ shortened. 23·9° (E) Preoperative dart-chirp. Note: signal was produced within ¼ inch of the end of the microphone. 24·4° (F) Postoperative dart-chirp: both rostral prongs ½ shortened. 23·9° (G) Preoperative trill. 24·4° (H) Postoperative trill: both rostral prongs ½ shortened. 23·9° (I) Preoperative trill. 21·1° (J) Postoperative trill: right rostral prong ½ shortened. 22·8° (K) Postoperative trill: right rostral prong ½ shortened. 25·0° (L) Postoperative trill: right rostral prong ½ shortened. 25·0° (M) Preoperative dart-chirp. 21·7° (N) Postoperative dart-chirp: right rostral prong ½ shortened. 21·7° Ordinate: frequency in kHz Abscissa: time in tenths of a second.
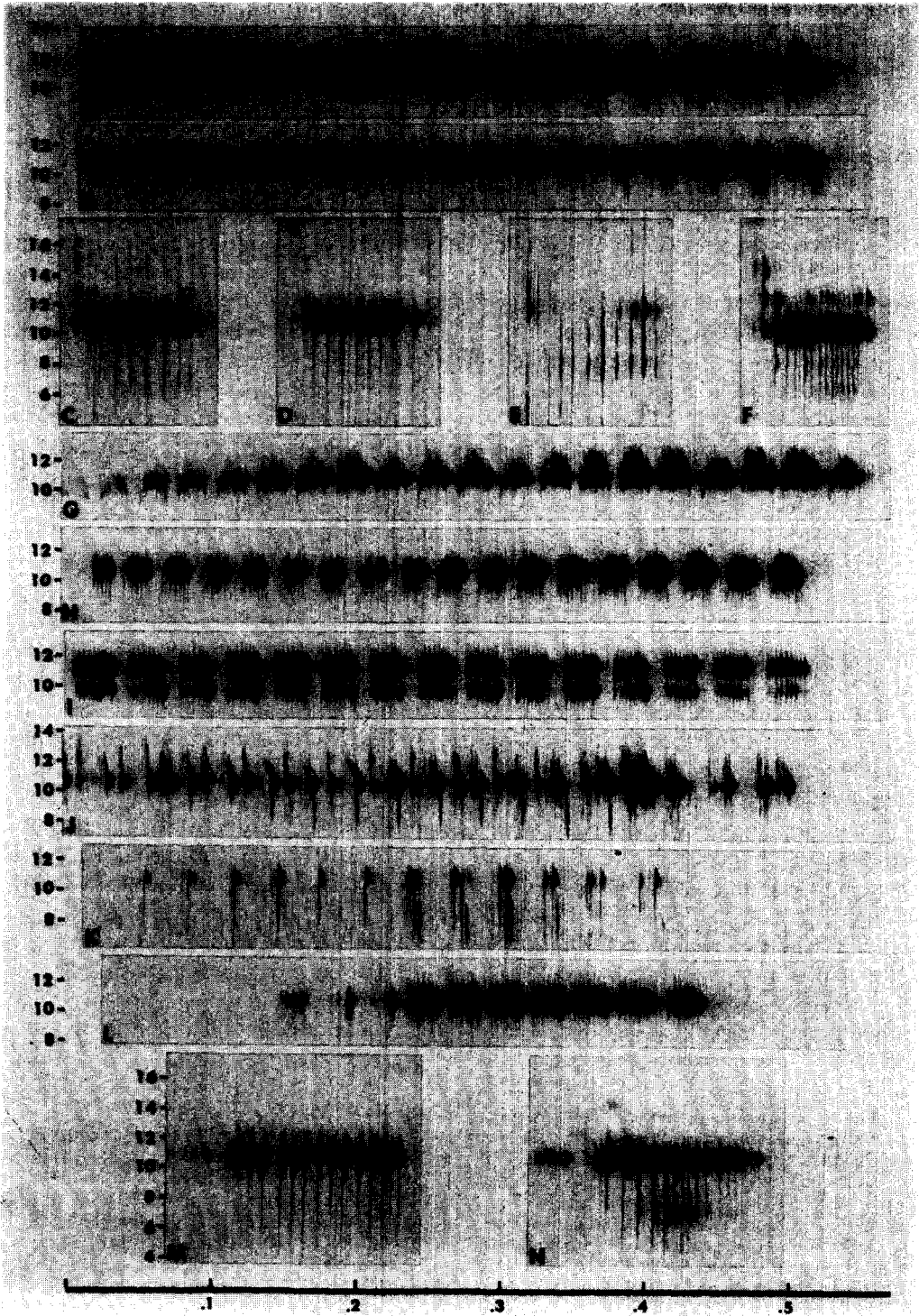
FIG. 5.

trill [Fig. 5, (L)]. The first postoperative trill presented for this individual (J) preceded the normal trill by about 2 seconds; and 5 trills recorded subsequent to the normal trill were all similar to (K). The results suggest that the rostral prongs are also involved in the production of trills and dart-chirps.

The frequency-generator

As discussed by Dumortier (1963b) and others, the frequency spectrum of a stridulatory signal may be generated by either or both (1) the rate at which file and scraper strike against one another, in which case the sound-radiating structure is forced to vibrate at the impact rate, and frequency increases or decreases as impact rate increases or decreases, or (2) the resonances inherent in a structure(s) which is part of or coupled to the stridulatory mechanism, in which case frequency is not related to impact rate. In *macrotibialis*, the file and scraper probably do not strike together rapidly enough to produce dominant frequencies in the 10 to 12 kHz range, as can easily be seen by noting the impact repetition rate in the figures of *macrotibialis* signals, with the assumption that each impact corresponds to the scraper striking one tooth of the file. Thus resonation seems more likely to be responsible for the frequency spectrum of *macrotibialis* signals. To test this idea, stridulatory rate was altered by temperature change, to see the effect this had on frequency.

Temperature change (1 *individual*). The chirp length and chirp interval of trills, the length of dart-chirps, and impact length and interval in both kinds of signal decreased by approximately one half as water temperature increased from 14·4 to 25·0°, indicating that the rate of leg movement in stridulation at 14·4° had increased by about twice at 25·0° (assuming the insect stridulated similarly throughout the experiment). However, the frequency spectrum showed no significant change in the experiment [Fig. 6, (A–F)]. These results indicate that in *macrotibialis* the frequency spectrum of trills and dart-chirps is generated by the inherent resonance of a structure or structures driven (caused to vibrate) by stridulation. I therefore plucked various body structures with a damped insect pin, in hopes of thereby eliciting the frequency spectrum characteristics of at least some signals.

Various structures plucked (1 *individual*). The plucking produced only broad frequencies, with intense frequencies below 8 kHz for any structure [Fig. 6, (H–M)]. The rubber operating platform probably dampened body vibration considerably, but there was nothing unusual damping the legs, tibial combs, or rostrum, thus eliminating these structures as possible frequency-generators, within the limits of the exercise. However, attempting to cause a structure to resonate by plucking it with a relatively large pin is a rather gross way to imitate the conditions under which such structures normally resonate. Altering various structures anatomically seemed to be a more effective way to cause alterations in frequency spectrum.

FIG. 6. Acoustic experiments on *macrotibialis* males. (A–F) (G) (H–M) and (N–Q) represent 3 different individuals respectively. (See text for further explanation.) (A–F) Temperature Changed (A) Trill recorded at 14·4° (B) Trill recorded at 20·0° (C) Trill recorded at 25·0° (D) Dart-chirp recorded at 15·0° (E) Dart-chirp recorded at 18·9° (F) Dart-chirp recorded at 25·0° (G) Male striking a glass partition with its head, in the recording aquarium. 21·1° (H–M) Various Structures Plucked (H) Rubber operating platform plucked. 21·7° (I) Vertex plucked. 23·3° (J) Inner distal end of right femur plucked. 24·4° (K) Left tibial comb scraped. 22·2° (L) Left rostral prong plucked. 22·2° (M) Dorsal part of third rostral segment plucked. 22·2° (N–Q) Rostrum Encircled by Rubber Band (N) Preoperative trill. 22·8° (O) Postoperative trill: rostrum encircled by rubber band. 22·2° (P) Preoperative dart-chirp. 22·8° (Q) Postoperative dart-chirp: rostrum encircled by rubber band. 22·2° Ordinate: frequency in kHz Abscissa: time in tenths of a second.
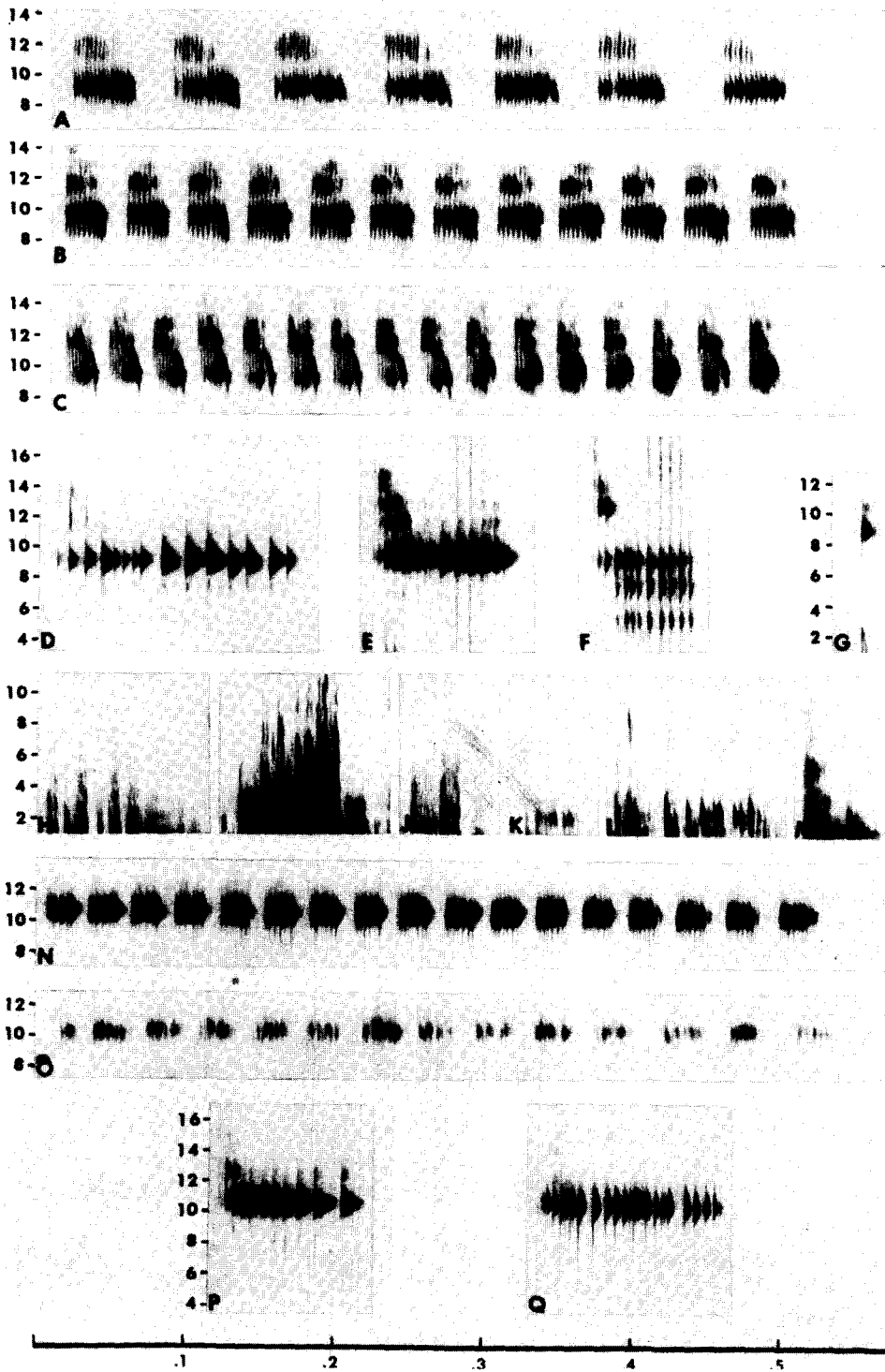
FIG. 6.

As shown in the postoperative trills in Figs. 3–5, alteration of the tibial combs and rostral prongs resulted mainly in downward increase in frequency span in trills, which made the 2 structures suspect as the frequency generators. However, the drastic alterations of the mass and shape of the tibial combs did not produce a wholesale shift in frequency spectrum. The results suggested instead that alteration of the tibial combs or rostral prongs altered not the frequency generator itself, but instead part of a mechanism which drove the frequency-generator, and consequently drove the generator in an altered way. The rostral prongs could hardly have produced the normal signal shown in Fig. 5, (L) if they were the frequency-generating structures, because of the irrevocable change in prong mass and shape. The prongs appeared instead to be part of the mechanism linking the driving force of the tibial combs to the frequency generator which, by elimination, seemed likely to be the body and/or the air bubble, in part or whole. These 2 possibilities were supported by the fact that when *macrotibialis* males strike their heads against hard objects, the most intense frequency band of the resulting sound is in the same range as that of signals [Fig. 6, (G)]. The likelihood that the rostrum transmits vibrations to the body was examined by positioning a rubber band around the rostrum.

Rostrum encircled by rubber band (2 *individuals*). The dart-chirps of one male showed no change except a greater number of impacts [Fig. 6, (Q)]. Trills were less intense and had longer chirp intervals than normal (N and O). The dart-chirps of the second male showed a decrease in length and loss of definition of impacts [Fig. 7, (F)]. All trills were diminished in intensity, and their frequency span was remarkably variable, being either most intense at the normal frequency span but strongly extended downward [Fig. 7, (C)] or restricted primarily to lower frequencies, up to about 9 kHz [Fig. 7, (D)]. One trill, however, appeared normal other than being less intense [Fig. 7, (B)]. This trill was preceded and succeeded by a number of the other 2 types of trills.

The differences between signals of the 2 males may have stemmed from differences in the rubber bands, which differed in shape, size, and tension, and probably position also. The changes in the signals of the second male especially, may reflect a change or changes in the mechanism driving the frequency-generator. The generator thus appeared likely to be a part or parts of the body or air bubble.

The air bubble carried by *Buenoa* extends along the entire ventral surface. Since bubble volume changes during a dive but the frequency spectra of signals do not change, the insects would have to maintain a portion of the bubble at a constant volume for each signal if the bubble were used as a frequency-generator. *Buenoa* can shift the bubble volume proportions back and forth between thoracic and abdominal portions of the body venter, and it is possible they could adjust a portion of the bubble to a repeatedly similar volume.

The 14·4–25·0°C temperature change was too slow to cause a change in bubble volume which the insect could not compensate by shifting bubble proportions. Likewise bubble volume changes occuring during changes in depth while stridulating would probably also be too slow. I therefore rapidly decreased and increased the volume of the bubble by about 21% during trills.

Air bubble volume change (1 *individual*). The results showed no significant change in trill frequency or intensity [Fig. 7, (G) and (H)]. It is very unlikely that the male was able to adjust bubble volume to such a rapid change so that no frequency change would occur. The experiment thus indicates that the air bubble is not directly involved in generating the frequency spectrum of trills, which leaves the body, in part or whole, as the likely frequency generator and acoustic amplifier.

Because the most intense frequency bands of grasping-chirps and cleaning-chirps are similar to the most intense bands of trills, chirps and dart-chirps [Fig. 2, (A–I)], the signals may all have a common frequency-generator. As the tibial combs are not in contact with the rostral prongs during the production of some cleaning-chirps, it seems likely that for
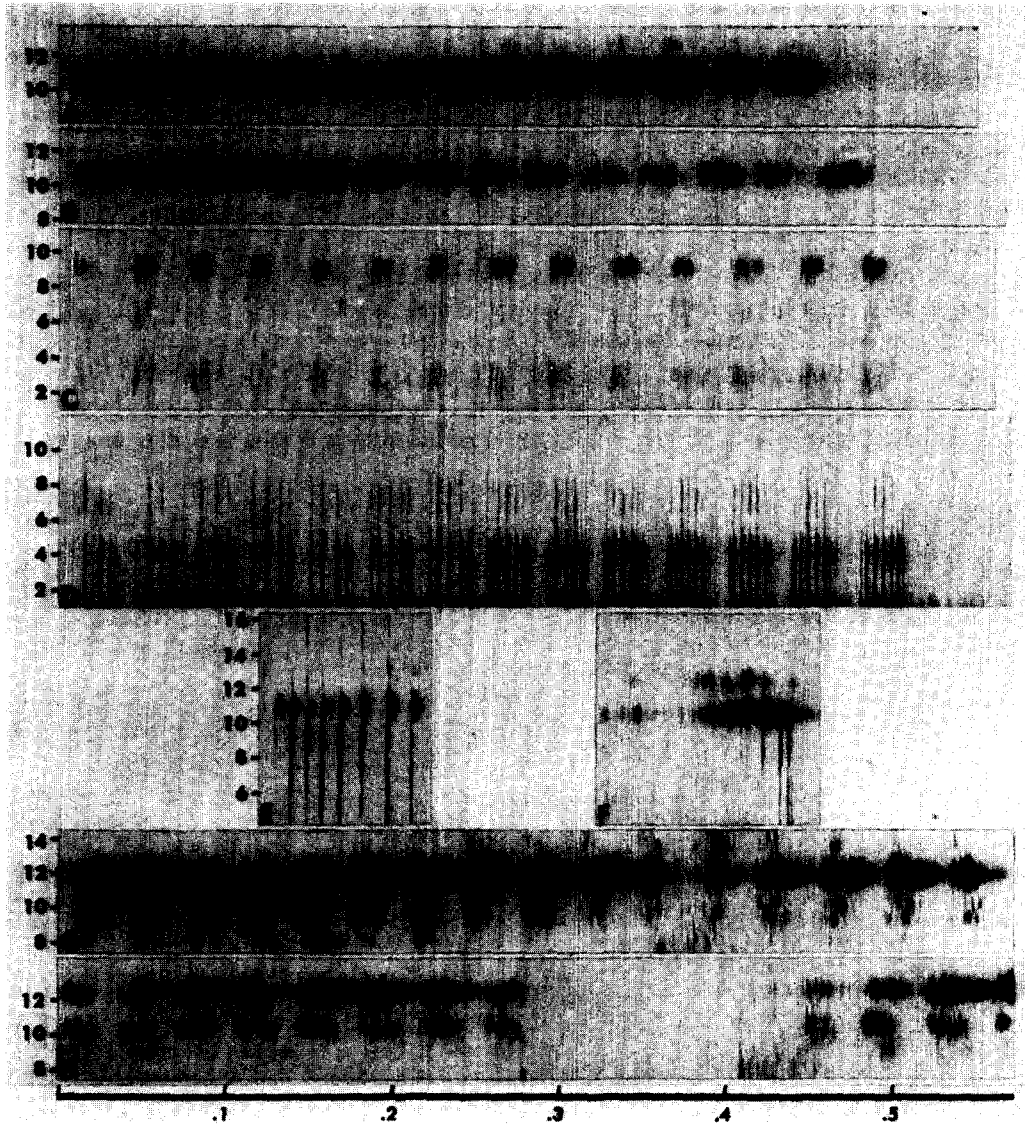

FIG. 7. Acoustic experiments on *macrotibialis* males. (A–F) (G–H) and (I–K) represent 3 different individuals respectively. (See text for further explanation.) (A–F) Rostrum Encircled by Rubber Band (A) Preoperative trill. 22·2° (B) Postoperative trill. 21·1° (C) Postoperative trill. 21·1° (D) Postoperative trill. 21·1° (E) Preoperative dart-chirp. 22·2° (F) Postoperative dart-chirp. 21·1° (G and H) Air Bubble Volume Changed. (G) Pressure increased during trill. Plunger hit bottom at black mark at center of audiospectograph. 23·3° (H) Pressure decreased during trill. Plunger pulled free at black mark at center of audiospectograph. 23·2° Ordinate: frequency in kHz Abscissa: time in tenths of a second.

cleaning-chirps, and perhaps grasping-chirps also, stridulatory vibrations are transmitted to the frequency-generator via the coxae alone and/or at least by some other structure besides the rostral prongs. In addition, vibrations created by stridulation of the tibial combs and rostral prongs could also be transmitted to the body via the coxae.

This study shows that in *macrotibialis*, 2 or possibly 3 sound-producing structures are located on the same appendage, and produced different signals with similar-appearing movements of the appendage. To my knowledge, this is a unique phenomenon among known stridulating arthropods.

The precopulatory signals of *Buenoa* are species specific. Natural hybrids are unknown, but *B. macrotibialis* females and *limnocastoris* males produce sterile hybrids in a laboratory cross (Wilcox, 1969). This information suggests that precopulatory acoustic signals function in sexual stimulation and reproductive isolation. With the relation of specific stridulatory mechanisms to specific signals verified in *macrotibialis*, and a certain amount of control established over the production of signals and some signal characteristics, it should be possible in future to begin examining the specific role of various male signals and signal characteristics in sexual stimulation and species recognition by females. Although artificially altered or generated playback signals might help elucidate these roles, playback signals alone would lack the courtship maneuvers and copulatory attempts of a behaviorally normal but acoustically altered male, giving an advantage to the live male technique.

REFERENCES

ALEXANDER, R. D. 1967. Acoustical communication in arthropods. *Annu. Rev. Entomol.* **12**: 495–526.
BARE, C. O. 1928. Haemoglobin cells and other studies of the genus *Buenoa* (Hemiptera, Notonectidae). *Univ. Kansas Sci. Bull.* **18**: 265–349.
DUMORTIER, B. 1963a. Morphology of sound emission apparatus in Arthropoda, pp. 277–345. In Busnel, R. G. (ed.) *Acoustic Behavior of Animals*, Elsevier, Amsterdam.
DUMORTIER, B. 1963b. The physical characteristics of sound emissions in arthropoda, pp. 346–373. In Busnel, R. G. (ed.) *Acoustic Behavior of Animals*, Elsevier, Amsterdam.
HALE, H. M. 1923. Studies in Australian aquatic Hemiptera. No. II. *Rec. So. Austral Mus.* **2**: 397–424.
HUNGERFORD, H. B. 1924. Stridulation of *Buenoa limnocastoris* Hungerford and systematic notes on the *Buenoa* of the Douglas Lake Region of Michigan, with a description of a new form. (Notonectidae—Hemiptera). *Amer. Entomol. Soc. Amer.* **17**: 223–27.
NOCKE, H. 1971. Biophysik der Schallerzeugung durch die Vorderflügel der Grillen. *Z. Vergl. Physiol.* **74**: 272–314.
POISSON, R. 1926. L'Anisops producta Fieb. (Hemiptera Notonectidae). Observations sur son anatomie et sa biologie. *Arch. Zool. Exp. Gen.* **65**: 181–208.
RITZMANN, R. 1973. Snapping behavior of the shrimp *Alpheus californiensis*. *Science* **181**: 459–460.
WILCOX, R. S. 1969. Acoustical behavior, sound-producing structures and biology of *Buenoa* (Hemiptera, Notonectidae). Ph.D. Thesis. Department of Zoology, The University of Michigan, Ann Arbor, Michigan 48104.