

# MORPHOLOGY AND FUNCTION OF FEMALE SOUND-PRODUCING STRUCTURES IN ENSIFERAN ORTHOPTERA WITH SPECIAL EMPHASIS ON THE PHANEROPTERINAE\*

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**Abstract**—We compared female stridulatory fields of 15 species (four genera) of phaneropterine katydids and determined that the stridulatory field has limited use as a character for identifying species. Female sound-producing structures and functions of the sounds are reviewed for Gryllotalpidae and three other subfamilies of Tettigoniidae.

The female stridulatory field of phaneropterine katydids is a complex of stout curved spines on the dorsal surface of the anal area of the right tegmen. Sounds of such females are produced in response to pair-forming signals of conspecific males and serve to attract males.

In five species of *Gryllotalpa* and *Neocurtilla major*, females have stridulatory files similar in structure and position to male files. In *Scapteriscus* species, females lack a stridulatory file, but on the dorsal surface of the left tegmen there are numerous cross-veins with a laminated ultrastructure reminiscent of the teeth on a stridulatory file. Females of *Scapteriscus vicinus*, *Neocurtilla major*, and three species of *Gryllotalpa* are known to produce sounds.

Females of *Ephippiger* have well-defined stridulatory files on the dorsal surface of the right tegmen. They produce sounds when a male signals nearby. These sounds presumably act at close range to finalize contact in pair formation.

Females of *Pterophylla camellifolia* have on the undersurface of the anal area of the left tegmen a network of veins bearing many short ridges. Sounds produced by these females perhaps reduce bird predation.

**Index descriptors** (in addition to those in title): Gryllotalpidae, Ephippigerinae, Meconematinae, Pseudophyllinae, stridulatory field.

## INTRODUCTION

FEMALE sound production in ensiferan Orthoptera has evolved independently in the Gryllotalpidae (Petrunkevitch and von Guaita, 1901; Baumgartner, 1905, 1910; Tindale, 1928) and in the tettigoniid subfamilies Phaneropterinae (Fulton, 1933; Spooner, 1964, 1968), Pseudophyllinae (Caudell, 1906), Meconematinae (de Baillon, 1921), and Ephippigerinae (Duijm and van Oyen, 1948; Busnel *et al.*, 1954, 1955, 1956; Grzeschik, 1969). However, the morphology of the sound-producing structures and functions of the sounds produced have not been well studied. Probably this neglect has occurred because pair-forming songs of crickets and most katydids are produced by males only, and in those species in which females also produce sound, the sounds are usually non-repetitive and of such low intensity as to escape notice by most workers.

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Among the ensiferan Orthoptera, phaneropterine or bush katydids are unusual in that of the 16 species (six genera) that have been examined acoustically, both sexes produce pair-forming signals (Spooner, 1968; Nickle, personal observation). The signals produced by males can be complex (Walker and Dew, 1972), but the sounds of females consist only of one or a few brief ticks in response to the male sound. The only descriptions of female stridulatory apparatus of bush katydids have been by Petrunkevitch and von Guaita (1901), Fulton (1933), and Leroy (1971).

In this paper we compare for the first time the female sound-producing apparatus of five sympatric species of bush katydids and, using other species to substantiate the data, discuss the taxonomic value of these structures as possible characters for species identification. In addition, we review the present knowledge of sound production in female ensiferan Orthoptera. This study was originally intended to correlate morphology of female sound-producing apparatus with frequency characteristics of the sounds produced (Nickle, 1973), but no satisfactory explanation of frequency spectra of female signals in terms of morphology was discovered.

#### MATERIALS AND METHODS

Specimens of 5 sympatric species from Gainesville, Florida, *Amblycorypha floridana* Rehn and Hebard, *Microcentrum rhombifolium* Saussure, *Scudderia cuneata* Brunner, *S. furcata* Morse, and *S. texensis* Saussure and Pictet, were collected or reared from eggs. All of these species have been observed singing in Gainesville at the same place and the same time (Nickle, personal observation). *Scudderia texensis*, *S. furcata*, and *Microcentrum rhombifolium* are bivoltine in Gainesville; the specimens in this study were of the second generation. T. J. Walker (personal communication) reports only a single generation of *S. cuneata* in Gainesville between July and October. Adults of *Amblycorypha floridana* occur in Gainesville between May and October.

TABLE 1. CHARACTERISTICS OF FEMALE STRIDULATORY FIELDS OF SPECIES OF BUSH KATYDIDS (N=SAMPLE SIZE FOR EACH SPECIES)

Species	N	No. of transverse veins anterior to posterior field		Average No. of spines/row for central 3 rows		Length of transverse vein area/posterior field		Total length of field	
		$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
<i>Microcentrum rhombifolium</i>	10	6.4	0.89	17.1	2.80	0.82	0.12	7.8	0.65
<i>M. retinerve</i>	5	7.2	1.83	12.2	2.23	0.79	0.30	7.7	0.73
<i>Amblycorypha floridana</i>	10	6.2	0.63	16.8	3.43	0.84	0.18	6.3	0.66
<i>A. carinata</i>	6	7.7	1.50	18.3	3.60	0.93	0.16	7.9	0.60
<i>A. rotundifolia</i>	3	7.2	0.96	17.8	3.09	0.98	0.21	5.7	0.69
“rattler” 008*									
<i>A. rotundifolia</i>	1	6.0	—	18.0	—	0.97	—	6.1	—
“clicker” 001									
<i>A. rotundifolia</i>	3	6.0	1.41	22.7	2.73	1.26	0.13	6.4	0.21
“fast-clicker” 005									
<i>Montezumina modesta</i>	5	7.8	0.45	10.3	2.94	2.20	0.51	6.2	0.68
<i>M. sinaloae</i>	5	10.2	1.30	10.1	2.98	2.50	0.29	6.1	0.42
<i>M. granti</i>	5	8.4	1.14	10.0	2.58	2.00	0.29	5.4	0.23
<i>M. bradleyi</i>	5	7.8	2.16	7.1	1.96	1.60	0.22	4.8	0.36
<i>M. species near oridiops</i>	5	7.3	1.53	10.2	1.64	2.00	0.21	5.0	0.43
<i>Scudderia furcata</i>	10	9.5	1.08	9.7	2.72	2.02	0.28	5.4	0.65
<i>S. cuneata</i>	10	9.7	1.32	9.4	1.82	1.78	0.44	5.7	0.55
<i>S. texensis</i>	10	8.4	1.26	9.3	2.14	1.53	0.65	5.8	0.34

\* University of Florida Insect Communication and Biosystematics Laboratory species-song reference number.

For light microscope examination, tegmina of 10 females of each species were dry-mounted between two glass slides. Tegmina used in scanning-electron micrographs were removed from living specimens and mounted on silver base paint. A Denton DV-502 High Vacuum Evaporator was used to deposit 200–300 Å gold in the subject. Scanning-electron micrographs were made with a Cambridge Mark II A Scanning Electron Microscope at the Insect Attractants and Basic Biology Laboratory, USDA, Gainesville.

In addition to these species, the stridulatory fields of 10 other phaneropterine species were examined to determine the value of this structure as a character for species identification. Although no micrographs were made for these species, measurements are summarized in Table 1. The additional species included *Microcentrum retinerve* (Burmeister), which also occurs sympatrically with the five species of this study; five species of *Montezumina*: *modesta* (Hebard) from Florida, *bradleyi* (Hebard) from Panama, *sinaloae* Hebard from Mexico, *granti* Nickle from Costa Rica, and an undescribed species near *oridiops* (S. & P.) from Honduras; and four species of *Amblycorypha*: *carinata* Rehn and Hebard, *rotundifolia* (Scudder), and two undescribed species near *rotundifolia*. These taxa were selected because although they are distinct species, in some cases it is difficult to separate morphologically the females within each genus.

### OBSERVATIONS

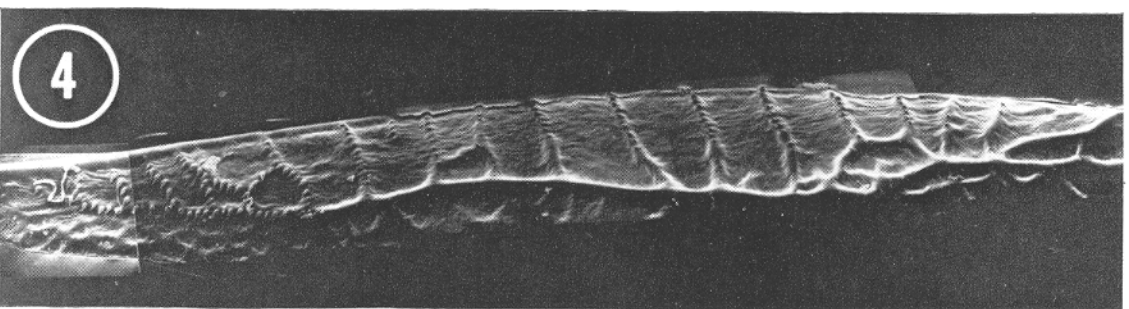
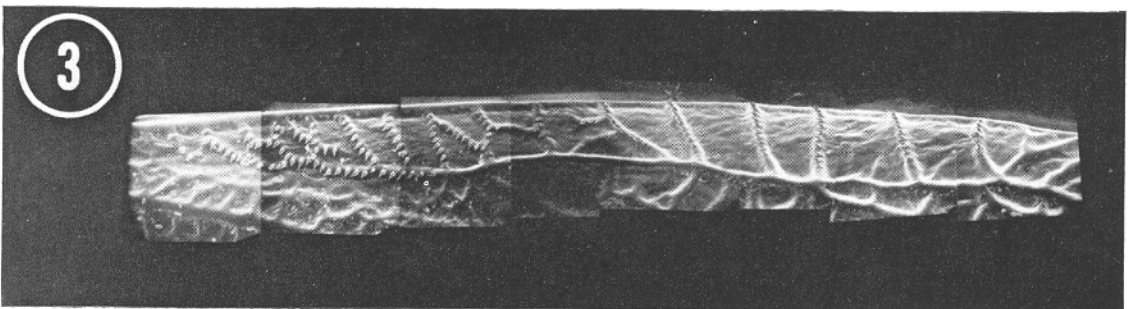
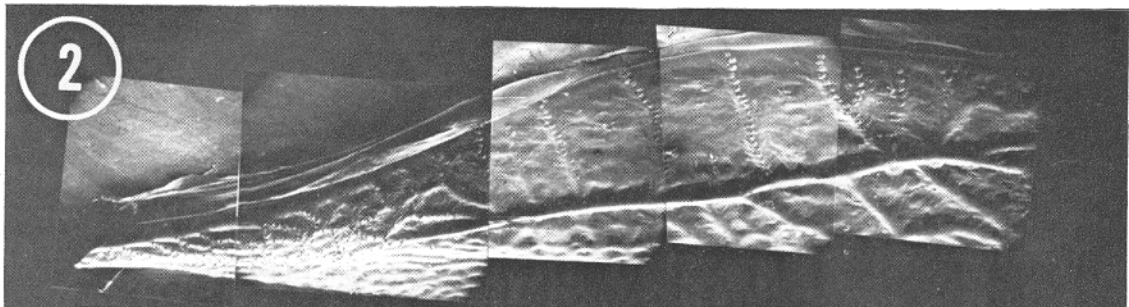
The female stridulatory field of bush katyids is a complex of stout curved spines on the dorsal surface of the anal area of the right tegmen. The arrangement is similar for all species except *Amblycorypha rotundifolia* (see below). A variable number of transverse veins located toward the base of the tegmen each bears 1–25 spines of similar shape and size. These spines are uniformly directed posteriorly (i.e. toward the apex of the tegmen), and their distal axes are parallel to the surface of the tegmen. Posterior to these transverse rows of uniformly oriented spines, and bordered by the distal half of the anal vein, is an area or field of many less-curved spines having no orderly arrangement. These spines point in a number of directions (through mainly abaxially), and their distal axes are parallel or at an acute angle to the surface of the tegmen. The scraper or surface that rubs across these spines is the sharpened anal margin of the left tegmen. This margin is thickened and curved downward, especially at the area overlapping the posterior field of spines. Scanning-electron micrograph montages of one female stridulatory field for the five sympatric species show some of the interspecific differences (Figs. 1–5).

Table 1 lists four diagnostic characteristics of female stridulatory fields. The number of transverse veins is determined by counting from the base of the field each vein that has at least one spine to the area where a latticed venation replaces the simple transverse veins. This latticed area is called the posterior field and is characterized in part by spines pointing in a number of directions. The ratio of the length of the tegmen occupied by the transverse veins to the length of the posterior field is determined by dividing the distance between the first and last transverse vein by the length of the posterior field.

### DISCUSSION

Although there is considerable intraspecific variation in the numbers of transverse veins and spines in each species, some generalizations may be made about interspecific differences of the female stridulatory fields.

*Microcentrum rhombifolium* has the most elaborate stridulatory field of the five species (Fig. 1). It averages seven transverse veins, has more spines on each vein than most other species, and many more spines in the posterior field than any of the other species. The transverse spines are also larger and often more bulbous at the base. The differences between spines from the transverse veins and from the posterior field are shown in Figs. 6 and 7,



FIGS. 1-5.

respectively. *Amblycorypha floridana* averages only six transverse veins (Fig. 2). Also, there is relatively more space between veins than occurs in *M. rhombifolium*. Figs. 8 and 9 show differences between spines from transverse veins and the posterior field. *Scudderia* species show the following interspecific differences: *texensis* averages fewer transverse veins than either *furcata* or *cuneata* (Figs. 3–5). Using Duncan's new multiple-range test on the ratios of the length of the area occupied by the transverse veins/posterior field area for the three species, it was found that *texensis* differed significantly ( $p = 0.05$ ) from *furcata* and *cuneata* but that the latter two species could not be separated at this level. The length of the spines on the transverse veins are longer in *cuneata* than in *furcata* (Figs. 10, 11).

As a character for identifying species, the female stridulatory field is limited, since all measured parameters overlap among the sympatric species studied. Although the field of *Scudderia texensis* can usually be distinguished from those of *furcata* and *cuneata*, the fields of the latter two species are often difficult or impossible to distinguish. However, since these two species are alike in many other characters as well, the fields of 10 other closely related species were compared to test the value of this structure.

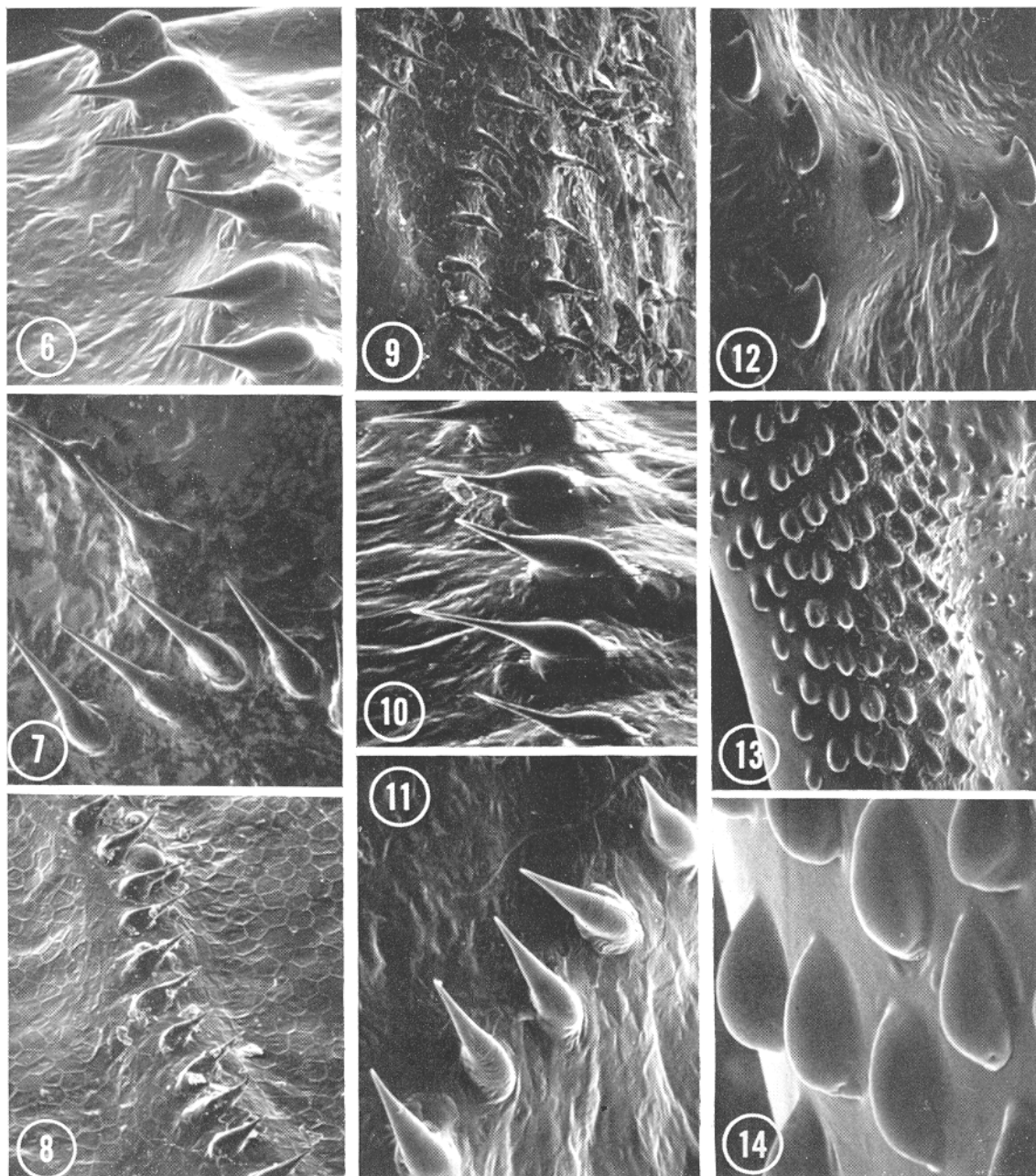
Within the genus *Amblycorypha*, two species complexes were examined. Comparing *carinata* and *floridana*, only one specimen of *carinata* ( $n = 6$ ) could not be distinguished from *floridana* ( $n = 10$ ) on the basis of a combination of the four field characters in Table 1. In the *rotundifolia* sibling group, *rotundifolia* ("fast clicker" 005) is easily distinguished from the other two species in that it has a latticed venation with spines both anterior and posterior to the rows of transverse veins. We could not identify females of *rotundifolia* "rattler" (008) or *rotundifolia* "clicker" (001) using their stridulatory fields.

*Microcentrum retinerve* averaged more transverse rows but fewer spines per row than *rhombifolium*. Only one specimen of *retinerve* ( $n = 5$ ) could not be distinguished from *rhombifolium*.

Of the five species of *Montezumina* examined, *sinaloae* and *bradleyi* were each easily separated from the other four species using the stridulatory field characters. *M. sinaloae* has more transverse rows than the other species, and the length of the transverse vein area is longer than the posterior area by at least 0.3 mm. *M. bradleyi*, which is a large species for the genus, has the smallest field and the smallest ratio of transverse row area/posterior field area of the five species. *M. modesta* differs from the other species in that its posterior field is reduced to two or three longitudinal rows of spines. *M. granti* and *M.* undescribed species near *oridiops* cannot be separated using their stridulatory fields.

This study suggests that although the female stridulatory field alone cannot be used to identify all species, some species can be identified, using this structure. For example, this character is used successfully to separate *Amblycorypha rotundifolia* (005) from its two sibling species, "rattler" (008) and "clicker" (001). It has been speculated that many of the known species of katydids have sibling species complexes, with well-defined behavioral differences but usually few morphological characters to identify them (Walker, 1964). Examination of the female stridulatory fields may reveal differences in some of these sibling complexes where more conventional characters fail.

FIGS. 1–5. Scanning-electron micrographs of female stridulatory fields on dorsal surface of anal area of right tegmen of bush katydids (attachment of the tegmen is to right): 1. *Microcentrum rhombifolium*,  $\times 13.2$ ; 2. *Amblycorypha floridana*,  $\times 16.8$ ; 3. *Scudderia furcata*,  $\times 16.3$ ; 4. *S. cuneata*,  $\times 20.3$ ; 5. *S. texensis*,  $\times 16.4$ .



FIGS. 6-14. Scanning-electron micrographs of ultrastructure of female stridulatory apparatus of katydids: 6. spines from center transverse vein of stridulatory field, *Microcentrum rhombifolium*,  $\times 246$ ; 7. spines from posterior field, *M. rhombifolium*,  $\times 254$ ; 8. center transverse vein of stridulatory field, *Amblycorypha floridana*,  $\times 89$ ; 9. spines from posterior field, *A. floridana*,  $\times 90$ ; 10-11. spines from center transverse vein of stridulatory field; 10. *Scudderia cuneata*,  $\times 353$ ; 1. *S. furcata*,  $\times 353$ ; 12-14. female stridulatory apparatus of *Pterophylla camellifolia*; 12. teeth on ventral surface of left tegmen,  $\times 237$ ; 13. scraper or anal margin of right tegmen,  $\times 109$ ; 14. same,  $\times 531$ .

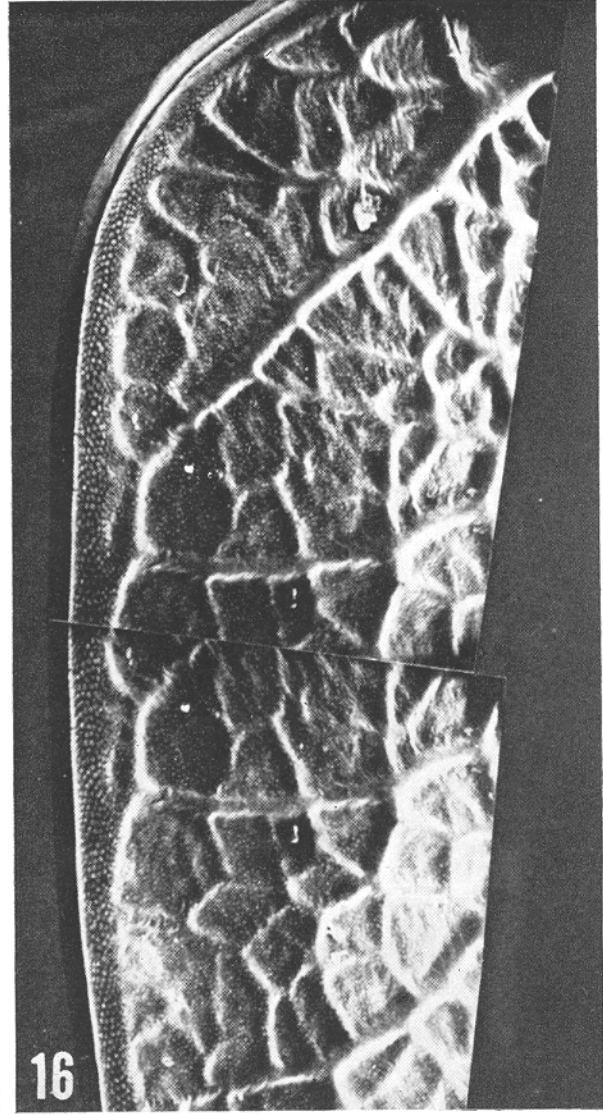
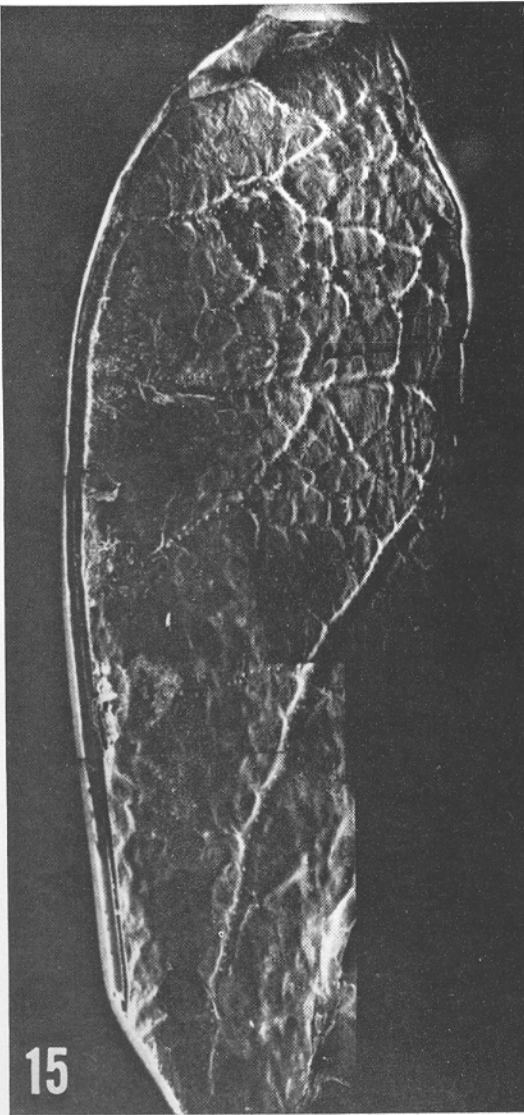


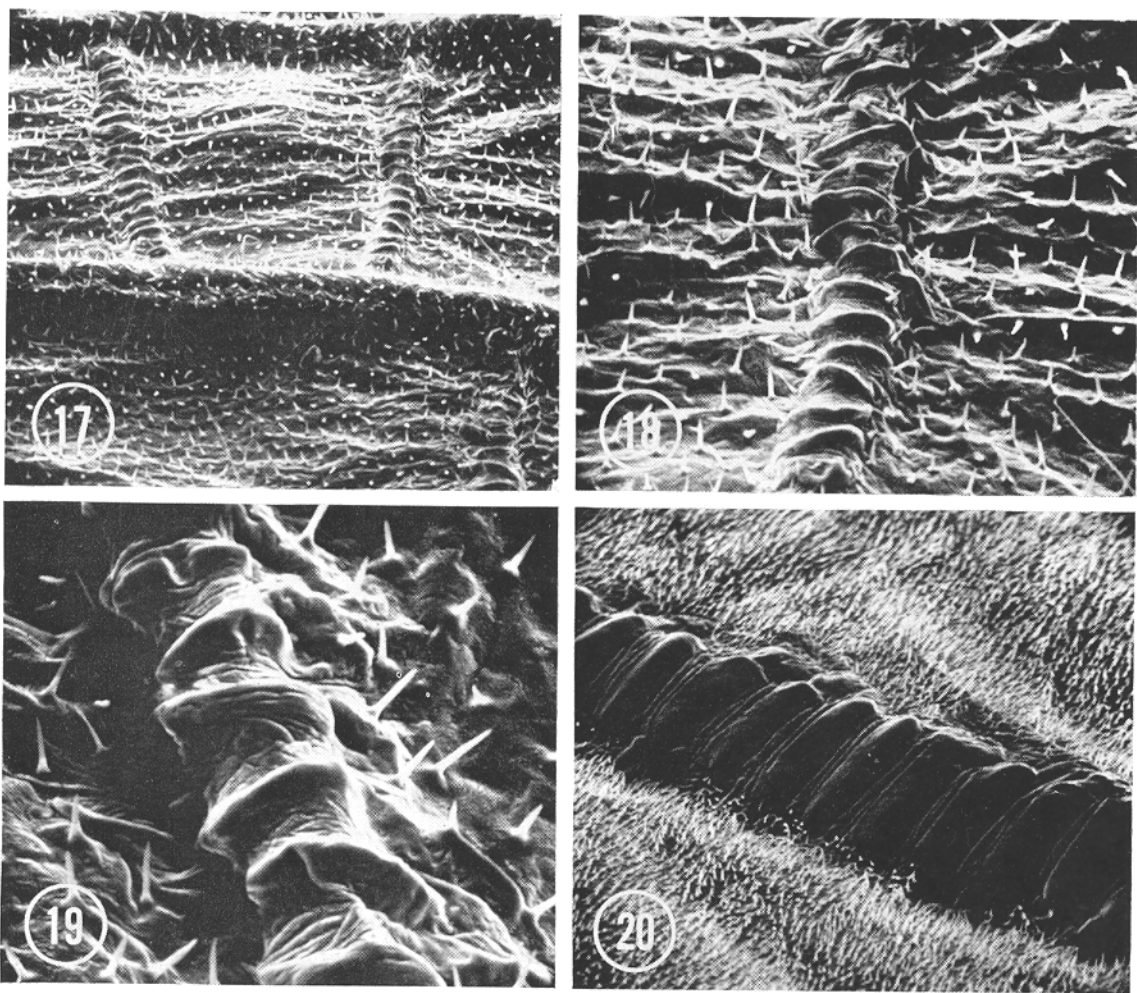
FIG. 15. Scanning-electron micrograph montage of ventral surface of left tegmen, *Pterophylla camellifolia* female, showing spatial distribution of teeth,  $\times 38$ .

FIG. 16. Scanning-electron micrograph of dorsal surface of right tegmen, showing anal margin or scraper *Pterophylla camellifolia* female,  $\times 22$ .

Among the phaneropterine katydids, female sounds are produced in response to pair-forming signals of conspecific males and serve to facilitate pair formation by attracting calling males (Spooner, 1964). How might the female stridulatory apparatus have evolved? Enhancement of the spines on the dorsal surface of the female tegmina could have evolved prior to the evolution of sound production as an improvement for holding the tegmina together in repose. Tegmina held fast together to maintain a foliage-like appearance, even when pecked at by birds or lizards or blown by stiff breezes, would have obvious selective

value, and selection would favor enhancement of spines. Evidence that these spines might have evolved in this context is found in females of other katydids such as *Neoconocephalus triops* (Copiphorinae) and species of *Orchelimum* (Conocephalinae) (Fulton, 1933; Nickle, personal observation). Females of these species have spines on the posterior field similar to those of phaneropterine katydids but the spines are somewhat smaller and not recurved, and no sound is produced. Male phaneropterine katydids also have posterior field spines but produce no sound with them.

Even less is known of the origin or function of female sound production in the Gryllotalpidae and the tettigoniid subfamilies Pseudophyllinae, Meconematinae, and Ephippigerinae. Baumgartner (1905, 1910) reported that females of *Gryllotalpa borealis* (probably *Neocurtilla major*) and of *Scapteriscus didactylus* (= *S. vicinis*) have the same kind of stridulatory apparatus as their males, although "much smaller and weaker". Tindale (1928)



FIGS. 17-19. Scanning-electron micrographs of transverse veins on dorsal surface of left tegmen of *Gryllus rubens* female; 17. transverse veins,  $\times 189$ ; 18. same,  $\times 378$ ; 19. same,  $\times 756$ .

FIG. 20. Scanning-electron micrograph of transverse vein on dorsal surface of left tegmen of *Scapteriscus acletis* female,  $\times 700$ .



listed five Australasian species of *Gryllotalpa* in which females had stridulatory files similar in structure to male files: *nitidula* Servile, *oya* Tindale, *gryllotalpa* L., *africana* Palisot de Beauv., and *pilosipes* Tindale. We examined two female *Gryllotalpa* specimens: one *gryllotalpa* from New Jersey and one undetermined species from Belle Glade, Florida. We also examined two females of *Neocurtilla major* from Vernon, Missouri. All four specimens had stridulatory files on the ventral surfaces of the right tegmina. No males were available for size comparison. Female *Neocurtilla hexadactyla* from southeastern United States do not have stridulatory files, nor do *Scapteriscus aetetus* or *S. vicinus*. However, on the dorsal surface of the left tegmen of *Scapteriscus* species there are numerous cross-veins with a peculiar laminated ultrastructure reminiscent of the teeth on a stridulatory file (Fig. 20). These structures also occur on the tegmina of *Gryllus* females (Figs. 17–19). Though no one has tape-recorded sounds from female *Gryllus* species, Ulagaraj (1974) has tape-recorded females of *Scapteriscus vicinus* producing sounds. Twenty females were placed in a small plastic box (10 × 20 × 30 cm) with some soil. Occasionally a female that was confronted by another female produced clearly audible sounds by rubbing the tegmina together.

Fulton (1933) described a sound-producing structure on females of *Pterophylla camellifolia* (Pseudophyllinae) quite unlike the structure found in bush katydids. On the under-surface of the anal area of the left tegmen is a network of veins bearing many short ridges or teeth, all directed parallel to the length of the tegmen (Fig. 15 and 16). The anal margin of the underlying right tegmen is thickened and well rounded above and is armed for most of its length with very small but prominent knobs arranged in regular diagonal rows (Figs. 12–14). Fulton also mentioned that in *P. camellifolia* there are spines similar to those of the phaneropterine katydids although they are fewer in number and scattered. The three specimens from New York that we examined lacked any spines on the dorsal surface of the right tegmen.

Females of the species of *Ephippiger* have well-defined stridulatory files on the dorsal surface of the right tegmen (Sellier, 1970). The scraper is the anal margin of the left tegmen and is thickened and recurved ventrally.

Females of species of *Meconema* have stout spines on both the dorsal surface of the right tegmen and the ventral surface of the left tegmen. These supposedly rub across each other, producing sound (de Baillon, 1921).

No function of female sound production has been demonstrated in most groups mentioned. Baumgartner (1905, 1910) concluded that the chirp of female mole crickets (*Gryllotalpa borealis*) is a recognition sound evolved as an adaptation to underground subsocial life. Tindale (1928) reported caged females of *Gryllotalpa oya* producing sounds apparently in response to calling songs of nearby males. He presented no evidence to confirm such a dialogue, however. Ulagaraj (personal communication) speculated that *Scapteriscus vicinus* females produce sounds as part of aggressive behavior. Zhantiev and Korsunovskaya (1973) reported the only example of female ensiferan Orthoptera producing more than one kind of sound. They analyzed sounds produced by both sexes of *Gryllotalpa gryllotalpa* and *G. unispina*. Females of these species produce 2 kinds of sounds: territorial and threatening. Territorial sounds of females of *G. unispina* are 5-pulsed, produced at a rate of 17 p/s. They have a narrow frequency spectrum (0.5–4 kHz) centered at 1 kHz. Threatening sounds consist of a single tick of 50 msec duration with a broad frequency spectrum (0–35 kHz) having 2 energy peaks at 3.5 and 16–18 kHz.

Caudell (1906) presumed the sounds of female pseudophylline katydids to be disturbance signals only, perhaps of use in startling vertebrate predators. Busnel and Dumortier (1954)

found that female ephippigerine katydids produce sounds when a male produces a sound nearby or when any insect lands on the branch on which she is resting. These sounds presumably act at close range to finalize contact between sexually responsive pairs. No one has reported upon the function(s) of sound produced by females of meconematine katydids.

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