STRIDULATORY FILE TEETH IN CRICKETS: TAXONOMIC AND ACOUSTIC IMPLICATIONS (ORTHOPTERA: GRYLLIDAE)

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Abstract—The file teeth of crickets show pronounced interspecific differences. Twenty-four species, representing eight subfamilies, were examined to determine whether such differences reflect differences in acoustic function. We found no relation between particular tooth structures and particular features of the calling song; however, such structures correlated with the major phyletic divisions of crickets.

Index descriptors (in addition to those in title): Ensifera, calling songs.

INTRODUCTION

Male crickets make their species-specific calling songs with specialized forewings. During calling, these tegmina are elevated and rubbed together. During each closing movement a portion of the anal edge of the left tegmen (the *scraper*) engages a toothed vein (the *file* or *pars stridens*) on the underside of the right tegmen resulting in a pulse of sound. Each pulse approximates a pure tone of the same frequency as the tooth-contact rate. Opening movements are silent. The pulses are produced at a temperature-dependent rate and may be grouped in simple or complex patterns (Walker, 1962b; Alexander, 1962). Calling songs differ among species in their carrier frequency, pulse rate, and pulse grouping. Within a genus or subgenus, the length of the stridulatory file and the number of file teeth are generally inversely correlated with pulse rate (Walker, 1963). No other correlations between file structure and calling song parameters are known, but when we discovered large and elaborate interspecific differences in file tooth structure, we undertook to systematically search for additional correlations. Such correlations could give clues to the physics of sound production, and provide ways to predict the songs of species known only from museum specimens.

MATERIAL AND METHODS

Three species from each of the eight major subfamilies of crickets were selected for their taxonomic and acoustic diversity (Table 1). Stridulatory files were cut from dry or alcohol-preserved specimens, attached to specimen stubs with silver-based paint, placed in a high-vacuum evaporator, and coated with a 200Å. layer of gold. The gold-coated files were studied and photographed with a scanning electron microscope

TABLE. 1. MAJOR SUBFAMILIES OF CRICKETS AND SPECIES EXAMINED, WITH NUMBER OF TEETH IN THE STRIDULATORY FILE AND CHARACTERISTICS OF THE CALLING SONGS

Subfamily Species	Locality	Number of file teeth*	Calling song at 25C†	
			Carrier frequency	Pulses/sec
Gryllotalpinae (2–3; 3–5)‡		25–95	1·7–3·1	60–135
Neocurtilla hexadactyla	Gainesville, Fla.	25	2·0	75
Scapteriscus abbreviatus	Lake Worth, Fla.	92	none	none
S. vicinus	Alachua Co., Fla.	66	3·1	135
Mogoplistinae (1–9; 2–30)		62–180	6·4–7·8	4–130
Cycloptilum antillarum	Dade Co., Fla.	70	7·5	102
C. bidens	Gilchrist Co., Fla.	75	6·7	54
C. trigonipalpum	Lowndes Co., Ala.	88	7·4	57
Trigonidiinae (3–23; 3–36)		69–485	5·3–7·3	6–92
Anaxipha latipennis	Jamaica, West Indies	485	6·0	12
Cyrtoxipha confusa	Dade Co., Fla.	88	7·1	92
Phyllopalpus pulchellus	Gainesville, Fla.	101	7·2	60
Oecanthinae (3–41; 3–21)		17–90	2·6–4·0	41–112
Neoxabea bipunctata	Licking Co., Ohio	22	3·3	112
Oecanthus exclamationis	Franklin Co., Ohio	17	2·8	81
O. quadripunctatus	Brown Co., Ohio	57	3·9	41
Eneopterinae (3–24; 4–29)		16–140	4·0–6·4	14–245
Hapithus agitator	Bradenton, Fla.	42	4·6	107
Orocharis diplastes	Tavernier, Fla.	135	5·8	14
O. gryllodes	Dry Tortugas, Fla.	27	5·8	212
Gryllinae (12–41; 16–49)		40–330	3·0–7·2	9–180
Anurogryllus arboreus	Alachua Co., Fla.	70	5·5	77
Gryllus ovisopis	Alachua Co., Fla.	141	none	none
G. rubens	Alachua Co., Fla.	103	4·8	56
Phalangopsinae (1–3; 1–5)		89–193	4·4–5·5	35–95
Amphiacusta sp. A	Haiti, West Indies	193	5·5	43
Amphiacusta sp. B	Haiti, West Indies	89	—	—
Amphiacusta sp. C	Dominican Republic, W.I.	98	5·1	95
Nemobiinae (3–14; 5–20)		20–228	5·0–9·4	8–99
Allonemobius fasciatus	Duval Co., Fla.	127	9·4	99
Eunemobius carolinus	Clay Co., Fla.	54	6·6	90
Hygronemobius alleni	Dade Co., Fla.	46	5·0	29

* For the subfamilies the extremes are given, and for the species either the mean for 2 or more files or the number of teeth in a single file is given. Data are from many sources including Leroy, 1966; Nickle and Walker, 1974; Vickery and Johnstone, 1973; Walker, 1962a, 1963, 1967, 1969a, 1969b, 1973.

† For the subfamilies the extremes of mean values are given, and for species mean values are given. Data are from many sources but mostly from Walker (unpublished). Pulses/sec refer to the rate during the most rapidly delivered pulse sequences within the calling song.

‡ Numbers in parentheses show the size of the sample that the subfamily values are based on: (no. of genera—no. of species for file data; no. of genera—no. of species for calling song data).

OBSERVATIONS

The teeth within a stridulatory file were similar in structure except for a few teeth at either end [Fig. 6(a)]. Individuals of the same species had almost identical file teeth, but individuals of different species often had dramatic differences in their file teeth (Figs. 1–16). These differences did not correlate with differences in carrier frequency, wingstroke rate, or pulse grouping of the calling song (Table 1 and below). In fact, species with very dissimilar

file teeth sometimes had nearly identical calling songs, and species with very similar file teeth often had widely divergent calling songs. The major differences in tooth structure correlated with the major phyletic divisions that have been established on the basis of comparisons of other features of crickets. It may prove possible to identify most crickets to subfamily solely on the basis of file tooth structure. File tooth structure in the eight subfamilies is discussed below.

Mogoplistinae (Scaly Crickets) [Figs. 1(a), (b) and (c)]. The three species examined represent both major groups of U.S. *Cycloptilum: antillarum* and *bidens* pair their pulses while *trigonipalpum*, like other species of its group, produces pulses in uniform sequences. Mogoplistine file teeth have greater width-to-height ratios than species of other subfamilies that have teeth without attenuated wings (i.e. without thin lateral extensions like those in Figs. 11, 14 and 15).

Trigonidiinae (Sword-Tailed Crickets) [Figs. 3(a) and (b); 4(a) and (b) and 5(a) and (b)]. The three species studied belong to different genera and have divergent pulse rates (Table 1). In *Anaxipha latipennis* the pulses are produced evenly, in *Cyrtoxipha confusa* they are paired (Walker, 1969b), and in *Phyllopalpus pulchellus* they are produced in small non-uniform groups (Walker, 1962b). In each case the teeth are thin and sharp-edged. *A. latipennis* has the most file teeth known for any cricket—Fig. 3(a) shows a portion of a 485–tooth file.

Oecanthinae (Tree Crickets) [Figs. 6(a) and (b); 7(a) and (b) and 8]. The species studied are from two of the three genera and represent two of the species groups in *Oecanthus*. Their songs vary substantially in carrier frequencies and pulse rates (Table 1). The teeth are thick and their rims are grooved longitudinally.

Eneopterinae (Bush Crickets) [Figs. 9(a) and (b) and 10(a) and (b)]. The 2 species of *Orocharis* studied show maximal differences in their calling songs (Table 1 and Walker, 1969a). The northern populations of *Hapithus agitator* produce no calling song. Eneopterine file teeth resemble those of oecanthines, and the two subfamilies are closely related. The teeth of *O. diplastes* and *H. agitator* (southern population) have longitudinal grooves in the rims, but *O. gryllodes* lacks such grooves.

Gryllotalpinae (Mole Crickets) [Fig. 2(a) and (b)]. We examined representatives of both North American genera and of the only species of mole cricket known to lack a calling song (Table 1). The teeth of the three species are very similar—thick, without grooves in the rim, and without wings.

Gryllinae (Field and House Crickets) [Figs. 11(a) and (b) and 12(a), (b) and (c)]. One of the two species of *Gryllus* studied is the only *Gryllus* known to lack a calling song (Table 1). *Anurogryllus* has sometimes been placed in the subfamily Brachytrupinae, but Walker (1973) concluded that it is a grylline. The two species of *Gryllus* have similar file teeth—nearly straight across the crest and with conspicuous wings [Fig. 11(a)]. The file teeth of the house cricket, *Acheta domesticus*, as illustrated by Sellier (1969) and Popov (1971), have the same appearance. The file teeth of *Anurogryllus arboreus* [Fig. 12(a), (b) and (c)] are conspicuously different from those of *Gryllus* spp. and *A. domesticus*. They lack wings and generally resemble the file teeth of Eneopterinae.

Phalangopsinae (Long-Legged Crickets) [Figs. 13(a) and (b) and 14(a) and (b)]. The three species studied were of the genus *Amphiacusta*. The crests of the file teeth vary from convex to straight to concave, but all have the sclerotized portion of the crest much broader than the base. The wings are prominent.

Nemobiinae (Ground Crickets) [Figs. 15(a), (b) and (c) and 16(a) and (b)]. We studied three species representing three genera and having widely varying calling songs (Table 1).
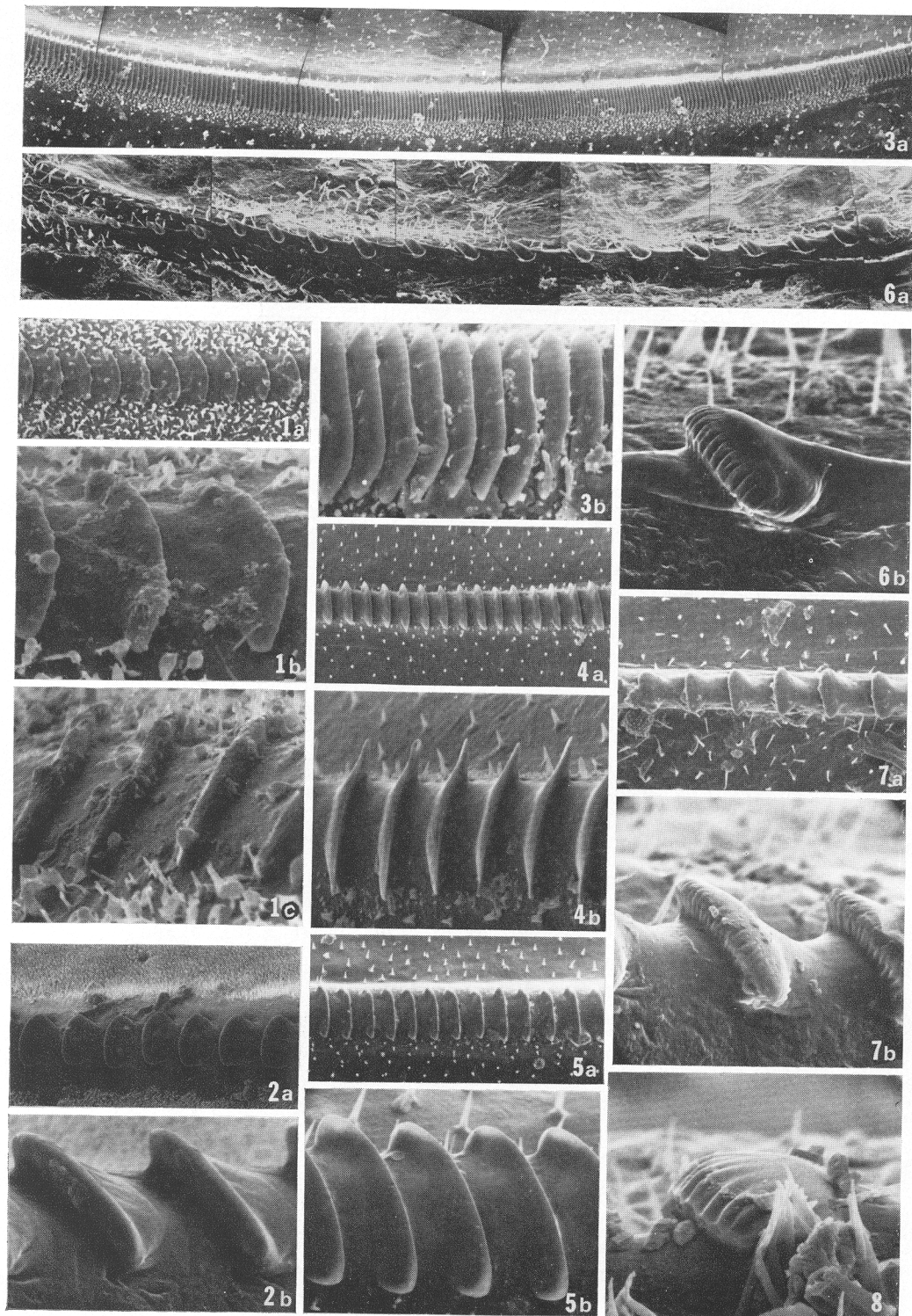
Figs. 1–8.

Sellier (1969) illustrated the file teeth of *Nemobius sylvestris*, which represents a fourth genus. The teeth of the four species are similar in being thin with convex crests and having well-developed wings.

DISCUSSION

The lack of correlation between details of tooth structure and any of the acoustic parameters measured does not deny the importance of the teeth in the production of the calling song, nor does it even prove that the details of tooth structure aren't important to particular aspects of the calling songs. Very different specializations may evolve independently in relation to the same function—compare the scales of moths, the body feathers of birds, and the fur of mammals in relation to homeothermy. Similarly the achievement of the same special features of calling songs could have occurred several times in cricket evolution with different morphological correlates each time.

The most direct way to determine whether particular features of the file teeth have acoustical effects is to modify the file or to substitute one file for another. If the crickets do not sing after such operations, the tegmina can be excised and mechanically driven (Bailey and Broughton, 1970). Another means of investigation would be to build and mechanically drive physical models of tegmina.

Some other aspects of possible acoustic function of file teeth specializations and of grosser features of the file deserve mention: (1) Most male crickets make courtship and aggressive songs that are quite different from their calling songs. Some of the features of the teeth may function in producing these other songs. (2) Some features of the teeth may be essential or important to sound production in ways that do not influence the quality of the sound produced—they may merely make possible or easy the production of whatever song is determined by other features of the mechanism. For instance, crickets that produce intense or long-continued songs might be expected to have tougher, better-buttressed teeth; crickets that produce much frictional heat during stridulation might be expected to have structures that would aid in radiating the heat or increasing air flow; etc. Comparative studies of the biophysics of cricket sound production are needed to give substance to this sort of speculation. Nocke (1971) discussed the few (non-comparative) studies done so far.

Number and density of file teeth are features that may have acoustical consequences. (3) The number of teeth in the file varies from 16 to 485. Since the number of sine waves in the pulse is apparently limited to the number of teeth in the file, the duration of the pulse at a given carrier frequency is limited by the number of teeth in the file. For instance, with 25 teeth and a frequency of 5 kHz the pulse could last only 5 msec, but with 250 teeth it could last 50 msec. Although the variation is great, most crickets make sound during at least 50% of the time they are moving their wings—i.e. the closing stroke occupies at least

FIGS. 1–8. Central portions of stridulatory files of crickets. (All files with ventral surfaces up. Acoustically effective stroke of scraper is against grain of teeth.) Fig. 1. Mogoplistinae. *Cycloptilum bidens*. a. ×400, b. and c. ×1600. Fig. 2. Gryllotalpinae. *Scapteriscus abbreviatus*. a. ×250, b. ×1000. Figs. 3–5. Trigonidiinae. 3. *Anaxipha latipennis*. a. Approximately two-fifths of file. ×173, b. ×1000. 4. *Cyrtoxipha confusa*. a. ×250, b. ×1000. 5. *Phyllopalpus pulchellus*. a. ×250, b. ×1000. Figs. 6–8. Oecanthinae. 6. *Oecanthus exclamationis*. a. Entire file. ×145, b. ×1000. 7. *O. quadripunctatus*. a. ×250, b. ×1000. 8. *Neoxabea bipunctata* ×1500. Figs. 1, 3–5. End of file nearest anal margin is to right (i.e., scraper moves from right to left during sound production). Figs. 2, 6–8. Anal end of file is to left. Figs. 1(a), 2(a), 3(a), 4(a), 5(a), and 7(a). Axis of view approximately 90° to dorsal field of tegmen. (Other figures are at other viewing angles selected to reveal additional details of tooth structure).
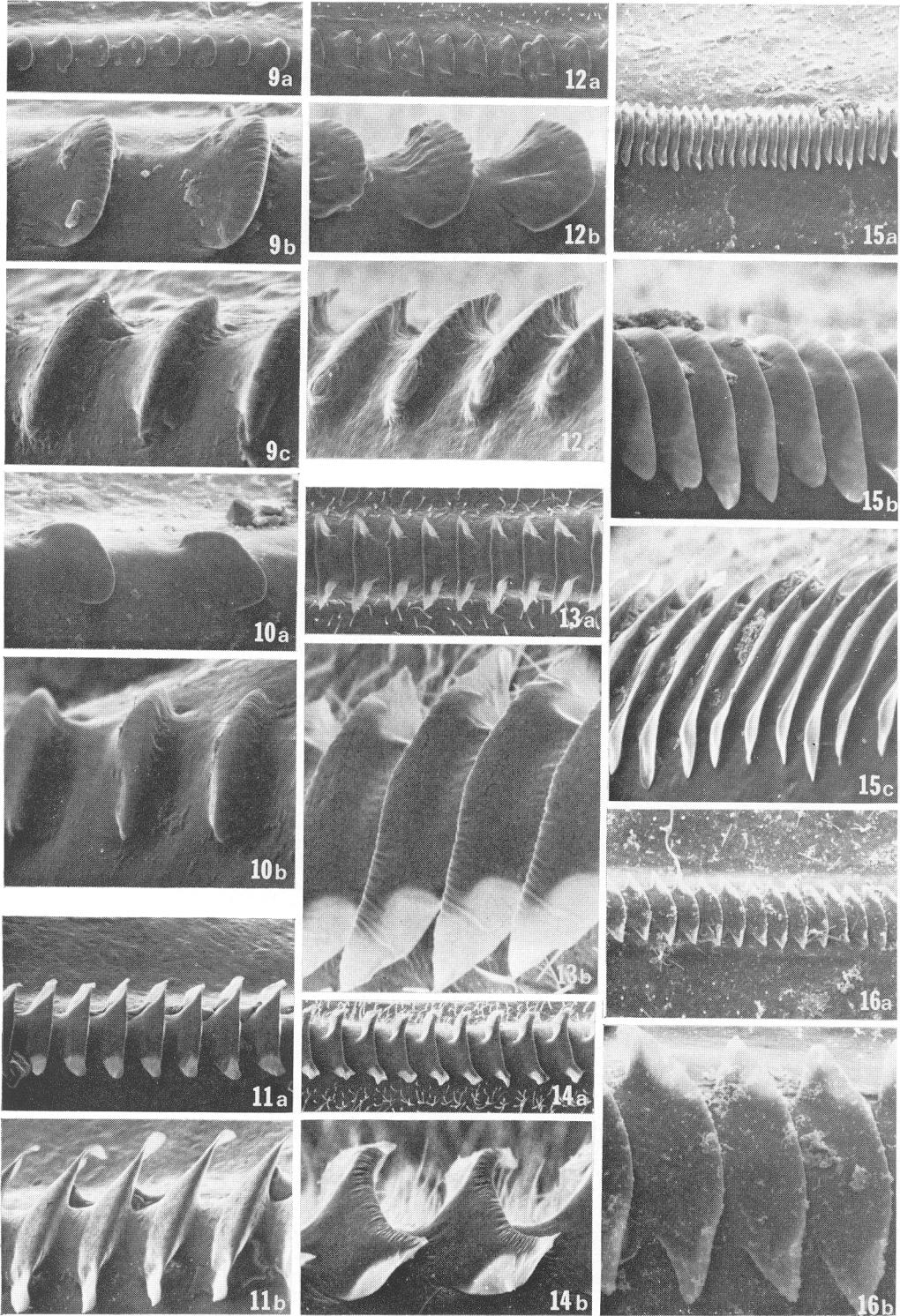
50% of the total time of a pulse-producing cycle of wing movement. Consequently, files with more teeth are correlated with songs with slower pulse rates (i.e. fewer cycles of wing movement per second, but more fundamental oscillations per tegminal closure). Complicating the relation of number of teeth to pulse duration is that in at least a few crickets less than half of the file is used during calling (e.g. *Gryllus veletis*, Rakshpal, 1960). (4) The tooth density (i.e. number of teeth per mm of file) is another feature of the file that varies immensely. For instance the files of *Anaxipha latipennis* and *Oecanthus exclamationis* [Figs. 3(a) and 6(a)] have 173 and 19 teeth/mm respectively. Since the carrier frequencies of their songs are 6·0 and 2·8 kHz, the scraper (relative to the file) must move at a speed of 35 mm/sec in *A. latipennis* and 147 mm/sec in *O. exclamationis*. Obviously, carrier frequency and pulse duration are correlated with number and spacing of the file teeth and the distance and speed of movement of the scraper.

Katydids (Tettigoniidae) are closely related to crickets and produce sounds by tegminal stridulation. Sellier (1969) and Anstee (1971) illustrated the files of six species of five sub-families of katydids, and Leroy (1970) compared the stridulatory files of 27 species of a single subfamily. The three authors documented astonishing diversity in file structure, but none discussed the relationships of the different structures to acoustic function. Bailey and Broughton (1970) and Morris and Pipher (1972) summarize what is known of such relationships in Tettigoniidae.

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FIGS. 9–16. Central portions of stridulatory files of crickets. (All files with ventral surfaces up. Acoustically effective stroke of scraper is against grain of teeth.) Figs. 9–10. Eneopterinae. 9. *Hapithus agitator*. a. ×250, b. and c. ×1000. 10. *Orocharis gryllodes*. a. ×500, b. ×1000. Figs. 11–12. Gryllinae. 11. *Gryllus ovisopis*. a. ×250, b. ×500. 12. *Anurogryllus arboreus*. a. ×125, b. and c. ×500. Figs. 13–14. Phalangopsinae. 13. *Amphiacusta* sp. C. a. ×250, b. ×1000. 14. *Amphiacusta* sp. B. a. ×125, b. ×500. Figs. 15–16. Nemobiinae. 15. *Allonemobius fasciatus*. a. ×250, b. and c. ×1000. 16. *Eunemobius carolinus*. a. ×250, b. ×1000. Figs. 9–12, 14–16. End of file nearest anal margin is to right. Fig. 13. Anal end of file is to left. Figs. 9(a), 11(a), 12(a), 13(a), 14(a), 15(a) and 16(a). Axis of view approximately 90° to dorsal field of tegmen. (Other Figs. at other viewing angles).

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