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Vibrational communication in Cercopoidea and Fulgoroidea (Homoptera: Cicadina) with notes on classification of higher taxa

Вибрационная коммуникация Cercopoidea и Fulgoroidea (Homoptera: Cicadina) с замечаниями по систематике высших таксонов

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KEY WORDS: Cercopoidea, Aphrophoridae, Fulgoroidea, Delphacidae, Cixiidae, Issidae, Caliscelidae, Cicadidae, Cicadina, planthoppers, froghoppers, taxonomy, signals, bioacoustics, vibrational communication.

КЛЮЧЕВЫЕ СЛОВА: Cercopoidea, Aphrophoridae, Fulgoroidea, Delphacidae, Cixiidae, Issidae, Caliscelidae, Cicadidae, Cicadina, пенницы, таксономия, сигналы, биоакустика, вибрационная коммуникация.

ABSTRACT. Oscillograms and descriptions of vibrational signals of 69 species of Cercopoidea and Fulgoroidea (Homoptera) totally from 10 families and also, oscillograms of sounds of 6 species of Cicadidae are presented. In 7 species, acoustic communication during mating behaviour is studied, in 6 ones signals of individuals from two localities remote from each other are investigated. Taxonomic status and relationships of certain taxa studied are discussed basing on bioacoustic characters.

РЕЗЮМЕ. Приведены осциллограммы и описания вибрационных сигналов 69 видов Cercopoidea и Fulgoroidea (Homoptera) из 10 семейств, а также осциллограммы звуков 6 видов Cicadidae. У 7 видов изучена акустическая коммуникация при половом поведении, у 6 видов исследованы сигналы особей из двух географически удаленных точек. На основании биоакустических признаков обсуждаются таксономический статус и родственные связи ряда таксонов.

Introduction

The fact that not only large singing cicadas (Cicadidae) but also, all other Cicadinea, so called small Auchenorrhyncha, produce highly elaborate acoustic signals became widely known after publication of the monograph by Ossiannilsson [1949]. Nevertheless, until recently there were very few if any data on vibrational signals of the representatives of the most part of families, subfamilies and tribes of this group. Almost all articles available contain oscillograms and descriptions of signals of one or several closely related species from 1–2 genera. It is evident, that both temporal pattern and a set of functional types of signals (repertoire) sometimes are quite unlike in different species, but the data existing are too insufficient for any conclusions. For this reason, more than ten years ago I have started comparative investigation of vibrational signals of small Auchenorrhyncha. Data on about 200 species of Membracoidea from the territory of Russia and adjacent countries were published recently [Tishechkin, 2000, 2001, 2003]. In the present paper acoustic signals of 15 species of Cercopoidea, 54 species of Fulgoroidea and of 6 Cicadidae species are described and illustrated by oscillograms on different speeds. Such conclusions concerning taxonomic status and relationships of taxa studied as can be done basing on this material are presented.

References on existing works on bioacoustics of one or another group are given after descriptions of signals in respective taxa. Description of methods of recording and analysis of signals as well as explanation of main bioacoustic terms are given in Tishechkin [2000]. Therefore, only brief comments concerning terminology are given below.

Calling signals are spontaneously produced by male when ready to copulation for attraction of female. As a rule, male does not demonstrate any specific behaviour when producing signals of this type, unless receptive female presents on the same plant.

Reply signals are produced by receptive female in reply to calling male. Occasionally, virgin females after certain time span begin to sing spontaneously.

Courtship signals. Signals produced by male occurring in close proximity with female and demonstrating courtship behaviour. The term is used only for signals differing distinctly in temporal pattern from calling ones. In certain species male emits the same signal both spontaneously and on all stages of mating behaviour. In such case I refer this signal as calling.

Copulatory signals. Signals produced by male on the last stage of courtship behaviour when mounting female, usually, at the moment of joining of genitalia of male and female or/and during copulation. As in the previous case, the term is used only for signals differing in structure from calling and courtship ones. It must be noted, that Booij [1982] distinguishes precopulatory and copulatory signals in *Muellerianella* species (Delphacidae).

Territorial signals. Signals with rather simple and variable structure, sometimes are similar in different species. Produced either by single individuals, or by several ones sitting on the same stem. As a rule, were registered in males, but in certain species present also in females. Evidently, play substantial role in regulation of distance between individuals on the plant. Not rarely insect producing these signals sits stationary not demonstrating any specific activity. For this reason in certain cases territorial signals are not easy to distinguish from calling ones.

Rivalry signals. Usually produced by males demonstrating competition behaviour in close proximity with each other. In contrast with territorial ones, these signals were never registered from single males. Among species studied were recorded in repertoire of some Aphrophoridae, Delphacidae and Caliscellidae. Occasionally, precede direct attacks and attempts to push adversary from the stem.

Call of distress. Produced by individuals of both sexes in various dangerous and stress situations, e.g. when seized by hand.

Continuous signal. Prolonged trill of uniform pulses, lasting occasionally for many minutes without breaks. Recorded in certain species of singing cicadas (Cicadidae) only. Sounds as incessant monotonous high noise for human ear. Signals of this type are almost indistinguishable in different species. Usually, singing male alternates portions of continuous signal with calling one. Function of the signals is obscure.

For elements of temporal structure of acoustic signals the following terms are used.

Pulse is a brief elementary fragment of signal (or succession of sine waves) with fast increase and following decrease of amplitude, i.e. separated from similar fragments by amplitude minimums.

Short fragments with constant temporal pattern usually repeating with regular intervals and consisting of uniform or different pulses are referred as **syllables** (= chirps, rolls in Booij, 1982, = series in Russian literature on bioacoustics of insects, ≈ syllables in literature on bioacoustics of Acrididae (Orthoptera), for instance, in Ragge, 1987; Bukhvalova, Vedenina, 1999). Long trains of uniform pulses repeating with constant period are **trills**. Succession of similar or different syllables, or even any more or less prolonged signal with complex structure (e.g. combination of several syllables and a trill) having determinable beginning and end is usually referred as **phrase**.

Diversity of temporal pattern of signals in small Auchenorrhyncha is exceedingly great, so sometimes it is impossible to refer every part of signal as pulse, syllable or trill with certainty. In such situations I prefer to use neutral terms (“fragment”, “succession”, “component”, etc.). Besides, the best and most adequate method of description of vibrational signals of Cicadinea is presenting of sufficient number of oscillograms on different speeds.

Superfamily CERCOPOIDEA

Family Cercopidae

Cercopis vulnerata Rossi, 1807
Figs 1–11.

LOCALITIES. Moscow Area: (1) environs of Zvenigorod Town, meadows on bank of Moskva River near Lutsyno Village, 8–9.VI.1984, signals of more than 10 ♂♂ are recorded at the temperature 23–24°C; (2) Serpukhov District, dry meadows on bank of Oka River near Luzhki Village, 7.VI.2002, signals of 1 ♀ are recorded at the temperature 20–21°C.

SIGNALS. Calling signal is a phrase lasting for 3–6 s (Figs 1–3). It consists of short syllables following each other with a period about 50 ms. As a rule, 2–3 pulses or clicks are distinguishable in each syllable (Figs 4–7). Male distinctly vibrates by abdomen and by wings during singing. Apparently, these movements play substantial role in generation of vibrational waves.

Walking along the plant or seldom even being motionless male emits successions of irregular pulses (Figs 8–9). These are obviously territorial signals. When seized by hand, individuals of both sexes produce call of distress (Figs 10–11).

Cercopis intermedia Kirschbaum, 1868
Figs 12–22.

LOCALITY. North Caucasus, North Ossetia, Tsey Canyon (Ardon River basin), polydominant meadow on right slope of canyon under Tsey waterfalls (1800 m above sea level). 5.VIII.1990. Signals of 2 ♂♂ are recorded at the temperature 22°C.

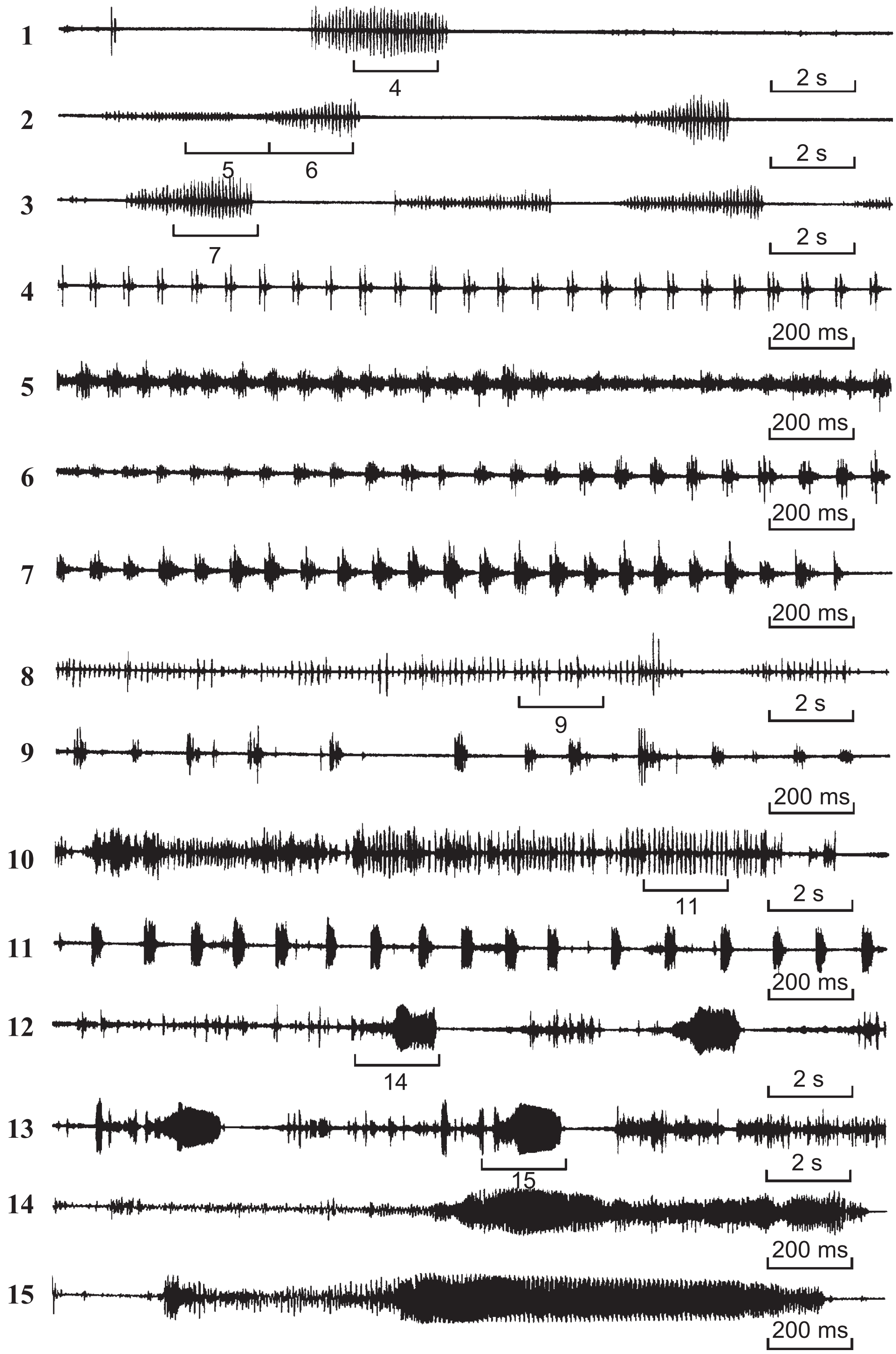
SIGNALS. Calling signal consists of syllables having duration approximately 1.5–2 s and repeating with irregular intervals (Figs 12–15). Pulses in syllables sometimes are indistinct. When courting female male produces courtship signal consisting of repeating phrases. Each phrase begins with successsion of pulses and ends with syllable, same as in calling (Figs 16–22).

As in the previous species, male when emitting signals of both types vibrates by abdomen. Waves resulting from these vibrations have rather low frequency, which is clearly visible on oscillograms on high speed (Figs 14–15, 19–22).

Eoscartopsis assimilis (Uhler, 1896)
Figs 23–29.

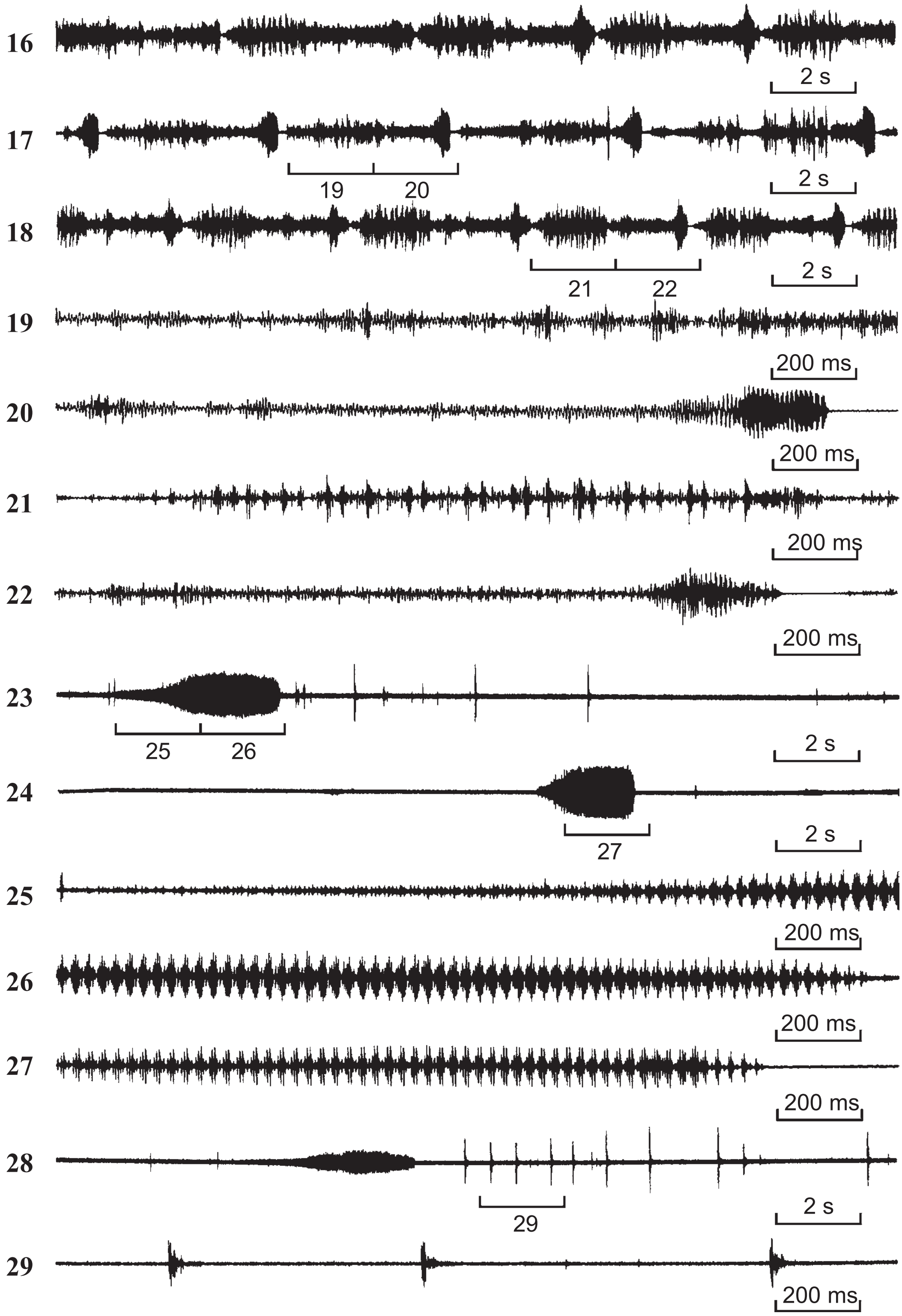
LOCALITY. The Russian Far East, Southern Maritime Province, Khankaiskiy District, 3–4 km north from Novokachalinsk Village, bank of Khanka Lake. 13–14.VII.2002. Signals of 5 ♂♂ are recorded at the temperature 21°C.

SIGNALS. As in *C. vulnerata*, calling signal is a phrase with a duration 2–4 s, but syllables repetition period in it is much shorter (about 30 ms). Male also produces territorial signals consisting of short pulses when moving or in the presence of other individuals (Figs 28–29).



Figs 1–15. Oscillograms of vibrational signals of *Cercopis vulnerata* Rossi (1–11) and *C. intermedia* Kbm. (12–15): 1–7 — *C. vulnerata*, calling signals, 8–9 — same, territorial signals, 10–11 — same, call of distress, 12–15 — *C. intermedia*, calling signals. Faster oscillograms of the parts of signals indicated as "4–7", "9", "11" and "14–15" are given under the same numbers.

Рис. 1–15. Осциллограммы вибрационных сигналов *Cercopis vulnerata* Rossi (1–11) и *C. intermedia* Kbm. (12–15): 1–7 — *C. vulnerata*, призывные сигналы, 8–9 — то же, территориальные сигналы, 10–11 — то же, сигналы протеста, 12–15 — *C. intermedia*, призывные сигналы. Фрагменты сигналов, помеченные цифрами "4–7", "9", "11" и "14–15", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 16–29. Oscillograms of vibrational signals of *Cercopis intermedia* Kbm. (16–22) and *Eoscartopsis assimilis* (Uhler) (23–29): 16–22 — *C. intermedia*, courtship signals, 23–27 — *E. assimilis*, calling signals, 28 — same, calling and territorial signals, 29 — same, territorial signals. Faster oscillograms of the parts of signals indicated as "19–22", "25–27" and "29" are given under the same numbers.

Рис. 16–29. Осциллограммы вибрационных сигналов *Cercopis intermedia* Kbm. (16–22) и *Eoscartopsis assimilis* (Uhler) (23–29): 16–22 — *C. intermedia*, сигналы ухаживания, 23–27 — *E. assimilis*, призывные сигналы, 28 — то же, призывный и территориальный сигналы, 29 — то же, территориальный сигнал. Фрагменты сигналов, помеченные цифрами "19–22", "25–27" и "29", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Family Aphrophoridae

Tribe Aphrophorini

Aphrophora alni (Fallén, 1805)
Figs 30–43.

LOCALITIES. 1. Moscow Area, environs of Mytishchi, on *Salix* sp. and *Rubus idaeus* L. 2.VIII.1991. Signals of 3 ♂♂ and 2 ♀♀ are recorded at the temperature 25°C.

2. The Russian Far East, Southern Maritime Province: (a) Khankaiskiy District, 3–4 km north from Novokachalinsk Village, bank of Khanka Lake, from *Salix udensis* Trautv. et Mey. 13.VII.2002. Signals of 1♂ are recorded at the temperature 23°C; (b) Pogranichny District, environs of Barabash-Levada Village. 20–22.VII.2002, signals of 4♂♂ are recorded at the temperature 20 and 26–27°C.

SIGNALS. Calling signal is a succession of short phrases usually repeating with a period about 1 s (Figs 30–33). Occasionally, male produces phrases with irregular intervals (Fig. 31). Phrase consists of 5–8 syllables including 2 pulses each (Figs 34–37). Signals of males from Moscow Area (Figs 30, 34) and from the Russian Far East (Figs 31–33, 35–37) have not any significant difference. Also, calling of males with usual coloration (Figs 31–32, 35–36) and of light-coloured ones, occurring in the far-eastern populations (Figs 33, 37) are indistinguishable.

Male territorial signals are similar with these in Cercopidae (Figs 38–39). Call of distress is a succession of pulses following each other with irregular intervals (Figs 40–41). Several males sitting on the same stem occasionally produce not only territorial signals, but also, rivalry ones (Figs 42–43).

Aphrophora pectoralis Matsumura, 1903
Figs 44–53.

LOCALITY. Moscow Area, environs of Mytishchi, on *Salix* sp. 1.VIII.1991. Signals of 2 ♂♂ and 1 ♀ are recorded at the temperature 24–25°C.

SIGNALS. Calling signal is similar with this of the previous species, but duration of phrases and their repetition period are much longer averaging 1.5–2 s and 5–9 s respectively (Figs 44–47). Male territorial (Figs 48–49) and rivalry (Figs 50–51) signals have the same temporal pattern as in *A. alni*. Territorial signal, similar in structure with the male one was also registered in female of this species (Figs 52–53).

NOTE. The species was known under the name *A. costalis* Matsumura, which is a junior synonym of *A. pectoralis* [Komatsu, 1997].

Aphrophora salicina (Goeze, 1778)
Figs 54–58.

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, from *Salix vinogradovii* A. Skvortsov. 13.VIII.1991. Signals of 2 ♂♂ are recorded at the temperature °C.

SIGNALS. Calling signal is quite similar with this of *A. pectoralis* (Figs 54–56). Territorial signal is the same as in other *Aphrophora* species. Rivalry signal consists of irregular trains of pulses (Figs 57–58).

Aphrophora obliqua Uhler, 1896
Figs 59–65.

LOCALITY. The Russian Far East, Southern Maritime Province, Pogranichny District, environs of Barabash-Levada Village. 23.VII.2002, signals of 3 ♂♂ are recorded at the temperature 18–19oC.

SIGNALS. Calling signal consists of single or repeating phrases (Figs 59–64). Duration of each phrase averages 5–8 s in my recordings. Syllables are almost indistinguishable in temporal pattern from these in signals of *A. pectoralis* and *A. salicina* (Figs 62–64). Territorial signal have the same structure as in other representatives of the genus (Figs 61, 65).

Tribe Lepyroniini

Lepyronia coleoptrata (Linnaeus, 1758)
Figs 66–86.

LOCALITIES. Moscow Area: (1) Serpukhov District, environs of Luzhki Village, 29.VI.1988, signals of 3 ♂♂ are recorded at the temperature 26°C; (2) Voskresensk District, environs of Beloozerskiy Town, 12.VII.1992, signals of 2 ♂♂ are recorded at the temperature 25°C; 14.VII.1992, signals of 2 ♂♂ are recorded at the temperature 26°C; 18.VII.1992, signals of 1♂ and 2 ♀♀ are recorded at the temperature 25–26°C; (3) environs of Pushkino, meadow on the bank of Ucha River, 23.VII.1992, signals of 2 ♂♂ and 2 ♀♀ are recorded at 26°C.

SIGNALS. Calling signal of this species is a long phrase with very complex and rather variable temporal structure (Figs 66–68). Typically, it begins with a succession of syllables; this succession sometimes lasts for more than 10 s (Fig. 66), or, on the contrary, is very short and includes less than 10 syllables (Fig. 68). Immediately after that several syllables of another type and a train of pulses follow (Figs 69–70, 72). The remaining part of a signal consists of rather short discrete fragments including one short syllable and a train of pulses each (Figs 71, 73). Repetition period and number of such fragments varies greatly. Occasionally, male produces one-two fragments only (Fig. 66), but sometimes he emits about 10 ones (Fig. 68).

Receptive female produces short successions of pulses in reply to calling male (Figs 78–80). After hearing female reply male starts singing almost unceasingly and walks along the plant in different directions. Female goes on producing reply signals at these moments, as a result the mates sing alternately or simultaneously (Figs 74–77). After finding female male emits one or two more signals sitting near her and starts copulation. When mounting female he produces copulatory signal, which is prolonged trill of somewhat variable pulses (Figs 81–82).

It must be noted, that in some cases observed male sitting in the same cage with female produced several calling signals, approached female and started copulation, but reply signals were not registered. Apparently, emitting of signals by female does not always necessary for successful mating.

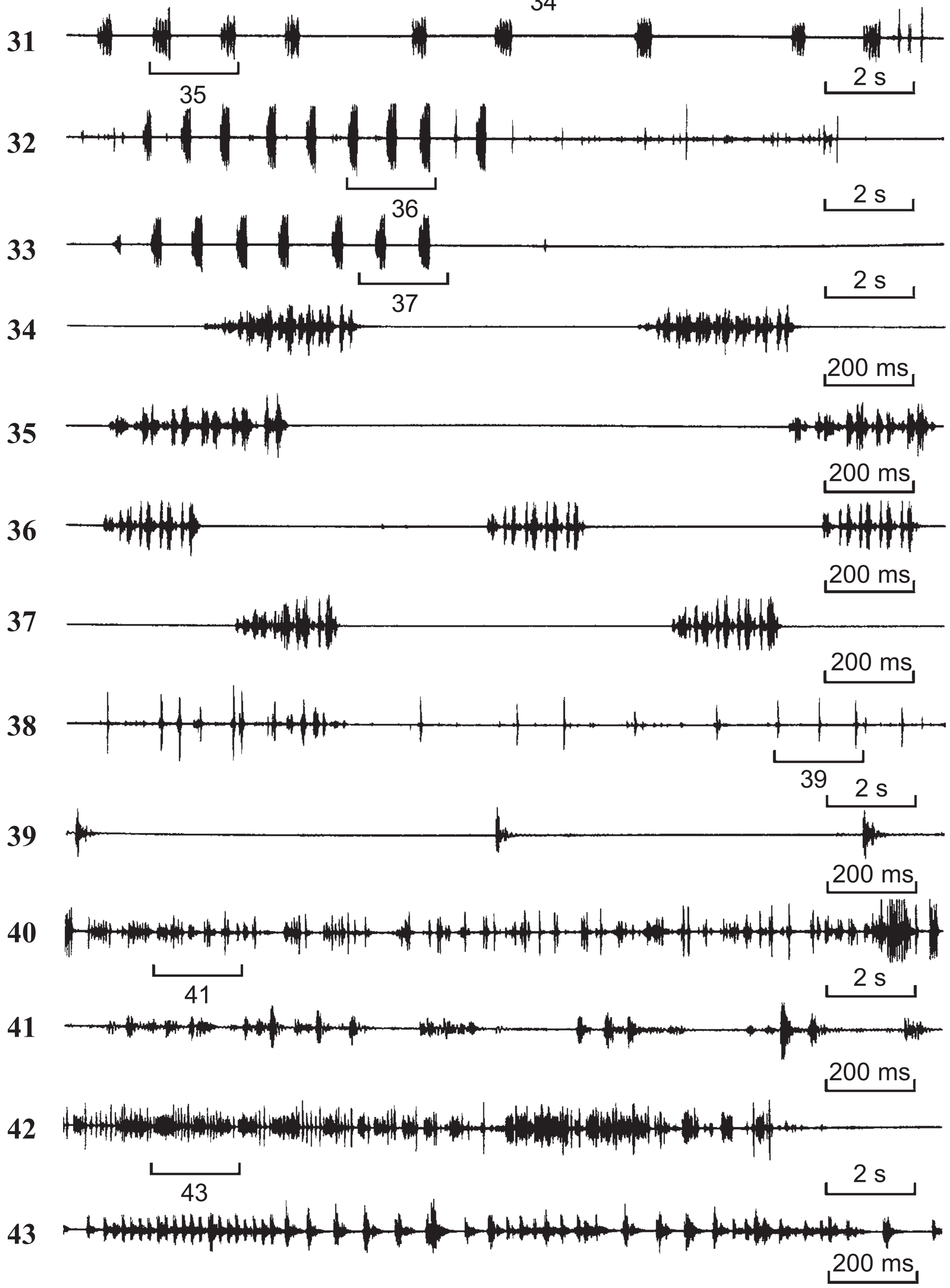
Individuals of both sexes produce call of distress when seized by hand (Figs 85–86). Signals of this type in males and females are similar. Also, both males and females sitting on the stem in close proximity with other individuals emit rivalry signals occasionally (Figs 83–84).

Tribe Philaenini

Aphilaenus ikumae (Matsumura, 1915)
Figs 87–91.

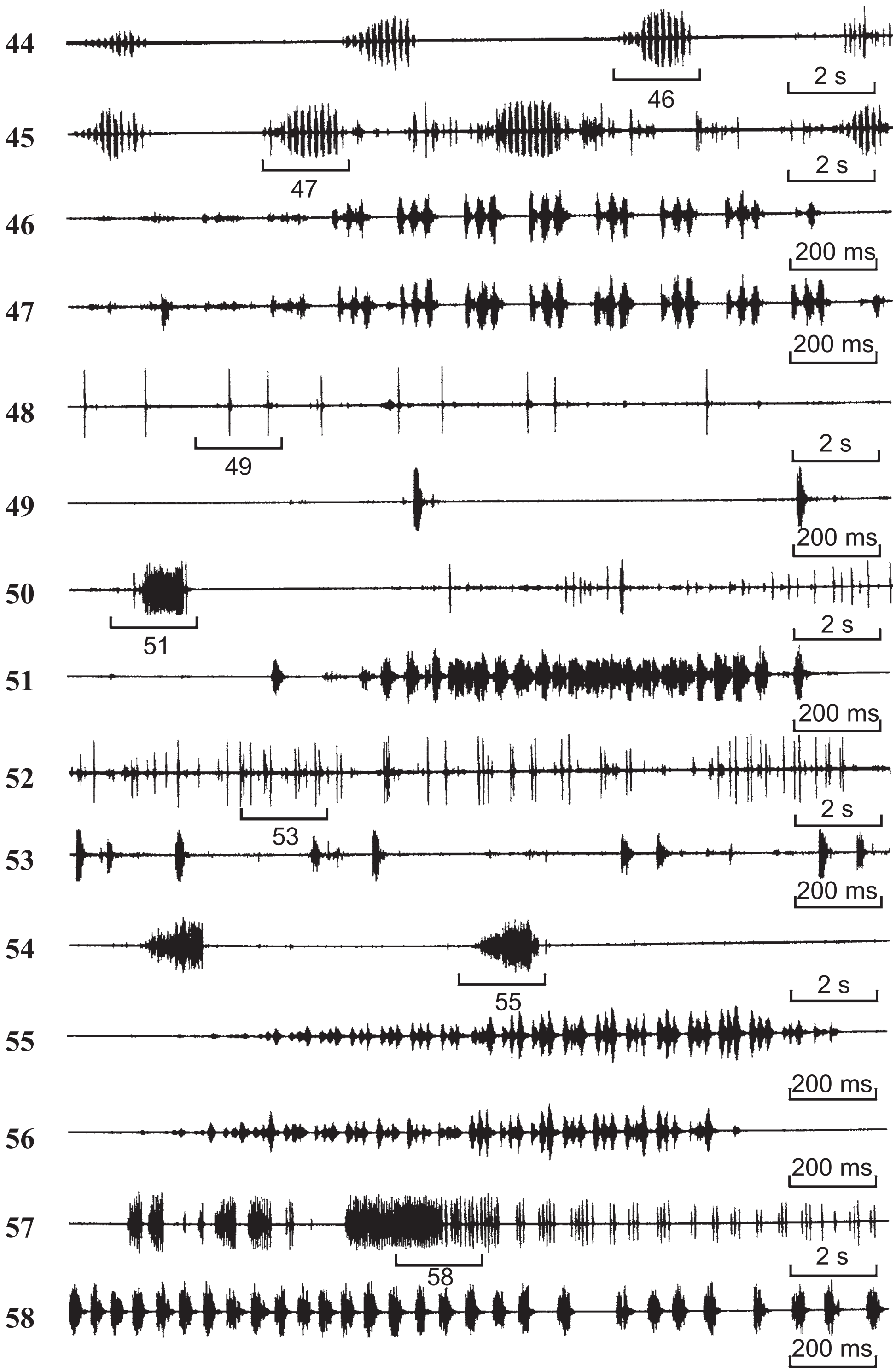
LOCALITY. The Russian Far East, Southern Maritime Province, Khankaiskiy District, 3–4 km north from Novokachalinsk Village, bank of Khanka Lake, from *Artemisia* sp. 16.VII.2002. Signals of 2 ♂♂ are recorded at the temperature 21–22°C.

SIGNALS. Calling signal consists of regularly repeated short syllables, separated by intervals from 3–4 up to 10 s.



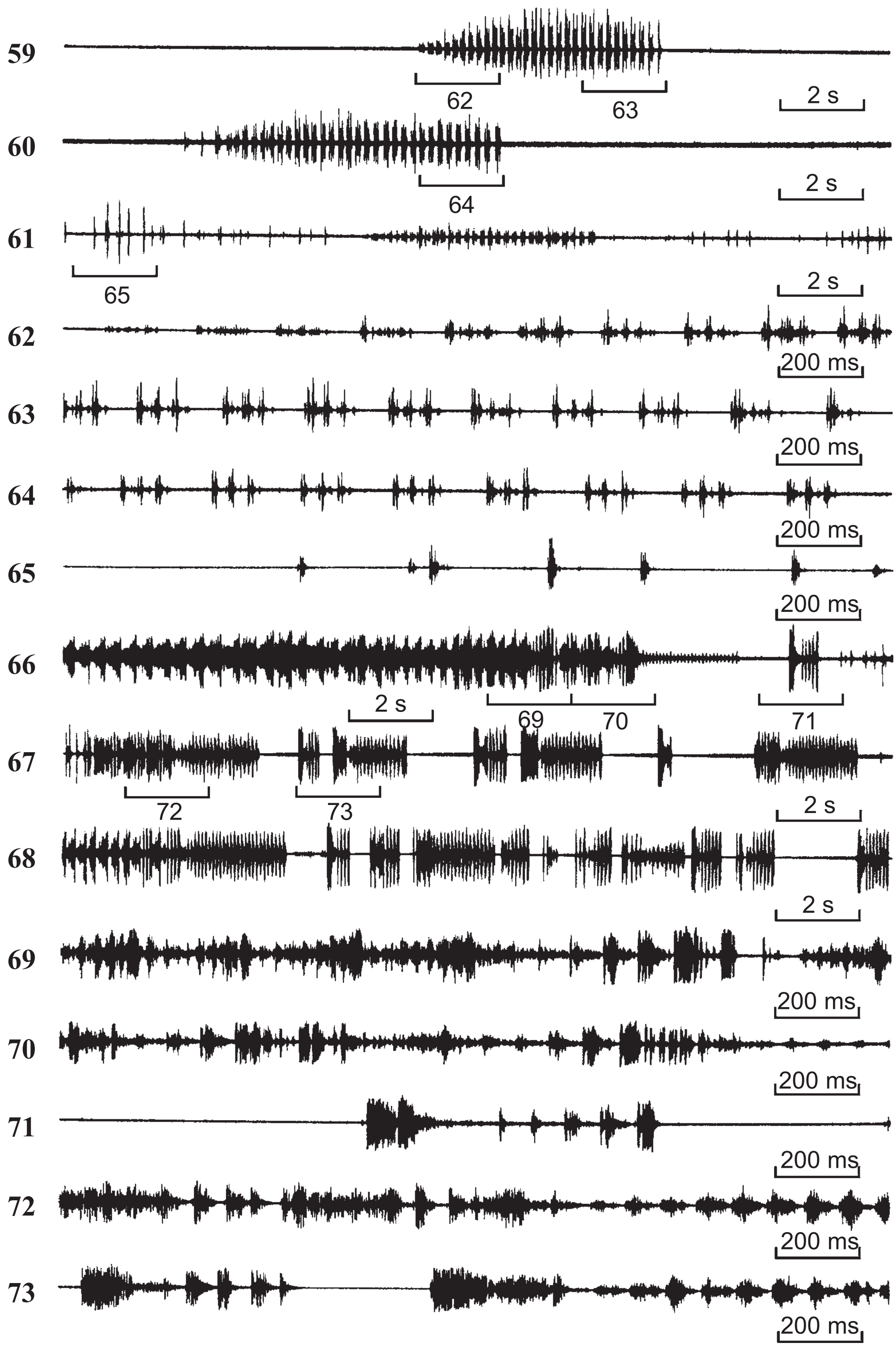
Figs 30–43. Oscillograms of vibrational signals of *Aphrophora alni* (Fall.): 30–37 — calling signals (30, 34 — specimen from Moscow Area, 31–32, 35–36 — specimens with typical coloration from the Russian Far East, 33, 37 — light-coloured male from the Far East), 38–39 — territorial signals, 40–41 — call of distress, 42–43 — rivalry signals. Faster oscillograms of the parts of signals indicated as "34–37", "39", "41" and "43" are given under the same numbers.

Рис. 30–43. Осциллограммы вибрационных сигналов *Aphrophora alni* (Fall.): 30–37 — призывные сигналы (30, 34 — экземпляр из Московской обл., 31–32, 35–36 — экземпляры с типичной окраской с Дальнего Востока, 33, 37 — светлоокрашенный самец с Дальнего Востока), 38–39 — территориальные сигналы, 40–41 — сигналы протеста, 42–43 — сигналы соперничества. Фрагменты сигналов, помеченные цифрами "34–37", "39", "41" и "43", представлены при большей скорости развертки на осциллограммах под такими же номерами.



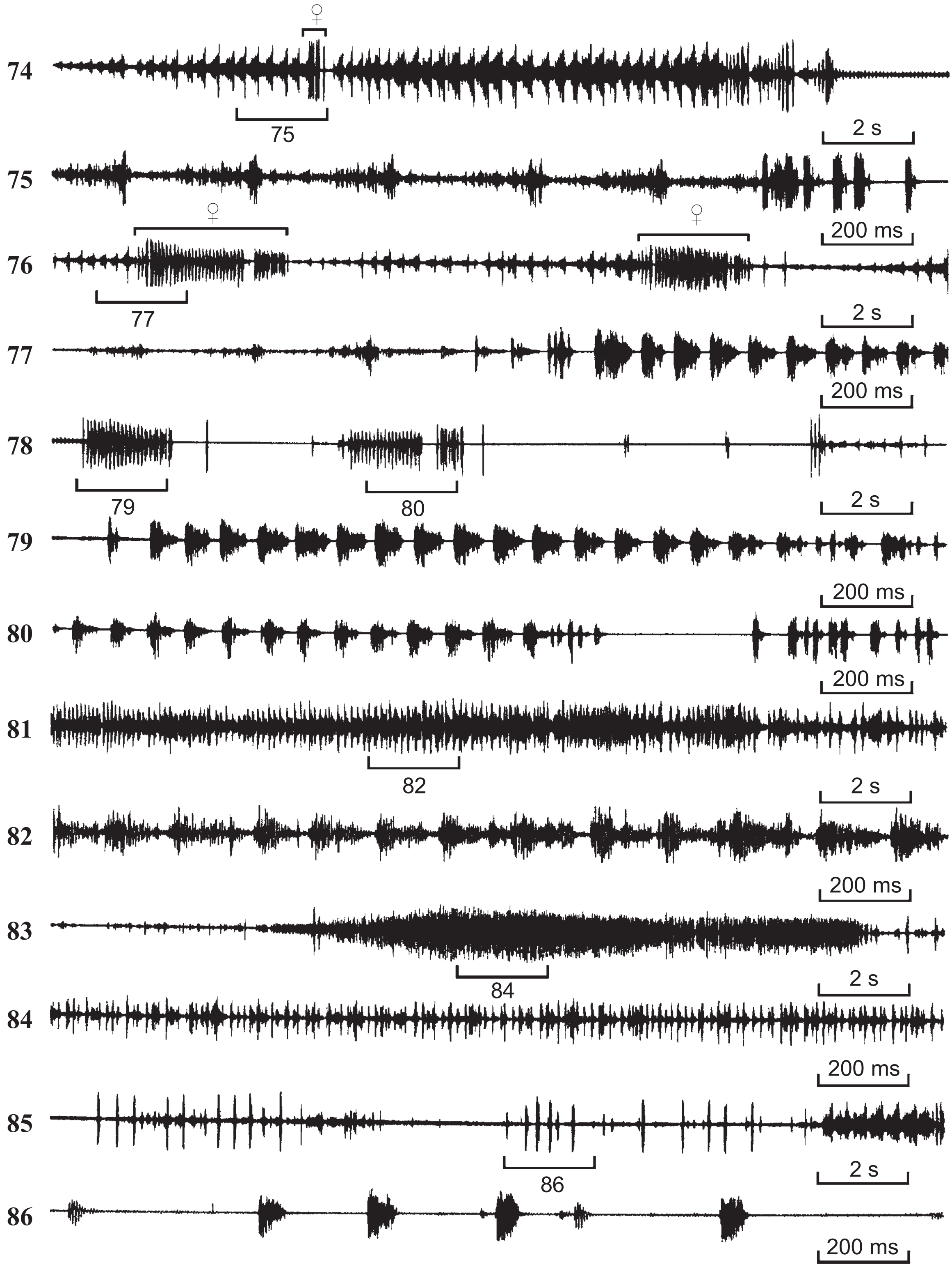
Figs 44–58. Oscillograms of vibrational signals of *Aphrophora pectoralis* Matsumura (44–53) and *A. salicina* (Goeze) (54–58): 44–47 — *A. pectoralis*, calling signals, 48–49 — same, territorial signals of male, 50–51 — same, rivalry signal, 52–53 — same, territorial signals of female, 54–56 — *A. salicina*, calling signals, 57–58 — same, rivalry signals. Faster oscillograms of the parts of signals indicated as “46–47”, “49”, “51”, “53”, “55” and “58” are given under the same numbers.

Рис. 44–58. Осциллограммы вибрационных сигналов *Aphrophora pectoralis* Matsumura (44–53) и *A. salicina* (Goeze) (54–58): 44–47 — *A. pectoralis*, призывные сигналы, 48–49 — то же, территориальные сигналы самца, 50–51 — то же, сигналы соперничества, 52–53 — то же, территориальные сигналы самки, 54–56 — *A. salicina*, призывные сигналы, 57–58 — то же, сигналы соперничества. Фрагменты сигналов, помеченные цифрами “46–47”, “49”, “51”, “53”, “55” и “58”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 59–73. Oscillograms of vibrational signals of *Aphrophora obliqua* Uhler (59–65) and *Lepyronia coleoptrata* (L.). (66–73): 59–60, 62–64 — *A. obliqua*, calling signals, 61 — same, calling and territorial signals, 65 — same, territorial signals, 66–73 — *L. coleoptrata*, calling signals. Faster oscillograms of the parts of signals indicated as "62–65" and "69–73" are given under the same numbers.

Рис. 59–73. Осциллограммы вибрационных сигналов *Aphrophora obliqua* Uhler (59–65) и *Lepyronia coleoptrata* (L.). (66–73): 59–60, 62–64 — *A. obliqua*, призывные сигналы, 61 — то же, призывный и территориальные сигналы, 65 — то же, территориальные сигналы, 66–73 — *L. coleoptrata*, призывные сигналы. Фрагменты сигналов, помеченные цифрами "62–65" и "69–73", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 74–86. Oscillograms of vibrational signals of *Lepyronia coleoptrata* (L.): 74–77 — male calling and female reply signals, 78–80 — female reply signals, 81–82 — copulatory signal, 83–84 — rivalry signals, 85–86 — call of distress. Faster oscillograms of the parts of signals indicated as “75”, “77”, “79–80”, “82”, “84” and “86” are given under the same numbers.

Рис. 74–86. Осциллограммы вибрационных сигналов *Lepyronia coleoptrata* (L.): 74–77 — призывные сигналы самца и ответные сигналы самки, 78–80 — ответные сигналы самки, 81–82 — копуляционные сигналы, 83–84 — сигналы соперничества, 85–86 — сигналы протеста. Фрагменты сигналов, помеченные цифрами “75”, “77”, “79–80”, “82”, “84” и “86”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

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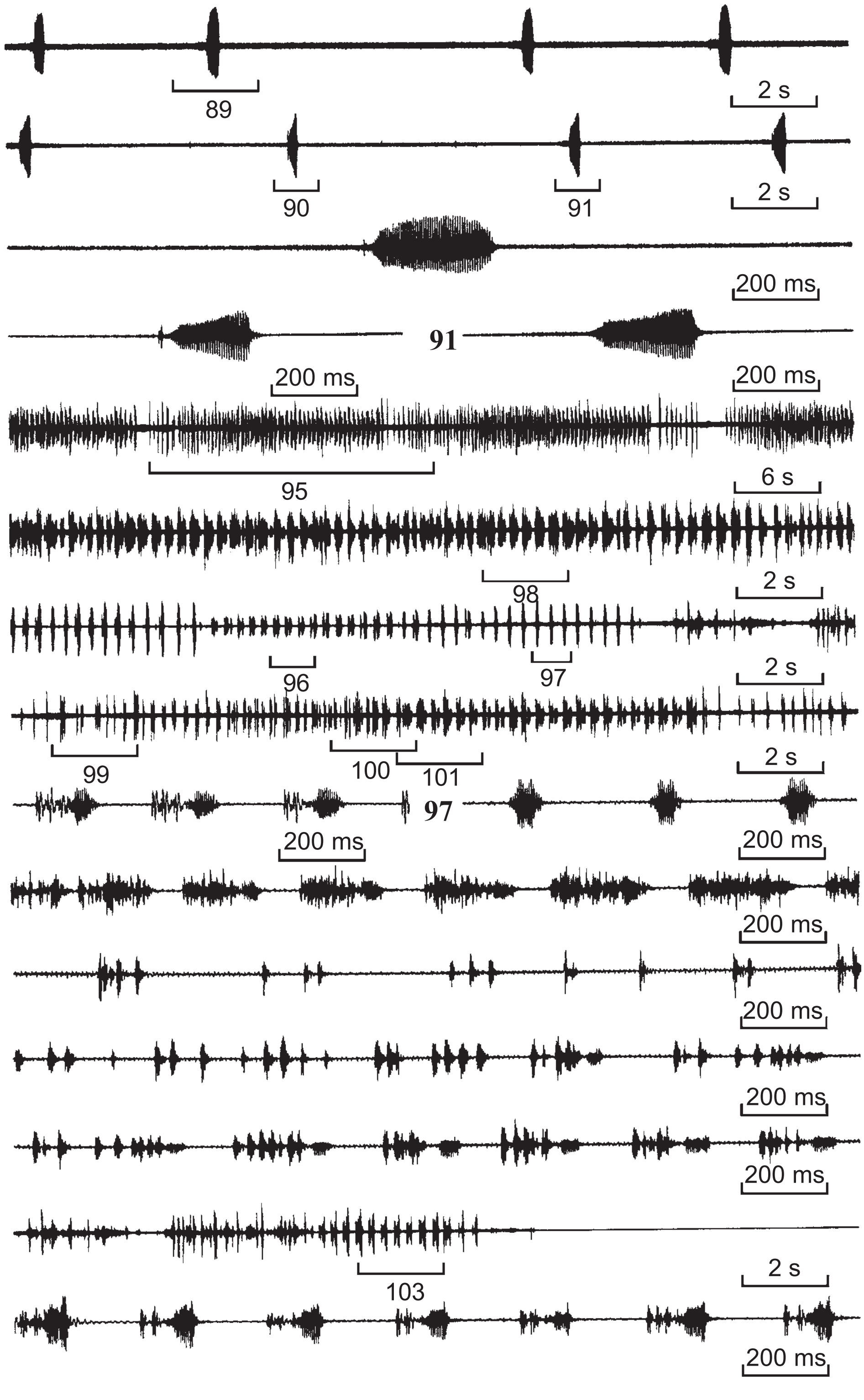


Figs 87–103. Oscillograms of vibrational signals of *Aphilaenus ikumae* (Matsumura) (87–91) and *Philaenus spumarius* (L.). (92–103): 87–91 — *A. ikumae*, calling signals, 92–101 — *Ph. spumarius*, calling signals, 102–103 — same, signals produced by male during copulation. Faster oscillograms of the parts of signals indicated as "89–91", "95–101" and "103" are given under the same numbers.

Рис. 87–103. Осциллограммы вибрационных сигналов *Aphilaenus ikumae* (Matsumura) (87–91) and *Philaenus spumarius* (L.). (92–103): 87–91 — *A. ikumae*, призывные сигналы, 92–101 — *Ph. spumarius*, призывные сигналы, 102–103 — то же, сигналы, издаваемые самцом во время копуляции. Фрагменты сигналов, помеченные цифрами "89–91", "95–101" и "103", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Occasionally, male can sing for several minutes.

Philaenus spumarius (Linnaeus, 1758)
Figs 92–103.

LOCALITIES. Moscow Area: (1) environs of Zvenigorod Town, meadows on bank of Moskva River near Lutsyno Village, 19.VII.1988, signals of 1 ♂ are recorded at the temperature 27–28°C; (2) environs of Pushkino, meadow on the bank of Ucha River, 22.VII.1988, signals of 3 ♂♂ are recorded at 28–29°C, 24.VII.1993, signals of 2 ♂♂ are recorded at 26–27°C.

SIGNALS. Calling signal is a succession of short syllables with total duration averaging 10–30 s (Figs 92–95). As a rule, temporal pattern of syllables changes gradually from the beginning to the end of signal (Figs 92, 94–97, 99–101), nevertheless, occasionally it remains constant throughout all the song (Figs 93, 98). Male can sing for more than ten minutes ceaselessly, producing one signal after another almost without pauses (Fig. 92).

I observed mating behaviour in this species more than once. In all cases male after producing several calling signals approached female and started copulation, but female reply was never registered. Copulation in this species often lasts for more than half an hour. During copulation male produces short fragments of calling signal from time to time (Figs102–103).

Paraphilaenus notatus (Mulsant et Rey, 1855)
Figs 104–108.

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, from *Artemisia campestris* L. 16, 18.VIII.1991. Signals of 2 ♂♂ are recorded at the temperature 25–26°C.

SIGNALS. Calling signal consists of single or repeated rather long syllables (Figs 104–105). Mating behaviour was observed twice in this species. In both cases male feeding on a plant in a cage with female after certain time span suddenly approached her not emitting any signals and started copulation. Female reply signals also were not registered. During copulation male every 30–40 s produced copulatory signals, which are single phrases, consisting of syllable, same as in calling and of a train of pulses each (Figs 106–108).

Neophilaenus exclamationis (Thunberg, 1782)
Figs 109–112.

LOCALITY. North Caucasus, North Ossetia, Tsey Canyon (Ardon River basin), subalpine meadow near Tsey Village (1800 m above sea level). 1.VIII.1990. Signals of 2 ♂♂ are recorded at the temperature 20°C.

SIGNALS. Calling signals consist of short syllables repeating with a period about 400–600 ms. Occasionally, male produces single syllables.

Neophilaenus campestris (Fallén, 1805)
Figs 113–115.

LOCALITY. Southern Azerbaidzhan, Talysh Mts., environs of Lerik Village. 14.VII.1987. Signals of 3 ♂♂ are recorded at the temperature 22°C.

SIGNALS. Calling signals are similar with these of the previous species, but syllables and intervals between them are about two or three times as long, as in *N. exclamationis*. Several males singing simultaneously usually produce syllables in turn (Fig. 114).

Neophilaenus lineatus (Linnaeus, 1758)
Figs 116–126.

LOCALITIES. Moscow Area: (1) environs of Zvenigorod Town, meadows on bank of Moskva River near Lutsyno Village, 10.VII.1988, signals of 2 ♂♂ are recorded at the temperature 24–25°C; (2) environs of Pushkino, meadow on the bank of Ucha River, 21.VII.1988, signals of 2 ♂♂ are recorded at 27–28°C.

SIGNALS. Calling signal in general structure is similar with this in the previous species, but has duration about 60–150 ms (Figs 116–120). Its initial part (succession of syllables) has noise frequency spectrum, whereas end one is almost pure-tone (Figs 120–121). Usually, male sings with irregular intervals.

In several males sitting in the same cage also short trills of pulses (? rivalry signals) were registered (Figs 122–123). During copulation male produce the same trills alternating this signal with calling (Figs 124–126). Observed mating behaviour in this species was quite similar with this in *Ph. spumarius* and *P. notatus*. Male approached female and started copulation without any prior acoustic interaction with her. Female reply signals were not registered at this moment.

Family Machaerotidae

Taichorina geisha Schumacher, 1915
Figs 127–135.

LOCALITY. The Russian Far East, Southern Maritime Province, Khankaiskiy District, 3–4 km north from Novokachalinsk Village, bank of Khanka Lake, from *Quercus mongolica* Fisch. ex Ledeb. 13.VII.2002. Signals of 4 ♂♂ are recorded at the temperature 21°C.

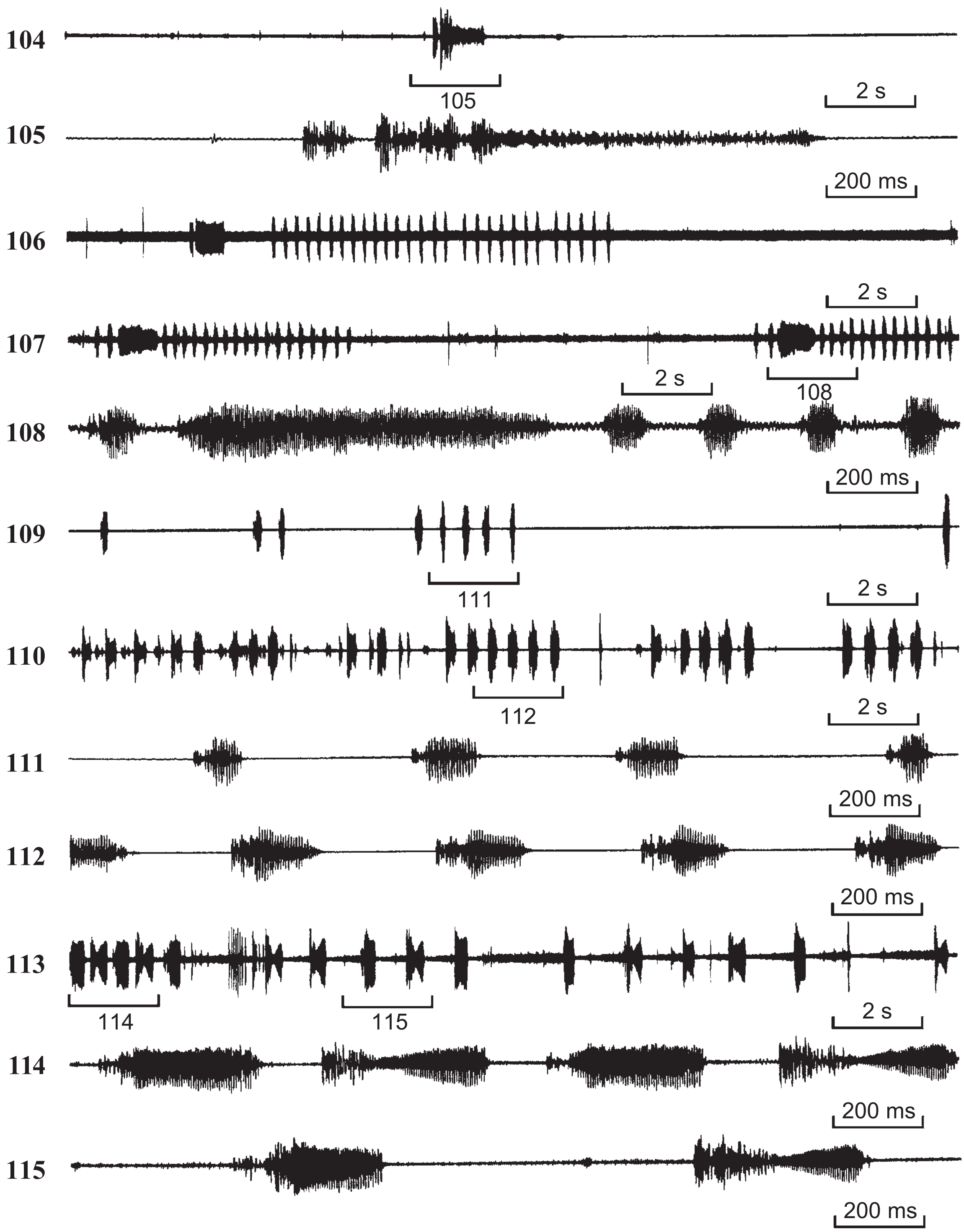
SIGNALS. Only calling signals were registered in this species. Signals of this type consist of alternating short and long phrases with similar temporal structure. Occasionally, two or three phrases of the same type follow one after another (Fig. 128). Total duration of signal usually does not exceed 30–40 s.

NOTE. Recently Hamilton [2001] redefined the limits of the family Clastopteridae including Machaerotidae as a subfamily. The only species studied by me belongs to the latter group, so I use here the traditional name Machaerotidae just to avoid possible misinterpretation.

The only attempt to investigate acoustic signals of Aphrophoridae, Cercopidae and Clastopteridae using present-day equipment was made by Moore [1961]. Sonograms of 10 species from three families mentioned above are presented in his work. Unfortunately, only female signals were registered in this study. It is most likely, judging from illustrations presented, that these are territorial and rivalry signals.

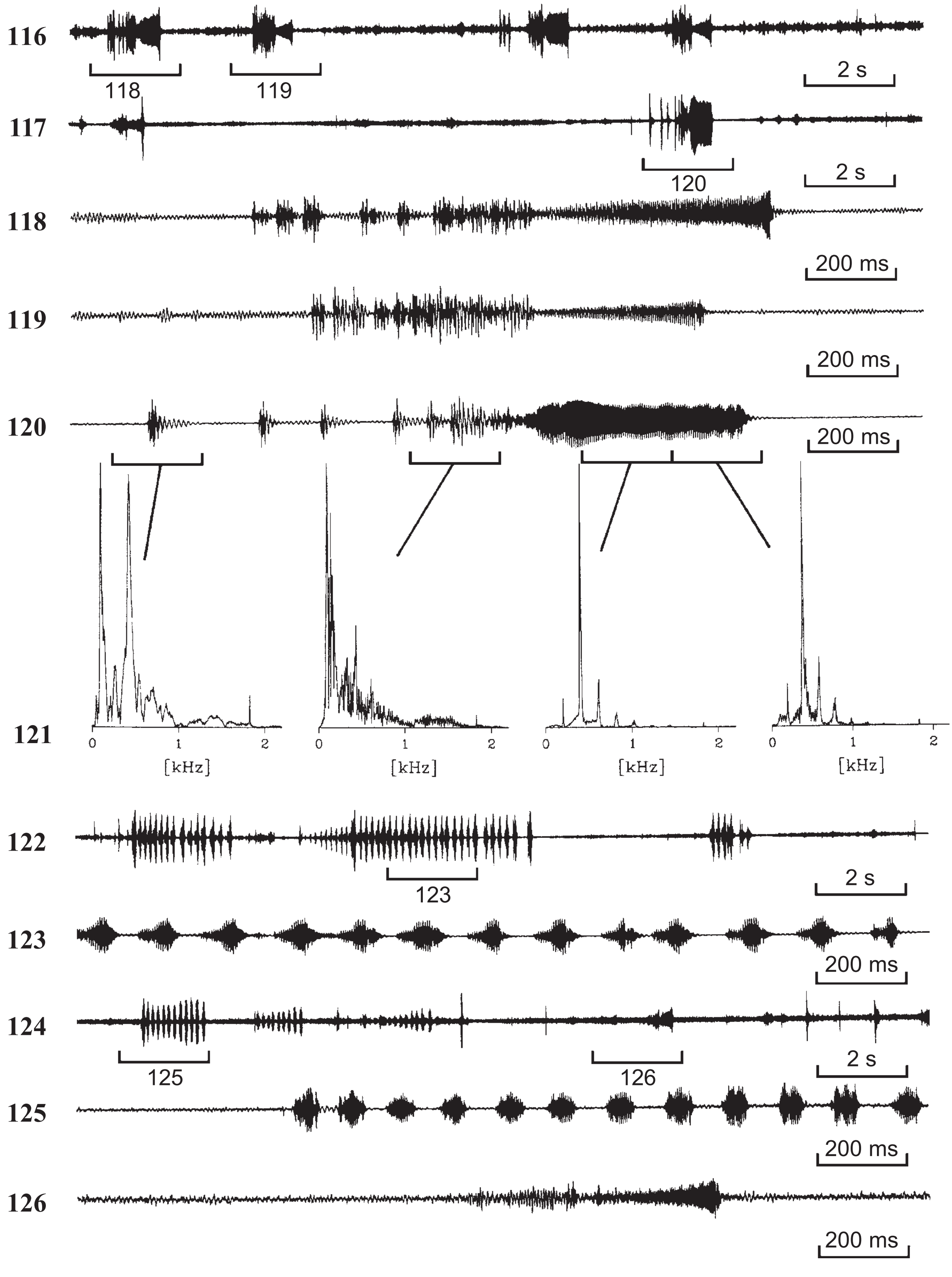
Also, brief description of calling signal of *Machaerota rastrata* (Walker, 1868) (Machaerotidae) from Java is available in literature [Morgan, Claridge, 1993]. Signal of this species is a succession of short syllables, following each other with a period of about 1–1.5 s. As in *T. geisha*, no other signals except calling were recorded in this species.

Judging from bioacoustic characters Cercopidae seem to be the least advanced family among Cercopoidea due to the presence of tremulation components in their



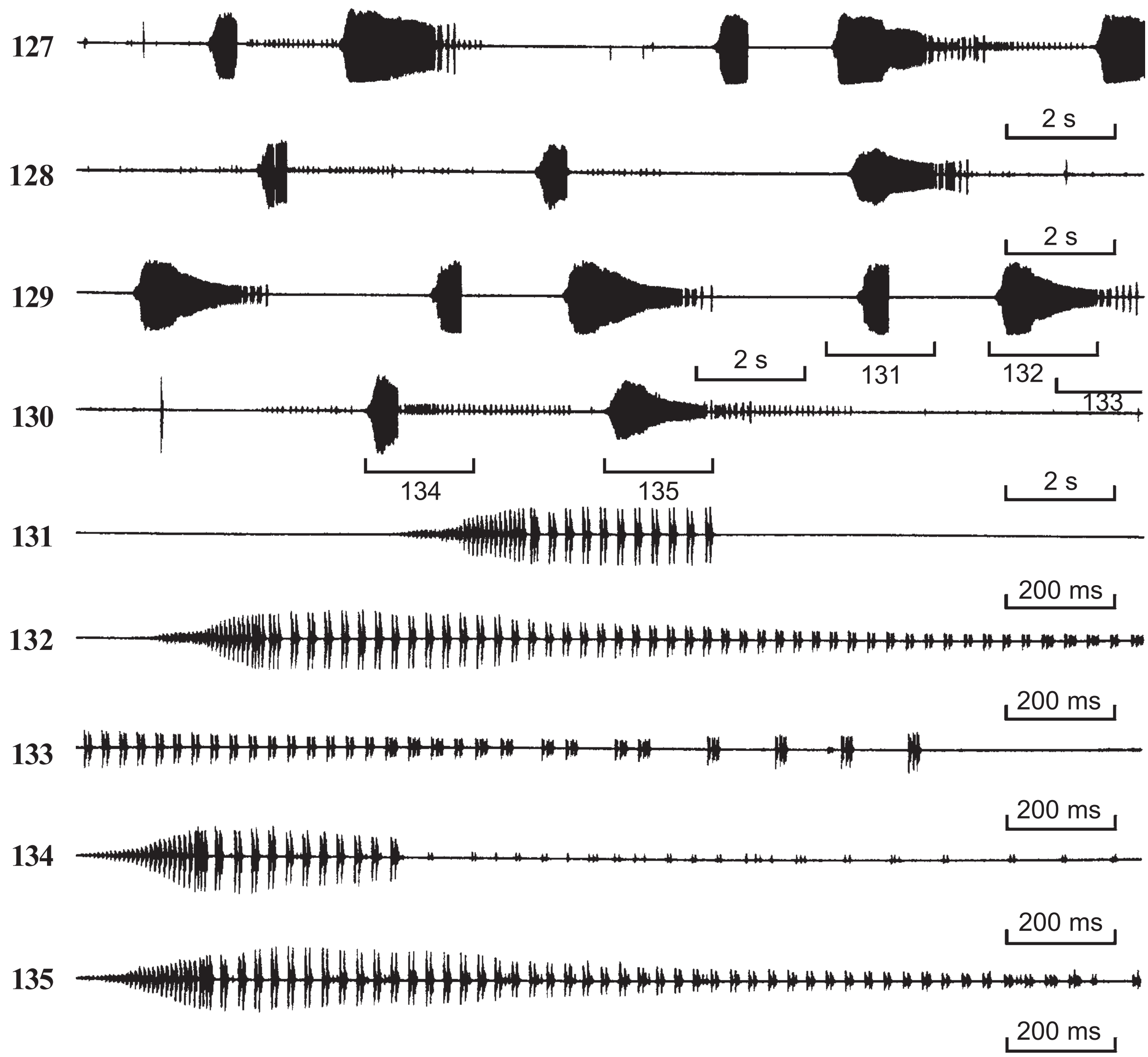
Figs 104–115. Oscillograms of vibrational signals of *Paraphilaenus notatus* (Mulsant et Rey) (104–108), *Neophilaenus exclamationis* (Thunb.) (109–112) and *N. campestris* (Fall.) (113–115): 104–105 — *P. notatus*, calling signals, 106–108 — same, copulatory signals, 109–112 — *N. exclamationis*, calling signals, 113–115 — *N. campestris*, calling signals. Faster oscillograms of the parts of signals indicated as "105", "108", "111–112" and "114–115" are given under the same numbers.

Рис. 104–115. Осциллограммы вибрационных сигналов *Paraphilaenus notatus* (Mulsant et Rey) (104–108), *Neophilaenus exclamationis* (Thunb.) (109–112) и *N. campestris* (Fall.) (113–115): 104–105 — *P. notatus*, призывные сигналы, 106–108 — то же, копуляционные сигналы, 109–112 — *N. exclamationis*, призывные сигналы, 113–115 — *N. campestris*, призывные сигналы. Фрагменты сигналов, помеченные цифрами "105", "108", "111–112" и "114–115", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 116–126. Vibrational signals of *Neophilaenus lineatus* (L.): 116–120 — oscillograms of calling signals, 121 — frequency spectra of different parts of calling signal, 122–123 — oscillograms of rivalry signals, 124–126 — oscillograms of signals produced by male during copulation. Faster oscillograms of the parts of signals indicated as "118–120", "123" and "125–126" are given under the same numbers.

Рис. 116–126. Вибрационные сигналы *Neophilaenus lineatus* (L.): 116–120 — осциллограммы призывных сигналов, 121 — частотные спектры разных частей призывного сигнала, 122–123 — осциллограммы сигналов протеста, 124–126 — осциллограммы сигналов, издаваемых самцом во время копуляции. Фрагменты сигналов, помеченные цифрами "118–120", "123" и "125–126", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 127–135. Oscillograms of calling signals of *Taichorina geisha* Schumacher. Faster oscillograms of the parts of signals indicated as "131–135" are given under the same numbers.

Рис. 127–135. Осциллограммы призывных сигналов *Taichorina geisha* Schumacher. Фрагменты сигналов, помеченные цифрами "131–135", представлены при большей скорости развертки на осциллограммах под такими же номерами.

signals. Tremulation, i.e. emitting of signals by means of vibration of the parts of body (usually, of abdomen) without using specialized structures is one of the most primitive methods of signals producing [Gogala, 1985]. Outside Cicadinea tremulation mechanism is known in a number of archaic groups, such as Megaloptera (Sialidae), Trichoptera and Mecoptera. Among Membracoidea it presents in Cicadellini s.str. (*Cicadella*, *Kolla*) from Cicadellides [Tishechkin, 2001], in Idiocerinae from Ulopides [Tishechkin, 2003] and in *Sagatus* from Macrostelini [Tishechkin, 2000].

Same opinion concerning the position of Cercopidae among Cercopoidea was expressed earlier by Emeljanov and Kirillova [1991] basing on karyological characters.

Three studied tribes of Aphrophoridae differ distinctly from each other in acoustic characters. In *Aphrophora* (Aphrophorini) territorial signals (short irregular pulses) may be heard almost always, when insects move along the plant. In *L. coleoptrata* (Lepyroniini) and in Philaenini such signals are absent. Rivalry signals, which present in repertoire of Aphrophorini and Lepyroniini, were not recorded in Philaenini (the only dubious exception are trills of pulses in *N. lineatus*, Figs 122–123).

Distinctive character of mating behaviour in most Cercopoidea species is rather prolonged copulation usually lasting at least for 10–20 minutes and usually more. Males of Philaenini produce calling or specialized copulatory signals during all the time of genital contact, whereas in *L. coleoptrata* such signal can be heard only at the initial stage of copulation. Unfortunately, there are no data on mating behaviour in Aphrophorini.

It is remarkable, that female reply signals evidently are not necessary for successful mating in Aphrophoridae. On the contrary, in most Cicadellidae and Fulgoroidea male as a rule absolutely ignore female if she does not produce signals in reply to his calling.

Temporal pattern of calling in three tribes is quite different. In Philaenini each syllable of calling signal typically is composed of one or several distinct pulses followed by monotonous fragment with more or less uniform structure throughout all its length. In certain species initial pulses can be absent (in *A. ikumae*, occasionally, in *Ph. spumarius*). Syllables can follow in trains or with irregular intervals. In *Aphrophora* calling signals consist of phrases, which are successions of syllables including 2–3 pulses each. Calling of *L. coleoptrata* has very complex structure differing from signals of representatives of both other tribes. On the other hand, in contrast with most Cicadellidae, temporal structure of calling within the genus or even the tribe in Aphrophoridae for the most part is quite similar (see, for instance, oscillograms of signals of *A. ikumae* and *Neophilaenus spp.*, Figs 89–91, 111–112, 114–115 and 118–120). Therefore, this character may appear to be not so reliable for distinguishing between closely related species or for elucidation of taxonomic status of dubious forms in Aphrophoridae, as it is in Cicadellidae. Still, acoustic analysis may be useful for correct tribal or even family placement of certain groups, because assigning of a number of Cercopoidea genera is incorrect at present [Hamilton, 2001].

Three tribes of Aphrophoridae differ from each other in acoustic characters on the same level as from Machaerotidae. This fact corroborates the opinion of Hamilton [2001], that Aphrophoridae is not natural group.

Available data on acoustic signals of Machaerotidae do not allow to make any definite conclusion concerning the relationships of this family. In both species studied only calling signals were recorded. In one of my experiments three males of *T. geisha* were placed in the cage on the same twig, still any competition behaviour including territorial or rivalry signals was not recorded. Similar situation in Cercopoidea is known also in Philaenini.

Superfamily CICADOIDEA

Family Cicadidae

Cicada orni (Linnaeus, 1758)
Figs 136–142.

LOCALITY. North Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town. 24.VI.1986. Signals of 3 ♂♂ are recorded at the temperature 35°C.

SIGNALS. Calling signal is a prolonged succession of syllables, following with a period averaging 250–500 ms (Figs 136–137). Duration of syllables varies from 40 up to 260 ms in different individuals (Figs 138–140). Insect, if not disturbed, can sing for about 15–20 min sitting on the same place. Call of distress in this species consists of trains of pulses with highly variable duration and repetition period (Figs 141–142).

Tibicen plebejus (Scopoli, 1763)
Figs 143–147.

LOCALITY. Southern Azerbaidzhan, Talysh Mts., environs of Lerik Village. 13.VII.1987. Signals of 1 ♂ are recorded at the temperature 28–30°C.

SIGNALS. Calling signal of this species consists of phrases following one after another without breaks (Figs 143–144). Duration of phrase averages 10–20 s. The main part of phrase is composed of short syllables, following with a period about 100 ms in my recordings. Temporal pattern of syllables changes gradually towards the end of signal (Figs 145–147). At the beginning and at the end of succession of syllables trains of simple pulses follow.

Cicadatra persica Kirkaldy, 1909
Figs 148–160.

LOCALITY. Southern Azerbaidzhan, Talysh Mts., environs of Lerik Village. 11–13.VII.1987. Signals of 3 ♂♂ are recorded at the temperature 28–30°C.

SIGNALS. Calling signal consists of short syllables following with intervals from 4–5 approximately up to 8–10 s (Figs 148–151). Sometimes, male clicks fore wings rapidly in pauses between syllables (Figs 152–154). Also, so called continuous signal was registered in this species (Figs 158–159). It sounds as monotonous high-frequency noise and lasts sometimes up to several minutes and more. On oscillograms on high speed it is visible, that pulses in the signal are grouped in syllables, including about 6–8 pulses each (Fig. 160). Singing male can alternate signals of these two types in his song. On Figs 155–157 changing from calling to continuous signal is shown. Also, inverse situation was observed quite often.

Cicadatra atra (Oliver, 1790)
Figs 161–165.

LOCALITY. North Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town. 24.VI.1986. Signals of 2 ♂♂ are recorded at the temperature 35°C.

SIGNALS. Calling signal is a long-lasting succession of syllables following each other with a period about 200–250 ms (Figs 161–163). Occasionally, male produces single click by fore wings in each interval between syllables. Call of distress is irregular succession of sort trills (164–165).

Cicadetta tibialis (Panzer, 1788)
Figs 166–167.

LOCALITY. North Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town. 24.VI.1986. Signals of 2 ♂♂ are recorded at the temperature 35°C.

SIGNALS. Calling signal consists of successions of short syllables interrupted by single more prolonged ones every 2–6 s. As in several other small species of Cicadidae, call of distress was not registered in this species.

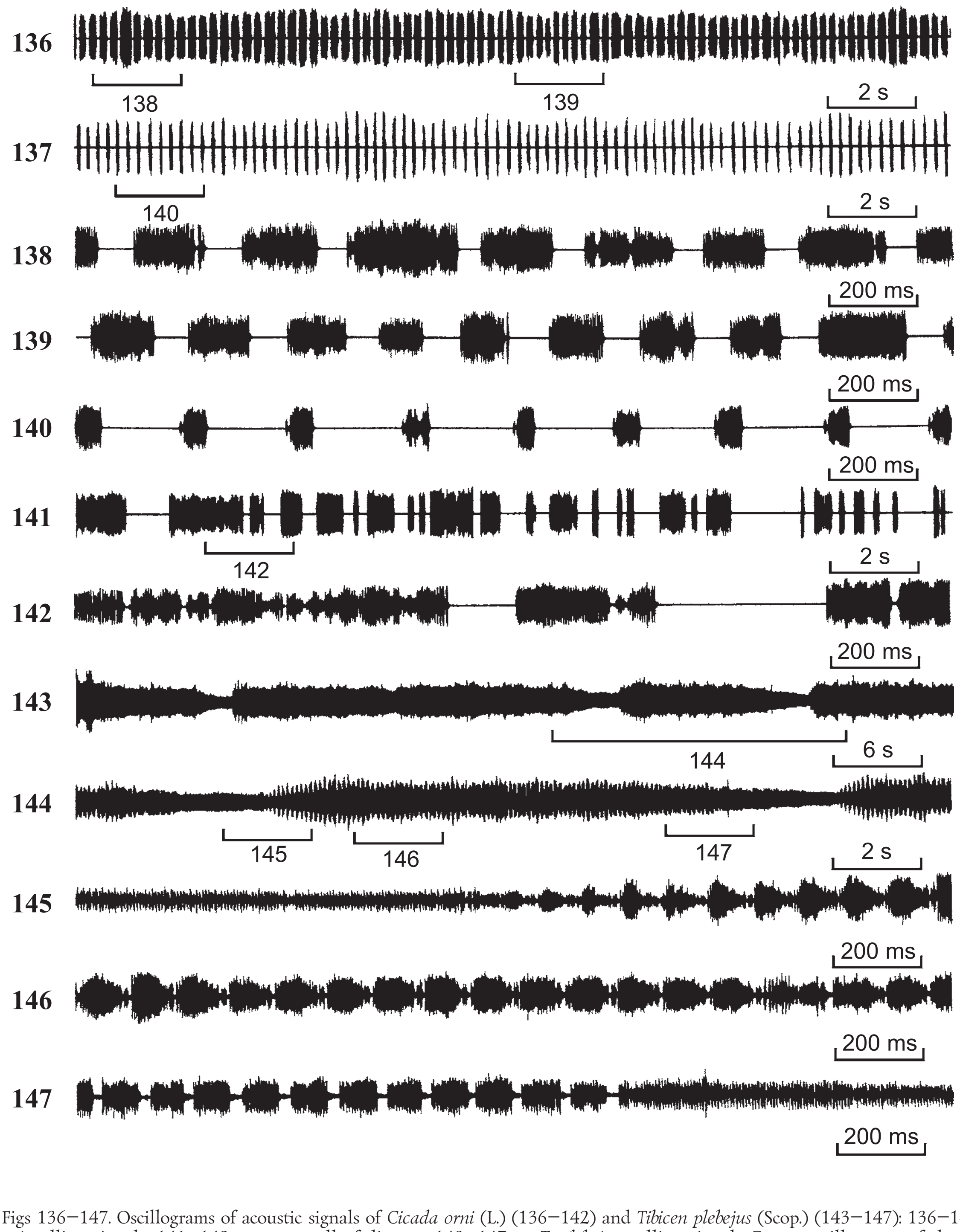
NOTE. Interpretation of species is accepted after Popov [1997].

Cicadetta dimissa (Hagen, 1865)
Figs 168–171.

LOCALITY. North Caucasus, Chechnya, Terskiy Mountain

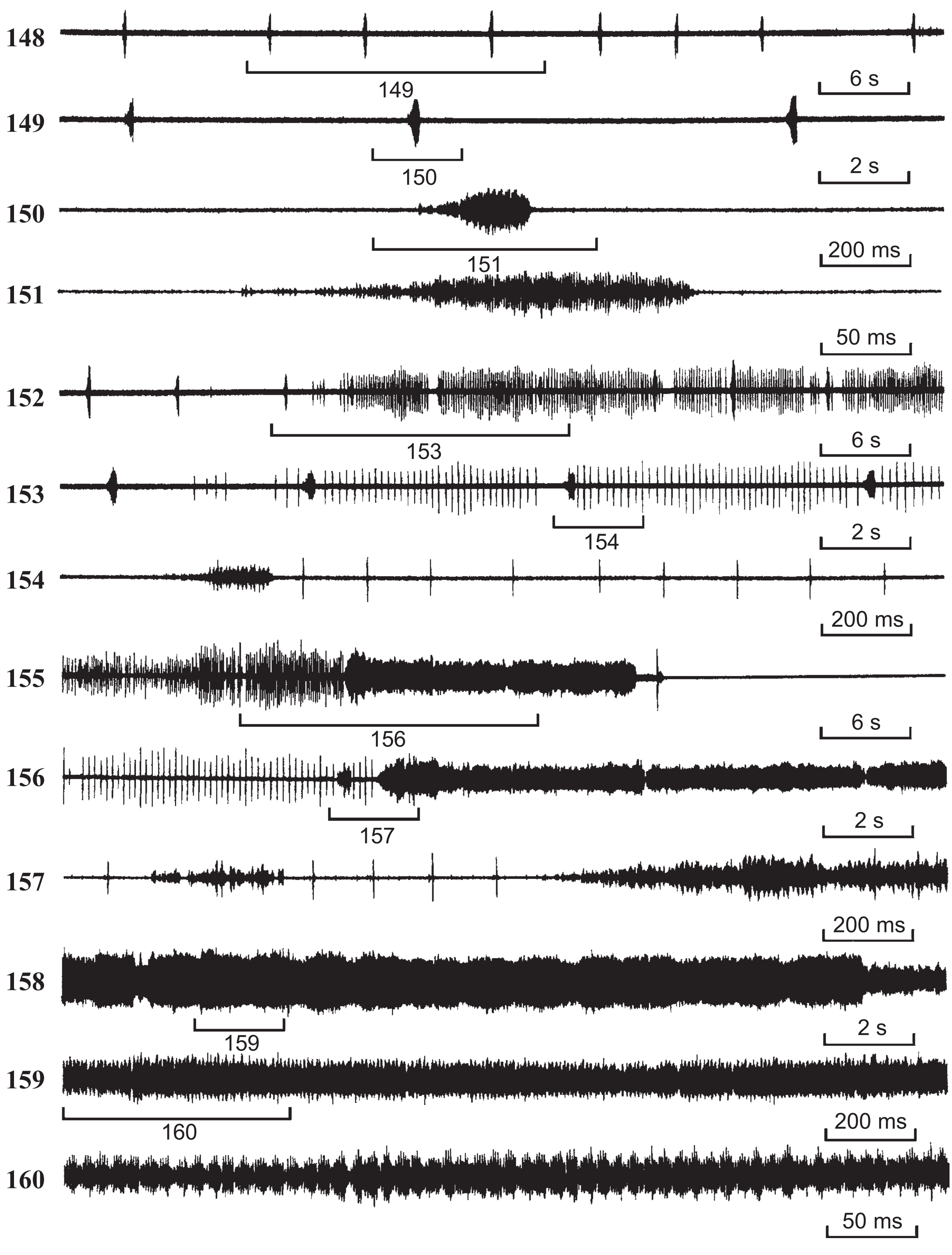
Ridge in the environs of Grozny Town. 26.VI.1986. Signals of 3 ♂♂ are recorded at the temperature 26–28°C.

SIGNALS. Calling signal is a continuous succession of phrases with rather complex structure (Fig. 168). Each phrase begins with a train of short syllables consisting of two pulses each and separated by distinct breaks. Then groups of 4–5 such syllables start alternating with more prolonged single ones, as in song of the previous species. After that a trill of pulses with



Figs 136–147. Oscillograms of acoustic signals of *Cicada orni* (L.) (136–142) and *Tibicen plebejus* (Scop.) (143–147): 136–140 — *C. orni*, calling signals, 141–142 — same, call of distress, 143–147 — *T. plebejus*, calling signals. Faster oscillograms of the parts of signals indicated as "138–140", "142" and "144–147" are given under the same numbers.

Рис. 136–147. Осциллограммы акустических сигналов *Cicada orni* (L.) (136–142) и *Tibicen plebejus* (Scop.) (143–147): 136–140 — *C. orni*, призывные сигналы, 141–142 — то же, сигналы протеста, 143–147 — *T. plebejus*, призывные сигналы. Фрагменты сигналов, помеченные цифрами "138–140", "142" и "144–147", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 148–160. Oscillograms of acoustic signals of *Cicadatra persica* Kirkaldy: 148–151 — calling signals, 152–154 — calling signals and wings clicks, 155–157 — calling and continuous signals, 158–160 — continuous signal. Faster oscillograms of the parts of signals indicated as “149–151”, “153–154”, “156–157” and “159–160” are given under the same numbers.

Рис. 148–160. Осциллограммы акустических сигналов *Cicadatra persica* Kirkaldy: 148–151 — призывные сигналы, 152–154 — призывные сигналы и щелчки крыльев, 155–157 — призывный и непрерывный сигналы, 158–160 — непрерывный сигнал. Фрагменты сигналов, помеченные цифрами “149–151”, “153–154”, “156–157” и “159–160”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

total duration about 3–5 s follows. Suddenly it changes into train of short syllables and so the next phrase begins.

In contrast with all other Auchenorrhyncha, Cicadidae for at least a half of a century are classical object of insects bioacoustics and neurophysiolgy due to their large size and loud signals, which can be easily registered by means of standard microphone. For this reason a considerable body of literature exists on this subject. The present work concerns vibrational signals of small Auchenorrhyncha, so comparative description of signals of Cicadidae is not a task of this paper. Here I present oscillograms of sounds of six species as an example and mention only few papers for the most part concerning Palaearctic representatives of the family.

In the works by Popov [Popov, 1969, 1975, 1981, 1989, 1990, 1997, 1998; Popov, Aronov, Sergeeva, 1985, 1991; Popov, Sergeeva, 1987] oscillograms and descriptions of sounds of a number of Cicadidae species from the territory of Russia and adjacent countries, including all species mentioned above with the exception of *C. persica* are given. In several cases signals temporal pattern was used as a character for solving of taxonomic problems, in particular for revealing of new species [Popov, 1989, 1990, 1997; Popov, Aronov, Sergeeva, 1985]. Similar investigations on bioacoustics and systematics of Cicadidae are in progress in Western Europe (see, for example, Joermann, Schneider, 1987; Boulard, Quartau, 1991; Boulard, 1992b; Gogala, Popov, Ribaric, 1996; Gogala, Popov, 1997; Gogala, Trilar, 1999) and in other regions [Fleming, 1984; Boulard, 1991, 1992a].

In communication system structure singing cicadas are quite dissimilar with other Cicadinea in a number of characters. First, they emit airborne waves, i.e. sounds, but not vibrational signals and, also, possess highly specialised tympanal organs for their reception. Second, only males can produce sounds in Cicadidae, whereas females are mute. Thus, acoustic communication in these insects is one-way, so receptive female comes to stationary singing male emitting no signals herself. Third, in contrast with small Auchenorrhyncha usually producing calling signals only from time to time or in short successions, males of Cicadidae as a rule sing ceaselessly for many minutes or even hours, as some crickets and bushcrickets do.

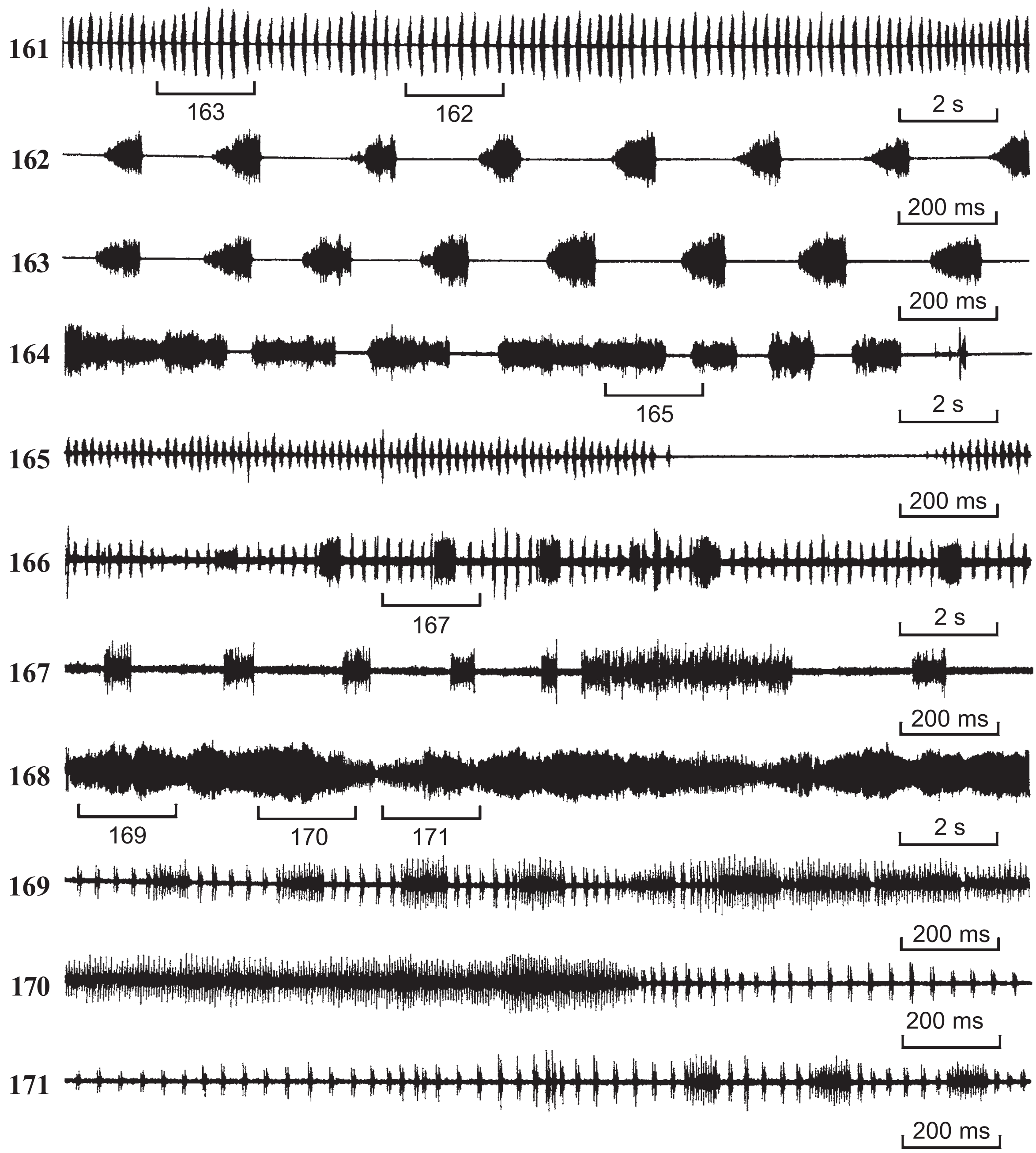
Still, both acoustic repertoire and temporal pattern of signals of cicadas do not differ much from these in other Cicadinea. Reply signals of female is the only type of signals, which is absent in Cicadidae, but presents in representatives of other families (with few exceptions in Cicadellidae, see Tishechkin, 2003). On the other hand, so called continuous signals recorded in several species of Cicadidae (see, for instance, descriptions of signals of *C. persica* above) were never registered in small Auchenorrhyncha. These signals are successions of uniform pulses lasting incessantly for several minutes and more. Signals of this type are almost indistinguishable in different species. Consequently, they cannot play any substantial role in recognition of conspecific individuals. Usually, singing male alternates continuous signals and calling ones in his song. Also, short loud shriek, produced by males of certain species, when leaving the plant being flushed, have no analogues among other Cicadinea. Certain Cicadidae species prefer to form aggregations during singing. On the other hand, in several species territorial behaviour, competition performance and signals of corresponding types were described [Popov, 1975, Cocroft, 1996].

In certain species both from Cicadidae and from other Cicadinea taxa males click fore wings during singing. In some species such clicks are facultative component of signals, which can be absent in a number of songs, whereas in other ones the wing-clicks is a necessary part of every signal.

Pure-tone signals presenting in several groups of small Auchenorrhyncha, e.g. in Typhlocybinae and related taxa of Cicadellidae [Tishechkin, 2001] are also recorded in representatives of Cicadidae [Moulds, 1975; Young, Josephson, 1983]. As in Cicadellidae, pure-tone signals of singing cicadas can be composed of distinct pulses (in one of the species of *Magicicada*, Young, Josephson, 1983), or are continuous trains of sine waves (in Australian cicada *Lembeja brunneosa* Distant, see Moulds, 1975).

Very interesting data on communication of the species from another family of Cicadoidea, namely, Tettigarctidae (*Tettigarcta crinita* Distant) were published recently [Claridge, Morgan, Moulds, 1999]. Two Australian species of *Tettigarcta* are the only recent representatives of this relict group, which was widespread during Jurassic and Cretaceous periods. Abdominal vibrations, i.e. producing of vibrational signals were observed in individuals of both sexes of *T. crinita* under natural conditions. Vibrational signals of males were registered in the laboratory. Signals consist of simple short syllables lasting for 0.24–0.74 s and following with breaks of 0.6–2.8 s, according to the paper cited. Recorded call sequence had total duration 2 min. In temporal pattern signals superficially resemble ones of some Cixiidae species, e.g. *Pentastiridius apicalis* (Uhler, 1896) (Figs 327–333) or *Hyalestes obsoletus* Signoret, 1865 (Figs 352–357).

This information is of great significance for understanding of evolution of acoustic communication system in Cicadinea. It now seems certain that intraspecific, mainly male-female two-ways interactions by means of vibrational signals is the basic type of acoustic communication in this group. Evidently, tremulation, i.e. vibration by abdomen without contact with a substrate was the first and most primitive method of signals producing. This mechanism does not require any special morphological structures and occurs until now in several rather archaic groups (see above discussion in the end of the item on Cercopoidea). Apparently, these are actually tremulation movements, but not motions during copulation, as it was supposed earlier [Pringle, 1957], which originate specialisation of some sclerites and their later modification into timbals, developed in more or less equal extent in both sexes. Thus, recently all Auchenorrhyncha with the exception of Cicadidae use two-ways vibrational communication. The latters are highly deviating group. It is unique among Cicadinea due to changing from vibrational to sound communication, which resulted in appearing of specialised tympanal organs for reception of airborne signals. Moreover,



Figs 161–171. Oscillograms of acoustic signals of *Cicadatra atra* (Oliver) (161–165), *Cicadetta tibialis* (Panzer) (166–167) and *C. dimissa* (Hagen) (168–171): 161–163 — *C. atra*, calling signals, 164–165 — same, call of distress, 166–167 — *C. tibialis*, calling signals, 168–171 — *C. dimissa*, calling signals. Faster oscillograms of the parts of signals indicated as "162–163", "165", "167" and "169–171" are given under the same numbers.

Рис. 161–171. Осциллограммы акустических сигналов *Cicadatra atra* (Oliver) (161–165), *Cicadetta tibialis* (Panzer) (166–167) и *C. dimissa* (Hagen) (168–171): 161–163 — *C. atra*, призывные сигналы, 164–165 — то же, сигналы протеста, 166–167 — *C. tibialis*, призывные сигналы, 168–171 — *C. dimissa*, призывные сигналы. Фрагменты сигналов, помеченные цифрами "162–163", "165", "167" и "169–171" представлены при большей скорости развертки на осциллограммах под такими же номерами.

females of Cicadidae lost timbals secondary, so communication between males and females became one-way in members of this family.

Superfamily FULGOROIDEA

Family Delphacidae

Subfamily Kelisiinae

Kelisia vittipennis (J. Sahlberg, 1867)
Figs 172–178.

LOCALITY. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, bog on the bank of lake. 6.VIII.1993, signals of 4 ♂♂ are recorded at the temperature 25°C; 16.VIII.1998, signals of 5 ♂♂ are recorded at the temperature 21–23°C.

SIGNALS. Calling signal consists of very long and complex phrases, including several different fragments each. Duration of phrase averages about 15–30 s. Usually male produces up to 4–5 phrases one after another. No other signals except calling were registered in males of this species.

Kelisia ribauti Wagner, 1938
Figs 179–184.

LOCALITY. North Caucasus, North Ossetia, Tsey Canyon (Ardon River basin), bog near spring in subalpine meadow (1800 m above sea level). 26.VII.1990. Signals of 2 ♂♂ are recorded at the temperature 22°C.

SIGNALS. In general structure, calling signal is similar with this of the previous species, but temporal pattern of phrases is quite different.

Subfamily Stenocraninae

Stenocranus major (Kirschbaum, 1868)
Figs 185–191.

LOCALITY. Moscow Area, environs of Pirogovo, bank of Klyaz'ma River. 4.VI.1989. Calling signals of 1 ♂ are recorded at 24–25°C.

SIGNALS. The main part of calling signal is a succession of syllables, following each other with a period about 1 s. Initial syllable in a phrase is somewhat longer than all subsequent ones. Occasionally, several irregular pulses precede the phrase. In the end of song several short syllables of another type presents; their number varies greatly from 2–3 up to 10–15.

Subfamily Delphacinae

Chloriona smaragdula Stål, 1853
Figs 192–195.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village. On *Phragmites australis* (Cav.) Trin. ex Steud. in irrigation ditch on roadside. 17.VI.2000. Signals of 3 ♂♂ are recorded at the temperature 21°C.

SIGNALS. Calling signal consists of syllables repeating with a period about 2–4 s (Figs 192–193). As a rule, short trains of pulses present in intervals between syllables (Fig. 193, 195).

NOTE. Signals of three European species of *Chloriona*, including *Ch. smaragdula* are described in details in Gillham, de Vrijer [1995]. Temporal pattern of signals of males from Western Europe and European Russia is quite similar.

Chloriona clavata Dlabola, 1960
Figs 196–200.

LOCALITY. Lower Volga Region, Astrakhan' Area, Dosang Railway Station, from *Phragmites australis* (Cav.) Trin. ex Steud. in irrigation ditch in a flood-land between Volga and Akhtuba rivers, 3.VII.2000. Signals of 5 ♂♂ were recorded at 26°C.

SIGNALS. In general scheme of temporal pattern calling is similar with this of the previous species. Syllables repetition period averages from 1–2 up to 6–7 s in my recordings. As in *Ch. smaragdula*, additional trains of pulses present between syllables in a number of signals (Figs 196–197, 199).

Delphax crassicornis (Panzer, 1796)
Figs 201–204.

LOCALITY. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, bog on the bank of lake, on *Phragmites australis* (Cav.) Trin. ex Steud. 28.VII.1994, signals of 1 ♂ are recorded at the temperature 23°C.

SIGNALS. Calling signal consists of short syllables following each other with intervals from 2–3 up to 10–15 s.

Megamelus notula (Germar, 1830)
Figs 205–212.

LOCALITY. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, bog in the flood-land of Moskva River. 20.VIII.1994. Signals of 5 ♂♂ are recorded at the temperature 20°C.

SIGNALS. Calling signal of this species is a succession of short syllables repeating with rather irregular intervals from 1 approximately up to 7–8 s (Figs 205–208). Occasionally, low-amplitude noise-like vibrations present in intervals between syllables (Figs 206, 208).

In several males sitting on the same leaf of host plant signal of another type was also registered. Sometimes it consists of short trains of pulses following each other with regular period of about 2–3 s (Figs 209–210). Occasionally, male can sing for 20–30 min in such a manner. In other cases length of successions of pulses, as well as intervals between them and pulses repetition period become more instable (Figs 211–212). At times male produce such signal simultaneously with calling (Fig. 212). Possibly, these signals are two different types of rivalry one. Similar variability of rivalry signals was described by Booij [1982] in one of the species of *Muellerianella*.

Megamelus flavus (Crawford, 1914)
Figs 213–216.

LOCALITY.South Siberia, Southern Tuva, environs of Erzin Village, flood-plain of Tes-Khem River, on *Carex* sp. in bog. 6.VIII.1989. Signals of 2♂♂ are recorded at the temperature 23°C.

SIGNALS. Calling signal is a short phrase consisting of 2–3 syllables. Occasionally, in intervals between syllables and even between phrases low-amplitude noise-like vibrations present (Figs 214, 216).

Hyledelphax elegantula (Boheman, 1847)
Figs 217–223.

LOCALITY. Altai Mountains, Altaiskiy Nature Reserve, S shore of Teletskoe Lake, in forest near Chiri River. 12.VII.1999. Calling signals of 2 ♂♂ are recorded at the temperature 24°C.

SIGNALS. Calling signal consists of 4–5 fragments (syllables or short phrases). Duration of signal averages 4–5 s. The first and sometimes also the last fragments in a signal have somewhat different temporal pattern, than the middle ones.

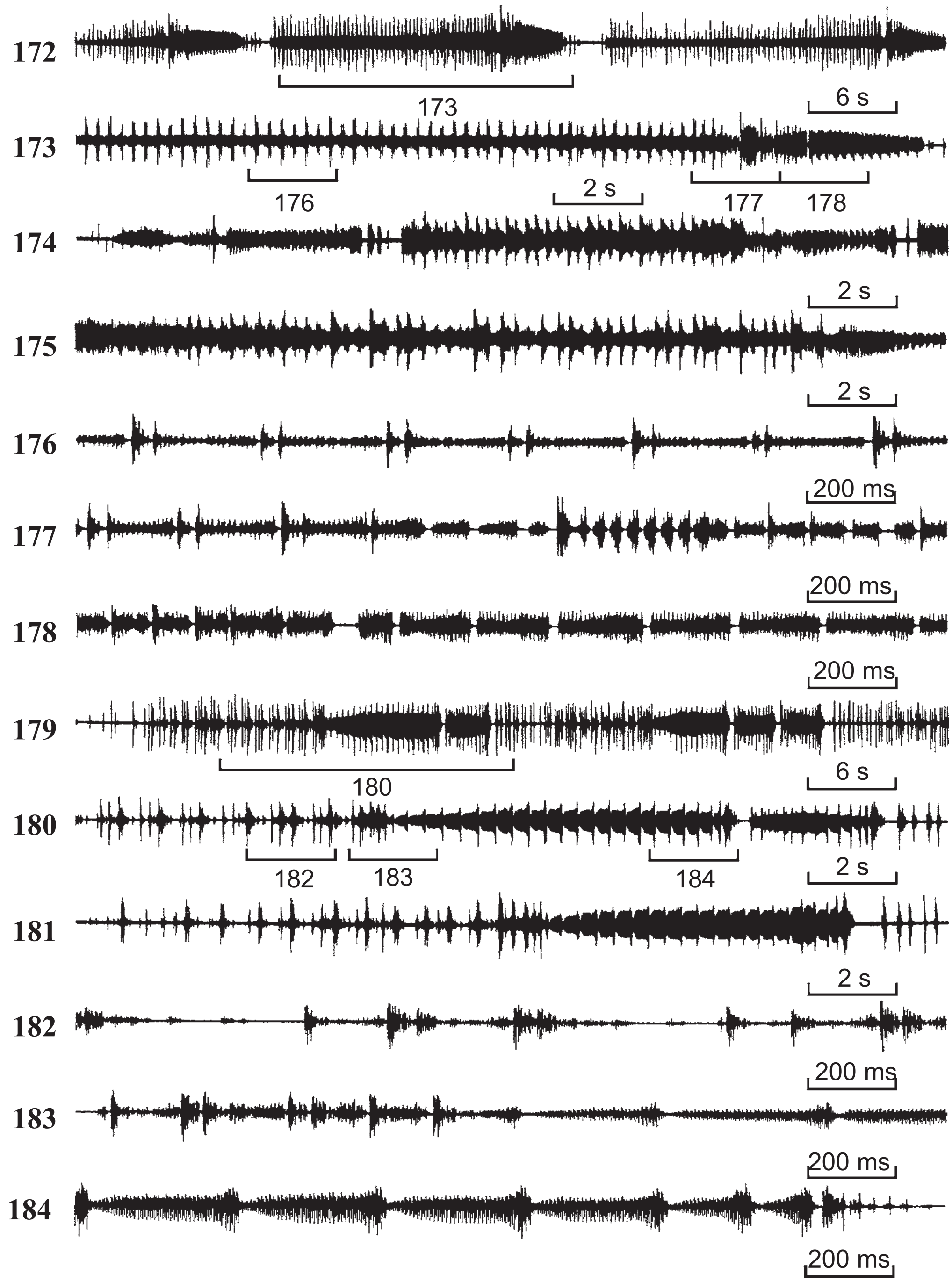
Struebingianella lugubrina (Boheman, 1847)
Figs 224–228.

LOCALITY. Moscow Area, forest in the environs of Naro-Fominsk Town. 14–15.VI.1987. Signals of 4 ♂♂ and 1 ♀ are recorded at the temperature 24–26°C.

SIGNALS. Male calling signal consists of repeating phrases (Figs 224–225). Each phrase begins with a trill composed of discrete pulses. Duration of trill can vary from 2–3 up to 7–10 s. Then a short fragment lasting for 1.5–2 s and consisting of partially merged pulses follows.

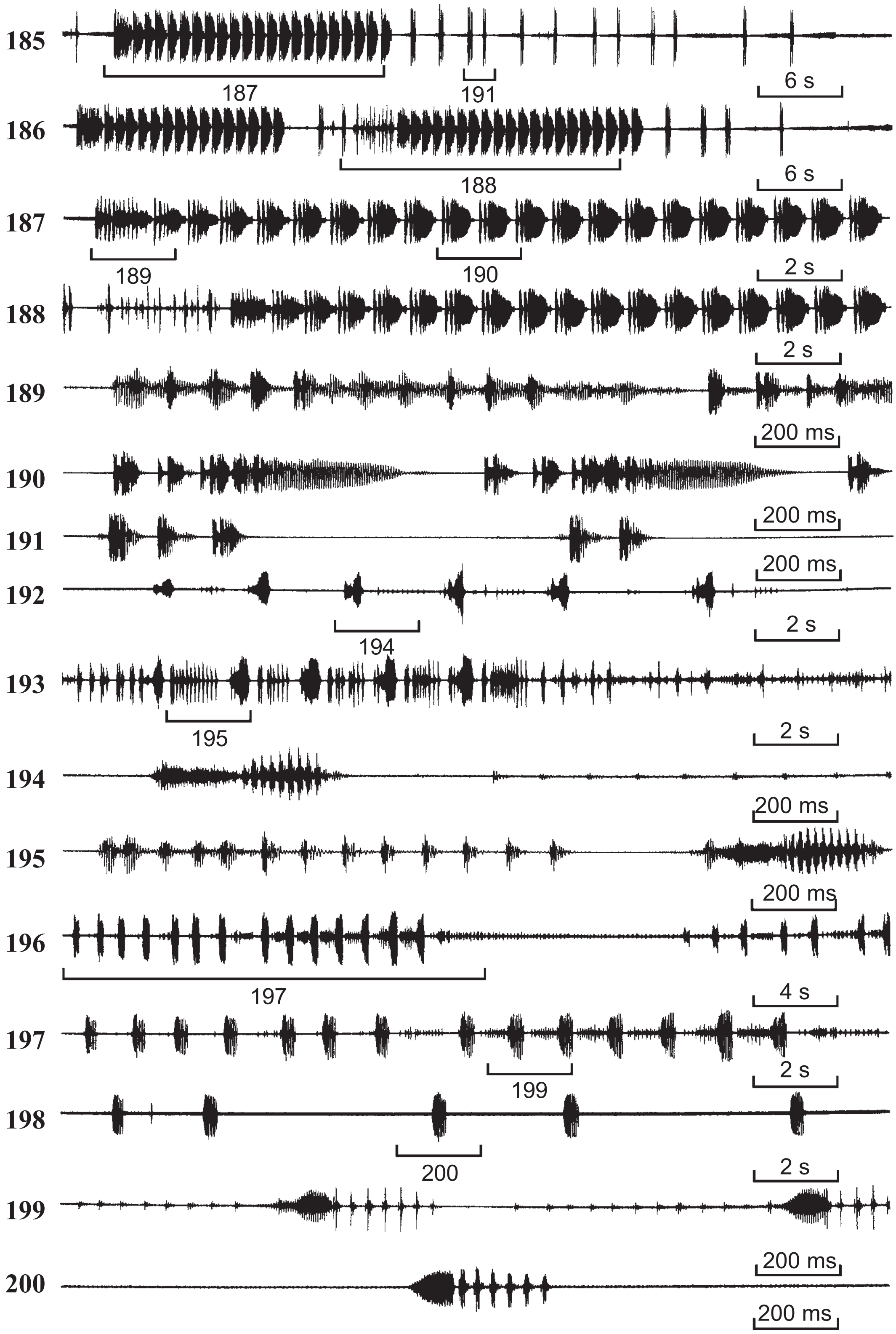
Receptive female produces reply signals in the end of each phrase of male calling (Fig. 226). As in all other species of Delphacidae studied, female reply in S. *lugubrina* is a train of simple pulses (Figs 227–228). For some time insects sing alternately, then male approaches female and starts copulation. In my experiment copulation lasted for 10 minutes. No other signals except male calling and female reply were recorded during mating behaviour.

NOTE. Also, calling signals of this species are described in Strübing, Rollenhagen [1988].



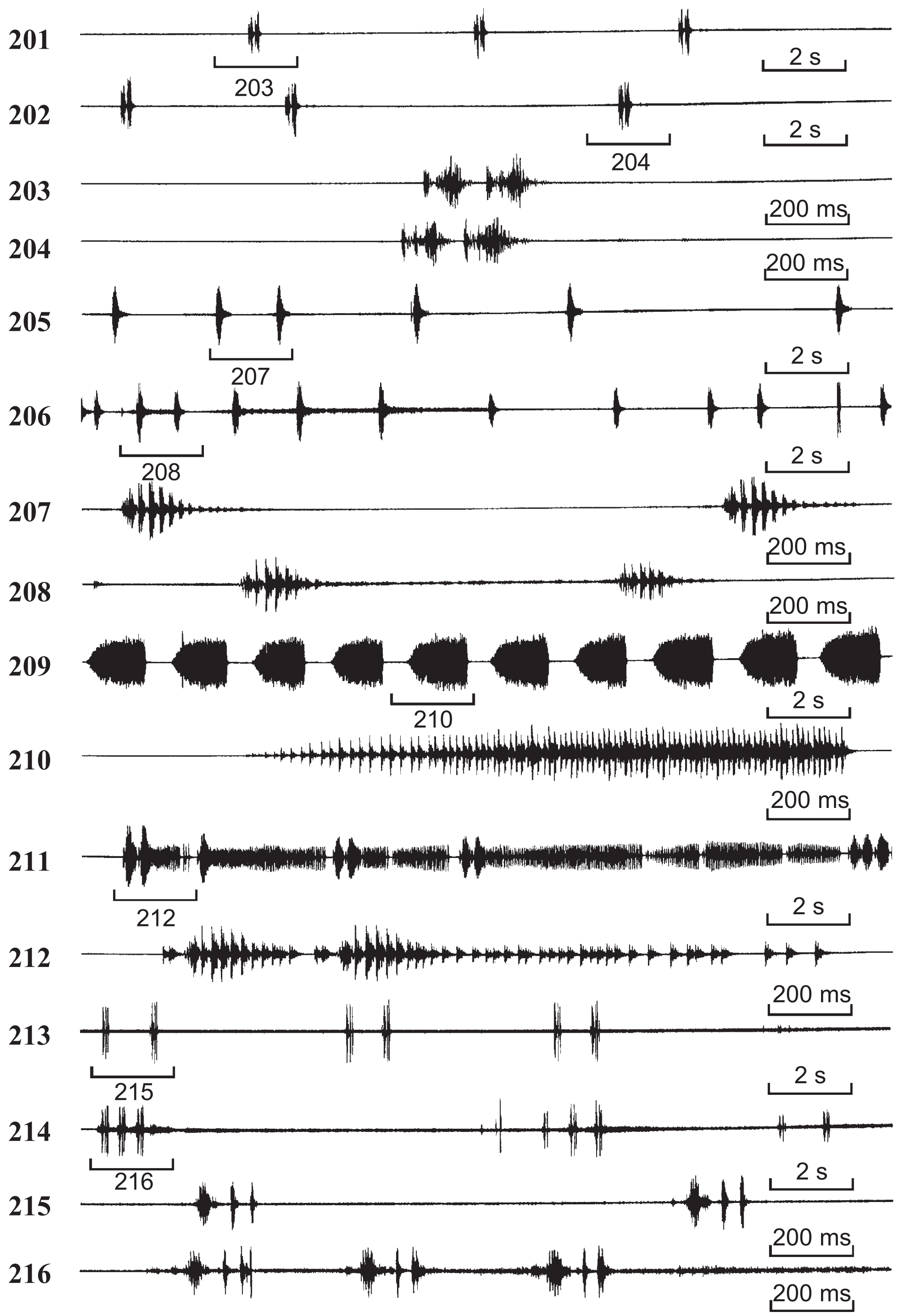
Figs 172–184. Oscillograms of calling signals of *Kelisia vittipennis* (J. Sahlb.) (172–178) and *K. ribauti* Wagn. (179–184). Faster oscillograms of the parts of signals indicated as “173”, “176–178”, “180” and “182–184” are given under the same numbers.

Рис. 172–184. Осциллограммы призывных сигналов *Kelisia vittipennis* (J. Sahlb.) (172–178) и *K. ribauti* Wagn. (179–184). Фрагменты сигналов, помеченные цифрами “173”, “176–178”, “180” и “182–184”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



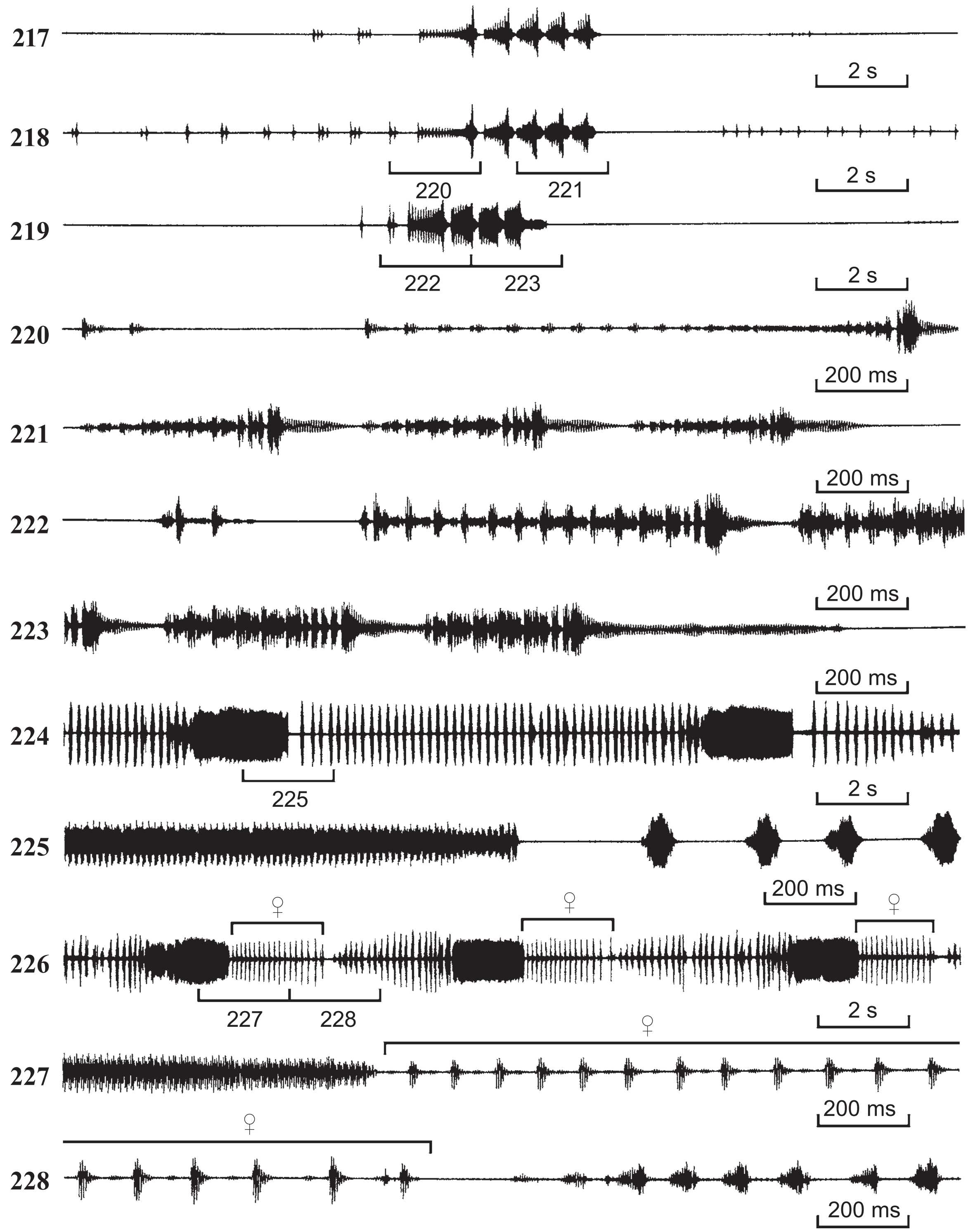
Figs 185–200. Oscillograms of calling signals of *Stenocranus major* (Kbm.) (185–191), *Chloriona smaragdula* Stål (192–195) and *Ch. clavata* Dlab. (196–200). Faster oscillograms of the parts of signals indicated as “187–191”, “194–195”, “197” and “199–200” are given under the same numbers.

Рис. 185–200. Осциллограммы призывных сигналов *Stenocranus major* (Kbm.) (185–191), *Chloriona smaragdula* Stål (192–195) и *Ch. clavata* Dlab. (196–200). Фрагменты сигналов, помеченные цифрами “187–191”, “194–195”, “197” и “199–200”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 201–216. Oscillograms of vibrational signals of *Delphax crassicornis* (Panzer) (201–204), *Megamelus notula* (Germ.) (205–212) and *M. flavus* (Crawford) (213–216): 201–204 — *D. crassicornis*, calling signals, 205–208 — *M. notula*, calling signals, 209–210 — same, rivalry signals, 211–212 — same, calling and rivalry signals, 213–216 — *M. flavus*, calling signals. Faster oscillograms of the parts of signals indicated as "203–204", "207–208", "210", "212" and "215–216" are given under the same numbers.

Рис. 201–216. Осциллограммы вибрационных сигналов *Delphax crassicornis* (Panzer) (201–204), *Megamelus notula* (Germ.) (205–212) и *M. flavus* (Crawford) (213–216): 201–204 — *D. crassicornis*, призывные сигналы, 205–208 — *M. notula*, призывные сигналы, 209–210 — то же, сигналы соперничества, 211–212 — то же, призывные сигналы и сигналы соперничества, 213–216 — *M. flavus*, призывные сигналы. Фрагменты сигналов, помеченные цифрами "203–204", "207–208", "210", "212" и "215–216", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 217–228. Oscillograms of vibrational signals of *Hyledelphax elegantula* (Boh.) (217–223) and *Struebingianella lugubrina* (Boh.) (224–228): 217–223 — *H. elegantula*, calling signals, 224–225 — *S. lugubrina*, calling signals, 226–228 — same, male calling and female reply signals. Faster oscillograms of the parts of signals indicated as "220–223", "225", and "227–228" are given under the same numbers.

Рис. 217–228. Осциллограммы вибрационных сигналов *Hyledelphax elegantula* (Boh.) (217–223) и *Struebingianella lugubrina* (Boh.) (224–228): 217–223 — *H. elegantula*, призывные сигналы, 224–225 — *S. lugubrina*, призывные сигналы, 226–228 — то же, призывные сигналы самца и ответные сигналы самки. Фрагменты сигналов, помеченные цифрами "220–223", "225", и "227–228", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Xanthodelphax xantha Vilbaste, 1965
Figs 229–235.

LOCALITY. Altai Mountains, Altaiskiy Nature Reserve, S shore of Teletskoe Lake, Chiri, mouth of Kyga River. 11.VII.1999. Calling signals of 2 ♂♂ are recorded at the temperature 23°C.

SIGNALS. Calling signal is a succession of phrases having complex temporal structure. Usually, phrases repeat with regular period averaging 2–3 s (Figs 229–230), occasionally, it reaches 4–5 s (Fig. 231).

Herbalima eforia (Dlabola, 1961)
Figs 236–240.

LOCALITY. Lower Volga Region, Astrakhan' Area, Dosang Railway Station, in irrigation ditch in a flood-land between Volga and Akhtuba rivers, 4.VII.2000. Signals of 6 ♂♂ were recorded at 26°C.

SIGNALS. Calling signals are single or repeating short syllables (Figs 236–238). Each syllable consists of several (8–12) high-amplitude pulses and monotonous low-amplitude part, which is visible on oscillograms at high amplification only (Fig. 240). Occasionally, trains of pulses present in intervals between syllables (Figs 236, 239).

Dicranotropis hamata (Boheman, 1847)
Figs 241–243.

LOCALITY. Moscow Area, environs of Pirogovo, bank of Klyaz'ma River. 4.VI.1988. Calling signals of 2 ♂♂ are recorded at 24–25°C.

SIGNALS. Calling signal consists of prolonged phrases somewhat similar in structure with these of *S. lugubrina*. Each phrase includes three parts with different pulses repetition period.

NOTE. Oscillograms of signals of this species are presented in Strübing, Rollenhagen [1988]. Signals of specimens from Germany are quite similar with these of males from the environs of Moscow.

Javesella (Javesella) obscurella (Boheman, 1847)
Figs 244–252.

LOCALITIES. Moscow Area: (1) forest in the environs of Naro-Fominsk Town, 14.VI.1987, signals of 1 ♂ are recorded at the temperature 25–26°C; (2) environs of Pirogovo, 11.VIII.1987, calling signals of 2 ♂♂ are recorded at 23–24°C; (3) Voskresensk District, environs of Beloozerskiy Town, 5.VIII.1987, signals of 1 ♂ are recorded at the temperature 22–24°C.

SIGNALS. In a most simple case calling signal is a succession of syllables with total duration about 1.5–3 s (Figs 247–248, 251–252). Sometimes, trains of pulses having different structure present between successions (Figs 244, 246), or even between syllables of the same succession (Figs 245, 250).

NOTE. Detailed study of acoustic signals of a number of European *Javesella* species including *J. obscurella* was provided by de Vrijer [1986]. Nonetheless, only simple variation of calling of this species (same as in Figs 247–248) is presented on oscillograms in his paper.

Javesella (Javesella) dubia (Kirschbaum, 1868)
Figs 253–258.

LOCALITY. Moscow Area, forest in the environs of Naro-Fominsk Town, 14.VI.1987, signals of 1 ♂ are recorded at the temperature 24–25°C.

SIGNALS. Most simple variation of calling signal is a succession of syllables with total duration varying from 2 up to 6 s (Fig. 253). Sometimes, additional trains of pulses or syllables present between main successions (Figs 254–255).

NOTE. Signals of *J. dubia* from European populations were studied by de Vrijer [1986], but as in the previous species, only simple variation of calling of *J. dubia* (as in Fig. 253) is presented on illustrations in the paper cited.

Javesella (Javesella) pellucida (Fabricius, 1794)
Figs 259–264.

LOCALITIES. Moscow Area: (1) forest in the environs of Naro-Fominsk Town, 14–15.VI.1987, calling signals of 2 ♂♂ are recorded at the temperature 25–26°C; (2) environs of Pirogovo, 11.VIII.1987, calling signals of 1 ♂ are recorded at 23–24°C.

SIGNALS. Calling signal is a long phrase consisting of several different parts and lasting for about 8–15 s. Duration of different components of a phrase can vary in different individuals (Figs 259–261).

NOTE. Signals of individuals from European Russia are quite similar with these of specimens from Western Europe, presented on oscillograms in the articles by de Vrijer [1984, 1986].

Javesella (Haffnerianella) stali (Metcalf, 1943)
Figs 265–272.

LOCALITY. Moscow Area, environs of Pirogovo, bank of Klyaz'ma River, on *Equisetum* sp. 3.VI.1988, calling signals of 2 ♂♂ are recorded at 24–25°C; 7.VI.1988, signals of 2 ♂♂ and 2 ♀♀ are recorded at 28–29°C.

SIGNALS. Calling signal is a continuous succession of repeating phrases (Figs 265–266). Each phrase includes short comparatively high-amplitude trill (Fig. 267) and low-amplitude train of syllables (Fig. 268). Occasionally, after the trill several discrete pulses follow (Figs 265–267). Male can sing ceaselessly for more than 10 minutes.

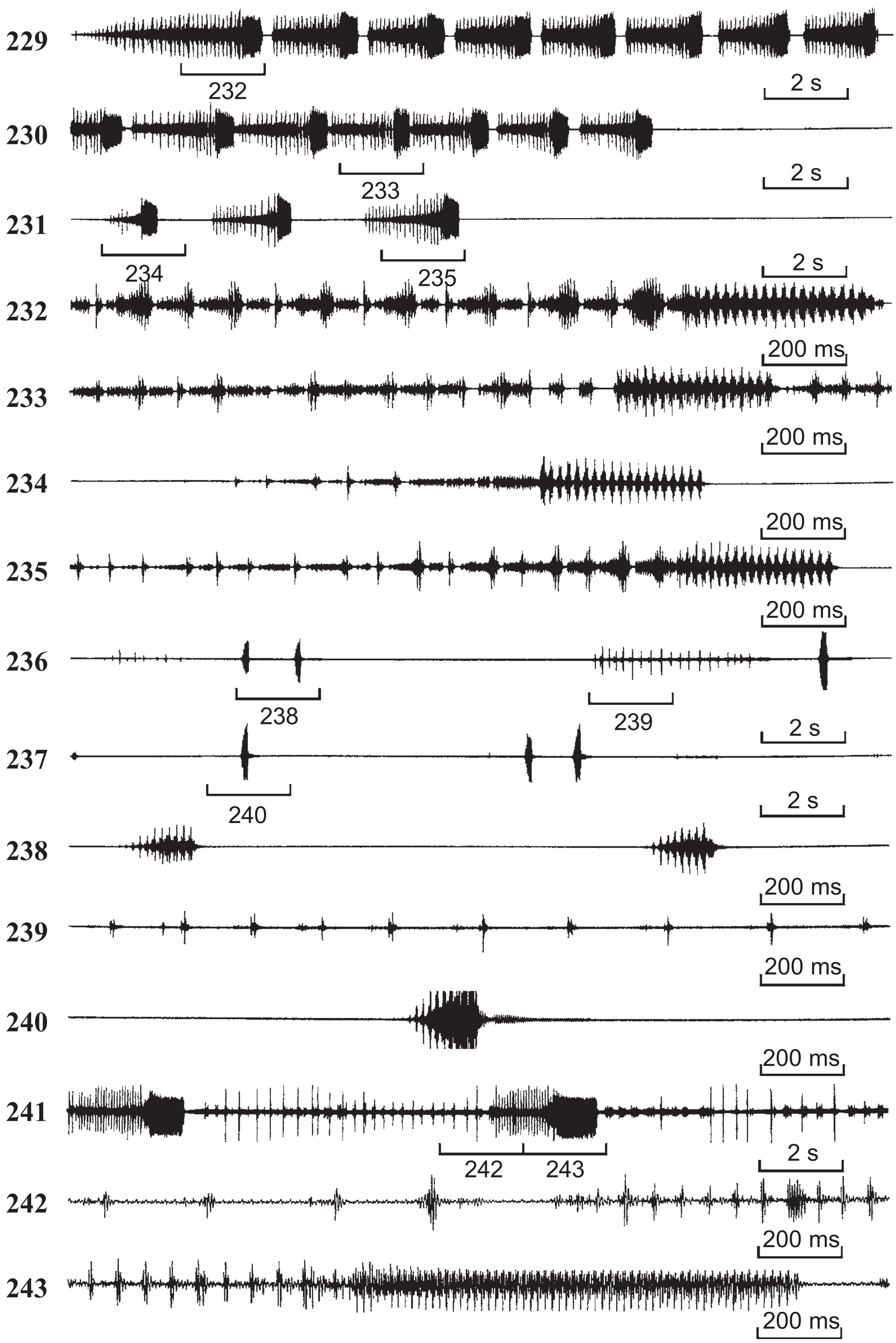
As in other planthoppers, female reply signals in *J. stali* are short trains of simple pulses (Figs 269–272). Immediately after hearing female reply male approaches her. For some time mates sing alternately (Figs 269–270), then they join their genitalia. Copulation lasts about 20–30 s, soon after it male starts singing again.

Metropis mayri Fieber, 1866
Figs 273–284.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village. On *Festuca* sp. on steppe slopes and meadows on the bank of Oka River. 3–4.VI.1987. Signals of about 10 ♂♂ are recorded at the temperature 20–21°C.

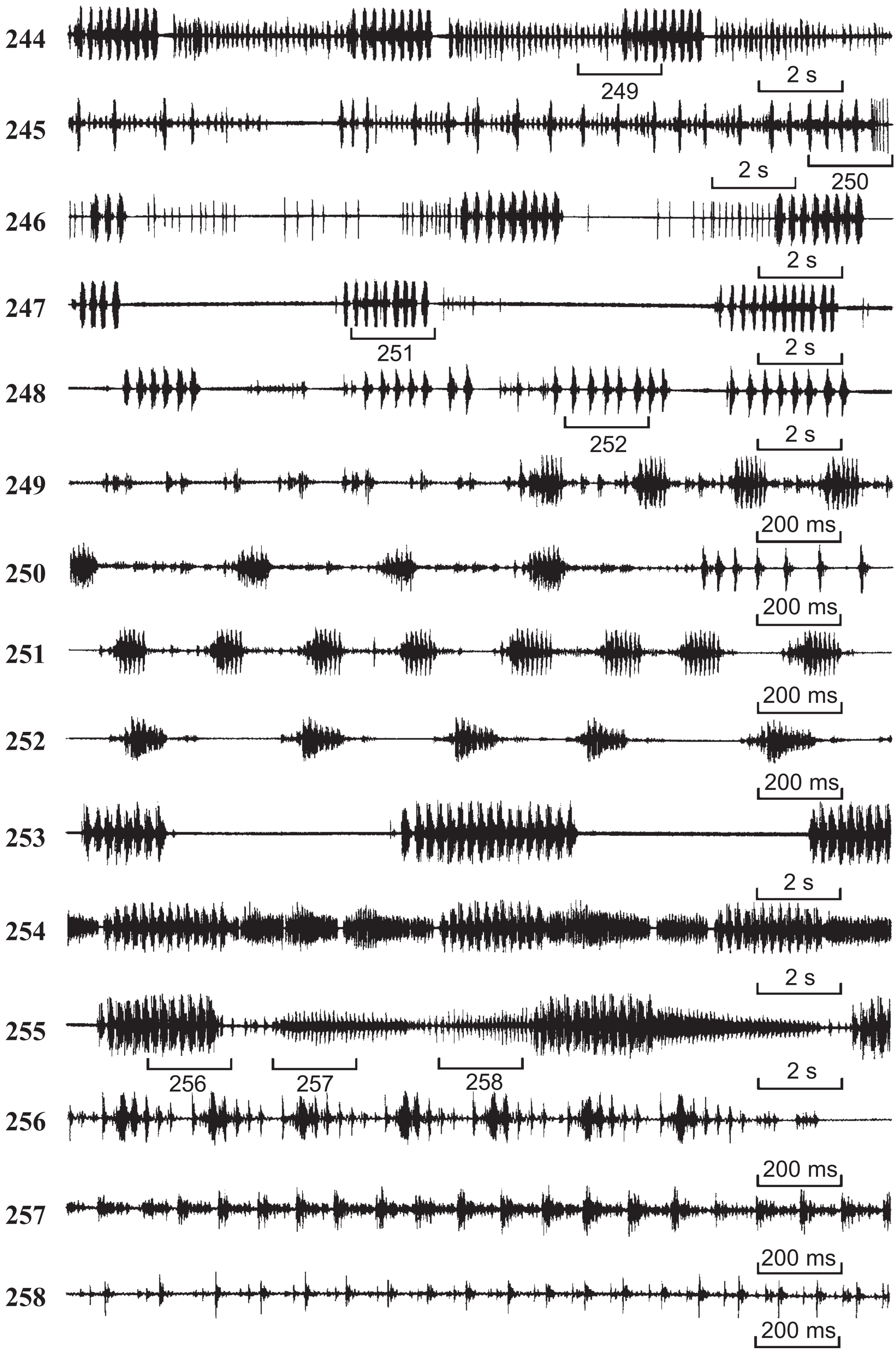
SIGNALS. Calling of *M. mayri* has rather complex temporal structure somewhat similar with this of the previous species (Figs 273–276). For the most part signal consists of trains of low-amplitude syllables alternating with single high-amplitude ones of another type (Figs 277, 280). Occasionally 2–3 such syllables follow one by one (Fig. 276, the beginning of the oscillogram). From time to time male produces additional syllable between two high amplitude ones (Fig. 278, the middle of the oscillogram, Fig. 281, the beginning of the oscillogram). Male can sing ceaselessly for 10 minutes and more.

Several males sitting in the same cage sometimes produce rivalry signals either spontaneously, or in reply to fragments of calling (Figs 282–284). They can even launch an attack, trying to push each other from the stem.



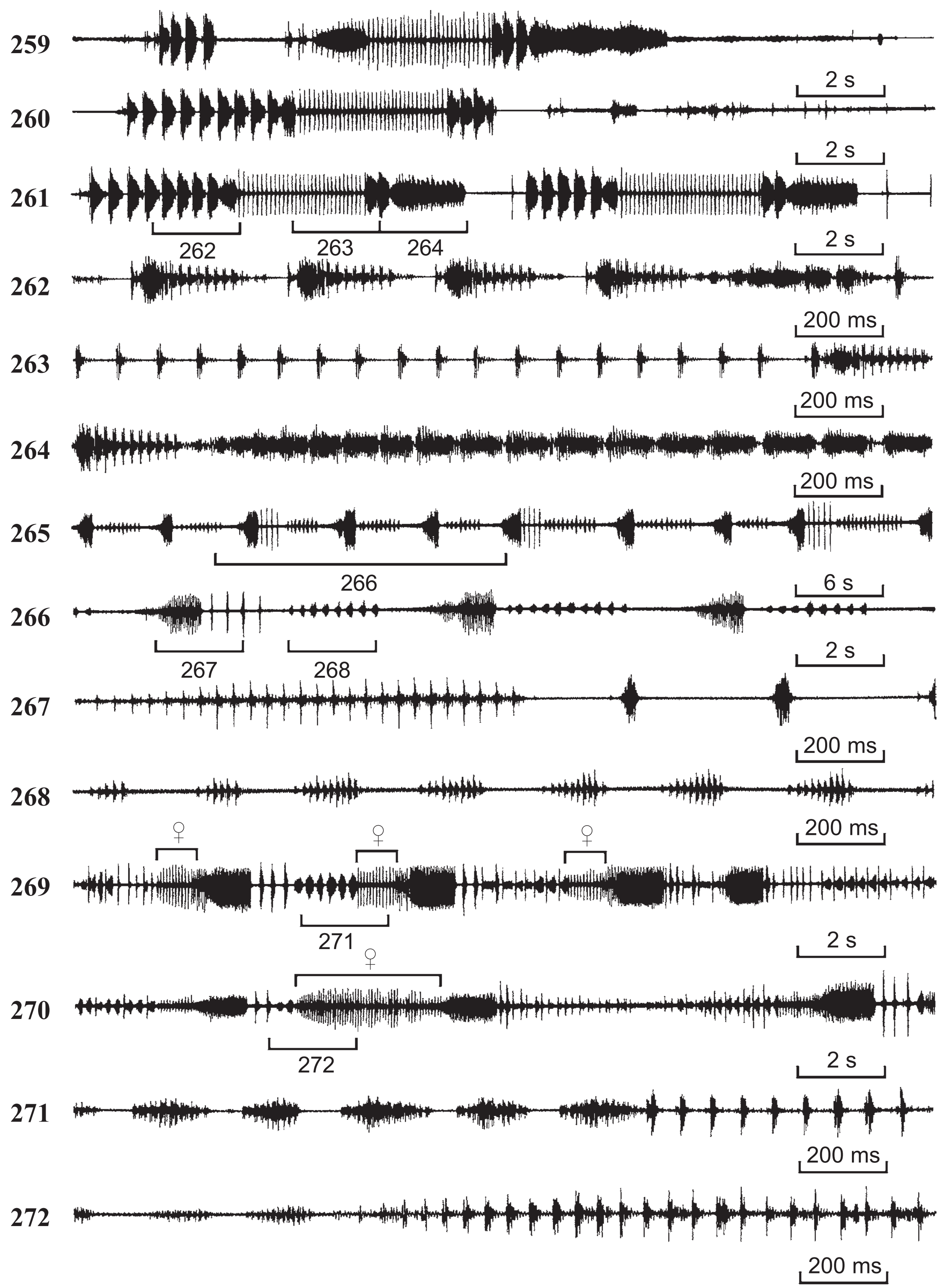
Figs 229–243. Oscillograms of calling signals of *Xanthodelphax xantha* Vilb. (229–235), *Herbalima eforia* (Dlab.) (236–240) and *Dicranotropis hamata* (Boh.) (241–243). Faster oscillograms of the parts of signals indicated as "232–235", "238–240" and "242–243" are given under the same numbers.

Рис. 229–243. Осциллограммы призывных сигналов *Xanthodelphax xantha* Vilb. (229–235), *Herbalima eforia* (Dlab.) (236–240) и *Dicranotropis hamata* (Boh.) (241–243). Фрагменты сигналов, помеченные цифрами "232–235", "238–240" и "242–243", представлены при большей скорости развертки на осциллограммах под такими же номерами.



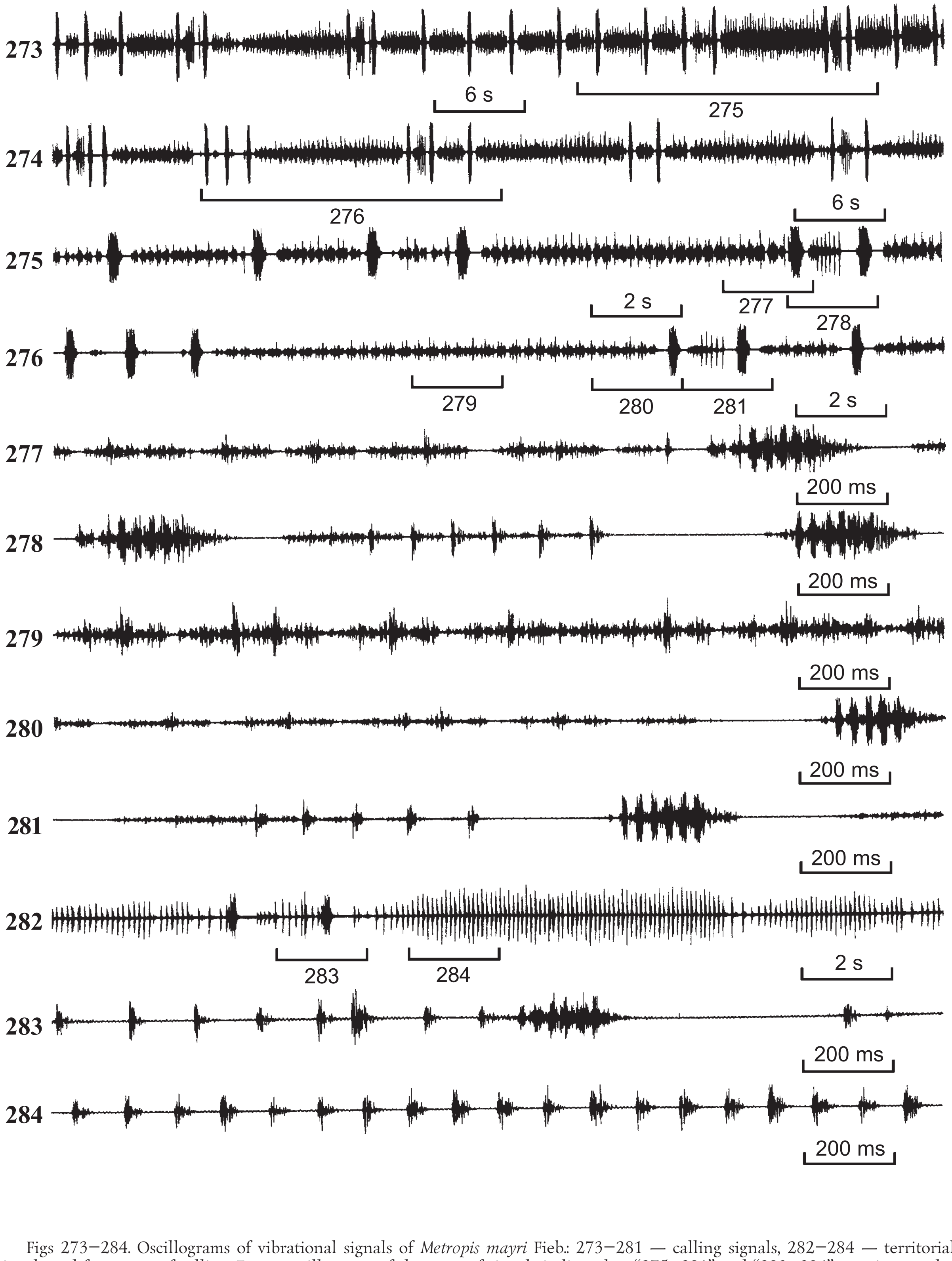
Figs 244–258. Oscillograms of calling signals of *Javesella obscurella* (Boh.) (244–252) and *J. dubia* Kbm. (253–258). Faster oscillograms of the parts of signals indicated as "249–252", and "256–258" are given under the same numbers.

Рис. 244–258. Осциллограммы призывных сигналов *Javesella obscurella* (Boh.) (244–252) и *J. dubia* Kbm. (253–258). Фрагменты сигналов, помеченные цифрами "249–252", и "256–258", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 259–272. Oscillograms of vibrational signals of *Javesella pellucida* (F.) (259–264) and *J. stali* (Metcalf) (265–272): 259–264 — *J. pellucida*, calling signals, 265–268 — *J. stali*, calling signals, 269–272 — same, male calling and female reply signals. Faster oscillograms of the parts of signals indicated as "262–264", "266–268", and "271–272" are given under the same numbers.

Рис. 259–272. Осциллограммы вибрационных сигналов *Javesella pellucida* (F.) (259–264) и *J. stali* (Metcalf) (265–272): 259–264 — *J. pellucida*, призывные сигналы, 265–268 — *J. stali*, призывные сигналы, 269–272 — то же, призывные сигналы самца и ответные сигналы самки. Фрагменты сигналов, помеченные цифрами "262–264", "266–268", и "271–272", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 273–284. Oscillograms of vibrational signals of *Metropis mayri* Fieb.: 273–281 — calling signals, 282–284 — territorial signals and fragments of calling. Faster oscillograms of the parts of signals indicated as "275–281" and "283–284" are given under the same numbers.

Рис. 273–284. Осциллограммы вибрационных сигналов *Metropis mayri* Fieb.: 273–281 — призывные сигналы, 282–284 — территориальные сигналы и фрагменты призыва. Фрагменты сигналов, помеченные цифрами "275–281" и "283–284", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Stiroma bicarinata (Herrich-Schäffer, 1835)
Figs 285–288.

LOCALITY. Moscow Area, environs of Pirogovo, bank of Klyaz'ma River. 3.VI.1988. Calling signals of 2 ♂♂ are recorded at 25–26°C.

SIGNALS. Calling signal consists of short syllables repeating with a period about 3–5 s (Figs 285, 287). Sometimes trains of rather low-amplitude pulses present between syllables (Figs 286, 288).

Stiroma affinis Fieber, 1866
Figs 289–298.

LOCALITY. Altai Mountains, Altaiskiy Nature Reserve, S shore of Teletskoe Lake, in forest near Chiri River. 12.VII.1999. Calling signals of 1 ♂ are recorded at the temperature 24°C.

SIGNALS. Calling signal consists of rather complex phrases with variable structure. All the variations presented on the oscillograms were recorded from the same male.

Among small Auchenorrhyncha, Delphacidae are the most popular objects of bioacoustic studies. Considerable part of works on vibrational signals of Cicadinea is concerned with species from this family. Still, only species from the family Delphacinae were studied by other authors until now.

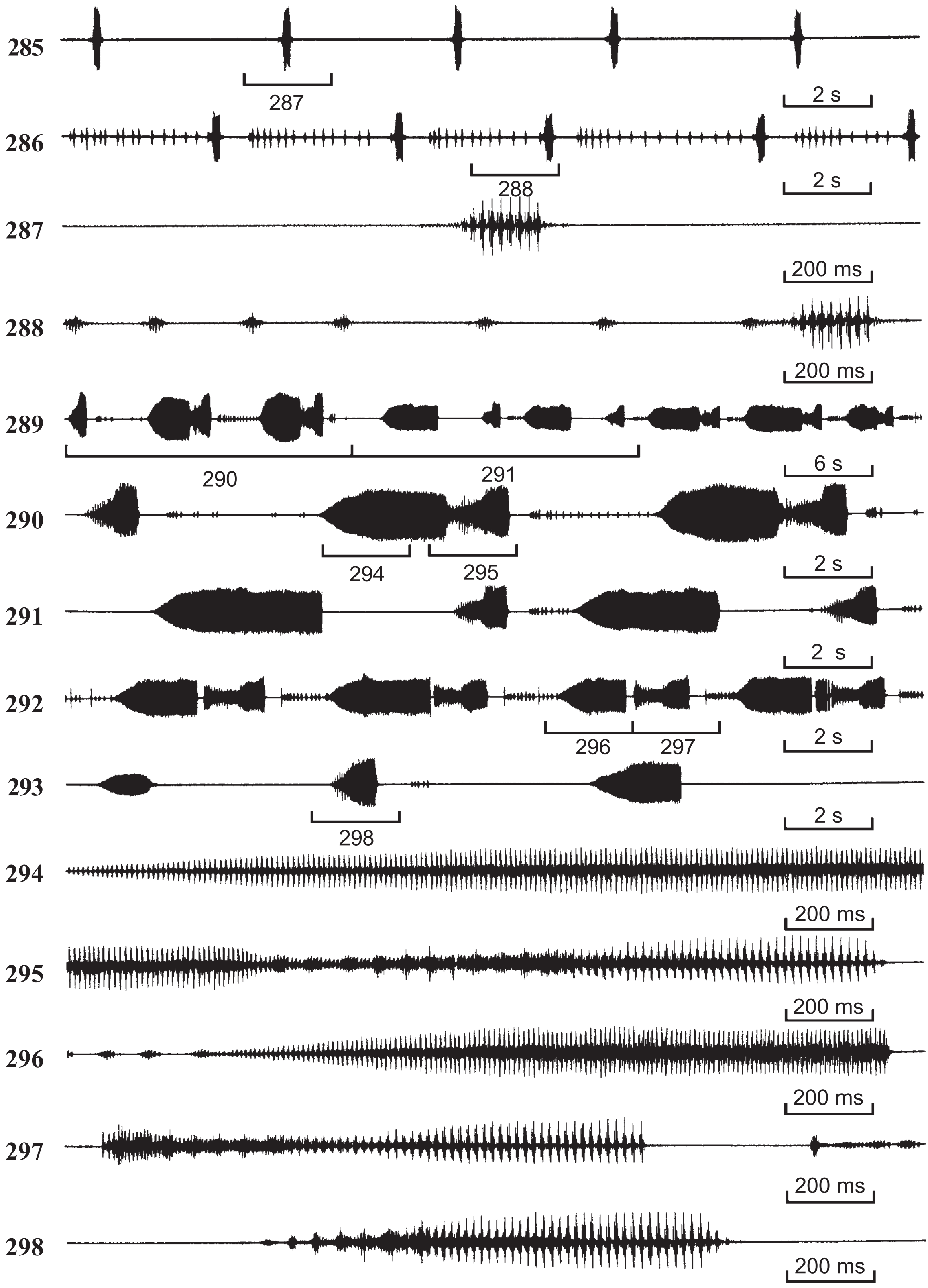
Three species of rice-dwelling planthoppers were the first representatives of small Auchenorrhyncha for which was proved conclusively, that their acoustic signals transmit via substrate i.e. leaves and stems of host plants [Ichikawa, Ishii, 1974; Ichikawa, Sakuma, Ishii, 1975; Ichikawa, 1976]. Later, detailed study of acoustic signals and associated behaviour of one of the most important rice pests, *Nilaparvata lugens* (Stål), was provided by a number of authors. Ichikawa [1982] demonstrated that competitive behaviour in males of this species depends much on population density at which individuals were reared. Competing males reared at a low density usually produce calling signals alternately or emit so called pre-aggressive signals being in close proximity with each other. Individuals reared at high density either produce rivalry signals or even launch attack trying to drive adversary away from the plant in similar situation. Variation in calling signals of *N. lugens* from different localities in India, South-East Asia and Northern Australia was investigated by Claridge and co-authors [Claridge, Den Hollander, Morgan, 1984, 1985a]. None of the populations studied demonstrated reproductive isolation from other ones in hybridisation tests. The success of hybridisation varied in different experiments and depended on difference in the pulse repetition period in calling signals of males from populations crossing, however. Also, the form feeding on weed grass *Leersia hexandra* was revealed. It differed from rice-associated populations in host and oviposition preference as well as in temporal parameters of acoustic signals [Claridge, Den Hollander, Morgan, 1985b, 1988]. It was supposed that this form represents separate biological species.

On the other hand, obvious differences in calling signals structure were found between different populations of *Nilaparvata bakeri* (Muir) closely related to *N. lugens*. In spite of such geographical variability mate choice experiments revealed no significant assortative mating between different populations. Thus, it was shown that difference in signals temporal pattern in planthoppers does not always indicate the presence of different biological species [Claridge, Morgan, 1993].

Both male calling and female reply signals in 5 european species of *Javesella* were studied by de Vrijer [1984, 1986]. Interspecific difference in signals temporal pattern appeared to be much more pronounced in males, than in females. Moreover, in two species female reply signals could not be distinguished. More detailed investigation of variability of signals was performed on *J. pellucida* [de Vrijer, 1986]. Waveform in a signal appeared to be extremely variable depending on physical properties of a substrate, but the basic temporal structure of signal remained unaffected. Most of time-related parameters are distinctly temperature dependent. Females showed high percentage of response reactions to play-back of male calling signals at temperatures differing by 5 °C from temperature at which male calling was recorded. Difference of 10 °C reduced female responsivity by more than 50 %.

Detailed investigation of vibrational signals of three *Muellerianella* species from West-European populations was provided by Booij [1982]. Not only male calling and female reply, but also, signals of other types were investigated. Males of all species produce rivalry signals either in reply to calling of another individual or being in close contact with each other. Normally, these signals are continuous trills, but in *M. brevipennis* in addition to typical rivalry calls another ones consisting of repeating syllables were registered. In contrast with all other Delphacidae studied, distinct changes in the structure of male signals during courtship behaviour were found in the representatives of the genus. Therefore, acoustic repertoire of *Muellerianella* species includes courtship, precopulatory and copulatory signals additionally. Further data on acoustic communication and mating behaviour in two bisexual species and one pseudogamous form of *Muellerianella* are presented in Drosopoulos [1985].

Comprehensive study of signals of several species of *Ribautodelphax* was undertaken by den Bieman [1986, 1987] and de Winter and Rollenhagen [1990]. General scheme of temporal pattern of calling signals is similar in all representatives of the genus, resembling this of *D. hamata* (Figs 241–243). Still, according to data given in the papers cited above, all species studied differ from each other in this character. Moreover, four new taxa were revealed basing on acoustic analysis. Detailed investigation of different types of variability of signals parameters with using of statistical methods was accomplished. In playback experiments females occasionally responded to calling of heterospecific males. However, even spontaneously calling females ceased singing immediately after hearing signals of non-congeneric males (*Javesella* and *Delphacodes*). Female reply signals in *Ribautodelphax* are trills of simple discrete pulses, as in all other Delphacidae studied. Both their duration and pulses repetition rate varies greatly within the species



Figs 285–298. Oscillograms of calling signals of *Stiroma bicarinata* (H.–S.) (285–288) and *S. affinis* Fieb. (289–298). Faster oscillograms of the parts of signals indicated as "287–288", "290–291" and "294–298" are given under the same numbers.

Рис. 285–298. Осциллограммы призывных сигналов *Stiroma bicarinata* (H.-S.) (285–288) и *S. affinis* Fieb. (289–298). Фрагменты сигналов, помеченные цифрами "287–288", "290–291" и "294–298", представлены при большей скорости развертки на осциллограммах под такими же номерами.

(studied in *R. pungens* and in so called Taxon 4, see den Bieman, 1987). On the other hand, it was shown that when offered a choice between female playback signals, male significantly more often moved towards the conspecific call. Consequently, not only females but also males are capable to recognise conspecific mate during acoustic interference [de Winter, Rollenhagen, 1990].

Investigation of signals of four *Chloriona* species was performed by Gillham and de Vrijer [1995] following the similar scheme. Calling and reply signals of individuals from several localities were studied. Statistical analysis of variability of temporal parameters both within and between populations was provided.

The role of acoustic signals in reproductive isolation of two closely related species of *Prokelisia* was studied by Heady and Denno [1991]. For each species both calling and reply signals were described and illustrated by oscillograms. It was shown that difference in signals structure alone does not provide full reproductive isolation. Occasionally, male and female in heterospecific pair produced signals, courted and attempted to join genitalia, but no copulations were successful.

Also, Delphacidae were used as a suitable object in investigations of physical aspects of vibrational communication in insects [Michelsen et al., 1982] and in development of recording equipment for registration of vibrational signals [Strübing, Rollenhagen, 1988].

Recently oscillograms of several Delphacidae species were published in my papers [Tishechkin, 1997, 1998]. In addition to Delphacinae s. str. signals of two *Kelisia* (Kelisiinae) and one *Stenocranus* (Stenocraninae) species were presented in these works.

During the last two decades considerable progress in systematics of Delphacidae was achieved due to the works by Asche [1985], Yang and co-authors [Yang, Yang, 1986; Yang, 1989], Emeljanov [1995] and other authors. The classification proposed by Asche [1985] became widely accepted recently in unchanged or somewhat modified form.

According to this system, all species which signals were studied until now belong to comparatively advanced subfamilies Kelisiinae (two *Kelisia* species), Stenocraninae (*S. major*) and Delphacinae (the rest of species). Emeljanov [1995] includes the former two groups into Delphacinae as tribes. It is impossible to discriminate these three taxa or to separate any groups within Delphacinae s. str. basing on material available. Calling signals with similar temporal pattern often can be found in representatives of different groups in Delphacidae. *M. notula* (Figs 205–208), *H. eforia* (Figs 236–240) and *S. bicarinata* (Figs 285–288) or *S. lugubrina* and *D. hamata* (Figs 224 and 241 respectively) can be mentioned as examples among species described above. On the other hand, structure of calling sometimes is quite different in the species of the same genus (see oscillograms of signals of *Javesella*, Figs 244–272). Female reply signals are extremely uniform in all species studied and consist of successions of simple uniform pulses. Males of most species demonstrate well-developed rivalry behaviour and readily produce signals of corresponding types in reply to calling of another male or in the presence of several individuals on the same plant. In all these characters the species considered are quite similar. Maybe, more detailed study of mating and rivalry behaviour in Kelisiinae and Stenocraninae and also, obtaining information on vibrational signals in other groups including Asiracinae will provide useful acoustic characters for discrimination of subfamilies and tribes in this group.

Family Cixiidae

Tribe Oecleini

Myndus musivus (Germar, 1825)
Figs 299–302.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village, from *Salix viminalis* on the bank of Oka River. 11.VI.1989. Signals of 2 ♂♂ are recorded at 26–27°C.

SIGNALS. Calling signals are prolonged trains of syllables including two pulses each. Syllables repetition period averages 160–200 ms in my recordings. Male can sing ceaselessly for about half a minute.

Tribe Cixiini

Cixius cunicularuis (Linnaeus, 1767)
Figs 303–306.

LOCALITY. Moscow Area, environs of Pirogovo, on *Salix caprea* L. 23.VII.1991. Calling signals of 1 ♂ are recorded at 24–25°C.

SIGNALS. Calling signal consists of short fragments (? phrases), usually following with regular intervals of 5–10 s. Each phrase is composed of uniform syllables including two pulses each. Syllables repetition period increases towards the end of signal.

Cixius nervosus (Linnaeus, 1758)
Figs 307–309.

LOCALITY. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, *Salix cinerea* L. in bog. 3.VIII.2000, signals of 1 ♂ are recorded at the temperature 24–25°C.

SIGNALS. Calling signal is similar with this of the previous species differing for the most part in more low syllable repetition frequency.

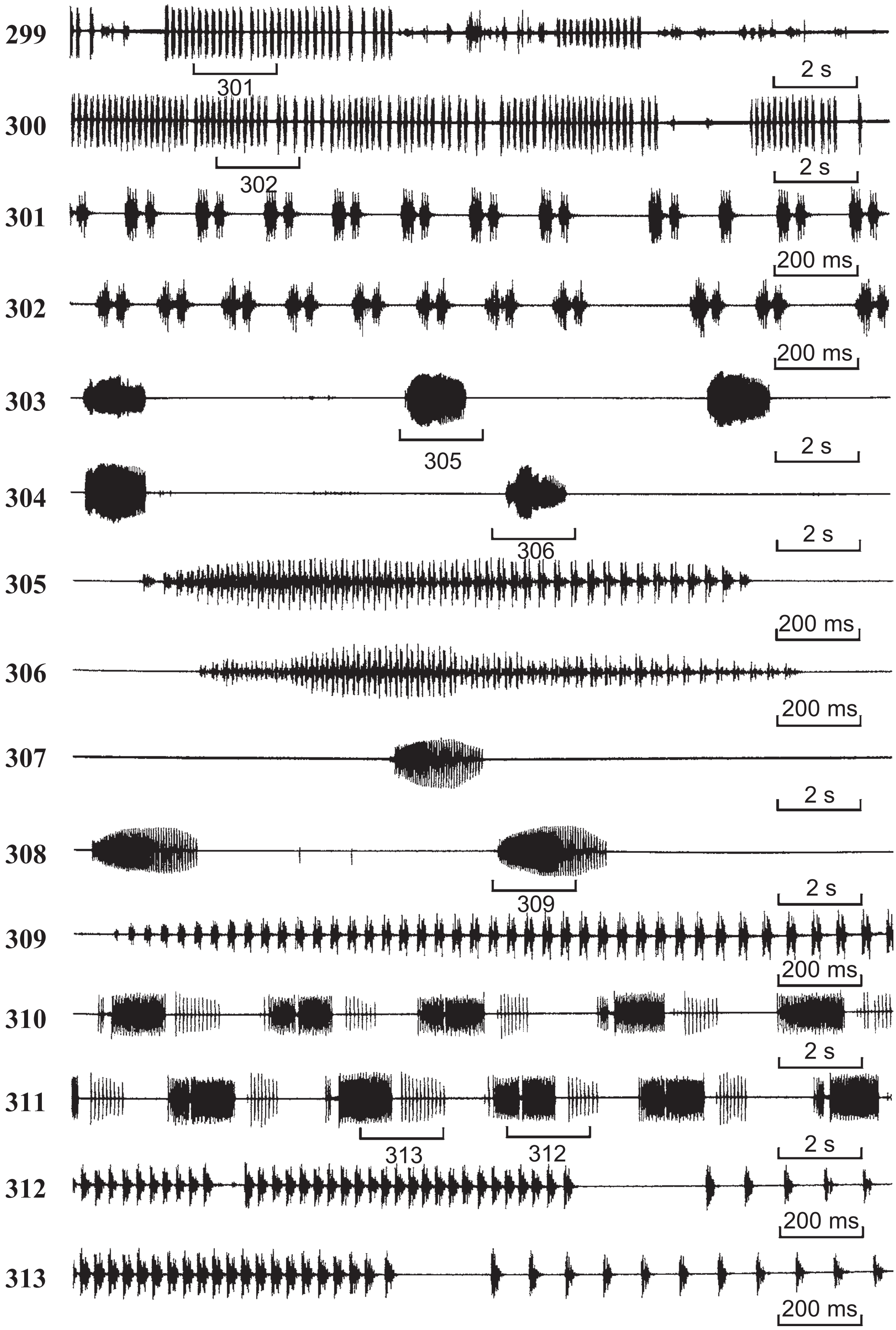
Cixius intermedius Scott, 1870
Figs 310–313.

LOCALITY. North Caucasus, North Ossetia, Ardon River flood-plain in the environs of Alagir Town, on *Hippophae rhamnoides* L. 14.VIII.1990. Signals of 2♂♂ are recorded at 25°C.

SIGNALS. Each phrase of calling signal includes two parts, the former being longer and having more high syllables repetition frequency, than the latter. Each syllable consists of two pulses but sometimes they merge and become indistinguishable. Occasionally, in the beginning of a phrase several additional pulses present. In certain phrases there is a short break in the middle of the first part.

In my experiment males sang incessantly for about 30 min producing phrases with a period of 3–4.5 s.

NOTE. Identification of species is based on Logvinenko [1975].



Figs 299–313. Oscillograms of calling signals of *Myndus musivus* (Germ.) (299–302), *Cixius cunicularuis* (L.) (303–306), *C. nervosus* (L.) (307–309) and *C. intermedius* Scott (310–313). Faster oscillograms of the parts of signals indicated as “301–302”, “305–306”, “309” and “312–313” are given under the same numbers.

Рис. 299–313. Осциллограммы призывных сигналов *Myndus musivus* (Germ.) (299–302), *Cixius cunicularuis* (L.) (303–306), *C. nervosus* (L.) (307–309) и *C. intermedius* Scott (310–313). Фрагменты сигналов, помеченные цифрами “301–302”, “305–306”, “309” и “312–313”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Tribe Pentastirini

Pentastiridius pallens (Germar, 1821)
Figs 314–318.

LOCALITY. Southern Turkmenistan, the road Dushak — Tedzhen 30 km East of Dushak, from *Phragmites australis* (Cav.) Trin. ex Steud. in irrigation ditch. 10.V.1994. Signals of 5♂♂ are recorded at the temperature 31°C.

SIGNALS. Calling signal is a succession of syllables following each other with a period 100–130 ms. Total duration of signal averages from 3–4 up to 10–12 s. Several males sitting in the same cage can sing alternately, but never demonstrate any other forms of competition behaviour.

Pentastiridius kaszabianus (Dlabola, 1970)
Figs 319–323.

LOCALITY. The Russian Far East, Southern Maritime Province, Pogranichny District, Komissarovka River near Barabash-Levada Village, on *Spiraea salicifolia* L. 20.VII.1995. Signals of 1 ♂ are recorded at the temperature 23°C.

SIGNALS. Calling of this species is a succession of short phrases repeating with a period about 2–3.5 s. Amplitude of phrases in the beginning of signal is distinctly lower than in its main part. Each phrase consists of uniform pulses forming several completely or partially separated groups. Total duration of signal averages about 15–20 s.

Pentastiridius leporinus (Linnaeus, 1761)
Figs 324–326.

LOCALITY. Lower Volga Region, East of Saratov Area, 10 km E of Ozinki Town towards Ural'sk, on *Salix cinerea* L. 24.VI.1996. Signals of 2 ♂♂ are recorded at the temperature 26–27°C.

SIGNALS. Calling signals are short phrases following with irregular intervals. Syllables in the first part of phrase consist of pulses with distinctly different structure. On the contrary, in most other studied species of Cixiidae signals are composed of uniform pulses.

Pentastiridius apicalis (Uhler, 1896)
Figs 327–333.

LOCALITY. The Russian Far East, Southern Maritime Province, Khankaiskiy District, bank of Khanka Lake about 5–6 km north from Novokachalinsk. 17.VII.2002. Signals of 4 ♂♂ are recorded at 26°C.

SIGNALS. Calling signal consists of syllables or trills varying in length from 200–300 ms up to 2–3 s. Several males sitting in the same cage can sing alternately or simultaneously, so that their calling signals overlap (Fig. 327), but they never produce signals of any other types.

Reptalus arcbogdulus (Dlabola, 1965)
Figs 334–337.

LOCALITY. Altai Mountains, Altaiskiy Nature Reserve, S shore of Teletskoe Lake, Chiri, rocky outcrops with steppe vegetation, from *Spiraea* sp. 19.VII.1999. Calling signals of 4♂♂ are recorded at the temperature 23°C.

SIGNALS. Calling signal is a phrase consisting of 4–10 syllables repeating with a period of 0.7–0.9 s. Usually, amplitude of syllables increases slightly towards the end of signal. Several males sitting on the same plant usually sing alternately, as other Cixiidae do.

Reptalus vilbastei Logvinenko, 1975
Figs 338–340.

LOCALITY. Lower Volga Region, Astrakhan' Area, Dosang Railway Station, *Artemisia arenaria* DC in sand desert. 1.VII.2000. Signals of 1 ♂ were recorded at 26°C.

SIGNALS. Calling signal is a phrase lasting for about 3 s. It consists of uniform pulses, but their repetition frequency in the first one third of signal is distinctly lower than in last two thirds.

Reptalus concolor (Fieber, 1876)
Figs 341–344.

LOCALITY. Kazakhstan, foothills of Zailiyskiy Alatau Mountain Ridge in the environs of Almaty. 2.VII.1994. Calling signals of 1 ♂ are recorded at 31°C.

SIGNALS. Calling signal is a single phrase consisting of several syllables with different temporal pattern. Total duration of phrase averages 3–4 s.

NOTE. Identification of species is based on Mityaev [1971].

Reptalus quinquecostatus (Dufour, 1833)
Figs 345–348.

LOCALITIES. 1. Crimea, environs of Pereval'noe Village (halfway from Simferopol to Alushta), from *Salix* sp. 16.VI.1997. Signals of 2 ♂♂ are recorded at 28–30°C.

2. Lower Volga Region, Volgograd Area, Ilovlya River about 5 km from the mouth, from *Salix* sp. 8.VI.1996. Signals of 1 ♂ are recorded at 24–25°C.

SIGNALS. Calling signal consists of single or repeating syllables composed of uniform pulses. Usually, syllables follow each other with intervals about 1–2 s. Signals of individuals from Crimea and Volgograd Area have not any significant difference.

Setapius apiculatus (Fieber, 1876)
Figs 349–351.

= *Oliarus fumatipennis* Dlabola, 1949

LOCALITY. Southern Urals, Orenburg Area, Guberlya River in the environs of Guberlya Railway Station 25 km W of Orsk Town, *Spiraea hypericifolia* L. on rocky slopes of hills. 8.VII.1996. Signals of 2 ♂♂ are recorded at the temperature 26°C.

SIGNALS. In general scheme of temporal pattern calling signal is similar with this of the previous species differing from it in quantitative characters. Duration of syllables averages 1.5–2 s, length of pauses between them is about 4 s. Several males sitting in the same cage occasionally sing simultaneously, but never demonstrate other forms of rivalry behaviour.

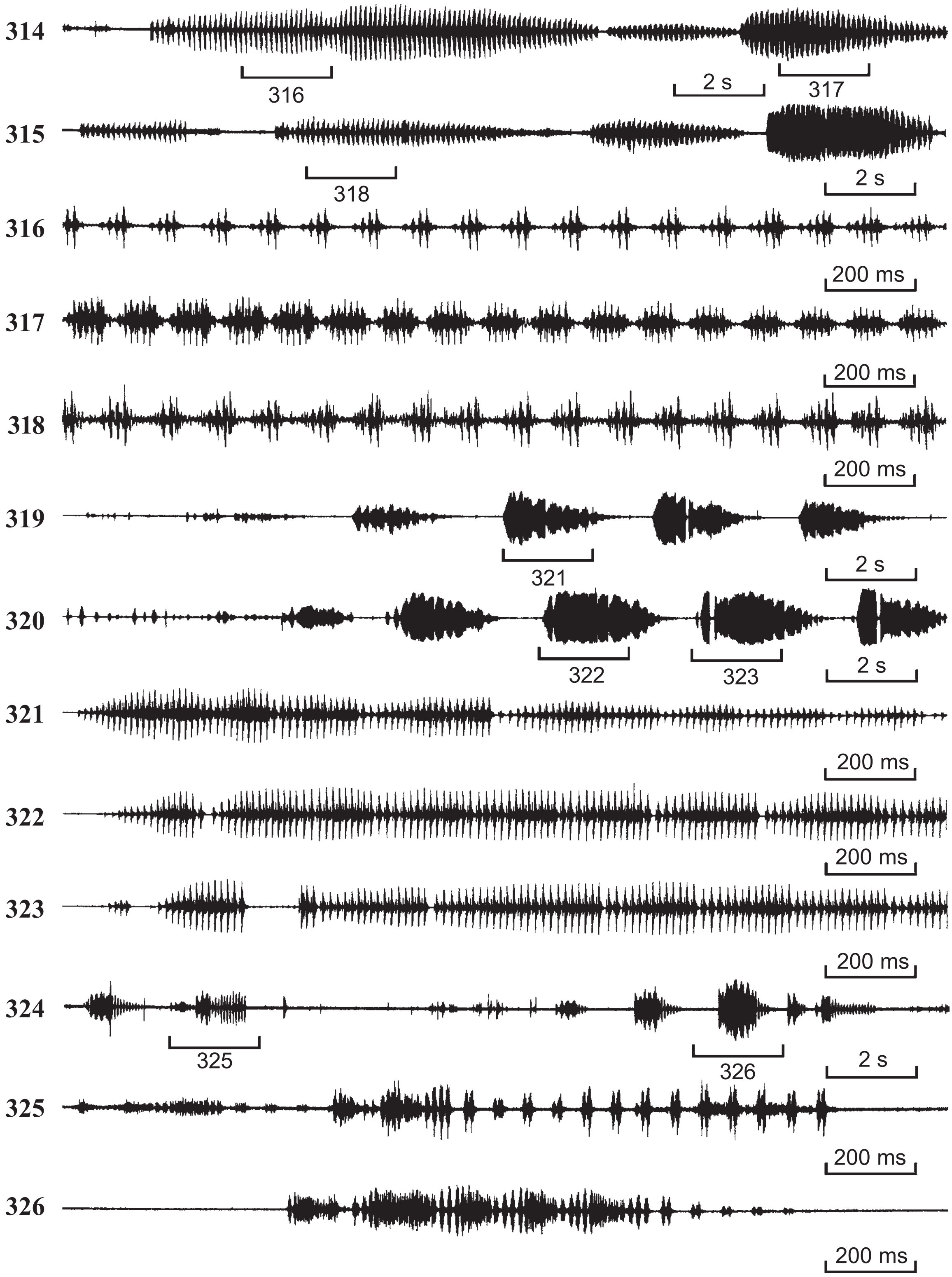
NOTE. Interpretation of species is based on Logvinenko [1975].

Hyalestes obsoletus Signoret, 1865
Figs 352–357.

LOCALITY. Southern Azerbaidzhan, Talysh Mts., environs of Lerik Village, from *Sambucus ebulus* L. 9.VII.1987. Signals of 2 ♂♂ are recorded at the temperature 22°C.

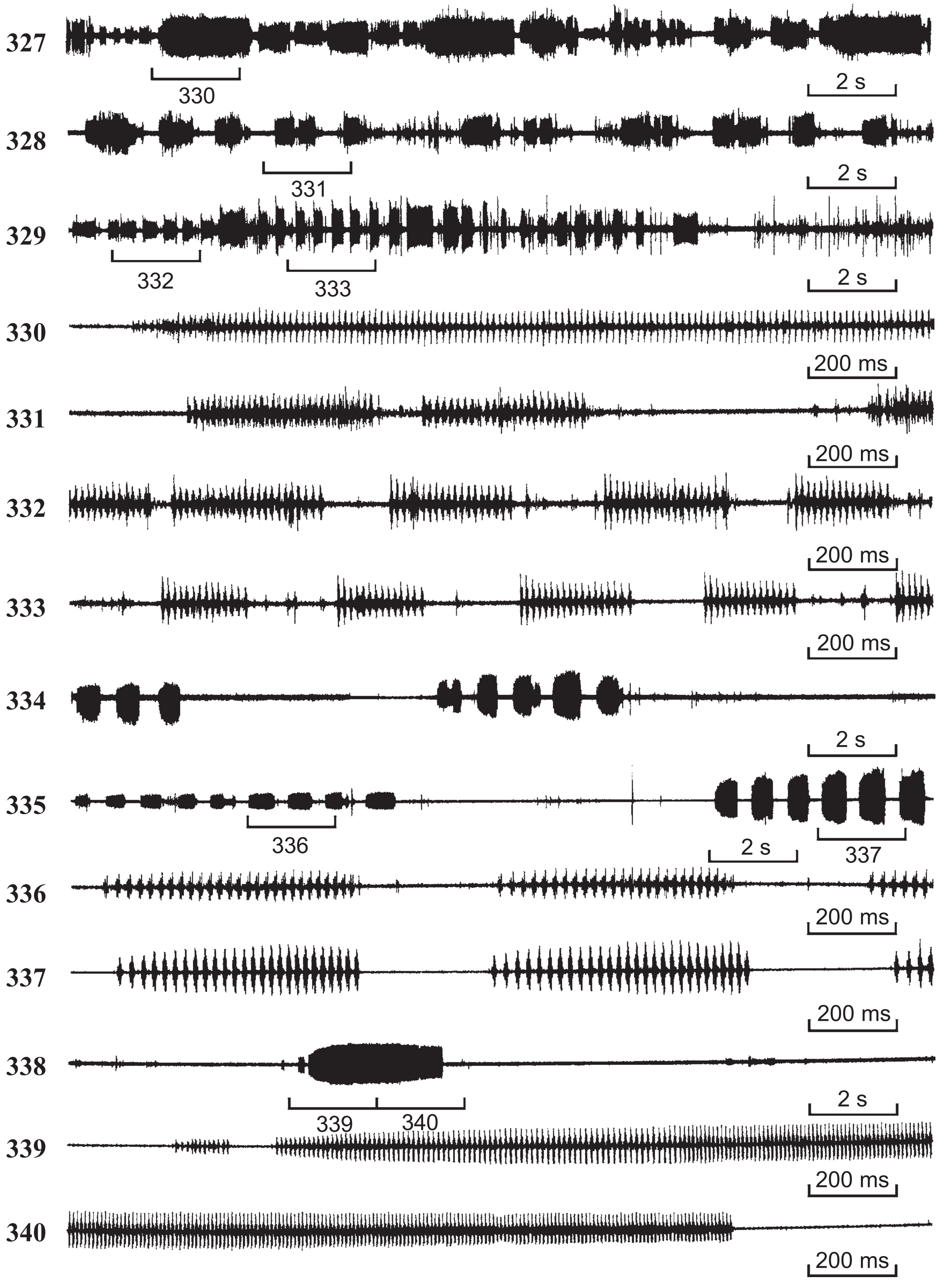
SIGNALS. Calling signals are long successions of short syllables with somewhat variable structure. As in the previous species, two males occurring on the same stem can sing simultaneously or one immediately after another.

NOTE. Determination of species is based on Logvinenko [1975] with due respect of Hoch, Remane [1985].



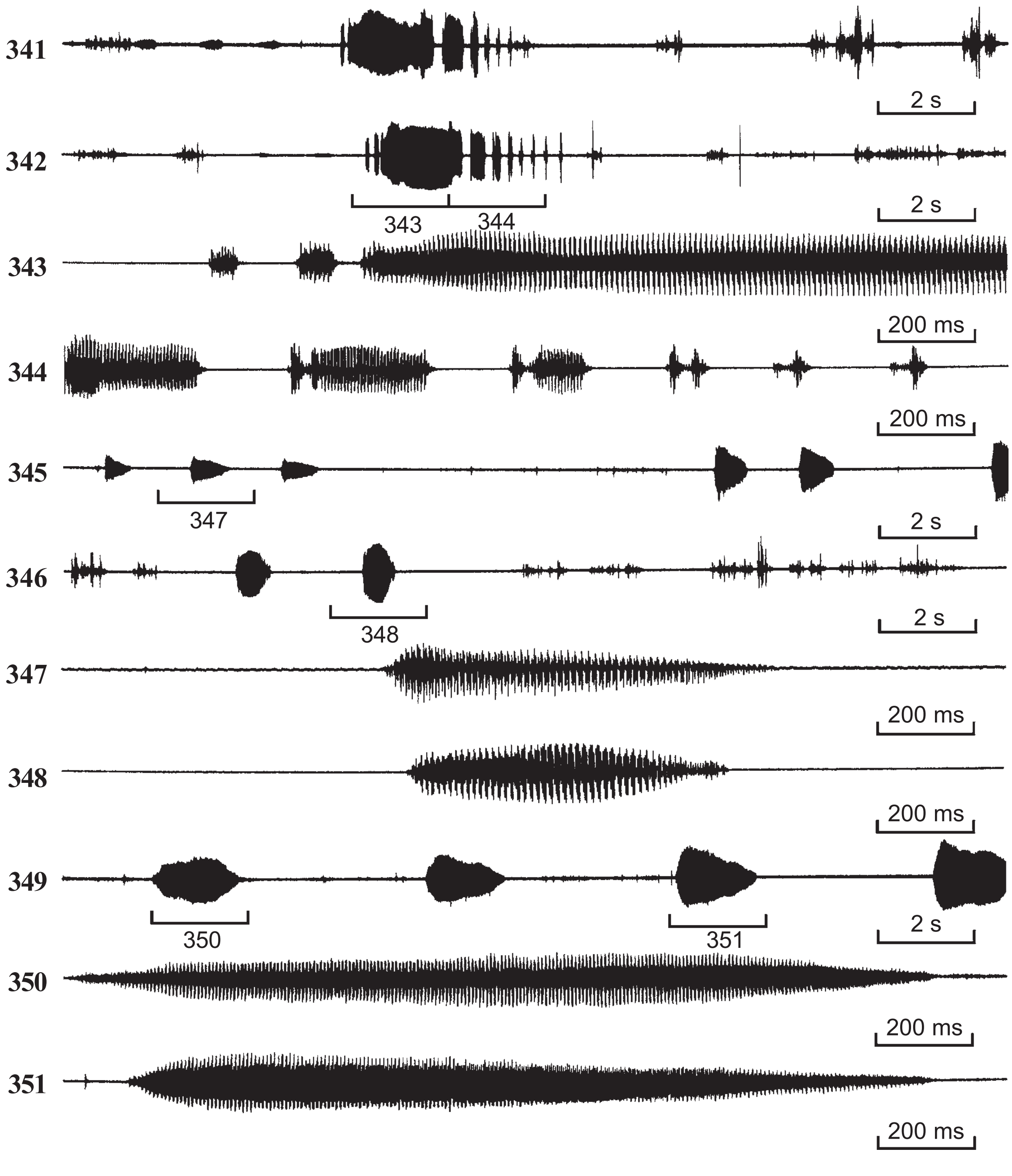
Figs 314–326. Oscillograms of calling signals of *Pentastiridius pallens* (Germ.) (314–318), *P. kaszabianus* (Dlab.) (319–323) and *P. leporinus* (L.) (324–326). Faster oscillograms of the parts of signals indicated as "316–318", "321–323" and "325–326" are given under the same numbers.

Рис. 314–326. Осциллограммы призывных сигналов *Pentastiridius pallens* (Germ.) (314–318), *P. kaszabianus* (Dlab.) (319–323) и *P. leporinus* (L.) (324–326). Фрагменты сигналов, помеченные цифрами "316–318", "321–323" и "325–326", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 327–340. Oscillograms of calling signals of *Pentastiridius apicalis* (Uhler) (327–333), *Reptalus arcbogdulus* (Dlab.) (334–337) and *R. vilbastei* Logv. (338–340). Faster oscillograms of the parts of signals indicated as "330–333", "336–337" and "339–340" are given under the same numbers.

Рис. 327–340. Осциллограммы призывных сигналов *Pentastiridius apicalis* (Uhler) (327–333), *Reptalus arcbogdulus* (Dlab.) (334–337) и *R. vilbastei* Logv. (338–340). Фрагменты сигналов, помеченные цифрами "330–333", "336–337" и "339–340", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 341–351. Oscillograms of calling signals of *Reptalus concolor* (Fieb.) (341–344), *R. quinquecostatus* (Dufour) (345–348) and *Setapius apiculatus* (Fieb.) (349–351). Faster oscillograms of the parts of signals indicated as "343–344", "347–348" and "350–351" are given under the same numbers.

Рис. 341–351. Осциллограммы призывных сигналов *Reptalus concolor* (Fieb.) (341–344), *R. quinquecostatus* (Dufour) (345–348) и *Setapius apiculatus* (Fieb.) (349–351). Фрагменты сигналов, помеченные цифрами "343–344", "347–348" и "350–351", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Calling signals of 10 species of Cixiidae were briefly described in my papers [Tishechkin, 1997, 1998]. In Tishechkin [1997] on the fig. 2 oscillograms designated in the legend as belonging to*R. concolor* actually belong to *R. quinquecostatus* and vice versa.

The only other description of vibrational signals of Cixiidae concerns several cave-dwelling Hawaiian forms belonging to morphological species *Oliarus polyphemus* Fennah [Howarth et al., 1990; Hoch, Howarth, 1993]. Both male calling and female reply signals in these forms are quite similar with these of surface-dwelling representatives of the family and consist of short trains of pulses. Moreover, in most forms male and female signals appeared to be almost identical. Within each form signals showed rather small range of variation but distinctly differed from signals of all other forms. These forms are evidently reproductively isolated for this reason and thus represent different biological species. In field experiments signals were find to be transmitted over distances of a few meters along roots on which the insects dwell. In both sexes acoustic activity started on an average of 7–10 days after the adult molt and persisted up to 51 days. In the majority of observed cases it was female, who initiated calling and throughout the courtship remained the more acoustic-active partner.

Also, changes in signals structure during maturing of individual were studied. Signals with the amplitude trough in the middle were registered in immature males producing their first calls 2 or 3 days after molting. Similar signals were recorded by me in *Dictyophara multireticulata* Mulsant et Rey, 1855 and *Caliscelis affinis* Fieber, 1867 (see below).

No other signals except male calling and female reply were registered in studied species of Cixiidae. Competing males sometimes can sing alternately, but never produce signals of any other types. Temporal pattern of calling signals is rather uniform in the representatives of the family. As a rule, signals consist of short simple pulses, which can be grouped in single succession (syllable or trill) either arranged in several trains of equal or different duration. Still, in most cases the shape of pulses remains constant in all trains. At least partly for this reason available material does not allow to separate the tribes studied basing on signals structure. Maybe, further investigation of signals of representatives of other tribes and subfamilies will allow to use acoustic analysis in systematics of higher taxa in this family.

Family Derbidae

Cedusa sarmatica (Anufriev, 1966)
Figs 358–360.

LOCALITY. NW Caucasus, Krasnodar Province, environs of Aderbievka Village east of Gelendzhik Town, from *Salix elbursensis* Boiss. 9.VII.1997. Signals of several ♂♂ are recorded at the temperature 27–30°C.

SIGNALS. Calling signal consists of repeating fragments including two syllables each, the first syllable being twice shorter than the second one. Occasionally, male produce two or three short syllables in succession.

Kirkaldy [1907] described corrugated areas, which were interpreted as stridulatory organs on the hind wings of several Derbidae species. Also, he presents a short account on observation of stridulatory movements in one of species. No other data on stridulation in Derbidae are available until now, yet the opinion that these structures on the wings of representatives of certain tribes are sound-producing mechanism became widely accepted.

The only species studied evidently produce signals in an ordinary way, i.e. by timbals. Besides, stridulatory organs were not found in Cedusini [Emeljanov, 1994].

Family Dictyopharidae

Subfamily Dictyopharinae

Dictyophara multireticulata Mulsant et Rey, 1855
Figs 361–364.

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, from *Quercus robur* L. 19.VIII.1992. Signals of 1 ♂ are recorded at the temperature 26°C.

SIGNALS. Calling signal is single succession of pulses lasting for about 2 s. Amplitude of pulses changes abruptly in the middle of a phrase.

NOTE. Signals of only one male were recorded, so it remained unclear, if the amplitude trough in the middle of syllable is typical for this species. Such sudden decreasing of amplitude in the middle of signal can occur in immature individuals of certain Cicadinea species [Howarth et al., 1990]. Similar phenomenon was observed also in *Caliscelis affinis* Fieber, 1867 (Caliscelidae, see below).

Dictyophara europaea (Linnaeus, 1767)
Figs 365–371.

LOCALITIES. 1. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, 16, 18.VIII.1991. Signals of 2 ♂♂ are recorded at the temperature 26°C.

2. Lower Volga Region, Astrakhan' Area, Dosang Railway Station, from ruderal vegetation in dry irrigation ditch in a floodland between Volga and Akhtuba rivers, 4.VII.2000. Signals of 2 ♂♂ were recorded at 26–27°C.

SIGNALS. Calling signal is a trill lasting for about 3 s and consisting of uniform pulses. As a rule, amplitude of pulses somewhat decreases towards the end of a phrase.

Dictyophara pannonica (Germar, 1830)
Figs 372–378.

LOCALITIES. 1. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, 15, 17.VIII.1991. Signals of 2 ♂♂ are recorded at the temperature 26°C.

2. Lower Volga Region, Astrakhan' Area, Dosang Railway Station, from ruderal vegetation in dry irrigation ditch in a floodland between Volga and Akhtuba rivers, together with the previous species, 4.VII.2000. Signals of 1 ♂ were recorded at 26–27°C.

SIGNALS. Calling signal is quite similar with this of *D. europaea*.

Subfamily Orgeriinae

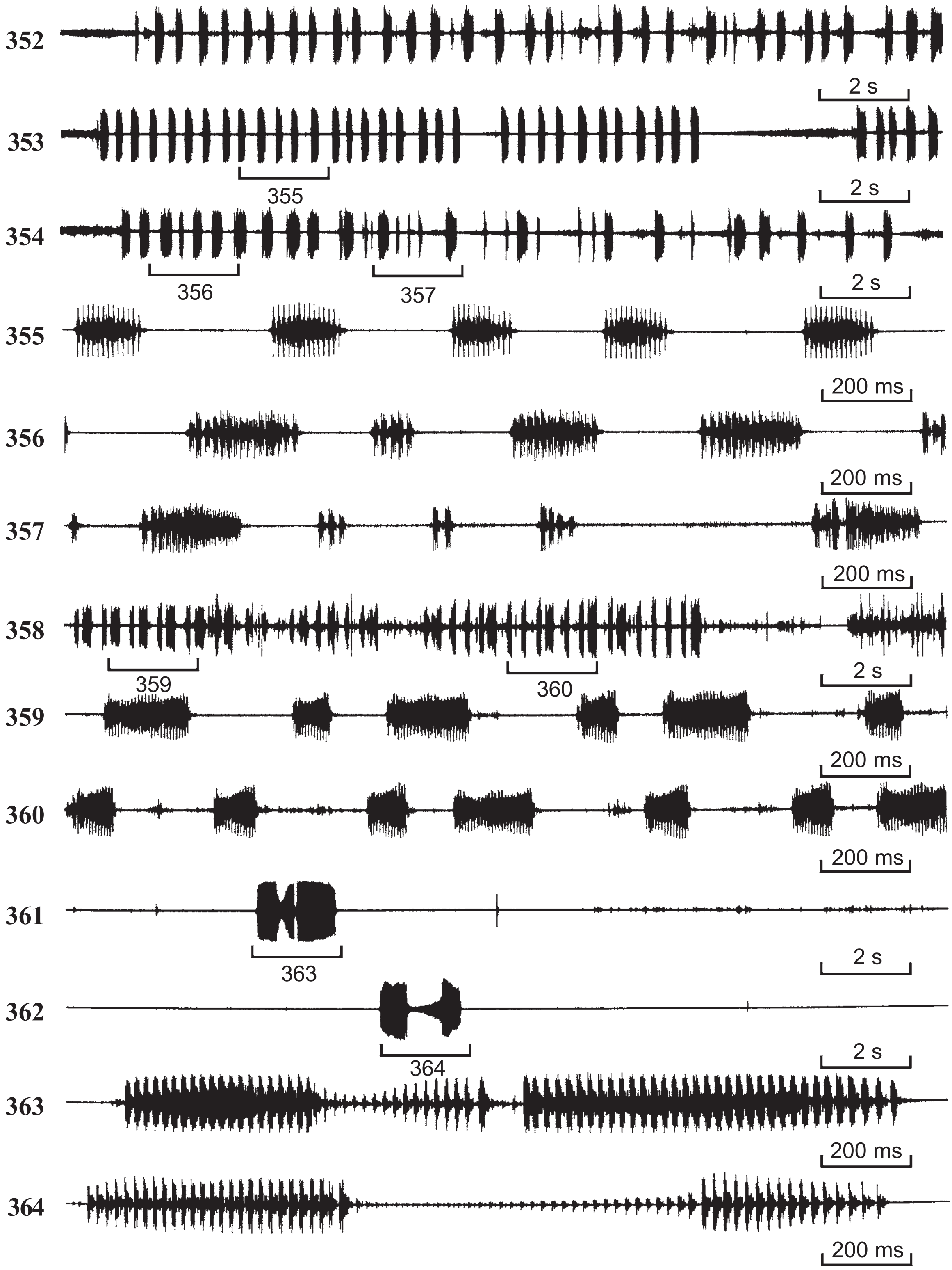
Phyllorgerius jacobsoni (Oshanin, 1913)
Figs 379–383.

LOCALITY. Southern Kazakhstan, foothills of Zailiyskiy Alatau Mountain Ridge in the environs of Almaty. 4.VII.1994. Calling signals of 4 ♂♂ are recorded at 30°C.

SIGNALS. Calling of this species is a long-lasting sucesssion of syllables consisting of several rather short pulses and single more prolonged one each. Occasionally, prolonged pulse in certain syllables can be missed (Fig. 380, 383).

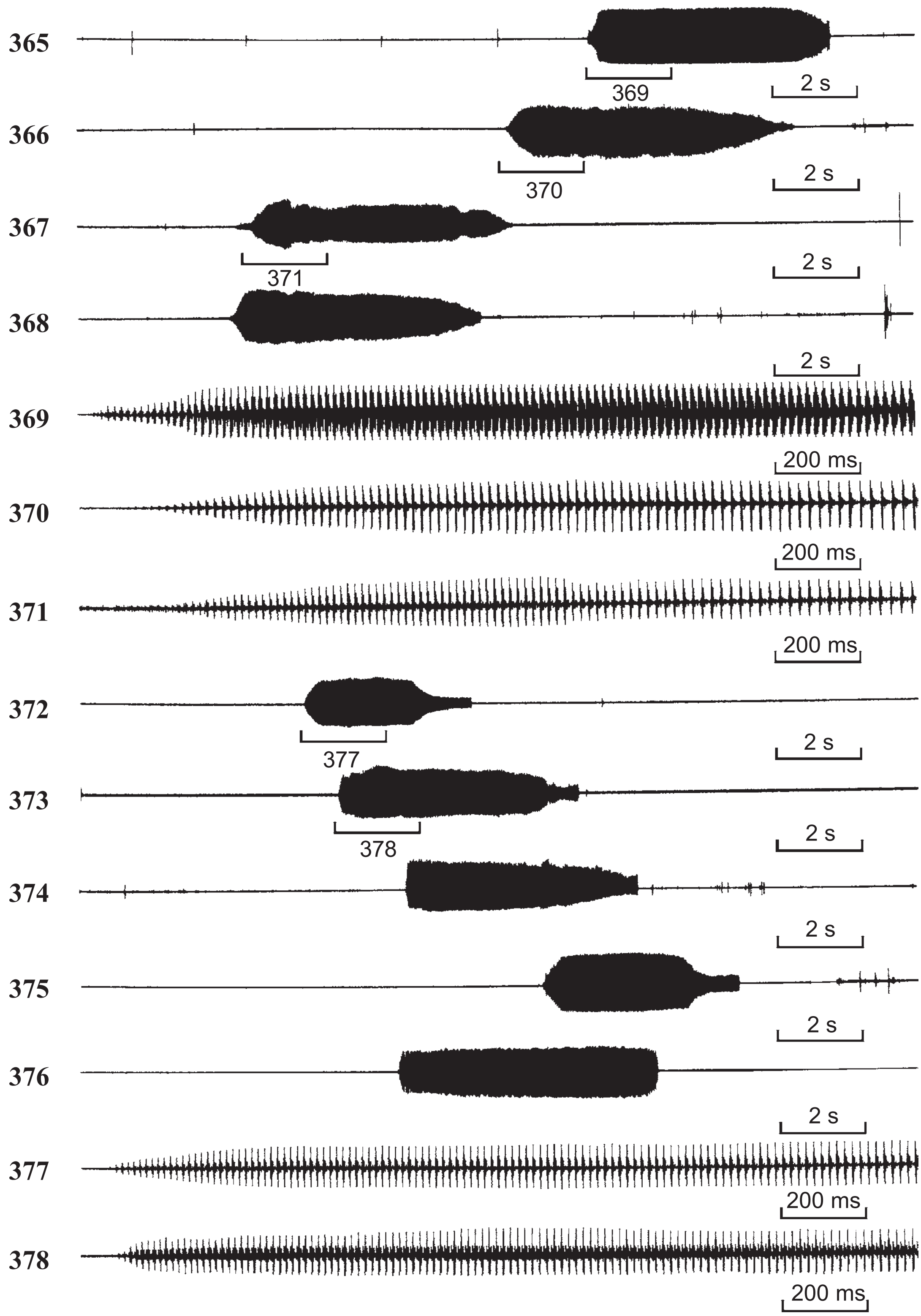
Sphenocratus hastatus Oshanin, 1912
Figs 384–391.

LOCALITY. Southern Kazakhstan, steppe in the environs of Chemalgan Village 20 km W of Almaty. 8–9.VII.1994. Signals of several ♂♂ are recorded at the temperature 27–30°C.



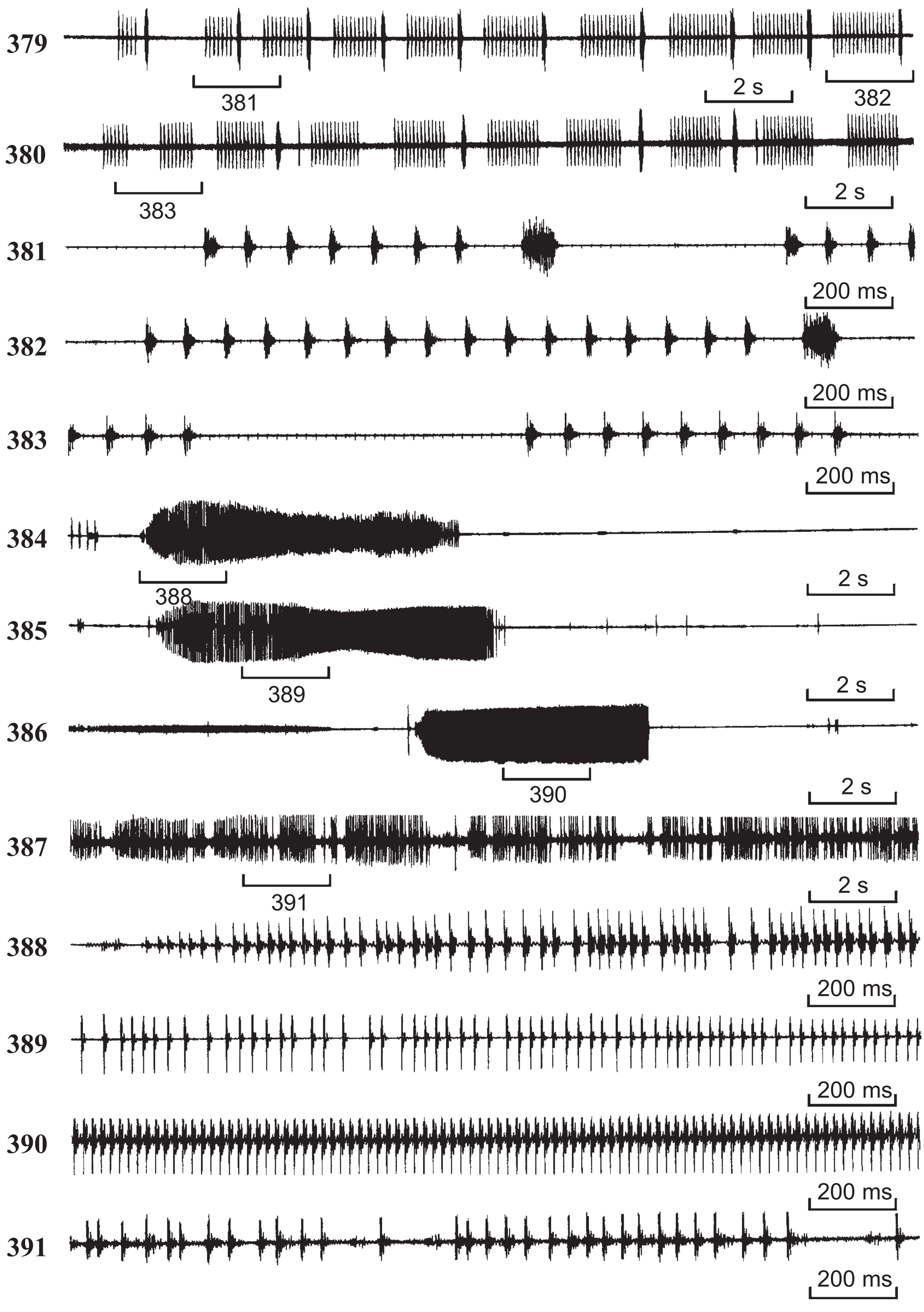
Figs 352–364. Oscillograms of calling signals of *Hyalestes obsoletus* Sign. (352–357), *Cedusa sarmatica* (Anufr.) (358–360) and *Dictyophara multireticulata* Mulsant et Rey (361–364). Faster oscillograms of the parts of signals indicated as “355–357”, “359–360” and “363–364” are given under the same numbers.

Рис. 352–364. Осциллограммы призывных сигналов *Hyalestes obsoletus* Sign. (352–357), *Cedusa sarmatica* (Anufr.) (358–360) и *Dictyophara multireticulata* Mulsant et Rey (361–364). Фрагменты сигналов, помеченные цифрами “355–357”, “359–360” и “363–364”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 365–378. Oscillograms of calling signals of *Dictyophara europaea* (L.) (365–371) and *D. pannonica* (Germ.) (372–378). Faster oscillograms of the parts of signals indicated as "369–371" and "377–378" are given under the same numbers.

Рис. 365–378. Осциллограммы призывных сигналов *Dictyophara europaea* (L.) (365–371) и *D. pannonica* (Germ.) (372–378). Фрагменты сигналов, помеченные цифрами "369–371" и "377–378", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 379–391. Oscillograms of vibrational signals of *Phyllorgerius jacobsoni* (Osh.) (379–383) and *Sphenocratus hastatus* Osh. (384–391): 379–383 — *Ph. jacobsoni*, calling signals, 384–386, 388–390 — *S. hastatus*, calling signals, 387, 391 — same, rivalry signals. Faster oscillograms of the parts of signals indicated as "381–383" and "388–391" are given under the same numbers.

Рис. 379–391. Осциллограммы вибрационных сигналов *Phyllorgerius jacobsoni* (Osh.) (379–383) и *Sphenocratus hastatus* Osh. (384–391): 379–383 — *Ph. jacobsoni*, призывные сигналы, 384–386, 388–390 — *S. hastatus*, призывные сигналы, 387, 391 — то же, сигналы соперничества. Фрагменты сигналов, помеченные цифрами "381–383" и "388–391, представлены при большей скорости развертки на осциллограммах под такими же номерами.

SIGNALS. Calling signal of this species is a trill more or less similar with these in *D. europaea* and *D. pannonica* (Figs 384–386, 388–390). Occasionally, signals of these three species are almost indistinguishable. Several males occurring in the same cage sometimes produce prolonged trills of another type having rather irregular pulses repetition period (Figs 387, 391). Evidently, these are rivalry signals.

Haumavarga fedtschenkoi (Oshanin, 1879)
Figs 392–396.

LOCALITY. Lower Volga Region, Astrakhan' Area, Bol'shoy Bogdo Mtn. near Baskunchak Lake, on *Artemisia lerchiana* Web. 22.VII.2001. Calling signals of 2 ♂♂ are recorded at the temperature 29°C.

SIGNALS. Calling signal consists of several short trills. Both their number and duration can vary greatly. Two males sitting on the same stem sometimes sing simultaneously, so that their signals overlap.

Mesorgerius tschujensis Vilbaste, 1965
Figs 397–404.

LOCALITY. South Siberia, southern Tuva, steppe in the environs of Erzin Village, on *Artemisia frigida* Willd. and *Ceratoides papposa* Botsch et Ikonn. 26.VII, 3.VIII.1989. Signals of 3 ♂♂ are recorded at the temperature 24–25°C.

SIGNALS. Calling signal is a short single trill, consisting of simple uniform pulses as in signals of other Dictyopharidae species (397–403). When in close contact with another individuals, male occasionally produces rivalry signals similar with these of *S. hastatus* (Figs 399, 404).

Description of vibrational signals and mating behaviour of *D. europaea* is given in Strübing [1977, 1999]. Calling signals of European specimens do not differ in structure from these of ones from Russian populations. Female reply is a succession of short syllables following each other with a period of about 0.5 s and lasting for 0.2–0.25 s each. Syllables consist of uniform pulses similar with these in male calling. After hearing female reply male starts producing courtship signal almost identical in structure with female ones. Female goes on singing on this stage of mating behaviour, answering courtship signals as well as calling.

Also, oscillograms of four species of Dictyopharidae (*D. multireticulata*, *Ph. jacobsoni*, *S. hastatus* and *M. tschujensis*) are given in Tishechkin [1997, 1998].

It is an extraordinary fact that calling signals of two strictly sympatric species of *Dictyophara* (*D. europaea* and *D. pannonica*) are indistinguishable in temporal pattern. Both in Rostov and Astrakhan' Areas I have found these species at the same time in the same biotope. In external appearance *D. europaea* differs distinctly from *D. pannonica*, which may prevent attempts of interspecific mating. Still, it is unclear how these insects recognize the conspecific individual during distant communication. Maybe, further more detailed investigation of acoustic signals in *Dictyophara*, including female reply ones could elucidate this problem. Also, in certain cases calling of these two species is quite similar with this of *S. hastatus* (see Figs 365–378 and 386, 390). The latter species occurs in Southern and South-Eastern Kazakhstan and in adjacent regions of Kyrgyzstan only, but the two *Dictyophara* species are widespread throughout all the territory of Kazakhstan, so the ranges of all three ones overlap.

As a whole, signals of the most part of studied species of Dictyopharidae are rather uniform in their temporal pattern. Available material is insufficient for separation of subfamilies or tribes in this group basing on acoustic characters.

Family Tropiduchidae

Trypetimorpha occidentalis Huang, Bourgoin, 1993
Figs 405–408.

= *T. fenestrata* auct. nec A. Costa, 1862

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River. 14.VIII.1992. Signals of 2 ♂♂ are recorded at the temperature 29–30°C.

SIGNALS. Calling signal consists of short phrases, repeating with regular period about 2–3 s. Two males sitting on the same stem can sing alternately (Fig. 405). No other forms of competition behaviour were observed in this species.

NOTE. Until recently *Trypetimorpha* species from Eastern Europe and Kazakhstan was regarded as belonging to *T. fenestrata*. Actually, it appeared to be a separate species *Trypetimorpha occidentalis* Huang, Bourgoin, 1993.

Family Issidae

Mycterodus intricatus Stål, 1861
Figs 409–412.

LOCALITY. Crimea, mountains 4–5 km E of Glubokiy Yar Village (N of Bakhchisaray), from oak. 8.VI.1997. Signals of 1 ♂ are recorded at the temperature 22–23°C.

SIGNALS. Calling signal consists of short successions of simple pulses (Figs 409–410). Also, in the male of this species prolonged trills of pulses were registered (Figs 411–412). Function of the latter signal is unclear.

Agalmatium bilobum (Fieber, 1877)
Figs 413–418.

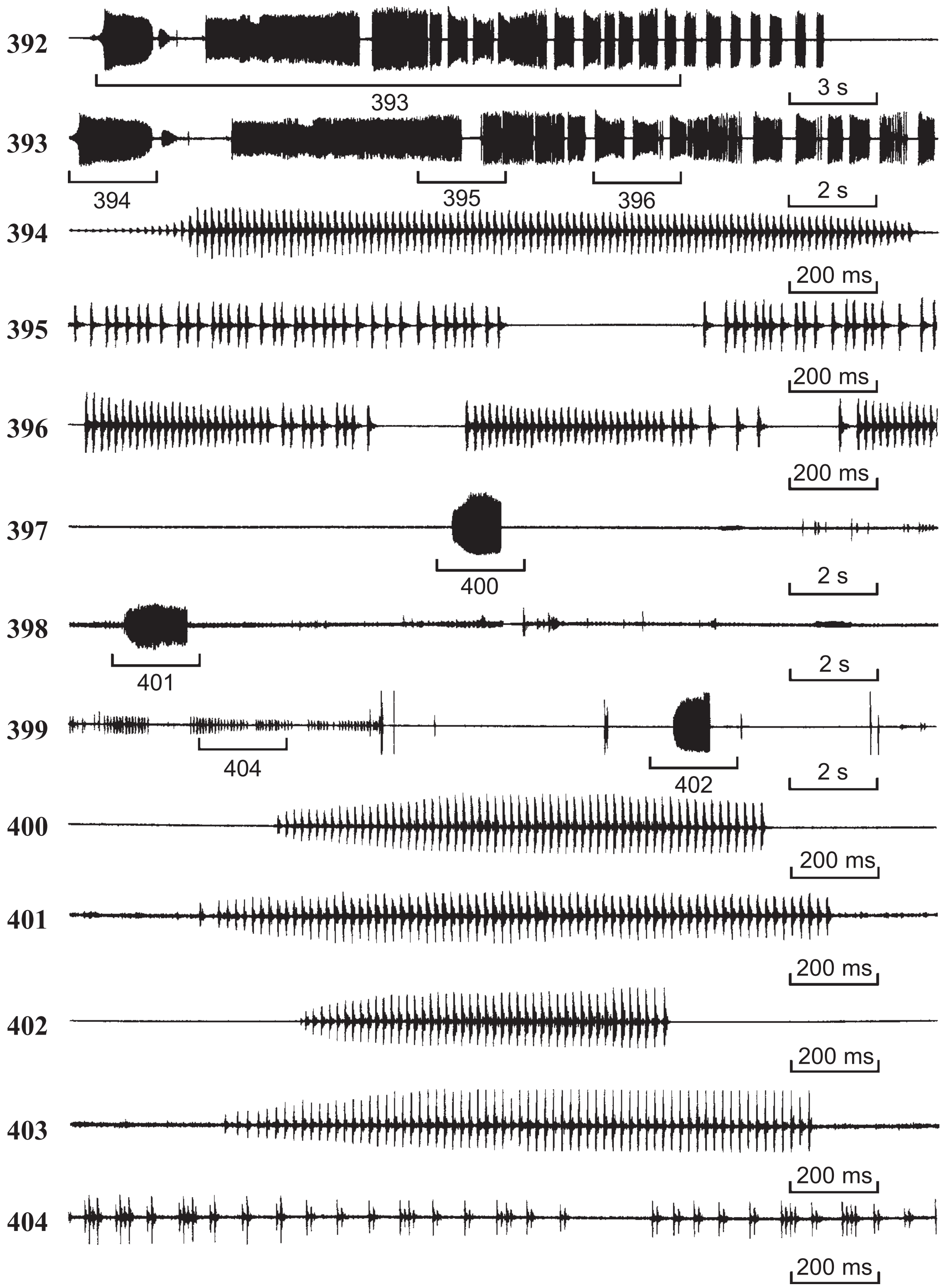
LOCALITY. Ukraine, Kherson Area, Sivash Lake, *Artemisia* sp. on seashore. 18.VIII.1986. Calling signals of 4 ♂♂ are recorded at the temperature 28°C.

SIGNALS. Calling signal is a long phrase normally lasting from 8–10 up to 20–30 s (Figs 413–414). The main part of a phrase consists of syllables, repeating with a period 400–600 ms and including two pulses each (Figs 416–417). Usually, a phrase ends with one or several syllables having more complex pattern (Fig. 418). Several males occurring in the same cage can sing alternately (Fig. 415). Duration of phrases in this case decreases considerably.

Scorlupella discolor (Germar, 1821)
Figs 419–421.

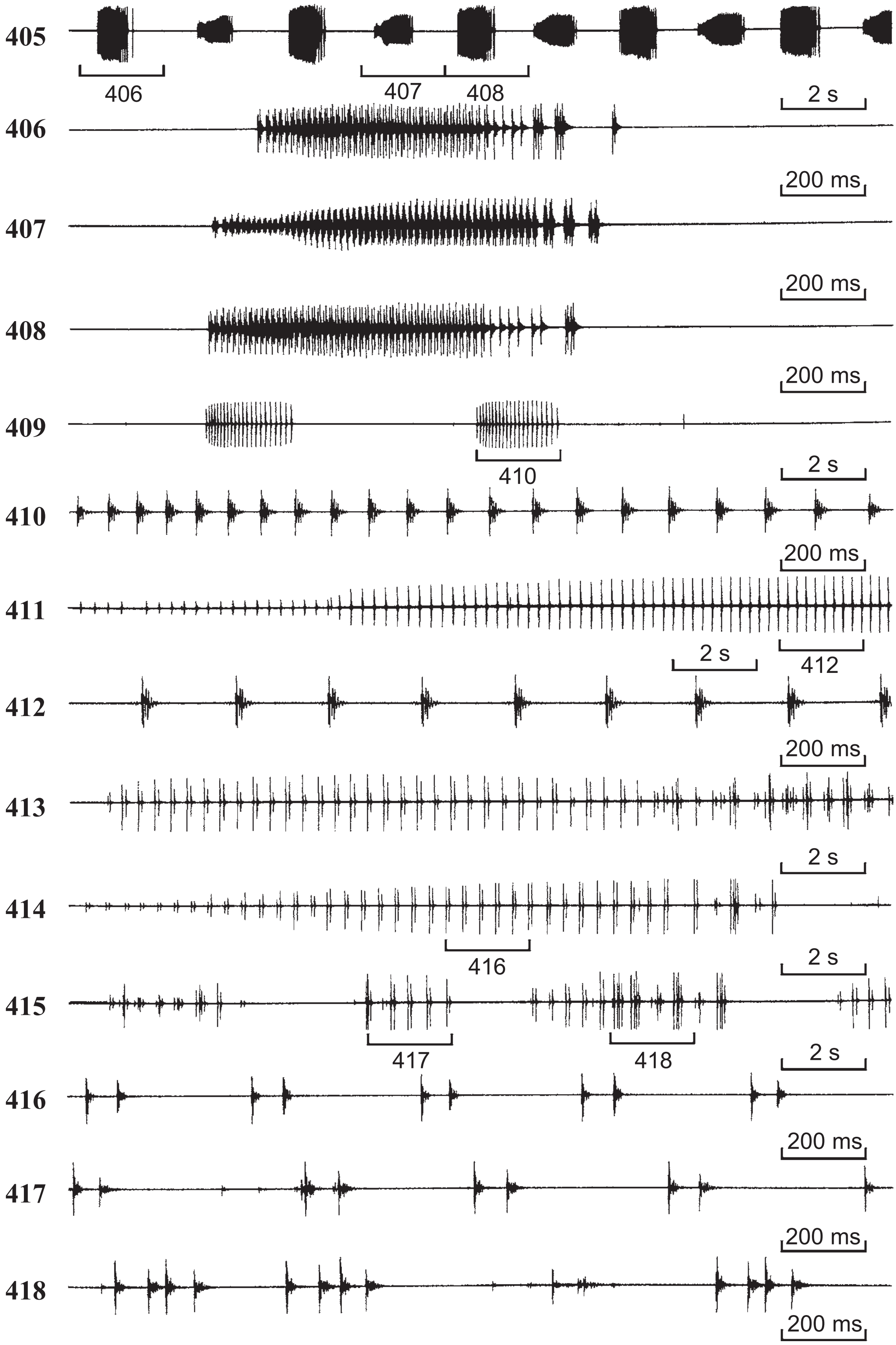
LOCALITY. Crimea, mountains 4–5 km E of Glubokiy Yar Village (N of Bakhchisaray). 8.VI.1997. Signals of 2 ♂♂ are recorded at the temperature 22°C.

SIGNALS. Calling signal consists of short phrases. Pulses in a phrase for the most part are united in pairs. Only in the first half of a phrase a short train of single pulses presents.



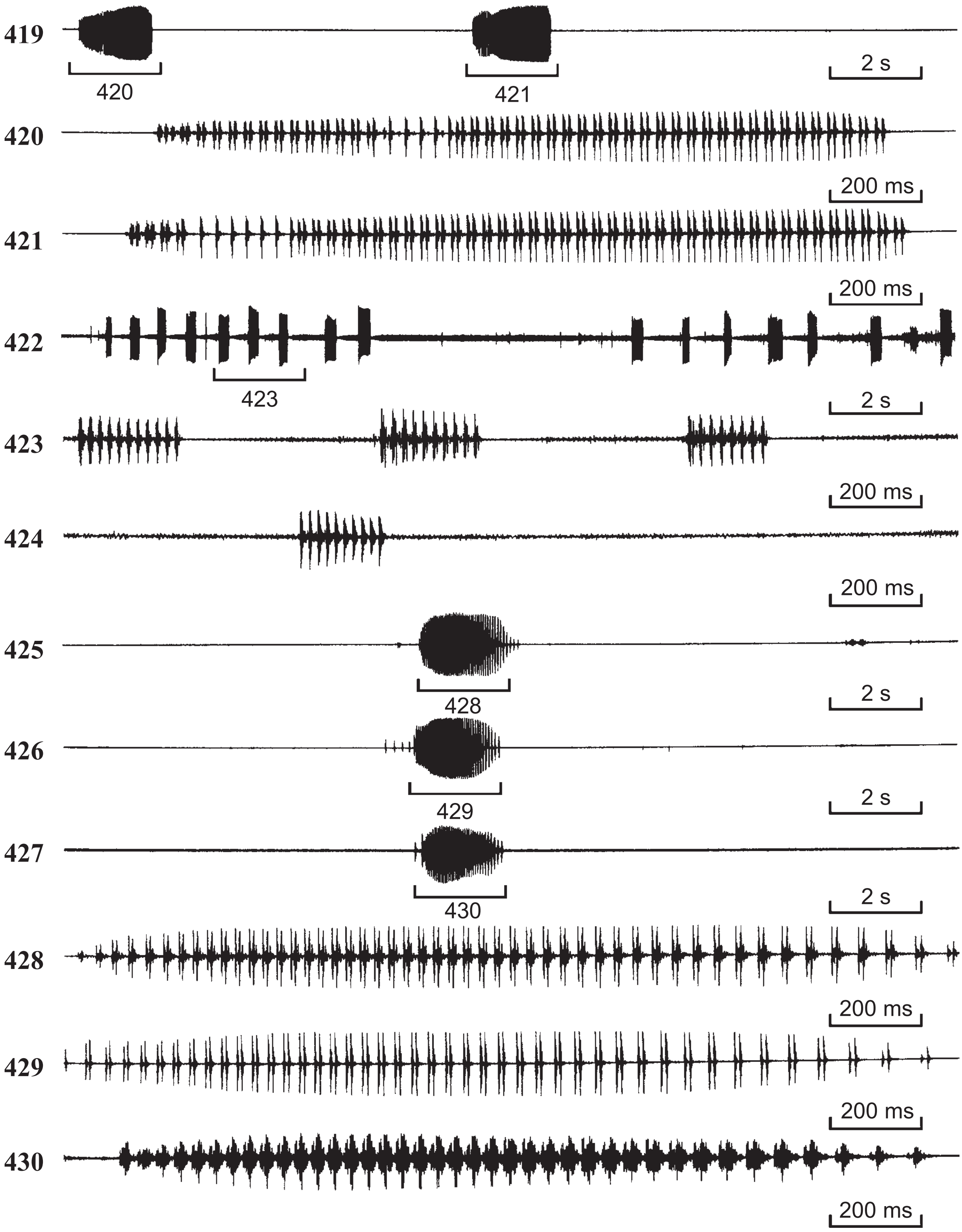
Figs 392–404. Oscillograms of vibrational signals of *Haumavarga fedtschenkoi* (Osh.) (392–396) and *Mesorgerius tschujensis* Vilb. (397–404): 392–396 — *H. fedtschenkoi*, calling signals, 397–398, 400–403 — *M. tschujensis*, calling signals, 399 — same, calling and rivalry signals, 404 — same, rivalry signals. Faster oscillograms of the parts of signals indicated as “393–396”, “400–402” and “404” are given under the same numbers.

Рис. 392–404. Осциллограммы вибрационных сигналов *Haumavarga fedtschenkoi* (Osh.) (392–396) и *Mesorgerius tschujensis* Vilb. (397–404): 392–396 — *H. fedtschenkoi*, призывные сигналы, 397–398, 400–403 — *M. tschujensis*, призывные сигналы, 399 — то же, сигналы соперничества и призывный сигнал, 404 — то же, сигналы соперничества. Фрагменты сигналов, помеченные цифрами “393–396”, “400–402” и “404”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 405–418. Oscillograms of calling signals of *Trypetimorpha occidentalis* Huang, Bourgoin (405–408), *Mycterodus intricatus* Stål (409–412) and *Agalmatium bilobum* (Fieb.) (413–418). Faster oscillograms of the parts of signals indicated as “406–408”, “410”, “412” and “416–418” are given under the same numbers.

Рис. 405–418. Осциллограммы призывных сигналов *Trypetimorpha occidentalis* Huang, Bourgoin (405–408), *Mycterodus intricatus* Stål (409–412) и *Agalmatium bilobum* (Fieb.) (413–418). Фрагменты сигналов, помеченные цифрами “406–408”, “410”, “412” и “416–418”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 419–430. Oscillograms of calling signals of *Scorlupella discolor* (Germ.) (419–421), *Scorlupaster asiaticum* (Leth.) (422–424) and *Alloscelis vittifrons* (Ivanov) (425–430). Faster oscillograms of the parts of signals indicated as “420–421”, “423” and “428–430” are given under the same numbers.

Рис. 419–430. Осциллограммы призывных сигналов *Scorlupella discolor* (Germ.) (419–421), *Scorlupaster asiaticum* (Leth.) (422–424) и *Alloscelis vittifrons* (Ivanov) (425–430). Фрагменты сигналов, помеченные цифрами “420–421”, “423” и “428–430”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Scorlupaster asiaticum (Lethierry, 1878)
Figs 422–424.

LOCALITY. Southern Turkmenistan, environs of Dushak Town, *Alhagi persarum* Boiss. et Buhse in desert. 20.V.1990. Calling signals of several ♂♂ are recorded at the temperature 30°C.

SIGNALS. Signal is a succession of syllables having total duration about 5–10 s (Fig. 422). Syllables follow each other with a period of approximately 0.5–2 s.

NOTE. Interpretation of species is based on Mityaev [1971].

Alloscelis vittifrons (Ivanov, 1885)
Figs 425–430.

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, from *Spiraea hypericifolia* L. 8–9.VIII.1991. Signals of 3 ♂♂ are recorded at the temperature 30–31°C.

SIGNALS. Generally, calling signal is similar with this of *S. discolor*, but the structure of a phrase is somewhat different. Occasionally, separate pulses in syllables are indistinct (Fig. 430).

NOTE. In the annotated check list of palaearctic Auchenorrhyncha by Nast [1972] the species was erroneously included into Caliscelidae (as Caliscelinae in Nast [1972]). This is an obvious mistake [Tishechkin, 1998; Gnezdilov, 2002].

Brief descriptions and oscillograms of signals of 5 species abovementioned are given in my papers [Tishechkin, 1997, 1998]. It must be noted that in the first article [Tishechkin, 1997] on the fig. 5 oscillograms erroneously designated as belonging to *A. vittifrons* actually belong to *S. asiaticum* and vice versa.

According to classification proposed recently by Gnezdilov [2002] for 20 west-palaearctic genera of Issinae, all the species studied belong to the same tribe Issini. *M. intricatus, A. vittifrons, S. discolor* and also *S. asiaticum* fall into subtribe Hysteropterina [Gnezdilov, 2002 and pers. comm.], whereas the genus *Agalmatium* was placed apart into separate subtribe Agalmatiina. Bioacoustic data corroborate this rearrangement. Calling signals of the first four species are quite similar and consist of rather short single or repeated successions of pulses or of short syllables. On the contrary, calling of *A. bilobum* as a rule is a long phrase consisting of syllables of two different types.

Family Caliscelidae

Subfamily Caliscelinae

Caliscelis affinis Fieber, 1867
Figs 431–444.

LOCALITIES. 1. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village, on the bank of Chir River. 13.VIII.1992. Signals of 2 ♂♂ are recorded at the temperature 28°C.

2. Crimea, Kerchenskiy Peninsula, E shore of Kazantipskiy Bay, environs of Zolotoe Village, from vegetation along salted dry river-bed. 26.VI.1997. Signals of 2 ♂♂ are recorded at 30°C.

SIGNALS. Calling signal is a long complex phrase having duration about 15–20 s (Figs 431–432). A phrase begins with a succession of syllables (Figs 433–434, 439–440). Towards the end of signal their repetition frequency and temporal pattern change gradually. Then prolonged monotonous trill follows (Figs 435–436, 441–442). Pulses repetition period and frequency spectrum of signal change suddenly in the middle of a trill (Figs 436, 441–444).

In signals of one of the males from Rostov Area abrupt decrease of amplitude in the middle of the second part of signal occurred (Figs 431, 438). Such phenomenon was observed by Hoch, Howarth [1993] in immature males of Cixiidae.

Signals of individuals from different populations are quite similar.

Aphelonema punctifrons (Horvath, 1865)
Figs 445–448.

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River. 8–9.VIII.1991. Signals of 3 ♂♂ are recorded at the temperature 30–31°C.

SIGNALS. Calling signal is a succession of syllables with total duration from 4–5 up to 10–12 s. Two males sitting on the same plant occasionally sang simultaneously, but never produced signals of any other types in my experiments.

Aphelonema eoa (Kusnezov, 1930)
Figs 449–453.

LOCALITY. Southern Kazakhstan, foothills of Zailiyskiy Alatau Mountain Ridge in the environs of Almaty. 4.VII.1994. Calling signals of 1 ♂ are recorded at 30°C.

SIGNALS. As in the previous species, calling signal is a succession of syllables, but their structure is much more complex (Figs 449–451). Also, territorial signals were registered in this species (Figs 452–453).

Aphelonema sp.
Figs 454–460.

LOCALITY. Southern Kazakhstan, foothills of Zailiyskiy Alatau Mountain Ridge in the environs of Almaty. 4.VII.1994. Calling signals of 1 ♂ are recorded at 30°C.

SIGNALS. Calling signal is similar with these of two previous species, but the temporal pattern of syllables is quite different (Figs 454–458). Territorial signal is a succession of pulses repeating with irregular intervals (459–460). Occasionally, male can produce this signal for several minutes with short pauses.

NOTE. *Aphelonema* sp. is a new species to be described by A. Emelyanov.

Subfamily Ommatidiotinae

Ommatidiotus dissimilis (Fallén, 1806)
Figs 461–486.

LOCALITIES. 1. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, bog on the bank of lake, on *Eriophorum vaginatum* L. 17.VIII.1987, signals of 1 ♂ and 3 ♀♀ are recorded at the temperature 18°C; 23, 26.VIII.1988, signals of 4 ♂♂ and 1 ♀ are recorded at the temperature 26–28°C; 27.VII.1992, signals of 1 ♂ and 1 ♀ are recorded at the temperature 26–27°C.

2. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, 16.VIII.1992. Signals of 4 ♂♂ are recorded at the temperature 31°C.

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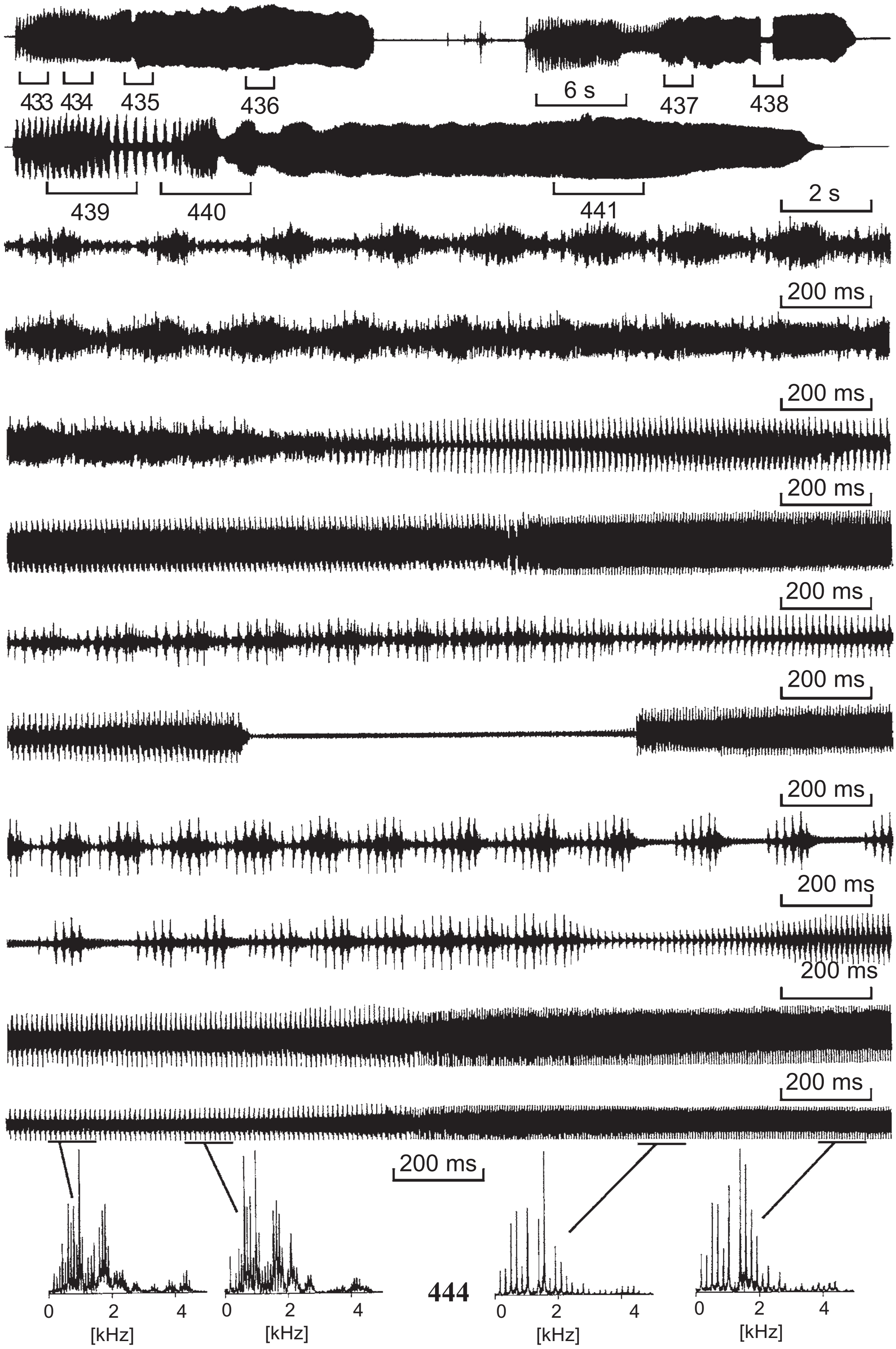
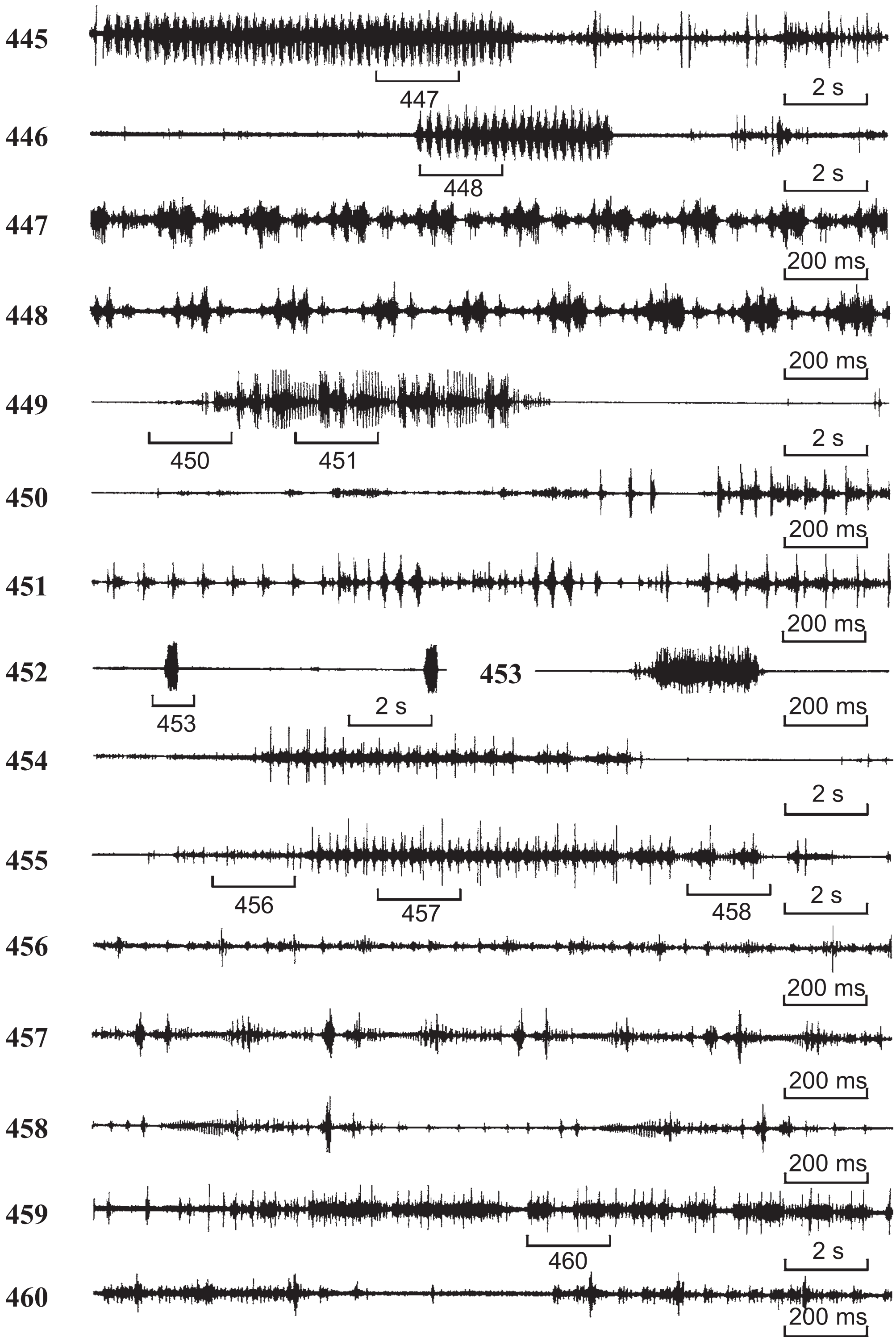


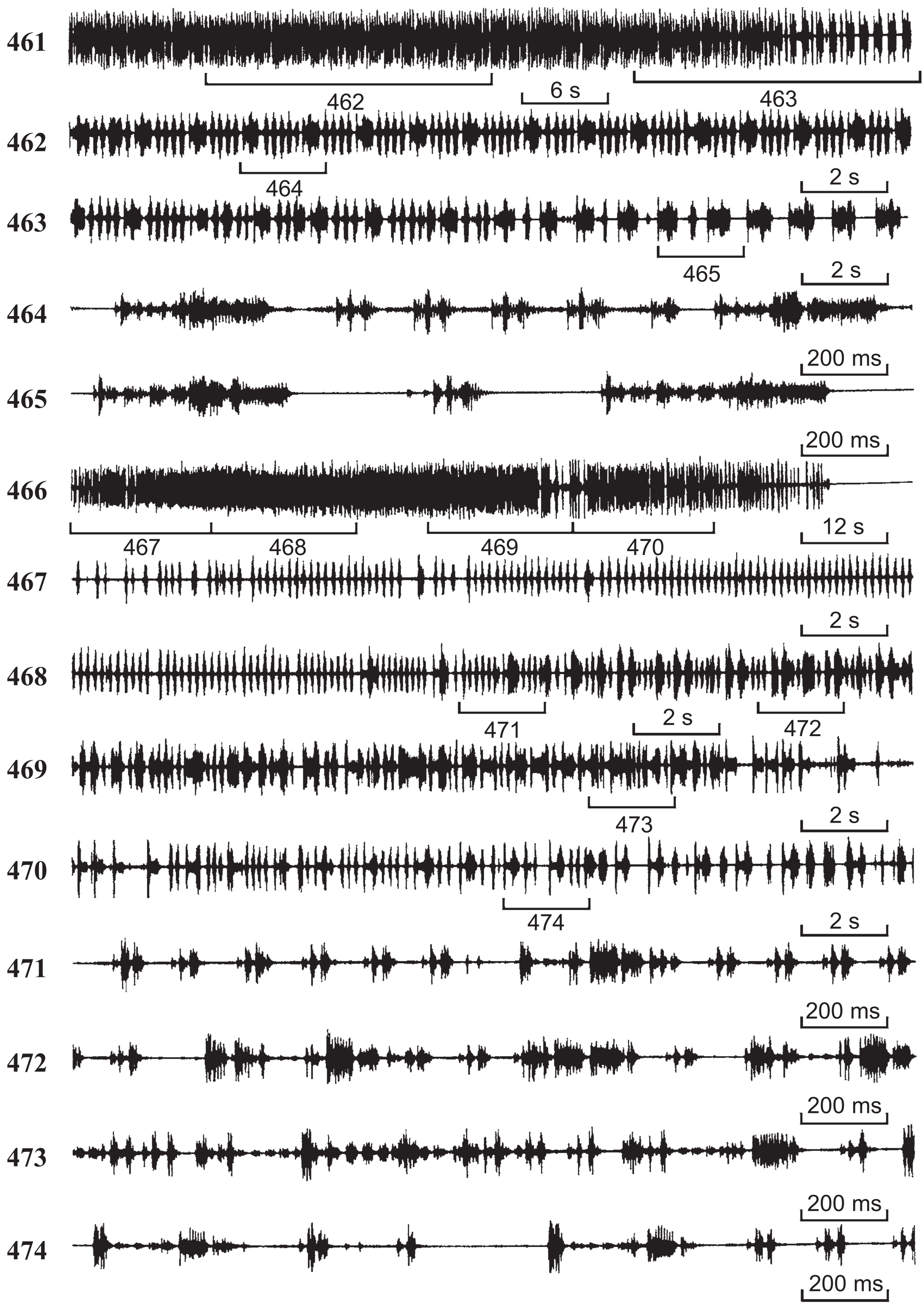
Figs 431–444. Calling signals *Caliscelis affinis* Fieb. 431, 433–438 — oscillograms of signals of males from Rostov Area, 432, 439–441 — same, male from Crimea, 442–444 — oscillogram and frequency spectra of different parts of signal. Faster oscillograms of the parts of signals indicated as "433–438" and "439–441" are given under the same numbers.

Рис. 431–444. Призывные сигналы *Caliscelis affinis* Fieb. 431, 433–438 — осциллограммы призывных сигналов самцов из Ростовской обл., 432, 439–441 — то же, самец из Крыма, 442–444 — осциллограмма и частотные спектры разных частей сигнала. Фрагменты сигналов, помеченные цифрами "433–438" и "439–441", представлены при большей скорости развертки на осциллограммах под такими же номерами.



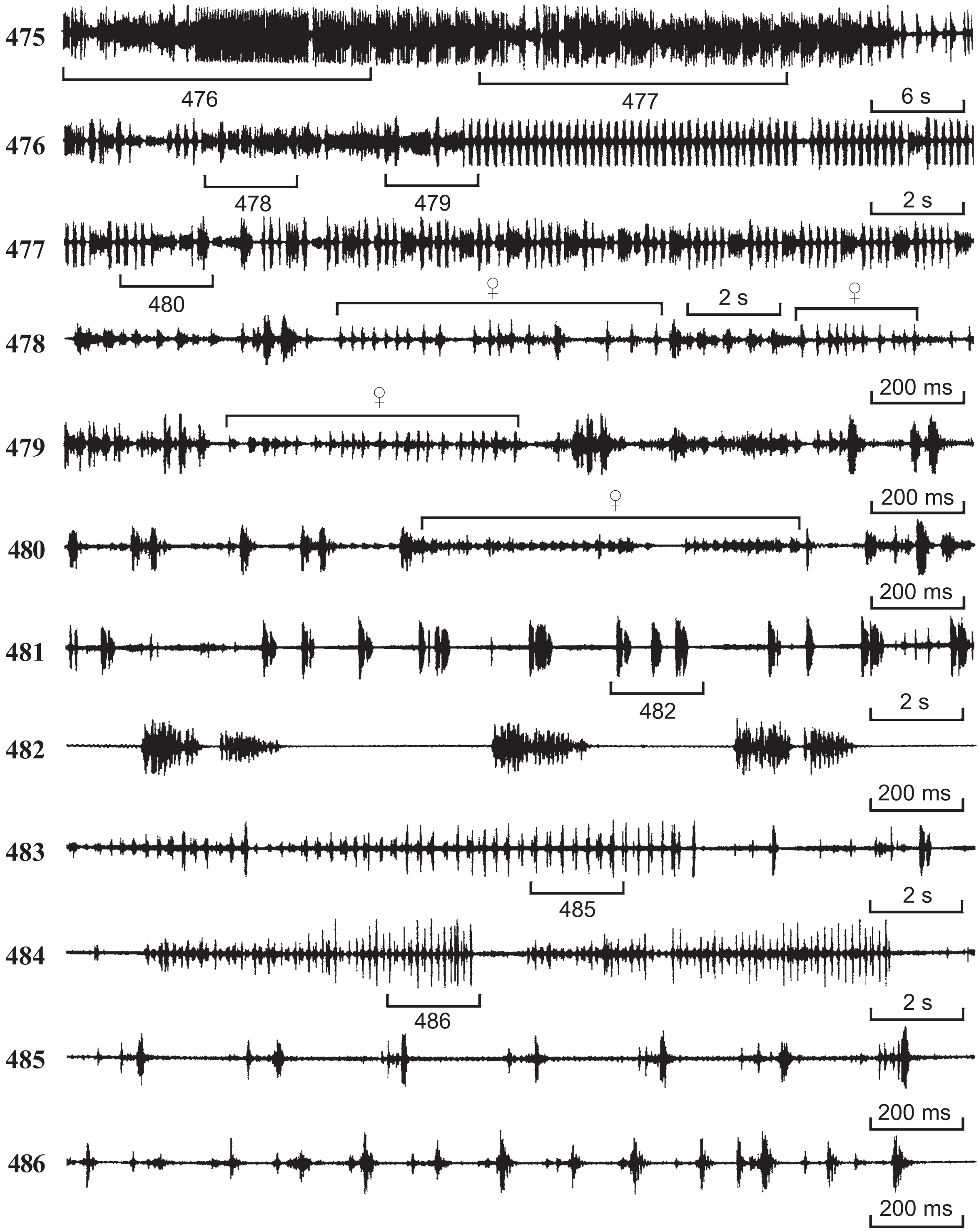
Figs 445–460. Oscillograms of vibrational signals of *Aphelonema punctifrons* (Horv.) (445–448), *A. eoa* (Kusn.) (449–453) and *Aphelonema* sp. (454–460): 445–448 — *A. punctifrons*, calling signals, 449–451 — *A. eoa*, calling signals, 452–453 — same, territorial signals, 454–458 — *Aphelonema* sp., calling signals, 459–460 — same, territorial signals. Faster oscillograms of the parts of signals indicated as “447–448”, “450–451”, “453”, “456–458” and “460” are given under the same numbers.

Рис. 445–460. Осциллограммы вибрационных сигналов *Aphelonema punctifrons* (Horv.) (445–448), *A. eoa* (Kusn.) (449–453) и *Aphelonema* sp. (454–460): 445–448 — *A. punctifrons*, призывные сигналы, 449–451 — *A. eoa*, призывные сигналы, 452–453 — то же, территориальные сигналы, 454–458 — *Aphelonema* sp., призывные сигналы, 459–460 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами “447–448”, “450–451”, “453”, “456–458” and “460”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 461–474. Oscillograms of calling signals of *Ommatidiotus dissimilis* (Fall.). Faster oscillograms of the parts of signals indicated as "462–465" and "467–474" are given under the same numbers.

Рис. 461–474. Осциллограммы призывных сигналов *Ommatidiotus dissimilis* (Fall.). Фрагменты сигналов, помеченные цифрами "462–465" и "467–474", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 475–486. Oscillograms of vibrational signals of *Ommatidiotus dissimilis* (Fall.): 475–480 — male calling and female reply signals, 481–482 — male territorial signals, 483–486 — female territorial signals. Faster oscillograms of the parts of signals indicated as "476–480", "482" and "485–486" are given under the same numbers.

Рис. 475–486. Осциллограммы вибрационных сигналов *Ommatidiotus dissimilis* (Fall.): 475–480 — призывные сигналы самца и ответные сигналы самки, 481–482 —территориальные сигналы самца, 483–486 — территориальные сигналы самки. Фрагменты сигналов, помеченные цифрами "476–480", "482" и "485–486", представлены при большей скорости развертки на осциллограммах под такими же номерами.

SIGNALS. Calling signal is a succession of syllables (Figs 461–463, 466–470). Its duration varies from several seconds up to 1–2 minutes. Temporal pattern of syllables can change significantly from the beginning towards the end of signal (Figs 462–465, 467–474). In short signals it usually remains constant. Pattern of calling signals in males from different localities is quite similar.

Female reply consists of short trains of pulses (Figs 478–480). On the first stage of mating behaviour female produces reply signals responding to spontaneously calling male (Figs 475–477). After hearing female reply male starts running along the plant in different directions until finding the mate. Occasionally, he stops to emit a part of calling. In a few seconds after meeting partners join genitalia. Male rises his tegmina and emits rather short, lasting for about 1.5 s buzzing copulatory signal at this moment (was not recorded).

In both sexes territorial signals were registered. Insects can produce these signals being single, but they sing much more readily in the presence of other individuals. In males, signals of this type consist of short syllables similar with these in *A. eoa* (Figs 481–482). In females, territorial signals are continuous trills or successions of short series (Figs 483–486). The mechanism of production of signals is rather peculiar and was not completely investigated. Under magnification about x7 it was visible that female presses the end of abdomen to substrate and moving right and left valves alternately in longitudinal direction back and forth, scrapes the surface of plant leaf by the halves of ovipositor.

Ommatidiotus inconspicuus Stål, 1863
Figs 487–509.

LOCALITY. Southern part of European Russia, Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, in sand steppe on *Carex* sp. 18, 20.VIII.1992. Signals of 9 ♂♂ and 4 ♀♀ are recorded at the temperature 27–31°C.

SIGNALS. Calling signal is somewhat similar with this of *C. affinis*. It consists of prolonged and rather variable succession of pulses followed by low-amplitude monotonous fragment (Figs 487–500). Occasionally, short trains of syllables same as in the beginning of signal present in monotonous part. Territorial signals in this species are quite similar with these of *O. dissimilis* (Figs 503–509). Several males occurring in the same cage sometimes produce rivalry signals in reply to calling of another individual (Figs 501–502).

Oscillograms and descriptions of vibrational signals of Caliscelidae are given in Tishechkin [1998]. None other data on bioacoustics of this group are known to me.

For a long time Caliscelidae were considered as a subfamily of Issidae. Nevertheless, this group differs clearly from Issidae s.str. as well as from the most part of other Fulgoroidea studied in general scheme of structure of male calling signals. Hamilton [1981] was the first who separated these two taxa regarding Caliscelidae as a family. For some time this opinion remained without any comments, but recently it was supported by a number of specialists basing both on morphological and on molecular and bioacoustics data [Chang, Yang, 1997; Cheng, Yang 1997; Yeh, Yang, Hui, 1998; Tishechkin, 1998; Emeljanov, 1999]. There is some superficial resemblance between temporal pattern of calling in certain Caliscelidae and Delphacidae, but it seems to be of convergent nature.

Two studied species from Caliscelinae and Ommatidiotinae (*C. affinis* and *O. inconspicuus* respectively) have similar structure of calling signals: succession of syllables followed by prolonged monotonous part. On the other hand, females of *Ommatidiotus* possess well-developed territorial behaviour and remarkable territorial signals, apparently produced by certain stridulatory mechanism on the ovipositor. It must be noted here, that Ommatidiotinae morphologically differ from Caliscelinae by the characteristic construction of ovipositor [Emeljanov, 1999]. Therefore, division of Caliscelidae into two subfamilies is also corroborated by acoustic characters.

In contrast with Membracoidea and Cercopoidea, temporal structure of calling signals in different Fulgoroidea families for the most part is rather uniform. In five of seven families studied (Cixiidae, Derbidae, Dictyopharidae, Tropiduchidae, Issidae) calling typically consists of trains of simple uniform pulses. Not rarely, signals of representatives of different families are quite similar. *Cixius nervosus* and *C. cunicularius* from Cixiidae (Figs 303–309) and *Scorlupella discolor* and *Alloscelis vittifrons* from Issidae (Figs 419–421, 425–430) can be mentioned as an example.

Nevertheless, two Fulgoroidea families, namely Delphacidae and Caliscelidae differ much in signals structure from other ones studied. Taxonomic status and position of Caliscelidae in relation to Issidae are discussed above. Delphacidae are regarded as one of the least advanced families of Fulgoroidea. In acoustic characters they stand out against both closely related Cixiidae and such rather non-related groups as Dictyopharidae and Issidae. These data correspond with phylogenetic scheme proposed by Emelyanov [1990]. In his cladogram Delphacidae are the sister-group of the common stem of all Fulgoroidea with the exception of Tettigometridae.

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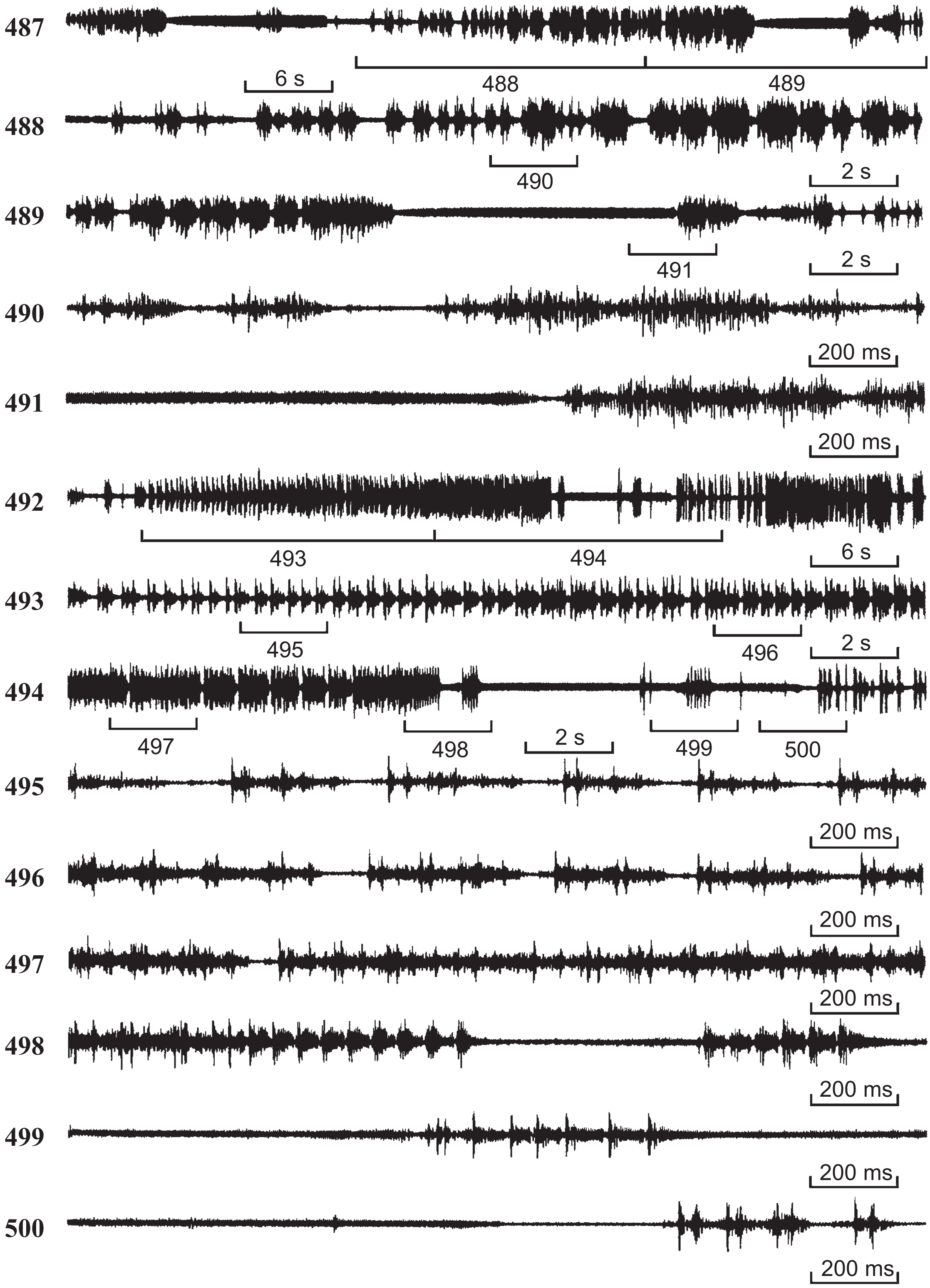
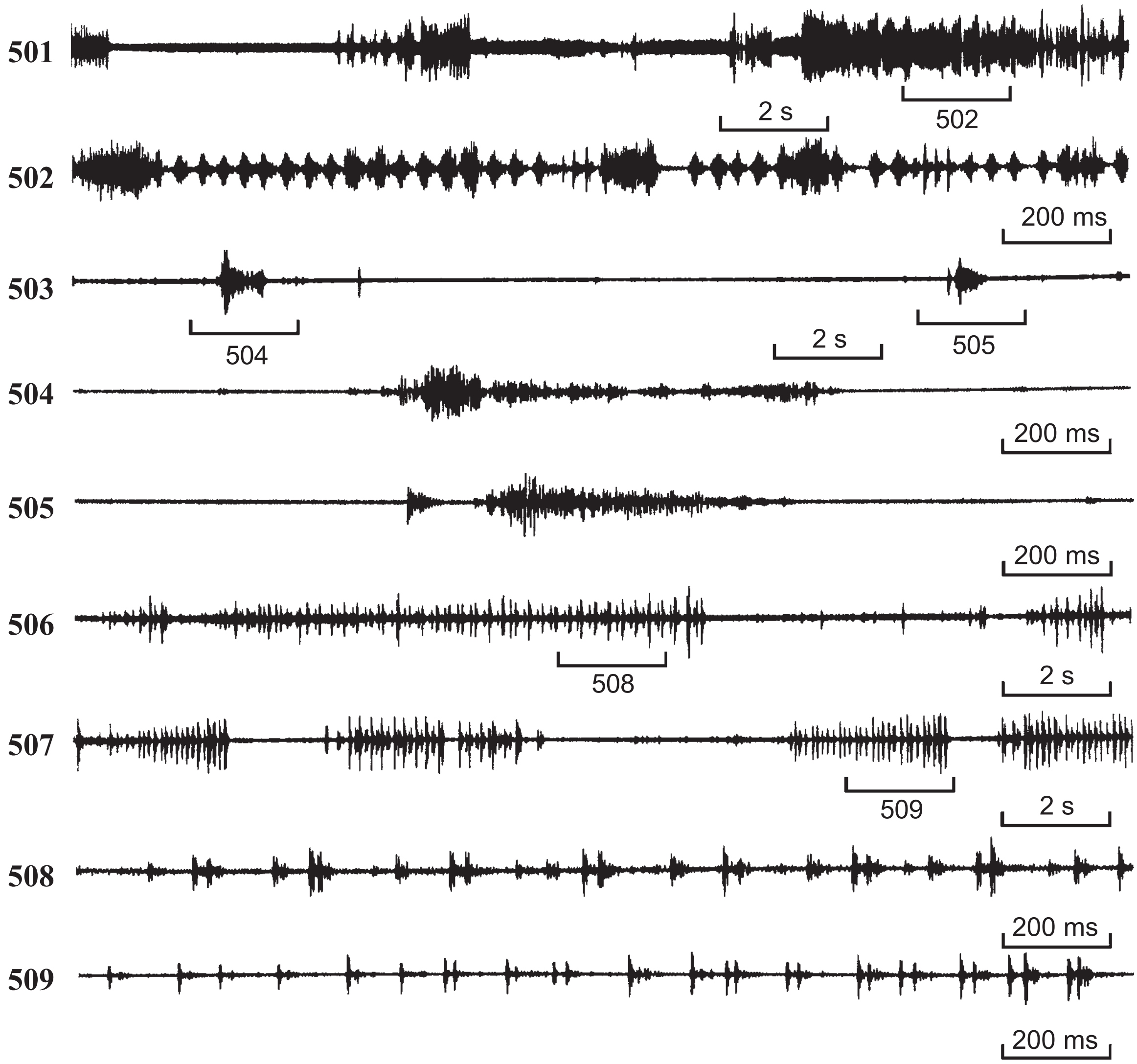


Figs 487–500. Oscillograms of calling signals of *Ommatidiotus inconspicuus* Stål. Faster oscillograms of the parts of signals indicated as “488–491” and “493–500” are given under the same numbers.

Рис. 487–500. Осциллограммы призывных сигналов *Ommatidiotus inconspicuus* Stål. Фрагменты сигналов, помеченные цифрами “488–491” и “493–500”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 501–509. Oscillograms of vibrational signals of *Ommatidiotus inconspicuus* Stål: 501–502 — male rivalry signals, 503–505 — male territorial signals, 506–509 — female territorial signals. Faster oscillograms of the parts of signals indicated as "502", "504–505" and "508–509" are given under the same numbers.

Рис. 501–509. Осциллограммы вибрационных сигналов *Ommatidiotus inconspicuus* Stål: 501–502 — сигналы соперничества самца, 503–505 — территориальные сигналы самца, 506–509 — территориальные сигналы самки. Фрагменты сигналов, помеченные цифрами "502", "504–505" и "508–509", представлены при большей скорости развертки на осциллограммах под такими же номерами.

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