Russian Entomol. J. 12 (1): 11–58

Vibrational communication in leafhoppers from Ulopides subfamilies group (Homoptera: Cicadellidae) and Membracidae with notes on classification of higher taxa

Вибрационная коммуникация цикадок группы подсемейств Ulopides (Homoptera: Cicadellidae) и Membracidae с замечаниями по систематике высших таксонов

D.Yu. Tishechkin
Д. Ю. Тишечкин

Department of Entomology, Faculty of Biology, M.V.Lomonosov Moscow State University, Vorobjevy Gory, Moscow 119899 Russia. E-mail: dt@3.entomol.bio.msu.ru

Кафедра энтомологии Биологического факультета Московского государственного университета имени М.В.Ломоносова, Воробьевы Горы, Москва 119899 Россия. E-mail: dt@3.entomol.bio.msu.ru

KEY WORDS. Cicadellidae, Membracidae, Cicadina, Idiocerinae, Macropsinae, Agalliinae, Adelungiinae, Megophthalminae, Ulopinae, leafhoppers, taxonomy, signals, bioacoustics, vibrational communication.

КЛЮЧЕВЫЕ СЛОВА. Cicadellidae, Membracidae, Cicadina, Idiocerinae, Macropsinae, Agalliinae, Adelungiinae, Megophthalminae, Ulopinae, цикадки, таксономия, сигналы, биоакустика, вибрационная коммуникация.

ABSTRACT. Oscillograms and descriptions of vibrational signals of 50 species of leafhoppers belonging to Idiocerinae, Macropsinae, Agalliinae, Adelungiinae, Megophthalminae and Ulopinae (Homoptera, Cicadellidae) and of 3 species of Membracidae are presented. Taxonomic status and relationships of the taxa studied are discussed basing on bioacoustic characters. The concept of Membracidae deriving from a group within Cicadellidae, being not a sister-group of this family, expressed earlier, is corroborated by bioacoustic data.

РЕЗЮМЕ. Приведены осциллограммы и описания вибрационных сигналов 50 видов цикадок из подсемейств Idiocerinae, Macropsinae, Agalliinae, Adelungiinae, Megophthalminae и Ulopinae (Homoptera, Cicadellidae) и 3 видов Membracidae. На основании биоакустических признаков обсуждается таксономический статус и родственные связи изученных таксонов. Высказанное ранее мнение о том, что Membracidae ведут свое начало от одной из групп Cicadellidae, а не являются сестринской группой этого семейства, подтверждается данными биоакустики.

Introduction

The results of the first study of acoustic signals in small Auchenorrhyncha (Cicadina with the exception of singing cicadas — Cicadidae) were published by F. Ossiannilsson [1949]. Nevertheless, until recently there was very few if any information on vibrational communication in most part of families, subfamilies and tribes of this group. Therefore, some time ago I started a comparative investigation of vibrational signals of Cicadina, trying to cover all the families, subfamilies and tribes represented in the fauna of Russia and adjacent territories as far as possible.

Recently I published data on Iassides (Aphrodinae sensu Hamilton [1975], i.e. including Deltocephalinae + Iassinae + Penthimiinae) and Cicadellides (Cicadellinae s.l. + Typhlocybinae) [Tishechkin, 2000c, 2001]. The present paper is the third in the series and the last, concerning Membracoidea. It includes descriptions of signals of species from the group of related subfamilies usually named Ulopides (Idiocerinae, Macropsinae, Agalliinae, Adelungiinae, Megophthalminae, Ulopinae, etc.) and also, of several species of Membracidae.

The number of articles, providing oscillograms of acoustic signals of representatives of one or another of subfamilies studied is quite different. Several genera of Macropsinae (*Macropsis*, *Oncopsis*, *Hephathus*) are rather well studied due to recent taxonomic works in which signals analysis was involved [Claridge, Howse, 1968; Claridge, Reynolds, 1973; Claridge, Nixon, 1986; Tishechkin, 1992, 2000a, 2000b, 2002]. On the other hand, only data on two and three species respectively are available on Agalliinae and Membracidae [Shaw, 1976; Hunt, 1993, 1994; Strübing, 1999). Idiocerinae, Megophthalminae and Ulopinae were never studied after Ossiannilsson [1949]. For this reason, only verbal descriptions of their signals and recordings made by means of radiograph, which is a pen recorder designed for registration of messages in Morse code, exist [Ossiannilsson, 1949]. All these works are discussed in more details after descriptions of respective taxa.

Methods of recording and analysis of vibrational signals are described in Tishechkin [2000c]. Only explanations of main bioacoustic terms used in the paper are given herein.

Calling signals. Signals produced by male ready to copulation for attracting receptive female. Male can produce signals of this type both being single and in the presence of other individuals. Usually, male remains motionless and does not demonstrate any activity after producing the signal, unless receptive female presents on the same stem.

Reply signals. Signals produced by receptive female in reply to calling male. In most species, after certain time span virgin female starts singing spontaneously.

Courtship signals. Signals produced by male courting female. The term is used only for signals differing distinctly in temporal pattern from calling ones.

Copulatory signals. Signals emitted by male in last moments before copulation and/or at the moment of joining of genitalia. As in the previous case, the term is used only if the signal differs from calling and courtship ones. There issome confusion in literature in using of this and previous terms. Occasionally, in species lacking courtship signals in a strict sense, signals produced immediately before copulation are referred as courtship ones. In species, having both courtship and copulatory signals in their repertoire, the latters sometimes are named as second type of courtship signals, courtship signals II, etc.

Territorial signals. Usually produced by stationary sitting male either in the presence of individuals of the same or opposite sex, or spontaneously. As a rule, no apparent change in insect behaviour is observed either before or after the signals were produced. For this reason, these signals sometimes may be hardly distinguished from calling ones. However, territorial signals for the most part have more simple and inconstant temporal pattern and sometimes are similar in different species. Moreover, they never evoke response reaction of receptive female. Evidently, signals of this type serves for regulation of the distance between individuals on the plant.

Rivalry signals. As a rule, emitted by male in reply to calling or rivalry signals of other individuals. Apparently, male usually produces signals of this type to drown calling of competing males. In contrast with territorial ones, these signals were never registered from single males. Occasionally, several males sitting close to each other on the same stem start producing rivalry signals spontaneously. For this reason, sometimes there is no any well-defined difference between this and previous types of signal. Present in repertoire of some Macropsinae and Adelungiinae only. In most part of other species studied male responds to calling of another one by producing calling or territorial signals.

Call of distress. Under experimental conditions as a rule was registered from individuals got in some narrow place (in a corner of a cage, between a twig and a wall of a cage, etc.) and trying to escape from there, or touched by hand.

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.

Repeated with constant intervals uniform groups of similar or different in structure pulses are referred as**syllables** (= rolls, chirps, series). Succession of similar or different syllables, or even any more or less prolonged signal with complex structure having determinable initial and end parts usually referred as **phrase**. Succession of undeterminable duration, not changing in structure distinctly throughout its length and consisting of uniform pulses, repeating with constant period, is a **trill**.

The terms for signals elements listed above are used only in obvious cases, when the fragment may be classified with certainty as pulse, syllable or trill. In dubious and intermediate situations I use neutral terms, such as “component”, “part”, etc.

For a long time analysis of Cicadina signals was used for discrimination between closely related species or for elucidation of the taxonomic status of dubious forms only. Recently I undertook an attempt to use acoustic characters for solving of taxonomic problems on subfamilies and tribes level in this group [Tishechkin, 2000c, 2001]. The main problems existing in systematics of higher taxa of Ulopides concern the status of Adelungiinae (separate subfamily or the tribe of Agalliinae) and the position of Megophthalminae and Ulopinae. Also, the supposition was expressed recently, that Membracidae, which were regarded as a sister-group of Cicadellidae, indeed are specialized lineage of leafhoppers related with Ulopinae, Megophthalminae and Agalliinae [Rakitov, 1998; Dietrich et al., 2001]. Such conclusions concerning these problems, as can be made basing on bioacoustic data available, are given after descriptions of signals in the respective groups.

Family Cicadellidae

Subfamily Idiocerinae

Idiocerus lituratus (Fallén, 1806)

Figs 1–3.

LOCALITY. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, from *Salix cinerea* L., 4.VIII.2000. Calling signals of 1 ♂ are recorded at 23–24°C.

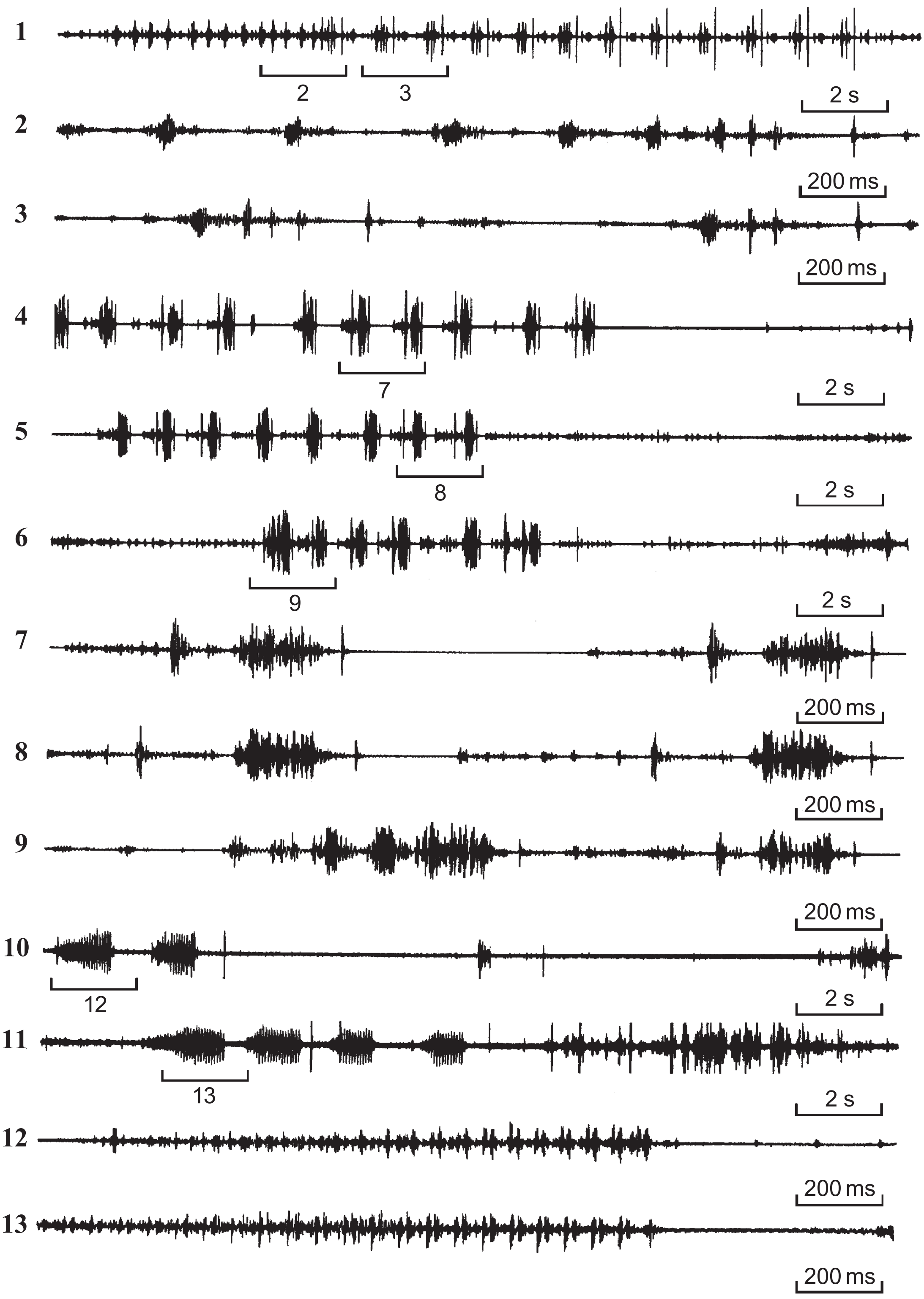
SIGNALS. Calling signal is a long phrase having duration up to 20–25 s and consisting of two parts. The first part is a succession of pulses, repeating with a period about 300–600 ms. Usually low-amplitude additional pulses are distinguishable on oscillograms between high-amplitude main ones (Fig. 2). The second part consists of syllables, repeating with period 1–1.3 s. Each syllable includes several rather low-frequency pulses, similar with ones from the first part of signal, and ends with short one having considerably higher carrier frequency (Fig. 3). For this reason terminal pulses in syllables look distinctly darker on oscillograms at high speed.

Idiocerus stigmaticalis Lewis, 1834

Figs 4–9.

LOCALITY. Moscow Area, environs of Bolshevo Town, from *Salix fragilis* L., 16.VII.1984. Signals of 2♂♂ are recorded at 23–24°C.

SIGNALS. Calling signal is a succession of syllables lasting up to 15–20 s. In general, it is similar with the second part of calling of the previous species. Each syllable consists of rather variable main part and short abrupt click. The click has more high carrier frequency than the main part of syllable. Occasionally, low-amplitude trill precedes or follows the signal (Figs 5–6).



Figs 1–13. Oscillograms of calling signals of *Idiocerus lituratus* (Fall.) (1–3), *I. stigmaticalis* Lew. (4–9) and *Populicerus laminatus* (Flor) (10–13). Faster oscillograms of the parts of signals indicated as "2–3", "7–9" and "12–13" are given under the same numbers.

Рис. 1–13. Осциллограммы призывных сигналов *Idiocerus lituratus* (Fall.) (1–3), *I. stigmaticalis* Lew. (4–9) и *Populicerus laminatus* (Flor) (10–13). Фрагменты сигналов, помеченные цифрами "2–3", "7–9" и "12–13", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Populicerus laminatus (Flor, 1861)
Figs 10–13.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village, from *Populus tremula* L., 21.VI.2000. Signals of 3 ♂♂ are recorded at the temperature 19–21°C.

SIGNALS. Calling signal is a short phrase with duration averaging 1.5–3 s. Its main component is a succession of pulses grouped in pairs, occasionally in the beginning of succession pulses are indistinct (Figs 12–13). After it 2–4 short low-amplitude pulses, separated by gaps about 150–250 ms follow (Fig. 12). Usually, low-frequency vibrations in the main part of signal are clearly visible on oscillograms. Male vibrates by abdomen distinctly when singing; low-frequency component of signal evidently results from abdomen movements. As a rule, male produces 2–5 phrases with intervals 0.5–1.5 s and then stops singing for several minutes. Two males sitting on the same twig can sing simultaneously, so that their signals alternate. No other forms of competition behaviour were observed in this species.

Populicerus populi (Linnaeus, 1761)
Figs 14–21.

LOCALITIES. 1. Moscow, "Sokol'niki" Park. 17.VII.1992. Signals of 2 ♂♂ are recorded at the temperature 25–26°C.

2. Moscow Area, environs of Bolshevo Town, from *P. tremula*, 11–12.VII.1984. Signals of 12 ♂♂ are recorded at 21–22°C.

SIGNALS. As in the previous species, calling signal is a phrase, consisting of two successions of pulses. Usually, male produces several phrases repeating with a period about 2–5 s (Figs 14–15). Occasionally, low-frequency trill precedes the phrase described above (Figs 16–19). It can have rather small duration of 2–3 s, or, on the contrary, averages 10–20 s and more. Such more complex signal as a rule was registered from male sitting in the same cage with female, but male never demonstrated courtship behaviour during or after singing. Similarly with *P. laminatus*, low-frequency components of signal are evidently emitted not only by timbals, but also by tremulation movements.

Several males occurring on the same twig produce short irregular trills of pulses during walking from time to time (Figs 20–21). Maybe, these are territorial signals.

Populicerus confusus (Flor, 1861)
Figs 22–25.

LOCALITY. Moscow Area, environs of Pushkino, from *Salix cinerea* L. on Ucha River bank. 14, 17.VII.1984. Signals of 6 ♂♂ are recorded at 23–25°C.

SIGNALS. In general structure calling is similar with this in two other *Populicerus* species, but it has somewhat more complex temporal pattern due to additional succession of pulses in the middle of a signal. Also, more prolonged form of calling with additional trill preceding the main part of signal, similar with this in *P. populi* was heard, but not recorded in this species. As in two previous species, a train of low-frequency pulses in the beginning of signal evidently is emitted both by timbals and abdomen tremulation.

All Idiocerinae studied distinctly vibrate by abdomen during singing. The mass of abdomen and amplitude of its movements is much higher, than in timbals, so tremulation movements certainly play substantial role in generation of signal. Apparently, low-frequency vibrations presenting on oscillograms are resulted from these movements.

Tremulation (vibration by the parts of body, usually, by abdomen without contact with substrate) is one of the most archaic and non-specialised mechanisms of acoustic communication in insects. For this reason, Idiocerinae seem to be the least advanced group among the studied taxa of Ulopides. This fact corroborates the point of view of Emelyanov and co-authors [Anufriev, Emelyanov, 1988; Emelyanov, Kirillova, 1989], who place this subfamily in the beginning of the list of Ulopides in their works.

Subfamily Macropsinae

Pediopsis tiliae (Germar, 1831)
Figs 26–45.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village, from small-leaved lime (*Tilia cordata* Miller), 14–17.VI.1989. Signals of 11♂♂ are recorded at the temperature 22–24°C.

SIGNALS. Calling signal is a single or repeating phrase consisting of three different parts (Figs 26–30). The first part consists of rather variable pulses or syllables and lasts from 2–3 s up to several minutes (Figs 31–34). The second one is composed of partially merged pulses repeating at a rate about 40/s, duration of this trill is about 1–1.5 s (Figs 32–34, 35–37). The third part is a succession of discrete pulses following each other with a period of 0.5–1 s. Number of pulses in it varies from 4–5 up to 20–30 (Figs 35–37).

I have never registered female reply signals in *P. tiliae*. Moreover, in this species, this is female, who walks in different directions along the twig before mating, searching for male, while the latter remains stationary, producing calling signals. Only after female approaches male within a distance of about 3–4 cm, he suddenly runs to her and starts copulation. During mounting female he produces copulatory signal, which is a succession of pulses (Figs 38–41).

Single male during grooming or not demonstrating any specific activity produces territorial signals, consisting of variable in structure irregular pulses (Figs 42–43).

Several males sitting on the same twig occasionally can react on each other's calling by rivalry signals, which are irregular trills of short pulses (Figs 44–45).

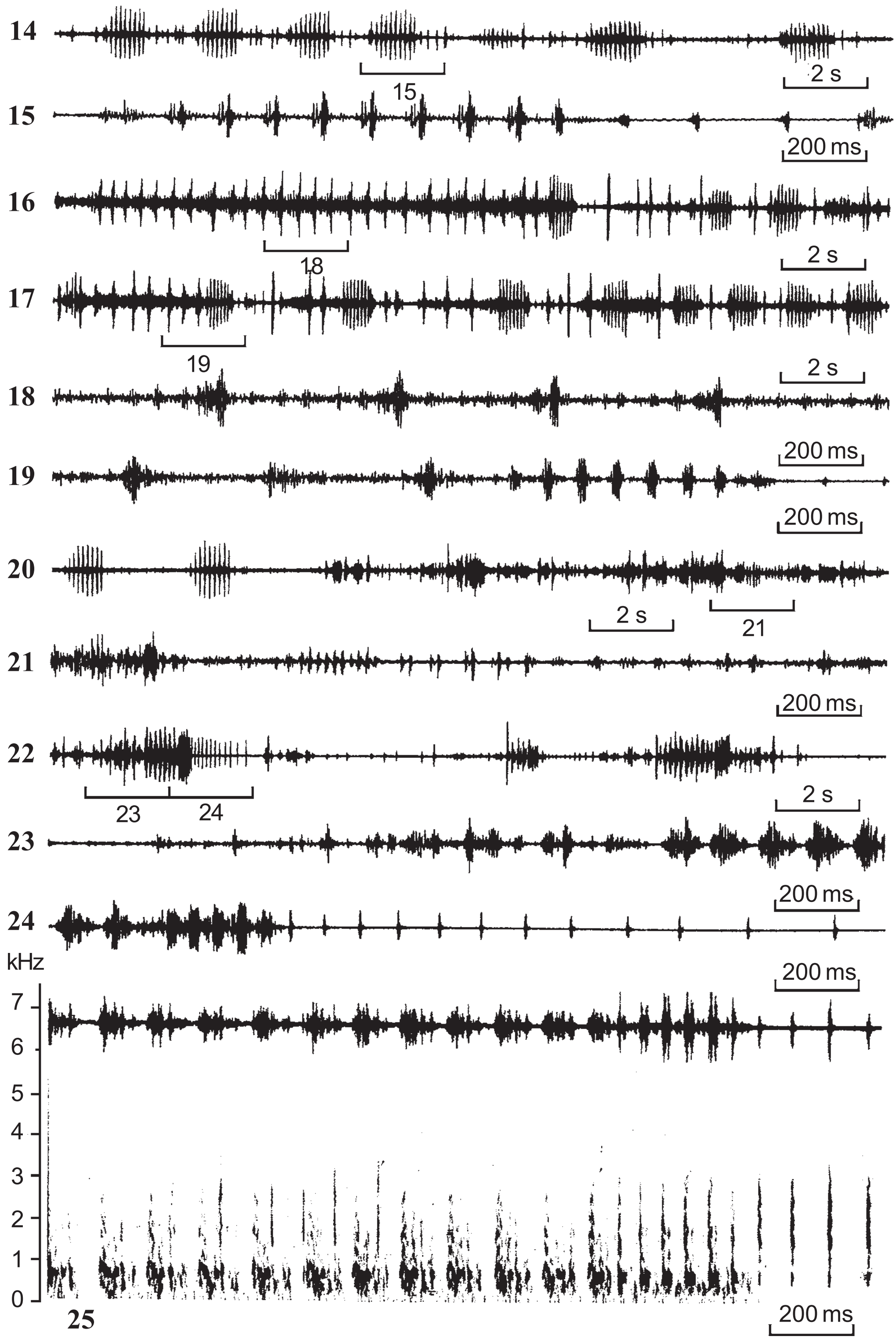
NOTE. Brief description of vibrational signals and mating behaviour of this species is given in Tishechkin [1994].

Pediopsoides kurentsovi (Anufriev, 1977)
Figs 46–49.

LOCALITY. The Southern Maritime Province, Pogranichny District, environs of Barabash-Levada Village, from *Juglans mandshurica* Maxim.; 1 ♂. 21.VII.1995. Shade air temperature — 27°C.

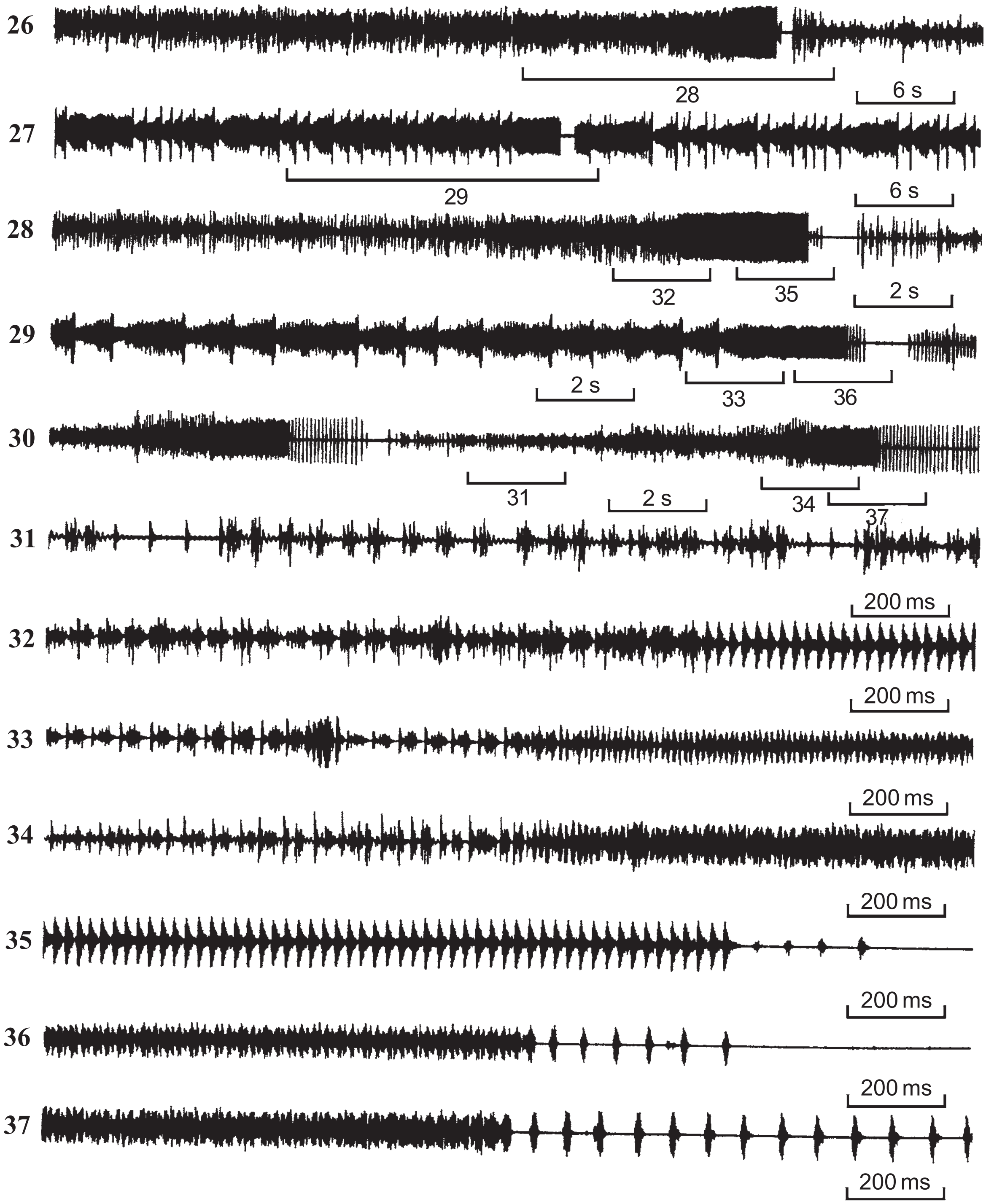
SIGNALS. Calling signal of this species is a long single phrase lasting for about 20 s. It consists of several successions of syllables, each syllable includes 4–6 low-amplitude pulses and one high-amplitude one. In the end of each succession several additional discrete pulses present.

NOTE. Interpretation of species is accepted after Hamilton [1980]. In Anufriev, Emelyanov [1988] the species is mentioned under the name *P. juglans* Mats.



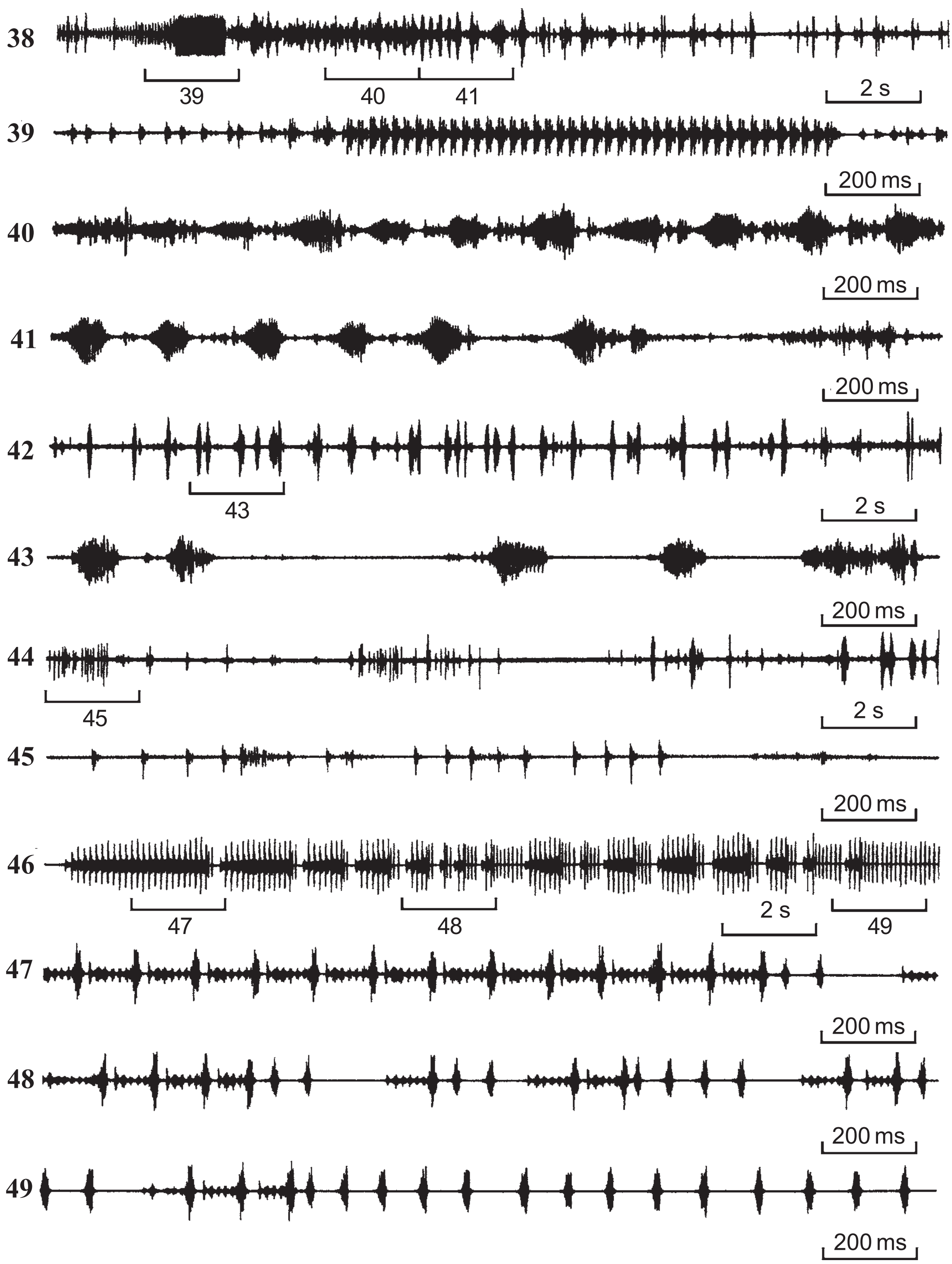
Figs 14–25. Vibrational signals of *Populicerus populi* (L.) (14–21), and *P. confusus* (Flor) (22–25): 14–15 — oscillograms of short form of calling signal of *P. populi*, 16–19 — same, long form, 20–21 — oscillograms of trills of pulses of males of *P. populi*, 22–24 — oscillograms of calling signal of *P. confusus*, 25 — same, oscillogram and sonogram. Faster oscillograms of the parts of signals indicated as “15”, “18–19”, “21” and “23–24” are given under the same numbers.

Рис. 14–25. Вибрационные сигналы *Populicerus populi* (L.) (14–21), и *P. confusus* (Flor) (22–25): 14–15 — осциллограммы короткой формы призывного сигнала *P. populi*, 16–19 — то же, полная форма, 20–21 — осциллограммы трелей пульсов самцов *P. populi*, 22–24 — осциллограммы призывных сигналов *P. confusus*, 25 — то же, осциллограмма и сонограмма. Фрагменты сигналов, помеченные цифрами “15”, “18–19”, “21” и “23–24”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 26–37. Oscillograms of calling signals of *Pediopsis tiliae* (Germ.). Faster oscillograms of the parts of signals indicated as "28–29" and "31–37" are given under the same numbers.

Рис. 26–37. Осциллограммы призывных сигналов *Pediopsis tiliae* (Germ.). Фрагменты сигналов, помеченные цифрами "28–29" и "31–37", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 38–49. Oscillograms of vibrational signals of *Pediopsis tiliae* (Germ.) (38–45) and *Pediopsoides kurentsovi* (Anufr.) (46–49): 38 — *P. tiliae*, calling and copulatory signals, 39 — same, calling signal, 40–41 — same, copulatory signal, 42–43 — same, territorial signals, 44–45 — same, rivalry signals, 46–49 — calling signal of *P. kurentsovi*. Faster oscillograms of the parts of signals indicated as "39–41", "43", "45" and "47–49" are given under the same numbers.

Рис. 38–49. Осциллограммы вибрационных сигналов *Pediopsis tiliae* (Germ.) (38–45) и *Pediopsoides kurentsovi* (Anufr.) (46–49): 38 — *P. tiliae*, призывный и копуляционный сигналы, 39 — то же, призывный сигнал, 40–41 — то же, копуляционный сигнал, 42–43 — то же, территориальный сигнал, 44–45 — то же, сигнал соперничества, 46–49 — призывный сигнал *P. kurentsovi*. Фрагменты сигналов, помеченные цифрами "39–41", "43", "45" и "47–49", представлены при большей скорости развертки на осциллограммах под такими же номерами.

Oncopsis flavicollis (Linnaeus, 1761) Figs 50–61.

LOCALITIES. 1. Moscow Area, Serpukhov District, Pushchino-na-Oke Town, from common birch (*Betula pendula* Roth), 5–8.VI.1985. Signals of more than 15♂♂ are recorded at 20–21°C.

2. Altai Mountains, N shore of Teletskoe Lake, Altaiskiy Nature Reserve, environs of Yaylyu Village, from common birch. 8.VII.1999. Calling signals of 1♂ are recorded at the temperature 30–35°C.

SIGNALS. Calling signal is a long single phrase, usually lasting from 10–15 up to 40–50 s (Figs 50–53). It begins with monotonous buzzing trill as a rule averaging several seconds. In the main part of signal trill is regularly (every 1–2 s) interrupted with short fragments of another kind (Figs 54–55). Their carrier frequency is always distinctly higher, than in the trill (Figs 56–57), but the amplitude varies greatly, depending on physical characteristics of substrate (twig or stem on which the insect sings). Signal ends with a short train of discrete pulses.

If male going along the twig contacts with another one sitting on his way, one individual or both of them as a rule produce rivalry signals (Figs 58, 60). Also, male emits signals of this type in reply to calling or rivalry signal of another one, sitting on the same stem (Figs 51, 59). Rivalry signal is a long trill; sometimes it also includes buzzing fragments of varying length.

Occasionally, male produces separate syllables with irregular intervals, not demonstrating any specific activity (Fig. 61). Evidently, these are territorial signals.

NOTES. Claridge and Nixon [1986], basing on both morphological and acoustic characters, came to the conclusion, that *O. flavicollis* sensu lato in Britain includes three closely related biological species. However, they did not give any scientific names to these forms, merely referring them as *O. flavicollis* 1, 2 and 3. All the material studied by me, both from Moscow Area and Altai Mts. belongs to *O. flavicollis* 2.

Oncopsis subangulata (J. Sahlberg, 1871) Figs 62–66.

LOCALITY. Moscow Area, environs of Pirogovo, the bank of Klyaz'ma River, from birch (*Betula* sp.): 17.VI.1985, signals of 2 ♂♂ are recorded at the temperature 21°C; 10.VI.1988, signals of 2 ♂♂ are recorded at the temperature 25°C.

SIGNALS. Calling is a long phrase, occasionally averaging more than a minute (Figs 62–64). It consists of alternating trills of two types. As in *O. flavicollis*, relation of their amplitudes varies from signal to signal (Figs 65–66). Trills of both types are composed of pulses or short syllables, but differ in the shape of pulses. Occasionally, pulses repetition rate somewhat decreases before the end of signal.

NOTE. Temporal pattern of calling signals in specimens studied is similar with this of songs of British ones, presented on oscillograms in Claridge, Nixon [1986].

Oncopsis tsejensis Tishechkin, 1992 Figs 67–71.

LOCALITY. North Caucasus, North Ossetia, Tsey Canyon (Ardon River basin) in the environs of Nizhniy Tsey Village (1700 m above sea level), from alder (*Alnus incana* (L.) Moench). 27.VII.1990. Signals of 2♂♂ are recorded at the temperature 19–20°C.

SIGNALS. As in the previous species, calling signal is a long phrase, consisting of alternating fragments with different waveform (Figs 67–69). Rivalry signals are similar with these of *O. flavicollis* (Figs 70–71).

Oncopsis carpini (J. Sahlberg, 1871) Figs 72–76.

LOCALITY. Crimea, environs of Pereval'noe Village (halfway from Simferopol to Alushta), from *Carpinus betulus* L. 21.VI.1997. Signals of 3 ♂♂ are recorded at 24-26°C.

SIGNALS. Calling signal in general is similar with these of two previous species, but differs both in repetition period and shape of pulses (Figs 72–74). Rivalry signal is similar with these of *O. flavicollis* and *O. tsejensis* (Figs 75–76).

Oncopsis alni (Schrank, 1801) Figs 77–87.

LOCALITY. Moscow Area, Serpukhov District, Pushchino-na-Oke Town, from black alder (*Alnus glutinosa* (L.) Gaertn.), 19–20, 24.VI.1985. Signals of more than 10 individuals of both sexes are recorded at 20–21°C.

SIGNALS. Calling signal is a long, monotonous, occasionally interrupting trill followed by succession of syllables, repeating at a rate of about 2–3/s (Figs 77–80). When mounting female, or sitting on her back during courtship, male produces copulatory signal, which is continuous trill (Figs 81–82). Territorial signals are rather variable syllables, following each other with irregular intervals (Fig. 83). Rivalry signals are similar with these in other *Oncopsis* species (Figs 84–86). Also, both males and females produce call of distress, when they are seized or jammed, for instance in a narrow place between a twig and a wall of a cage (Fig. 87).

Oncopsis tristis (Zetterstedt, 1840) Figs 88–91.

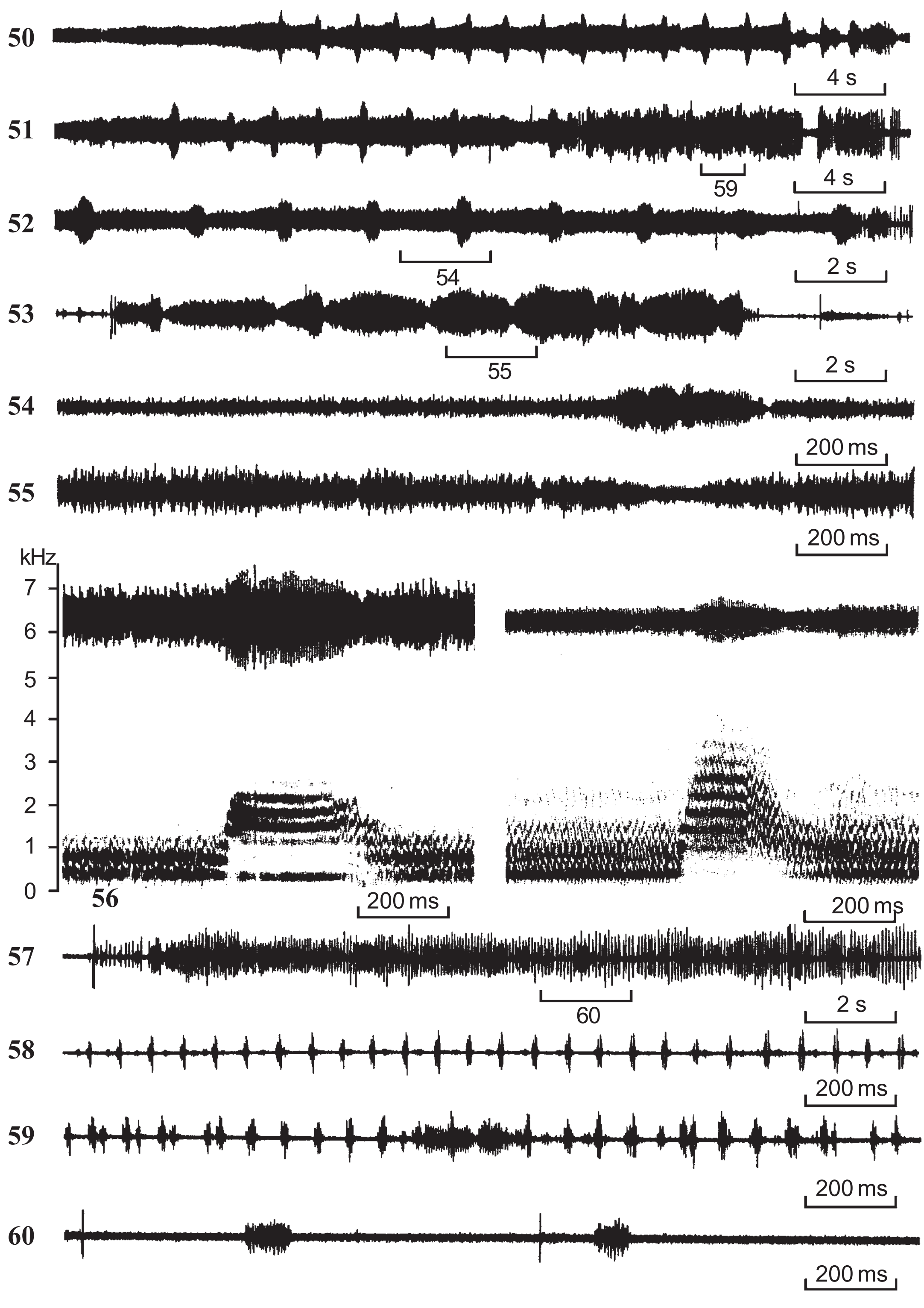
LOCALITIES. 1. Moscow Area: (1) environs of Bolshevo Town, from common birch, 27.VI.1984, signals of 2♂♂ are recorded at the temperature 21°C; (2) environs of Pushkino Town, from common birch, 29–30.VI, 6.VII.1984, signals of 9♂♂ are recorded at the temperature 21–22°C

2. Altai Mountains, N shore of Teletskoe Lake, Altaiskiy Nature Reserve, environs of Yaylyu Village, from common birch together with *O. flavicollis*. 5.VII.1999. Calling signals of 1 ♂ are recorded at the temperature 29°C.

SIGNALS. Calling signal is a long phrase, lasting up to 40–50 s. In general structure it is similar with signals of *O. subangulata*, *O. tsejensis* and *O. carpini*, but differs in the shape of pulses and syllables. Temporal pattern of signals of individuals from different populations is identical.

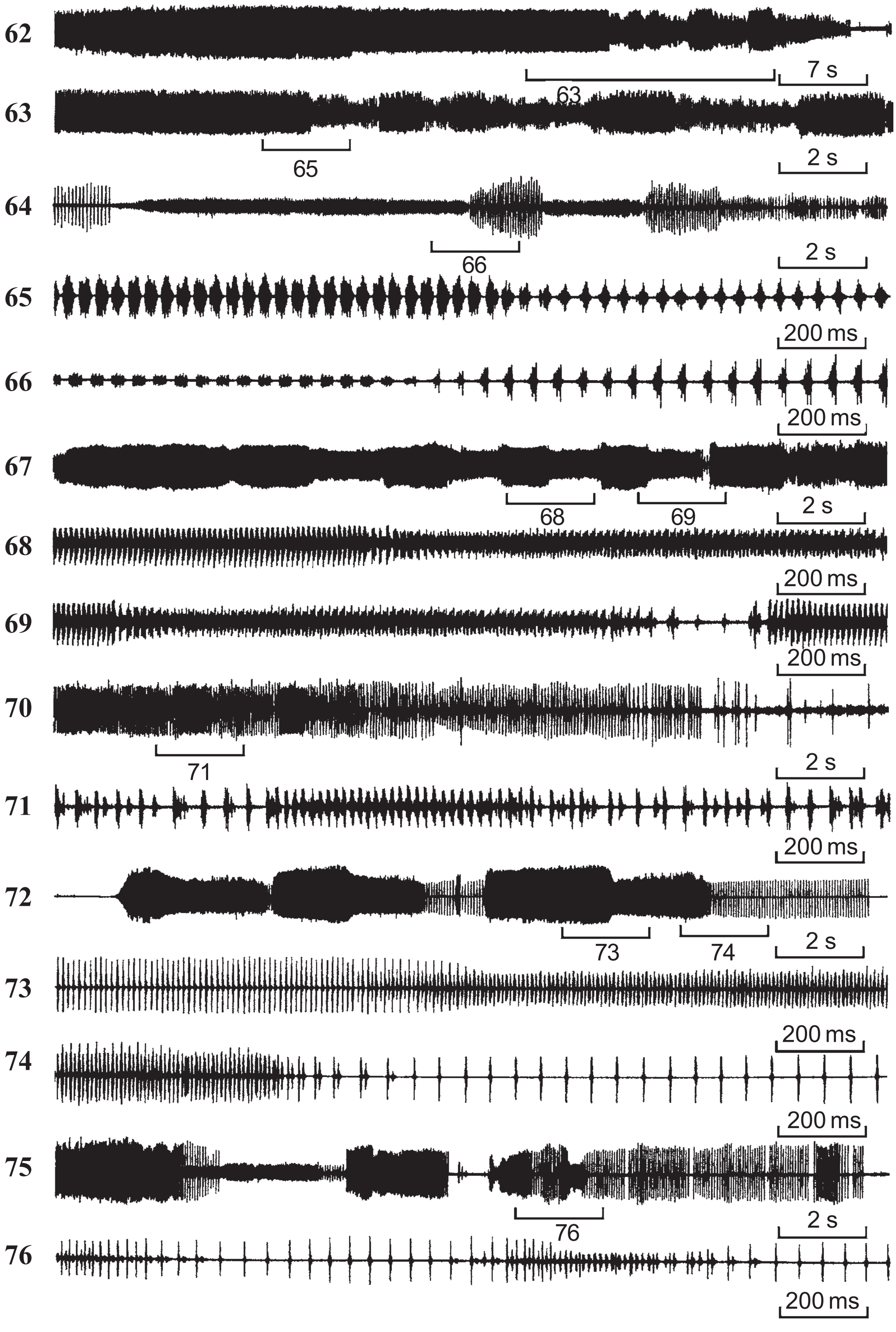
Acoustic signals of British *Oncopsis* species were studied by Claridge and co-authors (Claridge, Howse, 1968, Claridge, Reynolds, 1973, Claridge, Nixon, 1986). In the first two papers only signals produced by male during mounting female before copulation were studied. Authors refer these signals as courtship ones, but according to terminology used in the present paper these are rather copulatory signals. Copulatory signal of *O. tristis* is a long trill similar with this of *O. alni* [Claridge, Howse, 1968]. In species from *O. flavicollis* group (*O. flavicollis*, *O. avellanae* Edwards, 1920, *O. subangulata*, *O. carpini*) these signals are quite similar and consist of repeating phrases [Claridge, Reynolds, 1973]. Nevertheless, basing on signals analysis, authors came to the conclusion that all four forms are separate species.

More detailed study of British *Oncopsis* species from *O. flavicollis* group in Britain was provided by



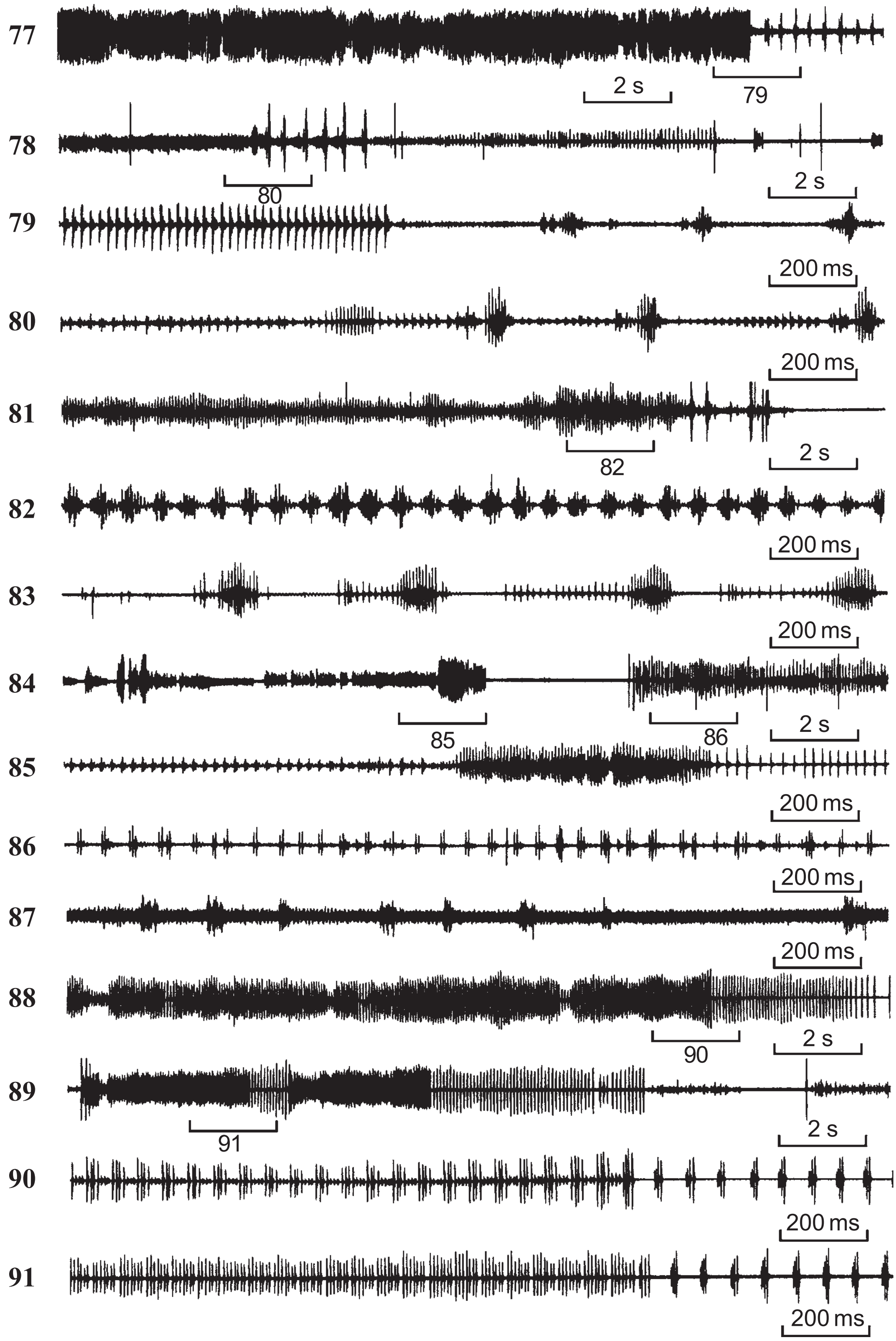
Figs 50–61. Vibrational signals of *Oncopsis flavicollis* (L): 50, 52–55 — oscillograms of calling signals, 51 — same, calling and rivalry signals, 56–57 — oscillograms and sonograms of calling signals, 58–60 — oscillograms of rivalry signals, 61 — oscillogram of territorial signal. Faster oscillograms of the parts of signals indicated as “54–55” and “59–60” are given under the same numbers.

Рис. 38–49. Осциллограммы вибрационных сигналов *Oncopsis flavicollis* (L): 50, 52–55 — осциллограммы призывных сигналов, 51 — то же, призывный сигнал и сигнал соперничества, 56–57 — осциллограммы и сонограммы призывных сигналов, 58–60 — осциллограммы сигналов соперничества, 61 — осциллограмма территориального сигнала. Фрагменты сигналов, помеченные цифрами “54–55” и “59–60”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 62–76. Oscillograms of vibrational signals of *Oncopsis subangulata* (J. Sahlb.) (62–66), *O. tsejensis* Tish. (67–71) and *O. carpini* (J. Sahlb.) (72–76): 62–66 — calling signals of *O. subangulata*, 67–69 — same, *O. tsejensis*, 70–71 — rivalry signals of *O. tsejensis*, 72–74 — *O. carpini*, calling signals, 75–76 — same, calling and rivalry signals. Faster oscillograms of the parts of signals indicated as "63", "65–66", "68–69", "71", "73–74" and "76" are given under the same numbers.

Рис. 62–76. Осциллограммы вибрационных сигналов *Oncopsis subangulata* (J. Sahlb.) (62–66), *O. tsejensis* Tish. (67–71) и *O. carpini* (J. Sahlb.) (72–76): 62–66 — призывные сигналы *O. subangulata*, 67–69 — то же, *O. tsejensis*, 70–71 — сигналы соперничества *O. tsejensis*, 72–74 — *O. carpini*, призывные сигналы, 75–76 — то же призывные сигналы и сигналы соперничества. Фрагменты сигналов, помеченные цифрами "63", "65–66", "68–69", "71", "73–74" и "76", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 77–91. Oscillograms of vibrational signals of *Oncopsis alni* (Schrk.) (77–87) and *O. tristis* (Zett.) (88–91): 77–80 — *O. alni*, calling signals, 81–82 — same, copulatory signals, 83 — same, territorial signals, 84–86 — same, rivalry signals, 87 — same, call of distress, 88–91 — calling signals of *O. tristis*. Faster oscillograms of the parts of signals indicated as “79–80”, “82”, “85–86” and “90–91” are given under the same numbers.

Рис. 77–91. Осциллограммы вибрационных сигналов *Oncopsis alni* (Schrk.) (77–87) и *O. tristis* (Zett.) (88–91): 77–80 — *O. alni*, призывные сигналы, 81–82 — то же, копуляционные сигналы, 83 — то же, территориальные сигналы, 84–86 — то же, сигналы соперничества, 87 — то же, сигнал протеста, 88–91 — призывные сигналы *O. tristis*. Фрагменты сигналов, помеченные цифрами “79–80”, “82”, “85–86” и “90–91”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Claridge and Nixon [1986]. Authors subdivided *O. flavicollis* into three forms differing in structure of both calling and copulatory signals and also, in some morphological characters. Only one of these forms (so called *O. flavicollis* 2) was found in Russia until now.

Oscillograms of calling signals of *O. flavicollis*, *O. subangulata* and *O. tsejensis* are also presented in Tishechkin [1992]. Very brief descriptions of signals of 4 species are given in Tishechkin [1994].

The genus *Macropsis* Lewis, 1834.

Calling signals of 39 species are described in my review of *Macropsis* from the territory of Russia [Tishechkin, 2000a, 2002]. In the present paper only signals of selected species are described with the purpose to illustrate as far as possible all the diversity of signals structure in the genus. Oscillograms showing variability of signals temporal pattern in each species for the most part are not given. Geographical variability of signals structure was not observed in the species of the genus. For this reason oscillograms of signals of the same species from different localities also are not presented.

Macropsis vicina (Horvath, 1897)
Figs 92–104.

LOCALITIES. 1. Moscow Area, Serpukhov District, Pushchino-na-Oke Town, from *Populus alba* L. 3.VII.1985. Signals of 5 ♂♂ are recorded at 21°C.

2. Volgograd Area, Ilovlya River about 5 km from the mouth, from *P. alba*. 10.VI.1996. Signals of 2♂♂ are recorded at 26–29°C.

3. North-west Caucasus, Krasnodar Province, valley of Sukko River 12 km S of Anapa. 30.VI — 1.VII.1997. Calling signals of 2 ♂♂ collected from *P. alba* are recorded at 27–28°C.

SIGNALS. There are two forms of calling signal in this species. The first (reduced) one is a succession of syllables, lasting for approximately 10–20 s (Figs 92–94). Syllables at the beginning of signal have duration about 200–300 ms, then several much longer ones (up to 1.5–2 s) follow. Their duration gradually decrease towards the end, so that initial and end syllables in a signal are almost equal in length.

Calling of the second (full) type also begins with a succession of syllables, but the last of the longer syllables suddenly changes into monotonous buzzing fragment after which a train of alternating short and long pulses follows (Figs 95–98). Single male can produce signals of both types, but when courting female he produces only full calling. After emitting one or several such signals male mounts female and produces copulatory one which is an end part of calling, i.e. the buzzing fragment and the train of pulses (Figs 99–102). In all cases observed copulation attempts were unsuccessful.

Male, being single or in the presence of other individuals, also produces territorial signals, consisting of short syllables, as in the beginning of calling, but following with greater intervals (Figs 103–104). Occasionally, he can sing in such a manner for half an hour and more.

Macropsis graminea (Fabricius, 1798)
Figs 105–118.

LOCALITIES. 1. Moscow Area, Serpukhov District, Pushchino-na-Oke Town, from *Populus nigra* var. *pyramidalis* Spach. 27–28.VI.1985. Signals of 3 ♂♂ are recorded at 21–22°C.

2. Crimea, environs of Pereval'noe Village (halfway from Simferopol to Alushta), from *P. nigra* L. 16.VI.1997. Signals of 2 ♂♂ are recorded at 21–22°C.

3. Volgograd Area, Ilovlya River about 5 km from the mouth, from *P. nigra*. 6–7.VI.1996. Signals of 5 ♂♂ are recorded at 18 and 21–22°C.

4. Orenburg Area, Sakmara River 20–25 km NNE of Kuvandyk Town, environs of Churaevo Village, from *P. nigra*. 29.VI.1996. Signals of 2 ♂♂ are recorded at 27°C.

SIGNALS. As in the previous species, there are two forms of calling signals in *M. graminea*. Reduced form consists of three different parts (Figs 105–108), in full calling two more parts similar with these in the signal of *M. vicina* present (Figs 109–116). Single male usually (but not always) produces reduced signals, whereas in the presence of female he as a rule emits full ones.

Territorial signal is a continuous trill consisting of pulses similar with these in the first part of calling, but following with longer and less regular intervals (Figs 117–118).

NOTES. In two other closely related species dwelling on *Populus* (*M. fuscinervis* (Boh., 1845) and *M. suspecta* Tishechkin, 1994) calling signals structure is quite similar with this in species described above.

Macropsis cerea (Germar, 1837)
Figs 119–126.

LOCALITIES. 1. Moscow Area. Several geographical points in central and southern parts. Signals of more than 15♂♂ collected from different species of willows were recorded at the temperature 21–26°C.

2. East of Saratov Area, 10 km from Ozinki Town towards Ural'sk, from *Salix vinogradovii* Skvortsov, 1 ♂. 24.VI.1996. Recording was made at the shade air temperature 28–30°C.

3. Orenburg Area, Sakmara River near Churaevo Village, 20–25 km NNE of Kuvandyk, from *Salix triandra* L., 1 ♂. 29.VI.1996. Recording was made at the shade air temperature 26–27°C.

4. Southern Tuva, environs of Erzin Village, from *Salix ledebouriana* Trautv. 30.VII.1989. Signals of 1♂ were recorded at the temperature 25°C.

5. Amur Area, approximately 30 km W of Svobodny, from *Salix udensis* Trautv. et Mey., 1♂. 6.VII.1995. Recording was made at the shade air temperature 25°C.

6. The Southern Maritime Province, Pogranichny District, Komissarovka River near Barabash-Levada Village, from *S. udensis*, 1 ♂. 13.VII.1995. Recording was made at the shade air temperature 25°C.

SIGNALS. Calling signal consists of repeating phrases, following each other with a period of 2–4 s (Figs 119–122). Also, male emits the same signal on all stages of courtship behaviour and immediately before copulation (Figs 123–124).

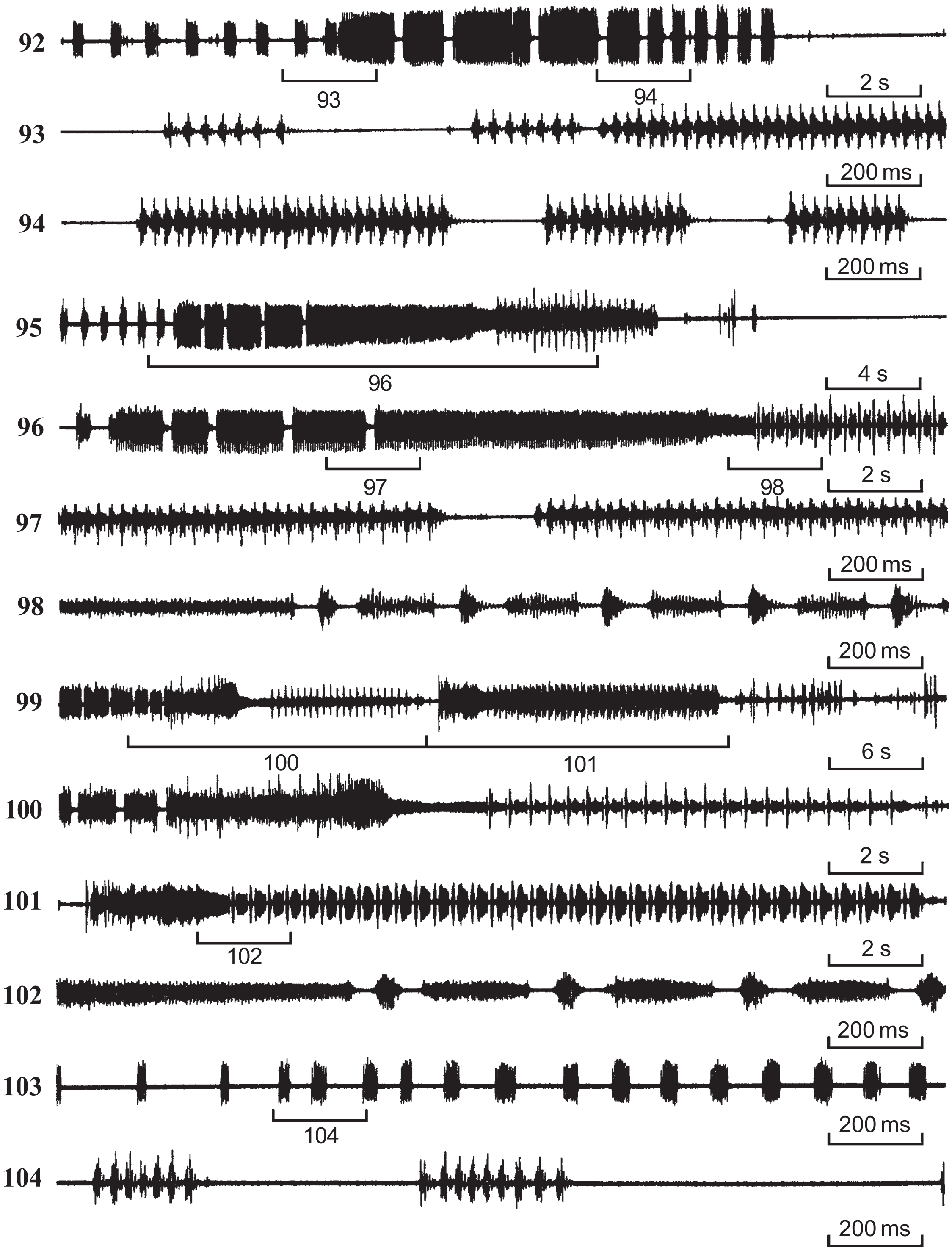
Single male during walking and occasionally also when sitting motionless produces continuous signal with highly varying parameters sounding like irregularly interrupting buzzing noise (Figs 125–126). Evidently, this is a territorial signal.

Macropsis prasina (Boheman, 1852)
Figs 127–133.

LOCALITIES. 1. Moscow Area, environs of Pushkino (about 15 km from the north-eastern boundary of Moscow), from *Salix cinerea* L. on the bank of Ucha River. 23, 25.VI.1984 and 24.VI.1988. Signals of 8♂♂ are recorded at the temperature 20–21 and 27°C.

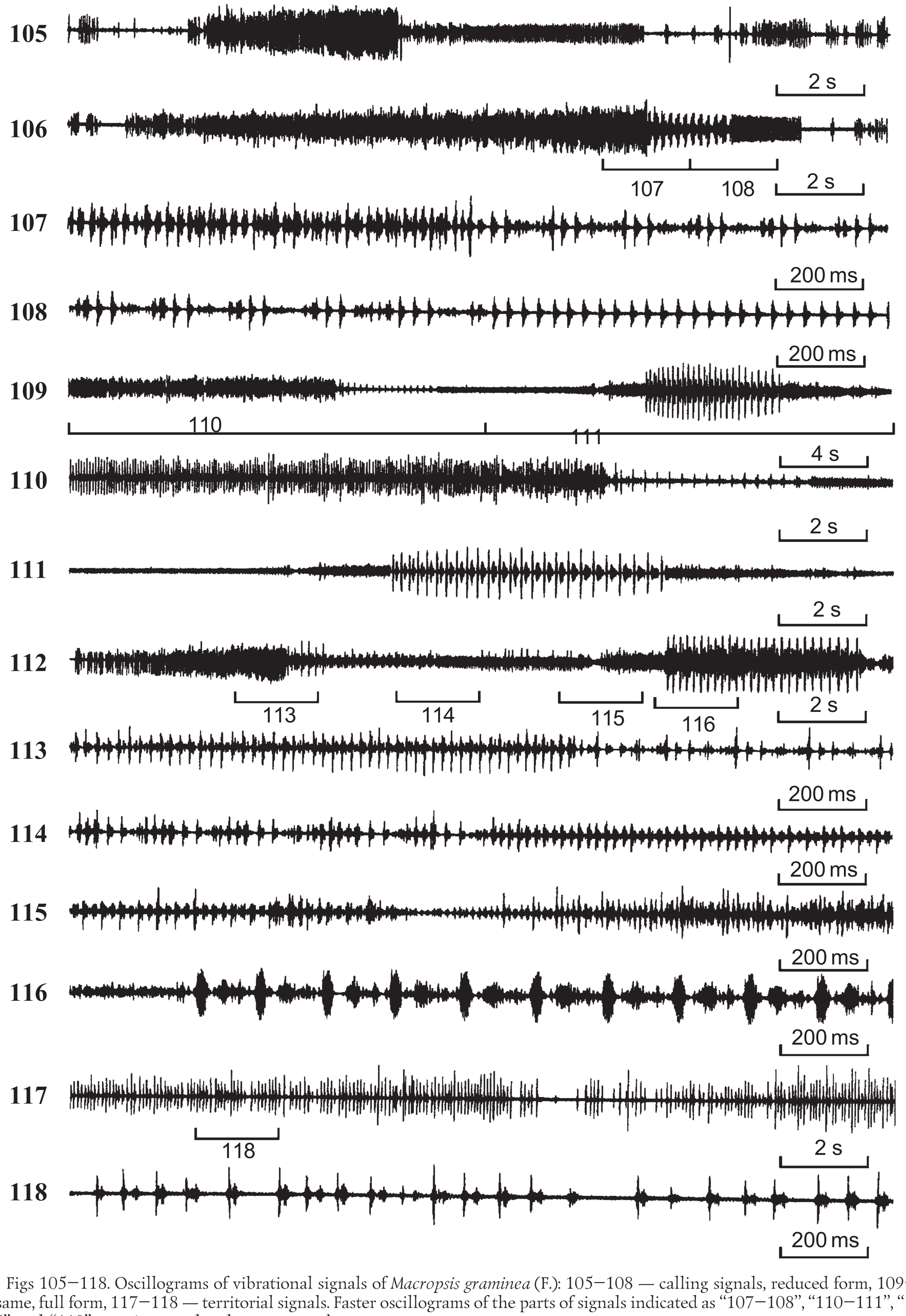
2. Northern part of Saratov Area, environs of Khvalynsk, near Ulyanino Village, from *S. cinerea*. 15, 17.VI.1996. Signals of 5♂♂ are recorded at the temperature 23 and 33°C.

3. East of Saratov Area, 10 km E of Ozinki Town towards Ural'sk, from *S. cinerea*. 24.VI.1996. Signals of 3♂♂ are recorded at the temperature 27–30°C.



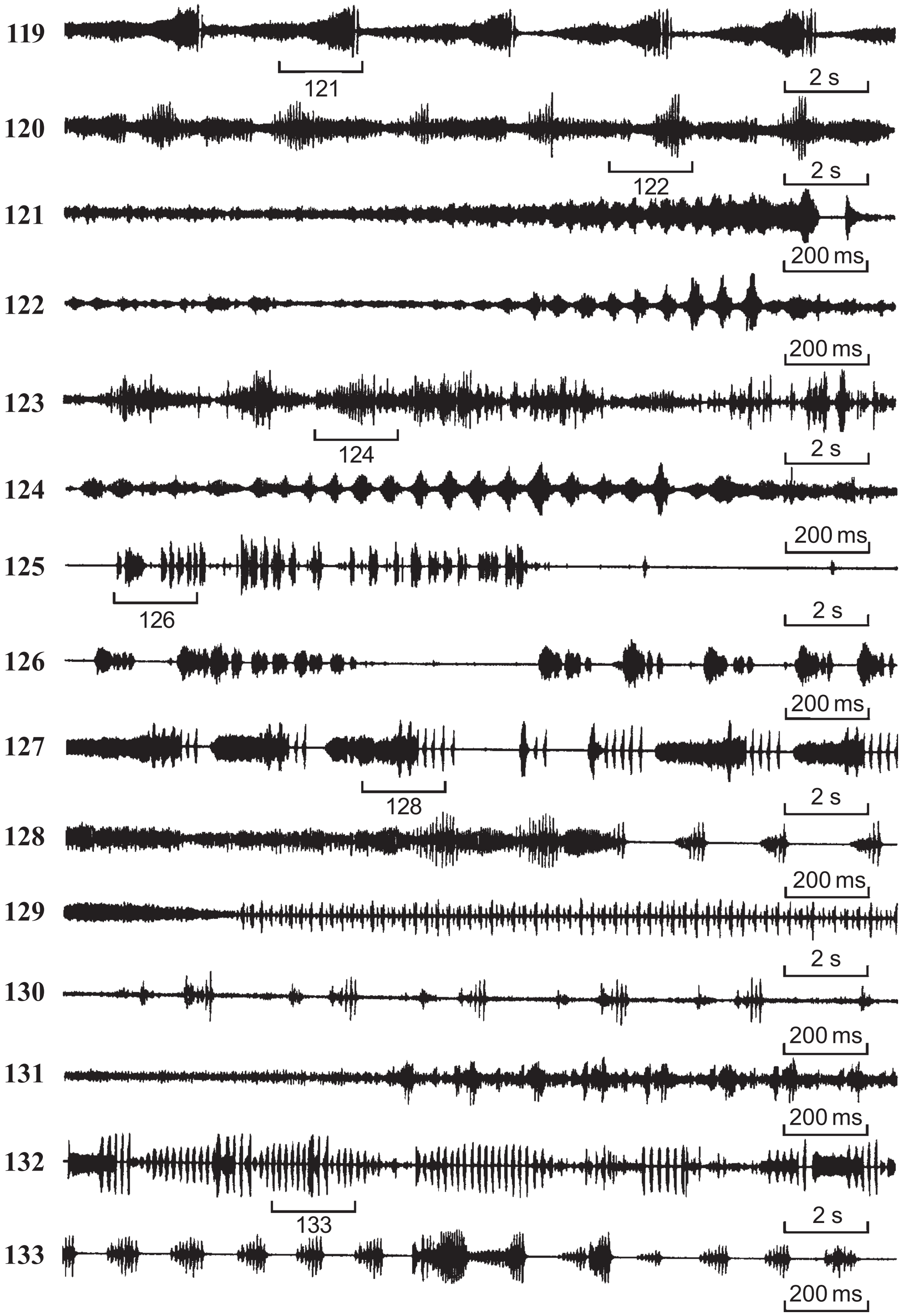
Figs 92–104. Oscillograms of vibrational signals of *Macropsis vicina* (Horv.): 92–94 — reduced form of calling signal, 95–98 — same, full form, 99 — calling and copulatory signals, 100 — calling signal, 101–102 — copulatory signals, 103–104 — territorial signals. Faster oscillograms of the parts of signals indicated as “93–94”, “96–98”, “100–102” and “104” are given under the same numbers.

Рис. 92–104. Осциллограммы вибрационных сигналов *Macropsis vicina* (Horv.): 92–94 — призывные сигналы, редуцированная форма, 95–98 — то же, полная форма, 99 — призывный и копуляционный сигналы, 100 — призывный сигнал, 101–102 — копуляционные сигналы, 103–104 — территориальные сигналы. Фрагменты сигналов, помеченные цифрами “93–94”, “96–98”, “100–102” и “104”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 105–118. Oscillograms of vibrational signals of *Macropsis graminea* (F.): 105–108 — calling signals, reduced form, 109–116 — same, full form, 117–118 — territorial signals. Faster oscillograms of the parts of signals indicated as “107–108”, “110–111”, “113–116” and “118” are given under the same numbers.

Рис. 105–118. Осциллограммы вибрационных сигналов *Macropsis graminea* (F.): 105–108 — призывные сигналы, редуцированная форма, 109–116 — то же, полная форма, 117–118 — территориальные сигналы. Фрагменты сигналов, помеченные цифрами “107–108”, “110–111”, “113–116” и “118”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 119–133. Oscillograms of vibrational signals of *Macropsis cerea* (Germ.) (119–126) and *M. prasina* (Boh.) (127–133): 119–122 — *M. cerea*, calling signals, 123–124 — same, signals, produced by male immediately before copulation, 125–126 — same, territorial signals, 127–128 — *M. prasina*, calling signals, 129–131 — same, copulatory signals, 132–133 — same, calling and rivalry signals. Faster oscillograms of the parts of signals indicated as “121–122”, “124”, “126”, “128” and “133” are given under the same numbers.

Рис. 199–133. Осциллограммы вибрационных сигналов *Macropsis cerea* (Germ.) (119–126) и *M. prasina* (Boh.) (127–133): 119–122 — *M. cerea*, призывные сигналы, 123–124 — то же, сигналы, издаваемые самцом непосредственно перед копуляцией, 125–126 — то же, территориальные сигналы, 127–128 — *M. prasina*, призывные сигналы, 129–131 — то же, копуляционные сигналы, 132–133 — то же, призывный сигнал и сигнал агрессии. Фрагменты сигналов, помеченные цифрами “121–122”, “124”, “126”, “128” и “133”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

4. Orenburg Area, Sakmara River near Churaevo Village, 20–25 km NNE of Kuvandyk Town, from *Salix viminalis* L., 2 ♂♂. 29.VI.1996. Shade air temperature — 27–28°C.

5. Altai Mountains, S shore of Teletskoe Lake, Chiri, mouth of Kyga River, from *S. viminalis*. 11.VII.1999. Calling signals of 1 ♂ are recorded at the temperature 22°C.

SIGNALS. Calling signal consists of short phrases usually repeating with a period about 3–8 s (Figs 127–128). Each phrase begins with monotonous trill, sounding like buzz, in the end part of it 2–4 fragments with another waveform present. Then several discrete syllables follow. Other males sitting on the same twig as a rule produce rivalry signals in reply to calling one (Figs 132–133). These signals are successions of syllables, same as in the second part of calling.

Male produces the same signal both being single and sitting next to female during courtship. After mounting female he emits another signal with quite different temporal structure (Figs 129–131). Undoubtedly, this is copulatory one, but in several cases it was also registered from single individual.

Macropsis verbae Anufriev, Zhiltsova, 1982
Figs 134–139.

LOCALITIES. 1. Moscow Area, Serpukhov District, Pushchino-na-Oke Town, from *Salix acutifolia* Willd. on the bank of Oka River. 2.VII.1985. Signals of 4 ♂♂ are recorded at 21°C.

2. Volgograd Area, Ilovlya River about 5–7 km from the mouth, from *S. acutifolia*. 10.VI.1996. Signals of 3♂♂ are recorded at 31–32°C.

SIGNALS. Calling signal consists of two different parts (Figs 134–137). The first part is a monotonous or modulated fragment lasting up to 5–8 s (Fig. 136), the second one consists of short repeating phrases (Fig. 137). Sometimes singing male omits the first part of signal.

Territorial signal is irregular buzzing trill (Figs 138–139).

Macropsis gravesteini Wagner, 1953
Figs 140–145.

LOCALITIES. 1. Crimea, environs of Pereval'noe Village halfway from Simferopol to Alushta, from *Salix alba* L. 16–17.VI.1997. Calling signals of 3 ♂♂ are recorded at the temperature 22–25°C.

2. Saratov Area, environs of Khvalynsk Town, near Ulyanino Village, from *S. alba* and *S. fragilis* L. 15, 17.VI.1996. Signals of 5 ♂♂ are recorded at 31 and 22°C.

3. Volgograd Area, Ilovlya River about 5–7 km from the mouth, from *S. alba*. 8.VI.1996. Calling signals of 3 ♂♂ are recorded at 20–26°C.

SIGNALS. Calling signal is a succession of short phrases, usually repeating with a period about 2–5 s (Figs 140–143). Territorial signal is a prolonged highly variable trill (Figs 144–145). Male emits signals of this type both being single and in reply to calling of another individual.

Macropsis leporina Tishechkin, 1997
Figs 146–153.

LOCALITIES. 1. Chita Area, Ingoda River 15 km E of Urul'ga (Karymskiy District), from *Salix schwerinii* E.Wolf, 7♂♂. 29.VI — 2.VII.1995. Shade air temperature — 25–27°C.

2. Amur Area, 30 km W of Svobodny, from *Salix udensis* Trautv. et Mey. 7–8.VII.1995. Signals of 4 ♂♂ are recorded at the temperature 21–22 and 27°C.

3. The Southern Maritime Province, Pogranichny District, environs of Barabash-Levada, from *S. udensis*. 13.VII.1995. Signals of 1 ♂ are recorded at the temperature 25°C.

SIGNALS. Calling signal is a succession of syllables, repeating with a period 300–600 ms (Figs 146–149). Total length of signal averages 5–20 s.

Several males sitting on the same twig can answer to one another's calling by short successions of pulses, which are rivalry signals (Figs 150–151). Territorial signal is similar with these in other willow-dwelling species and is a long trill with irregular temporal pattern (Figs 152–153).

Macropsis haupti Wagner, 1941
Figs 154–159.

LOCALITIES. 1. NW Caucasus, Krasnodar Area, Sukko River in the environs of Sukko Village 12 km South of Anapa, from *Salix elbursensis* Boiss. 30.VI.1997. Calling signals of 1♂ were recorded at 26°C.

2. Volgograd Area, Ilovlya River 5–7 km from the mouth, from *Salix vinogradovii* Skvortsov. 10.VI.1996. Calling signals of 2♂♂ were recorded at 22–25 and 29–30°C.

SIGNALS. Calling signal is a phrase consisting of rather low-amplitude trill, after which a succession of high-amplitude syllables follows (Figs 154–157). Duration of both parts and of phrase in total varies greatly. Territorial signal is similar with these in other species (Figs 158–159).

Macropsis ocellata Provancher, 1872
Figs 160–167.

LOCALITIES. 1. Moscow Area, Serpukhov District, environs of Luzhki Village, *Salix alba* L. on the bank of Oka River. 16.VII.1985 and 30.VII.1994. Signals of 6 ♂♂ were recorded at 22–23°C.

2. North-west Caucasus, 12 km S of Anapa, Sukko River, from *S. alba*, 4 ♂♂. 2.VII.1997. Shade air temperature — 29–31°C.

3. Astrakhan' Area, Dosang Railway Station, from *S. alba* (possibly, *S. alba* x *S. fragilis*) in a flood-land between Volga and Akhtuba rivers, 7.VII.2000. Signals of 2♂♂ were recorded at 26°C.

4. Orenburg Area, Sakmara River near Churaevo Village, 20–25 km NNE of Kuvandyk Town, from *S. alba*, 5 ♂♂. 29.VII.1996. Shade air temperature — 24–28°C.

SIGNALS. Full calling signal consists of train of short monotonous fragments, sounding like continuous regularly interrupting buzz, after which a trill of partially merged pulses follows (Figs 160, 162, 164). Total length of signal in some cases exceeds 30–40 s. Sometimes male omits the second part of signal (trill of pulses) (Figs 161, 165). Occasionally, inverse situation takes place and the first part may be almost entirely reduced, but the second one remains well-pronounced (Figs 163, 166–167).

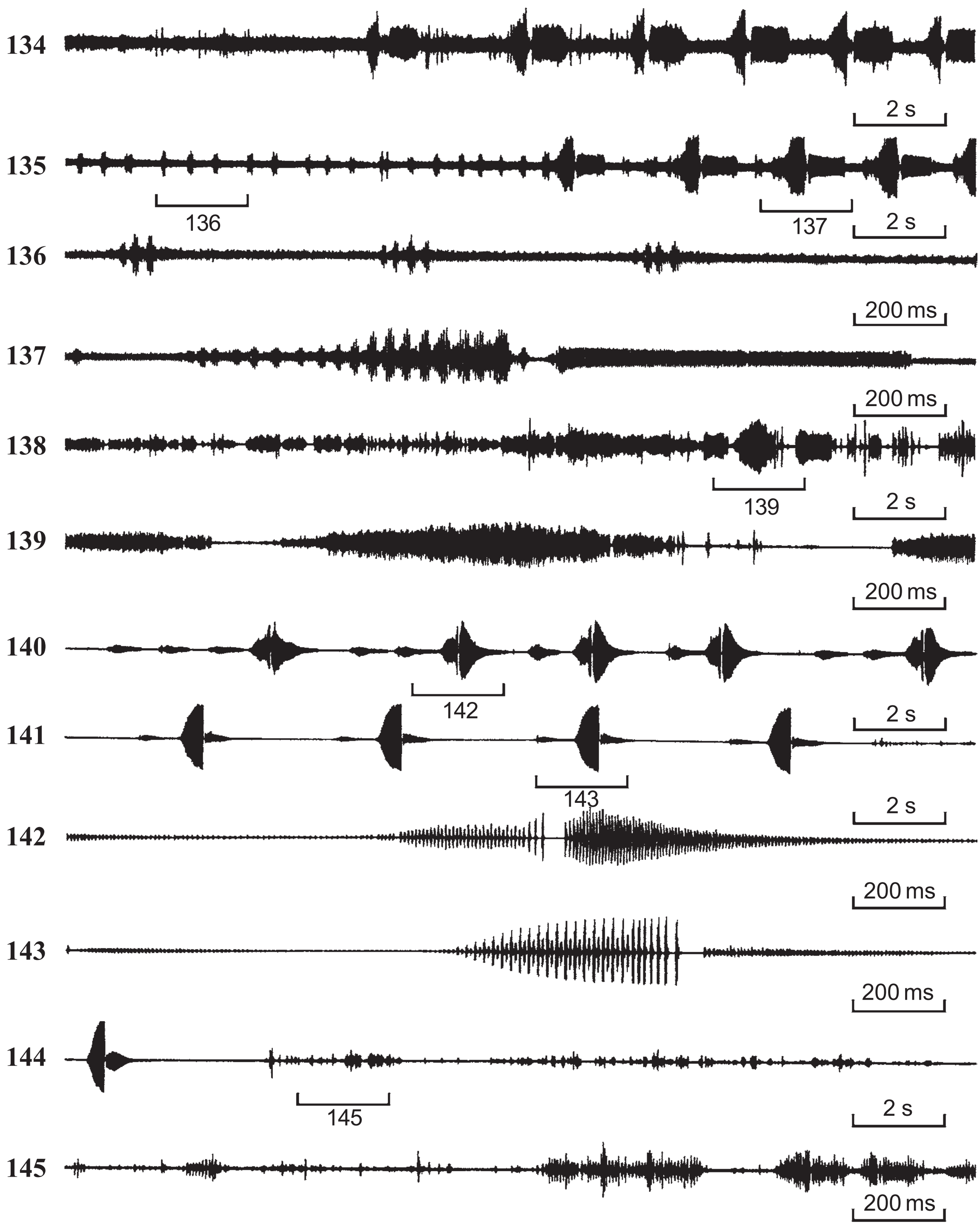
During the only observed attempt of copulation male emitted calling several times, sitting close to female. Then he mounted her back does not producing any signals at that moment. In several seconds female rejected male.

Macropsis fuscula (Zetterstedt, 1828)
Figs 168–173.

LOCALITIES. 1. Moscow Area: (a) environs of Serpukhov Town; (b) environs of Bronnitsy Town. Signals of more than 10 specimens collected from *Rubus idaeus* L., *R. caesius* L. and *R. nessensis* W. Hall were recorded at the temperature 24–26°C.

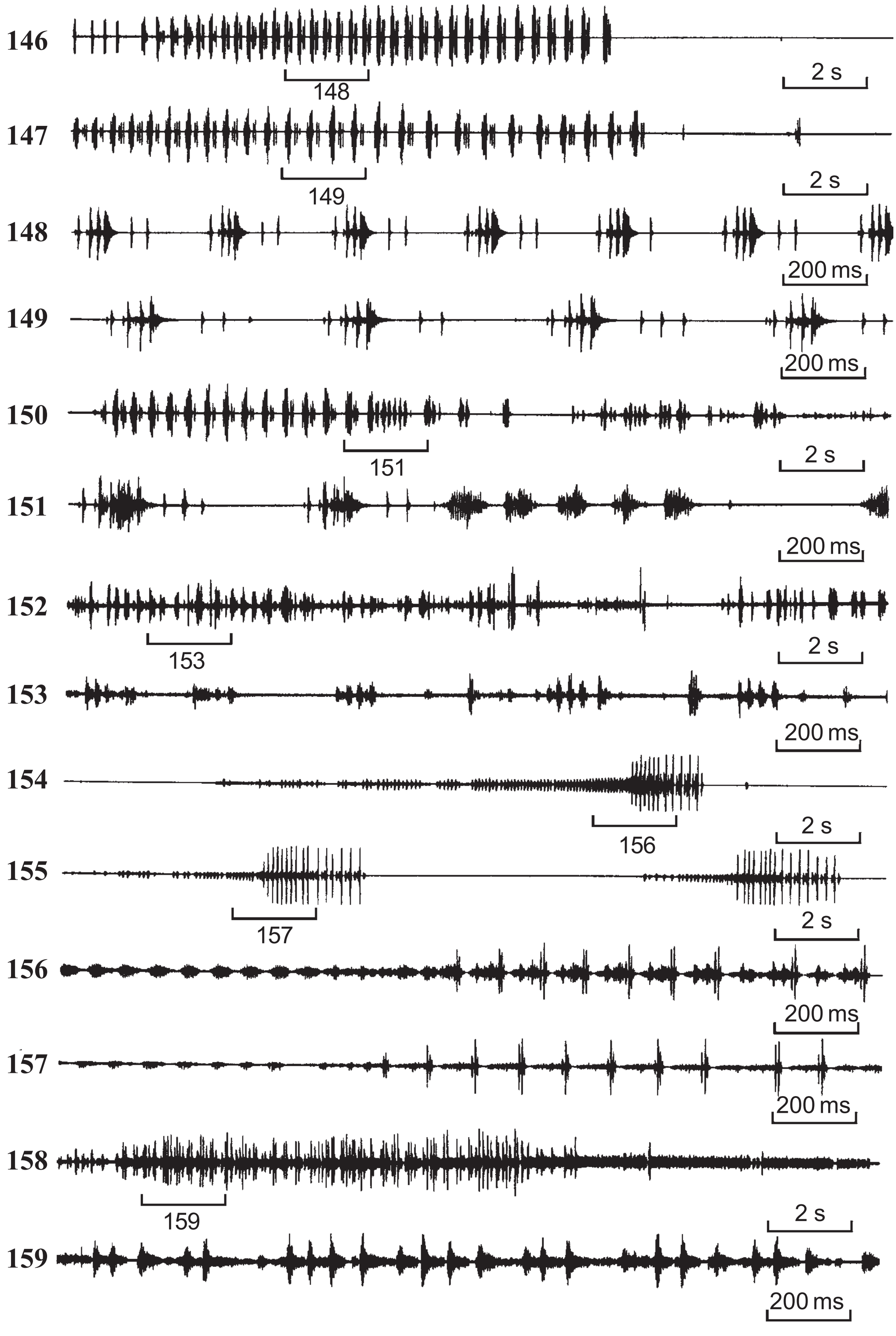
2. Southern Kazakhstan, Almaty and Zailiyskiy Alatau Mt. Ridge in the environs of the city, from *R. caesius*. 3.VII.1994. Signals of 4 ♂♂ were recorded at the temperature 30–31°C.

SIGNALS. Calling signal consists of short phrases repeating with a period from 1–2 up to 4–5 s (Figs 168–170). Two males sitting on the same stem sometimes sing simultaneously, so that phrases produced by different individuals alternate (Fig. 171). I have never registered rivalry signals in this species.



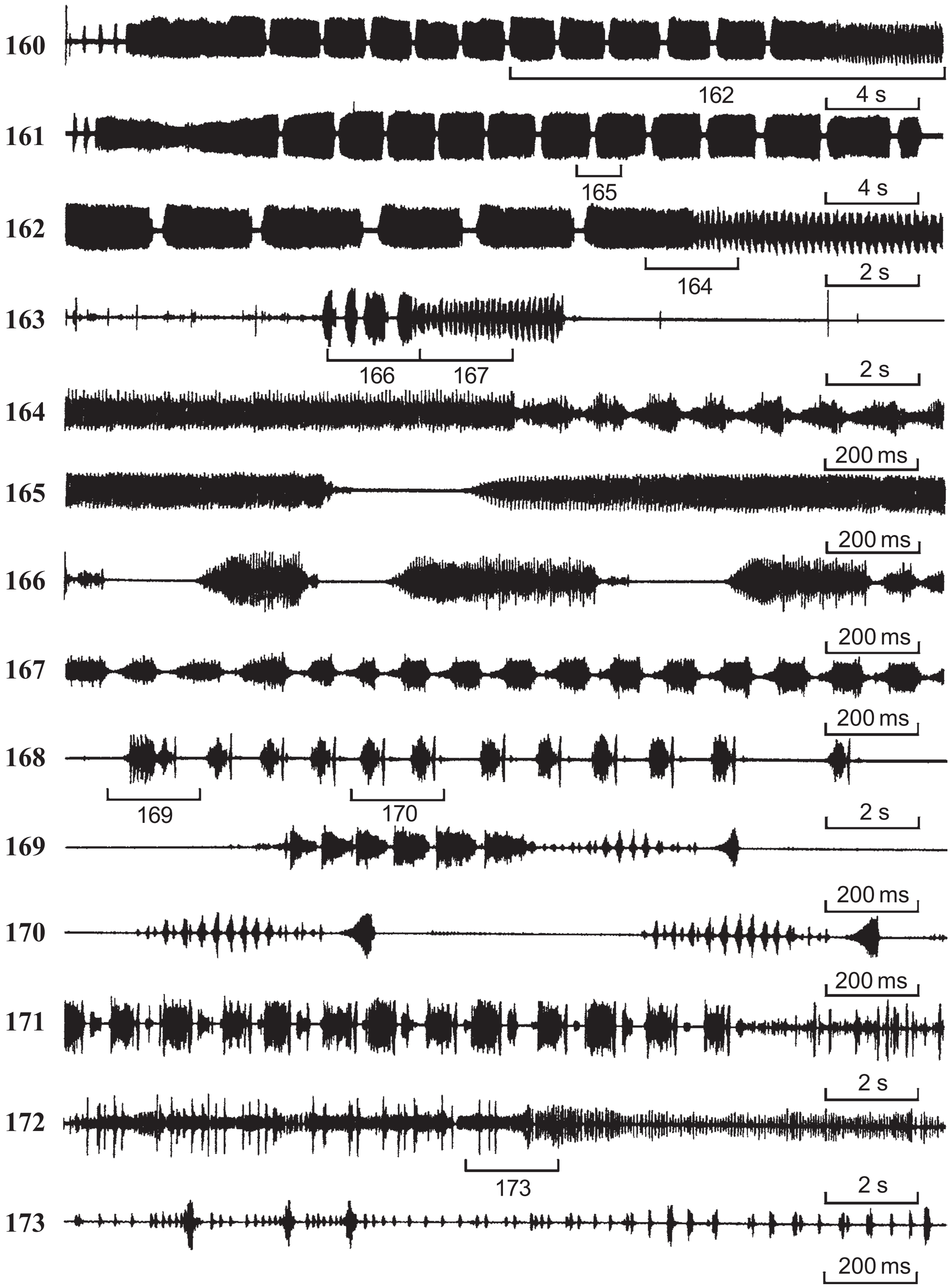
Figs 134–145. Oscillograms of vibrational signals of *Macropsis verbae* Anufr., Zhilts. (134–139) and *M. gravesteini* Wagn. (140–145): 134–137 — *M. verbae*, calling signals, 138–139 — same, territorial signals, 140–143 — *M. gravesteini*, calling signals, 144–145 — same, territorial signals. Faster oscillograms of the parts of signals indicated as "136–137", "139", "142–143" and "145" are given under the same numbers.

Рис. 134–145. Осциллограммы вибрационных сигналов *Macropsis verbae* Anufr., Zhilts. (134–139) и *M. gravesteini* Wagn. (140–145): 134–137 — *M. verbae*, призывные сигналы, 138–139 — то же, территориальные сигналы, 140–143 — *M. gravesteini*, призывные сигналы, 144–145 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами "136–137", "139", "142–143" and "145", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 146–159. Oscillograms of vibrational signals of *Macropsis leporina* Tish. (146–153) and *M. haupti* Wagn. (154–159): 146–149 —*M. leporina*, calling signals, 150–151 — same, rivalry signals, 152–153 — same, territorial signals, 154–157 —*M. haupti*, calling signals, 158–159 — same, territorial signals. Faster oscillograms of the parts of signals indicated as “148–149”, “151”, “153”, “156–157” and “159” are given under the same numbers.

Рис. 146–159. Осциллограммы вибрационных сигналов *Macropsis leporina* Tish. (146–153) и *M. haupti* Wagn. (154–159): 146–149 — *M. leporina*, призывные сигналы, 150–151 — то же, сигналы соперничества, 152–153 — то же, территориальные сигналы, 154–157 —*M. haupti*, призывные сигналы, 158–159 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами “148–149”, “151”, “153”, “156–157” и “159”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 160–173. Oscillograms of vibrational signals of *Macropsis ocellata* Prov. (160–167) and *M. fuscula* (Zett.) (168–173): 160–167 —*M. ocellata*, different types of calling signals, 168–170 —*M. fuscula*, calling signal, 171 — same, calling alternation of two males, 172–173 — same, territorial signals. Faster oscillograms of the parts of signals indicated as “162”, “164–167”, “169–170” and “173” are given under the same numbers.

Рис. 160–173. Осциллограммы вибрационных сигналов *Macropsis ocellata* Prov. (160–167) и *M. fuscula* (Zett.) (168–173): 160–167 —*M. ocellata*, разные типы призывного сигнала, 168–170 —*M. fuscula*, призывный сигнал, 171 — то же, чередующиеся призывные сигналы двух самцов, 172–173 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами “162”, “164–167”, “169–170” и “173”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Territorial signal is a prolonged succession of pulses with highly variable temporal structure (Figs 172–173).

Macropsis scutellata (Boheman, 1845)
Figs 174–178.

LOCALITIES. 1. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, from *Urtica dioica* L. 29.VII.1991. Signals of one ♂ were recorded at the temperature 24°C.

2. North-west Caucasus, Krasnodar Province, environs of Praskoveevka Village 15 km S of Gelendzhik, from *U. dioica*, 1 ♂. 12.VII.1997. Shade air temperature — 26°C.

SIGNALS. Calling signal consists of two parts with different temporal pattern (Figs 174–176). Its duration usually averages 20–30 s. Territorial signal is similar with this of the previous species (Figs 177–178).

Macropsis megerlei (Fieber, 1868)
Figs 179–187.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village, 12 and 16.VII.1990. Signals of 8♂♂ collected from *Rosa majalis* Herrm. were recorded at 22–23°C.

SIGNALS. Calling signal consists of alternating fragments of two different types, one of which is about twice shorter, than another (Figs 179–182). As a rule, after one long fragment 1–3 short ones follow. These signals were registered both from single male and from one sitting close to female. It was female, who was searching for the mate, whereas singing male was sitting stationary in my experiments. When female approached male within a distance about 1–2 cm, he suddenly ran towards her and mounted her back. After that he emitted copulatory signal and started copulation. Copulatory signal begins with a trill, then a succession of alternating syllables of two types follows (Figs 183–185).

Territorial signals in this species are continuous trains of syllables or single pulses with highly variable structure (Figs 186–187).

Macropsis idae Emeljanov, 1964
Figs 188–192.

LOCALITY. Signals of 6 ♂♂ collected from *Rosa* sp. in the Botanical Garden in Almaty (Kazakhstan) were recorded at 3.VII.1994 at the temperature 32°C.

SIGNALS. Calling signal consists of syllables repeating with a period of 1–1.5 s (Figs 188–191). Also, long trills of discrete pulses were registered in males of this species (Figs 188–189, 192). Male produces this signal either spontaneously or in reply to calling of another one. Thus, these trills act both as territorial and rivalry signal.

Macropsis elaeagni Emeljanov, 1964
Figs 193–200.

LOCALITIES. 1. Moscow, from ornamental trees of *Elaeagnus angustifolia* L. in the park near the Moscow State University. 14, 24.VII.1998. Signals of 7 ♂♂ are recorded at 25 and 29°C.

2. Crimea, Kerchenskiy Peninsula, E shore of Kazantipskiy Bay, Zolotoe Village, from cultivated *E. angustifolia*. 27.VI.1997. Signals of 5 ♂♂ are recorded at the temperature 30–31°C.

3. North-west Caucasus, 12 km S of Anapa, Sukko River, from *E. angustifolia*. 3.VII.1997. Signals of 5♂♂ are recorded at 27–28°C.

4. North Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town, from *E. angustifolia*. 19–22.VI.1986. Signals of 10 ♂♂ are recorded at the temperature 22–24°C.

5. Southern Urals, Guberlya River near Guberlya railway station, 25 km W of Orsk, from *E. angustifolia*. 5.VII.1996. Signals of 5 ♂♂ are recorded at 25–30°C.

6. Kazakhstan, Almaty and foothills of Zailiyskiy Alatau Mountain Ridge in the environs of the city, from *Elaeagnus* sp. 2.VII.1994. Signals of 5 ♂♂ are recorded at 31°C.

SIGNALS. Calling signal is a succession of syllables following each other with a period of about 2–4 s (Figs 193–194). Copulatory signal is also a succession of syllables, but their temporal pattern is quite different (Figs 195–197). The latter signal male normally produces when sitting on female's back immediately before attempt of copulation, but occasionally it was also registered from single individual. Call of distress is a train of pulses (Figs 197–198). Sitting stationary, especially during grooming, male produces short trains of pulses from time to time (Figs 199–200). Evidently, these are territorial signal.

Macropsis pictipes (Horvath, 1904)
Figs 201–206.

LOCALITIES. 1. Southern Tuva, environs of Erzin Village, flood-land of Erzin River, from *Hippophae rhamnoides* L. 21.VII.1989. Signals of 2 ♂♂ are recorded at 24°C.

2. Kazakhstan, environs of Almaty, Zailiyskiy Alatau Mountain Ridge, from *H. rhamnoides* near the river. 30.VI.1994. Signals of 1 ♂ are recorded at 31°C.

SIGNALS. Calling signal is a long phrase averaging up to 40–50 s and consisting of trill followed by succession of syllables (Figs 201–206). Sometimes male omits the trill and produces the train of syllables only. Two males singing on the same twig emitted syllables alternately, but never produced rivalry signals in my experiments.

Macropsis glandacea (Fieber, 1868)
Figs 207–214.

LOCALITIES. 1. North-west Caucasus, 12 km S of Anapa, Sukko River, from *Ulmus carpinifolia* Gled. 1.VII.1997. Signals of 1♂ are recorded at 27–29°C.

2. North-east Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town, from *U. carpinifolia*. 27.VI.1986. Signals of 4 ♂♂ are recorded at the temperature 24°C.

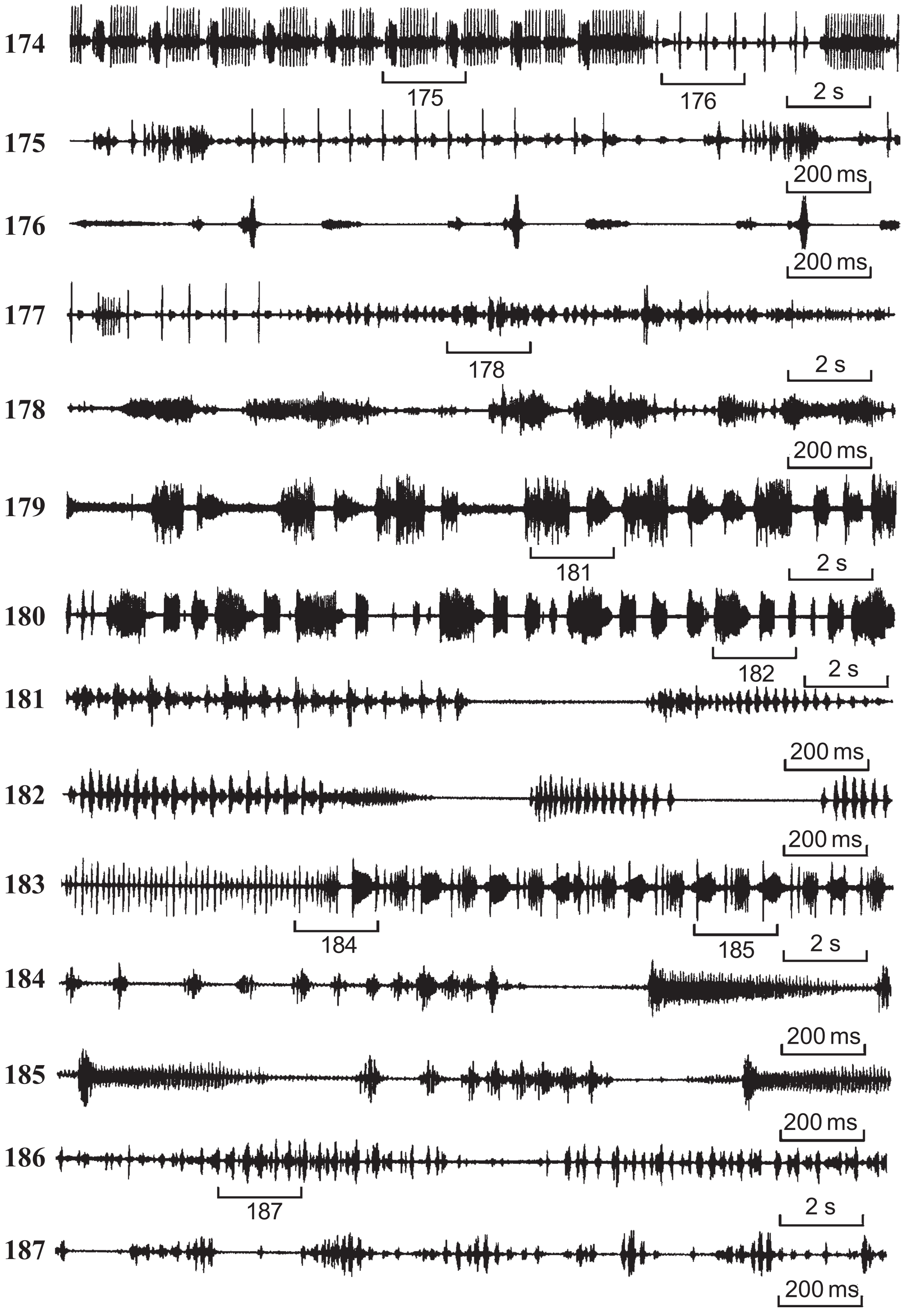
SIGNALS. Calling signal is a long succession of syllables (Figs 207–210). The same signal male emits sitting on female's back immediately before copulation (Figs 211–212). Territorial signal is a long trill (Figs 213–214).

Macropsidius abrotani Emeljanov, 1964
Figs 215–228.

LOCALITIES. 1. Moscow Area, Serpukhov District, from *Artemisia abrotanum* L. on Oka River bank in the environs of Luzhki Village, 11–12.VII.1985. Signals of more than 10 specimens of both sexes are recorded at the temperature 21–22°C.

2. East of Saratov Area, 10–15 km E of Ozinki Town. *A. abrotanum* on roadside in steppe. 22.VI.1996. Signals of 1 ♂ are recorded at the temperature 28–29°C.

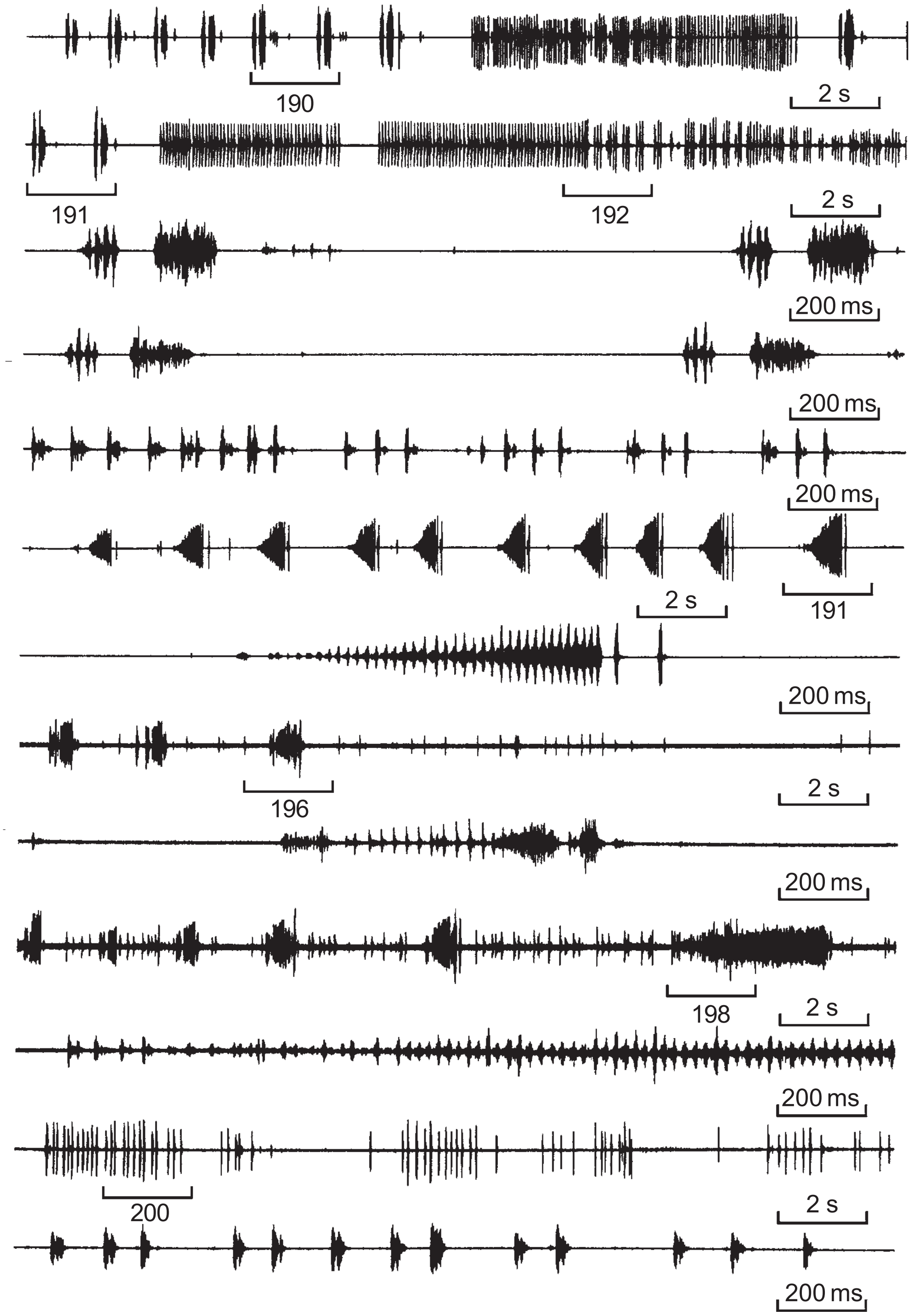
SIGNALS. Calling signal is a long single phrase, lasting for 20–30 s and more and consisting of three different successions of syllables (Figs 215–223). The shape of syllables depends much on physical characteristics of substrate on which the insect sings (Figs 220–222 and oscillograms on Fig. 223). As in other Macropsinae, male also produces this signal in close proximity with female. Only after mounting female he starts emitting copulatory signal, differing in structure from calling one (Figs 224–225). All observed copulation attempts were unsuccessful.



Figs 174–187. Oscillograms of vibrational signals of *Macropsis scutellata* (Boh.) (174–178) and *M. megerlei* (Fieb.) (179–187): 174–176 — *M. scutellata*, calling signals, 177–178 — same, territorial signals, 179–182 — *M. megerlei*, calling signals, 183–185 — same, copulatory signals, 186–187 — same, territorial signals. Faster oscillograms of the parts of signals indicated as “175–176”, “178”, “181–182”, “184–185” and “187” are given under the same numbers.

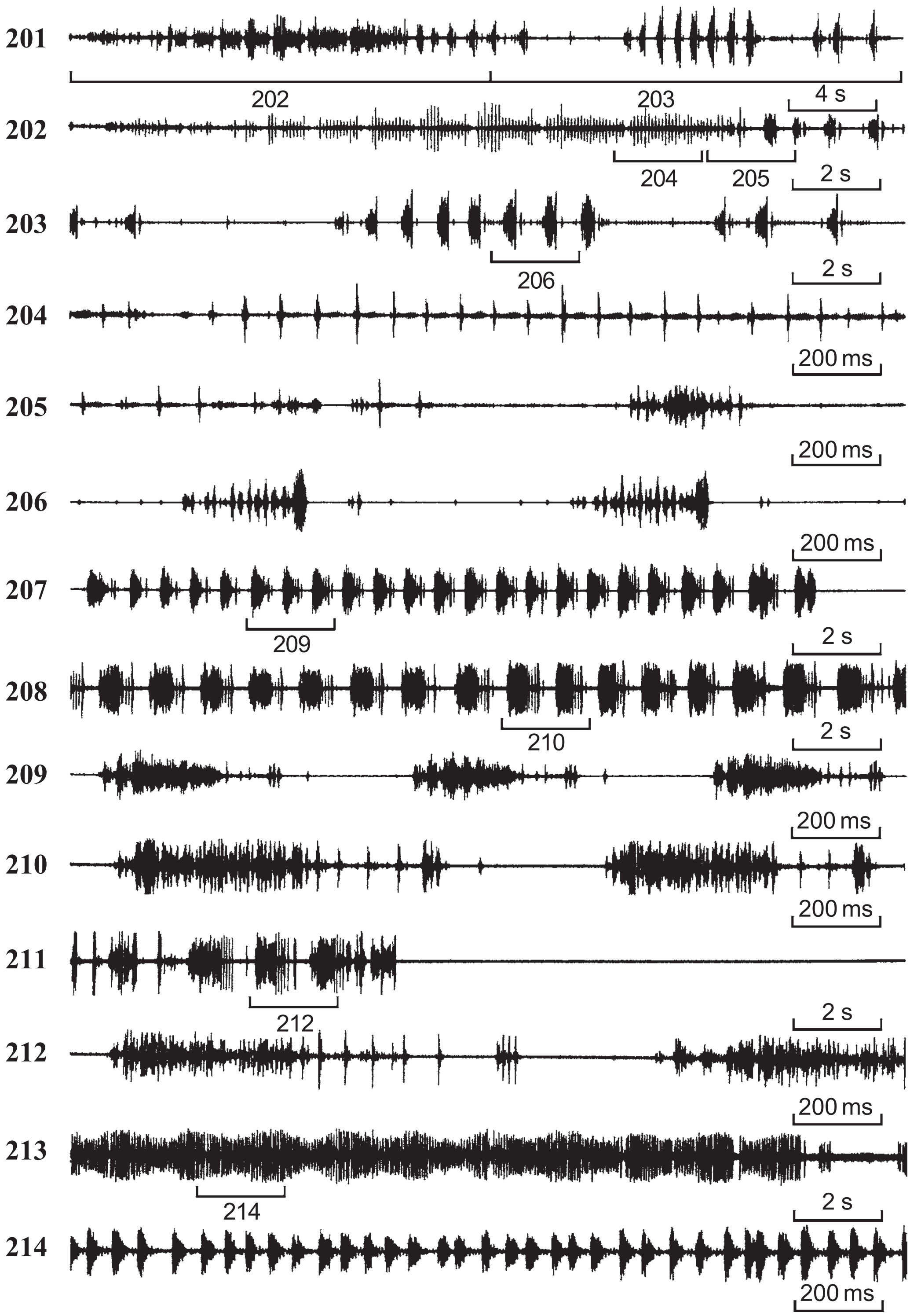
Рис. 174–187. Осциллограммы вибрационных сигналов *Macropsis scutellata* (Boh.) (174–178) и *M. megerlei* (Fieb.) (179–187): 174–176 — призывные сигналы *M. scutellata*, 177–178 — то же, территориальные сигналы, 179–182 — призывные сигналы *M. megerlei*, 183–185 — то же, копуляционные сигналы, 186–187 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами “175–176”, “178”, “181–182”, “184–185” и “187”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

188
189
190
191
192
193
194
195
196
197
198
199
200



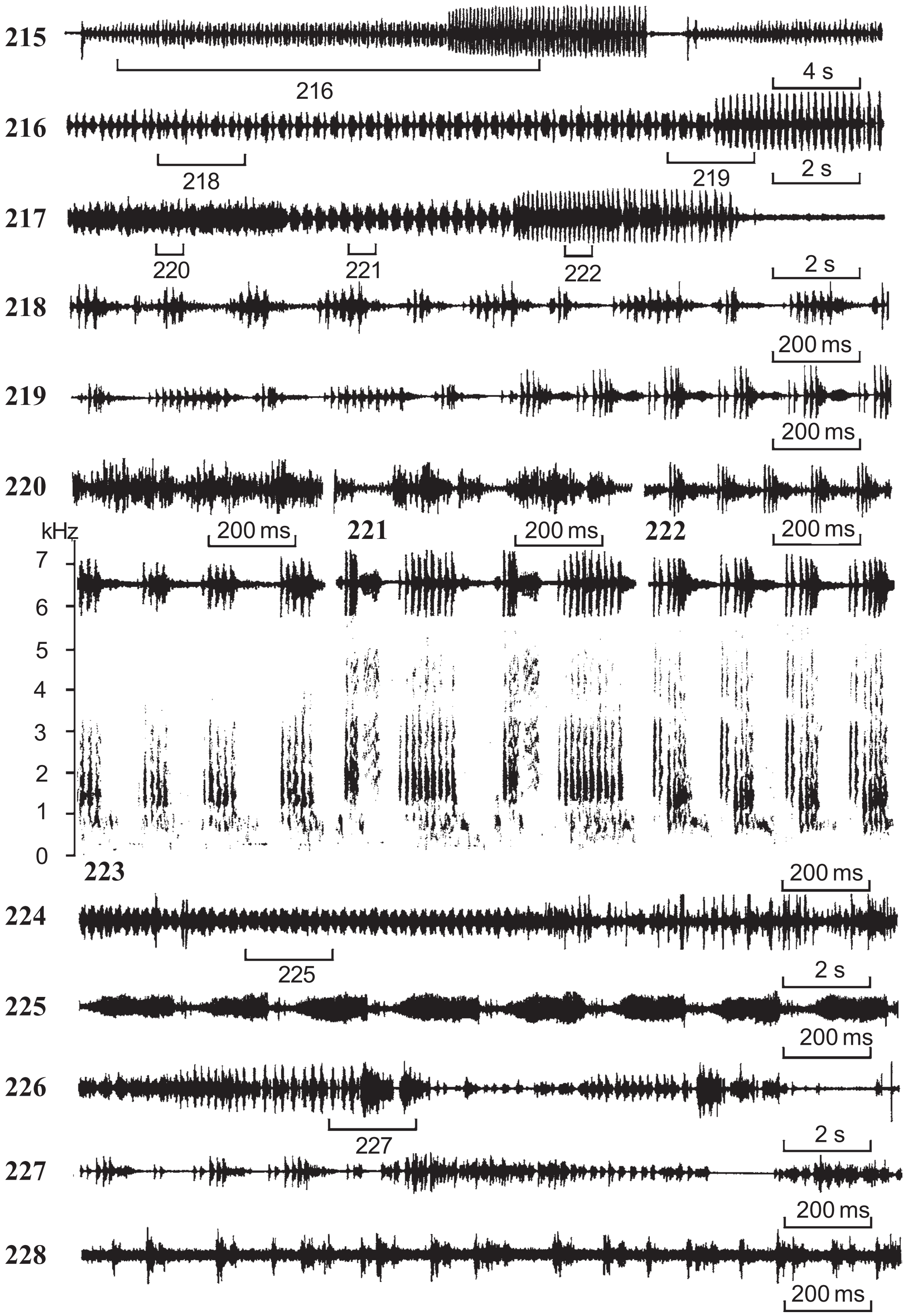
Figs 188–200. Oscillograms of vibrational signals of *Macropsis idae* Em. (188–192) and *M. elaeagni* Em. (193–200): 188–189 — *M. idae*, calling and rivalry signals, 190–191 — same, calling signals, 192 — same, rivalry signal, 193–194 —*M. elaeagni*, calling signals, 195–196 — same, copulatory signals, 197 — same, copulatory signals of one male and call of distress of another one; the former male attempts to copulate with the latter one, 198 — same, call of distress, 199–200 — same, territorial signals. Faster oscillograms of the parts of signals indicated as "190–192", "194", "196", "198" and "200" are given under the same numbers.

Рис. 188–200. Осциллограммы вибрационных сигналов *Macropsis idae* Em. (188–192) и *M. elaeagni* Em. (193–200): 188–189 — *M. idae*, призывные сигналы и сигналы соперничества, 190–191 — то же, призывные сигналы, 192 — то же, сигналы соперничества, 193–194 — *M. elaeagni*, призывные сигналы, 195–196 — то же, копуляционные сигналы, 197 — то же, копуляционные сигналы одного самца и сигналы протеста другого; первый самец пытается копулировать со вторым, 198 — то же, сигналы протеста, 199–200 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами "190–192", "194", "196", "198" и "200", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 201–214. Oscillograms of vibrational signals of *Macropsis pictipes* (Horv.) (201–206) and *M. glandacea* (Fieb.) (207–214): 201–206 — calling signal of *M. pictipes*, 207–210 — *M. glandacea*, calling signals, 211–212 — same, signals, produced by male immediately before copulation, 213–214 — same, territorial signals. Faster oscillograms of the parts of signals indicated as "202–206", "209–210", "212" and "214" are given under the same numbers.

Рис. 201–214. Осциллограммы вибрационных сигналов *Macropsis pictipes* (Horv.) (201–206) и *M. glandacea* (Fieb.) (207–214): 201–206 — призывный сигнал *M. pictipes*, 207–210 — *M. glandacea*, призывные сигналы, 211–212 — то же, сигналы, издаваемые самцом непосредственно перед копуляцией, 213–214 — то же, территориальные сигналы. Фрагменты сигналов, помеченные цифрами "202–206", "209–210", "212" and "214", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 215–228. Vibrational signals of *Macropsidius abrotani* Em.: 215–222 — oscillograms of calling signals, 223 — oscillograms and sonograms of three parts of calling signal, 224–225 — copulatory signal, 226–227 — calling and rivalry signals, 228 — call of distress. Faster oscillograms of the parts of signals indicated as “216”, “218–222”, “225” and “227” are given under the same numbers.

Рис. 215–228. Вибрационные сигналы *Macropsidius abrotani* Em.: 215–222 — осциллограммы призывных сигналов, 223 — осциллограммы и сонограммы трех частей призывного сигнала, 224–225 — копуляционный сигнал, 226–227 — призывный сигнал и сигнал соперничества, 228 — сигнал протеста. Фрагменты сигналов, помеченные цифрами “216”, “218–222”, “225” и “227”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Usually, male produces rivalry signals in reply to calling of another individual singing nearby (Figs 226–227). Same signals were registered from several males sitting close to each other in the same cage. Also, in female of this species call of distress similar with this in other Macropsinae was recorded (Fig. 228).

Calling signals of males from two different localities do not differ in temporal structure.

Macropsidius sahlbergi (Flor, 1861)
Figs 229–235.

LOCALITIES. Moscow Area: (1) environs of Zvenigorod Town, sandy slopes on bank of Moskva River near Lutsyno Village, from *Artemisia campestris* L. 27–28.VI.1988, signals of 4 ♂♂ are recorded at the temperature 26–28°C, 2.VII.1991, signals of 2♂♂ and 2 ♀♀ are recorded at the temperature 30°C; (2) Serpukhov District, from *A. campestris* on Oka River bank in the environs of Luzhki Village, 30.VII.1993. Signals of 1♂ are recorded at the temperature 25°C.

SIGNALS. Calling signal is a short phrase averaging in duration approximately 1–2 s. Single male can produce phrases with irregular intervals; after hearing female reply he starts singing more actively and regularly, emitting signals with pauses about 0.5 s (Figs 229–231).

Female reply is a short train of pulses (Figs 234–235). Usually it somewhat overlaps with the end part of male calling or follows immediately after it. As in most other leafhoppers, male runs along the plant searching for female, whereas the latter remains stationary during this alternate calling. After finding female male mounts her back, produces copulatory signal, lasting up to 20–30 s (Figs 232–233) and starts copulation. If copulation attempt appears to be unsuccessful, male emits copulatory signal once more before the next one.

Macropsidius serratus Logvinenko, 1965
Figs 236–241.

LOCALITY. Crimea, Kerchenskiy Peninsula, E shore of Kazantipskiy Bay, environs of Zolotoe Village, from *Artemisia* sp. along salted dry river-bed. 25–26.VI.1997. Signals of 5♂♂ were recorded at 27–29°C.

SIGNALS. Calling signal is a phrase consisting of initial fragment with irregular structure, sounding like buzz, and several syllables with higher amplitude (Figs 236–239). Normally, male emits several phrases one after another; in the first one initial part (buzz) can last for 20–30 s and more, in the successive phrases it is much shorter and does not exceed 2–3 s. Several males sitting on the same plant can sing alternately, but sometimes one male produces rivalry signals in reply to calling of another individual (Figs 240–241).

Macropsidius niger (Matsumura, 1915)
Figs 242–250.

LOCALITIES. 1. South Siberia, southern Tuva, environs of Erzin Village, from *Artemisia glauca* Pall. ex Willd. on the roadside. 11.VIII.1989. Signals of 3 ♂♂ were recorded at 27°C.

2. The Southern Maritime Province, Pogranichny District, environs of Barabash-Levada Village, from *Artemisia* sp. (Sect. *Artemisia*), 2 ♂♂. 13.VII.1995. Shade air temperature — 26°C.

SIGNALS. Calling signal is a succession of short syllables or pulses, repeating with a period 100–600 ms (Figs 242–248). Duration of signal varies greatly averaging from 1.5–2 up to 20–25 s in different cases. Also, in males call of distress was registered (Figs 249–250). Calling signals of males from different localities are similar.

The genus *Hephathus* Ribaut, 1952.

Revision of species of this genus from the territory of Russia was published recently [Tishechkin, 2000b]. The paper includes descriptions and oscillograms of calling signals, on which signals of individuals from different localities are presented and variability of their temporal pattern is shown. For this reason, only several most representative oscillograms for each *Hephathus* species are given in the present paper.

Hephathus nanus (Herrich–Schäffer, 1835)
Figs 251–255.

LOCALITIES. 1. Crimea, mountains 3–4 km E of Pereval'noe Village (halfway from Simferopol to Alushta), dry meadow with steppe vegetation in the mountains. 18.VI.1997. Calling signals of 2 ♂♂ were recorded at the temperature 25–26°C.

2. East of Saratov Area, about 15 km NE of Ozinki Town, dry ruderal vegetation on the roadside. 22.VI.1996. Calling signals of 1 ♂ were recorded at the temperature 33°C.

3. Southern Urals, Guberlinskiye Mountains in the environs of Guberlya railway station 25 km W of Orsk, rather wet hollow with high herbaceous steppe vegetation between the hills. 8–9.VII.1996. Calling signals of 2 ♂♂ were recorded at the temperature 26–28°C.

SIGNALS. Calling signal is a successions of syllables, following each other almost without gaps, or separated by intervals up to 1–1.5 s. In the former case, signal usually lasts up to 10 s (Figs 251, 253–254). If male produces syllables with rather long intervals, he can sing unceasingly for one minute and more (Figs 252, 255).

NOTES. In European Russia the species for a long time was confused with *H. achilleae* (see Tishechkin, 2000b). Signals of *H. achilleae* are presented under the name *H. nanus* in Tishechkin [1994].

Hephathus freyi (Fieber, 1868)
Figs 256–258.

LOCALITIES. 1. Rostov Area, Oblivskiy district, environs of Sosnovy (=Oporny) Village on Chir River. 8.VIII.1991, 17.VIII.1992. Calling signals of 4 ♂♂ were recorded at the temperature 27–30°C.

2. Volgograd Area, Ilovlya River about 5–7 km from the mouth. 10.VI.1996. Calling signals of 1♂ were recorded at the temperature 25°C.

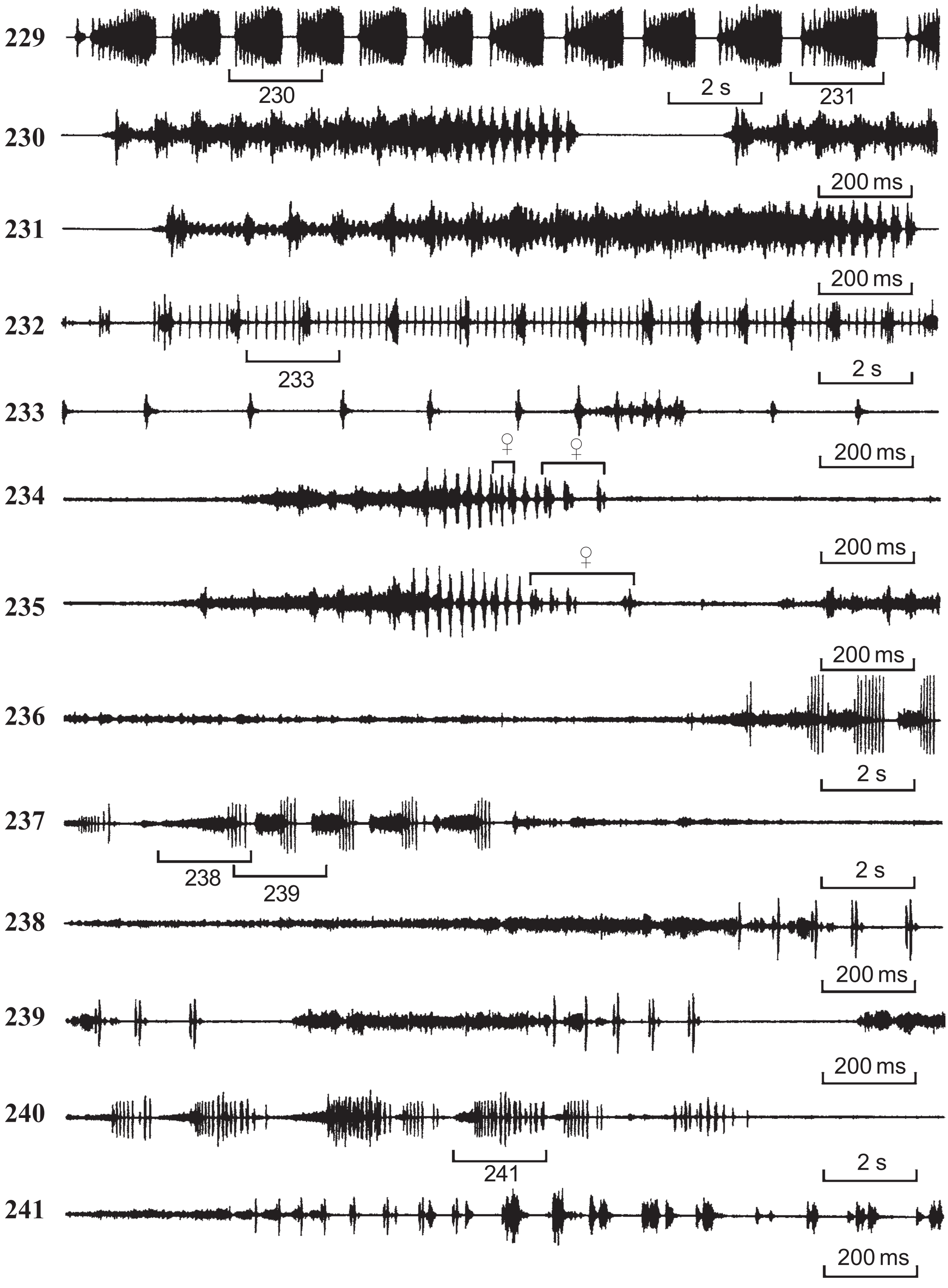
3. East of Saratov Area, about 15 km NE of Ozinki Town, dry ruderal vegetation on the roadside in the same biotope, where *H. nanus* was collected. 22.VI.1996. Calling signals of 1 ♂ were recorded at the temperature 31–32°C.

4. South-eastern Azerbaidzhan, Talysh Mountains, environs of Lerik Village. 10.VII.1987. Calling signals of 1♂ were recorded at the temperature 20°C.

5. Southern Turkmenistan, environs of Dushak Town. 9.V.1994. Calling signals of 1 ♂ were recorded at the temperature 31°C.

SIGNALS. Calling signal is a trill of discrete pulses, repeating with a period about 90–160 ms. Additional low-amplitude pulses present between main ones in the beginning of a signal. Overall duration of trill varies greatly and averages from 1–2 up to 30–40 s.

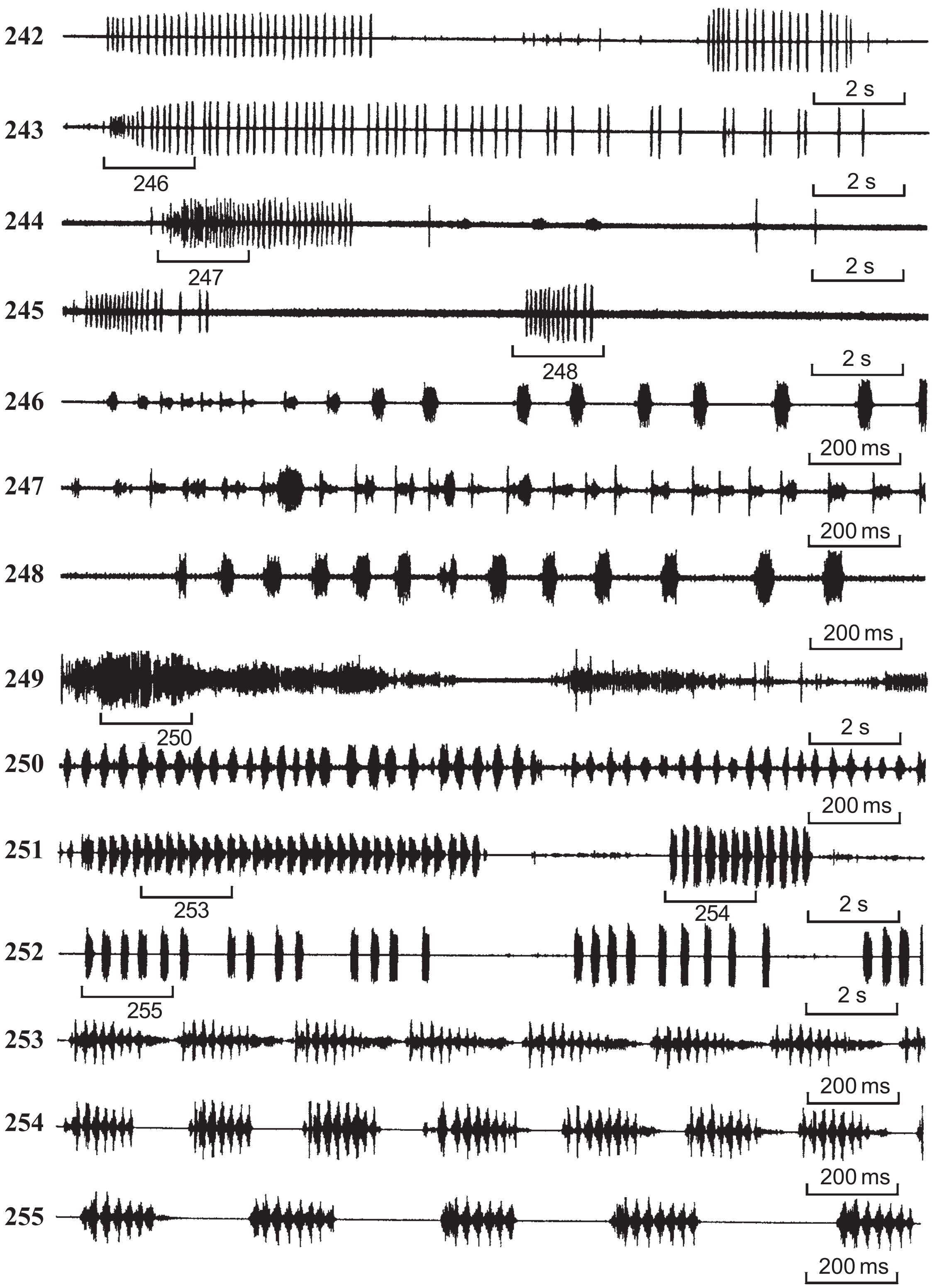
NOTES. From the territory of the former Soviet Union the species was recorded under the name *H. unicolor* (Lindberg, 1926), which is a junior synonym of *H. freyi* [Tishechkin, 2000b].



Figs 229–241. Oscillograms of vibrational signals of *Macropsidius sahlbergi* (Flor) (229–235) and *M. serratus* Logv. (236–241): 229–231 — *M. sahlbergi*, calling signals, 232–233 — same, copulatory signal, 234–235 — same, male calling and female reply, 236–239 — *M. serratus*, calling signals, 240–241 — same, calling and rivalry signals. Faster oscillograms of the parts of signals indicated as "230–231", "233", "238–239" and "241" are given under the same numbers.

Рис. 229–241. Осциллограммы вибрационных сигналов *Macropsidius sahlbergi* (Flor) (229–235) и *M. serratus* Logv. (236–241): 229–231 — *M. sahlbergi*, призывные сигналы, 232–233 — то же, копуляционный сигнал, 234–235 — то же, призыв самца и ответ самки, 236–239 — *M. serratus*, призывные сигналы, 240–241 — то же, призывные сигналы и сигналы соперничества. Фрагменты сигналов, помеченные цифрами "230–231", "233", "238–239" и "241", представлены при большей скорости развертки на осциллограммах под такими же номерами.

200 ms



Figs 242–255. Oscillograms of vibrational signals of *Macropsidius niger* (Mats.) (242–250) and *Hephathus nanus* (H.-S.). (251–255): 242–248 — *M. niger*, calling signals, 249–250 — same, call of distress, 251–255 — calling signals of *H. nanus*. Faster oscillograms of the parts of signals indicated as “246–248”, “250” and “253–255” are given under the same numbers.

Рис. 242–255. Осциллограммы вибрационных сигналов *Macropsidius niger* (Mats.) (242–250) и *Hephathus nanus* (H.-S.). (251–255): 242–248 — *M. niger*, призывные сигналы, 249–250 — то же, сигналы протеста, 251–255 — призывные сигналы *H. nanus*. Фрагменты сигналов, помеченные цифрами “246–248”, “250” и “253–255”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Hephathus achilleae Mityaev, 1967
Figs 259–265.

LOCALITIES. 1. Moscow Area, environs of Zvenigorod, dry sandy slopes on the bank of Moskva River near Lutsyno Village. 27–28.VI.1988. Calling signals of 7 ♂♂ were recorded at 26–28°C.

2. North Caucasus, Chechnya, steppe on the slopes of Terskiy Mountain Ridge in the environs of Grozny. 19.VI.1986. Calling signals of 2 ♂♂ were recorded at the temperature 23–24°C.

3. East of Saratov Area, 10 km E of Ozinki Town towards Ural'sk. 25.VI.1996. Calling signals of 2♂♂ were recorded at the temperature 30–31°C.

4. Southern Urals, Guberlinskiye Mountains in the environs of Guberlya railway station 25 km W of Orsk, rather wet hollow with high herbaceous steppe vegetation between the hills, together with *H. nanus*. 8.VII.1996. Calling signals of 2♂♂ were recorded at the temperature 26–27°C.

SIGNALS. Calling signal consists of syllables, having duration about 160–400 ms and repeating with irregular intervals (Figs 259–263). Sometimes several discrete pulses are visible on oscillograms in the initial part of syllable. Occasionally, this part lengthens greatly, so that the whole duration of syllable exceeds 1–2 s.

Also, call of distress was registered in *H. achilleae*. As in most other species, it is a continuous train of pulses with irregular structure (Figs 264–265).

NOTES. See the same item in the description of signals of *H. nanus*.

Some data on vibrational communication in Macropsinae were published earlier (Tishechkin, 1994), very brief descriptions and oscillograms of signals of several species are presented in this work.

Acoustic communication system in various genera of this subfamily is quite different. In representatives of *Pediopsis*, *Pediopsoides*, *Oncopsis* and, also, in poplar-feeding *Macropsis* species calling signals are long single phrases sometimes having very complex temporal pattern. In willow-dwelling *Macropsis* calling signals are either single or regularly repeating phrases, the latter case is more abundant. In species of the genus living on Rosaceae, Elaeagnaceae and plants from other families except Salicaceae calling usually consists of short repeating phrases or syllables, still their temporal pattern as a rule is rather complex. In the genus *Macropsidius* both long, complex phrases (*M. abrotani*) and short, simple signals (*M. sahlbergi*, *M. niger*) present. Calling signals of *Hephathus* are the simplest among Macropsinae.

Neither in *P. tiliae*, nor in several *Macropsis* species, in which mating behaviour was studied, female reply signals were registered. Moreover, in *P. tiliae* and *M. megerlei* it was female, who walked along the plant searching for the mate, whereas singing male remained on the same place (in other cases searching behaviour in female was not observed, because insects were sitting near each other before any of them started singing). Evidently, in these species female does not produce reply signals, and communication between representatives of different sexes becomes one-way, as in singing cicadas (Cicadidae).

In *Macropsidius* (*M. sahlbergi*) communication system and mating behaviour are typical for small Auchenorrhyncha: on the first stage male produces calling signals spontaneously, then receptive female starts singing in reply to his calling. For some time mates sing alternately, female being motionless, male running in different directions along the plant searching for her. After finding female male mounts her back, produces copulatory signal and starts copulation.

In no Macropsinae courtship signals were registered. In all cases, when mating behaviour was observed, male produced calling signals both being single and in close contact with female. Only when sitting on the back of female in last moments before copulation, male usually produces signals of another type, namely, copulatory ones. However, in some *Macropsis* species male goes on producing calling even at that moment. In several species of the genus copulatory signals occasionally were registered from single males. Maybe, these were individuals on the stage of most high sexual activity.

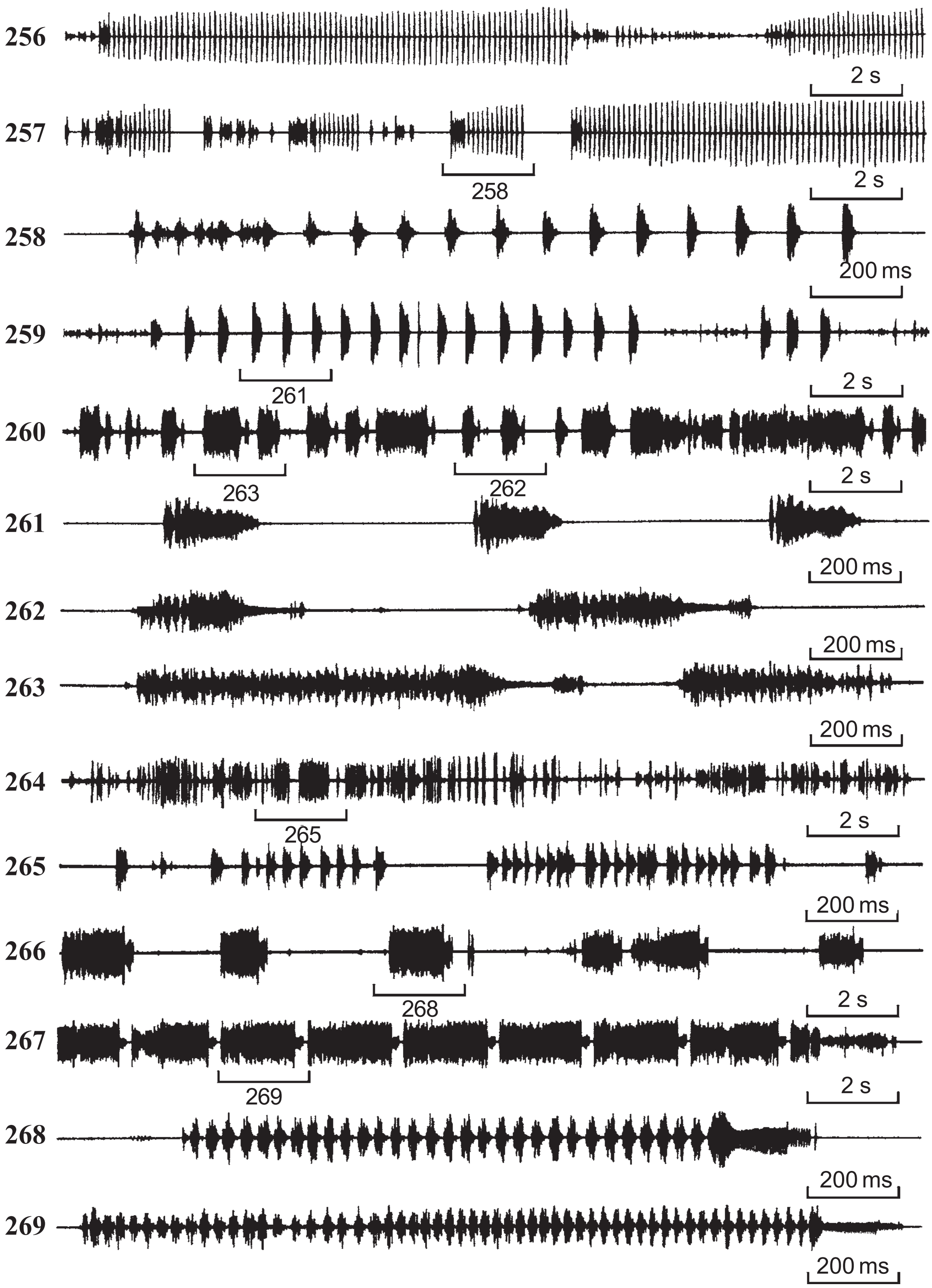
Arboreal Macropsinae (genera *Pediopsis*, *Pediopsoides*, *Oncopsis* and *Macropsis*) as a rule have territorial signals in their acoustic repertoire. Single males usually produce signals of this type during walking or grooming (when scraping the body surface by legs and creating on it the coating of brochosomes — for details see Rakitov, 1998) and before producing calling. More rarely signals of this type were registered from individuals sitting motionless and demonstrating no specific activity. In grass-dwelling species (*Macropsidius*, *Hephathus*) territorial signals were not recorded.

In all Macropsinae with the exception of *Hephathus* rivalry signals were registered in appropriate situations. Male produces signals of this type in reply to calling of another one. Also, several males sitting in the same cage can produce rivalry signals alternately or simultaneously from time to time. Among Cicadellidae such signals were also registered in Adelungiinae, in most other groups males demonstrating competition behaviour produce calling signals in turn.

Also, in representatives of all genera studied calls of distress were recorded both in males and in females. Insects produce these signals in various stress situations (being hold or got in some narrow place and trying to escape), or if male attempts to copulate with another one or with female not ready to mating.

It is possible, that some peculiar features of communication system in arboreal Macropsinae, such as absence of female reply signals and well-developed territorial and rivalry behaviour are resulted from their rather sedentary way of life. Males of *Pediopsis*, *Macropsis* and *Oncopsis* can sit on the same place for many hours producing calling with irregular intervals. In such situation territorial and rivalry signals may play important role in regulation of distance between individuals, because these insects leave long-occupied place only very reluctantly in contrast with most of other leafhoppers, for instance, Aphrodinae (= Deltocephalinae), Typhlocybinae, etc.

In actively moving insects female reply draws attention of male and thus prevents him from leaving the



Figs 256–269. Oscillograms of vibrational signals of *Hephathus freyi* (Fieb.) (256–258), *H. achilleae* Mit. (259–265) and *Agallia brachyptera* (Boh.) (266–269): 256–258 — calling signals of *H. freyi*, 259–263 — same of *H. achilleae*, 264–265 — call of distress of *H. achilleae*, 266–269 — calling signals of *A. brachyptera*. Faster oscillograms of the parts of signals indicated as “258”, “261–263”, “265” and “268–269” are given under the same numbers.

Рис. 256–269. Осциллограммы вибрационных сигналов *Hephathus freyi* (Fieb.) (256–258), *H. achilleae* Mit. (259–265) и *Agallia brachyptera* (Boh.) (266–269): 256–258 — призывные сигналы *H. freyi*, 259–263 — то же, *H. achilleae*, 264–265 — сигнал протеста *H. achilleae*, 266–269 — призывные сигналы *A. brachyptera*. Фрагменты сигналов, помеченные цифрами “258”, “261–263”, “265” и “268–269”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

plant on which receptive female occurs. In sedentary leafhoppers singing male does not change his location for a long time, so female can reach him being guided by his signals, not producing reply ones.

In general, judging by such acoustic characters as rather complex calling signals consisting of single or repeated phrases (or complicated syllables) and well-developed territorial and rivalry signals, Macropsinae seem to be most closely related with Agalliinae and Adelungiinae (see below).

Subfamily Agalliinae

Agallia brachyptera (Boheman, 1847)
Figs 266–282.

LOCALITIES. Moscow Area: (1) environs of Pirogovo, wet meadow on the bank of Klyaz'ma River, 30.VII.1987, signals of 2 ♂♂ are recorded at the temperature 22°C; (2) environs of Pushkino, meadow on the bank of Ucha River, 23.VII.1988, signals of 1♂ are recorded at the temperature 27–28°C; (3) Voskresensk District, environs of Beloozerskiy Town, from *Rumex acetosella* L. in pine forest, 26.VII.1988, signals of 1 ♂ are recorded at the temperature 26–27°C, 7.VII.1991, signals of 1 ♂ and 2 ♀♀ are recorded at the temperature 26–27°C.

SIGNALS. Calling signal is a short phrase lasting for 1–3 s (Figs 266–269). It consists of trill followed by short fragment in which pulses are indistinct (Figs 268–269). Frequency spectra of these two parts differ conspicuously, which is clearly audible even by human ear (Fig. 274). Male can produce phrases with irregular intervals from 1–2 s up to several minutes (Fig. 266), or sings ceaselessly for about half a minute or more (Fig. 267). In the latter case pauses between phrases do not exceed 100–200 ms.

Female reply signal is a continuous trill of pulses, repeating with approximately the same rate as in the first part of male calling (Figs 270–271). In my experiments female answered both to full calling and to its first part only (the trill of pulses).

After hearing female reply male starts running along the plant in different directions searching for the mate. His signals become more regular and long due to extending of the first part (Figs 272–273). Also, he flaps the wings several times at the end of each phrase (Figs 273–274); thus calling signal transforms into courtship one. After finding female male mounts her back. For several seconds he flaps wings rhythmically at a rate about 6–8/s and produces copulatory signal, which is a trill (Figs 275–280), then partners join their genitalia.

Male sitting motionless, both single and in the presence of other individuals also produces short pulses following with irregular intervals and sounding like clicks or ticking (Figs 281–282). Evidently these are territorial signals.

Anaceratagallia venosa (Fourcroy, 1785)
Figs 283–286.

LOCALITIES. Moscow Area, Voskresensk District, environs of Beloozerskiy Town, from *Rumex acetosella* L. in pine forest, 26.VII.1991, signals of 2♂♂ are recorded at the temperature 26–27°C.

SIGNALS. Calling signal is a long phrase lasting up to 20–30 s. It consists of two successions of syllables, differing both in temporal pattern and syllables repetition period. Usually phrases follow with irregular intervals from 1–2 seconds up to several minutes.

Anaceratagallia ribauti (Ossiannilsson, 1938)
Figs 287–289.

LOCALITIES. Moscow Area, Serpukhov District, dry meadow on bank of Oka River near Luzhki Village, 31.VII.1993, signals of 1 ♂ are recorded at the temperature 23–24°C.

SIGNALS. Calling signal is similar with this of the previous species, but temporal structure of syllables in the second part of phrase is quite different.

Anaceratagallia aciculata (Horvath, 1894)
Figs 290–296.

LOCALITY. Transvolga part of Astrakhan' Area, environs of Dosang Railway Station, flood–land between Akhtuba and Volga rivers, on ruderal vegetation in irrigation ditch. 4.VII.2000. Signals of 2 ♂♂ are recorded at the temperature 26–27°C.

SIGNALS. Calling signal is a very long phrase, occasionally having duration up to 1–2 minutes and more. As in two previous species, it consists of two parts differing both in temporal pattern and syllables repetition period.

Anaceratagallia chalchica Dlabola, 1967
Figs 297–299.

LOCALITY. South Siberia, southern Tuva, environs of Erzin Village, from *Artemisia glauca* Pall. ex Willd. on the roadside. 11.VIII.1989. Signals of 1 ♂ were recorded at 27°C.

SIGNALS. Calling signal is a phrase lasting for 5–6 s and consisting of more or less uniform pulses grouped in syllables. Temporal pattern of signal gradually changes towards the end, in the end part of phrase boundaries between syllables become indistinct.

NOTES. Determination of species is based on Dlabola [1967] (original description) and Vilbaste [1980].

Austroagallia sinuata (Mulsant et Rey, 1855)
Figs 300–308.

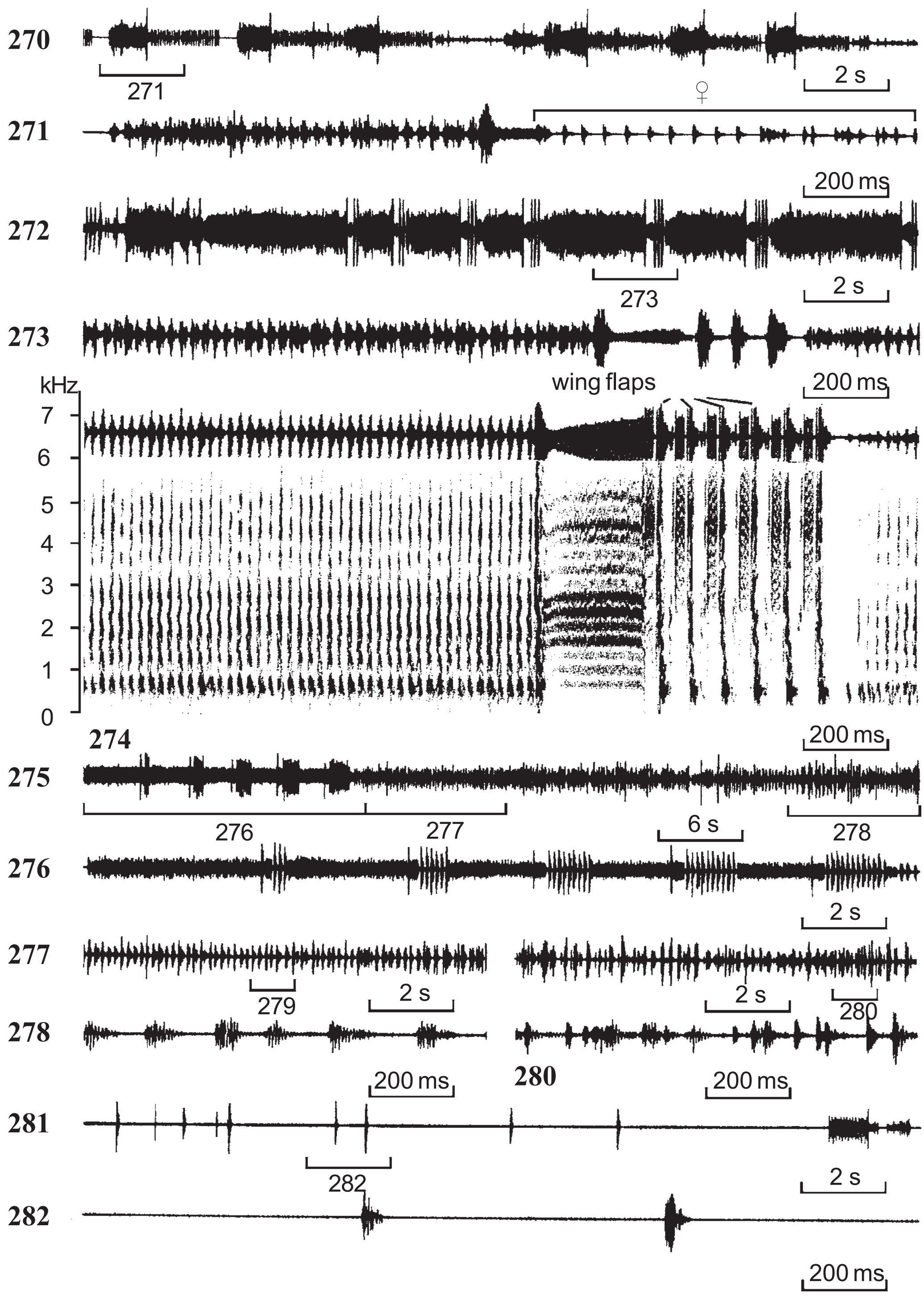
LOCALITIES. (1) North Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town. 4.VII.1986. Signals of 1 ♂ were recorded at 28°C.

(2) Ukraine, Kherson Area, Sivash Lake, steppe on seashore, from *Artemisia* sp. 16.VIII.1986. Signals of 1 ♂ were recorded at 28°C.

SIGNALS. As in some other Cicadellidae species, there are two forms of calling signal in*A. sinuata*. Usually, calling is a short phrase with a duration about 1.5 s, consisting of two syllables, the first being at least three times as long as the second. As a rule, male produces several phrases with intervals of 1.5–4 s (Figs 300–301, 303–306). Occasionally, the last phrase in the succession has rather long additional part, averaging 15–20 s and more (Figs 302, 307).

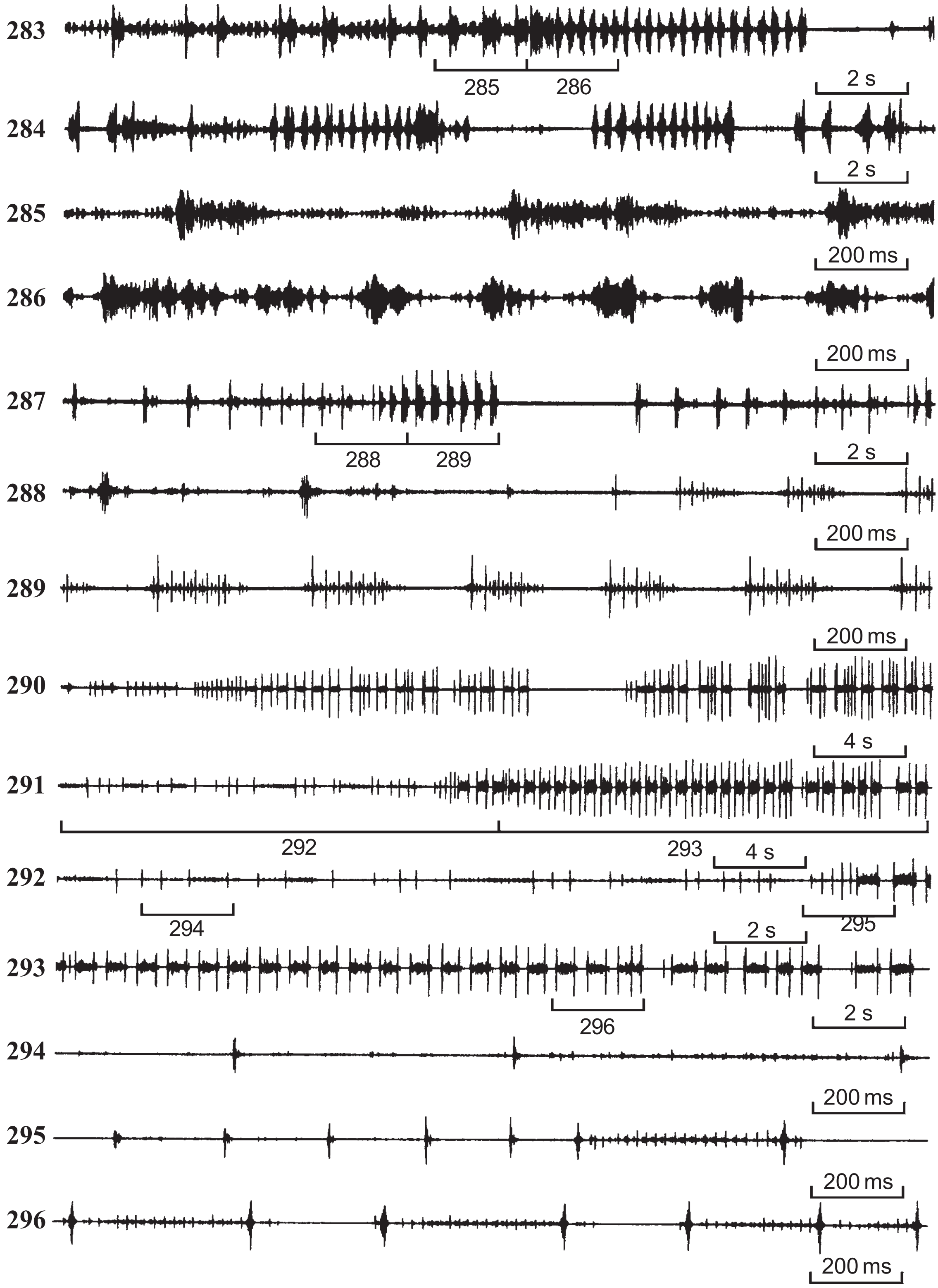
Also, call of distress consisting of short irregular successions of pulses once was registered in male of this species (Figs 308).

Detailed study of acoustic signals and associated behaviour of two Agalliinae species, namely, *Agallia constricta* van Duzee and *Agalliopsis novella* (Say) was provided by Shaw [1976]. Both signals temporal structure and set of their functional types, as well as mating behaviour in these species does not differ principally from these in ones involved in my study. Signals were registered by microphone, for this reason the author speaks of sounds, not of vibrational signals. Calling signals of both species (referred as "common sounds")



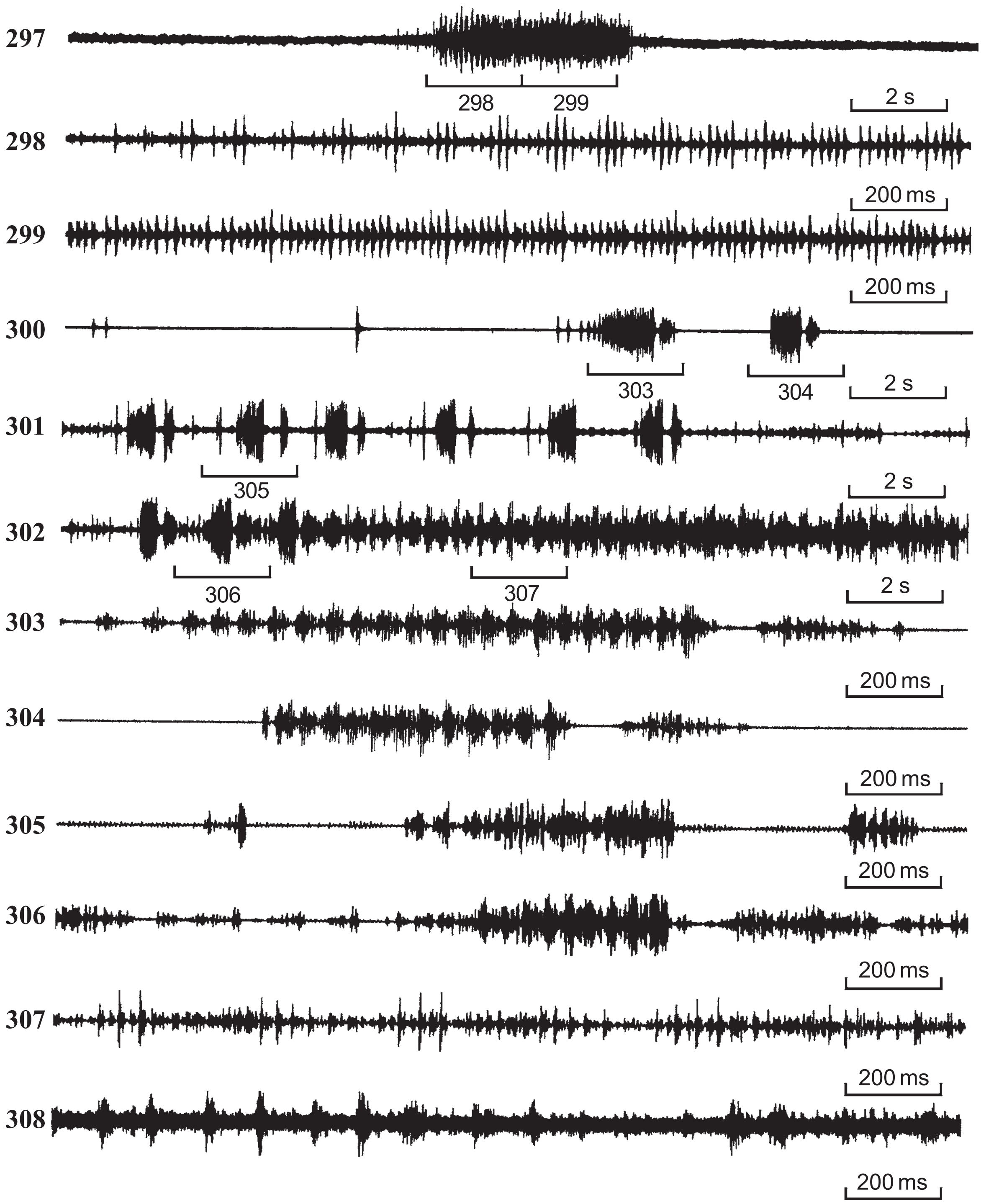
Figs 270–282. Vibrational signals of *Agallia brachyptera* (Boh.): 270–271 — oscillograms of male calling and female reply signals, 272–273 — oscillograms of courtship signal, 274 — same, oscillogram and sonogram, 275 — oscillogram of courtship and copulatory signals, 276 — oscillogram of courtship signal, 277–280 — oscillograms of copulatory signal (277, 279 — wing flaps, 278, 280 — signal, produced by timbals), 281–282 — oscillograms of territorial signals. Faster oscillograms of the parts of signals indicated as "271", "273", "276–280" and "282" are given under the same numbers.

Рис. 270–282. Вибрационные сигналы *Agallia brachyptera* (Boh.): 270–271 — осциллограммы призывного сигнала самца и ответного сигнала самки, 272–273 — осциллограммы сигнала ухаживания, 274 — то же, осциллограмма и сонограмма, 275 — осциллограмма сигнала ухаживания и копуляционного сигнала, 276 — осциллограмма сигнала ухаживания, 277–280 — осциллограммы копуляционного сигнала (277, 279 — удары крыльев, 278, 280 — сигнал, издаваемый при помощи тимбалов), 281–282 — осциллограммы территориальных сигналов. Фрагменты сигналов, помеченные цифрами "271", "273", "276–280" и "282", представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 283–296. Oscillograms of calling signals of *Anaceratagallia venosa* (Fourcroy.) (283–286), *A. ribauti* (Oss.) (287–289) and *A. aciculata*(Horv.) (290–296). Faster oscillograms of the parts of signals indicated as “285–286”, “288–289” and “292–296” are given under the same numbers.

Рис. 283–296. Осциллограммы призывных сигналов *Anaceratagallia venosa* (Fourcroy.) (283–286), *A. ribauti* (Oss.) (287–289) и *A. aciculata* (Horv.) (290–296). Фрагменты сигналов, помеченные цифрами “285–286”, “288–289” и “292–296”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 297–308. Oscillograms of vibrational signals of *Anaceratagallia chalchica* Dlab. (297–299) and *Austroagallia sinuata* (M. R.). (300–308): 297–299 — calling signals of *A. chalchica*, 300–301 and 303–305 — calling signals of *A. sinuata*, short form, 302, 306–307 — same, signal with additional part, 308 — same species, call of distress. Faster oscillograms of the parts of signals indicated as “298–299” and “303–307” are given under the same numbers.

Рис. 297–308. Осциллограммы вибрационных сигналов *Anaceratagallia chalchica* Dlab. (297–299) и *Austroagallia sinuata* (M. R.). (300–308): 297–299 — призывные сигналы *A. chalchica*, 300–301 и 303–305 — призывные сигналы *A. sinuata*, короткая форма, 302, 306–307 — то же, сигнал с дополнительной частью, 308 — тот же вид, сигнал протеста. Фрагменты сигналов, помеченные цифрами “298–299” и “303–307”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

are long and complex phrases lasting for 15–20 s and more, and consisting of several parts with different temporal pattern. In *A. constricta*, the first part of calling sometimes lengthens greatly reaching duration up to 3–4 minutes and more; such transformed signal was referred as “common sound II”. It must be noted, that oscillograms of “common sound I” of *A. constricta* and of “common sound” of *A. novella* on figs 1 and 3 respectively in the paper cited are overturned, so that the zero must be shifted to the right end of the time scale.

In both species receptive female answers male calling producing reply signals (“female common sounds”, according to terminology used in the paper). For some time insects sing alternately, during this duet male calling becomes shorter, its temporal structure somewhat changes, thus calling transforms into courtship signal. Female reply also changes slightly, so the author refers this modified signal as “female courtship sound”. In last seconds before copulation male produces rather variable trill of pulses — copulatory signal (= “precopulatory sound”). In *A. novella* male also vibrates by wings at this moment.

Also, both sexes of both species produce short pulses or clicks repeating with irregular intervals, so called “ticking sounds”. Signals of this type occur in many different behavioural contexts, both in motionless, spaced individuals and preceding or following any kind of activity, including walking, jumping, producing of calling signal, etc. Signals of the same kind I have registered in *A. brachyptera* (see above).

Subfamily Adelungiinae

Achrus albicosta (Kusnezov, 1929)
Figs 309–316.

LOCALITY. Southern Turkmenistan, the road Dushak — Tedzhen 30 km East of Dushak: (1) from *Haloxylon aphyllum* (Minkw.) Iljin, 27.V.1990, signals of 3 ♂♂ are recorded at the temperature 31°C; (2) from *Calligonum* sp., 10.V.1994, signals of 1 ♂ are recorded at the temperature 31°C.

SIGNALS. Calling signal is a succession of short phrases, following each other with a period about 1.5–3 s. Shape of pulses on oscillograms sometimes differs much in different signals depending on physical characteristics of substrate and relative position of singing insect and vibrotransducer (Figs 309, 311 and 310, 312). As in some Macropsinae species, male can answer the calling of another one by rivalry signals, consisting of short trains of discrete pulses (Figs 313–314). Territorial signals produced by male either being single or in the presence of other individuals consist of trills with irregular structure (Figs 315–316).

NOTES. The specimens recorded were identified by Prof. A.F. Emelyanov (St.-Petersburg).

Achrus nigronervosus Lindberg, 1924
Figs 317–322.

LOCALITY. Southern Turkmenistan, the road Dushak — Tedzhen 30 km East of Dushak, from *Calligonum* sp., 27.V.1990. Signals of 3 ♂♂ are recorded at the temperature 27°C.

SIGNALS. Calling signal is a succession of short syllables following each other at a rate 5–6/s. Succession ends with a fragment having irregular structure (Figs 317–320). Duration of signal varies from 4–5 up to 15–20 s. Other males sitting nearby on the same plant usually answer to calling by rivalry signals, consisting of syllables, similar in temporal pattern with these in calling one, but following with less regular intervals (Fig. 318). Quite often several males sitting close to each other on the same twig start producing rivalry signals spontaneously (Figs 321–322).

NOTES. The specimens recorded were identified by Prof. A.F. Emelyanov (St.-Petersburg).

Symphypyga repetekia Kusnezov, 1929
Figs 323–327.

LOCALITY. Transvolga part of Astrakhan’ Area, environs of Dosang Railway Station, from *Calligonum aphyllum* (Pall.) Gürke in sand desert. 6.VII.2000. Signals of 5 ♂♂ are recorded at the temperature 26–27°C.

SIGNALS. Calling signal is a succession of short syllables, somewhat similar with this of *A. nigronervosus* (Figs 323–325). Shape of syllables sometimes slightly changes from the beginning to the end of signal. As in most Adelungiinae species, other males answer to calling signal by rivalry ones (Figs 326–327).

Platyproctus tessellatus Lindberg, 1924
Figs 328–333.

LOCALITY. Transvolga part of Astrakhan’ Area, environs of Dosang Railway Station, from *Calligonum aphyllum* (Pall.) Gürke in sand desert. 30.VI, 5.VII.2000. Signals of more than 10♂♂ are recorded at the temperature 25–26°C.

SIGNALS. Spontaneously produced calling signal includes 2–4 phrases, following each other with a period 0.5–3 s (Figs 329, 332–333). Each phrase consists of low-amplitude succession of partly merged pulses and 1–3 high-amplitude ones, sounding like abrupt clicks. Several males usually sang alternatively (Fig. 329), but never produced territorial or rivalry signals in my experiments.

Male courting female sings more regularly and continuously (Figs 328, 330–331), running along the plant in different directions searching for the mate. Phrases of the signal at these moments become much longer, than in spontaneous calling due to elongation of the first (low-amplitude) part. Then male mounts female and starts copulation. I have neither registered, nor even heard female reply signals. Still, there is no doubt, that they present in acoustic repertoire of the species, because in all cases, when copulation was observed, it was male, who started searching for female, while the latter sat motionless. Evidently, reply signals were not discernible through the noises produced by moving male due to their low amplitude.

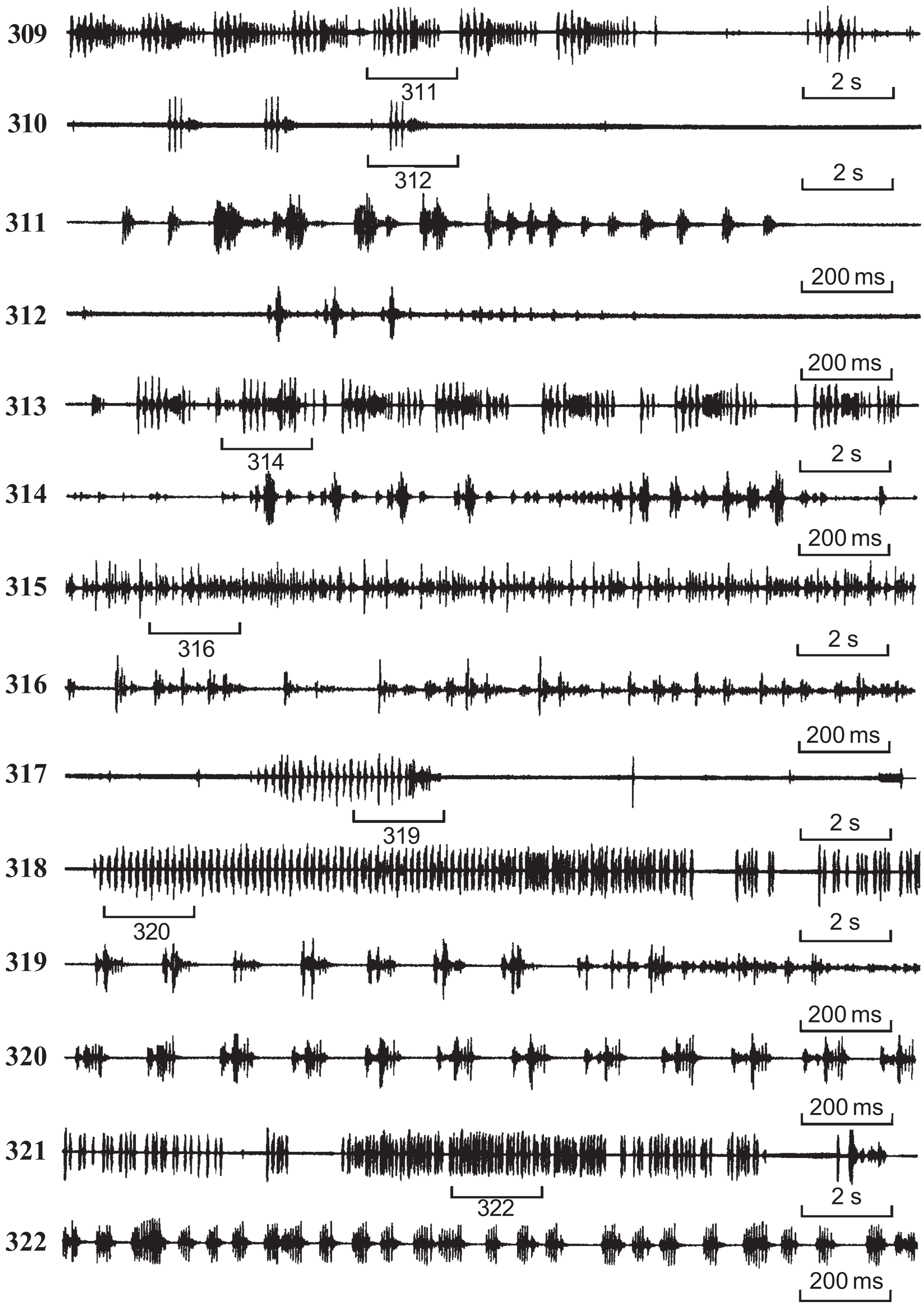
Melicharella callifrons Mitjaev, 1971
Figs 334–337.

LOCALITY. Transvolga part of Astrakhan’ Area, environs of Dosang Railway Station, from *Calligonum aphyllum* (Pall.) Gürke in sand desert. 15.VII.2000. Signals of 5 ♂♂ are recorded at the temperature 28°C.

SIGNALS. Calling signal is a short syllable (Figs 334–336). In my experiments males produced signals with irregular intervals. Other males presenting on the same stem as a rule answer to calling signal emitting continuous irregular rivalry ones (Figs 334, 337).

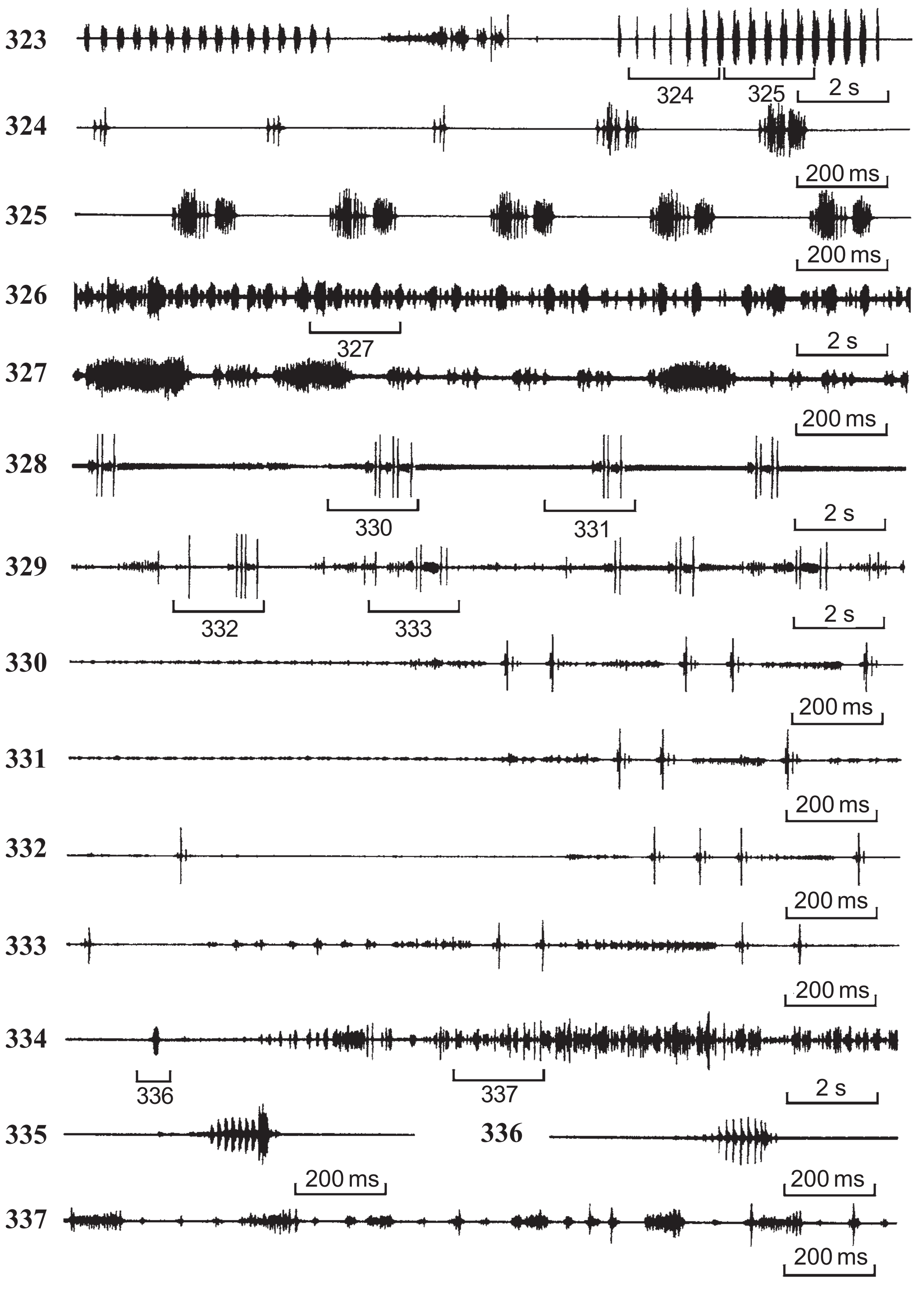
NOTES. Determination of species is based on Mityaev [1971].

200 ms



Figs 309–322. Oscillograms of vibrational signals of *Achrus albicosta* (Kusn.) (309–316) and *A. nigronervosus* Lindb. (317–322): 309–312 — *A. albicosta*, calling signals, 313–314 — same, calling and rivalry signals, 315–316 — same, territorial signals, 317, 319–320 — *A. nigronervosus*, calling signals, 318 — same, calling and rivalry signals, 321–322 — same, rivalry signals. Faster oscillograms of the parts of signals indicated as “311–312”, “314”, “316”, “319–320” and “322” are given under the same numbers.

Рис. 309–322. Осциллограммы вибрационных сигналов *Achrus albicosta* (Kusn.) (309–316) и *A. nigronervosus* Lindb. (317–322): 309–312 — *A. albicosta*, призывные сигналы, 313–314 — то же, призывные сигналы и сигналы соперничества, 315–316 — то же, территориальные сигналы, 317, 319–320 — *A. nigronervosus*, призывные сигналы, 318 — то же, призывные сигналы и сигналы соперничества, 321–322 — то же, сигналы соперничества. Фрагменты сигналов, помеченные цифрами “311–312”, “314”, “316”, “319–320” и “322”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 323–337. Oscillograms of vibrational signals of *Symphypyga repetekia* Kusn. (323–327), *Platyproctus tessellatus* Lindb. (328–333) and *Melicharella callifrons* Mit. (334–337): 323–325 — *S. repetekia*, calling signals, 326–327 — same, rivalry signals, 328–333 — calling signals of *P. tessellatus*, 334 — *M. callifrons*, calling and rivalry signals, 335–336 — same, calling signals, 337 — same, rivalry signals. Faster oscillograms of the parts of signals indicated as “324–325”, “327”, “330–333” and “336–337” are given under the same numbers.

Рис. 323–337. Осциллограммы вибрационных сигналов *Symphypyga repetekia* Kusn. (323–327), *Platyproctus tessellatus* Lindb. (328–333) и *Melicharella callifrons* Mit. (334–337): 323–325 — *S. repetekia*, призывные сигналы, 326–327 — то же, сигналы соперничества, 328–333 — призывные сигналы *P. tessellatus*, 334 — *M. callifrons*, призывный сигнал и сигналы соперничества, 335–336 — то же, призывные сигналы, 337 — то же, сигналы соперничества. Фрагменты сигналов, помеченные цифрами “324–325”, “327”, “330–333” и “336–337”, представлены при большей скорости развертки на осциллограммах под такими же номерами.

Adelungiinae form a well-defined group very closely related to Agalliinae and are regarded either as a tribe of this subfamily (for instance, Emelyanov, 1975) or as a separate group [Davis, 1975; Al-Ne'amy, Linnavuori, 1982; Rakitov, 1998, etc.]. Davis [1975] divides it into two tribes, Achrini and Adelungiini; among the genera studied the first two ones (*Achrus* and *Symphypyga*) belong to Achrini, and two others (*Melicharella* and *Platyproctus*) — to Adelungiini. Almost the same groups were outlined in Adelungiinae by Emelyanov [1975], but he never gave them any formal rank. I cannot find any difference between these two groups in acoustic characters. In representatives of both tribes (or subtribes if Adelungiini are regarded as a tribe) calling signals are single or repeating phrases (the only exception is *M. callifrons*). Also, in both groups males produce rivalry signals (not registered in *P. tessellatus*).

Communication systems in Agalliinae and Adelungiinae are similar in several features, but still differ at the same level, as in Agalliinae and Macropsinae for instance. Both in Agalliinae and in Adelungiinae male calling signals as a rule are rather complex single or repeating phrases.

Their temporal structure somewhat changes during courtship. However, in Agalliinae these changes are more distinct, besides, male produces copulatory signal on the last stage of courtship, whereas in Adelungiinae (*P. tessellatus*) signals of this type were not registered. Also, in contrast with Agalliinae, in males of most Adelungiinae competition behaviour is well developed. So, if any male produces calling, the ones sitting nearby almost immediately answer him by rivalry signals.

Consequently, judging from acoustic characters, Agalliinae and Adelungiinae are two groups, having rather the rank of subfamilies than tribes. At present, available material does not allow to outline any subdivisions in the latter group.

Subfamily Megophthalminae

Megophthalmus scanicus (Fallén, 1806)
Figs 338–345.

LOCALITY. Moscow Area, environs of Pirogovo, meadow on bank of Klyaz'ma River. 29–30.VII, 2.VIII.1987. Signals of 6 ♂♂ are recorded at the temperature 22–24°C.

SIGNALS. Calling signal is a train of syllables, repeating with a period about 0.25–0.5 s. The end pulse in each syllable as a rule has much higher amplitude, than all other ones.

Several males sitting in the same cage usually sing alternately. No other exhibitions of competition behaviour were observed. Courtship behaviour in this species was studied by Ossiannilsson [1949]. According to his description, courting male emits the same signals as a single one, but he sings more regularly, so that pauses between phrases are about as long as the phrase itself. During the pauses he performs rapid jerks and spasmodic movements with the body, for which the term "dancing" was used by the cited author. After mounting female male can continue his singing and dancing for about a minute if immediate attempt of copulation appears to be unsuccessful.

Subfamily Ulopinae

Utecha trivia (Germar, 1821)
Figs 346–358.

LOCALITY. North Caucasus, Chechnya, Terskiy Mountain Ridge in the environs of Grozny Town. 9.VII.1986. Signals of 7 ♂♂ are recorded at the temperature 30–32°C.

SIGNALS. Calling signal (Figs 348–354) usually begins with a long trill, consisting of hardly distinguishable or merged pulses and sounding like a continuous hiss. Now and then trill is interrupted by single high-amplitude pulses or short syllables consisting of 2–5 such ones, each repeating with irregular intervals (Figs 350, 352). Then male produces a short succession of low-amplitude pulses, delimited both in the beginning and in the end by several high-amplitude ones, same as in the preceding part of signal (Figs 351, 353). For the most part, song includes from 1 to 3–4 such successions separated by hissing trills of various length and has overall duration from 10–15 up to 30–40 s.

Courtship behaviour is similar with this, described for *M. scanicus* by Ossiannilsson [1949]. Singing male mounts female and performs rapid movements by all the body now running a little forward, now back, now sideways left or right on her back. Thus he runs approximately for 0.5–1.5 s. Then male stops for a moment, produces a succession of pulses, similar with this in the second part of calling and resumes his "dancing" again (Figs 355–358). It is impossible to ascertain, whether male sings during "dancing", because noises resulting from his movements drown all other sounds. This courtship ritual sometimes lasts for a minute or two. In all cases observed male leaved female and ceased singing after several unsuccessful copulation attempts.

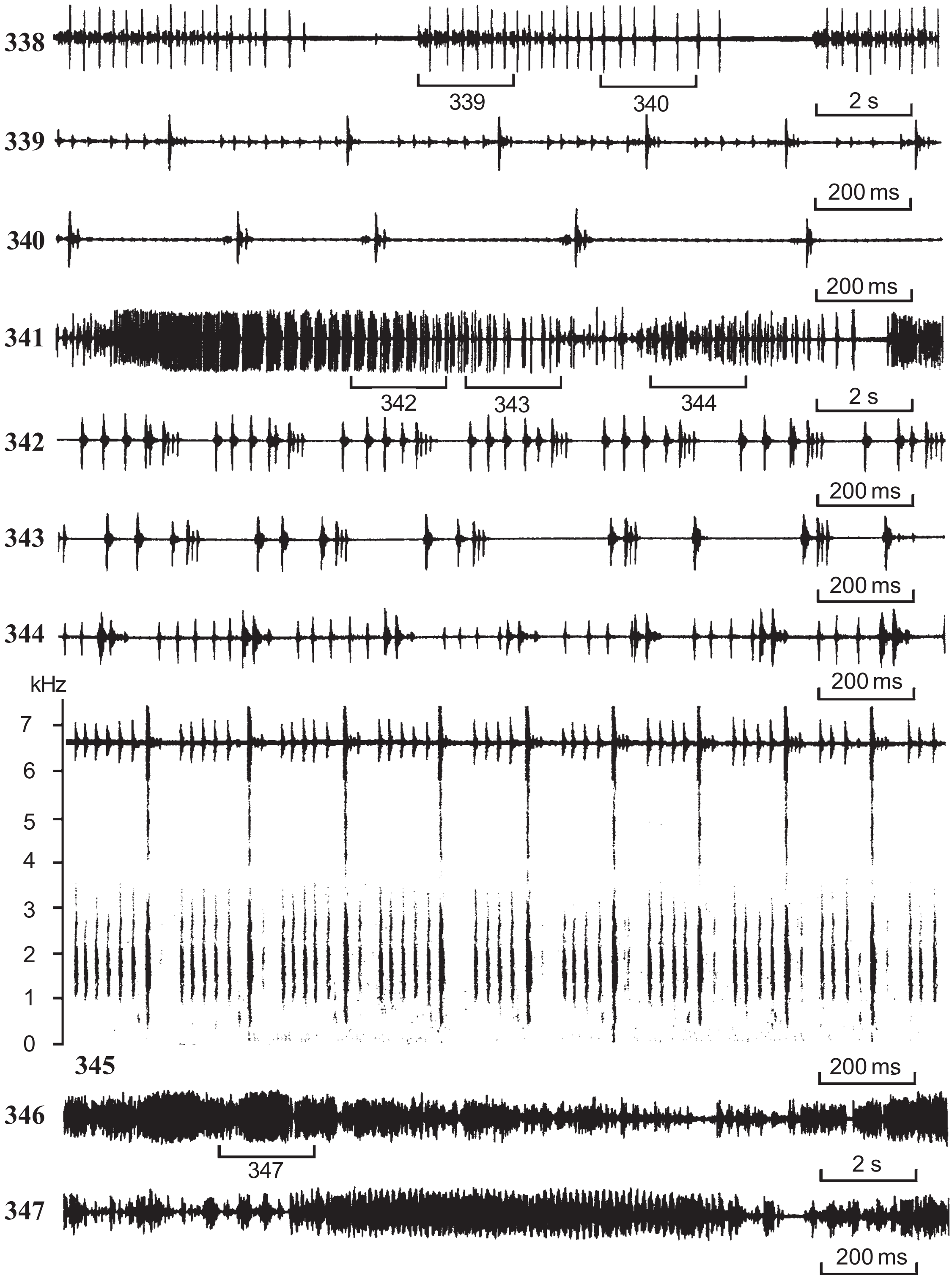
Several males sitting in one cage produce rivalry signals from time to time. Signals of this type consist of short trills similar with these in the second part of calling (Figs 346–347).

NOTES. The term "dancing" was also used for description of courtship performance in Alebrini and Empoascini (Typhlocybinae, see Saxena, Kumar, 1984; Tishechkin, 2001). In representatives of these tribes, courting male moves trotting by small pace and trembling by all the body. Such kind of behaviour is quite different from this in *Megophthalmus* and *Ulopa*, so these two types of "dancing" must not be confused.

There are different opinions concerning position and relationships of Ulopinae. Most authors regard this group as one the most primitive subfamilies among Cicadellidae. Evans [1947] places this subfamily at the base of his Ulopides stem which includes also Ledrinae, Hecalinae (Hecalini + Dorycephalini + Eupelicini + Paradorydiini), Aphrodinae (Aphrodini, incl. Doraturini, Anoterostemma and some others + Errhomenellini, etc.), Cicadellinae and Nirvaninae. Among other tribes he includes in Ulopinae also Megophthalmini.

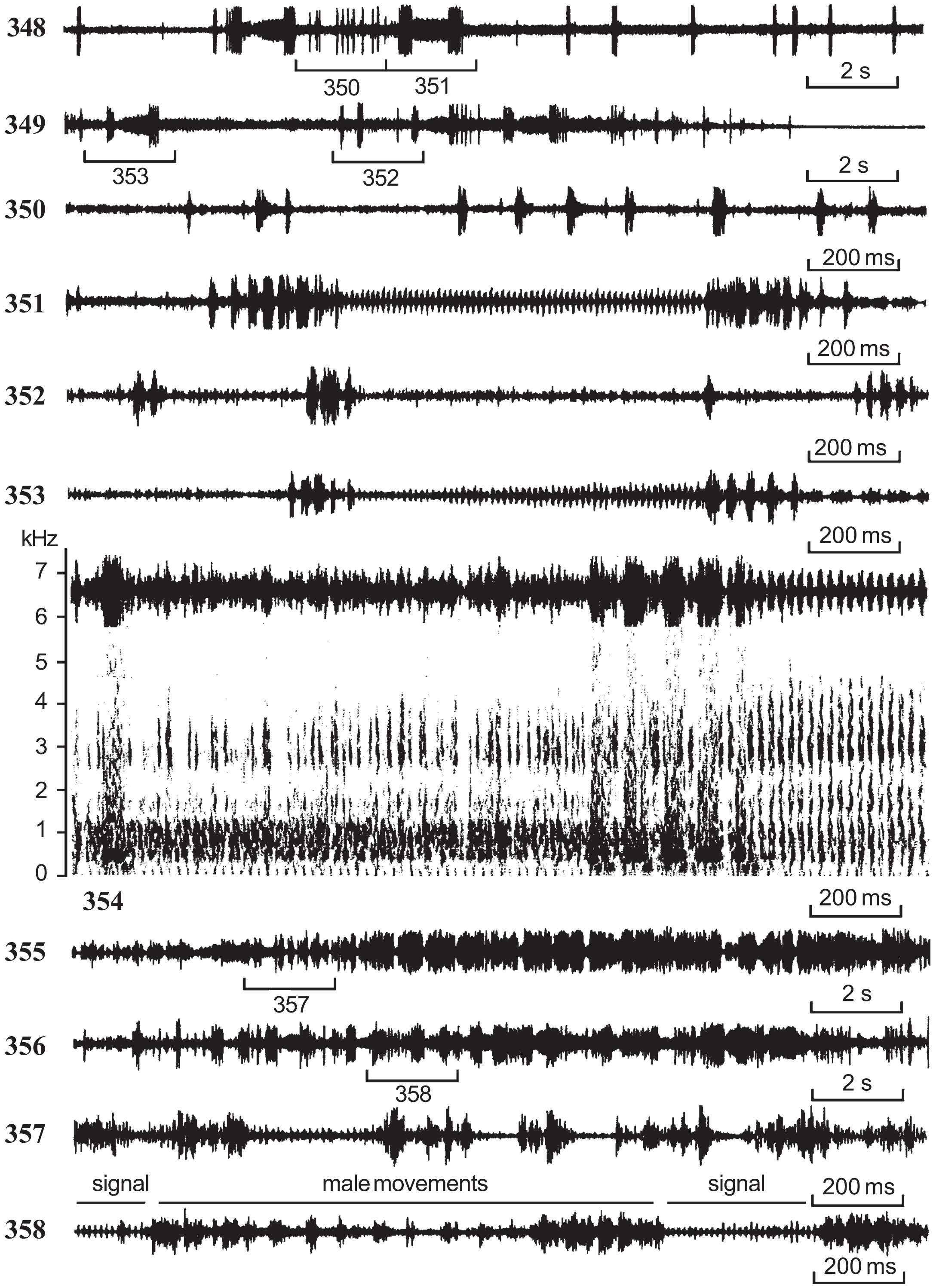
Wagner [1951] places Ulopinae at the base of his Cicadellides group (Aphrodinae sensu Hamilton [1975] + Penthimiinae + Cicadellidae sensu lato). On the other hand, Megophthalminae in his scheme are situated at the base of another stem, namely, Iassides (Iassinae + Macropsinae + Agalliinae + Idiocerinae).

Linnavuori [1972] also shares the opinion that Ulopinae are the most primitive group among Cicadellidae. He regards their relationship to Megophthalminae to be obscure, supposing that the latter group " … may be a derivative from Ulopinae stock from the Mesozoic era,



Figs 338–347. Vibrational signals of *Megophthalmus scanicus* (Fall.) (338–345) and *Utecha trivia* (Germ.) (346–347): 338–344 — oscillograms of calling signals of *M. scanicus*, 345 — same, oscillogram and sonogram, 346–347 — oscillograms of rivalry signals of *U. trivia*. Faster oscillograms of the parts of signals indicated as “339–340”, “342–344” and “347” are given under the same numbers.

Рис. 338–347. Вибрационные сигналы *Megophthalmus scanicus* (Fall.). (338–345) и *Utecha trivia* (Germ.) (346–347): 338–344 — осциллограммы призывных сигналов *M. scanicus*, 345 — то же, осциллограмма и сонограмма, 346–347 — сигналы соперничества *U. trivia*. Фрагменты сигналов, помеченные цифрами “339–340”, “342–344” и “347”, представлены при большей скорости развертки на осциллограммах под такими же номерами.



Figs 348–358. Vibrational signals of *Utecha trivia* (Germ.): 348–353 — oscillograms of calling signals, 354 — same, oscillogram and sonogram, 355–358 — oscillograms of courtship signals. Faster oscillograms of the parts of signals indicated as "350–353" and "357–358" are given under the same numbers.

Рис. 348–358. Вибрационные сигналы *Utecha trivia* (Germ.): 348–353 — осциллограммы призывных сигналов, 354 — то же, осциллограмма и сонограмма, 355–358 — осциллограммы сигналов ухаживания. Фрагменты сигналов, помеченные цифрами "350–353" и "357–358", представлены при большей скорости развертки на осциллограммах под такими же номерами.

but has differentiated so much, that it definitely deserves the rank of separate subfamily". However, he points out on evident relationship of Megophthalminae and Agalliinae.

Davis [1975] considers Agalliinae, Adelungiinae and Megophthalminae as three closely-related subfamilies, but he places Ulopinae somewhat apart from them.

Hamilton [1983] regards Ulopinae as a sister-group of Aetalionidae + Membracidae. He joins Megophthalminae in one tribe with Agalliinae (under the name Megophthalmini) and places them together with Macropsini, Idiocerini, Adelungiini and others in his subfamily Eurymelinae. It is necessary to note, that tribes in his work for the most part correspond to subfamilies of other authors.

Rakitov [1998] joins Ulopinae, Agalliinae, Adelungiinae, Macropsinae, Idiocerinae, Megophthalminae and some other subfamilies in his group Ulopides.

On the phylograms based on molecular data [Dietrich et al., 2001] Ulopinae form a group of closely-related taxa with Adelungiinae, Agalliinae and Megophthalminae. Membracidae appear to be a sister-group of their common stem.

Also, several authors rise Ulopinae to family rank [Ribaut, 1936; Emelyanov, Kirillova, 1987; Hamilton, 1999).

In acoustic characters Ulopinae seem to be most closely related with Megophthalminae, due to peculiar courtship behaviour, including male "dancing". Available material on these groups (single species from each subfamily) does not allow to make any definite conclusion concerning their relationships with Agalliinae, Macropsinae and Idiocerinae at present. However, if the suggestion of several authors about relation of Megophthalminae with Agalliinae is true, than the common stem of Ulopinae + Megophthalminae must be derived from the cluster, formed by Macropsinae, Idiocerinae, Agalliinae and related subfamilies. Consequently, in this case Ulopinae appear to be a derivative of one of small Cicadellidae stems, but not a sister-group of this family in a whole. Similar assumption was expressed earlier by Rakitov [1998] and Dietrich et al. [2001].

Family Membracidae

Subfamily Centrotinae

Gargara genistae (Fabricius, 1775)
Figs 359–372, 387.

LOCALITY. Moscow Area, Serpukhov District, environs of Luzhki Village, from *Genista tinctoria* L. and/or *Cytisus ruthenicus* Fisch. ex Woloszczak: 19.VII.1988, signals of 2 ♂♂ are recorded at the temperature 27°C; 14.VII.1990, signals of 1 ♂ are recorded at the temperature 22–23°C; 2–3.VIII.1992, signals of 10♂♂ and 3 ♀♀ are recorded at the temperature 24–25°C.

SIGNALS. Calling signal of this species is a short phrase, consisting of succession of pulses and monotonous fragment with indistinct structure (Figs 359–362). These two parts of signal differ distinctly from each other by frequency spectra (Fig. 387). Duration of phrase as a rule averages 1.2–1.5 s. Phrases follow with irregular intervals.

When several males present on the same twig, they can sing alternately. In this situation their signals become distinctly shorter. Nevertheless, their specific temporal pattern remains almost unchanged.

Female reply is a short (about 0.5 s) trill (Figs 363–364). After hearing reply signals male starts walking along the plant in different directions, searching for female. During walking he clicks the wings from time to time and stops occasionally to produce calling (Fig. 363). If female answers his signal, he usually produces one or several additional fragments at the end of her reply (about 0.8–1 s after the main part of calling signal, Fig. 364). When insects meet, male mounts female, performs short dancing movements on her back, as male of *U. trivia* do, and starts producing courtship signal. The signal consists of phrases, including two parts each. In breaks between phrases 1–2 wings clicks usually present (Figs 365–367). Occasionally, on the first stage of courtship female answers to each phrase of signal as well, as to calling (Figs 368–369). Overall length of courtship signal sometimes averages several minutes. In the last moments before copulation male changes his song and repeats second part of phrase several times without breaks; thus courtship signal changes into copulatory one (Figs 370–372). Immediately after that he makes an attempt to join his genitalia with female's. If the attempt appears to be unsuccessful, male usually starts courtship signal anew.

Centrotus cornutus (Linnaeus, 1758)
Figs 373–386, 388.

LOCALITIES. Moscow Area: (1) Serpukhov District, environs of Luzhki Village, 3.VI.1987, signals of 1 ♂ are recorded at the temperature 21°C; (2) Serpukhov District, environs of Pushchino-na-Oke Town, 9.VI.1987, signals of 2 ♂♂ are recorded at the temperature 25–26°C; (3) environs of Pirogovo, 27.V.1988, signals of 3 ♂♂ are recorded at the temperature 20°C.

SIGNALS. Calling signal is a long phrase lasting from 5–6 s up to 1 minute and more (Figs 373–375). Its main part is a continuous succession of syllables or pulses with variable temporal pattern (Fig. 376). As a rule, pulses repetition frequency increases and becomes more stable in the end of succession. Then a short trill of simple discrete pulses follows (Figs 377–378, 388).

Courting male comes close to female and starts singing more regularly. When producing courtship signal, he attaches additional part consisting of partially merged pulses in the end of each phrase of calling (Figs 379–382). He can sing for several minutes in such a manner. Immediately before and during copulation attempt male emits copulatory signal consisting of alternating last two parts of courtship one (Figs 383–384), i.e. male misses the first prolonged trill. When sitting on female's back, male performs abrupt jerks by all the body in some appointed moments during singing (Fig. 383). Evidently, these jerks are modification of "dancing" observed in *G. genistae*.

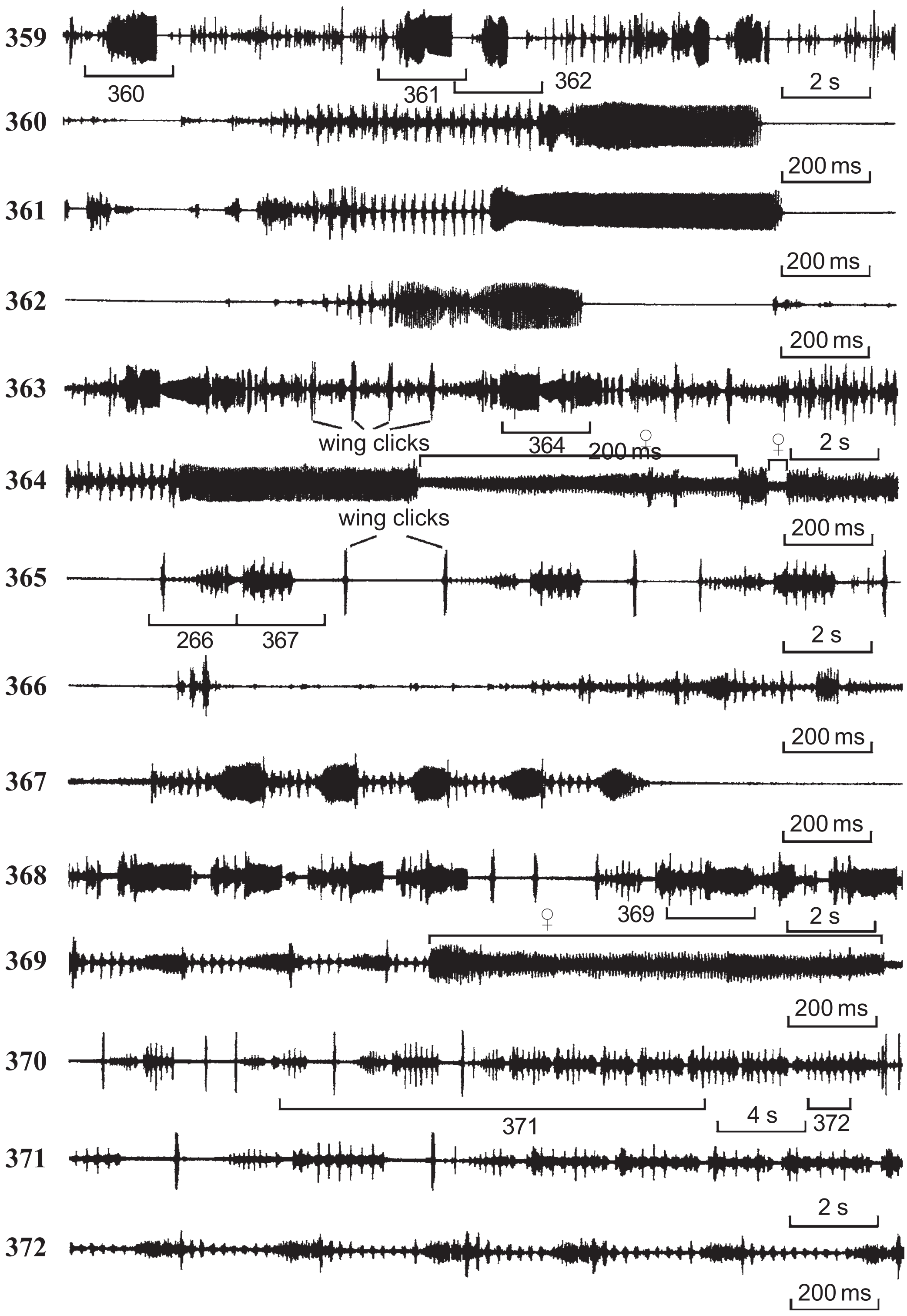
When seized or touched by hand, male produces call of distress (Figs 385–386).

Subfamily Smiliinae

Stictocephala bisonia Kopp, Yonke, 1977
Figs 389–403.

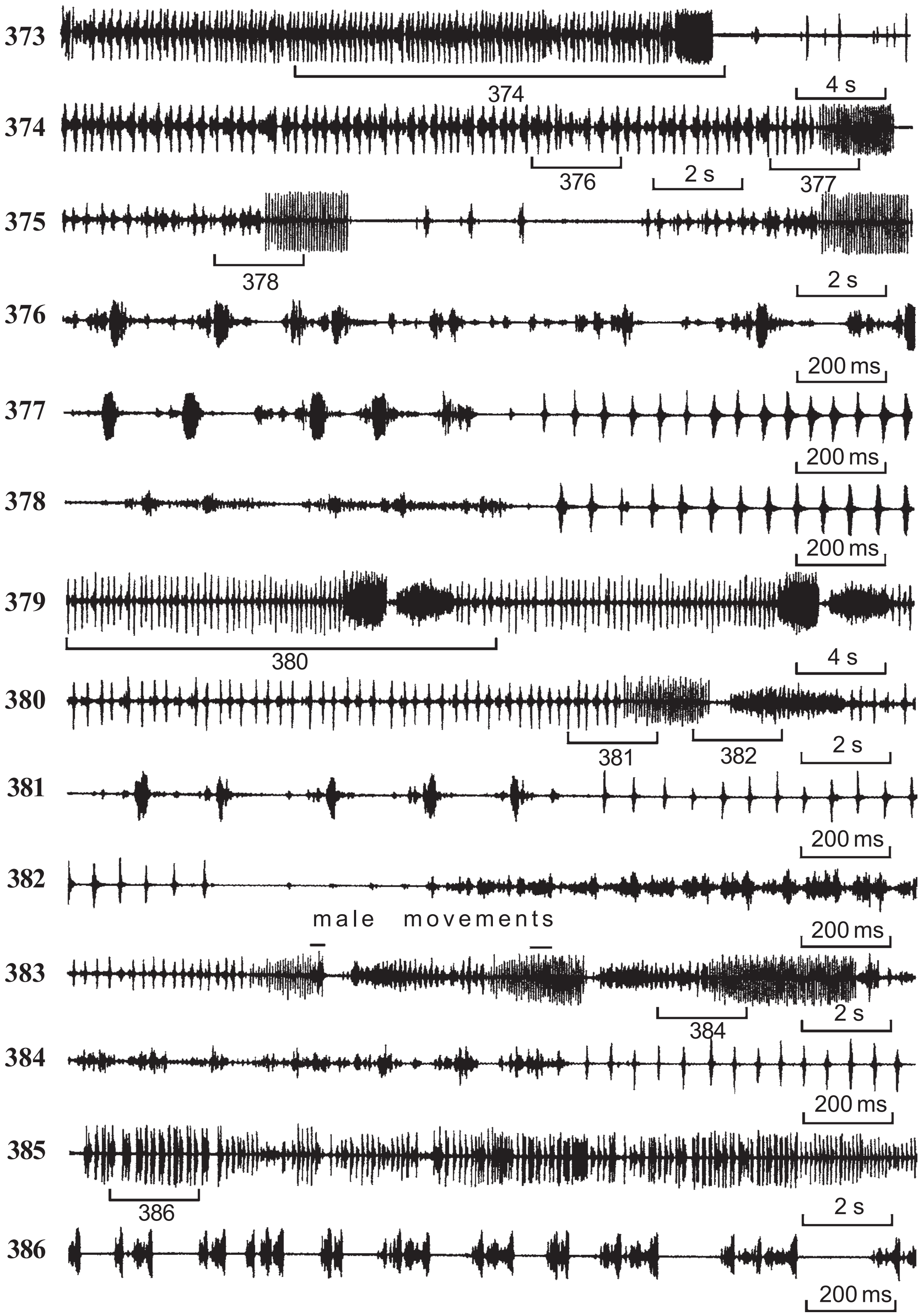
LOCALITY. Rostov Area, Oblivskiy District, environs of Sosnovy (=Oporny) Village on Chir River, from *Rosa* sp. on the roadside. 18–19.VIII.1992. Signals of 4 ♂♂ are recorded at the temperature 30–32°C.

200 ms



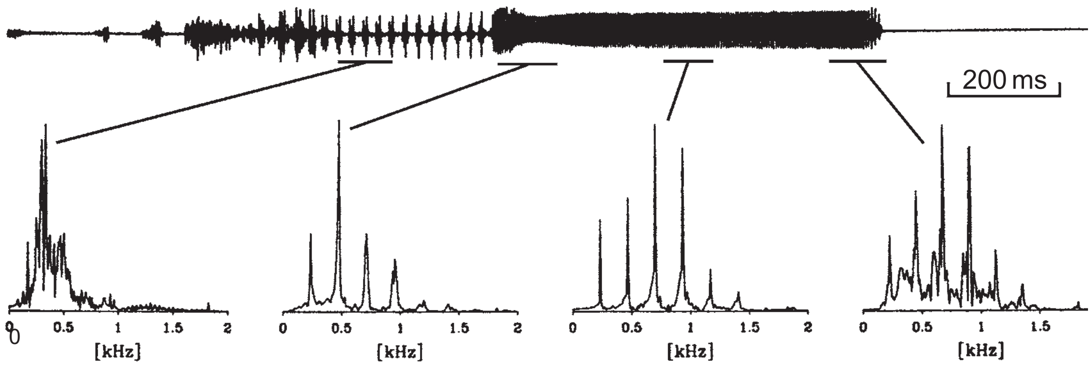
Figs 359–372. Oscillograms of vibrational signals of *Gargara genistae* (F.): 359–362 — calling signals, 363–364 — male calling and female reply, 365–367 — courtship signals, 368–369 — male courtship signal and female reply, 370–371 — courtship and copulatory signals, 372 — copulatory signal. Faster oscillograms of the parts of signals indicated as "360–362", "364", "366–367", "369", "371" and "372" are given under the same numbers.

Рис. 359–372. Осциллограммы вибрационных сигналов *Gargara genistae* (F.): 359–362 — призывные сигналы, 363–364 — призыв самца и ответ самки, 365–367 — сигналы ухаживания, 368–369 — сигнал ухаживания самца и ответ самки, 370–371 — сигналы ухаживания и копуляционный сигнал, 372 — копуляционный сигнал. Фрагменты сигналов, помеченные цифрами "360–362", "364", "366–367", "369", "371" и "372", представлены при большей скорости развертки на осциллограммах под такими же номерами.

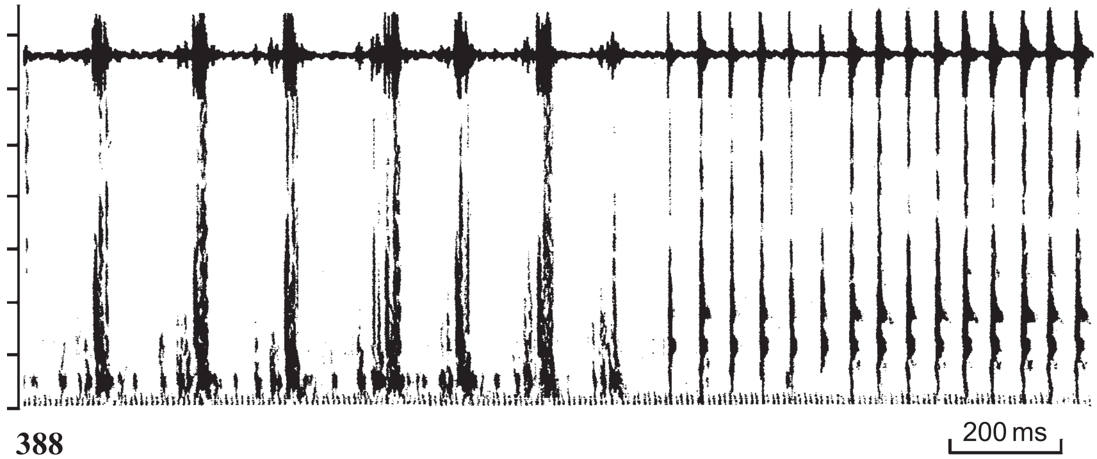


Figs 373–386. Oscillograms of vibrational signals of *Centrotus cornutus* (L.): 373–378 — calling signals, 379–382 — courtship signals, 383–384 — copulatory signals, 385–386 — call of distress. Faster oscillograms of the parts of signals indicated as "374", "376–378", "380–382", "384" and "386" are given under the same numbers.

Рис. 373–386. Осциллограммы вибрационных сигналов*Centrotus cornutus*(L.): 373–378 — призывные сигналы, 379–382 — сигналы ухаживания, 383–384 — копуляционные сигналы, 385–386 — сигнал протеста. Фрагменты сигналов, помеченные цифрами "374", "376–378", "380–382", "384" и "386", представлены при большей скорости развертки на осциллограммах под такими же номерами.



387



388

Figs 387—388. 387 — oscillogram and frequency spectra of different parts of calling signal of *Gargara genistae* (F.), 388 — oscillogram and sonogram of calling signal of *Centrotus cornutus* (L.).

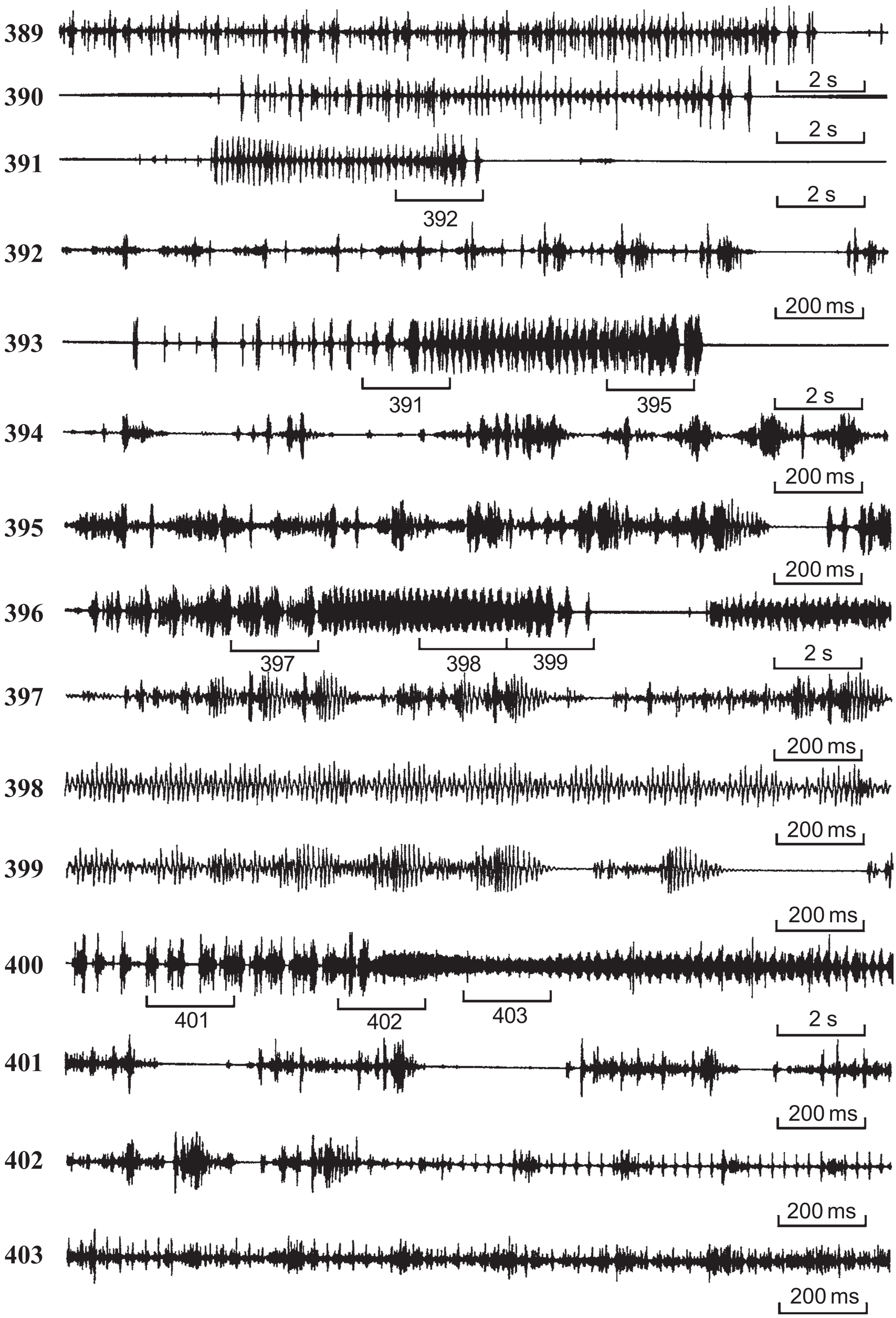
Рис. 387—388. 387 — осциллограмма и частотные спектры различных частей призывного сигнала *Gargara genistae* (F.), 388 — осциллограмма и сонограмма призывного сигнала *Centrotus cornutus* (L.).

SIGNALS. Only calling signals were registered in my experiments. These are single or irregularly repeating phrases lasting from 6–10 s up to 1–2 minutes (Figs 389–391, 393, 396). Usually phrase begins with a succession of rather variable pulses or syllables. Then syllables repetition rate becomes higher and more regular (Figs 389–390, 393, 396). Occasionally, male omits initial part of song (Fig. 391). The phrase ends with 1–2 syllables separated by intervals about 150–300 ms from the preceding part of signal. As in other Cicadina, the waveform in syllables depends on physical characteristics of substrate on which the insect occurs. For this reason, the shape of syllables sometimes varies much in different signals (Figs 392, 394–395, 397–399). Several males sitting on the same stem sometimes sing in turn, but never produce rivalry signals.

Occasionally, male produces signals with different end part, which is a prolonged succession of partially merged syllables (Figs 400–403). No any apparent changes in male behaviour were observed at these moments.

Mating behaviour of *S. bisonia* was studied by Strübing [1999]. As in most other Cicadina, receptive female responds to male calling by producing reply signals. In this species these are continuous non-modulated fragments lasting for about 5 s, sometimes followed by several discrete pulses. Normally, it is male, who walks along the plant searching for female, whereas the latter remains stationary. Any special courtship signals in this species were not registered.

Vibrational communication in two American species of Membracidae was described by Hunt [1993, 1994]. In *Spissistilus festinus* (Say) belonging to the subfamily Smiliinae, as *S. bisonia*, communication during mating behaviour is similar with this in the latter species [Hunt, 1993]. Male produces only one type of signal both being single and on all stages of courtship. It is a phrase lasting for approximately 8–9 s and consisting of two different parts. The first part is a pure-tone continuous fragment averaging about 7 s in length. Its carrier frequency somewhat changes from the beginning to the end of signal. The second part is a succession of discrete syllables having noise frequency spectrum. Female reply was observed if the distance between the insects was about 56 cm or less. The pause between male calling and female reply averaged 2 s. As



Figs 389–403. Oscillograms of calling signals of *Stictocephala bisonia* Kopp, Yonke. Faster oscillograms of the parts of signals indicated as "392", "394–395", "397–399" and "401–403" are given under the same numbers.

Рис. 389–403. Осциллограммы призывных сигналов *Stictocephala bisonia* Kopp, Yonke. Фрагменты сигналов, помеченные цифрами "392", "394–395", "397–399" и "401–403", представлены при большей скорости развертки на осциллограммах под такими же номерами.

in *S. bisonia*, after hearing female reply male started walking in different directions searching for the mate, but female remained sitting on the same place.

In *Enchenopa binotata* Say from the subfamily Membracinae, communication system is far more complex, than in two previous species. Individual male emits calling signals spontaneously . Each signal consists of two sections: the first one is an amplitude- and frequency-modulated wave-train, the second one consists of 2 to 10 pulses. Before climbing onto the side of female prior to copulation male emits a long and elaborate courtship signal. It includes several short repeating phrases followed by rumbling-like vibration, same as in the end part of each phrase, but lasting for about 5 seconds. Each signal ends by single wing flick. Duration of signal in total exceeds 20 s; usually male sings for several minutes, repeating his signals.

Immediately before copulation copulatory signal was detected (the author of the paper cited refers it as "second courtship song"). Its amplitude was very low and the identity of individual that produced the signal is not certain. Copulatory signal consists of two alternating parts and lasts less than one minute.

Also, there is a description of rather peculiar behaviour and parent-offspring communication in subsocial species of the genus *Umbonia* [Cockroft, 1999]. It is quite possible, that similar communication exists in some species of *Aetalion* (Aetalionidae), because both imago and nymphs in this genus have well developed timbals [Evans, 1957].

The structure of communication system during courtship in Centrotinae (*G. genistae*) and Membracinae (*E. binotata*, see Hunt, 1994) is similar, but is quite different from this in Smiliinae (*C. bisonia* and *S. festinus*, see Strübing, 1999 and Hunt, 1993). The data available are inconsistent for making any conclusions at present, but it is quite possible, that acoustic characters may be used in taxonomy of Membracidae on the subfamily or tribe level.

Membracidae or Membracidae + Aetalionidae usually are regarded as a sister-group of Cicadellidae (see for instance, Dietrich, Deitz, 1993). Hamilton [1983] divides Cicadellidae in two main branches on his phylogram and places Membracidae + Aetalionidae on the top of one branch with Ulopinae as their sister-group. Recently he somewhat modified the scheme: Ulopidae are raised to family status still remaining as a sister-group of Membracidae + Aetalionidae, but the common stem of all three families in its turn, is regarded as a sister-group of Cicadellidae [Hamilton, 1999].

Quite different opinion concerning the place of Membracidae among Membracoidea was expressed by Rakitov [1998] and Dietrich et al. [2001]. Basing on morphological, molecular and some other characters they suppose that Cicadellidae are paraphyletic with respect to Membracidae + Aetalionidae, i.e. treehoppers are specialized line deriving from within Cicadellidae, and are not their sister-group. Ulopinae, Megophthalminae, Agalliinae and Adelungiinae form common cluster with Membracidae on cladograms presented in Dietrich et al. [2001]; another cluster nearest to it includes among others Idiocerinae, Eurymelinae and, also, Macropsinae on one of two schemes.

Both temporal pattern and repertoire (a set of functional types) of signals in Membracidae are not unique among Membracoidea and does not allow to outline any kind of boundary between this family and Cicadellidae. In both species of Centrotinae studied male performs rapid, abrupt, jerky movements on female's back during courtship. Among other groups such peculiar behaviour was observed in Ulopinae (*U. trivia*) and Megophthalminae (*M. scanicus*, see Ossiannilsson, 1949) only. This seems to be the evidence of relationships between these three groups (Membracidae, Ulopinae and Megophthalminae). Thus, bioacoustic data corroborate phylogenetic reconstructions of Rakitov [1998] and Dietrich et al. [2001], but disagree with the opinion, that Membracidae are sister-group of Cicadellidae as a whole.

Finally, I give a summary of taxonomic conclusions both from the present article and from two my previous ones concerning vibrational communication of Cicadellidae [Tishechkin, 2000c, 2001]. Several authors (e.g. Evans, 1947; Wagner, 1951) unite all the subfamilies of Cicadellidae into 2–4 groups. In this series of papers I follow the system of Rakitov [1998].

Vibrational signals of more than 100 species of Iassides are described in Tishechkin [2000c]. Calling signals of the most part of Aphrodinae s. str. (*Aphrodes, Planaphrodes, Anoscopus* and *Stroggylocephalus*) are similar with these of Deltocephalini s. str. (*Deltocephalus*, *Graminella*) and *Chelidinus* from Paralimnini in general scheme of temporal pattern. By this character Deltocephalini (maybe, including Paralimnini) appear to be more closely related with Aphrodinae, than with many other tribes of Deltocephalinae. For this reason I share the opinion of Hamilton [1975, 1983], that Aphrodinae and Deltocephalinae must be joined in one subfamily under the valid name Aphrodinae.

Paralimnini are regarded either as a separate tribe or as a part of Deltocephalini. These taxa cannot be separated basing on acoustic characters, so bioacoustic data confirm the latter supposition.

Balclutini (*Balclutha punctata* (Fabricius, 1775)) do not differ much from Macrostelini s.str., so the joining of these two tribes in Macrostelini seems to be quite correct. Several *Macrosteles* species have the same scheme of calling signal pattern, as Aphrodini, Deltocephalini and *Chelidinus* from Paralimnini: the initial fragment being inconstant in structure and almost non-species-specific followed by the main part being constant, highly specific and elaborate. The presence of such a variable component may be interpreted as a primitive character, because it cannot play any substantial role in a process of recognition of conspecific male due to its non-species-specificity. Receptive female never answered to this component, but showed high percentage of reply reactions to isolated main part in the experiments with a playback of recordings of full signals and their different parts [Hunt et al., 1992]. Moreover, in several species male occasionally misses this component during singing. Thus, it is quite possible, that Aphrodini, Deltocephalini, Paralimnini and Macrostelini form a group of related tribes, deriving close to the base of common stem of Aphrodinae sensu Hamilton [1975]. Macrostelini seems to be most primitive group among these tribes due to the presence of tremulation fragments in signals of several species.

Opsiini are separate tribe closely related with Goniagnathini, judging by acoustic data. As the four previous ones, Opsiini + Goniagnathini seemingly form the group, deriving near the base of Aphrodinae stem, but it is not clear, whether it is closely related to Aphrodini + Deltocephalini + Paralimnini + Macrostelini.

The studied representatives of Hecalini (*Glossocratus foveolatus* Fieber, 1866, *Hecalus glaucescens* (Fieber, 1866)), Eupelicini (*Eupelix cuspidata* (Fabricius, 1775)) and Dorycephalini (*Dorycephalus hunnorum* Emeljanov, 1964) are quite similar in temporal pattern of calling signals. Apparently, these taxa must be regarded as three closely related tribes, or even as subtribes of a single tribe. Chiasmini (=Doraturini) seem to be a sister-group of their common stem.

Calling signals of *Nephotettix* spp. differ distinctly from these of other Chiasmini [Inoue, 1982]. So, *Nephotettix* and, apparently, also related genera joined in Stirellini by Emelyanov [1966] represent a separate group, which must be regarded as a tribe or maybe a subtribe of Chiasmini.

Athysanini s. str., Cicadulini and Platymetopiini differ in acoustic characters from each other and must be regarded as separate tribes. Communication systems in *Platymetopius* and *Fieberiella* are identical. For this reason I include Fieberiellini into Platymetopiini following Hamilton [1975].

Available data on Grypotini (*Grypotes puncticollis* (Herrich-Schäffer, 1834)) and Selenocephalini (*Selenocephalus obsoletus* (Germar, 1817)) do not allow to make any conclusion concerning their status.

Iassinae and Penthimiinae are similar with Aphrodinae sensu Hamilton [1975] in acoustic characters, but, on the other hand, differ from Macropsinae, Agalliinae and related subfamilies. So, I place these two subfamilies together with Aphrodinae into Iassides sensu Rakitov [1998].

Oscillograms and descriptions of vibrational signals of 36 species of Cicadellides (Cicadellinae s.l. and Typhlocybinae) are presented in Tishechkin [2001].

Cicadellini (*Cicadella*, *Kolla*) differ from all other Cicadellinae studied by tremulation mechanism of calling signals producing. For this reason the tribe seems to be the most primitive in the subfamily and standing somewhat apart from Errhomenini, Evacanthini and Mileewini.

Most of Cicadellinae and Typhlocybinae produce pure-tone signals or ones including particular fragments with almost regular sine carrier. Evidently, this character is a synapomorphy of these groups or even of all Cicadellides. It is impossible to outline any kind of well-defined boundary between these subfamilies basing on acoustic characters. This fact seems to be the evidence of their close relationships. Similar opinion was expressed by Young [1965] and Hamilton [1983] indirectly by transferring of Mileewini and Nirvanini respectively into Typhlocybinae.

All Typhlocybinae tribes studied may be arranged in several groups according to the scheme of acoustic communication during mating behaviour. Alebrini and Empoascini form one of the groups. Courtship pattern in these tribes is identical and includes male “dancing”, which was not observed in species from other groups. Forcipatini sensu Hamilton [1998] and Erythroneurini fall into another group: as in Alebrini + Empoascini, courting male in representatives of these tribes produces alternating calling and some additional component, but this component is far more developed and united with calling forming an integral signal; moreover, male does not “dance”. In *Vilbasteana oculata* (Lindberg, 1929) (the only studied species of Dikraneurini s.str., i.e., excluding *Notus* and *Forcipata*) courtship behaviour is exactly the same as in the previous group, but calling suffers more complex transformation when changes into courtship signal. Typhlocybini differ from all other tribes either by pattern of courtship behaviour (from Alebrini and Empoascini) or by temporal structure of courtship signal, which is thoroughly unlike calling in contrast with Erythroneurini, Forcipatini and Dikraneurini s. str.

Acoustic signals of 50 species of Ulopides (Idiocerinae, Macropsinae, Agalliinae, Adelungiinae, Megophthalminae and Ulopinae) and of 3 Membracidae ones are described in the present article.

Idiocerinae seem to be the most primitive among groups studied due to the presence of tremulation components in their signals.

Macropsinae are most closely related with Agalliinae and Adelungiinae. Two latter groups are related, but separate subfamilies, judging by acoustic characters.

Distinctive courtship behaviour, which is identical in males of Megophthalminae and Ulopinae, points out on close relationships between these groups. Similar courtship ritual was also observed in two species of Membracidae studied. This fact corroborates the opinion of Rakitov [1998] and Dietrich et al. [2001], that Membracidae derives from within Cicadellidae, namely, from Ulopides, but are not a sister-group of this family.

ACKNOWLEDGEMENTS. I am greatly indebted to Prof. Alexander F. Emelyanov (Zoological Institute of Russian Academy of Sciences, St.-Petersburg) for a number of valuable advises and consultations during the course of this study and for critical reading of the manuscript. On different stages this work was supported by grants of Russian Ministry of Higher Education (“Investigations in the field of fundamental natural Sciences”, head organization — St.-Petersburg State University and “Universities of Russia”, head organization — Moscow State University), and of Russian Foundation for Basic Researches (RFBR, grant № 01–04–49280).

References

Al-Ne'amy K.T., Linnavuori R. 1982. On the taxonomy of the subfamily Adelungiinae (Homoptera, Cicadellidae) // Ann. Ent. Fenn. Vol.48. No.4. P.109–115.

Anufriev G.A., Emelyanov A.F. 1988. [Suborder Cicadinea (Auchenorrhyncha)] // Opredelitel' nasekomykh Dal'nego Vostoka SSSR. Leningrad: Nauka Publ. Vol.2. P.12–495 [in Russian].

Claridge M.F., Howse P.E. 1968. Songs of some British *Oncopsis* species (Hemiptera: Cicadellidae) // Proc. Royal Entomol. Soc. London. Ser. A. Vol.43. No.4–6. P.57–61, 2 plates.

Claridge M.F., Nixon G.A. 1986. *Oncopsis flavicollis* (L.) associated with tree birches (*Betula*): a complex of biological species or a host plant utilisation polymorphism // Biol. J. Linn. Soc. Vol.27. P.381–397.

Claridge M.F., Reynolds W.J. 1973. Male courtship songs and sibling species in the *Oncopsis flavicollis* species group (Hemiptera: Cicadellidae) // J. Entomol. Ser. B. Vol.42. No.1. P.29–39.

Cockroft R. 1999. Parent-offspring communication in response to predators in a subsocial treehopper (Hemiptera: Membracidae: *Umbonia crassicornis*) // Ethol. Vol.105. P.553–568.

Davis R.B. 1975. Classification of selected higher categories of Auchenorrhynchous Homoptera (Cicadellidae and Aetalionidae) // Technical Bulletin of the United States Department of Agriculture. No.1494. P.1–52.

Dietrich C.H., Deitz L.L. 1993. Superfamily Membracoidea (Homoptera: Auchenorrhyncha). II. Cladistic analysis and conclusions // Syst. Entomol. Vol.18. P.297–311.

Dietrich C.H., Rakitov R.A., Holmes J.L., Black W.C., IV. 2001. Phylogeny of the mayor lineages of Membracoidea (Hemiptera: Cicadomorpha) based on 28S rDNA sequences // Molecular Phylogenetics and Evolution. Vol.18. No.2. P.293–305.

Dlabola J.1967. Ergebnisse der 1. mongolisch-tschechoslovakischen entomologisch-botanischen Expedition in der Mongolei. Nr. 1: Reisebericht, LakalitДtenьbersicht und Beschreibungen neuer Zikadenarten (Homopt. Auchenorrhyncha) // Acta Faunistica Entomologica Musei Nationalis Pragae. Vol.12. Nr.115. P.1–34.

Emelyanov A.F. 1966. [On the tribe Stirellini trib. n. and its taxonomic position (Homoptera, Cicadellidae)] // Zool. Zh. Vol.45. No.4. P.609–610 [in Russian, with English summary].

Emelyanov A.F. 1975. [Materials for the revision of the tribe Adelungiini (Homoptera, Cicadellidae)] // Entomol. Obozr. Vol.54. No.2. P.383–390 [in Russian].

Emelyanov A.F., Kirillova V.I. 1989. [Trends and modes of karyotype evolution in the Cicadinea (Homoptera)] // Ibid. Vol.68. No.3. P.587–603 [in Russian, with English summary].

Evans J.W. 1947. A natural classification of leafhoppers (Jassoidea, Homoptera). Pt. 3: Jassidae // Trans. Roy. Ent. Soc. London. Vol.98. P.105–217.

Evans W.J. 1957. Some aspects of the morphology and interrelationships of extinct and recent Homoptera // Ibid. Vol.109. Part 9. P.275–294.

Hamilton K.G.A. 1975. Review of the tribal classification of the leafhopper subfamily Aphrodinae (Deltocephalinae of authors) of the Holarctic region (Rhynchota: Homoptera: Cicadellidae) // Can. Entomol. Vol.107. No.5–6. P.477–498.

Hamilton K.G.A.1980. Contribution to the study of the world Macropsini (Rhynchota: Homoptera: Cicadellidae) // Ibid. Vol.112. No.9. P.875–932.

Hamilton K.G.A. 1983. Classification, morphology and phylogeny of the family Cicadellidae (Rhynchota: Homoptera) // Proc. 1st International Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Institute of Entomol. P.15–37.

Hamilton K.G.A. 1998. New World species of *Chlorita*, *Notus* and *Forcipata* (Rhynchota: Homoptera: Cicadellidae: Typhlocybinae) with a new tribe Forcipatini // Can. Entomol. Vol.130. P.491–507.

Hamilton K.G.A. 1999. The ground-dwelling leafhoppers Myerslopiidae, new family, and Sagmatiini, new tribe (Homoptera, Membracoidea) // Invertebrate Taxonomy. Vol.13. P.207–235.

Hunt R.E. 1993. Role of vibrational signals in mating behaviour of *Spissistilus festinus* (Homoptera: Membracidae) // Ann. Entomol. Soc. Amer. Vol.86. No.3. P.356–361.

Hunt R.E. 1994. Vibrational signals associated with mating behaviour in the treehopper, *Enchenopa binotata* Say (Hemiptera: Homoptera: Membracidae) // J. New York Entomol. Soc. Vol.102. No.2. P.266–270.

Hunt R.E., Fox J.P., Haynes K.F. 1992. Behavioral response of *Graminella nigrifrons* (Homoptera, Cicadellidae) to experimentally manipulated vibrational signals // J. Insect Behav. Vol.5. No.1. P.1–13.

Inoue H. 1982. Species-specific calling sounds as a reproductive isolating mechanism in *Nephotettix* spp. (Hemiptera, Cicadellidae) // Appl. Entomol. Zool. Vol.17. No.2. P.253–262.

Linnavuori R. 1972. Revision of the Ethiopian Cicadellidae (Hom.), Ulopinae and Megophthalminae // Ann. Ent. Fenn. Vol.38. No.3. P.126–149.

Mityaev I.D. 1971. [Cicadinea of Kazakhstan. Keys for identification of species]. Alma-Ata: Nauka Publ. 211 pp. [in Russian]

Ossiannilsson F. 1949. Insect drummers. A study on the morphology and function of the sound-producing organ of Swedish Homoptera Auchenorrhyncha with notes on their sound production // Opuscula Entomol. Suppl.10. P.1–145.

Rakitov R.A. 1998. On differentiation of cicadellid leg chaetotaxy (Homoptera: Auchenorrhyncha: Membracoidea) // Russian Entomol. J. Vol.6 (for 1997). No.3–4. P.7–27.

Ribaut H. 1936. Homoptères Auchénorrhynques. I. (Typhlocybidae) // Faune de France. Vol.31. 231 pp.

Saxena K.N., Kumar H. 1984. Acoustic communication in the sexual behaviour of the leafhopper, *Amrasca devastans* // Physiological Entomology. Vol.9. P.77–86.

Shaw K.C. 1976. Sounds and associated behaviour of *Agallia constricta* and *Agalliopsis novella* (Homoptera: Auchenorrhyncha: Cicadellidae) // J. Kansas Entomol. Soc. Vol.49. No.1. P.1–17.

Strübing H. 1999. Comments on the vibratory signals of *Stictocephala bisonia* Kopp et Yonke and *Dictyophara europaea* (L.) (Hemiptera: Auchenorrhyncha: Cicadomorpha et Fulgoromorpha: Membracidae and Dictyopharidae) // Reichenbachia. Staatl. Mus. Tierkunde Dresden. Bd.33. Nr.7. S.61–69.

Tishechkin D.Yu. 1992. [A new species of *Oncopsis* (Homoptera, Cicadinea, Cicadellidae) from the Northern Caucasus] // Zool. Zh. Vol.71. No.4. P.141–144 [in Russian with English summary].

Tishechkin D.Yu. 1994. [Acoustic communication system in Macropsinae leafhoppers (Homoptera, Cicadellidae): adaptive features and trends of evolution] // Entomol. Obozr. Vol.73. No.1. P.3–15 [in Russian with English summary].

Tishechkin D.Yu. 2000a. Review of the species of the genus *Macropsis* Lewis, 1834 (Homoptera: Cicadellidae: Macropsinae) from the Russian Far East and adjacent territories of Transbaikalia // Russian Entomol. J. Vol.8 (for 1999). No.2. P.73–113.

Tishechkin D.Yu. 2000b. Review of species of the genus *Hephathus* Ribaut, 1952 (Homoptera: Cicadellidae: Macropsinae) from the territory of Russia with notes on other Palaearctic species of the genus // Ibid. Vol.8 (for 1999). No.4. P.239–252.

Tishechkin D.Yu. 2000c. Vibrational communication in Aphrodinae leafhoppers (Deltocephalinae auct., Homoptera: Cicadellidae) and related groups with notes on classification of higher taxa // Ibid. Vol.9. No.1. P.1–66.

Tishechkin D.Yu. 2001. Vibrational communication in Cicadellinae sensu lato and Typhlocybinae leafhoppers (Homoptera: Cicadellidae) with notes on classification of higher taxa // Ibid. Vol.9. No.4 (for 2000). P.283–314.

Tishechkin D.Yu. 2002. Review of the species of the genus

Macropis Lewis, 1834 (Homoptera: Cicadellidae: Macropsinae) from European Russia and adjacent territories // Ibid. Vol.11. No.2. P.123–184.
Vilbaste Yu.G. 1980. [Fauna of Cicadinea of Tuva]. Tallinn: Valgus Publ. 219 pp. [in Russian with English summary]
Wagner W. 1951. Beitrag zur Phylogenie und Systematik der Cicadellidae (Jassidae) Nord- und Mitteleuropas // Commentationes biologicae. Vol.12. No.2. P.1–43.
Young D.A. 1965. Western Hemisphere Mileewanini // Zool. Beitrage (N.F.). Bd.11. S.369–380.