Russian Entomol. J. 27(3): 217–239

Contributions to the study of vibrational signals of Palearctic Cicadellidae (Homoptera: Auchenorrhyncha) — new recordings of interesting or rare species with notes on their taxonomy, biology and distribution

К изучению вибрационных сигналов палеарктических Cicadellidae (Homoptera: Auchenorrhyncha): новые записи интересных и редких видов с замечаниями по систематике, биологии и распространению

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KEY WORDS: Homoptera, Auchenorrhyncha, Cicadellidae, vibrational communication, vibrational signals, new records, host plants.

КЛЮЧЕВЫЕ СЛОВА: Homoptera, Auchenorrhyncha, Cicadellidae, вибрационная коммуникация, вибрационные сигналы, новые находки, кормовые растения.

ABSTRACT. Vibrational calling signals of 26 leafhopper species from the subfamilies Ulopinae, Ledrinae, Agalliinae, Xestocephalinae, Iassinae, Penthimiinae, Evacanthinae, and Deltocephalinae are described and illustrated by oscillograms and sonograms. *Ledra auditura* has nocturnal acoustic activity; males of all other species produce signals during daytime. Species rank of *Iassus dorsalis* is confirmed by signal analysis. *Utecha trivia* was recorded from Central European Russia, *Maiestas oryzae* — from Amur Oblast and Khabarovsk Krai for the first time; it is shown that records of *Stymphalus rubrostriatus* = *Varta rubrostriata* from the Russian Far East refer to *Varta japonica*. Examples of signal pattern similarity in different species are discussed. Both the type of frequency spectrum (noise or line) and signal temporal pattern bear phylogenetic information. Temporal pattern, compared to the frequency characteristics, is more exposed to the effect of natural selection resulting from competition for communication channels within insect communities. For this reason, it can be used in phylogenetic reconstructions only as an additional trait and by no means in all cases.

РЕЗЮМЕ. Приведены иллюстрированные осциллограммами и сонограммами описания вибрационных призывных сигналов 26 видов цикадок из подсемейств Ulopinae, Ledrinae, Agalliinae, Xestocephalinae, Iassinae, Penthimiinae, Evacanthinae и Deltocephalinae. *Ledra auditura* начинает петь после наступления темноты, все остальные виды издают сигналы в дневное время. Видовой статус *Iassus dorsalis* подтверждён анализом сигналов. *Utecha trivia* впервые отмечен в центральных районах европейской России, *Maiestas oryzae* — в Амурской области и Хабаровском крае; показано, что указания *Stymphalus rubrostriatus* = *Varta rubrostriata* с Дальнего Востока России относятся к *Varta japonica*. Обсуждаются случаи сходства сигналов у разных видов. Как тип частотного спектра (шумовой или линейчатый), так и временной рисунок сигналов несут филогенетическую информацию. Однако временной рисунок, по сравнению с частотными характеристиками, в большей степени подвержен естественному отбору в связи с конкуренцией за каналы связи в сообществах насекомых. Поэтому он может быть использован для филогенетических реконструкций только в качестве дополнительного признака и то далеко не во всех случаях.

How to cite this article: Tishechkin D.Yu. 2018. Contributions to the study of vibrational signals of Palearctic Cicadellidae (Homoptera: Auchenorrhyncha) – new recordings of interesting or rare species with notes on their taxonomy, biology and distribution // Russian Entomol. J. Vol.27. No.3. P.217–239. doi: 10.15298/rusentj.27.3.01

Introduction

For a long time, due to the lack of portable equipment investigations of vibrational communication signals of small Auchenorrhyncha (Homoptera) were conducted only under laboratory conditions. Consequently, all researchers had to confine themselves to a small number of model species cultivated in the laboratory. In the early 90-ies of the last century we adopted alternative approach and began a large-scale comparative study of vibrational signals of small Auchenorrhyncha using portable equipment specifically designed for field research. This made it possible to investigate in a short time the signals of several hundred species from many families, subfamilies, and tribes not studied before. Such an approach also opened up vast opportunities for using acoustic traits in leafhopper taxonomy for discrimination of cryptic species and for clarifying the status of dubious forms of the species rank. We must admit, however, that along with the merits, field studies also have disadvantages. Under field conditions, recording of calling signals produced by single male for attracting conspecific female is an easy task. Signals of this type are most useful for taxonomic analysis at the species level because interspecific differences in their temporal pattern provide the main precopulatory reproductive barrier. Detailed investigation of vibrational communication during mating behavior is very difficult outside laboratory, since it requires sufficient number of virgin females which are almost impossible to collect in nature. For this reason, for most species studied by us only recordings of calling signals are available.

The main results of the study of signals of small Auchenorrhyncha of Russia and adjacent territories were published in early 2000s [Tishechkin, 2000, 2001, 2003a, b]; these four articles include signal descriptions of more than 250 species. Later we published some additional data on signals of Fulgoroidea [Tishechkin, 2008, 2016] and Cicadellidae [Tishechkin, 2010]. Also, signal oscillograms and sonograms (dynamic spectrograms) of a number of species can be found in Tishechkin and Burlak [2013], but they do not give a complete picture of the signal structure. Since the article cited concerns investigation of pure-tone signals, detailed signal descriptions for every species studied was not part of its task.

For the present article, mostly species from small taxa poorly represented and rare in Palearctic were selected; most species were collected in the Russian Far East and in Central Asia. Calling signals of 26 species of Cicadellidae (Homoptera: Auchenorrhyncha) from eight subfamilies including two tribes of Evacanthinae and seven tribes of Deltocephalinae are described and illustrated by oscillograms and sonograms. Also, new data on host plants, biology, and distribution of some species are provided.

Since almost all recordings were made during expeditions, for most species only male calling signal descriptions are given. Only in *Paradorydium paradoxum* (Herrich-Schäffer, 1837) courtship signals produced by male in last moments before copulation were also recorded.

Material and methods

Leafhopper vibrational calling signals were recorded by means of portable recording equipment consisting of a piezocrystal gramophone cartridge GZP-311 connected to the microphone input of a cassette recorder Elektronika-302-1 (before 2005), minidisk recorder Sony Walkman MZ-NH900 (2004–2016), or Roland R-05 wave/mp3 recorder (2017) via a custom-made matching amplifier. For recording, a twig of the host plant about 10–15 cm in length was attached to the cartridge by a rubber ring so that the cartridge needle touched the stem slightly. Then a nylon cage containing a male leafhopper was put on the twig. After a time, the male usually sat on the twig and started singing.

Signal analysis was performed with Cool Edit Pro 2.1 software.

For elements of signal temporal pattern the following terms are used. **Pulse** is a brief elementary fragment of signal (or succession of sine waves) with rapid increase and subsequent decrease of amplitude, i.e. separated from similar fragments by amplitude minimums. Short fragments with constant temporal pattern usually repeated with regular intervals and consisting of similar or different pulses are referred to as **syllables**. To this category we also refer fragments not separated into pulses and consisting of uniform sine carrier. Any more or less prolonged signal with complex pattern (e.g. succession of similar or different syllables) is referred to as a **phrase**. **Repetition period** is a time interval from the beginning of one fragment of signal to the beginning of the next similar fragment. Since the diversity of a leafhopper signal patterns is very high, every part of signal cannot be classified with certainty as a pulse, syllable, or phrase. For this reason, in some cases we use neutral terms such as “sequence”, “fragment”, etc.

Specimens studied are deposited in the collection of Zoological Museum of M.V. Lomonosov Moscow State University, digital copies of signal recordings will be deposited in the Museum in the near future.

Results

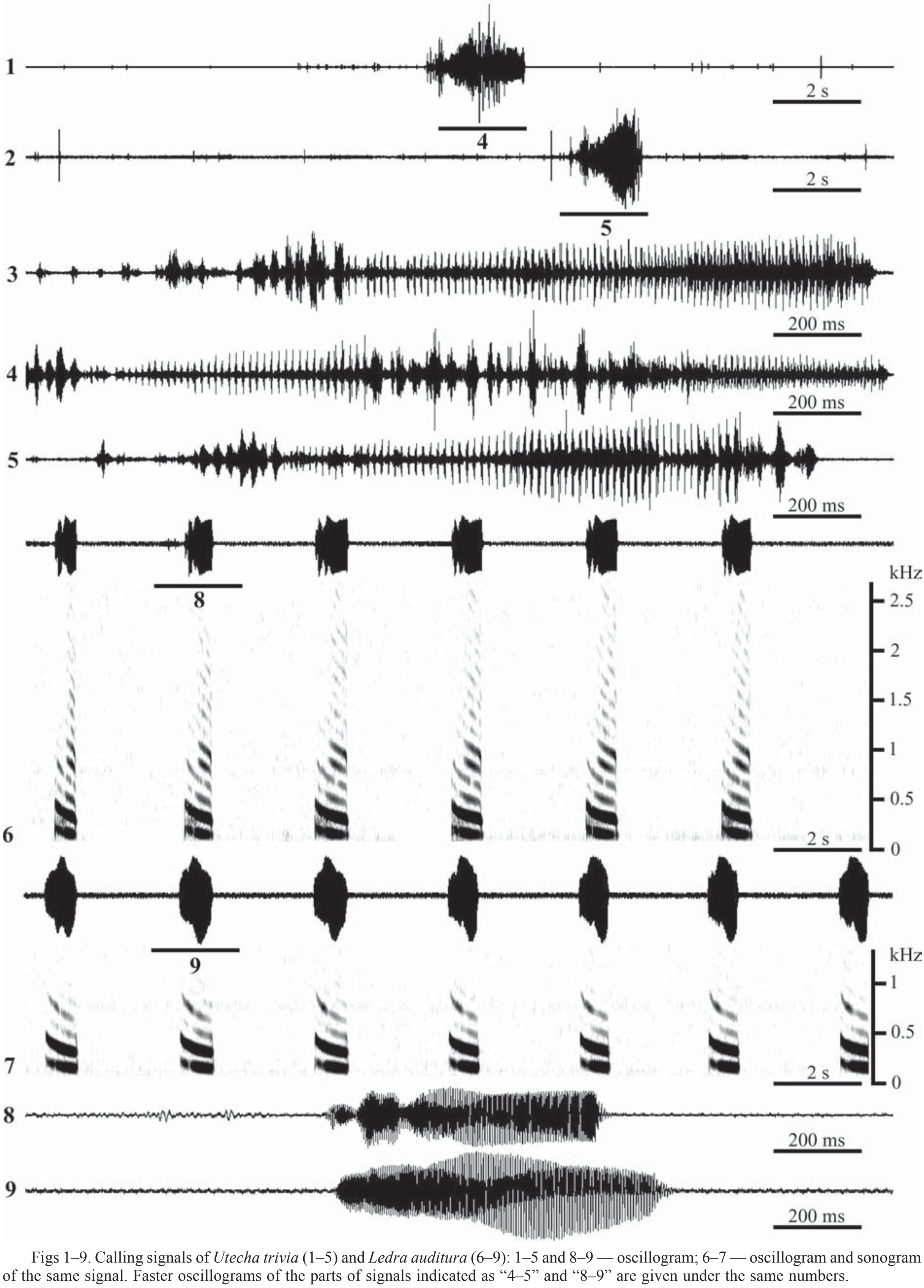
Subfamily Ulopinae

1. *Utecha trivia* (Germar, 1821)

Figs 1–5.

MATERIAL. Moscow Oblast, Voskresensk District, environs of Beloozerskiy Town, meadow with xerophyte vegetation on the shore of the lake, 1.VIII.2017, calling signals of 2 ♂♂ recorded on flash card at 30°C.

SIGNALS. Calling signal is a short phrase lasting for ca. 2 s (Figs 1–2). Phrases follow each other with irregular intervals from 5–10 s up to several minutes. Each phrase consists of alternating pulse successions of two types (Figs 3–5). Succession of the first type has irregular temporal pattern and lower pulse repetition frequency. Succession of the second type has more regular pattern and higher pulse repetition frequency. Phrase always begins with a succession of the first type; the number of successions in a phrase vary from 2 (Fig. 3) to 4 (Fig. 4) in our recordings.



Figs 1–9. Calling signals of *Utecha trivia* (1–5) and *Ledra auditura* (6–9): 1–5 and 8–9 — oscillogram; 6–7 — oscillogram and sonogram of the same signal. Faster oscillograms of the parts of signals indicated as “4–5” and “8–9” are given under the same numbers.

Рис. 1–9. Призывные сигналы *Utecha trivia* (1–5) и *Ledra auditura* (6–9): 1–5 и 8–9 — осциллограммы; 6–7 и 8–9 — осциллограмма и сонограмма одного и того же сигнала. Фрагменты сигналов, обозначенные цифрами “4–5” и “8–9”, представлены на осциллограммах под такими же номерами.

REMARKS. Until now *U. trivia* was reported only from the southern part of European Russia [Emelyanov, 1964]; locality in Moscow Oblast is a northernmost record of this species. In 2017 it was numerous on dry meadows dominated with *Hieraceum umbellatum* L. and *Tanacetum vulgare* L. (Asteraceae); in the laboratory, it fed upon *T. vulgare* and produced calling signals on this plant. *Echium* sp. (Boraginaceae), *Hippocrepis* sp. (Fabaceae), and *Plantago* sp. (Plantaginaceae) were reported as its possible hosts [Emelyanov, 1964; Biedermann, Niedringhaus, 2009], but neither of these plants were found in the habitats of this species in Moscow Oblast.

Oscillograms of calling signals of male, which was in the same cage with female, were published earlier; specimens were collected in the environs of Grozny City, North Caucasus [Tishechkin, 2000a]. On Figs 1–5 oscillograms of signals of a single male are shown.

Subfamily Ledrinae

2. *Ledra auditura* Walker, 1858
Figs 6–9.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 6–8.VIII.2010, calling signals of 6 ♂♂ recorded on disk at 24–25°C.

SIGNALS. Calling signal is a succession of pure-tone syllables with variable temporal pattern and regular sine carrier (Figs 8–9). In the signals of an actively singing male, syllables follow each other with a period of ca. 3–3.5 s (Figs 6–7); if the male sings seldom and reluctantly, syllable repetition period increases. The number of harmonics in a frequency spectrum (Figs 6–7) evidently, depends on filtering properties of a substrate.

Unlike most other leafhopper species, *L. auditura* produce signals only after dusk; also, this species readily flies at light sources. Nocturnal and evening acoustic activity was earlier reported for *Metcalfa pruinosa* (Say, 1830) (Homoptera: Flatidae) [Virant-Doberlet, Žežlina, 2007] and *Apartus michalki* (Wagner, 1948) (Homoptera: Cixiidae) [Kunz et al., 2014], respectively.

REMARKS. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

Anufriev [1978] reports that this species feeds on oak (*Quercus* sp.); Vilbaste [1968] collected one specimen from *Viburnum* sp. Males whose signals were recorded were collected at light; they fed upon *Acer* sp. for several days and produced calling signals on this plant.

Ossiannilsson [1949: 68] gave a verbal description of signals of a European member of this genus, *Ledra aurita* (Linnaeus, 1758). "The call consisted of a tone falling in pitch and repeated once per second"; it sounded like regularly repeated "tuuu", "tuuu", "tuuu" for human ear. Ossiannilsson heard this call twice, at 7.13 and 10.55 a.m. As far as can be judged from this description, signal of this species is quite similar to the signal of *L. auditura*.

Subfamily Agalliinae

3. *Onukigallia onukii* (Matsumura, 1912)
Figs 10–16.

MATERIAL. 1. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 6.VIII.2010, calling signals of 2 ♂♂ recorded on disk at 26°C.

2. Primorsky Krai, Pogranichny District, environs of Barabash-Levada Village, 23.VII.2002, calling signals of 1 ♂ recorded on tape at 19–20°C.

SIGNALS. Calling signal is a very variable phrase lasting for about 10–15 s (Figs 10–11, 14); its only constant component is a sequence of short simple pulses (Figs 12–13, second halves of oscillograms; Fig. 16). In males from "Kedrovaya Pad'" Nature Reserve successions of longer pulses precede and follow this component; an amplitude ratio of different parts can vary even within the song of the same male (Figs 12–13). In the male from the environs of Barabash-Levada Village a succession of short syllables precedes the main component of a phrase (Figs 14–16).

REMARK. Identification of species is based on Li et al. [2016].

Subfamily Xestocephalinae

4. *Xestocephalus guttatus* (Motschulsky, 1859)
Figs 17–24.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 8.VIII.2010, calling signals of 4 ♂♂ recorded on disk at 24–25°C.

SIGNALS. Calling signal is a phrase consisting of syllables repeated with a period of about 2.2–3.5 s (Figs 19–20). Temporal pattern of the initial part of a syllable varies greatly (Figs 22–24), occasionally, this part is almost completely reduced (Fig. 23). The main part of a syllable has more constant pattern and consists of 3–6 short pulses repeated with a period 100–200 ms; pulse amplitude and repetition period increase towards the end of a syllable. Occasionally, prolonged low-amplitude fragment with variable and indistinct pattern precedes the main part of a signal (Figs 17–18 and 21).

Subfamily Iassinae

5. *Iassus ulmi* (Kusnezov, 1929)
Figs 25–30.

MATERIAL. Transbaikalia, South-east of Chita Oblast, environs of Margutsek Village ca. 10 km West of Klichka Town, Klickinsky Mtn. Range at the crossing with the Urulunguy River, from *Ulmus pumila* L., 22–23.VII.2003, calling signals of 2 ♂♂ recorded on tape at 24 and 34°C.

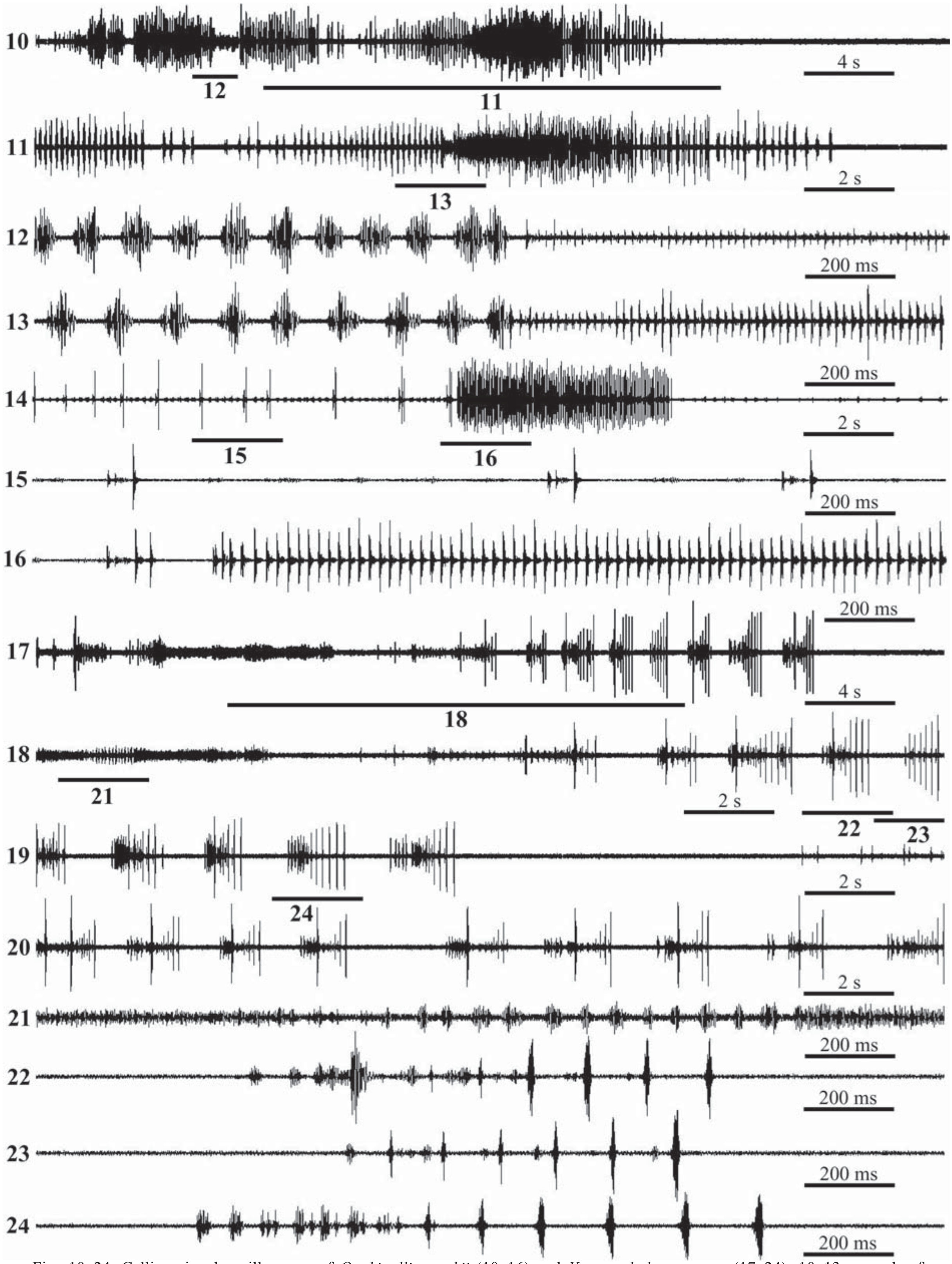
SIGNALS. Calling signal is a phrase lasting for ca. 3–4 s; usually, its amplitude clearly increases toward the end (Figs 25–27). Phrase consists of similar syllables repeated with a period 270–320 ms at 34°C (Figs 25–26 and 28–29) and 370–420 ms at 24°C (Figs 27 and 30).

6. *Iassus dorsalis* Matsumura, 1912
Figs 31–37.

MATERIAL. Southern Sakhalin, environs of Sokol Town, from *Ulmus japonica* (Rehd.) Sarg., 23.VII. 2015, calling signals of 1 ♂ recorded on disk at 25°C.

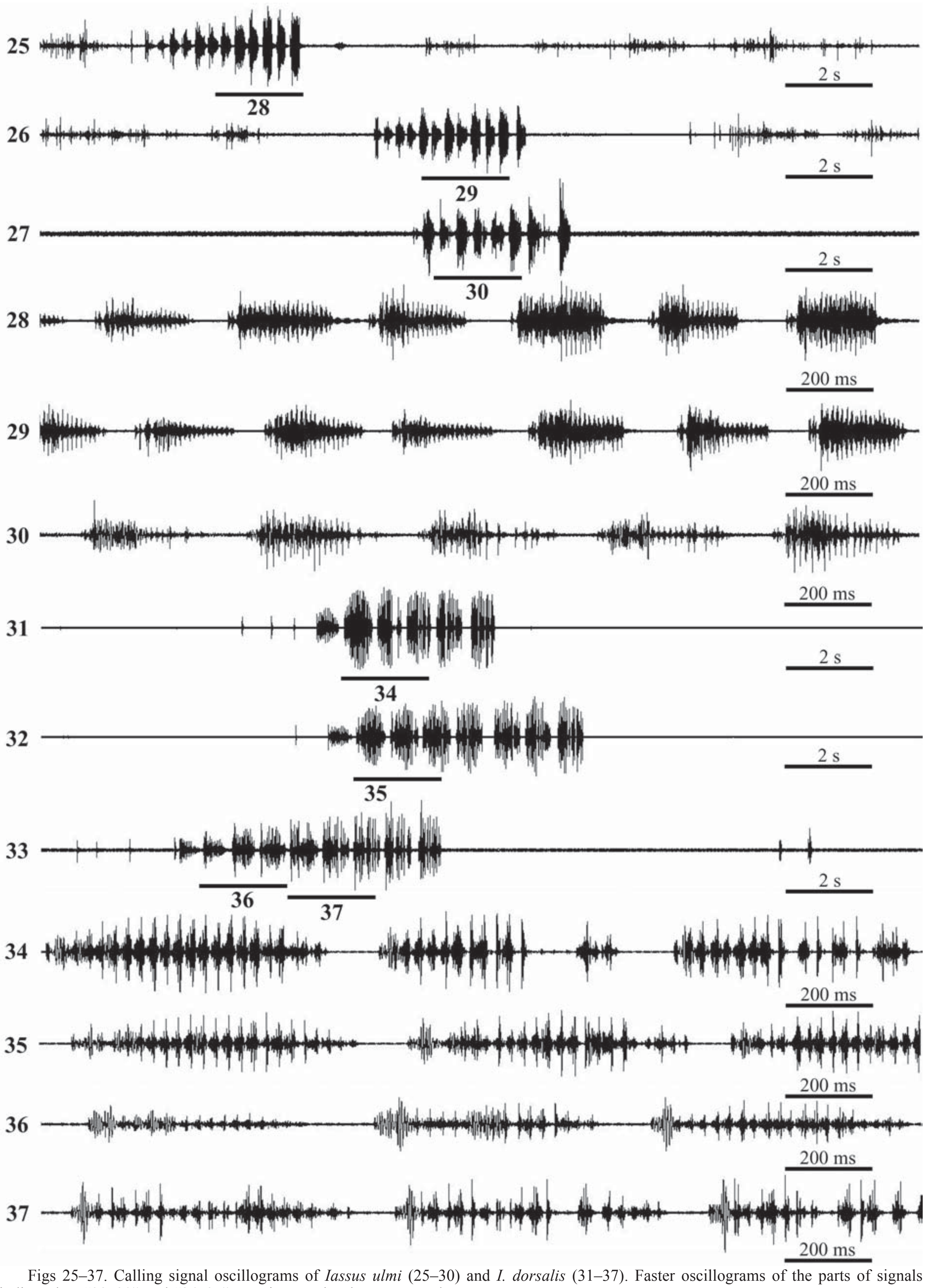
SIGNALS. In general structure, calling signal is similar to the signal of *I. ulmi* (Figs 31–33), but differs from it by longer syllables and by much greater repetition period of syllables and pulses (Figs 34–37). In particular, syllable repetition period averages 620–770 ms at 25°C.

REMARKS. This species was first described under the name *Macropsis dorsalis* Matsumura, 1912 from Japan. Anufriev [1977] described it in a rank of a subspecies, *I. ulmi nesaeus* Anufriev, 1977 from Kurile Islands because the only significant difference of this form from closely related *I. ulmi* is an absence of a denticle near the middle of ventral pygofer process. Ten years later Anufriev [1987] established a synonymy *I. matsumurai* Metcalf, 1955 = *M. dorsalis* Matsumura, 1912 non Provancher, 1899 [sic!] = *I. ulmi nesaeus* Anufriev, 1977 thus rising this form to the species rank and replacing the name given by Matsumura as a junior homonym. Actually, the name *dorsalis* introduced by Provancher was first used



Figs 10–24. Calling signal oscillograms of *Onukigallia onukii* (10–16) and *Xestocephalus guttatus* (17–24): 10–13 — males from "Kedrovaya Pad'" Nature Reserve, 14–16 — male from the environs of Barabash-Levada Village. Faster oscillograms of the parts of signals indicated as "11–13", "15–16", "18", and "21–24" are given under the same numbers.

Рис. 10–24. Осциллограммы призывных сигналов *Onukigallia onukii* (10–16) и *Xestocephalus guttatus* (17–24): 10–13 — самцы из заповедника «Кедровая Падь», 14–16 — самец из окрестностей с. Барабаш-Левада. Фрагменты сигналов, обозначенные цифрами "11–13", "15–16", "18" и "21–24", представлены на осциллограммах под такими же номерами.



Figs 25–37. Calling signal oscillograms of *Iassus ulmi* (25–30) and *I. dorsalis* (31–37). Faster oscillograms of the parts of signals indicated as "28–30" and "34–37" are given under the same numbers.

Рис. 25–37. Осциллограммы призывных сигналов *Iassus ulmi* (25–30) и *I. dorsalis* (31–37). Фрагменты сигналов, обозначенные цифрами "28–30" и "34–37", представлены на осциллограммах под такими же номерами.

in a combination *Pediopsis dorsalis* Provancher, 1890 (not 1899). Only once it was used in a combination *Macropsis dorsalis* (Provancher, 1890) by Oman [1949]; presently, this species is referred to *Oncopsis* Burmeister, 1838 [Hamilton, 1983]. Consequently, the name *Macropsis dorsalis* Matsumura, 1912 is valid and does not need replacement. It should be emphasized, that as far back as 1979 this name was used as valid by Viraktamath [1979] in a combination *Iassus dorsalis* Matsumura, 1912 in a revision of Iassinae described by S. Matsumura.

Comparison of male calling signals of *I. ulmi* and *I. dorsalis* testifies species rank of the latter form.

Subfamily Penthimiinae

7. *Penthimia scutellata* Lethierry, 1876 Figs 38–45.

MATERIAL. 1. South-west of Khabarovsk Krai, environs of Obluchye Town, from *Salix schwerinii* E. Wolf, 2.VII. 2002, calling signals of 1 ♂ recorded on tape at 30°C.

2. Primorsky Krai, Pogranichny District, environs of Barabash-Levada Village, from *Salix* spp., 17.VII.1995, calling signals of 1 ♂ recorded on tape at 24–25°C.

SIGNALS. Calling signal is a phrase lasting for 2–3 s and consisting of 4–5 syllables of the same shape (Figs 38–41). In our experiments males produced signals at irregular intervals of a few minutes. Syllables follow each other with a period of ca. 460–640 ms (Figs 42–44); syllable pattern somewhat varies even in the signals of the same male (Figs 43–44). Signals have line frequency spectra (Figs 38–39) and regular sine carrier (Fig. 45).

REMARK. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

8. *Penthimia nitida* Melichar, 1902 Figs 46–49.

MATERIAL. Primorsky Krai, ca. 33 km North-east of Chuguevka Town, environs of Zametnoe Village, 8.VII.2006, calling signals of 1 ♂ recorded on disk at 26°C.

SIGNALS. Calling signal is a syllable with abrupt leading and trailing edges (Figs 46–47). It lasts for about 0.8–1 s and consists of partially merged similar pulses (Figs 48–49). Unlike *P. scutellata*, signal of *P. nitida* has noise frequency spectrum.

Subfamily Evacanthinae

Classification of tribes and genera of Evacanthinae follows Dietrich [2004].

Tribe Evacanthini

9. *Evacanthus asiaticus* Oshanin, 1871 Figs 50–56.

MATERIAL. Kyrgyzstan, Chatkal Mtn. Range, Sary-Chelekskiy Biosphere Nature Reserve, environs of Arkyt Village, mesophyte glades in walnut forest, 22.VII.2008, calling signals of 1 ♂ recorded on disk at 22–23°C; 2.VII.2009, calling signals of 2 ♂♂ recorded on disk at 21–22°C.

SIGNALS. Calling signal is an elaborate phrase consisting of the components of two different types (Figs 50–54). Component of the first type is a group of 2–5 syllables; each syllable includes 2–4 partially merged pulses. Component of the second type is a monotonous fragment normally lasting for about 3–5 s; occasionally there are irregular amplitude modulations in it. Usually, a male produces components of two types in alternation (Figs 50 and 52). Quite often it can also produce these components one after another with very short gap so, that they form united phrase (Figs 51 and 54). More rarely, male produce single components of any type (Fig. 53).

All components of a signal have line frequency spectra and regular sine carrier (Figs 54–56).

REMARK. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

10. *Evacanthus ogumae* (Matsumura, 1911) Figs 57–62.

MATERIAL. 1. Primorsky Krai, ca. 35 km North-east of Chuguevka Town, environs of Zametnoe Village, from *Filipendula palmata* (Pallas) Maxim., 9.VII.2006, calling signals of 3 ♂♂ recorded on disk at 23–24°C.

2. Primorsky Krai, Khasan District, ca. 15 km Southwest of Slavyanka Town, environs of Ryazanovka Village, 9.VII.2012, calling signals of 2 ♂♂ recorded on disk at 23°C.

SIGNALS. Calling signal is a phrase consisting of 2–3 similar syllables (Figs 57–59). It is somewhat similar to the first component of calling signal of *E. asiaticus*, but in *E. ogumae* each syllable consists of 8–12 partially merged pulses (Figs 60–61). As in *E. asiaticus*, signal has line frequency spectrum and regular sine carrier (Figs 59 and 62).

11. *Onukia onukii* Matsumura, 1912 Figs 63–67.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, from unidentified Gramineae species under the forest canopy, 6–7.VIII.2010, calling signals of 5 ♂♂ recorded on disk at 25–26°C.

SIGNALS. Calling signal is a syllable consisting of 2–4 short pulses with noise frequency spectra and prolonged pure-tone fragment; overall duration of a syllable averages 1–1.3 s (Figs 63–67). Upper limit of a signal frequency spectrum can vary depending on physical properties of a substrate (Figs 63–64).

REMARK. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

Tribe Pagaroniini

12. *Epiacanthus stramineus* (Motschulsky, 1861) Figs 68–72.

MATERIAL. Primorsky Krai, Khasan District, environs of Andreevka Village, from *Adenocaulon himalaicum* Edgew. (Asteraceae), 6–13.VII.2006, calling signals of 7 ♂♂ recorded on disk at 27–28°C.

SIGNALS. Calling signal is a syllable lasting for 1.2–1.5 s. It consists of two parts separated by an amplitude minimum and differing from each other by the shape of vibrations (Figs 69–72) and, as a consequence, by frequency spectra (Fig. 68). The first part has regular sine carrier and line spectrum; its main frequency decreases towards the end of syllable. Vibrations in the second part are less regular; for this reason noise components appear in its spectrum.

REMARK. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

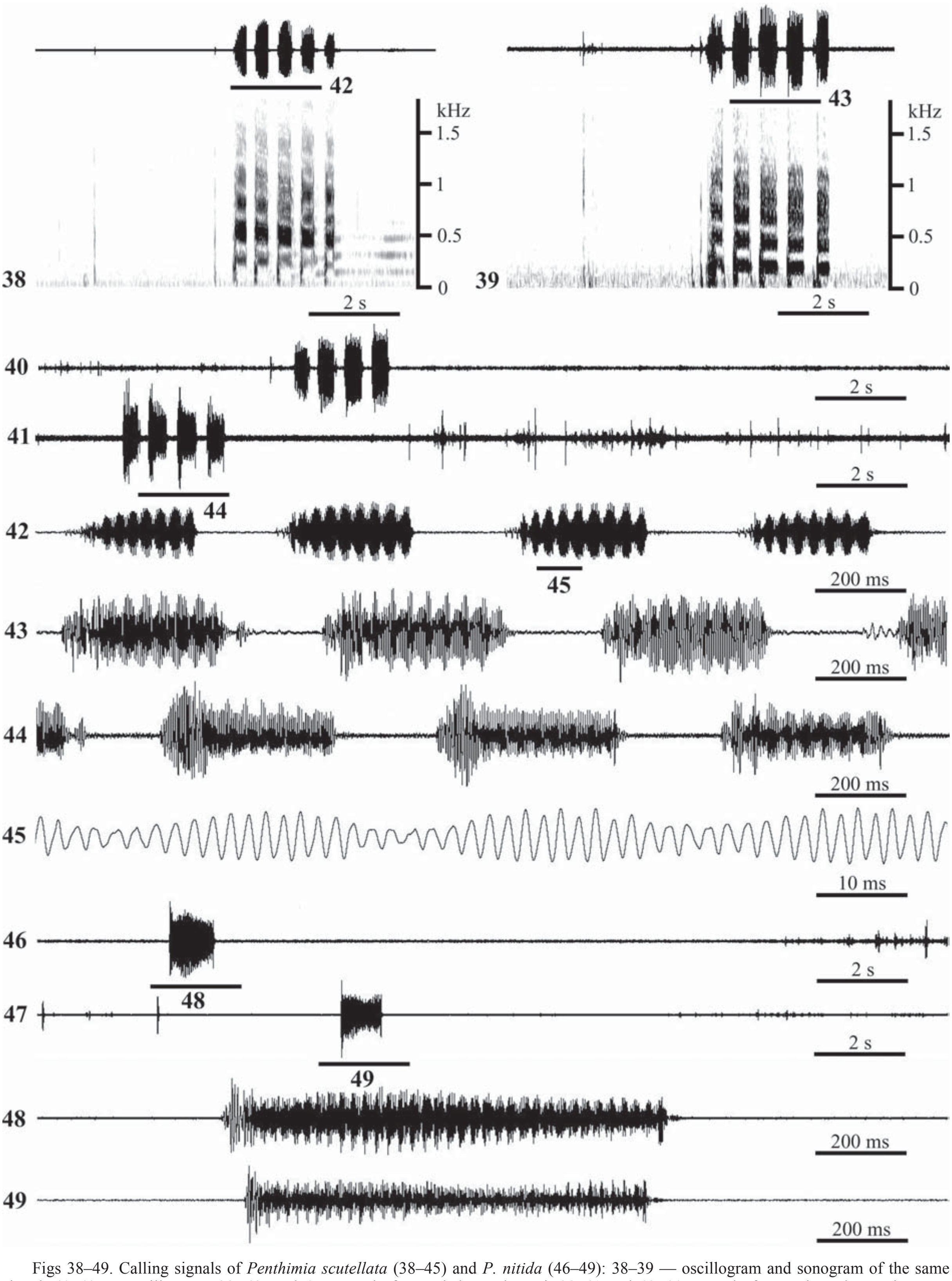
Subfamily Deltocephalinae

Classification of tribes and genera of Deltocephalinae follows Zahniser and Dietrich [2013].

Tribe Chiasmini

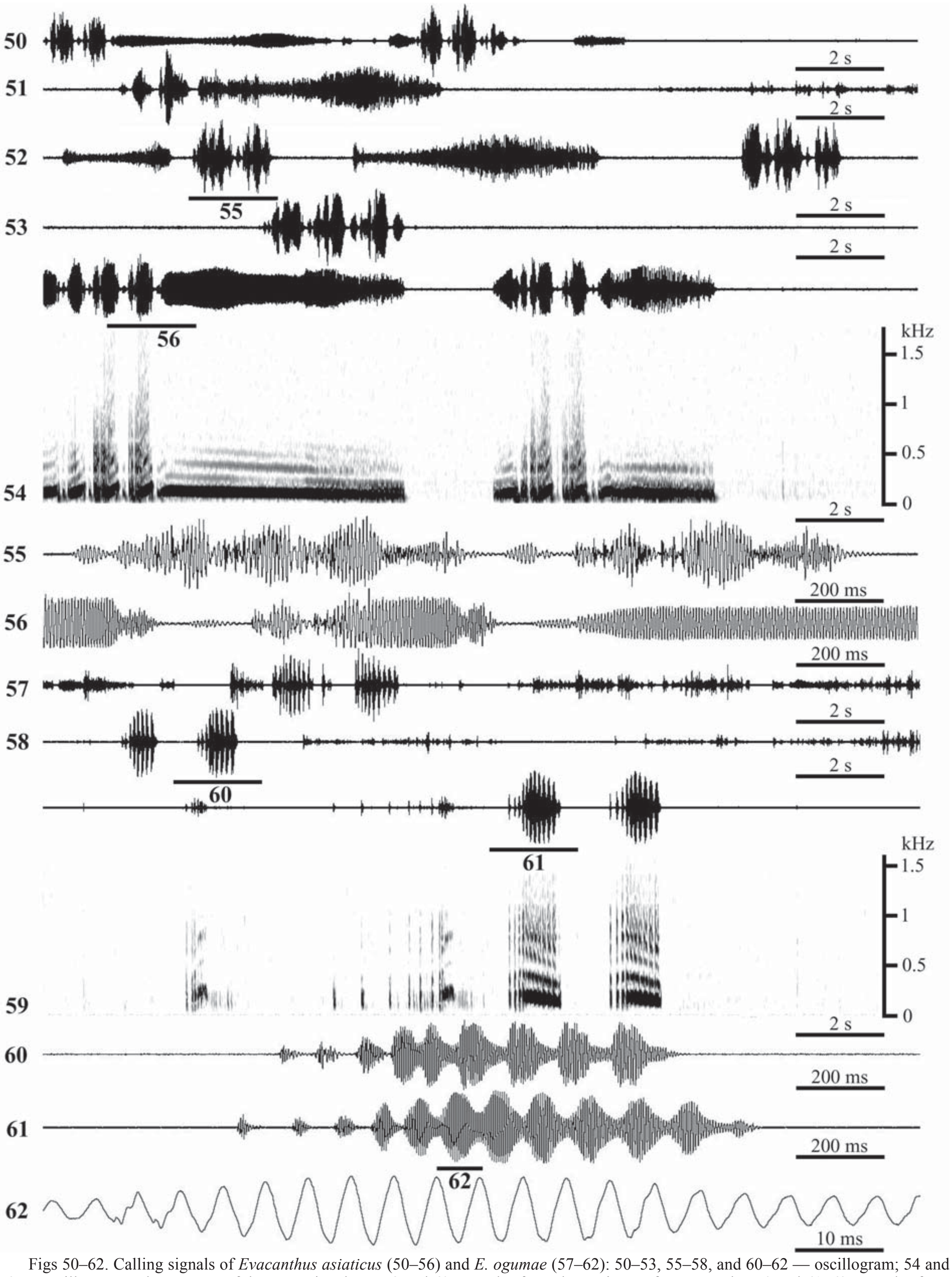
13. *Aconura volgensis* Lethierry, 1876 Figs 73–81.

MATERIAL. The Lower Volga Region, Dosang Railway Station 60 km North of Astrakhan', from *Aeluropus littoralis* (Gouan) Parl. on the bank of the Akhtuba River, 3.VII.2010, calling signals of 4 ♂♂ recorded on disk at 28–29°C.



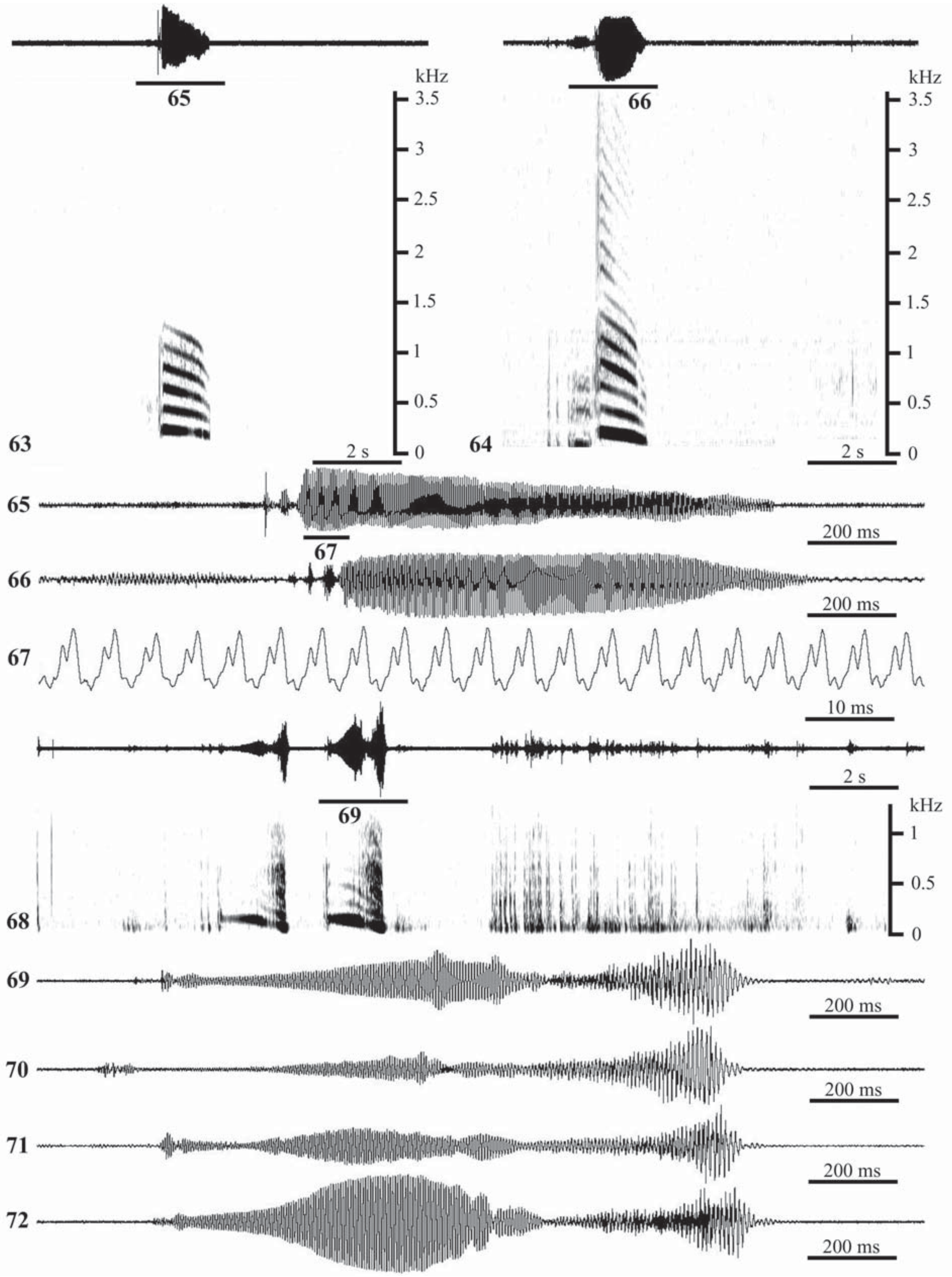
Figs 38–49. Calling signals of *Penthimia scutellata* (38–45) and *P. nitida* (46–49): 38–39 — oscillogram and sonogram of the same signal, 40–49 — oscillogram; 38, 42, and 45 — male from Khabarovsk Krai, 39–41 and 43–44 — male from Primorsky Krai. Faster oscillograms of the parts of signals indicated as “42–45” and “48–49” are given under the same numbers.

Рис. 38–49. Призывные сигналы *Penthimia scutellata* (38–45) и *P. nitida* (46–49): 38–39 — осциллограмма и сонограмма одного и того же сигнала, 40–49 — осциллограммы; 38, 42 и 45 — самец из Хабаровского Края, 39–41 и 43–44 — самец из Приморского Края. Фрагменты сигналов, обозначенные цифрами “42–45” и “48–49”, представлены на осциллограммах под такими же номерами.



Figs 50–62. Calling signals of *Evacanthus asiaticus* (50–56) and *E. ogumae* (57–62): 50–53, 55–58, and 60–62 — oscillogram; 54 and 59 — oscillogram and sonogram of the same signal; 57–58 and 60 — males from the environs of Ryazanovka; 59 and 61–62 — males from the environs of Chuguevka. Faster oscillograms of the parts of signals indicated as “55–56” and “60–62” are given under the same numbers.

Рис. 50–62. Призывные сигналы *Evacanthus asiaticus* (50–56) и *E. ogumae* (57–62): 50–53, 55–58 и 60–62 — осциллограммы; 54 и 59 — осциллограмма и сонограмма одного и того же сигнала; 57–58 и 60 — самцы из окрестностей Рязановки; 59 и 61–62 — самцы из окрестностей Чугуевки. Фрагменты сигналов, обозначенные цифрами “55–56” и “60–62”, представлены на осциллограммах под такими же номерами.



Figs 63–72. Calling signals of *Onukia onukii* (63–67) and *Epiacanthus stramineus* (68–72): 63–64 and 68 — oscillogram and sonogram of the same signal; 65–67 and 69–72 — oscillogram. Faster oscillograms of the parts of signals indicated as “65–67” and “69” are given under the same numbers.

Рис. 63–72. Призывные сигналы *Onukia onukii* (63–67) и *Epiacanthus stramineus* (68–72): 63–64 и 68 — осциллограмма и сонограмма одного и того же сигнала; 65–67 и 69–72 — осциллограммы. Фрагменты сигналов, обозначенные цифрами “65–67” и “69”, представлены на осциллограммах под такими же номерами.

SIGNALS. Calling signal consists of alternating pulse sequences and short fragments, which we quite conventionally classify as syllables; as a rule 2–3 such syllables alternate with 1–2 sequences (Fig. 73 and 75). Sometimes signal consists only of syllables following in pairs (Fig. 74 and 76) or with more or less equal intervals (Fig. 77). Each syllable includes 6–8 pulses (Figs 79–81). It should be noted however, that sometimes in these pulses distinct discrete elements are discernible; it is for this reason that their classification as pulses is somewhat arbitrary. Male can sing ceaselessly for several minutes.

14. *Aconura jakowlefi* Lethierry, 1876
Figs 82–88.

MATERIAL. The Lower Volga Region, Dosang Railway Station 60 km North of Astrakhan', from *Ae. littoralis* on the bank of the Akhtuba River in one sample with *A. volgensis*, 3.VII.2010, calling signals of 4 ♂♂ recorded on disk at 27–28°C.

SIGNALS. Calling signal consists of prolonged elaborate phrases alternating with rather short (ca. 1 s) simple low-amplitude pulse sequences, which can be classified as syllables (Figs 82–83). Each such syllable consists of short pulses repeated at a rate ca. 130–140/s (Fig. 84, first half of the oscillogram). Phrase duration averages 3–7 s. Usually, though not always the phrase begins quietly and reaches maximum intensity in 1.5–2 s (Figs 85 and 87). The main part of a phrase (first 0.6–0.8 of its duration) consists of the same pulses as in syllables described above, but their repetition rate is somewhat higher, ca. 150–170/s. Then follows a sequence of short syllables each including 3–4 pulses (Figs 86 and 88). Occasionally, in the end of a phrase male produce additional fragment consisting of high-amplitude single pulses alternating with 2–3 low-amplitude ones (Fig. 88).

REMARK. Description of calling signals of males from Sothern Turkmenistan was published earlier [Tishechkin, 2000]. In spite of the fact that two localities where insects for recording were collected are situated ca. 1500 km from each other, signals of males from the Lower Volga Region and Turkmenistan have no significant differences.

15. *Chiasmus conspurcatus* (Perris, 1857)
Figs 89–93.

MATERIAL. Kyrgyzstan, Batken Oblast, Northern Shore of the Tortkul' Reservoir 10 km South-west of Batken, from *Ae. littoralis*, *Cynodon dactylon* (L.) Pers., and unidentified Gramineae on the bank, 26.VI.2016, calling signals of 2 ♂♂ recorded on disk at 31–32°C.

SIGNALS. Calling signal is a phrase consisting of syllables repeated with a period 250–300 ms (Figs 89–90). Usually, all syllables in a phrase are similar to each other in shape and repetition period (Figs 91–93). Only occasionally certain syllables have high-amplitude leading and trailing edges and low-amplitude middle part (Fig. 89, the beginning and the end of the first phrase; Fig. 91, the last syllable).

REMARKS. Description of calling signal of one male from Southern Turkmenistan was published earlier [Tishechkin, 2000]. In its signal all syllables have high-amplitude trailing edge (sometimes also leading edge) and low-amplitude middle part. In our recordings from Kyrgyzstan such syllables present only in several signals. In other traits, including syllable repetition period, signals of males from two localities are indistinguishable in spite of the fact that a distance between these localities is ca. 1000 km.

As it was noted by Zahniser and Dietrich [2013], the species identity of *Chiasmus* specimens is difficult to determine; here we follow tradition and refer our specimens to *Ch. conspurcatus*. Comparative investigation of morphology and calling signals of males from different regions is necessary to elucidate a situation; at present, we can only state that our materials from Turkmenistan and Kyrgyzstan belong to the same species.

16. *Exitianus nanus* (Distant, 1908)
Figs 94–103.

MATERIAL. 1. Kyrgyzstan, Turkestan Mtn. Range, environs of Katran Village, the Layli-Mazar River 2–3 km upstream from the source of the Lyaylyak River, steppe on the mountain slope, 24.VI.2016, calling signals of 2 ♂♂ recorded on disk at 25°C.

2. Kyrgyzstan, Northern Shore of the Tortkul' Reservoir 10 km South-west of Batken, from *Ae. littoralis*, *C. dactylon*, and unidentified Gramineae on the bank, in one biotope with *Ch. conspurcatus*, 27.VI.2016, calling signals of 2 ♂♂ recorded on disk at 30°C.

SIGNALS. Calling signal is a phrase lasting for 15–30 s; it begins quietly and reaches maximum intensity in ca. 4–10 s (Figs 94–97 and 102). Usually, phrase consists of simple short similar syllables repeated with a period of ca. 280–340 at 25°C and 250–280 at 30°C (Figs 99–101 and 103). Sometimes, syllables in the beginning of a phrase have more complex pattern and gradually transit into more simple syllables typical for the middle and end parts of a phrase (Figs 98–99).

REMARK. On the shore of the Tortkul' Reservoir (locality No. 2) this species was found in strict sympatry with *Ch. conspurcatus*. General pattern of a phrase in these two species is different, but syllable repetition periods completely overlap (200–300 ms at 31–32°C in *Ch. conspurcatus* and 250–280 at 30°C in *E. nanus*).

Tribe Deltocephalini

17. *Recilia coronifer* (Marshall, 1866)
Figs 104–105.

MATERIAL. Primorsky Krai, Khasan District, environs of Andreevka Village, 15.VII.2006, calling signals of 1 ♂ recorded on disk at 32–33°C.

SIGNALS. Calling signal is a phrase consisting of syllables with elaborate temporal pattern (Figs 104–105). The shape of syllables on oscillograms somewhat changes from the beginning towards the end of a phrase.

18. *Maiestas latifrons* (Matsumura, 1902)
Figs 106–113.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 6.VIII.2010, calling signals of 3 ♂♂ recorded on disk at 24–25°C.

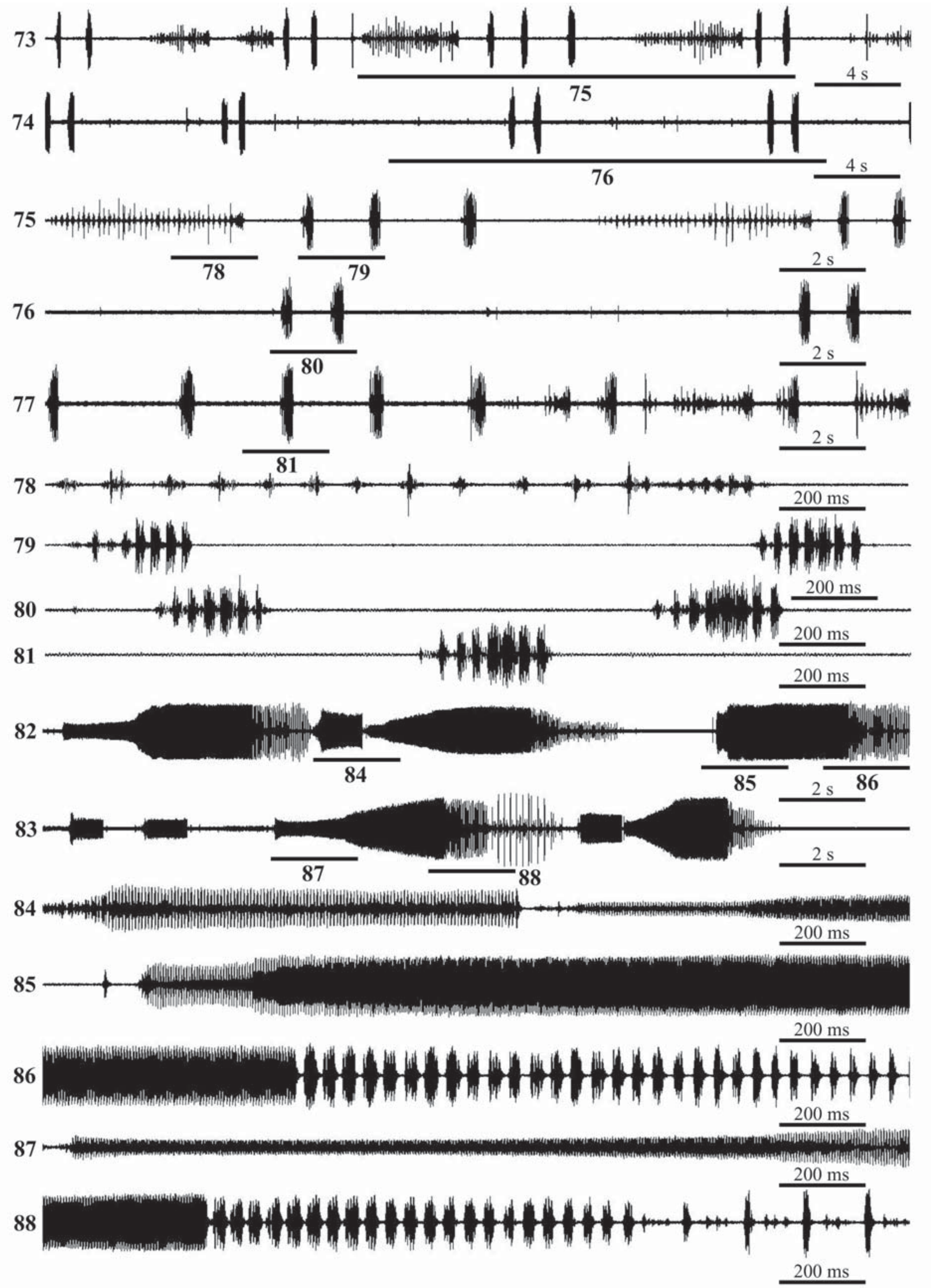
SIGNALS. Calling signal is a phrase lasting ca. from 4 to 33 s in our recordings (Figs 106–109). It consists of short syllables repeated with a period of 0.5–0.7 s. The shape of syllables gradually changes towards the end of a phrase due to reduction of short pulses at the end of a syllable; initial syllables in a phrase include three such pulses and last syllables include only one pulse or none (Figs 110–111 and 112–113).

REMARK. Identification of species is based on Zhang and Duan [2011].

19. *Maiestas oryzae* (Matsumura, 1902)
Figs 114–118.

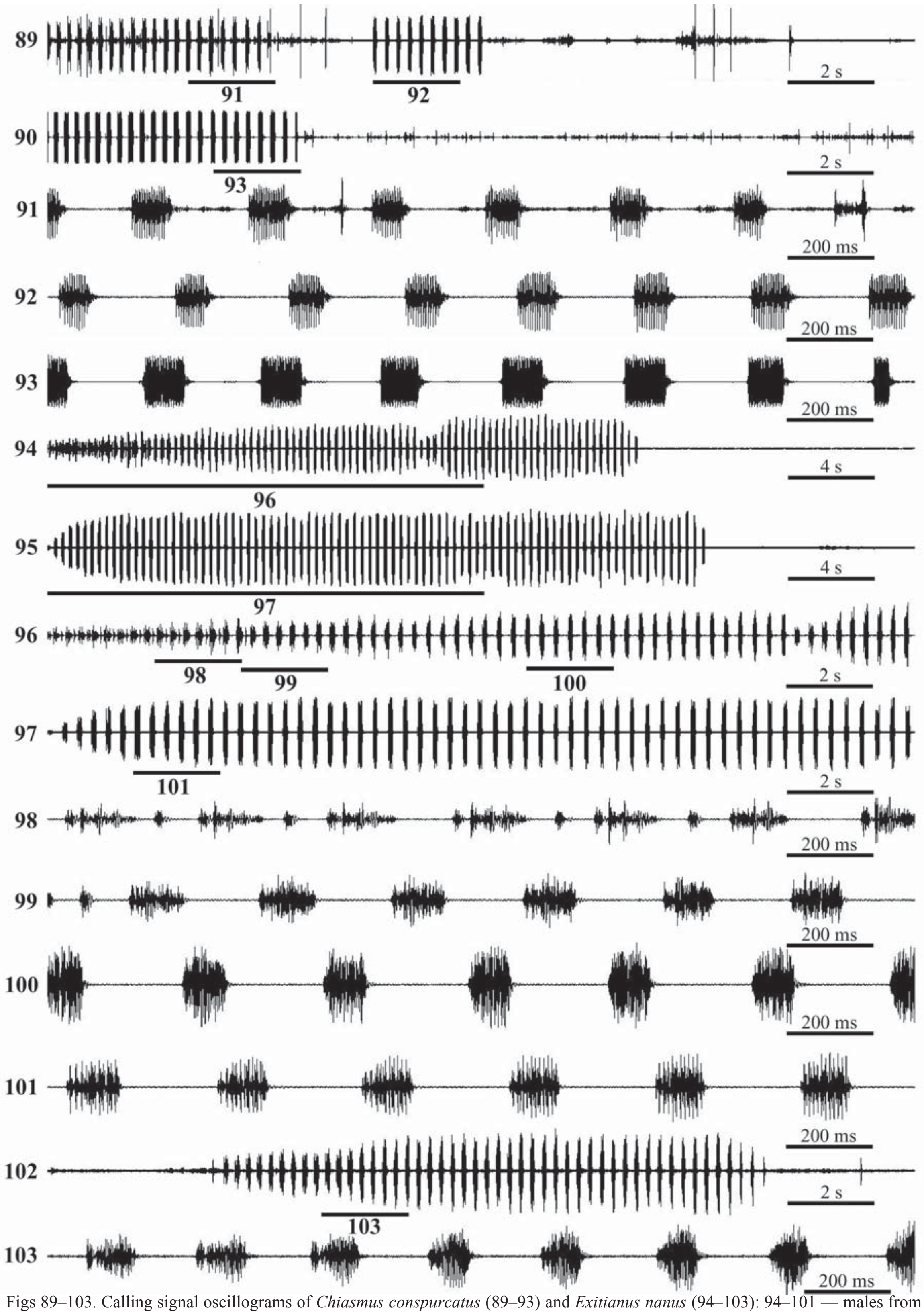
MATERIAL. South-west of Khabarovsk Krai, environs of Obluchye Town, meadow on the slope of the hill, 5.VII.2012, calling signals of 1 ♂ recorded on disk at 24°C.

SIGNALS. Calling signal is similar to this of *M. latifrons*, but syllables have not additional short pulses at the end and follow with distinctly shorter period, ca. 0.3–0.5 s (Figs 114–118).



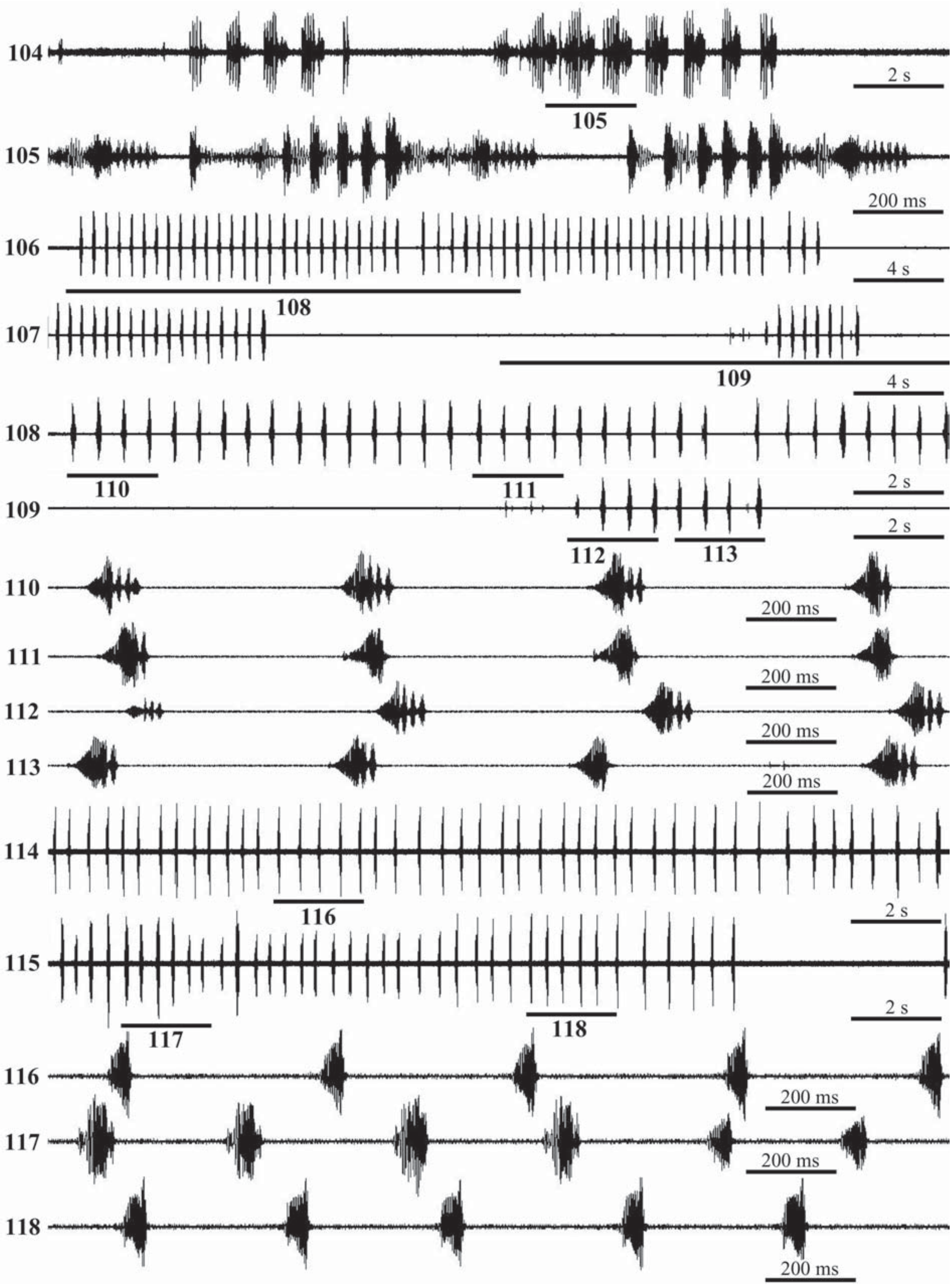
Figs 73–88. Calling signal oscillograms of *Aconura volgensis* (73–81) and *A. jakowlefi* (82–88). Faster oscillograms of the parts of signals indicated as “75–76”, “78–81”, and “84–88” are given under the same numbers.

Рис. 73–88. Осциллограммы призывных сигналов *Aconura volgensis* (73–81) и *A. jakowlefi* (82–88). Фрагменты сигналов, обозначенные цифрами “75–76”, “78–81” и “84–88”, представлены на осциллограммах под такими же номерами.



Figs 89–103. Calling signal oscillograms of *Chiasmus conspurcatus* (89–93) and *Exitianus nanus* (94–103): 94–101 — males from the Layli-Mazar River Valley, 102–103 — male from the Tortkul' Reservoir. Faster oscillograms of the parts of signals indicated as "91–93", "96–101", and "103" are given under the same numbers.

Рис. 89–103. Осциллограммы призывных сигналов *Chiasmus conspurcatus* (89–93) и *Exitianus nanus* (94–103): 94–101 — самцы из долины р. Лайли-Мазар, 102–103 — самцы с Торткульского водохранилища. Фрагменты сигналов, обозначенные цифрами "91–93", "96–101" и "103", представлены на осциллограммах под такими же номерами.



Figs 104–118. Calling signal oscillograms of *Recilia coronifer* (104–105), *Maiestas latifrons* (106–113), and *M. oryzae* (114–118): Faster oscillograms of the parts of signals indicated as "105", "108–113", and "116–118" are given under the same numbers.

Рис. 104–118. Осциллограммы призывных сигналов *Recilia coronifer* (104–105), *Maiestas latifrons* (106–113) и *M. oryzae* (114–118): фрагменты сигналов, обозначенные цифрами "105", "108–113" и "116–118", представлены на осциллограммах под такими же номерами.

REMARKS. Identification of species is based on Zhang and Duan [2011].

Vilbaste [1968] reported *M. oryzae* from Primorsky Krai, but he did not give the drawings of male genitalia of the specimens studied. His record was cited by Anufriev [1978], but *M. oryzae* was not included in the keys to Auchenorrhyncha of the Russian Far East [Anufriev, Emelyanov, 1988]. This is a first record of *M. oryzae* from Khabarovsk Krai; also, in 2012 we found it in Amur Oblast ca. 15 km North-east of Blagoveshchensk.

Tribe Hecalini

20. *Hecalus lineatus* (Horvath, 1899) Figs 119–127.

MATERIAL. Primorsky Krai, Khasan District, environs of Primorsky Village, meadows on the seashore, 13–14.VIII.2010, calling signals of 5 ♂♂ recorded on disk at 25–26°C.

SIGNALS. Calling signal is an elaborate and variable phrase lasting for ca. 10–20 s (Figs 119–122). It begins with a sequence of syllables following each other without gaps (Fig. 123); then several syllables separated by gaps of various durations follow (Figs 124–126). Some syllables consist of a monotonous fragment and 12–14 pulses (Figs 124–125), but in other syllables monotonous fragment is absent (Fig. 126, first syllable). Some fragments in the first (continuous) part of a phrase, and discrete syllables forming the second part have regular sine carrier and line frequency spectra (Figs 122 and 127).

REMARK. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

Tribe Eupelicini

21. *Paradorydium paradoxum* (Herrich-Schäffer, 1837) Figs 128–141.

MATERIAL. 1. Kyrgyzstan, Northern Shore of the Tortkul' Reservoir 10 km South-west of Batken, from *Ae. littoralis* and unidentified Gramineae on the bank, 27.VI.2016, calling signals of 2 ♂♂ and courtship signal of 1 ♂ recorded on disk at 30°C.

2. Kyrgyzstan, ca. 10 km North of Tash-Kumyr Town, from *Botriochloa ischaemum* (L.) Keng, 2.VII.2016, calling signals of 1 ♂ recorded on disk at 34°C.

SIGNALS. In the male from Tash-Kumyr (locality No. 2), signal consists of regularly repeated complex phrases; each phrase lasts for ca. 20 s and includs two different parts (Figs 128–131). In our experiment male produced such signals unceasingly for about 10 minutes. Less active males from the shore of the Tortkul' Reservoir (locality No. 1) produced single shorter phrases with simpler pattern (Figs 132–137). Duration of such phrase does not exceed 7–8 s, it lacks the first (low-amplitude) part, and in its end syllables have simpler pattern due to the absence of a sequence of short pulses at the beginning. Also, in the male from Tash-Kumyr these pulses are grouped in pairs, whereas in the males from the shore of the Tortkul' Reservoir they follow each other with equal intervals (Figs 131 and 135, respectively).

In one male from the shore of the Tortkul' Reservoir courtship signal was also recorded (Figs 138–141). It has very variable pattern and consists of syllables of different duration and shape. Male produced courtship signal for some time, then quickly moved to another place, stopped, produced a fragment of signal again, etc. Eventually it found receptive female, mounted it and started copulation. Since the male moved along the cage in search of the female and produced courtship signal continuously, its song and noises resulting from movements drowned out female reply signals.

In spite of the fact that signals of males from two localities are quite different in general appearance, on the oscillograms at high speed it is visible that they include similar elements. Full syllables from the second part of a phrase have similar temporal pattern (Figs 131 and 137). Courtship signal of the male from the shore of the Tortkul' Reservoir includes syllables similar to these in the first part of calling signal of male from Tash-Kumyr (Figs 130 and 141, first halves of oscillograms). This proves that all males whose signals were recorded are conspecific. Also, we failed to find any differences between them in the shape of genitalia.

REMARK. The species studied was repeatedly recorded from Eastern Europe and Central Asia under the name *P. lanceolatum* (Burmeister, 1839) [Dubovskiy, 1966; Mityaev, 1971, etc.]. D'Urso [1992] showed in her work that a valid name of this species is *P. paradoxum*.

Tribe Opsiini

Subtribe Achaeticina

22. *Achaetica anabasidis* Emelyanov, 1959 Figs 142–148.

MATERIAL. The Lower Volga Region, Dosang Railway Station 60 km North of Astrakhan', *Anabasis aphylla* L. in the desert, 30.VI.2010, calling signals of 1 ♂ recorded on disk at 28°C.

SIGNALS. Calling signal is a phrase lasting for 4–7 s and consisting of similar short syllables with abrupt leading and trailing edges (Figs 142–148). Syllables repeat with a period about 80–100 ms.

Subtribe Opsiina

23. *Hishimonus bucephalus* Emelyanov, 1969 Figs 149–154.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 14.VIII.2010, calling signals of 3 ♂♂ recorded on disk at 27°C.

SIGNALS. Calling signal is a phrase lasting from 5 to 11 s in our recordings (Figs 149–151). Syllables have more smooth edges than in *A. anabasidis* and repeat with a period of 110–140 ms (Figs 152–154).

REMARK. Insects were collected at light; they eagerly fed upon *Ulmus* sp. and produced calling signals on it in the laboratory.

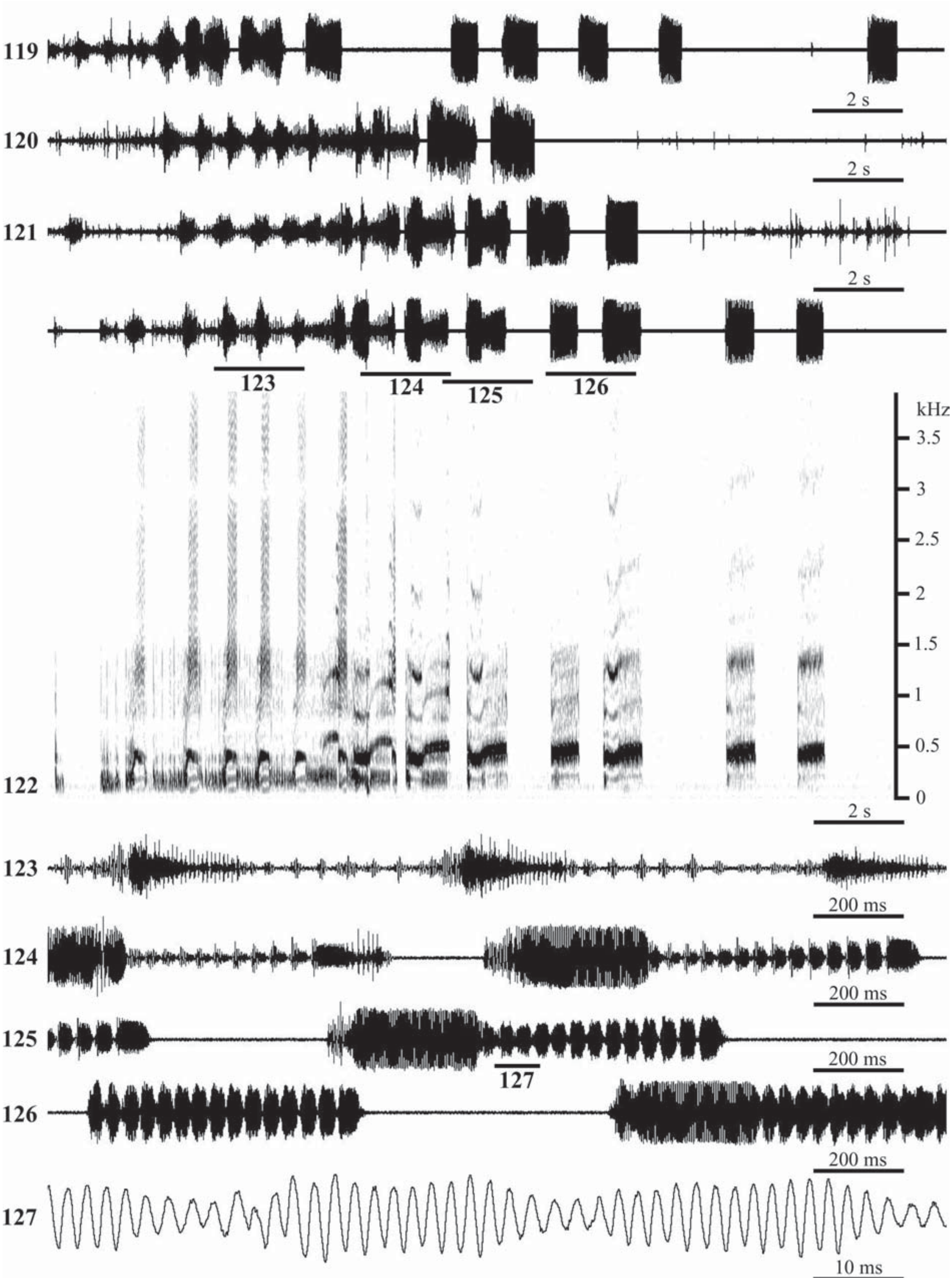
Tribe Scaphoideini

24. *Phlogotettix cyclops* (Mulsant et Rey, 1855) Figs 155–161.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 7 and 20.VIII.2010, calling signals of 3 ♂♂ recorded on disk at 25–26°C.

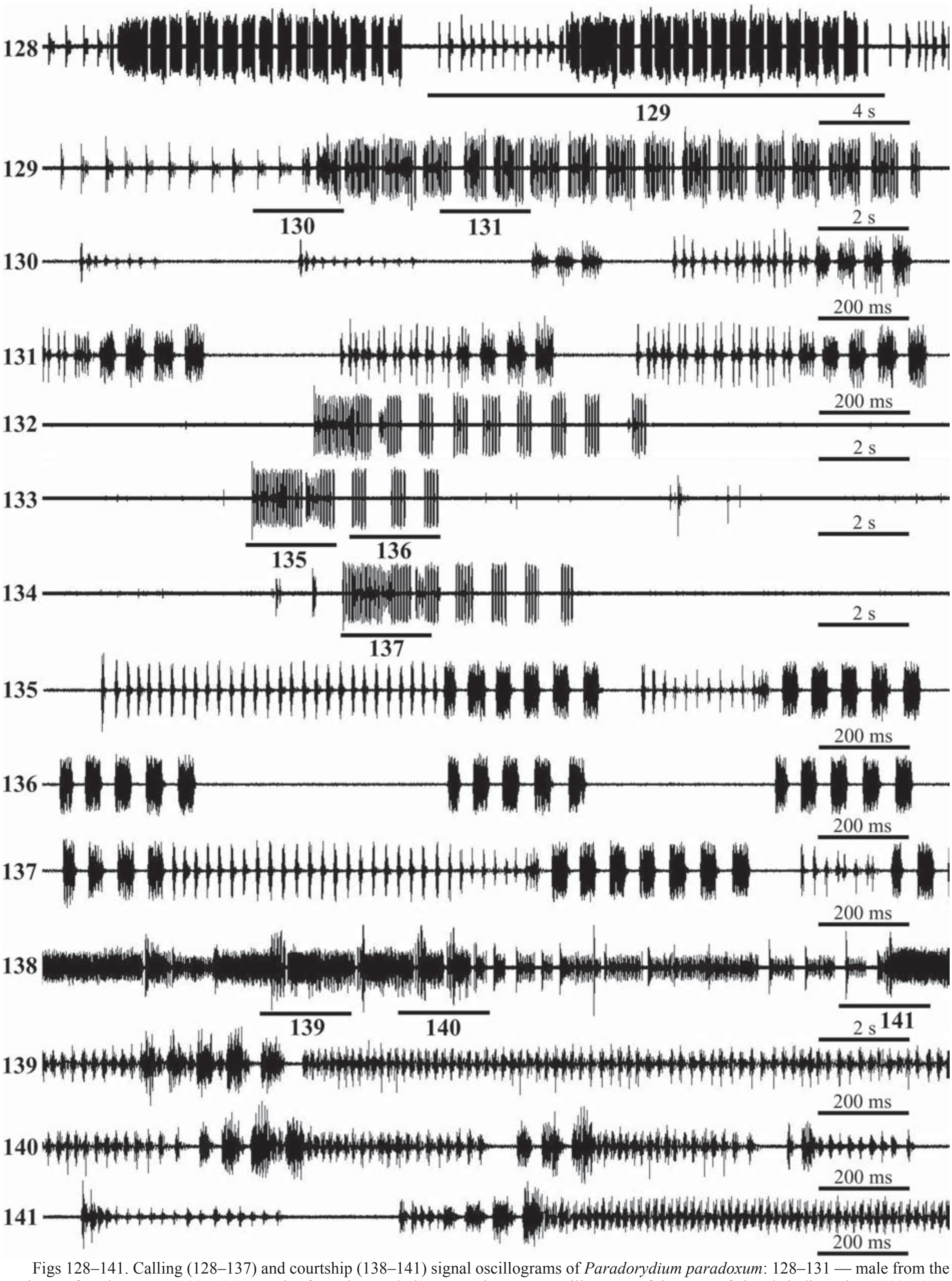
SIGNALS. Calling signal consists of syllables (perhaps it would be more correct to classify them as phrases). Syllables follow each other with a period of 4–7 s in our recordings (Figs 155–157). Each syllable consists of a sequence of low-amplitude pulses followed by high-amplitude part with regular sine carrier and line frequency spectrum (Figs 158–161). Duration of a sequence of low-amplitude pulses varies several-fold (Figs 158–159). High-amplitude pure-tone final part has more constant pattern; the number of discrete pulses at its beginning varies from two to four.

REMARK. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].



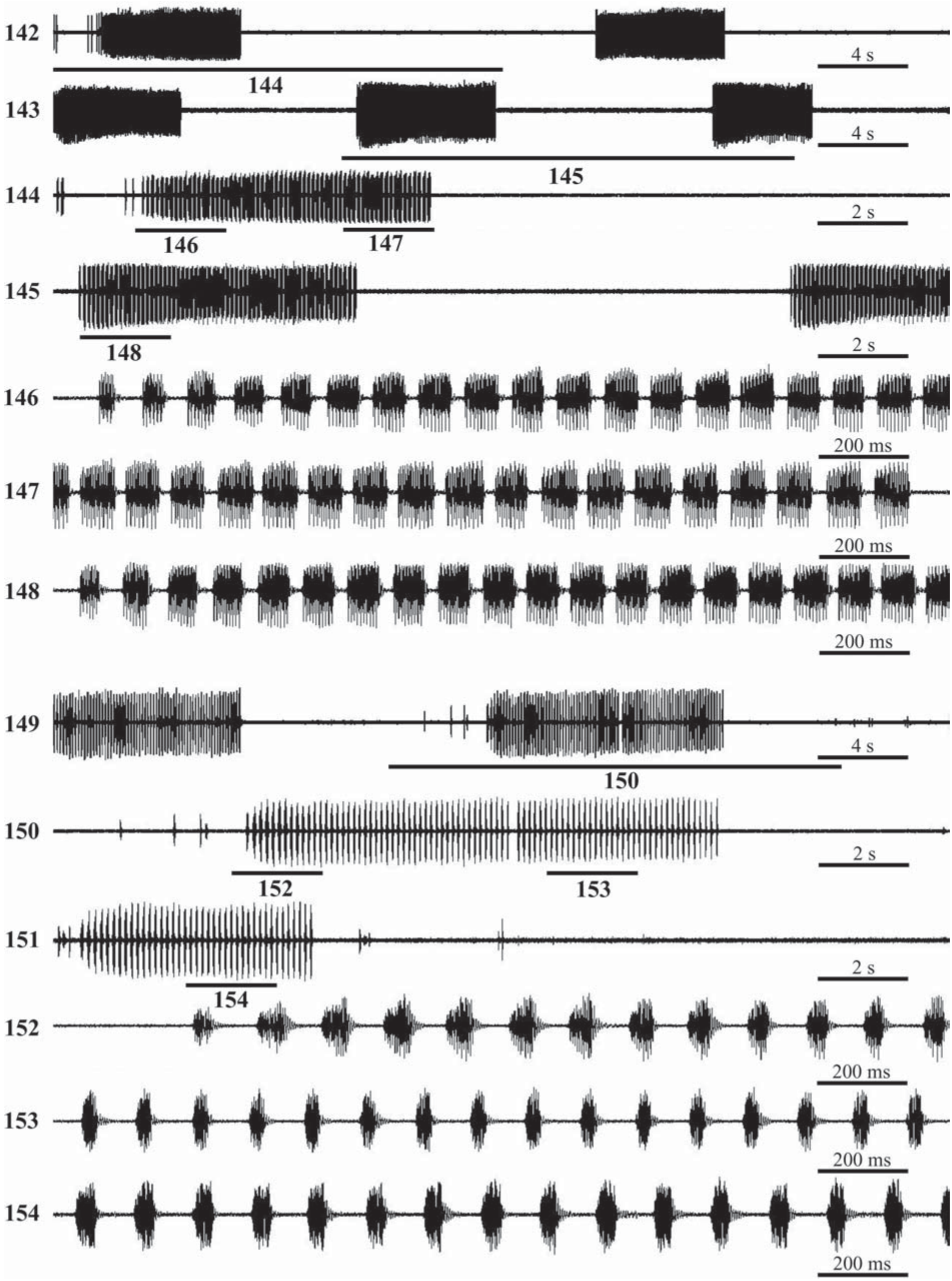
Figs 119–127. Calling signals of *Hecalus lineatus*: 119–121 and 123–127 — oscillogram, 122 — oscillogram and sonogram of the same signal. Faster oscillograms of the parts of signals indicated as "123–127" are given under the same numbers.

Рис. 119–127. Призывные сигналы *Hecalus lineatus*: 119–121 и 123–127 — осциллограммы, 122 — осциллограмма и сонограмма одного и того же сигнала. Фрагменты сигналов, обозначенные цифрами "123–127", представлены на осциллограммах под такими же номерами.



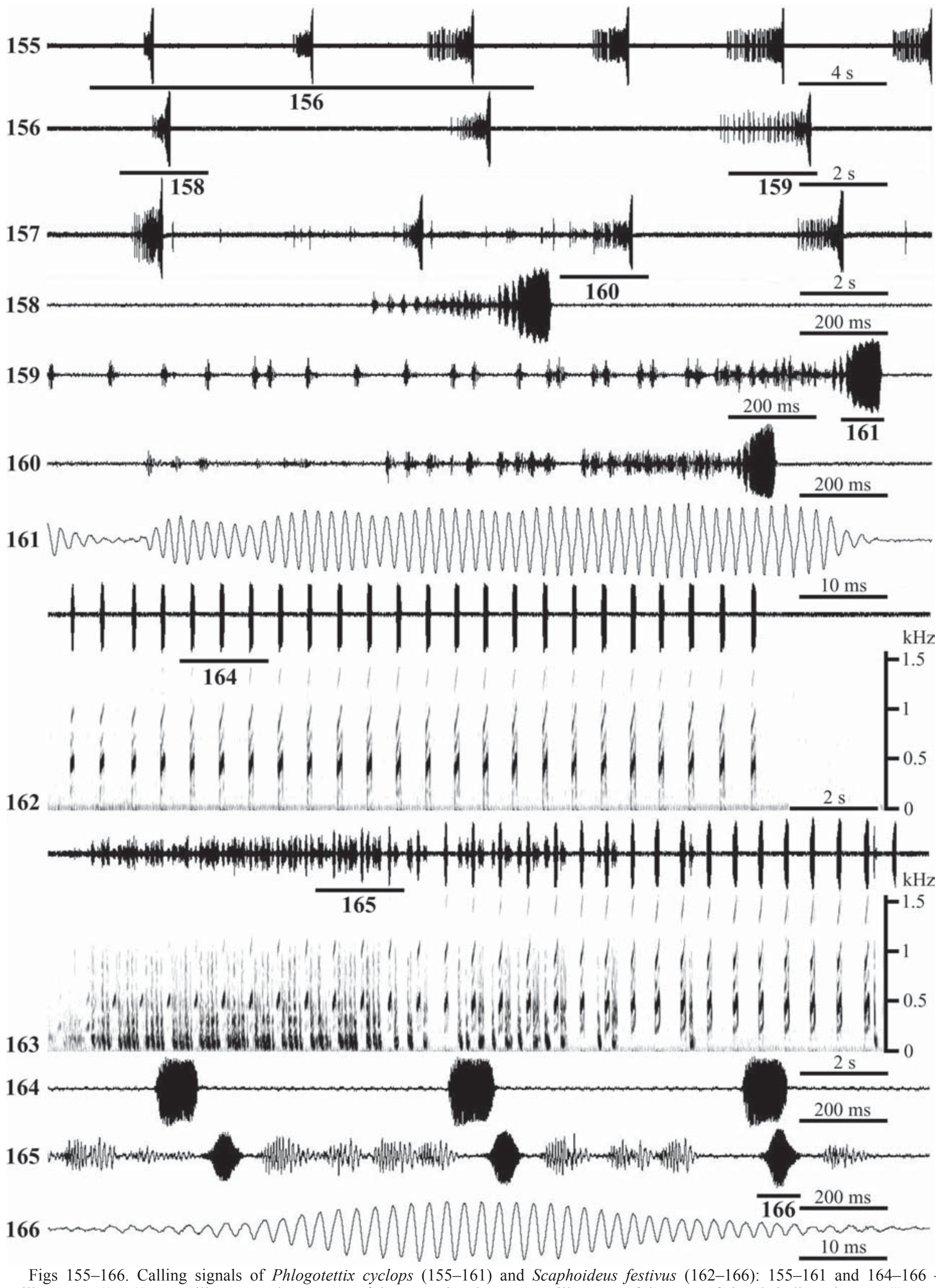
Figs 128–141. Calling (128–137) and courtship (138–141) signal oscillograms of *Paradorydium paradoxum*: 128–131 — male from the environs of Tash-Kumyr, 132–141 — males from the Tortkul' Reservoir. Faster oscillograms of the parts of signals indicated as "129–131", "135–137", and "139–141" are given under the same numbers.

Рис. 128–141. Осциллограммы призывных сигналов (128–137) и сигналов ухаживания (138–141) *Paradorydium paradoxum*: 128–131 — самец из окрестностей Таш-Кумыра, 132–141 — самцы с Торткульского водохранилища. Фрагменты сигналов, обозначенные цифрами "129–131", "135–137" и "139–141", представлены на осциллограммах под такими же номерами.



Figs 142–154. Calling signal oscillograms of *Achaetica anabasidis* (142–148) and *Hishimonus bucephalus* (149–154). Faster oscillograms of the parts of signals indicated as "144–148", "150", and "152–154" are given under the same numbers.

Рис. 142–154. Осциллограммы призывных сигналов *Achaetica anabasidis* (142–148) и *Hishimonus bucephalus* (149–154). Фрагменты сигналов, обозначенные цифрами "144–148", "150" и "152–154", представлены на осциллограммах под такими же номерами.



Figs 155–166. Calling signals of *Phlogotettix cyclops* (155–161) and *Scaphoideus festivus* (162–166): 155–161 and 164–166 — oscillogram, 162–163 — oscillogram and sonogram of the same signal. Faster oscillograms of the parts of signals indicated as “156”, “158–161”, and “164–166” are given under the same numbers.

Рис. 155–166. Призывные сигналы *Phlogotettix cyclops* (155–161) и *Scaphoideus festivus* (162–166): 155–161 и 164–166 — осциллограммы, 162–163 — осциллограмма и сонограмма одного и того же сигнала. Фрагменты сигналов, обозначенные цифрами “156”, “158–161” и “164–166”, представлены на осциллограммах под такими же номерами.

25. *Scaphoideus festivus* Matsumura, 1902 Figs 162–166.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 10 and 20.VIII.2010, calling signals of 4 ♂♂ recorded on disk at 25–26 and 27–28°C.

SIGNALS. In the simplest case, calling signal is a sequence of pure-tone pulses repeated with a period 0.6–0.7 s (Figs 162, 164). In more elaborate variant of a signal, pure-tone pulses alternate with 1–4 noise ones (Figs 163, 165–166). The number of noise pulses reduces towards the end of a signal; usually, in the last one-third of a phrase they are totally absent (Fig. 163). Duration of signal averages 15–20 s.

REMARKS. Brief description of calling signal of this species was published in Tishechkin and Burlak [2013].

S. festivus differs from all other Far-Eastern species of *Scaphoideus* by connective processes widened in distal parts in the shape of a knife blade. The shape of connective processes of males whose signals were recorded is exactly the same as in drawings of *S. festivus* in Anufriev and Emelyanov [1988], Kamitani and Hayashi [2013], and Wen et al. [2017]. In external appearance specimens studied are quite similar to *S. festivus* on the photo in Wen et al. [2017: fig. 3, D, I, N]. However, they distinctly differ from *S. festivus* on the photo in Kamitani and Hayashi [2013: fig. 5], but surprisingly, are similar to *S. aurantius* Kamitani et Hayashi, 2013 [Kamitani, Hayashi, 2013: fig. 7]. Either the photos on figs 5 and 7 in Kamitani and Hayashi [2013] were changed places by mistake, or under the name *S. festivus* more than one species exist.

Comprehensive study of vibrational signals and mating behavior in *Scaphoideus titanus* Ball, 1932 was performed by Mazzoni et al. [2009]. In general, male calling signal of this species is similar to this of *S. festivus*, but differs from it in pulse repetition period.

Tribe Vartini

26. *Varta japonica* Viraktamath, 2004 Figs 167–175.

MATERIAL. Primorsky Krai, Khasan District, "Kedrovaya Pad'" ("Cedar Valley") Nature Reserve, environs of Primorsky Village, 22.VIII.2010, calling signals of 1 ♂ recorded on disk at 25°C.

SIGNALS. Calling signal consists of 2–4 pure-tone syllables following each other with a period of 1.8–2.2 s (Figs 167–169). The shape of syllables varies considerably between the signals of the same male (Figs 170–172), but the shape of waves in a syllable is rather constant (Figs 173–175).

REMARKS. Brief description of calling signal of this species (as *Stymphalus rubrostriatus* (Horváth, 1907)) was published in Tishechkin and Burlak [2013].

S. rubrostriatus was the only species of Vartini recorded from the Russian Far East. Its misidentification resulted from absence of males in the material from this region; the drawings of male genitalia in Anufriev [1978] and Anufriev and Emelyanov [1988] were made from specimen from Western Turkmenistan [Anufriev, 1978: 190, figure captions]. Present identification of the species is based on Viraktamath [2004]. This is a first record of this species from the Russian Far East; apparently, all records of *S. rubrostriatus* from this territory refer to *V. japonica*.

Discussion

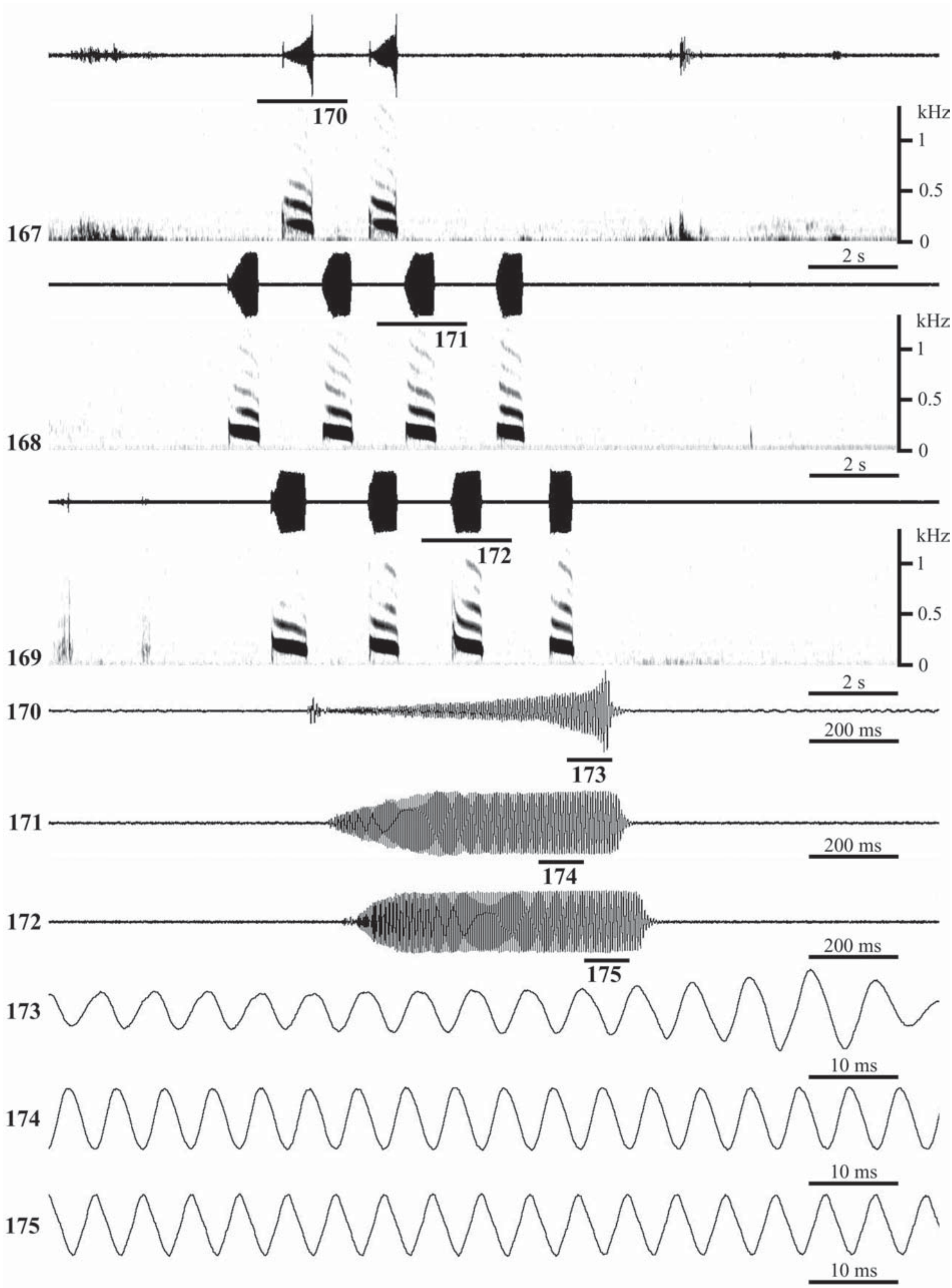
In many insect taxa, the male produces acoustic calling signals for attracting a conspecific female. Presently, it is common knowledge that, in such taxa, differences in calling signal patterns facilitate precopulatory reproductive isolation between closely related species. For this reason acoustic analysis in taxonomy is a useful tool for recognition of biological species similar in morphological traits.

Presently, in many poorly studied taxa of leafhoppers the primary task is the accumulation of signal recordings from different localities for comparative analysis, investigation of variability of signal pattern, and elucidation of status of dubious forms. The present article makes some contribution to the solution of taxonomic problems. Calling signal analysis confirmed species rank of *Iassus dorsalis*. Also, it was demonstrated that specimens of *Chiasmus conspurcatus* from Turkmenistan and Kyrgyzstan belong to the same species; its conspecificity with populations from Southern Europe still to be verified.

New examples of similarity of signal temporal pattern in sympatric species were revealed. For instance, calling signals of *Ledra auditura* and *Varta japonica* are quite similar in frequency spectra and temporal pattern (Figs 6–9 and 167–175). Both species were collected in the same locality, Primorsky Krai, Khasan District, "Kedrovaya Pad'" Nature Reserve, but they inhabit different biotopes. *L. auditura* lives on broadleaf trees, whereas *V. japonica* feeds upon Gramineae (mainly, on *Miscanthus* spp.) and was found only on high-grass meadows and glades. As a result, these two species never enter into acoustic contact, so signal similarity does not affect successful communication.

The above case shows that if two acoustically isolated forms do not differ in their signal pattern, they can still exist as biological species, since they do nor perceive each others signals; at present this regularity is well-known [e.g., Tishechkin, 2013]. Reproductive isolation in this case is provided by other mechanisms such as allopatry, differences in ecological preferences, seasonal or daily activity, etc. Thus, bioacoustic analysis may fail to produce a definite result when applied to allopatric forms. The Far-Eastern *Ledra auditura* and European *L. aurita* can be mentioned as an example. Both species dwell in broadleaf forests; evidently, their allopatry is a result of so-called nemoral disjunction i.e. division of broadleaf forest zone into two widely separated parts in temperate areas of Europe and East Asia during the Pleistocene glaciations. In morphological traits they are so similar that Anufriev [1978] assumed that they may belong to a single species with disjunctive range. Recordings of signals of *L. auditura* are currently available; as can be judged from verbal description of Ossiannilsson [1949], signals of *L. aurita* have similar pattern. However, recording of signals of *L. aurita* for comparison will not solve the problem of taxonomic status of these forms, since they are allopatric.

Each species producing acoustic signals occupies a certain communication channel, or the so-called acoustic niche. Segregation of acoustic niches is always observed in communities of species involved in acoustic contact. It is carried out through differences in



Figs 167–175. Calling signals of *Varta japonica*: 167–169 — oscillogram and sonogram of the same signal, 170–175 — oscillogram. Faster oscillograms of the parts of signals indicated as "170–175" are given under the same numbers.

Рис. 167–175. Призывные сигналы *Varta japonica*: 167–169 — осциллограмма и сонограмма одного и того же сигнала, 170–175 — осциллограммы. Фрагменты сигналов, обозначенные цифрами "170–175", представлены на осциллограммах под такими же номерами.

signal parameters such as general scheme of temporal pattern or, in the case temporal pattern is similar, the repetition period of signal rhythmical elements (pulses or syllables). Two strictly sympatric species of *Aconura* Lethierry, 1876, *A. volgensis* and *A. jakowlefi* provide an example of differences in general schemes of signal temporal patterns (Figs 73–81 and 82–88). These two species have identical ecological preferences and often can be found in the same biotope on the same host and their signals have nothing in common with each other. Examples of differences of similar signals in quantitative parameters were described earlier in Gomphocerinae (Orthoptera: Acrididae) [Tishechkin, Bukhvalova, 2010], *Aphrophora* Germar, 1821 (Homoptera: Aphrophoridae) [Tishechkin, 2011a], and *Doratura* J.Sahlberg, 1871 (Homoptera: Cicadellidae) [Tishechkin, 2011b].

Chiasmus conspurcatus and *Exitianus nanus* represent unusual and interesting case of acoustic niche segregation. These species were strictly sympatric on Gramineae, mainly *Aeluropus littoralis* and *Cynodon dactylon* on the saline meadow on the shore of the Tortkul' Reservoir 10 km South-west of Batken, Kyrgyzstan. Their calling signals differ in duration (2.5–7 s in *Ch. conspurcatus vs.* 15–30 s in *E. nanus*; Figs 89–90 and 94–97, 102); unlike *Ch. conspurcatus*, calling signal of *E. nanus* begins quietly and gradually reaches maximum intensity (Figs 94–97 and 102). In addition, initial syllables in a signal of *E. nanus* sometimes have more complex pattern, than syllables in the middle and in the end of a phrase (Figs 96 and 98). Still, the shape and repetition period of syllables in the middle of signals of these species are almost identical (Figs 91–93 and 100–101, 103).

Male calling signals are easier to record than signals of other types. Presently, illustrated descriptions of calling signals of several hundreds of small Auchenorrhyncha species are available in literature. The question arises, is it possible to use these data in phylogenetic analysis, or in other words, do the signal traits bear phylogenetic information?

In small Auchenorrhyncha, signals with noise frequency spectra prevail. Only ca. 10% of species studied produce pure-tone signals with regular sine carrier and line spectra. Distribution of species producing pure-tone signals among families, subfamilies, and tribes is far from random. In some taxa such species constitute the majority, in others, on the contrary, they are absent or their proportion is very low [Tishechkin, Burlak, 2013]. This clearly demonstrates that the type of frequency spectrum (noise or line) bears phylogenetic information. For example, among the species discussed above, pure-tone signals were recorded in all representatives of Evacanthinae (four species from two genera). Signals of both studied species of Scaphoideini include pure-tone components; similar situation is observed in *Scaphoideus titanus* [Mazzoni et al., 2009]. However, no taxonomic trait is universal, and the spectrum type is not an exception. For instance, calling signals of two studied species of *Penthimia* differ in the type of a frequency spectrum. Pure-tone signals were also recorded in *Ledra auditura* (Ledrinae), *Hecalus lineatus* (Deltocephalinae: Hecalini), and *Varta japonica* (Deltocephalinae: Vartini), but the significance of this fact is difficult to estimate, since we do not yet have sufficient comparative data on other representatives of these taxa.

Similarity of calling signal temporal pattern in small Auchenorrhyncha is not a rare phenomenon [Tishechkin, 2007, 2008]. If the signal pattern is rather simple, such similarity may be accidental or result from convergence. Examples of this kind among species studied are rather numerous. Phrases consisting of regularly repeated short similar syllables were recorded in *Maiestas* spp., *Chiasmus conspurcatus*, *Exitianus nanus*, *Achaetica anabasidis*, and *Hishimonus bucephalus*. In *A. anabasidis* and *H. bucephalus* (Deltocephalinae: Opsini; Figs 142–148 and 149–154), signal similarity hardly indicates their close relation, because they belong to different subtribes (Achaeticina and Opsiina, respectively), and the signals of other studied species of Opsiina have quite different patterns [Tishechkin, 2000]. Among Doraturini, in addition to *Ch. conspurcatus* and *E. nanus*, such signals were also described in several species of *Aconura* [Tishechkin, 2000: Figs 349–360 and 365–371], although signal patterns in other species of this tribe are different.

In *Maiestas* spp. (Figs 106–113 and 114–118) including *M. schmidtgeni* (Wagner, 1939) [see Tishechkin, 2000: figs 101–105], signal similarity is in a good agreement with their morphological similarity. It should be noted, that for a long time most species of *Maiestas* were included into the genus *Recilia*: they were excluded from it only recently [Webb, Viraktamath, 2009]. The studied representatives of these two genera distinctly differ in signal pattern (Figs 104–105 and 106–118); thus, acoustic traits support this taxonomic rearrangement.

Accidental emergence of similar signals with complex temporal pattern in unrelated species is hardly possible; for this reason similarity of elaborate signals may indicate phylogenetic relation. For example, in *Iassus ulmi* and *I. dorsalis* which are closely related to each other, general signal pattern is similar and signals of two species differ mostly in quantitative parameters i.e. pulse and syllable repetition period (Figs 25–30 and 31–37). Still, signals of congeneric species quite often have very different patterns, e.g. in *A. volgensis* and *A. jakowlefi* (Figs 73–81 and 82–88). Apparently, strong divergence of related species by this trait results from competition for communication channels within insect communities. For this reason, signal temporal pattern can be used in phylogenetic reconstructions only as an additional trait and by no means in all cases.

ACKNOWLEDGEMENTS. The study was supported by the Russian State program No. AAAA-A16-116021660095-7 (preparation of illustrations and manuscript) and Russian Science Foundation, grant No. 14-50-00029 (fieldwork in 2015–2017 and data handling).

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