

New data on the male calling signals of Palearctic Deltocephalinae (Homoptera: Cicadellidae)

Новые данные о призывных сигналах самцов палеарктических Deltocephalinae (Homoptera: Cicadellidae)

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КЛЮЧЕВЫЕ СЛОВА: цикадки, вибрационные сигналы, изменчивость, частотные спектры, тональные сигналы, Европа, Средняя Азия, Дальний Восток.

ABSTRACT. Illustrated descriptions of the male vibrational calling signals of 15 species of Palearctic Deltocephalinae from Europe, Central Asia, and the Russian Far East are published for the first time; signals of one more species were studied in a population located more than 2400 km from a previously studied locality. The signals of most species are characterized by strong intrapopulation variability. However, in two species for which signal recordings from localities situated at a distance of more than 2000 km apart were available, no geographical variability of signals was revealed. Signals of congeneric species can be similar in temporal patterns or, on the contrary, are very diverse and completely dissimilar in closely related species. *Rhoananus hypochlorus* (Paralimnini) produce pure-tone signals; signals of *Macrosteles fieberi* (Macrostelini) consist of noise and pure-tone components. Such signals were previously known in many species of Paralimnini but in Macrostelini they are described for the first time. In two species, distinct differences in frequency spectra between different components of the noise signals were revealed. Also, a brief overview and list of articles on vibrational signals of Deltocephalinae are presented.

РЕЗЮМЕ. Впервые опубликованы иллюстрированные описания вибрационных призывных сигналов самцов 15 видов палеарктических Deltocephalinae из Европы, Средней Азии и с Дальнего Востока; сигналы ещё одного вида изучены в популяции, расположенной на расстоянии более 2400 км от исследованной ранее. Сигналы большинства видов характеризуются значительной внутрипопуляционной изменчивостью. Однако у двух видов, для кото-

рых имелись записи сигналов из точек, расположенных на расстоянии более 2000 км друг от друга, географической изменчивости сигналов не выявлено. Сигналы видов из одного рода могут быть сходны по временному рисунку или, наоборот, чрезвычайно разнообразны и совершенно несходны у близкородственных видов. *Rhoananus hypochlorus* (Paralimnini) издает тональные сигналы; сигналы *Macrosteles fieberi* (Macrostelini) состоят из шумовых и тональных компонентов. Подобные сигналы ранее были известны у многих видов Paralimnini, но у Macrostelini они описаны впервые. У двух видов выявлены отчетливые различия в частотных спектрах разных компонентов шумового сигнала. Также представлены краткий обзор и список литературы по вибрационным сигналам Deltocephalinae.

Introduction

To distinguish between closely related insect species and clarify the taxonomic status of dubious forms, both morphological and non-morphological traits are currently used. Recently, in the taxonomy of Auchenorrhyncha (Homoptera), bioacoustic traits are used quite widely and make it possible to solve difficult problems in cases where morphological traits do not give a reliable result (reviews: Tishechkin [2013]; Tishechkin, Vedenina [2016]). For this reason, over the past 30 years, we have been conducting a systematic study of the male calling signals of small Auchenorrhyncha of Russia and adjacent countries. This article presents new data on the vibrational signals of Palearctic leafhoppers from the subfamily Deltocephalinae (Homoptera: Cicadellidae).

Deltocephalinae is the largest subfamily of leafhoppers. According to the excellent recent revision by Zahnizer & Dietrich [2013], it includes 38 tribes, 923 genera, and 6683 valid species distributed worldwide. Oscillograms and descriptions of acoustic signals of 89 species of Deltocephalinae from Russia and adjacent countries were published in one of our first works [Tishechkin, 2000]. Later, in our articles on a leafhopper bioacoustics, in particular on signal variability, communication channel segregation in sympatric species, etc., oscillograms of male calling signals of about 40 more species of Deltocephalinae from this territory were published [Tishechkin, 2005, 2007, 2009b, 2010, 2011, 2018, 2023a]. In addition, oscillograms of calling signals of 28 species were presented for the first time in our taxonomic works [Tishechkin, 2002, 2009a, 2019, 2021a, b, 2022a, 2023b]. Thus, in total, articles cited above contain illustrated descriptions of signals of more than 150 species of Deltocephalinae recorded during our field studies.

The efforts of other specialists were mainly focused on detailed investigations of the signal repertoire, communication system, and associated behavior of leafhoppers. Such studies can only be carried out on several model species; simultaneous study of many species is very difficult in these cases.

In one of the first studies of leafhopper vibrational signals using the example of the genus *Nephotettix* Matsumura, 1902 (Homoptera: Cicadellidae: Deltocephalinae: Chiasmmini), it was shown that it is differences in the male calling signal temporal patterns that represent a precopulatory reproductive barrier in Cicadellidae [Inoue, 1982]. Detailed descriptions of acoustic signals and mating behavior of several species of Macrostelini (Homoptera: Cicadellidae: Deltocephalinae) and of *Psammotettix alienus* (Dahlbom, 1850) (Homoptera: Cicadellidae: Deltocephalinae: Paralimnini) were published [Purcell, Lohr, 1976; Heady *et al.*, 1986, 1989; Nuhardiyati, Bailey, 2005; Derlink *et al.*, 2018]. Comprehensive investigation of acoustic behavior of *Graminella nigrifrons* (Forbes, 1885) (Homoptera: Cicadellidae: Deltocephalinae: Deltocephalini) made it possible to evaluate the significance of different elements of a complex signal for recognizing a conspecific mate and to describe the male communication strategy (so called “call-fly strategy”), which, as was later shown, is characteristic of many other species of small Auchenorrhyncha [Heady, Nault, 1991; Hunt, Nault, 1991; Hunt *et al.*, 1992; Hunt, Morton, 2001]. The study of vibrational communication of *Scaphoideus titanus* Ball, 1932 (Homoptera: Cicadellidae: Deltocephalinae: Scaphoideini) allowed to develop methods for acoustic control of leafhopper pests [Mazzoni *et al.*, 2009a, b]. A series of taxonomic works on European species of the genus *Euscelis* Brulle, 1832 (Homoptera: Cicadellidae: Deltocephalinae: Athysanini) using acoustic traits was published by Strübing [1965, 1970, 1976, 1980, 1983] and Strübing & Drosopoulos [2006].

In the present paper, previously unknown signals of 15 species of Deltocephalinae, mainly from the Asiatic

part of the Palearctic, are described and illustrated; for one more species, oscillograms of signals of the male from a population located more than 2400 km from a previously studied locality are presented. Classification of tribes and genera of Deltocephalinae follows Zahnizer & Dietrich [2013].

Material and methods

Leafhopper vibrational 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 (before 2005), minidisk recorder Sony Walkman MZ-NH900 (2005–2016), or Roland R-05 wave/mp3 recorder (since 2017) via a custom-made matching amplifier. For recording, a stem of the host plant about 10–15 cm in length was attached to the cartridge by a rubber ring with the cartridge needle slightly touching the stem. Then a nylon cage containing a male leafhopper was put on the twig. After some time, the male usually sat on the twig and started singing.

Oscillograms of signals were produced 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 repeated with regular intervals and consisting of uniform or different pulses are referred to as **syllables**. Any more or less prolonged signal with complex pattern (e.g. the sequence of similar or different syllables) is referred to as a **phrase**. It should be noted that the signals of small Auchenorrhyncha have a very complex and diverse temporal pattern. In this regard, a strictly unambiguous use of the above terms is not always possible.

Voucher specimens whose signals were recorded are deposited in the collection of the Zoological Museum of M.V. Lomonosov Moscow State University.

Signal descriptions

Tribe Athysanini

1. *Neomacednus marginatus* (Emeljanov, 1962)

Figs 1–4.

MATERIAL. The Russian Far East, Primorskiy Krai, western shore of the Khanka Lake, 10 km south of Turiy Rog, 19.VII.2006, signals of one male recorded at 28–30 °C.

SIGNALS. The male calling signal is a phrase lasting for 2.5–5 s (Figs 1–2). The phrase consists of uniform syllables; each syllable usually reaches the highest amplitude in the middle or in the end (Figs 3–4). Syllable repetition period averages 300–500 ms and gradually increases towards the end of the phrase. The pulse repetition period usually decreases sharply in the last third of a syllable.

2. *Allygidius atomarius* (Fabricius, 1794).

Figs 5–7.

MATERIAL. The Lower Volga Region, Saratov Oblast, Krasnokutskiy District, environs of Dyakovka village, 16.VII.2004, signals of one male recorded at 29–30 °C.

SIGNALS. The male calling signal is a short phrase lasting for 0.6–1.3 s (Fig. 5). It consists of uniform syllables including two or three pulses each; in some syllables, only one high-amplitude pulse is distinguishable (Figs 6–7). Syllable repetition period in a phrase averages 60–70 ms.

3. *Mimallygus lacteinervis* (Kirschbaum, 1868)
Figs 8–15.

MATERIAL. Moscow Oblast, Mytishchi, on cultivated *Salix purpurea* in the park, 22.VII.2022, signals of three males recorded at 27 °C.

SIGNALS. The male calling signal is a variable complex phrase lasting for about 10–30 s (Figs 8–11). The phrase begins with a sequence of syllables with a variable and indistinct pattern, repeating with a period of 0.9–2.0 s (usually about 1 s) (Fig. 12). As a rule, the amplitude of this sequence is significantly lower than that of the main part of the signal (Figs 8–9, 11), although sometimes it can be equal to it (Fig. 10). The middle part of the phrase consists of alternating longer and shorter syllables lasting approximately for 550–580 ms and 250–270 ms, respectively (Figs 13, 15). Syllables of both types have similar temporal patterns. Normally, they begin with an amplitude burst, followed by a long low-amplitude part; sometimes its amplitude gradually increases towards the end. The phrase usually ends with several syllables similar in temporal pattern to those in the middle part, but having lower amplitude and lasting for 570–700 ms (Fig. 14).

The above description concerns phrases with a typical pattern. Often the initial and/or final parts of a phrase can be almost completely reduced (Figs 10–11) and the middle part includes only 7–8 syllables (Fig. 10). The ratio of amplitudes of different parts of a syllable can be different from that described above, sometimes additional short component presents between main syllables, etc.; such an atypical syllable followed by an additional short component is shown in Fig. 15 (second half of the oscillogram).

REMARKS. This Western European species was only recently recorded from Russia [Tishechkin, 2022b].

4. *Cyanidius collinus* Dubovsky, 1966
Figs 16–20.

MATERIAL. Kyrgyzstan, Western Tien-Shan Mts., Chatkal Mtn. Range, Sary-Chelekskiy Nature Reserve, environs of Arkyt village, 30.VI.2009, signals of one male recorded at 21–22 °C.

SIGNALS. The male calling signal is a complex phrase lasting for 6–8 s (Figs 16–17). The phrase consists of three syllables lasting for 0.7–1.0 s each, alternating with shorter syllables lasting for about 100–200 ms or with single discrete pulses. The end parts of longer syllables usually differ somewhat from the main parts in the pulse repetition period or in their amplitude (Figs 19–20), but sometimes these differences are indistinct (Fig. 18).

REMARKS. The type locality of this species (environs of Ala-Buka Village) is situated on the same mountain range ca 60 km southwest from the recording site [Dubovsky, 1966].

5. *C. turkestanicus* Dubovsky, 1966
Figs 21–26.

MATERIAL. 1. Kyrgyzstan, Western Tien-Shan Mts., the bank of the Kara-Suu River ca 3.5 km from its confluence with the Naryn River (about 10 km north of Tash-Kumyr Town), from *Artemisia* subg. *Seriphidium*, 6.VII.2009, signals of two males recorded at 30–31 °C.

2. Kyrgyzstan, Western Tien-Shan Mts., semidesert in the hills about 12 km west of Tash-Kumyr Town, 41.301° N, 72.056° E, from *Artemisia* subg. *Seriphidium*, 9.VII.2023, signals of one male recorded at 31 °C.

SIGNALS. The temporal pattern of the male calling signal is generally the same as in *C. collinus*. The phrase consists of alternating sequences of 3–6 shorter syllables and one longer syllable, and always begins with a sequence of shorter syllables (Figs 21–23). Before the last longer syllable this sequence can be missing. The phrase duration is 9–10 s in males from the first locality (Figs 21–22) and about 4.5 s in the male from the second locality (Fig. 23). The duration of both longer and shorter syllables in males from different localities is almost the same and averages 1200–2200 ms and 95–140 ms, respectively. Sometimes the longer syllable begins with several pulses of higher amplitude (Figs 23, 26; the second long syllable on Fig. 22); at the end of some syllables, the pulse repetition period sharply decreases and their shape somewhat changes (Figs 25–26).

Signals of males from different localities clearly differ in duration, despite the fact that the distance between them is about 23 km and the recordings were made at almost the same temperature.

REMARKS. The type locality of this species (environs of Dzhanly-Dzhol Village) is situated ca 15 km north-northwest of the first recording site and ca 32 km north-northeast of the second recording site [Dubovsky, 1966].

6. *Euscelidius mundus* (Haupt, 1927)
Figs 27–28.

MATERIAL. The Lower Volga Region, Saratov Oblast, Krasnokutskiy District, environs of Dyakovka village, 15.VII.2004, signals of three males recorded at 30–31 °C.

SIGNALS. The male calling signal is a succession of short syllables following each other with a period of about 450–850 ms (Figs 27–28). The male can sing continuously for several tens of seconds.

7. *Streptanus aemulans* (Kirschbaum, 1868)
Figs 29–31.

MATERIAL. Kyrgyzstan, Western Tien-Shan Mts., Chatkal Mtn. Range, Sary-Chelekskiy Nature Reserve, meadows on the northern shore of the Sary-Chelek Lake, 26.VII.2008, signals of one male recorded at 24–25 °C.

SIGNALS. The male calling signal is a phrase lasting for 15–25 s (Figs 29–30). It consists of alternating syllables similar in the temporal pattern, but differing in the frequency spectra (Fig. 30). Syllables of both types include on average 6–8 pulses following each other with the repetition period of about 70–90 ms.

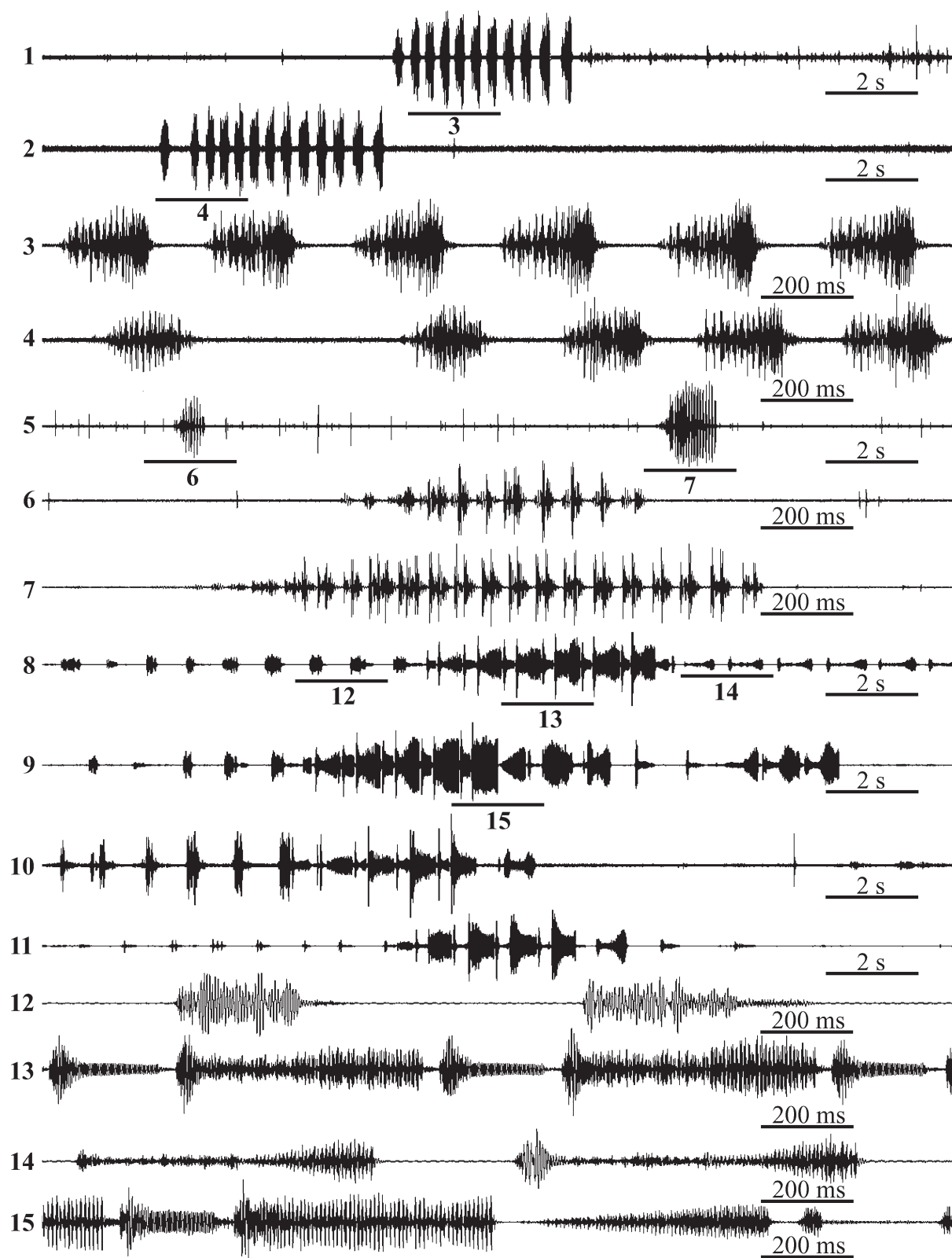
REMARKS. The structure of the male calling signals of *S. aemulans* is generally the same as in closely related *S. sordidus* (Zetterstedt, 1828) [Tishechkin, 2000: 47; figs 443–449], but differs in the pattern of syllables.

A remarkable feature of signals of *S. aemulans* is that syllables similar in the temporal pattern distinctly differ in frequency spectra.

Tribe Cicadulini

8. *Elymana pallidipennis* (Lindberg, 1929)
Figs 32–34.

MATERIAL. Primorskiy Krai, Khasan District, “Kedrovaya Pad’” (presently, “The Land of Leopard”) Nature Reserve, environs of Primorskiy Village, 17.VIII.2010, signals of one male recorded at 25 °C.



Figs 1–15. Oscillograms of male calling signals of Deltocephalinae. 1–4 — *Neomacednus marginatus*; 5–7 — *Allygidius atomarius*; 8–15 — *Mimallygus lacteinervis*. Faster oscillograms of the parts of signals indicated as “3–4”, “6–7”, and “12–15” are given under the same numbers.
Рис. 1–15. Осциллограммы призывных сигналов самцов Deltocephalinae. 1–4 — *Neomacednus marginatus*; 5–7 — *Allygidius atomarius*; 8–15 — *Mimallygus lacteinervis*. Фрагменты сигналов, помеченные цифрами “3–4”, “6–7” и “12–15”, представлены при большей скорости развёртки на осциллограммах под соответствующими номерами.

SIGNALS. The male calling signal consists of syllables lasting for 2.6–2.9 s and separated by gaps of approximately from 3 to 7–8 s (Figs 32–33). In our recordings, each signal includes 2–4 syllables. The syllable pattern is indistinct, and individual pulses in it are almost indistinguishable (Fig. 34).

REMARKS. In terms of the temporal pattern, the male calling signals of *E. pallidipennis* are almost the same as those of *E. sulphurella* (Zetterstedt, 1828), but distinctly differ from the signals of *E. koszevnikovi* (Zakhvatkin, 1938) [Tishechkin, 2000: 51–54; figs 480–494].

Tribe Fieberiellini

9. *Synophropsis lauri* (Horváth, 1897) Figs 35–37.

MATERIAL. Greece, Korfu Island, environs of Nissaki Village, ca 12 km north of Kerkyra, from *Laurus nobilis* L., 4.VI.2018, signals of two males recorded at 29 °C.

SIGNALS. The male calling signal is a phrase lasting for about 10–20 s. It consists of repeating components each including several short low-amplitude syllables and one longer syllable increasing in amplitude towards the end (Figs 35–37). Repetition period of these components averages 2.5–3.5 s. The duration of longer syllables is 350–450 ms; the duration of shorter syllables is more variable and ranges from 80 to 200 ms.

Tribe Goniagnathini

10. *Tamaricades decoratus* (Haupt, 1917) Figs 38–41.

MATERIAL. Kyrgyzstan, Western Tien-Shan Mts., ca 10 km north of Tash-Kumyr Town, 41.469° N, 72.212° E, from *Tamarix* sp., 4.VII.2023, signals of four males recorded at 29 and 35 °C.

SIGNALS. The male calling signal consists of syllables lasting from about 0.7–0.8 s up to 2–3 s (Figs 38–39). Syllables follow with prolonged irregular gaps or in groups from 2 to 5–6 syllables. The pulse repetition period is about 50–90 ms at 29 °C (Fig. 40) and is 25–30 ms at 35 °C (Fig. 41). In the middle of the longest syllables the pulse shape sometimes changes, and their repetition period decreases to 15–16 ms at 35 °C.

REMARKS. According to Mityaev [2002] and our observations in Kyrgyzstan, nymphs and young adults of *T. decoratus* live in dense aggregations usually consisting of 10–15 individuals. However, when we placed two mature males on the twig about 10 cm long, one of them, sitting in the same place, continuously produced calling signals, whereas the other ran several times in different directions, and then left the twig without producing signals. Apparently, the transition of insects to a solitary life begins when males became acoustically active.

Tribe Macrostelini

11. *Macrosteles fieberi* (Edwards, 1889) Figs 42–49.

MATERIAL. Moscow Oblast, Voskresenskiy Region, environs of Beloozerskiy Town, the bog in the floodplain of the Moskva River near Mikhalyovo Village, 20.VIII.2021, signals of four males recorded at 26 °C.

SIGNALS. The male calling signal is a phrase consisting of two or three different pulse sequences (Figs 42–45). The duration of the first sequence is 1.5–3.0 s, the pulse repetition period in it is about 120–150 ms; the pulse temporal pattern is very

variable (Fig. 46, the beginning of the oscillogram). Sometimes this sequence is reduced to a few pulses or is absent. The duration of the second sequence is about 0.8–1.2 s; it consists of pure-tone pulses following each other with a period of 39–41 ms (Figs 46–48). The duration of the third sequence is 1.8–2.7 s; it consists of pulses with a noise frequency spectrum, following each other with a period of 31–36 ms (Figs 47, 49). The total duration of a phrase consisting of three parts is 5.0–6.7 s. If the first part of the phrase is missing, it is reduced to 2.5–4.0 s.

REMARKS. Calling signals of four species of the genus *Macrosteles* Fieber, 1866 from European Russia and two morphologically similar forms of *Macrosteles fascifrons* (Stål, 1858) from North America were previously described [Purcell, Lohr, 1976; Tishechkin, 2000]. Judging by these data, calling signals in representatives of this genus are characterized by great diversity and, as a rule, a complex temporal pattern, and are often completely dissimilar in different species.

A remarkable feature of signals of *M. fieberi* is a combination of pure-tone and noise components.

Tribe Opsiini

12. *Achaetica anabasisidis* Emeljanov, 1959 Figs 50–52.

MATERIAL. Southeastern Kazakhstan, rocky desert between the Ili River and the lower Charyn River, about 4 km west of the Charyn River, 43.720° N, 79.324° E, from *Nanophyton iliense* U.P. Prato, 14.VI.2022, signals of one male recorded at 24 °C.

SIGNALS. The calling signal of the male from Southeastern Kazakhstan is a phrase lasting for 3.5–10.0 s (Figs 50–51). It consists of uniform syllables following each other with a period of 125–140 ms (Fig. 52).

REMARKS. Signals of the male from Kazakhstan are almost indistinguishable from the previously described signals of the male from Astrakhan Oblast [Tishechkin, 2018: 231; figs 142–148], despite the fact that the distance between recording sites exceeds 2400 km. The longer syllable repetition period in the signal of the male from Kazakhstan is explained by the fact that the recording was made at a lower temperature (24 °C in Kazakhstan vs 28 °C in Astrakhan Oblast).

13. *Diacra convexa* Emeljanov, 1961 Figs 53–58.

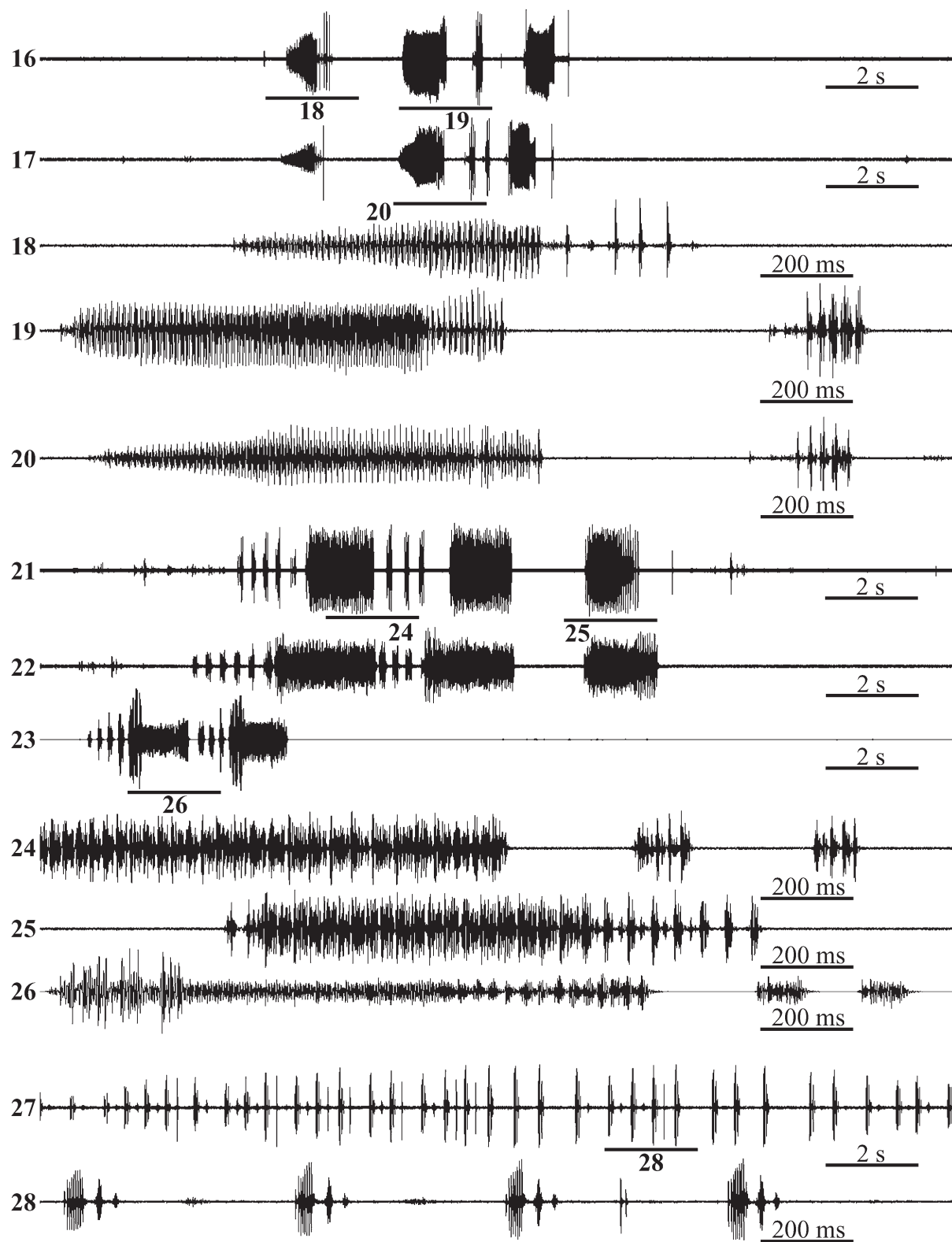
MATERIAL. Southeastern Kazakhstan, rocky desert between the Ili River and the lower Charyn River, about 4 km west of the Charyn River, 43.720° N, 79.324° E, from *Nanophyton iliense* U.P. Prato, together with the previous species, 14.VI.2022, signals of two males recorded at 24 °C.

SIGNALS. The male calling signal is a phrase lasting for 3.8–6.3 s and consisting of two parts with a syllable repetition period about 40–100 ms and 18–20 ms, respectively (Figs 53–58). Often in the end of the first part of the phrase, the pulse amplitude decreases and their repetition period increases and becomes very variable (Figs 53–54, 56).

Tribe Paralimnini

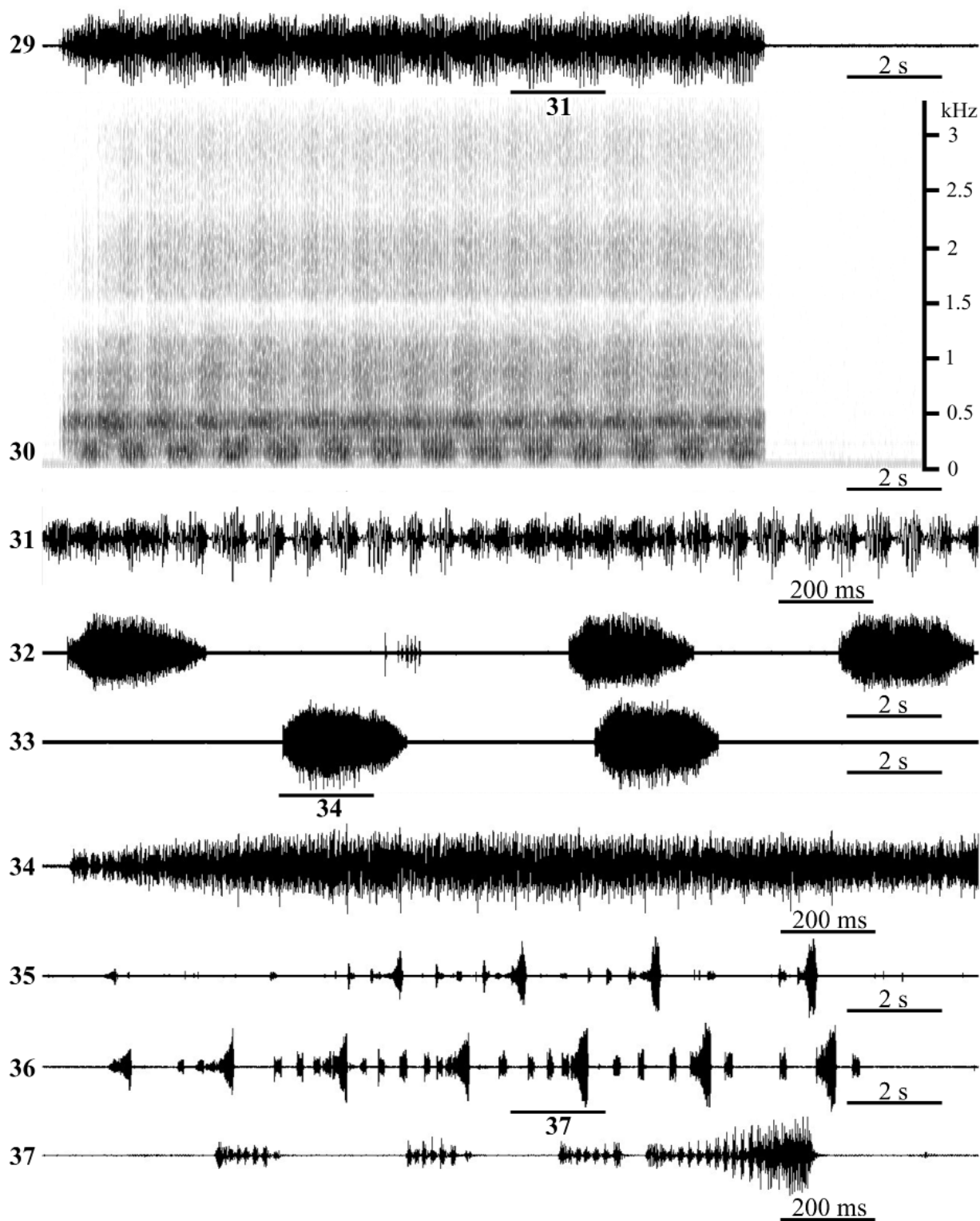
14. *Rhoananus hypochlorus* (Fieber, 1869) Figs 59–63.

MATERIAL. Kyrgyzstan, Inner Tien Shan Mts., steppe on the northern bank of the Western Karakol River, ca 25 km east-northeast of the Suusamy Village, 13.VII.2023, signals of two males recorded at 24 °C.



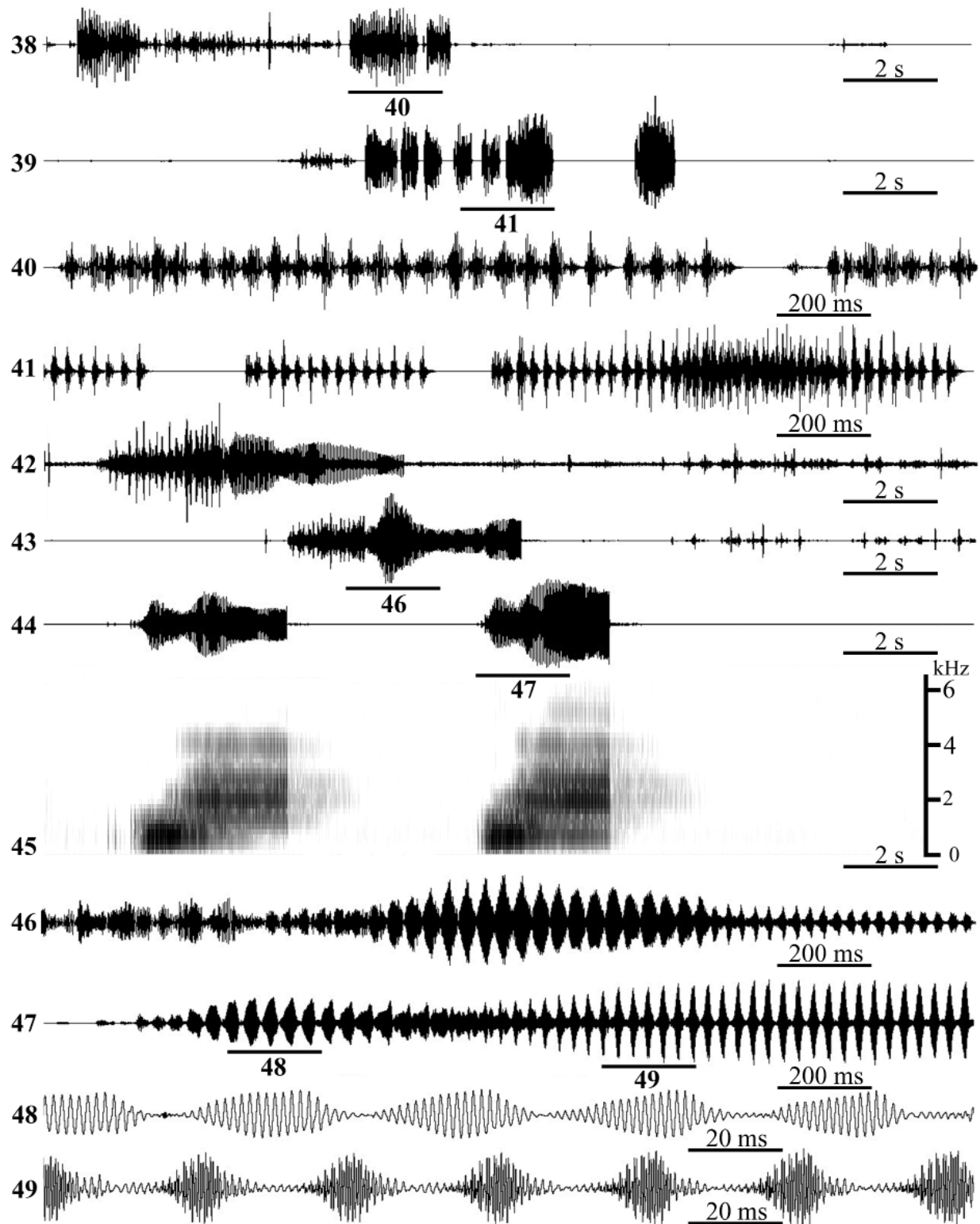
Figs 16–28. Oscillograms of male calling signals of Deltocephalinae. 16–20 — *Cyanidius collinus*; 21–26 — *C. turkestanicus*; 27–28 — *Euscelidius mundus*. Faster oscillograms of the parts of signals indicated as “18–20”, “24–26” and “28” are given under the same numbers.

Рис. 16–28. Осциллограммы призывных сигналов самцов Deltocephalinae. 16–20 — *Cyanidius collinus*; 21–26 — *C. turkestanicus*; 27–28 — *Euscelidius mundus*. Фрагменты сигналов, помеченные цифрами “18–20”, “24–26”, и “28”, представлены при большей скорости развёртки на осциллограммах под соответствующими номерами.



Figs 29–37. Male calling signals of Deltocephalinae. 29–31 — *Streptanus aemulans*; 32–34 — *Elymana pallidipennis*; 35–37 — *Synophropsis lauri*. 29–30 — oscillogram and sonogram of the same signal at the same speeds, 31–37 — oscillograms. Faster oscillograms of the parts of signals indicated as “31”, “34”, and “37” are given under the same numbers.

Рис. 29–37. Призывные сигналы самцов Deltocephalinae. 29–31 — *Streptanus aemulans*; 32–34 — *Elymana pallidipennis*; 35–37 — *Synophropsis lauri*. 29–30 — осциллограмма и сонограмма одного и того же сигнала при одной скорости развертки, 31–37 — осциллограммы. Фрагменты сигналов, помеченные цифрами “31”, “34” и “37”, представлены при большей скорости развёртки на осциллограммах под соответствующими номерами.



Figs 38–49. Male calling signals of Deltocephalinae. 38–41 — *Tamaricades decoratus*; 42–49 — *Macrosteles fieberi*. 38–43, 46–49 — oscillograms, 44–45 — oscillogram and sonogram of the same signal at the same speeds. Faster oscillograms of the parts of signals indicated as “40–41” and “46–49” are given under the same numbers.

Рис. 38–49. Призывные сигналы самцов Deltocephalinae. 38–41 — *Tamaricades decoratus*; 42–49 — *Macrosteles fieberi*. 38–43, 46–49 — осциллограммы, 44–45 — осциллограмма и сонограмма одного и того же сигнала при одной скорости развертки. Фрагменты сигналов, помеченные цифрами “40–41” и “46–49”, представлены при большей скорости развертки на осциллограммах под соответствующими номерами.

SIGNALS. The male calling signal consists of short syllables following each other with irregular gaps from 1.5–2.0 up to 5.0–10.0 s and more (Figs 59–60). Duration of syllable averages 400–520 ms (Figs 61–62). Pulse repetition period in the syllable increases from about 37–45 ms in the beginning to about 45–57 ms in the end. On oscillograms at high speed it is visible that the signal has a pure-tone carrier (Fig. 63).

REMARKS. Pure-tone signals are quite typical for Paralimnini and have previously been recorded in 22 out of 59 studied species of this tribe [Tishechkin, Burlak, 2013].

Tribe Phlepsiini

15. *Phlepsius intricatus* (Herrich-Schäffer, 1838) Figs 64–68.

MATERIAL. 1. The Lower Volga Region, Dosang Railway Station 60 km north of Astrakhan, *Artemisia arenaria* DC. in the desert, 29.VI.2010, signals of one male recorded at 29 °C.

2. Kyrgyzstan, Western Tien Shan Mts., the Naryn River Basin, Bekechal Gorge, 19 km southwest from Karakul Town, 41.536° N, 72.495° E, 3.VII.2023, signals of two males recorded at 36 °C.

SIGNALS. The male calling signal consists of single or repeated phrases lasting for about 2.1–2.6 s in the male from the Lower Volga Region and for 1.4–2.1 s in males from Kyrgyzstan. If the male produces several phrases one after another, the gaps between them average from 2 up to 6–7 s in our recordings (Figs 64–65).

The phrase consists of three sequences of pulses (Fig. 67). The initial and final sequences are identical, the middle, i. e., the second sequence differs from them in the shape of vibrations and, as a consequence, in the frequency spectrum (Fig. 66). In some signals, the first sequence is partially or entirely reduced. The pulse repetition period in the initial and final sequences is 10–12 ms at 29 °C and 7–8 ms at 35–36 °C. The pulse repetition period in the middle sequence is much longer and averages 20–22 and 15–20 ms, respectively. Often the pulses in the signal are poorly distinguishable (Fig. 68).

REMARKS. The distance between recording sites is approximately 2030 km, however, the signals of males from different populations are almost identical. The slight differences between them in temporal parameters are due to differences in temperature during recording.

A remarkable feature of signals of *P. intricatus* is that signal parts similar in the temporal pattern (Fig. 68) distinctly differ in frequency spectra (Figs 65–66).

16. *P. ornatus* (Perris, 1857) Figs 69–72.

MATERIAL. Kyrgyzstan, Western Tien Shan Mts., Torkent Village on the northern shore of the Toktogul Reservoir, the bank of the Torkent River, 41.841° N, 73.161° E, 11.VII.2023, signals of two males recorded at 25 °C.

SIGNALS. The male calling signal is a phrase lasting for 17–20 s and consisting of two parts (Figs 69–70). The first part has a duration of about 7 s. It consists of several syllables, each beginning with a sequence of low-amplitude pulses partially merged with each other and following with a period of 8–9 ms, and ending with one or two high-amplitude pulses (Fig. 71, the first half of the oscillogram). The second part of a phrase is a sequence of high-amplitude syllables, following with a period of about 0.7 s at the beginning and up to 1.5 s at the end of the sequence (Figs 71–72). At the beginning of the sequence between the main syllables there are sometimes ad-

ditional short syllables or separate pulses. The pulse repetition period in main syllables averages 45–80 ms.

REMARKS. In contrast to some other leafhopper genera, signals of two studied species of *Phlepsius* Fieber, 1866 are completely dissimilar in the temporal pattern.

Discussion

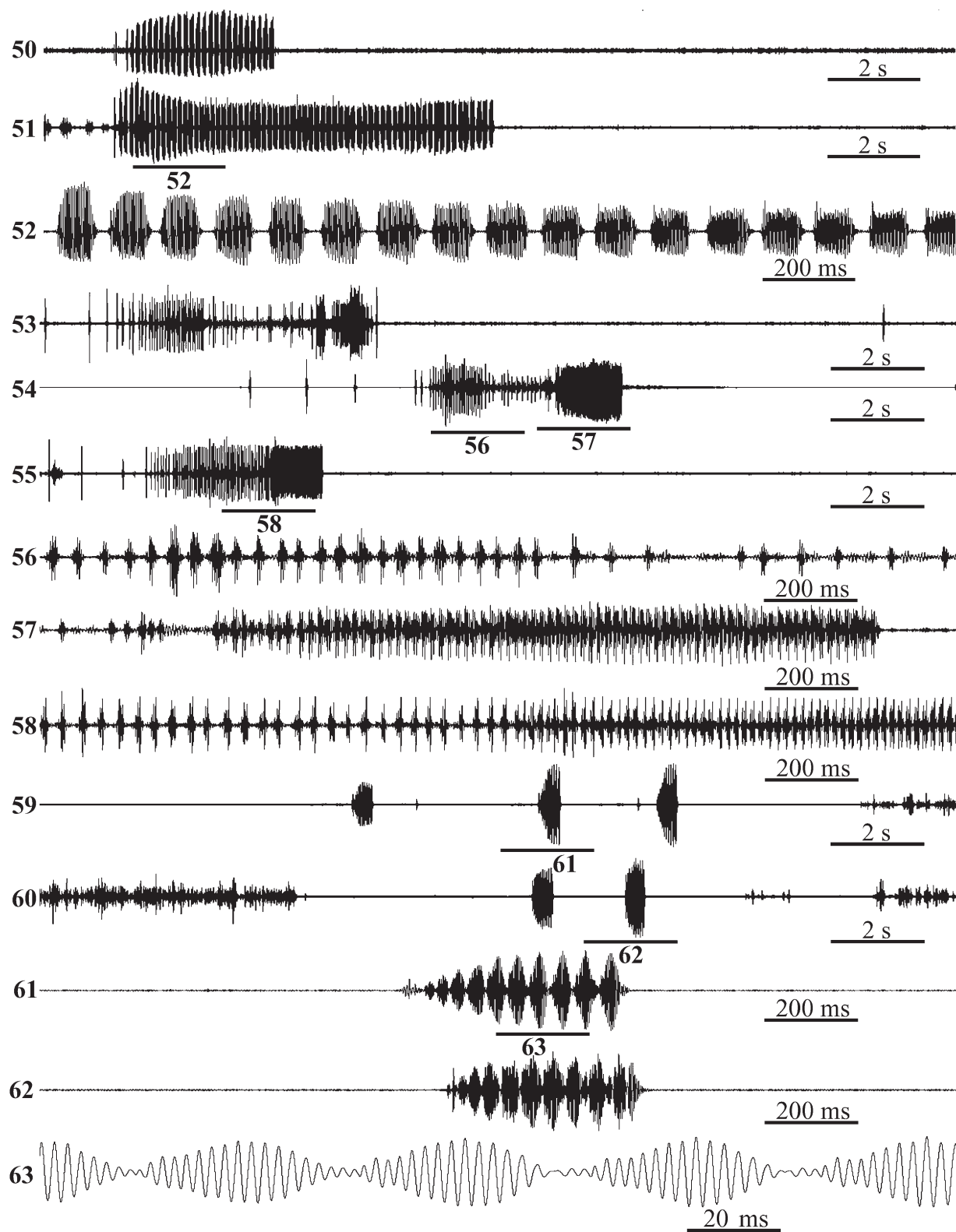
The results of the present study confirm some regularities revealed during the previous investigations of the leafhopper calling signals.

In small Auchenorrhyncha, the male calling signal temporal pattern is characterized by strong intrapopulation variability, and Deltocephalinae is no exception in this regard [Tishechkin, 2010]. Signals of different males from the same locality in most cases differ in the duration of phrases or the number of syllables. This is observed in *Mimallus lacteinervis* (Figs 8–11), *Cyanidius turkestanicus* (cf. Figs 21–22 and 23), *Synophropsis lauri* (Figs 35–36), and *Tamaricades decoratus* (Figs 38–39). Occasionally, additional components are present/absent in the signal, or the temporal pattern of one of the components changes greatly. For example, in *Macrosteles fieberi*, an additional sequence of pulses can be present in the beginning of the signal. Its duration is usually 1.5–3.0 s, but sometimes it is reduced to several pulses or is completely absent (cf. Figs 42–43 and 44). In *Diacra convexa*, a drop in the pulse amplitude and repetition frequency is sometimes observed in the middle of a phrase (cf. Figs 53–54 and 55). In both cases, these differences were observed between the signals of males from the same sample.

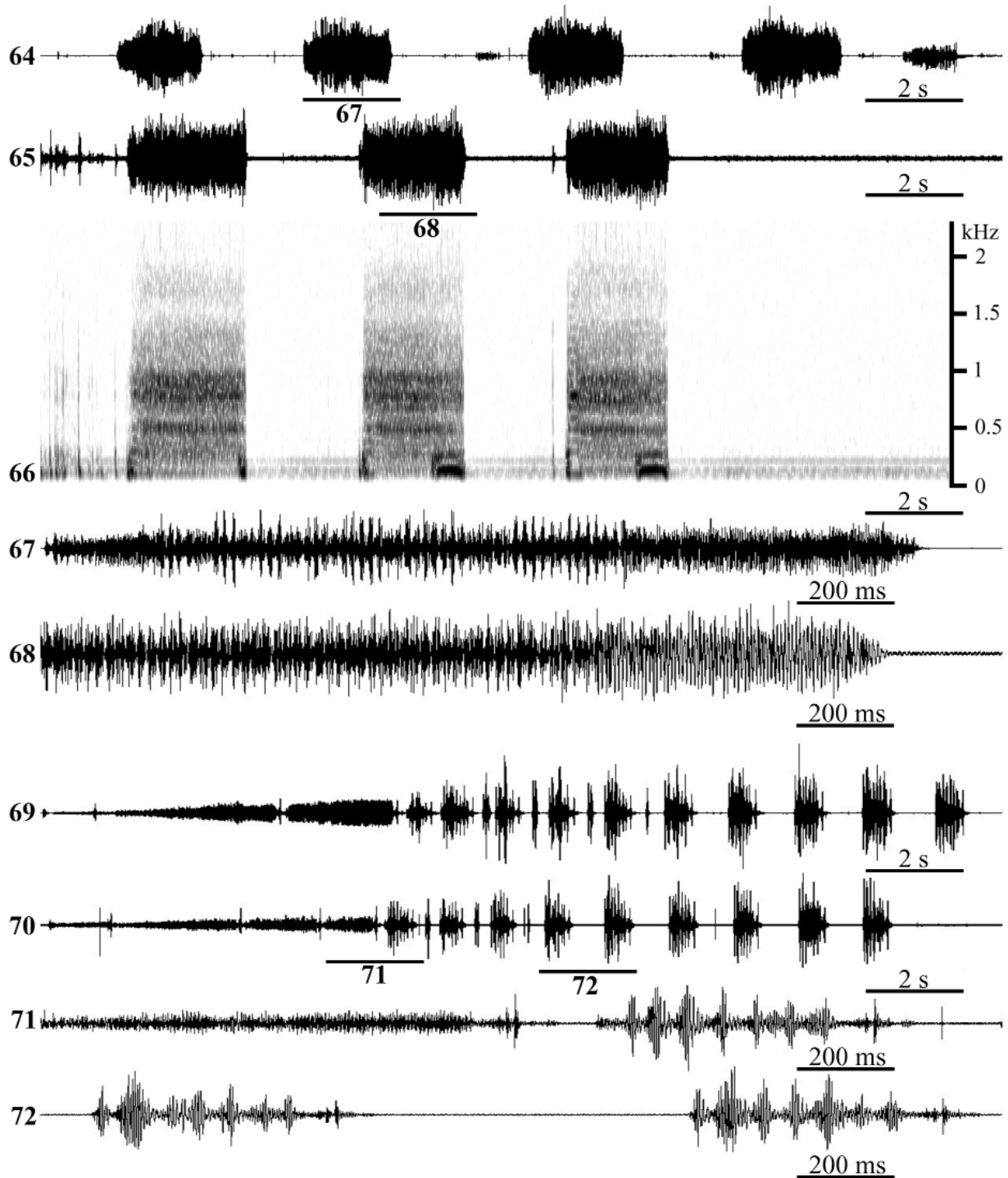
On the contrary, geographical variability of the leafhopper signal pattern is a very rare phenomenon and signals of males from different populations are similar [Tishechkin, 2013]. The examples of *Achaetica anabasis* and *Phlepsius intricatus* are fully consistent with previous data. In both species, signals of males from different populations are almost indistinguishable, despite the fact that the distance between them is about 2400 km in the first species, and about 2030 km in the second one.

Signals of congeneric species sometimes are similar in the temporal pattern. Among the studied material, examples of this kind can be found in the genera *Cyanidius* Emeljanov, 1964 (cf. Figs 16–17 and 21–23), *Streptanus* Ribaut, 1942, and, partially, in *Elymana* DeLong, 1936. On the other hand, in some genera the signal patterns are extremely diverse and completely dissimilar in closely related species, e.g. in *Macrosteles* Fieber, 1866 and *Phlepsius* Fieber, 1866 (cf. Figs 64–65 and 69–70).

Representatives of some taxa of small Auchenorrhyncha produce pure-tone signals with line frequency spectra, or the signals consisting of noise and pure-tone components [Tishechkin, Burlak, 2013]. At high speed, the pure-tone components in the oscillograms appear as a regular sine wave (Figs 48, 63). Such signals were also recorded in the two species considered in this article, *Rhoanenus hypochlorus* (Paralimnini) and *Macrosteles fieberi* (Macrostelini). In Paralimnini, the pure-tone signals were known previously [Tishechkin, 2007;



Figs 50–63. Oscillograms of male calling signals of Dectocephalinae. 50–52 — *Achaetia anabasidis*; 53–58 — *Diacra convexa*; 59–63 — *Rhoananus hypochlorus*. Faster oscillograms of the parts of signals indicated as “52”, “56–58”, and “61–63” are given under the same numbers.
Рис. 50–63. Осциллограммы призывных сигналов самцов Dectocephalinae. 50–52 — *Achaetia anabasidis*; 53–58 — *Diacra convexa*; 59–63 — *Rhoananus hypochlorus*. Фрагменты сигналов, помеченные цифрами “52”, “56–58” и “61–63”, представлены при большей скорости развёртки на осциллограммах под соответствующими номерами.



Figs 64–72. Male calling signals of Deltocephalinae. 64–68 — *Phlepsius intricatus*; 69–72 — *P. ornatus*. 64, 67–72 — oscillograms, 65–66 — oscillogram and sonogram of the same signal at the same speeds. Faster oscillograms of the parts of signals indicated as “67–68” and “71–72” are given under the same numbers.

Рис. 64–72. Призывные сигналы самцов Deltocephalinae. 64–68 — *Phlepsius intricatus*; 69–72 — *P. ornatus*. 64, 67–72 — осциллограммы, 65–66 — осциллограмма и сонограмма одного и того же сигнала при одной скорости развертки. Фрагменты сигналов, помеченные цифрами “67–68” и “71–72”, представлены при большей скорости развертки на осциллограммах под соответствующими номерами.

Tishechkin, Burlak, 2013], but in the tribe Macrostelini they are described here for the first time.

Differences in the frequency spectra between different components of the noise signal in small Auchenorrhyncha are usually very small or absent. However, in *Streptanus aemulans* and *Phlepsius intricatus* they are clearly visible on sonograms (Figs 30, 66). It is noteworthy that the differences in the temporal pattern between different signal components in these species are not so great.

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