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# Contributions to the study of the grasshopper (Orthoptera: Acrididae: Gomphocerinae) courtship songs from Kazakhstan and adjacent territories

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## Abstract

Male courtship songs of 9 grasshopper species of Gomphocerinae from Kazakhstan and Orenburg region and Altai Republic of Russia were studied. We analyzed not only the sound, but also the stridulatory movements of the hind legs to more entirely describe the songs. We also analyze the frequency spectra of the songs and the whole visual display during courtship. The courtship songs of three species, *Stenobothrus miramae, Chorthippus dubius* and *Ch. angulatus,* were studied for the first time. In four species, *Omocestus haemorrhoidalis, O. petraeus, Myrmeleotettix pallidus, Ch.karelini*, we found certain differences in temporal pattern of the courtship songs in comparison with the previous data on the respective species from other regions. In five species, *O. viridulus, S. miramae, M. pallidus, Ch. dubius* and *Ch. karelini*, various parts of elaborate courtship songs differed in the carrier frequency. In four species, *O. haemorrhoidalis, O. petraeus, M. pallidus* and *Ch. dubius*, the dominant frequencies of the courtship song were shown to lie in the range higher than 20 kHz. The conspicuous movements of antennae and legs during courtship were studied in *M. pallidus, S. miramae* and *Gomphocerus sibiricus*.

**Key words:** Gomphocerinae, courtship song, stridulatory leg movements, frequency spectrum, visual display

## Introduction

In many species of Orthoptera, the song is suggested to be the most important component of reproductive isolation. This is the reason why acoustic signals are often used in taxonomy, when sibling species are similar in morphology, but quite different in songs. Among Acrididae subfamilies, acoustic communication in Gomphocerinae is most developed in terms of structure of acoustic apparatus, temporal pattern of the song, and mating strategies (e.g., Otte, 1970; Helversen & Helversen, 1994; Ragge & Reynolds, 1998). The song is produced by stroking a stridulatory file of each hind femur across a raised vein on the fore wing. Using both hind legs, the grasshoppers have two separate sound-producing devices, which must be coordinated with one another. The stridulatory movements of the two legs often differ in amplitude and form, and the legs can exchange roles from time to time, which lead to increase of song complexity (Elsner, 1974; Helversen & Elsner, 1977; Elsner, 1994). Various species demonstrate different degrees of song complexity. The song in Gomphocerinae also varies according to the behavioral situation. A solitary male produces a calling song, listening for the response song of a female which is ready to mate. When a male finds a female, in many species the male begins a special courtship song, which may reach a high complexity and may be accompanied by conspicuous movements of different parts of the body such as abdomen, head, antennae or palps (Faber, 1953, Otte, 1970, Helversen & Helversen, 1994).

The courtship songs of Gomphocerinae are less studied than their calling songs. The reason for this may be due to the fact that the calling song is suggested to show a more species-specific structure, as this type of signal is often the only way to attract conspecific females. The courtship song being produced in the close vicinity of the female is often accompanied by chemical and visual stimuli of the male, which may weaken the selection pressure on the sound parameters of courtship. However, the courtship songs of different species were shown to possess a species-

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specific structure (Ragge & Reynolds, 1998; Vedenina & Helversen, 2009; Berger, 2008; Ostrowski *et al*., 2009; Berger & Gottsberger, 2010; Vedenina *et al*., 2012). In some recently diverged species (species of the *Stenobothrus* genus, of the *Chorthippus albomargintus* group), the calling songs are shown to be similar, whereas the courtship songs demonstrate many differences (Berger, 2008; Vedenina & Helversen, 2009). Thus, the courtship songs provide the only reliable key of species identification in these groups.

It is argued that the sound produced by Gomphocerinae has a broad frequency spectrum, so the specificity of the songs is believed to lie not in their frequency band but almost without exception in the pattern of amplitude over time. The songs of various species have usually a relatively broad-band maximum in the region between 20 and 40 kHz and a narrower peak between 5 and 15 kHz (Meyer & Elsner, 1996). The authors, however, found pronounced interspecific differences in the low-frequency peak, which was not correlated with the length of the body or of the elytra. This may indicate that not only the temporal parameters but also the carrier frequency of the sound can be used during species recognition. It was shown that male calling and female response songs may differ in the frequency spectra. In behavioural experiments on *Ch. biguttulus*, males reacted only to the low-frequency component, whereas females preferred spectra containing both, low and high frequency components (Helversen & Helversen, 1997). It was also shown that various parts of elaborate courtship songs may significantly differ in the carrier frequency (Vedenina *et al*., 2007; Ostrowski *et al*., 2009). The difference in the frequency spectra between the various song elements may influence the amplitude ratio on the oscillogram. If the song is recorded by portable recorders with a frequency range not exceeding 12.5–15 kHz, the amplitude ratio of different elements may be distorted (Vedenina & Shestakov, 2014).

In the current paper, we describe the courtship songs in 9 species of Gomphocerinae from Kazakhstan and adjacent territories. To gain a better description of the songs, we analyze not only the sound, but also the underlying stridulatory movements of the hind legs. The leg movement analysis may help in the sound analysis when the gaps between sound elements are not distinct because of the phase shift between the two legs. During the courtship behavior, a male may also demonstrate species-specific leg movements without producing the sound. We also take into account the whole visual display accompanying the courtship song in some species. And finally we analyze the frequency spectra of various parts of the song.

## Materials and methods

The courtship song was recorded when a male was sitting near-by a female. All song recordings were made in the laboratory. Both the sound and the movements of the hind legs were recorded with a custom-built opto-electronic device (Helversen & Elsner, 1977, Hedwig, 2000). A piece of reflecting foil was glued to the distal part of each hind leg femur of the male and two opto-electronic cameras were focused on the illuminated reflecting dots. Each camera was equipped with a position-sensitive photodiode that converted the upward and downward movements of the hind legs into voltage signals. These signals, together with the recordings of the sounds (a microphone type 4191, ½ inch; a conditioning amplifier type 2690; Brüel & Kjaer, Nærum, Denmark), were A/D-converted with a custom-built PC card. The sampling rate was 1325 Hz for recording the stridulatory movements and 100 kHz for sound recordings. The ambient temperature near the singing male was 30–32° C. The temporal parameters and power spectra of the songs were analyzed with COOLEDIT (Syntrillium, Seattle, WA) and TURBOLAB 4.0 (Bressner Technology, Gröbenzell, Germany). Courtship behaviour was also recorded with a Sony HDR-CX 260E digital video camera; the video signals were analyzed with the VIRTUAL DUB program.

Localities where the song recordings were made are shown in Fig. 1. The numbers of localities in the text correspond to the numbers on the map.

The basic map was taken from https://www.nationsonline.org/oneworld/asia_map.htm. Data on species distribution were obtained from Bei-Bienko & Mistshenko (1951) and Ragge & Reynolds (1998).

For the song description we used the following terms: *pulse*—the sound produced by one stroke of a hind leg and representing the shortest measurable unit; *syllable*—the sound produced by one complete up and down movement of the hind legs, starting when the legs leave their initial position and ending when the legs return to their original position; *element*—the sound produced by the same leg movements and usually including a series of equal syllables; *echeme*—series of consistent syllables separated by pauses (Fig. 2, 3).


**FIGURE 1.** Map of localities where the specimens were collected for the song recordings. Kazakhstan: 1—10 SE of Aktobe, near Aktjubinsk reservoir; 2—Akmola region, ab. 90 km SW of Kokshetau, near Balkashino; 3—Akmola region, ab. 60 km SE km of Nur-Sultan, environs of Vishnevka, near Vjacheslavskoe reservoir, 4—Akmola region, ab. 40 km NW of Ereimen-tau, Baysary; 5—Pavlodar region, ab. 48 km W of Ekibastuz, ab. 3 km W of Schiderty; 6—Pavlodar region, ab. 44 km SW of Pavlodar, environs of Pogranichnoe; 7—Pavlodar region, between Terenkol' and Beregovoe, near Irtysh river; 8—Pavlodar region, Zhelezinsky district, near Pyatiryzhsk; 9—Pavlodar region, environs of Irtyshsk; 10—Almaty region, ab. 60 km NE of Taldykorgan, near Kapal; 11- Almaty region, between Saryozek and Zharkent, environs of Basshi; 12—Almaty region, ab. 6 km SW of Zharkent; 13—Almaty region, ab. 4 km SE of Kegen, flood-lands of Kegen river; 14—Orenburg region, ab. 10 km W of Novosergievka; 15—ab. 10 km E of Orenburg, near Ural river; 16—Orenburg region, ab. 20 km NW of Orsk, environs of railway station Guberlja; 17—Altai Republic, ab. 26 km S of Shebalino, Semensky pass; 18—Altai Republic, ab. 26 km SE of Ongudai, environs of Kupchegen'.

## Results and discussion

### *Omocestus viridulus* (Linnaeus, 1758)

**Distribution.** From Western Europe to Siberia and Mongolia, moist habitats.

**Material. 17.** Russia, Altai Republic, ab. 26 km S of Shebalino, Semensky pass, 51°02.6' N, 85°36.3' E, 1705 m a.s.l., 07.08.2017, song recordings in 2 ♂.

**References to song.** Faber, 1953: verbal description only, calling and courtship songs; Elsner, 1974: recordings from Germany, courtship song; Waeber, 1989: recordings from Austria, courtship song; Hedwig & Heinrich, 1997: recordings from Germany, courtship song; Ragge & Reynolds, 1998: recordings from England, France and Spain, calling and courtship songs; Savitsky, 2005: recordings from the Caucasus, calling and courtship songs; Tishechkin & Bukhvalova, 2009a, b: recordings from Russia (Moscow region, Altai and Irkutsk region), calling song; Willemse *et al*., 2018: recordings from Greece, calling song.

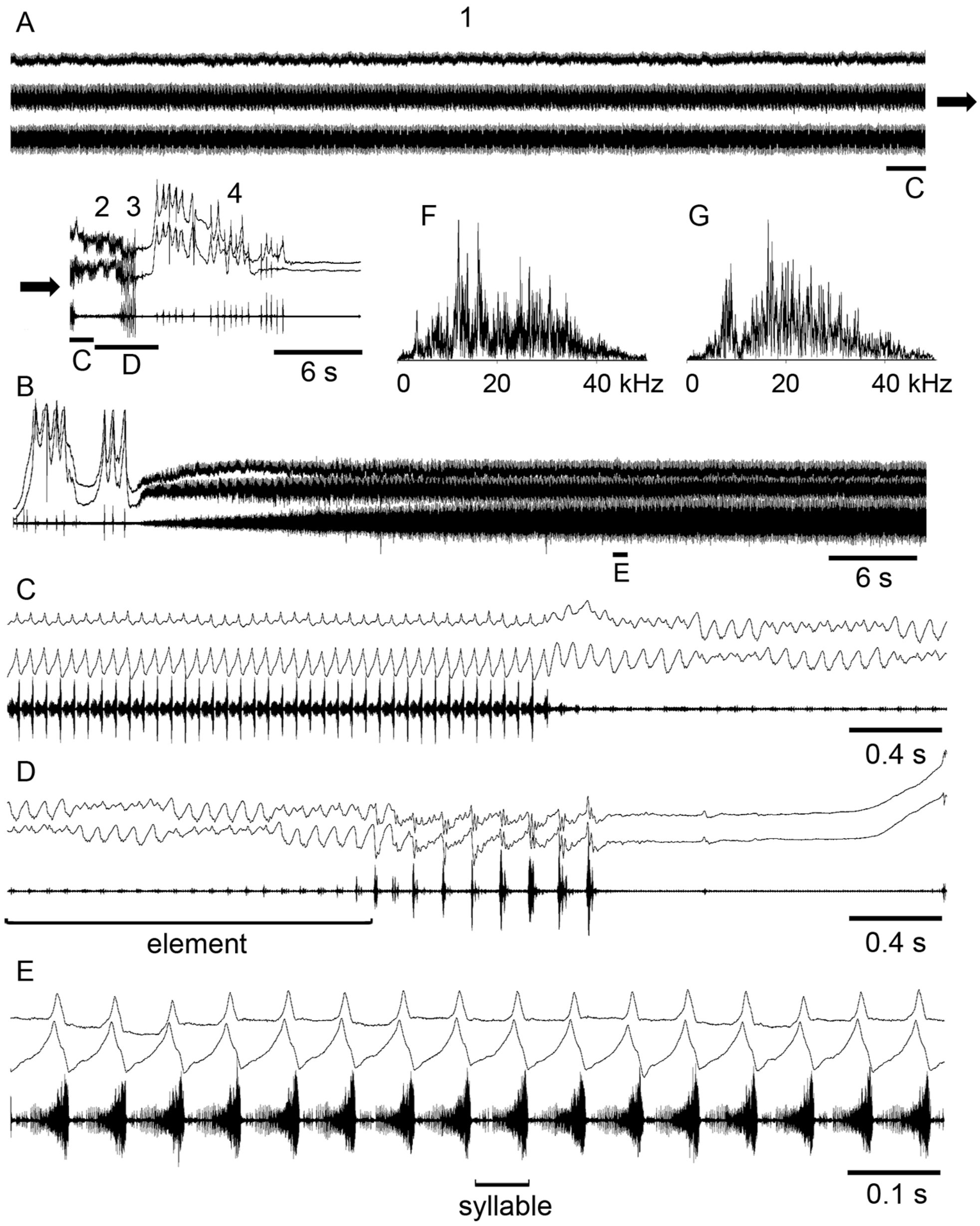


**FIGURE 2.** Oscillograms and frequency spectra of the courtship songs of two males (A, B) of *Omocestus viridulus* from Altai Republic. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in C–E). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–4. Frequency spectra shown for the elements 1 (F) and 3 (G).

**Song.** The first part of the courtship song (element 1) is similar to the calling song, but of longer duration (1–3 min, Fig. 2 A, B). It comprises an echeme consisting of syllables repeated at the rate of about 16–19/s. The echeme begins quietly reaching a maximum intensity after about 20 s. One hind leg is usually moved at a larger angle and with a slightly different pattern (leading leg) than the other leg (Fig. 2 C, E). After the element 1, there comes a completely different and much quieter echeme lasting 3–5 s (element 2, Fig. 2 C, D). The two legs start to alternate movements at the rate of about 13–15/s in a conspicuous manner: the leading leg moves with a larger amplitude producing simple up and down movements and the other leg moves with a smaller amplitude producing a more complex pattern. This complex pattern implies every two up and down leg-movements to be coupled in a characteristic way. Both legs repeatedly change their pattern in such a way that the leading leg produces the longer sequences of the high-amplitude movements than the other leg. This is followed by a series of loud syllables repeated at the rate of about 6–8/s (element 3, Fig. 2 D). During this element lasting about 1–1.5 s, the two legs are moved almost synchronously. Each syllable consists of one large and one or two small pulses. In about two seconds after the end of the element 3, the male raises both hind femora almost vertically and produces several pulses with irregular intervals of about 400–800 ms (element 4). These pulses, however, may also be produced just immediately before the first part of the courtship song (Fig. 2 B). The frequency spectra of the sound produced during various elements of the courtship song are broad, with a slightly different dominant frequencies for the first element (about 12 and 18 kHz) and for the third element (about 8 and 18 kHz) (Fig. 2 F, G).

**Comparative remarks.** Our recordings of the courtship songs of the specimens from Altai do not principally differ from the song recordings from Western Europe (Elsner, 1974; Waeber, 1989; Hedwig & Heinrich, 1997; Ragge & Reynolds, 1998). The authors, however, sometimes confused the pulses of the elements 3 and 4 of the courtship song, considering all of them as the pulses generated by 'precopulatory movements' that are followed by an attempt to copulate with a female. This confusion could originate from the similarity of the pulse structure in these elements of courtship. However, it must be emphasized that the above pulses are produced by completely different leg movements. Generation of the irregular pulses (the element 4) is apparently accompanied by a visual display. Ragge & Reynolds (1998) describe this visual display as kicking backwards with the hind tibiae. Unfortunately, we did not make video-recordings of courtship in *O. viridulus,* and therefore, we cannot confirm the statement about the kicking with the tibiae. On the other hand, the high raising of the hind legs on our oscillograms may indicate that this kicking could occur.

Savitsky (2005) distinguish only two parts in the courtship song of *O. viridulus* from Caucasus. These song parts could correspond to the elements 1 and 3 in our recordings. We, however, suppose that the element 2, very quiet part of the courtship song, is also present in the recordings of Savitsky but the pulses of the small amplitude are almost invisible on the oscillograms. It is very likely that this part of the song generated by alternating movements of the two legs serves rather as a visual cue than as a sound signal.

## *Omocestus haemorrhoidalis* (Charpentier, 1825)

**Distribution.** Transpalaearctic.

**Material.** Kazakhstan: **4.** Akmola region, ab. 40 km NW of Ereimentau, steppe near Baysary, 51°59.3' N, 72°42.1' E, 03.07.2019, song recordings in 1 ♂; **8.** Pavlodar region, Zhelezinsky district, environs of Pyatiryzhsk, 53°22.4' N, 75°33.6' E, 05.07.2019, song recordings in 2 ♂; **10.** Almaty region, environs of Kapal, 43° 08.4' N, 79° 01.3' E , 1220 m a.s.l., 01.07.2016, song recording in 1 ♂; **12.** Almaty region, ab. 6 km SW of Zharkent, pasture near fruit gardens, 44° 08.4' N, 79° 55.3' E, 06.07.2016, song recording in 1 ♂; **13.** Almaty region, ab. 4 km SE of Kegen, flood-lands of Kegen river, 42° 59.6' N, 79° 16.5' E, 07.07.2016, song recording in 1 ♂. Russia: **14.** Orenburg region, ab. 10 km W of Novosergievka, 52° 01.2' N, 53° 42.0' E, 13.07.2012, song recordings in 3 ♂; **15.** ab. 10 km E of Orenburg, near Ural river, 51º44.3' N, 55º20.8' E, 13–14.07.2012, song recordings in 2 ♂.

**References to song.** Faber, 1953: verbal description only, calling and courtship songs; Waeber, 1989: recordings from Spain and Turkey, calling song; Ragge & Reynolds, 1998: recordings from France, calling song; Savitsky, 2005, 2009: recordings from Russia (Volgograd and Astrakhan' regions), calling and courtship songs; Tishechkin & Bukhvalova, 2009a, b: recordings from Russia (Saratov region, Eastern Siberia, and Primorskiy Kray), calling song; Tishechkin, 2017: recordings from Kyrgyzstan, calling song; Willemse *et al*., 2018: recordings from Greece, calling song.

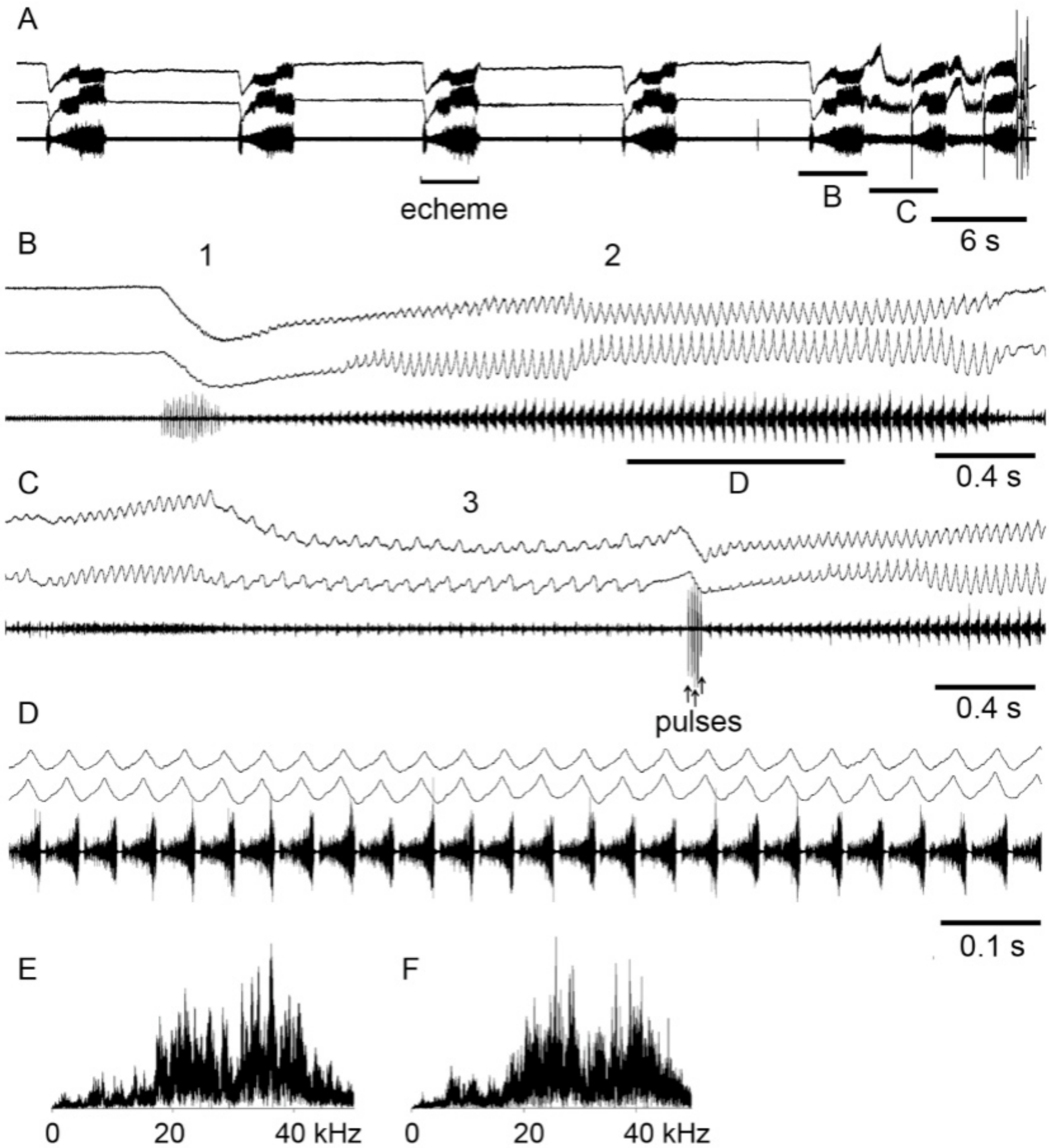


**FIGURE 3.** Oscillograms (A-D) and frequency spectra (E-F) of the courtship song of *Omocestus haemorrhoidalis* from Orenburg region. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in B–D). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–3. Frequency spectra shown for the elements 1 (E) and 2 (F).

**Song.** The courtship song (Fig. 3) starts with producing a single syllable of distinct pulses lasting about 100 ms (element 1, Fig. 3 B). This syllable is generated by synchronous down movements of both hind legs in a stepwise manner. The element 1 is immediately followed by an echeme similar to the calling song (element 2). It lasts about 3–4 s and consists of syllables repeated at the rate of about 25–30/s. The element 2 is also produced by almost synchronous leg movements. During calling, a male typically produces one echeme, whereas the courting male can emit many echemes containing both elements with the intervals varying in the range of about 8–20 s. In the developed courtship, one can distinguish the element 3 in the leg-movement pattern. After the element 2, the male raises both legs and produces similar up and down movements as before, which generate much quieter sound (Fig. 3 C). Then the legs are moved down and start to move in antiphase at the rate of about 10–13/s. During the element 3 that lasts about 1.4–2 s, the legs produce the low-amplitude pulses at the rate of about 22-25/s. The rate of these pulses is twice as high as the rate of the leg movements. The three elements are repeated from two to three times, followed by an attempt to copulate with a female (Fig. 3 A). The frequency spectra of the first and the second sound elements are broad and rather similar, but the dominant frequencies are much higher than in *O. viridulus*, with two maxima at around 22–25 kHz and 38–40 kHz.

**Comparative remarks.** Despite *O. haemorrhoidalis* often attracts the attention of bioacoustics, the courtship song of this species has been poorly studied. Savitsky (2005) describes courtship behaviour in one male from Astrakhan' region. The courtship song of this specimen includes two more elements that follow after the main echeme of the calling song type (element 2). These two elements, however, are completely different from those found in the courtship songs of our specimens from Orenburg region and Kazakhstan. According to the verbal description of Faber (1953), the courting males from Germany produce elements 1 and 2, but don't produce the element 3. Faber (1953) also mentions the difference in amplitude of movements between the two legs similarly to that we show in *O. viridulus* (Fig. 2 C, E). We, however, don't find the difference in the leg-movement amplitude in our specimens of *O. haemorrhoidalis*.

### ***Omocestus petraeus*** **(Brisout de Barneville, 1856)**

**Distribution.** From southern regions of Western Europe to southern Siberia.

**Material.** Russia: **14.** Orenburg region, ab. 10 km W of Novosergievka, 52° 01.2' N 53° 42.0' E, 13.07.2012, song recordings in 2 ♂; **15.** ab. 10 km E of Orenburg, near Ural river, N 51º44.3' E55º20.8', 13-14.07.2012, song recordings in 2 ♂; **3.** Kazakhstan, Akmola region, ab. 60 km SE km of Nur-Sultan, near Vjacheslavskoe reservoir, environs of Vishnevka, 50°54.6' N, 72°12.2' E, 11.07.2019, song recordings in 3 ♂.

**References to song.** Faber, 1953: verbal description only, calling and courtship songs; Waeber, 1989: recordings from former Yugoslavia and Turkey, calling and courtship songs; Ragge & Reynolds, 1998: recordings from France, calling and courtship songs; Savitsky, 2005, 2009: recordings from Russia (Volgograd and Astrakhan' regions), calling song; Tishechkin & Bukhvalova, 2009b: recordings from Russia (Saratov region), calling song; Willemse *et al*., 2018: recordings from Greece, calling song.

**Song.** The courtship song usually starts with the small-amplitude movements of one hind leg producing quiet pulses repeated at the rate of 13–19/s (element 1, Fig. 4 A–C). These quiet pulses are followed by an echeme of the calling song type (element 2). The element 2 consists of about 10–20 syllables. Each syllable lasts for about 250–400 ms reaching maximum intensity by half of its duration. All the syllables begin and end quietly, resulting to a spindle-shaped oscillogram. The syllable repetition rate is typically about 4/s at the beginning and about 2/s by the end. The syllables are produced either by synchronous (Fig. 4 E) or by antiphase movements (Fig. 4 F) of the hind legs. As a result, one could distinguish distinct double pulses separated by gaps or the pulses without gaps. The number of the leg movements producing a syllable varies in the range of about 20–30. Upon repetition of several echemes of the calling song type, the element 3 follows. One leg gradually rises and produces several up and down strokes until the leg reaches almost vertical position (Fig. 4 D). It is remarkable that almost no sound is produced during this gradual rise. After an abrupt down stroke, the legs vibrate at the rate of 4–6/s generating a syllable that lasts for about 300–400 ms. There come then several synchronous leg strokes followed by an attempt to copulate with a female. The main components of the frequency spectrum of the element 2 lie between 25 and 40 kHz (Fig. 4 G).

**Comparative remarks.** The courtship song of the specimens from Orenburg region and Kazakhstan basically differs from the courtship song of *O. petraeus* described by Ragge & Reynolds (1998) from France. The authors described the courtship syllables as the calling syllables but of a longer duration and with pulses repeated at the lower rate; no visual display (gradual rise of one leg) was documented in the specimens from France. Additionally, even the calling songs recorded from France (Ragge & Reynolds, 1998) and former Yugoslavia (Waeber, 1979) differ from the calling songs recorded from Russia (Savitsky, 2005; Tishechkin & Bukhvalova, 2009b) in the syllable duration (about 150 ms vs. 250–400 ms). The males recorded from Turkey (Waeber, 1989) also do not produce any visual display. At the same time, the specimens from Austria (Faber, 1953) produce single strokes with one leg after the main echeme, similarly to those recorded in specimens from Orenburg region and Kazakhstan.

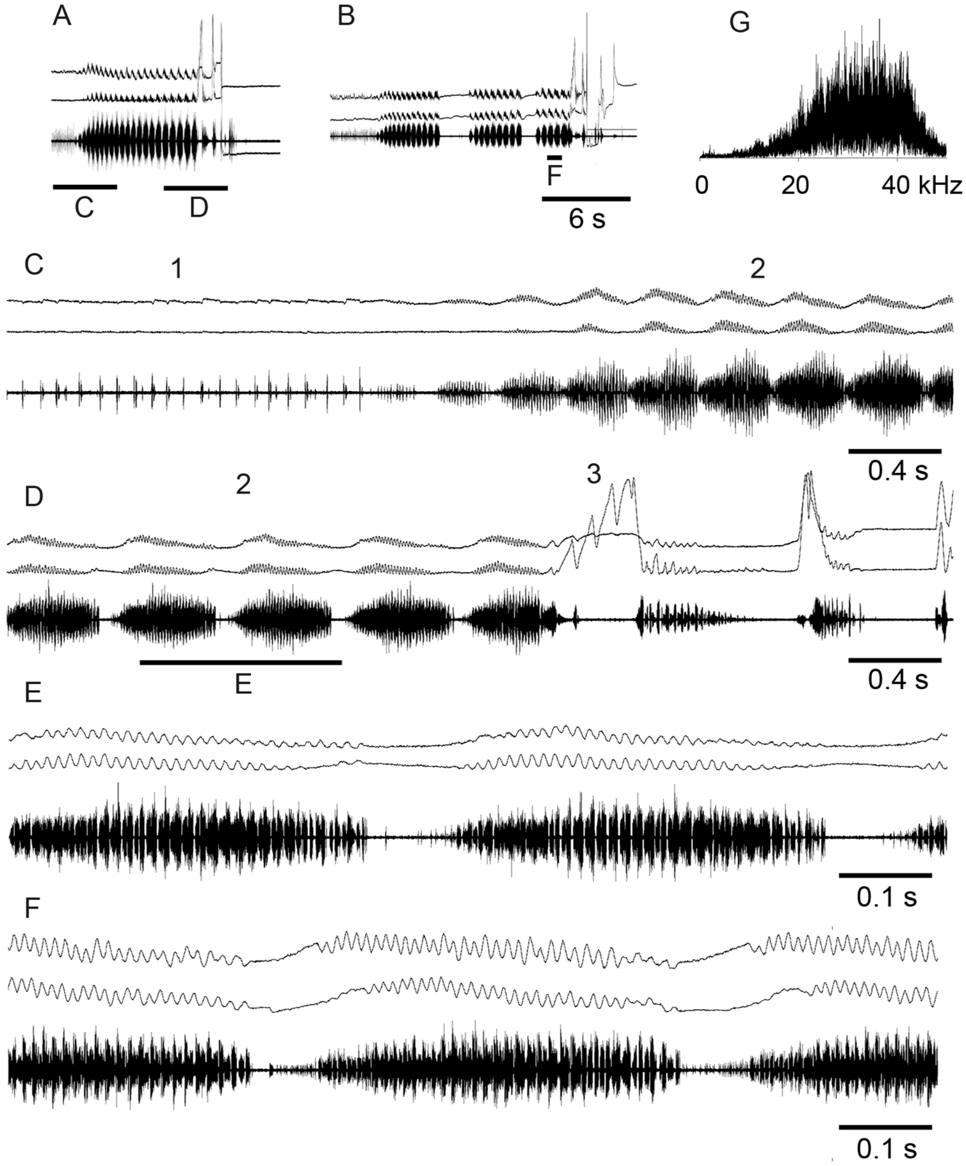


**FIGURE 4.** Oscillograms and frequency spectrum of the courtship songs of two males (A, B) of *Omocestus petraeus* from Orenburg region. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in C–F). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–3. Frequency spectrum (G) shown for element 2.

The visual display recorded in *O. petraeus* from Orenburg region and Kazakhstan appeared to be very similar to the visual display demonstrated by all species of the *Stenobothrus stigmaticus* group (Berger, 2008). Based on bioacoustics data, this group includes several west European species: *Omocestus antigay* (Bolivar, 1897), *O. bolivari* Chopard, 1939, *O. femoralis* Bolivar, 1908, *O. uhagonii* (Bolivar, 1876), *S. apenninus* Ebner, 1915, *S. ursulae* Nadig, 1986, and *S. stigmaticus* (Rambur, 1839). All species except *S. stigmaticus* are local endemics of Spain and Italy, and only *S. stigmaticus* has a wide distribution. During courtship, all these species produce up and down strokes at high amplitude by one leg, while the other leg does not move. Some of these species produce several strokes after the main echeme, with the two alternating legs (Berger, 2008). Similar visual display during courtship was also recorded in *O. minutus* Brullé, 1832 (Waeber, 1989; Vedenina, Mugue, 2011). It should be noted that all species attributed to the *S. stigmaticus* group and *O. minutus* have quite similar syllable structure of the calling song and of the main part of the courtship song. By contrast, the structure of the main syllables in *O. petraeus* greatly differs from the syllable pattern in the *S. stigmaticus* group and *O. minutus*. Nevertheless, all these species produce similar up and down strokes by one leg almost without sound in the end of courtship. The similarity of visual display in these species may indicate a common origin.

### *Myrmeleotettix pallidus* (Brunner von Wattenwyl, 1882)

**Distribution.** South-eastern part of European Russia, Kazakhstan, Altai, south-western Siberia.

**Material.** Kazakhstan: **4.** Akmola region, ab. 40 km NW of Ereimentau, steppe near Baysary, 51°59.3' N, 72°42.1' E, 03.07.2019, song recording in 1 ♂; **5.** Pavlodar region, ab. 48 km W of Ekibastuz, steppe ab. 3 km W of Schiderty, 51°42.9' N, 74°38.5' E, 04.07.2019, song recording in 1 ♂; **9.** Pavlodar region, environs of Irtyshsk, 53°20.2' N, 75°25.8' E, 05.07.2019, song recordings in 3 ♂.

**References to song.** Savitsky, 2005, 2009: recordings from Russia (Volgograd region), calling and courtship songs.

**Song.** The courtship song starts with alternating movements of the two hind legs (element 1, Fig. 5 A, C). One leg produces from 10 to 15 low-amplitude up and down movements, whereas the other leg doesn't move. Next, the legs change the roles. Despite the two legs demonstrate similar movement patterns, one leg produces the pulses of larger amplitude than the other leg. Thus, the syllables of larger pulses alternate with the syllables of the smaller pulses. Sometimes the legs do not show regular alternation of vibrations and pauses, in which case the pulse amplitude varies randomly (Fig. 5 D). The pulse repetition rate is typically about 40–55/s. This element lasting 6–10 s follows by the element 2 of the courtship song, which is similar to the calling song (Fig. 5 E). It lasts 1–3 s and consists of the syllables repeated at the rate of about 10–20/s. Each syllable is usually composed of 7–10 pulses that reach maximum intensity in the end of each syllable. During the element 2, the legs are moved almost synchronously (Fig. 5 F). The two elements alternate during several minutes. Thereupon, the element 2 is followed by the element 3 that is accompanied by a visual display (Fig. 5 E, G). The legs are lifted to an extra high position and are moved according to a specific pattern, which is nearly similar to the pattern of the element 2, but the very movements are larger in amplitude. The rate of the principal leg-movements is about 16/s, and superimposed on these movements there are the small-amplitude vibrations of the rate of about 90–110/s. The amplitude of syllables gradually increases so that the last syllable is the loudest. During the element 3, a male is also conspicuously moving his clubbed antennae in horizontal plane (Fig. 6). Immediately after the element 3, the element 4 is emitted. It is produced by synchronous, low-amplitude movements of the legs and lasts about 6–10 s. A low-amplitude pulse is produced during up-stroke, whereas a high-amplitude pulse is generated during down-stroke. Sometimes, the low-amplitude pulses are almost invisible on the oscillogram. The syllable rate in the element 4 is about 50–63/s. After the element 4, there is a sequence of the elements 1–4; several sequences are followed by precopulatory movements and an attempt to copulate with a female (Fig. 5 A, B). The frequency spectra of the sound produced during various parts of the courtship song are different. The frequency spectrum the element 2 has the main maxima around 25 and 28 kHz; the spectrum of the element 3 has many periodical peaks in the broad range of 15–45 kHz; the spectrum of the element 4 has main components between 25 and 45 kHz (Fig. 5 H–J).

**Comparative remarks.** Our recordings of the courtship song in *M. pallidus* from Kazakhstan do not basically differ from the recordings of this species from Volgograd region (Savitsky, 2005). However, there are some minor differences. First, we found the difference in the fine temporal structure of the syllables in the song element 4. In the song recordings from Volgograd, the pulses of the element 4 are of similar amplitude, whereas the analysis of the recordings from Kazakhstan reveals the alternation of the low-and the high-amplitude pulses. In addition, the syllables of the element 3 are the loudest ones in the recordings from Volgograd (Savitsky, 2005), whereas in our

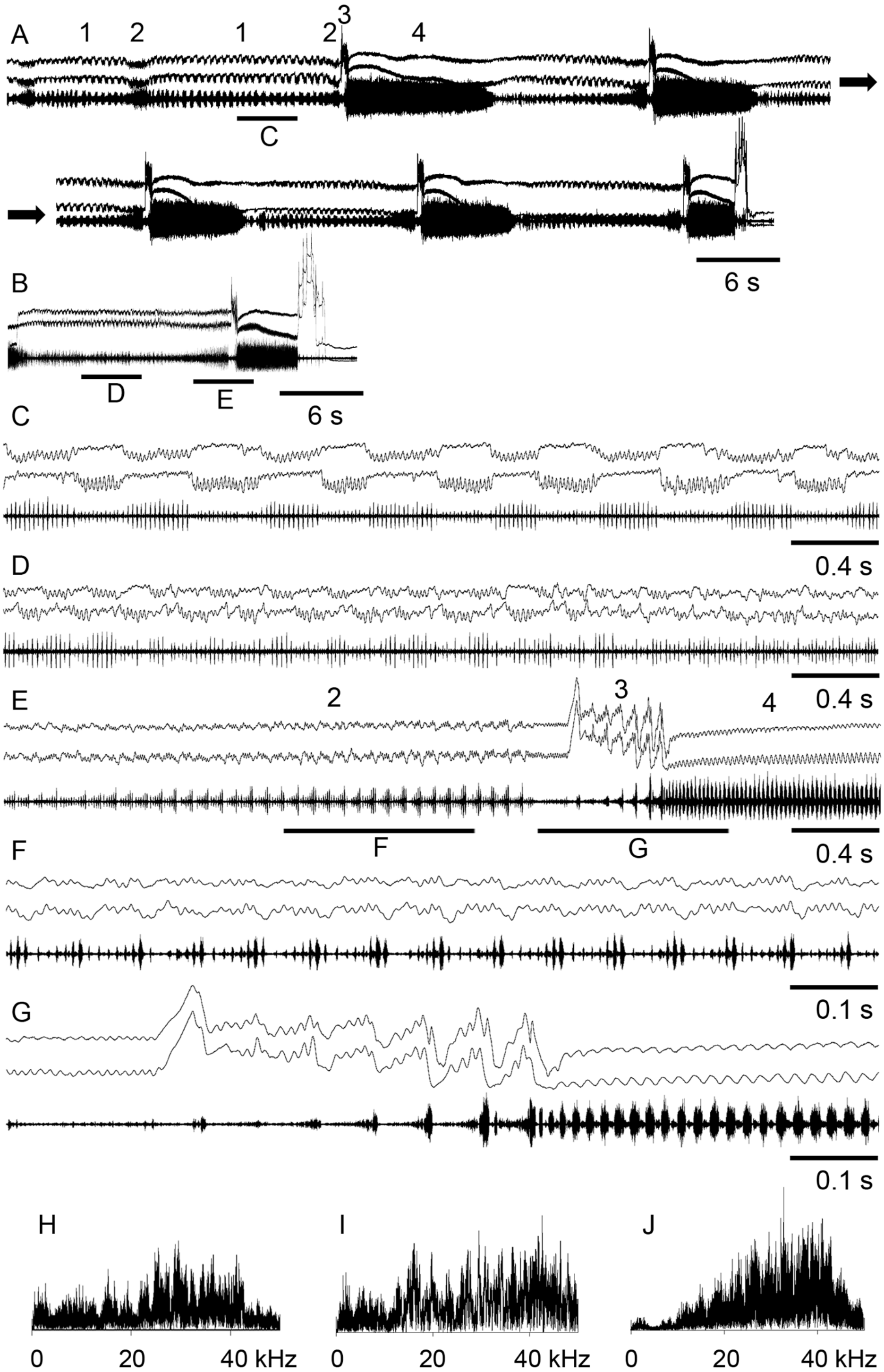


**FIGURE 5.** Oscillograms and frequency spectra of the courtship songs of two males (A, B) of *Myrmeleotettix pallidus* from Pavlodar region. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in C–G). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–4. Frequency spectra shown for the elements 2 (H), 3 (I) and 4 (J).

recordings, the element 4 is the loudest. This can be explained by different frequency characteristics of these two elements. A more broad-band sound is typical for the syllables of the element 3, whereas dominant frequencies of the element 4 shift to the ultrasound band (Fig. 5 I, J). The recordings of Savitsky (2005) were made in the field with cassette recorders; the upper frequency limit was not higher than 15 kHz. This could explain why the amplitude ratio of the elements 3 and 4 of the courtship song might be distorted in the recordings from Volgograd. The distortion of the frequency characteristics may also explain the difference in the pulse structure of the element 4 between the recordings from Volgograd region and Kazakhstan. Finally, Savitsky (2005) does not mention any movements with antennae during courtship.

The movements with antennae during courtship are typical for all three species of *Myrmeleotettix* studied so far. In *M. maculatus* (Thunberg, 1815) and *M. antennatus* (Fieber, 1853), antennae are moved in longitudinal plane—back and forth over the head (Bull, 1979; Berger & Gottsberger, 2010; Vedenina & Shestakov, 2014). In some other grasshopper species of the genera *Stenobothrus, Gomphocerus* and *Gomphocerippus* (Elsner, 1974; Ostrowski *et al*., 2009) antennae are also swung mainly in longitudinal plane. Strokes with antennae are supposed to originate from the disturbance reactions (Willey & Willey, 1969; Berger & Gottsberger, 2010), which can be frequently observed when animals are disturbed or touched by other animals or an experimenter. In this case the animals raise antennae into an opposite side of the disturbing interference, which usually means backwards. By contrast, in *M. pallidus* antennae are moved in horizontal plane (from side to side). Such pattern of the antennae movements seems to be unique among Gomphocerinae.

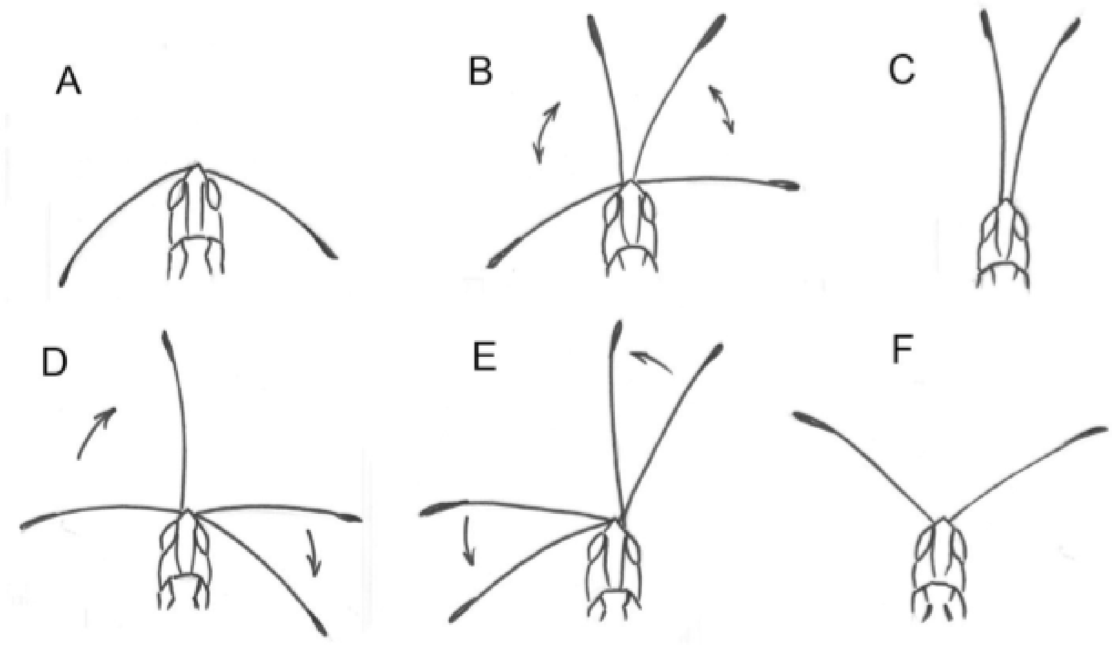


**FIGURE 6.** Movements of antennae during the element 3 of courtship in *Myrmeleotettix pallidus.* Figures A–F demonstrate successive stages of the antennae position.

### *Stenobothrus miramae* Dirsh, 1931

**Distribution.** South-eastern part of European Russia, Crimea, western Kazakhstan.

**Material. 16.** Russia, Orenburg region, ab. 20 km NW of Orsk, environs of railway station Guberlja, 51°17.2’ N, 58°10.6’ E, 29.06.2018, song recordings in 5 ♂.

**References to song.** Waeber, 1989: recordings *S. nigrogeniculatus* Kr. from Asia Minor, calling song; Bukhvalova & Vedenina, 1998: recordings from Crimea and Russia (Orenburg region), calling song; Tishechkin & Bukhvalova, 2009b: recordings from Crimea, calling song; Berger, 2008: recordings of *S. nigrogeniculatus* Kr. from Asia Minor, calling and courtship songs.

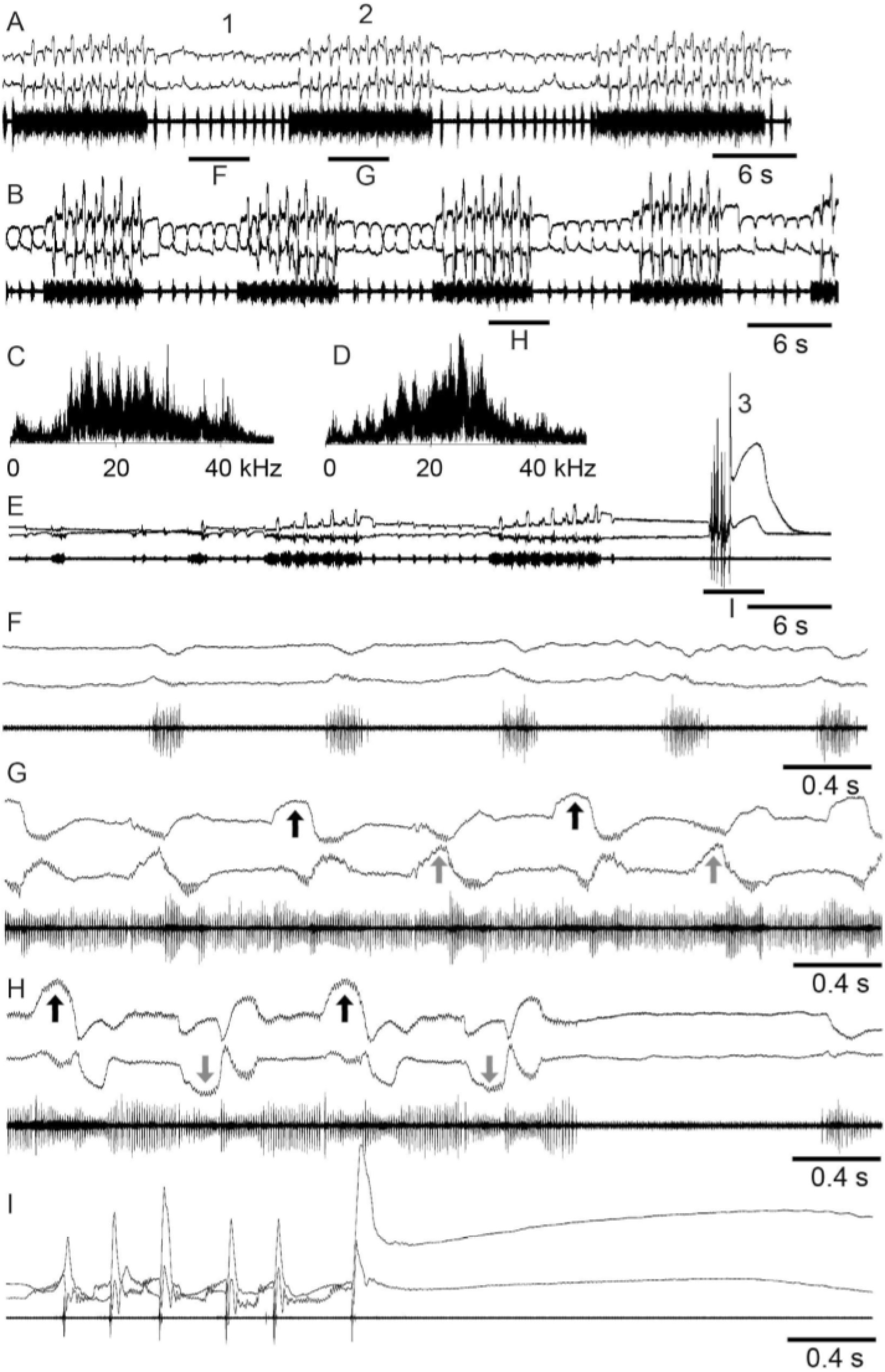


**FIGURE 7.** Oscillograms and frequency spectra of the courtship songs of three males (A, B, E) of *Stenobothrus miramae* from Orenburg region. Song recordings are presented at two different speeds (faster oscillograms of the indicated parts of the songs shown in F–I). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–3. The arrows (G, H) show the period of the leg movements. Frequency spectra shown for the elements 1 (C) and 2 (D).

**Song.** The courtship song of *S. miramae* (Fig. 7) contains no elements similar to the calling song. The element 1 of the courtship song is produced by the low-amplitude leg movements generating syllables repeated at the rate of about 1–1.5/s (Fig. 7 F). Each syllable lasting for about 200–250 ms is usually composed of approximately 20 pulses, repeated at the rate of about 95–105/s. In 4.5–7 s, the element 2 follows, lasting 6–8 s and generated by incredibly complex leg movements. The leg-movement analysis reveals about 5-8 long syllables repeated at the rate of about 0.6–0.7/s. One leg is moved up reaching the highest position, then it is moved down, and next it is slightly lifted and kept in intermediate position; in about 400 ms, the leg is moved down and then up, but the amplitude of these movements is lower than during the previous up and down movements (Fig. 7 G). Thereupon the leg is again kept in intermediate position, until the leg is moved up into the highest position. Superimposed on these slow movements are the small-amplitude vibrations of about 90–100/s. Another leg can be moved in about similar pattern but shifted in phase by half a period, or another leg can be moved in a completely different pattern, which can be interpreted as a mirror reflection of the first leg movement, and also with the phase shift (Fig. 7 H). The oscillographic analysis of the sound shows continuous series of pulses of varying amplitude repeated at the rate of about 90–100/s. The elements 1 and 2 are usually alternated for more than 2 min, and are finally followed by the element 3 (Fig. 7 E, I). A male sitting in front of a female hits the female several times with the head (Fig. 8 A). Then the male slowly raises both hind femora through an angle of more than 90° so that the knees appear to be over his head (Fig. 8 B) and keep them in this position for about 5–20 s. The frequency spectra of the elements 1 and 2 have many dominant peaks between 10 and 30 kHz, but one peak around 26 kHz is maximal on the spectrum of the element 2 (Fig. 7 C, D).

**Comparative remarks.** The courtship song of *S. miramae* is shown for the first time. However, it is almost identical to the courtship song of *S. nigrogeniculatus* Kr. (Berger, 2008). Taking into account the similarity in the calling songs between these species (e. g. Bukhvalova & Vedenina, 1998; Berger, 2008), one could suggest a synonymy of these species. According to Berger (2008), *S. nigrogeniculatus* has unusual history. This species was described by Krauss in 1878 from Dalmatia but afterwards, it was only recorded from Turkey. In all further works (e. g. Bei-Bienko & Mistshenko, 1951; Karabag, 1958; Demirsoy, 1977) the Turkish specimens were named under *S. nigrogeniculatus,* but they are suggested by Berger (2008) to be different in morphology and song from the animals described by Krauss. Thus, further taxonomic studies are necessary to solve the problem of the synonymy in this group.

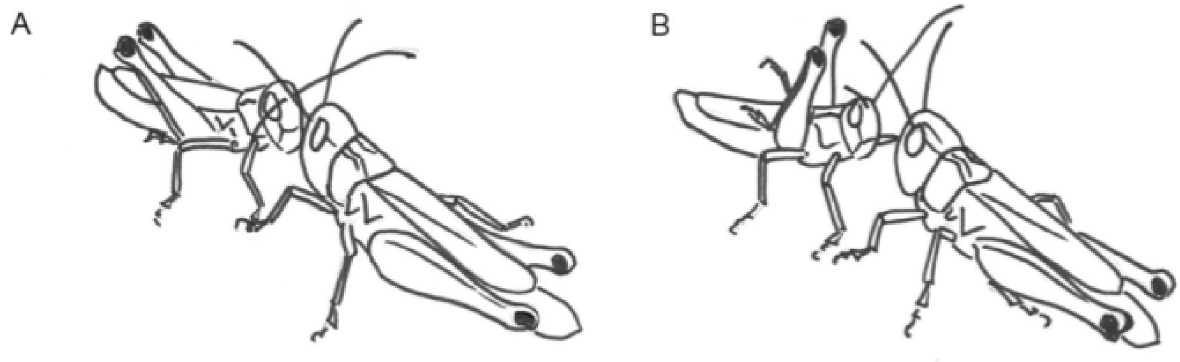


**FIGURE 8.** Positions of a male of *Stenobothrus miramae* during the element 3 of courtship. (A) The male hits a female several times with his head; (B) the male slowly raises both hind femora and keeps them over head.

### *Gomphocerus sibiricus* (Linnaeus, 1767)

**Distribution.** Scandinavia, northern half of European Russia, Siberia, northern part of the Russian Far East, steppes of Mongolia and northern China. Mountains of Western Europe, Asia Minor, the Caucasus, Central Asia and Tibet.

**Material. 2.** Kazakhstan, Akmola region, 90 km SW of Kokshetau, environs of Balkashino, meadows near the forest, 52°30,4’ N, 68°43,2’ E, 26.06.2018, song recordings in 4 ♂.

**References to song.** Faber, 1953: verbal description only, calling and courtship songs; Elsner, 1974: recordings from Switzerland, courtship song; Ragge & Reynolds, 1998: recordings from France and Italy, calling and

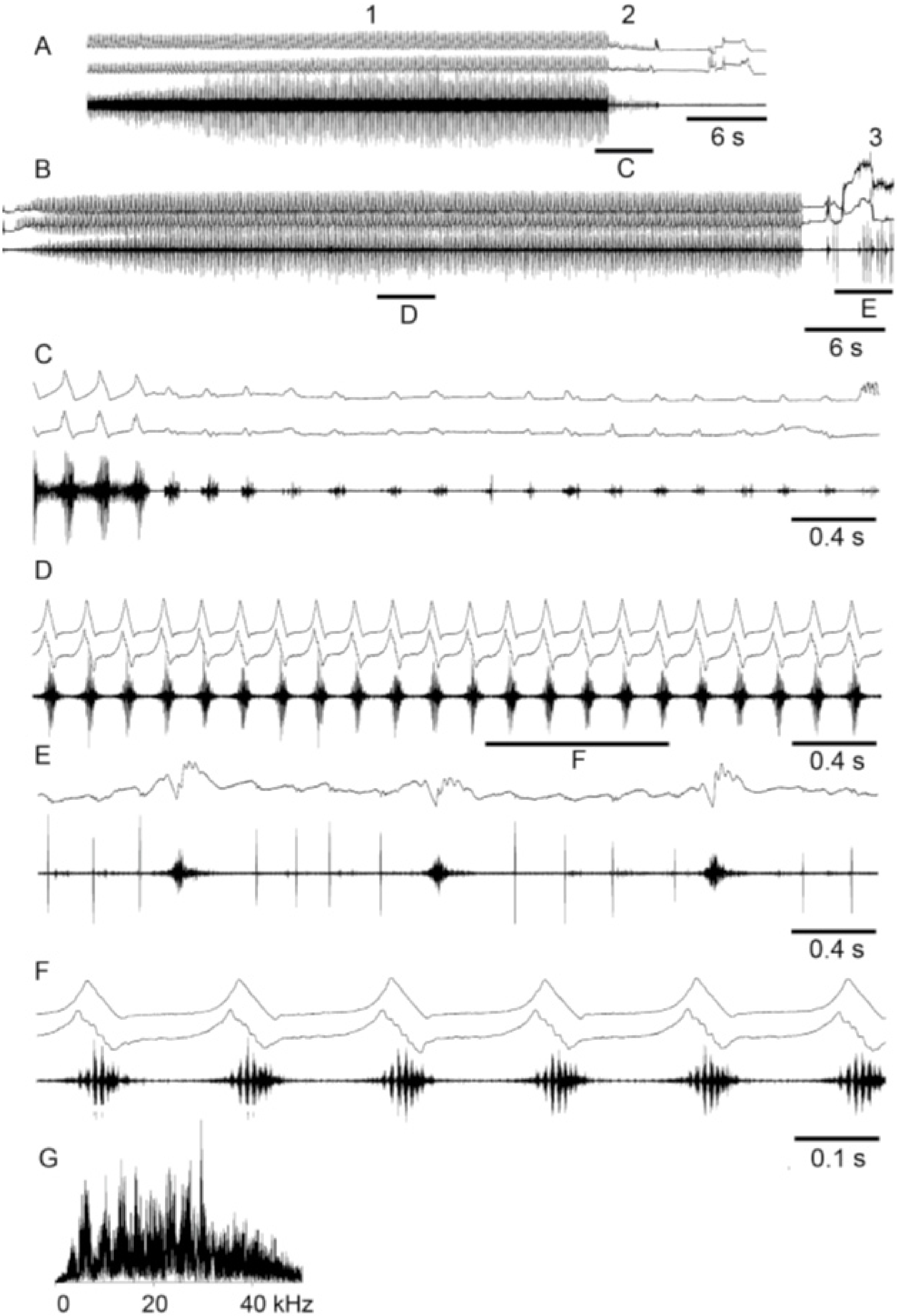


**FIGURE 9.** Oscillograms and frequency spectrum of the courtship songs of two males (A, B) of *Gomphocerus sibiricus* from Akmola region. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in C–F). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–3. Frequency spectrum shown for the element 1 (G).

courtship songs; Bukhvalova & Vedenina, 1998: recordings from Russia (Chita region), calling song; Tishechkin & Bukhvalova, 2009b: recordings from Russia (Buryatia), calling song; Tishechkin, 2017: recordings from Russia (Irkutsk region) and Kyrgyzstan, calling song; Willemse *et al*., 2018: recordings from Greece, calling song.

**Song.** The courtship song of *G. sibiricus* starts as an echeme similar to the calling song but lasting longer, up to 2 min (element 1). The echeme begins quietly, reaching maximum intensity in about 6–12 s (Fig. 9 A, B). The echeme consists of syllables repeated at the rate of about 5-6/s. The hind legs are almost synchronously moved up and down, but the sound (6-7 pulses) is only produced during the down-stroke (Fig. 9 F). One leg is usually moved down gradually, whereas another leg is moved down in a stepwise manner. The frequency spectrum of the sound occupies a broad band up to 50 kHz with many maxima in the range of 5–30 kHz (Fig. 9 G). The element 1 is sometimes followed by a series of much quieter syllables (element 2 or 'aftersong') repeated at the rate similar to that in the main echeme (Fig. 9 A, C). The main echeme with 'aftersong' or without it may be repeated several times until a male would reach a high degree of excitation. Then, the male demonstrates a complex visual display. The anterior part of the body is raised, the palps are moved, and the clubbed antennae are swung in such a way as they describe a cone (Fig. 10). Simultaneously with the antennae movements, the legs produce 3–4 short pulses and one longer pulse (Fig. 9 E). This visual display may be repeated several times before the male attempts to copulate with a female.

The attempt to copulate in *G. sibiricus* is accompanied by boxing movements with the fore legs unusual for other gomphocerine grasshoppers (Fig. 11). The *G. sibiricus* males have conspicuously swollen fore tibiae. During climbing on the female, the male beats her with his fore tibiae, lifting them almost vertically and dropping them at the rate of about 20/s.

**Comparative remarks.** Our recordings of *G. sibiricus* from Kazakhstan do not differ from the recordings made by various authors from other regions. However, in *G. sibiricus* from Switzerland (Elsner, 1974) both legs always produce identical stridulatory pattern. By contrast, it often happens in the specimens from Kazakhstan that one leg is moved down gradually, whereas another leg is moved down in a stepwise manner.

Despite courtship behaviour of *G. sibiricus* has been previously described from Western Europe (Faber, 1953; Elsner, 1974; Ragge & Reynolds, 1998), there are no figures that illustrate the antennae movements. The characteristic boxing movements that precede mating are also not comprehensively discussed in the literature, despite the video recordings of these movements are available in Internet (e.g. https://www.youtube.com/watch? v=F3e3kSuD-_A). The swollen fore tibiae of *G. sibiricus* are a characteristic feature of this species used in various taxonomic keys, but the function of this feature is not usually discussed. It is very likely that the males box the females to stimulate them to mate. Thus, sexual selection is suggested to be the main driving force for evolving the swollen fore tibiae in *G. sibiricus* males.

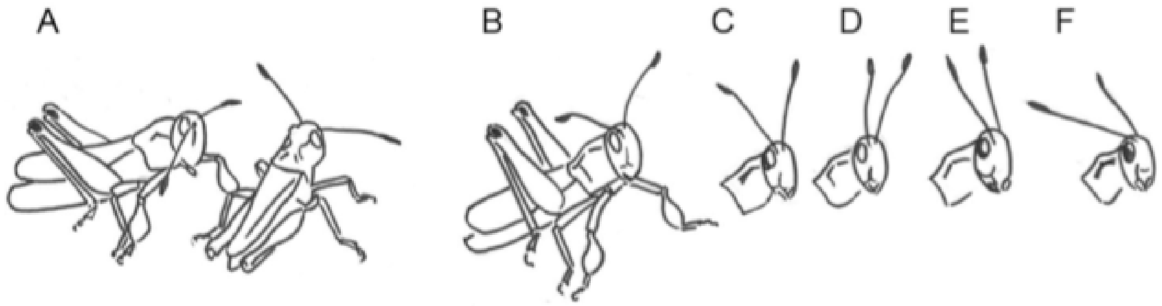


**FIGURE 10.** Positions of antennae in a male of *Gomphocerus sibiricus* during courtship, when producing the element 1 (A), when producing the element 3 (B–F). The antennae are swung in such a way as they describe a cone when producing one longer pulse and 3–4 shorter pulses (see Fig. 9 E).

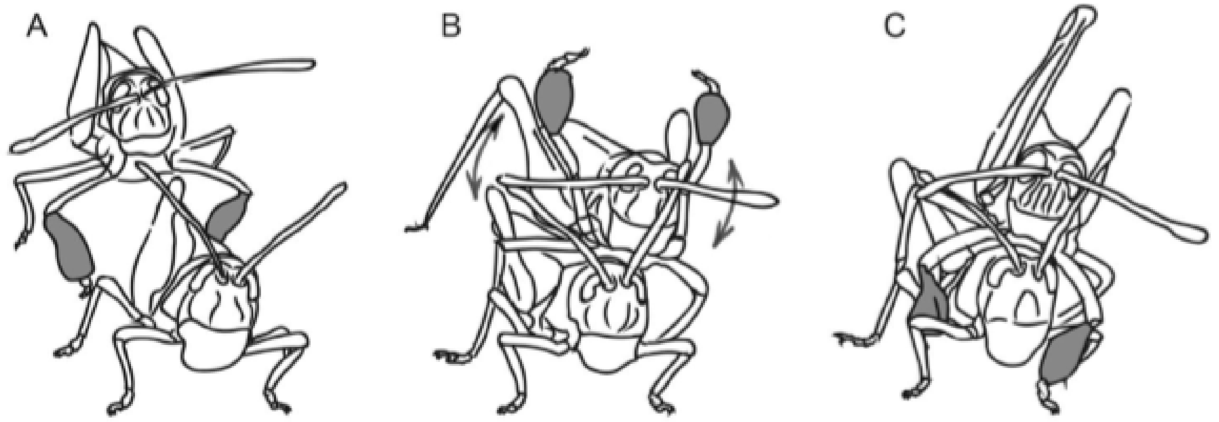


**FIGURE 11.** The boxing movements of a male of *Gomphocerus sibiricus* during mounting a female. (A) The male starts to climb the female; (B) the male lifts fore legs with swollen tibiae (marked by grey colour); (C) the male beats the female with swollen tibiae.

### *Chorthippus dubius* (Zubovski, 1898)

**Distribution.** South-eastern part of European Russia, Siberia, northern and eastern Kazakhstan, Mongolia, northern China.

**Material. 18.** Russia, Altai Republic, ab. 26 km SE of Ongudai, environs of Kupchegen', 50°37.3' N, 86°26.2' E, 922 m a.s.l., 08.08.2017, song recordings in 3 ♂.

**References to song.** Bukhvalova & Zhantiev, 1994: recordings from Tyva, calling song; Benediktov, 2005: recordings from southern Siberia, calling song.

**Song.** The courtship song of *Ch. dubius* starts as an echeme similar to the calling song but lasting longer, up to 20 s. The echeme begins quietly, reaching maximum intensity in about 8–10 s (element 1, Fig. 12 A). The element 1 contains syllables repeated at the rate of about 6–7/s. The hind legs are almost synchronously moved up and down. During the gradual up-stroke the legs produce a soft noisy sound, whereas during the stepwise down-stroke the legs generate 5–6 loud pulses (Fig. 12 D). This echeme can be repeated one-two times, and then 5–10 loud syllables of another temporal structure immediately follow (element 2, Fig. 12 C, E). They are repeated at the rate of about 13/s. In contrast to the element 1, the syllables of the element 2 are produced by gradual up- and down-strokes and do not contain distinct pulses. In about middle of the element 2, a male generates one high-amplitude stroke with the hind legs producing a syllable of dense pulses. The two elements can be repeated two–three times. The dominant frequencies of the spectrum lie between 20 and 40 kHz. The frequency spectrum of the element 1 has five clear harmonics in this band (Fig. 12 F), whereas the harmonics are not so obvious on the spectrum of the element 2 (Fig. 12 G).

**Comparative remarks.** The courtship song of *Ch. dubius* has been recorded for the first time.

### *Chorthippus karelini* (Uvarov, 1910)

**Distribution.** North-eastern part of Asia Minor, very locally in Ukraine (Askania-Nova), south-eastern part of European Russia, Transcaucasia, Kazakhstan, Siberia eastwards to Irkutsk region.

**Material.** Kazakhstan: **1.** 10 SE of Aktobe, near Aktjubinsk reservoir, 50°09.6' N, 57°18.8' E, 25.06.2018, song recordings in 4 ♂; **6.** Pavlodar reg., ab. 44 km SW of Pavlodar, environs of Pogranichnoe, 52° 05.4' N, 76°24.9' E, 04.07.2019, song recording in 1 ♂; **7.** Pavlodar region, between Terenkol' and Beregovoe, near Irtysh river, 53° 05.1' N, 75°56.6' E, 05.07.2019, song recordings in 2 ♂; **10.** Almaty region, ab. 60 km NE of Taldykorgan, near Kapal, 43° 08.4' N, 79° 01.3' E, 1220 m a.s.l., 01.07.2016, song recordings in 2 ♂.

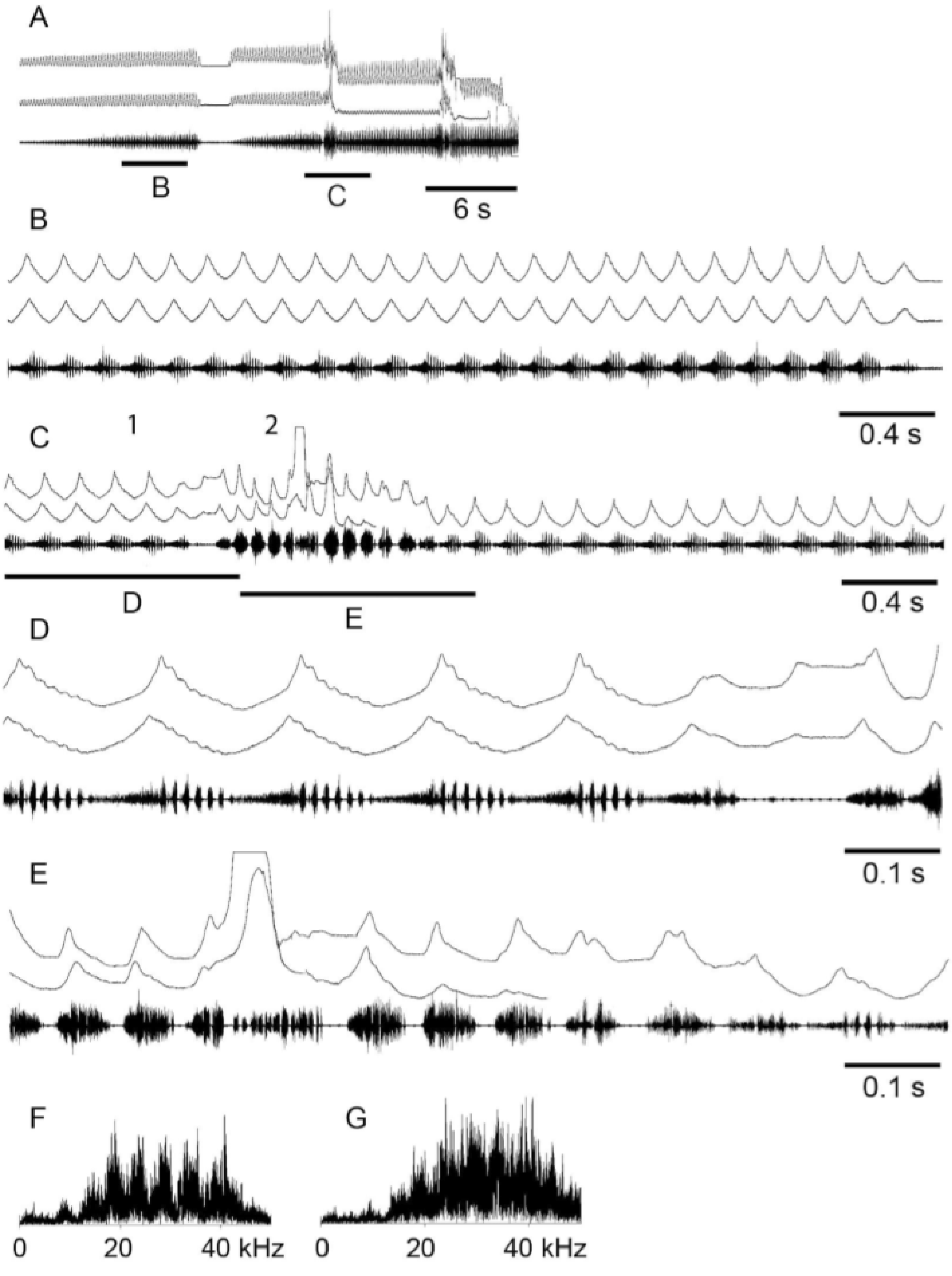


**FIGURE 12.** Oscillograms and frequency spectra of the courtship song of *Chorthippus dubius* from Altai. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in B–E). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–2. Frequency spectra shown for the element 1 (F) and the element 2 (G).

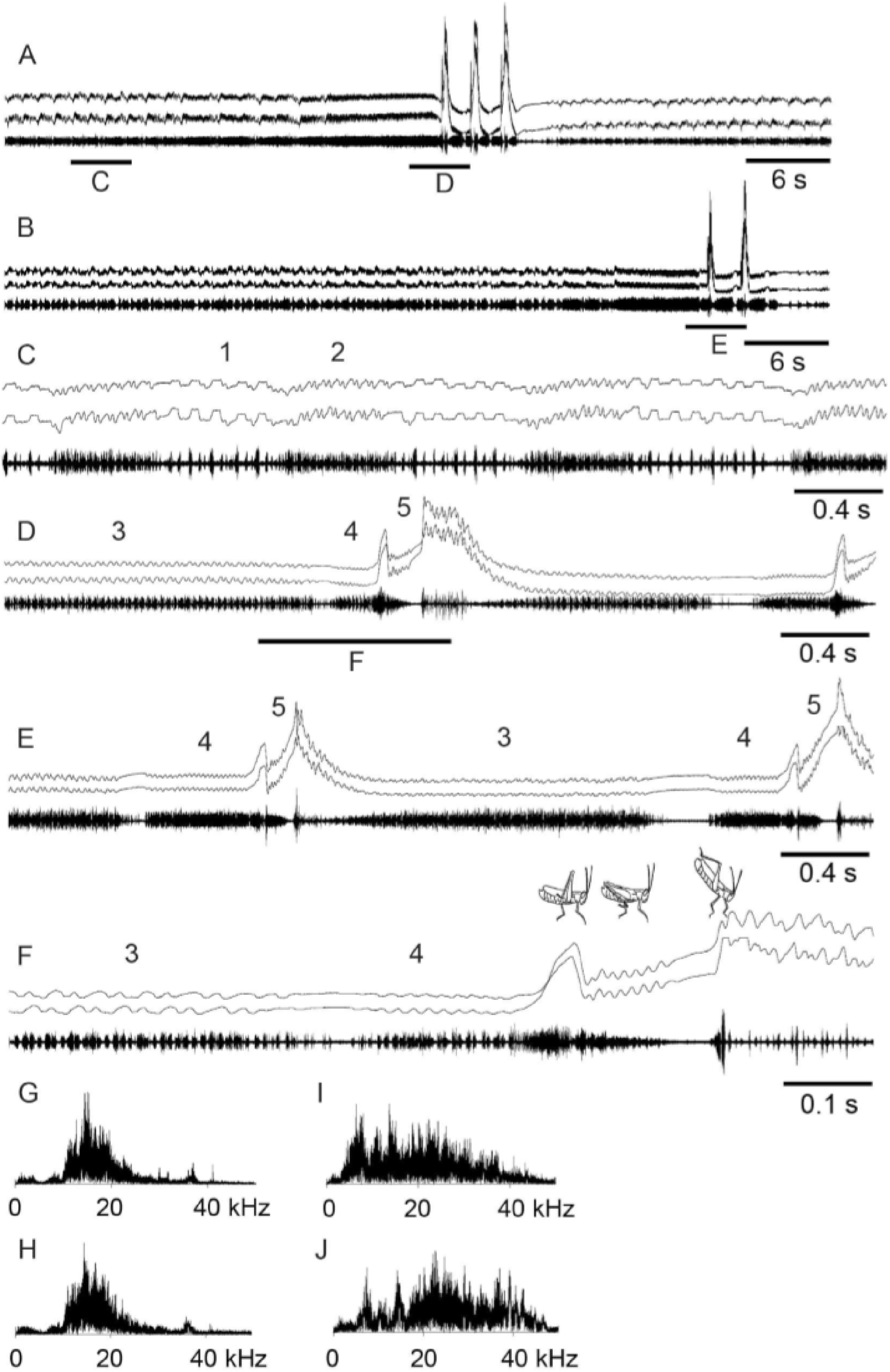


**FIGURE 13.** Oscillograms and frequency spectrum of the courtship songs of two males of *Chorthippus karelini* from Almaty region (A) and Aktobe region (B). Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in C–F). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–5, drawings show different positions of the hind legs and abdomen at the corresponding moments of the song. Frequency spectra shown for the element 3 (G), the element 4 (H), the element 5 (I–J).

**References to song.** Helversen, 1986: recordings from Asia Minor, calling and courtship songs; Vedenina & Bukhvalova, 2001: recordings from Russia (Altai and Tyva), calling song; Benediktov, 2005: recordings from southern Siberia, calling and courtship songs; Savitsky & Lekarev, 2007: recordings from Russia (Volgograd and Astrakhan' regions), calling and courtship songs; Bukhvalova & Tishechkin, 2009: recordings from Russia (Irkutsk region), calling song; Savitsky, 2009: recordings from Russia (Volgograd region), calling song; Vedenina & Helversen, 2009: recordings from Ukraine (Kherson region), Russia (Volgograd region), Turkey and Italy, calling and courtship songs; Vedenina, 2015: recordings from Ukraine (Kherson region) and Russia (Saratov, Samara and Orenburg regions), courtship song.

**Song.** The courtship song (Fig. 13) starts with alternation of two elements, which are repeated with the period of about 1 s (Fig. 13 C). When producing the element 1, the legs vibrate synchronously at the rate of about 10–11/s. When producing the element 2, the two hind legs vibrate with a phase shift at the rate of about 26–32/s in a complex pattern: every two up and down leg movements are coupled in a characteristic way. Oscillographic analysis shows that the syllables of the element 1 consist of the well pronounced pulses repeated at the rate of 21–24/s, whereas the syllables of the element 2 contain much more dense pulses following almost without gaps. The alternations of these two elements can last up to 2–3 min, followed by a complex of three more elements. The element 3 of the *Ch. karelini* song is similar to the element 2, but is remarkably longer, reaching 4–8 s in duration; the pulses of the element 3 are separated by gaps and repeated at the rate of about 98–103/s (Fig. 13 F). Then comes a rather short (200–400 ms), element 4; sometimes, one can distinguish in it the distinct pulses. The element 4 is produced by almost synchronous leg vibrations at the rate of about 40–53/s. A subsequent element 5 is accompanied by two fast strokes of the legs (Fig. 13 D–F). During a first stroke, a short (about 100 ms) noisy sound is generated; this is followed by high-frequency leg vibrations that also produce a noisy sound lasting for 100–200 ms. A second stroke is accompanied with lifting of abdomen and produced with the tibiae; the maximal angle between tibia and femur is 30°. Both strokes are produced with synchronous movements of the two legs, but most of the element 5 is generated by alternate leg movements (Fig. 13 F). During the second stroke, a short loud pulse is produced, followed by a quieter syllable of distinct pulses lasting for 200–300 ms. The element 5 reminds the calling song of *Ch. karelini*; however, both strokes in the element 5 are of higher amplitude and of shorter duration than in the calling song (Vedenina & Helversen, 2009). The complex of the elements 3, 4 and 5 is usually repeated 2–3 times, and then again followed by the alternation of the elements 1 and 2. A male tries to copulate with a female after the element 5. The frequency spectra of elements 3 and 4 are much more narrow (10–20 kHz) than the spectra of the element 5 (5–40 kHz) (Fig. 13 G–J).

**Comparative remarks.** The recordings of courtship song in *Ch. karelini* from Kazakhstan do not differ from the recordings from Asia Minor, Ukraine and south-east of European Russia (Vedenina & Helversen, 2009; Vedenina, 2015). Our recordings, however, slightly differ in the relative amplitude of the elements 3, 4 and 5 from those made by Benediktov (2005) and Savitsky & Lekarev (2007). The differences may arise from the distortions of the relative amplitude in various elements, similarly to those shown in *M. pallidus*. The recordings of Benediktov (2005) and Savitsky & Lekarev (2007) were made with the filed cassette recorders with the upper frequency limit not exceeding 15 kHz. Thus, the elements that have broader frequency spectra extending to the ultrasound band have smaller amplitude than the elements with the frequency spectra that lie below 20 kHz.

### *Chorthippus angulatus* Tarbinsky, 1927

**Distribution.** Southern and south-eastern Kazakhstan, Middle Asia.

**Material. 11.** Kazakhstan, Almaty region, between Saryozek and Zharkent, environs of Basshi, along stream. 44° 10.1' N, 78° 45.1' E. 05.07.2016. Song recordings in 2 ♂.

**References to song.** Bukhvalova & Vedenina, 1998: recordings from Kazakhstan, calling song.

**Song.** The courtship song of *Ch. angulatus* is completely different than the calling song. The courtship song starts with the small-amplitude movements of the hind legs, which generate short syllables repeated at the rate of about 5/s (element 1, Fig. 14 A, C). The syllables contain 3–4 pulses of variable amplitude, which are only produced during synchronous down leg-movements. In about 0.5–1 min, there comes the element 2; in contrast to the element 1, it is produced by rather complex leg movements. Each leg alternate low- and high-amplitude movements at the rate of about 2.5–3.5/s, and superimposed on these slow movements are small-amplitude vibrations of 20–30/s

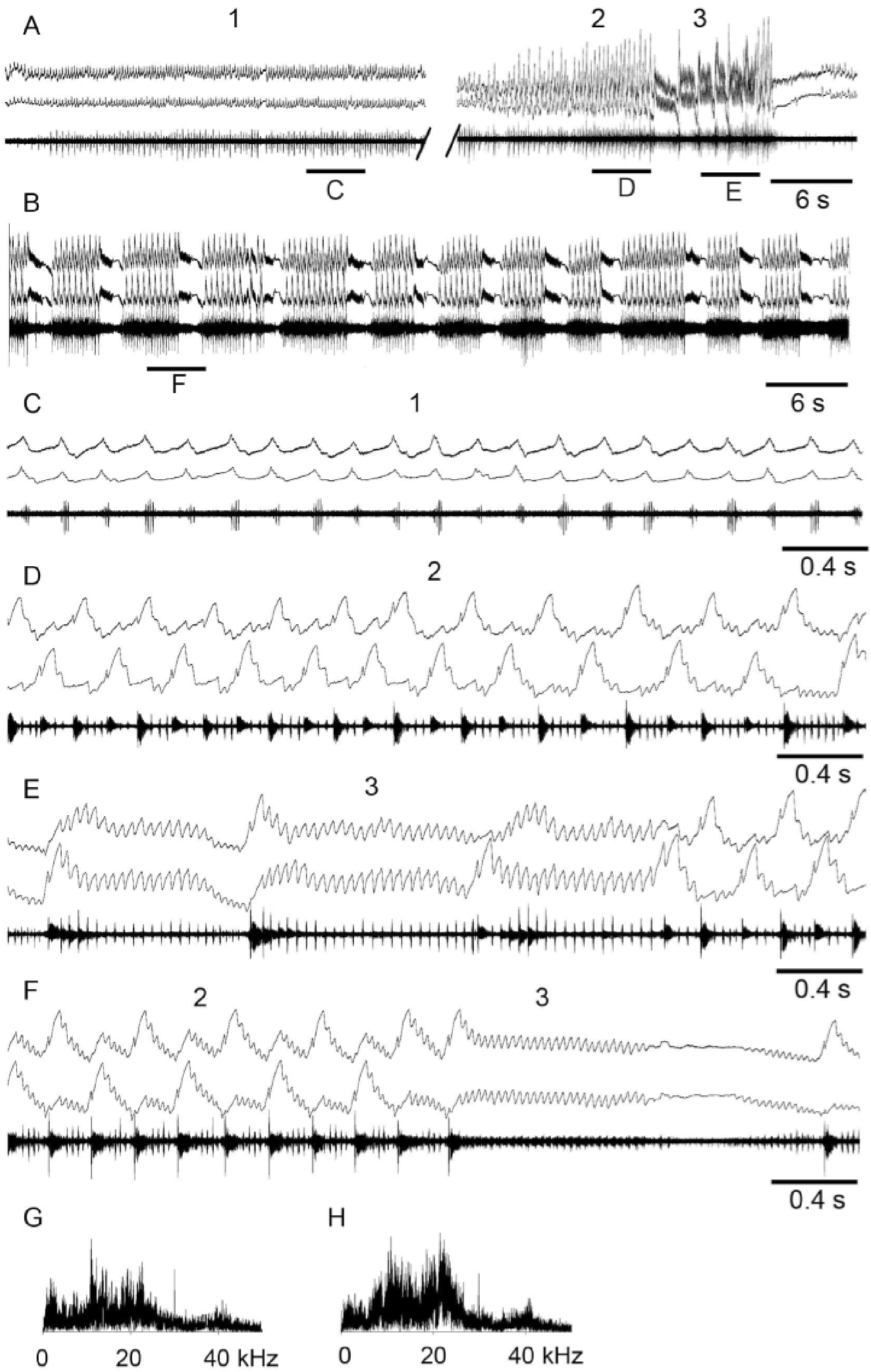


**FIGURE 14.** Oscillograms and frequency spectrum of the courtship songs of two males (A, B) of *Chorthippus angulatus* from Almaty region. Song recordings are presented at two different speeds (faster oscillograms of the indicated parts of the songs shown in C–F). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different elements of the courtship song are indicated by numbers 1–3. Frequency spectra shown for the element 1 (G) and the element 2 (H).

(Fig. 14 D, F). The two legs are moved alternately, so that one leg produces the high-amplitude stroke, whereas the other leg produces the low-amplitude stroke. During the slow up movements of the legs, a loud pulse of longer duration is generated; during the slow down movements, several (2–4) short, quieter pulses are produced. The pulses of longer duration are repeated at the rate of about 5-6/s. The element 2 lasting from 3 to 15 s is followed by the element 3. It starts with the high-amplitude stroke of one leg and the low-amplitude stroke of another leg, similarly to those of the element 2 (Fig. 14 E). However, there follow synchronous vibrations of both legs repeated at the rate of about 20–30/s and lasting about 800 ms–1.5 s. The next high-amplitude stroke is generated by another leg. During the high-amplitude stroke, the loud, long pulse is produced; then follows a series of short pulses repeated at the rate of about 25/s. Sometimes, the element 3 can alternate with the element 2 for more than 1 min (Fig. 14 B). The frequency spectra of all elements lie in the band of 6–25 kHz with two peaks at 12 and 23 kHz (Fig. 14 G, H).

**Comparative remarks.** The courtship song of *Ch. angulatus* has been presented for the first time.

## Conclusions

1. The analysis of the stridulatory leg movements allowed us to distinguish various courtship song elements and even syllables. The difference in sound pattern between the elements could be similar, whereas the leg-movement pattern differed to a larger degree (as in *O. viridulus, O. haemorrhoidalis, Ch. karelini*). We could explain such discrepancy between the sound and the leg movements by generation of additional visual signals with the leg movements during courtship. In various species, for example, the legs are moved alternately during certain periods of courtship producing a similar sound pattern as during synchronous leg movements. The change in the phase shift between the legs should be important for a female.
2. In four species studied from Kazakhstan and adjacent territories, we found some differences in courtship songs compared to the previous data on the respective species from other regions. This may be explained either by geographic variation (*O. haemorrhoidalis, O. petraeus*) or by the distortion in the amplitude ratio between different song elements due to cutting of high frequencies by the recording equipment (*M. pallidus, Ch. karelini*).
3. In five species (*O. viridulus, S. miramae, M. pallidus, Ch. dubius* and *Ch. karelini*), various parts of elaborate courtship songs differed in the carrier frequency, with the peaks laying either in the low-frequency or in the high-frequency ranges. This should be considered in future analysis of the songs recorded with portable equipment, having the frequency range restrictions. In four species (*O. haemorrhoidalis, O. petraeus, M. pallidus* and *Ch. dubius*), the dominant frequencies of the courtship song were shown to lie in the range higher than 20 kHz.
4. The courtship songs of three species (*S. miramae, Ch. dubius* and *Ch. angulatus*) are presented for the first time. The courtship song of *S. miramae* appeared to be almost identical to the courtship song of *S. nigrogeniculatus* from Turkey, which raises the question about the further taxonomic study.
5. In two species, *S. miramae* and *Ch. angulatus*, the courtship songs do not have the elements similar to the calling songs. In Gomphocerinae, one of the courtship elements is usually similar to the calling song (e. g. Vedenina & Mugue, 2011). Until now, it was considered that the calling song elements are only absent in the courtship songs of the species relative to *Ch. albomarginatus* (Vedenina & Helversen, 2009). However, we have showed that such feature can be found in the distantly related species, which supports our hypothesis that the increase of courtship complexity of Gomphocerinae has evolved independently and convergently (Vedenina & Mugue, 2011).
6. The analysis of visual display during courtship helped us to reveal unusual movements of antennae in horizontal plane in *M. pallidus*. Such pattern of the antennae movements seems to be unique among Gomphocerinae. The antennae movements during courtship and the boxing movements with conspicuously swollen fore tibiae in the beginning of mating were also studied in *G. sibiricus*.

## Acknowledgments

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