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Songs and morphology in grasshoppers of the *Stenobothrus eurasius* group (Orthoptera: Acrdidae: Gomphocerinae) from Russia and adjacent countries: clarifying of taxonomic status

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Abstract

On the basis of the song and morphological analyses, we revised the status of the subspecies *Stenobothrus eurasius eurasius* Zubowsky, 1898, and *S. eurasius hyalosuperficies* Vorontsovskii, 1927. The status of the subspecies *S. eurasius hyalosuperficies* Vor. has been changed to the species level. The most striking difference between *S. eurasius* and *S. hyalosuperficies* lies in the song parameters. The calling songs differ not only in temporal parameters but are also produced by different mechanisms. *S. eurasius* generates calling songs by common leg stridulation, whereas *S. hyalosuperficies* produces sound by wing clapping. The courtship songs of both species are complex (contain several elements) and very different in temporal structure. The morphological differences between the two species are not as striking as the differences in bioacoustics: we found the only differences in the hind wing venation. At the same time, we suggest these differences to be important since they might be due to different mechanisms of sound production. We revised the ranges of the two species on the territory of Ukraine, Russia and Kazakhstan. We also reviewed the type localities of *S. eurasius* Zub. and designated lectotype and paralectotype of this species.

Key words: Gomphocerinae, *Stenobothrus*, song, courtship, visual display, stridulation, wing clapping

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 to solve the problems at the species level, 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. In most species, the sound has a broad frequency spectrum, so that the specificity of the songs lies mainly in the pattern of amplitude over time. 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 shape, and the legs can exchange roles from time to time, which lead to increase of song complexity (Elsner, 1974; Helversen & Elsner, 1977; Elsner, 1994). Some species produce a sound also by another mechanism: the wings with sclerotized veins are clapped together and generated a sound, not while flying but during sit-ting on the ground (Elsner & Wasser, 1995; Bukhvalova & Vedenina, 1998; Berger, 2008). 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 that 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).

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The *Stenobothrus eurasius* group is suggested to be the species group that demonstrates courtship songs of increased complexity. Berger (2008) described the songs of *S. eurasius eurasius* Zubowsky, 1898, *S. euraisus bohemicus* Mařan, 1958, *S. eurasius clavicornis* nomen nudum, *S. eurasius macedonicus* Willemse, 1974, and *S. croaticus* Ramme, 1933, from the south-eastern Europe and Turkey. The song analysis revealed that *S. eurasius eurasius*, *S. euraisus* bohemicus and *S. eurasius clavicornis* could be one species and *S. eurasius* macedonicus and *S. croaticus* could represent another species (Berger, 2008). However, this was not revised taxonomically. Two subspecies of *S. eurasius* are suggested to inhabit Russia and adjacent countries: *S. eurasius eurasius* Zub. occurs in Kazakhstan, Kyrgyzstan and south of Siberia eastwards to Transbaikalia; *S. eurasius hyalosuperficies* Vorontsovskii, 1927, inhabits southern Ukraine and south of European part of Russia, Orenburg region and Bashkortostan (Tarbinskii, 1948; Bei-Bienko & Mishchenko, 1951).

Songs of *S. eurasius* have been described from Saratov region (Bukhvalova & Vedenina, 1998) and Astrakhan' region (Savitsky & Lekarev, 2007). The males recorded from these regions generated calling songs not by leg stridulation but by wing clapping. The courtship songs were generated by means of alternation of wing clapping and leg stridulation (Savitsky & Lekarev, 2007). In contrast to these recordings, the recordings from the south-eastern Europe and Turkey (Berger, 2008) represent the songs emitted by only leg stridulation and differ substantially from the recordings from Russia. However, Savitsky & Lekarev (2007) mentioned that the purely stridulating form of *S. eurasius* may occur on the territory of Russia, and supposed that *S. eurasius eurasius* and *S. eurasius hyalosuperficies* could be the different species.

The purpose of this study is to clarify a taxonomic status of the species of the *Stenobothrus eurasius* group on the territory of Ukraine, Russia and Kazakhstan. In the current paper, we analyzed not only the songs but also the underlying stridulatory movements of the hind legs and the whole visual display accompanying the courtship song. We also studied morphological characters used by different authors in their description of the subspecies (Bei-Bienko & Mishchenko, 1951; Mařan, 1958; Willemse, 1974). On the basis of the song and morphological analyses, we changed the status of the subspecies *S. eurasius hyalosuperficies* Vor. to the species level and clarified the ranges of the two species on the territory of Ukraine, Russia and Kazakhstan.

Material and methods

Morphological studies of the specimens were done with an MBS-9 light microscope at 8–56× magnification using an ocular micrometer. The following morphological features were measured: the length of the body, antennae, pronotum, fore wing and hind femur, the maximal width of radial, medial and cubital areas of hind wings and the number of stridulatory pegs. Figures were obtained using a Nikon 5100 SLR digital camera. Specimens examined in this study are deposited in Zoological Institute, Russian Academy of Sciences, St.-Petersburg (ZIN), Zoological Museum of Moscow State University (ZMMU) and in the personal collections of V. Vedenina in Moscow (CV).

The calling song was recorded from isolated males; the courtship song was recorded when a male was sitting close to 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 a 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 a singing male was 30–32° C. All recordings 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 transferred to a PC were analyzed with the VIRTUAL DUB program. All statistical analyses were performed using COOLEDIT (Syntrillium, Seattle, WA) and STATISTICA 6/Win v.

Localities where the song recordings were made are shown in Fig. 1 and Table 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.

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; in syllables one can sometimes distinguish *hemi-syllables*—the sound produced by up or down leg movement; *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 (Figs. 4–5).

FIGURE 1. Map of localities where the specimens were collected for the song recordings. *Stenobothrus eurasius* Zub. marked with triangles, *Stenobothrus hyalosuperficies* Vor. marked with circles. The details on localities shown in Table 1.

Results

We studied three type localities of *S. eurasius* Zub.: 1) Semipalatinsk province, Pjatoryzhsky poselok; 2) Semiretschje, Altyn-emel; 3) Semiretschje, Kehen (Zubowsky, 1898). In Pjatoryzhsky poselok (now Pjatiryzhsk, Pavlodar region), we found the males generated songs only by leg stridulation. Their songs were almost identical to the songs recorded from Hungary and Czech Republic (Berger, 2008). By contrast, the males from Altyn-emel and Kehen produced calling songs by wing beats and courtship songs by alternation of leg stridulation and wing beats. These recordings appeared to be similar to those from Saratov region (Vedenina & Bukhvalova, 1998) and Astrakhan' region (Savitsky & Lekarev, 2007). We suggest that the specimens from Pjatoryzhsky poselok should be considered as *S. eurasius eurasius* Zub., and the specimens from Altyn-emel and Kehen (now Almaty region) should be attributed to *S. eurasius hyalosuperficies* Vor.

We tried to find *S. eurasius hyalosuperficies* Vor. in the type locality (Vorontsovskii, 1927), in the western environs of Orenburg. Unfortunately, we have not found any material there because the city has grown up and the biotopes severely disturbed. Specimens found at the distances of about 20 km S of Orenburg (loc. 11) and 30 km E of Orenburg (loc. 12) produced wing clapping during the calling and courtship behaviour. Their songs were identical to the songs of the specimens from Almaty region (Altyn-emel and Kehen).

TABLE 1. Localities where the specimens were collected for the song recordings.

Species	Locality number	Number of males (recordings)	Collecting date	Geographical coordinates	Altitude, m a.s.l	Locality
Stenobothrus eurasius	1	5 (21)	26.06.2005	46°35.9' N 32°52.1' E	13	Ukraine, Kherson region, surr. of Tztyrjypinsk, Aleshkovskie peski
	2	7 (29)	27.06.2008	51°34'N 45°54'E	260	Russia, Saratov, slopes near Polivanovka
	3	5 (29)	4.07.2019	51°42.9' N, 74°38.5' E	226	Kazakhstan, Pavlodar region, Ekibastuz district, ab. 3 km W of Schidert
	4	4 (25)	5.07.2019	53° 05.1' N, 75°56.6' E	94	Kazakhstan, Pavlodar region, Terenkol' district, bank of the Irtysh river
	5	8 (35)	5.07.2019	53°22.4' N, 75°33.6' E	113	Kazakhstan, Pavlodar region, Zhelezinsky district, near Pyatiryzhsk
	6	1 (7)	8.08.2017	50°37.3' N 86°26.2' E	922	Russia, Altai Republic, ab. 26 km SE of Ongudai, environs of Kupchegen'
Stenobothrus hyalosuperficies	7	3 (20)	24.06.2008	51°32.4' N, 45°59' E	286	Russia, Saratov, Lysaja Gora
	8	11 (71)	29.06.2020	51°20.2' N, 48°13.4' E	257	Russia, Saratov region, Ershovsky district, Uchebny
	9	1 (7)	23.06.2018	51°06.4' N, 50°19.5' E	94	Kazakhstan, ab. 50 km W of Ural'sk, environs of Kamenka
	10	1 (4)	01.07.2018	52° 15.9' N 53° 16.7' E	173	Russia, Orenburg region, ab. 30 km S of Sorochinsk
	11	11 (75)	01.07.2020	51°33.4' N, 55°3.9' E	35	Russia, Orenburg region, Orenburgsky district, 3 km NE of Pervomaisky
	12	2 (5+10)	14.07.2012 01.07.2020	51° 51.6' N 55° 51.3' E	90	Russia, Orenburg region, ab. 30 km E of Orenburg, environs of Studentzy
	13	1 (15)	02.07.2020	52°11.3'N, 56°31.5'E	97	Russia, Bashkortostan, Zianchurinsky dist., near Yangi-Yul
	14	2 (7)	3.07.2016	44°12.6' N, 78°30.4' E	1683	Kazakhstan, Almaty region, Altyn Emel pass
	15	6 (54)	9.07.2016	43°07.8' N, 79°09.7' E	1959	Kazakhstan, Almaty region, ab. 14 km N of Kehen

Stenobothrus eurasius Zubowsky
(Figs. 2–5)

Stenobothrus eurasius Zubowsky, 1898: 75–78.

Material examined: 1 ♀ Lectotype. pr. Semipalatinsk Pjatoryzhsky poselok, 22.VII.1895 (ZIN); 1 ♀ paralectotype, pr. Semipalatinsk, Pjatoryzhsky poselok, 22.VII.1895 (ZIN); **Kazakhstan**: Pavlodar region, Zhelezinsky district, near Pjatiryzhsk, 5.VII.2019, 9 ♂ 1 ♀, leg. V. Vedenina, N. Sevastianov & T. Tarasova, song recordings in 7 ♂ (ZIN, CV); pr. Akmolinsk, Koktschetav, 20.VIII.1895, 1 ♀ syntype, leg. I. Ingenitzky (ZIN); pr. Akmolinsk, Koktschetav, 16.VII.1895(?), 1 ♂, leg. Ingenitzky (ZMMU); pr. Semipalatinsk, Balapan, 1.VIII.1895, 2 ♀ syntypes, leg. I.

Ingenitzky (ZIN); pr. Semipalatinsk, Lebjashje, 24.VII.1895, 1 ♀ syntype, leg. I. Ingenitzky (ZIN); Pavlodar region, Ekibastuz dist., ab. 3 km W of Schidert, 4.VII.2019, 5 ♂ 3 ♀, leg. V. Vedenina, N. Sevastianov & T. Tarasova (CV), song recordings in 5 ♂; Pavlodar region, Terenkol dist., bank of the Irtysh river, 5.VII.2019, 4 ♂, leg. V. Vedenina, N. Sevastianov & T. Tarasova (CV), song recordings in 4 ♂. **Czech Republic**: Bohemia, N. Mus., Oblik, 4.IX.1956, 3 ♂ 1 ♀ paratypes, leg. C. Stredohori (ZIN); Bohemia, N. Mus., Rana, 29.VIII.1956, 1 ♂, leg. C. Stredohori (ZIN); **Ukraine**: south-western Ukraine, B. Aleksandrovka, 7.VII.1928, 4 ♂ 4 ♀, leg: Znoiiko (ZIN); Kherson region, Chernomorsky reserve, Soljonoozerny uchastok, 25.VII–05.VIII.1995, 1 ♂ 4 ♀, leg. V. Vedenina (CV); Kherson region, surr. of Tztyrjypinsk, Aleshkovskie peski, 26.VI.2005, 6 ♂ 3 ♀, leg. V. Vedenina (CV), song recordings in 5 ♂; **Russia**: Saratov, Polivanovka, 27.VI.2008, 14 ♂ 9 ♀, leg. V. Vedenina (CV), song recordings in 7 ♂; Orenburg region, r. Donguz, VI.1935, 2 ♂ 1 ♀, leg. Zimin (ZIN); South Ural, Ilmenskii reserve, 11.VIII.1958, 1 ♂, leg. I. Stebaev, (ZMMU); Altai Republic, ab. 26 km SE of Ongudai, surr. of Kupchegen', 08.VIII.2017, 12 ♂ 11 ♀, leg. V. Vedenina & N. Sevastianov (ZIN, CV), song recordings in 1 ♂; Altai Republic, ab. 6 km SE of Chemal, surr. of Elekmonar, 06.VIII.2017, 1 ♂, leg. V. Vedenina & N. Sevastianov (ZIN, CV); Altay, Onguday. 20.VI.08, 1 ♂, leg. Steinfeld (ZIN); Altay, Rubtzovskoe ushel'je, 5.VII.1923, 1 ♂, leg. Koshkin (ZIN); Montes Altaiei rass steppa Inia, VII.1925, 1 ♂, leg. Bei-Bienko (ZMMU); Tomsk. gub., Biisk o., Onguday, 11.VII.1898, 1 ♂ 1 ♀, leg. A.Yakobson (ZIN); Sibiria, Minusinsk 19.VI.1897, 2 ♂ 1 ♀, leg. Vagner (ZIN); Sibiria, Minusinsk, VI.1902, leg. Molchanov (ZMMU); Krasnoyarskii krai, Yermakovskii dist., Otuk-Suk estuary, 08.VII–05.VIII.1990, 15 ♂, leg. L. Rybalov (ZMMU); Tuva, Tandinskii dist., Bolgazik, 1959, 1 ♂ leg. Filippov (ZIN); Russia, Tuva, Erzin, caragan steppe 26.VII–10.VIII.1989, 8 ♂, leg. M. Bukhvalova (ZMMU); U-Uda, 03.VII.1998, 1 ♂, leg. Ingenitzky (ZMMU); M. Uda 24–25.VII.1898, 1 ♀, leg. Ingenitzky (ZMMU); Russia, Zabaikal'je, surr. Ust'-Kjahta, 24.VII.1929, 1 ♂, leg. Strachovskii (ZIN).

Distribution. The range of this species extends from south-eastern Europe to southern Siberia, eastwards to Transbaikalia. In south-eastern Europe, the species can be found in lower Austria, Hungary, Czech, Slovakia, Romania, and very locally in Greece (Harz, 1975; Berger, 2008). Further to the east, the species occurs very likely in Moldova, in southern Ukraine, Saratov and Orenburg region, southern Ural, northern Kazakhstan. Altai, Krasnojarskii krai, Tyva and Transbaikalia. In the south-eastern part of European Russia, Orenburg region and Kazakhstan, the southern border of *S. eurasius* may overlap with the northern border of *S. hyalosuperficies* Vor.

Recognition (Figs. 2, 3A–B, Table 2). *S. eurasius* can be distinguished from S. hyalospurficies by morphology of the hind wings. The hind wings of *S. eurasius* are either transparent or brownish in the apical third. The apical part of costal area is slightly smoky. Medial area is hardly wider than radial area in their greatest width (1.1–1.4 times as wide as radial area in males and 1.1–1.3 in females). First and second cubital veins are parallel and distinctly separate.

Calling song (Fig. 4A–C). The calling song of *S. eurasius* is usually an echeme of quite variable duration (10–30 s). In the very beginning of the echeme, the legs vibrate at the rate of 23–28/s and produce pulses lasting about 7–12 ms (Fig. 4B). In about 1 s, the legs start to generate two types of movements: during the up movement, the legs vibrate at the rate of about 100–120/s, during the down movement—at the rate similar to that in the beginning of the echeme. These movements lead to alternation of two hemi-syllables: hemi-syllable A consists of the longer (11 ms) pulses, whereas hemi-syllable B consists of the shorter (2 ms) pulses (Fig. 4C). The syllables repeated at the rate of about 3.3–3.8/s.

Courtship song (Fig. 5, Table 3). The courtship song of *S. eurasius* usually starts with generating of the syllables of 3–6 pulses (element 1, Fig. 5A, D). The pulses are produced by the leg vibration at a rate of 23–28/s and their temporal structure is similar to that in hemi-syllable A of the calling song. The syllables are separated by gaps of about 150–180 ms. In about 6–10 s, the legs start to generate two types of movements similarly to those in the developed calling song (element 2). As a result, two hemi-syllables alternate with each other: one hemi-syllable contains short and frequent pulses, another—long and sparse pulses (Fig. 5E–H). The element 2 lasts for about 8–16 s. The elements 1 and 2 can alternate for 2 min and more. In the developed courtship, when a male reaches a high level of excitation, he produces the element 3 (Fig. 5F–G). The legs are abruptly stroked up producing hemi-syllable C, a noise with increasing amplitude. In the end of hemi-syllable C, the femora reach extra high position. During the longer down movement, the legs generate hemi-syllable B' that is similar to hemi-syllable B but of slightly longer duration. It is also interesting that the legs are moved up when producing hemi-syllable B; by contrast, hemi-syllable B' is produced during the down movements. The element C contains 5–12 syllables repeated at a rate of 3–4/s. After the element C, a male usually demonstrates an attempt of copulation.

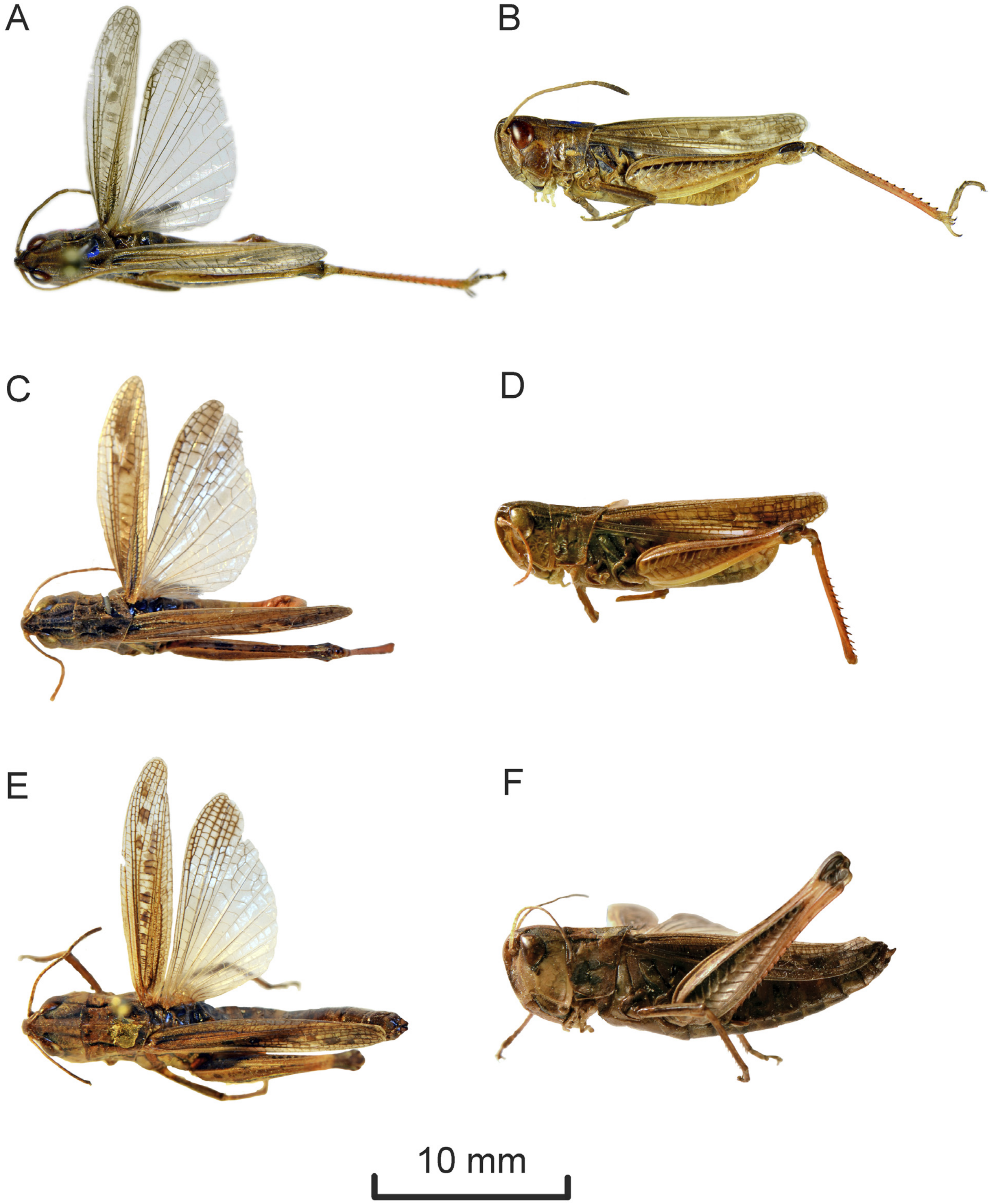

FIGURE 2. *Stenobothrus eurasius* Zub. Male from Pjatiryzhsk, Pavlodar region, A—dorsal view, B—lateral view; male from Kupchegen', Altai Republic, C—dorsal view, D—lateral view; female from Kupchegen', Altai Republic, E—dorsal view, F—lateral view

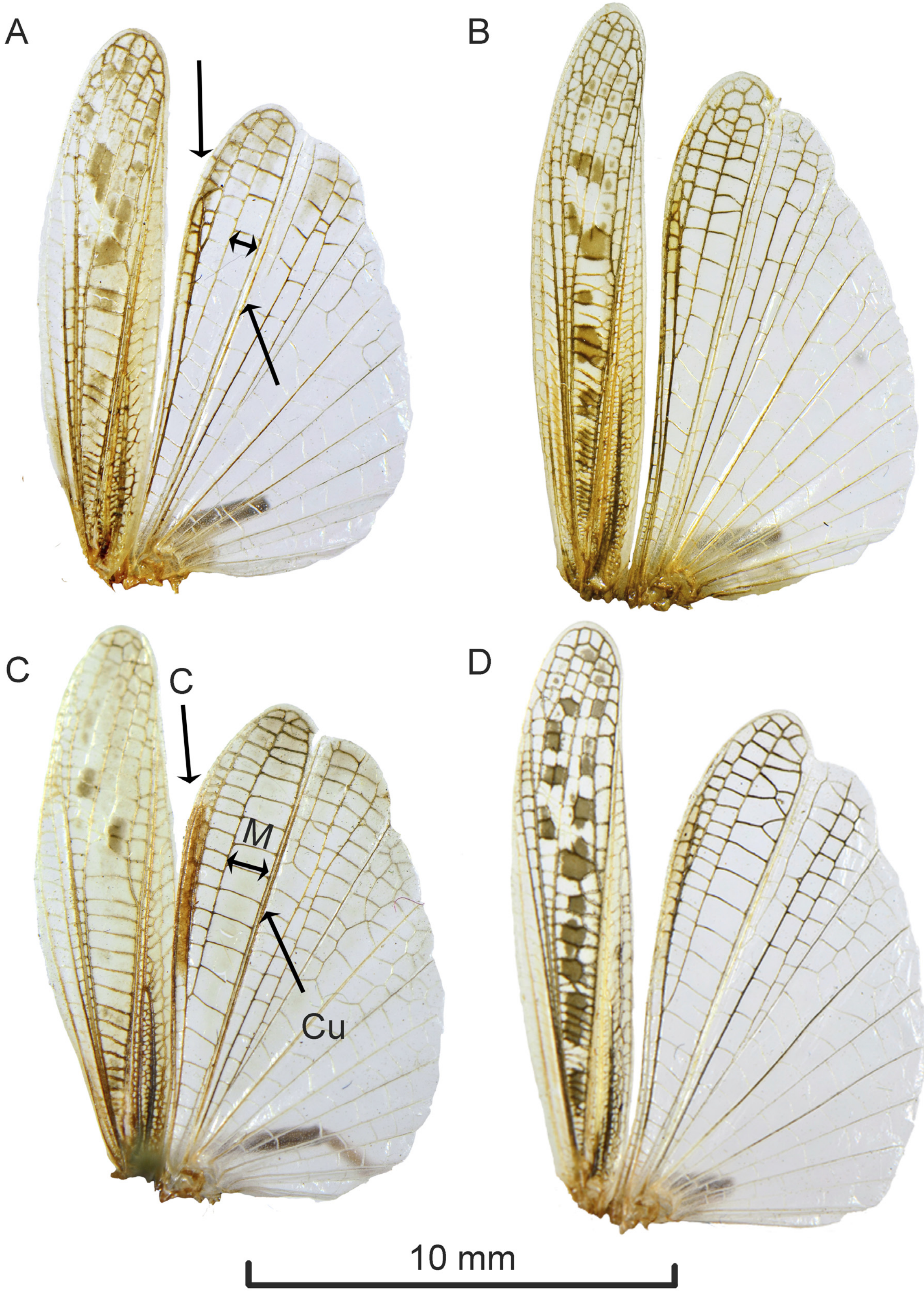

FIGURE 3. Wings of *Stenobothrus eurasius* Zub. (A—male from Pjatiryzhsk, Pavlodar region; B—female from Kupchegen', Altai Republic) and *Stenobothrus hyalosuperficies* Vor. (C—male from Pervomaisky, Orenburg region; D—female from Uchebny, Saratov region). Differences in hind wing venation of heterospecific males indicated with arrows: costal area (C), medial area (M), cubital area (Cu).

TABLE 2. Morphological parameters of *Stenobothrus eurasius* and *Stenobothrus hyalosuperficies*. Mean value, standard deviation and minimum – maximum are shown. N—the number of specimens.

	Stenobothrus eurasius		*Stenobothrus hyalosuperficies*	
	males	females	males	females
N	53	35	60	38
Body length, mm	15.52 ± 1.15	21.91 ± 1.32	16.14 ± 0.93	21.12 ± 1.37
	13.5 – 17.8	19.3 – 24.5	14.2 – 18.5	18.0 – 24.5
Antenna length, mm	8.62 ± 0.64	7.55 ± 0.65	8.45 ± 0.74	6.63 ± 0.50
	7.5 – 10.0	6.4 – 8.8	7.0 – 11.1	5.5 – 8.0
Pronotum length, mm	3.07 ± 0.17	4.01 ± 0.23	3.13 ± 0.18	3.94 ± 0.26
	2.6 – 3.4	3.3 – 4.4	2.8 – 3.6	3.6 – 4.5
Length of fore wing, mm	12.38 ± 0.60	14.75 ± 1.26	12.55 ± 0.62	14.25 ± 0.74
	11.2 – 13.6	10.7 – 16.4	11.3 – 14.2	12.1 – 15.5
Length of hind femur, mm	9.97 ± 0.65	13.75 ± 1.08	10.89 ± 0.87	13.91 ± 0.61
	8.2 – 11.5	11.8 – 15.8	9.7 – 13.6	12.7 – 15.4
Number of stridulatory pegs	227.5 ± 24.4	208.4 ± 23.6	219.8 ± 23.7	208.7 ± 21.4
	188 – 288	157 – 256	180 – 270	152 – 260
N, hind wings	99	35	86	57
Relative width of medial / radial areas	1.3 ± 0.2	1.2 ± 0.2	1.6 ± 0.2	1.5 ± 0.2
	1.0 – 1.9	0.8 – 1.5	1.3 – 2.2	1.1 – 2.1
Relative width of cubital / radial areas	0.3 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
	0.1 – 1.0	0.2 – 0.4	0.03 – 0.3	0.2 – 0.4

Stenobothrus hyalosuperficies **Vorontsovskii**
(Figs. 3, 4, 6, 7)
Stenobothrus eurasius hyalosuperficies Vorontsovskii, 1927: 7.

Material examined: Russia: Orenburg region, Orenburgsky dist., 3 km NE of Pervomaisky, 01.VII.2020, 12 ♂ 5 ♀, leg. A. Bykova & N. Ermilov & T. Tarasova & N. Sevastianov (ZIN, CV), song recording in 11 ♂; Orenburg region, ab. 30 km S of Sorochinsk, 01.VII.2018, 1 ♂, leg. V.Vedenina & N. Sevastianov (CV), song recording in 1 ♂; Orenburg region, ab. 30 km E of Orenburg, surr. of Studentzy, 14.VII.2012, 1 ♂, leg. V.Vedenina & L. Shestakov (CV), 01.VII.2020, 2 ♂, leg. T. Tarasova & N. Sevastianov (CV), song recording in 2 ♂; 7 km E of Orenburg, meadows near Ural river, 13.VII.2012, 1 ♂ 1 ♀, leg. V. Vedenina & L. Shestakov (CV); Bashkortostan, Zianchurinsky dist., near Yangi-Yul, 02.VII.2020, 1 ♂, leg. T. Tarasova & N. Sevastianov (CV), song recording in 11 ♂; Saratov region, Ershovsky dist., Uchebny, 29.VI.2020 21 ♂ 23 ♀, leg. A. Bykova & N. Ermilov & T. Tarasova & N. Sevastianov (ZIN, CV), song recording in 11 ♂; Saratov, Lysaja Gora, 24.VI.2008, 4 ♂ 1 ♀, leg. V. Vedenina (CV), song recording in 3 ♂; Saratov region, 10 km E of Ozinki, 26.VI.1996, 2 ♂, leg. D. Tishechkin (ZMMU), song recording in 1 ♂; surr. of Stalingrad, Naidyonova Balka, 05.VI.1950, 1 ♂, leg. I. Stebaev (ZMMU); Stalingrad region, Arshan'-Gudzhur, 15.VII.1950, 1 ♂ 2 ♀, leg. I. Stebaev (ZMMU); Stalingrad region, Tingut forestry, 05.VII.1950, 2 ♀, leg. I. Stebaev (ZMMU); Astrakhan' region, N of Arshan'-Zel'men', 1 ♂ (ZMMU); Astrakhan' region, W of Elista, 17.VII.1950, 1 ♀, leg. I. Stebaev (ZMMU); western slope of Ergeni, VII.1950, 2 ♀, leg. I. Stebaev (ZMMU); Checheno-Ingushetia, surr. Groznyi, 20–29.VI.1986, 4 ♂, leg. D. Tishechkin (ZMMU); Abkhazia, Azhary, 17.VIII.1950, 1 ♂, leg. I. Stebaev (ZMMU). **Kazakhstan**: western Kazakhstan, surr. of Kamenka, 23.VI.2018, 1 ♂, leg. V. Vedenina & N. Sevastianov (CV), song recording in 1 ♂; Semiretschje, Kyzyltschi 21.VII.1896, 1 ♂ syntype of *S. eurasius* Zub. (ZIN); Semiretschje, Kehen, 30.VI.1896, 3 ♂, leg. I. Ingenitzky (ZIN, ZMMU); Almaty region, ab. 14 km N of Kehen, 09.VII.2016, 8 ♂ 8 ♀, leg. V. Vedenina & T. Pushkar (ZIN, CV), song recording in 6 ♂♂; Semiretschje, Altyn-emel - Kopal, 14♀15.VII.1896, 1 ♂ 2 ♀ syntypes of *S. eurasius* Zub. (CV); Almaty region, Altyn Emel pass, 03.VII.2016, 11 ♂ leg. V. Vedenina & T. Pushkar (CV), song recording in 2 ♂; Tztyrjypinsk region, surr. of lake Zaisan, 23–28.VII.1935, 3 ♂ 5 ♀, leg. Sorokin (ZMMU). **Kyrgyzstan**: Semiretschje, Sasanovka, N of lake Issyk-Kul', 19–21.VI.1896, 1 ♂ syntype of *S. eurasius* Zub., leg.

I. Ingenitzky (ZMMU); E of lake Issyk-Kul', ravine Turchen'-Aksu, 25.VII.1953, 2 ♂, leg. D. Panfilov; lake Issyk-Kul', surr. Pokrovka, 25.VII.1956, 1 ♂, leg. D. Panfilov (ZMMU); ridge Terskei, Chonkyzylsu 22.VII.1953, 1 ♂, leg. D. Panfilov (ZMMU). **China**: Tien Shan, ridge Ketmen', S of Ak-su, 25.VII.1948, 2 ♂, 1 ♀, leg. Bei-Bienko (ZIN); Xinjiang, Barkulskaja vpadina, 27.VII.54, 1 ♂, leg. Tsyplenkov (ZIN).

Since *S. eurasius hyalosuperficies* Vor. has been described as variety without morphological description, we provide a description of the species.

Description (Figs. 3C–D, 6; Table 2). Ratio length of eye to length of subocular groove 3.4–4.2 in ♂, 2.8–3.3 in ♀. Fastigium verticis slightly pointed, on apex sometimes with the weak median carina that continues to the light median band. Light stripes from foveolae to vertex, dark stripes behind the eyes. Antennae far beyond lateral lobes of pronotum in ♂, slightly beyond them in ♀, straw-yellow or pale brown, apical segments dark, flattened and enlarged (1.5–2 times as wide as distal segments). Lateral pronotal keels weekly incurved (ratio between maximal and minimal widths between lateral keels 1.5–2), of the same colour as the rest pronotum or lighter than the rest pronotum, outlined on both sides by dark stripes; prozona commonly equal to metazona. Mesosternal interspace different in shape, its ratio width to length 0.5–1, mesosternal lobes slightly wider than mesosternal interspace. Fore and hind wings well developed, reaching (or slightly beyond) the knees of hind legs. Costal area of fore wing commonly with the light stripe, cubital area often light at the base; medial area wide, its width as large as (or slightly less than) total width of precostal, costal, subcostal and radial areas, medial area and distal part of fore wing often with dark spots; stigma in the distal part of the third quarter of fore wing, sometimes weakly expressed. Hind wings either transparent or smoky apically. Distal half of costal area smoky or brownish. Medial area distinctly wider than radial area, ratio maximal width of medial to radial area 1.6–2 in ♂, 1.3–1.8 in ♀. Cubital veins from more or less fused. Fore and mid legs brown, taupe or reddish. Hind femur 4 times as long as wide, brown or with olivaceous green upper area, with black longitudinal stripe; hind knees blackish brown, hind tibiae and tarsi orange or yellowish. The number of stridulatory pegs 205–268 in ♂, 157–243 in ♀. Apical part of abdomen in ♂ (less in ♀) light red or orange red from dorsal side; 10th tergite bordered in the same colour. Cerci almost 3 times as long as wide at the base in ♂, 2 times as long as wide at the base in ♀. Lobes of penis in profile thinly conical, their tips slightly incurved in cranial direction, lophi of epiphallus different in shape, but these differences with numerous transitional variants. Ovipositor corresponds to that for the genus. The whole body brownish, taupe, buffy, head and thorax sometimes with a green tint, dark and light patterns typical for the genus; downiness weak.

Distribution. *S. hyalosuperficies* occurs in south-eastern part of European Russia, very likely in the Caucasus, in Orenburg region, throughout Kazakhstan except of the northern regions, Kyrgyzstan, and north-western China.

Recognition (Fig. 3D–E). The hind wings in *S. hyalosuperficies* are distinguishable from those in *S. eurasius*, first, by the darker costal area, second, by the wider medial area than in *S. eurasius*, and third, by almost fused cubital veins in contrast to separate cubital veins in *S. eurasius*.

Calling song (Fig. 4D–E). The calling song of *S. hyalosuperficies* is generated by the wing clapping. The echemes are irregular, of variable duration in the range of 1 to 5 s. The wing beats are produced at a rate of 60–100/s.

Courtship song (Fig. 7, Table 3). The courtship song of *S. hyalosuperficies* usually starts with generating of single or double pulses repeated at the rate of 2–4/s (element 1). These pulses are produced by both up and down movements of the hind legs (Fig. 7C), whereas in *S. eurasius*, the pulses are only produced by the down movements. In *S. hyalosuperficies*, the element 1 can continue for 1.5 min, sometimes transforming to the element 1' (Fig. 7F). The latter element includes series of pulses that are similar to the pulses of the element 1 but repeated at the faster rate of 1.3–2.8/s. The element 1 or 1' can be abruptly followed by the element 3 (Fig. 7D). A male abruptly lifts the hind legs almost vertically and produces a stroke with the hind tibiae. An angle between femur and tibia usually is larger than 100°. At the same time, the male produces a backward movement with antennae. Then the tibiae are pressed to the femora, the femora are slightly lifted and the stroke with the tibiae is repeated (Fig. 7G). These movements result to generation of the noisy syllables repeated at the rate of 2–2.5/s. Every noisy syllable can contain

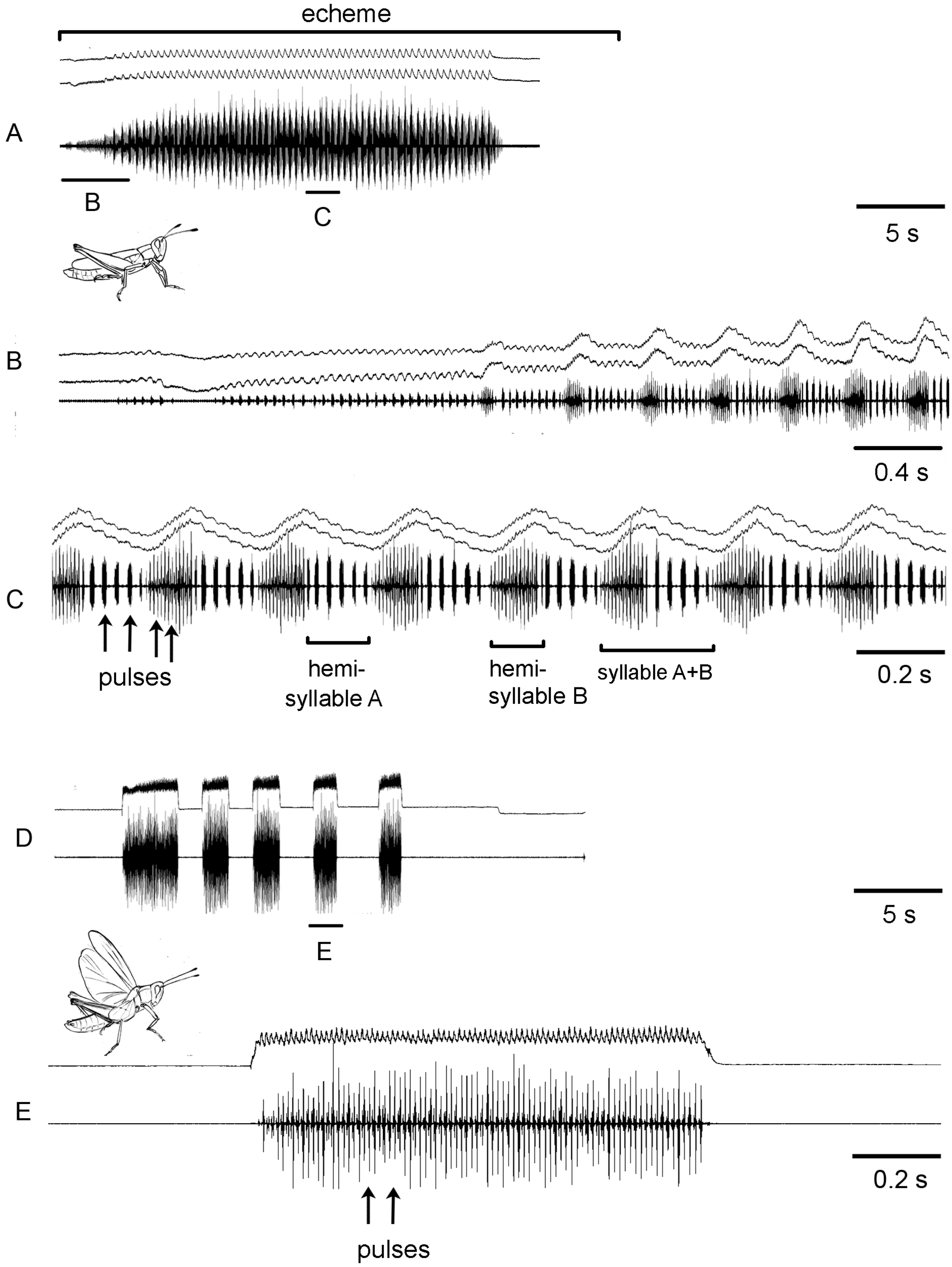

FIGURE 4. Oscillograms of the calling songs of *Stenobothrus eurasius* Zub. (A) from Pavlodar region and *Stenobothrus hyalosuperficies* (D) from West-Kazakhstan region. Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in B, C, and E). In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Drawings under oscillograms A and D demonstrate the leg and wing positions during singing of the corresponding species. Different song parameters indicated with brackets and arrows.

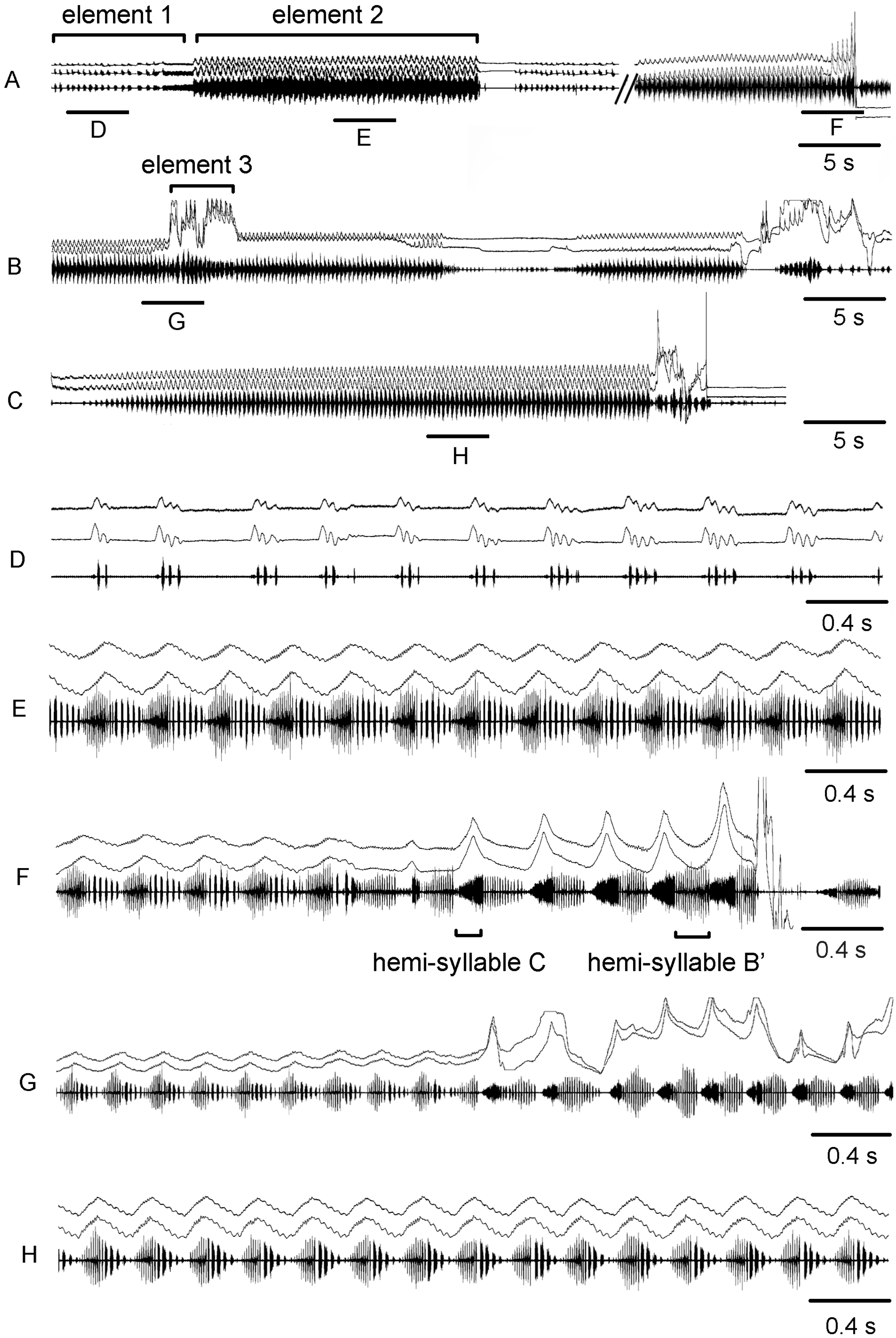

FIGURE 5. Oscillograms of the courtship songs of three males of *Stenobothrus eurasius* from Pavlodar region (A), Kherson region (B), and Altai Republic (C). Song recordings are presented at two different speeds (faster oscillograms of the indicated parts of the songs shown in D–H). D—element 1, E and H—element 2, F and G—elements 2 and 3. In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different song parameters indicated with brackets.

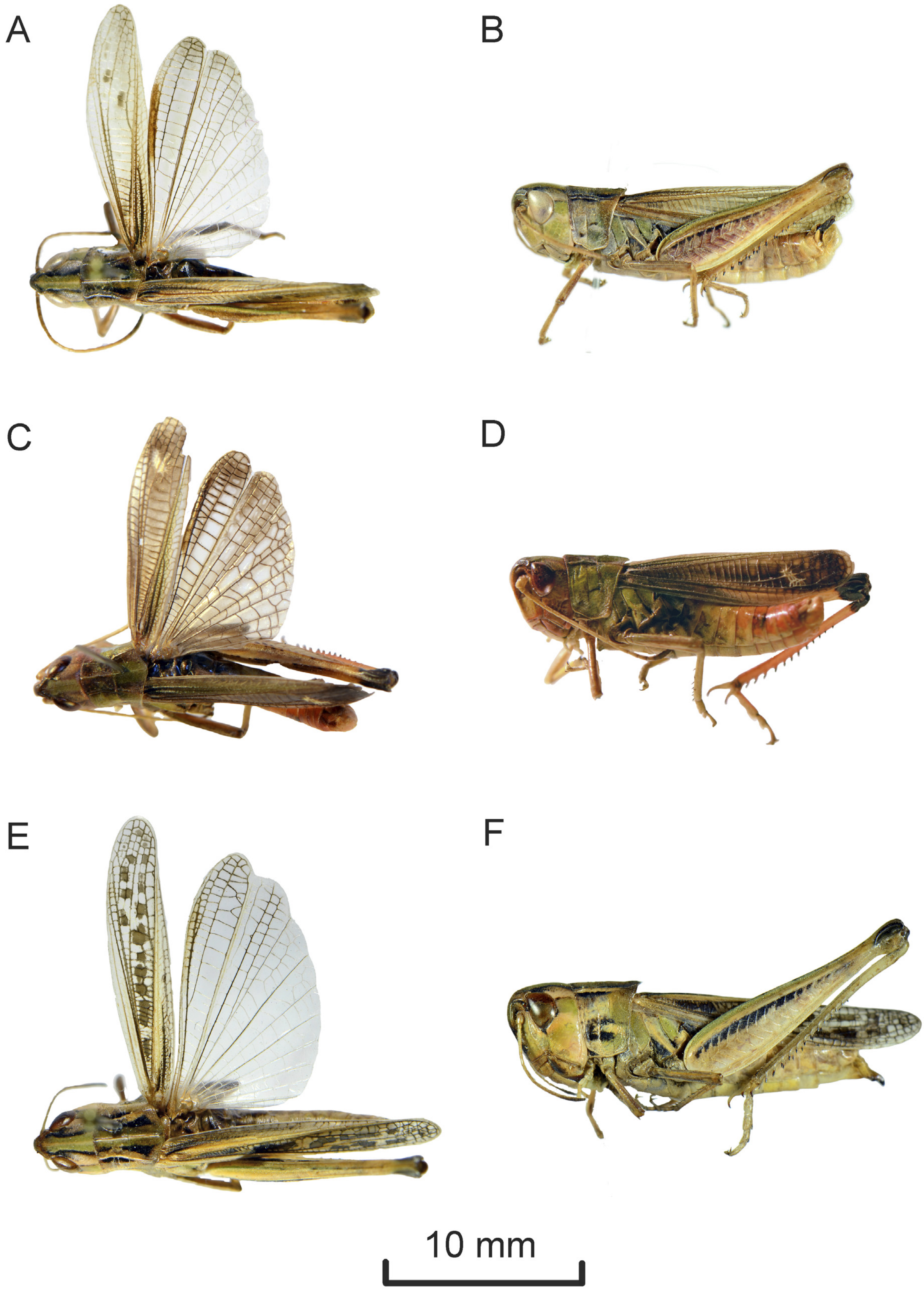

FIGURE 6. *Stenobothrus hyalosuperficies* Vor. Male from Pervomaisky, Orenburg region, A—dorsal view; male from Kehen, Almaty region, B—lateral view,C—dorsal view; female from Uchebny, Saratov region, D—lateral view, E—dorsal view, F—lateral view.

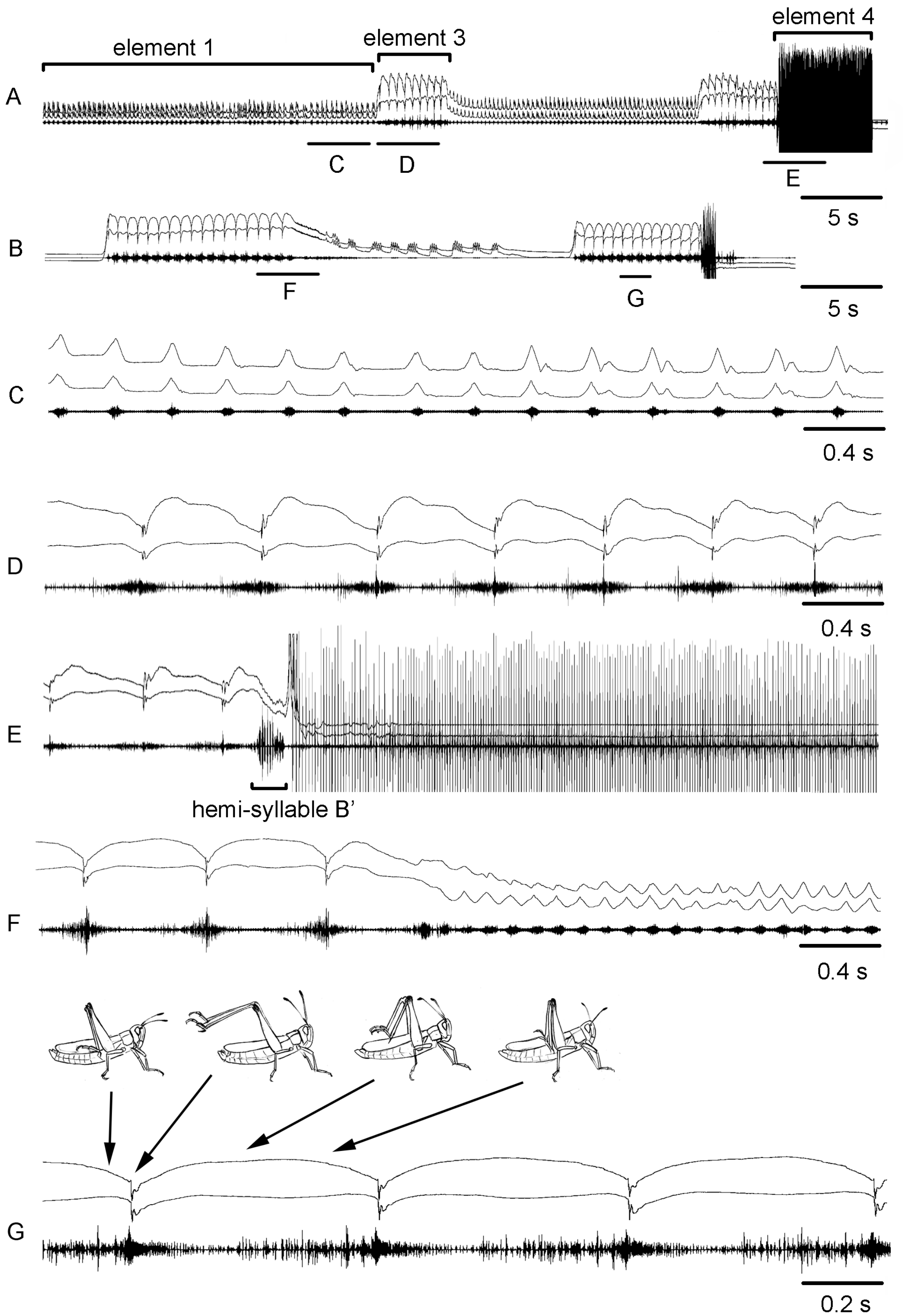

FIGURE 7. Oscillograms of the courtship songs of two males of *Stenobothrus hyalosuperficies* Vor. from Orenburg region (A), and Almaty region (B). Song recordings are presented at three different speeds (faster oscillograms of the indicated parts of the songs shown in C–G). C—element 1, D—element 3, E—elements 3 and 4, F—elements 3 and 1'. In all oscillograms the two upper lines are recordings of hind leg movements and the lower line is the sound recording. Different song parameters indicated with brackets. Drawings on oscillogram G demonstrate successive positions of tibiae and antennae during element 3.

one loud pulse that is usually produced during the stroke with the tibiae. At the end of the element 3, the legs can be moved down in a stepwise manner similarly to that how it is produced by *S. eurasius* in element 3 (Fig. 7E). As a result, the legs generate one syllable of pulses similar to hemi-syllable B' of *S. eurasius*. The element 3 can be followed by the element 4 that is identical to the calling song and generated by wing beats (Fig. 7E). The duration of the element 4 varies from 100 ms to 4 s, the pulses are repeated at the rate of 70–90/s. It should be noted that in *S. hyalosuperficies*, various elements are commonly produced in a random order, in contrast to *S. eurasius*. A copulation attempt in *S. hyalosuperficies*, however, usually occurs after the wing clapping.

Discussion

In the current study, we have revised the type localities of *S. eurasius Zub*. In the two type localities mentioned by Zubowsky (1898), Altyn-emel and Kehen, another species, *S. hyalosuperficies* Vor., occurs. We also suggest that other type localities in Semiretschje (Kysyltschi, Sasanovka and Verny) claimed by Zubowsky can't be the localities of *S. eurasius* anymore, since they are in the range of *S. hyalosuperficies*. We have designated lectotype and paralectotype of *S. eurasius* among the two females from Pjatoryzhsky poselok, pr. Semipalatinsk (now Pavlodar region of Kazakhstan), on the base of the study of the material collected on 5.VII.2019.

On the basis of the song and morphological analyses, we have changed the status of the subspecies *S. eurasius hyalosuperficies* Vor. to the species level. The most striking difference between *S. eurasius* and *S. hyalosuperficies* lies in the song parameters. The calling songs are different not only in temporal parameters but are also produced by different mechanisms (Fig. 4). In the courtship songs, one can find many differences between the two species even in the elements 1 and 3, which are suggested to be homological. In particular, the two species differ markedly in the pulse duration of the element 1 (Table 3) and in the temporal structure of the element 3. In *S. eurasius*, the element 3 comprises alternating syllables of the complex structure, which implies the noisy hemi-syllable C and the pulsed hemi-syllable B' (Fig. 5F). In *S. hyalosuperficies*, the element 3 contains noisy syllables of rather simple structure (Fig. 7D). However, when producing the last syllable of the element 3, the legs can vibrate at the rate of about 130–140/s and produce hemi-syllable B', similarly to *S. eurasius*. This testifies to the fact that the elements 3 can be homological in the two species, despite there are many differences in structure of this element between them. The *S. hyalosuperficies* males also demonstrate the conspicuous visual display during the element 3 (Fig. 7G), which is absent in all males of *S. eurasius* from Ukraine, Russia and Kazakhstan. The element 2 (alternation of hemi-syllables A and B) is only present in *S. eurasius*, whereas the element 4 (wing clapping)—in only *S. hyalosuperficies* (Table 3). Both elements are highly characteristic, and they can be easily recognized on the oscillogram even without leg-movement recordings.

The morphological differences between the two species are not as striking as the differences in bioacoustics. Most of the parameters measured do not differ between the species (Table 2, Figs. 2, 6). The differences may be only found in morphology of the hind wings (Fig. 3). The *S. hyalosuperficies* hind wings have the darker (and probably thickened) costal area and the wider medial area than the hind wings of *S. eurasius*, and cubital veins are almost fused in *S. hyalosuperficies* in contrast to separate cubital veins in *S. eurasius*. It is noteworthy that these features of *S. hyalosuperficies* may be an adaptation for producing sound by the wing clapping.

Until now, only one species of Gomphocerinae, *S. rubicundus*, has been known, which also produces sound by wings while the grasshopper is on the ground (Elsner & Wasser, 1995). This species is characterized by the extreme sclerotization of the costal, subcostal and medial veins and the wide medial area in the hind wings. Movement recordings have clearly shown that the leading edges of the hind wings touch one another at the end of the upstroke, and the sound is generated at this moment. We suppose that the mechanism of the sound production in *S. rubicundus* may be similar to that in *S. eurasius*. The weaker sclerotization of the hind wings in *S. eurasius* might be an indicator that this species represents an earlier stage of divergence than *S. rubicundus*. At the same time, the studies of the hybrid zone between *S. rubicundus* and *S. clavatus* (Vedenina *et al*., 2012; Sradnick *et al*., 2016) evidences that evolution of some morphological features could be driven very fast by sexual selection. Despite *S. rubicundus* and *S. clavatus* demonstrate an extremely different morphology, and *S. clavatus* doesn't produce any sound by wings, they hybridize and give fertile offspring, which could indicate their close relationship and recent divergence. The differences in the hind wing morphology between *S. eurasius* and *S. hyalosuperficies* are not as prominent as between *S. rubicundus* and *S. clavatus*; however, we suggest these differences to be very important. We expect that they would increase in the process of evolution.

TABLE 3. Courtship songs parameters of *Stenobothrus eurasius* and *Stenobothrus hyalosuperficies*. Medians and the lower, upper quartiles are shown.

	Stenobothrus eurasius					***Stenobothrus hyalosuperficies***					
Locality	1	2	3	4	5	7	8	11	12	14	15
Number of recorded males	5	7	5	4	8	3	11	11	2	2	6
Element 1, pulse duration. ms	11 8; 13	14 10; 18	11 8; 17	7 5; 10	7 4; 9	70 65; 78	53.5 38; 63	58.5 51; 70	76 72; 79	41 36; 56	70 55; 82
Element 1, syllable rate, Hz	3.1 2.4; 3.7	3 2; 7	3.4 2.3; 4	2.1 1.6; 3.9	4.1 3.6; 4.4	2.2 2; 3	3 2.5; 3.9	3 2; 4	2.9 2.4; 3.2	5 2.8; 6.2	3.9 2.6; 4.4
Element 1, pulses per syllable	3 3; 4	3 2; 7	3 2; 4	4.5 3; 7	3 2; 5	1 1; 2	1 1; 1	2 1; 3	1 1; 2	1 1; 1	1 1; 1
Element 2, pulse rate of hemi-syllable A, Hz	32 29; 39	31 27; 33	31 29; 35	39 35; 40	37 36; 40	n/a*	n/a	n/a	n/a	n/a	n/a
Element 2, pulse rate of hemi-syllable B, Hz	100 77; 111	200 167; 250	200 200; 250	250 250; 250	250 200; 250	n/a	n/a	n/a	n/a	n/a	n/a
Element 2, syllable A+B rate, Hz	3.8 3; 4	3.6 3.3; 3.9	3.3 3.1; 3.5	3.6 3.6; 3.7	3.8 3.6; 4.1	n/a	n/a	n/a	n/a	n/a	n/a
Element 3, syllable rate, Hz	4.1 3.5; 4.4	3.7 3.2; 4.5	3.6 3; 4	3.6 3.3; 3.9	3.6 3.4; 4.0	2.3 2.1; 5.2	2.4 1.7; 3.1	2.1 1.9; 2.4	1.8 1.5; 2.0	2.1 1.9; 2.3	1.8 1.7; 1.9
Element 3, number of syllables	12 5; 12	12 8.5; 15	5 3.5; 11	7 4; 12	7 6; 11	8 4; 8	6 4; 8	6 5; 8	6 5; 8	8 8; 9	14 13; 16
Element 4, pulse rate, Hz	n/a	n/a	n/a	n/a	n/a	91 76; 91	83 77; 91	83 77; 100	80 77; 83	67 66; 71	56 51; 63
Element 4, duration, s	n/a	n/a	n/a	n/a	n/a	1.69 1.16; 1.86	1.43 0.87; 2.00	1.06 0.37; 1.52	1.43 0.29; 2.17	0.12 –	0.21 0.15; 0.74

*n/a—non-applicable

The study of courtship behavior of almost all subspecies of *S. eurasius* from south-eastern Europe and Turkey showed that the males produce the visual display similar to that in *S. hyalosuperficies* (Berger, 2008). During element 3 of courtship (named as 'element C' by Berger), a male produces a stroke with the hind tibiae and a backward movement with antennae. This visual display, however, is shorter than in *S. hyalosuperficies* and is usually produced once per element. At the same time, we regard this as a convergence and an additional example of independent increasing complexity of courtship in Gomphocerinae (Vedenina & Mugue, 2011).

We have clarified the ranges of the two species on the territory of Ukraine, Russia and Kazakhstan. It was previously suggested that *S. eurasius eurasius* Zub. occurs in Kazakhstan, Kyrgyzstan and south of Siberia eastwards to Transbaikalia, whereas *S. eurasius hyalosuperficies* Vor. inhabits southern Ukraine and south of European part of Russia, Orenburg region and Bashkortostan (Tarbinskii, 1948; Bei-Bienko & Mishchenko, 1951). Now we state that the range of *S. eurasius* extends from the south-eastern Europe to southern Siberia, eastwards to Transbaikalia. It occurs in Austria, Czech, Slovakia, Hungary, Romania, southern Ukraine, Saratov and Orenburg regions, southern Ural, northern Kazakhstan, Altai, Krasnojarskii krai, Tyva and Transbaikalia. The range of the nominate subspecies of *S. eurasius* stretches at least from Ukraine to Altai. We suggest that the differences between the subspecies of *S. eurasius* lie in the song features and courtship behavior, and further studies should be done to clarify the borders between the ranges of the subspecies. Probably, the South-European populations could be attributed to another subspecies, since the courting males from Hungary, Czech and Greece usually produce visual display (Berger, 2008) that is absent in courtship of males from Ukraine, Russia and Kazakhstan.

The range of *S. hyalosuperficies* covers the south-eastern part of European Russia, very likely the Caucasus, Orenburg region, southern Bashkortostan, almost all Kazakhstan except of the northern regions, and Kyrgyzstan. In the south-eastern part of European Russia, in Orenburg region and in Kazakhstan, the southern border of the range of *S. eurasius* may overlap with the northern border of the range of *S. hyalosuperficies*.

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References

Bey-Bienko, G.Y. & Mistshenko, L.L. (1951) *Locusts and grasshoppers of the USSR andadjacent countries*. Part II. Academy of Sciences of USSR Publ., Moscow-Leningrad, 287 pp. [in Russian, English translation: 1964, Jerusalem, Israel Program for Scientific Translations]

Berger, D. (2008) *The evolution of complex courtship songs in the genus Stenobothrus Fischer 1853 (Orthoptera, Caelifera, Gomphocerinae).* Unpublished doctoral thesis, Friedrich- Alexander-Universität Erlangen-Nürnberg, Erlangen, 169 pp.

Bukhvalova, M.A. & Vedenina, V.Yu. (1998) Contributions to the study of acoustic signals of grasshoppers (Orthoptera: Acrididae: Gomphocerinae) from Russia and adjacent countries. I. New recordings of the calling songs of grasshoppers from Russia and adjacent countries. *Russian Entomological Journal*, 7 (3–4), 109–125.

Elsner, N. (1974) Neuroethology of Sound Production in Gomphocerinae Grasshoppers (Orthoptera: Acrididae) I. Song Patterns and Stridulatory Movements. *Journal of Comparative Physiology*, 88, 67–102.
https://doi.org/10.1007/BF00695923

Elsner, N. (1994) The search for the neural centres of cricket and grasshopper song. In: Schildberger K. & Elsner N. (Eds.), *Neural Basis of Behavioral Adaptations*. V. 39. Fortschritte der Zoologie. G. Fischer Verlag, Stuttgard, New-York, pp. 167–194.

Elsner, N. & Wasser, G. (1995) Leg and wing stridulation in various populations of the gomphocerine grasshopper *Stenobothrus rubicundus* (Germar 1817). I. Sound patterns and singing movements. *Zoology*, 98, 179–190.

Faber, A. (1953) *Laut- und Gebòrdensprache bei Insekten (Orthoptera).* Mitteilungen des Staatlichen Museums fьr Naturkunde, Stuttgart, 198 pp. [in German]

Harz, K. (1975) Die Orthopteren Europas II. *Series Entomologica,* 11, 939.

Hedwig, B. (2000) A highly sensitive opto-electronic system for the measurement of movements. *Journal of Neuroscience Methods*, 100, 165–171.
https://doi.org/10.1016/S0165-0270(00)00255-7

Helversen, O.von. & Elsner, N. (1977) The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. *Journal of Comparative Physiology,* 122, 53–64.
https://doi.org/10.1007/BF00611248

Helversen, O.von. & Helversen, D.von. (1994) Forces driving coevolution of song and song recognition in grasshoppers. *In:* Schildberger K. & Elsner N. (Eds.), *Neural Basis of Behavioral Adaptations.* V. 39. Fortschritte der Zoologie. G. Fischer Verlag, Stuttgart, New-York, pp. 253–284.

Mařan, J. (1958) Ueber das vorkommen *Stenobothrus* (subs. *Stenobothrodes* Tarb.) *eurasius* Zub. in der Tschechoslowakei Orthoptera – Acrididae. *Acta Entomologica Musei Nationalis Pragae*, 32 (525), 537–543. [in German]

Otte, D. (1970) A comparative study of communicative behavior in grasshoppers. *Miscellaneous Publications,* 141, 1–167.

Ragge, D.R. & Reynolds, W.J. (1998) *The Songs of the Grasshoppers and Crickets of Western Europe.* Harley Books, Natural History Museum, London, 591 pp.

Savitsky, V.Yu. & Lekarev, A.Yu. (2007) New data on acoustic communication and sexual behavior of grasshoppers (Orthoptera: Acridoidea) from semi-deserts and deserts of Russia and adjacent countries. *Russian Entomological Journal*, 16 (1), 1–38. [in Russian, English abstract]

Sradnick, J., Klöpfel, A., Elsner, N. & Vedenina, V. (2016) Variation in complex mating signals in an "island" hybrid zone between *Stenobothrus* grasshopper species. *Ecology and Evolution*, 6 (14), 5057–5075.
https://doi.org/10.1002/ece3.2265

Tarbinskii, S.P. (1948) Order Saltatoria (Orthoptera) – Prygajusjie prjamokrylye. *In:* Tarbinskii, S.P. & Plavilschikov, N.N. (Eds.), Opredelitel' nasekomykh evropeiskoi chasti SSSR. OGIZ-Sel'khozgiz, Moscow, St.-Petersburg, pp. 76–127. [in Russian]

Vedenina, V. & Mugue, N. (2011) Speciation in gomphocerine grasshoppers: molecular phylogeny versus bioacoustics and courtship behavior. *Journal of Orthoptera Research*, 20, 109–125.
https://doi.org/10.1665/034.020.0111

Vedenina, V., Sradnick, J., Klöpfel, A. & Elsner, N. (2012) A narrow hybrid zone between the grasshoppers *Stenobothrus clavatus* and *Stenobothrus rubicundus*: courtship song analysis. *Biological Journal of the Linnean Society*, 107, 383–397.
https://doi.org/10.1111/j.1095-8312.2012.01935.x

Vorontsovskii, P.A. (1927) Materialy k poznaniju fauny Acridodea Orenburgskogo kraja. *Izvestija Orenburgskoi stantzii zaschity rastenii, 1*, 5–7. [in Russian]

Willemse, F. (1974) *Stenobothrus (Stenobothrodes) eurasius macedonicus* subspec. nov. from Macedonia (Orthoptera, Acrididae). *Enthomologische Berichten*, 34, 180–184.

Zubowsky, N. (1898) Zur Acridiodea-Fauna des asiatischen Russlands. *Annuaire du Musee Zoologique de l'Academie des Sciences de St. Petersbourg,* 3, 68–110. [in German and Latin]