A re-examination of the taxonomy of the *Chorthippus albomarginatus* group in Europe on the basis of song and morphology (Orthoptera: Acrididae)

Varvara Yu. Vedenina & Otto von Helversen

A study of European sibling species of the *Chorthippus albomarginatus* group shows that the males could be well distinguished on the basis of the number and density of the stridulatory pegs. We recorded and analysed the calling and courtship songs of the males, as well as the stridulatory movements of the hind legs. Analysis of the stridulatory leg movements allowed us to reveal more differences between both the courtship songs and the calling songs of the European species of this group. On the basis of the morphology, calling and courtship song analysis, we describe a new species, *Ch. ferdinandi* sp. n., from Greece (Peloponnesus) and a new subspecies, *Ch. oschei pusztaensis* ssp. n., from the Balkans, Hungary, Moldova and Ukraine. *Ch. bruttius* Fontana & La Greca, 1999 is classified as a subspecies of *Ch. karelini.* We describe the phylogenetic relations between the European species of the *Ch. albomarginatus* group based on the courtship song complexity and courtship visual display.

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Introduction

Closely related grasshopper species belonging to the *Chorthippus albomarginatus* group are difficult to distinguish morphologically. Thus, for a long time, they were named as subspecies of *Ch. albomarginatus* (De Geer, 1773) (Bei-Bienko & Mishchenko 1951, Harz 1975). Recording and analysis of the acoustic signals allowed several authors to distinguish more species of this group (Helversen 1986, Fontana & La Greca 1999). To date, the following sibling species are reported to inhabit Europe: *Ch. albomarginatus* (De Geer, 1773) inhabiting northern and central Europe, eastward reaching western Siberia and Yakutia; *Ch. oschei* Helversen, 1986 inhabiting the Balkans, Moldova and south-western Ukraine; *Ch. karelini* (Uvarov, 1910) occurring in Asia Minor, south-eastern part of European Russia, Kazakhstan and Middle Asia, eastward reaching Irkutsk region of Russia; *Ch. lacustris* La Greca & Messina, 1975 endemic to a very small area around the lake of Joannina in northern Greece; *Ch. bruttius* Fontana & La Greca, 1999 described from southern Italy and *Ch. labaumei* Ramme, 1926 described from north-western Anatolia. Four species, *Ch. albomarginatus*, *Ch. oschei*, *Ch. karelini* and *Ch. lacustris*, have quite similar calling songs (the songs produced spontaneously by an isolated male) that are relatively simple in their temporal structure (Helversen 1986, Ragge & Reynolds 1998, Fontana & La Greca 1999, Vedenina & Bukhvalova 2001, Benediktov 2005). In contrast, their courtship songs (the songs produced by a male when close to a female) are very different

Tijdschrift voor Entomologie 152: 65–97, Figs 1–81. [ISSN 0040–7496]. http://www.nev.nl/tve

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** We announce with deep regret the death of the junior author on March 2, 2009.

and extremely complex in temporal pattern, and in three species, *Ch. oschei*, *Ch. karelini* and *Ch. lacustris*, the songs are accompanied by species-specific movements of the hind legs and antennae (Helversen 1986). Two species of this group, *Ch. albomarginatus* and *Ch. oschei,* were found to hybridize in a contact zone in Ukraine and Moldova (Vedenina & Helversen 2003). The hybrids can be easily produced under no-choice conditions; however, in choice mating experiments, females of the both species demonstrated a strong assortative mating. Comparison of the parental and hybrid viability revealed a reduced hatching and increased larval mortality in F_1 and F_2 hybrids (Vedenina et al. 2007 a). This indicated that reproductive isolation between *Ch. albomarginatus* and *Ch. oschei* was incomplete and mainly ethological isolating mechanisms evolved between the two species. It is generally agreed that the *Ch. albomarginatus* group in Europe is an assemblage of phylogenetically young species.

The existent literature does not contain a clear diagnosis for all European species of the *Ch. albomarginatus* group. On the other hand, more recent studies show that to distinguish the species of this group one can use the morphology of the stridulatory pegs situated on the inner side of the male hind femur. Thus the morphology of the stridulatory pegs was shown to be different in *Ch. bruttius* and *Ch. albomarginatus* (Fontana & La Greca 1999). Two species, *Ch. albomarginatus* and *Ch. oschei,* may be well recognized on the basis of the stridulatory file structure and the number of the stridulatory pegs as well (Vedenina et al. 2007 b). Moreover, recently collected material on the calling and courtship songs allows us to re-examine the European species of the group. As a result of this study: (i) the species of the *Ch. albomarginatus* group are reviewed on the basis of morphology and song parameters, (ii) a description of a new species and a new subspecies is given, (iii) one species is downgraded to the level of subspecies, (iv) the phylogenetic relations between the European species of the group are clarified and a hypothesis on their biogeography is presented.

Methods

Morphological measurements

Morphological studies of the specimens were done with a MBS-9 light microscope at 8–56× magnification using an ocular micrometer. The following morphological features were measured: the number of stridulatory pegs, the length and width of tegmen, the length and width of hind femur, the length of pronotum and prozona. Figures were obtained using a Sony DSC-W17 digital camera. Morphology of the stridulatory files was studied with a CamScan MV2300 scanning electron microscope. Specimens examined in this study are deposited in Zoological Institute, Russian Academy of Sciences, St.-Petersburg (ZIN), Zoological Museum of Moscow State University (ZMMU), Department of Entomology, Moscow State University (EDMU), in the personal collections of V. Vedenina in Moscow (CV) and of Fer Willemse in Eygelshoven, The Netherlands, a public collection in due time (CW), in the Zoological Museum of Akdeniz University, Antalya, Turkey (AUZM), in the Museum für Naturkunde der Humboldt-Universität, Berlin (MNHU), and in the British Museum of Natural History (BMNH).

Song recordings

The calling song was recorded from isolated males; the courtship song was recorded when a male was sitting close to a female. Most of the song recordings (from 185 males) were made in the laboratories of Zoological Institute in Erlangen and Institute for Information Transmission Problems in Moscow. During stridulation of the males studied in 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 microphone (½” Brüel and Kjaer) recordings of the sounds, were A/D-converted with a custom-built PC card. The sampling rate was 2 kHz for recording the stridulatory movements and 100 kHz for sound recordings. The ambient temperature near a singing male was 30–32° C. The smaller number of the song recordings (from 63 males) was made in the field with the cassette recorders; the upper frequency limit was 14 kHz. During the field recordings, the ambient temperature near a singing male varied in a range of 24–42° C; however, the recordings made at 30–32° C were only chosen to measure the song parameters and to show the oscillograms of the calling songs. All recordings were analyzed with a Turbolab 4.0 program (Germany, Bressner Technology). Courtship behaviour of 25 males was also recorded with a Sony DCR-TRV 355E digital video camera; the video signals were transferred to a PC for analysis of visual display.

The courtship song analysis allowed us to compare the homologous temporal song features. Earlier, we identified the homologous song elements in

Ch. albomarginatus and *Ch. oschei* (Vedenina & Helversen 2003, Vedenina et al. 2007 b). In the current paper, we describe the homologous song elements in other species on the basis of a similarity of the leg-movement pattern and also an order of the song element alternation. For the song description we used the following terms: *pulse* – the sound produced by one down or up movement of a hind leg; *gap* – the interval between pulses (Figs 28–29); *element* – the sound produced by the same leg movements (Fig. 53). All statistical analyses were performed using *Statistica* 6/Win v.

Results

Key to males based on morphological characters

1. Stridulatory file with fewer than 135 pegs (Fig. 2); in proximal third of stridulatory file pegs arranged sparsely in one straight row as in Figs 5–6; general colour brown to green; hind knee not darker than general colour; hind tarsi not pale or white, but of general colour .... *albomarginatus*
– Stridulatory file with more than 130 pegs (Fig. 2); in proximal third of stridulatory file pegs arranged in two-three rows as in Figs 7–10, 12–16; if pegs arranged in one row, starting from about 10th to 50th proximal pegs, they not organized in one straight file but in a wavy row of dense pegs as in Figs 11, 21, or in a wavy row of sparse pegs as in Fig. 17; general colour usually brown; hind knee darker brown or black, at least upper lobe; hind tarsi pale or white 2
2. In proximal part of stridulatory file pegs arranged very widely in two-three rows as in Fig. 12–16; number of pegs varies in range of 130–205 .... *karelini*
– In proximal part of stridulatory file pegs arranged more densely in two rows as in Figs 7–10 or in one wavy row as in Fig. 11 3
3. Number of stridulatory pegs varies in range of 205–240; stridulatory file long, last distal peg at level of second to third tooth of tibia when it pressed to femur; known only from Peloponnesus, Greece .... *ferdinandi*
– Stridulatory file with less than 205 pegs; last distal peg at level of about fourth tooth of tibia when it pressed to femur 4
4. Antennae long, reach to 3rd tergum; tips of antennae and hind tarsi distinctly white; proximal pegs arranged more widely as in Fig.17; known only from Ipiros, northern Greece .... *lacustris*
– Antennae shorter, reach to 2nd tergum; tips of antennae and hind tarsi pale but not distinctly white; proximal pegs arranged more densely as in Figs 7–11 5
5. Proximal stridulatory pegs arranged in one wavy row as in Fig. 11; known only from Northern Greece .... *oschei oschei*
– Proximal stridulatory pegs arranged in two rows as in Figs 7–10; widespread in Balkans (except for Greece) and adjacent countries .... *oschei pusztaensis*

Chorthippus albomarginatus (De Geer)

Figs 1–2, 5–6, 22–23, 28–29, 50–55

Acridium albo-marginatum De Geer, 1773: 480.

Material examined. Germany, Bavaria, 13 km N of Erlangen, Effeltrich, 20.vii.1999, 4♂, 20♀, 20–25.viii.2001, 10♂, 16♀, 25–30.vii.2002, leg. V. Vedenina (ZMMU, CV), song recordings in 20♂. **Poland,** 85 km S of Krakow, surroundings of Rabka, 574 m, 21.viii.2005, 18♂, 13♀, leg. V. Vedenina (CV), song recordings in 10♂. **Ukraine:** Ivano-Frankovskii region, Mikulichin, 12.viii.1996, 1♂, 2♀, 02.viii.1997, 3♂, 4♀, leg. V. Vedenina (CV), song recordings in 2♂; Ivano-Frankovskii region, 3 km E of Kolomyja, 2.viii.1997, 8♂, 7♀, leg. V. Vedenina (CV); 10 km E of Chernovtzy, meadow near highway, 3.viii.1997, 9♂, 5♀, leg. V. Vedenina (CV), song recordings in 3♂; Kiev, 29.viii.1998, 6♂, 3♀, leg. V. Vedenina (CV), song recordings in 5♂; Cherkassy region, Kanev reserve, 18–21.vi.1996, 12♂, 1♀, leg. V. Vedenina (CV); Poltava region, Mirgorod district, Velikie Sorochintzy, 25.07–20.viii.1994, 8♂, 12–14.viii.1997, 8♂, 11♀, leg. V. Vedenina (ZMMU, CV), song recordings in 10♂; Khar'kov region, Shevchenkovo district, Petrovka, 10.vii.1996, 4♂, 2♀, leg. V. Vedenina (CV); border between Donetzk and Dnepropetrovsk regions, 25 km W of Krasnoarmeisk, Kamjanka, 22.vii.2000, 12♂, 6♀, leg. V. Vedenina (CV), song recordings in 9♂; Zaporozh'je region, 40 km E of Melitopol, Vladimirovka, 20.vii.2000, 10♂, 2♀, 01.viii.2001, 10♂, leg. V. Vedenina (ZMMU, CV), song recordings in 10♂. **Russia:** Tver' region, ab. 37 km NE of Rzhev, Krutitzy, 25.viii.2004, 7♂, 3♀, leg. V. Vedenina (CV), song recordings in 6♂; Moscow, Bitzevskii park, 3.vii.2001, 5♂, 3–5.ix.2003, 22♂, 9♀, leg. V. Vedenina (ZMMU, CV), song recordings in 13♂; 12 km W of Tambov, near Arapovo, 7.viii.2001, 6♂, 3♀, leg. V. Vedenina (CV), song recordings in 5♂; Volgograd region, about 50 km SW of Surovikino, surroundings of Chernyshkovskii, 4.viii.2001, 9♂, 5♀, leg. V. Vedenina (CV), song recordings in 4♂.

Distribution

This species inhabits northern and central Europe, reaching western Siberia and Yakutia in the east. In Europe, its range extends northwards almost to the Arctic Circle and southwards to the Pyrenees (Ragge

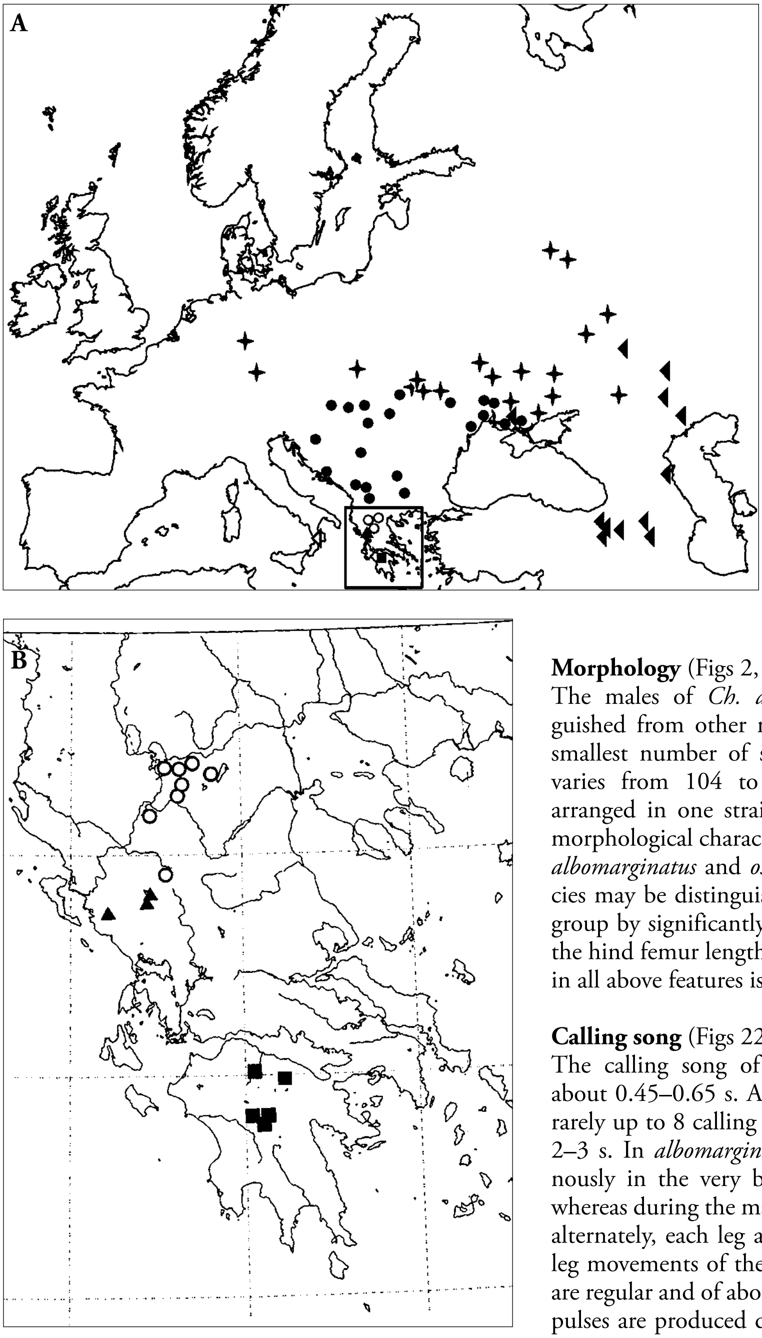


Fig. 1. Map of the localities of the *Chorthippus albomarginatus* group studied in Europe (a) and in Greece (b): ★ *Ch. albomarginatus,* ● *Ch. oschei pusztaensis,* ○ *Ch. o. oschei,* ◀ *Ch. k. karelini,* ◁ *Ch. k. bruttius,* ▲ *Ch. lacustris,* ■ *Ch. ferdinandi.*

& Reynolds 1998), probably Alps, Carpathian Mountains, the northern and eastern parts of Ukraine, Rostov and Volgograd regions in European Russia. Its range in Asiatic part of Russia remains to be clarified.

Morphology (Figs 2, 5–6, App. 1)
The males of *Ch. albomarginatus* can be distinguished from other members of the group by the smallest number of stridulatory pegs (mean value varies from 104 to 122). The pegs are always arranged in one straight row. The values of other morphological characters studied are quite similar in *albomarginatus* and *oschei.* However, these two species may be distinguished from other species of the group by significantly smaller values of tegmen and the hind femur length. In the females, the difference in all above features is insignificant.

Calling song (Figs 22–23, 28–29)
The calling song of *Ch. albomarginatus* lasts for about 0.45–0.65 s. As a rule, a male produces 3–4, rarely up to 8 calling songs separated by intervals of 2–3 s. In *albomarginatus,* the legs vibrate synchronously in the very beginning of the calling song, whereas during the main part of the song, they move alternately, each leg at a rate of about 40/s. All the leg movements of the main part of the calling song are regular and of about equal amplitude. The sound pulses are produced during either up and down leg movements. Thus, the sound pulses follow rather regularly at a rate of about 70–80/s, separating by distinct gaps. Quite often, one loud pulse produced in the beginning of the song is separated from the following pulses. The calling song of *albomarginatus* may be distinguished from the song of all other species of this group by the lower pulse rate and the presence of distinct gaps between pulses.

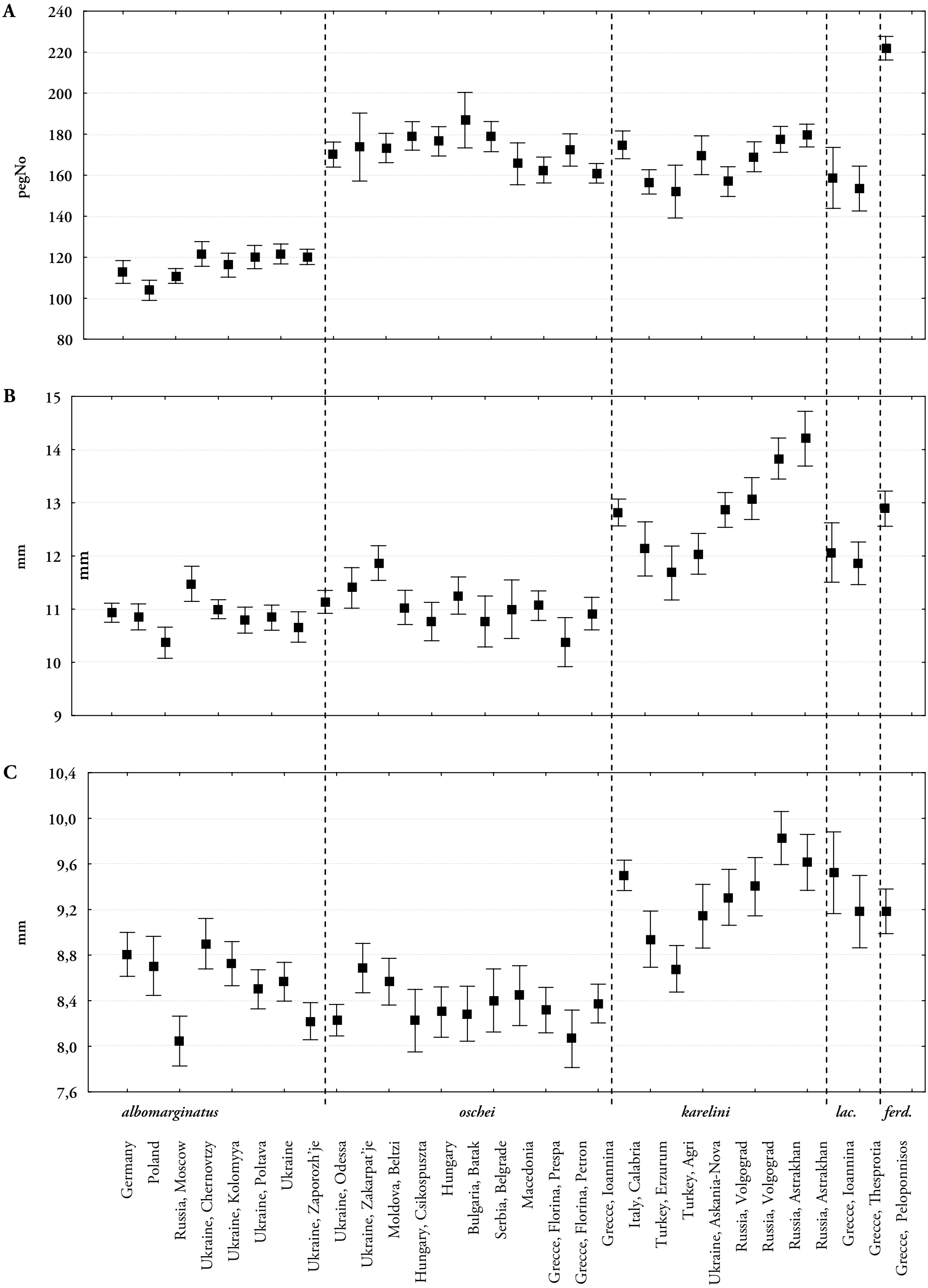


Fig. 2. The number of stridulatory pegs (a), length of tegmen (b), and length of hind femur (c) in males of five species of the *Ch. albomarginatus* group from different localities.

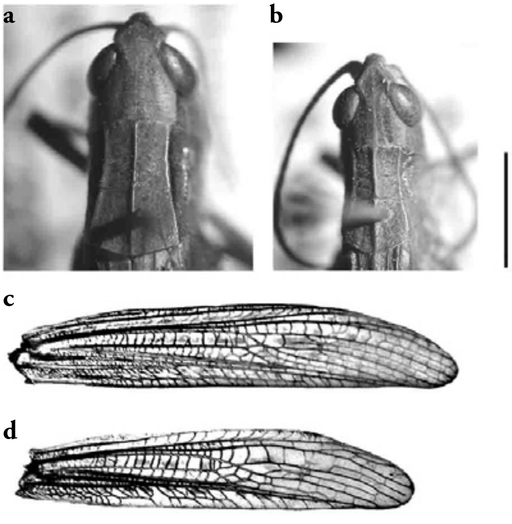


Fig. 3. *Chorthippus oschei pusztaensis* ssp. n., paratypes, head and pronotum, dorsal view in ♀ (a) and in ♂ (b), right tegmen in ♀ (c), and in ♂ (d); scale 3 mm.

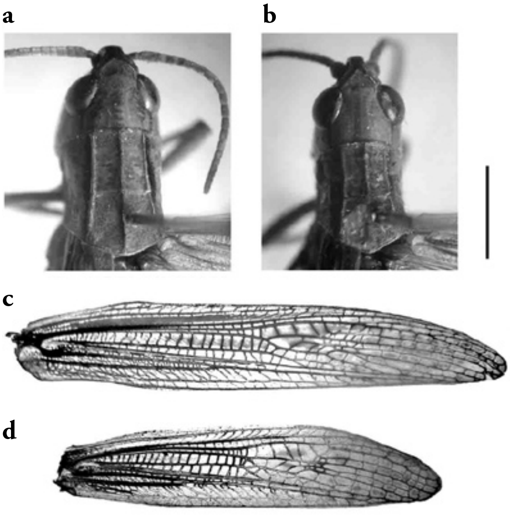


Fig. 4. *Chorthippus ferdinandi* sp. n., paratypes, head and pronotum, dorsal view in ♀ (a) and in ♂ (b), right tegmen in ♀ (c), and in ♂ (d); scale 3 mm.

Courtship song (Figs 50–55, App. 2)
Among all European species of the group, *Ch. albomarginatus* produces the simplest song regarding the number of the song elements and other features of the courtship behaviour. The courtship song of *albomarginatus* starts with an alternation of two elements, the A and B elements. The A elements are produced with legs vibrating rapidly (at 52–54/s) in a high position, the B elements are produced with legs held in a lower position and vibrating much more slowly (at 20–22/s). The A and B elements contain the pulses repeated at a rate of the corresponding leg vibration. About 15–30 s after the beginning of the courtship, a third C element appears. The last B element (B1), preceding the C element, has always a pause at about half of its duration. The element C is produced while the legs are in an extra-high position vibrating in a complex pattern: the low-amplitude vibrations alternate with the high-amplitude ones. Element C contains three-throw pulses; each middle pulse is often louder than the other two. In the very beginning of the C element, one louder and longer pulse is produced, called the C1 element. After the end of the C element, the A and B elements alternate again. In a fully developed courtship, each C element follows after 3–7 pairs of A/B elements. During A and B elements, the two legs are moved synchronously. In the very beginning of the C element, the legs are moved synchronously as well, but in the main part of the C element, the legs are moved alternately. In the beginning of courtship, A and B elements are almost of the same loudness (Helversen 1986), however, in the fully developed courtship, A elements are louder than B elements. There is some geographical variability in the number of A/B pairs between C elements and in the degree of the loudness increase of A elements during each cycle (compare Figs 50–52). Relative loudness of pulses in the C element slightly varies as well.

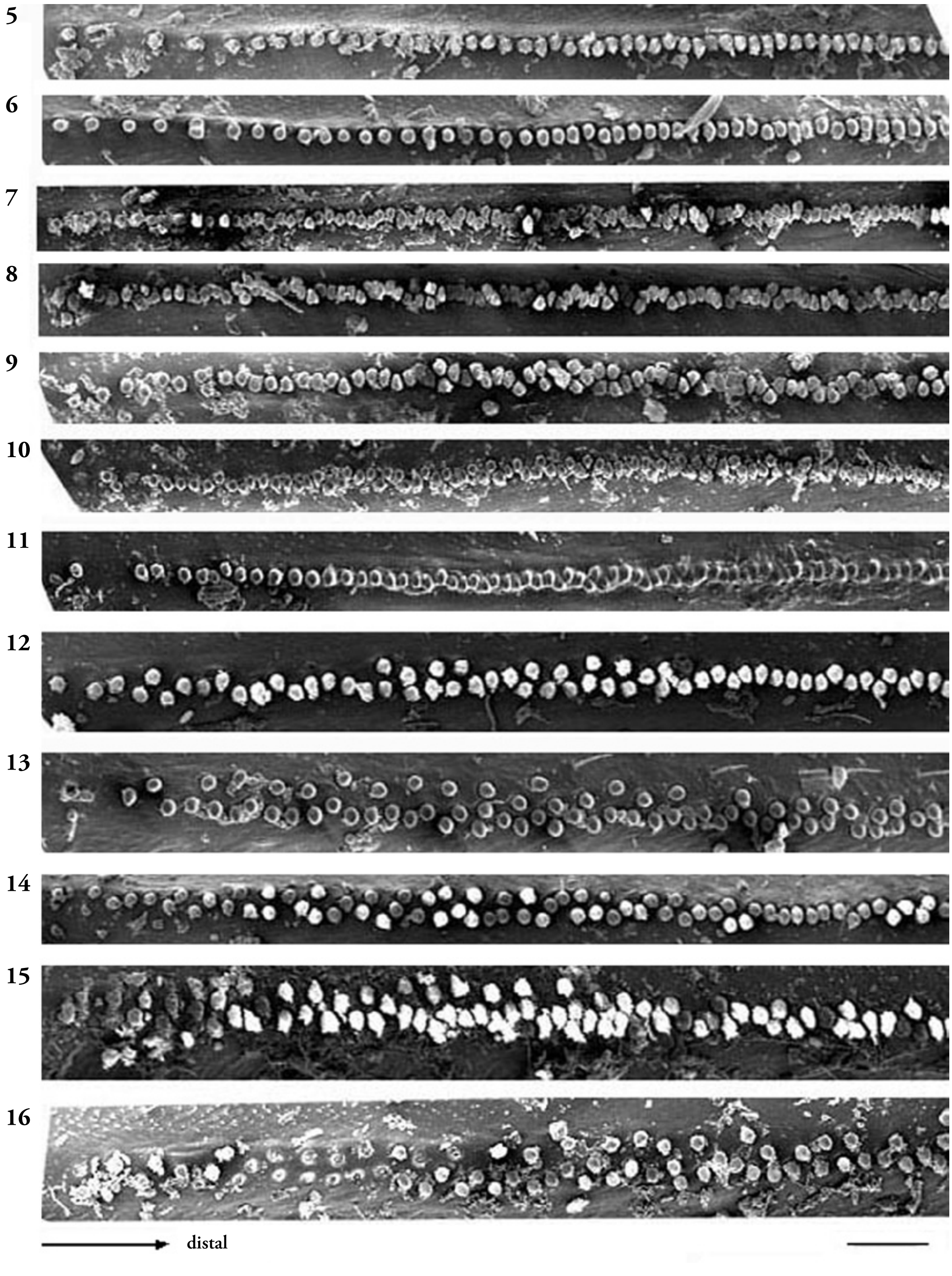
Chorthippus oschei Helversen

Figs 1–3, 7–11, 24–27, 30–33, 56–59

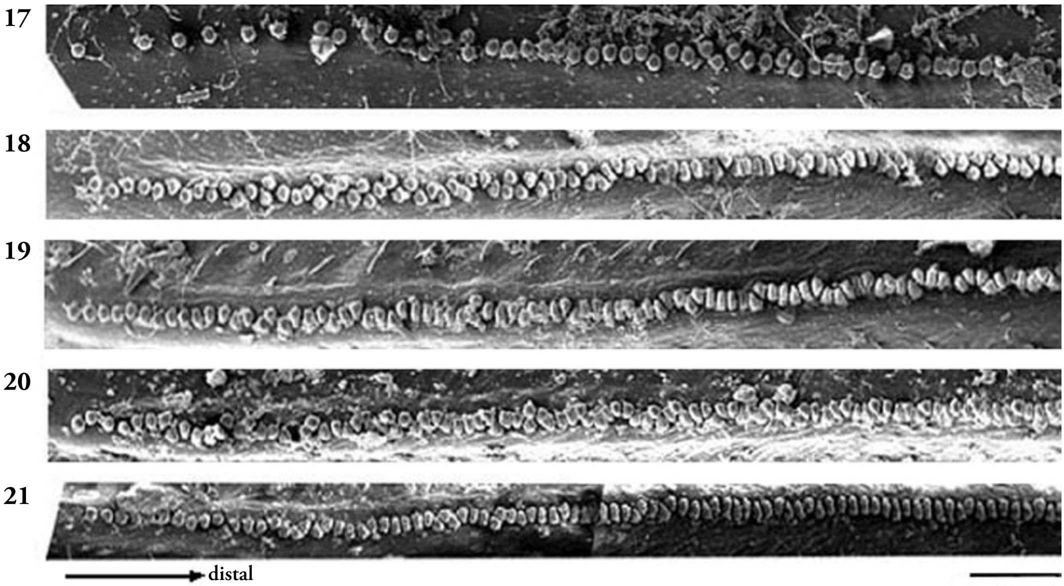
Chorthippus oschei Helversen, 1986: 322–323.

Chorthippus oschei oschei Helversen

We distinguish two subspecies of *Ch. oschei* in Europe on the basis of differences in two parameters of the courtship songs, the differences in calling songs and the morphology of the stridulatory file. The holotype of *Ch. oschei* Helversen, 1986 was described from NE of Florina town, Greece. The courtship song described was recorded from the Greek specimens as well (Helversen 1986). Therefore, the Greek form is regarded as the nominate subspecies. However, some paratypes mentioned by Helversen (1986) were from Croatia, Serbia and Montenegro. They should be regarded as *Ch. oschei pusztaensis* ssp. n.



Figs 5–16. Proximal part of the male stridulatory file on inner side of hind femur: 5, *Chorthippus albomarginatus*, Germany; 6, *Ch. albomarginatus*, Russia: Moscow; 7, *Ch. oschei pusztaensis*, Hungary: Kistompapuszta; 8, *Ch. oschei pusztaensis*, Bulgaria; 9, *Ch. oschei pusztaensis*, Moldova; 10, *Ch. oschei pusztaensis*, Ukraine: Odessa region; 11, *Chorthippus oschei oschei*; 12, *Ch. karelini bruttius*; 13, *Ch. k. karelini*, Turkey: Erzurum; 14, *Ch. k. karelini*, Turkey: Agri; 15, *Ch. k. karelini*, Ukraine: Askania-Nova; 16, *Ch. k. karelini*, Russia: Volgograd region. Scale 100 mkm.



Figs 17–21. Proximal part of the male stridulatory file on inner side of hind femur: 17, *Chorthippus lacustris*; 18–19, *Ch. ferdinandi*, Peloponnesus: Kalavrita; 20–21, *Ch. ferdinandi*, Peloponnesus: Mt. Mainalon. Scale 100 mkm.

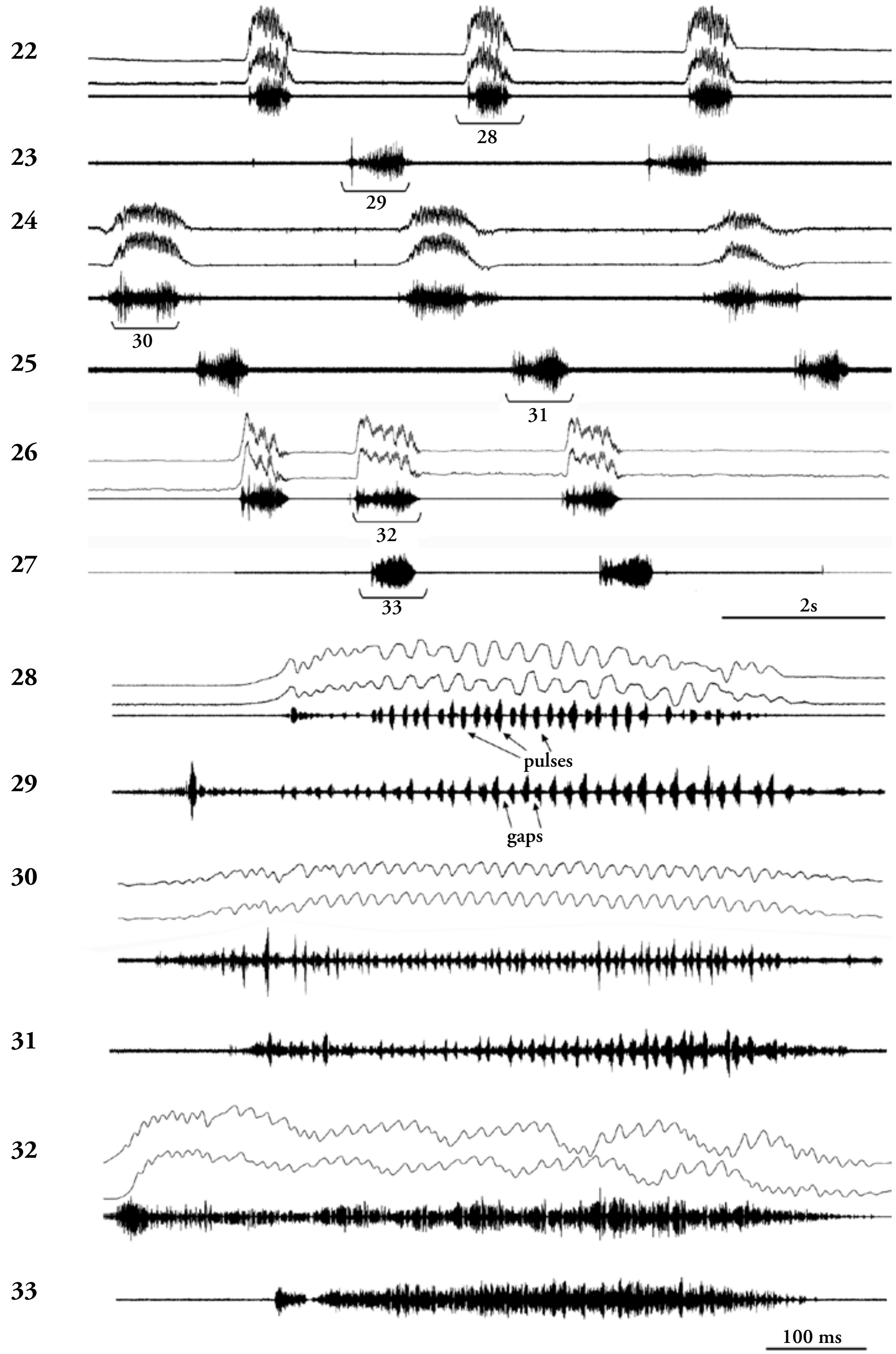
Material examined. Greece: Makedhonia, Florina, micro Prespa lake, 8.viii.1987, 1♂, leg. O. v. Helversen, song recording in 1♂; microlimni along lake Prespa, 800 m, 14.viii.1988, 10♂, 10♀, leg. F. Willemse (ZIN, CW); Makedhonia, Florina, Mt. Vernon, 1500–1600 m, 13.viii.1988, 7♂, 3♀, leg. F. Willemse (CW); Makedhonia, NE of Florina town (type locality), 19.vii.1978, 2♂, leg. O. v. Helversen, song recordings in 2♂; Makedhonia, Florina, lake Petron, 500 m, 15.viii.1988, 10♂, 9♀, leg. F. Willemse (CW); Makedhonia, Kastoria, Dispilio along lake Kastoria, 760 m, 12.viii.1988, 5♂, 3♀, leg. F. Willemse (CW); Makedhonia, Grammos, 17.ix.2001, 10♂, 5♀, leg. O. v. Helversen (ZMMU, CV), song recordings in 8♂; Ipiros, Ioannina, 5–12 km N of Metsovon, 12.viii.1988, 10♂, 5♀, leg. F. Willemse (CW), song recordings in 5♂; 6 km N of Metsovon, 27.vii.2004, 6♂, 7♀, leg. V. Vedenina (CV), song recordings in 6♂.

Chorthippus oschei pusztaensis Vedenina & Helversen, **ssp.n.**

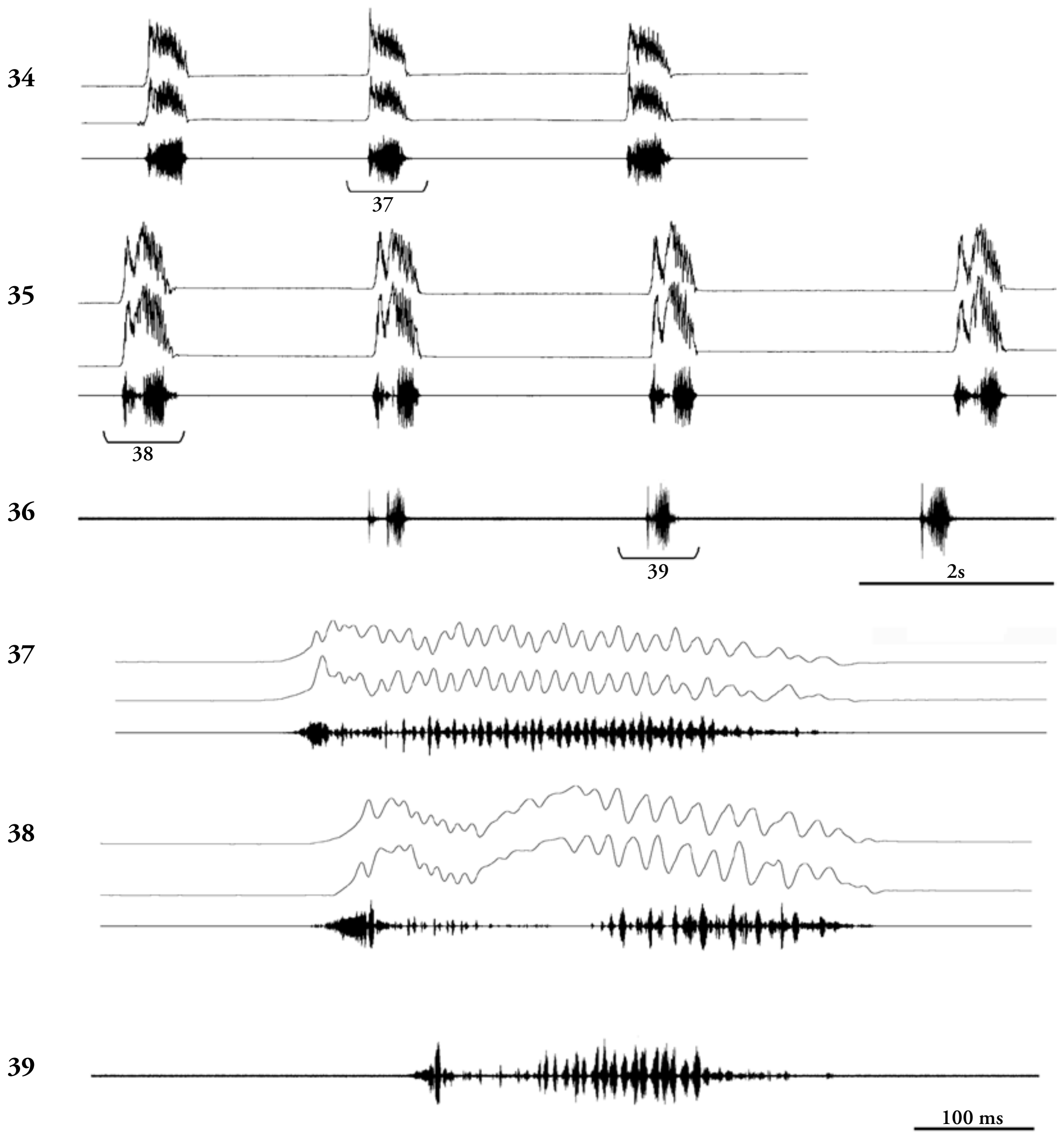
Type material. Holotype ♂. **Hungary:** province Békés, surroundings of Battonya, Csikospuszta, 16.vii.2002, leg. V. Vedenina (ZIN).

Paratypes. 11♂ and 5♀, same locality and date as holotype, leg. V. Vedenina (ZIN), song recordings in 7♂; Kistompapuszta, 16.vii.2002, 10♂ and 7♀, leg. V. Vedenina (ZIN), song recordings in 8♂. **Croatia:** Zagreb region, Kutina, 150 m, 29.vii.1963, 3♂, 1♀, leg. F. Willemse (CW). **Serbia:** Belgrade region, Vrcin, 200m, 17.viii.1966, 5♂, 8♀, leg. F. Willemse (CW). **Macedonia:** Tetovo region, Vratnica, 1.viii.1966, leg. F. Willemse (CW), 9♂, 11♀. **Hungary:** ab. 40 km S of Budapest, between Dabas and Bugai, 12.ix.1999, 12♂, 4♀, leg. K.Orci (CV); Kunhegyes, 11.ix.1990, leg. O. v. Helversen, song recording in 4♂. **Romania,** Huedin, Saula, 7.vii.2002 (D.Berger), 1♂, 1♀, leg. D.Berger (CV), song recording in 1♂. **Bulgaria:** about 2 km E of Vraza, 30.vi.2002, 2♂, 1♀, leg. V. Vedenina (CV), song recording in 1♂; 50 km SW of Plovdiv, near the lake Batak, 1230 m, 28.vi.2002, 11♂, 15♀, leg. V. Vedenina (CV), song recordings in 11♂. **Moldova,** Beltzi, 4.viii.1997, 12♂, 3♀, leg. V. Vedenina (CV), song recordings in 9♂. **Ukraine:** Zakarpat'je region, 4 km NW of Tjachev, 29.vii.1997, 7♂, 8♀, leg. V. Vedenina (CV), song recordings in 6♂; Odessa region, 20 km N of Belgorod-Dnestrovskii, beach of Dnestrovskii liman, surroundings of Semjonovka, 2.vii.1999, 12♂, 12♀, 8.vii.2001, 17♂, 18♀, leg. V. Vedenina (ZMMU, CV), song recordings in 16♂.

Other material, excluded from type series (damaged by *Anthrenus*). **Croatia:** Ploče, lake near Šipak, 13.viii.1974, 3♂, leg. O. v. Helversen, song recordings in 3♂. **Serbia:** Kosovo, near Peč, Dečani, 17.viii.1974, 1♂, leg. O. v. Helversen, song recording in 1♂. **Montenegro:** lake near Plav, 970 m, 16.viii.1974, 1♂, leg. O. v. Helversen, song recording in 1♂. **Hungary:** Györ, 6.viii.1991, 1♂, leg. O. v. Helversen, song recording in 1♂.



Figs 22–33. Oscillograms of the calling songs of the species of the *Chorthippus albomarginatus*-group at two different speeds: 22, 28, *Ch. albomarginatus,* Germany; 23, 29, Ukraine: Poltava region; 24, 30, *Ch. oschei pusztaensis,* Ukraine: Nikolaev region; 25, 31, Ukraine: Odessa region; 26, 32, *Ch. oschei oschei,* Greece: Florina; 27, 33, Greece: Ioannina, rec. F. Willemse. In figures 22, 24, 26, 28, 30 and 32 the two upper lines are recordings of hind leg movements and the lower line is the sound recording.



Figs 34–39. Oscillograms of the calling songs of the species of the *Chorthippus albomarginatus*-group at two different speeds: 34, 37, *Ch. karelini bruttius,* Italy: Calabria; 35, 38, *Ch. karelini karelini,* Turkey: Erzurum; 36, 39, Ukraine: Askania-Nova. In figures 34–35, 37–38 the two upper lines are recordings of hind leg movements and the lower line is the sound recording.

Description

Head from above as wide as pronotum, 0.7–0.8 times as short as pronotum (Fig. 3). Foveolae distinct, visible from above, 3.7–4 times as long as broad. Antennae filiform, in ♂ extend slightly beyond hind coxa, in ♀ hardly reach hind margin of pronotum, its longest medial segments in ♂ 2 times, in ♀ 1.6 times as long as wide. Pronotum with straight distinct lateral carina; prozona nearly as long as metazona. Radial vein of tegmen clearly sinuate (Fig. 3). Tegmina projecting slightly beyond apices of hind knees. Tegmen in ♂ 4.6, in ♀ 6 times as long as wide. Alae slightly shorter than tegmina. In male the number of stridulatory pegs on the inner side of hind femur varies in the range of 151–200. On the proximal third of the stridulatory file the pegs arranged very densely and often in two rows (Figs 7–10). Tympanal organ in ♂ 2.7 times, in ♀ 2 times as long as wide. Cerci conical, in ♂ reaching margin of supra-anal plate, in ♀ reaching half of supra-anal plate. Subgenital plate in ♂ bluntly conical. Ovipositor short, without lateral teeth. Hind femur in ♂ 4.7, in ♀ 5.4 times as long as its maximum width.

General colour brown, green forms rarely observed in males, more often in ♀. Apical segments of antennae pale or whitish in ♂, of general colour in ♀. Pronotum of general colour, in ♀ lateral keels ventrally often bordered with dark brown streak. Tegmen in ♂ of general colour, in ♀ commonly costal area with white stripe, contrasting with darker brown Sc and often also R vein and sometimes darker brown coloured subcostal, medial and basal part of radial fields. Hind femur of general colour. Hind knee in ♂ darker brown, especially upper lobe, in ♀ of general colour and often upper lobe only darker. Hind feet of general colour, third tarsus in ♂ whitish.

Measurements (in mm). Body length ♂ 14–15, ♀ 19–20; pronotum length ♂ 2.5–3, ♀ 2.9–3.2; tegmen length ♂ 10.5–12.3, ♀ 12.8–14; tegmen width ♂ 2.2–2.6, ♀ 2.1–2.2; femur length ♂ 7.8–9; ♀ 10.8–11.5; femur width♂ 1.6–1.9, ♀ 2–2.2; peg number in ♂ 155–194.

Etymology

This subspecies is described after specimens collected in the Hungarian Puszta.

Distribution

The nominate subspecies is known only from Northern Greece. *Ch. o. pusztaensis* inhabits almost all Balkans (except for Greece), Hungary, Moldova and south-western Ukraine. It occurs also in Austria (L. Zechner, pers. commun.), Slovakia (Holuša et al. submit.), and probably in Slovenia. The northern border of *Ch. o. pusztaensis* may overlap with the southern border of *Ch. albomarginatus*, and the two species may hybridize, as it was found in Ukraine and northern Moldova (Vedenina & Helversen 2003), as well as in Romania (Iorgu 2008) and Slovakia.

Morphology (Figs 2–3, 7–11, App. 1)

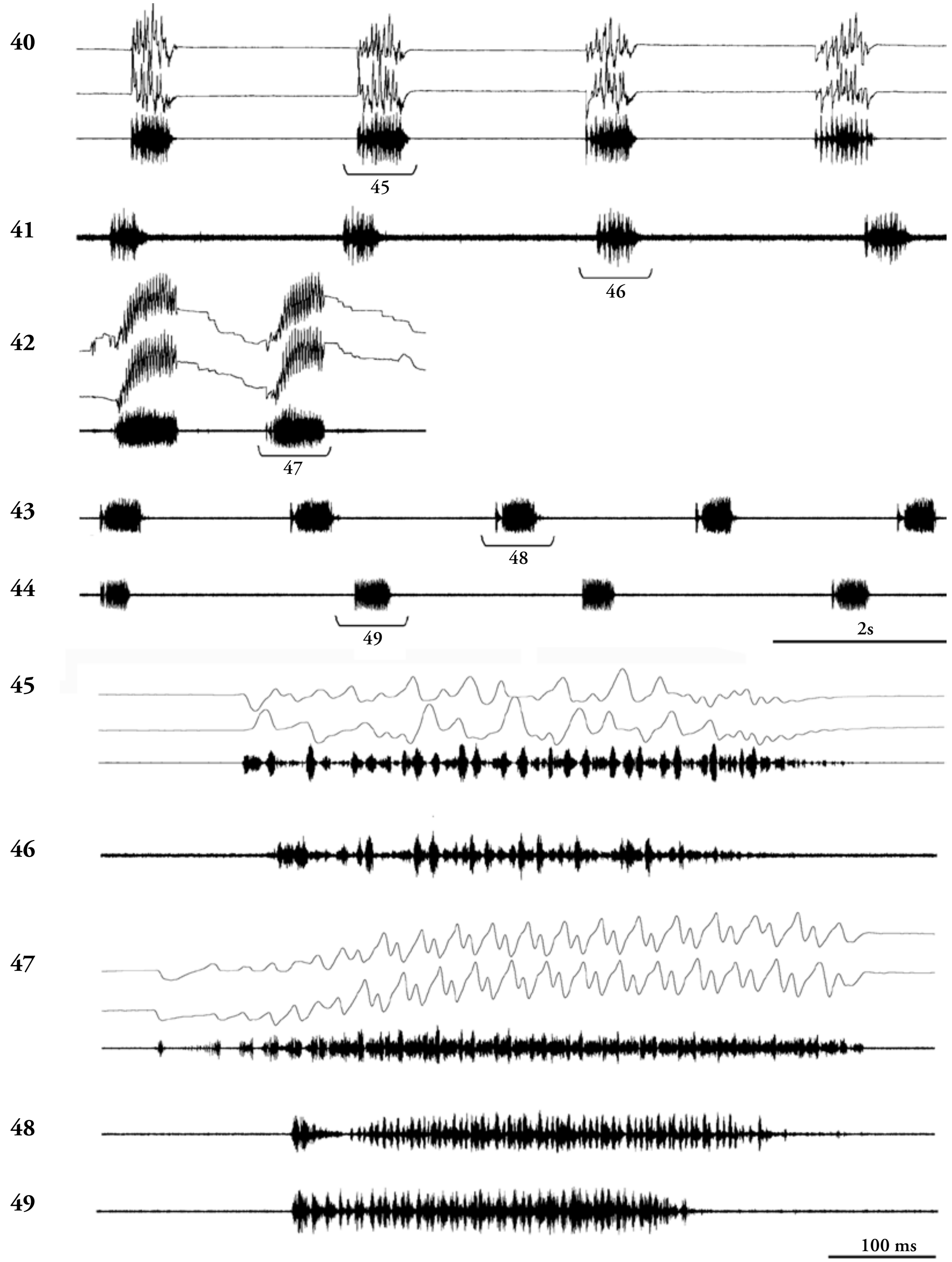
The mean number of stridulatory pegs in the males of *Ch. oschei* varied from 158 to 186 in different populations. In *Ch. o. pusztaensis*, the pegs are arranged very densely on the proximal third of the stridulatory file. Quite often they are arranged in two rows as in Figs 7–10. In the nominate subspecies, the pegs are usually organized in one wavy row as in Fig. 11; however, similarly to *pusztaensis*, the peg density is rather high. Other morphological characters (length of pronotum, tegmina and femora) studied are similar to those in *Ch. albomarginatus*. However, the length of the male antennae is different in the two species: in *albomarginatus* antennae do not extend beyond hind coxa, in *oschei* they are longer and reach the 2nd tergum. In living *oschei* males, the tips of antennae and hind tarsi are remarkably whitish, whereas in *albomarginatus* they are of general colour. Hind knee in *oschei* are darker brown or black, in *albomargiatus* they are of general colour.

Calling song (Figs 24–27, 30–33)

The calling song of *Chorthippus oschei pusztaensis* is different from the *albomarginatus* song by a higher rate of the leg movements (50/s) and a higher pulse rate (90–110/s). The legs in the nominate subspecies move even more frequently, at a rate of 60–65/s, and besides, these movements are modulated by a lower frequency of about 8/s. Oscillographic analysis shows that the gaps between pulses are sometimes distinct in the songs of *pusztaensis*, however, these gaps are completely absent from the songs of the nominate subspecies. In the latter subspecies, the sound is sometimes modulated in the amplitude. Other parameters of the calling song, like the number and duration of songs, are similar to those in *albomarginatus*.

Courtship song (Figs 56–59, App. 2)

Similarly to *Ch. albomarginatus*, the courtship song of *oschei* also starts with alternation of A and B elements. The rate of the leg vibrations during A and B elements, as well as the leg-movement pattern producing A elements, in *oschei* are quite similar to that in *albomarginatus*. However, the leg movement pattern producing B elements is more complex than in *albomarginatus*. The rate of sound pulses in A and B elements is similar to that in *Ch. albomarginatus*: about 59–62/s in the A element and about 22–24/s in the B element. However in *Ch. oschei*, B elements are always of a higher intensity than A elements. After about 20–30 alternations of A/B pairs, a complex of B1-A1-C elements follows. In *Ch. o. pusztaensis*, an amplitude of the leg movements during the B1 element gradually increases and the sound loudness essentially increases as well (3–4 times higher in comparison to the loudness of B element). The B1 element lasts for 2 s on average. During the up movement, the legs produce a low-amplitude pulse, during the down movement – a high amplitude pulse. The high amplitude pulses of the B1 element follow each other rather regularly at a rate of about 20–30/s. After that, a rapid leg vibration at a rate of about 75–80/s produces a very short (about 0.18 s) element A1 that contains the pulses following at the same rate. The complex element C starts with lifting



Figs 40–49. Oscillograms of the calling songs of the species of the *Chorthippus albomarginatus*-group at two different speeds: 40, 45, *Ch. lacustris,* Greece: NE of lake Ioannina (type locality); 41, 46, same locality, rec. F. Willemse; 42, 47, *Ch. ferdinandi,* Peloponnesus: Karkalou, N of Dimitsana; 43, 48, Peloponnesus: Kalavrita, rec. F. Willemse, paratype; 44, 49, same, holotype. In figures 40, 42, 45 and 47 the two upper lines are recordings of hind leg movements and the lower line is the sound recording.

of the abdomen at a maximal angle of 50°, accompanied with a fast movement of the legs into an extra-high position and a very characteristic stroke with the tibiae. The maximal angle between the tibia and femur is 100–130°; the tibial stroke lasts for 0.2–0.4 s. During the up-stroke, the C1 element is produced. Then the tibiae come again to their normal position and the legs vibrate in a complex pattern. In two subspecies, B1 and C elements are different. In the B1 element of the nominate subspecies, the pulses follow regularly only in the first third of the duration of B1 element; then the pulse rate starts abruptly to be very low (5/s). The B1 element is shorter, lasting for 0.8–1 s. When producing the C element, after finishing the tibiae stroke, the legs vibrate in a different pattern in the two subspecies. In *Ch. o. pusztaensis* the legs vibrate at a rate of 60–70/s modulated by the frequency of 15–20/s, whereas in *Ch. o. oschei* they vibrate at a similar rate of 55–60/s, however, this vibration rate is modulated by much lower frequency of 4–5/s. As a result, an amplitude-modulated hissing sound is produced in the nominate subspecies and a quieter sound without modulation of an amplitude is generated by *Ch. o. pusztaensis*.

Chorthippus karelini (Uvarov)

Figs 1–2, 12–16, 34–39, 60–71

Stenobothrus karelini Uvarov, 1910: 367–368.

Chorthippus karelini karelini (Uvarov)
Chorthippus karelini bruttius Fontana & La Greca, 1999, stat. n.

Material examined, subspecies *Ch. karelini karelini*. Ukraine: Kherson region, Askania-Nova, reserve steppe, 15.viii.2006, 19♂, 10♀, leg. V. Vedenina (ZMMU, CV), song recordings in 14♂. **Russia:** Volgograd region, 26 km E of Urjupinsk, along highway, wet meadow, 7.viii.2001, 15♂, 10♀, leg. V. Vedenina (CV), song recordings in 10♂; eastern border of Volgograd region, between Dzhanybek and Vishnjovka villages, 15–31.vii.1998, 15♂, 10♀, leg. V. Savitsky (EDMU); Astrakhan region, surroundings of Baskunchak lake, 30.vii.1995, 15♂, 10♀, leg. V. Savitsky (EDMU); 60 km N of Astrakhan, surroundings of Dosang, between Akhtuba & Volga rivers, 18–21.vi.1999, 15♂, 10♀, leg. V. Savitsky (EDMU); Daghestan, Kizljar district, 1928, 2♂, 2♀, leg. Polsmann, Popova, (MNHU). **Armenia:** Jelenovka, 1924, 6♂, leg. W. Ramme (MNHU). **Nakhichevan:** Daralag-Jangil, 6♂, 2♀, leg. Izmailov (MNHU). **Turkey:** province Erzurum, NW of Ispir, Mt. Tatos, 2150 m, 4.viii.1983, 4♂, leg. O. v. Helversen (CV), song recordings in 3♂; 6.viii.1987, 4♂, 1♀, leg. K. Reinhold, song recordings in 2♂; Erzurum, campus of Atatürk University, 1850 m, 24.viii.2000, 5♂, 4♀, leg. A. Mol (AUZM); province Erzurum, Cat-Bekcimen, Yaylasi, 2400 m, 24.viii.2000, 6♂, 5♀, leg. A. Mol (AUZM); province Agri, Eleskirt Yagmurlu Köyü, 1850 m, 18.viii.2000, 5♂, 2♀, leg. A. Mol (AUZM).

Subspecies *Ch. karelini bruttius*. Italy, Calabria, La Sila: Lago di Cecita, meadow near southern beach of the lake, 1130 m, 15.vi.1995, 2♂, leg. O. v. Helversen, song recordings in 2♂; Croce di Magara, meadow with *Juncus sp.*, 1200 m, 16.vi.1995, 1♂, leg. O. v. Helversen, song recording in 1♂; Lago Arvo, meadow at the southern beach of the lake, near Pino Collito, 1320 m, 16.viii.2002, 16♂, 4♀, leg. V. Vedenina (ZMMU, CV), song recordings in 7♂.

Distribution

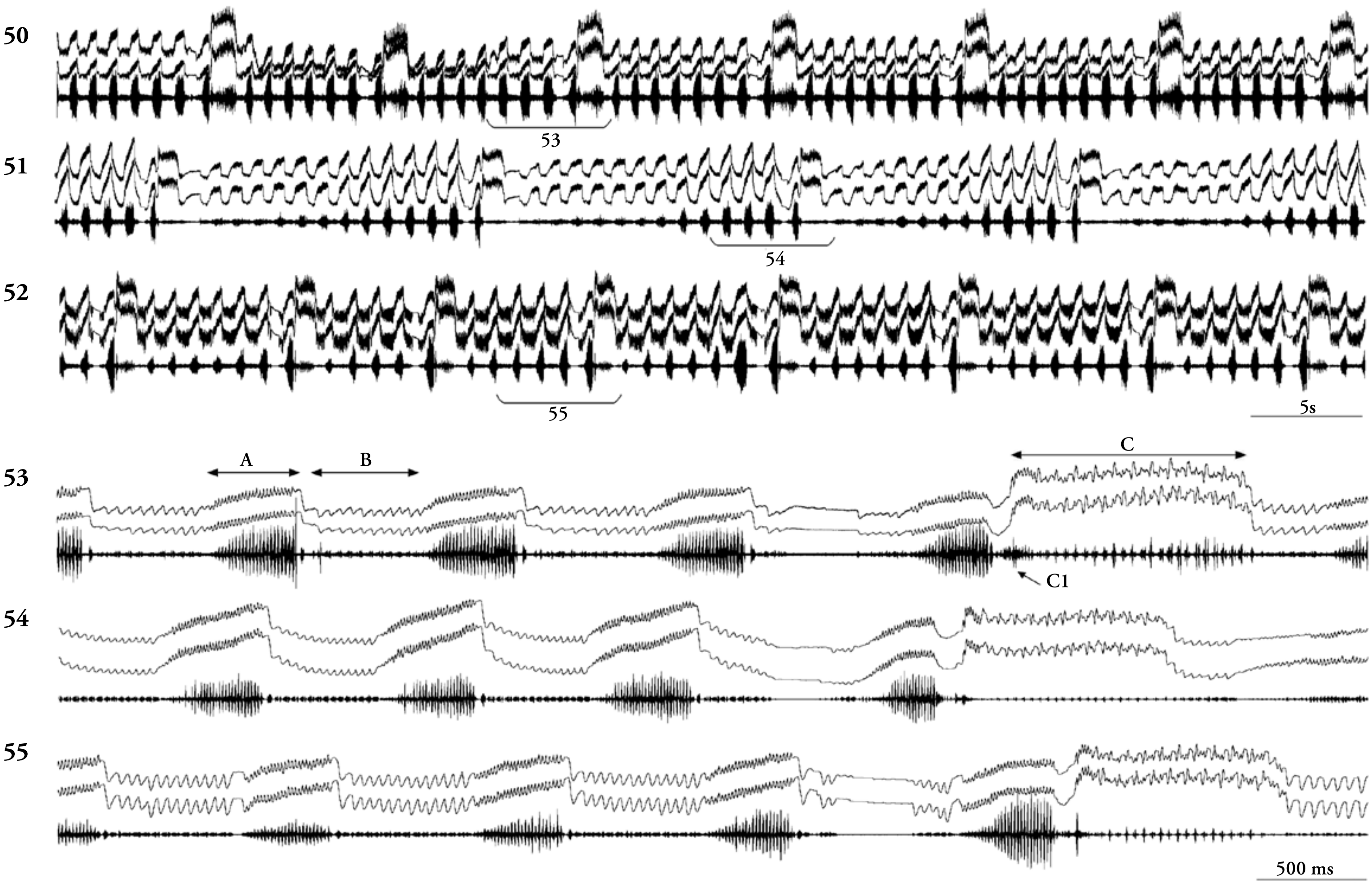
The nominate subspecies occurs in the north-eastern part of Asia Minor, very locally in Ukraine (Askania-Nova), in south-eastern part of European Russia, Transcaucasia, Kazakhstan, and probably Middle Asia. In Russia, its range very likely extends up to Irkutsk region in the east (Vedenina & Bukhvalova 2001, Benediktov 2005); however, the northern and southern limits in Asia remain unclear. The northern border of *Ch. karelini* may overlap with the southern border of *albomarginatus*, and the southern border of *karelini* may cross China and Mongolia, where it is replaced by purely Asiatic species of the group, *Ch. caliginosus* Mistshenko, 1951 (Vedenina & Bukhvalova 2001). *Ch. k. bruttius* inhabits southern Italy, Calabria, where it occurs very locally on the Sila plateau (Fontana & La Greca 1999).

Morphology (Figs 2, 12–16, App. 1)

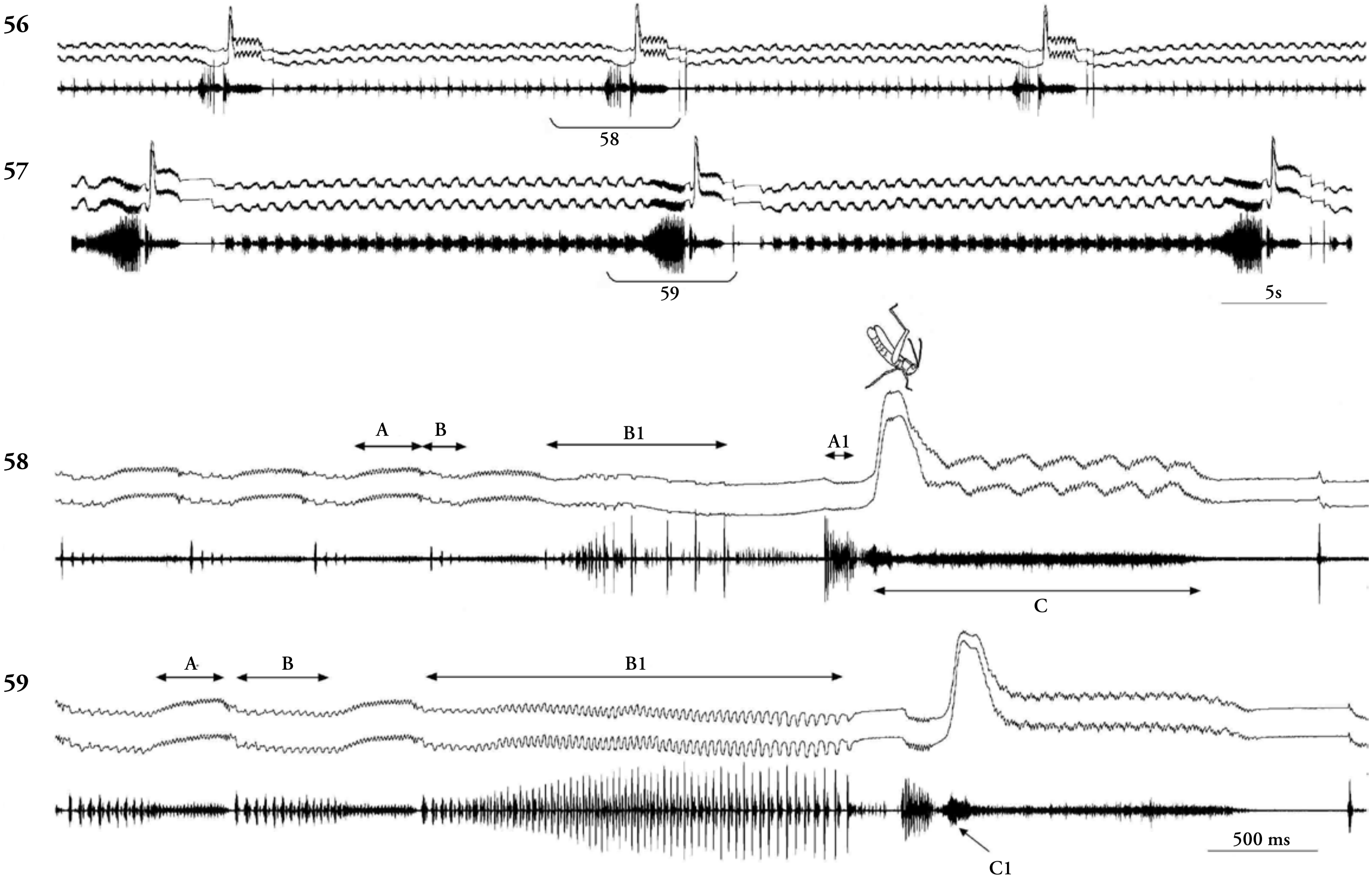
The mean peg number in *Ch. karelini* varies from 152 to 179 in different populations, and does not differ significantly from the peg number in *oschei* and *lacustris*. However, the position and the density of the pegs on the proximal third of the file are very different in *karelini*: the pegs are arranged in two or even three rows, but in contrast to *oschei*, they are organized very widely. On the basis of merely the peg morphology, it is possible to distinguish the males of *karelini* from the males of all other European members of the group. Males in *karelini* are remarkably larger than in *albomarginatus* and *oschei* in respect to the femur and tegmen length, but in females the difference is insignificant.

Calling song (Figs 34–39)

When producing the calling song, the male of *karelini* vibrates with the legs in a relatively simple pattern similar to the one of *albomarginatus* and *oschei pusztanesis*. During the main part of a song, the legs move alternately, each leg at a rate of about 45–60/s in *k. karelini* and at a rate of 70/s in *karelini bruttius*. In *k. karelini,* a first loud pulse and several subsequent quiet pulses are sometimes separated from the following pulses of a song by a pause.



Figs 50–55. Oscillograms of the courtship songs of *Chorthippus albomarginatus* at two different speeds: 50, 53, Russia: Tver' region; 51, 54, Russia: Tambov region; 52, 55, Ukraine: Poltava region. A, B and C are different song elements; in each figure the two upper lines are recordings of hind leg movements and the lower line is the sound recording.



Figs 56–59. Oscillograms of the courtship songs of *Chorthippus oschei* at two different speeds: 56, 58, *Ch. o. oschei*, Greece: Grammos; 57, 59, *Ch. oschei pusztaensis*, Hungary: Kunhegyes. A, B, B1, A1 and C are different song elements; drawing shows a stroke with the hind tibia at the corresponding moment of the song; in each figure the two upper lines are the recordings of hind leg movements and the lower line is the sound recording.

However, this feature may vary individually. The sound pulses of the main part of each song follow at a rate of 90–120/s in the nominate subspecies and at a higher rate of 130–140/s in *k. bruttius*.

Courtship song (Figs 60–71, App. 2)
The courtship song of *Ch. k. karelini* was analyzed on the basis of recordings from Ukraine (Askania-Nova), Russia (Volgograd region) and Turkey (Erzurum). The leg-movement pattern producing A and B elements in the nominate subspecies is quite different from that in *Ch. albomarginatus* and *oschei*. During B element, the legs vibrate at a rate of about 25–35/s in a complex pattern: every two up and down leg-movements are coupled in a characteristic way (Figs 64–66). During the A element, the legs vibrate at a much lower rate of 12–15/s and in a simple way. During the A element, the two legs vibrate synchronously, whereas during the B element, the legs vibrate with a phase shift. Oscillographic analysis shows that the sound elements A consist of the well-pronounced pulses repeated at a rate of 16–32/s, whereas the sound elements B contain the dense pulses following without gaps. After 30–50 alternations of A/B pairs, a complex of B1-A1-C elements follows. The B1 element of *k. karelini* is remarkably long, reaching 5–8 s in duration. As a rule, the duration of B elements increases from about 150 ms in the beginning of the cycle to about 1.15 s in the end of the cycle. After the long B1 element, a rather short (0.3–0.5 s) A1 element follows; it is produced by the leg vibrations at a rate of about 40/s. The following C element is quite characteristic: it is accompanied by two fast strokes of the legs (Figs 68–71). During the first stroke, a male does not lift its abdomen, and the tibiae are remaining in their normal position; the second stroke, however, is accompanied with lifting of abdomen at an angle of 30° and is produced with the tibiae, similarly to the stroke of *oschei*. However, in contrast to *oschei*, the maximal angle between tibia and femur is 30° in *k. karelini*, and after the second stroke, the legs vibrate in relatively simple patterns. During the first up-stroke, a short (0.1 s) sound pulse is generated, and after the first down-stroke, as a result of high-frequency leg vibrations, an element lasting for 0.1–0.2 s is produced. We distinguish a C1 element produced by the first up-stroke. During the second up-stroke, a short loud pulse is produced, and afterwards, an element lasting for 0.2–0.3 s follows. The first C element is followed by B element, and the A1/C pair is repeated. Sometimes, the third B-A1-C complex may follow, and then A/B pairs alternate again. When a male produces the complex of B1-A1-C elements, the legs always vibrate alternately or with a phase-shift; the only exception is when a male produces the strokes. Both strokes are produced with synchronous movements of the two legs. All sound elements, except for A element, consist of dense pulses without gaps.

The song of *Ch. k. bruttius* is basically similar to the song of the nominate subspecies. The characteristic leg-movements and sound patterns of B, B1, A1 and C elements are almost identical in the two subspecies. The main difference is the absence of A elements in the songs of *k. bruttius* (Fig. 67). This element is sometimes also poorly pronounced in the songs of some *k. karelini* specimens, especially in the very beginning of each cycle, but it is usually present in the end of the cycle. Another difference is in the period and duration of B elements. In the song of *k. bruttius*, B elements are on average of shorter duration, and they are repeated at a higher rate than in the *k. karelini* song (Appendix 2). The duration of B element is less variable in *k. bruttius* than in *k. karelini* song.

Remarks
Ch. bruttius was described as a new species on the basis of morphological characters and courtship songs (Fontana & La Greca 1999). However, the morphological characters of *bruttius* were compared with those of *albomarginatus* and not of other members of the group. Here we show a high similarity of the peg morphology and other morphological characters between *bruttius* and several populations of *karelini*. Fontana & La Greca (1999) stressed that there was only one type of the repeated elements (that we call B element) in the courtship song of *bruttius*, which they argued to be a characteristic feature of the *bruttius* song. We agree with this statement, however, as we showed above, other features of the *bruttius* courtship song are the same as in the *karelini* song. Thus, we consider this form from Italy to have a subspecies status.

Until recently, *Ch. k. karelini* was believed to be more widespread in central and eastern Anatolia. However, it is now becoming clear that the true *karelini* has a more restricted range in Anatolia. *Ch. labaumei* Ramme, 1926 described from central Anatolia was supposed to be the synonym of *karelini* (Helversen 1986). Our re-examination of the type specimens of *Ch. labaumei* (deposited at MNHU) revealed a completely different morphology of the stridulatory file as compared to *karelini* (Vedenina, unpubl.). We now suggest *labaumei* to be a separate species; although neither the calling nor the courtship song has been recorded. No new specimens were found since Ramme (1926) described the species. *Ch. albomarginatus hakkarikus* Demirsoy, 1977 from the province Hakkâri may be a synonym of *karelini* (Helversen 1986). However, there are no song recordings from this locality as well.

The specimens of *Ch. k. karelini* from Daghestan, Armenia and Nakhichevan deposited at MNHU were regarded as *Ch. albomarginatus fuliginosus* Ivan. by Ramme (1951).

Chorthippus lacustris La Greca & Messina

Figs 1–2, 17, 40–41, 45–46, 72–74

Chorthippus lacustris La Greca & Messina, 1975: 67–77.

Material examined. Greece, Ipiros: NE of lake of Ioannina, 470 m (type locality), 20.viii.1986, 8♂, 5♀, 28.vii.1987, 10♂, 7♀, leg. F. Willemse (ZIN, CW), song recordings in 3♂; 15 km S of Ioannina, Serviana, 29.vii.1978, 4♂, 4♀, song recordings in 2♂; 20.vi.2000, 12♂, 10♀, leg. O. v. Helversen (ZMMU, CV), song recordings in 6♂; Thesprotia, 5 km NW of Paramithia, near Kefalovriso, 28.vii.2004, 10♂, 8♀, leg. V. Vedenina (CV), song recordings in 9♂.

Distribution

This species only occurs in a small area in Ipiros, northern Greece.

Morphology (Figs 2, 17, App. 1)

The peg number in males of *Chorthippus lacustris* varies on average from 153 to 159. This number is lower than in *Ch. oschei* and *karelini*, however, it does not vary significantly in all three species. In the proximal third of the stridulatory file, the peg density is slightly higher than in *Ch. albomarginatus*, and the pegs tend to be organized in two rows. In general, this species is the most different in appearance from the other members of the group. *Ch. lacustris* is easy to distinguish by its very long antennae and by characteristic white colour of the antennae tips and hind tarsi (La Greca & Messina 1975; Helversen 1986).

Calling song (Figs 40–41, 45–46)

The male of *Ch. lacustris* produces 3–4 calling songs, each lasting 450–500 ms and separated by intervals of about 2 s. In contrast to other species of this group, when producing a calling song, the leg movements in *lacustris* are very irregular and the amplitude of the leg movements greatly varies. As a result, the amplitude and duration of sound pulses varies as well.

Courtship song (Figs 72–74, App. 2)

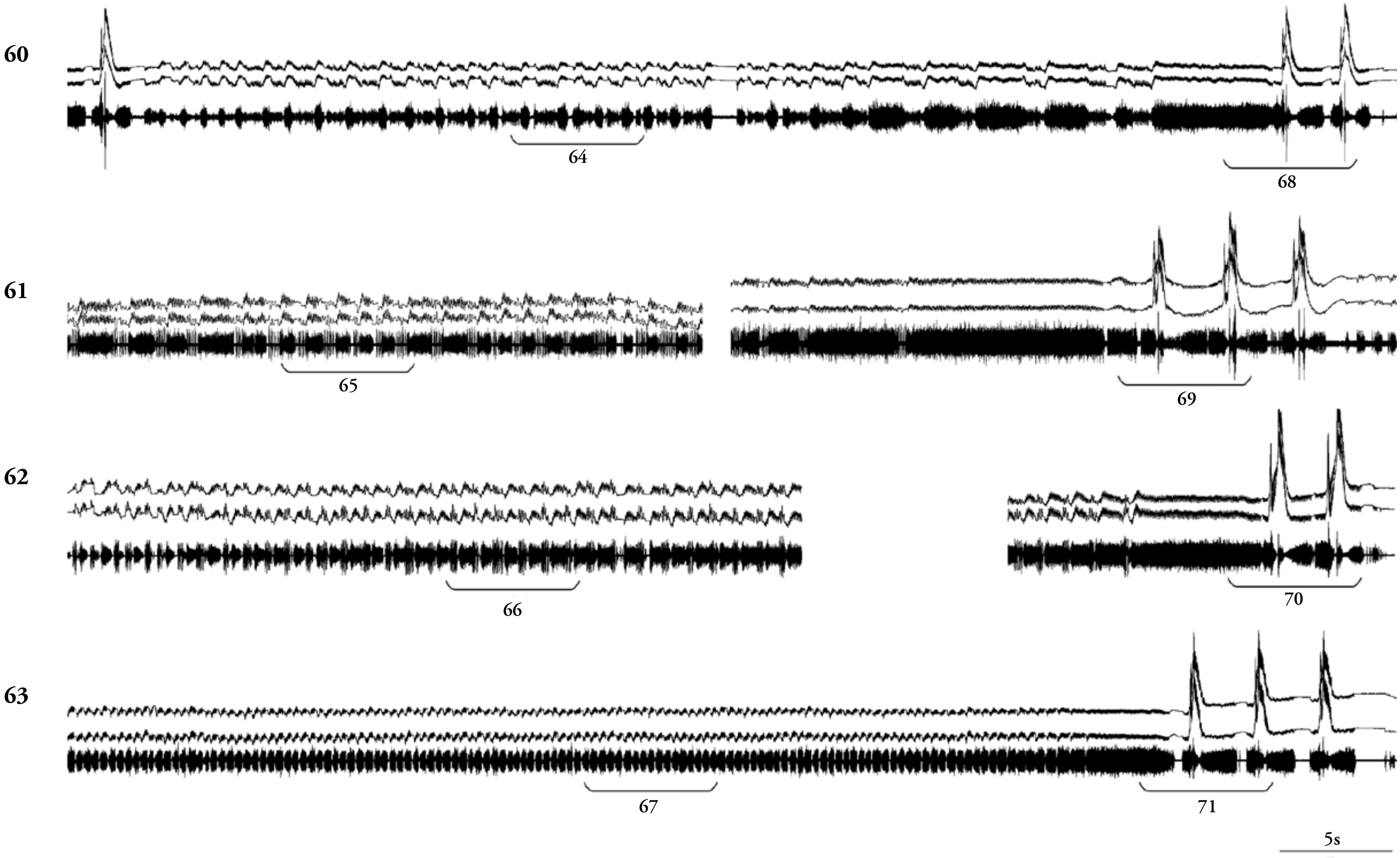
This species has the most remarkable courtship song among all members of the group because of its highly complex visual display. This conspicuous visual display was described in detail by von Helversen (1986). As usual in this group, the song starts with an alternation of A and B elements. The leg movement pattern producing A and B elements resembles that in *Ch. oschei*. During the A element, the legs vibrate more rapidly at a rate of about 40–45/s, during the B element, the legs are vibrated more slowly at a rate of about 14/s. Oscillographic analysis shows that sound is only produced during A elements, which consist of the pulses repeated at the rate of leg vibrations. After about 35–40 alternations of A and B elements, a complex of B1-A1-C elements follows. In contrast to other species of the group demonstrating the visual display, *lacustris* starts with lifting of its abdomen already during the B1 element. Then the A1 element follows, when the legs produce extremely low-amplitude vibrations at a very high rate of about 90/s, and after that, the first stroke with the tibiae follows. Then the femora go down but the legs straighten out even more. After that, the legs are slightly folded up and produce the second stroke with the tibiae. During about 2 s, the abdomen is kept in a lifted posture. The abdomen is lifted at a maximal angle of about 70°, whereas the maximal angle between femur and tibia is 140° on average. After that, the tibiae come to their normal position and the legs vibrate with small amplitude at a rather high rate of 80–85/s. The B1-A1-C complex repeats 4–5 times, and A/B pairs alternate again. Oscillographic analysis shows that the loudest elements of the song are A1 and C elements. In general, the courtship song of *lacustris* is much quieter than the songs of other species of the group.

Chorthippus ferdinandi Vedenina & Helversen sp. n.

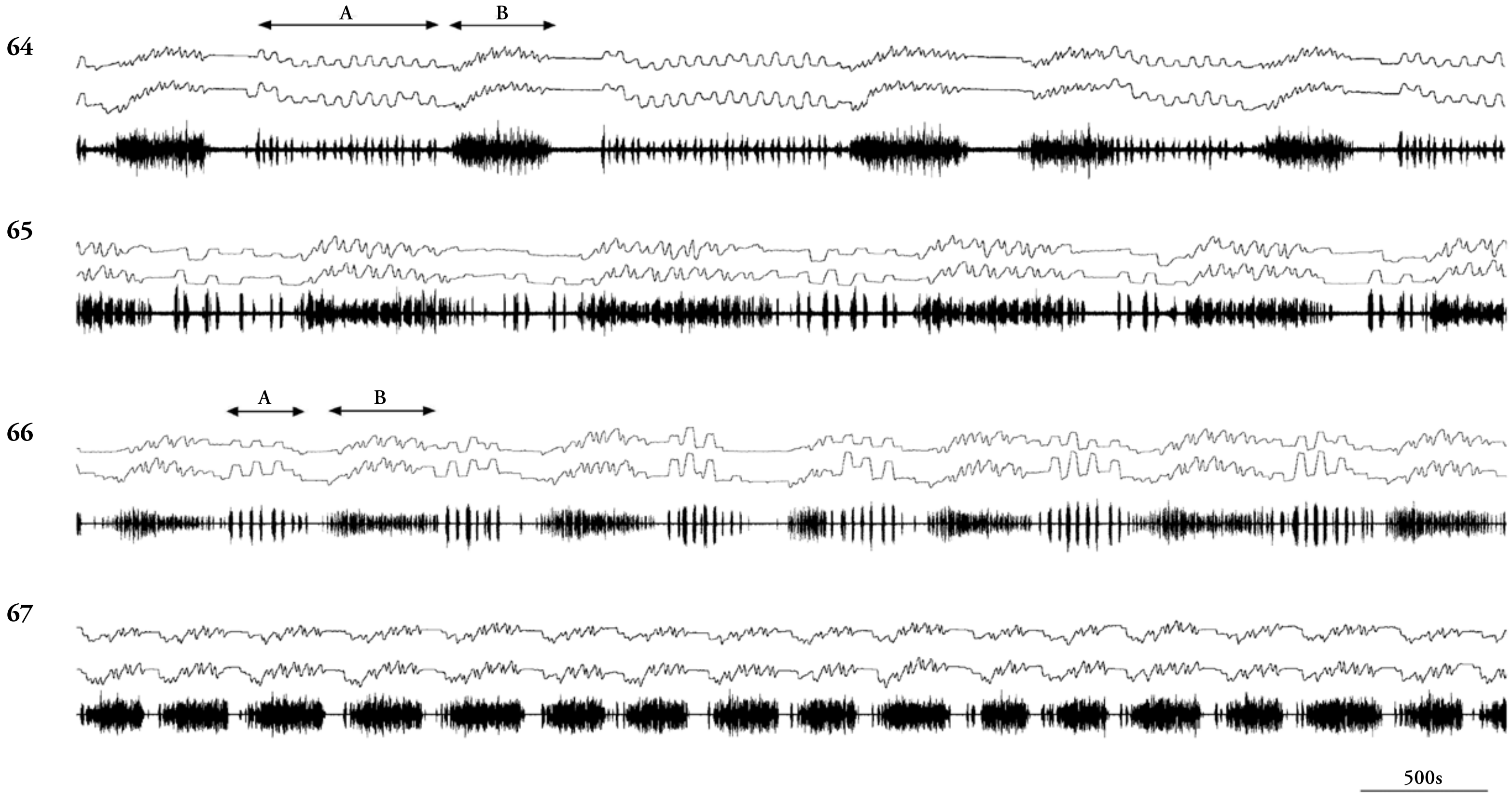
Figs 1–2, 4, 18–21, 42–44, 47–49, 75–79

Material examined

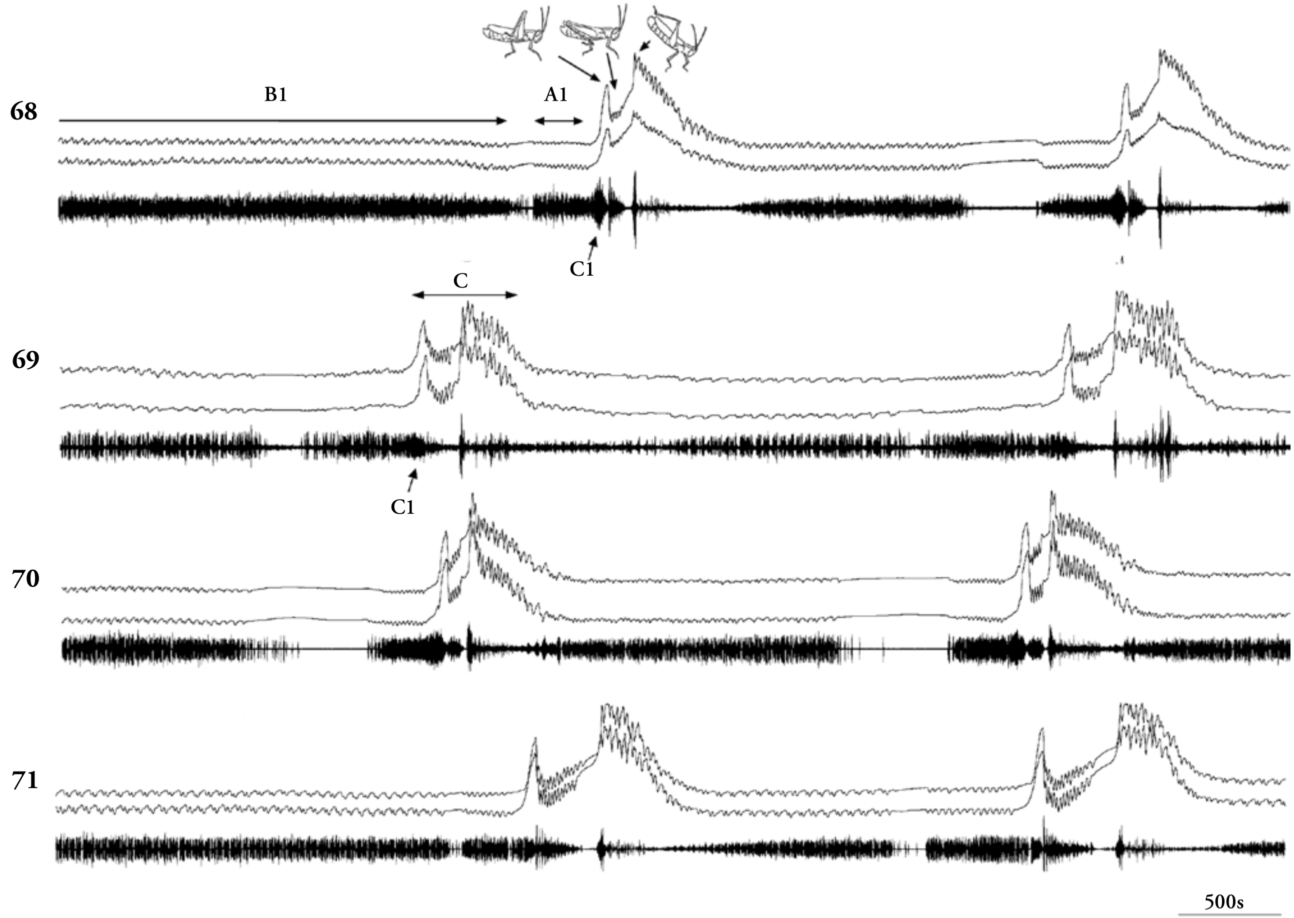
Type material. Holotype ♂. **Greece,** Peloponnesus: Akhaia, Kalavrita, 3 km W, 700 m, cultivated area, meadow with lush vegetation, 29.vii.1988, leg. F. Willemse (BMNH). **Paratypes.** 32♂, 22♀, same locality and date as holotype, leg. F. Willemse (CW, ZIN), song recordings in 3♂; Akhaia, Kalavrita, about 10 km W, near Vouraikos river, 28.viii.1986, 6♂, leg. O. v. Helversen (CV), 8.vi.2001, 3♂, 3♀, leg. O. v. Helversen as larvae (ZIN), song recordings in 4♂; 26.vii.2005, 1♂, leg. L. & J. Willemse (CW); Akhaia, Kalavrita, 800m, vii.1901, 2♂, 2♀, leg. Holtz (MNHU); Akhaia, Agridhi, 30 km S of Kalavrita, 750 m, 29.vii.1988, 3♂, leg. F. Willemse (CW); Arkadhia, Khrisovitsi, 3 km W, 1100 m, 12.vii.1974, 1♂, 4♀, leg. F. Willemse (CW); Arkadhia, Mt. Mainalon above Kardaras, 1500–1600 m, 10.vii.1974, 3♂, 27.vii.1975, 1♀, leg. F. Willemse (CW); 27.viii.1986, 8♂, 4♀, leg. O. v. Helversen (CV), song recording in 1♂;



Figs 60–63. Oscillograms of the courtship songs of *Chorthippus karelini*: 60, *Ch. k. karelini*, Ukraine: Askania-Nova; 61, Russia: Volgograd region; 62, Turkey: Erzurum; 63, *Ch. karelini bruttius*, Italy: Calabria. In each figure the two upper lines are the recordings of hind leg movements and the lower line is the sound recording.



Figs 64–67. Oscillograms of the courtship songs of *Chorthippus karelini*: 64, *Ch. k. karelini*, Ukraine: Askania-Nova; 65, Russia: Volgograd region; 66, Turkey: Erzurum; 67, *Ch. karelini bruttius*, Italy: Calabria. A and B elements are indicated; in each figure the two upper lines are the recordings of hind leg movements and the lower line is the sound recording.



Figs 68–71. Oscillograms of the courtship songs of *Chorthippus karelini*: 68, *Ch. k. karelini*, Ukraine: Askania-Nova; 69, Russia: Volgograd region; 70, Turkey: Erzurum; 71, *Ch. karelini bruttius*, Italy: Calabria. B1, A1 and C elements are indicated; drawings show different positions of the hind legs and abdomen at the corresponding moments of the song; in each figure the two upper lines are the recordings of hind leg movements and the lower line is the sound recording.

Korinthia, lake Dhasiou, 1500 m, 24.vii.2005, 8♂, 1♀, leg. L. & J. Willemse (CW).

Other material (damaged by *Anthrenus*). N of Dimitsana, near Kalo Neri, Karkalou, 28.viii.1989, 2♂, 1♀, leg. O. v. Helversen, song recordings in 2♂.

Description

Head from above as wide as pronotum, 0.6–0.7 times as short as pronotum (Fig. 4 a-b). Foveolae distinct, visible from above, 4.2–4.3 times as long as broad. Antennae filiform, in ♂ extend slightly beyond hind coxa, in ♀ hardly reach hind margin of pronotum, its longest medial segments 2 times as long as wide. Pronotum with straight distinct lateral carina; prozona nearly as long as metazona. Radial vein of tegmen clearly sinuate (Fig. 4 c-d). Tegmina projecting beyond apices of hind knees. Tegmen in ♂ 5.2, in ♀ 5.8 times as long as wide. Alae slightly shorter than tegmina. In male the number of stridulatory pegs on the inner side of hind femur is very high and varies from 206 to 240. In the proximal part of the stridulatory file, the pegs arranged very densely and sometimes in two rows (Figs 18–21). Tympanal organ in ♂ 2.4 times, in ♀ 2.1 times as long as wide. Cerci conical, in ♂ reaching margin of supra-anal plate, in ♀ reaching half of supra-anal plate. Subgenital plate in ♂ bluntly conical. Ovipositor short, without lateral teeth. Hind femur in ♂ 4.7, in ♀ 5 times as long as its maximum width.

General colour brown, green forms not observed. Antennae of general colour, ventral side of apical segments commonly darker brown, particularly in ♂. Pronotum of general colour, in ♂ dorsum sometimes slightly darker, in ♀ lateral keels ventrally often bordered with dark sepia brown streak and exceptionally also with dark brown median keel. Tegmen in ♂ of general colour, in ♀ commonly costal area with white stripe, contrasting with darker brown Sc and often also R vein and sometimes darker brown coloured subcostal, medial and basal part of radial fields. Hind femur of general colour, in ♂ outer and particularly upper side or keels often darker brown towards the hind knee, in ♀ much less obvious. Hind knee in ♂ darker brown, especially upper lobe, in ♀ of general colour and often upper lobe only darker. Hind tibia of general colour, ventral side often dark brown, particularly towards the apex, more obvious in ♂. Hind feet of general colour, in ♂ often slightly paler, particularly third tarsus but not white.

Measurements (in mm). Body length ♂ 15–16, ♀ 22–23; pronotum length ♂ 3.2–3.6, ♀ 3.8–4.5; tegmen length ♂ 12.3–14, ♀ 14–17; tegmen width ♂ 2.4–2.8, ♀ 2.44–3; femur length ♂ 8.6–9.7; ♀ 11.2–13; femur width ♂ 1.7–2, ♀ 2.2–2.6; peg number in ♂ 206–240.

Etymology

This species is named after Dr. Ferdinand Willemse (the name *willemsei* is already preoccupied in *Chorthippus willemsei* Harz), who collected most of the specimens in six of seven known localities, recorded the songs of several males, and noticed for the first time that the specimens from Peloponnesus are different from other specimens of this group (Willemse 1985).

Morphology (Figs 2, 4, 18–21, App. 1)

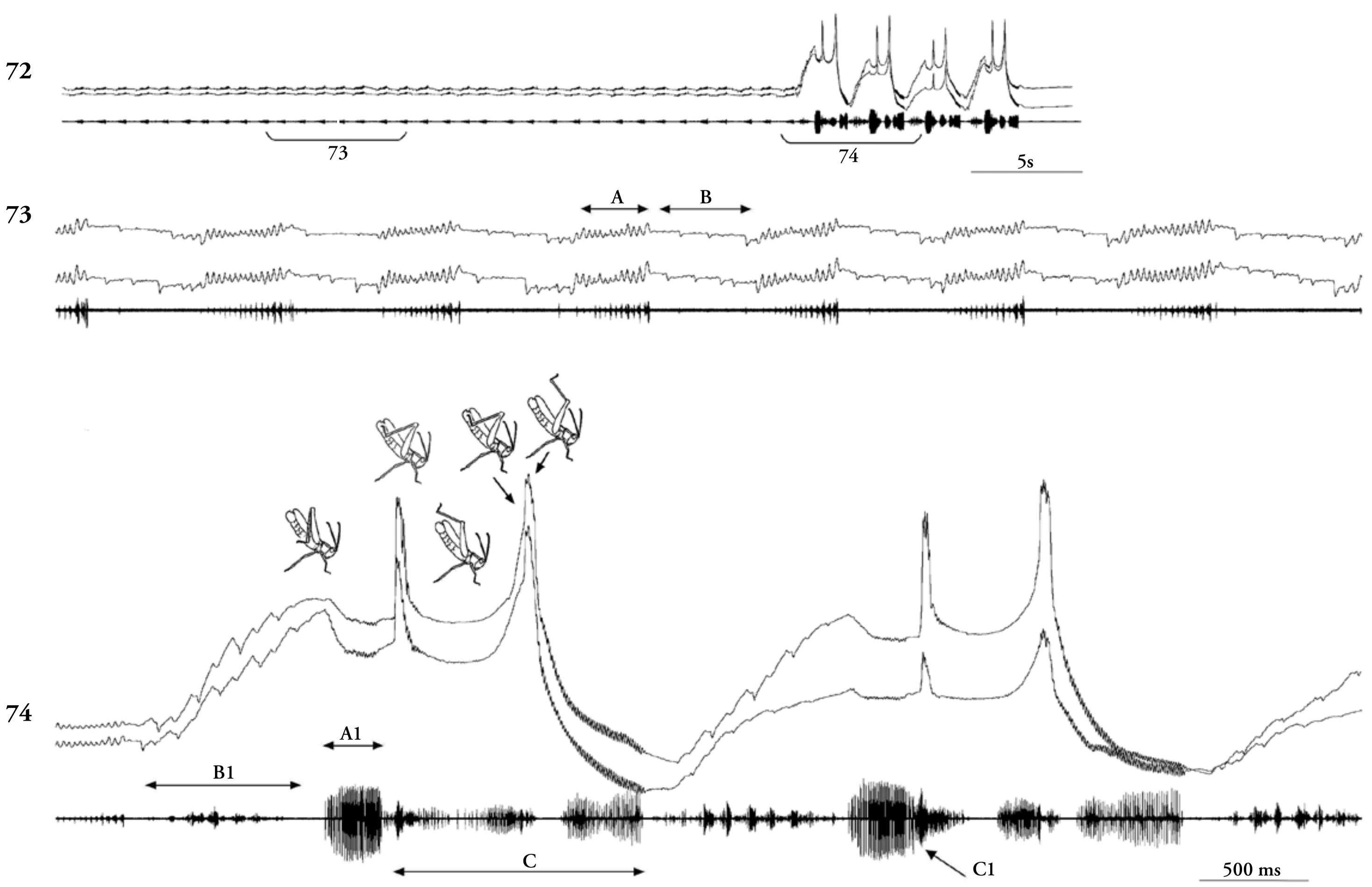
The males of this species have a significantly higher number of the stridulatory pegs (210–220 on average) than in all other species of the group. In the proximal part of the stridulatory file, the pegs are very densely arranged, usually in one row, but sometimes in two rows. The length of the male stridulatory file in the new species is more than in other species of the group: the last distal pegs reach the level of the second to third tooth of the tibia when it is pressed to the femur. This contrasts to the other members of the group, in which the last distal pegs reach the level of about the fourth tooth of the tibia. The length and width of tegmen and hind femur in both sexes of *ferdinandi* are the same as in *karelini* and *lacustris,* however, the length of pronotum is larger than in all other species of the group.

Calling song (Figs 42–44, 47–49)

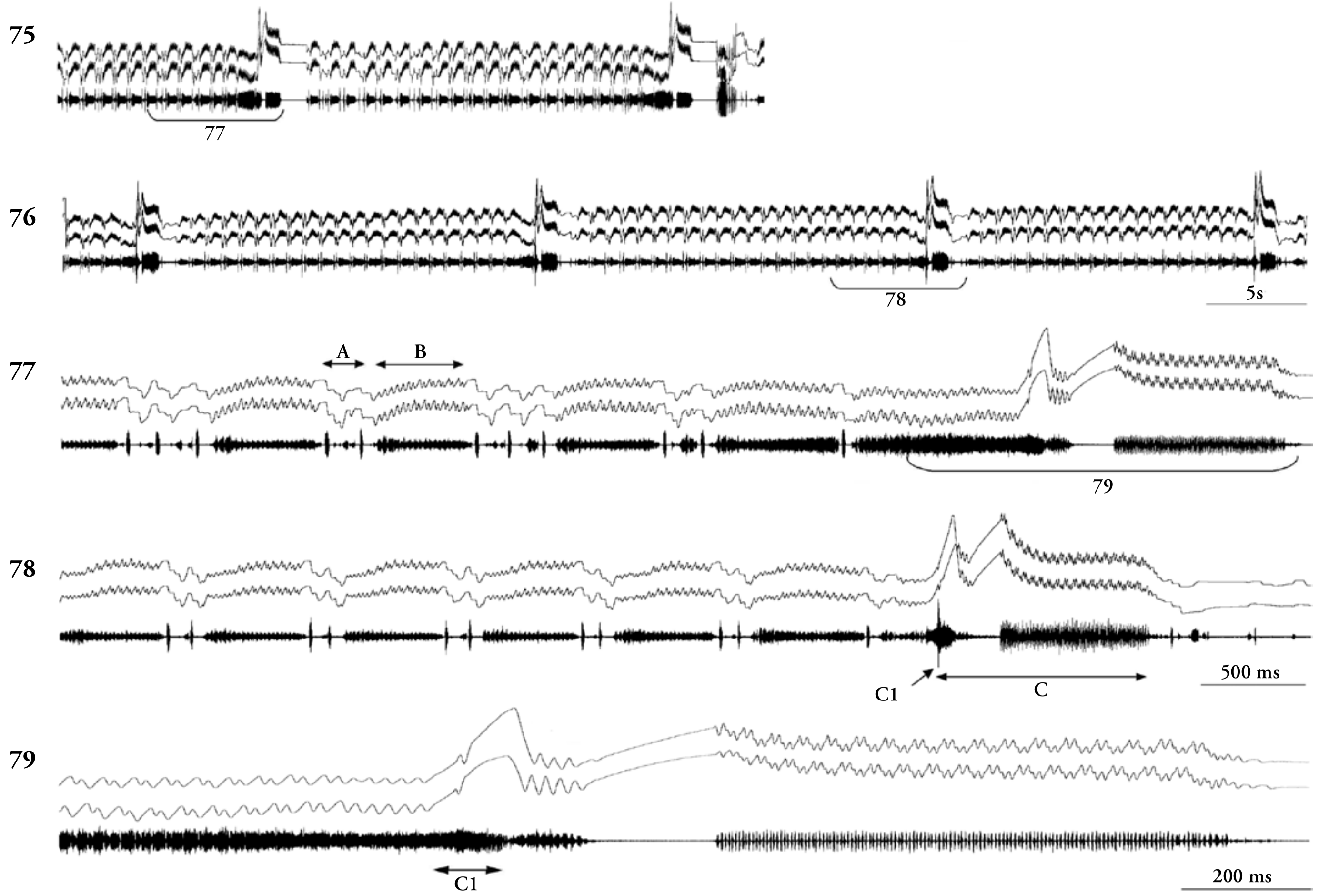
The male of *ferdinandi* produces up to 8 calling songs separated by intervals of 1.5–2 s. A song lasts for about 0.45–0.65 s. A leg-movement pattern producing a song is of a higher complexity in *ferdinandi* than in most species of the group: every two up-and-down leg-movements are coupled in such a way that a high-amplitude stroke alternates with a low-amplitude stroke. Oscillographic analysis shows that the sound pulses follow without gaps, and the low-amplitude pulses alternate with the higher-amplitude pulses. However, the sound pattern slightly varies in different populations and the sound pulses may be of about equal loudness.

Courtship song (Figs 75–79, App. 2)

The song starts with an alternation of A and B elements, which slightly resembles the corresponding elements in *k. karelini*. In the beginning of the B element of *ferdinandi*, the legs move synchronously in a rather simple pattern. After the first third of B element, they start to vibrate in a more complex pattern and with a phase-shift, like in *karelini,* but at a higher rate of 40–50/s. The leg movements producing the A element are much slower (about 5/s) and of a higher amplitude, than during the B element. The legs are moved synchronously during the A element.



Figs 72–74. Oscillograms of the courtship songs of *Chorthippus lacustris* at two different speeds: A, B, B1, A1 and C elements are indicated; drawings show different positions of the hind legs and abdomen at the corresponding moments of the song; in every figure two upper lines are recordings of hind leg movements and lower line is sound recording.



Figs 75–79. Oscillograms of the courtship songs of *Chorthippus ferdinandi* at three different speeds: 75, 77, 79, Peloponnesus: Mt. Mainalon; 76, 78, Peloponnesus: Kalavrita, paratype. A, B, and C elements are indicated; in each figure the two upper lines are recordings of the hind leg movements and the lower line is the sound recording.

Oscillographic analysis shows that several louder distinct pulses are sometimes visible in the beginning of the B element, and then quieter pulses without gaps follow. Each A element contains one to three loud pulses produced during the down-strokes, and sometimes one to three very quiet pulses produced during the up-stroke. In contrast, in *k. karelini*, the leg movements producing A and B elements are of about the same amplitude, and the sound pulses of A element produced by the up- and down-strokes are of equal loudness. In *ferdinandi*, the element C follows after alternating of about 18 A/B pairs. Leg movements producing the C element represent a peculiar kind of combination of the *oschei* and *karelini* leg-movement patterns. Similarly to *karelini,* the males of *ferdinandi* produce two relatively fast strokes. However, after the second stroke, the legs vibrate in a complex pattern similarly to the pattern of *Ch. oschei pusztaensis*. During the first stroke, an element of about 100ms-duration is produced (C1 element). Sometimes a loud pulse follows in the beginning of the element (Fig. 78). Thereafter the legs shortly vibrate in a simple pattern at a rate of 40–45/s and produce a quiet element of about 100 ms as well. After the second stroke the legs produce a longer element lasting for about 0.7–1 s and containing short distinct pulses following at a rate of 170–220/s. After one C element, the whole cycle is repeated.

Remarks

Material from the Peloponnesus was mentioned for the first time by Ramme (1951). He identified 2 males and 2 females deposited at MNHU as *Ch. albomarginatus fuliginosus* Ivan. We checked this material and found the high number of the stridulatory pegs (more than 210) and the long stridulatory file corresponding to *Ch. ferdinandi* sp. n.

Discussion

Song analysis

Analysis of the calling songs in the European species of the *Chorthippus albomarginatus* group performed in the present study, revealed a greater difference between the species than it was believed before. When producing a calling song, the legs generated regular up- and down-movements of a relatively equal amplitude in *albomarginatus, oschei pusztaensis* and *karelini*, the leg movements were regular but substantially more complex in *o. oschei* and *ferdinandi*, and the leg movements were very irregular and of variable amplitude in *lacustris.* Oscillographic analysis of the sound allows us to distinguish reliably between two groups: *albomarginatus*, *oschei pusztaensis, karelini* and *lacustris* represent the first group, and *o. oschei* and *ferdinandi* represent the other group. In the first group, calling song typically consists of distinct pulses separated by gaps, whereas in the second group, the sound pulses of calling song follow without gaps, which resulted in producing a hissing sound.

Comparison of the leg movements producing the calling and courtship songs reveals interesting correlations between the calling song and particular elements of the courtship song. In *karelini* and *o. oschei* the leg-movement pattern of the calling song is quite similar to that of the courtship element C (Fig. 80). In *ferdinandi* the calling leg-movement pattern is, however, similar to that of the courtship element B. In *albomarginatus, lacustris* and *oschei pusztaensis* the similarities between the calling and any of the courtship leg-movement patterns are not evident. There is even a contrast between relatively simple leg-movement patterns of the calling song and the complex patterns of the courtship C element in both *albomarginatus* and *oschei pusztaensis*. However, the hybrids between these two species produced the courtship songs with a rather simple leg-movement pattern of C element that was almost identical to the calling song pattern (Vedenina et al. 2007b). We assume that in ancestral species, the C element could originate from the calling song, however, it evolved to a more complex pattern in *albomarginatus, oschei pusztaensis, ferdinandi* and *lacustris*. We suggest that selection pressure favoring an increase in complexity acts stronger on the courtship song elements than on the calling song. The calling song is used for the communication at relatively long distances, and the calling song evolution is primarily driven by the acoustic surroundings and simultaneously singing other species. Thus, the calling song patterns are mainly under stabilizing selection. The courtship song being an important part of the close range communication system can serve for the evaluation of the mate “quality”, and the courtship song evolution is to a greater extent driven by sexual selection and, therefore, could proceed faster than the evolution of the calling song (Vedenina 2005; Heller 2006).

To hypothesize the phylogenetic relations between the European species of the *Ch. albomarginatus* group, one could consider the number of the courtship song elements, the degree of complexity of the leg-movement pattern and the visual display (Fig. 81). *Ch. albomarginatus* stands apart from all other members of the group since its courtship song contains the minimal element number (three) and not a single element is accompanied by the stroke

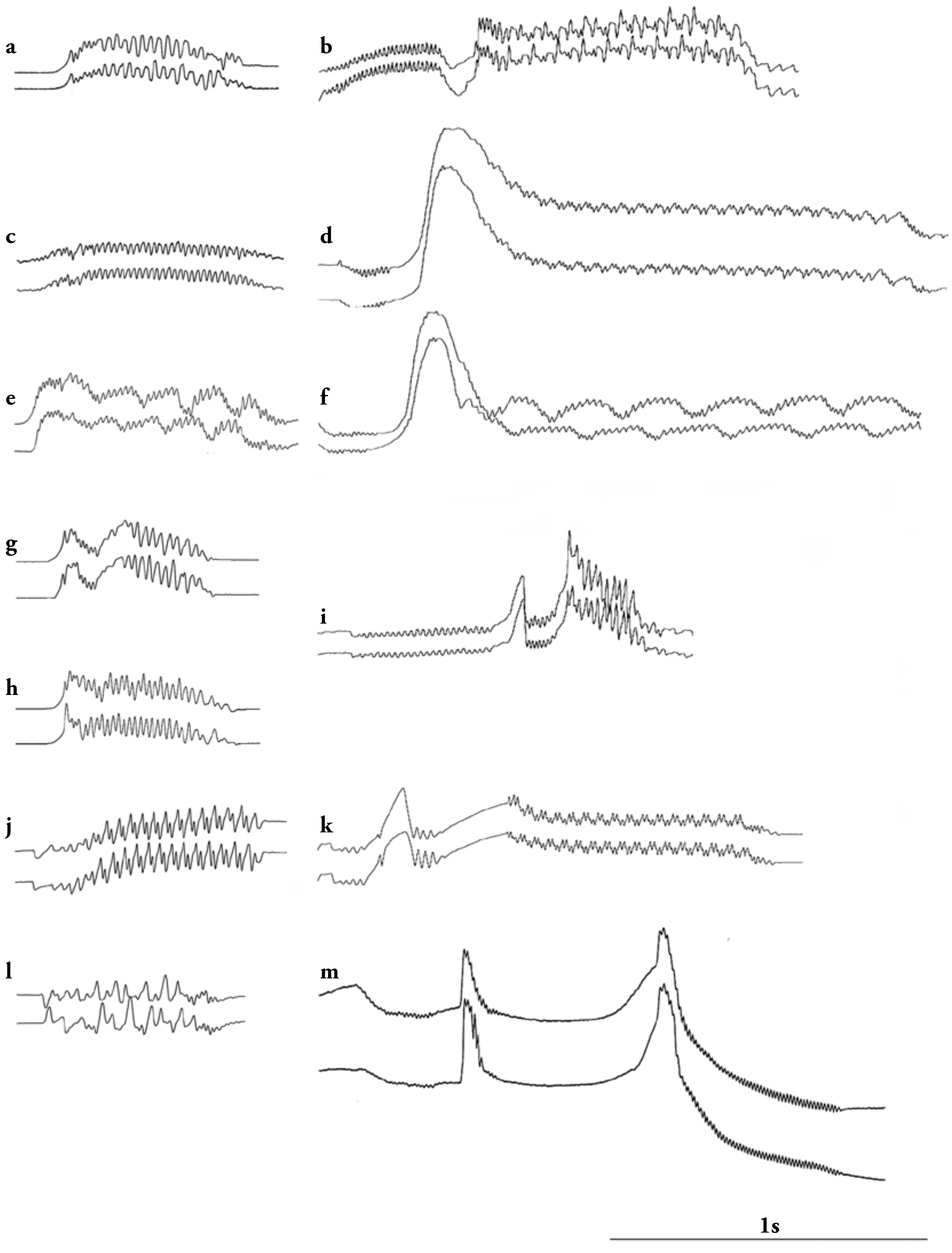


Fig. 80. Recordings of the hind leg movements producing calling song (from the left) and C element of the courtship song (from the right) in: a, b, *Chorthippus albomarginatus*; c, d, *Ch. oschei pusztaensis*; e, f, *Ch. o. oschei*; g, i, *Ch. k. karelini*; h, i, *Ch. karelini bruttius*; j, k, *Ch. ferdinandi*; l, m, *Ch. lacustris*. In three species, *Ch. o. oschei*, *Ch. karelini* and *Ch. ferdinandi*, there is a similarity between calling song and C element.

with the hind tibiae; A and B elements are produced by simple leg movements, whereas C element is produced by complex leg movements. This species is suggested to be the closest to an ancestral form. All other members of the group share one basic synapomorphy: C element is accompanied by lifting of the abdomen and by strokes of the hind tibiae. *Ch. oschei* is characterized by a single stroke of the hind tibiae during C element, the conspicuously loud B1 element and the highest number (5) of different courtship elements. Three other species, *karelini, ferdinandi* and *lacustris*, are characterized by a double stroke of the hind legs. The characteristic features of the *karelini* song are the following: relatively long B1 element, very short C element, and simple leg-movement pattern producing C element. Two other species, *lacustris* and *ferdinandi,* demonstrate more complex pattern of C element. In *ferdinandi*, this pattern reminds the pattern of *Ch. oschei pusztaensis*. One can speculate that C element of *ferdinandi* resulted from the hybridization between *karelini* and *oschei pusztaensis*. In *lacustris*, all the visual display lasts for a longer time, since not only the C element but also B1 and A1 elements are accompanied by the tibia strokes. The whole courtship is conspicuously quiet, A element is hardly audible, and the sound is not generated during the B element at all.

Ecological observations and distribution

All European species of the *Chothippus albomarginatus* group appear to be allopatric, although their ranges may overlap in the contact zones. Three species occur in Europe rather widely: the range of *Ch. albomarginatus* covers the northern and central Europe, *Ch. oschei* inhabits the Balkan Peninsula with some northern and eastern adjacent territories, and *Ch. karelini* occurs in the south-eastern part of European Russia, Transcaucasia, and the north-eastern part of Asia Minor. Occurrence of the latter species in southern Italy and very locally in Ukraine will be discussed later. Distribution of the two other species of the group, *Ch. lacustris* and *Ch. ferdinandi*, is very narrow and restricted to the particular regions of Greece: *Ch. lacustris* inhabits part of Ipiros in northern Greece, *Ch. ferdinandi* occurs in the Peloponnesus. In the south, the species of the group generally live at high altitudes, around 1000 m and higher. The habitats of *Ch. lacustris*, *Ch. ferdinandi*, and the southern populations of *Ch. karelini* and *Ch. oschei* are usually patchy moist meadows situated around water sources (lakes, springs, etc.). The northern plain habitats of *Ch. oschei pusztaensis* and *Ch. k. karelini*, as well as almost all habitats of *Ch. albomarginatus* may be characterized as meadows, pastures or steppe biotopes with domination of meso- and hygrophilous cereals. One locality of *Ch. karelini*, the reserve Askania-Nova in Ukraine, is of a special interest. During a period of more than 100 last years, the grass, in particular *Festuca stipa*, was not cut at the reserved steppe of Askania-Nova. An area of about 100 sq. km was used for a moderate pasture of the ungulate animals like the Przhevalsky horse, black bison, ox, buffalo and saiga antelope. *Ch. karelini* only occurs at this steppe, whereas *Ch. albomarginatus* and *Ch. oschei* may be found everywhere around the reserve.

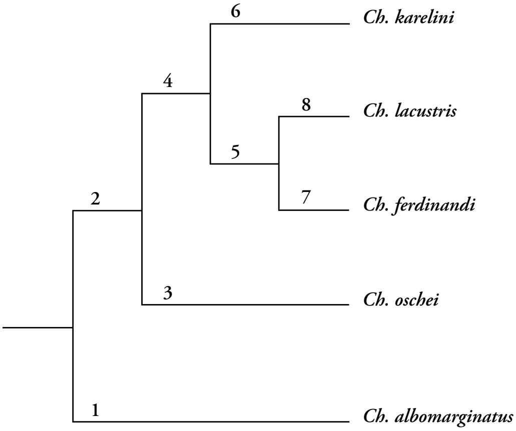


Fig. 81. Phylogenetic relations between the European species of the *Chorthippus albomarginatus* group based on the courtship song synapomorphies: **1**, no courtship element is accompanied by the stroke of the hind tibiae and lifting of abdomen; **2**, C element is accompanied by the stroke of the hind tibiae and lifting of abdomen; **3**, C element is accompanied by a single stroke of the hind tibiae; B1 element is conspicuously loud; **4**, C element is accompanied by a double stroke of the hind legs; **5**, B1 element is not longer than 1 s; during C element, the legs vibrate in a complex pattern; **6**, B1 element is very long, lasting for 5–8 s; during C element, the legs vibrate in a relatively simple pattern; **7**, during C element, after the second stroke, the legs vibrate in a complex pattern; C element is produced only once during each courtship cycle; **8**, lifting of abdomen starts during B1 element and lasts for about 2 s; C element is repeated four-five times during each courtship cycle; courtship song is conspicuously quiet.

Phylogeny and biogeography

The close resemblance in both morphology and calling songs found in all European species of the *Chorthippus albomarginatus* group suggests that they evolved from a common ancestor rather recently, probably during the Pleistocene period. According to

Hewitt's review (1996), the populations in southern refugia could easily have diverged from each other. During interglacial periods, populations in southern refugia were split into many subpopulations when ascending the mountains. These subpopulations were mixed again in the subsequent cold period, when they descended the mountains, and the process was repeated over several ice ages. In this process the subpopulations could diverge, form hybrid zones, and ultimately speciate. At the same time, the most northern expansions were driven extinct by each ice age. It is possible that *Ch. albomarginatus* originated from the northern population of an ancestral stock. In the course of warmer climatic phases such a population could be able to spread northwards, extending its range into most areas of western and eastern Europe. *Ch. oschei* and *Ch. karelini* could originate from the southern populations of the ancestral stock. One can infer that *Ch. karelini* was much more spread and invaded Italy, the Balkans, Turkey and the Caucasus, whereas *Ch. oschei* was only restricted to the Balkans. If we suggest the ancestral stock in the Balkan refugia, one could expect the highest diversity in this region, which corresponds to the situation in the *Ch. albomarginatus* group at the present time. *Ch. lacustris* and *Ch. ferdinandi* are very likely to be the derivatives of an ancestral *karelini* population. We assume that the Balkan diversity resulted from the hybridization that occurred during several interglacial periods. Due to hybridization, the rates of evolution in different refugia, such as Italy and the Balkans, could differ. As a result, *Ch. karelini* could remain in Italy, but it could diverge to *Ch. ferdinandi* and *Ch. lacustris* in the southern Balkans. The hybridization hypothesis is supported by the fact that the courtship song of *Ch. ferdinandi* possesses features of the songs of both *Ch. oschei* and *Ch. karelini*. The failure to find *Ch. karelini* in most of Turkey at the present time could be explained by the contraction of its population due to the destruction of suitable habitats, especially in the south of Anatolia. An extremely local and patchy distribution of many other Orthoptera species in Anatolia at the present time was documented as well (Çiplak 2004). Another member of the *Ch. albomarginatus* group, *Ch. labaumei*, could still occur in the central Turkey, however, we lack fresh material and song recordings.

A very recent event of about two-three centuries ago could influence the distribution of *Ch. karelini* in the southern Ukraine. This species was probably more widespread in Ukraine before, when this territory was not used for agriculture and was similar to the present steppe region of Askania-Nova. One may speculate that when the Ukrainian steppe was started to be ploughed, *Ch. karelini* was forced out by the other species, *albomarginatus* and *oschei*, who appeared to be more adapted to these conditions.

Our suggestion about the very recent divergence of the European species of the *Ch. albomarginatus* group is supported by some preliminary data of molecular analysis. According to the mitochondrial gene COI sequences, there are no fixed differences between the species of this group (Vedenina & Mugue 2005). The outstanding courtship song complexity in all species related to *Ch. albomarginatus* could be only explained by a rapid speciation via sexual selection. The evolution of the stridulatory pegs may be also rather fast in Gomphocerinae, since they function not only as a mechanic part of the stridulatory apparatus, but also as the mechanoreceptors (Hustert et al. 1999). In the species of the *Ch. albomarginatus* group, the peg number and density differ only at the proximal parts of the stridulatory files. The proximal pegs may participate in producing sound when the femora are kept at the extra-high, almost vertical, position, i.e., when the stroke with the hind tibiae is generated. Therefore, the divergence in visual display and the changes in the peg morphology could promote each other.

Acknowledgments

We are very grateful to F. Willemse (Eygelshoven, Netherlands) for supporting with material from Greece, organizing the work with the Orthoptera collection and for critical and helpful discussions. Our thanks to M. Bauer (Institute for Zoology, Erlangen) for technical help in song recordings and preparation of the figures, V. Andropov (A.N. Severtsov Institute of Ecology and Evolution, Moscow) for scanning electron microscopy, K.-G. Heller (Magdeburg), K. Orci (Budapest), D. Chobanov (Institute of Zoology, Sofia), and D. Berger (Institute for Zoology, Erlangen) for their help in collection of grasshoppers, B. Çiplak and Deniz Sirin (AUZM, Antalya) for organizing the work with the Orthoptera collection and for the song recordings of *Ch. karelini* from Turkey, V. Savitsky (Department of Entomology, Moscow University) for supporting with material from Volgograd region, M. Ohl (MNHU, Berlin) for his help with organizing the work with the Orthoptera collection, and V.S. Gavrilenko (reserve "Askania-Nova") for organizing the field work at the reserve territory. This work was partially supported by grants from the Alexander von Humboldt Foundation (IV-RUS 1054747) and from the Russian Foundation for Basic Research (04–04–48883 and 07–04–01698).

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Received: 17 March 2008
Accepted: 29 April 2009

Appendix 1

Morphometrical data of the species of the *Chorthippus albomarginatus* group. Minimum, maximum, mean, standard deviation and the number of specimens are presented.

Parameter	*albomarginatus*					
	Germany, Erlangen		Poland, Krakow reg.		Russia, Moscow	Ukraine, Chernovtzy
	males	females	males	females	males	males
Pronotum length (mm)	2.6-3.0 2.79±0.13 n=15	3.1-3.95 3.73±0.81 n=20	2.5-3.0 2.8±0.15 n=18	3.60-3.95 3.79±0.13 n=13	2.5-3 2.72±0.13 n=13	2.75-3.2 2.95±0.15 n=9
Prozona length (mm)	1.25-1.6 1.37±0.09 n=15	1.65-2.15 1.82±0.39 n=20	1.3-1.5 1.41±0.07 n=18	1.6-2 1.82±0.11 n=13	1.25-1.5 1.36±0.07 n=13	1.4-1.6 1.48±0.06 n=9
Tegmen length (mm)	10.6-11.5 10.93±0.32 n=15	12.7-16 13.94±3.03 n=20	10-12 10.86±0.49 n=18	12.5-14.5 13.52±0.55 n=13	9.5-11.2 10.4±0.5 n=13	11-12.1 11.48±0.43 n=9
Tegmen width (mm)	2.3-2.7 2.43± 0.12 n=15	n/m*	n/m	n/m	2.3-2.7 2.5±0.16 n=5	n/m
Femur length (mm)	8.2-9.3 8.81±0.35 n=15	10.9-12 11.46±2.43 n=20	8.0-10.1 8.71±0.52 n=18	10.7-12.4 11.42±0.49 n=13	7.5-8.8 8.05±0.36 n=13	8.6-9.4 8.9±0.29 n=9
Femur width (mm)	1.5-2.0 1.76±0.14 n=15	2.1-2.4 2.27±0.47 n=20	1.7-1.9 1.81±0.06 n=18	2.1-2.4 2.22±0.10 n=13	1.6-1.8 1.69±0.06 n=13	1.7-2 1.84±0.09 n=9
Stridulatory pegs (mm)	79-128 110.4±11.6 n=30	n/m	90-124 103.8±9.8 n=18	n/m	93-127 111.4±7.8 n=27	114-138 121.6±7.8 n=9

Parameter	*albomarginatus*				
	Ukraine, Kolomyja	Ukraine, Poltava reg., Velikie Sorochintzy		Ukraine, Dnepropetr. reg.	Ukraine, Zaporozhje
	males	males	females	males	males
Pronotum length (mm)	2.75-2.9 2.81±0.07 n=8	2.5-2.9 2.71±0.12 n=15	3.25-3.90 3.62±0.22 n=11	2.5-2.9 2.68±0.13 n=12	2.4-3 2.73±0.17 n=20
Prozona length (mm)	1.3-1.45 1.39±0.06 n=8	1.25-1.5 1.37±0.07 n=15	1.05-1.95 1.75±0.25 n=11	1.2-1.5 1.34±0.09 n=12	1.2-1.5 1.34±0.09 n=20
Tegmen length (mm)	10.8-11.4 11±0.21 n=8	9.7-11.3 10.79±0.44 n=15	11.5-16.5 13.74±1.28 n=11	10.3-11.5 10.84±0.37 n=12	9.8-11.7 10.67±0.61 n=20
Tegmen width (mm)	n/m	2.2-2.5 2.40±0.09 n=13	2.1-2.9 2.55±0.25 n=11	2.3-2.5 2.36±0.06 n=8	2.2-2.7 2.41±0.15 n=15
Femur length (mm)	8.5-9 8.73±0.23 n=8	7.7-9.0 8.50±0.31 n=15	10.4-12.4 11.22±0.62 n=11	8.1-9.1 8.57±0.27 n=12	7.4-8.7 8.22±0.35 n=20
Femur width (mm)	1.8-1.9 1.84±0.05 n=8	1.6-1.9 1.77±0.10 n=15	1.8-2.5 2.18±0.20 n=11	1.5-1.8 1.65±0.11 n=12	1.4-1.8 1.70±0.09 n=20
Number of stridulatory pegs	106-128 116.1±7.0 n=8	99-136 120.8±10.3 n=16	n/m	110-135 121.6±7.6 n=12	98-133 120.2±8.0 n=20

Para-meter	*oschei pusztaensis* ssp. n.							
	Serbia, Belgrade reg.		Makedonia, Tetovo reg.		Hungary, Csikospuszta		Hungary, Kistompapuszta	
	males	females	males	females	males	females	males	females
Pronotum length (mm)	2.44-2.75 2.61±0.11 n=5	3.13-3.75 3.55±0.2 n=8	2.5-3.1 2.7±0.17 n=9	3.2-3.5 3.3±0.11 n=11	2.5-3 2.68±0.15 n=12	2.9-3.2 3.05±0.13 n=4	2.35-2.75 2.61±0.12 n=15	3.15-3.55 3.35±0.14 n=10
Prozona length (mm)	1.25-1.37 1.3±0.06 n=5	1.56-1.81 1.7±0.1 n=8	1.25-1.56 1.36± 0.1 n=9	1.5-1.75 1.66±0.1 n=11	1.25-1.5 1.35±0.08 n=12	1.4-1.6 1.52±0.09 n=4	1.2-1.5 1.34±0.08 n=15	1.5-1.7 1.6±0.06 n=10
Tegmen length (mm)	10.3-11.2 10.8±0.4 n=5	13.3-15.8 14.6±0.8 n=8	9.7-12.3 11±0.72 n=9	12.3-14.3 13.2±0.7 n=11	10.5-12.3 11.03±0.5 n=12	12.8-14 13.65±0.57 n=4	9.7-12 10.8±0.6 n=15	12.5-14 13.2±0.45 n=10
Tegmen width (mm)	n/m	n/m	n/m	n/m	2.2-2.6 2.39±0.12 n=8	2.1-2.2 2.14±0.05 n=4	2.1-2.4 2.24±0.1 n=12	2.1-2.5 2.28±0.11 n=10
Femur length (mm)	8.2-8.7 8.4±0.22 n=5	10.8-12.7 11.8±0.6 n=8	8.2-9 8.44±0.3 n=9	9.8-11.75 10.9±0.5 n=11	7.8-9 8.23±0.43 n=12	10.8-11.5 11.17±0.33 n=4	7.8-9.1 8.3±0.40 n=15	10-11.3 10.84±0.4 n=10
Femur width (mm)	1.7-1.9 1.76±0.1 n=5	2.2-2.5 2.4±0.08 n=8	1.7-1.9 1.8±0.07 n=9	2.1-2.3 2.2±0.08 n=11	1.65-1.9 1.78±0.07 n=12	2-2.2 2.05±0.1 n=4	1.5-1.8 1.64±0.1 n=15	2-2.3 2.11±0.11 n=10
Number of stridul. pegs	173-187 178.8±6 n=5	n/m	151-188 165.6±13 n=9	n/m	155-194 178.5±11 n=13	n/m	153-196 176.5±13 n=15	n/m

Parameter	*oschei pusztaensis* ssp. n.				
	Bulgaria, Batak lake	Ukraine, Zakarpat'je Tjachev	Moldova, Beltzi	Ukraine, Odessa reg., Semjonovka	
	males	males	males	males	females
Pronotum length (mm)	2.4-2.8 2.59±0.13 n=7	2.7-2.95 2.84±0.10 n=7	2.75-3 2.85±0.09 n=12	2.45-2.9 2.64±0.14 n=21	3.4-3.75 3.52±0.1 n=10
Prozona length (mm)	1.2-1.3 1.28±0.04 n=7	1.3-1.55 1.41±0.08 n=7	1.3-1.5 1.43±0.07 n=12	1.2-1.45 1.31±0.09 n=21	1.55-1.7 1.66±0.06 n=10
Tegmen length (mm)	10.8-12 11.26±0.38 n=7	11-12 11.40±0.41 n=7	11.2-12.7 11.87±0.51 n=12	10.3-12 11.18±0.50 n=21	12.5-15 13.75±0.99 n=10
Tegmen width (mm)	2.3-2.5 2.41±0.07 n=7	2.3-2.6 2.47±0.1 n=6	n/m	2.1-2.5 2.37±0.13 n=19	n/m
Femur length (mm)	8-8.6 8.29±0.26 n=7	8.4-9 8.69±0.23 n=7	8-9 8.57±0.32 n=12	7.6-8.9 8.23±0.30 n=21	10.6-12 11.23±0.46 n=10
Femur width (mm)	1.5-1.7 1.64±0.07 n=7	1.6-1.8 1.73±0.1 n=7	1.4-1.9 1.75±0.13 n=12	1.5-1.9 1.72±0.13 n=21	2-2.5 2.35±0.15 n=10
Number of stridul. pegs	168-204 186.3±13.6 n=8	159-200 173.7±17.9 n=7	152-190 173.3±11.3 n=12	151-200 170.0±13.4 n=21	n/m

Parameter	***oschei oschei***					
	Greece, Ioannina, Metsovon		**Greece, Florina, lake Petron**		**Greece, Florina, lake Prespa**	
	males	**females**	**males**	**females**	**males**	**females**
Pronotum length (mm)	2.42-3.09 2.85±0.22 n=10	3.37-4.12 3.79±0.29 n=5	2.5-2.81 2.65±0.11 n=10	3.2-4 3.5±0.28 n=9	2.6-3 2.8±0.13 n=10	3.4-4.13 3.79±0.20 n=10
Prozona length (mm)	1.21-1.58 1.43±0.12 n=10	1.69-1.93 1.85±0.1 n=5	1.25-1.37 1.32±0.05 n=10	1.6-2 1.7±0.14 n=9	1.25-1.44 1.37±0.08 n=10	1.75-2 1.88±0.07 n=10
Tegmen length (mm)	10-12.2 11±0.6 n=10	13.17-14.17 13.57±0.38 n=5	9.3-11.3 10.4±0.64 n=10	12-14.3 13.3±0.9 n=9	10.3-11.7 11.07±0.39 n=10	13.3-15.8 14.13±0.7 n=10
Tegmen width (mm)	n/m	n/m	n/m	n/m	n/m	n/m
Femur length	7.8-8.8 8.4±0.35 n=10	10.7-12.2 11.2±0.59 n=5	7.5-8.5 8.07±0.35 n=10	10.7-12.2 11.4±0.6 n=9	7.8-8.7 8.32±0.28 n=10	10.8-12.7 11.51±0.53 n=10
Femur width	1.67-1.94 1.84±0.09 n=10	2.19-2.5 2.37±0.12 n=5	1.62-1.81 1.72±0.07 n=10	2.1-2.6 2.3±0.16 n=9	1.69-1.94 1.82±0.10 n=10	2.19-2.56 2.36±0.13 n=10
Number of stridul. pegs	150-175 158±8 8.1 n=10	n/m	153-191 172±11 n=10	n/m	152-178 162.5±8.8 n=10	n/m

Parameter	***karelini karelini***							
	Russia, Volgograd reg., Dzhanybek		**Russia, Astrakhan reg., Baskunchak**		**Russia, Astrakhan reg., Dosang**		**Russia, Volgograd reg., Urjupinsk**	
	males	**females**	**males**	**females**	**males**	**females**	**males**	**females**
Pronotum length (mm)	2.7-3.5 3.11±0.21 n=15	3.4-4 3.57±0.19 n=10	2.8-3.4 3.10±0.16 n=15	3.6-4.4 3.93±0.26 n=10	2.9-3.4 3.08±0.15 n=15	3.6-4.15 3.84±0.18 n=9	2.6-3.2 2.87±0.21 n=15	3.35-3.95 3.59±0.17 n=10
Prozona length (mm)	1.35-1.65 1.53±0.08 n=15	1.65-2 1.8±0.1 n=10	1.45-1.6 1.52±0.05 n=15	1.75-2.2 1.91±0.14 n=10	1.35-1.65 1.49±0.08 n=15	1.6-1.95 1.81±0.10 n=9	1.25-1.6 1.41±0.11 n=15	1.6-1.95 1.76±0.1 n=10
Tegmen length (mm)	12.2-15 13.1±0.7 n=15	14-17.5 15.06±1 n=10	12.5-15 13.83±0.1 n=15	15.5-18.5 16.78±1.1 n=10	12.8-15.8 14.21±0.9 n=15	16-18 16.74±0.6 n=9	12.1-14 12.9±0.59 n=15	15-16.8 15.8±0.56 n=10
Tegmen width (mm)	n/m	n/m	n/m	n/m	n/m	n/m	2.2-2.8 2.49±0.17 n=15	2.1-2.9 2.51±0.24 n=10
Femur length (mm)	8.5-10 9.4±0.46 n=15	11.1-12.7 11.9±0.57 n=10	9.2-10.7 9.83±0.42 n=15	11.8-15 13.11±0.1 n=10	9.1-10.5 9.61±0.44 n=15	11.1-13.5 12.4±0.8 n=9	8.5-10 9.31±0.44 n=15	10.8-12.8 12.2±0.59 n=10
Femur width (mm)	1.7-2.1 1.9±0.09 n=15	2-2.5 2.32±0.15 n=10	1.8-2.1 1.92±0.0 n=15	2.2-2.6 2.44±0.147 n=10	1.8-2.0 1.9±0.08 n=15	2.1-2.7 2.4 ± 0.19 n=9	1.5-2.0 1.76±0.12 n=15	1.9-2.6 2.32±0.24 n=10
Number of stridul. pegs	149-205 169±13.7 n=14	n/m	150-193 177±11.4 n=15	n/m	168-203 179.3±10 n=15	n/m	130-180 157±14.6 n=12	n/m

Parameter	*karelini karelini*					*karelini bruttius*
	Ukraine, Askania-Nova		Turkey, Erzurum, Cat-Bekcimen	Turkey, Erzurum, Ataturk Uni	Turkey, Agri, Eleskirt	Italy, Calabria, Lago Arvo
	males	females	males	males	males	males
Pronotum length (mm)	2.7-3.1 2.9±0.12 n=12	3.3-3.8 3.57±0.19 n=8	2.85-3 2.97±0.06 n=6	2.5-3 2.78±0.22 n=5	2.8-3 2.86±0.09 n=5	2.6-3.25 2.93±0.16 n=16
Prozona length (mm)	1.4-1.6 1.49±0.05 n=12	1.55-1.9 1.74±0.11 n=8	1.4-1.7 1.52±0.11 n=6	1.2-1.7 1.39±0.21 n=5	1.4-1.7 1.52±0.13 n=5	1.3-1.6 1.47±0.1 n=16
Tegmen length (mm)	11-13 12.04±0.6 n=12	14-16 15.2±0.6 n=8	11-12 11.75±0.4 n=6	10.8-13 11.7±0.98 n=5	11.2-12.2 11.68±0.4 n=5	11.8-13.6 12.8±0.47 n=15
Tegmen width (mm)	n/m	n/m	2.4-2.7 2.55±0.13 n=6	2.3-2.6 2.45±0.13 n=5	n/m	2.3-2.7 2.48±0.13 n=15
Femur length (mm)	8.5-10 9.1±0.4 n=12	11-12.5 11.8±0.56 n=8	8.7-9 8.9±0.13 n=6	8-9.3 8.62±0.54 n=5	8.5-8.8 8.68±0.16 n=5	8.9-9.8 9.5±0.25 n=15
Femur width (mm)	1.7-2.1 1.86±0.11 n=12	2.2-2.5 2.3±0.99 n=8	1.85-2 1.9±0.05 n=6	1.7-2 1.88±0.13 n=5	1.7-1.9 1.76±0.09 n=5	1.65-2 1.83±0.11 n=15
Number of stridul. pegs	143-193 169.7±15 n=12	n/m	141-183 156.3±15 n=6	149-167 157.2±6.6 n=5	139-167 152±10.4 n=5	156-199 174.8±13 n=15

Parameter	*lacustris*			*ferdinandi* sp. n.	
	Greece, Ioannina	Greece, Thesprothia		Greece, Peloponnesus, Kalavrita	
	males	males	females	males	females
Pronotum length (mm)	2.85-3.3 3.07±0.16 n=9	2.7-3.7 3.01±0.27 n=11	3.55-4.5 3.82±0.3 n=9	3.2-3.56 3.38±0.12 n=13	3.8-4.5 4.17±0.18 n=13
Prozona length (mm)	1.4-1.75 1.56±0.11 n=9	1.4-1.7 1.55±0.11 n=11	1.8-2.5 1.99±0.21 n=9	1.6-1.81 1.7±0.07 n=13	1.94-2.25 2.09±0.09 n=13
Tegmen length (mm)	11-13.4 12.07±0.73 n=9	10.8-12.7 11.86±0.6 n=11	14-16 14.73±0.61 n=9	12.3-14 12.89±0.05 n=13	14-17 15.44±0.91 n=13
Tegmen width (mm)	n/m	n/m	n/m	2.37-2.8 2.53±0.12 n=10	2.44-3 2.73±0.16 n=8
Femur length (mm)	8.8-10.2 9.52±0.47 n=9	8.1-9.8 9.18±0.47 n=11	11.4-13.5 12.23±0.67 n=9	8.6-9.67 9.18±0.32 n=13	11.2-13 12.17±0.56 n=13
Femur width (mm)	1.8-2.1 1.91±0.11 n=9	1.9-2.1 2.02±0.08 n=11	2.4-2.7 2.51±0.09 n=9	1.7-2 1.9±0.08 n=13	2.25-2.56 2.44±0.09 n=13
Number of stridulatory pegs	121-177 158.7±19.3 n=9	130-177 153.4±16.3 n=11	n/m	206-240 221.9±9.5 n=13	n/m

* n/m – no measurements

Appendix 2

Courtship song parameters of the species of the *Chorthippus albomarginatus* group. Mean, standard deviation and the number of males recorded (n) are presented. The ambient temperature near a singing male was 30-32o C.

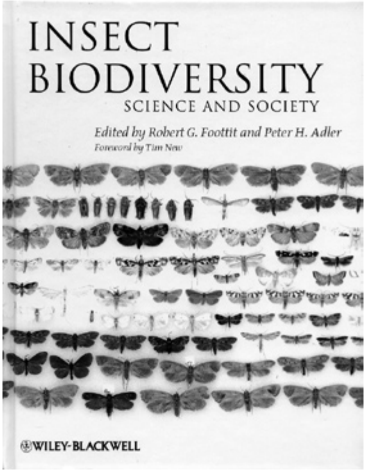
Parameter	***albomarginatus***			***oschei pusztaensis***		***o. oschei***
	Germany, Erlangen	**Poland, Krakow reg.**	**Russia, Moscow**	**Bulgaria, lake Batak**	**Ukraine, Odessa reg.**	**Greece, Ioannina**
	n=20	**n=10**	**n=13**	**n=11**	**n=16**	**n=8**
Number of A/B pairs in a courtship cycle	5±1	6±1	8.2±3.4	26.4±9.4	19.7±6.9	32.4±8.4
Relative B/A sound amplitude	0.14±0.05	0.24±0.15	0.39±0.16	3.3±1.5	3.2±1.7	3.0±1.4
Duration of A syllable (s)	0.47±0.08	0.48±0.15	0.52±0.15	0.36±0.04	0.34±0.07	0.45±0.11
Duration of B syllable (s)	0.66±0.11	0.62±0.11	0.53±0.09	0.32±0.06	0.33±0.10	0.30±0.08
Period of A/B pairs (s)	1.12±0.16	1.04±0.25	0.99±0.14	0.67±0.10	0.67±0.14	0.75±0.18
Rate of leg movements in A element (/s)	52.3±5.8	54.3±8.97	52.6±12.4	61.6±8.0	61.3±4.3	59.3±4.4
Rate of leg movements in B element (/s)	20.8±2.5	22±4.5	20.9±4.5	24.1±2.6	23.9±2.7	21.7±2.2
Duration of B1 syllable (s)	0.77±0.09	0.81±0.14	0.75±0.15	1.8±0.3	2.0±0.5	0.87±0.13
Duration of A1 syllable (s)	0.48±0.07	0.51±0.13	0.54±0.09	0.17±0.03	0.18±0.04	0.19±0.04
Rate of leg movements in A1 element (/s)	55.7±6.5	56.7±9.5	54.4±12.8	77.3±7.5	79.7±6.4	68.1±6.5
Relative A1/C1 sound amplitude	4.3±0.7	3.3±1.4	2.17±0.59	2.69±0.43	3.35±0.87	2.31±0.59
Duration of C element (s)	1.17±0.13	1.27±0.23	1.21±0.20	1.45±0.31	1.27±0.17	1.77±0.26
Number of C elements in a courtship cycle	1±0	1±0	1±0	1±0	1±0	1±0

Parameter	***karelini karelini***			***karelini bruttius***	***ferdinandi***	***lacustris***
	Ukraine, Askania-Nova	**Russia, Volgograd reg.**	**Turkey, Erzurum**	**Italy, Calabria, Lago Arvo**	**Greece, Peloponnesus, Kalavrita**	**Greece, Ioannina**
	n=12	**n=10**	**n=5**	**n=9**	**n=9**	**n=12**
Number of A/B pairs in a courtship cycle	41.6±13.3	34.2±9	49±14	57.8±24.4	17.8±6.7	39.7±7.5
Relative B/A sound amplitude	1.22±0.40	1.1±0.2	0.69±0.2	u/d	0.42±0.12	u/d
Duration of A syllable (s)	0.55±0.24	0.5±0.3	0.39±0.24	u/d	0.27±0.14	0.30±0.08
Duration of B syllable (s)	0.51±0.23	0.6±0.2	0.55±0.13	0.29±0.07	0.52±0.14	0.47±0.30
Period of A/B pairs (s)	1.06±0.29	1.1±0.4	1.07±0.32	0.36±0.07	0.77±0.29	0.78±0.39
Rate of leg movements in A element (/s)	15.11±2.23	12±4	14.1±2.1	u/d	4.98±2.04	44.7±2.4
Rate of leg movements in B element (/s)	32.4±3.31	25.3±3.2	31.4±4.7	35.1±4	48.6±7.8	14.5±3.7
Duration of B1 syllable (s)	5.3±0.9	7.1±3.5	8.5±3.8	3.49±0.62	0.78±0.21	0.53±0.11
Duration of A1 syllable (s)	0.32±0.07	0.51±0.1	0.40±0.11	0.33±0.02	0.09±0.03	0.22±0.03
Rate of leg movements in A1 element (/s)	49.9±6.1	42.2±7.3	43.4±4.2	51.4±3.6	39.8±9.3	92.8±9.4
Relative A1/C1 sound amplitude	0.44±0.11	0.55±0.2	0.5±0.3	0.61±0.23	0.35±0.28	2.24±0.37
Duration of C element (s)	0.52±0.05	0.7±0.1	0.68±0.21	0.57±0.09	1.11±0.20	1.01±0.15
Number of C elements in a courtship cycle	1.9±0.3	2.4±0.5	2±0	3.2±0.4	1.04±0.13	4.3±0.6

u/d* - unavailable data

Book review

Robert G. Foottit & Peter H. Adler (eds.), 2008.
Insect Biodiversity, Science and Society.
– Wiley-Blackwell, ISBN 978-1-4051-5142-9,
hardback, 632 pp. Price: EUR 90; USD 159.95.
Also available as e-book.



Books on biodiversity are hot, but frequently the term is misused as an advertisement for just any book on biology. Here we have two books (including the review on p. 184) on real biodiversity: the staggering diversity of insects is the subject of this title. It is not a book on classification, morphology or phylogeny, but in 25 chapters is giving a picture of the diversity of the real insects. The volume is a multi-authored, and the chapters are combined in three main groups: I: *regional examples*, II: *taxon examples*, III: *tools and approaches*. Two introductory chapters precede this. The editors provide a short overview of the total of known species per order, now totalling to 1,004,898, so we have passed the magic million! For a complete list of chapters see the publishers website.

As is clear from the titles of the parts, the book is not trying to be comprehensive, in the regional treatments we are badly missing the oriental region and in the taxon treatment such groups as Orthoptera, Dictyoptera or Neuropteroid orders. Having many authors inevitably also leads to sometimes very different treatments and personal choices. The treatment of the Palaearctic diversity (Konstantinov, Korotyaev & Volkovitsh) is a very extensive treatment with long lists with families and numbers (I think the first account of this kind), and a detailed review of major biogeographic regions, which these Russian authors know very well. But being all coleopterists, the treatment has also a 'beetle bias', albeit with very interesting sections, such as one on biodiversity of herbivores. Also the Amazonian and African chapters are written by coleopterists. Peter Cranston's chapter on Australasian insects is much more a narrative, with interesting details about some of the iconic species, such as the Lord Howe island stick insect and New Guinean birdwings. All these regional treatments make very interesting reading and are highly original, there have been very few comparable reviews published to date.

Some of the taxon treatments are very much an enumeration of taxonomic units with not much more than numbers and a little morphological and distribution information, and little information on importance, life strategies, etc. Pogue's treatment of the Lepidoptera is suffering from this, and in this way a bit disappointing, not offering much more than the Handbook of Zoology treatment (Kristensen ed.) of 1998, otherwise than some better estimates of species numbers. Even the new superfamily Andesianoidea described in 2000 by authors just a few doors away from this author, is missing. The chapters on Diptera and Coleoptera are both written by a consortium of four authors, and provide much more interesting information on the economic and societal importance of these groups than the other chapters. One chapter deals with aquatic insects throughout all orders, which in contrast to the rest of the book includes entognathous hexapods (Collembola).

The final section is the most diverse and provides also interesting reading, with some provocative chapters that show sometimes completely opposing opinions. Quentin Wheeler (*The science of insect taxonomy, prospects and needs*) is vigorously defending that all unknown insect species should be described and named, using new techniques and "cyber-enabled, international, taxon-focused 'knowledge communities' ". He proposes the use of the phylogenetic species concept, whereas Michael Claridge (*Insect species – concepts and practice*) advocates the use of the biological species concept as the most practical.

The book is well printed and bound, eight colour plates are bound together after page 314, but grey (a bit too pale) facsimiles are placed in the relevant positions and refer to the colour plates.

This book with its shortcomings, is a highly original account, providing many new insights and new summarised data that should not be missing on the shelves of any entomologist, and also other biologists and naturalists can benefit from this volume.

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