Systematics and Bioacoustics of the Genus Lithodusa (Orthoptera: Tettigoniidae) Including the Description of a New Species from Turkey and Comments on the Classification of the Drymadusini

Authors: Heller, Klaus-Gerhard, and Korsunovskaya, Olga

Source: Journal of Orthoptera Research, 18(1) : 5-13

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.018.0107

Journal of Orthoptera Research, August 12, 2009,18(1): 5-13

Systematics and bioacoustics of the genus Lithodusa (Orthoptera: Tettigoniidae) including the description of a new species from Turkey and comments on the classification of the Drymadusini

Accepted March 14, 2009

KLAUS-GERHARD HELLER AND OLGA KORSUNOVSKAYA

(KGH) Grillenstieg 18, 39120 Magdeburg, Germany. Email: heller.volleth@t-online.de
(OK) Department of Entomology, Moscow Lomonosov State University, Vorobiovy Gory, Moscow 119992, Russia
Email: korsuno@aport.ru

We dedicate this paper to Otto von Helversen (1943-2009), who initiated the excursion during which the new species was discovered, and devoted many years of his life to the understanding of orthopteran communication.

Abstract

The genus *Lithodusa* Bey-Bienko, 1951 is revised, including the description of a new species. Its two species differ in many aspects of morphology, mainly in genitalia, and can most easily be separated by length of tegmina. The calling songs of both species are quite similar in amplitude pattern, as well as in spectral properties. The genus is distributed from the Caucasus to northeast Turkey. The relationships of *Lithodusa* to other genera of the Tettigoniidae/-inae are discussed and a list of genera belonging to Drymadusini presented.

Key words

Drymadusini, *Lithodusa*, taxonomy, calling song, bioacoustics, new species, Russia, Turkey

Introduction

In the year 1983 Otto von Helversen and several of his students made an excursion to Turkey, mainly to study the acoustic behavior of acridid grasshoppers. The journey was very interesting and some of the participants subsequently became orthopterologists, or at least scientists working with and publishing about Orthoptera (Matthias Hennig, Jens Sachteleben, Helmut Kriegbaum and myself). Besides acridids we also looked for tettigoniids and their songs. Parts of the acoustic and systematic results of these observations have been published (Heller 1988, 1990; Çiplak & Heller 2001; Çiplak *et al.* 2002; Sevgili & Heller 2003; Çiplak & Heller 2005; Heller 2006; Heller *et al.* 2006). One form we had collected but could not identify was described as a new genus and species by another scientist, based on independent later findings (*Bolua turkiyae* Ünal 1999).

However, among the unidentified specimens was another problematic male. Relatively soon it turned out it did not belong to a species nor to a genus known from Turkey. From general morphology it could be suggested as a member of the Drymadusini, a group (see comments below) distributed with about 150 species, from North Africa eastwards to North America, mainly in Asia.

After examining the descriptions of most species of the Drymadusini and some specimens in museums, it became clear that our species was most similar to *Lithodusa daghestanica*. Fortunately this little known species (and genus) was studied bioacoustically by Korsunovskaya *et al.* in 2002. These data strongly support the inclusion of our specimen into this genus. A morphological comparison using the newly collected specimens of *L. daghestanica* indicates that it has to be considered as a separate new species.

While preparing the description we came across some problems in the systematics of the higher groups to which the genus belongs. These are discussed below.

Material and Methods

Depositories of material are abbreviated as follows: CH - Collection of Heller, Magdeburg; ZIN - Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZMB - Museum für Naturkunde der Humboldt-Universität, Berlin; NHM - Natural History Museum, London.

In the field sounds were recorded using a tape recorder (Uher 4200 IC) with microphone Uher M 645 (frequency response flat up to 20 kHz). In the laboratory sound recordings were made with a Racal store-4 DS tape recorder, with microphones Brüel & Kjaer 4133 and 4135 (frequency responses flat up to 40 and 70 kHz respectively). After digitizing the songs on a PC or Apple computer, oscillograms (after filtering) and sound analyses were done using a PC and the software Turbolab and Amadeus (Apple). Wing movements were registered by an opto-electronic device (Helversen & Elsner 1977, modified as in Heller 1988). The maps were produced using the software Versamap (http://www.versamap.com/).

Song terminology.—Calling song: song produced by an isolated male. Syllable: the sound produced by one complete apart (opening hemisyllable) and together (closing hemisyllable) stroke of the wing. Echeme: a first-order assemblage of syllables. Impulse: a simple, undivided, transient train of sound waves (here: the highly damped sound impulse arising as the impact of one tooth of the stridulatory file; see Elsner 1974).

Results

Genus *Lithodusa* Bey-Bienko, 1951

Translation of the diagnosis of the genus by Bey-Bienko 1951:

"Is close to Phytodrymadusa *Ramme and also characterized by not having a black stripe on the frons between the eyes. The elytra are shortened, but clearly protruding under the pronotum. The ovipositor is curved downwards.* [Lithodusa] *differs from this genus by the following characters. The body is grey, dimly-marble, without any greenish or yellowish colour tone.*

Elytra in both sexes slightly longer than pronotum, stridulatory vein completely exposed. Prosternum without obvious spines. Fore and middle femora on the lower side at the frontal edge without or with only weak spines. Ovipositor distinctly shorter than hind femora, strongly curved

Fig. 1. Male *Lithodusa helverseni* n. sp., holotype. For color version, see Plate I.

downwards. Subgenital plate with elongated groove in the middle.

Type of genus: Lithodusa daghestanica *gen. et sp. nov.*

Despite the morphological similarity to Phytodrymadusa *Ramme* [Lithodusa] *recalls more the representatives of* Paradrymadusa *Herm. The explanation for this may be found in the fact that this genus* [Lithodusa] *inhabits stony areas as* Paradrymadusa *Herm., whereas the species of* Phytodrymadusa *Ramme live on plants."*

According to this diagnosis *Lithodusa* can be separated from other genera of the Drymadusini as follows. The unarmed prosternum (see Uvarov 1942) seems to be quite important. Many genera of the Drymadusini (as well as the non-Drymadusini *Gampsocleis* and *Uvarovites*) possess a prosternum with spines (see Rentz & Colless 1990, character 5, state 1; also in *Delodusa*, own observations). However, the state of the prosternal armature "tuberculate" (= state 3) is difficult to separate from "absent" (own observations in *Anadolua, Scotodrymadusa, Paradrymadusa*). In addition, the state may be variable within a genus (*e.g., Scotodrymadusa*; Çiplak & Heller 2005; *Mixodusa, Novadrymadusa* own observations). The state "tuberculate" is mentioned for *Pezodrymadusa, Scotodrymadusa, Paradrymadusa, Phytodrymadusa* and *Anadolua*.

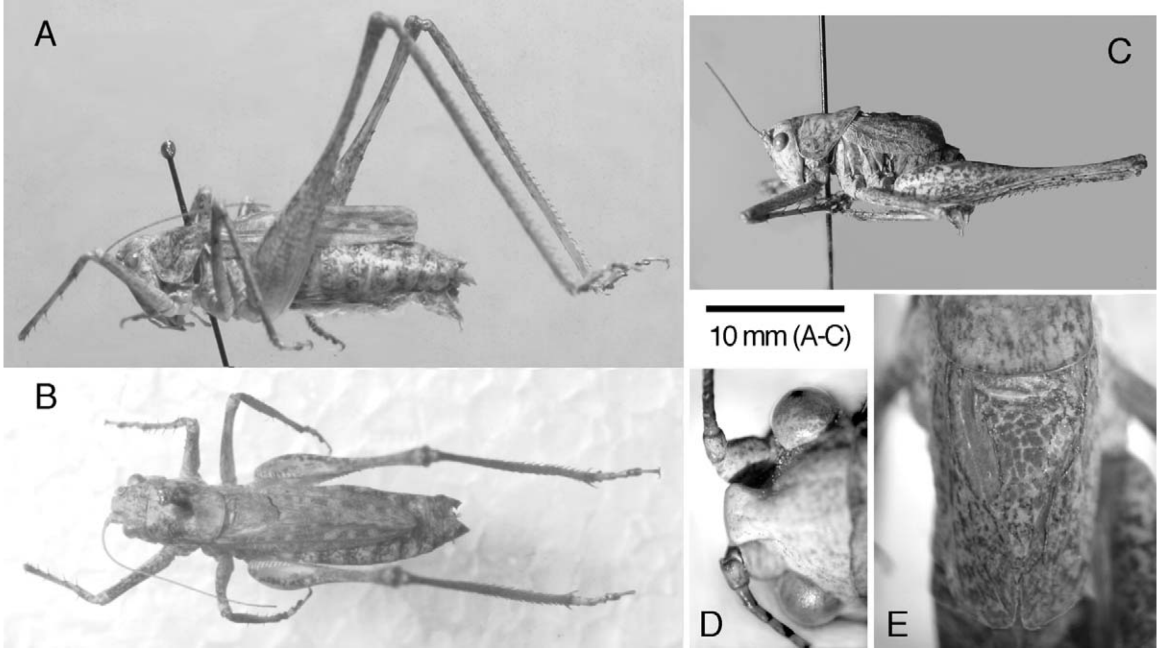
Pezodrymadusa is obviously closely related to *Drymadusa*, possessing the typical structure of the last tergite of that genus not found in *Lithodusa*. In *Anadolua*, the width of the fastigium is about the same as that of the scapus, while in *Lithodusa* it is 1.3 to 1.5 times wider. In addition, in *Anadolua* the stridulatory vein is covered by the pronotum. *Anadolua* has a straight ovipositor, *Scotodrymadusa* an upcurved ovipositor; *Paradrymadusa* has a black stripe between the eyes and *Phytodrymadusa* is typically green/yellow and has flattened apical arms of its titillators (see Table 1 in Demirsoy *et al.* 2002, also for differences from other small genera), all characters contrasting with the state in *Lithodusa*.

The prosternum is described as unarmed only in *Calopterusa* and *Iranusa*, both described by Uvarov in 1942. Uvarov (1942) himself was well aware of this important difference in the structure of the prosternum, obviously overlooked by Ramme in his revision of the group. *Lithodusa* differs from both above-mentioned genera at first glance, by the size and structure of the tegmina, *Iranusa* being macropterous (tegmina extending up to [*I. grisea*] or beyond hind knees) and *Calopterusa* being micropterous, with a thick membrane and callous thick veins and veinlets. More material is needed to show if *Lithodusa* is to be considered as a small, short-winged version of *Iranusa*. This genus, described on an eastern Iran species, is obviously much more widespread than previously assumed, with species in

Table 1. Measurements of *Lithodusa* species (in mm; data for *L. daghestanica* from Bey-Bienko 1951).

	L. daghestanica		*L. helverseni*
	male	female	male
Body	22.5 - 23.0	23.0	25.0
Pronotum	4.5 - 4.8	5.7	5.7
Tegmina	7.0	6.3	16.0
Hind femora	19.0 - 19.5	23.0	24.0
Ovipositor		13.0	

Fig. 2. Lateral and dorsal view of *Lithodusa helverseni* (A, B) and *L. daghestanica*. (C, E). D. Fastigium of *L. daghestanica*. Here and in Fig. 3 (B, D, F) and Fig. 4 (D, F) males of *L. daghestanica* from Daghestan, Gunib village are presented.



Pakistan (Ingrisch 1996) and central north Iran (Ünal 2006). Among the central and east Asian genera, the prosternum seems to be also unarmed in *Anatlanticus* ("tuberculate"), *Drymadusella, Uvarovina, Eulithoxenus* and *Bienkoxenus* (according to the data in Rentz and Colless 1990), and also in *Drymapedes*, *Lithoxenus*, *Microdrymadusa* and *Tadzhikia*.

All described species of these ten genera differ in one or more important characters from *Lithodusa*, but they will not be considered here in detail.

Both *Lithodusa* species (see below), especially *L. helverseni*, have relatively long tegmina, a situation resembling *Ferganusa* Uvarov, 1926, with its sole species *F. hemiptera*. *Ferganusa* however, has a prosternum armed "with a pair of thick conical spines" and its vertex is "distinctly narrower than the first joint of antennae" (Uvarov 1926).

Lithodusa daghestanica Bey-Bienko, 1951

Type locality.—Russian Federation: Daghestan: village Khodjal-makhi (=Khojal-makhi), Tzudakharski region, viii 1950, leg. N.G. Jolova; (Tsudakhar lat 42°33'N, long 47°09'E).

Type.—Holotype male, depository: ZIN Bey-Bienko 1951: 146 (description); Otte 1997: 302 (catalogue); Naskrecki & Otte 1999: (catalogue); Korsunovskaya *et al.* 2002: 339 (bioacoustics).

Distribution.—Known only from Daghestan: type locality, Kaptschugaj (= Kapchugay; Bey-Bienko 1951) and Gunib village (Korsunovskaya *et al.* 2002) (Fig. 6).

This little-known species and its genus are neither mentioned in Rentz & Colless' study of Tettigoniinae (1990), nor in a list of Orthoptera of Daghestan (Chernyakhovsky *et al.* 1994).

Lithodusa helverseni Heller n. sp.

Holotype male.— TURKEY: Erzurum: Çoruh Valley, 35 km northeast of Ispir, near bridge over Çoruh, lat 40°40'N, long 41°16'E, 900 m a.s.l., pebbles, some bushes, 5/6 viii 1983, leg. K.-G. Heller. Labels: "Türkei. Prov. Erzurum, Çoruh-Tal 35 km nö Ispir, Brücke über den Çoruh-Fluß. Flußschotter, teilweise Gebüsch, 900 m, 5/6. viii 1983"/"CH6051"/ "Racal" (on orange paper).

Type depository.—Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB) (Fig. 1).

Diagnosis.—Differs from *L. daghestanica* by the much longer tegmina of the male (see Table 1), structure of cerci, titillators and last tergite (Figs 2, 3), and also by details of the song (Fig. 4).

Description.— (Holotype, male).

Head. Shape conical; fastigium verticis about 1.3 times as wide as scapus; eyes protruding, slightly oval.

Thorax. Prosternum unarmed; pronotum without sulcus (only very weak groove at the end of first sixth) and without median keel, disc flat and smooth, its posterior edge convex, rounded (Fig. 2 B); shape of paranota as in Figs 1, 2. Tegmina covering more than three quarters of abdomen, quite long for a flightless member of Drymadusini.

Legs. Fore tibia on ventral side margins, 6 anterior and 6 posterior spines, dorsally with only 3 posterior spines. Middle tibia ventrally (left/right) with 5/6 anterior and 6/6 posterior spines, dorsally two anterior and four posterior spines. Hind tibia on ventral aspect with each margin having about 8 small anterior and posterior spines, on dorsal aspect many anterior and posterior spines. Femora without spines dorsally, ventrally fore femur with only 2/3 (left/right) anterior, middle femur only 1/2 anterior spinules, hind femur with about 8 anterior and 8 posterior spinules. Hind tibiae with two pairs of apical spurs. Plantulae shorter than half of metatarsus.

Abdomen. Last tergite with two triangular, rounded processes, separated by a rounded incision. Cerci see Fig. 3. Subgenital plate with sharp triangular incision, strong lateral and a weak median keel; styli slightly longer than incision width. Titillators with long and straight apical arms, anterior edge with small teeth at tip.

Coloration. Generally mottled grey, ventral side pale.

Female. Unknown.

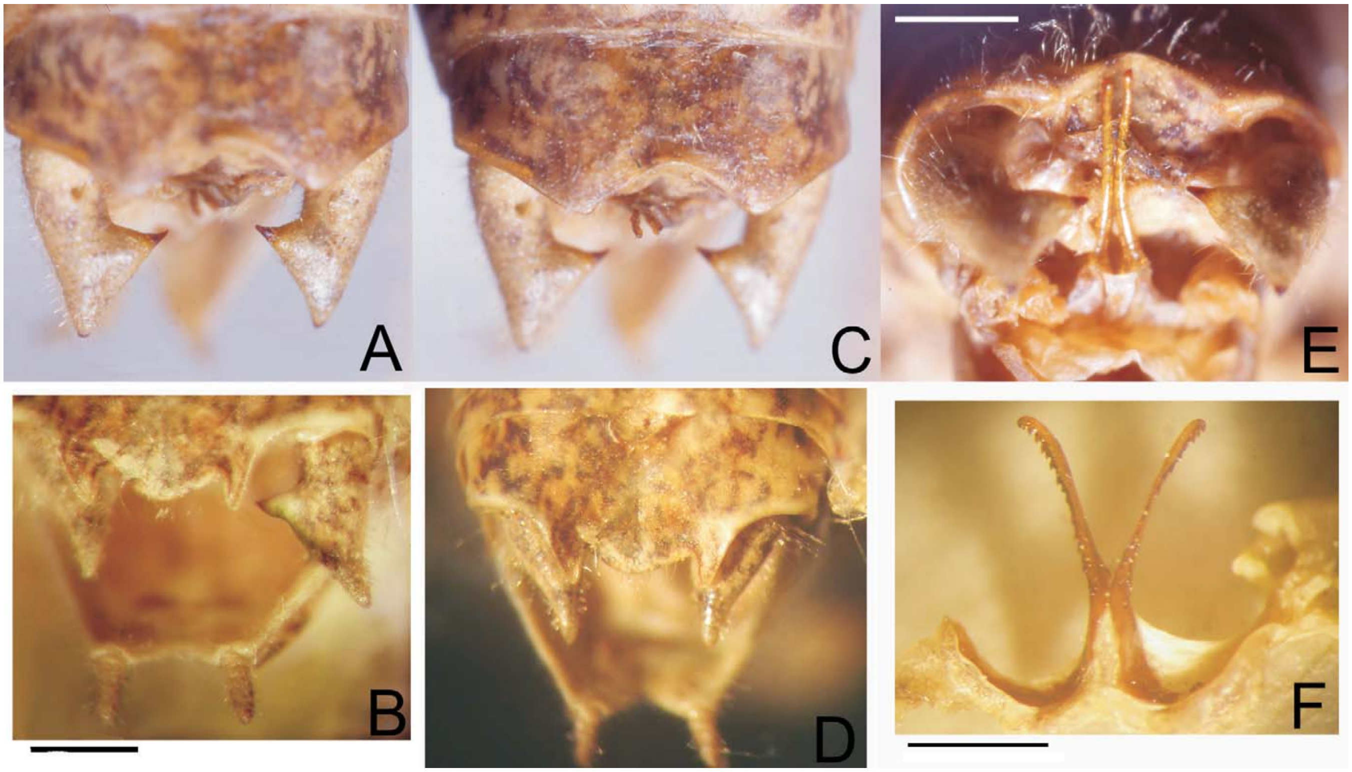


Fig. 3. Cerci, 10th tergite and titillators in *Lithodusa helverseni* (A, C, E) and *L. daghestanica* (B, D, F). Scale 1 mm. For color version, see Plate I.

Etymology.— This name is selected in remembrance of the recently deceased great zoologist Otto von Helversen, my teacher (KGH) in orthopterology.

Locality and habitat.—We spent the night from 5th to 6th August 1983 near the bridge over the river Çoruh northeast of Ispir, where the road from Ispir to Artvin changes from the southern to the northern side of the valley. Near our campsite we discovered the animal at night by its song. It was sitting on the stony ground near some bushes. The slopes of the valley were covered with sparse Mediterranean-type vegetation; near the river were mostly either stones or cultivated watered fields.

At night we heard the song of *Tettigonia viridissima* and *Anadrymadsa adzharica*, and a male of *Phaneroptera sparsa* was attracted to our light.

Bioacoustics.—The calling song consists of relatively long series of syllables (duration of series variable, 3 to 25 s recorded, Fig. 4). Within these series, however, the syllables were not repeated with a single repetition rate, rather syllables and syllable periods with slightly different durations changed regularly. After an initial crescending song phase (*ca* 1 to 2 s), groups (echemes) each containing three syllables, were repeated regularly. All syllables consisted of opening and closing hemisyllables of similar intensity, and both types of hemisyllables contained many impulses. Within an echeme, the first opening hemisyllable was the longest opening hemisyllable and the last closing hemisyllable, by far the longest closing hemisyllable (syllable periods 20.1±0.7 ms, 18.1±0.4 ms, 21.6±0.7ms, n = 16 each; measured from wing movements; durations of opening and closing hemisyllables: 1st syll. 6.6 ms, 8.8 ms; 2nd syll. 5.8, ms 8.2 ms; 3rd syll 5.0 ms, 11,4 ms; measured from sound) at about 30°C [27.5°C air temperature + 2.5 degree estimated increase of body temperature produced by the lamps of the recording device]). At the beginning of a syllable series usually a loud hemisyllable could be heard, and sometimes after the end of the syllable series a single sound, probably indicating the final closing of the wings (see Fig. 4 B, tegmina after the end of a series, not as closed as at the beginning). Both characters were also found in *L. daghestanica* (Korsunovskaya *et al.* 2002).

The structure of the song is quite similar to that of *L. daghestanica* (see Figs 4 C and D, 4 E and F). For the comparative figures different time scales (factor 2) were used to compensate for the different recording temperatures (20°C in *L. daghestanica*, 30°C in *L. helverseni*) corresponding to a van't Hoff temperature coefficient (Q_{10}) of 2. *L. daghestanica* shows a different structure of the opening hemisyllable, but the general rhythm seems to be the same in both species.

Calling songs built from series of echemes with three syllables are not common, but are known from some other tettigoniid species, *e.g.*, *Platycleis (Montana) macedonica* Berland & Chopard 1922 (Heller 1988).

Relatively large differences between opening and closing hemisyllable were found in the spectral composition of the song (Fig. 5). The opening hemisyllable had a broad maximum between 25 and 45 kHz (10 dB below peak; microphone 10 cm lateral of the animal), while the maximum of the closing hemisyllable is distinctly lower (15 to 40 kHz 10 dB below peak). This difference had the effect that in recordings with a good audio response (up to 20 kHz), the closing hemisyllable appeared much louder than the opening one, which could be nearly lost. The same difference can be seen in the song of *L. daghestanica*, although the spectra are narrower than in *L. helverseni* (an effect of the different size of the tegmina?).

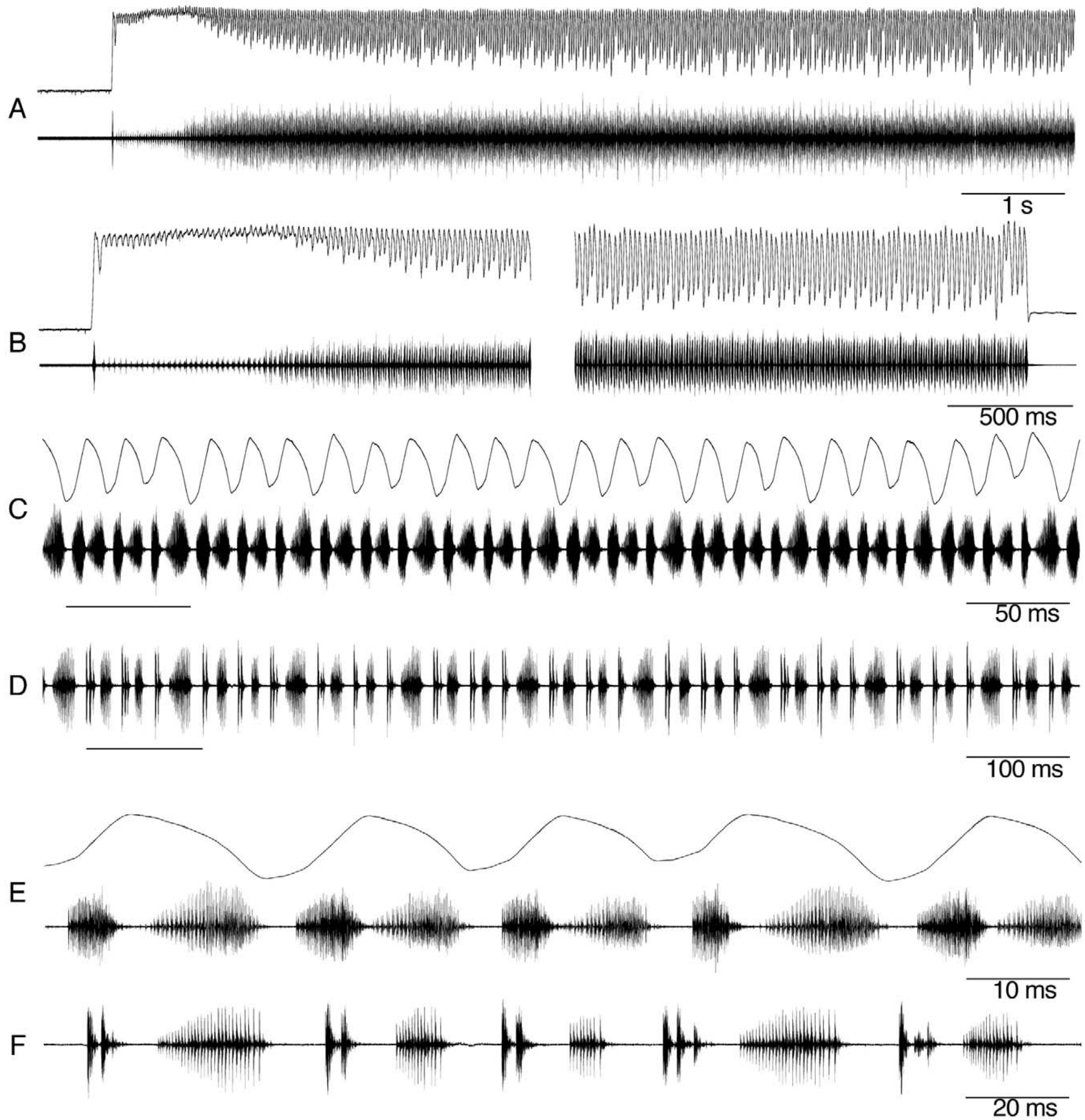


Fig. 4. Oscillograms of the stridulatory movements and song [synchronous registration of left tegmen movement (upward deflection represents opening, downward closing) and sound] of *Lithodusa helverseni* (A, B, C, E) at 30°C and of the song of *L. daghestanica*, (D, F) at 20°C. Because of the different recording temperatures, different time scales were used to make the songs of the two species comparable (see text).

Distribution.—The species is only known from its type locality (Fig. 6).

Comments on the classification of the Drymadusini Uvarov, 1924

Formal aspects.—The term Drymadusini was to our knowledge first used by Sergeev in his biogeographical study (1986). The designation as tribe, also used by Storozhenko (1986) and later Stolyarov (1994), was accepted by Otte (1997), but without giving an authorship, without (!) including the type genus *Drymadusa* and without incorporating many other genera mentioned by Sergeev. However, Sergeev had already used the name for a group of genera (see Table 2) assumed to be closely related. Storozhenko (2004) cites as author of this group Uvarov (1910), but this is obviously not correct. Uvarov seems to have mentioned Drymadusae as a group first in 1924 (p. 492) without definition. This name seems thus to be the first one used at a suprageneric level, fulfilling the criteria of a family group name (ICZN Art. 35.1). In 1924, from this group only the genera *Drymadusa*, *Ceraeocercus*, *Paradrymadusa*, *Bergiola* and *Atlanticus* had

Table 2. Genera of Drymadusini (see text for further details). Symbols: n = number of species; x = considered a member of Drymadusini; (x) = type species described as member of Drymadusini; - not covered in the respective paper (mostly more recent or out of range); b = considered a member of Bergiolini; p = considered a member of Platycleidini; t = considered a member of Tettigoniini. * = placed in Drymadusini according to comparisons made in the description of the genus; ° = the situation in *Bergiola* was not clear at the time of Ramme's study (see Ramme 1939).

Genus	Author, year	n	Type locality/localities of species included	Ramme 1939	Rentz & Colless 1990	Otte 1997	OSF 2006:	Sergeev 1993, 1995
Afrodrymadusa	Ramme, 1939	1	Tunisia	x	t	t	x	-
Ammoxenulus	Bey-Bienko, 1951	2	Turkmenistan	-	t	t	t	x
Anadolua	Ramme, 1939	4	Turkey	x	t	t	t	-
Anadrymadusa	Karabag, 1961	12	Caucasus, Crimea, Greece-Iran, Israel	(x)	t	t	x	-
Bergiola	Stshelkanovtsev, 1910	5	Iran, Kazakhstan, Pakistan, Turkmenistan	x°	t	t	b	x
Bienkoxenus	Cejchan, 1968	4	China, Mongolia, Russia: Tuva	-	p	p	b	x
Calopterusa	Uvarov, 1942	7	Afghanistan, Azerbaijan, Iran, Pakistan, Tajikistan	(x)	t	t	t	x
Ceraeocercus	Uvarov, 1910	1	Kazakhstan	x	t	t	t	x
Delodusa	Stolyarov, 1994	1	Iran	(x)	-	t	t	-
Drymadusa	Stein, 1860	2	Greece, Turkey	x	t	t	x	-
Drymadusella	Ramme, 1939	3	Afghanistan	x	t	t	x	x
Drymapedes	Bey-Bienko, 1967	1	Afghanistan	-	?	x	x	-
Eulithoxenus	Bey-Bienko, 1951	2	Mongolia	(x°)	p	p	b	x
Exodrymadusa	Karabag, 1961	1	Cyprus	(x)	t	t	x	-
Farsodecticus *	Mirzayans, 1991	1	Iran	-	-	?	?	-
Ferganusa	Uvarov, 1926	1	Uzbekistan	x	?	x	x	x
Iranusa	Uvarov, 1942	2	Iran, Pakistan	-	t	t	t	x
Leptodusa	Stolyarov, 1994	3	Turkey	(x)	-	t	t	-
Lithodusa	Bey-Bienko, 1951	2	Caucasus, Turkey	-	-	t	t	-
Lithoxenus	Bey-Bienko, 1951	4	Kazakhstan, Kyrgyzstan, Turkmenistan	(x°)	?	x	x	x
Microdrymadusa	Bey-Bienko, 1967	1	Afghanistan	-	?	x	x	-
Mixodusa	Stolyarov, 1994	2	Iran	(x)	-	t	t	-
Mongolodectes	Bey-Bienko, 1951	3	China, Mongolia	(x)	t	x	x	x
Novadrymadusa	Demirsoy et al., 2002	2	Iran, Turkey,	(x)	-	-	x	-
Paradrymadusa	Herman, 1874	11	Caucasus, Crimea, Tajikistan, Turkey, Uzbekistan	x	t	t	x	x
Pezodrymadusa	Karabag, 1961	13	Armenia, Iran, Turkey	(x)	t	t	x	-
Phytodrymadusa	Ramme, 1939	7	Caucasus, Iran, Pakistan, Turkey	x	t	t	x	x
Scotodrymadusa	Ramme, 1939	13	Turkey, Iran, Iraq, Caucasus (1)	x	t	t	x	-
Tadzhikia	Mistschenko, 1954	3	Afghanistan, Tajikistan	-	?	x	x	x
Uvarovina	Ramme, 1939	2	Mongolia, Russia: Irkutsk	x	p	p	b	x
Zagrosiella *	Mirzayans, 1991	1	Iran	-	-	?	?	-
Anatlanticus	Bey-Bienko, 1951	2	Korea, Russian Far East	-	t	t	t	x
Atlanticus	Scudder, 1884	28	China, North America, Russian Far East,	x	p	p	p	x
Paratlanticus	Ramme, 1939	3	Japan, Korea, Russian Far East	x	t	t	t	x

been described (see Table 2).

In the revision of all species related to *Drymadusa*, Ramme only once used a special name (1939, p. 93): he calls it "Gruppe Drymadusa" and lists at the same place all genera included. Bey-Bienko (1951) used as did Uvarov, "group Drymadusae" (1951, p. 148), but Karabag (1961) while splitting *Drymadusa*, did not employ any suprageneric terms.

Previously Brunner von Wattenwyl [1893; not 1878 as cited for Gampsocleidini by Storozhenko (*e.g.*, 2004, OSF 2006)] had included *Drymadusa* in his *Gampsoclees*.

The name Bergiolini for a subgroup of Drymadusini seems to have been introduced by Storozhenko (1994: p. 65) without any definition. We could not find a list of the 10 genera belonging to the tribe as stated by Storozhenko (2004). A reference to Uvarov (1928) for the name of the tribe (as made in Storozhenko 2004) is not correct, Uvarov did not mention any group name in this paper.

Taxonomic significance.—As the results from Rentz and Colless (1990) clearly show, it is very difficult to find characters useful for a supra-generic classification of the family Tettigoniidae (or Tettigoniinae). The two present solutions of this problem, to elevate many genera to tribes (Storozhenko, *e.g.*, 1994) and/or to use a disjunctive diagnosis (see Rentz & Colless 1990), have in our opinion not clarified the situation, and have not improved the understanding of the evolution of this family.

The group Drymadusini may or may not be a natural monophyletic grouping, but it is in any case a rough taxonomic "working hypothesis" that unites morphologically similar species. The diagnosis for the tribe given by Storozhenko (2004; repeated in Storozhenko & Paik 2007) is partly contradictory to the information given by Rentz & Colless (1990), being even incorrect for the type genus, and therefore not usable. Many (but not all) of the genera of the Drymadusini are grouped with Tettigoniini *sensu* Rentz & Colless (1990), but they are so different from *Tettigonia* itself (not to mention extra-Eurasian genera), that a group named after this genus would not convey the information an author would wish to convey to the experienced reader (as it is done, for example, by the

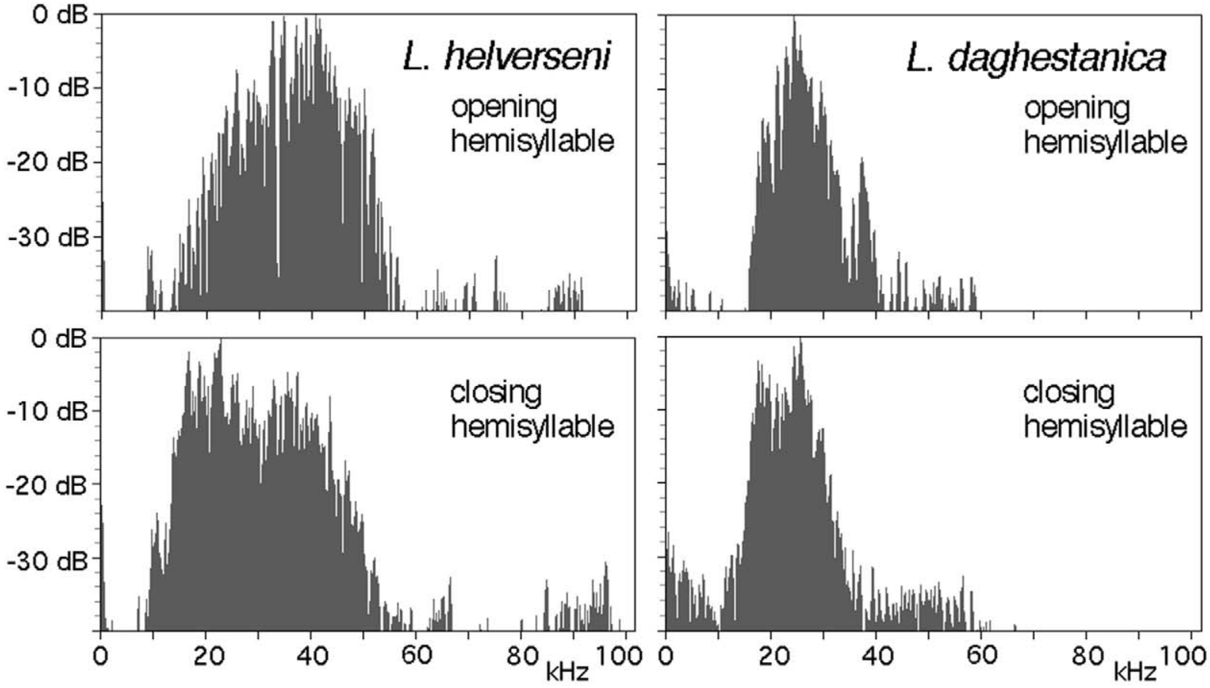


Fig. 5. Frequency spectra of *Lithodusa* calling songs.

use of this term by Sergeev 1986, Warchalowska & Bugrov 1996 and Korsunovskaya *et al.* 2002). Also for a taxonomic placement of unknown forms, such a working hypothesis may be more helpful than both of the above-mentioned approaches. All genera of a group of the Drymadusini distributed mainly in the western Palaearctic (except for *Anadolua*), cluster quite closely together in a phenetic diagram (Fig. 1 in Rentz & Colless 1990), where *Anadolua* is placed very near to *Bergiola*, both marked as Platycleidini, contrary to the text of that paper (p. 364, see also Fig. 2).

Table 2 gives a list of the genera we include in Drymadusini, mainly following Ramme's ideas (1939). The genera are placed in two blocks (Palaearctic and southeast Palaearctic-Nearctic), according to their center of distribution as indicated by Sergeev (1998), and are grouped alphabetically within each block. To our knowledge the list covers all described genera of the group. Following this table, it is a mainly Palaearctic group with one genus reaching the Nearctic region. However, the relationships to other Nearctic genera (see Rentz 1973, Table 1) remain unsolved. Uvarov (1928) considered *Idiostatus* Pictet, 1888 as next-related to *Bergiola*. *Idiostatus* is a genus with 25 species in the USA, that is not even mentioned in the recent field-guide of the Orthoptera of the USA (Capinera *et al.* 2004). Rentz (1973) assumed that the progenitor of *Steiroxys* and *Idiostatus*, which he considers to be closely related, immigrated to North America via the Bering arc.

From the Eurasian Tettigoniinae listed with uncertain tribal relationship in OSF (2006), *Pravdiniana* Sergeev & Pokivajlov, 1992 and also *Hermoniana* Broza, Ayal & Pener, 2004, clearly belong to Platycleidini according to their descriptions. *Kansua* Uvarov, 1933, obviously overlooked by Rentz & Colless (1990), is certainly not a member of Drymadusini, and for *Dreuxia* Chopard & Dreux, 1966 even the subfamily is uncertain. *Plicigastra* Uvarov, 1940, not studied and classified by Rentz & Colless (1990), is placed in Platycleidini by Otte (1997).

The definition of a group by a list based on the general similarity of the species included is certainly not a scientifically satisfying nor even a satisfactory solution, but it seems to us better than any other available at the moment. We have to wait until genetics can add a new dataset for phylogenetic analyses.

Acknowledgements

We would like to thank all members of our excursion to Turkey in 1983 (Peter Flache, Matthias Hennig, Otto von Helversen, Helmut Kriegbaum, Alois Liegl, Hermann Rübbelke, Jens Sachteleben, Marianne Volleth). In addition, our thanks go to Masha Sergeeva for her help with the translation, to Judith Marshall (NHM) for the loan of a paratype of *Delodusa humeralis* in 1999, to the staff of ZMB, to Michael Sergeev, Novosibirsk, for information about Drymadusini, and to Battal Çiplak for his comments on an earlier version of the manuscript.

References

Bey-Bienko G.Ya. 1951. Studies on long-horned grasshoppers of the USSR and adjacent countries (Orthoptera, Tettigoniidae). Trudy Vsesojuznogo Entomologicheskogo Obshchestva, Moskva, Leningrad [= Horae Societatis Entomologicae Unionis Soveticae] 43: 129-170 [Russian].

Brunner von Wattenwyl C. 1893. Révision du système des orthoptères et description des espèces rapportées par M. Leonardo Fea de Birmanie. Annali del Museo Civico di Storia Naturale 'Giacomo Doria', Genova 33: 1-230, pls 1-6.

Capinera J.L., Scott R.D., Walker T.J. 2004. Field Guide to Grasshoppers, Katydids, and Crickets of the United States. Cornell University Press. 1-246.

Çiplak B., Heller K.-G. 2001. Notes on the song of *Bolua turkiyae* and on the phylogeny of the genus *Bolua* (Orthoptera, Tettigoniidae, Tettigoniinae). Israel Journal of Zoology 47: 233-242.

Fig. 6. Distribution of *Lithodusa* species.

Çiplak B., Heller K.-G., Demirsoy A. 2002. Review and key to species of *Platycleis* from Turkey (Orthoptera: Tettigoniidae) with descriptions of *Yalvaciana* subgen. n. and two new species. Journal of Natural History 36: 197-236.

Çiplak B., Heller K.-G. 2005. Review of the south-west Asian genus *Scotodrymadusa* (Orthoptera, Tettigoniidae): systematics, phylogeny and biogeography of an eremial lineage. Insect Systematics and Evolution 36: 317-342.

Chernyakhovsky M.E., Litvinova N.F., Guseva V.S., Vorontsova L.I. 1994. Orthopteroidea of the west coast of the Caspian sea (Daghestan). Entomological Review 73: 112-120 [English translation in Zool. Zh. 73 (1994): 61-67].

Demirsoy A., Salman S., Sevgili H. 2002. *Novadrymadusa*, a new genus of bushcricket with a new species and notes on related genera (Orthoptera: Tettigoniidae). Journal of Orthoptera Research 11: 175-183.

Elsner N. 1974. Neuroethology of sound production in Gomphocerine grasshoppers (Orthoptera: Acrididae). I. Song patterns and stridulatory movements. Journal of Comparative Physiology 88: 67-102.

Heller K.-G. 1988. Bioakustik der Europäischen Laubheuschrecken. 1-358; Weikersheim (Verlag Josef Margraf).

Heller K.-G. 1990. Evolution of song pattern in east Mediterranean Phaneropterinae: constraints by the communication system, pp. 130-151. In: Bailey W.J., Rentz D.C.F. (Eds) The Tettigoniidae: Biology, Systematics and Evolution. Bathurst (Crawford House Press) & Berlin *et al.* (Springer).

Heller K.-G. 2006. Song evolution and speciation in bushcrickets. Pages 137–151. In: Drosopoulos Sakis, Claridge Michael F. [Eds]. Insect sounds and communication: physiology, behaviour, ecology and evolution. [Contemporary Topics in Entomology.] i –xvii, 1–532; London & New York [Taylor & Francis, Boca Raton]

Heller K.G., Korsunovskaya O.S., Sevgili H., Zhantiev, R.D. 2006. Bioacoustics and systematics of the *Poecilimon heroicus*-group (Orthoptera: Phaneropteridae: Barbitistinae). European Journal of Entomology 103: 853-865.

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.

Ingrisch S. 1996. Orthopteroide Insekten aus Nord-Pakistan. Ergebnisse der Forschungsreise von H. Hacker und L. Weigert im Herbst 1988. Esperiana 4: 231-244.

Karabag T. 1961. Revision of *Drymadusa* Stein and related genera (Orthoptera: Tettigoniidae). Bulletin British Museum (Natural History), Entomology Series 11: 1-41.

Korsunovskaya O.S., Zhantiev R.D., Savitsky V. Yu. 2002. The songs of the Palaearctic bush crickets of the tribe Drymadusini (Orthoptera: Tettigoniidae). Russian Entomological Journal 11: 335-350.

Mirzayans H. 1991. Three new genera and four new species of Orthoptera from Iran. Journal of Entomological Society of Iran Suppl. 6: 1-26.

OSF. 2006. = Eades D.C. D., Otte D. 2006. *Orthoptera Species File Online*. [2006/05/12]. <http://Orthoptera.SpeciesFile.org>.

Otte D. 1997. Orthoptera Species File 7. Tettigonioidea. 1-373. Philadelphia (Orthopterists' Society Academy of Natural Sciences of Philadelphia).

Naskrecki P., Otte D. 1999. An illustrated catalog of Orthoptera Vol. I. Tettigonioidea (Katydids or bush-crickets). CD-Rom published by the Orthopterists' Society at the Academy of Natural Sciences of Philadelphia.

Ramme W. 1939. Beiträge zur Kenntnis der palaearktischen Orthopterenfauna (Tettig. et Acrid.). III. Mitteilungen aus dem Zoologischen Museum, Berlin 24: 41-149, pls 2-3.

Rentz D.C.F. 1973. The shield–backed katydids of the genus *Idiostatus*. Memoirs American Entomological Society 29: 1-211.

Rentz D.C.F., Colless D.H. 1990. A classification of the shield-backed katydids (Tettigoniinae) of the world, pp. 352-377. In: Bailey W.J., Rentz D.C.F. (Eds). The Tettigoniidae: Biology, Systematics and Evolution. Bathurst (Crawford House Press) & Berlin *et al.* (Springer).

Sergeev M.G. 1986. Features of the distribution of Orthoptera in northern Asia. 1-236; Novosibirsk (Nauka Publ.) [Russian].

Sergeev M.G. 1993. The general distribution of Orthoptera in the main zoogeographical regions of North and Central Asia. Acta Zoologica Cracoviensia 36: 53-76.

Sergeev M.G. 1995. The general distribution of Orthoptera in the eastern parts of the Saharan-Gobian and Scythian subregions. Acta Zoologica Cracoviensia 38: 213-256.

Sergeev M.G. 1998. Patterns of distribution of phytophagous insects in grass ecosystems of the Holarctic. Izvestiya Akademii Nauk Seriya Biologicheskaya (Moscow) 4: 445-450 [Russian].

Sevgili H., Heller K.-G. 2003. A new species of the genus *Isophya* Brunner von Wattenwyl from Turkey (Orthoptera, Tettigoniidae, Phaneropterinae). Tijdschrift voor Entomologie 146: 39-44.

Stolyarov M.V. 1994. A revision of the genus *Phytodrymadusa* (Orthoptera, Tettigoniidae) with description of three new genera of the tribe Drymadusini from the Caucasus and adjoining areas. Vestnik Zoologii 2: 3-11; Kiev [Russian, English summary].

Storozhenko S.Yu. 1986. Orthopteroid Insects. 1-30, 161-172, 234-323, 431-451. In: Ler P.A. (Ed.). Keys to the insects of the Soviet Far East I. Leningrad (Nauka) [Russian].

Storozhenko S.Yu. 1994. Revision of the tribe Onconotini with a description of a new tribe (Orthoptera, Tettigoniidae, Tettigoniinae). Journal of Orthoptera Research 2: 65-68.

Storozhenko S.Yu. 2004. Long-horned orthopterans (Orthoptera: Ensifera) of the Asiatic part of Russia. 1-280; Dalnauka, Vladivostok [Russian].

Storozhenko S Yu., Paik, J Ch. 2007 Orthoptera of Korea. Dalnauka, Vladivostok. 1-231.

Ünal M. 1999. Notes on Orthoptera of Western Turkey, with description of a new genus and four new species. Journal of Orthoptera Research 8: 243-255.

Ünal M. 2006. Tettigoniidae (Orthoptera) from Turkey and the Middle East. Transactions American Entomological Society 132: 157-203.

Uvarov B.P. 1910. Material zur Orthoptera Fauna des Uralsk Gebietes. Trudy Russkago Entomologicheskago Obshchestva. [= Horae Societatis Entomologicae Rossicae] 39: 359-390; St. Petersburg [Russian with descriptions of new species in Latin].

Uvarov B.P. 1924. Notes on the Orthoptera in the British Museum. 3. Some less known or new genera and species of the subfamilies Tettigoniinae and Decticinae. Transactions of the Royal Entomological Society of London 1923: 492–537, pl. 28.

Uvarov B.P. 1926. Some Orthoptera from Central Asia. Russkoe Entomologiceskoe Obozrenie [= Revue Russe d' Entomologie] 20: 161-164.

Uvarov B.P. 1928. Orthoptera Palaearctica critica VI. Genus *Bergiola* Stschelk. (Tettig.). Eos. Revista Española de Entomologia 4: 243–251.

Uvarov B.P. 1942. New and less known southern Palaearctic Orthoptera. Transactions American Entomological Society 67 [1941]: 303–361, pls 25-29.

Warchalowska-Sliwa E., Bugrov A.G. 1996. Karyotype evolution of Drymadusini (Decticinae, Orthoptera). Cytologia (Tokyo) 61: 33-39.