

Re-evaluation of the genus *Phonochorion* (Orthoptera: Tettigoniidae: Phaneropterinae)

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Abstract. *Phonochorion* Uvarov (Orthoptera: Tettigoniidae: Phaneropterinae) is a little known genus consisting of three species: *Ph. satunini*, *Ph. artvinensis* and *Ph. uvarovi*. The objective of this study is to conduct a thorough distributional, taxonomic and systematic revision of the genus *Phonochorion* using both bioacoustic and external morphological characters. Field surveys indicate that the genus is distributed from the Trabzon region of Turkey to the Khulo province of Georgia however the exact limit of the eastern distribution of the genus remains unknown. *Phonochorion* species occur only on the northern slopes of the East Black Sea and Lesser Caucasus Mountains. The Coruh Valley, which separates the East Black Sea and Lesser Caucasus Mountain ranges, seems to be an effective physical and climatic barrier and determines the distribution of these species. *Ph. uvarovi* can clearly be distinguished from *Ph. satunini* and *Ph. artvinensis* by the calling songs of males and external morphological characters. *Ph. artvinensis* and *Ph. satunini* differ in several taxonomic characters but the males have virtually identical calling songs. From a character evolution perspective, although geographically more distant, *Ph. satunini* is more closely related to *Ph. uvarovi* than *Ph. artvinensis*. Morphological similarities in several characters indicate *Phonochorion* to be most closely related to *Polysarcus zacharovi* and the *Poecilimon heroicus*-group. Within the genus *Phonochorion*, song structure and morphological characters clearly indicate *Ph. uvarovi* to be the basal taxon.

INTRODUCTION

The genus *Phonochorion* (Orthoptera: Tettigoniidae: Phaneropterinae) is a little known group endemic to the East Black Sea and Lesser Caucasus mountains in North East Turkey and Western Georgia (Fig. 1). Only three species are described for this genus: *Ph. satunini* Uvarov, 1916 (type specimen), *Ph. artvinensis* Bei-Bienko, 1954 and *Ph. uvarovi* Karabağ, 1956. The first papers on this genus give little more than simple taxonomic descriptions and contain very little information on the biology of the species. In addition, the information on the distribution and range of the genus is poor as there are only a few locality records. Below is a brief summary based on information in the literature.

Apart from its type locality (SW, Jugum Adzaricum 1959 m, 16.viii.1902) there are no other records of *Ph. satunini* for Georgia, however Karabağ (1956), Heller (1990) and later Ünal (2005) record the same species from Turkey (İkizdere-Rize and Yusufeli-Artvin). *Ph. uvarovi* was initially recorded from İkizdere-Rize by Karabağ (1956) and later by Heller (1990) from the same locality. Therefore, current data would seem to suggest that *Ph. satunini* is distributed from Georgia to the İkizdere region of Turkey, where it occurs sympatrically with *Ph. uvarovi*. The third species of the genus, *Ph. artvinensis*, has only been recorded once in the Yalnızçam

Mountains of Turkey in the 1950s by Bei-Bienko (1954). Currently there are no other records of this species. Recently Salman (1978) failed to find this species at both the original locality in the Yalnızçam Mountains and the Artvin province of Turkey.

Karabağ (1956) revised this genus but did not examine any specimens of *Ph. artvinensis* or provide a taxonomic key. The calling songs of *Ph. satunini* and *Ph. uvarovi* were briefly described by Heller (1990), however taxonomic problems within the genus were not evaluated. Therefore, apart from the initial taxonomic descriptions and few distributional records there is no comprehensive systematic or biogeographic study of this group. In addition, the initial taxonomic description of *Ph. artvinensis* is both short and inadequate and there is very little and inadequate data on the distributions of all three species.

The objective of this study is to conduct a thorough revision of the taxonomy, systematics and distribution of the genus *Phonochorion* in order to clarify the taxonomic status and distribution of each of the species. For these reasons, specimens were collected in the field from the Trabzon province in Turkey to the Khulo province in Georgia. This paper presents results on the total range of the genus, geographic distribution of individual species and species delimitation based on calling songs and external morphological characters.

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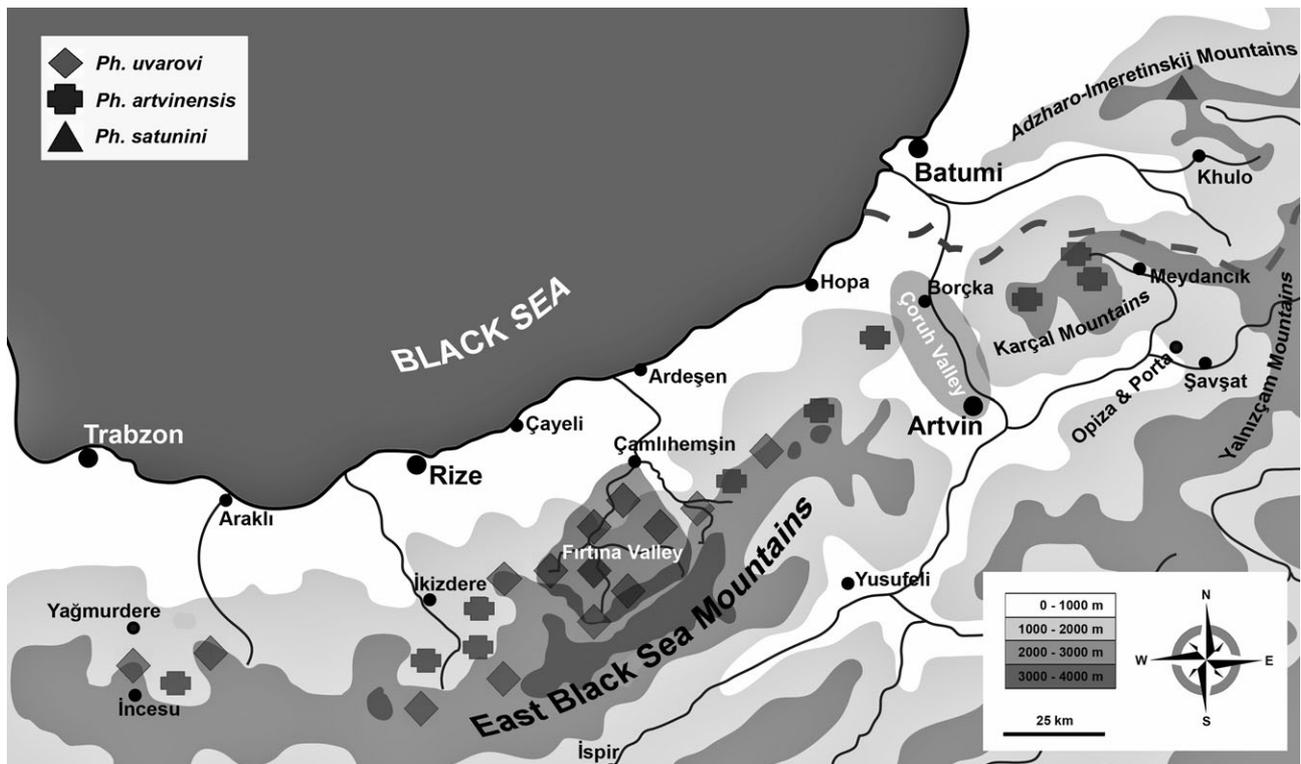


Fig. 1. Distribution of the species of the genus *Phonochorion*.

MATERIAL AND METHODS

Field studies

Field surveys were undertaken in the years 2003–2008, during the months of June, July and August, which are the months when these species are active. The total area sampled was 23,342 km² and included parts of the Trabzon, Rize and Artvin provinces of Turkey and the Khulo province of Georgia. In order to determine the presence or absence of species belonging to this genus, approximately 300 patches of characteristic habitat for this genus were visited in the study area. The presence of *Phonochorion* spp. was determined by listening for their characteristic calling songs and finding adults and nymphs. When no specimens were observed and no calling songs heard, the localities were rechecked the following year in order to prevent any bias that might arise due to seasonal changes in population abundance.

Depositories of the material collected are abbreviated as follows: CH – Collector Heller, Magdeburg; CHS – Collector Hasan Sevgili, Şanlıurfa; HUZOM – Hacettepe University, Zoology Museum, Ankara; CIKS – Collector İsmail K. Sağlam, ESRL – Hacettepe University Ecological Sciences Research Laboratories, Ankara; CSSC – Collector Selim S. Çağlar, ESRL – Hacettepe University Ecological Sciences Research Laboratories, Ankara; ZIN – Zoological Institute, Russian Academy of Sciences, St. Petersburg (type specimens of *Ph. satunini* and *Ph. artvinensis*).

Species delimitation: Taxonomic key and song analysis

Species were delimited using both morphological characters and recordings of males stridulating. A key to species is presented based on external morphological characters, which are illustrated in Figs 2–10. All characters were studied under a Leica MZ-7.5 stereoscopic zoom dissection microscope and photographed using a DC-300 digital camera system attached to the microscope.

Sounds were recorded in the field using a portable stereo audio recorder (TASCAM HD P2) fitted with a bat detector (TD 15-2 with HF-output via Mini-XLR, Laartech) or a M Audio Transit (mobile 24-bit/96kHz USB audio upgrade) and microphone (kondensator ansteckmicrophone, 30–30000 Hz, distance to microphone about 10–20 cm) attached to a notebook computer. Sounds were digitized at a sampling rate of 96 KHz and 24 bit resolution with Adobe Audition and Spectraplus software.

Oscillograms were generated using the above software after filtering out background noise. The following qualitative and quantitative parameters were analyzed: duration of the calling song, micro and macro syllable duration, syllable period, syllable group duration (echeme), number of syllables in each group, number of impulses in each syllable and amplitude modulation of syllables. Analyses were carried on a total of 32 calls recorded from 10 different populations of each of the three species. Terminology used in song descriptions are as follows (Ragge & Reynolds, 1998); *Calling song*: song produced by an isolated male; *Syllable*: the sound produced by one complete up (opening) and down (closing) stroke of the wing; *Syllable period*: time between the start of two consecutive syllables; *Echeme*: a first-order assemblage of syllables; *Impulse*: a simple, undivided, transient train of sound waves.

RESULTS

Genus: *Phonochorion* Uvarov, 1916

References. *Phonochorion* Uvarov: Uvarov (1916): 48; Tarbinskii (1940): 66; Bei-Bienko (1954): 363; Karabağ (1956): 49; Karabağ (1958): 89.

Type species. *Phonochorion satunini*.

Defining features

In males the pronotum distinctly rises vertically and the metazona widens anteriorly; in males the tegmina are well developed and highly chitinized; males have distinct and

TABLE 1. Diagnostic characters of *Phonochorion* species.

Characters	Description	<i>Ph. uvarovi</i>	<i>Ph. satunini</i>	<i>Ph. artvinensis</i>	
				East of ÇV*	West of ÇV*
Male overall colour	Black yellow	Yes	No (Black red-lilac)	No (Black red-lilac)	No (Black red-lilac)
Pronotum	With distinct tubercles on the sides	Yes	No	No	No
Female tegmen	Tegmina protrudes from under pronotum	No	No	Yes	Yes
Metanotal gland	folded into an inverted v shaped	Yes	No (curly bracket shaped)	No (curly bracket shaped)	No (curly bracket shaped)
Male subgenital plate	Colour light yellow	Yes	No (red-lilac)	No (red-lilac)	No (red-lilac)
	Neck stretches parallel towards apex	Yes	No (narrows down towards apex)	No (narrows down towards apex)	No (narrows down towards apex)
	neck length (mm)	1.60–3.00	2.00–2.70	2.10–3.00	3.00–4.30
	width/length (mm)	3.80–5.40/5.10–8.10	3.70–4.40/5.20–6.20	4.10–5.00/6.00–7.40	4.30–5.50/6.20–8.70
Female subgenital plate	acute projection on anterior end	Yes	Yes	No (blunt)	No (blunt)
	width/length (mm)	0.40–0.75/2.80–4.00	0.50–0.65/2.35–3.45	0.50–0.85/2.80–3.80	0.40–0.75/2.60–4.00
Fastigium	dorsal cavity deep, stretches to the tip	Yes	Yes	No (shallow, situated at base)	No (shallow, situated at base)
Width/Length of cerci (mm)	Male	0.60–0.90/2.90–3.50	0.70–0.80/2.85–3.00	0.80–1.00/3.40–3.80	0.80–1.10/3.50–4.45
	Female	0.40–0.60/1.75–2.50	0.41–0.57/1.55–1.86	0.43–0.56/1.84–2.15	0.38–0.56/2.10–2.60
Length of ovipositor (mm)		8.50–13.40	8.30–9.80	9.20–11.60	10.20–15.30
Length of pronotum (mm)	Male	3.75–5.00	3.90–4.60	3.90–4.90	3.90–5.50
	Female	5.00–7.10	5.60–6.85	5.00–6.00	5.30–7.00
Length of hind femur (mm)	Male	16.00–20.10	15.10–17.00	16.40–19.30	17.80–21.50
	Female	16.80–20.20	17.00–17.90	17.50–19.90	17.20–23.60

*ÇV = Çoruh Valley

large dorsal glands on the first tergum; in males the subgenital plate is long and curls vertically upwards; in both sexes there is a dorsal cavity on the fastigium; in males the coloration is aposematic.

Distribution and habitat characteristics

Results of the field surveys indicate that the genus is distributed from the Yağmurdere in the Gümüşhane province of Turkey to the Djvari Mindori plateau in the Khulo province of Georgia. The distributional range of the genus and species distributions are depicted in Fig. 1. Within this range species are found only on the northern slopes of the East Black Sea and Lesser Caucasus Mountains associated with local stands of various herbaceous plants and shrubs (mostly *Urtica dioica*, *Sambucus nigra* and *Rumex tuberosum*) and pasture vegetation forming discrete local populations in areas with a rainy, humid and cold climate. From the Yağmurdere to the Firtina Valley species are patchily distributed between 1400–2600 m. However, in the Firtina Valley species can be found in every suitable habitat patch (from shrubs to meadows) nearly forming a continuous population from 1000 to 2600 m. From east of the Firtina Valley to Georgia, populations of *Phonochorion* species occur locally in discrete patches usually at altitudes above 1800 m and exclusively on *Rumex tuberosum*.

The evaluation of the distribution of individual species indicates that the ranges of *Ph. uvarovi* and *Ph. artvinensis* overlap from Yağmurdere to Ardeşen in Rize (Fig. 1). The distributional range of *Ph. uvarovi* ends at Ardeşen, but that of *Ph. artvinensis* extends all the way to Meydancık in Artvin, near the Georgian border. Where the ranges of *Ph. uvarovi* and *Ph. artvinensis* overlap their populations do not mix as *Ph. uvarovi* is found mainly in habitats at high altitudes (1800–2500 m), whereas *Ph. artvinensis* occurs mainly at low altitudes (1200–1800 m). The distribution of *Ph. satunini* seems to be limited to the Khulo province of Georgia and does not extend into Turkey (Fig. 1). However the eastern limit of the distribution of this species is unknown.

Species delimitation

Diagnostic characters used for delimiting *Phonochorion* spp. are given in Table 1 along with linear measurements of external morphological characters. Below song characteristics and defining features of each species are described in detail.

Phonochorion uvarovi Karabağ, 1956

References. Karabağ (1956): 52 (description); Karabağ (1958): 89 (faunistic Catalogue); Çıplak et al. (2002): 684 (checklist, distribution); Ünal (2005): 442 (distribution); Heller (1990): 138, 144 (song).

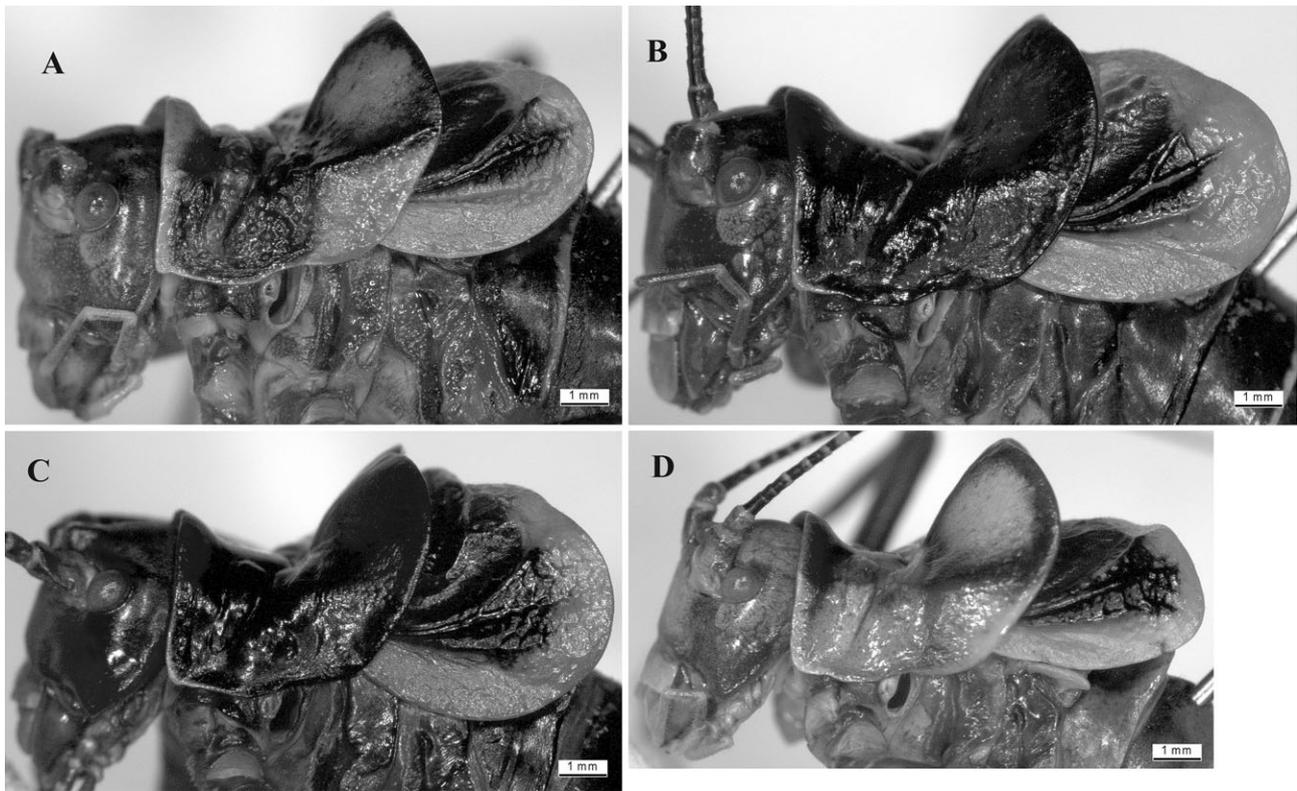


Fig. 2. Lateral view of male pronotum. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

Type locality. Turkey, Rize province, distr. İkizdere, Tatos dag: above Cimil, 2500 m, 27.viii.1952.

Type depository. Holotype, ♂ (BMNH).

Databanks. Orthoptera Species File (OSF)

Previous records. Rize province, distr. İkizdere, Tatos dag., above Cimil, 2500 m, 27.viii.1952, 3♂ (including type), 2♀; Pazar below as-Hemşin, 2000 m (in dry meadows and pasture), 02.ix.1952, 3♂, 3♀ (coll. P.H. Davis) Karabağ, 1956; Tatos dagları, Pasakoy, Demirtepe, 2500 m, 31.viii.1956, 18♂, 16♀ (coll. T. Karabağ) Karabağ, 1958; Gümüşhane: Soganli Gecidi, 7–7500 ft, 25.vii.1960, 16♂ (det. P.M. Stock); 6000 ft, 25.vii.1960, 3♂ (coll. K.M. Guichard and D.H. Harvey, det. M. Ünal) Ünal, 2005; Rize, pass south of İkizdere, 04.viii.1983.

Song. Heller (1990): 138, 144.

Material examined. Turkey: Rize: Çat Düzü, 13.vii.1991, 15♂, 27♀ (coll. A. Demirsoy); Çamlıhemşin, Çat Düzü, 09.vii.1990, 6♂, 6♀ (coll. S.S. Çağlar, 1♀ collected by A. Demirsoy); Çamlıhemşin, Çat Köyü, Vanksi yaylası, 09.vii.1990, 6♂, 1♀ (coll. A. Demirsoy & S.S. Çağlar); Çamlıhemşin, Verçenik, Atmeydanı gölü, 09.vii.1990, 4♂ (coll. A. Demirsoy & S.S. Çağlar); Vanksi Yaylası, 2150 m, 6♂ (A. Demirsoy); Çamlıhemşin, Çiçekli Yaylası, 1950 m, 25.viii.1983, 2♂ (coll. A. Demirsoy); Çamlıhemşin, Hemşin-Ortaköy, 09.vii.1990, 4♂, 2♀ (coll. S.S. Çağlar, 1♂ collected by A. Demirsoy); Kale-Hemşin yolu, 10.vii.1991, 20♂, 6♀ (coll. A. Demirsoy); Çamlıhemşin, Elevit Yaylası, 2400 m, 17.vii.1991, 3♂, 1♀ (coll. A. Demirsoy); Çamlıhemşin, Meydan Köyü, 1100 m, 18.vii.1991, 1♂ (coll. A. Demirsoy); Çamlıhemşin, Çat-Elevit yolu, 09.vii.1990, 47♂, 10♀ (coll. S.S. Çağlar & A. Demirsoy); Çamlıhemşin, Çat, 20.vii.1989, 42♂, 32♀ (coll. A. Demirsoy); Çamlıhemşin, 20.vii.1989, 1♀ (coll. A. Demirsoy); 1920 m, 40°40'14.1"N, 40°42'63.2"E, 27.vii.2002, 10♂, 2♀ (coll. H. Sevgili); Çamlıhemşin, Elevit,

Subalpine zone, 1890 m, 40°51'28.3"N, 41°00'77.0"E, 24.vii.2002, 8♂ (coll. H. Sevgili); Çamlıhemşin, Meydan Köyü Altı, 900 m, 40°54'38.2"N, 40°56'92.9"E, 23.vii.2002, 7♂ (coll. H. Sevgili); İkizdere, Ovit Dağı, Sivrikaya, İkizdere, Cimil, Başköy, 1800–2000 m, 29.–30.viii.1956, 1♂ (coll. T. Karabağ); İkizdere, Cimil, 2000 m, 29.viii.1956, 1♂ (coll. T. Karabağ); İkizdere, Cimil, Demirkoy, 2500 m, 31.viii.1956, 1♂ (coll. T. Karabağ) (These specimens are deposited in HUZOM). İkizdere, Çağrankaya Yaylası, 19.vii.2007, 1♂ (in alcohol) (coll. H. Sevgili); İkizdere, Anzer Plateo, 2154 m, 40°35'29.6"N, 40°31'02.5"E, 20♂, 6♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); İkizdere, Ovit Pass, 1857 m, 40°40'36.9"N, 40°42'30.9"E, 20♂, 8♀, (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Cayeli, Çağrankaya Plateo, 2226 m, 40°49'34.6"N, 40°38'47.3"E, 01.viii.2008, 20♂, 11♀ (in alcohol) (coll. İ.K. Sağlam); Çamlıhemşin, Demirkapi Village, 1024 m, 40°53'41.8"N, 40°56'23.1"E, 07.viii.2004, 9♂, 1♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Çamlıhemşin, Çat Duzlugu, 1228 m, 40°52'18.2"N, 40°55'34.1"E, 17.vii.2006, 20♂, 10♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Çamlıhemşin, Kale Village, 1811 m, 40°49'04.3"N, 40°56'40.9"E, 16.vii.2006, 20♂, 11♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Çamlıhemşin, Çiçekli Plateo, 2285 m, 40°47'29.5"N, 40°57'26.6"E, 04.viii.2006, 20♂, 14♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Çamlıhemşin, Amlakit Plateo, 2461 m, 40°52'02.8"N, 41°04'58.3"E, 12.viii.2006, 20♂, 6♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Çamlıhemşin, Aşağı Kavron Plateo, 1982 m, 40°54'26.9"N, 41°08'20.8"E, 18.vii.2006, 20♂, 6♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Ardeşen, Sirt Plateo, 2346 m, 41°02'51.4"N, 41°13'17.6"E, 11.viii.2007, 18♂, 10♀ (in alcohol) (coll. İ.K. Sağlam), these specimens are deposited in ESRL. Gümüşhane: Yağmurdere Village, 1774 m, 40°35'20.3"N, 39°52'25.3"E, 31.vii.2007, 9♂, 3♀ (in alcohol) (coll. İ.K. Sağlam, H. Sevgili, S. S. Çağlar), these specimens are

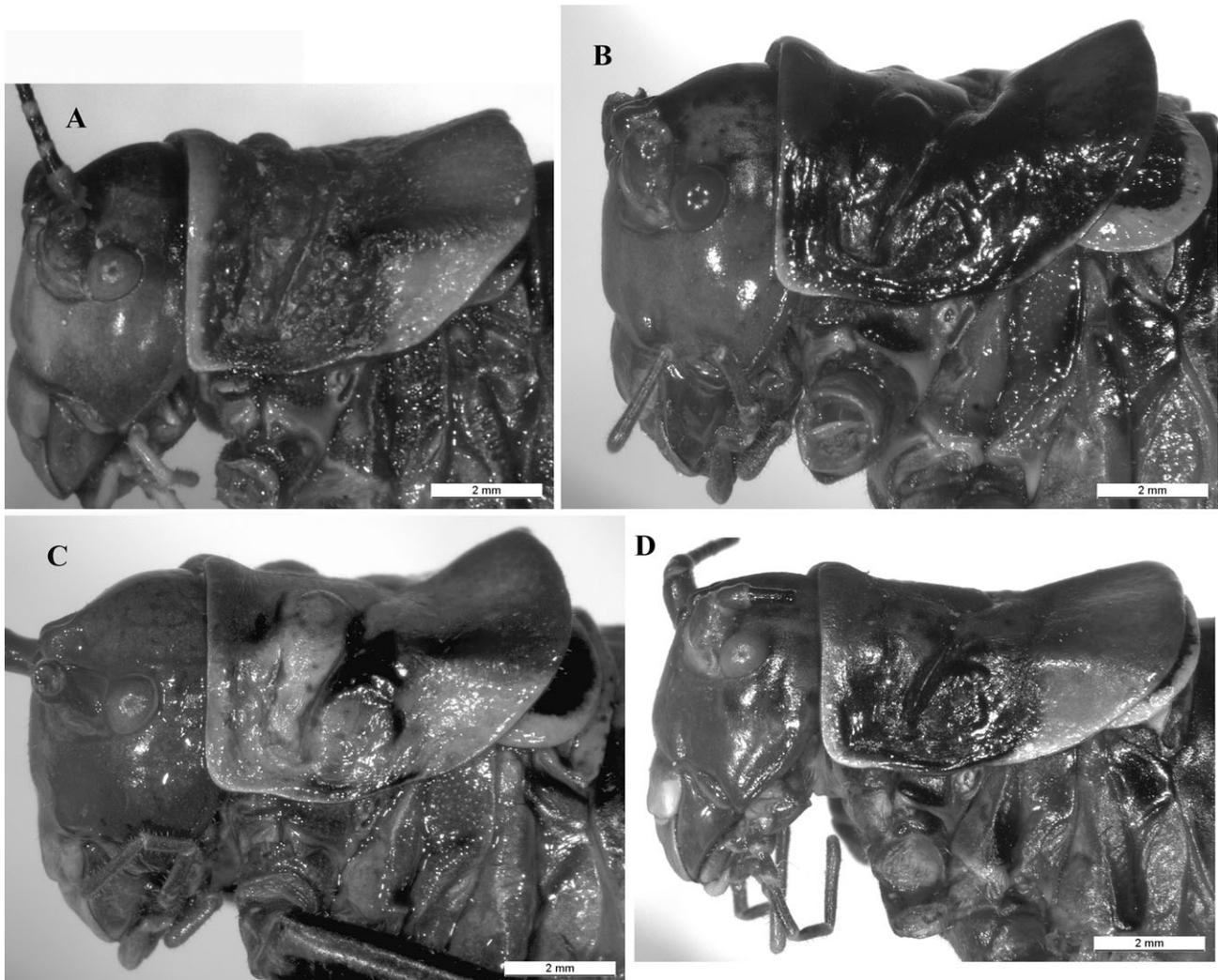


Fig. 3. Lateral view of female pronotum. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

deposited in ESRL. Trabzon: Araklı, Boğalı Village, 2139 m, 40°36'52.6"N, 40°02'08.4"E, 17.vii.2007, 2♂, 10♀ (in alcohol) (coll. İ.K. Sağlam, H. Sevgili), these specimens are deposited in ESRL.

Specimens used for sound recordings. Trabzon: Araklı, Boğalı Köyü, 2060 m, 17.vii.2007, 2♂ (in alcohol) (no. 6107-10, 6107-8); Rize: Ardeşen, Sırt Yaylası (Taprike), 2200 m, 09.viii.2007, 4♂ (in alcohol) (No. 5307-91, 5307-89, 5307-92, 5307-88); Çamlıhemşin, Çat Düzü, 15.vii.2008, 2♂ (in alcohol) (no. 5307-03, 5307-1); İkizdere, Anzer Yaylası, 20.vii.2007, 1♂ (in alcohol) (no. 5307-55); Gümüşhane: Yağmurdere, Bolahor, 31.vii.2007, 1♂ (in alcohol) (no. 2907-07); Yağmurdere arkası, 1774 m, 31.vii.2007, 1♂ (no. 2907-8) (coll. H. Sevgili).

Defining features. In both sexes there are distinct tubercles on the sides of the pronotum (especially on the mesozone) (Figs 2A and 3A); when the first tergum is viewed from above the metanotal glands are on either side of a distinct fold that rises upwards forming an inverted “v” shape (Fig. 4A); in males the subgenital plate is yellow, acutely narrows in the middle and neck stretches parallel towards apex (Fig. 5A); in females there is a clear protrusion at the anterior end of the subgenital

plate (Fig. 6A); body coloring mainly consists of black-yellow patterns.

Song. Songs were recorded at night at various temperatures (22, 25, 27 and 35°C). However the species is also bioacoustically active during the day. Sounds produced by males of *Ph. uvarovi* consist of orderly permutations of a single powerful crescendo type syllable (Fig. 11A–C). Duration of the crescendo type syllables produced by males is variable with a mean of 0.353 ms ± 0.133 SD (n = 83, min–max. 0.076–0.639 ms) and are repeated at 1.021 ms ± 0.442 SD (n = 81, min–max: 0.426–2.925 ms). On average the syllables consist of 111 impulses (n = 83, min–max. 33–172). Some individuals produce syllables that are a crescendo from start to finish, while in those produced by others only the last 16–68 (n = 46, mean 35.21 ± 14 SD) impulses are powerful crescendos.

Phonochorion satunini Uvarov, 1916

References. Uvarov (1916): 48–49 (description); Kartsivadze (1949): 144 (distribution); Bey-Bienko (1954): 364 (key), 365–366 (re-description).

Type locality. Georgia, Southwestern Georgia, Adzhar Range.

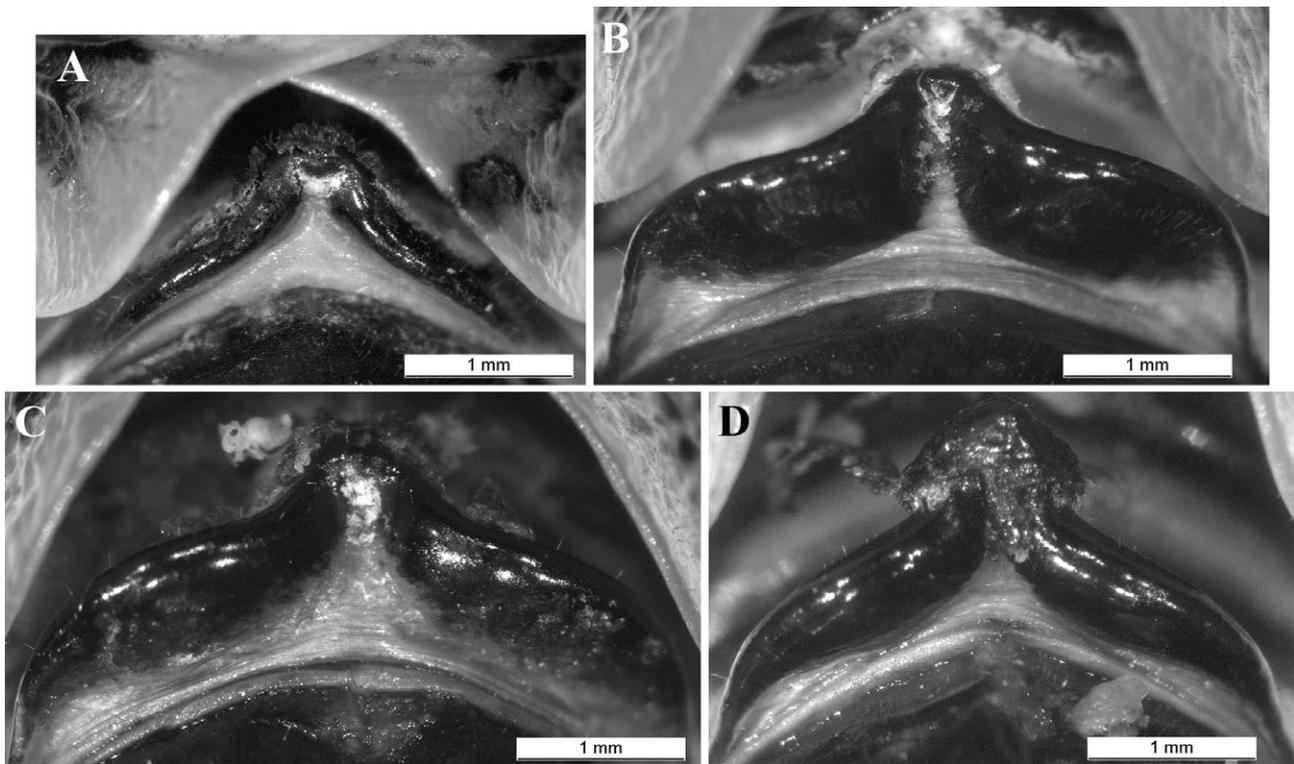


Fig. 4. Male metanotal gland. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

Type depository. ♂ (ZIN).

Previous records. Georgia: Jugum Adzaricum, 6430 feet, 16.viii.1902 (♂, coll. K.A. Satunin) Uvarov, 1916; South-western Georgia: Bakhmaro, mountains of Guria, 08.ix.1920, 1♂ (coll. A. Grossgeim); Bodishi, northern slopes of the Adzhar Range, altitude 1830 m, 07.viii.1939, in brush, 6♂ and ♀ (H. Kartsivadze); Adzhar Range, altitude 1950 m, 29.viii.1902, 1♂ (type) (coll. K. Satunin) Bei-Bienko, 1954.

Material examined. Georgia: Khulo, Gomista, Djvari Mindori Plateo, 2191 m, 41°45'31.6"N, 42°11'46.2"E, 09.viii.2007, 18♂, 11♀ (in alcohol) (coll. İ.K. Sağlam), these specimens are deposited in ESRL.

Specimens used for sound recordings. Khulo, Gomista, Djvari Mindori, 08.viii.2007, 2200 m, 5♂ (in alcohol) (no. ses-1, ses-2, ses-3, ses-4, ses-5) (coll. İ.K. Sağlam).

Defining features. Body size is relatively small; when the first tergum of the male is viewed from above the fold between the metanotal glands rises upwards forming a curled bracket or brace shape (Fig. 4D); in males the subgenital plate is red-lilac, and narrows gradually in the middle and neck narrows down towards apex (Fig. 5D); body coloring of males consists mainly of a pattern of black and lilac.

Song. Songs were recorded at high temperatures (35°C). Song consists of major (first group) and minor (second group) syllables (Fig. 12A–B). Mean duration of the first group is $9.63 \text{ s} \pm 3.24 \text{ SD}$, ($n = 49$) and is made up of powerful crescendo type major syllables (Fig. 12C–D). Number of major syllables in the first group ranges from 7–23. Mean duration and period of major syllables are $0.375 \text{ s} \pm 0.082$ and $1.050 \text{ s} \pm 0.114 \text{ SD}$, respectively. Number of impulses within major syllables

ranges from 102–153 (mean: 135, $n = 18$). Mean duration of the second group is $5.33 \pm 1.62 \text{ SD}$ ($n = 16$) and consists of minor syllables. Number of minor syllables in the second group ranges from 7–23, and 3–6 minor syllables are produced per second. Mean duration and period of minor syllables are $0.114 \text{ s} \pm 0.027$ and $0.367 \text{ s} \pm 0.030 \text{ SD}$ ($n = 35$), respectively.

Phonochorion artvinensis Bei-Bienko, 1954

References. *Ph. artvinensis*: Bei-Bienko (1954): 364 (key), 366–367 (description); Karabağ (1956): 49 (distribution); *Ph. satunini* nec Uvarov, 1916 (♂ from Yanlizçam, Artvin); Karabağ (1958): 89 (faunistic catalogue); Salman (1978): 20 (local catalogue); Çıplak et al. (2002): 684 (checklist, distribution: records from Rize province given as *Ph. satunini*); Ünal (2005): 442 (distribution: given as *Ph. satunini*); Heller (1990): 138, 144 (song, distribution: given as *Ph. satunini*).

Type locality. Turkey, Northeastern Turkey, Artvin (Opiza and Porta Monasteries).

Type depository. ♂ (Natural History Museum, St. Petersburg)

Previous records: As *Ph. artvinensis*: Artvin: Çoruh, Opiza-Porta, 2.viii.1909, 6♂ (including type), 2♀ (coll. P. Nesterov); 1.viii.1909, 1♀ (P. Nesterov) Bei-Bienko, 1954; Yanlizçam, ♂, Uvarov, 1916.

As *Ph. satunini* (misidentification): Rize: İkizdere, Tatos dağları (nr. Başköy), 2200 m, 28.viii.1952, 5♂, 5♀; Tatos dağları (above Cimil), 2500 m, 27.viii.1952, 1♀; Tatos dağları (at Yetimhoca), 2100 m, 27.viii.1952, 3♀ (coll. P.H. Davis) Karabağ, 1956; İkizdere, Cimil, Başköy, 2000 m, 30.viii.1956, 26♂, 30♀ (coll. T. Karabağ) Karabağ, 1958; 85 km South of Rize, Sivrikaya, 19.–25.viii.1959, 4♂, 13♀ (coll. K.M. Guichard, det. P.M. Stock); Artvin: Yusufeli, Olgunlar Köyü, 2200 m, 10.vii.2004, 1♂ (coll. N. İkinci) Ünal, 2005.

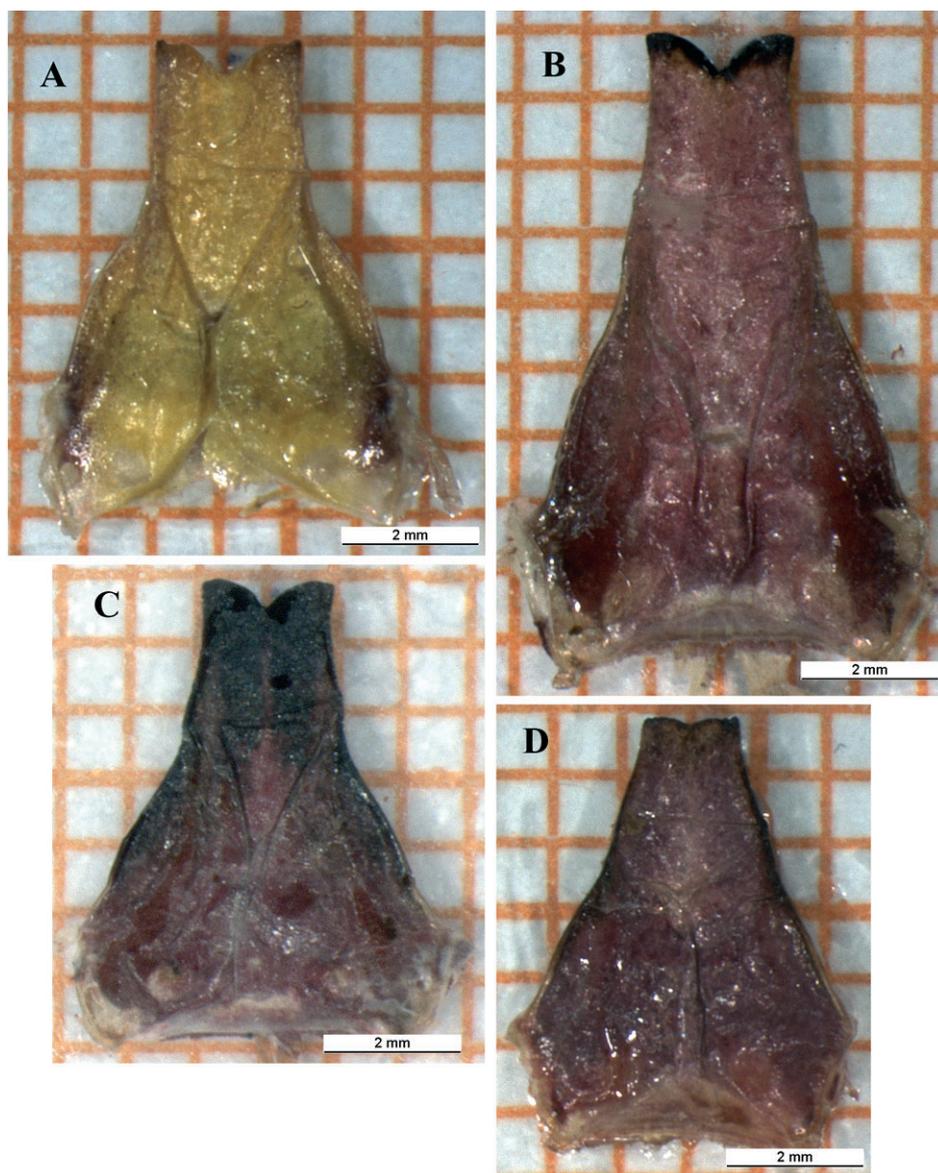


Fig. 5. Ventral view of male subgenital plate. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

Material examined. Rize: İkizdere, Cimil, 2000 m, 29.viii.–1.ix.1956, 1♂, 1♀ (coll. T. Karabağ); İkizdere, Cimil, Başköy, 1800–2000 m, 29.–30.viii.1956, 1♀ (coll. T. Karabağ); Cimil, Demirkoy, 31.viii.1956, 2500 m, 1♂ (coll. T. Karabağ); these specimens are deposited in HUZOM. İkizdere, Kama Village 1306 m, 40°39'47.1"N, 40°34'37.3"E, 9♂, 6♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); İkizdere, Çamlık Village, 1484 m, 40°42'14.5"N, 40°39'38.9"E, 16♂, 10♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); İkizdere, Cimil Waterfall, 1640 m, 40°44'44.9"N, 40°42'13.6"E, 16♂, 9♀, (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar); Çamlıhemşin, Aşağı Çaymakcur Plateo, 1996 m, 40°54'49.1"N, 41°09'51.4"E, 18.vii.2006, 20♂, 24♀ (in alcohol) (coll. İ.K. Sağlam, S.S. Çağlar) these specimens are deposited in ESRL. Artvin: Arhavi, Napopen Plateo, 2171 m, 41°11'01.8"N, 41°21'14.9"E, 17.viii.2005, 19♂, 6♀ (in alcohol) (coll. İ.K. Sağlam, H. Sevgili, S.S. Çağlar), Borçka, Beyazsu Plateo, 2316 m, 41°21'12.8"N, 41°57'12.1"E, 12.vii.2006, 20♂, 20♀ (coll. İ.K. Sağlam, S.S. Çağlar); Şavşat, Maden Village, 2316 m, 41°22'53.8"N, 42°07'32.1"E, 1996 m, 30.vii.2008, 20♂, 10♀ (in alcohol) (coll. İ.K. Sağlam); Şavşat, Sakorya Pla-

toe, 2401 m, 41°23'43.3"N, 42°06'35.4"E, 30.vii.2008, 18♂, 10♀ (in alcohol) (coll. İ.K. Sağlam), these specimens are deposited in ESRL. Trabzon: Araklı, Dağbaşı, Yaylaları, 28.vii.2005, 1♀ (Y. Durmuş), these specimens are deposited in HUZOM. Araklı, Erikli Village, 1802 m, 40°34'51.3"N, 39°56'33.6"E, 31.vii.2007, 18♂, 4♀ (in alcohol) (coll. İ.K. Sağlam, H. Sevgili, S.S. Çağlar) these specimens are deposited in ESRL.

Specimens used for sound recordings. Artvin: Borçka, Beyazsu Yaylası, 4.viii.2007, 2150 m, 5♂ (in alcohol) (no. 0807-11, 0807-18, 0807-34, 0807-34, 0807-78) (coll. H. Sevgili), Hatıla vadisi milli parkı, İskebe yaylası yolu, 1725 m, 2.viii.2007, 3♂ (in alcohol) (no. 0807-01, 0807-2, 0807-3) (coll. H. Sevgili); Rize: İkizdere-Ovit yolu, Çamlık üstü, 19.vii.2007, 4♂ (in alcohol) (no. 5307-22, 5307-30, 5307-31, 5307-62); İkizdere, Ovit, Sivrikaya, 20.vii.2007, 2♂ (in alcohol) (no. 5307-12, 5307-48); İkizdere, Anzer yolu, Kamanin dibi, 1320 m, 20.vii.2007, 2♂ (in alcohol) (no. 5307-40, 5307-41.)

Defining features. Body size is relatively large; when the fastigium is viewed from above, the dorsal cavity is

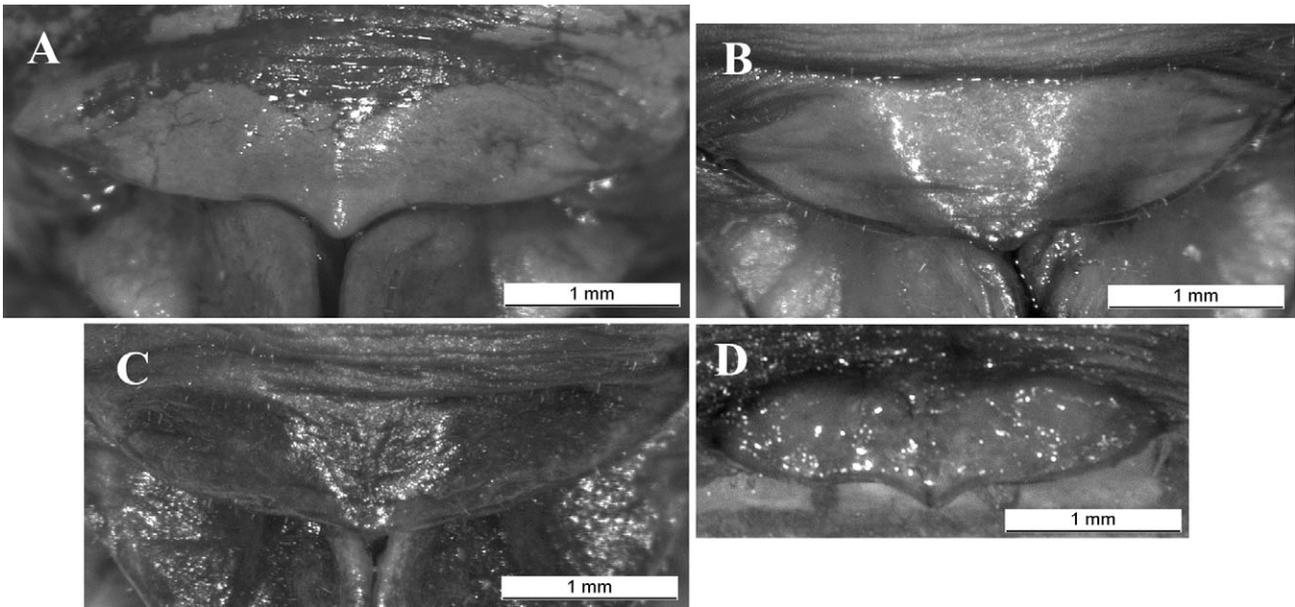


Fig. 6. Ventral view of female subgenital plate. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

concave at the sides, shallow and mainly located at the base (Fig. 7B and C); in females viewed from above the tegmina clearly protrudes from under the pronotum (Fig. 8B and C); in males when the first tergum is viewed from above the metanotal gland distinctly folds and rises upwards forming a curved bracket or brace shape (Fig. 4B and C); in males the subgenital plate is red-lilac, narrows gradually at the middle, the neck is long (3.00–4.30 mm) and narrows down towards apex (Fig. 5B) except in individuals from populations east of the Coruh Canyon, in which the neck is relatively short (2.10–3.00 mm) (Fig. 5C); in males the cerci are relatively thick (0.80–1.10 mm) and long (3.50–4.45 mm) (Fig. 9B and C); in females the protrusion at the anterior end of the subgenital plate is missing or very blunt (Fig. 6B and C); body coloring of males is mainly black and lilac.

Song. Songs were recorded at night at 24–27°C. The song pattern of *Ph. artvinensis* is similar to that of *Ph. satunini* and composed of two groups of echmes with the first consisting of major syllables and a second of minor syllables (Fig. 13A and B). Mean duration of the first group is $5.55 \text{ s} \pm 1.44 \text{ SD}$ ($n = 25$, min–max: 3.05–8.47 s) and is composed of powerful crescendo type major syllables. The main group is repeated at intervals of on average $41.30 \pm 10.14 \text{ SD}$ seconds (min–max: 20.73–58.17 s, $n = 20$). Number of major syllables within the first group ranges from 3–9. Mean duration and period of major syllables are $0.358 \text{ s} \pm 0.086 \text{ SD}$ and $1.27 \text{ s} \pm 0.15 \text{ SD}$ ($n = 99$), respectively. Number of impulses within the major syllables ranges from 57–135 (mean: $126.5 \pm 15.91 \text{ SD}$, $n = 16$). Impulses within major syllables start at low intensities and finish strongly. From time to time minor syllables similar to the ones recorded from the second group can be produced within the major syllables (Fig. 13C and D). On average these minor syllables are produced $0.280 \pm 0.038 \text{ s}$ after the main syllables.

This first group is followed by a second group composed of one section of crescendo type or two of minor syllables (Fig. 13A and B). If there are two types of syllables in the second group the first is a crescendo and the second a decrescendo. However, from time to time individuals produce only the second group and remain silent during the interval (Fig. 14A–C). Mean duration of the second group is $20.85 \text{ s} \pm 2.34 \text{ SD}$, ($n = 17$). Numbers of minor syllables in the second group ranges from 29–184 and 2–5 minor syllables are produced per second. Mean duration and period of minor syllables are $0.057 \pm 0.007 \text{ SD}$ and $0.309 \text{ s} \pm 0.089 \text{ SD}$, respectively. Numbers of pulses in minor syllables are quite variable ranging from 7–46 with a mean of $23.82 \pm 8.03 \text{ SD}$.

Key to species

Based on the above descriptions and characters given in Table 1 the following key to species was constructed:

- 1 In both sexes the pronotum is smooth with no distinct tubercles on the sides (Figs 2B–D, 3B–D); when the first tergum is viewed from above (especially in males) the metanotal gland distinctly folds and rises upwards forming a curved bracket or brace shape (Fig. 4B–D); in males the subgenital plate is red-lilac, narrowing in the middle and neck is gradual (Fig. 5B–D); body coloring of males is mainly black and lilac. 2
- In both sexes the pronotum has distinct tubercles on the sides (especially on the mesozone) (Fig. 2A and 3A); when the first tergum is viewed from above the region near the metanotal gland distinctly folds and rises up forming an inverted v shape (Fig. 4A); in males the base of the subgenital plate is quite wide and the narrowing in the middle is acute, neck is relatively short and stretches parallel towards apex (1.60–3.00 mm) (Fig. 5A); in females there is always a clear projection on the middle section of the subgenital plate (Fig. 6A); ovipositor length can range between 8.50–13.40 mm (Fig. 10A); body coloring of males is mainly black and yellow. *Ph. uvarovi*

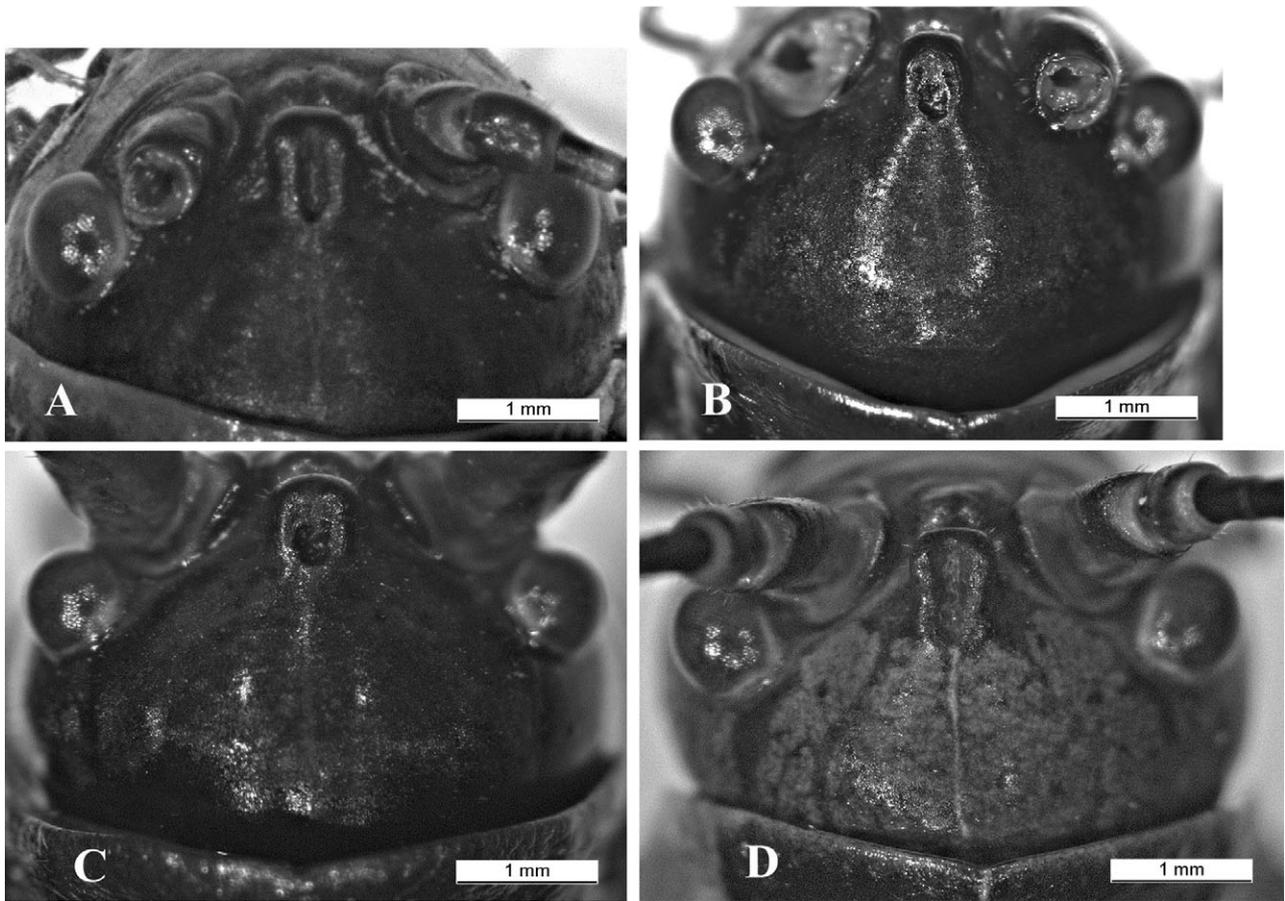


Fig. 7. Dorsal view of fastigium. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

- 2 When the fastigium is viewed from above the dorsal cavity is deep and usually extends all the way to the front (Fig. 7D); in females viewed from above the tegmina does not protrude from under the pronotum or only slightly (Fig. 8D); in males the neck of the subgenital plate is between 2.00–2.70 mm; in males the cerci are relatively thin (0.70–0.80 mm) and short (2.85–3.00 mm) (Fig. 9D); ovipositor length is between 8.30–9.80 mm (Fig. 10D). *Ph. satunini*
- When the fastigium is viewed from above the dorsal cavity is shallow and usually situated at the base (Fig. 7B and C); in females viewed from above the tegmina clearly protrudes from under the pronotum (Fig. 8B and C); in males the neck of the subgenital plate is elongated and relatively long (3.00–4.30 mm) in populations west of the Çoruh Valley (Fig. 5B), and in populations east of the Çoruh Valley of standard length (2.10–3.00 mm) (Fig. 5C); in females the subgenital plate has a blunt protrusion at the anterior end (Fig. 6B and C); in males the cerci are relatively thick (0.80–1.10 mm) and long (3.50–4.45 mm) (Fig. 9B and C); Ovipositor length can range between 9.00–15.30 mm (Fig. 10B and C). *Ph. artvinensis*

DISCUSSION

Distribution: Limiting factors and natural barriers

The general distribution of *Phonochorion* spp. indicates that this genus is restricted to the Colchic ecoregion and lives in high altitude montane habitats in the humid tem-

perate rain forests of the Caucasus. In addition, its limited vertical distribution (1200–2600 m) and preference for moist sub-alpine vegetation indicates this genus is an alpine endemic.

When the distribution of the genus is evaluated we can say with a fair amount of certainty that the westward distribution of the genus ends at Yağmurdere in the Gümüşhane province of Turkey since no specimens were found in suitable areas west of this region. The eastern limit of the genus is less certain since field expeditions in Georgia were limited and there is no information in the literature on the distribution of this genus in Georgia. Therefore how far the genus extends into the Lesser Caucasus is unknown. However, based on climatic and floristic similarities (McGinley, 2008) this is a distinct possibility.

The species of *Phonochorion* were only collected on the north facing slopes of the East Black Sea and Lesser Caucasus Mountains and no individuals were ever observed on the south facing slopes of these mountain ranges. This is not surprising since *Phonochorion* spp. are restricted to humid and wet conditions, which are prevalent on the Northern slopes of these mountains but not on the southern slopes due to a rain shadow effect. Continental polar air masses transporting dry and cold air from Siberia towards Anatolia take up moisture from the Black Sea, which condenses on the northern slopes of the North

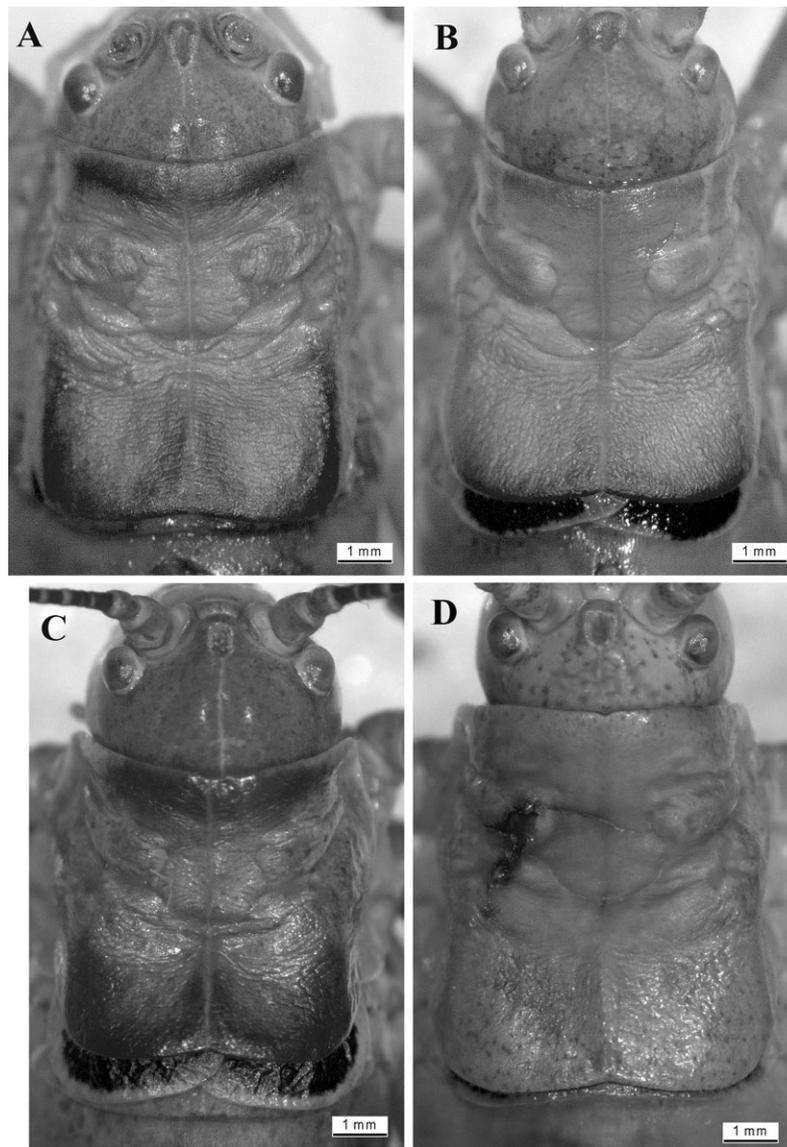


Fig. 8. Dorsal view of female pronotum + tegmina. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

East Anatolian Mountains resulting in heavy orographic rain fall (Akçar & Schluchter, 2005; Atalay, 2006). In addition, the high altitude of these mountain ranges also creates a natural barrier between coastal and internal areas resulting in a negative precipitation gradient towards inner Anatolia (Akçar & Schluchter, 2005). In the East Black Sea region a dramatic decrease in rainfall occurs as one moves 130 km inland from Rize (annual mean 2200 mm) to Erzurum (annual mean 400 mm) (Akçar & Schluchter, 2005). Therefore, due to the rain shadow and intense solar radiation (Atalay, 2006) the south facing slopes of these mountains are dominated by dry forest and scrub vegetation, which is an unsuitable habitat for *Phonochorion* species. This would also explain why *Ph. artvinensis* was not found at its type locality: the Yalnızçam Mountains and the Opiza and Porta Monastries. These localities lie well inland of the North East Anatolian Mountains where both the vegetation and climate are unsuitable for species of this genus.

Another important geographic feature affecting the distribution of species in this region would seem to be the Çoruh Valley. Like most orogenic mountains within Anatolia the North East Anatolian Mountains are dissected by rivers as a result of antecedent and superimposition events (Atalay, 2006). The largest of these river systems within the region is the Çoruh River, which by cutting through the North East Anatolian Mountains in a north-south direction creates a deep valley separating the Lesser Caucasus Mountains from the East Black Sea Mountains. The altitudinal difference between the river bed and the upper parts of the mountains is nearly 3000 m in the Çoruh Valley (Atalay, 2006). This deep valley has important implications for both the micro and macro climatic characteristics of the region. The north facing slopes of the East Black Sea Mountains are covered by humid forests and montane habitats as a result of abundant rainfall and reduced radiation (Atalay, 2006). On the other hand along the River Çoruh corridor humid-

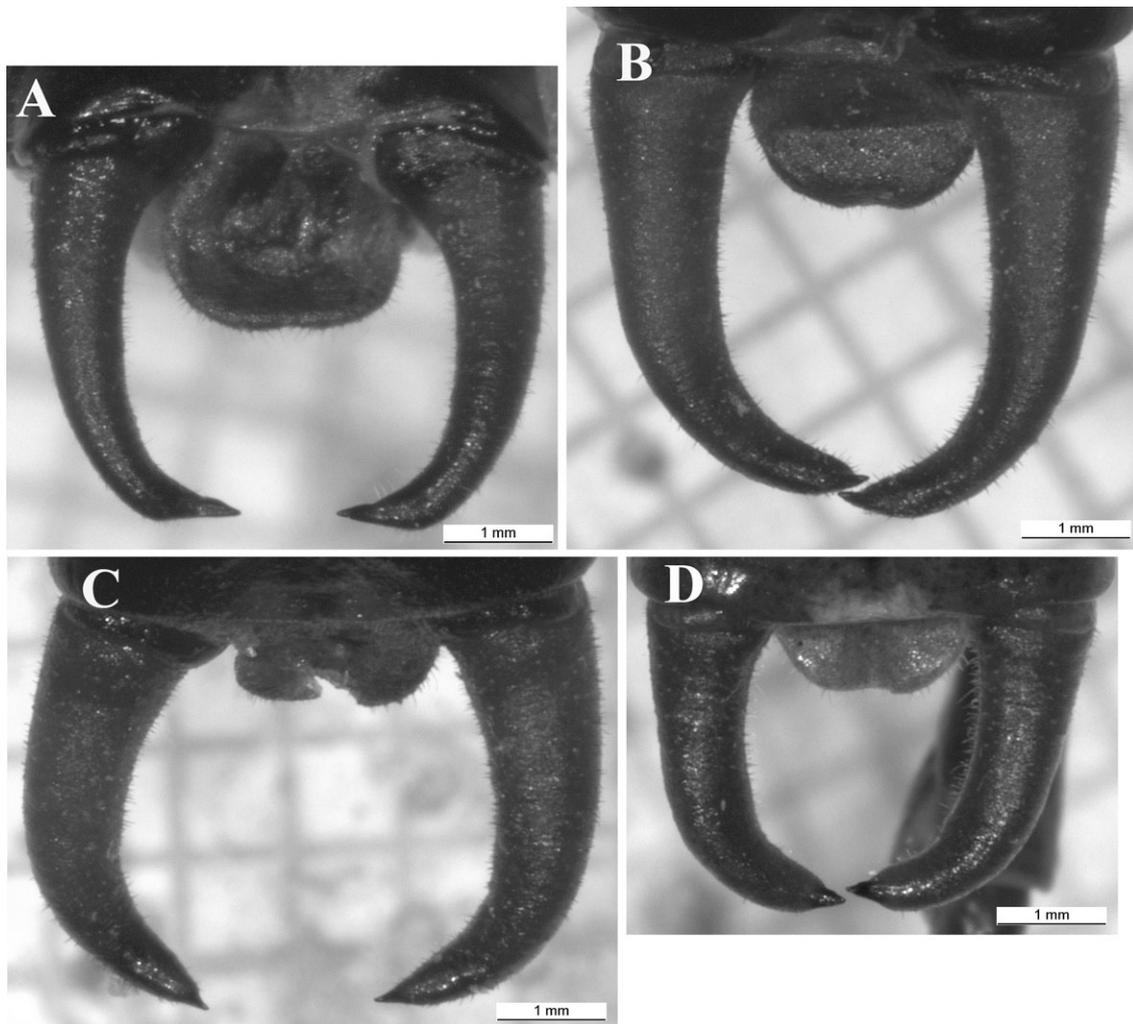


Fig. 9. Dorsal view of male cerci + epiproct. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

semiarid conditions and Mediterranean maquis vegetation prevail as a result of the absence of moisture and increased solar radiation (Atalay, 2006; Zengin et al., 2010).

Therefore, the Çoruh Valley would seem to be an important physical and climatic barrier to the dispersal and spread of species. If this is the case, then this valley effectively limits the westward distribution of *Ph. artvinensis* to east of the Çoruh Valley and its eastward distribution to west of the Çoruh Valley. Hence, the Çoruh Valley effectively separates the distribution of *Ph. satunini* and *Ph. artvinensis* in the Artvin region from that of *Ph. uvarovi* and *Ph. artvinensis* in the Rize and Trabzon regions.

Bioacoustics

The Phaneropterinae *Phonochorion* spp., *Polysarcus* spp. and *Poecilimon brunneri* species-groups produce the most complicated acoustic signals in terms of the temporal structure of their songs (Korsunovskaya, 2008). The songs of these bush-crickets usually contain several distinct components to which the females respond only to one (Korsunovskaya, 2008). Oscillograms of the songs of

two of the three species (*Ph. uvarovi* and *Ph. artvinensis*) were published earlier by Heller (1990). However Heller's (1990) recordings of *Ph. satunini* are of *Ph. artvinensis*. Based on similarities in the acoustic signatures (sequential repeats of structurally similar, simple, crescendo type syllables) and wing stroke patterns Heller (1990) classified *Ph. uvarovi* song as similar to that of the ancestral Barbitistini tribe. The Barbitistini tribe can be divided into two distinct phylogenetic groups depending on duration of the male call and male-female duet patterns: a clade where couples perform duets and a clade where male-female duets are absent (Heller, 1990; Bailey & Hammond, 2003). According to this classification it is hypothesized that short calling songs of males and short responses by females is the ancestral state and that species with long calling songs have evolved from this ancestral state. In this study the songs of females were not recorded. However, the structure of the wings of the females of *Phonochorion* indicates they can produce sounds. If as stated by Heller (1990) *Phonochorion* species performs duets, we would expect females to give short responses to male calling songs, which would place *Phonochorion* in the ancestral clade of the Barbitistini

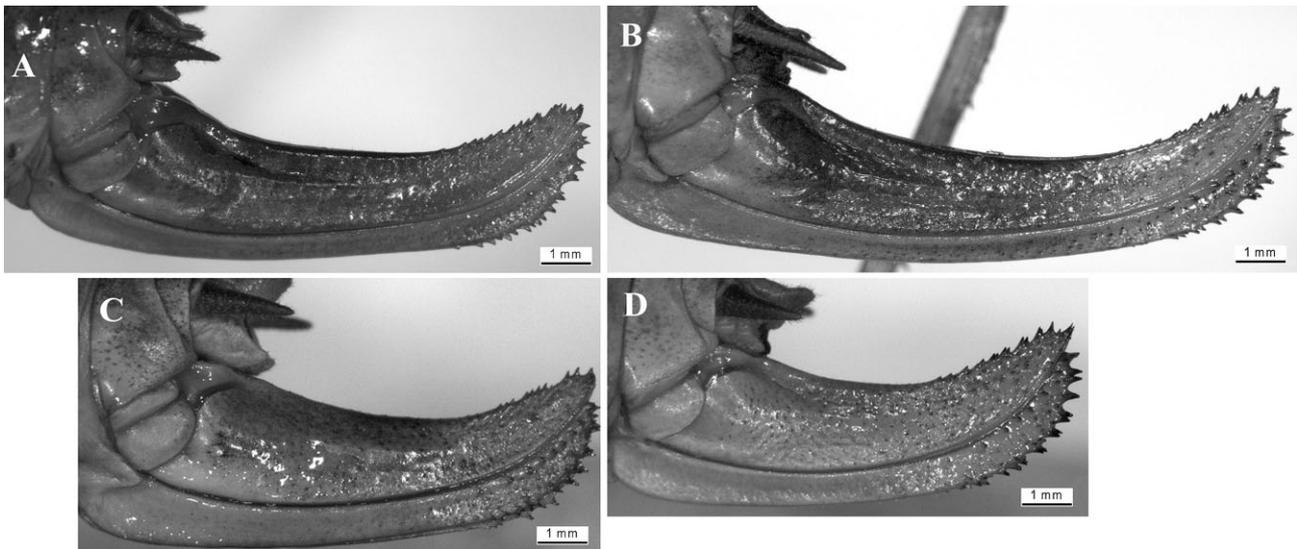


Fig. 10. Lateral view of ovipositor. A – *Ph. uvarovi*; B – *Ph. artvinensis* from west of Çoruh Valley; C – *Ph. artvinensis* from east of Çoruh Valley; D – *Ph. satunini*.

tribe. Short responses of this kind are also quite common in closely related groups, such as *Poecilimon* and *Isophya* (Heller, 1990; Bailey & Hammond, 2003; H. Sevgili, unpubl. data), which gives some support to this conclusion.

In the present study male calling songs of *Ph. satunini*, *Ph. artvinensis* and *Ph. uvarovi* were recorded at many different localities. When the calling songs of males of the three species are compared, those of *Ph. artvinensis* and *Ph. satunini* are clearly different from that of *Ph. uvarovi*. In all three species the main part of the calling song is composed of a powerful crescendo type syllable repeated at regular intervals. However in contrast to *Ph. uvarovi*, in *Ph. artvinensis* and *Ph. satunini* this main group is interrupted by a second group composed of rapid repeats of a minor two-piece syllable. In spite of this clear difference, divergence in calling songs between species does not seem to be totally complete as both *Ph. artvinensis* and *Ph. satunini* individuals may not produce this second group but remain silent during this period. In this form the calling songs produced by *Ph. artvinensis* and *Ph. satunini* are virtually identical to that of *Ph. uvarovi*. Therefore, based on acoustic data *Ph. uvarovi* has a simple song and seems to be the ancestral species, and *Ph. artvinensis* and *Ph. satunini* have complex songs and have diverged and evolved from this ancestral state.

Although calling songs enable us to discriminate *Ph. uvarovi* from the other two species the same cannot be said for discriminating between *Ph. artvinensis* and *Ph. satunini*. Songs produced by *Ph. satunini* and *Ph. artvinensis* are very similar with no significant differences between the structure of their songs. Although *Ph. satunini* and *Ph. artvinensis* show some differences in song structure in relation to duration and number of syllables these differences could easily be attributed to differences in the temperature at which they were recorded. Therefore, it is not possible to clearly differentiate between the two species using bioacoustic data.

External morphology

Although it is not possible to discriminate between *Ph. artvinensis* and *Ph. satunini* using bioacoustic data all three species are easily distinguishable using external morphological characters. *Ph. satunini* and *Ph. artvinensis* differ from *Ph. uvarovi* in the structure of its pronotum and metanotal gland, and in the colour and shape of the male subgenital plates. From a character evolution perspective, although geographically more distant, *Ph. satunini* is more closely related to *Ph. uvarovi* than *Ph. artvinensis* since the female tegmen, female subgenital plate, fastigium, male cerci and female ovipositor in *Ph. satunini* are identical with those in *Ph. uvarovi*. Retention of these characters in *Ph. satunini* also facilitates the differentiation between *Ph. satunini* and *Ph. artvinensis* as *Ph. artvinensis* differs in all the above characters.

Ph. artvinensis also shows substantial within species variation in the neck of male subgenital plates. The *Ph. artvinensis* populations east of the Çoruh Valley do not differ in this character from either *Ph. satunini* or *Ph. uvarovi*, but in the populations west of the Çoruh Valley the neck is very elongated. The male subgenital plate has proved a very useful character for delimitating Barbitistinae species (e. g. Heller et al., 2004; Sevgili et al., 2006) and given its importance in mating and spermatophore transfer (Helvesen & Helvesen, 1991); it is likely to be species specific. This along with the allopatric distribution of eastern and western *Ph. artvinensis* populations (in relation to the Çoruh Valley) might warrant the splitting of *Ph. artvinensis* into two sub species. However, since eastern and western populations of *Ph. artvinensis* do not differ in any of the remaining diagnostic characters the east and west populations of *Ph. artvinensis* are not classified here as two separate sub species. In addition there are numerous empirical studies showing the widespread occurrence of intra-specific variation in genitalia across insect taxa (Garnier et al., 2005; Mutanen et al., 2006; Polihronakis, 2006; Song & Wenzel, 2008). There-

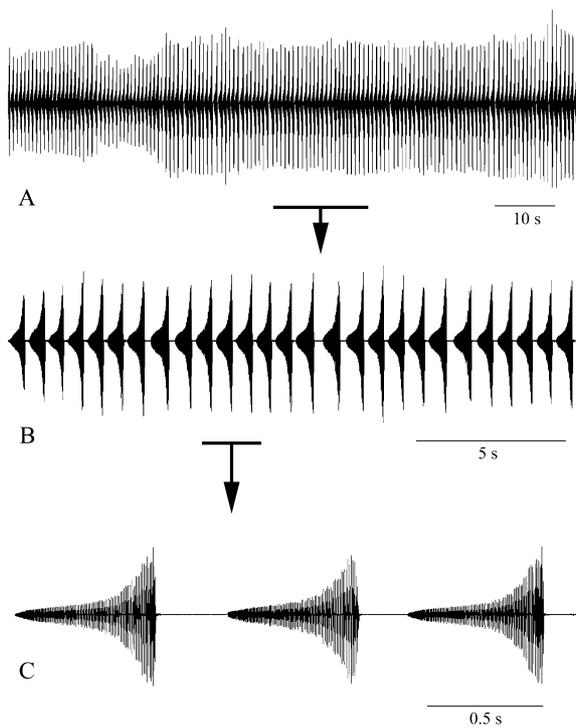


Fig. 11. Oscillograms of the song of *Ph. uvarovi*.

fore, we believe great care should be taken when assigning sub species status based on a single character.

Systematics

Based on morphological characteristics and bioacoustics *Phonochorion* spp. can be placed in the tribe Barbitistini, a group of short winged species within the subfamily Phaneropterinae (Tettigoniidae: Orthoptera) (Heller, 1990). However, its relation to other Barbitistine species is unclear. Morphologically *Phonochorion* spp. are most closely related to *Polysarcus zacharovi* and to members of the *Poecilimon heroicus*-group (*Poecilimon heroicus* Stshelkanovtzev, 1911; *Poecilimon bifenestratus* Miram, 1929; *Poecilimon tricuspis* Miram, 1926 and *Poecilimon tschorochensis* Adelung, 1907). Both *P. zacharovi* and the *Poecilimon heroicus*-group occur in north east Turkey and the latter is also widespread throughout the larger Caucasus region (Heller et al., 2006; Salman, 1978). They share the following features: general form of the pronotum (relatively wide, distinct rise in the metazona), relatively large tegmina, the presence of dorsal glands in males and the long upward curling subgenital plate in males.

Acoustically *Phonochorion* spp. and *P. zacharovi* are quite distinct from the *Poecilimon heroicus*-group. Acoustic signals of *Phonochorion* spp. and *P. zacharovi* are very complicated in their temporal structure (Korsunovskaya, 2008) and both groups produce a continuous song (Heller, 1990; Heller et al., 2006), whereas the temporal structure of the acoustic signals of the *Poecilimon heroicus*-group is less complicated (Korsunovskaya, 2008) and consist of isolated pairs of syllables (Heller et al., 2006). Due to the complexity of their song patterns

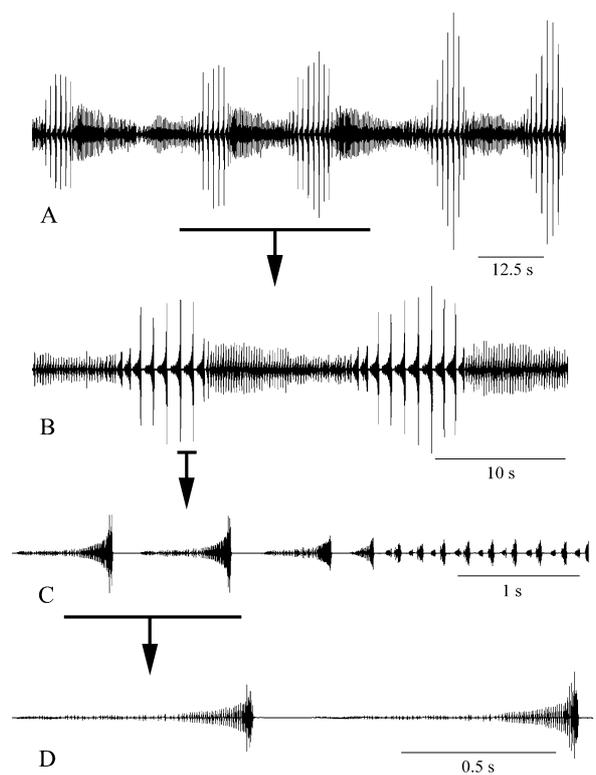


Fig. 12. Oscillograms of the song of *Ph. satunini*.

Phonochorion spp. and *P. zacharovi* can be classified as more derived clades to the *Poecilimon heroicus*-group.

Interestingly *Phonochorion* spp. shares several distinct features with the most basal taxon of the *Poecilimon heroicus*-group: *P. tschorochensis* (Heller et al., 2006). Females of *Phonochorion* species and *P. tschorochensis* have overlapping tegmina and are capable of responding acoustically to males whereas those of the other species in the *Poecilimon heroicus*-group have highly reduced non-overlapping tegmina and do not respond acoustically to males (Heller et al., 2006). Overlapping female tegmina and acoustic response of females to males also occurs in the genus *Polysarcus* (Korsunovskaya, 2008). In addition, *Phonochorion* spp. and *P. tschorochensis* share the ancestral cercal shape in which the cerci of males end in one simple tooth. *P. zacharovi* and all other species within the *Poecilimon heroicus*-group possess cerci with at least two teeth (Heller et al., 2006; Salman, 1978).

The similarity in distribution of *Phonochorion* spp., *P. zacharovi* and the *Poecilimon heroicus*-group and the closeness of *Phonochorion* spp., *P. zacharovi* and *P. tschorochensis* (the most basal taxon of the *Poecilimon heroicus*-group) suggests that these three groups might have diverged from a common ancestor distributed somewhere around the Circum-Caucasion region.

Within the genus *Phonochorion*, song structure clearly indicates *Ph. uvarovi* to be the basal taxon. Additional support can be inferred from morphological characteristics such as colour and shape of the male subgenital plate and the relatively small dorsal glands of *Ph. uvarovi*, all of which are relatively simple characters compared with

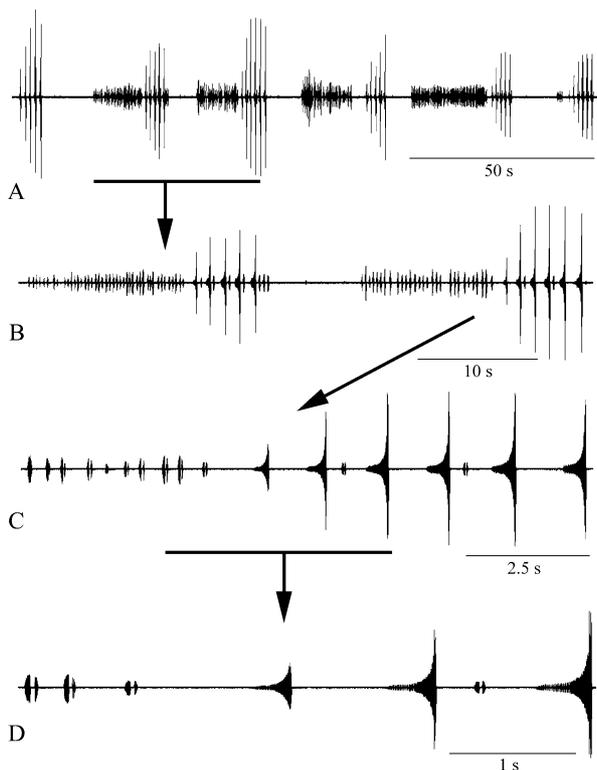


Fig. 13. Oscillograms of the song of *Ph. artvinensis* when two echmes were produced each containing a major and minor syllable.

the more derived characters of *Ph. satunini* and *Ph. artvinensis*.

The songs of *Ph. satunini* and *Ph. artvinensis* are not significantly different. This similarity suggests that morphological differentiation of the two species occurred after the initial split from *Ph. uvarovi*. The similarity in song raises the question of whether the two groups should be synonymized. However, although the two species look quite similar they differ significantly in important diagnostic traits such as male cerci and male and female subgenital plates. Therefore, the species status of *Ph. artvinensis* and *Ph. satunini* is retained until further information becomes available. The basic problem is that of sample size, as we have only one population of *Ph. satunini* to base our conclusions on. Further sampling, most notably in Georgia, is needed to clarify whether differences in traits truly reflect different species or intra-species variation.

Based on the acoustic and morphological data presented the following systematic relationship between *Phonochorion* spp is proposed. *Ph. uvarovi* (or its ancestral stock) is the most basal clade and gave rise to the (*Ph. satunini* + *Ph. artvinensis*) clade as a result of diversification in male calling song and overall male coloration. Later the ancestral (*Ph. satunini* + *Ph. artvinensis*) clade gave rise to *Ph. satunini* and *Ph. artvinensis*, most probably as a result of further character divergence in *Ph. artvinensis*.

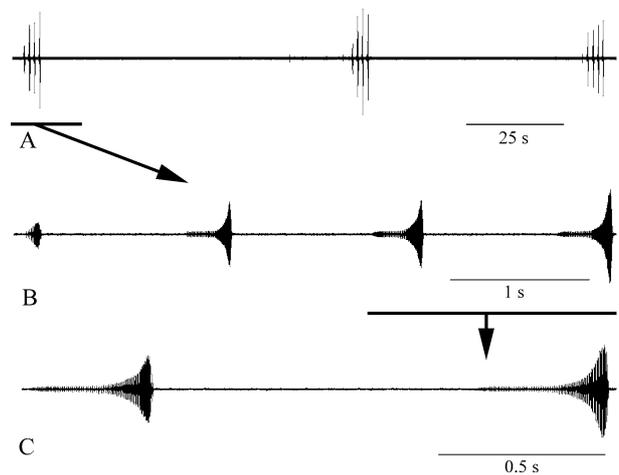


Fig. 14. Oscillograms of the song of *Ph. artvinensis* when only the first echme containing a major syllable was produced.

Conclusion

Both the bioacoustic and morphological data indicate that at the species level none of the characters of all of the extant taxa clearly differ. Therefore, it is likely that divergence within this group is quite recent and not yet complete. Furthermore the level and nature of the divergence between and within species suggests that both the level of bioacoustic and morphological divergence is stronger between species with overlapping ranges than those that are allopatric. Therefore divergence within the genus might be the result of ecological or reproductive character displacement. However, empirical tests are needed to substantiate the validity of this assumption.

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