

The Balkan *Psorodonotus* (Orthoptera: Tettigoniidae): Testing the existing taxa confirmed presence of three distinct species

SARP KAYA¹, DRAGAN P. CHOBANOV^{2,*}, JOSIP SKEJO³, KLAUS-GERHARD HELLER⁴ and BATTAL ÇIPLAK¹

¹Akdeniz University, Faculty of Sciences, 07058 Antalya, Turkey; e-mails: kaya_sarp@hotmail.com; ciplak@akdeniz.edu.tr

²Institute of Biodiversity and Ecosystem Research, 1 Tsar Osvoboditel Boul., 1000 Sofia, Bulgaria; e-mail: dchobanov@gmail.com

³Biology Students Association – BIUS, Rooseveltov trg 6, HR-10000 Zagreb, Croatia; e-mail: skejo.josip@gmail.com

⁴Grillenstieg 18, 39120 Magdeburg, Germany; e-mail: heller.volleth@t-online.de

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Abstract. A review of the Balkan representatives of the genus *Psorodonotus* was made with the aim of revealing the relationships between taxa and their systematic arrangement. For this purpose we used morphological (qualitative and quantitative), acoustic (amplitude-temporal song parameters) and molecular (mtDNA COI gene sequence) data. The analyses and comparisons with other taxa of *Psorodonotus* support the distinction of three species occurring on the Balkan Peninsula: *P. fieberi*, *P. illyricus* and *P. macedonicus*. Analysis of the COI sequences suggested the following relationships: outgroups + (*P. illyricus* + (*P. fieberi* + (*P. macedonicus* + *P. caucasicus*))). All available information on the distribution of the Balkan taxa was synthesized and mapped.

INTRODUCTION

Brunner von Wattenwyl (1861) established the genus *Psorodonotus* (originally a subgenus of *Decticus*) for *P. pancici* Brunner von Wattenwyl, 1861 (presently regarded a synonym of *P. fieberi* (Frivaldszky in Fieber, 1853) and the then known *Pterolepis fieberi* and *Pterolepis venosa* Fischer de Waldheim, 1839 (described under *Peltastes* Fischer de Waldheim, 1839, which was recognized by its author as a preoccupied name; Fischer de Waldheim, 1846). Later on, Brunner von Wattenwyl (1882) included in this genus also *Pterolepis specularis* Fischer de Waldheim, 1839 (also described under *Peltastes*). At present, the genus is thought to include 22 valid taxa (15 species) (Eades et al., 2014; Kaya et al., 2014), distributed in the mountainous regions of the Caucasus, Anatolia and the Balkan Peninsula. The highest diversity of species is concentrated in Eastern and Northeastern Anatolia and the Caucasus-Transcaucasus region. Three valid taxa are presently known from the Balkan Peninsula: *Psorodonotus fieberi fieberi* (Frivaldszky in Fieber, 1853), *Psorodonotus fieberi illyricus* Ebner, 1923 and *Psorodonotus fieberi macedonicus* Ramme, 1931. After their description, significant discrepancies existed between authors concerning the taxonomic status and systematics of the Balkan taxa. The taxa are regarded either as subspecies of two species (e.g., Ramme, 1931; Mikšić, 1965; Harz, 1969), separate species (Ramme, 1951) or subspecies of a single species (Heller, 1988; Eades et al., 2014). Most of the cited studies rely on morphological criteria. Heller (1988) used parameters of the male calling song in addition to general morphology to define the subspecies relationships of the three taxa, a

view that is currently accepted (Eades et al., 2014). Recent studies on related taxa in Anatolia (Ünal, 2013; Kaya et al., 2013, 2014; Taylan et al., 2014) revealed new distinct lineages in the genus with morphological and acoustic differences of the same order, which showed significant genetic differences (Kaya et al., data in prep.). Thus, the aim of the present study is to test the hypotheses concerning the taxonomic status of the Balkan taxa and reveal their relationships using molecular, morphological and acoustic data.

MATERIAL AND METHODS

Sampling

For the purposes of the present study we concentrated on collecting specimens from at least two mountain areas within the geographically outlined ranges of the known taxa (e.g., Mikšić, 1965; Harz, 1969). The material used for morphological and molecular studies is listed in Appendix 1.

Morphology

Specimens from the populations sampled were preserved in 70–96% ethanol in order to preserve original body shape. Upon preliminary identification (according to Ramme, 1951; Mikšić, 1965; Harz, 1969) specimens were arranged into respective taxonomic units (Appendix 1). We examined the morphological characters previously used for discriminating taxa. Respective morpho-structures were photographed, qualitatively examined and measured using a Leica MZ6/DC600 stereomicroscope equipped with a digital camera and Image J v. 1.36 software (<http://rsb.info.nih.gov/ij/>).

Previously, the Balkan representatives of *Psorodonotus* were distinguished mainly on their cercal morphology, titillator and ovipositor shape, and pronotum size (Ramme, 1951). Therefore, we conducted a geometric morphometrics analysis of all of these structures except the titillators. Illustrations of the pronotum and

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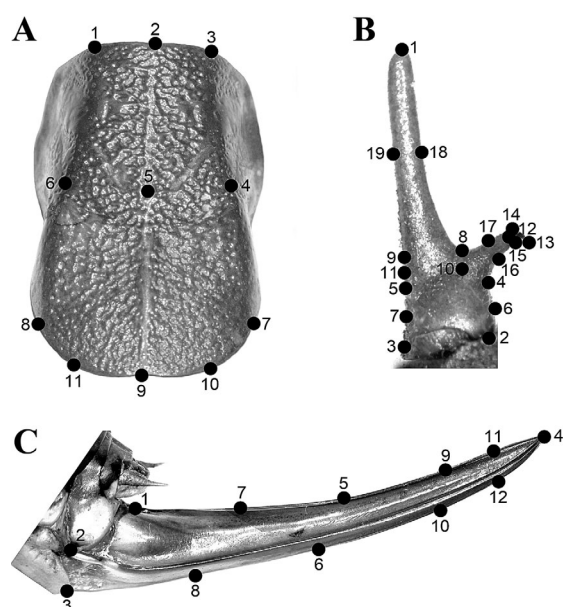


Fig. 1. Position of the homological landmarks on the three structures that were included in the Geometric morphometrics analysis: A – pronotum (*P. fieberi*); B – male cerci (*P. illyricus*); C – ovipositor (*P. fieberi*).

subgenital plate of males and females, tegmina, cerci and titillators of males and ovipositor of females were prepared for all available specimens (Appendix 1). In the case of uncertainty of the correct position of a structure in the photographs we used an additional image of the same structure. As a result, 54 images (*fieberi* – 18, *macedonicus* – 12, *illyricus* – 24) of the male and 35 (*fieberi* – 5, *macedonicus* – 10, *illyricus* – 20) of the female pronota, 88 (*fieberi* – 20, *macedonicus* – 19, *illyricus* – 49) of cerci and 31 (*fieberi* – 5, *macedonicus* – 7, *illyricus* – 19) of ovipositors were prepared. TPS files for each structure were created from images using tpsUtil v.1.26 following Rohlf (2004). Titillators were used only in the descriptive diagnoses. Eleven homologous landmarks for pronota, 19 for cerci and 12 for ovipositors were plotted manually in tpsDIG2 v.1.40 (Rohlf, 2002) according to

Kaya et al. (2013, 2014) (Fig. 1). The intersections marked in the TPS files were aligned using a Procrustes superimposition and matrices of partial warp scores for each structure were generated using MorphoJ v.1.03d (Klingenberg, 2011). Partial warp scores were analyzed using Canonical variate (CV) analysis using the same software.

Song

Male songs were recorded using the following equipment: (1) electret condenser microphone Knowles BT-1759-000 (with a cut-off at about 45 kHz; W. Schulze, Friedrich-Alexander Universität Erlangen-Nürnberg, pers. comm.), equipped with a custom-made preamplifier, connected to a ZOOM H2 handy recorder (Zoom Corporation) (96 kHz sampling rate); (2) Pettersson D500 external microphone (frequency range 1/2–>100 kHz) connected to a ZOOM H2 handy recorder; (3) UHER 4200 IC tape recorder with microphone UHER M645.

In addition we used some recordings available in the SysTax database (<http://www.biologie.uni-ulm.de/systax/index.html>) uploaded by Sigfrid Ingrisch via the DORSA project (<http://www.dorsa.de/>). For the specimens recorded and recording conditions see Table 1.

Bioacoustic terminology

Modified from Heller et al., 2004; Kaya et al., 2014. *Calling song*: the song produced by an isolated male; *phrase*: a group of densely arranged song elements or syllables forming main discrete part of the song; *syllable*: sound produced during one cycle of movements of tegmina (opening – often quiet – and closing – typically loud); here we termed the main distinguishable part of the song a *syllable*, which may be a single repeated unit of the *phrase* used by Kaya et al. (2014); *element*: a distinguishable compact oscillographic component that can be practically measured; *syllables repetition rate*: reciprocal of the syllable period (unit Hz = 1/s); *syllable period*: the duration of a syllable and the following silent interval until next syllable starts; *syllable duration*: the time interval starting from beginning of one repeated unit to its end; *impulse*: a recognizable undivided transient train of sound waves produced by the stridulatory tooth striking the plectrum (the anal edge of the opposite tegmen).

TABLE 1. Recordings of the male song of *Psorodonotus* used in this study.

Identification	Geographic range / Country	Locality, date	Geographic position	Recording equipment (Source)	Temperature
<i>fieberi</i>	Balkan Mts / Bulgaria	W Stara Planina Mts, Midzhur Peak, 1900 m, 9.09.2012	43.40810°N 22.66795°E	Knowles mic + ZOOMH2	28°C
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / Greece	Ionnina, Epirus, lake near Metsovon, 27.07.2004	39.817°N 21.133°E	UHER M645 + UHER 4200 IC	19°C
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / R Macedonia	Bistra Mt., Tonivoda highland, 1625–1700 m, 18.07.2013	41.64383°N 20.69788°E	Pettersson D500 + ZOOMH2	24°C
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Montenegro	Durmitor N.P., Pivska Planina Mt., Jarciste vill., 1500 m, 7.08.1990	43.13292°N 18.96944°E	AKG D202 + Kenwood KX880HX (SysTAX*)	? >32°C approximate estimate, rec. 1220 (27°C room T° but under incandescent lamp)
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Croatia	Rijeka, Učka Mt., 1000–1200 m, 12.08.2011 & Rijeka, Učka Mt., 21.07.1979	45.29194°N 14.20806°E & 45.33°N 14.18°E	AKG D202 + Kenwood KX880HX (SysTAX*) & UHER M645 + UHER 4200 IC	? >32°C approximate estimate, rec. 1016 (25°C room T° but under incandescent lamp) & ? >32°C approximate estimate (24°C air T° but animal exposed to sun)

*Recording by S. Ingrisch.

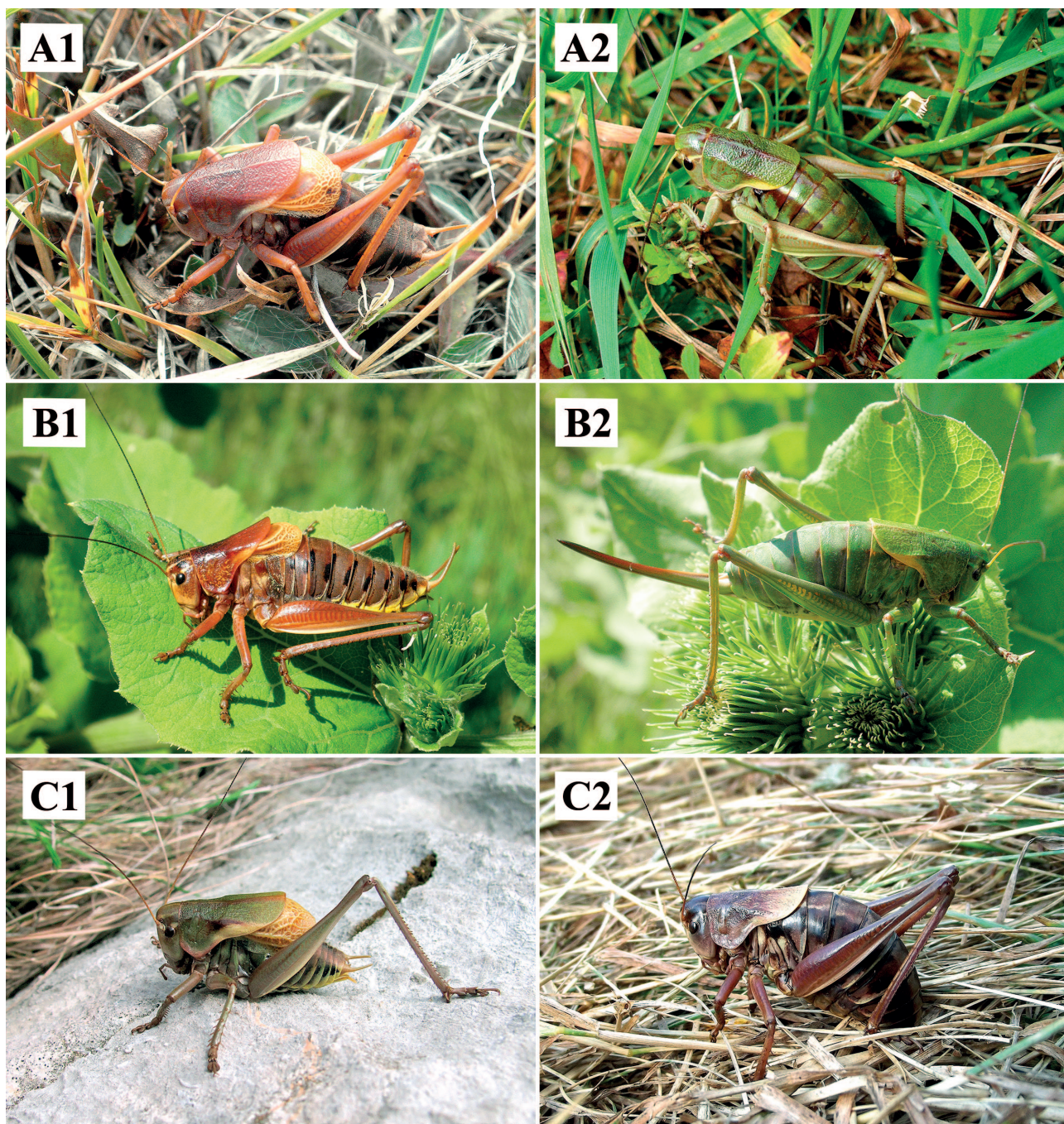


Fig. 2. General appearance of Balkan *Psorodonotus* (photographed in nature): A – *P. fieberi* (A1 – male, Bulgaria, W Stara Planina Mts, Vrachanska Planina; A2 – female, Bulgaria, C Stara Planina Mts, Ambaritsa); B – *P. macedonicus* (B1 – male, B2 – female, both photographed in the Republic of Macedonia, Korab Mt., Strezimir); C – *P. illyricus*, male (C1 – male, C2 – female, both photographed in Croatia, Obruč).

Song analysis

For manual and statistical comparisons of temporal song parameters between populations we selected the less variable and easily detectable part of the song: the second/main part of the syllable (see Results: Bioacoustics). As temperature (i.e., body temperature) is the most important factor affecting temporal song parameters in Orthoptera (e.g., Martin et al., 2000; Arias et al., 2012) we produced a subjective manual calibration of the recording temperature for the recordings of *P. illyricus* (see Results).

Molecular sequences and phylogenetic analysis

For determining the phylogenetic relationships between taxa we used Cytochrome c oxidase subunit I (COI) fragments of mitochondrial DNA (mtDNA). This region of mtDNA has revealed phylogenies of high resolution for bushcrickets (e.g., Ullrich et al., 2010) and also provided quality results for *Psorodonotus* (Kaya et al., in prep.).

Total DNA was extracted from muscle tissue using proteinase K digestion followed by the standard salt/isopropanol method (Aljanabi & Martinez, 1997). The universal primers forward C1-J-1718 or C1-J-1751 and reverse TL2-N-3014 were used to amplify the COI fragments (for the details of the structure of the

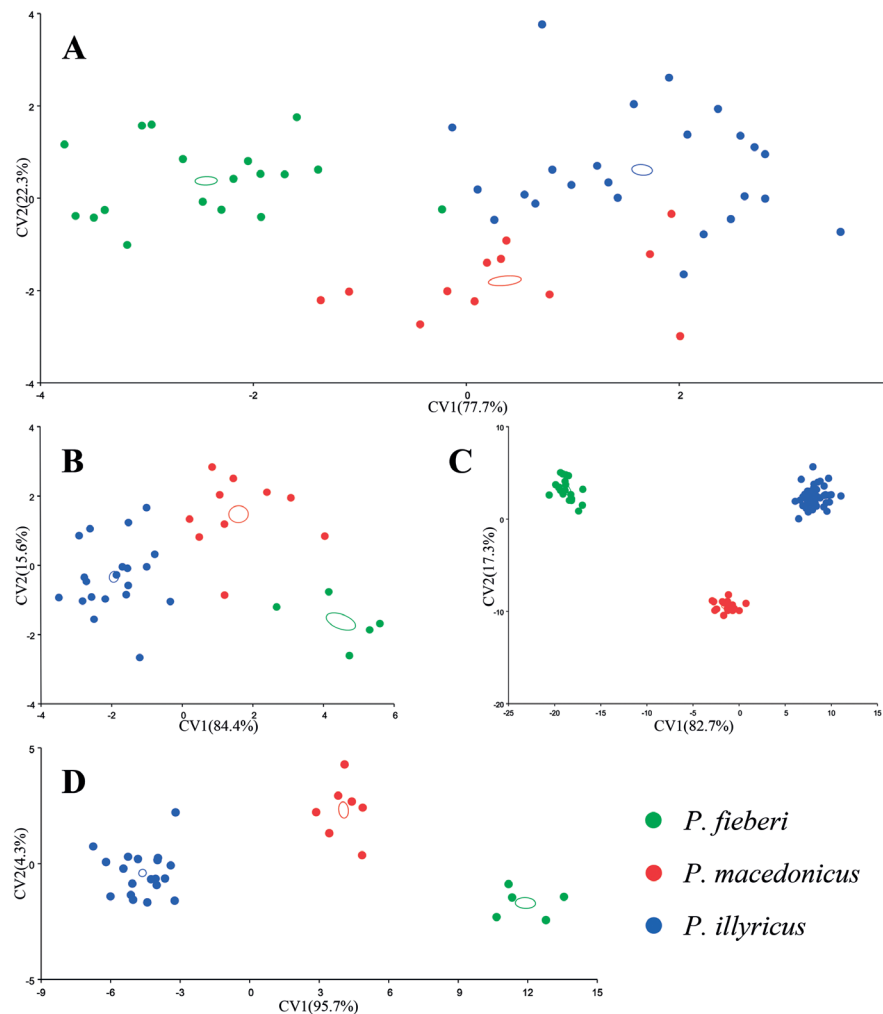


Fig. 3. Graph of CV analysis of centroid sizes of the morphological structures of Balkan *Psorodonotus*: A – male pronotum; B – female pronotum; C – male cerci; D – ovipositor.

primers see Simon et al., 1994). Amplification was performed in a 50- μ l volume containing 0.3 μ l of each primer (100 μ M), 1 μ l dNTP mix (10 mM), 2 μ l 50 mM MgCl₂, 5 μ l 10X Platinum PCR buffer (containing 200 mM Tris-HCl [pH 8.4], 500 mM KCl), 1.25 U Platinum TaqDNA polymerase (Invitrogen) and 0.5–1 μ l of 50–70 ng template DNA. Temperature cycling was carried out in an Eppendorf Mastercycler Personal. Amplification of the two fragments involved an initial cycle of denaturation at 94°C for 1 min, and 35 subsequent cycles of 94°C for 40 s, annealing temperature at 49°C for 30 s, extension temperature 72°C for 90 s, followed by a final extension step of 72°C for 10 min. Double-stranded sequence analysis (performed on a 23 ABI 3730XL DNA analyzer) and purifications were done by the Macrogen sequencing service (Macrogen Inc.). Nucleotide sequences of each unique haplotype identified in this study were deposited in the GenBank database under the Accession Numbers given in Appendix 3.

The sequences were aligned manually in Sequencher v. 4.1 (Gene Codes Corporation) and checked manually by eye. DnaSP v. 5 (Librado & Rozas, 2009) was used to determine unique haplotypes. The haplotype matrix was prepared using MEGA v. 5 (Tamura et al., 2011). A maximum parsimony (MP) analysis was carried out with 100 random additions following the heuristic search approach and the tree bisection-reconnection (TBR) algorithm using PAUP v. 4.10b (Swofford, 2000). A 10,000 non-parametric bootstrap resampling was used to assess the branching confidence

(Felsenstein, 1985). The parameters and best fit model were estimated using jModelTest v. 0.1.1. (Guindon & Gascuel, 2003; Darriba et al., 2012). The selected model was implemented in maximum likelihood (ML) and Bayesian phylogenetic inference (BI) analyses. ML was performed using a heuristic search procedure with TBR branch swapping and as-is addition replicates using PAUP v. 4.10b. Nonparametric bootstrapping (Felsenstein, 1985) was used to evaluate the support of nodes based on 1000 pseudoreplicates analyzed using ML. BI analysis was carried out in MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003; Ronquist et al., 2005) using four simulations of Markov chains, 2,000,000 generations and sampling every 100 generations. The software tool TRACER v. 1.5 (see Rambaut et al., 2014) was used to examine the parameters and determine the number of trees needed to reach stationarity. BI posterior branch probabilities were calculated using the majority rule consensus of the sampled trees, excluding the first 200 trees as burn-in. *P. specularis*, *P. venosus* and *P. caucasicus* were chosen as out groups. Pairwise genetic distances of species were calculated using MEGA.

RESULTS

Morphology

Preliminary identification of the populations sampled fitted the data from earlier sources very well (e.g., Ramme, 1951; Mikšić, 1965; Harz, 1969). Specimens also conform

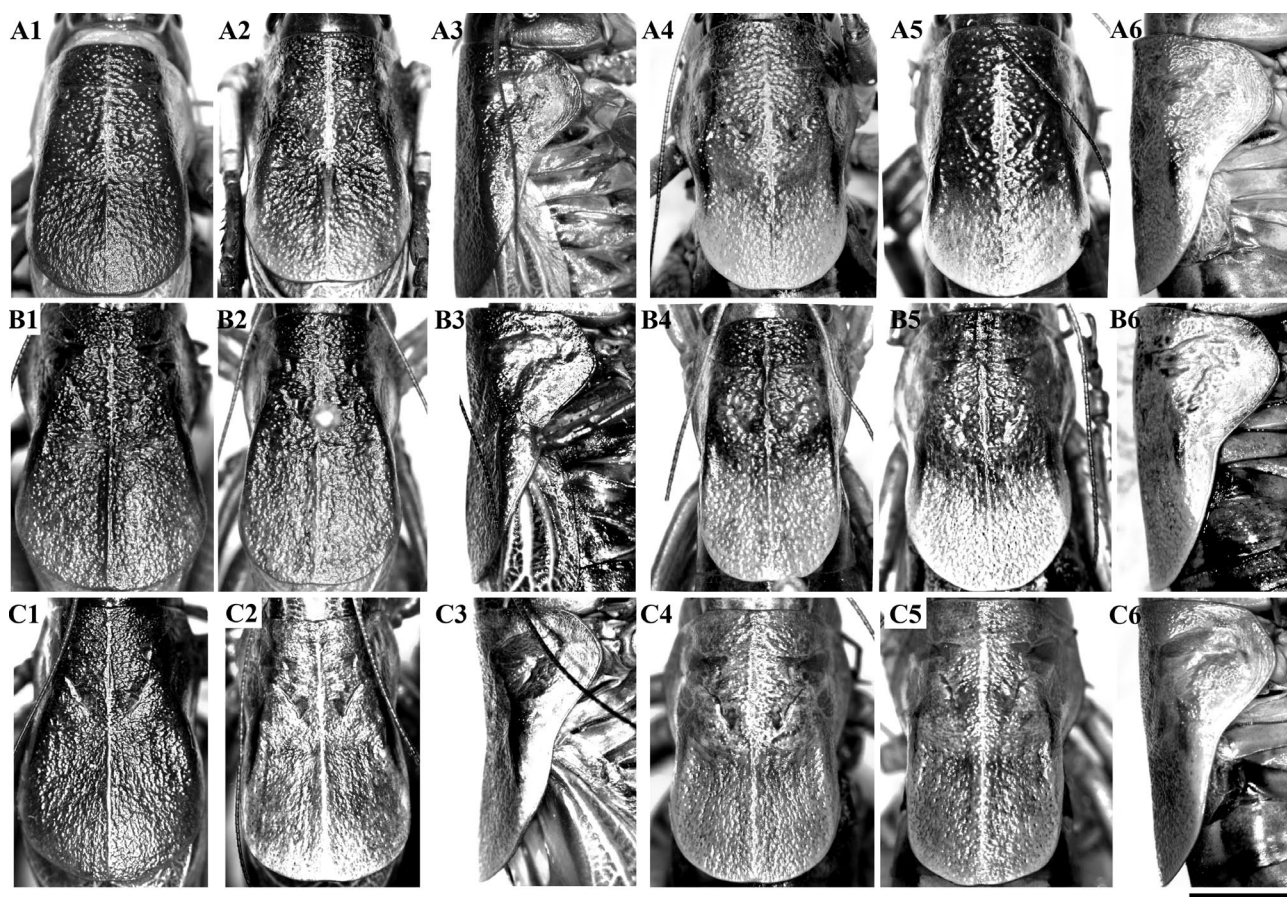


Fig. 4. Pronota of Balkan *Psorodonotus* (1–3 – males, 4–6 – females; 1, 2, 4, 5 – dorsal, 3, 6 – lateral views): A – *P. fieberi* (Bulgaria, Belassitsa Mt.); B – *P. macedonicus* (B2 – Greece, Oiti Mt.; the rest – Republic of Macedonia, Bistra Mt.); C – *P. illyricus* (Croatia, N.P. Sjevneri Velebit). Scale = 5 mm.

with the *Psorodonotus caucasicus* species group as defined by Kaya et al. (2013), which may be characterized morphologically by the dorsal surface of the pronotum being distinctly rugose but less so than in the *venosus* species group (smooth or slightly wrinkled in the *specularis* group). For their general appearance see Fig. 2. Graphs of the results of the CV analyses of matrices of partial warp scores recorded for male and female pronota, cerci and ovipositors are presented in Fig. 3.

CV analysis of male and female pronota (Fig. 3A, B) revealed significant variation within populations and a possible smooth transition between taxa, which is supported by the results of visual observations, which did not reveal clear distinctions between the extremes of variation, except in the short metazona of males of *P. fieberi* (compare Fig. 4). Combination of the results of the CV1 and CV2 analyses of the male pronotum separated *P. fieberi* from the other two taxa and revealed an overlap between *P. macedonicus* and *P. illyricus* (Fig. 3A). CV analysis of the partial warp scores for female pronota (Fig. 3B) revealed three bordering but non-overlapping clusters (Mahalanobis Distance, MD = 3.96 [*macedonicus* – *illyricus*], 4.24 [*fieberi* – *macedonicus*], 6.55 [*fieberi* – *illyricus*], p [10,000 permutation rounds] $\ll 0.05$), while, although the male pronota (Fig. 3A) were more similar, nevertheless the analysis also revealed three clusters (MD = 2.73 [*macedonicus* – *illyricus*],

3.54 [*fieberi* – *macedonicus*], 4.10 [*fieberi* – *illyricus*], $p \ll 0.05$).

CV analyses of male cerci (Fig. 3C) and the ovipositor (Fig. 3D) indicated three clear clusters, representing each of the existing taxa. Mahalanobis distances between taxa for cerci are 15.18 for *macedonicus* – *illyricus*, 21.46 for *fieberi* – *macedonicus* and 26.93 for *fieberi* – *illyricus* ($p \ll 0.05$) and those for ovipositors are 8.82 for *macedonicus* – *fieberi*, 9.09 for *macedonicus* – *illyricus* and 16.58 for *fieberi* – *illyricus* ($p \ll 0.05$). Male cerci (Fig. 5A2, A3, B3, B4, C2–4) are clearly qualitatively different although some specimens of *P. fieberi* and *P. macedonicus* are similar in this character and there is a clear transition in the shape of the ovipositors (Fig. 6A1, A2, B1, B2, C1, C2). In addition, there is a transition between taxa in the shape of the tegmina of males (Fig. 5A1, B1, B2, C1) and subgenital plate of males (Fig. 5A4, A5, B5, B6, C5, C6) and females (Fig. 6A3, B3, B4, C3–5), whereas the titillators (Fig. 7) were more useful for distinguishing taxa.

Bioacoustics

Acoustically, the *Psorodonotus caucasicus* group is characterized by a song consisting of syllables (monosyllabic phrases if compared to the other two species groups of this genus) that are composed of two isolated elements (possibly resulting from a step-interrupted closing move-

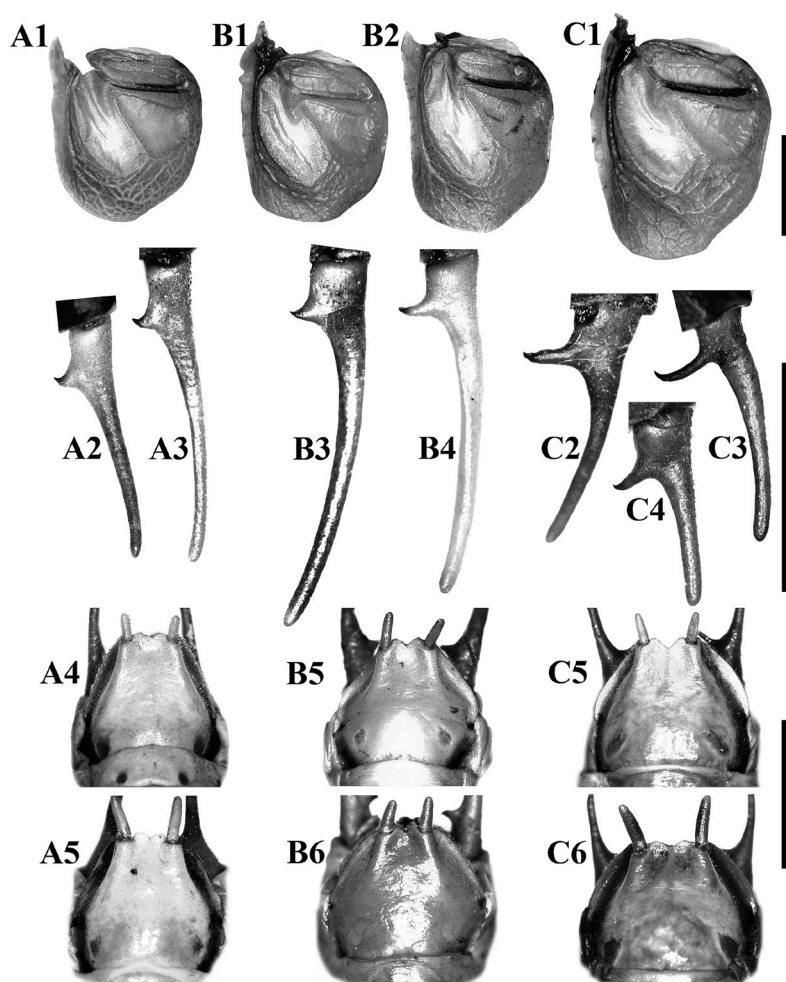


Fig. 5. Morphology of male tegmina (A1, B1, B2, C1), cerci (A2, A3, B3, B4, C2, C3, C4) and subgenital plate (A4, A5, B5, B6, C5, C6) of Balkan *Psorodonotus*: A – *P. fieberi* (A3 – Bulgaria, Stara Planina Mts; the rest – Bulgaria, Belassitsa Mt.); B – *P. macedonicus* (B4 – Montenegro, Bjelasica Mt.; the rest – Republic of Macedonia, Bistra Mt.); C – *P. illyricus* (C2 – Montenegro, Žabljak; C3 – Bosnia and Hercegovina, Donje Bare; the rest – Croatia, N.P. Sjeverni Velebit). Scale = 5 mm.

ment of the tegmina). This is the main difference between the *P. caucasicus* group and the *P. specularis* and *P. venosus* groups, in which two or more syllables are grouped into phrases (oscillographically consisting of three or more song elements) (Kaya et al., 2013, 2014).

The syllable (Fig. 8) consists of a quiet (low amplitude) first element, which may be compact (*P. fieberi*, *P. macedonicus*) or separated into two parts (*P. illyricus*), and after a short silent interval, a second (main) element. The main element starts with a crescendo of dense impulses, in which the maximum amplitude is reached and then the impulses become sparser at the end of the element. The main element may finish abruptly (in *P. illyricus*) or be followed by a few isolated impulses or after-clicks (*P. fieberi* and *P. macedonicus*). There is a tendency for the number of after-clicks to increase with decrease in body temperature. Syllable length and syllables repetition rate depend on temperature. As all the recordings of *P. illyricus* obtained in this study do not seem to reflect the real body temperature (the animals were exposed either to sun or to the light from an incandescent lamp, see Table 1) the approximate body temperature during recordings was determined by comparing the data of Keuper et al. (1988), Weidemann (1993)

and Jatho et al. (1994) and the temporal parameters in relation to the temperature change recorded in *P. macedonicus*. Weidemann (1993) records a 90–120 ms length of the main syllable element of *P. illyricus* at about 24°C, which we find the most reliable measurement. Furthermore, some differences in the syllables repetition rate were recorded (see Fig. 8, Table 2).

Molecular data and phylogeny

After alignment and trimming, the final length of COI sequences was 1111 bp. Of the 1111 aligned sites, 873 sites were constant, 238 were variable, and 178 were parsimony informative. We used 73 ingroup and 4 outgroup sequences, that represented 40 different haplotypes. Of those 15 ingroup and 4 outgroup haplotypes were used in the phylogenetic analyses. As early analyses indicated for haplotypes of *P. caucasicus* clustering within the haplotypes of the Balkan populations, one haplotype per *P. specularis* and *P. venosus* was used as the outgroup in later analyses and MP, ML and BI analyses with this setting are presented. jModeltest suggested the Tamura-Nei model based on the AIC value.

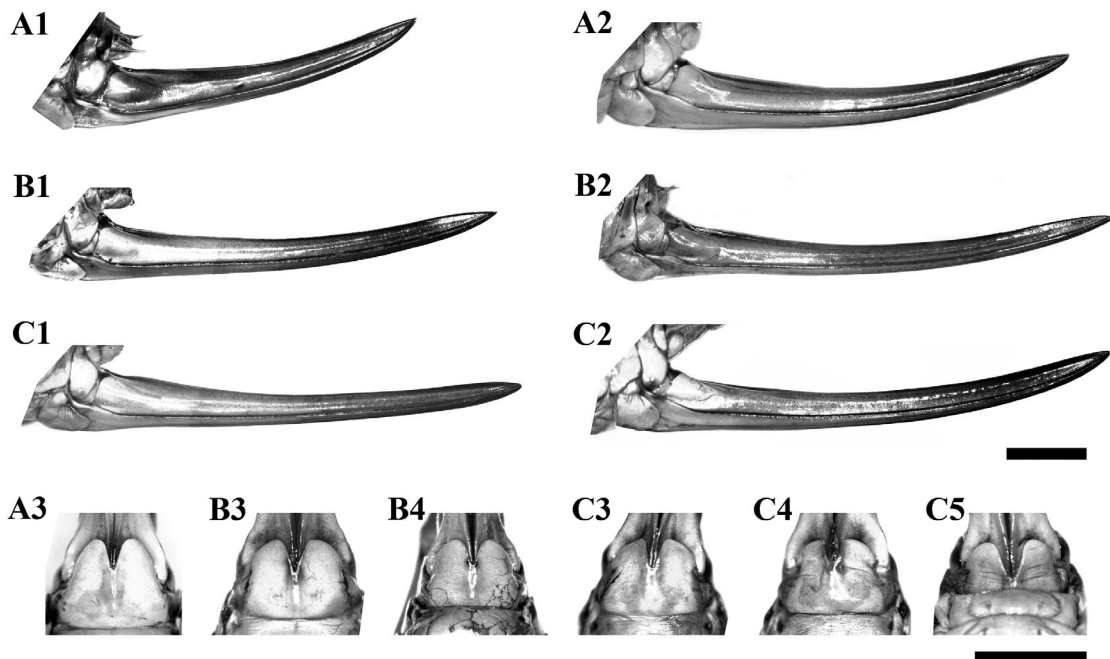


Fig. 6. Morphology of female ovipositor (A1, A2, B1, B2, C1, C2) and subgenital plate (A3, B3, B4, C3–C5) of Balkan *Psorodonotus*: A – *P. fieberi* (Bulgaria, Belassitsa Mt.); B – *P. macedonicus* (B1 – Republic of Macedonia, Bistra Mt; B2 – Greece, Metsovon); C – *P. illyricus* (Croatia, N.P. Sjeverni Velebit; Note: in C5 the base of plate is covered by the seventh sternite). Scale = 5 mm.

The MP, ML and BI analyses resulted in similar tree topologies (Fig. 9). Most of the nodes were constant in all trees with high bootstrap (MP and ML) or posterior probabilities (BI) supporting the following results: (1) *P. caucasicus* forms a clade together with the three Balkan taxa; (2) *P. caucasicus* and *P. macedonicus* form a monophyletic clade; (3) monophyly of haplotypes of each taxon. MP, ML and BI trees differed in topology for the relationships of the three main clades, (*P. caucasicus* + *P. macedonicus*), *P. fieberi* and *P. illyricus*. The BI indicated [(*caucasicus* + *macedonicus*) + *fieberi*] + *illyricus* whereas the MP/ML trees indicated trichotomy. Pairwise genetic distances among the three Balkan phylogroups (36 haplotypes) corrected by the Tamura-Nei model were as follows (net between mean/ between group mean): *fieberi* – *illyricus* = 0.069/0.080, *fieberi* – *macedonicus* = 0.072/0.080, *macedonicus* – *illyricus* = 0.078/0.085.

Discussion and taxonomic conclusions

So far, the Balkan populations of *Psorodonotus* have been treated in various systematic studies, either as three distinct species, three subspecies of two species, or subspecies of a single variable species (Ramme, 1931, 1951; Mikšić, 1965; Harz, 1969; Heller, 1988). New recently accumulated data indicate a better view of speciation within *Psorodonotus*, which in allopatric taxa have resulted in weaker morphological and acoustic differentiation, though genetic differences frequently point to early lineage separation (Kaya et al., in prep.). On the other hand, sympatric/parapatric taxa are clearly distinct (Kaya et al., 2014). Present data revealed good morphological distinction between *P. fieberi*, *P. macedonicus* and *P. illyricus*, similar to or even bigger than that recorded within well separated lineages of the *P. venosus* (Kaya et al., 2013) and *P. specularis*

(Kaya et al., 2014) species groups. Although the differences in song between the Balkan taxa are weaker (this paper) nevertheless they are within the interspecific range of distinction of the other lineages (see last citations). This is not surprising as divergence in song is usually slower in the case of allopatry (Heller, 2006; Çıplak et al., 2009). Most important support for the distinctiveness of the Balkan species comes from molecular data as all of the phylogenetic analyses confirmed the species are monophyletic. In addition, pairwise genetic divergence between species is high, about or above the mean for closely related allo-/parapatric orthopterans (e.g., Allegrucci et al., 2005; Shapiro et al., 2006) and even about the mean between-families distances recorded for some insect orders (Hebert et al., 2003). Our data indicated that the significant genetic distances between selected taxa were largest between *P. macedonicus* and *P. illyricus*. Interestingly, in all trees *P. caucasicus* is a sister group of *P. macedonicus*.

Our results do not support the opinion of Mikšić (1965) and Ingrisch & Pavičević (2012) that the populations in Montenegro are intermediate forms between *P. illyricus* and *P. macedonicus*. The specimens from Eastern Montenegro (Bjelasica Mt. S of Tara River) identified here as *P. macedonicus* grouped within the latter together with specimens from Western Macedonia and Northern Greece, while specimens from Northern Montenegro (N of Tara River) fit *P. illyricus* and group within it in the CV analysis. According to Mikšić (1965) the lengths of the cerci of specimens from Montenegro differ and the titillator shape is intermediate. Though the apical parts of cerci were indeed longer in specimens from Northern Montenegro and Southern Bosnia and Hercegovina (see Fig. 5C2, C3), the shape of their bases and the cercal spine clearly put these

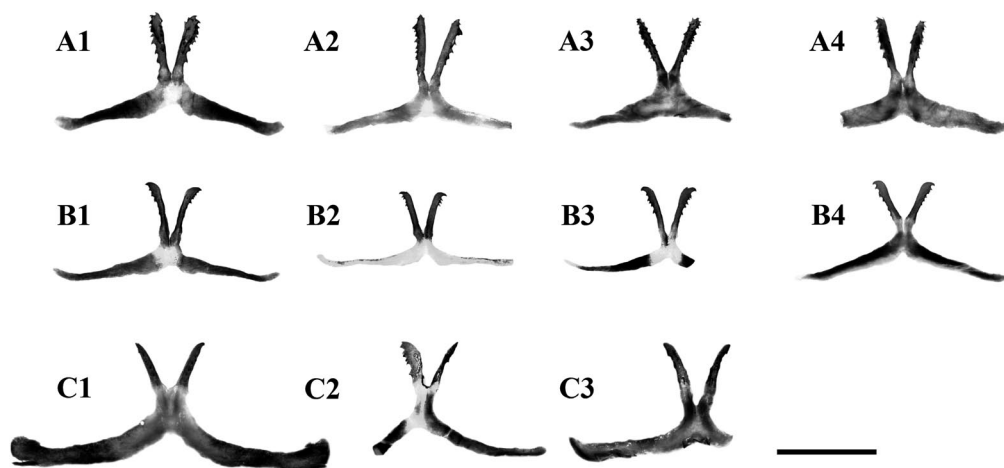


Fig. 7. Morphology of male titillators of Balkan *Psorodonotus*: A – *P. fieberi* (A1, 2 – Bulgaria, Belassitsa Mt.; A3, A4 – Bulgaria, Stara Planina Mts); B – *P. macedonicus* (B1, 2 – Republic of Macedonia, Bistra Mt.; B3 – R Macedonia, Jablanica Mt.; B4 – Montenegro, Bjelasica Mt.); C – *P. illyricus* (C1 – Croatia, Poštak Mt.; C2 – Bosnia and Herzegovina, Donje Bare; C3 – Montenegro, Šavnik). Scale = 2 mm.

animals within *P. illyricus*. Our small sample from this area cannot rule out the absence of intermediate forms. However all specimens studied could be related to a respective taxonomic unit. In terms of the male titillators, the specimens of *P. illyricus* and *P. macedonicus* in general differed with shorter and wider apical titillator arms in *P. illyricus* and more prominent with longer and stouter basal arms in *P. illyricus* (compare Fig. 7B with C). The gracile basal arms of the titillator of a specimen of *P. illyricus* from Bosnia and Herzegovina (Fig. 7C2; note the left apical arm is distorted) may be due to the weak sclerotization. Its geographic origin between Montenegro and Croatia indicates rather intraspecific variation than intermediate (i.e., hybrid) populations as stated by Mikšić (1965) and Ingrisch & Pavičević (2012) for specimens from Montenegro. In addition, differences in the shapes of the titillators of *P. illyricus* and *P. macedonicus* are similar to those among the latter taxa and other representatives of the *caucasicus* species group (*P. ebneri*, *P. caucasicus*) or even representatives of other species groups (e.g., *P. venosus*, *P. specularis*, etc.) (compare Ramme, 1951; Kaya et al., 2013, 2014). On the other hand, the shape of the titillator of *P. fieberi* (Fig. 7A) clearly distinguished this species.

Both the geometric morphometrics and molecular phylogeny presented in this study confirm the species status of the three taxa on the Balkan Peninsula: *P. fieberi*, *P. illyricus* and *P. macedonicus*. Our results also indicate an interesting phylogeographic pattern in the *P. caucasicus* species group with *P. caucasicus* placed within the Balkan lineage. However, in order to reveal the evolutionary history of the latter a comprehensive phylogeographic study based on mitochondrial and nuclear DNA phylogenetic

analyses (Kaya et al., in prep.) and ecological niche modelling is needed.

***Psorodonotus fieberi* (Frivaldszky in Fieber, 1853)**

Figs 2A, 3, 4A, 5A, 6A, 7A, 8A, 9, 10, Tables 2, 3

Pterolepis fieberi: Fryvaldszky [Frydvaldsky] in Fieber, 1853: 154.

Psorodonotus pancici: Brunner von Wattenwyl, 1861: 7(291).

Psorodonotus fieberi: Herman, 1874: 208.

Psorodonotus fieberi: Brunner von Wattenwyl, 1882: 367 (incl. *P. pancici*, syn. n.).

Psorodonotus fieberi fieberi: Ebner, 1923: 250, 251.

Psorodonotus fieberi: Mikšić, 1965: 203–213.

Psorodonotus fieberi fieberi: Heller, 1988: 134, 135 (sensu novo).

Morphological description

See the references above; Harz, 1969 (as *fieberi fieberi*).

Bioacoustics: Heller, 1988 (as *fieberi fieberi*).

General description and diagnosis

Males usually brownish (brownish-violet), females mostly green (rarely females also brown) (Fig. 2A1, 2). Male pronotal (Fig. 4A1–3) disc is strongly rugose (with distinct dense dents), less widened in the metazona (but some exceptions are present). The metazona is short with the transverse furrow behind the middle of the pronotum (rarely at its middle) and the hind pronotal sulcus reaching the median keel slightly before the middle of the pronotum. The female pronotal (Fig. 4A4–6) disc also usually with short and narrow metazona (though may be similar to that of male), less rugose than in male but more than in other species. Male tegmina (Fig. 5A) usually reach the third tergite. Male cerci (Fig. 5A2, 3) longer than cerci of *P. illyricus* and shorter than those of *P. macedonicus*, apical part

TABLE 2. Differences in the structure and amplitude-temporal song pattern of Balkan *Psorodonotus*.

Taxon	Syllables repetition rate at 23–28°C	Length of main element at ~25°C	Presence of after-clicks	Number of after-clicks
<i>fieberi</i>	(?0.2)0.3–0.6 Hz	70–100 ms	yes	>1
<i>macedonicus</i>	0.4–1 Hz	50–80 ms	yes	>1
<i>illyricus</i>	1–3 Hz	90–120 (–150?) ms	no/yes	0–1

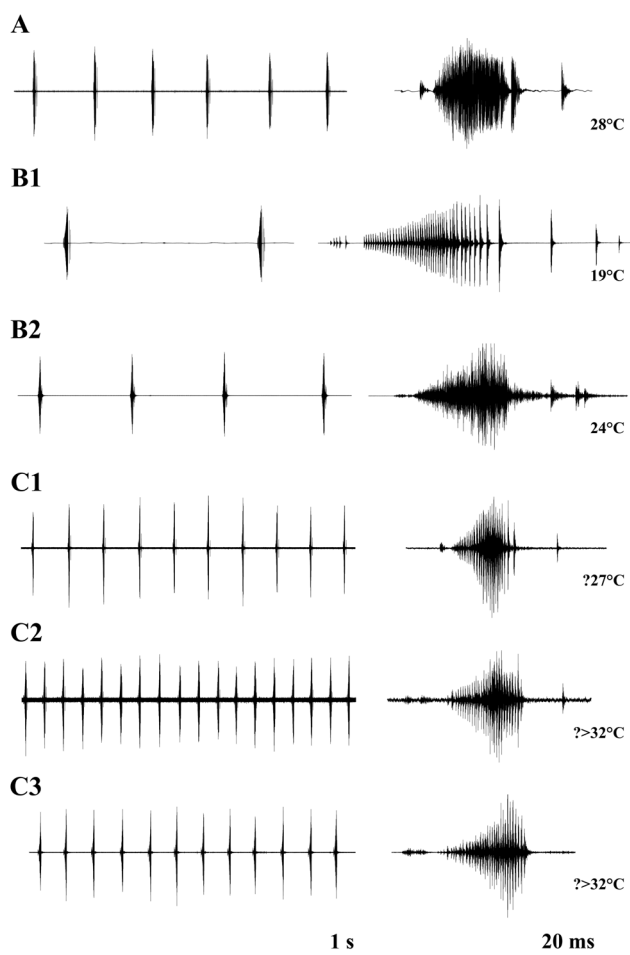


Fig. 8. Oscillograms of the song of Balkan *Psorodonotus*, recorded at different temperatures and two different speeds: A – *P. fieberi* (Bulgaria, W Stara Planina Mts, Midzhur Peak); B – *P. macedonicus* (B1 – Greece, Ioannina, Epirus, lake near Mets-ovon, rec. PSMA0401; B2 – Republic of Macedonia, Bistra Mt., Carevec pass); C – *P. illyricus* (C1 – Montenegro, Durmitor N.P., Pivska Planina Mt., Jarčište vill., rec. S. Ingrisch; C2 – Croatia, Rijeka, Učka Mt., rec. S. Ingrisch; C3 – Croatia, Rijeka, Učka Mt., rec. PSIL7904).

(from the tooth to the tip) over 2 times and up to 3.5 times longer than the basal part (from base to the tooth); base of cerci 3–4 times wider than the apex; cercal tooth similar in length but usually wider than that of *P. macedonicus*. Titillator (Fig. 7A) wider apically with strong teeth distributed in two or more rows; basal arms short, wide medially and narrowing laterally. Female subgenital plate (Fig. 6A3) elongated with a moderately deep incision being up to one-third of the length of the plate and forming narrow apical lobes. Ovipositor (Fig. 6A1, 2) variable in curvature and length (23.5–32 mm; Harz, 1969) but is usually stouter than in other taxa, wide at its base and gently narrowing towards the tip. Average length of ovipositor is the shortest among these three taxa (Table 3). Hind femora in the specimens studied contrary to the statement by Mikšić (1965) did not differ significantly in length (but mean values lower than in other taxa) or in the ratio length: width from those of the other two taxa (Table 3; see also Harz 1969).

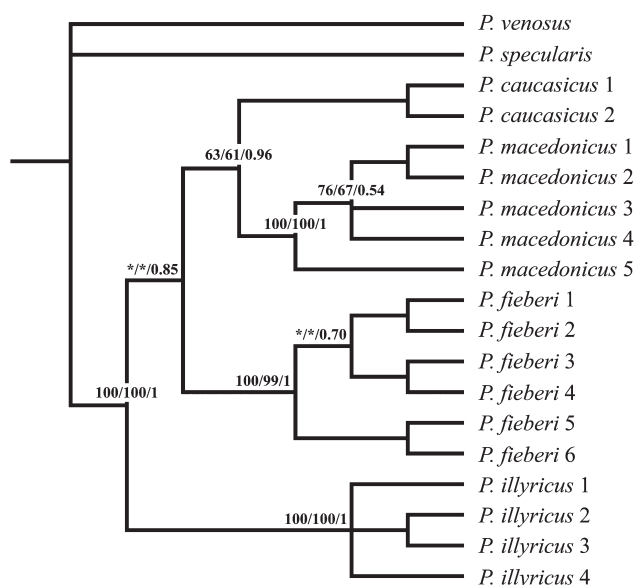


Fig. 9. Phylogenetic tree based on the Bayesian analysis of 15 haplotypes of Balkan and four haplotypes of Anatolian *Psorodonotus*. MP/ML bootstrap proportions (values > 50) and BI internode posterior probabilities (values > 0.50) are shown on BI-resolved internodes.

Song (Fig. 8A) consists of sparsely repeated syllables (0.3–0.6 Hz at 23–28°C) that contain a compact main element and well detached after-clicks.

Distribution

Fig. 10, Appendix 2. *P. fieberi* occurs in the Balkan (Stara Planina) Mountains, Macedonian-Thracian Massif (Rhodopean Mts s.l.) and the eastern arc of the Dinaric Mountain Range (Bulgaria, E Serbia, E Republic of Macedonia, NE Greece). The border of its range in the North is the Danube River valley, in the East – the lower parts of the Stara Planina Mts and Rhodope Mts, and in the South – the southern slopes of the Macedonian-Thracian Massif. In the West the known range of the species, mostly according to Mikšić (1965), borders the ranges of *P. macedonicus* and *P. illyricus*, approximately following the valleys of the Vapa, Lim, Drina, Ibar (Ibër), Sitnicë, Pchinja and Vardar Rivers, but it is not known where this border connects with the Pchinja and Sitnicë valleys. The exact border of its range, e.g., the locality “Tara Mt.” (Grebenshchikov, 1950; Mikšić, 1965) is not well defined.

The locality “Kasikoparan (Armenien)” (present Turkey) recorded by Ebner (1923; as *P. fieberi fieberi*) and “Armenia” (Jacobson & Bianchi, 1905) is herewith referred to *P. caucasicus* (Fischer von Waldheim, 1846). The record by Ebner (1923) from “Kalakend, Karabagh” (Kalakend Settlement in Nagorno-Karabakh Republic) is also possibly for *P. caucasicus*. The record by Ebner (1923) of *P. illyricus* from Bulgaria may either be a misidentification or the result of wrong labeling.

This species inhabits open grass-herbaceous plant associations, usually with *Juniperus communis alpina*, the bushes of which it uses for protection. It occurs within the altitudinal range 1100–2300/2400 m alt. (usually between 1500 and 2200 m).

TABLE 3. Measurements recorded for some of the morphological structures of Balkan *Psorodonotus*. Measurements are given in mm: first row – Min–Max values, in brackets – Average \pm Standard deviation and number.

	<i>P. fieberi</i>		<i>P. macedonicus</i>		<i>P. illyricus</i>	
	males	females	males	females	males	females
Pronotum length	11.1–12.7 (12.0 \pm 0.5, n = 16)	11.9–12.7 (12.4 \pm 0.3, n = 5)	10.1–13.7 (12.2 \pm 1.0, n = 11)	11.9–13.6 (12.8 \pm 0.6, n = 11)	11.6–14.6 (12.7 \pm 0.7, n = 25)	12.3–14.3 (13.1 \pm 0.4, n = 19)
Hind femur length	20–22.5 (20.8 \pm 0.7, n = 14)	21.5–23.5 (22.5 \pm 0.9, n = 4)	20.5–24 (22.4 \pm 1, n = 8)	21–26 (23.6 \pm 1.4, n = 12)	19–25.4 (22.6 \pm 1.7, n = 24)	21.6–27 (23.5 \pm 1.1, n = 24)
Ratio length : width of hind femur	4.6–5.7 (5.2 \pm 0.3, n = 14)	5.4–5.9 (5.7 \pm 0.2, n = 4)	4.9–5.8 (5.2 \pm 0.3, n = 8)	5.2–6 (5.7 \pm 0.3, n = 12)	4.4–5.8 (5.1 \pm 0.3, n = 24)	4.5–6 (5.2 \pm 0.4, n = 24)
Number of stridulatory teeth	88–124 (105 \pm 12, n = 16)	–	103–128 (112 \pm 9, n = 11)	–	91–125 (108 \pm 8.5, n = 11)	–
Ovipositor length	–	22.2–26.5 (23.6 \pm 1.6, n = 5)	–	23.1–29.2 (25.1 \pm 2.0, n = 9)	–	26.2–30.2 (28.3 \pm 1.1, n = 18)

Psorodonotus macedonicus Ramme, 1931

Figs 2B, 3, 4B, 5B, 6B, 7B, 8B, 9, 10, Tables 2, 3

Psorodonotus macedonicus: Ramme, 1931: 184.

Psorodonotus illyricus macedonicus: Mikšić, 1965: 203–213.

Psorodonotus fieberi macedonicus: Heller, 1988: 134, 135.

Morphological description

See the references above; Harz, 1969 (as *illyricus macedonicus*). *Bioacoustics*: Heller, 1988; Ingrisich & Pavičević, 2012 (partim[?] as *illyricus illyricus* / *illyricus macedonicus* intermediate form). *Karyology*: Warchałowska-Śliwa et al., 2005 (as *illyricus macedonicus*).

General description and diagnosis

Male usually brownish (brownish-violet), females mostly green (rarely are females also brown) (Fig. 2C1, 2). Male pronotal (Fig. 4B1–3) disc is less rugose than in *P. fieberi*, but similar to that of *P. illyricus*; metazona is strongly widened or sometimes elongated, shovel-like. The metazona is long with a transverse furrow (sulcus) before the middle of the pronotum (rarely at its middle). Female pronotal (Fig. 4B4–6) disc usually with a longer metazona than in *P. fieberi* and a less rugose surface; however, distinction by the female pronotum may be difficult. Male tegmina (Fig. 5B1, 2) similar in shape to those of *P. fieberi* or slightly elongated and reaching the third tergite. Male cerci (Fig. 5B3, 4) much longer than those of *P. illyricus* and longer or about the same length as those of *P. fieberi* but the basal part is very short, between over 5 to 6 times shorter than the apical part; base of cerci 2–3 times wider than the apical part; cercal tooth similar in length but narrower than that of *P. fieberi* and shorter than that of *P. illyricus*. Titrator (Fig. 7B) narrower apically bearing one row of teeth (rarely additional small teeth present on its dorsal surface); its basal part similar in length to that of *P. fieberi* but usually thinner, especially medially. Female subgenital plate (Fig. 6B3, 4) is shorter than that of *P. fieberi*, with wider apical lobes and incision reaching the middle of the sclerite. Ovipositor (Fig. 6B1, 2) varies in curvature and length (23.8–27 mm; Harz, 1969) but on average is longer than that of *P. fieberi* (Table 3); it is usually more slender than that of *P. fieberi* and generally slightly stouter or similar to that of *P. illyricus*. Hind femora in the specimens studied

slightly longer than in *P. fieberi* (mean values) and very similar in length to those of *P. illyricus*, but with greater ratio length: width (Table 3).

Song (Fig. 8B) consists of sparsely repeated syllables with a slightly higher repetition rate than recorded for *P. fieberi* (0.4–1 Hz at 23–28°C). The main element starts with a compact impulse series and usually ends (especially at low temperatures) with a sparse sequence of impulses, the last of which resemble after-clicks.

Distribution

Fig. 10, Appendix 2. Occurs throughout the Pindos Mountain Range, mountains of the Pelagonia horst-anticlinorium and southern part of the Dinaric Mountain Range (Greece except Peloponnese, Republic of Macedonia, Albania, W Kosovo, S Montenegro and possibly partly Serbia). The borders with the ranges of *P. fieberi* and especially *P. illyricus* are not clear. The border with the latter possibly passes along the Drina – Tara River Valleys, where contact between populations or a hybrid zone is suspected. The locality in Skopska Crna Gora Mt. (N R Macedonia) belongs to a geographically intermediate region between the Pindo-Dinaric Range and Macedonian-Thracian Massif, but as the specimens from there have not been included in a special study (e.g., by Mikšić, 1965), their taxonomic affinity needs to be confirmed.

This species inhabits open grass-herbaceous plant associations, usually with higher humidity than those inhabited by *P. fieberi* and is even recorded from peat bogs. This species is recorded within the altitudinal range (?1200) 1400–2500 (?2600) m alt., where it is common between 1500 and 2200 m.

Psorodonotus illyricus Ebner, 1923

Figs 2C, 3, 4C, 5C, 6C, 7C, 8C, 9, 10, Tables 2, 3

Psorodonotus fieberi illyricus: Ebner, 1923: 250, 251.

Psorodonotus illyricus illyricus: Mikšić, 1965: 203–213.

Psorodonotus fieberi illyricus: Heller, 1988: 134, 135.

Morphological description

See the references above; Ramme, 1931 (as *fieberi illyricus*); Harz, 1969 (as *illyricus illyricus*). *Bioacoustics*:

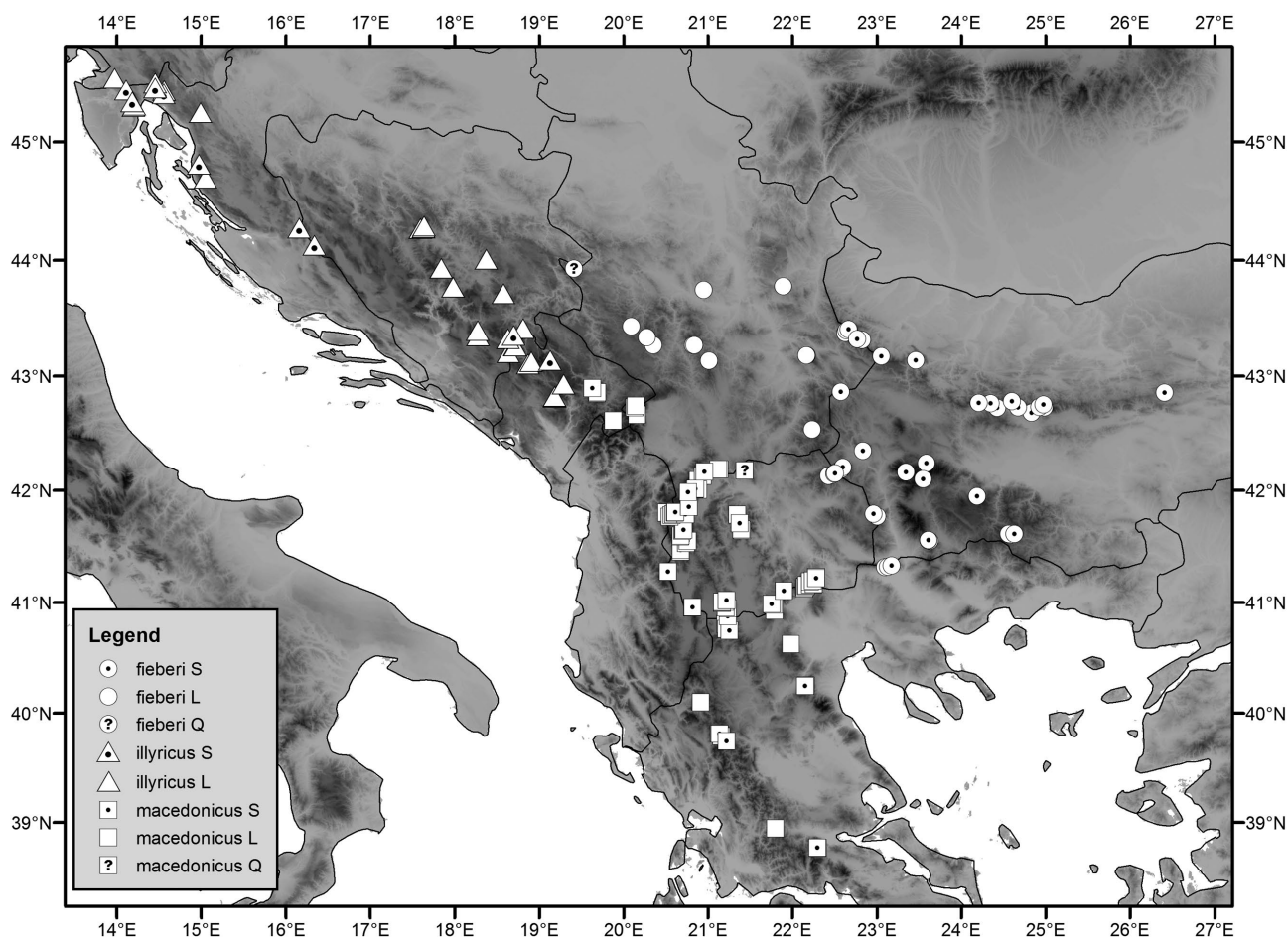


Fig. 10. Map showing the distribution of the genus *Psorodonotus* in the Balkan Peninsula: circles – *P. fieberi*, squares – *P. macedonicus*, triangles – *P. illyricus*. Open signs – literature data (L), signs with a centered dot – studied material (S), question mark – doubtful identification (Q).

Heller, 1988; Keuper et al., 1988; Weidemann, 1993; Jatho et al., 1994.

General description and diagnosis

Either a greenish or brownish (brownish-violet) colour seems to be common in this taxon, while in different populations one of these colours may dominate (Fig. 2C1, 2). Male pronotal (Fig. 4C1–3) disc is the least rugose of the three taxa with the metazona sometimes almost smooth. The metazona is notably wider and longer than the prozona if compared to *P. fieberi*, the transverse furrow (if visible) is located before the middle of the pronotum, and the hind pronotal sulcus reaches the median keel well before the middle of the pronotum. Female pronotal (Fig. 4C4–6) disc with notably elongated metazona, very similar to that of *P. macedonicus*. Male tegmina (Fig. 5C1) wider and longer than in the other two taxa and usually covering the third tergite. Male cerci (Fig. 5C2–4) much shorter than in the other two species with a very wide basal part and a long tooth; basal part 2–2.5 (rarely up to 3.5) times shorter than the apical part; base of cerci 3–7 times wider than the apical part. Titillator (Fig. 7C) similar to that of *P. macedonicus* apically but the arms are usually shorter and wider; its basal arms very wide, much stouter than those of *P. macedonicus* (with some exceptions, e.g., see Fig. 7C2), and

very long (longer than in the other taxa). Female subgenital plate (Fig. 6C3–5) resembles that of *P. macedonicus* but the excision may be wider and deeper, exceeding the middle of this sclerite. Ovipositor (Fig. 6C1, 2) varies in curvature and length (26–31 mm; Harz, 1969) but is usually more gracile than in *P. fieberi*, elongated and less wide at its base, and on average the longest of the three taxa (Table 3). Hind femora in the specimens studied the longest of the three species, with lowest ratio length: width, but the values overlap with the other taxa (Table 3).

Song (Fig. 8C) consists of densely repeated syllables (syllables repetition rate highest for these three taxa) (1–3 Hz at 23–28°C). The main element is the longest of the taxa studied at a particular temperature and lacks after-clicks (though at low temperatures the last impulses may be separated by longer intervals as in *P. macedonicus*).

Distribution

Fig. 10, Appendix 2. Occurs along the Dinaric Mountain Range from Istra Peninsula in S Slovenia and NW Croatia, through Bosnia and Herzegovina to the central regions of Montenegro. It is possibly isolated from populations of *P. macedonicus* to the South/South-east by the Drina and Tara River Valleys, where it is suspected populations come into contact and there may be a hybrid zone. Ebner (1923)

records a locality for *P. illyricus* in Bulgaria ("Bulgarien") but this may be the result of wrong label.

This species inhabits open grass/herbaceous plant associations in the colline to subalpine mountain zones. It seems less sensitive to drought and high temperature than the other two taxa. This species is recorded at altitudes between 800 and 1800 m.

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APPENDIX 1. Material of *Psorodonotus* used for geometric morphometrics and/or molecular phylogenetic analysis.

Identification	Geographic range / Country	Locality, date, number of studied specimens	Geographic position	Collector	Code of haplotypes used in the analysis
<i>fieberi</i>	Balkan Mts / Bulgaria	W Stara Planina Mts, Purshevitsa Lodge, 1350–1450 m, 18.09.2012, 1♂	43.14249°N 23.47067°E	D. Chobanov	<i>P. fieberi</i> 5
<i>fieberi</i>	Balkan Mts / Bulgaria	W Stara Planina Mts, Midzhur Peak, 1900 m, 9.09.2012, 1♂	43.40810°N 22.66795°E	D. Chobanov	<i>P. fieberi</i> 6
<i>fieberi</i>	Balkan Mts / Bulgaria	C Stara Planina Mts, Vezhen Peak, 1600 m, 22.09.2012, 1♂	42.72646°N 24.42808°E	D. Chobanov	<i>P. fieberi</i> 4
<i>fieberi</i>	Balkan Mts / Bulgaria	C Stara Planina Mts, Ravnets ridge above Karlovo, ~1950 m, 25.09.2012, 1♂	42.681°N 24.853°E	D. Chobanov	–
<i>fieberi</i>	Balkan Mts / Bulgaria	C Stara Planina Mts, Botev Peak, 2150 m, 30.09.2012, 1♂	42.73094°N 24.92817°E	D. Chobanov	<i>P. fieberi</i> 3
<i>fieberi</i>	Macedonian-Thracian Massif / Bulgaria	Belassitsa Mt., Kongur Peak, 1860 m, 12.08.2011, 11♂♂, 5♀♀	41.32459°N 23.17166°E	D. Chobanov	<i>P. fieberi</i> 1, 2
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / Greece	Oiti Mt., Ipati Refuge SW Lamia, 1800–1900 m, 11/13.08.1973, 1♂, 1♀	38.76667°N 23.3°E	F. Willemse	–
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / Greece	3 km N of Metsovon [Metsovo], 1400 m, F. Willemse, 1♂, 1♀	39.79°N 21.162°E	F. Willemse	–
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / R Macedonia	Jablanica Mt., Strizhek Peak, 1900–2000 m, 18/19.07.2006, 2♂♂	41.28°N 20.53°E	D. Chobanov	<i>P. macedonicus</i> 5
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / R Macedonia	Bistra Mt. (Mavrovo NP), 1800 m, 26.07.1969, 1♂, 1♀	–	F. Willemse	–
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / R Macedonia	Bistra Mt., Tonivoda highland, 1625–1700 m, 18.07.2013, 5♂♂, 7♀♀	41.64383°N 20.69788°E	D. Chobanov	<i>P. macedonicus</i> 3, 4
<i>macedonicus</i>	S Pindo-Dinaric Mt Range / R Macedonia	Korab Mt., Strezimir-Kobilino Pole, 1800–2300 m, 16.07.2013, 1♂, 2♀♀	41.79366°N 20.59361°E	D. Chobanov	<i>P. macedonicus</i> 1, 2
<i>macedonicus</i>	N Pindo-Dinaric Mt Range / Montenegro	Biogradska Gora NP, Virgin Forest Reserve, 1730 m, 25.07.2001, 1♂, 1♀	42.897°N 19.6324°E	M. Langourov	–
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Montenegro	Šavnik, Gvozd Peak, 1440 m, 2.08.1963, 1♂	42.9748°N 19.1476°E	F. Willemse	–
<i>illyricus</i>	N Pindo-Dinaric Mountain Range / Montenegro	Durmitor NP, Žabljak, 1450 m, 2.08.1963, 1♂	43.1357°N 19.133°E	F. Willemse	–
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Bosnia and Herzegovina	Sutjeska NP, Dragos Sedlo, 1000 m, 2.08.1963, 1♀	43.353°N 18.704°E	F. Willemse	–
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Bosnia and Herzegovina	Sutjeska NP, Donje Bare, 1500 m, 2.08.1963, 1♂	43.322°N 18.632°E	F. Willemse	–
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Croatia	NP Sjeverni Velebit, Vučjak peak, 1530 m, 11.08.2013, 6♂♂, 14♀♀	44.81175°N 14.97403°E	J. Skejo, N. Tvrtković	<i>P. illyricus</i> 3, 4
<i>illyricus</i>	N Pindo-Dinaric Mt Range / Croatia	Poštak Mt., Ljubina Poljana, 1050 m, 17.08.2013, 6♂♂	44.27246°N 16.15848°E	N. Tvrtković, M. Malenica	<i>P. illyricus</i> 1, 2
<i>illyricus</i>	N Pindo-Dinaric Mountain Range / Croatia	Istra Peninsula, Učka Mt., 700–1000 m, 15/16.08.1972, 1♂	45.306°N 14.2045°E	F. Willemse	–
<i>caucasicus</i>	Pontic Mountains / Turkey	Erzurum Prov., Tortum-Oltu, Yayla Pass, 2284 m, 3.08.2012, 2♂♂	40.44426°N 41.62466°E	B. Çıplak, S. Kaya	<i>P. caucasicus</i> 1, 2
<i>venosus</i>	Lesser Caucasus / Turkey	Ardahan Prov., Çıldır, 1940 m, 4.08.2012, 1♂	41.12459°N 42.190636°E	B. Çıplak, S. Kaya	<i>P. venosus</i>
<i>specularis</i>	Lesser Caucasus / Turkey	Ardahan Prov., Çıldır, 1940 m, 4.08.2012, 1♂	41.12459°N 42.190636°E	B. Çıplak, S. Kaya	<i>P. specularis</i>

APPENDIX 2. Locality list of the Balkan *Psorodonotus* from literature and unpublished data.

In the following list we present all published and unpublished localities of the Balkan *Psorodonotus* known to us. Data are arranged into respective taxonomic units after critical review. Doubtful records are shortly commented or related to “*Incertae sedis*”. The localities that were traceable are geographically ref-

erenced using decimal coordinates according to appropriate location and habitat and mapped (Fig. 10 in the text). The localities are arranged mostly in a north-south direction. For published data usually only original references (i.e. such reporting unpublished before information or treating the taxon in a different sense) are used given in brackets. Question marks indicate uncertainty about the respective information.

Abbreviations (others than widely used):

AU – Zoological Collection of the Faculty of Science of Akdeniz University; CC – Collectio Chobanov; CH – Collectio Heller; DC – D. Chobanov leg.; EA – E. Andreeva leg.; HMB – Historical Museum in Blagoevgrad, Bulgaria; JS – Josip Skejo leg. or obs. (nymphal stage); MM – Marta Malenica leg.; GP – Georgi Peshev leg.; MMNH – Macedonian Museum of Natural History, Skopje; SOFM – National Museum of Natural History, Sofia; NT – Nikola Tvrković leg.

Psorodonotus fieberi (Fieber, 1853)

“Rumelien” [either Bulgaria or Serbia] (Fryvaldsky [Frydvaldsky] in Fieber, 1853 as *Pterolepis fieberi*); “Bulgarien” (Ebner, 1923 as *P. fieberi illyricus* [wrong label or identification!]).

Bulgaria (all citations as *P. fieberi* unless specified): **Stara Planina Mts.**: Midzhur Peak, 1900–2000 m (43.40810°N, 22.66795°E), DC, CC; Kom Peak, 2015 m (43.1731°N, 23.0562°E) (Peshev, 1970); Vrachanska Planina, Purshevitsa Chalet, 1400 m (43.1399°N, 23.4631°E), DC, CC; Paskal Peak (42.7687°N, 24.2082°E), M. Vitanova leg., SOFM; Vezhen Peak, 1600 m (42.72646°N, 24.42808°E), DC, CC; Benkovski Chalet, 1800 m (42.7648°N, 24.3522°E) (Peshev, 1974b); “Central Balkan” N.P., 1400–1800 m (e.g., 42.681°N, 24.834°E) (Drenowski, 1929; Buresch & Peshev, 1958); Troyanski Prohod Pass, 1400–1500 m (42.782°N, 24.603°E) (Bey-Bienko & Peshev, 1960); Dermentkaya Chalet (42.728°N, 24.675°E) (Peshev, 1974b); Ravnets Ridge, 1950 m (42.681°N, 24.853°E), DC, CC; Botev Peak, 1800–2000 m (e.g., 42.7272°N, 24.984°E) (Peshev, 1974b) & 2150 m (42.73094°N, 24.92817°E), DC, CC; Tazha Chalet, 1700 m (42.7534°N, 24.9775°E), GP, SOFM; “Stara Planina, Sliven Region” (Nedelkov, 1908); Razboyna Peak, 1128 m (42.8586°N, 26.4134°E) (Peshev, 1974b wrongly as “Kotel surroundings, 600 m”; data corrected with material in SOFM); **Ruy Mt.**: Ruy Peak, 1600–1700 m (42.8638°N, 22.5768°E), DC, CC; **Konyavska Planina Mt.**: above Konyavo Vill. (42.3492°N, 22.8369°E), EA, HMB; **Ossogovska Planina Mts.**: “1500–2253 m” (Drenowski 1927 as *Psorodonotus (Podisma) fieberi* Scudd.; possibly printing error due to the same species name); Ruen Peak slopes, 1800–2200 m (42.1634°N, 22.533°E; 42.1676°N, 22.541°E), DC, CC; 1 km SW Begbunar Place, 1850 m (42.1871°N, 22.5792°E), DC, CC; Kyunek – Choveka Peaks, 1900–1950 m (42.2049°N, 22.5991°E), DC observed; **Maleshevska Planina Mts.**: Ilyov Vruh Peak, 1800 m (41.7691°N, 23.0086°E), DC, CC; **Vlakhina Mts.**: “1500–2000 m” (Peshev & Andreeva, 1986); Kadiytsa Peak, “1700–2000 m” (41.7914°N, 22.9646°E), EA, HMB; **Belassitsa Mt.**: “1600–2000 m” (Peshev 1962); Kongur – Radomir Peaks – Demir Kapiya Pass, 1700–1900 m (41.3330°N, 23.1767°E; 41.3211°N, 23.1351°E; 41.3192°N, 23.0982°E), DC, CC; “above Petrich”, 1600 m & 1700 m & 1800 m, GP, HMB; **Rila Mts.**: Elenin Vruh Peak (e.g., 42.1601°N, 23.3481°E) (Frey-Gessner, 1893); Borovets Resort, 1250 m & 1450 m (localities maybe partly extinct) (Buresch & Peshev, 1958) & to 2200 m (42.2400°N, 23.5900°E) (Peshev, 1990); **Pirin Mts.**: Orelek Peak, 1500–2000 m (41.5538°N, 23.6300°E; 41.5548°N, 23.6130°E; 41.5613°N, 23.6151°E), DC, CC & 1800–2050 m (Peshev & Andreeva, 1986); **W Rhodope Mts.**: “Rodopi” (Nedelkov, 1908; Buresch & Peshev, 1958); Batak Lake (41.9465°N, 24.1910°E) (Chobanov, 2012 as *P. f. fieberi*); Perelik Peak, 1700–2180 m (41.615°N, 24.634°E; 41.6072°N, 24.5784°E) (Peshev, 1975); Shiroka Laka Vill. (e.g., above the village, 41.613°N, 24.562°E) (Chobanov, 2012 as *P. f. fieberi*); Smolyan (not localized) (Chobanov, 2012 as *P. f. fieberi*); Stoykite Vill. (not localized) (Peshev, 1974a, 1975); “above Assenovgrad” (not localized) (Nedelkov, 1908).

Serbia: “alpius Serbiae” (Brunner von Wattenwyl, 1861 as *P. panicci*); **Rtanj Mt.** (Brunner von Wattenwyl, 1861, 1882; Ebner, 1923 as *P. f. fieberi*): 1500 m (43.7769°N, 21.8922°E) (Grebenschikov, 1950; Mikšić, 1965); **Stara Planina Mts.**: “Stara Planina”,

1600–2100 m (Grebenschikov, 1950); Krive [unclear locality position] (Mikšić, 1965); Žarkov Breg [unclear locality position] (Mikšić, 1965); Midžor – Trapanar [unclear locality position] (Mikšić, 1965); Midžor Peak (43.3957°N, 22.674°E) (Mikšić, 1965); Babin Zub (43.3765°N, 22.6275°E) (Mikšić, 1965); Tri Čuke Peak (43.317°N, 22.827°E) (Mikšić, 1965); Zlatibor (possibly Ilatibor in E Serbia) [comment based on data by Chobanov et al., 2013] (Grebenschikov, 1950 after Pančić, 1899); **Suha (Suva) Planina Mt.**: 1750 m (43.1811°N, 22.1741°E) (Brunner von Wattenwyl, 1861, 1882; Ebner, 1923 as *P. f. fieberi*; Grebenschikov, 1950; Mikšić, 1965); “Suva Planina Mt., Mt. Julio” [unclear locality position] (Grebenschikov, 1950; Mikšić 1965); **Besna Kobila Mt.** (42.5344°N, 22.235°E) (Mikšić, 1965); Ječmenište [Peak in **Gledička Planina Mt.** in Serbia; if mountain in Bosnia and Herzegovina, then not *P. fieberi*!] (43.747°N, 20.953°E) (Mikšić, 1965); Užice [possibly Javor Mt.] (Mikšić, 1965); **Javor Mt.** (“M. Javor-Uzica”) (43.431°N, 20.091°E) (Grebenschikov, 1950 after Pančić, 1899; Ebner 1923 as *P. f. fieberi*); **Golija Mt.**: Vrbena [unclear locality position] (Mikšić, 1965); Jankov kamen (43.336°N, 20.277°E) (Mikšić, 1965); 1500–1800 m (43.271°N, 20.357°E) (Grebenschikov, 1950); **Kopaonik Mt.**, 1700–2000 m (43.269°N, 20.825°E) (Grebenschikov, 1950 after Pančić, 1899); Treska [Peak of Kopaonik Mt.] (43.136°N, 21.016°E) (Mikšić, 1965); **Tara Mt.** [*?P. fieberi*] (43.93°N, 19.4125°E) (Grebenschikov, 1950; Mikšić, 1965).

R Macedonia: Ossogovska Plaina Mts.: Ruen ridge, 2000 m (42.1522°N, 22.5091°E), DC observed; Ruen peak slopes (Chashka-Ruen), 1800–2200 m (42.1483°N, 22.4983°E), DC, CC; Babina Cheshma-Tsarev Vruh, 1750–2085 m (42.1304°N, 22.4301°E & 42.1302°N, 22.4517°E), DC observed.

Psorodonotus illyricus Ebner, 1923

Slovenia (citations as *P. illyricus* unless specified): Slavnik (45.5348°N, 13.9726°E) (Us, 1992).

Croatia: Istra (Jacobson & Bianchi, 1905 as *P. fieberi*; Mikšić, 1965 as *P. i. illyricus*); Mountains near Rijeka (Weidemann 1993); Senj [possibly a locality in the mountains nearby] (Mikšić, 1965 as *P. i. illyricus*); Obruč Mt.: Trstenik, 1000 m (45.49°N, 14.455°E), photographed by J. Topić; Obruč Mt., W slopes, 800 m (45.45167°N, 14.455°E), NT; Čičarija Mt., Dol, 890 m (45.43414°N, 14.1122°E), JS & NT; Platak [Risnjak Mt.] (45.435°N, 14.559°E) (Nadig, 1987); E of Rijeka, Kamenjak hill (45.403°N, 14.5545°E) (Heller, 1988 as *P. fieberi illyricus*); Vela Učka, Mt. Maggiore (Istria) (45.3°N, 14.197°E) (Redtenbacher, 1900 as *P. fieberi*; Ebner, 1923 as *P. fieberi illyricus*); Učka Mt., 750–1100 m (45.306°N, 14.2045°E), JS; Istra, 15 km NE Opatija (Učka Mt.) (45.3356°N, 14.184°E) (Heller, 1988 as *P. fieberi illyricus*); Vel. Kapela, Brezje-Modruš (com. Fiume-Modrus) (45.249°N, 14.99°E) (Pungur, 1899); Velebit Mt., Vučjak – Kapelica sv. Ante, 1530–1560 m (44.81175°N, 14.974°E), JS & NT; Velebit Mt., Štirovaca (44.6985°N, 15.0521°E) (Ebner, 1923 as *P. fieberi illyricus*); Poštak Mt.: Ljubina Poljana, 1080 m (44.27246°N, 16.1585°E), JS, NT & MM.

Bosnia and Herzegovina: Ivan pl. [unclear locality position] (Grebenschikov, 1950 as *P. fieberi*; Mikšić, 1965 as *P. i. illyricus*); Paljenik Peak [Vlašić Mt.] (44.293°N, 17.638°E) (Mikšić, 1965 as *P. i. illyricus*); Galica [hut in Vlašić Mt.] (44.2729°N, 17.5945°E) (Mikšić, 1965 as *P. i. illyricus*); Devečani [summit/chalet in Vlašić Mt.] (44.2752°N, 17.6329°E) (Mikšić, 1965 as *P. i. illyricus*); Vlašić Mt. & Vlašić – Puhlovica – Devečani, 1780 m (44.2784°N, 17.636°E) (Mikšić, 1965 as *P. i. illyricus*); Paklarevo [in the foothills of Vlašić Mt.; unclear locality position] (Mikšić, 1965 as *P. i. illyricus*); Dinara Mt. (Mikšić, 1965 as *P. i. illyricus*); Dinara Mt., Risovac (BiH) near Brezovac (HR) (44.1243°N, 16.3392°E), leg. Müller, Trieste Natural History Museum; Čemerno [pass] (44.0099°N, 18.3788°E) (Ebner, 1923 as *P. f. fieberi*); Vranica Mt., Matorac, 1500–1800 m (43.933°N,

17.845°E) (Ebner, 1923, “Nordabhang des Matorac (Bosnien)”, as *P. fieberi illyricus*; Mikšić, 1965 as *P. i. illyricus*); Lisin (oder Lim; Herzegowina) (43.7702°N, 17.9832°E) (Ebner, 1923 as *P. fieberi illyricus*; Mikšić, 1965 as *P. i. illyricus*); Jahorina Mt., 1800 m (43.715°N, 18.581°E) (Grebenshchikov, 1950 as *P. fieberi*; Mikšić, 1965 as *P. i. illyricus*); Foča (SE Bosnia) [possibly Plješ Mt.] (43.415°N, 18.815°E) (Ebner, 1923 as *P. fieberi illyricus*); Ulog [Jakomir Ridge] (43.3956°N, 18.2729°E) (Grebenshchikov, 1950 as *P. fieberi*); Morine [Jakomir Ridge] (43.3498°N, 18.278°E) (Mikšić, 1965 as *P. i. illyricus*); Zelengora Mt., Sutjeska NP, Donje Bare Lake, 1500 m (43.322°N, 18.632°E), F. Willemse, AU; Zelengora Mt., Sutjeska NP, Dragos Sedlo, 1000 m (43.353°N, 18.704°E), F. Willemse, AU; Volujak (Herzegowina) (Ebner, 1923 as *P. fieberi illyricus*; Grebenshchikov, 1950 as *P. fieberi*); Volujak Mt., Suha jezerina [in Montenegro?] (43.2668°N, 18.7179°E) (Mikšić, 1965 as *P. i. illyricus*); Lebršnik Mt. (43.207°N, 18.639°E) (Mikšić, 1965 as *P. i. illyricus*);

Montenegro: Sinjajevina – Ljutovac (42.934°N, 19.292°E) (Mikšić, 1965 as *P. illyricus illyricus/macedonicus* intermediate form); Lokvice – Bare – Žurim [near Zurim Peak?] (42.8195°N, 19.1859°E) (Mikšić, 1965 as *P. illyricus illyricus/macedonicus* intermediate form); Durmitor (Grebenshchikov, 1950 as *P. fieberi*); Durmitor N.P., Žabljak, 1450 m (43.1357°N, 19.133°E) (Mikšić, 1965; Ingrisich & Pavičević, 2012; both as *P. illyricus illyricus/macedonicus* transitional form), F. Willemse, AU; Jarčište (43.1285°N, 18.909°E) (Ingrisich & Pavičević, 2012 as *P. illyricus illyricus/macedonicus* intermediate form); Borkovići (43.106°N, 18.8725°E) (Ingrisich & Pavičević, 2012 as *P. illyricus illyricus/macedonicus* transitional form).

***Psorodonotus macedonicus* Ramme, 1931**

Montenegro: “Belasica” [Bjelasica Mt.] (42.8535°N, 19.6856°E) (Mikšić, 1965 as *P. illyricus illyricus/macedonicus* transitional form); Bjelasica Mt., N.P. Biogradskia Gora, 1730 m (42.897°N, 19.6324°E), M. Langourov, AU; Visitor Mt., Murino vill. (“Visitor – Murina”) (42.614°N, 19.88°E) (Grebenshchikov, 1950 as *P. fieberi*; Mikšić, 1965 as *P. illyricus macedonicus*).

Kosovo (citations as *P. illyricus* unless specified): Hajla Mt., Pepici (42.7276°N, 20.1303°E) (Mikšić, 1965 as Albania, as *P. illyricus macedonicus*); Koprivnik Mt., 1800–2000 m (42.664°N, 20.16°E) (Grebenshchikov, 1950 as *P. fieberi*; Mikšić 1965 as *P. fieberi* citing Grebenshchikov, 1950); E ö Prizren (Prevalac Paß) (42.166°N, 20.963°E) (Heller, 1988 as *P. fieberi illyricus*); Shar Mts, 2000–2600 m [unclear locality position] (Grebenshchikov, 1950 as *P. fieberi*).

Albania: Korab Mt. (e.g., 41.8026°N, 20.5093°E) (Ebner, 1923 as *P. f. fieberi* but noted the female is similar to *P. f. illyricus*).

R Macedonia: Skopska Crna Gora Mt.: Ramno peak (42.1742°N, 21.4369°E) (Karaman, 1975) [*P. macedonicus*?]; Jakupica Mt. (Dimovski, 1968): Goleshnitsa Ridge – near Pepelak (41.784°N, 21.3514°E) (Ramme 1951; Mikšić 1965 as *P. illyricus macedonicus*); the subalpine zone, 1750–2130 m (41.7098°N, 21.3789°E), DC, CC; Cheples chalet – Plavnik place, 1500–1750 m (41.6531°N, 21.3976°E & 41.647°N, 21.4085°E), DC, CC; Shar Mts (Grebenshchikov, 1950 as *P. fieberi*; Harz 1969 as *P. illyricus macedonicus*); Ljuboten peak (42.185°N, 21.1388°E) (Us, 1938 as *P. fieberi*; Grebenshchikov 1950 as *P. fieberi*; Mikšić, 1965 as *P. illyricus macedonicus*); Crni Vrv (42.128°N, 20.942°E) (Ramme, 1951); Kobiliza (Kobilica) Peak (42.0739°N, 20.8816°E) (Ramme, 1951); Cerepašina [Cepirashina], 1700–2500 m (e.g., 42.0045°N, 20.8868°E) (Mikšić, 1965 as *P. illyricus macedonicus*; Chobanov & Mihajlova, 2010 as *P. fieberi*); Popova Shapka near Tetovo (41.98333°N, 20.7667°E), K.-G. Heller & M. Volleth, CH; Budimov grob – Mengulova kula, 2100–2200 m (41.8533°N, 20.7771°E), L. Stefanov leg. et coll.; Nichpurska Planina, under Lera Peak, 1900–1950 m (41.7898°N, 20.7388°E), DC, CC; Korab Mt. (Mikšić,

1965 as *P. illyricus macedonicus*); Strezimir Chalet, 1470 & 1620 m (41.80609°N, 20.6186°E & 41.8016°N, 20.6113°E), DC, AU; Kobilino Pole highland, 2250 m (41.7822°N, 20.5711°E), DC, AU; Dlaboka Reka Valley, 1850 m (41.767°N, 20.551°E), DC, CC; Bistra Mt. (Grebenshchikov, 1950 as *P. fieberi*); Trebiski čuk [not localised] (Mikšić, 1965 as *P. illyricus macedonicus*); E of Zhirovnitsa vill. (41.65°N, 20.716°E) (Heller, 1988 as *P. fieberi illyricus*); Mavrovo – Carevec pass (Chobanov & Mihajlova, 2010 as *P. fieberi*); Carevec Place – Tonivoda highland, 1625–1700 m (41.64899°N, 20.7095°E & 41.64383°N, 20.6979°E), DC, AU; Galičnik vill. (41.59°N, 20.673°E) (Mikšić, 1965 as *P. illyricus macedonicus*); above Lazaropole vill., 1450–1800 m (41.535°N, 20.7456°E & 41.5509°N, 20.7622°E), DC, CC; Stogovo Mt. (e.g., 41.4583°N, 20.6818°E & 41.4736°N, 20.6779°E) (Chobanov & Mihajlova, 2010); Jablanica Mt.: Strizhek Peak, 1900–2000 m (41.28°N, 20.53°E), DC, CC; Galichitsa Mt.: Oteshevo-Ohrid, 1600–1700 m (40.9552°N, 20.816°E), DC, CC & L. Stefanov, L. Stefanov coll.; Nidzhe Mt.: Redir place, 1600 m (40.9908°N, 21.7564°E), B. Micevski; under Kaymakchalan Peak, 1500–1900 m (40.9814°N, 21.7893°E), DC, CC; Baba Mt., Kopanki chalet – Jorgov Kamen place, 1600–1700 m (41.021°N, 21.223°E); Crveni Steni place, 1800 m (41.0068°N, 21.2088°E); Lovechka Koliba Place, 1850–2190 m (41.0079°N, 21.168°E & 41.0036°N, 21.1683°E & 40.9952°N, 21.1706°E); Rupa place, 2100 m (40.8775°N, 21.2376°E); Golemo Ezero – Muza Peak, 2000–2250 m (40.9468°N, 21.2377°E & 40.9556°N, 21.214°E) (all data for Baba Mt. by Micevski et al., 2003 as *P. fieberi*); Kozjak Mt.: Krusha place – the ridge, 1700 m (41.1072°N, 21.9044°E) (Chobanov, 2002 as *P. fieberi*); Kozhuf Mt.: Dve Ushi peak, 1700–1800 m (Grebenshchikov, 1950 as *P. fieberi*; Mikšić, 1965 [“Dvousje kod Gevgelije”] as *P. illyricus macedonicus*) (41.2213°N, 22.2847°E), DC, CC; Kechi Kaja peak, 1750–1787 m (41.1968°N, 22.2474°E), DC, CC; Mihajlovo – Dudica peak, 1600–2100 m (41.1698°N, 22.256°E), DC, CC; Dzhibara – Zelen Beg ridges, 1650–2000 m (41.1891°N, 22.2146°E & 41.1656°N, 22.2118°E), DC, CC; Mala Rupa ridge, 1600–2000 m (41.1651°N, 22.2491°E), DC, CC; Porta Peak, 2000–2100 m (41.1499°N, 22.1638°E & 41.1574°N, 22.1692°E), DC, CC; Zelen Beg-Dudica peaks, 1600–2100 m (41.1276°N, 22.144°E & 41.1391°N, 22.15°E), DC, CC.

Greece: Florina: Kaimakchalan Mt. (40.93111°N, 21.7892°E) (Werner, 1933 as *P. fieberi macedonicus*); Bela Voda Mt. (40.80972°N, 21.21°E) (Willemse, 1977 as *P. fieberi macedonicus*); Vernon Mt., 4 km E of Pisodheri (40.766°N, 21.2167°E) (Willemse, 1977 as *P. fieberi macedonicus*); Vernon Mt. (40.751°N, 21.257°E) (Heller, 1988 as *P. fieberi macedonicus*); Imathia: Vermion Mt., W of Naoussa, above refuge Tria Pigadhia (40.629°N, 21.985°E) (Willemse, 1977 as *P. fieberi macedonicus*); Kozani: Pieria Mt., above Katafiyio (40.2552°N, 22.1626°E) (Willemse, 1977 as *P. fieberi macedonicus*); Pieria Mt., 1680 m (40.25°N, 22.154°E) (Heller, 1988 as *P. fieberi macedonicus*); Ioannina: Smolikas Mt., above A. Paraskevi (40.1°N, 20.917°E) (Willemse, 1977 as *P. fieberi macedonicus*); Evritania, Timfristos Mt., above Karpenision (8.9435°N, 21.8015°E) (Willemse, 1977 as *P. fieberi macedonicus*); Peristeri (“Peristori, Metsovan”) (39.81667°N, 21.1333°E) (Harz, 1976 as *P. fieberi macedonicus*); Lake near Metsovon (39.8145°N, 21.142°E), K.-G. Heller & M. Heller, CH; 3 km N of Metsovon [Metsovo], 1400 m (39.79°N, 21.162°E) (Willemse, 1977 as *P. fieberi macedonicus*); Dokimi Mt., 10 km SE of Metsovon, Ski Centre Anilio, 1630–1650 m (39.7465°N, 21.225°E), K.-G. Heller & M. Heller, CH; Phthiotis: Oiti Mt., above Ipati (Willemse, 1977 as *P. fieberi macedonicus*); Oiti Mt., “Hochfläche zw. Pira und Pavliani (Herakles-Scheiterhaufen)”, 1000 m (38.76667°N, 22.3°E) (Heller, 1988 as *P. fieberi macedonicus*); 6–10 km NW of Pavliani (38.7639°N, 22.305°E) (Willemse, 1977 as *P. fieberi macedonicus*).

Incertae sedis

Psorodonotus illyricus / *macedonicus*?

Montenegro: Bilo [unclear locality position] (Grebenshchikov, 1950 as *P. fieberi*); Bijela Planina [unclear locality position] (Mikšić, 1965 as *P. illyricus illyricus/macedonicus* transitional form); Đuranica gora [unclear locality position] (Mikšić, 1965 as *P. illyricus illyricus/macedonicus* transitional form).

Psorodonotus fieberi / *macedonicus*?

Serbia: “Radoč (S Serbia)” [unclear locality position] (Ebner, 1923 as *P. f. fieberi* (female similar to *P. f. illyricus*);

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APPENDIX 3. GenBank Accession numbers of material used in this study.

Haplotype (see Fig. 9)	Haplotype no.	GenBank accession no.
<i>P. venosus</i>	1536cArdCv	KP639712
<i>P. specularis</i>	1020-1ArdCs	KP639730
<i>P. caucasicus</i> 1	1457ErmYc	KP639713
<i>P. caucasicus</i> 2	1458cErmYc	KP639714
<i>P. macedonicus</i> 1	1859cMacKfb	KP639725
<i>P. macedonicus</i> 2	1886cMacKfb	KP639728
<i>P. macedonicus</i> 3	1869cMacBfb	KP639726
<i>P. macedonicus</i> 4	1873cMacBfb	KP639727
<i>P. macedonicus</i> 5	1963cMacJfb	KP639729
<i>P. fieberi</i> 1	1240cBulBfb	KP639715
<i>P. fieberi</i> 2	1856cBulBfb	KP639720
<i>P. fieberi</i> 3	1637cBulSfb	KP639716
<i>P. fieberi</i> 4	1644cBulVzfb	KP639717
<i>P. fieberi</i> 5	1645cBulSfb	KP639718
<i>P. fieberi</i> 6	1646cBulSfb	KP639719
<i>P. illyricus</i> 1	2177cbHirPily	KP639721
<i>P. illyricus</i> 2	2178cbHirPily	KP639722
<i>P. illyricus</i> 3	2162cbHirVily	KP639723
<i>P. illyricus</i> 4	2164cHirVily	KP639724