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Research article

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On the diversity of subterranean beetles of the Dinarides: new leiodid taxa (Coleoptera: Leiodidae) from Serbia

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Abstract. Three subterranean leptodirine leiodid taxa, viz., *Bozidaria* Ćurčić & Pavićević gen. nov., *Bozidaria serbooccidentalis* Ćurčić & Pavićević gen. et sp. nov. and *Proleonhardella* (*Proleonhardella*) *tarensis* Ćurčić & Pavićević sp. nov., are described and diagnosed. *Bozidaria* Ćurčić & Pavićević

gen. nov. belongs to the phyletic series of "Leonhardella". The new beetle taxa differ from their closest relatives in numerous morphological characters. They most likely belong to phyletic lineages of Pliocene age. The new leiodid taxa are endemic to the Dinaric mountain chain of western Serbia. Keys to the leptodirine leiodid genera of the phyletic series of "Leonhardella" and to the taxa of the genus Proleonhardella Jeannel, 1910 are included.

Keywords. New genus, new species, endogean and cave-dwelling, Cholevinae, Leptodirini.

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Introduction

A moderately rich endogean and a relatively poor cave-dwelling fauna of leiodid beetles occur in Serbia. This diversity is highest in the western and southwestern parts of the country (Jeannel 1924; Perreau 2000; Ćurčić 2005; Ćurčić et al. 2006, 2008b, 2015, 2018). Most subterranean leptodirine taxa from Serbia are either bathyscioid (Magdelainella spp., Proleonhardella spp., Pavicevicia spp., Bathyscia montana apfelbecki Ganglbauer, 1899 and Pseudobathyscidius serbicus (Karaman, 1964)) or pholeuonoid (Pholeuonopsis spp.) (Jeannel 1924; Nonveiller 1983; Moldovan et al. 2018; Perreau 2019). Highly-evolved scaphoid taxa are the representatives of the genus Remyella Jeannel, 1931, which are distributed in a narrow Dinaric area in southwestern Serbia and northeastern Montenegro (Njunjić et al. 2017). Interestingly, no highly-evolved leptodiroid taxa are known from Serbia so far, although some species of Anthroherpon Reitter, 1889 inhabit certain areas close to the country's border (Njunjić et al. 2015). Most leiodid taxa from Serbia are associated with the Central Dinarides, a smaller amount with the Inner Dinarides, while the Carpathian-Balkan mountain system is characterized by only a few taxa (e.g., the endemic genus Pseudobathyscidius Karaman, 1964 and the endemic Magdelainella subgenus Derveniella Pavićević & Perreau, 2008) (Perreau 2015; Hlaváč et al. 2017).

The genus *Proleonhardella* Jeannel, 1910 currently includes 10 endemic taxa (eight species and two subspecies) (Perreau 2000, 2015; Hlaváč *et al.* 2017), which were all described in the first half of the twentieth century. *Proleonhardella* taxa are distributed in a narrow Dinaric area belonging to Bosnia and Herzegovina, Serbia, and Montenegro (Perreau 2000; Pavićević *et al.* 2012). The genus is divided into two subgenera: *Proleonhardella* Jeannel, 1910 and *Pholeuonillus* Breit, 1913. The former subgenus includes seven species and two subspecies inhabiting caves in the montane areas of central, eastern and southeastern Bosnia and Herzegovina, southwestern Serbia and northern Montenegro (Perreau 2000; Pavićević *et al.* 2012). The latter subgenus contains only one endogean montane species from southern Bosnia and Herzegovina (Perreau 2000). Two species of *Proleonhardella* occur in Serbia: *Proleonhardella* (*Proleonhardella*) *hirtella* Jeannel, 1934 (described from the Popova Pećina Cave, village of Seljane, near the town of Prijepolje, southwestern Serbia) and *P. (P.) remyi* Jeannel, 1934 (described from the Bjeloševačka (= Dvostruka) Pećina Cave, village of Bjeloševina, near the town of Pljevlja, northern Montenegro) (Fig. 9) (Perreau 2000).

In the chapter on the family Leiodidae in the recent Catalogue of Palaearctic Coleoptera, Perreau (2015) reported the presence of both species of *Proleonhardella* solely for Serbia (Pešter Plateau). In reality, the type localities of both species are not situated on the Pešter Plateau, but in its surroundings. Additionally, they inhabit the territory of Montenegro, as documented by Pavićević *et al.* (2012) and Hlaváč *et al.* (2017). Namely, *P.* (*P.*) *hirtella*, besides its type locality, is known to inhabit three caves and pits near the towns of Prijepolje and Priboj (southwestern Serbia) and one pit near the town of Pljevlja (northern

Montenegro) (Pavićević *et al.* 2012). On the other hand, *P.* (*P.*) *remyi*, besides its type locality, lives in numerous caves and pits in the area of Kamena Gora and near the towns of Prijepolje and Priboj (southwestern Serbia), as well as in two caves and one pit near the town of Pljevlja (northern Montenegro) (Pavićević *et al.* 2012). The two species cohabitate in some caves and pits (five such localities are known), where the populations of the latter are more abundant (Pavićević *et al.* 2012). Additionally, the type locality of *P.* (*P.*) *remyi* in northern Montenegro is erroneously reported by Perreau (2000) to be situated in Serbia.

On the basis of the current distribution of Serbian endogean and cave-dwelling leiodid taxa, we assumed that some taxa new to science (genera and species) might be discovered in certain karstic areas of the Dinaric Alps of Serbia, which were so far not investigated and from which no taxa of leiodids from the underground have been documented.

Several field surveys conducted by the staff of the Institute of Zoology, University of Belgrade - Faculty of Biology and the Institute for Nature Conservation of Serbia at a few speleological sites in western Serbia, as well as by the late Prof. Guido Nonveiller on Mt Bobija in western Serbia, resulted in the discovery of a new leptodirine genus, viz., *Bozidaria* Ćurčić & Pavićević gen. nov., and two new leptodirine species, *B. serbooccidentalis* Ćurčić & Pavićević gen. et sp. nov. and *Proleonhardella* (*Proleonhardella*) tarensis Ćurčić & Pavićević sp. nov., the descriptions and diagnoses of which are given in the current study.

Material and methods

The material of *Bozidaria serbooccidentalis* gen. et sp. nov. is comprised of a large series of individuals: four males and five females collected in traps for endogean fauna baited with rotten meat during 1980 on Mt Bobija, near the town of Ljubovija, western Serbia, as well as 30 males and 44 females collected by pitfall trapping during 2010 and 2017 in the Simina Jama Pit, village of Gornje Košlje, Debelo Brdo saddle, Mt Povlen, near the town of Ljubovija, western Serbia. That of *Proleonhardella (Proleonhardella) tarensis* sp. nov. includes four males and four females collected by pitfall trapping during 2014 in Pit 4-1-3-27, village of Kaluđerske Bare, Mt Tara, near the town of Bajina Bašta, western Serbia, as well as three males and five females collected by pitfall trapping during 2003 in the Sovljačka Pećina Cave, village of Šljivovica, Mt Tara, near the town of Bajina Bašta, western Serbia.

Type specimens were studied in the laboratories of the Institute of Zoology, University of Belgrade - Faculty of Biology, Belgrade, Serbia. The beetles were dissected, analysed in detail and photographed. Dry individuals were glued onto rectangular paper mounting cards. Extracted genitalia were fixed in a medium composed of Canada balsam and toluene and put onto rectangular transparent plastic mounting cards placed on the same entomological pin together with the mounting card of the dry individual.

Observations were conducted with a Carl Zeiss-Stemi 2000 binocular stereo microscope. A Nikon SMZ 18 stereo microscope combined with a Nikon DS-Fi1c digital camera, as well as a Leica DMLS light microscope combined with a Leica DC 300 camera, were used to photograph morphological details of the whole specimens and genitalia of new beetle taxa. The detailed morphology of the new taxa was imaged using scanning electron microscopy (SEM) at the Photonics Center, Institute of Physics Belgrade, University of Belgrade. SEM micrographs were made using a MIRA3 FEGSEM field-emission scanning electron microscope (FESEM) (Tescan, Brno, Czech Republic) in high vacuum mode, at a voltage of 15 kV. All samples were sputter coated with gold/palladium for 30 seconds. The index of intensity of the electron beam was 15.00. Pressure in the column was about 127 MPa.

Abbreviations of measurements

A1/A2 = ratio of length of antennomere I to length of antennomere II
A3/A2 = ratio of length of antennomere III to length of antennomere II
A3/A5 = ratio of length of antennomere III to length of antennomere V
A7/A6 = ratio of length of antennomere VII to length of antennomere VIII
A7/A8 = ratio of length of antennomere VIII to length of antennomere VIII

A8LW = ratio of length to width of antennomere VIII A9LW = ratio of length to width of antennomere IX

A9/A8 = ratio of length of antennomere IX to length of antennomere VIII

A10LW = ratio of length to width of antennomere X A11LW = ratio of length to width of antennomere XI

A11/A9+A10 = ratio of length of antennomere XI to length of antennomeres IX and X combined EL/EW = ratio of length of elytra (as linear distance between base to apex of elytra along

median suture) to maximum width of elytra

EL/PL = ratio of length of elytra (as linear distance between base to apex of elytra along

median suture) to length of pronotum

HL/HW = ratio of length of head (as linear distance between anterior margin of clypeus to

occipital carina) to maximum width of head

M = mean value for certain measurements P1LW = ratio of length to width of protarsomere I

PB/AM = ratio of length of pronotal base to length of anterior pronotal margin

PL/PW = ratio of length of pronotum to maximum width of pronotum

PL+EL/AL = ratio of length of pronotum and elytra combined (as linear distance between anterior

pronotal margin to apex of elytra along median suture) to total antennal length

R = range of measured values

TL = maximum body length from anterior margin of clypeus to apex of elytra along

median suture

Repositories

CDP = collection of Dragan Pavićević, Belgrade, Serbia

IZFB = Institute of Zoology, University of Belgrade - Faculty of Biology, Belgrade, Serbia

SBS = Serbian Biospeleological Society, Novi Sad, Serbia

Other abbreviations used in the text

Ma = million years

Mt = Mountain/Mount

Other material examined

Proleonhardella (Proleonhardella) hirtella Jeannel, 1934

SERBIA • 1 &; southwestern Serbia, municipality of Priboj, village of Krnjača, Tmuša Gorge, Goveđa Pećina Cave; 17 Jul. 2013; Dragan Antić leg.; IZFB.

Proleonhardella (Proleonhardella) remyi Jeannel, 1934

SERBIA • 6 ♂♂, 8 ♀♀; southwestern Serbia, municipality of Priboj, village of Krnjača, Tmuša Gorge, Goveđa Pećina Cave; 17 Jul. 2013; Dragan Antić leg.; IZFB • 8 ♂♂, 18 ♀♀; southwestern Serbia, municipality of Prijepolje, Kamena Gora, village of Kamena Gora, Bezdan Pit; 20 May–5 Nov. 2017; Miloš Kuraica leg.; pitfall traps; IZFB.

Results

Subphylum Hexapoda Latreille, 1825 Class Insecta Linnaeus, 1758 Order Coleoptera Linnaeus, 1758 Suborder Polyphaga Emery, 1886 Family Leiodidae Fleming, 1821 Subfamily Cholevinae Kirby, 1837 Tribe Leptodirini Lacordaire, 1854

Genus *Bozidaria* Ćurčić & Pavićević gen. nov. urn:lsid:zoobank.org:act:8CF69930-741E-4484-9F09-5E8C1FBC86AA

Type species

Bozidaria serbooccidentalis Ćurčić & Pavićević gen. et sp. nov., by monotypy.

Diagnosis

Bozidaria gen. nov. is most closely related to the following Dinaric genera of the group Théléomorphes belonging to the phyletic series of "Leonhardella" (Jeannel 1924): Proleonhardella, Blattochaeta Reitter, 1910, Augustia Zariquiey, 1927 and Pholeuodromus Breit, 1913. These genera share a similar body form, the presence of tetramerous tarsi in males, the absence of a comb on anterior tibiae, the first antennomere clearly shorter than the second antennomere, apically widened distal antennomeres, the absence of sutural striae, and the presence of a similar type of aedeagus.

The new genus differs from its closest relatives in the body shape (elliptical, elongate vs bathyscioid, oval/ovoid, mostly wide in Proleonhardella), TL (R 2.51–2.80 mm vs R 4.0–5.5 mm in Blattochaeta and R 3.8–4.6 mm in *Pholeuodromus*), body pubescence (short, recumbent vs long, erect in *Blattochaeta*), shape of antennae (elongate, thin, including distal antennomeres vs short, distal antennomeres wide. barely longer than wide in *Proleonhardella*), length of antennae (exceeding the middle of the body vs reaching, but not exceeding the middle of the body in Augustia and not reaching the middle of the body in *Pholeuodromus*), presence/absence of mesosternal carina (present vs absent in *Augustia*), shape of mesosternal carina (with no concavity on its anterior border, not atrophied vs with a concavity on its anterior border in *Blattochaeta* and atrophied posteriorly in *Pholeuodromus*), shape of lateral pronotal margins (arcuate vs weakly convex in Augustia), position of maximum pronotal length (sub-basally vs at base in *Pholeuodromus*), ratio of pronotum width to elytral width (pronotum slightly narrower than elytra vs pronotum as wide as elytra in Blattochaeta and Pholeuodromus and pronotum clearly narrower than elytra in Augustia), shape of elytra (more rounded, gradually narrowed distally vs less rounded, more pronouncedly attenuated distally in Augustia), shape of aedeagus (long, elongate vs short, wide in Blattochaeta and Augustia and mostly wide in Proleonhardella), shape of basal bulb (elongate, narrow vs short, rounded in *Proleonhardella*, *Blattochaeta* and *Augustia*) and its basal projection (long vs short in Proleonhardella and Augustia), and shape of parameral apex (narrow vs widened in Blattochaeta) (Jeannel 1910, 1924, 1930, 1931, 1934; Reitter 1910; Breit 1913; Zariquiey 1927; Knirsch 1928; Guéorguiev 1976).

Etymology

This genus is named after the late Academician Božidar Ćurčić, a well-known Serbian biospeleologist and zoologist.

Description

HABITUS. A small-sized elliptical leptodirine with short and wide head, transverse pronotum and elongate obovoid elytra. Blind, reddish-brown, body shiny, densely pubescent, dorsoventrally convex, finely punctate. Pubescence composed of short yellow hairs, on pronotum and elytra recumbent, while on head erect. Legs and antennae long and slender, densely pubescent. Microsculpture composed of isodiametric meshes.

HEAD. Anophthalmous, of almost equal length and width. Antennae inserted medially on head, elongate, thin, apically widened and flattened, exceeding middle of body, reaching basal third of elytral length. Antennomere I shorter than antennomere II. Antennomere III shorter than antennomere II and longer than antennomere IV. Antennomeres IV–VI of similar length. Antennomere VII elongate, apically widened. Antennomere VIII short, elongate, oval. Ultimate antennomere slender, ovoid, about as long as antennomeres IX and X combined. Occipital carina present.

THORAX. Pronotum almost twice as wide as long, with arcuate and well-rounded lateral margins, slightly narrower than elytra, widest slightly prior to pronotal base. Mesosternal carina well-developed, with no furrow, high, obtuse-angled, with an apical tooth.

ELYTRA. Elongate, much longer than pronotum, rounded medially, regularly arcuate distally, not attenuated. Scutellar striae absent. A part of pygidium not covered by elytra.

Legs. Extended and slender. Fore tarsi tetramerous. Male protarsi dilated. Tibiae with spines on external edges. No comb on external edges or apical parts of protibiae. Meso- and metatibiae with no apical baskets.

ABDOMEN. Median lobe of aedeagus slender, rounded sub-terminally, with an elongate triangular apex. Basal bulb elongate, narrow, with a long sub-triangular basal projection. Each paramere longer than median lobe, thin, sub-terminally widened, with three apical setae.

GONOSTYLI. Elongate, slender, almost straight.

Distribution

The new genus is currently known to inhabit deep soil on Mt Bobija and the Simina Jama Pit on Mt Povlen in the surroundings of the town of Ljubovija, western Serbia. It is probable that it might be present both in the soil and caves of the adjacent areas.

Key to the leptodirine leiodid genera of the phyletic series of "Leonhardella" (modified after Guéorguiev 1976) (Fig. 1)

Body of bathyscioid form, oval or ovoid, wide and short	
Mesosternal carina absent (Fig. 1A). Cavernicolous, Mt Čvrsnica, southwestern Bosnia and Herzegovina	27
Antennae short, not reaching middle of body	

4. Pubescence fine and recumbent, except in both lateral exterior border of elytra and apical elytral half, where long hairs occur. Antennae very short, barely exceeding pronotal base. Longer species

	(TL 2.5 mm). Mesosternal carina rounded. Basal lamina of tegmen of aedeagus without tooth. Cavernicolous, region of Kuči, vicinity of the city of Podgorica, eastern Montenegro
_	Pubescence entirely normal and recumbent. Antennae somewhat longer, but not reaching middle of body. Shorter species (TL 1.85 mm). Mesosternal carina triangular. Basal lamina of tegmen of aedeagus with a pronounced tooth basally. Cavernicolous, vicinity of the town of Karystos, island of Euboea, southern Greece ——————————————————————————————————
	Pubescence short and recumbent. Anterior border of mesosternal carina without concavity (Fig. 1C). Protarsi weakly dilated in males. Shorter species (TL 1.3–3.5 mm). Cavernicolous and endogean, central, eastern and southern Bosnia and Herzegovina, southwestern and western Serbia and eastern Montenegro
_	Pubescence long and erect. Anterior border of mesosternal carina with a deep concavity (Fig. 1D). Protarsi not dilated in males. Longer species (TL 4.0–5.5 mm). Cavernicolous, western, southwestern and eastern Montenegro, southern Bosnia and Herzegovina and southern Croatia
6.	Body of elliptical form (Fig. 1E). Pronotum regularly or almost regularly arcuate, slightly narrower than elytra or as wide as elytra
_	Body of pholeuonoid form (Fig. 1F). Pronotum campanuliform or strongly sinuated backwards, clearly narrower than elytra
7.	Body shorter (TL 1.8–2.0 mm). Antennae almost reaching middle of body. Elytra very attenuated apically, with sparse pubescence. Ventral border of mesosternal carina triangular and deeply grooved. Endogean and cavernicolous, southern Croatia and western Bosnia and Herzegovina
-	Body longer (TL 2.5–5.2 mm). Antennae reaching middle of body. Elytra regularly arcuate apically, with dense pubescence. Ventral border of mesosternal carina not grooved
8.	Body shorter (TL 2.5–3.0 mm). Mesosternal carina not atrophied. Protarsi dilated in males (Fig. 1G)
_	Body longer (TL 3.8–5.2 mm). Mesosternal carina atrophied posteriorly. Protarsi not dilated in males (Fig. 1H)
9.	Body very elongate and narrower. Pubescence long and erect. Median lobe more elongate, thin. Basal bulb small, with a short rounded basal projection (Fig. 1I). Paramerae distally widened. Cavernicolous, southern and southeastern Bosnia and Herzegovina and western Montenegro
_	Body less elongate and wider. Pubescence short and recumbent. Median lobe less elongate, wide. Basal bulb elongate, with a long sub-triangular basal projection (Fig. 1J). Paramerae distally narrow. Endogean and cavernicolous, Mts Bobija and Povlen, western Serbia
10	Body shorter (TL 3.8–4.6 mm). Pronotum as wide as elytra. Lateral pronotal margins regularly
10.	arcuate. Anterior border of mesosternal carina with no concavity. Paramerae with three setae. Endogean, central and southern Bosnia and Herzegovina
_	Body longer (TL 5.0–5.2 mm). Pronotum slightly narrower than elytra. Lateral pronotal margins weakly sinuate in basal third. Anterior border of mesosternal carina with a deep concavity. Paramerae with four setae. Cavernicolous, southeastern Bosnia and Herzegovina and northern Montenegro **Blattodromus** Bieti, 1915** Blattodromus** Reitter, 1904**

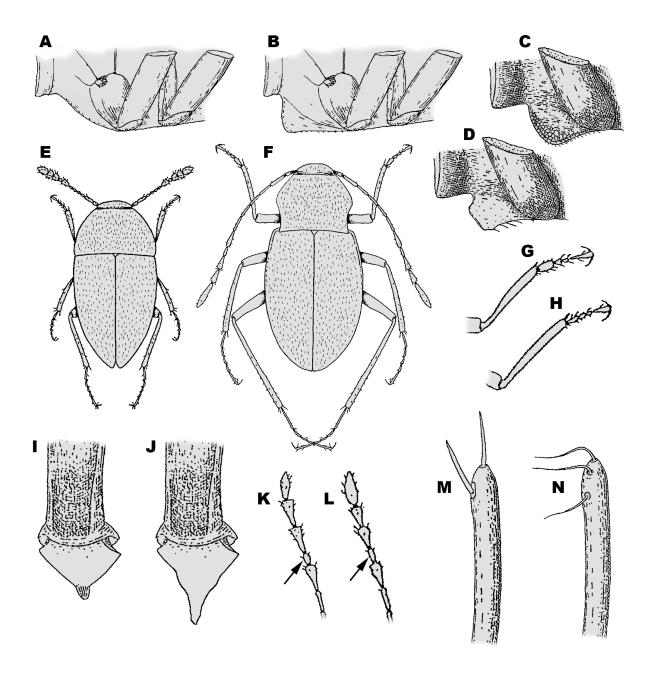


Fig. 1. Illustrations of morphological characters presented in the Key to the leptodirine leiodid genera of the phyletic series of "Leonhardella" (after Jeannel 1911, 1924; Ćurčić et al. 2008a). A. Absence of mesosternal carina. B. Presence of mesosternal carina. C. Absence of a concavity on mesosternal carina. D. Presence of a deep concavity on mesosternal carina. E. Presence of elliptical body shape. F. Presence of pholeuonoid body shape. G. Presence of dilated protarsi in males. H. Presence of undilated protarsi in males. I. Presence of a short rounded basal projection on basal bulbus. J. Presence of a long subtriangular basal projection on basal bulbus. K. Presence of subglobular antennomere VIII. L. Presence of elongate antennomere VIII. M. Presence of paramerae with two setae. N. Presence of paramerae with three setae.

- Body longer (TL 3.2–4.5 mm). Pronotum as long as wide or transverse, wider basally. Mesosternal carina high or atrophied. Paramerae with three setae (Fig. 1N)

Bozidaria serbooccidentalis Ćurčić & Pavićević gen. et sp. nov. urn:lsid:zoobank.org:act:A2B51421-4CD9-4696-BF46-7EACBC395C4E Figs 2–3

Diagnosis

The genus is currently monotypic and therefore a differential diagnosis for *Bozidaria serbooccidentalis* gen. et sp. nov. cannot be provided.

Etymology

The species is named after western Serbia, where its type locality and known localities are situated.

Type material

Holotype

SERBIA • &; western Serbia, town of Ljubovija, Mt Bobija; alt. 1000 m; 19 Apr. 1980; Guido Nonveiller leg.; traps for endogean fauna baited with rotten meat; IZFB-21/1.

Paratypes

SERBIA • 1 \circlearrowleft , 2 \circlearrowleft \circlearrowleft ; same collection data as for holotype; SBS-21/1 to 21/3 • 1 \circlearrowleft ; same collection data as for holotype; IZFB-21/2 • 2 \circlearrowleft \circlearrowleft , 2 \circlearrowleft \circlearrowleft ; same collection data as for holotype; CDP-21/1 to 21/4 • 10 \circlearrowleft \circlearrowleft , 14 \circlearrowleft \circlearrowleft ; western Serbia, town of Ljubovija, Mt Povlen, Debelo Brdo saddle, village of Gornje Košlje, Simina Jama Pit; 44°08′32.2″ N, 19°37′40.4″ E; 20 May–5 Nov. 2017; Miloš Kuraica leg.; pitfall trapping; IZFB-21/3 to 21/26 • 2 \circlearrowleft \circlearrowleft , 1 \hookrightarrow ; same locality as for preceding; 31 Dec. 2010; Iva Njunjić leg.; pitfall trapping; SBS-21/4 to 21/6 • 18 \circlearrowleft \circlearrowleft , 39 \hookrightarrow \hookrightarrow ; same collection data as for preceding; CDP-21/5 to 21/61 (Fig. 2).

Description

HABITUS. Body elliptical, TL R 2.51–2.80 mm (R 2.51–2.73 mm in males, R 2.67–2.80 mm in females), reddish-brown in colour, shiny, pubescent, with a fine punctuation (Fig. 2A).

HEAD. Short, wide, slightly wider than long (HL/HW M 0.97), without eyes (Fig. 2A). Antennae long and slender, apically gradually widened and flattened, ending slightly after basal third of elytra in males

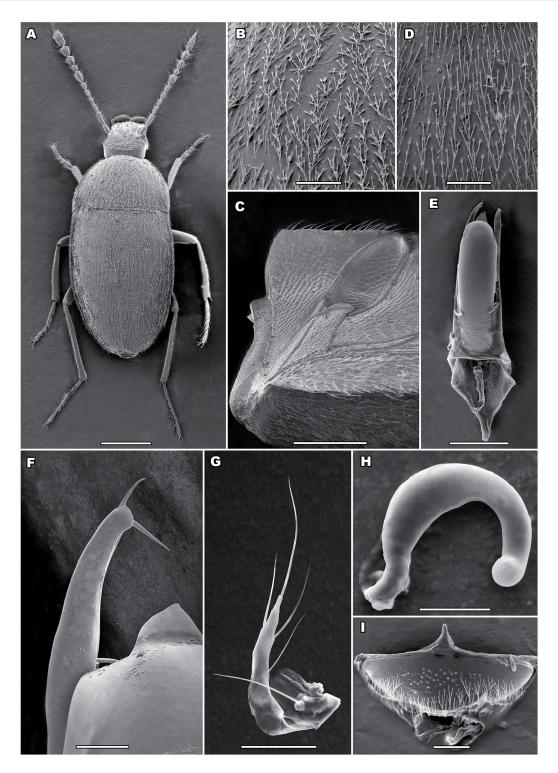


Fig. 2. *Bozidaria serbooccidentalis* Ćurčić & Pavićević gen. et sp. nov. from the Simina Jama Pit, village of Gornje Košlje, Debelo Brdo saddle, Mt Povlen, near the town of Ljubovija, western Serbia. **A–F**. Paratype male (IZFB-21/3). **A**. Habitus (dorsal view). **B**. Surface of pronotum (dorsal view). **C**. Mesosternal carina (lateral view). **D**. Surface of elytra (dorsal view). **E**. Aedeagus (dorsal view). **F**. Left paramere apex (dorsal view). **G–I**. Paratype female (IZFB-21/4). **G**. Left gonostylus (dorsal view). **H**. Spermatheca (lateral view). **I**. Abdominal segment VIII (ventral view). Scale bars: A = 500 μm; B, D, G, I = 100 μm; C, E = 200 μm; F = 25 μm; H = 50 μm.

or slightly prior to basal third of elytra in females. Antennomere II longer than antennomere I (A1/A2 M 0.795). A3/A2 M 0.67. A3/A5 M 1.24. Antennomeres IV–VI of similar length, of which IV narrowest and VI widest. Antennomere VII apically widened. A7/A6 M 1.56. Antennomere VIII slightly longer than half of antennomere VII (A7/A8 M 1.53), oval, somewhat elongate (A8LW M 1.52). Antennomere IX somewhat elongate, gradually widened distally (A9LW M 1.47). A9/A8 M 1.52 in males, M 1.42 in females. Antennomere X slightly longer than wide (A10LW M 1.24), more widened apically. Antennomere XI slender, ovoid, apically pointed, more elongate in males (A11LW M 2.45) than in females (A11LW M 1.97), as long as preceding two antennomeres combined or slightly shorter than the latter. Occipital carina present. Hairs yellow, erect. Microsculpture composed of small isodiametric meshes.

Thorax. Pronotum transverse, widest sub-basally, almost twice as wide as long (PL/PW M 0.59) (Fig. 2A). Lateral pronotal margins arcuate, rounded medially, sub-parallel prior to hind pronotal angles. Pronotal base more than twice as long as anterior pronotal margin (PB/AM M 2.13). Both anterior pronotal margin and pronotal base convex medially, the latter less pronouncedly. PL+EL/AL M 1.63 in males, M 1.89 in females. Fore angles prominent, obtuse, rounded, hind angles sharp, rounded, prominent, directed backwards. Microsculpture of pronotum composed of large isodiametric meshes. Hairs yellow, recumbent (Fig. 2B). Pronotal disc weakly convex. Mesosternal carina high, obtuse-angled, anterior margin strongly convex, posterior margin barely convex, almost straight, with hairs and teeth (Fig. 2C). Mesosternal carina with an apical tooth. Ventral border of mesosternal carina not grooved.

ELYTRA. Elongate (EL/EW M 1.38 in males, M 1.40 in females), more than 2.5 times as long as pronotum (EL/PL M 2.65), obovoid, sub-parallel below humeral angles, weakly narrowed basally, rounded medially, narrowed apically (Fig. 2A). Apex rounded. Sutural striae absent. Scutellum small, triangular. Elytra widest between basal third and mid-length. Microsculpture composed of large isodiametric meshes. Hairs yellow, recumbent (Fig. 2D). Elytral disc convex. Pygidium not completely covered by elytra.

Legs. Elongate and thin, with hairs (Fig. 2A). Tibiae with a few spines laterally. Anterior tarsi tetramerous in both genders, somewhat dilated in males (P1LW M 1.825 in males, M 1.88 in females).

ABDOMEN. Median lobe of aedeagus elongate, thin, sub-parallel, sub-apically rounded (Figs 2E, 3A). Apex elongate, triangular. Basal bulb relatively narrow, elongate, with a sub-triangular basal projection. Copulatory piece weakly chitinised, consisting of a basal phanera, median paired stripes and apical paired sclerotizations. Median lobe proximally straight, distally relatively curved, gradually narrowed distally in lateral view (Fig. 3B). Basal bulb narrow in lateral view. Parameres slender, thin, longer than median lobe, sub-terminally widened, terminally narrowed, apex slightly dilated, proximally arcuate and distally straight in lateral view, with three setae: one apical terminal, one apical inner and one sub-apical inner (Fig. 2F). Two apical parameral setae close-set. Parameral apices directed inwards. Parameres basally slightly curved, distally relatively straight in lateral view, sub-terminally widened, terminally narrowed in lateral view (Fig. 3B).

Gonostylli. Almost straight, elongate, thin, with one apical seta, three inner setae and one outer seta (Fig. 2G).

Spermatheca. Small, curved, widest in proximal third, apically sub-spherical (Fig. 2H).

Female abdominal sternite VIII. Large, transverse, setose both medially and distally, with a narrow, pointed anterior process. Microsculpture consisting of transverse polygonal meshes (Fig. 2I).

Bionomy, distribution and type locality

The type specimens were collected in traps for endogean fauna (cans) baited with rotten meat placed in the deep soil on Mt Bobija, near the town of Ljubovija, western Serbia, as well as by pitfall trapping with rotten meat as bait in the deep, totally dark parts of the Simina Jama Pit, village of Gornje Košlje, Debelo Brdo saddle, Mt Povlen, near the town of Ljubovija, western Serbia (Fig. 9). The type locality on Mt Bobija is located on its northern slope, at an altitude of 1000 m a.s.l., in a beech forest, close to several



Fig. 3. *Bozidaria serbooccidentalis* Ćurčić & Pavićević gen. et sp. nov. from the Simina Jama Pit, village of Gornje Košlje, Debelo Brdo saddle, Mt Povlen, near the town of Ljubovija, western Serbia. Holotype male (IZFB-21/1), aedeagus. **A.** Dorsal view. **B.** Lateral view. Scale bar = 200 μm.

streams. The entrance of the Simina Jama Pit is situated at 920 m a.s.l., the total length of its investigated channels is 270 m, while its depth is 56 m. It starts with a 31-m long vertical passage, which splits into two horizontal channels – left and right (Anđelić *et al.* 2011). Beetle specimens were found at the end and in the middle of the left horizontal channel with a clay muddy substrate and rocks, on the vertical limestone walls and floor with a high level of humidity (presence of trickling water). The places where the specimens were found in the pit are shown in Fig. 4. It is assumed that the species is actually endogean, as is the case with some other leiodid taxa (e.g., *Magdelainella* spp.), which inhabit the soil beneath deeply sunken rocks and forest detritus, but can also be found in caves and pits (Pavićević *et al.* 2012).

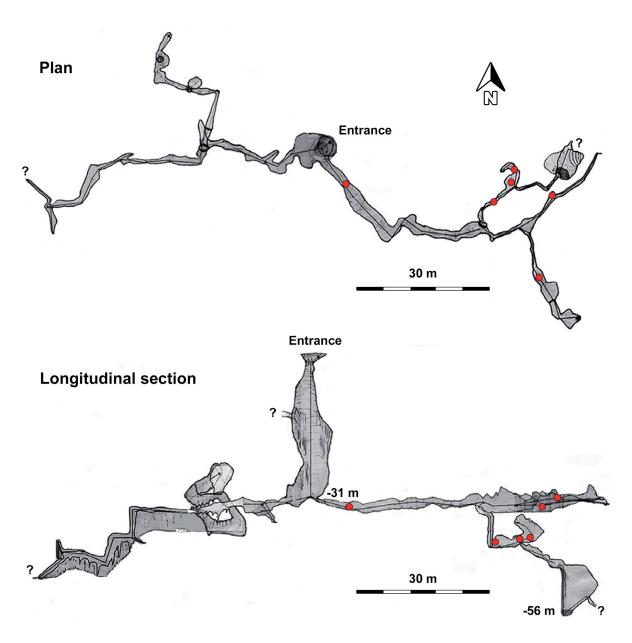


Fig. 4. A plan and a longitudinal section of the Simina Jama Pit, village of Gornje Košlje, Debelo Brdo saddle, Mt Povlen, near the town of Ljubovija, western Serbia (modified after Anđelić *et al.* 2011). The red circles indicate the places where specimens of *Bozidaria serbooccidentalis* Ćurčić & Pavićević gen. et sp. nov. were found.

Genus Proleonhardella Jeannel, 1910

Proleonhardella (*Proleonhardella*) *tarensis* Ćurčić & Pavićević sp. nov. urn:lsid:zoobank.org:act:E1B53D50-0C09-4E5C-AFB1-AC9F6EBBD426 Figs 5–6

Diagnosis

Proleonhardella (Proleonhardella) tarensis sp. nov. is most closely related to P. (P.) hirtella (from several caves and pits near the towns of Prijepolje (southwestern Serbia) and Pljevlja (northern Montenegro)), P. (P.) weiratheri (Reitter, 1913) (from the Vrteljka Cave, village of Đipi, Mt Sjemeć, near the town of Višegrad, eastern Bosnia and Herzegovina) and P. (P.) neumanni (Apfelbeck, 1901) (from a small unnamed cave, village of Podromanija, near the town of Sokolac, eastern Bosnia and Herzegovina) (Fig. 9) (Perreau 2000; Pavićević et al. 2012). Another congener from Serbia, P. (P.) remyi (from caves and pits in the area of Kamena Gora and near the towns of Prijepolje, Priboj (southwestern Serbia) and Pljevlja (northern Montenegro)), is of bathyscioid shape (P. (P.) tarensis sp. nov. is more elongate and of oval shape), it is significantly longer than the new species (TL R 3.0–3.5 mm vs 2.185–2.435 mm in P. (P.) tarensis sp. nov.) and has a quite different shape of aedeagus (stout, with a rounded apex, longer than parameres vs elongate, with a pointed apex, shorter than parameres in P. (P.) tarensis sp. nov.), indicating that these two species are not closely related (Jeannel 1934; Ćurčić et al. 2008a).

The new species differs from its closest congeners in the TL R (2.185–2.435 mm vs 1.6–1.8 mm in *P.* (*P.*) *hirtella* and 1.6–2.0 mm in *P.* (*P.*) *weiratheri*), antennal length (ending prior to basal third of elytra vs reaching only basal quarter of elytra in *P.* (*P.*) *hirtella* and exceeding middle of body in *P.* (*P.*) *weiratheri*), A1/A2 M (0.76 vs 0.80 in *P.* (*P.*) *neumanni*), A7/A6 M (1.66 vs 1.50 in *P.* (*P.*) *hirtella*), A7/A8 R (1.75–2.00 vs 3.00 in *P.* (*P.*) *hirtella*), A11/A9+A10 M (0.90 vs 1.00 in *P.* (*P.*) *weiratheri*), shape of antennomere VIII (oval and slightly longer than wide in males and spherical in females vs as long as wide in males and almost transverse in females in *P.* (*P.*) *weiratheri*), shape of antennomeres IX and X (slightly longer than wide vs as long as wide in *P.* (*P.*) *hirtella*), position of maximum width of pronotum (sub-basally vs at base in *P.* (*P.*) *hirtella* and *P.* (*P.*) *weiratheri*), shape of mesosternal carina (obtuse-angled vs almost right-angled in *P.* (*P.*) *neumanni*), shape of elytra (narrowed basally vs parallel basally in *P.* (*P.*) *hirtella* and *P.* (*P.*) *weiratheri* and clearly sinuate basally in *P.* (*P.*) *neumanni*), EL/EW (R 1.31–1.39 vs M 1.75 in *P.* (*P.*) *weiratheri*), position of maximum width of elytra (slightly after basal third vs prior to middle in *P.* (*P.*) *neumanni*), and shape of aedeagus (less elongate, with wider apex and larger basal bulb vs more elongate, with narrower apex and smaller basal bulb in *P.* (*P.*) *hirtella* (Apfelbeck 1901; Reitter 1913; Jeannel 1924, 1934).

Etymology

The species is named after Mt Tara in western Serbia, where its type locality is situated.

Type material

Holotype

SERBIA • &; western Serbia, town of Bajina Bašta, Mt Tara, village of Kaluđerske Bare, Pit 4-1-3-27; 43°54′30.712″ N, 19°33′11.585″ E; 5 Jul. 2014; Fabrizio Bosco leg.; pitfall trapping; IZFB-21/27.

Paratypes

SERBIA • 3 $\lozenge\lozenge\lozenge$, 3 $\lozenge\lozenge\lozenge$; same collection data as for holotype; IZFB-21/28 to 21/33 • 1 \lozenge ; same collection data as for holotype; SBS-21/7 • 1 \lozenge , 2 $\lozenge\lozenge\lozenge$; western Serbia, town of Bajina Bašta, Mt Tara, village of Šljivovica, Sovljačka Pećina Cave; 43°52′39.7″ N, 19°30′56.3″ E; 7 May 2003; Dragan Pavićević leg.; pitfall trapping; SBS-21/8 to 21/10 • 2 $\lozenge\lozenge\lozenge$, 3 $\lozenge\lozenge\lozenge$; same collection data as for preceding; CDP-21/62 to 21/66 (Fig. 5).

Description

Habitus. Body oval, relatively elongate, TL R 2.185–2.435 mm (R 2.185–2.32 mm in males, 2.435 mm in females), colour brownish-red (one teneral female specimen yellowish), shiny, pubescent and with a fine punctuation (Fig. 5A).

HEAD. Short, wide, slightly longer than wide (HL/HW R 1.00–1.06), anophthalmous (Fig. 5A). Antennae long and narrow, ending prior to basal third of elytra, apically widened and flattened. Antennomere II longer than antennomere I (A1/A2 M 0.76). Antennomeres III–VI small, narrow, of similar shape and length. A3/A2 M 0.58. A3/A5 M 1.19. Antennomere VII apically widened, obovoid. A7/A6 M 1.66. Antennomere VIII half as long as antennomere VII, oval and slightly longer than wide in males (A8LW M 1.31), while somewhat shorter (A7/A8 M 1.75), nearly as long as wide (A8LW M 1.04) and spherical in females. Antennomeres IX and X slightly longer than wide (A9LW M 1.28 and A10LW M 1.21, respectively), apically widened. A9/A8 M 1.60 in males, 2.00 in females. Antennomere XI ovoid, twice as long as wide in males, somewhat shorter in females (A11LW M 1.92), slightly shorter than two preceding antennomeres combined (A11/A9+A10 M 0.90). Occipital carina present. Hairs yellow, erect. Microsculpture composed of small isodiametric meshes.

THORAX. Pronotum transverse, almost twice as wide as long (PL/PW M 0.59), widest sub-basally (Fig. 5A). Lateral pronotal margins arcuate, most rounded medially, almost sub-parallel prior to hind pronotal angles. Anterior pronotal margin somewhat convex medially, base almost straight, around twice as long as anterior pronotal margin (PB/AM M 1.985). PL+EL/AL M 1.685 in males, 1.94 in females. Fore angles prominent, obtuse, rounded, hind angles sharp, rounded, prominent, directed backwards. Microsculpture of pronotum composed of large isodiametric meshes. Hairs yellow, recumbent (Fig. 5B). Pronotal disc weakly convex. Mesosternal carina high, obtuse-angled, anterior margin convex, posterior margin straight, setose and with unpronounced teeth (Fig. 5C). Mesosternal carina with an apical tooth.

ELYTRA. Elongate (EL/EW M 1.39 in males, 1.31 in females), more than twice as long as pronotum (EL/PL M 2.46), obovoid, sub-parallel below humeral angles, conspicuously narrowed basally, rounded medially, attenuated apically (Fig. 5A). Apex rounded. Sutural striae absent. Scutellum small, triangular. Elytra widest slightly after basal third. Microsculpture composed of large isodiametric meshes. Hairs yellow, recumbent (Fig. 5D). Elytral disc gently convex apically, more steeply distally. Pygidium completely covered by elytra.

Legs. Moderately elongate and thin, with hairs (Fig. 5A). Tibiae with a few spines. Anterior tarsi tetramerous in both genders, dilated in males (P1LW M 1.50 in males, 2.00 in females).

ABDOMEN. Median lobe of aedeagus elongate, thin, sub-parallel, sub-terminally somewhat widened, then narrowed apically (Figs 5E, 6A). Apex triangular. Basal bulb large, elongate, with a sub-triangular basal projection. Copulatory piece weakly chitinised, consisting of a basal phanera, median paired stripes and distal paired sclerotizations. Median lobe proximally weakly curved, distally more curved, gradually narrowed distally in lateral view (Fig. 6B). Basal bulb relatively narrow in lateral view. Parameres slender, thin, longer than median lobe, sub-terminally widened, terminally narrowed, basally arcuate and distally straight in lateral view, with three setae: one apical terminal, one apical inner and one sub-apical inner (Fig. 5F). Two apical parameral setae close-set. Parameral apices directed inwards. Parameres basally slightly curved, distally relatively straight, sub-terminally widened, terminally narrowed, apically directed downwards in lateral view (Fig. 6B).

GONOSTYLI. Straight, elongate, thin, with one apical seta, three inner setae and one outer seta (Fig. 5G).

Spermatheca. Small, hook-like, widest in middle, apically sub-spherical (Fig. 5H).

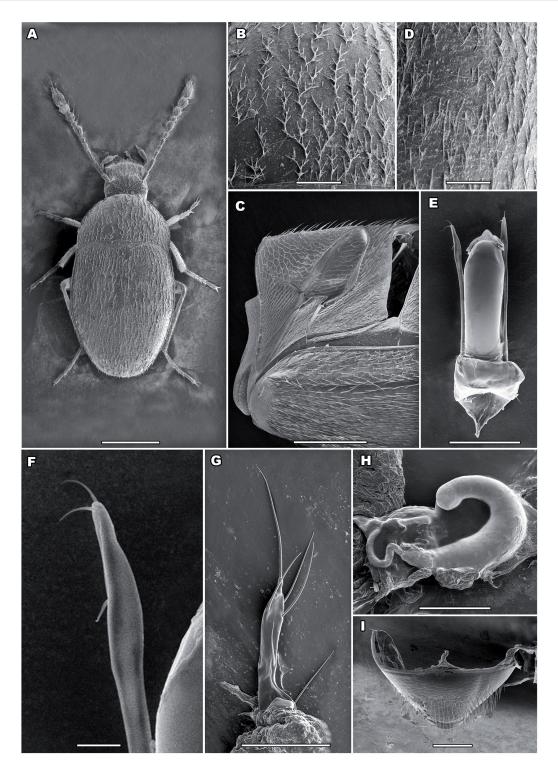


Fig. 5. *Proleonhardella* (*Proleonhardella*) *tarensis* Ćurčić & Pavićević sp. nov. from Pit 4-1-3-27, village of Kaluđerske Bare, Mt Tara, near the town of Bajina Bašta, western Serbia. **A–F**. Paratype male (IZFB-21/28). A. Habitus (dorsal view). **B**. Surface of pronotum (dorsal view). **C**. Mesosternal carina (lateral view). **D**. Surface of elytra (dorsal view). **E**. Aedeagus (dorsal view). **F**. Left paramere apex (dorsal view). **G–I**. Paratype female (IZFB-21/29). **G**. Left gonostylus (dorsal view). **H**. Spermatheca (lateral view). **I**. Abdominal segment VIII (ventral view). Scale bars: $A = 500 \mu m$; B, D, G, $I = 100 \mu m$; C, $E = 200 \mu m$; $F = 25 \mu m$; $H = 50 \mu m$.

Female abdominal sternite VIII. Large, transverse, setose in distal half, with a small, narrow anterior process. Microsculpture consisting of transverse polygonal meshes (Fig. 5I).

Comparisons

Proleonhardella (*P*.) *hirtella*, *P*. (*P*.) *weiratheri* and *P*. (*P*.) *tarensis* sp. nov. are somewhat elongate and their aedeagus is narrower than in the remaining congeners, suggesting their specific position within the genus. Based on these features, they are similar to *Bozidaria* gen. nov., but are much shorter (TL R 1.6–1.8 mm in *P*. (*P*.) *hirtella*, 1.6–2.0 mm in *P*. (*P*.) *weiratheri* and 2.185–2.435 mm in *P*. (*P*.) *tarensis* sp. nov.



Fig. 6. *Proleonhardella* (*Proleonhardella*) *tarensis* Ćurčić & Pavićević sp. nov. from Pit 4-1-3-27, village of Kaluđerske Bare, Mt Tara, near the town of Bajina Bašta, western Serbia. Holotype male (IZFB-21/27), aedeagus. **A.** Dorsal view. **B.** Lateral view. Scale bar = 200 μm.

vs 2.51–2.80 mm in *B. serbooccidentalis* gen. et sp. nov.), share other characteristics of *Proleonhardella* and additionally differ from the new genus in the shape of the antennae, the median lobe of the aedeagus, the basal bulb and its basal projection.

Proleonhardella (P.) tarensis sp. nov. and its closest relatives (P. (P.) hirtella, P. (P.) weiratheri and P. (P.) neumanni) share the presence of elongate, somewhat convex elytra, which are more than twice as long as the pronotum. Furthermore, the new species, P. (P.) hirtella and P. (P.) weiratheri have a somewhat elongate body shape, while the body shape in the remaining Proleonhardella taxa

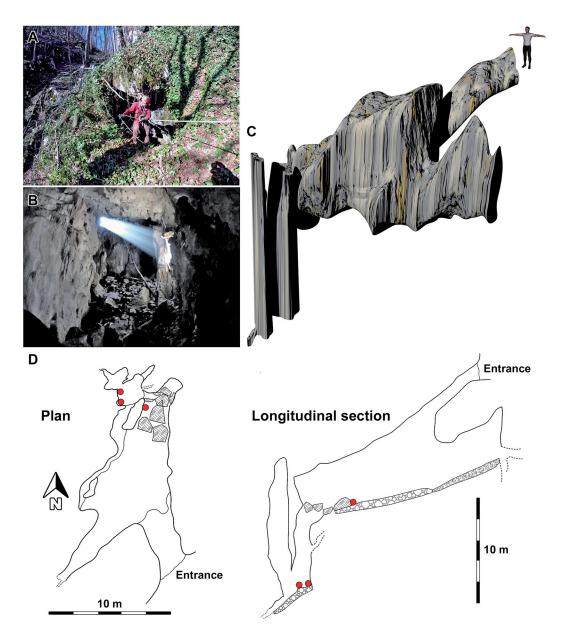


Fig. 7. Pit 4-1-3-27, village of Kaluđerske Bare, Mt Tara, near the town of Bajina Bašta, western Serbia (modified after Bosco 2016). **A.** Entrance. **B.** A chamber in which one type specimen of *Proleonhardella* (*Proleonhardella*) *tarensis* Ćurčić & Pavićević sp. nov. was collected. **C.** A 3D view. **D.** A plan and a longitudinal section. The red circles indicate the places where specimens of *P.* (*P.*) *tarensis* Ćurčić & Pavićević sp. nov. were found.

is more or less bathyscioid. These three species have an elongate aedeagus, contrary to other known congeners, in which the aedeagus is more or less short (Jeannel 1924, 1934). The shape of the aedeagus of *P*. (*P*.) *neumanni* wasn't mentioned in the description of the species or elsewhere (Apfelbeck 1901; Jeannel 1924).

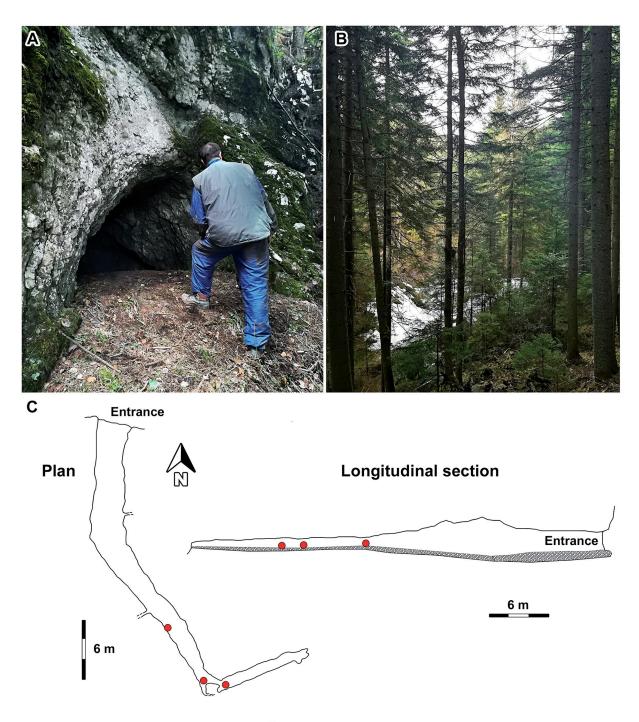


Fig. 8. Sovljačka Pećina Cave, village of Šljivovica, Mt Tara, near the town of Bajina Bašta, western Serbia (modified after Bosco 2016). **A.** Entrance. **B.** Immediate surroundings (a coniferous forest and view of the Sovljak stream). **C.** A plan and a longitudinal section. The red circles indicate the places where specimens of *P. (P.) tarensis* Ćurčić & Pavićević sp. nov. were found.

Bionomy, distribution and type locality

The type specimens were gathered using pitfall traps with rotten meat as bait in Pit 4-1-3-27 in the village of Kaluderske Bare, as well as in the Sovljačka Pećina Cave in the village of Šljivovica (Fig. 9). Both localities are situated on Mt Tara, near the town of Bajina Bašta, western Serbia. Beetles were found in the inner (from the middle to the innermost point), totally dark parts of the cave sites. The entrance of Pit 4-1-3-27 is situated at 868 m a.s.l., the total length of its investigated channels is 28 m, while its depth is 22 m. After a short vertical passage, the pit opens into a large chamber which contains big rocks at its lowest part. At this point another vertical passage starts, at the end of which is situated a small, moist semicircular chamber with a clay substrate and rocks (Bosco 2016). Beetle specimens were found in the inner part of the larger chamber, among rocks, and in the smaller chamber with a clay substrate and rocks, on the floor and vertical limestone walls with a high level of humidity (presence of trickling water). The entrance of the Sovljačka Pećina Cave is situated at 1080 m a.s.l. and its total length is 43 m (Bosco 2016). The cave is located in a coniferous forest in a valley where the Sovljak stream runs. It is entirely horizontal and consists of a single channel which is oriented to the left. Its height is slightly decreasing towards the end. Beetle individuals were found in the inner



Fig. 9. Map of the distribution of taxa of the genera *Bozidaria* Ćurčić & Pavićević gen. nov. and *Proleonhardella* Jeannel, 1910. White circles: *B. serbooccidentalis* Ćurčić & Pavićević gen. et sp. nov. Turquoise star: *P. (Pholeuonillus) adolfi* (Reitter, 1911). Light blue sun: *P. (Proleonhardella) matzenaueri matzenaueri* (Apfelbeck, 1907). Dark blue sun: *P. (P.) matzenaueri ottonis* Müller, 1917. Purple flower: *P. (P.) leonhardi* (Breit, 1913). Yellow cross: *P. (P.) apfelbecki* Jeannel, 1924. Brown circles: *P. (P.) remyi* Jeannel, 1934. Green squares: *P. (P.) hirtella* Jeannel, 1934. Pink pentagon: *P. (P.) neumanni* (Apfelbeck, 1901). Red triangle: *P. (P.) weiratheri* (Reitter, 1913). Orange rhombuses: *P. (P.) tarensis* Ćurčić & Pavićević sp. nov. Scale bar = 50 km.

part of the cave, on the floor among rocks, both on limestone and clay substrate, where a high level of humidity (presence of trickling water) was evident. Images of the cave localities and the places where the specimens were found in the caves are shown in Figs 7–8. The new species is most probably endogean and is likely to be found outside caves as well – in the deep soil strata and other speleological sites in the surroundings.

Key to the taxa of the genus *Proleonhardella* Jeannel, 1910 (modified after Jeannel 1924) (Figs 9–10)

(m	odined after Jeannel 1924) (Figs 9–10)
1.	Body more elongate, elliptical. Pronotum as wide as elytra, well constricted basally. Pronotal lateral margins well-rounded backwards. Mesosternal carina very low. Elytral punctuation rough and deep (subgenus <i>Pholeuonillus</i> Breit, 1913). Endogean, Mt Treskavica, southern Bosnia and Herzegovina
2.	Elytra shorter, more convex, less than twice as long as pronotum (Fig. 10A)
3.	Body of oval shape, longer (TL 1.8–2.2 mm). Antennae short, not reaching middle of body. Antennomere III not longer than antennomere V. Antennomere VIII globular in males (Fig. 10C). Cavernicolous, Mts Bjelašnica and Igman, central Bosnia and Herzegovina [<i>P. (Proleonhardella</i>)
-	matzenaueri (Apfelbeck, 1907)]
4.	Body of almost regular oval shape, longer (TL 2.0–2.2 mm). Elytra not widened towards middle. Cavernicolous, Mt Bjelašnica, central Bosnia and Herzegovina
-	Body narrower anteriorly, shorter (TL 1.8–2.0 mm). Elytra clearly widened medially. Cavernicolous, Mt Igman, central Bosnia and Herzegovina
5.	Body more elongate and convex, longer (TL 1.5 mm). Elytral punctuation finer and denser. Antennae shorter, with apical antennomeres thicker. Antennomere VIII barely longer than wide, antennomere IX as long as wide and antennomere X transverse in females. Cavernicolous, Mt Treskavica, southern Bosnia and Herzegovina
_	Body less elongate and convex, shorter (TL 1.3 mm). Elytral punctuation stronger and less dense. Antennae longer, with apical antennomeres less thick. Antennomeres VIII, IX and X longer than wide in females. Cavernicolous, village of Trnovo, vicinity of the city of Sarajevo, central Bosnia and Herzegovina
6.	Priboj and Pljevlja, southwestern Serbia and northern Montenegro
_	Body shorter (TL less than 2.435 mm)
7. –	Elytra parallel in basal half (Fig. 10E)

- Pubescence short. Punctuation finer. Apical antennomeres less widened. Pronotum more rounded.
 Apex of median lobe of aedeagus more bent ventrally. Elytral apex attenuated. Cavernicolous,
 Mt Sjemeć, eastern Bosnia and Herzegovina P. (Proleonhardella) weiratheri (Reitter, 1913)

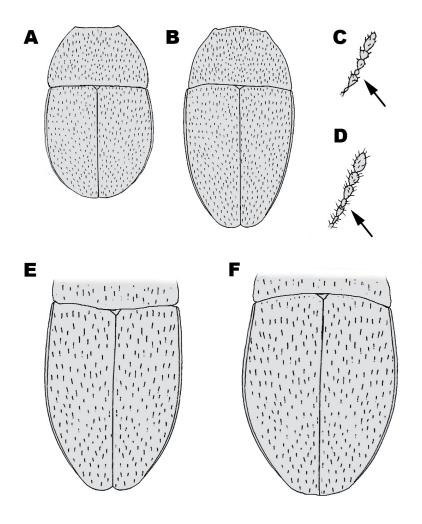


Fig. 10. Illustrations of morphological characters presented in the Key to the taxa of the genus *Proleonhardella* Jeannel, 1910 (after Jeannel 1924; Ćurčić *et al.* 2008a). **A.** Short elytra, less than twice as long as pronotum. **B.** Long elytra, more than twice as long as pronotum. **C.** Globular antennomere VIII in males. **D.** Slightly elongate antennomere VIII in males. **E.** Elytra parallel in basal half. **F.** Elytra narrowed in basal half.

Discussion

It should be noted that a new genus of leptodirines belonging to the phyletic series of "Leonhardella" was recently established. Ćurčić *et al.* (2008a) considered the status of *P.* (*P.*) *remyi* and described a new genus, Serboleonhardella S. Ćurčić & Schönmann, 2008, based on this taxon. Numerous differences between P. (P.) remyi and other members of the genus Proleonhardella, some of which are quite significant (body size and form, antennal length, shape of certain antennomeres, form of median lobe and shape of parameral apex), indicated a need to separate P. (P.) remyi as a distinct genus or at least to a specific position within the genus *Proleonhardella*. This genus was not reported in the catalogues of Perreau (2015) and Hlaváč et al. (2017), nor has it been synonymized so far. Even Jeannel (1934) recognised that P. (P.) remyi is quite remarkable for its large size compared to other congeners, which barely exceed 2 mm in length. The occurrence together of several congeners is a rare phenomenon in caves. Such is the case with P. (P.) remyi and P. (P.) hirtella, which were recorded together at five speleological sites in southwestern Serbia and northern Montenegro (Pavićević et al. 2012). This might also suggest that these taxa are indeed not congeneric. Additionally, Ćurčić et al. (2008a) proposed a new status for *Pholeuonillus* – as a full genus instead of a subgenus. Interestingly, *Pholeuonillus* was established by Breit (1913), who gave it generic rank. Later on, Jeannel (1924) treated it as a subgenus of *Proleonhardella* – a status that was maintained until now. It is recommended to study the taxa in question and other members of the genus *Proleonhardella* using molecular analyses in order to illuminate their phylogenetic relationships and to have their taxonomic status reconsidered and changed, if needed.

A series of high fluvial plateaus of the Inner Dinarides occur in western and southwestern Serbia (Zlatibor, Jabuka-Babine, etc.). According to their position in the area's relief, these plateaus are presumed to be of Pliocene age (Cvijić 1924, 1926). The palaeokarst in the areas of Mts Povlen and Tara was most probably formed at the same time as the Zlatibor plateau, in the second half of the Pliocene. Based on chronostratigraphic criteria by the International Commission on Stratigraphy (Gibbard *et al.* 2010; Gaudenyi & Jovanović 2012), it is estimated that the palaeokarst in question is around 3–3.5 Ma old. It is likely that the karstic areas of Mts Povlen and Tara were connected with other karstic regions in their vicinity, favouring links between their subterranean faunas in old geological times, as evidenced by the occurrence of two new endogean and cavernicolous leptodirine taxa and their closest relatives in the surrounding areas.

The tribe Leptodirini has a Palaearctic distribution with its highest diversity located in the Mediterranean (Perreau 2000, 2015). It has undergone extensive diversification in the subterranean environment (Ribera *et al.* 2010). In their comprehensive molecular approach to the phylogeny of western Mediterranean Leptodirini, including the fauna of the Iberian Peninsula, Ribera *et al.* (2010) revealed that the main subterranean lineages of the tribe were separated before the Early Oligocene.

The Dinaric mountain chain has provided suitable conditions for subterranean life for millions of years, which resulted in the presence of a rich and diverse cave-dwelling fauna (Zagmajster *et al.* 2008; Kozel *et al.* 2020; Sendra & Reboleira 2020). The leiodid beetle tribe Leptodirini is among the richest groups in the subterranean habitats (Sket 2005), comprising 175 species and 50 genera, most of which are endemic to the Dinarides. This mountain range is recognized for having the world's greatest species richness of subterranean fauna (Sket 2004; Culver *et al.* 2006; Deharveng *et al.* 2012). A very few studies dealing with phylogenetic relationships of certain subtribes within Dinaric Leptodirini exist. These studies were based only on morphology (Jeannel 1930; Perreau & Pavićević 2008; Perreau 2019) and in most cases they have not been tested with molecular data. Only recently, Njunjić *et al.* (2018) commented on the suprageneric classification of eastern Mediterranean Leptodirini based on molecular phylogeny data. The clade comprising the subtribes Bathysciina Horn, 1880 and Bathysciotina V. Guéorguiev, 1974 was estimated to have originated in the Oligocene (ca 30 Ma ago), while the tested genera of Bathysciina

belonging to the phyletic series of "Leonhardella" (Leonhardella and Proleonhardella) separated more recently – in the Miocene (ca 20 Ma ago) (Njunjić et al. 2018).

As in the study of Njunjić *et al.* (2018) only two taxa belonging to the subtribe Bathysciina (phyletic series of "Leonhardella") were subjected to molecular characterization (Leonhardella (Leonhardellina) antennaria Apfelbeck, 1907 and *P. (P.) remyi*), more Dinaric genera of Bathysciina should be included in future molecular analyses to establish their phylogenetic relationships and to understand their origin and the colonization of the region by the subterranean representatives of the group. Discoveries of fascinating new genera of Bathysciina in the underground of the Dinaric karst in the last few decades (Nonveiller & Pavićević 1999; Perreau 1999), including the one described herein, suggest that further investigations of the caves of the area are needed.

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