



This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

Research article

urn:lsid:zoobank.org:pub:E470EA58-7317-4643-9D1E-D3A6FF710DA0

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov., a new troglobitic leiodid beetle (Coleoptera: Leiodidae: Leptodirini) from southwestern Serbia

Srećko ĆURČIĆ^{1,*}, Maja VRBICA², Korana KOCIĆ³, Vukašin GOJŠINA⁴,
Sofija VRANIĆ⁵ & Nikola VESOVIĆ⁶

^{1,2,3,4,5,6}Institute of Zoology, University of Belgrade - Faculty of Biology, Studentski Trg 16,
11000 Belgrade, Serbia.

*Corresponding author: srecko@bio.bg.ac.rs

²Email: maja.vrbica@bio.bg.ac.rs

³Email: korana.kocic@bio.bg.ac.rs

⁴Email: vukasin.gojsina@bio.bg.ac.rs

⁵Email: sofija.vranic@bio.bg.ac.rs

⁶Email: nikola.vesovic@bio.bg.ac.rs

¹urn:lsid:zoobank.org:author:EFF0167C-0145-459F-A5CB-69778283E575

²urn:lsid:zoobank.org:author:47E4BA55-887B-4BDB-A6BF-C8490ACE633A

³urn:lsid:zoobank.org:author:FD666F7B-EB75-4083-86F7-BC4137661326

⁴urn:lsid:zoobank.org:author:7DFBCA49-0B7D-4516-96EE-8CB7C346E6DE

⁵urn:lsid:zoobank.org:author:B319CE00-2512-4780-BDFB-C8D5DCAC931D

⁶urn:lsid:zoobank.org:author:AA52F4F6-C952-4887-B257-FDBED464C5DA

Abstract. The genus *Remyella* Jeannel, 1931 consists of stenoendemic troglobitic leiodid beetles restricted to subterranean habitats in southwestern Serbia and northeastern Montenegro. A new subterranean leiodid species, *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov., from the Pećina na Đerekarskom Vrelu Cave (village of Đerekare, near the town of Tutin, Pešter Plateau, southwestern Serbia), is described and diagnosed. All taxonomically important morphological features of the new taxon are presented, including traits of both male and female genitalia. The new species is clearly distinguished from other congeners both morphologically and molecularly. Data on the sexual dimorphism of the new species are presented. Molecular analysis confirmed that *Remyella raskae* S. Ćurčić & B. Ćurčić, 2008 is a valid species. A key to the identification of the species of the genus *Remyella* is given. In addition, the species *Remyella hussoni* Jeannel, 1934 was found at another subterranean site in the village of Đerekare.

Keywords. Round fungus beetles, subterranean, endemic, cytochrome oxidase subunit I, Balkan Peninsula.

Ćurčić S., Vrbica M., Kocić K., Gojšina V., Vranić S. & Vesović N. 2025. *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov., a new troglobitic leiodid beetle (Coleoptera: Leiodidae: Leptodirini) from southwestern Serbia. *European Journal of Taxonomy* 997: 289–307. <https://doi.org/10.5852/ejt.2025.997.2941>

Introduction

The taxonomic history of *Remyella* Jeannel, 1931, a genus of subterranean leiodid beetles endemic to the Pešter Plateau in southwestern Serbia and northeastern Montenegro, begins with the description by Jeannel (1931), together with a single species – *Remyella scaphoides* Jeannel, 1931. Not long afterwards, Winkler (1933) added two new taxa: *Remyella propiformis* Winkler, 1933 and *R. propiformis borensis* Winkler, 1933. Further taxonomic studies of the genus were carried out by Jeannel (1934), which led to the description of two additional congeners – *Remyella propiformis hussoni* Jeannel, 1934 and *R. puncticollis* Jeannel, 1934. After the revision by Giachino & Etonti (1995), a new subspecies (*Remyella scaphoides droveniki* Giachino & Etonti, 1995) was introduced and *R. puncticollis* was synonymized with *R. scaphoides borensis* Winkler, 1933. Ćurčić *et al.* (2008, 2013) described three new species: *Remyella raskae* S. Ćurčić & B. Ćurčić, 2008, *R. javorensis* S. Ćurčić & B. Ćurčić, 2008 and *R. montenegrina* S. Ćurčić, Antić, N. Ćurčić & B. Ćurčić, 2013. A total of four species of *Remyella* were recognized at that time: *R. javorensis*, *R. montenegrina*, *R. raskae* and *R. scaphoides*, the latter of which comprised five subspecies: *R. scaphoides borensis*, *R. scaphoides droveniki*, *R. scaphoides hussoni* Jeannel, 1934, *R. scaphoides propiformis* Winkler, 1933 and *R. scaphoides scaphoides* Jeannel, 1931 (Ćurčić *et al.* 2013; Hlaváč *et al.* 2017).

Njunjić *et al.* (2017) conducted a more detailed molecular and morphological study on the taxa of the genus *Remyella*. A taxon from the Đalovića Pećina (= Pećina nad Vražjim Firovima) Cave, previously described as *R. montenegrina* by Ćurčić *et al.* (2013), was synonymized with *R. propiformis* based on the shape of the male genitalia. Using the morphological characteristics in combination with molecular data (with the exception of *R. scaphoides* and *R. raskae*) that seemed to be relevant for the separation of species, Njunjić *et al.* (2017) recognized five *Remyella* species: *R. javorensis*, *R. raskae*, *R. hussoni*, *R. propiformis* (this and the previous taxon were raised from subspecies level to species level) and *R. scaphoides*. According to these authors, there are no subspecies within the listed species. The subspecies *R. scaphoides borensis* and *R. scaphoides droveniki* were synonymized with *R. propiformis*. The species are distributed in three isolated karst areas on the edge of the Pešter Plateau (Fig. 1): i) the surroundings of the town of Sjenica (southwestern Serbia) is inhabited by *R. javorensis* [from the Baždarska Pećina Cave (its type locality), the village of Ursule and the Ušak cave system, the village of Ušak; ii) the surroundings of the city of Novi Pazar (southwestern Serbia) is inhabited by *R. raskae* (from the Pećina na Vrelu Raške Cave); iii) a karst zone on the Serbian-Montenegrin border is inhabited by *R. hussoni* [from the Pećina u Hamidovoj Vrtači Cave (its type locality), the village of Suvi Do, near the town of Sjenica, southwestern Serbia; the Jama na Sjera Poljani Pit, the Jama u Piskovoj Poljani Pit and the Ponor Ledenice Cave, all in the village of Đerekare, near the town of Tutin, southwestern Serbia; the Ledenica Cave and the Pećina u Vrh Livade Radojeve Cave, the village of Korita, near the town of Bijelo Polje, northeastern Montenegro], *R. propiformis* [from the Špela Hajnet Cave (its type locality), the Špela Vogel Cave, the sinkhole of the Boroštica river and the Špela Bores Cave, all in the village of Ugao, near the town of Tutin, southwestern Serbia; the Jama na Lopužinom Brdu Pit, Lopužino Brdo hill, Mt Giljeva, near the town of Sjenica, southwestern Serbia; the Uleva Pećina III Cave, the Pećina u Anin Kapeš Cave, the Pećina Ispod Gluare Cave, the Jama bez Dna Pit, the Pećina kod Jagodina Dola Cave and the Bezdán Kaćunova Ravan Pit, all in the villages of Doliće, Kapeš and Boljare, near the town of Sjenica, southwestern Serbia; the Jagoševa Pećina Cave and the Đalovića Pećina (= Pećina nad Vražjim Firovima) Cave, both in the village of Đalovići, near the town of Bijelo Polje, northeastern Montenegro] and *R. scaphoides* (from the Velika Pećina Cave, the village of Grgaje, near the town of Sjenica, southwestern Serbia) (Jeannel 1931, 1934; Winkler 1933; Pretner 1968; Guéorguiev 1990; Giachino & Etonti 1995; Perreau 2000, 2015; Ćurčić *et al.* 2008, 2013; Hlaváč *et al.* 2017; Moravec 2017; Njunjić *et al.* 2017; Čeplík 2023).

Two field trips to the Pešter Plateau (southwestern Serbia) conducted by the members of the Institute of Zoology of the University of Belgrade - Faculty of Biology (Belgrade, Serbia) in 2023 led to the

discovery of a number of adult specimens of a new leptodirine species – *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov., whose description and diagnosis are presented in the current study. A further task was to determine the phylogenetic position of the new species in relation to the other species of the genus *Remyella*, to verify the validity of *R. raskaе* and to report a new locality of *R. propiformis*.

Material and methods

Sampling information

The adult specimens of leptodirine leiodid beetles were collected both manually and with pitfall traps filled with propylene glycol and containing rotting meat or cheese as bait in the deepest accessible part of the Pećina na Đerekarskom Vrelu Cave in Đerekare, a village near the town of Tutin in southwestern Serbia, close to the Montenegrin border. The traps were placed both on the floor and on the walls in the dark part of the cave, where the humidity was high. The collected individuals were stored at room temperature in 70% ethanol, except for those destined for molecular analysis, which were stored in 96% ethanol and preserved in a freezer at -20°C.

Taxonomic and morphological analyses

We used the traditional method of examining insect morphology using bright-field microscopy. Furthermore, scanning electron microscopy (SEM) micrographs provided additional morphological details that were used for the description and diagnosis of the new species.

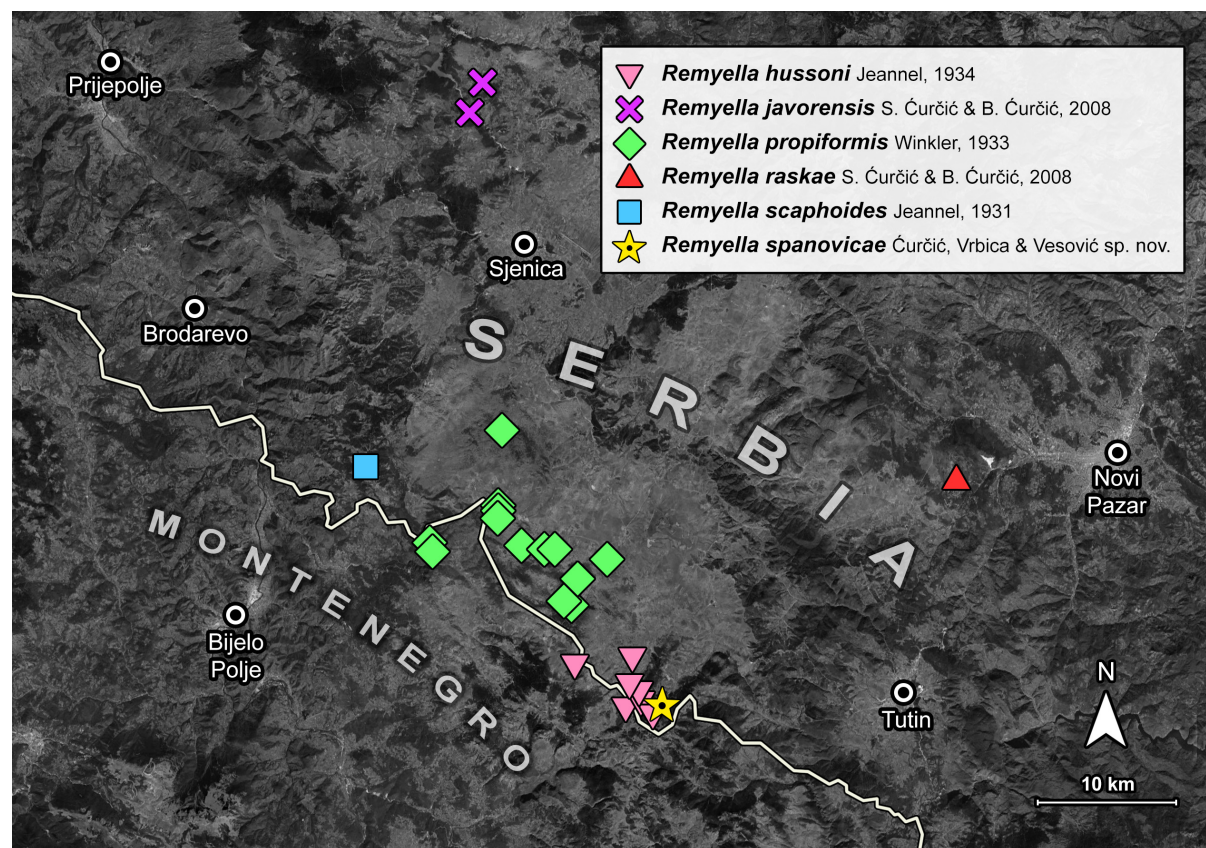


Fig. 1. Map of a part of southwestern Serbia and northeastern Montenegro (Pešter Plateau) with the localities of the species of *Remyella* Jeannel, 1931.

Bright-field microscopy

The type specimens of the new species were examined in a laboratory of the Institute of Zoology, University of Belgrade - Faculty of Biology (Belgrade, Serbia). They were dissected, thoroughly analysed and imaged. Both male and female genital structures were removed from the bodies, cleared in clove oil and then fixed on microscope slides in DPX medium. The beetles were then glued onto paper mounting cards and examined as dry specimens.

A total of 17 individuals (two males and 15 females) of the new species were measured (the values are given as averages and ranges in Table 1). All taxonomically important morphological traits were examined with a SMZ800N stereo microscope (Nikon, Tokyo, Japan), to which a DS-Fi2 digital camera (Nikon, Tokyo, Japan) was attached. A Nikon DS-L3 control unit was used for scale adjustment and precise measurements. An Intralux 5100 cold light source (Volpi, Schlieren, Switzerland) was used for additional illumination of the specimens under the stereo microscope. A DMLB light microscope (Leica, Wetzlar, Germany) equipped with a DFC295 camera (Leica, Wetzlar, Germany) was used to examine and photograph the genitalia.

Scanning electron microscopy (SEM)

A JSM-6390LV scanning electron microscope (SEM) (JEOL, Ltd., Akishima, Japan) at the University of Belgrade - Faculty of Agriculture (Belgrade, Serbia) was used to observe the detailed morphology of the new species. Prior to analysis, the beetle samples (three female specimens) were coated with gold for 100 s using an SCD005 sputter coater (BAL-TEC AG, Balzers, Liechtenstein). The high vacuum mode of the SEM with an accelerating voltage of 10 kV was used. The index of the electron beam intensity was 8.00, the electron beam current was 30 mA, while the pressure in the column was around 1.3×10^{-3} Pa.

Molecular analysis

DNA extraction, PCR amplification and sequencing

The Qiagen DNeasy® Blood & Tissue Kit (Qiagen Inc., Valencia, CA, USA) was used for non-destructive extraction of total DNA from whole specimens. The universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994) were used for PCR amplification of the cytochrome oxidase subunit I barcoding region (*COI*). The amplification mixture contained 32.6 µL of nuclease-free water, 10 µL of buffer, 1 µL of each primer pair, 1 µL of nucleotides, 0.4 µL of OneTaq DNA polymerase (New England BioLabs, Ipswich, MA, USA) and 4 µL of extracted DNA, so the final volume was 50 µL. The following PCR temperature profile was used: 60 s of initial denaturation (95°C), 35 cycles of 60 s of denaturation (94°C), 60 s of annealing (54°C), 90 s of extension (72°C) and 7 min of final extension (72°C). The amplification products obtained were sent to Macrogen Europe (Amsterdam, the Netherlands) for purification and sequencing. The sequences were analysed, trimmed and aligned using BioEdit software (Hall 1999). Evolutionary divergence analysis was performed with MEGA 11 software (Tamura *et al.* 2021) using the p-distance model. Bayesian evolutionary analysis was performed using BEAST 2.5 software (Drummond *et al.* 2012) with the initial dataset created using BEAUti ver. 1.10.4 (Drummond *et al.* 2012) with a designated strict clock type and the Yule process of speciation. The analysis ran for 10 million generations, sampling was performed every 1000 generations, while the first million trees were discarded as burn-in. The effective sample size (ESS) of the Markov chain Monte Carlo parameters was estimated using Tracer ver. 1.7.1 (Rambaut *et al.* 2018). The phylogenetic tree was visualized using FigTree ver. 1.4.3 software (Rambaut 2009).

The sequences obtained from *R. raskae* (one specimen), *R. spanovicæ* Ćurčić, Vrbica & Vesović sp. nov. (three specimens) and the outgroup sequence of the subspecies *Anthroherpon taxi remyi* Jeannel, 1931 (one specimen) were analysed together with the additional 15 sequences of four *Remyella* species (*R. javorensis*, *R. propiformis*, *R. hussoni* and *Remyella* sp.) acquired from the GenBank database. All

Table 1. Linear measurements and morphometric ratios in *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov. and its sexes. The values outside the parentheses are mean values, while those inside the parentheses are ranges (*values in mm).

Species and sex Character	<i>Remyella spanovicae</i> Ćurčić, Vrbica & Vesović sp. nov.		
	♂♀	♂	♀
TL*	4.48 (4.09–4.72)	4.14 (4.09–4.18)	4.53 (4.29–4.72)
HL/HW	1.17 (1.08–1.25)	1.14 (1.12–1.15)	1.18 (1.08–1.25)
HW/PW	1.02 (0.97–1.06)	1.01 (1.00–1.02)	1.02 (0.97–1.06)
AL*	4.22 (3.97–4.63)	4.63 (4.63)	4.16 (3.97–4.42)
AL/EL	1.49 (1.40–1.82)	1.79 (1.77–1.82)	1.45 (1.40–1.50)
AL/TL	0.94 (0.89–1.13)	1.12 (1.11–1.13)	0.92 (0.89–0.94)
A1L/A2L	1.04 (0.96–1.16)	0.98 (0.96–1.00)	1.05 (0.97–1.16)
A3L/A2L	1.37 (1.17–1.48)	1.41 (1.36–1.46)	1.37 (1.17–1.48)
A8L/A7L	0.82 (0.74–0.91)	0.87 (0.82–0.91)	0.81 (0.74–0.85)
A8L/A9L	0.91 (0.85–0.97)	0.93 (0.91–0.96)	0.91 (0.85–0.97)
A8W/A7W	0.64 (0.50–0.71)	0.67 (0.67)	0.63 (0.50–0.71)
A8W/A9W	0.65 (0.50–0.83)	0.67 (0.67)	0.65 (0.50–0.83)
PL/PW	1.19 (1.13–1.26)	1.20 (1.20–1.21)	1.18 (1.13–1.26)
PL/HL	1.00 (0.93–1.08)	1.05 (1.05)	1.00 (0.93–1.08)
PB/AM	0.92 (0.88–0.95)	0.94 (0.94)	0.92 (0.88–0.95)
EL/EW	2.30 (2.14–2.53)	2.49 (2.45–2.52)	2.27 (2.14–2.53)

sequences obtained in this study are deposited in the GenBank database (accession numbers are given in Table 2).

Abbreviations of measurements

- A1L/A2L = ratio of the length of the antennomere I to the length of the antennomere II
A3L/A2L = ratio of the length of the antennomere III to the length of the antennomere II
A8L/A7L = ratio of the length of the antennomere VIII to the length of the antennomere VII
A8L/A9L = ratio of the length of the antennomere VIII to the length of the antennomere IX
A8W/A7W = ratio of the width of the antennomere VIII to the width of the antennomere VII
A8W/A9W = ratio of the width of the antennomere VIII to the width of the antennomere IX
AL = total length of the antennae
AL/EL = ratio of the total length of the antennae to the length of the elytra
AL/TL = ratio of the total length of the antennae to the total length of the body
EL/EW = ratio of the length of the elytra (as a linear distance measured along the suture from the elytral base to the apex) to the maximum width of the elytra
HL/HW = ratio of the length of the head (as a linear distance measured from the anterior margin of the clypeus to the neck constriction) to the maximum width of the head (as the greatest transverse distance)
HW/PW = ratio of the maximum width of the head to the maximum width of the pronotum
M = mean value for certain measurements
PB/AM = ratio of the length of the pronotal base to the length of the anterior pronotal margin
PL/HL = ratio of the length of the pronotum to the length of the head
PL/PW = ratio of the length of the pronotum (as the greatest longitudinal distance) to the maximum width of the pronotum (as the greatest transverse distance)

Table 2. Specimens of Leptodirini Lacordaire, 1854 used for molecular analyses with GenBank accession numbers (*outgroup).

Locality	Taxon	GenBank
Pećina na Vrelu Raške Cave	<i>Remyella raskaе</i> S. Ćurčić & B. Ćurčić, 2008	PV138860
Pećina na Đerekarskom Vrelu Cave	<i>Remyella spanovicae</i> Ćurčić, Vrbica & Vesović sp. nov.	PV138858
Pećina na Đerekarskom Vrelu Cave	<i>Remyella spanovicae</i> Ćurčić, Vrbica & Vesović sp. nov.	PV138857
Pećina na Đerekarskom Vrelu Cave	<i>Remyella spanovicae</i> Ćurčić, Vrbica & Vesović sp. nov.	PV138859
Bracanovića Pećina Cave	<i>Anthroherpon taxi remyi</i> Jeannel, 1931*	PV138861

R = range of the total measurements performed

TL = total length of the body (measured from the anterior margin of the clypeus to the apex of the elytra)

Institutional abbreviations

CBSE = collection of the Center for Biospeleology of Southeast Europe, Belgrade, Serbia

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

Results

Taxonomy

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 *Remyella* Jeannel, 1931

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov.

urn:lsid:zoobank.org:act:02AFC9E8-9688-4B9F-95C4-C194658D018B

Figs 1–5; Tables 1–3

Diagnosis

A medium-sized, depigmented, anophthalmous, scaphoid leptodirine beetle with the character state of the genus *Remyella*, closely related to *R. hussoni* and *R. propiformis*, from which it differs mainly in the sides of the pronotum, which converge in a straight line from the point of maximum pronotal width to the anterior pronotal angles.

Differential diagnosis

The species geographically, morphologically and molecularly closest to the new species are *R. hussoni* and *R. propiformis*, with which *R. spanovicae* Ćurčić, Vrbica & Vesović sp. nov. shares the similar body length, the presence of the lateral rim of the pronotum extending from the pronotal base to $\frac{2}{3}$ – $\frac{3}{4}$ of the PL, the narrow median lobe of the aedeagus and the similar shape of the apex of the median lobe of the aedeagus (Winkler 1933; Jeannel 1934: 101, figs 12–13; Guéorguiev 1990; Giachino & Etonti 1995: 80, 82, figs 1–7; Njunjić *et al.* 2017: 150–151, figs 15, 31). The species *R. javorensis* and *R. raskaе* seem to be close to the new species based on the shape of the sides of the pronotum, which in these three species

converge in a straight line from the point of maximum pronotal width to the anterior pronotal angles (Ćurčić *et al.* 2008: 111, 113, figs 1–4; Njunjić *et al.* 2017: 151, figs 28–29, 32). The basic differences between *R. spanovicae* and all other species of the genus *Remyella* are listed below.

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov. differs from *R. hussoni* in the PL/PW (M 1.19 vs 1.10), the PW (slightly before the middle vs approximately in the middle), the shape of the lateral pronotal margins (converging in a straight line from the point of maximum pronotal width to the anterior pronotal angles vs convex in the anterior part), the density of the punctuation on the pronotal disc (relatively sparse vs dense) and the shape of the apex of the median lobe of the aedeagus (slightly extended vs sharp) (Jeannel 1934; Guéorguiev 1990; Giachino & Etonti 1995; Njunjić *et al.* 2017: 151, fig. 31).

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov. differs from *R. propiformis* in the shape of the lateral pronotal margins (converging in a straight line from the point of maximum pronotal width to the anterior pronotal angles vs convex in the anterior part), the PW (slightly before the middle vs approximately in the middle) and the shape of the apex of the median lobe of the aedeagus (slightly

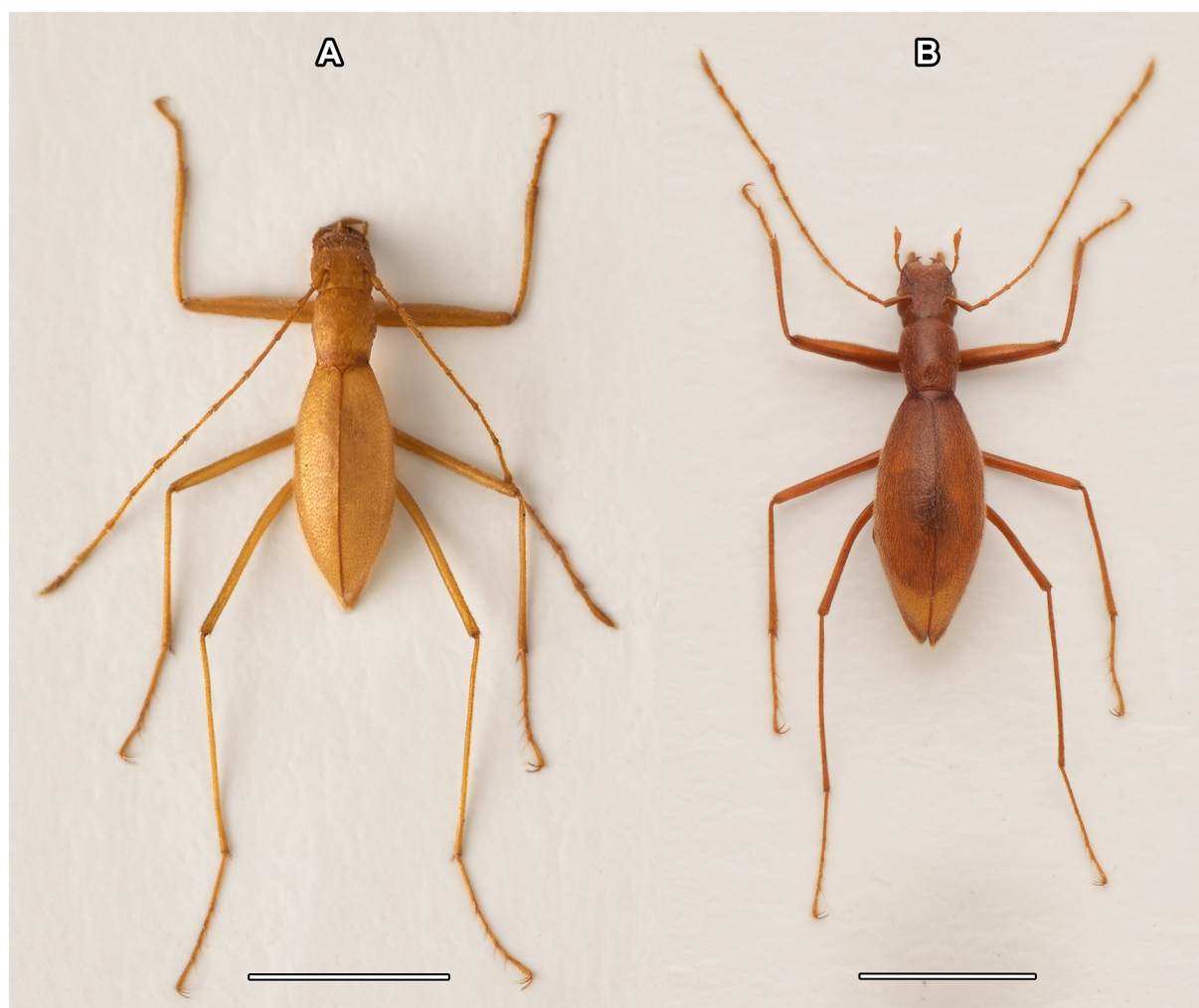


Fig. 2. Habitus of *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov., dorsal view. **A.** Holotype, ♂ (IZFB-24/15). **B.** Paratype, ♀ (IZFB-24/17). Scale bars = 2 mm.

extended vs sharp) (Winkler 1933; Jeannel 1934: 101, figs 12–13; Guéorguiev 1990; Giachino & Etonti 1995: 80, 82, figs 1–7; Njunjić *et al.* 2017: 150, fig. 15).

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov. differs from *R. javorensis* in the TL (on average smaller vs on average greater), the PL/PW (M 1.19 vs 1.25), the PW (slightly before the middle vs approximately in the middle), the shape of the lateral pronotal margins (less abruptly narrowed after the middle, then converging to the pronotal base vs more abruptly narrowed after the middle, then parallel to the pronotal base), the length of the lateral pronotal rim (extending from the pronotal base to $\frac{2}{3}$ – $\frac{3}{4}$ of the PL vs limited to the basal half of the pronotum) and the shape of the apex of the median lobe of the aedeagus (slightly extended vs bent upwards) (Ćurčić *et al.* 2008: 113, figs 3–4; Njunjić *et al.* 2017: 151, figs 29, 32).

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov. differs from *R. raskaе* in the TL (on average smaller vs on average greater), the PL/PW (M 1.19 vs 1.25), the PW (slightly before the middle vs in the posterior third), the shape of the lateral pronotal margins (less abruptly narrowed after the middle, then converging to the pronotal base vs more abruptly narrowed after the basal third, then parallel to the pronotal base), the length of the lateral pronotal rim (extending from the pronotal base to $\frac{2}{3}$ – $\frac{3}{4}$ of the PL vs limited to the basal half of the pronotum) and the shape of the apex of the median lobe of the aedeagus (slightly extended vs sharp) (Ćurčić *et al.* 2008: 111, figs 1–2; Njunjić *et al.* 2017: 151, fig. 28).

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov. differs from *R. scaphoides* in the PL/PW (M 1.19 vs 1.15), the PW (slightly before the middle vs approximately in the middle), the shape of the lateral pronotal margins (converging in a straight line from the point of maximum pronotal width to the anterior pronotal angles vs convex in the anterior part), the width of the median lobe of the aedeagus (narrow vs wide) and the shape of the apex of the median lobe of the aedeagus (slightly extended vs blunt) (Jeannel 1931: 261, 264, figs 6–8, 11; Winkler 1933; Jeannel 1934: 101, fig. 11; Winkler 1933; Guéorguiev 1990; Giachino & Etonti 1995; Njunjić *et al.* 2017: 150–151, figs 14, 30).

Etymology

Remyella spanovicae Ćurčić, Vrbica & Vesović sp. nov. is named after Ivana Španović, a famous Serbian athlete, one of the greatest female long jumpers of all time. She is the reigning world champion, two-time world indoor champion, two-time European champion, three-time European indoor champion, five-time winner of the Diamond League Trophy and Olympic medalist in the women's long jump.

Type material

Holotype

SERBIA • ♂ (Fig. 2A); southwestern Serbia, Pešter Plateau, town of Tutin, village of Đerekare, Pećina na Đerekarskom Vrelu Cave; 42°58'51.0" N, 20°07'13.0" E; 25 Jun.–15 Jul. 2023; Srećko Ćurčić and Vukašin Gojšina leg.; collected manually and with pitfall traps filled with propylene glycol and with rotten meat or cheese as bait; IZFB-24/15; IZFB.

Paratypes

SERBIA • 1 ♂; same data as for holotype; IZFB-24/16; IZFB • 75 ♀♀ (three of which are shown in Figs 2B, 3); same data as for holotype; IZFB-24/17-91; IZFB • 12 ♀♀; same locality as for holotype; 25 Jun. 2023; Nikola Vesović and Srećko Ćurčić leg.; collected manually; IZFB-24/92-103; IZFB.

Description

HABITUS. Medium-sized leptodirine beetle. Body length: TL M 4.48 mm (4.14 mm in males, 4.53 mm in females), R 4.09–4.72 mm (4.09–4.18 mm in males, 4.29–4.72 mm in females) (Table 1). Body colour

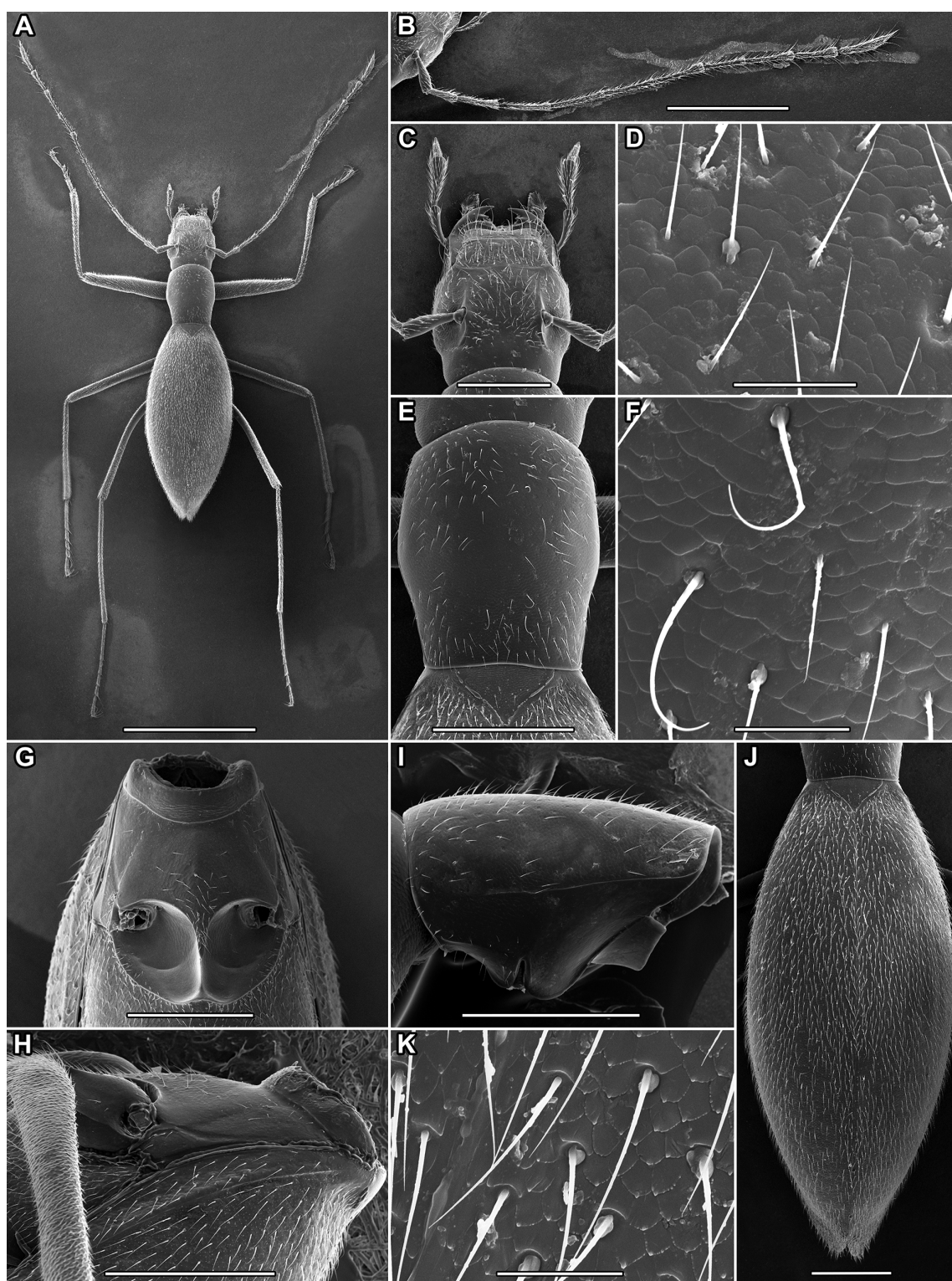


Fig. 3. *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov., SEM images of the external morphological features. **A–F, J, K.** Paratype, ♀ (IZFB-24/18). **G–I.** Paratype, ♀ (IZFB-24/19). **A.** Habitus, dorsal view. **B.** Right antenna, dorsal view. **C.** Head, dorsal view. **D.** Microsculpture of head, dorsal view. **E.** Pronotum, dorsal view. **F.** Microsculpture of pronotum, dorsal view. **G.** Mesoventrite, ventral view. **H.** Mesoventrite, lateral view. **I.** Pronotum, lateral view. **J.** Elytra, dorsal view. **K.** Microsculpture of elytra, dorsal view. Scale bars: A = 2 mm; B = 1 mm; C, E, G–J = 500 µm; D, F, K = 50 µm.

yellowish-brown, body shape scaphoid, tegument shiny (Figs 2, 3A). Head, pronotum and elytra with polygonal microsculpture (Fig. 3D, F, K).

HEAD. Elongate (HL/HW M 1.17, R 1.08–1.25), with slightly concave genae, covered with short and dense yellow erect setae and dense punctuation (Fig. 3C), about as wide as pronotum (HW/PW M 1.02, R 0.97–1.06). Eyes absent. Antennae elongate, thin, longer than elytra (AL/EL M 1.49, R 1.40–1.82), longer than body in males (AL/TL M 1.12, R 1.11–1.13) and shorter than body in females (AL/TL M 0.92, R 0.89–0.94) (Fig. 3B). Antennomere I widened apically, in most cases slightly longer than antennomere II (A1L/A2L M 1.04, R 0.96–1.16). Antennomere II slightly widened apically. Antennomere III longer than antennomere II (A3L/A2L M 1.37, R 1.17–1.48). Antennomeres IV–VI longer than preceding ones. Antennomere VI slightly shorter than antennomeres IV and V. Antennomere VIII shorter and narrower than antennomeres VII (A8L/A7L M 0.82, R 0.74–0.91; A8W/A7W M 0.64, R 0.50–0.71) and IX (A8L/A9L M 0.91, R 0.85–0.97; A8W/A9W M 0.65, R 0.50–0.83) (Table 1).

THORAX. Pronotum sub-bell-shaped, covered with sparsely distributed short yellow erect hairs (Fig. 3E), longer than wide (PL/PW M 1.19, R 1.13–1.26), about as long as head in females (PL/HL M 1.00, R 0.93–1.08) and slightly longer than head in males (PL/HL M 1.05, R 1.05) (Table 1). Widest slightly before middle in both sexes, about as wide as head (HW/PW M 1.02, R 0.97–1.06). Sides of pronotum gradually converging in straight line from point of maximum pronotal width to anterior pronotal angles, converging in concave line posteriorly to posterior pronotal angles. Lateral rim of pronotum starting at base and reaching $\frac{2}{3}$ – $\frac{3}{4}$ of PL. Posterior angles blunt, slightly obtusely angled, not extended posteriorly. Anterior pronotal margin slightly convex. Pronotal base almost straight, in some specimens barely concave medially. Pronotal disc regularly convex, with relatively sparse punctuation (Fig. 3E–F, I). Pronotal base slightly shorter than anterior pronotal margin (PB/AM M 0.92, R 0.88–0.95). Mesocoxal cavities close together. Mesosternal intercoxal apophysis not reaching anterior margin of metasternum (Fig. 3G). Metasternal intercoxal apophysis broad, with posterior processes separated from each other. Mesoventral carina absent (Fig. 3H).

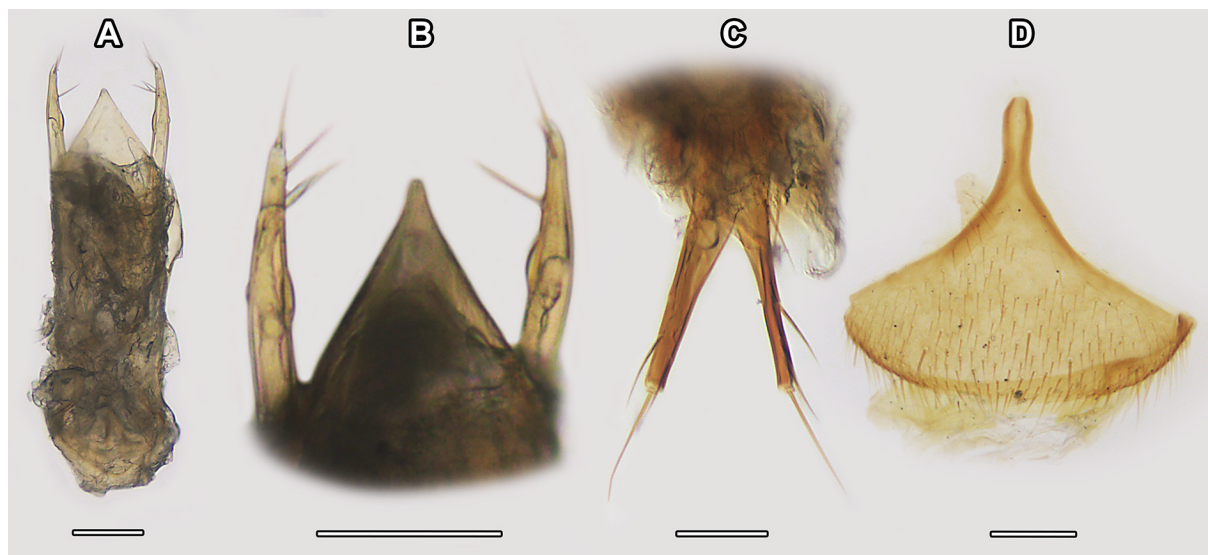


Fig. 4. *Remyella spanovicæ* Ćurčić, Vrbica & Vesović sp. nov. **A–B.** Holotype, ♂ (IZFB-24/15), morphological features of the genitalia. **C–D.** Paratype, ♀ (IZFB-24/20). **A.** Aedeagus, dorsal view. **B.** Apex of median lobe and parameres, dorsal view. **C.** Gonostyli, dorsal view. **D.** Abdominal ventrite VIII, ventral view. Scale bars = 100 µm.

ELYTRA. Scaphoid, elongate in relation to body (TL/EL M 1.58, R 1.53–1.61), narrow, oval, convex (Fig. 3J), widest just before middle in both sexes (Fig. 2), more elongate in males (EL/EW M 2.49, R 2.45–2.52) than in females (EL/EW M 2.27, R 2.14–2.53) (Table 1). Scutellum well developed, triangular, with transverse microsculpture (Fig. 3E). Sutural striae absent. Elytral apices rounded, separated from each other, covering pygidium in both sexes. Disc covered with dense and moderately deep punctures and relatively long, dense, recumbent yellow hairs (Fig. 3H, K).

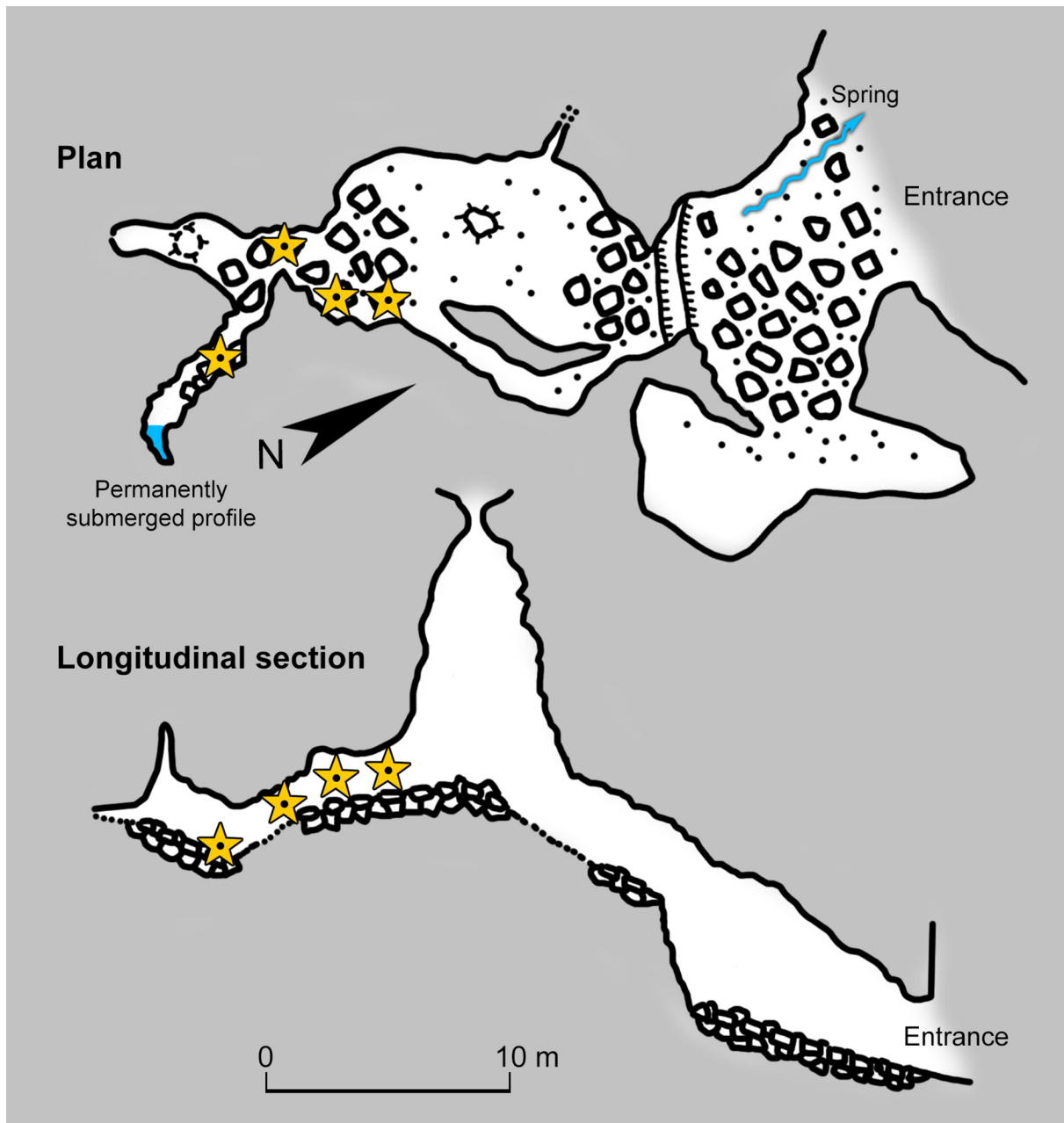


Fig. 5. Pećina na Đerekarskom Vrelu Cave, the type locality of *Remyella spanovicae* Ćurčić, Vrbica & Vesović sp. nov. and the sites where the specimens were collected (golden stars) (modified after Nešić 2015; reproduced with permission of Dragan Nešić).

LEGS. Very long and thin (Figs 2, 3A). Profemora slightly broadened basally, thicker than meso- and metafemora. Protibiae without external row of spines. Protarsi five-segmented in males, four-segmented in females, not dilated.

ABDOMEN. Aedeagus in dorsal view with relatively narrow median lobe. Sides of median lobe parallel from base to two-thirds of length, then converging and ending in equilateral triangle, with sharp, slightly extended apex (Fig. 4A–B). Each paramere with two apical setae and one subapical seta (Fig. 4A–B).

GONOSTYLI. Straight in dorsal view (Fig. 4C). Each stylus with one apical seta and three lateral setae. Anterior margin of female abdominal ventrite VIII angled. Apophysis located at top of angle (Fig. 4D).

Sexual dimorphism

Several features of sexual dimorphism have been observed in this new species: (i) the males are shorter than the females; (ii) the antennae are longer in the males than in the females, the AL/TL is larger in the males than in the females and the antennae are longer than the body in the males, whereas they are shorter than the body in the females; (iii) the elytra are more elongate in the males than in the females.

Distribution, type locality and bionomy

The new species inhabits only the Pećina na Đerekarskom Vrelu Cave, village of Đerekare, near the town of Tutin, Pešter Plateau, southwestern Serbia (Fig. 1). It is located at the Đerekare spring, the source of the Đerekarska Reka (= Boroštica) river, which is about 2 km upstream from the village of Đerekare (Petrović 1976). The total length of the cave is 100 m, while the difference in height between the entrance and the highest point is 23 m. The entrance channel has the form of a spacious hall with a structural extension on the left side and a higher level in the form of a channel connected to the entrance part of the cave by a 5 m high section. The higher level is in the form of a structural cavity with a small daylight hole and a crack, in the bottom of which there is stagnant water (Nešić 2015). The specimens of the new species were collected in the deepest part of the higher level of the cave, both on the damp limestone walls with trickling water and on the clay floor, in complete darkness (Fig. 5).

Remyella hussoni Jeannel, 1934

Figs 1, 6; Table 3

Material examined

SERBIA • 1 ♂, 1 ♀; southwestern Serbia, Pešter Plateau, town of Tutin, village of Đerekare, Zmijove Doline, Četiri Asa Pit; 22 Jul. 2007; Miloš Kuraica leg.; IZFB.

New finding

As comparative material we had a sample of the genus *Remyella* at our disposal, which was collected at a subterranean site on the Pešter Plateau in southwestern Serbia and belongs to the species *R. hussoni*. This sample (one male and one female) was gathered 18 years ago in the Četiri Asa Pit (Zmijove Doline, village of Đerekare, near the town of Tutin). This species is known from a number of caves and pits in the village of Đerekare (where the type locality of the new species is also located) (Njunjić *et al.* 2017), but so far it has not been found in the aforementioned pit.

Remyella javorensis S. Ćurčić & B. Ćurčić, 2008

Figs 1, 6; Table 3

Type material

Holotype

SERBIA • ♂; southwestern Serbia, Pešter Plateau, town of Sjenica, Mt Javor, village of Ursule, Baždarska Pećina Cave; 25 Aug. 2005; Srećko Ćurčić leg.; CBSE.

Paratypes

SERBIA • 6 ♂♂, 27 ♀♀; same data as for holotype; Srećko Ćurčić, Božidar Ćurčić and Nina Ćurčić leg.; CBSE.

Other material examined

SERBIA • 4 ♂♂, 10 ♀♀; same data as for holotype; 17 Aug. 2006; Srećko Ćurčić leg.; IZFB • 56 ♂♂, 135 ♀♀; same data as for holotype; 10 May 2016; Shuqiang Li leg.; IZFB • 1 ♂; southwestern Serbia, Pešter Plateau, town of Sjenica, village of Ušak, Ušak cave system; 23 Nov. 2014; Matija Petković leg.; IZFB • 6 ♂♂, 21 ♀♀; same data as for preceding; 22 Oct. 2016; Miloš Kuraica leg.; IZFB.

Remyella propiformis Winkler, 1933

Figs 1, 6; Table 3

Material examined

MONTENEGRO • 1 ♂, 1 ♀; northeastern Montenegro, Pešter Plateau, town of Bijelo Polje, village of Đalovići, Đalovića Pećina (= Pećina nad Vražjim Firovima) Cave; 5 Aug. 2012; Dragan Antić leg.; IZFB • 7 ♂♂, 16 ♀♀; same data as for preceding; 29 Jul. 2016; Matija Petković leg.; IZFB.

Remyella raskae S. Ćurčić & B. Ćurčić, 2008

Figs 1, 6; Table 3

Type material

Holotype

SERBIA • ♂; southwestern Serbia, Pešter Plateau, city of Novi Pazar, Pećina na Vrelu Raške Cave; 23 Aug. 2005; Srećko Ćurčić leg.; CBSE.

Paratypes

SERBIA • 5 ♂♂, 4 ♀♀; same data as for holotype; Srećko Ćurčić and Božidar Ćurčić leg.; CBSE.

Other material examined

SERBIA • 1 ♂; same data as for holotype; 11 May 2016; Đorđe Marković leg.; IZFB.

Molecular and phylogenetic analyses

Phylogenetic analysis of the barcoding region of the taxa of *Remyella* revealed five distinct clades corresponding to five species with evolutionary divergences between 4.2 and 12.0% (Fig. 6). A single sequence of *R. raskae* formed a distinct clade (Table 3) and was positioned as a sister group to *R. javorensis* with a genetic distance of 10.6%. Three sequences of *R. spanovicae* Ćurčić, Vrbica & Vesović sp. nov. and one sequence of *Remyella* sp. (accession number KX671646) clustered together with a minimum genetic distances of 0.0 to 0.1%. This clade separated from others with high evolutionary divergence

ranging from 9.5 (*R. hussoni*) to 12.0% (*R. raskaе*). *Remyella propiformis* and *R. hussoni* grouped together with a mean between-species genetic distance of 4.2%.

An identification key for the species of the genus *Remyella* Jeannel, 1931 (modified after Njunjić et al. 2017)

1. Sides of the pronotum converging in a straight line from the point of maximum pronotal width to the anterior pronotal angles (Ćurčić et al. 2008: 111, 113, figs 1, 3; Njunjić et al. 2017: 151, figs 28–29, 32; Figs 2A–B, 3A, E) 2
– Sides of the pronotum convex in the anterior part (Jeannel 1931: 261, figs 6–7; Giachino & Etonti 1995: 80, fig. 1; Njunjić et al. 2017: 151, figs 30–31) 4
2. Lateral rim of the pronotum extending from the base to slightly more than half the pronotal length (Ćurčić et al. 2008: 111, 113, figs 1, 3; Njunjić et al. 2017: 151, figs 28–29, 32) 3
– Lateral rim of the pronotum extending from the base to $\frac{2}{3}$ – $\frac{3}{4}$ of the pronotal length (Figs 2A–B, 3A, E) ***R. spanovicae*** Ćurčić, Vrbica & Vesović sp. nov.
3. Total length of the body greater: R 4.6–4.9 mm (males), 4.5–5.2 mm (females). Pronotum widest in the middle (Ćurčić et al. 2008: 113, fig. 3; Njunjić et al. 2017: 151, figs 29, 32). Male genital segment with lateral and central setae ***R. javorensis*** S. Ćurčić & B. Ćurčić, 2008
– Total length of the body smaller: 4.1–4.4 mm (males), 4.1–4.5 mm (females). Pronotum widest in basal third (Ćurčić et al. 2008: 111, fig. 1; Njunjić et al. 2017: 151, fig. 28). Male genital segment with lateral setae only (Njunjić et al. 2017: 150, fig. 18) ***R. raskaе*** S. Ćurčić & B. Ćurčić, 2008
4. Pronotal punctuation dense, uniformly distributed (Njunjić et al. 2017: 151, figs 31, 37)
..... ***R. hussoni*** Jeannel, 1934
– Pronotal punctuation very sparse and sporadic, generally denser at the base and sometimes along the median line (Giachino & Etonti 1995: 80, fig. 1; Njunjić et al. 2017: 151, figs 30, 36) 5
5. Median lobe of the aedeagus broad, with a blunt apex (Jeannel 1931: 264, fig. 11; Jeannel 1934: 101, fig. 11; Njunjić et al. 2017: 150, fig. 14) ***R. scaphoides*** Jeannel, 1931
– Median lobe of the aedeagus narrow, with a sharp apex (Jeannel 1934: 101, figs 12–13; Giachino & Etonti 1995: 82, figs 2–7; Njunjić et al. 2017: 150, fig. 15) ***R. propiformis*** Winkler, 1933

Discussion

All species of the genus *Remyella* live on the Pešter Plateau in a small area in southwestern Serbia and northeastern Montenegro between the following mountain ranges: Mts Jadovnik (1734 m a.s.l.), Javor (1520 m a.s.l.), Giljeva (1617 m a.s.l.), Ninaja (1358 m a.s.l.) and Žilindar (1616 m a.s.l.). Apart from the two geographically isolated species, *R. javorensis* and *R. raskaе*, the populations of the other species of *Remyella* are geographically very close to each other (Fig. 1). Surprisingly, these taxa inhabit caves/pits that are only a few kilometres apart, on a single karst plateau with no obvious geographical barriers (Njunjić et al. 2017). This is the case with *R. spanovicae* Ćurčić, Vrbica & Vesović sp. nov., which is only known from a subterranean site in the village of Đerekare. The same village is inhabited by another, somewhat more widespread species of *Remyella* (*R. hussoni*), which has been found there in a number of caves (Fig. 1). Interestingly, these caves are close to the type locality of *R. spanovicae* (Pećina na Đerekarskom Vrelu Cave), but they harbour two different species of *Remyella*. Our molecular analysis reveals a large genetic distance between them.

It is interesting to note that during our two visits to the cave only two males and 87 females of *R. spanovicae* Ćurčić, Vrbica & Vesović sp. nov. were found both manually and in pitfall traps. This is a very rare phenomenon, not only in leiodids but also in other beetles. In other species of the genus *Remyella* the females are more common, but the males are not as rare as in the new species (Ćurčić et al. 2008; Njunjić et al. 2017).

Morphological differences related to sexual dimorphism were found in the new species. As Jeannel (1924) stated, the females are larger and have broader elytra than the males. Although the males are smaller in size, they have longer antennae than the females. In addition, no sexually dimorphic differences were found in the shape of the head and pronotum.

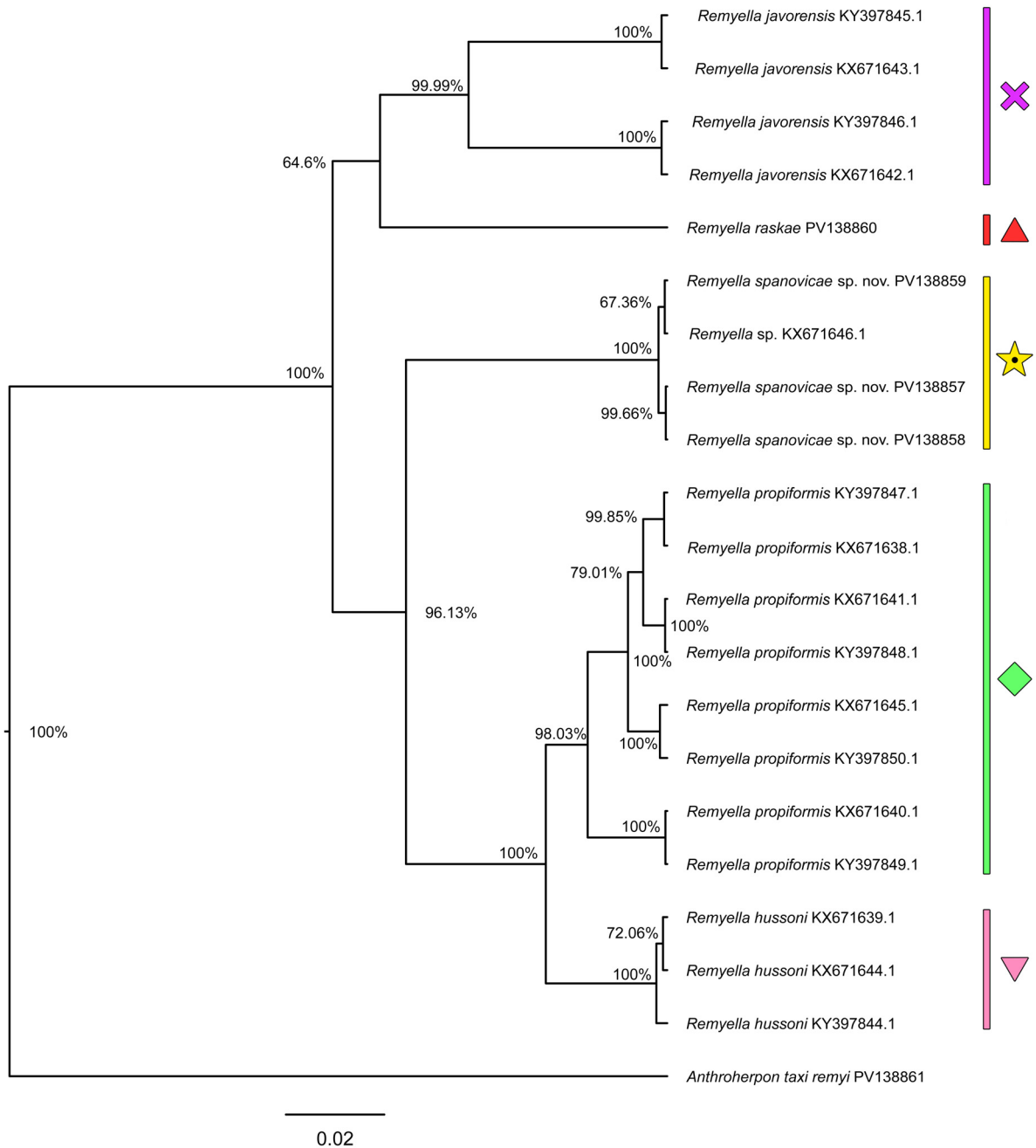


Fig. 6. Phylogenetic tree of the species of *Remyella* Jeannel, 1931 based on *COI* sequences, determined with Bayesian evolutionary analysis. Bootstrap values are indicated above/below the branches. *Anthroherpon taxi remyi* Jeannel, 1931 was used as outgroup taxon. The colours and symbols correspond to those used for the species of *Remyella* shown in Fig. 1.

Table 3. Mean between-species evolutionary divergence within the genus *Remyella* Jeannel, 1931.

Species	<i>R. spanovicae</i> Ćurčić, Vrbica & Vesović sp. nov.	<i>R. propiformis</i> Winkler, 1933	<i>R. hussoni</i> Jeannel, 1934	<i>R. raskaе</i> S. Ćurčić & B. Ćurčić, 2008
<i>R. spanovicae</i> Ćurčić, Vrbica & Vesović sp. nov.				
<i>R. propiformis</i> Winkler, 1933	0.0994			
<i>R. hussoni</i> Jeannel, 1934	0.0953	0.0425		
<i>R. raskaе</i> S. Ćurčić & B. Ćurčić, 2008	0.1200	0.1075	0.1118	
<i>R. javorensis</i> S. Ćurčić & B. Ćurčić, 2008	0.1063	0.0882	0.0935	0.1063

Near the sites of some species of *Remyella* in certain caves (Pećina na Vrelu Raške Cave and Pećina na Đerekarskom Vrelu Cave) there is flowing or stagnant groundwater (Ćurčić *et al.* 2008), which indicates their affinity for humid habitats.

The morphological traits originally used to distinguish the species of *Remyella* (Jeannel 1931, 1934; Winkler 1933) were further discussed by Giachino & Etonti (1995), who showed that the morphological differences in the ratio of length to width of the head, pronotum and elytra between the taxa are small and represent intrapopulation variation. One morphological character that Giachino & Etonti (1995) considered significant for taxonomy was the position of the three apical setae of the parameres and the relative distance between them. However, Njunjić *et al.* (2017) showed that the observed differences fall within the range of typical intrapopulation variability, suggesting that these differences may not be as significant as originally thought. According to Njunjić *et al.* (2017) and the results of our study, the morphological characters that seem to be most relevant for distinguishing the species of *Remyella* are the body length, the length of the lateral pronotal rim, the shape of the sides of the pronotum, the density of the punctuation of the pronotal disc, the shape of the apex of the median lobe of the aedeagus and the setation of the apical margin of the male genital segment.

The molecular analysis of the barcode region agrees with the morphological analysis of the taxa of *Remyella* and confirms the establishment of a new species. The three sequences of *R. spanovicae* Ćurčić, Vrbica & Vesović sp. nov. obtained in this study, together with a sequence from the GenBank database, represent two haplotypes with low genetic divergence between them (0.1%), which is to be expected since all specimens come from the same population and locality. In addition, this study confirmed *R. raskaе* for the first time as a valid species at the molecular level. Both species show a high evolutionary divergence, which separates them phylogenetically from the other taxa of *Remyella*. The sequence divergence values determined between the species of *Remyella* ($\geq 4.25\%$) are significant at the species level, as recently shown for some animal models (Hebert *et al.* 2003).

It is estimated that speciation within *Remyella* took place around two to five million years ago (Njunjić *et al.* 2017). This period coincides with the transition from the Miocene to the Pliocene, when the Pešter Plateau was periodically filled by shallow lakes that formed sedimentary deposits (Mojsilović *et al.* 1973). The distribution area of the species of *Remyella*, which occur on the edges of the Pešter Plateau, is probably influenced by the presence of these lakes. It is likely that the lakes acted as barriers and prevented the various populations from spreading more evenly over the entire area of the plateau.

Jeannel (1931) placed the genus *Remyella* in the subtribe Anthroherponina due to the insertion of the antennae in the posterior third of the head, but the shape of the claws differs from other genera of the subtribe (narrow in *Remyella* vs broad in Anthroherponina). Perreau & Pavićević (2008) excluded the

genus *Remyella* from the subtribe Anthroherponina and tentatively placed it in the subtribe Leptodirina. Njunjić *et al.* (2017) pointed out the close relationship between the genera *Remyella*, *Rozajella* S. Ćurčić, Brajković & B. Ćurčić, 2007 and *Nonveilleriella* Perreau & Pavićević, 2008. The polyphyly of the subtribe Leptodirina is supported and the assignment of the three listed genera to the mentioned subtribe should be reconsidered (Njunjić *et al.* 2017). The latter genus is treated by some authors as a synonym of the genus *Rozajella* (Fresneda *et al.* 2024). Other genera inhabiting the Dinaric Mountains need to be included in a comprehensive phylogenetic analysis to determine the actual relationships of the subterranean leiodirines in the region and to reveal the origin and colonization routes of the different lineages in the Balkan Peninsula.

The endemic differentiation of *Remyella* and related genera on the Balkan Peninsula was influenced by the great Alpine orogeny, various palaeoclimatic events and the subsequent evolution of the subterranean karst relief. These processes created numerous new hypogean niches which enabled the preservation of this ancient and autochthonous fauna (Ćurčić *et al.* 2013, 2021).

Most of the Pešter Plateau has not yet been biospeleologically investigated, and it is expected that new findings of the taxa of *Remyella* (including those new to science) will be recorded in the periphery of this area, especially in the eastern, northern and western parts, which will be attested by further investigations in this region.

Acknowledgements

This study was financially supported by the Ministry of Science, Technological Development and Innovation of the Republic of Serbia (contract numbers 451-03-137/2025-03/200178 and 451-03-136/2025-03/200178). Our thanks also go to Petar Ćurčić (Belgrade, Serbia), who helped us with the field research. We thank Prof. Dr Vladimir Pavlović (University of Belgrade - Faculty of Agriculture, Belgrade, Serbia), who took images of the new species with a scanning electron microscope. Dr Dragan Nešić (Institute for Nature Conservation of Serbia, Niš, Serbia) gave us permission to use his image in our article, for which we are particularly grateful. We are also indebted to an anonymous reviewer for constructive comments, which led to a significant improvement of the manuscript of our article.

References

- Čeplík D. 2023. Supplementary data and taxonomic changes in the subterranean beetles of the Balkan Peninsula from July 1st 2016 to September 30th 2023. *Zootaxa* 5383 (4): 401–440. <https://doi.org/10.11646/zootaxa.5383.4.1>
- Ćurčić S.B., Waitzbauer W., Zolda P., Brajković M.M. & Ćurčić B.P.M. 2008. New cave-dwelling species of the genus *Remyella* Jeannel (Leptodirini, Leiodidae, Coleoptera) from Serbia. *Archives of Biological Sciences* 60 (1): 109–115. <https://doi.org/10.2298/ABS1303217C>
- Ćurčić S.B., Antić D.Ž., Ćurčić N. & Ćurčić B.P.M. 2013. *Remyella montenegrina*, a new troglobitic leiodid beetle (Coleoptera: Leiodidae: Leptodirini) from northeastern Montenegro. *Archives of Biological Sciences* 65 (3): 1217–1222. <https://doi.org/10.2298/ABS1303217C>
- Ćurčić S., Pavićević D., Vesović N., Vrbica M., Kuraica M., Marković Đ., Petković M., Lazović V., Pantelić D. & Bosco F. 2021. On the diversity of subterranean beetles of the Dinarides: new leiodid taxa (Coleoptera: Leiodidae) from Serbia. *European Journal of Taxonomy* 782 (1): 55–81. <https://doi.org/10.5852/ejt.2021.782.1589>
- Drummond A.J., Suchard M.A., Xie D. & Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29 (8): 1969–1973. <https://doi.org/10.1093/molbev/mss075>

- Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Fresneda J., Giachino P.M., Salgado J.M., Faille A., Bourdeau C., Cieslak A. & Ribera I. 2024. A phylogenetic classification of Leptodirini (Coleoptera, Leiodidae, Cholevinae). *Memorie della Società Entomologica Italiana* 101: 3–936. <https://doi.org/10.4081/memoriesei.2024.3>
- Giachino P.M. & Etonti M. 1995. Il genere *Remyella* Jeannel, 1931 (Coleoptera Cholevidae Leptodirinae). *Atti del Museo Civico di Storia Naturale di Trieste* 46: 77–98.
- Guéorguiev V.B. 1990. Recherches sur les Bathysciinae (Coleoptera: Catopidae) de Yougoslavie. I. Anthroherponini. *Acta Entomologica Musei Nationalis Pragae* 43: 237–273.
- Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hebert P.D.N., Ratnasingham S. & de Waard J.R. 2003. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London B: Biological Sciences* 270: 596–599. <https://doi.org/10.1098/rsbl.2003.0025>
- Hlaváč P., Perreau M. & Čeplík D. 2017. *The Subterranean Beetles of the Balkan Peninsula: Carabidae, Leiodidae, Staphylinidae, Scarabaeidae, Bothrideridae, Zopheridae, Salpingidae, Brachyceridae, Curculionidae*. Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague.
- Jeannel R. 1924. Monographie des Bathysciinae. *Biospeologica L. Archives de Zoologie expérimentale et générale* 63: 1–436.
- Jeannel R. 1931. Bathysciinae nouveaux recueillis par P. Remy dans les grottes du Novi-Pazar. *Bulletin de la Société zoologique de France* 56: 258–266.
- Jeannel R. 1934. Bathysciinae recueillis par MM. P. Remy et R. Husson dans le Sandjak de Novi-Pazar et la Macédoine grecque. *Revue française d'Entomologie* 1: 89–103.
- Mojsilović S., Baklajić D. & Đoković I. 1973. *Tumač za list Sjenica*. Institute for Geological and Geophysical Research, Belgrade.
- Moravec J. 2017. Recent records of *Remyella propiformis* A. Winkler, 1933 (Coleoptera: Leiodidae: Cholevinae: Leptodirini) from the Đalovića Pećina Cave in Montenegro. *Studies and Reports, Taxonomical Series* 13 (2): 425–427.
- Nešić D. 2015. Results of the speleological exploration on Pešter Plateau. *Bulletin of the Serbian Geographical Society* 95 (4): 1–30. <https://doi.org/10.2298/GSGD1504001N>
- Njunjić I., Schilthuizen M., Pavićević D. & Perreau M. 2017. Further clarifications to the systematics of the cave beetle genera *Remyella* and *Rozajella* (Coleoptera: Leiodidae: Cholevinae: Leptodirini). *Arthropod Systematics & Phylogeny* 75: 141–158. <https://doi.org/10.3897/asp.75.e31881>
- Perreau M. 2000. Catalogue des Coléoptères Leiodidae Cholevinae et Platypsyllinae. *Mémoires de la Société entomologique de France* 4: 1–461.
- Perreau M. 2015. Family Leiodidae Fleming, 1821. In: Löbl I. & Löbl D. (eds) *Catalogue of Palaearctic Coleoptera. Volume 2/1. Hydrophiloidea – Staphylinoidea. Revised and Updated Edition*: 180–291. Brill, Leiden/Boston.
- Perreau M. & Pavićević D. 2008. The genus *Hadesia* Müller, 1911 and the phylogeny of Anthroherponina (Coleoptera, Leiodidae, Cholevinae, Leptodirini). In: Pavićević D. & Perreau M. (eds) *Advances in the*

Studies of the Fauna of the Balkan Peninsula. Papers Dedicated to the Memory of Guido Nonveiller: 215–239. Institute for Nature Conservation of Serbia, Belgrade.

Petrović J. 1976. *Jame i pećine SR Srbije*. Military Publishing Institute, Belgrade.

Pretner E. 1968. *Catalogus Faunae Jugoslaviae. III/6. Coleoptera. Fam. Catopidae. Subfam. Bathysciinae*. Slovenian Academy of Sciences and Arts, Ljubljana.

Rambaut A. 2009. FigTree Version 1.4.4. Available from <https://tree.bio.ed.ac.uk/software/figtree/> [accessed 25 Sept. 2023].

Rambaut A., Drummond A., Xie D., Baele G. & Suchard M. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904. <https://doi.org/10.1093/sysbio/syy032>

Tamura K., Stecher G. & Kumar S. 2021. MEGA11: molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38: 3022–3027. <https://doi.org/10.1093/molbev/msab120>

Winkler A. 1933. Zur Kenntnis der Blindkäfer Albaniens, Jugoslawiens und Rumäniens (Trechinae, Bathysciinae). *Koleopterologische Rundschau* 19 (1–2): 71–78.

Manuscript received: 1 July 2024

Manuscript accepted: 17 February 2025

Published on: 25 June 2025

Topic editor: Tony Robillard

Section editor: Maxwell Barclay

Desk editor: Eva-Maria Levermann

Printed versions of all papers are deposited in the libraries of four of the institutes that are members of the *EJT* consortium: Muséum national d’Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.