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The surprising discovery of two new subterranean Leptodirini of the genus *Spelaeobates* Müller, 1901 (Coleoptera, Leiodidae, Cholevinae) from Croatia after more than a century

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Abstract

Two new subterranean leiodid taxa of the genus *Spelaeobates* Müller, 1901 from three pits in northern Dalmatia (Croatia), *S. coriniensis* **sp. nov.** and *S. coriniensis nonveilleri* **ssp. nov.**, are described. The morphological traits of the new taxa are enumerated and illustrated. These two taxa are placed in the subgenus *Spelaeobates* Müller, 1901. The relationships of these two taxa and their close relatives are clarified. Data on the sexual dimorphism of the two new taxa and on the intrasubspecific variability of *S. coriniensis nonveilleri* **ssp. nov.** are presented. We also redescribed *S. novaki*, the type species of both the genus *Spelaeobates* and the subgenus *Spelaeobates* and the closest relative of the newly described species. A key for identification of the taxa of the genus *Spelaeobates* is included. The new taxa are endemic to the Dinaric Alps of Croatia. *Spelaeobates* (*Pretneriella*) *kraussi* Müller, 1903 and *S.* (*P.*) *pharensis langhofferi* Müller, 1931 were found for the first time outside their type locality.

Keywords
Balkan Peninsula, Dinarides, hypogean, leiodids, new species, new subspecies

Introduction

The genus *Spelaeobates* Müller, 1901 (Coleoptera, Leiodidae, Cholevinae, Leptodirini) includes the following six troglobitic species from Dalmatia (Croatia): *Spelaeobates bachofeni* Breit, 1913 (from an unnamed cave, near the town of Vis, island of Vis); *S. czernyi* Breit, 1913 (from another unnamed cave, near the town of Vis, island of Vis; the Špilja od Vore Cave and the Špilja na Bardorovici Cave, village of Kostirna, near the town of Komiža, island of Vis); *S. kraussi* Müller, 1903 (from the Dobra Jama Pit, Vidova Gora peak, village of Nerežišća, island of Brač); *S. peneckei* Müller, 1903 (from the Činjadra Špilja Cave, village of Škrip, island of Brač; Ješkalovica Pit and Studentski Ratac Pit, village of Selca, island of Brač; Kopačina Cave, village of Nerežišća, near the town of Supetar, island of Brač; and Ježulje Cave, village of Donji Humac, near the town of Supetar, island of Brač); *S. pharensis* Müller, 1901, with two subspecies: *S. pharensis pharensis* Müller, 1901 (from the Špilja pod Kapelu Cave, Smokovnik hill, island of Hvar; Jama u Pečarovu Stanu Pit, Propod Pit and "Neue *Spelaeobates* Höhle bei Lesina" Cave, near the town of Hvar, island of Hvar; and Jama u pod Kuse Pit, village of Brusje, island of Hvar) and *S. pharensis langhofferi* Müller, 1931 (from the Kruščica Cave, near the town of Stari Grad, island of Hvar); and *S. novaki* Müller, 1901 (from the Strašna Peć Cave, village of Savar, island of Dugi Otok; and Jezero Cave, village of Mali Iž, island of Iž) (Fig. 1) (Müller 1901, 1903, 1931; Breit 1913; Jeannel 1924; Pretner 1973; Guéorguiev 1990; Perreau 2000, 2015; Hlaváč et al. 2017). Perreau (2000, 2015) reported the presence of *S. novaki* only from the island of Iž, but it actually inhabits the nearby island of Dugi Otok as well (Pretner 1973; Guéorguiev 1990; Hlaváč et al. 2017). This genus is chiefly distributed on islands in northern (Dugi Otok and Iž) and central Dalmatia (Brač, Hvar, and Vis) in Croatia (Fig. 1) (Pretner 1973; Guéorguiev 1990; Perreau 2000, 2015; Hlaváč et al. 2017). Jalžić (1982) reported one finding of this genus from the mainland of northern Dalmatia (Croatia) (from the Golubnjača Cave, village of Kaštel Žegarski, near the town of Obrovac), indicating that the genus is not distributed only on the Dalmatian islands. However, it wasn't specified to which subgenus the taxon found in the Golubnjača Cave belongs (Jalžić 1982). The genus is highly specialised and is considered to be very old (Guéorguiev 1990). It comprises small-sized subterranean taxa with a narrow head, a narrow pronotum, convex pear-shaped physogastric elytra, and a very small, narrow, elongate, simple and unarmed endophallus (Jeannel 1924). The genus *Spelaeobates* is divided into two subgenera: *Spelaeobates* Müller, 1901 and *Pretneriella* V. Guéorguiev, 1976. The subgenera differ on the degree of punctuation on the pronotum, width of the first protarsomere in males, shape of the median lobe apex, and number of the parameral setae (Guéorguiev 1976). The nominotypic subgenus includes only the species *S. novaki*, while the subgenus *Pretneriella* comprises all remaining taxa of the genus *Spelaeobates*. The former subgenus is distributed only on two islands (Dugi Otok and

Figure 1. A map of part of Dalmatia (Croatia) showing localities where *Spelaeobates* taxa were registered **pink sun** *S.* (*P.*) *bachofeni* **yellow triangles** *S.* (*P.*) *czernyi* **black kites** *S.* (*P.*) *kraussi* **red circles** *S.* (*P.*) *peneckei* **lime squares** *S.* (*P.*) *pharensis langhofferi* **green squares** *S.* (*P.*) *pharensis pharensis* **light purple star** *S.* (*S.*) *coriniensis coriniensis* ssp. nov. **purple stars** *S.* (*S.*) *coriniensis nonveilleri* ssp. nov. **orange pentagons** *S.* (*S.*) *novaki* **light blue cross** *S.* sp.

Iž) belonging to northern Dalmatia, while the latter is recorded on three islands (Brač, Hvar, and Vis) in central Dalmatia. Generally, the genus *Spelaeobates* inhabits both the islands and mainland of northern and central Dalmatia (Croatia) and its taxa are subterranean (Perreau 2000, 2015). It is interesting to note that all known species of this genus were described in a short time interval at the beginning of the 20th century (from 1901 to 1913). The taxon of this genus which was described most recently (92 years ago) is the subspecies *S. pharensis langhofferi* (Perreau 2000, 2015).

The fauna of caves and pits of central and southern Dalmatia has been very well explored (Pretner 1973; Jalžić and Pretner 1977), while the biospeleological research of northern Dalmatia has been carried out on a very small scale, so the findings of numerous new taxa of subterranean leioids to science can be expected in this area.

Three field trips in northern Dalmatia (Croatia) conducted by the Špiljar Speleological Society (Split, Croatia) in 2019 at three subterranean sites resulted in the discovery of a number of adult individuals of two new leptodirine leiodid taxa (one species and one subspecies) belonging to the nominotypic subgenus of the genus *Spelaeobates*, whose

descriptions and diagnoses are presented in the current study. In 1997, the same team collected several adult specimens of the species *S.* (*S.*) *novaki* at its type locality (Strašna Peć Cave, village of Savar, island of Dugi Otok), which is redescribed in this paper.

Materials and methods

The adults of leptodirine leiodid beetles were collected manually in three pits and one cave in the vicinity of the town of Benkovac and the city of Šibenik, as well as on the island of Dugi Otok (northern Dalmatia, Croatia). These beetle individuals were studied in a laboratory of the Institute of Zoology, University of Belgrade - Faculty of Biology, Belgrade, Serbia. Their genitalia were extracted and conserved on microscope slides in a medium consisting of Canada balsam and toluene. Beetles were then glued on paper mounting cards and examined as dry specimens. We measured a total of seven individuals (three males and four females) of *S.* (*S.*) *coriniensis* sp. nov., nine individuals (five males and four females) of *S.* (*S.*) *coriniensis nonveilleri* ssp. nov., and four individuals (one male and three females) of *S.* (*S.*) *novaki* (values are given as averages and ranges in the Results). Taxonomically important morphological traits were studied for comparison using a Stemi 2000 binocular stereomicroscope (Carl Zeiss, Jena, Germany), a SMZ 18 binocular stereomicroscope (Nikon, Tokyo, Japan) with a DS-Fi1c digital camera (Nikon, Tokyo, Japan) appended, as well as an Axioskop 40 light microscope (Carl Zeiss, Jena, Germany). A Nikon DS-L3 control unit was used for scale bar adjustment and precise measurements. An Intralux 5100 cold light source (Volpi, Schlieren, Switzerland) was used for the additional illumination of beetles under binocular stereomicroscopes. A Tescan Mira 3 XMU field emission scanning electron microscope (FESEM) (Tescan, Brno, Czech Republic) at the University of Belgrade - Faculty of Technology and Metallurgy was used for observing the detailed morphology of the new taxa. Prior to analysis, beetle samples were coated with gold for 45 s using a Polaron SC502 Sputter Coater (Fisons, VG Microtech, East Sussex, UK). The high-vacuum mode of the FESEM at an acceleration voltage of 10 kV was used. The index of electron beam intensity was 8.00, the electron beam current was 364 μA, while the pressure in the column was around 1.3e–3 Pa.

The systematics used follow Jeannel (1924), Perreau (2000, 2015), and Hlaváč et al. (2017).

Abbreviations of measurements

A3L/A2L ratio of length of antennomere III to length of antennomere II;
A3L/A4L ratio of length of antennomere III to length of antennomere IV;
A6L/A3L ratio of length of antennomere VI to length of antennomere III;
A8L/A3L ratio of length of antennomere VIII to length of antennomere III;
A11L/A8L ratio of length of antennomere XI to length of antennomere VIII;
A11W/A10W ratio of width of antennomere XI to width of antennomere X;

AL total antennal length (including the scape);
EL/EW ratio of elytral length (as the linear distance measured along the suture from the elytral base to the apex) to maximum elytral width;
EW/PW ratio of maximum elytral width to maximum pronotal width;
HL/HW ratio of head length to maximum head width;
HW/PW ratio of maximum head width to maximum pronotal width;
M mean value;
M1L/M1W ratio of length to width of maxillary palpomere I;
M2L/M1L ratio of length of maxillary palpomere II to length of maxillary palpomere I;
M3L/M2L ratio of length of maxillary palpomere III to length of maxillary palpomere II;
PB/AM ratio of pronotal base length to anterior pronotal margin length;
PL/HL ratio of pronotal length to head length;
PL/PW ratio of pronotal length to maximum pronotal width;
P1W/P2W ratio of width of protarsomere I to width of protarsomere II;
R range of total measurements performed;
TL total body length (measured from the anterior margin of the clypeus to the elytral apex).

Collections

IZFB collection of the Institute of Zoology, University of Belgrade - Faculty of Biology, Belgrade, Serbia;
SSM collection of the Split Science Museum, Split, Croatia.

Other abbreviations

HT holotype;
PT paratype;
TR leg. Tonći Rađa.

Other examined taxa

Spelaeobates (*Pretneriella*) *kraussi* Müller, 1903: one male, one female, Croatia, central Dalmatia, island of Brač, village of Nerežišća, Vidova Gora peak, Vičja Jama Pit, 16.IV.2022, TR (IZFB).

Spelaeobates (*Pretneriella*) *pharensis langhofferi* Müller, 1931: two females, Croatia, central Dalmatia, island of Hvar, town of Jelsa, village of Pitve, Jama na Boroviku Pit, 9.XI.2013, TR (IZFB).

Spelaeobates (*Spelaeobates*) *novaki* Müller, 1901: one male, four females, Croatia, northern Dalmatia, island of Dugi Otok, village of Savar, Strašna Peć Cave, 1.VII.1997, TR (IZFB).

Results

Order Coleoptera Linnaeus, 1758
Family Leiodidae Fleming, 1821
Subfamily Cholevinae Kirby, 1837
Tribe Leptodirini Lacordaire, 1854
Subtribe Spelaeobatina V. Guéorguiev, 1974
Genus *Spelaeobates* Müller, 1901
Subgenus *Spelaeobates* Müller, 1901

***Spelaeobates* (*Spelaeobates*) *coriniensis* Ćurčić, Vesović, Vrbica & Rađa, sp. nov.**
https://zoobank.org/2F317FC3-634B-4EDB-886C-5BC4C008639A
Figs 2, 3, 6

Type material. ***Holotype*:** male (SSM) labeled as follows: "CROATIA, NORTHERN DALMATIA: town of Benkovac, settlement of Gornji Karin, village of Popovići, Jamurka (Rnjakuša II) Pit, 216 m a.s.l., 44°04'44.1"N, 15°41'00.3"E, 8.II.2019, TR" (white label, printed) / "Holotypus *Spelaeobates* (*Spelaeobates*) *coriniensis* sp. nov. Ćurčić, Vesović, Vrbica & Rađa det. 2022" (red label, printed).

Paratypes (three males and five females). The same data as for HT (IZFB). All paratypes are labeled with white, printed locality labels and with red printed labels "Paratypus *Spelaeobates* (*Spelaeobates*) *coriniensis* sp. nov. Ćurčić, Vesović, Vrbica & Rađa det. 2022" (Fig. 2).

Etymology. *Spelaeobates* (*Spelaeobates*) *coriniensis* sp. nov. is named after Corinium, a Roman town in the area of today's Gornji Karin, a settlement close to its type locality.

Diagnosis. The new species is most closely related to another species of *Spelaeobates* s. str., *S. novaki*, by the rimmed lateral pronotal margins, the presence of a dilated first protarsomere in males, a low, unangled mesoventral carina, the presence of its apically attenuated median lobe of the aedeagus, and by the presence of four parameral setae (Figs 2, 3, 7, 8) (Müller 1901; Jeannel 1924; Guéorguiev 1976).

Spelaeobates (*S.*) *coriniensis* sp. nov. is easily distinguished from *S.* (*S.*) *novaki* in terms of TL (R 2.37–2.50 mm vs. R 2.50–2.80 mm), length of antennae when stretched backwards (reaching end of elytra vs. not reaching end of elytra), length of first two antennomeres (antennomere II longer than antennomere I vs. antennomeres I and II approximately equal in length), A6L/A3L (M 0.93, R 0.88–1.00 vs. M 0.79, R 0.76–0.82), A8L/A3L (M 0.85, R 0.75–0.93 vs. M 0.65, R 0.59–0.71), A11L/A8L (M 1.94, R 1.77–2.08 vs. M 2.27, R 2.09–2.40), maximum width of head (between first quarter and third vs. between first third and middle), punctuation on pronotum (fine, punctures separated vs. strong, punctures merged), EL/EW in males (R 1.56–1.71 vs. R 1.53), maximum width of elytra (before middle vs. around at middle), EW/PW (R 2.15–2.34 vs. R 2.37–2.50), width of first protarsomere in males (less broadened vs. more broadened), and shape of median lobe of aedeagus in dorsal view (more narrowed distally, pointed apically vs. gradually narrowed distally, almost sub-parallel,

rounded apically) and in lateral view (less curved basally, almost straight apically vs. more curved basally, slightly bent downward apically) (Table 1, Figs 2, 3, 7, 8) (Müller 1901; Jeannel 1924; Guéorguiev 1976).

Description. Small-sized leptodirine. TL M 2.42 mm (2.43 mm in males, 2.41 mm in females), R 2.37–2.50 mm (2.37–2.50 mm in both males and females).

***Habitus*:** Body shape leptodiroid (Fig. 2A, B), colour yellowish.

***Integument*:** Lustrous, microsculptured both dorsally and ventrally (Fig. 2C, D, F–L). Sparsely distributed deep punctures present on head, while densely distributed, fine and separated on both pronotum and elytra (Fig. 2C, D, F, G, K, L). Entire body dorsally covered with yellow pubescence of short length (erect on head, while recumbent on both pronotum and elytra) (Fig. 2A, B).

***Head*:** About one and a half times as long as wide (HL/HW M 1.49, R 1.37–1.65), more elongate in males (HL/HW M 1.52 in males, M 1.46 in females), with no eyes, occipital carina in the shape of a curved concave line (Fig. 2A, C). Head widest between first quarter and third. Frons roundly impressed between antennal insertions. Labrum transverse, with a few long setae. First maxillary palpomere of similar length and width, shorter than second maxillary palpomere. Maxillary palpomeres II and III of similar length (M3L/M2L M 1.02, R 0.85–1.09). Penultimate maxillary palpomere widened apically. Ultimate maxillary palpomere short, slender, gradually narrowing apically. Antennae inserted in basal quarter of head, thin, narrow proximally (except for first two antennomeres, which are thickened), slightly widened distally, longer in males, AL M 1.83 mm, R 1.71–1.97 mm (1.88–1.97 mm in males, 1.71–1.82 mm in females),

Table 1. Linear measurements and morphometric ratios in *Spelaeobates* (*Spelaeobates*) *coriniensis coriniensis* ssp. nov., *S.* (*S.*) *coriniensis nonveilleri* ssp. nov., and *S.* (*S.*) *novaki*. Values outside parentheses are mean values, while those inside parentheses are ranges.

Species/subspecies	*S.* (*S.*) *coriniensis coriniensis* ssp. nov.	*S.* (*S.*) *coriniensis nonveilleri* ssp. nov.	*S.* (*S.*) *novaki*
Character			
TL*	2.42 (2.37–2.50)	2.46 (2.34–2.59)	2.63 (2.57–2.70)
HL/HW	1.49 (1.37–1.65)	1.57 (1.53–1.61)	1.47 (1.38–1.53)
HW/PW	0.89 (0.87–0.92)	0.91 (0.87–0.97)	0.93 (0.88–0.98)
AL*	1.83 (1.71–1.97)	1.86 (1.77–1.94)	1.81 (1.75–1.93)
A3L/A2L	1.26 (1.15–1.33)	1.34 (1.23–1.45)	1.37 (1.23–1.42)
A3L/A4L	1.09 (1.00–1.15)	1.21 (1.07–1.31)	1.24 (1.21–1.31)
A6L/A3L	0.93 (0.88–1.00)	0.86 (0.81–0.88)	0.79 (0.76–0.82)
A8L/A3L	0.85 (0.75–0.93)	0.75 (0.65–0.81)	0.65 (0.59–0.71)
A11L/A8L	1.94 (1.77–2.08)	2.03 (1.77–2.25)	2.27 (2.09–2.40)
A11W/A10W	0.78 (0.67–0.83)	0.84 (0.67–1.00)	0.75 (0.67–0.83)
M3L/M2L	1.02 (0.85–1.09)	0.97 (0.85–1.09)	1.09 (1.00–1.18)
PL/PW	1.24 (1.21–1.28)	1.30 (1.24–1.38)	1.29 (1.26–1.32)
PL/HL	0.95 (0.89–0.98)	0.91 (0.89–0.96)	0.96 (0.90–0.98)
PB/AM	0.86 (0.81–0.93)	0.89 (0.83–0.96)	0.86 (0.81–0.90)
EW/PW	2.25 (2.15–2.34)	2.28 (2.18–2.36)	2.44 (2.37–2.50)
EL/EW in males	1.64 (1.56–1.71)	1.64 (1.55–1.76)	1.53 (1.53)
P1W/P2W in males	1.75 (1.50–2.00)	1.20 (1.00–1.50)	1.67 (1.67)

* – values in mm.

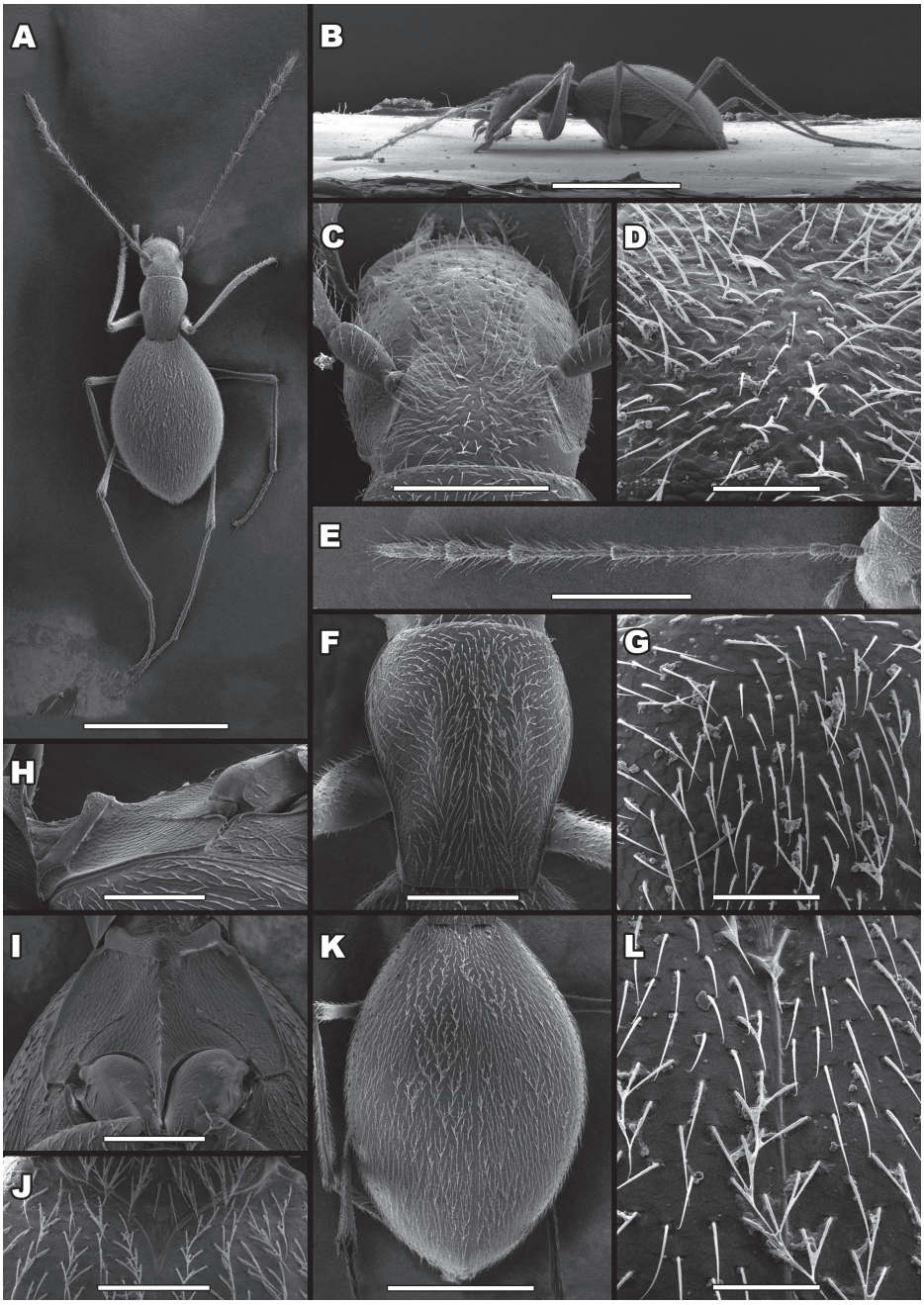

Figure 2. SEM images of the morphological structures of PT male (**A–G, J–L**) and PT female (**H, I**) of *Spelaeobates* (*Spelaeobates*) *coriniensis* sp. nov. from the Jamurka (Rnjakuša II) Pit, village of Popovići, settlement of Gornji Karin, town of Benkovac, northern Dalmatia, Croatia **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** microsculpture of head, dorsal view **E** right antenna, dorsal view **F** pronotum, dorsal view **G** microsculpture of pronotum, dorsal view **H** mesoventral carina, lateral view **I** mesoventrite, ventral view **J** scutellum, dorsal view **K** elytra, dorsal view **L** microsculpture of elytra, dorsal view. Scale bars: 1.0 mm (**A, B**); 0.5 mm (**E, K**); 0.2 mm (**C, F, H, I**); 0.1 mm (**J**); 0.05 mm (**D, G, L**).

reaching end of elytra in males (Fig. 2A, B, E). Antennomeres I and II short and wide, second of which slightly longer and narrower. Following four antennomeres thinner and slightly longer than antennomere II. Antennomere III longer than adjacent antennomeres (A3L/A2L M 1.26, R 1.15–1.33; A3L/A4L M 1.09, R 1.00–1.15). Antennomeres VII, IX, and X quite expanded distally. Antennomere VIII relatively short and narrow, shorter and narrower than anatennomeres VII, IX, X, and XI. Ultimate antennomere slender, widened sub-distally, then narrowing apically, narrower than penultimate one (A11W/A10W M 0.78, R 0.67–0.83). Antennomere I shortest, while antennomeres IX and XI longest. Other ratios of length of certain antennomeres: A6L/A3L M 0.93, R 0.88–1.00; A8L/A3L M 0.85, R 0.75–0.93; A11L/A8L M 1.94, R 1.77–2.08.

***Prothorax*:** Pronotum bell-shaped, elongate, longer than wide (PL/PW M 1.24, R 1.21–1.28; M 1.26, R 1.24–1.28 in males; M 1.23, R 1.21–1.27 in females), widest around anterior third, broader (HW/PW M 0.89, R 0.87–0.92) and shorter than head (PL/HL M 0.95, R 0.89–0.98) (Fig. 2A, F). Lateral margins rounded anteriorly, after which they constrict towards posterior end, slightly concave posteriorly. Pronotal base straight, somewhat shorter than elytral base. PB/AM M 0.86, R 0.81–0.93. Anterior margin barely convex medially, almost straight. Lateral margins and pronotal base rimmed. Fore pronotal angles weakly expressed, rounded, obtuse. Hind pronotal angles well-expressed, obtuse, not protruding backwards. Pronotal disc moderately convex (Fig. 2B).

***Mesothorax*:** Mesoventral carina very low, barely noticeable, with a few setae (Fig. 2H). No tooth, anterior and posterior margins observed. Mesoventrite with a long process between mesocoxae, which is gradually narrowing apically (Fig. 2I). Scutellum large, sub-triangular (Fig. 2K, J).

***Metathorax*:** Metaventrite without carina.

***Elytra*:** Wide, ovoid, almost of same width in males and females (EL/EW M 1.64, R 1.56–1.71 in males; M 1.64, R 1.60–1.69 in females), markedly wider than pronotum (EW/PW M 2.25, R 2.15–2.34) (Fig. 2A, K). Maximum width a little before middle. Lateral margins arcuate. Marginal furrows not visible from above. Shoulders barely visible, obtuse, covered by hind pronotal angles. Elytral disc markedly convex, steeply declining both basally and apically in lateral view (Fig. 2B). Parasutural stria absent. Elytral apex slightly attenuated, rounded. Pygidium covered by elytra.

***Legs*:** Elongate and slender (Fig. 2A, B). Femora widened basally, constricted in distal half. Tibiae thin, gently curved, gradually widening distally. Each protibia with a very fine comb over entire apical third of outer margin. Fore tarsi four-segmented in both sexes, only first protarsomere in males dilated (P1W/P2W M 1.75, R 1.50–2.00). Tarsal claws thin, elongate, curved, pointed apically.

***Male genitalia*:** Aedeagus elongate, slender, small, well chitinised (Fig. 3A, B). Median lobe in dorsal view straight, gradually narrowing distally, with a sharp apex, markedly longer than parameres (Fig. 3A). Median lobe in lateral view quite flattened, curved basally, almost straight proximally, narrowing apically (Fig. 3B). Basal bulb small, narrow, sub-parallel, slightly widened distally and bilobed in dorsal view (Fig. 3A), while elongate and widened basally in lateral view (Fig. 3B). Tegmen wide from above (Fig. 3A), in the shape of a ring around basal bulb (Fig. 3B). Parameres elongate, slender, arcuate, sub-apically curved exteriorly, each with a moderately widened rounded

Figure 3. Bright-field images of the male genitalia of HT of *Spelaeobates* (*Spelaeobates*) *coriniensis* sp. nov. from the Jamurka (Rnjakuša II) Pit, village of Popovići, settlement of Gornji Karin, town of Benkovac, northern Dalmatia, Croatia **A** aedeagus, dorsal view **B** aedeagus, lateral view. Scale bars: 0.1 mm.

apex in dorsal view (Fig. 3A), while straight, sub-parallel in lateral view (Fig. 3B). Each paramera bearing four apical close-set setae, two of which longer, while two shorter (Fig. 3A). No copulatory piece observed within inner sac (Fig. 3A, B).

***Female genitalia*:** Spermatheca small, chitinised, curved, markedly constricted medially, spherical both basally and apically (Fig. 6A). Gonostyli short, straight, moderately widened, gradually narrowing distally, pointed apically (Fig. 6B). Each gonostylus carrying one long apical seta.

***Male abdominal sternite IX (urite)*:** Small, narrowing apically, sub-triangular.

***Female abdominal ventrite VIII*:** Small, transverse, with no anterior process, hairy, especially posteriorly.

Sexual dimorphism. Some degree of sexual dimorphism was noted in this new species. Namely, it was found that: (i) antennae are longer in the males than in the females; (ii) antennomeres VIII–X are more elongate in the males than in the females; (iii) head is more elongate in the males than in the females; (iv) pronotum is slightly more elongate in the males than in the females; (v) first protarsomere is wider in the males than in the females.

Type locality. Jamurka (Rnjakuša II) Pit, village of Popovići, close to the settlement of Gornji Karin and the town of Benkovac, northern Dalmatia, Croatia.

Geographic distribution. The new species inhabits a few pits in the vicinity of the town of Benkovac and the city of Šibenik in northern Dalmatia (Croatia). Its type locality, the Jamurka (Rnjakuša II) Pit, represents the northernmost location of a *Spelaeobates* species. At the same time, this is the first official finding of a species of the genus *Spelaeobates* on the mainland, which confirms that this genus is distributed both on the islands and on the mainland of Dalmatia (Jalžić 1982). It is possible that the new species also inhabits the surrounding subterranean habitats in northern Dalmatia.

Bionomy and habitat. Individuals of *S.* (*S.*) *coriniensis* sp. nov. were collected by hand from the walls and floor in the innermost part of the Jamurka (Rnjakuša II) Pit, in places that were in complete darkness, with a high degree of humidity and the presence of trickling water.

***Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* Ćurčić, Vesović, Vrbica & Rađa, ssp. nov.**

https://zoobank.org/D92C0413-A52D-45A8-AE12-759986CD2F8F

Figs 4–6

Type material. ***Holotype*:** male (SSM) labeled as follows: "CROATIA, NORTHERN DALMATIA: city of Šibenik, island of Murter, settlement of Tisno, village of Jezera, Jezeranka Pit, 42 m a.s.l., 43°47'16.1"N, 15°37'25.3"E, 2.VI.2019, TR" (white label, printed) / "Holotypus *Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* ssp. nov. Ćurčić, Vesović, Vrbica & Rađa det. 2022" (red label, printed).

Paratypes (10 specimens). The same data as for HT [three males and five females, IZFB]; two males (IZFB) labeled as follows: "CROATIA, NORTHERN DALMATIA: city of Šibenik, village of Banjevci, Šušnjevača Pit, 149 m a.s.l., 43°53'29.9"N, 15°38'20.8"E, 5.XI.2019, TR". All paratypes are labeled with white, printed locality labels and with red printed labels "Paratypus *Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* ssp. nov. Ćurčić, Vesović, Vrbica & Rađa det. 2022" (Fig. 4).

Etymology. *Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* ssp. nov. is named after late Prof. Dr Guido Nonveiller, a famous Serbian and Croatian biospeleologist and an excellent connoisseur of the subterranean beetle fauna of the Balkans.

Diagnosis. The new subspecies is morphologically closest to the nominotypic subspecies *S.* (*S.*) *coriniensis coriniensis* ssp. nov., with which we compared it.

Spelaeobates (*S.*) *coriniensis nonveilleri* ssp. nov. differs from *S.* (*S.*) *coriniensis coriniensis* ssp. nov. with respect to head shape (more elongate and narrower vs. shorter and wider), A6L/A3L (R 0.81–0.88 vs. R 0.88–1.00), shape of certain antennomeres (antennomeres I–V and IX–XI more elongate in first subpecies, whereas antennomeres VI–VIII more elongate in second subspecies), shape of pronotum (more elongate, widest before level of first third, lateral margins strongly convex anteriorly, with right hind angles vs. less elongate, widest at level of first third, lateral margins rounded anteriorly, with obtuse hind angles), PL/PW (R 1.24–1.38 vs. R 1.21–1.28), shape of process between mesocoxae on mesoventrite (sub-parallel vs. gradually narrowing apically), shape of elytra (more narrowed apically vs. less narrowed apically), shape of basal bulb

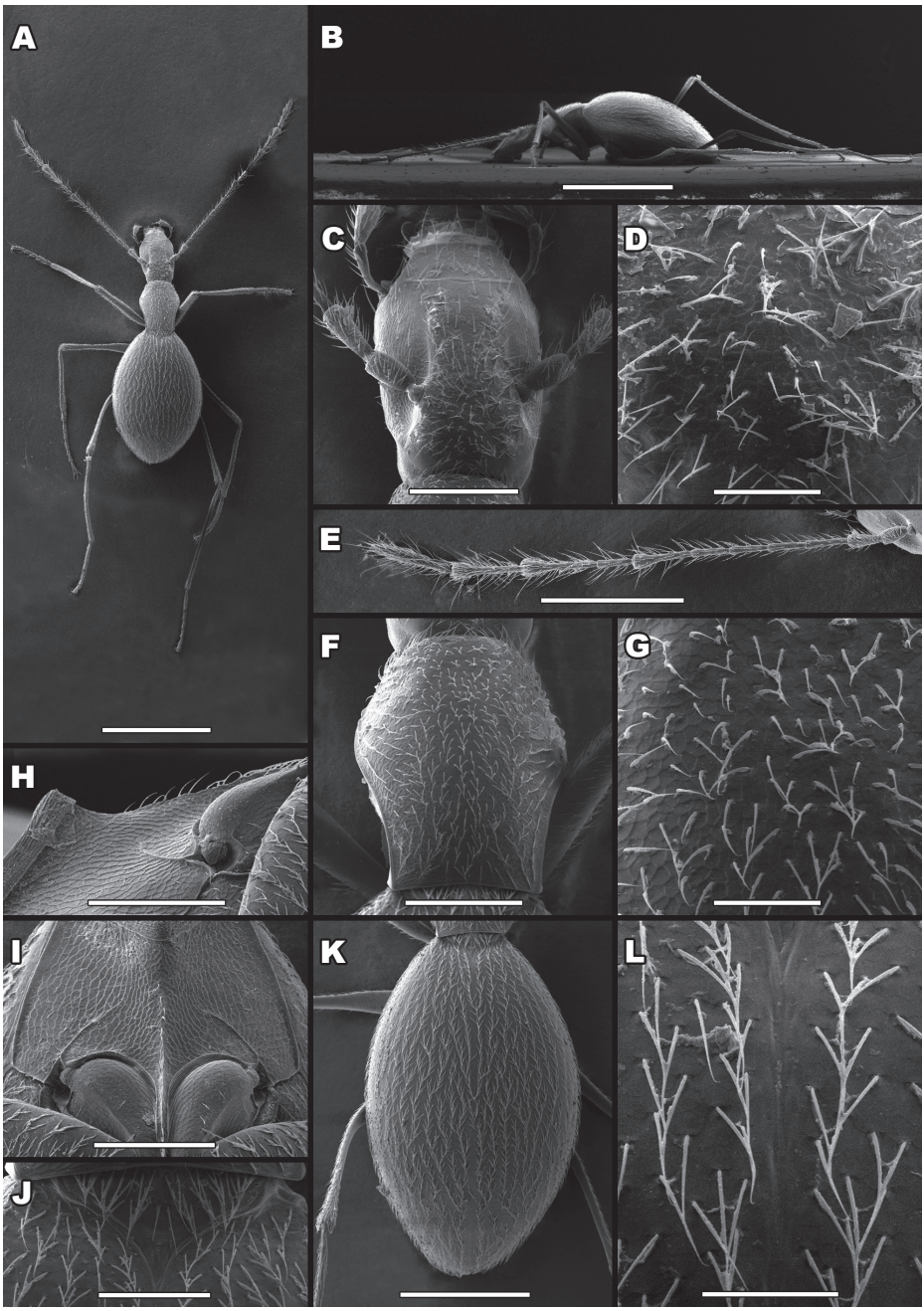

Figure 4. SEM images of the morphological structures of PT male (**A–G, J–L**) and PT female (**H, I**) of *Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* ssp. nov. from the Jezeranka Pit, village of Jezera, settlement of Tisno, island of Murter, city of Šibenik, northern Dalmatia, Croatia **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** microsculpture of head, dorsal view **E** right antenna, dorsal view **F** pronotum, dorsal view **G** microsculpture of pronotum, dorsal view **H** mesoventral carina, lateral view **I** mesoventrite, ventral view **J** scutellum, dorsal view **K** elytra, dorsal view **L** microsculpture of elytra, dorsal view. Scale bars: 1.0 mm (**A, B**); 0.5 mm (**E, K**); 0.2 mm (**C, F, H, I**); 0.1 mm (**J**); 0.05 mm (**D, G, L**).

in dorsal view (broadened distally vs. narrow, sub-parallel), and shape of spermatheca (less constricted medially vs. more constricted medially) (Table 1, Figs 2–6).

Description. Small-sized leptodirine. TL M 2.46 mm (2.42 mm in males, 2.52 mm in females), R 2.34–2.59 mm (2.34–2.52 mm in males, 2.47–2.59 mm in females).

***Habitus*:** Body shape leptodiroid (Fig. 4A, B), colour yellowish.

***Integument*:** Shiny, microsculptured both dorsally and ventrally (Fig. 4C, D, F–L). Sparsely distributed deep punctures present on head, while densely distributed, fine and separated on both pronotum and elytra (Fig. 4C, D, F, G, K, L). Entire body dorsally covered with yellow pubescence of short length (erect on head, while recumbent on both pronotum and elytra) (Fig. 4A, B).

***Head*:** More than one and a half times as long as wide (HL/HW M 1.57, R 1.53–1.61), with no differences in shape between males and females, anophthalmous, occipital carina in the shape of a curved concave line (Fig. 4A, C). Head widest in first quarter or between first quarter and third. Frons roundly impressed between antennal insertions. Labrum transverse, with a few long setae. First maxillary palpomere of similar length and width, shorter than second maxillary palpomere. Maxillary palpomeres II and III of similar length (M3L/M2L M 0.97, R 0.85–1.09). Penultimate maxillary palpomere widened apically. Last maxillary palpomere short, thin, gradually narrowing apically. Antennae inserted in basal quarter of head, slender, narrow proximally (except for first two antennomeres, which are widened), slightly widened distally, longer in males, AL M 1.86 mm, R 1.77–1.94 mm (1.86–1.94 mm in males, 1.77–1.85 mm in females), reaching end of elytra in males (Fig. 4A, B, E). Antennomeres I and II short and wide, second of which slightly longer and narrower. Following four antennomeres more slender and slightly longer than antennomere II. Antennomere III longer than adjacent antennomeres (A3L/A2L M 1.34, R 1.23–1.45; A3L/A4L M 1.21, R 1.07–1.31). Antennomeres VII, IX, and X quite dilated distally. Antennomere VIII relatively short and narrow, shorter and narrower than anatennomeres VII, IX, X, and XI. Ultimate antennomere thin, widened sub-distally, then narrowing apically, narrower than preceding (A11W/A10W M 0.84, R 0.67–1.00). Antennomere I shortest, while antennomeres IX and XI longest. Other ratios of length of certain antennomeres: A6L/A3L M 0.86, R 0.81–0.88; A8L/A3L M 0.75, R 0.65–0.81; A11L/A8L M 2.03, R 1.77–2.25.

***Prothorax*:** Pronotum bell-shaped, elongate, longer than wide (PL/PW M 1.30, R 1.24–1.38; M 1.29, R 1.24–1.33 in males; M 1.31, R 1.28–1.38 in females), widest between first fourth and third, wider (HW/PW M 0.91, R 0.87–0.97) and shorter than head (PL/HL M 0.91, R 0.89–0.96) (Fig. 4A, F). Lateral margins strongly convex anteriorly, then narrowing towards posterior end, markedly concave posteriorly. Pronotal base almost straight, slightly shorter than elytral base. PB/AM M 0.89, R 0.83–0.96. Anterior margin convex medially. Lateral margins and pronotal base rimmed. Fore pronotal angles weakly expressed, rounded, obtuse. Hind pronotal angles well-expressed, right, not protruding backwards. Pronotal disc moderately convex (Fig. 4B).

***Mesothorax*:** Mesoventral carina very low, barely noticeable, with a few setae (Fig. 4H). No tooth, anterior and posterior margins observed. Mesoventrite with a long, sub-parallel process between mesocoxae (Fig. 4I). Scutellum large, sub-triangular (Fig. 4K, J).

***Metathorax*:** Metaventrite with no carina.

***Elytra*:** Broad, ovoid, almost of same width in males and females (EL/EW M 1.63, R 1.55–1.76 in males; M 1.66, R 1.55–1.73 in females), markedly wider than pronotum (EW/PW M 2.28, R 2.18–2.36) (Fig. 4A, K). Maximum width a little before middle. Lateral margins arcuate. Marginal furrows not visible from above. Shoulders barely noticeable, obtuse, covered by hind pronotal angles. Elytral disc markedly convex, steeply declining basally and gently declining apically in lateral view (Fig. 4B). Parasutural stria absent. Elytral apex slightly attenuated, rounded. Pygidium covered by elytra.

***Legs*:** Elongate and thin (Fig. 4A, B). Femora broadened basally, constricted in distal half. Tibiae slender, gently curved, gradually widening distally. Each protibia with a very fine comb over entire apical third of outer margin. Fore tarsi four-segmented in both sexes, only first protarsomere in males slightly dilated (P1W/P2W M 1.20, R 1.00–1.50). Tarsal claws thin, elongate, curved, pointed apically.

***Male genitalia*:** Aedeagus elongate, thin, small, well chitinised, almost the same as in the nominotypic subspecies (Fig. 5A, B). Median lobe in dorsal view straight, gradually narrowing apically, with a sharp apex, barely longer than parameres (Fig. 5A). Median lobe in lateral view quite flattened, curved basally, almost straight proximally, narrowing apically (Fig. 5B). Basal bulb small, broadened distally and bilobed in dorsal view (Fig. 5A), elongate and broadened basally in lateral view (Fig. 5B). Tegmen wide from above (Fig. 5A), in the shape of a ring around basal bulb (Fig. 5B). Parameres elongate, thin, arcuate, sub-apically curved exteriorly, each with a moderately broadened rounded apex in dorsal view (Fig. 5A), while straight, sub-parallel in lateral view (Fig. 5B). Each paramera carrying four apical close-set setae, three of which longer, while one shorter (Fig. 5A). No copulatory piece observed within inner sac (Fig. 5A, B).

***Female genitalia*:** Spermatheca small, chitinised, curved, somewhat constricted medially, spherical both basally and apically (Fig. 6C). Gonostyli short, straight, moderately broadened, gradually narrowing distally, pointed apically. Each gonostylus with one long apical seta.

***Male abdominal sternite IX (urite)*:** Small, narrowing apically, sub-triangular (Fig. 6D).

***Female abdominal ventrite VIII*:** Small, transverse, with no anterior process, hairy, especially posteriorly (Fig. 6E).

Intrasubspecific variability. Some degree of intrasubspecific variability was noted in the new subspecies. It refers to the differences between the two known populations (one from the Jezeranka Pit, and the other from the Šušnjevača Pit). The following differences were observed between the individuals of the two populations mentioned: (i) head is widest in the first quarter in individuals from the population from the Jezeranka Pit vs. head is widest between the first quarter and third in specimens from the Šušnjevača Pit; (ii) antennomeres III, V, and IX, maxillary palpomere I, and elytra are more elongate in individuals from the Jezeranka Pit; (iii) antennomeres VI–VIII, X, and XI are more elongate in individuals from the Šušnjevača Pit; (iv) maxillary palpomere III is longer than maxillary palpomere II in individuals from the Šušnjevača Pit vs. maxillary palpomere III is shorter than maxillary palpomere II in individuals from

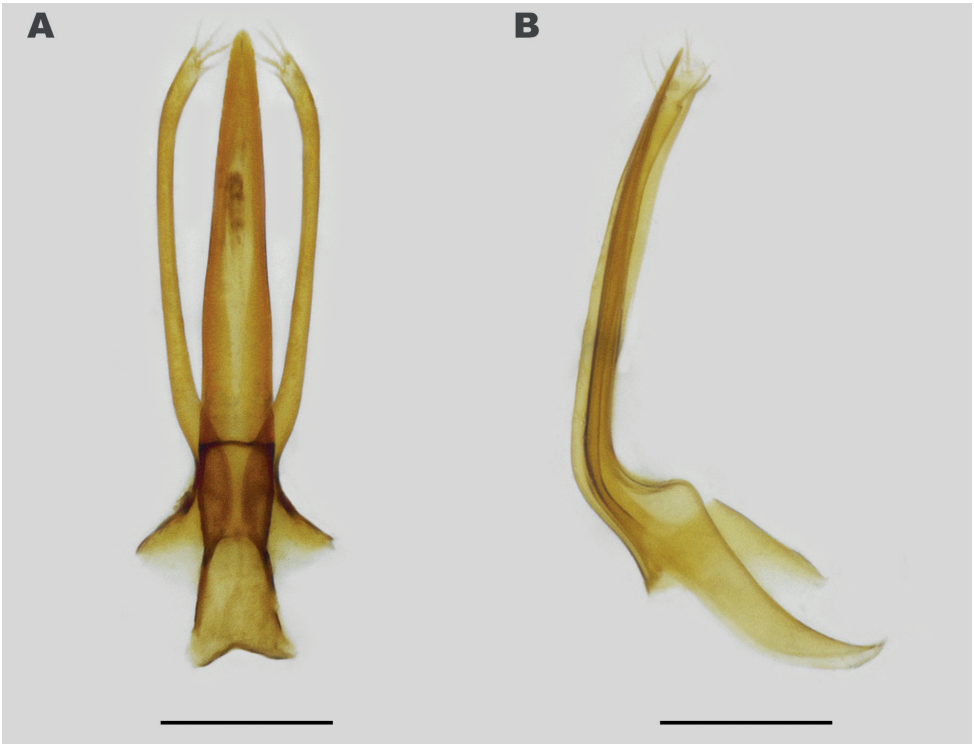

Figure 5. Bright-field images of the male genitalia of HT of *Spelaeobates* (*Spelaeobates*) *coriniensis nonveilleri* ssp. nov. from the Jezeranka Pit, village of Jezera, settlement of Tisno, island of Murter, city of Šibenik, northern Dalmatia, Croatia **A** aedeagus, dorsal view **B** aedeagus, lateral view. Scale bars: 0.1 mm.

the Jezeranka Pit. However, the identical shape of the aedeagus indicates that individuals from both populations belong to the same subspecies.

Sexual dimorphism. Some degree of sexual dimorphism was noted in this new subspecies. Namely, it was found that: (i) the females are slightly longer than the males; (ii) the antennae of the males are longer than those of the females; (iii) antennomeres VIII–X are more elongate in the males than in the females; (iv) first protarsomere is broader in the males than in the females.

Type locality. Jezeranka Pit, village of Jezera, close to the settlement of Tisno and the city of Šibenik, northern Dalmatia, Croatia.

Geographic distribution. This new subspecies is currently known from only two localities in the vicinity of the city of Šibenik, northern Dalmatia, Croatia – the Jezeranka Pit (type locality) in the village of Jezera, near the settlement of Tisno, and the Šušnjevača Pit in the village of Banjevci. The first site is on the island (Murter), while the second is on the mainland. At the same time, this is the second official finding of a species of the genus *Spelaeobates* on the mainland. It is likely that the new subspecies also lives at other insular and non-insular subterranean sites in the surrounding area in northern Dalmatia.

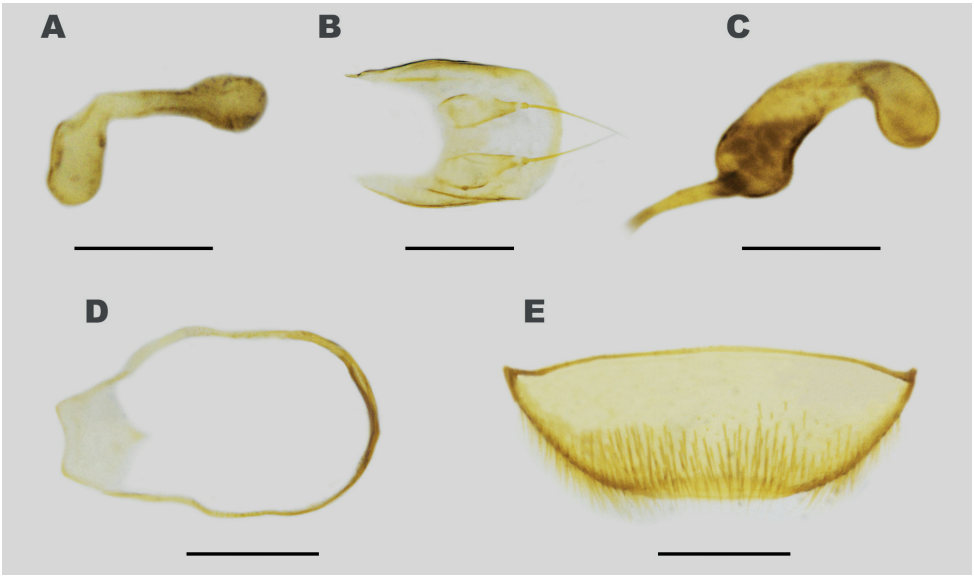

Figure 6. Bright-field images of certain morphological traits of *Spelaeobates* (*Spelaeobates*) *coriniensis coriniensis* ssp. nov. from the Jamurka (Rnjakuša II) Pit, village of Popovići, settlement of Gornji Karin, town of Benkovac, northern Dalmatia, Croatia (**A, B**) and *S.* (*S.*) *coriniensis nonveilleri* ssp. nov. from the Jezeranka Pit, village of Jezera, settlement of Tisno, island of Murter, city of Šibenik, northern Dalmatia, Croatia (**C–E**) **A, C** PT female, spermatheca, lateral view **B** PT female, gonostyli, dorsal view **D** HT male, abdominal sternite IX (urite) **E** PT female, abdominal ventrite VIII. Scale bars: 0.05 mm (**A, C**); 0.10 mm (**B, D, E**).

Bionomy and habitat. Specimens of *S.* (*S.*) *coriniensis nonveilleri* ssp. nov. were collected manually from the walls and floor in the innermost parts of the Jezeranka and Šušnjevača Pits, in places that were in complete darkness, with a high degree of humidity and the presence of trickling water.

Spelaeobates (*Spelaeobates*) *novaki* Müller, 1901

Figs 7, 8

Type material. ***Topotypes*:** one male and four females (IZFB) labeled as follows: "CROATIA, NORTHERN DALMATIA: island of Dugi Otok, village of Savar, Strašna Peć Cave, 70 m a.s.l., 44°00'16.6"N, 15°02'19.1"E, 1.VII.1997, TR". All topotypes are labeled with white, printed locality labels (Fig. 7).

Remarks. For purpose of comparisons, we have examined the topotype material of *S.* (*S.*) *novaki* collected by the last author of this study. This species is described on the basis of the type series of specimens collected in September 1900 by Josef Müller and Petar Novak in two caves on two northern Dalmatian islands – the Strašna Peć Cave, village od Savar, island of Dugi Otok, and a small cave in the village of Mali Iž, island

of Iž (Müller 1901). Later Pretner (1973) determined the correct name of the second cave site (its exact name is the Jezero Cave). In his original description of *S.* (*S.*) *novaki*, Müller (1901) did not indicate how many specimens are included in the type series, nor is there any information about their sex or where they were deposited. Based on the data and illustrations in the paper of Müller (1901), it can be concluded that the type series of this species consisted of both male and female specimens.

After reading both the original description of *S.* (*S.*) *novaki* by Müller (1901) and the subsequent morphological data on the species by Jeannel (1924), as well as a careful examination of the topotype specimens of *S.* (*S.*) *novaki*, we have found that some of the data given in the earlier literature on the morphology of the species do not agree with the characteristics of the topotype specimens we have observed. Namely, both Müller (1901) and Jeannel (1924) reported that the parameres of the aedeagus of *S.* (*S.*) *novaki* lack setae. Furthermore, in the drawing of the aedeagus by Müller (1901), no parameral setae are present. However, in the topotype male of *S.* (*S.*) *novaki*, we observed that each paramere has four apical setae, as in *S.* (*S.*) *coriniensis* sp. nov. In the work of Müller (1901), it was noted that the head of *S.* (*S.*) *novaki* is nearly twice as long as wide, the pronotum is 1.5 times longer than wide, antennomeres I and II are of similar width, the last antennomere is wider than the preceding ones, and the first protarsomere of the males is about twice as long as wide. However, in the specimens of the same species that we have examined, the head is about 1.5 times as long as wide, the pronotum is nearly one third longer than wide, antennomere I is wider than antennomere II, the last antennomere is narrower than the preceding ones, and the first protarsomere of the male is about 1⅔ times longer than wide (Table 1). Müller (1901) noted that the pronotum of *S.* (*S.*) *novaki* is finely punctate, but Jeannel (1924) reported that it is strongly punctate, which we also observed in our specimens. For these reasons, we have decided to redescribe the species *S.* (*S.*) *novaki* and add additional data on its morphology here.

Redescription. Small-sized leptodirine. TL M 2.63 mm (2.57 mm in males, 2.64 mm in females), R 2.57–2.70 mm (2.57 mm in males, 2.60–2.70 mm in females).

***Habitus*:** Body shape leptodiroid (Fig. 7A, B), colour yellowish-brown.

***Integument*:** Lustrous, microsculptured both dorsally and ventrally (Fig. 7C, E, F, H). Densely distributed deep punctures present on head, pronotum (often merged) and elytra (particularly strong) (Fig. 7C, E, F). Entire body dorsally covered with yellow pubescence of short length (erect on head, while recumbent on both pronotum and elytra) (Fig. 7A, B).

***Head*:** About one and a half times as long as wide (HL/HW M 1.47, R 1.38–1.53), slightly more elongate in males (HL/HW M 1.49 in males, M 1.46 in females), with no eyes, occipital carina in the shape of a curved concave line (Fig. 7A, C). Head widest between first third and half. Frons roundly impressed between antennal insertions. Labrum transverse, with a few long setae. First maxillary palpomere of similar length and width, shorter than second maxillary palpomere. Maxillary palpomeres II and III of similar length (M3L/M2L M 1.09, R 1.00–1.18). Penultimate maxillary palpomere widened apically. Ultimate maxillary palpomere

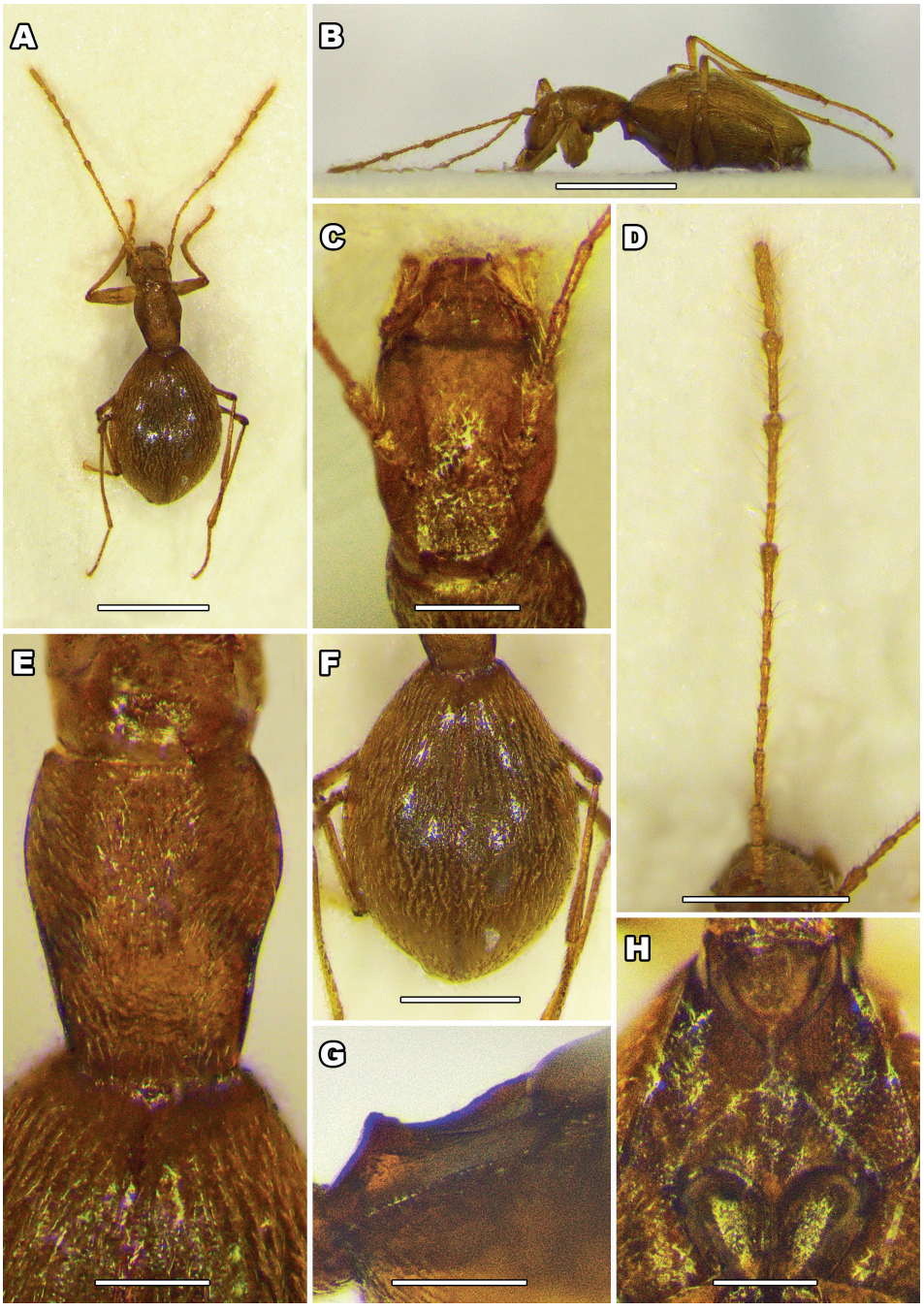

Figure 7. Bright-field images of the morphological structures of topotype male (**A–G**) and topotype female (**H**) of *Spelaeobates* (*Spelaeobates*) *novaki* from the Strašna Peć Cave, village of Savar, island of Dugi Otok, northern Dalmatia, Croatia **A** habitus, dorsal view **B** habitus, lateral view **C** head, dorsal view **D** left antenna, dorsal view **E** pronotum and scutellum, dorsal view **F** elytra, dorsal view **G** mesoventral carina, lateral view **H** mesoventrite, ventral view. Scale bars: 1.0 mm (**A, B**); 0.5 mm (**D, F**); 0.25 mm (**C, G**); 0.2 mm (**E, H**).

short, slender, gradually narrowing apically. Antennae inserted in basal quarter of head, thin, narrow proximally (except for first two antennomeres, which are thickened), slightly widened distally, longer in males, AL M 1.81 mm, R 1.75–1.93 mm (1.93 mm in males, 1.75–1.79 mm in females), not reaching end of elytra in both sexes (Fig. 7A, B, D). Antennomeres I and II short and wide, of similar length, second of which slightly narrower. Following four antennomeres thinner and slightly longer than antennomere II. Antennomere III longer than adjacent antennomeres (A3L/A2L M 1.37, R 1.23–1.42; A3L/A4L M 1.24, R 1.21–1.31). Antennomeres VII, IX, and X quite expanded distally. Antennomere VIII relatively short and narrow, shorter and narrower than anatennomeres VII, IX, X, and XI. Ultimate antennomere slender, widened sub-distally, then narrowing apically, narrower than penultimate one (A11W/A10W M 0.75, R 0.67–0.83). Antennomere VIII shortest, while antennomeres IX and XI longest. Other ratios of length of certain antennomeres: A6L/A3L M 0.79, R 0.76–0.82; A8L/A3L M 0.65, R 0.59–0.71; A11L/A8L M 2.27, R 2.09–2.40.

***Prothorax*:** Pronotum bell-shaped, elongate, longer than wide (PL/PW M 1.29, R 1.26–1.32; M 1.32, R 1.32 in males; M 1.28, R 1.26–1.30 in females), widest slightly before anterior third, broader (HW/PW M 0.93, R 0.88–0.98) and shorter than head (PL/HL M 0.96, R 0.90–0.98) (Fig. 7A, E). Lateral margins rounded anteriorly, after which they constrict towards posterior end, slightly concave posteriorly. Pronotal base straight, somewhat shorter than elytral base. PB/AM M 0.86, R 0.81–0.90. Anterior margin straight. Lateral margins and pronotal base rimmed. Fore pronotal angles weakly expressed, rounded, obtuse. Hind pronotal angles well-expressed, obtuse, not protruding backwards. Pronotal disc moderately convex (Fig. 7B).

***Mesothorax*:** Mesoventral carina very low, barely noticeable, with a few setae (Fig. 7G). No tooth, anterior and posterior margins observed. Mesoventrite with a long, sub-parallel process between mesocoxae (Fig. 7H). Scutellum large, sub-triangular (Fig. 7E, F).

***Metathorax*:** Metaventrite without carina.

***Elytra*:** Wide, ovoid, of similar width in males and females (EL/EW M 1.53, R 1.53 in males; M 1.55, R 1.49–1.60 in females), markedly wider than pronotum (EW/PW M 2.44, R 2.37–2.50) (Fig. 7A, F). Maximum width a little before middle. Lateral margins arcuate. Marginal furrows not visible from above. Shoulders barely visible, obtuse, covered by hind pronotal angles. Elytral disc markedly convex, steeply declining both basally and apically in lateral view (Fig. 7B). Parasutural stria absent. Elytral apex slightly attenuated, rounded. Pygidium not entirely covered by elytra.

***Legs*:** Elongate and slender (Fig. 7A, B). Femora widened basally, constricted in distal half. Tibiae thin, gently curved, gradually widening distally. Each protibia with a very fine comb over entire apical third of outer margin. Fore tarsi four-segmented in both sexes, only first protarsomere in males dilated (P1W/P2W M 1.67, R 1.67). Tarsal claws thin, elongate, curved, pointed apically.

***Male genitalia*:** Aedeagus elongate, slender, small, well chitinised (Fig. 8A, B). Median lobe in dorsal view straight, sub-parallel, gradually narrowing distally, with

Figure 8. Bright-field images of certain morphological traits of topotype male (**A, B**) and topotype female (**C, D**) of *Spelaeobates* (*Spelaeobates*) *novaki* from the Strašna Peć Cave, village of Savar, island of Dugi Otok, northern Dalmatia, Croatia **A** aedeagus, dorsal view **B** aedeagus, lateral view **C** spermatheca, lateral view **D** abdominal ventrite VIII. Scale bars: 0.2 mm (**A, B, D**); 0.1 mm (**C**).

a rounded apex, longer than parameres (Fig. 8A). Median lobe in lateral view quite flattened, curved basally, straight proximally and slightly bent downward distally, narrowing apically (Fig. 8B). Basal bulb small, narrow, sub-parallel and slightly widened distally in dorsal view (Fig. 8A), while elongate and widened basally in lateral view (Fig. 8B). Tegmen wide from above (Fig. 8A), in the shape of a ring around basal bulb (Fig. 8B). Parameres elongate, slender, arcuate, sub-apically curved exteriorly, each with a moderately widened rounded apex in dorsal view (Fig. 8A), while almost straight, sub-parallel in lateral view (Fig. 8B). Each paramera bearing four apical close-set setae, two of which longer, while two shorter (Fig. 8A, B). No copulatory piece observed within inner sac (Fig. 8A, B).

***Female genitalia*:** Spermatheca small, chitinised, straight basally, curved sub-apically, spherical both basally and apically (Fig. 8C). Gonostyli short, straight, moderately widened, gradually narrowing distally, pointed apically. Each gonostylus carrying one long apical seta.

***Male abdominal sternite IX (urite)*:** Small, narrowing apically, sub-triangular.

***Female abdominal ventrite VIII*:** Small, transverse, with no anterior process, hairy, especially posteriorly, slightly bilobed distally (Fig. 8D).

Geographic distribution. This species inhabits two caves located on two northern Dalmatian islands – the Strašna Peć Cave (island of Dugi Otok) and the Jezero Cave (island of Iž) (Pretner 1973). It is possible that it also inhabits other subterranean sites on the same and neighbouring islands.

Key to the taxa of the genus *Spelaeobates* [modified after Jeannel (1924)]

1 First protarsomere in males dilated, median lobe of aedeagus attenuated apically [*Spelaeobates* Müller, 1901] **2**

– First protarsomere in males narrow, median lobe of aedeagus bulging and club-like apically [*Pretneriella* V. Guéorguiev, 1976] **4**

2 Punctuation on pronotum strong, with merged punctures, elytra less elongate, median lobe of aedeagus sub-parallel, rounded apically .... ***S.* (*S.*) *novaki* Müller, 1901**

– Punctuation on pronotum fine, with separated punctures, elytra more elongate, median lobe of aedeagus narrowing distally, pointed at apex [*S.* (*S.*) *coriniensis* sp. nov.] **3**

3 Head shorter and wider, lateral pronotal margins rounded anteriorly, hind pronotal angles obtuse, elytra less narrowed apically, protarsomere I in males wider, basal bulb narrow, sub-parallel in dorsal view .... ***S.* (*S.*) *coriniensis coriniensis* ssp. nov.**

– Head more elongate and narrower, lateral pronotal margins strongly convex anteriorly, hind pronotal angles right, elytra more narrowed apically, protarsomere I in males narrower, basal bulb broadened distally in dorsal view..... ..... ***S.* (*S.*) *coriniensis nonveilleri* ssp. nov.**

4 Lateral margins of pronotum entirely rimmed, mesoventral carina high and toothed **5**

– Lateral margins of pronotum rimmed only basally, mesoventral carina not toothed **7**

5 Pronotum short, regularly narrowed and slightly sinuate basally, antennomere II not longer than antennomere I, elytra more convex, TL 2.6–2.8 mm [*S.* (*P.*) *pharensis* Müller, 1901] **6**

– Pronotum elongate, abruptly and deeply sinuate basally, antennomere II distinctly longer than antennomere I, elytra less convex, flattened in sutural region, TL 2.8–3.0 mm ..... ***S.* (*P.*) *czernyi* Breit, 1913**

6 Smaller, pronotum less elongate, with maximum width less forward, wider basally, punctuation and pubescence of elytra a little less dense .... ***S.* (*P.*) *pharensis pharensis* Müller, 1901**

– Larger, pronotum more elongate, with maximum width moved further forward, narrower basally, punctuation and pubescence of elytra a little denser .... ***S.* (*P.*) *pharensis langhofferi* Müller, 1931**

7 Punctuation on pronotum deep and strong, TL more than 2.8 mm .... ***S.* (*P.*) *kraussi* Müller, 1903**

– Punctuation on pronotum superficial and fine, TL less than 2.8 mm **8**

8 Pronotum shorter, more rounded anteriorly, more deeply sinuate posteriorly, TL 2.7 mm ..... ***S.* (*P.*) *bachofeni* Breit, 1913**

– Pronotum more elongate, less rounded anteriorly, less deeply sinuate posteriorly, TL 2.8 mm ..... ***S.* (*P.*) *peneckei* Müller, 1903**

New findings of the genus *Spelaeobates*

We had at our disposal as comparative material two samples of the genus *Spelaeobates*, collected on two islands in central Dalmatia by the last author of this study, which belong to the taxa *S.* (*P.*) *kraussi* and *S.* (*P.*) *pharensis langhofferi* (see the chapter Other examined taxa). A sample of *S.* (*P.*) *kraussi* (one male and one female) was collected last year in the Vičja Jama Pit (Vidova Gora peak, village of Nerežišća) on the island of Brač, while a sample of *S.* (*P.*) *pharensis langhofferi* (two females) was collected 10 years ago in the Jama na Boroviku Pit (village of Pitve, near the town of Jelsa) on the island of Hvar. Both taxa have been recorded so far only from their type locality – *S.* (*P.*) *kraussi* from the Dobra Jama Pit, Vidova Gora peak, village of Nerežišća, island of Brač, while *S.* (*P.*) *pharensis langhofferi* from the Kruščica Cave, near the town of Stari Grad, island of Hvar. We report herein the first findings of these two taxa outside their type locality.

Discussion

Our new findings of the genus *Spelaeobates* were completely surprising considering that more than a century has passed since the last species of this genus was described (Perreau 2000, 2015; Hlaváč et al. 2017). The taxa of this genus are very rare, which is indicated by a small number of species that have been described so far, despite the fact that detailed biospeleological explorations have been carried out in Dalmatia so far (Pretner 1973). Future biospeleological research should be intensified in northern Dalmatia (both on the islands and on the mainland), where additional new *Spelaeobates* species and subspecies to science could be expected.

It was thought for a long time that the genus *Spelaeobates* is endemic to the Adriatic islands, which belong to northern and central Dalmatia (Croatia). Namely, at the beginning of the 20th century, several new species of this genus to science were described, inhabiting a total of 17 subterranean localities (caves and pits) on the islands of Iž, Dugi Otok, Hvar, Brač, and Vis (Pretner 1973). Jalžić (1982) reported the first finding of this genus on the mainland. He found three specimens of *Spelaeobates* on bat guano in the Golubnjača Cave in the village of Kaštel Žegarski near the town of Obrovac in northern Dalmatia (Croatia) (Jalžić 1982). This taxon was not identified to the species level due to the small number of specimens available to Jalžić. Perhaps these specimens might belong to the nominotypic subspecies of *S.* (*S.*) *coriniensis* sp. nov., inhabiting the Jamurka (Rnjakuša II) Pit, which is located in the vicinity, too. The species from the Golubnjača Cave might belong to the subgenus *Spelaeobates*, considering that the two new taxa of this subgenus to science described in the current study are distributed in the surrounding area. One of the priorities is to collect additional *Spelaeobates* specimens (including males) from the Golubnjača Cave, which would make it possible to determine whether they belong to any of the known taxa. A comprehensive molecular study of all taxa of this genus would be helpful to determine their definitive phylogenetic relationships and taxonomic status.

Our study confirms that the insular genus *Spelaeobates* is also distributed on the mainland, where it inhabits a relatively wide area in northern Dalmatia, and its distribution range is probably even broader. Our findings of two new *Spelaeobates* taxa to science [one species from the Jamurka (Rnjakuša II) Pit and one subspecies from the Jezeranka and Šušnjevača Pits] are the first accurate findings of a species of this genus on the mainland. It is interesting to point out that the subspecies *S.* (*S.*) *coriniensis nonveilleri* ssp. nov. inhabits both the island of Murter and the nearby mainland (admittedly, this island is by far the closest to the mainland compared to all the other islands where taxa of the genus *Spelaeobates* have been found).

All taxa of the genus *Spelaeobates* are distributed in the proximity of the Adriatic Sea, whether recorded on the islands or on the nearby mainland. Also, subterranean sites where the members of this genus were found are located at low altitudes (42–216 m a.s.l. in the case of the locations where two new taxa of *Spelaeobates* to science were found).

Based on the presence of the first dilated protarsomere in males and the apically narrowed median lobe of the aedeagus, we classified both new taxa to science (a new species and a new subspecies) in the subgenus *Spelaeobates* s. str. In contrast, species of the subgenus *Pretneriella* have a narrow first protarsomere in males, as well as a bulging median lobe of the aedeagus, which is club-like apically (Jeannel 1924; Guéorguiev 1976). Also, both new taxa are geographically closer to *S.* (*S.*) *novaki*, the only species previously belonging to *Spelaeobates* s. str., than to species of the subgenus *Pretneriella* (Fig. 1). The definitive status of new and other taxa within the genus *Spelaeobates* and its subgenera will be resolved by studying a larger number of taxa, preferably using molecular techniques.

Intrasubspecific variability was found between two recorded populations of *S.* (*S.*) *coriniensis nonveilleri* ssp. nov. – one from the Jezeranka Pit and the other from the Šušnjevača Pit. In addition, morphological differences related to sexual dimorphism were noted in both new taxa. Females of both taxa were expected to be larger and have broader elytra compared to males (Jeannel 1924; Ćurčić et al. 2021). Interestingly, no differences in body length and elytral width between sexes were observed in *S.* (*S.*) *coriniensis coriniensis* ssp. nov. In addition, no differences in the shape of the head and pronotum and elytral width between males and females were detected in *S.* (*S.*) *coriniensis nonveilleri* ssp. nov.

During geotectonic events, the Adriatic microplate was pulled into orogenic processes, which formed the Dinarides. The island relief of the northeastern part of the Adriatic Sea was created in post-Pleistocene by rising sea level 100 m and it geotectonically belongs to the Outer Dinarides. The Adriatic archipelago is an inseparable part of the orogenic mountain system of the Dinarides and a connection of islands and mountains is visible due to its equal extension in northwest-southeast direction (Bognar 1999). Thirteen thousand years ago, the Adriatic Sea was a large valley with many mountains. Today, the peaks of the mountains and the hills represent the islands and the coast. The Adriatic Sea was formed by large post-glacial floods. Cycles of drying and flooding shaped small biogeographical units. The Messinian salinity crisis, the Zanclean flood, the sea-level decrease during the last glacial period, and the ultimate flood in the Adriatic basin as a consequence of ice melting that began 18,000 years ago may

explain the distributional patterns of species in the Adriatic basin (Van Straaten 1970; Maselli et al. 2014; Pellegrini et al. 2018), including the taxa of the genus *Spelaeobates*.

The fact that the territory of the former Yugoslavia, Bulgaria, and northern Greece was part of North Aegeis during most of the Tertiary indicates that the majority of terrestrial Balkan troglobites, including most of the endemic genera of the tribe Leptodirini, are of North Aegeid origin. This also applies to most representatives of the subtribes Bathysciotina and Leptodirina, as well as to all genera of the subtribes Anthroherponina and Spelaeobatina, including *Spelaeobates*. As most Balkan subterranean taxa of the tribe Leptodirini, two new *Spelaeobates* taxa to science described in the current study are also typical North Aegeid relicts, as evidenced by their location north of the Trans-Aegean fault (Popov et al. 2004).

The palaeokarst in the area of Dalmatia is very old (Gaudenyi and Jovanović 2012) and it is likely that the karstic areas of Dalmatian islands were once connected to karstic regions that now belong to the mainland of Dalmatia, which could favor the connection of their subterranean faunas in old geological times.

All previous authors agree that the genus *Spelaeobates* has a specific phylogenetic position within the tribe Leptodirini. Jeannel (1924) classified it in the phyletic series of *Spelaeobates*, while Guéorguiev (1974, 1977) established a separate subtribe Spelaeobatina, which contains only the genus *Spelaeobates*. Although the position of the antennal insertions (in the last quarter of the head) and the shape of the claws of the legs (enlarged and vertically blunt) indicated that Anthroherponina and Spelaeobatina are closely related subtribes (Jeannel 1924; Guéorguiev 1974, 1977), the prevailing opinion is that Spelaeobatina is actually closer to Bathysciina than to Anthroherponina (Perreau and Pavićević 2008; Njunjić et al. 2017), based on the analysis conducted by Casale et al. (1991). Thus, it can be assumed that the subtribes Spelaeobatina and Anthroherponina are not monophyletic since the phylogenetic significance of the position of the antennal insertions is debatable (Perreau and Pavićević 2008).

The genus *Prospelaeobates* Giachino & Etonti, 1996, which inhabits subterranean sites in southwestern Slovenia and northern Dalmatia (island of Cres, Croatia) (Perreau 2000, 2015), was thought to be related to *Spelaeobates* based on the presence of four tarsomeres in males and the structure of the aedeagus (Giachino and Etonti 1996). However, in the genus *Prospelaeobates*, the mesocoxal cavities are separated by an intercoxal process, which extends to the anterior margin of the metathorax (Giachino and Etonti 1996), in contrast to the genus *Spelaeobates*, where the mesocoxal cavities are fused (Giachino and Etonti 1995). Although originally considered related to *Spelaeobates* (Giachino and Etonti 1996), *Prospelaeobates* was later transferred to the subtribe Bathysciina (Newton 1998; Polak and Bognolo 2003).

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