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Original paper

A new genus and species of subterranean trechine beetle from Montenegro (Coleoptera: Carabidae: Trechini)

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Summary. Balkan's Dinaric karst is a continuous source of specialized, cave adapted fauna - so called troglobionts. Much of this exceptionally rich biodiversity is attributed to beetles (Coleoptera) from the ground beetle tribe Trechini (family Carabidae), with hundreds of species with different degrees of morphological modifications for life in subterranean habitats - so called troglomorphism. In this contribution, we present a discovery of one new genus and species of subterranean Trechine beetle, *Orcusiella prokletijensis* gen. et sp. nov. from a high-altitude pit situated on Prokletije Mountains, Montenegro. This new taxon is described, illustrated and compared with closely related taxa. An identification key for all so far known genera of Dinaric subterranean Trechini, as well as data on the distribution and ecology of these remarkable species are provided and discussed.

Keywords: Albania, Montenegro, *Neotrechus*, new genus, new species, *Orcusiella prokletijensis*, Prokletije Mountains, subterranean habitat, Trechinae, troglobiont.

INTRODUCTION

The Dinarides are recognized as a world hotspot of subterranean biodiversity, and are extremely rich in highly specialized troglomorphic invertebrates, especially insects (Sket 2004; Culver et al. 2006; Sket 2012). Among these, one of the best known and studied groups are Trechinae, especially the morphologically peculiar, so called aphaenopsoid Trechini beetles of the former „série phylétique *d´Aphaenops*" sensu Jeannel (1928). This specialized group is characterized by a strongly flattened body and long appendages, a more or less prolonged head without any traces of eyes, enlarged mandibles and, usually, a long and narrow pronotum coupled with an ovoid, basally narrowed elytra with effaced humeri. The pronotum and elytra bear very long sensorial setae (Jeannel 1928; Casale and Laneyrie 1982; Luo et al. 2018).

Up until the end of the 1980´s, four phyletic lines "série phylétique" sensu Jeannel (1928) of subterranean Trechini were known from the Dinaric Karst: *Duvalius*-phyletic line, *Neotrechus*-phyletic line, *Typhlotrechus*-phyletic line and *Aphaenops*-phyletic line. The first of these three lines were represented by a single genus each, while the *Aphaenops*-phyletic line included three genera; *Aphaenopsis* G. Müller, 1913 (Central Bosnia), *Scotoplanetes* Absolon, 1913 (southern Herzegovina and Montenegro) and *Adriaphaenops* Noesske, 1928 (Herzegovina, Montenegro and Albania). Traditionally, the *Aphaenops*-line was considered to be "ultra-evolved", "archaic", or "high or hyper-specialized" (Casale and Laneyrie 1982; Casale et al. 2012), and comprised species with a similar, so called "aphaenopsoid" or "aphaenopsian" habitus (Pretner 1959; Pavićević 1990, 2001; Quéinnec 2008; Quéinnec and Pavićević 2008; Quéinnec et al. 2008, Lohaj et al. 2016; Lohaj and Delić 2019).

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Over the following decades, new taxa of aphaenopsoid Trechini were discovered from all over the Dinaric karst, resulting in the description of nine new genera (*Dalmataphaenops* Monguzzi, 1993; *Albanotrechus* Casale & Guéorguiev, 1994; *Croatotrechus* Casale & Jalžić, 1999; *Minosaphaenops* Quéinnec, 2008; *Derossiella* Quinnec, 2008; *Jalzicaphaenops* Lohaj & Lakota, 2010; *Acheroniotes* Lohaj & Lakota, 2010; *Velebitaphaenops* Casale & Jalžić 2012 and *Velesaphaenops* Ćurčić & Pavićević, 2018. A significant contribution to these new discoveries (not only Coleoptera, but also other subterranean fauna) was the introduction of vertical caving techniques. This novelty enabled karst researchers to explore deeper hitherto inaccessible vertical pits or sections of caves and offered the possibility to sample new and otherwise barely accessible habitats, i.e. cave hygropetric (Lohaj and Delić 2019).

Despite the fact that the cave beetle fauna of this region has been systematically studied for almost two centuries, new taxa are discovered and described almost every year (Pavićević et al. 2008; Perreau and Pavićević 2008; Quéinnec 2008; Lakota et al. 2010; Lohaj and Lakota 2010; Casale et al. 2012; Hlaváč et al. 2019; Delić et al. 2020; etc.).

Similarly, speleological and biospeleological survey of newly unearthed pits on the Montenegrin part of the Prokletije Mountain range (in eastern Montenegro) by one of authors (MP), over the years 2011 – 2015, led to the discovery of a new, remarkable cave dwelling genus and species of "anisotopic" trechine beetles sensu Jeannel (1928), provisionally attributed to *Neotrechus*. The new taxon, *Orcusiella prokletijensis* gen. et sp. nov., is described below.

MATERIAL AND METHODS

Geomorphological framework and locality descriptions

Prokletije Mountains are a mountainous range in the southernmost part of the Dinarides. Their name (in English: Accursed Mountains) best describes the character of the range, often considered to be one of the most inaccessible mountain ranges in Europe, with an extremely harsh mountain environment providing extremely hard living conditions for its' inhabitants. The mountain range stretches for more than 64 km, from Skadar Lake along the Montenegrin - Albanian border in the southwest to Serbia (Kosovo and Metohija) in the northeast. The southern boundary of the Prokletije is defined by the Drim River and its tributary Valbona. The peak, Maja Jezercë in Albania at 2694 m a.s.l. is the highest peak of both the Prokletije range and the entire Dinarides. Both the highest mountain peak in Montenegro, Zla Kolata at 2534 m a.s.l., and the highest in Serbia, Djeravica at 2656 m a.s.l. are located here. The Prokletije Mountains present a typical high mountain range with a pronounced steep topography and paleo-glacial features. The complex paleogeology of the region produced the unusual zig-zag shape of Prokletije range, and induced a curving shape from the dominant northwestern – southeastern "Dinaric" direction towards northeast. In the western and central parts of the range the composition of the mountains is mainly uniform with Mesozoic limestones and dolomites of Jurassic and Cretaceous age. In eastern part of Prokletije, in addition to limestone and dolomite series, there are also rocks from the upper Paleozoic, Triassic volcanic rocks and Jurassic metamorphic rocks.

The idea for speleological research in the Prokletije Mountain range came up almost simultaneously from Serbian and Polish speleologists from the following clubs: Akademski speleološko-alpinistički klub, Belgrade, Serbia; Wielkopolski klub Taternictwa Jaskiniowego, Poznań, Poland and Speleoclub Swietokrzyski, Kielce, Poland.

Speleological exploration in the area started in 2006 and is still ongoing. The exploration was conducted at Bjelič limestone massif, in the vicinity of Gusinje (North-eastern Montenegro, 1014 m a.s.l.), on the border between Albania and Montenegro. The Bjelič massif is surrounded by two valleys, Ropojane in Montenegro and Valbona in Albania, in the form of a capital letter "U". The two most prominent peaks in the whole massif are Maja Kolata (2434 m a.s.l.) and Maja Rosit (2524 m a.s.l.). In this period, more than 50 caves, mainly vertical pits, were recognized, explored and surveyed. Four caves stand out by their length; i) Jaskinia Lodowa (1956 m of length, 451 m of depth, entrance at 1945 m a.s.l.), ii) Jaskinia Gigant (1635 m of length, 296 m of depth, entrance at 2116 m a.s.l.), iii) Jaskinia Gornicza (2019 m of length, 516 m of depth, entrance at 1218 m a.s.l.), and iv) Jaskinia Čardak (1054 m of length, depth of 175 m, entrance at 1969 m a.s.l.) (Kicińska and Najdek, 2013a, 2013b; Barović et al. 2018). In July 2011, speleobiologists from Belgrade, Momčilo Popović and Iva Njunjić, joined the expedition. In the next year, Michel Perreau from Paris (France), a renowned specialist for Coleoptera, joined the expedition along with four speleologists from ASBTP caving club from Nice (France). Between 2011 and 2015, twelve caves ranging in depth from 100 to 400 m were surveyed and biologically sampled. Several peculiar troglobiotic coleopterans were collected, among them a new genus and species of specialized subterranean trechine beetle, which is described below.

Laboratory work and morphology

The morphological structures of the collected beetles were examined using a stereoscopic microscopes Leica MZ 16 (Leica, Wetzlar, Germany) and Stemi 508 (Zeiss, Jena, Germany). Male and female genitalia were dissected, cleaned

in KOH or Carnation oil with ether, mounted in Canada balsam or Dimethyl–Hydantoin formaldehyde (DMHF) on transparent slides and pinned under the exanimated specimens. Fine structures of male and female genitalia were studied at magnifications up to 200× using an Olympus BHS (Olympus, Tokyo, Japan) and Laboval microscope (Zeiss, Jena, Germany). Macro photographs were taken using Canon 5D Mark II camera and edited using Adobe Photoshop software program.

Abbreviations of measurements used in the text are as follows:

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

L: overall length, from apex of mandibles to apex of elytra, measured along the suture.

HL: head length (measured from the anterior margin of the clypeus to the neck constriction)

HW: maximum width of head.

AL: antennal length (measured from the base of the antennal scape to the apex of terminal antennal segment).

PL: pronotal length (measured along the median line of pronotum).

PW: maximum width of pronotum, as greatest transverse distance.

EL: elytral length (measured as linear distance along the suture from the elytral base to the apex).

EW: maximum width of elytra.

HL/HW: ratio head length/maximum width of head.

PL/PW: ratio length of pronotum/maximum width of pronotum.

EL/EW: ratio length of elytra/maximum width of elytra.

Forward slash indicates separate labels.

Acronyms:

CDP - private collection of Dragan Pavićević (Belgrade, Serbia)

CMP - private collection of Momčilo Popović (Zemun, Serbia)

CRL - private collection of Roman Lohaj (Limbach, Slovakia).

Classification of the Trechini used here follows Jeannel (1928) and Belousov (2017).

RESULTS

Genus *Orcusiella* gen. nov.

Type species: *Orcusiella prokletijensis* sp. nov., by monotypy

Description

A large trechine species, characterized by the peculiar combination of the following characters: apterous, depigmented, elongated but robust; head, pronotum and elytra glabrous. Body flattened dorsoventrally, elytral striae almost absent, each elytra with 3-6 dorsal and 1 preapical setae. Humeral group of setae aggregated. Pronotum with two pairs of setae, anterior and posterior, legs and antennae very long and slender, densely pubescent. Male protarsi with the first tarsomere dilated. General shape of the body and size resembles the Alpine genus *Aphaenophidius* G. Müller, 1913 (Figs 1, 2).

Head large, dorsoventrally depressed, clearly wider and longer than the pronotum. Eyes absent. Frontal furrows very deep, markedly divergent, starting in the level of the first pair of supraorbital pores, hereafter becoming convergent, backwardly interrupted by the neck constriction. Sides of head with very narrow semi-lunar furrows at the level of reduced eyes, extending in temporal area in oval shallow depression connected with the frontal furrows in the level of the first pair of supraorbital pores. Genae subparallel and markedly narrowed to the neck, each with two to three laterally erected setae, one longer, the other very short, not in fixed position. Clypeus with the two pairs of setae, labrum with three pairs. Antennae elongated, robust, reaching the apex of elytra when stretched backwards. Submentum transversally furrowed, bearing a transverse row of six setae; Mandibles elongated but fairly stout, regularly curved; retinacle of the left mandible bidentate, retinacle of the right mandible tridentate. Mentum free, not fused with the submentum along the suture, with a pair of long labial setae and a pair of sensory pores; mentum tooth moderately bifid at apex, obtuse; ligula trapezoidal with the two very long setae at the middle of the truncated portion and three lateral setae on each side; paraglossae thin and moderately arcuate, densely pubescent on the inner margin, extending beyond the ligula (Fig. 3A).

Pronotum small-sized, nearly as long as wide, glabrous. Median furrow distinct, superficially impressed, not reaching basal margin. Lateral margins narrowly bordered, regularly curved, slightly narrowed to base. Anterior angles obtusely rounded, posterior rectangular, obtuse. Propleura visible in dorsal aspect in their middle part. Antero-lateral and baso-lateral setae present.

Elytra elongated, widened posteriorly, with maximum width in the apical fourth; humeral angles effaced; apical lobe and pre-apical sinuation evident. Disc moderately convex; striae completely absent, except juxta-scutallar striola and the apical recurrent stria; dorsal surface shiny, glabrous. Chetotaxy: one pair of basal setiferous pores near scutellum; three to six discal, asymmetrical setiferous pores and one pair of preapical pores; marginal umbilicate series of 8 pores aggregated, 4 setae of humeral group and 4 setae of apical group regularly situated along putative stria 8, close to the marginal furrow; latero-apical pore close to the apical stria; so called apical triangle complete (in the sense of Jeannel 1928). Abdominal sterna 4-6 with irregularly situated

setae along its posterior margins. Anal sternite of males and females with two pairs of setae.

Legs very long, markedly robust; femora with series of erected setae along margins of ventral sides; tibiae densely pubescent; protibae without external furrow; pro– and mesotarsi short, metatarsi elongate. First tarsomere of male protarsi distinctly dilated and produced at its internal margin.

Male genitalia (Figs 4A, B). Aedeagus: median lobe very elongate, narrow and slender, slightly sinuate in dorsal view, hooked at apex on the dorsal side. Basal bulb small, elongate, not inflated; sagittal carina very reduced in size. Endophallus with a small, sclerotized copulatory piece, close to the apex of the median lobe and in "anisotopic" position (in the sense of Jeannel, 1928).

Female genitalia (Fig. 3B): gonocoxite 1 with five short setae close to the distal margin; gonocoxite 2 short, rounded at apex, with three setae; sternal sensorial fovae small, with two short setae.

Etymology

Named after Orcus (Latin: Orcus), a Roman god of the underworld, punisher of broken oaths in Italic and Roman mythology. As with Hades, the name of the god was also used for the underworld itself.

***Orcusiella prokletijensis* Pavićević, Lohaj & Popović, sp. nov.**

(Figs 1–4)

Type series

Holotype, male labelled: Montenegro, Prokletije Mts., Bjelič massif, Maja Kolata, "Jama Kolektor" pit, 2052 m a.s.l., 20. 07. 2014 - 28. 07. 2015, traps, leg. M. Popović (white label, printed) / HOLOTYPUS *Orcusiella* gen. nov. *prokletijensis* sp. nov., D. Pavićević, R. Lohaj & M. Popović des. 2020 (red label, printed) (CDP).

Paratypes: 1 ♂ and 1 ♀, same data as holotype, 5 ♀♀, the same data as Holotype, but 25. 07. 2011 - 24. 07. 2012, traps, leg. Popović (CDP, CMP, CRL). All paratypes are labelled with white, printed locality labels and with red printed labels - PARATYPUS *Orcusiella* gen. nov. *prokletijensis* sp. nov., D. Pavićević, R. Lohaj & M. Popović des. 2020.

Description of holotype

TL 8.0 mm, L 8.6 mm. Color rufotestaceus, head, pronotum and basal antennomers dark redish; maxillae and palpomeres pale-yellow. Moderately shiny, with generally effaced microlines on the head and pronotum, more evident on the elytral surface, in the form of a transverse mesh pattern. Head and pronotum glabrous; elytra glabrous and shiny, without pubescence.

Head large, dorsoventrally depressed, wider and longer than pronotum, with its maximum width at the level of inseration of the anterior supraorbital setae. HL 1.70 mm, HW 1.30 mm (index HL/HW 1.31). Eyes totally absent. Genae obliquely convergent to neck constriction which is markedly evident; head at the level of the neck constriction with several transverse wavy-shaped wrinkles. Frontal furrows very deep, incomplete, ending before the level of posterior pair of supraorbital setae, curved in the middle and delimiting convex frontal area. Two pairs of supraorbital setae present; anterior pair located in the first third of head length, posterior pair before the neck constriction. Antennae long and slender, reaching the apex of elytra when stretched backwards, covered with short pubescence. AL 7.26 mm, length of antennal segments (from scape to terminal segment: 0.47, 0.50, 0.90, 1.10, 0.75, 0.73, 0.67, 0.63, 0.55, 0.48, and 0.48 mm. Mouth parts as in the genus description.

Prothorax small-sized. Pronotum narrower than the head, base slightly narrower than the anterior margin, almost as long as wide, PL 1.30 mm, PW 1.40 mm (index PL/PW 0.93). Disc moderately convex, with deep transverse wrinkles; median furrow distinct but superficially impressed, not reaching basal margin. Lateral sides regularly curved, slightly narrowed to the base and shortly sinuate before posterior angles; lateral margins not beaded; lateral groove completely effaced. Both anterior and posterior margins slightly concave in the middle; anterior and posterior angles obtusely rounded. Propleura visible in dorsal aspect from only in posterior third up to antero-lateral setae. Two pairs of setae present, first pair situated in the anterior sixth, second pair near posterior angles.

Elytra subovate elongated, convex, fused together, distinctly wider than prothorax, much longer than wide, widest behind posterior third, EL 4.20 mm, EW 2.30 mm (index EL/EW 1.83). Pre-humeral margins markedly oblique, humeri effaced. Disk markedly convex, striae superficial, almost vanished, except scutellar and apical striae which are more visible; dorsal surface irregularly and transversally wrinkled. Putative stria 3 with 6 long setae on both elytrons, 5 discal and 1 preapical. Ventral surface glabrous, abdominal ventrites 4-6 with 8-20 irregularly situated setae, anal vetrite with two pairs of setae, outer pair longer.

Legs very long, markedly robust; femorae with series of errected setae along margins of ventral sides; tibiae densely pubescent; protibae without external furrow; pro– and mesotarsi short, metatarsi elongate. Male protarsi with first tarsomerae dilated and produced at their internal margins, tarsal claws long and slender, slightly arcuate, without denticulation on the internal sides (Fig. 4D).

Aedeagus (Figs. 4A, B): median lobe very elongate, 1.8

mm long, narrow and slender, hooked at apex on the dorsal side, with apical part curved to left in dorsal view. Basal bulb small, elongate, not inflated; sagittal carina reduced in size. Endophallus with a small copulatory piece (0.25 mm long) in the shape of a folded lamella, only weakly sclerotized, situated close to apex of median lobe in lateral position. Parameres long and slender, length of parameres about half of length of aedeagus, left paramere more narrowed that right, each with four long setae at apex. Female genitalia (Fig. 3B): as in genus description.

Fig. 1. *Orcusiella prokletijensis* gen. et sp. nov. **A,** Paratype male; **B,** Paratype female.

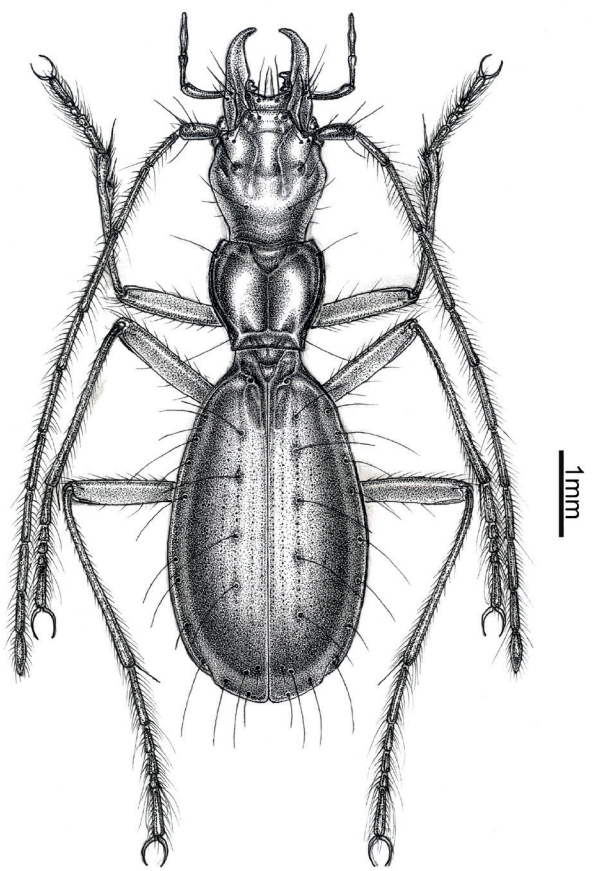

Fig. 2. *Orcusiella prokletijensis* gen. et sp. nov. Drawing of a paratype female with irregular number of elytral discal setae.

Variability

TL 7.3-8.6 mm, L 8.0-8.7 mm. Number of elytral setae 4-7 (3-6 discal plus one preapical), irregularly situated, one female specimen with different numbers of setae on left vs. right elytron (Fig. 2). Older specimens with abraded tips of mandibles as well as tarsal claws. Based on this we suppose that adult specimens can live for several years.

Etymology

Topotypic, referring to Prokletije Mts. where the new species was discovered.

Topographic location and ecology

Jama Kolektor pit (03-111, Jaskinia Kolektor, 42.49614°N, 19.89747°E). The entrance (Fig. 6) is situated at an altitude of 2052 m a.s.l. in a small valley adjacent to the northern part of Maja Kalata peak (2528 m a.s.l.). The cave is generally a vast old meander, over 600 m long, gradually descending into the massif, and has been explored to a depth of 93 m (Fig. 7). The name of the pit refers to its nature of collecting water from the surrounding slopes. During the wettest part of year, the pit is full of water and almost inaccessible. The main meander is a passage up to 20 m high and 7 m wide, with chimneys in the ceiling reaching a height of at least several dozen meters. There is a branched system of washed corridors rising up the massif, extending from the central part of the meander, which has been explored to the base of a steep chimney. The floor of the cave is covered with various types of sediments, both clay and gravel, sometimes reaching a thickness of several meters in cross-section. In corridors, on some fragments of the floor, there are numerous fungal infiltrates, forming specific, very fragile infiltration covers. At the lowest explored point of the cave, exploration was interrupted above a several-meter deep pit with strong air flow. Continued exploration is possible in the upper section, in the above-mentioned chimneys. The chimneys are probably connected with the caves located in the northern part of the Maja Kalata summit, at an altitude of 2400 m a.s.l., in the area of a large karst funnel with a diameter of about 200 m (http://www.prokletije.pl/Mapa/Pokaz/03/111, accessed on 31. 8. 2020).

The type series was collected during the years 2011 - 2012 and again in 2014 - 2015 by baited pitfall traps, 140 meters from the entrance. The traps were baited with rotten meat and vinegar was used as a preservation media. For this reason, collected specimens were not suitable for molecular analyses. Together with *Orcusiella prokletijensis* gen. et sp. nov., Leptodirine beetle *Anthroherpon taxi albanicum* (Apfelbeck, 1919) was collected.

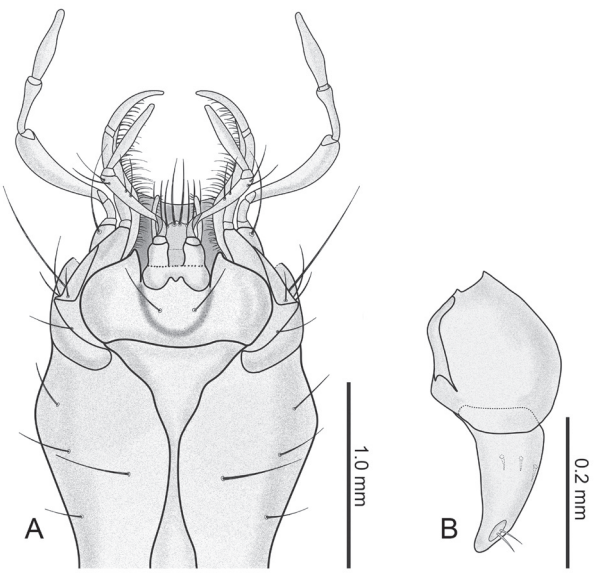

Fig. 3. *Orcusiella prokletijensis* gen. et sp. nov. **A,** Paratype female, head, ventral; **B,** Paratype female, apical segment of left gonostylus.

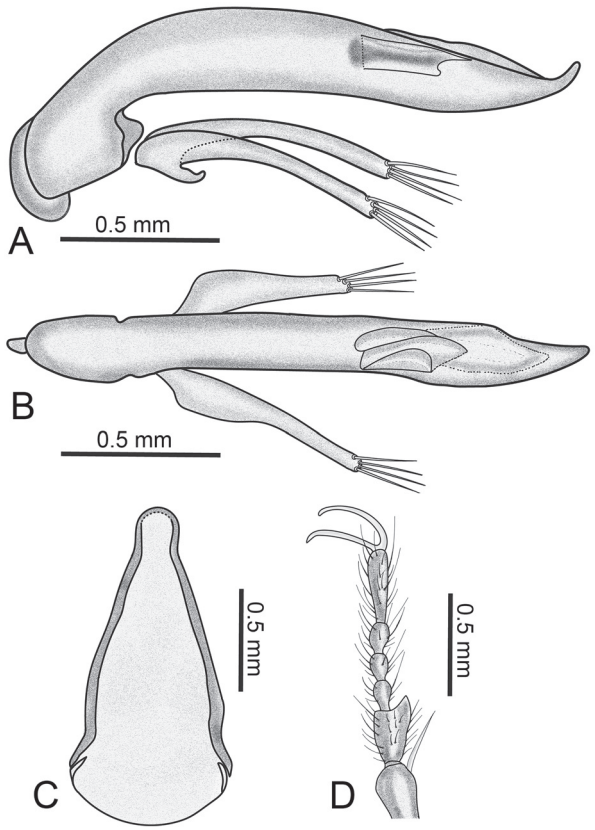

Fig. 4. *Orcusiella prokletijensis* gen. et sp. nov. **A,** Holotype male aedeagus left lateral view; **B,** Holotype male aedeagus dorsal view; **C,** Holotype male IX urite; **D,** Holotype male left protarsomera.

DISCUSSION

Subterranean beetles share common morphological characters, often referred to as troglomorphies, including sensory organs (touch chemoreceptors, hygroreceptors, thermoreceptors, pressure receptors), elongation of the appendages and foot modifications (elongated and sharp claws), pseudophysogastry, eye reductions, pigment and wing reductions and increased egg volume (Christiansen 1992).

According to the traditional view, virtually every species of subterranean Coleoptera developed its' troglomorphic characters independently (Faille et al. 2010; Ribeira et al. 2010). Recent work on the Pyrenean, western Mediterranean and Alpine subterranean Trechini beetles has changed this assumption by demonstrating a single origin for ancient and morphologically diverse clades of exclusively subterranean species (Faille et al. 2010, 2011, 2013).

Based on recent molecular analyses (Faille et al. 2013), most of the subterranean Trechini have an independent origin and are related to epigean taxa of the same geographical

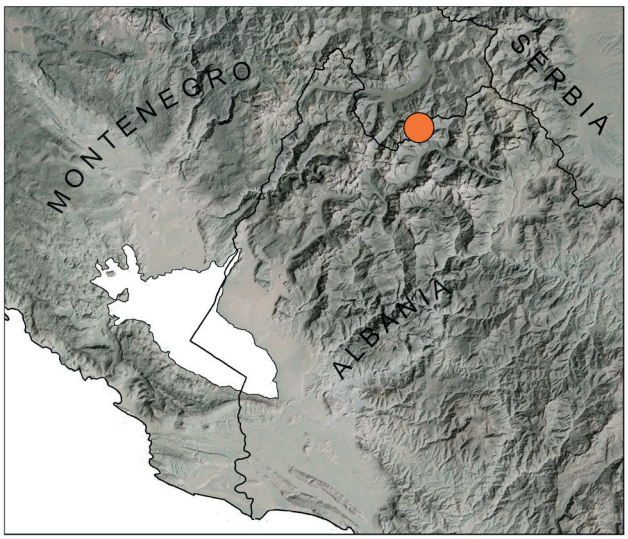

Fig. 5. Prokletije Mts., orange dot marks the position of the Kolektor pit.

area. At least three large monophyletic clades of exclusively subterranean species were confirmed: the Pyrenean lineage, a lineage including subterranean taxa from the eastern Alps and the Dinarides, and the lineage including the species rich genus *Anophthalmus* from the southeastern Alps. Additionally, smaller lineages, comprising of several species or genera, were also recognized. No matter the size, all lineages developed similar phenotypes independently, showing extensive morphological convergence or parallelism.

The first classification of subterranean Trechini was proposed by the famous French entomologist René Jeannel (1879-1965) in his masterpiece "Monographie des Trechinae, Les Trechini cavernicoles" (1928). Based on external and internal morphology (shape of the body, chaetotaxy and male genitalia), Dinaric subterranean taxa were divided into four phyletic lines: *Duvalius*-phyletic line, represented by a single genus *Duvalius* Delarouzée, 1859 s.l., *Neotrechus*-phyletic line, represented by a single genus *Neotrechus* J. Műller, 1913, *Typhlotrechus*-phyletic line represented by a single genus *Typhlotrechus* J. Műller, 1913, and finally, *Aphaenops*-phyletic line, represented by a group of genera with the so called aphaenopsoid habitus. In the same work, Jeannel also proposed a division of genera into two groups, based on differences in male genitalia, especially with respect to the internal structures of the aedeagus. In the so-called isotopic group, the endophallus has a symmetric copulatory piece in a ventral position (i.e. "série phylétique de *Duvalius*"), whereas in the so-called anisotopic group the copulatory piece is asymmetric and placed in a lateral position ("série phylétique de *Neotrechus*, *Typhlotrechus* and *Aphaenops*"). The correctness of this division has also been confirmed by

molecular analysis, where isotopic Trechini in the traditional sense were confirmed as monophyletic with strong statistical support (Faille et al. 2013; Delić et al. 2020).

In contrast with the isotopic group, which forms a monophylum, Dinaric anisotopic genera form a polyphyletic group (Faille et al. 2019). This result questions the extant -Jeannel's systematics, but at the same time, it is fully expected bearing in mind that at the time only 3 of 15 anisotopic genera from the Dinaric Karst were known.

In the Dinarides, all known genera, except for the morphologically highly polymorphic genera *Duvalius* and *Anophthalmus* are considered to be anisotopic genera. Some *Duvalius* representatives from the Dinarides are depigmented and blind, and inhabit subterranean habitats (caves, deep soil or MSS); but others are epigean, and live in forest litter and alpine pastures, and are slightly pigmented and/or with reduced eyes. In contrast, most of the anisotopic Trechini genera from the Dinarides (16 genera including newly recognized genus, *Orcusiella* gen. nov.), except for the genera *Neotrechus, Orotrechus* and *Typhlotrechus,* are represented by a morphologically well distinguished group. The group consists of morphologically derived, so called aphaenopsoid (also aphaenopsian) Trechini, of the former "série phylétique *d'Aphaenops*" sensu Jeannel. The common morphology of these genera is characterized by a more or less elongated head and pronotum, enlarged mandibles, and with ovoid and basally strongly narrowed elytra, which are distinctly wider than the fore body. This group was also stated to be „ultra-evolved", „archaic", or even „high or hyper-specialized" (Jeannel 1928; Casale and Laneyrie 1982; Casale et al. 2012; Luo et al. 2018). Such morphological characteristics are also present in other groups of the Balkan, Pyrenean, American and Asian specialized Trechini (Barr 1979; Belousov and Dolzhansky 1994; Faille et al. 2010; Luo et al. 2018; Delić et al. 2020), and is probably a consequence of directional selection driving the convergent evolution of elaborated traits in subterranean fauna. However, such morphological derivations still lack a proper evolutionary or functional explanation. For example, ground beetles from the genus *Cychrus* Fabricius, 1794 and subgenus *Damaster* Kollar, 1836 of the genus *Carabus* Linné, 1758 have a similarly modified fore body. Their narrowed head and pronotum, elongated and sharp mandibles with teeth are dietary specializations, used for predation of snails. Their specialized body shape allows them to penetrate deeply into usually narrow snail shells.

Fig. 6. Entrance of the Kolektor pit.

Neotrechus phyletic line sensu Jeannel (1928) included, as well as the Dinaric genus *Neotrechus*, also the Alpine genus *Orotrechus* J. Műller, 1913 (with one species *muellerianus* Schatzmayr, 1907 present in the Northern Dinarides, Trieste) and the Caucasian/Anatolian complex of genera *Nannotrechus* Winkler, 1926 (Jeannel 1928; Belousov 1998). This group of genera is characterized by dilatation of only the first male protarsomera (males of some taxa of *Nannotrechus* complex have simple first protarsomera, not dilated, similarly as females). The *Neotrechus* lineage of Jeannel was, therefore, accepted by all subsequent authors. However, recent molecular studies (Faille et al. 2013) did not support the assumed close relationship between the genera *Orotrechus* and *Neotrechus*, although this lack of support does not allow one to completely discard traditional hypotheses.

Based on the presented morphological features, and geographical origin, we hypothesize that *Orcusiella* gen. nov. is related to the genus *Neotrechus*. Both genera share many similarities, namely a pronotum with both an anterior and posterior pair of setae, mentum tooth bifid at apex, only the first male protarsomera is dilated and the shape of male genitalia – aedeagus long and slender, apex hooked, with copulatory piece in "anisotopic position", parameres long and slender, each with four apical setae. The main differences between the two genera are a humeral group of setae that are aggregated in *Orcusiella* gen. nov. versus not aggregated in *Neotrechus*, elytra with three to six pairs of dorsal setae in *Orcusiella* gen. nov versus two pairs in *Neotrechus*. *Orcusiella* gen. nov. resembles the Alpine genus *Aphaenopidius* from the isotopic Trechini group (see Delić et al. 2020 for *Aphaenopidius*). Prokletije Mountains and their nearby sur-

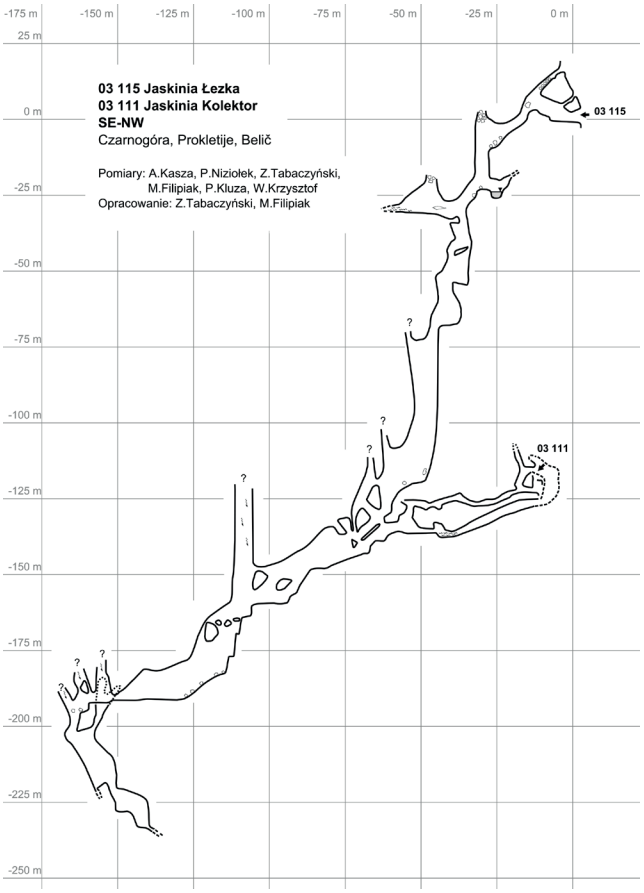

Fig. 7. Cross-section of Łezka and Kolektor pits.

roundings are inhabited by at least three *Neotrechus* species or subspecies: *N. lonae* s.l. G. Műller, 1914, *N. malissorum* G. Műller, 1914 and *N. suturalis pentheri* Winkler, 1926. All three mentioned *Neotrechus* representatives possess pubescent temporae, while *Orcusiella* gen. nov. has temporae with two or three setae.

Generally, very little is known about the bionomy of the Dinaric subterranean Trechini. The general assumption is that they are ecologically specialized predators, inhabiting various types of subterranean habitats. Genera occurring in the Dinarides, that do not share the so-called aphaenopsoid morphology (*Typhlotrechus*, *Neotrechus, Anophthalmus* and *Duvalius*) are frequently very abundant at cave entrances, under stones, in wet clay or debris. Similarly, these genera were also found outside caves, in forests or high-altitude habitats, under deeply inserted stones, or in MSS (see among others Jeannel 1928; Janák 2009; Janák and Moravec 2018).

On the other hand, representatives sharing the aphaenopsoid morphology are very rarely found. Most known taxa, with the exception of *Acheroniotes* (Lohaj and Lakota 2010), *Dalmataphaenops* (T. Delić, B. Jalžić, own observations, pers. comm.) and *Aphaenopsis apfelbecki* (Ganglbauer, 1891) are mostly known from only a few individuals caught by hand or, as in several cases, "accidentally" by long-term pitfall trapping. Common external morphology – a strongly flattened body with very long sensorial setae on the elytra and/or head and pronotum can indicate that these taxa are inhabitants of narrow spaces like fissures, slots, rock debris and MSS (Mesovoid Shallow Substratum or originally *Milieu Souterrain Superficiel* sensu Juberthie et al. 1980a, b, 1981). We suppose that the conditions (temperature, humidity) and the availability of food here is more stable than in the large cave spaces that they visit only occasionally. However, the large cave spaces are the only parts of the subterranean domain which are relatively easily visited by researchers. Therefore, most of our knowledge on these animals is based on findings from the later habitats. The morphology of their mandibles, which are very long and slender, apically pointed and usually with robust teeth at the base of the right mandible, indicates that they are active predators (Lakota et al. 2010; Lohaj and Lakota 2010; Casale et al. 2012). Interestingly, ecomorphological convergent evolution between Dinaric *Adriaphaenops* and Pyrenean *Hydraphaenops* species (eg. *H. vasconicus, H. navaricus, H. elhersi...*) provides evidence of adaptive processes as important drivers of phenotypic conservatism. Further research could develop these interesting topics.

Altogether, the Dinaric subterranean Trechini are now classified into 19 genera, 15 of them endemic, comprising ca 110 described species[1] (Belousov 2017; Lohaj and Delić 2019). They can be separated using the Identification key provided below.

Key to the identification of subterranean trechine genera of the Dinaric range

1(6) First tarsomere of male protarsi dilated.

2(5) Humeral group of setae not aggregated, first seta moved to elytral stria 7. Head smaller, usually narrower than pronotum.

3(4) Protibiae furrowed, glabrous. Small to large sized, 4-10.5 mm. 24 species in Bosnia & Hercegovina, Croatia, Montenegro and Albania ..... *Neotrechus* G. Műller, 1913

4(3) Protibiae not furrowed, pubescent. Small to medium sized, 3.2-7.1 mm. Ca 36 species in Italy, Slovenia and Austria, 1 in the Dinarides (Trieste) .... *Orotrechus* G. Műller, 1913

5(2) Humeral group of setae aggregated, all 4 setae regularly situated along putative stria 8. Head very large and robust, wider and longer than pronotum. Large sized, 8-8.6

[1] Second author (RL) and Teo Delić (Ljubljana, Slovenia) examined at least six new Dinaric Trechinae species from genera *Adriaphaenops*, *Jalzicaphaenops, Minosaphaenops* and *Scotoplanetes* from Bosnia & Hercegovina, Croatia and Montenegro. A study of these species including molecular analyses is in progress.

mm. Montenegro, Prokletije Mts. .... *Orcusiella* gen. nov.

6(1) First and second tarsomere of male protarsi dilated.

7(8) Anterior part of protibiae glabrous. Small to medium sized, 4.7-8 mm. Two species in Slovenia and Croatia ..... *Typhlotrechus* G. Műller, 1913

8(7) Anterior part of protibiae more or less pubescent.

9(12) Aedeagus with symmetric copulatory piece in ventral position, belonging to the "isotopic" group. Eyes partially reduced or completely missing.

10(11) Humeral group of setae aggregated. Species partially or completely depigmented. Habitus not aphaenopsoid. Small to large size, 4 – 9 mm. More than 350 described species, from Spain, France, Alps, Carpathians, Caucasus, Middle East and Iran, reaching the Tien Shan Mountains in China, ca 35 species distributed along the Dinarides .... *Duvalius* Delarouzée, 1859

11(10) Humeral group of setae not aggregated, first humeral seta located at the level of the second seta or between the level of the second and third humeral seta. Small to medium size, 3-7 mm. More than 50 described species distributed in Italy, Slovenia, Austria and Croatia, ca 20 species in the Dinarides ..... *Anophthalmus* Sturm, 1844

12(9) Aedeagus with asymmetric copulatory piece placed in the lateral position, "anisotopic" group. Eyes totally absent, species completely depigmented, habitus aphaenopsoid.

13(20) Pronotum with posterior pair of long setae situated near the hind angles.

14(15) Pronotal disc with pair of setae near the median furrow, situated in the anterior fifth, anterior angles of pronotum not protruding, obtuse, elytra with three pairs of setae (two discal and one preapical), without microchaetae. Small size, 3.9 mm. One species in Central Croatia, near Rakovica ..... *Jalzicaphaenops,* Lohaj & Lakota, 2010

15(14) Pronotal disc without pair of setae.

16(19) Head and pronotum with sparse pubescence.

17(18) Elytra with 3–5 pairs of discal setae, body sparsely pubescent. Submentum with 2-3 pairs of setae, cheeks with sparse pubescence. Small size, 3.4-4.6 mm. Three species in Montenegro, Hercegovina and Serbia .... *Acheroniotes,* Lohaj & Lakota, 2010

18(17) Elytra with 2 pairs of discal setae, body densely pubescent. Submentum with four pairs of setae, cheeks with dense pubescence. Small size, 3.7-3.9 mm. One species in Serbia, Tara, Mts. .... *Velesaphaenops* Ćurčić & Pavićević, 2018

19(16) Head and pronotum glabrous, without pubescence. Small size, 4.3-4.4 mm. One species in Croatia, Gorski Kotar ..... *Croatotrechus* Casale & Jalžić, 1999

20(13) Hind angles of pronotum without setae.

21(24) Head and pronotum pubescent.

22(23) Elytra with 3-4 pairs of setae (2-3 discal and one preapical), without microchetae, densely pubescent. Small to medium size: 3.8-5.0 mm. Thirteen species in Bosnia and Hercegovina, Montenegro and Albania .... *Adriaphaenops* Noesske, 1928

23(22) Elytra with 5 pairs of setae, 4 discal and one preapical, with additional microchetae, almost glabrous. Medium size, 5.1-5.7 mm. Two species in Montenegro and Croatia ..... *Minosaphaenops* Quéinnec, 2008

24(21) Head and pronotum glabrous.

25(26) Elytra densely pubescent. Largest in size, 12.3-14 mm. One species in Croatia, Velebit Mts., Crnopac .... *Velebitaphaenops* Casale & Jalžić, 2012

26(25) Elytra except sensorial setae glabrous.

27(28) Elytra with 7-11 setae in stria 3 and 3-6 setae in stria 5. Mentum without median tooth. Medium size, 6.1-6.8 mm. Two species in Hercegovina and Montenegro .... *Scotoplanetes* Absolon, 1913

28(27) Elytra with 3 – 4 setae in stria 3, stria 5 without setae. Mentum with simple or bifid median tooth.

29(32) Head wide, robust, globe-shaped, mentum with bifid median tooth.

30(31) Elytra with three pairs of setae (two discal and one preapical). Small to medium size: 4.5-6 mm. Two species in Bosnia ..... *Aphaenopsis* Müller, 1913

31(30) Elytra with four pairs of setae (three discal and one preapical). Large size, 9-10.5 mm. One species in Croatia, Biokovo Mts. ..... *Dalmataphaenops* Monguzzi, 1993

32(29) Head elongate, mentum with simple median tooth.

33(34) Elytra strongly narrowed on basis, humeri effaced. Hind angles of pronotum not protruding, obtuse. Small size, 5.1-5.3 mm, Two species in Croatia, Mosor and Biokovo Mts. ..... *Derossiella* Quéinnec, 2008

34(33) Elytra ovoid, with distinct humeri. Hind angles of pronotum protruding, acute. Medium size, 7.3-8.0 mm. One species in Albania, Rrëshen .... *Albanotrechus* Casale & Guéorguiev, 1994

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