

Research article

[urn:lsid:zoobank.org:pub:69DF8A05-F8E2-4EEC-9A52-4018F22E81ED](https://doi.org/10.5852/ejt.2020.717.1103)***Nemaspela borkoae* sp. nov. (Opiliones: Nemastomatidae),
the second species of the genus from the Dinaric Karst**Peter KOZEL^{1,*}, Teo DELIĆ² & Tone NOVAK³^{1,3}Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor,
Koroška 160, SI-2000 Maribor, Slovenia.¹Karst Research Institute ZRC IZRK SAZU, Titov trg 2, SI-6230 Postojna, Slovenia.²SubBio Lab, Department of Biology, University of Ljubljana, Jamnikarjeva ulica 101, SI-1000
Ljubljana, Slovenia.*Corresponding author: peter.kozel@um.si²Email: teo.delic@bf.uni-lj.si³Email: tone.novak@guest.um.si¹[urn:lsid:zoobank.org:author:8C33627F-2D3D-4723-A059-B87462535460](https://doi.org/10.5852/ejt.2020.717.1103)²[urn:lsid:zoobank.org:author:D38183EA-6034-4634-8DD1-45FF9C73D2B4](https://doi.org/10.5852/ejt.2020.717.1103)³[urn:lsid:zoobank.org:author:F6B51342-4296-473E-A3E8-AB87B0655F49](https://doi.org/10.5852/ejt.2020.717.1103)

Abstract. *Nemaspela* Šilhavý, 1966 (Opiliones: Nemastomatidae) is a genus of exclusively troglobiotic harvestmen species inhabiting caves in the Crimea, Caucasus and Balkan Peninsula. In this paper, *Nemaspela borkoae* sp. nov., recently found in four caves in Montenegro, is described. The new species is characterized by its small body, 1.5–2.1 mm long, and very long, thin appendages, with legs II about 15 times as long as the body. Although very similar, *Nemaspela ladae* Karaman, 2013 and *N. borkoae* sp. nov. can be easily distinguished by the terminally rounded vs conical glans, straight vs conspicuously ventrally bent pedipalp tarsus on its proximal portion and pedipalp tarsus measuring about $\frac{1}{2}$ vs $\frac{2}{3}$ tibia length. *Nemaspela ladae* and *N. borkoae* sp. nov. constitute the western *Nemaspela* group, both missing the male cheliceral apophysis present in all species of the eastern *Nemaspela* group from the Crimea and Caucasus, except in *N. femorecurvata* Martens, 2006. However, according to the glans morphology, *N. borkoae* sp. nov. seems much more closely related to several species from the Caucasus than to *N. ladae* from the Balkan Peninsula. We speculate that *N. ladae* and *N. borkoae* sp. nov. might originate from two epigeal ancestral lineages.

Keywords. Arachnids, *Hadzinia*, speleobiology, the Balkans, western *Nemaspela* group.

Kozel P., Delić T. & Novak T. 2020. *Nemaspela borkoae* sp. nov. (Opiliones: Nemastomatidae), the second species of the genus from the Dinaric Karst. *European Journal of Taxonomy* 717: 90–107. <https://doi.org/10.5852/ejt.2020.717.1103>

Introduction

During the past two centuries, following the establishment of speleobiology – the biology of subterranean habitats – in 1832 (Polak 2005; Sket 2012), an immense effort has been invested in the discovery of specialized

subterranean species. By the early 2000s, almost 1000 species adapted for living in these habitats, which seem simple and resource deprived, have been recognized in the western Dinaric Karst alone (Sket *et al.* 2004). The area has also been recognized as globally unique and as a hotspot for richness in subterranean species (Culver & Sket 2000; Culver *et al.* 2006); many new species have been discovered and scientifically described in the last two decades. In recent times, improvements in caving equipment and techniques have enabled access to deeper caves and allowed more time for fauna collection, along with the discovery of new species (e.g., Lukić *et al.* 2010; Andersen *et al.* 2016; Antić 2018; Delić *et al.* 2019; Trontelj *et al.* 2019).

New data on subterranean fauna revealed some peculiar distribution patterns that include groups of closely related organisms being distributed over various geological formations and geographic regions that are hundreds or even thousands of kilometers apart (e.g., Pérez-González *et al.* 2017; Taiti *et al.* 2018; Inäbnit *et al.* 2019; Lukić *et al.* 2019). Recognition of such patterns raises questions about the origin, dispersal potential and shared ancestry of animals that had been assumed to exhibit limited dispersal abilities. A similar spatial pattern has been found in the subterranean harvestman genus *Nemaspela* Šilhavý, 1966 (Opiliones: Dyspnoi: Nemastomatidae).

Once established (Simon 1872), the taxonomy of Nemastomatidae Simon, 1872 gradually progressed over the next hundred years (cf. Schönhofer 2013). This family, with a disjunctive Holarctic distribution, is currently represented by the two subfamilies: the Amphypacific Ortholasmatinae Shear & Gruber, 1983 and the predominantly western Palearctic Nemastomatinae Simon, 1872 (Shear & Gruber 1983; Gruber 2007; Schönhofer 2013; Zhang & Martens 2018). The taxonomic revision of the family was stepwise, with many contributing authors (Redikorzev 1936; Šilhavý 1956, 1966; Kratochvíl 1958; Ljovuschkin & Starobogatov 1963; Gruber & Martens 1968; Gruber 1976; Martens 1978; Shear & Gruber 1983). Although Grese (1911, under *Nemastoma*) described the first *Nemaspela* species, Ljovuschkin & Starobogatov (1963) provided the first penis drawings of the three *Nemaspela* (Ljovuschkin & Starobogatov 1963, under *Burešiolla*) species. In later works, Martens (2006), Chemeris (2009, 2013) and Karaman (2013) provided drawings and photographs of all known species of *Nemaspela*.

Species of *Nemaspela* have been reported from three geographically distant karstic regions: the Caucasus, the Crimea, and the Dinaric Karst. In this contribution, we therefore discuss two geographically limited *Nemaspela* groups: the eastern group distributed in the Caucasus and the Crimea (Martens 2006; Chemeris 2009, 2013), and the western one distributed in the Dinaric Karst (Karaman 2013). Based on the recent literature, there are no records of *Nemaspela* from the intermediate territory. Chemeris (2009) provided the first revision of the genus *Nemaspela* Šilhavý, 1966 in its main distribution area, i.e., the Caucasus and Crimea. The following seven species of the genus from the Caucasus and Crimea have been described: *Nemaspela caeca* (Grese, 1911) (Grese 1911), *N. abchasica* (Ljovuschkin & Starobogatov, 1963) and *N. sokolovi* (Ljovuschkin & Starobogatov, 1963) (Ljovuschkin & Starobogatov 1963), *N. birsteini* Ljovuschkin, 1972 (Ljovuschkin 1972), *N. femorecurvata* Martens, 2006 (Martens 2006), *N. kovali* Chemeris, 2009 (Chemeris 2009) and *N. gagrica* Chemeris, 2013 (Chemeris 2013). Recently, *Nemaspela ladae* Karaman, 2013 (Karaman 2013), the eighth species of the genus, was described from Bosnia and Herzegovina. In addition, it was the first *Nemaspela* representative to be found in the Dinaric Karst, more than 1000 km distant (Karaman 2013).

Here we describe the second species of *Nemaspela* from the Dinaric Karst. Recent speleobiological sampling resulted in the discovery of four new cave localities for *Nemaspela* in the mountainous area of Krivošije and Lovćen, Montenegro. The newly discovered localities are about 145 km in a straight line from the locality in Bosnia and Herzegovina where the first Dinaric species of *Nemaspela* was found. The discovery and description of the new species, *Nemaspela borkoae* sp. nov., raise questions about the historical biogeography of the genus and relations among the extant species of *Nemaspela*.

Material and methods

The habitat

In September 2014, the first specimen of a new species of *Nemaspela* was found in the “Dvogrla jama” cave (synonym: Njegoš Pećina) in Njeguši, Lovćen, Montenegro (42.43301° N, 18.83159° E; 873 m a.s.l.). The specimen was collected by hand on a wet flowstone wall in the cave section called “Veliki fosilni kanal”, at a depth of about 50 to 80 m (cave plan available at Speleologija.me 2020: www.speleologija.me). Further specimens were collected in 2018 and 2019 in three nearby localities. Three specimens were found on damp vertical rocks coated with moonmilk-like surface (Engel *et al.* 2013) in the “Moonmilk pitch” (at an approximate depth of 180 m) of the “PT4” cave (synonym: Pištet 4 cave) in Kameno more, Krivošije, Montenegro (42.55183° N, 18.73864° E; approximately 800 m a.s.l.) (Binding 2010, 2011). One specimen was found in the final chamber, the “Syphon chamber”, of the cave “Vodna jama” in Dragaljsko polje, Grahovo, Montenegro (42.60762° N, 18.68783° E; 615 m a.s.l. (diagram of the cave available in Lakota *et al.* 2010). The specimen was found walking on a vertical wet flowstone wall covered with organic sediment at an approximate depth of 135 m. The last two specimens were found in the “Pala Skala” cave in Zverinjačke rupe, Lovćen, Montenegro (42.36908° N, 18.83575° E; 1328 m a.s.l.), walking in a wet flowstone meander at a depth of 370 m. All collected specimens were found in wet habitats in close proximity to flowing water. The material is deposited in the Central Collection of Opiliones at the Slovenian Museum of Natural History (PMSL-Opiliones), Ljubljana. PK&TN: Peter Kozel & Tone Novak identification code.

Taxonomic investigation

Dissections were performed under a Nikon stereo microscope. External morphology and genitalia were studied under a Nikon Eclipse E800 compound microscope (Nikon, Japan), mounted with a digital Net DN100 camera and processed with NIS Elements ver. 4.20 software. Illumination from above was combined with classic microscopy procedures. Digital images captured at different focal planes were stacked using Helicon Focus ver. 7.5.8. Images were manipulated for optimal quality using various applications in GIMP ver. 2.10.8. Drawings were made under an Olympus CH30 microscope (Olympus, Japan), using the drawing tube. For observation, the specimens were preserved in glycerol. Measurements are in millimeters, if not otherwise indicated.

Results

Class Arachnida Lamarck, 1801
Order Opiliones Sundevall, 1833
Suborder Dyspnoi Hansen & Sørensen, 1904
Family Nemastomatidae Simon, 1872
Subfamily Nemastomatinae Simon, 1872
Genus *Nemaspela* Šilhavý, 1966

Nemaspela borkoae sp. nov.

urn:lsid:zoobank.org:act:D4139CAA-5F9A-4766-9FE5-6DABFA7BF26C

Figs 1–5, Table 1

Etymology

The species name *borkoae* is dedicated in honor of Špela Borko (Ljubljana), enthusiastic speleologist and speleobiologist, who collected the first specimen of this species.

Table 1. *Nemaspela borkoae* sp. nov. holotype, ♂ (allotype in parentheses). Length of appendage-segments in millimeters. In the rows for the legs I–IV, the upper row indicates the length of the segments and the lower row the number of pseudoarticles, and for tarsus the number of tarsomeres.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total length
Pedipalp	0.79 (0.70)	2.31 (2.39)	2.10 (2.33)	1.42 (1.51)	–	0.95 (0.93)	7.57 (7.86)
Leg I	0.24 (0.23)	4.55 (4.03)	0.73 (0.65)	3.08 (2.58)	6.03 (5.59)	3.08 (2.95)	
		20 (13)	–	–	8 (6)	17 (13)	17.71 (16.03)
Leg II	0.28 (0.27)	6.49 (6.83)	0.75 (0.76)	7.22 (4.53)	11.68 (12.48)	4.48 (5.67)	
		27 (23)	–	16 (0)	32 (31)	15 (28)	30.90 (30.54)
Leg III	0.28 (0.27)	4.60 (3.98)	0.74 (0.66)	3.03 (2.65)	6.37 (5.20)	3.57 (2.60)	
		16 (12)	–	–	6 (6)	15 (15)	18.59 (15.36)
Leg IV	0.26 (0.27)	6.73 (5.43)	0.76 (0.71)	3.96 (3.48)	7.11 (7.54)	4.28 (3.80)	
		19 (16)	–	–	7 (8)	15 (14)	23.10 (21.23)

Diagnosis

Small (1.5–2.1) long-legged *Nemaspela* species of the western *Nemaspela* group, without male cheliceral apophysis, and with disproportionately long pedipalp trochanter and tarsus. Pedipalp trochanter straight, pedipalp tarsus strongly (♂) bent ventrally. Glans with sparse minute spines gradually tapering into a short, slightly ventrally bent stylus. According to recent knowledge, endemic to the Krivošije karst plateau and Mt. Lovćen, Montenegro.

Material examined

Holotype

MONTENEGRO • ♂; Lovćen, Njeguši, Dvogrla jama; 42.43301° N, 18.83159° E; 873 m a.s.l.; 10 Sep. 2014; Špela Borko leg.; the cave section of “Veliki fosilni kanal”, depth: 50–80 m, on wet flowstone, collected by hand; PMSL-Opiliones-PK&TN 4/2019.

Paratypes

MONTENEGRO • ♀ allotype; Krivošije, Kameno more, PT4; 42.55183° N, 18.73864° E; approximately 800 m a.s.l.; 3 May 2018; Špela Borko leg.; the cave section of “Moonmilk pitch”, at an approximate depth of 180 m, on damp vertical rocks coated with moonmilk-like surface, collected by hand; PMSL-Opiliones-PK&TN 7/2019 • 2 ♂♂; same collection data as for preceding; 3 May 2018; Teo Delić leg.; PMSL-Opiliones-PK&TN 2/2019, PMSL-Opiliones-PK&TN 3/2019 • 1 ♀; Grahovo, Dragaljsko polje, Vodna jama; 42.60762° N, 18.68783° E; 615 m a.s.l.; 14 May 2019; Teo Delić leg.; the cave section of “Syphon chamber”, on a vertical wet flowstone wall covered with organic sediment, at an approximate depth of 135 m, collected by hand; PMSL-Opiliones-PK&TN 1/2019 • 1 ♂, 1 juv.; Lovćen, Zverinjačke rupe, Pala skala; 42.36908° N, 18.83575° E; 1328 m a.s.l.; 17 May 2019; Teo Delić leg.; on a wet flowstone meander, at a depth of 370 m, collected by hand; PMSL-Opiliones-PK & TN 8/2019.

Description

Male, holotype

BODY. Body length 1.57, width 0.86, body tender, with scutum magnum. Body color light beige (Fig. 1A–C). Dorsum weakly sclerotized, with dense, short mucronate, cuticular microtubercles (microtrichia) covering most of the cephalothorax and abdomen. Supracheliceral lamellae (Fig. 1D) large, with straight frontolateral margins and mammillary tubercles, similar to those in *N. ladae* (Karaman 2013; fig. 14). Ocular tubercle low but well pronounced, wider than long, starting about half its length behind anterior

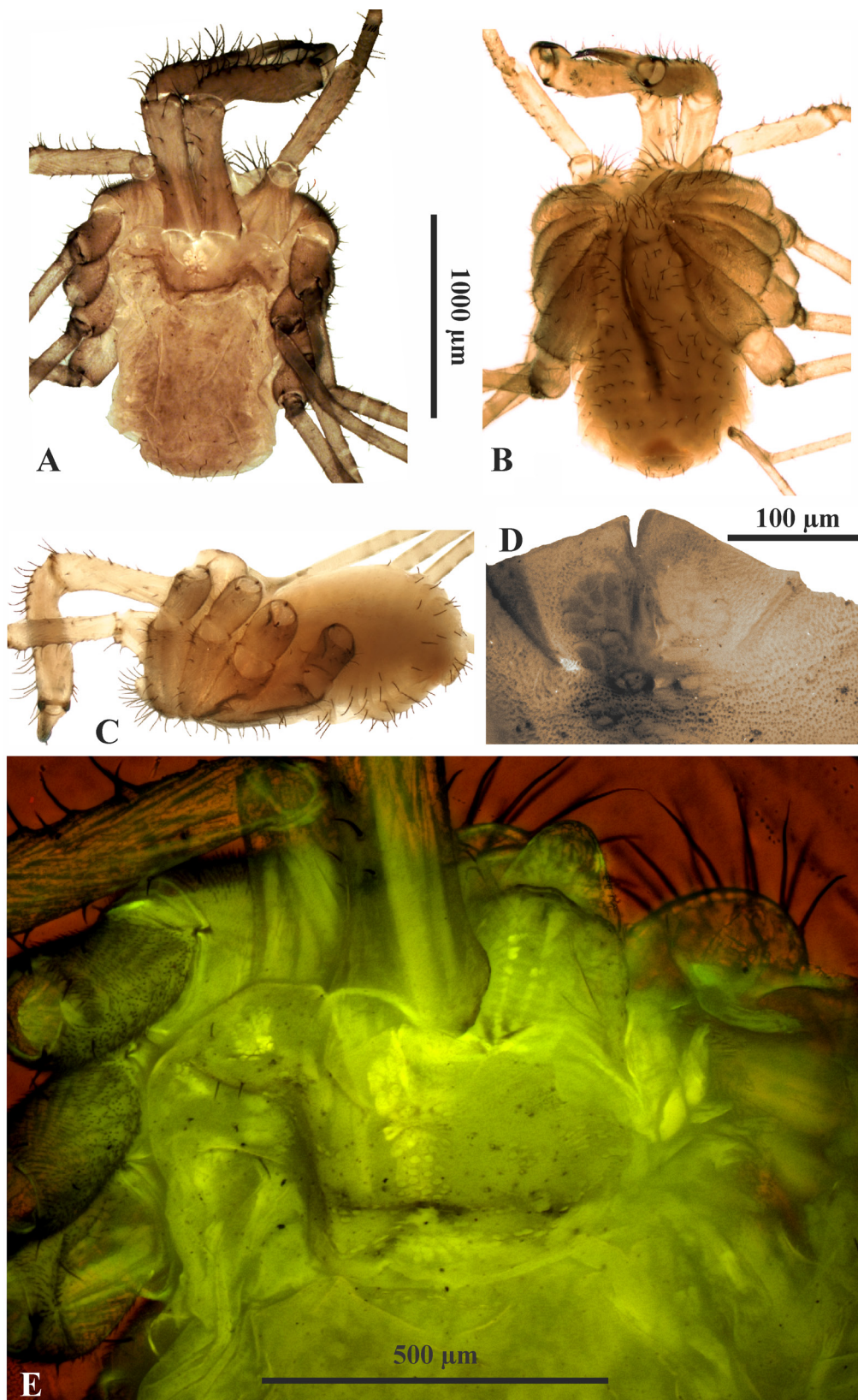


Fig. 1. *Nemaspela borkoae* sp. nov., ♂ holotype (PMSL-Opiliones-PK&TN 4/2019). A–C. Body, dorsal, ventral and lateral views (dry preparation). D. Supracheliceral lamellae. E. Body, dorsal view (fluorescence microscopy).

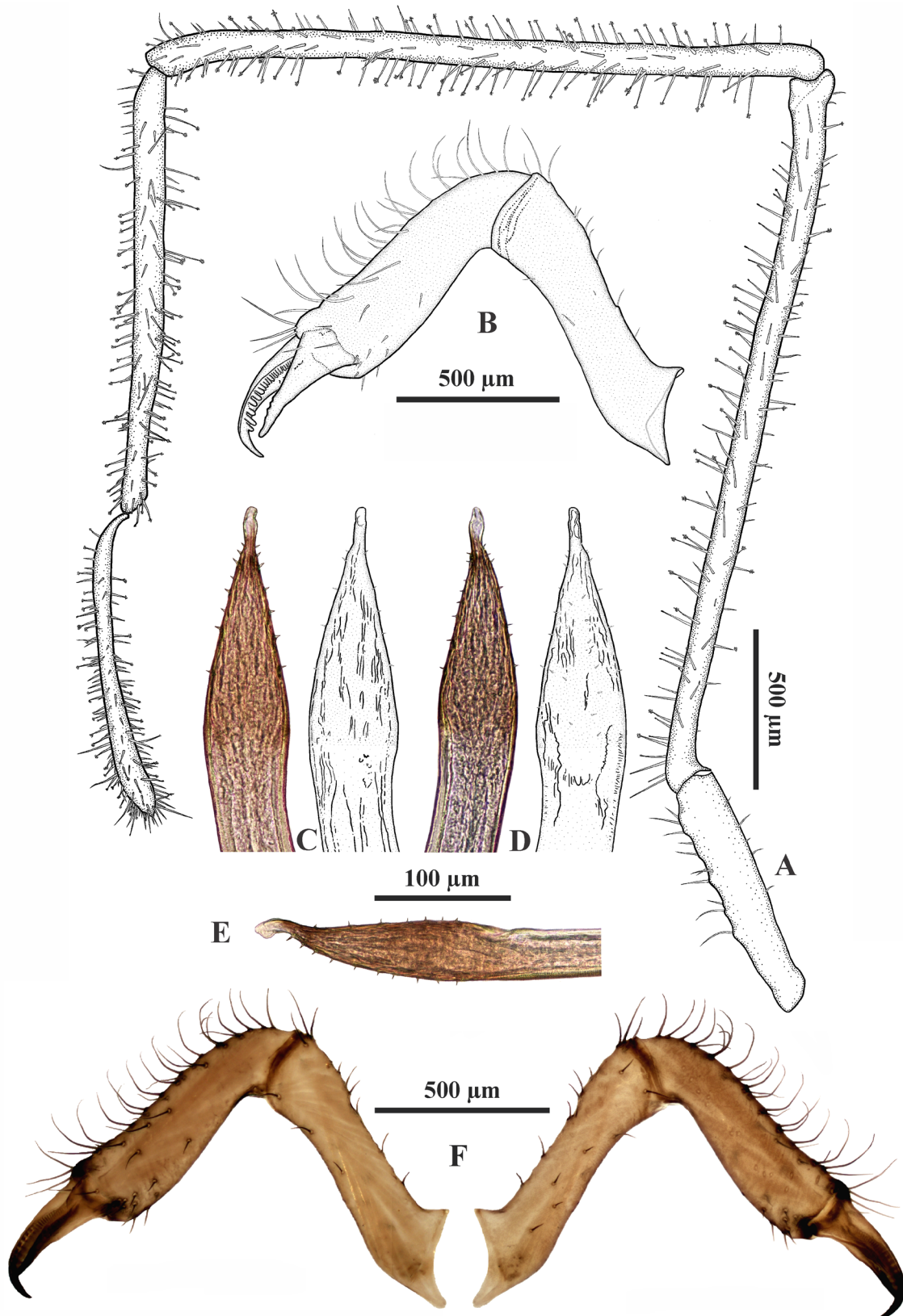


Fig. 2. *Nemaspela borkoae* sp. nov., ♂, holotype (PMSL-Opiliones-PK&TN 4/2019). **A.** Right pedipalp, medial view. **B.** Right chelicera, medial view. **C.** Penis, ventral view. **D.** Penis, dorsal view. **E.** Penis, lateral view. **F.** Right chelicera, medial (left) and lateral (right) views.

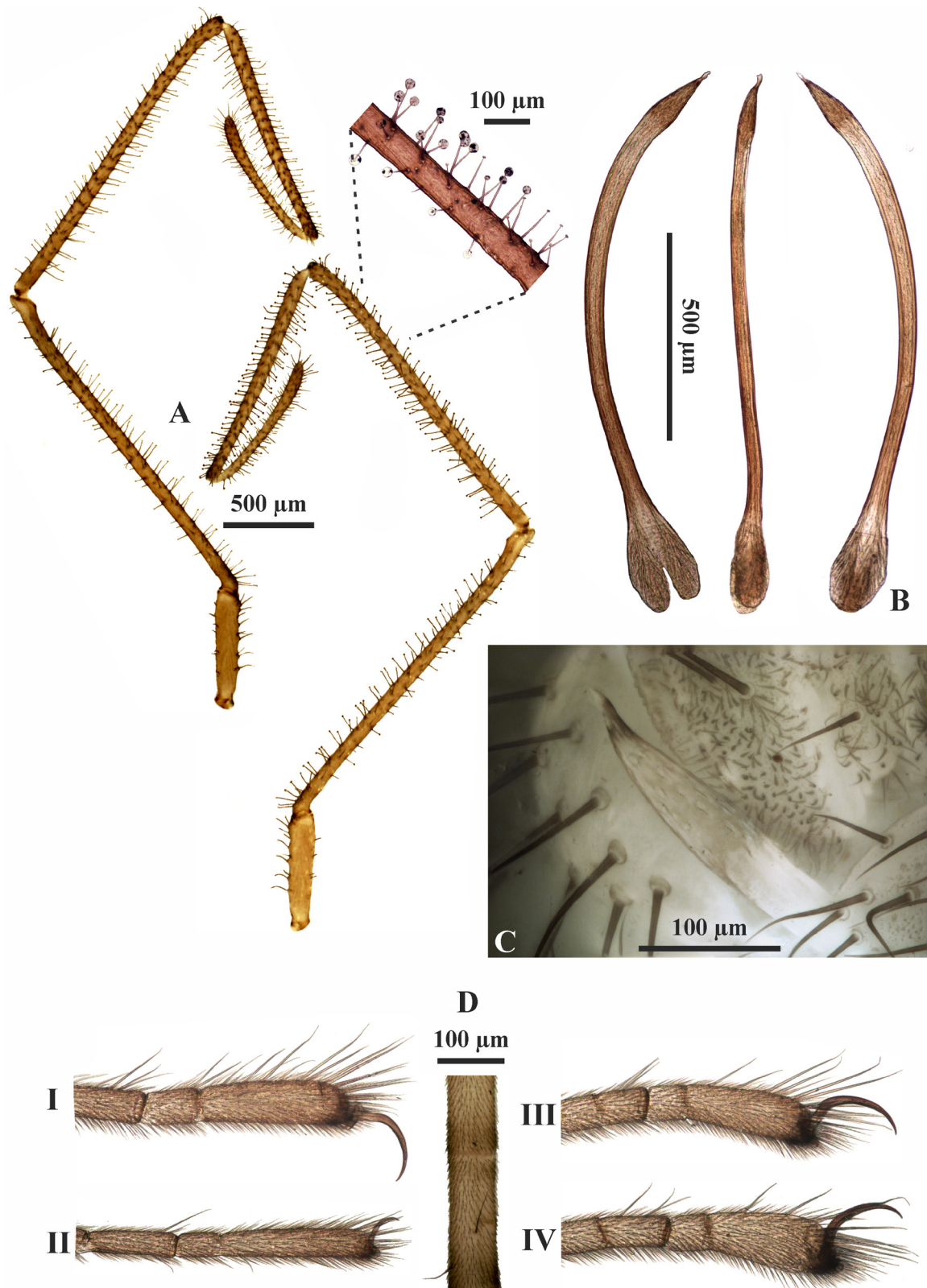


Fig. 3. *Nemaspela borkoae* sp. nov., ♂ holotype (PMSL-Opiliones-PK&TN 4/2019). **A.** Right pedipalp, lateral (left) and medial (right) views. **B.** Penis, ventral, lateral and dorsal view. **C.** Penis protruding through genital opening. **D.** Pseudoarticles in femur II, and distal tarsomerae I–IV with claws, lateral views.

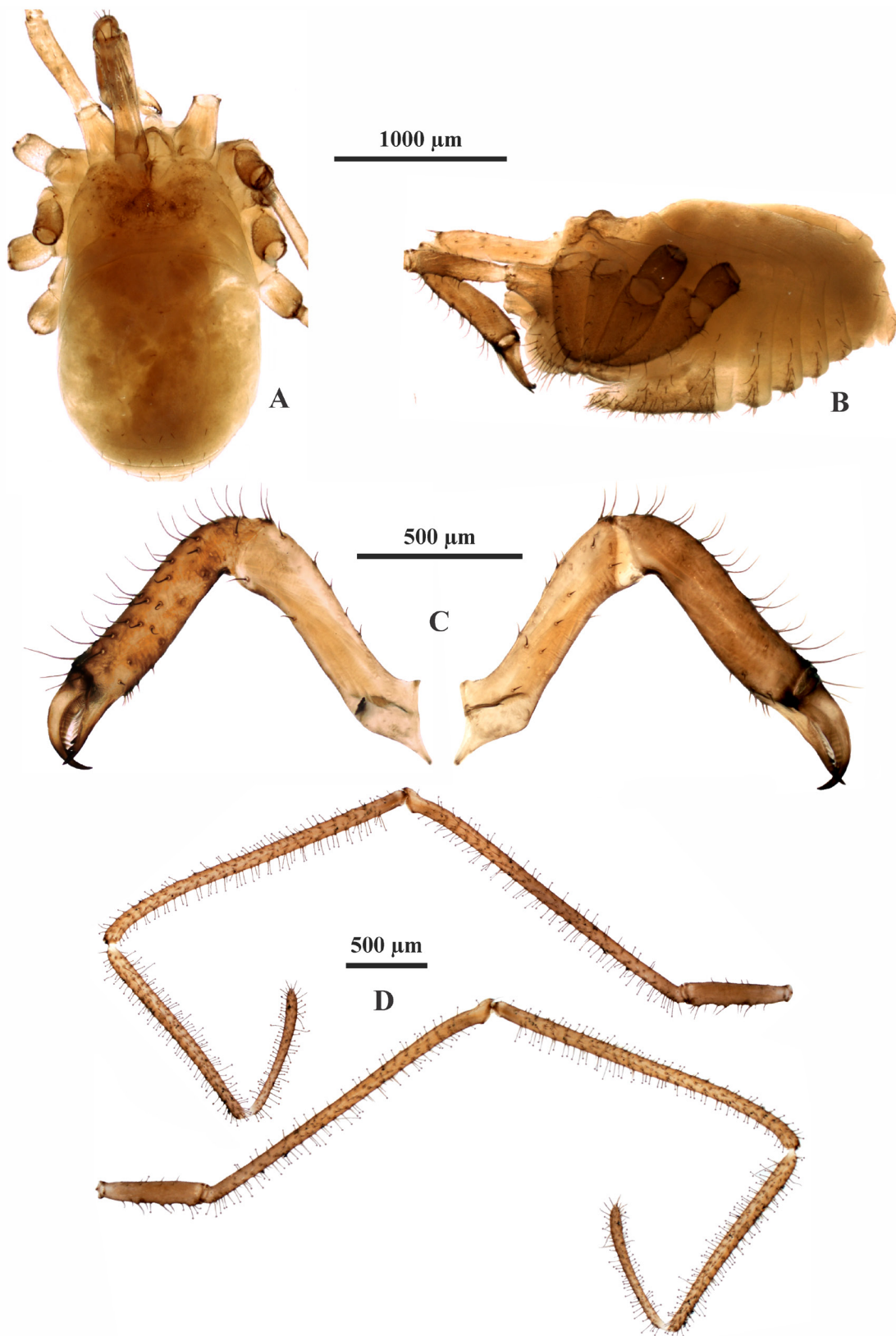


Fig. 4. *Nemaspela borkoae* sp. nov., ♀, allotype (PMSL-Opiliones-PK&TN 7/2019). **A–B.** Body, dorsal and lateral views (dry preparation). **C.** Right chelicera, medial (left) and lateral (right) views. **D.** Right pedipalp, medial (upper) and lateral (lower) views.

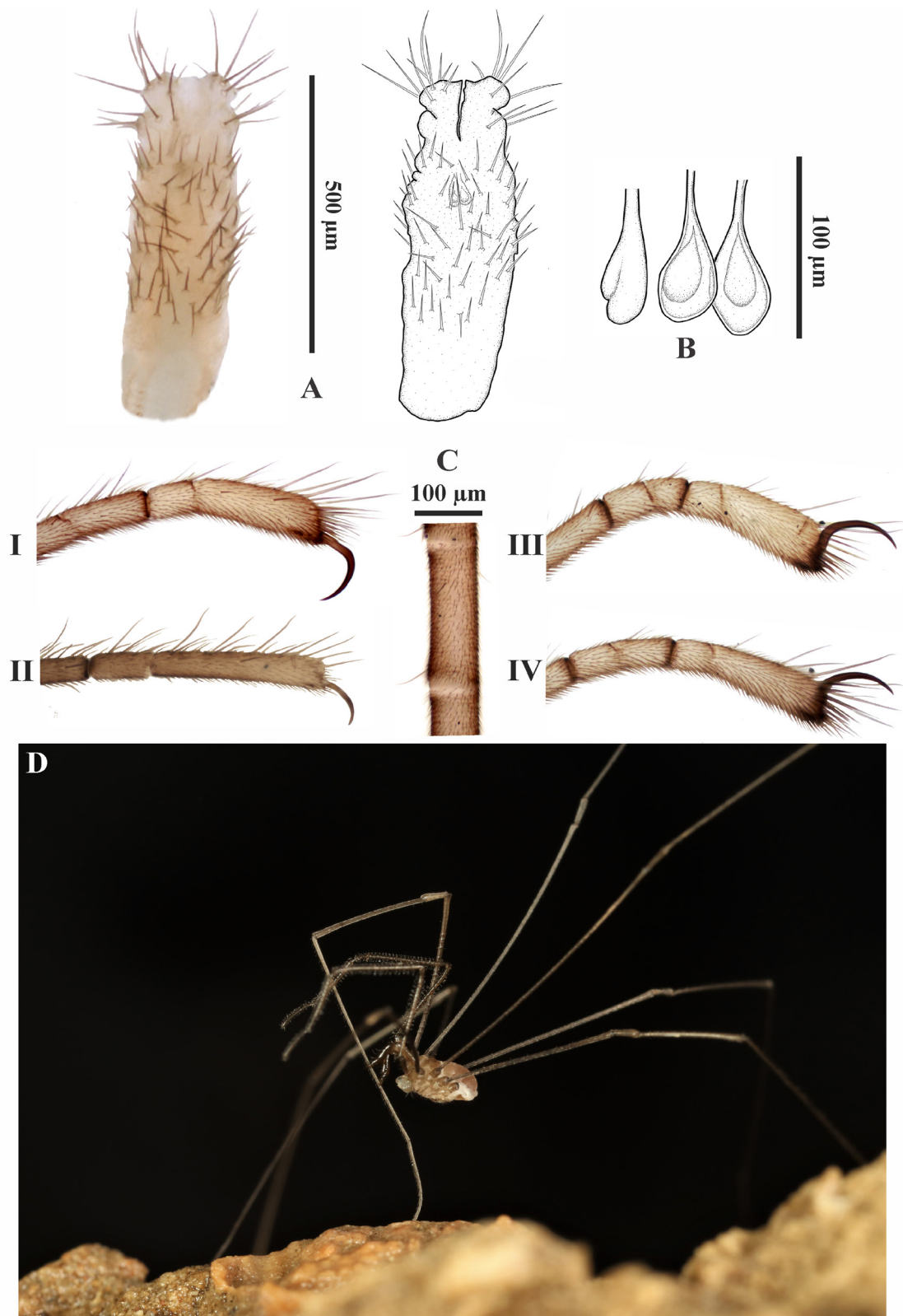


Fig. 5. *Nemaspela borkoae* sp. nov., ♀, allotype (PMSL-Opiliones-PK&TN 7/2019). **A.** Ovipositor, ventral view. **B.** Receptacula seminis, lateral (left) and ventral (right) views. **C.** Pseudoarticles in femur II, and distal tarsomeres I–IV with claws, lateral views. **D.** Female (PMSL-Opiliones-PK&TN 8/2019) in the natural habitat in Vodna jama u Dragalju Cave. Photograph by T. Deliċ.

edge of dorsal scutum. Cuticle of cephalothorax thicker in center and thinner towards edges, with scattered oval and irregularly shaped spots of thinner parts (Fig. 1E). Eyes completely reduced. Coxae and ventral side of the body with sparse long setae in a transverse row in the middle of each sternite (Fig. 1B–C).

CHELICERAE. Beige-brown, long and slender (Fig. 2B, F), without apophysis and gland openings. Lengths of basal article, distal article and movable finger, 0.99, 1.19 and 0.37, respectively. Basal segment basally and terminally widened. Distal segment distally enlarged, frontally evenly set with long bristles, the longest ones shorter than the article diameter. Fixed finger with a series of 21, movable finger with 23 diaphanous teeth.

PEDIPALPS. Light beige-brown, without secondary sexual characteristics (Figs 2A, 3A), very long, slender, with scattered, very densely set clavate glandular setae on all articles, except trochanter, diminishing in size from femur to tarsus, and giving a voluminous appearance in live animals. Femur straight, terminally slightly enlarged. Patella slightly shorter than femur, straight, with one long bristle dorso-distally. Tibia distally gradually narrowing. Tarsus long, slightly club-like, at the very proximal portion conspicuously bent ventrally at an angle of ca 45°, with a few long bristles. For article lengths, see Table 1.

LEGS (Fig. 3D, Table 1). Beige with darker article endings, very long and thin (L body: L leg II = 1:15.7), with numerous pseudoarticulations. Claws simple, ventrally bent. Leg articles cylindrical, with dense cover of fine bristles, interspersed by a few long ones (Fig. 3D).

PENIS (Figs 2C–E, 3B, on Fig. 3C protruding glans). 1.43 long, glans 0.18, basis 0.31. Truncus slightly dorsally bent, distally gradually slightly widened, narrowest near the basis, slightly dorso-ventrally compressed. Basis straight, bulbous, incised for about two-fifths its length. Glans brownish, conical and basally slightly wider than truncus, with sparse minute spines, terminally gradually tapering into a short stylus.

Female

BODY. Body length 2.11, width 1.48, body egg-shaped, with scutum magnum. Color of body light beige (Figs 4A–B, 5D).

CHELICERAE. As in male, more robust (Fig. 4C). Lengths of basal article, distal article and movable finger 1.01, 1.19 and 0.48, respectively.

PEDIPALPS (Fig. 4D). As in male, for lengths of articles see Table 1.

LEGS (Table 1; Fig. 5D; distal tarsomerae Fig. 5C). As in male, but shorter. Claws as in male.

OVIPOSITOR (Fig. 5A, left: lateral view, right: ventral view). ca 0.62 long, receptacula seminis monovesicular, with tear-like anterior bulge, ca 85 µm (Fig. 5B).

Relationships

Nemaspela borkoae sp. nov. is, besides *N. ladae*, the second species of *Nemaspela* in the Balkans. Both belong to the western group of *Nemaspela*, and are missing the male cheliceral apophysis. The cheliceral apophysis is, except in *N. femorecurvata*, present in all species of the eastern group of *Nemaspela*. The two Balkan species can be distinguished by the following ♂ characteristics (♀ of *N. ladae* unknown at the time; Karaman 2013):

1. Pedipalp trochanter about $\frac{1}{4}$ femur length, tarsus straight, about $\frac{1}{2}$ tibia length, glans terminally rounded, stylus wide-flattened, tube-like, curved *N. ladae* Karaman, 2013
- Pedipalp trochanter $\frac{1}{3}$ femur length, tarsus on very proximal portion conspicuously bent ventrally, about $\frac{2}{3}$ tibia length, glans gradually tapering into a short stylus slightly bent ventrally
..... *N. borkoae* sp. nov.

Distribution

Nemaspela borkoae sp. nov. has been found in four caves in Dragaljsko polje, the Krivošije karst plateau and Mt. Lovćen (Fig. 6).

Ecology

All the specimens of *N. borkoae* sp. nov. were collected in four caves situated in western Montenegro within the maximum linear extent of 30 km, in an area that receives the highest amount of precipitation in Europe (Ducić *et al.* 2012). The specimens were found at depths from about 50 to 370 m, at temperatures between 4.8 and 7.8°C. They were all found in places close to running water or in places susceptible to water level oscillation. However, three different habitat types can generally be distinguished: i) the vertical wet flowstone covered with organic sediment; ii) wet flowstone meanders subjected to occasional flooding; and iii) cave walls coated with the moonmilk-like surface. Some of the habitats were shared with other specialized subterranean fauna belonging to the following genera: *Verhoeffiella* Absolon, 1900 (Collembola: Entomobryidae), *Neotrechus* G. Muller, 1913 (Coleoptera: Carabidae), *Abasola* Strand, 1915 (Opiliones: Travuniidae). The relatively long appendages in *Nemaspela borkoae* sp. nov. suggest adaptation to spacious habitats, while their movable, pointed claws enable efficient clinging in slippery and water-drenched sites.

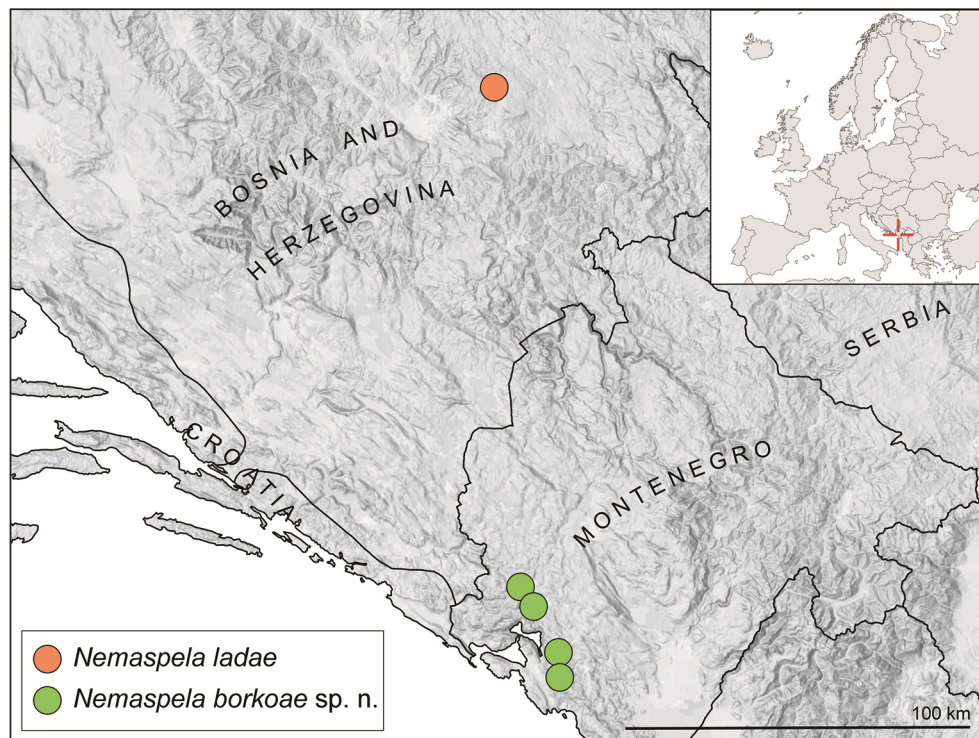


Fig. 6. Distribution of species of *Nemaspela* Šilhavý, 1966 in the Balkans. The locality for *N. ladae* Karaman, 2013 from Karaman (2013).

Discussion

There are two geographically separate *Nemaspela* groups, 1200 km distant from each other: the eastern one in the Caucasus and Crimea (Martens 2006; Chemeris 2009, 2013), and the western one in the Dinaric Karst (Karaman 2013). There is no recent evidence for a more continuous pattern of *Nemaspela* distribution, but this might indicate a much larger ancestral distribution range (Karaman 2013). Similar patterns of geographically distant but closely related species from the Caucasus and the Dinaric Karst have been noted in both surface and subterranean taxa (Zakšek *et al.* 2007; Tarkhnishvili 2014; Sidorov *et al.* 2018; Hrivniak *et al.* 2020). The main reason for such disjunct distribution patterns may be orogeny processes during the Miocene, which fundamentally changed the physical geography of the wider area, including the Dinaric Karst, Asia Minor, Caucasus, Rhodopes, etc. (Popov *et al.* 2004). Despite this poorly understood insular-like distribution (Karaman 2013; Nadolny & Turbanov 2015), we think that *Nemaspela* reports might be expected in the intermittent karstic regions between Caucasus and Crimea and the Balkans, namely in the southern Ukraine karst, and the karst regions in Romania, Bulgaria and eastern Serbia. This is because deep caves are still largely undersampled. Congruently, in a region of Montenegro with many deep caves that have recently been thoroughly explored, *N. borckoae* sp. nov. have regularly been found (see Material examined). Thus, the present data do not provide conclusive insight into *Nemaspela* distribution. On the other hand, where present, *Nemaspela* individuals are permanently recorded. In the western Crimea karst, *N. caeca* have been readily reported (Grese 1911; Ljovuschkin & Starobogatov 1963; Ljovuschkin 1972; Nadolny & Turbanov 2015) for over a hundred years, even in caves with a high recreational load (Nadolny & Turbanov 2015). *Nemaspela borckoae* sp. nov. likely inhabit many deep, neighboring caves in western Montenegro and thus occupy a larger karstic territory. Besides, in many large, deep caves, researchers might have overlooked *Nemaspela* individuals, which are hard to spot. This suspicion was lately (in January 2020) confirmed by discovery of habitually similar *Hadzinia ferrani* Novak & Kozel, 2014 (Novak & Kozel 2014) in Križna jama, Slovenia, which lies 30 km in a straight line from the type locality Ferranova buža, and is the second known locality, with no finding places in between. This happened even though Križna jama is one of the best explored and biologically sampled caves in Slovenia and has experienced organized tourism since the nineteen fifties (Bosák *et al.* 2010). Thus, further discoveries of specialized subterranean species in the karstic regions between the Balkans and the Caucasus can be expected, since this karst is presumably a constitutive part of the ridge exhibiting the highest biodiversity of terrestrial subterranean fauna in Europe (Culver *et al.* 2006).

Considering the glans morphology, *N. borckoae* sp. nov. seems to be much more closely related to *N. sokolovi*, *N. abchasica*, *N. birsteini*, *N. femorecurvata* and *N. gagraica* from the Caucasus than to *N. ladae*. In these species, the glans is gradually tapering into a straight stylus, while in *N. ladae* the glans is short, slightly dorso-ventrally flattened, with flattened tube-like, bent stylus. We speculate that *N. borckoae* sp. nov. and *N. ladae* eventually originate from two epigeal ancestors that colonized subterranean habitats.

Šilhavý (1966) reproduced Ljovuschkin & Starobogatov's (1963) drawings of the described species of *Nemaspela* and selected *N. sokolovi* as the type species of the newly established genus *Nemaspela*. When establishing the genus *Hadzinia* Šilhavý, 1966, Šilhavý redrew and enlarged the very inaccurate Hadži's original drawing of the glans of the type species *H. karamani* (Hadži, 1940) (Hadži 1940). This sketch, later reproduced by Schönhofer & Martens (2012), clearly exhibits *Nemaspela* characteristics (much resembling *N. femorecurvata*, described 40 years later; Martens 2006), but does not correspond to any species of *Hadzinia*, namely *H. karamani* and *H. ferrani*. Consequently, this blurred the taxonomic relation between the presumably closely related genera (the genetic evidence is still missing) *Nemaspela* and *Hadzinia* (Karaman 2013). However, typically, in *Nemaspela*, the glans gradually tapers into a mostly long stylus, while in *Hadzinia*, the glans is truncated, with a short, apparently inserted stylus, well

delimited from the glans (Novak & Kozel 2014). These two are the only exclusively troglolithic genera of the family (Karaman 2013) with very similar external morphology, which additionally complicates any morphology-based taxonomic conclusions.

All species of *Nemaspela* are eyeless and depigmented and show a high degree of adaptation for living in the subterranean environment. In contrast to *Hadzinia ferrani* (Novak & Kozel 2014) with a very similar habitus and external morphology, fluorescent microscopy in *N. borchoae* sp. nov. did not reveal any residual cuticular formation, spotting the emergence site of the optic nerve, nowadays reduced. We assume that this is true for all *Hadzinia* vs *Nemaspela* species, indicating two possible explanations: i) either *Nemaspela* ancestors colonized the subterranean habitat earlier; or ii) the reduction of the optic system took place in different ways in the two genera.

Nemaspela seems to be a subterranean offshoot of the *Giljarovia* ancestor (Martens 2006). There are no seceding characteristics in the genital morphology between the two geographical *Nemaspela* groups, but perhaps some external morphology features matter. Generally, the external morphology is of rather minor value in considering relations among the species in question, since interspecific competition may significantly influence the morphology of closely related animals (Fišer *et al.* 2012; Vergnon *et al.* 2013; Delić *et al.* 2019), and convergent adaptation of distantly related species is common in the subterranean habitat (Derkarabetian *et al.* 2010; Pipan & Culver 2012; Delić *et al.* 2017). However, *N. femorecurvata* is the only species in the eastern *Nemaspela* group missing the male cheliceral apophysis, which is a normal condition in both Balkan species, *N. ladae* and *N. borchoae* sp. nov. The other eastern species differ in this characteristic by having a small, but conspicuous, e.g., *N. abchasica*, to huge, e.g., *N. kovali*, apophysis (Chemeris 2009). Such variability indicates that this, presumably ancestral character, retained more or less the original function, in a varying degree, during adaptation to the subterranean habitat. It seems not likely that such a complex, energy consuming organ (cf. Hüppop 2012; Fišer 2019), as the cheliceral apophysis, would be preserved in so many species, if it had completely lost its function; however, this issue should be properly addressed prior any conclusive statements. Consequently, although the shape of the cheliceral apophysis alone is insufficient to identify the nemastomatid genera (Dunlop & Mitov 2009), we speculate that the absence/presence of the apophysis might be of some help in tracing the relations among species of *Nemaspela*. Eventually, this feature indicates two adaptational groups within the genus: the one that evolved from an ancestor with the apophysis, and the other being a descendant of an ancestor primarily missing the apophysis. On the other hand, the absence of the apophysis in particular species may be due to various selection pressures in further adaptational processes to various subterranean microhabitats (Fišer *et al.* 2012; Delić *et al.* 2016; Kralj-Fišer *et al.* 2020). Note that the genital morphology is not congruent with the presence/absence of the cheliceral apophysis. For the time being, we still lack a molecular phylogeny of the genus, which would help to uncover these relations.

Acknowledgements

We are indebted to Špela Borko, who provided the first specimen of *N. borchoae* sp. nov. Michelle Gadpaille valuably improved the English. The authors are grateful to two anonymous referees for their insightful comments and suggestions during the review process. Teo Delić would like to thank his irreplaceable caving colleagues, without whom this study could not have been prepared: Špela Borko, Ester Premate, David Škufca, Maja Zagmajster and Aja Zamolo. This study was partly supported by the Slovenian Research Agency (program P1-0184), the Karst Research programme (research core funding No. P6-0119), Project "DEVELOPMENT OF RESEARCH INFRASTRUCTURE FOR THE INTERNATIONAL COMPETITIVENESS OF THE SLOVENIAN RRI SPACE – RI-SI-LifeWatch" (the operation is co-financed by the Republic of Slovenia, Ministry of Education, Science and Sport and the European Union from the European Regional Development Fund) and a bilateral project between

Slovenia and Montenegro (BI-ME/18-20-001). The collection of the material was undertaken with permissions issued by the state nature conservation of Montenegro (UPI–101/2–02–387/1 and 02-UPI-500/7).

Corrigendum

In the description of *Hadzinia ferrani* (Novak & Kozel 2014), the authors erroneously reported pedipalp trochanter lengths of 1.15 (1.21), instead of 0.58 (0.61); consequently, the total pedipalp lengths were 5.78 (6.66), not 6.35 (7.26).

References

- Andersen T., Baranov V., Hagenlund L.K., Ivković M., Kvifte G.M. & Pavlek M. 2016. Blind flight? A new troglobiotic Orthoclad (Dipera, Chironomidae) from the Lukina jama - Trojama cave in Croatia. *PLoS ONE* 11 (4): e0152884. <https://doi.org/10.1371/journal.pone.0152884>
- Antić D. 2018. From the depths: *Heterocauseuma deprofundum* sp. nov., the world's deepest-occurring millipede (Diplopoda, Chordeumatida, Anthroleucosomatidae) from caves in the western Caucasus. *Zootaxa* 4377: 110–124. <https://doi.org/10.11646/zootaxa.4377.1.7>
- Binding C.J. 2010. Expedition to the Kameno-more region, Montenegro, 2009: The exploration of cave Pištet 4. *Proceedings of the University Bristol Speleological Society* 25 (1): 35–46.
- Binding C.J. 2011. Expedition to the Kameno-more region, Montenegro: Further exploration in cave Pištet 4. *Proceedings of the University Bristol Speleological Society* 25 (2): 125–131.
- Bosák P., Pruner P., Zupan Hajna N., Hercman H., Mihevc A. & Wagner J. 2010. Križna jama (SW Slovenia): Numerical- and correlated-ages from cave bear-bearing sediments. *Acta Carsologica* 39 (3): 529–549. <https://doi.org/10.3986/ac.v39i3.82>
- Chemers A. 2009. New data on the harvestman genus *Nemaspela* Šilhavý, 1966 (Arachnida: Opiliones). *Bulletin of the British Arachnological Society* 14 (7): 286–296. <https://doi.org/10.13156/arac.2009.14.7.286>
- Chemers A. 2013. Two new harvestman species (Arachnida: Opiliones) from the collection of the Siberian Zoological Museum. *Arthropoda Selecta* 22 (1): 41–46. <https://doi.org/10.15298/arthsel.22.1.03>
- Culver D.C. & Sket B. 2000. Hotspots of Subterranean Biodiversity in Caves and Wells. *Journal of Cave and Karst Studies* 62 (1): 11–17.
- Culver D.C., Deharveng L., Bedos A., Lewis J.J., Madden M., Reddell J.R., Sket B., Trontelj P. & White D. 2006. The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography* 29: 120–128. <https://doi.org/10.1111/j.2005.0906-7590.04435.x>
- Delić T., Trontelj P., Zakšek V. & Fišer C. 2016. Biotic and abiotic determinants of appendage length evolution in a cave amphipod. *Journal of Zoology* 299 (1): 42–50. <https://doi.org/10.1111/jzo.12318>
- Delić T., Trontelj P., Rendoš M. & Fišer C. 2017. The importance of naming cryptic species and the conservation of endemic subterranean amphipods. *Scientific Reports* 7: 3391. <https://doi.org/10.1038/s41598-017-02938-z>
- Delić T., Kapla A. & Colla A. 2019. Orogeny, sympatry and emergence of a new genus of Alpine subterranean Trechini (Coleoptera: Carabidae). *Zoological Journal of the Linnean Society* 189 (4): 1217–1231. <https://doi.org/10.1093/zoolin/zlzl157>
- Derkarabetian S., Steinmann D.B. & Hedin M. 2010. Repeated and time-correlated morphological convergence in cave-dwelling harvestmen (Opiliones, Laniatores) from montane western North America. *PLoS ONE* 5 (5) e10388. <https://doi.org/10.1371/journal.pone.0010388>

- Ducić V., Luković J., Burić D., Stanojević G. & Mustafić S. 2012. Precipitation extremes in the wettest Mediterranean region (Krivošije) and associated atmospheric circulation types. *Natural Hazards and Earth System Science* 12: 687–697. <https://doi.org/10.5194/nhess-12-687-2012>
- Dunlop J.A. & Mitov P.G. 2009. Fossil harvestmen (Arachnida, Opiliones) from Bitterfeld amber. In: Stoev P., Dunlop J. & Lazarov S. (eds) *A life caught in a spider's web. Papers in arachnology in honour of Christo Deltchev*. *ZooKeys* 16: 347–375. <https://doi.org/10.3897/zookeys.16.224>
- Engel S.A., Paoletti M.G., Beggio M., Dorigo L., Pamio A., Gomiero T., Furlan C., Brillì M., Dreon A.L., Bertoni R. & Squartini A. 2013. Comparative microbial community composition from secondary carbonate (moonmilk) deposits: implications for the *Cansiliella servadeii* cave hygropetric food web. *International Journal of Speleology* 42: 181–192. <https://doi.org/10.5038/1827-806X.42.3.2>
- Fišer C., Blejcek A. & Trontelj P. 2012. Niche-based mechanisms operating within extreme habitats: a case study of subterranean amphipod communities. *Biology Letters* 8 (4): 578–581. <https://doi.org/10.1098/rsbl.2012.0125>
- Fišer Ž. 2019. Adaptation to low food. In: White W.B., Culver D.C. & Pipan T. (eds) *Encyclopedia of caves, third edition*: 1–7. Academic Press, London.
- Grese N. 1911. Über eine blinde *Nemastoma*-Art aus einer Höhle in der Krim (*Nemastoma caecum* sp. nov.). *Zoologischer Anzeiger* 37: 108.
- Gruber J. 1976. Ergebnisse zoologischer Sammelreisen in der Türkei: Zwei neue Nemastomatidenarten mit Stridulationsorganen, nebst Anmerkungen zur systematischen Gliederung der Familie (Opiliones, Arachnida). *Annalen des Naturhistorischen Museums in Wien* 80: 781–801.
- Gruber J. 2007. Dyspnoi – Historical systematic synopsis and family chapters. In: Pinto-da-Rocha R., Machado G. & Giribet G. (eds) *Harvestmen: the biology of Opiliones*: 131–159. Harvard University Press, Cambridge.
- Gruber J. & Martens J. 1968. Morphologie, Systematik und Ökologie der Gattung *Nemastoma* C.L. Koch (s. str.) (Opiliones, Nemastomatidae). *Senckenbergiana biologica* 49: 137–172.
- Hadži J. 1940. Dve nove zanimljive vrste opilionskog roda *Nemastoma*. *Glasnik Skopskog naučnog društva* 22: 1–17.
- Hrivniak L., Sroka P., Bojková J., Godunko R.J., Soldán T. & Staniczek A.H. 2020. The impact of Miocene orogeny for the diversification of Caucasian *Epeorus* (*Caucasiron*) mayflies (Ephemeroptera: Heptageniidae). *Molecular Phylogenetics and Evolution* 146: 106735. <https://doi.org/10.1016/j.ympev.2020.106735>
- Hüppop P. 2012. Adaptation to low food. In: White B.W. & Culver D.C. (eds) *Encyclopedia of caves, second edition*: 1–9. Academic Press, Amsterdam.
- Inäbnit T., Jochum A., Kampschulte M., Martels G., Ruthensteiner B., Slapnik R., Nesselhauf C. & Neubert E. 2019. An integrative taxonomic study reveals carychiid microsnails of the troglobitic genus *Zospeum* in the Eastern and Dinaric Alps (Gastropoda, Ellobioidea, Carychiinae). *Organisms Diversity and Evolution* 19: 135–177. <https://doi.org/10.1007/s13127-019-00400-8>
- Karaman I. 2013. *Nemaspela ladae* sp. n., a new troglobitic nemastomatid (Opiliones, Dyspnoi, Nemastomatidae) from a Dinaric cave. *Zootaxa* 3694 (3): 240–248. <https://doi.org/10.11646/zootaxa.3694.3.4>
- Kralj-Fišer S., Premate E., Copilaș-Ciocianu D., Volk T., Fišer Ž., Balázs G., Herczeg G., Delić T. & Fišer C. 2020. The interplay between habitat use, morphology and locomotion in subterranean crustaceans of the genus *Niphargus*. *Zoology* 139: 125742. <https://doi.org/10.1016/j.zool.2020.125742>

- Kratochvíl J. 1958. Höhlenweberknechte Bulgariens (Palpatores-Nemastomatidae). *Práce Brněnské Základny Československé Akademie Věd* 30 (12): 523–576.
- Lakota J., Lohaj R. & Dunay G. 2010. Taxonomical and ecological notes on the genus *Scotoplanetes* Absolon, with the description of a new species from Montenegro (Coleoptera: Carabidae: Trechini). *Natura Croatica* 19 (1): 99–110.
- Ljovuschkin S.T. 1972. [Harvestmen of the family Nemastomatidae from caves of USSR]. *Biospeologica Sovietica*, XLVI. *Sbornik Trudov Zoologičeskogo Muzeja MGU* 12: 61–73. [in Russian].
- Ljovuschkin S.T. & Starobogatov Y.I. 1963. [The cavernicolous Opilionidea in the Crimea and Caucasus]. *Biospeologica Sovietica*, XVIII. *Byulletin Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologičeskii* 68 (1): 41–51. [in Russian].
- Lukić M., Houssin C. & Deharveng L. 2010. A new relictual and highly troglomorphic species of Tomoceridae (Collembola) from a deep Croatian cave. *Zookeys* 69: 1–16. <https://doi.org/10.3897/zookeys.69.739>
- Lukić M., Delić T., Pavlek M., Deharveng L. & Zagmajster M. 2019. Distribution pattern and radiation of the European subterranean genus *Verhoeffiella* (Collembola, Entomobryidae). *Zoologica scripta* 49 (1): 86–100. <https://doi.org/10.1111/zsc.12392>
- Martens J. 1978. Spinnentiere, Arachnida - Weberknechte, Opiliones. *Die Tierwelt Deutschlands* 64: 1–464.
- Martens J. 2006. Weberknechte aus dem Kaukasus (Arachnida, Opiliones, Nemastomatidae). *Senckenbergiana biologica* 86 (2): 145–210.
- Nadolny A.A. & Turbanov I.S. 2015. Rasprostranenie *Nemaspela caeca* (Arachnida: Opiliones) v Krymu [Distribution of *Nemaspela caeca* (Arachnida: Opiliones) in Crimea.] In: Turbanov I.S., Marin I.N. & Gongalsky K.B. (eds) *Materialy vserossijskoj molodežnoj konferencii Biospeleobiologija Kavkaza i drugih rajonov Rossii*: 46–48. Institute of Ecology and Evolution A.N. Severtsov RAS and Institute of Biology of Inland Waters I.D. Papanin RAS, Moskva. [In Russian]
- Novak T. & Kozel P. 2014. *Hadzinia ferrani*, sp. n. (Opiliones: Nemastomatidae), a highly specialized troglobiotic harvestman from Slovenia. *Zootaxa* 3841 (1): 135–145. <https://doi.org/10.11646/zootaxa.3841.1.8>.
- Pérez-González A., Ceccarelli F.S., Monte B.G.O., Proud D.N., DaSilva M.B. & Bichuette M.E. 2017. Light from dark: A relictual troglobite reveals a broader ancestral distribution for kimulid harvestmen (Opiliones: Laniatores: Kimulidae) in South America. *PLoS ONE* 12 (11): e0187919. <https://doi.org/10.1371/journal.pone.0187919>
- Pipan T. & Culver D.C. 2012. Convergence and divergence in the subterranean realm: a reassessment. *Biological Journal of the Linnean Society* 107(1): 1–14. <https://doi.org/10.1111/j.1095-8312.2012.01964.x>
- Polak S. 2005. Importance of discovery of the first cave beetle *Leptodirus hochenwartii* Schmidt, 1832. *ENDINS* 28: 71–80.
- Popov S.V., Rögl F., Rozanov A.Y., Steininger F.F., Shcherba I.G. & Kovac M. 2004. *Lithological-Paleogeographic maps of Paratethys 10 maps Late Eocene to Pliocene*. Courier Forschungsinstitut Senckenberg, Stuttgart.
- Redikorzev V.V. 1936. Materialy k faune Opiliones SSSR. *Trudy Zoologičeskogo Instituta, Akademija Nauk SSSR* 3: 33–57.
- Schönhofer A.L. 2013. A taxonomic catalogue of the Dyspnoi Hansen and Sørensen, 1904 (Arachnida: Opiliones). *Zootaxa* 3679 (1): 1–68. <https://doi.org/10.11646/zootaxa.3679.1.1>

- Schönhöfer A.L. & Martens J. 2012. The enigmatic Alpine opilionid *Saccarella schilleri* gen. n., sp. n. (Arachnida: Nemastomatidae) – isolated systematic placement inferred from comparative genital morphology. *Organisms Diversity & Evolution* 12 (4): 409–419. <https://doi.org/10.1007/s13127-012-0073-7>
- Shear W.A. & Gruber J. 1983. The opilionid subfamily Ortholasmatinae (Opiliones, Troguloidea, Nemastomatidae). *American Museum Novitates* 2757: 1–65.
- Sidorov D., Taylor S.J., Sharina S. & Gontcharov A. 2018. Zenkevitchiidae fam. nov. (Crustacea: Gammaroidea), with description of new subterranean amphipods from extremely deep cave habitats. *Journal of Natural History* 52: 1509–1535. <https://doi.org/10.1080/00222933.2018.1482017>
- Šilhavý V. 1956. *Sekáči – Opilionidea*. Fauna ČSR, 7. Nakladatelství Československé Akademie Věd, Praha.
- Šilhavý V. 1966. Über die Genitalmorphologie der Nemastomatidae (Arach., Opiliones). *Senckenbergiana biologica* 47 (1): 67–72.
- Simon E. 1872. Notices sur les arachnides cavernicoles et hypogés. *Annales de la Société Entomologique de France*, série 5 (2): 214–244.
- Sket B. 2012. Diversity patterns in the dinaric karst. In: White W.B. & Culver D.C. (eds) *Encyclopedia of Caves, second edition*: 228–238. Academic Press, Amsterdam.
- Sket B., Paragamian K. & Trontelj P. 2004. A census of the obligate subterranean fauna in the Balkan Peninsula. In: Griffiths H.I. & Krystufek B. (eds) *Balkan Biodiversity*: 309–322. Springer, Dordrecht.
- Speleologija.me 2020. Available from <http://www.speleologija.me/p/najdublje-jame-u-crnoj-gori.html> [Accessed 30 Mar. 2020].
- Taiti S., Argano R., Marcia P., Scarpa F., Sanna D. & Casu M. 2018. The genus *Alpioniscus* Racovitza, 1908 in Sardinia: Taxonomy and natural history (Isopoda, Oniscidea, Trichoniscidae). *ZooKeys* 801: 229–263. <https://doi.org/10.3897/zookeys.801.24102>
- Tarkhishvili D. 2014. *Historical Biogeography of the Caucasus*. Nova Science Publishers, New York.
- Trontelj P., Borko Š. & Delić T. 2019. Testing the uniqueness of deep terrestrial life. *Scientific Reports* 9: 15188. <https://doi.org/10.1038/s41598-019-51610-1>
- Vergnon R., Leijs R., van Nes E.H. & Scheffer M. 2013. Repeated parallel evolution reveals limiting similarity in subterranean diving beetles. *The American Naturalist* 182 (1): 67–75. <https://doi.org/10.1086/670589>
- Zakšek V., Sket B. & Trontelj P. 2007. Phylogeny of the cave shrimp *Troglocaris*: evidence of a young connection between Balkans and Caucasus. *Molecular Phylogenetics and Evolution* 42: 223–235. <https://doi.org/10.1016/j.ympev.2006.07.009>
- Zhang C. & Martens J. 2018. Ancient home or in exile? The easternmost species of genus *Starengovia* Snegovaya, 2010 found in China (Opiliones, Nemastomatidae, Nemastomatinae). *ZooKeys* 770: 105–115. <https://doi.org/10.3897/zookeys.770.25491>

Manuscript received: 9 April 2020

Manuscript accepted: 27 July 2020

Published on: 28 September 2020

Topic editor: Rudy Jocqué

Desk editor: Marianne Salaiün

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Botanic Garden Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain; Zoological Research Museum Alexander Koenig, Bonn, Germany; National Museum, Prague, Czech Republic.