**Nemaspela borkoae** sp. nov. (Opiliones: Nemastomatidae),
the second species of the genus from the Dinaric Karst

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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 ½ vs ⅔ 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 epigean ancestral lineages.

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

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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.
KOZEL P. et al., First Nemaspela species from Montenegro

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)| 17 (13)      |
| 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)| 15 (28)      |
| 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)| 15 (15)      |
| 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)| 15 (14)      |

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, V odna 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 mammillar 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 tarsomerae 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. Delić.
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 ¼ femur length, tarsus straight, about ½ tibia length, glans terminally rounded, stylus wide-flattened, tube-like, curved ................................. \textit{N. ladae} Karaman, 2013

– Pedipalp trochanter ⅓ femur length, tarsus on very proximal portion conspicuously bent ventrally, about ⅔ tibia length, glans gradually tapering into a short stylus slightly bent ventrally ................................. \textit{N. borkoae} sp. nov.

\subsection*{Distribution}

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

\subsection*{Ecology}

All the specimens of \textit{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 \textit{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: \textit{Verhoeffiella} Absolon, 1900 (Collembola: Entomobryidae), \textit{Neotrechus} G. Muller, 1913 (Coleoptera: Carabidae), \textit{Abasola} Strand, 1915 (Opiliones: Travuniidae). The relatively long appendages in \textit{Nemaspela borkoae} sp. nov. suggest adaptation to spacious habitats, while their movable, pointed claws enable efficient clinging in slippery and water-drenched sites.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{map.png}
\caption{Distribution of species of \textit{Nemaspela} Šilhavý, 1966 in the Balkans. The locality for \textit{N. ladae} Karaman, 2013 from Karaman (2013).}
\end{figure}
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. borkoae 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 borkoae 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. borkoae sp. nov. seems to be much more closely related to N. sokolovi, N. abchasica, N. birsteini, N. femorecurvata and N. gagrica 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. borkoae sp. nov. and N. ladae eventually originate from two epigean 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 troglobiotic 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. borkoae* 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. borkoae* 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.

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**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).

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