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## Research article

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# *Kryptonesticus deelemanae* gen. et sp. nov. (Araneae, Nesticidae), with notes on the Mediterranean cave species

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**Abstract.** This paper describes and illustrates a new genus and a new species belonging to the family Nesticidae based on morphology and supported by molecular data. The new genus, *Kryptonesticus* gen. nov., groups eight species spread from Bulgaria and Turkey to Croatia, including Montenegro, Bosnia and Herzegovina and Crete. As a result, seven new combinations are proposed: *K. eremita* (Simon, 1879) comb. nov., *K. arenstorffi* (Kulczyński, 1914) comb. nov., *K. fagei* (Kratohvil, 1933) comb. nov., *K. beroni* (Deltshev, 1977) comb. nov., *K. beshkovi* (Deltshev, 1979) comb. nov., *K. henderickxi* (Bosselaers, 1998) comb. nov. and *K. dimensis* (López-Pancorbo, Kunt & Ribera, 2013) comb. nov., all ex *Nesticus*. *Kryptonesticus deelemanae* gen. et sp. nov. is described on the basis of both sexes and its phylogenetic relationships with closely related species are discussed based on morphological and molecular data (the *cox1*, *rrn* and *H3* genes). In addition, the species of this new genus (except for *K. eremita*) are clear candidates for protection: they have highly restricted ranges and some of them show a high degree of adaptation to the subterranean environment.

**Keywords.** Nesticidae, taxonomy, caves, endemism, Dinarides.

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## Introduction

The Nesticids inhabit dark and damp places and are common cave-dwellers in the northern Mediterranean Basin. So far, 52 different species belonging to four genera have been discovered in this area: *Nesticus* Thorell, 1869, *Typhlonesticus* Kulczyński, 1914, *Carpathonesticus* Lehtinen & Saaristo, 1980 and *Aituaria* Esyunin & Efimik, 1998 (World Spider Catalog 2016). As far as we know, only one of these 52 species (*C. lotriensis* Weiss, 1983) has not been recorded in caves because it lives in a non-karstic area, although it is usually found in the walls and ceilings of hollows in rocky walls in shaded areas within

its distribution range. Two more genera occur in bordering areas: *Canarionesticus* Wunderlich, 1992, endemic to the Tenerife (Canaries), and *Nesticella* Lehtinen & Saaristo, 1980, which is broadly spread throughout the Asian continent and recorded in Azerbaijan (*N. moguera* (Yaginuma, 1972)).

At the species level, most of them are well described and illustrated, but the taxonomy of the whole group is not well established at the genus level. With only a cursory review of the Mediterranean *Nesticus* species, we realize that there are conspicuous differences in both male and female genital morphology, suggesting the existence of independent evolutionary lineages. These morphological differences were already pointed out by Lehtinen & Saaristo (1980), and López-Pancorbo & Ribera (2011).

In the Dinarides seven nesticid species have been recorded so far: two *Typhlonesticus* species, the type species of the genus *T. absoloni* (Kratohvíl, 1933) from Montenegro, and *T. idriacus* (Roewer, 1931) from Slovenia; one *Carpathonesticus* species, *C. parvus* (Kulczyński, 1914) from Bosnia and Herzegovina; and four *Nesticus* species, two widespread species, *N. cellulanus* (Clerck, 1757) and *N. eremita* Simon, 1879, and two narrowly distributed species, *N. arenstorffi* Kulczyński, 1914 from Bosnia and Herzegovina and Montenegro and *N. fagei* Kratochvíl, 1933 from Bosnia and Herzegovina. In Croatia, only *N. cellulanus* and *N. eremita* have been recorded so far (Nentwig *et al.* 2016). *Nesticus speluncarum* Pavesi, 1873, an endemic species from a small part of Italy, is wrongly listed for Dinaric countries, probably because of the misidentification of *N. eremita* samples. The most relevant authors in taxonomic studies of Dinaric nesticids are Władysław Kulczyński and Josef Kratochvíl. Kulczyński described two species (Kulczyński 1914) while Kratochvíl's 1933 paper, besides the description of two new species from Dinarides, gave an overview of all European nesticids known at that time and divided species of *Nesticus* into three groups based mostly on paracymbium morphology: the hercynian, dinaric and transylvanic groups (Kratohvíl 1933). In later papers, he made a great contribution to the distribution areas of the known species (Kratohvíl 1934, 1935) and compared the body coloration and leg length of different nesticid species, which he related to their adaptation to cave life (Kratohvíl 1978).

Research of the Croatian cave fauna, including cave spiders, intensified with the foundation of the Croatian Biospeleological Society (CBSS) in 1996. One of the intensively researched areas is Biokovo Mountain, known for its large number of endemic and relict taxa from many cave dwelling groups of animals (Ozimec & Jalzic 1999). The result of a project, “Inventory and Mapping of the Subterranean and Spring Fauna”, undertaken by CBSS and the Biokovo Nature Park, as well as later field trips, was the discovery of many interesting and new cave taxa that included a new nesticid species.

This discovery prompted us to perform a review of the species described so far, especially those showing a strong morphological similarity. These were *N. fagei* Kratochvíl, 1933 and *N. arenstorffi* Kulczyński, 1914, two species geographically and morphologically closest to the new one, but also *N. henderickxi* Bosselaers, 1998, *N. dimensis* López-Pancorbo, Kunt & Ribera, 2013, *N. eremita* Simon, 1879, *N. beroni* Deltshv, 1977 and *N. beshkovi* Deltshv, 1979. In order to check the evolutionary relationships between these species, a molecular phylogenetic analysis based on nuclear and mitochondrial gene sequences was performed, including the type species of the Mediterranean genera *Nesticus* (*N. cellulanus*), *Typhlonesticus* (*T. absoloni*) and *Carpathonesticus* (*C. fodinarum*).

This paper aims to describe a new genus and a new species belonging to the Nesticidae. The new genus, *Kryptonesticus* gen. nov., shows conspicuous and synapomorphic characters in male and female genital organs that allow a clear differentiation from other nesticid genera, which is why we propose seven new combinations of the above mentioned species. Finally, the new species is related to the geographically closest species, *N. fagei* and *N. arenstorffi*, for which we also provided redescriptions of both sexes.

## Material and methods

### Molecular data

#### Sampling and molecular data collection

In order to assess the phylogenetic affinities of the new genus we conducted molecular analysis on representatives of the Mediterranean genera *Nesticus*, *Carpathonesticus* and *Typhlonesticus*, including the type species from each of them. We could not include representatives of the genus *Aituaria* due to lack of suitable material for molecular analysis. We also included all representatives of the new genus, except *N. beshkovi* and *N. beroni* due to lack of specimens.

Specimens were collected in the field, fixed in 96% or absolute ethanol and stored at 4°C. Total genomic DNA was extracted with QIamp® DNA Mini Kit and DNeasy Blood & Tissue Kit (QIAGEN) following the manufacturer's protocols. The approximate concentration and purity of the DNA obtained were verified using 1% agarose/TBE gel electrophoresis and a BioSpec-nano Spectrophotometer.

Partial fragments of two mitochondrial (cytochrome oxidase I: *cox1* and 16S rRNA: *rrnL*) and one nuclear (Histone 3: *H3*) gene were selectively amplified in polymerase chain reactions (PCR) that were conducted following Ribera *et al.* (2014) and sequenced at the Macrogen sequence center in the Netherlands. Raw sequences were edited and assembled with Geneious v. 4.6.5 (<http://www.geneious.com>; Kearse *et al.* 2012). All new sequences obtained were deposited in GenBank (see Appendix 1 for localities and GenBank accession numbers of all used samples).

#### Alignment, partitioning analyses and evolutionary model selection

Alignment of the *cox1* and *H3* gene fragments was trivial due to the absence of length polymorphism. The *rrnL* sequences were aligned using the online version of MAFFT, applying the Q-INS-i algorithm (Kato & Toh 2008) with the default options. With the “user-specific schemes” option in PartitionFinder v. 1.0.1 (Lanfear *et al.* 2012), we explored eight alternative partitioning schemes. Partitioning schemes ranged from all the gene fragments together as one partition, to a highly partitioned scheme, with each gene fragment considered as an independent partition and the third codon position separated from the first and second in *cox1* and *H3*. We used the Bayesian information criterion to select among the partition schemes and evolutionary models (Lanfear *et al.* 2012). We obtained the uncorrected pairwise (p)-distance genetic divergences between and within evolutionary lineages using MEGA v. 7.0.14 (Kumar *et al.* 2016) removing alignment gaps in pairwise comparisons.

### Phylogenetic analyses

A Maximum Likelihood (ML) analysis was performed using RAxML v. 7.4.2 (Stamatakis 2006), through the graphical front-end RAxMLGUI 1.3; Silvestro & Michalak 2012). The GTR + G nucleotide substitution model was applied to each of the partitions corresponding to the best partition scheme selected and nonparametric bootstrap support analysis of 1000 pseudoreplicates was conducted. *Typhlonesticus absoloni* was used to root the tree.

### Morphological observations

All measurements are in millimeters (mm). Specimens were hand collected using forceps. Body color descriptions were based on live observations and digital images taken in situ with a Canon Eos 400D camera.

The vulva was removed and treated with 30% KOH. After observation, drawing and taking photographs, the vulva was washed in distilled water and stored in 70% ethanol. The left male palp was illustrated and photographed in all cases. Terminology for the body measurements and copulatory organs follows López-Pancorbo & Ribera (2011).

Specimens were examined under a Zeiss Stereo Discovery V12 stereo microscope equipped with an Infinity X DeltaPix digital camera and under a Zeiss SteREO Discovery V20 stereo microscope equipped with an Axiocam 105 color microscopy camera. The digital microscopic images were edited using DeltaPix DpxWiew Pro AZ v. 13.6 software with an enhanced focus function. For viewing and tracking the insemination ducts a Leitz DMRB Progres C3 microscope equipped with a digital camera was used. The drawings were hand-drawn in ink using a “camera lucida” attached to the Leica MZ160A binocular stereoscope.

#### **Abbreviations used**

b	=	bulge in the inner MA side
BTA	=	basal tegular apophysis
dm	=	dorsomedian apophysis of do
do	=	dorsal paracymbium process
E	=	embolus
id	=	insemination duct
juv.	=	juv.enile
lr	=	longitudinal ridge of tegulum
MA	=	median apophysis
me	=	membranous extension of ventral process
od	=	oval depression
OL	=	opisthosoma length
OW	=	maximum opisthosoma width
P	=	paracymbium
PL	=	prosoma length (from the posterior edge of the carapace to the front edge of the clypeus, measured at the midline)
poe	=	pointed outer MA edge
PW	=	maximum prosoma width
rs	=	round swelling of tegulum
S	=	spermathecae
T	=	tegulum
TL	=	total body length
TTA	=	theridioid tegular apophysis
TTA p1	=	process 1 of TTA
TTA p2	=	process 2 of TTA
v	=	ventral paracymbium process
wr	=	wrinkled outer rim of MA proximal part

#### **Eyes**

AL	=	anterior lateral
AM	=	anterior median
PL	=	posterior lateral
PM	=	posterior median

#### **Collection acronyms**

CBSS	=	Croatian Biospeleological Society collection, part of the Croatian Natural History Museum collection, Zagreb, Croatia
SMF	=	Senckenberg Museum, Frankfurt, Germany

## Results

Class Arachnida Cuvier, 1812  
Order Araneae Clerck, 1757  
Family Nesticidae Simon, 1894

*Kryptonesticus* gen. nov.

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Figs 1–5

## Type species

*Kryptonesticus deelemanae* gen. et sp. nov.

## Diagnosis

*Kryptonesticus* gen. nov. differs from other nesticid genera by the morphology of both male and female copulatory organs. In males, the most conspicuous diagnostic character is the shape and size of the median apophysis (MA), which is large and conspicuous, highly developed and thickly sclerotized, emerging from the middle part of the tegulum and reaching its apical part. This characteristic is shared among a group of species including *K. eremita*, *K. dimensis*, *K. henderickxi*, *K. fagei* and *K. arenstorffi* (males of *K. beshkovi* and *K. biroi* are unknown). In other nesticid genera, the MA is absent, inconspicuous or poorly developed (*Nesticella* Lehtinen & Saaristo, 1980; *Wraios* Ballarin & Li, 2015; *Nescina* Ballarin & Li, 2015; *Hamus* Ballarin & Li, 2015; *Gaucelmus* Keyserling, 1884; *Cyclocarcina* Komatsu, 1942; *Typhlonesticus* Kulczyński, 1914; *Canarionesticus* Wunderlich, 1992); in the form of a small, curved and pointed hook (*Carpathonesticus* Lehtinen & Saaristo, 1980); compact, transverse and not very developed (*Eidmannella* Roewer, 1935); more conspicuous and transverse (*Aituaria* Esyunin & Efimik, 1998) or it is well developed (*Nesticus cellulanus* (Clerck, 1757) and *Pseudonesticus* Liu & Li, 2013), but in this case the MA is long, thin and extended laterally. In *Kryptonesticus* gen. nov., the MA extends laterally at its base and then stretches towards the apex of the tegulum, parallel to the embolus. The theridioid tegular apophysis (TTA) is more compact than in *N. cellulanus* or *Pseudonesticus*. This is a very important character, since the TTA and MA are actively involved in sperm transfer (Huber 1993). *Kryptonesticus* gen. nov. also differs from other nesticid genera in the shape, ramification and modifications associated with the paracymbium. *Kryptonesticus* gen. nov. shows a well-developed dorsal process and a poorly differentiated ventral one. Distal and paradistal apophyses are absent and the dorsomedian apophysis is short and pointed, inconspicuous or absent. Females of this new genus show characteristic slender spermathecae, oval-shaped, with a shallow constriction in the middle, located above or just behind the apical part of the internal chitinous structures of the vulva. Insemination ducts depart from the basal part of the spermathecae, make a sharp turn-out and continue ventro-laterally, reaching the copulatory orifices.

## Etymology

The prefix “*Krypto*”, from Ancient Greek κρυπτός (*kruptós* “hidden”), alludes to the long time it took to diagnose this evolutionary line.

## Distribution

From Bulgaria and Turkey to Croatia, including Montenegro, Bosnia and Herzegovina and Crete. All these species are known only from the type locality, or have small distribution ranges. *K. eremita* is an exception; this species is linked to human activities and can be found in hangars, cellars and cottages. It has been cited from France and Italy to Bulgaria and Turkey. It is a potentially invasive species, found in an abandoned air-raid tunnel in Auckland, New Zealand (Vink & Dupérré 2011).

### Taxonomic remarks

The morphology of both male and female copulatory organs of this group of species shows important differences with respect to *N. cellulanus* (the type species of the genus *Nesticus*) and the western Mediterranean *Nesticus* species, as well as the representatives of *Carpathonesticus* and *Typhlonesticus*. The asymmetrical development of the paracymbial ramification, the shape, size and arrangement of the median apophysis and some differences in the size and arrangement of the TTA p1 and p2 processes constitute the major differences in males. The number and position of spermathecae and the features of the insemination ducts are the most obvious characteristics in females. *K. beroni* and *K. beshkovi* are only known from females. Regardless, the shape and position of the spermathecae and the insemination ducts undoubtedly allow us to transfer these two species to the *Kryptonesticus* evolutionary lineage.

Concerning species of *Nesticus* from other parts of the world (e.g., East Asia, North and South America) we can state that they do not show the diagnostic characters of the new genus described here. Surely this is a polyphyletic group that could be considered as a wastebasket group, and its inclusion within the genus *Nesticus* must be revised since the morphology of their genitalia is remarkably different from the type species of the genus (*N. cellulanus*). Of course, this affirmation must be tested in a phylogenetic framework including all species of *Nesticus* described so far. Preliminary results on the phylogeny of European nesticids, including some American and Asian representatives (results not shown), indicate the polyphyly of *Nesticus* species described from other parts of the world.

### Composition

*Kryptonesticus deelemanae* gen. et sp. nov., *K. eremita* (Simon, 1879) comb. nov. (Southern and Central Europe, introduced in New Zealand, potentially invasive species), *K. arenstorffi* (Kulczyński, 1914) comb. nov. (Bosnia and Herzegovina and Montenegro), *K. fagei* (Kratohvíl, 1933) comb. nov. (Bosnia and Herzegovina), *K. beroni* (Deltshév, 1977) comb. nov. (Bulgaria), *K. beshkovi* (Deltshév, 1979) comb. nov. (Crete), *K. henderickxi* (Bosselaers, 1998) comb. nov. (Crete) and *K. dimensis* (López-Pancorbo, Kunt & Ribera, 2013) comb. nov. (Turkey).

*Kryponesticus deelemanae* gen. et sp. nov.

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Figs 1, 2A, 3A–C, 4A, D, 5A, D

### Diagnosis

The most prominent character of the male bulb is a large and conspicuous median apophysis which emerges from the middle part of the tegulum and reaches its apical part. The most obvious differences between the new species and the closest ones, *K. fagei* and *K. arenstorffi*, are: distal part of MA in the new species is massive and slightly thinner toward the top, while in *K. arenstorffi* the whole distal part is slender and the top is more narrowed; the proximal part of MA of the new species has a round process on the outer edge, while in *K. fagei* and *K. arenstorffi* it has no process. Another important feature is the tooth-like dorsomedian apophysis of the paracymbium's dorsal process, which is not present in *K. fagei* and *K. arenstorffi*. The inner side of the distal part of MA, the curve between the proximal and distal parts of MA, the shape of the tegulum, the basal tegular apophysis and the dorsal paracymbium process are also diagnostic. The epigyne is most similar to that in *K. fagei* and *K. arenstorffi*, from which it differs in the outline of the posterior epigyne margin which is triangular in *K. fagei* and sinuous in other two species. The difference between the new species and *K. arenstorffi* is in the posterior epigyne border, lateral of the central chitinous arches, which is straight in the new species and slightly notched in *K. arenstorffi*. The vulva can be distinguished by the position of the spermathecae, whose apical part in the new species reaches over the vulvar chitinous structures, while it does not in *K. fagei* and *K. arenstorffi*.

### Etymology

The specific name is a patronym in honor of Christa Laetitia Deeleman-Reinhold, an important Dutch arachnologist and a dear friend. Her work has vastly raised the knowledge of the cave spider fauna of Dinarides. The species name is in possessive genitive.

### Material examined

#### Holotype

CROATIA: 1 ♂, Biokovo Mt, Samogorska špilja, 43°19'5.71" N, 17°7'29.9" E, elevation 717 m, 23 Jan. 2016, leg. Marko Lukić (CBSS/AR 3934-1).

#### Paratypes

CROATIA: 1 ♀ (CBSS/AR 3934-2), 1 ♂, 6 ♀♀ (CBSS/AR 3934-5), leg. Marko Lukić; 1 ♂, 1 ♀, leg. Marko Lukić (SMF); 1 ♂, 7 ♀♀, leg. Tin Rožman (CBSS/AR 3932). All with same collection data as the holotype.

#### Other material examined

CROATIA: 1 ♂, Biokovo Mt, Kuna jama, 27 Aug. 1998, leg. Roman Ozimec (CBSS/AR 1495); 1 ♂, Biokovo Mt, Crna Ledenica, 24 Oct. 2006, leg. Marko Lukić (CBSS/AR 1277); 1 ♂, Biokovo Mt, Stonjska peć donja, 27 Oct. 2003, leg. Roman Ozimec (CBSS/AR 1287).

#### Comparative material

TURKEY: *K. dimensis* (López-Pancorbo, Kunt & Ribera, 2013), 1 ♂, 1 ♀, Antalya Province, Alanya District, Kestel Town, Dim Valley, Dim Cave, 3 Dec. 2011, leg. Kadir Boğaç Kunt.

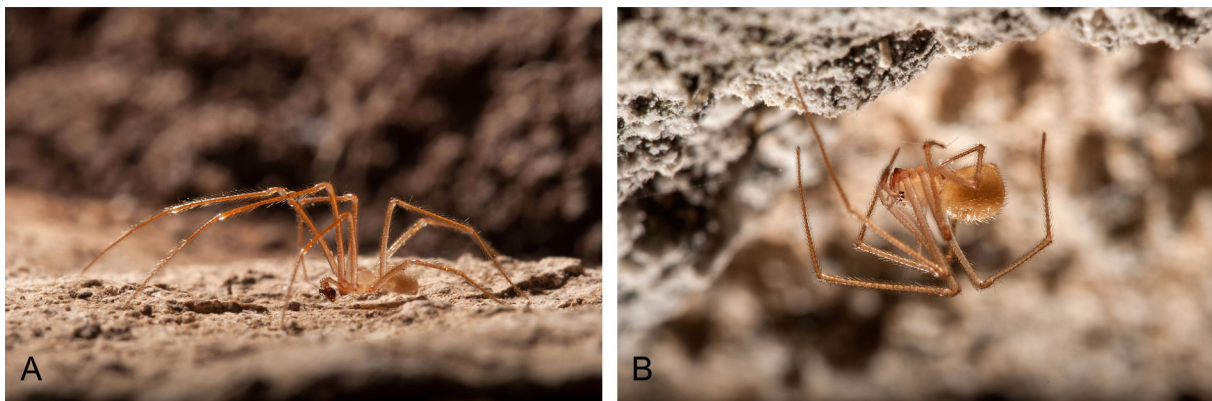
CROATIA: *K. eremita* (Simon, 1879), 2 ♀♀, 2 ♂♂, 2 juv.. (CBSS/AR 1160), Dubrovnik, Osojnik, Močiljska špilja, 21 June 2001, leg. Roman Ozimec. *K. arenstorffi* (Kulczyński, 1914) and *K. fagei* (Kratochvíl, 1933): see below.

### Description

#### Male (holotype)

COLORATION. Carapace uniform whitish, opisthosoma yellowish without marked darker patches. Sternum of the same color as carapace. Appendages slightly darker, especially the distal segments (Fig. 1A).

PROSOMA. Approximately circular in dorsal view. Cephalic region not differentiated from rest of prosoma. Fovea and thoracic grooves visible. Eyes normally developed. Eye size and interocular distances: AM =



**Fig 1.** Habitus of *Kryptonesticus deelemanae* sp. nov. **A.** Male, body length 3.6 mm. **B.** Female, body length 4.3 mm. (Photos by M. Pavlek.)

0.042; AL = 0.081; PM = 0.085; PL = 0.077; AM–AL = 0.07; AM–AM = 0.067; PM–PL = 0.075; PM–PM = 0.129; PL–AL = 0.02.

OPISTHOSOMA. Sub-elliptical in dorsal view.

CHELICERA. Mesal part of promargin with three teeth of about the same size.

MALE PALP. Paracymbium with a well-developed dorsal and very simple ventral processes. Dorsal process with two branches, apical branch parallel to cymbium's longer axis and shorter basal branch pointing to cymbium. Apical branch with parallel rims in proximal part, slightly dilated in middle with distal part acuminate, dagger-shaped. Basal branch with convex upper rim and with distal part sharp and tilted upward (Figs 2A, 3B). Dorsomedian apophysis tooth-like, small with broad base. Ventral process (Figs 2A, 3A) broad, rounded, with transparent middle part and a membranous extension on rim (Figs 2A, 3A). Tegulum with a shallow, rounded and broad longitudinal groove (visible in apical view, Fig. 3C) and with a broad, roughly circular basal apophysis on base (in ventral view). Median apophysis remarkably well developed, V-shaped, distal arm reaching almost to apical part of tegulum. Proximal part of MA with wrinkled outer rim which in posterior view looks like a small process. Outer edge between proximal and distal part equally rounded, distal part of MA mildly narrowing toward top, bluntly ended, with slightly serrated upper edge. Inner side of distal part of MA slightly swollen. Conductor absent. TTA with two processes: TTA p1 and TTA p2 (homologous to processes p1–p6 of the conductor complex in Huber 1993). TTA p1 saddle-shaped, longer than wide, with slim, rounded and pale process on top and in central area with three small dark teeth in a row, middle one smallest and proximal one faintly rounded. TTA p2 located in an apical position, with one sharp and pointed process, the rest forming groove where tip of embolus lodges and which serves as a conductor. Filamentous embolus partially borders tegulum and reaches its apex in semicircular course (Figs 2A, 3A). Measurements: PL: 1.552; PW: 1.407; OL: 2.075; OW: 1.412; TL = 3.627. Leg formula: I > IV > II > III.

Leg	coxa	troch.	femur	patella	tibia	meta.	tarsus	total
I	0.18	0.18	4.20	0.66	4.32	4.12	1.52	15.18
II	0.17	0.20	3.24	0.60	2.97	2.91	1.20	11.30
III	0.17	0.14	2.54	0.53	1.88	2.12	0.91	8.30
IV	0.20	0.17	3.46	0.61	2.92	2.83	1.15	11.34

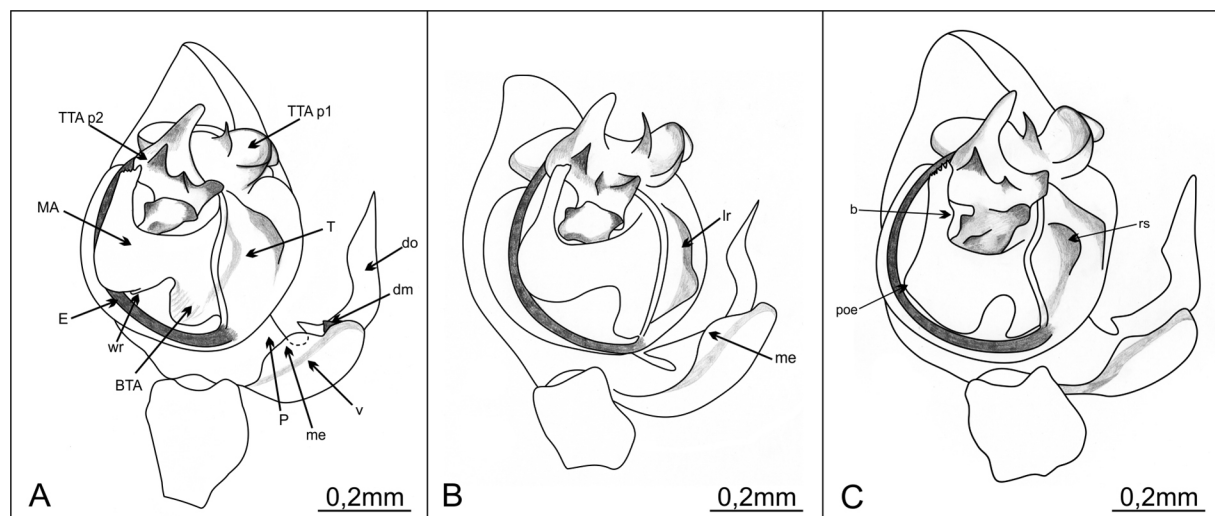
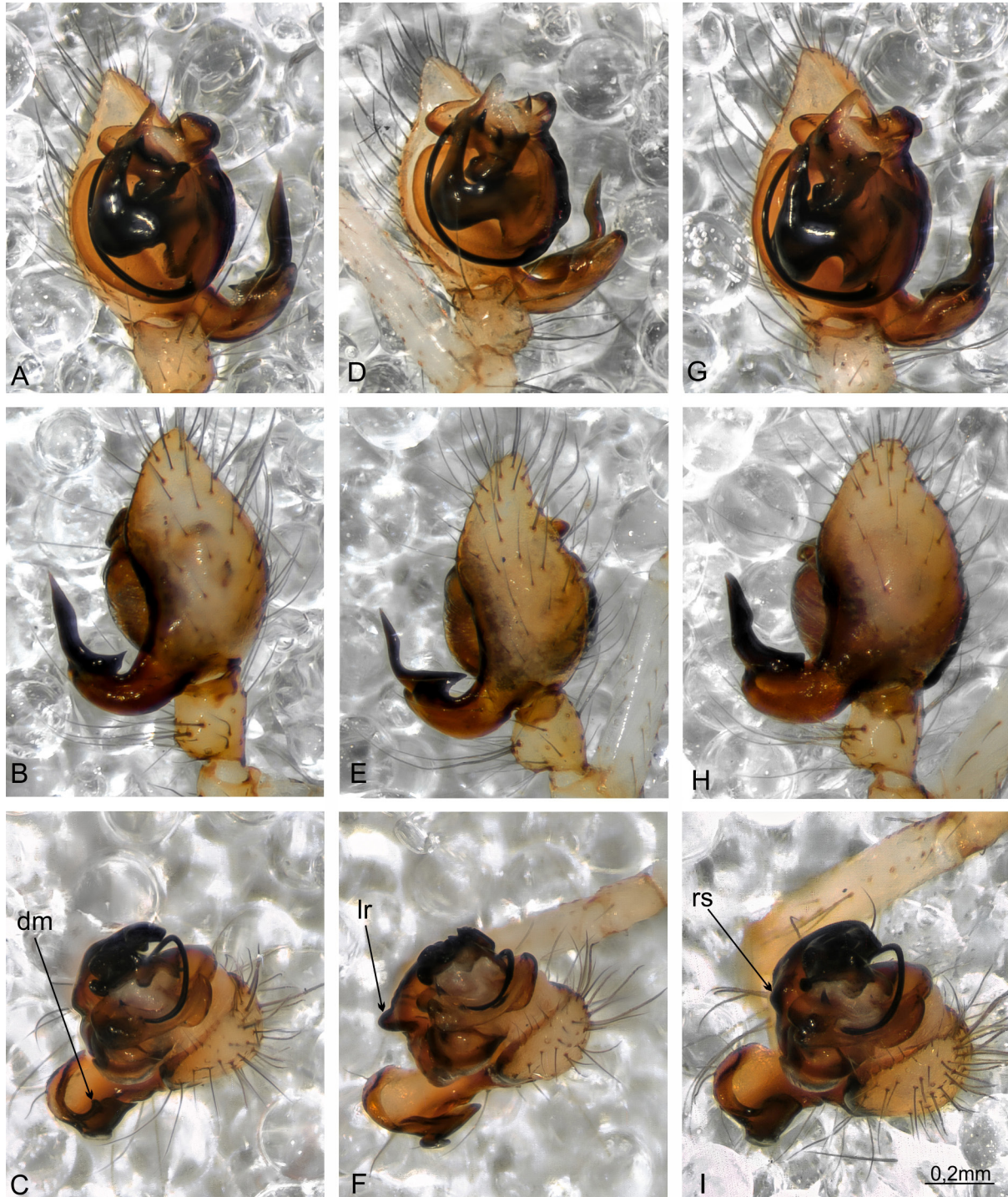


Fig 2. Male bulbus. A. *Kryptonesticus deelemanae* gen. et sp. nov. B. *K. fagei* (Kratochvíl, 1933). C. *K. arenstorffi* (Kulczyński, 1914).



**Female** (paratype CBSS/AR 3934-2)

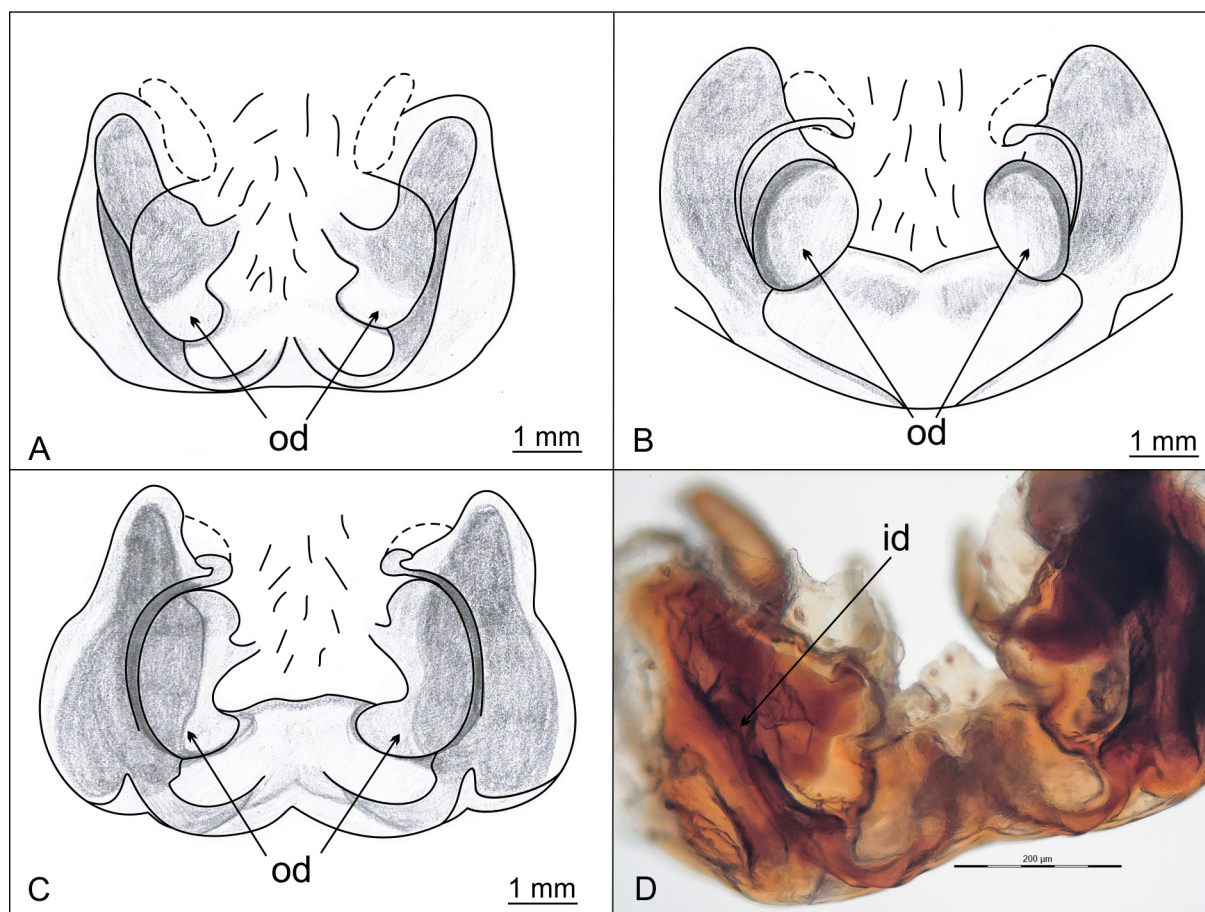
SOMATIC CHARACTERS (Fig. 1B) As in male, except that eye size and interocular distances are a bit different and body length a little larger: AM = 0.052; AL = 0.095; PM = 0.085; PL = 0.076; AM-AL = 0.061;



**Fig 3.** Male bulbus. **A–C.** *Kryptonesticus deelemana* gen. et sp. nov. **D–F.** *K. fagei* (Kratochvíl, 1933). **G–I.** *K. arenstorffi* (Kulczyński, 1914). **A, D, G.** Ventral view. **B, E, H.** Dorsal view. **C, F, I.** Apical view. The scale (shown on I) is the same for all photos.

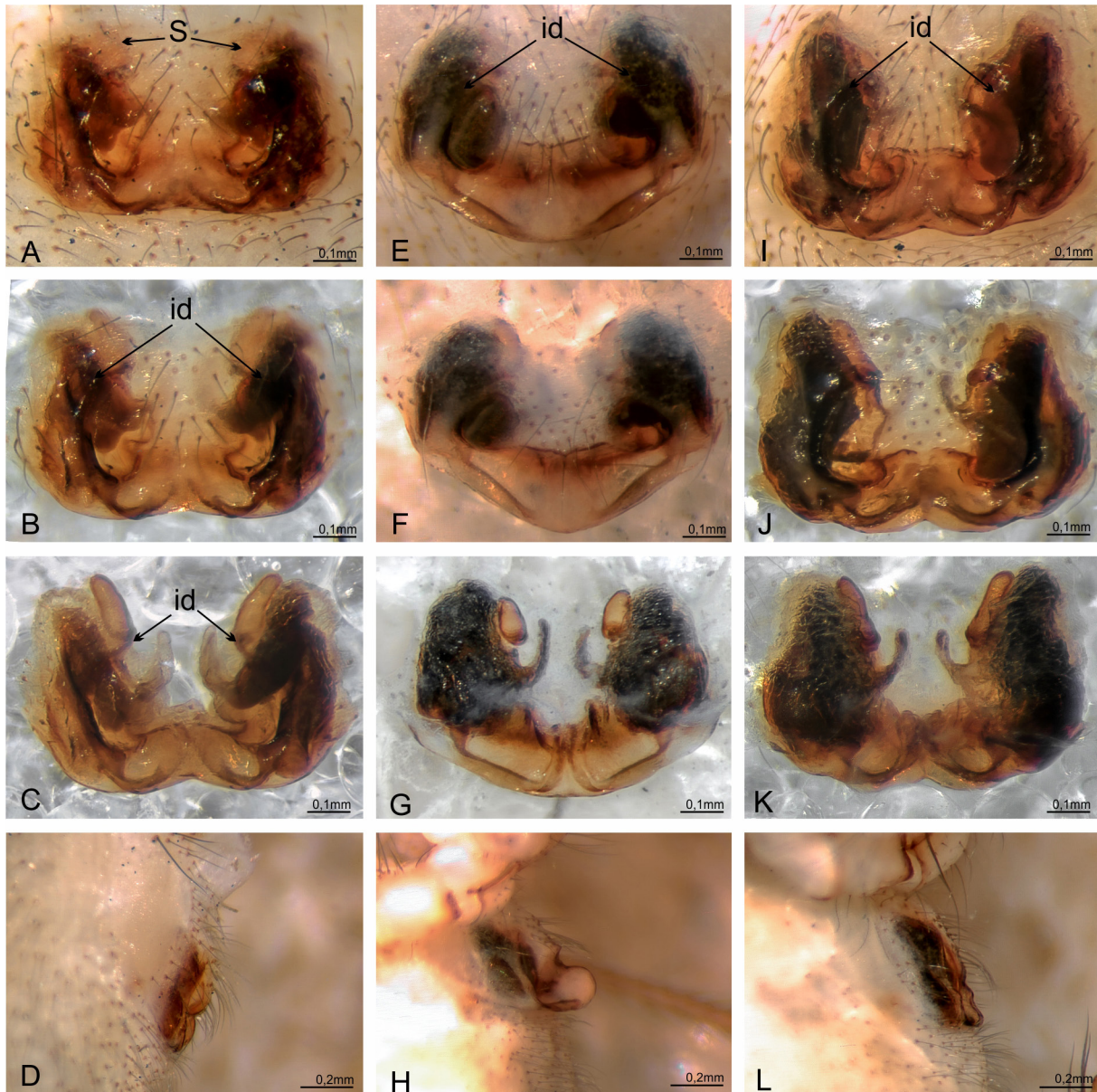
AM–AM = 0.070; PM–PL = 0.128; PM–PM = 0.1112; PL–AL = 0.015. Epigyne slightly wider than long, in lateral view not much protruding (Fig. 5D). Lateral lobes with oval depressions in posterior part, reaching middle of epigyne. Posterior epigyne border made of two semicircular chitinous arches, flanking depressions, coming together in middle and forming a small, pale, inconspicuous convex tubercle. A ridge apically bordering tubercle and depressions faintly visible. Epigyne outline, laterally from semicircular chitinous arches, straight, with no notches (Figs 4A, 5A–B).

**VULVA.** Lateral sides of vulva made of compact dark chitinous structures enclosed in a firm transparent membrane (lateral pouches). Oval shaped spermathecae, with a shallow constriction in middle, located just above chitinous vulval structures (dorsal view). Narrower, upper part of spermathecae protrudes above chitinous vulval structures (Fig. 5C). Insemination ducts depart from spermathecae at bottom (Fig. 5C), make a sharp turn outwards and continue ventro-laterally in semicircular course to reach copulatory orifices (Fig. 4D). In ventral view, spermathecae slightly visible above lateral dark structures, while chitinous curves, through which insemination ducts run visible on both sides of epigyne (Fig. 4A). Two chitinous narrow, horn-like apophyses protrude from inner sides of dark chitinous vulval structures, in apical direction, to empty middle part of vulva (Fig. 5C). Measurements: PL: 1,666; PW: 1,414; OL: 2,609; OW: 1,872; TL = 4,275. Leg formula: I > IV > II > III.



**Fig 4.** Epigyne and vulva. **A.** *Kryptonesticus deelemanae* gen. et sp. nov., epigyne. **B.** *K. fagei* (Kratochvíl, 1933), epigyne. **C.** *K. arenstorffi* (Kulczyński, 1914), epigyne. **D.** *K. deelemanae* gen. et sp. nov. vulva. Broken lines mark the positions of the spermathecae.

Leg	coxa	troch.	femur	patella	tibia	meta.	tarsus	total
I	0.26	0.18	4.09	0.72	4.15	3.79	1.45	14.64
II	0.19	0.15	3.14	0.63	2.81	2.58	1.18	10.69
III	0.17	0.14	2.44	0.54	1.68	1.88	0.90	7.74
IV	0.18	0.16	3.52	0.64	2.76	2.70	1.08	11.04



**Fig 5.** Epigyne and vulva. **A–D.** *Kryptonesticus deelemanae* gen. et sp. nov. **E–H.** *K. fagei* (Kratochvil, 1933). **I–L.** *K. arenstorffi* (Kulczyński, 1914). **A, E, I.** Epigyne in ventral view. **B, F, J.** Epigyne in ventral view after detachment from the opisthosoma. **C, G, K.** Vulva after treatment with 30% KOH. **D, H, L.** Epigyne in lateral view.

## Distribution

The new species is endemic to Croatia; it is distributed on Biokovo Mt in central Dalmatia, a coastal region in Croatia. So far it has been recorded in 20 caves scattered through the whole mountain, from the south-west sea side to the north-east continental side, from the 310 to 1640 asl (Fig. 6A). Data on all records of *K. deelemanae* gen. et sp. nov. are given in Appendix 2. The distribution area of *K. deelemanae* gen. et sp. nov. is more than 80 km away from that of *K. fagei* and more than 100 km from that of *K. arenstorffi* (Fig. 6B).

## Natural history

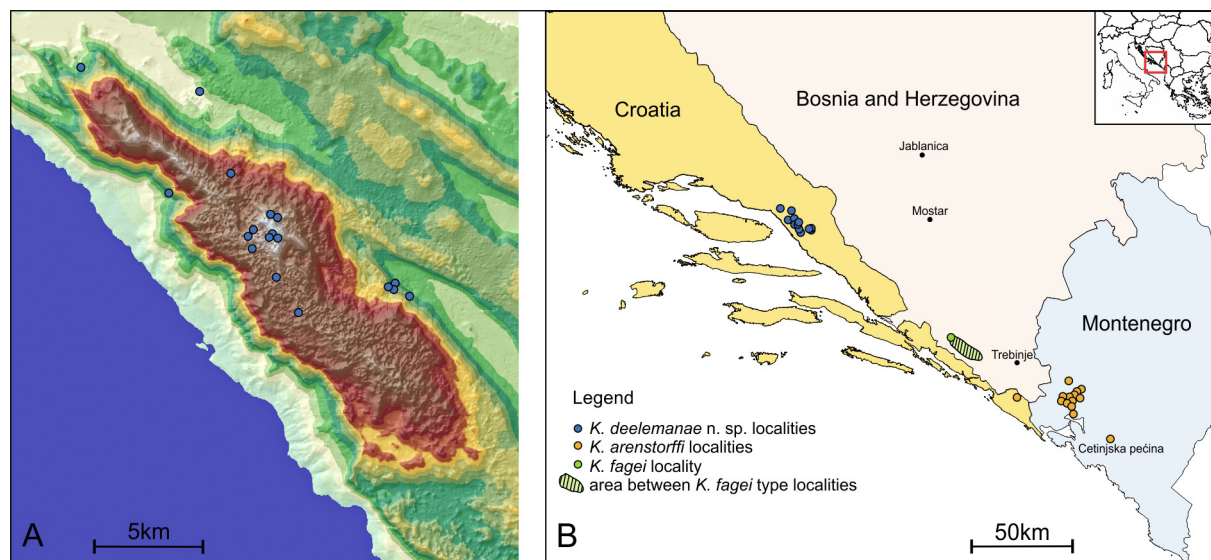
The type locality, Samogorska špilja, is a small cave with two entrances (Fig. 7). On the date of the last collection, 23 Jan. 2016, the air temperature in the cave was 0.5°C with cold air streaming through the cave, mostly near the cave floor. Spiders were found freely walking on the ceiling of the chamber (probably avoiding the cold air flow at the bottom) and on the side walls of the cave. The temperature in other caves where *K. deelemanae* gen. et sp. nov. is found ranges from 0 to 15°C. Some of those caves are very small and are greatly influenced by outside conditions (like the type locality), while the others are quite big, have a true cave microclimate and harbor diverse types of cave habitats (for example Pretnerova jama, a 254-meter deep pit). No other nestigid species are found in caves on Biokovo Mt.

*Kryptonesticus fagei* (Kratohvil, 1933) comb. nov.  
Figs 2B, 3D–F, 4B, 5E–H

*Nesticus fagei* Kratochvil, 1933: 44, 64, pl. 1, fig 4, pl. 2, fig 22, pl. 4, figs 37–40.

*Nesticus fagei* – Gasparo & Thaler 2000: 32, figs 3–4. — Le Peru 2011: 364, fig. 630.

*Ivesia fagei* – Lehtinen & Saaristo 1980: 51.



**Fig 6.** Distribution maps. **A.** Map of Biokovo Mt with distribution of *Kryptonesticus deelemanae* gen. et sp. nov. **B.** Map with distributions of *K. deelemanae* gen. et sp. nov., *K. fagei* (Kratohvil, 1933) and *K. arenstorffi* (Kulczyński, 1914). Marked is the town of Trebinje, near the type locality for *K. arenstorffi*, and also the towns of Mostar and Jablanica, between which is Čudna jama, a dubious record for *K. arenstorffi*. Also marked is Cetinjska pećina, the southernmost locality for *K. arenstorffi*.

## Diagnosis

Proximal part of MA without process on outer edge, inner side of distal part of MA straight, curve between proximal and distal parts of MA equally rounded. Tegulum with longitudinal ridge stretching through entire surface, basal apophysis of tegulum triangular. Apical branch of dorsal paracymbium process curved in “S” shape, dorsomedian apophysis absent. Epigyne triangular in ventral view, protruding in lateral view. Spermathecae not reaching over vulvar lateral chitinous structures.

## Type material

Not examined. The exact position of the type localities is not known and the surrounding area is at the moment inaccessible (for details see Distribution).

## Material examined

BOSNIA AND HERZEGOVINA: Popovo polje, Bjelušica: 1 ♂ (CBSS/AR 3701-1), 1 ♀ (CBSS/AR 3701-2), 1 ♂ (CBSS/AR 3690), 26 Oct. 2015, leg. Martina Pavlek; 3 ♀♀, 1 juv. ♂, 1 juv., 26 Oct. 2015, leg. Vedran Sudar (CBSS/AR 3692); 1 ♀ (CBSS/AR 1510), 1 ♂, 1 juv. ♂, 1 juv. (CBSS/AR 1513), 16 Aug. 2004, leg. Roman Ozimec; 1 ♀, 4 Jun. 2014, leg. Martina Pavlek (CBSS/AR 3389).

## Redescription

### Male (CBSS/AR 3701-1)

Paracymbium with a well-developed dorsal and simple ventral process. Basal branch of dorsal process with straight upper rim, distal part longer and less sharp than in *K. deelemanae* gen. et sp. nov., more pronounced. Apical branch slender, curved in “S” shape, distal part acuminate and sharp (Figs 2B, 3E). Ventral process larger than in *K. deelemanae* gen. et sp. nov., broad and round, most of its surface transparent and with small membranous extension on rim. Dorsomedial apophysis absent (Fig. 3D). Tegulum with longitudinal ridge (in apical view) stretching through entire surface and reaching broad-based triangular basal apophysis (Figs 2B, 3F). Median apophysis well developed, V-shaped, distal arm reaching almost to the apical part of tegulum. Outer edge between proximal and distal part equally rounded, distal part of MA

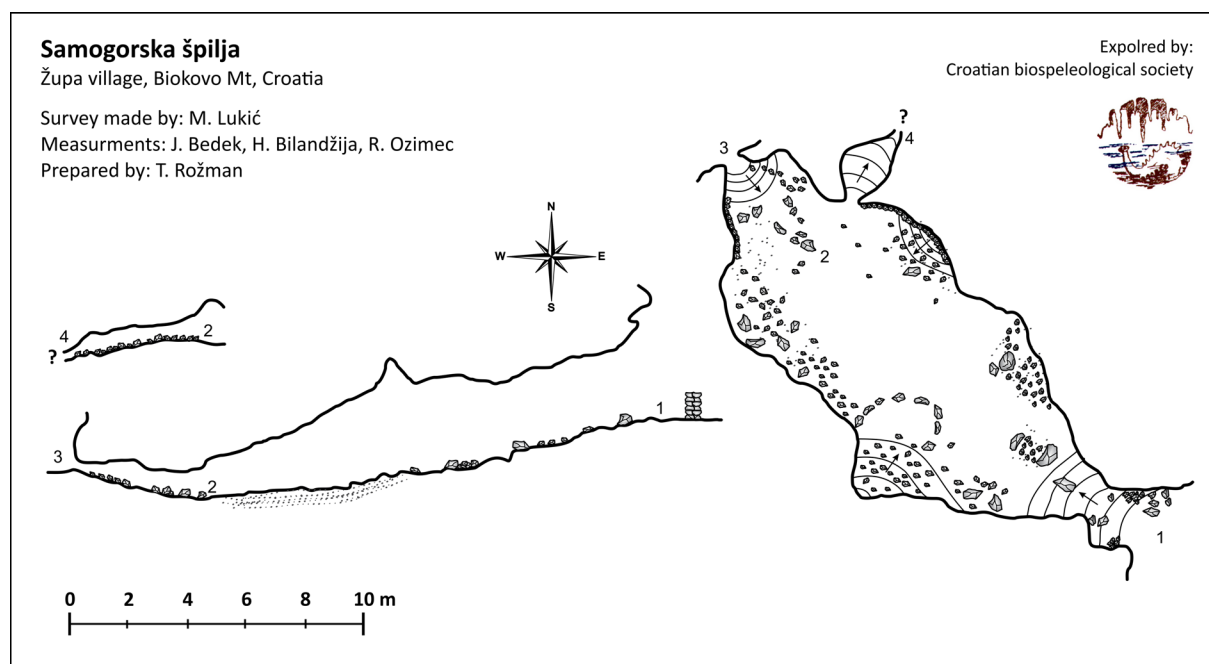


Fig 7. A survey of the *K. deelemanae* gen. et sp. nov. type locality: Samogorska špilja.

narrowing toward top, which ends bluntly with slightly serrated upper edge. Inner side of distal part of MA straight. Embolus, TTA p1 and TTA p2 of TTA similar to in *K. deelemanae* gen. et sp. nov. (Figs 2B, 3D).

#### **Female** (CBSS/AR 3701-2)

**EPIGYNE.** Slightly wider than long. Lateral lobes with oval depressions in posterior part, reaching middle of epigyne. Posterior epigyne border triangular in ventral view, made of two straight chitinous arches which flank depressions, come together in middle and after sharp inward turn form broad and pale convex tubercle (Figs 4B, 5E–F), protruding in lateral view (Fig. 5H). Insemination ducts visible on both sides of epigyne in a form of chitinous curves (Figs 4B, 5E–F).

**VULVA.** Lateral sides of vulva made of compact dark chitinous structures enclosed in firm transparent membrane (lateral pouches). Spermathecae oval-shaped, with shallow constriction in middle, narrower in upper part and less slender than in *K. deelemanae* gen. et sp. nov., located meso-apically behind dark chitinous lateral structures. Insemination ducts depart from bottom of spermathecae, make sharp turn outwards and continue to epigynal base. Two chitinous narrow, horn-like structures protrude from inner sides of dark chitinous vulval structures, in apical direction, to empty middle part of vulva (Fig. 5G).

#### **Distribution**

This species was described based on the material collected by Kratochvíl in several caves in Herzegovina, on the north-west border of Popovo polje: Pećina kod Tamnicam and Jama za Jamskim vrhom near Belenići village and Pčelina pećina near Nevada village (Kratochvíl 1933). The type material is deposited in the National Museum in Prague (Ružička *et al.* 2005). The area where the type localities are is inaccessible at the moment because of the mine fields left after the civil war in Bosnia and Herzegovina in the 1990s. The species is known from only one more locality, Bjelušica (Dresco 1966; Kratochvíl 1936), a horizontal cave around 4 km north of Belenići village (Fig. 6B). The material for this redescription was collected there. The species is endemic for Bosnia and Herzegovina and the citation of ‘Montenegro’ in ‘The Spiders of Europe’ (Nentwig *et al.* 2016) is erroneous.

#### **Natural history**

Bjelušica is a small cave, around 150 m long. From the semi-dark entrance chamber departs a narrowing, 1 × 2 meters wide passage that leads to the main channel which, after the first few meters that are slightly lighter, is always in complete darkness. The spiders were found right after the narrowing and all along the cave. They were mostly hanging from their nets on the walls and between the big stones on the cave floor, or freely walking on the walls of the cave. The temperature in the cave is around 13.5°C. In his paper with the description of *K. fagei* (Kratochvíl 1933), Kratochvíl also listed *K. eremita* at one of the type localities, Jama za Jamskim vrhom. Since it is not common for two species of the same genus to inhabit the same cave, we wanted to check the original material, but that was unfortunately impossible since the specimens deposited in the museum in Prague are without pedipalps (personal communication with Petr Dolejš, curator of the spider collection). In the last 20 years, researchers from CBSS have visited many caves around the town of Trebinje, in the Popovo polje area, and in the hilly region between Popovo polje and Croatia, but have so far recovered no *K. eremita*.

*Kryptonesticus arenstorffi* (Kulczyński, 1914) comb. nov.

Figs 2C, 3G–I, 4C, 5I–L

*Nesticus arenstorffi* Kulczyński, 1914: 378, pl. 16, fig. 50.

*Nesticus arenstorffi* – Kratochvíl 1933: 42, 64, pl. 1, fig. 5, pl. 4, figs 34–36. — Le Peru 2011: 361, fig. 620.

*Ivesia arenstorffi* – Lehtinen & Saaristo 1980: 51.

### Diagnosis

Proximal part of MA without process on outer edge, inner side of distal part of MA with bulge in middle, edge between proximal and distal part of MA pointed. Tegulum with triangular basal apophysis. Dorsomedian apophysis of paracymbium absent. Posterior epigyne outline wavy, ridge apically bordering lateral depressions well visible. Spermathecae not reaching over vulvar lateral chitinous structures.

### Type material

Not examined. The exact position of the type locality is unknown (for details see Distribution).

### Material examined

MONTENEGRO: 1 ♂ (CBSS/AR 3288-1), 1 ♀ (CBSS/AR 3288-2), Kotorski zaljev, Golodražnica, 31 Mar. 2012, leg. Ana Komerički; 1 ♀ (CBSS/AR 3641-1), 1 ♀, 3 ♂♂, Cetinje, Cetinjska pećina, 28 Oct. 2015, leg. Martina Pavlek (CBSS/AR 3641-2).

### Redescription

#### Male (CBSS/AR 3288-1)

Paracymbium with well-developed dorsal and simple ventral process. Basal branch of dorsal process with slightly convex upper rim which ends in the shape of an indistinct minor blunt tooth. Longer apical branch similar to that in *K. deelemanae* gen. et sp. nov. but more robust, dilated in middle and attenuated towards top (Figs 2D, 3H). Ventral process broad and round, with transparent middle part and no membranous extension on rim. Dorsomedial apophysis absent (Fig. 3G). Tegulum with inconspicuous groove, low round swelling in apical part (Fig. 2B, in apical view in Fig. 3I), and with triangular broad-based basal apophysis. Median apophysis well developed, V-shaped, distal arm reaching almost to apical part of tegulum. Outer edge between proximal and distal part pointed, not equally rounded as in *K. deelemanae* gen. et sp. nov. and *K. fagei*. Distal part of MA narrowing toward top; top bluntly ended with serrated upper edge. Inner side of distal part of MA with bulge in middle. Embolus, TTA p1 and TTA p2 of TTA similar to those in *K. deelemanae* gen. et sp. nov. (Figs 2D, 3G).

#### Female (CBSS/AR 3641-1)

EPIGYNE. Slightly wider than long. In lateral view not protruding very much (Fig. 5L). Lateral lobes with oval depressions in posterior part, reaching middle of epigyne. Posterior epigyne border made of two semicircular chitinous arches, flanking depressions and coming together in middle, forming a small, pale, inconspicuous convex tubercle. Ridge apically bordering tubercle well visible. Epigyne outline, laterally of semicircular chitinous arches, with shallow notches. In ventral view, chitinous curves through which insemination ducts extend visible on both sides of epigyne (Figs 4C, 5I–J).

VULVA. Lateral sides of vulva made of compact dark chitinous structures enclosed in firm transparent membrane (lateral pouches). Spermathecae slender, oval-shaped, with shallow constriction in middle, located meso-apically behind dark chitinous lateral structures. Insemination ducts depart at bottom and extend to epigynal base. Two chitinous narrow, horn-like structures protrude from inner sides of dark chitinous lateral structures, in apical direction, to empty middle part of vulva (Fig. 5K).

### Distribution

The type locality is Laketićeva pećina near the town of Trebinje in Bosnia and Herzegovina (Kulczyński 1914). Since the original description, it has not been collected at the type locality and its exact position is at the moment unknown. In the surroundings of the town of Trebinje no cave with such a name is known. The type material is deposited in the National Museum in Prague (Ružička *et al.* 2005). The species is also known from Čudna jama near Mostar (Fage 1931) and from 19 more caves in Montenegro (Kratochvíl 1933, 1935; Deeleman-Reinhold 1974). Recently, the species has been recorded in three

more caves: Cetinjska pećina as reported by Deltšev *et al.* (2014) and personal observations, Pećina Vojvode Dakovića (pers. obs.) in Montenegro, and from cave Jezero on Sniježnica Mt which is the first record for Croatia (all records from the CBSS collection are listed in Appendix 3). All localities are marked on the map in Fig. 6B. In the last 20 years, researchers from CBSS visited many caves around the town of Trebinje, in the Popovo polje region and in other parts of Bosnia and Herzegovina, but recovered no *K. arenstorffi*. Čudna jama near Mostar is far away from all certain *K. arenstorffi* localities and we wanted to check that material, deposited in the National Museum in Prague, but unfortunately there are only two subadult males and a juvenile inside the vial (personal communication with Petr Dolejš, curator of the spider collection) so the taxonomical status of the samples could not be confirmed. We consider that locality dubious. The citation of Serbia in ‘The Spiders of Europe’ (Nentwig *et al.* 2016) is erroneous.

### Natural history

*K. arenstorffi* specimens were mostly found hanging upside down from the webs, in the entrance part but also deeper in the caves. The temperature in the caves where *K. arenstorffi* has recently been collected ranges between 5°C and 15°C. Generally, in all caves where *K. arenstorffi* was recorded no other nesticid species was present, except in Cetinjska pećina in the town of Cetinje in Montenegro. This cave is inhabited by the troglotic species *Typhlonesticus absoloni* as reported by Christa Deeleman-Reinhold (1974), and it has also been collected recently (Appendix 4). It is worth noting that in her 1974 paper, Christa Deeleman-Reinhold did not mention the presence of *K. arenstorffi*. Her collecting trip was in 1972, before Cetinjska pećina was adapted for touristic visits and before a tunnel was dug into the cave from the outside (in the 1980s). The tunnel has surely changed the microclimatic conditions in the cave by introducing a constant air flow, so it could have made some parts of the cave less suitable for the troglotic *Typhlonesticus absoloni* (found only in deeper parts), but more accommodating for the less troglomorphic *K. arenstorffi*.

### Molecular data

Specimens, localities and sequences with corresponding GenBank accession numbers analyzed in the present study are listed in Appendix 1. The concatenated matrix used in phylogenetic analyses includes 12 terminals and 1699 aligned characters (*cox1* = 931, *rrn* = 451 and *H3* = 317). Primer fidelity across taxa was not always consistent in *cox1*, which is why some specimens have slightly truncated sequence lengths. The preferred partitioning scheme included three partitions: the first and second position of the *cox1* and *H3* gene fragments; the third codon position of *cox1* and *H3*; and *rrnL*. Uncorrected *cox1* pairwise (p)-distances among terminal taxa and within and between genera are summarized in Appendix 5.

Fig. 8 shows the ML tree inferred using the combined data matrix. *Kryptonesticus*, *Nesticus* and *Carpathonesticus* show high bootstrap support (81, 90 and 100 respectively). Among representatives of *Kryptonesticus*, the new species clusters with *K. arenstorffi* and *K. fagei*, the geographically closest species, with a low bootstrap value. The remaining three species (*K. henderickxi*, *K. eremita* and *K. dimensis*) are poorly supported (low bootstrap support) and do not allow us to determine its internal relationships. *N. cellulanus*, the type species of the genus *Nesticus*, is the sister species of the representatives of *Carpathonesticus* included in this analysis.

The topologies of the partial analyses of the three genes separately were almost identical at the genus level and no inconsistencies were detected. In *cox1* and *rrn*, *N. cellulanus* is the sister species of the *Carpathonesticus* evolutionary line, while *Kryptonesticus* gen. nov. is the sister group of the clade formed by *Nesticus* and *Carpathonesticus*. In *H3* partial sequences, these three evolutionary lines are



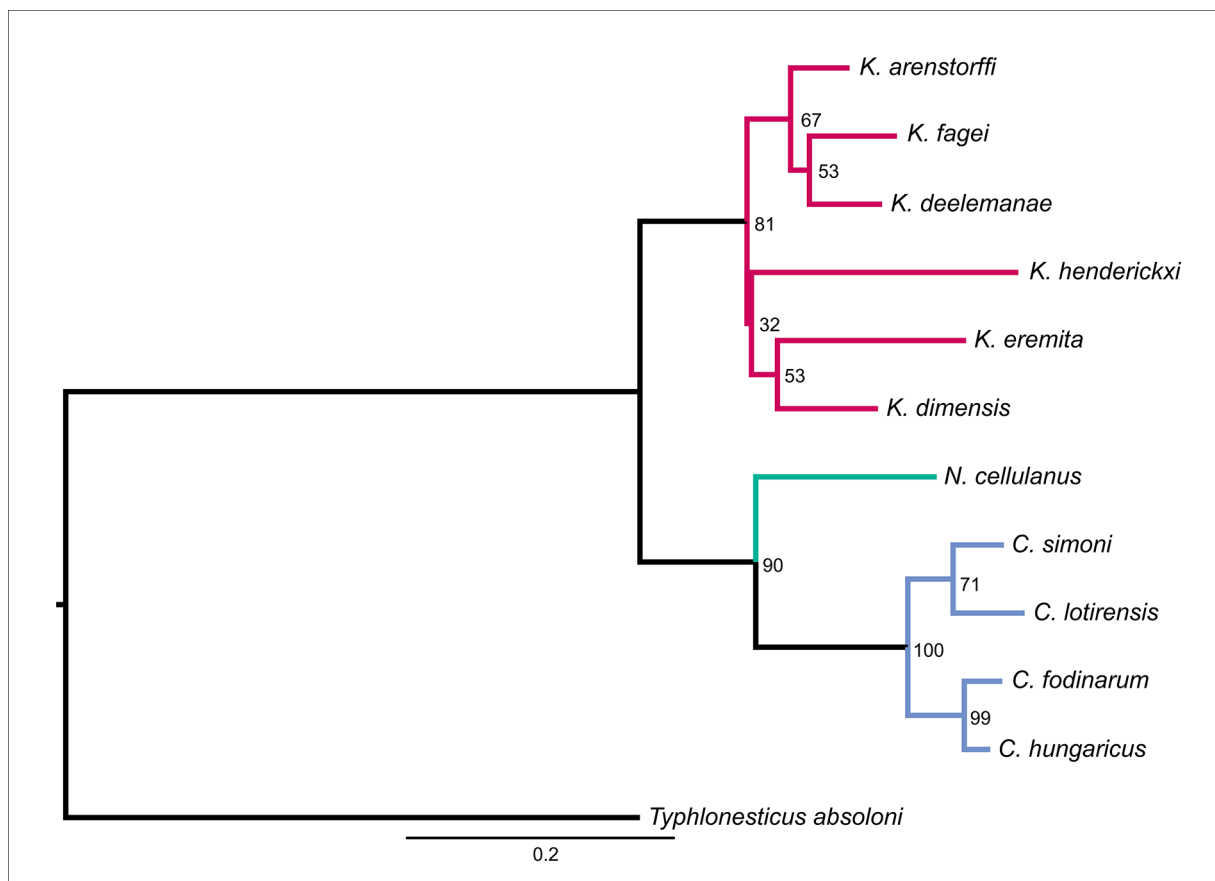
also present (*N. cellulanus*, *Kryptonesticus* and *Carpathonesticus*) but forming a polytomy at the generic level.

Within the *Kryptonesticus* clade, only *H3* shows good bootstrap support for *K. fagei*, *K. arenstorffi* and *K. deelemanae* gen. et sp. nov. (90%), while with *rrnL* only *K. deelemanae* gen. et sp. nov. and *K. arenstorffi* show bootstrap support, although very low (59%), while with *cox1* no support exists for these species.

The mean uncorrected p-distances of *cox1* between and within taxa analyzed (Appendix 5) show high values. The mean p-distance between genera ranges from 17.5% (*Typhlonesticus* vs *Carpathonesticus*) to 10.9% (*Nesticus* vs *Carpathonesticus*). The genetic divergences between *Kryptonesticus* gen. nov. and *Typhlonesticus*, *Carpathonesticus* and *Nesticus* are 16.6, 11.7 and 12.1%, respectively. The average evolutionary divergence between representatives within the new genus is 8.2% (6.2% among the three species from Dinarides).

## Discussion

This paper describes a new genus belonging to the Nesticidae. The molecular phylogenetic analysis includes the type species of the genera *Nesticus*, *Carpathonesticus* and *Thyphlonesticus*, all from the Mediterranean Basin. It indicates that *Nesticus cellulanus*, the type species of *Nesticus*, is sister to a



**Fig 8.** ML tree inferred from a concatenated matrix of *cox1* and *rrn* mtDNA and *H3* nuDNA gene fragments. Numbers next to nodes correspond to bootstrap support values. The tree was rooted using *Typhlonesticus absoloni* (Kratochvíl, 1933).

group containing all the species of *Carpathonesticus* included in the analysis (bootstrap support 90%), including the type species. The new genus constitutes a well-defined and independent evolutionary lineage with a high bootstrap support and shows mean uncorrected p-distances of *cox1* of 11.7 versus *Carpathonesticus* and 12.1 versus *Nesticus cellulanus*. *Typhlonesticus* is clearly more distanced (16.6). From a morphological point of view, *Kryptonesticus* gen. et sp. nov. is also well defined. The large size and the shape of the median apophysis in males, and the shape and position of spermathecae and insemination ducts in females, constitute the main diagnostic characteristics. This is in accordance with Kratochvíl's Dinaric group, in which he placed *K. fagei* and *K. arenstorffi* (Kratochvíl 1933), the only species now referred to *Kryptonesticus* gen. nov. known at that time. It does not include *K. eremita* which is morphologically the most aberrant within the genus. Accordingly, we propose the following new combinations:

*Kryptonesticus eremita* (Simon, 1879) comb. nov. (ex *Nesticus eremita* Simon, 1880: 258)  
*Kryptonesticus arenstorffi* (Kulczyński, 1914) comb. nov. (ex *Nesticus arenstorffi* Kulczyński, 1914: 378)  
*Kryptonesticus fagei* (Kratochvíl, 1933) comb. nov. (ex *Nesticus fagei* Kratochvíl, 1933: 44)  
*Kryptonesticus beroni* (Deltshev, 1977) comb. nov. (ex *Nesticus beroni* Deltshev, 1977: 75)  
*Kryptonesticus beshkovi* (Deltshev, 1979) comb. nov. (ex *Nesticus beshkovi* Deltshev, 1979: 53)  
*Kryptonesticus henderickxi* (Bosselaers, 1998) comb. nov. (ex *Nesticus henderickxi* Bosselaers, 1998: 9)  
*Kryptonesticus dimensis* (López-Pancorbo, Kunt & Ribera, 2013) comb. nov. (ex *Nesticus dimensis* López-Pancorbo *et al.*, 2013: 185)

The presence of “pipette setae” (Grall & Jäger 2016) in males of *Kryptonesticus* gen. nov. supports the proposition that it is a potential new diagnostic character for Nesticidae (we can also confirm its presence in males of *Typhlonesticus absoloni*).

There is great confusion about the identity of *N. speluncarum* Pavesi, 1873, an endemic species from northern Italy. Several authors have considered it a subspecies of *N. eremita* (Simon 1929; Kratochvíl 1934); however, the drawings of the male palp (not the female) of this species clearly separate it from other known species (Brignoli 1971; Caporiacco 1934; Dresco 1966). Its distribution is also not clear, although quite restricted. In our last two papers on nesticids (López-Pancorbo *et al.* 2013; Ribera *et al.* 2014) we included partial sequences of *cox1* and *H3* (GenBank accession numbers KF417421 and KF417405) from *N. speluncarum*. After a revision of the material identified, we noticed an error in the identification of this species. It is not *N. speluncarum*, but *K. eremita*, and for that reason it has not been included in this work.

A very special trait of several species of this new genus (*K. beroni* from Bulgaria, *K. beshkovi* and *K. henderickxi* from Crete, and *K. dimensis* from Turkey) is their possession of highly troglomorphic characteristics, such as the absence of, or very reduced, eyes (size and number), and the lack of body pigmentation. In addition, these species are known from a single or a small number of caves. These data suggest that these species are probably very sensitive to disturbances in their environment and are thus clear candidates for protection: they have highly restricted ranges and show a high degree of adaptation to the subterranean environment.

## Acknowledgments

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Balabanić for advice on the Latin name of the new species and to Nevenka Meštrović Radan, a mentor of the ESF project. Also thanks to Miguel A. Arnedo for using the lupa, Marcos Roca-Cusachs for help with drawing and Humbert Salvadó for using the microscope. Thanks to Lida Lamza and Rebecca J. Wilson for English check.

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**Appendix 1.** Specimens, localities and sequences with corresponding GenBank accession numbers analyzed in the present study (sequences with \* are new for this study).

Species	Locality	<i>Cox1</i>	<i>rmL</i>	<i>H3</i>
<i>K. deelemanae</i> gen. et sp. nov.	Samogorska špilja, Biokovo Mt., Croatia (43°19'5,71" N, 17°7'29,9" E, 717 m)	KX632167*	KX632160*	KX611237*
<i>K. fagei</i>	Bjelušica, Popovo polje, Bosnia and Herzegovina (42°50'41" N, E 17°58'43" E, 350 m)	KX632166*	KX632159*	KX611236*
<i>K. arenstorffi</i>	Čora pećina, Crni nugli, Dragaljsko polje, Gornje Krivošije, Selakov do, Risan Distr., Montenegro (42°35'36,5" N, E 18°41'41,6" E, 750 m)	KF417407	KF417403	KF417422
<i>K. eremita</i>	Pišurka (=Paganetijeva pećina), town of Korčula, Korčula Isl., Croatia (42°57'33,83" N, E 17°7'45,26" E, 58 m)	KX632165*	KF417400	–
<i>K. henderickxi</i>	Kournas Cave, Kournas, Crete	KX632164*	KF417404	–
<i>K. dimensis</i>	Dim Cave, Taurus Mountains, Alanya District. Turkey (36°32'337" N, 32°06'599" E, 189 m)	KF417406	KF417401	KF417420
<i>N. cellulanus</i>	Manantiales Monte Castro, Sueces, Castelló, Spain	KX632163*	EU746444	KX611235*
<i>C. fodinarum</i>	Pesterea Cave, Poarte lui Joarnele, Giarda, Alba, Garda, Romania	KX632162*	KX632158*	
<i>C. lotriensis</i>	Unnamed cave in Lotrioara Valley, Lotrului Mountains, Sibiu, Romania (45°34'45,8319" N, 24°11'16,7493")	KX632161*	KF417399	KF417418
<i>C. hungaricus</i>	Pestera cave, Liliecilor, Cheile Ampoitei Gorges, Romania (46°08'21,7748" N, 23°23'39,8507")	KF417412	KF417402	KF417419
<i>C. simoni</i>	Unnamed cave in Bisbrita Gorges, Stogu-Vinturarita Mts., Romania (45°11'42,2789" N, 24°02'03,2702" E, 491 m)	KF417408	KF417398	KF417417
<i>T. absoloni</i>	Baba Tuša cave, Trnovo, Virpazar Distr., Montenegro (42°17'25,1" N, 19°02'10,8" E, 350 m)	KF417410	KF417397	KF417416

**Appendix 2.** All records of *K. deelemanae* gen. et sp. nov. from the CBSS collection. Date format: dd.mm.yyyy.

CBSS coll. number	Cave name	Location of the cave	Collection date	Collector	Number and gender of specimens
AR: 1268	Kukor	Croatia, Biokovo Mt., Bast village	8.9.2005	Roman Ozimec	1 ♀
AR: 1269	Ograđena špilja pod Sv. Jurem	Croatia, Biokovo Mt., Sv. Jure	21.6.2003	Branko Jalžić	2 juv.
AR: 1271	Matijaševa peć	Croatia, Biokovo Mt., Župa village	4.4.2006	Helena Bilandžija	1 juv.
AR: 1272	Kukor	Croatia, Biokovo Mt., Bast village	27.7.2004	Roman Ozimec	1 juv.
AR: 1273	Špilja u Radinovicima	Croatia, Biokovo Mt., Zagvozd, Rastovac village	25.10.2006	Roman Ozimec	2 ♀♀, 2 ♂♂, 2 juv.
AR: 1274	Poskokova rupa	Croatia, Biokovo Mt., Župa village	25.5.2004	Roman Ozimec	1 ♀
AR: 1275	Kukor	Croatia, Biokovo Mt., Bast village	19.6.2002	Roman Ozimec	1 ♀, 2 juv.
AR: 1276	Kukor	Croatia, Biokovo Mt., Bast village	29.10.2006	Roman Ozimec	1 ♀
AR: 1277	Crna Ledenica	Croatia, Biokovo Mt., Sv. Jure	24.10.2006	Marko Lukić	1 ♂
AR: 1281	Ledenica kod Stare škole	Croatia, Biokovo Mt., Sv. Jure, Barišna torina	28.6.2002	Branko Jalžić	2 juv.
AR: 1284	Spasiteljica špilja	Croatia, Biokovo Mt., Gornja Brela, Bartulovići village	23.3.2003	Jana Bedek	1 ♀
AR: 1285	Mala jama u stijenama	Croatia, Biokovo Mt., Kaoci	20.6.2003	Branko Jalžić	1 juv.
AR: 1286	Kukor	Croatia, Biokovo Mt., Bast village	6.4.2006	Martina Pavlek	1 juv.
AR: 1287	Stonjska peć donja	Croatia, Biokovo Mt., Župa village	27.10.2003	Roman Ozimec	1 ♂, 1 juv.
AR: 1288	Kuna špilja	Croatia, Biokovo Mt., Kadulja peak	15.6.2002	Roman Ozimec	1 juv. ♂
AR: 1289	Kukor	Croatia, Biokovo Mt., Bast village	6.4.2006	Roman Ozimec	1 juv.
AR: 1290	Samogorska špilja	Croatia, Biokovo Mt., Župa village	4.4.2006	Roman Ozimec	1 juv. ♂
AR: 1291	Kuna špilja	Croatia, Biokovo Mt., Kadulja peak	28.4.2002	Roman Ozimec	1 juv. ♂
AR: 1292	Jama iznad Lipog dočića	Croatia, Biokovo Mt., Sv. Jure, Lipi dočić	26.2.2001	Jana Bedek	1 juv. ♂
AR: 1293	Pretnerova jama	Croatia, Biokovo Mt., Radov dolac	28.10.2006	Marko Lukić	1 ♀
AR: 1294	Crna Ledenica	Croatia, Biokovo Mt., Sv. Jure	25.4.2004	Branko Jalžić	1 ♀, 1 juv. ♂
AR: 1296	Kukor	Croatia, Biokovo Mt., Bast village	27.7.2004	Roman Ozimec	1 ♀
AR: 1297	Špilja u Radinovicima	Croatia, Biokovo Mt., Zagvozd, Rastovac village	25.10.2006	Martina Pavlek	2 ♀♀, 1 ♂, 7 juv.
AR: 1298	Samogorska špilja	Croatia, Biokovo Mt., Župa village	4.4.2006	Helena Bilandžija	1 ♀
AR: 1299	Špilja u Radinovicima	Croatia, Biokovo Mt., Zagvozd, Rastovac village	26.10.2006	Hrvoje Cvitanović	2 ♀♀, 2 juv.
AR: 1401	Kukor	Croatia, Biokovo Mt., Bast village	28.7.2006	Roman Ozimec	1 juv.
AR: 1402	Matijaševa peć	Croatia, Biokovo Mt., Župa village	19.11.2005	Hrvoje Cvitanović	1 juv.
AR: 1481	Kukor	Croatia, Biokovo Mt., Bast village	17.8.2000	Roman Ozimec	1 ♀, 1 juv.
AR: 1495	Kuna špilja	Croatia, Biokovo Mt., Kadulja peak	27.8.1998	Roman Ozimec	1 ♂
AR: 2050	Kukor	Croatia, Biokovo Mt., Bast village	2.1.1999	Roman Ozimec	1 ♀, 1 juv.
AR: 2067	Crna Ledenica	Croatia, Biokovo Mt., Sv. Jure	24.5.2004	Helena Bilandžija	1 juv. ♂
AR: 2084	Kukor	Croatia, Biokovo Mt., Bast village	29.12.1997	Roman Ozimec	1 ♀, 1 juv.
AR: 2085	Kukor	Croatia, Biokovo Mt., Bast village	7.8.2000	Roman Ozimec	1 ♀, 7 juv.
AR: 2088	Kukor	Croatia, Biokovo Mt., Bast village	25.3.2004	Jana Bedek	1 juv.
AR: 2093	Kukor	Croatia, Biokovo Mt., Bast village	26.3.2004	Marko Lukić	1 ♀, 1 juv.
AR: 2104	Čavlenovača jama	Croatia, Biokovo Mt., Radov dolac	18.6.2002	Roman Ozimec	1 juv.
AR: 2111	Golubnjača jama	Croatia, Biokovo Mt., Gornja Brela, Bartulovići village	23.3.2003	Marko Lukić	2 juv.

AR: 2114	Kukor	Croatia, Biokovo Mt., Bast village	23.9.1999	Roman Ozimec	1 juv.
AR: 2377	Crna Ledenica	Croatia, Biokovo Mt., Sv. Jure	18.6.2011	Alen Kirin	1 ♀
AR: 3253	Romanova jama	Croatia, Biokovo Mt., Kupušnjak	30.9.1995	Roman Ozimec	1 juv.
AR: 3906	Špilja u Radinovicima	Croatia, Biokovo Mt., Zagvozd, Rastovac village	1.5.2014	Branko Jalžić, Petra Bregović	2 juv. ♂
AR: 3909	Jama pod Svetim Jurom	Croatia, Biokovo Mt., Sv. Jure	11.10.2014	Branko Jalžić	1 juv.
AR: 3912	Špilja u Radinovicima	Croatia, Biokovo Mt., Zagvozd, Rastovac village	15.10.2014	Petra Bregović	1 juv.
AR: 3915	Kašogijeva jama	Croatia, Biokovo Mt., Sv. Jure	11.10.2014	Petra Bregović	1 ♀
AR: 3932	Samogorska špilja	Croatia, Biokovo Mt., Župa village	23.1.2016	Tin Rožman	1 ♂, 7 ♀♀, 3 juv. ♂, 3 juv.
AR: 3933	Samogorska špilja	Croatia, Biokovo Mt., Župa village	23.1.2016	Martina Pavlek	9 ♀♀
AR: 3934	Samogorska špilja	Croatia, Biokovo Mt., Župa village	23.1.2016	Marko Lukić	8 ♀♀, 2 ♂♂, 2 juv.
AR: 3936	Samogorska špilja	Croatia, Biokovo Mt., Župa village	23.1.2016	Martina Pavlek	3 juv., 1 juv. ♂
AR: 3938	Stonjska peć gornja	Croatia, Biokovo Mt., Župa village	22.1.2016	Martina Pavlek	2 ♀♀, 1 juv.
AR: 3941	Stonjska peć gornja	Croatia, Biokovo Mt., Župa village	22.1.2016	Martina Pavlek	2 ♀♀, 1 ♂
AR: 3944	Stonjska peć donja	Croatia, Biokovo Mt., Župa village	22.1.2016	Tin Rožman	3 juv.
AR: 3945	Stonjska peć donja	Croatia, Biokovo Mt., Župa village	22.1.2016	Tin Rožman	1 ♀
AR: 3947	Stonjska peć donja	Croatia, Biokovo Mt., Župa village	22.1.2016	Martina Pavlek	5 ♀♀
AR: 3949	Kukor	Croatia, Biokovo Mt., Bast village	21.1.2016	Tin Rožman	2 ♀♀
AR: 3950	Kukor	Croatia, Biokovo Mt., Bast village	21.1.2016	Marko Lukić	1 ♀, 4 juv.
AR: 3953	Matijaševa peć	Croatia, Biokovo Mt., Župa village	23.1.2016	Marko Lukić	1 ♀, 1 juv.
AR: 3955	Matijaševa peć	Croatia, Biokovo Mt., Župa village	23.1.2016	Marko Lukić	3 juv.
AR: 3957	Matijaševa peć	Croatia, Biokovo Mt., Župa village	23.1.2016	Martina Pavlek	2 juv.
AR: 3973	Stonjska peć donja	Croatia, Biokovo Mt., Župa village	22.1.2016	Martina Pavlek	1 juv. ♂, 1 juv.
AR: 3977	Stonjska peć gornja	Croatia, Biokovo Mt., Župa village	22.1.2016	Martina Pavlek	1 juv. ♂



**Appendix 3.** All records of *K. arenstorffi* (Kulczyński, 1914) from the CBSS collection. Date format: dd.mm.yyyy.

CBSS coll. number	Cave name	Location of the cave	Collection date	Collector	Number and gender of specimens
AR: 823	Jezero	Croatia, Sniježnica Mt	28.5.2004	Karla Fabrio	1 ♀
AR: 824	Jezero	Croatia, Sniježnica Mt	28.5.2004	Helena Bilandžija	1 ♀, 2 juv.
AR: 1578	Golodražnica	Montenegro, Bay of Kotor, town of Risan	24.4.2010	Jana Bedek	2 ♂♂, 2 juv. ♂♂, 3 juv.
AR: 1579	Golodražnica	Montenegro, Bay of Kotor, town of Risan	24.4.2010	Jana Bedek	1 ♀, 1 ♂, 1 juv. ♂
AR: 1580	Golodražnica	Montenegro, Bay of Kotor, town of Risan	24.4.2010	Alen Kirin	1 ♀, 1 ♂, 1 juv. ♂, 1 juv.
AR: 2777	Jezero	Croatia, Sniježnica Mt	16.3.2002	Roman Ozimec	1 ♀, 5 juv.
AR: 3288	Golodražnica	Montenegro, Bay of Kotor, town of Risan	31.3.2012	Ana Komerički	2 ♂♂, 2 ♀♀, 1 juv.
AR: 3291	Golodražnica	Montenegro, Bay of Kotor, town of Risan	31.3.2012	Marko Lukić	1 ♀, 1 juv. ♂, 1 juv.
AR: 3292	Golodražnica	Montenegro, Bay of Kotor, town of Risan	31.3.2012	Jana Bedek	4 ♀♀
AR: 3293	Golodražnica	Montenegro, Bay of Kotor, town of Risan	31.3.2012	J. Bedek, M. Lukić, A. Komerički	1 ♀, 1 juv. ♂
AR: 3459	Pećina kod Dvoriškog ždrijela	Montenegro, Dragaljsko polje	3.12.2014	Martina Pavlek	1 ♂
AR: 3461	Pećina kod Dvoriškog ždrijela	Montenegro, Dragaljsko polje	3.12.2014	Martina Pavlek	1 ♂, 2 ♀♀
AR: 3465	Golodražnica	Montenegro, Bay of Kotor, town of Risan	4.12.2014	Marko Lukić	1 ♂, 1 ♀
AR: 3641	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Martina Pavlek	2 ♀♀, 3 ♂♂
AR: 3645	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Martina Pavlek	1 ♂, 1 ♀
AR: 3649	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Vedran Sudar	1 ♂, 3 ♀♀, 2 juv.
AR: 3673	Vilina pećina	Montenegro, Dragaljsko polje	30.10.2015	Martina Pavlek	1 ♀, 1 ♂
AR: 3783	Pećina Vojvode Dakovića	Montenegro, Grahovo village	6.11.2015	Marko Lukić	1 ♂

**Appendix 4.** Records of *Typhlonesicus absoloni* (Kratochvíl, 1933) from Cetinjska pećina from the CBSS collection. Date format: dd.mm.yyyy.

CBSS coll. number	Cave name	Location of the cave	Collection date	Collector	Number and gender of specimens
AR: 3634	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Jana Bedek	1 ♀, 1 juv. ♂
AR: 3636	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Jana Bedek	1 ♀, 1 juv. ♂
AR: 3638	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Tin Rožman	2 juv. ♂♂, 1 juv.
AR: 3643	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Tin Rožman	1 ♀
AR: 3644	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Nikolina Kuharić	1 juv. ♀
AR: 3646	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Martina Pavlek	1 juv. ♂, 1 juv.
AR: 3647	Cetinjska pećina	Montenegro, town of Cetinje	28.10.2015	Vedran Sudar	1 ♂, 2 ♀♀, 1 juv. ♂, 2 juv.
AR: 3768	Cetinjska pećina	Montenegro, town of Cetinje	8.11.2015	Alen Kirin	2 juv.
AR: 3769	Cetinjska pećina	Montenegro, town of Cetinje	8.11.2015	Marko Lukić	3 ♀♀

**Appendix 5.** Estimates of genetic p-distances between species of Nesticidae included in this study (below the diagonal). In the inset the genetic p-distances between genera are provided.

	<i>deelemanae</i> gen. et sp. nov.	<i>fagei</i>	<i>arenstorffi</i>	<i>eremita</i>	<i>henderickxi</i>	<i>dimensis</i>	<i>cellulanus</i>	<i>hungaricus</i>	<i>lotriensis</i>	<i>fodinarum</i>	<i>simoni</i>
<i>K. fagei</i>	0.065										
<i>K. arenstorffi</i>	0.067	0.058						<i>Nesticus</i>	0.121		
<i>K. eremita</i>	0.104	0.084	0.080					<i>Typhlonesticus</i>	0.166	0.165	
<i>K. henderickxi</i>	0.097	0.087	0.100	0.097				<i>Carpathonesticus</i>	0.117	0.109	0.175
<i>K. dimensis</i>	0.087	0.074	0.069	0.084	0.087						
<i>N. cellulanus</i>	0.128	0.119	0.119	0.117	0.130	0.115					
<i>C. fodinarum</i>	0.119	0.113	0.097	0.117	0.117	0.093	0.097				
<i>C. lotriensis</i>	0.143	0.130	0.108	0.117	0.121	0.104	0.115	0.076			
<i>C. hungaricus</i>	0.119	0.115	0.102	0.119	0.123	0.102	0.104	0.028	0.078		
<i>C. simoni</i>	0.139	0.130	0.115	0.128	0.130	0.102	0.119	0.065	0.052	0.067	
<i>T. absoloni</i>	0.156	0.165	0.160	0.186	0.167	0.165	0.165	0.169	0.180	0.175	0.177