2019. Journal of Arachnology 47:142–153

A new critically endangered species of the harvestman genus *Lola* Kratochvíl, 1937 (Opiliones: Laniatores: Phalangodidae) from the Dalmatian karst, with notes on troglomorphy in European phalangodids

Darrell Ubick[1] and **Roman Ozimec**[2]: [1]Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, California 94118, U.S.A. E-mail: dubick@calacademy.org [2]ADIPA: Society for Croatian Natural History Diversity Research & Conservation, Orehovečki ogranak 37, 10040 Zagreb, Croatia

Abstract. Recent collecting in the Dalmatian karst uncovered a fascinating new species of cave-obligate harvestman, here described as *Lola konavoka* sp. nov. The new species closely resembles *Lola insularis* Kratochvíl, 1937, the type species of the genus, in male secondary sexual structures (presence of cheliceral boss and labial prongs) and genitalia (glans sigmoid and with basal lobes), supporting these characters as diagnostic for the genus. Males of *L. konavoka* have smaller dimorphic structures and genitalia with unbranched stylus and basal lobes, unlike in *L. insularis*. Somatically, *L. konavoka* is more strongly troglomorphic, having a smaller eyemound, longer legs, and higher tarsal count which exceeds that of all European Phalangodidae, including the most troglomorphic member, *Paralola buresi* Kratochvíl, 1951. All species were compared and ranked in degree of troglomorphy. The least modified, troglophiles, include two primarily surface-dwelling species (*Scotolemon doriae* Pavesi, 1878, and *S. terricola* Simon, 1872) and one cave-obligate species showing little modification (*S. lucasi* Simon, 1872). The remaining species, troglobites, have some degree of eye loss [*Ptychosoma espagnoli* (Rambla, 1973), *Ptychosoma balearicum* (Rambla, 1977), both *Lola* spp., and *Paralola buresi*]. The distribution of the cavernicolous species is plotted. The troglophiles occupy the central region (Pyrenees through greater Italy). The troglobitic species are in a linear arrangement, with the least troglomorphic (*Ptychosoma espagnoli*) in the west and most troglomorphic (*Paralola buresi*) in the east. Clinal variation in troglomorphy has previously been recorded in the Nearctic phalangodid genera *Texella* Goodnight & Goodnight, 1942, and *Banksula* Roewer, 1949, where the most troglomorphic members are also to the east as well as north.

Keywords: Troglobiont, cline, Dinarides, Croatia, systematics

ZooBank publication: http://zoobank.org/References/E973ABB5-F734-4340-83F0-FA4D02048F8A

The harvestman genus *Lola* Kratochvíl, 1937, was among the least known of the European Phalangodidae. Its single specimen, the holotype of *L. insularis* Kratochvíl, 1937, was not described in detail, even its gender remained uncertain (Kratochvíl 1937), and shortly thereafter was lost amidst the chaos of WWII. Despite Kratochvíl's incomplete description, the specimen was distinctive based on somatic morphology, as it was strongly cave adapted, and was the first blind phalangodid harvestman recorded from the European continent. Some years later he described the second blind harvestman, *Paralola buresi* Kratochvíl, 1951, in another new, monotypic genus (Kratochvíl 1951). Erecting genera based on only somatic structures is now ill-advised as the most informative characters are in the reproductive structures. In the case of *Lola*, however, Kratochvíl was correct. Some 66 years after the original study, an expedition to the type locality, Špilja pod Kapelu (Hvar Island, Croatia), successfully collected specimens of *Lola insularis* (Ozimec 2003). This allowed a redescription of the species, which revealed several unique structures supporting the genus. As expected, the diagnostic features are in the male genitalia, where the glans has a complex folding pattern which is possibly unique in the fauna (Ubick & Ozimec 2005, fig. 4A); and in secondary sexual structures, with coxae II bearing large labial processes and the chelicerae with an ectobasal boss (Ubick & Ozimec 2005, fig. 3B), which are not known from other European Phalangodidae (Ubick 2007). Globally, only the character combination is unique to *Lola* as these structures occur singly in some Nearctic phalangodids which, interestingly, range at the opposite sides of the continent. Labial prongs are found in *Phalangodes* Tellkampf, 1844 and related genera, representing several mostly cavernicolous species of the southeastern USA, whereas the cheliceral boss is found only in *Megacina cockerelli* (Goodnight & Goodnight, 1942), which is restricted to the redwood forest region of coastal California to southern Oregon (Ubick & Briggs 1992, 2008; Ubick 2007).

Recent collecting expeditions in the karst of the Konavle region in southern Croatia discovered another blind phalangodid, a second species of *Lola*, here named *Lola konavoka* sp. nov. The new species is clearly congeneric with *L. insularis*, which it resembles in genital conformation and secondary structures, reinforcing the validity of the genus. *Lola konavoka* differs from the type species in several features. Somatically, the new species is more troglomorphic, having longer legs, increased tarsal count, and a slightly reduced eye mound (Figs. 1A, 1D, 3, 4A–C). Also, the male dimorphic structures are slightly smaller (compare Ubick & Ozimec 2005, fig. 3B, to Figs. 2D–E, 4B, 4D), and the male genitalia lack accessory lobes on both the basal lobes and stylus (Figs. 5C–E), which are present in *L. insularis* (Ubick & Ozimec 2005, figs. 4B, 4F). The high troglomorphy in *L. konavoka* ranks it second in the European phalangodid fauna, surpassed only by *Paralola buresi*, as will be discussed later in this paper.

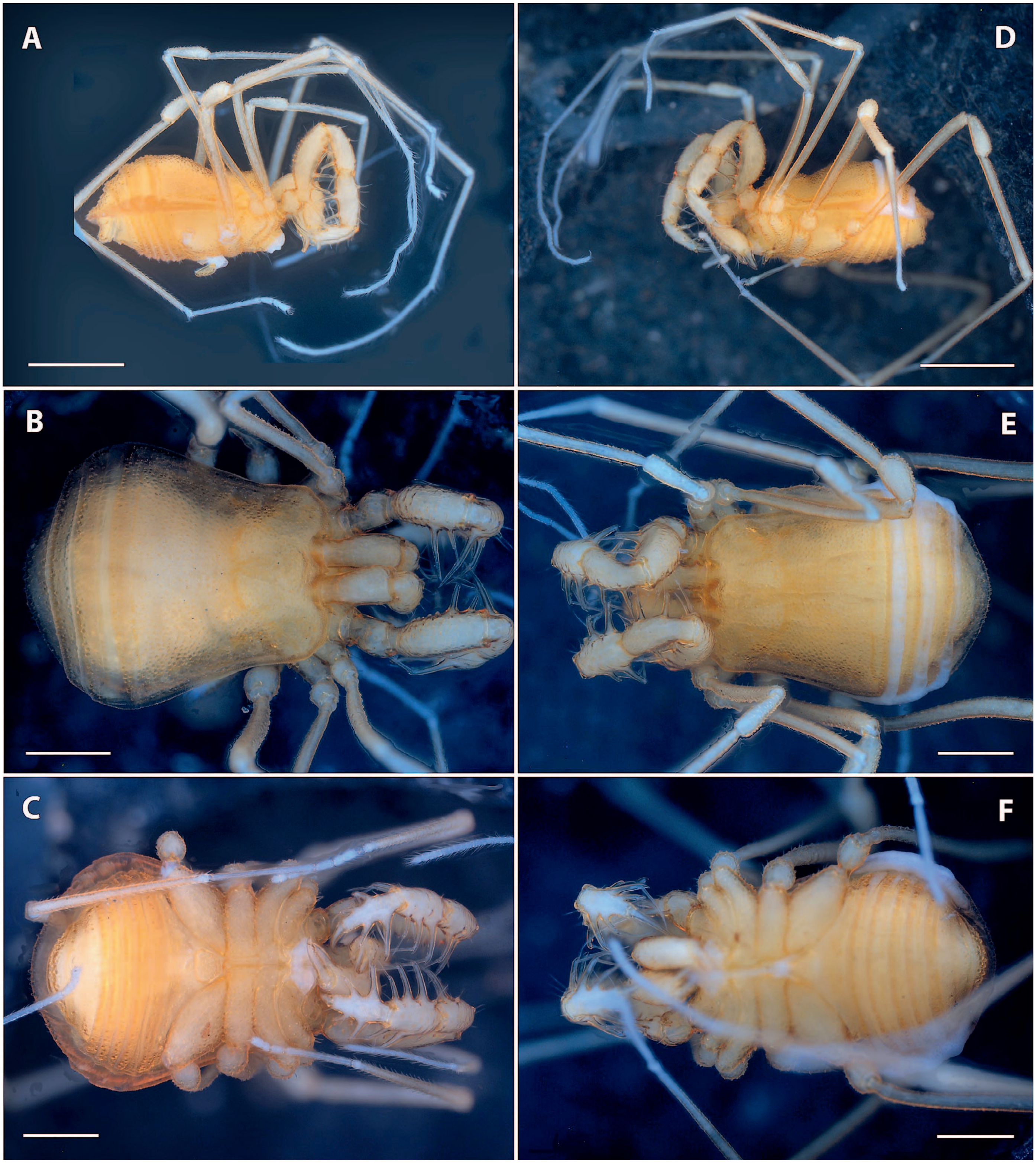

Figure 1.—*Lola konavoka*, sp. nov., habitus of female (A–C) and male (D–F). A, D. Lateral view. B, E. Dorsal view. C, F. Ventral view. Scale bars: A, D = 1.0 mm; B, C, E, F = 0.5 mm.

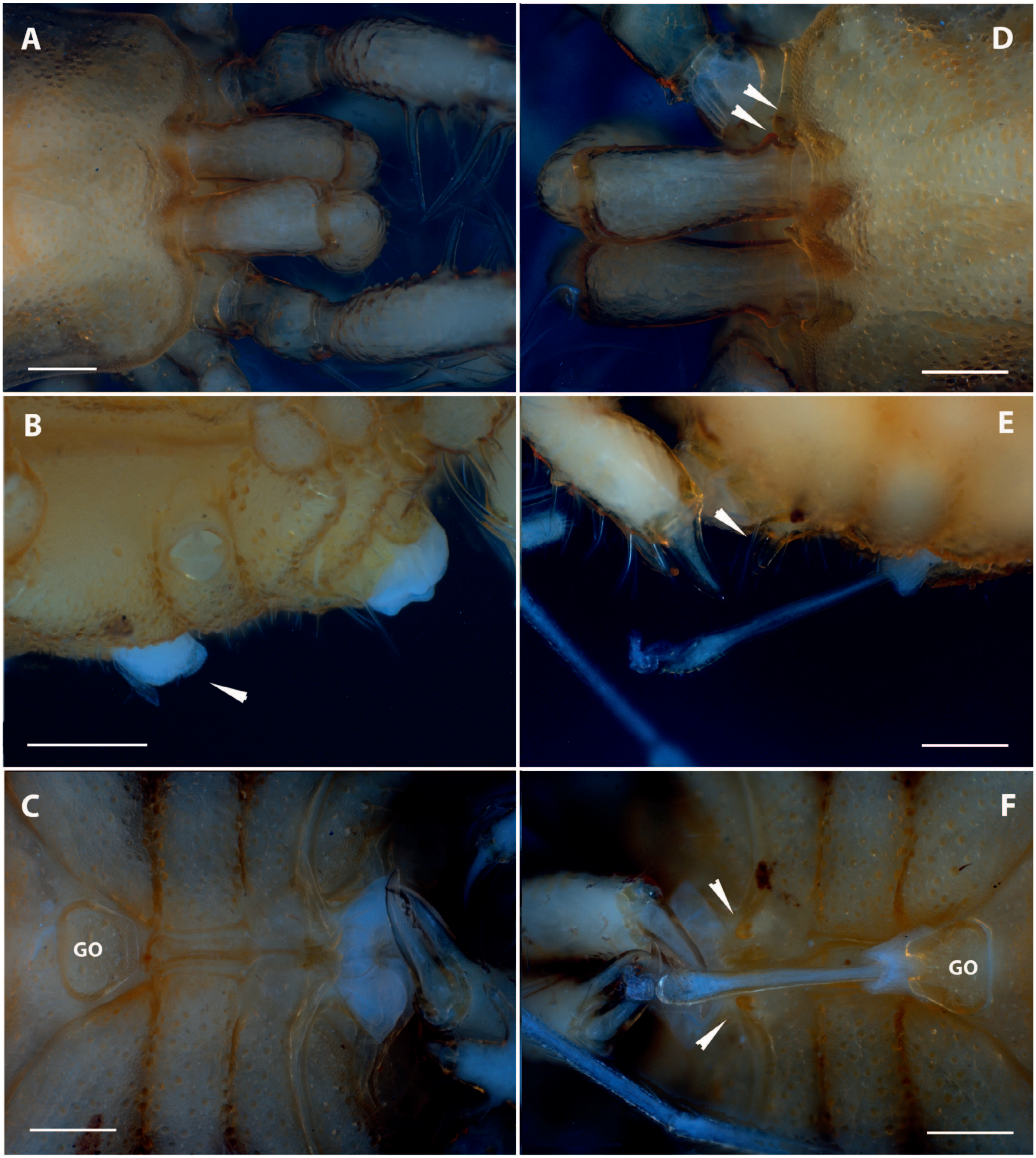

Figure 2.—*Lola konavoka*, sp. nov., anterior prosoma of female (A–C) and male (D–F). A, D. Dorsal views showing eye region and chelicerae, with arrows (D) to male dimorphic structures. B, E. Lateral views of the oral-genital region showing the extruded ovipositor (B) and penis (D), with arrow to the ovipositor and male labial process. C, F. Ventral views showing genital opercula (GO) and extended male genitalia (F) with arrows to labial processes. Scale bars: 0.2 mm.

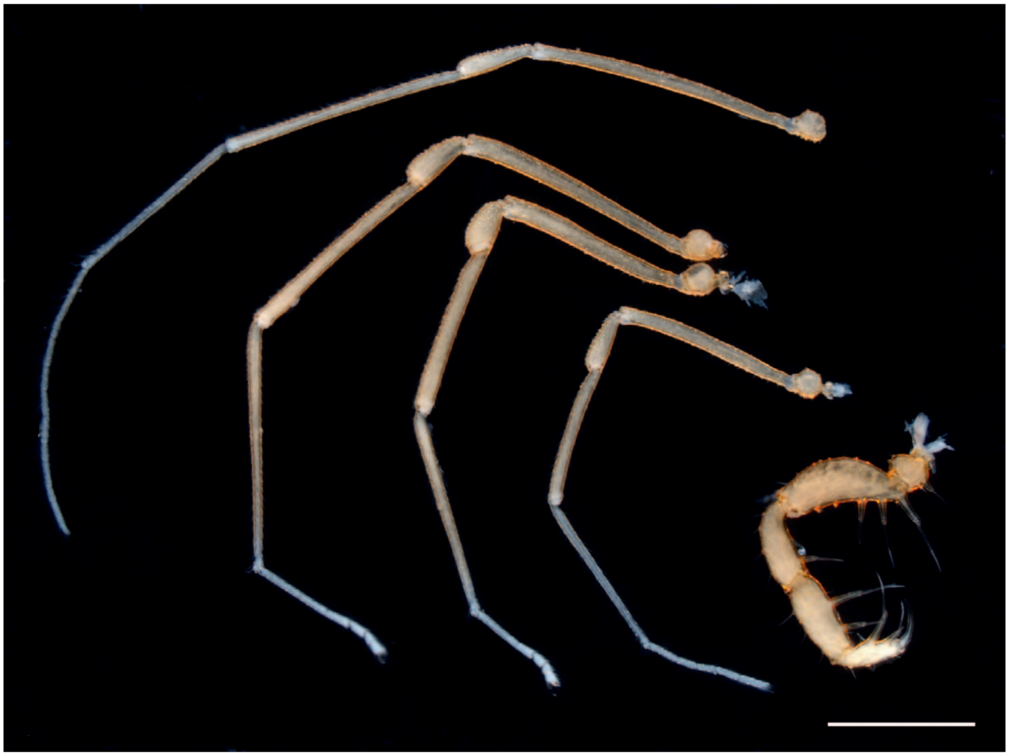

Figure 3.—*Lola konavoka*, sp. nov., male appendages in retrolateral view; from right to left: palp, leg I, leg III, leg IV, and leg II. Scale bar: 1.0 mm.

METHODS

Specimen preparation and observation follow the format in Ubick & Briggs (1989, 2008). Leg lengths are given as: total length (femur, patella, tibia, metatarsus, tarsus). All measurements not indicated otherwise are in millimeters. 'Fig.' and 'Figs.' refer to this paper, 'fig.' and 'figs.' to the previously published works. The cave conditions, including air movement, were recorded with a Kestrel 3000 Pocket Environmental Meter (see online at http://e-ecodb.bas.bg/rdb/en/vol2/Paburesi.html).

The phalangodid distribution map (Fig. 6B) is based on the published records in Dresco (1950), Brignoli (1968), Martens (1972, 1978), Thaler (1996) and Novak (2004) and in their included references. Localities were plotted using Google Earth and rendered with Adobe Photoshop and Illustrator.

Abbreviations.—BL = basal lobe of glans; GO = genital operculum; H = height; L = length; LII/SL = leg II length to scute length; S = stylus; SL = scute length; TBL = total body length; TC = tarsal count; W = width.

Specimens are deposited with the Roman Ozimec Collection (ROC) and the Croatian Natural History Museum (CNHM), Zagreb, except for the SEM-prepared male which is at the California Academy of Sciences (CAS), San Francisco.

SYSTEMATICS

Family **Phalangodidae** Simon, 1879
Lola Kratochvíl, 1937

Lola Kratochvíl 1937: 48.

Type species.—*Lola insularis* Kratochvíl, 1937 by monotypy.

Diagnosis.—Males of *Lola* can be distinguished from other phalangodid genera most readily by the sexually dimorphic chelicera (with ectobasal boss, Figs. 2D, 4D) and coxa II (with labial prong, Figs. 2E, 5A), structures unique in the European fauna and, in combination, are unique globally. The penis has an entire ventral plate and glans with a sigmoid folding pattern (Fig. 5), which also may be a unique combination in the family. A comparison of female genitalia is not possible as the ovipositor morphology is unknown for most species; in *Lola* the ovipositor lacks microspines and bears 8 pairs of short apical setae (Ubick & Ozimec 2005, fig. 5). Both sexes can be distinguished from other European phalangodids, except *Paralola*, by the high degree of troglomorphy, including the complete absence of eyes (including cornea) and a tarsal count of > 4-5-5-5 (Figs. 1, 3, 4). *Paralola* is more troglomorphic and has attenuated palpi (Kratochvíl 1958, figs. 13, 14, 20), which are unmodified in *Lola* (Figs. 1, 4B)

Lola konavoka, sp. nov.

http://zoobank.org/NomenclaturalActs/91A0D562-7D39-4DEC-A1DD-B94E516D5BBD
Figs. 1—6

Type material.—*Holotype male*. CROATIA: *Dalmatia*: Konavle: Mihanići, Jama pod Brk (cave) [42.567° N, 18.338° E], 16 January 2015, N. Hanžek, Geonatura (CNHM).

Paratypes: CROATIA: *Dalmatia*: Konavle: 1 ♂, 1 ♀, collected with holotype (CNHM); 3 ♂, same locality and date,

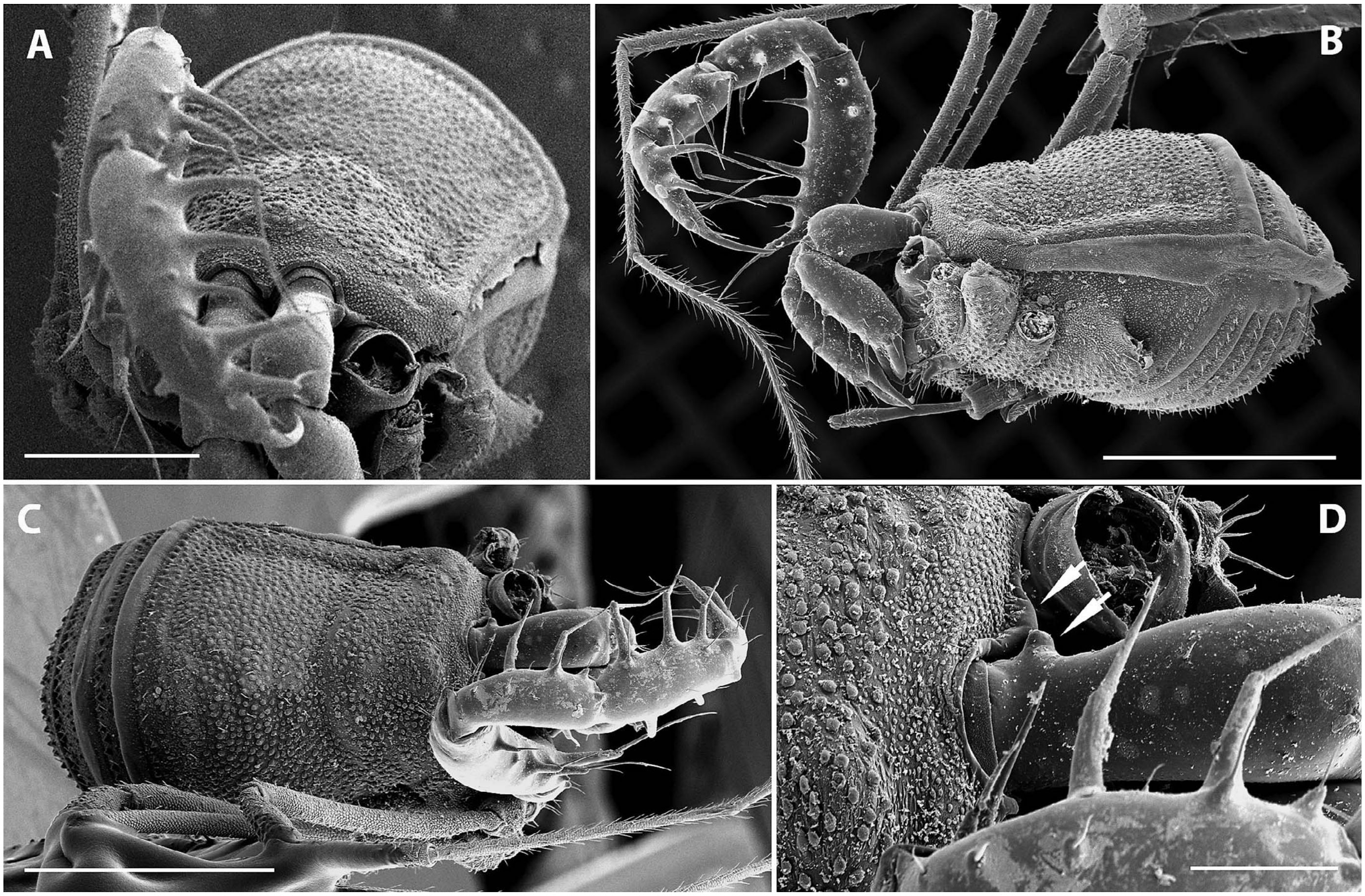

Figure 4.—*Lola konavoka*, sp. nov., male soma. A. Anterior view. B. Lateral view. C. Dorsal view. D. Same, magnified view of cheliceral base showing dimorphic structures (arrows). Scale bars: A–C = 1.0 mm; D = 0.2 mm.

G. Rnjak, Geonatura (ROC); 1 ♂ (SEM preparation), same locality, 29 August 2014, A. Ćukušić, Oikon (CAS).

Diagnosis.—*Lola konavoka* most closely resembles *L. insularis* in general morphology, including troglomorphic eye degeneration and appendage elongation, and in male genital conformation (the glans has multiple folds, appearing sigmoid in lateral view, and has a pair of basal lobes; Figs. 5C–E) and dimorphic structures (coxae II with labial processes and chelicerae with ectobasal boss; Figs. 2D–F, 4D, 5A,B). It differs in being more strongly troglomorphic, having a smaller eyemound ($H < L$; but $H = L$ in *L. insularis*), longer legs (LII/SL = 5.2 – 5.6; but 4.6 – 5.0 in *L. insularis*), and a higher tarsal count (4 or 5-8 to 10-5-5; but 4-6-5-5 in *L. insularis*. The male differs in several genital features, especially that the S and BL are unbranched (Fig. 5), but with accessory lobes in *L. insularis* (fig. 4 in Ubick & Ozimec 2005).

Description (male holotype).—Color: body pale orange, appendages yellowish, tarsi white. Dorsum evenly tuberculate, cephalic region with small tubercles, thorax and anterior tergal margins smooth, posterior with short sharp tubercles; cephalothoracic groove deep; scute margin lacking anterior tubercles. Eyemound small and rounded, $H < L$; cornea and retina absent. Venter with prominent tubercles at coxae and along posterior tergal margins; endites of coxae II with ventral process. Chelicera large, proximal segment with ectobasal swelling, distal with setose tubercles along dorsal surface. Palpal megaspines: trochanter 1 ventral; femur 4 ventrobasal, 2 mesodistal; patella 1 ectal, 2 mesal; tibia 2 ectal, 3 mesal; tarsus 2 ectal, 2 mesal. Palpal femur lacking dorsal tubercles. Trochanter IV with small ventral tubercles.

Genital operculum (GO) unarmed and relatively small: GO W / scute W = 0.16. Penis (Fig. 5) with truncus long and slender, slightly enlarged distally. Ventral plate rounded apically, lacking apical spine, with about 22 pairs of short slender setae. Glans folds along two axes, appearing sigmoid in lateral view, with one pair of unbranched claw-like basal lobes; stylus broad with lateral fringe, lacking lobes.

Total body length 1.88. Scute length 1.28, width 1.40. Eyemound length 0.15, width 0.22, height 0.07. Genital operculum length 0.22, width 0.22. Leg II length 6.56; LII/SL = 5.2. Leg I: 4.45 (1.21, 0.29, 0.95, 1.14, 0.86). Leg II: 6.56 (1.72, 0.38, 1.60, 1.20, 1.66). Leg III: 4.89 (1.29, 0.39, 1.10, 1.39, 0.72). Leg IV: 5.95 (1.62, 0.49, 1.40, 1.63, 0.81). Tarsal count: 5-9-5-5.

Female (paratype).—Similar to male but without the dimorphic structures. Total body length 1.77. Scute length 1.29, width 1.59. Eyemound length 0.15, width 0.23, height 0.07. Genital operculum length 0.18, width 0.23; GO W/ scute W = 0.145. Leg II length 6.85; LII/SL = 5.3. Leg I: 4.22 (1.14, 0.38, 0.88, 1.15, 0.67). Leg II: 6.85 (1.57, 0.48, 1.62, 1.28, 1.90).

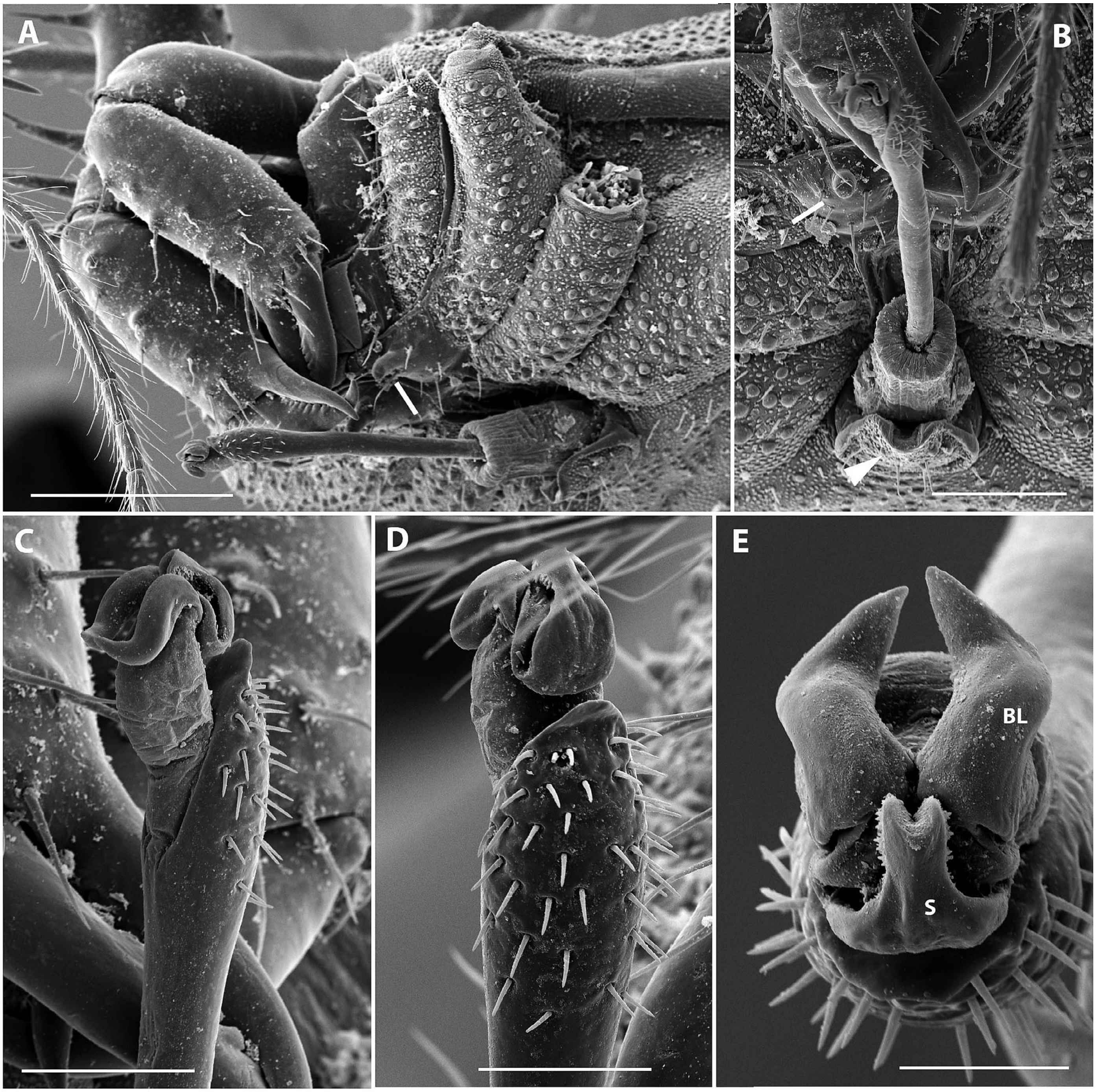

Figure 5.—*Lola konavoka*, sp. nov., male genitalia. A. Ventrolateral view showing fully extended penis. B. Ventral view showing curved apex of genital operculum (arrow) and labial process (dash). C. Dorsolateral view showing sigmoid curvature of glans. D. Ventrolateral view. E. Apical view of glans showing large claw-like basal lobes (BL) and a stylus apically indented and with a lateral fringe (S). Scale bars: A = 0.5 mm; B–D = 0.1 mm; E = 0.05 mm.

Leg III: 4.67 (1.26, 0.36, 1.03, 1.34, 0.68). Leg IV: 6.22 (1.52, 0.52, 1.43, 1.70, 1.05). Tarsal count: 4-8/9-5-5.

Ovipositor (Fig. 2B), not examined in detail.

Variation.—The two paratype males are slightly larger than the holotype in body length (2.05, 2.15), scute length (1.33, 1.40), scute width (1.40, 1.67), leg II length (7.19, 7.81), and have a higher LII/SL ratio (5.4, 5.6). These males also have higher tarsal counts: 5-10-5-5 in the larger male and 5-9/10-5-5 in the other, which has asymmetry in leg II tarsomeres. The female is similarly asymmetrical, having 4-8/9-5-5.

Sexual dimorphisms.—The male differs from the female in having the following modifications:

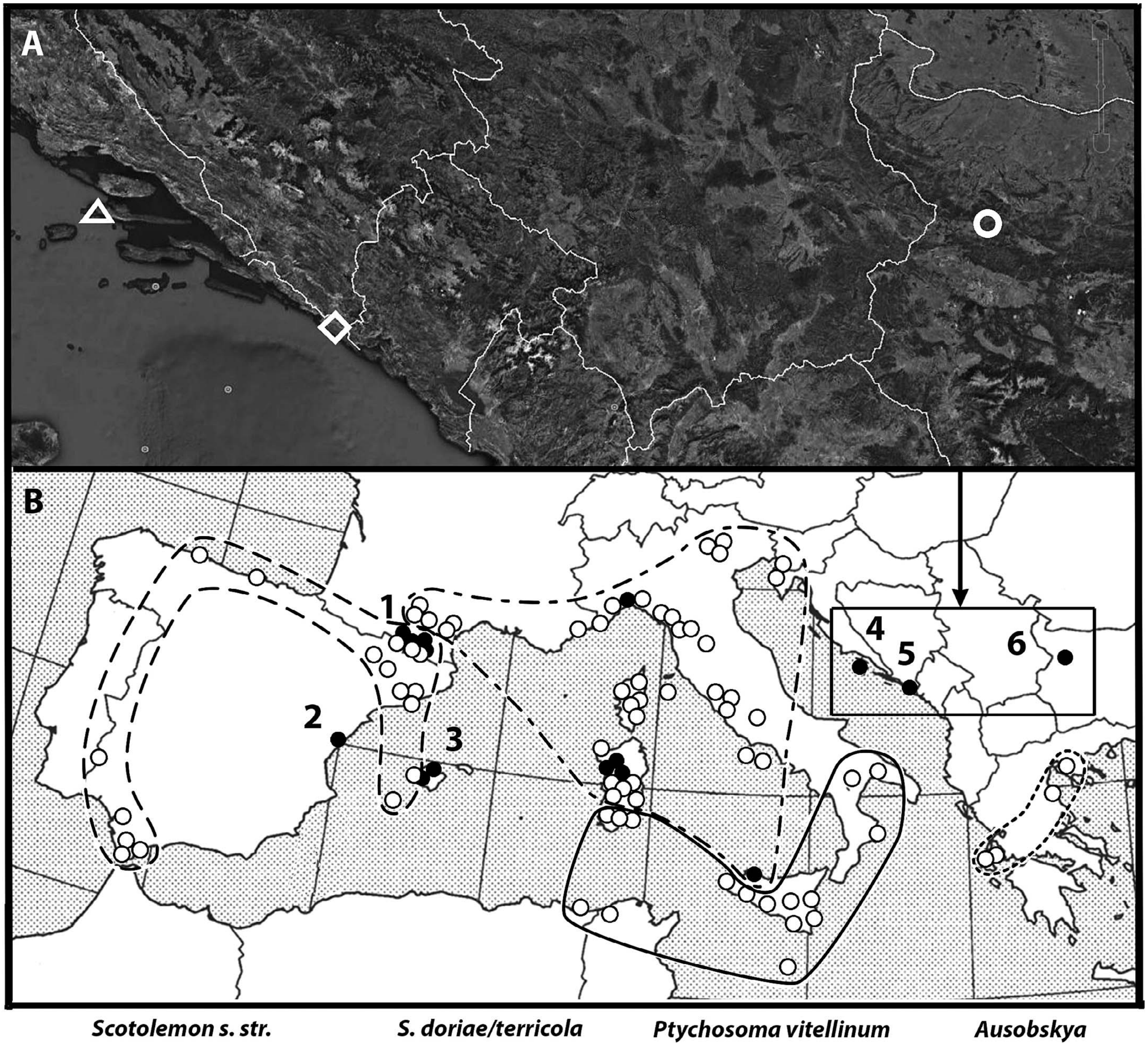

Figure 6.—A. Map of southeastern Europe showing distribution of *Lola* and *Paralola*: *Lola insularis* is the westernmost location (triangle), *Paralola buresi* is easternmost (circle), and *Lola konavoka* sp. nov., in the middle (diamond). B. Distribution of European Phalangodidae with the epigean (white) and cave (black) localities indicated. Encircled areas show genus-level groupings: *Scotolemon s. str*. (dashes), *Scotolemon doriae* and *S. terricola* (dash-dot line), *Ptychosoma vitellinum* Soerensen (solid line), and *Ausobskya* Martens (dots). Numbers identify the cave-obligate species in order of increasing troglomorphy (listed by rank in Table 1).

(1) coxa II with mesoventral labial process, which may function as a guide for the expanded penis (Fig. 5A);

(2) chelicera with prominent ectobasal boss (Figs. 2D, 4D), very small in female (Fig. 2A);

(3) anterior scutal margin with swelling adjacent to cheliceral boss (Figs. 2D, 4D), unmodified in female (Fig. 2A);

(4) GO somewhat narrower in male ($L \geq W$, Fig. 2F) than female ($L < W$, Fig. 2C), with apex curved outward (straight in female) and forming groove with the sternal excavation through which the genitalia project (Figs. 5A,B); and

(5) males have a higher tarsal count on the anterior legs (5-9 or 10-5-5, but only 4-8 or 9-5-5 in the female).

Research history.—Extensive speleological and biospeleological research of the continental part of the Dubrovnik-Neretva Parish was conducted during 2014 and first part of 2015, in collaboration with the project, 'Research on cave and karstic source habitats of the wider Dubrovnik area with the aim of evaluating biodiversity and the assessment of the acceptability of the construction of hydropower facilities', organized by Oikon Ltd, Geonatura Ltd., and the Croatian Natural History Museum. During the course of the project, 115 speleological features, underground buildings, karst springs and karstic wells were researched and extensively studied. The project study was produced in May 2015 with some 282 troglobitic and stygobiotic fungi and animal taxa recorded from the research area, including 45 potentially new taxa (Ozimec et al. 2015a). In this study, the first specimen of *Lola konavoka* was recognized by the second author as a new species. The speleological results were published as speleo-inventory (Ozimec et al. 2015b), but the biospeleological results await publication.

Type locality.—The pit, Jama pod Brk, is located in vertical southern slopes of Snježnica Mt., some 425 m.a.s.l. and above Mihanići village in the Konavle region, southeast of Dubrovnik. The pit is currently known to a depth of 46 m and length of 106 m and consists entirely of narrow meandering passageways, making it difficult for researchers, and also dangerous because of unstable stones. The pit map was published by Ozimec et al. (2015b).

Habitat ecology.—After a very small entrance of about 40 × 50 cm, the pit spreads as a vertical fissure, generally narrow, around 60 cm wide. The standard qualities of total darkness, moderate temperature, and high humidity start immediately after the entrance. During the first visit, in August 2014, the cave had an air temperature of 16.6°C, humidity of 98.4 %, and without air movement but with dripping water (outside conditions: 26.1°C; humidity 62.6 %). During the second visit, in January 2015, it was slightly colder with an air temperature of 16.4°C, humidity of 100 %, and again without air movement, just water dripping (outside conditions: 15.0°C, humidity 65.5 %).

Bionomy.—All specimens were found beneath embedded stones, mostly in places with dripping water, a microhabitat of even higher humidity. This habitat is very similar to that of the other cave phalangodids, for example *Lola insularis* on Hvar island, and the genera *Banksula* Roewer, 1949 and *Texella* from the western Nearctic.

Associated fauna.—During the course of researching the type locality, eight additional cavernicolous taxa were discovered. Three of these species are troglophiles: *Apfelbeckia* sp. (Diplopoda: Schizopetalidae), *Dolichopoda araneiformis* (Burmeister, 1838) (Orthoptera: Rhaphidophoridae), and *Nelima troglodytes* Roewer, 1910 (Opiliones: Sclerosomatidae). The remaining five species are troglobites: *Brachydesmus* sp. (Diplopoda: Polydesmidae), *Cyphonethes herzegowinensis* Verhoeff, 1900 (Isopoda: Trichoniscidae), *Roncus* sp. nov. (Pseudoscorpiones: Neobisiidae), *Speonesiotes* (*Speonesiotes*) *narentinus latitarsis* Apfelbeck, 1919 (Coleoptera: Leiodidae), and *Stalagtia hercegovinensis* Nosek, 1905 (Araneae: Dysderidae).

Distribution.—*Lola konavoka* is currently known only from the type locality, the cave "Jama pod Brk", on the southern slopes of Snježnica Mt., above Mihanići village, in southern Croatia (Fig. 6A).

Biogeography.—According to the established biogeographical regions, *L. konavoka* is endemic to the Dinarid mountain range and belongs to the South Dinaric endemics. The endemic taxa spread from the Neretva fracture to the border of the Dinarid range with the Taurid mountain range (Ozimec 2009a). As the stenoendemic taxa located on Snježnica Mt. are part of a complex of the Orjen massif, the three-border area of southeast Herzegovina, west Montenegro and south Croatia, this opens the possibility that undescribed taxa may occur in similar habitats in the adjacent countries.

Conservation.—Due to its rarity, relictual status and single known locality, *L. insularis* was declared critically endangered: CR B1ab(iii)+2ab(iii) (Ozimec 2009b), which is similar to the critically endangered *Paralola buresi*: B2a, b (ii)(iv)(v); C2a (i) (Mitov 2015). It is unclear why those taxa are not included in The IUCN Red List of Threatened Species (www.iucnredlist.org/). As *Lola konavoka* n. sp. is known from only a single locality, it should also be considered critically endangered (CR).

Etymology.—In Croatian, according to the local dialect, *konavoka* is a woman from Konavle, the region south of Dubrovnik, where this species occurs. To be treated as a noun in apposition.

TROGLOMORPHY

Harvestmen of the family Phalangodidae are cryptozoic creatures and occur in moist dark microhabitats, such as in leaf litter and on the undersurfaces of rocks, and are frequently found in caves. With the addition of *L. konavoka*, the European phalangodid fauna now includes eight cavernicolous species (Table 1), or 42% of the known species. [Actually, there is a ninth species, which is known but not formally described. A new species of *Scotolemon* was listed by Prieto (2008:62) from a cave in Spain (Valencia Province), and characterized by a "high ocularium with inconspicuous eyes". The associated images (Prieto 2008, fig. 19) show retinal loss (at least), which would make this species the first troglobitic *Scotolemon*. As Prieto's listing lacks relevant measurements, it was not possible to include the species in the discussion. However, by including this species in the above tallies, the European cavernicole ratio increases to 45% (9/20), and is identical to that in the Nearctic.] A similar ratio is found in the much larger Nearctic fauna, whose 49 cavernicoles represent 45% of the total phalangodid species (Ubick & Briggs 2004, 2008; Elliott et al. 2017).

Cavernicolous species differ in their dependence on the cave and in the degrees of troglomorphy, or structural modification for cave life. The least modified are species which also occur on the surface, termed troglophiles. In this case, the cave populations closely resemble their surface counterparts but are depigmented to varying degrees and have longer legs, as has been recorded in some species of the Nearctic genera *Calicina* Ubick & Briggs, 1989, *Texella* Goodnight & Goodnight, 1942, and *Sitalcina* Banks, 1911 (Ubick & Briggs 1989, 1992, 2008). Two species of European phalangodids are similarly troglophilic in having both epigean and cave populations. *Scotolemon doriae* Pavesi, 1878 is widely distributed from southeastern France to northern Sicily and S. *terricola* Simon, 1872 is restricted to Corsica and Sardinia, where it is parapatric with *S. doriae*. Both species occur in several caves on Sardinia, whereas *S. doriae* is also recorded from a cave in NW Italy and one in N Sicily (Brignoli 1968, Marcellino 1970, 1980). A comparison of the cave and epigean morphologies has not

Table 1.—Comparative troglomorphy in European Phalangodidae. The eight cavernicolous species are listed and the cave-restricted species ranked in order of increasing troglomorphy. Ecology refers to troglophile, either facultative (TPF) or obligate (TPO), or troglobite (TB). Eye reduction is measured by the presence (Y), absence (N), or partial loss (±) of the retina and cornea, and by reduction in eye mound (EM) size, with L = large, fully developed, M = with some reduction, and S = very strongly reduced. The tarsal formula and leg/ body ratios are measures of appendage elongation. Three species show variation in tarsal counts; in *Ptychosoma balearicum* the numbers give the frequency in the 13 specimens studied. For the leg/ body ratios, the rows are TBL (total body length), SL (scute length), LIIL (leg II length), LII/ SL, LII/ TBL, and *n* (number of specimens measured). Reference abbreviations: Mar/ Lin = Martens & Lingnau (1985); Ubi/ Ozi = Ubick & Ozimec (2005); Kra = Kratochvíl; and Sta = Staręga (1976).

	Species	***Scotolemon terricola***	***Scotolemon doriae***	***Scotolemon lucasi***	***Ptychosoma espagnoli***	***Ptychosoma balearicum***	***Lola insularis***	***Lola konavoka***	***Paralola buresi***
	Habitat	epigean (+ cave)	epigean (+ cave)	cave	cave	cave	cave	cave	cave
	Ecology	TPF	TPF	TPO	TB	TB	TB	TB	TB
	Rank			**1**	**2**	**3**	**4**	**5**	**6**
Eye	Retina	Y	N	Y	±	±	N	N	N
	Cornea	Y	Y	Y	Y	Y	N	N	N
	EM size	L	L	L	M	M	S	S	S
Tarsal Formula	3-3-4-4								
	3-4-5-5					1			
	3-5-4-5	▭	▭	▭					
	3-5-5-5				▭	2			
	3-6-5-5								
	4-5-5-5					10			
	4-6-5-5						▭		▭
	4-7-5-5								▭
	4-8-5-5							▭	
	4-9-5-5							▭	
	5-9-5-5							▭	
	5-10-5-5							▭	
Leg/ Body Ratios	TBL	1.6	1.6	2.0-2.6	1.6	2.1	2.1-2.2	1.8-2.2	1.2-1.9
	SL	1.0-1.1	0.9-1.2	1.2-1.5	1.25	1.4	1.2-1.5	1.3-1.4	0.8-1.3
	LIIL	3.7-3.8	3.3-4.1	7.5-9.0	6.6	8.6	6.2-7.0	6.6-7.8	7.8-9.4
	LII/ TBL	2.3-2.4	2.1-2.6	3.4-3.9	4.1	4.1	3.0-3.2	3.6-3.7	4.9-6.9
	LII/ SL	3.5-3.7	3.0-4.1	6.0-6.2	5.3	6.1	4.7-5.0	5.2-5.6	7.2-9.7
	n	2	2	many	1	1	3	4	5
	Refs	Thaler 1996	Thaler 1996	Mar/ Lin 1985	Rambla 1973, 1977a	Rambla 1977b	Ubi/ Ozi 2005	this paper	Kra 1958, Sta 1976

been conducted, but at least some leg elongation is expected in the cave populations. Interestingly, the primary difference between the two species is eye development, as members of *S. doriae* lack retinal pigments. Although eye loss is a common troglomorphy, given that *S. doriae* is a predominantly surface-dwelling species, this loss requires a different explanation. Apart from this difference, the two species are quite similar, especially in reproductive structures, and may represent only a single polymorphic species (Brignoli & Raffaelli 1978).

The remaining six phalangodid species are all restricted to caves and may be grouped ecologically as troglobites, or troglobionts, the latter of which Sket (2008) argues is the preferred term. He also uses "troglobiont" in a broad sense to include species showing little morphological modification. However, if morphology is taken into consideration, a troglobite needs to show significant troglomorphy. What is considered significant may vary for different organisms, but for Nearctic phalangodids, we have used the loss of eyes, even partial loss of the retina, for designating troglobites (Ubick & Briggs 1992). Under this grouping, cave-restricted species showing no eye reduction would be regarded as troglophiles, but these would clearly be of a higher level, given their cave dependency, than in the previous examples. For this, the term "obligatory troglophile" has been used for cave-restricted species with little troglomorphy, to differentiate them from the previous "facultative troglophiles" (Peck 1970). Of the European phalangodids, *Scotolemon lucasi*, a species recorded from many caves in the eastern Pyrenees, belongs to this category as it has well-developed eyes. This species is also very similar to the sympatric but surface-dwelling *S. lespesi* Lucas, 1860, but is somewhat depigmented, slightly smaller in size, and has relatively longer legs. Apart from that, the two are otherwise morphologically similar enough to possibly represent only one species (Martens & Lingnau 1985). If this is indeed so, and *S. lucasi* represents the cave-inhabiting populations of *S. lespesi*, then its category would need to be downgraded to a *facultative* troglophile.

The remaining species all show some degree of eye loss, with the least in *Ptychosoma espagnoli*, known from a single cave in eastern Spain, and *P. balearicum* (Rambla, 1977), from several caves on Mallorca (Rambla 1977a, b). Both species show some loss of retinal pigment and have slightly reduced eye mounds, but still retain the cornea (= lens). Of the two, *P. balearicum* is more troglomorphic in having a higher tarsal count as most individuals are 4-5-5-5, but only 3-5-5-5 in *P. espagnoli* (Rambla 1977b).

The last three species are more troglomorphic than the previous in having complete eye loss, including the cornea, and further reduction of the eye mound. The two species of *Lola* are each known from single caves in Croatia and, as discussed earlier, *L. konavoka* is more troglomorphic than *L. insularis* in several features, including a higher tarsal count, longer appendages, and a somewhat smaller eye mound. Finally, *Paralola buresi* Kratochvíl, the most troglomorphic of the species, is known from the type locality, Temnata Dupka (cave), and three nearby caves (Zidanka, Svinskata and Kozarskata), all in vicinity of the railway station of Lakatnik, the Western Stara Planina Mountains in Bulgaria (Mitov

2015). It differs from the other species in having the greatest appendage elongation, not only in leg length, but also in the extreme elongation of the palpi and palpal megaspines (Kratochvíl 1958, figs. 13, 14, 20).

Character transformation.—Summary of the above discussion is presented in Table 1, which compares the species in degree of eye degeneration and appendage elongation. Eye loss proceeds in stages, beginning with the reduction and loss of the retina, followed by the cornea (= lens), and finally to the extreme reduction of the eye mound to vestigial proportions. The standard measure of appendage elongation is the length of leg II, the longest leg, which is antenna-like in function and of obvious survival value in a cave. As larger harvestmen tend to have longer legs, size-related bias is offset by using the ratio of leg length to body size. For this, the scute length is a more stable indicator of size than is total body length, since the abdomen fluctuates in size depending on digestive and reproductive activity. Most of the referenced descriptions provided only the total body lengths and the scute lengths were extrapolated from the habitus drawings. Here, both the total body lengths (TBL) and scute lengths (SL) are used in the table. Related to appendage elongation is an increase in tarsomere number. The tarsal count variants of all European species are listed, with two categories not represented by cavernicoles.

The measurements of the two facultative troglophiles (*S. terricola* and *S. doriae*) are from surface-dwelling specimens, as cave representatives have not been studied. These are included here as placeholders for their cavernicolous representatives and also in showing epigean character states, apart from the anomalous retinal loss in *S. doriae*.

The remaining species are all cave obligates with different degrees of troglomorphy and can be unambiguously ranked from (1), the least troglomorphic *S. lucasi*, to (6), the most troglomorphic *P. buresi*. As troglomorphies are derived states, they can be used to define groups on the basis on "syntroglomorphies". In this usage, the groups are not clades in the phylogenetic sense, but rather grades supported by shared adaptive states. As each level is relatively more derived, the species can be arranged, using the epigean state as outgroup, as: (1 (2 (3 (4 (5 (6)))))).

This suggests a single, stepwise transformation, from the least to most troglomorphic, for all the characters. For example, it would be expected that the most troglomorphic species (6) has the most troglomorphic character states and, similarly, that the least troglomorphic (1) should have the least. However, this turns out not to be the case as species (5) has a higher tarsal count than (6) and species (1) has longer legs than many of the species showing eye degeneration.

To examine this discordance more closely, the species are grouped on the basis of individual characters. Eye degeneration: 1(2, 3 (4 (5, 6))), with the grades defined by retinal reduction, corneal loss, and extreme reduction of the eye mound.

Tarsal count: 1, 2 (3 (4, 6 (5))), based on increased tarsomere numbers.

These two indicators are compatible and, when added, result in: 1(2 (3 (4 (5, 6)))); with 5 and 6 unresolved with this character selection.

However, different results come from the leg elongation.

For LII/TBL: 4 (1, 5 (2, 3 (6))); and for LII/SL: 4 (2, 5 (1, 3 (6)))

It is not clear why some highly troglomorphic species (4, 5) have relatively shorter legs than species showing little to no eye degeneration (1, 2). Perhaps the problem lies with the measurements, either because of small sample size or errors in the published descriptions. However, this would not alter the values for species (1), which was studied in great detail (Martens & Lingnau 1985), and clearly has longer legs than would be expected. Apart from this species, the others show the expected pattern, but not taken as a whole. Three species (4, 5, 6) clearly show increasing leg lengths in all measures, and (2, 3) shows it with the LII/SL ratio. Based on this, it can be concluded that increased leg lengths do correlate with other troglomorphic traits within smaller clusters of species.

Perhaps a clue to the leg length concordance lies in the species' phylogeny. If the ancestor had longer legs, then the troglophile has a higher starting point. This seems to be the case for *S. lucasi*, which is most closely related to *S. lespesi* and *does* have long legs. Although its LII/TBL ratio of 2.7—3.0 is below that of the cavernicolous species, its LII/SL ratio of 4.7—5.0 equals that of the highly troglomorphic *L. insularis* (Martens & Lingnau 1985).

The other cavernicolous species traditionally included in *Scotolemon* are not closely related to *S. lespesi*, the type species, as they differ in genitalic and secondary sexual structures, the latter being the most easily visible characters. Males of *S. lespesi* have a pair of short prongs on the hind legs, one each on trochanter and femur IV, which probably function as claspers (van der Hammen 1985, fig. 31C), and which are not found in the other species. The troglobitic species lack sexual dimorphisms (Rambla 1973, 1977b), and were recently (and correctly) transferred to *Ptychosoma*, as *P. espagnoli* and *P. balearicum* (Prieto 2008). The troglophilic species, *S. terricola* and *S. doriae*, have dimorphic males, but they differ from those of *S. lespesi* in having a single long process on trochanter IV (Thaler 1996, figs. 23–25). Given these differences, as well as those in genitalic characters (compare figs. 16–21 with figs. 38–41 in Thaler 1996), these species are clearly misplaced in the genus. *Scotolemon* has long been a source of taxonomic problems, being traditionally based on somatic characters, such as tarsal formula, which are poor phylogenetic indicators, and which has resulted in misplaced species and much discussion (Roewer 1935; Kraus 1961; Brignoli 1968; Rambla 1977b; Thaler 1996).

Distribution.—Additional differences between the cavernicolous species are in their distribution patterns, which are plotted in Fig. 6B, showing the caves as black dots and the epigean localities as white dots. The most obvious difference is in the size of the species' distributions. The facultative troglophiles, encircled by a dash-dot line, occupy the largest region and the obligate troglophile (species 1) the next largest. The troglobitic species (2—6) have the narrowest distributions, with two of the species (*Lola*) known only from single caves and one (*Paralola*) from four caves in a small, restricted region. Thus, a species' distribution size decreases with increasing troglomorphy.

Another interesting pattern is in the alignment of the troglobites (2—6), which shows increasing troglomorphy from west to east. Clinal variation in troglomorphic characters has been previously recorded in the Nearctic Phalangodidae. A similar west-to-east trend occurs in the Californian genus *Banksula* Roewer. Its westernmost member, *B. incredula* Ubick & Briggs, 2002, is epigean; *B. melones* Briggs, 1974, a large eyed cavernicole, is intermediate; and the easternmost populations of *B. grahami* Briggs, 1974, have degenerate eyes, lacking both the retina and cornea (Ubick & Briggs 2002). In the genus *Texella*, three clades in Texas and New Mexico show clinal variation, but with the most troglomorphic members being to the north (*T. reyesi* Ubick & Briggs, 1992) or northeast (*T. mulaiki* Goodnight & Goodnight, 1942, and *T. welbourni* Ubick & Briggs, 2004) of the less modified species (Ubick & Briggs 1992, 2004).

The fact that the cavernicolous phalangodids show different degrees of troglomorphy suggests a gradual, stepwise acquisition of troglomorphies, with the extant species representing different stages of a single transformation series. As change is a function of time, it seems safe to assume that it applies here, and that increased troglomorphy means more time spent underground. In this case, the most modified species (6) were the earliest cave colonizers, and the remaining species must have entered the caves sequentially from (5) to (2). This suggests some gradual change, from east to west, which must have isolated the species from their epigean counterparts.

ACKNOWLEDGMENTS

The authors are grateful to Goran Rnjak, Nikola Hanžek and Anđela Ćukušić for collecting the specimens, Predrag Rade and Alan Kovačević for type locality research, and to Geonatura and Oleg Antonić for general support. For determinations of associated fauna we are grateful to: Dražina Tvrtko (Diplopoda), Jalžić Branko (Coleoptera) and Karaman Ivo (Isopoda; Opiliones: Sironidae). Special thanks go to Gordan Polić, Nikša Bojanić and Darijan Ozimec for their companionship and field assistance in exploring caves on Hvar in search of *Lola*. A big thanks goes to the meticulous reviewers of the manuscript, Abel Perez Gonzalez, James C. Cokendolpher, and Mark S. Harvey, who corrected many errors and provided a most important reference.

LITERATURE CITED

Brignoli, P.M. 1968. Note su Sironidae, Phalangodidae e Trogulidae italiani, cavernicoli ed endogei (Opiliones). Fragmenta entomologica 5:259–293.

Brignoli, P.M. & E. Raffaelli. 1978. Nuovi dati e problem aperti su alcuni opilioni italiani (Arachnida, Opiliones). Bollettino della Società entomologica italiana (Genoa) 110:86–99.

Dresco, E. 1950. Opilions Capturés en Corse et description d'une espèce nouvelle. Bulletin du Muséum national d'Histoire Naturelle, Paris XXI (6) 1949:676–679.

Elliott, W.R., J.R. Reddell, D.C. Rudolph, G.O. Graening, T.S. Briggs, D. Ubick et al. 2017. The cave fauna of California. Proceedings of the California Academy of Sciences (series 4) 64:1–311.

Kratochvíl, J. 1937. *Lola insularis* nov. gen. nov. spec. (fam. Phalangodidae) a *Travunia* (?) *jandai* nov. spec. (fam. Travuniidae), dva noví jeskynní sekáči z jihodalmatinských ostrovu. *Lola insularis* nov. gen. nov. spec. (fam. Phalangodidae) et *Travunia* (?) *jandai* nov. spec. (fam. Travuniidae) deux Opilions Cavernicoles nouveaux des iles de la Dalmatie méridionale. Entomologické Listy (Folia entomologica), Brno 1(1937–1938):44–54.

Kratochvíl, J. 1951. Výsledki bulharské biospeologie v jeskyni "Temnata dupka". Československý Kras 4(1/2):8–12.

Kratochvíl, J. 1958. Die Höhlenweberknechte Bulgariens (Cyphophthalmi und Laniatores). Brnenske Zakladny Československe Akademie Ved 30:371–396.

Kraus, O. 1961. Die Weberknechte der Iberischen Halbinsel (Arach., Opiliones). Senckenbergiana biologica 42:331–363.

Marcellino, I. 1970. Su alcuni Opilioni (Arachnida) della Sicilia sud-orientale e centrale. Bollettino delle sedute dell'Accademia Gioenia di Scienze naturali in Catania 4(10):283–308.

Marcellino, I. 1980. Opilioni di Sardegna (Arachnida, Opiliones). Lavori della Società Italiana di Biogeografia, Nuova Serie 8:323–345.

Martens, J. 1972. *Ausobskya athos*, der erste Krallenweberknecht aus Griechenland (Opiliones: Phalangodidae). Senckenbergiana biologica 53(5/6):431–440.

Martens, J. 1978. Spinnentiere, Arachnida: Weberknechte, Opiliones. Die Tierwelt Deutschlands. Vol. 64. VEB Gustav Fischer Verlag Jena.

Martens, J. & M. Lingnau. 1985. Die Weberknechte *Scotolemon lespesi* Lucas und *Scotolemon lucasi* Simon aus den Pyrenäen – zwei valide Arten? (Arachnida: Opiliones: Phalangodidae). Mémoire Biospéologie 12:111–126.

Mitov, P. 2015: Paralola / *Paralola buresi* Kratochvil, 1951. In: Golemansky (ed.), Red Data Book Republic of Bulgaria_Animals Vol_2. Online at http://e-ecodb.bas.bg/rdb/en/vol2/Paburesi.html.

Novak, T. 2004. An overview of harvestmen (Arachnida: Opiliones) in Croatia. Natura Croatica 13(3):231–296.

Ozimec, R. 2003. *Lola* pronađena nakon 65 godina (*Lola* found after 65 Years). Meridijani 76:17.

Ozimec, R. 2009a. Endemism. Pp. 30–32. *In* Red Book of Croatian cave dwelling fauna. (R. Ozimec & L. Katušić, eds.). Ministry of Culture, State Institute for Nature Protection, Republic of Croatia.

Ozimec, R. 2009b. Hvarska lola / Hvar lola / *Lola insularis* Kratochvil, 1938. Pp. 101–102. *In* Red Book of Croatian cave dwelling fauna. (R. Ozimec & L. Katušić, eds.). Ministry of Culture, State Institute for Nature Protection, Republic of Croatia.

Ozimec, R., B. Jalžić, I. Mihoci, N. Hanžek, G. Rnjak, M. Grgurev et al. 2015a. Study of the Main Assessment of Acceptability of the Project for the Ecological Network of HPP Ombla, Book 3: Biodiversity of Speleological Objects in Wider Area of Intervention, Professional Elaborate, Oikon-Croatian Natural History Museum-Geonatura, 198 pp. + Attachments, 118 pp.

Ozimec, R., G. Rnjak, B. Jalžić, D. Lacković, H. Cvitanović, D. Basara et al. 2015b. Spelaeologia Ragusina 1: Cadaster of speleological objects, underground structures, karst springs and karstic wells of the land area of the Dubrovnik-Neretva County. Subterranea Croatica 13, Supplementum 1:1–152.

Peck, S.B. 1970. The terrestrial arthropod fauna of Florida caves. Florida Entomologist 53:203–207.

Prieto, C.E. 2008. Updating the checklist of the Iberian opiliofauna: corrections, suppressions and additions. Revista Ibérica de Aracnología 16:49–65.

Rambla, M. 1973. Contribución al conocimiento de los Opiliones de la fauna ibérica. Estudio de los subórdenes Laniatores y Palpatores (pars.). Secretaria de Publicaciones, Universidad de Barcelona. Resúmen Tesis Doctoral: 1–21.

Rambla, M. 1977a. Nota sobre dos Laniatores de la Peninsula ibérica e Ibiza (Arach., Opiliones, Laniatores, Phalangodidae). Graellsia 31:267–275.

Rambla, M. 1977b. Un nuevo *Scotolemon* cavernicola de la isla de Mallorca (Arachnida, Opiliones, Phalangodidae). Speleon 23:7–13.

Roewer, C.F. 1935. Opiliones (Fünfte série). Zugleich eine Revision aller bisher bekannten europäischen Laniatores. Pp. 1–96. *In* Biospeleologica LXII. Archives de Zoologie Expérimentale et Générale 78(1).

Sket, B. 2008. Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42:1549–1563.

Staręga, W. 1976: Die Weberknechte (Opiliones, excl. Sironidae) Bulgariens. Annales Zoologici (Polska Akademia Nauk) 33(18):287–433.

Thaler, K. 1996. Neue Funde europäischer Krallenweberknechte (Arachnida, Opiliones: Phalangodidae, Travuniidae). Berichte des naturwissenschaftlichen-medizinischen Verein Innsbruck 83:135–148.

Ubick, D. 2007. Phalangodidae. Pp. 217–221. *In* Harvestmen, The Biology of Opiliones. (R. Pinto da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press.

Ubick, D. & T.S. Briggs. 1989. The harvestman family Phalangodidae. 1. The new genus *Calicina*, with notes on *Sitalcina* (Opiliones: Laniatores). Proceedings of the California Academy of Sciences 46(4):95–136.

Ubick, D. & T.S. Briggs. 1992. The harvestman family Phalangodidae. 3. Revision of *Texella* (Opiliones: Laniatores). Texas Memorial Museum Speleological Monograph 3:155–240.

Ubick, D. & T.S. Briggs. 2002. The harvestman family Phalangodidae. 4. A review of the genus *Banksula* (Opiliones: Laniatores). Journal of Arachnology 30:435–451.

Ubick, D. & T.S. Briggs. 2004. The harvestman family Phalangodidae. 5. New records and species of *Texella* Goodnight and Goodnight (Opiliones: Laniatores). Texas Memorial Museum Speleological Monograph 6:101–141.

Ubick, D. & T.S. Briggs. 2008. The harvestman family Phalangodidae. 6. Revision of the *Sitalcina* complex (Opiliones: Laniatores). Proceedings of the California Academy of Sciences (Fourth Series) 59:1–108.

Ubick, D. & R. Ozimec. 2005. On the harvestman genus *Lola* Kratochvíl (Opiliones: Laniatores). Natura Croatica 14:161–174.

van der Hammen, L. 1985. Comparative studies Chelicerata III. Opilionida. Zoologische Verhandelingen 220:1–60.

Manuscript received 12 May 2018, revised 24 September 2018.