

Cavernicolous Scorpions of the Balkans: Redescription of *Euscorpium studentium*

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Article

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Redescription of *Euscorpius studentium* Based on Adult Specimens; Updated Classification of Cavernicolous Euscorpiidae; and Review of Cavernicolous Scorpions in the Balkans

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Abstract: Cavernicolous scorpions are difficult to collect and study due to their often inaccessible habitats. Some have evolved unique morphological adaptations, known as troglomorphies, including reduced sclerotization and pigmentation, reduction and/or loss of eyes, attenuation and elongation of the appendages, which assist them to thrive in dark, humid and low-energy input environments. Cavernicolous scorpions are classified into accidentals, troglonexes, troglophiles, and troglobites. The Balkans, and particularly the Dinaric Karst region, host a diverse cave-adapted fauna, including scorpions. Despite an 1895 report of a blind scorpion from Bosnia and Herzegovina, the first truly troglobitic European scorpion, *Euscorpius studentium* Karaman, 2020, was only described a few years ago, based on two immature specimens. In the present contribution, this unique species is redescribed based on the first adult specimens; the ecological classification of all currently known cavernicolous Euscorpiidae Laurie, 1896, is updated; a key to the identification of cavernicolous scorpions occurring in the Dinaric Karst is provided; and the historical and geographical factors affecting the distribution and conservation of cavernicolous scorpions in the Balkans is reviewed.



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1. Introduction

Over millions of years, cavernicolous taxa adapted to the unique conditions of the subterranean environment, especially the absence of light, stable microclimate, and low energy input [1–3], by evolving specialized behavior, physiological responses, and ecomorphological adaptations known as troglomorphies. Among scorpions, such troglomorphies include anophthalmia (i.e., loss or reduction of median and lateral ocelli), reduction of sclerotization and pigmentation, and attenuation of the appendages [4–8].

Several classifications, building on the original Schiner-Racovitza System [9,10], have been proposed for cavernicolous and troglomorphic biota, depending on the phenotype, ecological niche and degree of specialization (e.g., [11–16]). Prendini et al. [8] reviewed these classifications as applied to scorpions and presented a key to classify cavernicolous and troglomorphic species according to their ecology and morphology. The key, which was based on Trajano and Carvalho's [15] redefinition of the three classical Schiner-Racovitza categories, troglonexes, troglophiles and troglobites, and a fourth category, accidentals, differentiated between epigean, endogean, and hypogean scorpions, corresponding to those living on the surface, within the soil or leaf litter, and in subterranean environments,

respectively. The differences between the redefined Schiner-Racovitza categories for scorpions, as outlined by Prendini et al. [8], can be summarized as follows: accidentals typically inhabit epigean habitats but occasionally enter caves either by mishap or in search of a milder climate; troglonexes can thrive and establish stable populations in both epigean and hypogean habitats; troglaphiles occur exclusively within hypogean habitats but exhibit few or no troglomorphic traits; troglobites or troglobionts are exclusively found within hypogean habitats and generally exhibit marked troglomorphies (i.e., loss or reduction of ocelli and pigmentation).

The Balkans, a group of nations in southeastern Europe, including Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Greece, Kosovo, Montenegro, North Macedonia, Serbia, Slovenia and Romania, contain extensive cave systems, representing global hotspots of troglobitic fauna [17–23]. The complex and dynamic geoclimatic history of the Dinaric Karst region (Figures 1–3) in the western Balkans has resulted in unprecedented speciation through the colonization and isolation of different taxa, especially invertebrates [18,23–26]. This area acted as a refugium during the Miocene Climatic Transition and Plio-Pleistocene glacial cycles, sheltering relictual taxa, e.g., the descendants of hygrophilous and/or humicolous epigean fauna from the Tertiary [19,27,28] and promoted the diversification of younger, karst-adapted lineages, generating pronounced geographical structure in several groups. Subterranean radiations were fostered by the complex geotectonics, orogeny, fluvial networks, vast cave systems, and localized pits and cavities of the region [19,23,29].

Despite an early report of a blind scorpion from Bosnia and Herzegovina (“Les cavernes du sud de la Bosnie . . . on y trouve . . . et une petite espèce de Scorpion aveugle” (p. 23: [30]), no cavernicolous scorpions were described from the Dinarides until the last decade [31–36]. Like some other subterranean fauna, cavernicolous scorpions may occupy the *milieu souterrain superficiel* [37,38], i.e., not only the large chambers of caves but the network of narrow crevices and fissures interconnecting them. These restricted cavities are usually impossible to access, greatly limiting biospeleologists from obtaining comprehensive series of cavernicolous taxa for study [5,6,33]. The challenges involved in collecting cavernicolous taxa may create a false impression of rarity and provide a mere glimpse of their true diversity, a phenomenon referred to as the “Racovitza impediment” [39].

The Dinaric Karst is now the only part of Europe, aside from Greece and Sardinia, known to harbor troglonexes, troglaphiles, and troglobites scorpions, and it contains the highest diversity among the three regions, with at least five species in two genera of the family Euscorpiidae Laurie, 1896, *Alpiscorpius* Gantenbein et al., 1999, and *Euscorpius* Thorell, 1876, occurring exclusively within caves (Table 1).

Euscorpius studentium Karaman, 2020, the first truly troglobitic European scorpion (Figure 4), displaying several marked troglomorphies (e.g., absence of median ocelli, reduction of lateral ocelli, and reduction of pigmentation), was described based on immature specimens from a cave in Montenegro (Figures 1–3). No further data were published about the morphology and biology of this species in the ensuing years. In the present contribution, this unique species is redescribed based on the first adult specimens; the ecological classification of all currently known cavernicolous Euscorpiidae is updated; a key to the identification of cavernicolous scorpions occurring in the Dinaric Karst is provided; and the historical and geographical factors affecting the distribution and conservation of cavernicolous scorpions in the Balkans is reviewed.

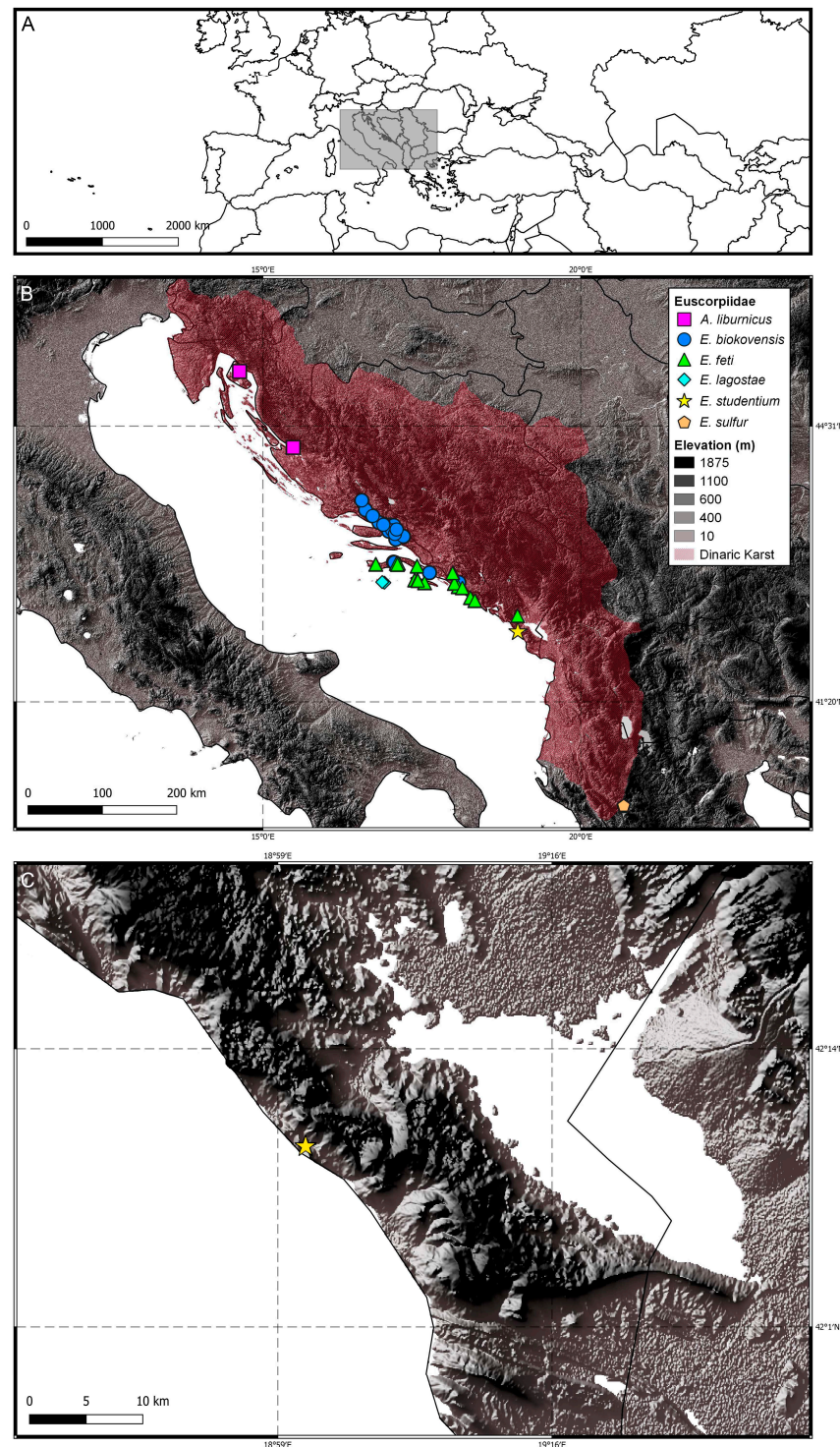


Figure 1. (A). Map of the Western Palearctic with international borders. Rectangle indicates area in (B). (B). Map illustrating extent of the Dinaric Karst from southern Slovenia across southern Croatia, Bosnia and Herzegovina and Montenegro, to Albania, and cavernicolous species of Euscorpiidae Laurie, 1896, occurring in the area. (C). Map indicating location of Spila Skožnica Cave, type locality of *Euscorpius studentium* Karaman, 2020, amid mountains surrounding Skadar Lake. Stars (B,C) indicate cave locality of *E. studentium*; squares, cave localities of *Alpiscorpius liburnicus* Tvrtković & Rebrina, 2022; circles, cave localities of *Euscorpius biokovensis* Tropea & Ozimec, 2020; triangles, cave localities of *Euscorpius feti* Tropea, 2013; diamonds, cave localities of *Euscorpius lagostae* Caporiacco, 1950; pentagon, cave locality of *Euscorpius sulfur* Kovařík et al., 2023.

Table 1. Genera and species of cavernicolous, troglotitic, and troglomorphic Euscorpiidae Laurie, 1896, with countries of occurrence, cave records, summary of troglomorphies, and ecological classification based on Prendini et al. [8].

Alpiscorpius liburnicus Tvrtković & Rebrina, 2022: CROATIA. Habitat: inside cave.

Troglomorphies: pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Classification: hypogean: troglophile.

Citations: [8,33–35,40–43].

Alpiscorpius pavicevici Tropea, 2021: SERBIA. Habitat: inside cave; surface habitats, in leaf litter or under stones. Classification: endogean: accidental. Troglomorphies: none. Citations: [44].

Euscorpius aquilejensis (C.L. Koch, 1837): CROATIA, ITALY, SLOVENIA. Habitat: inside cave; surface habitats, in rock crevices or under tree bark. Troglomorphies: pedipalps, legs, and metasoma attenuate. Classification: epigean, hypogean: accidental. Citations: [8,32,34–36,45–49].

Euscorpius biokovenski Tropea & Ozimec, 2020: BOSNIA AND HERZEGOVINA, CROATIA. Habitat: inside caves. Troglomorphies: pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Classification: hypogean: troglophile. Citations: [8,32–36,49].

Euscorpius birulai Fet et al., 2014: GREECE. Habitat: inside cave. Troglomorphies: median ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Classification: hypogean: troglophile. Citations: [8,32,33,36,48,50,51].

Euscorpius canestrinii (Fanzago, 1872): ITALY. Habitat: inside cave; surface habitats, in rock crevices. Troglomorphies: none. Classification: epigean, hypogean: accidental. Citations: [52].

Euscorpius concinnus (C.L. Koch, 1837): ITALY. Habitat: inside cave; surface habitats, in rock crevices, leaf litter, or under stones. Troglomorphies: none. Classification: epigean: accidental. Citations: [8,45,53–55].

Euscorpius deltshevi Fet et al., 2014: BULGARIA, SERBIA. Habitat: inside cave; surface habitats, in rock crevices, leaf litter or under stones. Troglomorphies: none. Classification: epigean: accidental. Citations: [8,56,57].

Euscorpius feti Tropea, 2013: BOSNIA AND HERZEGOVINA, CROATIA, MONTENEGRO. Habitat: both inside and outside cave. Troglomorphies: pigmentation and sclerotization slightly reduced; pedipalps, legs, and metasoma attenuate. Classification: epigean, hypogean: troglaxene. Citations: [8,31–36,47–49].

Euscorpius giachinoi Tropea & Fet, 2015: GREECE. Habitat: both inside caves and outside. Troglomorphies: median ocelli reduced; pigmentation and sclerotization reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Classification: epigean, hypogean: troglaxene. Citations: [8,33,36,47,51].

Euscorpius lagostae Caporiacco, 1950: CROATIA. Habitat: both inside and outside caves. Troglomorphies: pedipalps, legs, and metasoma slightly attenuate. Classification: epigean, hypogean: troglaxene. Citations: [34,58].

Euscorpius sulfur Kovařík et al., 2023: ALBANIA, GREECE. Habitat: inside cave. Troglomorphies: pigmentation and sclerotization slightly reduced. Classification: hypogean: troglophile. Citations: [36].

Euscorpius studentium Karaman, 2020: MONTENEGRO. Habitat: inside cave. Troglomorphies: median and lateral ocelli reduced; pigmentation and sclerotization reduced; pectinal teeth count reduced; pedipalps, legs, and metasoma attenuate; telson vesicle enlarged. Classification: hypogean: troglotite. Citations: [8,33–36].



Figure 2. *Euscorpius studentium* Karaman, 2020, habitat at type locality. (A). View of mountain range concealing Spila Skožnica Cave, as seen from Skadar Lake. (B). Entrance to Spila Skožnica Cave. (C). Twilight zone in Spila Skožnica Cave, with guano-coated soil and stones.

2. Materials and Methods

Specimens were collected inside the cave, by shining on the walls with ultraviolet (UV) lamps [59] and turning stones in loose and guano-coated soil. Adult specimens were preserved in 70% ethanol for morphological examination and a single juvenile in 95% ethanol for DNA isolation. Material is deposited in the collections of the American Museum of Natural History (AMNH), including the Ambrose Monell Cryocollection for Molecular and Microbial Research (AMCC), and the zoological collection of the Department of Biology and Ecology, University of Novi Sad, Serbia (ZZDBE). The newly collected material of *E. studentium* was compared morphologically with closely related species, using material deposited at the AMNH, as follows:

Euscorpius biokovens Tropea & Ozimec, 2020: **CROATIA: Dalmatia Region: Splitsko-Dalmatinska County:** Bartulovići, Drinova II Cave, vicinity of Biokovo Nature Park, 43°24'28" N 16°56'34.5" E, 557 m, 11.viii.2022, J. Blasco-Aróstegui and P. Vicent, on walls and under stones inside cave, 1 ♂, 1 ♀(AMNH), 1 ♀(AMCC [LP 18574]); Župa, ca. 5.5 km NW on road 62 to Zagvozd, 43°20'51.6" N 17°05'57.5" E, 11.v.2023, A. Ullrich, 1 ♀(AMCC [LP 19477]); Biokovsko Selo, unnamed cave, 43°20'51.8" N 17°05'58" E, 780 m, 21.v.2024, J. Blasco-Aróstegui and H. Tahirović, inside cave, in crevices and under stones, 2 ♂, 2 ♀(AMNH), 2 ♀(AMCC [LP 20616, 20617]).

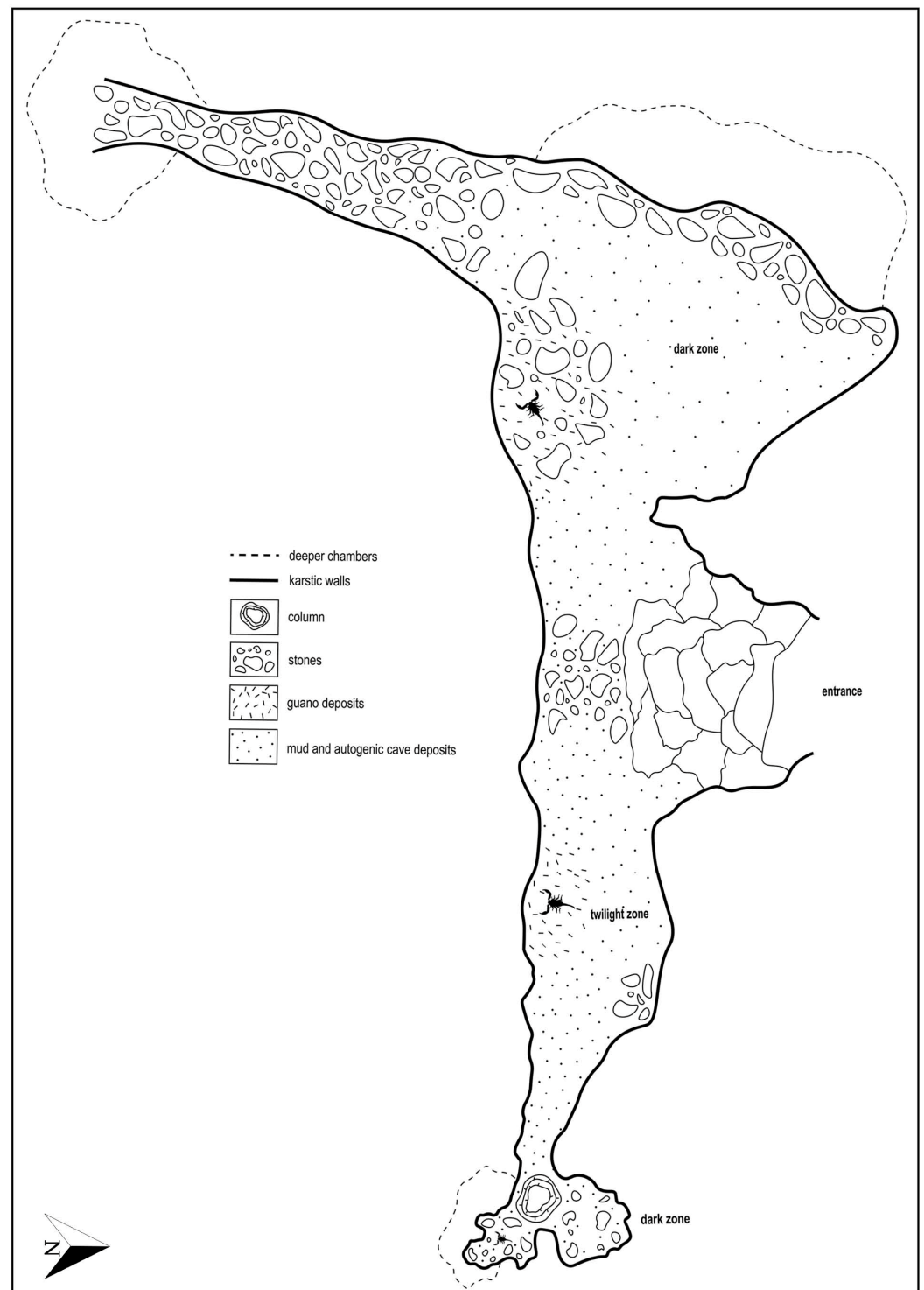


Figure 3. Schematic drawing of Spila Skožnica Cave layout, indicating zones in which scorpions were collected.

Euscorpius feti Tropea, 2013: **CROATIA: Dalmatia Region: Dubrovačko-Neretvanska County: Pelješac Peninsula: Janjina, Gorska Jama Pit**, 42°55'37.3" N 17°25'29.7" E, 243 m, 12.viii.2022, J. Blasco-Aróstegui and P. Vicent, in crevice of depression in steep rock, 1 ♀(AMCC [LP 18284]); **Korčula, in Pišurka Cave**, 42°57'34.3" N 17°07'45.1" E, 105 m, 12.viii.2022, J. Blasco-Aróstegui and P. Vicent, crevices at entrance, on floor and under stones in first chambers of cave, 5 ♂(AMNH), 3 ♀(AMCC [LP 18290, 18523, 18591]).



Figure 4. *Euscorpius studentium* Karaman, 2020, live habitus, dorsal aspect. (A). ♂(AMNH). (B). ♀(AMNH).

Live habitus photographs were taken inside the cave using a Google Pixel Pro 7 camera. Digital images of preserved adult specimens were taken in visible and long-wave UV light with a Microptics™ ML-1000 digital photomicrography system at the AMNH. Morphological examination of specimens was conducted using a Nikon SMZ1500 stereoscope. Measurements (Tables 2 and 3) were taken following Stahnke [60] and Sissom et al. [61], using the ocular micrometer of a Nikon SMZ1500 stereoscope.

The cave location was georeferenced using a portable Garmin 64s GPS Navigation System. However, the exact coordinates have been withheld due to the sensitive nature of the site, which hosts a bat colony and a potentially endangered scorpion species. A

map showing the approximate location and vicinity of the cave was created from a digital elevation layer available at DIVA-GIS using QGIS v.3.4. An approximate reconstruction of the cave's internal layout was prepared using Adobe Illustrator 2020.

The style of the species description follows previous works on *Euscorpius* systematics by the authors [49]. Morphological terminology follows Prendini et al. [62] for carapace topography and surface ornamentation; Loria and Prendini [63] for lateral ocelli; Vachon [64] and Prendini [65] for carinae and surfaces of pedipalps and legs, replacing “external” and “internal” with “retrolateral” and “prolateral”, respectively; Prendini [65] for the patellar process, a spiniform apophysis on the prolateral surface of the pedipalp patella, teleologically referred to as the “patellar spur” in some literature; Vachon [66] for cheliceral dentition, replacing “external” and “internal” with “retrolateral” and “prolateral”, respectively; Prendini and Loria [67] and Blasco-Aróstegui and Prendini [49] for lobes and notches on the pedipalp chela fingers; Vachon [64,68] for trichobothrial notation, with trichobothrial homology following Stockwell [69], in part; a modified version of Prendini [70] for tergal, sternal, and metasomal carinae; Volschenk and Prendini [5], Vignoli and Prendini [6], and Prendini et al. [7,8] for troglomorphies; Vachon [64] and Stahnke [60] for other characters.

Table 2. Measurements (mm) of adult male and female specimens of *Euscorpius studentium* Karaman, 2020, deposited in the American Museum of Natural History (AMNH), New York. Abbreviations: H, height; L, length; W, width. Notes: ¹ sum of prosoma, mesosoma, and metasoma; ² sum of tergites I–VII measured along midline; ³ sum of metasomal segments I–V and telson; ⁴ sum of pedipalp femur, patella, and chela; ⁵ measured from movable finger condyle to fingertip; ⁶ measured at median notch; ⁷ measured at median lobe.

		AMNH				AMNH	
		♂	♀			♂	♀
Total length ¹		41.9	40.28	Telson vesicle	L	4.5	3.62
Carapace	L	5.53	5.47		W	2.56	1.65
	Anterior W	3.87	3.63		H	2.22	1.93
	Posterior W	5.07	4.9	Aculeus	L	0.88	1.2
Mesosoma	L ²	13.03	12.67	Pedipalp	L ⁴	23.24	21.6
Metasoma	L ³	23.34	22.14	Femur	L	5.55	5.26
Segment I	L	2.62	2.49		W	1.79	1.75
	W	1.96	1.64		H	1.12	1.1
	H	1.38	1.22	Patella	L	5.94	5.62
Segment II	L	3.08	2.96		W	1.9	1.85
	W	1.78	1.49		H	1.64	1.61
	H	1.37	1.29	Chela	L ⁵	11.75	10.72
Segment III	L	3.22	3.12	Manus	L	6.7	6.18
	W	1.64	1.43		W	3.38	3.21
	H	1.38	1.25		H	2.67	2.49
Segment IV	L	3.82	3.46	Fixed finger	L	5.05	4.54
	W	1.57	1.34		W ⁶	0.61	0.65
	H	1.38	1.25		H ⁶	0.94	0.89
Segment V	L	6.1	5.29	Movable finger	L	5.93	5.48
	W	1.51	1.26		W ⁷	0.58	0.58
	H	1.45	1.39		H ⁷	1.1	0.81
Telson	L	5.38	4.82	Pectines	L	2.45	1.84

Table 3. Meristic data for known specimens of *Euscorpius studentium* Karaman, 2020, deposited in the University of Novi Sad (ZZDBE), Serbia, and the American Museum of Natural History (AMNH), New York. Counts (sinistral/dextral) of median denticle subrows, prolateral accessory denticles (PAD) and retrolateral accessory denticles (RAD) on fixed and movable fingers of pedipalp chela; retrolateral and ventral trichobothria on pedipalp chela and patella; ventromedian spinules (VMS) on telotarsi of legs I–IV; and pectinal teeth; - indicates missing data.

			♂	♀	Holotype subad. ♂	juv. ♂	Paratype juv. ♀
			AMNH	AMNH	ZZDBE SC1/01	AMNH	ZZDBE SC2/02
Pedipalp chela	Fixed finger subrows		7/7	7/7	7/7	7/7	-/-
	Fixed finger PAD		11/11	11/11	-/11	11/11	-/-
	Fixed finger RAD		7/7	7/7	7/7	7/7	-/-
	Movable finger subrows		7/7	7/7	7/7	7/7	-/-
	Movable finger PAD		11/11	11/11	-/11	11/11	-/-
	Movable finger RAD		7/7	7/7	-/7	7/7	-/-
	External trichobothria	<i>Et</i>	5/5	5/5	5/5	5/5	5/5
		<i>Est</i>	1/1	1/1	1/1	1/1	1/1
		<i>Esb</i>	1/1	1/1	1/1	1/1	1/1
		<i>Eb</i>	3/3	3/3	3/3	3/3	3/3
		<i>et</i>	1/1	1/1	1/1	1/1	1/1
		<i>est</i>	1/1	1/1	1/1	1/1	1/1
		<i>esb</i>	1/1	1/1	1/1	1/1	1/1
		<i>eb</i>	1/1	1/1	1/1	1/1	1/1
Pedipalp patella	Ventral trichobothria	<i>V</i>	4/4	4/4	4/4	4/4	4/4
	External trichobothria	<i>et</i>	6/6	6/6	6/6	6/6	6/6
		<i>est</i>	4/4	4/4	4/4	4/4	4/4
		<i>em</i>	4/4	4/4	4/4	4/4	4/4
		<i>esb</i>	2/2	2/2	2/2	2/2	2/2
		<i>esb_a</i>	4/4	4/4	4/4	4/4	4/4
		<i>eb</i>	4/4	4/4	4/4	4/4	4/4
Telotarsal VMS	Ventral trichobothria	<i>v</i>	7/7	7/7	7/7	7/7	7/7
	Leg I		7/7	6/6	-/-	-/-	-/-
	Leg II		7/6	7/7	-/-	-/-	-/-
	Leg III		8/7	5/7	-/7	-/-	-/-
	Leg IV		9/9	-/8	-/-	-/-	-/-
Pectines	Teeth		7/7	6/6	7/7	7/7	7/7

3. Key to Identification of Cavernicolous Scorpions in the Dinaric Karst

1. Pedipalp patella retrolateral surface with three trichobothria in *em* series *Alpiscorpius liburnicus*
- Pedipalp patella retrolateral surface with four trichobothria in *em* series 2
2. Median ocelli absent, lateral ocelli reduced *Euscorpius studentium*
- Median ocelli present, lateral ocelli well-developed 3
3. Pedipalp patella retrolateral surface with four trichobothria in *eb* series and four trichobothria in *eb_a* series 4
- Pedipalp patella retrolateral surface with five trichobothria in *eb* series and 6–8 trichobothria in *eb_a* series *Euscorpius lagostae*
4. Pedipalp patella retrolateral surface with six trichobothria in *et* series; ventral surface with 7–9 trichobothria in *v* series 5
- Pedipalp patella retrolateral surface with more than six trichobothria in *et* series; ventral surface with 11–12 trichobothria in *v* series *Euscorpius feti*
5. Metasomal segment V, ventrolateral and ventromedian carinae obsolete, intercarinal surfaces smooth *Euscorpius biokovensis*
- Metasomal segment V, ventrolateral and ventromedian carinae distinct, intercarinal surfaces finely granular *Euscorpius sulfur*

4. Systematics

Family Euscorpiidae Laurie, 1896

Genus *Euscorpius* Thorell, 1876

Euscorpius studentium Karaman, 2020

Figures 1–12; Tables 1–3

Euscorpius studentium Karaman, 2020: 1–18, Figures 1–7, 11A and 15 [33].

Type Material. MONTENEGRO: Coastal Region: Bar Municipality: Čanj, Spila Skožnica Cave [42°10' N 19°01' E], 7.v.2017, I. Karaman, 1 subad. ♂holotype (ZZDBE SC1/01), 2.vi.2017, I. Karaman, 1 juv. ♀paratype (ZZDBE SC1/02). According to I. Karaman, the paratype was donated to G. Tropea (Rome, Italy).

Diagnosis. *Euscorpius studentium* can be separated from all other European species of Euscorpiidae, in which the ocelli are present and fully developed, by the absence of median ocelli and reduction of lateral ocelli (Figure 6). Additionally, the second-most proximal denticle in the first median denticle subrow of the movable finger is larger than the other denticles in *E. studentium* (Figures 8B and 9B), unlike other European species of Euscorpiidae, in which these denticles are similar in size.

Euscorpius studentium most closely resembles *E. biokovensis* and *E. feti*, two troglomorphic species inhabiting humid caves in the Dinaric Karst of Bosnia and Herzegovina, Croatia, and Montenegro, which also exhibit attenuation and elongation of the pedipalps and marked dorsoventral compression (Figures 4–12). However, in addition to the absence of median ocelli and reduction of lateral ocelli (Figure 6), *E. studentium* can be separated from these species by the following characters. Although the base coloration is similar (dark or reddish-brown to lighter brown, with carapace and pedipalps darker than mesosoma and metasoma) in all three species, *E. studentium* is notably paler (Figure 4). The pedipalp patella is also more elongate and slender in *E. studentium* (width 32.4% of length; Table 2) than in *E. biokovensis* (width 37.3% of length) and *E. feti* (width 37.1% of length) with the patellar process notably more developed, especially in the male, in *studentium* (height 135.1% of width; Figure 7) than in *E. biokovensis* (height 116.3% of width) and *E. feti* (height 113.8% of width) [31,32,48]. Whereas *E. studentium* possesses six trichobothria in the *et* series of the pedipalp patellar retrolateral surface and seven trichobothria in the *v* series of

the patellar ventral surface (Figure 7), *E. biokovensis* possesses six and 7–9 trichobothria in these series, respectively, and *E. feti*, seven or eight and 11–12 trichobothria in these series, respectively [31,32,48]. Whereas the pedipalp chela is slender and compressed in all three species, the manus is more elongate in *E. studentium* (manus width 29.4% of chela length; Table 2; Figures 8 and 9) than in *E. biokovensis* (manus width 31.1% of chela length) and *E. feti* (manus width 33.6% of chela length). Unlike *E. studentium*, however, the chela fingers are more elongate and attenuate in the male of *E. biokovensis* and especially *E. feti*, which exhibits a more pronounced gap in the fixed finger and a wider median lobe on the movable finger. The pectinal tooth counts of *E. biokovensis* and *E. studentium* are generally lower, 7/7 (σ) or 6/6 (φ) (Table 3; Figure 6), than those of *E. feti*, 8–9/8–9 (σ) or 7–8/7–8 (φ) [31,32,48]. The legs, especially the terminal segments (i.e., basitarsi and telotarsi), exhibit similar attenuation in all three species, but this is more pronounced in *E. studentium* (Figure 10). The telotarsal ungues of *E. feti* and *E. studentium* (Figure 10) are more elongated and curved than those of *E. biokovensis*, which are slightly shorter and more robust. The ventrolateral and ventromedian carinae of metasomal segment V are distinct in *E. feti*, obsolete in *E. biokovensis*, and absent in *E. studentium* (Figure 11). The telson vesicle of the adult male is less globose in *E. biokovensis* and *E. studentium* (Figure 12A,B) than in *E. feti*.

Description. The following description is based on an adult male and an adult female (Figure 5), the first adults reported for the species (see Tables 2 and 3 for measurements and meristic data).

Total length: Medium-sized, 41.9 mm (σ ; $n = 1$) or 40.3 mm (φ ; $n = 1$) (Table 2).

Coloration: Uniformly depigmented (Figure 4). Carapace reddish-brown, darker in female, with posterior and posterolateral margins lighter. Pedipalps medium brown, slightly darker in female. Pedipalp carinae dark, blackish. Legs pale brown, darker in female. Tergites light brown, with posterior and lateral margins pale. Telson vesicle pale, with three slightly darker stripes longitudinally, one pair along ventrolateral sulci and one between anterodorsal sulci, more noticeable in female; aculeus black.

Chelicerae: Manus dorsal and retrolateral surfaces entirely smooth, with few scattered setae; prolateral and, to a lesser extent, ventral surfaces densely setose (Figure 6A,B). Fixed finger dorsal margin with four teeth: distal, subdistal, median and basal; distal and subdistal teeth well separated, median and basal fused into a bicuspid. Movable finger dorsal margin with five teeth: one prodistal, two subdistal, one median, and one basal; prodistal (DI) and retrodistal (DE) teeth asymmetric, DI twice length of DE; subdistal teeth small, separated; median teeth large; basal teeth small.

Carapace: Carapace anterior width of posterior width, 76.3% (σ ; $n = 1$) or 74.1% (φ ; $n = 1$); posterior width of length, 91.7% (σ ; $n = 1$) or 89.6% (φ ; $n = 1$) (Table 2). Carapace anterior margin sublinear, with obsolete anteromedian notch; anteromedian sulcus distinct, narrow, shallow; posteromedian sulcus shallow, more pronounced than anteromedian sulcus; posterolateral sulci shallow. Median ocelli absent; two pairs of small lateral ocelli, posterolateral major (PLMa) and median lateral major (MLMa), similar in size. Median ocular tubercle and superciliary carinae absent (Figure 6A,B). Anteromedian and posteromedian surfaces smooth; lateral surfaces very finely and sparsely granular; margins costate-granular. Carapace surfaces almost asetose; anterior margin with three or four microsetae; location of median ocular tubercle demarcated by two microsetae.

Sternum: Shape subpentagonal (Figure 6C,D) with marked posterior depression. Surface with four macrosetae and few additional microsetae.

Pedipalps: Femur width of length, 32.3% (σ ; $n = 1$) or 33.3% (φ ; $n = 1$) (Table 2). Prodorsal and proventral carinae complete, costate-granular, each with several large spiniform and subspiniform granules (Figure 7A,B). Retrodorsal carina complete, granular, discontinuous. Promedian and retroventral carinae complete, costate-granular, each with discontinuous spiniform granules and few macro- and microsetae. Ventromedian carinae partial, granular, becoming obsolete distally. Other carinae absent. Dorsal and ventral intercarinal surfaces finely granular in male, almost smooth in female. Prolateral and retrolateral intercarinal surfaces smooth or nearly so.



Figure 5. *Euscorpius studentium* Karaman, 2020, habitus, dorsal (A,C) and ventral (B,D) aspects. (A,B). ♂ (AMNH). (C,D). ♀ (AMNH). Scale bar = 10 mm.

Patella elongate, width of length, 32% (♂; $n = 1$) or 32.9% (♀; $n = 1$) (Table 2). Proventral carina complete, granular to costate-granular (Figure 7G,H). Prodorsal carina reduced to series of spiniform granules (Figure 7C,D). Retrodorsal and retroventral carinae complete, costate-granular (♂; Figure 7C,E,G) or granular (♀; Figure 7D,F,H), except at proximal and distal margins of segment. Retromedian carina partial, reduced to discontinuous row of granules (Figure 7E,F). Other carinae absent. Dorsal and ventral intercarinal surfaces finely granular to smooth (Figure 7C,D,G,H). Prolateral surface with distinct, elongate patellar process, more spiniform in male (Figure 7C,G) than in female (Figure 7D,H); surface of process smooth, with few microsetae and two macrosetae, one situated basally, the other apically (Figure 7C,D,G,H). Retrolateral intercarinal surface smooth (Figure 7E,F).

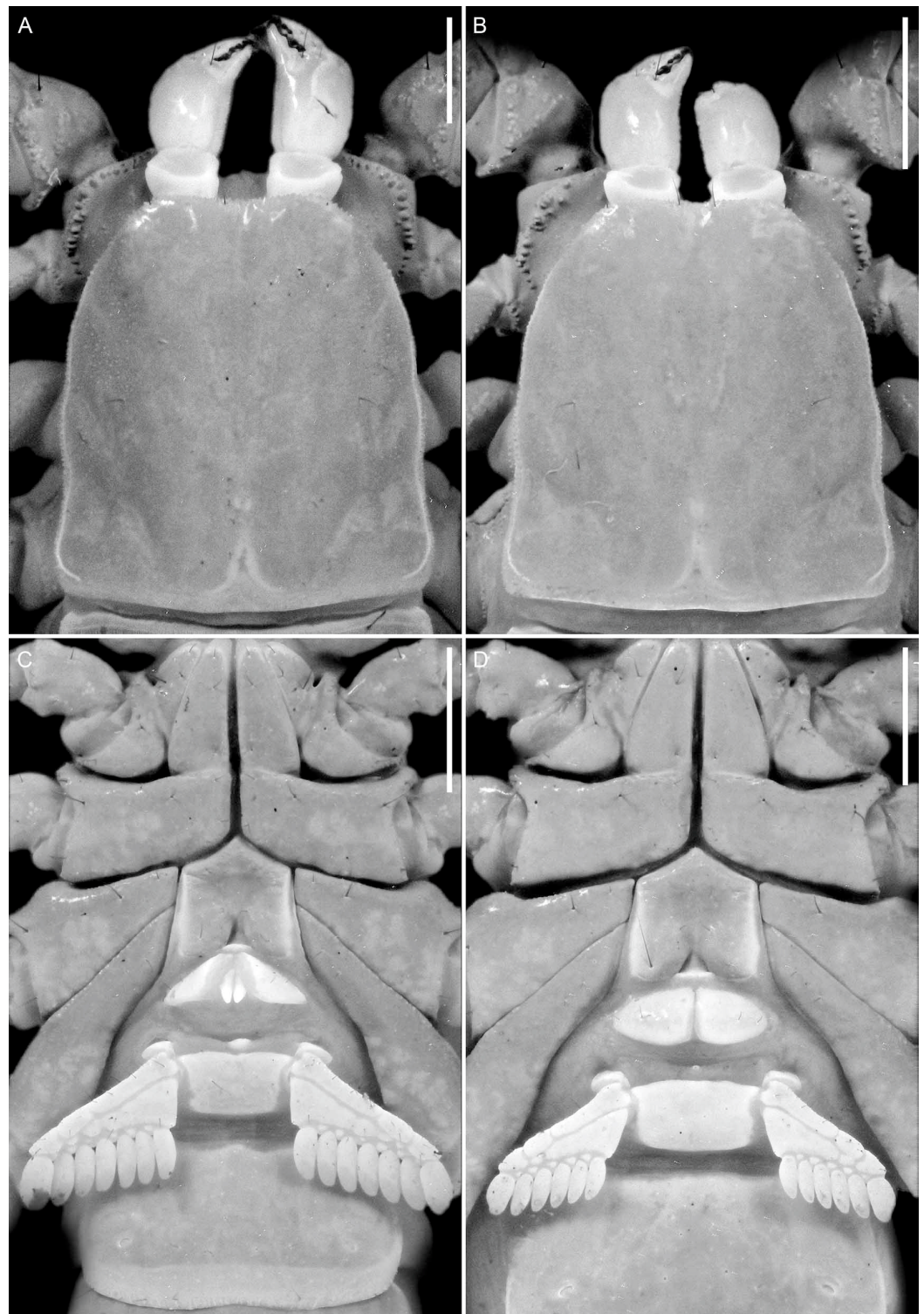


Figure 6. *Euscorpius studentium* Karaman, 2020, carapace, dorsal aspect (A,B) and sternum and pectines, ventral aspect (C,D). (A,C). ♂(AMNH). (B,D). ♀(AMNH). Scale bars = 2 mm.

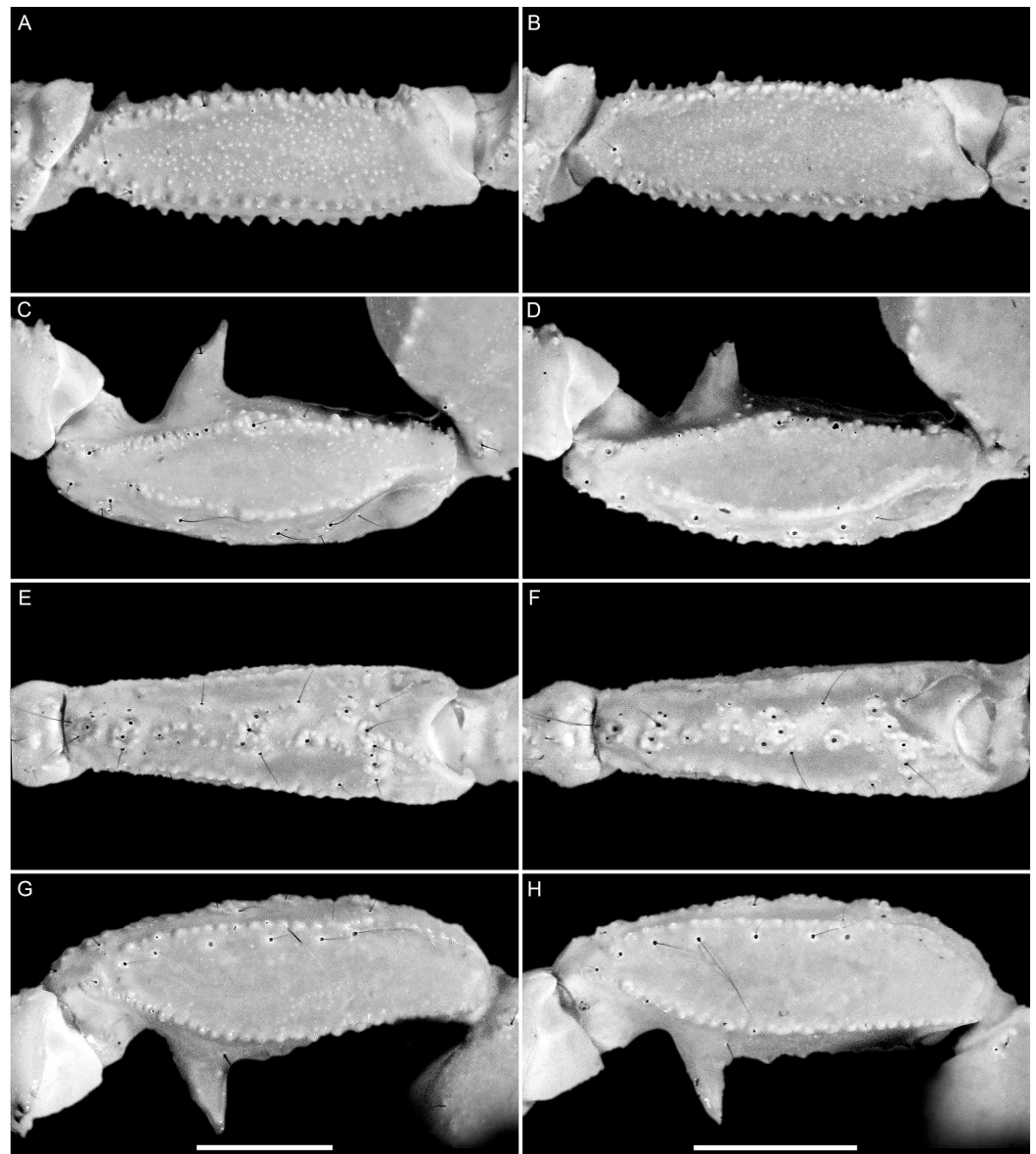


Figure 7. *Euscorpius studentium* Karaman, 2020, dextral pedipalp femur, dorsal aspect (A,B), and patella, dorsal (C,D), retrolateral (E,F), and ventral (G,H) aspects. (A,C,E,G). ♂(AMNH). (B,D,F,H). ♀(AMNH). Scale bars = 2 mm.

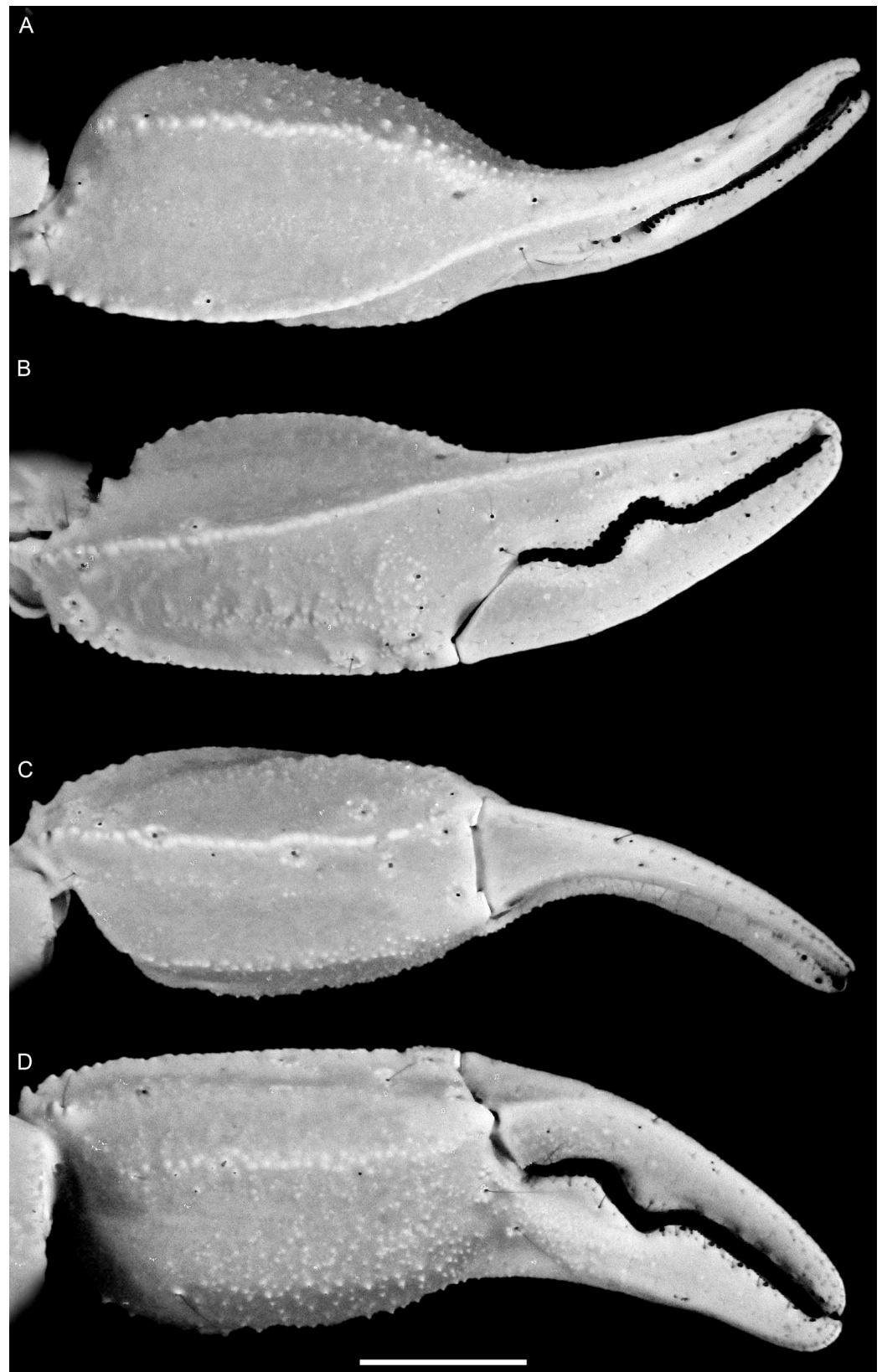


Figure 8. *Euscorpius studentium* Karaman, 2020, ♂(AMNH), dextral pedipalp chela, dorsal (A), retrolateral (B), ventral (C), and prolateral (D) aspects. Scale bar = 2 mm.

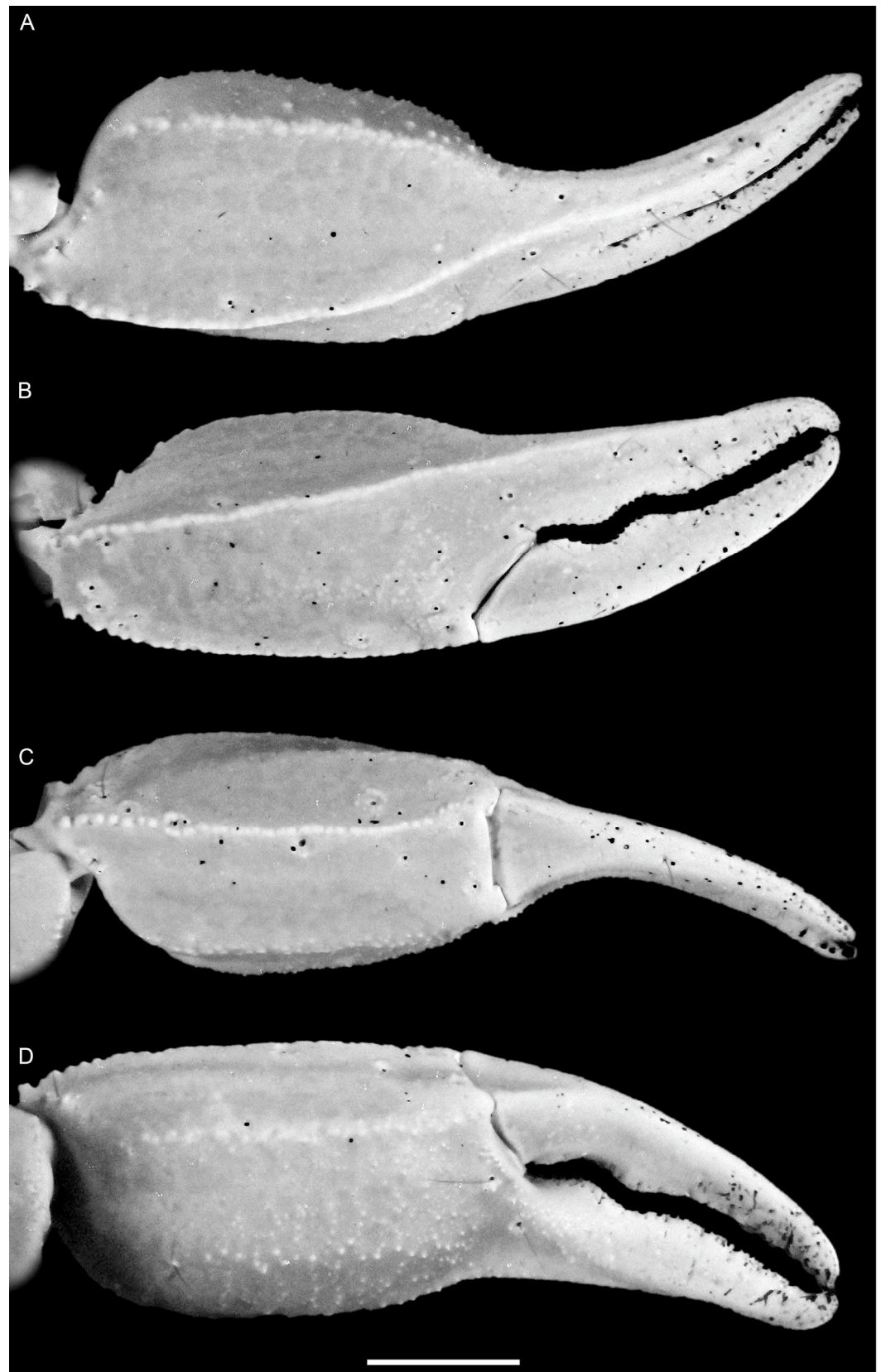


Figure 9. *Euscorpius studentium* Karaman, 2020, ♀(AMNH), dextral pedipalp chela, dorsal (A), retrolateral (B), ventral (C), and prolateral (D) aspects. Scale bar = 2 mm.

Chela slender, with elongate manus, fingers curved and narrower in male (Figure 8) than female (Figure 9); chela length of manus width, 28.8% (σ ; $n = 1$) or 29.9% (φ ; $n = 1$); manus width of length, 50.4% (σ ; $n = 1$) or 51.9% (φ ; $n = 1$); manus height of width, 79% (σ ; $n = 1$) or 77.6% (φ ; $n = 1$); movable finger length of manus length, 89% (σ ; $n = 1$) or 88.7% (φ ; $n = 1$); fixed finger width of length, 12.7% (σ ; $n = 1$) and 14.3% (φ ; $n = 1$); movable finger width of length, 9.8%, (σ ; $n = 1$) or 10.6%, (φ ; $n = 1$). Chela dorsal surface flat (Figures 8A,B and 9A,B), sloping slightly from proximal to distal margin, more so in male. Prolateral surface convex proximally, moderately (φ ; Figure 9A,D) to markedly (σ ; Figure 8A,D) concave distally (proximal to fixed finger). Retrolateral surface slightly (φ ; Figure 9B) to markedly (σ ; Figure 8B) convex medially. Ventral surface flat, sloping slightly from proximal to distal margin in female; proximal margin curved (Figures 8C and 9C). Proventral carina granular, incomplete, absent in proximal part of segment but notably more developed than ventromedian carina, which is obsolete (Figures 8C,D and 9C,D). Promedian carina obsolete, finely granular, extending to base of fixed finger (Figures 8D and 9D). Prodorsal carina obsolete, granular, comprising discontinuous row of granules in distal part of segment (Figures 8A,B and 9A,B). Dorsomedian carina costate-granular, partial, reduced to discontinuous row of subspiniiform granules becoming obsolete in distal part of segment (Figures 8A,B and 9A,B). Dorsal secondary carinae vestigial. Digital carina costate-granular, reduced to discontinuous row of subspiniiform granules distally (Figures 8A,B and 9A,B). Subdigital carina vestigial, reduced to few granules at proximal margin of segment (Figures 8A,B and 9A,B). Retromedian carina incomplete, comprising obsolete row of granules decreasing in size distally (Figures 8B,C and 9B,C). Retrolateral secondary and secondary accessory carinae vestigial, reduced to distal quarter of segment, proximal to movable finger condyle (Figures 8B,C and 9B,C). Retroventral carina complete, costate-granular, comprising subspiniiform granules in proximal part of segment (Figures 8B–D and 9B–D). Ventromedian carina vestigial, reduced to fine granules proximally (Figures 8C,D and 9C,D). Dorsal and ventral intercarinal surfaces sparsely setose and smooth to glabrous. Prolateral and retrolateral intercarinal surfaces sparsely setose and finely granulo-reticulate (Figures 8 and 9). Fixed and movable fingers with pronounced proximal and medial lobes, respectively, and correspondingly deep proximal and medial notches in male (Figure 8B,D); proximal and medial lobes wider than high, but medial lobe higher and medial notch deeper; medial lobe fits evenly with median notch, leaving little to no gap between fingers, when closed. Proximal and medial lobes, and corresponding notches, of fixed and movable fingers shallower in female (Figure 9B,D). Median denticle rows of fixed and movable fingers each comprising seven subrows (Table 3) forming sub-linear row, discontinuous at accessory denticles (Figures 8 and 9); second-most proximal denticle of first subrow on movable finger, distal to condyle, noticeably larger than other denticles (Figures 8B and 9B); fixed and movable fingers each with eleven prolateral and seven retrolateral accessory denticles ($n = 4$; Table 3) and single terminal denticle, interlocking unevenly, such that movable finger moderately displaced retrolaterally when closed (Figures 8 and 9). Intercarinal surfaces of fingers smooth, fairly setose (Figures 8 and 9).

Femur with three full-sized trichobothria (Figure 7A,B), two on dorsal surface (d_1 , d_2), one on prolateral surface (i). Patella with 34 trichobothria, one petite (esb_2), 33 full sized (Table 3; Figure 7C–H): seven on ventral surface (v_1 – v_7); 24 on retrolateral surface (et_1 – et_6 , est_1 – est_4 , em_1 – em_4 , esb_1 , esb_2 , esb_{a1} – esb_{a4} , eb_1 – eb_4); two on dorsal surface (d_1 , d_2); one on prolateral surface (i). Chela with 26 trichobothria, two petite (Et_4 , Esb), 24 full sized (Table 3; Figures 8 and 9): eighteen on manus, four on ventral surface (V_1 – V_4), ten on retrolateral surface (Et_1 – Et_5 , Est , Esb , Eb_1 – Eb_3), two on dorsal surface (Dt , Db), two on prolateral surface (it , ib); eight on fixed finger, four on dorsal surface (dt , dst , dsb , db), four on retrolateral surface (et , est , esb , eb).

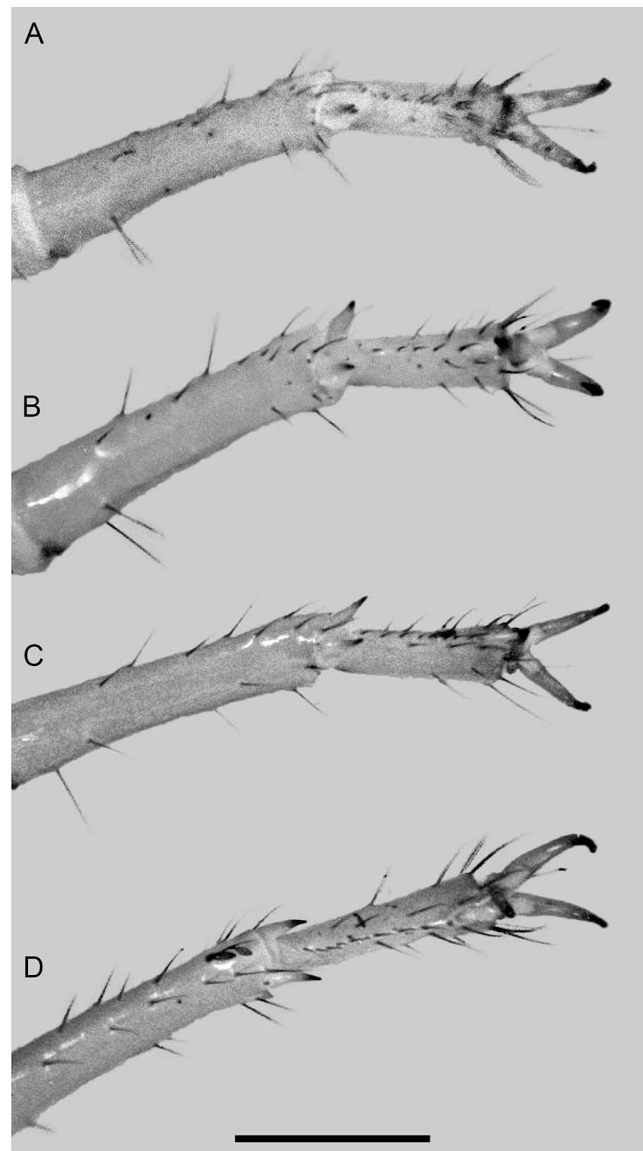


Figure 10. *Euscorpius studentium* Karaman, 2020, ♂ (AMNH), dextral legs I–IV, basitarsi and telotarsi, proventral aspect (A–D). Scale bar = 1 mm.

Legs: Femora with costate-granular proventral carina complete on legs I–III, partial, restricted to proximal three-quarters on IV, and granular retrodorsal carina partial, restricted to proximal three-quarters, on I and IV, complete on legs II and III, other carinae absent; prolateral and retrolateral surfaces finely granular; few macrosetae on carinae and other surfaces. Patellae with costate-granular prodorsal carina on legs I and II, acarinate on III and IV, other carinae absent; few macrosetae on carina and other surfaces; pro- and retrolateral surfaces finely granular to smooth. Tibiae acarinate, with few setiform macrosetae on prolateral and retrolateral surfaces; tibial spurs absent. Basitarsi acarinate; prolateral and retrolateral surfaces sparsely setose; prolateral and retrolateral pedal spurs present distally. Telotarsi attenuate, each with single ventromedian row of six or seven elongate spinules on legs I and II, seven or eight on III, and eight or nine on IV ($n = 2$; Table 3); unguis elongate, narrow, curved, and equal in length; dactyl pronounced (Figure 10).

Genital operculum: Opercula suboval, sclerites completely separated longitudinally (Figure 6C,D). Genital papillae well developed, protruding medially from below opercula (♂; Figure 6C) or absent (♀; Figure 6D).



Figure 11. *Euscorpius studentium* Karaman, 2020 (AMNH), metasomal segments I–V, dorsal (A,D), lateral (B,E), and ventral (C,F) aspects. (A–C). ♂(AMNH). (D–F). ♀(AMNH). Scale bars = 2 mm.

Pectines: Basal plate rectangular, slightly oval; shallow anteromedian invagination in male, absent in female (Figure 6C,D). Three short marginal lamellae, proximal sclerite considerably longer than medial and distal sclerites; median lamellae count, 4/4. Pectinal tooth count, 7/7 (♂; $n = 3$) or 6–7/6–7 (♀; $n = 2$) (Table 3). Surfaces with macro- and microsetae, mostly on marginal lamellae but also on teeth.

Tergites: Pre-tergites and post-tergites progressively increasing in length. Pre-tergites glabrous; post-tergites III–VII surfaces acarinate and smooth medially, finely granular submedially and along posterior margins.

Sternites: Sternites III–VII surfaces acarinate, entirely smooth, and sparsely setose medially, each with several microsetae along lateral and posterior margins; III–VI each with pair of kidney-shaped spiracles sublaterally.



Figure 12. *Euscorpius studentium* Karaman, 2020, telson, ventral (A,C) and lateral (B,D) aspects. (A,B). ♂ (AMNH). (C,D). ♀ (AMNH). Scale bars = 2 mm.

Metasoma: Segments I–V narrow and slender, progressively increasing in length and decreasing in width (Table 2). All segments acarinate, except for few obsolete granules posteriorly on segments I–III (Figure 11). Anal arch of segment V with ten obsolete ventral lobes, two pairs of lateral lobes and rounded dorsal depression (Figure 11). Dorsal, lateral and ventral surfaces smooth on segments I–IV (Figure 11), almost completely smooth on V, except dorsolateral surfaces, finely granular (Figure 11B,E). Macrosetae arranged in groups of eight or nine per segment, situated ventrolaterally on segments I–IV, with few additional setae on V (Figure 11B,C,E,F).

Telson: Vesicle globose in male, elongate and slightly flattened ventrodistally in female (Figure 12); with anterodorsal and paired ventrolateral sulci; surfaces smooth with scattered macro- and microsetae mostly anterior to aculeus. Aculeus short, curved, forming obtuse angle with vesicle, angle broader in female (Figure 12); base of aculeus aligned diagonally to ventral surface of vesicle, more prominent in male (Figure 12).

DISTRIBUTION: Only known from Spila Skožnica Cave near Čanj, in the Coastal Region of Montenegro. An unidentified blind scorpion from a cave in Bosnia and Herzegovina (p. 23: [30]) may be closely related.

ECOLOGY: *Euscorpius studentium* is an obligate troglobite, restricted to a single cave in the Dinaric Karst (Figures 1–4). It displays pronounced troglomorphies, including absence of the median ocelli and reduction of the lateral ocelli, reduction in sclerotization and pigmentation, and attenuation of the pedipalps and legs (Figures 4–10 and 12). *Euscorpius biokovenski*, a closely related species with a wider distribution in the Dinaric Karst, has also only been found inside caves, but presents moderate to weak troglomorphies and is considered a troglophile (Table 1). *Euscorpius feti*, another species found both inside and outside caves in the Dinaric Karst, exhibits moderate to weak troglomorphies and is considered a troglaxene (Table 1).

The three specimens of *E. studentium* reported in the present contribution were collected with UV light detection, during daytime. The adult male of *E. studentium* was found walking on a humid limestone wall, in the twilight zone of the cave, near moist muddy soil covered with guano (Figure 3). The adult female and juvenile were taken from under stones situated directly beneath bat roosts, where the soil was moist and covered with guano, in the dark zones of the cave (Figure 3). Despite extensive searches, including the initial expeditions of I. Karaman and a subsequent visit to the cave in August 2022 by the first author, no additional specimens were collected (although exuviae were observed), suggesting that these scorpions are seasonally active and require high humidity. All specimens

were collected in late spring, from May to early June, coinciding with the presence of bats and fresh guano deposits in the cave. The apparently greater activity of these scorpions in the upper chambers of the cave is probably associated with an increased energy input to the cave, resulting in a higher abundance of guanivores and other invertebrates, as well as higher levels of humidity during the rainy season.

An unidentified species of *Euscorpius* was collected in crevices near the cave entrance and surrounding forest in the foothills of the mountain.

CONSERVATION STATUS: *Euscorpius studentium* inhabits a small, humid cave in a low-elevation hill, known as Golo Brdo, on the coast of Montenegro (Figures 1–3). The cave is situated on a slope, surrounded by karren bedrock with patches of vegetation [33]. It houses a medium-sized colony of bats that become active in spring and depart the cave in summer, suggesting it serves as a winter roost. The cave interior, as well as the sub-Mediterranean forest on the foothills of the mountain in which it is located, are relatively undisturbed. However, the proximity of the cave to the tourist settlement of Čanj poses a potential threat to the cave and its occupants.

Euscorpius studentium is a highly stenotopic species, presently known from only three juveniles and two adults, collected in a single cave. Due to its very limited extent of occurrence, specific habitat requirements, and possibly low abundance, *E. studentium* may be vulnerable to anthropogenic environmental impacts, including climate change and habitat destruction or degradation. As this species is potentially at risk of extinction in an uncertain future, it would be advisable to list it as Endangered on the IUCN Red List of Threatened Species (<https://www.iucnredlist.org>, accessed on 27 November 2024). As a further recommendation to ensure the preservation of the scorpion and the bat colony, the cave should be designated a National Protected Area by the Environmental Protection Agency of Montenegro (<https://epa.org.me>, accessed on 27 November 2024).

MATERIAL EXAMINED: MONTENEGRO: Coastal Region: Bar Municipality: Čanj, Spila Skožnica Cave, 42°10' N 19°01' E, 149 m, 22.v.2024, J. Blasco-Aróstegui and H. Tahi-rović, inside karstic cave, in humid and guano covered area, walking along karstic wall and under stones, 1 ♂, 1 ♀(AMNH), 1 juv. ♂(AMCC [LP 20621]).

5. Discussion

The evolution of troglobitism has long interested biologists. Many researchers argue that it represents an evolutionary dead-end, as the extreme specialization and isolation of cave-dwelling species, which often leads to limited genetic diversity and reduced adaptability outside the cave environment, are presumed to be difficult to overcome [33,71–73]. Competing with epigeal species that are already well adapted to surface habitats may further disadvantage hypogean species [73]. However, Humphreys [74] suggested that the removal of potential competitors might allow troglobitic species to recolonize endogean and epigeal habitats—assuming suitable external conditions such as a highly humid environment—challenging the notion that troglobitism is a definitive evolutionary dead-end. More recent evidence from troglomorphic scorpions supports this view. Prendini et al. [7] found that endogean, humicolous scorpions of the North American family Typhlochactidae Mitchell, 1971, were evolutionarily younger than their hypogean counterparts. The hypogean condition was recovered as ancestral, indicating that endogean species evolved from hypogean ancestors on more than one occasion. Volschenk and Prendini [5] proposed that lithophily, the adaptation to rocky habitats, could be an evolutionary precursor to troglomorphy. This raises the question as to whether humicolous (endogean) habitats could represent a transitional stage between cave (hypogean) habitats and surface (epigeal) habitats in some taxa. Leaf litter or soil microhabitats often share ecological characteristics with cave environments, e.g., higher levels of humidity and more stable temperatures than other surface microhabitats [75,76].

The troglobitic fauna of the Balkans is singularly ancient. It is assumed that the region's past tropical climate with an abundance of humid habitats promoted the diversification of an early humicolous and hygrophilous fauna during the Tertiary [19,27,28]. Part of

this “proto-fauna” survived successive climatic transitions, including Miocene aridification and the Quaternary glaciations at the end of the Pliocene, by retreating to hypogean refugia, i.e., as climate relicts [19,26,77–79]. The presence of deep limestone sediments and subsequent processes of karstification (Figure 1B) facilitated the divergence of subterranean taxa in isolated hypogean niches, ultimately creating a remarkably diverse troglomorphic and troglobitic fauna [18,23,26]. The extant cavernicolous species of the Balkans are, in effect, Darwin’s (p. 136: [80]) “wrecks of ancient life”, remnants of an ancient biota that evolved and adapted to subterranean environments over millions of years, diversifying through niche divergence and allopatric speciation.

Among Balkan cavernicolous taxa, scorpions are a rarity. Eleven of the thirteen euscorpoid species recorded from inside caves have been reported from the Balkans (Table 1), and little is known about their biology, ecology or genetic relationships. Five of these species are exclusively cavernicolous, each with varying degrees of specialization to subterranean environments. Noteworthy examples of differential adaptation to cave habitats include *E. biokovensis*, *E. feti*, and *E. studentium*. Using the ecological key of Prendini et al. [8], *E. feti* was classified as a troglone, which occasionally ventures into caves but is not entirely dependent on them. *Euscorpius feti* has often been recorded outside of caves [31–33,48], including in the present study, indicating a broader ecological tolerance (eurytopy). In contrast, *E. biokovensis* and *E. studentium* are considered a troglophile and troglobite, respectively. Both species are restricted to karstic systems, to which they exhibit different degrees of specialization [32–34]. Whereas *E. biokovensis* only displays attenuation of the appendages and slight reduction in sclerotization and pigmentation, *E. studentium* is an obligate troglobite, exhibiting pronounced troglomorphies (i.e., anophthalmia, reduced sclerotization and pigmentation, and attenuation of the appendages). Other remarkable Balkan cavernicolous *Euscorpius* species include the troglomorphic *Euscorpius birulai* Fet et al., 2014, which appears to be restricted to a single cave on the Greek island of Euboea [50] and *Euscorpius sulfur* Kovařík et al., 2023, discovered within a sulfur cave on the border between Albania and Greece [36]. The other species in Table 1 represent sporadic records of typically epigean species in cave environments, displaying broad ecological tolerances and an ability to thrive in diverse environments. The opportunistic ability of euscorpoids to exploit a range of ecological niches probably contributed to their dispersal across Europe and beyond [81–83]. The only two cave-restricted species which have been studied phylogenetically appear to represent the most basal branch of their clade, in the case of *E. feti*, or to lack epigean relatives, in the case of *E. biokovensis* [34], consistent with the “Climate Relict” model [1,84,85]. Although the phylogenetic position of the troglobitic *E. studentium* has yet to be tested, it may represent another ancient lineage of Euscorpidae, along with the montane species of the predominantly humicolous genus *Alpiscorpius* and the widely distributed genus *Tetratrachobothrius* Birula, 1917. Further evidence supporting the Climate Relict model in the Balkans is provided by several radiations of Dinaric Karst invertebrates in which unique, ancient lineages coexist with evolutionary younger, karst-adapted taxa [86–89]. For example, molecular analyses of pseudoscorpions inhabiting the Dinaric Karst identified several relictual species and revealed that at least 65% of the species in the region are endemic [23].

The restricted distributions, specific habitat requirements, and typically low abundance of cavernicolous taxa, either due to their occurrence in deeper cave chambers or because they follow a K-selected life history strategy, common to many troglone [33], render these species particularly susceptible to anthropogenic environmental impacts, including climate change and habitat destruction or degradation. Anthropogenic pressure on subterranean ecosystems and species is intensifying [90]. Climate change is the main factor altering the microclimate within caves, whereas habitat degradation, driven by pollution, mining, recreational tourism, and other forms of land use, threatens their structural integrity [90–92]. Troglobitic organisms frequently possess low thermal tolerance and limited vagility, rendering them particularly vulnerable [1,2,16]. Without prompt and effective conservation strategies, unique subterranean habitats and the specialized species

they shelter face an inevitable decline [90]. The present contribution adds to a growing body of knowledge about the unique diversity of cavernicolous invertebrates, highlighting the need for continued exploration and conservation of these fragile ecosystems before it is too late.

Author Contributions: Conceptualization, J.B.-A. and L.P.; methodology, J.B.-A. and L.P.; software, J.B.-A.; validation, J.B.-A. and L.P.; formal analysis, J.B.-A.; investigation, J.B.-A. and L.P.; resources, L.P.; data curation, L.P.; writing—original draft preparation, J.B.-A.; writing—review and editing, J.B.-A. and L.P.; visualization, J.B.-A. and L.P.; supervision, L.P.; project administration, L.P.; funding acquisition, J.B.-A. and L.P. All authors have read and agreed to the published version of the manuscript.

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