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Cave-adapted campodeids (Hexapoda, Diplura, Campodeidae) from the Dinarides and adjacent karst regions

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Abstract: Five new species are described, *Plusiocampa (Didymocampa) cvijici* Sendra & Antić, sp. nov., *Plusiocampa (Plusiocampa) atom* Sendra & Antić, sp. nov., *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov., *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. and *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. This brings the number of cave-adapted species of campodeids known from the Dinarides, Eastern Alps, Balkan System and Rodope Massif to 28 (one species in the genus *Campodea* and 27 in *Plusiocampa*). Among *Plusiocampa*, four out of five subgenera are present (*Pentachaetocampa* is not present in the region studied): *Didymocampa* (one species), *Plusiocampa* s. str. (15 species), *Stygiocampa* (eight species) and *Venetocampa* (three species), whereby *Stygiocampa* and *Venetocampa* are endemic to the studied region. These results reveal the importance of the Dinarides karst region as a centre of diversification for campodeids and for cave animals in general. A monophyletic subgroup, consisting of *Stygiocampa*, *Venetocampa* and *Plusiocampa* s. str. and characterized by the absence of medial posterior thoracic macrosetae, presumably colonized the Dinaric plate during the middle of the Cenozoic and occurs in that area since then.

Keywords: *Plusiocampa* - *Stygiocampa* - *Venetocampa* - *Didymocampa* - Plusiocampinae - taxonomy - biogeography - colonization.

INTRODUCTION

The order Diplura encompasses ten families with 1009 species, of which the Campodeidae and the Japygidae are the most diversified, comprising 85% of the total diversity (Koch, 2009; Sendra *et al.*, 2021). Diplurans live in cryptic hypogean habitats all over the world, except for the polar circles and regions with permafrost soils (Condé, 1956; Sendra *et al.*, 2021). They have successfully colonized cave ecosystems, particularly so the family Campodeidae, which encompasses 144 cave-adapted species that represent 30% of the total family diversity (Sendra *et al*., 2020a, b). Seventy percent of cave-adapted Campodeidae are distributed in European and Mediterranean karst regions (Sendra *et al*., 2020a). Prior to our study, 22 obligate cave-dwelling campodeid species were known from the Dinarides and adjacent karst regions, from the Eastern Alps to the Balkan System, and the Rhodope Massif (Sendra *et al*., 2020a). The number of cave-restricted species of different taxa is exceptionally high in the Dinarides and this region has been recognized as one of the world's major hotspot of subterranean biodiversity (Culver *et al.,* 2006; Sket *et al.,* 2004; Sket, 2012; Zagmajster *et al.,* 2014; Antić & Makarov, 2019). Two campodeid genera inhabit

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the studied region: *Campodea* Westwood, 1842 and *Plusiocampa* Silvestri, 1912, with one endemic subgenus *Stygiocampa* Silvestri, 1934 (Bareth & Condé, 2001; Condé & Bareth, 1996; Sendra *et al.,* 2020a).

The study of cave-adapted campodeids in the Dinaric and adjacent karst regions has a long history, starting with Joseph (1882) who described the troglomorphic species *Campodea nivea* Joseph, 1882 from the Jama v Košanskih Grižah Cave near Pivka (Slovenia). The species description encompasses only a short diagnosis, as it is the case with many other species described during this period (Sendra *et al.,* 2020b). Denis (1923) and later Silvestri (1934, 1947) redescribed *C. nivea* in detail and proposed a new combination (Silvetri, 1934): *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882). Further research revealed 11 new cave-adapted *Plusiocampa* species throughout the western Balkans: four in the subgenus *Stygiocampa* and seven in the subgenus *Plusiocampa* (Condé, 1947, 1948, 1950, 1959; Silvestri, 1931; 1933a, b). Ten new descriptions of cave-adapted campodeids followed at the end of the 20th and the beginning of the 21st century (Bareth, 1988; Bareth & Condé, 1984, 2001; Condé, 1974; Condé & Bareth, 1996; Neuhertz, 1984). Recently, Sendra *et al*. (2020a) revealed more than two hundred records of 22 cave-adapted campodeids species throughout the study area, identifying this region as a possible centre of campodeid diversification in caves, along with other well-sampled and rich regions as the Pyrenees and Cantabria (Sendra *et al.,* 2020a, b). Recently collected diplurans from caves in the Dinarides and adjacent regions point to an overlooked diversity hotspot in that region. In the present paper we describe five new species from 15 caves and give additional biogeographic data on cave-adapted campodeids of the region.

MATERIAL AND METHODS

The specimens stored in ethanol 70-75% were washed using distilled water, mounted on microscope slides in Marc André II solution, and examined under a phase-contrast optical compound microscope (Leica DMLS). The illustrations were made with a drawing tube, while measurements were taken with an ocular micrometer. To measure body length, the specimens were mounted *in toto* and measured from the base of the distal macrochaetae of the frontal process to the supra-anal valve of the abdomen. Several specimens were coated with palladium-gold and used for SEM (Hitachi S-4100) photography and measurement of the sensilla.

The morphological descriptions and abbreviations follow Condé (1956). We use the term "gouge sensilla" for the concave-convexly-shaped sensilla on the antennae, and "gard setae" for the characteristic two short setiform sensilla near the lateral anterior sensillum of each labial palp (Bareth & Condé, 1981). For the position of macrosetae we adopt the abbreviations of Condé (1956): *ma* = medial-anterior, *la* = lateral-anterior, *lp* = lateral-posterior, and *post* = posterior; *sma, sla, slp, spost* for submacrosetae. For head macrosetae we follow Wygodzinsky (1944): *asl* = anterior-sublateral, *psm* = posterior-submedia, and *psl* = posterior-sublateral macrosetae.

The type specimens and other material studied are kept in the following institutions:

IZB	Institute of Zoology, University of Belgrade, Serbia
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
NHMB	Natural History Museum of Barcelona, Spain
Coll. AS	private collection of Alberto Sendra, València, Spain
NHMZOO	Natural History Museum & Zoo, Split, Croatia
PMSL	Slovenian Museum of Natural History, Ljubljana, Slovenia.

TAXONOMY

Family Campodeidae Meinert, 1865
Subfamily Plusiocampinae Paclt, 1957
Genus *Plusiocampa* Silvestri, 1912
Subgenus *Didymocampa* Paclt, 1957

Plusiocampa (Didymocampa) cvijici Sendra & Antić, sp. nov.

Figs 1-6, Table 1

Type material: IZB; male holotype; western Serbia, Hadži-Prodanova pećina Cave, near the village of Raščići, Ivanjica, 650 m asl.; 28th June 2018; leg. D. Antić. – Coll. AS; one male and one juvenile paratypes; collected together with the holotype. – Coll. AS; one female paratype; same cave and collector; 17th October 2018. All specimens mounted in Marc André II solution.

Other material studied: Coll. AS; one specimen of unknown sex collected together with the holotype; mounted on an aluminium stub and coated with palladium-gold.

Etymology: This species is named after Prof. Dr Jovan Cvijić (1865-1927), a widely known Serbian geomorphologist, former president of the Serbian Royal Academy of Sciences, and one of the first explorers of the Hadži-Prodan Cave in 1914. The epithet is a name in the genitive case.

Description:

Body: Body lengths 3.9 mm (female paratype), 3.3 mm (holotype), 3.4 mm (male paratype) and 2.6 mm (juvenile paratype) (Fig. 1). Epicuticle smooth when examined under an optical microscope. Body clothed with few

Fig. 1. Habitus of *Plusiocampa (Didymocampa) cvijici* Sendra & Antić, sp. nov. from Hadži-Prodanova pećina Cave, Raščići, Ivanjica, western Serbia (photograph by Dragan Antić).

medium-sized, thin, smooth (or with one thin distal barb) setae.

Head: Antennae of same length as body in juvenile and slightly shorter in adults (Table 1), with 27 (female paratype), 29 (juvenile paratype), and 30 (male holotype) antennomeres. Bacilliform sensillum of third antennomere in ventral position, between macrosetae *d* and *e,* 20 µm long. Medial antennomeres slightly elongated: 1.5-1.6 times longer than wide; apical antennomere 1.5 longer than wide. Each medial and distal antennomere with 18-20 thin gouge sensilla (30 µm) in a single distal whorl, as well as with two conical sensilla (7 µm) in same whorl. Cupuliform organ occupying 1/3 of total length of last antennomere; with 12-16 spheroidal olfactory chemoreceptors with an eccentric or centric column surrounded by concentric, incompleted expansions covered by a visible polygonal net with porous surface (Figs 2-3). Protruding frontal process carrying numerous tubercular setae. Length ratios of three macrosetae along each side of line of insertion of antennomere and *x* setae being 30/37/30/42, a/i/p/x in holotype. Three pairs of longer macrosetae on dorsal side of head in *asl, psm, psl* position. Labial palps suboval, each with conical latero-external sensillum near two gard setae, seven normal setae in anterior portion, and up to 60-80 neuroglandular setae in medial and posterior position.

Thorax: Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 $lp_{2,3}$ macrosetae; mesonotum with 1+1 *ma*, 3+3 (3+2) la_{1-3}, 2+2 $lp_{2,3}$; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 $lp_{2,3}$; long, thin notal macrosetae with barbs in distal half; few smooth (or with a thin distal barb) clothing setae (holotype: 5+3, 14+13, 15+14 on pronotum, mesonotum, and metanotum) (Fig. 4). Metathoracic legs reaching eighth abdominal segment, with two dorsal femoral macroseta of 0.25-0.20 mm length, with thin barbs in distal three-fourths, as well as two ventral macrosetae similar in shape and length as dorsal macrosetae (Fig. 5); two tibial metathoracic macrosetae with 1-5 thin distal barbs; calcars with long, thin barbs in several rows on one side; tarsus with two ventral rows of larger setae with distal barbs and with two dorsal and two ventral subapical smooth macrosetae; slightly unequal claws (posterior claw 1.2 longer than anterior claw) with large lateral crests; posterior claw with a small backward overhang.

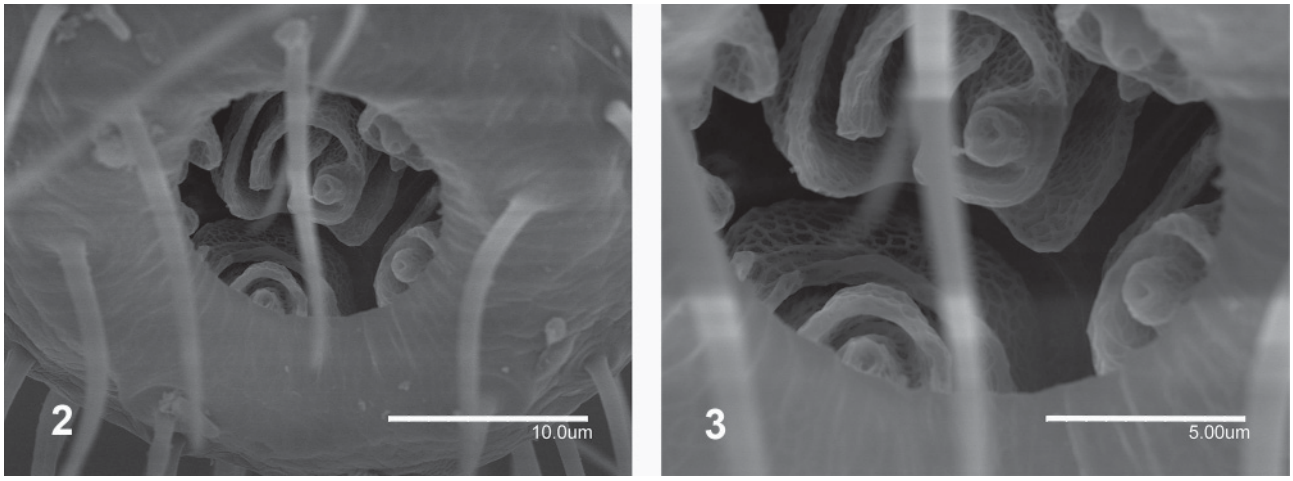
Abdomen: Urotergites I-III with 1+1 $post_1$ macrosetae; urotergite IV with 1+1 *la*, 2+2 $post_{1,2}$ macrosetae; urotergite V with 1+1 *la*, 5+5 $post_{1-5}$; urotergite VI with 2+2 (1+1) *la*, 5+5 $post_{1-5}$; urotergite VII with 2+2 *la*, 5+5 $post_{1-5}$; urotergite VIII with 6+6 *post*; abdominal segment IX with 8+8 (8+7) *post* macrosetae; all urotergal macrosetae long and barbed in distal three-fourths; urosternite I with 7+7 macrosetae, urosternites II-VII with 5+5, and urosternite VIII with 2+2 macrosetae. Stylar setae with a few barbs: apical seta with basal tooth and two thin barbs, subapical seta with two or three thin barbs, and medio-sternal seta with a long distal barb and a thin short one. Complete cercus of holotype 1.3 times longer than body, with base divided into three secondary articles followed by nine primary articles (Table 1); each primary cercus bearing 2-10 irregularly arranged whorls of long barbed macrosetae, 1-2 distal whorls of smooth long setae, and one apical whorl of short thin setae with tiny distal barbs.

Secondary sex characters: First urosternite of males with two rows of up to 43 glandular g_1 setae, subcylindrical appendages slightly enlarged in distal area, with up to 25 glandular a_1 setae (Fig. 6). Females with subcylindrical appendages carrying up to nine glandular a_1 setae.

Taxonomic affinities: *Plusiocampa (Didymocampa) cvijici* sp. nov. shares some taxonomical features

Table 1. *Plusiocampa (Didymocampa) cvijici* Sendra & Antić, sp. nov. Length (in mm) of body, antennae, femur, tibia and tarsus of metathoracic legs and of cerci, in addition to number of antennomeres and cercal primary articles.

specimen	body	antennae	number of antennomeres	femur	tibia	tarsus	number of primary cercal articles	cercus
Paratype, juvenile	2.6	2.6	29	-	-	-	-	-
Holotype, male	3.3	3.2	30	0.48	0.53	0.44	9	4.3
Paratype, male	3.4	-	-	0.50	0.64	0.45	-	-
Paratype, female	3.9	3.4	34	0.52	0.58	0.45	-	-



Figs 2-3. *Plusiocampa (Didymocampa) cvijici* Sendra & Antić, sp. nov. (2) Cupuliform organ of last antennomere. (3) Detail olfactory receptors of cupulifom organ.

with two species of the presumably paraphyletic subgenus *Didymocampa*: *Plusiocampa (Didymocampa) evallonychia* Silvestri, 1949 from Crimenan caves and *Plusiocampa (Didymocampa) euxina* Condé, 1996 from Movile Cave in Romania. Among other taxonomical features we point out the following: the absence of medial posterior macrosetae on mesonotum and metanotum; 1+1 posterior macrosetae on first to third urotergites; 5+5-6+6 macrosetae on second to seventh urosternites; stylar setae with a few thin barbs (Condé, 1996; Sendra *et al.,* 2020a; Silvestri, 1949). *Plusiocampa (D.) cvijici* sp. nov. differs from both species by some taxonomical features: 3+3 and 1+1 lateral anterior macrosetae on mesonotum and metanotum [*vs.* 2+2 *la*, 1+2 *la* in *P. (D.) euxina* and 1+1 *la*, 0+0 *la* in *P. (D.) evallonychia*], 8+8 post macrosetae on abdominal segment IX [*vs*. 9+9 in *P. (D.) euxina* and *P. (D.) evallonychia*]. *Plusiocampa (D.) euxina* is geographically and taxonomically closest to *P. (D.) cvijici* sp. nov. due to similarities in the macrosetae distribution pattern, their slightly subequal claws, and few smooth notal clothing setae. The new species differs from *P. (D.) euxina* not only in the aforementioned number of lateral anterior notal macrosetae and the number of macrosetae on the eighth abdominal segment, but *P. (D.) euxina* also has few tubercular setae on the frontal process, three ventral tibial macrosetae, short lateral processes with a few barbs on the pretarsus, and barbed subapical tarsal setae. *Plusiocampa (D.) cvijici* sp. nov. is distinguished from *P. (D.) euxina* by more tubercular setae, two ventral tibial macrosetae, longer smooth lateral processes protruding beyond the tips of the claws, and smooth subapical tarsal setae.

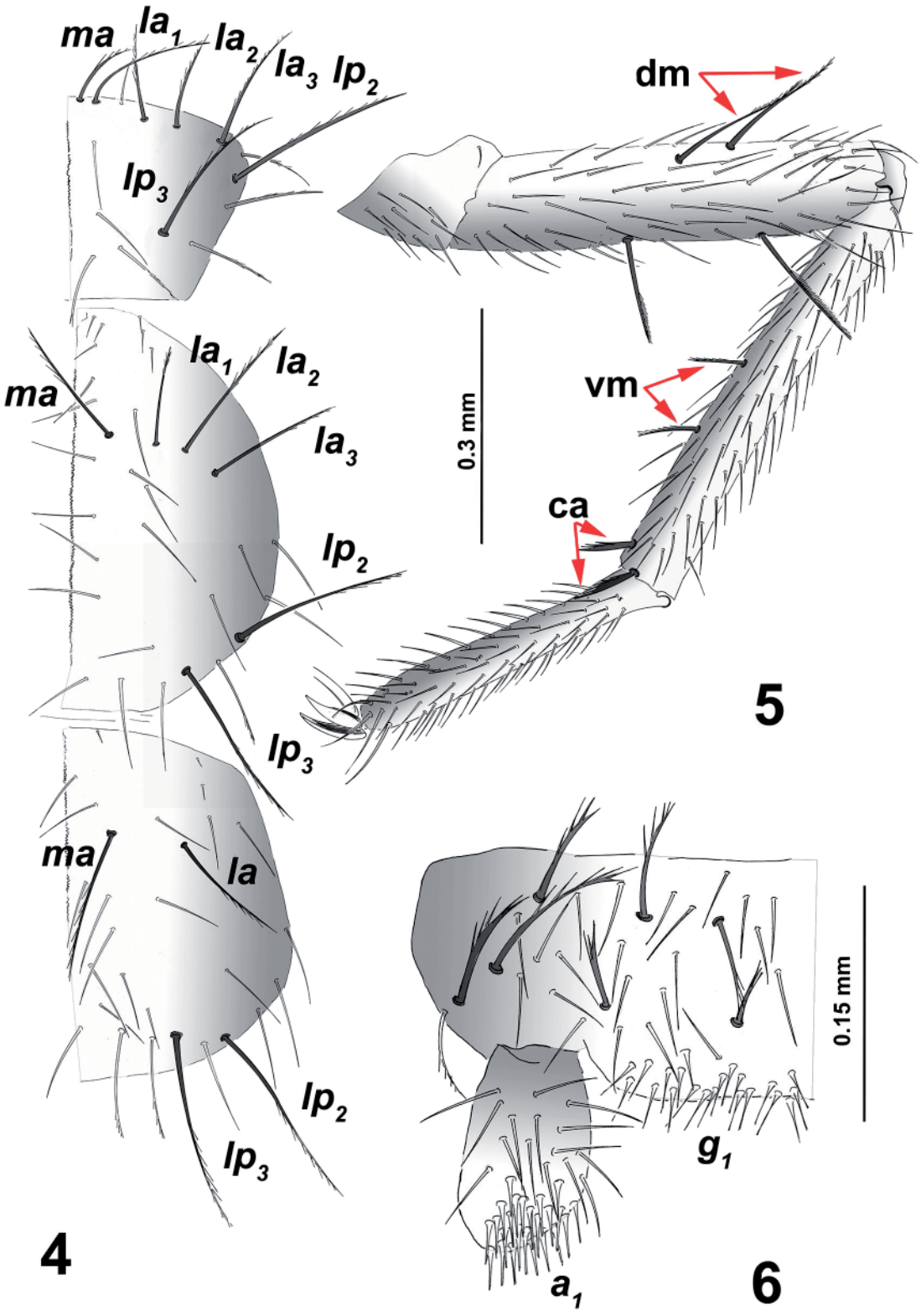
Type locality: The Hadži-Prodanova pećina Cave, located in western Serbia (the Dinarides), is a national natural monument and a well-known Palaeolithic site rich in late Pleistocene mammal fossils (Mihailović & Mihailović, 2003; Bogićević *et al.,* 2017) (Fig. 7). The entrance of this multilevel cave with a length of 420 m is situated at 630 m a.s.l. The cave is mainly dry, without a cave stream, and it consists of three main chambers: the lower, middle and upper one. It is a residence for six Chiroptera species (Paunović, 2016). Besides, the cave is rich in arthropods, of which the most important are Balkan troglophiles, viz., the harvestman *Mitostoma cancellatum* (Roewer, 1917), the millipedes *Apfelbeckia insculpta* (L. Koch, 1867) and *Brachydesmus herzogowinensis* Verhoeff, 1897, as well as Serbian troglobionts such as the springtail *Pseudosinella ivanjicae* Ćurčić, Lučić & Boškova, 1999 and the ground beetle *Duvalius starivlahi* Guéorguiev, Ćurčić & Ćurčić, 2000, both only known from the Hadži-Prodanova pećina Cave. The new species was found under stones in the main (middle) chamber of the cave.

Subgenus *Plusiocampa* s. str. Silvestri, 1912

Plusiocampa (Plusiocampa) atom Sendra & Antić, sp. nov.

Figs 8-10, Table 2

Type material: MHNG; female holotype; Bosnia & Herzegovina, Lukina pećina Cave, Srednja stijena, Tajan, Zavidovići; 11th July 2018; leg. D. Antić. – MHNG; one male a one female paratypes (labelled ♂2 paratype and ♀7 paratype) collected from the same cave on 17th November 2019; leg. A. Bajraktarević, E. Balić, D. Zgonjanin, A. Sinković. – NHMB; two female paratypes (labelled ♀2 paratype and ♀6 paratype) collected together with the holotype. – Coll. AS.; one male, three female and one juvenile paratypes (labelled ♂1 paratype, ♀2, ♀3, ♀7 paratypes and J1 paratype) collected together with the holotype.



Figs 4-6. *Plusiocampa (Didymocampa) cvijici* Sendra & Antić, sp. nov., holotype. (4) Pronotum, mesonotum and metanotum of right side of body (5) Right metathoracic leg; dm = dorsal macrosetae, vm = ventral macrosetae; ca = calcars. (6) First urosternite of right side; a_1 = glandular a_1 setae, g_1 = glandular g_1 setae.

Other material studied: Coll. AS; one female collected together with the holotype. – Coll. AS; three females and one juvenile; same cave and collectors, sampled on 17th November 2019; mounted in Marc André II solution. – Coll. AS; one specimen of unknown sex collected together with the holotype; mounted on an aluminium stub and coated with palladium-gold.

Etymology: This species is named in honor of the members of the "Atom" Sport and Science-Research Club, Zavidovići, Bosnia and Herzegovina, for their determination and hard work at protecting speleological objects in Bosnia and Herzegovina, for collecting cave animals, as well as for saving human lives in the mountains of Bosnia and Herzegovina whilst risking their own lives. Additionally, D.A. is grateful to them for their long-lasting friendship. Noun in apposition.

Description:

Body: Body length 4.4 mm (males), 4.5-6.5 mm (females) and 3.6 mm in one juvenile (Fig. 8) (Table 2). Epicuticle smooth when seen under optical microscope; body with numerous medium-sized, smooth (or with a distal thin barb) clothing seta.

Head: Antennae length 0.73-0.84, shorter than body (Table 2), with 32-38 antennomeres (perhaps regenerated distal antennomers). Bacilliform sensillum of third antennomere in a ventral position, between macrosetae *d* and *e,* 15 µm long. Medial antennomeres slightly elongated, 1.7 times longer than wide; apical antennomere 2.3 times longer than wide. Eight to ten thin gouge sensilla (28 µm) in a single distal whorl on each medial and distal antennomere; two conical sensilla (9 µm) in same whorl. Cupuliform organ occupying less than 1/3 of total length of last antennomere, with 7-9 spheroidal olfactory chemoreceptors with an eccentric or centric column surrounded by a concentric fold. Non-protruding frontal process with three smooths anterior macrosetae and no tubercular setae. In holotype these macrosetae along each side of line of insertion of antennomere and smooth *x* setae with length ratios of *a/i/p/x,* 36/34/29/39, respectively. Three pairs of slightly longer smooth macrosetae on dorsal side of head in *ma, la, lp* position. Labial palps suboval, each with a conical latero-external sensillum near two gard setae, six normal setae in anterior portion, and up to 60 neuroglandular setae in medial and posterior position.

Thorax: Pronotum with 1+1 *ma*, 4+4-3+3 *la*, 2+2 $lp_{2,3}$ macrosetae; mesonotum with 1+1 *ma*, 3+3 la_{1-3}, 2+2 $lp_{2,3}$; and metanotum with 1+1 *ma*, 1+1 *la*, 2+2 $lp_{2,3}$; long barbed notal macrosetae with barbs in distal two-

Fig. 7. Entrance of the Hadži-Prodanova pećina Cave, Raščići, Ivanjica, western Serbia (photograph by Bojan Ilić).

Fig. 8. Habitus of *Plusiocampa (Plusiocampa) atom* Sendra & Antić, sp. nov. (left) from Lukina pećina Cave, Srednja stijena, Tajan, Zavidovići, Bosnia & Herzegovina. On the right is a specimen of *Brachydesmus mulaomerovici* Makarov, Ćurčić & Antić in Antić *et al.*, 2013 (photograph by Dragan Antić).

Table 2. *Plusiocampa (Plusiocampa) atom* Sendra & Antić, sp. nov. Length (in mm) of body, antennae, femur, tibia and tarsus of metathoracic legs, in addition to number of antennomers. Asterisks indicate presence of telescoped body segments.

specimen	body	antennae	number of antennomeres	femur	tibia	tarsus
J1 paratype	3.6	-	-	0.64	0.62	0.60
♂1 paratype	4.4 (*)	-	-	0.77	0.80	0.72
♂2 paratype	4.4	3.7	34	0.56	0.57	0.52
♀1 paratype	4.5 (*)	-	-	0.78	0.79	0.72
♀6 paratype	4.8	4.0	32	0.90	1.00	0.80
♀5 paratype	5.3	-	-	0.93	0.84	0.81
♀ holotype	5.4	4.3	38	0.74	0.78	0.67
♀7 paratype	6.4	4.7	36	0.81	0.89	0.77
♀4 paratype	6.5	-	-	1.05	1.00	0.84

thirds; smooth clothing setae or clothing setae with a thin distal barb, and longer marginal setae with thin distal barbs in their distal half (Fig. 9). Metathoracic legs reaching the ninth abdominal segment, with similar lengths of femur, tibia and tarsus, including pretarsus (Fig. 9) (Table 2). One dorsal femoral macroseta in distal half with thin 0.20-0.30 mm long barbs; three barbed ventral macrosetae slightly shorter than dorsal macrosetae; three short tibial metathoracic macrosetae barbed in distal half; calcars with thin barbs in several rows on one side; tarsus with two ventral rows of slightly larger setae with distal barbs; two smooth dorsal subapical setae and two barbed ventral setae on tarsus; claws slightly unequal (posterior claw 1.2-1.3 times longer than anterior claw), with large lateral crests and smooth setiform lateral processes; posterior claw with large backward overhang (Fig. 10).

Abdomen: Urotergites I-III with 1+1 $post_1$ macrosetae; urotergite IV with 1+1 *la*, 3+3 (4+3) $post_{1-3}$ macrosetae; urotergite V-VII with 1+1 *la*, 5+5 $post_{1-5}$; urotergite VIII with 6+6 *post*; abdominal segment IX with 8+8 *post* macrosetae; all urotergal macrosetae long and barbed in distal three-fourths; urosternite I with 7+7 macrosetae; urosternites II-VII with 5+5; urosternite VIII with 2+2 macrosetae; urosternal macrosetae with a few long distal barbs. Stylus with smooth apical seta carrying a basal tooth, subapical and medio-sternal setae with four or five long thin barbs. No intact cercus in any specimen; the most complete cercus 4.5 mm long (♀6-paratype), with basal article divided into three secondary articles followed by eight primary articles; each primary cercal article bearing 2-8 irregulary shaped whorls of long macrosetae with thin distal barbs, one distal whorl of smooth long setae, and one apical whorl of short thin setae with tiny distal barbs.

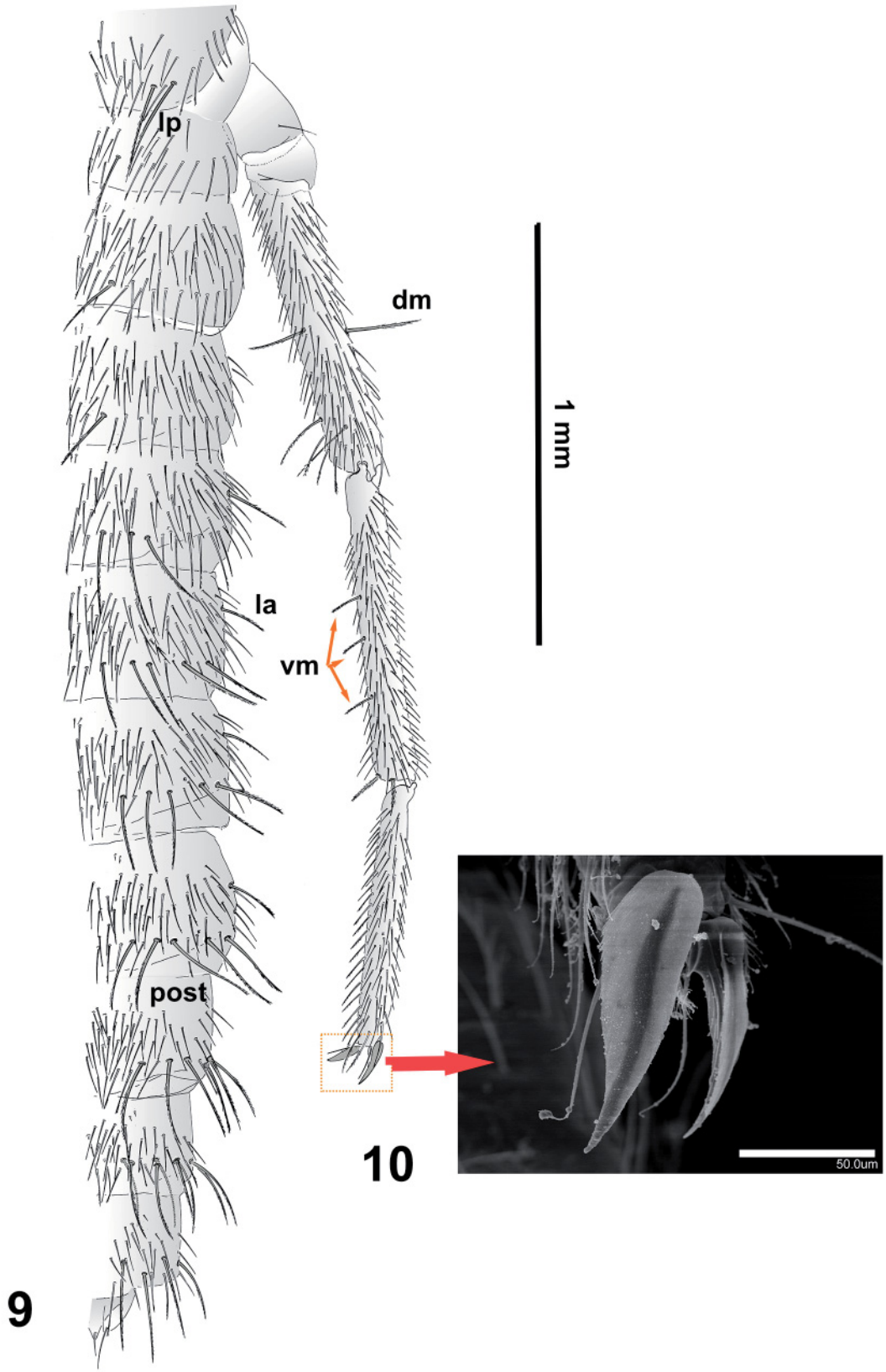
Secondary sex characters: First urosternite of males bearing a narrow field with one or two rows of up to 29 glandular g_1 setae; subcylindrical appendages with a small field of up to 15 glandular a_1 setae; females possessing subcylindrical appendages with up to 13 glandular a_1 setae.

Taxonomic affinities: *Plusiocampa (P.) atom* sp. nov. shows similarities with *P. (P.) latens* Condé, 1948, a species with several known localities in the Dinaric karst (Sendra *et al.,* 2020a). Both species have equal macrosetae patterns on thorax and abdomen (Condé, 1948). *Plusiocampa (P.) atom* sp. nov. differs from *P. (P.) latens* in two characters: it has three ventral macrosetae and up to 38 antennomeres, whereas *P. (P.) latens* has only two ventral macrosetae and 24-27 antennomeres.

Type locality: The Lukina pećina Cave is located in the "Tajan" Nature Monument, in central Bosnia and Herzegovina (Fig. 11). This is a cave system with two entrances close to each other and a total length of 247 m. It is well-known for its remains of an autochthonous Upper Pleistocene fauna and for traces of the cave bear (Lukić-Bilela *et al.,* 2009). As far as arthropods are concerned, two other troglobites were found in the cave, viz., the millipede *Brachydesmus mulaomerovici* Makarov, Ćurčić & Antić in Antić *et al.*, 2013 and the woodlouse *Cyphonethes tajanus* Karaman & Horvatović, 2018, both recently discovered and described, and endemic to subterranean habitats in the "Tajan" Nature Monument.

Plusiocampa (Plusiocampa) aff. *elongata* Ionescu, 1955

Material studied: Coll. AS; three males and five females; Serbia, Pričevska pećina Cave, Pričevac, Papratna, Stara Planina; 17th June 2019; leg. D. Antić & D. Stojanović.



Figs 9-10. *Plusiocampa (Plusiocampa) atom* Sendra & Antić, sp. nov., holotype. (9) Posterior portion of metathorax and abdomen, right side of body; dm = dorsal macrosetae, vm = ventral macrosetae. (10) Pretarsus, dorsal view.

Fig. 11. Entrances of Lukina pećina Cave, Srednja stijena, Tajan, Zavidovići, Bosnia & Herzegovina (photograph by Emir Balić).

Subgenus *Stygiocampa* Silvestri, 1934

***Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov.**

Figs 12-41, Table 3

Type material: MHMZOO; male holotype; Croatia, Grabovčića jama Cave, Radošić; 4th November 2014; leg T. Rađa. – MHMZOO; one male and five female paratypes (labelled ♂2 paratype, and ♀5 to ♀9 paratypes); same cave and collector as holotype sampled 27th October 2014. – MHNG; two female paratypes (labelled ♀1 paratype and ♀4 paratype); same cave, data and collecter as holotype. – NHMB; one female paratype (labelled ♀11 paratype); same cave and collector as holotype; sampled 27th October 2014. – Coll. AS; two female paratypes (labelled ♀2 paratype and ♀3 paratype); same cave, data, and collector as holotype. – Coll. AS; one male and three female paratypes (labelled ♀10 paratype, ♀12 paratype, ♀13 paratype and ♂3 paratype); same cave and collector as holotype sampled 27th October 2014.

Other material studied: Coll. AS; two males and two females from the same cave and collector; sampled on 27th October 2014; mounted on an aluminium stage and coated with palladium-gold.

Etymology: This species is dedicated to the French zoologist Camille Bareth, who has been working with diplurans throughout her prolific career and described 27 new species and 3 subspecies of troglobitic campodeids. She also worked intensely on the morphology and physiology of the group, to which she devoted more time and effort than any other researcher. In addition, she is the co-author of an article where she and her colleague Dr Bruno Condé suggested the possibility that the specimens identified by them as *Plusiocampa (Stygiocampa)* cf. *remyi*, could belong to a new taxon. This is confirmed and the new species is described below. The specific epithet is a name in the genitive case.

Description:

Body: Body length 3.4-5.9 mm (males, n= 3), 5.5-8.7 mm (females, n= 11) (Table 3). Epicuticle smooth under

optical microscope, when seen at high magnification, weakly reticulated, showing irregular polygonal structures of various sizes (Fig. 20); body set with numerous moderately long clothing setae with thin barbs almost all over over surface.

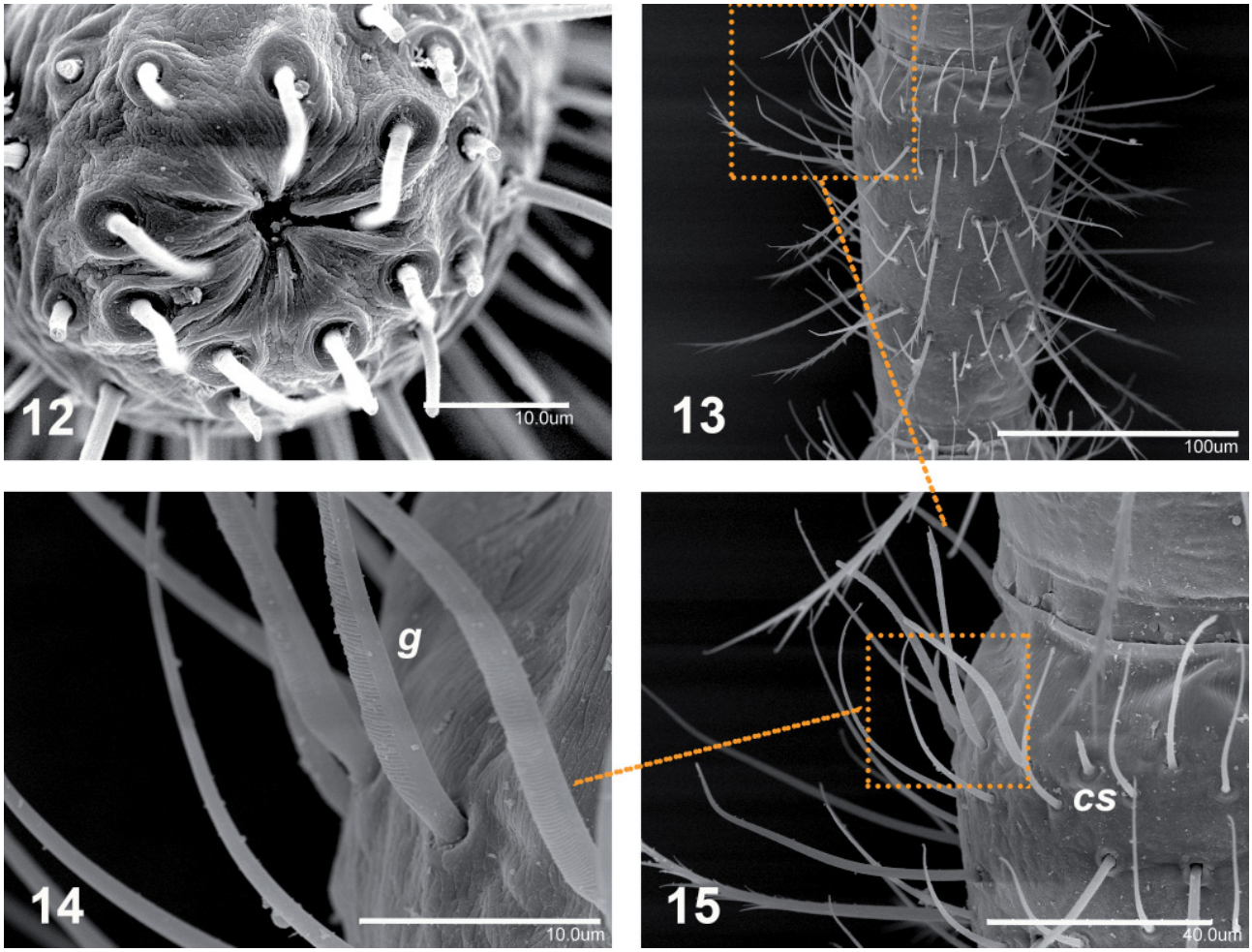
Head: Eleven apparently complete and intact antennae with 40-50 antennomeres; antennae 1.07-1.25 times longer than body (Table 3); medial antennomeres 2-3 times longer than wide; apical antennomere 3 times longer than wide. Cupuliform organ with several uncountable, complex and apparently laminar olfactory chemoreceptors opening to the exterior through a very narrow hole (Fig. 12). Distal and central antennomeres with three whorls of macrosetae carrying distal barbs and scattered smooth setae, as well as a single distal whorl of 16-18 long gouge sensilla (26-38 µm long), and up to two conical 8 µm long sensilla (Figs 13-15). Proximal antennomeres with typical trichobothria, plus a small bacilliform sensillum (8 µm long) on third antennomere in a ventral position. Frontal process with a moderate conical protrusion covered with a few tuberculate setae carrying a few thin barbs (Fig. 17). The three macrosetae along each side of line of insertion of antennomere and *x* setae with thin distal barbs; length ratios of *a/i/p/x* being 23/27/26/29. Labial palps large and suboval, with a conical latero-external sensillum, two guard setae, up to thirteen setae on anterior border, and up to 250 neuroglandular setae (Fig. 16).

Thorax: Thoracic macrosetae: pronotum with 1+1 *ma*, 3+3 la_{1-3}, 2+2 $lp_{2,4}$ macrosetae; mesonotum with 1+1 ma, 2+2 $lp_{2,4}$ macrosetae; metanotum with 2+2 (2+1; 1+1) $lp_{2,3}$ macrosetae (Figs 18-21). All thoracic macrosetae long and with thin barbs almost all over; thin marginal setae slightly longer than clothing setae, both with thin distal barbs almost all over their surface (Figs 19-21). Legs elongated, metathoracic legs reaching beyond end of abdomen; femur, tibia and tarsus with pretarsus similar in length (Table 3). Femora carrying well-differentiated long subapical ventral macrosetae. Calcars completely covered with thin barbs (Fig. 23). Tarsus with two rows of ventral setae, these similarly barbed but larger than clothing setae, plus several thin long setiform sensilla all over tarsus. Tarsus with three dorsal and two ventral subapical setae with thin barbs all over. Claws unequal in size, posterior claw longer than anterior claw (posterior claw : anterior claw ratio = 1.5-1.6 : 1), both claws with large lateral crests. Ventral side of claws noticeably ridged and covered with a micro-granular surface; posterior claw large, with a backward overhang. Lateral processes of pretarsus setiform, with a few thin proximal barbs (Figs 22, 24-25).

Abdomen: Distribution of abdominal macrosetae on tergites: 1+1 *la* on IV; 1+1 *la*, 1+1 $post_5$ on IV; 1+1 *la*, 3+3 $post_{3,4,5}$ on VI-VII; 5+5 $post_{1-5}$ on VIII; 8+8 *post* on IX. All tergal abdominal macrosetae long and well-differentiated, with thin barbs in distal four-fifths. Urosternite I with 24+24-21+21 (18+18 in smaller specimen: ♂2 paratype) well-barbed macrosetae (Figs 26-31); urosternites II-VII with 15+15-13+13 (11+11 in smaller specimen = ♂2 paratype) macrosetae (Figs 32-33); urosternite VIII with

Table 3. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. Length (in mm) of body, antennae, femur, tibia and tarsus of metathoracic legs; number of antennomeres.

specimen	body	antennae	number of antennomeres	femur	tibia	tarsus
♂2 paratype	3.9	4.3	48	0.60	0.63	0.61
♂3 paratype	4.6	5.8	48	0.85	0.86	0.75
♀2 paratype	5.5	-	-	0.95	1.02	1.00
♀12 paratype	5.6	7.0	48	0.94	1.04	0.90
♀3 paratype	5.8	7.1	50	0.97	1.10	0.98
♂1 holotype	5.9	7.1	45	0.94	1.08	0.95
♀13 paratype	6.0	6.8	40	1.00	1.09	0.79
♀4 paratype	6.2	7.6	43	1.08	1.25	1.10
♀8 paratype	6.5	-	-	1.02	1.17	0.99
♀6 paratype	6.6	7.8	41	1.25	1.41	1.10
♀1 paratype	6.7	8.3	44	1.15	1.35	1.05
♀7 paratype	7.4	7.9	41	1.26	1.45	1.08
♀9 paratype	7.5	8.2	45	1.12	1.34	1.11
♀5 paratype	7.6	-	-	1.15	1.28	1.08
♀10 paratype	7.7	-	-	1.15	1.35	1.10
♀11 paratype	8.7	-	-	1.30	1.58	1.13

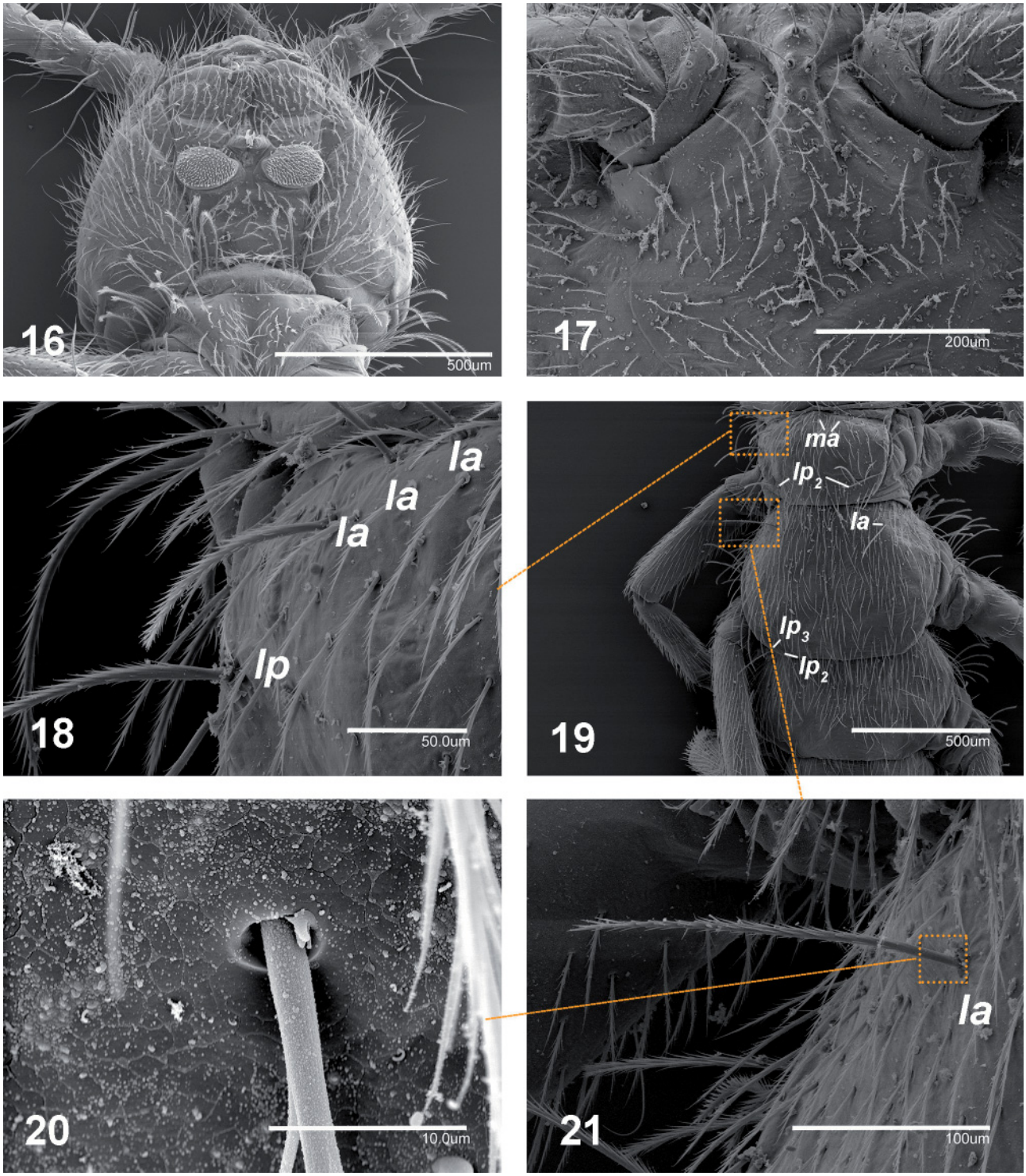


Figs 12-15. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (12) Apical view of last antennomere with narrow hole of cupuliform organ. (13) Medial antennomeres. (14) Lateral distal detail of a medial antennomere with gouge sensilla (*g*). (15) Lateral distal portion of a medial antennomere with gouge sensilla (*g*) and one conical sensillum (c*s*).

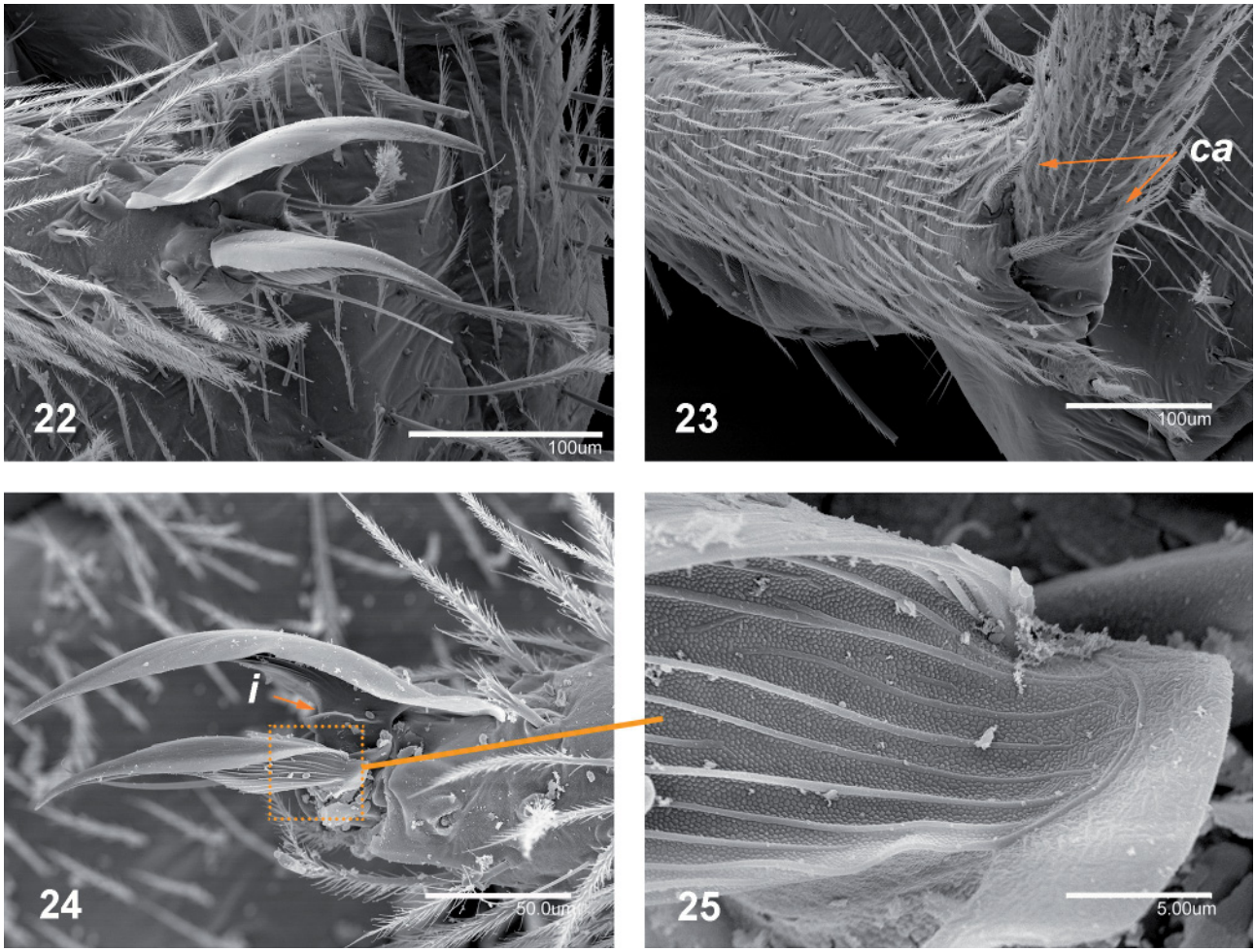
3+3-4+4 macrosetae (Fig. 36); urosternal macrosetae of medium length or longer and with long barbs, some divided into micro-barbs all over distal two-thirds (Figs 28-29, 33). Stylar apical setae including a long basal tooth, subapical setae completely covered with barbs all around; medial setae thinner than others, with short barbs in distal two-thirds (Figs 34, 37). Eversible vesicles large, with two different surface textures (Figs 34-35). No intact cerci available in studied material; the most complete cercus present on ♀6 paratype: basal article with 12 secondary articles followed by 18 primary articles, total length 12 mm. Length of cercal articles increasing from proximal to distal articles. Each article with a variable number of irregular whorls of almost completely barbed macrosetae, from three on proximal articles to 18 on distal articles, mixed with few irregular whorls of long smooth setae. All primary articles with a short, thin, distally barbed whorl of seta (Figs 38-39).

Secondary sex characters: Female urosternite I with subcylindrical appendages, each one bearing up to 17 glandular a_1 setae in a distal field (Figs 30-31). Male urosternite I with enlarged appendages, each one bearing up to 80 glandular a_1 setae in a distal field; posterior edge of urosternite I with a field of up to 240 glandular g_1 setae arranged in four rows; additionally about eighty short setae in an anterior position, these clearly differentiated from clothing setae by their barbed middle portion (Figs 26-27).

Taxonomic affinities: More than two decades ago, Condé & Bareth (1996) referred to one male and two females sampled in the Vranjača pećina Cave near Kotlenice (Split, Croatia) as *Plusiocampa (Stygiocampa)* cf. *remyi* because of differences in secondary sex characters of the male. These traits consist of enlarged appendages with a large apical field of glandular a_1 setae and a large field of glandular g_1 setae on the posterior border (Figs 26-31). The same structures are found in four males collected in the



Figs 16-21. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (16) Head, ventral view. (17) Frontal process, dorsal view. (18) Lateral left side of prothorax, dorsal view. (19) Prothorax, mesothorax and metathorax, dorsal view. (20) Detail of surface and insertion of lateral anterior mesonotal macroseta. (21) Lateral anterior portion of mesonotum.



Figs 22-25. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (22) Pretarsus, dorso-lateral view. (23) Joint between tibia and tarsus with calcars (*ca*). (24) Pretarsus, lateral view (*i* = intermediate sheet). (25) Detail of ventro-lateral portion of anterior claw.

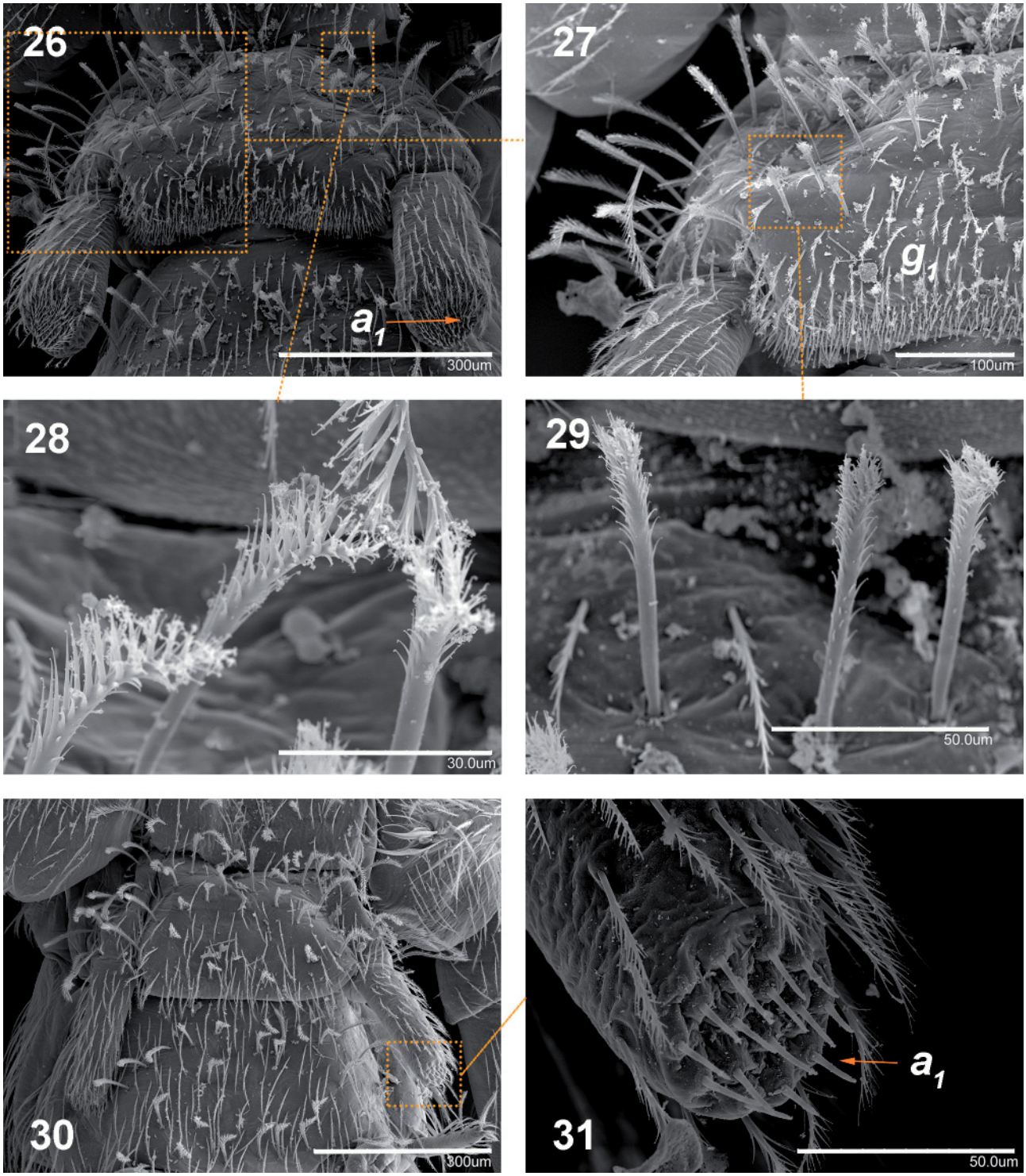
nearby Grabovčića jama Cave (Radošić, Croatia). This morphological distinction encouraged us to propose a new species from the Vranjača pećina and Grabovčića jama specimens, i.e. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. In addition to the characters mentioned above, there are several other differences between *P. (S.) barethae* sp. nov. and *P. (S.) remyi,* such as shorter and thinner gouge sensilla in *P. (S.) remyi*; 1+1 lateral anterior macrosetae on third urotergite in *P. (S.) remyi,* which are absent in *P. (S.) barethae* sp. nov.; and 9+9 to 11+11 posterior macrosetae on the ninth abdominal segment in *P. (S.) remyi* instead of 8+8 posterior macrosetae as in *P. (S.) barethae* sp. nov.

Type locality: The Grabovčića jama Cave, with a narrow, approximately 1 x 0.6 m wide entrance, is situated at 230 m a.s.l (Fig. 40). The bottom, at 45 m depth, is reached through a series of small pits. The interior of the cave is humid, with an annual mean temperature of about 10°C. The specimens were collected on flowstone at a depth of approximately 30 m (Fig. 41), in complete darkness. More than ten individuals of different sizes were spotted on our third visit to the cave.

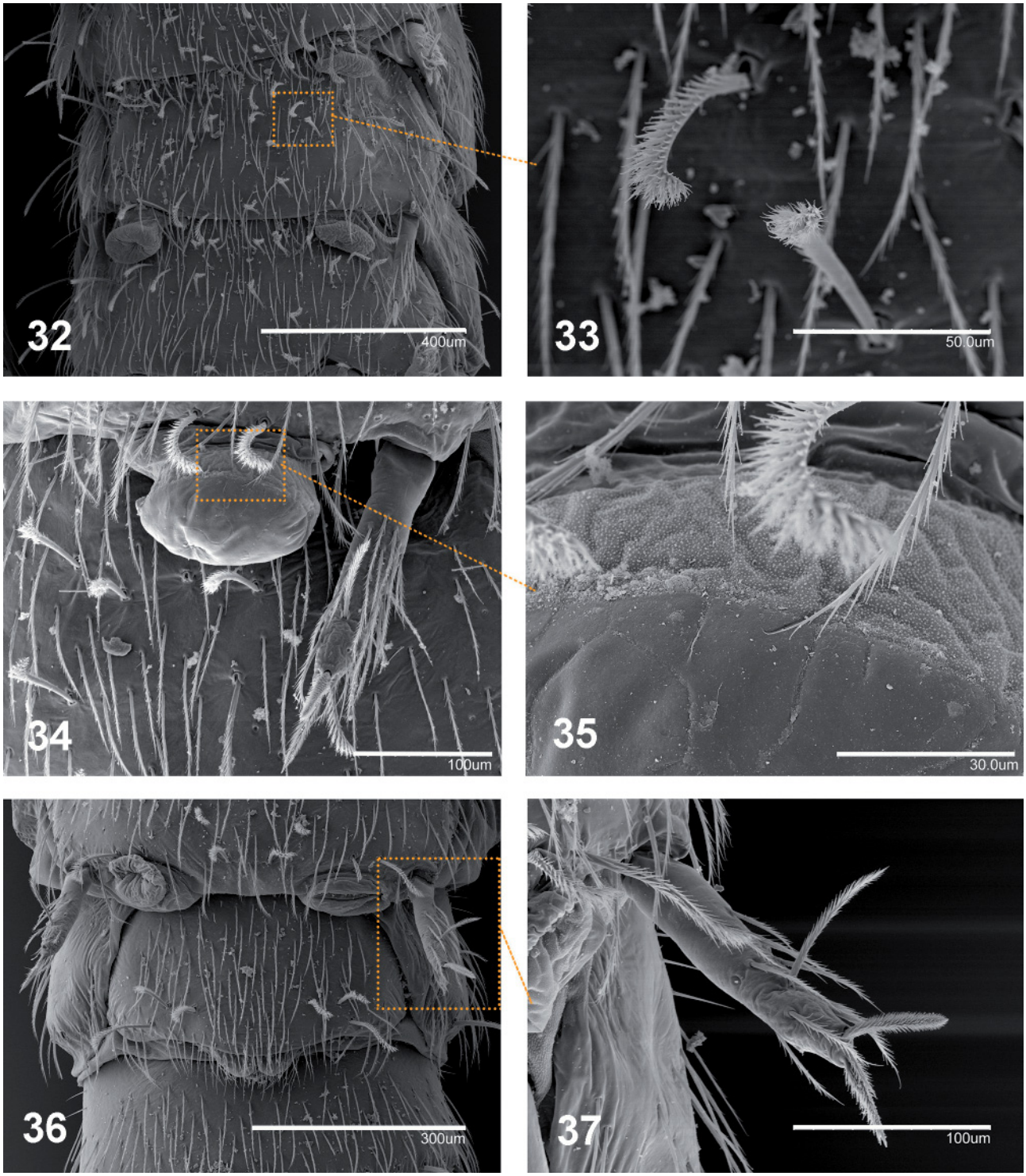
Plusiocampa (Stygiocampa) christiani Condé & Bareth, 1996

Figs 44-61

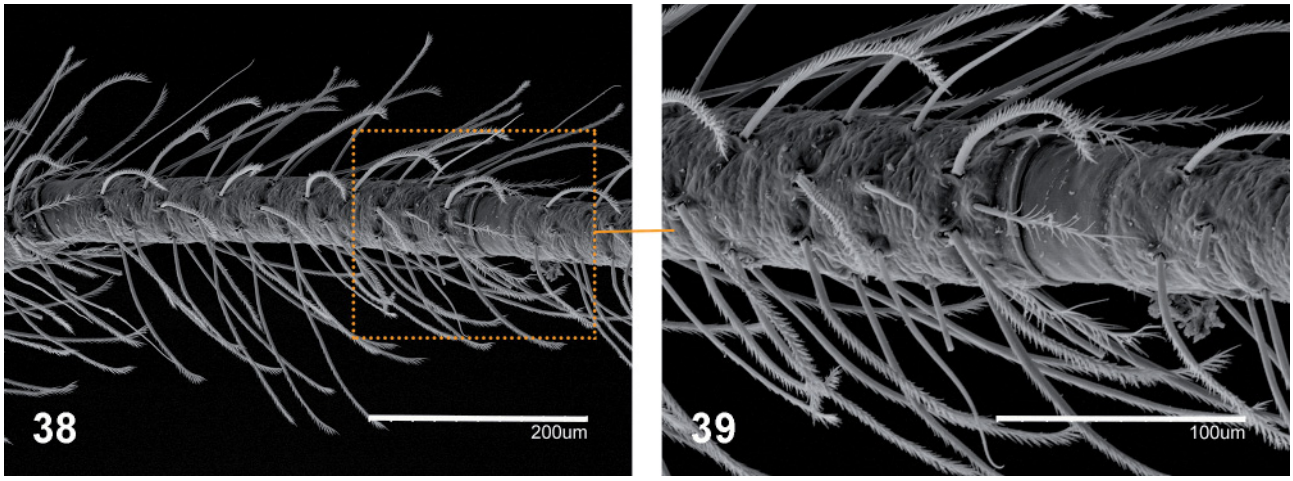
Material studied: Coll. AS; one male and thirteen females; Serbia, Izviđačka Cave, canyon of the river Suvaja, Mt Beljanica, near Despotovac; 14th July 2018; leg Đ. Marković. – Coll. AS; one male and five females; from the same cave; 6th June 2018; leg. S. Ćurčić. – Coll. AS; two females and one juvenile; Serbia, Vlaška Cave, Mt Beljanica; 11th April 2010; leg. I. Njunjić. – Coll. AS; three females; Serbia, Lazareva (Zlotska) Cave, village of Zlot, Kučaj Mts, near Bor; 15th November 2018; leg. D. Antić, D. Stojanović. – Coll. AS; three females; Serbia, Lazareva (Zlotska) Cave,



Figs 26-31. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (26) First and anterior portion of second urosternites of an adult male. (27) Lateral right side of first urosternite of an adult male. (28) Distal part of urosternal macrosetae. (29) Urosternal macrosetae. (30) First and anterior portion of second urosternites of an adult female. (31) Distal portion of one appendage of first urosternite of an adult female.



Figs 32-37. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (32) Posterior portion of fourth to sixth abdominal segment, ventral view. (33) Detail of macrosetae on fifth abdominal segment. (34) Lateral posterior portion of sixth urosternite. (35) Detail of eversible vesicle with two different kinds of surface microstructures. (36) Posterior portion of seventh abdominal segment to anterior portion of ninth abdominal segment, ventral view. (37) Left stylus of eighth abdominal segment, ventral view.



Figs 38-39. *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (38) Fourth primary cercal article. (39) Detail of distal portion of fourth primary cercal article.

village of Zlot, Kučaj Mts, near Bor; 16th June 1996; leg. S. Ognjenović. – Coll. AS; one female; Serbia, Jama u Vrtačelju Pit, Vrtačelje, Kučaj Mts; 17th October 2007; leg. S. Ognjenović. – Coll. AS; three females and six specimens; Serbia, Vernjikica Cave, village of Zlot, Kučaj Mts, near Bor; 15th November 2018; leg. D. Antić, D. Stojanović. – Coll. AS; three females; Serbia, Bogovinska Cave, village of Bogovina, Kučaj Mts, Boljevac; 16th November 2018; leg. D. Antić, D. Stojanović.

Taxonomic notes: SEM observations have revealed and supplemented some taxonomic features, such as a narrow hole of the cupuliform organ (Fig. 44); very long shafts of trichobothria (Fig. 45); a quadrangular protruding frontal process with non-tuberculated setae (Figs 46-47); thin and long neuroglandular setae on subspherical labial palps with enlarged asymmetrical openings (Figs 48-49); slightly elongated nota with macrosetae on pronotum (1+1 *ma*, 3+3 *la*, 1+1 lp_2), a lack of macrosetae on mesonotum and metanotum with a microreticulated surface visible under SEM (Figs 50-53); tibia with barbed calcars (Fig. 56); claws unequal (posterior claw: anterior claw ratio = 1.45 : 1); tarsal setae with long barbs from base to tip; dorsal surface of claws almost smooth, longitudinal grooves on ventral side with a pattern of tiny transversal ridges between them (Figs 54-55, 57); first urosternite of females carrying subcylindrical appendages ending in a small field of glandular a_1 setae (Figs 58-59); long urosternal macrosetae with long, thin barbs in half to three-fourths of distal portion (Figs 58, 60); styli carrying short apical setae with a few long barbs, and longer subapical and medial setae with long barbs almost from base to tip (Fig. 61); large eversible vesicles with two well-differentiated areas (Fig. 61).

Biogeographical note: The new localities of the material studied slightly enlarge the previously known geographical range.

Plusiocampa (Stygiocampa) dalmatica Condé, 1959

Material studied: Coll. AS; one juvenile; Montenegro, Začirska Cave, village of Začir, near Rijeka Crnojevića, Cetinje; 25th June 2018; leg. D. Antić, Đ. Marković. – Coll. AS; one female; Bosnia & Herzegovina, Jazvina Cave, Kamešnica; 1st July 2018; leg. T. Rađa.

Taxonomic note: The female from Jazvina Cave is without medial anterior macrosetae on its metanotum.

Biogeographical note: The new localities of the material studied slightly enlarge the previously known geographical range.

Plusiocampa (Stygiocampa) dulcici Sendra & Rađa, sp. nov.

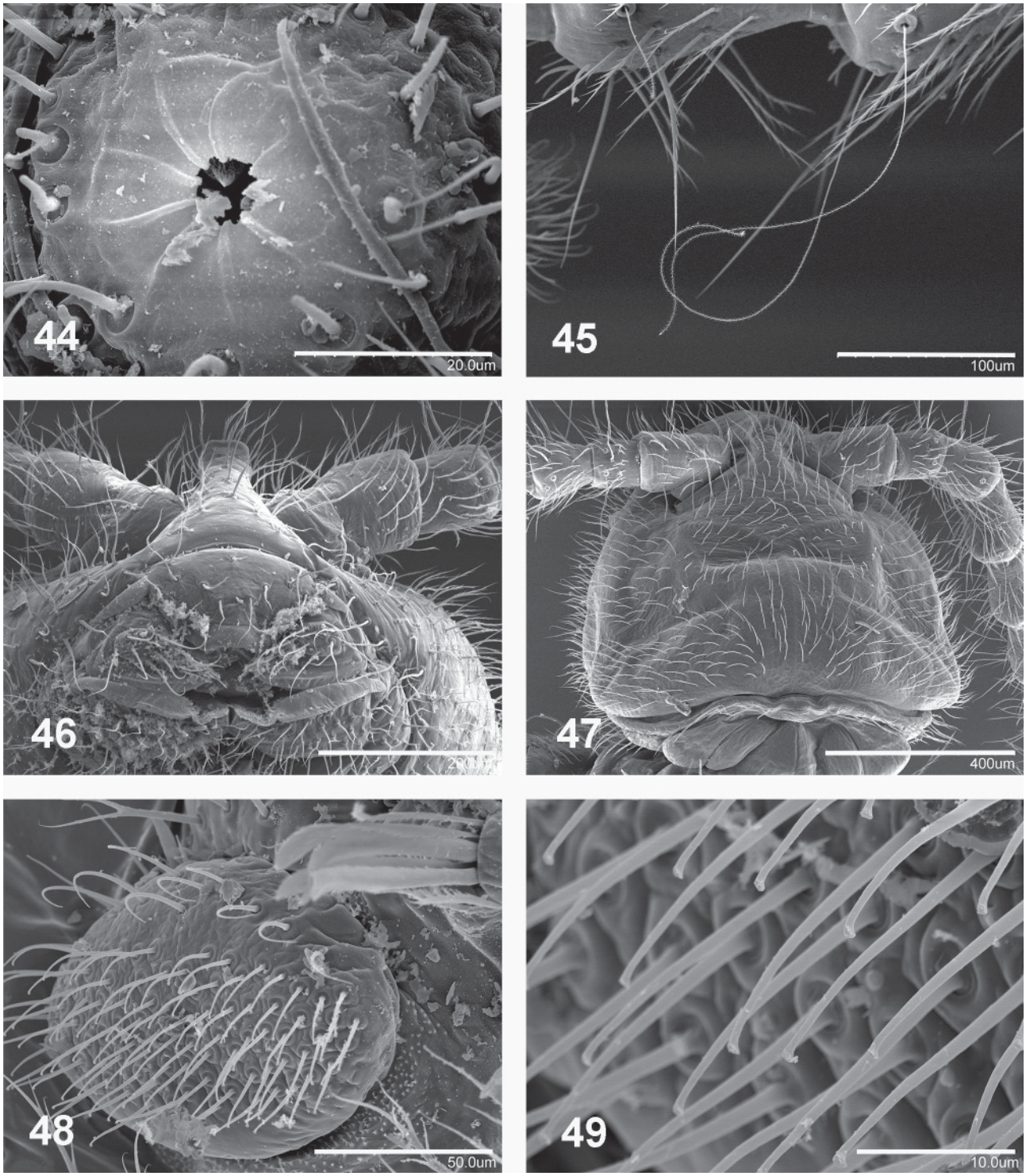
Figs 42-43, 62-76

Type material: MHMZOO; female holotype; Croatia, Golubinka pod Kraljevcom Cave, Radošić; 10th September 2014; leg. T. Rađa. – MHNG; one male paratype (labelled ♂1 paratype); same cave and collector; 15th November 2014. – Coll. AS; one male paratype (labelled ♂2 paratype); same cave and collector; 18th April 2014. All material mounted in Marc André II solution.

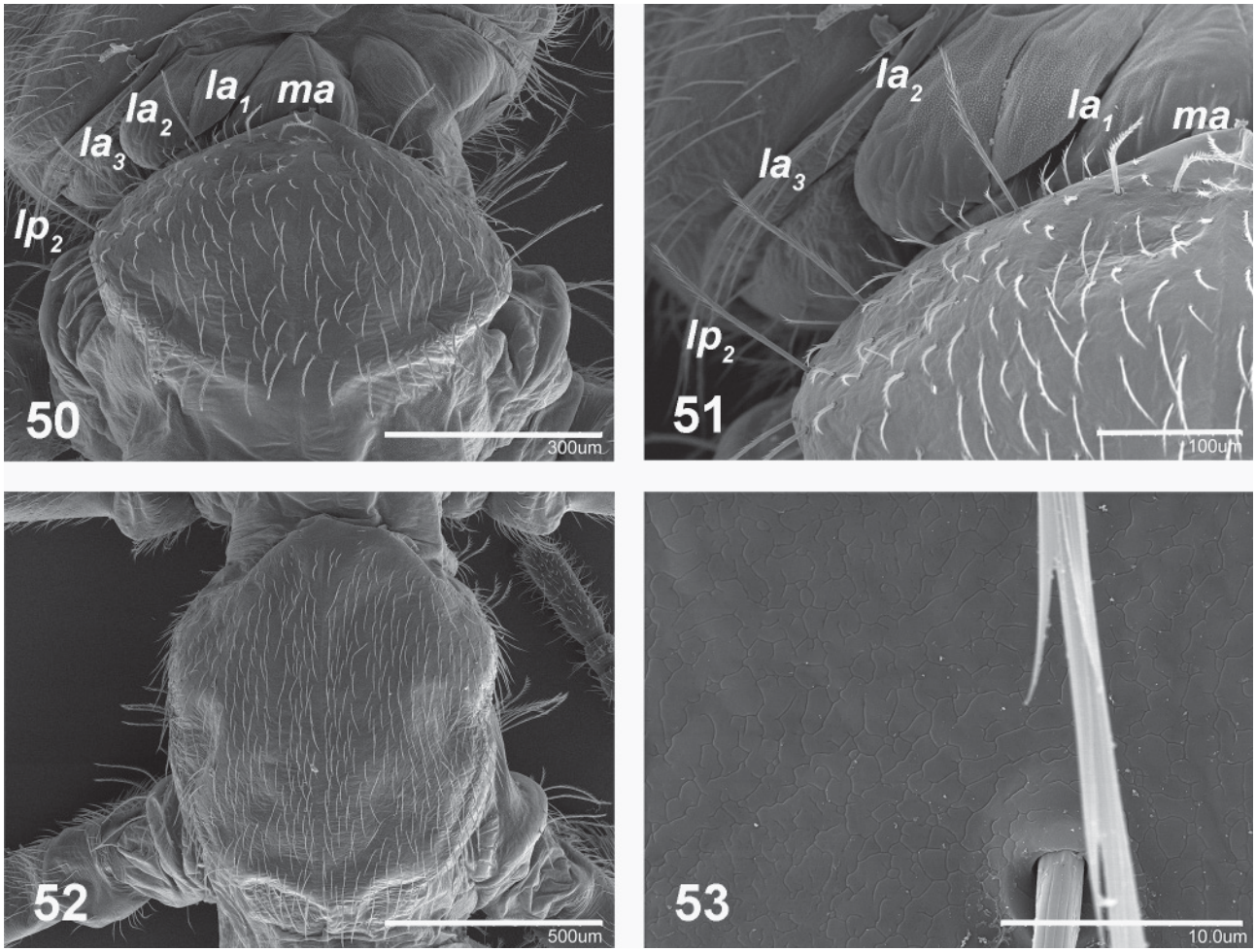
Other studied material: Coll. AS; two specimens of unknown sex; collected together with holotype; mounted on an aluminium stub and coated with palladium-gold.

Etymology: This species is named after Vicko Dulčić

Figs 40-43. Type localities of *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. and *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. (40) Narrow entrance of Grabovčića jama Cave, Radošić, Croatia; type locality of *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (41) Flowstone where *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. was collected at approximately 30 m depth in the Grabovčića jama Cave. (42) Stony surface where *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. was collected under small stones at 22 m depth in the Golubinka pod Kraljevcom Cave. (43) Entrance of the Golubinka pod Kraljevcom Cave, Radošić, Croatia; type locality of *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov.



Figs 44-49. *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996. (44) Apical view of last antennomere with hole of cupuliform organ. (45) Lateral view of third and fourth antennomeres with their trichobothria. (46) Anterior frontal view of head. (47) Dorsal view of head. (48) Labial palp. (49) Detail of labial palp.



Figs 50-53. *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996. (50) Prothorax, dorsal view. (51) Lateral left view of dorsal side of prothorax. (52) Mesothorax, dorsal view. (53) Detail of surface of mesothorax.

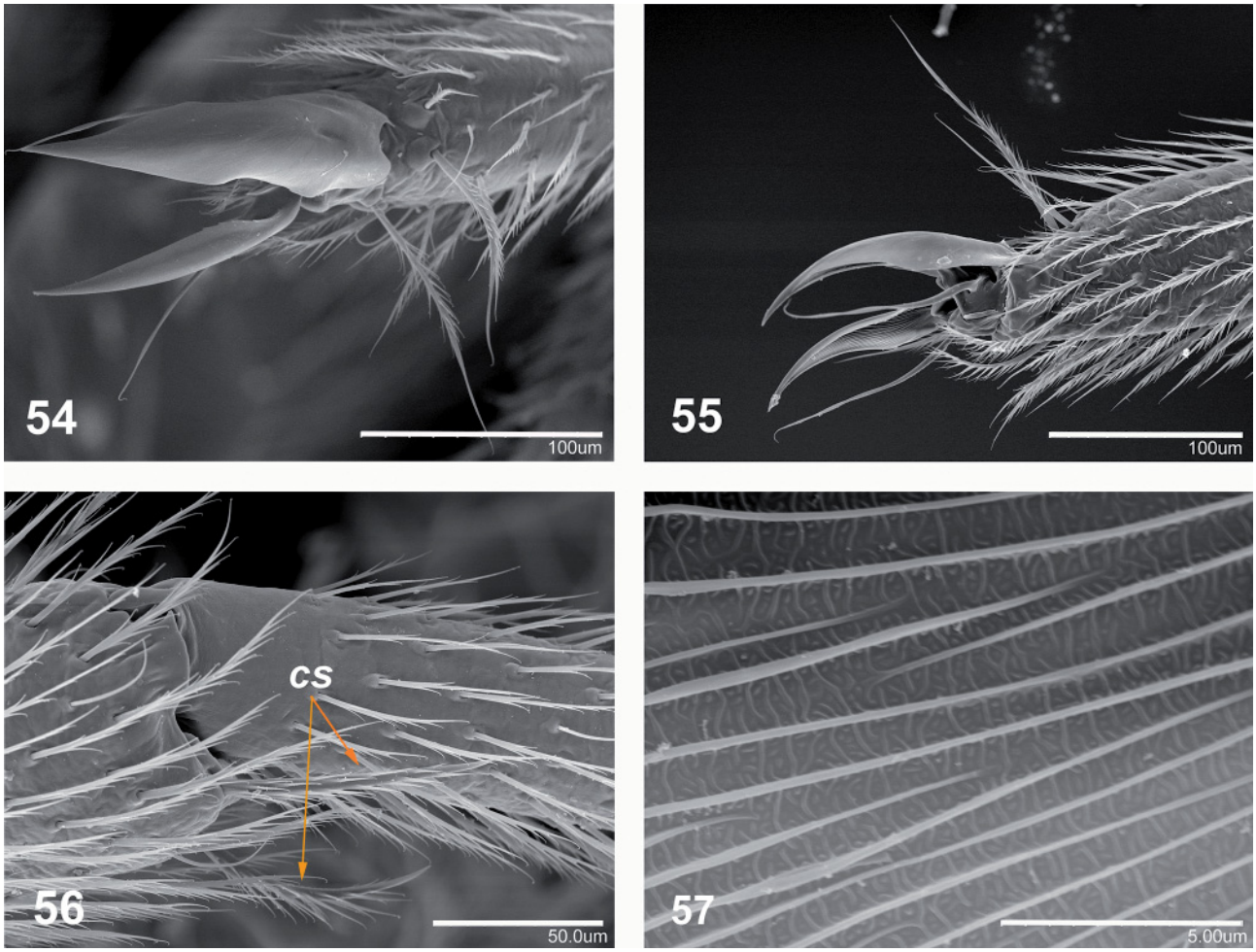
(1923-1985), a Croatian caver and founder of the Speleological Society "Špiljar", Split, Croatia. Name in the genitive case.

Description:

Body: Body length 4.7 mm (♀ holotype), 3.2 and 4.5 mm (♂1 and ♂2 paratypes). Epicuticle smooth when examined under optical microscope, thin reticular under high magnification (SEM, up to 1000x) (Fig. 70); body with thin, medium-sized, barbed clothing setae.

Head: Antennae length similar to body length (antennae length : body lenght ratio = 0.98 : 1), with 38 antennomeres. Bacilliform sensillum of third antennomere in a ventral position, between macrosetae *d* and *e,* 18 µm in length. Medial antennomeres elongated and 1.7 times longer than wide; apical antennomere 1.5 times longer than wide. Twelve to fourteen thin gouge sensilla (28 µm) in a single distal whorl on each medial and distal antennomere, plus one long bacilliform sensillum (13 µm) in same whorl (Figs 63-65). Cupuliform organ occupying less than 1/3 of total length of last antennomere, with numerous complex olfactory chemoreceptors with a centric column surrounded by radial folds; entire surface covered with a polygonal net with pores (Fig. 62). Frontal process with double protrusion above several tubercular setae (Figs 67-68). The three macrosetae along each side of line of insertion of antennomere and *x* setae with 4-8 thin barbs; length ratios of *a/i/p/x* in holotype being 39/45/38/56 (Fig. 68). Head carrying three pairs of moderately long, smooth macrosetae in *asl, psm, psl* position on dorsal side. Suboval labial palps, each with a bacilliform latero-external sensillum near two gard setae, with twelve normal setae in anterior portion and with up to 125 neuroglandular setae in medial and posterior position.

Thorax: Pronotum with 1+1 *ma*, 4+4-5+5 *la*, 2+2 $lp_{2,3}$ macrosetae; mesonotum with 1+1 *ma*, 1+1 *la*, 3+3 lp_{1-3}; metanotum with 1+1 *ma*, 3+3 lp_{1-3}; long barbed notal macrosetae with barbs in distal two-thirds; marginal setae longer than clothing setae, with thin distal barbs (Figs 66, 69-70). Metathoracic legs reaching tenth abdominal segment; without ventral macrosetae and



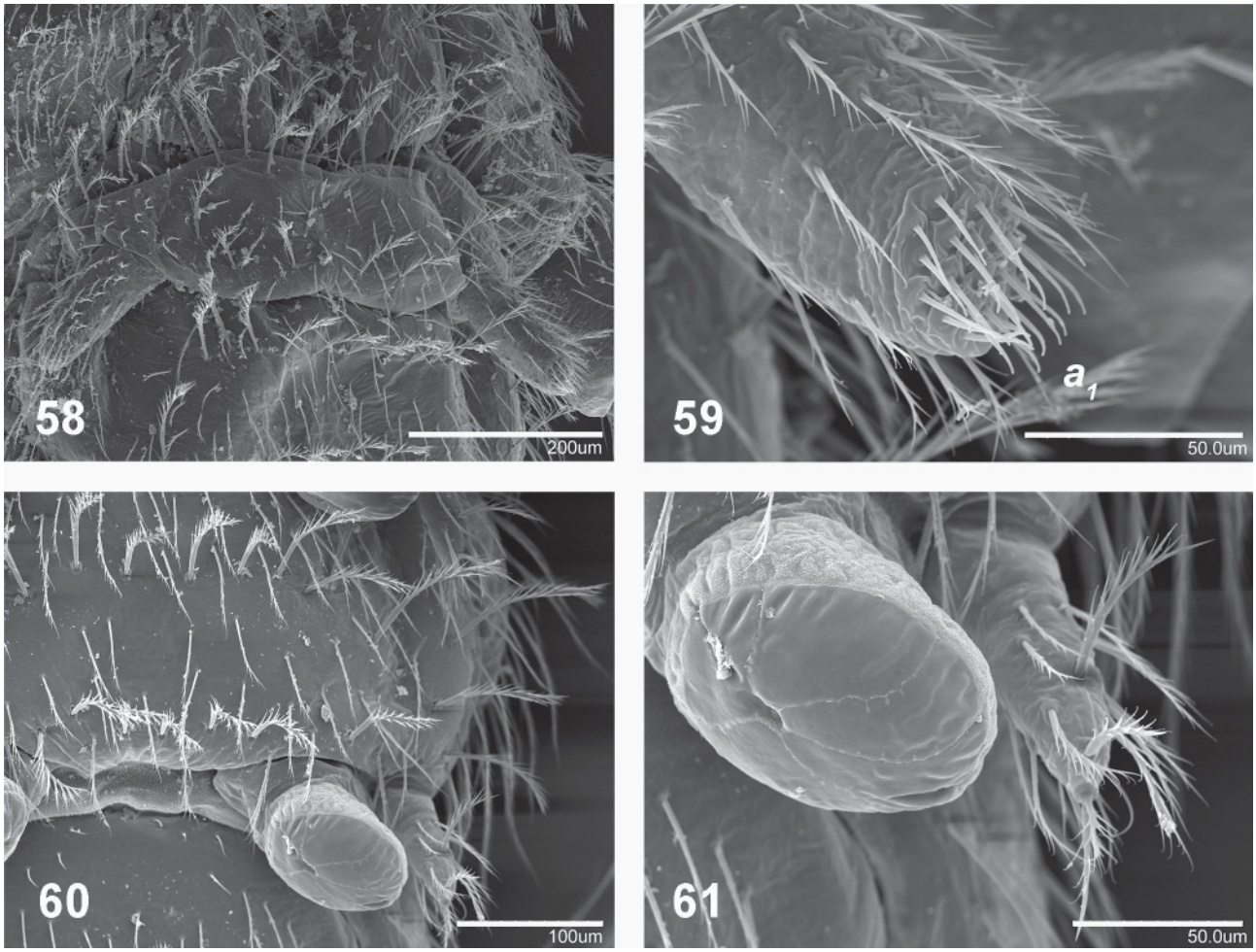
Figs 54-57. *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996. (54) Pretarsus of metathoracic leg, dorsal view. (55) Pretarsus of metathoracic leg, lateral view. (56) Joint between tarsus and tibia with the calcars (*cs*). (57) Detail of lateral ventral side of anterior claw of a metathoracic leg.

tibial macroseta; calcars with numerous long thin barbs in a few rows; tarsus with two ventral rows of larger, longer and more densely barbed setae than clothing setae, with numerous setiform sensilla among clothing setae (Fig. 73) and with two dorsal and two ventral subapical barbed setae; claws unequal (posterior claw 1.3 times longer than anterior claw), with large lateral crests and smooth setiform lateral processes or with a couple of barbs; posterior claw with large backward overhang; claws almost smooth on dorsal side, ventral side noticeably ridged and covered with micro-granular surface (Figs 71-72).

Abdomen: Urotergite I with 1+0 (0+0) $post_1$ macrosetae; urotergite II with 1+1 (0+1) $post_1$; urotergite III with 1+1 $post_1$; urotergite IV with 2+2 (2+1) $post_{1\text{-}2}$; urotergites V-VII with 1+1 *la*, 4+4 $post_{1\text{-}4}$; urotergite VIII with 6+6 *post*; abdominal segment IX with 9+9 (8+9) *post*; all urotergal macrosetae long and barbed in distal three-fourths; urosternite I with 7+7 macrosetae; urosternites II-VII with 6+6; urosternite VIII with 2+2; urosternal macrosetae with long medial and distal barbs (Fig. 75). Apical seta with a basal double tooth and two or three long thin barbs; subapical seta completely covered by short barbs; medio-ventral setae with four or six long thin barbs (Fig. 74). Eversible vesicles large, with proximal and distal areas of different microtexture (Fig. 76). Best preserved cercus broken; each primary article bearing from two to eight irregular whorls of long barbed macrosetae, one distal whorl of long smooth setae, and one apical whorl of short thin setae with tiny distal barbs.

Secondary sex characters: First urosternite of males with subcylindrical appendages, each bearing 10 and 8 glandular a_1 setae; posterior border of urosternite I with 90 and 4 glandular g_1 setae in two males studied: one adult male (♂1 paratype) and one young male (♂2 paratype); female holotype with subcylindrical appendages, each carrying up to 16 glandular a_1 setae.

Taxonomic affinities: *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. is closely related to



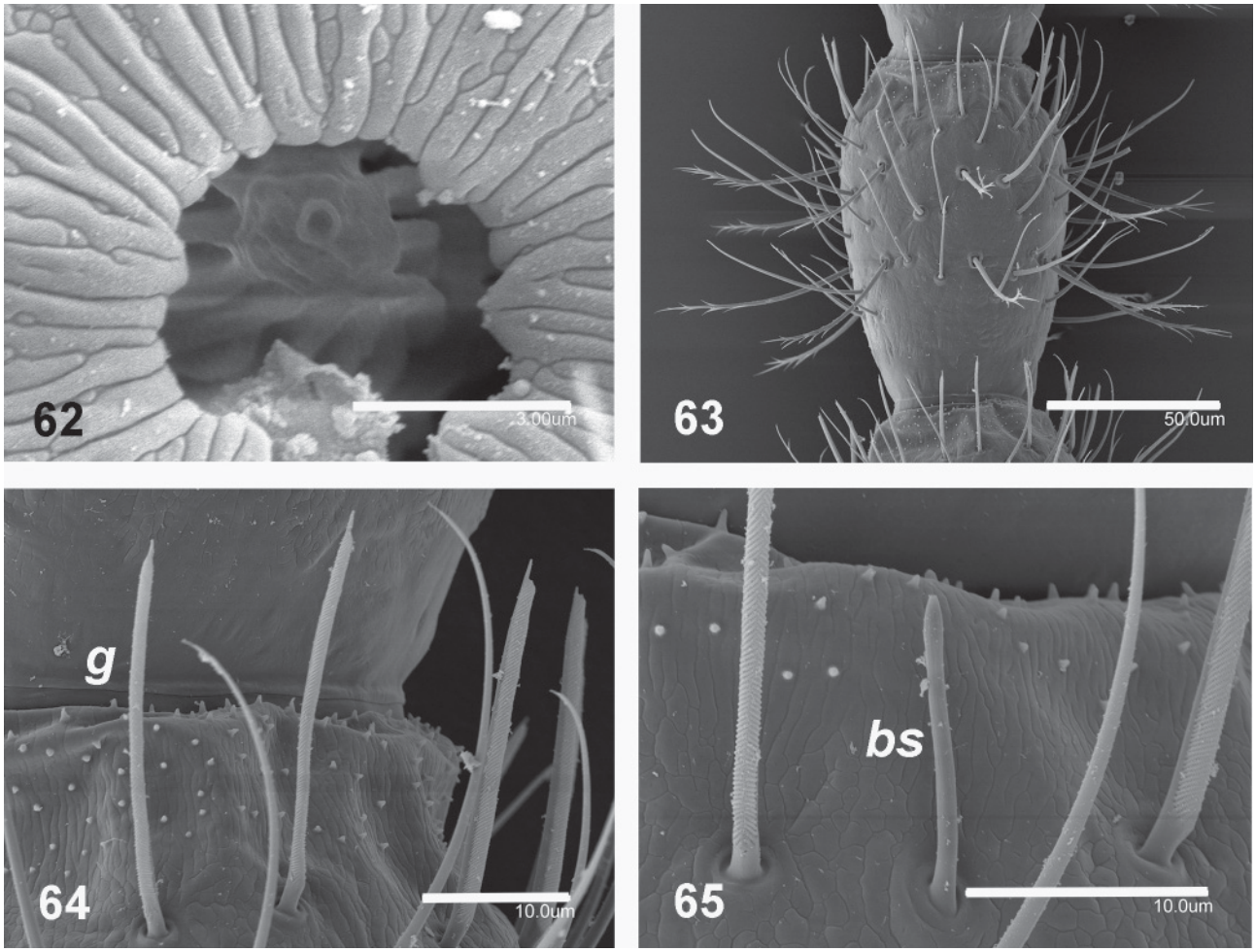
Figs 58-61. *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996. (58) First abdominal segment of a female, ventral view. (59) Distal portion of left appendage of first urosternite of a female. (60) Medial and lateral left side of fourth abdominal segment, ventral view. (61) Eversible vesicles and stylus of left side of fourth urosternite.

Pluciocampa (Stygiocampa) denisi Condé, 1947 due to similarities in the distribution pattern of urotergal and urosternal macrosetae, both with 1+1 lateral anterior and 4+4 posterior macrosetae on the sixth and seventh urotergites, and 7+7 and 2+2 urosternal macrosetae on the first and seventh urosternites (Condé, 1947). A remarkable distinction from *P. (S.) denisi* is the number of lateral posterior macrosetae on the mesonotum and metanotum: *P. (S.) dulcici* sp. nov. has 3+3 such macrosetae on the mesonotum and metanotum, whereas *P. (S.) denisi* has 1+1 lateral posterior macrosetae on the mesonotum but none the metanotum. Other taxonomical features that differ between *P. (S.) dulcici* sp. nov. and *P. (S.) denisi* are the presence of macrosetae on the first to the third urotergites in *P. (S.) dulcici* sp. nov. *vs.* their absence in *P. (S.) denisi,* and the 6+6 macrosetae on the second to the seventh urosternite in *P. (S.) dulcici* sp. nov. *vs.* 5+5 in *P. (S.) denisi*.

Type locality: The Golubinka pod Krajevcem Pit is about 25 m deep and about 30 m long, with two entrances (Fig. 43) at 233 m a.s.l. through which the daylight reaches the bottom of the pit, allowing a Mediterranean shrub and moss community to grow. The final chamber is large, 20 x 24 m, with a mean annual temperature of around 10°C. Several specimens of the new species were collected under small stones at 22 m depth (Fig. 42). During the wet season the cave is very humid. Golubinka pod Kraljevcem is renowned for being the habitat of several cave species, i.e., *Troglaegopis mosorensis* (Kuščer, 1933) (Mollusca: Gastropoda), *Neotrechus dalmatinus* (L. Miller, 1861) (Insecta: Coleoptera), *Psychoda* sp. (Insecta: Diptera), *Solentanodesmus insularis* Antić & Reip in Antić *et al.,* 2014 (Myriapoda: Diplopoda).

Plusiocampa (Stygiocampa) remyi Condé, 1947

Material studied: Coll. AS; one male; Montenegro, Cetinjska Cave, Cetinje; 24th June 2018; leg. D. Antić. – Coll. AS; one male; Montenegro, Velika (Njegoševa)



Figs 62-65. *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. (62) Hole of cupuliform organ of last antennomere. (63) Medial antennomeres. (64) Detail of lateral anterior side of a medial antennomere with some gouge sensilla (g). (65) Detail of lateral anterior side of a medial antennomere with one bacilliform sensillum (*bs*).

Cave, Njeguši, Mt Lovćen, Cetinje; 24th June 2018; leg. D. Antić. – Coll. AS; one female; Montenegro, Vojvode Dakovića Cave, Grahovo, Nikšić; 28th July 2018; leg. S. Ćurčić, N. Vesović. – Coll. AS; one male and two females; Bosnia & Herzegovina, Golubinka, Dabarsko Polje, Berkovići/Bileća; 18th June 2003; leg. S. Ognjenović. – Coll. AS; one male; Montenegro, Arapova Cave, Gornja Grabovica, Mt Durmitor; 29th July1993; leg. D. Pavićević. – Coll. AS; three males and three females; Montenegro, Vojvode Dakovića Cave, Grahovo, Nikšić; 28th July to 27th October 2018; leg. S. Ćurčić, N. Vesović, M. Kuraica. – Coll. AS; one male; Montenegro, Izeta Cave, Knežlaz, Kameno more, Kotor; 28th July to 27th October 2018; leg. S. Ćurčić, N. Vesović, M. Kuraica. – Coll. AS; three females; Montenegro, Lipska Cave, Lipa, Cetinje; 29th July to 28th October 2018; leg. N. Vesović. – Coll. AS; one male; Montenegro, Bijela Cave, Gornji Kazanci, near Nikšić; 17th November 2019; leg. D. Antić.

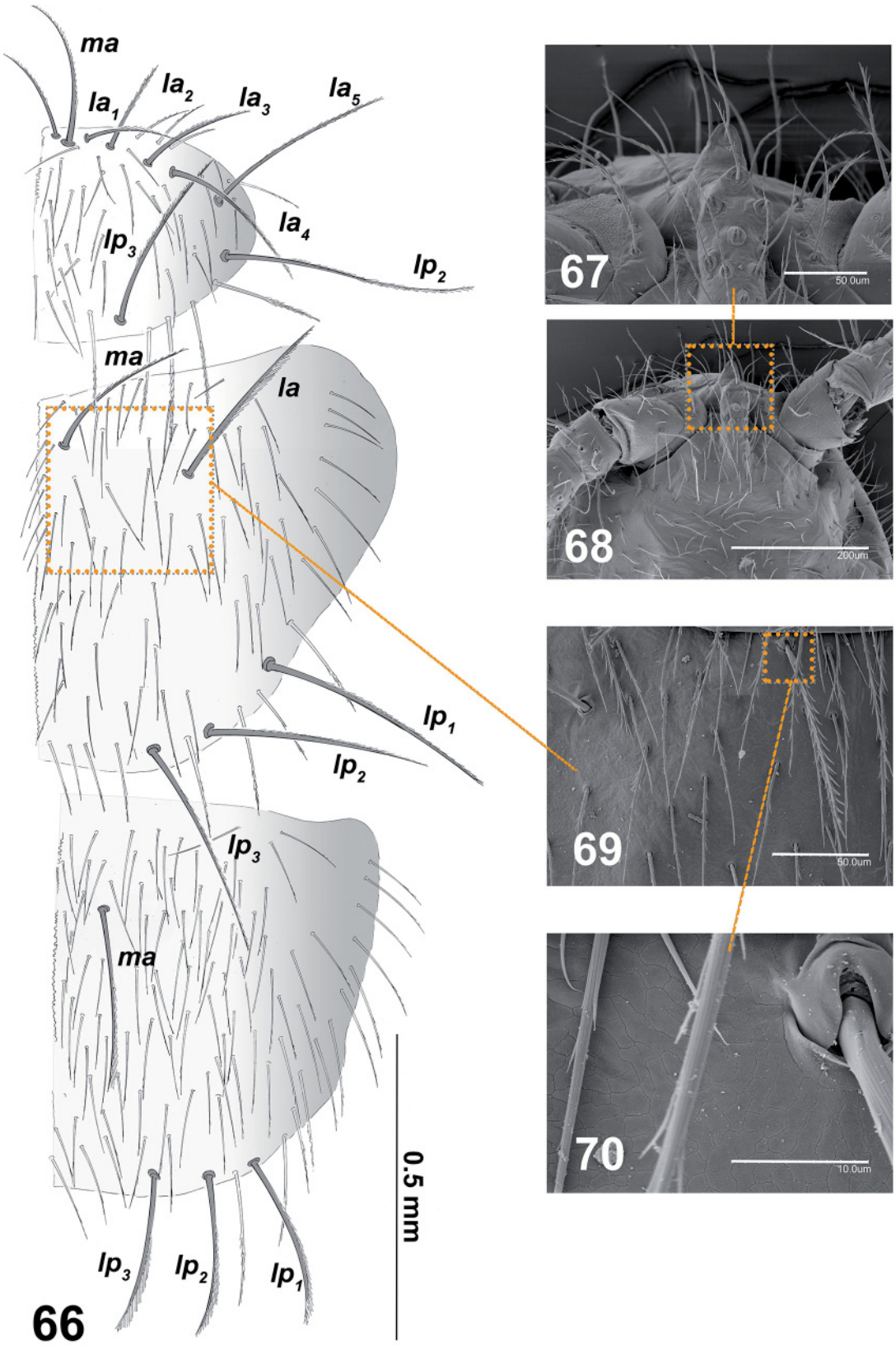
Biogeographical note: These localities extend the known distribution range of the species.

Subgenus *Venetocampa* Bareth & Condé, 1984

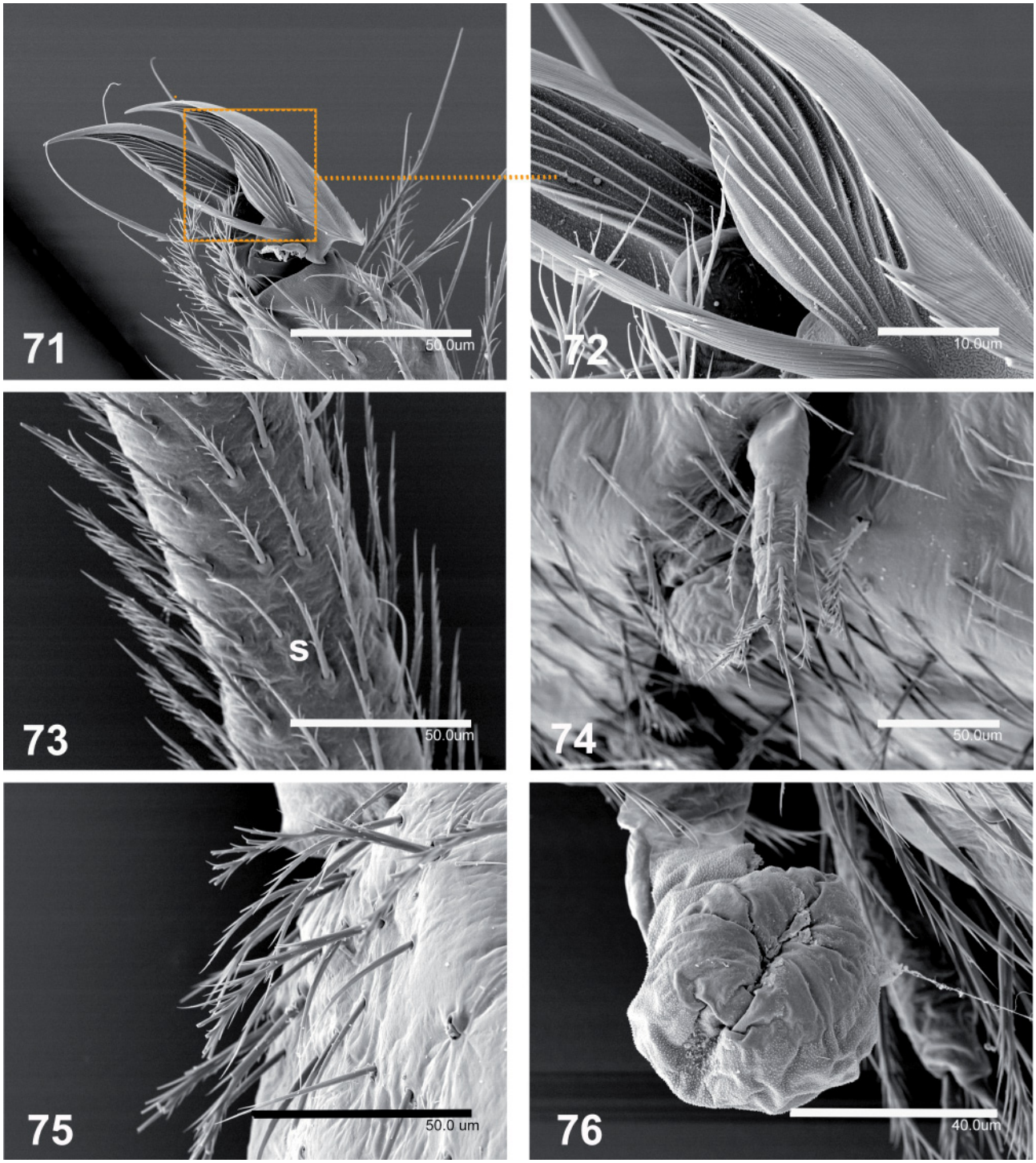
Plusiocampa (Venetocampa) pirnati Sendra & Borko, sp. nov.

Figs 77-97, Table 4

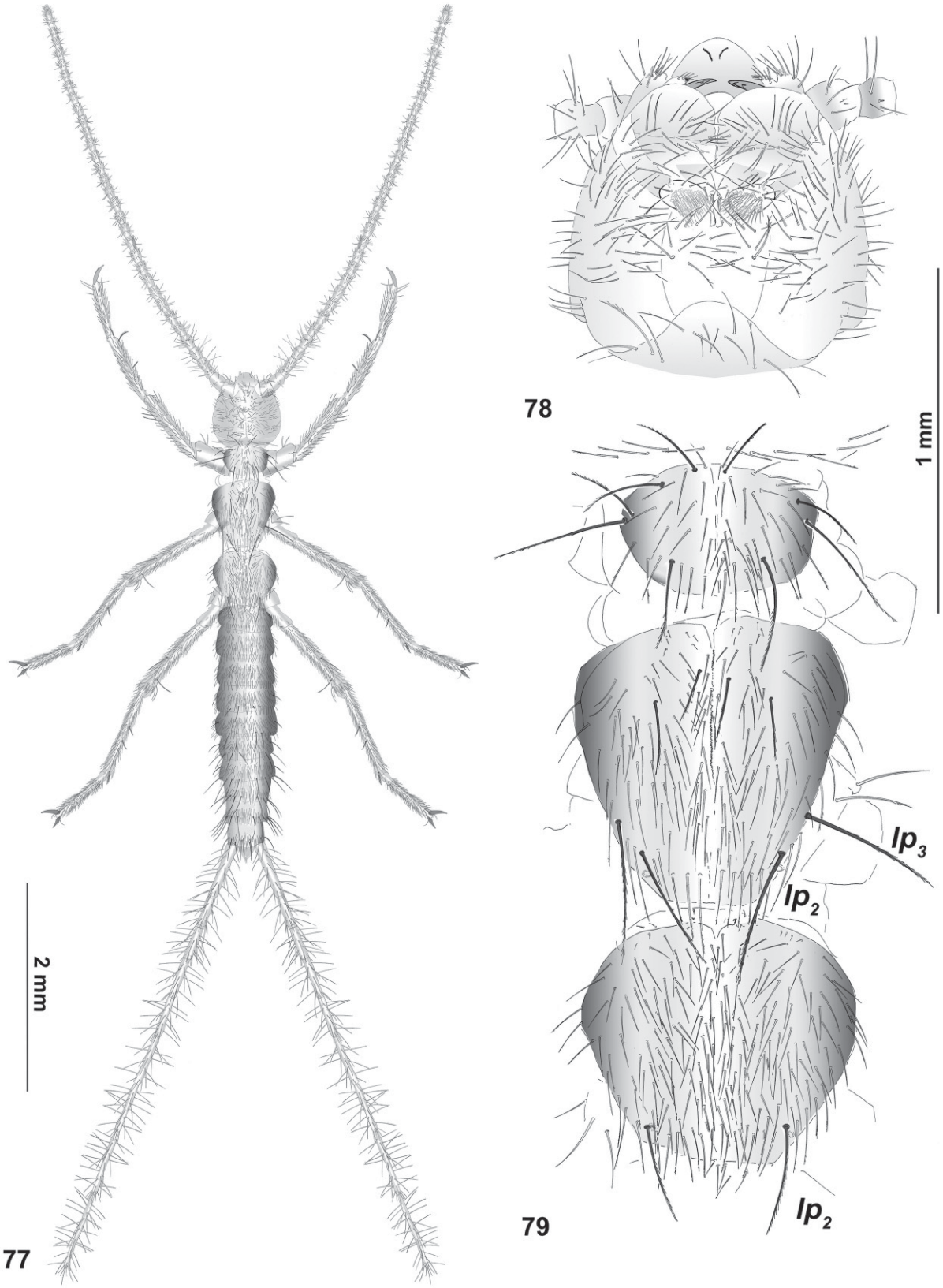
Type material: PSML; male holotype; Slovenia, cave P4, Kanin, Bovec; 3rd August 2018; leg. Š. Borko. – PSML; one female paratype (labelled ♀1 paratype); same cave, data, and collector. – MHNG; one male and two female paratypes (labelled ♀2 paratype, ♀3 paratype, ♂5 paratype); same cave, data, and collector. – Coll. AS; four male, one female and one juvenile paratypes (labelled ♀4 paratype, ♂2 paratype, ♂3 paratype, ♂4 paratype, ♂6 paratype and J1 paratype); same cave, data, and collector.



Figs 66-70. *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. (66) Pronotum, mesonotum and metanotum of holotype. (67) Detail of anterior portion of frontal process, dorsal view. (68) Frontal process on head, dorsal view. (69) Detail of mesonotum surface with partial view of medial anterior and lateral anterior macrosetae. (70) Detail of insertion of medial anterior macrosetae of mesonotum and partial view of clothing setae.



Figs 71-76. *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. (71) Pretasus, lateral view. (72) Detail of posterior claw of pretarsus with anterior claw in the background. (73) Lateral view of tarsus with setiform sensilla (s). (74) Stylus of fourth urosternite. (75) Urosternal macrosetae on first urosternite. (76) Eversible vesicle of fifth urosternite.



Figs 77-79. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (77) Habitus, dorsal view. (78) Head, ventral view. (79) Pronotum, mesonotum and metanotum, dorsal view.

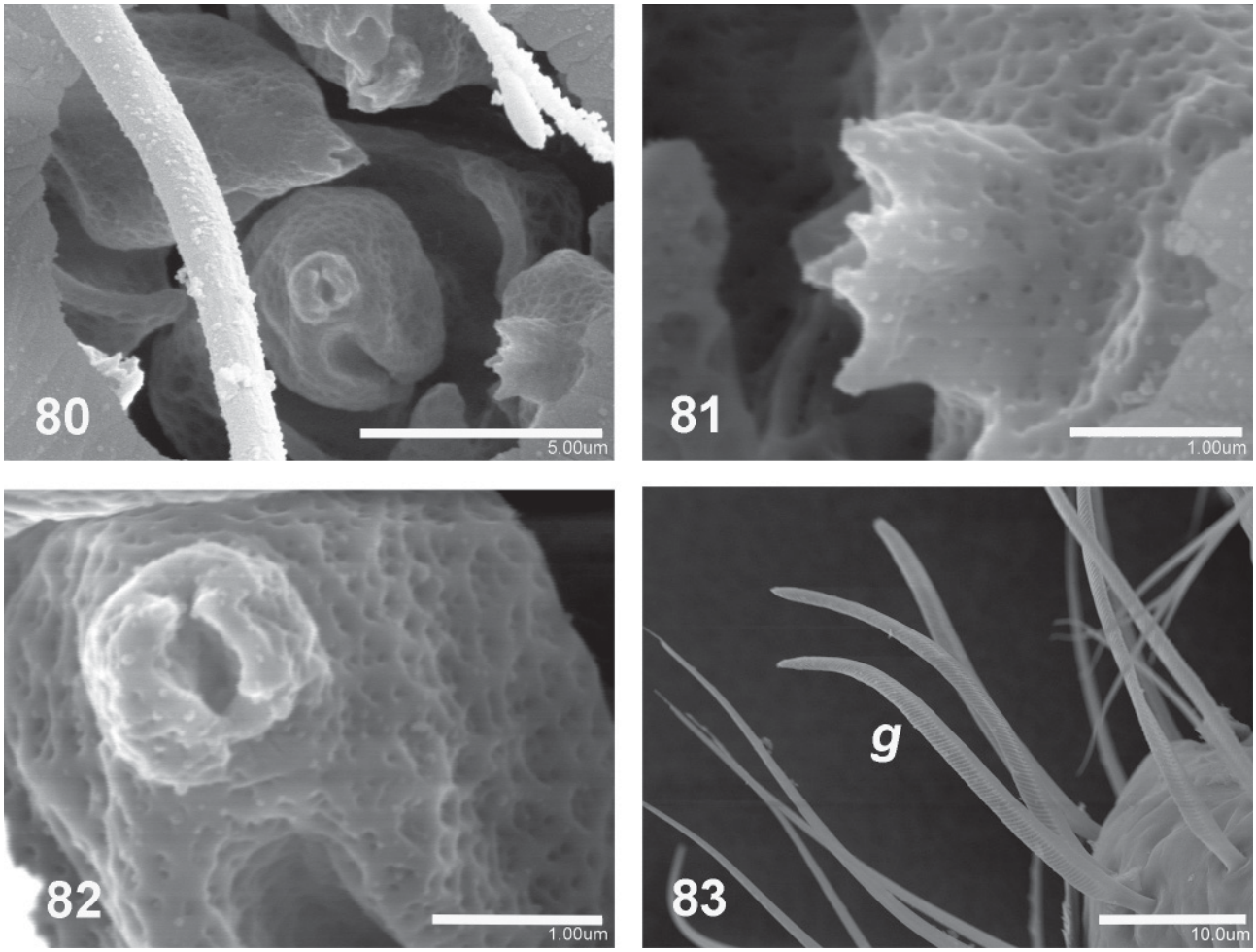
Other material studied: Coll. AS; five males and thirteen females; same cave, data, and collector as for type material mounted in Marc André II solution. – Coll. AS; six specimens of unknown sex; same cave, data, and collector; mounted on an aluminium stub and coated with palladium-gold.

Etymology: The new species is named after Joško Pirnat, a caver who significantly contributed to the speleological exploration of the area and without whom these remote sites could not have been explored. Name in the genitive case.

Description:

Body: Body length 4.3-4.9 mm (males), 4.1-5.6 mm (females) and 2.9 mm in one juvenile (in type series) (Fig. 77). Epicuticle smooth under optical microscope, weakly reticulated under high magnification (SEM, up to 1000x) (Figs 84-85); body covered with numerous thin, medium-sized clothing setae bearing two to five thin distal barbs.

Head: Antennae lengths ranging from 109% of body length in small specimens to 86% of body length in larger specimens, with 34-36 antennomeres (Table 4). Bacilliform sensillum of third antennomere in a ventral position, between macrosetae *d* and *e,* 13 µm in length. Medial antennomeres slightly elongated and 1.4 times longer than wide; apical antennomere 2.5 times longer than wide. Ten to fifteen thin and long gouge sensilla (30-38 µm long) in a single distal whorl on each medial and distal antennomere (Fig. 83); two conical sensilla (8 µm) in the same whorl. Cupuliform organ occupying less than 1/4 of total length of last antennomere, with eight to ten spheroidal olfactory chemoreceptors with a centric column surrounded by a concentric fold; entire surface covered with a polygonal net with pores (Figs 80-82). Non-protruding frontal process with three smooth, slightly tubercular anterior macrosetae and without tubercular setae. The three macrosetae along each side of line of insertion of antennomere and *x* setae with 2-4 long thin barbs; length ratios of *a/i/p/x* in holotype being 32/39/33/38. A pair of slightly longer smooth macrosetae on dorsal side of head in *a psl* position. Labial palps



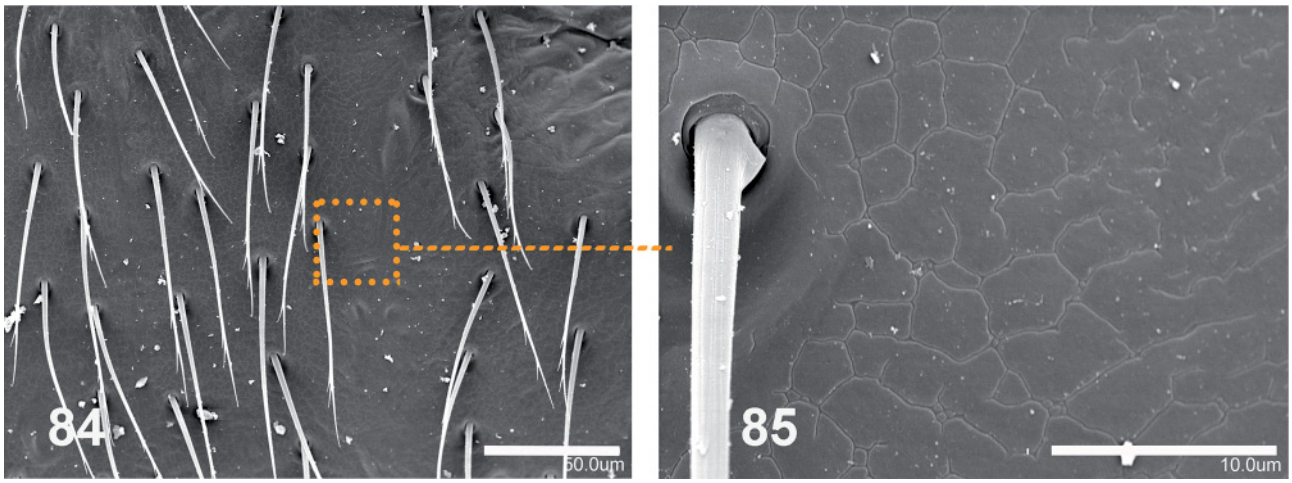
Figs 80-83. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (80) Interior of cupuliform organ of last antennomere. (81-82) Different details of olfactory chemoreceptor of cupulifom organ. (83) Lateral distal portion of a medial antennomere with gouge sensilla (*g*).

suboval, each with a conical latero-external sensillum near two gard setae, with five normal setae in anterior portion, and with up to 62 neuroglandular setae in a medial and posterior position. Narrow submentum with two posterior macrosetae with 3-5 long, thin distal barbs and a smooth anterior row of setae (Fig. 78).

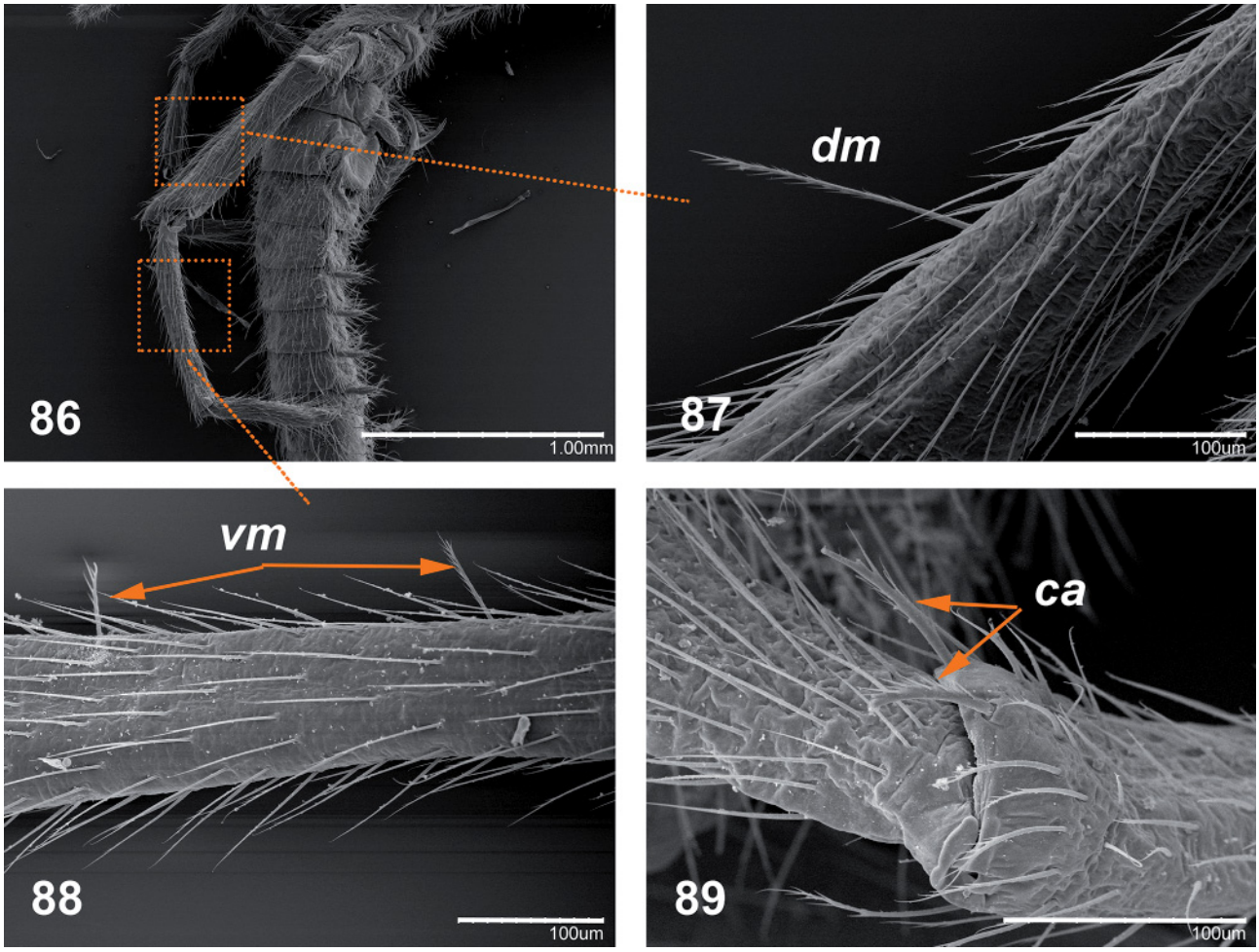
Thorax: Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 $lp_{2,3}$ macrosetae; mesonotum with 1+1 s*ma*, 1+1 s*la* or 1+0 *sla* - 0+1 *la*, 2+2 $lp_{2,3}$; metanotum with 1+1 lp_2; long, thin, barbed notal macrosetae in distal two-thirds; marginal setae slightly longer than clothing setae, with a few thin distal barbs (Fig. 79). Metathoracic legs reaching beyond end of abdomen; femur and tibia being the longest articles with a similar length (Table 4). One dorsal femoral macroseta in distal half with thin barbs 0.20-0.25 mm in length, and with three slightly shorter barbed ventral macrosetae (Figs 86-87); two (rarely three) short metathoracic tibial macrosetae barbed in distal half (Fig. 88); calcars with long thin barbs in two rows on one side (Fig. 89); tarsus with two ventral rows of smooth setae slightly larger and longer than clothing setae; two dorsal and two ventral subapical smooth setae on tarsus; very unequal claws (posterior claw 1.5-1.6 longer than anterior claw), with large lateral crests and smooth setiform lateral processes; posterior claw with large backward overhang; claws almost smooth on dorsal side, ventral side with a micro-bacilliform to granular surface between noticeable crests; an intermediate small, thin irregular structure present between the claws (Figs 90-93).

Table 4. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. Length (in mm) of body, antennae, femur, tibia and tarsus of metathoracic legs and of cerci.

specimen	body	antennae	number of antennomeres	femur	tibia	tarsus	number of primary cercal articles	cercus
J1 paratype	2.9	3.0	35	0.55	0.56	0.54	-	-
♀4 paratype	4.1	4.4	36	0.90	0.81	0.70	-	-
♂4 paratype	4.3	4.7	35	1.05	0.95	0.70	-	-
♂5 paratype	4.4	4.3	34	0.81	0.90	0.65	9	4.6
♂3 paratype	4.5	4.1	35	1.00	0.95	0.73	-	-
♂2 paratype	4.7	4.6	35	0.91	1.05	0.75	-	-
♂1 holotype	4.8	4.6	35	0.92	0.91	0.73	8	4.7
♀2 paratype	4.8	4.6	35	0.97	1.02	0.80		
♂6 paratype	4.9	4.3	35	0.86	0.98	0.73		
♀3 paratype	5.1	-	-	0.97	1.02	0.73	9	4.6
♀1 paratype	5.6	4.8	36	1.01	1.11	0.76	11	6.2



Figs 84-85. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (84) Detail of mesonotum with clothing setae. (85) Detail of mesonotum with insertion of a clothing seta.

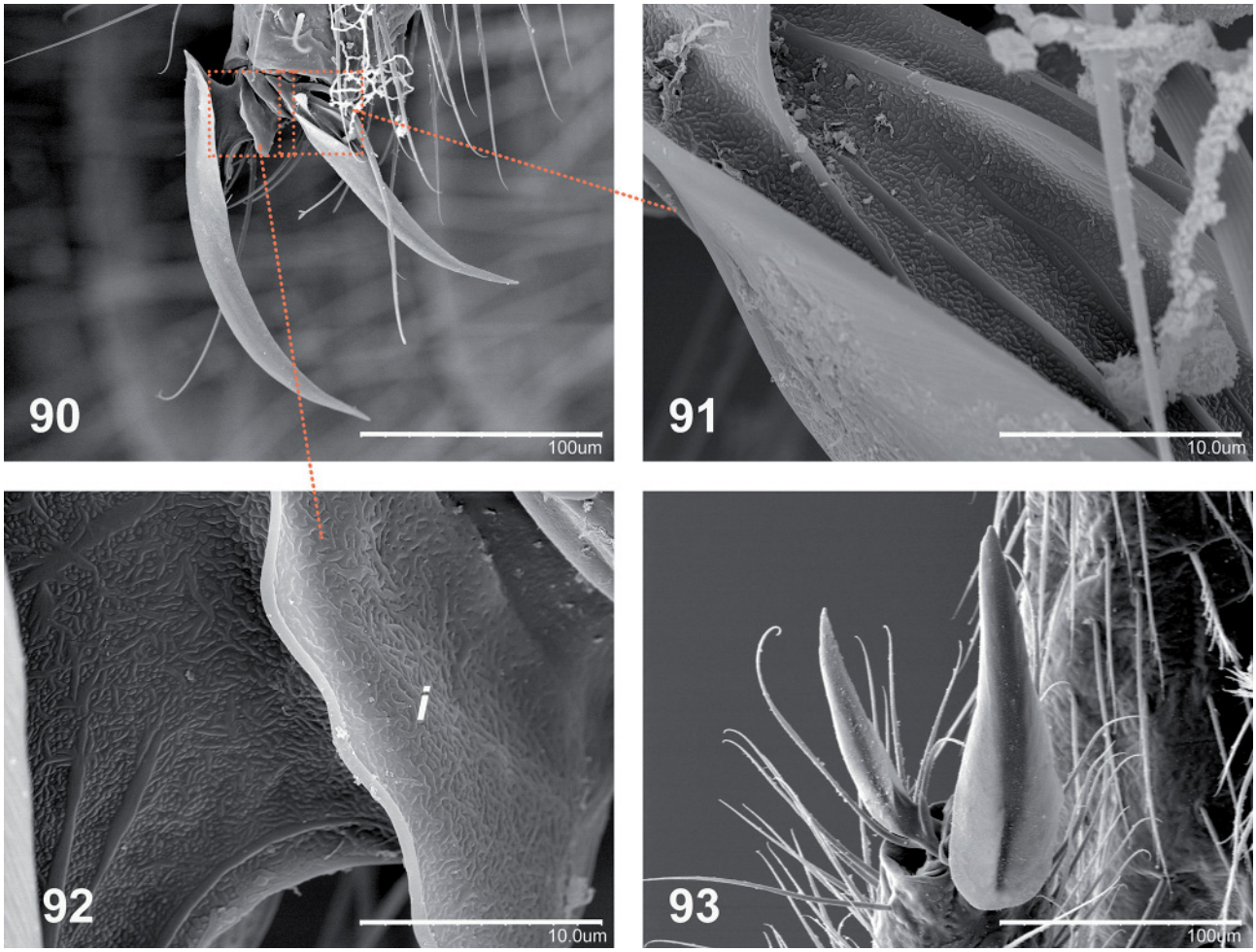


Figs 86-89. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (86). Metathorax to eighth abdominal segment and metathoracic leg of a female, lateral view. (87) Central portion of femur of metathoracic leg with dorsal macrosetae (*dm*). (88) Central portion of tibia of metathoracic leg with two ventral macrosetae (v*m*). (89) Joint between tibia and tarsus of metathoracic leg with calcars (*ca*).

Abdomen: Urotergites III with 0+0 (rarely 0+1 $post_1$) macrosetae; urotergite IV with 0+0, 0+1 or 1+1 *la*, 1+1-2+1 $post_{1-2}$ macrosetae or 1+1-0+1 $spost_1$ submacrosetae; urotergite V with 1+1 *la*, 3+3-2+3 $post_{1-2,4}$ macrosetae or 2+1 $spost_{1-2}$ submacrosetae; urotergites VI-VII with 1+1 *la*, 4+4 $post_{1-4}$ macrosetae; urotergite VIII with 6+6 *post*; abdominal segment IX with 8+8 *post* macrosetae; all urotergal macrosetae long and barbed in distal three-fourths; urosternite I with 7+7 macrosetae; urosternites II-VII with 5+5; urosternite VIII with 2+2; urosternal macrosetae with a few long distal barbs. Apical seta with a basal tooth and two or three long thin barbs, subapical and medio-sternal setae with four or six long thin barbs (Fig. 96). Four cerci from four different specimens apparently complete and of similar length as body, except in ♀1 paratype (the largest) with cercus being 1.22 times longer than body; basal article divided into three or four secondary articles, followed by eight to eleven primary articles (Table 4); each primary cercus bearing two to ten irregular whorls of long barbed macrosetae, one to two distal whorls of smooth long setae, and one apical whorl of short thin setae with tiny distal barbs (Fig. 97).

Secondary sex characters: First urosternite of males carrying very large spherical appendages with a large field of up to 200 glandular a_1 setae (Figs 94-95); females with subcylindrical to conical appendages with up to 18 glandular a_1 setae.

Taxonomic affinities: The noticeable taxonomic traits in *Plusiocampa (Venetocampa) pirnati* sp. nov., such as the macroseta distribution pattern on nota and abdomen and the very unequal claws (posterior claw more than 1.5 longer than anterior claw), show strong similarities with *Plusiocampa* (*Plusiocampa*) *hoelzeli* (Neuherz, 1984), described from a cave in Carinthia (Austria) and recently reported from Renejevo brezno, Kanin Mountain, in Slovenia (Sendra *et al.,* 2020a) (uncertain affinity, see discussion below). The absence of glandular g_1 setae and the presence of huge spherical appendages

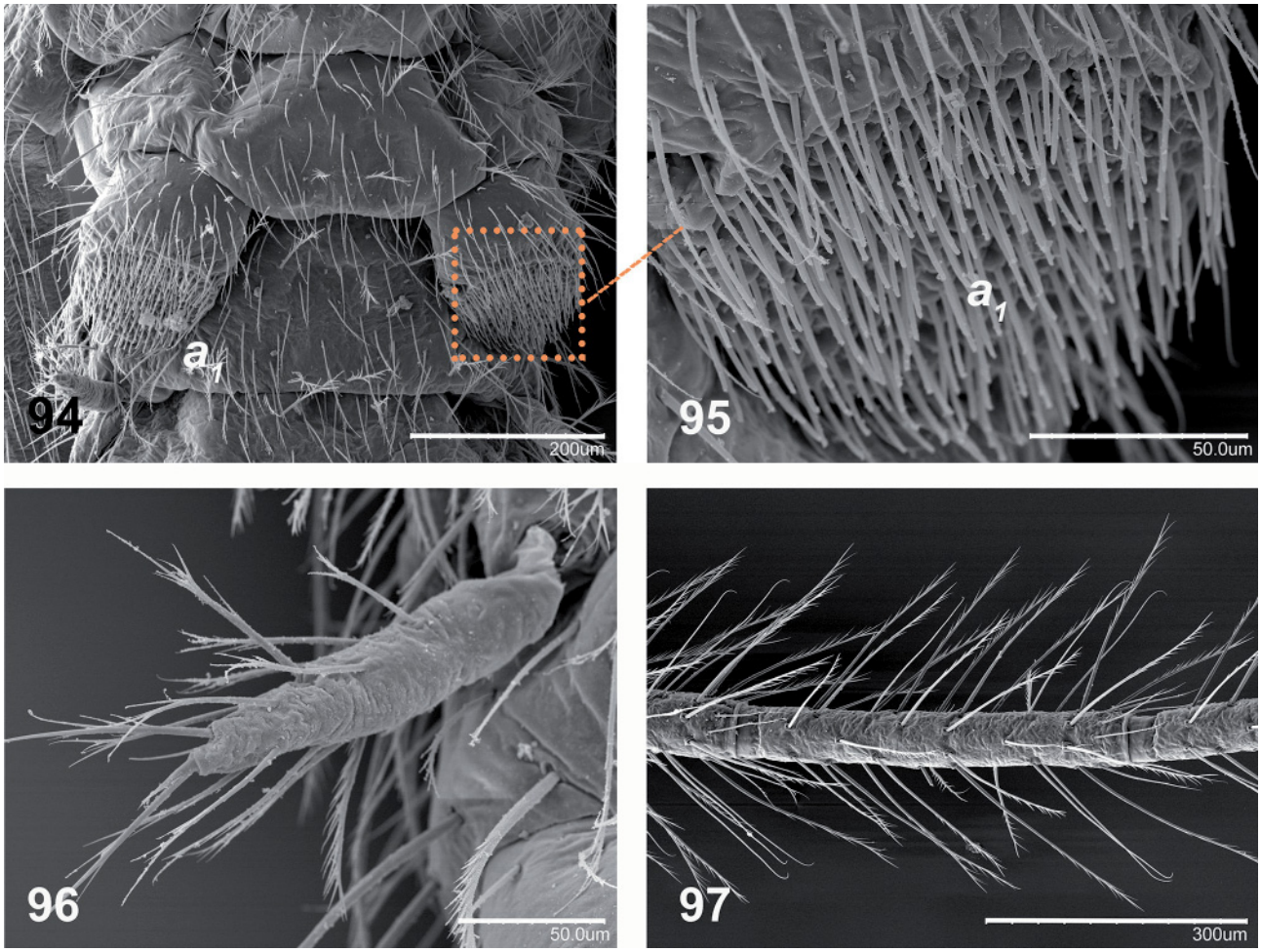


Figs 90-93. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (90) Pretarsus of metathoracic leg, lateral view. (91) Detail of proximal portion of anterior claw in lateral view. (92) Detail of intermediate structure between claws (*i* = intermediate sheet). (93) Pretarsus of metathoracic leg, dorsal view.

with numerous glandular a_1 setae in males show close similarities with *Plusiocampa* (*Venetocampa*) *paolettii* Bareth & Condé, 1984, described from a (not too distant) cave in Belluno, in the Italian Alps. At present, *P.* (*V.*) *paolettii* is considered to be closely related to *P. (V.) pirnati* sp. nov. and to belong in the controversial subgenus *Venetocampa* (see discussion). Both species are distinguished by the following traits: urotergal macrosetae present on the fourth urotergite, and 4+4 posterior macrosetae present on the sixth and seventh urotergite in *P. (V.) pirnati* sp. nov.; in *P. (V.) paolettii* the urotergal macrosetae on the fourth urotergite are absent and only 2+2 and 1+1 posterior macrosetae on the sixth and seventh urotergite are present; *P. (V.) pirnati* sp. nov. has 6+6 and 8+8 posterior macrosetae on the eighth urotergite, and on the ninth abdominal segment 4+4 macrosetae *vs.* 7+7 in *P. (V.) paolettii*. Lastly, *P. (V.) pirnati* sp. nov. has two or three ventral tibial macrosetae, whereas in *P. (V.) paolettii* such macrosetae are absent.

Type locality: Cave P4 (n. 1529) lies in the Kanin mountains (Bovec, Slovenia), in the western part of the Julian Alps (Figs 98-100). The cave entrance is located on the Kanin plateau, 2121 m above sea level, in a rocky area with an alpine vegetation. Cave P4 is part of a cave system that is 1320 m deep and 12 km long. The cave temperature varies with depth, from 1˚C in the upper parts to 3˚C at 1 km below the surface. Species richness and abundance is highest in the deeper parts of the cave. Animals were mostly collected with baited pitfall traps and very rarely by manual collecting from the surfaces. Most specimens were collected in the deep horizontal parts of the cave: always in wet areas, near constant drip water, on walls or in traps placed in gravel, but never on clay or sand. They were found together with *Anophthalmus* sp. beetles, Acari and several species of Collembola.

Renejevo brezno Cave (cave catalogue number 7090), where *Plusiocampa (Plusiocampa) hoelzeli* was found (Sendra *et al.,* 2020a), is part of the same cave system as



Figs 94-97. *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (94) First and second abdominal segment of a male, ventral view. (95) Apical portion of appendage of first urosternite with glandular a_1 setae in a male. (96) Stylus of fourth urosternite. (97) Fifth primary cercal article.

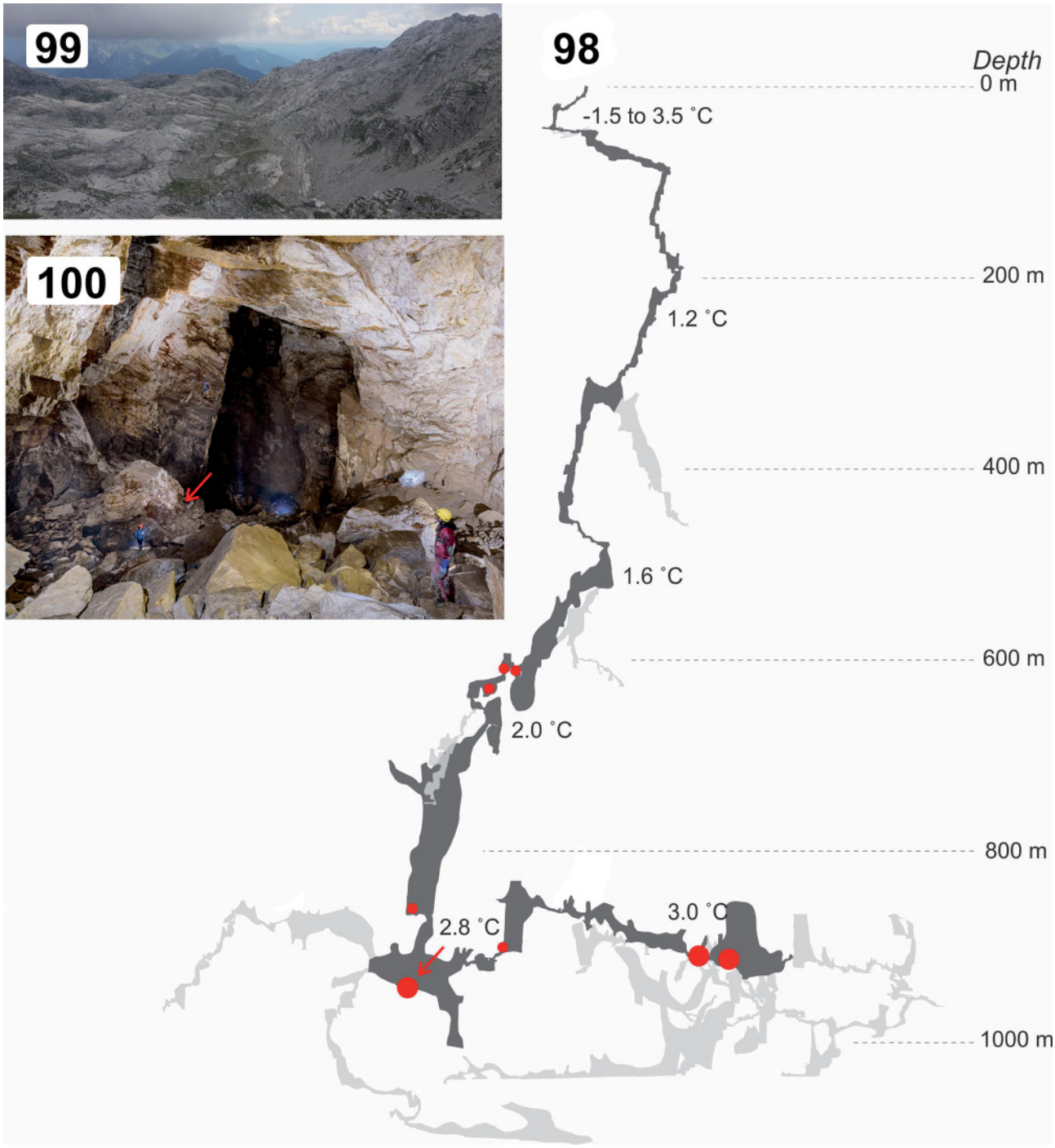
P4. The entrances of both caves are 1 km apart. In both caves diplurans were found at similar depths (always in deep parts of the caves). It is possible that the diplurans from Renejevo brezno Cave belong *to P. (V.) pirnati,* but the available specimens are too strongly damaged for a reliable identification. More diplurans from Renejevo brezno are needed to confirm taxonomic affinity.

DISCUSSION

Phylogeny, habitat and distribution: Diplurans are represented by 28 species of Campodeidae (one of the two dipluran families with troglobites around the world) in the cave ecosystems of the Dinarides, Eastern Alps, Balkan Mountains, and Rhodope Massif. Two out of five campodeid subfamilies inhabit this region: Campodeinae with one species and Plusiocampinae with 27 species.

The family Campodeinae comprises currently 355 species and worldwide distribution. It is characterized by a cuticle with roseate microstructures; the pronotal macrosetae formula is 1+1 medial anterior, 1+1 lateral anterior, 1+1 lateral posterior; the claws are subequal, simple, smooth, regularly curved and rarely have plain lateral crests; the uroterga carry up to one pair of medial and lateral anterior macrosetae and one to three pairs of lateral posterior macrosetae. Most Campodeinae live in soil habitats, and 15% of the species have adapted to cave ecosystems (Sendra *et al.,* 2020b). Its only representative in the study area is *Campodea (Paurocampa) pretneri* which occurs in the Eastern Alps and the western Dinaric Mountains (Table 5, Fig. 101).

Plusiocampinae have a Eurasian distribution, with 83% of the species living mostly in caves (Sendra *et al.*, 2020b). Two genera, the monotypic *Condeicampa* Ferguson, 1996 from a single cave in Nevada (USA), and *Silvestricampa* Condé, 1950, a genus with five soil-dwelling species from South Africa, are outside the main distribution area of Plusiocampinae in Eurasia. These species are characterized by a pronotum with at least 4+4 macrosetae, numerous lateral anterior and posterior



Figs 98-100. (98) Map of Cave P4 in the Kanin mountains (Bovec, Slovenia), with locations marked where *P. (V.) pirnati* sp. nov. was found. Cave passages that have been sampled at least once are marked in dark grey, whereas passages that have not been sampled yet are marked in light grey. Large red dots represent locations where we sampled five or more specimens, and small red dots are locations where less than five specimens where found. (99) View of the landscape from the cave entrance (photograph by Matic Di Batista). (100) Big chamber at 950 m depth where a high number of specimens were collected in one trap (red arrow indicates same location in Fig. 98 (photograph by Uroš Kunaver).

Table 5. Cave-adapted campodeids from the Dinarides, Eastern Alps, Balkan Mountains and Rhodope Massif.

Species	Dinarides	Eastern Alps	Balkan and Rhodope
Campodea (Paurocampa) pretneri Condé, 1974	x	x	
Plusiocampa (Didymocampa) cvijici Sendra & Antić, sp. nov.	x		
Plusiocampa (Plusiocampa) atom Sendra & Antić, sp. nov.	x		
Plusiocampa (Plusiocampa) bulgarica Silvestri, 1931			x
Plusiocampa (Plusiocampa) beroni Bareth & Condé, 2001			x
Plusiocampa (Plusiocampa) caprai Condé, 1950		x	
Plusiocampa (Plusiocampa) aff. *elongata* Ionescu, 1955			x
Plusiocampa (Plusiocampa) gueorguievi Bareth & Condé, 2001			x
Plusiocampa (Plusiocampa) hoelzeli (Neuherz, 1984)		x	
Plusiocampa (Plusiocampa) aff. *isterina* Condé, 1993	x		
Plusiocampa (Plusiocampa) friulensis Bareth & Condé, 1984		x	
Plusiocampa (Plusiocampa) grandii Silvestri, 1933		x	
Plusiocampa (Plusiocampa) latens Condé, 1948	x		
Plusiocampa (Plusiocampa) schweitzeri Condé, 1947	x		
Plusiocampa (Plusiocampa) strouhali Silvestri, 1933		x	
Plusiocampa (Plusiocampa) ternovensis Sendra & Borko, 2020 in Sendra *et al.,* 2020a	x		
Plusiocampa (Plusiocampa) vodniensis Bareth & Condé, 2001			x
Plusiocampa (Stygiocampa) barethae Sendra & Rađa, sp. nov.	x		
Plusiocampa (Stygiocampa) bureschi Silvestri, 1931			x
Plusiocampa (Stygiocampa) christiani Condé & Bareth, 1996	x		x
Plusiocampa (Stygiocampa) dalmatica Condé, 1959	x		
Plusiocampa (Stygiocampa) denisi Condé, 1947	x		
Plusiocampa (Stygiocampa) dulcici Sendra & Rađa, sp. nov.	x		
Plusiocampa (Stygiocampa) nivea (Joseph, 1882)	x		
Plusiocampa (Stygiocampa) remyi Condé, 1947	x		
Plusiocampa (Venetocampa) ferrani Sendra & Delić, 2020 in Sendra *et al.,* 2020a	x		
Plusiocampa (Venetocampa) paolettii Bareth & Condé, 1984		x	
Plusiocampa (Venetocampa) pirnati Sendra & Borko, sp. nov.		x	

macrosetae on several urotergites, and elbowed claws with mostly well-developed lateral crests. In our study area Plusiocampinae are represented by the hightly diversified genus *Plusiocampa* (divided into five subgenera), of which only the monotypic *Pentachaetocampa* Sendra & Weber, 2018, found in a single cave in southwestern Germany, is absent. The genus *Plusiocampa* has 76 described species, most of which are cave-adapted, although 16 of these species lack troglomorphic features. These species live in the soil and occasionally reach the deepest soil layer, sometimes called the mesovoid shallow substratum, and they are rarely found in caves (Sendra *et al.,* 2020a). In the study area there are species of four subgenera: *Didymocampa* Paclt, 1957 with one species described herein; *Plusiocampa* s. str. Silvestri, 1912 with 15 species including one described herein; *Stygiocampa* Silvestri, 1934 with eight species of which two are described herein; and *Venetocampa* Bareth & Condé, 1984 with three species, including one described herein (Table 5, Fig. 102).

Didymocampa was established on the basis of the presence of two dorsal femora macrosetae in two species from distant localities: *P. (D.) evallonychia* from a Crimean cave and *Plusiocampa sinensis* Silvestri, 1931 found in Chinese soil (Paclt, 1957). Much later Condé & Sendra (1989) added one more species from a cave

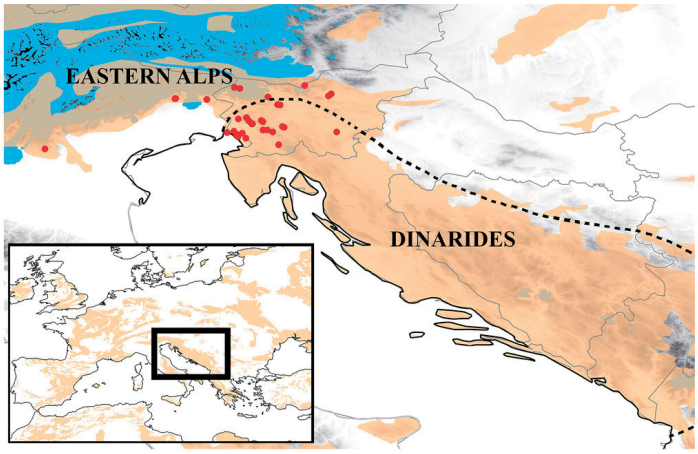
in the south of the Iberian Peninsula, *Plusiocampa (Didymocampa) alhamae* Condé & Sendra, 1989. Condé (1993) described a new cave-adapted species from China, *Plusiocampa (Didymocampa) lipase* Condé, 1993, and last Condé (1996) added one more species from Movile Cave in Romania, *P. (D.) euxina* Condé, 1996. Recently, the disjunct subgenus *Didymocampa* started to crumble; *P. (D.) lipsae* was transferred to *Hubeicampa* Sendra & Lips in Sendra *et al.,* 2020b, to which the highly cave-adapted Chinese species *Hubeicampa melissa* Sendra & Lips, 2020 in Sendra *et al.,* 2020b was added. It is also necessary to reconsider the position of *P. sinensis* due to the presence of 1+1 macrosetae on the eighth urosternite, which is not present in any other *Plusiocampa* species (Sendra *et al.,* 2020b). We suggest keeping the subgenus *Didymocampa* for the European species, including *Plusiocampa (Didymocampa) cvijici* sp. nov. from the Dinarides (Fig. 102).

The subgenus *Plusiocampa* has 58 described species of which 73% are exclusively found in caves (Sendra *et al.,* 2020a). They are spread over the Euro-Mediterranean region, from southern Europe and a small karst area in northern Africa (Kabylian Mountains, Tell Atlas) throughout the south of Central Europe to southeastern Europe, together with some isolated localities in the Anatolian and Crimean peninsulas and in the western Caucasus (Sendra *et al.,* 2020a). *Plusiocampa* s. str. seems to be a monophyletic group because species share numerous macrosetae on nota and urotergites and possess one dorsal femoral macroseta and 1-4 ventral tibial macrosetae. The presence or absence of medial posterior macrosetae on the mesonotum and metanotum splits *Plusiocampa* s. str. into two biogeographically distinct subgroups (Condé, 1956; Sendra *et al.,* 2019; Sendra *et al.,* 2020c). In our study area six species of *Plusiocampa* s. str. belong to the group without thoracic medial posterior macrosetae. They presumably evolved on the Dinaric plate. *Plusiocampa atom* sp. nov., *P.* aff. *isterina, P. latens, P. schweitzeri* and *P. ternovensis* occur in the Dinarides, and only one species, *P. gueorguievi,* lives in Central Predbalkan caves. Nine species belong to the group with medial posterior macrosetae on the thorax, representing recent colonizers of the surroundings of the Dinarides: *P. caprai, P. friulensis, P. grandii, P. hoelzeli* and *P. strouhali* inhabit the Eastern Alps, and *P. bulgarica, P. beroni, P.* aff. *elongata* and *P. vodniensis* live in the Balkan System (Stara Planina) and in the Rhodope Massif (Table 5, Fig. 103).

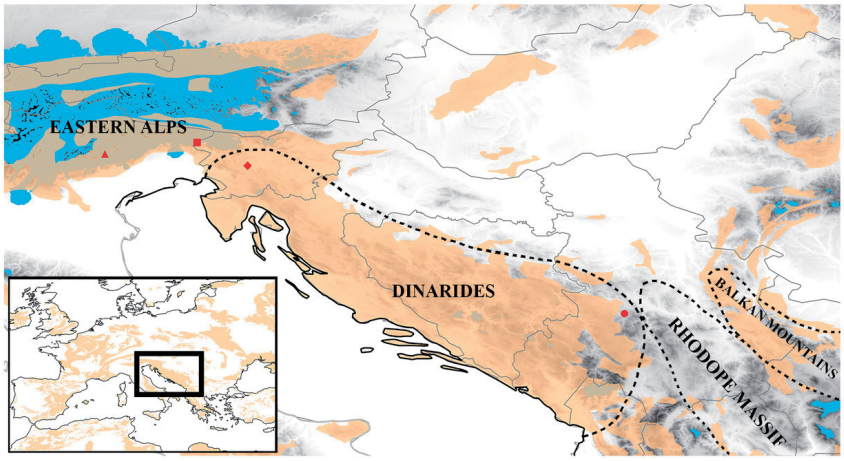
Most species in the subgenus *Stygiocampa* are restricted to the Dinaric Karst: *P. (S.) barethae* sp. nov., *P. (S.) dalmatica, P. (S.) denisi, P. (S.) dulcici* sp. n., *P. (S.) nivea* and *P. (S.) remyi*. In addition, *P. (S.) christiani* and *P. (S.) bureschi* can be found in the Balkan Mountains (Table 5, Fig. 104). *Stygiocampa* is a presumably monophyletic group of large species in the genus *Plusiocampa* (6-9 mm body size), which are highly adapted to cave ecosystems and characterized by a trend towards macrosetae reduction on nota, urotergites and legs. They show noticeable troglomorphic features, including a peculiar cupuliform organ with a very narrow entrance, complex and unique olfactory chemoreceptors, long antennae and legs, and mostly long cerci that are two times (or almost three times) the body length (Condé, 1956; Sendra *et al.,* 2020a). Two groups within *Stygiocampa* can be defined based on the presence or absence of extra macrosetae on the first to the eighth urosternites. *Plusiocampa (S.) barethae* sp. nov., *P. (S.) christiani, P. (S.) dalmatica*, *P. (S.) nivea* and *P. (S.) remyi* have extra macrosetae (18+18-24+24, 11+11-15+15, 3+3-4+4 macrosetae formula on first, second to seventh and eighth urosternite, respectively), whereas *P. (S.) bureschi, P. (S.) denisi* and *P. (S.) dulcici* sp. nov. have no extra urosternal macrosetae (7+7, 5+5, 2+2 macrosetae instead).

The subgenus *Venetocampa* has three species [*P. (V.) ferrani*, *P. (V.) paolettii* and *P. (V.) pirnati* sp. nov.] that occur between the Italian and Slovenian Alps, the Eastern Alps and the extreme northwest of the Dinarides (Table 5, Fig. 102). *Venetocampa* is defined by the presence of one dorsal femoral macroseta, in addition to the absence of ventral tibial macrosetae, which is a combination of characters close to that present in *Plusiocampa* s. str. and *Stygiocampa*. The three *Venetocampa* species have other chracteristics in common with *P. (P.) ternovensis* and *P. (P.) hoelzeli,* such as their small body sizes, unequal anterior and posterior claws, and occurrence in cave ecosystems. Interestingly, all species except *P. (V.) ferrani* are from caves located at high altitudes, with *P. (V.) ferrani* also found in a relatively deep cave (-350 m) although not in the mountains. At least three species are known from great depths: *P. (P.) ternovensis* from 900 m below ground, *P. (V.) pirnati* sp. nov. from -1000 m, and *P. (P.) hoelzeli* from -1200 m which holds the record of being the dipluran from the deepest cave locality.

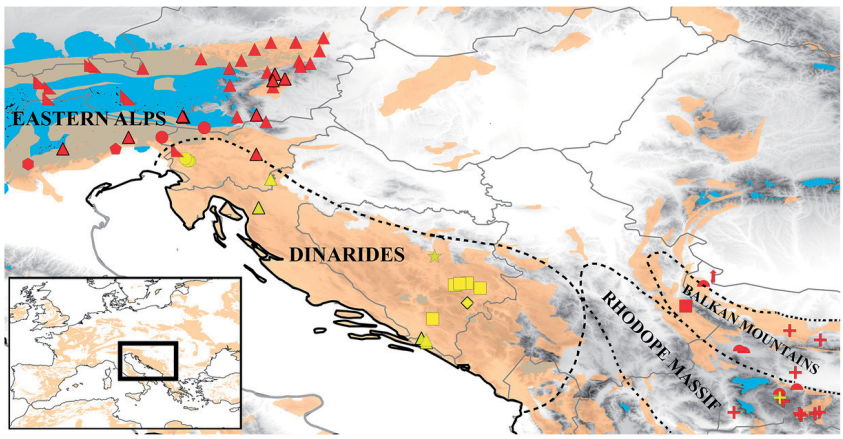
Biodiversity and distribution patterns in the Dinaric and adjacent karst regions: The Dinarides is a region with high endemicity of troglobionts from many different terrestrial arthropod groups (Bedek *et al.,* 2011; Hlavač *et al.,* 2017). The geographical ranges of these troglobionts are generally small and fragmented (Trontelj *et al.*, 2009; Zagmajster *et al.,* 2014; Bregović *et al.,* 2019). Our data on cave-dwelling campodeids in the Dinarides and adjacent regions revealed a somewhat different pattern. Most of the troglobiotic dipluran species have large ranges, in particular species of the subgenus *Stygiocampa,* such as *Plusiocampa (Stygiocampa) nivea*, *Plusiocampa (Stygiocampa) remyi* and the extreme case of *Plusiocampa (Stygiocampa) dalmatica,* with a maximum distance of 350 km between localities (Fig. 104). Such large ranges are rare for terrestrial troglobionts and have been recorded only within some taxonomic groups such as centipedes, millipedes, isopods and spiders (Antić *et al.,* 2015; Karaman & Horvatović, 2018; Stoev, 2001). Large ranges are probably methodological artefacts, i.e.



101



102



103

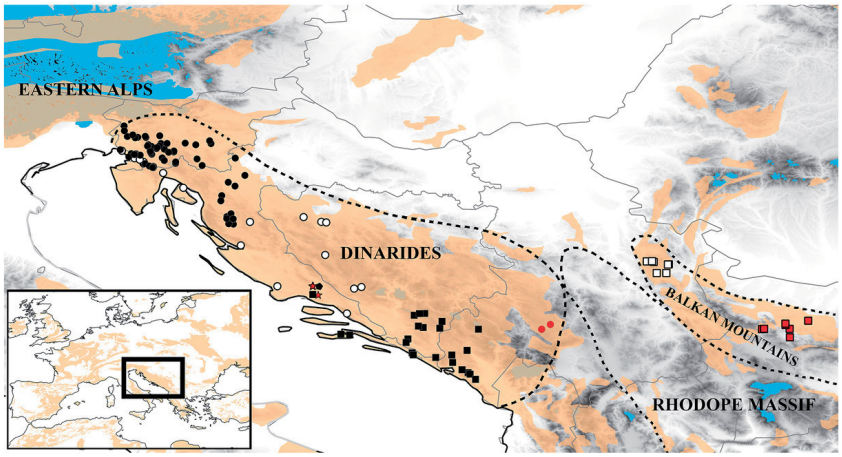


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Fig. 101. Localities of *Campodea (Paurocampa) pretneri* Condé, 1974 (red circles). In brown: karst areas (source: Chen *et al.,* 2017). In blue: ice cover during the Last Glacial Maximum (source: Ehlers *et al.,* 2011).

Fig. 102. Localities of *Plusiocampa (Venetocampa) paolettii* Bareth & Condé, 1984 (red triangle), *Plusiocampa (Venetocampa) pirnati* Sendra & Borko, sp. nov. (red square), *Plusiocampa (Venetocampa) ferrani* Sendra & Delić, 2020 in Sendra *et al.,* 2020a (red diamond) and *Plusiocampa (Didymocampa) cvijici* Sendra & Antić, sp. nov. (red circle). In brown: karst areas (source: Chen *et al.,* 2017). In blue: ice cover during the Last Glacial Maximum (source: Ehlers *et al.,* 2011).

Fig. 103. Localities of *Plusiocampa (Plusiocampa) strouhali* Silvestri, 1933a (red triangles), *Plusiocampa (Plusiocampa) hoelzeli* (Neuherz, 1984) (red circles), *Plusiocampa (Plusiocampa)* aff. *elongata* Ionescu, 1955 (red squares), *Plusiocampa (Plusiocampa) caprai* Condé, 1950 (red half squares), *Plusiocampa (Plusiocampa) friulensis* Bareth & Condé, 1984 (red pentagon), *Plusiocampa (Plusiocampa) grandii* Silvestri, 1933b (red hexagon), *Plusiocampa (Plusiocampa) bulgarica* Silvestri, 1931 (red crosses), *Plusiocampa (Plusiocampa) beroni* Bareth & Condé, 2001 (red semicircles), *Plusiocampa (Plusiocampa) vodniensis* Bareth & Condé, 2001 (red arrow), *Plusiocampa (Plusiocampa) ternovensis* Sendra & Borko, 2020 in Sendra *et al.,* 2020a (yellow circles), *Plusiocampa (Plusiocampa) atom* Sendra & Antić, sp. nov. (yellow star), *Plusiocampa (Plusiocampa) latens* Condé, 1948 (yellow triangles), *Plusiocampa (Plusiocampa) schweitzeri* Condé, 1947 (yellow squares), *Plusiocampa (Plusiocampa)* aff. *isterina* Condé, 1993 (yellow diamond), *Plusiocampa (Plusiocampa) gueorguievi* Bareth & Condé, 2001 (yellow cross). In brown: karst areas (source: Chen *et al.,* 2017). In blue: ice cover during the Last Glacial Maximum (source: Ehlers *et al.,* 2011).

Fig. 104. Localities of *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882) (black circles), *Plusiocampa (Stygiocampa) dalmatica* Condé, 1959 (white circles), *Plusiocampa (Stygiocampa) remyi* Condé, 1947 (black squares), *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996 (white squares), *Plusiocampa (Stygiocampa) barethae* Sendra & Rađa, sp. nov. (black hexagon), *Plusiocampa (Stygiocampa) dulcici* Sendra & Rađa, sp. nov. (red stars), *Plusiocampa* (*Stygiocampa*) *denisi* Condé, 1947 (red circles) and *Plusiocampa (Stygiocampa) bureschi* Silvestri, 1931 (red squares). In brown: karst areas (source: Chen *et al.,* 2017). In blue: ice cover during the Last Glacial Maximum (source: Ehlers *et al.,* 2011).

morphology alone, without molecular analyses, cannot untangle taxonomic relationships within subterranean groups with a multitude of cryptic species. Another peculiar feature of campodeid diversity is that there are no endemic genera or subgenera in the Dinarides in constrast to all other taxonomic groups that have strongly diversified in the subterranean habitats of the region. Cave-adapted species of the subgenera *Campodea (Paurocampa)* and *Plusiocampa (Venetocampa)* are distributed across the Eastern Alps and western Dinarides, representing Alpine-Dinaric lineages, a pattern documented in several other taxonomic groups (Antić *et al.,* 2018). *Plusiocampa (Plusiocampa)* and *Plusiocampa (Didymocampa)* have a wide Euro-Mediterranean distribution. *Plusiocampa (Stygiocampa)* exhibits a holodinaric distribution, but two species are also known to be present in the Kučaj and Beljanica Mountains, in the Serbia and Stara Planina Mountains (all part of the Balkan Mountains) (Figs 101-104). The alternating range pattern of different subgenera, together with their regional overlaps, suggest complex colonization and speciation events of the subterranean habitats in the study regions. This is particulary evident in Slovenia, at the junction of the Dinaric and the Alpine biogeographic regions, where the pattern of co-occurrences of Alpine and Dinaric lineages was already documented in different cave groups (Faille *et al.,* 2013).

Colonization: Multiple hypotheses have been suggested to explain the colonization of the Euro-Mediterranean basin by campodeid diplurans (Sendra *et al.*, 2004; Sendra *et al.,* 2019; Sendra *et al.,* 2020a, c, d). These colonization hypotheses use families, subfamilies, genera, and subgenera of cave-adapted species of campodeids as groups to compare with their current well-known distribution ranges. Thus, we suggest that dispersal, vicariance and extinction processes that have taken place during hundreds of millions of years explain the current distribution of cave campodeids in the Balkan region. No tachycampoids species, *Podocampa* or *Litocampa* (a presumably monophyletic linage in the subfamily Campodeinae), are present in either the central or eastern Euro-Mediterranean karst regions. Tachycampoids, *Podocampa* and *Litocampa* occur in the extreme western European karst regions, with disjunct distribution ranges at both sides of the Atlantic Ocean, and they are considered as relicts of Pangea from the Mesozoic (Sendra *et al.,* 2020a). At the beginning of the Cenozoic, new European microplates emerged and gave the opportunity for new colonization (Sendra *et al.,* 2004; Sendra *et al.,* 2019). In such a paleogeographical scenario Plusicampinae could have arrived through two possible connections from eastern Laurasia: one when the Turgai Strait closed during the Eocene-Oligocene transition (Decourt *et al.,* 2000), and another, more recent, at the beginning of Miocene, through the Anatolian peninsula to the Balkans (Sendra *et al.,* 2004). Both connections could have allowed the arrival of the first Plusiocampinae wave represented by Plusiocampinae species without medial macrosetae on the mesonotum and metanotum. This hypothetic monophyletic group contains all *Stygiocampa, Venetocampa, Pentachaetocampa, Patrizicampa* and *Cycladicama* species, as well as some species

of *Cestocampa, Didymocampa* and *Plusiocampa* s. str. These first newcomers are currently located in the Dinaric karst, Gargano Promontory, and the rest of the Protoliguric massif: Catalanides Range, Sardinia, Kabylias and Internal Baetic Zone, in addition to the small Irakelia Island in the Cyclades Islands where *Cycladicampa* Sendra, 2020 has been recently discovered (Sendra *et al.,* 2020c). A second wave of Plusiocampinae could have colonized the land emerging during the Messinian, at the end of the Miocene. These second newcomers are represented by Plusiocampinae with medial macrosetae on the mesonotum and metanotum, as in many species of *Plusiocampa* s. str., including also *Vandelicampa, Hystrichocampa,* some *Didymocampa* and *Cestocampa* species (Sendra *et al.,* 2019). This second lineage is currently distributed in the external Baetic Mountains, Rhone Valley region, Alpes, Italian peninsula, and many Mediterranean islands such as the Balearic Islands or Crete. The Dinarides harbour only ancestors of the first wave of colonizers, that is Plusiocampinae with medial macrosetae: *Stygiocampa, Didymocampa, Venetocampa* and *Plusiocampa* s. str. species. Adjacent karst regions, such as the Alps and the Balkan Mountains, received only *Plusiocampa* species from the second colonization wave, that is Plusiocampinae without medial macrosetae. Relatively stable climatic conditions inside caves and their subterrestrian surroundings allowed campodeids to survive in Dinaric cave-ecosystems during the Cenozoic. The diplurans from regions to the north of the Dinarides were wiped out during the Pleistocene glaciations (Sendra *et al.,* 2020c).

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