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## Monograph

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# Flourishing in subterranean ecosystems: Euro-Mediterranean Plusiocampinae and tachycampoids (Diplura, Campodeidae)

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**Abstract.** Diplura is a group of entognathous hexapods, often considered a sister group to insects. They play an important role in recycling organic matter in soil and subterranean terrestrial ecosystems. The Campodeidae is the most diverse family, divided into four subfamilies. The subfamily Plusiocampinae has a subterranean life-style with many species distributed in the Euro-Mediterranean area. The *incertae sedis* tachycampoids (“lignée Tachycampoïde”) is a group within the family Campodeidae that share with the Plusiocampinae a strong preference for subterranean habitats and several morphological characters, such as slender body shape, elongated appendages, considerable increment in the number of antennomeres and cercal articles, and complexity of sensorial structures. The present monograph provides a taxonomic revision of the subfamily Plusiocampinae and the genera belonging to the tachycampoid lineage from Europe and the Mediterranean region. It comprises detailed morphological descriptions and illustrations together with data on the habitats and distributions of 87 species, 10 subspecies and 11 affinis forms. Seven new species are described among those, namely: *Plusiocampa (Plusiocampa) apollo* Sendra, Giachino & Vailati sp. nov., *P. (P.) chiosensis* Sendra & Gasparo sp. nov., *P. (P.) dublanskii* Sendra & Turbanov sp. nov., *P. (P.) hoffmanni* Sendra & Paragamian sp. nov., *P. (P.) rhea* Sendra sp. nov., *P. (P.) ternovensis* Sendra & Borko sp. nov. and *P. (Venetocampa) ferrani* Sendra & Delić sp. nov.

**Keywords.** Dipluran, cave fauna, troglobite, Europe, circum-Mediterranean.

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## Introduction

Diplura is a group of eyeless entognathous hexapods, often considered a sister group to insects, which colonize terrestrial habitats, presenting a tracheal system, rudimentary Malpighian tubules and sperm transfer via a spermatophore (Beutel *et al.* 2017; Denis 1949). About 1000 extant dipluran species are named and described in 10 dipluran families. Half of this diversity belongs to the Campodeidae (Condé 1955a; Pagés 1959; Sendra 2015). The family Campodeidae is characterized by soft pluriarticular cerci

without glands and is divided into four subfamilies: Campodeinae Condé, 1956, Lepidocampinae Condé, 1956, Hemicampinae Condé, 1956 and Plusiocampinae Paclt, 1957.

Campodeids live in terrestrial habitats from soil to subterranean ecosystems, where they are active decomposers of decaying organic matter, opportunistic scavengers or spore feeders (Christian & Bauer 2007). Within campodeids, the subfamily Campodeinae is the most diverse, distributed worldwide (Condé 1955a), while Lepidocampinae and Hemicampinae are restricted to tropical regions. Unlike Hemicampinae, both Campodeinae and Lepidocampinae have species distributed in subterranean ecosystems, mainly in the campodeine genera *Litocampa* Silvestri, 1933 and *Podocampa* Silvestri, 1932 (Condé 1955a). Nonetheless, the subfamily Plusiocampinae is the most diverse in subterranean habitats, with over 50 species described from the Euro-Mediterranean region. Only 10 species of Plusiocampinae, belonging to five genera, are found beyond the Euro-Mediterranean region (Holarctic realm) and throughout the Indomalayan and possibly the Afrotropical realms (Condé 1955a; Paclt 1957; Sendra *et al.* 2016, 2017a).

In addition, some other genera with an uncertain position among the different subfamilies of Campodeidae are referred to under the informal term coined by Bareth & Condé (1981) as the “lignée Tachycampode,” which is named the tachycampoid lineage in this text. This lineage currently contains five genera and 17 species, and it has a disjunct distribution on both sides of the Atlantic Ocean, in Mexico, Guatemala and eastern Brazil and in the western Euro-Mediterranean region (Sendra *et al.* 2016). Plusiocampinae and tachycampoids share a strong preference for subterranean habitats and several common morphological characters: slender body shape, elongate appendages, a considerable increment in the number of antennomeres and cercal articles, and numerous and complex sensorial structures.

Historically, campodeids have been placed in a single genus, *Campodea* Westwood, 1842, including species from European caves (Joseph 1882; Viré 1897). *Plusiocampa* Silvestri, 1912 was established based on their elevated number of macrosetae and the lateral crests on their claws. Subsequently, some of the former *Campodea* were transferred into the Plusiocampinae (Denis 1923; Condé 1955a), and many species were described, especially in the genus *Plusiocampa*. All species of Plusiocampinae are characterized by their pattern of pronotal macrosetae, with more than 3+3 macrosetae (Paclt 1957).

Five subgenera of *Plusiocampa* occur in the Euro-Mediterranean region: *Plusiocampa* s. str. from the Mediterranean basin and the Alps; *Stygiocampa* Silvestri, 1934, endemic to the subterranean environment of the Dinaric Mountains and part of the Balkan System; the controversial subgenus *Dydimocampa* Paclt, 1957, extending from Crimea to the Iberian Peninsula; *Venetocampa* Bareth & Condé, 1984, in the Italian and Slovenian Alps; and *Pentachaetocampa* Sendra & Weber, 2018, only known from a cave in the Black Forest, Germany.

Four other genera closely related to *Plusiocampa* occur in the Euro-Mediterranean region: *Cestocampa* Condé, 1956, *Hystrichocampa* Condé, 1948, *Patrizicampa* Condé, 1956 and *Vandelicampa* Condé, 1956. Six genera of Plusiocampinae are distributed outside the Euro-Mediterranean region: *Anisuracampa* Xie & Yang, 1991 in China; *Silvestricampa* Condé, 1950 in South Africa; *Simlacampa* Condé, 1956 in caves of the Indian Himalayas; *Plutocampa* Chevrizov, 1978, with two species in northeastern Asia; *Condeicampa* Ferguson, 1996; and the recently described *Turkmenocampa* Sendra & Stoev, 2017 from a single cave in Central Asia. In addition to these, we plan to describe new genera, mostly from Southeast Asia, in the near future.

The first species described in the tachycampoid lineage was *Tachycampa lepineyi* Silvestri, 1936, collected in a cave in the western Rif Mountains, northwest Africa. The phyletic group also comprises *Paratachycampa* Wygodzinsky, 1944, *Juxtlacampa* Wygodzinsky, 1944, *Jeannelicampa* Condé, 1952 and *Oncinocampa* Condé, 1982. Recently, new tachycampoid species have been described on both

sides of the Atlantic and the nine American and eight Euro-Mediterranean species clearly indicate a disjunct distribution of the group. Some species of *Oncinocampa*, *Paratachycampa* and *Tachycampa* show amphi-Atlantic distributions (Bareth & Condé 1981; Sendra *et al.* 2016).

A taxonomic revision of most plusiocampine and tachycampoid genera from the Euro-Mediterranean region is provided (see complete list of previously published reports in [Table S1](#) in Supplementary Material), together with the description of seven new species. The present monograph also provides detailed descriptions and illustrations of the morphological characters, as well as data on habitats and distribution maps, based on material from several collections and freshly sampled specimens.

## Material and methods

During the last decade, an enthusiastic group of friends and colleagues, speleologists, biospeleologists and biologists have gathered many samples of Plusiocampinae and tachycampoids. This material was sampled in soil and hypogean habitats, including the deepest dipluran ever collected at 1180 m below the surface of the Kanin Mountains, in Slovenia. This large sampling effort extended over the Euro-Mediterranean region, including many Mediterranean islands. It resulted in a total of 4243 specimens from 182 localities, most of them in carbonate caves. Details on the specimens collected for each species are given in the ‘Habitat and distribution’ sections, including all localities of the Euro-Mediterranean species. A complete list of collecting events, organized by taxon, is presented in [Table S2](#) in the Supplementary Material.

Specimens were washed using distilled water, mounted on slides in Marc André II solution and studied under a phase-contrast microscope (Leica DMLS). The illustrations were made using a drawing tube. Measurements were taken with an ocular micrometer. The specimens mounted ‘*in toto*’ were measured from the distal macrosetae on the frontal process to the abdominal supra-anal valve. For scanning electron microscopy (SEM) some specimens were critical point-dried, coated with palladium-gold and studied under a Hitachi S-4100 SEM.

The identification keys to genera, subgenera and species of Plusiocampinae and tachycampoids were generated from a DELTA database (Dallwitz 2005) and modified to improve readability. For each taxon, a diagnosis has been generated, as well as a habitat and distribution section. Taxonomic notes and character illustrations are provided for the seven newly described species.

For indications of ecological context used in the text we have applied the following definitions (Racovitza 1907; Juberthie & Decu 1994; Giachino & Vailati 2010; Ortuño *et al.* 2013; Moldovan *et al.* 2018):

- Hypogean habitats: refers to those found below the surface, as opposed to those above the surface (epigean habitats). Hypogean habitats are always aphotic with less influence from the surface.
- Edaphic habitats: superficial hypogean habitats that extend through the spaces in the soil (A and B horizons) where the edaphic fauna or soil-dwelling fauna live.
- Endogean fauna: animals living in the B horizon of soils, where smaller voids occur.
- Subterranean habitats: deep hypogean habitats extending through a network of spaces (caves) developed in the bedrock, where subterranean or cave-dwelling fauna live.
- Mesovoid Shallow Substratum (MSS): terrestrial habitats in the interstitial mid-size voids below the soil or directly under the surface in colluvial or alluvial environments, inhabited by soil and subterranean fauna and MSS specialized fauna.

Troglobites are cave-adapted fauna living permanently in subterranean habitats, exhibiting similar convergent evolutionary traits (troglomorphisms) such as unpigmented and elongated bodies and appendages, as well as hypertrophy of sensorial organs.

A complete database including the localities where each species has been found was built using our own observations and locality data from an intensive literature review. Locality names and addresses were used to obtain the corresponding GPS coordinates from Google maps using the Import[] function implemented in the Mathematica ver. 11.0 software package (Wolfram Inc., USA). Coordinates obtained from the locality names cited in the literature do not correspond to the exact collecting spot (e.g., cave entrance) in most cases, but rather to the closest town to the sampling site. Distribution maps were built for Plusiocampinae and tachycampoids, genera, subgenera or morphogroups using the GeoListPlot[] function in Mathematica.

The type and studied material is kept at the following institutions:

Coll. AS = private collection of Alberto Sendra, València, Spain  
MZB = Museu de Zoologia de Barcelona, Spain  
PMSL = Slovenian Museum of Natural History, Ljubljana, Slovenia  
ZMMU = Zoological Museum of Moscow University, Moscow, Russia

Other specimens mentioned in [Table S2](#) in Supplementary Material have been used for taxon identification.

## Results

### *Taxonomic characters in Plusiocampinae and tachycampoid genera*

The 10 extant dipluran families differ clearly in morphology, but uniformity prevails within the families and lower taxa. This applies also to Campodeidae and to the subordinate Plusiocampinae and tachycampoids. Interspecific differences in these groups are based mainly on the position of the mechanoreceptor setae (in particular the macrosetae that have a fixed place of insertion), the shape of the pretarsus, including the claws and its outer lateral processes, and the secondary sexual characters of the first urosternite.

### General characters

#### Integument

The cuticle is thin and most species show a smooth epicuticle under the optical microscope, but a reticulate structure is frequently visible using SEM. The surface of the cuticle has microdenticles in a few taxa (e.g., *Tachycampa*; Sendra *et al.* 2016).

Relevant taxonomic characters are the mechanoreceptor setae and other sensorial structures (Condé 1955a; Bareth 1968). The macrosetae, large setae with a discernible base in an upright position, improve the mechanoreceptor function. Macrosetae occupy a fixed position on the body during post-embryonic development (Orelli 1956). They are longer and thicker than ordinary setae, and they have larger bases and usually more barbs. Exceptionally, in very few species macrosetae are substituted by submacrosetae, which are thinner, shorter and less barbed than the typical macrosetae. Apart from macrosetae on appendages, three main macrosetal formulas along the body are also used to characterize most genera and species: the notal, the urotergal and the urosternal formulas (Condé 1955a; Paclt 1957).

Notal macrosetal formula. Macrosetae can occupy six main positions on each notum: *ma* = medial anterior; *la* = lateral anterior; *lp* = lateral posterior; *mp* = medial posterior; *mi* = medial intermediate; and *li* = lateral intermediate. In the groups under consideration here, the pronotum never has less than 4+4 *ma*, *la*, *lp*<sub>2,3</sub> (*ma*, *la*<sub>1,4</sub>, *lp*<sub>3</sub> in *Plusiocampa* (*Stygiocampa*) *christiani* Condé & Bareth, 1996); the mesonotum and metanotum can bear from zero to an astonishingly high number of macrosetae. The South African *Silvestricampa lawrencei* Condé, 1949, for instance, has 10+10 (*ma*, *la*<sub>1-3</sub>, *mi*, *li*, *lp*<sub>1-4</sub>) and 6+6 (*ma*, *mi*, *li*, *lp*<sub>1-3</sub>). In tachycampoids the notal formula is consistently 3+3 (*ma*, *la*, *lp*), 2+2 (*ma*, *la*) and 1+1 (*ma*).

Urotergal macrosetal formula. Macrosetae can occupy two different positions on each urotergite: *post*, posterior and *la*, lateral anterior. Three regions can be distinguished: (1) anterior urotergites with 0+0 to 3+3 *post* and without *la* macrosetae; (2) medial urotergites with up to 6+6 *post* and up to 3+3 *la* macrosetae; and (3) urotergite VIII and adominal segment IX with up to 10+10 *post* macrosetae and without *la* macrosetae.

Urosternites usually have short, well-barbed macrosetae. Three urosternal regions can be distinguished: (1) urosternite I frequently with 7+7–8+8 to numerous extra macrosetae (up to about sixty in total); (2) urosternites II–VII with 5+5 up to 14+14 macrosetae; and (3) urosternite VIII with 1+1 to up to 4+4 macrosetae.

Macrosetae on appendages. The most relevant characters to differentiate species and subgenera are the number of dorsal femoral macrosetae, from 0 to 5; the number of short ventral tibial macrosetae, from 0 to 4; and the long or short, more or less barbed cercal macrosetae.

Stylus setae and the calcars on the tibiae show differences in the degree of barbulation and may also be used in taxonomy, together with the eversible vesicles observed under the SEM.

Sensillum of the third antennomere. One (exceptionally three) isolated subcylindrical to spheroidal sensillum can occupy two main positions (dorsal and ventral) among the crown of macrosetae, which encircle the third antennomere. To determine the position of this sensory organ, the macrosetae are named as *a* macrosetae between the two trichobothria, as *b* macrosetae when situated on the exterior side, and as *c*, *d* and *e* when they continue on up to the crown macrosetae (Condé 1955a).

Cupuliform organ. This sensory organ is an invagination of the integument at the end of the apical antennomere crammed with olfactory chemoreceptors (Juberthie-Jupeau & Bareth 1980). These increase in number and shape complexity in subterranean species, reaching a remarkable diversity (Sendra *et al.* 2017a).

Gouge sensilla (Bareth & Condé 1981). These are situated in an apical whorl on medial and distal antennomeres and show a slight variability of forms. Nevertheless, their taxonomical value has not yet been explored.

### **Pretarsus**

The shape of the distal structure of the tarsus, with two claws and usually each with an outer lateral process, has been used to define genera. The main claw types are: (1) the more frequent, elbow-like claws, with lateral crests; (2) less frequent, subequal smooth claws, regularly curved without lateral crests, found in *Silvestricampa* and *Jeannelicampa*; and (3) elbow-like claws with a sharp side-shoot, as in *Turkmenocampa*. The lateral processes are also taken into account for generic delimitation; they vary from setiform to laminar and with or without short to long pubescence or dense barbs.

### **Sexual characters**

Secondary sex characteristics are present on the first urosternite: the shape of the posterior border and appendages, and the number and type of glandular setae. A complete area of glandular  $g_1$  setae along the posterior border is frequently present in males and exceptionally in females (Sendra & Weber 2018). The appendages of the first urosternite are generally subcylindrical in females, while they are enlarged in males. Both sexes have glandular  $a_1$  setae, and glandular  $a_2$  setae can be present in males and less frequently in females.

Spermatozoid fascicles, a packed group of spermatozoons in a spiral structure, are produced by a pair of testicles located in the abdomen of the male. These spirals can vary in length, size and shape, but are usually short and thick in Plusiocampinae (Bareth 1968).

## Taxonomy of *Plusiocampinae* Paclt, 1957

Class Diplura Börner, 1904  
Family Campodeidae Meinert, 1865  
Subfamily *Plusiocampinae* Paclt, 1957

*Plusiocampinae* Paclt, 1957: 42.

### Diagnosis (Condé 1955a; Paclt 1957; Sendra *et al.* 2017a)

Since the only diagnostic character of *Plusiocampinae* (as suggested by Paclt 1957) is the higher number of macrosetae on the pronotum, this taxon seems to be paraphyletic. The pronotum never has less than 4+4 macrosetae. However, many of the genera can be considered monophyletic within *Plusiocampinae*. This is the case for *Anisuracampa*, *Cestocampa*, *Condeicampa*, *Hystrichocampa*, *Patrizicampa*, *Plusiocampa*, *Plutocampa*, *Simlacampa* and *Vandelicampa*, characterized by pretarsal lateral crests. Nonetheless, these lateral crests are absent in *Silvestricampa* and *Turkmenocampa*, clearly isolating them from the other genera.

### Key to the genera of *Plusiocampinae*

1. Pretarsal claws with lateral crests .....2  
– Pretarsal claws without lateral crests .....7
2. Pretarsal lateral processes setiform .....3  
– Pretarsal lateral processes laminar barbed or absent .....5
3. Pretarsal lateral processes pubescent .....*Hystrichocampa* Condé, 1948  
– Pretarsal lateral process smooth .....4
4. 4+4 macrosetae on urosternites II–VII, 1+1 macrosetae on urosternite VIII .....  
.....*Condeicampa* Ferguson, 1996 and *Plusiocampa (Dydimocampa) sinensis* Silvestri, 1931  
– No less than 5+5 macrosetae on urosternites II–VII and 2+2 macrosetae on urosternite VIII .....  
.....*Plusiocampa* Silvestri, 1912
5. Pretarsal lateral processes absent .....*Plutocampa* Chevrizov, 1978  
– Pretarsal lateral processes laminar barbed .....6
6. Pretarsal lateral processes laminar .....*Cestocampa* Condé, 1955,  
*Vandelicampa* Condé, 1955, *Patrizicampa* Condé, 1956, *Anisuracampa* Xie & Yang, 1991,  
*Plusiocampa (Didymocampa) lipsae* Condé, 1993 and *Plusiocampa kashiensis* (Chou & Tong, 1980)  
– Pretarsal lateral processes narrow .....*Simlacampa* Condé, 1956
7. Simple claws; pretarsal lateral processes absent, medial-intermediate and lateral-intermediate  
macrosetae on mesonotum and metanotum .....*Silvestricampa* Condé, 1950  
– Pretarsal claws with sharp side-shoot; pretarsal lateral processes laminar, without medial posterior  
macrosetae on mesonotum and metanotum .....*Turkmenocampa* Sendra & Stoev, 2017

This key includes 11 accepted genera plus three species, *Plusiocampa (Dydimocampa) sinensis*, *Plusiocampa (Dydimocampa) lipsae* and *Plusiocampa kashiensis* from China, which remain in an uncertain position (Sendra *et al.* 2012a). Three new troglomorphic genera from China, Indochina and the Aegean islands, which are currently under description (Sendra, in prep.), are excluded.



*Cestocampa* Condé, 1955

*Cestocampa* Condé, 1955a: 132.

**Diagnosis** (Condé 1955a; Sendra *et al.* 2012a)

Non-protruding frontal process with non-tubercular setae. Mesonotum with 1+1 medial anterior, 3+3 lateral anterior and 2+2 lateral posterior macrosetae; metanotum with 1+1 medial anterior, 2+2 lateral anterior and 2+2 lateral posterior macrosetae. With or without medial posterior notal macrosetae. One dorsal femoral macroseta. Two to three ventral tibial macrosetae. Subequal elbow-like claws, posterior claw equal (1.0) to subequal (1.1) to anterior claw. Laminar pretarsal lateral processes with long, rigid, ventral hook-tipped barbs. Urotergites I–II with 1+1–2+2 posterior macrosetae; urotergite III with 2+2–4+4 posterior macrosetae; urotergites VI–VII with 3+3 lateral anterior and 5+5 posterior macrosetae. Urosternite I with 7+7 (15+15 in *C. iberica* Sendra & Condé, 2012), urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Males without  $g_1$  glandular setae but with  $a_2$  glandular setae on first urosternite appendages. Females with subcylindrical appendages with  $a_1$  glandular setae.

**Habitat and distribution**

Two of the four species of *Cestocampa* occupy the subterranean habitat in caves from the south of the Italian Peninsula (*C. gasparoi* Bareth, 1988) and the east of the Iberian Peninsula (*C. iberica*). The other two are soil-dwelling species (*C. italica* (Silvestri, 1912) and *C. balcanica* Condé, 1986) that have been reported from the Italian Peninsula and Dinaric Mountains (Fig. 210).

**Key to the species of *Cestocampa***

1. 1+1 medial posterior mesonotal and metanotal macrosetae .....2  
 – Without medial posterior mesonotal and metanotal macrosetae .....3
2. 1+1 posterior macrosetae on urotergite I; 2+2 posterior macrosetae on urotergite II; 5+5 posterior macrosetae on urotergite IV; 6+6 macrosetae on urosternite I .....*Cestocampa balcanica* Condé, 1955  
 – Without posterior macrosetae on urotergites I–II; 4+4 posterior macrosetae on urotergite IV; 15+15 macrosetae on urosternite I .....*Cestocampa iberica* Sendra & Condé, 2012
3. 2+2 posterior macrosetae on urotergite I; 4+4 posterior macrosetae on urotergite III; 2+2 lateral anterior macrosetae on urotergite IV; 3+3 lateral anterior macrosetae on urotergite V .....*Cestocampa italica* (Silvestri, 1912)  
 – 1+1 posterior macrosetae on urotergite I; 2+2 posterior macrosetae on urotergite III; 1+1 lateral anterior macrosetae on urotergite IV; 2+2 lateral anterior macrosetae on urotergite V .....*Cestocampa gasparoi* Bareth, 1988

*Cestocampa balcanica* Condé, 1955

*Cestocampa balcanica* Condé, 1955: 57.

**Diagnosis** (Condé 1955a; Sendra *et al.* 2012a)

Non-troglophic species. With 25 antennomeres in a regenerated antenna; frontal process with non-tubercular setae. Pronotum with 1+1  $ma$ , 2+2  $la$ , 2+2  $lp$  macrosetae; mesonotum with 1+1  $ma$ , 3+3  $la$ , 2+2  $lp$ , 1+1  $mp$  macrosetae; metanotum with 1+1  $ma$ , 2+2  $la$ , 2+2  $lp$ , 1+1  $mp$  macrosetae; long, barbed notal macrosetae; sparse smooth notal clothing setae. Two ventral tibial macrosetae; subequal small claws (1.03) with small lateral crests, posterior claw without a backward overhang. Urotergite I with 1+1  $post$  macrosetae; urotergites II–III with 2+2  $post$  macrosetae; urotergite IV with 1+1  $la$ , 5+5

*post* macrosetae; urotergite V with 2+2 (2+1) *la*, 5+5 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 (8+7) *post* macrosetae; urosternite I with 7+1+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female subcylindrical appendages with  $a_1$  glandular setae.

#### Habitat and distribution

Soil-dwelling species found in two remote localities, the type locality in Rabitlje, south-eastern Dinaric Mountains, and on Monti Aurunci, Lazio, central Italian Peninsula.

#### *Cestocampa gasparoi* Bareth, 1988

*Cestocampa gasparoi* Bareth, 1988: 49, fig 3a–f.

#### Diagnosis (Bareth 1988)

Troglomorphic species. Antennae with 27–29 antennomeres (perhaps regenerated); 12–13 simple olfactory chemoreceptors in cupuliform organ; frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3–4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; notal setal clothing sparse, long, smooth or with two apical barbs. Two ventral tibial macrosetae; subequal small claws with small lateral crests, posterior claw without a backward overhang. Urotergite I with 1+1 *post* macrosetae; urotergite II with 1+2 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergite V with 2+2 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae, enlarged subcylindrical appendages with thin and long glandular  $a_2$  setae. Spermatozoid fascicle wheels with 2½ turns of 350 µm long and 8 µm wide filament. Female unknown.

#### Habitat and distribution

Subterranean species found in Grotta Superiore di Sant'Angelo Calabria, south Italian Peninsula.

#### *Cestocampa iberica* Sendra & Condé, 2012

*Cestocampa iberica* Sendra & Condé in Sendra *et al.*, 2012a: 47, figs 2–3.

#### Diagnosis (Sendra *et al.* 2012a)

Troglomorphic species. Antennae with 34–41 antennomeres; 8–10 complex olfactory chemoreceptors in cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; middle-sized, barbed notal macrosetae; notal clothing setae sparse, smooth or with thin distal barbs. Two or three ventral tibial macrosetae; subequal claws (1.05–1.10) with large lateral crests, posterior claw without a backward overhang. Urotergite I with 1+1 *post* macrosetae; urotergite II with 2+2 *post* macrosetae; urotergite III with 1+1 *la*, 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 4+4 *post* macrosetae; urotergites V–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae; abdominal segment IX with 9+9 *post* macrosetae; urosternite I with 15+15, urosternites II–VII with 5+5, urotergite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae, enlarged subcylindrical appendages with glandular  $a_2$  setae; female with subcylindrical appendages with glandular  $a_1$  setae. Spermatozoid fascicle wheels with 1½ turns of 70–90 µm long and 4–5 µm wide filament.

### Habitat and distribution

Subterranean species found in 11 caves around the Castilian-Valencian Branch of the Iberian Mountain Range and its border with the northwest of the Pre-Baetic Mountains, eastern Iberian Peninsula.

#### *Cestocampa italica* (Silvestri, 1912)

*Plusiocampa italica* Silvestri, 1912: 145, fig. xxx.

### Diagnosis (Silvestri 1912; Condé 1955a)

Non-trogomorphic species. Antennae with 22 antennomeres. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae. Two ventral tibial macrosetae; subequal small claws with small lateral crests, posterior claw without a backward overhang. Urotergites I–II with 2+2 *post* macrosetae; urotergite III with 4+4 *post* macrosetae; urotergite IV with 2+2 *la*, 5+5 *post* macrosetae; urotergites V–VII with 3+3 *la*, 5+5 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae and slightly enlarged appendages.

### Habitat and distribution

Soil-dwelling species known from the type locality in Strongoli, Calabria, southern Italian Peninsula, and northern Macedonia.

#### *Hystrichocampa* Condé, 1948

*Hystrichocampa* Condé, 1948a: 5.

### Diagnosis

Mesonotum and metanotum with medial posterior macrosetae. Five dorsal femoral macrosetae; one or two ventral and two dorsal tibial macrosetae. Unequal, elbow-like claws. Thick, subcylindrical, setiform, pubescent lateral process of pretarsus. Urotergites with up to 3+3 lateral anterior and 5+5 posterior macrosetae.

#### *Hystrichocampa pelletieri* Condé, 1948

*Hystrichocampa pelletieri* Condé, 1948a: 5, fig. 2.

### Diagnosis (Condé 1948a, 1955a; Bareth 1968, 2006)

Trogomorphic species. Antennae with 31–36 antennomeres; 8 to 10 olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; sparse long, thin clothing setae. Unequal, elbow-like claws (1.2) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 4+4 *post* macrosetae; urotergite V with 2+2 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with glandular *g*<sub>1</sub> setae, enlarged subcylindrical appendages with glandular *a*<sub>1</sub> setae; female subcylindrical appendages with glandular *a*<sub>1</sub> setae. Spermatozoid fascicles 57–80 µm in diameter and 7–9 µm in width; wheels with 1½ turns of 150–200 µm long and 7–8 µm thick filament.

### Habitat and distribution

Subterranean species widespread in the Jura karst mountains between France and Switzerland, where it is found in 18 caves (Fig. 210).

### *Patrizicampa* Condé, 1962

*Patrizicampa* Condé, 1962: 199.

### Diagnosis (Condé 1962)

Without dorsal femoral macrosetae or ventral tibial macrosetae; abundant macrosetae on all urosternites, including 3+3 macrosetae on urosternite VIII. Its apomorphic feature, the shape of the laminar pretarsal lateral process, is unique among diplurans. It starts with a large laminar lateral process, well barbed on the ventral side and ending in a thin, smooth, pointed process.

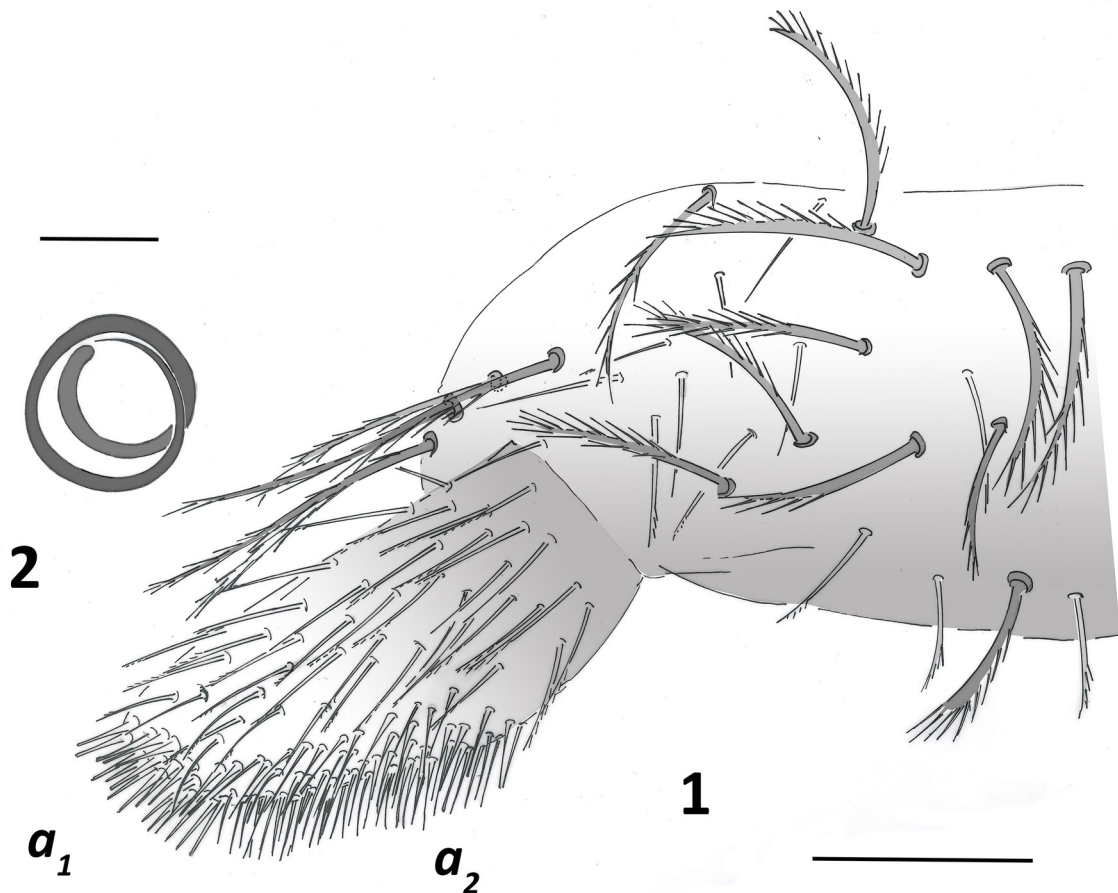
### *Patrizicampa sardoa* Condé, 1962

Figs 1–2

*Patrizicampa sardoa* Condé, 1962: 199, figs a–b.

### Diagnosis (Condé 1962)

Troglomorphic species. Cupuliform organ with 10–14 complex olfactory chemoreceptors. Protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum



**Figs 1–2.** *Patrizicampa sardoa* Condé, 1956, 5 mm long ♂, from Murgulavó Cave, Sardinia (Coll. AS). 1. First urosternite, right side. 2. Spiral filament. Scale bars: 20 µm.

with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; long clothing setae covered with thin barbs. Subequal elbow-like claws (1.1) with large lateral crests, posterior claw with a backward overhang. Urotergite III with 1+1 *la*, 0+0–1+1 *post* macrosetae; urotergite IV with 2+2 *la*, 1+1–3+3 *post* macrosetae; urotergite V with 2+2–3+3 *la*, 2+2–4+4 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8–8+9 *post* macrosetae. Urosternite I with 15+15–16+16, urosternites II–VII with 7+7–8+8, urosternite VIII with 3+3 macrosetae. Male without glandular *g*<sub>1</sub> setae, slightly subtrapezoidal appendages with glandular *a*<sub>1</sub> and *a*<sub>2</sub> setae; females with subcylindrical appendages and an apical area with glandular *a*<sub>1</sub> setae.

#### Remarks (Figs 1–2)

The study of many specimens collected in 6 new caves (see Table S2 in Supplementary Material) allowed us to complete Condé's diagnosis, as well as to supplement it with some minor taxonomic details. Medial antennomeres with 10–12 gouge sensilla 40–50 µm long. End of metathoracic leg reaches end of abdomen; calcaria covered with barbs; subapical setae with thin barbs almost from base up to two-thirds of length. Stylus with an apical seta with a few thin barbs and a large, thick basal tooth, medial and subapical setae covered with thin barbs. Male appendages with up to 60 glandular *a*<sub>2</sub> setae and 20 *a*<sub>1</sub> glandular setae (Fig. 1); female appendages with up to 18 *a*<sub>1</sub> glandular setae. Spermatozoid fascicle wheels with 2 turns of 140–160 µm long and up to 4 µm wide filament (Fig. 2).

#### Habitat and distribution

Subterranean species found in eight caves in eastern Sardinia (Fig. 210).

#### *Plusiocampa* Silvestri, 1912

*Plusiocampa* Silvestri, 1912: 141.

#### Diagnosis (Silvestri 1912; Condé 1955a; Sendra & Weber 2018)

Apparently smooth epicuticle, usually reticulated at high magnification, rosetta pores absent. Head with a frontal process with or without tuberculate setae. In non-trogloform species, cupuliform organ with four or five spheroidal olfactory chemoreceptors with polygonal net, with pore surface made by at least one cup-shaped fold and a central structure ending in a terminal pore. In troglobiiform species, spheroidal olfactory chemoreceptor with more folds in spiral, radial or other complex shape and a more visible polygonal net with pore surface. Sensillum of third antennomere in ventral position. Meso- and metathorax with a few macrosetae but frequently with medial anterior, lateral anterior, lateral posterior and medial posterior (exceptionally medial intermediate and lateral intermediate) macrosetae. Femur with one to five dorsal macrosetae; tibia with one to three ventral macrosetae. Elbow-like claws with usually large lateral crests and setiform lateral processes, rarely with a few barbs on proximal part. Abdomen with lateral anterior and posterior macrosetae and never with medial anterior macrosetae. Sternal macrosetae: sternite I with 6+6 up to 60 macrosetae; sternites II–VII with 4+4 up to 14+14 macrosetae; sternite VIII with 2+2 up to 4+4 macrosetae. Secondary sexual differences in shape of first urosternite appendages and number of glandular setae.

#### Habitat and distribution

This is the most diverse genus of Plusiocampinae, with a clear preference for the subterranean ecosystems (Condé 1955a; Sendra & Weber 2018). It has 72 species (including the seven new ones described here) and 10 subspecies, distributed around the Mediterranean Basin (Figs 210–211). The exceptions are three Chinese species considered representatives of *Plusiocampa* by Silvestri (1931a), Condé (1993a) and Sendra *et al.* (2012a): *P. sinensis* Silvestri, 1931, *P. lipsae* Condé, 1993 and *P. kashiensis* Chou & Tong,

1980. Nevertheless, these species must be removed from *Plusiocampa* due to the macrosetal formula on urosternites II to VIII.

**Key to the subgenera and species of *Plusiocampa***

The genus *Plusiocampa* has been divided into four subgenera based on two characters: the presence of the femoral dorsal macrosetae (Condé 1955a; Paclt 1957; Sendra & Weber 2018) and the number of tibial ventral macrosetae (Bareth & Condé 1984). Based on these synapomorphies and other characters, the following taxonomic key is proposed for the current five subgenera and 69 species.

1. Femoral macrosetae absent .....2  
 – Femoral macrosetae present .....7
2. Lateral posterior mesonotal macrosetae absent .....  
 .....*Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996  
 – Lateral posterior mesonotal macrosetae present .....3
3. 2+2 lateral posterior mesonotal macrosetae .....4  
 – 1+1 lateral posterior mesonotal macrosetae .....6
4. Lateral expansions on posterior side of first urosternite absent in adult males; males without  $g_1$  glandular setae; urosternal appendages in adult males enlarged, thick and subcylindrical .....  
 .....*Plusiocampa (Stygiocampa) nivea* (Joseph, 1882)  
 – Lateral expansions on posterior side of first urosternite present in adult males; males with  $g_1$  glandular setae; urosternal appendages in males subcylindrical .....5
5. 1+1 medial anterior mesonotal and metanotal macrosetae; 2+2 lateral anterior mesonotal macrosetae; 1+1 lateral anterior metanotal macrosetae .....  
 .....*Plusiocampa (Stygiocampa) dalmatica* Condé, 1959  
 – Medial anterior mesonotal and metanotal macrosetae absent; 1+1 lateral anterior mesonotal macrosetae; lateral anterior metanotal macrosetae absent .....  
 .....*Plusiocampa (Stygiocampa) remyi* Condé, 1947
6. 2 ventral tibial macrosetae; unequal pretarsal claws (1.2–1.6); males with  $g_1$  glandular setae; urosternal appendages in adult males subcylindrical .....  
 .....*Plusiocampa (Stygiocampa) denisi* Condé, 1947  
 – Ventral tibial macrosetae absent; slightly unequal pretarsal claws (1.1–1.2); males without  $g_1$  glandular setae; urosternal appendages in adult males enlarged and subcylindrical .....  
 .....*Plusiocampa (Stygiocampa) bureschi* Silvestri, 1931
7. 5 dorsal femoral macrosetae .....  
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– Urosternal appendages in adult females subcylindrical; olfactory chemoreceptors simple .....	
..... <i>Plusiocampa (Plusiocampa) djurdjurae</i> Condé, 1984	
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– Medial anterior metanotal macrosetae absent; 4+4 posterior macrosetae on urotergites VI–VII; 5+5 posterior macrosetae on urotergite VIII .... <i>Plusiocampa (Plusiocampa) hoelzeli</i> (Neuherz, 1984)	
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 – Urosternal appendages in adult males subcylindrical; 6+6 posterior macrosetae on urotergite VIII;  
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 – 1+1 lateral anterior metanotal macrosetae; 4+4 posterior macrosetae on urotergites VI–VII;  
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Subgenus *Dydimocampa* Paclt, 1957

*Dydimocampa* Paclt, 1957: 46.

**Diagnosis** (Paclt 1957; Condé 1996)

*Dydimocampa* shares with *Plusiocampa* s. str. the same taxonomic features, with the exception of the two dorsal femoral macrosetae. This fact, together with their distribution patterns, suggests that

*Dydimocampa* is an artificial subgenus based on a single apomorphic feature that has probably appeared several times in *Plusiocampa* s. str.

#### **Habitat and distribution**

The three species treated here are cave-dwellers with a subterranean life-style and they are distributed in three disjunct karst areas in Europe (Fig. 211).

#### ***Plusiocampa (Dydimocampa) alhamae* Condé & Sendra, 1989**

*Plusiocampa alhamae* Condé & Sendra, 1989: 612, figs 1–3, tables 1–3.

#### **Diagnosis** (Condé & Sendra 1989)

Troglomorphic species. Antennae with 35–40 antennomeres; up to 17 digitiform complex olfactory chemoreceptors on cupuliform organ; slightly protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae with thin barbs; sparse long, barbed notal clothing setae. Two to four ventral tibial macrosetae, femur/tibia ratio 0.69; subequal, elbow-like claws with large lateral crests, posterior claw with a small backward overhang; long lateral process. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 0+0–1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2–4+4 *post* macrosetae; urotergite V with 1+1 *la*, 4+4–5+5 *post* macrosetae; urotergites VI–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with up to 8+8 macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular *g*<sub>7</sub> setae, subcylindrical appendages with glandular *a*<sub>7</sub> setae; female appendages like male appendages. Spermatozoid fascicle wheels with 1½ turns of 100–140 µm long and 2 µm wide filament.

#### **Habitat and distribution**

Troglomorphic species found in four caves around the Sub-Baetic Interior Mountain Range, from Antequera (Málaga) to Sierra María (Almería), southern Iberian Peninsula.

#### ***Plusiocampa (Dydimocampa) euxina* Condé, 1996**

*Plusiocampa euxina* Condé, 1996: 102, figs 1–6.

#### **Diagnosis** (Condé 1996)

Troglomorphic species. Antennae with 44–45 antennomeres; eight to ten complex olfactory chemoreceptors in cupuliform organ; slightly protruding frontal process with a few anterior tubercular setae. Pronotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+2 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; sparse short, smooth notal clothing setae. Three ventral tibial macrosetae; unequal claws (1.25) with large lateral crests, posterior claw with a small backward overhang; short lateral processes. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 4+4 *post* macrosetae; urotergite V with 2+2 *la*, 4+4 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 9+9 *post* macrosetae; urosternite I with 8+7, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>7</sub> setae, enlarged subcylindrical appendages with a large area of glandular *a*<sub>7</sub> setae; adult female unknown.

#### **Habitat and distribution**

Subterranean species inhabiting the Movile Cave, Southern Dubrudja, Romania.

**Table 1.** *Plusiocampa (Dydimocampa) evallonychia* Silvestri, 1949. Length of the body, antennae, metathoracic legs and cerci (measurements in mm), in addition to the number of antennomeres and cercal articles.

Specimens (Coll. AS)	Body length	No. of antennomeres	Antenna length	Metathoracic leg length	No. of cercal articles	Cercus length
juv., Mamut-Tshokarak Cave	3.45	40	3.10	1.8	–	–
♀, Mamut-Tshokarak Cave	4.9	35	5.3	3.3	base + 6	9.20
♀, Kuban Cave	5.2	–	–	2.95	–	–
♀, Nassonova Cave	5.3	34	4.3	–	–	–

*Plusiocampa (Dydimocampa) evallonychia* Silvestri, 1949

Figs 3–8; Table 1

*Plusiocampa evallonychia* Silvestri, 1949: 29, figs ii–iii.

**Diagnosis** (Silvestri 1949; Condé 1996)

Troglomorphic species. Antennae with 33 antennomeres. Protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *lp* macrosetae; long, barbed macrosetae. Two ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang; short lateral anterior process and long lateral posterior process. Urotergites I–III with 1+1 *post* macrosetae; urotergites IV–VI with 1+1 *la*, 2+2 *post* macrosetae; urotergite VII with 1+1 *la*, 5+5 *post* macrosetae. Urosternite I with 7+7, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male unknown; female with subcylindrical appendages with glandular *a*<sub>1</sub> setae.

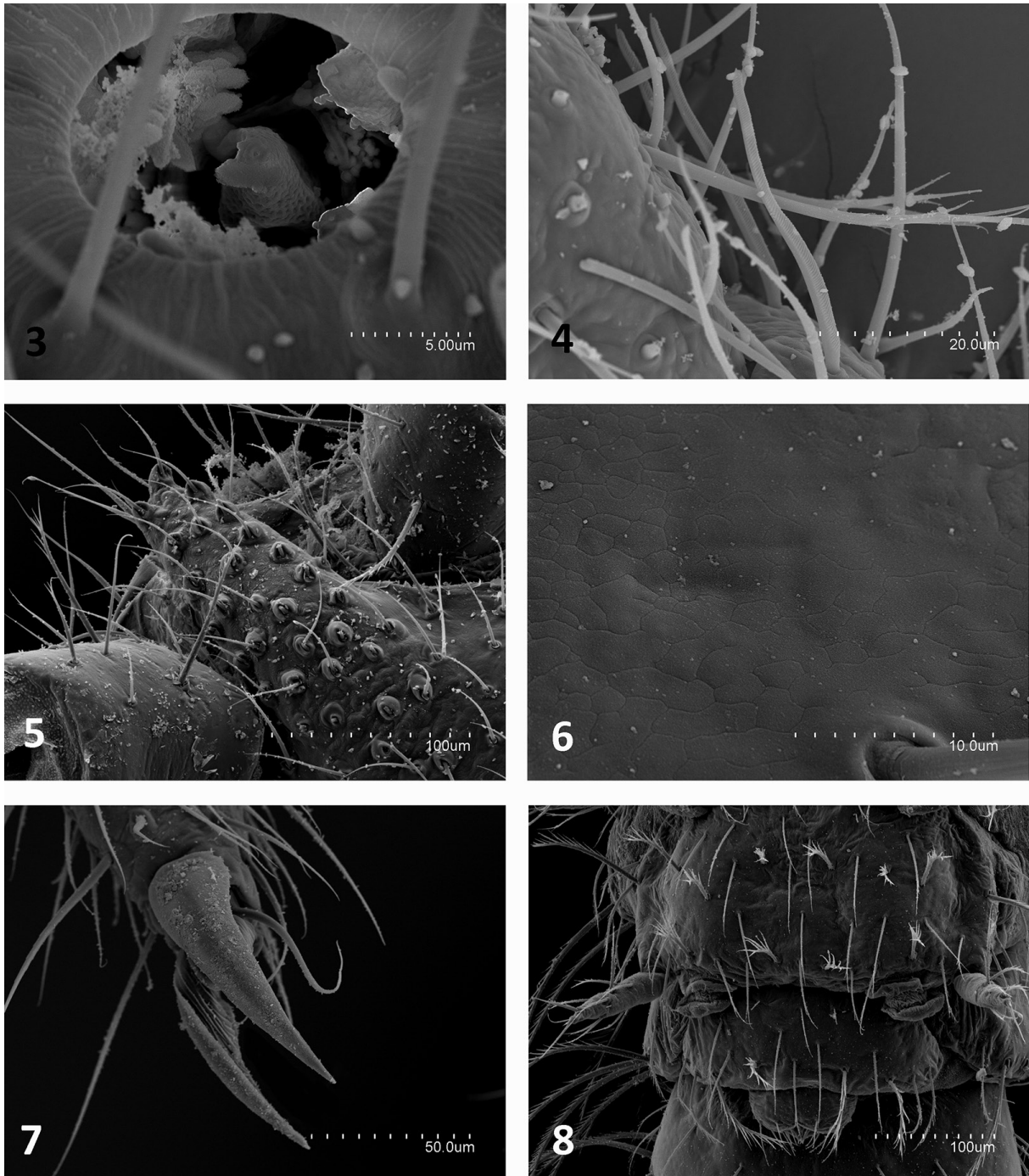
**Remarks**

The study of four specimens, a juvenile and 3 females, collected in three caves (see Table S2 in Supplementary Material) allowed a comparison with the species description, but new topotype material is needed to clarify the taxonomic status of this species (Table 1). The epicuticle of dorsal sclerites is reticulate when observed in high magnification (Fig. 6). Antennae with 34 and 35 antennomeres in two adults, and 40 in the juvenile; adult medial antennomeres 1.6× as long as wide, apical antennomere 2.5× as long as wide; one distal whorl with 20–22 gouge sensilla in each medial and distal antennomere, 36–38 μm in length (Fig. 4). Cupuliform organ occupies 1/5 of total length of last antennomere, with more than ten spheroidal olfactory chemoreceptors with a central column unfolded in complex expansions with a visible polygonal net with porous surface (Fig. 3). Protruding frontal process with abundant tubercular setae (Fig. 5). Pronotum with 3+3 *la* macrosetae (2+2 *la* in original description). Unequal claws (1.4–1.5) with large lateral crests (Fig. 7), posterior claw with a large backward overhang; short lateral anterior pretarsal processes, less than half length of claw, and long lateral posterior pretarsal anterior process overpassing end of claw, as described in type form. Calcars with two rows of long barbs almost from base; smooth subapical tarsal setae. Urotergites with important differences from type form: 2+2 (3+2) *la* and 4+4–5+5 *post* on urotergites VI–VII; 6+6 *post* on urotergite VII; 9+9 *post* macrosetae on abdominal segment IX (undescribed in type form). Styler setae with a few long, thin barbs. Urosternite I with 7+7, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae (Fig. 8). Cerci 1.9× as long as body, with only 6 articles plus base.

**Habitat and distribution**

Subterranean species found in four caves, including the type locality in the I-El Koba (= Kizil-Koba, Krasnaya) Cave in the Crimean Mountains. The occurrence of such a distribution for *P. (D.) evallonychia*

in the currently unrelated isolated karst regions of the Crimean Mountains is probably associated with the recent colonization of the caves by the edaphic form of this species in the Würm glacial stage. Such a recent isolation of the populations of this species might explain the absence of differences between them.



**Figs 3–8.** *Plusiocampa (Dydimocampa) evallonychia* Silvestri, 1949, from Mamut-Tshokrak Cave, Baidarsko-Balaklavsky karst massif, Crimean Peninsula (Coll. AS). **3.** Cupuliform organ. **4.** Lateral side of a middle antennomere with several gouge sensilla. **5.** Frontal process. **6.** Surface of metanotum. **7.** Metathoracic claws. **8.** Urosternites VII–IX.

Subgenus *Pentachaetocampa* Sendra & Weber, 2018

*Pentachaetocampa* Sendra & Weber, 2018: 3.

**Diagnosis** (Sendra & Weber 2018)

Mesothoracic and metathoracic femora with five dorsal macrosetae, up to three on prothoracic femur; presence of a narrow area of glandular  $g_1$  setae in adult females.

*Plusiocampa (Pentachaetocampa) inopinata* Sendra & Weber, 2018

*Plusiocampa (Pentachaetocampa) inopinata* Sendra & Weber, 2018: 5, figs 1–17, table 1.

**Diagnosis** (Sendra & Weber 2018)

Troglomorphic species. Sparse thin and long clothing notal setae with thin barbs. Antennae in adults with 32–33 antennomeres. Cupuliform organ with 12–14 complex olfactory chemoreceptors. Frontal process developed, with slightly tubercular setae and macrosetae. Pronotum with 1+1  $ma$ , 4+4  $la$ , 2+2  $lp$  macrosetae; mesonotum with 1+1  $ma$ , 3+3  $la$ , 2+2  $lp$ , 1+1  $mp$  macrosetae; metanotum with 1+1  $ma$ , 1+1  $la$ , 2+2  $lp$ , 1+1  $mp$  macrosetae; long, thin macrosetae, with very thin barbs; subequal to slightly unequal claws (posterior claw 1.05–1.15) with large lateral crests; posterior claw with backward overhang; pretarsal lateral process long, smooth and setiform with several short proximal barbs. Urotergites I–II with 1+1  $post_1$  macrosetae; urotergite III with 1+1  $la$ , 1+1  $post$  macrosetae; urotergite IV with 1+1  $la$ , 2+2 (3+2, 3+3)  $post$  macrosetae; urotergites V–VII with 1+1  $la$ , 5+5  $post$  macrosetae; urotergite VIII with 6+6 (5+6, 5+5)  $post$  macrosetae; abdominal segment IX with 8+8 (8+7)  $post$  macrosetae. Urosternite I with 7+7 (7+6), urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a narrow area with glandular  $g_1$  setae, enlarged subcylindrical appendages with glandular  $a_1$  setae; female with glandular  $g_1$  setae with subcylindrical appendages, thinner than in male.

**Habitat and distribution**

Monotypic subgenus known only from a single cave in southwest Germany (Fig. 211).

Subgenus *Plusiocampa* s. str. Silvestri, 1912

**Diagnosis** (Silvestri 1912; Condé 1955a; Sendra & Weber 2018)

Lateral crests on claws from small to large, with subequal to very unequal, elbow-like claws; one dorsal femoral; from one to four ventral tibial macrosetae; setiform and smooth (in several species with a few proximal barbs) pretarsal lateral processes. Sternite I with 6+6–9+9, sternites II–VII with 4+4–7+7 and sternite VIII with 2+2 macrosetae (with the exception of *P. (P.) dargilani*). Cerci elongated, with long articles covered in long, thin macrosetae with thin barbs and thin, smooth clothing setae.

**Habitat and distribution**

Within humid soils and MSS, but with a preference for the deep subterranean spaces found in caves, including the deepest caves in the world. The 60 species and 9 subspecies of this subgenus are well-spread around the Euro-Mediterranean region, from Southern Europe, including a small karst area in North Africa (Kabylian Mountains, Tell Atlas), throughout south of Central to Southeastern Europe and also reaching some spots in the Anatolian and Crimean peninsulas and Western Caucasus (Fig. 211).

*Plusiocampa (Plusiocampa) affinis* Condé, 1947

*Plusiocampa affinis* Condé, 1947a: 25, fig. 4.



**Diagnosis** (Condé 1947a)

Non-troglophic species. Antennae with 23–26 antennomeres. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; smooth or distally barbed notal clothing setae. Two ventral tibial macrosetae; unequal claws (1.30) with large lateral crests, posterior claw with backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular *g*<sub>1</sub> setae, subcylindrical appendages with glandular *a*<sub>1</sub> setae; female appendages like male appendages.

**Habitat and distribution**

This species is only known from Županska pećina, Lubnice, Berane Municipality, Montenegro.

*Plusiocampa (Plusiocampa) apollo* Sendra, Giachino & Vailati sp. nov.

[urn:lsid:zoobank.org:act:6B496C95-E094-4688-BE14-60BDDE1105C8](https://zoobank.org/act:6B496C95-E094-4688-BE14-60BDDE1105C8)

Figs 9–11; Table 2

**Etymology**

The specific name ‘apollo’ is proposed since the Parnassos Mountain, its type locality, is the home of the divinity ‘Apollo’.

**Material examined****Holotype**

GREECE • 1 ♀; Viotia, O. Parnassós, crevices; 1660 m a.s.l.; 20 Jun. 2004–9 Jun. 2005; Pier Mauro Giachino and Dante Vailati leg.; MSS habitat; pitfall trap; MZB 2019-1032.

**Paratypes**

GREECE • 4 ♀♀; same collection data as for holotype; Coll. AS • 9 ♂♂, 18 ♀♀; Fokída, Ori Vardoússia; 1575 m a.s.l.; 10 Jun. 2005–8 Jun. 2006; Pier Mauro Giachino and Dante Vailati leg.; MSS habitat; pitfall trap; Coll. AS.

**Description**

**BODY.** Body length 4.5 to 6.1 mm (females) and 5.0 to 6.4 mm (males). Epicuticle smooth under optical microscope; body with thin, middle-sized clothing, covered or not by a few thin barbs.

**HEAD.** Two intact antennae in a 5.6 mm long female paratype with 28 antennomeres and a 5.1 mm long female paratype with 32 antennomeres, in both shorter than body length (Table 2). Small subcylindrical sensillum of third antennomere located in ventral position between *c* and *d* macrosetae. Central antennomeres 1.8× as long as wide, apical antennomere 2.0× as long as wide. Cupuliform organ occupying ¼ of total length of apical antennomere, with 8–9 complex olfactory chemoreceptors. Gouge sensilla 30–38 µm long, in a single distal whorl of 16–18 sensilla on each medial and distal antennomere. Frontal process plain, with non-tubercular setae and macrosetae with a few barbs along distal half; macrosetae along line of insertion of antennomere and *x* setae longer than other macrosetae (*a/i/p/x* with relative lengths of 40/48/37/68 in holotype). Suboval labial palps with a small, coniform latero-external sensillum, with two guard setae, up to 9 setae on anterior border and up to 190 neuroglandular setae.

**Table 2.** *Plusiocampa (Plusiocampa) apollo* Sendra, Giachino & Vailati sp. nov. Length of the body, antennae and metathoracic legs (measurements in mm), in addition to the number of antennomeres.

Specimen	Body length	Antennae		
		No. of antennomeres	Length	Metathoracic leg length
♀, paratype (Coll. AS)	4.5	–	–	2.3
♀, paratype (Coll. AS)	4.7	–	–	2.5
♂, holotype (MZB 2019-1032)	4.8	–	–	2.6
♀, paratype (Coll. AS)	5.0	–	–	2.7
♀, paratype (Coll. AS)	5.0	–	–	2.6
♀, paratype (Coll. AS)	5.1	32	3.7	2.4
♀, paratype (Coll. AS)	5.6	28	3.1	2.8
♂, paratype (Coll. AS)	6.2	–	–	2.8
♂, paratype (Coll. AS)	6.4	–	–	3.2

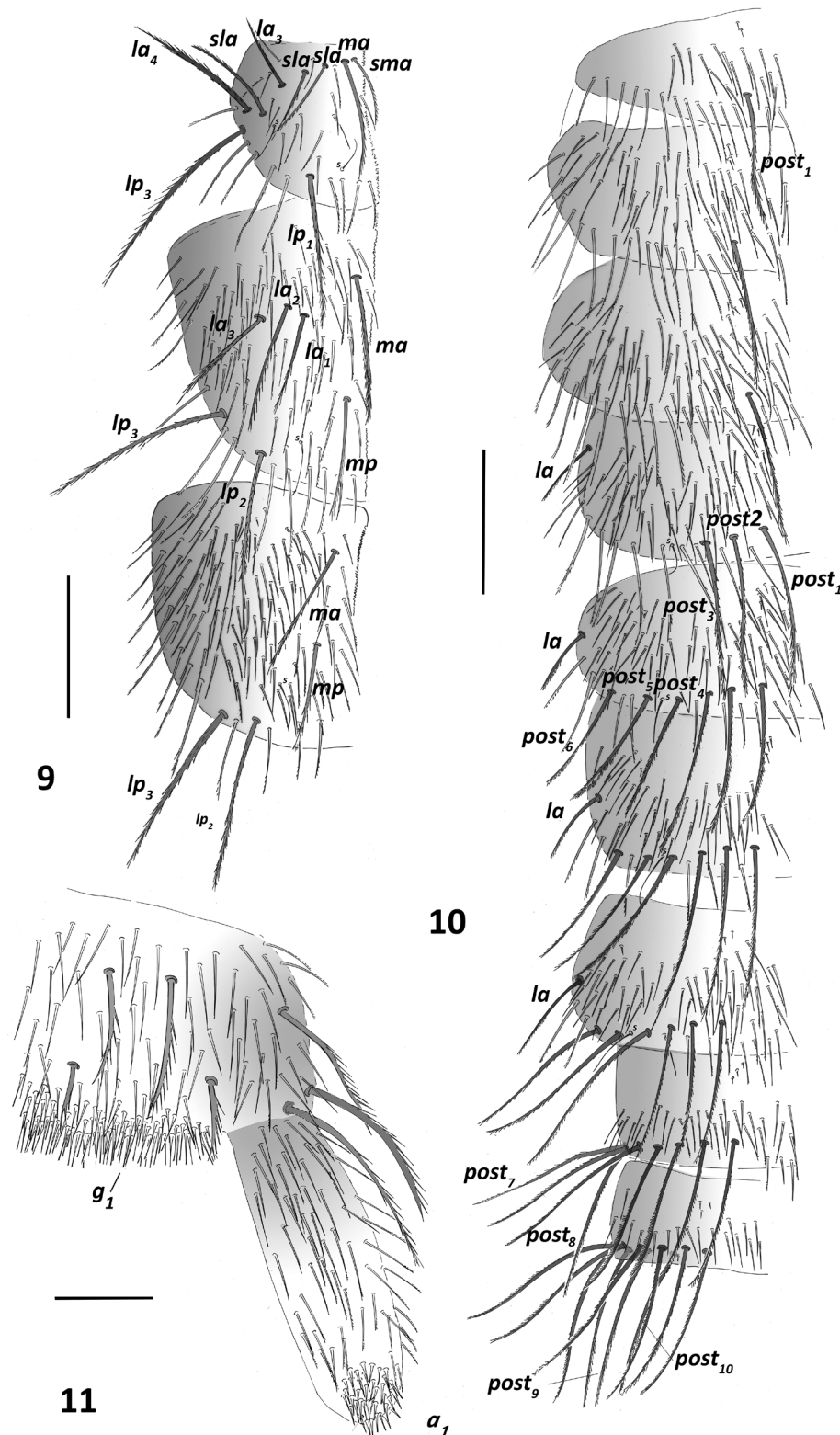
THORAX. Thoracic macrosetal distribution (Fig. 9): pronotum with 1+1 *ma*, 2+2 *la*<sub>3,4</sub> and 3+3 *sla*, 2+2 *lp*<sub>2,3</sub> (additionally, 1+1 extra *sma* appear near sagittal plane); mesonotum with 1+1 *ma*, 3+3 *la*<sub>1,2,3</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*; metanotum with 1+1 *ma*, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*. All notal macrosetae long and robust, covered by thin barbs almost from their base; submacrosetae *sla* and *sma* thinner and shorter than notal macrosetae, but with same large base; marginal setae longer than clothing setae, covered by thin barbs along distal half. Legs elongated, pretarsus of metathoracic legs slightly overpassing end of abdomen (Table 2). Femur I without dorsal macrosetae, but with one long, barbed ventral macroseta; femora II–III with one long, barbed dorsal and one long, barbed ventral macroseta. Tibia I with one short, barbed ventral macroseta; tibiae II–III with two short, barbed ventral macrosetae. Calcars with 2–3 rows of long barbs from base to tip, smooth on one narrow side along calcar. Dorsal and lateral subapical tarsal setae smooth. Subequal claws (posterior claw 1.1 × as long as anterior one); posterior claw without backward overhang; lateral crests well developed. Pretarsal process long and setiform, reaching extremities of claws.

ABDOMEN. Distribution of abdominal macrosetae on tergites (Fig. 10): 1+1 *post*<sub>1</sub> on I–III; 1+1 *la*, 3+3 (also 2+2, but less frequent) *post*<sub>1,2,3</sub> on IV; 1+1 *la*, 6+6 *post*<sub>1,5</sub> on V–VII; 8+8 *post* on VIII; 10+10 *post* on abdominal segment IX. All *post* urotergal macrosetae thick, long and covered by thin barbs along distal four-fifths; *la* urotergal macrosetae shorter than *post* macrosetae, covered by barbs along distal half. Urosternite I with 7+7 macrosetae; urosternites II–VII with 5+5 macrosetae; urosternite VIII with 2+2 macrosetae; all urosternal macrosetae robust and large, covered by long barbs along distal three-fourths to four-fifths. Apical, subapical and ventromedial setae with abundant long barbs.

SECONDARY SEX CHARACTERS. Male urosternite I (Fig. 11) with up to 180 glandular *g*<sub>1</sub> setae arranged in up to five rows, with enlarged subcylindrical appendages each bearing up to 52 glandular *a*<sub>1</sub> setae. Female appendages slightly thinner, with up to 38 glandular *a*<sub>1</sub> setae.

### Phyletic affinities, habitat and distribution

The modest subequal claws, including the posterior claw lacking a backward overhang, and the absence of lateral anterior macrosetae on the metanotum relate *P. (P.) apollo* sp. nov. to *P. (P.) festae*. Nonetheless the more abundant posterior urotergal macrosetae, with 6+6 *post* on urotergites IV–VII, as well as 8+8 and 10+10 *post* on abdominal segments VIII–IX in *P. (P.) apollo* sp. nov., rather than 5+5 on urotergites IV–VII, and 7+7 and 9+9 on abdominal segments VIII–IX in *P. (P.) festae* (Silvestri 1933a), separate the two species. Interestingly, the new species was collected in traps placed in MSS over the forest line



**Figs 9–11.** *Plusiocampa (Plusiocampa) apollo* Sendra, Giachino & Vailati sp. nov. **9–10.** Holotype, ♀, 4.8 mm long, from Viotia, O. Pamassós, Greece (MZB 2019-1032). **9.** Pronotum, mesonotum and metanotum (s = setiform sensillum). **10.** Urotergites I–VII and abdominal segment IX, right side (s = setiform sensillum). **11.** Paratype, ♂, 6.4 mm long, from the type locality (Coll. AS); urosternite I, left side. Scale bars: 9–10 = 30 µm; 11 = 10 µm.

(type locality) or in *Abies* Mill. forest (all the other sites), at altitudes from 1075 to 1660 m a.s.l. This large range of hypogean habitats also occurs in *P. (P.) festae* (see below).

***Plusiocampa (Plusiocampa) arbanasiensis* Bareth & Condé, 2001**

*Plusiocampa (Plusiocampa) arbanasiensis* Bareth & Condé, 2001: 23, figs 7a–g, 8a–b [name emended to *arbanasiensis*].

**Diagnosis** (Bareth & Condé 2001)

Non-troglophic species. Antennae with 23 and 26 antennomeres; five simple olfactory chemoreceptors in cupuliform organ; slightly protruding frontal process with slightly tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 (2+1) *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; abundant barbed notal clothing setae. Two ventral tibial macrosetae; subequal claws (1.05–1.1) with large lateral crests, posterior claw with a small backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergites IV–V with 1+1 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 (2+1) *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with glandular *g<sub>i</sub>* setae, subcylindrical appendages with glandular *a<sub>i</sub>* setae; female appendages similar to those of male.

**Remarks**

The studied material allowed us to complete the above description. The complete antennae of a female from Jama 1 v Kanjaducah show 23 antennomeres with five simple olfactory chemoreceptors within the cupuliform organ; it has a distal whorl of 8–11 gouge sensilla that are 25 µm long. All specimens show a simple frontal process with non-tubercular setae; smooth subapical tarsal setae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I of male with a narrow area of up to 80 glandular *g<sub>i</sub>* setae arranged in two or three rows; subcylindrical appendages with up to 12 glandular *a<sub>i</sub>* setae; females with subcylindrical appendages as in male, with up to 9 glandular *a<sub>i</sub>* setae. Nevertheless, the large distance from the type locality casts serious doubts regarding the correct identification of this rare species.

**Habitat and distribution**

Hypogean species found in two geographically distant karst regions, the Lyashkata Peshtera Cave, Balkan Mountains in Bulgaria, and two caves in the Slovenian Dinaric Mountains.

***Plusiocampa (Plusiocampa) baetica* Sendra, 2004**

Figs 12–23

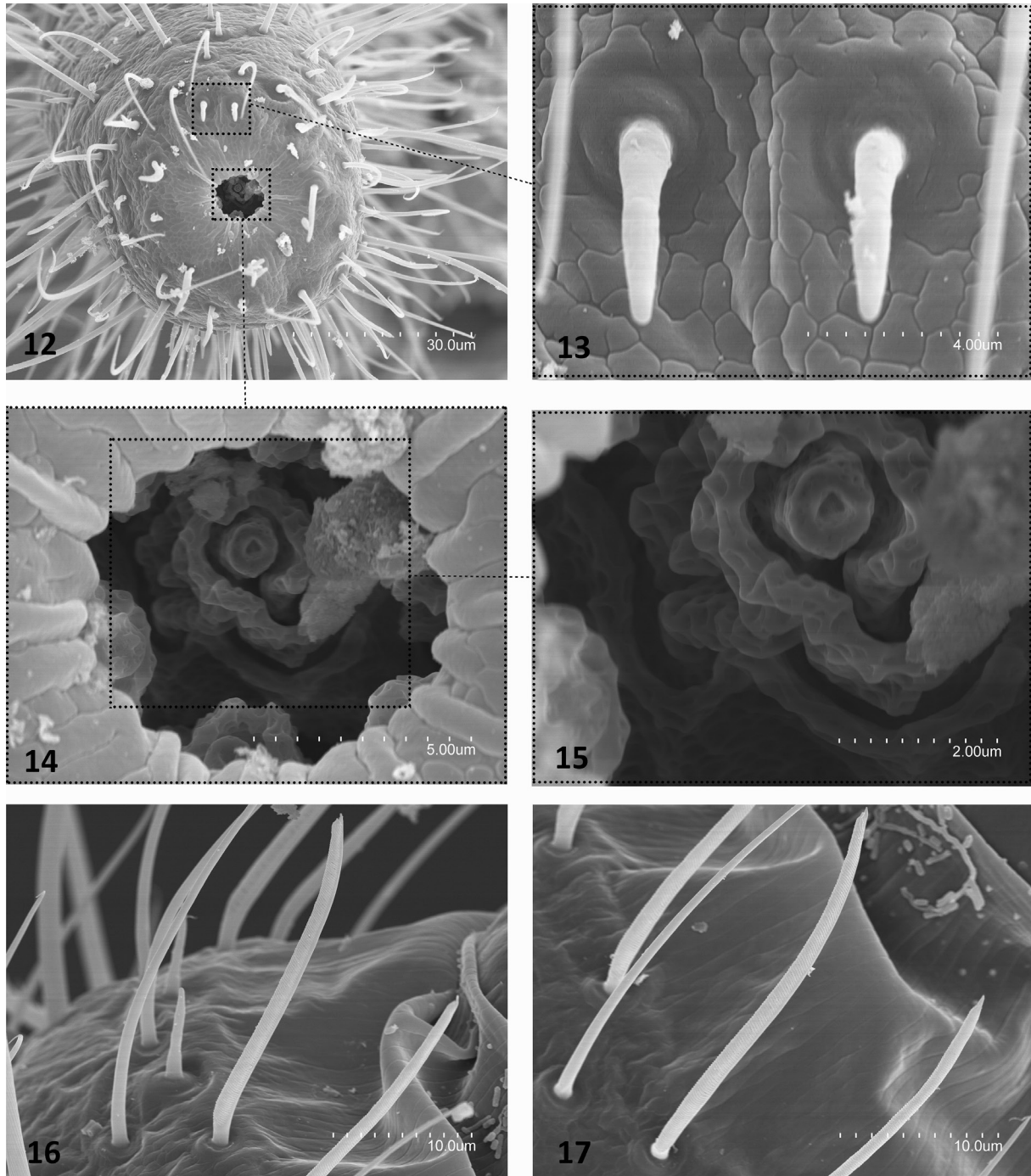
*Plusiocampa baetica* Sendra in Sendra *et al.*, 2004: 114, figs 1–4, tables 1–4.

**Diagnosis** (Sendra *et al.* 2004)

Troglophic species. Antennae with 39 antennomeres; 12 very complex olfactory chemoreceptors in a large cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum 1+1 with *ma*, 2+2 *lp* macrosetae; metanotum without macrosetae; short, barbed notal macrosetae except pronotal *lp*; sparse smooth clothing setae. Two ventral tibial macrosetae; slightly unequal claws (1.16) with large lateral crests, posterior claw with a short backward overhang. Urotergites V–VI with 1+1 *la*, 1+1 *post* macrosetae; urotergite VII with 1+1 *la*, 2+2–3+3 *post* macrosetae; urotergite VIII with 5+5–6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 8+8, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a narrow area of glandular *g<sub>i</sub>* setae, with subcylindrical appendages similar to those of female, with glandular *a<sub>i</sub>* setae.

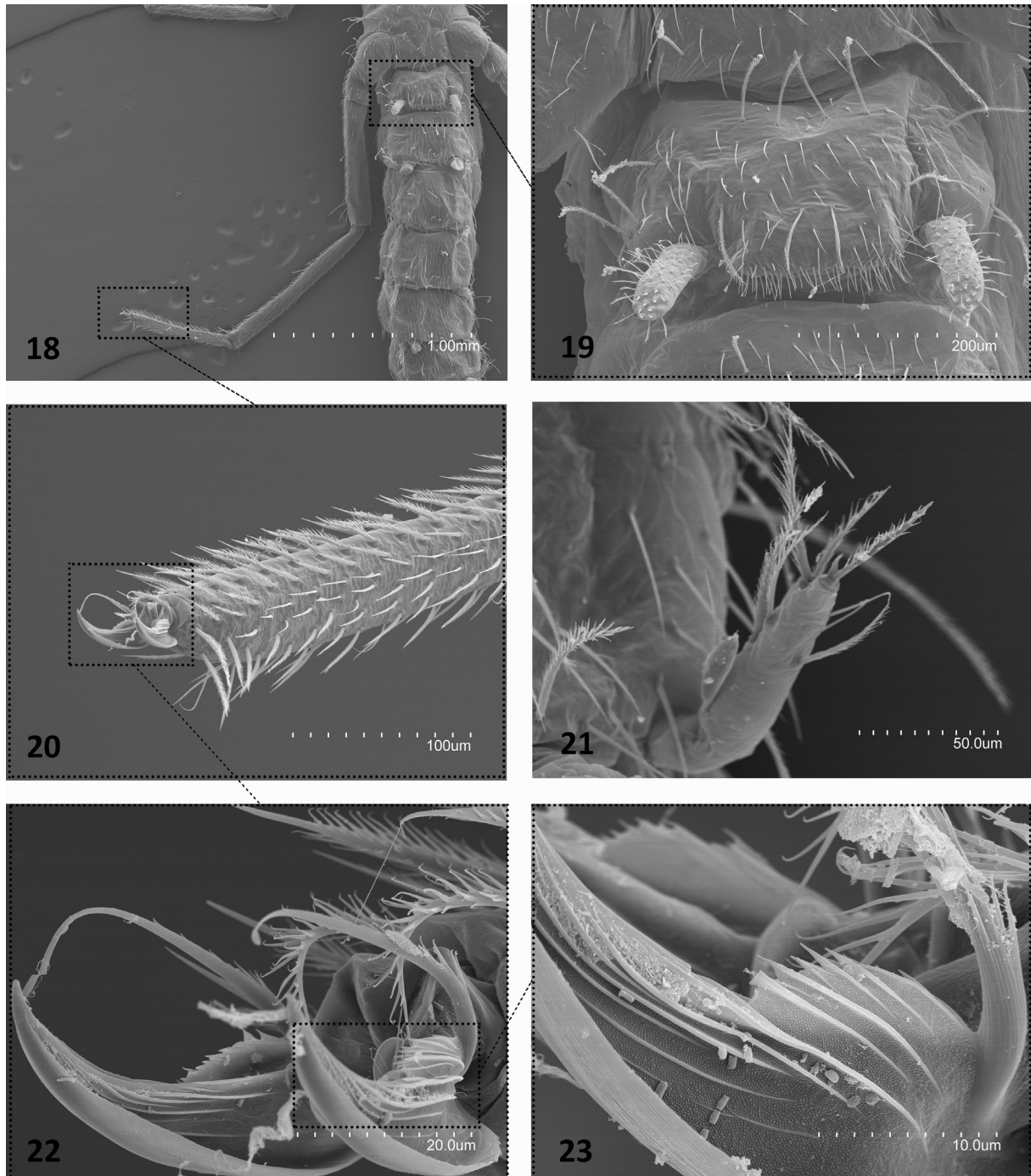
**Remarks**

SEM observations have shown several taxonomical features to complete the original description (Sendra *et al.* 2004). Each olfactory chemoreceptor shows a spiral fold with a central cylindrical structure, all with a multiporous surface, all tightly open to the exterior through a small opening (Figs 12, 14–15), surrounded by tiny coniform sensilla (Figs 12–13) that are present in the whorl of thin gouge sensilla



**Figs 12–17.** *Plusiocampa (Plusiocampa) baetica* Sendra, 2004, from Cueva de Nerja, Nerja, Málaga, Spain (Coll. AS). **12.** Apical view of last antennomere. **13.** Coniform sensilla of last antennomere. **14.** Cupuliform organ. **15.** Olfactory chemoreceptor. **16.** Lateral side of medial antennomere. **17.** Gouge sensilla.

on each medial and distal antennomere (Figs 16–17). Tibia longer than femur and tarsus (Fig. 18). Pretarsus with subequal claws with large lateral crests, the claws carved by longitudinal ridges and a micro-tuberculated surface (Figs 20, 22–23). Lateral process smooth, with several thin basal barbs (Figs 22–23). Stylar setae with abundant barbs (Fig. 21). Male with subcylindrical appendages with only glandular  $a_1$  setae and a narrow area of glandular  $g_7$  seate (Fig. 19).



**Figs 18–23.** *Plusiocampa (Plusiocampa) baetica* Sendra, 2004, from Cueva de Nerja, Nerja, Málaga, Spain (Coll. AS). **18.** Incomplete abdomen and thorax, ventral view, including metathoracic right leg. **19.** Urosternite I, ♂. **20.** Metatarsus of metathoracic leg. **21.** Abdominal stylus. **22.** Pretarsus of metathoracic leg, latero-anterior view. **23.** Lateral anterior claw of metathoracic leg, detail.

### Habitat and distribution

Subterranean species known only from Nerja Cave, a touristic cave in the internal zone of the Baetic Mountain Range, southern Iberian Peninsula.

#### *Plusiocampa (Plusiocampa) balsani* Condé, 1947

*Plusiocampa balsani* Condé, 1947: 46, fig. 3f.

*Campodea staphylinus* Viré, 1897: 7, figs 1–2.

### Diagnosis (Condé 1947b, 1948b; Bareth 2006)

Troglomorphic species. Antennae with 30–40 antennomeres; 12 complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum 1+1 *ma*, 1+1–2+2 *la*, 2+2 *lp* macrosetae; large, long, barbed notal macrosetae; scarce barbed clothing setae. One or two ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 0+0–1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male with a narrow area of glandular *g*<sub>1</sub> setae, with subtrapezoidal appendages with glandular *a*<sub>2</sub> setae; female with subcylindrical appendages with glandular *a*<sub>1</sub> setae. Spermatozoid fascicles with a diameter of 55–60 µm and a width of 15 µm, its filament wheels with 2½ turns of 460 µm long and 12–13 µm diameter filament.

### Habitat and distribution

Subterranean species found in 49 caves around the Central Massif, France.

#### *Plusiocampa (Plusiocampa) beroni* Bareth & Condé, 2001

*Plusiocampa beroni* Bareth & Condé, 2001: 16, figs 3b, 4a–e.

### Diagnosis (Bareth & Condé 2001)

Slightly troglomorphic species. Antennae with 26–29 antennomeres; 5–6 complex olfactory chemoreceptors on cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 (2+1) *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae. Two ventral tibial macrosetae; unequal claws (1.30) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae (1+1 *la*, 1+1 *post* on one specimen from Novata Peștera, western Rhodope); urotergite IV with 1+1 *la*, 4+4–5+5 *post* macrosetae; urotergite V with 1+1–2+2 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2–3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular *g*<sub>1</sub> setae, subcylindrical appendages with glandular *a*<sub>1</sub> setae (adults from Gruffre Padez, Sofia with short, thick appendages with a large area of glandular *a*<sub>1</sub> setae); female with subcylindrical appendages with glandular *a*<sub>1</sub> setae. Spermatozoid fascicle wheels with 2 turns of 50 µm long and 5 µm diameter filament.

### Habitat and distribution

Subterranean species found in six caves in different karst regions of the Bulgarian Balkan Mountains (= Stara Planina Mts).

***Plusiocampa (Plusiocampa) bonadonai bonadonai* Condé, 1948**

*Plusiocampa bonadonai* Condé, 1948c: 50, figs 2–3.

**Diagnosis** (Condé 1948c, 1949, 1950; Condé & Poivre 1982; Bareth 2006)

Troglomorphic species. Antennae with 31–37 antennomeres; 7–8 complex olfactory chemoreceptors in cupuliform organ. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; sparse notal clothing setae with a few distal barbs. Two or three ventral tibial macrosetae; subequal claws (1.05) with large lateral crests, posterior claw with a small backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergites IV–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with abundant glandular  $g_1$  setae, subcylindrical appendages like female appendages, with glandular  $a_1$  setae.

**Habitat and distribution**

Subterranean species found in 11 caves and at one edaphic site in the Île Saint-Honorat caves around the Western Alps, in the mountain reliefs near the Mediterranean coast in the Provence Alps, France.

***Plusiocampa (Plusiocampa) bonadonai lanzai* Condé, 1961**

*Plusiocampa bonadonai lanzai* Condé, 1961: 399.

**Diagnosis differential against the type form** (Condé 1961; Condé & Poivre 1982)

Troglomorphic subspecies. Antennae with 27–33 antennomeres. Urotergite III with 2+2 *post* macrosetae. No adult males have been observed, and the young males from Valais do not have glandular  $g_1$  setae, without glandular  $a_2$  setae.

**Habitat and distribution**

Subterranean subspecies found in a cave of Valais (Switzerland) as well as in two caves in Brescia and Toscana (Italy), around the Western Alps.

***Plusiocampa (Plusiocampa) bonadonai pavani* Condé & Poivre, 1982**

*Plusiocampa bonadonai pavani* Condé & Poivre, 1981: 171.

**Differential diagnosis against the type form** (Condé & Poivre 1982)

Troglomorphic subspecies. Antennae with 31–36 antennomeres; urosternite VIII with 7+7 *post* macrosetae.

**Habitat and distribution**

Subterranean subspecies found in 13 caves around the Western Alps.

***Plusiocampa (Plusiocampa) bonneti bonneti* Condé, 1948**

Figs 24–29

*Plusiocampa pouadensis bonneti* Condé, 1948c: 54, fig. 4b.

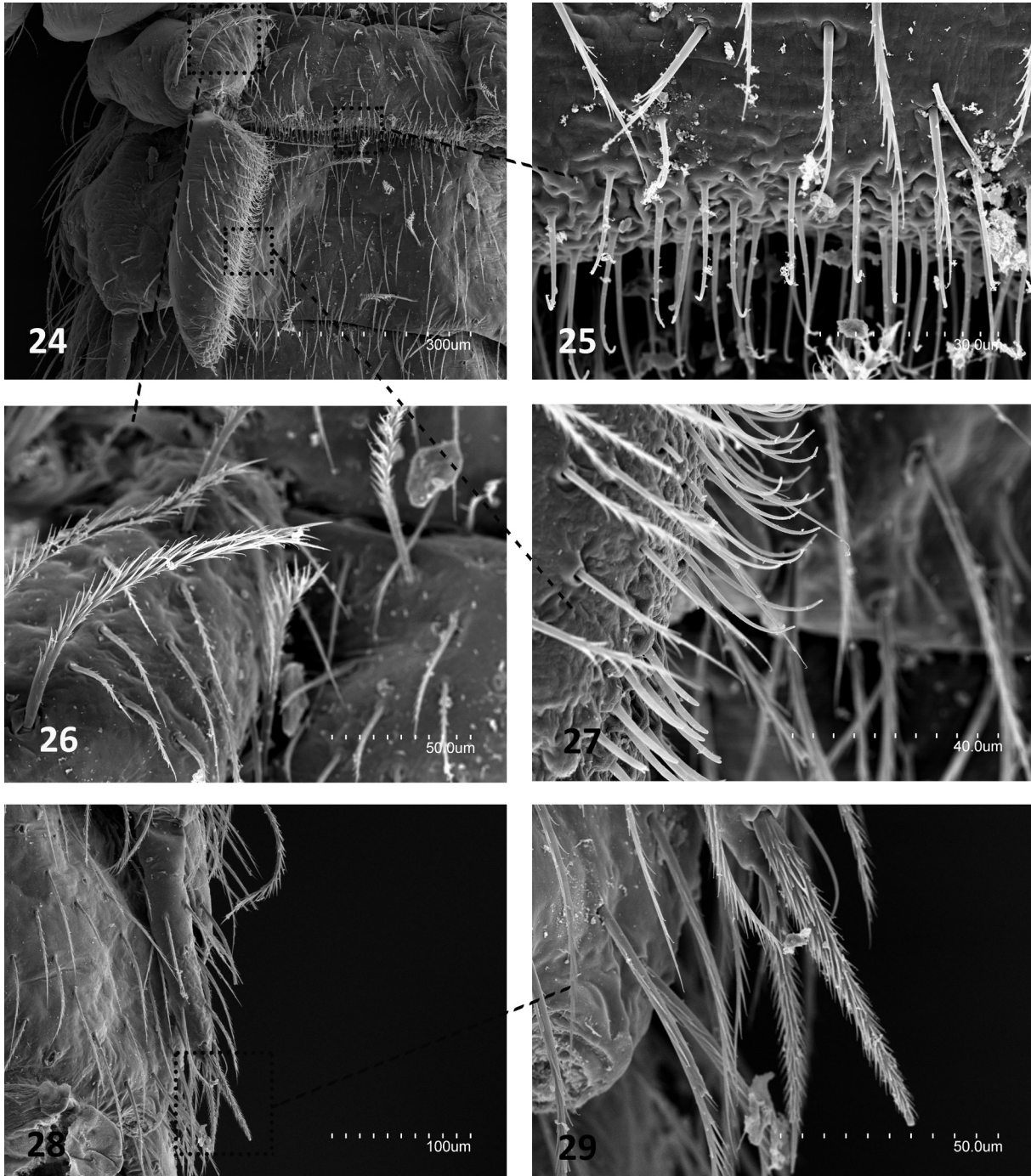
*Plusiocampa bonneti escolai* Sendra, 1985: 123, fig. 2b.

**Diagnosis** (Condé 1948c; Sendra 1985; Bareth & Condé 1996; Sendra & Escolà 2004; Bareth 2006)

Troglomorphic species. Antennae with 28–40 antennomeres; nine to ten complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum



with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae with distal barbs. Two ventral tibial macrosetae; slightly unequal claws (1.1–1.2) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergite V with 1+1–2+2 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment



**Figs 24–29.** *Plusiocampa (Plusiocampa) boneti boneti* Condé, 1948, ♂, from Cova Mora, Huesca, Spain (Coll. AS). **24.** Urosternite I, right side. **25.** Urosternite I, detail of glandular  $g_1$ -setae. **26.** Macrosetae of urosternite I. **27.** Appendage of urosternite I, glandular  $a_1$  and  $a_2$  setae. **28.** Stylus of left urosternite VI. **29.** Distal stylus of left urosternite VI, detail.

IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a large area of glandular  $g_1$  setae, subtrapezoidal appendages with glandular  $a_2$  setae; female with subcylindrical appendages with glandular  $a_1$  setae.

#### Habitat and distribution

Subterranean species found in three caves in the southern reliefs of France, west of the Rhône River, and in 34 caves distributed from the Central Pyrenees to the Pre-Pyrenees without reaching the Ebro Basin.

***Plusiocampa (Plusiocampa) bonneti condei*** Sendra & Escolà, 2004  
Figs 30–41

*Plusiocampa bonneti condei* Sendra & Escolà, 2004: 892.

*Plusiocampa pouadensis bonneti* – Condé 1951: 61.

#### Differential diagnosis against the type form (Sendra 1985; Sendra & Escolà 2004)

Antennae with 30–43 antennomeres; eight to nine complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with slightly tubercular setae. Spermatozoid fascicle wheels with 2–2½ turns of 300–400 µm long and 7 µm diameter filament.

#### Remarks (Figs 24–35)

One male of *P. (P.) bonneti bonneti* from Cova Mora (San Juan de la Peña, Huesca, Spain) and six specimens of *P. (P.) bonneti condei* from Cova Toll (Moià, Barcelona, Spain) (see [Table S2](#) in Supplementary Material) were used for SEM to remark on some features that are difficult to observe under the optical microscope. In *P. (P.) bonneti bonneti*, the first urosternite shows very long subtrapezoidal appendages with a large area of glandular  $a_2$  setae and a large area of glandular  $g_1$  setae, with the surface covered by barbed clothing setae and well-barbed macrosetae (Figs 24–27). In *P. (P.) bonneti condei*, the epicuticle varies from completely smooth to gently reticulate (Fig. 35); antennomeres with a whorl of gouge sensilla, 16–18 µm long (Figs 31, 33). Olfactory chemoreceptors with a central column unfolded in several layers with a reticulate surface covered by pores (Fig. 30). Protruding frontal process with slightly tubercular macrosetae and setae (Figs 32, 34). Claws with large lateral crest with ventral longitudinal grooves separated by reticulate surfaces (Figs 36–39). Styler setae totally covered by short, thin barbs (Fig. 40). Large eversible vesicles (Fig. 41).

#### Habitat and distribution

Subterranean subspecies found in 35 caves in the Eastern Pyrenees and the northern part of the Catalan Mediterranean Mountain System.

***Plusiocampa (Plusiocampa) bonneti deharvengi*** Bareth & Condé, 1996

*Plusiocampa bonneti deharvengi* Bareth & Condé, 1996: 128, figs 1–2, table 1.

#### Differential diagnosis against the type form (Bareth & Condé 1996)

Antennae with 34–38 antennomeres; six to seven simple olfactory chemoreceptors in cupuliform organ; slight protruding frontal process with a few anterior tubercular setae; abundant barbed notal clothing setae. One ventral tibial macroseta. Unequal claws with large lateral crests, posterior claw with a backwards overhang. Urotergites IV–VII with 1+1 *la*, 5+5 *post* macrosetae. Male with an area of glandular  $g_1$  setae; subtriangular appendages with glandular  $a_2$  setae. Spermatozoid fascicle wheels with 1½–2 turns of 8 µm diameter filament.

#### Habitat and distribution

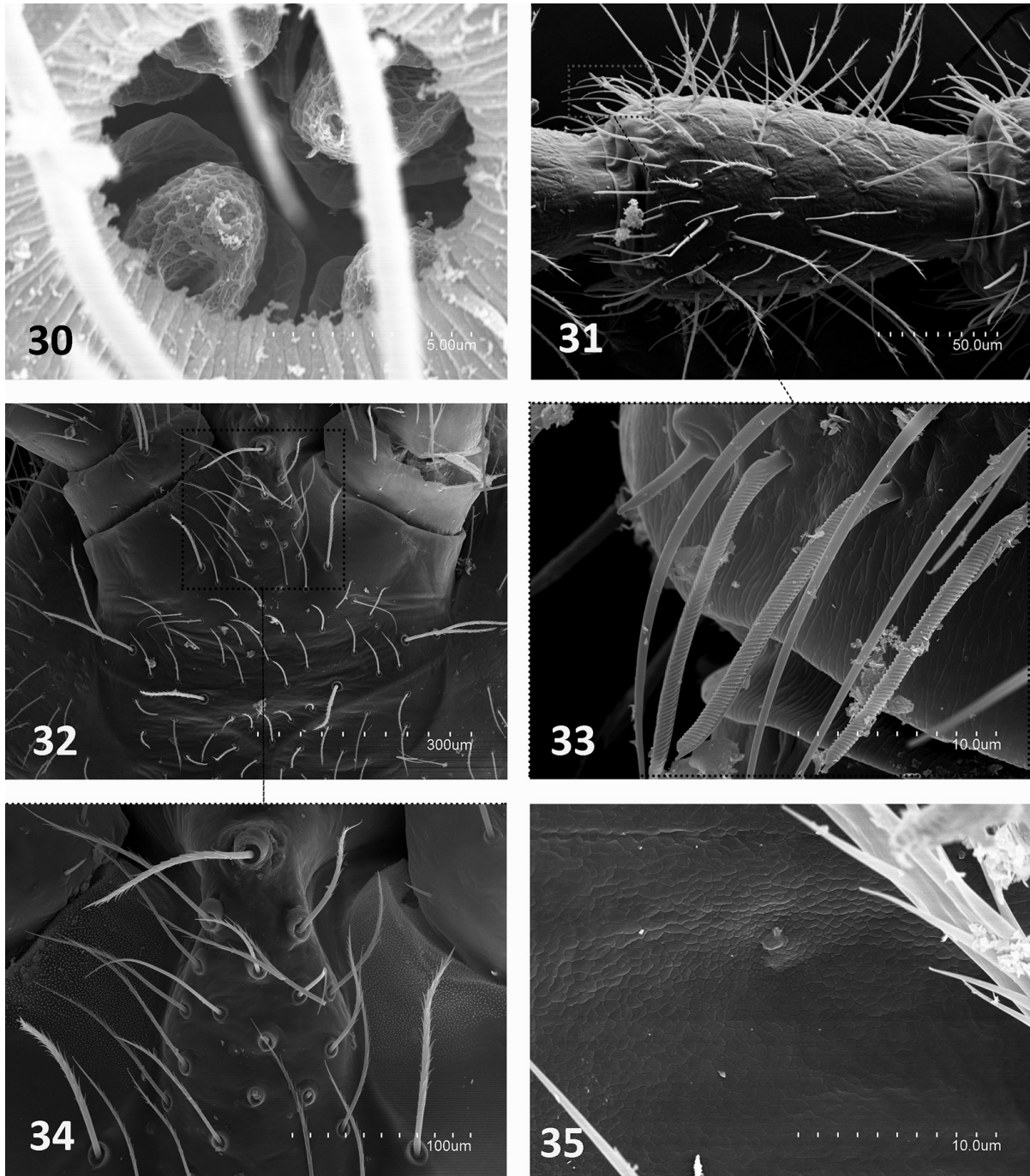
Subterranean subspecies found in two caves in the northern part of the Eastern Pyrenees.

*Plusiocampa (Plusiocampa) breviantennata* Loksa, 1960

*Plusiocampa breviantennata* Loksa, 1960: 258, figs 2–9.

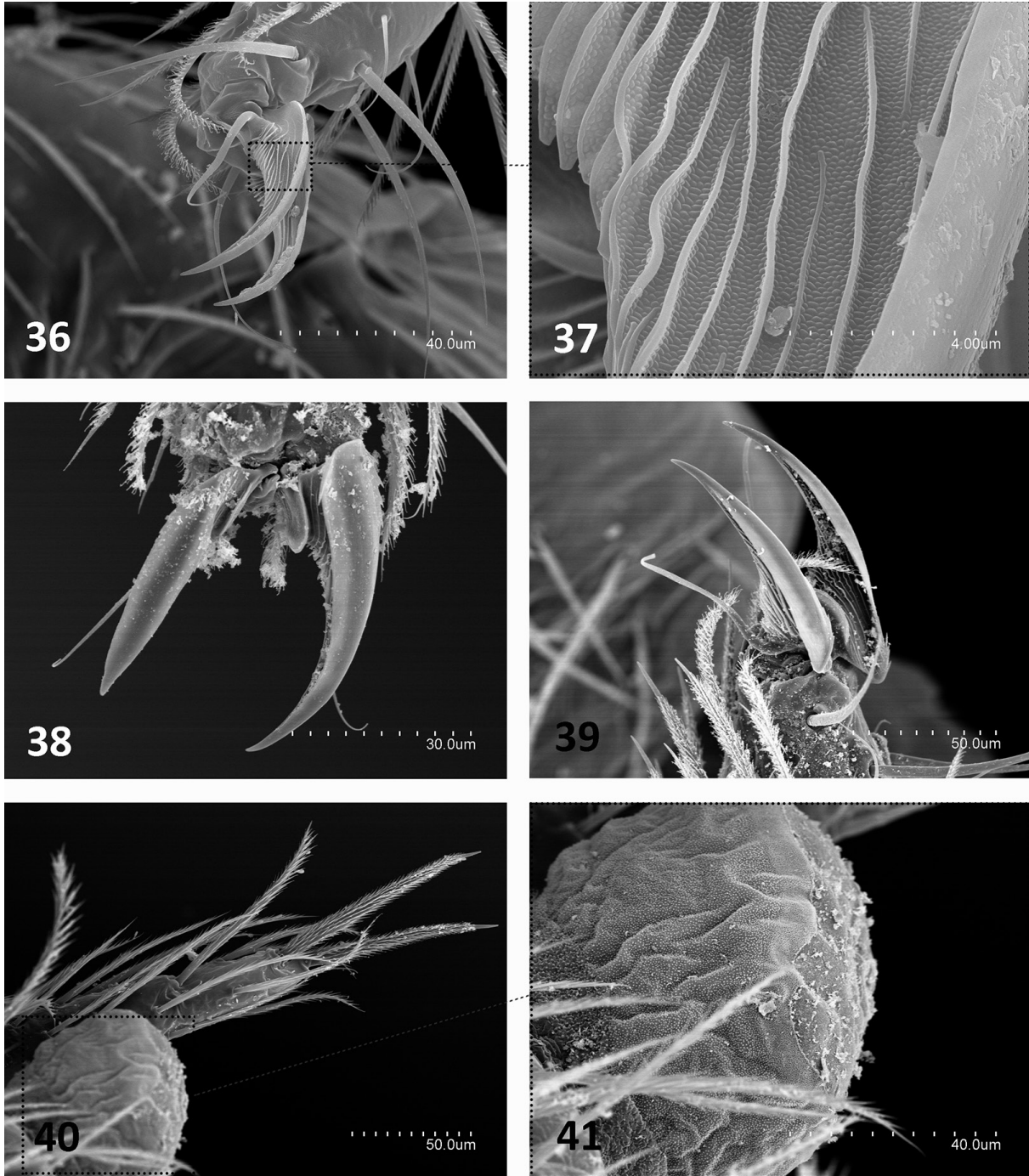
**Diagnosis** (Loksa 1960)

Non-trogloformic species. Antennae with 19–20 doliiform antennomeres. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1



**Figs 30–35.** *Plusiocampa (Plusiocampa) bonneti condei* Sendra & Escolà, 2004, from Cova del Toll, Moià, Barcelona, Spain (Coll. AS). **30.** Cupuliform organ. **31.** Medial antennomere. **32.** Frontal process. **33.** Lateral distal view of medial antennomere, with gouge and coniform sensilla **34.** Protruding frontal process. **35.** Surface of metanotum.

*la*, 2+2 *lp* macrosetae; thin notal macrosetae; sparse notal clothing setae. Two ventral tibial macrosetae. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 3+3 *post* macrosetae; urotergites IV–VII with 4+4 *post* macrosetae; *la* macrosetae not mentioned in original description.



**Figs 36–41.** *Plusiocampa (Plusiocampa) bonneti condei* Sendra & Escolà, 2004, from Cova del Toll, Moià, Barcelona, Spain (Coll. AS). **36.** Lateral posterior pretarsus of metathoracic leg. **37.** Lateral detail of posterior claw of metathoracic leg. **38.** Frontal view of pretarsus of metathoracic leg. **39.** Lateral anterior view of pretarsus. **40.** Stylus and abdominal eversible vesicle of urosternite. **41.** Detail of abdominal eversible vesicle.

### Habitat and distribution

Hypogean species, only found in Lóczy Cave, Balatonfüred, in the Balaton Uplands, southern Transdanubian Mountains, Hungary.

#### *Plusiocampa (Plusiocampa) breuili* Condé, 1955

*Plusiocampa breuili* Condé, 1955b: 125, figs 2, 3a–c.

#### **Diagnosis** (Condé 1955b; Condé & Sendra 1989; Sendra *et al.* 2004)

Troglomorphic species. Antennae with 30 and 32 antennomeres; 21 complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae, sparse notal clothing setae. 3 or 4 ventral tibial macrosetae (ratio of femur/tibia 0.66); subequal claws (1.1) with large lateral crests, posterior claw with a small backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 0+0–1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 2+2 (2+1) *la*, 5+5 *post* macrosetae; urotergites V–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 8+8, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular  $g_1$  setae, subcylindrical appendages with glandular  $a_1$  setae; female with subcylindrical appendages with glandular  $a_1$  setae.

#### *Plusiocampa (Plusiocampa) aff. breuili* Condé, 1955

#### **Differential diagnosis against the type form** (Sendra *et al.* 2004)

Frontal process with tubercular setae and 1+1 *la* macrosetae on urotergites VI–VII.

### Habitat and distribution

Subterranean species inhabiting two caves in Eivissa and four caves in Formentera, two of the Balearic Islands. *Plusiocampa (P.) aff. breuili* is only known from a cave in the eastern Baetic Mountains, southeastern Iberian Peninsula.

#### *Plusiocampa (Plusiocampa) bulgarica* Silvestri, 1931 Figs 42–43

*Plusiocampa bulgarica* Silvestri, 1931b: 103, figs vi–viii.

#### **Diagnosis** (Silvestri 1931b; Bareth & Condé 2001)

Troglomorphic species. Antennae with 24–30 antennomeres; 10 complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; a few long, distally barbed notal clothing setae. Two or three ventral tibial macrosetae; unequal claws (1.30) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 0+0–1+1 *la*, 1+1–2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergite V with 2+2 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a large area of glandular  $g_1$  setae and slightly enlarged appendages with glandular  $a_1$  setae; female with subcylindrical appendages with glandular  $a_1$  setae.

## Remarks

The study of 38 specimens collected from two new caves (see [Table S2](#) in Supplementary Material) allowed the addition of information to the diagnosis, including the observation of the pretarsal structures (Figs 42–43).

## Habitat and distribution

Subterranean species found in 16 caves in the Balkan and Rhodope Mountains, Bulgaria.

### *Plusiocampa (Plusiocampa) caprai* Condé, 1950

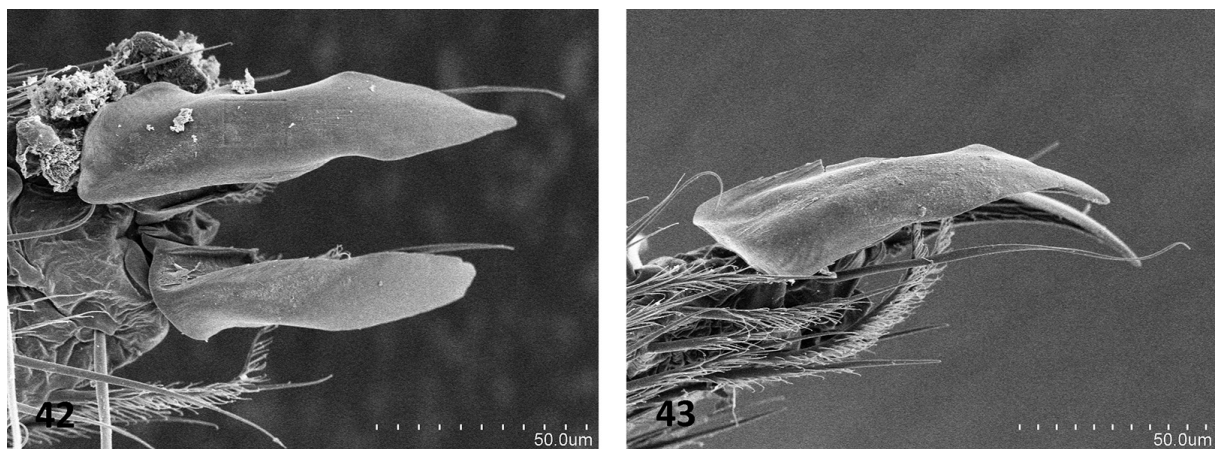
*Plusiocampa caprai* Condé, 1950: 1, figs a–e.

## Diagnosis (Condé 1950, 1954a; Christian *et al.* 1996)

Slightly troglomorphic species. Antennae with 28–30 antennomeres. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae, either smooth or with a few thin barbs. Three ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 (4+4) *post* macrosetae; urotergite V with 2+2 (1+1) *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae. Urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae, slightly enlarged subcylindrical appendages with *a*<sub>1</sub> glandular setae; female with subcylindrical appendages with *a*<sub>1</sub> glandular setae.

## Remarks

One male and one female of *P. (P.) caprai* from Babja jama (Slovenia) have been studied. However, two females collected from an MSS habitat in Corinthia (Peloponnese Peninsula) (see [Table S2](#) in Supplementary Material) appear to be very closely related to *P. (P.) caprai*, although the substantial geographical distance between these two areas and the observation of only females cast doubts on this specific attribution. Furthermore, all antennae and cerci are broken. The frontal process shows a protrusion and bears tubercular setae.



**Figs 42–43.** *Plusiocampa (Plusiocampa) bulgarica* Silvestri, 1931, from Sbrikovata Cave, Pamporovo, Bulgaria (Coll. AS). **42.** Pretarsus, dorsal view. **43.** Pretarsus, latero-posterior view.

**Habitat and distribution**

Hypogean species inhabiting subterranean and soil habitats, found in six caves, one mine and two soil and MSS habitats in the Austrian, Italian, Slovenian and Swiss Alps.

*Plusiocampa (Plusiocampa) chiosensis* Sendra & Gasparo sp. nov.

urn:lsid:zoobank.org:act:B3F3B66C-8C7C-48BF-A841-EAD3DF711C47

Figs 44–46; Tables 3–4

**Etymology**

The name ‘chiosensis’ is proposed based on the island of Chios, where it occurs in its deep subterranean habitat.

**Material examined****Holotype**

GREECE • ♀; Chios Island, Sykias; 10 Jun. 2006; Fulvio Gasparo leg.; MZB 2019-1030.

**Paratypes**

GREECE • 2 ♂♂; same collection data as for holotype; Coll. AS.

**Description**

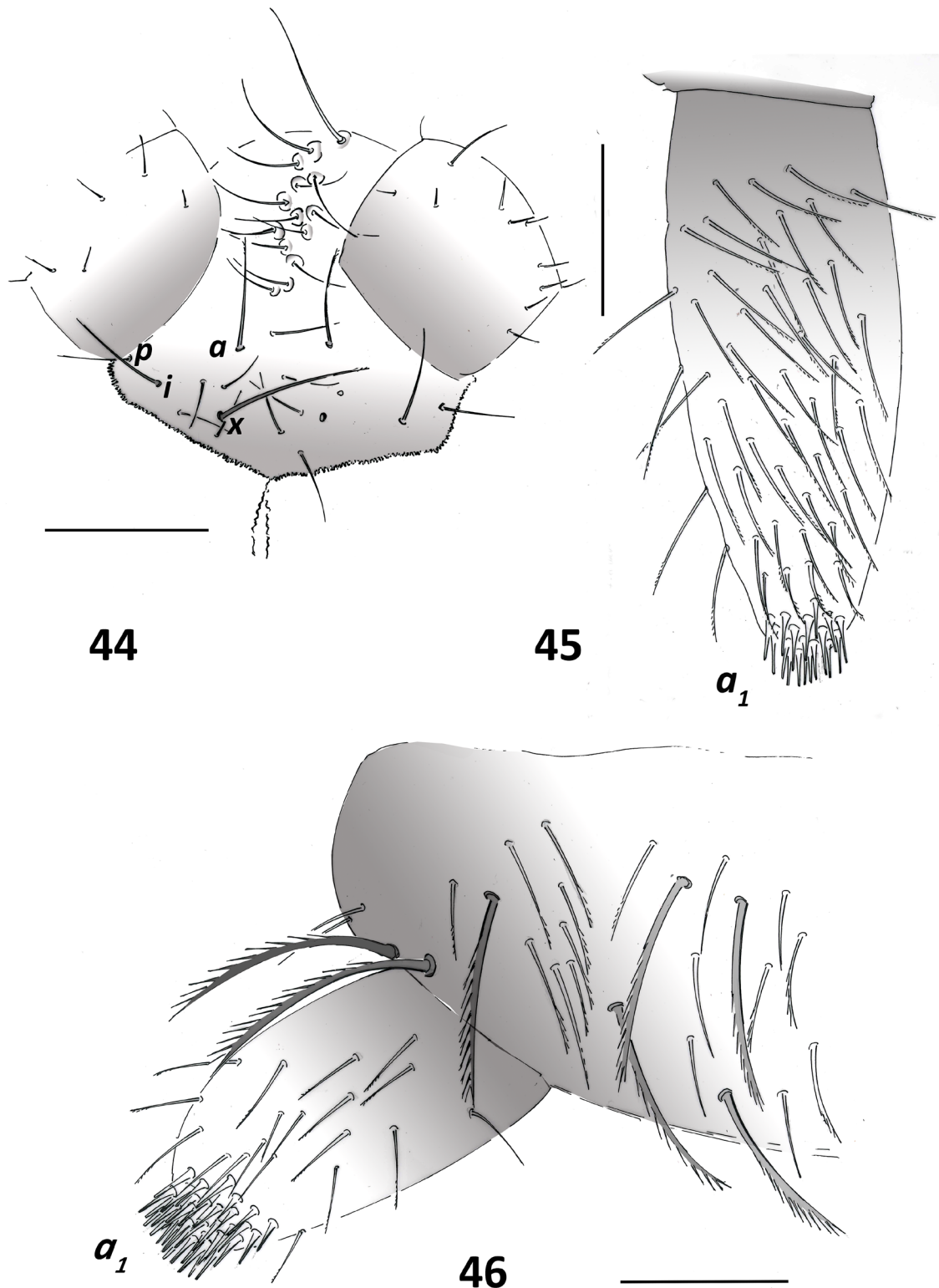
**BODY.** Body length 4.4 and 4.9 mm (males, paratypes) and 7.8 mm (female, holotype). Epicuticle smooth under optical microscope; body with sparse thin, long clothing, covered or not by a few thin distal barbs.

**HEAD.** Holotype with two intact antennae of 54 antennomeres, 14.8 mm long. Small coniform sensillum of third antennomere located in ventral position between *c* and *d* macrosetae. Central antennomeres  $3.8\times$  as long as wide, apical antennomere  $3.6\times$  as long as wide. Small cupuliform organ occupying  $\frac{1}{9}$  of total length of apical antennomere, with 6–7 complex olfactory chemoreceptors. Thin and long gouge sensilla (44–47  $\mu\text{m}$  long) in a single distal whorl of 10–13 sensilla on each medial and distal antennomere. Frontal process developed, with tubercular setae and macrosetae with thin barbs. Three macrosetae along line of insertion of antennae poorly differentiated, only anterior one with 1–2 thin apical barbs; *x* setae longer than these macrosetae, with a couple of thin apical barbs (Fig. 44). Suboval labial palps with latero-external sensillum larger than sensillum of third antennomere, with two guard setae, up to 12 setae on anterior border and up to 130 neuroglandular setae.

**THORAX.** Distribution of thoracic macrosetae: pronotum with 1+1 *ma*, 4+4–3+3 *la*<sub>1,2,3,4</sub>, 2+2 *lp*<sub>2,3</sub> (additionally in the three type specimens, 1+1 extra *ma* near the sagittal plane); mesonotum with 1+1 *ma*, 1+1 (0+1) *la*<sub>2</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*; metanotum with 1+1 *ma*, 1+1 *lp*<sub>2</sub> and 1+1, 0+1 or 0+0 *mp*. All notal macrosetae long, thin, covered by very thin barbs along distal third up to half; marginal setae

**Table 3.** *Plusiocampa (Plusiocampa) chiosensis* Sendra & Gasparo sp. nov. Length of the body, metathoracic legs and their segments: trochanter, femur, tibia and tarsus (measurements in mm).

Specimen	Body length	Metathoracic leg				Total length
		Trochanter	Femur	Tibia	Tarsus	
♂, paratype (Coll. AS)	4.4	0.20	0.9	1.10	1.01	3.20
♂, paratype (Coll. AS)	4.9	0.22	1.04	1.31	1.14	3.71
♀, holotype (MZB 2019-1030)	7.8	0.40	1.60	2.20	1.60	5.80



**Figs 44–46.** *Plusiocampa (Plusiocampa) chiosensis* Sendra & Gasparo sp. nov. **44–45.** Holotype, ♀, 7 mm long, from Spilaio Sykias Cave, Chios Island (MZB 2019-1930). **44.** Frontal process (*a*, *i* and *p* macrosetae of antennal insertion and *x* setae). **45.** Right appendage of urosternite I. **46.** Paratype, ♂, 4.9 mm long, from type locality (Coll. AS); urosternite I, right side. Scale bars: 44 = 0.2 mm; 45–46 = 0.1 mm.



**Table 4.** *Plusiocampa (Plusiocampa) chiosensis* Sendra & Gasparo sp. nov. Length of one cercus in the holotype (MZB 2019-1030) (measurements in mm).

Base	1 <sup>st</sup>	2 <sup>nd</sup>	3 <sup>rd</sup>	4 <sup>th</sup>	5 <sup>th</sup>	6 <sup>th</sup>	7 <sup>th</sup>	8 <sup>th</sup>	Total
2.80	1.10	1.45	1.65	2.05	2.35	2.80	2.70	2.80	19.70

longer than clothing setae, covered by thin barbs along distal half up to two thirds; spare clothing setae, with 14, 21 and 23 clothing setae on each heminotum of pronotum, mesonotum and metanotum, respectively (holotype). Legs elongated, metathoracic legs overpassing end of abdomen in middle of tibia; measurements as in Table 3. Femora II–III with one long dorsal macroseta and one longer ventral macroseta. Tibiae I–III with two ventral macrosetae surrounded all along by thin, short barbs. Calcars surrounded from base to tip by thin, short barbs. Dorsal and lateral subapical tarsal setae completely covered by thin barbs almost from base and almost to tip. Subequal claws (posterior claw 1.0–1.05× as long as anterior claw); posterior claw with a small backward overhang; lateral crests well developed, noticeably ridged on ventral side. Pretarsal lateral process setiform, with plenty of very short proximal barbs.

ABDOMEN. Distribution of abdominal macrosetae on tergites: 1+1 *post*<sub>1</sub> on I–III; 1+1 *la*, 2+2 *lp*<sub>1,2</sub> on IV; 1+1 *la*, 5+5 *post*<sub>1-5</sub> on V–VII, 8+8 *post* on VIII; 11+11 (11+12) *post* on abdominal segment IX. All *post* urotergal macrosetae thick, long, covered by thin barbs along distal four-fifths; *la* urotergal macrosetae shorter than *post* macrosetae, covered by barbs along distal half. Urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae; all urosternal macrosetae robust and large, covered by long barbs along distal half up to four-fifths. Apical subapical and ventro-medial setae completely surrounded by short abundant barbs.

CERCI. One complete cercus in holotype with eight articles in addition to basal article, 19.70 mm long (Table 4), 2.53 mm longer than body length; articles show whorls of long macrosetae covered by thin barbs along distal two-thirds, combined with whorls of smooth, thin setae shorter than macrosetae.

SECONDARY SEX CHARACTERS. Female urosternite I (Fig. 45) with enlarged subcylindrical appendages, each bearing up to 16 glandular *a*<sub>1</sub> setae in a distal area. Male urosternite I (Fig. 46) without glandular *g*<sub>1</sub> setae, with moderated large subcylindrical appendages thicker than those of female, each bearing up to 33 glandular *a*<sub>1</sub> setae.

#### Phyletic affinities, habitat and distribution

Although *P. (P.) chiosensis* sp. nov. has medial posterior macrosetae on the mesonotum and metanotum (sometimes absent in one or two heminota), as do many previously described species of *Plusiocampa* s. str., a similar reduction in the number of lateral anterior and lateral posterior macrosetae on the mesonotum and metanotum is present in another troglomorphic species, *P. (P.) glabra* from continental Greece (Condé 1984a). *Plusiocampa (P.) chiosensis* sp. nov. also shares a couple of noticeable taxonomical features with *P. (P.) glabra* in their subequal claws and the number of urosternal macrosetae. Nevertheless, the presence of 1+1 lateral anterior macrosetae on the mesonotum, the more abundant macrosetae on all urotergites, including the eighth abdominal segment, and the absence of glandular *g*<sub>1</sub> setae in males in *P. (P.) chiosensis* sp. nov. distinguish it from *P. (P.) glabra*.

*Plusiocampa (P.) chiosensis* sp. nov. is only known from one cave and occupies the deep subterranean spaces, showing highly troglomorphic features (elongation of appendages, antennomeres and articles, and the strengthening of sensorial equipment of the antennae).

***Plusiocampa (Plusiocampa) corcyraea corcyraea* Silvestri, 1912**

*Plusiocampa corcyraea* Silvestri, 1912: 142, figs xxvii–xxviii.

**Diagnosis** (Silvestri 1912; Condé 1947a, 1984a)

Non-trogomorphic species. Antennae with 18–21 antennomeres. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae; small subequal claws with small lateral crests, posterior claw with no backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 3+3 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female with enlarged appendages with glandular *a*<sub>1</sub> setae.

**Habitat and distribution**

Soil-dwelling species found at two localities on Kerkyra (Corfu), one of the main Ionian islands, and at three localities in continental Greece, in the Epirus region in the east of the Balkan Peninsula.

***Plusiocampa (Plusiocampa) corcyraea abdominalis* Condé, 1984**

*Plusiocampa corcyraea abdominalis* Condé, 1984a: 194.

**Differential diagnosis against the type form** (Condé 1984a)

Antennae with 22 antennomeres; urotergite III with 1+1 *post* macrosetae, instead of 2+2; urotergite IV with 2+2 *post* macrosetae, instead of 3+3; urotergites V–VII with 3+3 *post* macrosetae, instead of 4+4.

**Habitat and distribution**

Soil-dwelling subspecies found only on Ithaca and other large Ionian islands.

***Plusiocampa (Plusiocampa) cyrnensis* Condé, 1953**

*Plusiocampa (Plusiocampa) corcyraea cyrnensis* Condé, 1953a: 566, figs. 2d–f.

**Differential diagnosis against *P. (P.) corcyraea corcyraea*** (Condé 1953a)

Non-trogomorphic species. Antennae with 20–21 antennomeres. Mesonotum with 2+2 *la* macrosetae, instead of 3+3; metanotum without *la* macrosetae, instead of 1+1 *la*.

**Habitat and distribution**

Soil-dwelling species found at two localities on Corsica.

***Plusiocampa (Plusiocampa) dallai* Bareth & Condé, 1984**

*Plusiocampa dallai* Bareth & Condé, 1984: 138, fig. 3.

**Diagnosis** (Bareth & Condé 1984)

Trogomorphic species. Antennae with 32 antennomeres; 8 complex olfactory chemoreceptors with an atypical multi-sheet shape in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; thin, barbed notal

clothing setae. Three ventral tibial macrosetae; unequal claws (1.25) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergites V–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown, female with subcylindrical appendages with glandular  $a_1$  setae.

### Habitat and distribution

Subterranean species only known from Grotta di Montenero, in the Gargano Promontory part of the Apulia Carbonate Platform, Italian Peninsula.

#### *Plusiocampa (Plusiocampa) dargilani* (Moniez, 1894)

*Campodea dargilani* Moniez, 1894: 82.

*Campodea staphylinus* – Viré 1897: 7, figs 1–2 (not Westwood, 1852).

*Troglocampa dargilani* – Denis 1930 pars: 231, figs 25–28.

### Diagnosis (Denis 1923; Condé 1946; Bareth 2006)

Troglomorphic species. Antennae with 40–48 antennomeres; eight to nine complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2–1+1 *lp* macrosetae; thin, poorly barbed notal macrosetae; sparse long, thin, barbed notal clothing setae. No ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergite III with 1+1 *la* macrosetae; urotergite IV with 1+1 *la*, 1+1 *post* macrosetae; urotergites V–VII with 1+1 *la*, 3+3–4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 11+11, urosternites II–VII with 9+9, urosternite VIII with 3+3 macrosetae. Male with a narrow area of glandular  $g_1$  setae; subtrapezoidal appendages with an area of glandular  $a_2$  setae; female with subcylindrical appendages with glandular  $a_1$  setae. Spermatozoid fascicles 60–65  $\mu\text{m}$  in diameter and 25–30  $\mu\text{m}$  wide, wheels with 2½–3 turns of 650  $\mu\text{m}$  long and 13  $\mu\text{m}$  diameter filament.

### Remarks

The study of one female from Puech Cave, Grands Causses, France (see [Table S2](#) in Supplementary Material) has allowed us to supplement the former description, including regarding the presence of only 1+1 *lp* metanotal macrosetae.

### Habitat and distribution

Subterranean species, well-spread around the Grands Causses, where it is found in eight caves, living alongside the troglobite *P. (P.) balsani*.

#### *Plusiocampa (Plusiocampa) djurdjurae* Condé, 1984

*Plusiocampa djurdjurae* Condé, 1984b: 244.

### Diagnosis (Condé 1984b)

Troglomorphic species. Antennae with 34–35 and 38 antennomeres; 28 simple olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3–2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed macrosetae; barbed notal clothing setae. Two or three ventral

tibial macrosetae; unequal claws (1.4) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 0+0–1+1 *la*, 2+2–3+3 *post* macrosetae; urotergites V–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5–6+6, urosternite VIII with 2+2 macrosetae. Young male with an area of glandular  $g_1$  setae, enlarged appendages with glandular  $a_1$  setae; female with subcylindrical appendages with glandular  $a_1$  setae.

#### Habitat and distribution

Subterranean species found in two caves, Ifri Samedane and Ifri Maareb, in the Djurdjura Mountains, Tell Atlas, Algeria, on the former Kabylean microplate.

#### *Plusiocampa (Plusiocampa) dohati* Condé, 1975

*Plusiocampa dohati* Condé in Dobat, 1975: 321.

#### Diagnosis (Condé 1993a; Sendra & Weber 2018)

Troglomorphic species. Antennae with 27–29 antennomeres; 7–9 complex olfactory chemoreceptors on cupuliform organ; protruding frontal process characterized by a frontal and lateral rim with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2–3+3 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2–3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1–2+2 (2+1) *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; smooth notal clothing setae. Two ventral tibial macrosetae; unequal claws (1.3) with large lateral crests, posterior claw with a backward overhang; lateral processes smooth and short. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 (2+1) *post* macrosetae; urotergite IV with 0+0–1+1 (0+1) *la*, 2+2 (1+2) *post* macrosetae; urotergite V with 1+1 (1+2) *la*, 5+5 *post* macrosetae; urotergite VI with 2+2 (1+2, 2+3) *la*, 5+5 *post* macrosetae; urotergite VII with 2+2 (1+2) *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae; short enlarged subcylindrical appendages with glandular  $a_1$  setae; female with subcylindrical appendages, with glandular  $a_1$  setae.

#### Habitat and distribution

Subterranean species found in 13 caves around Swabian Alb, Germany.

#### *Plusiocampa (Plusiocampa) dolichopoda* Bareth & Condé, 1984

*Plusiocampa dolichopoda* Bareth & Condé, 1984: 141, fig. 4.

#### Diagnosis (Bareth & Condé 1984)

Troglomorphic species. Frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *lp* macrosetae; long, barbed notal macrosetae. One ventral tibial macroseta; subequal claws with small lateral crests, posterior claw with no backward overhang. Urotergites I–IV with 1+1 *post* macrosetae; urotergites V–VII with 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Adults unknown.

#### Habitat and distribution

Description based on a single juvenile from only one cave, Grotta Trojano, Jacotenente, the Gargano Promontory part of the Apulia Carbonate Platform, Italian Peninsula.

*Plusiocampa (Plusiocampa) dolichopoda inguscioni* Bareth, 2002

*Plusiocampa dolichopoda inguscioni* Bareth, 2002: 122, figs 1–2.

**Differential diagnosis against the type form** (Bareth 2002)

Pronotum with 3+3 lateral posterior macrosetae, instead of 2+2 in the type form.

**Habitat and distribution**

Subterranean subspecies inhabiting one cave, Grotte Scaloria, Manfredonia, Gargano, Italian Peninsula, near the type locality.

*Plusiocampa (Plusiocampa) dublanskii* Sendra & Turbanov sp. nov.  
[urn:lsid:zoobank.org:act:66D5D570-F8DC-43CF-936B-DE8512631B55](https://zoobank.org/act:66D5D570-F8DC-43CF-936B-DE8512631B55)  
Figs 47–48

**Etymology**

This species is named in honour of Professor V.N. Dublyansky (1930–2012), who was the instigator of complex karstological and speleological studies of the Kizil-Koba (= Krasnaya) Cave.

**Material examined**

**Holotype**

CRIMEA • 1 ♂; Simferopol District, Dolgorukovsky karst massif, Kizil-Koba (= Krasnaya) Cave; 5 Nov. 2014; I.S. Turbanov leg.; ZMMU Dip0006.

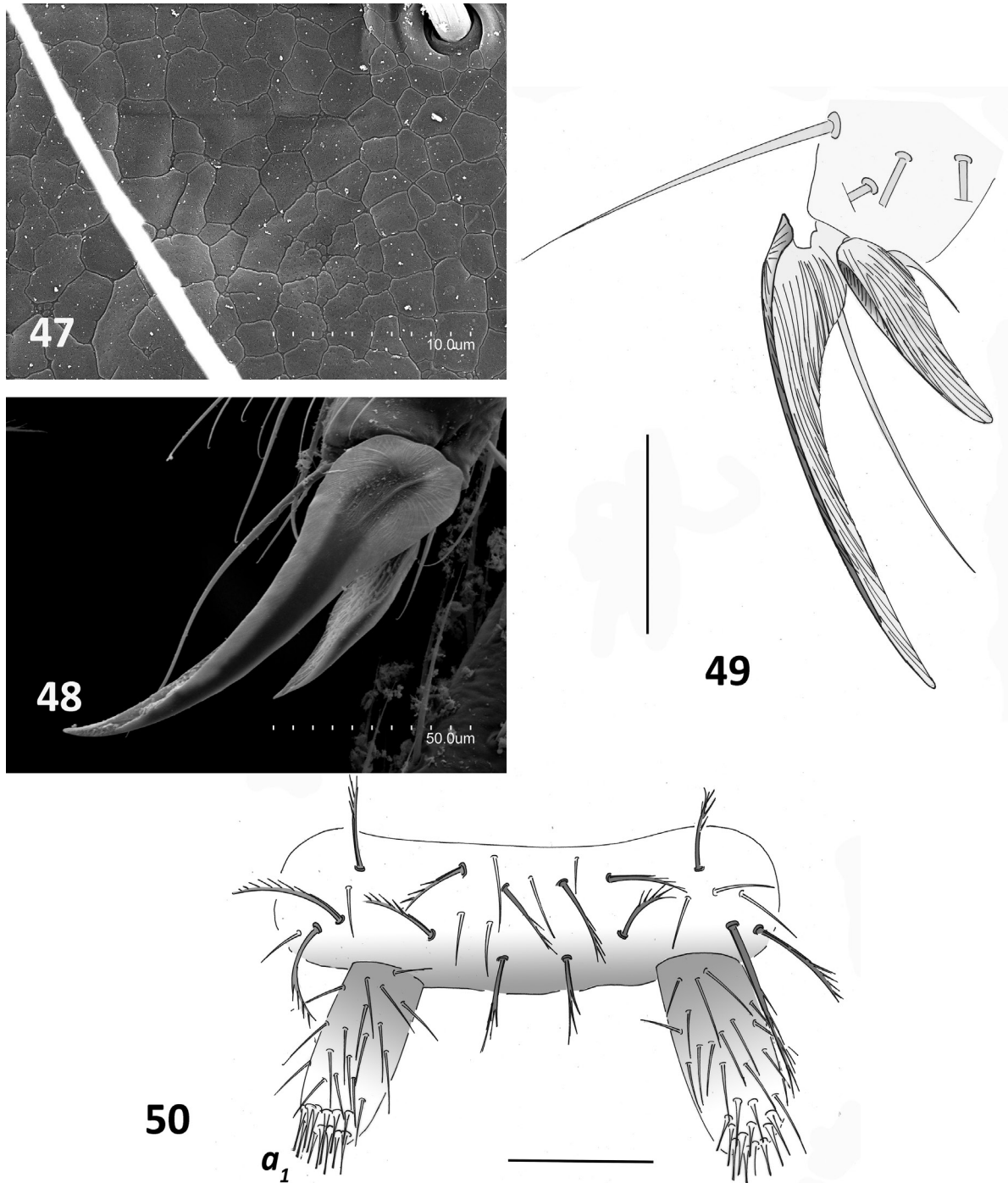
**Description**

**BODY.** Body length 2.7 mm. Epicuticle smooth under optical microscope but with a reticulate surface under SEM (Fig. 47); body with sparse thin and middle-sized clothing setae with 1–3 thin distal barbs.

**HEAD.** Two intact antennae with 35 antennomeres, longer than body length (3.2 mm); thin subcylindrical sensillum on third antennomere in ventral position between macrosetae *d* and *e*; central antennomeres 2.1× as long as wide, apical antennomere 3.0× as long as wide; cupuliform organ occupying 1/3 of its length, with nine complex olfactory chemoreceptors; gouge sensilla 40–50 µm long in a single whorl of 10–12 sensilla on each medial and distal antennomere; a small, thin subcylindrical sensillum on third antennomere. Non-protruding frontal process with very slightly tubercular frontal macrosetae. Frontal process plain, with very slight tubercular frontal macrosetae; macrosetae along line of insertion of antennomere and *x* setae similar in length and with a few distal barbs (*a/i/p/x* with relative lengths of 29/19/24/25). Small suboval labial palps with a large subcylindrical sensillum, two guard setae, five normal setae and up to 20 neuroglandular setae.

**THORAX.** Thoracic macrosetal distribution: pronotum with 1+1 *ma*, 2+2 *la*<sub>2</sub>, 2+2 *lp*<sub>2,3</sub>; mesonotum with 1+1 *ma*, 2+2 *la*<sub>2,3</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*; metanotum with 1+1 *ma*, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*. All notal macrosetae long and barbed along distal two-thirds; marginal setae similar to clothing setae, but a bit longer. Legs elongated (1.53 mm long), overpassing end of abdomen. Femur I without dorsal macrosetae; femora II–III with one dorsal macroseta inserted on distal third. No ventral tibial macrosetae. Calcars with 2–3 rows of long barbs, from base with a smooth and narrow lateral side along each calcar. Dorsal and lateral subapical tarsal macrosetae smooth. Very unequal claws, posterior claw 1.80–2.05× as long as anterior one, including a large backward overhang in posterior claw; ventral surface of claws with grooves, dorsal surface including large lateral crests with thin stripes. Posterior claw with a long, setiform pretarsal process reaching claw; anterior claw with short pretarsal processes without reaching extremity of this short claw (Figs 48–49).

ABDOMEN. Distribution of abdominal macrosetae on tergites: 1+1  $post_1$  on I–III; 1+1  $la$ , 1+1  $post_1$  on IV; 1+1  $la$ , 2+2  $post_{1,2}$  on V; 1+1  $la$ , 3+3  $post_{1,2,3}$  on VI; 1+1  $la$ , 4+4  $post_{1,2,3,4}$  on VII; 5+5  $post$  on VIII; 8+8  $post$  on abdominal segment IX. All  $post$  urotergal macrosetae long, robust, barbed;  $la$  urotergal



**Figs 47–50.** – 47–48. *Plusiocampa (Plusiocampa) dublanskii* Sendra & Turbanov sp. nov. 47. Specimen from Kizil-Koba (= Krasnaya) Cave, Dolgorukovsky karst massif, Crimean Peninsula (Coll. AS); surface of metanotum, detail. 48. Holotype, ♂, 2.7 mm long, from same locality (ZMMU Dip0006); pretarsus, dorsal view. – 49–50. *P. (P.)* aff. *dublanskii* Sendra & Turbanov sp. nov., ♂, 2.8 mm long, from Abrskila Cave, Abkhazia, Western Caucasus (ZMMU). 49. Metathoracic pretarsus. 50. Urosternite I. Scale bars: 49 = 50  $\mu$ m; 50 = 0.1 mm.

macrosetae much shorter, with thin distal barbs. Urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae; all urosternal macrosetae robust, large, covered by long barbs along distal half to three-fourths. Thick stylus with almost smooth stylar setae.

SECONDARY SEX CHARACTERS. Male urosternite I without glandular  $g_1$  setae, with subcylindrical, short and enlarged appendages with up to 15 large glandular  $a_1$  setae, with spermatozoid fascicles. Female unknown.

*Plusiocampa (Plusiocampa) aff. dublanskii* sp. nov.

Fig. 49–50

**Material examined**

WESTERN CAUCASUS • 1 ♂; Abkhazia, Ochamchira District, near Otap Village, Abrskila Cave; 9 Sep. 2014; I.S. Turbanov leg.; ZMMU.

**Remarks**

Body length 2.8 mm. It shows some differences from the type form in the number of macrosetae on the pronotum (1+2  $la_{2,3}$ ), metanotum (1+1  $la$ ), urotergite IV (without  $la$  macrosetae), urotergite V (without  $la$  and 1+1  $post_1$ ), urotergite VI (1+1  $la$ , 2+2  $post_{1,2}$ ), urotergite VII (2+2  $la_{2,3}$ , 2+2  $post_{1,2}$ ), urotergite VIII (4+4  $post$ ) and abdominal segment IX (7+7  $post$ ).

**Phyletic affinities, habitat and distribution**

Among the described species of *Plusiocampa* s. str., *P. (P.) bulgarica*, *P. (P.) elongata*, *P. (P.) vodniensis* and *P. (P.) beroni* from the Balkan karst region (Condé 1954a; Bareth & Condé 2001; Sendra *et al.* 2012b), *P. (P.) strouhali*, *P. (P.) caprai*, *P. (P.) grandii* and *P. (P.) hoelzeli* from the Alps (Condé 1954a; Neuherz 1984) and *P. (P.) fagei* from caves on Mallorca (Condé 1955b) share two important taxonomic characters with *P. (P.) dublanskii* sp. nov.: the distinctly unequal claws with large lateral crests and an evident backward overhang on the posterior claw, and the presence of medial posterior macrosetae on the mesonotum and metanotum. Nonetheless, the absence of ventral tibial macrosetae or the extremely unequal claws with unequal lateral pretarsal processes suggest a completely different relationship with the unclear subgenus *Venetocampa* from the Veneto region, northern Italian Peninsula. These new troglomorphic taxa live in two separated karst regions in the north (Crimea) and the east (Western Caucasus) of the Black Sea. The important differences between the two studied specimens are remarkable, in particular the number and distribution of the macrosetae on the urotergites and abdominal segment, something that should be reviewed in the future with further samples.

*Plusiocampa (Plusiocampa) elongata* Ionescu, 1955

*Plusiocampa elongata* Ionescu, 1955: 43, figs 18–19.

**Diagnosis** (Ionescu 1955, Sendra *et al.* 2012b)

Troglomorphic species. Antennae with 30–35 antennomeres; cupuliform organ with four complex olfactory chemoreceptors; protuding frontal process with very slightly tubercular setae. Pronotum with 1+1  $ma$ , 4+4  $la$ , 2+2  $lp$  macrosetae; mesonotum with 1+1  $ma$ , 3+3  $la$ , 2+2  $lp$ , 1+1  $mp$  macrosetae; metanotum with 1+1  $ma$ , 2+2  $la$ , 2+2  $lp$ , 1+1  $mp$  macrosetae; long, barbed notal macrosetae; abundant notal clothing setae. Two or three ventral tibial macrosetae; unequal claws (1.15–1.30) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1  $post$  macrosetae; urotergite III with 0+0–1+1  $la$ , 3+3–4+4  $post$  macrosetae; urotergite IV with 1+1–2+2–3+3  $la$ , 4+4  $post$  macrosetae; urotergite V with 2+2–3+3  $la$ , 5+5  $post$  macrosetae; urotergites VI–VII with 3+3  $la$ , 5+5  $post$  macrosetae; urotergite VIII with 6+6  $post$  macrosetae; abdominal segment IX with 8+8  $post$  macrosetae; urosternite I with 8+8, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae, with enlarged, thick subtrapezoidal appendages with a large area of

glandular  $a_1$  setae; female with enlarged, thick subcylindrical appendages with a few glandular  $a_1$  setae. Spermatozoid fascicles 70  $\mu\text{m}$  in diameter, wheels with  $2\frac{1}{2}$  turns of 400  $\mu\text{m}$  long and 7  $\mu\text{m}$  wide filament.

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

**Differential diagnosis against the type form** (Sendra *et al.* 2012b)

Urotergite I with 0+0–0+1–1+1 *post* macrosetae; urotergites II–III with 1+1 *post* macrosetae; urotergite IV with 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae.

**Habitat and distribution**

Subterranean species found in nine caves around the Carpathian Mountains in Romania; *P. (P.) aff. elongata* has only been found in one cave, the Peștera Cloșani cave.

*Plusiocampa (Plusiocampa) exsulans* Condé, 1947

*Plusiocampa exsulans* Condé, 1947a: 27, fig. 5.

**Diagnosis** (Condé 1947a, 1955a, 1966; Bareth 1988)

Non-trogomorphic species. Antennae with 21–25 antennomeres; four simple olfactory chemoreceptors in cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; smooth notal clothing setae. Two ventral tibial macrosetae. Small subequal claws (1.05) with middle-sized lateral crests, posterior claw with no backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergites IV–V with 1+1 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 (2+1) *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular  $g_1$  setae, subcylindrical enlarged appendages with glandular  $a_1$  setae; female with slender subcylindrical appendages with glandular  $a_1$  setae. Spermatozoid fascicle wheels with  $1\frac{1}{2}$  turns of 150  $\mu\text{m}$  long and 10  $\mu\text{m}$  diameter filament.

**Remarks**

The study of five specimens from two caves in Slovenia and Trieste, Italy, and one from Faedo San Michele, Trento, Italy (see [Table S2](#) in Supplementary Material) allowed the addition of information to the diagnosis.

**Habitat and distribution**

Hypogean species found in caves and frequently in soil. A total of 20 localities are reported from around Central Europe, from the Czech Republic and Slovakia to the Italian and Dinaric Mountains, reaching Croatia and Bosnia and Herzegovina towards the east and France towards the west, where it has been found in garden soils. This species is often found in urban soils, e.g., at ca 20 sites in Vienna (Christian 1992). The presence of *P. (P.) cf. exsulans* on the Anatolian Peninsula (Sendra *et al.* 2006) must be confirmed.

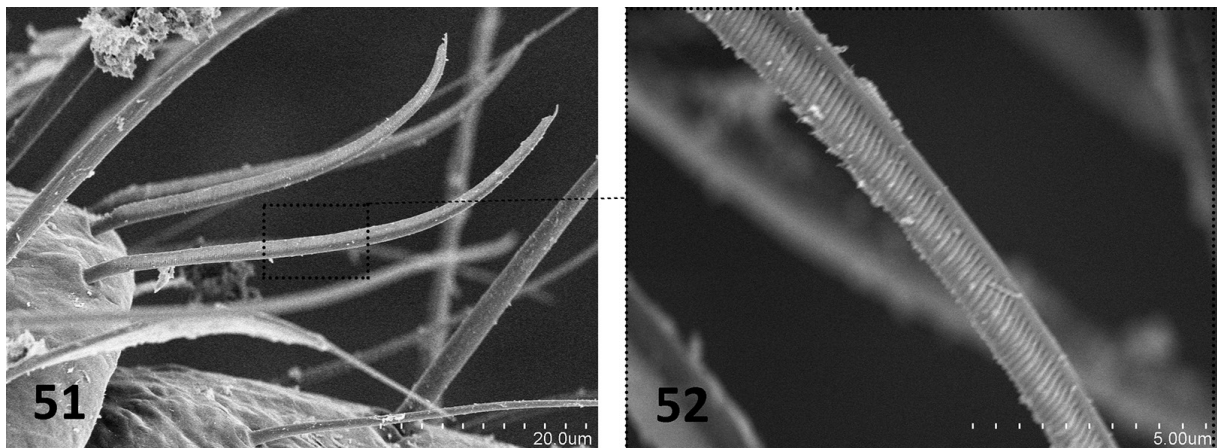
*Plusiocampa (Plusiocampa) fagei* Condé, 1955  
Figs 51–52

*Plusiocampa fagei* Condé, 1955b: 129, figs 3d, 4.

**Diagnosis** (Condé 1955b)

Trogomorphic species. Antennae with 39–48 antennomeres; 21 complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2





**Figs 51–52.** *Plusiocampa (Plusiocampa) fagei* Condé, 1955, from Cova Sa Gleda, Manacor, Mallorca Island (Coll. AS). **51.** Lateral distal side of a medial antennomere. **52.** Detail of a gouge sensillum.

*la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; sparse notal clothing setae. Two or three ventral tibial macrosetae; unequal claws (1.25) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 0+0–1+1 *la*, 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2–4+4 *post* macrosetae; urotergites V–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 6+6–8+8, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a narrow area of glandular *g*<sub>1</sub> setae and very long cylindrical appendages with glandular *a*<sub>1</sub> setae; female with thin subcylindrical appendages with glandular *a*<sub>1</sub> setae.

### Remarks

Two specimens from Cova Sa Gleda, Manacor, Mallorca (see [Table S2](#) in Supplementary Material) were used for SEM to look at some features that are difficult to observe under an optical microscope, such as their thin gouge sensilla, 48–50 μm long with an external transversal striped surface (Figs 51–52).

### Habitat and distribution

Subterranean species inhabiting 19 caves in Mallorca, Balearic Islands, mainly in the Tramuntana mountain chain on the north of the island.

### *Plusiocampa (Plusiocampa) festae* Silvestri, 1932

*Plusiocampa festae* Silvestri, 1932: 75, figs x–xi.

*Plusiocampa festae coi* Silvestri, 1932: 78.

### Diagnosis (Silvestri 1933a; Condé 1984a)

Slightly troglomorphic species. Antennae with 25 and 35 antennomeres. Non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae. Two (rarely three) ventral tibial macrosetae; subequal claws (1.1) with large lateral crests; posterior claw with no backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 1+0 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2–3+3 *post* macrosetae; urotergites V–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae; abdominal segment IX with 9+9 *post* macrosetae; urosternite I with 7+7, urosternites II–VII

with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular  $g_1$  setae and enlarged appendages with glandular  $a_1$  setae.

### Remarks

The studied material (see Table S2 in Supplementary Material) from MSS habitats was collected from inland Greece. Three specimens from Évia show variability in the number of *post* macrosetae on the third urotergite; they have 2+1, 2+2 and 3+3 *post* macrosetae, showing the dubious value of the subspecies *P. (P.) festae coi*. In addition, a juvenile from Montes Orno, Crete, has also been studied and it matches in all chaetotaxic characters with *P. (P.) festae festae*. In conclusion, we suggest that *P. (P.) festae coi* should be synonymized with the nominate subspecies.

### Habitat and distribution

Soil-dwelling species previously found on Karpathos and Leros, islands of the Dodecanese Archipelago; also collected in endogean environments at two sites on Crete and at a locality near Izmir, Anatolia, Turkey. It seems to inhabit MSS, where it has also been found at 14 localities in continental Greece.

### *Plusiocampa (Plusiocampa) friulensis* Bareth & Condé, 1984

*Plusiocampa friulensis* Bareth & Condé, 1984: 136, fig. 2.

### Diagnosis (Bareth & Condé 1984)

Slightly troglomorphic species. Antennae with 27 antennomeres; seven simple olfactory chemoreceptors in cupuliform organ; frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae. Unequal claws (more than 1.2) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 4+4 *post* macrosetae; urotergite V with 1+1 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a large area of glandular  $g_1$  setae and enlarged appendages with a large area of glandular  $a_1$  setae; female appendages thinner than those of male, with glandular  $a_1$  setae.

### Habitat and distribution

Subterranean species found at Inghiottoio di Val dei Pai, Montereale Valcellina, Pordenone, Carnic Pre-Alps, Italy.

### *Plusiocampa (Plusiocampa) gadorensis* Sendra, 2001

*Plusiocampa gadorensis* Sendra, 2001: 73, figs 1–4, tables i–ii.

### Diagnosis (Sendra 2001)

Troglomorphic species. Antennae with 46–52 antennomeres; 15–18 complex olfactory chemoreceptors in cupuliform organ; small protruding frontal process with a few slightly tubercular setae. Pronotum with 1+1 *ma*, 2+2–3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 (2+3) *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 (2+3) *lp* macrosetae; long, barbed notal macrosetae; short notal clothing setae. Two or three ventral tibial macrosetae; slightly unequal claws (1.15) with large lateral

crests, posterior claw with no backward overhang. Urotergite II with 0+0–1+1 (0+1) *post* macrosetae; urotergite III with 0+0–1+1 *la*, 1+1–2+2 (0+1) *post* macrosetae; urotergite IV with 1+1 (1+2) *la*, 3+3–4+4 (4+5) *post* macrosetae; urotergite V with 1+1 (1+2) *la*, 4+4–5+5 (4+5) *post* macrosetae; urotergite VI with 1+1 (1+2) *la*, 5+5 (4+5) *post* macrosetae; urotergite VII with 1+1 *la*, 5+5 (4+5) *post* macrosetae; urotergite VIII with 6+6 (6+5) *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7–8+8 (8+9), urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular  $g_1$  setae, subcylindrical appendages with glandular  $a_1$  setae; female and male appendages identical.

### Habitat and distribution

Subterranean species endemic to the isolated karst of Sierra de Gádor, in the Peni-Baetic System, southeastern Iberian Peninsula. It is known from seven natural caves and one mine.

### *Plusiocampa (Plusiocampa) glabra* Condé, 1984

*Plusiocampa glabra* Condé, 1984a: 195, figs 7–9.

### Diagnosis (Condé 1984a)

Troglomorphic species. Antennae with 43 antennomeres; 14 olfactory chemoreceptors within cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *lp*, 1+1 *mp* or *sm* macrosetae; thin, poorly barbed notal macrosetae; very sparse notal and urotergal clothing setae. Two ventral tibial macrosetae; subequal claws (1.0–1.1) with large lateral crests, posterior claw with a small backward overhang. Urotergites I–IV without macrosetae; urotergite V with 2+2 (1+2, 2+3) *post* macrosetae; urotergite VI with 1+1 *la*, 2+2 to 4+4 *post* macrosetae; urotergite VII with 1+1 *la*, 3+3–4+4 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae; abdominal segment IX with 9+9 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a row of glandular  $g_1$  setae and thin subcylindrical appendages with glandular  $a_1$  setae; female and male appendages identical.

### Habitat and distribution

Subterranean species found in Greece, namely at Spilaio Tripa tou Kalivaki, Klenia, Corinthos, southern Balkan Peninsula.

### *Plusiocampa (Plusiocampa) grandii* Silvestri, 1933

*Plusiocampa grandii* Silvestri, 1933b: 1, figs i–ii.

### Diagnosis (Silvestri 1933b; Condé 1954a)

Troglomorphic species. Antennae with 33–38 antennomeres. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; abundant clothing setae. Three ventral tibial macrosetae; unequal claws (1.25) with large lateral crests, posterior claw with a backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergites V–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male unknown; female with subcylindrical appendages bearing glandular  $a_1$  setae.

*Plusiocampa (Plusiocampa) aff. grandii* Silvestri, 1933

**Differential diagnosis against the type form**

Observation of a single female from Inamila Cave in Evia, Greece (Coll. AS). It shows remarkable differences from the type form, such as the more anterior insertion position of *mp* mesonotal and metanotal macrosetae and *post* macrosetae on urotergites I–III. In addition, this Greek form shows important differences in the number and distribution of urotergal macrosetae: urotergite III with 1+0 *la*, 1+1 *post*; urotergite IV with 1+1 *la*, 4+5 *post*; urotergites VI–VII with 3+3 *la*, 5+5 *post*. Others features are: protruding frontal process with abundant tubercular setae; subequal claws with large lateral crests, posterior claw with a backward overhang; smooth subapical tarsal setae; stylus setae with abundant but separated barbs.

**Habitat and distribution**

Subterranean species only found in Bus del Globo Cave, in Trentino, Italian Alps. The aff. form from a cave in Greece should be accepted with caution, as it could be a new taxon.

*Plusiocampa (Plusiocampa) gueorguievi* Bareth & Condé, 2001

*Plusiocampa gueorguievi* Bareth & Condé, 2001: 24, fig. 9.

**Diagnosis** (Bareth & Condé 2001)

Troglomorphic species. Antennae with 29–31 antennomeres; six simple olfactory chemoreceptors in cupuliform organ on probably regenerated antenna; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 0+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; barbed notal clothing setae. Two ventral tibial macrosetae; unequal claws (1.5) with large lateral crests, posterior claw with a backward overhang. Urotergite IV with 1+1 *la*, 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular *g*<sub>1</sub> setae, enlarged appendages with glandular *a*<sub>1</sub> setae.

**Habitat and distribution**

Subterranean species found in Toplya Cave, Stara Planina Mountains (= Balkan Mts), Bulgaria.

*Plusiocampa (Plusiocampa) hoelzeli* (Neuherz, 1984)

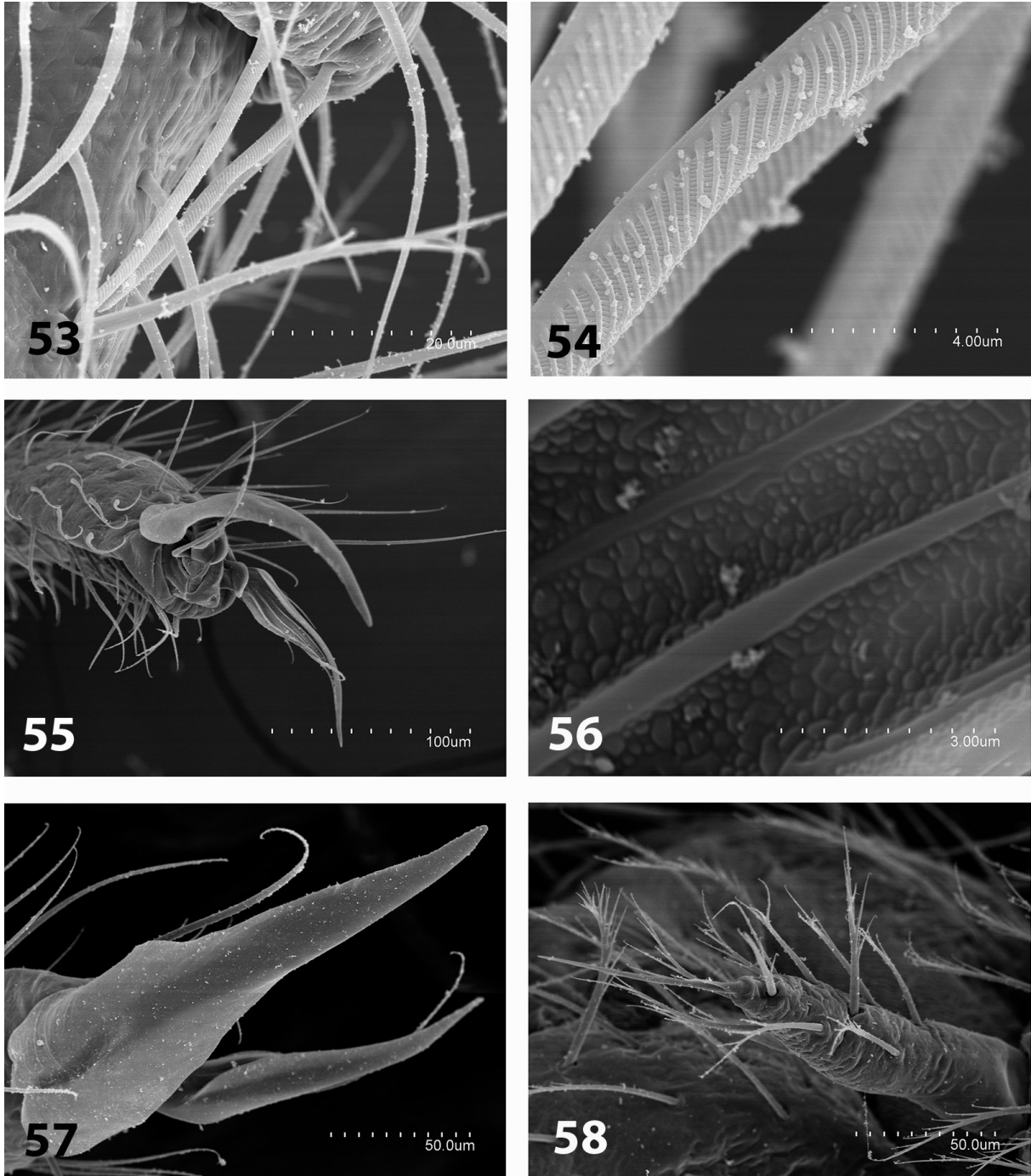
Figs 53–58; Table 5

*Torocampa h lzeli* Neuherz, 1984: 416, figs 1–23, tables i–ii.

**Diagnosis** (Neuherz 1984)

Troglomorphic species. Antennae with 34–35 antennomeres; 10–12 complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2–3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *sma*, 1+1 *la*, 2+2 *lp*, 1+1 (0+1) *smp* macrosetae; metanotum with 1+1 *lp* macrosetae; long, barbed notal macrosetae; long, abundant notal clothing setae. One ventral tibial macroseta (two and three in Renejevo brezno); unequal claws (1.5) with large lateral crests, posterior claw with a backward overhang. Urotergite IV with 0+0–1+1 *la*, 1+1 *post* macrosetae; urotergite V with 1+1 *la*, 2+2–3+3 *post* macrosetae; urotergites VI–VII with 1+1 *la*, 4+4

*post* macrosetae; urotergite VIII with 5+5 *post* macrosetae; abdominal segment IX with 7+7–8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with glandular  $g_1$  setae, slightly enlarged subcylindrical appendages with abundant glandular  $a_1$  setae; female with subcylindrical appendages with glandular  $a_1$  setae.



**Figs 53–58.** *Plusiocampa (Plusiocampa) hoelzeli* (Neuherz, 1984), from Renejevo brezno Cave, collected at a depth of 1180 meters, Kanin Mountains, Slovenia (Coll. AS). **53.** Lateral side of a middle antennomere with several gouge sensilla. **54.** Medial portion of several gouge sensilla, detail. **55.** Pretarsus, lateral posterior view. **56.** Ventral surface of anterior claw, detail. **57.** Pretarsus, with posterior claw in the foreground, dorsal view. **58.** Abdominal stylus.

**Table 5.** *Plusiocampa (Plusiocampa) hoelzeli* (Neuherz, 1984) from Renejevo brezno. Length of the body, antennae, cerci, metathoracic legs and their segments: trochanter, femur, tibia and tarsus (measurements in mm), in addition to the number of antennomeres and cercal articles

Specimen (Coll. AS)	Body length	Antennae		Metathoracic legs						Cerci	
		Length	No. of antennomeres	Coxa	Trochanter	Femur	Tibia	Tarsus	Total	Length	No. of articles
juv.	3.4	2.80	35	0.10	0.10	0.55	0.45	0.50	1.70	1.95	base + 3
♂01	4.7	–	–	0.20	0.20	0.80	0.85	0.70	2.75	4.60	base + 7
♀02	4.8	3.95	34	0.20	0.20	0.85	0.90	0.80	2.95	–	–
♀01	5.1	4.80	34	0.25	0.25	1.00	1.15	0.80	3.45	5.60	base + 9

### Remarks

Five specimens (three females, one male and one juvenile) of *Plusiocampa* were collected at a very deep location, >1180 m deep in Renejevo brezno, Kanin Mountain, Slovenia (see Table S2 in Supplementary Material). No other dipluran has yet been found at such a depth, with the exception of specimens of *Plusiocampa (Stygiocampa)* sp. presently under study from the Lukina jama–Trojama cave system in Croatia, collected by Branko Jalžić (Kazimir Micilinić, pers. obs.). These specimens match the thoroughly described population of *P. (P.) hoelzeli* found only in Hafnerhöhle, Karawanken Mountains in Carinthia. Nevertheless, there is some variability in important taxonomic features. First, the number of ventral tibial macrosetae on the metathoracic leg, with two (three in one leg) rather than only one; presumably, only the prothoracic legs were observed in the original description. In addition, there is variability in the antennomeres and cercal articles; their measurements are recorded (Table 5). Body length from 3.4 to 5.1 mm; antennae shorter than body length, with 10–12 complex olfactory chemoreceptors in cupuliform organ; a whorl of gouge sensilla, 34–38 µm long, on each medial and distal antennomere, with an oblique striation (Figs 53–54); small protruding frontal process with slightly tuberculate anterior macrosetae; pronotum with 1+1 *ma*, 1+1–2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *la*, 2+2 *lp* macrosetae; metanotum with 1+1–0+0 *lp* (0+1–1+1 *slp*) macrosetae; unequal claws, posterior claw 1.4–1.5× as long as anterior claw; posterior claw with a large backward overhang (Figs 55–57); urotergite IV with 1+1 *la*, 1+1 (2+1) *post* macrosetae; urotergite V with 1+1 *la*, 2+2–3+3 (3+1) *post* macrosetae; urotergites VI–VII with 1+1 *la*, 4+4 (4+3) *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 7+7–8+8 (8+7) *post* macrosetae; apical stylus setae with one or two medial thin barbs, subapical and medial setae with a few thin barbs (Fig. 58); cerci longer than body length in adult specimens (Table 5), with several whorls of long, barbed macrosetae on each article in addition to a whorl of smooth, shorter setae in distal position and a characteristic whorl of short, thin setae with a few thin distal barbs in apical position.

### Habitat and distribution

Subterranean species found in a cave in Carinthia (Austria) and another one in the Kanin Mountains (Slovenia).

*Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov.  
[urn:lsid:zoobank.org:act:7C4D40A0-3013-48A3-B3DF-529E78F99DDC](https://zoobank.org/act:7C4D40A0-3013-48A3-B3DF-529E78F99DDC)

Figs 59–94, 204; Tables 6–8

### Etymology

This species is named in honour of Luc Hoffmann (1923–2016), an extraordinary man, a naturalist and philanthropist, who helped create many international conservation organisations and supported conservation research and actions in the Mediterranean and elsewhere.

**Table 6.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov. Length of the body and antennae (measurements in mm), in addition to the number of antennomeres.

Specimen	Depository	Locality	Body length	No. of antennomeres	Antennal length
♀, holotype	MZB	Spilaio Doxa	5.9	53	9.3
♂, paratype	Coll. AS	Spilaio Sfentoni Trypa	7.4	53	telescoped
♀, paratype	Coll. AS	Varathro Stou Bokou ton Poro	5.9	46	7.5
♀, paratype	Coll. AS	Varathro Stou Bokou ton Poro	6.1	53	8.3
♀, paratype	Coll. AS	Varathro Psistraki	5.8	48	8.0
♂, paratype	Coll. AS	Varathro Psistraki	6.5	52	8.9
juv., paratype	Coll. AS	Varathro Psistraki	4.8	49	5.2

### Material examined

#### Holotype

GREECE • ♀; Crete, Marathos nomos Iraklion, Spilaio Doxa (n. 1065); 490 m a.s.l.; 11 May 2005; Fulvio Gasparo leg.; MZB.

#### Paratypes

GREECE – Crete • 2 ♂♂, 2 ♀♀; same collection data as for holotype but 2 Jun. 2002; Coll. AS • 1 ♀; Zoniana nomos Rethymon, Spilaio Sfentoni Trypa (n. 701); 630 m a.s.l.; 11 Apr. 2003; Kaloust Paragamian leg.; Coll. AS • 6 ♀♀; Krousonas, Malevizi, Krousaniotiko Livadi, Varathro Stou Bokou ton Poro; 1 Jul. 1990; Kaloust Paragamian leg.; Coll. AS • 1 ♀; Mylopotamos, Livadia, Varathro Sipouli; 24 Mar. 1990; Kaloust Paragamian leg.; Coll. AS • 1 ♂, 2 ♀♀; Malevizi, Gonies, Varathro Psistraki; 20 Nov. 2005; Kaloust Paragamian and S. Paragamian leg.; Coll. AS.

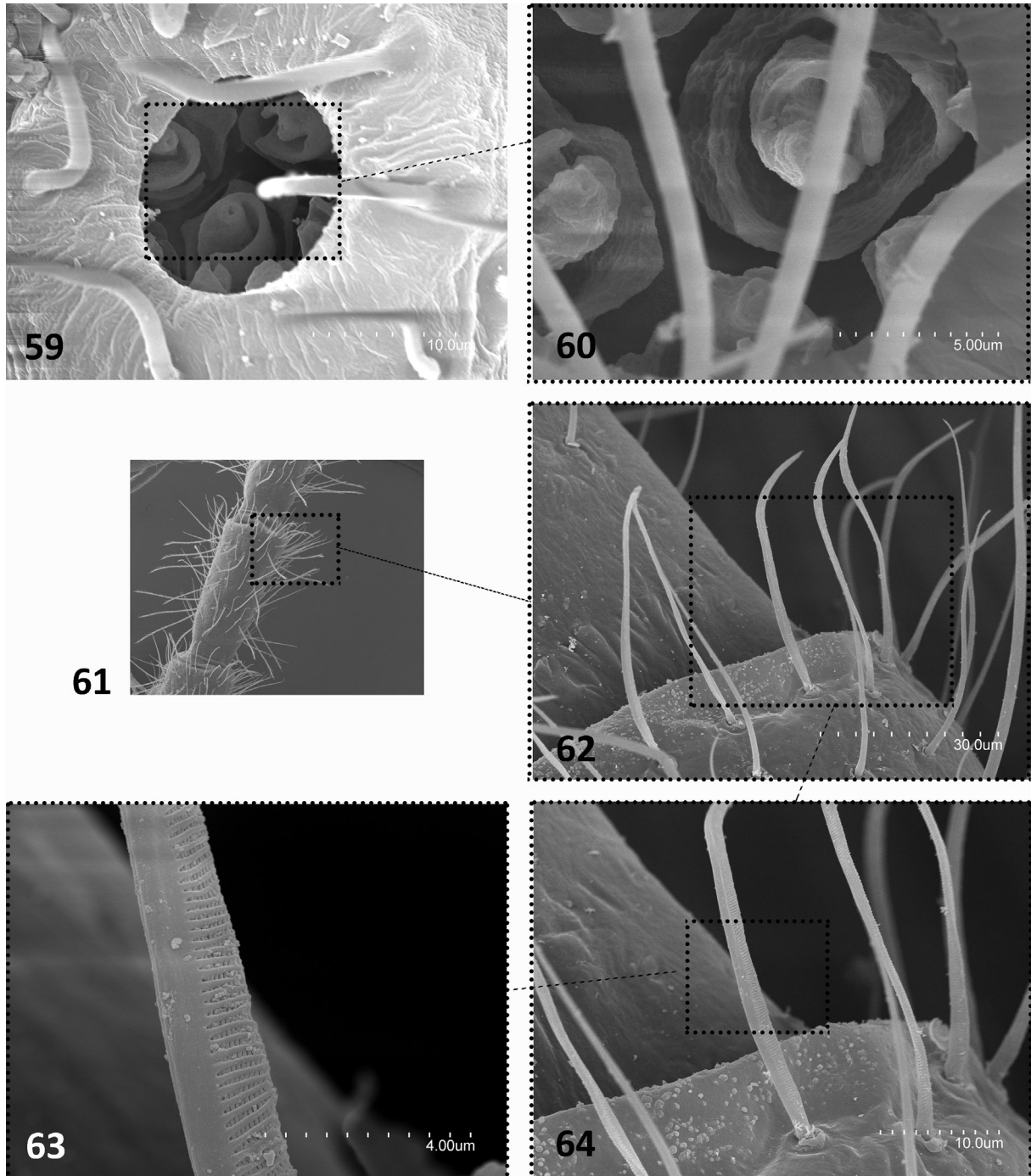
### Description

**BODY.** Body length: 4.8 mm (juvenile), 4.7 and 5.4 mm (males from Spilio Doxa), 5.9 and 6.4 mm (females from Spilio Doxa), and 7.4 mm (male from Sfentoni Trypa). Epicuticle smooth under optical microscope, but reticulate at high magnification (Figs 68–69); body with thin, long clothing, smooth or with a few thin distal barbs on dorsal side and well barbed on ventral side, legs and urosternal appendages.

**HEAD.** Antennae with 44–53 antennomeres; central antennomeres 2.5–3× as long as wide, apical antennomere 2.5× as long as wide (Fig. 61). Large cupuliform organ occupying ¼ of total length of apical antennomere, with 8–10 complex olfactory chemoreceptors (Figs 59–60). Small coniform sensillum of third antennomere located in ventral position between *c* and *d* macrosetae. Thin and long gouge sensilla, 38–50 µm long, in a single distal whorl of 10–14 sensilla on each medial and distal antennomere (Figs 62–64). Protruding frontal process with tubercular setae and macrosetae with thin barbs. Three macrosetae along line of insertion of antennomere and *x* setae relatively long, covered from distal third to fourth (Figs 65–66).

**THORAX.** Thoracic macrosetal distribution (Fig. 67): pronotum with 1+1 *ma*, 4+4 *la*<sub>1,2,3,4</sub>, 2+2 *lp*<sub>2,3</sub>; mesonotum with 1+1 *ma*, 3+3 *la*<sub>1,2,3</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*; metanotum with 1+1 *ma*, 0+0, 0+1, 1+1, 1+2 *la* or 0+1, 1+1 *sla*, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*. All medial posterior macrosetae in a forward position. All long, thin notal macrosetae with very thin barbs along distal third or half; marginal setae longer than clothing setae, covered by a few thin distal barbs. Legs elongated, metathoracic legs overpassing end of abdomen at beginning of tarsus. Tibia longest part of leg, 1.11–1.30× as long as tarsus and 1.21–1.37× as long

as femur (Table 7). Ratios between lengths of tibia, tarsus and femur seem more or less fixed (Table 7). Femora II–III with one long, thin dorsal macroseta and one shorter ventral macroseta. Tibiae I–III with two or three ventral macrosetae surrounded by thin, short barbs. Calcars surrounded from base almost to tip by thin, short barbs. Metatarsus with a pseudo-articulation on distal third. Typical double rows



**Figs 59–64.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., from Varathro Stou Bokou ton Poro, Krousonas, Crete (59, 62–64) and Varathro Mythia Kabathoura, Rethymno, Crete (60–61) (Coll. AS). **59.** Cupuliform organ. **60.** Olfactory chemoreceptors. **61.** Medial antennomere. **62.** Latero-distal view of medial antennomere with gouge sensilla. **63.** Gouge sensilla, detail. **64.** Gouge sensilla of medial antennomere.

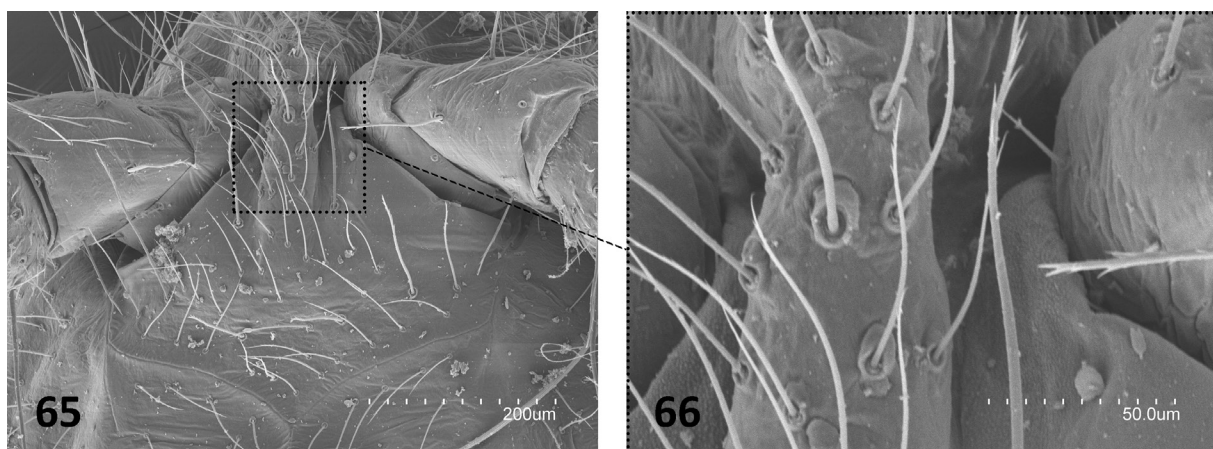


**Table 7.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov. Length of the body, metathoracic legs and their segments: trochanter, femur, tibia and tarsus (measurements in mm).

Specimen	Depository	Locality	Body length	Femur	Tibia	Tarsus	Tibia/Femur	Tibia/Tarsus	Tarsus/Femur
juv., paratype	Coll. AS	Varathro Psistraki	3.7	0.70	0.85	0.75	1.21	1.13	1.07
♂, paratype	Coll. AS	Spilaio Doxa	4.7	0.71	0.95	0.82	1.34	1.16	1.16
juv., paratype	Coll. AS	Varathro Psistraki	4.8	0.8	1.0	0.9	1.25	1.11	1.12
♂, paratype	Coll. AS	Spilaio Doxa	5.4	1.15	1.50	1.17	1.30	1.28	1.02
♀, paratype	Coll. AS	Varathro Psistraki	5.5	1.15	1.5	1.3	1.30	1.15	1.13
♀, paratype	Coll. AS	Varathro Psistraki	5.7	1.1	1.5	1.25	1.36	1.20	1.14
♀, paratype	Coll. AS	Varathro Psistraki	5.8	1.30	1.65	1.35	1.27	1.22	1.04
♀, holotype	MZB	Spilaio Doxa	5.9	1.19	1.47	1.21	1.24	1.22	1.02
♀, paratype	Coll. AS	Varathro Stou Bokou ton Poro	6.1	1.25	1.6	1.4	1.28	1.14	1.12
♀, paratype	Coll. AS	Spilaio Doxa	6.4	1.18	1.62	1.34	1.37	1.21	1.14
♂, paratype	Coll. AS	Varathro Psistraki	6.5	1.35	1.75	1.35	1.30	1.30	1.00
♀, paratype	Coll. AS	Varathro Psistraki	6.7	1.3	1.75	1.40	1.35	1.25	1.08
♀, paratype	Coll. AS	Varathro Sipouli	7.4	1.4	1.75	1.5	1.25	1.17	1.07

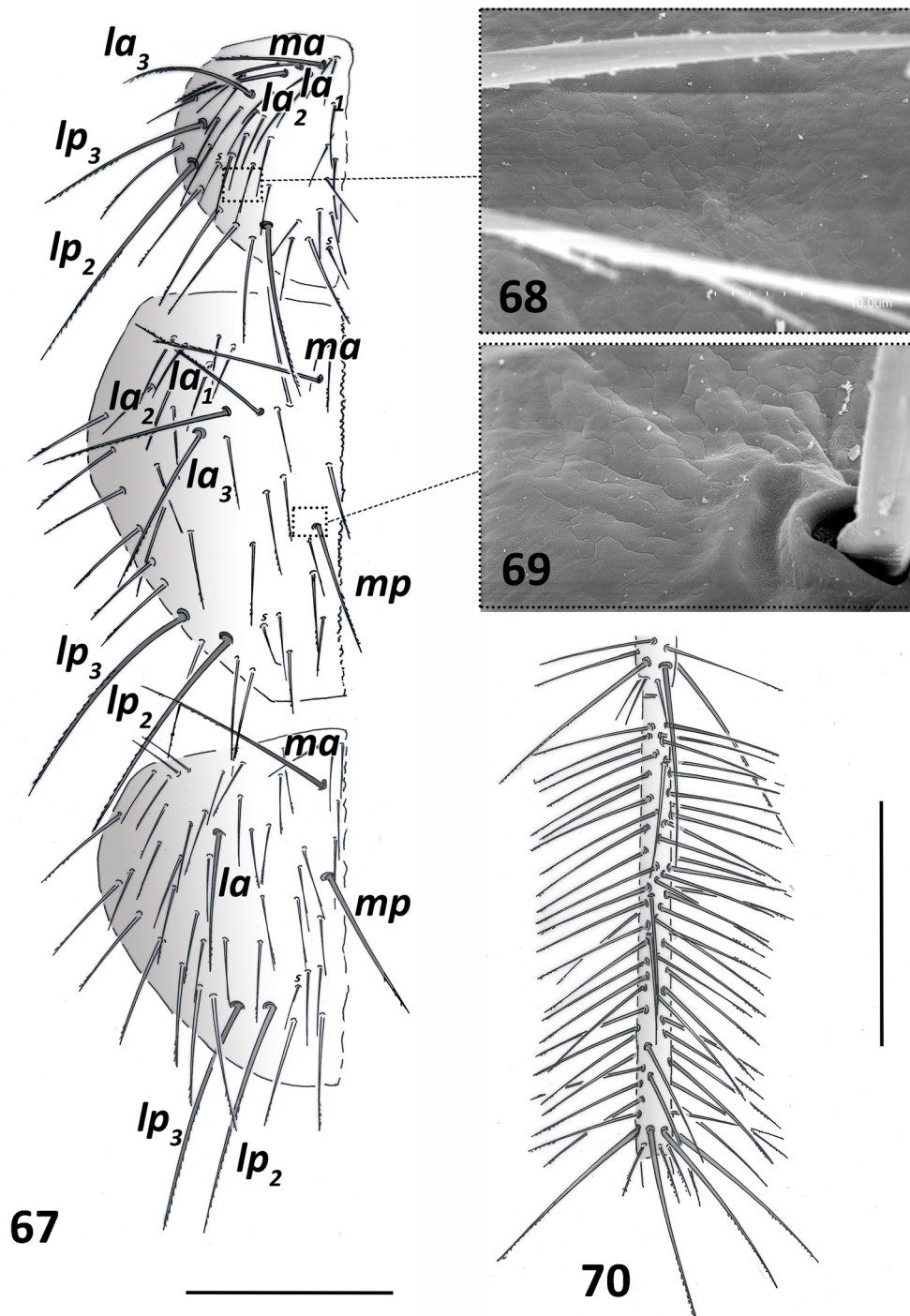
of thick, completely barbed setae along ventral side of tarsus. Dorsal and lateral subapical tarsal setae completely covered by thin barbs nearly from base almost to tip. Subequal to slightly unequal claws (posterior claw  $1.05\text{--}1.15\times$  as long as anterior one), with large lateral crests well developed on posterior claw prolonged backwards. Ventral side of claws with longitudinal ridges separated by a surface of micro-hemispherical structures. Pretarsal processes setiform, with abundant, very short proximal barbs (Figs 71–82).

ABDOMEN. Distribution of abdominal macrosetae on tergites:  $1+1\ post_1$  on I–II;  $1+1-0+0\ la$ ,  $1+1\ post_1$  on III;  $1+1\ la$ ,  $3+3-4+4\ post_{1,2,4,5}$  on IV;  $1+1\ la$ ,  $5+5\ post_{1-5}$  on V–VII,  $7+7\ post$  on VIII;  $8+8-9+9\ post$  on abdominal segment IX. Urosternite I with  $7+7-9+9$ , urosternites II–VII with  $5+5-7+7$ , urosternite VIII with  $2+2$  macrosetae; all urosternal macrosetae robust, large, covered by long barbs along distal half to four-fifths (Figs 87–88). Stylus with subapical setae longer and more barbated, in fact completely



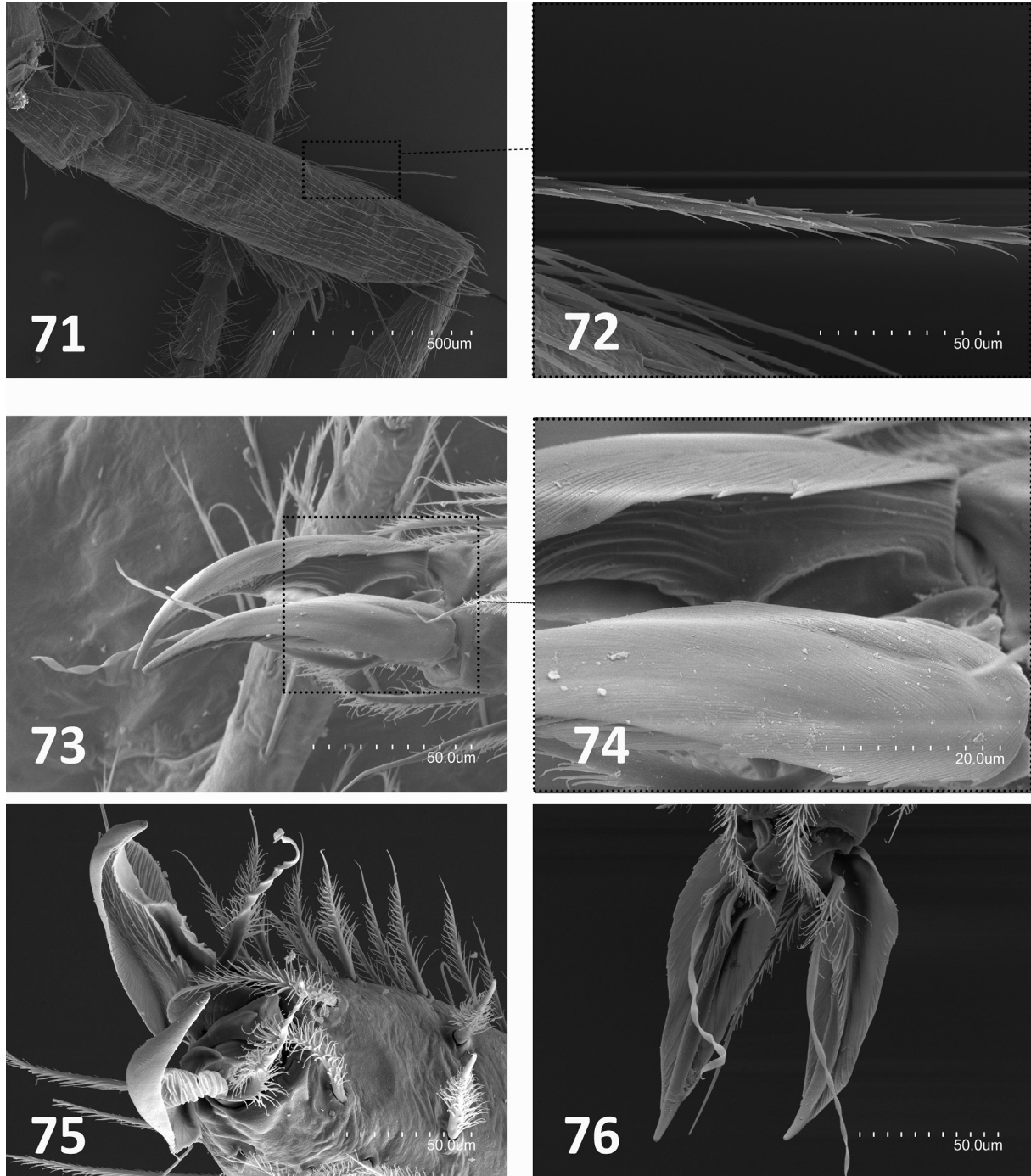
**Figs 65–66.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., from Varathro Stou Bokou ton Poro, Krousonas, Crete (Coll. AS). **65.** Frontal process. **66.** Anterior zone of frontal process.

surrounded by short, abundant barbs, more numerous on apical and ventromedial setae (Figs 92–93); large eversible vesicles (Figs 92, 94). Two complete cerci, 2.37 and 1.71 × as long as body; this ratio higher in an incomplete 14.50 mm long cercus of 5.4 mm long male (Table 8); up to 11 articles, covered



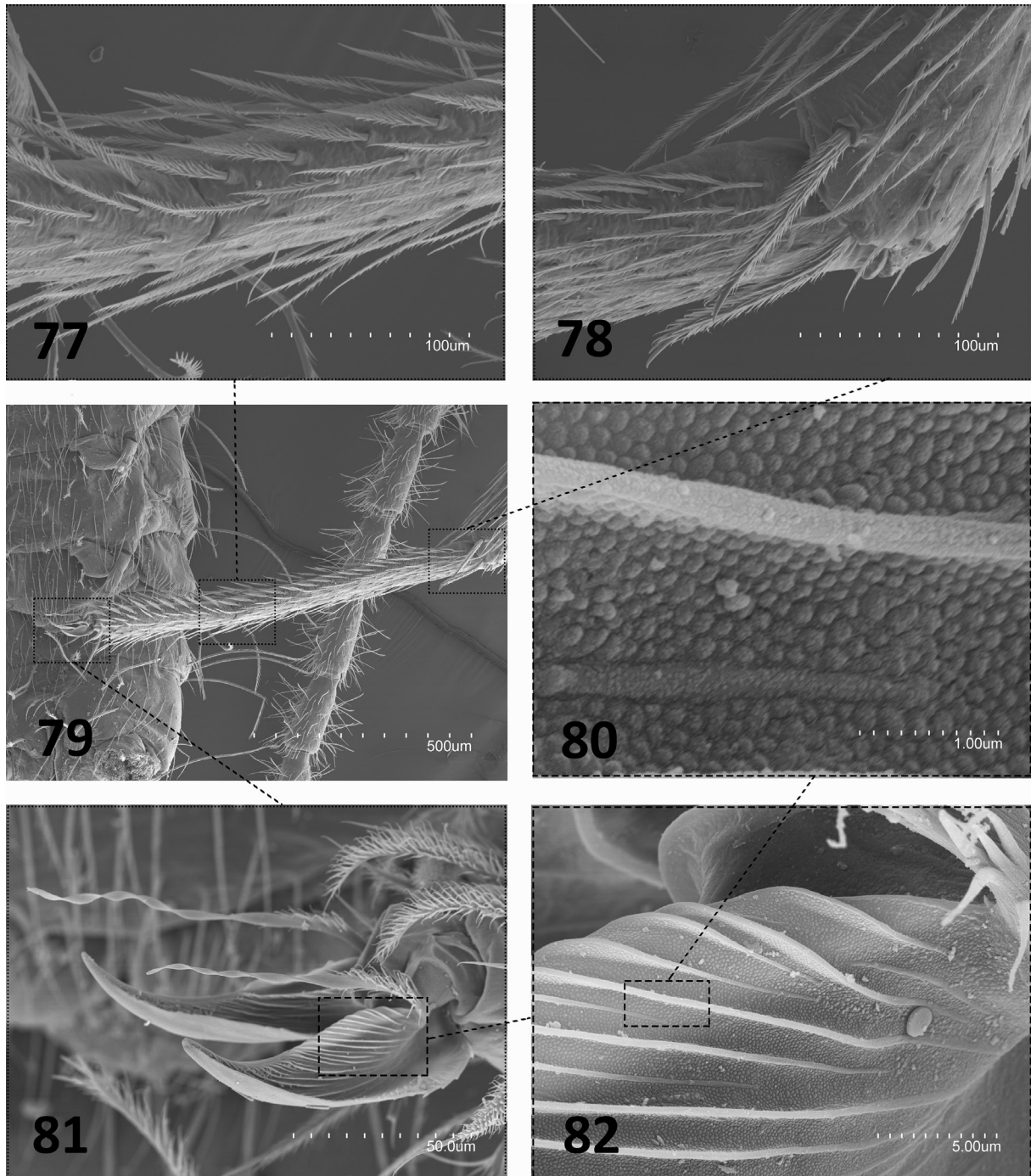
**Figs 67–70.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov. **67, 70.** Paratype, ♂, 5.4 mm long, from Spilaio Doxa, Marathos, Irakleo Prefecture, Crete (MZB). **68–69.** Specimen from Varathro Mythia Kabathoura, Rethymno, Crete (Coll. AS). **67.** Pronotum, mesonotum and metanotum, left side. **68.** Surface of pronotum. **69.** Surface of mesonotum. **70.** Fourth cercal article. Scale bars: 67 = 0.4 mm; 70 = 0.5 mm.

with numerous disorganized, long, thin macrosetae with thin barbs along distal half, in addition to a distal whorl of longer, thicker macrosetae on each article plus an apical whorl of barbed, thin, short clothing setae (Fig. 70).



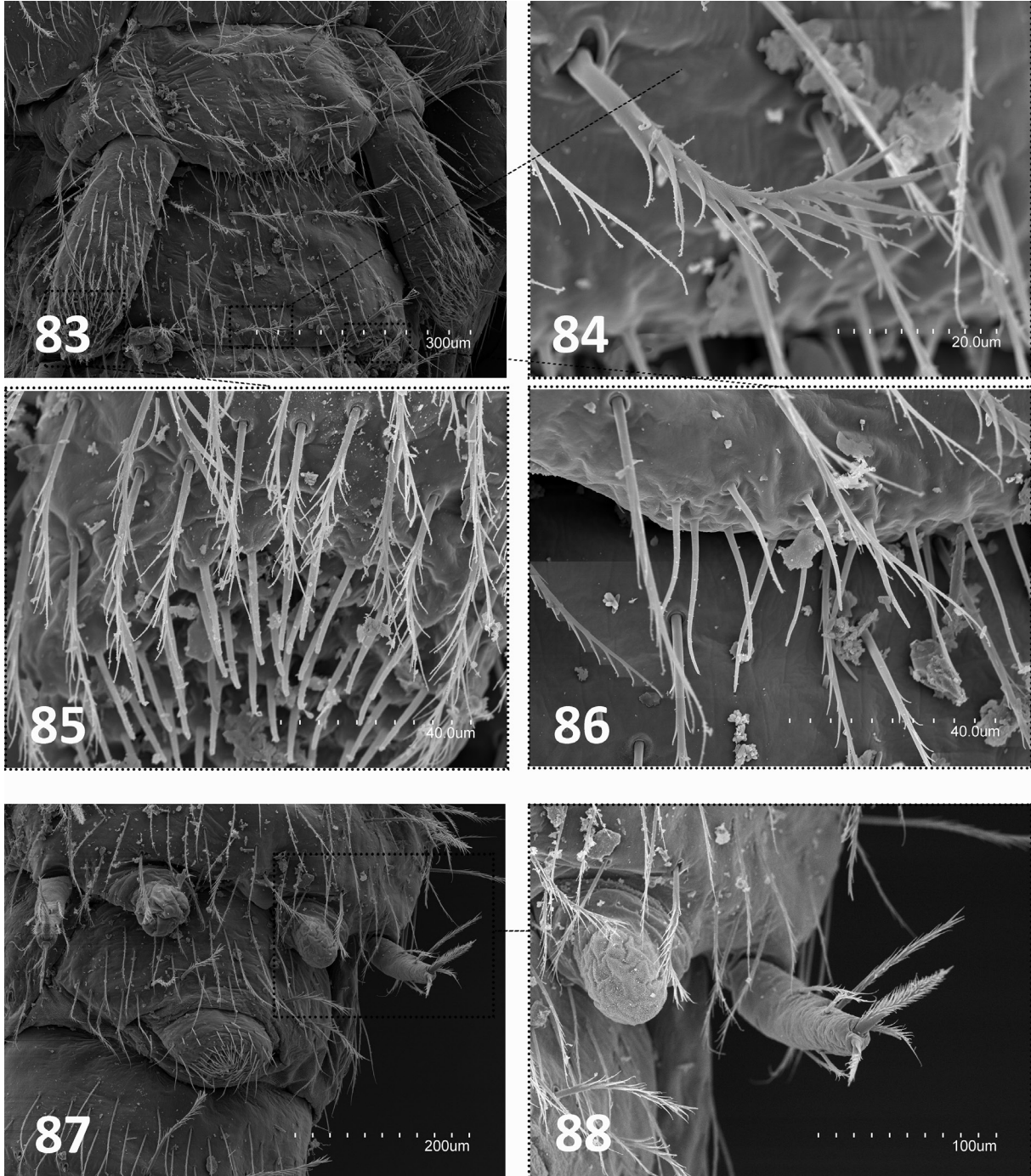
**Figs 71–76.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., from Varathro Stou Bokou ton Poro, Krousonas, Crete (71–74) and Varathro Mythia Kabathoura, Rethymno, Crete (75–76) (Coll. AS). **71.** Femur of metathoracic leg. **72.** Dorsal femoral macroseta, metathoracic leg. **73.** Dorso-lateral view of pretarsus, posterior claw in the foreground. **74.** Detail of preceding, posterior claw in the foreground. **75.** End of tarsus, with pretarsus in ventral view. **76.** Pretarsus, ventral view.

SECONDARY SEX CHARACTERS. Female urosternite I with subcylindrical appendages, each bearing up to 18 glandular  $a_1$  setae in a distal area (Figs 89–91). Male urosternite I (Figs 83–86) with a posterior area of up to 160 glandular  $g_1$  setae in larger male from Sfedoni Trypa (absent in smaller male); with



**Figs 77–82.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., metathoracic leg of ♀ from Varathro Stou Bokou ton Poro, Krousonas, Crete (Coll. AS). **77.** Medial portion of tarsus in latero-ventral view, with a visible pseudo-articulation. **78.** Joint between tibia and tarsus with their calcaria. **79.** Tarsus. **80.** Detail of ventral side of anterior claw, lateral view. **81.** Pretarsus, lateral anterior view. **82.** Anterior claw, detail.

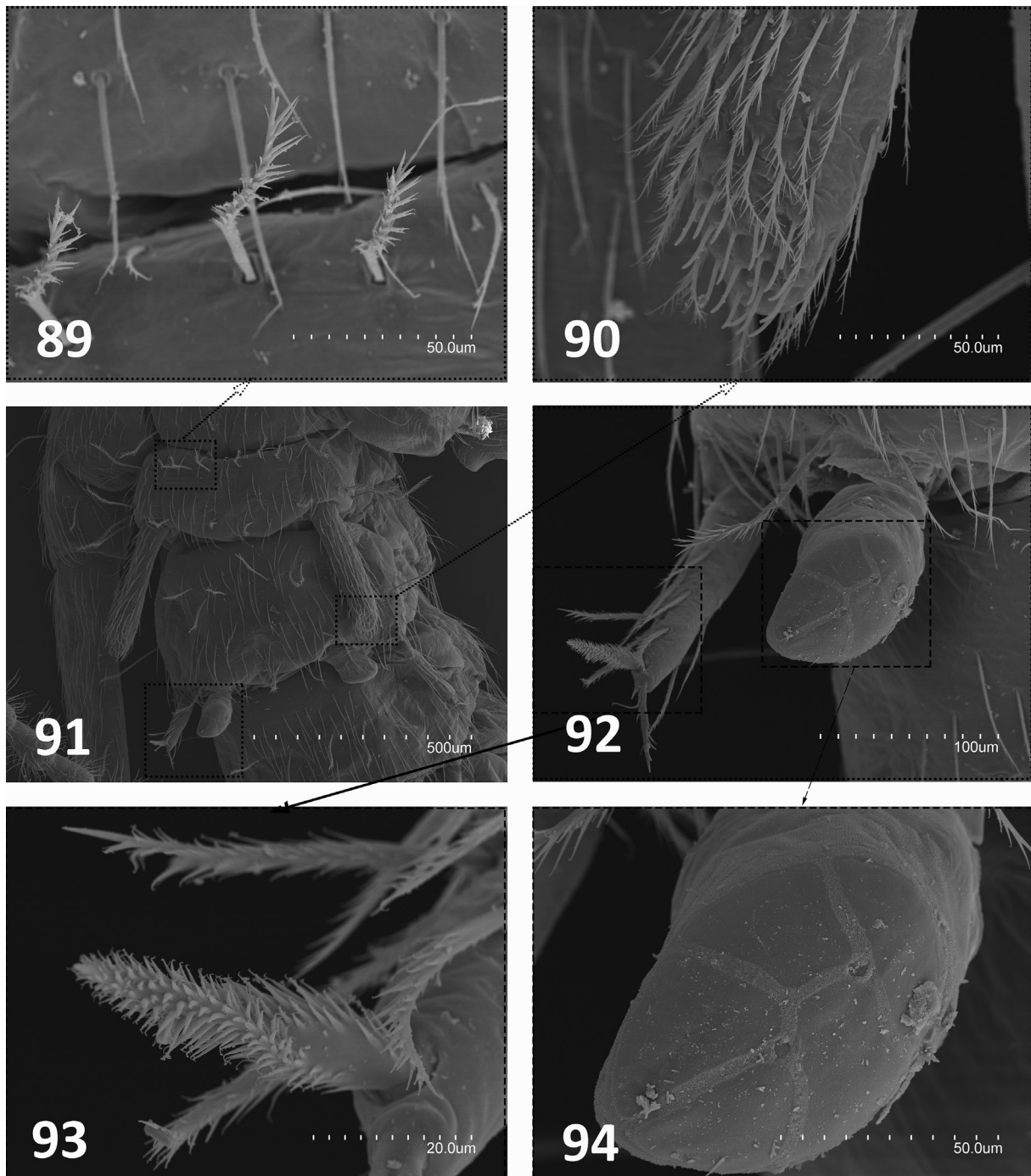
thick, large, subcylindrical appendages, much thicker than female appendages, each bearing up to 100 glandular  $a_1$  setae in a large distal area in two largest adults. Spermatozoid fascicles with a thick spiral filament.



**Figs 83–88.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., ♂, from Varathro Mythia Kabathoura, Rethymno, Crete (Coll. AS). **83.** Urosternites I–II. **84.** Macroseta on posterior portion of urosternite I. **85.** Tip of urosternal appendage. **86.** Latero-interior portion of posterior edge, with glandular  $g_1$  setae. **87.** Urosternites VII–IX. **88.** Left latero-posterior portion of urosternite VII.

### Phyletic affinities, habitat and distribution

The presence of medial posterior macrosetae on the mesonotum and metanotum relates *P. (P.) hoffmanni* sp. nov. to almost half of the species in the subgenus *Plusiocampa*, all living in the European region, including most of the Mediterranean islands. Among them, *P. (P.) festae* is probably the closest related species due to the distribution pattern of their notal macrosetae; in spite of the fact that both species live



**Figs 89–94.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., ♀, from Varathro Stou Bokou ton Poro, Krousonas, Crete (Coll. AS). **89.** Macrosetae on anterior portion of urosternite I. **90.** Distal portion of an appendage on urosternite I. **91.** Urosternites I–II. **92.** Stylus and abdominal eversible vesicle. **93.** Detail of a stylus with subapical seta. **94.** Abdominal eversible vesicle, detail.

**Table 8.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov. Length of the body, cerci and their articles (measurements in mm).

Specimen	Depository	Locality	Body length	Base	1 <sup>st</sup>	2 <sup>nd</sup>	3 <sup>rd</sup>	4 <sup>th</sup>	5 <sup>th</sup>	6 <sup>th</sup>	7 <sup>th</sup>	8 <sup>th</sup>	9 <sup>th</sup>	10 <sup>th</sup>	11 <sup>th</sup>	Total
♂, paratype	Coll. AS	Spilaio Doxa	5.4	1.1	0.6	0.7	0.9	1.0	1.3	1.5	1.9	2.1	2.4	incompl.	–	14.50
♀, paratype	Coll. AS	Varathro Psistraki	6.7	2.4	0.6	0.7	0.8	0.85	0.9	0.95	1.1	1.5	1.9	1.95	2.2	15.85
♀, paratype	Coll. AS	Varathro Sipouli	7.4	1.1	0.75	0.8	1.15	1.35	1.95	2.35	3.2	–	–	–	–	12.65

in Crete (Condé 1984a; Silvestri 1933a), they occupy different habitats, *P. (P.) hoffmanni* sp. nov. in deep subterranean habitats, *P. (P.) festae* in soil and subterranean superficial habitats. In addition to this ecological difference, there are several important features that allow them to be separated. *Plusiocampa (P.) hoffmanni* sp. nov. has troglomorphic traits, with longer appendages than *P. (P.) festae* and more antennomeres and cercal articles, with more complex and more numerous olfactory chemoreceptors within the cupuliform organ. In *P. (P.) hoffmanni* sp. nov., the claws are slightly unequal to subequal, but with large lateral crests and a backward prolongation of the posterior claws. Additionally, *P. (P.) hoffmanni* sp. nov. shows a protruding frontal process covered by tuberculated setae, 8+8 macrosetae on the first urosternite and 6+6 on the second to seventh urosternites. Some of these features also separate *P. (P.) hoffmanni* sp. nov. from *P. (P.) rybaki*, a poorly described troglomorphic species from the southern Balkan Peninsula (Condé 1956). *Plusiocampa (P.) hoffmanni* sp. nov. has been collected from the deep zone of 14 caves in the numerous karst areas of Crete (Fig. 204).

***Plusiocampa (Plusiocampa) humicola* Ionescu, 1951**

*Plusiocampa humicola* Ionescu, 1951: 528, figs 1–6.

**Diagnosis** (Ionescu 1951; Sendra *et al.* 2012b)

Non-troglomorphic species. Antennae with 21–23 doliiform antennomeres; four or five olfactory chemoreceptors; frontal process without non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae; slightly unequal claws (1.1–1.2) with large lateral crests, posterior claw without backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 4+4 *post* macrosetae; urotergite V with 1+1 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae; subcylindrical appendages with glandular *a*<sub>1</sub> setae. Appendages of female slightly thinner, subcylindrical, with glandular *a*<sub>1</sub> setae.

**Habitat and distribution**

Soil-dwelling species found at four sites around the South Carpathian Mountains, including the Transylvanian reliefs, Romania.

***Plusiocampa (Plusiocampa) hystricula* Bareth & Condé, 1984**

*Plusiocampa hystricula* Bareth & Condé, 1984: 133, fig. 1.

**Diagnosis** (Bareth & Condé 1984)

Troglophilic species. Antennae with 31 antennomeres (regenerated antenna); frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae. Two ventral tibial macrosetae; slightly unequal claws (1.2) with large lateral crests, posterior claw with a small backward overhang. Urotergite I with 2+2 *post* macrosetae; urotergite II with 2+3 *post* macrosetae; urotergite III with 3+3 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergites V–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae; abdominal segment IX with 9+9 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female with subcylindrical appendages bearing glandular  $a_1$  setae.

**Habitat and distribution**

Subterranean species, found only in Bus de Bec Cave, Brescia, Italian Alps.

*Plusiocampa (Plusiocampa) isterina* Condé, 1993

*Plusiocampa isterina* Condé, 1993a: 736, figs 1a, 2, 3a, 4, 6a.

**Diagnosis** (Condé 1993a, 1996)

Non-troglophilic species. Antennae with 23 antennomeres; four simple olfactory chemoreceptors in cupuliform organ; slightly protruding frontal process with some slightly tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 (2+1) *la*, 2+2 *lp* macrosetae; long, thin, barbed notal macrosetae; short, smooth clothing setae. Two ventral tibial macrosetae; unequal claws (1.29) with large lateral crests, posterior claw with a backward overhang; pretarsal processes short, with a few sparse barbs. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergites IV–V with 1+1 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; subcylindrical female appendages bearing glandular  $a_1$  setae.

*Plusiocampa (Plusiocampa) aff. isterina* Condé, 1993

**Differential diagnosis against the type form**

This record is based on seven specimens found in Ledenjača Cave, Bosnia and Herzegovina (see [Table S2](#) in Supplementary Material). Due to their clear differences from the type of *P. (P.) isterina*, described from Movile Cave, they have been identified as *P. (P.) aff. isterina*. Specimens from Ledenjača Cave have a higher number of antennomeres (25–28), six olfactory chemoreceptors in a relatively large cupuliform organ (occupying one third of a short antennomere) and a clearer protruding frontal process with remarkable tuberculate setae.

**Habitat and distribution**

Non-troglophilic species. The nominate form is found in Peștera Movile Cave, Southern Dobruja, Romania. The aff. form is found in a cave in the Dinaric Mountains, Bosnia and Herzegovina.



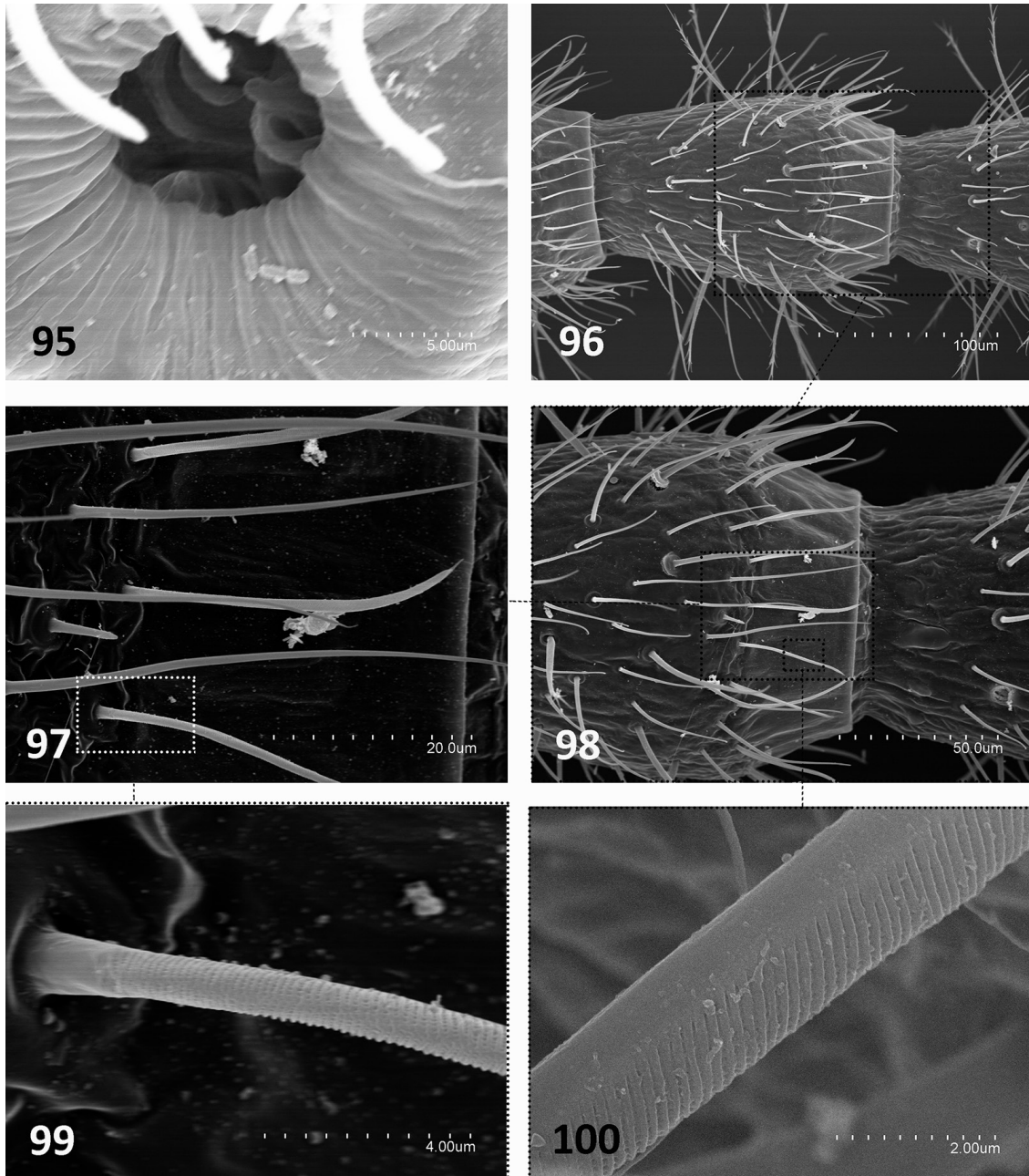
*Plusiocampa (Plusiocampa) lagari* Sendra & Condé, 1987

Figs 95–118, 203

*Plusiocampa lagari* Sendra & Condé, 1987: 741, figs 1–4, tables 1–3.

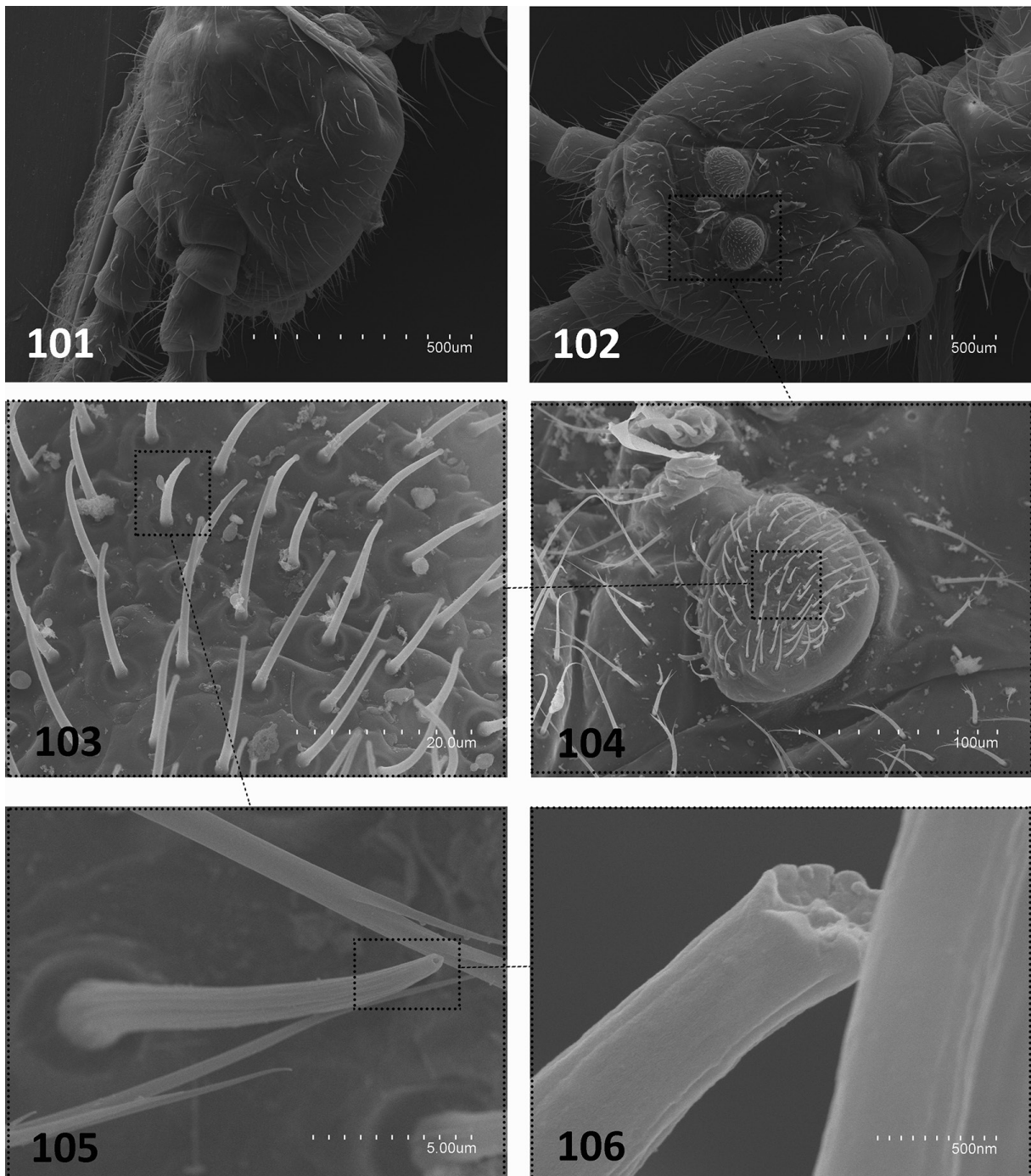
**Diagnosis** (Sendra & Condé 1987; Sendra 2001; Sendra *et al.* 2004)

Troglomorphic species. Antennae with 32–34 antennomeres; 15–18 complex olfactory chemoreceptors in cupuliform organ; slightly protruding frontal process with non-tubercular setae. Pronotum with 1+1



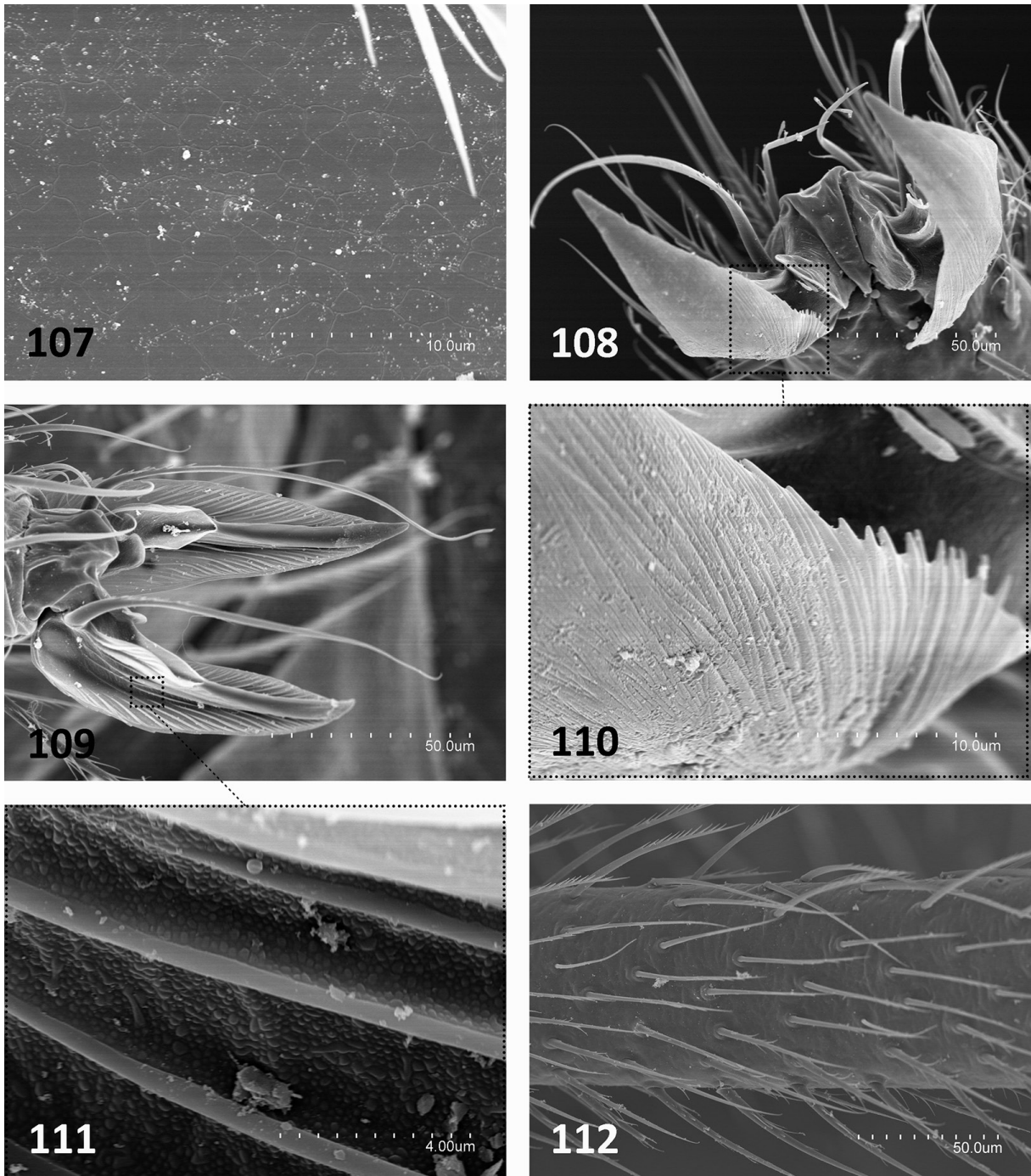
**Figs 95–100.** *Plusiocampa (Plusiocampa) lagari* Sendra & Condé, 1987, from Chorros Cave, Riopar, Albacete, Spain (Coll. AS). **95.** Cupuliform organ. **96.** Medial antennomere. **97.** Gouge and coniform sensilla. **98.** Medial antennomere, detail with gouge and coniform sensilla. **99.** Base of gouge sensillum, detail. **100.** Medial portion of gouge sensillum, detail.

*ma*, 3+3 (4+3) *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* (1+1 *lp* supplementary in some populations), 1+1 *mp* macrosetae. Two or three ventral tibial macrosetae; subequal claws (1.1) with large lateral crests, posterior claw with a small backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2–3+3–4+3 *post* macrosetae; urotergites V–VII with 1+1 *la*, 5+5 (4+5) *post* macrosetae; urotergite



**Figs 101–106.** *Plusiocampa (Plusiocampa) lagari* Sendra & Condé, 1987, from Chorros Cave, Riopar, Albacete, Spain (Coll. AS). **101.** Head, dorso-lateral view. **102.** Head, ventral view. **103.** Detail of labial palp. **104.** Labial palp. **105.** Neuroglandular seta. **106.** Tip of neuroglandular seta.

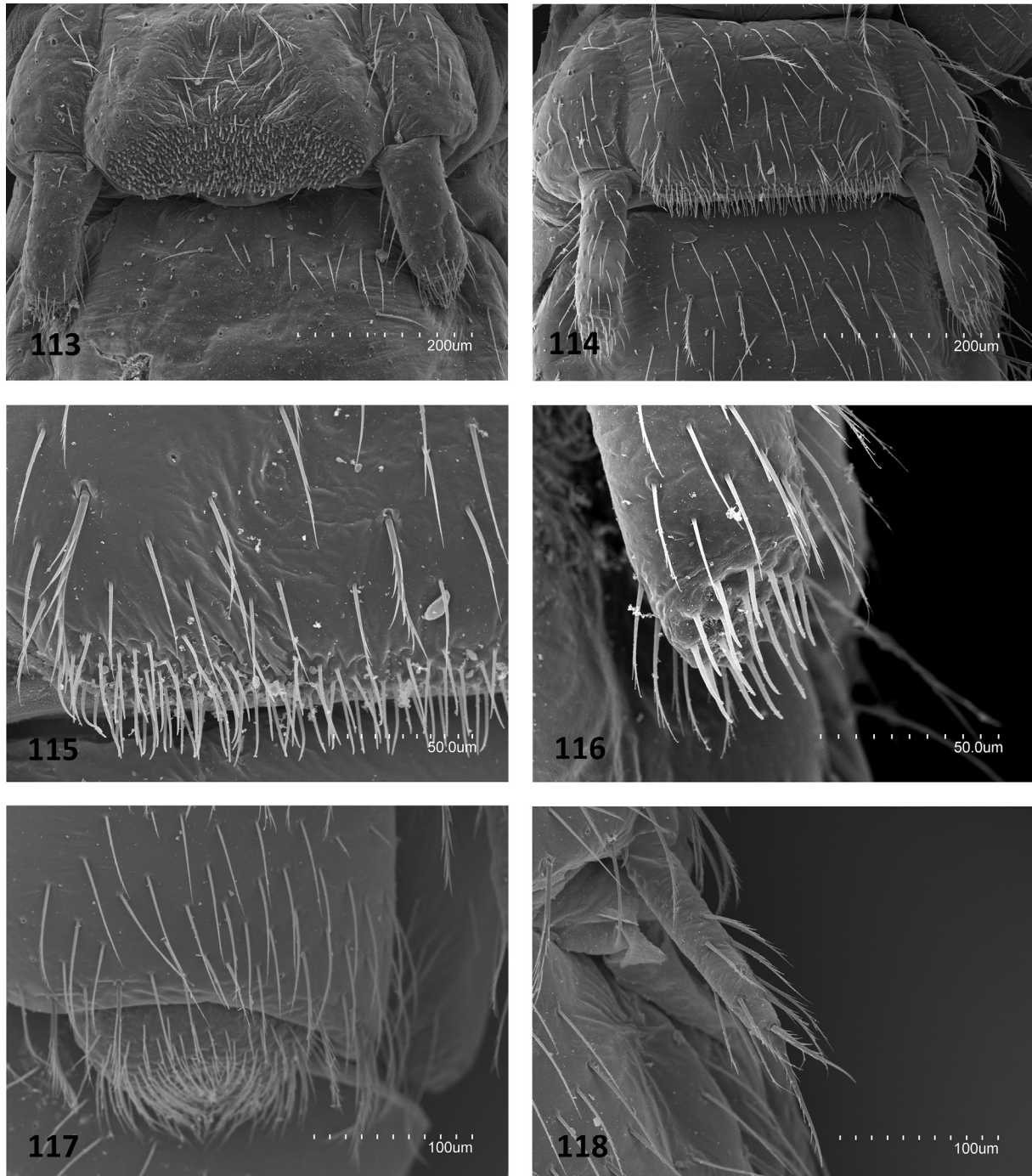
VIII with 6+6 (6+5, 6+7) *post* macrosetae; abdominal segment IX with 8+8 (8+9) *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a narrow area of glandular  $g_1$  setae, subcylindrical appendages with glandular  $a_1$  setae; female with subcylindrical appendages bearing glandular  $a_1$  setae. Spermatozoid fascicle wheels with  $1\frac{1}{2}$  turns of 110–140  $\mu\text{m}$  long and 6  $\mu\text{m}$  wide filament.



**Figs 107–112.** *Plusiocampa (Plusiocampa) lagari* Sendra & Condé, 1987, from Chorros Cave, Riopar, Albacete, Spain (Coll. AS). **107.** Surface of metanotum, detail. **108.** Pretarsus, frontal-dorsal view. **109.** Pretarsus, ventral view. **110.** Lateral crest of posterior claw, detail. **111.** Lateral crest, ventral view, detail. **112.** Portion of medial tarsus.

### Remarks

Ten specimens from the Chorros and Farallón Caves in Riopar, Albacete, Spain (see [Table S2](#) in Supplementary Material) were used for SEM to study some features that are difficult to observe under an optical microscope. Epicuticle slightly reticulate, with large polygonal pattern (Fig. 107); antennomeres



**Figs 113–118.** *Plusiocampa (Plusiocampa) lagari* Sendra & Condé, 1987, adult ♂♂, from Farallón Cave, Riopar, Albacete, Spain (Coll. AS). **113.** Urosternite I of a large adult ♂. **114.** Urosternite I. **115.** Distal portion of appendage of a urosternite. **116.** Detail of posterior portion of urosternite I with glandular  $g_j$  setae. **117.** Urosternite VIII. **118.** Lateral part of urosternite VII, with stylus.

with a whorl of thin gouge sensilla, 34–36 µm long, with an external transversal striped surface (Figs 96–100). Cupuliform organ with spheroidal olfactory chemoreceptors in a complex spiral shape (Fig. 95). Head suboval with slightly protruding frontal process (Figs 101–102). Labial palp with short neuroglandular setae (Figs 103–106). Tarsus with two ventral barbed rows (Fig. 112). Claws with large lateral crest with dorsal striated surface and with ventral longitudinal grooves separated by a multi-hemispherical surface (Figs 108–111). Male with a large area of glandular  $g_1$  setae and slightly thicker subcylindrical appendages (Figs 113–117). Styler setae covered by a few thin, short barbs (Fig. 118).

### Habitat and distribution

Subterranean species found in 31 caves in the external zone of the Baetic Mountain Range, around the carbonate areas of the Cazorla, Segura, Alcaraz and Castril Mountains and the peripheral karst areas of Filabres Mountain and the Yesos de Sorbas, southeastern Iberian Peninsula (Fig. 203).

#### *Plusiocampa (Plusiocampa) lagoi* Silvestri, 1932

*Plusiocampa lagoi* Silvestri, 1932: 78, figs xiii–xiv.

### Diagnosis (Silvestri 1932a)

Non-trogomorphic species. Antennae with 23–26 antennomeres; non-protruding frontal process with simple setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae; subequal claws (1.05) with large lateral crests without prolonged backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergites V–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae; urosternite I with 8+8, urosternite II–VII with 5+5, urosternite VIII with 2+2 macrosetae.

#### *Plusiocampa (Plusiocampa) aff. lagoi* Silvestri, 1932

### Differential diagnosis against the type form

One female and two juveniles (Coll. AS) collected in a couple of Croatian caves (see [Table S2](#) in Supplementary Material) show several differences from the type form in: the non-trogomorphic shape; antennae with 24 antennomeres and four simple olfactory chemoreceptors; the number of urotergal macrosetae, with 1+1 *post* macrosetae on urotergite III, 6+6 *post* macrosetae on urotergite VIII and 8+8 *post* macrosetae on abdominal segment IX; and a unique ventral tibial macroseta.

### Habitat and distribution

Hypogean species found in edaphic habitats. The nominate form is known from a couple of localities in Marizza and Cremastò, Ródos, Greece. The aff. form was found in two caves in the Dinaric Mountains.

#### *Plusiocampa (Plusiocampa) latens* Condé, 1948

*Plusiocampa latens* Condé, 1948d: 49, fig. 1.

### Diagnosis (Condé 1948d)

Slightly troglomorphic species. Antennae with 24–27 with antennomeres. Small protruding frontal process with slightly tuberculated setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae; unequal claws (1.4) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV

with 1+1 *la*, 3+3 *post* macrosetae; urotergites V–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with glandular  $g_1$  setae, subcylindrical appendages with glandular  $a_1$  setae; female and male appendages identical.

### Remarks

Among the studied material there is a male from Žira jama and another male from Crnulja ponor from Bosnia and Herzegovina (see Table S2 in Supplementary Material) which match the original description and allowed the completion of the previous diagnosis (Coll. AS).

### *Plusiocampa (Plusiocampa) aff. latens* Condé, 1948

#### Differential diagnosis against the type form

One male and one female from Vidovića špilja, Croatia (see Table S2 in Supplementary Material) show notable differences compared to the type form. Antennae with 25 doliiform antennomeres; non-tubercular setae on simple frontal process. Pronotum with 1+1 *sma*, 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergite IV with 0+1 *la*, 4+4–5+5 *post* macrosetae; urotergite V with 1+1 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+7 *post* macrosetae. Urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae, mostly short with long barbs. Subequal claws (1.1) with small backward overhang. Male with glandular  $g_1$  setae and enlarged appendages with thick glandular  $a_1$  setae; female with enlarged subcylindrical appendages with glandular  $a_1$  setae. Styolar setae with a few barbs.

#### Habitat and distribution

Hypogean species found in three caves (Baba pećina, Crnulja ponor and Žira jama) in Bosnia and Herzegovina for the type form and one cave for the aff. form (Vidovića špilja, Croatia); all localities in the Dinaric Mountains.

### *Plusiocampa (Plusiocampa) lindbergi* Condé, 1956

Fig 119

*Plusiocampa lindbergi* Condé, 1956a: 7, figs 1–2.

#### Diagnosis (Condé 1956a)

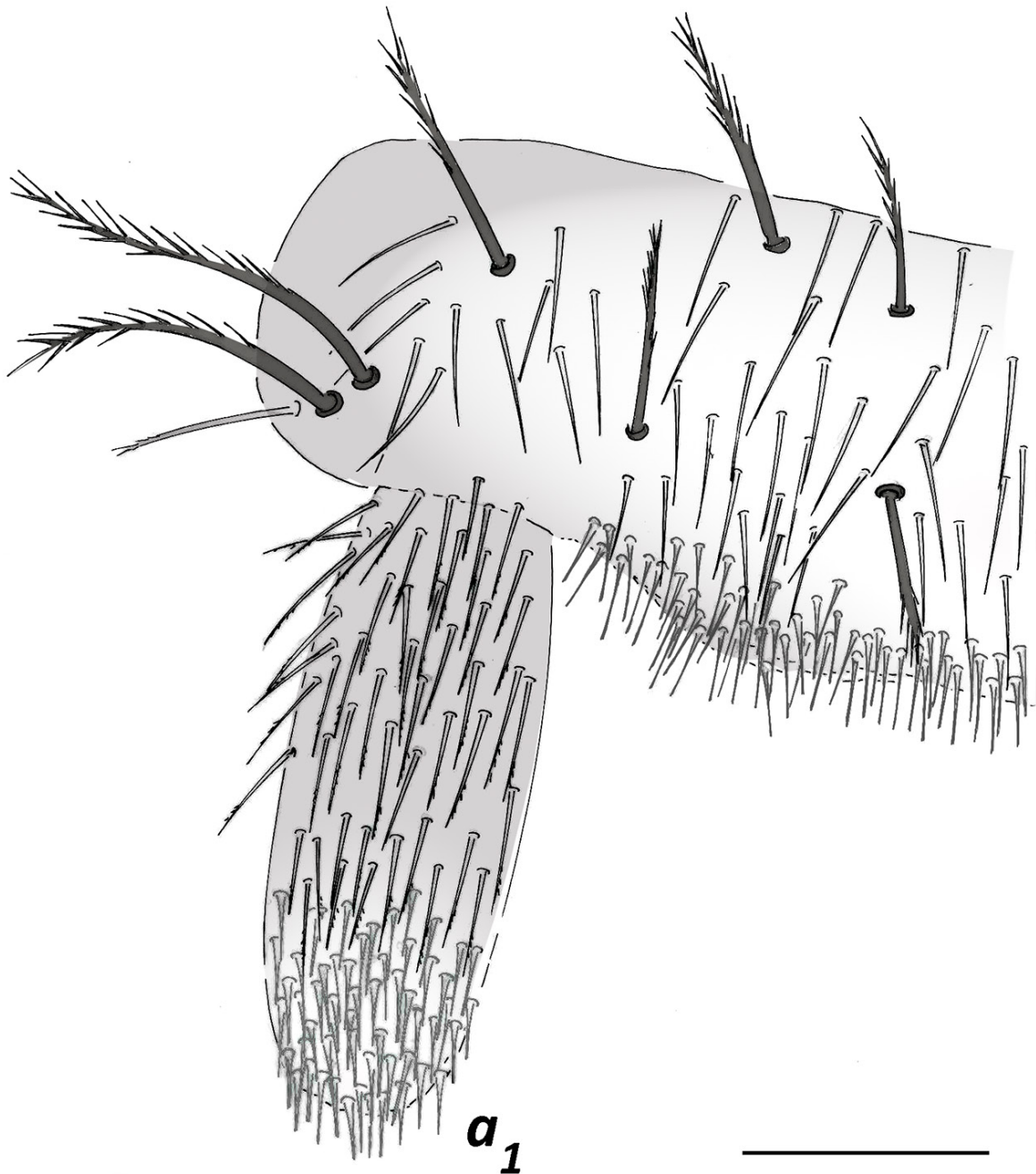
Slightly troglomorphic species. Antennae with 34–37 antennomeres; five olfactory chemoreceptors in cupuliform organ of a possibly regenerated antenna; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *lp* macrosetae; long, large, barbed notal macrosetae; smooth clothing setae. Two ventral tibial macrosetae; subequal claws (1.05–1.1) with middle-sized lateral crests, posterior claw with no backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with glandular  $g_1$  setae, enlarged subcylindrical appendages with glandular  $a_1$  setae; female with slender, subcylindrical appendages.

### Remarks

The study of one male adult of 4.6 mm body length collected from the MSS habitat in Xánthi, Géraças, Greece (see [Table S2](#) in Supplementary Material) allows the addition of information on the urosternites of the male. It has a narrow area of 96 glandular  $g_1$  setae, arranged in 2–3 rows; enlarged and subcylindrical appendages with a distal area of up to 60 glandular  $a_1$  setae (Fig. 119).

### Habitat and distribution

Subterranean species known from Saint-Jean-le-Prodrome Cave (Spilaio Pelade) and from the MSS habitat near Xánthi, both on the Balkan Peninsula, in the Macedonian and Greek regions.



**Fig. 119.** *Plusiocampa (Plusiocampa) lindbergi* Condé, 1956, ♂, 4.6 mm long, from MSS in Géraças, Greece (Coll. AS). First urosternite, right side, glandular  $g_1$  and  $a_1$  setae. Scale bar: 0.1 mm.

***Plusiocampa (Plusiocampa) lucenti* Sendra & Condé, 1986**

*Plusiocampa lucenti* Sendra & Condé, 1986: 971, figs 1–3, table 1.

**Diagnosis** (Sendra & Condé 1986; Sendra *et al.* 2004)

Troglomorphic species. Antennae with 37–40 antennomeres; 17–21 complex olfactory chemoreceptors in cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2–3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2–3+3 *la*, 2+2 *lp*, 1+1 (0+1) *mi*, 1+1 (0+1) *li* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mi*, 1+1–0+0 *li* macrosetae; long, barbed notal macrosetae; sparse notal clothing setae. Two or three ventral tibial macrosetae; unequal claws (1.30) with large lateral crests, posterior claw with backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 1+1 *la*, 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae. Urosternite I with 7+7 (7+1+7), urosternites II–VII with 5+5–6+6, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae, slightly subcylindrical appendages with glandular *a*<sub>1</sub> setae; female appendages like male appendages. Spermatozoid fascicle wheels with 2 turns of 140–160 µm long and 1.5 µm wide filament.

**Habitat and distribution**

Subterranean species inhabiting seven caves around the north-eastern Pre-Baetic reliefs on the Iberian Peninsula. Furthermore, it slightly extends its distribution to three more caves in the south of the Iberian Mountain Range.

***Plusiocampa (Plusiocampa) magdalenae* Condé, 1957**

*Plusiocampa magdalenae* Condé, 1957: 9, fig. 1.

**Diagnosis** (Condé 1957, 1961, 1983; Bareth 2006)

Troglomorphic species. Antennae with 31–33 antennomeres; ten olfactory chemoreceptors in cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2–3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 (2+2) *la*, 2+2 *lp*, 0+1 *mp* (1+0 *sm**p*) macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *sm**p* macrosetae; long, barbed notal macrosetae; sparse notal clothing setae. Three or four ventral tibial macrosetae; slightly unequal claws with large lateral crests, posterior claw with a small backward overhang. Urotergite I with 1+1 *post* macrosetae; urotergite II with 1+1–2+2 *post* macrosetae; urotergite III with 2+2–3+4 *post* macrosetae; urotergite IV with 2+2 *la*, 5+5 *post* macrosetae; urotergite V with 3+3 *la*, 5+5–5+4 *post* macrosetae; urotergite VI with 3+3 *la*, 5+5 *post* macrosetae; urotergite VII with 3+3 *la*, 4+5–5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; thick clothing setae on abdominal segments IX–X; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female appendages slightly enlarged, from subcylindrical to conical in shape, with glandular *a*<sub>1</sub> setae.

**Habitat and distribution**

Subterranean species found in two adjacent caves, Grotte du Pertuis and Trou Miette, north of Méailles, Alpes de Haute-Provence, southeastern France.

***Plusiocampa (Plusiocampa) notabilis* Silvestri, 1912**

*Plusiocampa notabilis* Silvestri, 1912: 143, fig. xxix.



**Diagnosis** (Silvestri 1912; Condé 1978; Bareth 2006)

Non-trogomorphic species. Antennae with 25–27 antennomeres. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, thin barbed macrosetae; sparse smooth, long notal clothing setae. Two ventral tibial macrosetae; small subequal claws with small lateral crests, posterior claw with no backward overhang. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergites IV–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with glandular *g*<sub>1</sub> setae, subcylindrical appendages with glandular *a*<sub>1</sub> setae; female appendages like male appendages.

**Habitat and distribution**

Soil-dwelling species found at six edaphic sites on the island of Corsica, one on Isola Zannone and two at inland localities in Calabria and Lazio, Italian Peninsula.

*Plusiocampa (Plusiocampa) pouadensis pouadensis* (Denis, 1930)

Figs 120–123

*Troglocampa pouadensis* Denis, 1930: 37, figs 28–35.

**Diagnosis** (Denis 1930; Condé 1948b; Bareth 2006)

Trogomorphic species. Antennae with 33–35 antennomeres, protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 3+3 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 3+3 *lp* macrosetae; long, barbed notal macrosetae; barbed notal clothing setae. Two ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergites V–VI with 1+1–2+2 *la*, 5+5 *post* macrosetae; urotergite VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae. Urosternite I with 8+8, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male with a area of glandular *g*<sub>1</sub> setae, developed large appendages with a large area of glandular *a*<sub>2</sub> setae and an apical area of glandular *a*<sub>1</sub> setae; female with subcylindrical appendages with glandular *a*<sub>1</sub> setae.

**Remarks**

The studied material from Pouade Cave (see [Table S2](#) in Supplementary Material) has allowed a better observation of the first urosternite with its very large appendages in males (Fig. 120), as well as a large area of glandular *a*<sub>2</sub> setae. The first urosternite of females has subcylindrical appendages (Figs 121, 123) and the surface is completely smooth (Fig. 122).

**Habitat and distribution**

Subterranean species only found in Grotte de Pouade, Banyuls de la Marenda, on the French side of the Eastern Pyrenees.

*Plusiocampa (Plusiocampa) pouadensis fouresi* Condé, 1955

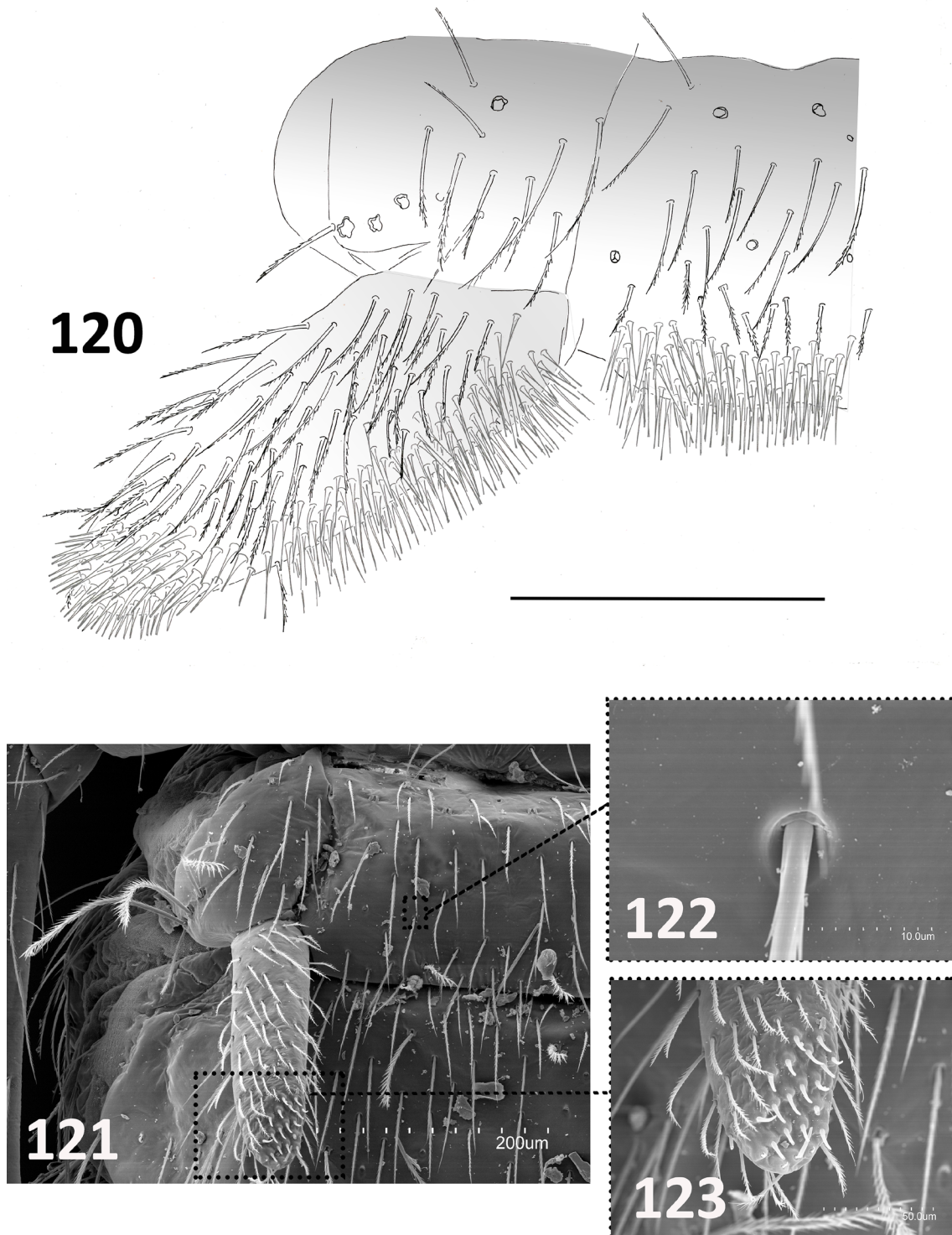
*Plusiocampa pouadensis fouresi* Condé, 1955a: 27.

**Differential diagnosis against the type form** (Condé 1955a; Bareth & Condé 1996)

Urotergite III with 2+2 *post* macrosetae; urotergites V–VII with 2+2 *la*, 6+6 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae.

### Habitat and distribution

Subterranean subspecies inhabiting two caves on the French side of the Eastern Pyrenees.



**Figs 120–123.** *Plusiocampa (Plusiocampa) pouadensis pouadensis* (Denis, 1930), from Grotte Pouade, Banyuls-sur-Mer, France (Coll. AS). **120.** ♂, urosternite I, right side, with glandular  $g_1$ ,  $a_1$  and  $a_2$  setae. **121.** ♀, urosternite I. **122.** Surface of urosternite I, detail. **123.** ♀, urosternite I appendage. Scale bar: 120 = 0.2 mm.

*Plusiocampa (Plusiocampa) pouadensis leoni* Condé, 1951

*Plusiocampa pouadensis leoni* Condé, 1951: 60, fig. 2.

**Differential diagnosis against the type form** (Condé 1951, 1955a; Bareth & Condé 1996)

Antennae with 28–33 antennomeres. Urotergite III with 2+2 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae.

**Habitat and distribution**

Subterranean subspecies inhabiting three caves on the Spanish side of the Eastern Pyrenees.

*Plusiocampa (Plusiocampa) provincialis provincialis* Condé, 1949

*Plusiocampa provincialis* Condé, 1949: 166, figs a–b, d–h.

**Diagnosis** (Condé 1949, 1957, 1981a, 1983; Bareth 2006)

Troglomorphic species. Antennae with 30–36 antennomeres; sensillum of third antennomere very long, in ventral position; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; barbed notal clothing setae. Two ventral tibial macrosetae; subequal claws (1.06) with large lateral crests, posterior claw with a small backward overhang. Urotergites I–II with 2+2 *post* macrosetae; urotergite III with 2+2–3+3 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergite V with 2+2 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 7+7 *post* macrosetae; thick clothing setae on abdominal segments IX–X; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a large area of glandular  $g_1$  setae and appendages with glandular  $a_2$  setae.

**Habitat and distribution**

Subterranean species found in nine caves around Massif de Marseilleveyre and the Sainte-Baume Massif, Alps de Provence, southeastern France.

*Plusiocampa (Plusiocampa) provincialis praedita* Condé, 1949

*Plusiocampa provincialis praedita* Condé, 1949: 169, fig. c.

**Differential diagnosis against the type form** (Condé 1949, 1983; Bareth 2006)

Protruding frontal process with slightly tubercular setae. Two ventral tibial macrosetae. Thick clothing setae on abdominal segments VIII–X. Male with slightly enlarged appendages with glandular  $a_1$  setae; female appendages like male appendages.

**Habitat and distribution**

Subterranean subspecies found in Grotte du Saint-Trou in the Saint-Baume Massif, northeast of Événos, Alps de Provence, southeastern France.

**Table 9.** *Plusiocampa (Plusiocampa) rhea* Sendra sp. nov. Length of the body, antennae and metathoracic legs (measurements in mm), in addition to the number of antennomeres.

Specimen (Coll. AS)	Body length	No. of antennomeres	Antennal length	Metathoracic leg length
♂, holotype	4.9	32	4.0	2.2
♂, paratype	4.0	30	3.6	–
♂, paratype	3.8	33	3.8	1.9

*Plusiocampa (Plusiocampa) rhea* Sendra sp. nov.

[urn:lsid:zoobank.org:act:79F00B32-CCCA-4195-BB1F-52D3B2225C20](https://zoobank.org/act:79F00B32-CCCA-4195-BB1F-52D3B2225C20)

Fig. 124; Table 9

### Etymology

This species is named in honour of Rhea, mother of the Greek god Zeus and daughter of Gaea, the Earth goddess. She gave birth and cared for her son Zeus in the Ideon Andron Cave located in Mount Psiloritis, the highest mountain in Crete, where this new species was found.

### Material examined

#### Holotype

GREECE • 1 ♂; Crete, Anogeia, Ideon Antron Cave (Zeus Cave) at twilight zone area, near entrance; 1174 m a.s.l.; 22 Mar. 2006; Alberto Sendra leg.; MZB 2019-1033.

#### Paratypes

GREECE – Crete • 1 ♂; Pombia; 211 m a.s.l.; Alberto Sendra leg.; MSS habitat; Coll. AS • 1 ♂; Sissarha; 601 m a.s.l.; MSS habitat; Alberto Sendra leg.; Coll. AS.

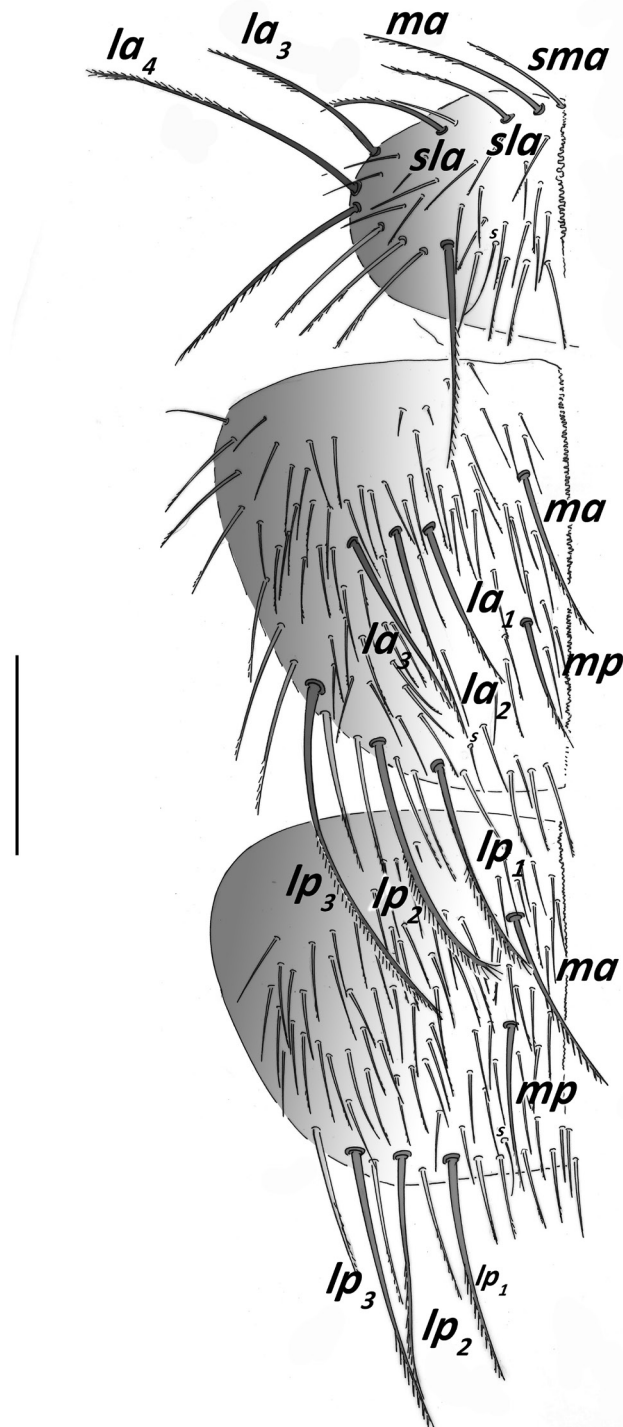
### Description

**BODY.** Body length 3.8–4.9 mm. Epicuticle smooth under optical microscope; body with thin, middle-sized clothing, covered or not by a few thin barbs.

**HEAD.** Three intact antennae in holotype and paratypes, with 30, 32 and 33 antennomeres, slightly shorter than body length (Table 9). Small coniform sensillum of third antennomere located in ventral position between *c* and *d* macrosetae. Central antennomeres 1.5× as long as wide, apical antennomere 1.6× as long as wide. Cupuliform organ occupying 1/5 of total length of apical antennomere, with 8–9 complex olfactory chemoreceptors. Gouge sensilla 30–32 µm long in a single distal whorl of 12–16 sensilla on each medial and distal antennomere. Frontal process plain, with non-tubercular setae and macrosetae with barbs along half to two-thirds; macrosetae along line of insertion of antennomere and *x* setae with similar lengths (*a/i/p/x* with relative lengths of 36/42/35/52 in holotype). Suboval labial palps with latero-external sensillum larger than sensillum of third antennomere, with two guard setae, up to 12 setae on anterior border and up to 180 neuroglandular setae.

**THORAX.** Distribution of thoracic macrosetae (Fig. 124): pronotum with 1+1 *ma*, 2+2 *la*<sub>3,4</sub> and 2+2 *sla*<sub>1,2</sub>, 2+2 *lp*<sub>1,3</sub> (with additional 1+1 extra *sma* near the sagittal plane); mesonotum with 1+1 *ma*, 3+3 *la*<sub>1,2,3</sub>, 3+3 *lp*<sub>1,2,3</sub>, 1+1 *mp*; metanotum with 1+1 *ma*, 3+3 *lp*<sub>1,2,3</sub>, 1+1 *mp*. All notal macrosetae long, robust, covered by thin barbs along distal third or half; submacrosetae *sla*<sub>1,2</sub> and *sma* thinner and shorter than notal macrosetae, but with same large base; marginal setae longer than clothing setae, covered by thin barbs along distal three-fourths. Legs elongated, pretarsus of metathoracic legs slightly overpassing end of abdomen (Table 9). Femur I without dorsal macrosetae but with one long, barbed ventral macroseta; femora II–III with one long, barbed dorsal and one long, barbed ventral macroseta. Tibia I with one

short, barbed ventral macroseta; tibiae II–III with two short, barbed ventral macrosetae. Calcars with 2–3 rows of long barbs from base to tip, smooth on one narrow side along calcar. Dorsal and lateral subapical tarsal setae smooth. Slightly unequal claws (posterior claw 1.15–1.2× as long as anterior one); posterior claw without backward overhang; lateral crests well developed. Pretarsal processes long, setiform, reaching extremities of claws.



**Fig. 124.** *Plusiocampa (Plusiocampa) rhea* Sendra sp. nov., holotype, ♂, 4.9 mm long, from Ideon Antron Cave entrance, Anogeia, Crete (MZB 2019-1033). Pronotum, mesonotum and metanotum, left side (s = setiform sensillum). Scale bar: 0.3 mm.

ABDOMEN. Distribution of abdominal macrosetae on tergites: 1+1 *post*<sub>1</sub> on I–III (0+1 *la* on III); 1+1 *la*, 2+2 *post*<sub>1,2</sub> on IV; 1+1 *la*, 5+5 *post*<sub>1–5</sub> on V–VII; 7+7 *post* on VIII; 9+9 *post* on abdominal segment IX. All *post* urotergal macrosetae thick, long and covered by thin barbs along distal four-fifths; *la* urotergal macrosetae shorter than *post* macrosetae, covered by barbs along distal half. Urosternite I with 9+9, urosternites II–VII with 5+5; urosternite VIII with 2+2 macrosetae; all urosternal macrosetae robust and large, covered by long barbs along distal three-fourths to four-fifths. Apical, subapical and ventromedial setae with abundant long barbs.

CERCI. One incomplete cercus on 4 mm long paratype with six articles in addition to basal article, 3.8 mm long; their articles show whorls of long macrosetae covered by thin barbs along distal two-thirds, combined with whorls of smooth, thin setae, shorter than macrosetae, in addition to one apical whorl of short setae with a few distal barbs.

GENITAL ORGANS. Male urosternite I with up to 160 glandular *g*<sub>1</sub> setae arranged in up to five rows with slightly enlarged subcylindrical appendages, each bearing up to 19 glandular *a*<sub>1</sub> setae.

### Phyletic affinities, habitat and distribution

*Plusiocampa* (*P.*) *rhea* sp. nov. has 3+3 lateral posterior macrosetae on the mesonotum and metanotum, a feature only found in *P.* (*P.*) *pouadensis* (Condé 1948c; Sendra & Escolà 2004). Nevertheless, *P.* (*P.*) *rhea* sp. nov. has medial posterior mesonotal and metanotal macrosetae, which are absent in *P.* (*P.*) *pouadensis*. Furthermore, *P.* (*P.*) *pouadensis* is a troglomorphic species from the Eastern Pyrenees, whereas *P.* (*P.*) *rhea* sp. nov. has been found in hypogean habitats, in soil, MSS and the twilight zones of caves at three locations on Crete.

#### *Plusiocampa* (*Plusiocampa*) *romana* Condé, 1954

*Plusiocampa romana* Condé, 1954b: 37, figs a–e.

#### Diagnosis (Condé 1954b, 1983; Ramellini 1990)

Troglomorphic species. Antennae with 26 antennomeres; 12 complex olfactory chemoreceptors in cupuliform organ; frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; thin, barbed notal macrosetae; sparse notal clothing setae. Two to four ventral tibial macrosetae; slightly unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergite I with 1+1 *post* macrosetae; urotergite II with 2+2 *post* macrosetae; urotergite III with 4+4 *post* macrosetae; urotergite IV with 2+2 *la*, 5+5 *post* macrosetae; urotergite V with 2+2–3+3 *la*, 5+5 *post* macrosetae; urotergites VI–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosteronite VIII with 2+2 macrosetae. Male unknown.

#### Habitat and distribution

Subterranean species found on the Italian Peninsula in two caves, Grotta di Santa Liberata (Toscana) and Grotta dell'Inferniglio (Latium), and in soil habitat on Monti Ausoni, central Apennine Mountains.

#### *Plusiocampa* (*Plusiocampa*) *rudnica* Blesić, 1992

*Plusiocampa rudnica* Blesić, 1992: 145, figs 1–4.

#### Diagnosis (Blesić 1992)

Non-troglomorphic species. Antennae with 27–28 antennomeres. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2

*lp*, 1+1 *mp* macrosetae. Two or three ventral tibial macrosetae. Subequal claws with large lateral crests, posterior claw with a small backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergites IV–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. This species should be judged with caution due to the fact that it is poorly described.

#### Habitat and distribution

Soil-dwelling species distributed in Rudnik Mountain (Serbia) on the west of the Balkan Peninsula.

#### *Plusiocampa (Plusiocampa) rybaki* Condé, 1956

*Plusiocampa rybaki* Condé, 1956a: 11.

#### Diagnosis

*Plusiocampa (P.) rybaki* was poorly described by Condé, based on specimens from three caves, one in Attica, Greece (Cave I in Rachi, northern part of Mt Ymittos) and two on Crete (Achyrospilo Cave on the Acrotiri Peninsula, Chania and Sarchos Cave, Irakleio). Troglomorphic species. Antennae with 40–44 antennomeres, large cupuliform organ with 13–21 olfactory chemoreceptors; frontal process with tubercular setae. Mesonotum with 3+3 *la* macrosetae, and mesonotum and metanotum with *mp* macrosetae. Pretarsus with large lateral crests. Urotergites V–VII with 5+5 *post* macrosetae.

#### Remarks

The specimens from Crete reported by Condé (1956a) as *P. (P.) rybaki*, as well as two specimens collected by P. Strinati on Crete (deposited in the Natural History Museum of Geneva on two slides labelled by B. Condé as *Plusiocampa rybaki*: 1 male from Melidoni Spilia, 2 Aug. 1983 and 1 female from Grotta “Sentoni”), are here considered to belong to *P. (P.) hoffmanni* sp. nov.

#### *Plusiocampa (Plusiocampa) sardiniana* Condé, 1981

*Plusiocampa sardiniana* Condé, 1981b: 593, fig. 1b.

*Plusiocampa provincialis?* – Condé 1953: 36.

#### Diagnosis (Condé 1953b, 1981b, 1983)

Troglomorphic species. Antennae with 33–38 antennomeres; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae. Two ventral tibial macrosetae; slightly unequal claws (1.15) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 2+2 *post* macrosetae; urotergite IV with 1+1 (0+1) *la*, 5+5 *post* macrosetae; urotergite V with 1+1 (1+2) *la*, 5+5 *post* macrosetae; urotergite VI with 2+2 (1+2) *la*, 5+5 *post* macrosetae; urotergite VII with 2+2–3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; thick clothing setae on abdominal segments IX–X; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae or glandular  $a_2$  setae, with the exception of 1+1  $g_1$  and 2–3  $a_2$  in one specimen; female with subcylindrical appendages with glandular  $a_1$  setae.

#### Habitat and distribution

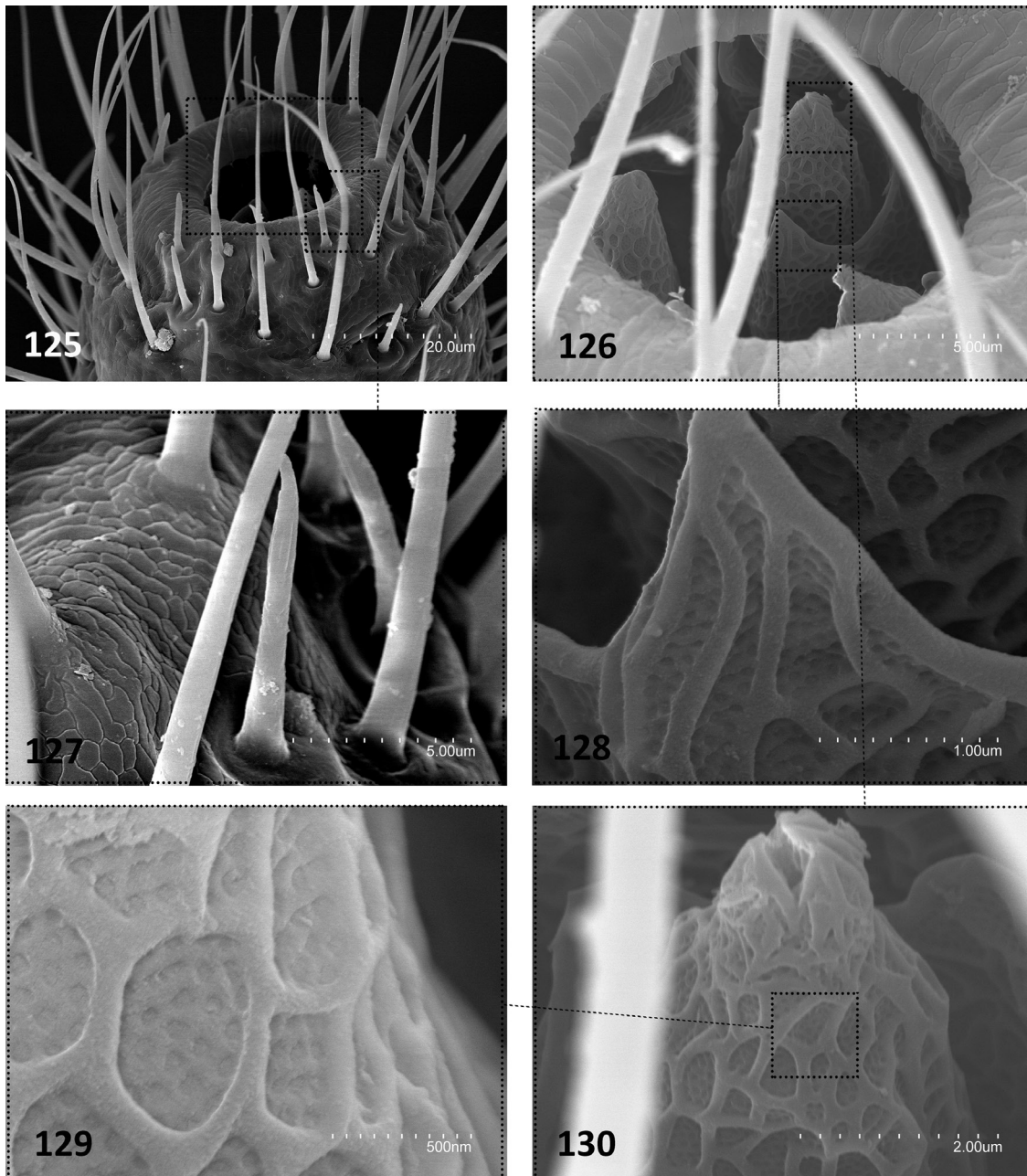
Subterranean species found only in the San Giovanni Caves, Sardinia.

*Plusiocampa (Plusiocampa) schweitzeri* Condé, 1947  
Figs 125–134

*Plusiocampa schweitzeri* Condé, 1947a: 23, fig. 3.

**Diagnosis** (Condé 1947a)

Troglomorphic species. Antennae with 22–29 antennomeres; cupuliform organ with seven or eight complex olfactory chemoreceptors. Protruding frontal process with tubercular setae. Pronotum with 1+1



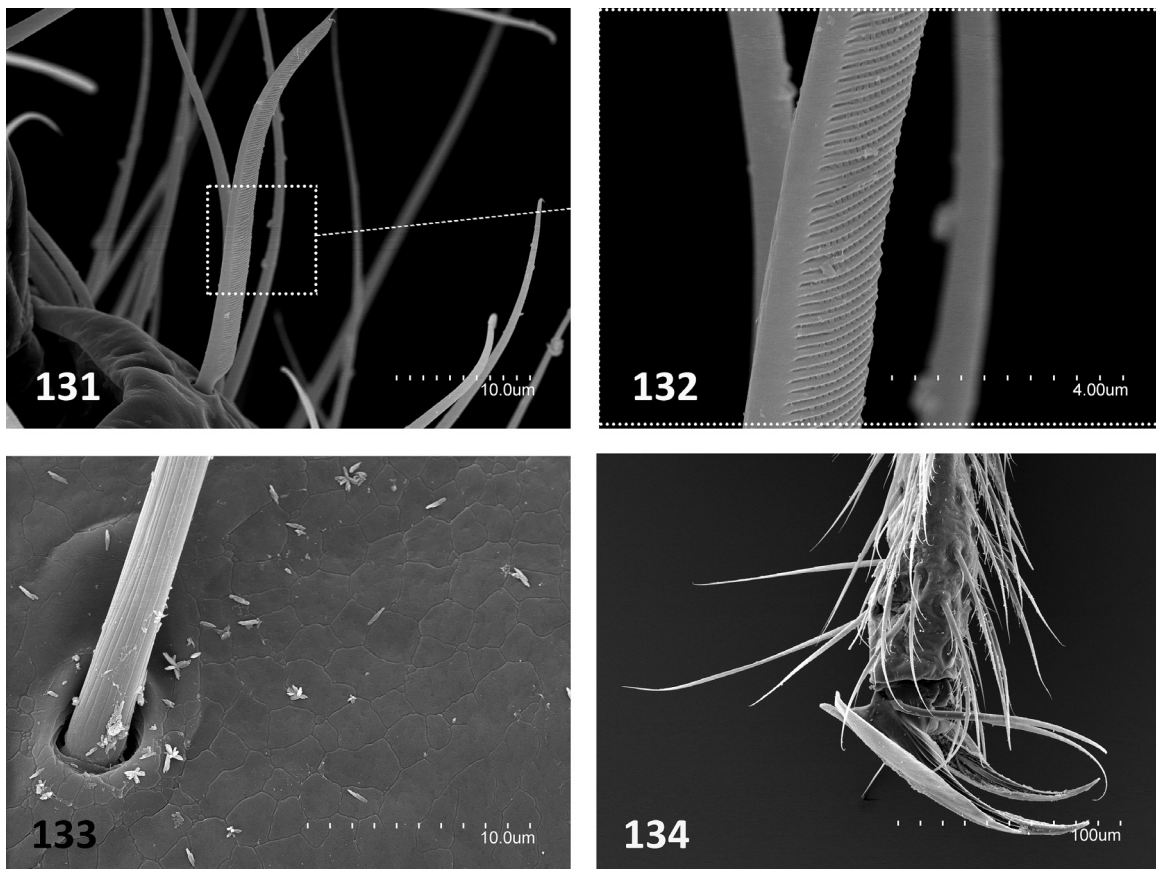
**Figs 125–130.** *Plusiocampa (Plusiocampa) schweitzeri* Condé, 1947, from Govještica, Banja stijena, Rogatica, Bosnia and Herzegovina (Coll. AS). **125.** Tip of last antennomere. **126.** Cupuliform organ. **127.** Detail of rim of cupuliform organ with a coniform sensillum. **128.** Olfactory chemoreceptor, detail. **129.** Apical portion of an olfactory chemoreceptor. **130.** Surface of olfactory chemoreceptor, detail.



*ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2–2+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal setae; abundant barbed notal clothing setae. Two ventral tibial macrosetae; unequal claws (1.3–1.5) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2–3+3 *post* macrosetae; urotergite V with 1+1 *la*, 4+4–5+5 *post* macrosetae; urotergites VI–VII with 1+1–2+2 *la*, 5+5 (4+5) *post* macrosetae; urotergite VIII with 6+6 macrosetae; abdominal segment IX with 8+8–8+9 macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with an area of glandular *g*<sub>1</sub> setae, subcylindrical and slightly enlarged appendages with glandular *a*<sub>1</sub> setae; female appendages like male appendages.

### Remarks

The 17 specimens studied, from four caves in the Dinaric Mountains (Bosnia and Herzegovina) (see Table S2 in Supplementary Material), allowed us to clarify some characters: five complete antennae preserved show 28–29 antennomeres, elongated antennomeres with a distal whorl of 12–14 long gouge sensilla (30–32 µm) (Figs 131–132); cupuliform organ with seven or eight spheroidal olfactory chemoreceptors, each with a jagged fold surrounding a central coniform structure covered by a highly visible, multiperforated polygonal net surface (Figs 125–130). Protruding frontal process with tubercular setae. Surface of epicuticle reticulate (Fig. 133). Smooth tarsal subapical setae and calcars with long barbs from base, pretarsus claws with large lateral crests (Fig. 134). Furthermore, they show a wider range in the number of urotergal macrosetae than mentioned in the diagnosis above.



**Figs 131–134.** *Plusiocampa (Plusiocampa) schweitzeri* Condé, 1947, from Govještica, Banja stijena, Rogatica, Bosnia and Herzegovina (Coll. AS). **131.** Medial antennomere, latero-distal view. **132.** Medial portion of a gouge sensillum, detail. **133.** Surface of metanotum, detail. **134.** Distal portion of tarsus and pretarsus, lateral view.

*Plusiocampa (Plusiocampa) aff. schweitzeri* Condé, 1947

**Differential diagnosis against the type form**

The five studied specimens from Karakaya Cave in Turkey (see [Table S2](#) in Supplementary Material) share the same macrosetal distribution found in the specimens from Bosnia and Herzegovina, with the exception of 7+7 *post* macrosetae on urotergite VIII and 9+9 *post* macrosetae on abdominal segment IX. Furthermore, two other important features separate these two forms, i.e., the shape of the claws (subequal claws and posterior claw with no backward overhang in the form from Karakaya Cave) and features of the frontal process (simple frontal process without tubercular setae in specimens from Karakaya Cave). However, more material is needed to describe these specimens with different features from Karakaya Cave, Mihalliçik as a new species.

**Habitat and distribution**

Subterranean species found in five caves of Bosnia and Herzegovina in the Dinaric Mountains. The aff. form was found in a cave in the northeast of the Anatolian Peninsula.

*Plusiocampa (Plusiocampa) socia* Condé, 1983

*Plusiocampa socia* Condé, 1956b: 200 (nomen nudum).

*Plusiocampa socia* Condé, 1983: 900, figs 1a, 2–4.

**Diagnosis** (Condé 1983)

Troglophic species. Antennae with 36 antennomeres; nine complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae, smooth or with a few distal barbs. Two ventral tibial macrosetae; subequal claws (1.05) with large lateral crests, posterior claw with a small backward overhang. Urosternite I with 2+1 *post* macrosetae; urotergite II with 2+2 *post* macrosetae; urotergite III with 0+1 *la*, 2+2 *post* macrosetae; urotergites IV–V with 1+1 *la*, 2+2 *post* macrosetae; urotergite VI with 3+3–2+2 *la*, 4+4 *post* macrosetae; urotergite VII with 3+3 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; urosternite I with 8+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; subcylindrical appendages with glandular *a*<sub>1</sub> setae in females.

**Habitat and distribution**

Subterranean species found only in Grotta di Gana ‘e Gortoe, Siniscola, Eastern Sardinia.

*Plusiocampa (Plusiocampa) solerii* Silvestri, 1932

*Plusiocampa solerii* Silvestri, 1932: 72, figs viii–ix.

**Diagnosis** (Silvestri 1933a; Sendra *et al.* 2006)

Non-troglophic species. Antennae with 22–25 antennomeres; frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae; slightly unequal claws (1.15) with large lateral crests, posterior claw with no backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 2+2 *post* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 macrosetae; urosternite I with 7+7, urosternites II–VII with

5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female with long subcylindrical appendages with glandular  $a_j$  setae.

***Plusiocampa (Plusiocampa) aff. solerii* Silvestri, 1932**

**Differential diagnosis against the type form**

The only specimen collected is a female, a troglomorphic form found in a cave on the island of Cyprus (Coll. AS). This specimen shows several taxonomical differences from the type form. Body length 5.6 mm (metathoracic leg 3.2 mm long); 8.7 mm long antenna with 49 antennomeres; elongated antennomeres with 16–18 long gouge sensilla, more than eight complex sensilla in cupuliform organ; 2 or 3 ventral tibial macrosetae; 1+1 lateral anterior and 1+1 posterior macrosetae on fourth urotergite and 2+2 anterior lateral macrosetae on seventh urotergite.

**Habitat and distribution**

The type form was found in soil habitat on the island of Ródos (Greece) and at Izmir on the west coast of the Anatolian Peninsula, but the aff. troglomorphic form was found on Cyprus.

***Plusiocampa (Plusiocampa) spelaea* Stach, 1930**

Table 10

*Plusiocampa spelaea* Stach, 1930: 278.

**Diagnosis** (Stach 1930; Condé 1954a; Paclt 1957)

Non-troglomorphic species. Antennae with 20–22 antennomeres. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae. Two ventral tibial macrosetae. Urotergites I–II with 1+1 *post* macrosetae; urotergite III with 2+2 *post* macrosetae; urotergites IV–VII with 1+1 *la*, 5+5 *post* macrosetae; urosternite I with 8+8?, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae.

**Remarks**

The study of five females and one juvenile collected in four caves (see [Table S2](#) in Supplementary Material) has allowed the completion of the former description, although new specimens from the type locality are needed for a proper redescription of this species. Nevertheless, a complementary and differential description has been made using the studied material.

Non-troglomorphic species (Table 10). Antennae with 21 and 23 doliiform antennomeres, apical antennomere 1.3× as long as wide, with a small cupuliform organ occupying  $\frac{1}{3}$  of antennomere, with four simple olfactory chemoreceptors. Small ventral sensillum of third antennomere between *d* and *e* macrosetae. Non-protruding frontal process with non-tubercular setae. Labial palp suboval with a thick lateral anterior sensillum, two guard setae, up to five normal setae and 75 neuroglandular setae. Pronotum with 2+2 *la* to 3+3 *la* macrosetae; long, barbed notal macrosetae; notal clothing setae long, smooth or with one or two distal barbs. Calcars with two rows of long barbs. Smooth subapical tarsal setae. Slightly unequal claws (1.15–1.20) with large lateral crests and a small backward overhang. Urotergite IV with 4+4 *post* macrosetae (5+5 according to redescription in Paclt 1957); urotergites VI–VII with 2+2 *la* macrosetae (1+1 *la* according to Paclt 1957); urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 4+4, urosternite VIII with 2+2 macrosetae. Styler setae with a few long, thin bars. Female with subcylindrical appendages bearing up to 9 glandular  $a_j$  setae.

**Table 10.** *Plusiocampa (Plusiocampa) spelaea* Stach, 1930. Length of the body, antennae, metathoracic legs and cerci (measurements in mm), in addition to the number of antennomeres and cercal articles.

Specimen (Coll. AS)	Body length	No. of antennomeres	Antennal length	Metathoracic leg length	No. of cercal articles (base included)	Length of cercus
juv., Domica Cave	2.35	23	1.40	0.90	4	0.53
♀, Vass Imre barlang Cave	3.6	23	1.70	1.25	7	2.05
♀, Vass Imre barlang Cave	3.9	23	2.00	1.50	7	2.01
♀, Jaskyňa nad Kadlubom Cave	4.3	23	1.95	1.35	7	1.85
♀, Jaskyňa nad Kadlubom Cave	4.6	–	–	1.45	7	2.00
♀, Drienovská jaskyňa Cave	4.9	21	2.10	1.60	–	–

### Habitat and distribution

Apparently, this species only lives in caves, but its non-trogomorphic shape reveals a more superficial habitat (MSS or soils). It has been found in six caves in the southern karst areas of the Western Carpathians, where it was described from the Domica-Baradla cave system in the Slovak and Aggtelek Karst, on the border between Slovakia and Hungary.

### *Plusiocampa (Plusiocampa) strouhali strouhali* Silvestri, 1933

*Plusiocampa strouhali* Silvestri, 1933c: 30, tables i–ii.

### Diagnosis (Silvestri 1933c; Condé 1954a)

Trogomorphic species. Antennae with 40–41 antennomeres. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed macrosetae; abundant notal clothing setae. Three ventral tibial macrosetae; unequal claws (1.4) with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 5+5 *post* macrosetae; urotergites V–VII with 2+2 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae on first urosternite. Female and male with subcylindrical appendages bearing glandular *a*<sub>1</sub> setae.

### Habitat and distribution

Subterranean species reported from 10 caves, with a wide distribution area in the Austrian Alps.

### *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943

Figs 135–152; Table 11

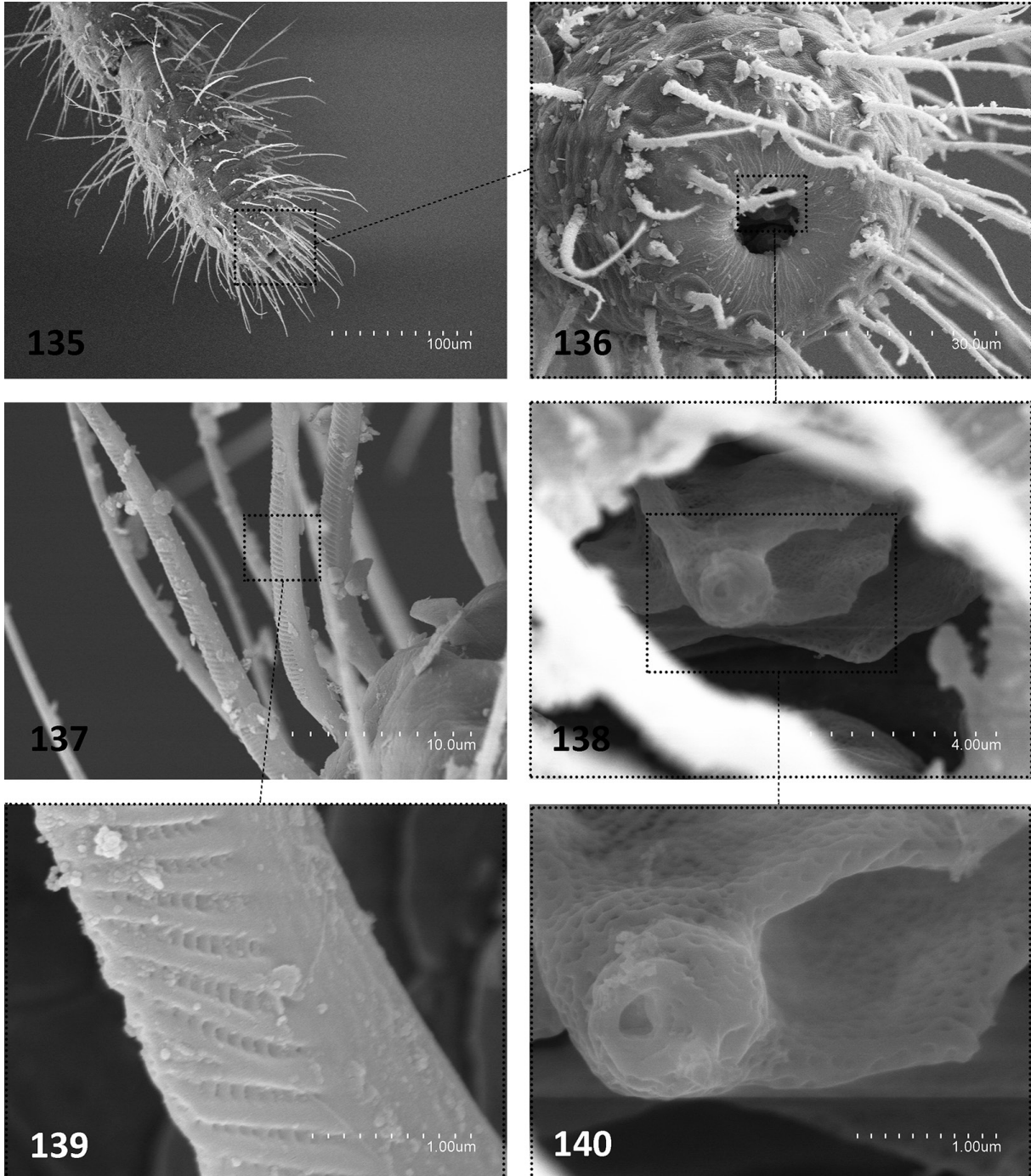
*Plusiocampa strouhali cavicola* Vornatscher, 1943: 235.

### Differential diagnosis against the type form (Condé 1954a)

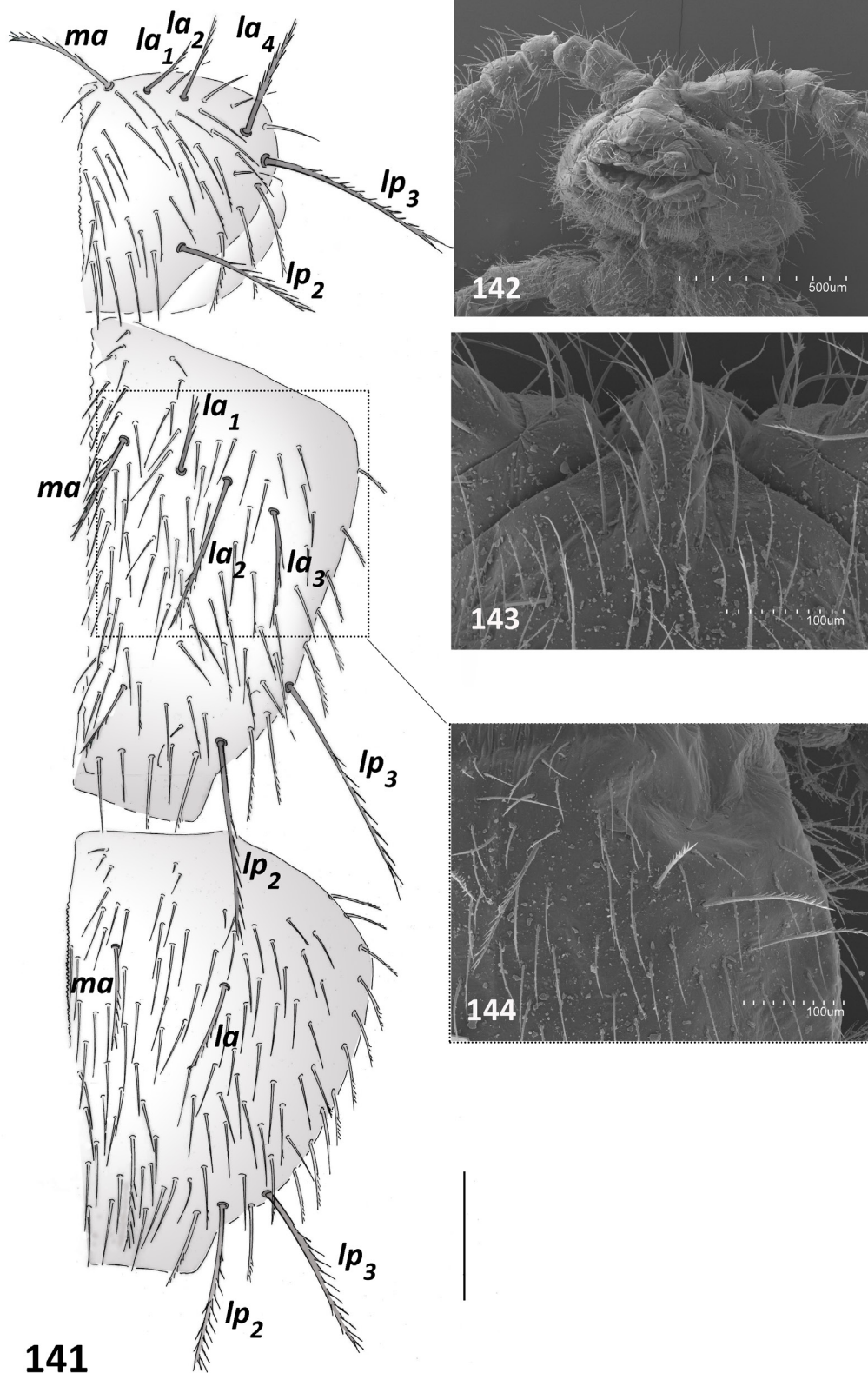
Trogomorphic subspecies. Antennae with 25–28 antennomeres. Until now, the only character used to separate *P. (P.) strouhali strouhali* from *P. (P.) strouhali cavicola* has been the number of antennomeres (Condé 1954a). This characteristic had been used to sort out the subspecies (Vornatscher 1943; Strouhal & Vornatscher 1975), and it was applied to the study material (see Table S2 in Supplementary Material). On the basis of this weak taxonomic character, the population from Odelsteinhöhle in the Gesäuse National Park, Austria has been classified as *P. (P.) strouhali cavicola*.

**Description**

Troglomorphic subspecies. Body length: females 3.4–7 mm, males 3.45–6.15 mm, juveniles 2.95–3.7 mm. Epicuticle smooth under optical microscope; clothing setae thin, middle-sized, smooth or with a few distal barbs (Fig. 144). Antennae with 30–35 antennomeres in adults (Table 11). Length of antennae equal to or slightly shorter than body length in adults and juveniles. Sensillum of third



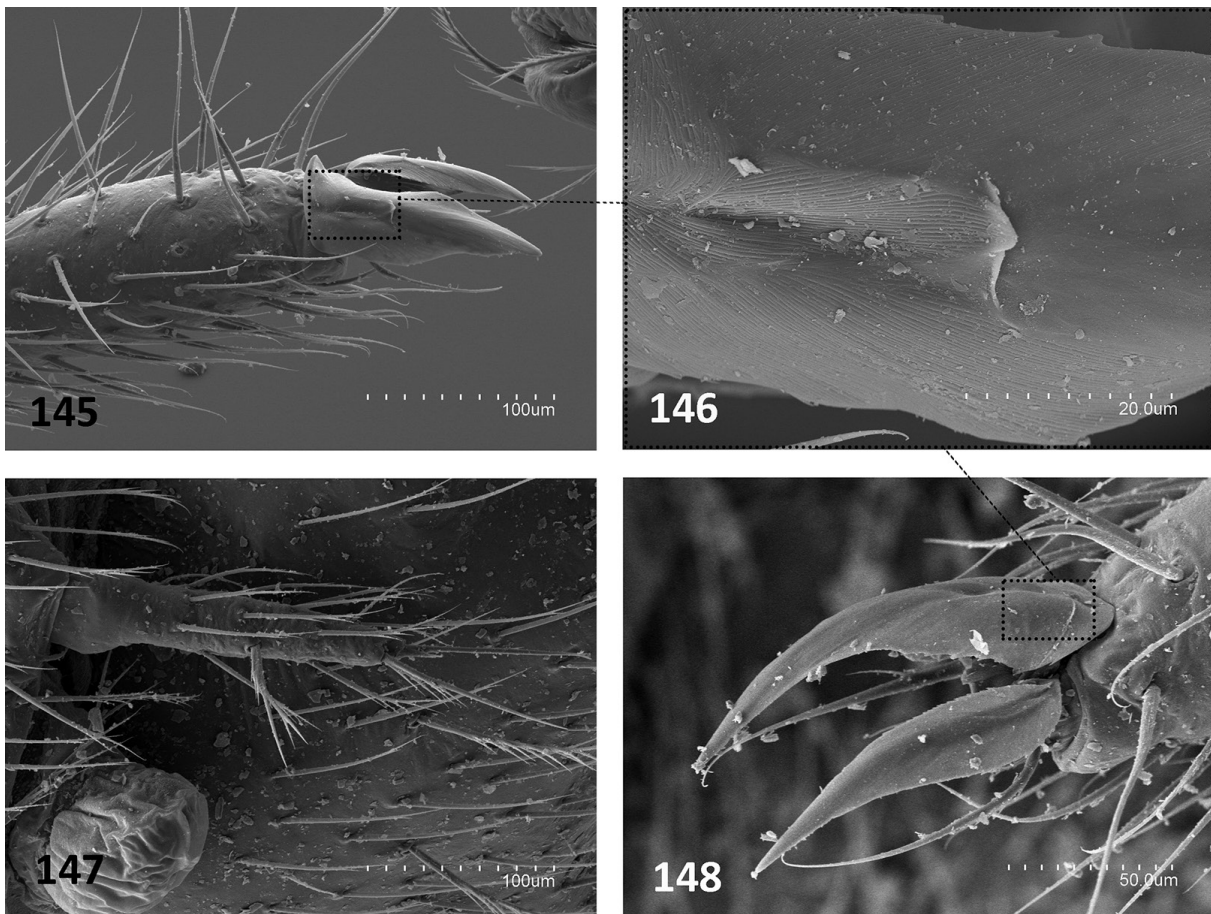
**Figs 135–140.** *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943, from Odelsteinhöhle, Styria, Austria (Coll. AS). **135.** Apical and distal antennomeres. **136.** Tip of apical antennomere. **137.** Lateral distal view of medial antennomere. **138.** Olfactory chemoreceptor. **139.** Medial portion of a gouge sensillum, detail. **140.** Central portion of a gouge sensillum, detail.



Figs 141–144. *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943, from Odelsteinhöhle, Styria, Austria (Coll. AS). 141. Pronotum, mesonotum and metanotum, right side (*s* = setiform sensillum). 142. Head, frontal view. 143. Frontal process. 144. Detail of mesonotum, right side, with *ma* and *la*<sub>1,2,3</sub> macrosetae. Scale bar: 141 = 0.2 mm.

antennomere subcylindrical, sharply pointed, in ventral position between macrosetae *d* and *e*. Central antennomeres  $1.6\times$  as long as wide. Twelve to twenty thin gouge sensilla ( $28\text{--}40\ \mu\text{m}$ ) in a single distal whorl on each medial and distal antennomere (Figs 137, 139–140). Cupuliform organ with 8–10 spheroidal olfactory chemoreceptors with a complex central structure surrounded by folds with visible polygonal net with porous surface (Figs 135–136, 138). Protruding frontal process with three distal, slightly tubercular macrosetae and a few posterior setae (Figs 142–143).

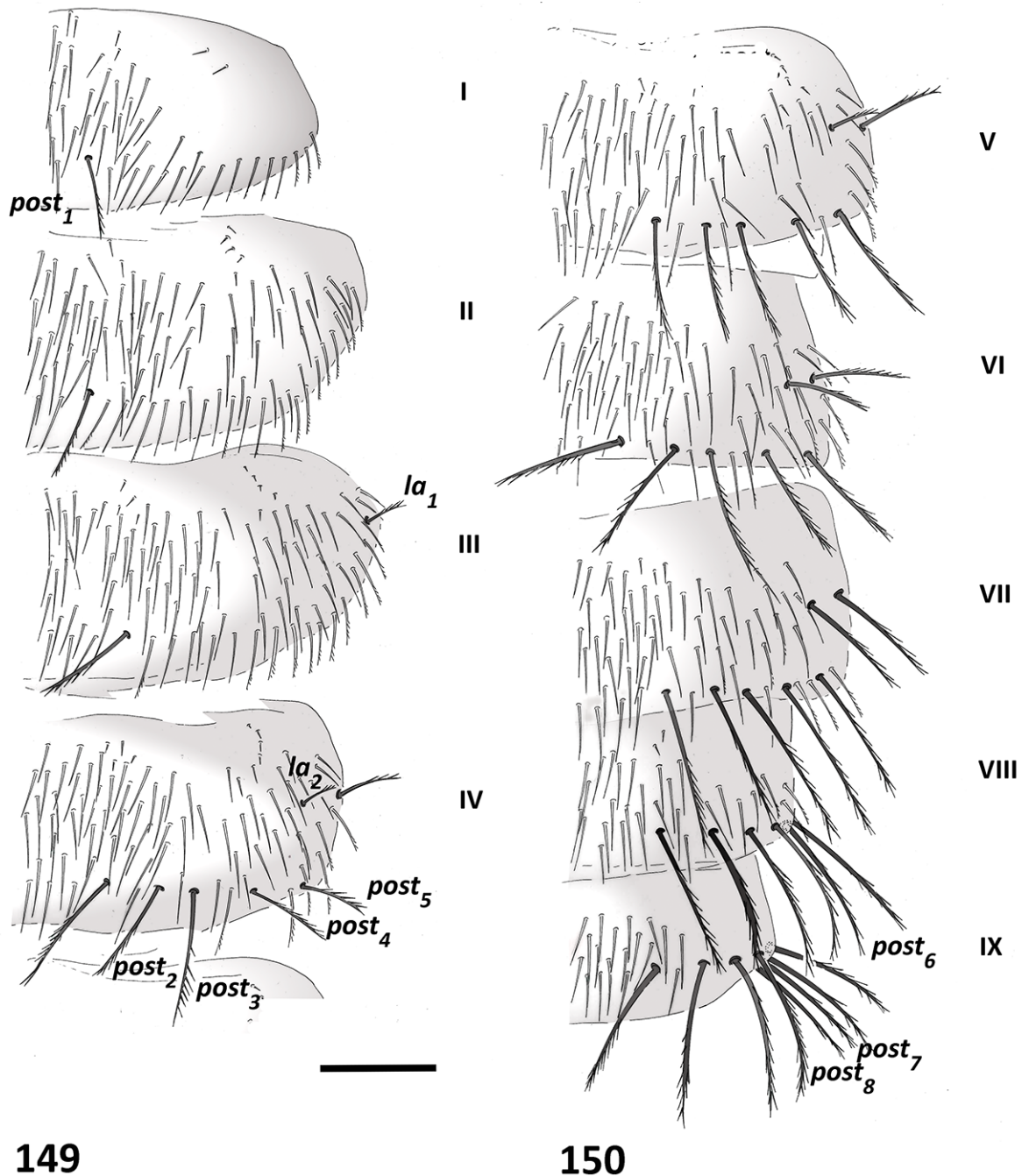
Notal macrosetae (Fig. 141): pronotum with 1+1 *ma*, 3+3 (3+2) *la*, 2+2 *lp*<sub>2,3</sub>; mesonotum with 1+1 *ma*, 3+3 *la*<sub>1,2,3</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *smp* submacrosetae (or 1+1 *mp*); metanotum with 1+1 *ma*, 1+1 *la*<sub>3</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp*; all notal macrosetae long, with long barbs along distal four-fifths (Fig. 144); marginal setae slightly longer than clothing setae, with thin barbs along distal half in lateral ones. Legs elongated, metathoracic legs reaching abdominal segment IX. Femur with one long dorsal macroseta, barbed along distal four-fifths. Tibia with 2–5 ventral macrosetae, barbed almost from base to tip. Calcars barbed from base to tip. Dorsal and lateral tarsal setae smooth. Unequal claws (1.1–1.4) with large lateral crests; ventral surface of claws noticeably ridged, dorsal surface slightly ridged but more evident on backward overhang of posterior claw; pretarsal processes smooth and setiform, with 0–4 thin, small basal barbs (Figs 145–146, 148).



**Figs 145–148.** *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943, from Odelsteinhöhle, Styria, Austria (Coll. AS). **145.** Distal portion of tarsus and pretarsus. **146.** Dorsal view of a posterior claw, detail. **147.** Lateral portion of urosternite VI with stylus and abdominal eversible vesicle. **148.** Pretarsus, laterodorsal view.

Distribution of abdominal macrosetae on tergites (Figs 149–150): 1+1 *post*<sub>1</sub> on I–II; 1+1 (0+0) *la*, 1+1 *post*<sub>1</sub> on III; 1+1–2+2 *la*, 5+5 (4+5) *post*<sub>1–5</sub> on IV; 2+2 *la*, 5+5 *post*<sub>1–5</sub> on V–VII; 6+6 (7+6) *post* on VIII; 8+8–9+9 *post* on abdominal segment IX. All *post* macrosetae long, covered with long barbs along distal four-fifths; *la* macrosetae shorter and less barbed than *post* macrosetae.

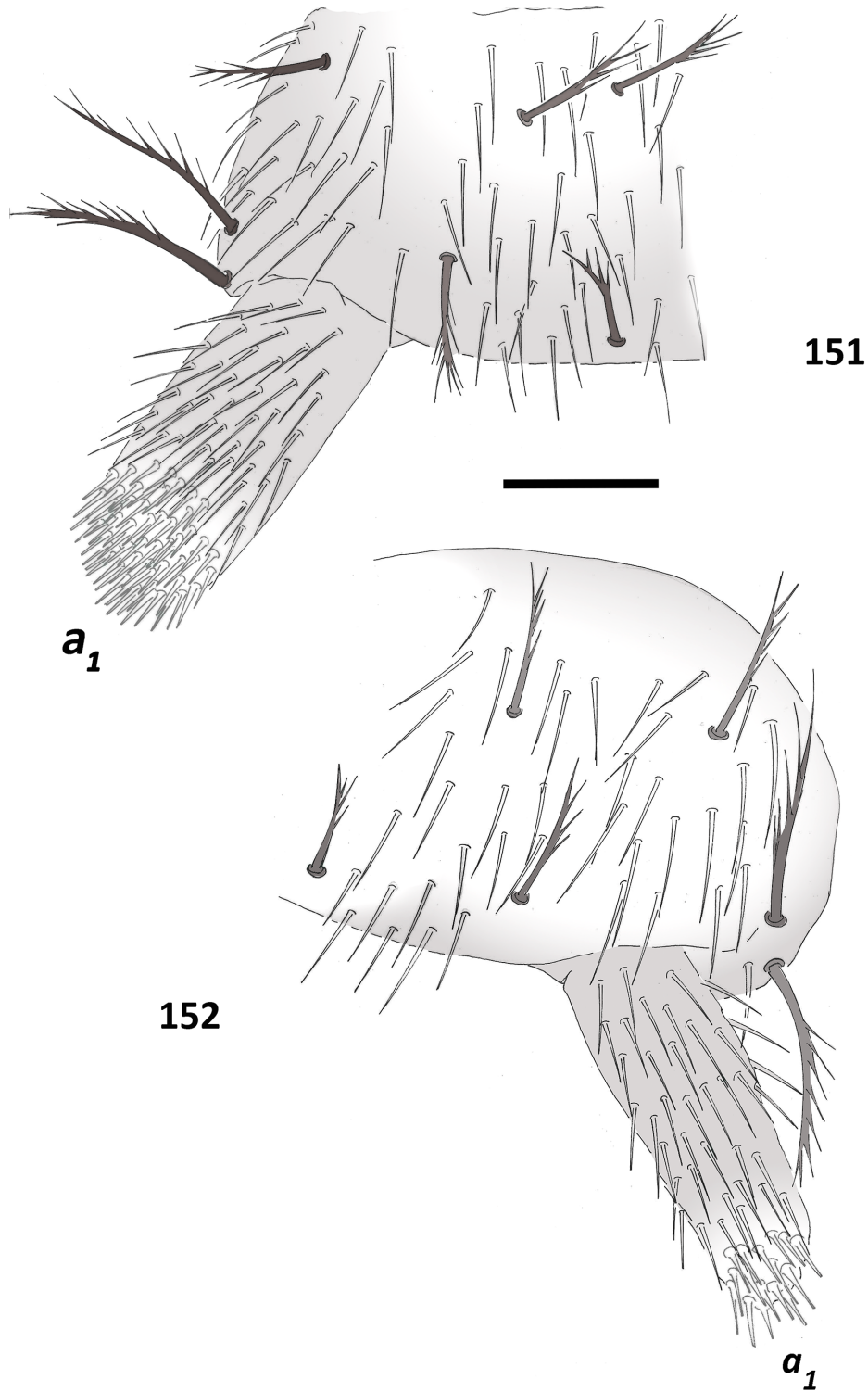
Urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Apical setae of styli smooth, with basal tooth; subapical setae with 2–4 long proximal barbs; medial sternal setae with 4–6 long medial barbs (Fig. 147).



**149** **150**  
**Figs 149–150.** *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943, from Odelsteinhöhle, Styria, Austria (Coll. AS). **149.** Urotergites I–IV, right side. **150.** Urotergites V–VIII and abdominal segment IX, right side (*s* = setiform sensillum). Scale bar: 0.2 mm.



Cerci up to 6.7 mm long (in 4.7 mm long female), with eight primary articles plus basal one, twice the length in juveniles (see Table 11). Articles with whorls of long macrosetae covered with thin barbs along distal two-thirds, combined with whorls of smooth, thin setae shorter than macrosetae.



**Figs 151–152.** *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943, from Odelsteinhöhle, Styria, Austria (Coll. AS). **151.** ♂, 6.3 mm long; urosternite I, right side. **152.** ♀, 6.3 mm long; urosternite I, left side. Scale bar: 0.1 mm.

**Table 11** (continued on next page). *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943 from Odelsteinhöhle, Austria. Length of the body, antennae, metathoracic legs and cerci (measurements in mm), in addition to the number of antennomeres and cercal articles.

Specimen (Coll. AS)	Body length	No. of antennomeres	Antennal length	Metathoracic leg length	No. of cercal articles (base included)	Cercus length
juv.	2.95	34	3.05	1.55	–	–
juv.	3.10	34	3.00	1.80	–	–
juv.	3.10	34	3.10	1.40	–	–
juv.	3.15	32	3.10	1.45	5	2.70
juv.	3.15	32	3.40	1.50	–	–
juv.	3.20	34	2.90	1.50	6	4.00
juv.	3.20	34	3.20	1.80	6	3.60
juv.	3.30	34	3.25	1.70	–	–
juv.	3.45	35	3.20	1.70	–	–
juv.	3.70	33	3.10	1.60	6	3.60
juv.	3.70	33	2.95	1.30	6	3.25
juv.	3.90	35	3.35	1.60	–	–
♀	3.40	34	3.45	1.55	–	–
♂	3.45	33	3.35	1.80	–	–
♀	3.60	35	3.60	1.95	–	–
♀	3.70	34	3.20	1.90	6	3.40
♂	4.50	34	4.70	2.15	–	–
♀	4.6	–	–	2.45	9	5.90
♀	4.70	31	4.95	2.60	9	6.70
♂	4.70	31	4.70	2.40	–	–
♂	4.80	35	4.40	2.30	–	–
♀	4.90	31	4.85	2.70	–	–
♀	5.00	35	5.50	2.70	–	–
♂	5.25	33	5.40	2.60	–	–
♂	5.30	31	4.50	2.45	–	–
♀	5.30	35	5.60	2.60	–	–
♂	5.35	30	5.00	2.35	9	6.10
♀	5.40	33	4.90	2.50	–	–
♂	5.40	33	4.50	2.45	–	–
♀	5.40	32	5.10	2.50	–	–
♀	5.55	34	5.10	2.50	–	–
♂	5.60	35	5.10	2.50	–	–
♂	5.60	34	4.55	2.15	–	–
♂	5.60	31	4.85	2.65	–	–
♂	5.70	34	4.70	2.35	–	–
♂	5.80	34	5.10	2.55	–	–

**Table 11** (continued from preceding page). *Plusiocampa (Plusiocampa) strouhali cavicola* Vornatscher, 1943 from Odelsteinhöhle, Austria. Length of the body, antennae, metathoracic legs and cerci (measurements in mm), in addition to the number of antennomeres and cercal articles.

Specimen (Coll. AS)	Body length	No. of antennomeres	Antennal length	Metathoracic leg length	No. of cercal articles (base included)	Cercus length
♀	5.90	34	5.30	2.75	–	–
♂	6.00	32	4.80	2.60	–	–
♀	6.10	31	4.70	2.50	–	–
♀	6.10	35	5.00	2.35	–	–
♂	6.15	34	5.10	2.60	–	–
♀	6.30	34	5.30	2.40	–	–
♀	6.30	31	5.00	2.60	–	–
♀	6.40	31	4.90	2.55	–	–
♀	6.50	32	5.10	2.90	–	–
♀	6.70	34	5.15	2.70	–	–
♀	7.00	32	5.10	2.70	–	–

In males, urosternite I (Fig. 151) with large subcylindrical appendages, each bearing up to 60 glandular  $a_1$  setae in a distal area. In females, urosternite I (Fig. 152) with subcylindrical appendages thinner than male appendages, each bearing up to 20 glandular  $a_1$  setae in a distal area.

### Habitat and distribution

Subterranean subspecies found in 21 caves in the Austrian Alps, where it is the common form in caves of the Northern Calcareous Alps. The areas of the two subspecies are overlapping, which casts serious doubt on the validity of the subspecies.

#### *Plusiocampa (Plusiocampa) suspiciosa* Condé & Mathieu, 1957

*Plusiocampa suspiciosa* Condé & Mathieu, 1957: 467, fig. xi, 45–52.

### Diagnosis (Condé & Mathieu 1957)

Non-trogloformic species. Antennae with 20–21 antennomeres; four olfactory chemoreceptors in cupuliform organ; non-protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 3+3–2+1 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; sparse smooth notal clothing setae. Two or three ventral tibial macrosetae; subequal small claws with small lateral crests, posterior claw with no backward overhang. Urotergites I–II with 2+2 *post* macrosetae; urotergite III with 4+4 *post* macrosetae; urotergites IV with 2+2 *la*, 5+5 *post* macrosetae; urotergites V–VII with 3+3 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female with subcylindrical to conical appendages with glandular  $a_1$  setae.

### Habitat and distribution

The locality of this species is still not clear, as a label confusion may have occurred between two localities, one endogean habitat in France (Tarn-et-Garonne, La Capelle-Livran, Caylus) and a small cave in Sicily (Scaletta Zanclea, south of Messina).

*Plusiocampa (Plusiocampa) ternovensis* Sendra & Borko sp. nov.  
urn:lsid:zoobank.org:act:D1AE6C14-8920-4505-9B42-B518BB1A6FB0

Figs 153–156; Table 12

### Etymology

The specific name comes from the geographic area where this new species was found, the plateau called Trnovski gozd (Trnovo Forest).

### Material examined

#### Holotype

SLOVENIA • ♀; Ajdovščina, Predmeja, Bela Griža 1 n. 7937; 2 Oct. 2014; Špela Borko leg., PMSL Diplura-001.

#### Paratypes

SLOVENIA • 2 ♀♀, 2 ♂♂; same collection data as for holotype; Coll. AS • 7 ♀♀, 2 ♂♂, 3 juv.; Ajdovščina, Predmeja, Velika ledena jama v Paradani n. 742; Coll. AS • 1 ♂; same collection data as for preceding; PMSL Diplura-002 • 1 ♀; same collection data as for preceding; PMSL Diplura-003.

#### Other material

See [Table S2](#) in Supplementary Material.

### Description

**BODY.** Body length 3.9–5.4 mm (females), 3.2–4.35 mm (males) and 2.7–3.7 (juveniles). Epicuticle smooth under optical microscope; body with thin, middle-sized barbed clothing.

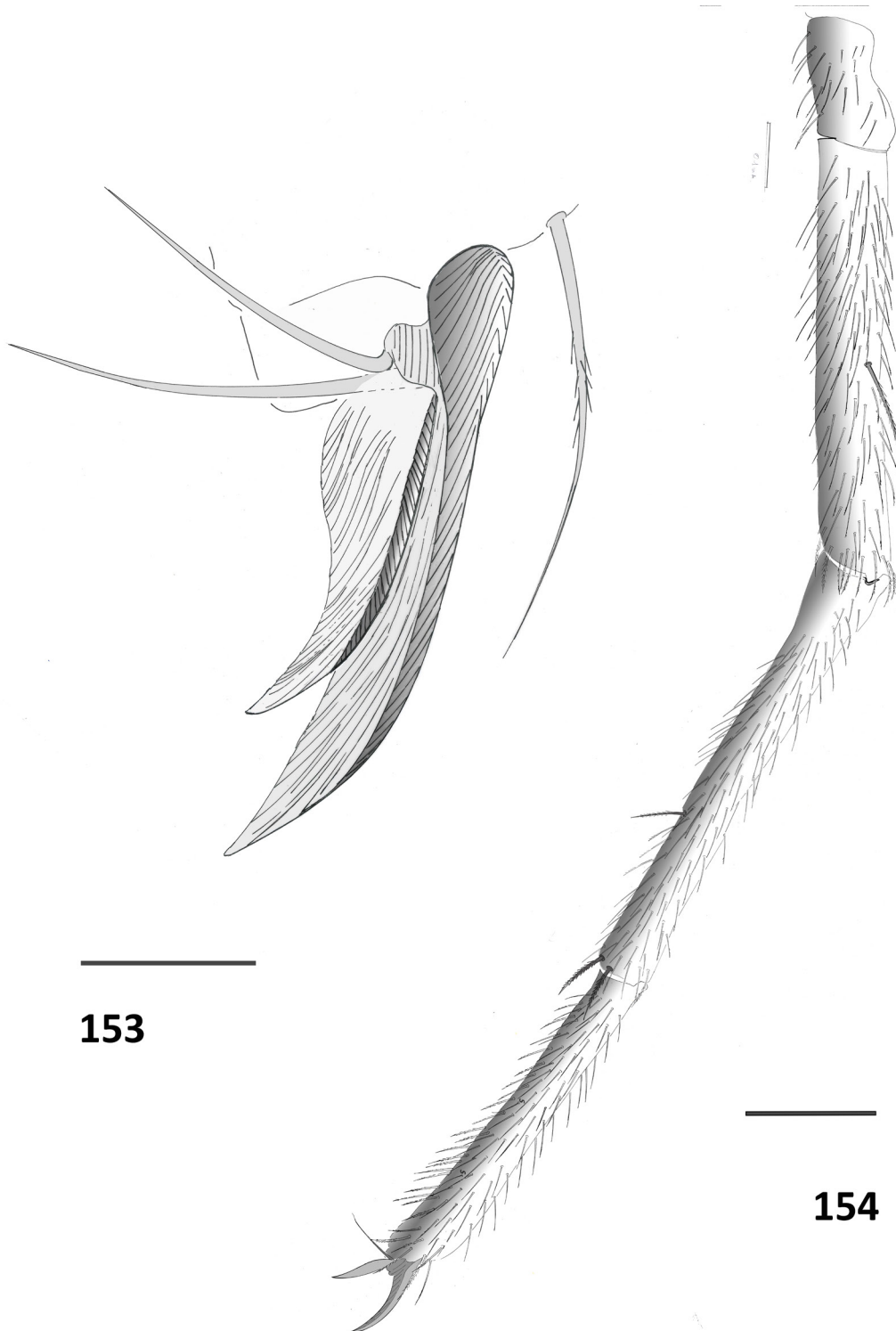
**HEAD.** Only two complete antennae, in a juvenile with 40 antennomeres. Bacilliform sensillum of third antennomere in ventral position between macrosetae *d* and *e*. Central antennomeres 1.3× as long as wide. Eighteen to twenty thin gouge sensilla (30–34 µm) in a single distal whorl on each medial and distal antennomere; 2–3 coniform sensilla in same whorl, but also present in last antennomere. Cupuliform organ on apical antennomere with about eight complex olfactory chemoreceptors. Non-protruding frontal process, with non-tubercular setae.

**THORAX.** Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 2+2 (1+1, 3+2) *la*, 2+2 *lp* macrosetae; long, barbed macrosetae; long, thin, barbed notal macrosetae; clothing setae smooth or with up to four distal thin barbs. One dorsal femoral macroseta, barbed all along with thin, short barbs; one barbed tibial metathoracic macroseta and none on prothoracic or mesothoracic tibiae; calcars with thin, long barbs in several rows; very unequal claws (1.7–1.8) with large lateral crests; posterior claw with a large backward overhang (Figs 153–154).

**ABDOMEN.** Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 (1+0) *la*, 3+3–2+2 *post* macrosetae; urotergite V with 1+1 (0+1) *la*, 4+4 *post* macrosetae; urotergite VI with 1+1 *la*, 4+4 *post* macrosetae; urotergite VII with 2+2 (2+1) *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7–8+8, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Stylus setae with a few barbs, smooth apically, with basal tooth; 3–5 thin distal barbs on subapical and mediosternal setae.

**CERCI.** Incomplete cerci, a maximum of 5 primary articles have been observed in several specimens. Each primary cercus bears from six to ten disorganized whorls of long, barbed macrosetae, one distal whorl of smooth, long setae and an apical whorl of short, thin setae.

GENITAL ORGANS. Male with two to four rows of up to 200 glandular  $g_1$  setae, subcylindrical appendages with a small distal area of up to ten glandular  $a_1$  setae; female with subcylindrical appendages with up to 8 glandular  $a_1$  setae (Figs 155–156).

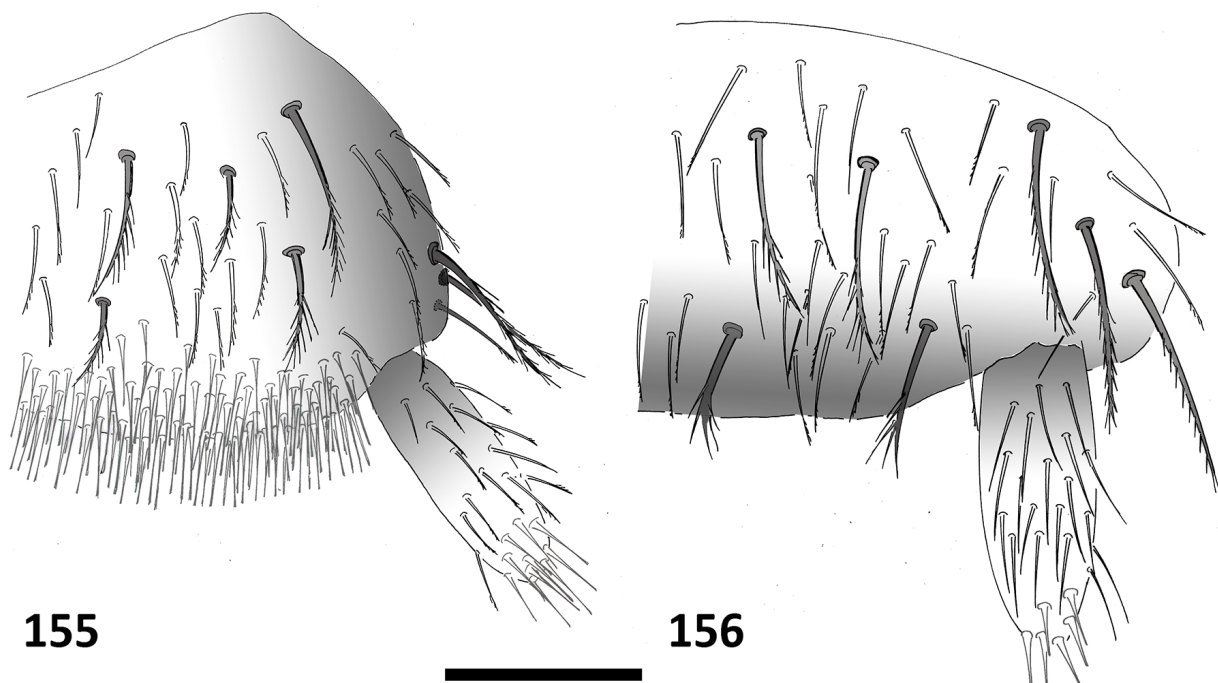


**Figs 153–154.** *Plusiocampa (Plusiocampa) ternovensis* Sendra & Borko sp. nov., paratype, ♀, 4.4 mm long, from Velika ledena jama v Paradani, Predmeja, Slovenia (PMSL Diplura-003). **153.** Metathoracic leg. **154.** Metathoracic pretarsus, lateral anterior side. Scale bars: 153 = 100  $\mu\text{m}$ ; 154 = 50  $\mu\text{m}$ .

### Phyletic affinities, habitat and distribution

Several species of *Plusiocampa* s. str. share important taxonomical features with *P. (P.) ternovensis* sp. nov., such as the clearly unequal claws with large lateral crests, the posterior claw with a backward overhang and the absence of medial posterior macrosetae on mesonotum and metanotum, but only *P. (P.) balsani* and *P. (P.) affinis* share a similar distribution pattern of notal and urotergal macrosetae. Nonetheless, the secondary sexual features of *P. (P.) balsani*, with the male having subtrapezoidal appendages and glandular  $a_2$  setae, unambiguously isolate it from *P. (P.) ternovensis* sp. nov. Morphologically and geographically speaking, its closest related species is *P. (P.) affinis*, but some clear differences separate them. The very unequal claws (1.7–1.8), presence of only one ventral tibial macroseta and the 2+2 lateral macrosetae on the urotergites are features of the new species that are not present in *P. (P.) affinis*, which has unequal claws (1.3), two ventral tibial macrosetae and 1+1 lateral macrosetae on the urotergites.

*Plusiocampa (P.) ternovensis* sp. nov. has been sampled in three caves at the edge of a karst plateau north of the town of Ajdovščina, in Slovenia. This karst area is in the northern part of the Dinaric Mountains, a transitional zone between the Mediterranean, Alpine, Dinaric and Central European biogeographic regions. In two of the caves, the species lives together with *P. (Stygiocampa) nivea*, although they segregate differently within the cave. *Plusiocampa (P.) ternovensis* sp. nov. lives at a wider range of depths, while *P. (S.) nivea* occupies a deeper zone of the cave, at a depth of 500 m in the Velika ledena jama v Paradani and Bela Griža 1 caves. The temperatures in these two deep caves increase with depth, from permanently under 0°C (Velika ledena jama v Paradani, with permanent ice in the upper parts) to more than 4°C in parts deeper than 500 m. In Ledenica pri Dolu, an ice cave with temperatures below 2°C, we found only *P. (P.) ternovensis* sp. nov., while in the Bošnarjev brezen Cave (5.9°C to 7.0°C) we found only *P. (S.) nivea*. This suggests that *P. (P.) ternovensis* sp. nov. may be considered better cold-adapted than *P. (S.) nivea*.



**Figs 155–156.** *Plusiocampa (Plusiocampa) ternovensis* Sendra & Borko sp. nov. **155.** Paratype, ♂, 4.7 mm long (PMSL Diplura-002); urosternite I, left side. **156.** ♀, 5.3 mm long (Coll. AS); urosternite I, left side. Scale bar: 0.1 mm.

**Table 12.** *Plusiocampa (Plusiocampa) ternovensis* Sendra & Borko sp. nov. Length of the body, femur, tibia and tarsus (including pretarsus) (measurements in mm).

Specimen	Depository	Body length	Femur	Tibia	Tarsus
♀ 01, paratype	Coll. AS	4.4	0.70	0.72	0.72
♀ 02, paratype	Coll. AS	3.9	0.75	0.80	0.78
♀ 03, paratype	Coll. AS	4.6	0.76	0.83	0.72
♀, holotype	PMSL Diplura-001	5.4	0.85	0.93	0.77
♀ 05, partype	PMSL Diplura-003	5.4	0.92	1.02	0.84
♀ 06, paratype	Coll. AS	4.7	0.80	0.86	0.78
♀ 07, paratype	Coll. AS	4.4	0.78	0.82	0.72
♀ 08, paratype	Coll. AS	4.2	0.78	0.87	0.78
juv. 01, paratype	Coll. AS	2.7	0.44	0.46	0.50
♀ 09, paratype	Coll. AS	5.3	0.85	1.04	0.81
♂ 01, paratype	PMSL Diplura-002	4.4	0.72	0.84	0.71
♂ 02, paratype	Coll. AS	3.2	0.65	0.70	0.68
juv. 02, paratype	Coll. AS	3.0	0.65	0.72	0.68
juv. 03, paratype	Coll. AS	3.7	0.64	0.72	0.68
♀ 10, paratype	Coll. AS	5.0	0.84	1.02	0.80

***Plusiocampa (Plusiocampa) tinoamorei*** Sendra & Nicolosi, 2019

*Plusiocampa (Plusiocampa) tinoamorei* Sendra & Nicolosi in Sendra *et al.*, 2019: 298, figs 1–22, tables 1–2..

**Diagnosis** (Sendra *et al.* 2019)

Troglomorphic species. Antennae with 37–41 antennomeres. Very slight protruded frontal process with slightly differentiated smooth macrosetae. Pronotum with 1+1 *ma*, 4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; body with a small number of thin clothing setae with thin distal barbs. Two or three ventral tibial macrosetae; slightly unequal claws (1.08–1.12) with large lateral crests, posterior claw with backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 3+3 *post* macrosetae; urotergites V–VII with 1+1 *la*, 5+5 *post* macrosetae; urotergite VIII with 6+6 (6+5) *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Styler setae with a few thin barbs. Male with an area of glandular *g*<sub>1</sub> setae, subcylindrical appendages with glandular *a*<sub>1</sub> setae; appendages of female slightly thinner than those of male.

**Habitat and distribution**

Subterranean species found in three caves near Siracusa, southeastern Sicily.

***Plusiocampa (Plusiocampa) vedovinii*** Condé, 1981

*Plusiocampa vedovinii* Condé, 1981b: 590, fig. 2.

**Diagnosis** (Condé 1981b)

Troglomorphic species. Antennae with 39 antennomeres; eight simple olfactory chemoreceptors in cupuliform organ, highly likely regenerated; non-protruding frontal process with non-tubercular setae.

Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *lp* macrosetae; long, barbed notal macrosetae. Two ventral tibial macrosetae; unequal claws with large lateral crests. Urotergite IV with 1+1 *la*, 1+0 *post* macrosetae; urotergites V–VII with 1+1 *la*, 3+3 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown; female with subcylindrical appendages bearing glandular *a*<sub>1</sub> setae.

#### Habitat and distribution

Subterranean species found in Grouffre des Encanaux, Auriol, Sainte-Baume Massif, Bouches-du-Rhône, southeastern France.

#### *Plusiocampa (Plusiocampa) vodniensis* Bareth & Condé, 2001

*Plusiocampa vodniensis* Bareth & Condé, 2001: 18, figs 5–6.

#### Diagnosis (Bareth & Condé 2001)

Troglomorphic species. Antennae with 31, 36 and 38 antennomeres; six simple olfactory chemoreceptors on cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3 *la*, 2+2 *lp* macrosetae; mesonotum 1+1 *ma*, 3+3 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; metanotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp*, 1+1 *mp* macrosetae; long, barbed notal macrosetae; clothing setae abundant, smooth or with a few distal barbs. Two or three ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergites I–III with 1+1 *post* macrosetae; urotergites IV–V with 1+1 *la*, 4+4 *post* macrosetae; urotergites VI–VII with 2+2 *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; abdominal segment IX with 8+8 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male unknown.

#### Habitat and distribution

Subterranean species known only from the Vodni Pech Cave, Vidin town area, in the Balkan Mountains, Bulgaria.

#### Subgenus *Stygiocampa* Silvestri, 1934

*Stygiocampa* Silvestri, 1934: 180.

#### Diagnosis (Condé & Bareth 1996; Bareth & Condé 2001)

No dorsal femoral macrosetae; without medial posterior notal macrosetae and with an overall reduction in mesonotal and metanotal macrosetae; extra macrosetae on first to eighth urosternites (with the exception of *Plusiocampa (Stygiocampa) bureschi* Silvestri, 1931 and *P. (S.) denisi* Condé (1947)).

#### Habitat and distribution

Subterranean subgenus found almost exclusively in the Dinaric Mountains, but also in part of the Balkan Mountains (Fig. 211).

#### *Plusiocampa (Stygiocampa) bureschi* Silvestri, 1931

*Plusiocampa bureschi* Silvestri, 1931b: 100, figs iii–v.

*Plusiocampa (Stygiocampa) rauseri* Rusek, 1965: 94, figs 18–24.

#### Diagnosis (Silvestri 1931b; Condé 1955a, 1959; Condé & Bareth 1996; Bareth & Condé 2001)

Troglomorphic species. Antennae with 39–54 antennomeres; seven to nine complex olfactory chemoreceptors in cupuliform organ. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with



1+1 *ma*, 1+1 *lp* macrosetae; metanotum without macrosetae; long, barbed notal macrosetae; abundant notal clothing setae. No ventral tibial macrosetae; slightly unequal claws (1.1) with large lateral crests, posterior claw with a small backward overhang. Urotergite VII with 2+2 *post* macrosetae; urotergite VIII with 4+4 *post* macrosetae; abdominal segment IX with 6+6–7+7 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae, subcylindrical slightly enlarged appendages with glandular *a*<sub>1</sub> setae; female with subcylindrical appendages with glandular *a*<sub>1</sub> setae. Spermatozoid fascicles 50 µm in diameter, 25 µm wide; wheels with 3½ turns of 300–350 µm and 5.6 µm diameter filament.

### Habitat and distribution

Subterranean species found in 13 caves in a karst region on the left bank of the Iskar River, Sofia District, Balkan Mountains, Bulgaria.

#### *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996

Fig. 202

*Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996: 374, figs 1, 3, 4e, tables 1–4.

### Diagnosis (Condé & Bareth 1996)

Troglomorphic species. Antennae with 29–33 antennomeres; 12–14 complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 1+1 *lp* macrosetae; mesonotum with 0+0–1+1 *sla* macrosetae; metanotum without macrosetae; long, barbed macrosetae; abundant barbed notal clothing setae. No ventral tibial macrosetae; unequal claws (1.35) with large lateral crests, posterior claw with a large backward overhang. Urotergite VII with 0+0–1+1 *post* macrosetae; urotergite VIII with 3+3–2+2 *post* macrosetae; abdominal segment IX with 7+7 *post* macrosetae; urosternite I with 21+21–29+25, urosternites II–VII with 11+11–14+12, urosternite VIII with 4+4 (3+3, 4+5) macrosetae. Male without glandular *g*<sub>1</sub> setae, thick slightly short subcylindrical appendages without glandular *a*<sub>2</sub> setae; female with subcylindrical appendages without glandular *a*<sub>2</sub> setae. Spermatozoid fascicles 50 µm in diameter and 10–12 µm wide; wheels with 1½ turns of 140–150 µm long filament.

### Remarks

The study of 26 specimens collected from three caves (see [Table S2](#) in Supplementary Material) allowed us to add characters to the diagnosis (Coll. AS).

### Habitat and distribution

Subterranean species found in several caves in the Kučaj and Beljanica Mountains, eastern Serbia Balkan System (Fig. 202).

#### *Plusiocampa (Stygiocampa) dalmatica* Condé, 1959

Figs 205, 208

*Plusiocampa dalmatica* Condé, 1959: 48, fig. 2.

### Diagnosis (Condé 1959; Bareth 1988; Condé & Bareth 1996)

Troglomorphic species. Antennae with 41–47 antennomeres; numerous sheet-shaped complex olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3–4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; long, barbed notal macrosetae; long, barbed notal

clothing setae. No ventral tibial macrosetae; unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergite III with 0+0–1+1 (1+0) *la* macrosetae; urotergite IV with 1+1 *la*, 0+1 *post* macrosetae; urotergite V with 1+1 *la*, 4+4 (3+4) *post* macrosetae; urotergites VI–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 5+5–6+6 *post* macrosetae; abdominal segment IX with 8+8–9+9 (10+9) *post* macrosetae. Urosternite I with 14+15–21+20, urosternites II–VII with 9+9–12+12, urosternite VIII with 2+2–3+3 macrosetae. Male with lateral expansions of posterior margin occupied by an area of glandular  $g_i$  setae in adults (no expansion in juveniles and little expansion in young males), subcylindrical appendages without glandular  $a_2$  setae; female with subcylindrical appendages with glandular  $a_1$  setae.

### Remarks

The studied material (see Table S2 in Supplementary Material) allowed us to make additions to the diagnosis (Coll. AS).

### Habitat and distribution

Subterranean species well distributed around the northwestern Dinaric Mountains, found in 18 caves (Figs 205, 208).

#### *Plusiocampa (Stygiocampa) denisi* Condé, 1947

*Plusiocampa denisi* Condé, 1947a: 21, fig. 2.

### Diagnosis (Condé 1947a)

Troglomorphic species. Antennae with 29–34 antennomeres. Pronotum with 1+1 *ma*, 3+3 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1–2+1–2+2 *la*, 1+1 *lp* macrosetae; metanotum with 1+1 *ma* macrosetae; long, barbed notal macrosetae, abundant notal clothing setae, smooth or with a few distal barbs. Two ventral tibial macrosetae. Unequal claws with large lateral crests, posterior claw with a backward overhang. Urotergite IV with 1+1 *la*, 1+1 *post* macrosetae; urotergite V with 1+1 *la*, 2+2 *post* macrosetae; urotergites VI–VII with 1+1 *la*, 4+4 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with a large area with glandular  $g_i$  setae, subcylindrical appendages with glandular  $a_1$  setae; female appendages like those of male.

### Habitat and distribution

Subterranean species found in the Pećina u Hamidovoj vrtači and Špela Hajnet (= Špela Maja Hajnet) caves in southwestern Serbia, Dinaric Mountains.

#### *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882)

Figs 157–180, 207

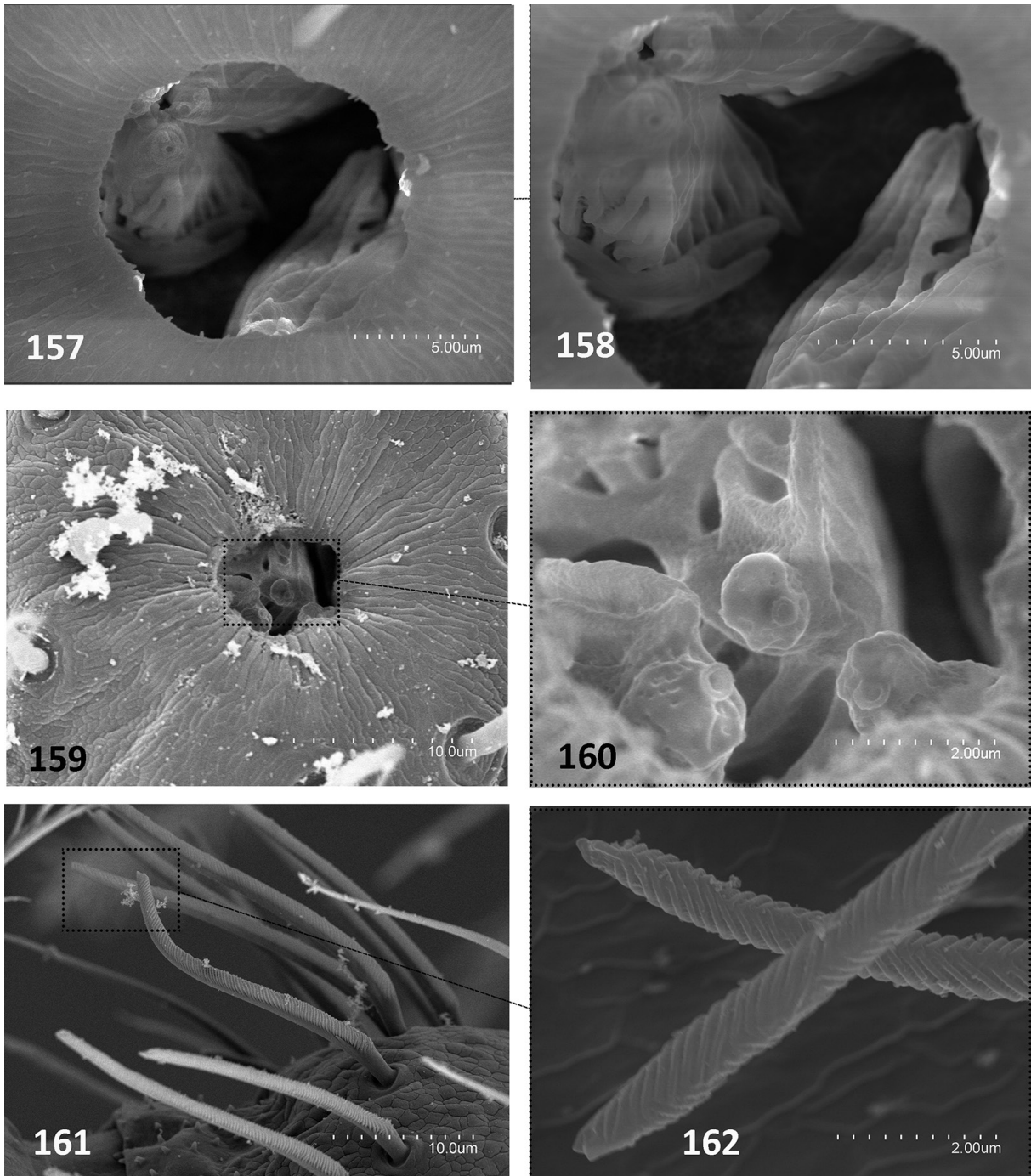
*Campodea nivea* Joseph, 1882: 25.

*Campodea erebophila* Hamann, 1896: 153, figs i–ii, table 3.

### Diagnosis (Denis 1923; Condé 1947a, 1959; Silvestri 1947; Bareth 1968)

Troglomorphic species. Antennae with 28–36 antennomeres; abundant sheet-shaped olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1 *ma*, 3+3–4+4 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *la*, 2+2 (3+2) *lp* macrosetae; metanotum with 2+2 *lp* macrosetae; long, barbed notal macrosetae; abundant barbed notal clothing setae. No ventral tibial macrosetae; unequal claws (1.35) with large lateral crests, posterior claw with a backward overhang. Urotergite IV with 0+0–1+1 *la* macrosetae; urotergites V–VII with 1+1 *la*, 4+4 *post* macrosetae; urotergite VIII with 5+5–6+6 *post* macrosetae; abdominal segment IX with 8+8–9+9

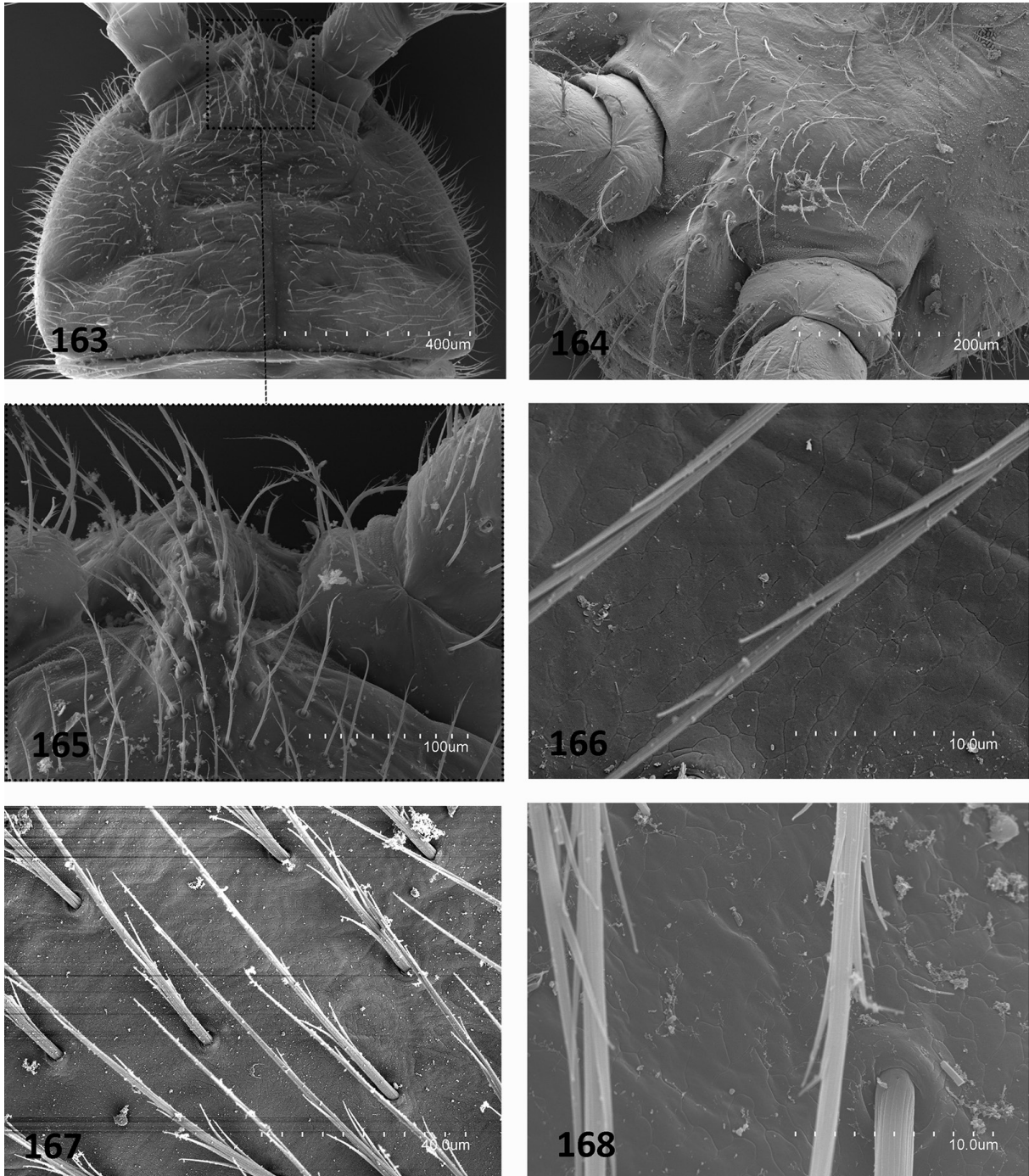
(9+10) *post* macrosetae; urosternite I with 11+1+11–15+15 (15+16), urosternites II–VII with 11+11–14+14, urosternite VIII with 2+2–4+4 macrosetae. Male without glandular  $g_1$  setae, thick subcylindrical appendages without glandular  $a_2$  setae; female with subcylindrical appendages without glandular  $a_2$  setae.



**Figs 157–162.** *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882), from Habečkov Brezen, Idrijski Log Idrija, Slovenia (157–158), Velika ledena jama v Paradani, Predmeja, Slovenia (159–160, 162) and Volčja jama, Postojna, Slovenia (161) (Coll. AS). **157.** Cupuliform organ. **158.** Olfactory chemoreceptors. **159.** Cupuliform organ. **160.** Olfactory chemoreceptors. **161.** Lateral distal portion of a medial antennomere. **162.** Distal portion of two gouge sensilla.

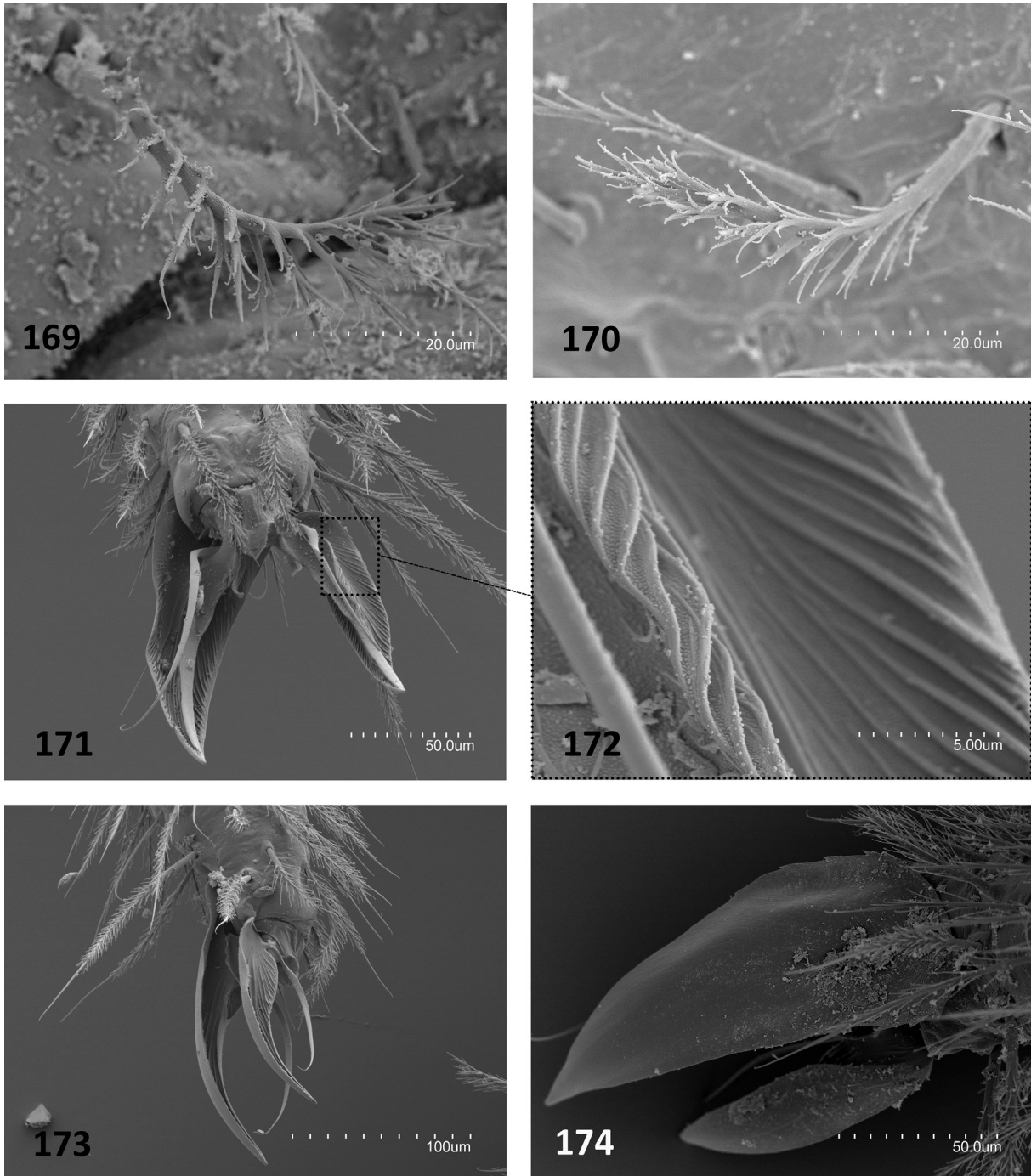
## Remarks

The new material studied (see [Table S2](#) in Supplementary Material) allowed the addition of minor taxonomic details revealed by SEM microscopy. The epicuticle, apparently smooth in optical microscopy, shows a subtle reticulate surface (Figs 166, 168) covered by well-barbed clothing setae (Figs 167–168). The macrosetae are also well barbed, but the multi-barbed urosternal macrosetae (Figs 169–170) are



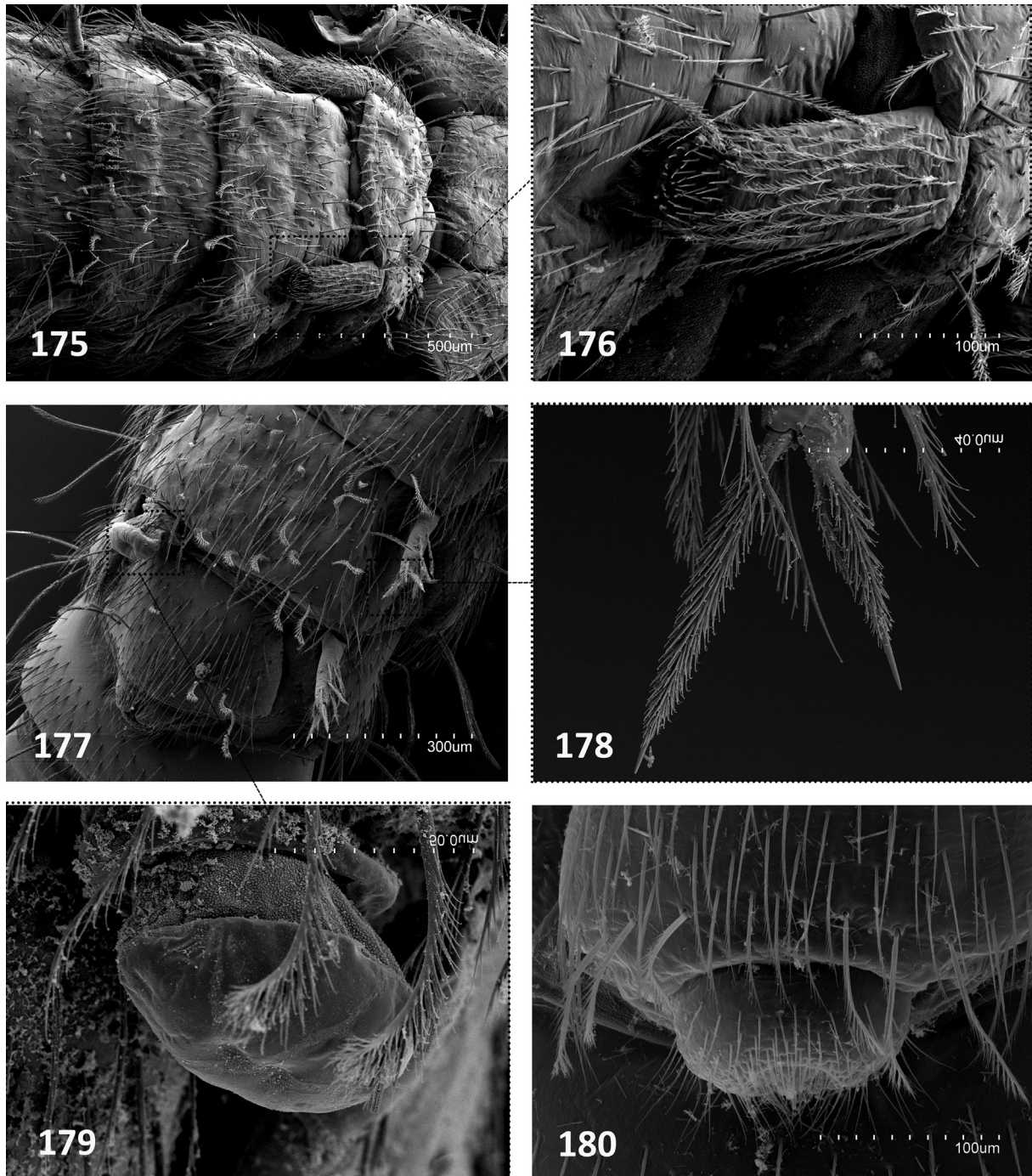
**Figs 163–168.** *Plusiocampa* (*Stygiocampa*) *nivea* (Joseph, 1882), from Velika ledena jama v Paradani, Predmeja, Slovenia (163–166, 168) and Volčja jama, Postojna, Slovenia (167) (Coll. AS). **163.** Head, dorsal view. **164.** Head, lateral frontal view. **165.** Frontal process. **166.** Surface of mesonotum, detail. **167.** Clothing setae of metanotum. **168.** Surface of metanotum, detail.

remarkable. The gouge sensilla are abundant and as long as 28  $\mu\text{m}$ , with transversal stripes in a V shape (Figs 161–162). The cupuliform organ has a narrow hole that does not allow an adequate observation of the olfactory chemoreceptors; however, these can be described under the optical microscope as having a multiple laminal shape and under SEM as a central structure with a pronounced terminal pore,



**Figs 169–174.** *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882), from Velika ledena jama v Paradani, Predmeja, Slovenia (169, 171–174) and Jabčina (Pečina Jabčinov stržen), Račice, Podgrad, Slovenia (170) (Coll. AS). **169.** Macrosetae on urosternite I. **170.** Macrosetae on urosternite I. **171.** Pretarsus, ventral view. **172.** Ventral side of claw, detail. **173.** Lateral side of pretarsus with anterior claw in the foreground. **174.** Pretarsus, dorsal side.

semiradially and irregularly folded (Figs 157–160). The protruding frontal process with tubercular setae is clearly visible under SEM (Figs 163–165). Claws have well-developed lateral crests with a complex, grooved ventral surface (Figs 171–174). The completely barbed abundant macrosetae and setae cover the entire surface of the sternites (Figs 169–170). The entire length of the stylar setae is totally covered



**Figs 175–180.** *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882), from Volčja Jama, Postojna, Slovenia (175–177), Velika ledena jama v Paradani, Predmeja, Slovenia (178–179) and Roupa Cave, Banjščice, Slovenia (180) (Coll. AS). **175.** ♂, urosternites I–III. **176.** ♂, left appendage of urosternite I. **177.** ♀, urosternites VII–VIII. **178.** Apical and subapical setae on abdominal stylus. **179.** Abdominal eversible vesicle. **180.** ♂, urosternite VIII.

by barbs (Figs 177–178) and the eversible vesicles are large (Fig. 179). Males have large subcylindrical appendages with a large area of glandular  $a_1$  setae (Figs 175–176, 180).

### Habitat and distribution

Subterranean species, well distributed around the northwestern Dinaric Mountains, so far found in 75 caves (Fig. 207).

***Plusiocampa (Stygiocampa) remyi* Condé, 1947**  
Figs 181–192

*Plusiocampa remyi* Condé, 1947a: 17, fig. 1.

### Diagnosis (Condé 1947a; Condé & Bareth 1996)

Troglomorphic species. Antennae with 46–52 antennomeres; abundant sheet-shaped olfactory chemoreceptors in cupuliform organ; protruding frontal process with tubercular setae. Pronotum with 1+1  $ma$ , 3+3–4+4  $la$ , 2+2  $lp$  macrosetae; mesonotum with 1+1  $la$ , 2+2  $lp$  macrosetae; metanotum with 2+2  $lp$  macrosetae; barbed notal macrosetae; clothing setae abundant, completely barbed. No ventral tibial macrosetae; unequal claws with large crests, posterior claw with a backward overhang. Urotergite III with 1+1 (0+1)  $la$  macrosetae; urotergite IV with 1+1  $la$  macrosetae; urotergites V–VII with 1+1  $la$ , 3+3  $post$  macrosetae; urotergite VIII with 5+5  $post$  macrosetae; abdominal segment IX with 9+9–11+11  $post$  macrosetae; urosternite I with 17+17–22+22, urosternites II–VII with 13+13–19+19, urosternite VIII with 3+3–6+6 macrosetae. Male with lateral expansions of posterior margin occupied by an area of glandular  $g_1$  setae in adults (no expansions in juveniles and small expansions in young males), subcylindrical appendages without glandular  $a_2$  setae; females with long subcylindrical appendages without glandular  $a_2$  setae.

### Remarks

The studied material (see [Table S2](#) in Supplementary Material) allowed the addition of information to the diagnosis. The specimens from Njegoš pećina, Njeguši (Kotor, Montenegro) and Đatlo pećina, Lebršnik, Gacko (Bosnia and Herzegovina) revealed new diagnostic characters in SEM microscopy: antennomeres with a whorl of thin gouge sensilla, 40–47  $\mu\text{m}$  long with an external transversal striped surface in a V pattern (Figs 181–182, 184), claws with large lateral crest with ventral longitudinal grooves separated by reticulate surfaces (Figs 183, 185–186). The first urosternite of the adult male has lateral expansions, bearing plenty of glandular  $g_1$  setae (Figs 187–188), and abundantly long and completely barbed urosternal macrosetae (Figs 189, 192), like the stylar setae (Fig. 190), and similar to but thinner than the cercal macrosetae (Fig. 191).

***Plusiocampa (Stygiocampa) aff. remyi* Condé, 1947**

### Differential diagnosis against the type form (Condé & Bareth 1996)

Antennae with 50 antennomeres; urosternite without lateral expansions, with a large area of glandular  $g_1$  setae; enlarged subcylindrical appendages with a distal glandular  $a_1$  seta.

### Habitat and distribution

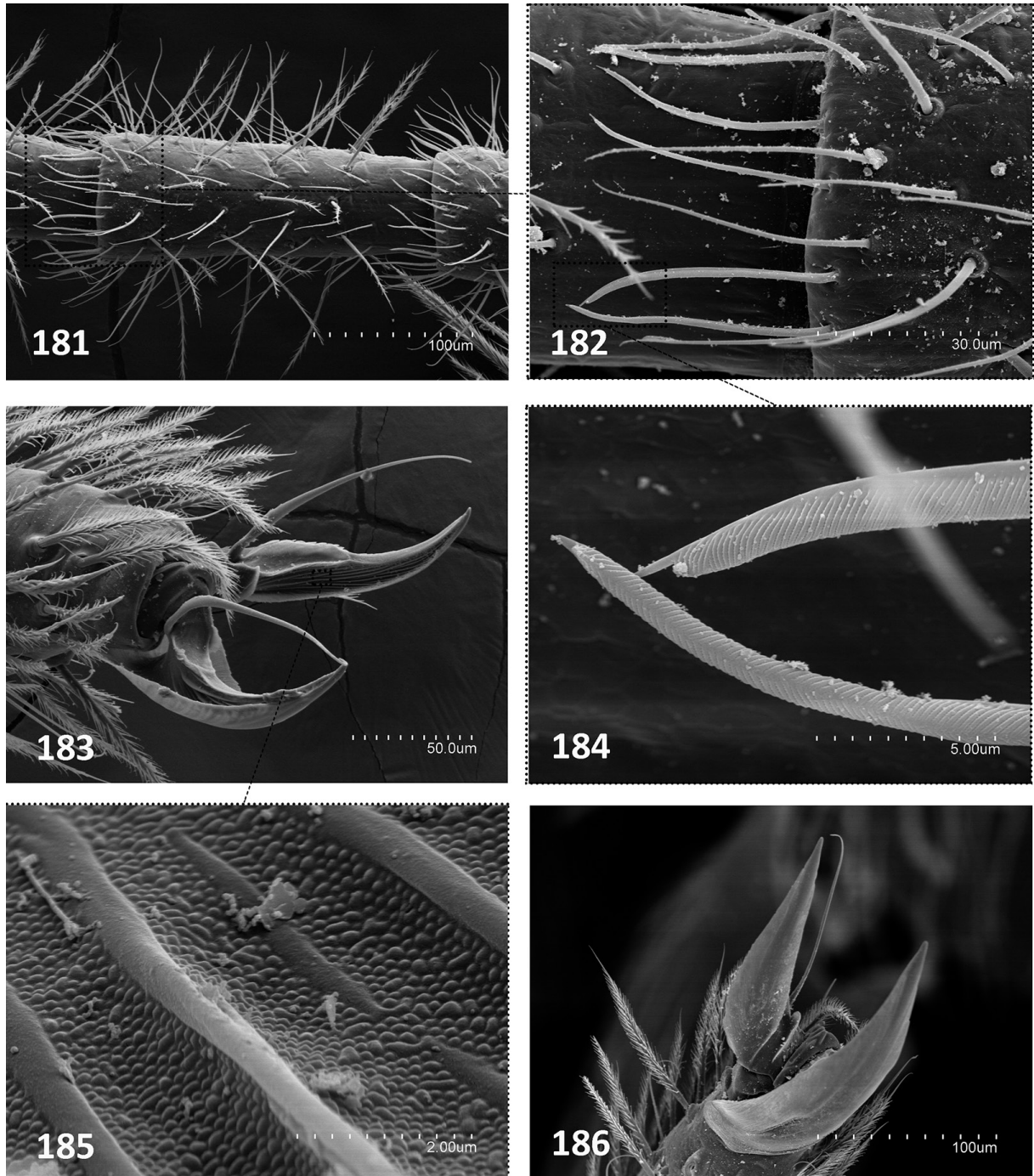
Subterranean species widespread in 21 caves of karst regions of the southeastern Dinaric Mountains. *Plusiocampa (S.) aff. remyi* occurs in Vranjača (cave), Croatia.

Subgenus ***Venetocampa*** Bareth & Condé, 1984

*Venetocampa* Bareth & Condé, 1984: 143.

**Diagnosis** (Bareth & Condé 1984)

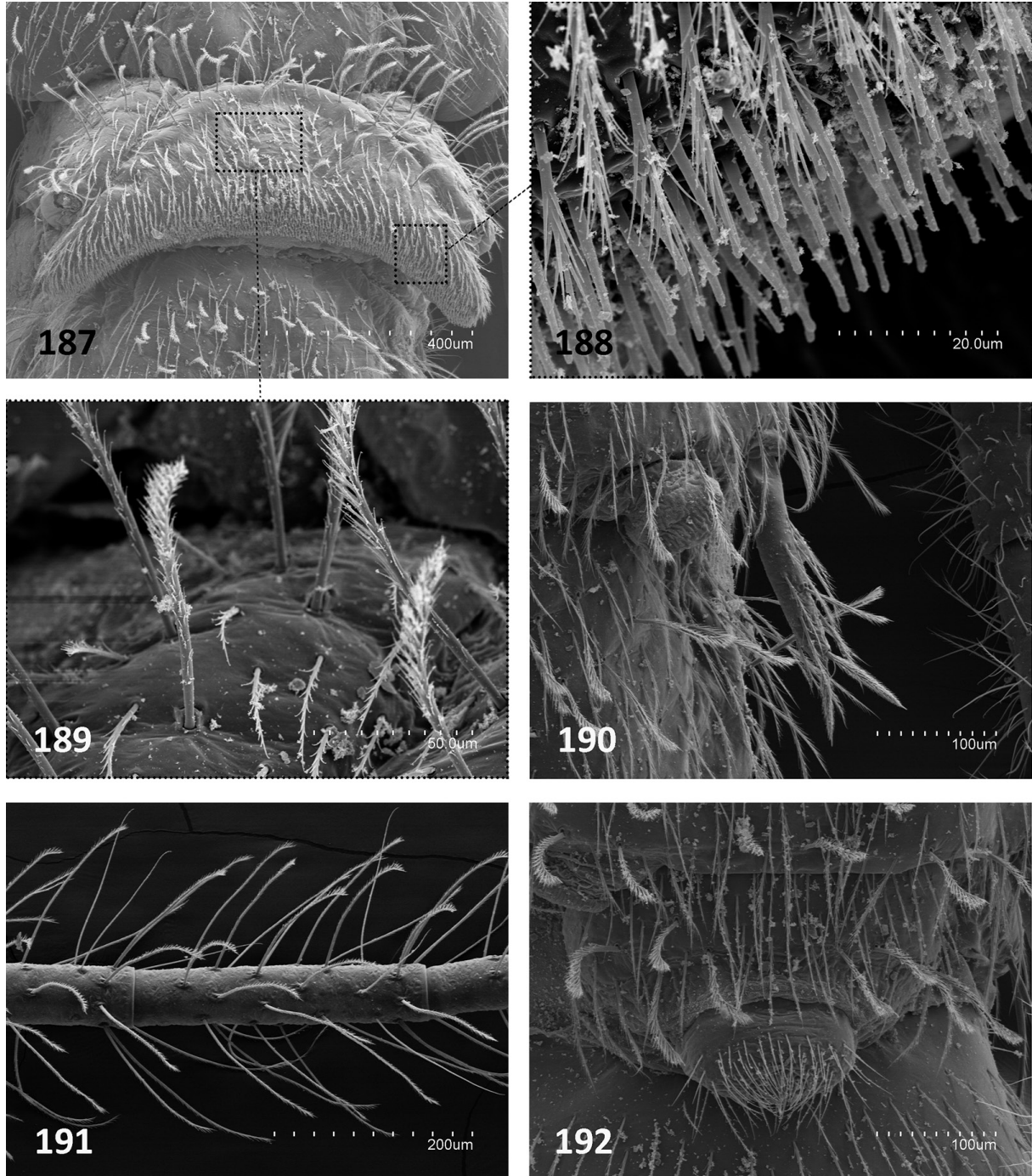
Mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *lp* or 1+1 *ma*, 1+1 *la*, 2+2 *lp* macrosetae; without *mp* notal macrosetae. One dorsal femoral macroseta; without ventral tibial macrosetae. Very unequal, elbow-like claws with large lateral crests, posterior claw with a large



**Figs 181–186.** *Plusiocampa* (*Stygiocampa*) *remyi* Condé, 1947, from Njegoš pećina, Njeguši, Kotor, Montenegro (Coll. AS). **181.** Medial antennomere. **182.** Distal portion of a medial antennomere. **183.** Pretarsus of a metathoracic leg, lateral view with posterior claw in the foreground. **184.** Distal portion of two gouge sensilla. **185.** Ventral side of anterior claw, detail. **186.** Pretarsus of a metathoracic leg, dorsal side.



backward overhang. Urotergites with at most 1+1 lateral anterior and 4+5 posterior macrosetae starting from sixth urotergite; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male with thick, enlarged appendages with a large area of glandular *a*<sub>1</sub> setae.



**Figs 187–192.** *Plusiocampa (Stygiocampa) remyi* Condé, 1947, from Njegoš pećina, Njeguši, Kotor, Montenegro (187–190, 192) and Đatlo pećina, Lebršnik, Gacko, Bosnia and Herzegovina (191) (Coll. AS). **187.** ♂, urosternite I (appendages missing). **188.** ♂, edge of urosternite I, detail. **189.** ♂, macrosetae on urosternite I, detail. **190.** Lateral posterior view of urosternite V. **191.** Second cercal article. **192.** ♂, urosternite VIII.

### Habitat and distribution

The two species of the subgenus *Venetocampa*, which inhabit the subterranean habitat, are found in two caves of the Veneto Region, northern Italian Peninsula (Fig. 211).

*Plusiocampa (Venetocampa) ferrani* Sendra & Delić sp. nov.

[urn:lsid:zoobank.org:act:27DC5E1D-B0E4-4BAD-B12E-20ADF1BF16FB](https://zoobank.org/act:27DC5E1D-B0E4-4BAD-B12E-20ADF1BF16FB)

Figs 193–195

### Etymology

This species is named after Milan Ferran, an enthusiastic caver, discoverer and explorer of the type locality in Ferranova buža (meaning Ferran's hole), Slovenia.

### Material examined

#### Holotype

SLOVENIA • ♂; Vrhnika, Ferran buža; 16 Feb. 2013; T. Delić, T. Novak and M. Feron leg.; MZB 2019-1031.

#### Paratype

SLOVENIA • 1 juv.; same collecting data as for holotype; Coll. AS.

### Description

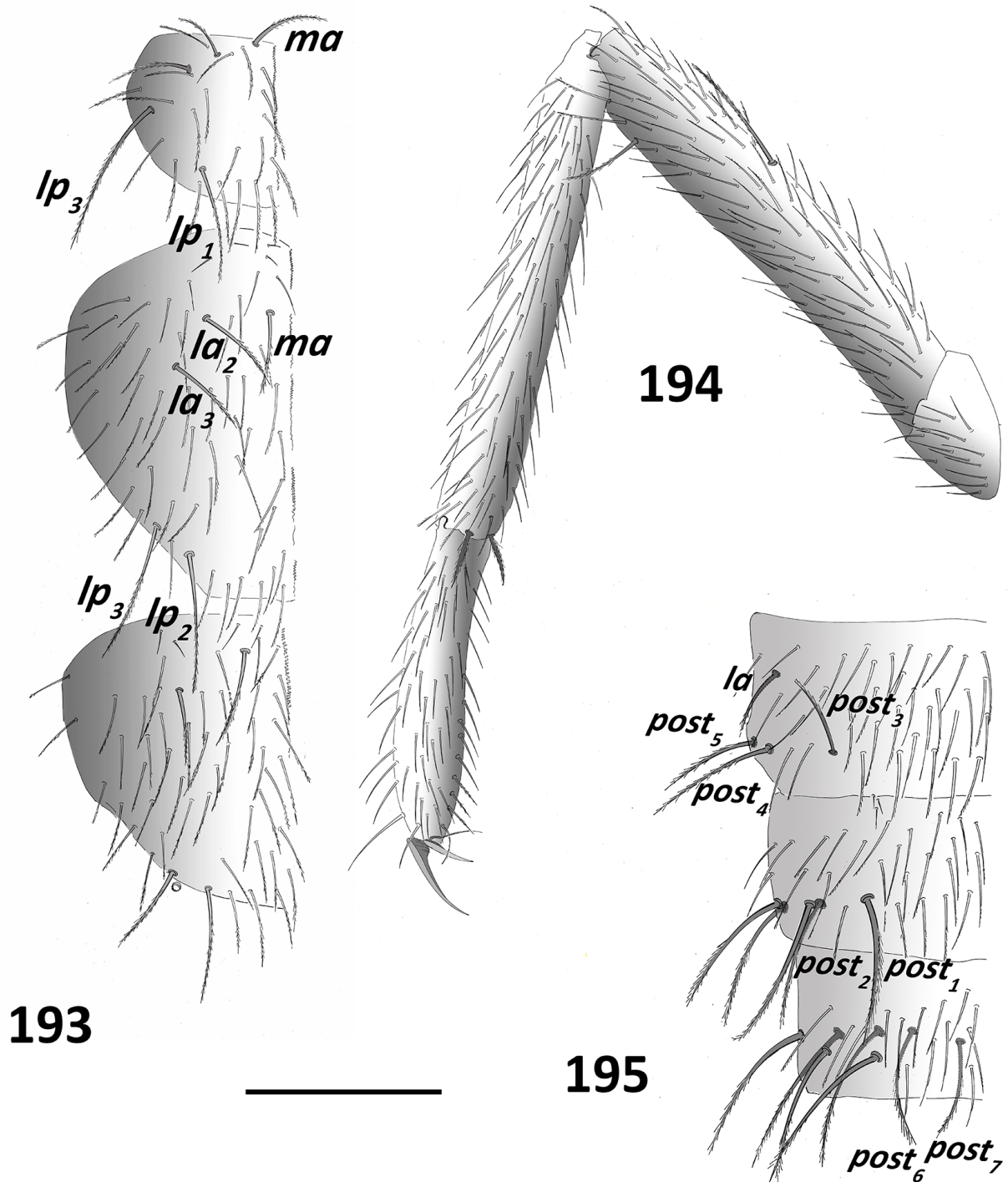
**BODY.** Body length 3.0 mm (holotype) and 2.8 mm (paratype). Epicuticle smooth under optical microscope; body with sparse middle-sized clothing setae, distal two-thirds with thin barbs.

**HEAD.** Two intact antennae in holotype, slightly longer than body length (3.5/3.6 mm), with 32/33 antennomeres, in paratype slightly shorter than body length (2.76/2.75 mm), with 32/32 antennomeres. Small, subcylindrical sensillum of third antennomere in ventral position between *c* and *d* macrosetae; central antennomeres 1.7× as long as wide, apical antennomere 2.0× as long as wide; cupuliform organ occupies 1/6 of its length, with 7 or 8 spheroidal olfactory chemoreceptors, each with at least two folds, in cupuliform organ; gouge sensilla starting on ventral side of third antennomere, with an apical row of eight gouge sensilla; fourth antennomere with 12 ventral gouge sensilla and 1 dorsal gouge sensillum; fifth antennomere with 12 ventral and 2 dorsal gouge sensilla; sixth antennomere with 13 ventral and 4 dorsal gouge sensilla; seventh antennomere with 15 ventral and 6 dorsal gouge sensilla; eighth antennomere with 14 ventral and 7 dorsal gouge sensilla; ninth antennomere with 12 ventral and 8 dorsal gouge sensilla; after tenth antennomere a complete apical whorl of gouge sensilla on each antennomere, with about 20 on medial antennomeres and 15 on distal ones. Frontal process with non-tubercular macrosetae or setae; macrosetae along line of insertion of antennomere and *x* setae similar in length, with long, thin distal barbs, on distal two-thirds (*a/i/p/x* with relative lengths of 33/30/26/39 in holotype). Small suboval labial palps with a long subcylindrical sensillum, two guard setae, four normal setae and up to 72 neuroglandular setae.

**THORAX.** Pronotum with 1+1 *ma*, 2+2 *la*<sub>2,3</sub>, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*<sub>2,3</sub>, 2+2 *lp*<sub>1,3</sub> macrosetae; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*<sub>2,3</sub> macrosetae; long notal macrosetae, barbed along distal four-fifths; long marginal setae with barbs along distal two-thirds (Fig. 193). Legs elongated (1.84 mm long in holotype and 1.54 mm in paratype), overpassing end of abdomen. Femur with one long dorsal macroseta, barbed almost from its base, inserted around middle of article. No ventral tibial macrosetae. Calcars with 2–3 rows of long barbs from base, with a smooth and narrow lateral side along each calcar. Dorsal and lateral subapical tarsal macrosetae smooth. Very unequal claws, posterior claw 1.6–1.8× as long as anterior one, including a large backward overhang on posterior claw; ventral surface

of claws with grooves, dorsal surface including large lateral crests with thin stripes. Setiform pretarsal processes reaching extremities of claws (Fig. 194).

ABDOMEN. Distribution of abdominal macrosetae on tergites: 1+1 (holotype) or 0+0 (paratype) *la*, 2+3 *post*<sub>3,4,5</sub> on urotergite VII; 5+5 *post* on urotergite VIII; 7+7 *post* on abdominal segment IX. All *post*



**Figs 193–195.** *Plusiocampa (Venetocampa) ferrani* Sendra & Delić sp. nov., holotype, ♂, from Ferranova buža, Vrhnika, Slovenia (MZB 2019-1031). **193.** Pronotum, mesonotum and metanotum, left side. **194.** Metathoracic leg. **195.** Urotergites VII–VIII and abdominal segment IX, right side. Scale bar: 0.2 mm.

urotergal macrosetae long, robust, barbed on distal four-fifths; *la* urotergal macrosetae much shorter, barbed along distal half (Fig. 195). Urosternite I with 6+6, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae; all urosternal macrosetae robust, covered by very long barbs along distal half to three-fourths. Pseudoarticulated stylus with barbed setae with long barbs, apical setae shorter than medial and subapical setae.

SECONDARY SEX CHARACTERS. Male urosternite I without glandular  $g_1$  setae, subcylindrical short, enlarged appendages with up to 21 large glandular  $a_1$  setae. Adult female unknown.

#### Phyletic affinities, habitat and distribution

*Plusiocampa (V.) ferrani* sp. nov. is the second representative of the subgenus *Venetocampa*. It is a cave-dwelling species closely related to *P. (V.) paoletti*, found in the vicinity of Belluno, Italian Alps (Bareth & Condé 1984). Nonetheless, the macrosetal distribution patterns on the nota and urotergites show enough differences to describe these specimens as a new taxon.

#### *Plusiocampa (Venetocampa) paoletti* Bareth & Condé, 1984

*Plusiocampa paoletti* Bareth & Condé, 1984: 143, figs 5–6.

#### Diagnosis (Bareth & Condé 1984)

Troglomorphic species. Antennae with 33 antennomeres; eight to nine simple olfactory chemoreceptors in perhaps a regenerated antennae; non-tubercular setae in frontal process. Pronotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*, 2+2 *lp* macrosetae; metanotum with 1+1 *ma*, 1+1 *lp* macrosetae; long, barbed notal macrosetae; abundant notal clothing setae. One dorsal femoral macroseta; no ventral tibial macrosetae; very unequal claws (2.5), posterior claw with a backward overhang, with large lateral crests; short anterior lateral process and long posterior lateral process. Urotergite V with 0+1 *la* macrosetae; urotergite VI with 1+1 *la*, 2+2 *post* macrosetae; urotergite VII with 1+1 *la*, 1+1 *post* macrosetae; urotergite VIII with 4+5 *post* macrosetae; abdominal segment IX with 7+7 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae, short and very thick appendages with abundant glandular  $a_1$  setae; female unknown.

#### Habitat and distribution

Subterranean species found in Biga de le Agnelezze Cave, Piani Eterni, Belluno, Italian Alps.

#### Genus *Vandelicampa* Condé, 1955

*Vandelicampa* Condé, 1955c: 407.

#### Diagnosis (Condé 1955c)

Monotypic genus with 1+1 medial anterior, (2+2) 3+3 lateral anterior, 1+1 medial posterior and 2+2 lateral posterior macrosetae on mesonotum and with 1+1 medial anterior, 1+1 (2+2) lateral anterior, 1+1 lateral posterior and 2+2 lateral posterior macrosetae on metanotum. One dorsal femoral macroseta. Two or three ventral tibial macrosetae. Subequal, elbow-like claws with large lateral crests. Laminal pretarsal process with a sharp ending covered with long ventral barbs. Urosternite I with 8+8, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae, subcylindrical appendages without glandular  $a_2$  setae.

*Vandelicampa tisserandi* Condé, 1955

*Vandelicampa tisserandi* Condé, 1955c: 407, figs 3–4.

**Diagnosis** (Condé 1955c)

Troglophobic species. Antennae with 29–38 antennomeres; eight to ten olfactory chemoreceptors in cupuliform organ. Long, barbed notal macrosetae; sparse, smooth, long notal clothing setae. One dorsal femoral macroseta; two or three ventral tibial macrosetae; subequal claws (1.04) with large lateral crests, posterior claw without a backward overhang; laminar pretarsus processes with a sharp ending covered with long ventral barbs. Urotergites I–III with 1+1 *post* macrosetae; urotergite IV with 1+1 *la*, 3+3 *post* macrosetae; urotergites V–VII with 3+3 (2+2) *la*, 4+4 *post* macrosetae; urotergite VIII with 6+6 *post* macrosetae; urosternite I with 8+8, urosternites II–VII with 6+6, urosternite VIII with 2+2 macrosetae. Male with subcylindrical appendages of first urosternite similar to those of female.

**Habitat and distribution**

Subterranean species found in three caves in the karst areas of Lebanon (Fig. 210).

***Tachycampoid phyletic lineage*****Other genera related to Plusiocampinae, the tachycampoid phyletic lineage**

Bareth & Condé (1981) originally proposed a unique and different tachycampoid phylogenetic lineage (“lignée Tachycampoïde”) for a number of previously described genera: *Tachycampa* Silvestri, 1936 with one species from a cave in the western Rif Mountains (Silvestri 1936); *Paratachycampa* Wygodzinsky, 1944 with three species, one from a cave in Nuevo León (Mexico) and two from several caves in the eastern Iberian Peninsula (Wygodzinsky 1944; Bareth & Condé 1981); *Juxtalcampa* Wygodzinsky, 1944 with two species, one from a cave in Guerrero (Mexico) and another from a cave in Alta Verapaz (Guatemala) (Wygodzinsky 1944); and *Jeannelicampa* Condé, 1955 with one species from caves in Tell Atlas (Algeria) (Condé 1952, 1954c). Much later, Condé (1982) proposed a new genus within this phyletic lineage, *Oncinocampa* Condé, 1982, for a subterranean species from the north of the Iberian Peninsula and another one from Sardinia (Condé 1981b, 1982). A few years later, the diversity of *Oncinocampa* was increased with four more species, two from the same karst region in the Cantabric Mountain Range on the northern Iberian Peninsula (Sendra & Condé 1988, Bareth 1989) and two from caves in the Americas, one near São Paulo, Brazil (Condé 1997) and another in Veracruz, Mexico (Sendra *et al.*, 2016). The number of species in *Tachycampa* has also been expanded with three new cave-dwelling species from Mexico (Sendra *et al.* 2016) (Fig. 209).

**Diagnosis** (Bareth & Condé 1981; Sendra *et al.* 2016)

Three main morphological features support the phyletic line of the tachycampoid group, although exceptions exist. First, the elbow-like claws with lateral crests (absent in *Jeannelicampa stygia* Condé, 1952). Second, the notal macrosetal formula: pronotum with 3+3 *ma*, *la* and *lp*; mesonotum with 2+2 *ma* and *la*; metanotum with 1+1 *ma* or fewer (with only 1+1 *lp* pronotal macrosetae in *Oncinocampa genuitei* (Bareth, 1989); *Paratachycampa hispanica* Bareth & Condé, 1981 and *P. penyoensis* Bareth & Condé, 1981 have an extra lateral anterior macroseta). Finally, dorsal macrosetae are absent from the femur, with the exception of a small, thin macroseta in *O. asonensis* Sendra & Condé, 1988 and *O. paclti* Condé, 1981. Additionally, all species inhabit subterranean ecosystems, except *O. paclti*, which has non-troglophobic features.

**Taxonomic key to Euro-Mediterranean tachycampoid genera and species**

- |   |   |
|---|---|
| 1. 2+2 macrosetae on urosternite VIII ..... | 2 |
| – 1+1 macrosetae on urosternite VIII .....  | 4 |

2. 9+9 macrosetae on urosternites II–VII .....*Paratachycampa penyoensis* Bareth & Condé, 1981  
– 6+6 or 7+7 macrosetae on urosternites II–VII .....3
3. 6+6 macrosetae on urosternites II–VII .....*Jeannelicampa stygia* Condé, 1952  
– 7+7 macrosetae on urosternites II–VII .....*Paratachycampa hispanica* Bareth & Condé, 1981
4. Pretarsal claws without lateral crests .....*Jeannelicampa stygia* Condé, 1952  
– Pretarsal claws with lateral crests .....5
5. Pretarsal claws with large lateral crests, but without backward overhang .....  
.....*Tachycampa lepineyi* Silvestri, 1936  
– Pretarsal claws with small lateral crests .....6
6. Appendages of urosternite I in adult males piriform or subtrapezoidal .....7  
– Appendages of urosternite I in adult males short, thick and large .....8
7. Appendages of urosternite I in adult males piriform .....  
.....*Oncinocampa asonensis* Sendra & Condé, 1988  
– Appendages of urosternite I in adult males subtrapezoidal .....*Oncinocampa pacti* (Condé, 1981)
8. 1+1 lateral anterior macrosetae or submacrosetae on pronotum, mesonotum and metanotum; 1+1 lateral anterior pronotal macrosetae or submacrosetae .....*Oncinocampa falcifer* Condé, 1982  
– Without notal macrosetae, except 1+1 long lateral posterior pronotal macrosetae .....  
.....*Oncinocampa genuitei* Bareth, 1989

Genus *Jeannelicampa* Condé, 1952

*Jeannelicampa* Condé, 1952: 64.

**Diagnosis** (Condé 1952, 1954c)

Pronotum with 3+3 medial anterior, lateral anterior and lateral posterior macrosetae; mesonotum with 1+1 medial anterior macrosetae and with or without 1+1 lateral anterior submacrosetae; metanotum with or without 1+1 medial anterior submacrosetae. No dorsal femoral macrosetae; one ventral tibial macroseta. Simple and slightly curved claws with smooth, laminar lateral process. Urotergal macrosetae start from urotergite V or VII. 9+9 macrosetae on first urosternite. Male unknown.

*Jeannelicampa stygia* Condé, 1952

*Jeannelicampa stygia* Condé, 1952: 65, fig. 2.

**Diagnosis** (Condé 1952, 1954c)

Troglomorphic species. Antennae with 40–48 antennomeres; 20–28 olfactory chemoreceptors in cupuliform organ; protruding frontal process with non-tubercular setae. Pronotum with 1+1 *ma*, 1+1 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 short *ma* macrosetae and 0+0–1+1 *sla* submacrosetae; metanotum with 0+0–1+1 *sma* submacrosetae; long, barbed pronotal macrosetae, short mesonotal macrosetae; clothing setae barbed along distal three-fourths. No dorsal femoral macrosetae; one ventral tibial macroseta; subequal, slightly curved claws without lateral crests; narrow, laminar, smooth pretarsal processes. Urotergites V–VII with 0+0–1+1 *la* macrosetae; urotergite VIII with 2+2–3+3 (2+1) *post* macrosetae; urosternite I with 9+9, urosternites II–VII with 6+6, urosternite VIII with 1+1–2+2 macrosetae. Female appendages of urosternite I subcylindrical, with glandular *a*<sub>1</sub> setae; male unknown.

### Habitat and distribution

Subterranean species located in two caves: Bou Iacor and Misserghin Ravine in Oran, Tell Atlas, Algeria (Fig. 210).

Genus *Oncinocampa* Condé, 1982

*Oncinocampa* Condé, 1982: 71.

**Diagnosis** (Sendra & Condé 1988; Condé 1997; Sendra *et al.* 2016)

Pronotum with 3+3 medial anterior, lateral anterior and lateral posterior macrosetae; mesonotum with 2+2 medial anterior and lateral anterior macrosetae; metanotum with 1+1 medial anterior macrosetae. Dorsal femoral macrosetae absent (with the exception of *O. asonensis* and *O. paclti*); ventral tibial macrosetae absent (exceptions: one in *O. paclti* and *O. trajanoae* Condé, 1997); elbow-like claws with small lateral crest, without a backward overhang; setiform, smooth lateral process; one pair of lateral anterior and lateral posterior urotergal macrosetae on medial urotergites (absent in *O. bolivarurrutiai* Sendra & García, 2016); apical, subapical and medial setae of stylus with a few small barbs.

### Habitat and distribution

The six current species of this genus have been found in caves, although two are non-troglophic. They have an amphi-Atlantic distribution, with one species in Mexico, one in Brazil, three in the center of the Cantabrian Mountain Range on the Iberian Peninsula and one in Sardinia (Fig. 210).

*Oncinocampa asonensis* Sendra & Condé, 1988

*Oncinocampa asonensis* Sendra & Condé, 1988: 1019, figs 1–4, table 1.

**Diagnosis** (Sendra & Condé 1988)

Troglophic species. Epicuticle smooth under optical microscope. Antennae with 53–64 antennomeres; protruding frontal process with non-tubercular setae; nine or ten complex olfactory chemoreceptors. Pronotum with 1+1 *ma*, 1+1 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la* macrosetae; metanotum with 1+1 *ma* macrosetae; long, barbed notal macrosetae; smooth, long clothing setae. Dorsal femoral macrosetae absent; ventral tibial macrosetae absent; subequal, elbow-like claws with small lateral crests; setiform, smooth pretarsal processes. Urotergites V–VII with 1+1 *la*, 1+1 *lp* macrosetae; urotergite VIII with 4+4 *post* macrosetae; abdominal segment IX with 6+6 *post* macrosetae; urosternite I with 7+1+7–11+1+11, urosternites II–VII with 6+6–7+7 (6+9), urosternite VIII with 1+1 macrosetae. Male with remarkable large lateral expansion on posterior border with glandular *g<sub>1</sub>* setae; piriform appendages with glandular *a<sub>1</sub>* and *a<sub>2</sub>* setae; subcylindrical appendages with glandular *a<sub>1</sub>* and *a<sub>2</sub>* setae.

### Habitat and distribution

Subterranean species found in seven caves in the karst areas around Ason Valley, in the Cantabro-Basque sector of the Cantabrian Mountain Range, northern Iberian Peninsula.

*Oncinocampa falcifer* Condé, 1982

*Oncinocampa falcifer* Condé, 1982: 71, figs 1–2.

**Diagnosis** (Condé 1982)

Troglophic species. Epicuticle smooth under optical microscope. Antennae with 39–40 antennomeres; six complex olfactory chemoreceptors in cupuliform organ; non-tubercular frontal process setae.

Pronotum with 1+1 *ma*, 1+1 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la* macrosetae; metanotum with 1+1 *ma* macrosetae; long, thin macrosetae with a few barbs; short, smooth clothing setae. One weak dorsal femoral macroseta; ventral tibial macrosetae absent; unequal, elbow-like claws with very small lateral crests; setiform, smooth pretarsal process. Urotergites VI–VII with 1+1 *la*, 1+1 *lp* macrosetae; urotergite VIII with 3+3 *post* macrosetae; abdominal segment IX with 5+5 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 4+4, urosternite VIII with 1+1 macrosetae. Male without glandular  $g_1$  setae; short, thick and enlarged appendages with glandular  $a_1$  and  $a_2$  setae; female unknown.

*Oncinocampa* aff. *falcifer* Condé, 1982

**Differential diagnosis against the type form**

Two specimens (Coll. AS), in poor condition and difficult to observe under the microscope, were collected in two adjacent caves, Sima de Landubia and Sistema de la Cubada Grande (Burgos) in the southeast of the Cantabrian Mountain Range. Mesonotum and metanotum with *lp* macrosetae, in addition to some variation in urotergal macrosetae. Nevertheless, new specimens should be collected before establishing a new species.

**Habitat and distribution**

Subterranean species known only from Cueva de la Marniosa (Treviso, Cantabria), Picos de Europa, Central Cantabrian Mountain Range. The aff. form was found in two caves in the southeast of the Cantabrian Mountains, northern Iberian Peninsula.

*Oncinocampa genuitei* Bareth, 1989

*Oncinocampa genuitei* Bareth, 1989: 131, fig. 1.

**Diagnosis** (Bareth 1989)

Troglomorphic species. Epicuticle smooth under optical microscope. Non-protruding frontal process, non-tubercular setae. Pronotum with 1+1 *lp* macrosetae, long and poorly barbed; mesonotum and metanotum without macrosetae; smooth, short notal clothing setae. No dorsal femoral macrosetae; ventral tibial macrosetae absent; without developed calcars; very unequal, elbow-like claws with small lateral crests; setiform, smooth pretarsal process. Urotergite IV with 1+1 *lp* macrosetae; urotergites V–VII with 1+1 *la* and 1+1 *lp* macrosetae; urotergite VIII with 3+3 *post* macrosetae; abdominal segment IX with 6+6 *post* macrosetae; urosternite I with 7+7, urosternites II–VII with 4+4, urosternite VIII with 1+1 macrosetae. Male without glandular  $g_1$  setae; short, thick, enlarged appendages with glandular  $a_1$  and  $a_2$  setae; female unknown.

**Habitat and distribution**

Subterranean species known only from Sima del Trave, collected at a depth of 550 meters, Picos de Europa, Central Cantabrian Mountain Range, northern Iberian Peninsula.

*Oncinocampa paclti* (Condé, 1981)

*Litocampa paclti* Condé, 1981a: 96, fig. 1.

*Plusiocampa* (*Stygiocampa*) sp. – Paclt 1979: 222.

**Diagnosis** (Paclt 1979; Condé 1981a; Sendra & Condé 1988)

Non-troglomorphic species; epicuticle with microdenticles; antennae with 18–25 doliiform antennomeres; gouge sensilla thick and short; four to six simple olfactory chemoreceptors in cupuliform



organ; non-developed frontal process, with non-tubercular setae. Pronotum with 1+1 *ma*, 1+1 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la* macrosetae; metanotum with 1+1 *ma* macrosetae; middle-sized notal macrosetae with a few distal long barbs, *la* pronotal and *ma* macrosetae with one or two distal barbs; short, smooth clothing setae. No dorsal femoral macrosetae; one ventral tibial macroseta; small, subequal, elbow-like claws with very small lateral crests; setiform, smooth pretarsal processes. Urotergites I–IV with 1+1 *ma* macrosetae; urotergites V–VII with 1+1 *ma*, 1+1 *la*, 1+1 *lp* macrosetae; urotergite VIII with 1+1 *ma*, 3+3 *post* macrosetae; abdominal segment IX with 1+1 *ma*, 5+5 *post* macrosetae; urosternite I with 6+6, urosternites II–VII with 4+4, urosternite VIII with 1+1 macrosetae; male with glandular  $g_1$  setae; small, subtrapezoidal appendages with glandular  $a_1$  and  $a_2$  setae; female with subcylindric appendages with glandular  $a_1$  setae.

### Habitat and distribution

Non-trogomorphic species found in one cave and within soil at two adjacent localities in the east of Sardinia.

### Genus *Paratachycampa* Wygodzinsky, 1944

*Paratachycampa* Wygodzinsky, 1944: 371.

### Diagnosis (Wygodzinsky 1944; Bareth & Condé 1981)

Pronotum with 1+1 *ma*, 1+1–2+2 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 *mp*, 1+1 *la* macrosetae; metanotum with 1+1 *ma* macrosetae. Dorsal femoral macrosetae absent; ventral tibial macrosetae absent. Claws with lateral crest, with a backward overhang. Pretarsal lateral processes from setiform to laminar and well barbed on ventral side. Urotergal macrosetae start on urotergite III or IV. Stylus with pubescent apical, subapical and medial setae. Extra urosternal macrosetae on first urosternite and 2+2 on eighth urosternite. Male with elongate appendages, covered with a large area of glandular  $a_2$  setae.

### Habitat and distribution

All three known species are highly cave-adapted to the deep subterranean ecosystems. The genus *Paratachycampa* has an amphi-Atlantic distribution, with one species in Mexico and two on the Iberian Peninsula (Fig. 210).

### *Paratachycampa hispanica* Bareth & Condé, 1981

Figs 196–201, 206

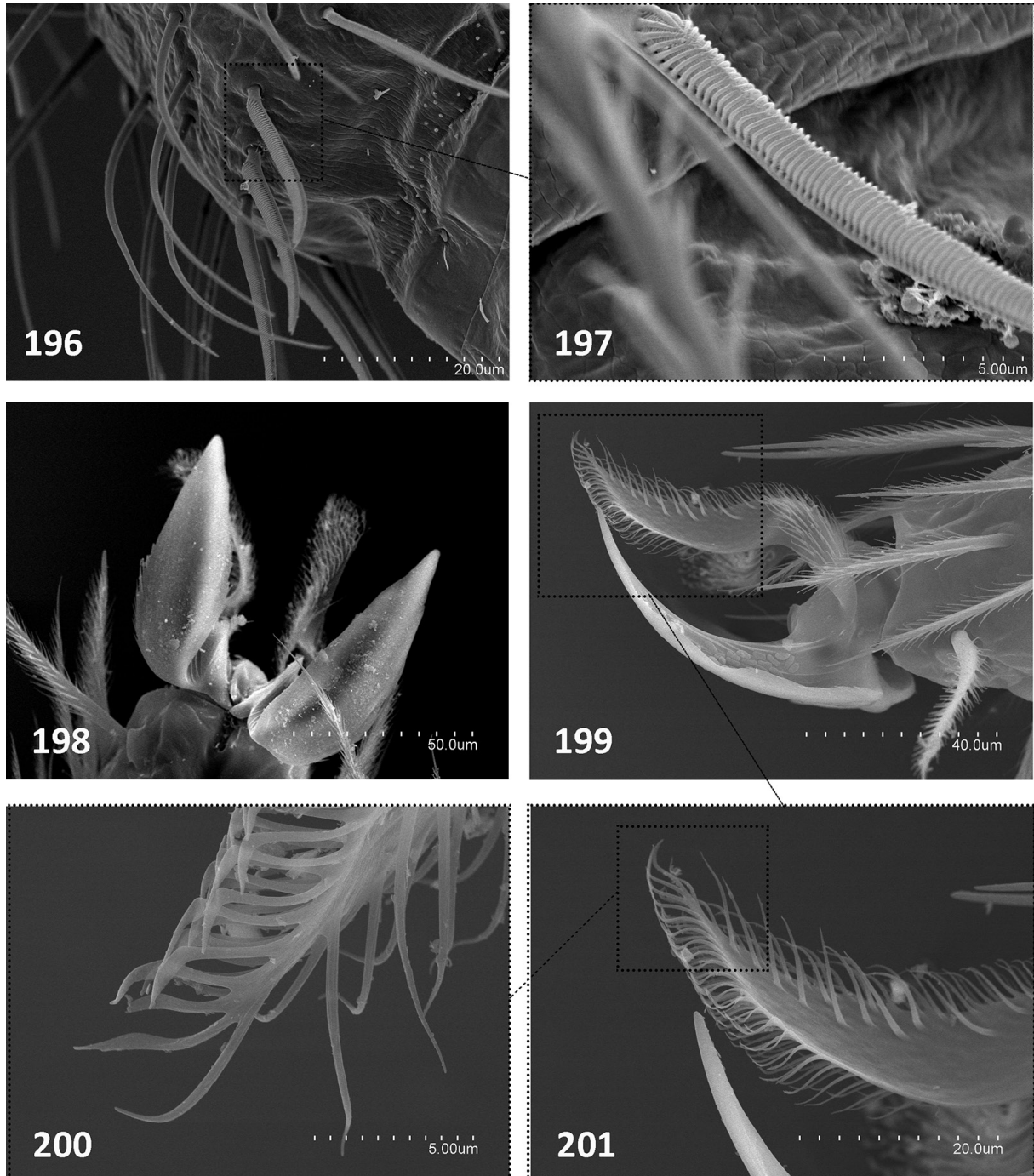
*Paratachycampa hispanica* Bareth & Condé, 1981: 776, figs 1a–c, 2a–c, 3a–c, 4a–c, 5a, c, e.

### Diagnosis (Bareth & Condé 1981; Sendra 1988; Sendra & Escolà 2004)

Trogomorphic species. Epicuticle smooth. Antennae with 34–40 elongated antennomeres; 12–16 complex olfactory chemoreceptors in cupuliform organ. Protruding frontal process with abundant tubercular setae. Pronotum with 1+1 *ma*, 2+2 *la*, 1+1 *lp* macrosetae; mesonotum with 1+1 *ma*, 1+1 *la* macrosetae; metanotum with 1+1 *ma*, 1+1 *la* macrosetae; long, thin notal macrosetae with a very few barbs; long, thin smooth clothing setae. Subequal, elbow-like claws with large lateral crests, posterior claw with a backward overhang; laminar, barbed ventral pretarsal processes. Urotergites III–VII with 1+1 *la* macrosetae; urotergite VIII with 4+4 *post* macrosetae; abdominal segment IX with 7+7 *post* macrosetae; urosternite I with 22+22, urosternites II–VII with 7+7, urosternite VIII with 2+2 macrosetae. Male without glandular  $g_1$  setae; overdeveloped appendages with a large area of glandular  $a_2$  setae and an apical area of glandular  $a_1$  setae; subcylindrical female appendages with glandular  $a_1$  and  $a_2$  setae.

### Remarks

The studied material (see [Table S2](#) in Supplementary Material) allowed us to add taxonomic details revealed by SEM microscopy. Gouge sensilla abundant, as long as 28  $\mu\text{m}$ , with thick transversal stripes with alternating rows of pores between them (Figs 196–197). Subequal claws with well-developed



**Figs 196–201.** *Paratachycampa hispanica* Bareth & Condé, 1981, from Cova dels Encenalls, Sant Mateu, Spain (Coll. AS). **196.** Lateral distal view of a medial antennomere with gouge sensilla. **197.** Basal view of a gouge sensillum. **198.** Pretarsus of a metathoracic leg. **199.** Lateral view of pretarsus, metathoracic leg. **200.** Distal part of lateral process of pretarsus, metathoracic leg. **201.** Apical part of lateral process of pretarsus, metathoracic leg.

lateral crests (Figs 198–199). Lateral processes of pretarsus with S-shape, its ventral side covered with long, hooked barbs (Figs 200–201).

### Habitat and distribution

Subterranean species found in nine caves throughout the coastal karst reliefs in the east of the Iberian Peninsula (Fig. 206).

#### *Paratachycampa penyoensis* Bareth & Condé, 1981

*Paratachycampa peynoensis* Bareth & Condé, 1981: 780, figs 1d, 2d, 3d, 4d–e, 5b, d, f [corrected here to *penyoensis*].

### Diagnosis (Bareth & Condé 1981; Sendra 1988)

Troglomorphic species. Epicuticle smooth under optical microscope. Antennae with 30–38 elongated antennomeres. Protruding frontal process well developed, with tuberculated, barbed setae. Pronotum with 1+1 *ma*, 2+2 *la*, 1+1 *lp* macrosetae; mesonotum with 1+ *ma*, 1+1 *la* macrosetae; metanotum with 1+1 *ma* macrosetae; middle-sized, barbed notal macrosetae; short, barbed clothing setae. Subequal, elbow-like claws with large lateral crests, with backward overhang; laminar, barbed ventral pretarsal processes. Urotergites III–V with 1+1 *la* macrosetae; urotergite VI with 1+1 *la*, 1+1–2+1 *lp* macrosetae; urotergite VII with 1+1 *la*, 2+2–3+4 *lp* macrosetae; urotergite VIII with 4+4–6+6 *post* macrosetae; abdominal segment IX with 6+6–7+7 *post* macrosetae; urosternite I with 21+21–22+22, urosternites II–VII with 5+5, urosternite VIII with 2+2 macrosetae. Male without glandular *g*<sub>1</sub> setae; developed, large appendages with a large area of glandular *a*<sub>2</sub> setae and an apical area of glandular *a*<sub>1</sub> setae; subcylindrical female appendages with glandular *a*<sub>1</sub> and *a*<sub>2</sub> setae.

### Habitat and distribution

Subterranean species found in two caves, Cova del Penyó (type locality) and the Soterranya Cave (Serra, València), Calderona Massif, eastern Iberian Peninsula.

#### Genus *Tachycampa* Silvestri, 1936

*Tachycampa* Silvestri, 1936: 86.

### Diagnosis (Silvestri 1936; Sendra *et al.* 2016)

Epicuticle with microdenticles on surface. Pronotum with 3+3 medial anterior and lateral posterior macrosetae, and lateral anterior submacrosetae; mesonotum with 2+2 medial and lateral anterior submacrosetae; metanotum with 1+1 medial anterior submacrosetae. Dorsal femoral macrosetae absent. One small ventral tibial macroseta. Subequal, elbow-like claws with large lateral crests, posterior claw without a backward overhang; setiform, smooth pretarsal processes. With 3+3 and 6+6 posterior macrosetae on urotergite VIII and abdominal segment IX, respectively; urosternite I with 8+8–11+11, urosternites II–VII with 8+8, urosternite VIII with 1+1 macrosetae. Male urosternite I with glandular *g*<sub>1</sub> setae; short, thick, large appendages with a large area of glandular *a*<sub>1</sub> and *a*<sub>2</sub> setae; female with subcylindrical appendages with glandular *a*<sub>1</sub> setae.

### Habitat and distribution

The four species of this genus are found in subterranean habitats, in the deep areas of caves. It has an ampho-Atlantic distribution, with three species in Mesoamerica and another one in the Rif Mountains, northwestern Africa (Fig. 210).

*Tachycampa lepineyi* Silvestri, 1936

*Tachycampa lepineyi* Silvestri, 1936: 86, figs 1–11.

**Diagnosis** (Silvestri 1936; Condé 1952)

Troglophobic species. Epicuticle with microdenticles. Antennae with 36–38 antennomeres; about 20 small complex olfactory chemoreceptors in cupuliform organ; protruding frontal process, with non-tubercular setae. Pronotum with 1+1 *ma* and 1+1 *lp* macrosetae and 1+1 *sla* submacrosetae; mesonotum with 1+1 *sma* and 1+1 *sla* submacrosetae; metanotum with 1+1 *sma* submacrosetae; short, smooth notal macrosetae; short, smooth notal clothing setae. Dorsal femoral macrosetae absent; one small ventral tibial macroseta; subequal, elbow-like claws with large lateral crests, posterior claw without a backward overhang; setiform pretarsal processes. Urotergite VIII with 3+3 *post* macrosetae; abdominal segment IX with 6+6 *post* macrosetae; urosternite I with 8+8–11+11, urosternites II–VII with 8+8, urosternite VIII with 1+1 macrosetae. Male urosternite I with a wide area of glandular  $g_1$  setae; short, thick, large appendages with a large area of glandular  $a_1$  and  $a_2$  setae; female with enlarged subcylindrical appendages with glandular  $a_1$  setae.

**Remarks**

The study of many specimens collected from five new caves (Coll. AS) (see [Table S2](#) in Supplementary Material) allowed the addition of information to the diagnosis and the inclusion of other minor taxonomic characters: ventral sensillum in third antennomere; labial palps with thick sensilla, two guard sensilla, nine simple setae and about 80 neuroglandular setae; metathoracic leg reaching end of abdomen; calcars with long barbs running up from base in two rows; smooth subapical tarsal setae; stylar setae covered with a few long barbs, apical setae with large basal tooth.

**Habitat and distribution**

Subterranean species found in nine caves in the karst areas near Taza in the Middle Atlas Mountains, Morocco.

**Discussion**

**Species diversity, phylogenetic groupings and distribution**

The systematic groups are here maintained as those previously suggested for Campodeidae (Silvestri 1912; Condé 1955a; Paclt 1957; Bareth & Condé 1981, 1984; Condé & Bareth 1996; Sendra *et al.* 2016, 2017a, 2018; Sendra & Weber 2018). Using morphological characters, a phylogenetic grouping seems natural for the five subfamilies of Campodeidae (Paclt 1957) plus the tachycampoid phyletic lineage proposed by Bareth & Condé (1981). Nevertheless, not all genera and subgenera seem monophyletic within Plusiocampinae and the tachycampoids. This is the case for the Asian and African species of Plusiocampinae (Condé 1993b; Sendra *et al.* 2012a, 2017a). However, the European and Mediterranean genera of Plusiocampinae and tachycampoids belong to two well-differentiated phyletic lineages with a distinct biogeographical pattern. The five Euro-Mediterranean genera of Plusiocampinae (*Cestocampa*, *Hystrichocampa*, *Patrizicampa*, *Plusiocampa* and *Vandelicampa*) share remarkable morphological characters: 1) the ventral position of the sensillum on the third antennomere; 2) the pattern of macrosetal distribution on the pronotum, with two pairs of lateral posterior macrosetae; 3) the elbow-like claws with lateral crests; and 4) two pairs of macrosetae on the eighth urosternite. They also have some taxonomically less important similarities, such as a smooth cuticle as seen in an optical microscope (cuticle often appears reticulated in SEM) and the absence of pores on the dorsal sclerites. For the tachycampoid lineage, the four studied genera (*Jeannelicampa*, *Oncinocampa*, *Paratachycampa* and *Tachycampa*) show notable differences in several morphological characters, for instance the simple claws in *J. stygia* or the presence of medial anterior macrosetae on the urotergites in *O. paclti* (Figs 209–210).



**Figs 202–204.** **202.** *Plusiocampa (Stygiocampa) christiani* Condé & Bareth, 1996, from Lazareva Cave, Serbia (photo: Dragan Antić). **203.** *Plusiocampa (Plusiocampa) lagari* Sendra & Condé, 1987, from Chorros Cave, Albacete, Spain (photo: Toni Pérez). **204.** *Plusiocampa (Plusiocampa) hoffmanni* Sendra & Paragamian sp. nov., from Splialio Sfontone Trypa Cave, Crete (photo: Kaloust Paragamian).

The Euro-Mediterranean Plusiocampinae represent the vast majority of the entire subfamily, with 78 species out of the total 91 species around the world. *Plusiocampa* is the most diverse genus of Plusiocampinae, with 71 species and 10 subspecies from the Euro-Mediterranean region (Table 13, Fig. 211; see also Table S1 in Supplementary Material). The remaining genera are far less diversified: *Cestocampa* includes four species, while *Hystrichocampa*, *Patrizicampa* and *Vandelicampa* are monotypic (Fig. 210). This biodiversity estimate does not consider the Asian species of *Plusiocampa* and *Cestocampa*, proposed to be placed in new genera by Sendra *et al.* (2012a, 2017a). The European region appears to be the center of origin for Plusiocampinae, but new evidence of undescribed taxa from East Asia has emerged (Sendra, unpubl. data), suggesting Asia as the most likely center of origin. Nonetheless, more sampling efforts and studies in Central and East Asia are required to reach a clearer view of the origin and possible colonization scenario for this subfamily, highly diversified in subterranean ecosystems.

The evolutionary relationships among taxa are not clear within the Euro-Mediterranean Plusiocampinae. *Cestocampa*, *Patrizicampa* and *Vandelicampa* are split from *Plusiocampa* by a single character: the laminar processes of the pretarsus are covered by pubescence instead of being smooth and setiform, as in species of *Plusiocampa*. *Hystrichocampa* is separated by the unique pubescent, thick setiform lateral processes of the pretarsus. The subgenera of *Plusiocampa* are not well supported. *Dydimocampa* and *Venetocampa* might be paraphyletic and *Plusiocampa* s. str. might contain two different monophyletic groups (Sendra 2003; Sendra *et al.* 2004). Furthermore, in the case of *Dydimocampa*, *P. (D.) evallonychia*, *P. (D.) euxina* and a probable new species found in a cave in southwestern Serbia (D. Antić leg.) seem very closely related. Species of *Stygiocampa* certainly form a monophyletic subgenus, sharing several common characters, such as the reduction of mesonotal and metanotal macrosetae, the absence of dorsal femoral macrosetae, and the presence of several extra urosternal macrosetae in four of these species. In addition, they are geographically restricted to subterranean ecosystems around the Dinaric and Balkan Mountains (Bareth & Condé 2001). The monotypic *Pentachaetocampa*, with its five dorsal femoral macrosetae and the unique presence of glandular *g*, setae in females, is only found in a cave in southwestern Germany (Sendra & Weber 2018). Finally, *Plusiocampa* s. str., including 60 species and 10 subspecies, is widespread across the entire European and Mediterranean region (Table 13, Fig. 211; see also Table S1 in Supplementary Material). The two suggested monophyletic groups within *Plusiocampa* are characterized by two formula patterns in the distribution of notal macrosetae: the presence or the absence of medial posterior macrosetae or submacrosetae on the mesonotum and metanotum. A peculiar distribution formula pattern is revealed using this taxonomical criterion. Part of *Plusiocampa* s. str., specifically 25 species and 6 subspecies that do not have medial posterior or intermediate thoracic macrosetae, occupy the ancient European plates, the current Dinaric and Catalanian regions. The other 35 species and 4 subspecies of *Plusiocampa* s. str., which have medial posterior thoracic macrosetae, occupy more recently emerged plates in the east and west of the emerged Mediterranean plates (Table 13, Fig. 212; see also Table S1 in Supplementary Material) (Sendra *et al.* 2004).

The tachycampoid lineage is less diversified than Plusiocampinae. It has four genera and eight species in the Eastern Mediterranean region (Table 14, Fig. 209; see also Table S1 in Supplementary Material). Three of these genera have amphi-Atlantic distributions, with species in Mesoamerica (*Oncinocampa*, *Paratachycampa* and *Tachycampa*) and Brazil (*Oncinocampa*) (Bareth & Condé 1981; Sendra *et al.* 2016).

### Habitats and troglomorphism

Campodeids were considered by Racovitza (1907: 426–427, 443) as “le Cavernicole idéal”, the ideal troglobite. All campodeids are eyeless with positive thigmotaxis, they have a soft body with a tracheal respiratory system and a thin cuticle, traits associated with a cryptic, subsurface life-style. Many campodeids, mainly within Plusiocampinae and the tachycampoids, inhabit the deep subterranean

**Table 13** (continued on next two pages). Genera, subgenera, species, subspecies and affinis forms of Plusiocampinae Paclt, 1957 in the Euro-Mediterranean Region.

<b>Taxon</b>	<b>Habitat</b>	<b>Distribution</b>
<i>Cestocampa</i> Condé, 1955	hypogean	Southern Euro-Mediterranean Region
<i>C. balcanica</i> Condé, 1955	edaphic	Dinaric Mountains and Italian Peninsula
<i>C. gasparoi</i> Bareth, 1988	subterranean	Southern Italian Peninsula
<i>C. iberica</i> Sendra & Condé 2012	subterranean	Eastern Iberian Peninsula
<i>C. italica</i> (Silvestri, 1912)	edaphic	Dinaric Mountains and Italian Peninsula
<i>Hystrihocampa pelletieri</i> Condé, 1948	subterranean	Jura Mountains (France and Switzerland)
<i>Patrizicampa sardoa</i> Condé, 1962	subterranean	Eastern Sardinia
<i>Plusiocampa</i> Silvestri, 1912	hypogean	Euro-Mediterranean Region
<i>Plusiocampa (Dydimocampa)</i> Paclt, 1957	subterranean	European Region
<i>P. (D.) alhamae</i> Condé & Sendra, 1989	subterranean	Southern Iberian Peninsula
<i>P. (D.) euxina</i> Condé, 1996	subterranean	Movile Cave, Dobruja (Romania)
<i>P. (D.) evallonychia</i> Silvestri, 1949	subterranean	Crimean Peninsula
<i>Plusiocampa (Pentachaetocampa) inopinata</i> Sendra & Weber, 2018	subterranean	South Black Forest (Germany)
<i>Plusiocampa (Plusiocampa) s. str.</i> Silvestri, 1912	hypogean	Euro-Mediterranean region
<i>Plusiocampa (Plusiocampa) s. str.</i> (with medial posterior or intermediate macrosetae)	hypogean	Central, Southern and Southeastern Europe
<i>P. (P.) apollo</i> Sendra, Giachino & Vailati sp. nov.	MSS	Southern Balkan Peninsula (Greece)
<i>P. (P.) beroni</i> Bareth & Condé, 2001	subterranean	Balkan Mountains (Bulgaria)
<i>P. (P.) bonadonai bonadonai</i> Condé, 1948	subterranean	Provence Alps (France)
<i>P. (P.) bonadonai lanzai</i> Condé, 1961	subterranean	Valais (Switzerland) and Northern Apennines (Italy)
<i>P. (P.) bonadonai pavani</i> Condé & Poivre, 1982	subterranean	Lombardy (Italy)
<i>P. (P.) breuili</i> Condé, 1955	subterranean	Pityuses, Balearic Islands
<i>P. (P.)</i> aff. <i>breuili</i> Condé, 1955	subterranean	Southeastern Iberian Peninsula
<i>P. (P.) bulgarica</i> Silvestri, 1931	subterranean	Balkan and Rhodope Mountains (Bulgaria)
<i>P. (P.) caprai</i> Condé, 1950	hypogean	Alps
<i>P. (P.) chiosensis</i> Sendra & Gasparo sp. nov.	subterranean	Chios (Greece), coast of Anatolian Peninsula
<i>P. (P.) dublanskii</i> Sendra & Turbanov sp. nov.	subterranean	Crimean Peninsula
<i>P. (P.)</i> aff. <i>dublanskii</i> Sendra & Turbanov sp. nov.	subterranean	Western Caucasus
<i>P. (P.) elongata</i> Ionescu, 1955	subterranean	Carpathian Mountains (Romania)
<i>P. (P.)</i> aff. <i>elongata</i> Ionescu, 1955	subterranean	Peștera Cloșani, Carpathian Mountains (Romania)
<i>P. (P.) fagei</i> Condé, 1955	subterranean	Tramuntana Mountains, Mallorca, Balearic Islands
<i>P. (P.) festae</i> Silvestri, 1932	hypogean	Aegean Islands and Anatolian Peninsula
<i>P. (P.) friulensis</i> Bareth & Condé, 1984	subterranean	Carnic Pre-Alps (Italy)
<i>P. (P.) glabra</i> Condé, 1984	subterranean	Southern Balkan Peninsula
<i>P. (P.) grandii</i> Silvestri, 1933	subterranean	Italian Alps
<i>P. (P.)</i> aff. <i>grandii</i> Silvestri, 1933	subterranean	Southern Balkan Peninsula
<i>P. (P.) hoelzeli</i> (Neuherz, 1984)	subterranean	Austrian and Slovenian Alps
<i>P. (P.) hoffmanni</i> Sendra & Paragamian sp. nov.	subterranean	Crete (Greece)
<i>P. (P.) humicola</i> Ionescu, 1951	edaphic	Carpathians Mountains (Romania)
<i>P. (P.) hystricula</i> Bareth & Condé, 1984	subterranean	Italian Alps
<i>P. (P.) lagari</i> Sendra & Condé, 1987	subterranean	Baetic Mountains Range (Spain)

**Table 13** (continued). Genera, subgenera, species, subspecies and affinis forms of Plusiocampinae Paclt, 1957 in the Euro-Mediterranean Region.

<b>Taxon</b>	<b>Habitat</b>	<b>Distribution</b>
<i>P. (P.) lagoi</i> Silvestri, 1932	hypogean	Ródos (Greece)
<i>P. (P.)</i> aff. <i>lagoi</i> Silvestri, 1932	hypogean	Dinaric Mountains (Croatia)
<i>P. (P.) lucenti</i> Sendra & Condé, 1986	subterranean	East Pre-Baetic Mountains, Eastern Iberian Peninsula
<i>P. (P.) magdalanae</i> Condé, 1957	subterranean	Alpes de Provence (France)
<i>P. (P.) notabilis</i> Silvestri, 1912	edaphic	Southern Italian Peninsula
<i>P. (P.) provincialis provincialis</i> Condé, 1949	subterranean	Alpes de Provence (France)
<i>P. (P.) provincialis praedita</i> Condé, 1949	subterranean	Alpes de Provence (France)
<i>P. (P.) rhea</i> Sendra sp. nov.	hypogean	Crete (Greece)
<i>P. (P.) romana</i> Condé, 1954	subterranean	Central Apennine Mountains, Italian Peninsula
<i>P. (P.) rudnica</i> Blesic, 1992	edaphic	Western Balkan Peninsula (Serbia)
<i>P. (P.) rybaki</i> Condé, 1956	subterranean	Southern Balkan Peninsula
<i>P. (P.) sardiniana</i> Condé, 1981	subterranean	Sardinia
<i>P. (P.) socia</i> Condé, 1983	subterranean	Eastern Sardinia
<i>P. (P.) spelaea</i> Stach, 1930	hypogean	Western Carpathians
<i>P. (P.) suspiciosa</i> Condé & Mathieu, 1957	hypogean	(dubious locality)
<i>P. (P.) strouhali strouhali</i> Silvestri, 1933	subterranean	Austrian, Italian and Slovenian Alps
<i>P. (P.) strouhali cavicola</i> Vornatscher, 1943	subterranean	Austrian and Slovenian Alps
<i>P. (P.) tinoamorei</i> Sendra & Nicolosi, 2019	subterranean	Southeastern Sicily
<i>P. (P.) vodniensis</i> Bareth & Condé, 2001	subterranean	Balkan Mountains (Bulgaria)
<i>Plusiocampa (Plusiocampa) s. str.</i> (without medial posterior and intermediate macrosetae)	hypogean	European Basin
<i>P. (P.) affinis</i> Condé, 1947	hypogean	Dinaric Mountains (Montenegro)
<i>P. (P.) arbanasiensis</i> Bareth & Condé, 2001	hypogean	Balkan Mountain and Dinaric Mountains
<i>P. (P.) baetica</i> Sendra, 2004	subterranean	Internal zone of Baetic Mountain Range, Southern Iberian Peninsula
<i>P. (P.) balsani</i> Condé, 1947	subterranean	Central Massif (France)
<i>P. (P.) bonneti bonneti</i> Condé, 1948	subterranean	Central Pyrenees and Pre-Pyrenees (France and Spain)
<i>P. (P.) bonneti condei</i> Sendra & Escolà, 2004	subterranean	Eastern Pyrenees and Catalan Mediterranean Mountain System
<i>P. (P.) bonneti deharvengi</i> Bareth & Condé, 1996	subterranean	Eastern Pyrenees
<i>P. (P.) brevantennata</i> Loksa, 1960	hypogean	Southern Transdanubian Mountains (Hungary)
<i>P. (P.) corcyraea corcyraea</i> Silvestri, 1912	edaphic	Southern Balkan Peninsula and Corfu
<i>P. (P.) corcyraea abdominalis</i> Condé, 1984	edaphic	Ithakia (Greece)
<i>P. (P.) cyrnensis</i> Condé, 1953	edaphic	Corsica
<i>P. (P.) dallai</i> Bareth & Condé, 1984	subterranean	Gargano Promontory on the Apulian Carbonate Platform, Italian Peninsula
<i>P. (P.) dargilani</i> (Moniez, 1894)	subterranean	Grands Causses (France)
<i>P. (P.) djurdjurae</i> Condé, 1984	subterranean	Djurdjura Mountains, Tell Atlas (Algeria)
<i>P. (P.) dohati</i> Condé, 1975	subterranean	Swanian Alb (Germany)
<i>P. (P.) dolichopoda</i> Bareth & Condé, 1984	subterranean	Gargano Promontory on the Apulian Carbonate Platform, Italian Peninsula
<i>P. (P.) exsulans</i> Condé, 1947	hypogean	Central Europe, Italian and Dinaric Mountains



**Table 13** (continued). Genera, subgenera, species, subspecies and affinis forms of Plusiocampinae Paclt, 1957 in the Euro-Mediterranean Region.

<b>Taxon</b>	<b>Habitat</b>	<b>Distribution</b>
<i>P. (P.) gadorensis</i> Sendra, 2001	subterranean	Sierra Gador, Southeast Iberian Peninsula
<i>P. (P.) gueorguievi</i> Bareth & Condé, 2001	subterranean	Stara Planina (Bulgaria)
<i>P. (P.) isterina</i> Condé, 1993	hypogean	Movile Cave, Dobruja (Romania)
<i>P. (P.)</i> aff. <i>isterina</i> Condé, 1993	subterranean	Dinaric Mountains (Bosnia and Herzegovina)
<i>P. (P.) latens</i> Condé, 1948	hypogean	Dinaric Mountains (Bosnia and Herzegovina)
<i>P. (P.)</i> aff. <i>latens</i> Condé, 1948	hypogean	Dinaric Mountains (Croatia)
<i>P. (P.) lindbergi</i> Condé, 1956	hypogean	Greek Macedonia, Balkan Peninsula
<i>P. (P.) pouadensis pouadensis</i> (Denis, 1930)	subterranean	Eastern Pyrenees (France)
<i>P. (P.) pouadensis fouresi</i> Condé, 1956	subterranean	Eastern Pyrenees (France)
<i>P. (P.) pouadensis leoni</i> Condé, 1951	subterranean	Eastern Pyrenees (Spain)
<i>P. (P.) schweitzeri</i> Condé, 1947	subterranean	Dinaric Mountains (Bosnia and Herzegovina)
<i>P. (P.)</i> aff. <i>schweitzeri</i> Condé, 1947	subterranean	Northeast Anatolian Peninsula
<i>P. (P.) solerii</i> Silvestri, 1932	edaphic	Ródos (Greece) and Izmir (Anatolian Peninsula)
<i>P. (P.)</i> aff. <i>solerii</i> Silvestri, 1932	subterranean	Cyprus
<i>P. (P.) ternovensis</i> Sendra & Borko sp. nov.	subterranean	Dinaric Mountains (Slovenia)
<i>P. (P.) vedovinii</i> Condé, 1981	subterranean	Alpes de Provence (France)
<i>Plusiocampa (Stygiocampa)</i> Silvestri, 1934	subterranean	Dinaric Mountains and Balkan Mountains
<i>P. (S.) bureschi</i> Silvestri, 1931	subterranean	Balkan Mountains (Bulgaria)
<i>P. (S.) christiani</i> Condé & Bareth, 1966	subterranean	Kučaj and Beljanica Mts, part of Balkan Mt System (Serbia)
<i>P. (S.) dalmatica</i> Condé, 1959	subterranean	Dinaric Mountains (Italy, Bosnia and Herzegovina, Croatia and Slovenia)
<i>P. (S.) denisi</i> Condé, 1947	subterranean	Dinaric Mountains (Serbia)
<i>P. (S.) nivea</i> (Joseph, 1882)	subterranean	Dinaric Mountains (Croatia, Italy and Slovenia)
<i>P. (S.) remyi</i> Condé, 1947	subterranean	Dinaric Mountains (Bosnia and Herzegovina, Croatia and Montenegro)
<i>P. (S.)</i> aff. <i>remyi</i> Condé, 1947	subterranean	Dinaric Mountains (Croatia)
<i>Plusiocampa (Venetocampa)</i> Bareth & Condé, 1984	subterranean	Italian and Slovenian Alps
<i>P. (V.) ferrani</i> Sendra & Deliđ sp. nov.	subterranean	Slovenian Alps
<i>P. (V.) paolettii</i> Bareth & Condé, 1984	subterranean	Italian Alps
<i>Vandelicampa tisserandi</i> Condé, 1955	subterranean	Middle East (Lebanon)

environment and show troglomorphic adaptations: elongation of the body and appendages, including the increase and complexity of their sensory organs. These traits are associated with a troglomorphic evolution of morphological characters (Christiansen 1965).

Only 11 of 97 taxa of Plusiocampinae inhabit edaphic environments, with a clear preference for humid habitats (Table 13, Fig. 213). All edaphic species have smaller bodies compared to subterranean Plusiocampinae. They have shorter appendages and a lower number of cercal articles (up to seven) and antennomeres (18 to 27), which are all doliiform. Their cupuliform organs are simple and enclose four olfactory chemoreceptors with one simple fold. Species found in soils, but also in shallow subterranean habitats (MSS) and caves, have slightly longer bodies, elongated appendages and an increased number of antennomeres (from 19 to 32), cercal articles and olfactory chemoreceptors. Currently, 13 taxa of Plusiocampinae and one species of tachycampoid (*O. placti*) can be considered as non-troglomorphic,



**Figs 205–206.** 205. *Plusiocampa* (*Stygiocampa*) *dalmatica* Condé, 1959 and the beetle *Parapropus vitorogensis* Ćurčić *et al.*, 2012 (Leptodirini) feeding on a dead cave cricket, *Troglophilus* sp., in Vaganska pećina, Bosnia and Herzegovina (photo: Slavko Polak). 206. *Paratachycampa hispanica* Bareth & Condé, 1981, from Cirat Cave, Castellón, Spain (photo: Sergio Montagud).



**Figs 207–208.** 207. *Plusiocampa (Stygiocampa) nivea* (Joseph, 1882), from Košanski spodmol (n. 902) Obrov, Podgrad, Slovenia (photo: Fulvio Gasparo). 208. *Plusiocampa (Stygiocampa) dalmatica* Condé, 1959, from Grotta Bac, VG 49, 400 m a.s.l., Trieste, Italy (photo: Fulvio Gasparo).

**Table 14.** Tachycampoid species and affinis forms in the Euro-Mediterranean Region.

Taxon	Habitat	Distribution
<i>Jeannelicampa stygia</i> Condé, 1952	subterranean	Tell Atlas (Algeria)
<i>Oncinocampa</i> Condé, 1982	hypogean	Cantabric Mountains, Northern Iberian Peninsula, and E Sardinia
<i>O. asonensis</i> Sendra & Condé, 1988	subterranean	Cantabric Mountains, Northern Iberian Peninsula
<i>O. falcifer</i> Condé, 1982	subterranean	Cantabric Mountains, Northern Iberian Peninsula
<i>O. aff. falcifer</i> Condé, 1982	subterranean	Cantabric Mountains, Northern Iberian Peninsula
<i>O. genuitei</i> Bareth, 1989	subterranean	Picos de Europa, Cantabric Mountains, Northern Iberian Peninsula
<i>O. pacti</i> Condé, 1981	hypogean	E Sardinia
<i>Paratachycampa</i> Wygodzinsky, 1944	subterranean	Southern North America and Eastern Iberian Peninsula
<i>P. hispanica</i> Bareth & Condé, 1981	subterranean	Eastern Iberian Peninsula
<i>P. penyoensis</i> Bareth & Condé, 1981	subterranean	Calderona Massif, Eastern Iberian Peninsula
<i>Tachycampa</i> Silvestri, 1936	subterranean	Mesoamerica and Middle Atlas (Morocco)
<i>T. lepinyi</i> Silvestri, 1936	subterranean	Middle Atlas (Morocco)

occupying a wide variety of hypogean habitats from edaphic to shallow subterranean habitats (MSS) and occasionally caves (Table 14, Fig. 213). Several of these hypogean species are almost only reported from MSS habitats. This is the case for *P. (P.) festae* and *P. (P.) apollo* sp. nov., as has been shown by the sampling effort carried out mainly in Greece by P.M. Giachino and D. Vailati in MSS habitats, both in karst and non-karst areas. The marked preference of these two species for MSS habitats has also been observed in other diplurans and collembolans studied in colluvial and alluvial MSS (Bareth 1983; Ortuño *et al.* 2013; Baquero *et al.* 2017; Sendra *et al.* 2017b). Nevertheless, the most frequent habitats for most of the Plusiocampinae and tachycampoids are the subterranean spaces in the vadose zone of the bedrock. A total of 73 species, subspecies or affinis forms of Plusiocampinae and eight species of tachycampoids inhabiting the Euro-Mediterranean region are cave-dwelling species – named in the text as subterranean species – found mostly in caves, with clear troglomorphic features (Tables 13–14, Fig. 213; see also Table S1 in Supplementary Material). They have larger bodies, up to 9 mm; the antennae are up to 2× and the cerci up to 3× as long as the body length. Furthermore, the antennae have more than 30 antennomeres, although there are a few exceptions in which a smaller number of antennomeres could be an indication of a regenerated antenna. Some species of Plusiocampinae, such as *P. (P.) gadorensis* and *P. (P.) hoffmanni* sp. nov. (Table 6) have 50 antennomeres and there are up to 54 in *P. (P.) chiosensis* sp. nov. and *P. (S.) bureschi* (Bareth & Condé 2001; Sendra 2001). In the tachycampoid *O. asonensis*, the antennae have up to 64 antennomeres (Sendra & Condé 1988). The antennomeres of these highly troglomorphic species are usually elongated, the middle antennomeres being 2× or 3× as long as wide. Another remarkable troglomorphic trait is the length of the cerci (Tables 1, 4–5, 8, 11), with clear differences between the non-troglomorphic species such as *P. (P.) spelaea*, showing cerci shorter than the body length (0.4–0.5× as long) (Table 10), the slightly troglomorphic species such as *P. (P.) strouhali cavicola* and *P. (P.) hoelzeli* (Tables 5, 11), with cerci somewhat longer than the body, and the most troglomorphic species such as *P. (D.) evallonychia* and *P. (P.) hoffmanni* sp. nov. (Tables 1, 8), with cerci almost twice as long as the body. The longest cerci of all Plusiocampinae have been recorded in *P. (P.) chiosensis* sp. nov., with cerci 2.52× as long as the body length (Table 4). A recent study of cerci elongation in campodeids suggests that the elongation of these appendages is an adaptation to improve sensitivity in subterranean environments, with two different growth patterns: the cerci of Campodeinae and Lepidocampinae have a positive allometric growth, whereas it is isometric in Plusiocampinae (Sendra *et al.* 2017a). This difference between subfamilies might be regarded as an adaptation to the different habitats they colonize. While the majority of species of Campodeinae and Lepidocampinae are non-troglobites, many of them being edaphic-endogean species thriving in the small spaces of the soil, most species of Plusiocampinae are troglobites inhabiting the deep subterranean ecosystems.

Another remarkable progressive troglomorphic trait in campodeid species is the notable increase of complexity in shape, size and abundance of the sensorial equipment on the antennae. Although the troglomorphic species have a similarly invariable number of trichobothria as epigeal species, they have longer flagella. The gouge sensilla (with an unknown function) were first described in two highly troglomorphic species of *Paratachycampa* (Bareth & Condé 1981) and later found in all campodeid species (Reboleira *et al.* 2010; Sendra *et al.* 2010). Furthermore, troglomorphic campodeids show some differences in gouge sensilla compared with non-troglomorphic campodeids; in the troglobites they are more abundant (up to 20) and are usually, but not always, longer and thinner than in non-troglomorphic taxa (Sendra *et al.* 2017c). The most remarkable changes in the sensory organs caused by a subterranean life-style are observed in the olfactory chemoreceptors of the cupuliform organ. Olfactory chemoreceptors are spheroid sensilla surrounded by tiny folds or ‘collarettes’. The cuticular invagination and the sensilla have a perforated surface, and these pores are more numerous in troglomorphic than in non-troglomorphic species (Juberthie-Jupeau & Bareth 1980). Outstanding examples are found in many troglobites such as *J. stygia*, which has the highest known number of sensilla (28) in each cupuliform organ (Condé 1954c). The SEM observation of these chemoreceptors in a few species shows a great complexity of folds, with a multiperforated surface that adopts some spiral patterns in *Plusiocampa* (Figs 14–15, 30, 53–54, 95, 126, 128–130, 138, 140, 157–160). Other troglomorphic Plusiocampinae have more complex chemoreceptor shapes, such as *Turkmenocampa mirabilis*, with sphaeriform and ramiform chemoreceptors (Sendra *et al.* 2018), or the network of coralliform structures in an undescribed Plusiocampinae from southern Asia (Sendra, unpubl. data). Plusiocampinae and tachycampoids share convergent evolutionary traits associated with the selective pressures of subterranean ecosystems (see Culver 1982; Hüppop 2000; Christiansen 2012), where the absence of light and patchiness of nutrients might promote the lengthening of appendages (Culver 1982; Bellés 1987; Christiansen 2012; Sendra *et al.* 2017c).

The ecological role of Plusiocampinae and tachycampoids still has to be studied. Field and laboratory observations suggest that they might be secondary consumers in the food web. Plusiocampinae and tachycampoids feed on the remains of organic matter coming from the surface, microorganisms and fungi, but also on dead animals (Fig. 205). The observation of the digestive tube of troglomorphic species often reveals complete body parts of microarthropods, such as small acari or insect larvae (Sendra, pers. obs.). This has already been recorded for soil-dwelling campodeids, although very rarely (Gunn 1992), and might suggest an opportunistic predatory behavior.

Campodeids are often found in syntopy in edaphic habitats, which is less frequent in subterranean habitats. Up to four species of campodeids are known to live in the same cave (Bareth & Condé 1981), and co-occurrence of two species is not rare (Condé 1948a). Data on the spatial distribution of cave Diplura within cave systems are scarce and we report here the presence of *Plusiocampa (S.) nivea* and *P. (P.) ternovensis* sp. nov. in two caves where they seem to be spatially segregated, occupying different cave depths (see Table S2 in Supplementary Material). These observations reveal a complex mutual relationship of syntopically occurring species pairs, as well as habitat preferences of certain species within the subterranean ecosystem.

### **Paleobiogeography, dispersion and colonization of subterranean ecosystems**

Plusiocampinae and tachycampoids share strong troglomorphic features due to their hypogean life-style in deep subterranean ecosystems. They represent two of the most diversified, disperse and abundant groups of dipluran troglobites in karst areas of the Euro-Mediterranean region. Their current distribution suggests an old colonization of this region under different paleogeographical scenarios of the fragmented Tethys Sea. Distributions might be explained mainly through tectonic plates and microplate drift theory, and the dispersal, vicariance and extinction processes that have taken place for hundreds of millions of years.

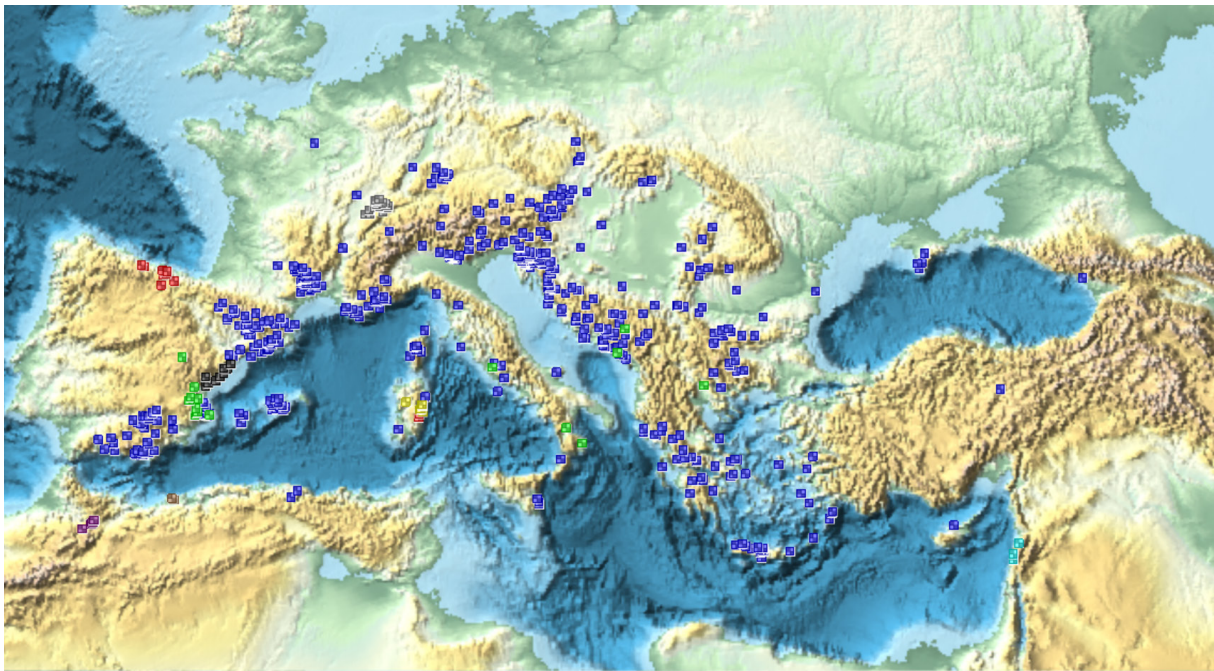
Following a chronological paleobiogeographical history, tachycampoids might be the oldest phyletic group of the Campodeidae. Their disjunct distribution across the Atlantic, encompassing limited distribution areas in karst regions in West Europe, Northwest Africa, Mesoamerica and East Brazil, supports the hypothesis of a Pangean origin during the Mesozoic. These facts also support the ancient colonization of subterranean ecosystems (Bareth & Condé 1981; Sendra *et al.* 2016).

Due to the absence of dated molecular phylogenies, a plausible scenario is suggested based on morphological characters. Plusiocampinae might have originated in the center of Eastern Laurasia, from where they dispersed throughout European regions, reaching a few African karst areas, perhaps since the Eocene–Oligocene, when the closing of the Turgai Strait allowed the European-Asian connection (Decourt *et al.* 2000). At least two dispersal waves might have occurred for the two doubtful monophyletic groups of Euro-Mediterranean Plusiocampinae during the Cenozoic. These groups are separated by the absence or presence of medial posterior macrosetae on the mesonotum and metanotum (Sendra *et al.* 2004). Following these criteria, the ancestors of *Plusiocampa* s. str. without thoracic medial posterior macrosetae (Table 13, Fig. 212), *Stygiocampa* and *Patrizicampa* could have reached the fragmented Europe soon after the connection with Asia through the Turgai Strait. They might have dispersed around Europe up to the western European regions (western Occitania, Basque Country, Cantabrian and Lusitanian regions), where other members of the subfamily Campodeinae and the tachycampoids occurred, perhaps already occupying the subterranean habitats (Sendra 1988, 2003). These are the genera *Podocampa* Silvestri, 1932 and *Litocampa* Silvestri, 1933 among Campodeinae, and the genera *Oncinocampa* and *Paratachycampa* among tachycampoids.

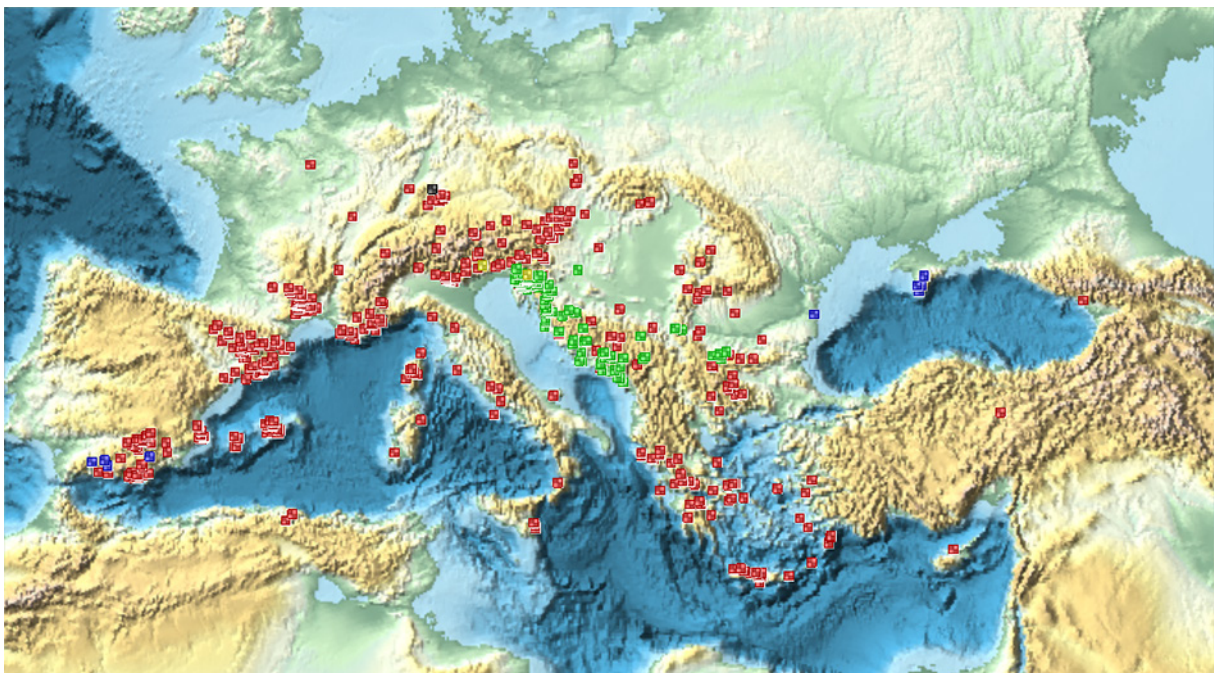
This first dispersal wave might have been limited in Africa by the earlier presence of two tachycampoid genera, *Tachycampa* and *Jeannelicampa*, with an exception on the Kabylean microplate, which moved towards the African plate much later (Rosenbaum *et al.* 2002; Schettino & Turco 2006). The wave of *Plusiocampa* without medial posterior macrosetae included the monotypic *Patrizicampa* of Sardinia, the subgenus *Stygiocampa* of the Dinaric Mountains and the Balkan System, and perhaps the subgenus *Venetocampa* of the Italian Mountains. This first dispersal could have settled and still be living today in



**Fig. 209.** Distribution map of Plusiocampinae Paclt, 1957 (red squares) and the tachycampoid phyletic group species (black squares) in the Euro-Mediterranean area.



**Fig. 210.** Distribution map of Plusiocampinae Paclt, 1957 and tachycampoid phyletic group genera in the Euro-Mediterranean area: *Cestocampa* Condé, 1956 (green squares), *Hystrichocampa* Condé, 1948 (grey squares), *Jeannelicampa* Condé, 1952 (brown squares), *Oncinocampa* Condé, 1982 (red squares), *Paratachycampa* Wygodzinsky, 1944 (black squares), *Patrizicampa* Condé, 1956 (yellow squares), *Plusiocampa* Silvestri, 1912 (navy blue squares), *Tachycampa* Silvestri, 1936 (violet squares) and *Vandelicampa* Condé, 1955 (light blue squares).



**Fig. 211.** Distribution map of subgenera of *Plusiocampa* Silvestri, 1912: *Dydimocampa* Paclt, 1957 (blue squares), *Pentachaetocampa* Sendra & Weber, 2018 (black square), *Plusiocampa* s. str. (red squares), *Stygiocampa* Silvestri, 1934 (green squares) and *Venetocampa* Bareth & Condé, 1984 (yellow squares).

the Dinaric Alps, the isolated carbonate platform in Apulia and the later-fragmented eastern microplates of the Iberian Peninsula. This fragmentation of the eastern microplates (Santanach *et al.* 1986) explains the vicariant distribution of the Plusiocampinae found in French Provence, Catalonia, Sardinia, Kabylia



**Fig. 212.** Distribution map of species of Plusiocampinae Paclt, 1957 with medial posterior (or intermediate) notal macrosetae (red squares) and without these macrosetae (black squares).



**Fig. 213.** Distribution map of Plusiocampinae Paclt, 1957 and tachycampoid phyletic lineage species in their habitats: subterranean, including natural and artificial caves (red squares), edaphic (black squares), MSS (green squares).



and the rest of the Alboran plate in the Interior Zone of the Baetic Mountains (Fig. 212) (Sendra 2003; Sendra *et al.* 2004).

The second dispersal wave of the Plusiocampinae with thoracic medial posterior macrosetae (Table 13) could have happened much later, in the late Miocene, from Anatolia along the Miocenic Alps. This connection was open during this epoch (Rögl & Steiniger 1984) and allowed their dispersal into the Apennine, Jura, Carpathian, Rhodopes, Crimean and Caucasus Mountains, and onto the Mediterranean islands, as has previously been suggested for Leptodirini beetles (Giachino *et al.* 1998; Moldovan & Rajka 2007), so well represented in European subterranean ecosystems (Moldovan 2008). It is possible that these Plusiocampinae newcomers had reached the new lands emerged from the Tethys Sea on the Balkan Peninsula and the Aegean islands, Italian Peninsula, Rhône Valley, and Western Mediterranean, including the islands and the Pre-Baetic Mountains in the south of the Iberian Peninsula. The connected lands during the Messinian period might have allowed a much wider dispersion of *Plusiocampa* s. str., subgenera of *Plusiocampa* and genera of Plusiocampinae with *mp* thoracic macrosetae. This could have been the case for species of *Plusiocampa* s. str., but also for *Cestocampa balcanica*, *C. iberica*, *P. (Dydimocampa) alhamae*, *P. (P.) inopinata* and the monotypic *Hystrichocampa* and *Vandelicampa* (Fig. 212) (Sendra 1988, 2003).

The present distribution areas of subterranean and edaphic Plusiocampinae and tachycampoids are probably not simply marked by ancient paleogeographic events, but might also have been affected during Pleistocene climatic changes. This could explain the total absence of Plusiocampinae and tachycampoids north of latitude 50° N, which roughly follows the southern frontier of the Last Glacial Maximum from Belgium to Crimea. The same may have occurred for all other troglomorphic diplurans, with the remarkable exception of *Haplocampa wagnelli* Sendra, 2019. This fact was pointed out early by Racovitză (1907) and confirmed in recent cave biogeography studies (e.g., Culver *et al.* 2006). The absence of subterranean fauna would then be related to the lack of organic material, not reaching the caves and underground networks because of glaciation (Sendra & Reboleira 2014; Jiménez-Valverde *et al.* 2017). All northern species of Plusiocampinae distributed near the limits of the Last Glacial Maximum are non-troglomorphic members of *Plusiocampa*, which have short antennae with doliiform antennomeres and four simple cupuliform sensilla, as well as a small body with short legs and cerci. This is the case for *P. (P.) humicola*, *P. (P.) spelaea* and *P. (P.) corcyraea* (Sendra & Weber 2018). In this scenario of continuous climatic changes, Plusiocampinae and tachycampoid species that settled in northern European regions could have been wiped out several times during glacial periods. After these harsh climatic events, campodeids would not have been able to colonize or recolonize the subterranean habitats of northern Europe (Figs 209, 213).

During the Mesozoic and Cenozoic, the Plusiocampinae and tachycampoid groups of the Euro-Mediterranean regions probably suffered countless extinctions. These phyletic lineages could have undergone speciation and diversification by vicariance after the split of land masses. Over time, subterranean colonization would have occurred when an empty niche was available (Sendra & Reboleira 2014). As pointed out by Bellés (1991), survival (subterranean spaces as immediate refuges), opportunism (empty subterranean niches to colonize) or convenience (to escape from the competitive pressures of surface habitats) could be the main forces driving the colonization of deep meso- and macro-spaces underground.

Molecular phylogenetic studies are expected to shed new light on the systematics of Plusiocampinae and tachycampoids and may help us to understand their flourishing success in subterranean habitats, contributing to complete a better picture of the ancient colonization of the Euro-Mediterranean region.

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