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**An unexpected discovery of a new subgenus and a species of  
*Plusiocampa* (Campodeidae, Diplura) alongside an overview  
of Central European subterranean campodeids**

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**Abstract.** An unexpected new subgenus and species of Campodeidae (Diplura), *Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov., a troglobitic species found in Schallsinger Höhle in an isolated karstic region in southwestern Germany is described. The new taxon shows two unique characters for the genus *Plusiocampa*: five dorsal femoral macrosetae and the presence of  $g_7$ -glandular setae in females. Two other *Plusiocampa* species have been studied and taxonomic remarks made for them; both are also cave dwelling species from Germany: *Plusiocampa dohati* Condé in Dobat, 1975 studied from eight caves in the Swabian Alb, and one unnamed species of *Plusiocampa* (*Plusiocampa*) from four caves in the Franconian Alb. The biogeographical and taxonomic affinities among *Plusiocampa* species of Central Europe are discussed. The distribution of *Plusiocampa* species in Central Europe runs alongside the frontier of the Pleistocene glaciations, with non-troglomorphic *Plusiocampa* species adjacent to the glacial limits and troglomorphic *Plusiocampa* species below. Worthy of note is the presence only in the northeast of the Central Alps of two relict *Plusiocampinae* species, the already known *Hystrichocampa pelletieri* Condé, 1948 and the new species *P. (P.) inopinata* subgen. et sp. nov.

**Keywords.** Germany, troglobite, *Pentachaetocampa* subgen. nov., glacial distribution.

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## Introduction

Cave-dwelling campodeid diplurans have been known from Central Europe since the end of the nineteenth century (Joseph 1882). Nowadays, about fifteen troglobitic species are known of. This subterranean fauna is well spread throughout the Dinaric Alps (Condé & Bareth 1996) and on both sides of the Alps, in Austria (Condé 1954) and Switzerland (Condé 1962), including the northern karstic Italian regions (Bareth & Condé 1984), and extending towards the northeast along the Inner Western Carpathian Mountains, in the north of Hungary (Stach 1929), and also within caves in the south of Slovakia (Lubomir Kováč pers. com.). In Germany only one troglobitic campodeid was found by Dobat (1975) in the Swabian Alb caves. Much later, samples from seven Swabian caves were used to properly describe (Condé 1993) the endemic species cited only by its name and a short description using a letter from Condé (Dobat 1975): *Plusiocampa* (s. str.) *dobati* Condé in Dobat, 1975.

Recently some accurate biospeleological studies have been made including sampling of cave-dwelling animals in North Rhine-Westphalia, Hesse, Rhenish-Palatinate, Saarland, Baden-Württemberg (mainly Swabian Alb), and Bavaria (mainly Franconian Alb), where more than 10.000 caves and artificial caverns are known, resulting in the discovery in a single cave (Schallsinger Höhle, Baden-Württemberg) of a new and remarkable subgenus (Figs 1–2) of the genus *Plusiocampa*, already well known from subterranean habitats in the Euro Mediterranean region. Furthermore, taxonomic remarks are added on the species *P. dobati*, known from several northern caves in Swabian Alb, and on the uncertain *Plusiocampa* (*Plusiocampa*) sp., which has been located in caves of the Franconian Alb, Bavaria.

## Material and methods

### Sampling methods

The new material of *P. dobati* was collected from eight caves in the Swabian Alb, Baden-Württemberg, Germany. In the Vetterhöhle, some specimens were caught by using an exhaustor and were directly transferred to 96% ethanol. In addition, two ethan-diol-1,2-traps were used to collect further specimens. The collections from the traps were also transferred to 96% ethanol. In the Bärenalhöhle, *P. dobati* was collected by hand and directly transferred to 96% ethanol. *Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov. was collected in the Schallsinger Höhle, southern Black Forest, Baden-Württemberg, Germany. It was collected by using a wet paint brush and transferred directly to 96% ethanol. It was only found in the “Great Hall” between 195 and 230 m away from the entrance of the cave, where the cave is highly humid. Some specimens were found on organic material, others on the surface of a cave lake, several of them already dead.

### Material processing and identification

The specimens were washed using distilled water and were put between slides and glass coverslips to be examined under a phase-contrast optical microscope (Leica DMLS) using Marc André II solution. The illustrations were made with a drawing tube, and the measurements were taken with an ocular micrometer. For measuring the length of the body, the specimens were mounted *in toto* and were measured from the base of the frontal process distal macrochaetae to the abdomen’s supra-anal valve. For scanning electron microscopy (Hitachi S-4100), six specimens were coated with palladium-gold and used for scanning electronic microscopic photography and measurement of the sensilla.

The morphological descriptions and abbreviations used in this paper follow Condé (1956). We use gouge sensilla for the concavo-convexly shaped sensilla located on the antennae, described by Bareth & Condé (1981) and whose function is still unknown. For the position of macrosetae we follow the terms of Condé (1956): *ma*, medial-anterior; *la*, lateral-anterior; *lp*, lateral-posterior; *mp*, medial-posterior and *post*, posterior.

**Collection abbreviations**

- AS = collection of Alberto Sendra, Alcalá de Henares, Madrid, Spain  
 MCNB = Museum de Ciències Naturals de Barcelona, Spain  
 ZMUC = Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Denmark

**Results**

Class Hexapoda Blainville, 1816  
 Order Diplura Börner, 1904  
 Suborder Rhabdura Cook, 1896  
 Family Campodeidae Lubbock, 1873  
 Subfamily Plusiocampinae Paclt, 1957  
 Genus *Plusiocampa* Silvestri, 1912

*Pentachaetocampa* subgen. nov.

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**Type species**

*Plusiocampa (Pentachaetocampa) inopinata* subgen. et sp. nov.

**Diagnosis**

Mesothoracic and metathoracic femur having five dorsal macrosetae (Fig. 12), up to 3 on prothoracic femur; presence of a narrow field of  $g_1$ -glandular setae in adult females (Figs 6, 15–16). In addition to these unique features, there are other characters in common with *Plusiocampa* species, such as: notal macrosetal formula (1+1  $ma$ , 4+4  $la_{1,2,3,4}$ , 2+2  $lp_{2,3}$  pronotum, 1+1  $ma$ , 3+3  $la_{1,2,3}$ , 2+2  $lp_{2,3}$ , 1+1  $mp$  mesonotum, and 1+1  $ma$ , 1+1  $la_1$ , 2+2  $lp_{2,3}$ , 1+1  $mp$  metanotum) (Fig. 3); 2–3 ventral macrosetae on tibia (Fig. 12); slightly unequal elbow-like claws with short extension at the basal end of the posterior claw; lateral crests well developed (Figs 13–14); urotergal macrosetal formula (1+1  $post_1$  on I–II; 1+1  $post_1$ , 1+1  $la$  on III; 2+2–3+3  $post_{1,2,3}$ , 1+1  $la$  on IV; 5+5  $post_{1-5}$ , 1+1  $la$  on V–VII, 6+6–5+5  $post$  on VIII; 8+8  $post$  on IX) (Fig. 4); urosternal macrosetal formula (7+7 on I; 5+5 on II–VII; 2+2 on VIII urosternites); female and male urosternite I with a narrow posterior field of  $g_1$ -glandular setae and subcylindrical appendages having a field of  $a_1$ -glandular setae (Figs 5–6).

**Etymology**

*Penta* in addition to *chaetae* (*chaeta*–), both from the Greek words which means five setae in reference to the noticeable five dorsal macrosetae on the femur.

**Phyletic affinities of the subgenera of *Plusiocampa***

Recently, weak support was found for the classification of Campodeidae (Sendra *et al.* 2017), specifically within Plusiocampinae Paclt, 1957, based on the sparse number of solid characters and the high intraspecific and interspecific variation of many of them. This makes the taxonomy of the Plusiocampinae a delicate subject, with only a few synapomorphic features that can be used to put some order into the problematic subfamily proposed by Paclt (1957). All Plusiocampinae have at least 1+1  $ma$ , 1+1  $la$  and 2+2  $lp_{2,3}$  on its pronotum, known in all the ten previously described genera (Sendra *et al.* 2017). Among them, *Plusiocampa* with 57 species distributed around the Mediterranean Basin (Condé 1956) is the most diversified. The exceptions are the two Chinese species *Plusiocampa (Dydimocampa) sinensis* Silvestri, 1931 and *Plusiocampa (Didymocampa) lipsae* Condé, 1993, although both should be removed from *Plusiocampa* due to the macrosetal formula on urosternites II to VIII. Furthermore,

a laminar telotarsal process is present in the case of *P. lipsae*. As a consequence, a new diagnosis of *Plusiocampa* is proposed: telotarsus with lateral crests and smooth-setiform lateral processes; pronotal formula with 1+1 *ma* and 2+2 *lp* macrosetae and from 2+2 to 4+4 *la* macrosetae; no less than 3+3 *post* macrosetae on urotergites VI–VII; no less than 5+5 macrosetae on urosternites II–VII and 2+2 macrosetae on urosternite VIII; and sensillum of antennomere III in a ventral position.

The genus *Plusiocampa* was divided into four subgenera based on two features, the dorsal macrosetae on the femur (Paclt 1957) and the ventral macrosetae on the tibia. Using these two synapomorphic features and additional ones, the following taxonomic key is proposed for the current five subgenera, *Pentachaetocampa* subgen. nov. included.

### Key of the subgenera of *Plusiocampa*

1. No dorsal femoral macrosetae; without medial posterior notal macrosetae; extra macrosetae on the first to the eighth urosternites (with the exception of *Plusiocampa (Stygiocampa) bureschi* Silvestri, 1931 and *Plusiocampa (Stygiocampa) denisi* Condé, 1947) ..... ***Stygiocampa*** Silvestri, 1934
  - One, two or five dorsal femoral macrosetae; with or without medial posterior notal macrosetae. No extra macrosetae on the first to the eighth urosternites (with the exception of *Plusiocampa (Plusiocampa) dargilani* (Moniez, 1894)) ..... 2
2. One or two dorsal femoral macrosetae; with or without medial posterior notal macrosetae; without glandular setae *g<sub>1</sub>* in females ..... 3
  - Five dorsal femoral macrosetae; two to four ventral tibial macrosetae; with medial posterior notal macrosetae; with glandular setae *g<sub>1</sub>* in females ..... ***Pentachaetocampa*** subgen. nov.
3. One dorsal femoral macroseta; zero to four ventral tibial macrosetae ..... 4
  - Two dorsal femoral macrosetae; two to four ventral tibial macrosetae .... ***Dydimocampa*** Paclt, 1957
4. One to four ventral tibial macrosetae; with or without medial posterior notal macrosetae; subequal to unequal claws but upmost the posterior claw is 2 times as longer as the anterior claw ..... ***Plusiocampa*** s. str. Silvestri, 1912
  - No ventral tibial macrosetae; without medial posterior notal macrosetae; very unequal claws (posterior claw 2.5 times as long as anterior claw) ..... ***Venetocampa*** Bareth & Condé, 1984

For *Plusiocampa* s. str., its 47 species and 10 subspecies bear one dorsal femoral macroseta and 1–3 ventral tibial macrosetae. They are distributed from the Pontic Mountains in the northwest of the Anatolian Peninsula to the Betic Mountains on the Iberian Peninsula, colonizing the Balkan, Iberian and Italian peninsulas the Central French Massif included, and also the Aegean and most of the west-Mediterranean islands, reaching the Alps and the Carpathians Mountain ranges towards the north and in the south an isolated location in the Kabylie Mountains, northern Algeria. Most of its species inhabit subterranean ecosystems (Condé 1956) and only eight species and two subspecies can be considered soil-dwelling.

*Stygiocampa* has six species, all of them sharing the absence of dorsal femoral macrosetae in addition to a progressive reduction of the notal and urotergal macrosetae formula. Furthermore, four of these species have an increase in the number of macrosetae on the urosternites. All of this shows remarkable troglomorphic features, its species inhabiting the subterranean ecosystems around the Dinaric Alps (Condé & Bareth 1996).

The two species of *Dydimocampa* share the possession of two dorsal femoral macrosetae and in both the *mp* meso- and metanotal macrosetae are absent. They have been found at two unique locations, a



cave in the Crimean Peninsula (Silvestri 1949) and in the Movile Cave (Condé 1996) in the southeast of Romania, both near the Black Sea.

Only one species is proposed in *Venetocampa*: *Plusiocampa (Venetocampa) paoletti* Bareth & Condé, 1984, collected from a single cave in the Feltrine Alps. It is characterized by the absence of ventral tibial macrosetae and the progressive reduction of the notal and urotergal macrosetae, sharing these features with *Stygiocampa*, and the presence of dorsal femoral macrosetae as its differential feature (Bareth & Condé 1984). With this definition, another troglobitic species, *Plusiocampa (Plusiocampa) dargilani* (Moniez, 1984) could be included in *Venetocampa*. *Plusiocampa dargilani* was found in many caves in the Central Massif, southern France (Condé 1997), and in addition, it shares with most of the species of *Stygiocampa* an increase in macrosetae on the urosternites.

Finally, the new subgenus *Pentachaetocampa* subgen. nov. bears two synapomorphic features that separate it from other already-known Plusiocampinae: the five dorsal macrosetae on the meso- and metathoracic femur and the presence of a narrow field of  $g_1$ -glandular setae on the first urosternite in adult females. No other species of *Plusiocampa* has five dorsal femoral macrosetae, although this does occur in another genus of Plusiocampinae. This is the case for *Hystrichocampa* Condé, 1948, a monospecific genus with a widely distributed species, *H. pelletieri* Condé, 1948, from several caves and mines from karst regions around the French and Swiss Jura (Condé 1948, 1962). Nevertheless, many solid features differentiate *Hystrichocampa* from *Pentachaetocampa* subgen. nov. Among them the most noticeable are: the shape and pubescence of the telotarsal processes, the absence of  $g_1$ -glandular setae in females and the unequal claws in *Hystrichocampa*. Furthermore, no other *Plusiocampa* or Plusiocampinae females bear  $g_1$ -glandular setae on the first urosternite.

***Plusiocampa (Pentachaetocampa) inopinata* subgen. et sp. nov.**

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Figs 1–17, Table 1

### Etymology

Unopinatus, inopinata, inopinatum, a Latin adjective meaning unexpected or surprising, which describes how we felt after the discovery of this remarkable troglobitic new taxon in German caves.

### Type material

#### Holotype

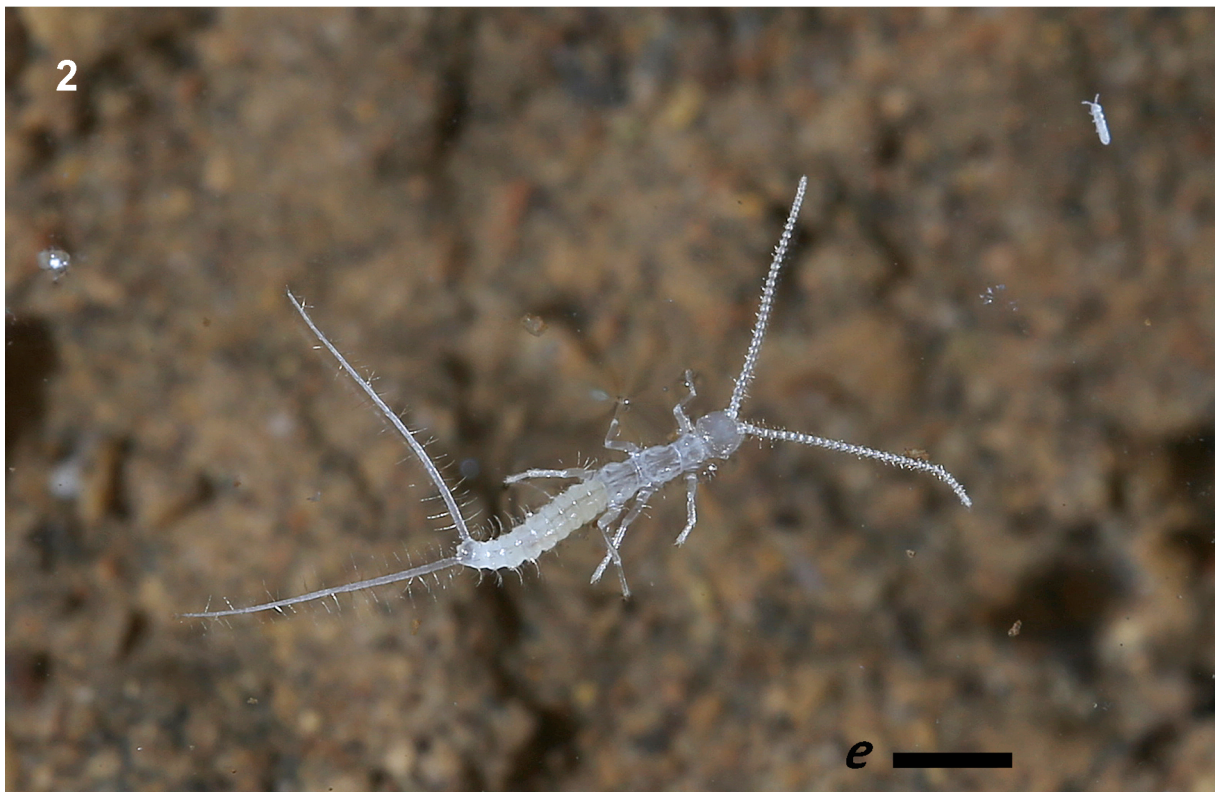
GERMANY: ♀, Schallsinger Höhle, Malsburg-Marzell, Baden-Württemberg, 11 May 2014, Dominik Fröhlich and M. Sieber leg. (ZMUC).

#### Paratypes

GERMANY: 4 ♀♀, 2 ♂♂, from the type locality, 11 May 2014, Dominik Fröhlich leg. (ZMUC); 1 ♂, 8 Jun. 2013, Hannes Köble leg. (AS); 1 ♂, 11 Jun. 2016, Dominik Fröhlich, Tobias Helling and Dieter Weber leg. (MNCB); 3 juvs, 11 Jun. 2016, Dominik Fröhlich, Tobias Helling and Dieter Weber leg. (AS); 1 ♀, 1 juv., 11 Jun. 2016, Dominik Fröhlich, Tobias Helling and Dieter Weber leg. (AS); 1 spec. and 1 juv., 11 Jun. 2016, Dominik Fröhlich, Tobias Helling and Dieter Weber leg., mounted in Marc André solution (AS).

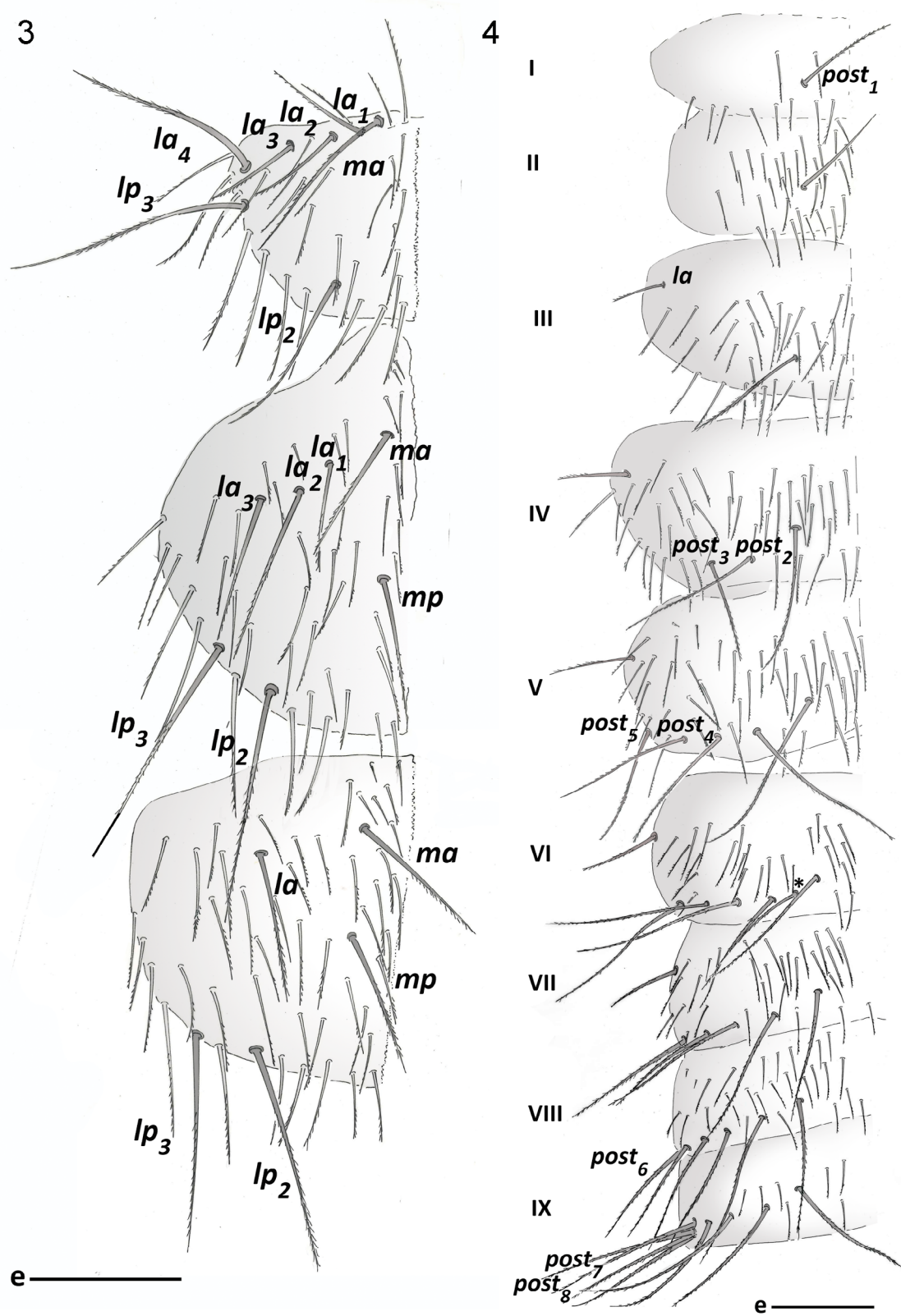
### Other material examined

GERMANY: 2 ♀♀, Schallsinger Höhle, Malsburg-Marzell, Baden-Württemberg, Germany, 11 June 2016, Dominik Fröhlich, Tobias Helling and Dieter Weber leg. (AS).

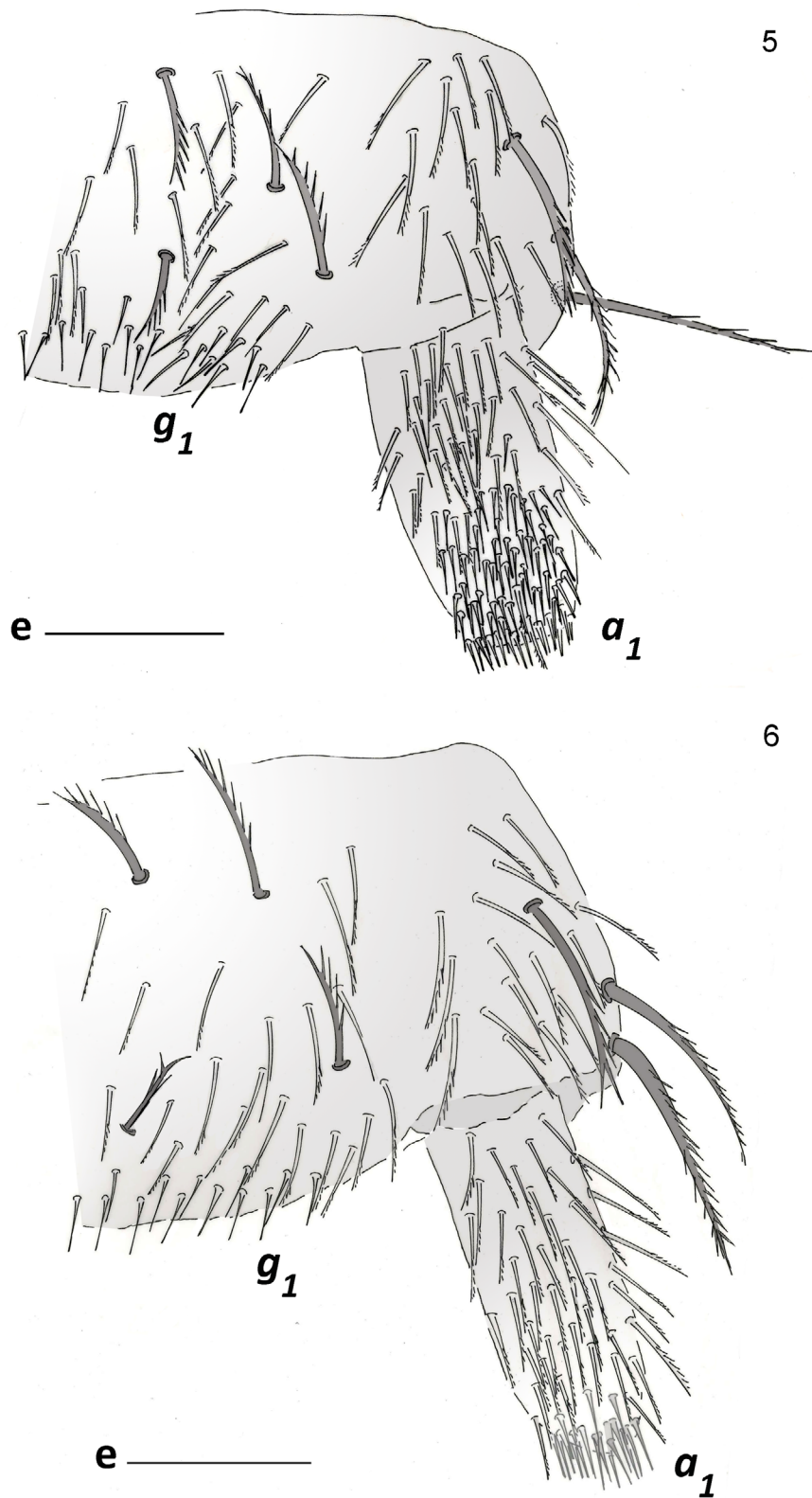


**Figs 1–2.** *Plusiocampa (Pentachaetocampa) inopinata* subgen. et sp. nov. **1.** On a clay surface. **2.** On the surface of a puddle from Schallsinger Höhle. Courtesy of Mirjam Widmer. Scale bars = 2 mm.





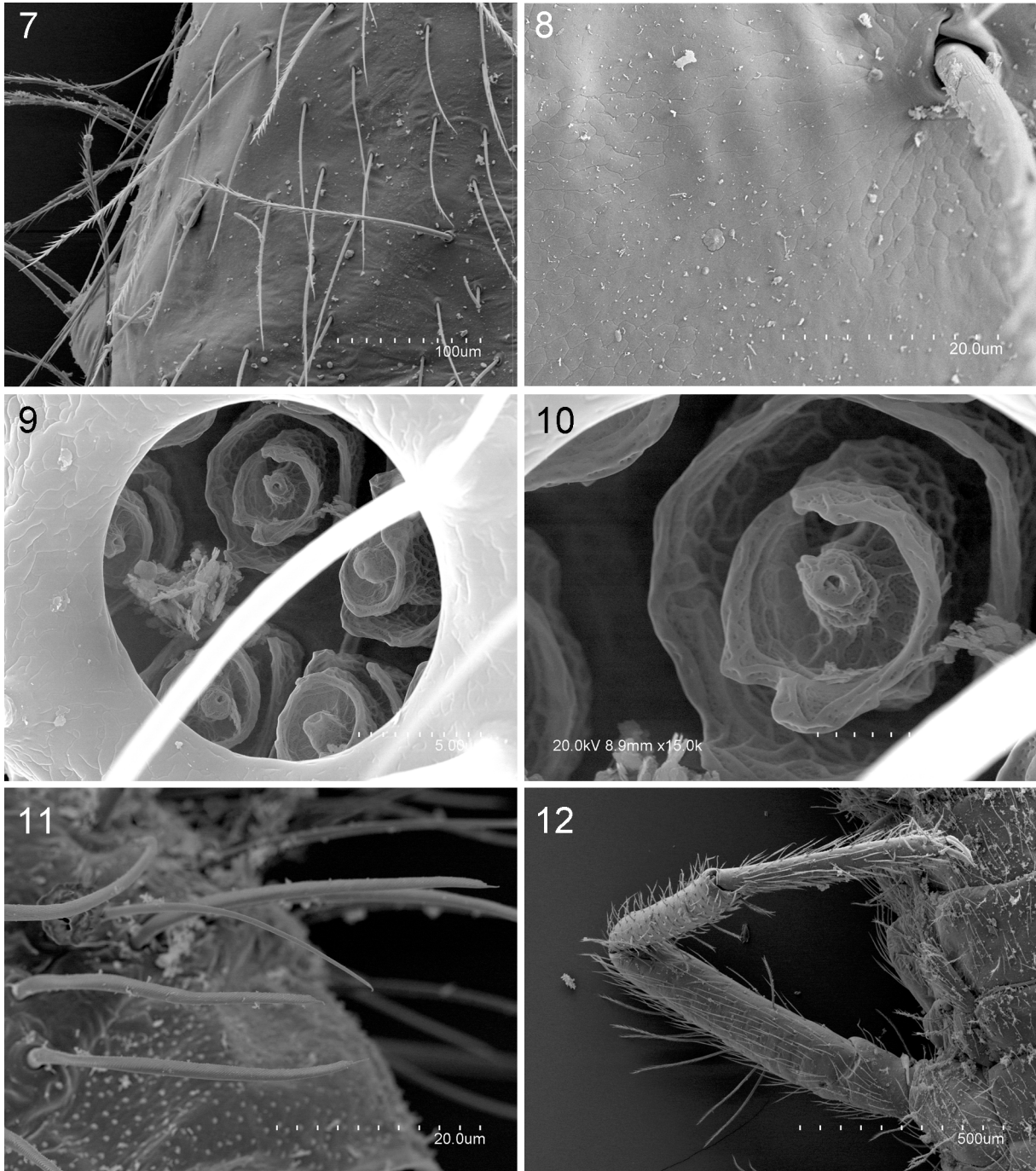
**Figs 3–4.** *Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov., holotype, ♀. **3.** Pro-, meso- and metanotum, left side. **4.** Urotergites I–IX, left side. Scale bars = 0.2 mm.



**Figs 5–6.** *Plusiocampa (Pentachaetocampa) inopinata* subgen. et sp. nov. Urosternite I. **5.** Male. **6.** Female.  $a_1$  =  $a_1$ -glandular setae,  $g_1$  =  $g_1$ -glandular setae. Scale bars: = 0.1 mm.

**Description**

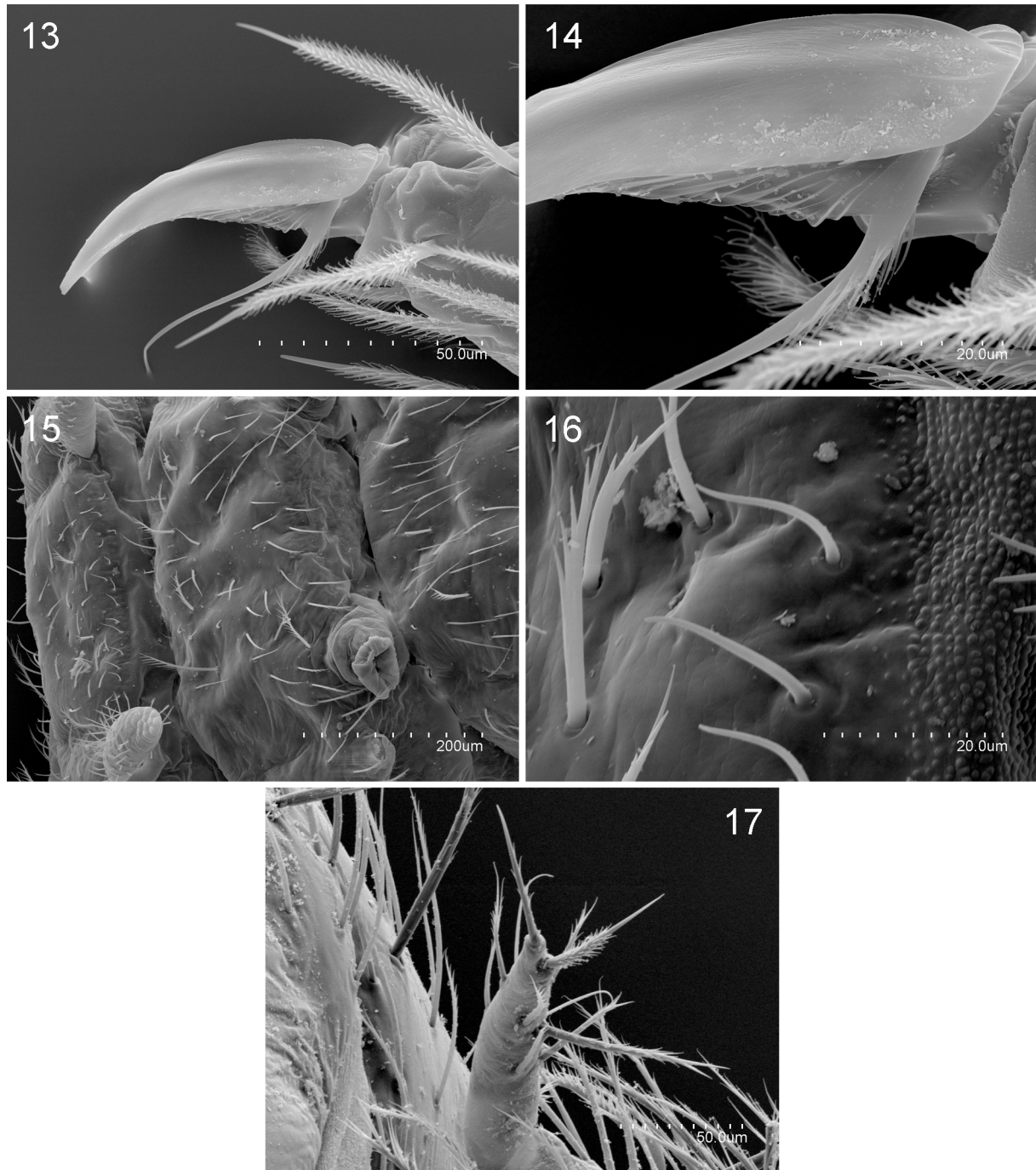
MEASUREMENTS. Body length 3.1–5.5 mm (males), 3.9–5.4 mm (females) and 2.2–2.3 mm (juveniles) (Figs 1–2; see [Supplementary File 2](#)). Epicuticle smooth under optical microscope but slightly reticulated in high magnifications; body with sparse thin and long clothing, covered with thin barbs along the distal one third to one half (Figs 7–8).



**Figs 7-12.** *Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov. 7–8. Metanotum. 7. Macrosetae  $la_{1,2,3}$  and  $mp$ . 8. Detail of surface. 9. Cupuliform organ of last antennomere. 10. Sensillum of cupuliform organ. 11. Gouge sensilla. 12. Metathoracic leg. Scale bars in  $\mu\text{m}$ .



HEAD. Two intact antennae in adults with 32 and 33 antennomeres and three in juveniles with 32, 32 and 33 antennomeres. Small sensillum of third antennomere located in ventral position between *d* and *e* macrosetae. Central antennomeres 1.5 times as long as wide in adults and juveniles, 2.0 times in the apical antennomere. Large cupuliform organ occupying  $\frac{1}{6}$  of total length of apical antennomere with 12–14 olfactory chemoreceptors with 2–3 collarettes, each one covered completely by small pores



**Figs 13–17.** *Plusiocampa (Pentachaetocampa) inopinata* subgen. et sp. nov. **13.** Tarsal end of metathoracic leg. **14.** Detail of telotarsal claw. **15.** Urosternites I-II of a female. **16.**  $g_1$ -glandular setae of urosternite I of a female. **17.** Stylus of urosternite VII. Scale bars in  $\mu\text{m}$ .

**Table 1.** *Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov., length of the body, antennomeres, metathoracic leg and cerci (units in mm), and number of antennomeres and cercal articles.

| Specimen                | Body length | Antennae     |        | Length metathoracic leg | Cerci                    |        |
|-------------------------|-------------|--------------|--------|-------------------------|--------------------------|--------|
|                         |             | Antennomeres | Length |                         | Articles, basal included | Length |
| Paratype, juvenile (AS) | 2.3         | 32           | 2.0    | 1.3                     | 7                        | 2.0    |
| Paratype, juvenile (AS) | 2.5         | 32           | 2.2    | 1.4                     | –                        | –      |
| Paratype, juvenile (AS) | 2.6         | 33           | 2.2    | 1.3                     | –                        | –      |
| Paratype, ♂ (MNCB)      | 3.2         | –            | –      | 1.8                     | –                        | –      |
| Paratype, ♀ (ZMUC)      | 3.9         | 33           | 2.8    | 2.0                     | –                        | –      |
| Holotype, ♀ (ZMUC)      | 4.1         | –            | –      | 2.3                     | –                        | –      |
| Paratype, ♀ (ZMUC)      | 4.2         | –            | –      | 2.4                     | 8                        | 4.2    |
| Paratype, ♀ (ZMUC)      | 4.5         | –            | –      | 2.5                     | –                        | –      |
| Paratype, ♂ (ZMUC)      | 4.6         | 32           | 3.3    | 2.4                     | –                        | –      |
| Paratype, ♂ (ZMUC)      | 4.6         | –            | –      | –                       | –                        | –      |
| Paratype, ♀ (ZMUC)      | 5.1         | –            | –      | 2.5                     | –                        | –      |
| Paratype, ♀ (AS)        | 5.4         | –            | –      | 2.7                     | –                        | –      |
| Paratype, ♂ (AS)        | 5.5         | –            | –      | 2.6                     | –                        | –      |

(Figs 9–10). Thin and long gouge sensilla (Fig. 11) 30–35  $\mu\text{m}$  long in a single distal whorl of 12–15 sensilla on each medial and distal antennomere. Frontal process developed with slightly tuberculate setae and macrosetae with thin barbs. The three macrosetae along the line of insertion of antennomere and  $x$  setae with thin barbs along distal one third. Suboval labial palps with latero-external sensillum similar to sensillum of third antennomere, with two guard setae, up to 8 setae on anterior border and up to 120 neuroglandular setae.

THORACIC CHAETOTAXY. Thoracic macrosetae distribution (Fig. 3): 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*, 1+1 *la*<sub>1</sub>, 2+2 *lp*<sub>2,3</sub>, 1+1 *mp* macrosetae. All macrosetae long, thin, covered by very thin barbs along distal four fifths (Fig. 7); marginal setae longer than clothing setae, covered by thin barbs along distal half to two thirds. Legs elongated, metathoracic legs reaching abdominal segment X. Femur II–III with 5 dorsal macrosetae (6 on femur III of two adults) (Fig. 12); femur I with 3 dorsal macrosetae. Tibia with two or three ventral

macrosetae covered by thin short barbs along distal half to four fifths (Fig. 12). Calcars well barbed from base to tip with long barbs (Fig. 12). Dorsal and lateral tarsal setae completely covered with thin barbs almost from base almost to tip (Fig. 13). Slightly unequal, elbow-like claws (posterior claw 1.05–1.15 as long as anterior one), with short extension at basal end of posterior claw; lateral crests well developed, noticeably ridged on ventral side (Figs 13–14) and almost smooth on dorsal side. Telotarsal process smooth and setiform, with several short proximal barbs (Figs 13–14).

ABDOMINAL CHAETOTAXY. Distribution of abdominal macrosetae on tergites (Fig. 4): 1+1 *post*<sub>1</sub> on I–II; 1+1 *post*<sub>1</sub> and 1+1 *la* on III; 2+2 (3+2, 3+3) *post*<sub>1,2</sub> and 1+1 *la* on IV; 5+5 *post*<sub>1–5</sub> and 1+1 *la* on V–VII, 6+6 (5+6, 5+5) *post* on VIII; 8+8 (8+7) *post* on IX. All *post* urotergal macrosetae long and covered by thin barbs along distal two thirds to four fifths; *la* urotergal macrosetae shorter than *post* macrosetae, covered by barbs along distal half; position of *post*<sub>1</sub> macrosetae always a little bit anterior before marginal setae insertion. Urosternite I with 7+7 (7+6) macrosetae; urosternites II to VII with 5+5 macrosetae; urosternite VIII with 2+2 macrosetae; all urosternal macrosetae covered by long barbs along distal half to four fifths. Apical setae of styli with a short tooth with 2–5 small thin barbs in middle of setae; subapical and ventromedial setae covered with numerous thin barbs in middle portion of setae (Fig. 17). Cerci in adults with seven articles in addition to basal article, as long as body length; 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 (Table 1).

FEMALE UROSTERNITE I (Figs 6, 15–16). With subcylindrical appendages thinner than male appendages, each bearing up to 20 *a*<sub>1</sub>-glandular setae in a distal field; and a narrow marginal field with up to 25 *g*<sub>1</sub>-glandular setae in larger female adults.

MALE UROSTERNITE I (FIG. 5). With moderated large subcylindrical appendages, each bearing up to 70 *a*<sub>1</sub>-glandular setae in a large field covering almost distal half of its ventral and apical side; and a narrow marginal field with up to 35 *g*<sub>1</sub>-glandular setae in longer male adults.

### Phyletic affinities

*Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov. is a clearly recognizable species due to the presence of five femoral macrosetae and the presence of *g*<sub>1</sub>-glandular setae in females. It differs strongly from members of other subgenera in the previously mentioned characters; but without these two differential features, *P* (*P*) *inopinata* subgen. et sp. nov. seems to be most closely related to *Plusiocampa* (*Plusiocampa*) *bonadonai* Condé, 1948, based on similarities in the macrosetal formula of the thorax and abdomen and in the size and shape of the telotarsus. It is also a cave-dwelling species known from several caves, also found in endogean habitats (Condé & Poivre 1982) in the Maritime Alps, southeastern France.

### *Plusiocampa* (*Plusiocampa*) *dobati* Condé in Dobat, 1975

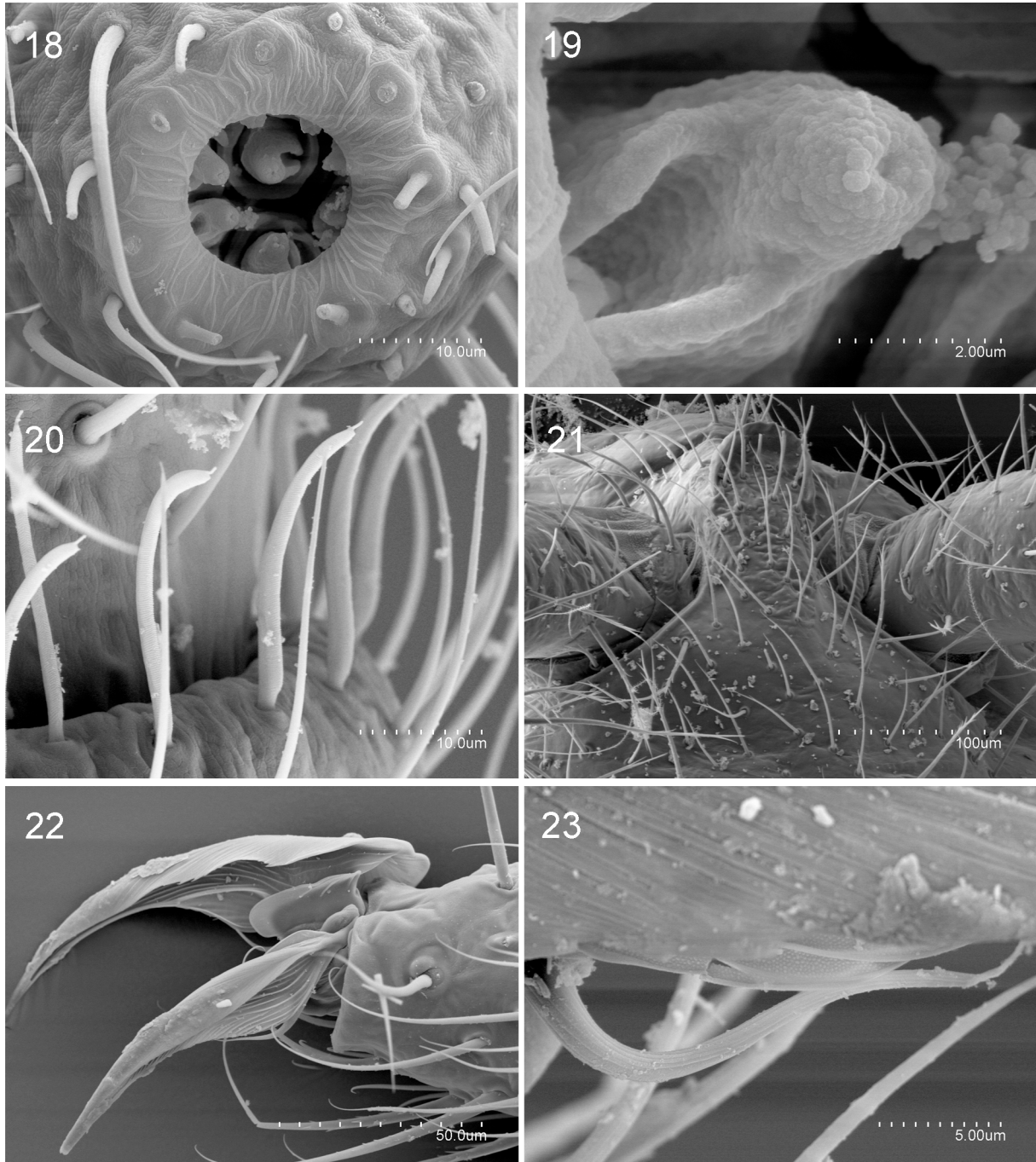
Figs 18–25

### Material examined

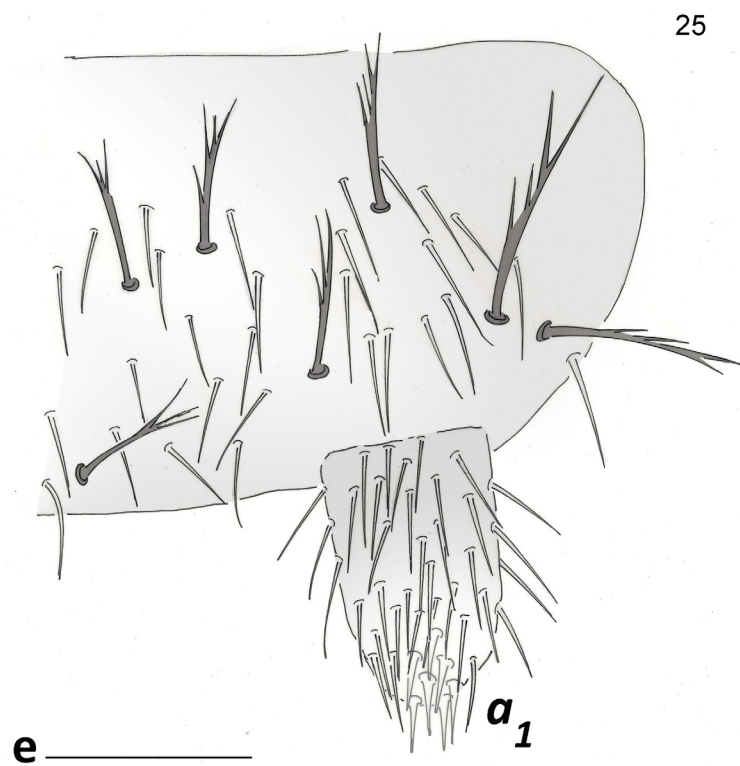
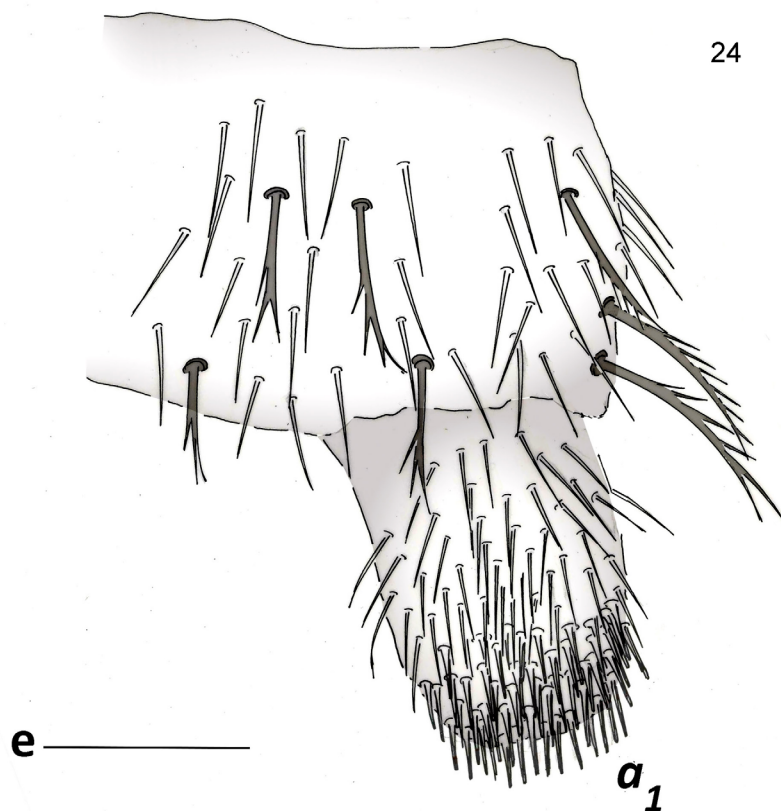
GERMANY (All Swabian Alb, Baden-Württemberg): 1 ♂, Todsburger Höhle, 29 Jun. 2013, Hannes Köble leg. (AS); 1 ♀, Todsburger Höhle, 14 Jul. 2013, Hannes Köble leg. (AS); 1 ♀, Blautopfhöhle, 12 Oct. 2012, S. Bauer leg. (AS); 1 ♀, Blautopfhöhle, 12 Oct. 2012, S. Bauer leg. (AS); 1 ♀, Blautopfhöhle, 29 Oct. 2012, S. Bauer leg. (AS); 1 ♂, Blautopfhöhle, 21 Sep. 2013, Hannes Köble leg. (AS); 1 juv., Blautopfhöhle, 21 Sep. 2013, Hannes Köble leg. (AS); 1 ♀, Blautopfhöhle, 21 Sep. 2012, S. Bauer leg. (AS); 1 ♀, Bärenalhöhle, 20 Mar. 2013, Petra Boldt leg. (AS); 1 ♂, 1 ♀, Bärenalhöhle, 13 Sep. 2013, Petra Boldt leg. (AS); 1 ♀, 1 juv., Bärenalhöhle, 27 Nov. 2012, Petra Boldt leg. (AS); 1 ♀, Bärenalhöhle, 11 May 2013, Petra Boldt leg. (AS); 1 ♂, 1 ♀, Bärenalhöhle, 13 Sep. 2013, Petra



Boldt leg. (AS); 1 ♀, Bärentalhöhle, 15 Feb. 2014, Hannes Köble leg. (AS); 1 ♂, Bärentalhöhle, 5 Aug. 2014, Hannes Köble leg. (AS); 1 ♂, 1 ♀, Falkensteiner Höhle, 31 Mar. 2013, Hannes Köble leg. (AS); 1 ♀, Falkensteiner Höhle, 25 Apr. 2013, Hannes Köble leg. (AS); 1 ♂, Vetterhöhle, 24 Feb. 2013, Holger Döhmman leg. (AS); 2 ♂♂, Vetterhöhle, 1 Aug. 2013, Petra Boldt leg. (AS); 1 ♂, Vetterhöhle,



**Figs 18–23.** *Plusiocampa (Plusiocampa) dobatii* Condé in Dobat, 1975. **18.** Cupuliform organ of the last antennomere. **19.** Central cylindrical structure of an olfactory chemoreceptor sensillum of the cupuliform organ. **20.** Gouge sensilla. **21.** Frontal process. **22.** Telotarsal end of metathoracic leg. **23.** Detail of telotarsal claw. Scale bars in µm.



**Figs 24–25.** *Plusiocampa (Plusiocampa) dobati* Condé in Dobat, 1975. Urosternite I. **24.** Male. **25.** Female.  $a_1$  =  $a_1$ -glandular setae. Scale bars = 0.1 mm.

20 May 2013, Petra Boldt and Udo Wohlketter leg. (AS); 1 ♂, 1 ♀, Vetterhöhle, 7 Mar. 2013, Otto Schwabe and Udo Wohlketter leg. (AS); 1 ♀, Vetterhöhle, 24 Nov. 2013, Hannes Köble leg. (AS); 1 ♂, Glemser Höllenloch, 17 Jul. 2014, Hannes Köble leg. (AS); 2 ♂♂, 2 ♀♀, Wiemsener Höhle, 24 Mar. 2010, R. Straub leg. (AS); 1 ♀, Wimsener Höhle, 27 Mar. 2010, R. Straub leg. (AS); 1 juv., Hausener Bröller, 2 May 2014, Hannes Köble leg. (AS).

### Taxonomic remarks

Antennae with 28 and 29 antennomeres in adults and 28 in one juvenile. Cupuliform organ with eight complex olfactory chemoreceptor sensilla characterized by a cylindrical central structure without noticeable pores, surrounded by one concentric fold (Figs 18–19). Gouge sensilla long (25 µm), with a tip on the end (Fig. 20). Frontal process with a frontal and lateral rim (Fig. 21). The shortness of their telotarsal processes and the shape of the claws are confirmed (Figs 23–24). The urosternites of male and female were mentioned in the original description but no drawings were produced. In the first urosternite of both males and females there are no  $g_1$ -glandular setae and the appendages support up to 54  $a_1$ -glandular setae in males and up to nine in females (Figs 24–25).

### *Plusiocampa (Plusiocampa)* sp.

Table 2

### Material studied

GERMANY (all Franconian Alb, Bavaria): 1 juv., Geisloch near Oberfellendorf, 17 Apr. 2014, Hardy Schabdach leg. (AS); 2 ♀♀, Geisloch near Oberfellendorf, 17 Apr. 2014, Hardy Schabdach leg. (AS); 1 ♂, Fischerhöhle near Heuchling, 7 Jul. 2011, Hardy Schabdach leg. (AS); 1 ♀, Sophienhöhle near Rabenstein, 10 Jan. 2012, Hardy Schabdach leg. (AS); 1 ♀, Geisloch near Müzinghof, 10 May 2011, Hardy Schabdach leg. (AS).

### Taxonomic remarks

Body length 2.0 mm in a juvenile and 3.0–3.8 mm in adults; short antennae with 20–21 doliiform antennomeres (1–1.1 times as long as wide in middle antennomeres and 1.5 times in last one); four simple olfactory chemoreceptors in cupuliform organ; small sensillum of third antennomere in ventral position, between  $d$  and  $e$  macrosetae; frontal process without protrusion nor tuberculate setae; pronotum with 1+1  $ma$ , 4+4  $la$ , 2+2  $lp$ ; mesonotum with 1+1  $ma$ , 3+3  $la_{1,2,3}$ , 2+2  $lp_{2,3}$ , 1+1  $mp$ ; metanotum with 1+1  $ma$ , 1+1  $la$ , 2+2  $lp_{2,3}$ , 1+1  $mp$ ; short legs reaching seventh abdominal segment, with two ventral tibial macrosetae; telotarsal process with small claws slightly unequal (1.1–1.2), with very short extension at basal end of posterior claw and large lateral crests; urotergites with 1+1  $post$  on I–II; 0–1+1  $la$ , 2+2  $post_{1,2}$  on III, 1+1  $la$ , 4+4  $post_{1,2,3,4}$  on IV, 2+2 or 1+1  $la$ , 5+5  $post_{1-5}$  on V, 2+2  $la$ , 5+5  $post_{1-5}$  on VI–VII; 6+6  $post$  on VIII and 10+8 to 9+9 on abdominal segment IX; male with slightly enlarged appendages, having  $a_1$ -glandular setae in addition to a field of  $g_1$ -glandular setae; female appendages slightly thin, having  $a_1$ -glandular setae; cerci approximately half of body length with 6–7 articles plus base.

### Phyletic affinities

This small *Plusiocampa* s. str. sp. from Franconian Alb caves is characterized by its short appendages, modest claws, low number of antennomeres and cercal articles in addition to only four olfactory chemoreceptors in the cupuliform organ; all of these non-troglophile features indicate a not exclusively subterranean life for this species. Due to this, *Plusiocampa* s. str. sp. can be considered a troglophile form that can live in subterranean superficial habitats or humid soils. This troglophile life-style can be seen in other *Plusiocampa* species described from Hungarian caves (Stach 1929; Loksa 1960). This is the case for *Plusiocampa (Plusiocampa) spelaeae* Stach, 1929 from Baradla Cave (Gömör, northern Hungary) and *Plusiocampa (Plusiocampa) brevi antennata* Loksa, 1960 from Lóczy Cave (Balatonfüred,

**Table 2.** *Plusiocampa (Plusiocampa)* sp. from Franconian Alb caves, length of the body, antennomeres, metathoracic leg and cerci (units in mm), and number of antennomeres and cercal articles.

| Sex           | Body length | Antennae     |        | Metathoracic leg length | Cerci    |        |
|---------------|-------------|--------------|--------|-------------------------|----------|--------|
|               |             | Antennomeres | Length |                         | Articles | Length |
| Juvenile (AS) | 2.0         | –            | –      | –                       | –        | –      |
| ♂ (AS)        | 3.2         | 21           | –      | –                       | –        | –      |
| ♀ (AS)        | 3.5         | –            | –      | –                       | –        | –      |
| ♂ (AS)        | 3.7         | 20           | 1.8    | 1.4                     | 6 + base | 1.6    |
| ♀ (AS)        | 3.4         | 21           | 2.1    | 1.4                     | –        | –      |
| ♀ (AS)        | 3.8         | 21           | 1.9    | 1.4                     | 7 + base | 2.0    |

Hungary). Nevertheless, both cave-dwelling Hungarian species were poorly described and nowadays it is impossible to make a complete comparison with other species of *Plusiocampa*. Furthermore, both Hungarian species apparently lack medial posterior macrosetae on the mesonotum and metanotum.

The traits related with the small size observed in this Franconian Alb *Plusiocampa* s. str. sp., in addition to the presence in this species of thoracic medial posterior macrosetae, are found in a soil-dwelling species, *Plusiocampa (Plusiocampa) humicola* Ionescu, 1951, recently redescribed by Sendra *et al.* (2012). However, in the males of *P. (P.) humicola*  $g_1$ -glandular setae are absent and that species was also found far from Germany in Cluj (Romania).

It is also possible to look into the affinities of *Plusiocampa* s. str. sp. from Franconian caves in a species of *Plusiocampa* from a less distant area. The latter was informally referred to as *Plusiocampa strohuali cavicola* Vornatscher, 1943 and it has been reported from several Austrian caves (Condé 1954). Nevertheless, further sampling of material from the type location is the only solution to unravelling the taxonomic mess of several *Plusiocampa* species from Central Europe.

## Discussion

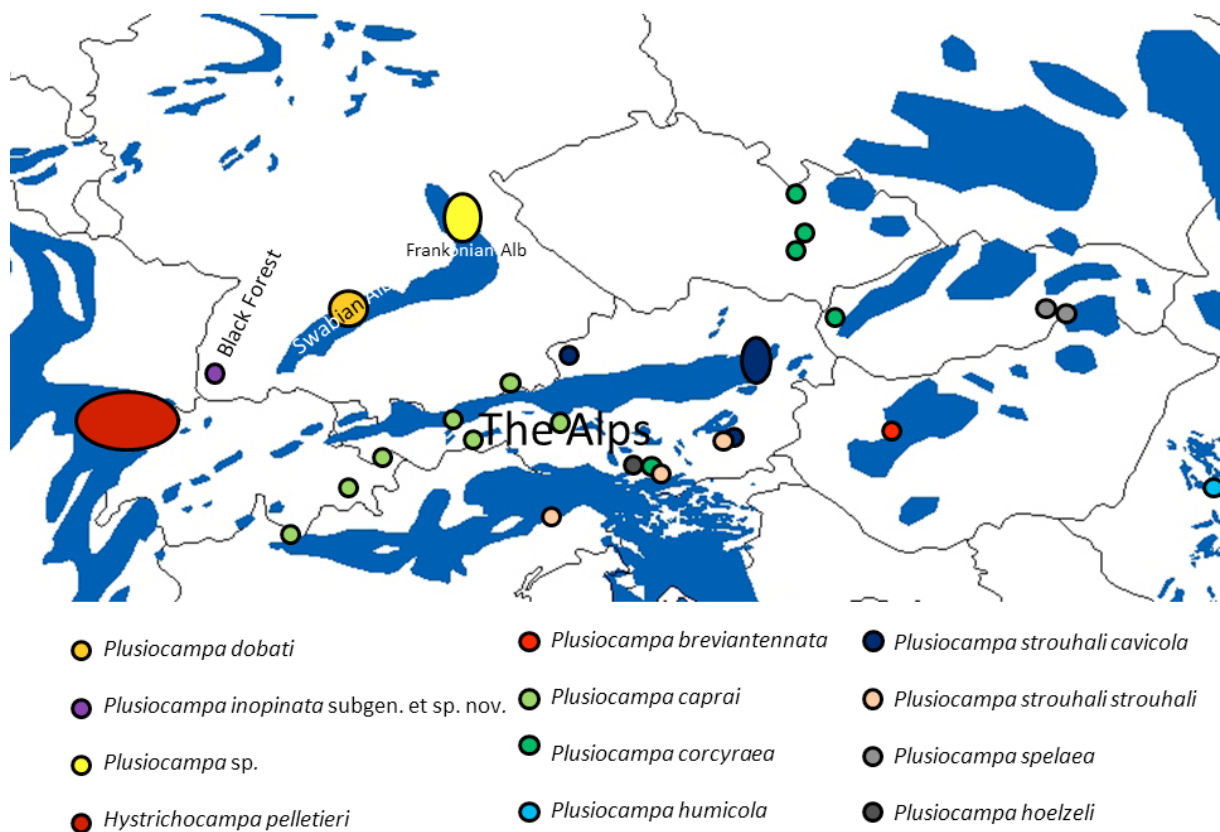
### Current knowledge of subterranean Campodeidae fauna in Central Europe

The distribution of the subterranean campodeids around the European Mediterranean region has its northern limits from Belgium to the Crimea Peninsula, going along the southern limit of the Pleistocene glaciations. This lack of subterranean fauna under the glacial influence was pointed out early by Racovitza (1907) and remarked on in more recent distributional studies from Europe (Culver *et al.* 2006, for instance). The reason for this absence of subterranean fauna was also remarked on by Racovitza (1907), citing the lack of food in the form of organic material that could not reach the caves through the network of voids in the vadose zone (Sendra & Reboleira 2014; Jiménez-Valverde *et al.* 2017).

In the case of *Plusiocampa* and *Hystrichocampa*, both included in the subfamily Plusiocampinae (Paclt 1957), the northern limits, always below the 50th parallel north, are occupied by four non-trogloglomorphic species of *Plusiocampa* (Fig. 26; see [Supplementary File 1](#)), all species with short antennae

with doliform antennomeres plus four simple cupuliform sensilla, and also a small body with short legs and cerci. Four non-troglobitic species are distributed from west to east: *P. (P.) humicola* found in soil habitats in Romania (Sendra *et al.* 2012); *P. (P.) spelaea* described from two caves, one from the north of Hungary (Stach 1929) and another from the south of Slovakia (Paclt 1956); *Plusiocampa (Plusiocampa) corcyraea* Silvestri, 1912, another soil-dwelling species found in the Czech Republic (Paclt 1961, 1979; Rusek 1964) and Slovakia (Paclt 1965); and *Plusiocampa (Plusiocampa) sp.* known from the Franconian Alb caves in this study. Among these non-troglobitic species, *P. (P.) brevi antennata*, found in a single cave in the center of Hungary (Loksa 1960), can also be included (Fig. 26).

Towards the south-west of these non-troglobitic species and surrounded by the Central Alps, in lower mountains regions and consequently less affected by glaciations, there are caves inhabited by troglobitic species of *Plusiocampa* and *Hystrichocampa*. In the Austrian Alps, caves are occupied by *Plusiocampa (Plusiocampa) strouhali* Silvestri, 1933 and its subspecies *P. (P.) strouhali cavicola*; *Plusiocampa (Plusiocampa) caprai* Condé, 1950, which is also known from shallow subterranean habitats, is the only species whose distribution reaches the extreme east of Switzerland (Condé 1950, 1962; Janetschek 1952; Christian *et al.* 1996); and the remarkable species *Plusiocampa (Plusiocampa) hoelzeli* (Neuherz, 1984), described from a single cave in Carinthia (Neuherz 1984). In regions north of the Alps, German caves are occupied by three species: *P. (P.) dobati* in the Swabian Alb, *Plusiocampa (Plusiocampa) sp.* from the Franconian Alb and the new *P. (Penturochaeta) inopinata* subgen. et sp. nov. in a small karst area in the south of the Black Forest. *Plusiocampa (P.) dobati* and the new one represent the only troglobiont diplurans from Germany, not far from the northern-most troglobiont diplurans in Europe.



**Fig. 26.** Distribution of Plusiocampinae (*Plusiocampa* Silvestri, 1912 and *Hystrichocampa* Condé, 1962) in Central Europe; blue indicates karst regions.



And finally, in caves of the Western Central Alps the relict species *Hystrichocampa pelletieri* Condé, 1962 can be found (Fig. 26).

The current phylogeny and the palaeobiogeographical data known for species of Plusiocampinae suggest that the colonization of Europe occurred during the first half of the Cenozoic, probably from Asia (Sendra *et al.* 2004). The Plusiocampinae settled in Central Europe and suffered continuous climatic changes, mainly during the Pleistocene, that could have wiped out different Plusiocampinae species several times. This glaciation frontier is nowadays occupied by four non-troglobitic species of *Plusiocampa* s. str. living in subterranean and edaphic habitats. However, only slightly towards the south troglobitic *Plusiocampa* s. str. species appear. Surprisingly, two species from different genera appear, both considered as relict due to their northeastern distribution in Europe and their unique features: the unexpected *P. (Pentachaetocampa) inopinata* subgen. et sp. nov. and *H. pelletieri*, both troglobites inhabiting the north-east of the Central Alps.

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## **Electronic supplementary material**

### [Supplementary File 1](#)

Table localities of Plusiocampinae from Central Europe.

### [Supplementary File 2](#)

Video of *Plusiocampa* (*Pentachaetocampa*) *inopinata* subgen. et sp. nov. from Schallsinger Höhle, Malsburg-Marzell, Baden-Württemberg; courtesy of Hannes Köble.