

***Whittencampa troglobia*, a new genus and species of troglomorphic Plusiocampinae from China (Diplura: Campodeidae)**

Alberto Sendra^{1*} & Louis Deharveng²

Abstract. *Whittencampa troglobia*, new genus and new species, is a highly troglomorphic Diplura of the Plusiocampinae subfamily described from Lian Hua Dong Cave in southern China. *Whittencampa* belongs to the Plusiocampinae subfamily, which is widely distributed in the European region, but also has four species in China. *Whittencampa* is characterised by its thick setiform pretarsal processes completely covered with long barbs with a tiny hooked tip. *Whittencampa* shares important features with other members of the subfamily, in particular the distribution pattern of notal, femoral and abdominal macrosetae, including the presence of an isolated pair of macrosetae on the eighth urosternite; the last trait characterises the Chinese Plusiocampinae. Scanning electron microscopy reveals new features for this subfamily such as the large subtriangular ending of the neuroglandular setae on the labial palps, the epidermal glands on the labial palps and the bifurcated or double sac ending of the eversible abdominal vesicles. *Whittencampa troglobia* has remarkable troglomorphic traits: the most elongated antennae, and the largest number of antennomeres (56) among Plusiocampinae, and cerci up to 2.3 times longer than the body. It lives with other highly troglomorphic arthropods at the type locality, Lian Hua Dong, and provides additional evidence that southern China is one of the major biodiversity world hotspots for subterranean fauna.

Key words. subterranean fauna, East Asia, *Whittencampa troglobia*, troglomorphy

INTRODUCTION

With the high number of cave-adapted millipedes (Golovatch, 2015), Collembola (Zhang et al., 2016) and Trechinae beetles (Tian et al., 2016) discovered in caves of South China, this region has emerged as a major biodiversity hotspot for most of the large invertebrate groups of the subterranean fauna (Deharveng et al., 2008). Regarding ground beetles and millipedes, the high ratio of troglomorphic taxa in this region is unmatched elsewhere in the world (Deharveng & Bedos, 2018). In contrast, only two species of troglomorphic campodeid diplurans have been described from China, while the soil-dwelling species of the country are rather well-known. Almost a century passed since Silvestri (1931) published the first important contribution to the knowledge of Chinese campodeids with the description of 14 species, of which 10 were new to science. Currently, 23 campodeid species are known in China, including six species from five endemic genera (*Anisuracampa* Xie & Yang, 1990; *Leniwytzmania* Paclt,

1957; *Pseudolibanocampa* Xie & Yang, 1990; *Sinocampa* Chou & Chen, 1981; *Syncampa* Silvestri, 1931). Thirteen of these species belong to Campodeinae, six to Lepidocampinae, and four to Plusiocampinae (Condé, 1993; Ferguson, 1997; Io & Tong, 1980; Xie, 2000; Xie & Yang, 1991). Only the smallest campodeid subfamily, Hemicampinae, which includes four species from tropical and subtropical areas (Paclt, 1957), is not represented in China. The majority of campodeid species of Eastern Asia are soil-dwelling species, and only three have been found in the subterranean environment: *Plusiocampa lipsae* Condé, 1993, a troglomorphic species restricted to a single cave in southern China (Hubei) and two troglomorphic representatives of *Pacificampa* recently described from Japan (Sendra et al., 2018). In addition, an undescribed non-troglomorphic species of *Pacificampa* Chevrizov, 1978 is present in China (Ferguson, 1997), another undescribed species of Plusiocampinae is mentioned by Condé (1993) near Xing'an in Guangxi (China), and new material collected by Josiane Lips is currently under study. Diplura are actually very rare in the caves of the richest region of the Chinese karst (northern Guangxi and southern Guizhou), which has been extensively sampled over the last 10 years. The discovery in 2010 of a large population of a highly troglomorphic new genus and species of diplura in a small cave of Guangxi was unexpected. Both taxa are described in the present paper under the names *Whittencampa*, new genus, and *W. troglobia*, new species.

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MATERIAL AND METHODS

The specimens, stored in ethanol 95%, were washed using distilled water, mounted in a slide with Marc André II solution, and examined under a phase-contrast optical microscope (Leica DMLS). The illustrations were made with a drawing tube, and measurements taken with an ocular micrometer. For measuring body length, the specimens were mounted in toto and measured from the base of the frontal process distal macrochaetae to the abdomen's supra-anal valve. Six specimens coated with palladium-gold were used for SEM (Hitachi S-4100) photography and measurement of the sensilla.

The morphological descriptions and abbreviations follow Condé (1956). We use the term gouge sensilla for the concavo-convexly shaped sensilla on the antennae (Bareth & Condé, 1981). For the position of macrosetae we adopt the abbreviations of Condé (1956): *ma*, medial-anterior; *la*, lateral-anterior; *lp*, lateral-posterior; *post*, posterior.

SYSTEMATICS

Class Hexapoda Blainville, 1816

Order Diplura Börner, 1904

Suborder Rhabdura Cook, 1896

Family Campodeidae Lubbock, 1873

Subfamily Plusiocampinae Paclt, 1957

Whittencampa, new genus

(Figs. 1–3, 5–20)

Type species. *Whittencampa troglobia*, new species.

Etymology. *Whittencampa* is named in honour of Tony Whitten, who passed away in November 2017. Tony was an enthusiastic initiator and efficient facilitator of biospeleological expeditions in China, which allowed the discovery of this new genus, among many other remarkable taxa. Gender: feminine.

Diagnosis. On pronotum 1+1 *ma*, 1+1 *la*, and 2+2 *lp*_{1,3}, on meso- and metanotum 1+1 *ma*, 1+1 *la*, and 2+2 *lp*_{2,3} (Figs. 1–3); two dorsal femoral macrosetae; without tibial macrosetae; unequal claws with lateral-crests (Figs. 12, 13); two thick setiform pretarsal processes completely covered with long barbs (Figs. 12, 13, 15); male and female without glandular field on the posterior part of the first urosternite; first urosternite of male with large subcylindrical appendages with conical ending and carrying long glandular *a*₁ and *a*₂ setae (Figs. 16, 17); female with small subcylindrical appendages with concal ending on first urosternite, with long glandular *a*₁ setae; sac of eversible vesicles with double ending (Figs. 18, 19); 1+1 *post* urotergal macrosetae on III–IV, 4+4 *post* on V–VII, 5+5 *post* on VIII and 7+7 *post* on

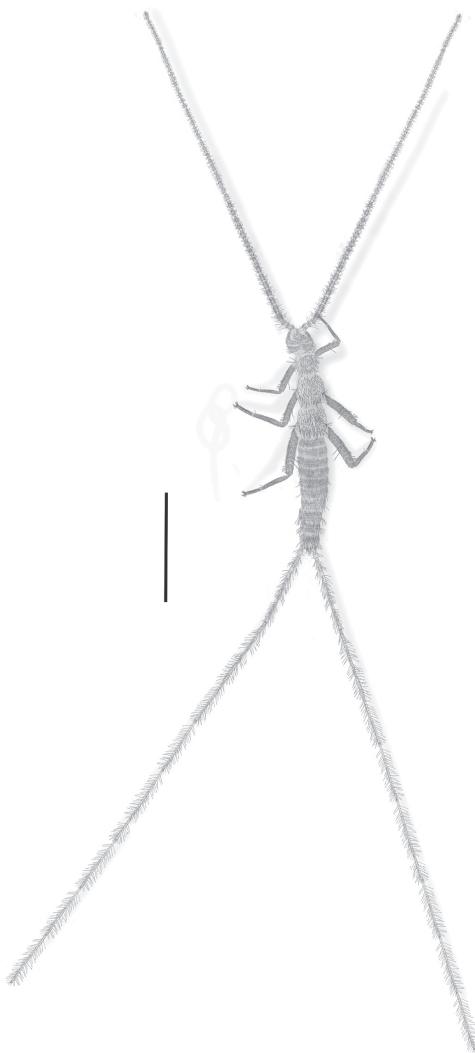


Fig. 1. *Whittencampa troglobia*, new species; habitus. Scale bar = 3 mm.

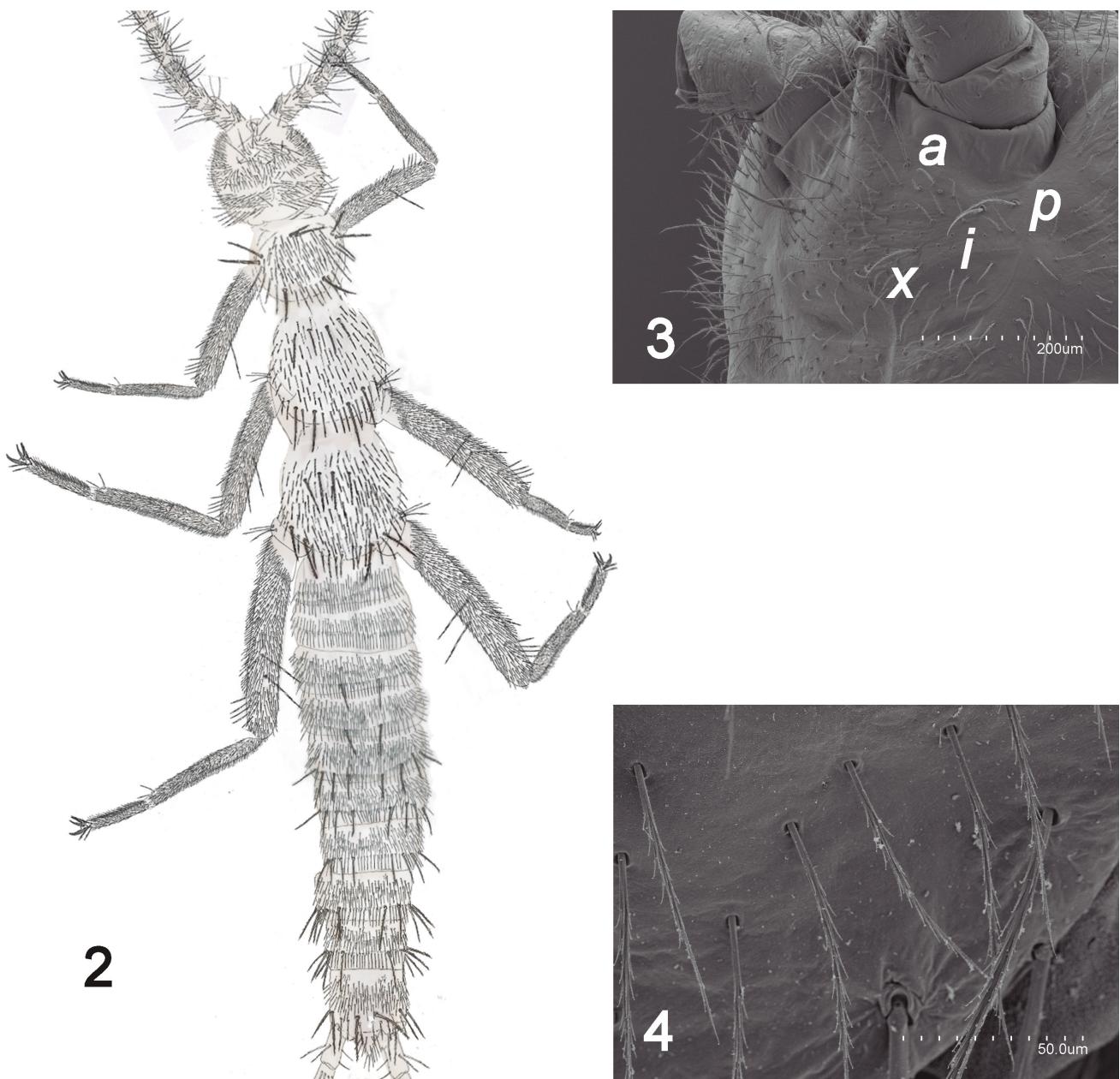
IX; 13+13–10+10 macrosetae on urosternite I, 5+5 on II–VII and 1+1 macrosetae on VIII (Fig. 20); large subtriangular ending of neuroglandular setae and epidermal glands on labial palps (Figs. 5–10, under SEM magnification); dense barbs on macrosetae on abdominal sternites, legs and calcars (Fig. 11); glandular *a*₁ and *a*₂ setae long and slender (Fig. 17).

Whittencampa troglobia, new species

(Figs. 1–20, Table 1)

Etymology. The epithet emphasises the ecology of the new species, strictly linked to subterranean habitats (from the greek trogle (τρόγλη), which means hole).

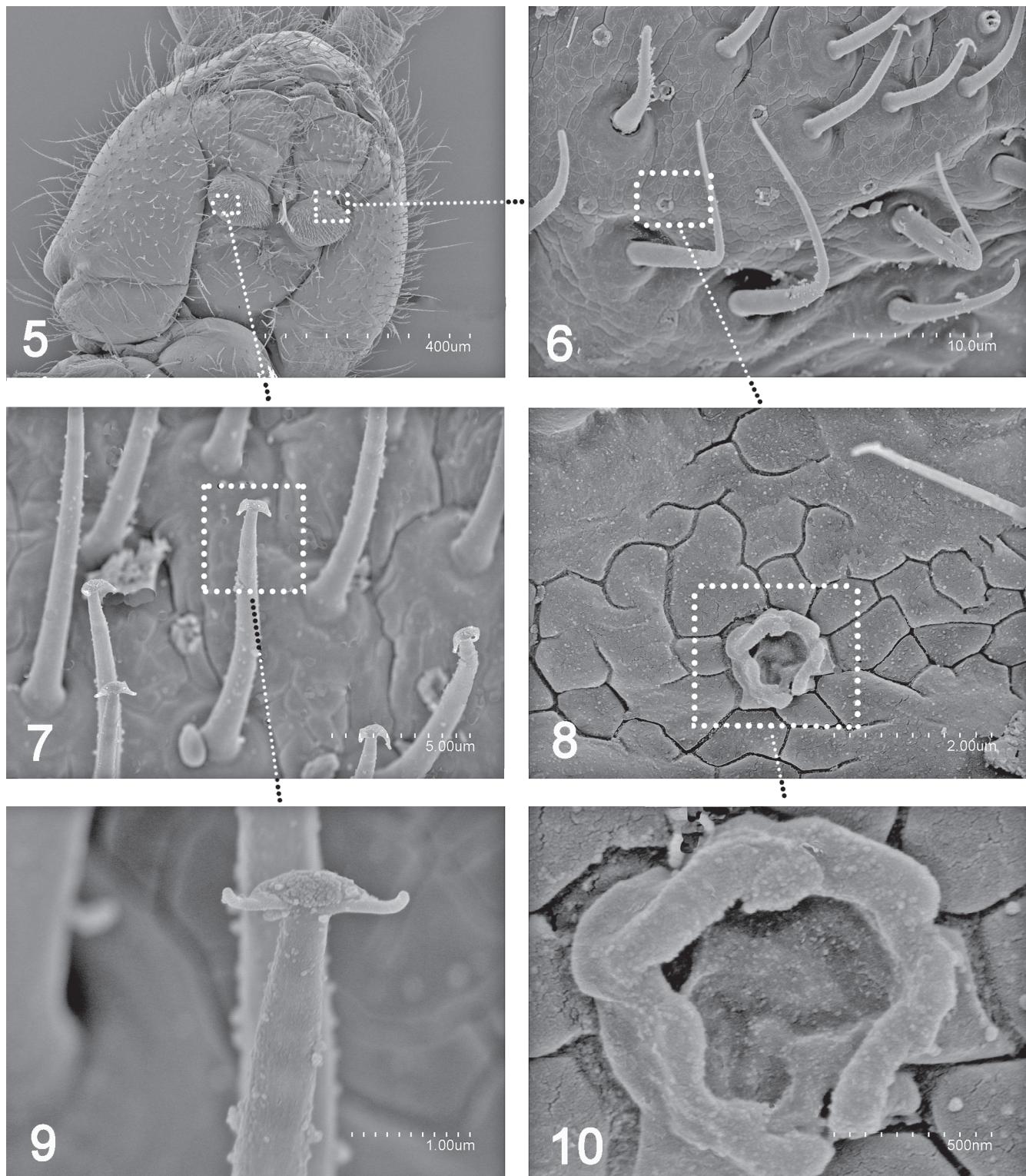
Type material. Holotype on slide: male 1, China: Guangxi: Hechi: Du'an Xian: Liu Zhu village: Lian Hua Dong Cave, 23.99483°N 108.10519°E, alt. 161 m, coll. Louis Deharveng, Anne Bedos and Tian Mingyi, 27 April 2010, by aspirator around baits placed close to a small pool on 25 April 2010, sample code CHIgx10–69. Paratypes on slides: 1 male and 2 females (respective sample codes: male 2, CHIgx10–69;



Figs. 2–4. *Whittencampa troglobia*, new species. 2, Habitus without antennae and cerci (scale bar = 1.5 mm). 3, Head anterior portion with frontal process. Abbreviations: a, anterior; i, intermediate; p, posterior macrosetae of insertion line and x setae. 4, Lateral posterior border of metanotum, right side.

Table 1. *Whittencampa troglobia* metrics (in mm): length of the body, antennomeres, metathoracic leg, cerci, and number of antennomeres and cercal articles.

	body length	antennomeres	length antennae	length metathoracic leg	cercal articles, basal included	length cerci
Male 1, holotype CHigx10.69	6.95	54	9.10	2.80	8 incomplete	9.1 incomplete
Female 2, paratype CHigx10.69	6.30	56	8.50	3.20	—	—
Female 1, paratype CHigx10.69	5.90	—	—	2.65	—	—
Male 2, paratype CHigx10.69	5.20	—	—	2.70	—	—



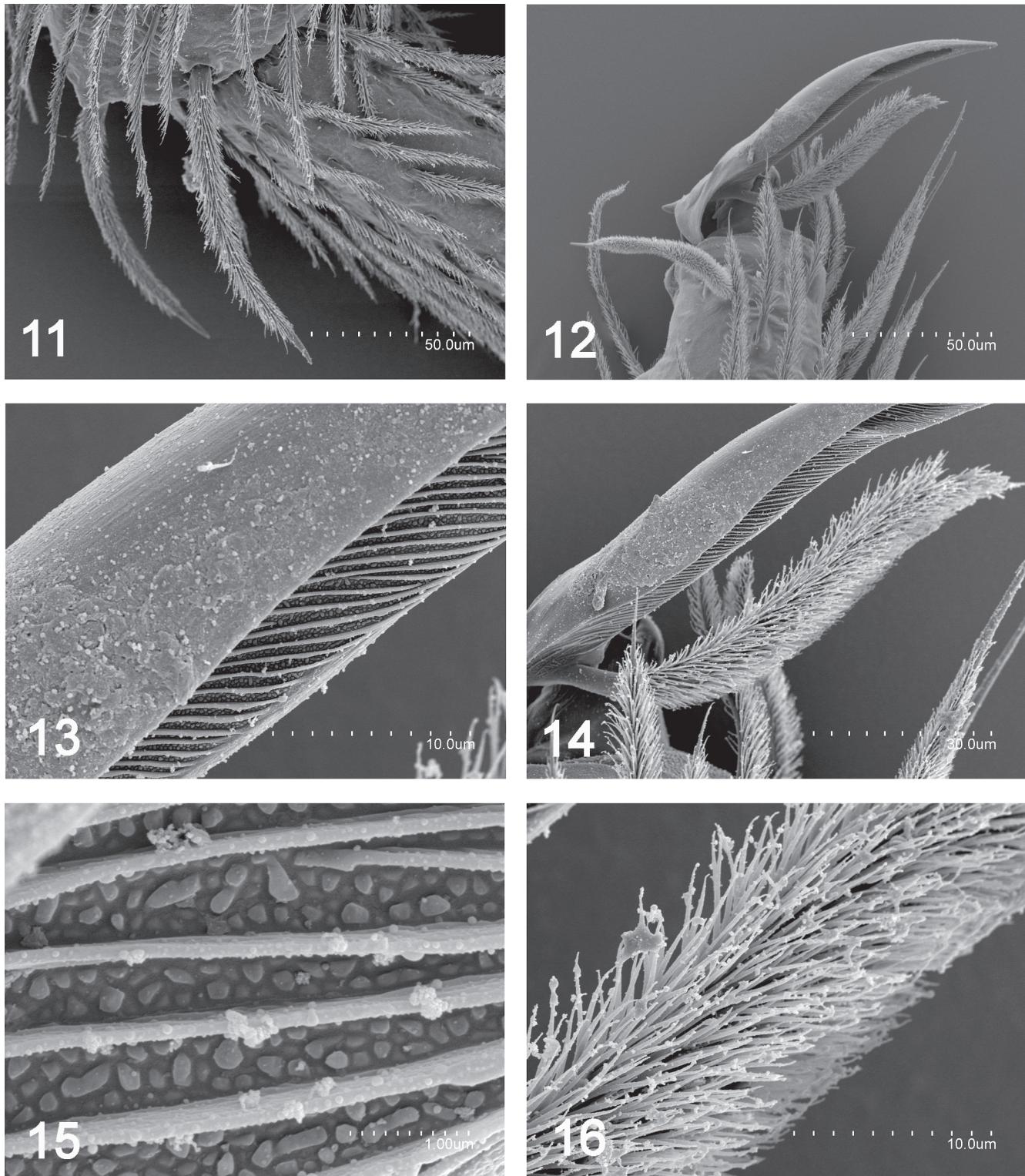
Figs. 5–10. *Whittencampa troglobia*, new species. 5, Head, ventral side. 6, Anterior border of labial palp. 7, Detail of labial palp. 8, Epidermal gland of the labial palp. 9, Ending neuroglandular setae of labial palp. 10, Epidermal gland of labial palp at higher magnification.

female 1, CHIgx10–69; female 2, CHIgx10–69), same data as holotype; 3 specimens in ethanol, labelled CHIgx10–69, same data as holotype; 3 specimens in ethanol, sample CHIgx10–60, same data as holotype, except coll. Louis Deharveng and Li Youbang, 25 April 2010, by aspirator near the small pool of the sample CHIgx10–69.

Type deposition. Holotype male and 1 paratype female on slide, 2 paratypes in alcohol deposited in South China

Agricultural University (SCAU), Guangzhou (China); 1 paratype male on slide, 2 paratypes in alcohol and 2 paratypes coated with palladium-gold deposited in A. Sendra, private dipluran collection (Spain); 1 paratype female on slide, 2 paratypes in alcohol deposited in Muséum national d'Histoire naturelle, Paris (France).

Other material. We report to *Whittencampa troglobia* one female on slide, China: Guangxi: Hechi: Huanjiang Xian:



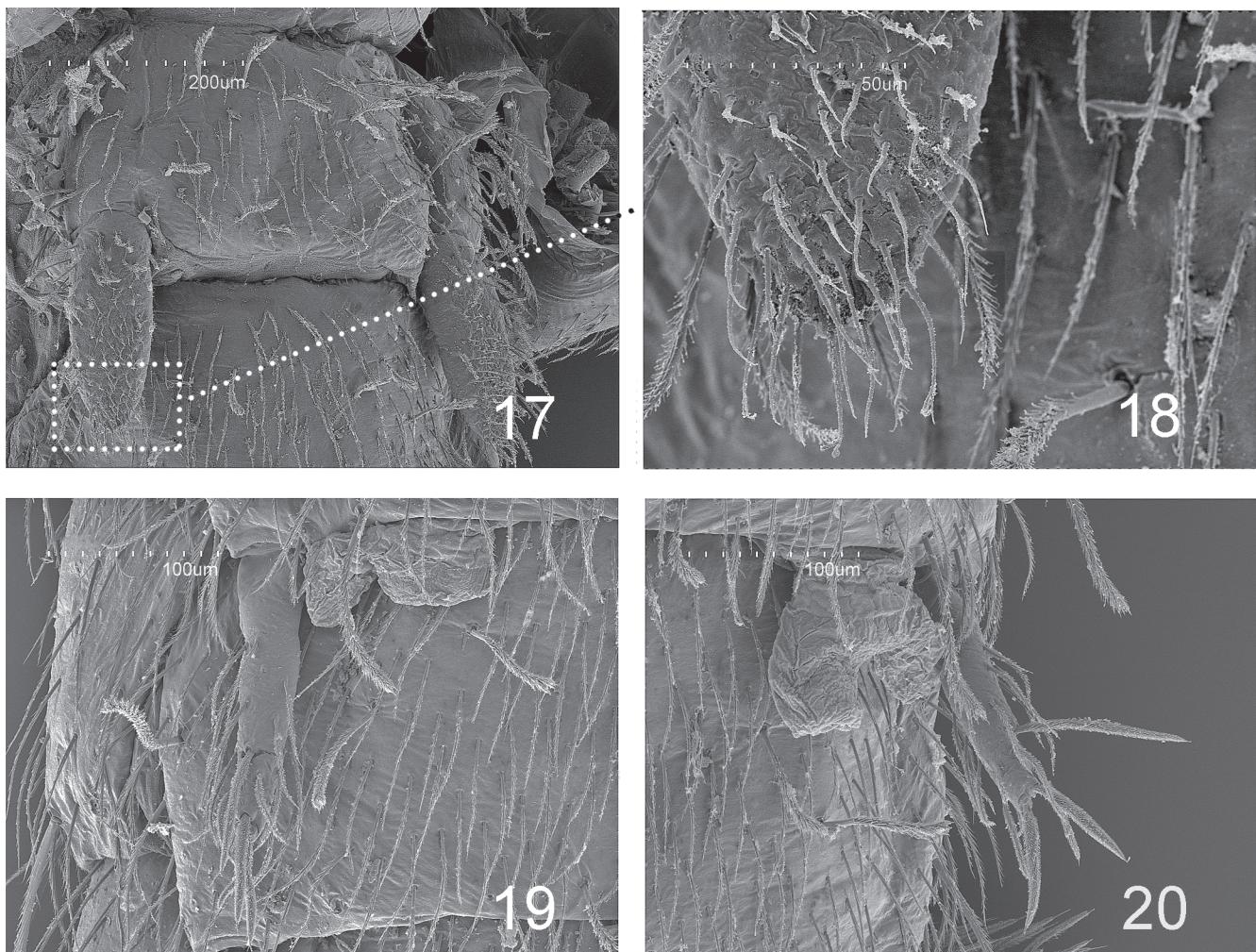
Figs. 11–16. *Whittencampa troglobia*, new species. 11, Distal part of tibia with calcars. 12, Pretarsus. 13, Detail of medial portion of a claw. 14, Detail of pretarsus. 15, Detail of claw, ventral side. 16, Detail of pretarsal lateral process.

Shuiyuan Zhen: Sancai village: Ji Dong also called Shuiku Dong Cave, 24.82935°N 108.091733°E, alt. 280 m, coll. Wei Chun Tao and Louis Deharveng, by aspirator on very humid calcite formation, 9 November 2009, sample code CHIgx09–090.

Description. Body length 5.20 and 6.95 mm (males) and 5.90–6.30 mm (females) (Figs. 1, 2, Table 1). Epicuticle smooth under optical microscope but well reticulated at high

magnifications (Fig. 4); body covered with thin clothing setae with long thin barbs over almost entire length (Fig. 4).

Two intact antennae in adults with 56 (in one female) and 54 (in one male, holotype) antennomeres. Thick sensillum of third antennomere located in ventral position between *d* and *e* macrosetae, similar in size and shape to maxillary and labial setae. Central antennomeres 2.3 times longer than wide, 4.0 for apical antennomere. Large cupuliform organ



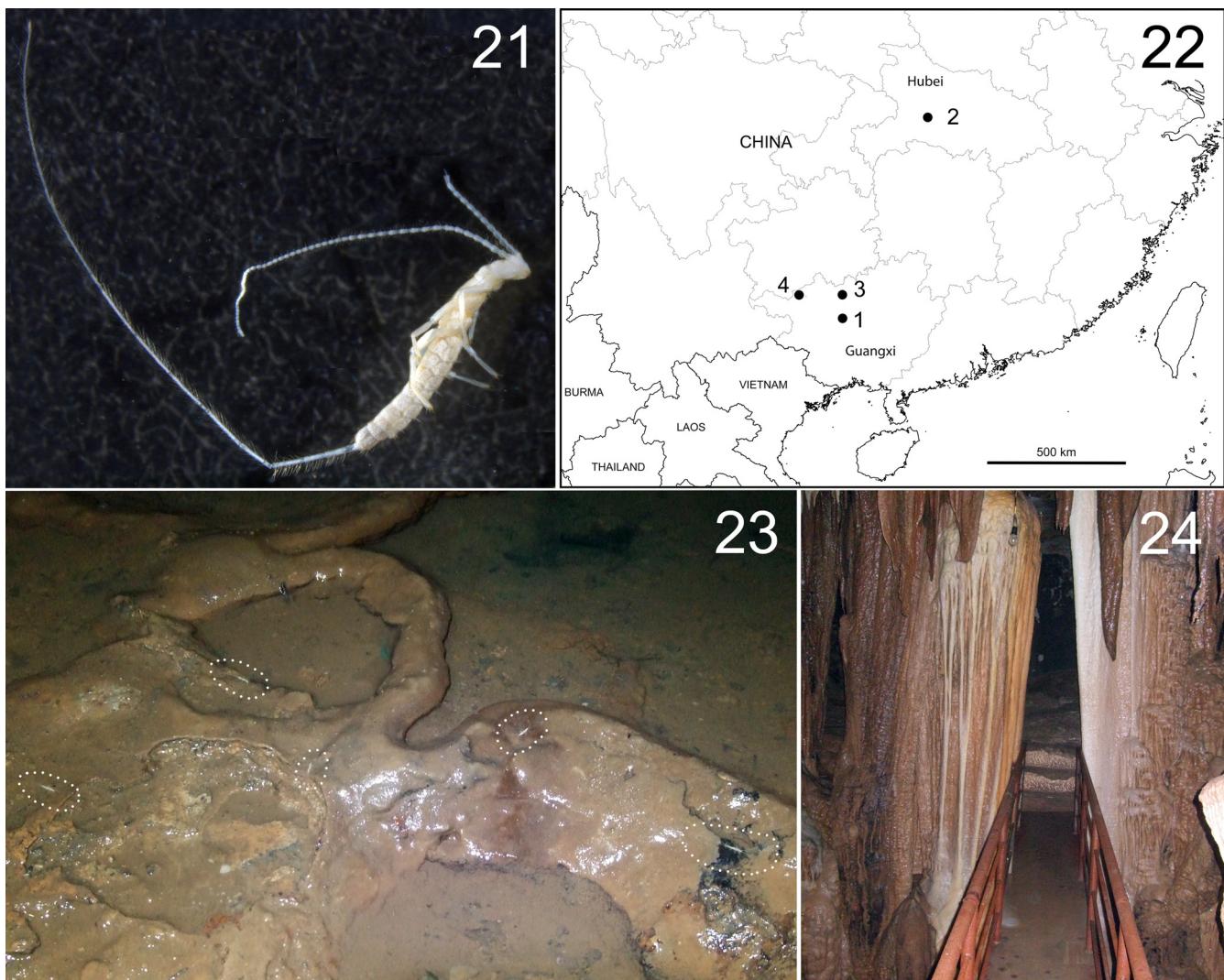
Figs. 17–20. *Whittencampa troglobia*, new species. 17, First urosternite of a male. 18, Apical portion of right appendage on first urosternite of a male. 19, Sixth and seventh urosternites, right side. 20, Sixth and seventh urosternites, left side.

occupying 1/14 of total length of apical antennomere with about 10 complex olfactory chemoreceptors. Thin and long gouge sensilla 35–40 μm long in a single distal whorl of 7–9 sensilla on each medial and distal antennomere. Frontal process slightly developed with an anterior rim and three triangular macrosetae with thin barbs except in distal part (Fig. 3). Three macrosetae along line of insertion of antennomere and x setae similar in shape to frontal macrosetae (Fig. 3). Suboval labial palps (Fig. 5) with latero-external sensillum, two guard setae, up to 8 setae on anterior border and up to 130 neuroglandular setae with a singular ending with two large subtriangular expansions (Figs. 6, 7, 9) (tiny in other campodeids; Bareth & Juberthie-Jupeau, 1977); on its reticulated surface, sparsely distributed tiny epidermal glands (Figs. 8, 10) similar to “rosette” gland of other campodeids (Bareth & Juberthie-Jupeau, 1996).

Distribution of thoracic macrosetae (Fig. 2). Pronotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{1,3}; mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{2,3}; metanotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{2,3}, macrosetae. All macrosetae long, thin, covered with thin barbs almost from their bases; marginal setae much longer than clothing setae, covered with barbs almost from their bases (Fig. 4). Legs elongated, metathoracic legs reaching the end of the abdomen. Femur II–III with 2 dorsal

macrosetae, femur I with one dorsal macroseta (Figs. 1, 2). Tibia without ventral macrosetae (relation femur/tibia about 1). Calcars completely covered with barbs except the extreme end (Fig. 11). Dorsal and lateral tarsal setae completely covered with barbs except the extreme tip. Unequal elbow-like claws (posterior claw 1.35–1.60 longer than anterior one) with an extension at the basal end of the posterior claw; lateral crests well developed, showing marked ridges with pebble-dash between on ventral side and thin stripes on dorsal side (Figs. 12–15). Pretarsal processes short, setiform and completely covered with long barbs with a tiny hook (Figs. 12, 14, 16).

Distribution of abdominal macrosetae on tergites (Figs. 1, 2). 0+0, (0+1) *post*, on II; 1+1 *post*, on III; 1+1 (1+2, 3+2) *post*_{1,2} on IV; 4+4 *post*_{1–4} on V–VII; 5+5 *post*_{1–5} on VIII, 7+7 *post* on IX. All *post* urotergal macrosetae long and covered with barbs almost from their bases. Urosternite I with 13+13–10+10 macrosetae; urosternites II to VII with 5+5 (5+6) macrosetae; urosternite VIII with 1+1 macrosetae; all urosternal macrosetae completely covered with long barbs almost from their bases (Figs. 17–20). Apical setae of styli, subapical and ventromedial setae completely covered with long barbs from their bases (Figs. 19, 20); eversible vesicles with a double sac (Figs. 19, 20).



Figs. 21–24. 21. Habitus of *Whittencampa troglobia*, new species. 22, Distribution map of troglomorphic cave Campodeidae in China: (1) *Whittencampa troglobia*, Lian Hu Dong near Du'an (Guangxi); (2) *Plusiocampa lipsae*, Grotte des Quatre Porches near Yishang (Hubei); (3) *Whittencampa* cf. *troglobia*, Ji Dong near Huanjiang (Guangxi); (4) Campodeidae sp., Yan Wu Dong near Leye (Guangxi). 23, Microhabitat of *W. troglobia* in Lian Hu Dong cave, with specimens around small pools (in white dotted circles). 24, Well decorated passage in Lian Hu Dong cave.

Only one incomplete cercus with eight articles (basal article included) preserved in holotype (Table 1). It is 9.1 mm long, longer than body, covered with 2 to 16 whorls of thin and long macrosetae with tiny barbs on distal third, combined with whorls of smooth thin setae shorter than macrosetae.

Female urosternite I with coniform appendages thinner than male appendages, each bearing up to 23 thin and long glandular a_1 setae in a distal field.

Male urosternite I (Figs. 17–20) with large and enlarged subcylindrical appendages, each bearing up to 24 long glandular a_1 setae and a large field of up to 34 thin and long glandular a_2 setae.

DISCUSSION

Phyletic affinities. Plusiocampinae Paclt, 1957 as a subfamily of Campodeidae is characterised by one

synapomorphic feature, the formula of notal macrosetae (Paclt, 1957). Currently the 78 species of this subfamily are assigned to ten genera (Sendra et al., 2017b), or eleven if the poorly described *Anisuracampa* Xie & Yang, 1990 is valid. They have at least 1+1 *ma*, 1+1 *la* and 2+2 *lp*_{2,3} macrosetae on the pronotum. The pattern of macrosetae in Plusiocampinae is characterised by *la*, *lp* (*post* in urotergites) macrosetae more numerous than in other Campodeidae, and sometimes the presence of *mp*, *mi* and *li* macrosetae on nota and on sterna (Condé, 1956). Eight of ten Plusiocampinae genera share the presence of lateral crests on the pretarsus, an important character also present in *Whittencampa*. Another important feature of Campodeinae is the telotarsal process; although it shows intraspecific variability in *Podocampa* Silvestri, 1932 (Condé, 1959; Condé & Geeraert, 1962; Sendra et al., 1986), it remains a valid taxonomical character in Plusiocampinae. There are two well distinguishable barbed lateral pretarsal processes in *Whittencampa*, new genus. These processes are usually smooth and setiform in *Plusiocampa* Silvestri, 1912, the most

diversified Plusiocampinae genus with five subgenera and 58 species around the Mediterranean Basin (Condé, 1956; Sendra & Weber, 2018) and in the monospecific genus *Condeicampa* Ferguson, 1996, known from a single cave in Nevada, Western USA (Ferguson, 1996). Less frequently, pretarsal processes are laminar and barbed, a morphology known in four monotypic genera from caves: *Patrizicampa* Condé, 1956 (Sardinia), *Vandelicampa* Condé, 1955 (Lebanon), *Simlacampa* Condé, 1956 (India), and *Anisuracampa* (China); as well as in *Cestocampa* Condé, 1956, a genus with two soil-dwelling and two cave-dwelling species from the Mediterranean Basin (Sendra et al., 2012). These laminar barbed or pubescent processes are also observed in some *Plusiocampa* species of uncertain taxonomical position: the soil-dwelling *Plusiocampa* (?) *kashiensis* (Chou & Tong, 1980) and the cave-dwelling *P. lipsae* Condé, 1993, both from China. Exceptionally, the telotarsal process is absent in the three species of *Plutocampa* Chevrevizov, 1978 from caves in the Russian Far-East (Chevrevizov, 1978). Lastly, in the troglobitic species of the monotypic *Hystrichocampa* Condé, 1948 from the Jura range (France), there is a unique pretarsal processes: setiform and thick with a medial section covered with a thin pubescence. The shape of this process in *Hystrichocampa* has some similarities with those of *Whittencampa*, being also a thick setiform process, but completely covered with long barbs with a tiny hooked end.

Noticeable is the similarity of the macrosetae formula of *Whittencampa* with other species of China (*P. kashiensis*, *P. lipsae* and the soil-dwelling species *Plusiocampa* (?) *sinensis* Silvestri, 1931), as well as with the recently described *Turkmenocampa* Sendra & Stoev, 2017 from a single cave in Turkmenistan, Central Asia (Sendra et al., 2017b). All of them have a similar distribution of macrosetae: 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{1,3} with an atypical position of the second pair of macrosetae near to the sagittal plane on pronotum, and up to 1+1 *ma*, 1+1 *la* and 2+2 *lp*_{2,3} on meso and metanotum; only *post* macrosetae on urotergites I–VII with up to 5+5 *post*_{1,3}; up to 13+13 macrosetae on first urosternite, 5+5 on II–VII and 1+1 on VIII; and finally, 1 dorsal femoral macroseta in *P. kashiensis* and *T. mirabilis*, and 2 dorsal femoral macrosetae in *P. sinensis* and *P. lipsae*. This character, also present in *Whittencampa*, supports the inclusion of *P. sinensis* and *P. lipsae* in *Dydimocampa*, a subgenus of *Plusiocampa* (Condé, 1993). In fact, including *P. lipsae*, *P. sinensis* and *P. kashiensis* into *Whittencampa* is a tantalising idea, but the vast sampling gaps for subterranean diplurans in this poorly known East Asian region prevents us from formally endorsing such a taxonomic decision.

Other features of *Whittencampa* are potentially interesting, such as the dense barbulation of the sternal and leg macrosetae and calcars, and the shape of the labial and urosternal sensilla. These characters are poorly known in others campodeids because they require SEM examination, which came into use for taxonomical descriptions only recently (Sendra et al., 2012; 2015; 2016; 2017a; 2017b; 2018; Sendra & Weber, 2018). SEM was previously used for morphological and physiological studies (Bareth &

Juberthie-Jupeau, 1977, 1984, 1996). The bifurcate or double sac ending in the eversible vesicle has been seen for the first time in Campodeidae species.

Whittencampa troglobia, new species, described from Lian Hua Dong Cave in Du'an Xian of Guangxi province, was also collected in Ji Dong (=Shuiku Dong) Cave in Huanjiang Xian (Sancai village) of Guangxi province. The single specimen from Ji Dong Cave matches the description of *W. troglobia* in observed features. It is assigned to this species with some doubt, as the cave where it has been collected is located about 100 km north of Du'an city, in a karst unit not connected with that of Du'an. If this identification is confirmed by additional material, it would constitute an unusually large distribution for a highly troglomorphic species of Chinese cave invertebrates.

Troglomorphy. A large part of Plusiocampinae species, with the exception of several species among the genera *Plusiocampa* and *Cestocampa* and all *Silvestricampa* Condé, 1950, are troglobionts with considerable modifications of traits considered as adaptive to the subterranean environment. A total of 57 species of the 78 Plusiocampinae species live in subterranean environments, i.e., 73% of the subfamily, a very high percentage compared to the 28% troglobionts in the whole Campodeidae family. *Whittencampa troglobia* shows the most highly troglomorphic features among Campodeidae (Figs. 1, 2, Table 1), clearly regressive traits such as the absence of microdenticles on the epicuticle that characterise edaphic species, and several progressive features such as the elongation of appendages. An almost complete cercus of a paratype is 2.3 times longer than the body, and an incomplete cercus of the holotype of *W. troglobia* is 1.7 times longer. These data match the results of a recent study of cercal length in edaphic and troglobiont Campodeidae (Sendra et al., 2017a). In the subfamily Plusiocampinae, there is a significant positive allometric relation between cerci and body length ($r^2 = 0.21$) but in contrast to other campodeid subfamilies it seems that edaphic and troglobiotic Plusiocampinae do not differ in relative cerci length. *Whittencampa troglobia* is also among the Plusiocampinae with the most elongated antennae and the highest number of antennomeres: no other species reaches 56 antennomeres, and only five exceed 50 (*Plusiocampa* (*Plusiocampa*) *gadorensis* Sendra, 2001; *Plusiocampa* (*Stygiocampa*) *bureschi* Silvestri, 1931, *Plusiocampa* (*Stygiocampa*) *remyi* Condé, 1947 and two undescribed species of *Plusiocampa* sensu stricto from caves in the Aegean Islands (Crete and Chios, Greece; Sendra, unpubl.). However, the highest numbers of antennomeres (70–84) in Diplura were found in two other subfamilies, i.e., the cave-dwelling Lepidocampinae *Lepidocampa beltrani* Sendra, 2017 from Réunion Island with 70–84 antennomeres, and the troglobitic Campodeinae *Podocampa simonini* Condé, 1955 from Guipuzcoa (Spain) with 64 antennomeres (Condé, 1956; Sendra et al., 2017a). The elongation of the antennomeres in *W. troglobia* is also remarkable: middle antennomeres are 2.3 times longer than wider and the apical antennomere is 4.0 times longer than wide. The only other troglomorphic

species from China, *P. lipsae* shows less elongation of body and appendages, and has only 43–44 elongated antennomeres.

Like other troglobitic campodeids, *W. troglobia* has long and thin gouge sensilla on the antennomeres and about ten complex olfactory chemoreceptors within the cupuliform organ. SEM inspection was not possible because the prepared specimens had broken antennae.

ECOLOGY

Lian Hua Dong Cave is closed by a door and used as a local tourist attraction, but not intensively. It was explored for about 200 meters. The habitats in the cave include very humid calcite formations with small pools, and clay slopes in lower passages, both apparently devoid of trophic resources. The cave is developed southwest of a small limestone outcrop (about 5 km long for 1 km wide) close to the village of Liu Zhu Cun and separated from the very large karst of Du'an (several hundred km²) by a narrow valley a few km long. The many caves surveyed biologically in the Du'an karst (Tian et al., 2014) and in Guangxi only provided rare and isolated specimens of troglomorphic Campodeidae. On the contrary, *W. troglobia* was abundant in Lian Hua Dong.

Whittencampa troglobia was found during a first visit on rocks and calcite formations of the cave, in oligotrophic and very wet microhabitats of the dark zone. It was found in even greater numbers during a second visit two days after baiting. In this microhabitat, it co-occurred with another highly troglomorphic species, a large undescribed springtail of the genus *Coecobrya* Yosii, 1956. In the same cave but in less wet micro-habitats, the fauna was limited to a large pseudoscorpion of the genus *Megachernes* Beier, 1932, some Psocoptera probably linked to the disturbance brought by tourist visits, and another moderately troglomorphic *Coecobrya* species. Surprisingly, no species of *Dongodytes* Deuve, 1993 was collected in this cave, while these extremely troglomorphic beetles are well diversified in the surrounding karsts of Du'an (Tian et al., 2014).

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