

September 2017

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A striking new genus and species of troglobitic Campodeidae (Diplura) from Central Asia

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Academic editor: O. Moldovan | Received 21 June 2017 | Accepted 3 August 2017 | Published 21 September 2017

<http://zoobank.org/9294E54B-C84C-41DE-8C7B-2313FC24419E>

Citation: Sendra A, Boris Sket B, Stoev P (2017) A striking new genus and species of troglobitic Campodeidae (Diplura) from Central Asia. Subterranean Biology 23: 47–68. <https://doi.org/10.3897/subtbiol.23.14631>

Abstract

A striking new genus and species of Campodeidae (Diplura), *Turkmenocampa mirabilis* Sendra & Stoev, **gen.n.**, **sp.n.**, found in Kaptarhana cave in Eastern Turkmenistan is described. This represents the first record of Diplura from Central Asia and also the first terrestrial troglobiont found in Turkmenistan. The new taxon shows several unique characters such as the lack of crests on the telotarsus, the presence of a side-shoot process and the shape of barbs on the ventral side of the laminar telotarsal processes hitherto unknown in other members of this family. Although *T. mirabilis* is tentatively placed in the subfamily Plusiocampinae, its true affinities remain uncertain. The new finding provides further support to the importance of Kaptarhana as a refuge for a number of endemic invertebrates.

Keywords

Turkmenistan, Koytentag Mountain, *Turkmenocampa mirabilis*, identification key, Plusiocampinae, cave fauna

Introduction

Central Asia is a geographical region which covers an area of approximately 4 million square kilometres stretching from the Caspian Sea in the west to the border of China in the east and from the southern borders of Russia in the north to the northern borders of Iran, Afghanistan and China in the South. This vast geographical area is composed of the territories of five independent countries, the former Soviet republics of Kazakhstan, Uzbekistan, Tajikistan, Kyrgyzstan and Turkmenistan. It is also occasionally referred to as Middle Asia, with other mainly dry and ecologically similar parts of Afghanistan, Pakistan, Mongolia, and at times Xinjiang and Tibet in western China and southern Siberia in eastern Russia are also included in this definition. The complex political history and highly diverse geography and diverse landscape, the latter including high mountains (Tian Shan), deserts (Karakum, Kyzylkum, Taklamakan) and steppes, as well as the comparatively low level of economic development and transport networks, significantly hampered the zoological explorations in the area.

Diplura is one of the four classes that comprise the subphylum Hexapoda. According to Koch (2009) and Zhang (2013), at present it includes 976 extant and 1 fossil species. Despite their worldwide distribution, diplurans are virtually unknown from Central Asia. A few species have hitherto been recorded from the adjacent to Central Asian countries, but most records refer to species found distant from the region or even in other zoogeographical realms. The Japygidae genus *Kohjapyx*, with three species, including the troglobiotic species *Kohjapyx lindbergi* Pagés, 1962 from a cave near Kabul have been described from Afghanistan (Pagés 1953, 1962; Paclt 1958). In a recent study on the Campodeidae of North Iran, Azadbakhsh and Nozari (2016) recorded the soil-dwelling species *Campodea* (*Dicampa*) *sprovierii* Silvestri, 1932 and *Campodea* (*Campodea*) *fragilis* Meinert, 1865 from the provinces Mazandaran and Alburz. Even in other, better explored areas in Asia, the knowledge is rather poor. For instance, the cave fauna of mainland Asia is known to harbour only seven species (Bareth and Condé 1972; Condé 1956b, 1993; Chevrizov 1978; Ferguson 1997). *Simlacampa clayae* Condé, 1956 is known from three caves in Punjab, India (Condé 1956b). *Plusiocampa* (*Didymocampa*) *lipsae* Condé, 1993 is recorded from several caves in the south of China (Condé 1993). From caves in the Russian Far East, Primorskij kraj (or Primor'e) Chevrizov (1978) described two genera – *Plutocampa* and *Pacificampa*, with respectively 3 and 2 troglomorphic species. Furthermore, Ferguson (1997) reported a new species of *Pacificampa* (Diplura: Campodeidae) from a cave in China. Given the general shortage of dipluran material and the low rate of sampling in almost all parts of Asia, many new species of subterranean diplurans are expected to be found in the near future, especially when large collections such as that of Dr. Louis Deharverg (MNHN) from Chinese caves have been studied.

In this paper, a remarkable new genus and species of the dipluran family Campodeidae, found from Kaptarhana cave in South East Turkmenistan, is described. This represents the first formal record of the subclass from the entire Central Asia and also the first terrestrial trogllobiont found in Turkmenistan.

The true affinities of the new taxon remain uncertain as it departs significantly from all the currently established campodeid genera. It is tentatively placed in subfamily Plusiocampinae but this may change in future when combined morphological and molecular phylogenetic analysis of Diplura has been undertaken.

The exploration of Kaptarhana cave begun at the end of the summer of 1963 when a group of speleologists from Moscow led by V. Andreyev visited the cave and collected some foraminifers, isopods and harpacticoids from the lake. In November 1963, intrigued by these interesting findings, the cave was visited by the leading (at that time) Soviet biospeleologist S. Ljovuschkin (see Birstein and Ljovuschkin 1965). Ljovuschkin later (1969) published short report on the fauna of the cave mentioning the barklice *Psyllipsocus ramburii* Selys-Longchamps, 1872 (Insecta: Psocodea) an undetermined species of Pseudoscorpiones and Oniscoidea. Furthermore, in 1972 Starobogatov (1972) described the cave hydrobiid gastropod *Pseudocaspia ljovuschkini*. Until the study of Pavel Stoev and Boris Sket in 2015, almost no other biospeleological work was carried out in the cave. The new sampling revealed that the cave is also inhabited by spiders, springtails, parasitic flies and cryptophagid beetles. There is also a large colony of horseshoe bats, *Rhinolophus bocharicus*.

Material and methods

Sampling methods

The material was collected by Pavel Stoev and Boris Sket from the cave Kaptarhana (see details below) in the course of a rapid speleobiological assessment of the caves of Koytendag State Nature Reserve of Turkmenistan undertaken in 2015. The mission was carried out under the Memorandum of Understanding between the State Committee on Environment Protection and Land Resources of Turkmenistan and the Royal Society for the Protection of Birds to protect birds and other biodiversity in Turkmenistan. For sampling, pitfall traps, with Ethylene glycol and smelly cheese as bait, were set along the main gallery of the cave, mostly in humid places, in close proximity to large boulders and guano heaps. Pitfall traps were exposed for several days in the last week of May. Subsequently, all the captured animals were transferred to a container with 95% alcohol solution and properly labelled. Despite the fact that both collectors spent 7–8 hours altogether in the cave, no specimens were found by visual observations, all specimens being caught by pitfall trapping. The cave was very spacious, with large boulders and passages at different levels, making the process difficult for the collection and discovery of cryptic animals (such as diplurans) by methods other than pitfall trapping.

Material processing and identification

Specimens were washed in distilled water and inserted between slides and glass coverslips to be examined under a phase-contrast optical microscope (Leica DMLS) us-

ing Marc André II solution. The illustrations were made with a drawing tube and the measurements were taken with an ocular micrometer. For measuring the body length, 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 measurement of the sensilla and for examination of some minute anatomical parts, six specimens were coated with palladium-gold and studied in a Hitachi S-4100 scanning electron microscope.

The morphological descriptions and abbreviations used in this paper follow Condé (1956a). Although its function is still unknown, the term ‘gouge sensilla’ is used for the concavo-convexly shaped sensilla located on the antennae (as described by Bareth and Condé 1981). For the position of macrosetae on the occiput, *ma*, *la* and *lp*, Wygodzinsky (1944) was followed.

Abbreviations

NMNHS National Museum of Natural History, Sofia.

For notal macrosetae: *ma*, medial-anterior, *la*, lateral-anterior and *lp*, lateral-posterior; for urotergal macrosetae: *post*: posterior.

Results

Taxonomy

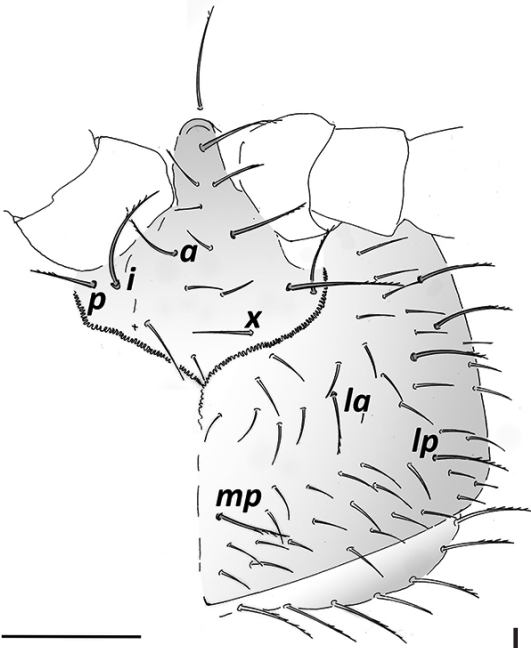
Turkmenocampa Sendra & Stoev, gen. n.

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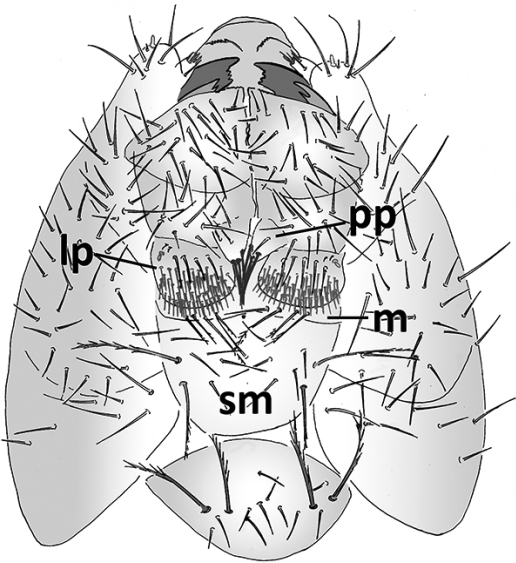
Type species. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n.

Etymology. *Turkmenocampa* is a composite name comprising “Turkmeno”-referring to the type locality and the suffix ‘-campa’ traditionally used in Campodeidae taxonomy. Gender: feminine.

Diagnosis. Head with a frontal process without tuberculate setae (Fig. 1); mentum and submentum short (Fig. 2). Cupuliform organ shallow, having three types, large oval, smaller oval and tree shaped, olfactory chemoreceptors (Figs 8–12). Thorax with 4+4 (*ma*, *la*, *lp*_{2,3}) macrosetae on pronotum and mesonotum, 3+3 (*ma*, *lp*_{2,3}) on metanotum (Fig. 3). Femur having one dorsal macroseta; tibia with one ventral macroseta. Claws simple, with a medial external expansion with laminar lateral processes covered with long barbs on the ventral side (Figs 17–18). Abdomen entirely lacking lateral-anterior macrosetae, with 1+1 to 4+4 *post* macrosetae on I to VII tergites (Fig. 4). Sternal macrosetae: I sternite: 7+7; II–VII sternites: 4+4 (Fig. 7), VIII sternite: 1+1. Sexual secondary characters almost absent; *a*₁ glandular setae present in both sexes in the distal part of subcylindrical appendage (Figs 5–6).

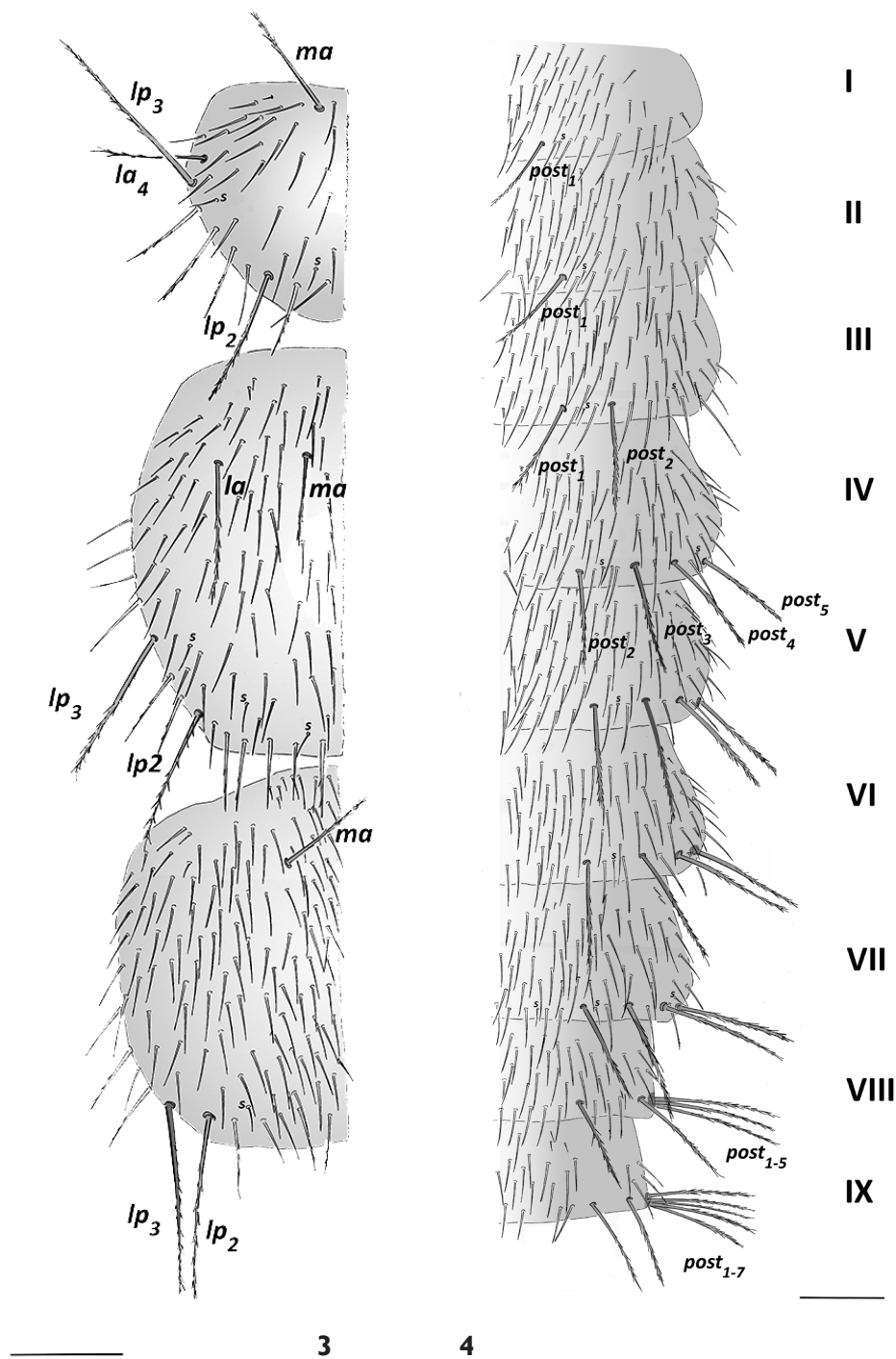


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Figures 1–2. *Turkenocampa mirabilis* Sendra & Stoev, sp. n. **1** Dorsal view of the frontal process and right side of the head, holotype **2** Head, ventral view, E23 female paratype. Scale bars: 0.2 mm.



Figures 3–4. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n. **3** Pro-, meso- and metanotum, left side, holotype **4** Urotergites I-IX, right side, holotype. Scale bars: 0.2 mm

A key to the genera of Plusiocampinae Paclt, 1957

- 1(2) Claws with lateral crests3
- 2(1) Claws without lateral crests 13
- 3(4) Telotarsal processes setiform 5
- 4(3) Telotarsal processes lacking or laminar barbed 9
- 5(6) Telotarsal processes pubescent *Hystrichocampa* Condé, 1948
- 6(5) Telotarsal process smooth 7
- 7(8) 4+4 macrosetae on II-VII urosternites, 1+1 macrosetae on VIII urosternite ..
..... *Condeicampa* Ferguson, 1996 and *Plusiocampa* (*Dydymocampa*)
sinensis Silvestri, 1931
- 8(7) Not less than 5+5 macrosetae on II-VII urosternites and 2+2 macrosetae on
VIII urosternite *Plusiocampa* Silvestri, 1912
- 9(10) Telotarsal processes lacking *Plutocampa* Chevrizov, 1978
- 10(10) Telotarsal processes laminar barbed 11
- 11(12) Telotarsal processes broad
..... *Cestocampa* Condé, 1956; *Vandelicampa* Condé, 1955; *Patrizicam-*
pa Condé, 1956 and *Plusiocampa* (*Didymocampa*) *lipsae* Condé, 1993
- 12(11) Telotarsal processes narrow *Simlacampa* Condé, 1956
- 13(14) Simple claws, without telotarsal processes, medial-intermediate and lateral-in-
termediate meso- and metanotal macrosetae *Silvestricampa* Condé, 1950
- 14(13) Claws with a side-shoot sharp, laminar and telotarsal processes, without me-
dial posterior meso- and metanotal macrosetae *Turkmenocampa* gen. n.

Turkmenocampa mirabilis Sendra & Stoev, sp. n.

<http://zoobank.org/DD725FD0-83CD-45F6-994C-A4C103CB9592>

Material examined. Holotype: female, 5.8 mm, Turkmenistan, Lebap Province, Koytendag District, v. Gurshun Magdanly (=Svintsovyi rudnik), cave Kaptarhana, N37°49' E66°24', alt. 550–600 m asl, numerous gypsum boulders, guano heaps, cave lakes, pitfall traps with a bait, 24–30.V.2015, P. Stoev, B. Sket leg. preserved in slide with Marc André II, deposited in the NMNH labelled E01. **Paratypes:** 16 females and 11 males, same locality, date and collectors, preserved in slide with Marc André II, deposited in the NMNHS (labelled E02 to E21) and in A. Sendra personal collection (labelled E22 to E28).

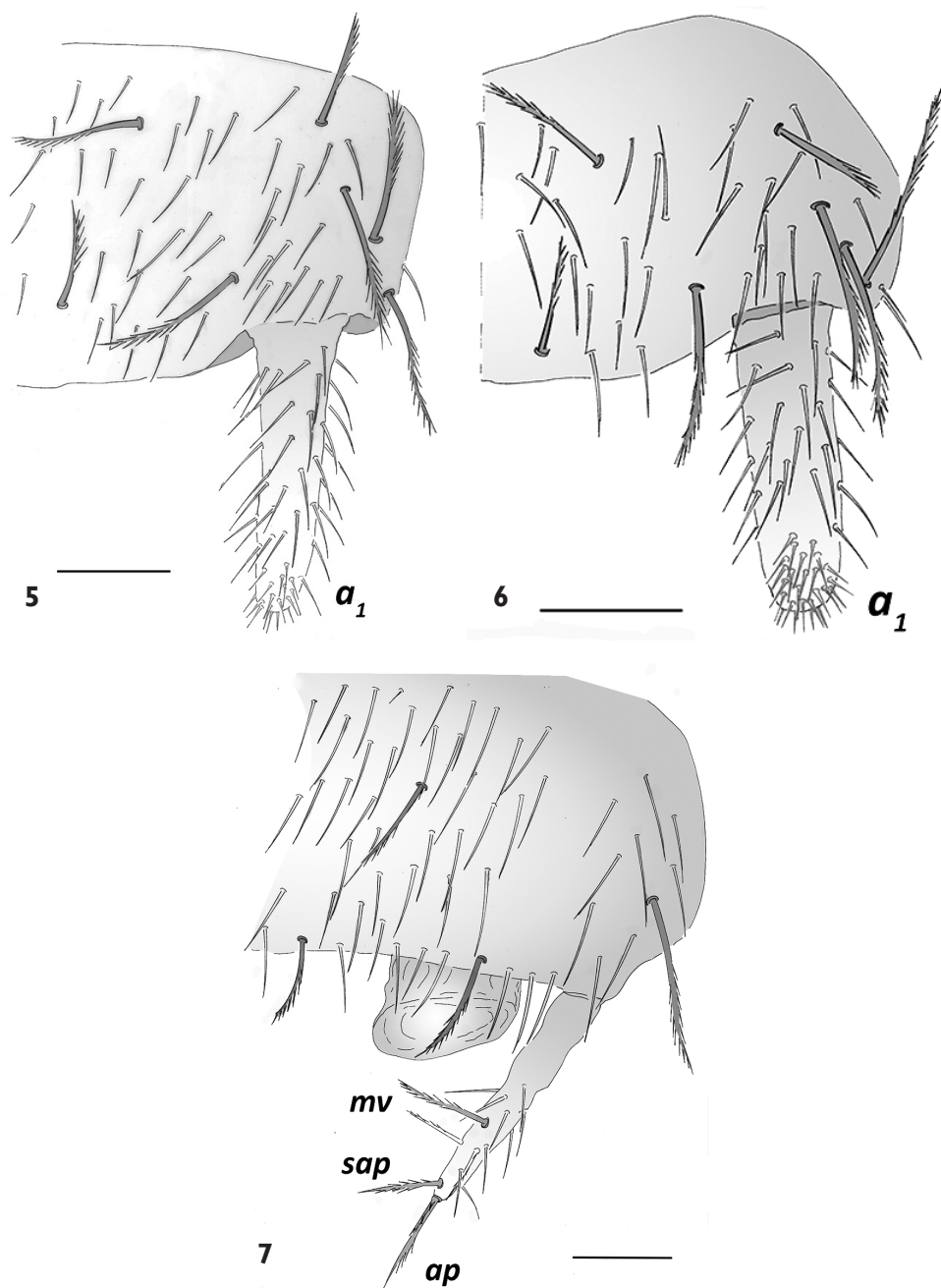
Etymology. ‘*mirabilis*’ is a Latin adjective meaning “unusual, amazing, wonderful, remarkable”. The specific epithet refers to the unique micro-sensilla in the cupuliform organ which resemble sponges and micro-corals.

Description. Body: length of males 3.2–4.9 mm, females 3.5–6.2 mm (Table 1). Epicuticle smooth; body with long, thin and smooth clothing setae (Figs 3–4) which are much shorter and less numerous on the head (Fig. 1); micro-sensilla present on the labial palps and appendages of the first urosternite (Figs 16 and 19).

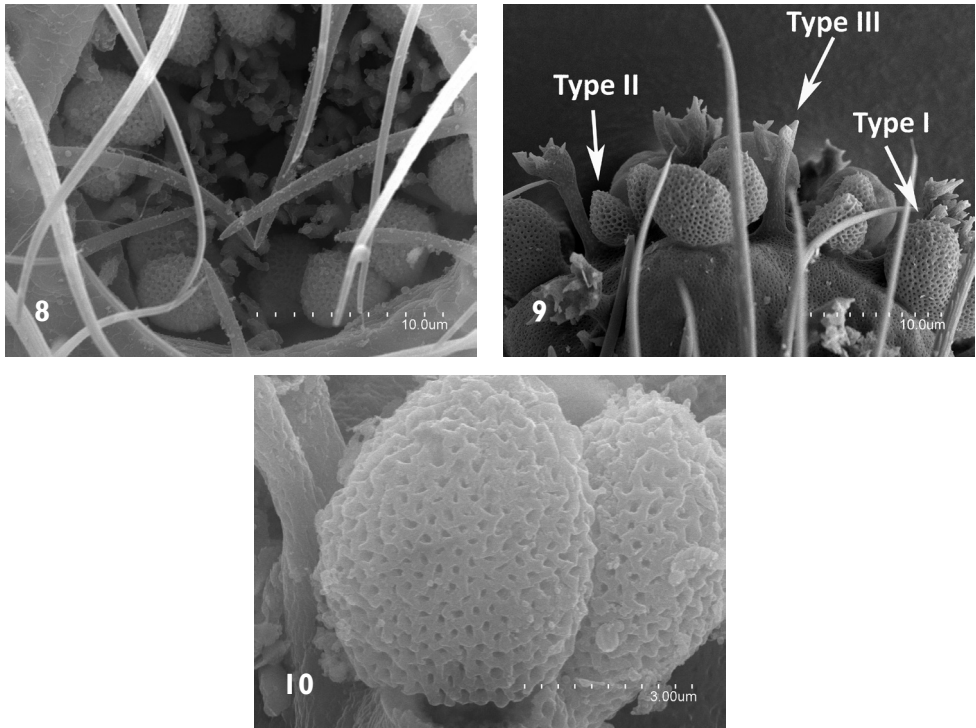
Table 1. Body measurements of *Turkmenocampa mirabilis*. (-) Absent or difficult for observation or measurement trait.

Specimen #	Sex	Length (mm)	Length of antennae (mm)	Number of antennomeres	Leg III length (mm)	Number of <i>aI</i> glandular setae on one appendage
E22, paratype	♂	3.2	1.9	33	1.4	-
E12, paratype	♂	3.3	1.8	33	1.3	8
E28, paratype	♂	3.4	-	-	1.7	-
E17, paratype	♀	3.5	-	-	1.6	9
E24, paratype	♀	3.7	-	-	1.7	-
E08, paratype	♀	3.8	-	-	1.8	12
E27, paratype	♂	4.0	-	-	2.3	23
E11, paratype	♂	4.3	-	-	2.2	-
E14, paratype	♂	4.3	-	-	2.1	26
E07, paratype	♂	4.5	-	-	2.0	22
E18, paratype	♂	4.7	-	-	2.4	29
E20, paratype	♀	4.7	3.1	33	2.3	13
E16, paratype	♂	4.8	3.0	31	2.3	-
E13, paratype	♀	4.9	2.6	32	2.0	15
E03, paratype	♂	4.9	-	-	2.2	25
E19, paratype	♀	4.95	-	-	2.5	-
E15, paratype	♀	5.0	-	-	2.7	20
E06, paratype	♀	5.1	-	-	2.3	20
E04, paratype	♀	5.2	-	-	2.5	15
E21, paratype	♀	5.2	3.6	30	2.3	-
E26, paratype	♀	5.2	-	-	2.4	15
E23, paratype	♀	5.3	-	-	2.3	10
E10, paratype	♀	5.6	3.1	31	2.5	21
E01, holotype	♀	5.8	-	-	2.7	17
E25, paratype	♀	5.8	4.2	32	2.6	19
E09, paratype	♀	5.9	3.9	33	2.6	-
E02, paratype	♀	6.2	4.0	33	2.6	18

Head: Antennae shorter than body; composed of 30–33 antennomeres (Table 1). Sensillum of the third antennomere subcylindrical, slightly swollen, similar in size and shape to the maxilla and labial palps (Fig. 2); sensillum located in ventral position between macrosetae *d* and *e*, middle antennomeres in adults 2–2.5 times longer than wide. Gouge sensilla (Fig. 13) 18–26 µm long, with their outside surface lightly grooved and with a pointed apex. Gouge sensilla distributed in a single distal whorl of 6–10 sensilla on each medial and distal antennomere. Last antennomere is twice the size of the penultimate, with a noticeable shallow cupuliform organ having a wide opening of 25 µm of diameter measuring 1/12th of its length (Fig. 8). Cupuliform organ tightly packed with two types of unknown sensilla and having three different types of olfactory chemoreceptors all covered with pores: about fourteen type I, two oviform structures of 7–8 µm long; about six type II, two oviform structures of 3.5–4 µm long and about



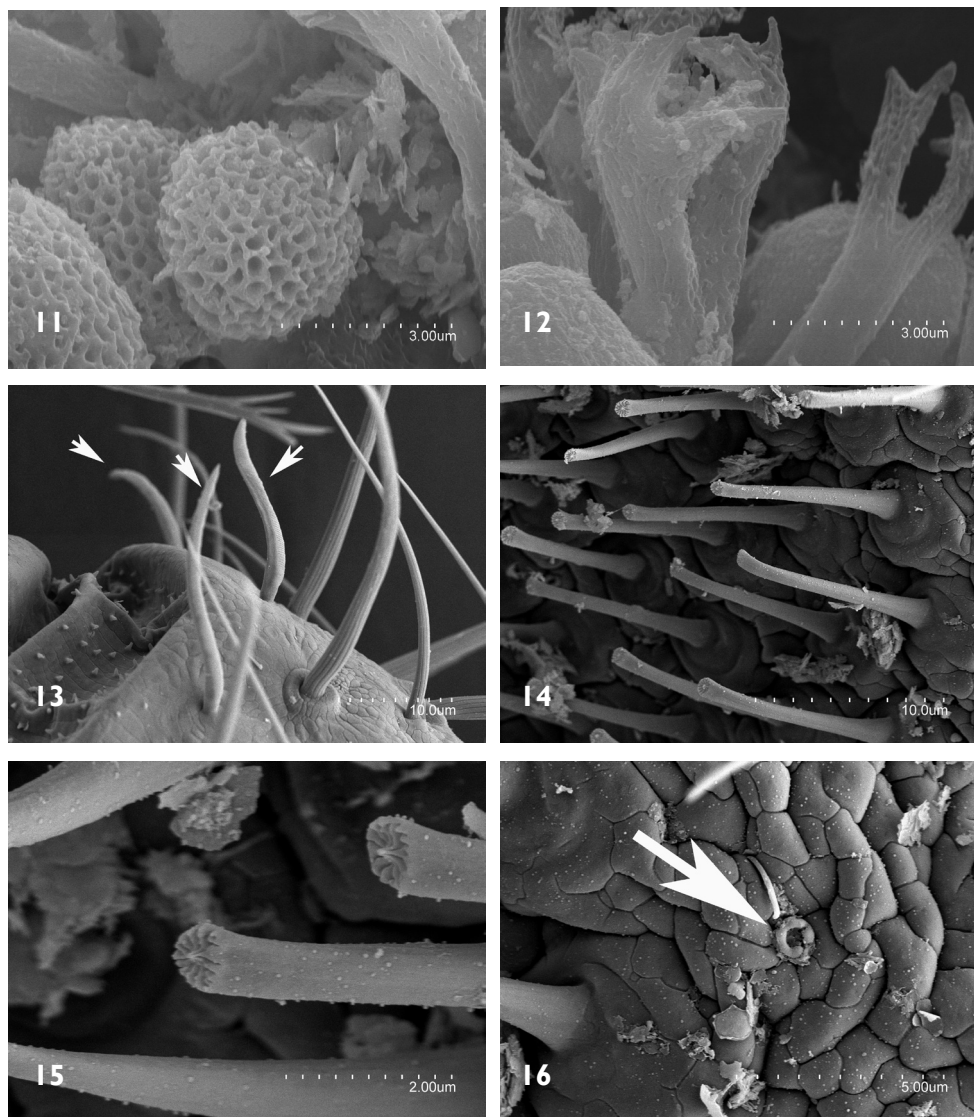
Figures 5–7. *Turkenocampa mirabilis* Sendra & Stoev, sp. n. **5** Urosternite I of male, left side, E03 male paratype **6** Urosternite I of female, left side, E02 female paratype; **7** Urosternite VII, left side, E02 female paratype. Abbreviations: apical (*ap*), subapical (*sap*) and medio-ventral (*mv*) setae, glandular *a1*-setae. Scale bars: 0.1 mm.



Figures 8–10. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n. **8** Cupuliform organ of the latest antennomere in an adult specimen **9** Cupuliform organ of the latest antennomere in an adult specimen with all olfactory chemoreceptors visible after an artificial outpouching of the organ presumably produced by the ethylene glycol in the trap (type I large oval, type II, small oval and type III, tree olfactory chemoreceptors) **10** Type I large oval olfactory chemoreceptor in the cupuliform organ.

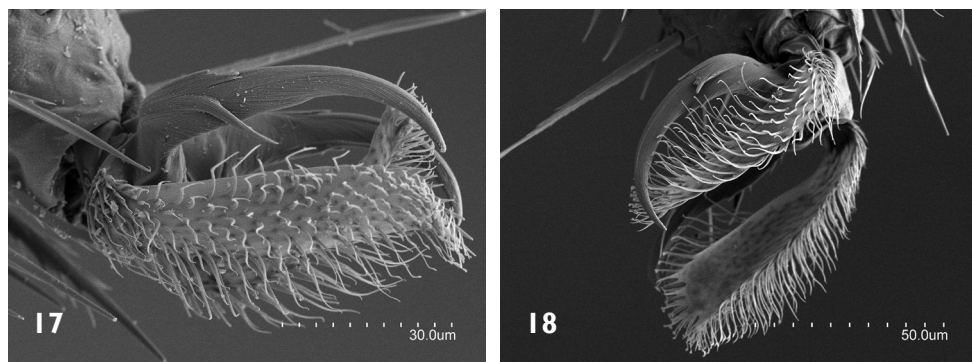
twenty type III, tree-shaped structures with branches that overhang the types I and II sensilla (Figs 8–12). Frontal process slightly developed (Fig. 1), with one long apical and two short posterior setae with 1–2 tiny distal barbs. Three macrosetae along the line of the insertion of antennae and x setae, in female holotype length ratios: *anterior* = 0.7, *posterior* = 0.6, *intermediate* = 1, x = 0.5; all macrosetae with a few thin barbs along the distal one-third. Occiput of the dorsal head with 6+6 macrosetae, including 3+3 *ma*, *la*, *lp* macrosetae (Fig. 1). Labium (Fig. 2) with a short submentum (**sm**) with 2+2 long macrosetae barbed along the distal half and shorter mentum (**m**) with 4+4 short macrosetae with a few distal barbs. Typical labial palps (**lp**) and palpiform processes (**pp**). Labial palps covered by more than one hundred neuroglandular setae ending truncated with radial micro-crests on the top (Figs 14–15); nearby are observed a few micro-sensilla (Fig. 16) adjacent to the row of a few banal setae and the labial sensillum.

Thorax: Slightly elongated thoracic nota. Distribution of macrosetae (Fig. 3): pronotum and mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{2,3} and metanotum with 1+1 *ma*, 2+2 *lp*_{2,3}. All macrosetae long, with thin barbs along the distal half to four-fifths; marginal setae longer than clothing setae and with a few distal barbs. Legs slightly



Figures 11–16. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n.: **11** Type II small oval olfactory chemoreceptor in the cupuliform organ **12** Type III tree olfactory chemoreceptor in the cupuliform organ **13** Gouge sensilla on the lateral external side of a medial antennomere in an adult specimen (indicated with arrows) **14** Neuroglandular setae of the labial palp in an adult specimen **15** Tips of some neuroglandular setae on the labial palp in an adult specimen **16** Microsensillum on the labial palp in an adult specimen (indicated with arrows).

elongated, metathoracic legs reaching abdominal segment VIII. Femur II–III with one long dorsal macrosetae barbed along four-fifths. One short ventral macrosetae on tibia I–III well barbed almost from its base. Calcars well barbed from base to tip with long barbs. Tarsus with two ventral rows of setae covered by long thin barbs



Figures 17–18. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n., telotarsal process of the metathoracic leg in an adult specimen: **17** Lateral view **18** Lateroventral view.

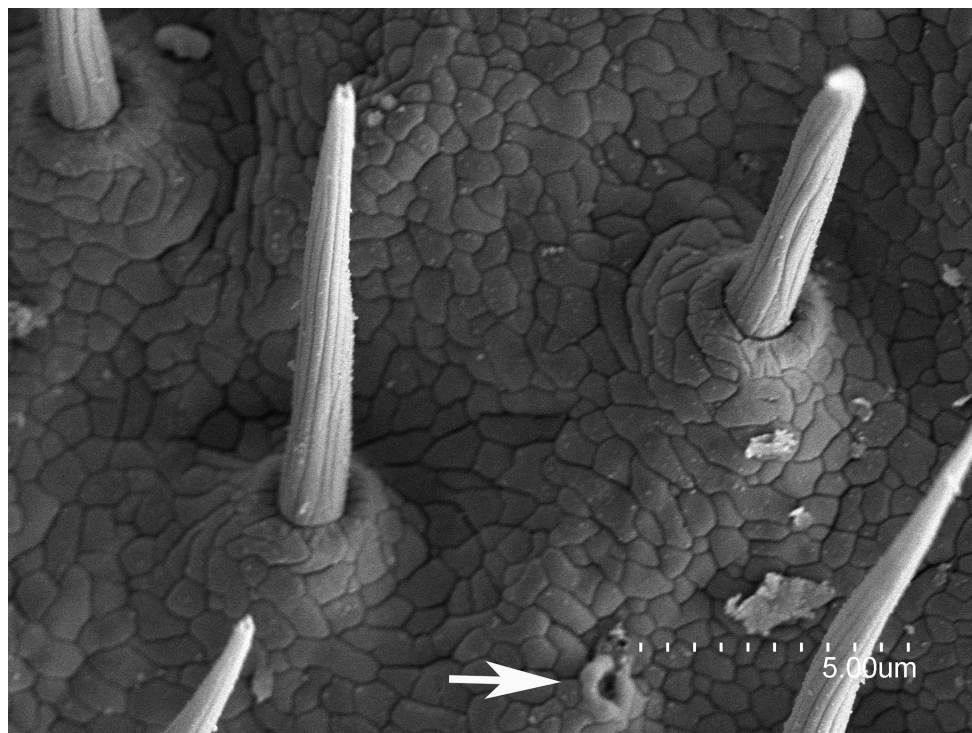


Figure 19. *Turkmenocampa mirabilis* Sendra & Stoev, sp. n.: Apex appendage of the first urosternite in an adult female showing some a_1 glandular setae.

on the medial portion. Distal tarsus with smooth subapical setae or with a few thin distal barbs. Subequal claws curved in the medial distal comprising a thick base and a remarkable sharp-ending external expansion or side-shoot, the whole body of the claws with fine longitudinal and semi-transversal striate laminar telotarsal processes and only ventral face covered with long barbs with tip ending in a hook-shape along

the laminar processes and with a flat expansion-shape at the end of the laminar processes (Figs 17–18).

Abdomen: Abdominal distribution of macrosetae (Fig. 4): 1+1 $post_1$ macrosetae on tergites I–II, 2+2 $post_{1,2}$ on III, 4+4 $post_{2-5}$ on IV–VII, 5+5 $post$ on VIII and 7+7 $post$ IX, all long and barbed on the distal two-thirds. Urosternite I with 7+7 (7+8 in three paratypes) well developed macrosetae barbed on the distal two-thirds; II–VII with 4+4; VIII with 1+1 (2+1 in paratype female 5 mm, E05) (Figs 5–7). Styli with a long basal tooth with barbs, apical, subapical and medio-ventral setae well barbed (Fig. 7). One complete cerci isolated: 6.7 mm long, with 9 elongated articles plus base, each article progressively longer and covered with long macrosetae with thin tiny barbs along the distal one-third.

Sexual secondary features: Male urosternite I (Fig. 5) with two subcylindrical appendages, each bearing 8 $a1$ glandular setae in paratype E12 (a young male, 3.3 mm long) and up to 29 $a1$ in paratype E18 (adult male, 4.7 mm long) (Table 1). Female urosternite I (Fig. 6) with two subcylindrical appendages thinner than in the males, each bearing 9 to 20 $a1$ glandular setae (see Table 1 and Fig. 19)

Description of Kaptarhana cave

Turkmenocampa mirabilis is hitherto known only from the cave Kaptarhana situated near the village Gurshun Magdany, Koytendag District, Lebap Province, Turkmenistan (Figs 20, 21). Kaptarhana (also spelt Kaptar-Khana) means ‘house of pigeons’ in Turkmen language as its entrance is used by pigeons for nesting. The cave is located at the foot of Koytendag Mountain (also known as Koytendag, Köýtendag, Kugitang, Koitendag, Kugitangtau, Kugitang-Tay, Kugitangtou) in the northern part of Hojapil Sanctuary, on the left bank of the Koyten river. The cave is approximately 450 m long and is situated in Late Jurassic gypsum (Birstein and Ljovuschkin 1965, Ljovuschkin 1969). There are two main galleries starting from the entrance, one orientated west (160 m long) and the second, approximately 300 m long, in a northeastern direction. Part of the cave is occupied by lakes with saline water. According to Birstein and Ljovuschkin (1965), the salinity is 11.68‰ and the pH is 7.8. The same authors provide a detailed chemical analysis of the water comparing it with the neighbouring river Amu Darya, Aral and Caspian seas and the World Ocean. The ionic composition of the lakes shows a high similarity to that of the ocean water and little resemblance to those of the neighbouring water basins. Additional support to the relict origin of the lakes comes from their rich foraminiferan, harpacticoid, isopod and gastropod fauna comprising a number of endemic species of marine origin.

A list of species known from Kaptarhana

Aquatic: Foraminifera: *Entzia macrescens* (Brady, 1870) =? *Entzia zernovi* (Schmalhausen, 1950), =? *Entzia polystoma* (Bartenstein & Brand, 1938) subsp. *casifica* Mayer,

Habitat

Although *Turkmenocampa mirabilis* has so far been found only in the larger gallery of the cave, some 200–250 m inside the cave, it might well be that it also inhabits the other main passage of the cave. The species is a troglobiont, all records deriving from the aphotic zone of the cave. No specimens were however observed during the exploration of the cave, those that were trapped being found in humid locations, rich in guano.

Discussion

Phyletic affinities

The classifications of Campodeidae (Condé 1956a; Paclt 1957) and Diplura (Pagés 1959) are rather outdated and badly in need of revision. Only some of the higher taxa proposed in Campodeidae seem natural as they appear to receive geographical support. This is particularly so for the diplurans from the Holarctics but, outside this region and towards its edges, most phylogenetic groups appear more or less artificial. The traits currently applied in the taxonomy of the group are of little help in clarifying the natural grouping and for developing a sound phylogenetic hypothesis. The shape and distribution of macrosetae and setae, the shape and complexity of pretarsal structures, as well as the secondary sexual characters, are the major taxonomic traits used for classifying the existing campodeid taxa. Molecular methods have only recently been applied to the group (Sendra et al. 2012) and the data are still insufficient for drawing a more robust phylogenetic analysis. Despite all these taxonomic weaknesses in the current classification, the traits demonstrated by *Turkmenocampa mirabilis* are solid enough to justify the description of a new species and genus within Campodeidae. The new taxon possesses a combination of several features not present in the other genera, one of which – the specific morphology of the olfactory chemoreceptor sensilla of the cupuliform organ – is unique in the whole family.

Plusiocampinae seems to be a paraphyletic taxon with regard to its only diagnostic character – the additional macrosetae on the pronotum – as suggested by Paclt (1957). Nevertheless, many of its genera can be considered monophyletic. This refers to the genera *Cestocampa* Condé, 1956, *Condeicampa* Ferguson, 1996, *Hystrichocampa* Condé, 1948, *Patrizicampa* Condé, 1956, *Plusiocampa* Silvestri, 1912, *Plutocampa* Chevrizov, 1978, *Simlacampa* Condé, 1956 and *Vandelicampa* Condé, 1956, all of which have lateral crests in their telotarsus. The absence of this important taxonomical trait in *Silvestricampa* Condé, 1950 and *Turkmenocampa* clearly distinguish them from the other Plusiocampinae. With regards to the subfamily position of the new genus, the presence of more than 3+3 macrosetae on pronotum (vs. up to 3+3 in Campodeinae Condé, 1956) and the absence of scales covering part of the body (vs. present as in Hemicampinae Condé, 1956 and Lepidocampinae Condé, 1956), places *T. mirabilis* within Plusiocampinae. However, the absence of lateral crests in *T. mirabilis* and all members of genus



Figure 21. Entrance of the cave Kaptarhana. Photo credit: Aleksandr Degtyarev.

Silvestricampa, the latter being solely known from the Afrotropical realm (Silvestri 1913; Condé 1950), raises doubts about their placement in *Plusiocampinae*.

The high number of macrosetae in *Silvestricampa*, with 7+7 macrosetae on the pronotum and presence of medial and lateral intermediate macrosetae on meso- and metanotum as well as the absence of telotarsal processes, clearly differentiate *Turkmenocampa* from *Silvestricampa*. Close examination of the genera *Plusiocampa* and *Cestocampa*, reveals that several species do not match their original diagnoses. This is the case with subgenus *Dydimocampa* of *Plusiocampa* defined by Paclt (1957) with the presence of two dorsal femoral macrosetae. The subgenus is known with two species from China (Condé 1993; Silvestri 1931): the soil-dwelling *Plusiocampa* (*Dydimocampa*) *sinensis* Silvestri, 1931 and the cave-dwelling *Plusiocampa* (*Dydimocampa*) *lipsae* Condé, 1993. Their chaetotaxy show close similarities with *T. mirabilis* except for the additional macrosetae on II-VII urosternites present in *P. lipsae*. Furthermore, *P. lipsae* has laminar telotarsal processes although with a short sternal pubescence, while they are setiform in *P. sinensis*. *P. sinensis* has clear lateral crests while they are very small in *P. lipsae*.

Another allied species, the soil-dwelling *Plusiocampa kashiensis* from West China (Chou and Chen 1980), was recently transferred from *Cestocampa* (Sendra et al. 2012). Despite its poor original description, *P. kashiensis* shares some similarities with *T. mi-*

mirabilis in the distribution of macrosetae on the nota and abdomen and also in having barbed laminar telotarsal processes and claws without crests. However, the species can readily be distinguished from *T. mirabilis* by the short and abundant clothing setae (vs. long and thin in *T. mirabilis*) and the lack of extension of the claws or side-shoot (at least not mentioned in its original description). It might well be that *P. kashiensis* is actually a member of *Turkmenocampa* but, until a new or type material is studied, a formal transfer has not been suggested at this time. This also refers to the genus *Anisuracampa* Xie & Yang, 1990 which was described from subtropical China (Xie and Yang 1991) and shows morphological similarities with *Dydimocampa*.

Finally, worthy of special mention is the presence of the latero-outside side-shoot of the claw in *T. mirabilis*. It can be considered as a convergent character as it is known in *Metriocampa* (*Notocampa*) *afra* Condé, 1950 and is also present basally in *Oreocampa minutella* (Silvestri, 1918), as well as in *Haplocampa* Silvestri, 1912. It has never been found in combination with telotarsal processes (Condé 1956a) until the discovery of *T. mirabilis*.

Derived morphological characters, troglomorphies

It should be emphasised that all Diplura are without external eyes, although George (1963) presumably gave a light-perceptive function to its lateral sense organs, each one being below the integument in the latero-ventral position in the head. Furthermore, Diplura and Campodeidae, in particular show thin integument with no pigment or sclerotized cuticle. These traits are in all soil- and cave-inhabiting species. Nevertheless, the features which clearly define the troglobiotic campodeids are: increased body size, elongation of appendages and body, more numerous antennomeres and cercal articles, as well as specialisation of sensory organs. Considering all these features, *Turkmenocampa mirabilis* is undoubtedly a strict cave-dweller showing slightly elongated body and appendages (including the cercal articles and the antennomeres); and a moderate increase in the number of antennomeres reaching up to 33 and up to 10 elongated gouge sensilla in the medial and distal antennomeres. Furthermore, the species possesses three striking features which could also be related to its subterranean living environment (see also Condé 1956a; Sendra et al. 2017).

Firstly, the olfactory chemoreceptors within the cupuliform organ, which are usually present in troglobiotic campodeids. In *T. mirabilis*, the shape of these olfactory chemoreceptors have no analogue in any other Campodeidae (Figs 8–12). All troglobiotic campodeids show an increase in size and complexity of the olfactory chemoreceptors and their surface. Troglobionts have more and larger pores than soil-dwellers (Juberthie-Jupeau and Bareth 1980). The increase in complexity demonstrates a similar pattern showing a multiplication of tiny folds (or collarets) around a spheroid sensilla (Condé 1956a). In the most complex cases (Bareth and Condé 1984; Condé 1974; Condé and Sendra 1989), these folds have a sheet-like shape, in *Plusiocampa dallai* Bareth & Condé, 1984 and *Plusiocampa alhamae* Condé & Sendra, 1989; or digit-shape, in *Campodea* (*Paurocampa*) *pretneri* Condé, 1974.

Inside the cupuliform organ, *T. mirabilis* has three types of olfactory chemoreceptors, about forty sensilla tightly packed in a shallow cuticular invagination perforated by tiny pores (Figs 8–9). These sensilla are produced by microscopic evagination at the bottom of the cupuliform organ producing three different types of olfactory chemoreceptor sensilla. Type I and II have a wide and very short base, difficult to observe, which increases in size into two oval-shaped structures completely covered by pores. In type I, the oval structures are 7–8 μm long by 5–6 μm wide with pores of 0.1–0.25 μm diameter (Figs 9–10); in type II, the oval structures are 3.5–4 μm by 3–4 μm with pores of 0.25–0.35 μm (Figs 9, 11). Type III are tree-shaped sensilla covered by irregular pores (0.05–0.08 μm diameter) that start from the cupuliform organ base with a trunk-shaped structure 4.5–6 μm high and 1.1–1.4 μm wide, that it is divided into 2, 3 or 4 branches of 1.1–2.6 μm long extending into 1–2–3–4 spines (Figs 9, 12). The type III sensilla slightly overhang the types I and II and are mostly (Fig. 8) in the centre of the cupuliform organ surrounded generally by types I and II.

Thus in *T. mirabilis*, the increase in number, complexity and porous surface in olfactory chemoreceptors sensilla follow another evolutionary path, different from the pattern observed in numerous trogllobiotic species in *Plusiocampa* and *Cestocampa*, where these sensilla have been examined (eg., Condé 1956a).

The other two remarkable features of *T. mirabilis* refer to the telotarsus and both could be an adaptation for walking on wet and soft surfaces in subterranean environment. The claws are 50–60 μm long and curved only at the distal end where they are also slightly thinner. The whole surface of the claws is marked with fine longitudinal and semi-transversal striate of 0.3 μm thickness. At approximately 15 μm from the base on the lateral external side of the claw, there is a pointed side-shoot process of 12–15 μm length (Figs 17–18). If side-shoots of the claws have a similar function to the function of lateral crests present in several trogllobiotic species of *Plusiocampa*, *Cestocampa*, *Paratachycampa* and *Juxtlacampa*, which are usually regarded as adaptations to subterranean lifestyle (see, for example Conde 1956a; Bareth and Pagés 1994), then they should also be considered derived traits resulting from the long cave evolution. The third interesting feature is the shape of the barbs (about 120 thin barbs 3–18 μm long) on the ventral side of the laminar telotarsal processes, ending mostly in a hook but in a flat extension in the apical barbs (Fig. 17). These two types of laminar barbs have also been observed in other trogllobiotic campodeids (Sendra et al. 2012, 2016) and were considered as an adaptation to facilitate movement on wet surfaces (Sendra et al. 2017).

Biogeography

The cave fauna of Central Asia is outstanding with its poverty of terrestrial trogllobionts (Birstein and Ljovuschkin 1967, Ljovuschkin 1969). Kniss (2001) enumerated from the Central Asian caves altogether 80 species, of which 27 were stygo- and trogllobionts. However, out of 27 strict cave-dwellers, only the springtail *Pseudacherontides stachi* (Ljo-

vuschkin, 1972), found from the Amir-Temir Cave on the western spur of Zeravshan Range of Uzbekistan, is considered troglobiont (Turbanov et al. 2016b). All others, including one fish, inhabit underground waters. Likewise, in adjacent Iran, the cave fauna comprise only 89 species, of which 16 are strict cave-dwellers. Of these, only three are terrestrial troglobites – the spider *Trilacuna garzi* Malek Hosseini & Grismado, 2015, the millipede *Chiraziulus troglopersicus* Reboleira, Malek Hosseini, Sadeghi & Enghoff, 2015 and the isopod *Protracheoniscus gakalicus* Kashani, Malek Hosseini & Sadeghi, 2013 (Malek-Hosseini and Zamani 2017).

Based on climatic, lithological and soil characteristics, Turkmenistan is divided into thirteen ecological regions. Koytendag Mountains form a region of its own and is characterised by desert landscapes on mountainous relief, highly dissected by ravines, foothills with ridges and cuernas and fan plains. Karst processes are well developed in the region. The average annual temperature is about 17°C and annual precipitation is approximately 150 mm (Babaev 1994). The flora contains more than 1,900 species, including 332 endemics (see Rustamov et al. 2009). Lying at the intersection of three biomes – the Eurasian high mountains (Alpine and Tibetan), the Irano-Turanian mountains and the Sino-Himalayan temperate forests – the area supports a high faunal and floral diversity with a number of endemic plant, fish and invertebrate species (UNESCO Nomination dossier 2015).

Due to its remote location, difficult accessibility and restricted border control, as well as the lack of active speleobiologists in Turkmenistan, the biological aspect of the Koytendag caves has only been marginally studied. Despite the great number of caves in the area (some estimates give 300), until now only the invertebrate fauna of the caves Kaptarhana, Gap-Gotan, Hashym Oyuk and Gulshirin, an unnamed cave near v. Svincovyi rudnik, have been explored from the biological viewpoint (Birstein and Ljovuschkin 1965, Ljovuschkin 1969, Starobogatov 1972, Kniss 2001, Turbanov et al. 2016a, b, c). Kniss (2001) reviewed the existing knowledge in his catalogue “Fauna of the caves of Russia and adjacent countries” and Turbanov et al. (2016a, b, c) provided a checklist of all cave species known from Russia and the former Soviet republics. Until the present time, terrestrial troglobionts have not been registered in Koytendag.

The specific composition of the brackish lake in the cave Kaptarhana and its unique stygofauna comprised of species of marine origin suggest a completely different geological history of the cave compared to the rest of the region. It is very likely that the saline waters belong to another hydrographic entity, without connection to the subterranean waters of the neighbouring Koyten and Garlyk areas where the stygofauna is represented by other species such as *Troglocobitis starostini*, *Stenasellus asiaticus*, *Bogidiella ruffoi*, *Gammarus* spp., copepods, etc. (Turbanov et al. 2016 ab, Boris Sket, unpublished).

It is noteworthy that the terrestrial fauna of the cave also shows differences compared to the other caves of Koytendag. The authors’ attempts to find *T. mirabilis* in any of the other caves were unsuccessful despite the fact that the same collecting method (baited pitfall traps) was applied in the cave Gap-Gotan. Furthermore, the ptinid beetle *Niptus hololeucus* (Faldermann, 1835), which is otherwise very abundant in the Gap-Goutan cave (mostly on porcupine scats), is missing in Kaprahana, where the group is repre-

sented by an unidentified species of family Cryptophagidae. The unique character of the fauna of Kaptarhana is supported by the finding of very likely new species of Collembola (L. Deharveng, in progress). It may well be that the existing hydrological barrier between Kaptarhana and the other caves also prevents distribution of terrestrial organisms.

Taking into consideration that the caves of Central Asia are poorly studied, the possibility is not excluded that this taxon or new species of *Turkmenocampa* will be found in future in other caves in Koytendag or in the neighbouring parts of Uzbekistan and Afghanistan.

Acknowledgements

Pavel Stoev and Boris Sket would like to express their deepest gratitude to Stephanie Ward and Elizabeth Ball (both RSPB) for their overall support during the field mission in Turkmenistan, as well as Nurmuhamet Imamov and Dr. Shaniyaz Menliev of Koytendag State Nature Reserve for their guidance and expert local knowledge. We are grateful to Atamyrat Veyisov and Aleksandr Degtyarev for providing the source map of Turkmenistan and the photograph of the cave entrance respectively. We also thank Enrique Navarro and Pilar Gómez from the Electron microscopy facility at the Universitat de València (Spain) for their help in taking the SEM photographs. Journal editor Oana Moldovan and the referees Yun-Xia Luan and Yun Bu provided valuable comments that helped us improve the manuscript.

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