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A new species of an interesting cave-adapted dipluran (Diplura, Campodeidae, Plusiocampinae) from the Kopet Dagh Mountains in Iran

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Abstract. A new species of Plusiocampinae (Diplura, Campodeidae), *Anatoliocampa pax* Sendra & Mehrafrooz sp. nov., is described from specimens collected in an unexplored cave system in the Kopet Dagh Mountains, northeastern Iran, near the Turkmenistan border. This is the second known species of the genus *Anatoliocampa*, previously represented only by *Anatoliocampa diclesis* Sendra, Tusun & Satar, 2022, from a cave in the Anatolian Peninsula. The relationship between these two species highlights the biogeographical relevance of *Anatoliocampa* as a genus within the well-established subfamily Plusiocampinae, which has a Palearctic distribution; East Asia is probably the evolution center of this subfamily, with representatives that occupy mostly deep subterranean ecosystems. An updated taxonomical key for the 15 known genera of Plusiocampinae subfamily is provided.

Keywords. Cave-dwelling fauna, *Anatoliocampa*, taxonomical key, biogeography.

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Introduction

Although Diplura Börner, 1904 represent a small group of entognathous arthropods, with just over a thousand species, 1008 according to the latest checklist (Sendra *et al.* 2021c), a significant proportion of this diversity (up to 15%) inhabits cave environments. These organisms exhibit remarkable morphological and sensory adaptations that enable them to thrive in dark, food-scarce, and atmospherically stable subterranean habitats (Racovitză 1907; Pagés 1964; Bareth & Pagés 1994; Sendra *et al.* 2021c).

The number of dipluran is particularly low in arid regions of the world, of which Iran is no exception. Moreover, the sampling effort in Iran—and generally across the entire Eastern-Palaearctic region, where records are scarce—has been insufficient. To date, only 56 species have been described in this area (Sendra *et al.* 2021d), representing a small fraction of the global dipluran diversity. No species of dipluran had been recorded in Iran until the study by Azadbakhsh & Nozari (2016), which reported 45 specimens collected from three soil samples in a mountainous forest area in the western part of Mazandaran Province, northern Iran. This contribution identified two Campodeidae Meinert, 1865 species: *Campodea (Campodea) fragilis* Meinert, 1865 and *Campodea (Dicampa) sprovierii* Silvestri, 1932, both of which are well known in the Euro-Mediterranean region (Condé 1956a; Sendra & Reboleira 2020).

A team of biologists recently explored a cave in the Kopet Dag Mountains of northeastern Iran to investigate its cave-dwelling arthropod fauna. As a result, a previously unknown dipluran taxon was discovered and is described herein. This finding has motivated the development of a taxonomic key for the genera of Plusiocampinae Paclt, 1957, as well as a discussion about the phylogenetic implications and geographical distribution of this subfamily within Campodeidae.

Material and methods

Study area

Cave description

Moghan Cave, located in the Razavi Khorasan Province near a village of the same name, lies approximately 34 kilometres from Mashhad City. This cave is located at an elevation of 2193 meters above sea level (36°06'59" N, 59°22'06" E) within the eastern part of the Kopet Dag Mountains (Fig. 1A–B). The cave has two entrances: a smaller one, about 3 meters wide and 1.5 m high, and a main entrance on the right side, about 4 m high and approximately 6 m long (Fig. 1C–D). The cave's total length is about 500 m and it is 44 m deep. The twilight area, which has a completely dry floor, extends about 50 meters inward and slopes gently toward the deeper section of the cave. The cave comprises two levels, five galleries, and various wells, each gallery differing in height. The deepest well reaches approximately 25 meters. In the final chamber, which is 23 meters long, there is a permanent lake of approximately 5.66 × 6.93 meters in area and 30–60 cm deep (Mehrafrooz Mayvan *et al.* 2024) (Fig. 1E). Air temperature and relative humidity (RH) were measured in July 2024 using an HTC-2 digital thermometer and hygrometer, recording values of 9°C and 84%, respectively. All specimens of the new species were collected from the floor and stones within this area.

Sampling methods

Diplurans were collected in the dark zones of Moghan Cave using two sampling methods. In 2022, specimens were hand-collected with the aid of an aspirator near a stalagmite. In 2024, additional specimens were obtained both manually—from rocks and stones—and using pitfall traps made from plastic cups filled with 10% formaldehyde. All collected specimens were transferred to vials containing 96% ethanol for preservation. Type material and other studied specimens was deposited (pending numbers) at the following institutions:

Coll. AS = Collection of Alberto Sendra, Museu Ciències Naturals de València, València, Spain
MCNB = Museu de Ciències Naturals de Barcelona, Barcelona, Spain
UPJŠ = Institute of Biology & Ecology, Faculty of Science, P.J. Šafárik University Košice, Slovakia
ZMFUM = Zoology Museum of Ferdowsi University of Mashhad, Mashhad, Iran

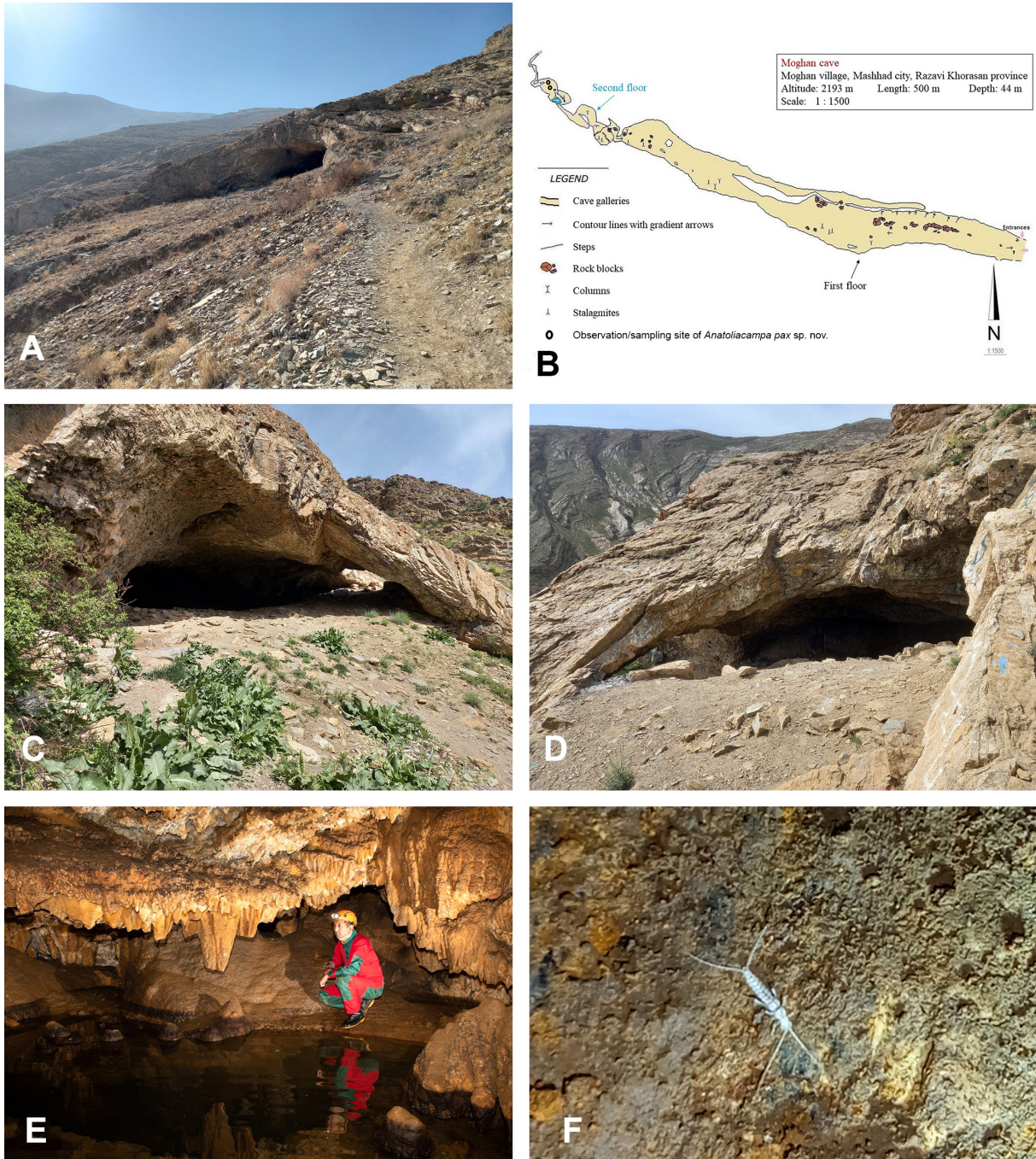


Fig. 1. Moghan Cave, northeast Iran. **A.** Entrance and surroundings of Moghan Cave in autumn. **B.** Map of the Moghan cave. **C.** Main entrance of the cave in spring. **D.** Second entrance. **E.** Pool situated at the end of the cave on the second floor. **F.** *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov. in Moghan Cave. Photos: A, C–D, F: M. Mehrafrooz; E: Vahid Ashrafi; B: Sketched by V. Ashrafi.

Morphological study

Specimens were washed with distilled water, mounted on a slide with Marc André II solution, and examined under a phase-contrast optical microscope (Leica DMLS). Illustrations were made with a drawing tube, and measurements were taken with an ocular micrometre. To determine body length, specimens were mounted in toto and measured from the base of the distal macrosetae on the frontal process to the supra-anal abdominal valve. Four specimens were coated with palladium-gold for SEM photography (Hitachi S-4900) and sensilla measurements. The morphological descriptions and abbreviations follow Condé (1956a): *la* = lateral-anterior; *lp* = lateral-posterior, *ma* = medial-anterior; *mp* = medial posterior and *post* = posterior. The term gouge sensilla is used for the concavo-convex shaped sensilla on the antennae, following Bareth & Condé (1981).

Results

Class Diplura Börner, 1904
Superfamily Campodeoidea Lubbock, 1873
Family Campodeidae Meinert, 1865
Subfamily Plusiocampinae Plact, 1957
Genus *Anatoliacampa* Sendra, Tusun & Satar, 2022

Anatoliacampa pax Sendra & Mehrafrooz sp. nov.
[urn:lsid:zoobank.org:act:2F134DDB-AFE1-4B24-AB32-E1926A8AE2E2](https://zoobank.org/act:2F134DDB-AFE1-4B24-AB32-E1926A8AE2E2)
Figs 1F, 2–7, 10, Table 1–2

Diagnosis

Body robust, length 4–6 mm; epicuticle is smooth; 32–38 antennomeres; cupuliform organ with about 10 complex olfactory chemoreceptors compounded by a central column surrounded by a spiral fold of 5–6 turns; pronotum with 1+1 *ma*, 2+2–4+4 *la*_{1–4}, 2+2 *lp*_{2,3} macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*_{2–3}, 2+2 *lp*_{2–3}, 1+1 *mp* and 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{2–3}, 1+1 *mp* long macrosetae; metathoracic legs reach the eighth abdominal segment; tibia is 1.1–1.3 times as long as the femur or tarsus; femora II–III have 3 long dorsal macrosetae; tibia II–III with 3–2 ventral macrosetae; calcars with long barbs almost all over; end part of the tarsus has two dorsal and one lateral long robust pubescens setae; claws are similar in size, both with large lateral crests; lateral processes have a basal laminar boarder that narrows along the distal half and all borders prolonged in long fringes; 1+1 post1 macrosetae on I–III urotergites, 1+1 *la*₁, 3+3 post1–3 macrosetae on IV urotergite, 1+1 *la*₁, 5+5 *post*_{1–5} macrosetae on V urotergite; 2+2–3+3 *la*_{1–3}, 5+5 *post*_{1–5} macrosetae on VI–VII urotergites, 7+7–8+8 post macrosetae on VIII urotergites and 11+11 post macrosetae on IX abdominal segment; urosternite I with 10+10–13+13 well-barbed macrosetae; urosternites II–VII with 7+7 macrosetae, urosternite VIII with 2+2 macrosetae; the stylus setae are well barbed with almost complete thin barbs; female urosternite I with subcylindrical appendages, each with 26 glandular *a*₁ setae and male with larger subcylindrical appendages with up to 34 glandular setae *a*₁.

Etymology

The specific epithet '*pax*' is a Latin noun meaning 'peace'. It is used here as a noun in apposition and does not change to agree in gender with the genus name. The name is intended as a symbolic tribute to peace, reflecting a personal aspiration for harmony in both nature and society; and a relevant desire in these times of war in the area studied.

Type material

Holotype

IRAN • ♀; Moghan Cave, Moghan village, Mashhad City, Razavi Khorasan Province; 36°06'59" N, 59°22'06" E; 2193 m a.s.l.; 29 Jul. 2024; Mahmood Mehrafrooz Mayvan leg.; ZMFUM-MoAn101IR.

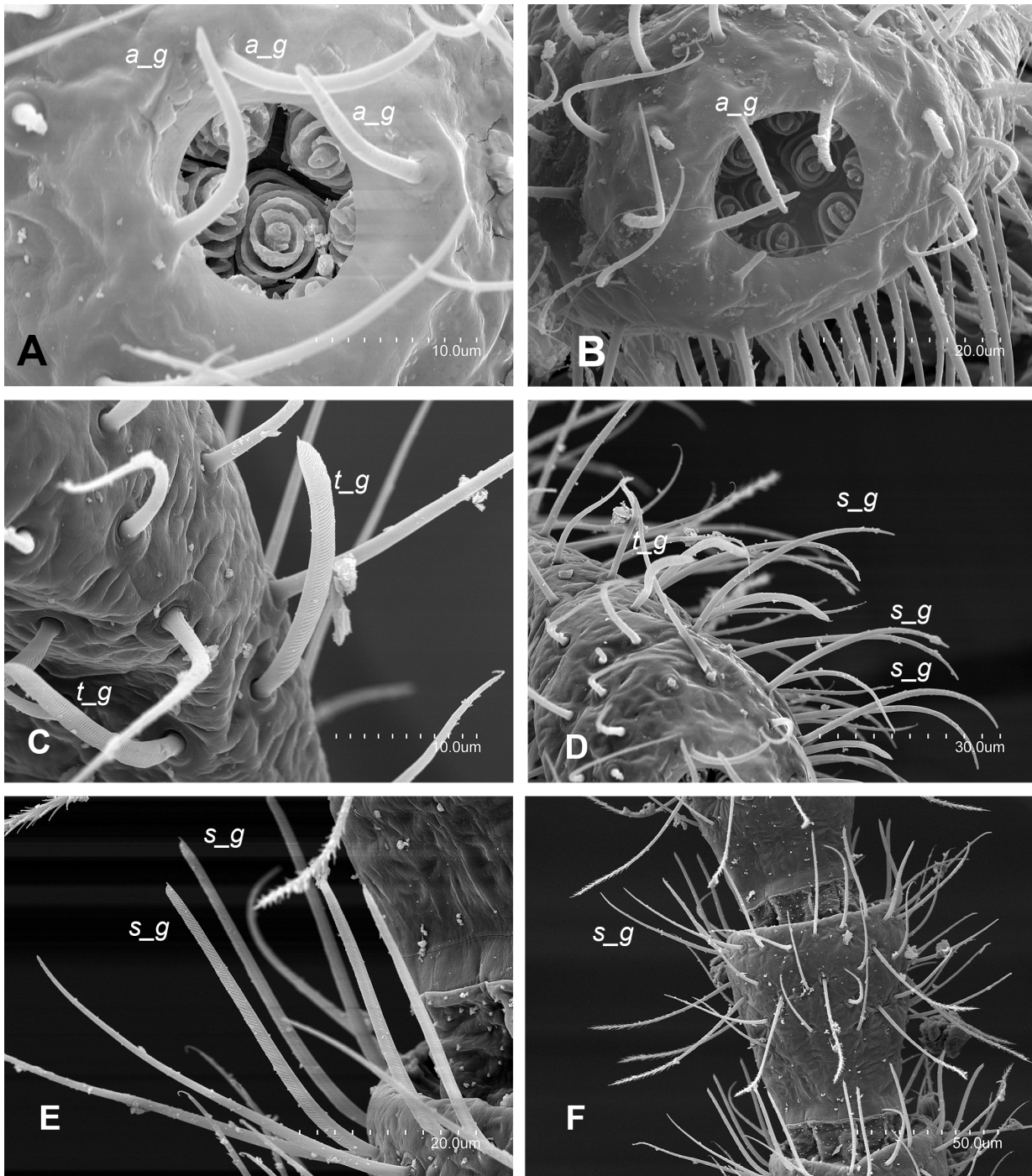


Fig. 2. *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov.; male AS, coll. **A.** Cupuliform organ on the apical antennomere. **B.** Cupuliform organ on the apical antennomere. **C.** Detail of apical antennomere. **D.** Detail of apical antennomere. **E.** Latero-distal portion of medial antennomere. **F.** Medial antennomere. Abbreviations: *a_g* = apical glandular setae; *s_g* = slim gouge setae; *t_g* = thick gouge setae.

Paratypes

IRAN • 1 ♂; Moghan Cave, Moghan village, Mashhad City, Razavi Khorasan province; 36°06'59" N, 59°22'06" E; 2193 m a.s.l.; 29 Jul. 2024; Mahmood Mehrafrooz Mayvan leg; ZMFUM-MoAn104IR. • 1 ♂; same collection data as for holotype; ZMFUM-MoAn102IR • 1 ♂; same collection data as for holotype; ZMFUM-MoAn103IR. • 1 ♂; same collection data as for holotype; MUVHN-ZE6928 • 1 ♀; same collection data as for holotype; MUVHN-ZE6976 • 1 ♀; same collection data as for holotype; MCNB-2025-7270 • 1 ♂; same collection data as for holotype; MCNB-2025-7271 • 1 ♂ same collection data as for holotype; UPJŠ-01-25 • ♂ same collection data as for holotype; UPJŠ-02-25.

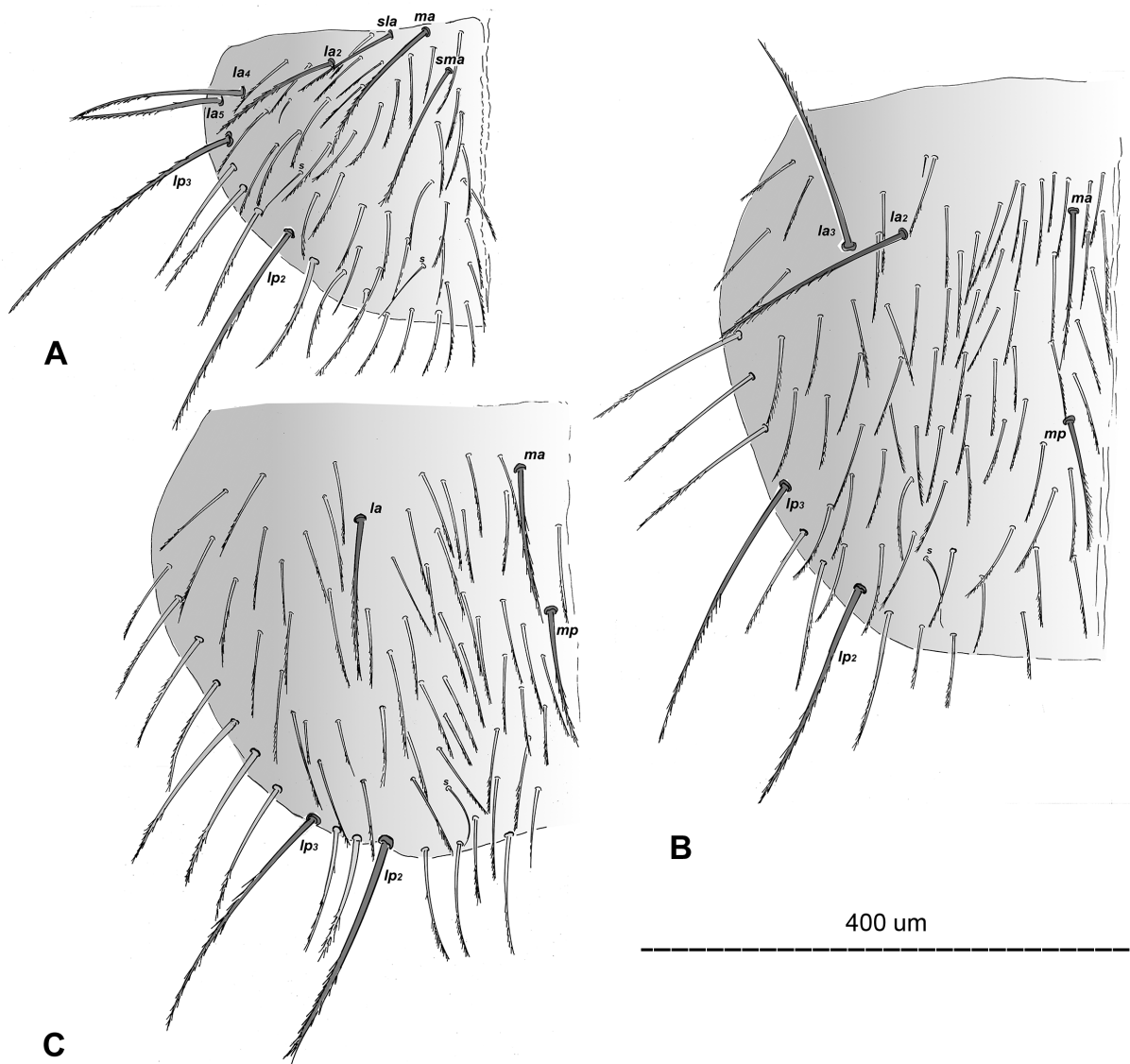


Fig. 3. *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov. Holotype, ZMFUM-MoAn101IR. **A.** Pronotum. **B.** Mesonotum. **C.** Metanotum. Abbreviations: *la* = lateral posterior macrosetae; *lp* = lateral posterior macrosetae; *ma* = medial anterior macrosetae; *mp* = medial posterior macrosetae; *s* = sensillum setiform; *sla* = sub lateral anterior macrosetae.

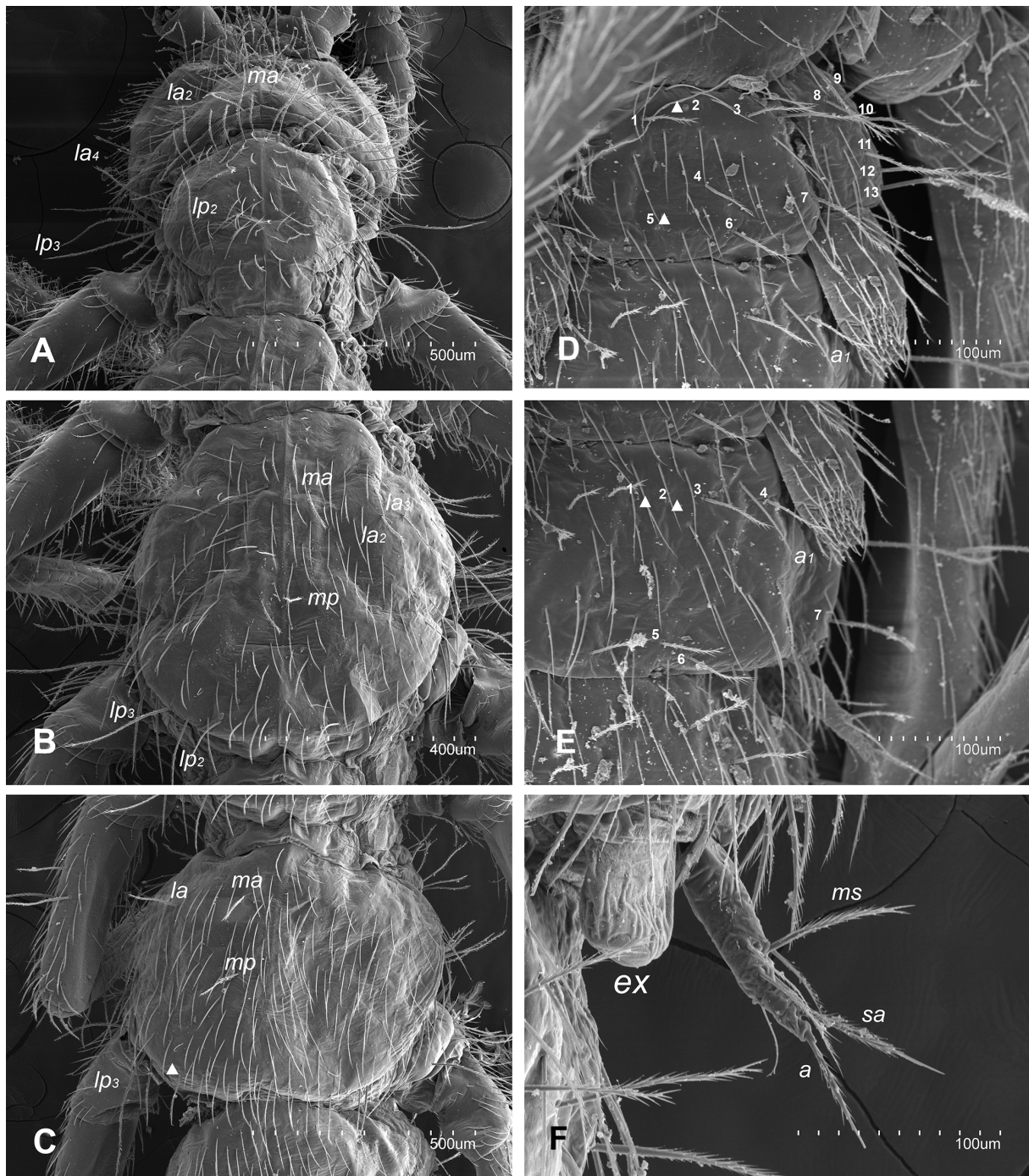


Fig. 4. *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov., female (A–C), male (D–F), AS coll. **A.** Head and prothorax. **B.** Mesothorax. **C.** Metathorax. **D.** First abdominal segment of a male, ventral view. **E.** Second abdominal segment, ventral view. **F.** Lateral posterior part of fourth abdominal segment, ventral view. Abbreviations: *a* = apical stylus setae; *a*₁ = glandular *a*₁ setae; *ex* = exertil vesicle; *la* = lateral posterior macrosetae; *lp* = lateral posterior macrosetae; *ma* = medial anterior macrosetae; *mp* = medial posterior macrosetae; *ms* = medial sternal stylus setae; *sa* = subapical stylus setae; triangle = insertion of macrosetae; 1, 2, 3, ... = order disposition of macrosetae in a sclerite.

Table 1. Body measurements of *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov., (*) = telescoped abdomen.

Specimen	Body length (mm)	Antennae length	Antennomeres	Metathoracic leg length (mm)					Total length
				Coxa	Trochanter	Femur	Tibia	Tarsus plus pretarsus	
Juv. (♀)	3.1	2.2	29	0.10	0.09	0.39	0.46	0.40	1.44
♂05	4.0 (*)	4.0	32	0.18	0.17	0.60	0.68	0.54	2.17
♂03	4.1	3.5	38	0.12	0.11	0.49	0.55	0.45	1.17
♂06	4.2	3.7	34	0.18	0.15	0.55	0.66	0.54	2.08
♂01	4.4	3.8	36	0.16	0.15	0.60	0.70	0.55	2.16
♂04	4.9	3.9	35	0.11	0.10	0.60	0.70	0.53	2.04
♂02	5.0	4.0	35	0.21	0.20	0.58	0.65	0.55	2.19
♀02	5.1	4.3	36	0.18	0.15	0.65	0.78	0.63	2.39
♀01, holotype	6.0	5.1	35	0.25	0.24	0.70	0.90	0.72	2.81

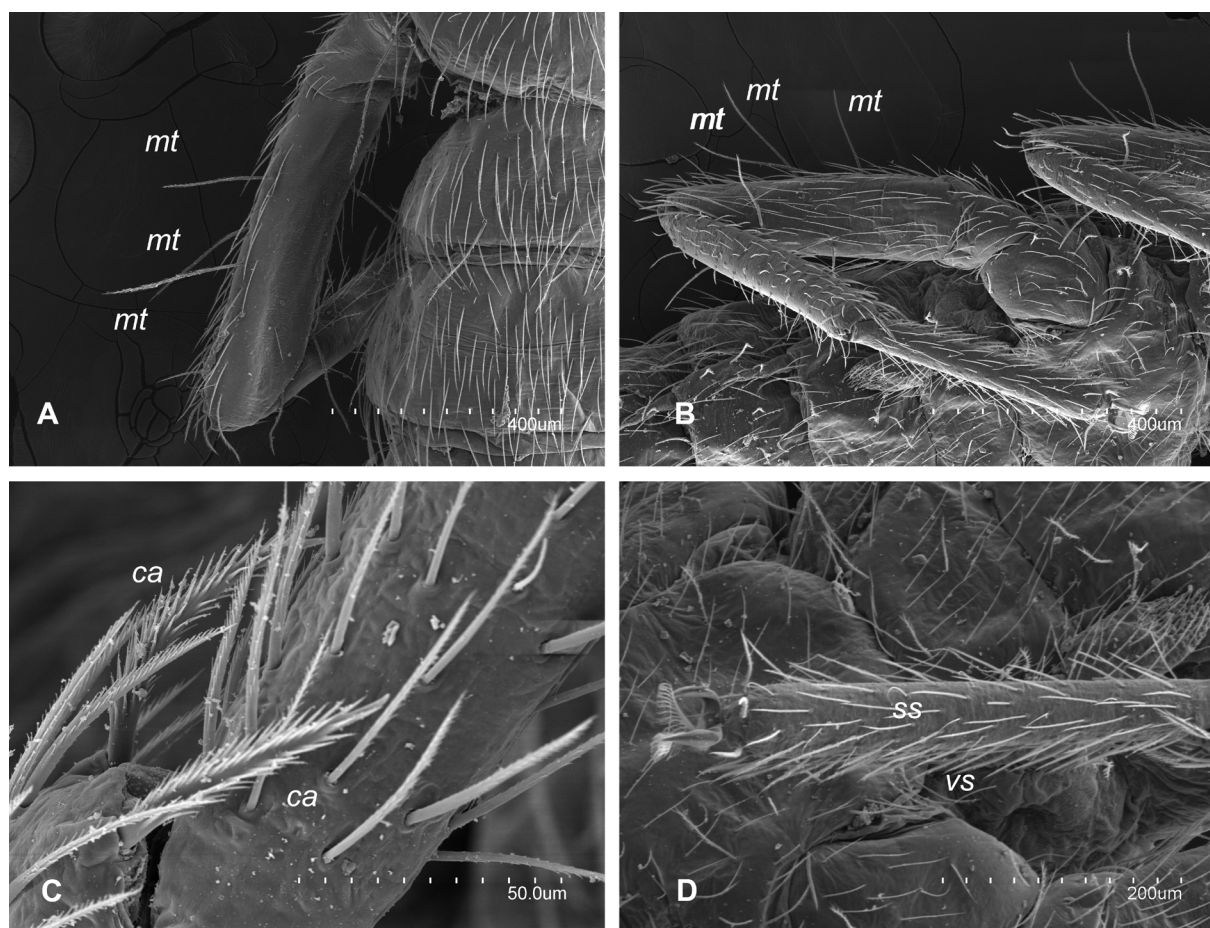


Fig. 5. *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov., female, AS coll. **A.** Left lateral side of abdominal segments first to second and metathoracic leg, dorsal view. **B.** Metathoracic leg and ventral view of metathorax and first to second abdominal segments. **C.** Joint tibio-tarsal with calcaria. **D.** Metatarsus, latero-dorsal view. Abbreviations: ca = calcaria; mt = tergal macrosetae; ss = setiforme sensillum; vs = ventral setae.

Other studied material

IRAN • 2 ♂♂, 4 ♀♀; Moghan Cave, Moghan village, Mashhad City, Razavi Khorasan Province, 36°06'59" N, 59°22'06" E, 2193 m a.s.l.; 29 Jul. 2024; Mahmood Mehrafrooz Mayvan leg.; AS coll. Used for scanning electron microscopy.

Taxa description

BODY. Body length 4–5 mm in males, 5.1–6 mm in females, and 3.1 mm in a juvenile (Fig. 1F). The epicuticle is smooth even under high magnifications (Fig. 4A–C); body robust and covered by clothing setae with thin barbs along half to one-third distal portion.

HEAD. Antennae have 32–38 antennomeres in intact adult antennae, and 28 antennomeres in a female juvenile; antennae ~0.88–0.80 times as long as the body's length, with medial antennomeres 1.5 times as long as wide and apical antennomere more than two times as long as wide. Two types of gouge sensilla and glandular setae cover the last antennomere: numerous long and slim gouge sensilla, scarce large and thick gouge sensilla, and an apical whorl of glandular setae around the cupuliform organ (Fig. 2C–D). The cupuliform organ occupies $\frac{1}{11}$ of total length in the last antennomere and has about 10 complex olfactory chemoreceptors compounded by a central column surrounded by a spiral fold of five to six turns (Fig. 2A–B). The distal and central antennomeres have three whorls of slightly barbed macrosetae, in addition to smooth, thin setae. They also have a distal whorl of 12–14 long, slim gouge sensilla (38–

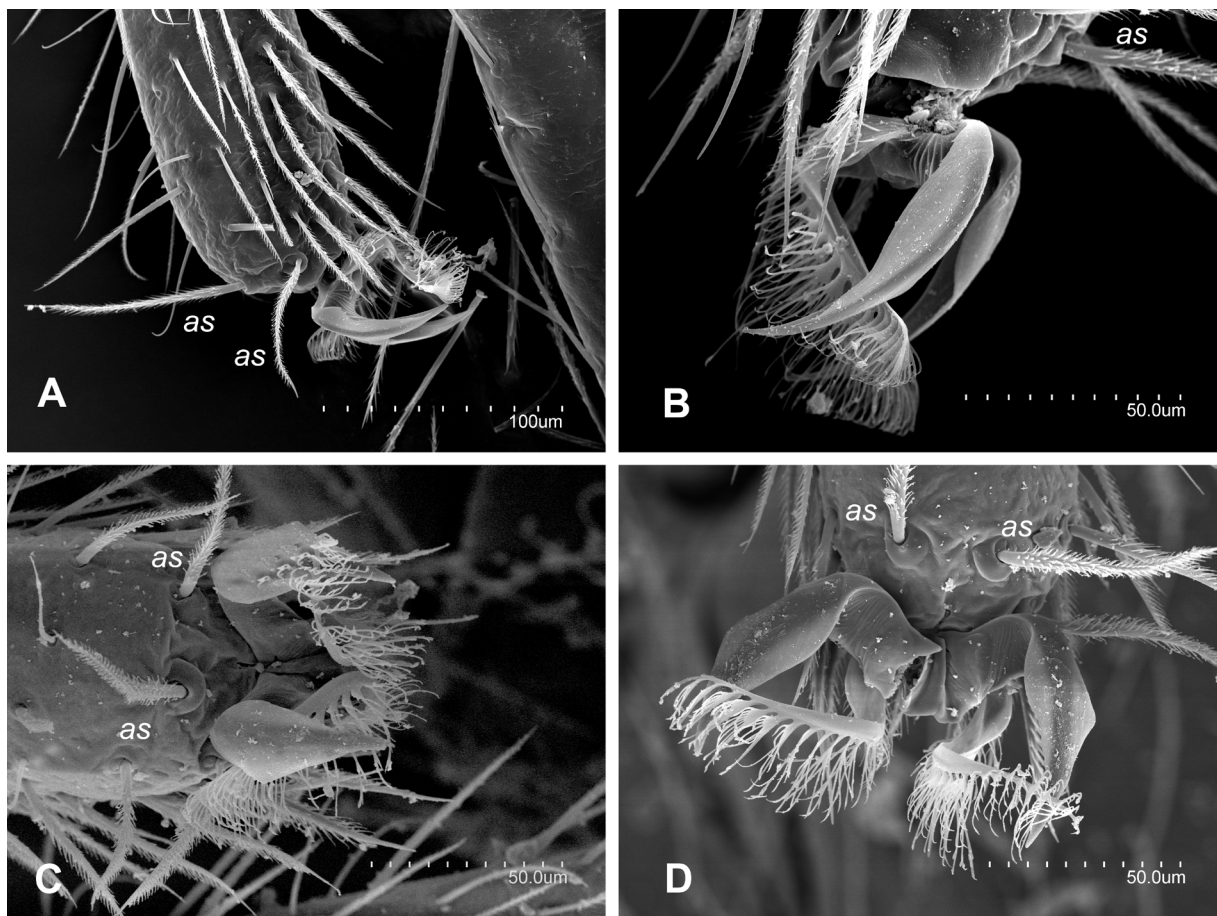


Fig. 6. *Anataliacampa pax* Sendra & Mehrafrooz sp. nov., female, AS coll. **A.** Pretarsus, lateral view. **B.** Pretarsus, lateral view. **C.** Pretarsus, dorsal view. **D.** Pretarsus, frontal view. Abbreviation: as = apical setae.

50 µm long) (Fig. 2E–F). The proximal antennomeres have typical trichobothria, plus a small bacilliform sensillum on the third antennomere in ventral position. The frontal process has a slightly protrusion with one distal smooth macroseta, plus three shorter macrosetae with a few distal barbs; the three-insertion line macrosetae and *x* macrosetae bear a few distal barbs, and their length ratios are: *a*/*i*/*p*/*x* 43/49/41/62, respectively, in the holotype; occiput of the dorsal head with 3+3 *ma*, *la*, *lp* macrosetae bears a few distal barbs. The labial palps are large and suboval with large coniform latero-external sensillum, two guard setae, up to fourteen setae on anterior border, and up to 100 neuroglandular setae in the holotype.

THORAX. Thoracic macroseta distribution: pronotum with 1+1 *ma*, 2+2–4+4 *la*_{1–4}, 2+2 *lp*_{2–3} macrosetae; mesonotum with 1+1 *ma*, 2+2 *la*_{2–3}, 2+2 *lp*_{2–3}, 1+1 *mp* and 1+1 *ma*, 1+1 *la*, 2+2 *lp*_{2–3}, 1+1 *mp* long macrosetae (Figs 3, 4A–C). All macrosetae are long and with thin barbs along 2/3 of their basal length; marginal setae are thin and barbed along two-thirds of the distal portion and double the length of the clothing setae. The legs are slightly elongated, and the metathoracic legs reach the eighth abdominal segment. The tibia is 1.1–1.3 times as long as the femur or tarsus. Femora II–III have 3 long dorsal macrosetae, 2 in a few specimens (femora I with 2 dorsal macrosetae); tibia II–III with 3–2 ventral macrosetae (Fig. 5A–B, D). The calcars have long barbs almost all over (Fig. 5C). The tarsus has two ventral rows of ventral setae with barbs on medial portion setae and a few setiform sensilla; the end part of the tarsus has two dorsal and one lateral long robust pubescens setae (Fig. 6A–D). The claws are

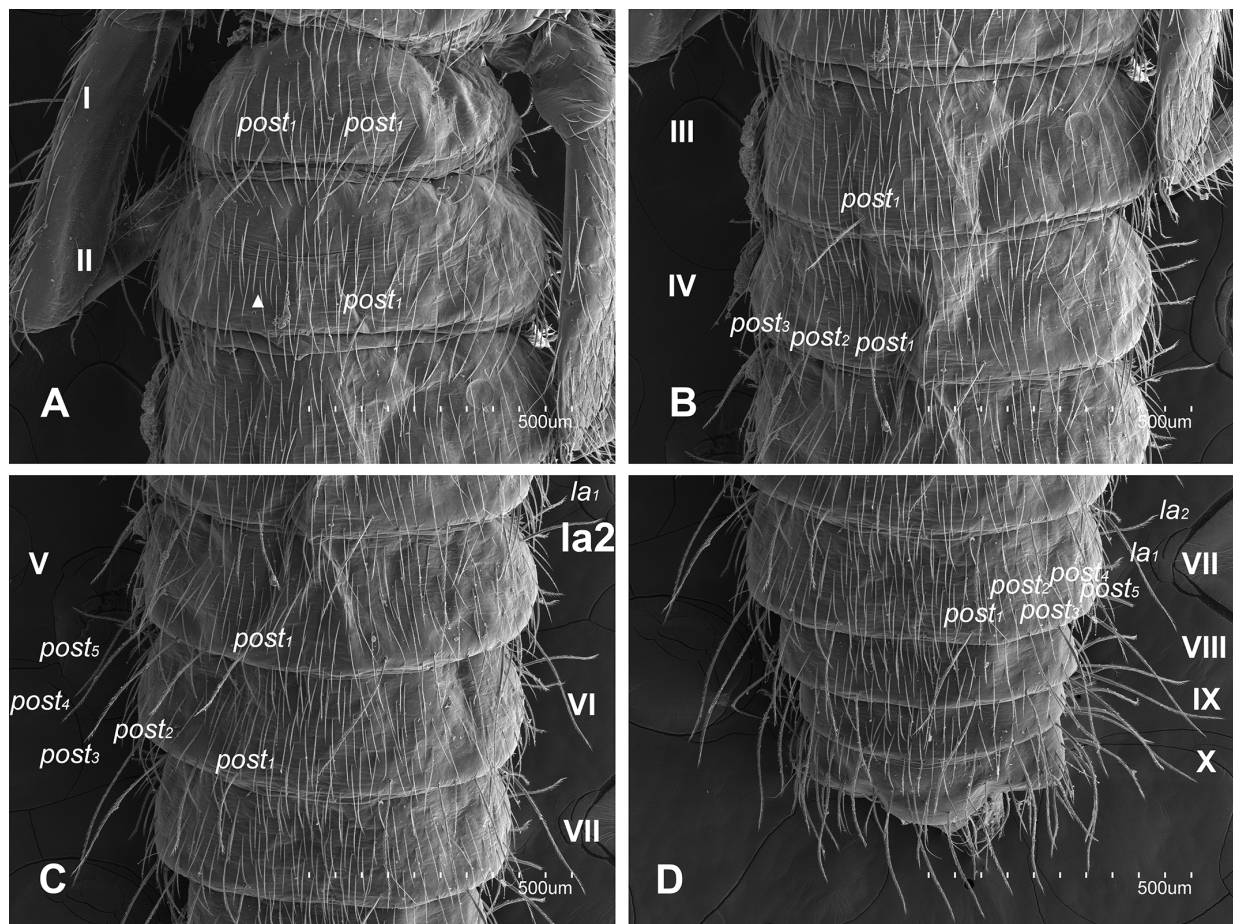


Fig. 7. *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov., female, AS coll. **A.** First and second abdominal segments, dorsal view. **B.** Third and fourth abdominal segments, dorsal view. **C.** Fifth to seventh abdominal segments, dorsal view. **D.** Telescoped seventh to tenth abdominal segments, dorsal view. Abbreviation: *la* = lateral posterior macrosetae; *post* = posterior macrosetae.

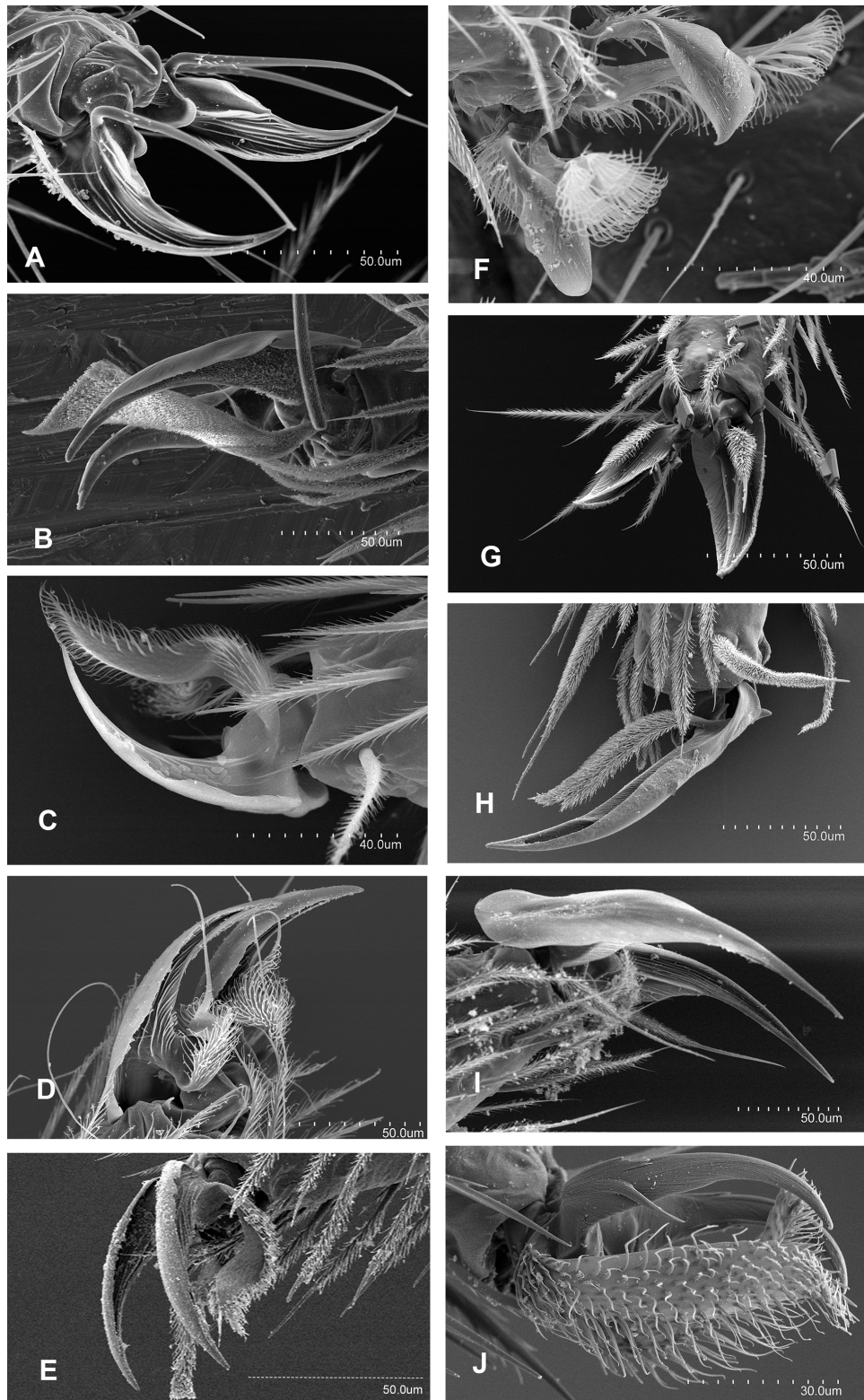


Fig. 8. Pretarsus of. **A.** *Anisuracampa ywangana* Sendra & Komerički, 2021. **B.** *Cycladiacampa irakleiae* Sendra, 2020. **C.** *Whittencampa troglobia* Sendra & Deharveng, 2020. **D.** *Hystrichocampa pelletieri* Condé, 1948. **E.** *Turkmenocampa mirabilis* Sendra & Stoev, 2017. **F.** *Plusiocampa lagari* Sendra & Condé, 1987. **G.** *Hubeicampa melissa* Sendra & Lips, 2021. **H.** *Paratachycampa hispanica* Barteh & Condé, 1981. **I.** *Patrizicampa sardoa* Condé, 1956. **J.** *Cestocampa iberica* Sendra & Condé, 2012.

Table 2. Cerci measurements of *Anataliacampa pax* Sendra & Mehrafrooz sp. nov.

Specimen	Cerci length (mm)								Total length
	Basal	Primary articles			Primary articles				
		First	Second	Third	Fourth	Fifth	Sixth	Seventh	
♂05	0.90	0.35	0.42	0.49	0.55	0.62	broken		-
♂04	0.98	0.45	0.50	0.60	0.70	0.80	0.90		4.93
♀01, holotype	1.10	0.45	0.53	0.60	0.78	0.80	1.00	1.05	6.41

similar in size, both with large lateral crests. Lateral processes have a basal laminar boarder that narrows along the distal half and all borders prolonged in long fringes (Fig. 6A–D).

ABDOMEN. Distribution of abdominal macrosetae on tergites: 1+1 *post*₁ macrosetae on I–III urotergites, 1+1 *la*₁, 3+3 *post*₁₋₃ macrosetae on IV urotergite, 1+1 *la*₁, 5+5 *post*₁₋₅ macrosetae on V urotergite; 2+2–3+3 *la*₁₋₃, 5+5 *post*₁₋₅ macrosetae on VI–VII urotergites, 7+7–8+8 *post* macrosetae on VIII urotergites and 11+11 *post* macrosetae on IX abdominal segment (Fig. 7A–D). All tergal abdominal macrosetae are long and well-differentiated with thin barbs along most of their length (Fig. 7A–D). Urosternite I with 10+10–13+13 well-barbed macrosetae (Fig. 4d), urosternites II–VII with 7+7 macrosetae (Fig. 4E), urosternite VIII with 2+2 macrosetae; urosternal macrosetae barbed with thin barbs almost from the base to two-thirds. The stylus setae is well barbed with almost complete thin barbs. (Fig. 4F).

Two completed cerci with six (paratype ♂04) and seven (holotype) primary articles slightly longer from proximal to distal, one in addition to a basal article divided into three secondary articles, both slightly longer than the body length, 1.2 for the paratype ♂04 and 1.1 for holotype; primary article bears 6–12 whorls of long macrosetae with thin barbs along distal $\frac{1}{3}$, one distal whorl of smooth setae, and one apical whorl of thin setae with thin barbs along distal $\frac{1}{3}$.

SECONDARY SEX CHARACTERS. Female urosternite I with subcylindrical appendages, each bearing up to 26 glandular *a*₁ setae in a distal field. Male with larger subcylindrical appendages than the female, each bearing up to 34 glandular setae *a*₁ (Fig. 4D).

***Taxonomical key of genera of Plusiocampinae* (Fig. 8)**

1. Pretarsal claws with lateral crests 2
- Pretarsus claws without lateral crests 14

2. Pretarsal lateral processes setiform 3
- Pretarsal lateral processes laminar 5
- Pretarsal lateral processes absent *Plutocampa* Chevrizov, 1978

3. Pretarsal lateral setiform with barbs covered almost completely the whole surface 12
- Pretarsal lateral process setiform and smooth 4

4. 4+4 macrosetae on urosternites II–VII, 1+1 macrosetae on urosternite VIII
..... *Condeicampa* Ferguson, 1996 and *Plusiocampa* (?) *sinensis* Silvestri, 1931
- No less than 5+5 macrosetae on urosternites II–VII and 2+2 macrosetae on urosternite VIII *Plusiocampa* Silvestri, 1912

5. Pretarsal lateral processes laminar with barbs or micro-barbs 6
- Pretarsal lateral processes laminar cut into fringes 10

6. Laminar pretarsal lateral processes with barbs 7
 – Laminar pretarsal lateral processes with micro-bars with the appearance of pubescent surface *Hubeicampa* Sendra & Lips, 2021
7. All nota with 2+2 lateral posterior macrosetae 8
 – Only pronotum with 1+1 lateral posterior macrosetae *Paratachycampa* Wygodzinsky, 1944
8. Broad laminar pretarsal processes with abrupt narrowing in distal portion
 *Patrizicampa* Condé, 1955
 – Broad laminar pretarsal processes with abrupt narrowing in distal portion 9
9. Broad laminar pretarsal processes with square ending *Cestocampa* Condé, 1955
 – Broad laminar pretarsal processes gradual narrowing *Vandelicampa* Condé, 1955
10. One dorsal macrosetae on femora, lateral posterior notal macrosetae on meso. and metanotum absent *Simlacampa* Condé, 1956
 – Two or three dorsal macrosetae on femora, at least 2+2 lateral posterior macrosetae on meso and metanotum 11
11. Sternite VIII with 1+1 macrosetae; basal portion of claws covered with spiniform formations *Anisuracampa* Xie & Yang, 1991
 – Sternite VIII with 2+2-3+3 macrosetae; without spiniform formation on basal portion of claws *Anatoliacampa* Sendra, Tusun & Satar, 2022
12. Macrosetae macrosetae on meso. and metanotum absent; one dorsal macroseta on femora *Cycladiacampa* Sendra, 2020
 – Macrosetae on meso. and metanotum present; two to five dorsal macrosetae on femora 13
13. Urosternite VIII with 1+1 macrosetae, two dorsal macrosetae on femora *Whittencampa* Sendra & Deharveng, 2020
 – Urosternite VIII with 2+2 macrosetae; five dorsal macrosetae on femora
 *Hystrihocampa* Condé, 1948
14. Claws simple; pretarsal lateral processes absent, medial-intermediate and lateral-intermediate macrosetae on mesonotum and metanotum present *Silvestricampa* Condé, 1950
 – Claws with sharp side-shoot; pretarsal lateral processes laminar, medial posterior macrosetae on mesonotum and metanotum absent *Turkmenocampa* Sendra & Stoev, 2017

Discussion

Taxonomic position

Anatoliacampa Sendra, Tusun & Satar, 2022, —a genus characterized by laminar lateral broader pretarsal processes with long lateral and distal fringes— was recently described in Sendra *et al.* (2022). These pretarsal processes in *Anatoliacampa* are similar to the lateral pretarsal processes in the genus *Anisuracampa* Xie & Yang, 1991 (see Figs 6, 11A) (Sendra *et al.* 2021a). However, *Anatoliacampa* shares a macrosetae distribution pattern typical of most species within the subfamily Plusiocampinae, with 2+2–3+3 macrosetae on the VIII urosternite, whereas *Anisuracampa* has only 1+1 macrosetae on this sclerite.

Within the genus *Anatoliacampa*, *A. pax* Sendra & Mehrafrooz sp. nov. exhibits clear and numerous taxonomic differences compared to the type species, *Anatoliacampa diclensis* Sendra, Tusun & Satar, 2022. Notable differences include the presence of medial posterior macrosetae on the mesonotum and

metanotum in *A. pax* (Fig. 4), which are absent in *A. diclensis*; the presence of three dorsal macrosetae on the femora in *A. pax* (Fig. 6A–B), compared to only two in *A. diclensis*; and up to 3+3 lateral anterior macrosetae on the VI–VII urotergites in *A. pax*, whereas *A. diclensis* has only 1+1. Another remarkable difference is in the structure of the complex sensilla within the cupuliform organ, a feature particularly relevant since both *Anatoliacampa* species are cave-adapted. In *A. pax*, the sensilla consist of a central column surrounded by a spiral fold with 5–6 turns (Fig. 2A–B), whereas in *A. diclensis*, the sensilla comprises a central column with the typical apical hole, surrounded by irregular, cauliflower-like folds (Sendra *et al.* 2022). Additionally, in *A. pax* the body shape is robust, while in *A. diclensis* it is slender, in addition to the less elongated appendages in *A. pax* compared to *A. diclensis*. These morphological traits suggest that *A. pax* sp. nov. exhibits a less pronounced degree of cave adaptation than *A. diclensis*.

***Plusiocampinae* subfamily**

The description of the remarkable *Anatoliacampa pax* Sendra & Mehrafrooz sp. nov., together with the latest taxonomic contributions to the subfamily Plusiocampinae (Sendra *et al.* 2021a; Sendra & Deharveng 2022), provides a solid foundation to propose an updated and more comprehensive taxonomic key for the Plusiocampinae genera, thus expanding upon those previously published by Sendra *et al.* (2017b, 2020). Plusiocampinae currently comprises 15 genera, 103 species, and 9 subspecies, with a distribution primarily concentrated in the Palearctic Realm. Its northern limit appears to coincide with the extent of the Last Glacial Maximum (Figs 9–10), and there is a marked preference for the Euro-Mediterranean region (Fig. 10). However, six species have been recorded outside this realm: four species of the genus *Silvestricampa* from KwaZulu-Natal, South Africa (*Silvestricampa africana* (Silvestri, 1913), *Silvestricampa lawrencei* Condé, 1950, *Silvestricampa proxima* Condé, 1950, and *Silvestricampa nexa* Condé, 1955); the monotypic genus *Condeicampa*, represented by *Condeicampa langei* Ferguson, 1996 from a cave in Nevada, USA; and *Paratachycampa boneti* Wygodzinsky, 1944, the only species of its genus (see Supp. file 1). The genus *Plusiocampa* Silvestri, 1912, remains the most diverse within the subfamily, comprising 74 species and 9 recognized subspecies in the Euro-Mediterranean region (Fig. 10). Notably, *Plusiocampa sinensis* Silvestri, 1931, may require reassignment to another genus, although further morphological studies are necessary to confirm this taxonomic revision.

As previously noted, (Sendra *et al.* 2021a, 2022), although most of the described species of Plusiocampinae are concentrated in Europe, seven genera are currently known from the East Palearctic region: *Plutocampa* Cherizov, 1978; *Anisuracampa* Xie & Yang, 1991, *Simlacampa* Condé, 1956; *Cestocampa* Condé, 1955; *Turkmenicampa* Sendra & Stoev, 2017; *Hubeicampa* Sendra & Lips, 2021; and *Anatoliacampa* Sendra, Tusun & Satar, 2022. Most of these genera are considered endemic to that region, with the exception of *Cestocampa*, which is also known to be in the Mediterranean region (Sendra *et al.*, 2012). This distributional pattern suggests that East Asia may represent the centre of origin for the Plusiocampinae subfamily. Further support for this hypothesis lies in the fact that current knowledge of species diversity is based on limited sampling efforts, as evidenced by the relatively sparse literature drawn from only 11 key studies (Silvestri 1931; Condé 1956b, 1993; Bareth & Condé 1972; Chevrizov 1978; Chou & Tong 1980, 1981; Sendra *et al.* 2017b, 2021a, 2021b, 2022; Sendra & Deharveng 2020). Increasing sampling efforts in East and Central Asia is likely to reveal a high number of new species, primarily those inhabiting subterranean ecosystems. In fact, most Plusiocampinae species live in both shallow and deep subterranean habitats such as caves. Approximately 82% of all species show cave-adapted morphological traits, including slender bodies, elongated appendages, and highly developed sensory structures (Condé 1956a; Bareth & Pagés 1994; Sendra *et al.* 2017a, 2021c).

Anatoliacampa pax Sendra & Mehrafrooz sp. nov. is a cave-adapted member of the subfamily Plusiocampinae, although its morphology is not fully consistent with the typical troglomorphic condition. Its body is relatively robust, and the antennae are shorter than its body's length, features that resemble those of soil-dwelling species. However, it exhibits 32 to 38 antennomeres, and the cerci are 1.1 to

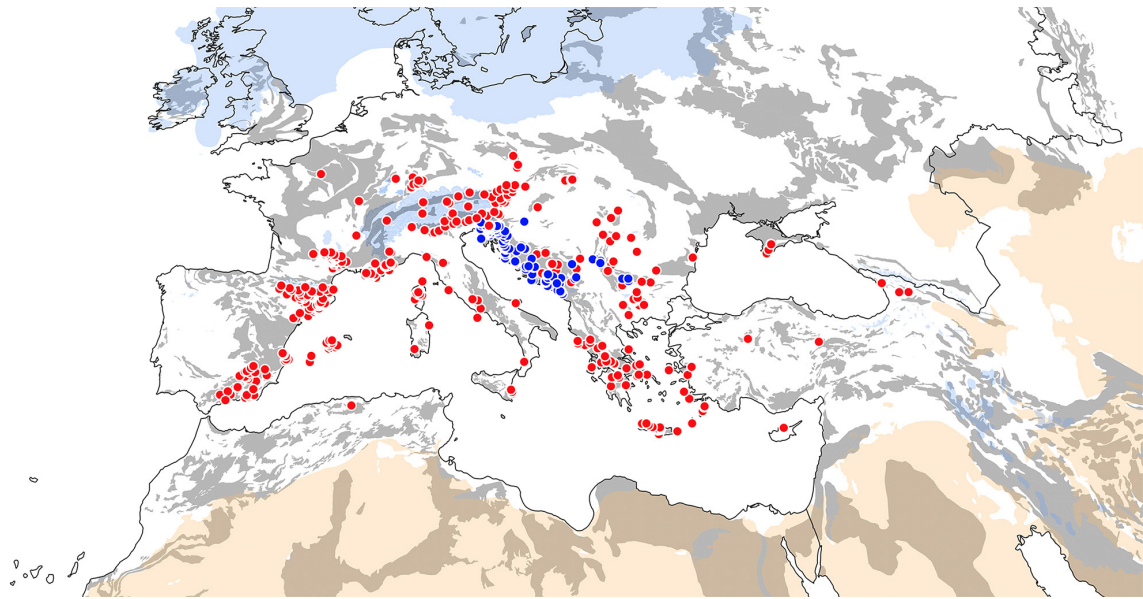


Fig. 9. Euro-Mediterranean distribution of *Plusiocampa*. In dotted grey: karst areas (Chen *et al.* 2017). In orange: deserts (Olson & Dinerstein 2002). In blue: ice cover during the Last Glacial Maximum (Ehlers *et al.* 2011). Red circles: *P. (Plusiocampa)* spp. Blue circles: *P. (Stygiocampa)* spp.

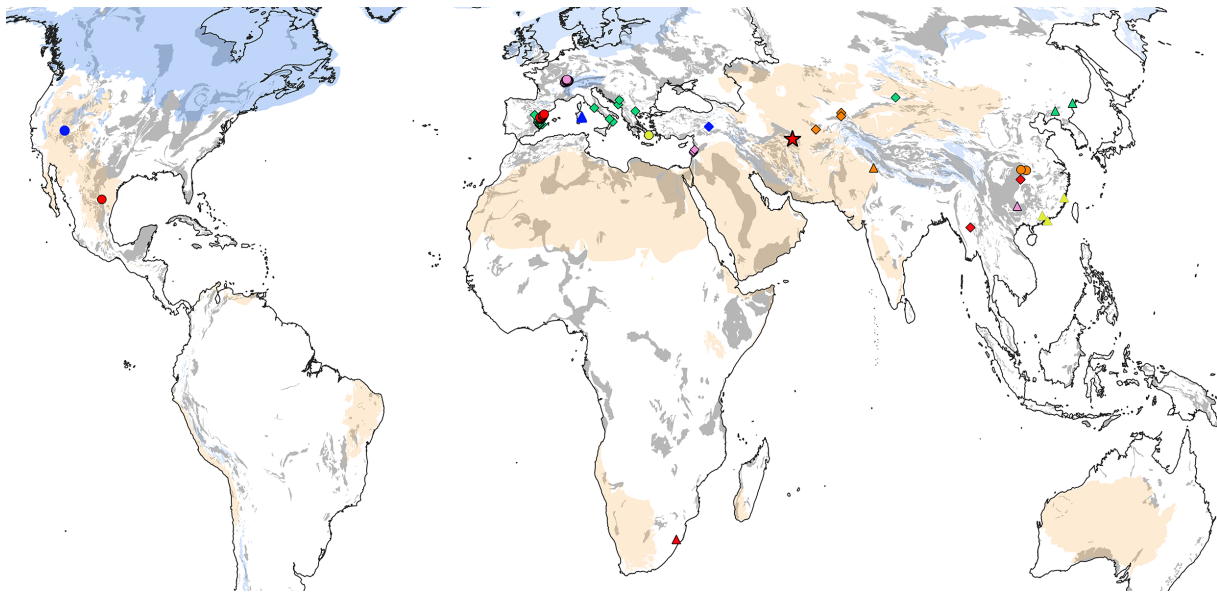


Fig. 10. Worldwide distribution of Plusiocampinae (excluding *Plusiocampa* for clarity, see Fig. 8). In dotted grey: karst areas (Chen *et al.* 2017). In orange: deserts (Olson & Dinerstein 2002). In blue: ice cover during the Last Glacial Maximum (Ehlers *et al.* 2011). Blue diamond: *Anatoliacampa* spp. also red star for *A. pax* Sendra & Mehrafrooz sp. nov. Red diamonds: *Anisuracampa* spp. Green diamonds: *Cesticampa* spp. Blue circle: *Condeicampa* spp. Green circles: *Cycladiacampa* spp. Orange circles: *Hubeicampa* spp. Pink circle: *Hystrichocampa* spp. Red circles: *Paratachycampa* spp. Blue triangles: *Patricicampa* spp. Green triangles: *Plutocampa* spp. Red triangles: *Silvestricampa* spp. Orange triangles: *Simlacampa* spp. Orange diamonds: *Turkmenocampa* spp. Pink diamonds: *Vandelicampa* spp. Pink triangle: *Whittencampa* spp.

1.2 times as long as the body length, values that exceed the average for edaphic species and are similar to those observed in other cave-adapted Campodeidae (Condé 1956a; Sendra *et al.* 2017a). In addition to this cave-adapted features, the sensory apparatus of *A. pax* includes numerous long and slender gouge sensilla, as well as approximately 10 complex olfactory chemoreceptors in the cupuliform organ. These chemoreceptors are composed of a central column surrounded by a spiral fold with five to six turns (Fig. 2A–D), a configuration characteristic of cave-adapted species (Sendra *et al.* 2021c).

From a palaeogeographical perspective, this new finding—the second known species of the genus *Anatoliacampa*—reinforces the hypothesis suggested by Sendra *et al.* (2022) that Anatolia and the nearby eastern karst areas of Iran may have functioned as a land bridge facilitating the colonization of the Euro-Mediterranean region by cave-adapted Plusiocampinae and their few soil-dwelling relatives.

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Supplementary file

Supp. 1. List of species of Plusiocampinae. <https://doi.org/10.5852/ejt.2026.1034.3159.14061>