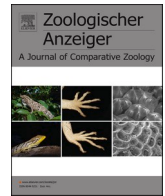


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New evidence for an Anatolian bridge: Colonization of Euromediterranean lands by cave-adapted Plusiocampinae (Diplura, Campodeidae), with establishment of a new genus

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ABSTRACT

A new genus of Plusiocampinae (Diplura, Campodeidae), *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov., is described from specimens found in the Southeastern Anatolian Peninsula in Dicle cave (Bozaba village, Dicle district, Diyarbakir province, Turkey). Based on its morphological characteristics and molecular analysis, the new taxon undoubtedly belongs to the well-established subfamily Plusiocampinae and occupies, like most species of the subfamily, cave habitats. *Anatoliacampa diclensis* has two important features: its unique pretarsus and the abundant distribution of urosternal macrosetae. The finding of this new taxon is of high palaeogeographic interest, as it provides new evidence for establishing Anatolia as a land bridge for the colonization of the Euro-Mediterranean lands by cave-adapted Plusiocampinae and their few soil-dwelling relatives.

1. Introduction

The Diplura are a primitive group of entognathan hexapods closely related to Insecta (Koch, 2009). Its primitive origin as a terrestrial group, given that it is wingless and tightly dependent on high humidity levels, causes it to have poor dispersal capacity, which in turn makes dipluran species an ideal subject for biogeographical studies (Sendra et al., 2021a). Cave-adapted species are particularly relevant for studies with palaeogeographical implications (Sendra et al., 2020b), and Diplura is one of the hexapod orders with the highest proportion of troglobites (Deharveng & Bedos, 2018). Campodeidae is the most diverse family of diplurans, accounting for 49% of the total number of extant species in the order and it is by far the best represented in cave ecosystems (Sendra et al., 2020b). Currently, about 500 species of campodeids have been described, of which 31% (i.e., 156 species) are cave-adapted taxa

(Sendra et al., 2020b; 2021b; 2021c; 2021d). Campodeidae comprises four subfamilies, with Plusiocampinae having the largest number of cave-adapted species (83 species), most of which present a Euro-Mediterranean distribution (Sendra et al., 2020a). The exception to this distribution is the Anatolian Peninsula, where the only Plusiocampinae are three soil-dwelling species: *Plusiocampa (Plusiocampa) exsulans* Condé, 1947, *Plusiocampa (Plusiocampa) festae* Silvestri, 1933, and *Plusiocampa (Plusiocampa) solerii* Silvestri, 1933 (Sendra et al., 2006; 2010). The existence of cave-adapted species belonging to Plusiocampinae – or any cave diplurans for that matter – was unknown until two authors from this study (ST and AS) conducted field sampling in an isolated cave in the Dicle region of the eastern Anatolian Peninsula.

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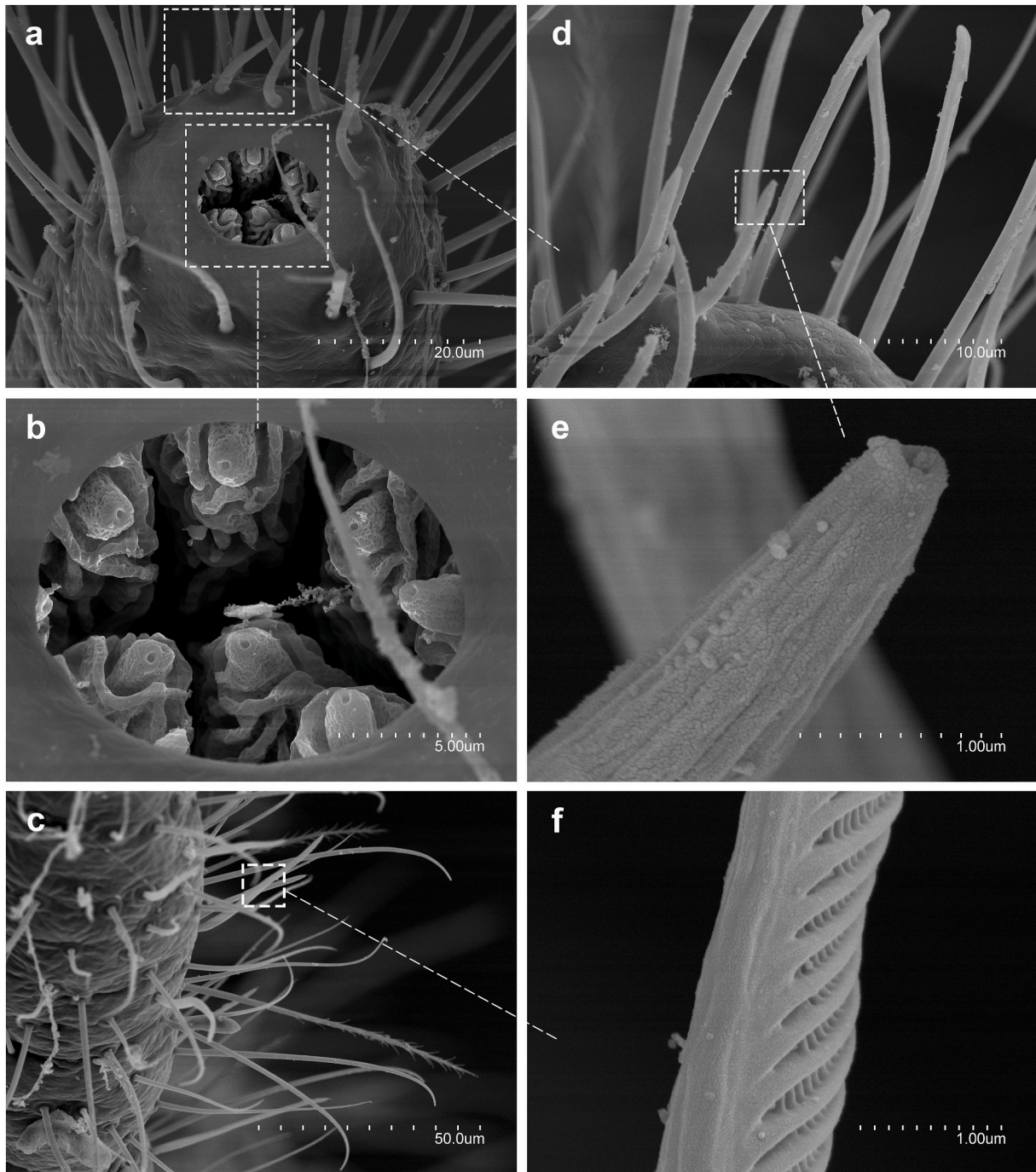


Fig. 1. SEM micrographs of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov. (a) Cupuliform organ of the apical antennomere. (b) Detail of sensilla of the cupuliform organ. (c) Lateral view of the apical antennomere. (d) Glandular setae on the exterior rim of the cupuliform organ. (e) Detail of apical portion of glandular setae. (f) Detail of medial portion of gouge sensilla.

2. Material and methods

Diplurans, three specimens in total, were sampled by hand using an aspirator in the dark zones of Dicle cave during 2018 and 2019. The specimens were transferred to vials containing 70% ethanol. The holotype is deposited at the Zoology Museum (DUZM), Dicle, Turkey; and the paratype at the Museu de Ciències Naturals de Barcelona (MZB, MCNB), Barcelona, Spain. The third specimen used for scanning electron microscopy (SEM) and DNA analysis is in the private collection of Alberto Sendra (coll. AS), València, Spain.

2.1. 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 of the head to the supra-anal abdominal valve. One specimen was coated with palladium-gold for SEM photography (Hitachi S-4900) and sensilla measurements. The morphological descriptions and abbreviations

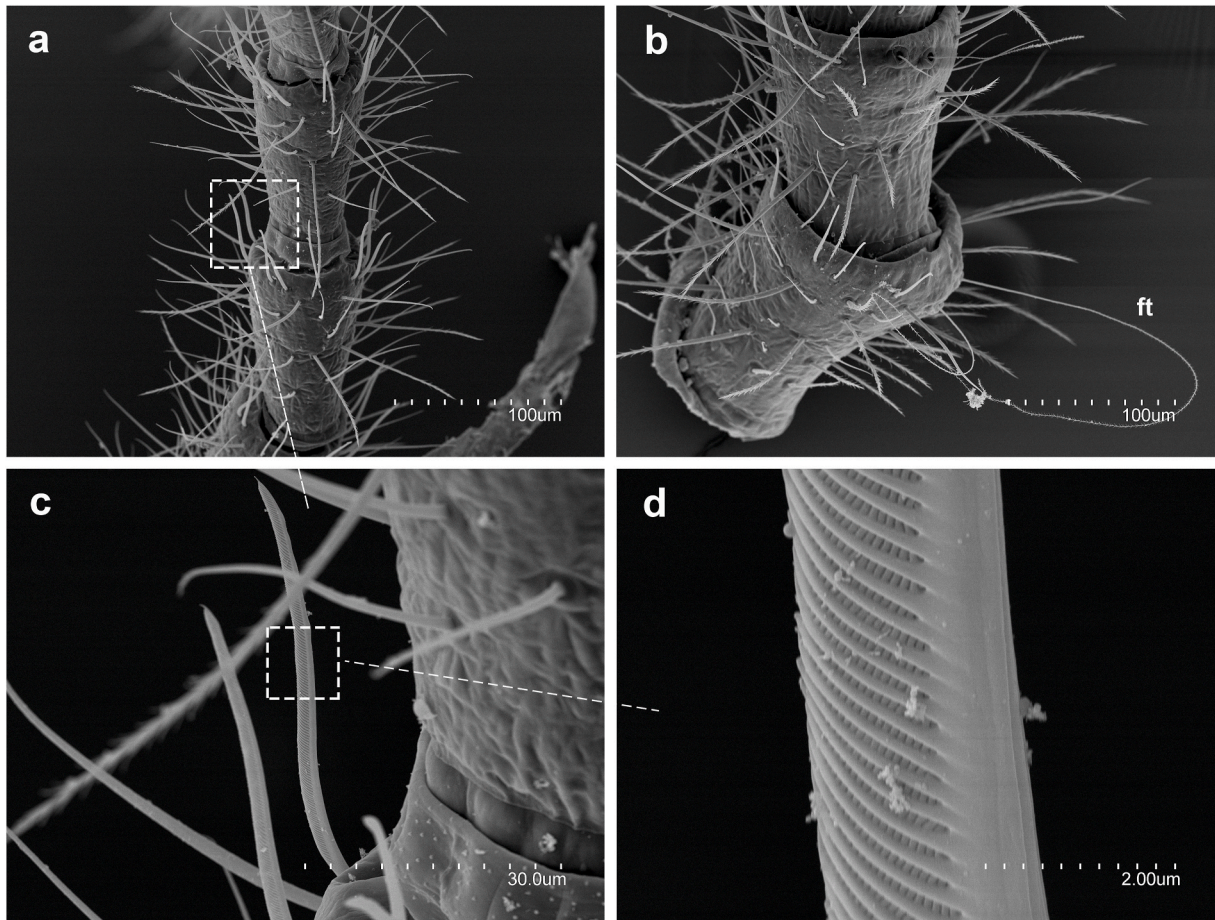


Fig. 2. SEM micrographs of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov. (a) Medial antennomeres. (b) Proximal antennomeres. (c) Distal gouge sensilla on a medial antennomere. (d) Detail of central portion of gouge sensilla. Abbreviation: ft, flagellum of the trichobothria.

follow Condé (1956a): *ma*, medial-anterior, *la*, lateral-anterior, *lp*, lateral-posterior, *mp*, medial posterior and *post*, posterior. The term gouge sensilla is used for the concavo-convex shaped sensilla on antennae, following Bareth & Condé (1981).

2.2. Molecular analysis

Total genomic DNA extraction was performed using the Chelex-resin method (Palero et al., 2010) after morphological examination and drawing of the specimens. In order to amplify the standard COI gene region, we used the pair of primers proposed by Krehenwinkel et al. (2018) specifically for arthropod studies [ArF1: 5' – GCNCCWGAYATRGCNTTYCCNCG – 3' (Gibson et al., 2014) and Fol-degen-rev: 3' – TANACYTCNGGRTGNCCRAARAAYCA – 5' (Yu et al., 2012)]. Amplifications were carried out using ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1 × buffer (Amersham), 0.2 mM of each primer, and 0.12 mM dNTPs. The polymerase chain reaction (PCR) thermal profile was 94 °C for 4 min for initial denaturation, followed by 30 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s, and a final extension at 72 °C for 4 min. Amplified PCR products were cleaned with Exo-SAP enzyme and sequenced using the Big-Dye Ready-Reaction kit ver. 3.1 (Applied Biosystems) on an ABI Prism 3770 automated sequencer (Macrogen, Spain).

Chromatograms for each DNA sequence were checked with BioEdit v7.2.5 (Hall, 1999) and all sequences were translated into amino acids to detect possible insertions and/or stop codons to rule out the presence of pseudogenes. Sequence alignment was conducted using the program Muscle v3.6 (Edgar, 2004) with default parameters. The model selection was carried out according to the BIC criterion, as implemented in MEGA

X (Kumar et al., 2018), and the selected model was used to obtain the maximum-likelihood (ML) phylogenetic tree using RAxML.

3. Results

3.1. Systematics

Class Diplura Börner, 1904.

Superfamily Campodeoidea Lubbock, 1873.

Subfamily Plusiocampinae Paclt, 1957.

Genus *Anatoliacampa* Sendra, Tusun & Satar gen. nov.

Type species. *Anatoliacampa diclensis* Sendra, Tusun & Satar sp. nov.

Etymology. The genus is named in reference to the Anatolian Peninsula and the suffix -campa, traditionally used in Campodeidae taxonomy. The gender of the name is feminine.

Diagnosis. Troglomorphic body and appendages. Cupuliform organ of antennae with complex olfactory chemoreceptors; frontal process of head slightly protruding, with non-tubercular setae. Pronotum 1 + 1 *ma*, 2 + 2 *la*_{1,3}, 2 + 2 *lp*_{2,3}; mesonotum and metanotum 1 + 1 *ma*, 2 + 2 *la*_{1,2}, 2 + 2 *lp*_{2,3}. Femora I–III with two dorsal macrosetae. Tibiae II–III without macrosetae. Claws subequal, with well-developed crests. Pretarsal process start in a laminar shape and extend to a narrow axis, divided into multiple fringes: simple or subdivided with a hook ending. Urotergites 1 + 1 *post*₁ on I–IV; 0 + 0 or 1 + 1 *la*, 3+3–4+4 *post*_{1–4} on V–VII, 5+5–6+6 *post*_{1–6} on VIII, and 8 + 8 *post*_{1–8} on IX. Urosternite I with up to 32 macrosetae; urosternites II–VII with up to 16 macrosetae; urosternite VIII with 3 + 3 macrosetae. Male urosternite I appendages subcylindrical, with up to 200 glandular *a*₁ setae. Female urosternite I appendages coniform, with up to 11 glandular *a*₁ setae.



Fig. 3. Thoracic nota of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov., ♀-holotype (DUZM-2121).

Anatoliacampa diclensis Sendra, Tusun & Satar sp. nov.

Etymology. The specific epithet refers to both the name of the cave and the name of the region of the type's locality.

Type locality. Dicle Cave, Bozaba village, Dicle district, Diyarbakir province, Southeastern Anatolian region, Turkey.

Holotype. TURKEY. ♀ (labelled as holotype-♀ DUZM-2121). Dicle Cave, Bozaba village, Dicle district, Diyarbakir province, Southeastern Anatolian region, 38°19'23" N, 40°06'25" E. Sadreddin TUSUN and Ali SATAR leg.

Paratype. TURKEY. ♂ (labelled as paratype-♂1 MZB (MCNB) 2022-5694), same locality, date, and collectors as holotype.

Other material. ♀ (coll. AS), same locality, date and collectors as types; specimen used for scanning electron microscopy (SEM) and DNA analysis.

Description. Body. Body length 5.6 mm (female, holotype) and 5.8 mm (male, paratype). Epicuticle smooth under compound microscope and SEM; with thin, medium-sized clothing covered by thin distal barbs.

Head. Antennae complete (Figs. 1 and 2), with 41 antennomeres. Small, subcylindrical sensillum on third antennomere located in ventral position between *c* and *d* macrosetae; flagellum of the trichobothria very long (Fig. 2b). Central antennomeres $2.3 \times$ as long as wide, with large barbed and short setae distributed in two to three whorls, in addition to one distal whorl of about 12 thin gouge sensilla 40–50 μm long (Fig. 2a, c, d). Apical antennomere with sensorial equipment of: cupuliform organ with about 12 complex olfactory chemoreceptors (each chemoreceptor is composed of a central column with the typical apical hole surrounded by irregular folds in a cauliflower shape and its surface is entirely reticulated and perforated) (Fig. 1a and b); numerous gouge sensilla 25–50 μm long (Fig. 1c, f); a few short bacilliform sensilla; several glandular setae on the edge of the hole of the cupuliform organ (Fig. 1a, d, e); and numerous long barbed setae. Frontal process slightly protruding, plain, and with one distal and two posterior non-tubercular setae; macrosetae along the insertion line of antennomere I similar in length, *x* setae the longest (*a/i/p/x* with relative lengths of 23/25/21/40 in holotype), all with very thin distal barbs. Labial palpus suboval, with a bacilliform latero-external sensillum, two guard setae on internal side, up to 8 setae on anterior border, and up to 150 neuroglandular setae in holotype, and 180 neuroglandular setae in paratype.

Thorax. Macrosetal distribution (Fig. 3): pronotum with 1 + 1 *ma*, 2 + 2 *la*_{1,3}, 2 + 2 *lp*_{2,3}; mesonotum with 1 + 1 *ma*, 2 + 2 *la*_{1,2}, 2 + 2 *lp*_{2,3}; metanotum with 1 + 1 *ma*, 2 + 2 *la*_{1,2}, 2 + 2 *lp*_{2,3}. All notal macrosetae long and with thin barbs along distal half to two thirds; marginal setae longer than clothing setae, with thin barbs along distal half. Legs elongated, pretarsus of metathoracic leg overpasses end of abdomen. Lengths of metathoracic leg segments on holotype/paratype: coxa 0.26/0.30, trochanter 0.20/0.25, femur 0.98/1.05, tibia 1.19/1.30, tarsus 0.88/0.90; total: 3.51/3.80. Femora I–III with two long barbed dorsal macrosetae in the distal third of femur and one shorter barbed ventral macroseta inserted near central position (Fig. 4a). Tibia I with one or two short barbed ventral macrosetae; tibiae II–III without macrosetae. Calcars on tibiae covered with thin, short barbs. Tarsi with two rows of thick ventral setae with very thin barbs except on the apical portion. Four long barbed setae on dorsal subapical end of the tarsi. Claws (Fig. 4b–f) subequal with well-developed crests and a slightly backward overhang on both claws; the dorsal side is almost smooth and the ventral side has thin longitudinal grooves. Pretarsal lateral process start in laminar shape and extend into a narrow axis overpassing the end of the claws, which is divided into multiple fringes: simple or subdivided and with a hook ending.

Abdomen. Distribution of macrosetae on tergites: 1 + 1 *post*₁ on I–IV; 0 + 0, 0 + 1 *la*, 3 + 3 *post*_{1–3} or 4 + 4 *post*_{1–4} on V; 0 + 0, 0 + 1, 1 + 1 *la*, 4 + 4 *post*_{1–4} on VI–VII; 5 + 5 or 6 + 6 *post*_{1–6} on VIII, and 8 + 8 *post*_{1–8} on abdominal segment IX. All post urotergal macrosetae long and covered by thin barbs along distal four-fifths; *la* urotergal macrosetae shorter than *post* macrosetae, covered by barbs along distal half. Urosternite I with 11 + 12 macrosetae on holotype and 15 + 17 macrosetae on

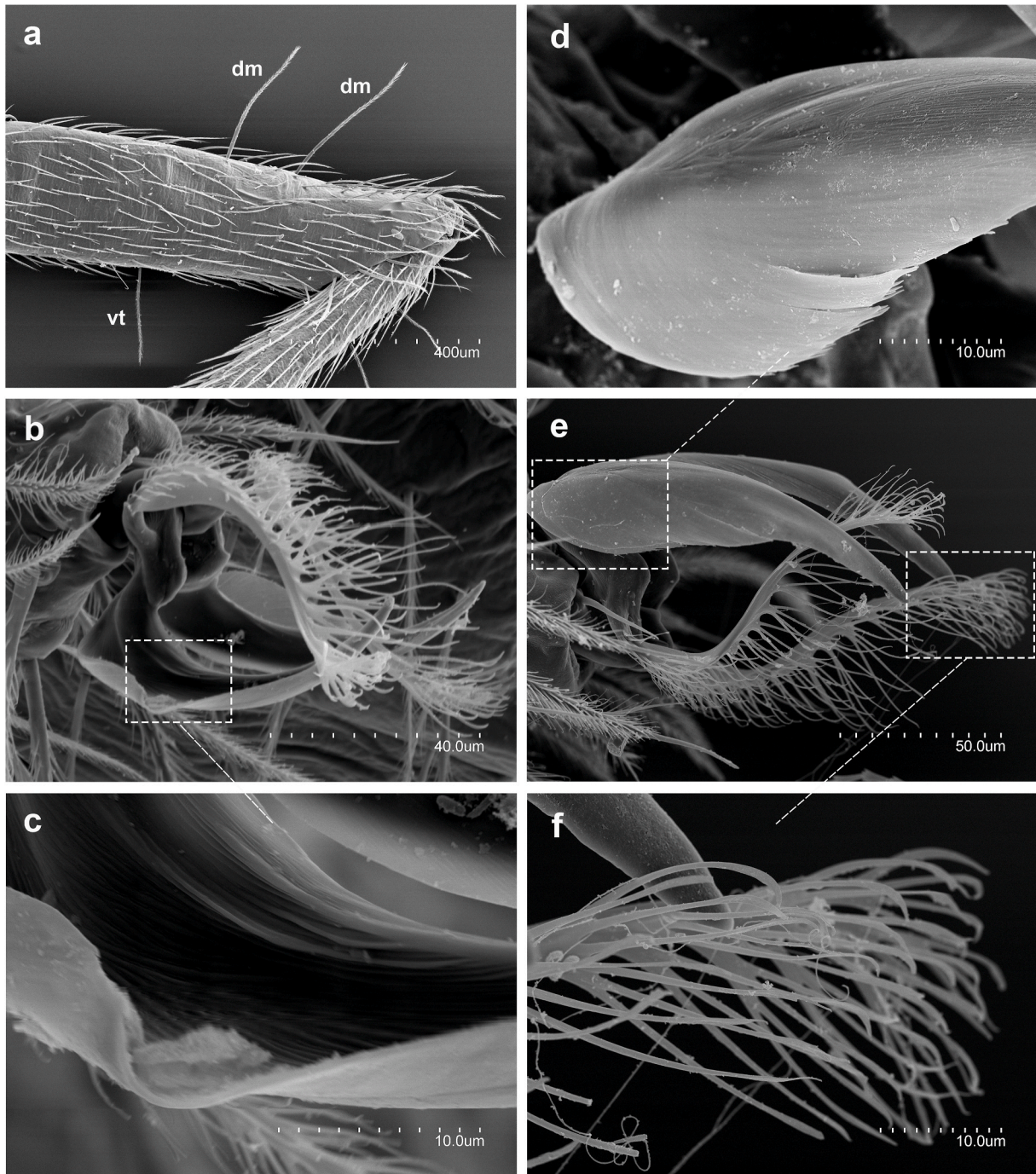


Fig. 4. SEM micrographs of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov., metathoracic leg. (a) Distal portion of the metathoracic leg. (b) Lateral view of pretarsus in upward position. (c) Detail of lateral crest of the pretarsus. (d) Dorsal proximal portion of lateral crest. (e) Lateral view of pretarsus in downward position. (f) Distal portion of the lateral processes of the pretarsus. Abbreviations: dm, dorsal macrosetae; vt, ventral macrosetae.

paratype (Fig. 5a and b); urosternites II–VII with 7+7–8+8 macrosetae; urosternite VIII with 3 + 3 macrosetae; all urosternal macrosetae robust and large, covered by long barbs along distal third to four-fifths. Styli with apical, subapical, and ventromedial setae completely surrounded by thin and short barbs (Fig. 6b). Eversible vesicles large, with two distinct zones: the distal one with an almost smooth surface with a sinuous border and the proximal one with a rough surface densely covered by minute dots (Fig. 6a). Gonopore of the genital papilla surrounded by 19 short setae (in paratype male). Cerci lost in all three specimens.

Secondary sex characters. Male urosternite I (Fig. 5a) with very

large appendages, almost subcylindrical, with up to 200 glandular α_1 setae. Female urosternite I (Fig. 5b) with thinner subcylindrical appendages, almost coniform, with up to 11 glandular α_1 setae.

3.2. Molecular analysis

The new COI sequences have been uploaded to Genbank with codes: OM680964–OM680970. The selected nucleotide substitution model after alignment was GTR + G + I (BIC = 8561.95), with the proportion of invariant sites (I = 0.45) and estimated alpha parameter for the gamma distribution ($\alpha = 0.99$), indicating a significant heterogeneity in

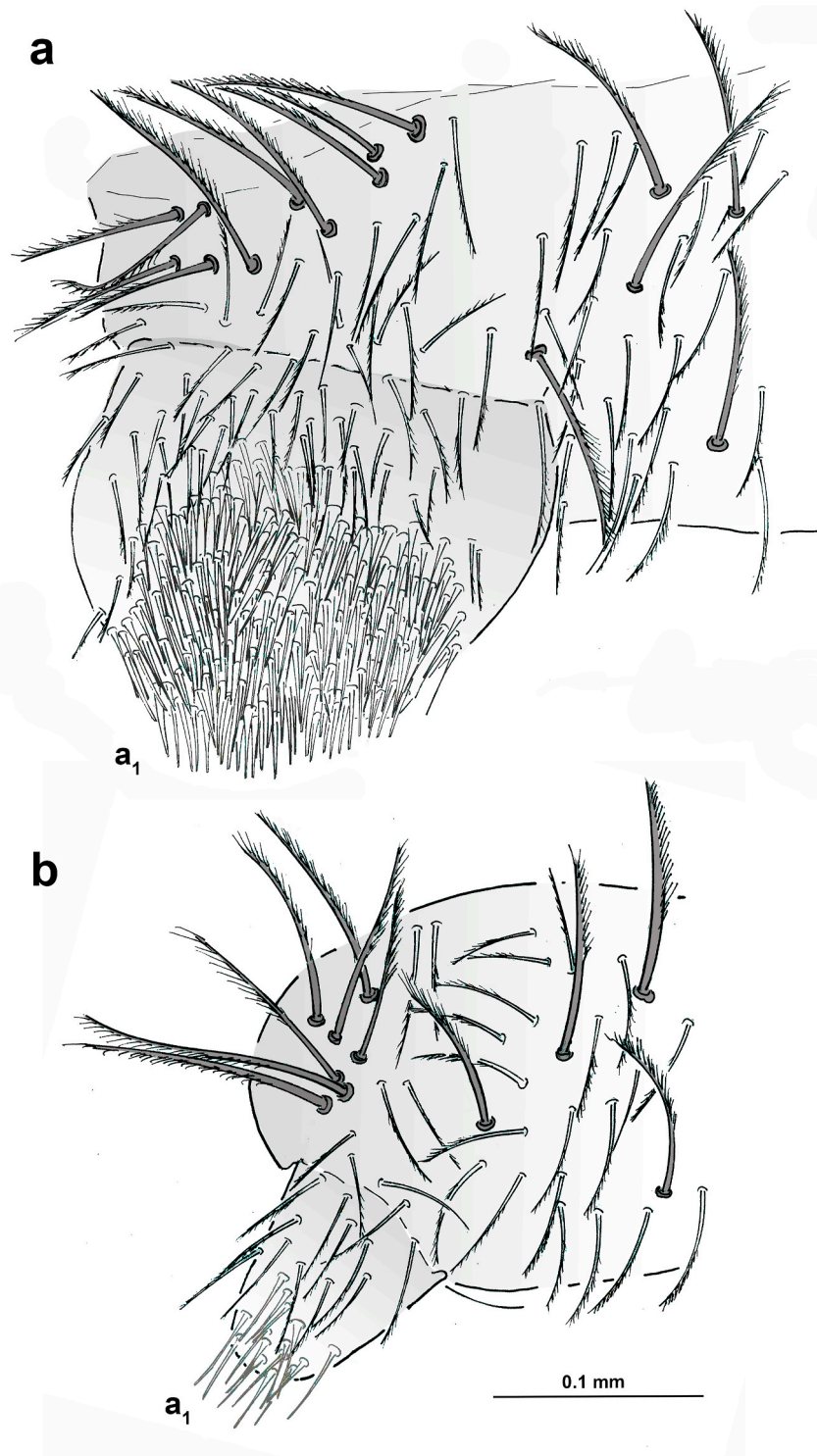


Fig. 5. *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov. (a) Urosternite I of the male, δ - paratype (MZB (MCNB) 2022-5694). (b) Urosternite I of the female, ♀ - holotype (DUZM-2121). Abbreviation: a_1 , glandular a_1 setae.

the DNA substitution among sites. The ML phylogenetic tree showed Plusiocampinae sequences form a well-supported clade, nested within Campodeidae and clearly distinct from Japygidae (Fig. 9). *Anatoliacampa diclensis* Sendra, Tusun & Satar sp. nov. grouped with *Plusiocampa* (*Plusiocampa*) *imereti* Sendra & Barjadze, 2021 (Sendra et al., 2021d) from Georgia and *Plusiocampa* (*Stygiocampa*) *bureschi* Silvestri, 1931 from Bulgaria, whereas *Plusiocampa* taxa from Iberian Peninsula [e.g. *Plusiocampa* (*Plusiocampa*) *gadorensis* Sendra, 2001, *Plusiocampa*

(*Plusiocampa*) *baetica* Sendra, 2004 (Sendra et al., 2004) or *Cestocampa iberica* Sendra & Condé, 2012 (Sendra et al., 2012)] clustered in separate clades.

3.3. Habitat

Dicle cave is excavated in carbonate rocks of the Firat formation, Eocene to Miocene in age. It has one artificial entrance, 2 m \times 1.5 m size,

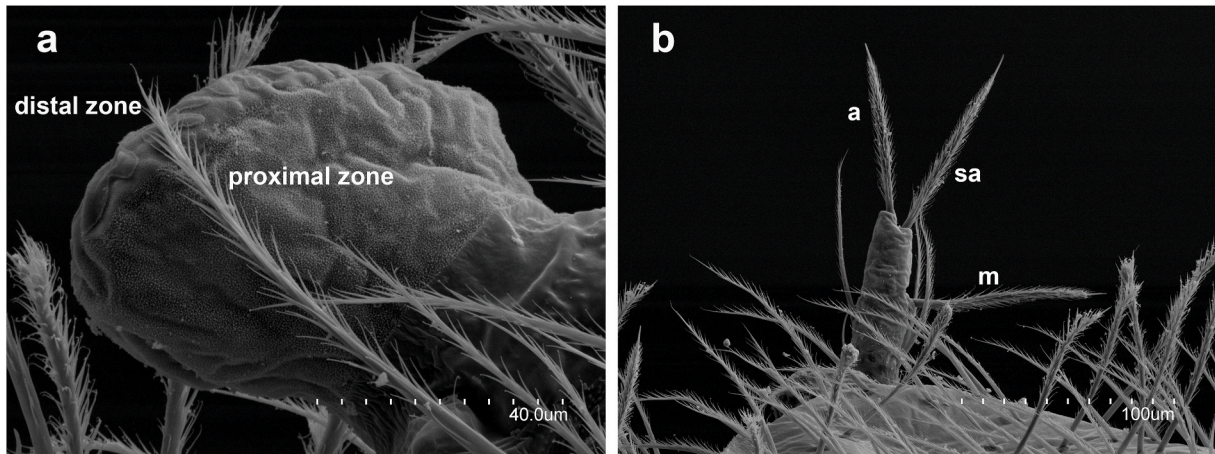


Fig. 6. SEM micrographs of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov. (a) Right eversible vesicle on an abdominal segment. (b) Right stylus on abdominal segment IV. Abbreviations: a, apical; sa, subapical; and m, medial macrosetae.



Fig. 7. Deep zone in Dicle cave, type locality of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov.

protected by a metal grid. It gives access to a large room with plenty of speleothems, 80 m long and 60 m wide, which goes down to a depth of 13 m (Fig. 7). The cave has no water pools or watercourse but some deep corners have hidden places where specimens of *Anatoliacampa diclensis* Sendra, Tusun & Satar gen. et sp. nov. were sampled. In summer, the outside environment reaches 35 °C and 27% humidity, while the general atmosphere inside the cave stays at 23 °C and 60% humidity.

4. Discussion

4.1. Phyletic affinities

Anatoliacampa Sendra, Tusun & Satar gen. nov., a new genus with highly cave-adapted features, is another remarkable surprise in the recent discoveries of Plusiocampinae taxa. In the last five years four genera for the Euro Asiatic region have been described: *Turkmenocampa* Sendra & Stoev, 2017 (Sendra et al., 2017), *Whittencampa* Sendra & Deharveng, 2020, *Cycladiacampa* Sendra, 2020 (Sendra et al., 2020c), and *Hubeicampa* Sendra & Lips, 2021 (Sendra et al., 2021c); in addition to 19 other species (Sendra et al., 2019; 2020a; 2021b; Sendra & Weber

2018). Although the number of DNA sequences from dipluran taxa available on public databases (e.g. Genbank or BOLD) remains low, include poor identifications and show strong biases, our new molecular data suggest some affinities with taxa from Bulgaria and Georgia (*Plusiocampa* (*Stygiocampa*) *buresschi* and *Plusiocampa imereti*, respectively). Nevertheless, *Anatoliacampa diclensis* presents a distinctive combination of characters that supports its establishment as a separate genus, namely: gouge sensilla and glandular setae on last antennomere; fringed lateral processes on the pretarsus; subequal claws with large lateral crests; pronotum with no more than 1 + 1 *ma*, 1 + 1 *la* and 2 + 2 *lp* macrosetae (synapomorphic feature share with Plusiocampinae e.g., Condé, 1956a; Paclt, 1957; Sendra et al., 2020a), and meso- and metanotum without medial posterior macrosetae; metathoracic legs with two dorsal macrosetae on femora and no macrosetae on tibiae; large suboval appendages on first urosternite in males with *a*₁ glandular setae and no *g*₁ glandular setae; calcars and styler setae completely barbed; up to 32 macrosetae on first urosternite, up to 16 macrosetae on urosternites II–VII, and 3 + 3 macrosetae on urosternite VIII; and 1 + 1 *post* macrosetae on urotergites I–IV, and 1 + 1 *la* plus 4 + 4 *post* on urotergites VI–VII.



Fig. 8. Colonization way of Euromediterranean lands during the end of the Oligocene, 25 m. a. Abbreviations, taxonomic groups: Ces: *Cestocampa*; Par: *Paratychycampa*; Pat: *Patrizicampa*; Sty: *Stygiocampa*; Cycl: *Cycladiacampa irakleiae*; Anat: *Anatoliacampa diclensis*; Red highlights the current distribution of *Plusiocampinae* in Euromediterranean lands; the red arrow indicates the direction of the *Plusiocampinae* arrival from East Asia. source map © 2020 Colorado Plateau Geosystems Inc. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The unique sensorial equipment on the last antennomere, with glandular setae and gouge sensilla, is an apomorphic taxonomic character that defines the new taxon *Anatoliacampa diclensis* Sendra, Tusun & Satar sp. nov. The pretarsus shape, with fringed lateral process, places *Anatoliacampa* Sendra, Tusun & Satar gen. nov. close to *Anisuracampa* Xie & Yang, 1991, represented by two species from Southeast Asia (*Anisuracampa suoxiensis* Xie & Yang, 1991 a soil-dwelling species from Hunan Province in southeastern China and *Anisuracampa ywangana* Sendra & Komerički, 2021 (Sendra et al., 2021c) a cave-dwelling species from Myanmar), and *Simlacampa* Condé, 1956 (Condé, 1956a, b) with a single cave-dwelling species (i.e. *Simlacampa clayae* Condé, 1956 (Condé, 1956a, b) from northwest India. Nevertheless, the ventral side of claws have spiniform formations in *Anisuracampa* and *Simlacampa*, which are completely absent in *Anatoliacampa*. Both *Anisuracampa* and *Anatoliacampa* share the presence of more than one dorsal macrosetae on femora, but they are differentiated by the number and distribution of notal macrosetae and the numerous urosternal macrosetae on all urosternites. While *Anatoliacampa* has 3 + 3 macrosetae on urosternite VIII, *Anisuracampa* has a common distribution pattern, that is, I, II–VII and VIII (7 + 7, 5 + 5 and 1 + 1 macrosetae). These numerous urosternal macrosetae, in addition to calcars and completely barbed stylar setae, are also found in a few species of *Plusiocampa* Silvestri, 1912, mostly within species of the *Stygiocampa* Silvestri, 1934 subgenus, *Cestocampa iberica* Sendra & Condé, 2012 (Sendra et al., 2012), and two monotype genera: *Patrizicampa* Condé, 1962 and *Cycladiacampa* Sendra, 2020 (Sendra et al., 2020c). Furthermore, this character is shared with *Paratychycampa* Wygodzinsky, 1944 genus (Bareth & Condé, 1981; Sendra et al., 2020a; 2021b). In conclusion, *Anatoliacampa* showcases two important features: its unique pretarsus and the abundant urosternal macrosetae distribution.

4.2. Palaeogeography and geological setting of anatolian and colonization way

The arrival of the subfamily *Plusiocampinae* at the end of the Mesozoic and during the Cenozoic in the emerged European lands was

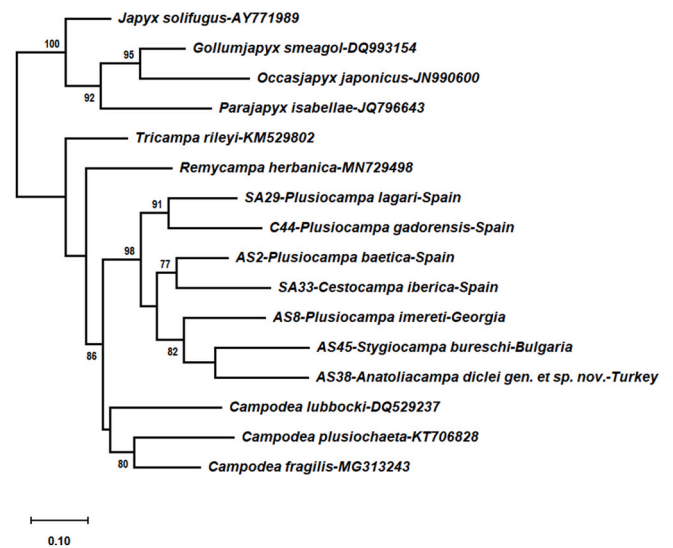


Fig. 9. Maximum likelihood (ML) tree obtained from CO1 sequence data showing significant (>70) bootstrap support values. *Anatoliacampa* clustered with *Plusiocampinae* representatives from Turkey and Bulgaria.

probably possible across the Anatolian land bridge that appeared due to the movement of the Arabic plate against Eurasia (Fig. 8). In this palaeogeographical scenario, the colonization of Europe from Asia was possible for terrestrial fauna (Briggs, 1995; Hallan, 1994; Popov et al., 2004; Rögl, 1999). The Anatolian bridge could have allowed the monophyletic *Plusiocampinae* to enter the Balkans and Dinarides and to probably reach the east and south of the Iberian lands at the end of Oligocene (ca. 25 m. a.), consequently moving through the Alps and the emerged lands of the Protoliguric massif (Sendra et al., 2004). At this time the European continent was connected to the microplates of Corsica and Sardinia, as well as to the Balearic and Kabylies in the

Protoliguric massif (Decourt et al., 2000). The ancestors of campodeids probably belonged to some genera of Campodeinae (such as *Campodea* Westwood, 1842, *Podocampa* Silvestri, 1932 and *Litocampa* Silvestri, 1933) and already inhabited the few European emerged lands during the Mesozoic and early Cenozoic (Sendra et al., 2004; 2019). The ancestors of Plusiocampinae were able to reach the European peri-Mediterranean regions by probably occupying the deep subterranean habitats where they flourished with great success up to today, which is showcased by the fact that most of their species have strong cave-adapted features such as increased sensitive equipment and enlarged and elongated bodies and appendages (Sendra et al., 2020a). *Stygiocampa* Silvestri, 1934 subgenus in the Dinarides and other less diverse genera such as *Cestocampa* in the Iberian and Italian Peninsulas, *Patrizicampa* in Sardinia, *Cycladiacampa* in the Cyclades Islands and *Vandelicampa* in the coast of the eastern Mediterranean seem to be the most primitive groups to reach the Mediterranean landmass. These first newcomers, as suggested by the distribution of different putative genera and subgenera of Plusiocampinae in the Mediterranean area (Sendra et al., 2020a), were followed much later by other Plusiocampinae, nowadays represented by many species among *Plusiocampa* s.str. Silvestri, 1912, *Didymocampa* Paclt, 1957, *Pentachaetocampa* Sendra & Weber, 2018 and *Venetocampa* Bareth & Condé, 1984, all subgenera of *Plusiocampa*. The current Plusiocampinae distribution might be explained mainly by tectonic plates and microplates drift theory, along with the dispersal, vicariance, and extinction processes that have taken place for hundreds of millions of years (Sendra et al., 2020b).

In such palaeogeographical context, *Anatoliacampa diclensis* could be considered a living fossil linking the Plusiocampinae of Asia and Europe as it is located in a cave-ecosystem in the middle of both emerged lands. This is another piece of evidence to support the hypothesis of the colonization of the European lands by the cave-adapted diplurans across the Anatolian bridge. As shown by recent studies (Sendra & Deharveng, 2020; Sendra et al., 2021b), East Asia has been suggested as the centre of origin for Plusiocampinae given the high diversity of this still poorly known region. Furthermore, the close similarities among *Anisuracampa*, *Simlacampa*, and the new *Anatoliacampa* support this idea.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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