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Systematics of the Sierra Nevada endemic earwig: *Eulithinus analis* (Forficulidae, Dermaptera)

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Abstract. Since the description of *Eulithinus analis* (Rambur, 1838) the taxonomic position of this Sierra Nevada endemic earwig has been controversial. It has been subdivided in different taxa, assigned to various genera or transferred to different subfamilies. With the aim of clarifying its systematics, we performed a mitochondrial phylogeographic analysis using specimens from different localities of Sierra Nevada representing the diverse phenotypes treated as differentiated taxa until now, and a phylogenetic analysis including representatives of apparently distant, but morphologically close, relatives. The phylogenetic and phylogeographic results obtained using mitochondrial (cytb, cox1) and nuclear (ITS2) markers and the study of morphological characters, indicate that the Sierra Nevada Mountain Range harbors a single species of the genus *Eulithinus*. Based on these molecular data, the morphological characters used to date in the internal taxonomy of this group of earwigs, especially size and shape of the cerci, lack diagnostic validity and show a large inter- and intra-populational variability. These results imply the synonymy of *Eulithinus montanus* (Steinmann, 1981) with *Eulithinus analis* (Rambur, 1838) syn. nov. and the reconsideration of *Eulithinus analis* outside the subfamily Allodahliinae. We established the synonymy between *Eulithinus analis* (Rambur, 1838) and *Forficula brevis* Rambur, 1838 syn. nov., a name that must be removed from the synonymy of *Forficula decipiens* Gené, 1832.

Keywords. Allodahliinae, *Pseudochelidura*, morphology, phylogeography, taxonomy.

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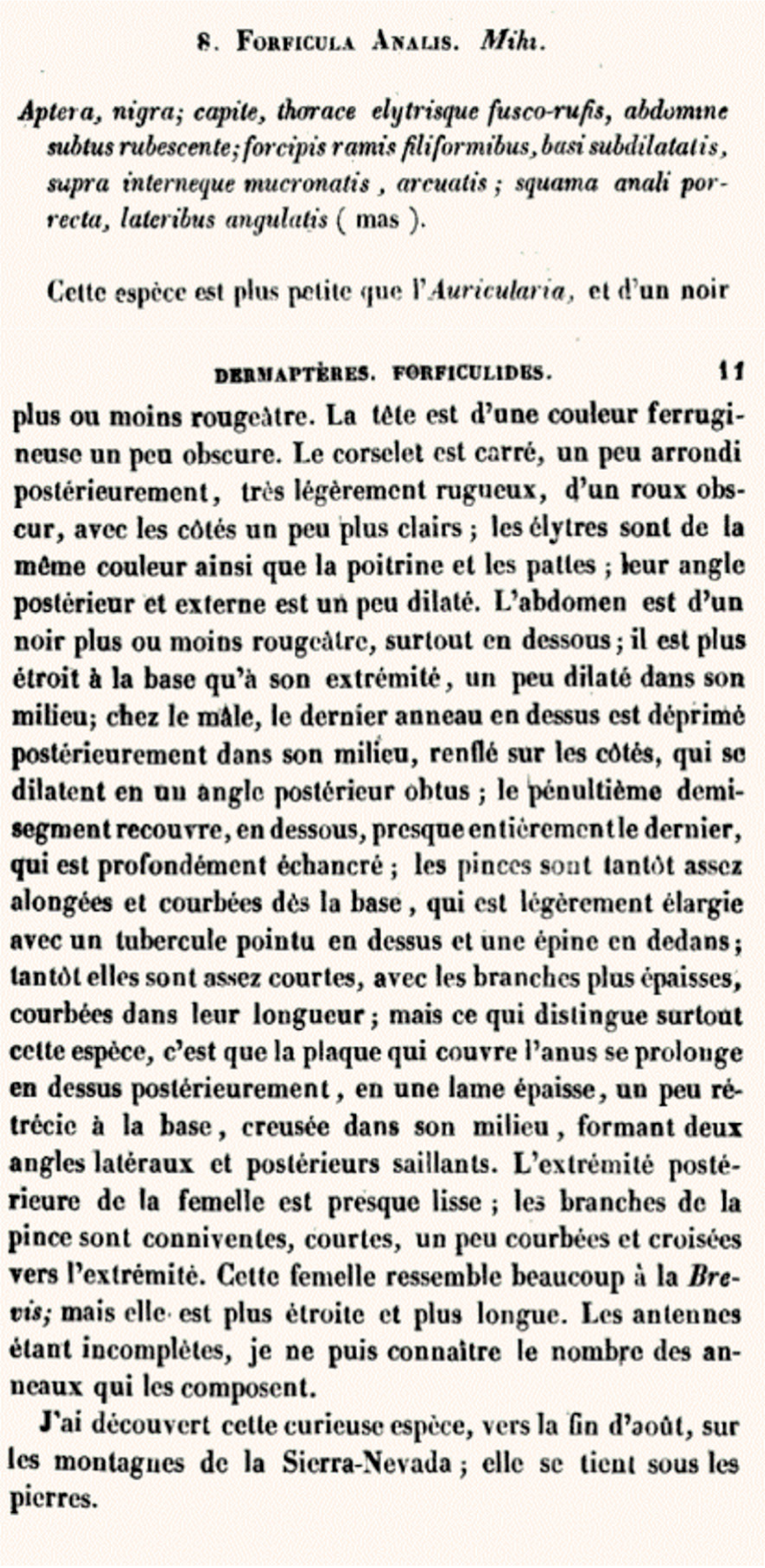
Introduction

The high elevations of the Sierra Nevada mountains, in southern Spain, are inhabited by an endemic set of earwigs, traditionally included in the genus *Eulithinus* Hincks, 1935 within the family Forficulidae Latreille, 1810. The discovery of the Sierra Nevada earwig was made by Rambur (1838), along a period of intense zoological exploration of the mountains of southern Spain (Waltl 1839; Rosenhauer 1856). The zoological exploration of today's Sierra Nevada National Park has been almost continuous since then. The Sierra Nevada mountain chain, which includes the highest elevations in continental Spain (Mulhacén, 3482 m), harbours an impressive list of endemic taxa (e.g., *Agriades zullichi* Hemming, 1933; *Polyommatus golgus* (Hübner, 1813); *Mylabris nevadensis* (Escalera, 1915); *Dinodes baeticus* Rambur, 1837; *Baetica ustulata* Rambur, 1838; *Eumigus rubioi* Harz, 1973) (Ruano & Tinaut 2003; Ruano *et al*. 2013).

Rambur's (1838) description of *Forficula analis* Rambur, 1838 depicted unambiguously the Sierra Nevada earwig: "This species is smaller than *auricularia*, and more or less reddish black. The colour of the head is a slightly obscure ferruginous. The corselet is square, a little rounded posteriorly, very slightly coarse, obscure red, with the sides a little lighter; the elytra are of the same colour as the prothorax and legs; their posterior and external angle is a little dilated. The abdomen is more or less reddish black, especially on the underside; it is narrower at the base than at the tip, and a little dilated in the middle; in the male, the last terguite is depressed posteriorly in the middle, and swollen on the sides, which dilate to form an obtuse posterior angle; the penultimate half-segment almost entirely covers the last, which is deeply indented, on the underside; the claws are either fairly long and curved from the base, which is slightly enlarged with a pointed tubercle on top and a spine on the inside; or they are fairly short, with the thicker branches curved along their length; but what particularly distinguishes this species is that the plate which covers the anus extends posteriorly into a thick blade, slightly narrowed at the base, hollowed out in the middle, forming two prominent lateral and posterior angles. The posterior end of the female is almost smooth; the branches of the claw are connivent, short, a little curved and crossed towards the end. This female is very similar to *brevis*, but narrower and longer. As the antennae are incomplete, I do not know how many rings they have. I discovered this curious species towards the end of August in the Sierra Nevada mountains; it lives under rocks" (translated from original in French; Fig. 1). But the taxonomic position of the species was controversial since then. The taxon was included subsequently in the genera *Chelidura* Latreille, 1825 (type species: *Forficula aptera* Mégerlé, 1825) by Dubrony (1878), *Lithinus* Burr, 1909 (type species: *Forficula analis* Rambur, 1838) by Burr (1909), *Eulithinus* Hincks, 1935 (replacement name for *Lithinus*) by Hincks (1935), *Pseudochelidura* Verhoeff, 1902 (type species: *Forficula sinuata* Germar, 1825) by Burr (1908) and Steinmann (1981), and *Eulithinus* again by most modern authors (e.g., Ebner 1959; Steinmann 1975, 1984; Harz & Kaltenbach 1976; Sakai 1992, 1996; Herrera Mesa 1999; Pérez-Valcárcel *et al*. 2022). The genus *Lithinus*, and its replacement name *Eulithinus*, were created to include only the Sierra Nevada earwig (Burr 1911; Hincks 1935), and although all recent authors retained the genus *Eulithinus* as valid, there is a long-standing controversy on its phylogenetic position. Most of the authors dealing with Sierra Nevada earwigs, included them in the subfamily Forficulinae Latreille, 1810, or Anechurinae Burr, 1907. However, Steinmann (1975), followed by Sakai (1992, 1996) and Herrera Mesa (1999) included them in the subfamily Allodahliinae Verhoeff, 1902, a subfamily previously considered to be restricted to eastern Asia (Srivastava 1993).



8. **FORFICULA ANALIS.** *Mihi.*

Aptera, nigra; capite, thorace elytrisque fusco-rufis, abdomine subtus rubescente; forcipis ramis filiformibus, basi subdilatatis, supra interneque mucronatis, arcuatis; squama anali porrecta, lateribus angulatis (mas).

Cette espèce est plus petite que l'*Auricularia*, et d'un noir

DERMAPTÈRES. FORFICULIDES. 11

plus ou moins rougeâtre. La tête est d'une couleur ferrugineuse un peu obscure. Le corselet est carré, un peu arrondi postérieurement, très légèrement rugueux, d'un roux obscur, avec les côtés un peu plus clairs ; les élytres sont de la même couleur ainsi que la poitrine et les pattes ; leur angle postérieur et externe est un peu dilaté. L'abdomen est d'un noir plus ou moins rougeâtre, surtout en dessous ; il est plus étroit à la base qu'à son extrémité, un peu dilaté dans son milieu; chez le mâle, le dernier anneau en dessus est déprimé postérieurement dans son milieu, renflé sur les côtés, qui se dilatent en un angle postérieur obtus ; le pénultième demi-segment recouvre, en dessous, presque entièrement le dernier, qui est profondément échancré ; les pinces sont tantôt assez alongées et courbées dès la base, qui est légèrement élargie avec un tubercule pointu en dessus et une épine en dedans ; tantôt elles sont assez courtes, avec les branches plus épaisses, courbées dans leur longueur ; mais ce qui distingue surtout cette espèce, c'est que la plaque qui couvre l'anus se prolonge en dessus postérieurement, en une lame épaisse, un peu rétrécie à la base, creusée dans son milieu, formant deux angles latéraux et postérieurs saillants. L'extrémité postérieure de la femelle est presque lisse ; les branches de la pince sont conniventes, courtes, un peu courbées et croisées vers l'extrémité. Cette femelle ressemble beaucoup à la *Brevis;* mais elle est plus étroite et plus longue. Les antennes étant incomplètes, je ne puis connaître le nombre des anneaux qui les composent.

J'ai découvert cette curieuse espèce, vers la fin d'août, sur les montagnes de la Sierra-Nevada ; elle se tient sous les pierres.

Fig. 1. Original description of *Eulithinus analis* by Rambur (1838) in the *Faune entomologique de l'Andalousie Vol. II.*

To complicate matters, Steinmann (1981, 1984, 1989, 1993), after a series of taxonomic inconsistencies involving Sierra Nevada earwigs (see García-París 2017 for the problems in Anisolabididae Verhoeff, 1902) described a second taxon within the genus *Eulithinus*: *Eulithinus montanus* (Steinmann, 1981), also endemic to Sierra Nevada. Since then, the systematics of the Sierra Nevada earwig became unsettled. Some authors followed more or less strictly Steinmann's (1975, 1979, 1981, 1984) taxonomic proposals (Herrera Mesa 1999; Haas 2010; Pérez-Valcárcel *et al*. 2022), while those with local knowledge of the Sierra Nevada fauna simply disregarded part of Steinmann's criteria without further comments (Lapeira & Pascual 1980; Pascual & Barranco 2013).

We had the opportunity to examine some of the type specimens used by Steinmann (1979, 1981, 1984) for his descriptions. At the same time, we were able to collect for study, specimens representing all the phenotypes treated as separate taxa of *Eulithinus* in the Sierra Nevada National Park, allowing us to perform morphological and molecular analyses.

The objective of this work is to clarify the systematics of the endemic Sierra Nevada earwigs related to the Rambur' species (originally *Forficula analis*), in order to solve the taxonomic problems that complicate their ecological study and especially their conservation. The particular objectives are (1) to identify how many evolutionary units inhabit the high elevations of Sierra Nevada, and (2) to evaluate their phylogenetic position, including their subfamily placement.

Material and methods

Morphological study

We studied 12 specimens of *Eulithinus* at the collection of the Magyar Természettudományi Múzeum (Hungarian Natural History Museum, Budapest, Hungary: HNHM). Three of these specimens are the holotype of *Pseudochelidura montana* Steinmann, 1981 (= *E. montanus*), and respective paratypes of *Eulithinus hispanicus* Steinmann, 1984 (= *E. montanus*), and *Pseudochelidura minor* Steinmann, 1979. Type specimens of *E. analis* and *F. brevis* were not studied; according to Steinman (1993) the former are holded in the Natural History Museum of London. Additional 229 dry-mounted specimens of *Eulithinus* were studied at the Entomology collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain) (MNCN_Ent); 71 ethanol preserved specimens were collected along the Sierra Nevada mountain range, and stored at -20°C at the MNCN collection. Dry-mounted and alcohol preserved specimens were used to identify variability in cerci size and shape under the stereo microscope. Extended depth-of-focus images of dry-mounted specimens were taken with a digital camera Nikon and a lens Nikon AF-S VR Micro-Nikkor 105 mm f/2.8G IF-ED, using the software Helicon Remote ver. 3.9.11 and Helicon Focus ver. 7.6.4.

(1) Dry mounted specimens (Fig. 2)
SPAIN – **Andalucía: Granada** • 7 specs; Sierra Nevada; Cámara leg.; MNCN_122579 to 122585 • 29 specs; Barranco de San Juan; 20 Jul. 1913; C. Bolívar leg.; MNCN_Ent 65069, 122017 to 122040, 122564 to 122567 • 1 spec.; Barranco Goterón, R.Vacares; 26 Jun. 1950; J. Mateu leg.; MNCN_122586 • 3 specs; Cerro Pelado; 23 Jun. 1950; Mateu-Suárez leg.; MNCN_Ent 122568, 122570, 122588 • 5 specs; Cerro Pelado; 5 Jul. 1951; MNCN_Ent 122590, 122591, 122593, 122594, 122622 • 1 spec.; Cerro Pelado; 24 Nov. 1953; J. Suárez leg.; MNCN_Ent 122592 • 1 spec.; Laguna de las Yeguas; 14 Nov. 1936; C. Bolívar leg.; MNCN_Ent 65068 • 143 specs; Laguna de las Yeguas; 14 Sep. 1935; C. Bolívar leg.; MNCN_Ent 69459, 69478, 69505, 69512, 69572, 69593, 69605, 121917 to 122016, 122042 to 122071, 122558 to 122563 • 4 specs; Laguna de las Yeguas; 3000 m a.s.l.; Aug. 1965; Fidel Fdez. Rubio leg.; MNCN_Ent 122617, 122619 to 122621 • 1 ♂; Laguna de las Yeguas; 2800 m a.s.l.; 14 Sep.; R. Ebner leg.; (gen. prep. No. 620 det. Dr Steinmann, *Eulithinus analis* Ramb. det. Dr H. Steinmann, Dt 2381); HNHM • 24 specs; Lagunillos de la Virgen; 2950 m a.s.l.; Aug. 1964; Fidel Fdez. Rubio leg.; MNCN_Ent 122595 to 122616, 122618 • 1 spec.; Lanjarón; Pérez Arcas leg.; MNCN_Ent 122575

• 1 ♂; P. [Pico] de Veleta; 14 Sep. 1935; gen. prep. No. 621 det. Dr Steinmann, Dt 2379; HNHM • 2 ♀♀; P. [Pico] de Veleta; 14 Sep. 1935; *Eulithinus analis* Ramb. det. Dr Steinmann, Dt 2380; HNHM • 1 spec.; Puerto del Lobo; Mateu-Cobos leg.; MNCN_Ent 122587 • 1 spec.; Puerto del Lobo; 22 Jun. 1950; Mateu-Suárez leg.; MNCM_Ent 122041 • 3 specs; Puerto de la Ragua; 2000 m a.s.l.; 17 Jul. 1903; Escalera leg.; MNCN_Ent 122576 to 122578 • 5 ♂♂; Réf. [Refugio] Universitario; 2600 m; Jul. 1979; G. Osella leg.; (Dt 2378); HNHM. – **Almería** • 5 specs; Sierra de Filabres, Bacares; Martínez leg.; MNCN_Ent 122569, 122571 to 122574.

(2) Ethanol preserved specimens (Fig. 2)
SPAIN – **Andalucía: Granada** • 12 ♂♂; Sierra Nevada, Laguna de Río Seco; 37°03′07.16″ N, 3°20′45.57″ W; 3029 m a.s.l.; 17 Aug. 2011; P. Pavón Gozalo, M. García París and J.M. Barea Azcón leg.; field number MNCN tij11935; MNCN_Ent 344345, 344346, 344352 to 344360 • 2 ♂♂; Borreguiles del Río San Juan; 37°05′05.06″ N, 3°22’30.81″ W; 2546 m a.s.l.; 16 Aug. 2011; P. Pavón Gozalo and M. García París leg.; MNCN_Ent 344349, 344350 • 1 ♂; same collection data as for preceding; 22 Aug. 2011; MNCN_Ent 344351 • 1 ♂, 1 ♀; Monachil, Pradollano; 37°05′30.66″ N, 3°23′47.51″ W; 2214 m a.s.l.; 19 Aug. 2011; M. García París and G. García Martín leg.; field number MNCN tij11503; MNCN_Ent344344 • 1 ♀, 2 nymphs; Arroyo Albergue de San Francisco; 37°06′13.51″ N, 3°22′54.61″ W; 2194 m a.s.l.; 17 Aug. 2011; P. Pavón Gozalo, M. García París and J.M. Barea Azcón leg.; MNCN_Ent 344347, 344348, 344361.

(3) Type material studied (HNHM)
Paratype of *Pseudochelidura minor* Steinmann, 1979 (type locality: “Pic du Midi, Pyrennes”)
SPAIN • ♂; “Spain, 2700 m Sierra Nevada Dr. H. Steinmann” [typed] // “legit 18.6.1976 Dr. H. Steinmann” [date hand written] // “Paratypus *Pseudochelidura minor* Dr. H. Steinmann” [name hand written, white label red edges] // “Dt 1936 [printed]”; morphologically assignable to *Eulithinus analis*; HNHM (Fig. 3A).

Holotype of *Pseudochelidura montana* Steinmann, 1981
SPAIN • ♂; “Spain, 2700 m Sierra Nevada Dr. H. Steinmann [typed] // legit 18.6.1976 Dr. H. Steinmann [date hand written] // Holotypus *Pseudochelidura montana sp. nov.* Dr. H. Steinmann [name hand

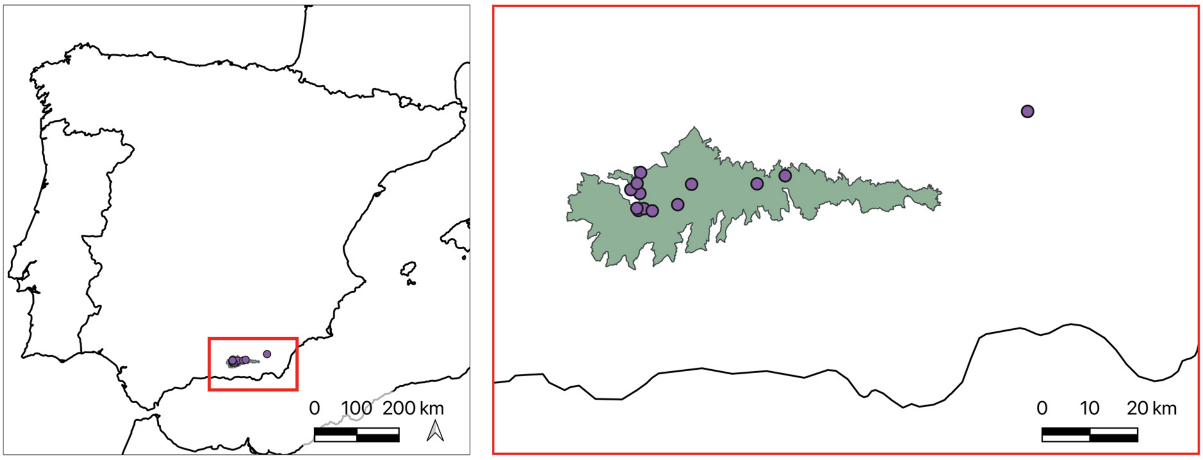


Fig. 2. Geographic distribution of *Eulithinus analis* (Rambur, 1838). The green shading on the map represents the area of the Sierra Nevada National Park usually considered as the general area of the species. The purple dots correspond to the records of the species based on the specimens studied from the Entomology collection of the Museo Nacional de Ciencias Naturales, including dry mounted and ethanol preserved material.

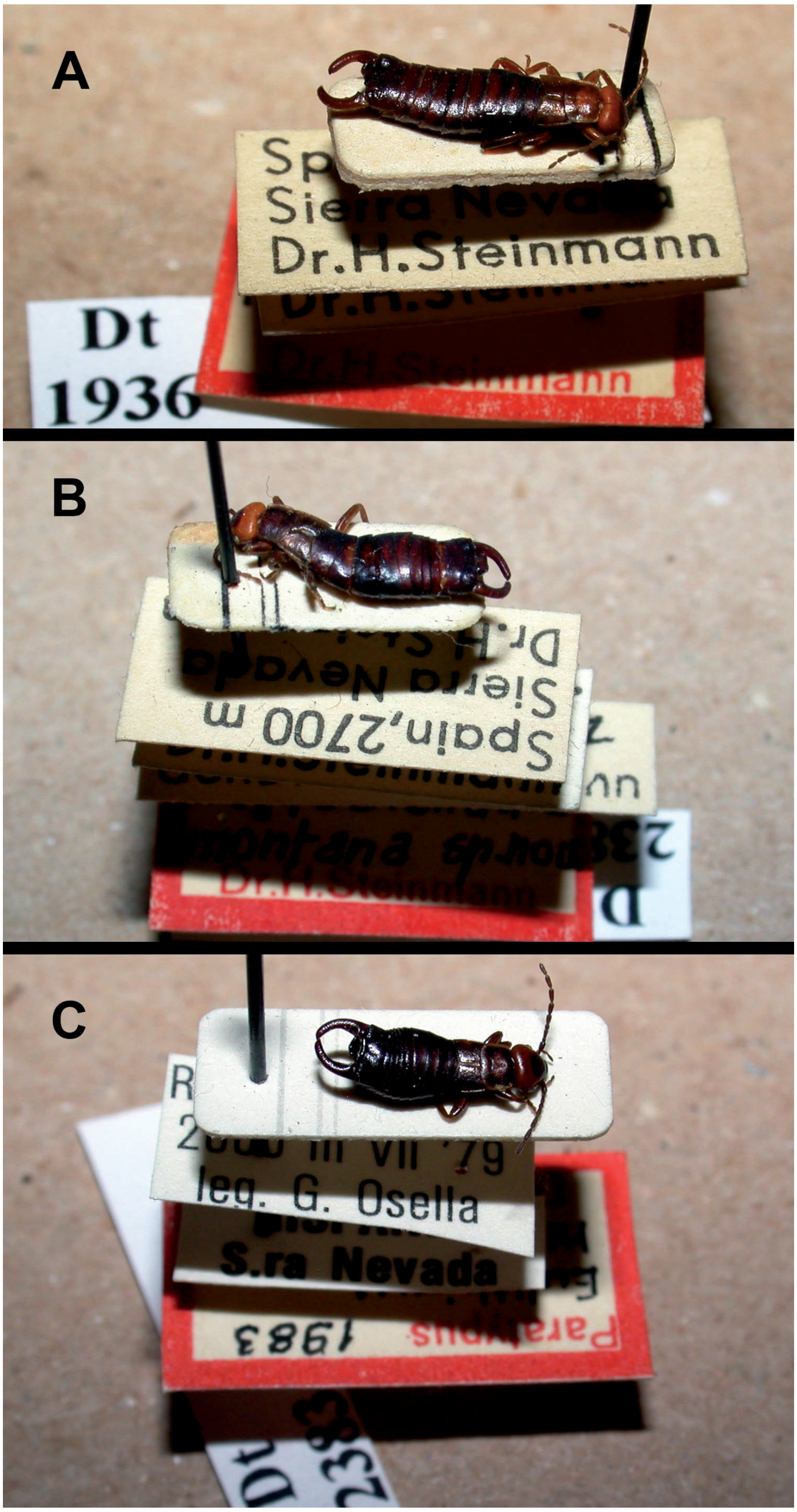


Fig. 3. Type specimens collected in Sierra Nevada mountains. **A**. Paratype of *Pseudochelidura minor* Steinmann, 1979 (HNHM), a male labelled as collected in “Spain, 2700 m Sierra Nevada Dr. H. Steinmann”. **B**. Holotype of *Pseudochelidura montana* Steinmann, 1981, a male from “Spain, 2700 m Sierra Nevada Dr. H. Steinmann”. **C**. Paratype of *Eulithinus hispanicus* Steinmann, 1984, a male collected from Sierra Nevada in “Réf. Universitario 2600 m VII ‘79 leg. G. Osella”.

written, white label red edges] // Dt 2382 [printed]"; specimen reported by Steinmann (1981); HNHM (Fig. 3B).

Paratype of *Eulithinus hispanicus* Steinmann, 1984

SPAIN • ♂; "Réf. Universitario 2600 m VII '79 leg. G. Osella [printed]" // "Hispania S.ra Nevada [typed]" // "Paratypus 1983 *Eulithinus hispanicus* Dr. H. Steinmann [name hand written, white label red edges]" // Dt 2383 [printed]"; HNHM (Fig. 3C).

DNA extraction, sequencing, sequence alignment, and phylogenetic analyses

A total of 20 specimens of *Eulithinus* collected by biologists of the Sierra Nevada National Park Service (see Acknowledgements) and us, on three expeditions in July 2010, June 2011 and June 2010 (Ruiz & García-París 2011; García-París 2017) to Sierra Nevada, were selected for molecular analyses (Table 1). Nine of these specimens corresponded to the morphology of typical *E. analis* according to Rambur's (1838) original criterion, three correspond to Steinmann's (1981) criterion for *E. montanus*, and, four additional male specimens corresponding to intermediate cerci morphology as described by Ebner (1959). Two additional specimens were females, and two more, nymphs.

DNA extractions were performed from one leg of each specimen. DNA was extracted with a DNeasy Blood & Tissue Kits (QIAGEN NV, Hilden, Germany, Europe). Polymerase chain reaction was used to amplify fragments of two mitochondrial genes, the cytochrome c oxidase I (cox1, 658 pb) with the pair of primers LCOI1490/HCOI2198 (Folmer *et al*. 1994) and the cytochrome b gene (cytb, 385 pb) using the set of primers CB-J-10933 (Simon *et al.* 1994) and CB4 (Pons 2006); plus one nuclear region, the ribosomal internal transcribed spacer 2 (ITS2, 336 pb), amplified using the pair of primers CAS5p8sFc/CAS28sB1d (Ji *et al.* 2003). PCR amplifications were performed in a final volume of 25 µl, including 3 mM $MgCl_2$, 0.4 mM of each dNTP, 0.2 µM of each primer, template DNA (10–100 ng), and DNA polymerase (1 unit; Biotools). PCRs run for 40 cycles (denaturing at 94°C for 60 s, annealing at 42°C (cox1 and cytb) or 48°C (ITS2) for 60 s, and extension at 72°C for 60 s) with an initial denaturing step at 96°C for 5 min and a final extension at 72°C for 5 min. Sequencing reactions were performed using both strands in standard conditions and sequenced at Macrogen Inc. (Macrogen Spain).

To compile, assemble and edit all sequences, we used Geneious R11 ver. 11.0.5 (Biomatters, Auckland, New Zealand). Sequences were automatically aligned with MAFFT web portal (Katoh & Toh 2008) and subsequently, manually verified with Mesquite ver. 3.04 (Maddison & Maddison 2015). Preliminary analyses and pairwise comparisons of observed proportional sequence divergence (p-distance) (Table 2) were obtained using the computer program PAUP* ver. 4.0b10 (Swofford 2002).

To evaluate the phylogenetic placement of the Sierra Nevada earwigs we combined our cytb dataset with the data set from *Pseudochelidura* generated in Cuesta-Segura *et al*. (2023). We used the cytb data set instead of cox1 because, as reported by Cuesta-Segura *et al*. (2023), amplifications of cox1 from Pyrenean *Pseudochelidura* consistently yielded *Wolbachia* (Rickettsiales) (Werren *et al.* 2008) sequences. Phylogenetic analyses were carried out under Bayesian inference (BI) methods using a dataset that included 19 specimens of *Pseudochelidura sinuata* (Germar, 1825), 13 specimens of *Pseudochelidura cantabrica* (Cuesta-Segura *et al.*, 2023), four specimens of *Eulithinus analis* (sensu Hincks 1935), and one specimen of *Mesochelidura bolivari* (Dubrony, 1878) used as distant outgroup. We also include as outgroups the *Eudohrnia metallica* (Dohrn, 1865) and *Paratimomenus flavocapitatus* (Shiraki, 1905) cytb fragment obtained from their partial mitochondrial genome available in GenBank (Table 1).

To identify patterns of cox1 variation as a function of geography or morphological traits (cerci shape) within *Eulithinus* (sensu Hincks 1935), we produced haplotype networks with Population Analysis with

Table 1 (continued on next two pages). Taxon sampling. Specimens of *Eulithinus* Hincks, 1935, *Pseudochelidura* Verhoeff, 1902, *Mesochelidura* Verhoeff, 1902, *Eudohrnia* Burr, 1907 and *Paratimomenus* Steinmann, 1974 included in the molecular study.

Species	Morphotype cerci	Population	Specimen code	Latitude	Longitude	Male/ Female	Stadio	Genbank cytb	Genbank ITS2	Genbank cox1
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344352	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864777
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344353	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864778
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	tij11935	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864779
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_ent344356	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864782
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344359	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864785
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344360	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864786
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344346	37°03′07.16″ N	3°20′45.57″ W	male	adult	OR863402		OR864771
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Borreguiles del Río San Juan, 2546 m	MNCN_Ent344350	37°05′05.06″ N	3°22′30.81″ W	male	adult	OR863404	OR855735	OR864775
Eulithinus analis	1 large	Spain: Andalucía: Granada: Sierra Nevada: Monachil, Pradollano, 2214 m	MNCN_Ent344344	37°05′30.66″ N	3°23′47.51″ W	male	adult			OR864768
Eulithinus analis	2 small	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344358	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864784
Eulithinus analis	2 small	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_ent344345	37°03′07.16″ N	3°20′45.57″ W	male	adult	OR863401		OR864770
Eulithinus analis	2 small	Spain: Andalucía: Granada: Sierra Nevada: Borreguiles del Río San Juan, 2546 m	MNCN_Ent344349	37°05′05.06″ N	3°22′30.81″ W	male	adult	OR863403	OR855734	OR864774
Eulithinus analis	3 intermediate	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344354	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864780
Eulithinus analis	3 intermediate	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344357	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864783
Eulithinus analis	3 intermediate	Spain: Andalucía: Granada: Sierra Nevada: Laguna de Río Seco, 3029 m	MNCN_Ent344355	37°03′07.16″ N	3°20′45.57″ W	male	adult			OR864781
Eulithinus analis	3 intermediate	Spain: Andalucía: Granada: Sierra Nevada: Borreguiles del Río San Juan, 2546 m	MNCN_Ent344351	37°05′05.06″ N	3°22′30.81″ W	male	adult			OR864776
Eulithinus analis		Spain: Andalucía: Granada: Sierra Nevada: Arroyo Albergue de San Francisco, 2194 m	MNCN_Ent344361	37°06′13.51″ N	3°22′54.61″ W	female	adult			OR864787
Eulithinus analis		Spain: Andalucía: Granada: Sierra Nevada: Arroyo Albergue de San Francisco, 2194 m	MNCN_Ent344347	37°06′13.51″ N	3°22′54.61″ W		nymph			OR864772
Eulithinus analis		Spain: Andalucía: Granada: Sierra Nevada: Arroyo Albergue de San Francisco, 2194 m	MNCN_Ent344348	37°06′13.51″ N	3°22′54.61″ W		nymph			OR864773
Eulithinus analis		Spain: Andalucía: Granada: Sierra Nevada: Monachil, Pradollano, 2214 m	tij11503	37°05′30.66″ N	3°23′47.51″ W	female	adult			OR864769

Table 1 (continued). Taxon sampling. Specimens of *Eulithinus* Hincks, 1935, *Pseudochelidura* Verhoeff, 1902, *Mesochelidura* Verhoeff, 1902, *Eudohrnia* Burr, 1907 and *Paratimomenus* Steinmann, 1974 included in the molecular study.

Species	Morphotype cerci	Population	Specimen code	Latitude	Longitude	Male/ Female	Stadio	Genbank cytb	Genbank ITS2	Genbank cox1
Pseudochelidura sinuata		France: Ariége: Coll de Pailhéres, 1958 m	MNCN_Ent331186	42°44″07.7″ N	1°59′53.5″ E			OP893680	OP908089	
Pseudochelidura sinuata		France: Ariége: Coll de Pailhéres, 1958 m	MNCN_Ent331187	42°44′07.7″ N	1°59′53.5″ E			OP893681	OP908090	
Pseudochelidura sinuata		France: Ariége: Coll de Pailhéres, 1958 m	MNCN_Ent331188	42°44′07.7″ N	1°59′53.5″ E			OP893682	OP908091	
Pseudochelidura sinuata		France: Ariége: Coll de Pailhéres, 1958 m	MNCN_Ent331191	42°44′07.7″ N	1°59′53.5″ E			OP893683	OP908092	
Pseudochelidura sinuata		France: Ariége: Coll de Pailhéres, 1958 m	MNCN_Ent331193	42°44′07.7″ N	1°59′53.5″ E			OP893684	OP908093	
Pseudochelidura sinuata		France: Ariége: Coll de Pailhéres, 1958 m	MNCN_Ent331197	42°44′07.7″ N	1°59′53.5″ E			OP893685	OP908094	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331198	42°36′44.2″ N	1°38′16.0″ E			OP893686	OP908095	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331199	42°36′44.2″ N	1°38′16.0″ E			OP893687	OP908096	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331200	42°36′44.2″ N	1°38′16.0″ E			OP893688	OP908097	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331201	42°36′44.2″ N	1°38′16.0″ E			OP893689	OP908098	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331203	42°36′44.2″ N	1°38′16.0″ E			OP893690	OP908099	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331205	42°36′44.2″ N	1°38′16.0″ E			OP893691	OP908100	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331210	42°36′44.2″ N	1°38′16.0″ E			OP893692	OP908101	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331212	42°36′44.2″ N	1°38′16.0″ E			OP893693	OP908102	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331215	42°36′44.2″ N	1°38′16.0″ E			OP893694	OP908103	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331215h	42°36′44.2″ N	1°38′16.0″ E			OP893695	OP908104	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331216	42°36′44.2″ N	1°38′16.0″ E			OP893696	OP908105	
Pseudochelidura sinuata		Andorra: Canillo: Coma de Ransol, 1940 m	MNCN_Ent331216h	42°36′44.2″ N	1°38′16.0″ E			OP893697	OP908106	
Pseudochelidura sinuata		Spain: Aragón: Huesca: Bielsa: Valle de Pineta, 1299m	MNCN_Ent331171	42°40′47.84″ N	0°04′47.68″ E			OP893679	OP908088	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de la Ventana, 1588 m	MNCN_Ent331172	43°03′27.62″ N	6°00′15.15″ W			OP893666	OP908075	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de la Ventana, 1588 m	MNCN_Ent331175	43°03′27.62″ N	6°00′15.15″ W			OP893667	OP908076	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de la Ventana, 1588 m	MNCN_Ent331176	43°03′27.62″ N	6°00′15.15″ W			OP893668	OP908077	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de la Ventana, 1588 m	MNCN_Ent331179	43°03′27.62″ N	6°00′15.15″ W			OP893669	OP908078	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de la Ventana, 1588 m	MNCN_Ent331182	43°03′27.62″ N	6°00′15.15″ W			OP893670	OP908079	

Table 1 (continued). Taxon sampling. Specimens of *Eulithinus* Hincks, 1935, *Pseudochelidura* Verhoeff, 1902, *Mesochelidura* Verhoeff, 1902, *Eudohrnia* Burr, 1907 and *Paratimomenus* Steinmann, 1974 included in the molecular study.

Species	Morphotype cerci	Population	Specimen code	Latitude	Longitude	Male/ Female	Stadio	Genbank cytb	Genbank ITS2	Genbank cox1
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de Vegarada, 1684 m	MNCN_Ent331219	43°01′54.95″ N	5°28′34.17″ W			OP893671	OP908080	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de Vegarada, 1684 m	MNCN_Ent331220	43°01′54.95″ N	5°28′34.17″ W			OP893672	OP908081	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de Vegarada, 1684 m	MNCN_Ent331221	43°01′54.95″ N	5°28′34.17″ W			OP893673	OP908082	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de Vegarada, 1684 m	MNCN_Ent331222	43°01′54.95″ N	5°28′34.17″ W			OP893674	OP908083	
Pseudochelidura cantabrica		Spain: Castilla y León: León: Puerto de Vegarada, 1684 m	MNCN_Ent331223	43°01′54.95″ N	5°28′34.17″ W			OP893675	OP908084	
Pseudochelidura cantabrica		Spain: Castilla y León: Burgos: Puerto de las Estacas de Trueba, 1128 m	MNCN_Ent331224	43°6′48.55″ N	3°42′4.69″ W			OP893676	OP908085	
Pseudochelidura cantabrica		Spain: Castilla y León: Burgos: Puerto de Lunada, 1270 m	MNCN_Ent331225	43°10′20.98″ N	3°38′39.49″ W			OP893677	OP908086	
Pseudochelidura cantabrica		Spain: Castilla y León: Burgos: Puerto de Lunada, 1270 m	MNCN_Ent331226	43°10′20.98″ N	3°38′39.49″ W			OP893678	OP908087	
Mesochelidura bolivari		Spain: Castilla y León: Palencia: Triollo, 1314 m	MNCN_Ent331218	42°55′59.5″ N	4°40′14.8″ W			OP893698	OP908107	
Eudohrnia metallica								KX091853		
Paratimomenus flavocapitatus								KX091861		

Table 2. Uncorrected (p) pairwise genetic distance matrix between specimens (code and morphotype cerci) used in the mitochondrial (cox1) network analyses of *Eulithinus analis* (Rambur, 1838).

		MNCN_ Ent 344344	tij11503	MNCN_Ent 344347-50	MNCN_Ent 344351	MNCN_Ent 344345-6 344352-60 tij11935
		Large	**Female**	**Large, small, nymph**	**Intermediate**	**Large, intermediate, small**
MNCN_Ent 344344	**Large**	–				
tij11503	**Female**	0.002				
MNCN_Ent 344347-50	**Large, small, nymph**	0.005	0.003			
MNCN_Ent 344351	**Intermediate**	0.009	0.008	0.005		
MNCN_Ent 344345-6 344352-60 tij11935	**Large, intermediate, small**	0.011	0.009	0.012	0.017	
MNCN_Ent 344361	**Female**	0.006	0.005	0.001	0.006	0.014

Reticulate Trees (PopART), using a Median Joining Network. Haplotype networks were edited with Adobe Photoshop CS5 ver. 12.0 (Adobe Systems Incorporated).

Species concept

To delimit how many singular and evolutionary independent taxa can be defined within *Eulithinus* (sensu Hincks 1935), we adopted the evolutionary species concept (Wiley 1978) as discussed in Ruiz & García-París (2015) and Sánchez-Vialas *et al*. (2020). This concept considers a species as "a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978: 18). Testing for cohesion was performed identifying levels of concordance between morphology and nuclear and mitochondrial markers (Sainz-Escudero *et al*. 2021; Cuesta-Segura *et al*. 2023).

Results

Morphological study and phylogeographic and phylogenetic analyses

Male specimens studied from the Sierra Nevada mountain range are quite homogeneous in external characters (including pattern coloration). Only size and shape of cerci and pygidum are conspicuously variable (Figs 4–5) and may vary within populations as described in detail by Ebner (1959). The type series of *P. montana* consisted on the holotype and one paratype, both from Sierra Nevada (the paratype held at the Zoologiske Museum of the University at Copenhagen). We studied the holotype (Fig. 3B) and it corresponds to a male specimen of *E. analis* with short cerci.

The phylogeographic networks based on the mitochondrial gene cox1 marker (Fig. 6) showed six different haplotypes for *Eulithinus* (sensu Hincks 1935) in our sample. One haplotype was recovered from 12 male specimens collected in the Laguna de Río Seco that differed in cerci morphology: seven with large cerci (MNCN_Ent 344346, 344352, 344353, 344356, 344359, 344360 and field number MNCN tij11935), three with intermediate cerci (MNCN_Ent 344354, 344355 and 344357), and two with small cerci (MNCN_Ent 344345 and 344358). A second haplotype is shared by four specimens, two of them nymphs (MNCN_Ent 344347, 344348) from Arroyo del Albergue de San Francisco, and two males (MNCN_Ent 344350 with large cerci and MNCN_Ent 344349 with small cerci), from the Borreguiles del Río San Juan. Four additional haplotypes were represented by single specimens, a female (MNCN_Ent 344361) from Arroyo del Albergue de San Francisco, a male with intermediate cerci (MNCN_Ent 344351) from Borreguiles del Río San Juan, and a female (field number MNCN tij11503) and a male with large cerci (MNCN_Ent 344344) from Pradollano. These sequences were poorly differentiated, showing a genetic distance (uncorrected p_{distance}) between 0 and 0.017 (Table 2).

Phylogenetic analyses of *Eulithinus* (sensu Hincks 1935) morphologically ascribable to *E. analis*, *E. montanus*, *P. sinuata*, and *P. cantabrica* cytb sequences (Fig. 7) resulted in all sequences being part of a single well-structured monophyletic group (PP = 0.92) in which Sierra Nevada sequences break the monophyly of *Pseudochelidura*. *Eulithinus* samples are sister to *P. sinuata* (PP = 1) while *P. cantabrica* is sister to the well-supported *Eulithinus*–*P. sinuata* clade (PP = 0.92).

Nuclear ITS2 data were only obtained for two specimens from Borreguiles del Río San Juan (MNCN_Ent 344349, 344350) representing small- and large-cerci male phenotypes respectively. Both sequences were 100% identical, supporting that male cerci variation is part of a single evolutionary unit. Phylogenetic analyses of these sequences together with the available *Pseudochelidura* ITS2 sequences, resulted in a

Fig. 4. Habitus variability in males of *Eulithinus analis* (Rambur, 1838) from Sierra Nevada (Spain). **A**. Small specimen with short cerci, corresponding to the original description of *Eulithinus montanus* (Steinmann, 1981) from Laguna de las Yeguas at 2859 m of altitude (MNCN_Ent 122048). **B**. Large specimen with long cerci also from Laguna de las Yeguas (MNCN_Ent 121966).

well-structured clade with *Elithinus analis* sister to the species of *Pseudochelidura*, rendering *Eulithinus* and *Pseudochelidura* lineages reciprocally monophyletic (Fig. 8). The topology of the ITS2 hypothesis is not consistent with the mitochondrial hypothesis (Fig. 7) differing in the relative position of *Eulithinus* with respect to *Pseudochelidura.*

Discussion and conclusions

The taxonomic status of *Pseudochelidura montana* and *Eulithinus analis*

Morphology-based taxonomic studies resulted in two non-congruent hypotheses for the taxonomy of the Sierra Nevada endemic earwigs. On the one hand, Rambur (1838), Dubrony (1878), de Bormans & Krauss (1900), Burr (1911), Hincks (1935), Ebner (1959), Lapeira & Pascual (1980), Ruano & Tinaut (2003), and Ruano *et al*. (2013) considered that all the variability observed in male cerci corresponded to a single taxon: *E. analis.* On the other hand, Steinmann (1981, 1984, 1989, 1993) followed by Herrera Mesa (1999), Haas (2010), and Pérez-Valcárcel *et al*. (2022), considered that the genus *Eulithinus* was integrated by two species, *E. analis* and *E. montanus*, both endemic to Sierra Nevada. Steinmann based his classification on the shape of the cerci, pygidium and male genitalia.

The history of the problem begins in 1979 when Steinmann described the Pyrenean species *Pseudochelidura minor*. Steinmann (1979) included a paratype from Sierra Nevada within the type series of the Pyrenean *P. minor*. We studied this paratype (Fig. 3A) and it is a male specimen of *E. analis* with short cerci. Steinmann thus believed that *P. minor* was present also in the Sierra Nevada mountains. This mistake was possible because, at a first glance, the external appearance of *Pseudochelidura* and *Eulithinus* is quite similar (size, coloration pattern, elytral development, and cerci morphology), but easy to reject upon examination of the external margin of the tegmina.

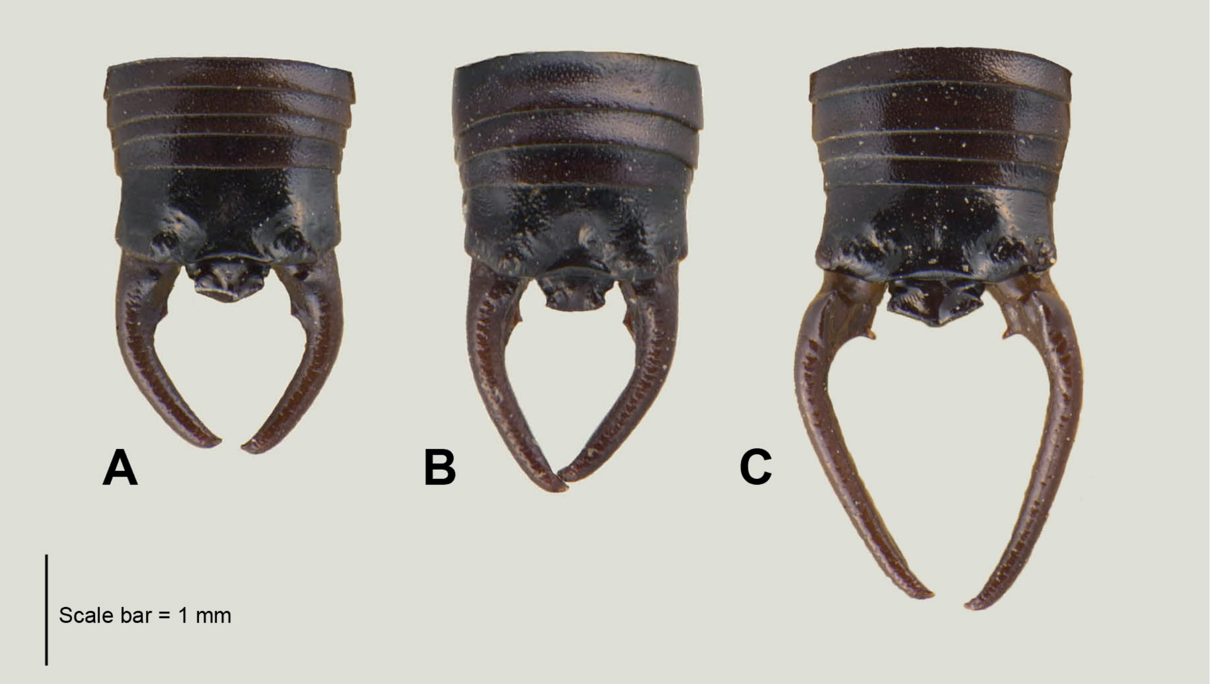


Fig. 5. Cerci variation in *Eulithinus analis* (Rambur, 1838) males. **A**. Laguna de las Yeguas at 2859 m of altitude (MNCN_Ent 122048). **B**. Lagunillos de la Virgen at 2945 m of altitude (MNCN_Ent 122612). **C**. Laguna de las Yeguas (MNCN_Ent 121966).

Steinmann in 1981, still believing that *Pseudochelidura* was present in Sierra Nevada, described a new species: *Pseudochelidura montana*. To complicate matters, in 1984, Steinmann described one more taxon, using materials exclusively from Sierra Nevada: *Eulithinus hispanicus* (Fig. 3C).

Years later, Steinmann (1989) became finally aware of the morphological similarity between the genera *Eulithinus* and *Pseudochelidura.* Consequently, he synonymized *E. hispanicus* and *P. montana*, and transferred them to *Eulithinus* establishing the new combination: *Eulithinus montanus* (Steinmann, 1981).

According to the specimen labels, the holotype of *P. montana* Steinmann, 1981, and a paratype of *P. minor* Steinmann, 1979, were collected the same day by Steinmann himself at Sierra Nevada at 2700 m of altitude. The paratype of *E. hispanicus* Steinmann, 1984, was collected by G. Osella at the Refugio Universitario at 2600 m of altitude, together with five other male specimens identified by Steinmann as typical *E. analis*. These specimens represent some of the different morphs reported and described by Ebner (1959) as part of his study of *E. analis* population variability.

The characters used by Steinmann (1981, 1984, 1989, 1993) in the description and the key to separate *E. montanus* and *E. analis*, were focused on the relative shape of male last tergite, including pygidium and forceps shape. In 1993, Steinmann indicated that male of *E. analis* presents "forceps strongly curved in basal section, and apically straightened; inner margins with one prominent tooth basally and pygidium ornamented with a lateral tooth" (Figs 4B, 5C). However, according to Steinmann (1993), the male of *E. montanus* present "forceps strongly curved basally and apically; inner margins with a small tooth medially. Pygidium ornamented with two lateral teeth" (Figs 4A, 5A). A direct examination of the morphological characters of the material of *E. analis* at the collection of MNCN and the type material used by Steinmann (1979, 1981) in the description of *E. montanus* (= *P. montana*) at the collection of HNHM, shows that the external characters used by Steinmann (1979, 1981, 1984) to separate *E. montanus* from *E. analis* correspond to the intraspecific variability as already considered by Ebner (1959) (Figs 4–5, 9).

Pygidium and male forceps morphology are traits widely used as diagnostic taxonomic characters, however these are characters with high intraspecific variability in earwigs (Dohrn 1867; Diajonov 1925; Ollason 1970; Simpson & Mayer 1990; Tomkins & Simmons 1996; García-París 2017; Kirstová *et al*. 2020; Fontana *et al*. 2021; García-París *et al*. 2021; Jurado-Angulo *et al*. 2021; Cuesta-Segura *et al*. 2023). It has been recently demonstrated by morphological and molecular analyses (Fontana *et al*. 2021; Jurado-Angulo *et al*. 2021; Cuesta-Segura *et al*. 2023), that the misinterpretation of the morphological variability of male cerci in *Chelidura* and *Pseudochelidura* led to errors in the determination of the geographic distribution of the species and in the delimitation of independent evolutionary units (e.g., species).

Just as there is variability in the morphology of male cerci, there is also intraspecific variability in male genitalia within *Eulithinus*. Male genitalia of *E. analis* and *E. montanus* were studied in detail and illustrated by Steinmann (1981, 1993). According to Steinmann (1993) males of *E. analis* present "genitalia normally developed; central parameral plate somewhat narrowed basally, and expanded apically; virga within genital lobe of *Forficula*-type, short; external parameres comparatively long, straight, obtuse apically" (Steinmann 1993: fig. 586). Steinmann (1993) also indicated that males of *E. montanus* present "genitalia simple, *Forficula*-type; central parameral plate well developed, broad, oval, virga within genital lobe short, with basal vesicle; external parameres fully developed, more or less straight, with a very small spine at tips" (Steinmann 1993: fig. 589). These two diagnoses do not differ significantly between them, being its differences within the intraspecific levels of variability shown for example in *P. cantabrica* (Cuesta-Segura *et al.* 2023).

In addition, our phylogeographic analyses performed with specimens collected at Sierra Nevada National Park show that, at the mtDNA level, most individuals from a given population share a common cox1 haplotype with independence of cerci morphotype (Fig. 6). For example, the 12 males sequenced from the population of Laguna de Río Seco, that included specimens with cerci representing typical *E. analis*, typical *E. montanus*, and intermediate morphotypes (as described by Ebner 1959, and Steinmann 1993), share a common haplotype. All localities and specimens together are represented by 6 haplotypes in total, with a maximum divergence of 10 base pair changes between them (maximum uncorrected $p_{\text{distance}} = 0.017$) (Table 2). Some specimens from Borreguiles del Río San Juan and Arroyo del Albergue de San Francisco share a common haplotype. Maximum internal haplotype divergence within a single population is represented by three base changes within the Borreguiles del Río San Juan population (uncorrected $p_{\text{distances}} = 0.005$) (Table 2). Studied populations are clustered in three relatively isolated haplogroups, with apparently little exchange among them (Fig. 6): a) the high altitude specimens from the eastern-most sequenced population (Laguna de Río Seco; Figs 9E–F, 10B, D); b) the specimens from Borreguiles del Río San Juan (Fig. 9C) and Arroyo del Albergue de San Francisco, separated by a few hundred meters, and likely part of a unique population; and c) the low elevation specimens from the human modified area at the westernmost area of Pradollano (Figs 9A–B, D, 10C).

According to the morphological data (all male morphotypes are present at a single locality, and all are represented across all other populations), and the phylogeographic information (haplotypes are not segregated according to male morphotype) we suggest that all specimens studied with independence of their cerci morphology are part of single species, and therefore, *E. analis* and *E. montanus* are different names applied to a unique evolutionary unit. Thus, we propose the new synonymy: *Forficula analis* Rambur, 1838 = *Pseudochelidura montana* Steinmann, 1981 syn. nov.

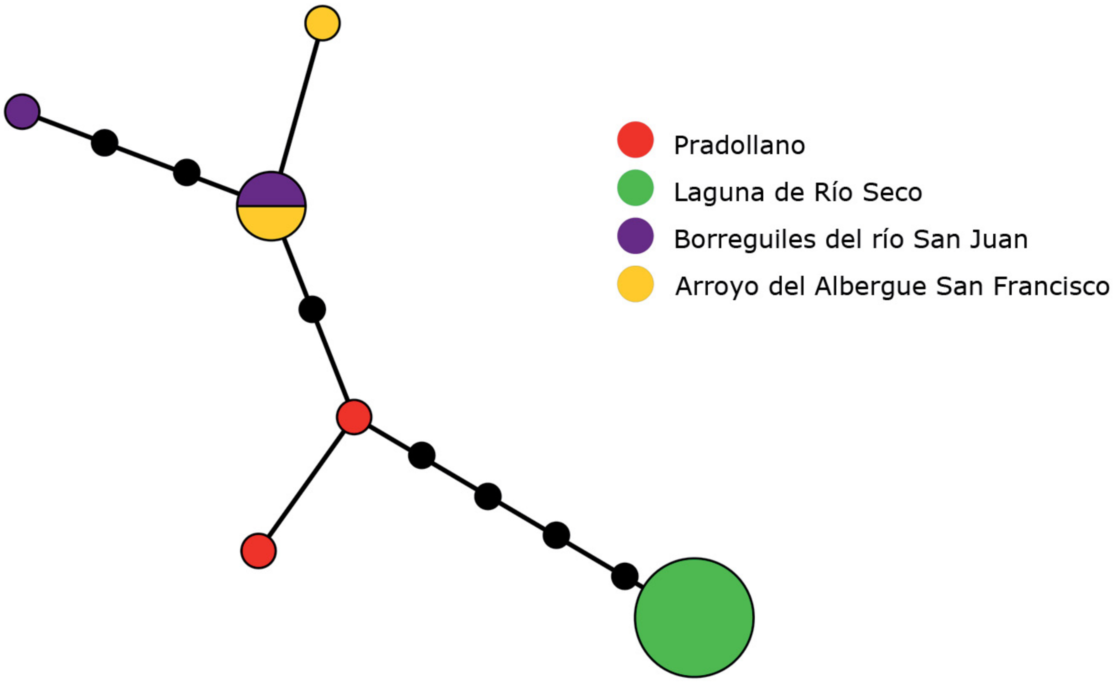


Fig. 6. Mitochondrial (cox1) network analyses of specimens of *Eulithinus analis* (Rambur, 1838) from Sierra Nevada. Specimens from Laguna del Río Seco are colored in green, from Pradollano in red, from Arroyo del Albergue San Francisco in yellow and from Borreguiles del Río San Juan in purple.

A few pages before the description of *F. analis*, Rambur described *Forficula brevis* Rambur, 1838 using two female specimens from Sierra Nevada. Rambur (1838) mentioned in the original description of *F. brevis* that the two specimens known at the time, were similar to female specimens of *F. analis*, but lighter in coloration, more reddish, larger (smaller than *Forficula auricularia*), but relatively stout with the maximum abdominal width placed a little further than the middle. Fieber (1853) suggested that *F. brevis* likely represented the female of *F. analis*. The same year, Fischer (1853: 75) proposed with doubts and only studying female specimens, the synonymy of *F. brevis* with *Forficula decipiens* Gené, 1832 (type locality: "nei contorni de Genova... sugli Apennini liguri"), probably influenced by the indications of Rambur about the absence of wings and larger size than in *F. analis*, and believing that,

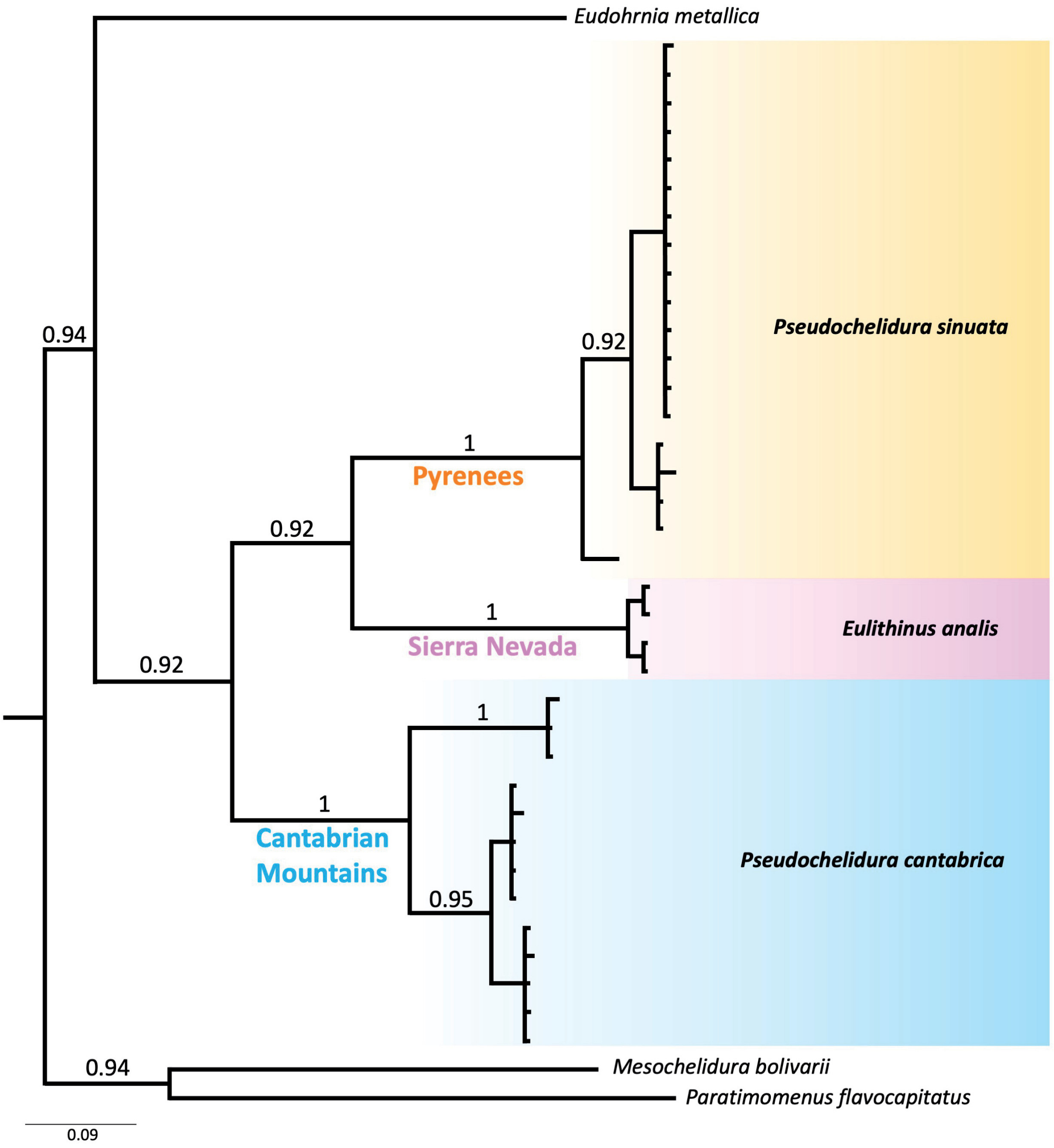


Fig. 7. Bayesian phylogenetic tree based on cytb sequences of *Eulithinus* Hincks, 1935 and *Pseudochelidura* Verhoeff, 1902. Species and clade names correspond to the new classification adopted in this work. Posterior probabilities are indicated above branches. Background colours represent species and names below branches represent geographic areas.

akin to other Mediterranean countries, *F. decipiens* was a common species in southern Spain. Since then, all recent authors treated *F. brevis* as a synonym of *F. decipiens*. However, we do not find evidences that support Fischer's (1853) synonymy. Despite detailed prospections, *F. decipiens* has never been found in the Sierra Nevada mountain chain (Pascual & Barranco 2013) and female specimens of *F. decipiens* do not show the reddish coloration or the particular body shape described by Rambur (1938). On the contrary, some particularly large females of *E. analis* (Fig. 11) with a general shape and coloration very similar to Rambur's (1838) original description, appear occasionally mixed with typical specimens of *E. analis*. These specimens not only fit precisely the description of *F. brevis* but also, they are found under stones in the Sierra Nevada mountains as indicated by Rambur (1838). Taking into consideration these arguments we formalize the suggestion of Fieber (1853) and propose the synonymy of *Forficula*

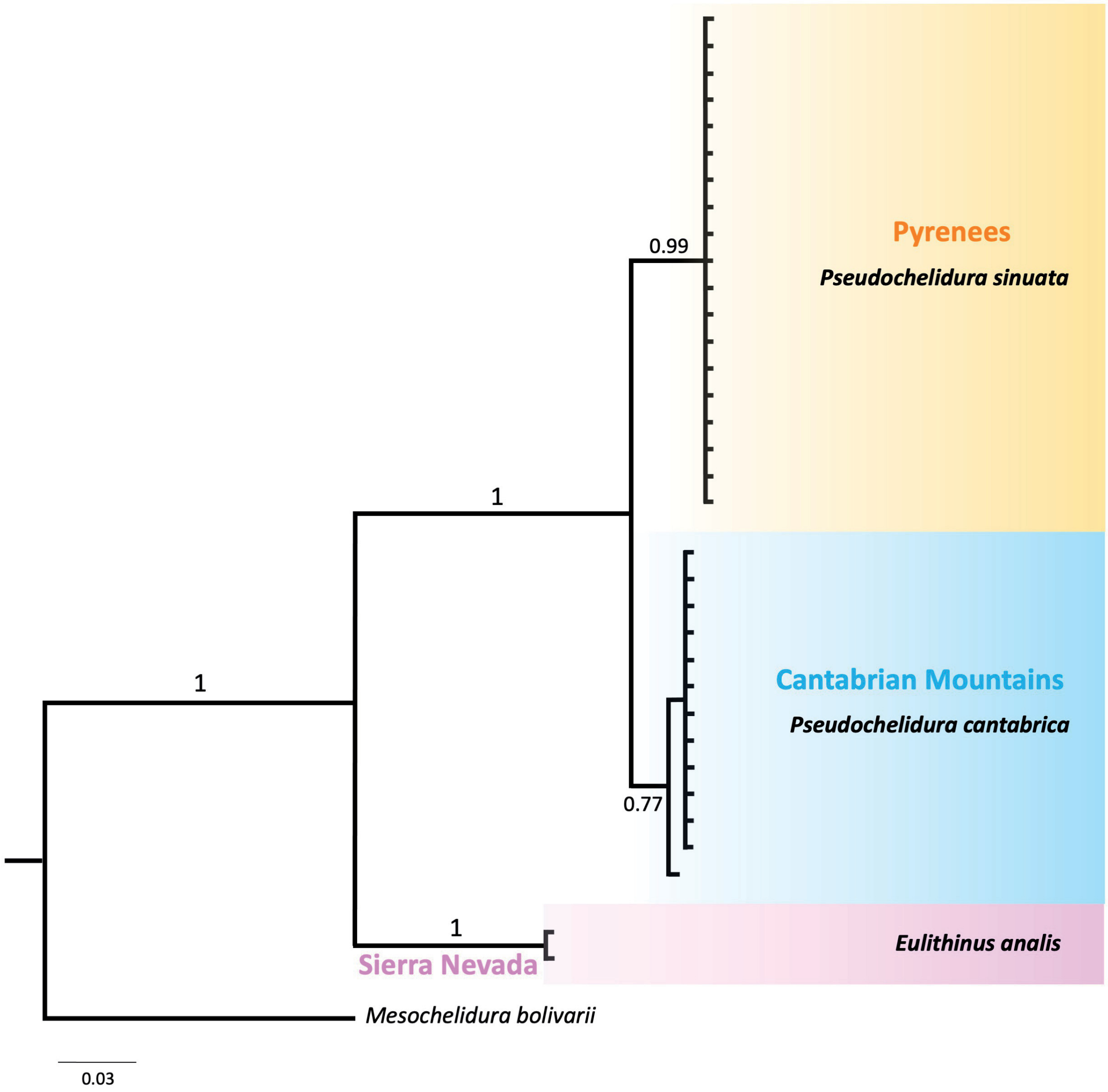


Fig. 8. Bayesian phylogenetic tree based on ITS2 sequences of *Eulithinus* Hincks, 1935 and *Pseudochelidura* Verhoeff, 1902. Species and clade names correspond to the new classification adopted in this work. Posterior probabilities are indicated above branches. Background colours represent species and names below branches represent geographic areas.

brevis Rambur, 1838 with *Forficula analis* Rambur, 1838 syn. nov. Since *F. brevis* and *F. analis* were described in the same work, *F. analis* can be retained as the valid name for the species despite of being described a few pages latter (article 24.2 of International Code of Zoological Nomenclature; ICZN 1999).

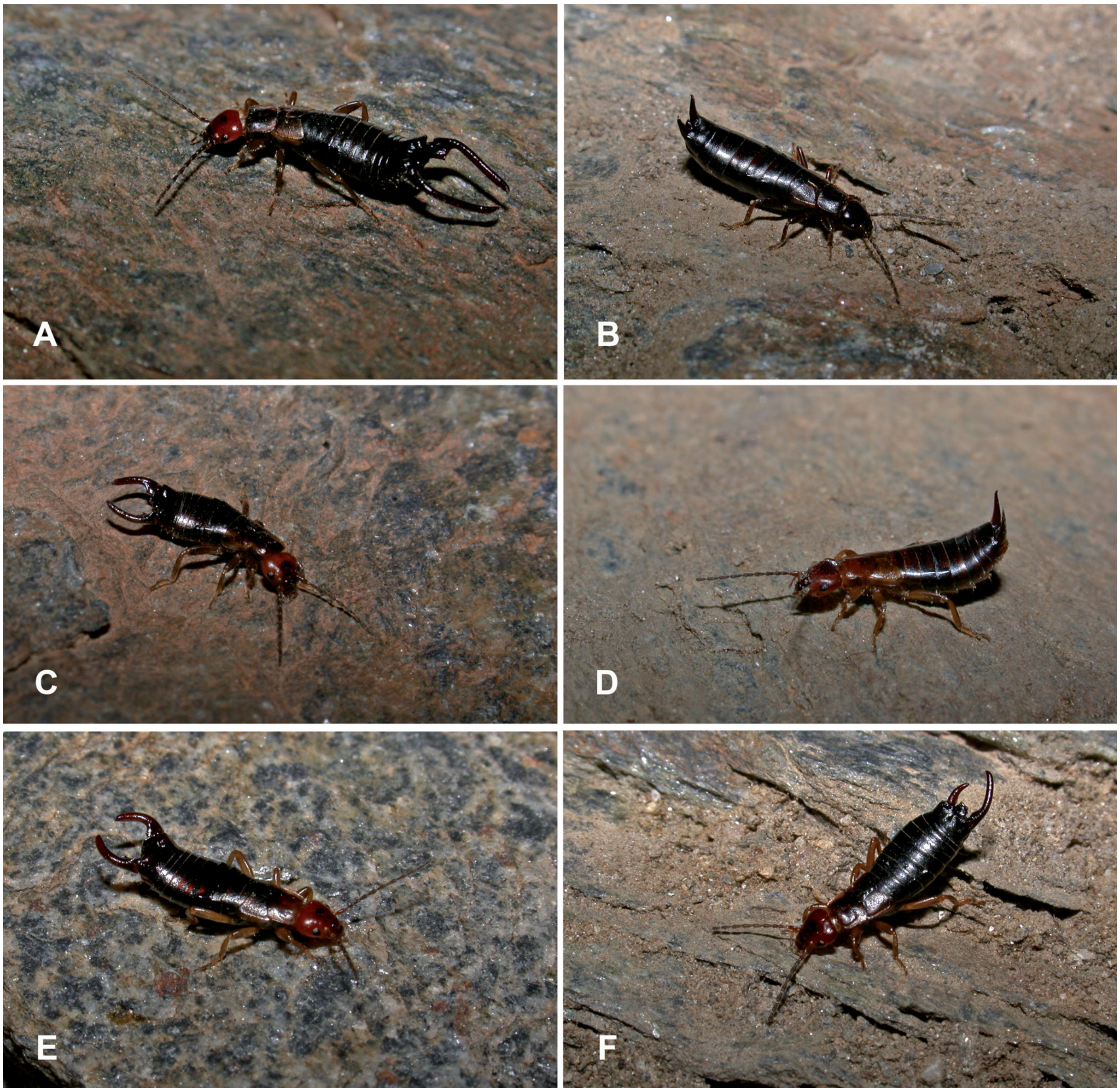


Fig. 9. Habitus of live specimens of *Eulithinus analis* (Rambur, 1838) from Sierra Nevada (Spain). **A**. Male specimen with long cerci from Pradollano. **B**. Typical female with dark coloration and brown head from Pradollano. **C**. Male with intermediate sized cerci from Borreguiles del Río San Juan (MNCN_Ent433449). **D**. Light colored female with reddish head and pronotum from Pradollano. **E**. Male displaying short cerci from Laguna de Río Seco (MNCN_Ent344345). **F**. Male with each cercus of different size from Laguna de Río Seco. Photographs ex situ by MG-P.

Taxonomic output

Class Insecta Linnaeus, 1758
Order Dermaptera De Geer, 1773
Family Forficulidae Latreille, 1810
Genus *Eulithinus* Hincks, 1935

Nuclear and molecular markers indicate that cerci variation in *Eulithinus* is part of the phenotypic plasticity within a single evolutionary unit. Under this scenario we consider that all the species level taxa described from Sierra Nevada using as diagnostic characters the shape and size of cerci and pygidium are part of a single species: *E. analis* (see Discussion, section The taxonomic status of *Pseudochelidura montana* and *Eulithinus analis*, p. 13).

The synonymic list of *Eulithinus analis* remains as follows:

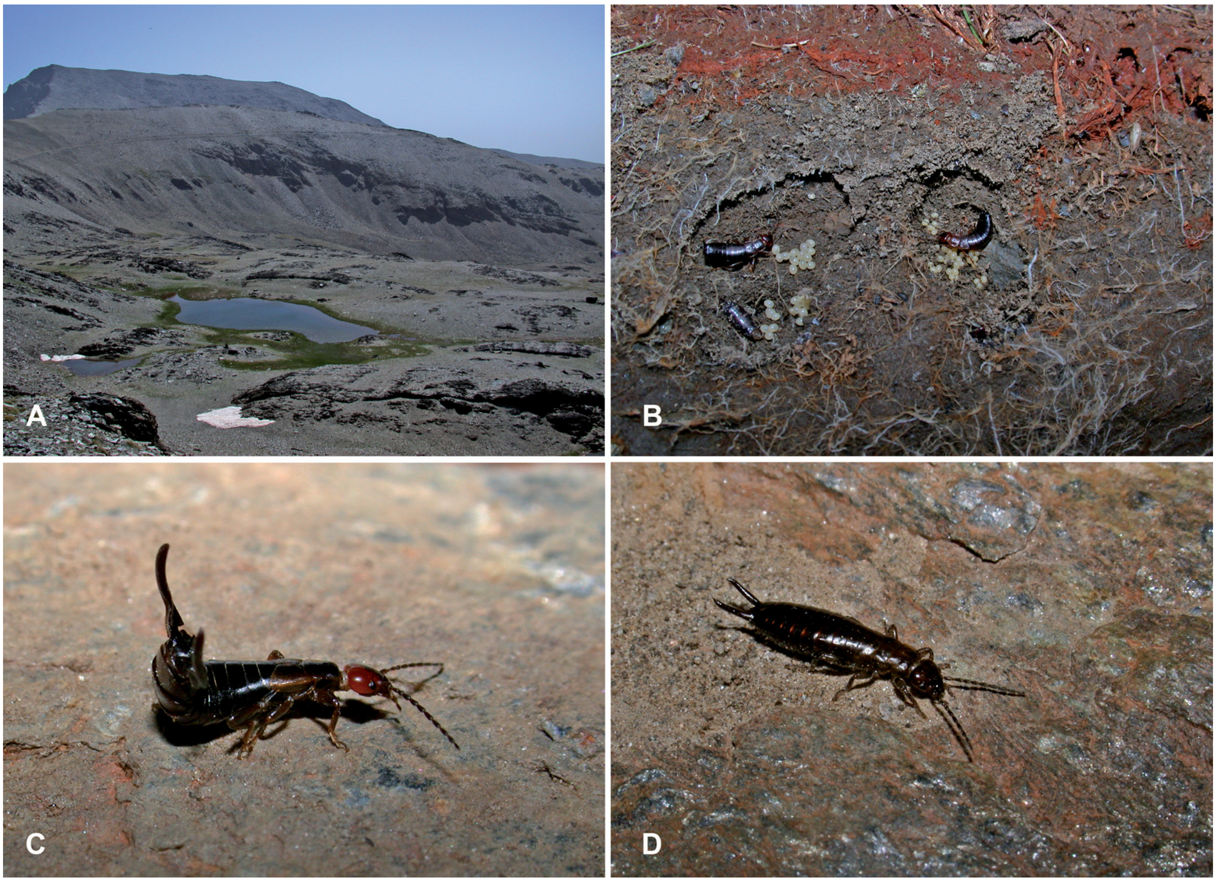


Fig. 10. General view of the habitat and natural history notes of *Eulithinus analis* (Rambur, 1838) in Sierra Nevada (Spain). **A**. Typical landscape occupied by *E. analis*; in front Laguna de Río Seco, where numerous female specimens were observed taking care of their eggs under stones in August. **B**. Two females taking care of their eggs under the same stone at Laguna de Río Seco; note the remains of a dead male on the left, and the different development degree of the two egg masses; a few minutes later, females clustered the eggs into compact masses. **C**. Male with intermediate long sized cerci running in alert display at Pradollano. **D**. Last instar nymph from Laguna de Río Seco; note the general similarity with nymphs of *Pseudochelidura cantabrica* (Cuesta *et al*. 2023: fig. 5c). Photographs by MG-P.

Eulithinus analis (Rambur, 1838)

Forficula analis Rambur, 1838: 10. Terra typica: "… sur les montagnes de la Sierra Nevada… sous les pierres". Type specimen at the Natural History Museum (London, UK) (Steinmann 1989).
Forficula brevis Rambur, 1838: 9. Terra typica: "sous les pierres, dans les montagnes de la Sierra-Nevada". Type placement unknown (Steinmann 1989). **Syn. nov.**
Chelidura analis var. *macrolabia* Dubrony, 1878: 436 (unavailable name).
Chelidura analis var. *cyclolabia* Dubrony, 1878: 436 (unavailable name).
Pseudochelidura montana Steinmann, 1981: 189. Terra typica: "Spain, Sierra Nevada, 2700 m". Holotype at the Hungarian Natural History Museum (Budapest, Hungary) and paratypes at Zoologiske Museum (Copenhagen, Denmark). **Syn. nov.**
Eulithinus hispanicus Steinmann, 1984: 202. Terra typica: "Spain, Sierra Nevada, Réf. Universitario, 2600 m". Holotype at the Museo Civico di Storia Naturale (Verona, Italy) and paratypes at the Hungarian Natural History Museum (Budapest, Hungary) (Steinmann 1989). Synonymy of *E. hispanicus* Steinmann, 1984, with *E. montanus* proposed by Steinmann (1989).

Chelidura analis – Dubrony 1878: 434.
Pseudochelidura analis – Burr 1908: 11.
Lithinus analis – Burr 1909: 327.
Eulithinus analis – Hincks 1935: 276.
Eulithinus montanus – Steinmann 1989: 744.

Fig. 11. Female specimen of *Eulithinus analis* (Rambur, 1838) from Borreguiles del Río San Juan (Sierra Nevada) with atypical body proportions and with coloration matching the descriptions of *Forficula brevis* Rambur, 1838. The presence of atypical specimens mixed with typical females of *E. analis* in the high elevations of Sierra Nevada supports the synonymy between *F. analis* and *F. brevis*.

Phylogenetic placement of the Sierra Nevada earwig and comments on the systematics of Forficulidae

The Sierra Nevada earwig shares with the species of *Pseudochelidura* a similar general morphology, including similar complex patterns of male cerci and pygidial variation and a common general habitus (Cuesta-Segura *et al*. 2023). Morphological resemblance between species both of *Eulithinus* and *Pseudochelidura* partially agrees with the mitochondrial phylogenetic results, which showed that the Sierra Nevada specimens are deeply nested within *Pseudochelidura* and sister to the Pyrenean *P. sinuata* (Fig. 7). However, we are well aware of the problems of using only mitochondrial DNA data for taxonomic purposes (Sainz-Escudero *et al*. 2021), because organismic evolution is nuclear and therefore mtDNA can only be used as a proxy when no nuclear evidence suggest otherwise (Moritz *et al*. 1987; Rissler *et al*. 2006; Singhal & Moritz 2013), because mtDNA introgression is very common across species with postzygotic isolation mechanisms (Shimizu & Ueshima 2000; Alves *et al*. 2003; Babik *et al*. 2005; Barbanera *et al*. 2009; Zakharov *et al*. 2009; Nunes *et al*. 2010; Mastrantonio *et al*. 2016), and most importantly, because its haploid nature and maternal inheritance generate very different demographic dynamics with respect to nuclear genes (Avise *et al*. 1987, 1988; White *et al*. 2008). However, it is generally considered that mitochondrial DNA data are particularly useful to depict the biogeographic and past evolutionary history of a taxon (precisely because its maternal inheritance and lack of recombination allow for its long population persistence through time, as shown since the early works of Moritz *et al*. 1992; García-París *et al*. 2003). In our case, the cytb data clearly indicates that *E. analis* and *P. sinuata* became isolated from a common ancestor much more recently than they did with respect to *P. cantabrica*. However, the ITS2 phylogeny clearly placed *Eulithinus* as the sister taxon to the Iberian *Pseudochelidura*, supporting, or at least not questioning their generic status.

In this situation of morphological similarity, in which, however, the presence of a marked edge in the lateral side of the tegmina of *Eulithinus* could be clearly interpreted as a generic diagnostic character, and with mtDNA supporting *Eulithinus* as deeply nested within *Pseudochelidura*, we cannot make a proper decision on the taxonomic status of *Eulithinus*. The inclusion in the analyses of the Italian species of *Pseudochelidura* (*P. galvagnii* Vigna Taglianti, 1999, and *P. orsinii* (Gené, 1833)) might shed some additional light on whether *Eulithinus* should remain as a valid genus or if, alternatively, it should be transferred to *Pseudochelidura*. Even Steinmann (1979, 1981) while including Sierra Nevada specimens as paratypes of his Pyrenean *Pseudochelidura minor* (= *P. sinuata*) (Cuesta-Segura *et al*. 2023), or while describing his Sierra Nevada species *Pseudochelidura montana*, mixed *Eulithinus* and *Pseudochelidura.*

Following the classification criteria used by Burr in 1907, many authors who dealt with the earwigs of Sierra Nevada, included them in the subfamily Forficulinae or Anechurinae. However, Steinmann (1975), followed by Sakai (1992, 1996) and Herrera Mesa (1999) included them in the subfamily Allodahliinae Verhoeff, 1902. Steinmann (1975) considered that the criterion "border on the sides of the elytra" given by Verhoeff (1902), which also served to describe *Allodahlia* Verhoeff, 1902, was a sufficiently important characteristic feature to elevate the group to the rank of subfamily. For this reason, Steinmann included in Allodahliinae all species that possess this character state including *Allodahlia* and *Eulithinus*.

Since *Eulithinus* is close to or nested within *Pseudochelidura*, it appears that the presence of a marked edge in the humeral angle of *Eulithinus* tegmina, absent in *Pseudochelidura*, is a homoplastic trait with respect to the same structure present in *Allodahlia*. In other words, *Allodahlia* and *Eulithinus* would present similar traits in the tegmina by mere convergence and not by presenting a close phylogenetic relationship between them. This inference renders Allodahliinae without a proper diagnostic definition. We consider that the use of subfamilies within Forficulidae should be avoided until a robust phylogenetic analysis of the entire Forficulidae would define properly internal monophyletic subunits (subfamilies) within it.

The close relationship between endemics of Sierra Nevada and Pyrenean taxa is a common theme in the biogeography of European arthropods. Some of the most emblematic insects of Sierra Nevada as *Agriades zullichi* or *Mylabris nevadensis* are sister to their Pyrenean, often extended over other European mountain systems, counterparts, and allied species, as *Agriades glandon glandon* (von Prunner, 1798) plus *A. g. aquilo* (Boisduval, 1832), and *Mylabris flexuosa* Olivier, 1811 (Martin *et al*. 2002; Wiemers *et al*. 2020). The isolation of the Sierra Nevada and Pyrenean (Western European) taxa have been considered a result of the extinction of the intervening populations during the interglaciar periods. Cold adapted species inhabiting the dry and thermoclimatic areas of southeastern Spain would only survive at high elevations, becoming isolated from all other mountain systems in Western Europe (Hewitt 2001; Wilson *et al*. 2005; Ploquin *et al.* 2013). Our cytb data support that Sierra Nevada populations are related to Pyrenean populations in a well-supported monophyletic group, leaving the Cantabrian populations as sister to them.

Natural history notes and conservation

Eulithinus analis is an endemic taxon to the Sierra Nevada and the adjacent Sierra de Filabres mountain chains in the Penibetic Region of southeastern Spain. The species occurs at high elevations, from 2039 (Pilar de las Yeguas, Puerto de la Ragua) to 3029 m (Laguna de Río Seco; Fig. 10A) (Ebner 1959; own data). It is not uncommon in the western area of its range, but it becomes more sporadic towards the east. We have failed to locate the species in the Sierra de Filabres (Almería), where early 20th century explorers located some specimens (see the historical MNCN Material examined) and where general conditions seem favourable for the species; in any case, the taxonomic status of these populations require further analyses. *Eulithinus analis* is relatively frequent in open areas within rocky valleys partially covered with grass, and associated with humidity, as small lakes, streams and "borreguiles" (peat bogs) (Ebner 1959) (Fig. 10), but also at the edge of pine forests (Puerto de la Ragua). Adults are usually found under stones or active at night in humid areas of beneath decaying wooden logs in pine forests during summer months (June to August). Females attend their eggs during this period, sometimes aggregated under the same stone, and often with the remains of dead males nearby (Fig. 10B).

During the explorations to localize *E. analis* in Sierra Nevada and Sierra de Filabres, we often found specimens of *Forficula mediterranea* González-Miguéns & García-París, 2020 (in González-Miguéns *et al.* 2020), a member of the *F. auricularia* species group. The presence of this species at low-mid elevations of Sierra Nevada was expected, but we also observed large densities at high elevations areas in which *E. analis* typically occurs. In mid-August 2011, we observed more than 300 specimens of *F. mediterranea* and *F. dentata* at Puerto de la Ragua, about 50 at Laguna de Aguas Verdes at 3058 m (37°02′53″ N, 3°22′06″ W), and one female at Laguna de Río Seco. The specimen at Laguna de Río Seco (Fig. 9F) was located under a stone where females of *E. analis* were tending egg clutches (Fig. 10B), but we did not observe any interaction between them. At Laguna de Aguas Verdes we did not find a single specimen of *E. analis*, while at Puerto de la Ragua, *F. mediterranea* clearly dominated, but *E. analis* was not uncommon. Species of the *F. auricularia* complex appear in company of species of *Pseudochelidura* in the Cantabrian Mountains (Cuesta-Segura *et al*. 2023), but these limited observations were not designed to identify patterns of interaction between the high elevation specialists of the genus *Psudochelidura* and the widespread euryoic species of the *F. auricularia* species group. Unfortunately, we do not have previous data on the presence of *F. mediterranea* (even under the name of *F. auricularia*) at high elevations in Sierra Nevada.

Most of the area occupied by *E. analis* is currently under the protection of the Sierra Nevada National Park, so we do not expect immediate threats for the survival of the species other than the consequences of climate change, including a likely reduction of their presence area. It is imperative to acknowledge that the coexistence of species from the *F. auricularia* complex in the same areas as *E. analis* may constitute a potential threat to the latter species. This is attributed to the fact that species within the

F. auricularia complex exhibit substantial competitive abilities, and the ongoing climatic changes are fostering their adaptation to higher altitudes (Pavón-Gozalo *et al.* 2011). We believe it is important to determine if the populations of *E. analis* from Sierra de Filabres still exist or if they have already disappeared. In this respect, we like to call attention to the record of a specimen of *Chelidura*, reported in Fontana *et al.* (2021) from Pico de Veleta, treated as doubtful by Jurado-Angulo *et al.* (2021), but that requires further exploring.

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