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Research article

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Taxonomy of the Iberian species of *Pseudochelidura* (Dermaptera: Forficulidae)

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Abstract. Male cerci variability was used as the main source of information to separate taxonomic units in the genus *Pseudochelidura*. Based on these data it was considered that three species of *Pseudochelidura* coexisted in the Pyrenees: *P. sinuata*, *P. minor* and *P. montuosa*. However, our phylogeographic and phylogenetic analyses based on molecular data (mitochondrial cytb and nuclear ITS2) do not support those conclusions. Combining these analyses with morphological studies we concluded that: 1) the Pyrenees are inhabited by a single evolutionary unit: *P. sinuata* (Germar, 1825) (= *P. minor* Steinmann, 1979 syn. nov., = *P. montuosa* Steinmann, 1981 syn. nov.). 2) Cantabrian and Pyrenean populations are reciprocally monophyletic and morphologically diagnosable representing two independent evolutionary units: *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. and *P. sinuata*. And, 3) their conservation status needs to be evaluated in the light of current taxonomic changes. We have shown that the use of male cerci for species identification is problematic. Patterns of variation possibly affected by sexual selection (e.g., intrapopulational variability) appear to be very difficult to separate from variation driven by natural selection or genetic drift (i.e., character divergence in geographical isolation). The large sequence divergence observed between Pyrenean and Cantabrian populations of *Pseudochelidura* suggest a lasting genetic and geographic isolation between them, rendering difficult to ascertain their phylogenetic relationships.

Keywords. Earwigs, intraspecific character variability, geographic isolation, sexual variation, systematics.

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Introduction

The mountain systems of Western Europe are inhabited by a set of genera of earwigs, *Chelidura* Latreille, 1825, *Eulithinus* Hincks, 1935, *Mesochelidura* Verhoeff, 1902, and *Pseudochelidura* Verhoeff, 1902, characterized by presenting a series of adaptations typical of species inhabiting high elevation areas, including lack of wings, wide abdominal segments, relatively short antennae, and often, complex male cerci (Albouy & Caussanel 1990; Steinmann 1993; Kočárek 2004; Kirstová *et al.* 2020; Fontana *et al.* 2021b; Jurado-Angulo *et al.* 2021). Most of these genera were placed in the subfamily Anechurinae Burr, 1907, although their affinities and relationships with other members of the family Forficulidae Latreille, 1810 are still unresolved (Kirstová *et al.* 2020; Fontana *et al.* 2021b).

The most species-rich among these genera, *Pseudochelidura*, endemic to Italy, France, Andorra, and Spain, was considered to include five species: *P. sinuata* (Germar, 1825), *P. minor* Steinmann, 1979, *P. montuosa* Steinmann, 1981, *P. galvagnii* Vigna Taglianti, 1999, and *P. orsinii* (Gené, 1833) (Steinmann 1981; Albouy & Caussanel 1990; Herrera-Mesa 1999; Fontana *et al.* 2021a). The high elevation areas of the Pyrenean mountains, lying between France and Spain, are thought to be inhabited by three species of *Pseudochelidura*, one of them, *P. montuosa*, considered extremely rare (Steinmann 1981; Albouy & Caussanel 1990; Caussanel *et al.* 1990; Cuesta-Segura 2012). The taxonomic and nomenclatural history of the Pyrenean species is complex and not without controversy. The early works (e.g., Serville 1839) considered the existence of two species, consisting basically of two different male morphs, one with distorted and sinuated cerci (*P. sinuata*), and a second one with much shorter and curved cerci (*P. minor* = *F. dufourii* Serville, 1839). This status was maintained until Dubrony (1878), followed by Chopard (1951) and Harz & Kaltenbach (1976), included all the morphological diversity previously described in cerci and pygidium as variability of a single taxon, under the name *P. sinuata*. However, Steinmann (1979) reconsidered the situation of the Pyrenean populations describing *P. minor* and *P. montuosa* as new species. Subsequent authors followed Steinmann's criteria for the Pyrenean populations (Albouy & Caussanel 1990; Herrera Mesa 1999), while other authors reported the presence of *P. sinuata* or *P. minor* in the Cantabrian Mountains in northern Spain (Harz & Kaltenbach 1976 sub *P. sinuata*; Lapeira & Pascual 1980 sub *P. sinuata*; Bivar de Sousa 1997 sub *P. sinuata*; Neira Artidiello 2009 sub *P. sinuata*; Cuesta-Segura 2012 sub *P. minor*; Pérez-Valcárcel *et al.* 2022 sub *P. sinuata)*.

However, there are problems with the current taxonomic status of the Cantabrian and Pyrenean *Pseudochelidura*. A revision of Steinmann's type material (see García-París 2017) revealed that this author had some trouble naming and labelling some of this material, including specimens from the type series of *P. minor*. These problems involved the inclusion of specimens of *Eulithinus analis* (Rambur, 1838), a genus and species endemic to the Sierra Nevada (Southern Spain), quite similar at a first glance to *Pseudochelidura*, as either paratypes of *P. minor* or types of a new species, *Eulithinus montanus* Steinmann, 1981, that Steinmann originally labelled as "*Pseudochelidura montana*" (sic) (see García-París 2017). These mistakes, together with an evident lack of studies determining male cerci polymorphism in the Pyrenean and Cantabrian populations of *Pseudochelidura*, render their taxonomic adscription and status at least questionable.

During a recent revision of the Iberian Dermaptera De Geer, 1773 (García-París 2017; González-Miguéns *et al.* 2020; García-París *et al.* 2021; Jurado-Angulo *et al.* 2021), we had the opportunity of collecting and examining live specimens of *Pseudochelidura* from all the areas where the genus was reported in the Pyrenees and the Cantabrian Mountains. In addition, we had the opportunity to examine large series of Iberian specimens held at the Museo Nacional de Ciencias Naturales (MNCN, CSIC) (Madrid, Spain).

Observations made during field work in the Pyrenees, including the simultaneous presence of male specimens corresponding to typical *P. sinuata*, typical *P. minor*, and typical *P. montuosa*, all together

under the same or close by stones, generally accompanied by female specimens. These findings made us wonder, whether these three taxa corresponded to independent evolutionary units or rather represented three phenotypic variants of pygidium and cerci development of a single taxon as some authors previously considered (Dubrony 1878; Harz & Kaltenbach 1976). We observed a similar pattern of variation in populations of *Pseudochelidura* from the Cantabrian Mountains, although in this case, the morphology of the cerci of each phenotype differed consistently from those present in the Pyrenean specimens (as already shown in the figures presented by Harz & Kaltenbach 1976). Based on those observations, our working hypotheses are that (1) the Pyrenean and the Cantabrian populations correspond to two independent evolutionary units, while (2) all the morphological diversity represented by Pyrenean *P. sinuata*, *P. minor*, and *P. montuosa*, correspond to a single, highly polymorphic taxon. Trying to obtain an independent (e.g., not morphological) source of information, we obtained partial sequences of the cytochrome b mitochondrial gene (cytb) and the nuclear second internal transcribed spacer (ITS2) from specimens representing the main different phenotypes from diverse localities in the Pyrenees and the Cantabrian Mountains.

The main goal of this work is thus to revise the taxonomic status of the Cantabrian and Pyrenean populations of *Pseudochelidura*, with the following particular objectives: (1) identify the evolutionary units of *Pseudochelidura* inhabiting the Iberian Peninsula, describing their morphological variation, (2) settle the taxonomy of the genus in the area, by describing a new species endemic to the Cantabrian Mountains, and stablishing the new required synonymies for the Pyrenean populations, (3) discuss the problems of using secondary sexual characters for species delimitation in Dermaptera, and (4) evaluate the need of revising the conservation status of Iberian *Pseudochelidura* in the light of the new taxonomic results.

Material and methods

Studied material

A total of 458 specimens morphologically assignable to *Pseudochelidura* were included in this study: 32 were used for the DNA analyses (Table 1) and 426 for the morphological analyses (see also Paratypes section).

We studied 12 additional specimens assigned to *Pseudochelidura* by Steinmann in the collection of the Hungarian Natural History Museum (HNHM). Four of these specimens are the holotype of *Pseudochelidura montana* Steinmann, 1981, and respective paratypes of *Pseudochelidura minor* Steinmann, 1979. Of the 458 studied non-type specimens of *Pseudochelidura*, 333 dry mounted specimens are held in the collection of the Museo Nacional de Ciencias Naturales (Madrid) (MNCN, CSIC) (156 from the Cantabrian Mountains, 162 from the Pyrenees, and 15 *P. orsinii*), 26 dry mounted specimens from the Cantabrian Mountains at the A.D. Cuesta-Segura collection (ADC-S), 56 specimens preserved in absolute ethanol at the MNCN collection (23 from the Cantabrian Mountains and 33 from the Pyrenees), and 43 specimens preserved in 70% ethanol at the ADC-S collection (38 from the Cantabrian Mountains and 5 from the Pyrenees). Recently collected specimens were photographed in the field when possible and georeferenced using the WGS84 datum system prior to being preserved in absolute ethanol and then stored at –20°C at the MNCN, CSIC or dry mounted.

Type material

Paratypes of *Pseudochelidura minor* Steinmann, 1979

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.

Table 1 (continued on next page). Specimens used for DNA analyses with their corresponding MNCN Entomology Collection codes (voucher number) and GenBank accession numbers.

Taxon	Voucher number	Locality	Coordinates	GenBank cytb	GenBank ITS2
Pseudochelidura sinuata	MNCN_Ent 331186	France: Ariège: Coll de Pailhères, 1958 m a.s.l.	42º44′07.7″ N 1º59′53.5″ E	OP893680	OP908089
Pseudochelidura sinuata	MNCN_Ent 331187	France: Ariège: Coll de Pailhères, 1958 m a.s.l.	42º44′07.7″ N 1º59′53.5″ E	OP893681	OP908090
Pseudochelidura sinuata	MNCN_Ent 331188	France: Ariège: Coll de Pailhères, 1958 m a.s.l.	42º44′07.7″ N 1º59′53.5″ E	OP893682	OP908091
Pseudochelidura sinuata	MNCN_Ent 331191	France: Ariège: Coll de Pailhères, 1958 m a.s.l.	42º44′07.7″ N 1º59′53.5″ E	OP893683	OP908092
Pseudochelidura sinuata	MNCN_Ent 331193	France: Ariège: Coll de Pailhères, 1958 m a.s.l.	42º44′07.7″ N 1º59′53.5″ E	OP893684	OP908093
Pseudochelidura sinuata	MNCN_Ent 331197	France: Ariège: Coll de Pailhères, 1958 m a.s.l.	42º44′07.7″ N 1º59′53.5″ E	OP893685	OP908094
Pseudochelidura sinuata	MNCN_Ent 331198	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893686	OP908095
Pseudochelidura sinuata	MNCN_Ent 331199	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893687	OP908096
Pseudochelidura sinuata	MNCN_Ent 331200	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893688	OP908097
Pseudochelidura sinuata	MNCN_Ent 331201	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893689	OP908098
Pseudochelidura sinuata	MNCN_Ent 331203	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893690	OP908099
Pseudochelidura sinuata	MNCN_Ent 331205	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893691	OP908100
Pseudochelidura sinuata	MNCN_Ent 331210	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893692	OP908101
Pseudochelidura sinuata	MNCN_Ent 331212	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893693	OP908102
Pseudochelidura sinuata	MNCN_Ent 331215	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893694	OP908103
Pseudochelidura sinuata	MNCN_Ent 331215h	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893695	OP908104
Pseudochelidura sinuata	MNCN_Ent 331216	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893696	OP908105
Pseudochelidura sinuata	MNCN_Ent 331216h	Andorra: Canillo: Coma de Ransol, 1940 m a.s.l.	42º36′44.2″ N 1º38′16.0″ E	OP893697	OP908106
Pseudochelidura sinuata	MNCN_Ent 331171	Spain: Aragón: Huesca: Bielsa: Valle de Pineta, 1299 m a.s.l.	42º40′47.84″ N 0º04′47.68″ E	OP893679	OP908088
Pseudochelidura cantabrica sp. nov.	MNCN_Ent 331172	Spain: Castilla y León: León: Puerto de la Ventana, 1588 m a.s.l.	43º03′27.62″ N 6º00′15.15″ W	OP893666	OP908075
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331175	Spain: Castilla y León: León: Puerto de la Ventana, 1588 m a.s.l.	43º03′27.62″ N 6º00′15.15″ W	OP893667	OP908076

Table 1 (continued).

Taxon	Voucher number	Locality	Coordinates	GenBank cytb	GenBank ITS2
Pseudochelidura cantabrica sp. nov.	MNCN_Ent 331176	Spain: Castilla y León: León: Puerto de la Ventana, 1588 m a.s.l.	43º03′27.62″ N 6º00′15.15″ W	OP893668	OP908077
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331179	Spain: Castilla y León: León: Puerto de la Ventana, 1588 m a.s.l.	43º03′27.62″ N 6º00′15.15″ W	OP893669	OP908078
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331182	Spain: Castilla y León: León: Puerto de la Ventana, 1588 m a.s.l.	43º03′27.62″ N 6º00′15.15″ W	OP893670	OP908079
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331219	Spain: Castilla y León: León: Puerto de Vegarada, 1684 m a.s.l.	43°01′54.95″ N 5°28′34.17″ W	OP893671	OP908080
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331220	Spain: Castilla y León: León: Puerto de Vegarada, 1684 m a.s.l.	43°01′54.95″ N 5°28′34.17″ W	OP893672	OP908081
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331221	Spain: Castilla y León: León: Puerto de Vegarada, 1684 m a.s.l.	43°01′54.95″ N 5°28′34.17″ W	OP893673	OP908082
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331222	Spain: Castilla y León: León: Puerto de Vegarada, 1684 m a.s.l.	43°01′54.95″ N 5°28′34.17″ W	OP893674	OP908083
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331223	Spain: Castilla y León: León: Puerto de Vegarada 1684 m a.s.l.	43°01′54.95″ N 5°28′34.17″ W	OP893675	OP908084
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331224	Spain: Castilla y León: Burgos: Puerto de las Estacas de Trueba, 1128 m a.s.l.	43°6′48.55″ N 3°42′4.69″ W	OP893676	OP908085
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331225	Spain: Castilla y León: Burgos: Puerto de Lunada, 1270 m a.s.l.	43°10′20.98″ N 3°38′39.49″ W	OP893677	OP908086
Pseudochelidura cantabrica sp. nov	MNCN_Ent 331226	Spain: Castilla y León: Burgos: Puerto de Lunada, 1270 m a.s.l.	43°10′20.98″ N 3°38′39.49″ W	OP893678	OP908087
Mesochelidura bolivari	MNCN_Ent 331218	Spain: Castilla y León: Palencia: Triollo, 1314 m a.s.l.	42º55′59.5″ N 4º40′14.8″ W	OP893698	OP908107

WITHOUT LOCALITY DATA • 1 ♂; "Hab.? Europa [hand written] // Paratypus *Pseudochelidura minor* Dr. H. Steinmann [name hand written, white label red edges] // Dt 1937 [printed]"; morphologically assignable to *P. sinuata* sensu novo; HNHM • 1 ♂; "*P. sinuata var.* [typed] // *Pseudochelidura sinuata* Lafr. determ. ex coll. Mus. Stettin [hand written] // gen. prep. No. 397 det. Dr. Steinmann [number hand written] // Paratypus *Pseudochelidura minor* Dr. H. Steinmann [name hand written, white label red edges] // Dt 1935 [printed]"; morphologically assignable to *P. sinuata* sensu novo; HNHM.

Holotype of *Eulithinus montanus* (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 written, white label red edges] // Dt 2382 [printed]"; specimen reported by Steinmann (1981); HNHM.

Non-type specimens

Pseudochelidura cantabrica Cuesta-Segura, Jurado-Angulo & García-París sp. nov.

(1) Dry mounted specimens

SPAIN – **Asturias** • 1 ♂; Puerto de Ventana; 43°3′31.6″ N, 6°0′10.02″ W; 1603 m a.s.l.; 19 Aug. 2017; ADC-S leg.; ADC-S • 1 ♂; same collection data as for preceding; 17 Sep. 2017; ADC-S leg.; ADC-S. – **Cantabria** • 2 ♂♂, 1 ♀; Picos de Europa, Peña Vieja; 1700 m a.s.l.; Aug. 1935; C. Bolívar and F. Escalera leg.; MNCN_Ent 123682 to 123684 • 2 ♂♂; Picos de Europa, Puerto de Áliva; 43°10′26.81″ N, 4°47′54.21″ W; 1890 m a.s.l.; 24 Jul. 2021; ADC-S leg.; ADC-S. – **Castilla y León: Burgos** • 1 ♂, 2 ♀♀; Puerto de Las Estacas de Trueba; 43°6′48.55″ N, 3°42′4.69″ W; 1128 m a.s.l.; 13 Sep. 2017; ADC-S leg.; MNCN_Ent 167449, 167450, 167484 • 1 ♂, 4 ♀♀; Puerto de Lunada; 43°10′20.98″ N, 3°38′39.49″ W; 1270 m a.s.l.; 13 Sep. 2017; ADC-S leg.; MNCN_Ent167451 to 167454, 167480. **León** • 1 ♂, 1 ♀; LaCeana [Laciana]; Lauffer leg.; MNCN_Ent 123599, 123600 • 1 ♂; Puerto de Vegarada; 43°2′17.08″ N, 5°28′42.39″ W; 1560 m a.s.l.; 1–21 Jun. 2008; in pitfall trap; ADC-S leg.; ADC-S • 1 ♂; same collection data as for preceding; 43°01′54.95″ N, 5°28′34.17″ W; 1684 m a.s.l.; 22 Jul. 2017; ADC-S leg.; ADC-S • 1 ♂; same collection data as for preceding; 15 Jul. 2021; ADC-S leg.; ADC-S • 1 ♀; same collection data as for preceding; 43°02′15.64″ N, 5°28′34.45″ W; 1543 m a.s.l.; 24 Jul. 2017; ADC-S leg.; ADC-S • 1 ♀; Puerto de Ventana; 43°03′13.5″ N, 6°0′31.6″ W; 1559 m a.s.l.; 19 Aug. 2017; ADC-S leg.; ADC-S • 1 ♂; same collection data as for preceding; 43°03′11.3″ N, 6°00′09.6″ W; 1543 m a.s.l.; 20 Aug. 2017; ADC-S leg.; ADC-S • 1 ♀; Torrestío; 43°03′50.22″ N, 6°04′37.62″ W; 1700 m a.s.l.; 15 Jul.–4 Aug. 2010; ADC-S leg.; in pitfall trap; ADC-S • 1 ♀; same collection data as for preceding; 4–22 Aug. 2010; ADC-S leg.; in pitfall trap; ADC-S • 1 ♂; same collection data as for preceding; 22 Aug.–11 Sep. 2010; ADC-S leg.; in pitfall trap; ADC-S • 4 ♂♂, 2 ♀♀; Puerto de La Farrapona; 43°2′51.99″ N, 6°5′18.10″ W; 1651 m a.s.l.; 17 Sep. 2017; ADC-S leg.; ADC-S. – **Province not indicated** • 16 ♂♂, 5 ♀♀; Picos de Europa; Aug.; Bolívar leg.; MNCN_Ent 123601 to 123621.

(2) Ethanol preserved specimens

SPAIN – **Asturias** • 1 ♀; Puerto de La Farrapona; 43°03′28.81″ N, 6°05′37.99″ W; 1685 m a.s.l.; 17 Sep. 2017; ADC-S leg.; ADC-S • 1 ♀; Puerto de Vegarada; 43°01′51.6″ N, 5°29′29.3″ W; 1723 m a.s.l.; 3 Aug. 2022; ADC-S leg.; ADC-S • 3 ♂♂, 3 ♀♀; Puerto de Ventana; 43°3′31.6″ N, 6°0′10.02″ W; 1603 m a.s.l.; 19 Aug. 2017; ADC-S leg.; ADC-S • 1 ♂; same collection data as for preceding; 17 Sep. 2017; ADC-S leg.; ADC-S. – **Castilla y León**: **Burgos** • 1 ♀; Puerto de las Estacas de Trueba; 43°6′48.55″ N, 3°42′4.69″ W; 1128 m a.s.l.; 13 Sep. 2017; ADC-S leg.; MNCN_Ent 331224 • 2 ♀♀; Puerto de Lunada; 43°10′20.98″ N, 3°38′39.49″ W; 1270 m a.s.l.; 13 Sep. 2017; ADC-S leg.; MNCN_Ent 331225, 331226. **León** • 2 ♂♂, 2 ♀♀; Picos de Europa, Canal de Pedavejo; 43°08′48.86″ N, 4°51′05.33″ W; 2033 m a.s.l.; 29 Aug. 2019; ADC-S leg.; ADC-S • 1 ♂ (last tergite and cerci), 1 nymph (moult); Picos de Europa: Torre de Llambrión; 43°10′9.55″ N, 4°51′51.38″ W; 2152 m a.s.l.; 5 Jul. 2015; Grupo Ibérico de Anillamiento (GIA) leg.; by vacuum sampling; ADC-S • 1 ♂; same collection data as for preceding; 10 Aug. 2015; GIA leg.; by vacuum sampling; ADC-S • 1 nymph (moult); same collection data as for preceding; 43°10′7.15″ N, 4°51′48.93″ W; 2160 m a.s.l.; 14 Jul. 2015; GIA leg.; by vacuum sampling; ADC-S • 2 ♂♂ (last tergite and cerci), 1 ♀; same collection data as for preceding; 43°10′3.25″ N, 4°51′43.41″ W; 2179 m a.s.l.; 4 Aug. 2015; GIA leg.; by vacuum sampling; ADC-S • 1 ♂ (last tergite and cerci); same collection data as for preceding; 43°10′1.62″ N, 4°51′40.83″ W; 2184 m a.s.l.; 4 Jul. 2015; GIA leg.; by vacuum sampling; ADC-S • 1 ♂ (last tergite and cerci), 1 nymph (moult); same collection data as for preceding; 43°10′1.02″ N, 4°51′35.32″ W; 2180 m a.s.l.; 4 Aug. 2015; GIA leg.; by vacuum sampling; ADC-S • 1 nymph (moult); same collection data as for preceding; 43°10′1.38″ N, 4°51′25.50″ W; 2112 m a.s.l.; 23 Jun. 2015; GIA leg.; by vacuum sampling; ADC-S • 1 ♀ (last tergite and cerci); same collection data as for preceding; 4 Aug. 2015; GIA leg.; by vacuum sampling • 4 ♀♀; Torrestío; 43°03′50.22″ N, 6°04′37.62″ W; 1700 m a.s.l.; 15 Jul.–4 Aug. 2010; ADC-S leg.; in pitfall trap; ADC-S • 1 ♂; same collection data as for preceding; 4–22 Aug. 2010; ADC-S leg.; in pitfall trap; ADC-S • 1 ♀; same collection data as for preceding; 22 Aug.–11 Sep. 2010; ADC-S leg.;

in pitfall trap; ADC-S • 1 ♂; same collection data as for preceding; 11 Sep. 2010; ADC-S leg.; ADC-S • 1 ♂; Puerto de Vegarada; 43°2′17.08″ N, 5°28′42.39″ W; 1560 m a.s.l.; 1–21 Jun. 2008; ADC-S leg.; in pitfall trap; ADC-S • 2 ♀♀; same collection data as for preceding; 1–23 Aug. 2008; ADC-S leg.; in pitfall trap; ADC-S • 1 ♀; same collection data as for preceding; 43°02′18.69″ N, 5°28′36.59″ W; 1554 m a.s.l.; 9 Apr. 2017; ADC-S leg.; ADC-S • 3 ♀♀; Puerto de Ventana; 43°03′13.5″ N, 6°0′31.6″ W; 1559 m a.s.l.; 19 Aug. 2017; ADC-S leg.; ADC-S • 1 ♀, 1 nymph; same collection data as for preceding; 43°03′26.3″ N, 6°00′11.7″ W; 1590 m a.s.l.; 20 Aug. 2017; ADC-S leg.; ADC-S • 1 ♂; same collection data as for preceding; 43°03′16.02″ N, 6°00′13.95″ W; 1486 m a.s.l.; 20 Aug. 2017; ADC-S leg.; ADC-S.

Pseudochelidura sinuata (Germar, 1825)

(1) Dry mounted specimens

FRANCE – **Ariège** • 3 nymphs; Lhospitalet [L'Hospitalet-près-l'Andorre]; Dr. Martin leg.; MNCN_Ent 201806-08. – **Haute-Garonne** • 3 ♂♂, 4 ♀♀; Luchon [Bagnères-de-Luchon], P. Venasque [Port de Vénasque]; MNCN_Ent 8215, 201785 to 201791 • 1 ♀; Luchon [Bagnères-de-Luchon], P. Venasque [Port de Vénasque]; MNCN_Ent 201803 • 1 ♀; same collection data as for preceding; H. du Buysson leg.; MNCN_Ent 201802 • 2 ♀♀; same collection data as for preceding; MNCN_Ent 201801, 201804. – **Hautes-Pyrénées** • 2 ♂♂, 2 ♀♀; Bagnères-de-Bigorre; 5 Oct. 1886; Col. A. Finot; MNCN_Ent 201797 to 201800 • 1 ♂; Circo de Gavar [Cirque de Gavarnie]; Sep. 79; Bormans leg; MNCN_Ent 201792 • 1 ♀; Gavarnie [Cirque de Gavarnie]; Dr. Martin leg.; MNCN_Ent 201805 • 3 ♂♂, 1 ♀; Pic du Midi; Marquet leg.; MNCN_Ent 201793 to 201796 • 1 ♂; same collection data as for preceding; 2500 m a.s.l.; HNHM.

SPAIN – **Aragón: Huesca** • 1 ♂; Biescas; 25 Jul. 1918; C. Bolívar leg.; MNCN_Ent 123564 • 1 ♂; Canfranc, Candanchú; 1400 m a.s.l.; Aug. 1943; J.M. Dusmet leg.; MNCN_Ent 123589 • 7 ♂♂, 5 ♀♀; Hospital de Benasque; 7 Aug. 1918; C. Bolívar leg.; MNCN_Ent 123543 to 123546, 123552, 123576 to 123578, 123581, 123584, 123585, 123591 • 6 ♂♂, 7 ♀♀; Panticosa; MNCN_Ent 123624 to 123636 • 1 ♂; same collection data as for preceding; Escalera leg.; MNCN_Ent 123623 • 1 ♀; same collection data as for preceding; Jul. 1921; Dusmet leg.; MNCN_Ent 123622 • 2 ♂♂, 2 ♀♀; same collection data as for preceding; 1800 m a.s.l.; 16–18 Jul. 1943; Exp. Inst. de Entomología leg.; MNCN_Ent 123565 to 123568 • 1 ♂, 8 ♀♀, 2 nymph; Plan, Puerto de Sahún; 2000 m a.s.l.; 5 Aug. 1918; C. Bolívar leg.; MNCN_Ent 123536 to 123538, 123547 to 123550, 123553, 123555, 123556, 123579 • 4 ♂♂, 9 ♀♀; Puerto de Bujaruelo; MNCN_Ent 123637, 123639 to 123649, 123690 • 1 ♀; Puerto de Castanesa; 2000–2200 m a.s.l.; MNCN_Ent 123650 • 1 ♂, 1 ♀; Sallent [Sallent de Gállego]; 1268 m a.s.l.; 4–12 Aug. 1949; Exp. Inst. de Entomología leg.; MNCN_Ent 123701, 123744 • 3 ♂♂, 1 ♀; Selva de Oza; 1230 m a.s.l.; 6 Jul. 1943; Exp. Inst. de Entomología leg.; MNCN_Ent 123569 to 123572 • 5 ♂♂, 8 ♀♀; Valle de Canfranc; 1200–1400 m a.s.l.; 19 Jul. 1918; C. Bolívar leg.; MNCN_Ent 123539 to 123542, 123551, 123554, 123560, 123563, 123582, 123586, 123590, 123638, 123746 • 2 ♂♂, 1 ♀; Valle de Ordesa; MNCN_Ent 123573 to 123575 • 3 ♂♂, 2 ♀♀; same collection data as for preceding; F. Bonet leg.; MNCN_Ent 123653 to 123657 • 1 ♂; same collection data as for preceding; C. Bolívar leg.; MNCN_Ent 123658 • 1 ♂, 1 ♀; same collection data as for preceding; Jul. 1934; C. Bolívar leg.; MNCN_Ent 123587, 123588 • 4 ♂♂, 3 ♀♀; Ordesa; Jul. 1934; E. Mor [E. Morales] leg.; MNCN_Ent 123592 to 123598. – **Cataluña**: **Lleida** • 9 ♂♂, 5 ♀♀; Puerto Pallás [Pallars]: Virgen de Arés [Alt Àneu]; MNCN_Ent 123667 to 123680 • 2 ♂♂, 2 ♀♀, 2 nymphs; same collection data as for preceding; 1928; M. Escalera leg;. MNCN_Ent 123659 to 123662, 123664, 123666 • 5 ♂♂, 11 ♀♀; Salardú; 1260 m a.s.l.; Aug. 1948; E. Morales and Exp. Inst. de Entomología leg.; MNCN_Ent 123583, 123685 to 123689, 123691 to 123700 • 1 ♂, 1 ♀; Valle de Arán [Val d'Aran]; C. Bolívar leg.; MNCN_Ent 123561, 123562 • 1 ♀; Valle de Arán [Val d'Aran], Artiga de Lin; 2 Aug. 1948; Exp. Inst. de Entomología leg.; MNCN_Ent 123681 • 2 ♀♀; Valle de Arán [Val d'Aran]: Llenas; MNCN_Ent 123651, 123652 • 1 ♂; Baños de Tredós; 1695 m a.s.l.; Aug. 1948; E. Morale leg.; MNCN_Ent 123580.

WITHOUT LOCALITY DATA • 1 ♀; "*Ch. sinuata* var. *Dufouri*, Mus. Zool. Polonicum Warszawa 12/45, *Pseudochelidura sinuata* Lafr. det Dr. Steinmann, Dt 1931"; HNHM • 1 ♂; "*Pseudochelidura sinuata* Lafr. det Dr. Steinmann, Dt 1931"; HNHM • 1 ♂; "white square, red circle, Mus. Zool. Polonicum Warszawa 12/45, *Pseudochelidura sinuata* Lafr. det Dr. Steinmann, gen. prep. No. 397 det. Dr. Steinmann, Dt 1934"; HNHM.

(2) Ethanol preserved specimens
ANDORRA • 8 ♂♂, 8 ♀♀ (some with eggs or nymphs), 4 nymphs; Canillo, Coma de Ransol; 42°36′44.2″ N, 1°38′16.0″ E; 1940 m a.s.l.; 21 Jun. 2013; MNCN_Ent 331198 to 331217.

FRANCE – **Ariège** • 4 ♂♂, 7 ♀♀ (some with eggs or nymphs), 1 nymph; Coll de Pailhères; 42°44′07.7″ N, 1°59′53.5″ E; 1958 m a.s.l.; 19 Jun. 2013; MNCN_Ent 331186 to 331197. – **Hautes-Pyrénées** • 1 ♂, 1 ♀, 3 nymphs; Cirque de Gavarnie; 42°41′59.82″ N, 0°00′22.91″ W; 1633 m a.s.l.; 27 Jul. 2013; ADC-S collection.

SPAIN – **Aragón**: **Huesca** • 1 ♂; Bielsa, Valle de Pineta; 42°40′47.84″ N, 0°04′47.68″ E; 1299 m a.s.l.; 29 Jun. 2011; MNCN_Ent 331171.

Pseudochelidura orsinii (Gené, 1833)
Dry mounted specimens
ITALY – **Abruzzo** • 1 ♂, 1 ♀; La Mela; 18 Aug. 1912; Ebner leg.; MNCN_Ent 201809, 201811 • 1 ♂, 1 ♀; Gran Sasso; 9 Aug. 1912; Ebner leg.: MNCN_Ent 201810, 201812. – **Campania** • 2 ♀♀; Matese, Monte Miletto; 1600–2000 m a.s.l.; 20 Aug. 1949; M. La Greca leg.; MNCN_Ent 201820, 201821. – **Emilia-Romagna** • 2 ♂♂, 2 ♀♀; Piandelagotti; Aug. 1922; C. Menozzi leg.; MNCN_Ent 201814, 201816, 201817, 201819 • 2 ♂♂; Sestola; 10 Aug. 1921; C. Menozzi leg.; MNCN_Ent 201815, 201818. – **Marche** • 2 ♂♂, 1 ♀; Forca Viola, Monti Sibillini; 1900 m a.s.l.; 9 Aug. 1954; Galvagni leg.; MNCN_Ent 201822 to 201824.

Morphological study and distribution data

Description of nymphal stages was based on the study of 34 nymphs obtained from a single female from Puerto de Vegarada (León, Spain) collected during the summer of 2017, kept in captivity, individualized in small Petri dishes of 55 mm in diameter with a wet paper on the bottom and fed with small pieces of cheese, turkey ham, walnuts, homemade quince jelly, cooked potato and banana, offered at the same time and constantly. Additional nymphs were obtained from the field and kept in captivity from similar way.

External characters were measured under the stereo microscope Zeiss 47 50 57, in the Zoology Area of the University of León, at highest possible magnification. Dry-mounted specimens from the MNCN Entomology collection were photographed with a digital camera Nikon and a lens Nikon AF-S VR Micro-Nikkor 105mm f/2.8G IF-ED, using the software Helicon Remote ver. 3.9.11 and Helicon Focus ver. 7.6.4. We followed the protocol described in Fontana *et al.* (2002) with minor modifications to extract male genitalia. The nomenclature of the different parts of the male genitalia is based on Burr (1915). Male genitalia from specimens of the Cantabrian Mountains, including six paratypes of *P. cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp, nov. (MNCN_Ent 167421, 167488, 167500, ADC-S col. Derm_0005-6, 0008), were studied in detail and photographed. Description of the new taxon follows the structure of Matzke & Kočárek (2015). The distribution map of *P. cantabrica* was generated with the QGIS program (QGIS 2022) from bibliographic and own data (see examined material).

DNA sequencing and phylogenetic analyses

For molecular analyses, total DNA was extracted from 33 specimens: 19 from the Pyrenees and 13 from the Cantabrian Mountains representing all three phenotypes assignable to *P. sinuata*, *P. minor*,

and *P. montuosa* (following Albouy & Caussanel 1990 and Steinmann 1981), plus one specimen of *Mesochelidura bolivarii* (Dubrony, 1878), used as outgroup to root the phylogenetic analyses. DNA was extracted from one or two legs, depending on specimen size, using the DNeasy Blood and Tissue Isolation Kit (Qiagen, Hilden, Germany), according to the manufacturer's instructions, and then stored at 4°C until further processed.

Polymerase chain reaction (PCR) was used to amplify fragments of the cytochrome b gene (cytb) using the set of primers CB-J-10933 (Simon *et al.* 1994) and CB4 (Pons 2006), and fragments of the nuclear second internal transcribed spacer (ITS2) using the primers CAS5p8SFc and CAS28SB1d (Ji *et al.* 2003). All PCR amplifications were conducted 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 DNApolymerase (1 unit; Biotools). Thermocycling conditions consisted of an initial denaturation at 95°C for 5 min, followed by 40 cycles of denaturation at 94°C for 1 min, annealing at 40°C (cytb) or 48°C (ITS2) for 1 min and extension at 72°C for 1 min, and a final elongation step at 72°C for 5 min. PCR products were checked in a 1% agarose gel and products with the expected length were sent for sequencing to Macrogen Inc. (Macrogen Europe, Madrid, Spain). Sequences were checked, edited and aligned using BioEdit ver. 7.0.9 (Hall 1999). Uncorrected (p) pairwise genetic distances were estimated using PAUP* ver. 4.0a (Swofford 2002). Cytb was selected to provide mitochondrial information for phylogeographic analyses in this study, instead of the generally used cox1 (González-Miguéns *et al.* 2020; Kirstová *et al.* 2020; Jurado-Angulo *et al*. 2021), because we had consistent PCR amplifications of *Wolbachia* (Rickettsiales) (Werren *et al*. 2008) cox1 in leg tissues of *Pseudochelidura*.

A Bayesian inference analysis was conducted in MrBayes ver. 3.2.6 (Ronquist *et al.* 2012) using a concatenated mitochondrial-nuclear dataset. We used JModelTest ver. 2.1.10 (Darriba *et al.* 2012) to determine the best substitution model for each marker (Posada & Buckley 2004) under the Bayesian Information Criterion (BIC; Schwarz 1978). The selected models were: HKY+I for the cytb and F81 for the ITS2. MrBayes analysis consisted of two simultaneous runs of 10 million generations, sampling trees every 100 generations. The resulting consensus tree was constructed after discarding the first 10% trees as burn-in, and then edited in FigTree ver. 1.4.3 (Rambaut 2012).

To present a hypothesis on how many singular and evolutionary independent taxa can be defined within the Iberian *Pseudochelidura*, we followed the evolutionary species concept (Wiley 1978) as discussed in Sánchez-Vialas *et al.* (2020). This concept combines implications derived from the phylogenetic species concept such as reciprocal monophyly with additional subjective properties, such as phenetic distinguishability and reproductive isolation (Ruiz & García-París 2015).

Results

Phylogenetic analyses

The tree topology of the combined data set (mtDNA cytb and nuclear ITS2) recovered two well-supported main clades within *Pseudochelidura* (Bayesian Posterior Probability PP = 1) (Fig. 1). The first clade included the Pyrenean specimens (PP = 1; in purple in Fig. 1) and the second clade (PP = 1; in orange in Fig. 1) grouped the specimens from the Cantabrian Mountains. Separate analyses for each marker yielded totally compatible topologies, only differing in resolution (ITS2 produced a large polytomy including all Pyrenean samples). Uncorrected 'p' distances between different groups based on cytb are summarized in Table 2.

Pyrenean samples (Andorra: Canillo: Coma de Ransol; France: Ariège: Coll de Pailhères; Spain: Huesca: Valle de Pineta) include male specimens with cerci and pygidium assignable to the morphological concept of *P. sinuata* (MNCN_Ent 332186, 331203, 331205), specimens assignable to *P. minor*

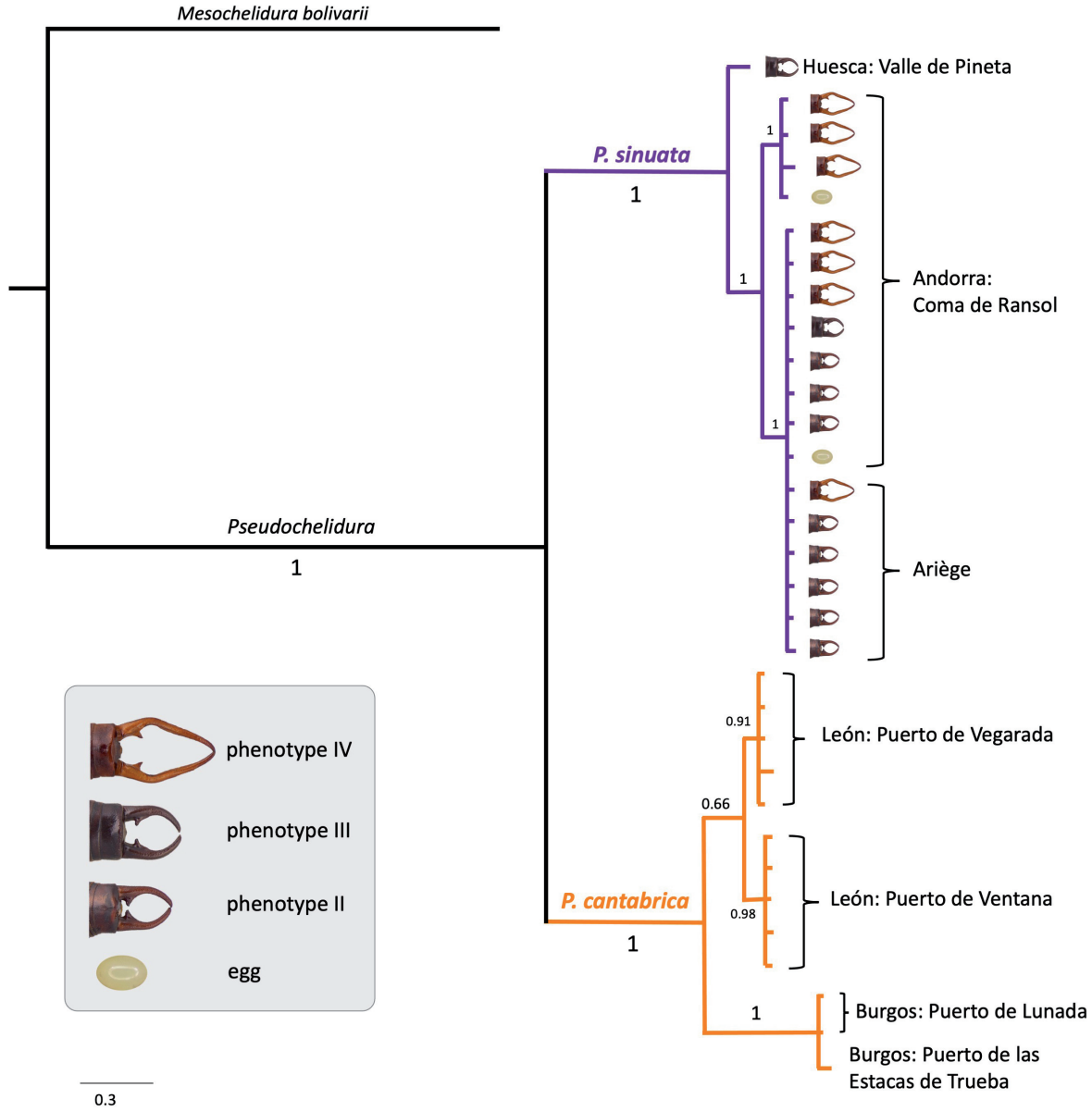

Fig. 1. Bayesian tree obtained using the concatenated mitochondrial-nuclear data set (cytb + ITS2). Independent analyses using cytb and ITS2 data provided totally congruent topologies. Posterior probabilities are indicated below branches. Branch colors represent the two species of *Pseudochelidura* Verhoeff, 1902 studied: *P. sinuata* (Germar, 1825) and *P. cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. A synthetic representation of the cerci phenotype of each analyzed male specimen of *P. sinuata* is represented next to its branch. The three phenotypes corresponded to the three previously recognized Pyrenean species of *Pseudochelidura* synonymized in this work (*P. sinuata* = *P. minor* Steinmann, 1979 = *P. montuosa* Steinmann, 1981 syn. nov.). DNA from two eggs was also sequenced. Specimens of *P. cantabrica* used in the analyses covered all range of male cerci variability (see Fig. 3).

(MNCN_Ent 331187–8, 331199–201), and to *P. montuosa* (MNCN_Ent 331171, 331198) (Figs 2–3). All these samples, irrespective of their morphological ascription, form a monophyletic group. Sequence divergence was low for mtDNA sequences (uncorrected mitochondrial $p_{distance}$ = 0.000–0.057) and non-existent for nuclear sequences (Fig. 1; Table 2).

Cantabrian samples (Spain: León: Puerto de Vegarada; Puerto de Ventana and Burgos: Puerto de las Estacas de Trueba; Puerto de Lunada) also included male specimens with a different cerci morphology: including long slightly curved cerci (MNCN_Ent 331220), long curved cerci (MNCN_Ent 331219, 331221), short curved cerci (MNCN_Ent 331222–23), and short, slightly curved cerci (MNCN_Ent 331172, 331175) (Fig. 3). Samples from the Cantabrian clade appear to be geographically structured in two main subclades, one including samples from the eastern area (Puerto de las Estacas de Trueba and Puerto de Lunada, PP = 1), and the second including samples from the western areas (Puerto de Vegarada and Puerto de Ventana,

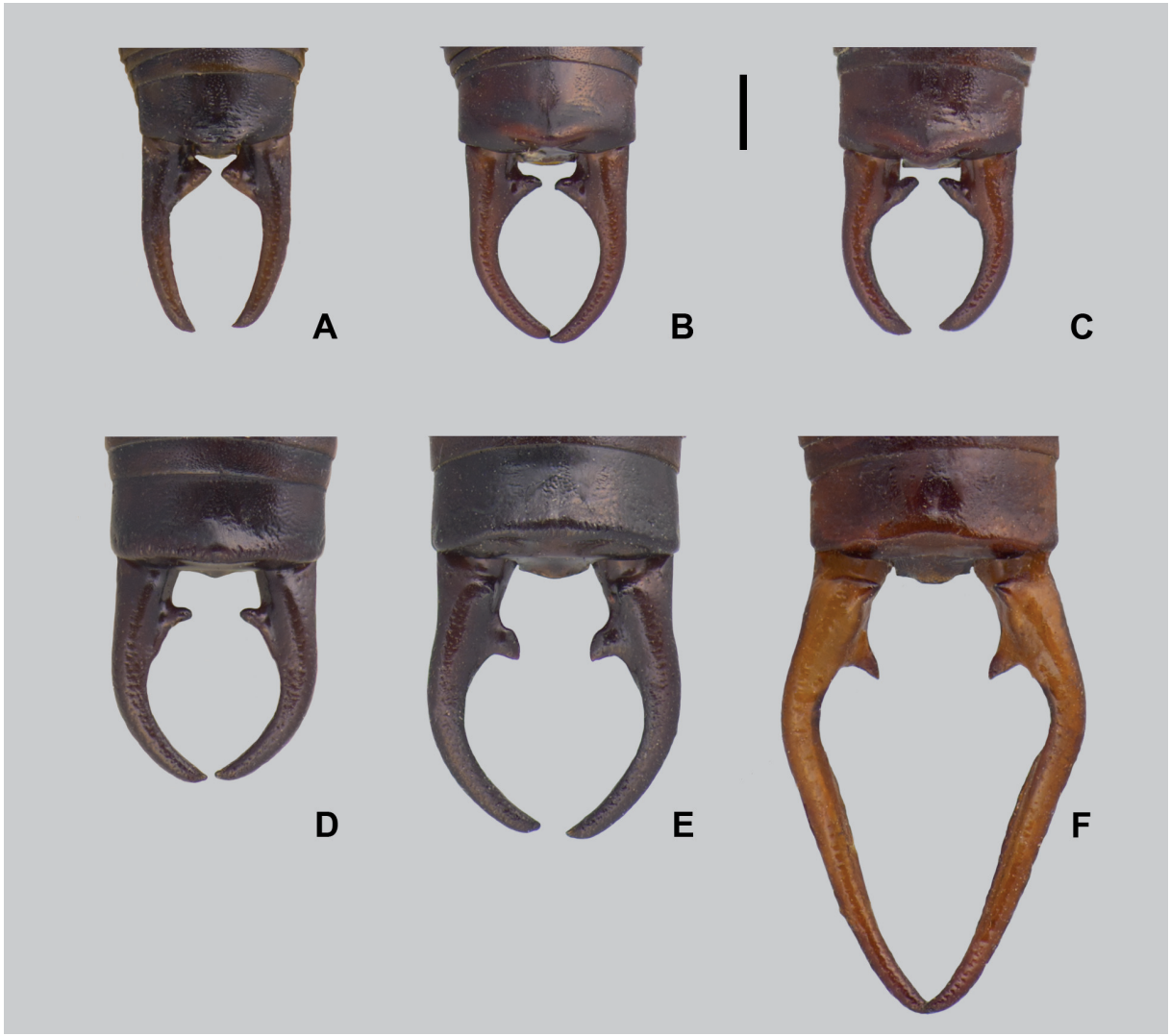

Fig. 2. Cerci variation in *Pseudochelidura sinuata* (Germar, 1825), males. **A**. Valle de Canfranc (Huesca, Spain) (MNCN_Ent 123563). **B**. Salardú (Lleida, Spain) (MNCN_Ent 123689). **C**. Puerto Pallars, Virgen de Arés (Lleida, Spain) (MNCN_Ent 123674). **D**. Panticosa (Huesca, Spain) (MNCN_Ent 123568). **E**. Puerto de Bujaruelo (Huesca, Spain) (MNCN_Ent 123639). **F**. Puerto Pallars, Virgen de Arés (Lleida, Spain) (MNCN_Ent 123668). Scale bar = 1 mm.

PP = 0.66). Mitochondrial and nuclear sequences of the Cantabrian clade show a poor differentiation across geographic areas (uncorrected mitochondrial $p_{distance}$ = 0.000–0.0123; uncorrected nuclear $p_{distance}$ = 0.000–0.003). In contrast, the genetic distance between Pyrenean and Cantabrian samples is considerably larger (uncorrected mitochondrial $p_{distance}$ = 0.205–0.251) (Fig. 1; Table 2).

Taxonomic output

Our phylogenetic analyses reveal that the variation of the male pygidium and cerci used to describe diverse taxa from the Pyrenees (*Forficula sinuata* Germar, 1825; *Forficula dufourii* Serville, 1839; *Forficula sinuata* var. *macrolabia* Fieber, 1853; *Forficula sinuata* var. *cyclolabia* Fieber, 1853; *Chelidura sinuata* var. *opisthogona* Borelli, 1905; *Pseudochelidura minor* Steinmann, 1979; and *Pseudochelidura montuosa* Steinmann, 1981) corresponds to an intra-populational variability of a single evolutionary unit (Fig. 2). This taxon should retain the oldest available name, *P. sinuata* (Germar, 1825). All other names applied to Pyrenean *Pseudochelidura* are junior synonyms of *P. sinuata* (see catalogue below).

Pyrenean and Cantabrian samples are reciprocally monophyletic, and, as discussed below, patterns of cerci variability differ among them. In accordance, we hypothesize that the geographically isolated populations of Pyrenean and Cantabrian *Pseudochelidura* represent two independent species. The description of the Cantabrian species is presented below.

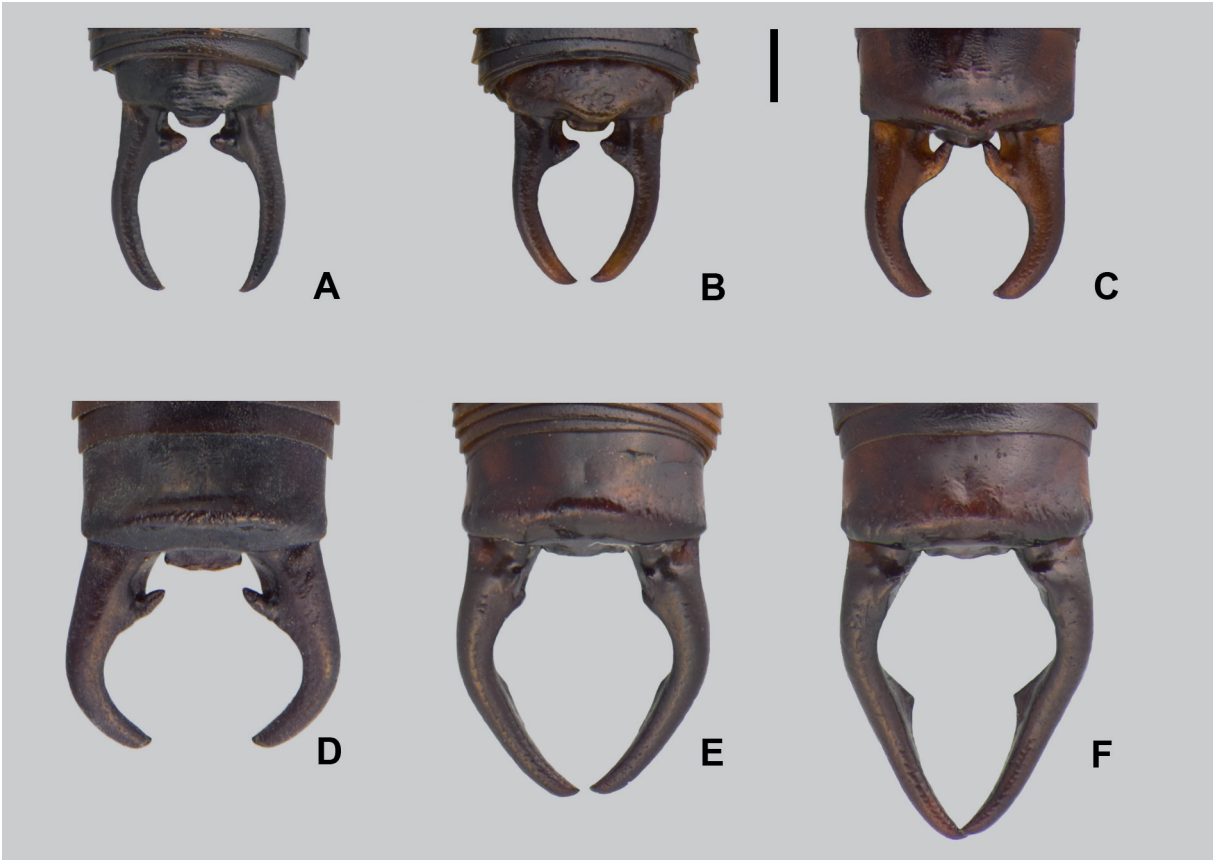

Fig. 3. Cerci variation in *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov., males. **A**. Puerto de Ventana (Asturias, Spain) (MNCN_Ent 167428). **B**. Puerto de La Farrapona (León, Spain) (MNCN_Ent 167426). **C**. Somiedo (Asturias, Spain) (MNCN_Ent 123721). **D**. León (Spain) (MNCN_Ent 167420). **E**. Puerto de La Farrapona (León, Spain) (MNCN_Ent 167419). **F**. Puerto de La Farrapona (León, Spain) (MNCN_Ent 167418). Scale bar = 1 mm.

Table 2. Uncorrected mitochondrial (p) pairwise genetic distance matrix between Cantabrian and Pyrenean specimens of *Pseudochelidura* Verhoeff, 1902 (phenotype IV–II–I | Puerto de Ventana – Puerto de Vegarada – Burgos (Puerto de Lunada and Puerto de las Estacas de Trueba)) used in the phylogenetic analyses.

		Pseudochelidura sinuata			***Pseudochelidura cantabrica*** sp. nov.		
		Phenotype IV	Phenotype II	Phenotype I	P. Ventana	P. Vegarada	Burgos
Pseudochelidura sinuata	Phenotype IV	0.000–0.034					
	Phenotype II	0.000–0.055	0.055	0.000–0.057			
	Phenotype I	0.000–0.034	0.000–0.057	0.000–0.003			
Pseudochelidura cantabrica sp. nov.	P. Ventana	0.216–0.221	0.205–0.218	0.216–0.221	0.000–0.002		
	P. Vegarada	0.229–0.234	0.218–0.231	0.229–0.234	0.026–0.034		
	Burgos	0.240–248	0.225–0.248	0.245–0.251	0.120–0.123	0.112–123	

Description of a new species of Pseudochelidura Verhoeff, 1902

Class Insecta Linnaeus, 1758
Order Dermaptera De Geer, 1773
Family Forficulidae Latreille, 1810
Genus *Pseudochelidura* Verhoeff, 1902

Pseudochelidura cantabrica Cuesta-Segura, Jurado-Angulo & García-París sp. nov.
urn:lsid:zoobank.org:act:62F051DC-0763-4A90-A97B-A5F4E79FFFDC
Figs 3–8

Diagnosis

Dry-mounted specimens light brown, although the head may remain somewhat orange. In living specimens, anterior part of body orange more or less intense (head, first antennomere, pronotum, tegmina and legs), sometimes with darkened areas (Figs 4–5). Antennae light brown, with 12 antennomeres; antennomere 1 almost equally long than 2–3 combined. All antennomeres pubescent; a dense, fine and white pubescence covers from the middle of the third antennomere, less frequently from the fourth, to the apical end. Postfrontal sutures do not reach the eyes generally. Pronotum smooth, 1.2 times as long as wide, parallel-sided or slightly wider posteriorly. Tegmina short, truncated obliquely. Wings reduced to a small scale that can be perceived beneath the tegmina. Abdomen reddish brown to blackish brown, darkened toward the posterior end, cerci blackish brown. Tegument surface punctate, shiny. Total body length without cerci: ♂♂: 7.00–10.06 mm (mean = 8.77 mm; n = 16); ♀♀: 8.25–10.62 mm (mean = 9.10; n = 18). Length of cerci: ♂♂: 2.13–4.00 mm (mean = 2.47; n = 16); ♀♀: 1.83–2.10 mm (mean = 1.95; n = 18) (Table 3).

Etymology

The name '*cantabrica*' is a feminine gender Latin adjective derived from '*cantabricus*' that means belonging to or related to the Cantabrian Sea or the land adjacent to that sea, reason for which the mountain range parallel to this sea is called Cantabrian Mountains, in Spanish 'Cordillera Cantábrica'.

Type material

Holotype

SPAIN • ♂; "España, Castilla y León: León: Torrestío, Puerto de La Farrapona, 43°02′51″ N, 6°05′18″ W, 1651 m, 17-IX-2017, A.D. Cuesta-Segura leg. // MNCN_Ent 167418 // Holotipo *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París, des. 2022" [red label, printed]; MNCN_Ent 167418 (Figs 6–7).

Paratypes

All carrying a red or white label printed (if preserved in ethanol) with "Paratipo *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & Gª-París, 2022", from the following localities:

(1) Dry mounted specimens

SPAIN – **Asturias** • 18 ♂♂, 12 ♀♀; Valle del Lago, Somiedo; 1565 m a.s.l.; 26–30 Jul. 1949; Exp. Inst. Esp. Entomología leg.; MNCN_Ent 123702, 123706 to 123716, 123718 to 123722, 123724, 123726 to 123737 • 1 ♂; same collection data as for preceding; 4–12 Aug. 1949; MNCN_Ent 123717 • 2 ♂♂, 2 ♀♀; same collection data as for preceding; 20–30 Jul. 1950; MNCN_Ent 123703, 123725, 123738, 123739 • 2 ♂♂, 2 ♀♀; same collection data as for preceding; 1–10 Aug. 1950; MNCN_Ent 123704, 123705, 123741, 123742 • 1 ♂; Puerto de Leitariegos; 1575 m a.s.l.; 1–10 Aug. 1950; Exp. Inst. Esp.

Fig. 4. Live specimens of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. and cerci variation. **A**. Male from Puerto de la Farrapona (León, Spain). **B**. Male from Puerto de Vegarada (León, Spain) (ADC-S col. Derm_0006). **C**. Male from Puerto de Ventana (León, Spain). **D**. Male from Puerto de Áliva (Cantabria, Spain) (ADC-S col. Derm_0008). Photographs ex situ by ADC-S (A–B, D) and MG-P (C).

Entomología leg.; MNCN_Ent 123723 • 2 ♀♀; same collection data as for preceding; 1675 m a.s.l.; 1–10 Aug. 1950; Exp. Inst. Esp. Entomología leg.; MNCN_Ent 123740, 123743 • 8 ♂♂, 9 ♀♀; Puerto de Ventana; 43°3′31.6″ N, 6°0′10.02″ W; 1603 m a.s.l.; 19 Aug. 2017; ADC-S leg.; MNCN_Ent 167422, 167424, 167428, 167429, 167438 to 167441, 167446, 167455, 167468, 167469, 167478, 167499 to 167501, 167503. – **Castilla y León**: **León** • 1 ♂; Puerto de Vegarada; 43°2′17.08″ N, 5°28′42.39″ W; 1560 m a.s.l.; 1–23 Aug. 2008; ADC-S leg.; in pitfall trap; MNCN_Ent 167420 • 2 ♂♂; same collection data as for preceding; 43°01′54.95″ N, 5°28′34.17″ W; 1684 m a.s.l.; 15 Jul. 2021; ADC-S leg.; ADC-S col. Derm_0005, 0006 • 1 ♂, 5 ♀♀; Puerto de Ventana; 43°03′13.5″ N, 6°0′31.6″ W; 1559 m a.s.l.; 19 Aug. 2017; ADC-S leg.; MNCN_Ent 167431, 167434, 167442, 167444, 167447, 167498 • 4 ♂♂, 8 ♀♀; same collection data as for preceding; 43°03′11.3″ N, 6°00′09.6″ W; 1543 m a.s.l.; 20 Aug. 2017; ADC-S leg.; MNCN_Ent 167421, 167430, 167432, 167433, 167435 to 167437, 167445, 167448, 167475, 167479, 167497 • 2 ♂♂, 1 ♀; same collection data as for preceding; 43°03′26.3″ N, 6°00′11.7″ W; 1590 m a.s.l.; 20 Aug. 2017; ADC-S leg.; MNCN_Ent 167443, 167476, 167477 • 19 ♂♂, 19 ♀♀; Torrestío, Puerto de La Farrapona; 43°2′51.99″ N, 6°5′18.10″ W; 1651 m a.s.l.; 17 Sep. 2017; ADC-S and M. Sánchez Gutiérrez leg.; MNCN_Ent 167419, 167423, 167425 to 167427, 167456 to 167467, 167470 to 167474, 167481 to 167483, 167485 to 167496, 167502 • 3 ♂♂, 2 ♀♀; same collection data as for preceding; ADC-S col. Derm_0001 to Derm_0004, Derm_0007.

Fig. 5. Live specimens of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. **A**. Female from Puerto de la Farrapona (León, Spain). **B**. Female from Puerto de Ventana (León, Spain). **C**. Early instar nymph from Puerto de Ventana (León, Spain). **D**. Eggs from Puerto de Vegarada (León, Spain). Photographs in situ by ADC-S (A, D) and ex situ by MG-P (B–C).

(2) Ethanol preserved specimens
SPAIN – **Castilla y León**: **León** • 5 ♂♂; Puerto de Vegarada; 43°01′54.95″ N, 5°28′34.17″ W; 1684 m a.s.l.; 22 Aug. 2017; ADC-S leg.; MNCN_Ent 331219 to 331223 • 1 ♂, 3 ♀♀, 3 nymphs; Puerto de Ventana; 43°03′27″ N, 6°00′15″ W; 1588 m a.s.l.; 15 Sep. 2011; M. García-París and P. Pavón leg.; MNCN_Ent 331179 to 331185 • 2 ♂♂, 2 ♀♀, 3 nymphs; same collection data as for preceding; 16 Sep. 2011; M. García-París and P. Pavón leg.; MNCN_Ent 331172 to 331178.

Description

Male (holotype, MNCN_Ent 167418)

General aspect and coloration. Male specimen, large, robust with the maximum width at posterior third of body (Figs 6–7). General coloration of live specimen reddish brown; head lighter, almost orange; pronotum, tegminae, legs and first abdominal segments, also lighter, dark-orange to honey-yellow; pronotum and tegminae somewhat transparent, not homogeneously colored because of the subjacent structures; eyes deep-black, antennae brownish, densely covered by short decumbent setae that provides gray hue to general appearance, specially to central and apical tergites; abdominal segments chestnut-brown with anterior portion of each segment lighter, dark-red; cerci chestnut-brown colored darkened toward basis (Fig. 7).

Measurements. Total body length without cerci of 9.38 mm. Cerci length 4.00 mm (Table 3).

Head. Transverse (1.97 mm maximum width; 1.48 mm length without clypeus), about 0.75 times as long as wide (Fig. 6). Postfrontal and coronal sutures fine but distinct, postfrontal sutures shorter than distance between them and eyes. Two deep transverse short incisions internal to eyes. Frons flat, slightly darkened. Posterior margin of the head feebly emarginated at middle. Eyes black, almost triangularly shaped, length approximately 0.5 times that of head behind eyes. Antennae with 12 antennomeres (right

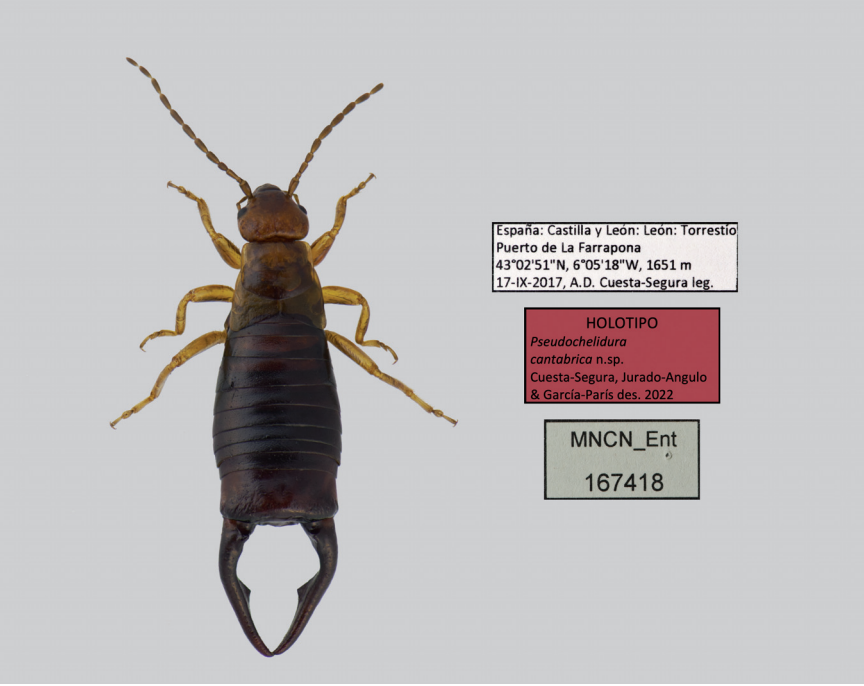

Fig. 6. *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov., holotype, ♂ (MNCN_Ent 167418), deposited in the collection of the Museo Nacional de Ciencias Naturales (MNCN, CSIC).

one missing two); antennomere I long (0.48 mm), narrowed basally, widened terminally, almost equal to antennomeres II–III combined (I/II+III = 0.97); antennomere II short (0.14 mm), but longer than wider; antennomere III (0.34 mm) longer than antennomere IV (0.26 mm), slightly widened terminally. Antennomeres II–III cylindrical, all others sub-conical. All antennomeres pubescent; dense, fine and white pubescence from middle of third antennomere to apical end. Maxillary palpi with articles I and II relatively long but shorter than third, sub-cylindrical and slightly widened distally. Article III sub-ellipsoidal, elongated, with very thin base.

Pronotum. Smooth, subquadrate (1.67 mm long, 2.04 wide; 1.22 times as wide as long), sides slightly widened posteriorly (Fig. 6). Anterior margin nearly straight, anterior angles with well-marked ridge that continues along lateral margin, sometimes less clearly marked. Posterior margin rounded. Median sulcus fine but distinct up to half of pronotum. Mesonotum and metanotum not visible. Sternal plates typical for genus. Tegmina short, truncated, with inner edge shorter than outer, clearly wider than pronotum and wider at end than at base. Wings reduced to small scale visible under tegmina.

Fig. 7. *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov., holotype, ♂ (MNCN_Ent 167418). **A**. Photographed alive at Puerto de la Farrapona (León, Spain) . **B**. Lateral view of the cerci. Photographs in situ by ADC-S.

Table 3. Measurements and indices of female and male (including the four different phenotypes of males, Ph. = phenotype) specimens of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. Phenotype IV corresponds to the holotype.

	♀♀	♂♂				
MEASUREMENTS	(n = 18)	Average (n = 16)	Ph. I (n = 6)	Ph. II (n = 7)	Ph. III (n = 2)	Ph. IV (n = 1)
Body length without cerci	9.10	8.64	8.38	8.68	9.97	9.38
Cerci length	1.95	2.36	2.37	2.24	2.81	4.00
Body length	10.95	10.72	10.53	10.61	12.31	12.94
Head length	1.39	1.42	1.38	1.42	1.48	1.48
Head width	1.92	1.82	1.79	1.87	1.95	1.97
Pronotum length	1.60	1.46	1.38	1.47	1.57	1.67
Pronotum width	1.97	1.82	1.74	1.83	1.90	2.04
INDICES						
Head (length/width)	0.73	0.77	0.77	0.76	0.76	0.75
Pronotum (length/width)	1.23	1.25	1.26	1.25	1.21	1.22
Eye length/head behind the eye	0.50	0.49	0.50	0.48	0.49	0.50
Metatarsomeres (1/2+3)	0.94	0.97	0.98	0.96	0.98	0.94
Antennomeres (1/2+3)	0.97	0.94	0.93	0.96	0.94	0.97

Legs. With femora and tibiae compressed. Profemora much more swollen meso- and metafemora, with more than 15 strong setae on inside of anterior side, a few setae on mesofemora and none on metafemora. Tibiae covered with thick and fine golden setae. Three tarsal segments, metatarsomere I long and subcylindrical, longer than pro- and mesotarsomeres, II spatulated, incorporating insertion of third, III elongated widened distally accommodating two strong curved claws, directed ventrally. Length of metatarsomere I (0.78 mm) almost equal to metatarsomeres II and III combined (0.76 mm; I/II+III = 0.94).

Abdomen. Stout, relatively long and depressed, slightly widened in posterior third; fine and densely punctate; tergites convex (Fig. 6). Lateral glandular folds feeble-marked almost as scars, well visible on tergites 3–4. Last tergite transverse; surface partially rugose and punctuated. Penultimate sternite with semicircular posterior margin, with slightly prominent apex. Last tergite with slightly concave sides; slightly broadened posteriorly. Posterior margin of last tergite rounded and very slightly elevated. Pygidium completely visible, very wide, rectangular. Cerci long, sinuous and curved, with two teeth very apparent. First one (dorsal tooth) at base of cerci, in dorsal position and of triangular shape, dorso-internally directed and with apex pointing forward; visible in dorsal and lateral views. Second one (internal tooth) is at approximately $^{3}/_{5}$ of the length of cerci, in ventro-internal position, laminar and triangle-shaped with broad base, visible in dorsal and ventral views.

Genitalia. Robust (described from large number of paratypes, Fig. 8A). Metaparameres fully developed, short, robust, straight and slightly narrowed at apex and with obtuse or rounded tips slightly directed inwards. Virga almost straight, slightly sinuous and short, shorter than metaparameres. Basal vesicle relatively small, kidney-shaped, strongly curved, with small sclerotized plate lacking supplementary sac associated to basal vesicle (present in smaller specimens) (Fig. 8A).

Fig. 8. Male genitalia of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. **A**. Phenotype III–IV from Puerto de Áliva (Cantabria, Spain) (ADC-S col. Derm_0008). **B**. Phenotype II from Puerto de Vegarada (León, Spain) (ADC-S col. Derm_0005). Photographs by ADC-S.

Variability in males

Male cerci and last tergite extremely variable, but most specimens can be classified in four different phenotypes (I, II, III, and IV) (Figs 3–4, 7). In addition to these phenotypes, there are also specimens with intermediate characteristics (I–II, II–III, and III–IV) (Figs 3–4).

Phenotype IV: as described in the holotype.

Phenotype III: last tergite with slightly concave sides; slightly broadened posteriorly; posterior margin with central protuberance projected upwards and rough at its edge; with the posterior side slightly inclined forward and visible in dorsal view, leaving the pygidium completely visible. Pygidium very wide, rectangular. Cerci symmetrical, broad at the base and separated from each other, medium size (2.81 mm) and curved, with a digitiform tooth at the inner edge located approximately ⅓ of its length, which is initially directed inwards and then upwards. In lateral view, these teeth do not protrude or protrude very slightly from the upper part of the cerci, which are slightly convex. The cerci in their final ⅔ are narrower, being of almost round section, except for a flat area located interno-ventrally clearly visible in ventral view.

Phenotype II: last tergite with parallel sides, with a median longitudinal furrow not very marked but visible; posterior margin with a triangular central protuberance projected backwards that partially or totally covers the pygidium. Pygidium narrow. Cerci similar to phenotype III, except for their smaller size (2.24 mm) and by the more robust digitiform tooth. In lateral view, these teeth protrude slightly but clearly from the upper part of the cerci.

Phenotype I: last tergite with parallel sides, with a median longitudinal furrow not very marked but visible; posterior margin with a central protuberance emarginated, paralleled to the body axis; this protuberance covers partially or totally the pygidium. Pygidium narrow. Cerci symmetrical, long (2.37 mm), broad at the base but clearly separated from each other, short and slightly curved, thinner and longer than in phenotype II; with a robust triangular tooth at the inner edge located near to the base and tilted up about 45 degrees. In lateral view, cerci are practically straight; the inner teeth do not protrude or protrude very slightly in lateral view. The cerci in their apical ⅔ are tapering, with almost round section, except for a flat section area located interno-ventrally visible in ventral view.

Males of *P. cantabrica* sp. nov. have fully developed metaparameres, slightly narrowed at the apex and with obtuse or rounded tips (Fig. 8). However, just as there is variability in the morphology of male cerci, there is also intraspecific variability in male genitalia, including the size of the parameres and the basal vesicle shape. Small specimens present a supplementary sac associated to the basal vesicle, which is absent in large specimens (phenotype III–IV). The latter (phenotype III–IV) present a small sclerotized plate on the basal vesicle.

Female

Similar to male in most characters except last tergite with slightly concave sides, clearly narrowed posteriorly; with a median longitudinal furrow. Two very small protuberances on the posterior margin, just above the insertion of the cerci. Female cerci have simple and straight contiguous branches, short, wide at the base and slightly curved inwards just at the apex (Fig. 5A–B).

Eggs

Eggs ivory yellow (Fig. 5D). Some may be somewhat deformed, presenting small flat areas by contact with other eggs. The egg masses remain grouped. Eleven eggs laid in captivity by one female from Puerto de La Farrapona were measured (average, minimum-maximum measures): length (mean = 1.15 mm, range = 1.13–1.17 mm, n = 11), width (mean = 0.94 mm, range = 0.92–0.95 mm, n = 11) and a length/width ratio (mean = 1.22 mm, range = 1.18–1.27 mm, n = 11).

Table 4. Characterization of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. nymphal stages. Nymphs measured were obtained from Puerto de Vegarada, Puerto de La Farrapona, Puerto de Lunada and Puerto de las Estacas de Trueba. Average and minimum-maximum values are shown.

Characters	Instar					Adult
	1	2	3	4	5	
N	22	21	5	12	29	34
Head width (mm)	0.83 (0.77–0.87)	0.94 (0.90–0.98)	1.12 (1.08–1.15)	1.24 (1.17–1.29)	1.49 (1.33–1.61)	1.89 (1.74–1.99)
Body length without cerci (mm)	3.88 (3.54–4.30)	4.51 (4.06–5.60)	5.41 (4.94–6.25)	6.60 (5.90–8.70)	8.49 (6.06–10.0)	8.94 (7.0–10.63)
Forceps length (mm)	0.88 (0.79–0.97)	1.05 (0.88–1.11)	1.17 (1.08–1.23)	1.44 (1.34–1.61)	1.66 (1.44–1.90)	2.20 (1.83–4.0)
Number of antennomeres	8	10	10	10	11	12

Nymphs

A female from Puerto de Vegarada with 34 1st instar nymphs was held for study. As the nymphal stages aged, the number of antennomeres, the width of the head and the length of the body and cerci increase (Table 4). Width of head seems reliable to determine nymphal stage, since ranges across stages do not overlap. The rest of the characteristics are common for the different nymphal stages (Fig. 5C). 1st and 2nd instar: head and dorsum of body dark. Legs almost transparent except for femora with central ring and base of tibiae slightly darkened. Dark antennomeres, pale at both ends. Postfrontal sutures reaching eyes and coronal suture extending to first abdominal segment, this included. Cerci with very fine granulation on inner edge, only visible under stereo microscope. From 3rd instar on: body completely dark, except light legs. Darkened ring of femora generally wider, occupying almost basal half. Anterior half of tibiae darkened. Cerci with marked granulation on interior edge.

Comparisons

Pseudochelidura cantabrica sp. nov. differs morphologically from all other species of the genus (*P. sinuata*, *P. galvagnii* and *P. orsinii*) and also genetically from the more similar species, *P. sinuata*.

Male cerci are extremely variable in *P. cantabrica* sp. nov. and *P. sinuata* (Figs 2–4, 9), with marked differences in the shape of the cerci of the larger males: phenotypes III–IV (Figs 2E, 3E) and IV (Figs 2F, 3F), but not so clear across other phenotypes (Cuesta-Segura 2012). In the phenotype III–IV, the internal tooth located at ⅓ of the cerci is almost non-existent in *P. cantabrica*, while it is very distinct, flat, with a curved anterior edge and a straight posterior edge in *P. sinuata*. In addition, *P. cantabrica* has slightly marked internal teeth, located at ½ of the cerci, which do not exist in *P. sinuata*. Males of *P. sinuata* phenotype IV have longer cerci and a more marked dorsal tooth at its base than in *P. cantabrica*. The internal teeth in *P. sinuata* are at ¼ of the cerci, triangle-shaped with a narrow base, pointing posteriorly, and are visible in dorsal, ventral and lateral views. However, the internal teeth of *P. cantabrica* are at approximately ³/₅ of the cerci, triangle-shaped with a very wide base, pointing inwards and visible only in dorsal and ventral views. Differences in cerci between males of phenotypes I, II and III are subtle, involving teeth shape and direction (see Figs 2–3). Females are so far indistinguishable.

Steinmann (1979, 1981) provided an illustration of the male genitalia of three phenotypes (II, III and IV) of *P. sinuata* (sub *P. sinuata*, *P. montuosa* and *P. minor*) from the Pyrenees. The genitalia of male specimens from the Pyrenees (MNCN_Ent 123583, 123639, 123640) match the description presented by Steinmann (1979, 1981) and Albouy & Caussanel (1990). Male genitalia of *P. sinuata* and *P. cantabrica* sp. nov. do not differ significantly. Both species have metaparameres fully developed, slightly narrowed at the apex and with obtuse or rounded tips. The virga is relatively short and thick and is located within the genital lobe, with a basal vesicle of the "forficuloid" type (Steinmann 1979). Our study supports

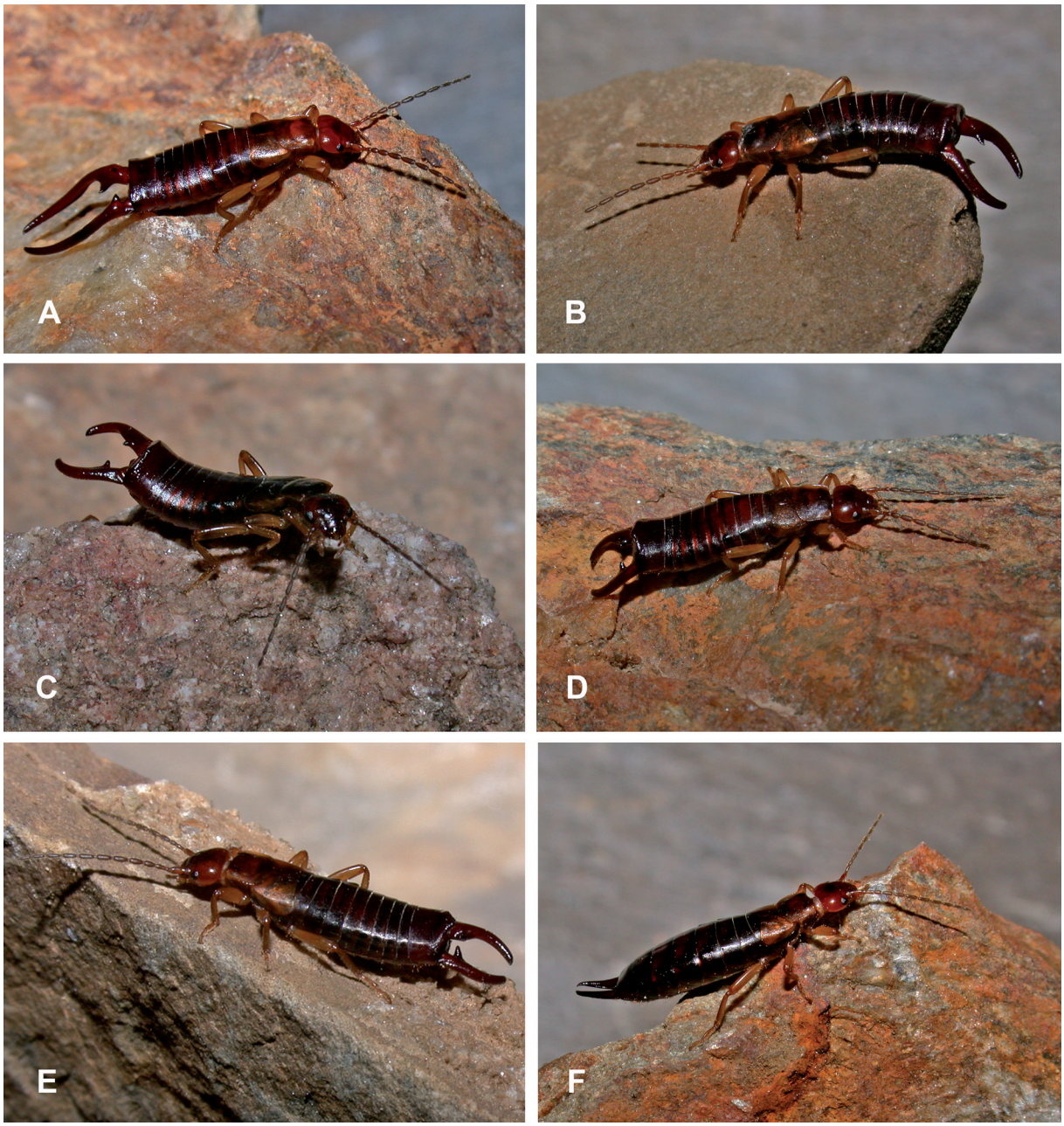

Fig. 9. Live specimens of *Pseudochelidura sinuata* (Germar, 1825) and cerci variation. **A**. Male from Ransol (Andorra). **B**. Male from Coll de Pailhères (Ariège, France). **C**. Male from Valle de Pineta (Huesca, Spain). **D**. Male from Ransol (Andorra). **E**. Male from Ransol (Andorra). **F**. Female from Ransol (Andorra). Photographs ex situ by MG-P.

Steinmann's (1979, 1981) descriptions of phenotypes II (sub *P. minor*) and III (sub *P. montuosa*) differing from phenotype IV by showing a supplementary sac associated to the basal vesicle. Small specimens of *P. cantabrica* also present a supplementary sac associated to the basal vesicle. In addition, phenotype IV of *P. sinuata* and *P. cantabrica* presents a small sclerotized plate on the basal vesicle.

Male cerci of *P. galvagnii* and *P. orsinii* show limited morphological diversity when compared with those of *P. cantabrica* sp. nov. and *P. sinuata*. Vigna-Taglianti (1999: figs 7–9) reported two main phenotypes in *P. galvagnii*. A first one with large curved cerci, very similar to those of *P. cantabrica* (Fig. 3F) with a dorsal tooth near the base and a long laminar ventrolateral internal projection and a second one with long, thinner cerci, slightly curved, almost straight, with a reduced dorsal tooth and a poorly developed ventrolateral internal projection. This second phenotype (Vigna-Taglianti 1999: fig. 9) does not show correspondence in *P. cantabrica*, where all males present markedly curved cerci. Large curved cerci of the first phenotype in *P. galvagnii* (Vigna-Taglianti 1999: figs 7–8) present a series of internal denticles at the dorsal projection level, that are totally absent in *P. cantabrica*. Male virga of *P. galvagnii* is markedly arcuate distally (Vigna-Taglianti 1999: fig. 11). Male cerci of *P. orsinii* are very different from those of *P. cantabrica*. Male cerci of *P. orsinii* present the lateral inner projection strongly directed inwards resulting in a double concavity that make cerci appearing '3' shaped, even those of specimens with smaller cerci (Vigna-Taglianti 1999: figs 2–4). As in the case of *P. galvagnii*, the phenotype of *P. orsinii* with smaller cerci is not similar to those in *P. cantabrica*, where all males present markedly curved cerci, and not almost straight. Male virga of *P. orsinii* is slighltly arquate distally (Maccagno 1933: fig. 11; Vigna-Taglianti 1999: fig. 6) while it is relatively short and thick in *P. cantabrica*.

Differences between *P. galvagnii* and *P. orsinii* are basically at the same level as those reported here between *P. sinuata* and *P. cantabrica* sp. nov., but intraspecific diversity is much limited in *P. galvagnii* and *P. orsinii* (Vigna-Taglianti 1999).

Geographic range

Pseudochelidura cantabrica sp. nov. occurs along to the Cantabrian Mountains (Fig. 10). At the moment, the species has been located in the Spanish provinces of Asturias, Burgos, Cantabria, and León, at altitudes between 1128 and 2184 m.

In addition to the localities included in the type series and in the material and methods section (see above), *P. cantabrica* sp. nov. has previously been reported from diverse localities under different names (see also comments at the end of the synonymy list). According to the illustrations provided by Harz & Kaltenbach (1976), the records of *P. sinuata* from Peña Vieja and Asturias (Picos de Europa, Spain) correspond to *P. cantabrica*. Most of the specimens in the MNCN Collection mentioned by Lapeira & Pascual (1980) sub *P. sinuata* from the Cantabrian Mountains: Peña Vieja (Picos de Europa, Spain), Valle del Lago and Leitariegos (Asturias, Spain), are considered paratypes of *P. cantabrica* in the present work, except the specimens from "Sorbea [Gorbea], Bilbao" and "Torrebarrio, León" which correspond to female specimens of *Forficula* (possibly *F. lesnei* Finot, 1887). We have not found the two specimens mentioned by Lapeira & Pascual (1980) sub *P. sinuata* with the labels "Ladera del Coriscao, Santander, 21-VII-54 (Peris)" and "W. from Lagoa Comprida, Serra Estrella, Portugal, 28-VIII-42 (Machado)". Bivar de Sousa (1997) commented that the specimen from Lagoa Comprida corresponded to a nymph of *Mesochelidura bolivari*, and that consequently there were no confirmed records of *Pseudochelidura* in Portugal. On the contrary, because of the proximity of Ladera del Coriscao to known localities of *Pseudochelidura*, we consider that this specimen likely corresponds to *P. cantabrica*. According to the description provided by Neira Artidiello (2009), the male of *P. sinuata* captured in the Macizo de las Ubiñas (Asturias, Spain) corresponds to *P. cantabrica*. The specimens from Torrestío and Redipuertas (León, Spain) cited as *P. minor* by Cuesta-Segura (2012) and studied in the present work, also correspond to *P. cantabrica*.

Finally, the male from Fuente Dé (Cantabria, Spain) cited as *P. sinuata* by Pérez-Valcárcel *et al*. (2022) also corresponds to *P. cantabrica*.

Notes on natural history

Pseudochelidura cantabrica sp. nov. is usually found in mountain meadows and pastures (Fig. 11). These mountain pastures are usually grazed by transhumant cattle during the summer, usually cows, sheep and horses. In a biodiversity study using pitfall traps at the mountain pass of Vegarada in the summers of 2004 and 2008, specimens of *P. cantabrica* were found only in the pastures, but not under the bushes (mixed *Calluna* Salisb. and *Vaccinium* L.) (Cuesta-Segura 2012, 2016 sub *P. minor*).

Pseudochelidura cantabrica sp. nov. is an uncommon species occasionally found under rocks or dry cow dung and can locally be abundant but populations are not continuous, patchily distributed and difficult to locate. A study surveying 15 mountain passes along the Western Cantabrian range, by using pitfall traps, only detected the presence of the species at a single locality (Cuesta-Segura 2012 sub *P. minor*). Populations of *P. cantabrica* coexist with the ubiquitous *Forficula dentata* Fabricius, 1775. Abundance percentages of one or the other species vary across zones, *P. cantabrica* being less abundant in most cases (Table 5). Both species, but especially *P. cantabrica*, were more abundant in locations facing north (Table 5, zones 2 and 8).

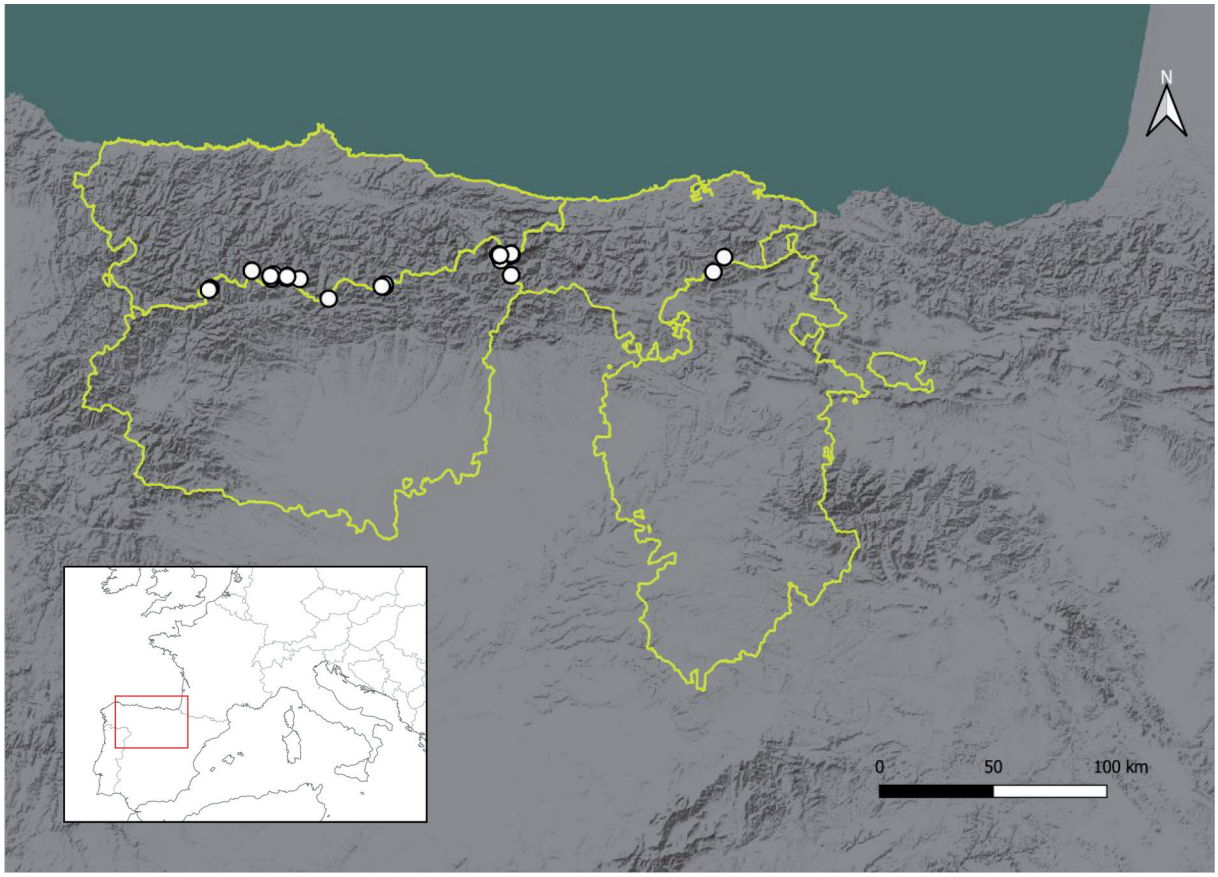

Fig. 10. Map of central northern Spain depicting the geographic distribution range of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. The inset map of part of western Europe indicates the area included in the larger map. Yellow lines identify regional or provincial limits that include records of the species. White dots correspond to the species records (see text sections of type series, material examined and previous records of *P. cantabrica* for precise localities).

During the summer of 2017, females were more frequent than males (Table 5). Males with a diverse cerci morphology (phenotypes I, II, III and IV) and females (one of which with nymphs) were observed together in the Vegarada mountain pass under a single cow pat. In general, phenotypes I and II were the most abundant, III and IV being scarce. As an example, at Puerto de La Farrapona, 17 Sep. 2017, we observed (only a few specimens collected), 95 nymphs, 46 females and 33 males; 23 males (70%) corresponding phenotype I, four (12%) to phenotype II, one (3%) to phenotype III, one (3%) to phenotype IV (the holotype), and four (12%) to intermediate phenotypes (I–II, II–III, and III–IV). One of the females kept alive from Puerto de La Farrapona laid 27 eggs and while initially she took care of them, about two weeks later she ate them. The same female laid 17 eggs three weeks later, and ate them too.

Synonymy list and nomenclatural combinations of Iberian Pseudochelidura Verhoeff, 1902

Pseudochelidura cantabrica Cuesta-Segura, Jurado-Angulo & García-París sp. nov.

Pseudochelidura cantabrica Cuesta-Segura, Jurado-Angulo & García-París sp. nov. Terra typica: "España: Castilla y León: León: Torrestío, Puerto de La Farrapona, 43°02′51″ N, 6°05′18″ W, 1651 m".

Fig. 11. Typical landscape in the Cantabrian Mountains where *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. is located. **A**. Puerto de Ventana (zone 1 in Table 5). **B**. Puerto de Ventana (zone 3 in Table 5). **C**. Puerto de Vegarada (zone 5 in Table 5). **D**. Puerto de La Farrapona (type locality; zone 8 in Table 5). Photographs by ADC-S.

Table 5. Relative abundances of *Pseudochelidura cantabrica* Cuesta-Segura, Jurado-Angulo & García-París sp. nov. and *Forficula dentata* Fabricius, 1775, adults and nymphs, in different sampling areas of the Cantabrian Mountains in Summer 2017. Asturias (AS), Burgos (BU) and León (LE).

Puerto de	**Ventana**			**Vegarada**		**Lunada**	**Las Estacas de Trueba**	**La Farrapona**
Sampling areas	Zone 1 (LE)	Zone 2 (AS)	Zone 3 (LE)	Zone 4 (LE)	Zone 5 (LE)	Zona 6 (BU)	Zona 7 (BU)	Zona 8 (LE)
Dates	19 Aug. 2017	19 Aug. 2017	20 Aug. 2017	22 Aug. 2017	24 Aug. 2017	13 Sep. 2017	13 Sep. 2017	17 Sep. 2017
Points with Dermaptera	39	90	62	11	13	43	8	87
Stone	15.4%	76.7%	90.3%	45.5%	92.3%	95.3%	100%	100%
Dry cow dung	84.6%	23.3%	9.7%	54.5%	7.7%	4.7%	0%	0%
Forficula dentata	74.4%	78.9%	79%	54.5%	61.5%	83.7%	25%	16.1%
Pseudochelidura cantabrica sp. nov.	12.8%	5.5%	11.3%	9.1%	7.7%	9.3%	50%	63.2%
Both species together	12.8%	15.6%	9.7%	36.4%	30.8%	7%	25%	20.7%
Total n. of Dermaptera (Adults/Nymphs)	96 / 11	454 / 13	201 / 23	47 / 41	37 / 2	121 / 12	6 /5	124 / 95
Forficula dentata (A / N)	95.8% / 18.2%	95.4% / 30.8%	95.5% / 47.8%	63.8% / 12.2%	86.5% / 0%	97.5% / 50%	83.3% / 0%	36.3% / 0%
Pseudochelidura cantabrica sp. nov. (A / N)	4.2% / 81.8%	4.6% / 69.2%	4.5% / 52.2%	36.2% / 87.8%	13.5% / 100%	2.5% / 50%	16.7% / 100%	63.7% / 100%

Pseudochelidura sinuata (Germar, 1825)

Forficula sinuata Germar, 1825: 16. Terra typica: "Habitat in Pyrenaeis".
Forficula dufourii Serville, 1839: 49, pl. 1 (non *F. dufouri* Desmarest, 1820). Terra typica: "France meridionale. Feu".
? *Forficula pyrenaea* Herrich-Schäffer, 1840: 31. Terra typica not indicated. A synonym of either *Chelidura pyrenaica* (Mégerlé, 1825) or *P. sinuata* (Germar, 1825) (Herrich-Schäffer 1840).
Forficula sinuata var. *macrolabia* Fieber, 1853: 256. Terra typica: not specified.
Forficula sinuata var. *cyclolabia* Fieber, 1853: 256. Terra typica: not specified.
Chelidura sinuata var. *opisthogona* Borelli, 1905: 50. Terra typica: "... Port-de-Gavarnie, ... massif de l'Astajou, ... environs de Gavarnie". Harz & Kaltenbach (1976: 97) and Herrera Mesa (1999: 59) wrote the name as "*Chelidura sinuata* var. *opithogona*".
Pseudochelidura minor Steinmann, 1979: 167 **syn. nov.** Terra typica: "Pic du Midi, Pyrennes".
Pseudochelidura montuosa Steinmann, 1981: 189 **syn. nov.** Terra typica: "Andorra".

Chelidura sinuata – Fischer von Waldheim 1846: 48.
Chelidura dufouri – Dohrn 1867: 342 (unavailable name).
Pseudochelidura sinuata – Verhoeff 1902: 196.
Pseudochelidura dufouri – Albouy 1984: 177 (unavailable name).

Two additional names have been included or mentioned as possible synonyms of *Pseudochelidura sinuata*: *Chelidura vittigera* Fischer von Waldheim, 1846 and *Forficula paupercula* Gené, 1832. The type locality of *C. vittigera* "dans le Caucase" and its original description, based on a single female specimen, make us exclude the name from the synonymy of *P. sinuata*. The correct allocation of *C. vittigera* requires the examination of new specimens from the Caucasus, but according to the location it should likely be placed in the genus *Chelidura* as originally proposed by Fischer von Waldheim (1846).

Fontana (1999) discussed the problematic situation of *F. paupercula*. The name was applied to a single male specimen from the "Alpi della Savoia" (Gené 1832) apparently lost (Fontana 1999). Harz & Kaltenbach (1976) treated *F. paupercula* as an independent species within *Pseudochelidura*, but according to Fontana (1999) the specimens examined by Harz & Kaltenbach (1976) were not part of the type series of Gené's *F. paupercula*, representing a phenotype of *Pseudochelidura* similar to *P. minor*, but not matching the original description of *F. paupercula*. Gené's (1832) description of *F. paupercula* does not support its inclusion in the synonymy of any species of *Pseudochelidura*, including *P. sinuata*, as already mentioned by different authors that assimilated the name to *Chelidura aptera* (including de Bormans & Krauss 1900; Sakai 1995), however a detailed prospection of the Savoyan Alps is needed to confirm the presence of populations of *Pseudochelidura* in the region (considered possible by Harz & Kaltenbach 1976 and Albouy & Caussanel 1990). The results of these prospections would allow for a proper discussion of Gené's *F. paupercula*.

Discussion

Defining evolutionary units using discrete traits is often a challenge because of problems overestimating phenotypic variability (Pomorski 1990; Jurado-Angulo *et al.* 2021; Sottile e*t al.* 2022) or, on the contrary, underestimating it (Posso-Terranova & Andrés 2018; Sánchez-Vialas *et al.* 2020). Pyrenean populations of *Pseudochelidura* have been treated as three different taxonomic units, *P. sinuata*, *P. minor* and *P. montuosa*, based on the shape of male cerci and pygidium (Steinmann 1979, 1981; Albouy & Caussanel 1990; Caussanel *et al.* 1990; Herrera Mesa 1999; Cuesta-Segura 2012), a set of characters widely used for taxonomic inference in Dermaptera (Albouy & Caussanel 1990; Kočárek 2004; Anlaş & Kočárek 2012; Kirstová *et al.* 2020; Fontana *et al.* 2021b).

Our concordant nuclear and mtDNA molecular data unequivocally demonstrate that the general variability observed in pygidium and cerci shape within Pyrenean *Pseudochelidura* is larger than the variability observed across isolated geographic areas (Pyrenees and Cantabrian Mountains), thus rendering impossible the use of pygidium and cerci shape as diagnostic taxonomic characters in *Pseudochelidura* when local variability occurs. Coexisting phenotypes in the Pyrenees representing three supposedly independent taxonomic units, *P. sinuata*, *P. montuosa* and *P. minor*, are only extreme variations of a highly variable unique evolutionary entity (Fig. 2). It appears that patters of variation possibly affected by sexual selection (i.e., intrapopulational variability in male cerci) seem to be very difficult to separate from variation driven by natural selection or genetic drift in Forficulidae (i.e., character divergence in geographical isolation). Separating these sources of variation require the use of appropriate phylogeographic or phylogenetic analyses, rendering taxonomic decisions very difficult without them.

Intraspecific variability of male cerci in earwigs is well known (Dohrn 1867; Diajonov 1925; Ollason 1970; Srivastava 1970; Mourier 1986; Simpson & Mayer 1990; Fontana *et al.* 2021b; García-París *et al.* 2021; Jurado-Angulo *et al.* 2021); however, the levels of variability found in males of *Pseudochelidura* (Figs 2–3) are probably among the highest. It is thus somewhat counterintuitive that morphological differences in cerci shape between Pyrenean and Cantabrian populations (Figs 2–3) are relatively small and more limited than intrapopulational variability, but this is a situation relatively similar to that described for the French Massif Central and Pyrenean populations of *Chelidura* (Jurado-Angulo *et al.* 2021).

Saturation of the morphospace (e.g., intraspecific variability reaching all possible morphological diversification) might impose an evolutionary restriction to further morphological change (Oyston *et al.* 2015). Therefore, it is possible that complex hypervariable morphological structures as male cerci in *Pseudochelidura* might have occuppied the overall morphospace available for their lineage, with an internal intraspecific variability almost as large as that shown by the entire Anechurinae, thus leaving little room for character change across species. This hypothesis might be supported by the close similarity in male cerci variability displayed by the Iberian endemic genus *Eulithinus*, a set of species apparently not closely related to *Pseudochelidura* (Steinmann 1993), but so similar to them that Steinmann (1979, 1981) included specimens of *Eulithinus* as paratypes of his *Pseudochelidura minor*. In depth analyses of cerci morphospace, including representatives of *Eulithinus*, *Anechura* Scudder, 1876 and related genera, are necessary to test this hypothesis.

The large sequence divergence observed between Pyrenean and Cantabrian specimens of *Pseudochelidura* suggests a lasting genetic and geographic isolation between these populations (Fig. 1; Table 2). At the same time, phylogenetic and morphological analyses suggest that Cantabrian and Pyrenean populations have their own independent historical and future evolutionary trajectory (Wiley 1978). The misinterpretation of intraspecific morphological variability had consequences in determining the geographical distribution area of each species. According to our results, the presence of *P. sinuata* in the Cantabrian Mountains can be rejected, so all records of *P. sinuata* and *P. minor* from this region correspond to *P. cantabrica* sp. nov. This last point has conservation implications, because changing the distribution range of a species would also change its conservation status, specially with the added challenge of climate change in the mountain ranges. The conservation status of *P. cantabrica* and *P. sinuata* needs to be evaluated in light of the current taxonomic changes.

The fauna of southern Europe, especially of the Iberian Peninsula, has a high level of endemism possibly related to the existence of faunal refuges during the Pleistocene glaciations (Hewitt 1999; Macher *et al.* 2015; Martínez-Freiría *et al.* 2015; Schröder *et al.* 2021). Rising temperatures during interglacial times led many species to take refuge in nearby mountains where suitable habitat was available, and they became

isolated in these "cold" refugia (Recuero & García-París 2011; Dufresne *et al.* 2020). The differentiation of Cantabrian and Pyrenean populations of *Pseudochelidura* possibly matches the suggested Pleistocene scenario, although their genetic divergence suggests a much older scenario of isolation. In fact, a close relationship between Cantabrian and Pyrenean taxa is not straightforward for many other lineages. The rock lizards of the genus *Iberolacerta* Arribas, 1999 present an endemic Pyrenean clade formed by 3 taxa, sister to another clade that includes species distributed across the Cantabrian Mountains, Galicia and Portugal, but also Hungarian and Central Iberian species (Crochet *et al*. 2004; Arribas *et al.* 2006; Rojo *et al.* 2013). A similar situation occurred between *Rana parvipalmata* (López Seoane, 1885) and *R. temporaria* Linnaeus, 1758, the former endemic to the Galician and Cantabrian Mountains, the latter extended from the Pyrenees to a large area of the Palaearctic Region (Dufresnes *et al.* 2020). It is thus possible that the closest affinities of *P. sinuata* would not be with *P. cantabrica* sp. nov. but with species not included in our analyses as *P. galvagnii* and *P. orsinii*. A robust phylogenetic hypothesis including all species of *Pseudochelidura* and related genera is necessary to discuss the evolutionary history of the clade.

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