

The Pyrenean species of *Chelidura* (Dermaptera, Forficulidae)

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Abstract

The Pyrenees are inhabited by scattered populations of earwigs of the genus *Chelidura* Latreille, 1825. There is some controversy about the specific assignment of these populations: while most authors assign them to *C. pyrenaica* (Gené, 1832), others consider that *C. aptera* (Mégerlé, 1825) is also present in the Pyrenees. The main objective of this work was to revise the identity and synonyms of Pyrenean *Chelidura*. Specimens from recent fieldwork and collections (MNCN-CSIC) were used for morphological and molecular studies (cytochrome oxidase 1). All Pyrenean specimens shared similar *cox1* sequences, very divergent from those of Alpine *C. aptera*. As a consequence, the variability observed in male cerci morphology from the Pyrenees, ranging from long and slightly curved to short and very curved, corresponded to *C. pyrenaica*, and the presence of *C. aptera* in the Pyrenees can be rejected. As previously suggested by Maccagno (1933) and Fontana et al. (2021), the revision of the synonymic list uncovered the misplacement of the name *F. simplex* Germar, 1825 under the synonymy of *C. aptera*, while it rather represents a synonym of *C. pyrenaica* (**syn. nov.**). *Forficula simplex* has nomenclatural priority over *C. pyrenaica*, however both names meet the requirements of the article 23.9.1 of the International Code of Zoological Nomenclature to retain the prevailing usage of *C. pyrenaica* (**nomen protectum**) over *F. simplex* (**nomen oblitum**). Additionally, we discuss the taxonomic status of *Chelidura arverna* David & Van Hereweghe, 1973 **stat. nov.** from the French Massif Central.

Key Words

Chelidura aptera, *Chelidura arverna*, *Chelidura pyrenaica*, Cytochrome oxidase 1, earwigs, geographic distribution, intraspecific variation, morphology, taxonomy

Introduction

One of the most characteristic genera of Dermaptera in the high elevations of the European Mountains is *Chelidura* Latreille, 1825, represented by robust large-sized species often found in the upper limit of the coniferous forests. After the recent revision by Kirstová et al. (2020) who reconsidered the status of *Mesochelidura* Verhoeff, 1902 and *Chelidurella* Verhoeff, 1902, previously synonymized with *Chelidura* by Steinmann (1993), the genus *Chelidura* includes 13 species confined to mountains of the Palaearctic region (Kočárek 2004; Kirstová et al. 2020). However, the genus is still in need of a rigorous

taxonomic revision to determine the status of the Asian species (Kirstová et al. 2020).

The species of *Chelidura* are characterized by absence of wings, a broad and large body with rudimentary tegmina, abdomen strongly dilated towards the posterior end, and flat, rounded and not protruding pygidium (Albouy and Caussanel 1990; Kočárek 2004; Kirstová et al. 2020; Fontana et al. 2021). The Pyrenean Mountain Chain is inhabited by scattered populations of *Chelidura*, distributed over the Spanish, Andorran and French sides of the chain (Lapeira and Pascual 1980; Albouy and Caussanel 1990; Herrera-Mesa 1999; Fontana et al. 2021). The specific ascription of these Pyrenean populations is subject

to discussion. Some authors only mentioned the presence of *C. pyrenaica* (Gené, 1832) in the Pyrenees (Marquet 1877; Finot 1890; de Bormans and Krauss 1900; Houbert 1900; Xambeu 1903; Kirby 1904; Burr 1904; Xambeu 1907; Hamon 1956; Popham 1968; Vancassel and Foraste 1980; Dauphin 1987; Fontana 1999; Dusoulier 2004; Fontana et al. 2021), while some others considered that *C. pyrenaica* and also *C. aptera* (Megerle, 1825), are both present in the Pyrenees (Serville 1839; Fieber 1853; Bolívar 1878; Cazurro Ruiz 1888; Chopard 1922; Chopard 1951; Boeseman 1954; Amiet 1961; Sakai 1973; Harz and Kaltenbach 1976; Lapeira and Pascual 1980; Caussanel and Albouy 1987; Albouy and Caussanel 1990; Herrera-Mesa 1999).

Chelidura pyrenaica and *C. aptera* are two European species with ecological similarities. Both species are found in mountains at relatively high elevations, between 1000 and 2500 m of altitude (Albouy and Caussanel 1990). Most reports and descriptions indicate that *C. aptera* and *C. pyrenaica* are easily differentiated morphologically by the shape of male cerci (see Finot 1890; Azam 1901; Chopard 1922; Albouy and Caussanel 1990). According to those authors, males of *C. aptera* have long, relatively thin and slightly curved cerci, while males of *C. pyrenaica* have short, broad and very curved cerci. In both species, cerci of females are short, thin and practically straight, with a slight curvature at the apex. However, Dohrn (1867), followed by Brunner von Wattenwyl (1882), Maccagno (1933) and Fontana et al (2021) considered that long, thin and slightly curved cerci together with short, broad and very curved cerci were part of the intraspecific variability of each taxon, and questioned the presence of *C. aptera* in the Pyrenees (or the presence of *C. pyrenaica* in the Alps). To complicate matters, as already noted by Maccagno (1933), the earliest descriptions of Pyrenean specimens of *Chelidura* as a differentiated taxon correspond to *Forficula simplex* Germar, 1825, which was described based on long cerci Pyrenean specimens (Germar 1825). *Forficula simplex* was subsequently included in the synonymy of *C. aptera* by Dohrn (1867), followed by Bolívar (1876), Brunner von Wattenwyl (1882), Finot (1890), Kirby (1904), Burr (1904), Sakai (1973), Harz and Kaltenbach (1976), and Herrera-Mesa (1999) among others, or treated as a variety of *C. aptera* (Dubrony 1878).

The known distribution range of *Chelidura* in the Pyrenees is quite limited, with very few records in Andorra and the Spanish (Lapeira and Pascual 1980) and French slopes (Albouy and Caussanel 1990) (see “Species accounts” section). During field surveys aimed to document the persistence of the species in some of the classical localities, we were surprised to find consistently specimens with long cerci (referred to as *C. aptera* in the literature; e.g. Lapeira and Pascual 1980; Albouy and Caussanel 1990), and short cerci (referred to as *C. pyrenaica*; op. cit.) coexisting at the same localities. These observations, together with the lack of consensus on the presence of *C. aptera* in the Pyrenees (see references above), prompt-

ed us to carry out a study to determine the correct identification of long and short cerci specimens of Pyrenean *Chelidura*. For this purpose, we obtained cytochrome oxidase 1 (*cox1*) partial sequences of a few Pyrenean specimens, a representative of each cerci morphology, and we also raised under controlled conditions, a series of nymphs collected from the same clutch till they metamorphose. The results of these analyses revealed that both long and short cerci males corresponded to a single taxonomic entity.

With this main aim, the specific objectives of this work are: (i) to confirm the taxonomic identification of *Chelidura* specimens with long and short cerci present in the Pyrenees, (ii) discuss the taxonomic entity of the subspecies *C. pyrenaica arverna* from the French Massif Central, and (iii) provide a species account including all known localities and synonymies of Pyrenean *Chelidura*.

Material and methods

Studied material, morphological study and distribution data

Sampling was conducted in different localities of the Catalonia Pyrenees (Girona, Lleida), Andorra and Italy (Valle d'Aosta). A total of 104 specimens, 95 specimens of *C. pyrenaica* and 9 specimens of *C. aptera* (see below) were collected. All specimens were collected by hand, photographed in the field (when possible) and geo-referenced prior to being preserved in absolute ethanol, and then stored at -20 °C at the Museo Nacional de Ciencias Naturales (MNCN-CSIC) (Madrid, Spain). A set of 124 additional specimens of *C. aptera* and *C. pyrenaica* from the MNCN-CSIC collection were used for the morphological study. A series of last instar nymphs from Tossa d'Alp were maintained under controlled conditions until metamorphosis, previous to preservation (11 males were obtained from nymphs). The 228 specimens studied are from:

***Chelidura pyrenaica* (Gené, 1832): ANDORRA:** Sant Julià de Lòria: Bixessarri: Coll de la Gallina, 1933 m, 42°27'33.6"N, 1°27'03.7"E: 20-VI-2013, 2 females with eggs, M. García-París, G. García-Martín (MNCN_Ent 296001, 296015); La Rabassa, 1963 m, 42°26'21.7"N, 1°31'26.4"E: 20-VI-2013, 3 nymphs IV, 1 nymph V, 2 males, 5 females with eggs, M. García-París, G. García-Martín (MNCN_Ent 296016–296017, 269444, 296003–296010). – **FRANCE: Ariège:** L'Hospitalet-près-l'Andorre: 2 nymphs, 1 female, Dr. Martin (MNCN_Ent 283428–283430). **Hauts-Pyrénées:** Bagnères-de-Bigorre: 20-IX-1886, 1 male, 1 female, Collection A. Finot (MNCN_Ent 7850, 283422). **Pyrénées-Orientales:** Canigou: 1 female, Col. Marquet (MNCN_Ent 283425); 1 male, Masferrer (sub *C. aptera*) (MNCN_Ent 7849); Coll d'Ares, 1508m, 42°21'58.7"N, 2°27'31.5"E: 17-VI-2013, 1 female, M. García-París, G. García-Martín (MNCN_Ent 295998); Mont-Louis: 1 male, 1 female, E. Simon leg., I. Bolívar det. (MNCN_Ent 283426–283427). – **SPAIN: Catalonia: Bar-**

celona: Berga: Rasos de Peguera: 23-V-1991, 1 female, C. Martín (MNCN_Ent 122647); Montseny: 1 nymph, 3 males, 2 females, Masferrer (MNCN_Ent 122705, 122720–122721, 122723–122725); **Girona:** Campredó, 950 m: 15-IX-40, 5 males, J. Mat [J. Mateu] (MNCN_Ent 122699, 122736–122739), 25-IX-40, 2 male, 2 females, J. Mat [J. Mateu] (MNCN_Ent 122697–122698, 122700–122701); La Molina: Tossa d'Alp, 2343 – 2484 m, 42°19'30.07"N, 1°54'10.89"E / 42°19'12.78"N, 1°53'45.57"E: 5-VII-2011, 22 nymphs, 8 females, 10 males, P. Pavón-Gozalo, M. García-París, V. Salvador de Jesús (MNCN_Ent 269465–269466, 269468–269471, 269474, 269443, 269480–269485, 296013–296014, 295972–295995); Puigcerdà: 2 males, Zariquey (MNCN_Ent 122637, 122722); Puigmal, 2909 m: 1 male, Cazurro (MNCN_Ent 122729); Setcases: Vallter, 1736 m, 42°24'11.50"N, 2°17'12.82"E: 4-VII-2011, 8 nymphs, P. Pavón-Gozalo, M. García-París, V. Salvador de Jesús (MNCN_Ent 269460–269461, 269467, 269487, 295968–295971); 2174 m, 42°25'40.53"N, 2°15'58.56"E: 4-VII-2011, 23 nymphs, 2 males, 4 females, P. Pavón-Gozalo, M. García-París, V. Salvador de Jesús (MNCN_Ent 269462–269464, 269472–269473, 269442, 269475, 269477–269479, 269486, 269489–269491, 295953–295966, 13276); 2175 m, 42°25'36.7"N, 2°15'41.0"E: 17-VI-2013, 1 nymph IV, 1 nymph V, M. García-París, G. García Martín (MNCN_Ent 295999–296000); Toses: 26-IX-1932, 1 male, 1 female, A. Vilarrubia (MNCN_Ent 122726–122727); **Lleida:** Bellver: 10-903 [X-1903], 1

male (MNCN_Ent 122728); Caldes de Boí: VIII-1945, 3 males, Montada, (MNCN_Ent 122730–122732); Llès de la Cerdanya, 1935 m, 42°25'39.39"N, 1°39'51.73"E: 5-VII-2011, 4 nymphs, P. Pavón-Gozalo, M. García-París, V. Salvador de Jesús (MNCN_Ent 269476, 269488, 295996–295997); Pto. Payás [Pallars]: Virgen de Arés [Alt Aneu]: 32 females, 29 males (MNCN_Ent 122638–122644, 122646, 122648–122659, 122661–122677, 122679–122689, 122703, 122707–122718), 1923, 1 male, 2 females, M. Escalera (MNCN_Ent 122690, 122694–122695), VIII-1928, 4 females, 5 males, M. Escalera (MNCN_Ent 122660, 122678, 122702, 122704, 122706, 122691–122693, 122696); Salardú, 1.260 m: VIII-48, 1 nymph, E. Morales (MNCN_Ent 122645); Valle de Arán: Llenas: 1 nymph, 2 females (MNCN_Ent 122733–122735); **Pirineos** (without further indication): 1 male, Martorell (MNCN_Ent 122719); 1 female, 3 males, Col. Marquet (MNCN_Ent 283423–283424, 283439–283440) (specimens referenced from Pyrenees by Dubrony 1878 and Azam 1901) (Fig. 1).

Chelidura aptera (Megerle, 1825): **FRANCE: Savoie:** Mont-Cenis: 1 female, H. Martin (MNCN_Ent 283431); Saint-Bernard [Col du Petit Saint Bernard]: 1 male, Brunner (MNCN_Ent 283438). – **ITALY:** 3 females, 1 male, Durieu (MNCN_Ent 283434–283437). Gressoney la T. [Trinité] (Piemonte, M. Rosa): VIII-935 [1935], 1 male, 1 female (C. Alzona) (MNCN_Ent 283432–283433); **Valle d'Aosta:** Val Veny: Pré de Pascal, 1856 m, 45°48'20.2"N,

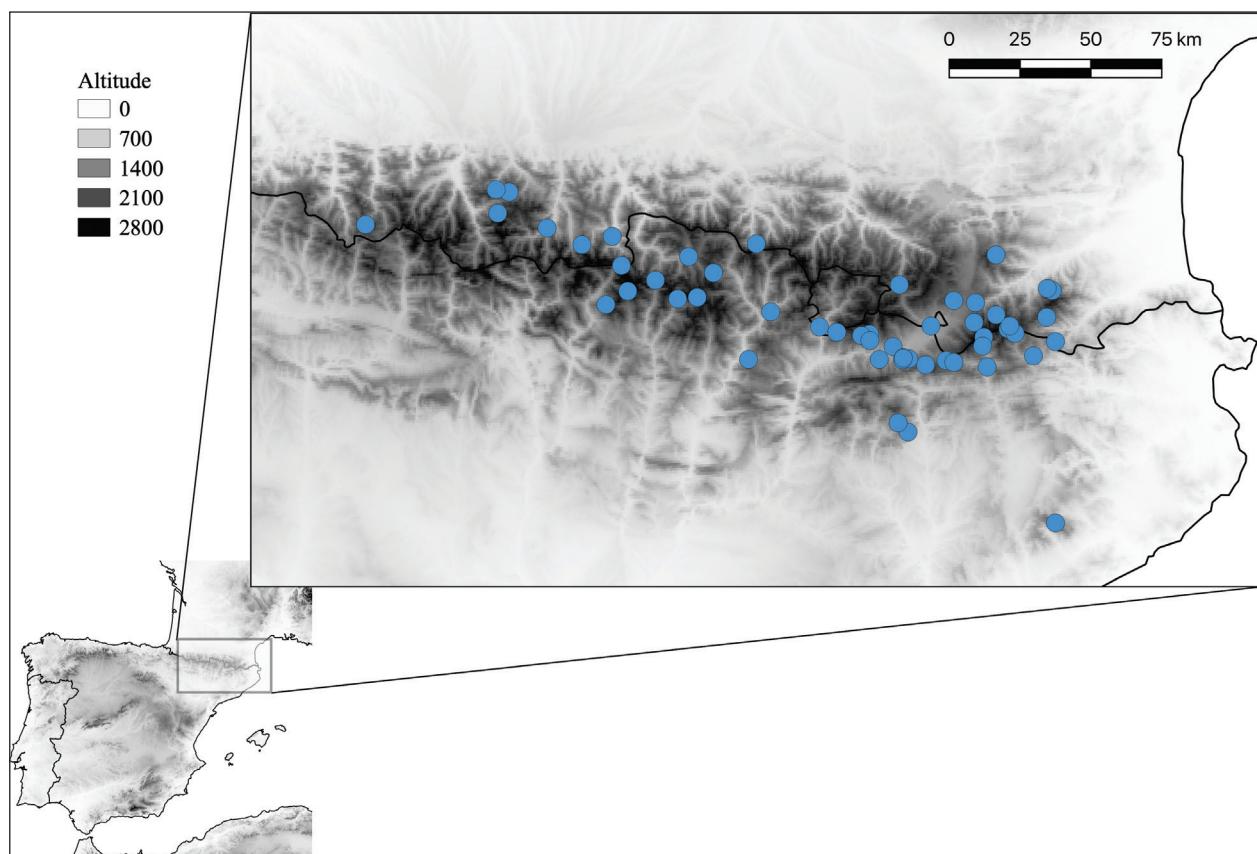


Figure 1. Geographic distribution of *Chelidura pyrenaica*. Blue dots correspond to the species records, including both recent and old (see material and methods and species accounts for the localities).

6°56'35.5"E: 28-VI-2012, 5 nymphs V, 2 females, 2 males, M. García-París, G. García-Martín (MNCN_Ent 269452–269458, 296011–296012).

Dry-mounted specimens were examined under a stereomicroscopy. Live specimens were photographed in the field with a Nikon digital camera. 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 105mm f/2.8G IF-ED and the software Helicon Remote v. 3. 9. 11 and Helicon Focus v. 7. 6. 4. Male genitalia were extracted and studied following the protocol described in Fontana et al. (2002) with minor modifications. The map depicting distribution range (Fig. 1) was made using the Natural Earth basemap, as implemented in QGIS vs. 3.8.

DNA extraction and amplification

Total DNA was obtained from six specimens (Table 1). DNA was extracted from one leg, using the DNeasy Blood and Tissue Isolation Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions, and then stored at 4 °C until further processed. The polymerase chain reaction (PCR) consisted of, with occasional minor variations, 18.8 µL of distilled water, 2.5 µL of 10 × PCR buffer, 1 µL of dNTP mix (10 mM), 0.5 µL of MgCl₂ (50 mM), 0.5 µL of each primer (10 µM), 0.2 µL of DNA polymerase (5U/µL) and 1 µL of DNA template, consisting of a final reaction volume of 25 µL. The universal pair of primers LCO1490 and HCO2198 (Folmer et al. 1994) were used to amplify a fragment of *cox1*, with the following PCR cycling profile: initial denaturation at 96 °C for 5 min, followed by 40 cycles at 94 °C for 30 s, 42 °C for 45 s and 72 °C for 1 min, and a final extension step at 72 °C for 5 min. After the amplification, 4 µL of the reaction was analyzed by electrophoresis on a 1% agarose gel. Samples with single bands were sent to the company Macrogen Inc. (Macrogen Europe, Madrid, Spain) for sequencing in both directions.

Phylogenetic analyses and species concept

The *cox1* data set included four Pyrenean specimens (with diverse cerci morphology), two specimens from the Italian Alps, one specimen of *C. p. arverna* from Kirstová et al. (2020), and six additional specimens of *C. aptera* from Fontana et al. (2021) (Table 1). One additional specimen of *Chelidurella vignai* Galvagni, 1995 and another of *Chelidurella thaleri* Harz, 1980 (from Kirstová et al. 2020; Table 1) were used as closely related outgroups. We also included one specimen of *Mesochelidura occidentalis* Fernandes, 1973 and another of *Anechura bipunctata* (Fabricius, 1781) (from Kirstová et al. 2020; Table 1) as distant outgroups to root the phylogenetic analyses. Gen Bank accession numbers for the newly sequenced specimens are provided in Table 1.

The obtained *cox1* partial sequences were aligned with MAFFT v.7 (Katoh et al. 2019) using default parameters. Uncorrected (p) pairwise genetic distances were estimated using PAUP* v.4.0a (Swofford 2002). The best substitution model obtained using PartitionFinder2 (Lanfear et al. 2016) was HKY + I + γ. An XML File was generated with BEAUTi v.2.5.0 (Bouckaert et al. 2019) using a birth-death process model, and an uncorrelated relaxed lognormal clock model under default parameters. Bayesian analyses were performed using in MrBayes v.3.2.6 (Ronquist et al. 2012) and BEAST v.2.6.3 (Bouckaert et al. 2019), through the CIPRES Science Gateway v.3 (Miller et al. 2010). The length of MCMC chain was 1,000,000 sampling every 1000. To check for convergence of the Markov chains Monte Carlo (MCMC), posterior trace plots and effective sample sizes (ESS) were examined in TRACER v.1.7 (Rambaut et al. 2018). The first 25% of sampled trees were discarded, and using TreeAnnotator v.1.8.4 (Drummond et al. 2012), the results were summarized in a maximum clade credibility tree (MCC) and selecting a length of the nodes based on the median. Visualization and editing of the phylogenetic tree were carried out in FigTree v1.4.4 (Rambaut et al. 2018).

Table 1. Specimens used for DNA analyses with their corresponding MNCN Entomology Collection codes (or original publication) and GenBank accession numbers.

Species	Specimen code	Geographic origin	Coordinates	GenBank COI
<i>Chelidura aptera</i>	MNCN_Ent 296011	Italy: Valle d'Aosta: Val Veny: Pré de Pascal	45°48'20.2"N, 6°56'35.5"E	MZ325323
<i>Chelidura aptera</i>	MNCN_Ent 296012	Italy: Valle d'Aosta: Val Veny: Pré de Pascal	45°48'20.2"N, 6°56'35.5"E	MZ325324
<i>Chelidura pyrenaica</i>	MNCN_Ent 296013	Spain: Girona: La Molina: Tossa d'Alp	42°19'30.07"N, 1°54'10.89"E	MZ325325
<i>Chelidura pyrenaica</i>	MNCN_Ent 296014	Spain: Girona: La Molina: Tossa d'Alp	42°19'30.07"N, 1°54'10.89"E	MZ325326
<i>Chelidura pyrenaica</i>	MNCN_Ent 296015	Andorra: Sant Julià de Lòria: Bixessarri: Coll de la Gallina	42°27'33.6"N, 1°27'03.7"E	MZ325327
<i>Chelidura pyrenaica</i>	MNCN_Ent 296016	Andorra: Sant Julià de Lòria: La Rabassa	42°26'21.7"N, 1°31'26.4"E	MZ325328
<i>Chelidura arverna</i>		France: Chalmazel (Kirstová et al. 2020)	45°40'33"N, 03°49'32"E	MH853428
<i>Chelidura aptera</i>	5b-1	Switzerland, Valais, Col du Grand Saint-Bernard, Liddes, 2160 m	45°53'11.24"N, 7°11'24.35"E	Fontana et al. (2021)
<i>Chelidura aptera</i>	5b-5	Switzerland, Valais, Col du Grand Saint-Bernard, Liddes, 2160 m	45°53'11.24"N, 7°11'24.35"E	Fontana et al. (2021)
<i>Chelidura aptera</i>	2a-1	Italy, Piedmont (Biella), Pennine Alps, Lago del Mucrone, Oropa, 1910 m	45°37'43.54"N, 7°56'38.24"E	Fontana et al. (2021)
<i>Chelidura aptera</i>	2a-3	Italy, Piedmont (Biella), Pennine Alps, Lago del Mucrone, Oropa, 1910 m	45°37'43.54"N, 7°56'38.24"E	Fontana et al. (2021)
<i>Chelidura aptera</i>	17-1	Italy, Lombardy (Sondrio), Western Rhaetian Alps, Franscia, Lanzada, 1480 m	46°17'21.4"N, 9°54'41.14"E	Fontana et al. (2021)
<i>Chelidura aptera</i>	18	Italy, Lombardy (Sondrio), Western Rhaetian Alps, Franscia, Lanzada, 1480 m	46°17'21.4"N, 9°54'41.14"E	Fontana et al. (2021)
<i>Chelidurella vignai</i>		Italy: Trento (Kirstová et al. 2020)	46°07'11"N, 11°15'40"E	MH853430
<i>Chelidurella thaleri</i>		Slovakia: Pol'ana (Kirstová et al. 2020)	48°40'52"N, 19°30'29"E	MH853433
<i>Mesochelidura occidentalis</i>		Portugal: Monchique (Kirstová et al. 2020)	37°19'03"N, 08°35'18"W	MH853427
<i>Anechura bipunctata</i>		Mongolia: Ikh-tamir (Kirstová et al. 2020)	47°35'33"N, 101°12'60"E	MH853426

Evolutionary (taxonomic) units within *Chelidura* were defined using the evolutionary species concept as discussed in Sánchez-Vilas et al. (2020). The evolutionary species concept considers species as “a single lineage of ancestral descendant populations of organisms that maintain its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley 1978, 1981; Wiley and Mayden 2000).

Results

Based on the phylogenetic analyses, studied specimens of *Chelidura* compose three well-supported clades (posterior probabilities = 1) (Fig. 2). A clade includes the Pyrenean specimens (PP = 1), a second clade includes the Massif Central specimen, and the third clade includes the Alpine specimens (Valle d’Aosta – Biella – Sondrio – Valais: Grand Saint Bernard) (PP = 1). The Alpine samples are geographically structured in two main subclades, one including samples from Valle d’Aosta and Col du Grand Saint Bernard (PP = 0.99), the second from Biella and Sondrio (PP = 0.94). Uncorrected “p” distances between different groups based on *cox1* partial sequences are summarized in Table 2.

Pyrenean specimens (Andorra and Girona) form a monophyletic group of poorly differentiated sequences (uncorrected $p_{distance}$ ranging from 0 to 0.03) (Fig. 2; Table 2). These samples include male specimens from Tossa d’Alp (Girona) and La Rabassa (Andorra) with typical short cerci (MNCN_Ent 296014, 296016) and specimens from Tossa d’Alp (Girona) with very long cerci (MNCN_Ent 296013). The sister taxon relationship of the Alpine

clade with respect to the Pyrenean and Massif Central clades is poorly resolved (PP = 0.72) forming a possible polytomy with respect to *Chelidurella*. Genetic distance between the specimens of the Pyrenean and the Alpine clades is very large (uncorrected $p_{distance}$ = 0.19–0.22) (Table 2). It is almost as high as those found among different genera of Forficulidae (Table 2), suggesting that nucleotide changes in *cox1* might be already saturated at that level.

Male specimens included in the Pyrenean clade (Girona and Andorra) present large variability in the shape of the cerci. Cerci range from long, almost straight convergent cerci (Figs 3A, 4A), to very curved, broad, short cerci (Fig. 3D). Short cerci present the maximum curvature at the middle, forming an angle of approximately 90°; cerci are wider at the base, strongly narrowed at the area of greatest curvature (Fig. 3D, E), and maintaining a more or less constant width up to the apex (Fig. 3D). Long cerci are sub-cylindrical, slightly curved at their maximum width near the base, progressively narrowed towards the apex, acuminate at the end (Fig. 3A). Cerci may present a ridge on the inner margin (Fig. 3B–F) or not (Fig. 3A). This ridge, when present, arises after the point of greatest curvature of the cerci and can continue to the apex of the cerci (Fig. 3D, E) or ending earlier, resembling a broad tooth (Fig. 3F). Intermediate specimens between these extreme shapes also occur (Figs 3B, C, F, 4C, D). In the same way, the diameter of the cerci is variable, including specimens with thick cerci compared to others with finer cerci. In all the individuals studied, cerci diameter expands over half or more of the width of the last segment. Males raised under controlled conditions from a single group of last instar nymphs from

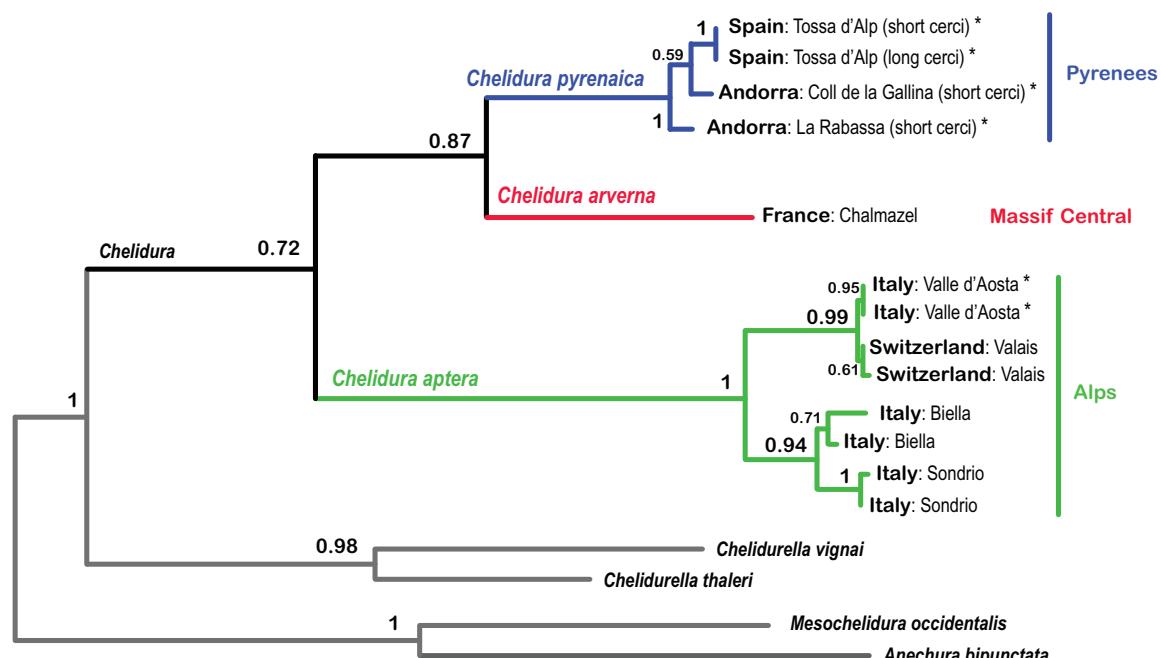


Figure 2. Bayesian phylogenetic tree based on *cox1* partial sequences. The colours represent species and geographic areas: Pyrenees (blue), Massif Central (red) and Alps (green). Posterior probabilities are indicated for each clade. Sequences marked with an asterisk (*) were obtained for this study, all other sequences were recovered from Kirstová et al. (2020) and Fontana et al. (2021).

Table 2. Uncorrected (p) pairwise genetic distance matrix between specimens (short – long cerci) and taxa used in the phylogenetic analyses.

		<i>Chelidura</i>						<i>Chelidurella vignai</i>	<i>Chelidurella thaleri</i>	<i>Anechura bipunctata</i>	<i>Mesochelidura occidentalis</i>
		<i>C. aptera</i>			<i>C. pyrenaica</i>		<i>C. arverna</i>				
		Valle d'Aosta	Valais	Biella	Sondrio	Long cerci	Short cerci				
<i>Chelidura</i>	<i>C. aptera</i>	Valle d'Aosta	0.00								
		Valais	0.00-0.01	0.00							
		Biella	0.08-0.09	0.08-0.09	0.02						
		Sondrio	0.09	0.08-0.09	0.03-0.04	0.00					
<i>C. pyrenaica</i>	Long cerci			0.19-0.21							
	Short cerci			0.19-0.22		0.00-0.03	0.02-0.03				
<i>C. arverna</i>				0.18-0.21		0.15	0.14-0.15				
	<i>Ch. vignai</i>			0.20-0.21		0.21	0.20-0.21	0.20			
	<i>Ch. thaleri</i>			0.20-0.21		0.19	0.19-0.20	0.21	0.15		
<i>Anechura</i>	<i>A. bipunctata</i>			0.22-0.23		0.22	0.22	0.22	0.20	0.20	
<i>Mesochelidura</i>	<i>M. occidentalis</i>			0.24-0.25		0.20	0.20	0.21	0.23	0.22	0.19

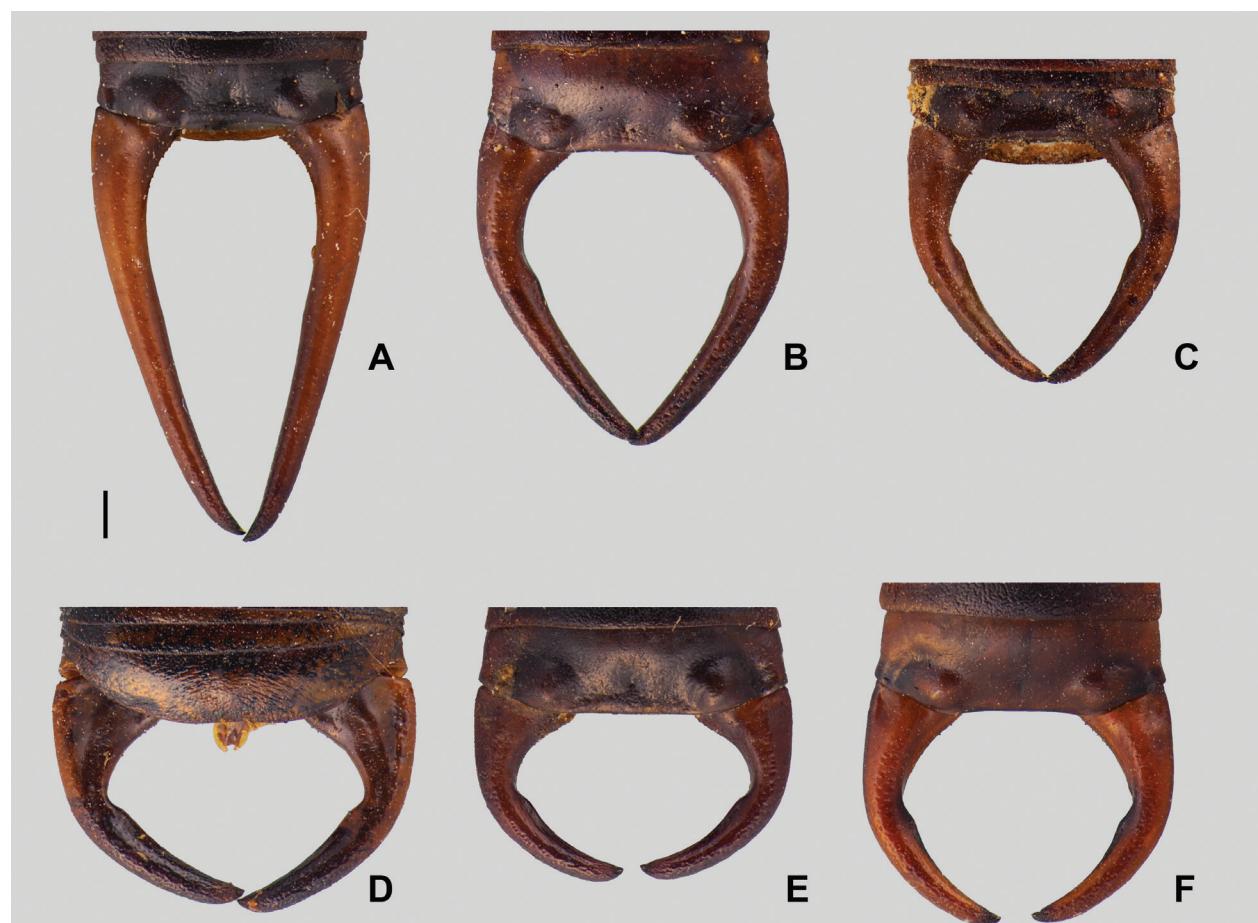


Figure 3. Cerci variation in *Chelidura pyrenaica* (Gené, 1832) males. Specimens from: (A) Puigcerdà (Girona, Spain) (MNCN_Ent_122637); (B) Pyrenees (Spain) (MNCN_Ent_122719); (C) Camprodon (Girona, Spain) (MNCN_Ent_122738); (D) Pyrenees (MNCN_Ent_283424); (E) Caldes de Boí (Lleida, Spain) (MNCN_Ent_122732); (F) Montseny (Barcelona, Spain) (MNCN_Ent_122721). Scale bar = 1 mm.

Tossa d'Alp present long, short and intermediate cerci (Fig. 4A, C, D).

The specimens studied from the Alpine clade present long cerci with little curvature, cylindrical apically, progressively narrowed towards the apex and the inner margins without teeth or with one tooth. The diameter of the cerci of those specimens studied is generally smaller than that of the specimens of the Pyrenean clade. However, our sample is not representative of the

variability already reported for the Alpine clade (Burr 1912; Amiet 1961; David and Van Herrewege 1973; Sakai 1973; Caussanel and Albouy 1987; Albouy and Caussanel 1990; Herrera-Mesa 1999). Fontana et al. (2021) indicated that cerci variability in *C. aptera* is larger than previously considered, pending of a detailed geographic analysis.

The Pyrenean clade is sister to the single sequence representing the Massif Central clade (PP = 0.87). The

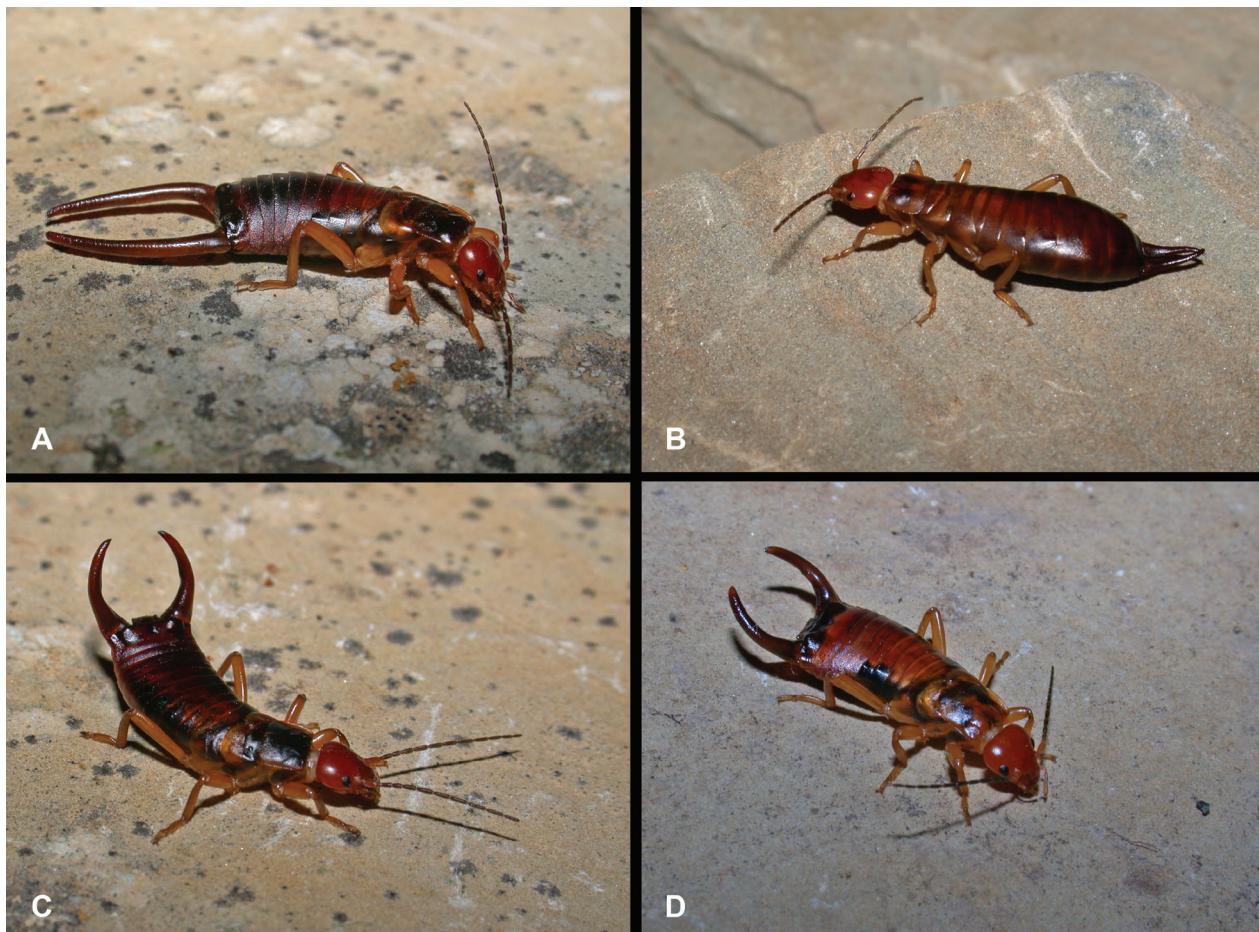


Figure 4. Live specimens of *Chelidura pyrenaica* (Gené, 1832) and cerci variation. **A.** Male from Tossa d'Alp (Girona, Spain) (MNCN_Ent 296013). **B.** Female from Coll de La Rabassa (Andorra). **C.** Male from Tossa d'Alp (Girona, Spain) (MNCN_Ent 269481). **D.** Male from Tossa d'Alp (Girona, Spain). Photographs ex situ by M. G.-P.

genetic distance between Pyrenean and Massif Central populations is quite large (uncorrected $p_{\text{distance}} = 0.14$ –0.15). Among the large series of Pyrenean specimens studied we did not find the cerci morphology described for *C. p. arverna* by David & Van Herrewege (1973), Kirstová et al. (2020) and Fontana et al (2021). Cerci of the specimen included in the Massif Central clade, from Chalmazel (France), are more robust, relatively wider and less curved than cerci of the specimens of the Pyrenean clade. David and Van Herrewege (1973) confirmed that the morphology of the Pyrenean populations and those of the Massif Central (morphometric traits and male cerci), differ statistically.

Male genitalia from specimens of the Pyrenees, Alpine and Massif Central clades, including the lectotype of *C. pyrenaica*, the neotype of *C. aptera* and the holotype of *C. p. arverna*, were studied in detail and photographed by Fontana (1999) and Fontana et al. (2021). Maccagno (1933) also provided an illustration of the male genitalia of Pyrenean specimens corresponding to *C. pyrenaica*. The genitalia of the male specimens of *C. pyrenaica* we examined (Virgen de Ares, Lleida) match the description presented by Maccagno (1933) and Fontana (1999); variability is however large, including

size of parameres. They differ from those of the Alpine specimens, by showing thinner parameres with almost parallel margins (shorter and curved on the external margin in Alpine specimens). Male genitalia of typical *C. pyrenaica* and the holotype of *C. p. arverna* do not differ significantly, although *C. p. arverna* seems to present a more arcuate vesicle.

Species accounts

Chelidura arverna David & Van Herrewege, 1973 stat. nov.

Chelidura pyrenaica arverna David & Van Herrewege, 1973: 40. Terra typica: «Massif Central: Mont Mézenc». Holotype at the Muséum d'Histoire naturelle de Paris (David & Van Herrewege 1973). Albouy & Caussanel (1990: 180) wrote the species name as “*C. p. averna*”.

Published records. FRANCE: **Cantal** (Chopard 1922 sub *C. aptera*; Chopard 1951 sub *C. aptera*; Sakai 1973 sub *C. aptera*; Harz and Kaltenbach 1976 sub *C. aptera*); Le Lioran (Burr 1904 sub *C. aptera*); Le Lioran, prairies voisines de la station (Finot 1890 sub *C. aptera*). **Haute-**

Loire: Massif Central (Amiet 1961 sub *C. aptera*; Caussanel and Albouy 1987 sub *C. aptera* and *C. pyrenaica*; Albouy and Caussanel 1990 sub *C. aptera* and *C. pyrenaica*; Herrera-Mesa 1999 sub *C. pyrenaica*); Mont Mézenc (David and Van Herrewege 1973; Albouy and Caussanel 1990 sub *C. pyrenaica* spp. *averna* [*arverna*]). **Loire:** Chalmazel: Station de Chalmazel, 1137 m, 45°40'33"N, 3°49'32"E (Fontana et al. 2021). **Lozère** (Chopard 1922 sub *C. aptera*; Chopard 1951 sub *C. aptera*; Sakai 1973 sub *C. aptera*; Harz and Kaltenbach 1976 sub *C. aptera*). **Puy-de-Dôme** (Chopard 1922 sub *C. aptera*; Chopard 1951 sub *C. aptera*; Sakai 1973; Harz and Kaltenbach 1976 sub *C. aptera*): Mont Doré (Fontana et al. 2021). **Dubious assignment: FRANCE:** **Ardèche** (Harz and Kaltenbach 1976 sub *C. aptera*): Astet (Chopard 1951 sub *C. aptera*).

Chelidura pyrenaica (Gené, 1832)

Forficula simplex Germar, 1825: pl. 17 (*nomen oblitum*) syn. nov. Terra typica: "... in Pyrenaeis...".

Forficula pyrenaica Gené, 1832: 227 (*nomen protectum*). Terra typica: "...Pirenei...". Lectotype designated by Fontana (1999) (male, specimen number 2363 at MRSNT). The neotype designation mentioned by Harz and Kaltenbach (1976) with specimens from "Riba Freser" (sic), is not valid (Fontana 1999).

Forficula dilatata Burmeister, 1838: 755. Terra typica "In den Pyrenäen" ? *Forficula pyrenaea* Herrich-Schäffer, 1840: 31. Terra typica not indicated. A synonym of either *C. pyrenaica* or *Pseudochelidura sinuata* (Germar, 1825) (Herrich-Schäffer 1840).

Chelidura dilatata (Burmeister, 1838): Brunner von Wattenwyll 1882: 25

Chelidura pyrenaica (Gené, 1832): de Bormans and Krauss 1900: 108. Sakai (1973: 175) wrote by mistake «*Chelidura pyrenatica*».

Published records. ANDORRA (David and Van Herrewege 1973; Steinmann 1981 sub *C. aptera*). – **FRANCE:** **Ariège** (Dubrony 1878 sub *C. aptera*; Finot 1890 sub *C. dilatata*; Azam 1901 sub *C. dilatata*; Chopard 1951; Sakai 1973): 1500 m (Chopard 1922); Anglade [Cirque d'Anglade] (David and Van Herrewege 1973); L'Hospitalet-près-l'Andorre (Dusoulier 2004); Montagnes de l'Ariège (Marquet 1877 sub *C. dilatata*); Sollau [not found] (David and Van Herrewege 1973). **Haute-Garonne** (Marquet 1877 sub *C. dilatata*): Vallé d'Esquieres Luchon bei 1400 m [Bagnères-de-Luchon] (Fieber 1853 sub *F. dilatata*). **Hautes-Pyrénées** (Dubrony 1878 sub *C. aptera*; Brunner von Wattenwyll 1882 sub *C. dilatata*; Chopard 1951 sub *C. aptera*; Sakai 1973): au-dessus de 1500 m (Chopard 1922); à une hauteur de 2000 à 2500 m (Finot 1890 sub *C. dilatata*); à partir de 1000 m (Chopard 1922 sub *C. aptera*); Bagnères-de-Bigorre (Azam 1901 sub *C. dilatata*; Chopard 1951); Bagnères-de-Bigorre, au lac Bleu (Azam 1901 sub *C. dilatata*); environs de Bagnères-de-Bigorre (Finot 1890 sub *C. dilatata*); Glacier de Neouvielle (Burr 1912 sub *C. dilatata*; Sakai 1973); Pic de Nère (David and Van Herrewege 1973); Pic-du-Midi (Finot 1890 sub *C. dilatata*; Chopard 1951); Pic du

Midi de Big 2000–2800 m (Harz and Kaltenbach 1976 sub *C. aptera*); Saint-Lary [Saint-Lary-Soulan] (Dauphin 1987); Seincourt [not found] (David and Van Herrewege 1973). **Pyrénées-Atlantiques** (Albouy and Caussanel 1990). **Pyrénées-Orientales** (Dubrony 1878 sub *C. aptera*; Finot 1890 sub *C. dilatata*; Azam 1901 sub *C. dilatata*; Chopard 1922): au-dessus de 1500 m (Chopard 1922); Canigó (Finot 1890 sub *C. dilatata*; Azam 1901 sub *C. dilatata*; Borelli 1905 sub *C. dilatata*; Burr 1912 sub *C. dilatata*; Amiet 1961; Sakai 1973; David and Van Herrewege 1973); Canigou, à partir de 1000 mètres (Xambeu 1907 sub *C. dilatata*; Chopard 1951); Canigó, à partir de 1200 m d'altitude, jusqu'à 2400 (Xambeu 1903 sub *C. dilatata*); Coubezet (Xambeu 1907 sub *C. dilatata*); Font-Romeu [Font-Romeu-Odeillo-Via] (Borelli 1905 sub *C. dilatata*; Sakai 1973; Vancassel and Foraste 1980; Vancassel 1984); Le Vernet [Vernet-les-Bains] (Dubrony 1878 sub *C. aptera*; Azam 1901 sub *C. dilatata*); Le Vernet [Vernet-les-Bains], près Prades (Finot 1890 sub *C. dilatata*; Chopard 1951); Mont-Louis (Amiet 1961; Steinmann 1981 sub *C. aptera*); Rouquette [Pic de la Rouquette] à partir de 1200 m d'altitude, jusqu'à 2400 (Xambeu 1903 sub *C. dilatata*); Thuès, Haute vallée de la Carança (Hamon 1956); Val d'Eyne (Chopard 1951; Hamon 1956); Vallée supérieure du Tech (Borelli 1905 sub *C. dilatata*; Sakai 1973). **Pyrénées** (département not indicated) (Serville 1839 sub *F. aptera* and *F. simplex*; Fieber 1853 sub *F. simplex* and *F. dilatata*; Dubrony 1878 sub *C. aptera* and *C. a. var. simplex*; Brunner von Wattenwyll 1882 sub *C. dilatata*; de Bormans and Krauss 1900; Azam 1901 sub *C. aptera*; Kirby 1904; Borelli 1905 sub *C. dilatata*; Amiet 1961; David and Van Herrewege 1973; Caussanel and Albouy 1987; Albouy and Caussanel 1990): les parties élevées (Azam 1901 sub *C. dilatata*); localités élevées (Houlbert 1900 sub *C. dilatata*); southern Europe from Pyrenees and Southern France (Sakai 1973 sub *C. aptera*). – **SPAIN** (province not indicated): Espagne en montagne, entre 1000 et 2500 m d'altitude (Albouy and Caussanel 1990 sub *C. aptera*); Norte de España (Cazurro Ruiz 1888 sub *C. dilatata*). **Aragón:** **Huesca:** Coll de Basibé, 2000–2200 m (Borelli 1926; Sakai 1973); Hospital de Benasque, Maladeta, 1775 m (Borelli 1926; Sakai 1973); Valibierne-Tal bei Benasque, 2000–2400 m (Borelli 1926; Sakai 1973). **Catalunya:** **Barcelona** (Herrera-Mesa 1999): Espinalbet (Lapeira and Pascual 1980); Montseny (Lapeira and Pascual 1980). **Girona** (Herrera-Mesa 1999): Camprodón (Cazurro Ruiz 1888 sub *C. dilatata*; Novellas 1901); Camprodón 950 m (Lapeira and Pascual 1980); Camprodón ("a native of the upper regions of the Pyrenees, where it occurs at an elevation of 6000ft.–8000ft.") (Burr 1904); Col de Tosas [Collada de Toses] (David and Van Herrewege 1973); Nuria [Vall de Núria] (Lapeira and Pascual 1980); Nuria, pinar de la Virgen, a más de 2000 metros (Navás 1921); Puigcerdà (Lapeira and Pascual 1980); Puigmal [Puigmal d'Er], 2909 m (Lapeira and Pascual 1980); Riba Freser [Ribes de Freser] (Harz and Kaltenbach 1976; Albouy and Caussanel 1990; Fontana 1999);

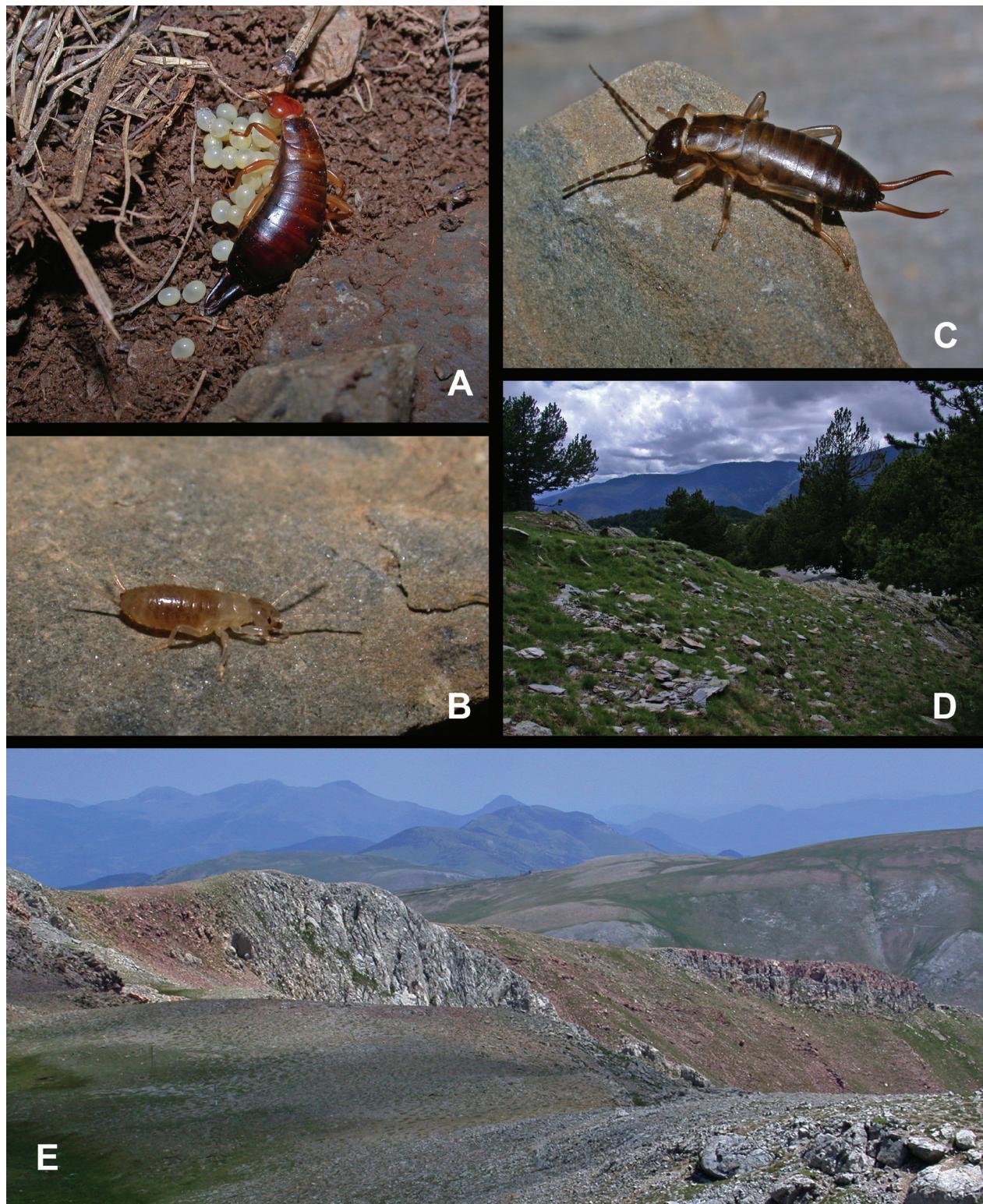


Figure 5. Live specimens of *Chelidura pyrenaica* (Gené, 1832) from Andorra and typical habitat. **A.** Female with eggs from Coll de la Gallina (Andorra). **B.** Early instar nymph from Coll de La Rabassa (Andorra). **C.** Late instar nymph from Coll de la Rabassa (Andorra). **D.** Typical habitat where *C. pyrenaica* complete its development (Coll de la Gallina, Andorra; June). **E.** Slopes of Tossa d'Alp (Girona; July) where specimens of *C. pyrenaica* showing a wide variability of cerci shape coexist. Photographs by M. G.-P.

Ripollès: Toses [Collada de Toses] (Lapeira and Pascual 1980); Riu (BVdb 2021); Ull de Ter [Ulldeter] (Lapeira and Pascual 1980). Lleida (Herrera-Mesa 1999): Aransa [Aràns] (BVdb 2021); Bellver [Bellver de Cerdanya]

(Lapeira and Pascual 1980); Bellver de Cerdanya (BVdb 2021); Bor (BVdb 2021); Caldas Bohí [Caldes de Boí] (Lapeira and Pascual 1980); Martinet (Boeseman 1954; Sakai 1973; Sakai 1973 sub *C. aptera*); Parque Nacio-

nal de Aigues Tortes (Balcells et al. 1962); Pto. Payás [Pallars]: Virgen de Ares [Alt Àneu] (Lapeira and Pascual 1980); Tírvia (BVdb 2021); Tornafont (BVdb 2021); Valle de Arán [Val d’Aran] (Lapeira and Pascual 1980); Val d’Aran: Port de Viella (Borelli 1926; Sakai 1973; Lapeira and Pascual 1980); Val d’Aran: Salardú, 1260 m (Lapeira and Pascual 1980). **Pirineos** (provincia not indicated) (Fischer 1853 sub *C. dilatata*; Bolívar 1878 sub *C. aptera*; Martorell Peña 1879; Cazurro Ruiz 1888 sub *C. aptera* and *C. dilatata*; Burr 1910; Popham 1968; Sakai 1973; Harz and Kaltenbach 1976; Lapeira and Pascual 1980; Caussanel and Albouy 1987; Steinmann 1989; Fontana 1999; Herrera-Mesa 1999; Guillet and Vancassel 2001; Kirstová et al. 2020 sub *Chelidura*; Fontana et al. 2021) (Fig. 1).

Fontana et al. (2021: fig. 13) commented on a specimen morphologically assignable to *C. pyrenaica* from the Sierra Nevada Mountains in Southern Spain (Picacho de Veleta; Museum National d’Histoire Naturelle, Paris). As Fontana et al. (2021) discussed, it is quite possible that the specimen could be mislabelled, as it has already happened with other specimens of Dermaptera labelled erroneously from the Sierra Nevada Mountains, otherwise a quite well explored mountain chain (García-París 2017). The presence of *Chelidura* in the Sierra Nevada Mountains should be treated as doubtful until additional specimens come to light.

Notes on Natural History

Chelidura pyrenaica is found in mountain slopes, between 1000 and 2500 m, usually in pastures in areas covered by flat stones, near the forest edge or in open areas (Fig. 5D, E) (Borelli 1905; Chopard 1922; Chopard 1951; David and Van Herrewege 1973; Albouy and Caussanel 1990). The geologic substrates of the area are diverse and complex, dominated by schists and limestone (see for a general overview Dendaletche 1982). Adult specimens are usually found under stones, bark of fallen trees and clods of earth in summer and fall (Azam 1901; Xambeu 1903; Chopard 1922; Albouy and Caussanel 1990). Xambeu (1903, 1907) and Chopard (1951) mentioned that *C. pyrenaica* can be also found in spring. Mating takes place in April or May, in galleries that earwigs dig under their shelters. Females lay the eggs grouped in a shallow excavation at the end of one of these galleries and take care of them until the larvae hatch (Xambeu 1903; Caussanel and Albouy 1987; Albouy and Caussanel 1990). We observed female attending eggs in the second half of June in Andorra (Fig. 5A). Upon disturbance females hide in small burrows, but usually return soon to the egg mass and start moving the eggs to the burrow, holding them one by one with their mandibles. Herter (1943) indicates that females may lay 40–45 eggs per clutch. Diverse nymphal stages were observed in the second half of June in Andorra and in the first half of July in Coll d’Ares (Girona) also attended by females (Fig. 5B, C).

Discussion

There is a strict correspondence between mtDNA clades and geographic areas, with all samples from the Pyrenees included in a well-supported clade, sister to the Massif Central specimen, and those, in turn, related to the Alpine specimens. Sequences of the specimens from Tossa d’Alp (with short and long cerci respectively) are closer to each other than to the short cerci specimens from Andorra, therefore, at the molecular level, specimens with short and long cerci from the Pyrenees correspond to a single taxon. Results from the nymphs raised under controlled conditions, with adult males including long (see for example MNCN_Ent 296013; Fig 4A), short, and intermediate cerci (MNCN_Ent 269481; Fig. 4C) also support that cerci variability corresponds to a single taxon.

Populations of *Chelidura* from the French Massif Central have been treated as a differentiated subspecies, *C. pyrenaica arverna* (David and Van Herrewege 1973; Kirstová et al. 2020). The large genetic distance observed between Pyrenean and Massif Central populations of *Chelidura* suggests that they have been isolated for long time. Lasting isolation between the Pyrenean and Central Massif populations is also supported by the morphological differentiation observed in male cerci. Reciprocal monophyly, long isolation reflected by large sequence divergence, and cerci morphological differentiation at morphometric level, suggest that *C. arverna* likely represents a separate taxonomic unit with respect to *C. pyrenaica* as previously suggested by Fontana et al. (2021). Using the evolutionary species concept (Wiley 1978, 1981; Wiley and Mayden 2000), there is little doubt that the Massif Central populations of *Chelidura* can be considered to represent an independent species: *Chelidura arverna* David and Van Herrewege, 1973 stat. nov.

Intraspecific variability of morphological structures, as pygidium or cerci, is well known in earwigs (Srivastava 1970; Simpson and Mayer 1990; Tomkins and Simmons 1996; García-París 2017; Kirstová et al. 2020). Many species of Dermaptera show large variability in the size and shape of male cerci (Dohrn 1867; Diakonov 1925; Ollason 1970; Srivastava 1970; Mourier 1986; Simpson and Mayer 1990; González-Miguens et al. 2020; García-París et al. in press). The level of variability found in Pyrenean *Chelidura* is apparently higher than the levels of variability found by these previous authors in other taxa (Fontana et al. 2021; Fig. 3). This large variability in male sexual characters might be a consequence of strong sexual selection (Kawano 2006; Brown 2007). Alternatively, the large variability observed could be a consequence of the absence of directional selective pressures as Kirstová et al. (2020) mentioned as a possible explanation for the variability of the shape of the pygidium in some species of *Chelidurella*.

The taxonomic implications of the large shape variability in male cerci need to be addressed in the case of Pyrenean *Chelidura*. The presence of specimens of *C. pyrenaica* in the Pyrenees with long cerci was already mentioned by Borelli (1905), who said: “Parmi les in-

dividus trouvés sur les flancs du Canigou, trois ont les branches de la pince très allongées, légèrement arquées, ne se touchant pas à l'extrémité et pourvues en dedans, vers le milieu, d'une petite dent à peine visible...". Dohrn (1867) also mentioned that he had seen specimens of *C. pyrenaica* (sub *C. dilatata*) with long narrow cerci not typical for this species. More recently, Maccagno (1933) and Fontana et al. (2021), based on examination of male genitalia made a clear statement indicating that Pyrenean specimens with long cerci corresponded to *C. pyrenaica*. But many other authors disregarded these considerations treating long cerci Pyrenean specimens as *C. aptera*, and consequently reporting the presence of this species in the Pyrenees (Serville 1831, 1839; Fieber 1953; Bolívar 1878; Dubrony 1878; Cazurro Ruiz 1888; Azam 1901; Chopard 1922; Chopard 1951; Boeseman 1954; Amiet 1961; Sakai 1973; Harz and Kaltenbach 1976; Lapeira and Pascual 1980; Steinmann 1981; Caussanel and Albouy 1987; Albouy and Caussanel 1990; Herrera-Mesa 1999).

Most of the confusion derived from the early synonymization of *Forficula simplex* Germar, 1825, described based on Pyrenean specimens displaying long cerci (Germar, 1825), with *C. aptera* (Dohrn 1867; Bolívar 1876; Brunner von Wattenwyll 1882; Finot 1890; Kirby 1904; Burr 1904; Sakai 1973; Harz and Kaltenbach 1976; Herrera-Mesa 1999). The treatment of *F. simplex* as a synonym of *C. aptera* carried two consequences, first the early inclusion of the Pyrenees within the geographic range of *C. aptera*, leading to the current confusion, and second, the unnecessary descriptions of *Forficula pyrenaica* Gené, 1832 and *Forficula dilatata* Burmeister, 1838, based on specimens also from the Pyrenees. According to the principle of priority (article 23 of International Code of Zoological Nomenclature, ICZN 1999), the name *Forficula simplex* Germar, 1825 has nomenclatural priority over *Forficula pyrenaica* Gené, 1832. However, both names meet the provisions of the article 23.9.1 (ICZN, 1999) to retain prevailing usage in order to assure nomenclatural stability. In consequence, we propose the reversion of precedence of *F. simplex* with respect to *F. pyrenaica*. *Forficula simplex* Germar, 1825 has not been used as a valid species name after 1899, and *Forficula pyrenaica* Gené, 1832 has been used in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years (see for example David and Van Herrewege 1973; Sakai 1973; Harz and Kaltenbach 1976; Lapeira and Pascual 1980; Vancassel and Foraste 1980; Shah 1984; Vancassel 1984; Caussanel and Albouy 1987; Dauphin 1987; Pascual 1988; Steinmann 1989, 1993; Albouy and Caussanel 1990; Dendaletche 1982; Coutin 1983; Plate 1987; Haas 1995; Herrera-Mesa 1996, 1999; Guillet and Vancassel 2001; Klass 2001; Barrientos 2004; Dusoulier 2004; Matzke and Klass 2005; Costa 2006; Leraut 2007; Kirstová et al. 2020; Fontana et al. 2021). Therefore, and according to the Article 23.9.2. of the International Code of Zoological Nomenclature (ICZN 1999), the name *Forficula pyrenaica* Gené, 1832 is considered a *nomen*

protectum with nomenclatural precedence over the name *Forficula simplex* Germar, 1825, a *nomen oblitum*.

Chelidura pyrenaica has been recorded in the Alps (Burr 1912; Amiet 1961; David and Van Herrewege 1973; Sakai 1973; Caussanel and Albouy 1987; Albouy and Caussanel 1990; Herrera-Mesa 1999) and *C. aptera* in the Massif Central (Finot 1890; Burr 1904; Chopard 1922; Chopard 1951; Amiet 1961; Sakai 1973; Harz and Kaltenbach 1976; Caussanel and Albouy 1987; Albouy and Caussanel 1990), but we conclude, totally in agreement with Fontana et al. (2021), that the reports of *C. pyrenaica* from the Alps, and those of *C. aptera* in the Massif Central, should be disregarded, and assigned to *C. aptera* and *C. arverna* respectively.

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