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Current knowledge of the genus *Chelidura* Latreille, 1825 in the Alps, with descriptions of two new species (Dermaptera, Forficulidae)

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Abstract

Chelidura Latreille, 1825 is a genus of robust apterous earwigs with a Palaearctic distribution. Thanks to research carried out in Italy, Spain and France, the recent general reassessment of the European alpine species of *Chelidura* has clarified its distribution across Europe. Only one species, *Chelidura aptera* (von Charpentier, 1825), has been distinguished in the Alps so far, and we have subjected its populations to detailed morphometric and molecular analyses. The results revealed cryptic diversity and allowed us to define the presence of at least five species in the Alps: *C. aptera* (von Charpentier, 1825), *C. montana* (Gené, 1832), **stat. nov.**, *C. alpina* (Gené, 1832), **comb. nov.**, *C. rhaetica* **sp. nov.** and *C. osellarum* **sp. nov.** The diagnostic morphological characters of recognized species are described and illustrated, and an identification key for males of Western European *Chelidura* is provided. The distribution of *Chelidura* species is patchy, with most occurring in subalpine and alpine zones at altitudes between 1,600 and 2,300 metres in the Alps. The occupied habitat is characterized by rocky landscapes with sparse vegetation. According to current knowledge, all recognized species exhibit allopatric distribution patterns, and their ranges do not overlap. The recent decline in the numbers of *Chelidura* specimens sighted at many historical localities may suggest possible local extinctions or a shift to higher elevations in response to environmental changes.

Key Words

Europe, phylogeny, taxonomy, threatened species

Introduction

In recent years, the use of genetic analyses alongside traditional morphological taxonomy has led to a reappraisal of the European Dermaptera. This group has been moderately well studied historically, but there are a few unclear issues, such as *Chelidurella* Verhoeff, 1902, and *Chelidura* Latreille, 1825. For example, the revision of *Chelidurella* by Kirstová et al. (2020) confirmed the hypotheses of Antonio Galvagni (Galvagni 1994, 1995, 1996, and 1997), whereas the revision of *Forficula auricularia* Linnaeus, 1758 by Gonzales et al. (2020) highlighted the existence of a cryptic species complex, confirming previous suggestions of Guillet et al. (2000). In addition, a recent study by Cuesta-Segura et al. (2023) reviewed the status and distribution of *Pseudochelidura* Verhoeff, 1902, in the Iberian Peninsula. Even the European *Chelidura* Latreille, 1825, after several years of absolute nomenclatural confusion, now seems to be on the way to a more solid understanding, compatible with the original literature and consistent with morphological and molecular data and above all with current biogeographic knowledge.

Maccagno (1933), Vigna Taglianti (1994) and Felice Capra (in Fontana et al. 2021) had the merit to begin the reorganization of the European *Chelidura*, starting from the taxonomic issues affecting the genus and the morphological distinction of *Chelidura aptera* (von Charpentier, 1825) and *Chelidura pyrenaica* (Gené, 1832). These studies made it possible to recognise *C. aptera* as a species of the Western Alps and *C. pyrenaica* as a species of the Pyrenees and the Massif Central. The population from Massif Central was subsequently recognized as a subspecies of *C. pyrenaica*, and later separate species *C. arverna* David & Van Herrewege, 1973 (Jurado-Angulo et al. 2021).

The discovery of part of the type material of species described by Carlo Giuseppe Gené (1800–1847) in his papers from 1832 and 1837, and above all of the autograph descriptions of Francesco Andrea Bonelli (1784–1830), on which some of these descriptions were based (Fontana 1999), allowed the designation of the lectotypes for *Chelidura pyrenaica* as well as for *Forficula alpina* and *Forficula montana*, considered as synonyms of *C. aptera* (Fontana 1999).

In the last few years, three distinct research groups have addressed the European *Chelidura*, covering the entire distribution range of the genus and converging to a common overall vision (Dierkens et al. 2021; Fontana et al. 2021; Jurado-Angulo et al. 2021). Dierkens et al. (2021) confirmed, based on male genitalia, that *C. pyrenaica pyrenaica* occurs only in the Pyrenees, *C. pyrenaica arverna* in the Massif Central, and *C. aptera* in the Alps. Subsequently, Fontana et al. (2021) thanks to the meticulous review of the literature combined with DNA barcodes of *Chelidura* specimens from the Alps and the Massif Central, attributed the paternity of the genus *Chelidura* to Pierre André Latreille and established the neotype of *Chelidura aptera*, type species of the genus. In the same study, the authors highlighted that the specimens collected in Colle Grand San Bernardo Hospice and Liddes (Switzerland) (topotypes), which morphologically match the lectotype of *Forficula montana* (*sensu* Gené 1832), were genetically and morphologically distinct from *C. aptera* specimens belonging to the designated neotypical population (Italy, Cottian Alps, Monte Mucrone, Biella). These observations indicated identity mismatch between *C. aptera* and *F. montana*, suggesting the existence of more than one *Chelidura* species in the Alps and the possible validity of *Forficula alpina* (Fontana et al. 2021).

Fontana et al. (2021) also introduced a previously unknown *Chelidura* population from the Rhaetian Alps (Italy, Lombardy), a location that significantly extends the distribution of the genus to the east. Preliminary analyses highlighted that the population of the Alps Retiche was more genetically related to *Forficula montana* from the Colle Grand San Bernardo than to the geographically related *C. aptera* from Monte Mucrone, thus suggesting its attribution to a yet undescribed taxon. The three alpine populations examined by Fontana et al. (2021) also proved to be genetically distinct from those from Massif Central.

Based on an extensive series of specimens from the Pyrenees, the Massif Central, and the Alps (Italy, Valle d'Aosta), Jurado-Angulo et al. (2021) subsequently confirmed the attribution of Alpine, Pyrenean and Central Massif populations to three distinct species. The authors considered *C. pyrenaica* to be endemic to the Pyrenees and elevated the Massif Central endemic *C. arverna* David & Van Herrewege, 1973, to species level.

The recent availability of further historical material originating from previously unknown Italian localities, in combination with newly collected DNA-grade samples, allowed us to uncover a diversity of the genus *Chelidura* in the Italian Alps that was hitherto only partially expected. The aim of this study is to reevaluate alpine populations of *Chelidura* via both morphological and genetic data, to describe newly recognized species, and to revalidate previously synonymized species.

Materials and methods

Specimen collection

In September 2019, 2021, and 2025, a series of field expedition across Italy, Switzerland, and France was organized in the Western Alps to collect new samples among localities known from collection records or the literature (Fontana et al. 2021). Val Maira, Colle Sampéire, and related areas (Piedmont, Italy) were sampled in July 2020 (Paolo Fontana and Valeria Malagnini) and August 2021 (Paolo Fontana and Cinzia Vivian). The specimens used for DNA analyses were stored in 96% ethanol as soon as they were collected in the field.

Examined material

All the materials mentioned in this paper are deposited in the following collections:

FMCR	Paolo Fontana collection, Fondazione Museo Civico di Rovereto (Rovereto, Italy),
MRSNT	Regional Museum of Natural Sciences of Turin (Turin, Italy),
OUCO	Petr Kočárek collection, Department of Biology and Ecology, University of Ostrava (Ostrava, Czech Republic).

Citizen science records

In addition to the occurrences derived from collected specimens, we retrieved data from iNaturalist to better depict the range of *Chelidura* species. On January 30, 2024, 77 records were found on iNaturalist for the genus *Chelidura*, including 7 species recorded by 61 observers and identified by 21 identifiers (https://www.inaturalist.org/observations?taxon_id=333635). Of these 77 records, excluding those not falling within the geographical area considered in this article, 60 records were selected for which at least the identification at genus level was considered reliable. Some juvenile stages and a few females that could also be identified as *Chelidurella* were eliminated. Most of these 60 records were made between 2023 and 2024, and the least recent dates back to 2007. The observation dates are distributed practically throughout the year. Of the 36 records of *Chelidura pyrenaica*, more than half of the total were made in France (24), Spain (11), and Andorra (1), therefore all from the Pyrenees. *Chelidura aptera* has 3 records, all from Italy, not far from the type locality of the neotype. *Chelidura arverna* has 6 records, all from France (Massif Central). Some records from the Western Alps attributed to *C. aptera* are presumably partly attributable to *Chelidura alpina* (3 records from France) and partly to *C. montana* (2 from Switzerland and 1 from Italy). For some records from the Western Alps and attributed to *C. aptera*, 6 from Italy and 3 from France, it is not possible at present to attribute them to one of the *Chelidura* species clearly defined to date. Until a few years ago, the records for the genus *Chelidura* were very limited and, above all, there was a certain amount of confusion in the identification. It is evident that the recent articles published on the genus *Chelidura* (Fontana et al. 2021 and Jurado-Angulo et al. 2021) have contributed significantly to a better knowledge and that naturalists who access iNaturalist keep up to date through scientific literature. The data present on iNaturalist, always regarding the area considered in this article, all fall within the known distribution of the genus *Chelidura* and do not highlight unexpected populations.

Morphology and measurements

Male genitalia of dry-mounted and alcohol-stored specimens were prepared according to the methods of Fontana et al. (2002): the genitalia were removed, cleared by immersion in 10% KOH solution at room temperature for 20 minutes, dehydrated by passages in alcohols of increasing concentration and in xylene, and finally mounted in Canadian balsam on a microscope slide or a transparent holder. The specimens and the male genitalia were measured (Fig. 1 and Suppl. material 1: table S1) with a micrometric lens (Meopta H 8xm 10) via a stereomicroscope (Optech). The nomenclatural and morphological terminology follow those used by Steinmann (1993) for general morphology, and by Kamimura (2014) for the male terminalia and genitalia.

Morphological measurements of adult males were taken according to the scheme shown in Fig. 1: **A**) Total length without cerci; **B**) Total length with cerci; **C**) Hind femur length; **D**) Hind femur width; **E**) Intraocular distance; **F**) Maximum head width; **G**) Maximum pronotum width; **H**) Maximum pronotum length; **I**) First antennomere length; **J**) Third antennomere length; **K**) Ultimate tergite width; **L**) Pygidium width; **M**) Cerci basal width; **N**) Cerci inner total length; **O**) Cerci outer total length; **P**) Cerci diagonal length; **Q**) Cerci maximum curvature; **R**) Cerci width at maximum curvature; **S**) Parameter length; **T**) Parameter maximum width; **U**) Virga total length; **V**) Seminal vesicle maximum length.

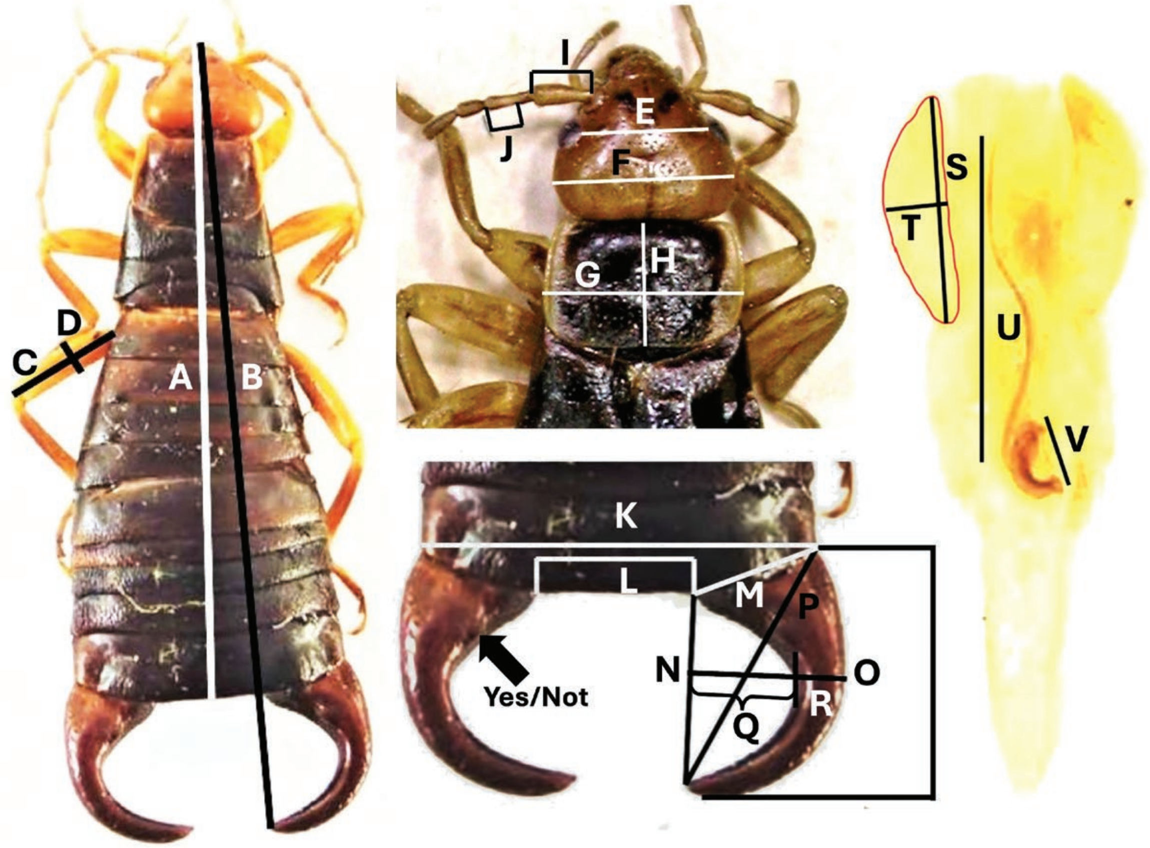

Figure 1. Explanatory plate resuming of the measurements made on the *Chelidura* specimens.

Morphometric analyses were conducted using the R software (RStudio Team, 202x). As an initial step, a Principal Component Analysis (PCA) was performed using the 'prcomp' function from the *stats* R core package, to identify the main variables contributing to the variance among specimens. Given the challenges in collecting linear measurements unaffected by the preservation state and desiccation of the specimens, we opted to use also ratios of the most sclerotized body parts. This approach allowed us to obtain values not influenced by relative size differences. Autocorrelation among both linear and ratio measurements was assessed using Pearson's correlation coefficient, with values above 0.7 considered indicative of strong correlation. Based on this initial exploratory analysis, we opted to use ratios over linear measurements, as they proved to be fully informative and not mutually correlated.

A linear discriminant analysis (LDA) was performed using the MASS (Venables and Ripley 2002) and caret (Kuhn 2008) packages to identify linear combinations of variables that best discriminate among predefined classes. To ensure the robustness and generalizability of the model, a 10-fold cross-validation approach was applied. In this procedure, the dataset is divided into 10 equal parts (folds); in each iteration, nine folds are used for training and one for validation, with the process repeated 10 times so that each subset serves once as the test set. The *ggplot2* package (Wickham 2016) was used to generate scatterplots of the PCA and LDA results.

DNA barcoding and phylogenetic analyses

The six legs of each specimen used in the molecular analyses were removed and used for DNA extraction. After lyophilization, total DNA was isolated via a commercial kit (NucleoSpin® Tissue; Macherey-Nagel, Düren, Germany). The cytochrome oxidase subunit I (COI) gene was amplified with the primer pair LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al. 1994). The polymerase chain reaction (PCR) conditions used were previously reported (EPPO, 2021). After purification with the Illustra ExoProStar1-Step kit (GE Healthcare, Little Chalfont, UK), PCR products were sequenced with the Big Dye Terminator v3.1 cycle sequencing kit (Applied Biosystems, Foster City, CA, USA) on an Applied Biosystems 3130 xl Genetic Analyser (Carlsbad, CA, USA). The sequences were manually checked via BIOEDIT (Hall 1999).

COI sequences belonging to *Chelidura* species were retrieved from GenBank and BOLD System (Ratnasingham and Hebert 2007) and cross-checked against the related literature. Newly produced sequences were deposited in GenBank with the accession numbers OR922626–OR922644. The species *Chelidurella acanthopygia* (Gené, 1832) (seq. id: MH571978.1), *Chelidurella thaleri* Harz, 1980 (MH571979.1), and *Forficula auricularia* Linnaeus, 1758 (MT072843.1 were selected as the outgroup).

Maximum likelihood (ML) and Bayesian Inference (BI) were performed via IQTree (Minh et al. 2020) and BEAST2 (version 2.7.4; Bouckaert et al. 2019), whereas Maximum Parsimony (MP) analysis was run via MEGA 11 (Tamura et al. 2021). The pairwise genetic distances between sequences were calculated via MEGA 11 under default settings.

Results and discussion

The genus *Chelidura* Latreille, 1825

A recent paper by Kirstová et al. (2021) established the separation between *Chelidura* Latreille, 1825, and *Chelidurella* Verhoeff, 1902, which in the past had been considered a single genus (*Chelidura*) by several authors (e.g., Steinmann 1989; Steinmann 1993, Sakai and Liu 1995). The species of the genus *Chelidura sensu* Kirstová et al. (2021) are distributed throughout Europe and Palaearctic Asia and are characterized by a generally large and broad body, rudimentary tegmina with a short, medially overlapping section, and a lack of wings. The abdomen is more or less dilated from base to apex, and male forceps are stout, remote at the base, arcuate and without conspicuous denticulations. The pygidium is flat, rounded, and not protruding.

In recent years, the following 18 species have been assigned to the genus *Chelidura*:

Chelidura aptera (von Charpentier, 1825); terra typica: Europe
Chelidura arverna David & Van Herrewege, 1973; terra typica: France
Chelidura carpathica Steinmann & Kis, 1990 in Steinmann, 1990; terra typica: Romania
Chelidura dalijiashana Chen, 2025; terra typica: China: Gansu
Chelidura euxina (Semenov, 1907); terra typica: Russia
Chelidura farkaci Kočárek, 2004; terra typica: Tibet
Chelidura gansuensis Chen, 2024; terra typica: China: Gansu
Chelidura nuristanica Steinmann, 1977; terra typica: Afghanistan
Chelidura pyrenaica (Gené, 1832); terra typica: Pyrenees
Chelidura przewalskii (Semenov, 1908); terra typica: Tibet
Chelidura redux (Semenov, 1908); terra typica: China: Gansu
Chelidura russica Steinmann, 1977; terra typica: Caucassus
Chelidura semenovi Bey-Bienko, 1934; terra typica: China: Szechwan
Chelidura siguniangshana Chen, 2024; terra typica: China: Sichuan
Chelidura specifica Steinmann, 1989; terra typica: Caucassus

Chelidura thoracica Fischer von Waldheim, 1846; terra typica: Finland (nomen dubium)
Chelidura tibetana (Semenov & Bey-Bienko, 1935); terra typica: Tibet
Chelidura transsilvanica Ebner, 1932; terra typica: Romania

On the basis of molecular and morphometric data and biogeographical considerations, at least 5 species of the *Chelidura* genus are currently identifiable in the Alps: *C. aptera* in the Biella Alps, *C. montana* from western Switzerland and Val d'Aosta (Italy), *C. alpina* in France (Savoy) and two new species described below, both from Italy; one from the Rhaetian Alps (Italy, Lombardy) and one from the Cottian Alps (Italy, Piedmont).

Nomenclature considerations

According to Fontana et al. (2021), the genus *Chelidura* was named by the French entomologist Pierre André Latreille (1762–1833) in Toussaint von Charpentier (1779–1847) [and not Johann Carl Megerle von Mühlfeld (1765–1842)] and von Charpentier is recognized as the original author of *Chelidura aptera*, type species of the genus. In fact, the note that appears under the title *'Forficula aptera*', '(Meg. De Muehlfeld.)' simply indicates the origin of the material received in the study and not the authorship. This interpretation is confirmed by the introduction notes wrote by von Charpentier himself (von Charpentier, 1825): *Gratias permagnas debeo clarissimo Megerle de Muehlfeld… qui sui muesi copiam Orthopterorum omnem ad me transmisit, eamque exploranda per plures menses concessit* (My sincere thanks to the illustrious Megerle de Muehlfeld... who sent me the entire collection of Orthoptera from his museum and allowed it to be examined for several months).

On the other hand, it is more difficult to interpret and adopt the nomenclature to be used for species attributable to Franco Andrea Bonelli and Carlo Giuseppe Gené in some way. In fact, Gené (1832) wrote that his publication corresponds to a monograph by Bonelli which remained unpublished due to his premature death in 1830. Gené, however, clearly writes that the descriptions are in his own hand and that, instead, the indications of locality and habitat derive mainly from Bonelli's autograph notes present in the General Catalogue of the Collections of the Zoological Museum of the University of Turin (still preserved today at the Regional Museum of Natural Sciences of Turin - MRSNT). In this catalogue, Bonelli listed the specimens with a number corresponding to the labels inserted on the pins with the insects (Fontana 1999). Many of these insects catalogued by Bonelli are still preserved to this day, and among these, some specimens with any doubt are identifiable as *Chelidura*. Bonelli also named these species *Forficula longicauda*, *F. alpina* (in Bonelli's handwritten notes this species was initially called *F. lunata*, a name that Bonelli himself later cancelled in his manuscript, replacing it with *F. alpina*), and *F. pyrenaica* (also for this species in the manuscript notes the first name written was "*F. crassicauda"*, later cancelled in his manuscript by Bonelli himself and replaced with *F. pyrenaica*). Describing these species, Gené attributed the paternity of two of the three species treated in his paper to Bonelli, referring to them as "*F. alpina* Bon." and "*F. pyrenaica* Bon." where "Bon." stands for Bonelli. The third species (*F. montana* in Borelli's notes) instead becomes "*F. montana* Nob." where "Nob." stands for *nobis* meaning "ours". Therefore, according to article 50.1 of the International Code of Zoological Nomenclature (ICZN 1999), the three species mentioned must be attributed to Gené (Gené 1832). In fact, despite Gené did not used his own original names except for one, and referred to Bonelli's handwritten notes, he is the first providing a description of the species.

A fourth species was described by Gené in 1932, "*Forficula paupercula* Nob."; however, the type specimen of this taxon is most plausibly lost (Fontana 1999). This species was historically attributed by most authors to the genera *Chelidura* or *Pseudochelidura*. Dubrony (1878) considered *F. paupercula* as a synonym of *Forficula sinuata* Germar, 1825 (now *Pseudochelidura sinuata*), whereas Burr (1913) hypothesized that the species could be an immature specimen. In 1976, Harz and Kaltenbach (Harz and Kaltenbach 1976) treated *F. paupercula* simultaneously in two distinct taxonomic assignments in their list, one as a synonym of *C. aptera* and one as *Pseudochelidura paupercula*, but did not include this species in the identification keys. Recently, Kirstová et al. (2020) treated *F. paupercula* as synonym of *Chelidurella mutica* (Krauss, 1886), quoting *Chelidura paupercula* Heller & Dalla Torre, 1882. Since it is impossible to attribute a proper identity to *Forficula paupercula* Gené, 1832, the name is here considered *nomen dubium*.

The nomenclature adopted, based on the literature and the results and considerations presented in this study, for the Western European species certainly belonging to *Chelidura* known to date is therefore the following:

Chelidura aptera (von Charpentier, 1825)
Chelidura montana (Gené, 1832), stat. nov.
Chelidura alpina (Gené, 1832), stat. nov.
Chelidura pyrenaica (Gené, 1832)
Chelidura arverna David & Van Herrewege, 1973

Molecular phylogeny

The phylogenetic analyses produced the same topology across the three methods of reconstruction (ML, MP and BI), with high node support values. The phylogenetic reconstruction (Fig. 2) revealed three clearly distinct clades with strongly supported topologies (bootstrap values > 0.70) among the sequences obtained from the western Alpine *Chelidura*, confirming the existence of three different taxa. Interestingly, two geographically well

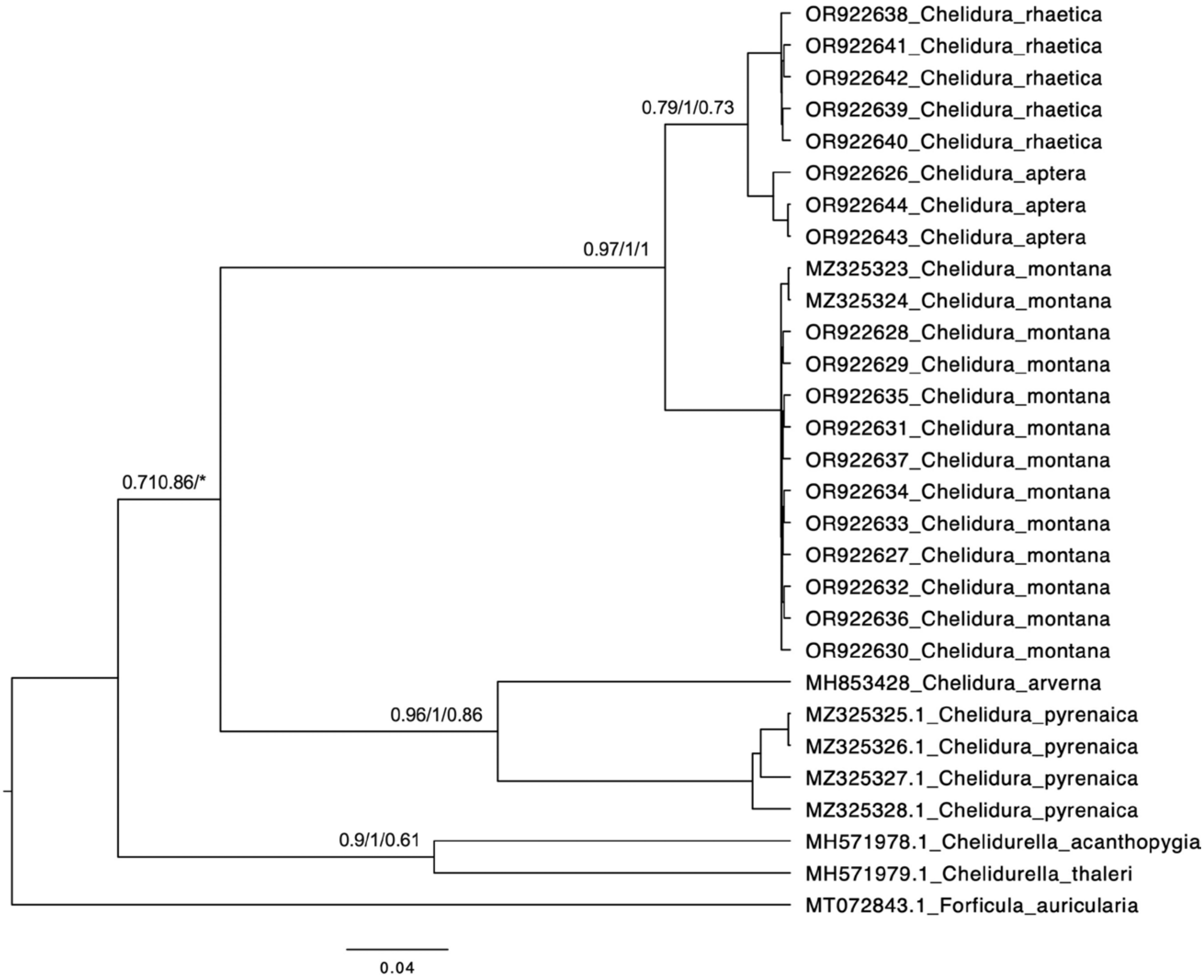

Figure 2. Phylogenetic tree inferred by Maximum Likelihood (ML), Bayesian inference (BI) and Maximum parsimony (MP) analyses of the cytochrome c oxidase subunit I (COI) gene fragment of the genus *Chelidura*. The topology shows the best ML tree with Bootstrap probabilities from the ML (left), Posterior probabilities from BI (center) and Bootstrap values from the MP (right). Asterisks indicate bootstrap probabilities lower than 50% and posterior probabilities lower than 95%.

separated taxa, *Chelidura rhaetica* sp. nov. and *C. aptera*, presented relatively low genetic distances (d = 7.9%) compared with the spatially closely related *C. aptera* and *C. montana* (d = 24%). In addition, the phylogenetic reconstruction revealed that the specimens previously identified as *C. aptera* by Jurado-Angulo et al. (2021) (MZ325323– MZ325323) belong to *C. montana*.

Morphological variability and morphometric analysis

In Dermaptera, intraspecific variability in the shape and size of male cerci is a widespread phenomenon. Forms with highly developed cerci are referred to as macrolabic, while those with small cerci are termed cyclolabic or brachylabic (Fontana et al. 2021). Between these two extremes, many intermediate forms, known as mesolabic, are commonly observed.

The genus *Chelidura* also exhibits substantial variability in male cercal morphology. However, this variability has contributed to taxonomic confusion among species from the Alps, the Pyrenees, and the Massif Central. Males of the macrolabic form (with strongly developed cerci) often exhibit similar cercal shapes across different species. For instance, macrolabic males of *C. pyrenaica* can be easily confused with those of *C. arverna*, whereas the cyclolabic forms of these same species display clearly distinct, reduced cerci. Despite their morphological similarity in the macrolabic form, *C. pyrenaica* and *C. arverna* are genetically distinct based on molecular analyses (Jurado-Angulo et al. 2021). Notably, the male genitalia of both species are highly similar—a trait that nonetheless allows their separation from Alpine species of the genus (Fontana et al. 2021).

Examination of Alpine *Chelidura* material reveals some specific patterns in cercal morphology. In several species, *C. aptera*, *C. alpina* stat. nov., and *C. osellarum* sp. nov., a true macrolabic form has not been confirmed to date. Conversely, in species *C. montana* stat. nov. and *C. rhaetica* sp. nov., a well-defined cyclolabic form characterized by strongly curved cerci (Fig. 3), appear to be absent. This pattern is particularly evident in *C. osellarum*, as none of the 33 males collected over several years from Val Maira (Piedmont, Italy, Cottian Alps) showed traits assignable to the macrolabic form. This observation is further supported by two additional males from Colle Sampéire (also in the Cottian Alps), which have been assigned to the same new species. Finally, the coexistence of multiple *Chelidura* species within the Alps suggests the possible presence of more than one species in certain localities. This scenario appears to be supported by a few specimens from a site located in an area where the species composition of the *Chelidura* population remains unresolved.

Preliminary PCA analyses (results not shown) were used to identify the most informative predictors. Accordingly, both the final PCA and the LDA included the following variables: total length ratio (B/A), femoral ratio (C/D), first-to-third antennomere ratio (I/J), and paramere ratio (S/T).

PCA of the morphometric data revealed a well-defined structure of morphological variation, indicating that specific measurements have a greater influence on the overall variance. The first three principal components (PC1, PC2, and PC3) account for a cumulative 91.4% of the total variance (Suppl. material 1: table S2). This suggests that the three principal components sufficiently capture the majority of morphological variation among the species. The LDA model reached an overall accuracy of 68.8% in distinguishing among the four species. The Kappa statistic was 0.5556, indicating moderate agreement between the predicted and observed species classifications. This suggests that the LDA model performs reasonably well in distinguishing among the different *Chelidura* species based on the selected morphological parameters (Fig. 4). The prior probabilities assigned to each group reflect the species distribution in the training dataset (Suppl. material 1: table S3). *Chelidura osellarum* was the most represented species (43.6%), followed by *C. montana* and *C. rhaetica*, each accounting for 25.0% of the sample.

As shown in Suppl. material 1: table S4, the coefficients of the linear discriminants reflect the extent to which each morphological trait contributes to the separation of species within the LDA model. The linear discriminant analysis showed that B/A ratio was the most influential variable for both LD1 and LD2, whereas I/J had the strongest contribution to LD3, highlighting the importance of these morphological traits in distinguishing species along the corresponding discriminant functions (Suppl. material 1: table S4).

The confusion matrix (Suppl. material 1: table S5) provides an overview of the performance of the LDA model in predicting *Chelidura* species based on morphological parameters (Fig. 4). LDA correctly identified 100% of the specimens morphologically classified as *C. montana* (4 of 4) and *C. rhaetica* (3 of 4), and correctly classified a substantial proportion of *C. osellarum* specimens (4 of 7). This suggests that the morphological traits of *C. montana*, *C. rhaetica*, and *C. osellarum* are distinctive enough to recognize each as separate taxa from the other species included in this analysis. The uncertain classification of *C. aptera* is likely due to the fact that only a single specimen was measured. *Chelidura montana* demonstrated perfect classification accuracy (100%), followed by *C. rhaetica* (83.3%) and *C. osellarum* (67.5%). In contrast, *C. aptera* showed a considerably lower accuracy of 43.4%, likely due to the previously mentioned reason.

Taxonomy

Family Forficulidae Latreille, 1810
Subfamily Anechurinae Verhoeff, 1902
Genus *Chelidura* Latreille, 1825

Chelidura aptera (von Charpentier, 1825)

Figs 3, 5, 6

Note. Detailed redescription of *Chelidura aptera* as well as the designation of its neotype and of its *locus typicus restricus* have been recently published (Fontana 1999 and Fontana et al. 2021); therefore, providing the same identical information is considered superfluous.

Diagnosis. *Chelidura aptera* is characterized by a robust body, a very dark overall colouration, lighter legs, and a reddish head. A notable feature is the pronounced dilation of the posterior part of the body, with the ratio between head length and the width of the last tergite averaging 0.47. The cerci are strongly curved inward, with a broad base positioned on the inner side of the dorsal surface, and bear a well-developed tooth. Regarding the male genitalia, the parameres exhibit the greatest maximum width relative to their length among all known *Chelidura* species.

Examined material. Italy, Piedmont (Biella), M. Mucrone, 30.VIII.1971, leg. Pace R., 1 male (Neotype) and 1 female, FMCR; Italy, Piedmont (Biella), Alpi Pennine, Lago Mucrone, 1902 m, VII.1911, leg. Burlini, 1 male, FMCR; Italy, Piedmont (Biella), Monte Mucrone, Lago Mucrone, 1903 m, 24.IX.2003, leg. Fontana P., Buzzetti F. M. and Tirello P., 1 male and 1 female, FMCR; Italy, Piedmont (Novara), Mottarone, 20.V.1995, leg. G. Osella, 1 male, FMCF.

Distribution. Mount Mucrone (Biellese Alps, Italy) is the *locus typicus restrictus* of *Chelidura aptera* and the collection site of the neotype recently designated for the species (Fontana et al. 2021). This mountain, which reaches an elevation of 2,335 m, is located in the southern portion of the Pennine Alps and is also referred to as the Biella Alps (formerly known as the Biella Prealps). A male specimen from Mount Mottarone has also been assigned

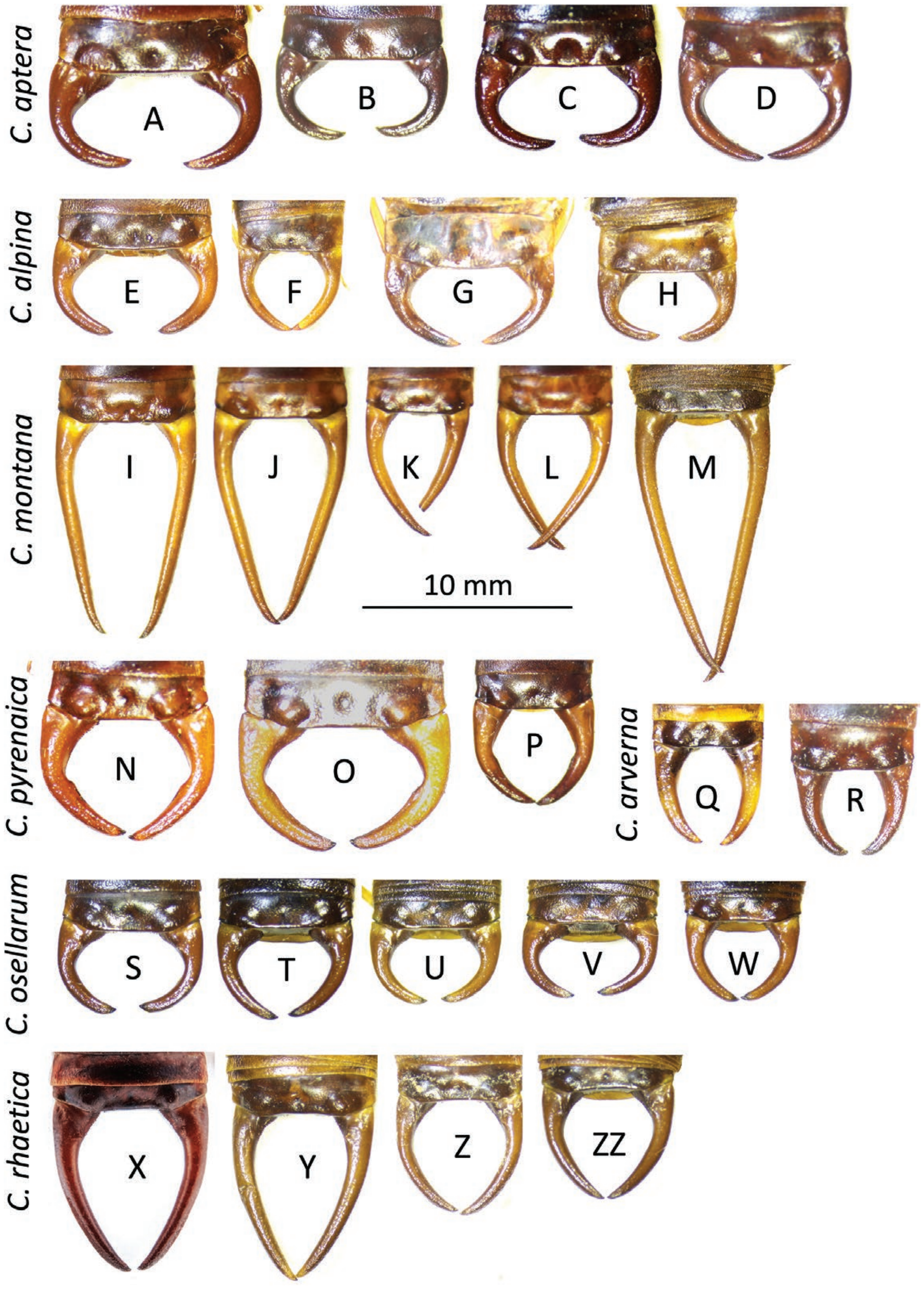

Figure 3. Variability in male terminalia of the species of the genus *Chelidura* Latreille, 1825 distributed in the Western Europe, including the species here reconsidered valid and the two new species described below. **A–C.** *Chelidura aptera* (von Charpentier, 1825) from Monte Mucrone (n° 1 is the Neotype) and Lago Mucrone (Italy, Piedmont, Pennine Alps); **D.** *C. aptera* (von Charpentier, 1825) from Mottarone (Italy, Piedmont, Pennine Alps); **E–H.** *C. alpina* (Gené, 1832), stat. nov., from Val-d'Isère (France, Savoie); **I–L.** *C. montana* (Gené, 1832), stat. nov. from Colle Grand San Bernardo (Switzerland, Valais); **M.** *C. montana* (Gené, 1832), stat. nov. from Gressoney-La-Trinité (Italy, Valle d'Aosta, Mount Rosa); **N–P.** *C. pyrenaica* (Gené, 1832), cyclolabic form, from Pyrénées-Orientales (France); **Q–R.** *C. arverna* David & Van Herrewege, 1973, cyclolabic form, from Chalmazel (France, Loire) and Satilleu (France, Ardeche); **S–V.** *C. osellarum* sp. nov. from Val Maira (Italy, Piedmont, Alpi Cozie); **W.** *C. osellarum* sp. nov. from Colle Sampéire (Italy, Piedmont, Alpi Cozie); **X–ZZ.** *Chelidura rhaetica* sp. nov. from Lanzada (Italy, Lombardy, Western Rhaetian Alps).

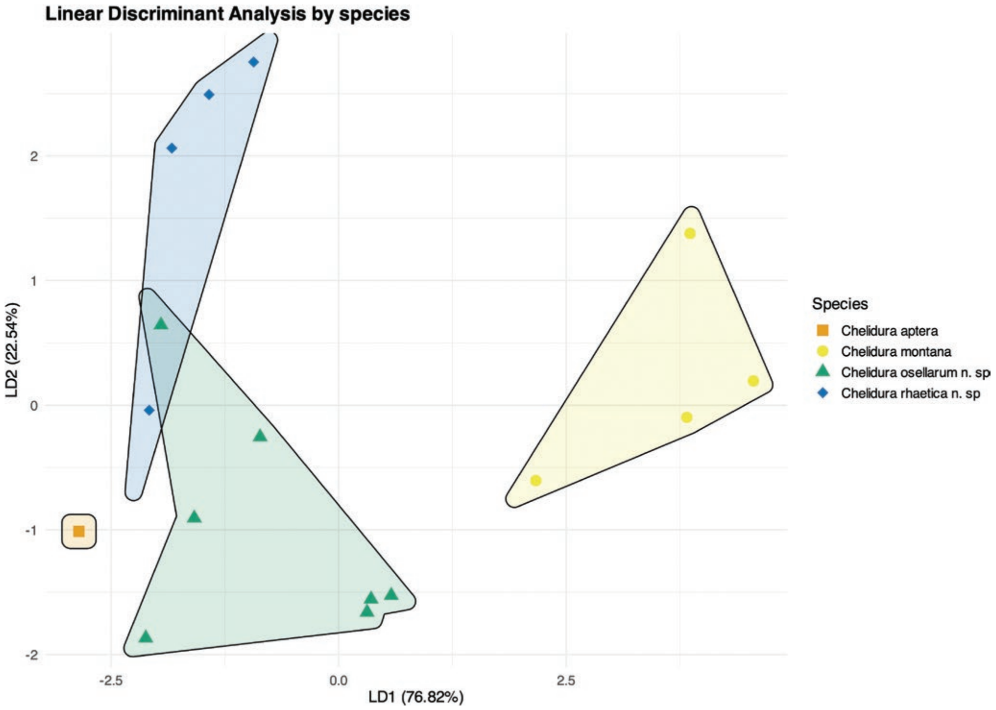

Figure 4. Linear Discriminant Analysis (LDA) plot illustrating the separation of *Chelidura* species based on selected morphological variables. Each point represents an individual specimen, colour-coded by species. The plot shows how the linear discriminant functions differentiate specimens according to species groups, highlighting the degree of overlap and separation among them.

to this species, as it shares all diagnostic characteristics with the neotype material. Mottarone is a mountainous ridge situated on the border between Piedmont and Lombardy, rising to 1,492 m a.s.l., and separates Lake Maggiore from Lake Orta. Mounts Mucrone and Mottarone lie near opposite ends of a chain of peaks, many of which exceed 2,000 m, extending diagonally from southwest to northeast along the edge of the Po Valley, defining this section of the southern Alps.

Chelidura alpina (Gené, 1832), stat. nov.

Figs 3, 5, 6

Note. The Type material, the original description as well as the redescription, was provided by Fontana (1999). The type locality is not in Italy, as suggested by Fontana (1999), but in France. The locality reported by Bonelli in the general catalogue of the Zoological Museum of the University of Turin and now at the MRSNT and published later by Gené (1832) is "*Moncenisio, tra la Croce e l'Ospizio, dal lato che guarda settentrione"* (Mont-Cenis, between the Cross and the hospice, facing north). The Hospice du Mont-Cenis is a religious establishment located at the Col du Mont-Cenis, which has now disappeared. It was built on February 14, 825 AD, by Lothair I (795–855), the king of Lotharingia and Carolingian emperor from 840, near the banks of Lake Mont-Cenis. With the construction of the hydroelectric dam in 1970, the lake level increased considerably, causing the building to disappear underwater. The cross referred to by Bonelli and later by Gené is certainly the Gran Croce (in French Grand Croix), a hamlet of Val-Cenis in the French Val Cenischia at the foot of Mount Lamet and not far from Lake Moncenis, the Moncenis Pass and the border with Italy. Until 1947, it was a hamlet of the village of Moncenisio in the province of Turin (Italy), but following the Treaty of Paris in 1947, it was annexed to France despite being on the southern side of the Alps; the hamlet was abandoned following the construction of the new dam on Lake Moncenisio in 1968 and became definitively uninhabited in 1986. The typical locality of *F. alpina* is therefore between two localities today in French territory and lies under Lake Mont Cenis. On the basis of Fontana's (1999) description of the Lectotype of *F. alpina*, as well as its geographical proximity, the examined specimens from Val-d'Isère (Savoie, France) can be assigned to *C. alpina*.

The specimens considered here were *C. alpina* (Gené, 1832), stat. nov. are similar in general structure and, above all, concerning the cerci and the last abdominal segment, to *Chelidura aptera*, as defined by Fontana et al. (2021). The smaller size and less dark colour, as well as geographical isolation, are, however, elements that today suggest maintaining the identity of the *Chelidura* from the Savoy. Only more in-depth studies on an adequate number of samples from different localities will be able to establish the real relationships between *C. alpina* and other Alpine species and populations of the genus.

Diagnosis. *Chelidura alpina* is characterized by its very small size, brown body colouration, lighter legs, and a reddish head. Similar to *C. aptera*, it exhibits a pronounced

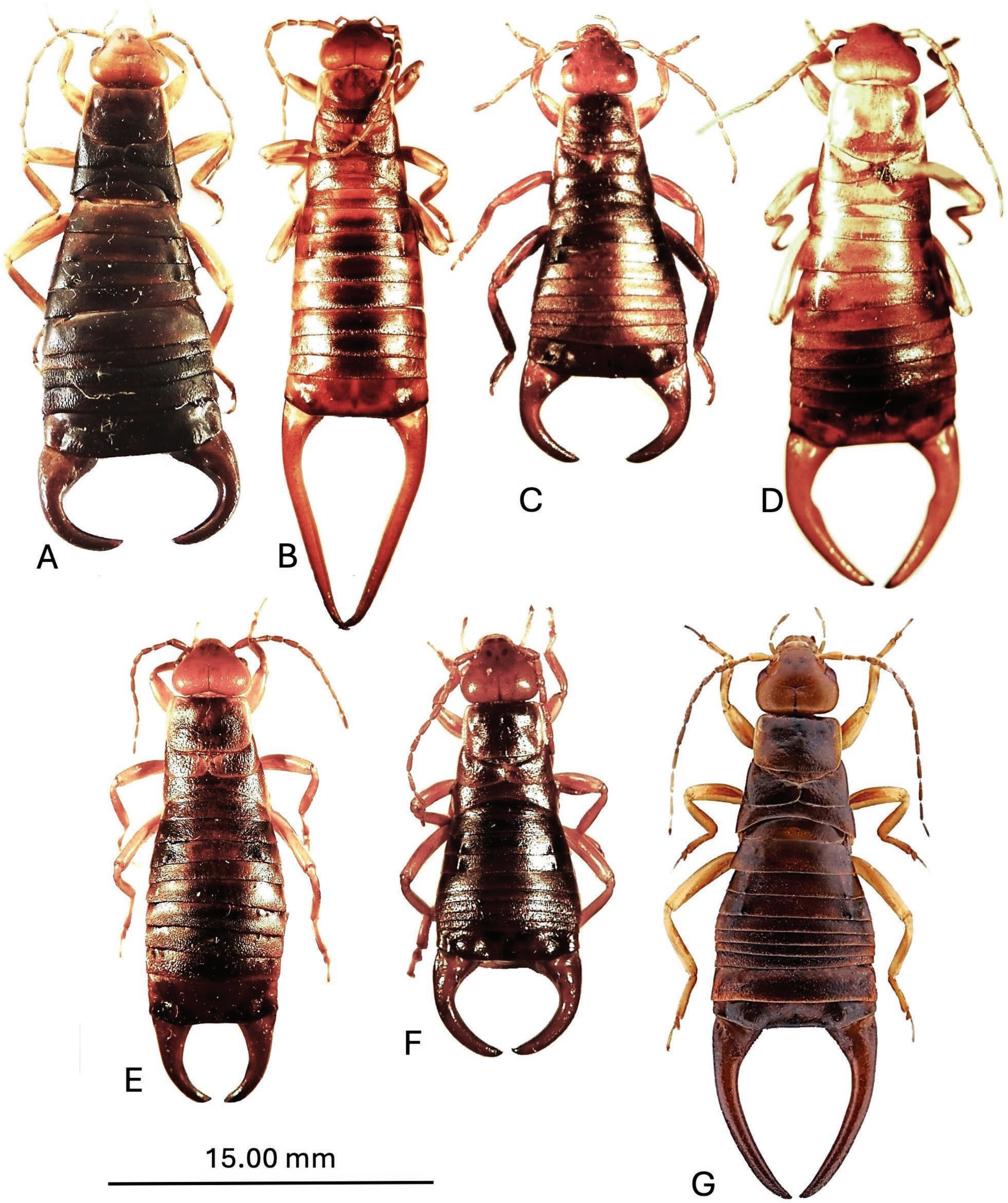

Figure 5. Males of the species of the genus *Chelidura* Latreille, 1825 known for the Western Europe, including the species here reconsidered valid and the two new species described below. **A.** *Chelidura aptera* (von Charpentier, 1825); **B.** *Chelidura alpina* (Gené, 1832), stat. nov.; **C.** *Chelidura montana* (Gené, 1832), stat. nov.; **D.** *Chelidura pyrenaica* (Gené, 1832), cyclolabic form; **E.** *Chelidura arverna* David & Van Herrewege, 1973, cyclolabic form; **F.** *Chelidura osellarum* sp. nov. and **G.** *Chelidura rhaetica*. sp. nov.

dilation of the posterior part of the body, with the ratio between the maximum head length and the width of the last tergite averaging 0.50. The cerci are strongly curved inward, with a very broad base positioned on the inner side of the dorsal surface, forming a small tubercle. The male genitalia are the smallest recorded among all known *Chelidura* species, with parameres that are semilunar in shape and relatively broad in proportion to their length.

Examined material. Lectotype (male) of *Forficula alpina* Gené, 1832 (Fontana 1999): round label with number 1886, corresponding to "Moncenisio, tra la Croce e l'Ospizio, dal lato che guarda settentrione" (= France, Mont-Cenis, between the Cross and the hospice, on the side facing north); MRSNT.

Additional material. France, Savoie, Val-d'Isère, 2000 m, 1960, 4 males and 2 females, leg. Amiet, FMCR; France, Savoie, Val-d'Isère, VIII-1955, 1960, 1 male, leg. J. Briel, FMCR.

Distribution. *Chelidura alpina* is currently known only from Savoie (France), based on the limited material available to date. However, its presence in adjacent areas of Italy cannot be excluded.

Chelidura montana (Gené, 1832), stat. nov.

Figs 3, 5, 6

Note. The type material and the species redescription were presented by Fontana (1999). The identity of this species and its distinct species both from *C. aptera* and from the population of the Rhaetian Alps have already been highlighted by Fontana et al. (2021). The samples from the Italian side of the Colle Grand San Bernardo as well as those from the Monte Rosa group reported among the examined materials are also assigned to this species. Gené also assigned this species to samples collected by Mr. Zumstein on Monte Rosa (Gené 1832).

Diagnosis. *Chelidura montana* is characterized by a very elongated body, a light brown colouration with legs and a head that is not markedly lighter than the rest of the body. It is characterized by scarce dilation of the posterior part of the body, with a ratio between the maximum length of the head and the width of the last tergite having an average value of 0.56. The cerci are long, gently curved inwards and without tubercles on the dorsal surface of their base. The male genitalia are characterized by parameters that are semilunar in shape, with a reduced width compared with their length.

Examined material. Switzerland, Valais, Colle Grand San Bernardo, Liddes, 2160 m, (45°53'11,24"N, 7°11'24,35"E), 18.IX.2019, Fontana P. and Marangoni F. leg., 3 males and 2 females, FMCR; Switzerland, Valais, Colle Grand San Bernardo, Liddes, 2160 m, (45°53'11,24"N, 7°11'24,35"E), 25.IX.2021, Fontana P. and Vivian C. leg., 2 males, FMCR; Switzerland mer., Valais, SAAS FEE Gletschergrotte, 2000 m, 05.VIII.2006, M. Fikáček, 1 male, FMCR; Italy Val d'Aosta, Gran San Bernardo, 1900 m, 5.VII.1979, leg. Rocchi S., 1 male, FMCR; Italy Valle d'Aosta, Gran San Bernardo, 1900 m, 5.VII.1979, leg. Rocchi S., 1 male, FMCR; Italy, Valle d'Aosta, M. Rosa, Gressoney-La-Trinité (Aosta), VII.1935, 4 males and 1 female, leg. C. Alzona, FMCR; Italy, Piedmont, M. Rosa, Macugnaga (Verbano-Cusio-Ossola), 20.VIII.1958, 2 males, FMCR; Italy, Valle d'Aosta, Val Veny, Monte Bianco, 2000 m, 18.VIII.1967, 1 female, leg. M. la Greca, FMCR.

In addition to the material here considered, all the specimens treated as *C. montana* by Jurado-Angulo et al. (2021), coming from Valle d'Aosta (Italy), Val Veny, Pré de Pascal [Courmayeur] (45°48'20.2"N, 6°56'35.5"E), 28.VI.2012, lrg. M. García-París, G. García-Martín (MNCN_Ent 269452–269458, 296011–296012), need to be considered as such. Consequently, the female from Val Veny and stored at FMCR is assigned to *C. montana*.

Community science data: Switzerland, Valais, La Fouly, Camping des Glaciers, 1640 m, (45.93458, 7.090132), 26.VIII.2023, Patrick Favre observ., 1 male documented by photo (GBIF.org 2023).

Distribution. *Chelidura montana* is known from various localities between southern Switzerland and north-western Italy. Its presence also appears probable in the bordering areas of France.

Chelidura pyrenaica (Gené, 1832)

Figs 3, 5, 6

Note. The type material, the original description and the redescription are given in Fontana (1999). A detailed and exhaustive discussion of this species, particularly regarding the Spanish populations, has been published by Jurado-Angulo et al. (2021).

Diagnosis. *Chelidura pyrenaica* is a large-sized species among Western European species and is characterized by a clear dilation of the male terminalia. It has a uniform buff colour with legs and head of a colour that is slightly different from the rest of the dry samples. The main characteristics of this species are the dilation on the internal side of the male cerci of the cyclolabic form and the parameres of the male genitalia, which are very elongated and have parallel sides and are not semilunar, as in other Western European species known to date, with the only exception being C. arverna, which has parameters almost identical to those of *C. pyrenaica*. For *C. pyrenaica*, the macrolabic form of the male cerci is known. In these cases, the specimens are very similar to individuals of the macrolabic form of *C. arverna* and, in part, of *C. montana*.

Examined material. Lectotype (male) and Paralectotype (female) of *Forficula pyrenaica* Gené, 1832 (Fontana, 1999): round labels with numbers 2363 (Lectotype) and 2364 (Paralectotype), corresponding to "Trovata sui Pirenei dal Sig. Moncarel, ed avuta nel 1813 dal signor Dupare di Parigi" (= Pyrenees, leg. Moncarel), MRSNT.

Additional material. France, Source des Tech, Pyr. Orient. (vallée superior du Tech), VII-VIII.1904, 1 male, Borelli A. leg., 1 male, FMCR; France, Pyrénées-Orientales, Roussillon, Foret de Marcaille, Canigou, 1600 m, 1.X.195, Barthes leg., 1 male, FMCR; France, Pyrénées-Orientales, Roussillon, La Llagone, Route des Bouillouses, Niveau centrale electr., Sous pierre en foret, 1700 m, 11.IV.1988, Hamon J. leg., FMCR; France, Pyrénées-Orientales, Roussillon, Canigou, IV.1939,

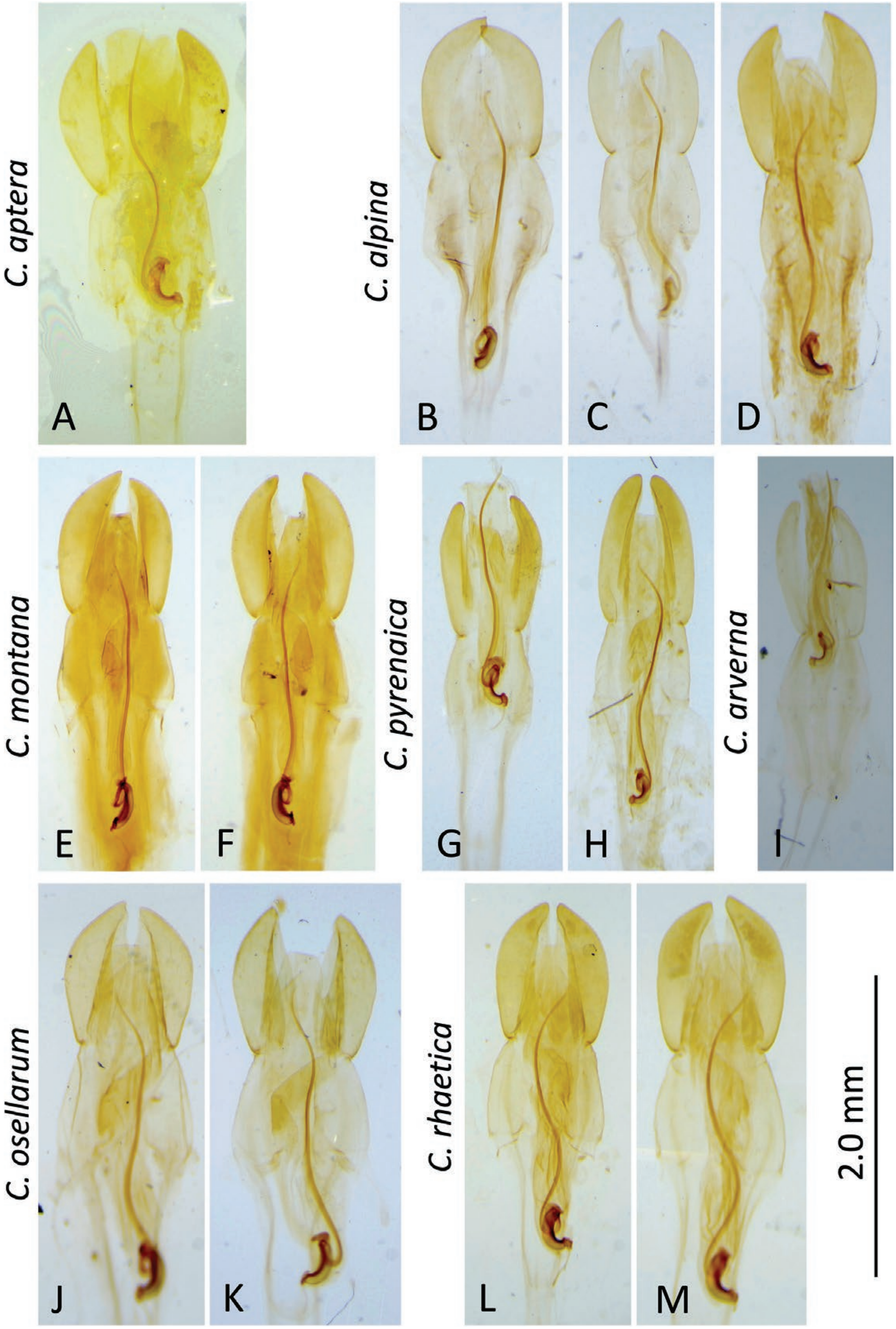

Figure 6. Male genitalia of the species of the genus *Chelidura* Latreille, 1825, known for western Europe, including the species here reconsidered valid and the two new species described below. **A.** *Chelidura aptera* (von Charpentier, 1825) Neotype from Monte Mucrone (Italy, Piedmont, Pennine Alps); **B–D.** *C. alpina* (Gené, 1832), stat. nov., from Val-d'Isère (France, Savoie); **E–F.** *C. montana* (Gené, 1832), stat. nov. from Colle Grand San Bernardo (Switzerland, Valais); **G–H.** *C. pyrenaica* (Gené, 1832), from Pyrénées-Orientales (France); **I.** *C. arverna* David & Van Herrewege, 1973, cyclolabic form, from Chalmazel (France, Loire); **J.** *C. osellarum* sp. nov. (holotype) from Val Maira (Italy, Piedmont, Alpi Cozie); **K.** *C. osellarum* sp. nov. (paratype) from Colle Sampéire (Italy, Piedmont, Alpi Cozie); **L, M.** *Chelidura rhaetica* sp. nov. (paratypes) from Lanzada (Italy, Lombardy, Western Rhaetian Alps).

Bolivar I. leg., 1 male, FMCR; France, Hautes-Pyrénées, Seincourt, 2300 m. IX.1933, Reymond leg., 1 male, FMCR; France, Pyrénées-Orientales, Roussillon, Ariege, cirque d'Anglade, Coiffart leg., 2 males, FMCR.

Distribution. *Chelidura pyrenaica* is known only from the Pyrenees (France, Spain, and Andorra) and quite homogenous populations from both morphological and genetic features (Jurado-Angulo et al. 2021).

Chelidura arverna David & Van Herrewege, 1973

Figs 3, 5, 6

Note. *Chelidura arverna* was described as a subspecies of *C. pyrenaica* (David & Van Herrewege, 1973), and it has only recently been elevated to species (Jurado-Angulo et al. 2021). Interestingly, this taxon is phylogenetically closely related to the Pyrenean species than to the *Chelidura* of the Alps.

Diagnosis. *Chelidura arverna* is a medium-sized species among Western European species and is characterized by a moderate dilation of the male terminalia, especially in cyclolabic males. It has a dark brown body, lighter legs and reddish-brown head. The male cerci in the macrolabic form are very similar to those of *C. pyrenaica*, whereas in the cyclolabic form, they are very simple, short, and without teeth, tubercles or enlargements; they are regularly conical and slightly curved inwards. The parameres are very elongated and parallel and not semilunar, as in other Western European species known to date, with the only exception for *C. pyrenaica*. For *C. arverna*, the macrolabic form of the male cerci is known. In these cases, the specimens are very similar to individuals of the macrolabic form of *C. pyrenaica* and, in part, of *C. montana*.

Examined material. France, Loire, Station de Chalmazel, Chalmazel, 1137 m, (45°40'33"N, 03°49'32"E), 31.VIII.3016, Christophe Girod leg., 1 male and 1 female, FMCR; France, Ardeche, surr. Satilleu, 1000 m, 13.VI.1994, Andrei Gourov leg., 1 male and 1 female, FMCR.

Distribution. *Chelidura arverna* is known only from the Massif Central and its offshoots (France).

Chelidura osellarum Fontana, Kočárek & Ruzzier, sp. nov.

https://zoobank.org/A136BD3F-B3A6-41AE-AC52-630BF0FB405B

Figs 3, 5–7

Diagnosis. *Chelidura osellarum* sp. nov. is characterized by a small size, blackish-brown body, brown legs and reddish-brown head. It is characterized by a reduced dilation of the posterior part of the body, with a ratio between the maximum length of the head and the width of the last tergite having an average value of 0.56. The cerci are well curved inwards, with a very wide base; base of the cerci bearing a small tubercle, sometimes hardly detectable. Male genitalia are characterized by short, semi-lunar parameres, a long virga, and a long seminal vesicle.

Type material (33 males and 5 females): Italy, Piedmont (Cuneo), Alpi Cozie, Val Maira, Chiappera di Acceglio, 1800 m, 05.VIII.1996, G. Osella leg., 25 males (Holotype and 24 paratypes) and 5 females paratypes, FMCR (23 males and 4 females) and OUCO (2 males and 1 female, Italy, Piedmont (Cuneo), Alpi Cozie, Val Maira, Chiappera di Acceglio, 1700 m, 09.VIII.1995, G. Osella leg., 8 males (paratypes), FMCR).

Additional material. Italy, Piedmont (Cuneo), Alpi Cozie, Colle Sampéire, 2050 m, 10.VIII.1996, leg. G. Osella, 1 male, FMCR; Italy, Piedmont (Cuneo), Alpi Cozie, Colle Sampéire North, 1600–1900 m, 07.VIII.1996, leg. G. Osella, 1 male, FMCR.

Description of the holotype. Body, incl. forceps, blackish-brown, shiny; head light brown, legs and antennae light brown. The cuticle is slightly rugose and shiny. Tegmina of the *Chelidura*/*Chelidurella* type, scarcely rugose, rudimentary, with a short section overlapping medially; wings absent. Total body length without forceps: 17.28 mm, length of forceps: 3.68 mm (male of forma cyclolabia).

Head slightly wider as long (Ratio: 1.13), with a maximal width of 3.04 mm; frons convex, postfrontal and coronal sutures distinct, posterior margin slightly concave in middle. Eyes small, shorter than length of the 1st antennomere and shorter than the length of the head behind eyes; distance between eyes 1.8 mm. Antennae with 13 antennomeres; antennomere 1 length 0.72 mm, narrowed basally, distal half parallel-sided, shorter than 3rd and 4th antennomeres combined and shorter than distance between antennal bases; antennomere 2 as long as wide; antennomere 3 narrower and longer than antennomere 4, both subconical; antennomeres 5–13 cylindrical; antennomeres gradually narrow from antennomere 5 up to antennomere 13, each antennomere 3 to 4× longer than wide; all antennomeres shortly pubescent.

Pronotum transverse (3.20 × 2.16 mm), subequal in width to head, with nearly parallel lateral margins and nearly straight posterior margins; posterior corners of the pronotum broadly rounded in dorsal view; disc of pronotum flat, median sulcus fine but distinct. Tegmina rugose, rudimentary, with a short section overlapping medially, with distal and internal edges broadly rounded.

Mesonotum dorsally visible as distally broadly rounded mesoscutellum; metanotum transverse, wider than long, posteriorly broadly emarginate. Prosternum longer than wide, angularly constricted in the distal third; mesosternum as long as wide, broadly rounded; metasternum transversal, distal part truncate, lateral sides tapering distally. Legs uniformly light brown; femora moderately thickened; tibiae clad with thick and fine setae, shallowly furrowed at the distal apex dorsally; metatarsomere 1 cylindrical, longer than tarsomeres 2 and 3 combined; metatarsomere 2 triangular, widened posteriorly; and metatarsomere 3 cylindrical.

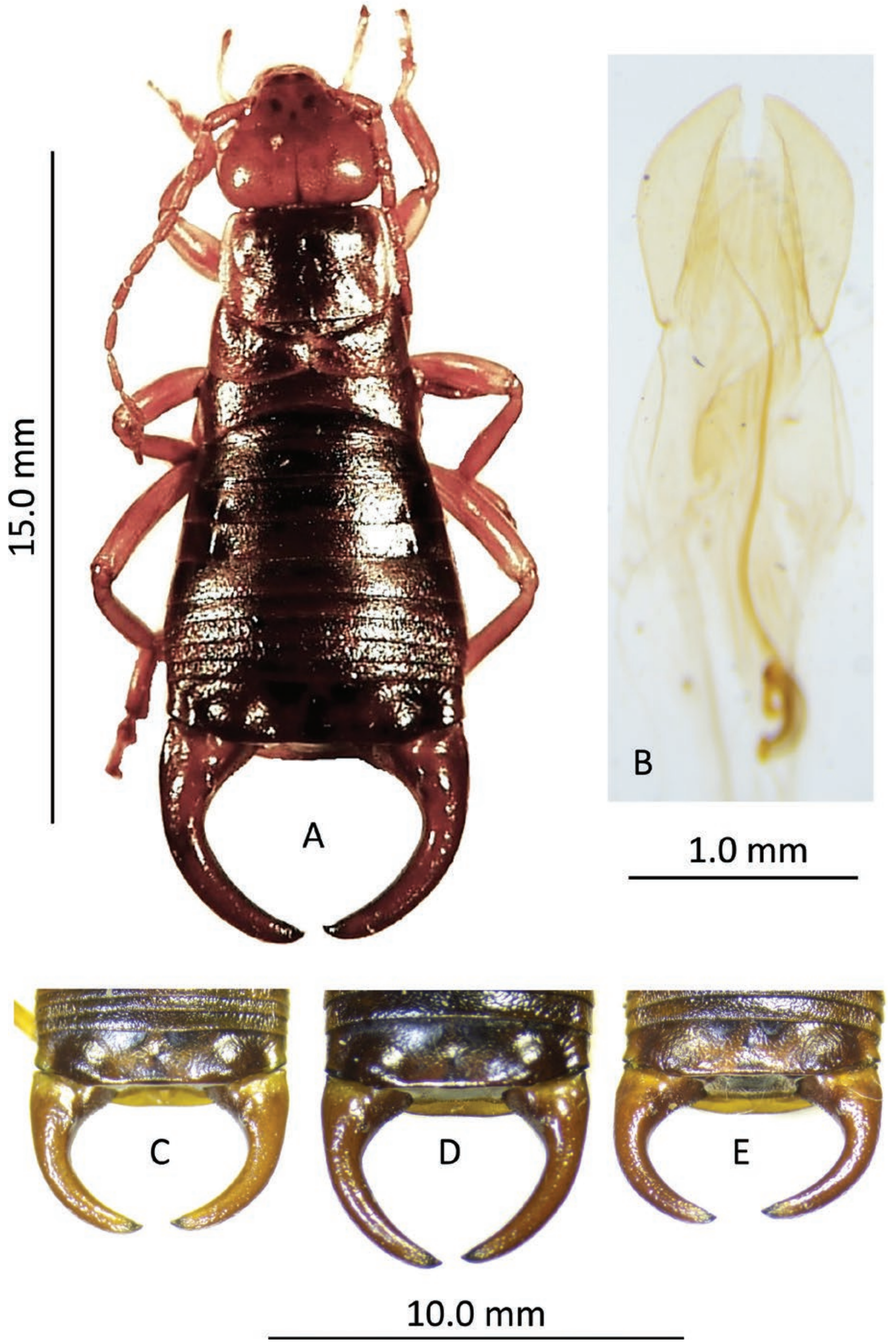

Figure 7. *Chelidura osellarum* sp. nov. **A.** Male holotype in dorsal view; **B.** Genitalia of the holotype; **C–E.** Male terminalia of 3 paratypes from Val Maira.

Abdomen slightly widened posteriorly, widest part of abdomen in correspondence of the 9th tergite; very small lateral glandular folds present on tergites 3 and 4; ultimate tergite (10th) strongly transverse, median part concave near posterior margin, disc with a pair of rounded tubercles above the forceps bases; pygidium very broad and flat, strongly transverse, simple, covered by ultimate tergite in dorsal view; ninth sternite (subgenital plate) transverse, 3× wider than long, apical margin slightly broadly rounded with shallow concavity in middle. Forceps arcuate, branches cylindrical, with small tubercles near the base of each branch dorsally, with the inner margin scarcely denticulated from the base to the dorsal tooth; forceps shorter than the width of the ultimate tergite.

Genitalia robust, with short and wide penis lobe and broadly rounded parameres laterally; parameres approximately 4× longer than wide; penis lobe 2× wider than parameres apically, apex truncate, external margin convex, internal margin gently emarginated in basal fourth; virga sinuated, well sclerotized, elongated, less than 2× longer than parameres; brown; basal vesicle thin, longer than maximal paramere width, reniform, slightly wider at basal half and enlarged at both apexes.

Variability in males. Body length without forceps was 11.20–15.2 mm. The holotype and all the paratypes are cyclolabic males.

Female. Body length without forceps 11.52–12.80 mm (female paratype 12.89 mm), with an average length of 12.45 mm; length of forceps 3.04–3.20 mm (female paratype 3.04 mm), with an average length of 3.14 mm. Body shape and colouration similar to those of the holotype; the widest part of the abdomen is located in correspondence of the 6th tergite; abdomen tapering from the 6th to 10th tergite. Pygidium prominent, with pointed lateral angles and concave middle part; forceps simple, light in colour, sinuate from dorsal view, tapering, inner margin serrated in the basal half.

Derivatio nominis. The new species is named after the illustrious Italian entomologist Prof. Giuseppe (“Beppe”) Osella (1936–2022) and his wife Margherita Pogliano Osella both of Piedmontese origin. The Osella couple collected and lately donated to the first author all the specimens upon the description of this species is based.

Distribution. *Chelidura osellarum* sp. nov. is known from a long series of specimens collected in Val Maira (Cottian Alps) in the Chiappera di Acceglio area, and from two males collected at Colle Sampéire (Cottian Alps). The two locations are about 16 km apart in a straight line, and it is probable that the species occurs in a fairly large area in the Cottian Alps. Unfortunately, the repeated searches carried out in recent years both in Val Maira and on Colle Sampéire have not yielded any results; therefore, it cannot be ruled out that the species may have become rarefied or that it has moved to higher altitudes.

Chelidura rhaetica Fontana, Kočárek & Ruzzier, sp. nov.

https://zoobank.org/FD413DC4-568A-485C-A171-C6EF7086F200

Figs 3, 5, 6, 8

Diagnosis. *Chelidura rhaetica* sp. nov. is characterized by a medium–large body size, brown body integuments, yellowish legs and a reddish-brown head. It is characterized by a clear dilation of male terminalia, with a ratio between the maximum length of the head and the width of the last tergite having an average value of 0.55. The cerci are scarcely curved inwards, conical, with a small tubercle near the base of each branch dorsally. Male genitalia with semilunar, elongated and quite wide parameres, virga quite long as well as seminal vesicles.

Type material. Holotype (male) and one female paratype, labelled: Italy, Lombardy (Sondrio), Western Rhaetian Alps, Franscia, Lanzada, 1480 m, (46°17'21,4"N, 9°54'41,14"E), 22.VII.2019, Mario Grosser leg.; Paratypes: 3 males, 1 female: the same data as the holotype. The holotype is deposited in the Petr Kočárek collection of OUCO, whereas 3 male and 2 female paratypes are deposited in the collection of FMCR.

Description of the holotype. Body, including forceps, brown, shiny; head fulvous, legs and first antennomere yellowish, rest of antennae fulvous. Cuticle punctured, shiny. Tegmina of the *Chelidura*/*Chelidurella* type, rugose, rudimentary, with a short section overlapping medially; wings entirely absent. Body length without forceps: 14.20 mm, length of forceps: 6.73 mm (male of forma cyclolabia).

Head as wide as long, with maximal width 3.15 mm; frons convex, postfrontal, and coronal sutures distinct, posterior margin slightly concave in the middle. Eyes small, shorter than length of the 1st antennomere and shorter than length of head behind eyes, distance between eyes 2.21 mm. Antennae with 13 antennomeres; antennomere 1 length 0.94 mm, narrowed basally, distal half parallel-sided, as long as 3rd and 4th antennomeres combined and shorter than distance between antennal bases; antennomere 2 transverse, only little longer than wide; antennomere 3 narrower and slightly longer than antennomere 4, both subconical; antennomeres 5–13 cylindrical; antennomeres gradually narrow from antennomere 5 up to antennomere 13, each antennomere 3–5× longer than wide; all antennomeres shortly pubescent.

Pronotum transverse (3.24 × 2.22 mm), subequal in width to head, with nearly parallel lateral margins and nearly strait posterior margin, distal corners broadly rounded; disc of pronotum flat, median sulcus fine but distinct. Tegmina rugose, rudimentary, with a short section overlapping medially, distal and internal edges broadly rounded. Mesonotum dorsally visible as distally broadly rounded mesoscutellum; metanotum transverse, wider than long, posteriorly broadly emarginate. Prosternum longer than wide, angularly constricted in distal third; mesosternum as long as wide, broadly rounded; metasternum transversal, distal part truncate, lateral sides tapering distally. Legs uniformly yellowish; femora stout; tibiae clad with thick and fine setae, shallowly furrowed at distal apex dorsally; metatarsomere 1 cylindrical, longer than tarsomeres 2 and 3 combined, metatarsomere 2 triangular, widened posteriorly, metatarsomere 3 cylindrical.

Abdomen widened posteriorly, widest part of abdomen in 9th tergite; lateral glandular folds present on tergites 3 and 4; ultimate tergite (10th) strongly transverse, median part concave near posterior margin, disc with a pair of rounded tubercles above the forceps bases; pygidium very broad and flat, strongly transverse, simple, covered by ultimate tergite in dorsal view; ninth sternite (subgenital plate) transverse, 3× wider than broad, apical margin slightly broadly rounded with shallow concavity in middle. Forceps arcuate, branches cylindrical, with small peg near base of each branch dorsally, inner margin denticulated from basis to dorsal tooth; forceps shorter than width of ultimate tergite.

Genitalia robust, with short and wide penis lobe and broadly rounded parameres laterally; parameres 3× longer than wide; penis lobe 2× wider than parameres apically, apex truncate, external margin convex, internal margin gently emarginated in basal fourth; virga sinuated, well sclerotized, elongated, less than 2× longer than parameres; dark brown; basal vesicle thin, longer than maximal

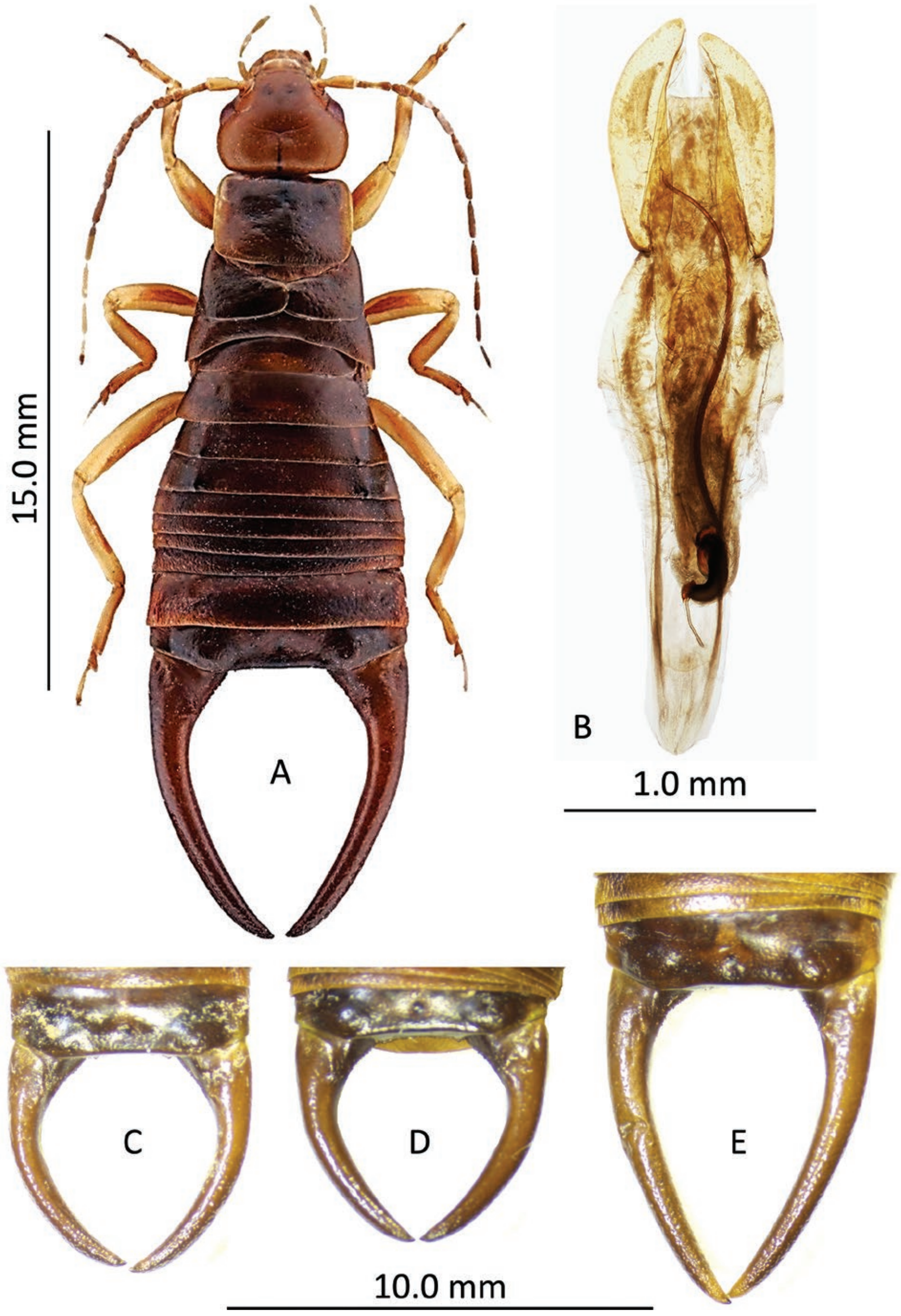

Figure 8. *Chelidura rhaetica* sp. nov. **A.** Male holotype in dorsal view; **B.** Genitalia of the holotype; **C–E.** Male terminalia of 3 paratypes from Val Maira.

paramere width, reniform, slightly wider at basal half and enlarged at both apexes.

Variability in males. Body length without forceps 14.20–15.20 mm. The four examined males of *C. rhaetica* sp. nov., despite having differences in the length of the cerci, cannot be distinguished into macrolabic and cyclolabic.

Female. Body length without forceps 15.20–16.00 mm, length of forceps 3.90 mm (one female paratype has cerci with broken apex). Body shape and colouration similar to holotype male; widest part of abdomen in 6th tergite, distally from 6th tergite abdomen continuously tapering to 10th tergite. Pygidium prominent, with pointed lateral angles and concave middle part; forceps simple, sinuate from dorsal view, tapering, inner margin serrated in basal third.

Derivatio nominis. The new species is named after the Rhaeti civilization and the Rhaetian Alps. The Rhaeti (Raeti, Rheti or Rhaetii) were a confederation of alpine tribes that, before the Roman conquest, inhabited present-day Tyrol in Austria, eastern Switzerland and the alpine regions of northeastern Italy. The Rhaeti civilization developed between the end of the Bronze Age and the early Iron Age. The Rhaetian Alps are located in the centre of the Alps chain across Italy, Switzerland, Liechtenstein and Austria and extend from the Spluga Pass to the Brenner Pass.

Distribution. The locality in the Rhaetian Alps (Italy) where specimens of *Chelidura rhaetica* sp. nov. were discovered, Lanzada (Sondrio), is situated well outside the typical distribution range of the *Chelidura* genus in the Alps, extending its known eastern range by approximately one-third of its longitudinal extent. At present, only a single population is known from this area, and it remains unclear whether other populations, of this or other *Chelidura* species, exist between this site in the Rhaetian Alps and Mount Mottarone, previously considered the easternmost limit of the genus in the Alpine region.

Key for the identification of males of the genus *Chelidura* in the Western Europe

1 Parameres decidedly elongated, with almost parallel sides and 5.5–6.5× their maximum width in length (Fig. 6G–I). Massif Central (France) and Pyrenees (France, Andorra and Spain) 2

– Parameres less elongated, distinctly semilunar, with a widely curved outer side and 3.5–4× their maximum width in length (Fig. 6A–F, J–M). Central Western Alps (Italy, Switzerland and France 3

2 Abdomen significantly dilated posteriorly with the last tergite markedly wider than the pronotum (Fig. 5D). Cerci of the cyclolabia form with a dilation at the internal margin (Fig. 3N–P); Brown-reddish colouration generally uniform. Pyrenees (France, Andorra and Spain) .... *C. pyrenaica* (Gené, 1832)

– Abdomen less dilated posteriorly with last tergite slightly wider than the pronotum (Fig. 5E). Cerci of the cyclolabia form very stocky and slightly curved and always without a dilation at the internal margin (Fig. 3Q, R); Colouration of the body and cerci generally very dark, with head and legs generally brown-reddish. Massif Central (France) .... *C. arverna* David & Van Herrewege, 1973

3 Abdomen significantly dilated posteriorly (Fig. 5A, B, F); cerci of the cyclolabia form very curved (Fig. 3A–H, S–W). Macrolabia form unknown. Body and cerci colouration very dark, with head and legs often reddish-brown 4

– Abdomen less markedly dilated posteriorly (Fig. 5C, G). Cerci of the cyclolabia form slightly curved (Fig. 3K, L, Z, ZZ); macrolabia form sometimes present and even predominant 6

4 Larger in size, with total length without cerci about 14–20 mm and width of the last tergite about 7–8 mm. Macrolabia form unknown. Body colouration very dark brown (Fig. 5A). Pennine Alps (Italy) .... *C. aptera* (von Charpentier, 1825)

– Smaller in size, with total length without cerci about 10–18 mm and width of the last tergite about 5–6 mm. Body colouration lighter, reddish-brown (Fig. 5B, F) 5

5 Abdomen very dilated posteriorly with very broad last tergite (Fig. 5B, C, F–H). Colouration generally brown. Graian Alps (France and Italy) .... *C. alpina* (Gené, 1832)

– Abdomen less dilated posteriorly with last tergite less broad (Figs 3S–W, 5F). Colouration darker, almost spruce-brown with lighter head and legs. Cottian Alps (Italy) .... *C. osellarum* sp. nov.

6 Very elongated body shape and abdomen little or not at all dilated posteriorly (Fig. 5C). Cerci slender and moderately long and slightly curved in the cyclolabia form; macrolabia form very frequent with cerci often rectilinear for most of their length (Fig. 3C–M). Uniform light brown colouration. Pennine Alps (Switzerland, Italy) .... *C. montana* (Gené, 1832)

– Less elongated body shape and abdomen clearly dilated posteriorly (Fig. 5G). Robust cerci, especially at the base, of variable length and moderately curved both in cyclolabic as well in macrolabic forms (Fig. 3X–ZZ). Uniform dark brown colouration with lighter legs. Rhaetian Alps (Italy) .... *C. rhaetica* sp. nov.

Distribution of Chelidura in the Alps

Until a few years ago, the genus *Chelidura* was known in the Alps only from the western sector of the range, in the border area between Switzerland, Italy, and France (e.g., Vigna Taglianti 1994; Dierkens et al. 2021; Jurado-Angulo et al. 2021). In Italy, records were limited to Piedmont and Valle d'Aosta (Vigna Taglianti 1994). The discovery of a new population in Lombardy, far to the east of the previously known distribution and here described as *C. rhaetica* sp. nov., raises the question of whether additional populations of *Chelidura* may occur in the central Alpine arc, both in Italy and, especially, in Switzerland. Although a few records come from elevations of around 1,000 m (which we consider likely to result from labelling errors), most known localities, particularly the more reliable ones, are situated between 1,600 and 2,300 m a.s.l., corresponding to the montane and alpine belts. As high-altitude insects often inhabiting the coldest slopes, *Chelidura* species are known from a limited number of sites, resulting in a discontinuous and markedly patchy distribution. The current state of knowledge presented in this work, still far from complete, confirms this discontinuous pattern, while also revealing a taxonomic complexity that better reflects the true situation (Figs 9, 10).

Final remarks

The order Dermaptera is among the least studied insect groups, both globally and within Europe. The number of species recorded at most sites is usually low. Their collection generally relies on active searching on the ground or vegetation, or the incidental capture of specimens using

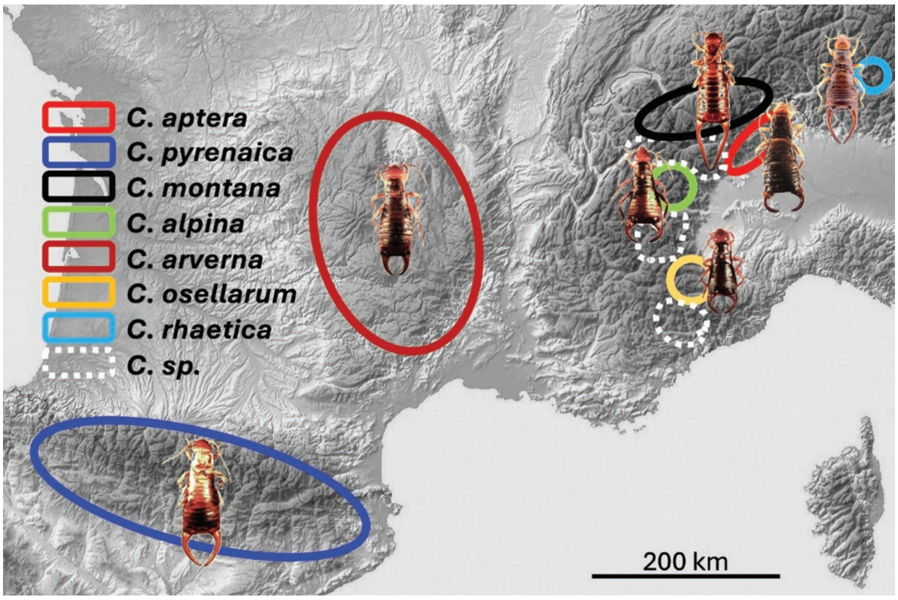

Figure 9. Distribution of the taxa of the genus *Chelidura* in Western Europe. *Chelidura* sp. illustrates the occurrence of specimens that could not be assigned to the recognized species. These are either females or records based on iNaturalist for which documentary material missing.

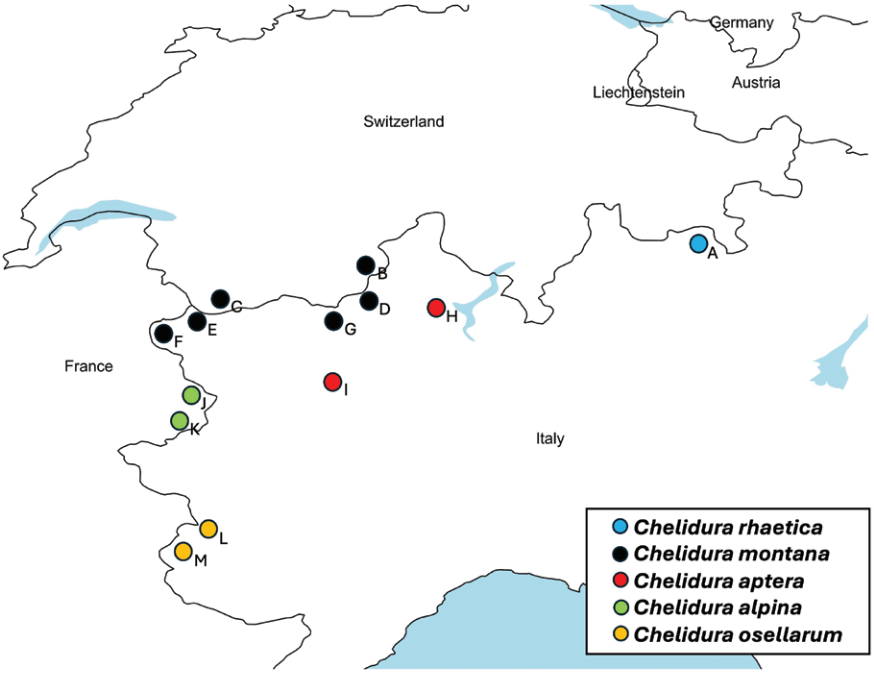

Figure 10. Localities of specimens used in this study. *Chelidura rhaetica*: A. Italy, Lombardy (Sondrio), Western Rhaetian Alps, Franscia, Lanzada, 1480 m. *Chelidura montana*: B. Switzerland mer., Valais, SAAS FEE Gletschergrotte, 2000 m; C. Switzerland, Valais, Colle Grand San Bernardo, Liddes, 2160 m; D. Italy, Piedmont, M. Rosa, Macugnaga; E. Italy Vallle d'Aosta, Colle Grand San Bernardo, 1900 m; F. Italy, Valle d'Aosta, Val Veny, Pré de Pascal (Courmayeur); G. Italy, Valle d'Aosta, M. Rosa, Gressoney-La-Trinité. *Chelidura aptera*: H. Italy, Piedmont (Novara), Mottarone; I. Italy, Piedmont (Biella), M. Mucrone. *Chelidura alpina*: J. France, Savoie, Val-d'Isère, 2000 m; K. France, Mont-Cenis, between the Cross and the hospice, on the side facing north. *Chelidura osellarum*: L. Italy, Piedmont (Cuneo), Alpi Cozie, Colle Sampéire North, 1600–1900 m; M. Italy, Piedmont (Cuneo), Alpi Cozie, Val Maira, Chiappera di Acceglio, 1700 m.

pitfall traps and other non-selective methods. Consequently, the majority of Dermaptera specimens were not collected by specialists in the order. Instead, they are often gathered by researchers working on other insect groups, who understandably pay only limited attention to recording detailed collection data for earwigs. These specimens are then either integrated into general collections or passed on to specialists in the order Dermaptera for further study.

The species of the genus *Chelidura* inhabit mountainous and alpine environments. They crawl on the ground and frequently take shelter under debris, particularly stones. Consequently, most specimens are captured using pitfall traps, typically deployed to study ground beetles (particularly Carabidae). However, in high-altitude settings, these traps cannot be checked frequently due to logistical constraints, so various preservatives must be used. Specimens collected in this way must then undergo further treatment, either for dry mounting or preservation in 70% ethanol.

Once in the hands of researchers specialising in Dermaptera, such material is often re-softened and prepared for the extraction of genitalia or processed for morphological identification. These repeated manipulations significantly reduce the likelihood of obtaining viable DNA for molecular analysis. This is the case, for example, with *Chelidura* specimens from Val Maira (Piedmont, Italy, Cottian Alps), where the condition of the preserved material limits its suitability for genetic studies.

The difficulty of collecting fresh material and the poor condition of many specimens in historical collections highlight the need for a multidisciplinary approach. Combining molecular and morphometric analyses with ecological and biogeographical data could provide a more comprehensive framework for resolving taxonomic uncertainties and reconstructing species relationships.

Diversity of *Chelidura* in the Alps and its possible origin

As the largest European high mountain system, the Alps form a major feature in molding the phylogeography of many species, and they are specific to many endemic species (Rabitsch and Essl 2009). Cold-adapted species had the largest distribution areas during glacial periods, whereas the subsequent interglacials led to retreats of these taxa into mountain ranges followed by the generation of new alpine lineages (Ehl et al. 2021). Schmitt (2009) postulated several characteristic biogeographical differentiation patterns of the species restricted to the Alps. One pattern follows the allopatric model of biological speciation, which involves the splitting of a pre-existing species distribution, followed by genetic divergence in isolation. Taxa with wide distributions in the Alps often have two to four or more surviving genetic lineages, some of which have the status of cryptic species. In many cases, these lineages are the result of several centres of glacial survival in perialpine areas (Schönswetter et al. 2005; Schmitt 2009). Other studies, yet fewer in number, have suggested survival at nunataks, i.e., mountain tops above the glaciers (e.g., Stehlik et al. 2002), or even north of the mountain chain of the Alps (Schmitt et al. 2006). With respect to the phylogeographic patterns of high mountain taxa, a highly repetitive pattern has been shown for the Alps (Schmitt et al. 2016), whereas examples can be found in various groups of arthropods, such as harvestmen of the genus *Megabunus* Meade, 1855 (Wachter et al. 2016), ants of the genus *Formica* Linnaeus, 1758 (Bernasconi et al. 2011), or endemic cryptic species of *Euscorpius* Thorell, 1876 (Štundlová et al. 2019).

The five Alpine *Chelidura* lineages identified in this study fit well with the patterns detected in other insect groups. The currently isolated distribution islands of individual *Chelidura* species correspond to islands of assumed distributions of *Boloria* Moore, 1900 (Lepidoptera: Nymphalidae) during the last ice age (Ehl et al. 2021), so it can be assumed that both groups experienced similar evolutionary histories with the same refuges for the survival of ice ages. Geographical barriers combined with the limited ability of dispersal in this flightless genus led to long-term isolation of populations without the possibility of subsequent gene flow among them. A similar case of Alpine speciation was also recorded among related Dermaptera species of the genus *Chelidurella* Verhoeff, 1902 (Kirstová et al. 2021). However, today's Alpine species of this genus are probably derived from the species currently (and probably also historically) widely distributed outside the Alps, i.e., *C. acanthopygia* (Gené, 1832) and *C. thaleri* Harz, 1980. During the glacial period, some populations were isolated in rugged alpine terrain, and after the retreat of glaciers, the newly diverged genetic lineages spread from their refugia. As species of the genus *Chelidurella* are not as strictly cold-adapted as *Chelidura*, their current occurrence is wider, and their ranges are more fragmented. This is apparently a consequence of the subsequent expansion of differentiated populations during interglacial periods, and the subsequent interactions between these populations. Kirstová et al. (2021) did not observe direct evidence of reproduction barriers between *Chelidurella* species, but according to genetic identifications, only one species was always collected at one locality. Because the majority of species exhibit similar habitat associations and similar phenologies, we can assume that competition between the species or their crossbreeding results in infertile offspring (or offspring with reduced fertility). This would lead to competitive exclusion, and only one of the species at the locality would remain (Hardin 1960; Hochkirch et al. 2007). Similarly, we did not observe syntopic occurrence in the newly described *Chelidura*. However, syntopy seems unlikely in this genus because of the long-term isolation of high-altitude populations surrounded by lower locations, which are apparently an insurmountable barrier for these species

Ecology and conservation

Alpine environments represent the typical habitat for *Chelidura* species. These ecosystems are exceptionally rich in European endemics and threatened species (Franzén and Molander 2012). According to the red lists of the International Union for Conservation of Nature (IUCN), the southern slopes of the Alps and the Pyrenees rank among the most biodiverse regions (Hochkirch et al. 2023) and simultaneously host the largest number of *Chelidura.*

The ecological preferences of the *Chelidura* species reveal notable distinctions. Alpine populations of *Chelidura* typically inhabit environments at high altitudes, generally residing above 1,400 m, and extending to over 2,000 m (Fontana et al. 2021). These habitats are primarily subalpine and alpine zones, characterized by rocky landscapes with sparse vegetation. For example, *Chelidura pyrenaica* is found at elevations ranging from approximately 1,300 to 2,800 m (Jurado-Angulo et al. 2021), sharing similar habitat characteristics with populations in the Alps. In contrast, *Chelidura arverna* is known to thrive at relatively lower altitudes, even below 1,000 m. This species is endemic to the Massif Central, a region of mountain ranges primarily situated between 800 and 1,200 m, with the Puy de Sancy, the highest peak at 1,885 m, located approximately 35 km southeast of Clermont-Ferrand. Notably, *C. arverna* occupies both forested areas and open high-altitude habitats, suggesting that Alpine *Chelidura* species might similarly inhabit diverse environments.

Very little is known about the reproductive cycles or dietary habits of the different species of *Chelidura*. Observations of adults of Alpine species have been reported from May to September, with most records in July and August. Adults of *C. osellarum* sp. nov. have only been observed in the first half of August (four independent observations), while adults of *C. rhaetica* sp. nov. have only been observed once in the second half of July. Adults of *C. montana* stat. nov. have been observed from beginning of July to the end of September. Citizen science databases comprise several unidentified *Chelidura* records from May/June (iNaturalist) and here we present a record of *C. aptera* observed on 20 May. However, repeated observations of the *C. montana* population at Colle Grand San Bernardo (2,160 m) in September 2019, 2021 and 2025 confirm the co-occurrence of adult individuals of both sexes and nymphs of various ages. It is common for females of the earwig family Forficulidae to care for nymphs until the second instar, after which they die, while males usually die earlier (e.g. Albouy and Caussanel 1990). During this period, populations usually consist of only females and young nymphs (Kočárek 1998; Kirstová et al. 2017). The presence of nymphs of different ages alongside males in *C. montana* is highly unusual and suggests a potential two-year development cycle. Copulation was also observed during this period (Fig. 11), suggesting that these are not merely longer-surviving males from previous reproductive period. The most likely explanation is a two-year development cycle, whereby adults from the previous year and nymphs from the previous year's reproduction meet at the same time of year.

The phenology and life cycles of the genus *Chelidurella* have been studied in the most common and widely distributed species, *C. acanthopygia* (Gené, 1832) (Kočárek 1998; Fontana and Cogo 2001). The adults of this species overwinter, then reproduce in spring, and the nymphs reach adulthood in late summer/autumn. The overwintering adults became active in the spring (May and June), after which the adults of the next generation appear from August to October and subsequently overwintering (Kočárek 1998). However, quantitative observations are made at low altitudes. At higher altitudes, it has been occasionally observed that development and overwintering in the nymphal stage are prolonged (Franke 1985; Irmler and Hingst 1993, personal observation by P. Kočárek). Unlike *Chelidura montana*, however, *Chelidurella acanthopygia* is observed in autumn only as last instar nymphs, not as small nymphs together with adults. Jurado-Angulo et al. (2021) reported occasional observation of female of *C. pyrenaica* attending eggs in the second half of June in Andorra, which fits into the assumed general scheme of the reproductive cycle of earwigs of the genus *Chelidura*. However, targeted research on the life cycle of *Chelidura* in the Alps is lacking, and year-round phenological observations are necessary to clarify them.

The recent decline in sightings of *Chelidura* specimens at many historical localities may suggest possible local extinctions or a shift to higher elevations in response to environmental changes (Brandmayr and Pizzolotto 2016;

Figure 11. The copulation of *Chelidura montana* (Gené, 1832), stat. nov. observed in Colle Grand San Bernardo (45°53'13"N 7°11'16"E) at an altitude 2,160 m on 16 September 2025, and the habitat occupied by this species (photo P. Fontana).

Scalercio et al. 2014). In orthopteroid insects, there is in fact evidence of a northward expansion of southern-type species (Buzzetti et al. 2013) and as well as the ascent of thermophilic species to higher altitudes (Fontana, pers. obs.). In recent years, the earwig *Anechura bipunctata* (Fabricius, 1781) has become more prevalent in areas where *Chelidura* populations were previously known to occur but have not been recorded recently (personal observation). This shift supports the hypothesis that climate change may benefit *Anechura*, potentially leading to competitive interactions with *Chelidura* over resources or a shared ecological niche.

Conclusions

This study demonstrates substantial knowledge gaps in many insect groups, particularly those with restricted distributions resulting from ecological specialization and those difficult to collect. Biodiversity hotspots such as the Alps remain especially understudied in this regard. Progress in the study of species with limited distribution, such as the mountain species of the *Chelidura* genus, hinges on three key factors: the collection of new specimens for genetic analyses, the systematic revision of historical material, and the vital role of museums in safeguarding natural, cultural and scientific heritage. The results of an extensive comparative study presented in this study revealed hidden diversity within the Alpine *Chelidura* and enabled us to define the presence of at least five species in the Alps: *C. aptera* (von Charpentier, 1825), *C. montana* (Gené, 1832), stat. nov., *C. alpina* (Gené, 1832), comb. nov., *C. rhaetica* sp. nov., and *C. osellarum* sp. nov. More extensive molecular and morphometric analyses are required to assign populations from numerous localities in the Western Alps to well-defined *Chelidura* species or describe additional new species. Indeed, the potential existence of undescribed species, intermediate forms, and the coexistence of multiple species within single sites cannot be excluded. For instance, the identity of specimens from Mont Blanc and Gran Paradiso remains unresolved, while material from Aiguilles (Hautes-Alpes, France) and Valli di Lanzo (Turin, Piedmont, Italy) appears to represent promising candidates for further new species. It is clear that the conservation of these taxa, threatened by climate change and human-induced disturbances to their habitats, depends fundamentally on gaining a deeper understanding of them.

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Supplementary material 1

Additional information

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Data type: xlsx

Explanation note: **table S1.** Main measurements and ratios of the examined male specimens of the alpine *Chelidura*. **table S2.** Coefficients of principal components PC1, PC2, and PC3, with the standard deviation, the proportion of variance explained per component and the cumulative proportion of variance explained. **table S3.** Prior probabilities for the four *Chelidura* species as incorporated into the LDA model. **table S4.** Linear discriminant coefficients for the LDA model, indicating how each morphological measurement contributes to the three discriminant functions (LD1, LD2, LD3) that distinguish the species. **table S5.** Confusion matrix showing the results of the second LDA model, comparing the number of predicted individuals (columns) with the observed individuals (rows) for each species.

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