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Research article

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***Desoria calderonis* sp. nov., a new species of alpine cryophilic springtail
 (Collembola: Isotomidae) from the Apennines (Italy),
 with phylogenetic and ecological considerations**

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Abstract. We describe and delimit with integrative taxonomy the new springtail species *Desoria calderonis* sp. nov. (Collembola: Isotomidae). This cryophilic species is strictly linked to the supraglacial stony debris of the isolated Calderone glacier (Central Apennines, Italy), one of the southernmost glaciers of Europe. *Desoria calderonis* sp. nov. could belong to the *nivalis*-complex, a group of European mountain species included in the *violacea*-group. Genetic analysis (COI mtDNA barcoding) confirms the morphological attribution to the genus *Desoria* Nicolet in Desor, 1841, but highlights that the genus, in its current definition, is polyphyletic. We specify the peculiar micro-habitat preferences and highlight the threat of extinction for this cryophilic species in the context of the ongoing climate change and subsequent risk of complete disappearance of the glacier.

Keywords. Glacial biodiversity, glacial refugia, peripheral mountains, vanishing glaciers, unknown biodiversity.

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Introduction

Cryophilic springtails (Hexapoda: Collembola) are cold- and moisture-requiring organisms, whose typical habitat is near or above ice or snow (Deharveng *et al.* 2008; Fjellberg 2010; Buda *et al.* 2020; Valle *et al.* 2020; Jureková *et al.* 2021). *Desoria saltans* Nicolet, 1841 (Entomobryomorpha: Isotomidae) is among the best known cryophilic springtails and is commonly known as the “glacier flea”. This species was already cited by the Italian geologist Stoppani in his early essay “Il Bel Paese” (Stoppani 1876) for its showy, swarming and large assemblages on Alpine glaciers. Nowadays there are indications that “glacier fleas” include multiple taxa of cryophilic Isotomidae related to the genus *Desoria*: *Desoria* Nicolet in Desor, 1841, *Gnathisotoma* Cassagnau, 1957 and *Myopia* Christiansen & Bellinger, 1980 (Najt 1981; Fjellberg 2010). These organisms appear to be differentiated among isolated glacial areas (Deharveng 1975; Lauga-Reyrel & Lauga 1995). By comparing different European glacier forelands, Hågvar *et al.* (2020) observed how the species belonging to this group, and to a few other pioneer genera, are important not only as components of supraglacial communities (see also Gobbi *et al.* 2021), but also as early colonisers of recently-deglaciated terrains. High diversity of cryophilic Isotomidae was observed in southern Alaska and in the Canadian Rocky Mountains in North America (Fjellberg 2010). Therefore, we can assume high diversity of the genera related to *Desoria* at similar sites in Europe.

The genus *Desoria* comprises 101 described species (Bellinger *et al.* 1996–2021), mostly distributed in the Holarctic, especially at high latitudes (Potapov 2001). *Desoria* differs from the closely related genus *Isotoma* Bourlet, 1839 by the number of apical setae on tibiotalpi (11, with the exception of the *pjasini*-group), and the absence of ventroapical spine-like setae on the manubrium (Potapov 2001; Fjellberg 2007). From the ecological point of view, *Desoria* also differs from *Isotoma* by being more frequent at cold and wet sites and thus including many hygrophile and cold-adapted species (Potapov 2001). Species belonging to the genus *Desoria* overwinter in the adult stage and are often active on snow or ice, on which they feed (Hao *et al.* 2020) and migrate (Hågvar 2000; Zhang *et al.* 2017). Among these cold-adapted species, *Desoria* and taxonomically related genera like *Agrenia* Börner, 1906, *Gnathisotoma*, *Myopia* and *Kaylathalia* Stevens & D’Haese, 2016 (Najt 1981; Fjellberg 2010; Stevens & D’Haese 2017) include cryophilic species (Potapov 2001; Fjellberg 2007, 2010). Cryophilic species, in particular, are of great interest because they are particularly threatened by the current global warming and are good candidates as indicators for conservation projects aimed at investigating refugial glaciated areas (Gobbi *et al.* 2021).

Several works carried out on alpine cryophilic springtails (e.g., Deharveng 1975; Najt 1981; Lauga-Reyrel & Lauga 1995; Fjellberg 2010; Makowska *et al.* 2016; Hittorf 2017; Buda *et al.* 2020) indicated a significant knowledge gap on springtail biodiversity in glaciated areas of the World. The cryophilic collembolan fauna is still poorly described especially from Southern Europe, where it should be particularly differentiated in relation to the glacial history of the peripheral and southernmost European massifs (Deharveng 1975; Najt 1981; Lauga-Reyrel & Lauga 1995). Furthermore, the taxonomy of *Desoria* is still uncertain, as both morphological and genetic evidence indicates that this genus is polyphyletic, as it includes different subgroups (Stevens *et al.* 2006; Fjellberg 2007; Stevens & D’Haese 2017).

In this work, we present a description of a new species of *Desoria* found in one of the southernmost European relict glacial areas, the Calderone glacier (Central Apennines, Italy; Grunewald & Scheithauer 2010). This species is thus a good indicator of a “cold-spot” of the local glacial biodiversity (Cauvy-Fraunié & Dangles 2019) in the Mediterranean region. In order to provide a robust taxonomic classification for this new species, we applied both morphological and genetic approaches, to obtain a phylogenetic framework. In addition, we provide remarks on its habitat and microhabitat preferences.

Material and methods

Study area and data collection

Specimens were collected by the flotation method (Marshall *et al.* 1994) on the Calderone glacier. The Calderone glacier is located on the Gran Sasso Massif, in the Central Apennines (Italy, Abruzzo; 42°28'16.4" N, 13°34'01.4" E). Presently, it is classified as glacieret (total surface < 0.04 km²; Smiraglia & Diolaiuti 2015) and it is almost totally covered by stony debris. We searched for *Desoria calderonis* sp. nov. in all glacial environments, on the supraglacial debris and on the Little Ice Age (LIA) moraines. In order to better verify its distribution, both flotation and pitfall trap methods were used for 15 sampling points on the supraglacial debris as well as 6 sampling points on LIA moraines as controls. In order to better characterize the ecology of *Desoria calderonis* sp. nov., we recorded micrometeorological (temperature and humidity) and soil data of its habitat and of the surrounding habitat where it was not found, in particular:

- temperature was recorded on supraglacial debris by 15 and on LIA moraines by 2 dataloggers (iButton 1922) for the period 9 July 2020 – 27 July 2021; using this data, we calculated the mean annual temperature, the mean temperature during the snow-free period, the minimum and the maximum temperatures and the duration of the snow-cover;
- relative humidity was recorded in both environments by a datalogger (Tinytag Plus) for the same period; with this data we calculated the mean annual value and the mean value during the snow-free period;
- soil samples were collected for 15 points on the supraglacial debris and 6 points on LIA moraines. In soil samples we measured the value of carbonate calcium content, organic matter content and pH.

All dataloggers were positioned 10 cm under the surface.

Specimen conservation and preparation

Specimens (1 holotype and 15 paratypes), preserved in 90% ethanol at -20°C, were initially cleared by a short immersion in 10% KOH solution and then mounted on slides using lactic acid or Marc André as a preservative solution. Additional specimens (five) were prepared for scanning electron microscopy: they were completely dehydrated in absolute ethanol, before critical point drying in a Balzers Union (FL-9496) apparatus and the subsequent sputter coating with gold in an Edwards Sputter Coater S150B. Morphological observations were performed with a Leica Laborlux S light microscope and a Quanta400 (FEI) scanning electron microscope.

Molecular analysis

Whole genomic DNA was extracted from 10 specimens, individually, using the Wizard®SV Genomic DNA Purification System (Promega, Madison, WI, USA). The mitochondrial marker analyzed –cytochrome *c*

oxidase subunit 1, 5P fragment (*cox1*) – was amplified with a universal primer pair (Folmer *et al.* 1994). PCRs were prepared in a 25 µL reaction volume containing: 2.5 µL of whole genomic DNA, 1.25 µL of both forward and reverse primers (10 µM), 2.5 µL of MgCl₂ (2.5 mM), 2.5 µL of deoxynucleotides (dNTPs, 10 mM), 5 µL of Green GoTaq Flexi Buffer (Promega, Madison, WI, USA), 0.125 µL of GoTaq® G2 Flexi DNA Polymerase (Promega, Madison, WI, USA), 5 µL and 9.875 µL of ddH₂O. Amplifications were run on a GeneAmp® PCR System 2700 (Applied Biosystems, Foster City, CA, USA) thermal cycler with the following conditions for each of the 35 cycles: a denaturation step at 95°C for 1 min, an annealing step at 50°C for 1 min and an elongation step at 60°C for 90 s. An additional initial denaturation step was set at 95°C for 5 min as well as a final extension step at 72°C for 7 min. PCR products were purified with the kit Wizard®SV Gel and PCR Clean-up System (Promega, Madison, WI, USA) and sequenced on both strands using a DNA Analyzer ABI 3730 at Biofab (Rome, Italy). Sequences were then manually corrected and assembled in Sequencher ver. 4.2.2 (Gene Codes, Ann Arbor, MI, USA).

Phylogenetic analysis

Given the current uncertainties on the monophyly of the genus *Desoria* (Stevens *et al.* 2006; Stevens & D’Haese 2017) and of its closest relatives, a preliminary analysis was conducted to identify *Desoria* as well as phylogenetically related sequences in order to bypass the assumption of a monophyletic *Desoria* in the process of taxa selection. All records belonging to the family Isotomidae were downloaded from the BOLD database (Ratnasingham & Hebert 2007) with their metadata (last download 30 June 2021). The 8483 records were filtered to retain only those including information for the COI-5P *cox1* fragment and having an assigned bin. The longest sequence for each bin was extracted using the R package 'bold' (ver. 1.2.0, written by Scott Chamberlain) and used as representative for the bin in the following analysis. For all records, metadata associated with a specific bin were revised to identify the taxonomic attribution(s), if available, of each bin, whereas bins with no taxonomic information below the family level in any sequence were discarded. Records were associated with 728 bins in BOLD, 348 of which included sequences with at least some associated taxonomic information. After the addition of the new species, *D. calderonis* sp. nov. (mean uncorrected divergence within the species is 0.4%, S.D. 0.2), the total dataset was composed of 349 sequences by 438 aligned positions (1st and 2nd positions only). The dataset was aligned with MAFFT (Katoh 2002) in order to calculate both uncorrected p-distances and phylogenetic relationships. These latter were obtained, using 1st and 2nd codon position data set, by IQ-TREE (ver. 1.6.12, default settings with 1000 fast bootstrap replicates and the model was optimized using ModelFinder; Nguyen *et al.* 2015). A reasonably supported node (bootstrap 92) was identified, including all *Desoria* sequences – with the exception of *Desoria trispinata* (3 bins, 18 sequences) and *Desoria tshernovi* (1 bin, 1 sequence, unrelated to 6 *D. tshernovi* sequences within the node) – as well as sequences from other genera. This subdataset, inclusive of related species and three outgroups (*Cryptopygus terranovus*, *Parisotoma notabilis* and *Folsomia quadriculata*, grouping outside the *Desoria* cluster), accounted for 89 sequences by 438 aligned positions and was reanalyzed as above to investigate the phylogenetic position of the new species in the context of *Desoria* and related species. Once a final phylogenetic tree had been obtained, records that appeared phylogenetically related to *D. calderonis* sp. nov. were further revised in the BOLD database metadata or in the original literature to assess the existence of ecological and/or phylogeographic similarities.

Abbreviations used in the text

Abd	=	abdominal segment
<i>accp</i> -setae	=	accessory p-row <i>s</i> -setae
<i>al</i> -setae	=	antero-lateral <i>s</i> -setae
Ant	=	antennal segment
AOIII	=	antennal organ III
<i>as</i> -setae	=	antersubmedial <i>s</i> -setae

bl	=	basolateral field (mentum)
bm	=	basomedian field (submentum)
ms-setae	=	micro <i>s</i> -setae
PAO	=	post antennal organ
Px	=	proximal field
Th	=	thoracic segment
Tita	=	tibiotarsus
VT	=	ventral tube

Results

Phylum Arthropoda Latreille, 1829
Class Collembola Lubbock, 1870
Order Entomobryomorpha Börner, 1913
Family Isotomidae Schäffer, 1896
Subfamily Isotominae Schäffer, 1896
Genus *Desoria* Nicolet in Desor, 1841

Desoria calderonis Valle sp. nov.

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Figs 1–5

Diagnosis

Desoria calderonis sp. nov. belongs to the *violacea*-group sensu Potapov, 2001, with quadridentate mucro without seta, maxillary palp bifurcate, apical folds on labrum sharp. Differences from closely related species are analysed in the section ‘Taxonomic and ecological consideration’.

Etymology

The epithet of the new species reflects the name of the site from which holotype and paratypes derive, Calderone glacier (Italy, Abruzzo, Gran Sasso massif).

Material examined

Holotype

ITALY • ♀; Abruzzo (Central Italy), Gran Sasso massif, Apennines, Calderone Glacier, supraglacial stony debris; 42°28′16.2″ N, 13°34′05.8″ E; alt. 2700 m a.s.l.; 8 Jul. 2020; B. Valle and M. Di Musciano leg.; collected with flotation method; Genbank (NCBI) MZ686962-70; Collembola collection, Department of Life Sciences, University of Siena, Italy.

Paratypes

ITALY • 15 spec. (♂ and ♀); same collection data as for holotype; Collembola collection, Department of Life Sciences, University of Siena, Italy.

Description

BODY. Mean body length. 1.5 mm (standard deviation: 0.1 mm on 12 specimens, see Table 1). Colour violet-black on abdomen and antennae, lighter on furca and legs, which are brownish (Fig. 1); juveniles are much paler, bluish. Cuticle granulation fine and regularly distributed; all dorsal tergites clearly separated from each other. Abd. III and IV of approximately same width.

CHAETOTAXY. Terga plurichaetotic, consisting of micro-, meso- and macrosetae, these latter well differentiated on last abdominal tergites (Abd. IV–VI, in median position), but not well distinguished

from ordinary setae on other tergites (Fig. 2A). On every segment, longer setae concentrated along the lateral and posterior edges of tergite. All setae smooth. Macrosetae on Abd. V 0.9–1 times median length of tergite and 1.8–2.4 times as long as inner edge of Claw III (Table 1). Sensory chaetotaxy constituted by *ms*-setae, *accp*-, *al*- and *as*-setae. Only Th. II and Abd. III have *ms*-setae (formula 10/001). Dorsal *s*-setae constituted by single *al*-seta on Th. II and Th. III, single *as*-seta on Abd. V and by *accp*-setae (4–7 on each tergite from Th. II to Abd. V) normally set within *p*-row (Fig. 2B). The number of *accp*-setae can be expressed as 5–6,6/5–6,5,7,6–7,4 (Fig. 2B). The number of ordinary setae between *accp*-setae may vary by 1 (rarely 2) with respect to the scheme presented in Figure 2B (after Potapov 1989).

HEAD. Antennae longer than cephalic diagonal ($D/A = 0.79$). Ratio among Ant. I/Ant. II/Ant. III/Ant. IV is 1/1.75/1.57/2.57. Some *s*-setae well differentiated, others thick and hardly differing from ordinary setae (hereafter ‘seta-like *s*-setae’). There are often cases of asymmetry among *s*-setae between antennae of the same specimen. Ant. I has about 54 setae, 6–11 short, thick and cylindrical *s*-setae and 4 seta-like *s*-setae in ventro-lateral position; 2–3 microsetae in ventro-proximal position (Fig. 2E). Ant. II has about 90 setae, 4 *s*-setae and 2–3 seta-like *s*-setae (Fig. 2E). Ant. III has about 84 setae and a sensory field that includes 2 *s*-setae of AO III, about 8 *s*-setae and 6 seta-like *s*-setae (Figs 2E; 5C). Ant. IV plurichaetotic with more than 300 setae, with few *s*-setae and several seta-like *s*-setae; one simple small subapical, rod-shaped organite and a clearly bifurcate pin-like seta (Fig. 2D). Eye spots strongly dark pigmented with 8 + 8 ocelli (G and H usually hardly visible; Figs 2C, 5A). PAO elongated, with a weak median constriction, about 2 times as long as diameter of nearest ocellus (Fig. 2C). Prelabral setae 4. Labral formula as 5, 5, 4 and 4 sharp papillae (Fig. 4C). Maxillary palp bifurcate and maxillary outer lobe with 4 sublobal hairs (Fig. 4F). Labial palp with 5 papillae and a total of 16 guard setae (Fjellberg 1999) distributed as: A_1 , B_{1-4} , C_0 , D_{1-4} , E_{1-7} (Fig. 4B). Hypostomal papilla with H as long as h_1/h_2 . Proximal (px), basomedian (bm) and basolateral (bl) fields of labium with 4, 4 and 5 setae, respectively (Fig. 4A).



Fig. 1. *Desoria calderonis* sp. nov., general aspect.

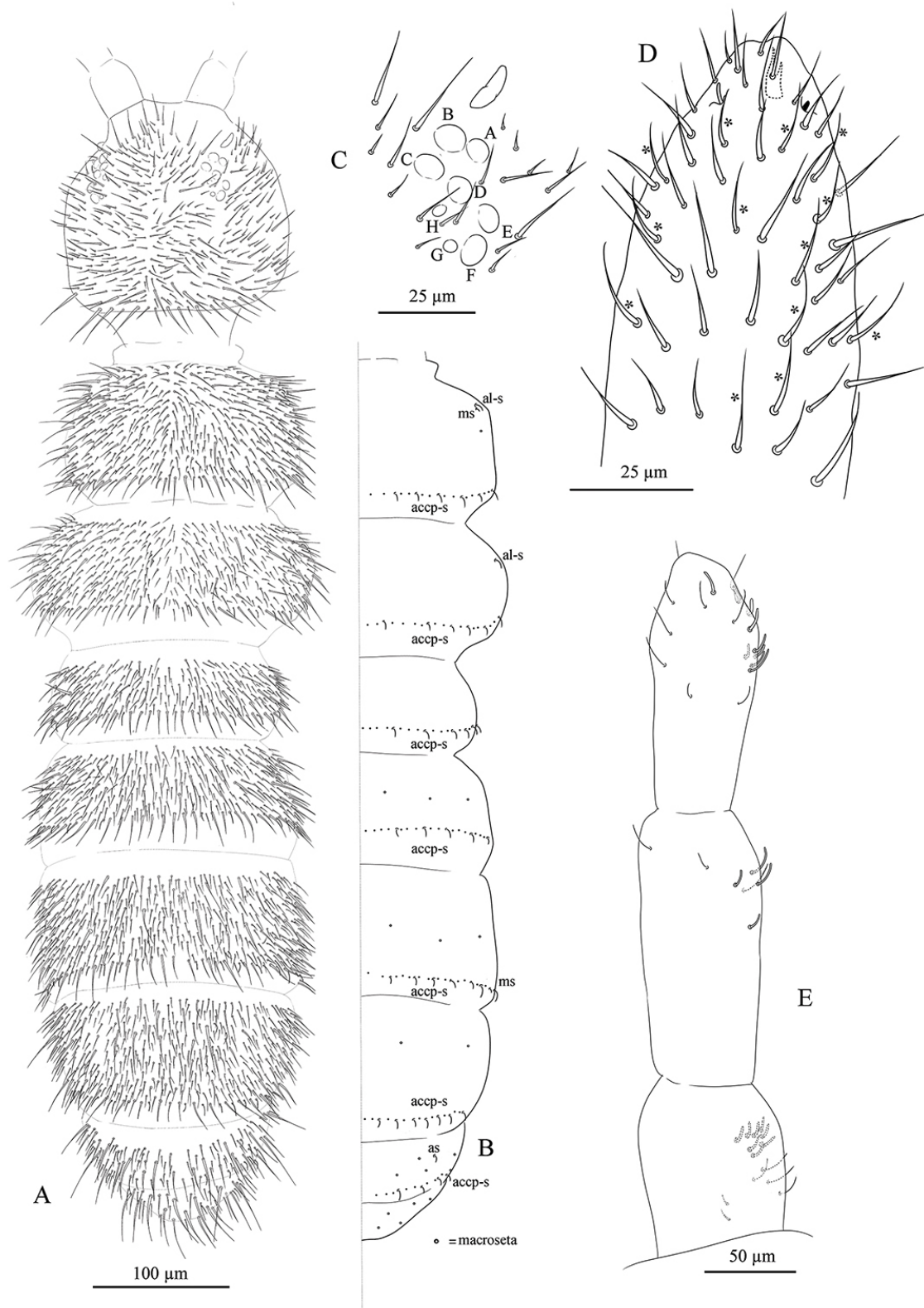


Fig. 2. *Desoria calderonis* sp. nov. **A.** Dorsal chaetotaxy. **B.** Number and distribution of dorsal *s*-setae (*accp-s*: *accp*-setae; *al-s*: *al*-setae; *as*: *as*-setae) and *ms*-setae (*ms*). **C.** Ocular plate (A–H: eyes) and PAO. **D.** Ant. IV apical dorsal part; asterisk = seta-like *s*-seta. **E.** Ant. I–III, dorsal view, with *s*-setae (double line) and seta-like *s*-setae (simple line); on ventro-proximal part of Ant. I, two isolated microsetae present.

Table 1. Body measurements of *Desoria calderonis* sp. nov.

	Length (µm)										
	Head (dorsal)	Body	Ant. I	Ant. II	Ant. III	Ant. IV	Cephalic diagonal	Furca	Mac (Abd. V)	Abd. V	Inner edge of Claw3
Mean value (µm)	311	1171	61	107	97	164	338	495	191	193	95
Standard deviation	20	82	8	11	12	15	39	43	10	13	8
Number of measurements	11	12	12	12	12	12	5	12	11	10	11

Maxilla of normal shape as in Fig. 4E, with lamellae shorter than capitulum. Ventral line of head with 9 + 9 postlabial setae (Fig. 4A). Mandible with well-developed molar plate as in Fig. 4D. VT with 2–4 + 2–4 anterior, 4 + 4 latero-distal and 4 posterior setae with 2 in apical transverse row (Fig. 4I). Retinaculum with 4 teeth and 7–8 setae (Figs 3F, 5D).

FURCA. Well-developed; ratio of mucro/dens/manubrium = 1/41/19 (Fig. 3D–E). Ventral setae on manubrium numerous (about 88) and ventro-apical setae (10–12) larger than the others (Fig. 3D), with the exception of 2 + 2 short apical setae; more than 70 dorsal setae (Fig. 3E). Dens with dorsal crenulations, about 200 ventral and 18 dorsal setae (Fig. 3D–E). Mucro quadridentate with apical tooth much smaller than subapical one (Fig. 3G).

LEGS. Upper and lower subcoxa of Leg I with 1 outer seta (Fig. 3A). Upper subcoxa of Leg II with 7, lower subcoxa with 6 outer setae (Fig. 3B). Upper subcoxa of Leg III with 10, lower subcoxa with 19 outer setae (Fig. 3C). Coxa with 5, 10, 24 setae, respectively, on leg I, II, III (Fig. 3A–C). Trochanter with 20, 21, 20 setae, respectively, on leg I, II, III. Femur with 36, 42, 74, respectively, on leg I, II, III. Tita with 45, 54, 96 setae, respectively, on Leg I, II, III; tenent hair pointed (Fig. 3I). Claw of normal shape with lateral and inner teeth; empodium with a small inner tooth; pretarsus with a pair of setae (Fig. 3I).

Measurements

See Table 1.

Ecology

Desoria calderonis sp. nov. was found only on supraglacial stony debris of the Calderone glacier at 2650–2700 m a.s.l. (Appendix 1A). The supraglacial stony debris (carbonate: dolomite and limestone) is very coarse and the fine component is poorly represented (Appendix 1B). In this mineral, inorganic soil, *D. calderonis* sp. nov. was found mostly where the debris is in contact with the ice (Appendix 1B). In this environment, the vegetation cover is almost absent, with the rare exception of sporadic seedlings of *Arabis alpina* ssp. *caucasica* (Willd.) Briq. On supraglacial debris the mean annual temperature is 0.67°C (4.6°C during the snow-free period), the minimum recorded was -7.7°C and maximum 36.1°C; the snow cover persists on average for 250 days a year; the relative humidity is on average 95.7% during the whole year (85.9% during the snow-free period). Since *D. calderonis* sp. nov. was found only on supraglacial stony debris, and not in the surrounding habitats (LIA moraines: mean annual temperature = 1.3°C, mean temperature during snow-free period = 4.4°C; minimum = -9.8°C; maximum = 40.7°C; annual relative humidity = 88.7%; mean relative humidity during the snow-free period = 84.7°C; snow cover duration = 146 days), we can consider this species as cryophilic. On supraglacial debris, pH is 8.6, the organic matter content is 1.7 g/kg and carbonate calcium content is 96.2%, while on LIA moraine, pH is 8.3, organic matter content is 3.9 g/kg and carbonate calcium content is 91.4%.

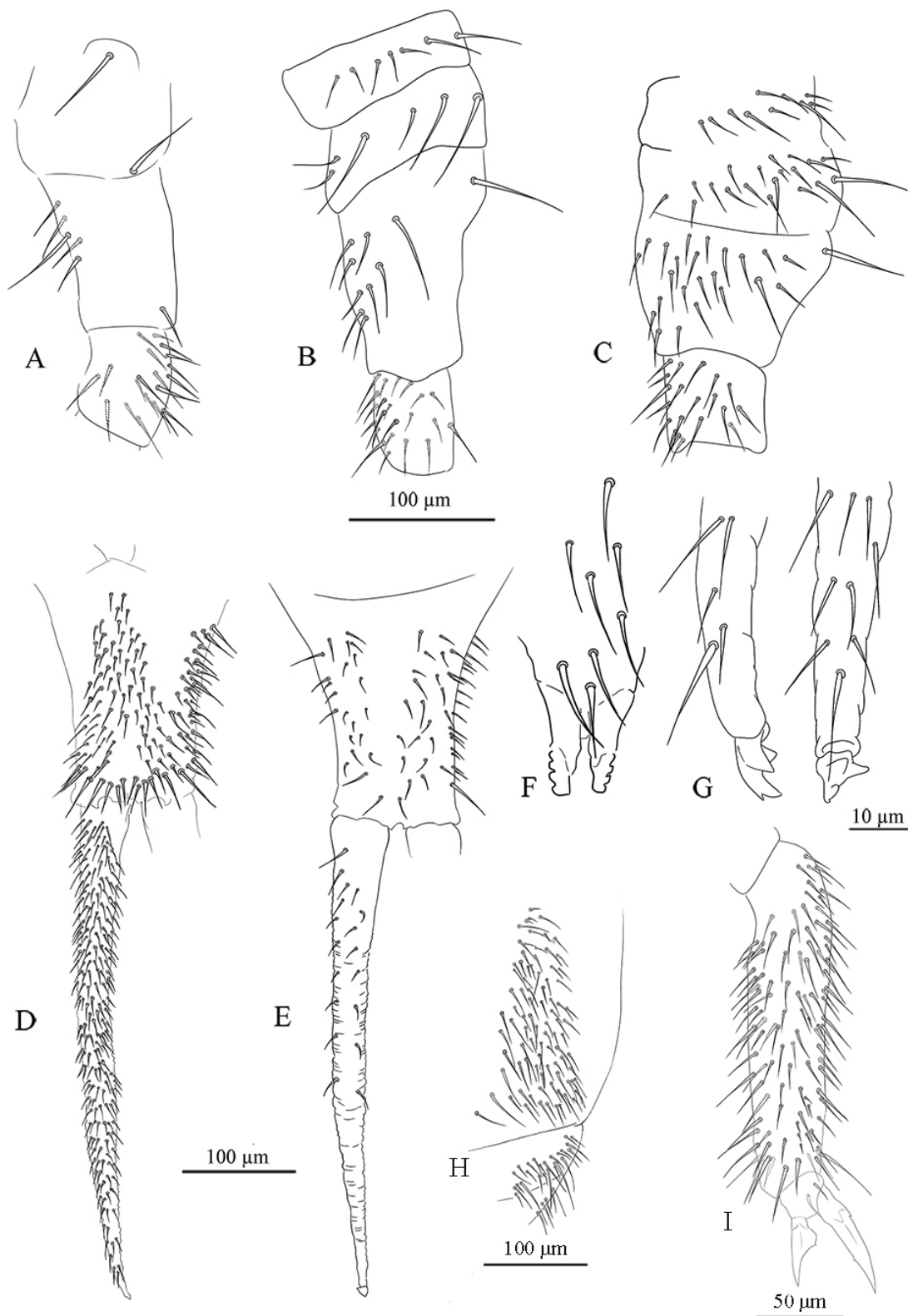


Fig. 3. *Desoria calderonis* sp. nov. **A.** Leg I, left; upper and lower subcoxa, coxa and trochanter. **B.** Leg II, left; upper and lower subcoxa, coxa and trochanter. **C.** Leg III, left; upper and lower subcoxa, coxa and trochanter. **D.** Ventral side of furca. **E.** Dorsal side of furca. **F.** Retinaculum. **G.** Mucro and apical part of dens, lateral and dorsal views. **H.** Lateral part of Abd. IV–V sternites. **I.** Tita III and Claw III.

Table 2 (continued on next page). Characters important for *Desoria* taxonomy are compared for the species of the *violacea*-group. The green colour highlights characteristics common between *D. calderonis* sp. nov. and all other known species of the group (with an inclusive criterion, in order not to overestimate differences, but, at least, to underestimate them).

Species of <i>violacea</i> -group	<i>D. hiemalis</i> (Schött, 1893)	<i>D. duodecemoculata</i> (Denis, 1927)	<i>D. blufusata</i> (Fjellberg, 1978)	<i>D. blekeni</i> (Leimaas, 1980)	<i>D. alaskensis</i> (Fjellberg, 1978)	<i>D. calderonis</i> Valle sp. nov.
Colour	dark bluish-grey or bluish-violet. With extremities paler	violet to bluish-grey	dark violet-blue	dark violet-blue	blue-red to bluish-black	violet-black on abdomen and antennae, lighter on furca and legs, which are brownish (Fig. 1); juvenile much paler, bluish
Pin-seta	bifurcate	bifurcate	bifurcate	with basal process	bifurcate	bifurcate
Short and thick sensilla on Ant I	no	no	no	no	no	x
Laterodistal setae on VT	11/23 + 11/23	4 + 4	6/13 + 6/13	5/5 + 5/6	10/26 + 10/26	4 + 4
Anterior setae on VT	10/19 + 10/19	1 + 1	5/9 + 5/9	2/4 + 2/4	–	2/4 + 2/4
Posterior setae on VT	14/22	5	6/11	6/7	12/20	4
Short apical setae on Mandible	2/3 + 2/3	2 + 2	1/2 + 1/2	1 + 1	3 + 3 (rarely less)	2 + 2
Posterior setae on dens	9/14	8	20/40	9/11	25/45	18
Dimension of apical tooth on mucro with respect to the subapical one	equal or larger	smaller (sometimes apical one hardly visible)	equal or larger	equal or larger	larger	smaller
Basomedian setae on labium	5	4	5/6	4	5	4
Maxilla lamellae	short	short	short	short	short	short
PAO length with respect to the nearest OMMA diameter	0.9/1.2	1.5/2.0	1.4/1.8	0.9/1.1	1.8/2.3	2.0
Abd V–VI fused	separated or partly fused	no	x	no	x	no
Length of Abd.V macroseta with respect to median length of tergite (and of Claw3)	2.0/2.3 (3.0/4.0)	1.1 (–)	– (2/2.8)	1.1/1.5 (2.8/3.0)	– (3.0/4.0)	0.9/1.0 (1.8–2.4)
Number of characteristics in common with <i>D. calderonis</i>	5	10	4	6	3	3

Table 2 (continued).

Species of <i>violacea</i> -group	<i>D. violacea</i> (Tullberg, 1876) sensu Fjellberg 1979	<i>D. taimyrica</i> (Martynova, 1974)	<i>D. nivea</i> (Schäffer, 1896)	<i>D. nivalis</i> (Carl, 1910)	<i>D. neglecta</i> (Schäffer, 1900)
Colour	dark violet blue/black.; with head, posterior part of ventral and lateral sides withish	intensively green, greyish, or dark olive green	white, eye region black	deeply black. Dens, Ant II–III and distal part of legs white	grey, greyish brown, greyish green or red
Pin-seta	bifurcate	bifurcate	simple	with basal process	simple
Short and thick sensilla on Ant I	no	no	x	no	no
Laterodistal setae on VT	7/22 + 7/22	6/13 + 6/13	7/13 + 7/13	4/5 + 4/5	7/13 + 7/13
Anterior setae on VT	3/10 + 3/10	3/8 + 3/8	4/7 + 4/7	4 + 4	7/13 + 7/13
Posterior setae on VT	4/10	5/9	4/6	4	7/14
Short apical setae on Mandible	1/3 + 1/3	2 + 2	1/3 + 1/3	2/4 + 2/4	2/3 + 2/3
Posterior setae on dens	12/19	14/19	7/11	8	15/30
Dimension of apical tooth on mucro with respect to the subapical one	equal or larger	equal or smaller	equal or larger	smaller	equal or larger
Basomedian setae on labium	5	5	5	4	5
Maxilla lamellae	short	short	long	short	short
PAO length with respect to the nearest OMMA diameter	1.2/1.5	1.2/1.5	2.0	1.5	2.0/2.4
Abd V–VI fused	no	no	no	no	no
Length of Abd. V macroseta with respect to median length of tergite (and of Claw3)	1.1/1.5 (2.3/3.1)	1.1/1.3 (2.4/2.9)	0.5/0.6 (1.1/1.2)	1.1 (–)	0.8/1.2 (2.2/2.7)
Number of characteristics in common with <i>D. calderonis</i>	8	7	6	10	6

Distribution

Desoria calderonis sp. nov. is currently known only for the type locality.

Type locality

Gran Sasso massif, Apennines, Calderone glacier (42°28'16.2" N, 13°34'05.8" E). Supraglacial stony debris of Calderone glacier, altitude: 2650–2700 m a.s.l.

Taxonomic and ecological considerations

Desoria calderonis sp. nov. belongs to the *violacea*-group sensu Potapov 2001, having mucro quadridentate, without seta, maxillary palp bifurcate, apical folds on labrum sharp. It differs from most species of this group (Table 2) by the reduced number of setae on VT (with the exception of *D. duodecemoculata* (Denis, 1927) and *D. nivalis* (Carl, 1910), which also have few setae, but in a different number). *Desoria calderonis* sp. nov., in addition, has a characteristic sensory field on Ant I with short, thick and cylindrical *s*-setae; this characteristic is common, for Palearctic *Desoria*, to many species of the *fennica*-group (sensu Potapov 2001) – *D. atkasukiensis* (Fjellberg, 1978), *D. fennica* (Reuter, 1895) sensu Fjellberg 1979, *D. fjellbergi* (Najt, 1981), *D. iuxta* (Dunger, 1982), *D. kaszabi* (Dunger, 1982), *D. saltans*, *D. tigrina* Nicolet, 1842 – two species of *olivacea*-group – *D. infusata* (Murphy, 1959) and *D. olivacea* (Tullberg, 1871) sensu Fjellberg 1979 – and only one species of the *violacea*-group – *D. nivea* (Schäffer, 1896). Among species of the *violacea*-group, another peculiarity of *D. calderonis* sp. nov. is the number of dorsal setae on the dens, similar only to that in *D. neglecta* (Schäffer, 1900) sensu Fjellberg 1978, *D. taimyrica* (Martynova, 1974) and *D. violacea* (Tullberg, 1876) sensu Fjellberg 1979. In general, *D. calderonis* sp. nov. differs by a combination of at least four important characters (Table 2) from every species of the group.

Within the group, considering the number of common characteristics, *D. calderonis* sp. nov. appears most similar to *D. duodecemoculata* – present in Italy, Austria, Spain and France (Potapov 2001) – and *D. nivalis*, present in the Alps (France, Switzerland, Austria) and possibly in eastern Europe (Potapov 2001) (Table 2). Nevertheless, some features allow us to discriminate the new species from these. First, *D. duodecemoculata* and *D. nivalis* do not have short, thick and cylindrical, but only hair-like *s*-setae on Ant I. In addition, the new species differs from *D. duodecemoculata* by the chaetotaxy of VT and the number of dorsal setae on the dens; it differs from *D. nivalis* by having Ant II-III violet-black (white in *D. nivalis*), a longer PAO and by the number of dorsal setae on the dens.

Both *D. duodecemoculata* and *D. nivalis* belong to the *nivalis*-complex, a group of European mountain species included in the *violacea*-group. *Desoria nivalis*, in particular, is known to live near snow fields and other cold sites in high mountains (Handschin 1924; Franz & Serrl-Butschek 1954), while the ecology and the taxonomy of the other members of the complex need to be revised (Potapov 2001). Because of these similarities in morphology and ecology, we could ascribe our species to this *nivalis*-complex, even if we reported marked differences, in particular the presence in *D. calderonis* sp. nov. of the sensory field on Ant. I.

Phylogenetic context

The phylogenetic tree (Fig. 6), with a log-likelihood of 3077.45, is characterized by good support at recent nodes but low support at deeper nodes. It appears subdivided into three major clusters, two dominated by *Isotoma* and *Isotomurus*, respectively, and one by *Desoria*, with records representing 14 different *Desoria* species as well as others incompletely identified as *Desoria* sp. This latter cluster also included scattered sequences from the following genera: *Vertagopus*, *Pseudisotoma*, *Isotoma*, *Skadisotoma*, *Proisotoma*, *Isotomurus*, *Agrenia*, *Metisotoma*, *Axelsonia*, *Chionobora* and *Kaylathalia*. Within the *Desoria* cluster, *Desoria calderonis* sp. nov. clustered with high support (99) with one bin

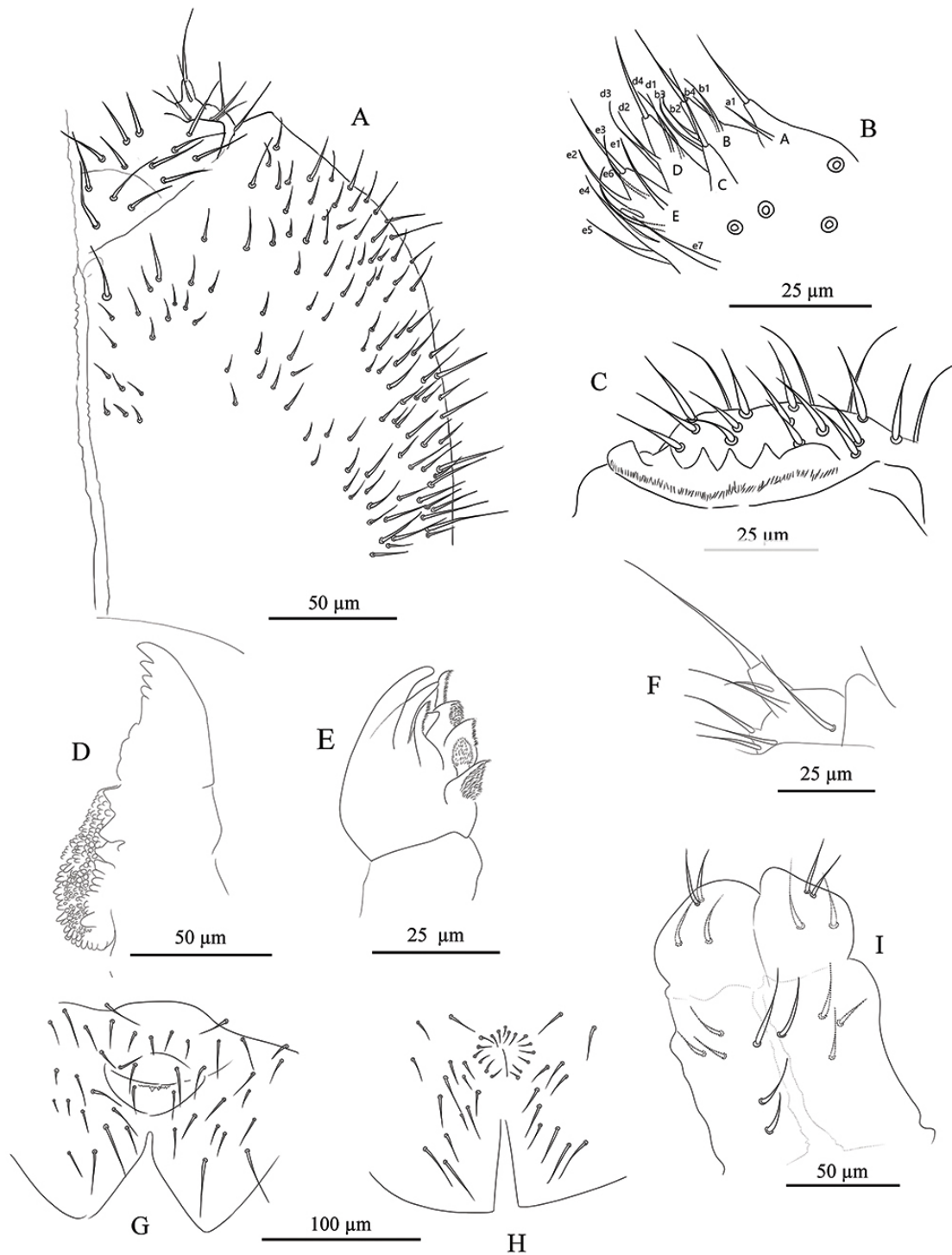


Fig. 4. *Desoria calderonis* sp. nov. **A.** Ventral chaetotaxy of head. **B.** Labial palps. **C.** Labrum. **D.** Mandible. **E.** Maxilla. **F.** Maxillary palp. **G.** Female genital opening. **H.** Male genital opening. **I.** VT in posterior view.

(AAO3603) identified as *Desoria* (with no indication on the species, 4 sequences from France) and *Vertagopus arboreus* (1 sequence from Ontario, Canada). The mean divergence between *D. calderonis* sp. nov. and this bin is 16.9% (S.D. 0.2). Both bins were associated (support 97) with one record of *D. tigrina* and this latter cluster, although with lower support, was associated with records of *D. blufusata*, *D. germanica*, *D. intermedia* and *D. violacea*.

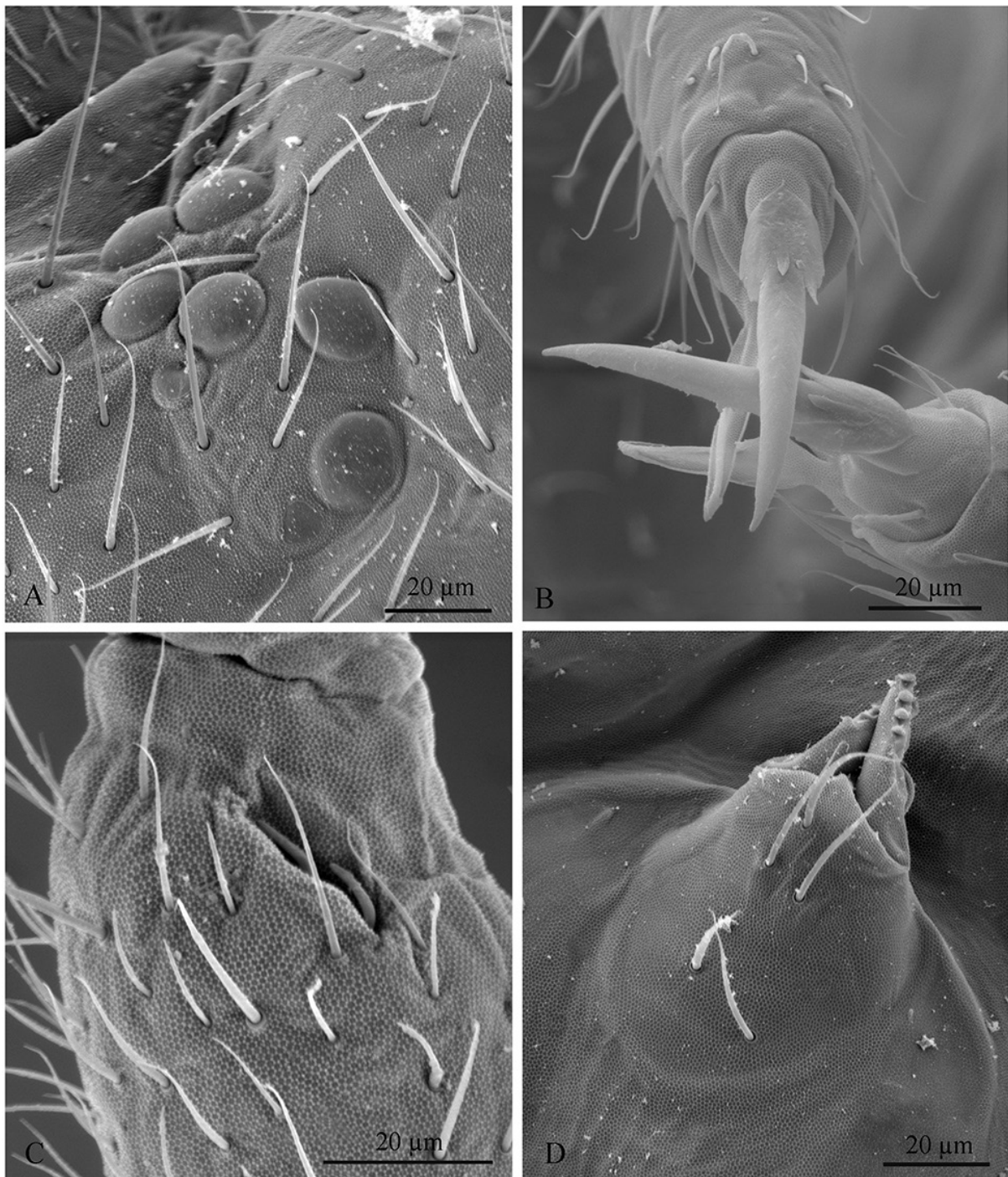


Fig. 5. *Desoria calderonis* sp. nov., scanning electron microscopy. **A.** Ocular plate. **B.** Claws. **C.** Antennal organ III. **D.** Retinaculum.

Apart from *D. violacea* (BOLD:AEA8472), *D. tigrina* (BOLD:ACS3918), *Vertagopus arboreus* (BOLD:AAO3603), and individual records mined from GenBank with no location information, all other reports come from areas characterized by a markedly cold climate, mostly in Northern Europe. Similarly to *D. calderonis* sp. nov., *D. blufusata* (BOLD:ACT9239, 3 records), *D. intermedia* (BOLD:AAI9461, 4 records) and *D. germanica* (BOLD:AAI9461, 2 records; see Stevens *et al.* 2006 for sampling information) were collected in low-temperature habitats, specifically in Norway and Sweden, with two records of *D. intermedia* explicitly associated to a snow covered setting. At variance, *Desoria* sp. (BOLD:AAO3603), for which species level identification is missing, originated from British Columbia (Canada) as well as the Ile-de-France (France).

Discussion

Our analysis supports the idea that *Desoria* is a polyphyletic group, as already observed by Stevens & D’Haese (2017). In particular, *Desoria* clustered with *Vertagopus*, *Pseudisotoma*, *Isotoma*, *Skadisotoma*, *Proisotoma*, *Isotomurus*, *Agrenia*, *Metisotoma*, *Axelsonia*, *Chionobora* and *Kaylathalia*. Most of the *Desoria* records came from areas characterized by a markedly cold climate and here cluster with other strictly cold-adapted and cryophilic organisms. In particular, *Agrenia* Börner, 1906 is a Holarctic genus living in damp and cold habitats such as banks of cold-water streams and the shores of lakes in tundra and mountain zones (Fjellberg 1988), on or near snow (Fjellberg 1976, 1986, 1994) and polar deserts (Chernov *et al.* 1977). Hågvar (2010) reported *A. bidenticulata*, *Desoria olivacea* and *D. infuscata* as the most pioneer species of the proglacial succession along Midtdalsbreen glacier (Norway). *Skadisotoma* Greenslade & Fjellberg, 2015 is a mountain endemic Australian genus linked to snow patches (Greenslade & Fjellberg 2015) and taxonomically related to *Desoria*. *Chionobora* Greenslade & Potapov, 2015 is an endemic hygrophilous Tasmanian genus, living around the lakes of the Central Plateau, the largest area of high ground in Tasmania. *Kaylathalia* is an Antarctic isotomid and was regarded as belonging to *Desoria* until Stevens & D’Haese (2017). *Isotoma* and *Isotomurus* are present in this cluster with a few sparse sequences identified at the genus level, but most of the sequences belonging to these genera were grouped in two alternative well defined groups outside the *Desoria* cluster. Thus, we hypothesize that the sparse *Isotoma* and *Isotomurus* sequences clustering with *Desoria* could be phylogenetically misplaced or not properly identified specimens. Therefore, we suppose that the genera more strictly related to *Desoria* are *Vertagopus*, *Skadisotoma*, *Agrenia*, *Metisotoma*, *Axelsonia*, *Chionobora* and *Kaylathalia*.

The position of the new species in a cluster composed entirely of *Desoria* sequences (with the exception of a single sequence of *Vertagopus*) supports its morphological identification as belonging to the genus. *Desoria calderonis* sp. nov. is dissimilar (17.8% genetic variability) to all other sequences present in the BOLD database. Morphologically, *D. calderonis* sp. nov. is more similar to *D. nivalis* and *D. duodecemoculata* of the mountain and cold-adapted *nivalis*-complex (*violacea*-group). However, this affinity was not testable phylogenetically with the available dataset, since no sequences from this complex are present.

In terms of subgeneric relationships, *D. calderonis* sp. nov. appears to be related to species belonging to both the *fennica*- (*D. tigrina*: bin BOLD:ACS3918; *D. germanica* and *D. intermedia*: bin BOLD:AAI9461) and *violacea*-group (*D. blufusata*: bin BOLD:ACT9239 and *D. violacea*: BOLD:AEA8472), leaving the question of its morphological assignment to the *violacea*-group untestable. In general, our phylogenetic results do not support the morphological groups reported by Potapov (2001) as natural assemblages.

From a methodological standpoint, the *Desoria* phylogeny presented here is difficult to interpret due to the possibility that some key groups are polyphyletic, the lack of sequence data for crucial elements and the uncertainty in the attribution of some sequences. In fact, building robust phylogenetic trees would require the combination of data from a large number of genes, integrating nuclear and mitochondrial

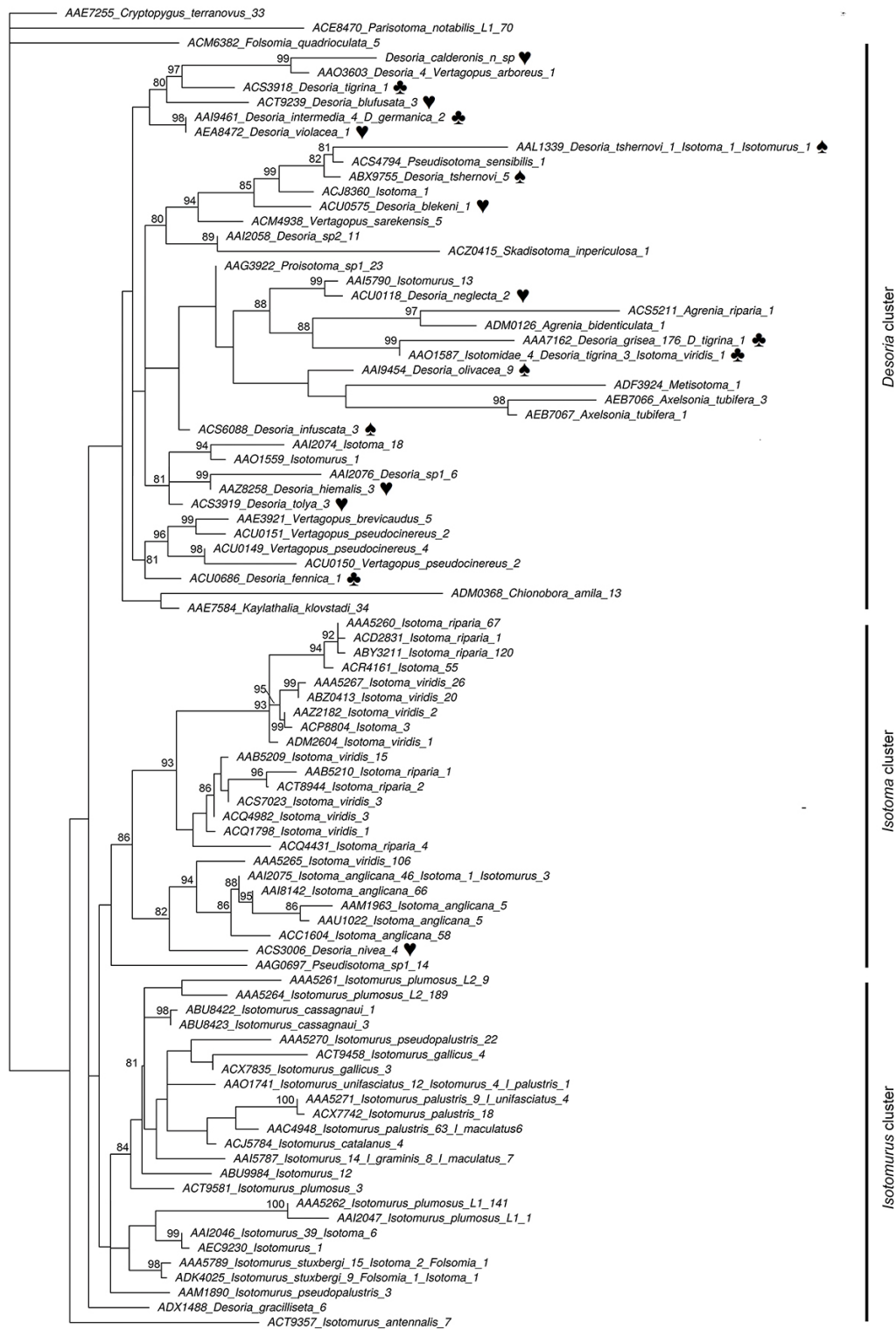


Fig. 6. Phylogenetic tree of *Desoria calderonis* sp. nov. and related species, on the basis of the *coxI* gene. Names include the BOLD bin number, as well as the taxonomic attribution and number of sequences included in the bin. Genera were abbreviated where unambiguous within the bin. When records of the same bin had multiple taxonomic attributions, the one at the lowest level was retained if all were compatible. Alternatively, all were listed separately. Bootstrap support is indicated if > 80. ♠: *olivacea*-group; ♣: *fennica*-group; ♥: *violacea*-group of *Desoria*.

information, and the *coxI* barcoding fragment is suboptimal in terms of resolution, especially at deeper nodes. Nevertheless, a great advantage of *coxI* is the availability of a large number of sequences in the BOLD database, including sequences from rare or difficult to sample species. Thus, the use of this gene allows for preliminary considerations on the phylogenetic context of the new species even in the absence of a consolidated taxonomy of the group, which would require more complete phylogenetic analyses.

Desoria species, with few exceptions (e.g., *D. violacea*, xerophilic, *D. blekeni*, mesophilic; Fjellberg 1975, 1988; Leinaas 1980), are cold and wet adapted organisms (Potapov 2001). Cold and wet environments are more common in northern Europe also in mountain forests, ponds and rivers. In Mediterranean regions, these environments are extremely fragmented and there is evidence that cryophilic springtails could find suitable habitat – ice – only in isolated refugial areas, like caves (Raschmanová *et al.* 2018) or alpine glaciers, glacierets, the banks of glacial streams and permanent snowfields (Lauga-Reyrel & Lauga 1995; Fjellberg 2010). This fragmentation of suitable habitats is compatible with the notion of a great undescribed cryophilic endemic biodiversity, largely constituted by springtails taxonomically related to the *Desoria* genus (Deharveng 1975; Najt 1981; Lauga-Reyrel & Lauga 1995; Fjellberg 2010; Hittorf 2017).

Desoria calderonis sp. nov. was described for the Calderone glacier, a relict, isolated glacier of the Apennines, a peripheral mountain chain without other existing glaciers. This is in line with the hypothesis of an undescribed fragmented glacial springtail biodiversity in refugial areas. It is noteworthy that, these glacial areas are highly threatened by climate change (Grunewald & Scheithauer 2010). We do not know the fate of the cold adapted and cryophilic collembolan fauna in these areas, but extinction seems to be a likely scenario (Greenslade & Fjellberg 2015). This underlines the importance of studying these unique environments and preserving their biodiversity in order to know it before its definitive disappearance.

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Appendix 1A. Calderone glacier, lower tongue mostly covered by stony debris. Photo taken on 8 Jul. 2020, when there was still a high snow cover. Red arrows indicate the sampling points where *Desoria calderonis* sp. nov. was sampled with the flotation method.



Appendix 1B. Supraglacial debris where *D. calderonis* sp. nov. was discovered. This is a coarse mineral soil in contact with the ice of the Calderone glacier: *D. calderonis* sp. nov. lives at the ice-stony debris interface. Red arrows indicate *D. calderonis* sp. nov. specimens moving on the ice and cold debris.

