



Alpine blooming of “snow fleas”: the importance of snow for Alpine springtails (Hexapoda: Collembola) ecology and biodiversity

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Abstract

Springtails can occur in large populations on the snow surface. This peculiar habitat hosts specialized winter-active springtails living in colonies and using this seasonal habitat for feeding, effective dispersal and migration. Snow-active species have never been studied in Southern European Alps: the aim of this work is to study snow-active springtails of Adamello-Brenta Nature Park (“PNAB”; Italy), a peripheral mountain range of relevant biogeographic interest using integrative taxonomy. Springtail “bloomings” were sampled for 17 months by an environmental assistant of the park. Nine assemblages of springtails were found when temperatures were higher than 0 °C; eight were monospecific, with a total of five species found. The snow-active springtail fauna found includes both common Central-Northern European nival species like *Desoria hiemalis* (first record for Italy, although genetically differentiated from Northern Alps populations), *Ceratophysella sigillata* (known in Italy mainly from caves) and three species likely new to science (*Hypogastrura* cf. *kelmendica* sp1, *Hypogastrura* cf. *kelmendica* sp2, *H.* cf. *peloponnesica*, all belonging to the *Hypogastrura socialis* group). Snow is an important ephemeral habitat for springtails, for the biodiversity hosted and for its importance as an ecological corridor. We could hypothesize that snow, especially in peripheral mountain chains, acts as a fragmentary ephemeral habitat for those cold-adapted springtails. This could constitute a relevant aspect to take into consideration for conservation biology, especially in the context of the ongoing climate change. On the other hand, the Alpine chain probably acts as an ecological barrier for nival species, since isolated species and populations were found in PNAB.

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Graphical Abstract



snow-active springtails of European Alps poorly studied



aim: surveying springtails blooming on snow in an area of relevant biogeographic interest in Southern European Alps, Adamello Brenta Nature Park (Italy)

methods: - sampling by park environmental assistants;
- integrative taxonomy

9 assemblages,
5 species found

detected when
temperature > 0°C



Desoria hiemalis



Ceratophysella sigillata



three species likely new for sciences belonging to *Hypogastrura socialis*-group



peculiar biodiversity, populations probably isolated from Northern Alps.

snow, on European Alps, may act as a fragmentary azonal habitat for cold-loving springtails

Keywords Cold-adapted species · Collembola · Ecological corridors · Integrative taxonomy · Mountain ecology · Nival fauna · Snow-active · Winter ecology

1 Introduction

Among snow-active arthropods (Leinaas 1981a; Vanin and Turchetto 2007; Hågvar 2010), springtails (Hexapoda: Collembola) are particularly active on the snow surface, and are well known for showing large mass occurrences (e.g., 4000 animals per m² snow surface in coniferous forest in Norway; Hågvar 2000; Leinaas 1981a), also visible with naked eyes by unskilled observers.

In particular, the supranival environment hosts specialized winter-active springtails (Leinaas 1981b,c) — typically living in colonies (Leinaas 1983) — that could use this seasonal habitat not only for feeding (Zettel et al. 2002; Hao et al. 2020), but also for effective dispersal and migration (Hågvar 1995, 2000; Zhang et al. 2017). Using sun position, and probably thanks to their high mobility via jumps on the

smooth and moist snow surface (Hågvar 2000), migrations of hundreds of meters per day are possible (Hågvar 1995; Zhang et al. 2017). In many podurids (Poduromorpha; e.g., *Hypogastrura socialis*, *Ceratophysella sigillata*), this is possible also thanks to the presence of specialized anal vesicles that allow them to adhere to the substratum after landing (Leinaas 1988; Zerneck 1999). Usually, new colonies are established after migration (Hågvar 2010; Leinaas 1983). In addition, this winter behavior may be an efficient way of exchanging genes between populations that live separated during summer (Leinaas 1981a). In fact, these winter-active species usually live in a patchy and temporary micro-habitat during the snow-free period (Leinaas 1983; Hågvar 2000), as it is known for *Hypogastrura socialis*, typically inhabiting in summer well-drained heaps of needle litter below spruce trees (Leinaas 1981a). Thus, during winter, snow acts as an

ecological corridor. In general, intraspecific aggregations are promoted in springtails by pheromones (Tosi et al 1977; Mertens and Bourgoigne 1977; Krool and Bauer 1987) facilitating: (i) the attraction of the opposite sex, and (ii) the aggregation on feeding resources (Hopkin 1997). For example, Zernecke (1999) observed that *H. socialis* feeds on spruce pollen.

The peak of activity on snow occurs during mild (i.e., sunny days with partial snow melting, maybe also because they need sun for orientation) and humid weather (i.e., in a dry period, springtails swarm at the first rain), and springtails move down in the subnivean environment, more temperature-buffered (average temperature of ca. 0 °C), when the weather gets colder (Leinaas 1981a; Hågvar 2000). During the day, activity peak occurs in hours when mild temperatures are recorded (Zhang et al. 2014). Activity at low temperatures requires physiological adaptations; for instance, the presence of antifreeze agents in certain Alpine springtails was demonstrated by Zettel (1984).

In Europe, specialized species that are known to be regularly active and migrating on the snow surface are *Hypogastrura socialis*, *H. lapponica*, *Vertagopus westerlundii*, *Desoria hiemalis*, *D. tolya* (Hågvar 2010; Leinaas 1981c), and *Ceratophysella sigillata* (Zettel et al. 2002). *Hypogastrura peloponnesica* (Danyi 2013) is a recently described species, found swarming on the Menalo Mts. (Greece) among melting snow patches. In China, Zhang et al. (2014) and Hao et al. (2020) documented the activity on the snow surface of three unidentified species belonging to the genus *Desoria*.

If, for Northern Europe, detailed ecological studies have already been published (e.g. Leinaas 1981c; Hågvar 2000, 2010), the knowledge of snow-active species in the European Alps is still incomplete (Thaler 1999): for Northern European Alps, only some ecophysiological studies have been performed on few documented snow-active springtails (Zettel and Zettel 1994; Zettel et al. 2002) and no studies are available for Southern European Alps. Our expectation is that snow habitats in Southern European Alps would host the same species that inhabit the snow habitat of Northern Alps and Northern Europe, since those species are widespread in Europe (e.g., *Desoria hiemalis*, *Hypogastrura socialis*; *Ceratophysella sigillata*; Potapov 2001; Thibaud et al. 2004).

The aim of this work is to provide a first insight about snow-active springtails in a protected area of the Southern European Alps, the Adamello-Brenta Nature Park.

We selected this area because: (i) it represents a peripheral mountain range of relevant biogeographic interest given the a large amount of endemic species of plants and arthropods (Gobbi et al. 2021; Rota et al. 2022); (ii) the Brenta

mountain group belongs to the Dolomites chain, and thus, it is an UNESCO World Heritage Site (<https://whc.unesco.org/en/list/1237/>, accessed on 16 June 2023); (iii) it is deeply affected, as the rest of the Southern European Alps, by the ongoing climate change in terms of glacier disappearance and snow cover reduction (Edwards et al. 2007; Zebre et al. 2021; Marta et al. 2023).

2 Material and methods

2.1 Study area

The study was performed in the Adamello-Brenta Nature Park (“PNAB”; Central-Eastern Italian Alps), the largest (620 km²) protected area in Trentino-Alto Adige region with an altitude that spans between 477 and 3.558 m a.s.l. (Fig. 1). The park exhibits a great environmental heterogeneity — including habitats from the valley floor (e.g., broadleaved and coniferous forests, seminatural and natural grasslands) to glacial environment — also because of the occurrence of two distinct lithological, and thus geomorphological, areas: the granitic massif of Adamello-Presanella and the limestone massif of Brenta Dolomites, separated by the Rendena Valley (46°07′07.1″N 10°45′10.7″E).

2.2 Sampling activity

Sampling was performed in the period December 2019 – April 2021, by collecting springtail bloomings all the year (Table 1). The term “bloomings” refers to two different situations: “dense” blooming with at least 20 cm² of the surface completely covered by springtails, and “sparse” blooming in which springtails extend for hundreds of meters, but they do not cover completely the surface. The sampling activity was performed by an environmental assistant of the Park (M.Z.) during faunistic transects aimed at monitoring the presence and distribution of target species of vertebrates and of red wood ant nests (*Formica rufa*) between 800 and 2100 m a.s.l.; for each springtail “bloomings” found on snow, a variable number of individuals (range: 30–200) were collected and preserved in 96% ethanol. In addition, two other springtail assemblages were found on the bare ground (i.e., not on snow) and on water surface, and they were also sampled as a comparison.

Videos and photos in macro-mode were taken by M.Z. during the sampling procedures to obtain original documentation about morphology and behavior. Multimedia material was taken with two cameras: Nikon Coolpix P900 and Nikon D5500, both potentiated with a Ryanox macroscopic

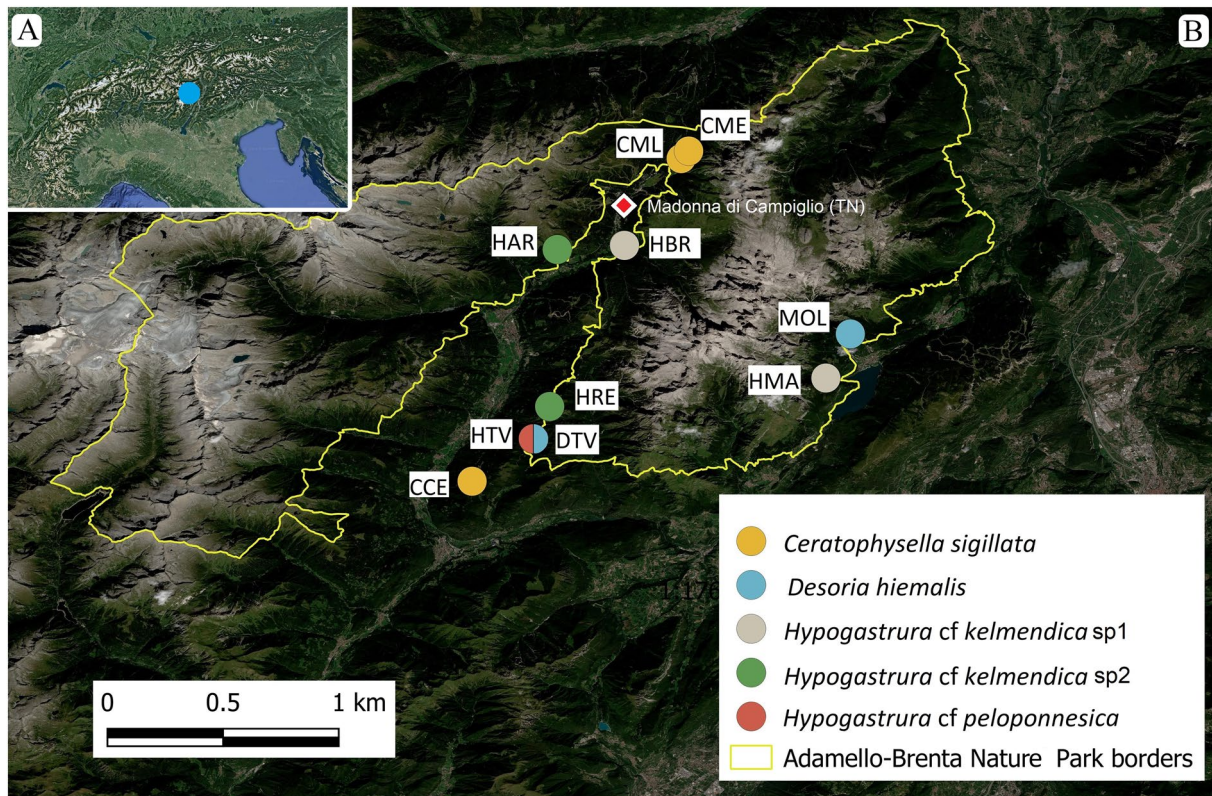


Fig. 1 Position of THE Adamello-Brenta Nature Park on European Alps (A) and sites where springtail populations have been sampled (B); Legend for population codes: see Table 1

lens (Model M-250) for macro videos and photos (Appendix Fig. 5, Supplementary material 1).

All sampling sites and all populations found are reported in Table 1 and in Fig. 1, while in Appendix Fig. 5, pictures of the sampled species and their habitat are reported.

Air temperature of each sampling site at the sampling hour has been obtained by applying a thermal gradient of 0.6 °C/100 m to meteorological data (meteotrentino.it) of the two main areas in which populations have been found: Molveno weather station (835 m a.s.l.) for population “MOL” and “HMA”, occurring in the Valley of Molveno lake, and Giustino weather station (877 m a.s.l.) for the other ones, all belonging to the Rendena Valley. Since weather data have been collected every 15 min, sampling hours were rounded accordingly.

2.3 Specimens' preparation, morphological identification and preservation

For slide preparation, springtails were passed in boiling alcohol for removing fats and cleared by short immersion in 10% KOH solution (1–5 min). Then, after a Chlorophenol

bath, they were mounted on slides using Swann medium as a preservative solution (Rusek 1975). Morphological observations and pictures were made with a Leica DM2500 with phase and DIC contrasts and drawing arm and Carl Zeiss Axiolab 5 with phase-contrast light microscopes. Identification has been performed according to Thibaud et al. (2004), Potapov (2001), Skarżyński and Smolis (2003), Danyi (2013). Specimens preserved in alcohol and permanent slides are preserved at the MUSE-Science Museum of Trento (Italy).

For comparison, we extracted DNA and sequenced the barcode fragment (5'-end of the COI mitochondrial gene) from 5 specimens of *H. kelmendica* Peja, 1985 (population “HKE”, sampled the 13/02/2022 in Poland, near Olsztyn, Kraków-Częstochowa Upland; 50°44'55.5"N 19°16'34.6"E, 300 m asl. Leg. D.S.).

2.4 Molecular data

According to Potapov et al. (2020), both morphological and genetic analyses of integrative taxonomy were performed, to check cryptic diversity. Genomic DNA was extracted

Table 1 Species found and information on micro-habitat (snow, water and ground) and type of blooming (sparse/dense: see “sampling activity” chapter). Station data and sampling data are here reported, and also air temperature at the sampling hour, obtained from weather station data corrected with the thermal gradient (see “sampling activity” chapter)

Species	Code	Data	Hour	Site	Habitat	Coordinates (WGS84, 32 T)	Altitude (m a.s.l.)	Micro habitat	Type of blooming	Air tem- perature (°C)
<i>Hypogastrura cf. kelmendica</i> sp1	HBR	31/12/2019	12:20	Val Brenta, Tre Ville_ Val Fonda (Valles-inella)	<i>Picea excelsa</i> and <i>Fagus sylvatica</i> forest	46°12'21.0"N 10°49'37.6"E	1369	on snow	sparse	2.5
<i>Hypogastrura cf. kelmendica</i> sp1	HMA	17/11/2020	11:57	Val di Ceda (Molveno)	<i>Picea excelsa</i> and <i>Fagus sylvatica</i> forest	46°07'56.2"N 10°56'21.1"E	1087	on water	sparse	9.0
<i>Hypogastrura cf. kelmendica</i> sp2	HRE	07/05/2020	10:15	Val Rendena, Pinzolo	Coniferous forest (<i>Picea excelsa</i>)	46°06'57.6"N 10°47'08.1"E	1737	on snow	dense	10.8
<i>Hypogastrura cf. kelmendica</i> sp2	HAR	14/05/2020	15:30	Val Rendena, Pinzolo	Coniferous forest (<i>Picea excelsa</i>)	46°12'13.8"N 10°47'23.6"E	1695	on snow	dense	14.4
<i>Desoria hiemalis</i>	MOL	29/01/2020	14:32	Rifugio Montanara (Molveno)	<i>Picea excelsa</i> and <i>Fagus sylvatica</i> forest	46°09'24.6"N 10°57'09.8"E	1518	on snow	sparse	1.4
<i>Desoria hiemalis</i>	DTV	23/12/2020	11:59	Val Manez (Tre Ville)	<i>Picea excelsa</i> and <i>Fagus sylvatica</i> forest	46°05'53.6"N 10°46'36.5"E	1675	on snow	sparse	0.2
<i>Hypogastrura cf. pelo-pomesica</i>	HTV									
<i>Ceratophysella sigillata</i>	CCE	08/06/2020	10:27	Monte Amolo (Val Rendena) – loc. Tre Ville, passo Daone	<i>Picea excelsa</i> and <i>Fagus sylvatica</i> forest	46°04'28.8"N 10°44'33.9"E	1301	on litter	dense	7.8
<i>Ceratophysella sigillata</i>	CME	27/04/2021	09:13	Val Meledrio (Dimaro Folgarida) campione 1/2	<i>Picea excelsa</i> and <i>Fagus sylvatica</i> forest	46°15'30.5"N 10°51'47.2"E	1508	on snow	sparse	3.0
<i>Ceratophysella sigillata</i>	CML	27/04/2021	10:05	Val Meledrio (Dimaro Folgarida) campione 2/2	Coniferous forest (<i>Picea excelsa</i>)	46°15'15.6"N 10°51'32.4"E	1542	on snow, water and litter	dense	3.5

from five specimens (whole animal) from each population (with the exception of HBR, for which only one sequence is available), using the Wizard[®]SV Genomic DNA Purification System (Promega, Madison, WI, USA); DNA was eluted in 50 µl of H₂O. A fragment of the mitochondrial cytochrome *c* oxidase subunit 1 (*cox1*) was amplified with the primers 5'-GGTCAACAAATCATAAAGATATTGG-3' (LCO1490) and 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (HCO2198) (Folmer et al. 1994). PCR reactions were prepared in a 25 µL volume containing: 2.5 µL of both forward and reverse primers (10 µM), 16 µl of H₂O, 4 µl of 1:10 diluted DNA template and lyophilised PCR beads (illustra[™] PuReTaq RTG PCR-Cytiva). Amplifications were run with the following conditions: an initial denaturation of 5 min at 95 °C, followed by 34 cycles of denaturation (30 s at 95 °C), annealing (30 s at 52 °C) and extension (40 s at 72 °C). A final extension of 10 min at 72 °C was added. For the HBR population the PCR product had to be reamplified (with the same conditions) to obtain enough material for sequencing. PCR products were sequenced on both strands using 3730xl DNA Analyzer by Macrogen Inc. Sequences were assembled in Geneious 8.1.9 and aligned, then manually corrected, and aligned using BIOEDIT version 7.0.5.3 (Hall 1999).

2.5 Genetic analysis

The sequences produced for this work were analyzed with those from the same species (when available) and other species from the same genera (GeneBank accessions numbers and BoldDatabase sequence ID are reported in Supplementary material 2).

Distance analyses were performed with MEGA7 (Kumar et al. 2016), using a Neighbor-Joining (Saitou and Nei 1987) algorithm with the Kimura-2 parameter model (K2P – Kimura 1980) to estimate genetic distances. The robustness of nodes was evaluated through bootstrap reanalysis of 1000 pseudoreplicates. The trees were replotted using the R package ggtree (Xu et al. 2022).

3 Results

3.1 Biodiversity of snow-dwelling and “blooming” springtails

Overall, nine assemblages of springtails were found, with eight of which monospecific and one comprising two species (Table 1, Fig. 1, Appendix Fig. 5). In total, five species were found: *Hypogastrura* cf. *kelmendica* sp1, *Hypogastrura*

cf. *kelmendica* sp2, *Hypogastrura* cf. *peloponnesica* Danyi 2013, *Desoria hiemalis* (Schött, 1893) (Table 1, Appendix Fig. 5) and *Ceratophysella sigillata* (Uzel, 1891). *Desoria hiemalis* and *Hypogastrura* cf. *kelmendica* sp2 have been found only on snow, while the others were also collected in other microhabitats. Specifically, *Hypogastrura* cf. *kelmendica* sp1 and *Ceratophysella sigillata* were found also on the water surface and *C. sigillata* also on ground.

Among the five species found, two were already described in literature: *Desoria hiemalis* and *Ceratophysella sigillata*. Two species are likely new for science and morphologically close to *H. kelmendica*: *Hypogastrura* cf. *kelmendica* sp1 and *Hypogastrura* cf. *kelmendica* sp2. The last one, *H. cf. peloponnesica*, morphologically corresponds to the *H. peloponnesica* recently described from Greece and only known from the type locality. All specimens of *Desoria hiemalis* exhibit the typical “winter form” (sensu Potapov 2001). The most frequent species is *C. sigillata*, found in three populations, two of them temporally and spatially very close to each other (CME, CML; Table 1). All the other species, except *H. cf. peloponnesica* found in a single site, have been found in two populations.

3.2 Genetic analysis

In the three genera analyzed, a clear barcode gap and a clear differentiation was found between intra and interspecific distances (GenBank accession numbers in Appendix Fig. 6).

In *Ceratophysella* (Table 2, Fig. 2), among the species from the *armata* group — excluding the *C. sigillata* from PNAB and Germany — mean intraspecific distance is 0.38% (range: 0.06–1.08%) and mean interspecific distance is 24.47% (range: 21.25–27.87%). The PNAB/German *C. sigillata* cluster exhibits an intraspecific divergence of 0.33% (with 2.34% divergence between PNAB and the German sequences) and a mean interspecific divergence with all the other species included in the analysis of 22.93% (range: 18.95–28.24%). In *Hypogastrura* (Table 2, Fig. 3), mean intraspecific distance is 0.44% (0–2.42%) and mean interspecific distance is 21.14%. Without *H. cf. kelmendica* sp1 and *H. cf. kelmendica* sp2., mean interspecific distance is 21.34% (range: 17.67–26.14%) and without *H. cf. peloponnesica* is 21.15%. These two potential new species close to *H. kelmendica*, exhibit a mean interspecific distance of 15.53% and respectively a mean intraspecific divergence of 0.34% and 0.41%. Their respective mean divergences with the *H. kelmendica* cluster is 13.08% and 15.20%. In *Desoria* (Table 2, Fig. 4), without the *D. hiemalis* cluster, mean intraspecific distance is 0.15% (range: 0–0.46%) and mean interspecific distance is 22.13% (range: 19.26–25.38%). Within *D. hiemalis*, two clusters are identified (A Norway/

Table 2 Mean intra and interspecific K2P distances in *Ceratophysella*, *Hypogastrura*, and *Desoria*. PNAB = Adamello-Brenta Nature Park

		Intraspecific	Interspecific						
			1	2	3	4	5	6	7
1	<i>C. bengtssoni</i>	0.06							
2	<i>C. cavicola</i>	0.23	26.45						
3	<i>C. granulata</i>	1.08	23.91	21.25					
4	<i>C. longispina</i>	0.52	25.81	24.12	23.38				
5	<i>C. scotica</i>	0.24	27.72	21.53	27.39	27.87			
6	<i>C. pseudarmata</i>	0.15	25.45	23.25	24.86	19.85	24.23		
7	<i>C. sigillata</i> PNAB/Germany	0.33	28.24	23.76	23.63	20.61	22.40	18.95	
			1	2	3	4	5	6	7
1	<i>H. cf. kelmendica</i> sp1 PNAB	0.34							
2	<i>H. cf. kelmendica</i> sp2 PNAB	0.41	15.53						
3	<i>H. cf. peloponnesica</i> PNAB	0.00	20.96	20.88					
4	<i>H. kelmendica</i>	0.00	13.08	15.20	20.46				
5	<i>H. macrotuberculata</i>	0.00	21.50	19.61	21.57	21.72			
6	<i>H. sahlbergi</i>	0.00	20.18	20.80	23.98	19.38	20.40		
7	<i>H. socialis</i>	0.22	19.06	19.44	26.14	17.67	24.07	22.92	
8	<i>H. tooliki</i>	2.42	23.63	23.83	25.74	23.25	25.10	23.89	21.82
			1	2	3	4	5	6	
1	<i>D. blufusata</i>	0.00							
2	<i>D. calderonis</i>	0.46	21.84						
3	<i>D. hiemalis</i> Norway/German pre-Alps	0.10	24.80	21.82					
4	<i>D. hiemalis</i> PNAB	1.64	23.41	20.71	8.29				
5	<i>D. neglecta</i>	0.00	21.34	23.37	21.73	21.80			
6	<i>D. nivea</i>	0.31	22.68	22.90	20.16	21.36	25.38		
7	<i>D. tolya</i>	0.00	21.36	19.26	18.47	17.53	22.70	20.48	

German pre-Alps' cluster and a PNAB one), with a distance of 8.29% (Fig. 4, Table 2). The mean intercluster distance between these two *D. hiemalis* clusters was 8.29%. Intraspecific variability inside *D. hiemalis* PNAB cluster is 1.64% (Table 2).

3.3 Temporal distribution of specimens along the sampling period

Specimens were found in January, April, May, June, November and December (Fig. 4). The longest period in which no swarming springtails could be found was from June 2020 to November 2020 (about 5 months, mainly corresponding to the snow-free period). *Ceratophysella sigillata* and

Hypogastrura cf. kelmendica sp2 were found only during spring (respectively, in April and June the first one and in May the other ones), *Desoria hiemalis* and *Hypogastrura cf. peloponnesica* only during winter (respectively, in January and December), while *Hypogastrura cf. kelmendica* sp1 in autumn and winter (November and December) (Fig. 4). In relation to daytime, of the five populations sampled in spring (HRE, HAR, CCE, CME and CML), four populations were found before 10:30 AM and one at 15:30 (HAR). Otherwise, the four populations sampled in colder seasons, autumn and winter (HBR, MOL, HMA and HTV-DTV), were found after 11:30 AM (Table 1). According to the weather stations used in this study, all springtail "bloomings" were found when temperature was higher than 0 °C (Fig. 4).

Fig. 2 Neighbor joining tree (K2P) based on the COI 5' sequences of (a) specimens of *C. sigillata* collected in PNAB / Germany along with those from (b) six other *Ceratophysella* species from the armata group. The upper and lower sides of the triangle represent respectively the maximum and minimum of genetic distances within the species. Nodes supported by $\geq 99\%$ bootstrap values are marked with an asterisk

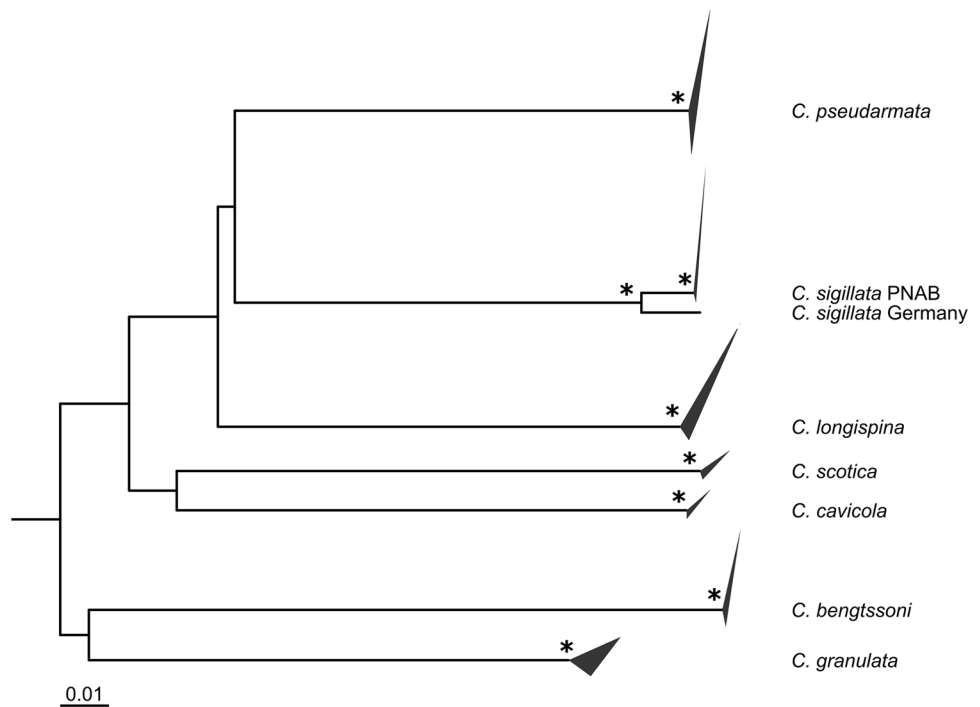


Fig. 3 Neighbor joining tree (K2P) based on the COI 5' sequences of (a) specimens of *H. cf. kelmendica* (sp1 and sp2) and *H. cf. peloponnesica* collected in PNAB along with those from (b) six other *Hypogastrura* species (comprising sequences from specimens formally identified as *H. kelmendica*). The upper and lower sides of the triangle represent respectively the maximum and minimum of genetic distances within the species. Nodes supported by $\geq 99\%$ bootstrap values are marked with an asterisk

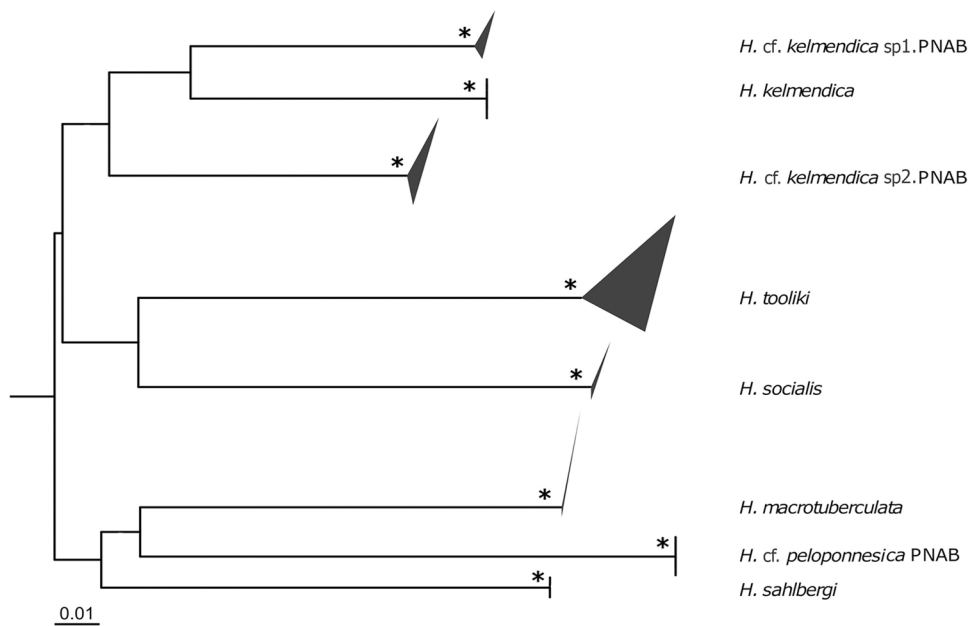
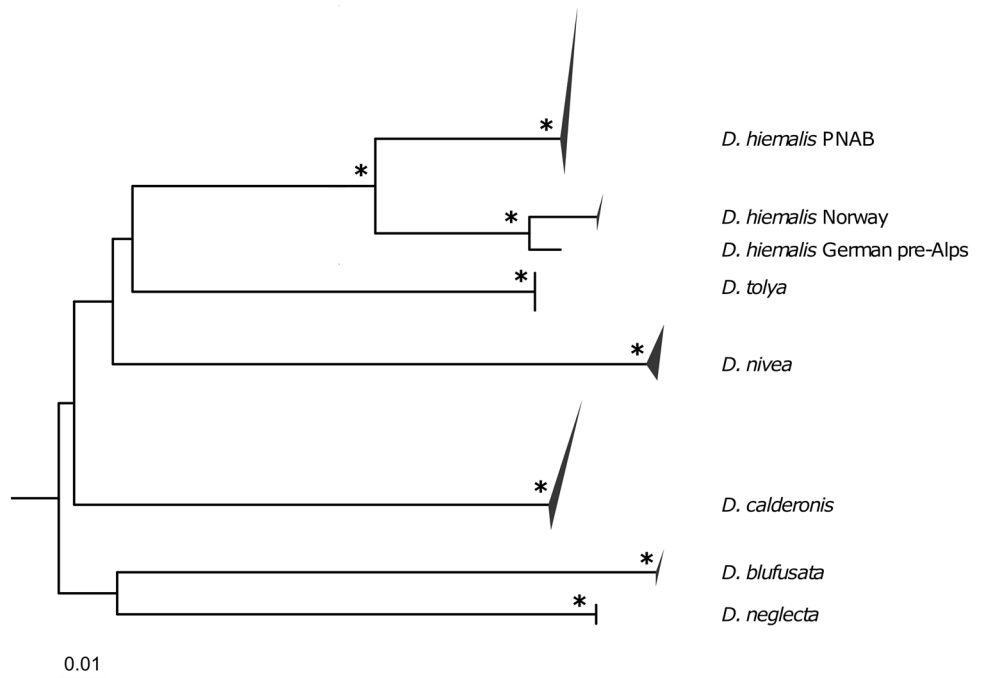


Fig. 4 Neighbor joining tree (K2P) based on the COI sequences of (a) specimens of *D. hiemalis* collected in PNAB and Norway / German pre-Alps along with those from (b) five other *Desoria* species. The upper and lower sides of the triangle represent respectively the maximum and minimum genetic distances within the species. Nodes supported by $\geq 99\%$ bootstrap values are marked with an asterisk



4 Discussion

4.1 Snow-swarming biodiversity still to be described

Our data suggest that the snow-active springtail fauna found in the Adamello-Brenta Natural Park is partially different from that of Northern Europe (Hågvar 2010; Leinaas 1981c). Specifically, more than a half of the snow-active collembolan species in the study area are likely new for science (e.g., *H. cf. kelmendica* sp1 and *H. cf. kelmendica* sp2) or only recently described (*H. cf. peloponnesica*; Danyi 2013) (see following paragraph). The remaining taxa, *Desoria hiemalis* and *Ceratophysella sigillata*, are widespread species. *Desoria hiemalis* is a nival species from Central and Northern Europe, already found in the European Alps (Block and Zettel 1980), but this is the first report for Italy. In the European part of Russia, *D. hiemalis* is “a very common xeromesophilic species”, found in coniferous forests (Potapov 2001), which is compatible with our samples collected in a spruce and beech forest. *Ceratophysella sigillata* is the only springtail from temperate habitat known to have its main reproductive season in winter and to spend the warm season in dormancy, as reported also from Northern European Alps (Zettel and Zettel 1994; Jureková, et al 2021). We documented that this cold-loving species is active in the Southern Alps in mild spring on snow, as observed in Crete, Greece (Schulz 2010). *Ceratophysella sigillata* was mainly known from the Northern European Alps (Palissa 1964; Block and Zettel 2003). According to Dallai and

Malatesta (1982), *C. sigillata* was recorded in Italy only in caves, with the exception of two records, from the Dolomites (Marcuzzi 1983a) and from the Apennines on Gran Sasso (Marcuzzi 1983b). Thus, the finding of both species in the Adamello-Brenta Nature Park represents an important record for the Alpine collembolan fauna. Despite the expectations, *Hypogastrura socialis* was not found. However, two of the three *Hypogastrura* species found in the Adamello-Brenta Nature Park belong to the *Hypogastrura socialis* group (see following paragraph).

4.2 Morphological and genetic diversity of snow-active springtails in PNAB

In terms of biodiversity, the most interesting group of snow-active springtails found was represented by the genus *Hypogastrura*, for which we found three different species. *Hypogastrura cf. kelmendica* sp1 and sp2 are morphologically very close to *Hypogastrura kelmendica* Peja, 1985 described from Central and Southeast Europe and belonging to the *Hypogastrura socialis* group. They differ from *H. kelmendica* and from each other in their body and antennae chaetotaxy and tegumentary granulation. In particular, *Hypogastrura cf. kelmendica* sp1 is morphologically similar to *Hypogastrura socialis* found in large swarms in Mount Amiata (Central Italy; Dallai and Ferrari 1970) and re-attributed by Skarżyński and Smolis (2003) to the *H. kelmendica* complex.

The genetic divergence between *H. kelmendica* and *H. cf. kelmendica* sp1 and sp2 is lower than the interspecific divergence observed between other well-defined *Hypogastrura*

species (albeit higher than the intraspecific divergence in those species). This lower genetic divergence could be due to a recent — or even ongoing (and therefore incomplete) — speciation (Porco et al. 2018). Their specific status could be further investigated with nuclear gene sequencing; meanwhile, it is important to flag them as distinct genetic entities.

Globally, both putative species exhibit a clear morphological and genetic differentiation, suggesting that they could be considered as two independent species. These forms, which are thus likely species new to science, will be formally described in separate taxonomic studies. In general, species of the *Hypogastrura socialis* group seems to include a great diversity of species, with a weak and inconstant morphological diversification; thus, as shown in this study, the use of integrative taxonomy for approaching snow-active *Hypogastrura* species would be highly advisable.

Concerning *H. cf. peloponnesica*, despite a correspondence with the diagnosis, we suspect a possible differentiation from the nominal species (a snow-active springtail from Peloponnese, Greece) because of clear differences in the shape of setae and in the body and leg chaetotaxy. Unfortunately, it was not possible to perform a genetic comparison on the original material that could have brought further support to this hypothesis. More investigations are needed to reach conclusions on this topic.

Regarding the *Ceratophysella* cluster, *C. sigillata* sequences from PNAB do not cluster with *C. pseudarmata* sequences from Canadian specimens, i.e., they were found as genetically divergent as the other clusters from the other *Hypogastrura* species analyzed. This could further support the synonymisation of *C. sigillata* from North American populations with *C. pseudarmata* (Babenko et al. 2019).

Regarding the genus *Desoria*, the distances between the sequences obtained from populations of *D. hiemalis* from PNAB and from Germany and Norway lay within the known intraspecific range found among populations of a same species in Collembola (e.g., Porco et al. 2014; Schneider et al. 2016). The mean genetic distances found between this cluster (Germany/Norway) and the sequences produced from PNAB populations of *D. hiemalis* ranged between the mean intraspecific and interspecific distances found among other *Desoria* species. Nevertheless, in other Collembola groups, interspecific distances were previously found to range from 8% (between well-defined *Hypogastrura* species—Hogg and Hebert 2004) and up to 11.71% (among *Micranurida* morphospecies — Porco et al. 2014). Moreover, in this study, the genetic distances found for *Desoria* species other than *D. hiemalis* comprised only one population each, thus potentially not reporting the full actual range of the intraspecific variation within species of the genus.

From the morphological point of view, no differences was found regarding diagnostic characteristic of the species, but further investigation should be done.

This finding calls for further investigations with nuclear genes and/or more abundant samplings for COI (e.g., Porco et al. 2018). This could help elucidating the nature of the high intraspecific divergence found between PNAB and Norway/Germany populations in *D. hiemalis*, and deciding if this divergence is at species level or if it is the result of an incomplete ongoing speciation process.

4.3 Snow as a fragmentary habitat and European Alps as biogeographic barrier

On a broader perspective, we could hypothesize that snow, especially in peripheral mountain chains like the Adamello-Brenta mountain group, acts as a fragmentary ephemeral habitat for those cold-adapted springtails that are known to be present in Southern Europe, but mainly active in winter or in cold and stable microhabitats like caves, as suggested by Cassagnau (1973) for *H. socialis* and *C. sigillata*. Indeed, Arbea and Pérez Fernández (2020) recently reported the first occurrence of *H. socialis* for the Iberian Peninsula, in a cave habitat. Also at smaller scale, Jureková et al. (2021) and Raschmanová et al. (2018a) found that *C. sigillata* prefers cold micro-habitats in Slovak karstic areas. Likewise other species that have a high cold tolerance, this species also shows a remarkable heat tolerance (Raschmanová et al. 2018b) that could enhance its migration capability and explain its wide distribution range in Europe. As suggested by Thaler (1999) for Alpine nival fauna in general, springtails too could have sustained a biogeographic differentiation on Alps; for example, the genetic divergence found between PNAB and German/Norway *Desoria hiemalis* could support the hypothesis of such a differentiation between Northern and Southern Alps. In addition, the co-presence of the two closely related species of the *H. kelmendica* complex (*H. socialis* group), probably new for sciences, indicates a local differentiation of Northern species. Based on our data and on morphological descriptions of historical records of *H. socialis* on European Alps (e.g., Handschin 1924, where *H. socialis* has only 6–7 sens on antennomeres IV rather than 10–12), we hypothesize that this group also includes several other species still unknown closely related to *H. socialis* on Alpine mountain chains. In general, European Alps could act as a biogeographic barrier for some nival species between Northern and Southern areas and Southern European Alps seem to constitute a peculiar biogeographic region for snow-active springtails.

However, population genetic studies would be necessary for assessing gene flow and migration dynamics.

4.4 Conservation issues of snow habitat

It is already known from the literature that ground-dwelling springtails have a general decrease in activity during the warmest and driest seasons (Badejo and van Straalen 1993). Populations collected in the Adamello-Brenta Nature Park confirm this observation and suggest that summer is not a good “blooming” period for springtails; however, we cannot exclude that the lack of “blooming” occurrence in the summer is due to an increased difficulty in detecting springtails when snow is not present. Concerning sampling time, it was observed that, while in spring springtails swarm earlier in the morning, in colder season, springtails swarm usually in later (and milder) hours, confirming the expectations (Zhang et al. 2014). According to this, springtail “bloomings” were always found in Adamello-Brenta Nature Park when the air temperature was above 0 °C.

From the ecological point of view, we consider interesting the hypothesis that snow cover could act as an ecological corridor able to connect, in temperate and cold-temperate regions, populations of cold-adapted springtails that are spatially separated during the snow-free period. It, therefore, favors gregarism and easier dispersal ability for the individuals in a bidimensional space (rather than tridimensional as in the soil). For this reason, it is important to know how many species use snow as habitat for foraging, reproduction, and for connecting populations.

In addition, the use of the snow surface as habitat and/or ecological corridor could be relevant in conservation biology in the context of the ongoing climate changes. Several arthropods, specifically those active during the winter, seem to be negatively affected by the reduction of the duration of the snow cover (see Slatyer et al. 2017; Templer et al. 2012). As reported in the literature, springtail abundance decreases during the snow-free period and, more generally, it is negatively affected by soil drought (Badejo and van Straalen 1993). Changes in the frequency and magnitude of snow cover are significantly impacting the Alpine ecosystems (Marta et al. 2023) that rely on snowmelt to satisfy their water demands. A recent research by Colombo et al. (2023) clearly demonstrated unprecedented snow-drought conditions in the Italian Alps during the early 2020s which is part of a recent

pattern of increased intensity and frequency of snow-drought events since the 1990s. Soil arthropods are negatively impacted by extreme warming events (Harvey et al. 2023), also during the cold season (Bokhorst et al. 2012). Thus, we can expect, for the future, a significant reduction of the role of snow as an ecological corridor, potentially bringing the populations to a higher risk of spatial separation, that could lead to a higher extinction risk.

Interestingly, no cryophilic species (i.e., linked to ice) was found during our samplings. Cryophilic Alpine springtails are among the most spatially fragmented and threatened fauna (Valle et al. 2021). Thus, whether the snow could act as an ecological corridor for glacial organisms remains to be tested.

5 Conclusions

Snow is an important ephemeral habitat for springtails, not only for the biodiversity hosted and its ecological importance for cold-adapted springtails. The Southern European Alps could be an important area of diversification for snow-active species, probably for the effect of Alps as a biogeographic barrier.

In practical terms, snow also facilitates the detection and sampling of springtails by untrained persons, whose activity might be useful for finding new species, as it happened in our study where samplings were performed during monitoring activities. This makes the collection of snow-active springtails an ideal topic for citizen science projects. On the other hand, despite the relative simplicity in sampling springtail “blooming” on snow, this biodiversity is still understudied and poorly described. The description of this biodiversity is fundamental for future ecological and zoogeographical research, as they strictly depend on the progress of the taxonomic knowledge (Thaler 1999): without precise taxonomic information, it is not possible even a proper evaluation of fieldwork.

Appendix

See Figs. 5, 6

Fig. 5 A-G. Photos of the populations and species sampled. (Photos by M.Z.). **A:** *Desoria hiemalis* in Molveno, Rifugio Montanara on snow (population “MOL”) and the habitat where it was found. **B:** *Ceratophysella sigillata* from Monte Amolo swarming on spruce and beech forest litter (population “CCE”). **C:** *Ceratophysella sigillata* from Val Meledrio (population “CME”), before (left) and after (right) protruding anal vesicles and antennal vesicles for jumping. **D:** *Ceratophysella sigillata* from Val Meledrio (population “CML”). **E:** *Hypogastrura* cf. *peloponnesica* on snow (population “HTV”). **F:** *Hypogastrura* cf. *kelmendica* sp1 in Vallesinella on snow (population “HBR”). In the second photo anal vesicles are extruded before jumping. **G:** *Hypogastrura* cf. *kelmendica* sp1 in Val di Ceda on the water in a fountain (population “HMA”). In the second photo the fountain where it was found

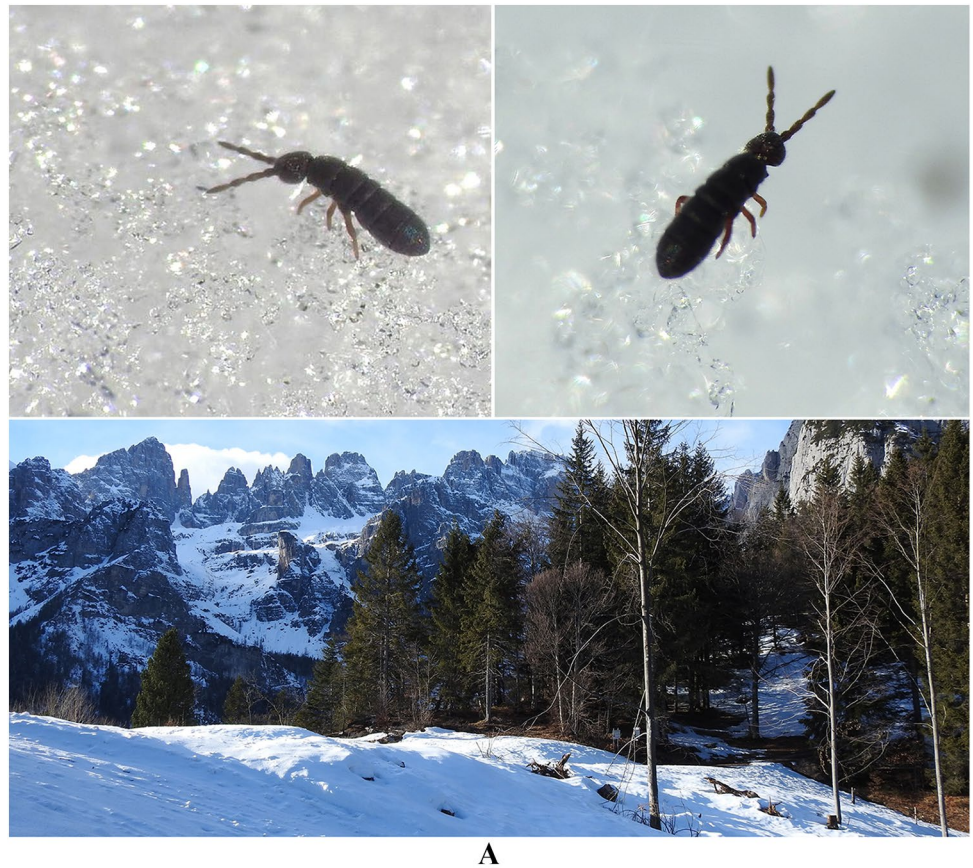


Fig. 5 (continued)



C



D

Fig. 5 (continued)



E



F

Fig. 5 (continued)



G

Fig. 5 (continued)

Fig. 6 GenBank accession numbers of *cox1* sequence obtained for this work (for further information about the sampling, see “Material and Methods”)

Species	locality	Sequence code	Accession number
<i>Desoria hiemalis</i>	Italy, PNAB	MOL1 COX1	OR105947
<i>Desoria hiemalis</i>	Italy, PNAB	MOL2 COX1	OR105948
<i>Desoria hiemalis</i>	Italy, PNAB	MOL3 COX1	OR105949
<i>Desoria hiemalis</i>	Italy, PNAB	MOL4 COX1	OR105950
<i>Desoria hiemalis</i>	Italy, PNAB	MOL5 COX1	OR105951
<i>Desoria hiemalis</i>	Italy, PNAB	DTV3 COX1	OR105952
<i>Desoria hiemalis</i>	Italy, PNAB	DTV1 COX1	OR105953
<i>Desoria hiemalis</i>	Italy, PNAB	DTV2 COX1	OR105954
<i>Desoria hiemalis</i>	Italy, PNAB	DTV4 COX1	OR105955
<i>Desoria hiemalis</i>	Italy, PNAB	DTV5 COX1	OR105956
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HAR2 COX1	OR105957
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HAR3 COX1	OR105958
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HAR4 COX1	OR105959
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HAR1 COX1	OR105960
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HAR5 COX1	OR105961
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HRE2 COX1	OR105962
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HRE3 COX1	OR105963
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HRE4 COX1	OR105964
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HRE5 COX1	OR105965
<i>Hypogastrura cf. kelmendica</i> sp2	Italy, PNAB	HRE1 COX1	OR105966
<i>Hypogastrura kelmendica</i>	Poland	HKE5 COX1	OR105967
<i>Hypogastrura kelmendica</i>	Poland	HKE2 COX1	OR105968
<i>Hypogastrura kelmendica</i>	Poland	HKE3 COX1	OR105969
<i>Hypogastrura kelmendica</i>	Poland	HKE4 COX1	OR105970
<i>Hypogastrura kelmendica</i>	Poland	HKE1 COX1	OR105971
<i>Hypogastrura cf. peloponnesica</i>	Italy, PNAB	HTV2 COX1	OR105972
<i>Hypogastrura cf. peloponnesica</i>	Italy, PNAB	HTV4 COX1	OR105973
<i>Hypogastrura cf. peloponnesica</i>	Italy, PNAB	HTV3 COX1	OR105974
<i>Hypogastrura cf. peloponnesica</i>	Italy, PNAB	HTV1 COX1	OR105975
<i>Hypogastrura cf. peloponnesica</i>	Italy, PNAB	HTV5 COX1	OR105976
<i>Ceratophysella sigillata</i>	Italy, PNAB	CCE2 COX1	OR105977
<i>Ceratophysella sigillata</i>	Italy, PNAB	CCE3 COX1	OR105978
<i>Ceratophysella sigillata</i>	Italy, PNAB	CCE1 COX1	OR105979
<i>Ceratophysella sigillata</i>	Italy, PNAB	CCE5 COX1	OR105980
<i>Ceratophysella sigillata</i>	Italy, PNAB	CCE4 COX1	OR105981
<i>Ceratophysella sigillata</i>	Italy, PNAB	CML4 COX1	OR105982
<i>Ceratophysella sigillata</i>	Italy, PNAB	CML5 COX1	OR105983
<i>Ceratophysella sigillata</i>	Italy, PNAB	CML1 COX1	OR105984
<i>Ceratophysella sigillata</i>	Italy, PNAB	CML3 COX1	OR105985
<i>Ceratophysella sigillata</i>	Italy, PNAB	CML2 COX1	OR105986
<i>Ceratophysella sigillata</i>	Italy, PNAB	CME2 COX1	OR105987
<i>Ceratophysella sigillata</i>	Italy, PNAB	CME4 COX1	OR105988
<i>Ceratophysella sigillata</i>	Italy, PNAB	CME5 COX1	OR105989
<i>Ceratophysella sigillata</i>	Italy, PNAB	CME1 COX1	OR105990
<i>Ceratophysella sigillata</i>	Italy, PNAB	CME3 COX1	OR105991
<i>Hypogastrura cf. kelmendica</i> sp1	Italy, PNAB	HMA1 COX1	OR105992
<i>Hypogastrura cf. kelmendica</i> sp1	Italy, PNAB	HMA3 COX1	OR105993
<i>Hypogastrura cf. kelmendica</i> sp1	Italy, PNAB	HMA4 COX1	OR105994
<i>Hypogastrura cf. kelmendica</i> sp1	Italy, PNAB	HMA5 COX1	OR105995
<i>Hypogastrura cf. kelmendica</i> sp1	Italy, PNAB	HMA2 COX1	OR105996
<i>Hypogastrura cf. kelmendica</i> sp1	Italy, PNAB	HBR3 COX1	OR105997

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sequences are available in Genbank (see Appendix Fig. 6 for accession numbers).

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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