From a volcanic area on the Kamchatka peninsula (Northeast Asia) to a rock glacier in the Swiss Alps: a new record of *Aspilota umbrosa* Belokobylskij, 2007 (Hymenoptera, Braconidae)

Francisco Javier Peris-Felipo[1], José D. Gilgado[2,3*], Sergey A. Belokobylskij[4] & Bruno Baur[3]

[1] *Bleichestrasse 15, CH-4058 Basel, Switzerland.*
[2] *Grupo de Investigación de Biología del Suelo y de los Ecosistemas Subterráneos, Departamento de Ciencias de la Vida, Facultad de Ciencias, Universidad de Alcalá, E-28805, Alcalá de Henares, Madrid, Spain.*
[3] *Section of Conservation Biology, Department of Environmental Sciences, University of Basel, CH-4056 Basel, Switzerland.*
[4] *Zoological Institute of the Russian Academy of Sciences, St Petersburg, 199034, Russia.*
* *Corresponding author: josedomingo.gilgado@gmail.com*

Abstract: The species *Aspilota umbrosa* Belokobylskij, 2007 is recorded for the first time in Europe. The first photographs of this species, both of the holotype and of the new record, the second in the world, are provided. The holotype was found near the Klyuchevskaya Sopka volcano (Kamchatka peninsula, Russia). The new specimen of this species was collected in a superficial subterranean habitat (the MSS – Milieu Souterrain Superficiel) in the rock glacier in Val Sassa (Swiss National Park, Grisons, Switzerland) by a subterranean trap in 2020. This is the first record of *A. umbrosa* in the MSS of the Swiss Alps and in a rock glacier. A key to the known Swiss species of *Aspilota* is provided.

Keywords: High mountains - MSS - new records - Subterranean habitats - Switzerland - wasps.

INTRODUCTION

Superficial subterranean habitats have received increasing attention in recent decades (Culver & Pipan, 2014). The most researched of them is the "Milieu Souterrain Superficiel", widely known as MSS (Mammola *et al.,* 2016). This habitat comprises the network of voids between stony debris that lies beneath the surface. MSSs have different origins (colluvial, volcanic or alluvial) and different properties (among others, size of the stones, voids, and presence of soil layers) (Ortuño *et al.,* 2013). MSSs are inhabited by species with different ecological requirements (epigean, edaphobionts, and troglobionts, among others) (e.g., Nitzu *et al.,* 2014; Jiménez-Valverde *et al.,* 2015; Mammola *et al.,* 2016). Recently, new and rarely captured species have been frequently discovered in MSSs (e.g., Baquero *et al.,* 2017; Gilgado *et al.,* 2017; Ledesma *et al.,* 2019; Jordana *et al.,* 2020), allowing for a deeper understanding of the ecology of soil and subsoil habitats (Rendoš *et al.,* 2012, 2016; Nitzu *et al.,* 2014; Nae & Băncilă, 2017; Ledesma *et al.,* 2020; Nae *et al.,* 2021). MSS-research began in the Pyrenees (Juberthie *et al.,* 1980, 1981) and has been largely conducted in Europe (Mammola *et al.,* 2016). Some entomological faunistic records in MSSs of the Alps have been documented (Vailati, 1990; Christian *et al.,* 1996; Růžička & Thaler, 2002; Zacharda & Kučera, 2006; Christian & Spötl, 2010), but there is no information on such habitats in Switzerland. Moreover, MSSs have never been sampled in rock glaciers.

Rock glaciers are defined as "lobate or tongue-shaped bodies of perennially frozen unconsolidated material supersaturated with interstitial ice and ice lenses that move downslope or downvalley by creep" (Haeberli, 1985). These landscape features are not uncommon in the Alps and other high mountains in temperate zones (Clark *et al.,* 1998). Rock glaciers are formed by several processes (Clark *et al.,* 1998), and the percentage of ice or permafrost in them is variable (Barsch, 1996). Rock glaciers have been studied from a biological perspective, including their plant and animal communities, and their role as climatic refugia (e.g., Cannone & Gerdol,

Manuscript accepted 20.09.2023
DOI: 10.35929/RSZ.0114

2003; Millar *et al.,* 2015; Tampucci *et al.,* 2017; Gobbi *et al.,* 2020; Cannone & Piccinelli, 2021). So far, however, there have been no studies on the subterranean fauna of rock glaciers. We have collected hundreds of different specimens in a series of sampling efforts in the superficial subterranean environment of a rock glacier in the Swiss National Park. Among them, a parasitoid species the genus *Aspilota* Foerster, 1863 (Hymenoptera, Braconidae, Alysiinae) was identified.

The genus *Aspilota* is one of the most species-rich taxa of the Alysiinae with approximately 250 species described from almost all zoogeographical regions. *Aspilota* species are parasitoids of flies (Diptera), mainly of the families Phoridae and Drosophilidae; other families listed (Anthomyiidae, Lonchaeidae, Muscidae, Platypezidae, Sarcophagidae, Syrphidae and Tephritidae) (Yu *et al*., 2016) may have been erroneously included and need to be confirmed. This genus is well defined by the presence of large paraclypeal fovea, almost connected to the inner margin of the eye, and the presence of fore wing vein cuqu1 (2-SR) (van Achterberg, 1988; Peris-Felipo & Belokobylskij, 2016a).

In this study, we provide the first record of the Far Eastern species *Aspilota umbrosa* Belokobylskij, 2007 in Europe. We also present the first photographs of the species, and a key to identifying the eight known species of *Aspilota* from Switzerland.

MATERIAL AND METHODS

Sampling was carried at the rock glacier in Val Sassa, and the surrounding scree habitats, in the Swiss National Park (SNP) in the Eastern Alps, Grisons, Switzerland (46º39'N, 10º12' E)(Fig. 1). The SNP is a strict nature reserve (category Ia; IUCN/WCMC, 1994), with no habitat and wildlife management. Public access to the SNP is only permitted on marked paths during the summer months (Baur & Scheurer, 2014). The upper layer of this rock glacier consists mainly of dolomite rock and sediments (Trümpy *et al.,* 1997). The lower end of the rock glacier is at an elevation of 2100 m, while its higher part reaches up to 2600 m.

We installed eight subterranean sampling devices (SSD) on 24.07.2019: four in a line on the surface of the rock glacier, two in its foreland and two in the lateral screes. The SSDs were modified from the design of previous research (López & Oromí, 2010; Mammola *et al.,* 2016; Baquero *et al.,* 2017) (Fig. 1). A SSD consisted of a 1 m long PVC tube, 11 cm in diameter, buried vertically in the ground with the upper end at surface level. The tubes had several lateral perforations (each 8 mm in diameter) below the first 40 cm, allowing invertebrates to enter the interior of the tube. A pitfall trap containing propylene glycol was placed at the bottom of each tube. The pitfall traps were recovered by means of a metal rod attached to it and emptied. This happened after two months (25.09.2019), 12 months (28.07.2020), and 14 months (23.09.2020). The captured animals were transported to the University of Basel, where they were sorted in the lab using a stereomicroscope.

The terminology of the morphological features, sculpture, and measurements, as well as the wing venation nomenclature followed Peris-Felipo *et al.* (2014), and in parenthesis van Achterberg (1993). To identify the *Aspilota* specimen we used the keys of Fischer (1976, 1978), Belokobylskij & Tobias (2007), and Papp (2008). The material was imaged using Digital Microscope Keyence® VHX-2000 and Adobe Photoshop® imaging system. The specimen is kept in the collection of the Bündner Naturmuseum Chur (BNM), Switzerland, in accordance with the guidelines of the Swiss National Park. The holotype of *Aspilota umbrosa* deposited in the Zoological Institute of the Russian Academy of Sciences in St. Petersburg, Russia (ZISP) was also studied and photographed.

TAXONOMIC PART

Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1811
Subfamily Alysiinae Leach, 1815
Genus *Aspilota* Foerster, 1863

***Aspilota umbrosa* Belokobylskij, 2007**
Figs 2-4

Type material: Holotype (Fig. 4): female; Russia, Kamchatka, Kozyrevsk, mixed forest; 24.07.1985; collected near the active volcano Klyuchevskaya Sopka; S. Belokobylskij *leg*. (ZISP).

Material collected: BNM; 1 female; Switzerland, Grisons, rock glacier in Val Sassa, Swiss National Park, 46°37'44"N 10°6'44"E, 2250 m; 23.09.2020; collected by subterranean sampling devices (SSD); J. D. Gilgado *leg*. (Figs 2-3).

Main characters of the species (Swiss specimen): Body length 2.0 mm. Head in dorsal view 1.8 times as wide as its median length and 1.4 times as wide as mesoscutum. Face 1.8 times as wide as high. Mandible 1.3 times as long as wide. Lower tooth wider than upper tooth. Antenna 18-segmented. First flagellar segment 5.2 times as long as its apical width. Sixth flagellar segment almost twice as long as its width. Mesosoma in lateral view 1.2 times as long as high. Mesoscutum 0.8 time as long as its maximum width. Notauli mostly absent. Dorsal mesoscutal pit absent. Prescutellar depression smooth, with medial and two lateral carinae. Precoxal sulcus present, crenulate, not reaching anterior and posterior margins of mesopleuron. Upper part of posterior mesopleural furrow crenulated, while the lower part is smooth. Propodeum with pentagonal areola delineated by distinct carinae. Propodeal spiracles small.

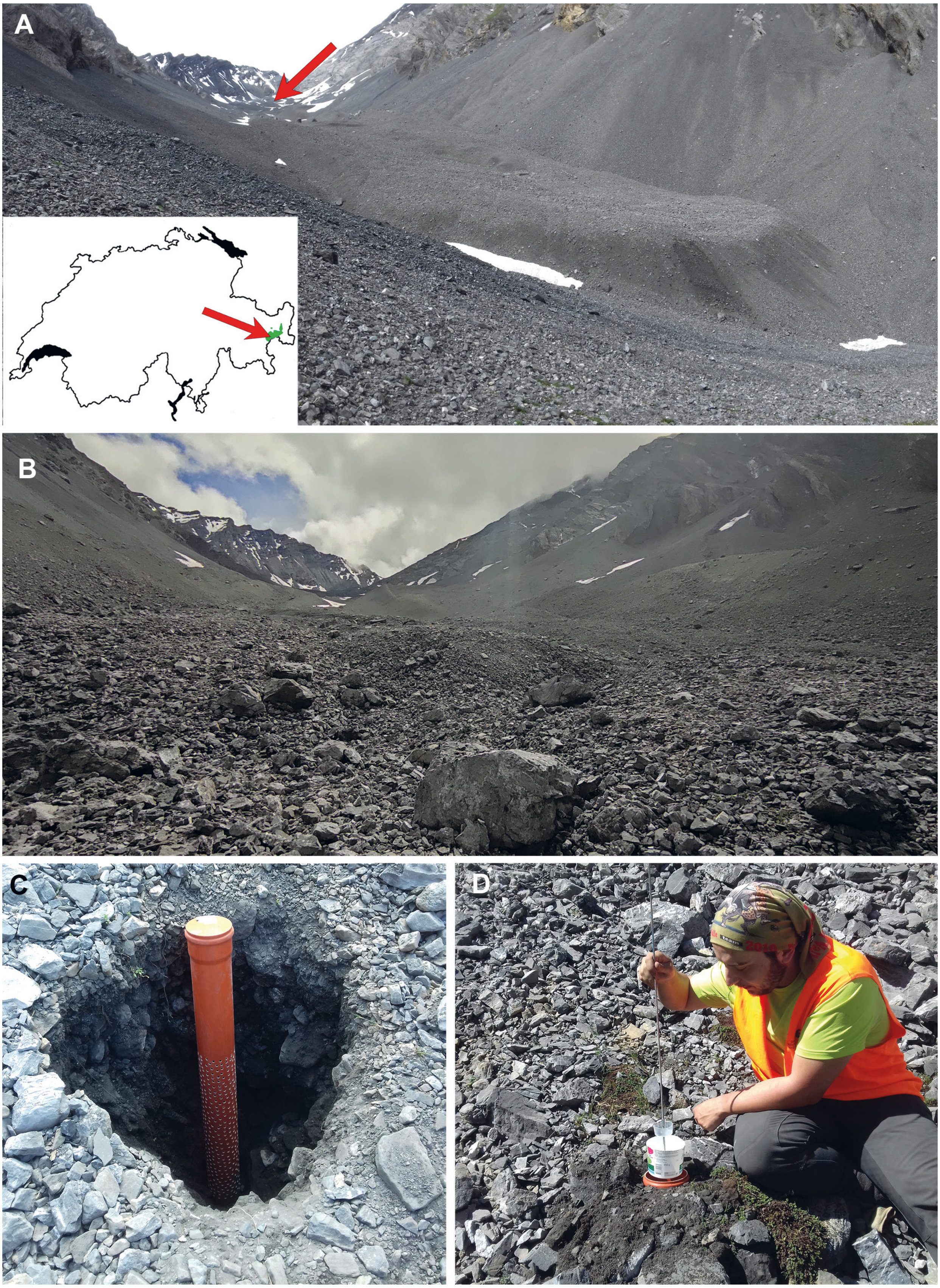

Fig. 1. (A) Location of the sampling site on the rock glacier in Val Sassa in the Swiss National Park. (B) Surface of the rock glacier at the sampling site. (C) Subterranean Sampling Device (SSD) just before burying it. (D) Installation of the pitfall trap in the tube once it was buried.

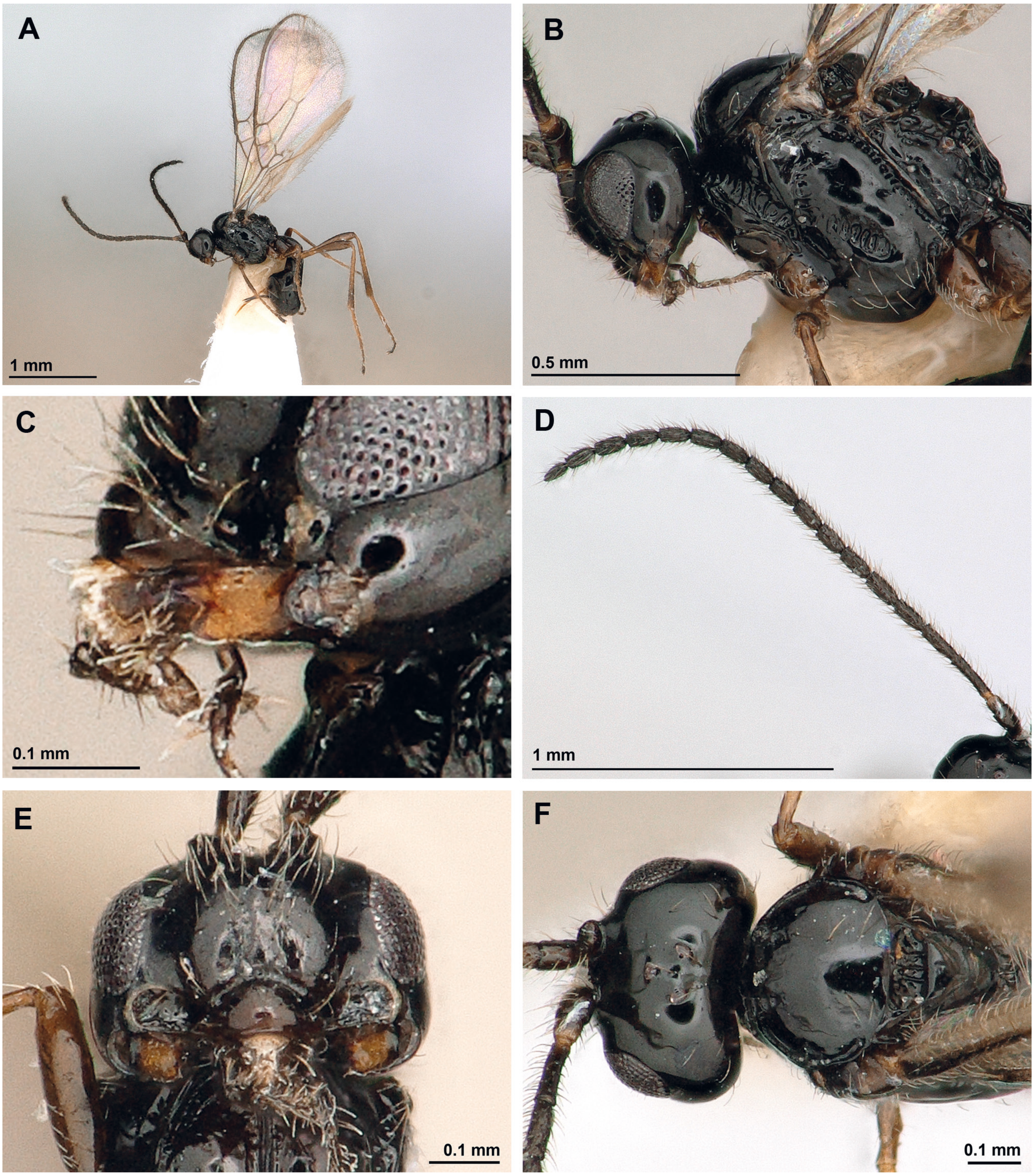

Fig. 2. *Aspilota umbrosa* Belokobylskij, 2007 (female, Swiss specimen). (A) Habitus, lateral view. (B) Head and mesosoma, lateral view. (C) Mandible. (D) Antenna. (E) Head, front view. (F) Head, dorsal view.

Hind femur 4.4 times as long as its maximum width. First metasomal tergite twice as long as its apical width, striate. Ovipositor 1.5 times as long as first tergite, shorter than metasoma, as long as hind femur. Body, antenna, and pterostigma dark brown, mandibles and legs brown.
Male. Unknown.

Variation with holotype: Face 1.5 times as wide as high (1.8 times in the Swiss specimen). Antenna 17-segmented (18-segmented in the Swiss specimen). First flagellar segment 4.0 times as long as its apical width (4.4 times in the Swiss specimen). Body, antenna, and pterostigma brown (dark brown in the Swiss specimen). Mandible and legs yellowish brown (brown in the Swiss specimen). Otherwise, characters are similar.

Key to the known Swiss species of *Aspilota*

1 Vein 2-SR of fore wing absent. First flagellar segment 1.2 times as long as its maximum width. Upper tooth wider than lower tooth. First metasomal tergite 2.0 times as long as its maximum width. Body length 1.6-1.8 mm. Austria, Bulgaria, China, Finland, Germany, Hungary, Russia (Far East), Sweden, Switzerland .... *A. (Eusynaldis) parvicornis* (Thomson)

– Vein 2-SR of fore wing present. First flagellar segment 3.0-5.2 times as long as its maximum width. Lower tooth wider than upper tooth 2

2(1) Propodeum with rather large areola, distinctly delineated by carinae. First metasoma tergite 2.0-2.5 times as long as its apical width 3

– Propodeum without areola, distinctly sculptured. First metasoma tergite 1.6-1.8 times as long as its apical width.... 6

3(2) Precoxal sulcus not reaching anterior margin of mesopleuron 4

– Precoxal sulcus reaching anterior margin of mesopleuron 5

4(3) First flagellar segment 4.5 times as long as its maximum width. Head in dorsal view 1.7 times as wide as mesoscutum. Hind femur 4.0 times as long as its maximum width. First metasomal tergite 2.3 times as long as its apical width. First metasomal tergite lighter than second and third tergites. Ovipositor as long as first tergite. Body length 1.8 mm. Austria, former Czechoslovakia, Denmark, Faeroe Islands, Germany, Hungary, Netherlands, Sweden, Switzerland .... *A. (Aspilota) hirticornis* Thomson

– First flagellar segment 5.2 times as long as its maximum width. Head in dorsal view 1.4 times as wide as mesoscutum. Hind femur 4.4 times as long as its maximum width. First metasomal tergite 2.0 times as long as its apical width. First metasomal tergite similar in colour to second and third tergites. Ovipositor 1.5 times as long as first metasomal tergite. Body length 2.0 mm. Russia (Far East), Switzerland .... *A. (Aspilota) umbrosa* Belokobylskij

5(4) First metasomal tergite similar in colour to second and third tergites. First flagellar segment 5.5 times as long as its maximum width. Hind femur 5.0 times as long as its maximum width. Ovipositor 1.5 times as long as first metasomal tergite. Body length 1.9 mm. Austria, Hungary, Korea, Spain, Switzerland .... *A. (Aspilota) flagellaris* Fischer

– First metasomal tergite paler than second and third tergites. First flagellar segment 5.0 times as long as its maximum width. Hind femur 4.5 times as long as its maximum width. Ovipositor as long as first metasomal tergite. Body length 2.2 mm. Austria, Bosnia-Herzegovina, Denmark, Hungary, Switzerland .. *A. (Aspilota) furtnerana* Fischer

6(2) Precoxal sulcus not reaching anterior margin of mesopleuron. First flagellar segment 4.5 times as long as its maximum width. Body length 2.7-3.2 mm. Austria, former Czechoslovakia, Germany, Hungary, Poland, Russia, Spain, Sweden, Switzerland .... *A. (Aspilota) efoveolata* (Thomson)

– Precoxal sulcus reaching anterior margin or anterior and posterior margins of mesopleuron. First flagellar segment 3.0 times as long as its maximum width 7

7(6) Precoxal sulcus reaching anterior margin of mesopleuron. Hind femur 4.0 times as long as its maximum width. Face 1.9 times as high as long. Head in dorsal view 1.4 times as wide as its length. Ovipositor shorter than first metasomal tergite. Body length 2.5-3.0 mm. Austria, Belgium, Croatia, former Czechoslovakia, Denmark, Germany, Hungary, Montenegro, Netherlands, Poland, Romania, Serbia, Sweden, Switzerland, Turkey, United Kingdom .... *A. (Aspilota) ruficornis* (Nees)

– Precoxal sulcus reaching anterior and posterior margins of mesopleuron. Hind femur 3.5 times as long as its maximum width. Face 1.5-1.6 times as high as long. Head in dorsal view 1.25 times as wide as its length. Ovipositor 1.3 times as long as first metasomal tergite. Body length 1.6 mm. Austria, Hungary, Israel, Switzerland .... *A. (Aspilota) latitemporata* Fischer

DISCUSSION

In our project we collected some parasitoid wasps in the subterranean traps. However, *Aspilota umbrosa* in our samples was a surprising finding for several reasons. Firstly, its disjunct distribution as the only known individual of this species to date has been found near the Klyuchevskaya Sopka volcano (Kamchatka, Russia), which is some 8600 km from Val Sassa in the Swiss National Park. It is possible that the species has a wide distribution, with many undiscovered populations between these locations. Alternatively, it is conceivable that the alpine population of *A. umbrosa* is a relict of past ice ages, remaining isolated from the north-eastern population (Schmitt *et al.,* 2010). Furthermore, the alpine population could be a result of a modern dispersal event (Schmitt *et al.,* 2010). Interestingly, the habitat at the type location is mixed forest, a completely different habitat than that of our record. However, the landscapes of both regions share some characteristics, such as mountain reliefs and snowfields. The currently known distribution of *Aspilota umbrosa* suggests that it is a boreo-alpine species.

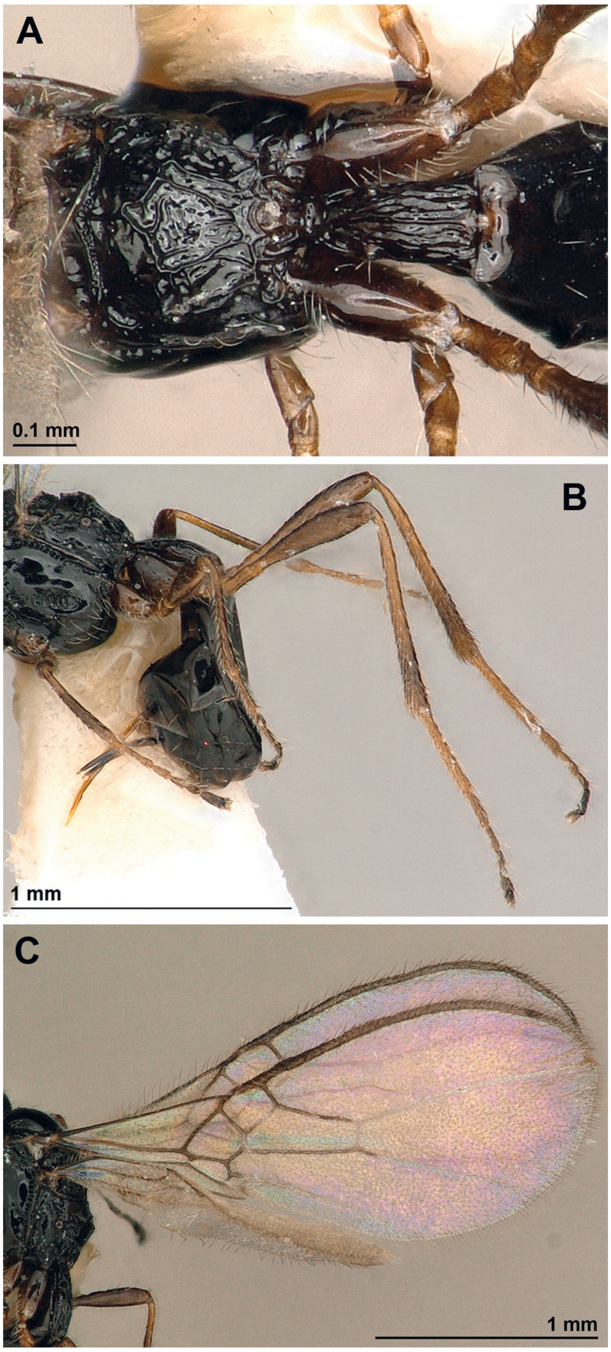

Fig. 3. *Aspilota umbrosa* Belokobylskij, 2007 (female, Swiss specimen). (A) Propodeum and first metasomal tergite, dorsal view. (B) Hind leg, metasoma and ovipositor, lateral view. (C) Fore and hind wings.

The identification of the captured specimen with the keys of Fischer (1976, 1978), Belokobylskij & Tobias (2007), and Papp (2008) led us to *Aspilota umbrosa*, but the significant geographical separation between the two locations made us consider that our specimen could belong to a closely related new species. However, further examination of their morphology showed only subtle differences between our specimen and the holotype of *Aspilota umbrosa*, consistent with a distance of 8600 km between collection sites, and not enough to justify the establishment of a new species. Moreover, minimal morphological differences are known to occur in other insects with boreo-alpine distributions (Paill *et al*., 2021). We contemplated the possibility of conducting a barcoding analysis as an additional source of information, but none of the authors involved had the possibility to perform it in the recently captured specimen, or the holotype of *Aspilota umbrosa* stored in Russia. In addition, we also considered that even if they belonged to the same species, the large distance between the two collecting sites would most surely show in the barcoding analysis, possibly not providing a conclusive result. On the other hand, even large differences in barcode sequences are not enough to justify species descriptions by themselves (Zamani *et al.,* 2022). Thus, we consider that the morphological study is for the time being enough evidence to consider the identity of the newly captured specimen as *Aspilota umbrosa*, and the observed minor differences are consistent with a boreo-alpine distribution and a distance among collecting sites of 8600 km.

Another interesting feature of the present record is the microhabitat in which *Aspilota umbrosa* was found. This is not the first record of a braconid wasp in the subterranean realm (Peris-Felipo & Belokobylskij, 2016b), and specimens of the genus *Aspilota* have also been trapped in caves (Peris-Felipo *et al.,* 2016). However, our record is the first of a braconid parasitoid in the MSS. At the same time, our finding is the first published record of an arthropod species inhabiting the scree layer (MSS) of a rock glacier in the Swiss Alps. The MSS acts as a shelter, reducing the diurnal and seasonal fluctuations in temperature and humidity at the surface (Jiménez-Valverde *et al.,* 2015; Mammola *et al.,* 2016;

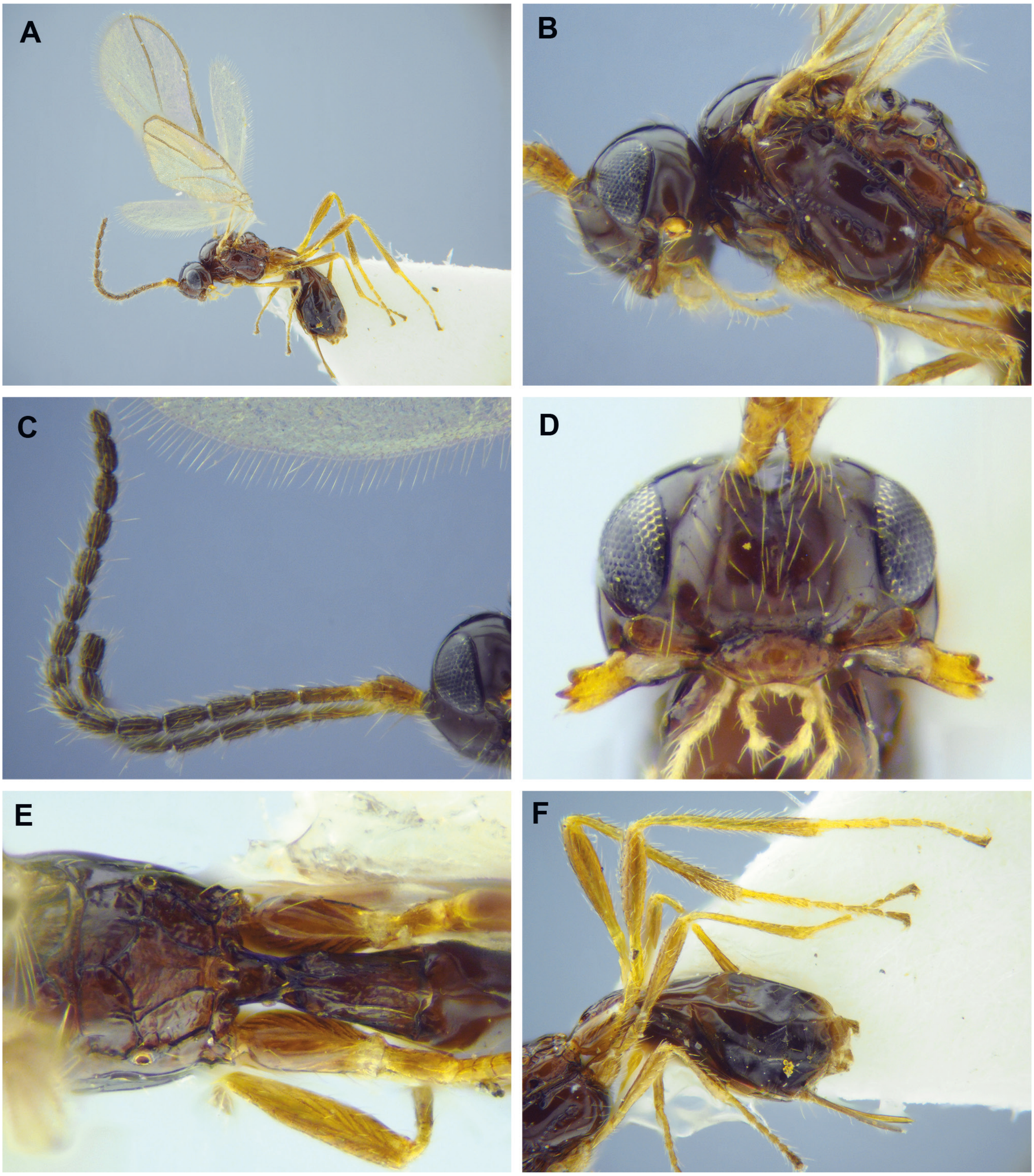

Fig. 4. *Aspilota umbrosa* Belokobylskij, 2007 (female, holotype). (A) Habitus, lateral view. (B) Head and mesosoma, lateral view. (C) Antenna. (D) Head, front view. (E) Propodeum and first metasomal tergite, dorsal view. (F) Hind leg, metasoma and ovipositor, lateral view.

Ledesma *et al.,* 2020). This can help preserve populations of high mountain species that are otherwise rare on the surface (e.g., Gilgado *et al.,* 2014, 2015; Ledesma *et al.,* 2019; Ortuño *et al.,* 2019). Some of these species may be glacial relicts (Růžička *et al.,* 2012), as could be the case with *Aspilota umbrosa*. This type of MSS on a rock glacier with permafrost underneath can sustain particularly cold temperatures in summer. It is worth noting that the SSDs only collected individuals below the first 40 cm of the scree layer to prevent accidental capture of epigean species. It is likely that *A. umbrosa* or its hosts use the MSS during at least a part of their life cycle. Further samplings can strengthen this idea.

Finally, we do not have enough information to assess the conservation status of *Aspilota umbrosa*. However, the Alps are currently being affected by global warming, leading to melting glaciers, and changing the distribution ranges of many species, including arthropods (Vitasse *et al.,* 2021; Gilgado *et al.,* 2022a, b). Thus, the alpine population of *A. umbrosa* may be also affected.

ACKNOWLEDGEMENTS

The SNP direction granted permission for fieldwork in the SNP and provided logistical support. Funding was provided by the SNP Research Commission. We thank Sonja Wipf, Christian Rossi, Samuel Wiesmann, Seraina Campell Andri and Stania Bunte (all staff members of SNP) for advice and help during fieldwork. We thank the staff of the Chamanna Cluozza for the accommodation during fieldwork. We are thankful to Alejandro Criado, Ignacio Gilgado, Luca Yapura, Noah Meier, Sophie Fröhlicher, José Muñoz and Sandro Meyer for assistance during fieldwork, and Etienne Cudré-Mauroux, Evelin Pandiamakkal and Luca Yapura for sorting the arthropods sampled in the traps, and to Noah Meier for sorting the wasps by families. We also want to thank especially Miriam Conti and Matthias Borer (Naturhistorisches Museum Basel, Switzerland) for their kindness and help during our work with the photosystem in the Museum. We are also thankful to Ueli Rehsteiner and Stephan Liersch (Bündner Naturmusem Chur) for their help with preparing the specimen for the collection. Additional funding was obtained from the 'Stiftung Sammlung Naturmuseum Chur'. SAB was also funded in part by State Research Project No 122031100272-3.

REFERENCES

Achterberg C. van. 1988. The genera of the *Aspilota*-group and some descriptions of fungicolous Alysiini from Netherlands (Hymenoptera: Braconidae: Alysiinae). *Zoologische Verhandelingen Leiden* 247: 1-88.

Achterberg C. van. 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandelingen Leiden* 283: 1-189.

Baquero E., Ledesma E., Gilgado J.D., Ortuño V.M., Jordana R. 2017. Distinctive Collembola communities in the Mesovoid Shallow Substratum: First data for the Sierra de Guadarrama National Park (Central Spain) and a description of two new species of *Orchesella* (Entomobryidae). *PLoS One* 12(12): e0189205.

Barsch D. 1996. Welche geoökologischen und klimatischen Aussagen erlauben aktive, inaktive und fossile Blockgletscher. *Heidelberger Geographische Arbeiten* 100: 32-39.

Baur B., Scheurer T. (eds). 2014. Wissen schaffen – 100 Jahre Forschung im Schweizerischen Nationalpark. Nationalpark-Forschung in der Schweiz 100/I. *Haupt Verlag, Bern,* 391 pp.

Belokobylskij S.A., Tobias V.I. 2007. Fam. Braconidae. Subfam. Alysiinae. Group of genera close to *Aspilota* (pp. 9-133). In: Lelej A.S. (ed.). Key to insects of the Russian Far East. Neuropteroidea, Mecoptera, Hymenoptera. Vladivostok. *Dal'nauka* 4(5).

Cannone N., Gerdol R. 2003. Vegetation as an ecological indicator ofsurface instability in rock glaciers. *Arctic, Antarctic, and Alpine Research* 35(3): 384-390.

Cannone N., Piccinelli S. 2021. Changes of rock glacier vegetation in 25 years of climate warming in the Italian Alps. *Catena* 206: 105562.

Christian E., Spötl C. 2010. Karst geology and cave fauna of Austria: a concise review. *International Journal of Speleology* 39(2): 71-90.

Christian E., Graf W., Moog O. 1996. *Plusiocampa caprai* – Ein "Höhlentier" in den Kärntner Zentralalpen. *Carinthia II* 186/106: 387-392.

Clark D.H., Steig E.J., Potter Jr. N., Gillespie, A.R. 1998. Genetic variability of rock glaciers. *Geografiska Annaler: Series A, Physical Geography* 80(3/4): 175-182.

Culver D.C., Pipan, T. 2014. Shallow subterranean habitats: ecology, evolution, and conservation. *Oxford University Press, USA*, 258 pp.

Fischer M. 1976. Erste Nachweise von *Aspilota*-Wespen in Burgenland (Hymenoptera, Braconidae, Alysiinae). *Annalen des Naturhistorisches Museum Wien* 80: 343-410.

Fischer M. 1978. Neue Alysiinen von Neu Guinea, Neu Britannien und den Philippinen (Hymenoptera, Braconidae, Alysiinae). *Annalen des Naturhistorisches Museum Wien* 81: 479-497.

Gilgado J.D., Ledesma E., Cuesta E., Arrechea E., Zapata de la Vega J.L., Sánchez-Ruiz A., Ortuño V.M. 2014. *Dima assoi* Pérez Arcas 1872 (Coleoptera: Elateridae): from montane to hypogean life. An example of exaptations to the subterranean environment? *Annales de la Société entomologique de France (NS)* 50(3-4): 264-271.

Gilgado J.D., Enghoff H., Tinaut A., Ortuño V.M. 2015. Hidden biodiversity in the Iberian Mesovoid Shallow Substratum (MSS): New and poorly known species of the millipede genus *Archipolydesmus* Attems, 1898 (Diplopoda, Polydesmidae). *Zoologischer Anzeiger* 258: 13-38.

Gilgado J.D., Ledesma E., Enghoff H., Mauriès J.-P., Ortuño V.M. 2017. A new genus and species of Haplobainosomatidae (Diplopoda: Chordeumatida) from the MSS of the Sierra de Guadarrama National Park, central Spain. *Zootaxa* 4347(3): 492-510.

Gilgado J.D., Rusterholz H.-P., Baur B. 2022a. Millipedes step up: species extend their upper elevational limit in the Alps in response to climate warming. *Insect Conservation and Diversity* 15(1): 61-72.

Gilgado J.D., Rusterholz H.-P., Braschler B., Zimmermann S., Chittaro Y. & Baur B. 2022b. Six groups of ground-dwelling arthropods show different diversity responses along elevational gradients in the Swiss Alps. *PLoS One,* 17(7): e0271831.

Gobbi M., Caccianiga M., Compostella C., Zapparoli M. 2020. Centipede assemblages (Chilopoda) in high-altitude landforms of the Central-Eastern Italian Alps: Diversity and abundance. *Rendiconti Lincei. Scienze Fisiche e Naturali* 31(4): 1071-1087.

Haeberli W. 1985. Creep of mountain permafrost: Internal structure and flow of Alpine rock glaciers. *Mitteilungen der VAW-ETH Zürich,* vol. 77, 142 pp.

IUCN/WCMC 1994. Guidelines for protected area management categories. *IUCN, Gland, Switzerland/Cambridge, U.K.*

Jiménez-Valverde A., Gilgado J.D., Sendra A., Pérez-Suárez G., Herrero-Borgoñón J.J., Ortuño V.M. 2015. Exceptional invertebrate diversity in a scree slope in Eastern Spain. *Journal of insect conservation* 19(4): 713-728.

Jordana R., Baquero E., Ledesma E., Sendra A., Ortuño V.M. 2020. Poduromorpha (Collembola) from a sampling in the mesovoid shallow substratum of the Sierra de Guadarrama National Park (Madrid and Segovia, Spain): Taxonomy and Biogeography. *Zoologischer Anzeiger* 285: 81-96.

Juberthie C., Delay D., Bouillon M. 1980. Extension du milieu souterrain en zone non calcaire: description d'un nouveau milieu et de son peuplement par les Coléoptères troglobies. *Mémoires de Biospéologie* 7: 19-52.

Juberthie C., Bouillon M., Delay B. 1981. Sur l'existence du milieu souterrain superficiel en zone calcaire. *Mémoires de Biospéologie* 8: 77-93.

Ledesma E., Jiménez-Valverde A., de Castro A., Aguado-Aranda P., Ortuño V.M. 2019. The study of hidden habitats sheds light on poorly known taxa: spiders of the Mesovoid Shallow Substratum. *ZooKeys* 841: 39-59.

Ledesma E., Jiménez-Valverde A., Baquero E., Jordana R., de Castro A., Ortuño V.M. 2020. Arthropod biodiversity patterns point to the Mesovoid Shallow Substratum (MSS) as a climate refugium. *Zoology* 141: 125771.

López H., Oromí P. 2010. A type of trap for sampling the mesovoid shallow substratum (MSS) fauna. *Speleobiology Notes* 2: 7-11.

Mammola S., Giachino P.M., Piano E., Jones A., Barberis M., Badino G., Isaia M. 2016. Ecology and sampling techniques of an understudied subterranean habitat: the Milieu Souterrain Superficiel (MSS). *The Science of Nature* 103(11): 1-24.

Millar C.I., Westfall R.D., Evenden A., Holmquist J.G., Schmidt-Gengenbach J.R., Franklin R.S., Nachlinger J., Delany D.L. 2015. Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. *Quaternary International* 387: 106-121.

Nae I., Băncilă R.I. 2017. Mesovoid shallow substratum as a biodiversity hotspot for conservation priorities: analysis of oribatid mite (Acari: Oribatida) fauna. *Acarologia* 57(4): 855-868.

Nae I., Nae A., Scheu S., Maraun M. 2021. Oribatid mite communities in mountain scree: stable isotopes (15 N, 13 C) reveal three trophic levels of exclusively sexual species. *Experimental and Applied Acarology* 83(3): 375-386.

Nitzu E., Nae A., Băncilă R., Popa I., Giurginca A., Plăiaşu R. 2014. Scree habitats: ecological function, species conservation and spatial-temporal variation in the arthropod community. *Systematics and Biodiversity* 12(1): 65-75.

Ortuño V.M., Gilgado J.D., Jiménez-Valverde A., Sendra A., Pérez-Suárez G., Herrero-Borgoñón J.J. 2013. The "alluvial mesovoid shallow substratum", a new subterranean habitat. *PLoS One* 8(10): e76311.

Ortuño V.M., Ledesma E., Jiménez-Valverde, A., Pérez-Suárez G. 2019. Studies of the mesovoid shallow substratum can change the accepted autecology of species: the case of ground beetles (Coleoptera, Carabidae) in the Sierra de Guadarrama National Park (Spain). *Animal Biodiversity and Conservation* 42(2): 213-226.

Paill W., Koblmüller S., Friess T., Gereben-Krenn B.A., Mairhuber C., Raupach M.J., Zangl L. 2021. Relicts from glacial times: The ground beetle *Pterostichus adstrictus* Eschscholtz, 1823 (Coleoptera: Carabidae) in the Austrian Alps. *Insects* 12(1): 84.

Papp J. 2008. Seven new species of *Aspilota* Foerster from the Palaearctic region (Hymenoptera: Braconidae, Alysiinae). *Annales Historico-Naturales Musei Nationalis Hungarici* 100: 245-269.

Peris-Felipo F.J., Belokobylskij S.A. 2016a. First record of the genus *Dinotrema* Foerster, 1863 (Hymenoptera, Braconidae, Alysiinae) from the Neotropical region with description of four new species and a key to the New World taxa. *European Journal of Taxonomy* 179: 1-23.

Peris-Felipo F.J., Belokobylskij S.A. 2016b. Avispas parasitoides de la familia Braconidae en ambientes subterráneos. *Actas Espeleo Meeting Ciudad de Villacarrillo* 45-48.

Peris-Felipo F.J., Belokobylskij S.A., Jiménez-Peydró R. 2014. Revision of the Western Palaearctic species of the genus *Dinotrema* Foerster, 1862 (Hymenoptera, Braconidae, Alysiinae). *Zootaxa* 3885(1): 1-483.

Peris-Felipo F.J., Becerra R.G., Belokobylskij S. 2016. *Aspilota ajara* sp. n. (Hymenoptera, Braconidae, Alysiinae), the first species of the genus *Aspilota* Foerster from caves. *Journal of Hymenoptera Research* 52: 153-162.

Rendoš M., Mock A., Jászay T. 2012. Spatial and temporal dynamics of invertebrates dwelling karstic mesovoid shallow substratum of Sivec National Nature Reserve (Slovakia), with emphasis on Coleoptera. *Biologia* 67(6): 1143-1151.

Rendoš M., Mock A., Miklisová D. 2016. Terrestrial isopods and myriapods in a forested scree slope: subterranean biodiversity, depth gradient and annual dynamics. *Journal of Natural History* 50(33-34): 2129-2142.

Růžička V., Thaler K. 2002. Spiders (Araneae) from deep screes in the Northern Alps (Tyrol, Austria). *Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck* 89: 137-141.

Růžička V., Zacharda M., Němcová L., Šmilauer P., Nekola J.C. 2012. Periglacial microclimate in low-altitude scree slopes supports relict biodiversity. *Journal of Natural History* 46(35-36): 2145-2157.

Schmitt T., Muster C., Schönswetter P. 2010. Are disjunct alpine and arctic-alpine animal and plant species in the Western Palearctic really "relics of a cold past"? In: Habel J.C., Assmann T. (eds). Relict Species. *Springer, Berlin, Heidelberg*, 442 pp.

Tampucci D., Gobbi M., Marano G., Boracchi P., Boffa G., Ballarin F., Pantini P., Seppi R., Compostella C., Caccianiga M. 2017. Ecology of active rock glaciers and surrounding landforms: climate, soil, plants and arthropods. *Boreas* 46: 185-198

Trümpy R., Schmid S., Conti P., Froitzheim N. 1997. Erläuterungen zur Geologischen Karte 1:50'000 des Schweizerischen Nationalparks. Geologische Spezialkarte Nr. 122. Parc Naziunal Svizzer, SANW/ASSN. *Nationalpark Forschung in der Schweiz* 87(1): 1-40.

Vailati D. 1990. *Insubriella paradoxa* nuovo genere nuova specie di Bathysciinae delle Prealpi Italiane (Coleoptera Catopidae). *Natura Bresciana* 25: 213-229.

Vitasse Y., Ursenbacher S., Klein G., Bohnenstengel T., Chittaro Y., Delestrade A., Monnerat C., Rebetez M., Rixen C., Strebel N., Schmidt B.R., Wipf S., Wohlgemuth T., Yoccoz N.G., Lenoir J. 2021. Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews* 96(5): 1816-1835.

Yu D.S., Achterberg C. van & Horstmann K. 2016. Taxapad 2016, Ichneumonoidea 2015. Taxapad, Ottawa, Ontario. [database on flash-drive].

Zacharda M., Kučera T. 2006. Diversity of predatory Rhagidiid mites (Acari: Rhagidiidae) inhabiting montane stony debris in the Otztal Alps, North Tyrol. *Arctic, Antarctic, and Alpine Research* 38(2): 292-300.

Zamani A., Fric Z.F., Gante H.F., Hopkins T., Orfinger A.B., Scherz M.D., Bartoňová A.S., Pos D.D. 2022. DNA barcodes on their own are not enough to describe a species. *Systematic Entomology* 47: 385-389.