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Campanula bergomensis (Campanulaceae), a new species from Bergamo Prealps (Northern Italy)

BARBARA VALLE^{1,5,6,7*}, ELENA EUSTACCHIO^{2,5,8}, GUIDO ROBERTO GALLO^{2,9}, MARIO BERETTA^{3,10}, MARCO BONELLI^{1,4,11}, ALICE ZANZOTTERA^{2,12}, LUCA GIANFRANCESCHI^{2,13}, GERMANO FEDERICI^{5,14}, FEDERICO MANGILI^{5,15}, LUCA MANGILI^{5,16}, GIOVANNI PERICO^{5,17}, MYRIAM TRAINI^{5,18} & MARCO CACCIANIGA^{3,19}

¹Department of Life Sciences, Università degli Studi di Siena, Via A. Moro 2, 53100 Siena (SI), Italy.

²Department of Biosciences, Università degli Studi di Milano, Via G. Celoria 26, 20133 Milano (MI), Italy.

³“Città Studi” Botanical Garden, Department of Biosciences, Università degli Studi di Milano, Via G. Celoria 26, 20133 Milano (MI), Italy.

⁴Research and Museum Collections Office, Climate and Ecology Unit, MUSE—Museo delle Scienze, 38122 Trento (TN), Italy.

⁵FAB—Flora Alpina Bergamasca APS, Via G. Crescenzi 82, 24123, Bergamo (BG), Italy.

⁶NBFC, National Biodiversity Future Center, Palermo (PA), Italy.

⁷✉ valle.barbara94@gmail.com; <https://orcid.org/0000-0003-4829-4776>

⁸✉ elena.eustacchio@unimi.it; <https://orcid.org/0000-0001-9488-203X>

⁹✉ guido.gallo@unimi.it; <https://orcid.org/0000-0001-5980-0326>

¹⁰✉ mario.beretta1@unimi.it; <https://orcid.org/0000-0002-6962-5207>

¹¹✉ marco.bonelli@unimi.it; <https://orcid.org/0000-0003-2853-6598>

¹²✉ alice.zanzo96@gmail.com; <https://orcid.org/0009-0004-8427-0987>

¹³✉ luca.gianfranceschi@unimi.it; <https://orcid.org/0000-0002-7644-5968>

¹⁴✉ germano.federici@gmail.com; <https://orcid.org/0009-0004-2816-1313>

¹⁵✉ f.mangili@yahoo.it; <https://orcid.org/0009-0005-7746-6225>

¹⁶✉ luca.mangili@gmail.com; <https://orcid.org/0009-0002-8680-268X>

¹⁷✉ mimmo.perico@gmail.com; <https://orcid.org/0009-0002-8825-5122>

¹⁸✉ myriamtraini@gmail.com; <https://orcid.org/0009-0008-8532-5475>

¹⁹✉ marco.caccianiga@unimi.it; <https://orcid.org/0000-0001-9715-1830>

*Corresponding author

Abstract

A new species of *Campanula* (Campanulaceae), *C. bergomensis* sp. nov., is described from the Bergamo Prealps (Orobic Prealps, Lombardy, Northern Italy), based on both morphological and molecular evidence. The new species was considered in the past as an isolated population of *C. cespitosa*, which presents an eastern Alpine distribution. *C. bergomensis* is morphologically well distinguishable from *C. cespitosa* on the number of flowers in the racemose inflorescence, the corolla shape, and the whitish-yellow pollen surface with many spinulae. Genetically, the presence of an insertion of 81-bp in the *trnL-F* sequences is very characteristic. Further studies are needed to better define the phylogenetic relationship among the three closely related species, *C. bergomensis*, *C. cespitosa* and *C. cochleariifolia*. *C. bergomensis* inhabits dolomitic debris cones at low elevations. The species is range-restricted and is severely threatened by human activities. Therefore, it is urgent to adopt protection and conservation measures for the new species.

Key words: Biodiversity, *Campanula cespitosa*, Endemism, Genetics, Morphology

Introduction

The Bergamo Prealps (Lombardy, Northern Italy), located in the southwestern portion of the Eastern Alps, are known as a biodiversity hotspot, due to the very high number of narrow endemic species (Merxmüller, 1954; Fenaroli, 1973; Aeschimann *et al.*, 2011, Martini *et al.*, 2012), the highest in the Alps (Aeschimann *et al.*, 2004). This high rate of endemism is caused by the complex geomorphological and climatic history of this Alpine sector (Cesati, 1848; Giacomini, 1943; Kunz & Reichstein, 1959; Pitschmann & Reischigl, 1959). The proximity of this area to the margins of the Quaternary ice sheet allowed the formation and maintenance of refugia (Tribsch & Schönswetter, 2003). Currently, its central position forms a bridge between the western and eastern Alpine floras, under a favourable climatic condition characterized by mild winters and high summer precipitation (Martini *et al.*, 2012).

Among the Alpine genera, *Campanula* L. has the highest number of endemic species (Aeschimann *et al.*, 2004). In the Bergamo Prealps this is underlined by several endemic *Campanula* taxa: *C. raineri* Perp., *C. elatinoides* Moretti, *C. carnica* Schiede ex Mert. & W.D.J.Koch *subsp. puberula* Podlech, (Martini *et al.*, 2012), *C. martinii* F.Fen., Pistarino, Peruzzi & Cellin. (Fenaroli *et al.*, 2013). Another endemic is *C. cespitosa* Scop., an eastern Alpine species with two distinct ranges, north and south of the Alpine chain (Pawlowski, 1970): from the Viennese to the Steyr Alps in the north, and from Slovenia to the river Adige in the south. Its presence in the Bergamo Prealps was first observed by Rota (1843), Bergamaschi (1853), Chenevard (1915), and later confirmed by Hess *et al.* (1967), Ravazzi (2007), and Martini *et al.* (2012) (Fig. 1). Surprisingly, despite all these confirmed records, the presence of this species in the Bergamo Prealps is reported only in local floras (Martini *et al.*, 2012), but it is missing from national or international floras. In fact, it is not reported in the Bergamo Prealps in Aeschimann *et al.* (2004), Pignatti (1982; 2017–2019) and in the most recent updated checklist of the Italian flora (Bartolucci *et al.*, 2018). Considering the high degree of endemism of *Campanula* in the Alps and the poorly known occurrence of *C. cespitosa* in the Bergamo Prealps, in addition to the significant distance between these populations from the rest of its distribution range, we decided to further study this taxon in Lombardy. Based on multiple phytogeographic, morphological and genetic evidence, we concluded that the populations from the Bergamo Prealps represent a species new to science, which we propose to name *Campanula bergomensis*.

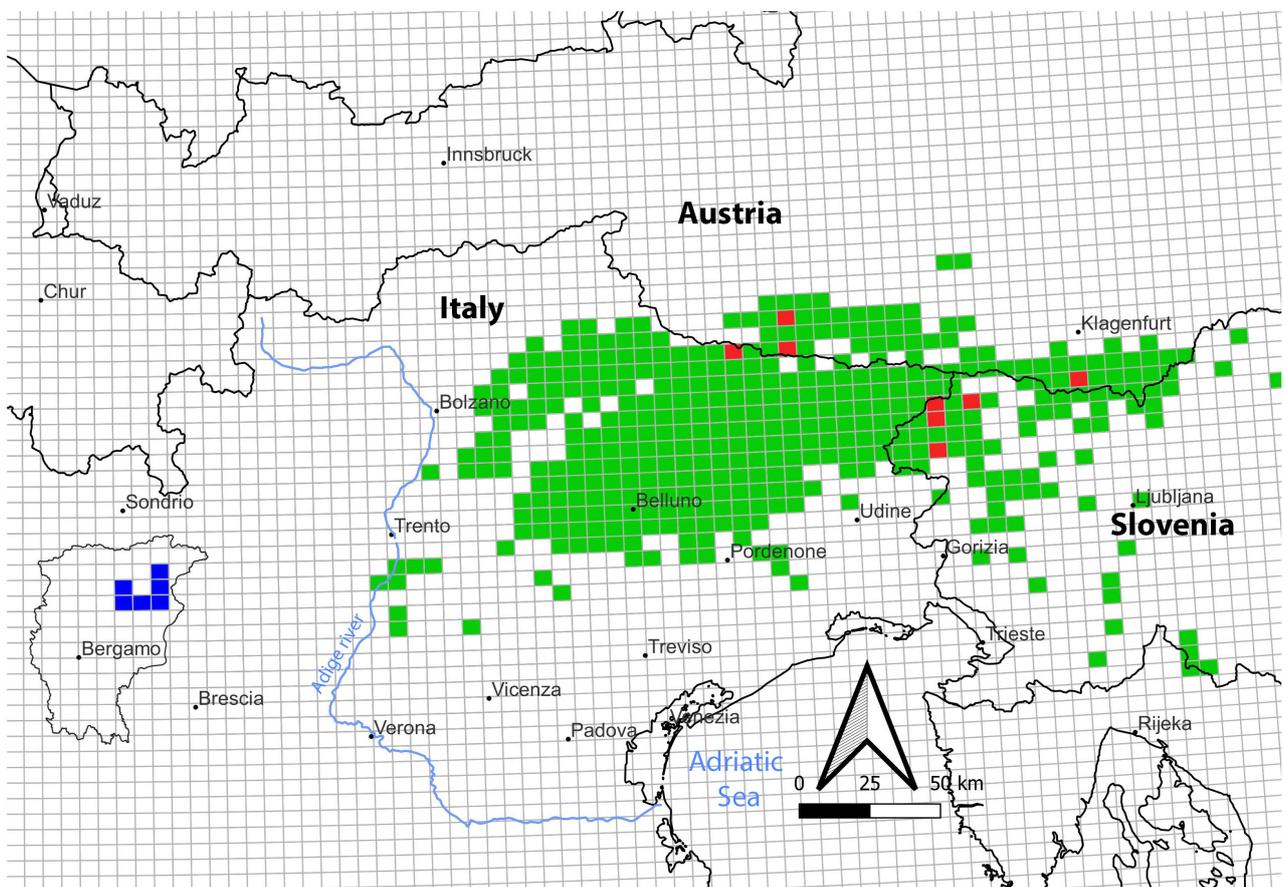


FIGURE 1. Distribution of *Campanula bergomensis* (blu squares) and *C. cespitosa* (green and red squares). Red squares indicate the grids where *C. cespitosa* samples for genetic analysis were collected. Cartographic grid is taken from Ehrendorfer and Hamann (1965). Bibliographic data of *C. cespitosa* are: Andreatta *et al.* 2020 (Veneto, Italy), Martini *et al.* 2023 (Friuli-Venezia Giulia, Italy), Wilhelm *et al.* 2014 (Alto Adige, Italy), Jogan *et al.* 2001 (Slovenia), Hartl *et al.* 1992 and Staudinger *et al.* 2009 (Austria).

Materials and methods

The morphological analysis of *Campanula bergomensis* was performed on samples collected in three valleys (Table 1); from each valley, 40–50 individuals (130 in total) were collected. The morphological comparison with the closely related species *C. cespitosa* was performed using 10–20 individuals of this species from three different sites (50 in

total) (Table 1). For leaf trait measurements, individuals were collected and preserved in moistened blotting paper until traits were measured.

For the pollen analysis and comparison, at least 3 flowers in full anthesis from each population sampled of *C. bergomensis* and *C. cespitosa* were collected and dried (Table 1). For *C. cespitosa*, the pollen from an herbarium specimen was also included (Table 1).

For the genetic analysis, *C. bergomensis* samples were collected in summer 2022. In order to perform detailed genetic comparison with the closely related *C. cespitosa*, the latter was sampled in three different areas within its distribution range (see Fig. 1). Samples of *C. cochleariifolia*, a species closely related to *C. cespitosa*, were also collected (Table 1). For genetic analysis, five specimens of each investigated species were sampled (four *C. cochleariifolia*) (Table 1). From each specimen 5 to 15 young leaves were collected. Specimens were preserved in plastic bags hermetically closed and filled with silica gel to reduce moisture and dehydrate the leaves. Bags were then preserved under cool and dry conditions.

TABLE 1. Sampling dates for morphological and genetic analysis. “-” indicates missing data. * samples from Val Resia (UD) are from *Herbarium* F. Martini of Museo Friulano di Storia Naturale Udine (Italy) (*leg.* F. Martini).

Species	Country, region	Site	Elevation (m asl)	Sampling date for plant morphology	Sampling date for pollen morphology	Sampling date for genetics	Sample IDs for genetics
<i>C. bergomensis</i>	Italy, Lombardy	Songavazzo (BG), Valle di Frucc	920–930	20 Jul. 2019	20 Jul. 2019	-	-
	Italy, Lombardy	Onore (BG), Val dei Dadi	770–850	21 Jul. 2019	21 Jul. 2019	8 Aug. 2022	BG1–2
	Italy, Lombardy	Clusone (BG), Valle Cabrosna	515–745	25 Aug. 2019	25 Aug. 2019	8 Aug. 2022	BG5
	Italy, Lombardy	Onore (BG), Valle di Tede	710	-	-	8 Aug. 2022	BG3–4
<i>C. cespitosa</i>	Italy, Veneto	Cortina d’Ampezzo (BL), Passo Tre Croci	1210	30 Jul. 2019	30 Jul. 2019	-	-
	Italy, Friuli-Venezia Giulia	Resia (UD), Valle del Rio Barman	600	-	Herbarium *	-	-
	Italy, Friuli-Venezia Giulia	Sauris (UD)	1240	1 Aug. 2020	-	-	-
	Italy, Veneto	Sappada-Presenari (BL), Piave river springs	1085–1890	-	-	8 Aug. 2022	CeP1–5
	Italy, Trentino	Primiero San Martino (TN), Val Canali	1410–1580	2 Aug. 2020	-	-	-
	Slovenia, Gorizia Region	Žaga- Kobarid; Robič- Staro selo; Predel- Bovec; Log pod Mangartom; Kranjska Gora	240–1520	-	-	18 Aug. 2022	CeS1–5
	Austria, Carinthia	Ferlach, Loibl Pass; Galbass (Oberdrau); Kötschach-Mauthen, Plöcken Pass	700–980	-	-	19 Aug. 2022	CeA1–5
<i>C. cochleariifolia</i>	Italy, Lombardy	Bormio (SO), Passo dello Stelvio	2200	-	-	11 Jul. 2023	CoV2–5

Seeds from specimens from Val dei Dadi were collected in the field on 14th September 2019 in order to cultivate the new species *ex situ* in “Città Studi” Botanical Garden (University of Milan). 450 seeds were sown in the tropical greenhouse on 26 January 2021, although only 14 seedlings germinated and, on 3 October 2023, only two plants had survived, which are currently cultivated outdoors.

Following the method proposed by Pierce *et al.* (2013), the CSR (competitive-stress tolerant-ruderal) strategy was calculated for the new species using three leaf parameters: leaf dry matter content (LDMC), specific leaf area (SLA), and leaf area (LA). In particular, 130 cauline and 30 basal leaves were measured from samples from Val Dei Dadi, Val di Frucc and Val Cabrosna (Table 1).

Light Microscopy (LM) and Scanning Electron Microscopy (SEM) observations were conducted using pollen grains acetolyzed according to Bonelli *et al.* (2020). The measurements of acetolyzed pollen, mounted in glycerine jelly, were taken in LM with a 100x immersion objective lens on a Leica DM–RD microscope equipped with a Leica

MC170 HD camera (Leica Camera AG, Wetzlar, DE). For pollen grain shape, P (polar axis), E (equatorial diameter), and P/E ratio, 50 pollen grains in equatorial view were measured and analyzed for each population (Eustacchio *et al.*, 2023). The measurements were performed with ImageJ software (Schneider *et al.*, 2012). For SEM observations, acetolyzed and air-dried pollen was sputtered with a 25-nm layer of gold in argon plasma (AGAR Automatic Sputter Coater Mod. B7341, Scientific Limited, Stansted, UK) equipped with a quartz crystal thickness monitor. At least 30 pollen grains in equatorial and polar view were observed under the electron microscope (Model Leo-1430, Zeiss Inc., Thornwood, NY, USA). Palynological terminology follows Rodondi *et al.* (2004), Punt *et al.* (2007) and Hesse *et al.* (2009).

DNA was extracted within two months from sample collection. Genomic DNA was extracted and purified using DNeasy Plant Pro Kit (QIAGEN©, Germantown, MD, USA) starting from 10 mg of dry leaves. For the genetic analysis two plastidal markers were PCR-amplified and sequenced. For the PCR amplification of *matK* and *trnL-F* genes primers from Crowl *et al.* (2014) were used. Amplifications of plastidal genes were performed with the following PCR cycles: an initial denaturation step at 96 °C for 90 s, followed by 34 cycles at 95 °C for 30 s, 50 °C for 60 s, and 72 °C for 90 s, and a final extension step of 20 min at 72 °C. Amplification products were checked on a 1.5% agarose gel and sequenced by an external sequencing service provider (Eurofins Genomics, Italy), using the same two primers as used for amplification.

Prior to phylogenetic analyses, sequence electropherograms were visually inspected using Benchling (Benchling, 2023) to detect mis-calls. Besides the sequences from *C. bergomensis* and *C. cespitosa* generated by us, we added all taxa with publicly available *matK* and *trnL* sequences included in the J clade (the one with *C. cespitosa*) from the phylogenetic tree in Crowl *et al.* (2014). To further complement the phylogenetic reconstruction, *C. hawkinsiana* and *C. lasiocarpa* were added at the time the analysis was conducted; they were within the first four species with the highest total alignment score after a nucleotide blast against *Campanula* (taxid:40568; organism field) using BG5 *trnL-F* sequence as a query. *Jasione montana* was used as outgroup. Alignments were performed using Muscle included in AliView v1.28 (Larsson, 2014). After manual trimming of upstream and downstream unaligned portions, multialignments built from *matK* and *trnL-F* sequences were manually merged to build a concatenated plastidal dataset. Phylogenetic analyses were run using MEGA v11.0.13 (Tamura *et al.*, 2021). The best substitution model was estimated using the appropriate MEGA function. A maximum likelihood (ML) tree was constructed with the following parameters: General Time Reversible model (gamma distributed with invariant sites), four discrete gamma categories, use all sites, 5000 bootstrap replications (all other options were left to default parameters). Single-nucleotide polymorphic sites (SNPs) in the multialignment were counted using the SNP-sites v2.5.1 tool (Page *et al.*, 2016). Small insertions/deletions (indels) were counted by visual inspection of the alignments. For both variant types, a variant was counted if occurring at least in one species of the multialignment. GenBank accession numbers of sequences used in this study are reported in Table S1a in supplementary material.

Results

The analysis of morphological traits indicates a clear separation between *C. bergomensis* and the closely related species *C. cespitosa* (see section on taxonomic relationships).

New sequences and trace files generated in this work have been uploaded to GenBank (Table S1b in supplementary material). The alignment of *trnL-F* sequences from all species considered revealed the presence of an 81bp (base pair) long tandem repeat in the *C. bergomensis* accessions. A total of 194 SNPs and 3 indels were identified comparing the *matK* sequence of all species. For *trnL-F*, SNP number was lower (96), but a higher number of indels was detected (17). The genetic variants identified in these sequences allowed a phylogenetic reconstruction (ML tree) which provides a robust support for considering the three related groups *C. bergomensis* (99 bootstrap value; Fig. 2, purple vertical line), *C. cespitosa* (95 bootstrap value; Fig. 2, blue vertical line) and *C. cochlearifolia* (96 bootstrap value; Fig. 2, green vertical line) as distinct species. On the other hand, although *C. cespitosa* and *C. cochlearifolia* species are clearly separated, their relationship remains unresolved due to the low bootstrap value (40) of their ancestral node. Importantly, the significant bootstrap value supporting the *C. bergomensis* group (99) suggests its separation from the other two related entities. The congruence among the morphological, genetic and geographic evidence supports the recognition of *C. bergomensis* as a species new to science.

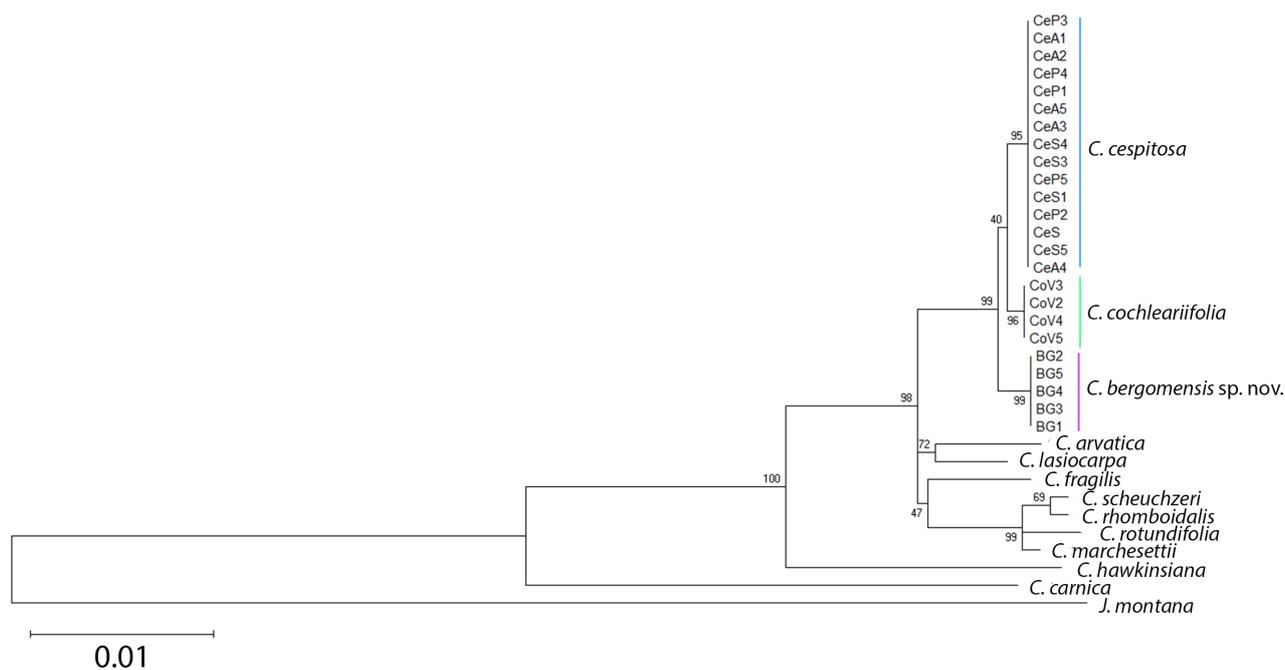


FIGURE 2. ML phylogenetic reconstruction of relevant *Campanula* species. Species selection is explained in the methods section. Bootstrap values are shown on each node. *Jasione montana* is selected as the outgroup.

Taxonomy

Campanula bergomensis F. Mangili & L. Mangili sp. nov. (Figs. 3–8)

Description:—Perennial herb, (4–) 10–20 (–30) cm tall, with ascending-erect, glabrous or sparsely hairy, square-cross-section stems, with strong, horizontal creeping rhizomes from which a rosette of leaves develops (Fig. 3A–C; Fig. 4). Roots robust, branched and elongated underground. Basal leaves forming rosettes, with 10–20 mm long petioles, lamina oval-rhomboid 9–12 x 6–7 mm, glabrous, margin weakly toothed, sometimes sparsely hairy, often withered during summer anthesis (Fig. 3A–D; Fig. 4); stem leaves numerous, sessile, linear-lanceolate, acute, (7–) 15–21 (–30) mm, glabrous, margin entire, on lower portion of stem close together, then spaced and decreasing upwards (Fig. 3A, Fig. 4). Inflorescence a raceme with 2–4 flowers, supported by long peduncles (Fig. 3A; Fig. 4). Calyx glabrous, with lacinae 2–3 mm slightly larger than the tube and appressed to the corolla (Fig. 3E, Fig. 4). Buds and flowers pendulous; corolla (9–) 11–12 (–14) mm, hemispherical-campanulate, not constricted in upper part, light blue (Fig. 3E–F, Fig. 4); trifold stigma not protruding. Fresh pollen color whitish, becoming yellow when drying out; mature pollen grains suboblate ($P/E = 0.87$), released as free monads of medium size (30 μm); grains radially symmetric, isopolar, triporate and zonoporate (Fig. 5); tectum discontinuous with muri (thickness around 0.20 μm) and lumina; spinulae present, shorter than 3 μm ; sometimes granules present; ornamentation rugulate-microreticulate and echinate (Fig. 5). Capsule pendulous, ovoid, dehiscent. Seeds about 0.9 mm long (Fig. 3G; Fig. 4).

Type:—ITALY, Val Borlezza BG, Clusone, Ponte della Selva, Val Cabrosna, sentiero di fondovalle, 625 m, ghiaione ricco di calcare, 15.VIII.2007, *Leg. Perico*, 18 Apr. 2023 (holotype BER!; isotypes in BER!; paratypes ibidem 15.VIII.2007, *leg. Perico*), (Fig. 6).

Synonyms:—*Campanula cespitosa sensu* Martini *et al.* (2012), non Scop., Fl. Carniol., ed. 2, 1: 143 (1771); *Campanula rotundifolia pro parte sensu* auct. fl. bergomensis, non L., Sp. Pl.: 163 (1753).

Phenology:—Flowering from mid-July to mid-August.

Habitat and ecology:—*Campanula bergomensis* grows on dolomitic debris cones, ledges of rough grassland, generally on poorly developed and well-drained soils (Fig. 3B). Its elevational distribution ranges from 450 to 1,250 m a.s.l. The area of occurrence is characterized by an annual average temperature of 11 °C in Clusone (data from Ufficio Idrografico del Po, 1958–1982°) and rainy climate (1500 ml/y in Clusone; Ceriani & Carelli, 1990). The species is particularly associated with wide and flat debris cones, an unusual geomorphological feature in the Lombardian

Prealps. *C. bergomensis* can be found on the edge of *Pinus mugo* Turra vegetation (with *Amelanchier ovalis* Medik., *Sesleria coerulea* (L.) Ard., *Calamagrostis varia* (Schrad.) Host, *Hieracium* sp., *Dryas octopetala* L., *Globularia cordifolia* L.), where the slopes are sparsely vegetated. *C. bergomensis* shows a S-R strategy (leaf traits and CSR graph are reported in supplementary material in Table S2 and Fig. S1, respectively).

Distribution range:—*Campanula bergomensis* occurs in a few areas of the Orobie Prealps, within the borders of Bergamo Province (Lombardy, Italy). (Fig. 1, 7).



FIGURE 3. Morphological features of *C. bergomensis* A: plant habitus (scale bar 5 cm). B: the plant in its habitat. C: winter habitus. D: leaf shapes (scale bar 1 cm). E, F: flower shape and fresh pollen color (scale bars 1 cm). G: seeds on millimetre paper to show shape and size.

Campanula bergomensis sp. nov.

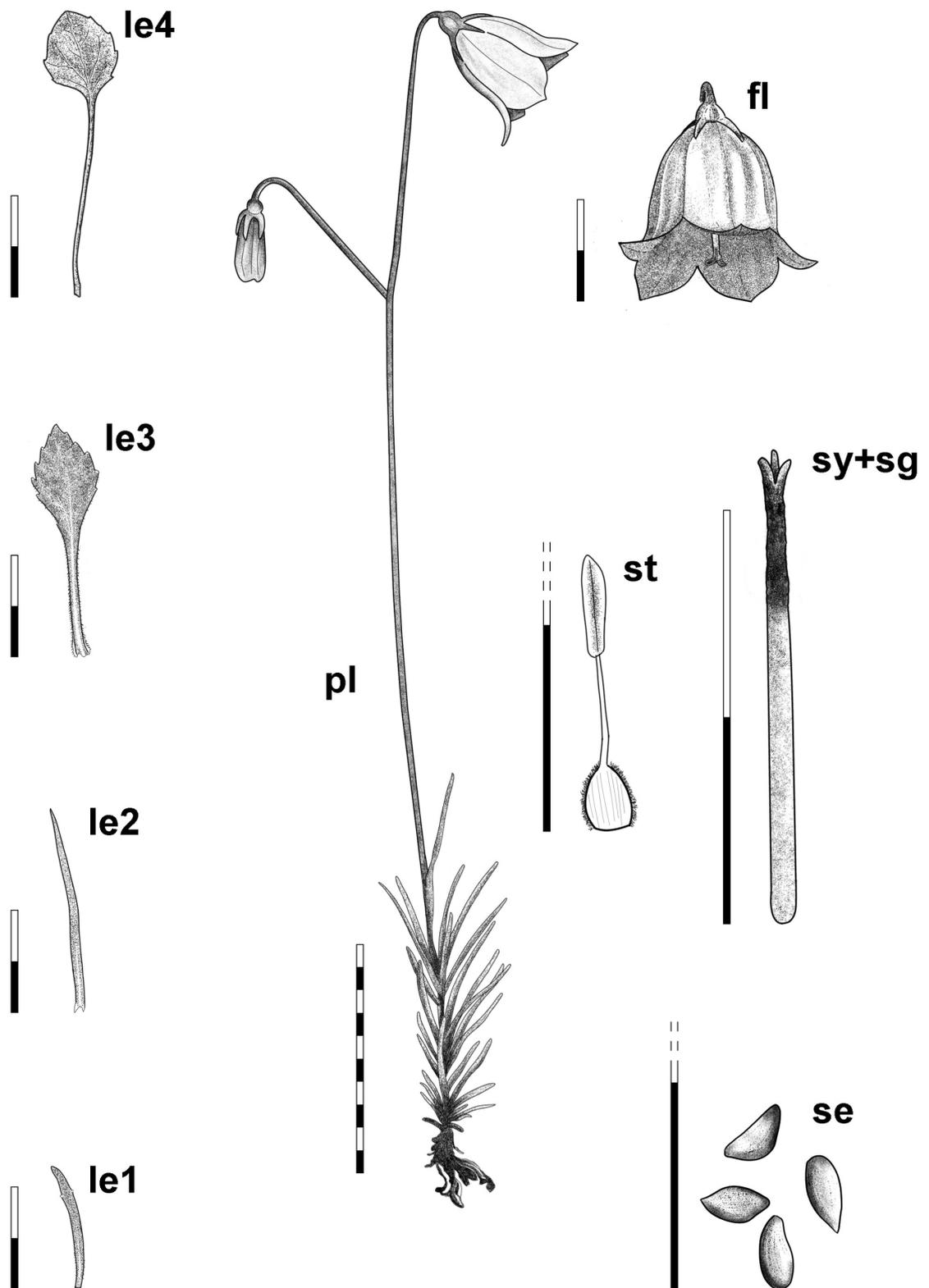


FIGURE 4. Illustration of *C. bergomensis* (bars subdivisions 5 mm). “le”= leaf, “pl”=plant, “fl”=flower, “st”=stamen”, “sy”= style”, “sg”= stigma, “se”=seeds”.

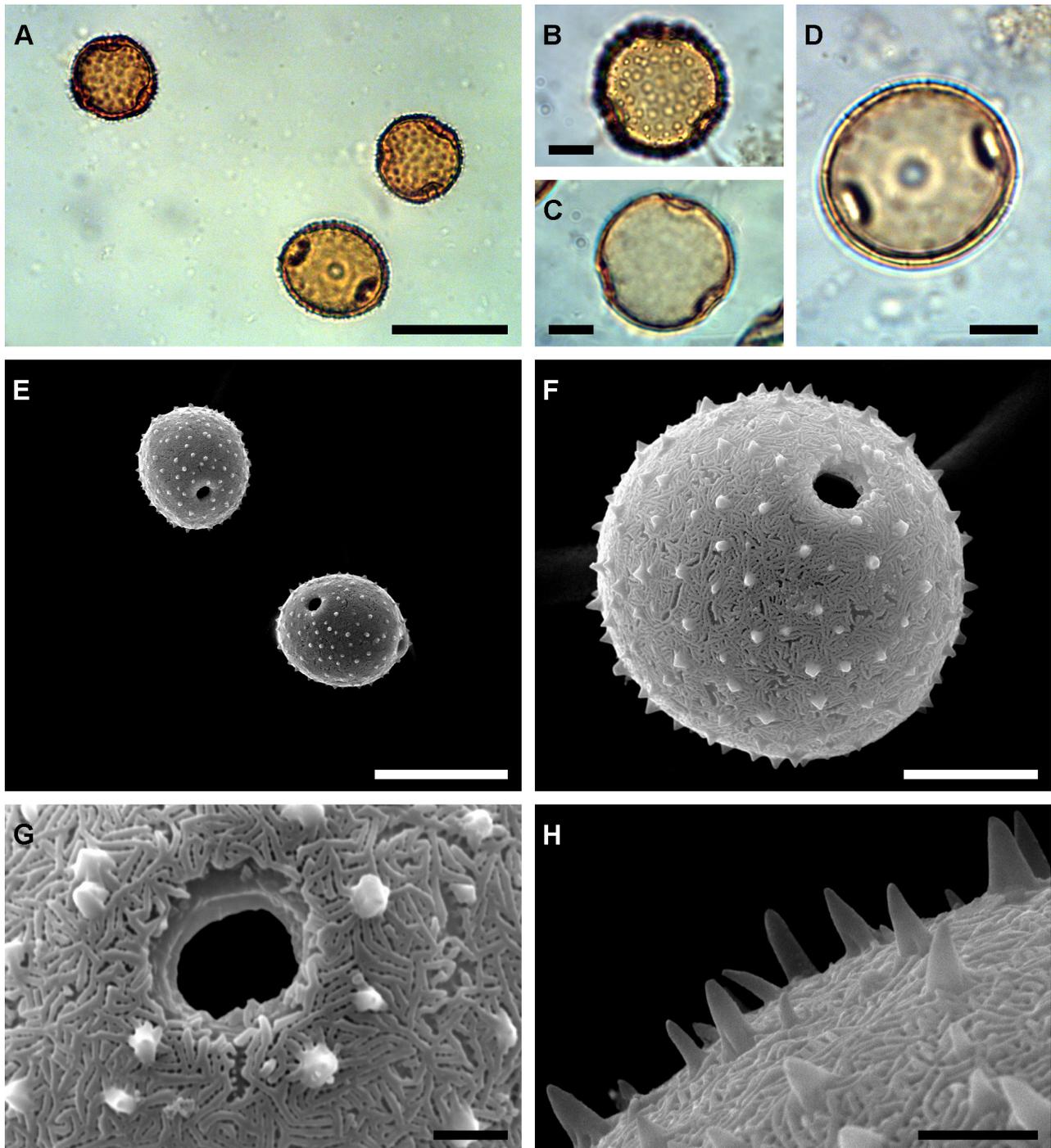


FIGURE 5. Pollen morphology of *C. bergomensis*. **A–D:** LM micrographs; **E–H:** SEM micrographs. **A:** Pollen grains as free monads showing the pores and the echinate ornamentation (scale bar = 30 μm). **B:** Pollen grain in polar view, the focal plane is on the echinate pole (scale bar = 10 μm). **C:** Pollen grain in polar view, the focal plane is on the equator showing the equatorial position of the pores (scale bar = 10 μm). **D:** Pollen grain in equatorial view, showing the suboblate shape (scale bar = 10 μm). **E:** Pollen grains as free monads showing echinate ornamentation (scale bar = 30 μm). **F:** Pollen grain showing the rugulate-microreticulate and echinate ornamentation (scale bar = 10 μm). **G:** The rugulate-microreticulate ornamentation stops near the pore margin (scale bar = 2 μm). **H:** The echinate ornamentation coexists with a rugulate-microreticulate pattern (scale bar = 2 μm).



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F. MARTINI		15 NOV. 2007

NUMERO DI INVENTARIO 083980

3771 *Campanula caespitosa* Scop.

WHB PG 4e 01251 CLUSONE BG, Clusone, Ponte della Selva, Val Cabrosna, sul sentiero di fondo valle (3); F x 625 625 15/08/2007

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REVISIONI	da	in data	Note
1 DET	<i>Campanula caespitosa</i> Scop.	Perico G.	15/08/2007
2 CONF	<i>Campanula caespitosa</i> Scop.	Martini F.	15/11/2007

Erbario Flora Alpina Bergamasca

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3771

Campanula caespitosa Scop.
Subsp.

Val Borlezza
BG, Clusone, Ponte della Selva, Val Cabrosna, sul sentiero di fondo valle (3);

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Hb PERICO Giovanni Leg. Perico G. 15/08/2007
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FIGURE 6. Holotype of *C. bergomensis* sp. nov.

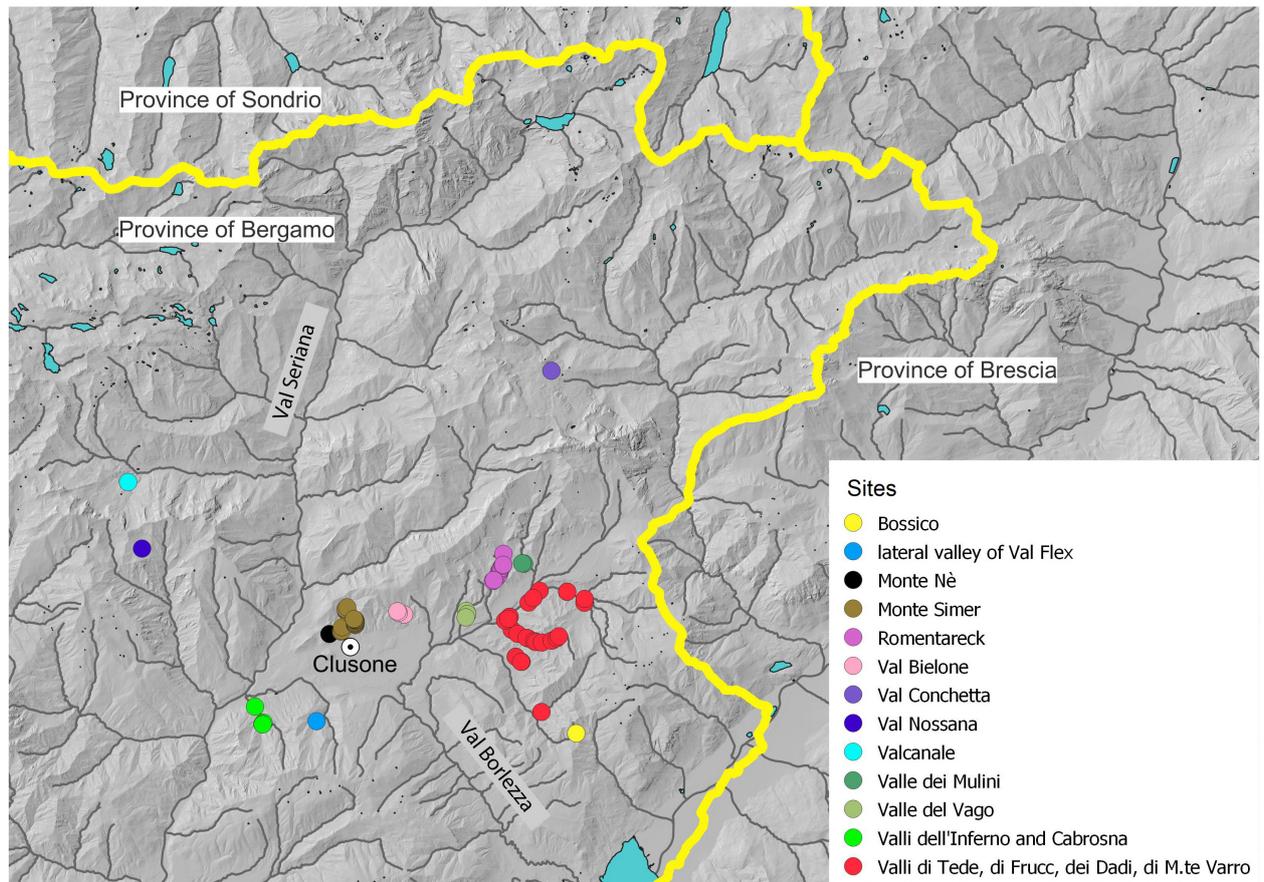


FIGURE 7. Distribution of *Campanula bergomensis*.

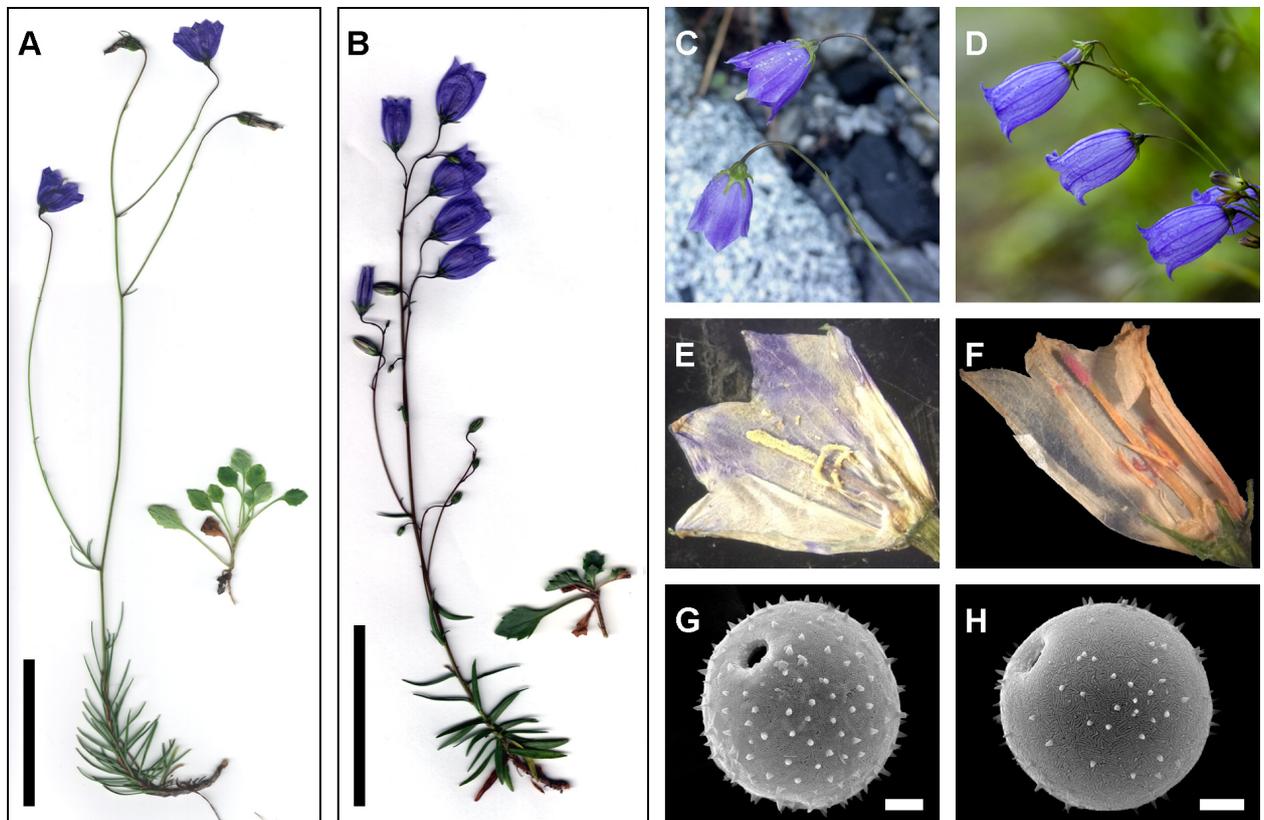


FIGURE 8. Morphological comparison between *C. bergomensis* sp. nov. (A, C, E, G) and *C. cespitosa* (B, D, F, H). A, B: plants habitus (scale bars 5 cm). C, D: flower shape. E, F: dried pollen color. G, H: pollen ornamentation observed with SEM (scale bars 5 μ m).

Etymology:—The epithet refers to the Province of Bergamo (called “Bergomum” in Roman antiquity), where all known populations of the new species are found.

Taxonomic remarks:—Morphological and genetic evidence support *Campanula bergomensis* as a species new to science. In particular, it is morphologically distinguished from *C. cespitosa* for having 1) the racemose inflorescence with less flowers compared to *C. cespitosa* (2–3 and 6, on average, respectively; Fig. 8 and Fig. S2); 2) the shape of the corolla (not constricted at the apex, like in *C. cespitosa*); and 3) the whitish-yellow pollen surface with many spinulae, instead of pink and with few spinulae like in *C. cespitosa* (Fig. 8). Genetically, *C. bergomensis* is well-distinguished from, though close to both *C. cespitosa* and *C. cochleariifolia* (Fig. 2), which have been consistently recovered as sister species (Mansion *et al.* 2012; Crowl *et al.* 2014, 2016). Although morphology would suggest that *C. bergomensis* is closer to *C. cespitosa* than to *C. cochleariifolia*, which is macroscopically very different, our genetic data are not so clear in confirming the phylogenetic relationships among these three closely related species and further investigations are needed, possibly including the comparison of more genes.

Discussion

Biogeographic considerations

Among the three closely related species, *C. cochleariifolia*, has the widest distribution range, being a South-European orophyte, which includes that of *Campanula bergomensis* and *C. cespitosa*. The co-occurrence of *C. cochleariifolia* and *C. bergomensis* was documented in phytosociological relevés from Val dei Dadi (Ravazzi, 2007). In contrast, *C. bergomensis* and *C. cespitosa* have clearly separated distribution ranges, the first being present only in a few sites of the Bergamo Prealps (Central-Southern Alps), the second occurring in the Eastern Alps, at least 100 km apart (the westernmost record is from Monte Finonchio—Folgaria, TN; Prosser *et al.*, 2019). The two disjunct, though closely related species *C. bergomensis* and *C. cespitosa* may have originated in isolation resulted from the Pleistocene Ice Ages, a well-known driver of such distributional pattern in the Alps, particularly important in the unglaciated peripheral areas (Merxmüller, 1954, Schönswetter *et al.*, 2003). However, a pre-glacial origin has been suggested for some endemic taxa occurring in the same area as a result of the late Tertiary dismantling of a once continuous southern Prealpine karstic platform characterized by limestone/dolomitic substrate (Bini, 1978, Ravazzi, 2007). The occurrence of *C. bergomensis* on peculiar carbonate landforms, such as flat and wide debris cones, uncommon in the Central Prealps but distinctive in the Eastern Alps, may support that hypothesis. In addition, Crowl *et al.* (2016) dated the split between *C. cespitosa* and *C. cochleariifolia* between 0.3 and 4.6 million years: this range, although wide, would support this hypothesis.

Threats

Some populations of *Campanula bergomensis* grow within a protected area of the Natura 2000 Network, Habitat Directive. In particular, populations of Val Bielone, Romentareck, Val dei Mulini (Colle di Passeraia), Monte Simer are included in the SAC (Special Area of Conservation) “Val Sedornia, Valzurio, e Pizzo della Presolana” (IT2060005); Val Nossana population is included in SAC “Val Nossana—Cima di Grem” (IT2060009). The main threat to *C. bergomensis* is currently the high frequency of motorcycles on and off the trails, and also off-trail, in all the valleys where the largest populations of the new species subsist (Val di Tede, Val di Monte Varro, Val Righenzolo, Val dei Dadi). The frequent passage of mountain bikes and motorcycles severely disrupts the stability of the debris conoids where *C. bergomensis* grows. Less critical is the episodic hydro-geological thread due to sudden floods caused by heavy precipitation events (Ravazzi *et al.*, 2007). The IUCN conservation status of the new species is under evaluation.

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