

Woodsia pulchella in the Western Carpathians: a relict species at the northern limit of its distribution

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In the Western Carpathians, we identified a strongly isolated stand of a species belonging in the fern genus *Woodsia*. Based on morphological characters, nuclear DNA content analysis and chromosome counts, we determined that the species occurring in the Polish Tatra Mts. is *W. pulchella* and not *W. alpina*, as was supposed before. The population is situated 365 km from the nearest one in the eastern Alps in Austria. *Woodsia pulchella* grows on northern slopes of the Giewont massif in the Western Tatra, on dolomite rocks between 1100–1480 m a.s.l. at two closely-situated localities. The current distribution of *W. pulchella* in Europe is detailed and the evolutionary origin of this very rare and relict species is discussed.

Introduction

The fern genus *Woodsia* (Woodsiaceae) comprises about 36 species and five hybrids distributed nearly exclusively in the northern hemisphere (Brown 1964, <http://homepages.caverock.net.nz/~bj/fern/woodsia.htm>). Only one species, *W. montevidensis*, reaches the southern hemisphere, where it occurs in South America and South Africa (Brown 1964). China, with 20–22

species of *Woodsia*, including eight endemics, stands out as a centre of diversity at the species level (Luo & Zhang 2012).

In Europe, three *Woodsia* species of circumboreal distribution are present: *W. alpina*, *W. ilvensis* and *W. glabella* (Hultén & Fries 1986). *Woodsia pulchella* (*W. glabella* subsp. *pulchella*), a species morphologically close to *W. glabella*, is known mainly from the Alps (Hultén & Fries 1986). It is regarded as a European

endemic distributed mainly in the central and eastern Alps, with isolated stands in east Pyrenees and south Carpathians. It occurs mainly in the subalpine and alpine zone, usually between 1400–1900 m a.s.l., but in the Italian Alps it has been found as low as 1000 m a.s.l. and as high as 2330 m a.s.l. (Pichi-Sermolli 1956). *Woodsia pulchella* grows exclusively on carbonate rocks, on cliffs, and in rock crevices in partially-shattered, usually north-exposed stands. The species is rare in most of the countries where it occurs and is included in local Red Lists or Red Books with the status critically endangered (CR) or endangered (EN).

From the Carpathians, *W. pulchella* was not reported until recently. Only *W. glabella*, reported from one stand in the Southern Carpathians, was known (Sündermann 1916). However, recent revision of the herbarium material and new findings revealed that the species occurring in this area is actually *W. pulchella* (Ciocârlan & Pop 2003).

In the present study, we identified *W. pulchella* in the Polish Tatra Mts. based on ecology, morphology, DNA content and cytological analysis. Our finding extends the general distribution area of this relict species considerably further north.

Material and methods

Field studies in the Polish Tatra Mts. were conducted during the years 2012 and 2013. Geographical coordinates of the stands were determined with a Garmin Legend HCx GPS receiver. The plants were documented using a Nikon Coolpix P500 camera. Distribution map of *Woodsia* species in the Tatra Mts. was prepared using a fragment of the map *Mapa Tatry w całości* 1:50 000 (www.sygmatra.com.pl). When available (for Austria, Germany, Slovenia), the stands were given in 10' × 6' MTB (Messtischblatt) grid or 5' × 3' quadrants.

Flow cytometry

For the measurements, *W. alpina* was obtained from the natural stand in Mały Śnieżny Kocioł

(the Sudetes Mts.), as well as from *in vitro* cultures of the Botanical Garden, University of Wrocław (the lines were derived from plants occurring in Mały Śnieżny Kocioł); *W. ilvensis* was obtained from a natural stand in Gorce Mts.; and *W. cf. pulchella* was obtained from Koński Żleb in the Polish Tatra Mts.

For nuclear DNA content estimation, nuclei were released simultaneously from young leaves of a sample species and an internal standard (*Secale cereale* 'Dankowskie', 16.19 pg/2C; Doležel et al. 1998) by chopping the leaves in a Petri dish in 1 ml of Galbraith's buffer (Galbraith et al. 1983), with addition of propidium iodide (PI; 50 µg cm⁻³) and ribonuclease A (50 µg cm⁻³). An antioxidant, PVP-10, 1% (v/v), was added to the buffer to neutralize staining inhibitors present in the leaf cytosol of *Woodsia* species. The suspension was passed through a 50 µm mesh nylon filter and analysed using a CyFlow SL (Partec GmbH, Münster, Germany) flow cytometer equipped with a high-grade solid-state laser with green light emission at 532 nm, long-pass filter RG 590 E, DM 560 A, as well as with side (SSC) and forward (FSC) scatters. For each species analyses were performed on three plants and replicated three times for each plant. For each sample, DNA content was established for 3000–5000 nuclei. Histograms were analysed using FloMax (Partec GmbH, Münster, Germany) software. Coefficient of variation (CV) of the G₀/G₁ peak of *Woodsia* spp. ranged between 4.44% and 6.63%. Nuclear DNA content was calculated using a linear relationship between the ratio of the 2C peak positions *Woodsia/Secale* on a histogram of fluorescence intensities.

Results

Woodsia alpina was reported from the Tatra Mts., the highest mountain range of the Carpathians, from 13 localities situated mostly in the Slovakian Tatras (Piękoś-Mirkowa & Delimat 2002). Since it is known that, in contrast to *W. alpina* and *W. ilvensis*, *W. pulchella* is exclusively bound to dolomite or limestone bed-rock, we undertook thorough studies of *Woodsia* populations occurring on dolomite rocks in the Polish



Fig. 1. Habit of *Woodsia pulchella* from Koński Żleb (Western Tatras) grown in laboratory.

Table 1. Morphological differences between *Woodsia alpina*, *W. pulchella* and *W. glabella* (Poelt 1952, Prosser 1990, J. Kruk. pers. obs.).

Characters	<i>W. alpina</i>	<i>W. pulchella</i>	<i>W. glabella</i>
Fronds	broadly to narrowly lanceolate, 20–30 mm wide	broadly to narrowly lanceolate, 8–14(19) mm wide	linear to linear-lanceolate, 6–10 (12) mm wide
Pinnae	in upper part of frond obtuse, loosely arranged	in upper part of frond ± acute, loosely arranged	round-shaped, strongly obtuse, densely arranged
Scales	abundant on stipe and rachis	few and minute on stipe or stipe glabrous	absent
Glandular hairs	absent or minute on rachis	numerous on stipe, rachis and pinnae	absent

Western Tatras in order to determine their taxonomical status. These populations were known for years (Szafer & Sokołowski 1927, Piękoś-Mirkowa & Delimat 2002, 2008), but the plants occurring there were always regarded as *W. alpina*. Three *Woodsia* species that were taken into consideration as possible candidates for the investigated populations were *W. alpina*, *W. pulchella* and *W. glabella*. The species have some consistent morphological differences (Table 1).

The investigated *Woodsia* plants had numerous glandular hairs on stipes, rachis and pinnae (Figs. 1 and 2), while minute scales were present only in the lower part of the stipe (Figs. 1 and 2A). The other, less distinct morphological characters also indicated that the plants belonged to *W. pulchella*.

We performed a cytometric estimation of nuclear DNA content (2C values) of this taxon, as well as of the other *Woodsia* species (as a reference), i.e., *W. ilvensis* originating from the

Gorce Mts., the only presently known stand of this species in Poland, and *W. alpina* from the Sudetes Mts. Currently, the plant DNA C-values database (<http://data.kew.org/cvalues/>) has no entries for any *Woodsia* species, therefore in our studies the reference species were required. The three taxa had different 2C values (Table 2). The 2C value of *Woodsia* from the Tatra Mts.

Table 2. DNA content (pg/2C) of *Woodsia alpina*, *W. ilvensis* and *W. cf. pulchella*. In the case of *W. alpina*, the plants originated from natural stands or *in vitro* culture. The values given are means with their standard deviations. Three independent plants of each species in two or three replicates were analyzed.

Species	DNA content (pg/2C)
<i>W. alpina</i>	6.295 ± 0.184
<i>W. alpina</i> (<i>in vitro</i> culture)	6.277 ± 0.104
<i>W. ilvensis</i>	7.542 ± 0.090
<i>W. cf. pulchella</i>	4.868 ± 0.099

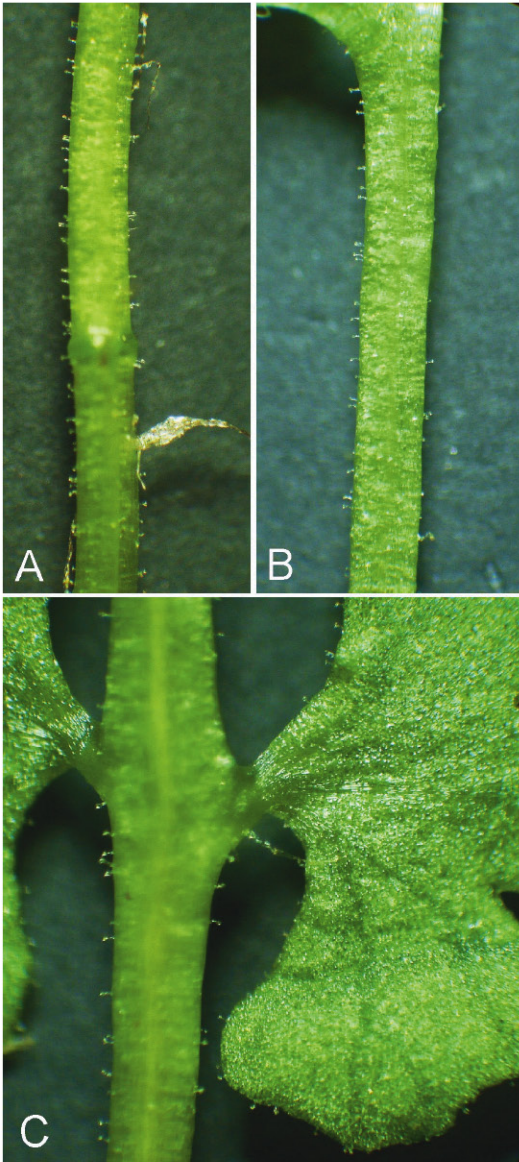


Fig. 2. Close-ups of glandular hairs of *Woodsia pulchella* from Koński Żleb (Western Tatras). — **A:** Lower part of stalk. — **B:** Upper part of stalk. — **C:** Rachis and pinnae.

was the lowest (4.9 pg/2C) and clearly different from that of *W. alpina* (6.3 pg/2C) from the Sudetes Mts. Interestingly, although the reported chromosome numbers for *W. ilvensis* and *W. pulchella* are the same ($2n = 78$) (Ma 1985), their genomes are very different in size. On the other hand, the DNA content of *W. alpina*, an allotetraploid ($2n = 156$), is intermediate between

the other two studied species. It is supposed that *W. alpina* is a fixed hybrid of *W. ilvensis* ($2n = 78$, $2C = 7.5$ pg/2C) and *W. glabella* ($2n = 78$) (Brown 1964), and our results are in agreement with that hypothesis, assuming similar 2C values for *W. pulchella* and *W. glabella*. Unfortunately, we were not able to obtain reliable reference material of *W. pulchella* to compare its 2C value with that of the *Woodsia* specimens from the Polish Tatra Mts. The DNA content analysis revealed that *Woodsia* specimens from the Polish Tatra Mts. are clearly different from those of *W. alpina* and support the notion that the examined taxon is *W. pulchella*.

The present analysis included *W. alpina* specimens from the natural stand in the glacial circus Mały Śnieżny Kocioł in the Karkonosze Mts. (the Sudetes Mts.), and propagated *in vitro* (Kromer et al. 2008). Similar 2C values obtained for *W. alpina* plants originating from those two sources indicate that *in vitro* propagation of this critically-endangered species in Poland does not affect its nuclear DNA content.

Since *W. pulchella* ($2n = 78$) and *W. alpina* ($2n = 156$) differ in chromosome numbers, we analyzed specimens originating from Koński Żleb (stand 1 in Fig. 3). For this purpose, we prepared cytological squashes from pinna tips, sporocytes and root tips. Only in the latter case, the metaphase plate could be found, where ca. 60 (70) chromosomes could be observed (data not shown). The exact number of chromosomes could not be estimated due to aggregation of chromosomes. For this reason, the obtained $2n$ number is certainly underestimated to some extent. Nevertheless, it is close to the $2n$ number reported for *W. pulchella* and these data preclude the possibility that the investigated individuals belonged to *W. alpina*.

Our data unequivocally demonstrate that the species occurring in the Polish Tatra Mts. is *W. pulchella* and not *W. alpina*, as was supposed before, representing the first, strongly isolated stand in the Western Carpathians. The stand is situated 365 km from the nearest population of this species in eastern Austria.

Woodsia pulchella grows on northern slopes of the Giewont massif in the Western Tatra on dolomite rocks between 1100–1480 m at two closely situated stands: Koński Żleb (locality 1



Fig. 3. Distribution of *Woodsia pulchella* (squares) and *W. alpina* (dots) in the Tatra Mts. See text for more detailed localization and description of the stands. Published with permission of SYGNATURA.

in Fig. 3), 1100–1200 m on three rocks, the populations altogether not exceeding 20 individuals (Piękoś-Mirkowa & Delimat 2002); Suchy Wierch, 1480 m a.s.l. (locality 2 in Fig. 3), from where it was described as *W. alpina* (Szafer & Sokołowski 1927) and confirmed in 2013 (49°15'31.6''N, 19°56'27.8''E, 1479 m a.s.l., N exposition); the plants were found in two groups comprising ca. 10 individuals, with a similar number of adult plants and seedlings (Fig. 4). In both localities, the species grows in floristically poor communities. The most frequent accompanying species are *Asplenium viride*, *A. trichomanes*, *Campanula cochlearifolia*, *Primula auricula*, *Leontopodium alpinum* and *Trisetum alpestre* (Piękoś-Mirkowa & Delimat 2008).

The locality of *W. alpina* in the Polish Tatra (locality 3 in Fig. 3, below the Szpiglasowa Pass, ca. 1900 m) is doubtful. It was not confirmed in the present study and no suitable habitat was found in this area. The literature data regarding this stand (Fabiszewski & Piękoś-Mirkowa 2001) are not documented by herbarium material. The

other localities of *W. alpina*, according to the literature (Piękoś-Mirkowa & Delimat 2002), are (numbers refer to localities in Fig. 3): (4) Kriváň Mt., N slope; (5) Bielovodská valley near České pleso between the Mlynár and Ganek Mts., 1425–1555 m a.s.l.; between Bielovodská and Česká valley, 1400 m a.s.l.; (6) Kvetnicová veža Mt. above the Velická valley, 1790–1810 m a.s.l.; (7) Gerlach Mt., E slope, ca. 1900 m a.s.l.; (8) Slavkovský Mt. above Vel'ká Studená valley, 1550–1575 m a.s.l.; (9) Malý Ladový Mt., SE slope, ca. 2600 m a.s.l.; (10) Kežmarský Mt., 2450 m a.s.l.; (11) Vel'ká Sviš'ovka, 1700–2000 m a.s.l.

Although we have not verified the taxonomical status of *Woodsia* from the Slovak Tatras (Fig. 3), it is most probably *W. alpina*, taking into account that the bedrock is silicate (granite or mylonite) in the whole area. Our data indicate that *W. alpina* does not occur in the Polish Tatra Mts. and the only existing relict locality of that species in Poland is in the Karkonosze Mts.

Below we present the current distribution of *W. pulchella* in other countries, based on litera-



Fig. 4. Adult and juvenile plants of *Woodsia pulchella* in a natural stand at Suchy Wierch Mt. (Western Tatras).

ture data and personal communications (see also Fig. 5). When known, the accompanying species are named. The numbers (e.g. 8359/2) are MTB quadrats (see Material and methods)

Romania (O. Pop pers. comm. and the cited literature). In 1889, F. Sündermann discovered in Bucegi Massif (above Mălăești chalet on Mt. Buceșoiu) a species that was published as *Woodsia glabella* (Sündermann 1916). However, a recent revision of the herbarium specimen revealed it is *W. pulchella* (Ciocârlan & Pop 2003). During the years 2000–2002, new stands of *W. pulchella* were discovered in the Piatra Craiului Massif near Zărnești (Ciocârlan & Pop 2003), ca. 20 km NW from the Buceșoiu Peak: Zărnești Gorges (Prăpăștiile Zărneștilor) (ca. 1300 m a.s.l. on limestone rocks); Bârsa Valley near Gura Bârsei chalet; Padina Lăncii; western slopes of the main ridge between Timbalul Mic and Sbirii Peak. The species occurs in the Piatra Craiului Massif from 1000 to 1800 m a.s.l. in very small populations (2–3 individuals) (Ciocârlan & Pop 2003). The stands are not further than 7 km apart from each other.

The Alps. *Woodsia pulchella* inhabits almost exclusively two large, continuous belts of calcareous or dolomitic bedrock that run in west–eastern direction through the external ranges, viz. the northern ranges from Canton Vaud (W. Switzerland) in the west unto NE Styria (Steiermark, Austria) in the east, and the southern ranges from M. Generoso in Canton Ticino (S. Switzerland) in the west unto Slovenia in the east. In contrast, according to the sources quoted below, only very few stands exist in the scattered calcareous or dolomitic areas of the interior ranges: near Passo di Spluga (Splügenpass) in Lombardy, and on Mt. Endkopf (Jaggl) near Passo di Resia (Reschenpass) in South Tyrol (both in Italy).

Austria (H. Niklfeld pers. comm. and the cited literature), reliable records of the species exist for three regions.

— Steiermark (Styria), 8359/2, Farfel in Schneeealpe, ca. 1600 m a.s.l., W exposition, on a limestone rock face with *Potentilla clusiana*, *Draba stellata*, *Asplenium viride* and *Campanula cochlearifolia* or together with *Carex firma*, *Moehringia muscosa*, *Saxifraga caesia*, *S. paniculata*, *Sesleria varia* and *Trisetum alpestre* (Gutermann 1978); this is an isolated, most northeastern stand of *W. pulchella* in the Alps (Fig. 5) and the closest to that in the Tatra Mts.; 8456/2, Mt. Messnerin, 1835 m a.s.l., herbarium material, leg. *Portenschlag*, ca. 1800 a.s.l. (Gutermann 1978), the latter locality was never confirmed afterwards though searched by several botanists (Heber 2013). — Kärnten (Carinthia), 9343/3, Karnische Alpen: Gamsboden above Obere Valentinalm, ca. 1750 m a.s.l. (Melzer 1980); 9345/1, Gailtaler Alpen: Gössering, NW of Weißbriach, N exposed rock built of limestone conglomerate (Melzer, 1980), ca. 900 m a.s.l.; 9552/2; Karawanken Mts.: SW foot of Mt. Obir (Hochobir), near Zell Pfarre (Sele Fara), close to Freibach, ca. 810 m a.s.l. on dolomitic limestone rock, NW exposition (Melzer 1990). — Tirol, 8728/1, Allgäuer Alpen, upper part of Höhenbach valley, N of Holzgau (Gutermann 1960).

Germany (Paul 1952, Dostál & Reichstein 1984, Bennert 1999, Wilfried Bennert pers. comm.). The species was found only in the Allgäuer Alps and the Berchtesgaden Alps in six populations, of which only two had more than ten individuals; 8627/1, Breitachklamm near Oberstdorf, probably extinct; 8528/1, near Hinterstein at 1460 m a.s.l., six plants; 8528/1, below Ochsenalphütte at 1560 m a.s.l., > 20 plants; 8628/1, Hofäts; 8242/4, Weißbachschlucht between Bad Reichenhall and Inzell, SW (?) of Mauthäusl (extinct); 8443/4, at Grünsee, eight plants; 8543/2, Teufelsmühle at Funtensee, ca. 1600 m a.s.l., with *Cystopteris fragilis* and *Grimmia andreoides*, 70 plants.

Slovenia (Nejc Jogan, pers. comm.). Julijske Alpe (Julian Alps), 9647/3, Kanin, 1200 m a.s.l.; 9647/1, Bovec, Planina Goričica, 1351 m a.s.l.; 9647/1, Bovec, Mt. Čuklja,



Fig. 5. General distribution of *Woodsia pulchella*. The stands in different countries are shown by the following coloured dots: Spain = yellow-green, Switzerland = green, Italy = pink, Germany = blue, Austria = yellow, Slovenia = bright-violet, Poland = red, Romania = orange. The diameter of the dots is ca. 10 km. Crosses indicate localities where the species is extinct. See text for detailed localization and description of the stands. Two or more locations might be represented by one symbol.

1767 m a.s.l.; 9647/2, Bovec, Zgornja Bavščica, Bala, 1553 m a.s.l.; 9548/3, Bovec, Trenta, Gorenja Trenta–Zapoden, 877 m a.s.l.; 9647/2, Bovec, Bala, Planina Bala, 1184 m a.s.l.; Mt. Šuštar-Kotni vrh, 1604 m a.s.l.; 9747/2 and 9748/1, Mt. Krn, eight records from altitudes between 1396 and 2232 m a.s.l.; 9749/4, Tolmin, Bača pri Podbrdu; Kamniške-Savinjske Alpe (Kamnik and Savinja Alps): 9653/3, Krvavec, Kokrsko sedlo, 1797 m a.s.l.; Karavanke Mts.: 9550/1, Mt. Baba, 1849 m a.s.l. (doubtful locality). According to Čušin and Dakskobler (2001): 9548/3, Zapoden v Trenti, lonely rock under Ušje-Plešivec ridge, ca. 1100 m a.s.l. together with *Viola biflora*, *Cystopteris fragilis* and *Asplenium trichomanes*; only slightly higher with *Crepis kernerii*, *Campanula zoyssii*, *C. cochlearifolia*, *Astrantia carniolica*, *Carex firma*, *Sesleria albicans*, *Rhodothamnus chamaecistus*, *Selaginella selaginoides*, *Valeriana saxatilis* and *Aquilegia einseleana*; 9749/4, Šoštar (Kotni vrh), E of Mt. Črna prst, ca. 1590 m a.s.l., with *Salix glabra*, *Pinus mugo*, *Campanula zoyssii*, *C. cochlearifolia*, *Carex firma*, *Rhodothamnus chamaecistus*, *Primula auricula*, *Sesleria albicans*, *Pinguicula alpina*, *Selaginella selaginoides*, *Saxifraga crustata*, *S. squarrosa*, *Tofieldia calyculata*, *Silene pusilla*, *Pedicularis rostratocapitata*, *Valeriana saxatilis*, *Paederota lutea*, *Ranunculus hybridus*, *Asplenium viride* and *Crepis kernerii*.

Switzerland (Becherer 1973). — Canton Bern, Berner Oberland, in der Klus above Kandersteg, 1350 m a.s.l., in association with *Cystopteris fragilis*, *Saxifraga caesia*, *Erica carnea*, *Primula auricula*; above Gemniweg behind Kandersteg, 1425 m a.s.l., with *Cystopteris fragilis*, *Asplenium viride*, *Carex firma*, *Ranunculus alpestre*, *Arabis pumila*, *Primula auricula*, *Gentiana clusii*; on the northwestern foot of Unteres Tatlishorn in the Schwarzbach valley (a side valley of Gasterental), 1710–1730 m a.s.l. — Canton Obwal-

den, near Engelberg: Gentidossen (Gentifluh) between Ober- and Unter-Trübsee, ca. 1740 m a.s.l. — Canton St. Gallen, Gamserrugg, NE side, 1890 m a.s.l.; Alp Naus above Grabs, 1600 m a.s.l.; Flürentobel above Wildhaus, 1310 m a.s.l. — Canton Appenzell (Alpsteingebirge, between Potersalp and Nasenlöchern on a rock tower, 1600 m a.s.l.; Gartenalp, between Schäfler and Ebenalp, on a small rock wall, 1730 m a.s.l.; above Hogsberer, between Seealpsee and Alp Siegel resp. Bogartenfirst, 1410 m a.s.l.; in Stiefel, between Fählensee and Sämtiseralp, 1440 m a.s.l.; Brühltoebel near Brütli-sau, 1260–1270 m a.s.l. — Canton Ticino (Tessin), Monte Generoso, 1380 m a.s.l., 1550–1600 m a.s.l. — Other localities in Switzerland (distribution maps available at <http://www.infoflora.ch>): — Canton Bern, region of St. Stephan and Lenk in Simmental. — Canton Ticino (Tessin), Airola region. — Canton Schwyz, Muotatal region. — According to the database (<http://www.infoflora.ch>) and by courtesy of Michael Jutzi (reports from between 1983–2013): Iffigtal (S of Lenk); S of Kandersteg; S of Hinterthal near Schwyz; Tour d’Aï Massif near Montreux (canton Vaud; this is the westernmost stand of the species in the Alps).

Italy. This is the country where *W. pulchella* is most widely distributed, from the Grigna massif near Lago di Como in the West unto the border with Slovenia in the East. Most numerous stands were reported from the Dolomites, followed by other parts of Trentino-Alto Adige/Südtirol, Lombardy, Veneto, the Carnic and the Julian Alps (Alpi Carniche and Alpi Giulie). In Valle di Revolto, north of Verona, *W. pulchella* reaches its southern limit in the Alps. According to Bona (2005) and Beck and Wilhelm (2010) the species was reported from 53 squares of 10' long. × 6' lat., resp. from 82 quadrants of 5' × 3'. A list of the Italian localities known up to that time was published by Pichi-Sermolli (1956); from one locality in

the Dolomites of South Tyrol (Massif of Sciliar/Schlern: Col di Spiedl/Grünser Bühl), he quoted as companion species *Potentilla nitida*, *Leontopodium alpinum*, *Phyteuma sieberi*, *Erigeron uniflorus*, *Euphrasia minima*, *Silene quadrifida*, *Daphne* sp., *Asplenium viride* and *Cystopteris fragilis*.

Spain. The species is known from only one locality in eastern Pyrenees: Pedraforca Massif (between Sierra del Cadi and Rasos de Peguera y Sierra d'Encija), 2100 m and 2300 m a.s.l., at the latter altitude together with *Petrocallis pyrenaica* and *Saxifraga caesia* (Rivas-Martínez & Costa 1968). The presence of *W. pulchella* in Pedraforca was confirmed recently (Saez & Talavera 2010), where only seven individuals were observed between 2100 and 2300 m a.s.l. (five reproductive).

Woodsia pulchella is presently a rare relict, distributed mainly in the Alps, with extremely isolated small populations in the Pyrenees and the Carpathians. Most probably an ancestor of *W. pulchella* is *W. glabella* which occupied mountains of Europe during glacial periods and afterwards evolved in a warmer climate into a distinct taxon. Therefore, *W. pulchella* can be regarded as a glacial or postglacial relict. It is uncertain if the species is limited to Europe or if the southernmost populations regarded as representing *W. glabella* in the Caucasus or in Japan are actually *W. pulchella*.

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