

Observations on *Primula elatior* in the High Sudeten Mts.

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ABSTRACT: The Western and Eastern Sudeten are known to differ considerably in the composition of their floras and striking dissimilarities can also be seen in the behaviour of some species that are common to both the mountain ranges. *Primula elatior* (L.) HILL, represented by subsp. *elatior* and subsp. *tatrensis* (DOMIN) SOÓ growing mixed together and intergrading with each other, is widespread and variable in the Eastern Sudeten but has failed to produce an endemic taxon, even though two of the populations are spatially isolated. On the other hand, in the Western Sudeten, *P. elatior* (L.) HILL subsp. *elatior* is only locally frequent but has given rise to an endemic taxon, var. *corcontica* DOMIN. Possible causes of this unusual situation are briefly considered. Based on an analysis of morphological characters and taking into account its allopatric distribution, a taxonomic reassessment in the rank of subspecies is proposed for var. *corcontica* DOMIN. Observations are also made on geographical distribution, ecology, phenology and biology.

KEYWORDS: *Primula elatior*, Sudeten Mts., isolating mechanisms, endemism, morphology, geographical distribution.

Introduction

When comparing the flora of the Western Sudeten (Krkonoše Mts.) and Eastern Sudeten (Králický Sněžník Mts., Hrubý Jeseník Mts.), one is struck by the many conspicuous differences in the composition of their floras that are difficult to account for rationally. Several attempts have been made to compile a list of plants that differentiate between the West and East (see e.g. FIEK 1881, SCHUSTLER 1918, DOMIN 1924, ŠMARDÁ 1951, JENÍK 1961).

One may wonder for instance why *Agrostis rupestris* ALL., *Androsace obtusifolia* ALL., *Arabis alpina* L., *Baeothryon caespitosum* (L.) A. DIETR. subsp. *austriacum* (PALLA) Á. et D. LÖVE, *Carex magellanica* LAM., *Comarum palustre* L., *Cryptogramma crispa* (L.) R. BR. ex HOOKER, *Festuca versicolor* TAUSCH, *Galium hircynicum* WEIGEL, *Gentiana asclepiadea* L., *Geum montanum* L., *Gnaphalium supinum* L., *Linnaea borealis* L., *Luzula spicata* (L.) DC., *Myosotis alpestris* F. W. SCHMIDT, *Pedicularis sudetica* WILLD., *Pinus mugo* TURRA subsp. *mugo*, *Poa laxa* HAENKE, *Primula minima* L., *Pulsatilla scherfelii* (ULLEP.) SKALICKÝ, *Rubus chamaemorus* L., *Saxifraga moschata* WULFEN subsp. *basaltica* BR.-BL., *S. nivalis* L., *S. oppositifolia* L., or *Veronica bellidioides* L. occur, albeit some of them extremely rarely, in the Krkonoše Mts. but are absent from the Eastern Sudeten Mts., or, vice versa, why *Agrostis alpina* SCOP., *Aster alpinus* L., *Campanula barbata* L., *Cardamine trifolia* L., *Carex acutiformis* EHRH., *C. montana* L., *Carlina vulgaris* L. subsp. *stricta* (ROUY) DOMIN, *Cerastium fontanum* BAUMG., *Conioselinum tataricum* HOFFM., *Crepis sibirica* L., *Dianthus carthusianorum* L. s.l., *Gentiana punctata* L., *G. verna* L., *Helianthemum nummularium* (L.) MILL. subsp. *grandiflorum* (SCOP.) SCHINZ et THELL., *Helictotrichon planiculme* (SCHRAD.) PILGER, *Hieracium villosum* JACQ., *Laserpitium archangelica* WULF., *Ligusticum mutellina* (L.) CRANTZ, *Plantago atrata* HOPPE s.l., *Poa alpina* L., *Prunella grandiflora* (L.) SCHOLLER, *Pteridium aquilinum* (L.) KUHN, *Salix hastata* L., *Saxifraga paniculata* MILL., *Scrophularia scopolii* HOPPE or *Valeriana tripteris* L. are present in the Hrubý Jeseník Mts. but are missing from the Krkonoše Mts.

Both the Western and Eastern Sudeten have a similar geological past and a similar florogenesis. Both had their own glaciers, with the Nordic glacier ending not far from their northern foothills. While the Eastern Sudeten saw an influx of plants from the Carpathians during the glacial era, such an event is less likely in the Western Sudeten. *Conioselinum tataricum* HOFFM., *Crepis sibirica* L. and *Scrophularia scopolii* HOPPE apparently stopped in the Hrubý Jeseník Mts. on their way west from the Carpathians but why the basically Alpine *Campanula barbata* L. colonized S. Norway by way of the Eastern and not Western Sudeten is a mystery. Both the Western and Eastern Sudeten received a number of plants from the North as well as from the Alps and it is not always easy to decide which came from where. Both the Western and Eastern Sudeten are notable for their endemics.

There are no less startling differences in the distribution and frequency of certain plants that occur in both the mountain systems. A good example is *Primula elatior* (L.) HILL, where an interesting taxonomic diversification is accompanied by inequalities in spatial spread (whether sympatric or allopatric), phytogeographical relationships, variation and biology (see Tab. 1).

P. elatior varies widely in terms of leaf shape, length of petiole, hairiness (of leaves, scapes, pedicels and calyx), shape and length of calyx, length of calyx teeth and length and shape of corolla limb. Some characters, most notably the size of the leaves and hairiness, undergo considerable changes during ontogenic development. It is important therefore that to avoid confusion plants in the same stage of development are compared. Variation is largely continuous however and much of the variation trends combine freely with each other.

Tab. 1. Differences (other than morphological) between the Western Sudeten and Eastern Sudeten *Primula elatior*

	Western Sudeten	Eastern Sudeten
Taxa represented	<i>elatior</i> , <i>corcontica</i>	<i>elatior</i> , <i>tatrensis</i>
Their distribution	Allopatric	Sympatric
Occurrence	Locally abundant (<i>elatior</i>) Rare and local (<i>corcontica</i>)	Frequent (both <i>elatior</i> and <i>tatrensis</i>)
Transitions	Rare	Large scale
Endemic taxon	Present	Absent

Surprisingly, none of the early students of the Sudeten flora said anything particular about *P. elatior*. The first to register it, as a species, were probably WIMMER & GRABOWSKI (1827) who reported *P. elatior* as occurring near what is now the Schronisko pod Łabskim Szczytem Chalet, Polish Karkonosze Mts. WIMMER later (1844) added: "an das Hochgebirge hinaufsteigend ... Kupferberg, Hirschberg bis zu den Schlesischen Bauden hinauf".

***Primula elatior* in the Eastern Sudeten**

In the Eastern Sudeten *P. elatior* is found scattered throughout both the Hrubý Jeseník Mts. and the Králický Sněžník Mts., forming locally large populations. Taxonomically the plants belong partly to subsp. *tatrensis* (DOMIN) SOÓ which extends from the Carpathians and is typically only sparsely hairy and has doubly crenate-dentate to (in the lower part) lobulate leaf blades, and partly to subsp. *elatior*. The two almost always grow side by side and intergrade on a large scale. Subsp. *tatrensis* (DOMIN) SOÓ is prevalent in the Hrubý Jeseník Mts. but is less frequent in the Králický Sněžník Mts. (which are more remote from the Carpathians) where subsp. *elatior* and the intermediates prevail. Small, spatially isolated topodemes of "pure" subsp. *tatrensis* (DOMIN) SOÓ occur in the Velká kotlina and Malá kotlina glacial cirques where they extend up to 1320 m (see KOVANDA 1992). While elsewhere in these mountains the plants flower prolifically and produce a lot of viable seed, flowering is of extremely rare occurrence in these particular populations. Even though the glacial cirques are renowned as the scene of speciation processes for a number of plant taxa, no taxonomically deviating race of *P. elatior* has evolved and no indication of such process can be observed. *P. montana* OPIZ, described from the Králický Sněžník Mts., is merely a synonym of *P. elatior* (L.) HILL, based on a specimen collected "unter einer *Petasites*, welche sich durch äusserst hohe Blattstiele und kolossale Blätter auszeichnet" (see BERCHTOLD & OPIZ 1839).

***Primula elatior* in the Western Sudeten**

The situation in the Western Sudeten (Krkonoše Mts.) is quite different. Here *P. elatior* is locally frequent in the foothills but extends only rarely into the mountains

Tab. 2. List of topodemes sampled

No.	Locality
Krkonoše Mts.:	
1	Herlíkovice, near Vrchlabí, wet meadow near ski-lift, 820 m
2	Strážné, near Vrchlabí, spring terrain on road to Šestidomí, 880 m
3	Přední Labská, dry meadow near bell tower, 870 m
4	Špindlerův Mlýn, meadow near Hromovka house, 870 m
5	Svoboda nad Úpou, along a stream SW of town, 620 m
6	Hofmannovy boudy, near Janské Lázně, small alder grove, 750 m
7	Rýchory Mts., meadow NW of Kraví hora, 660 m
8	Pec pod Sněžkou, steep slope opposite bus terminal, 860 m
9	Velká Úpa, slope opposite post office, 830 m
10	Janovy boudy, near Velká Úpa, spring terrain, 890 m
11	Spálený Mlýn, near Dolní Malá Úpa, along a stream, 890 m
12	Dolní Malá Úpa, meadow just off the cemetery, 960 m
13	Černá Voda, near Pomezní Boudy, spring terrain, 980 m
14	Rokytnice nad Jizerou, along a stream at Hoření Domky, 890 m
15	Chmelná hůra, near Jilemnice, along road to Roubenka house, 580 m
16	Velká kotelná jáma glacial cirque, scree cone, 1200 m
Hrubý Jeseník Mts.:	
17	Mt. Petrovy kameny, slope above the Ovčárna Chalet, 1350 m
18	Velká kotlina glacial cirque, spring terrain in a <i>Betula carpatica</i> growth in the upper part, 1260 m
19	Velká kotlina glacial cirque, bottom, 1190 m
20	Along the Moravice stream below Velká kotlina glacial cirque, 1150 m
21	Along the Moravice stream below Velká kotlina glacial cirque, 940 m
22	Peat bogs at Karlov, 674 m
23	Wet meadow at Nová Rudná, 720 m
24	Proposed nature reserve at Raná, 760 m
25	Malá Morávka, along a stream in the upper part, 680 m
Králický Sněžník Mts.:	
26	Spring terrain along state boundary between Vlačovčí skály rocks and Mt. Malý Sněžník, 1350 m
27	Along the Morava stream below the Tvarožné díry caves, 840 m

proper. Its populations are taxonomically homogeneous, consisting entirely of subsp. *elator*. Subsp. *tatrensis* (DOMIN) SOÓ and intermediates are missing. Elsewhere in these mountains, *P. elator* is extremely rare and local, occurring only in a few sites between around 1220 and 1400 m. This is an endemic taxon, appropriately named var. *corcontica* DOMIN¹. Unlike subsp. *tatrensis* (DOMIN) SOÓ in the Eastern Sudeten, it is clear cut in terms of morphology and is fully allopatric in relation to subsp. *elator* (Tab.1).

¹ "To Askiburgion Oros Korkontoi", name of the Sudeten on Ptolemy's map of Europe (2nd century A.D.).

Characteristic features of var. *corcontica* DOMIN include:

- (1) The narrowly winged, entire petiole. - This proved to be a constant character of all plants examined. It is extremely rare in populations of subsp. *elatior* from other parts of the distribution range and is never in such cases correlated with other characters of var. *corcontica* DOMIN. It is not known to occur in subsp. *tatrensis* (DOMIN) SOÓ.²
- (2) The minutely dentate leaf blade. - Again, this is a character of the highest constancy in var. *corcontica* DOMIN. No transitions to leaf blade grossly dentate to lobulate as in subsp. *tatrensis* (DOMIN) SOÓ could be seen.
- (3) The cordate base of the leaf blade. - Generally, in *P. elatior*, the shape of the blade is subject to unusual variation even within a given population. In var. *corcontica* DOMIN, the cuneate base, which is of frequent occurrence elsewhere, seems to be entirely missing (see Tab. 2, 3, 4).

Of the other characters mentioned by DOMIN (1930), the following can be used as supplementary: petiole (during florescence) often longer than blade, calyx tubulose-campanulate, divided to 1/3, corolla limb slightly concave, 6.8-7.8(-8.2) mm long. The indumentum of the leaves, scapes and calyces varies considerably from one plant to another and becomes generally sparser as the ontogenic development continues.

The morphological characterization and allopatry in distribution justify treating var. *corcontica* DOMIN as a subspecies:

***Primula elatior* (L.) HILL subsp. *corcontica* (DOMIN) KOVANDA, comb. nova**

Bas.: *Primula elatior* HILL var. *corcontica* DOMIN Věda Přírodní 11 : 239, 1930.

The rank of species could perhaps be considered but in view of the immense variation range of the species, such assessment appears inappropriate.

It is interesting to note that DOMIN, who is known to have described new species freely, was extremely restrained in the case of *P. elatior*. He obviously did not attach much importance to his intraspecific taxa, some of which have since been elevated to the rank of subspecies [subsp. *tatrensis* (DOMIN) SOÓ, subsp. *poloninensis* (DOMIN) DOSTÁL] or even species [*P. poloninensis* (DOMIN) FEDOROV], having failed to mention them at all in his *Plantarum Čechoslovakiae Enumeratio* (DOMIN 1935).

DOMIN described var. *corcontica* on plentiful material gathered by his assistants V. KRAJINA (1905-1993) and P. SILLINGER (1905-1938) at 900 m in the Elbe valley on 18 May 1929 (see DOMIN & KRAJINA, *Flora Čechoslovenica exsiccata* no. 284; subsp. *elatior* admixed), where KRAJINA had collected it previously at 800 m on 10 May 1929. DOMIN also refers to a herbarium collection made by KRAJINA on the famous outcrop of

² In herbarium material, especially of young plants, the characters of the petiole are often poorly preserved due to the revolute vernation. A typically dentate petiole may then appear as entire.

basalt in the Mały Kocioł Śnieżny, Polish Karkonosze Mts., on 8 July 1928. Surprisingly, neither record has been confirmed by subsequent research. J. ŠOUREK, an acknowledged authority on the Krkonoše flora, does not mention these stations at all in his Flora (ŠOUREK 1969), even though GÖPPERT (1864), FIEK (1881), SCHUSTLER (1918) and LIMPRICHT (1930) listed "*P. elatior*" as occurring in the latter locality. Another record cited by DOMIN, from near Svoboda nad Úpou ("Vrajt"), is doubtful. It is based on a poor herbarium collection made by an enigmatic collector in April 1902 who signed his name illegibly. (DOMIN quotes himself as the collector.) The material available represents typical subsp. *elatior*. The locality lies too low (510 m) for subsp. *corcontica* to occur. All herbarium material documenting these data is deposited in the Herbarium of the Department of Botany, Charles University, Prague (PRC). A fourth locality listed by DOMIN (1930), Mt. Studničná hora, does not appear to have ever been verified, either in herbaria or in literature. The following relatively recent reports of *P. elatior* are probably referable to subsp. *corcontica*: Luční bouda, 1400 m (PROCHÁZKA & ŠTURSA 1972), Liščí hora, 1360 m and Výrovka, 1355 m (one and three plants, respectively; ŠTEFFAN 1986). It is unclear whether the early reports of *P. elatior* from near Schronisko na Hali Szrenickiej and Schronisko pod Łabskim Szczytem (WIMMER & GRABOWSKI 1827, WIMMER 1844) are referable to var. *corcontica* or not. PAWŁOWSKA (1963) reports var. *corcontica* summarily from the Polish part of the mountains without any precise locality.

Herbarium specimens of subsp. *corcontica* seen

Czech Republic

"montes Krkonoše (Riesengebirge), in pratis montanis in valle rivi Labe supra Vrchlábí, altitudine circa 900 m s.m.", Krajina et Sillinger 1929 PRC (lectotype)

"Labské údolí", Krajina 1929 PRC

"Velká Kotelná jáma" (Kotel, Velký Kotel, Kesselgrund, Grosser Kessel), Cypers 1893 PR, Čelakovský fil. 1907 PR, anon. 1916 PR, Sillinger 1927 PRC, Šourek 1951 PR, Kovanda 1994 PR

Poland

"begraste Felsen über dem Kalkofen in Ober-Schmiedeberg", Schneider 1886 PR

"in valle praerupto Malá Sněžná jáma (Kleine Schneegrube), solo basaltico", Krajina 1928 PRC

At present, subsp. *corcontica* is demonstrably known to occur only in two sites on the E. to S. E. side of Mt. Kotel (Kokrháč), the Malá Kotelná jáma (1350 m) and Velká Kotelná jáma (1220 - 1250 m) glacial cirques in the Czech part of the Krkonoše Mts., not far from the locus classicus (cf. JENÍK 1961, ŠOUREK 1969).

In the Velká kotelná jáma glacial cirque, a topodeme of about 60 individuals occurs in a plant community of the alliance *Calamagrostion arundinaceae* on a stabilized vegetated scree cone (granite, c. 40° slope, S. E. facing) associated with *Achillea millefolium* L. subsp. *sudetica* (OPIZ) WEISS, *Alchemilla glabra* NEYGENF., *Aconitum*

callibotryon REICHENB., *Allium schoenoprasum* L. subsp. *sibiricum* (L.) ČELAK., *Anemone narcissiflora* L., *Arabis sudetica* TAUSCH, *Bartsia alpina* L., *Blechnum spicant* (L.) ROTH, *Bupleurum longifolium* L., *Botrychium lunaria* (L.) SW., *Calamagrostis arundinacea* (L.) ROTH, *Calluna vulgaris* (L.) HULL, *Daphne mezereum* L., *Delphinium elatum* L., *Digitalis grandiflora* MILL., *Galium boreale* L., *G. sudeticum* TAUSCH, *Gentiana asclepiadea* L., *Hypericum maculatum* CRANTZ, *Leontodon hispidus* L. s.l., *Lilium martagon* L., *Myosotis nemorosa* BESSER, *Phyteuma spicatum* L., *Poa chaixii* VILL., *Potentilla aurea* L., *P. erecta* (L.) RÄUSCHEL, *Pulmonaria obscura* DUMORT., *Pulsatilla Scherfelii* (ULLEP.) SKALICKÝ, *Thalictrum aquilegiifolium* L., *Thesium alpinum* L., *Thymus alpestris* TAUSCH ex A. J. KERNER, *Trollius altissimus* CRANTZ, *Vaccinium myrtillus* L., *Viola biflora* L., etc. The cone is watered profusely during the thaw but remains dry for most of the growing period, except after heavy showers. JENÍK (1961) lists "*Primula elatior*" in a relevé of the association *Bupleuro-Calamagrostidetum arundinaceae* (ZLATNÍK 1928) JENÍK 1961 at 1220 m in the same locality.

Subsp. *corcontica* starts to flower very early, when the bottom of the cirque nearby is still occupied by a mass of granulated snow. Together with *Daphne mezereum* L., it is the first plant to flower on the scree cone. The onset of flowering varies greatly depending on the weather, from late May to early June. Usually no flowers open prior to 20 May. A peculiar feature of subsp. *corcontica* is the sparsity of flowering. In the period of study (1980-1996), only 2 to 6 plants (not necessarily the same ones) flowered in any given year. The remaining were surviving as rosettes generating a few new leaves each growing season but no scapes or flowers. Those flowering produced very little or no seed.

The failure of the vast majority of plants of subsp. *corcontica* to flower regularly is apparently caused by adverse environmental conditions. A rosette (only one, in view of the extreme rareness of occurrence) transferred to the experimental plot at Průhonice in 1990 has been producing a scape with an umbel of flowers every year since.

The poor fertility of the plants which manage to flower in the natural habitat can be attributed to the scarcity of pollen vectors in early spring rather than to any intrinsic factors.

It is remarkable that so ill-adapted a race could have evolved, become established and survived to the present day. Perhaps it was more vigorous in the warm Boreal and Atlantic eras and was reduced to its present state by the onset of the cool Subatlantic.

Discussion

It is tempting to speculate why an endemic *Primula* evolved in the Western Sudeten but not in the Eastern Sudeten. The differentiation process has obviously operated with material from different sources and has, of necessity, yielded different effects.

In the Eastern Sudeten, an ancestral *elatior* was superimposed upon and locally absorbed by the alien, vigorous, eastern *tatrensis* (or its evolutionary predecessor) with little propensity to spatial isolation. This is the case in the Velká kotlina and Malá kotlina glacial cirques but, for reasons unknown, it has failed to bring about any perceivable

Tab. 3. Representation (in per cent) of nine characters in the topodemes.

Characters studied									
Shape of petiole	Margin of leaf blade			Shape of leaf blade					
A ₁ not distinct from the blade, the latter decurrent	B ₁ doubly dentate to lobulate in the lower part			C ₁ cordate					
A ₂ distinct from the blade, winged, dentate	B ₂ dentate to grossly dentate			C ₂ abruptly contracted					
A ₃ distinct from the blade, wingless, entire	B ₃ finely dentate			C ₃ cuneate					
Topodeme no.	Character								
	A ₁	A ₂	A ₃	B ₁	B ₂	B ₃	C ₁	C ₂	C ₃
1	0	88	12	0	90	10	76	24	0
2	0	96	4	0	100	0	70	20	10
3	0	96	4	0	100	0	86	14	0
4	0	92	8	0	96	4	92	4	4
5	0	90	10	0	92	8	76	14	10
6	0	94	6	0	100	0	68	8	24
7	0	92	8	0	100	0	48	40	12
8	0	90	10	0	100	0	84	16	0
9	0	98	2	0	100	0	44	24	32
10	0	96	4	0	100	0	36	56	8
11	0	96	4	0	100	0	48	36	16
12	0	96	4	0	100	0	52	16	32
13	0	100	0	0	96	4	72	24	4
14	0	92	8	0	100	0	60	24	16
15	0	90	10	0	100	0	0	24	76
16	0	4	96	0	0	100	92	8	0
17	96	4	0	72	28	0	0	68	32
18	98	2	0	96	4	0	0	72	28
19	100	0	0	80	20	0	0	64	36
20	100	0	0	80	20	0	4	72	28
21	100	0	0	72	28	0	0	48	52
22	100	0	0	94	6	0	0	8	92
23	100	0	0	80	20	0	0	32	68
24	96	4	0	96	4	0	0	28	72
25	100	0	0	98	2	0	0	22	78
26	52	34	14	62	36	2	50	30	20
27	94	0	6	82	18	0	20	12	68

Fifty individuals per site were examined. Topodemes no. 1-15 correspond to subsp. *elatior*. The most characteristic features of subsp. *corcontica*, viz. the wingless petiole (A₃) and finely dentate margin of the leaf blade (B₃) appeared, at a low frequency, in topodemes of subsp. *elatior*, the first in 14, the latter only in 4 out of 15. No individual combining these two characters showed up in the entire set of 750 plants examined. The shape of the blade varies greatly in subsp. *elatior* but leaf blade cuneate at base (C₃) is rather rare. The decurrent leaf blade is missing. Topodeme no. 16 is a typical subsp. *corcontica*. Topodemes no 17-25 comprise typical subsp. *tatrensis* and transitions to subsp. *elatior*. The last two topodemes (no. 26-27) proved highly aberrant in differing markedly from each other and amalgamating characters of all three subspecies. They require further study. Some plants come very close to subsp. *corcontica*.

Tab. 4. The distinguishing characters of the three subspecies

	subsp. <i>elatior</i>	subsp. <i>corcontica</i>	subsp. <i>tatrensis</i>
Petiole	Winged, dentate	Wingless, entire	Broadly winged, blade decurrent, dentate
Blade	Flat or moderately undulate at base	Flat	Distinctly undulate at base
Margin of leaf blade	Dentate to grossly dentate	Finely dentate	Doubly dentate to lobulate in the lower part
Base of leaf blade	Cordate, abruptly contracted or rarely cuneate	Cordate	Cuneate or abruptly contracted

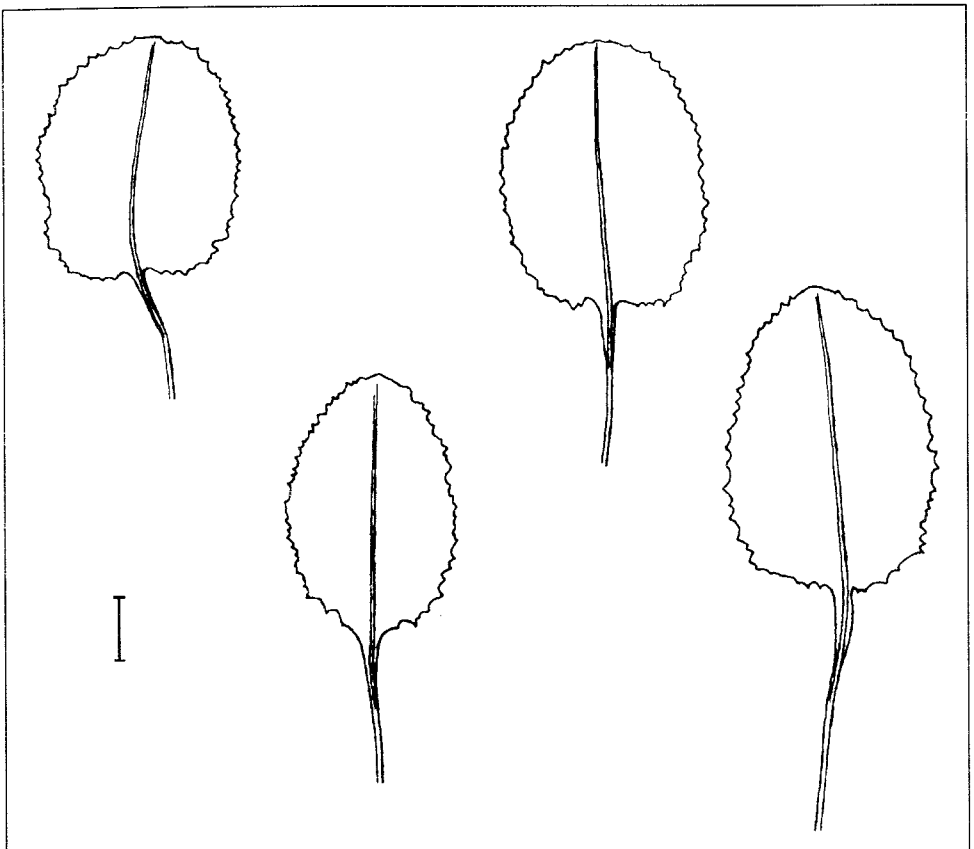


Fig. 1. Showing variation in the leaf shape in *P. elatior* subsp. *corcontica*. (Venation not shown). (Orig. J. Soják, scale bar: 1 cm)

results there. In the Western Sudeten there was a homogeneous population of *elatior* in the foothills free from any introgression which in some way or other managed to colonize new isolated habitats above the tree line. Here speciation processes may have been operating for thousands of years though hampered seriously by the limited possibilities of gene exchange. Yet they succeeded in producing a well defined local endemic. What is even more interesting, the differentiation took place solely at the diploid level, $2n = 22$.

It is important to note that subsp. *corcontica* is not an evolutionary parallel to subsp. *tatrensis*; indeed its morphological characteristics are in many respects contrary to it.

As suggested by STEBBINS (1950), in the evolution of geographically isolated subspecies or species, initial separation and divergence have been caused by the response of the ancestral population to different selection pressures; this results from ecological differentiation in various parts of its originally more uniform environment. Most geographical races may therefore have arisen primarily as ecotypes and their separate distribution may be an accidental secondary result of ecotypic differentiation. Subsp. *corcontica* seems to be one such example.

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References

- BERCHTOLD F. & OPIZ F. M. (1839): Oekonomisch-technische Flora Böhmens nach einem ausgedehnten Plane bearbeitet 2/2. – Prag.
- DOMIN K. (1924): Úvahy a studie o regionálním členění Čech z hlediska geobotanického. – Spisy Přírod. Fak. Karl. Univ. 1924/9: 1-38.
- DOMIN K. (1930): O variabilitě prvosenky bleďožluté (*Primula elatior* Hill.) v Československu. – Věda Přír. 11: 236-242.
- DOMIN K. (1935): Plantarum Českoslovakiae enumeratio species vasculares indigenas et introductas exhibiens. – Preslia 13-15: 1-305.
- FIEK E. (1881): Flora von Schlesien preussischen und österreichischen Antheils. – Breslau.
- GÖPPERT H. R. (1864): Eine botanische Exkursion ins Riesengebirge vom 26. bis 29. Juni 1863. – Österr. Bot. Zeitschr. 14: 305-312.
- JENÍK J. (1961): Alpínská vegetace Krkonoš, Králického Sněžníku a Hrubého Jeseníku. – Praha.
- KOVANDA M. (1992): 1. *Primula L.* - prvosenka. – In: HEJNÝ S. & SLAVÍK B. (eds.): Květena České republiky 3, p. 246-252.
- LIMPRICHT W. (1930): Die Pflanzenwelt der Schneeegruben im Riesengebirge (Phanerogamen und Archegoniaten). – Bot. Jber. 63, Beibl. 142: 1-74.
- PAWLOWSKA S. (1963): Rodzina: Primulaceae, Pierwosnkowate. – In: PAWŁOWSKI B. (ed.): Flora Polska 10, p. 39-76.
- PROCHAZKA F. & ŠTURSA J. (1972): Příspěvek ke květeně Krkonoš. – Opera Corcont. 9: 134-164.
- SCHUSTLER F. (1918): Krkonoše. Rostlinozeměpisná (fytogeografická) studie. – Arch. Přírod. Výzk. Čech 16/4: 1-181.
- STEBBINS G. L. (1950): Variation and evolution in plants. – New York.

- ŠMARD A J. (1951): Srovnání květeny Hrubého Jeseníku se sousedními horskými masivy. – Přírod. Sborn. Ostrav. Kraje 11: 176-182.
- ŠOUREK J. (1969): Květena Krkonoš. – Praha.
- ŠTEFFAN O. (1982): Příspěvek ke květeně Krkonoš (7). – Opera Corcont. 25: 119-139.
- WIMMER F. (1844): Flora von Schlesien preussischen und österreichischen Antheils 1. Ed. 2. – Breslau.
- WIMMER F. & GRABOWSKI H. (1827): Flora Silesiae 1. – Vratislaviae.

Appendix

List of German topographical names (in common use before 1945)

Czech Republic

Černá Voda	Schwarzwasser
Černý potok	Schwarzbach
Dolní Malá Úpa	Nieder-Kleinaupa
Herlíkovice	Hackelsdorf
Hofmannovy boudy	Hofmannsbauden
Hoření Domky	Obere Häuser
Hrubý Jeseník	Hochgesenke
Janské Lázně	Johannisbad
Karlovy	Karlsdorf
Kotel, Kokrháč	Kesselkoppe
Králický Sněžník	Glatzer Schneeberg, Grulicher Schneeberg, Spieglitzer Schneeberg
Kraví hora	Kuh-Berg
Krkonoše	Riesengebirge
Labe	Elbe
Labský důl	Elbegrund
Liščí hora	Fuchs-Berg
Luční bouda	Wiesenbaude
Malá Kotelná jáma	Kleine Kesselgrube
Malá Kotlina	Kleiner Kessel
Malá Morávka	Kleinmohrau
Malý Sněžník	Klein-Schneeberg
Morava (river)	March
Moravice	Mohra
Nová Rudná	Neu-Vogelseifen
Ovčárna	Schäferei
Pec pod Sněžkou	Petzer
Pomezní Boudy	Grenzbauden
Přední Labská	Ochsengraben
Raná	Morgenland
Rokytnice nad Jizerou	Rochlitz a. d. Iser
Rýchory	Rehorn

Spálený mlýn
Strážné
Studniční hora
Svoboda nad Úpou
Šestidomí
Špindlerův Mlýn
Tvarožné díry
Velká Kotelná jáma
Velký kotel
Velká kotlina
Velká Úpa
Vlaštovčí skály
Vrchlabí
Výrovka

Poland

Jelenia Góra
Karkonosze
Kowary Górne
Mały Kocioł Śnieżny
Miedzianka
Schronisko na Hali Szrenickiej
Schronisko pod Łabskim Szczytem
Śnieżnik Kłodzki

Mohornmühle
Pommerndorf
Brunnberg
Freiheit
Sechsstätten
Spindelmühle
Quarklöcher
Grosse Kesselgrube
Grosser Kessel (in the Krkonoše Mts.)
Grosser Kessel (in the Hrubý Jeseník Mts.)
Grossaupa
Schwalbenfelsen
Hohenelbe
Geiergucke

Hirschberg
Riesengebirge
Ober-Schmiedeberg
Kleine Schneegrube
Kupferberg
Neue Schlesische Baude
Alte Schlesische Baude
Glatzer Schneeberg

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