

Hieracium × *grofiae* – a rediscovered diploid hybrid from the Ukrainian Carpathians

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Abstract: Diploid hybrid plants ($2n = 18$) between sexual diploid cytotypes of *Hieracium alpinum* and *H. umbellatum* were found in the Ukrainian Eastern Carpathians. They were identified with *H. ×grofiae* WOL., originally used for the combination *H. decipiens* × *H. umbellatum* var. *lactaris*. As *H. decipiens* sensu WOL. (non TAUSCH) does not produce viable pollen grains and is most probably a polyploid apomict, it is unlikely to produce diploid hybrid plants with diploid *H. umbellatum*. Both parent species, *Hieracium alpinum* and *H. umbellatum* are also given by WOŁOSZCZAK from the original locality. Thus we conclude that *H. ×grofiae* is result of hybridization between *H. alpinum* and high mountain form of *H. umbellatum*. Hybrid plants are morphologically intermediate between the parent species, and moreover resemble closely or they are identical with the experimental hybrids of the same parent combination. Hybrids produce rather high amount of homogeneously sized pollen grains (values of standard deviation and coefficient of variation lower than upper limits for diploids – $3\mu\text{m}$ or 7.5%, respectively), and might probably serve as male parents in further crosses; on the other hand, they are fully seed-sterile. A lectotype of *H. ×grofiae*, a second proved nothotaxon in the genus *Hieracium* s.str., is designated. Localities of *H. ×grofiae* are located in subalpine belt of the Marmarosh Mts, the Svydovets' Mts and the Horhany Mts (all in the Ukrainian Eastern Carpathians). Biotopes of hybrid plants usually represent secondary formed and disturbed pastures allowing close contact of altitudinally vicariant parent taxa.

Key words: Asteraceae, chromosome numbers, homoploid hybridization, lectotype

Introduction

Hieracium L. s. str. (*Hieracium* subgen. *Hieracium*, 'Archieracium' as defined by ZAHN, 1921–1923) is one of the world's most species-rich plant groups (Royal Botanical Gardens Kew, 1993). It includes perennial herbs distributed predominantly in temperate regions of Europe, Asia, and North America. Polyploidy and diplosporous agamospermy seem to prevail in the genus (e.g., GUSTAFSSON, 1946–1947; SCHUHWERK, 1996). Sexuality is confined to a few diploid species, distributed mostly in South Europe (MERXMÜLLER, 1975; CHRTEK et al., 2004).

Two different species concepts appeared in the genus: i) broad species concept, utilized e.g. by NÄGELI & PETER (1885, 1886) and ZAHN (1921–1923, 1930–1939), and ii) narrow species concept (applied first of all by British, Scandinavian and East European authors, e.g. PUGSLEY, 1948; ÜKSIP, 1960). In the former, the

broadly defined species are (usually) divided into subspecies, and (if necessary) to varieties and lower taxonomic units. In the latter, binomial 'microspecies' ('agamospecies') are recognized, species groups (aggregate species, usually analogous to species in a broad sense) then accommodate one to many 'microspecies'.

Two kinds of species in the broad sense are distinguished. While the main species ('species principales collectivae') possess usually an unique set of morphological characters (although their definition is sometimes rather arbitrary), the intermediate ones ('species principales intermediae') share a morphologically intermediate position between two or more main species. The latter are usually thought to be a result of extensive past hybridization and polyploidization, nowadays there are mostly fixed by agamospermous mode of reproduction. However, their origin is still a contentious issue. Taxonomically, they are usually treated as hybridogeneous species (e.g. ZAHN 1921–1923).

In contrast, recent hybridization seems to be a very rare phenomenon. It is most likely confined to crosses between diploid sexual species (MRÁZ et al., 2005; MRÁZ & PAULE, 2006) or diploid sexuals (as mother parents) and pollen producing polyploids (pollen donors) (MRÁZ & PAULE, 2003; PAULE, 2004; MRÁZ & TOMČÍKOVÁ, 2004). So far, spontaneous hybridization in the wild has only been documented between diploid *Hieracium alpinum* L. and *H. transsilvanicum* HEUFF. in the Ukrainian an Rumanien Eastern Carpathians (MRÁZ et al., 2005). MERXMÜLLER (1975: 193) mentioned that allegedly spontaneous hybrids, morphologically intermediate between the two diploids *H. porrifolium* L. and *H. umbellatum* L., were found in his *Hieracium* garden collection at Munich Botanical Garden.

During field excursions to the Marmarosh Mts in 1996 (J.C. and P.M.) and 2005 (J. ZAHRADNÍČEK) and to the Svydovets' Mts in 1999 (P.M.) we found plants that superficially resembled the *Hieracium fritzei* group (*H. alpinum* > *H. prenanthoides*). This aggregate species (species group) is rather common in the highest mountains of the Sudeten range (N Czech Republic, SW Poland) and the Western Carpathians, a small area is situated in Rumanian Carpathians (ZAHN, 1921–1923, 1930–1939; CHRTEK & MARHOLD, 1998). It has also been reported from the Ukrainian Eastern Carpathians (ZAHN, l.c.; ŮKSIP, 1960; CHOPYK, 1977, MALYNOVSK'YJ, 1980; PROKUDIN, 1987; SHLYAKOV, 1989; MOSYAKHIN & FEDORONCHUK, 1999). However, further detailed morphological studies showed affinities with *H. umbellatum*, which reaches its upper altitudinal limit on the secondary mountain grasslands ("poloniny").

Both sexual diploids ($2n = 18$) and apomictic triploids ($2n = 27$) are known in *H. umbellatum* (for references see e.g. SCHUHWERK, 1996; MÁJOVSKÝ et al., 1987 and other chromosome number indexes); plants from the Ukrainian Carpathians were proved to be diploid (see diploids counts given by CHRTEK, 1996 as *H. conicum* ARV.-TOUV. and MRÁZ, 2003 as *H. hryniawiense* WOŁ.; and other yet unpublished counts by J.C. and P.M.). Distinct influence of diploid sexual *Hieracium alpinum* rather widespread in the area (CHRTEK, 1997; MRÁZ, 2001) lead us to conclusion, that our plants may represent hybrids between *H. alpinum* and high mountain morphotype of *H. umbellatum*. Several identical plants from the same region were found in herbaria PR, SAV and GLM.

A correlation between pollen size heterogeneity and ploidy level has been documented in *Hieracium* s. str. (homogeneously-sized pollen in diploids, heterogeneously-sized pollen in polyploids, MRÁZ et al., 2002; KOVALČIKOVÁ, 2004). We use here the heterogeneity of pollen size as an indirect method to estimate the ploidy level in herbarium specimens.

The aim of the present paper is: (1) to find evidence about the recent hybrid origin of our plants, (2) to find a

name, which can be applied for them, and (3) to provide a list of localities in the Ukrainian Carpathians.

Material and methods

Plants

Putative hybrid plants were collected by J. C. and R. LETZ (1996), P. M. and V. JURKOVIČOVÁ (1999) and J. ZAHRADNÍČEK (2005) in the Ukrainian Carpathians. Living plants from 2005 (Mt. Berlebasha) were transferred in the experimental garden of the Institute of Botany, Průhonice and used for chromosome counting. Herbarium specimens from following institutions were examined (acronyms according to HOLMGREN et al., 1990): BP, GLM, KRA, KRAM, PR, PRA, PRC, SAV, W.

Pollen was examined in herbarium plants from the original material of *H. × grofae* (KRAM) and in plants collected by P.M. at Mt. Unharias'ka (the Svydovets' Mts) and Mt. Berlebasha (the Marmarosh Mts) (Fig. 1A–C). Furthermore, it was examined in herbarium plants of *Hieracium alpinum* and *H. umbellatum* from the Ukrainian Carpathians, as well as in experimental diploid hybrids between high mountain form of diploid *H. umbellatum* (mother plant) and diploid *H. alpinum* (pollen donor) (for details cf. MRÁZ & PAULE, 2006; cross no. X9 ut *H. umbellatum* × *H. alpinum*, Fig. 1D). The localities of the plants examined are summarized in Appendix 1.

Chromosome number, pollen grains

Chromosome counts were estimated in two cultivated plants originating from Mt. Berlebasha. Root tips of mature plants were used for karyological studies. The material was pretreated with a saturated solution of p-dichlorobenzene, fixed in a mixture of ethanol and acetic acid (3:1 v/v) and stored in 70% ethanol. The squash method and staining by lacto-propionic orceine were used (DYER, 1963).

The pollen (its shape and size) was observed using light microscope. After acetolysis following ERDTMAN (1960) the pollen grains were observed using light microscope. Usually three to five flowers per plant in the stage before anthesis were used and at least 30 pollen grains per plant were measured (all values include echinae).

Results

Extensive search in public herbarium collections lead us to conclusion that our plants are identical with those described by E. WOŁOSZCZAK as *Hieracium × grofae* WOŁ.

Hieracium × grofae WOŁ. Spraw. Komis. Fizjogr. 27: 142, 1892

Ind. loc. (WOŁOSZCZAK 1892: 143): "Galicia in regione Mughii montis Grofae Lomnicensis, Carpathorum orientatum 1600 m s. m."

Lectotypus (hoc loco designatus): W dziedzinie koso-drzewa na Grofie, Karp. Wsch. okol. rz. Lomnicy [in dwarf-pine stands at Mt. Grofa, the Eastern Carpathians, near the river of Lomnica], ca 1550 m, 20. lip. [July] 1889, leg. WOŁOSZCZAK, KRAM no. 148408. (Fig. 1A).



Fig. 1. Herbarium specimens of diploid hybrid *Hieracium* × *grofiae*. **A.** Original voucher selected as a lectotype (KRAM 148408). **B.** Plants collected W of Mt. Unharias'ka. **C.** Plants collected on Mt. Berlebasha. **D.** Plants from experimental hybridization. Scale bar = 10 cm (on Fig. 1A).

Table 1. Main distinguishing characters of *Hieracium alpinum*, *H. × grofae* and *H. umbellatum*. Delimitation of *H. alpinum* follows that in CHRTEK (1997). Thus, plants completely lacking simple eglandular hairs, occurring in some parts of the Ukrainian Carpathians, are treated separately [*H. augusti-bayeri* (ZLATNÍK) CHRTEK f.]. The data for *H. umbellatum* refer to plants from the Ukrainian Carpathians only, do not cover the whole variation range of the species.

Character	<i>H. alpinum</i>	<i>H. × grofae</i>	<i>H. umbellatum</i>
Height of plants (cm)	6–24	15–30	10–80
Basal leaves	distinct rosette of basal leaves	usually withering in the flowering time	plants without basal leaves
No. of stem leaves	0–1(–2)	4–8, the lower sometimes withering in the flowering time	10–40
Shape of stem leaves	(if present) linear to linear-lanceolate	oblong-elliptical to lanceolate	lanceolate, elliptical-lanceolate, oblong-elliptical, elliptical
Indumentum of leaves	numerous (less often scattered) simple eglandular hairs, on the margins of leaves scattered minute yellowish glands	scattered, on the margins numerous simple eglandular hairs (on the upper site sometimes nearly glabrous around the midrib), on the margins of leaves scattered minute yellowish glands	leaves glabrous, sometimes with short simple eglandular hairs on the margins, without minute yellowish glands
No. of heads	1	1–4	10–40 (high mountain type 3–5 only)
Simple eglandular hairs at the apex of ligules	numerous	very few	none
Colour of styles and stigmas	purely yellow	olivaceous with black scales	yellow to olivaceous with black scales

Description

Phyllopodous or hypophyllopodous. Stem 15–30 cm high, simple (unbranched), usually slightly flexuous, usually purplish below, with scattered to numerous pale towards the top of stem pale but dark-based 1.5–2.5(–3.0) mm long simple eglandular hairs, scattered 0.2–0.4 mm long dark glandular hairs in the upper part and with numerous stellate hairs in the middle and upper parts. Leaves medium green, slightly glaucous below, with scattered, on the margins numerous, (0.8–)1.0–2.0(–2.6) mm long pale simple eglandular hairs (sometimes nearly glabrous around the midrib above), scattered 0.10–0.13 mm long yellowish glandular hairs mainly on the margins, and stellate hairs. Basal leaves 1–3, usually withering at the time of flowering, petiolate, oblanceolate to oblong-elliptical, 5–7 × 1.2–1.6 cm, rounded at apex, attenuate to a petiole or cuneate-based, entire with remote mucronate glands. Cauline leaves 4–8, gradually decreasing in size towards the top of stem, the lower cauline leaves (sometimes withering at the flowering time) ± petiolate, oblong-elliptical to lanceolate, rounded to obtuse-acute at apex, cuneate-based; the middle cauline leaves lanceolate to oblong-elliptical, 3.2–7.5 × 1.0–1.5 cm, obtuse-acute to acute at apex, abruptly narrowed to a sessile base, entire (with remote mucronate glands) to remotely denticulate with teeth to 1 mm long; upper cauline leaves lanceolate, linear-lanceolate to linear, acute at apex, narrowed (often abruptly) to a sessile base, entire or occasionally remotely denticulate. Heads solitary or 2–4 (accladium 1.6–1.8 cm long); peduncles blackish-green, with scattered to nu-

merous, 1–2 mm long, shortly (1/5–1/4 of their length) dark-based simple eglandular hairs, scattered to numerous 0.2–0.5 mm long dark glandular hairs and numerous to dense stellate hairs. Involucres barrel-shaped, (10–)12–14 mm long; phyllaries linear-lanceolate, obtuse at apex, brownish to blackish-green, the inner with paler margins, the outer with numerous to 2.5 mm long pale but dark-based (1/4–1/3 of their length) simple eglandular hairs and numerous glandular hairs, the inner with scattered eglandular and glandular hairs. Ligules flat, yellow, with few, very short hairs at the apex, the outer ligules 14–16 mm long. Styles olivaceous with black scales. Achenes 3.1–3.4 mm long, brown, empty. Flowering from July to August.

According to our study (chromosome number, morphological studies – see Tab. 1) the hybrid formula should be *H. alpinum* × *H. umbellatum*, instead of *H. decipiens* × *H. umbellatum*.

Hieracium × grofae can be easily distinguished from its parents. It is in general appearance more similar to *H. alpinum*, but clearly differs first of all in the leafy stems, usually 2–3(–4) heads and dark (olivaceous with black scales) styles (Tab. 1, Fig. 1A–D).

Chromosome number

2n = 18 (Ukrainian Eastern Carpathians, Marmarosh Mts, Mt. Berlebashka, coll. J. ZAHRADNÍČEK, 4 August 2005, counted by J.C., 2005, 2 plants).

Pollen size in *H. × grofae*, *H. alpinum* and *H. umbellatum*

All measured samples including putative parental taxa

Table 2. Size of acetolyzed pollen grains (including echinae) of parental *Hieracium* taxa and their natural and experimental hybrids. For parental taxa, the pollen measurements were taken from two or more individual plants per taxon; for hybrids, each line represents just one plant. Origin, number of studied plants and codes are given in Appendix 1. N – number of pollen grains.

Taxon (and code or other characteristic)	N	Equatorial size $x \pm SD$ (μm)	cv (%)	Polar size $x \pm SD$ (μm)	cv (%)
<i>alpinum</i>	312	44.3 ± 2.2	4.9	42.2 ± 2.3	5.5
<i>umbellatum</i> (lower altitude morphotype)	117	37.4 ± 2.0	5.2	35.4 ± 2.2	6.2
<i>umbellatum</i> (high mountain morphotype)	119	39.6 ± 2.7	6.8	37.6 ± 2.7	6.7
× <i>grofae</i> (lectotype specimen KRAM 148408)	30	37.3 ± 1.8	4.8	34.5 ± 2.2	6.4
× <i>grofae</i> (Ber1)	43	36.8 ± 2.3	6.3	34.7 ± 2.3	6.6
× <i>grofae</i> (Ungar1)	30	36.1 ± 2.1	5.8	33.4 ± 2.3	6.9
× <i>grofae</i> (Ungar2)	49	36.6 ± 1.6	4.4	34.3 ± 1.6	4.7
× <i>grofae</i> (X9/35, 1 headed plant)	35	38.4 ± 2.3	6.0	36.1 ± 2.3	6.4
× <i>grofae</i> (X9/29, 5 headed plant)	47	34.0 ± 1.8	5.3	31.5 ± 2.1	6.6

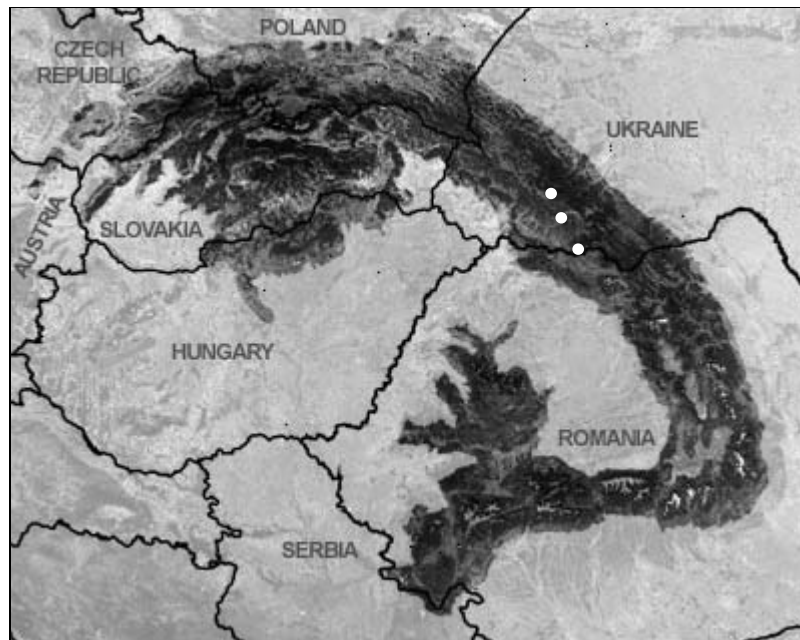


Fig. 2. Distribution of *Hieracium* × *grofae*. The easternmost dot represents a group of localities in the Pip Ivan massif (Marmarosh Mts).

and putative natural hybrids and progeny from experimental hybridization produced homogeneously sized pollen with standard deviations and coefficients of variation lower than upper limit values for diploids – 3 μm or 7.5%, respectively (Tab. 2). This suggests that the hybrid plants found in Mt. Unharias’ka and lectotype specimens from the locus classicus are also diploids. *Hieracium alpinum* produced the largest pollen grains, while *H. umbellatum* and their hybrids *H. × grofae* smaller ones. We found a variation in pollen size between lowland and mountain morphotypes of *H. umbellatum*. Similarly, two experimental hybrids analyzed show differences in pollen size.

Ecology

Subalpine secondary grasslands (less intensively grazed

or abandoned pastures, usually more or less disturbed places) and rocky outcrops.

Distribution

Local and very rare in the Marmarosh Mts, the Svydovets’ Mts and the Horhany Mts (all the Ukrainian Eastern Carpathians, Fig. 2), occurring in very small number of individuals on the localities. Its occurrence in adjacent part of Rumanian Eastern Carpathians, mainly in the Munții Maramureșului, is highly probable.

Specimens studied:

Ukraine

Oblasť Ivano-Frankivs’ka: [Horhany Mts] Galicia in regione Mughii montis Grofae Lomnicensis,

Carpathorum orientaliu 1600 m s. m. (20. VII. 1889 WOŁOSZCZAK, KRAM; Fig. 1A).

Oblasť Zakarpats'ka: [Svydovets' Mts] Svidovec, ca 2 km V od kóty Ungariaska (1711), na hrebeni, ca 1600 m (7. VIII. 1996 P. MRÁZ & V. JURKOVIČOVÁ, herb. P. MRÁZ, det. P. MRÁZ 2003 ut *Hieracium fritzei* f. *marmarosense*, rev. P. Mráz ut *H. alpinum* × *H. hryniawiense*; Fig. 1B). – [Marmarosh Mts] Huculské Alpy, hřeben mezi Žerbánem a Pop Ivanem (VIII. 1938 s. coll., SAV). – Marmaroš, in graminosis et saxosis montis Pop Ivan prope vicum Trebušany, solo granitico, alt. 1650-1940 m s.m. (VIII. 1933 M. DEYL, PR, SAV). – Marmaros: Alpenmatten des Popp Ivan, Glimmerschiefer, 1800-1900 m (24. VIII. 1894 WEBERBAUER, SAV). – Marmaroš, Berlebaška Mt., skaly pod vrcholom, ca 1800 m (31. VII. 1996 R. LETZ, herb. P. MRÁZ, det. P. MRÁZ 2004 ut *Hieracium alpinum* × *hryniawiense* (*conicum* agg.); Fig. 1C). – Ostkarpaten, 13 km SE Rachiv: Marmaroski Alpi, Berlebaška, W unterhalb des Gipfels, 1700 m, 47°57.2' N, 24°18.9' E, Gneisfelsen (31. VII. 1996, S. BRÄUTIGAM & J. CHRTEK jun., GLM, PRA). – Marmarosh, Dilove: Mt. Berlebashka, W slope below the top, 10.5 km ENE of Dilove (plant cultivated at the experimental garden in Průhonice, leg. 20 September 2005, J. CHRTEK; collection in the field 4 August 2005, J. ZAHRADNÍČEK).

Discussion

The chromosome number ($2n = 18$, diploid) supports our hypothesis of a recent hybrid origin of the plants from *H. alpinum* and *H. umbellatum*. All stabilized hybridogeneous species in *Hieracium* s.str. are polyploids (triploids and tetraploids, very rarely pentaploids). The studied plants produce homogeneously sized pollen and would most likely serve as pollen parents in backcrosses or in hybridization with another sexual *Hieracium* species (either the parent species or *Hieracium transilvanicum* co-occurring in the area). Similarly, pollen production and quite high stainability of pollen grains (75 and 85%) was reported for experimental hybrids *H. × grofae* (MRÁZ & PAULE, 2006; cf. Tab. 2, cross no. X9). Only empty achenes were found in all examined plants of *H. × grofae*; it is most probably completely seed sterile (examination of heads of the herbarium specimens), similar to *H. × krasanii* WOŁ. (MRÁZ et al., 2005). Nearly complete seed sterility has also been documented in experimental hybrids between *H. alpinum* and *H. umbellatum* (MRÁZ & PAULE, 2006). Moreover, the morphological comparison of natural hybrids with those from an experimental hybridization (MRÁZ, 2003; MRÁZ & PAULE, 2006; cross no. X9 *H. umbellatum* × *H. alpinum*) revealed that they are identical.

The original plants of *H. × grofae* collected by E. WOŁOSZCZAK are with high probability diploid as is evident from the pollen size homogeneity, an indirect indicator of diploidy, found in lectotype voucher. While

particular ploidy levels in *Hieracium* s. str. do not differ significantly from each other in the mean pollen size, pollen from diploids strongly differs from that in polyploids with respect to its size homogeneity. In diploids, values of standard deviation and coefficient of variation do not exceed 3 μm or 7.5%, respectively. In contrast, triploid and tetraploid apomictic taxa (if they produce pollen at all) produce lower quantity of heterogeneously sized pollen grains (values of standard deviation and coefficient of variation always exceed 3 μm or 7.5%, respectively) (MRÁZ et al., 2002; KOVALČIKOVÁ, 2004). In the genus *Taraxacum*, STERK et al. (1982) found that diploids have standard deviation lower than 3 μm and polyploids higher than 3 μm . Considering the genus *Hieracium* as a whole, there is probably a correlation between the number and size of capitula and pollen size. Plants with small number of capitula per plant produced usually larger pollen than the plants with higher number of small capitula per plant. Although, this tendency was observed also in other analyzed diploid taxa (KOVALČIKOVÁ, 2004), more detailed studies should be undertaken.

WOŁOSZCZAK (1892) proposed the parentage of *H. × grofae* as *H. decipiens* × *H. umbellatum* var. *lactaris* BERTOL. However, he was aware that this decision was rather arbitrary and he was not convinced that it was really correct. He has found the hybrids growing with *H. umbellatum* var. *lactaris*, *H. alpinum* and *H. decipiens* (from the taxonomical point of view, the plants determined by Wołoszczak as *H. decipiens* do not match *H. decipiens* TAUSCH and cannot be referred to it). While the parentage of *H. umbellatum* was clear, WOŁOSZCZAK (1892: 143) much doubted about the second parent (*H. alpinum* vs. *H. decipiens*).

According to our studies, plants from the Ukrainian Eastern Carpathians determined by E. WOŁOSZCZAK as *H. decipiens* (e.g. from Mt. Guretvyn, herb. W no. 15285) have no pollen grains and could hardly be involved in any natural hybridization. Unfortunately, we do not know the ploidy level of this taxon. However, morphologically nearly identical plants collected in 2003 by J.C. and P.M. at Mt. Pikuj (the Beskyds'ke vysokohir'ya Mts, the Ukrainian Carpathians) were found to be tetraploid (J.C. unpubl.). Thus, even if these plants had produced viable pollen grains, their hybrids with diploid plants (*H. umbellatum*) should have been triploid. *Hieracium alpinum* is much more likely to be a parent – it is diploid and sexual in the Ukrainian Eastern Carpathians (CHRTEK, 1997; MRÁZ, 2001, 2003) and its capability to produce hybrids with other *Hieracium* species from different section has been proved experimentally (MRÁZ & PAULE, 2006). Furthermore, *H. decipiens* sensu WOŁ. non TAUSCH has distinctly dentate leaves, while hybrid plants have entire to finely denticulate leaves (similarly to *H. alpinum* and *H. umbellatum*). Thus, we are sure that the hybrid formula should be *H. alpinum* × *H. umbellatum*.

Although many polyploid *Hieracium* species occur

pying an intermediate position between two or more other species are undoubtedly results of past hybridization and introgression processes, recent spontaneous hybrids in *Hieracium* (s. str.) are most likely extremely rare. Besides *H. ×grofae*, only the hybrid between *H. alpinum* and *H. transsilvanicum* (*H. ×krasanii*) has been reported in the literature (MRÁZ et al., 2005). Two common features of the two hybrids deserve brief discussion:

(1) Both of them were discovered in the Ukrainian and/or Rumanian Eastern Carpathians. This part of the Carpathian arc harbours 3 diploid sexual hawkweed species, i.e. *Hieracium alpinum*, *H. transsilvanicum* and *H. umbellatum* (both lower altitude and high mountain morphotypes). Intermingled populations have never been observed mostly due to their different ecological demands. However, they are sometimes found in rather close vicinity allowing effective pollination (all hawkweeds are entomophilous) and hybrid formation.

(2) Both *H. ×grofae* and *H. ×krasanii* are very rare, only individual plants are found in the nature. This can be explained by only occasional effective pollination, due to distance between the parent plants, and/or by prezygotic fertilization barriers (competition between conspecific and heterospecific pollen/pollen tubes). Hybrid zones are situated on the secondary mountain grassland (“poloniny”), thus low germination rates due to an absence of suitable gaps and disturbed places can also play an important role. Low seedling vigour and competitive ability should also be suggested.

Hieracium ×grofae resembles taxa of the *Hieracium fritzei* group, but differs by having nearly glabrous ligule apices (ligules at apex with scattered to numerous short hairs in the *H. fritzei* group), obtuse phyllaries (acute in the *H. fritzei* group) and obtuse leaves (rather acute in the *H. fritzei* group). Plants of *H. ×grofae* are diploid and produce regularly-sized pollen grains, the *H. fritzei* group embraces tri- and tetraploid agamosperms with disturbed microsporogenesis (aborted or irregularly sized pollen). The total geographic range of the *H. fritzei* group includes the high Sudeten mountains (the Krkonoše Mts, Mt. Králický Sněžník), highest parts of the Western Carpathians, and Rumanian South Carpathians, but the occurrence in the Ukrainian Eastern Carpathians is unclear. ZAHN (1930–1939) listed 5 localities from this area, namely “B. [Berg] Gorgan ilemski”, “Grofa”, “Alpe Sywula”, “Pop Ivan” and “Czorna hora”. The former 3 lie in the Horhany Mts; the latter localities (“Pop Ivan” and “Czorna hora”) are situated in (or nearby) the area where we have discovered the hybrid plants and have never observed plants referring to the *H. fritzei* group. CHOPYK (1977) reported *H. fritzei* from the Chornohora Mts, PROKUDIN (1987) gave only brief note “V Karpatach” [in the Carpathians]. Unfortunately, we have not found the respective herbarium voucher specimens and thus the occurrence of *H. fritzei* in the Mar-marosh Mts (Mt. Pip Ivan) and the Chornohora Mts

remains a moot point. However, based on our own observation (excursion in 1996) we are fairly certain that the two localities in the ZAHN’s monograph refer to *H. ×grofae* and that *H. fritzei* is absent from this area.

Hieracium umbellatum, one of the parent species of *H. ×grofae*, is well-known by an extreme range of variation mainly in the total height, number of stem leaves, leaf shape, and number and size of capitula (e.g. TURESSON, 1922; ZAHN 1930–1939; LÖVKVIST, 1962). Particular morphologically distinct types are often classified as varieties (SENNIKOV, 2003). All plants from the mountain grasslands in our area are characterized by distinctly broad cauline leaves. Moreover, the plants from the subalpine or even alpine belt of the Ukrainian Carpathians growing on exposed slopes of glacial cirques have only few (usually 3–5) large heads. This mountain morphotype is morphologically stable in cultivation and clearly distinct from lowland populations of *H. umbellatum*. In our previous papers we have used the names *H. conicum* (CHRTEK, 1996) or *H. hryniawienne* (MRÁZ, 2003) for these diploid mountain populations. The former taxon was described from the Western Alps, for the latter name we have recently discovered an original herbarium material in KRAM. Neither of the names can be clearly applied to our mountain populations, and for this reason we treat them under the name *H. umbellatum* in this paper.

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Appendix 1

Origin of plant material used for pollen measurements

Localities are abbreviated and simplified; voucher specimens are deposited in the Herb. P. MRAZ, except for lectotype specimen *H. × grofae* (deposited in KRAM). Abbreviations: Sk – Slovakia, Uk – Ukraine.

H. alpinum (diploid cytotype; other plants from identical populations were counted karyologically, cf. CHRTEK, 1997; MRAZ, 2001, 2003)

Uk, Svydovets' Mts, Mt. Unharias'ka, coll. P. MRAZ & V. JURKOVIČOVÁ 1999 (1 plant)

Uk, Svydovets' Mts, Mt. Tatul, coll. P. MRAZ & V. JURKOVIČOVÁ 1999 (1 plant)

Uk, Svydovets' Mts, Mt. Blyznytysia, coll. P. MRAZ & V. JURKOVIČOVÁ 1999 (2 plants)

Uk, Chornohora Mts, Mt. Hoverla, coll. P. MRAZ et al. 1996 (1 plant)

H. × grofae – natural diploid hybrids

Uk, Horhany Mts, Mt. Grofa, coll. E. WOŁOSZCZAK 1889 (KRAM 148408)

Uk, Marmarosh Mts, Mt. Berlebashka, coll. R. LETZ 1996 (1 plant, Ber1)

Uk, Svydovets' Mts, E of Mt. Unharias'ka, coll. P. MRAZ & V. JURKOVIČOVÁ 1999 (2 plants, Ungar1 and 2)

H. × grofae – experimental diploid hybrids

X9/29 and X9/35 (for details on provenience of parental species, crossing scheme, chromosome numbers etc. see MRAZ, 2003 and MRAZ & PAULE, 2006)

H. umbellatum – morphotype of low altitude (diploid cytotype; diploid chromosome number for plant for the first locality was published in MRAZ, 2003):

Sk, Volovské vrchy Mts, village of Prakovce, coll. P. MRÁZ 1999 (1 plant, cult. no. 736).

Sk, Volovské vrchy Mts, town of Gelnica, coll. P. MRÁZ 1999 (1 plant)

H. umbellatum– high mountain morphotype (diploid cytotype; cf. CHRTEK, 1996 ut *H. conicum*; MRÁZ, 2003 ut *H. hryniawiense*)

Uk, Svydovets' Mts, Mt. Unharias'ka, coll. P. MRÁZ & V. JURKOVIČOVÁ 1999 (1 plant)

Uk, Svydovets' Mts, Mt. Heryshas'ka, coll. P. MRÁZ & V. JURKOVIČOVÁ 1999 (1 plant)