Chromosome numbers and reproductive systems in selected representatives of *Hieracium* subgen. *Pilosella* in the Krkonoše Mts (the Sudeten Mts) – 2.

Počty chromozomů a reprodukční systémy vybraných zástupců jestřábníků (*Hieracium* subgen. *Pilosella*) Krkonoš – 2.

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Dedicated to the memory of Zdeněk Černohorský

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Chromosome numbers and reproductive systems of the following species are reported from the Krkonoše Mts (the Sudeten Mts): (a) species not previously studied within this area: *H. fuscoatrum* Nägeli et Peter (2n = 36, apomictic), *H. blyttianum* Fr. (2n = 36, apomictic), *H. tubulascens* Norrl. (2n = 36, apomictic), *H. bauhini* Besser (2n = 45, apomictic), *H. onegense* (Norrl.) Norrl. (2n = 18, sexual); (b) new cytotypes recorded: *H. floribundum* Wimm. et Grab. (2n = 18, sexual), *H. apatelium* Nägeli et Peter (2n = 45, apomictic), *H. iseranum* Uechtr. (2n = 45, apomictic), *H. aurantiacum* L. (2n = 45, apomictic), *H. stoloniflorum* Waldst. et Kit. (2n = 45); (c) additional data on distribution and reproduction mode of species previously studied: *H. pilosella* L. (2n = 36, sexual), *H. lactucella* Wallr. (2n = 18), *H. caespitosum* Dumort. (2n = 36, apomictic), *H. aurantiacum* L. (2n = 36, apomictic), *H. schultesii* F. W. Schultz (2n = 36, apomictic), *H. glomeratum* Froel. (2n = 45, apomictic), *H. floribundum* Wimm. et Grab. (2n = 36, apomictic), *H. piloselliflorum* Nägeli et Peter (2n = 36, both sexual and apomictic; 2n = 45, apomictic; 2n = 54, apomictic). Chromosome numbers are given for the first time for *H. fuscoatrum* and *H. tubulascens*, the record of diploid sexual plants is a novelty for *H. floribundum*. New ploidy levels are also reported for *H. apatelium* and *H. iseranum*. The richness of the Krkonoše Mts in *Hieracium* subgen. *Pilosella* is discussed with respect to number of basic (5) and sexual (7) species. In the Czech Republic as well as in the Sudeten Mts, two species of this subgenus (*H. fuscoatrum* and *H. tubulascens*) were recorded for the first time.

Keywords: *Hieracium* subgen. *Pilosella*, chromosome numbers, breeding systems, Krkonoše Mts, Czech Republic

Introduction

The taxonomic complexity of the genus *Hieracium* has long attracted the attention of botanists. For example, Mendel, in 1869 described several interspecific crosses within the subgenus *Pilosella*. Since then there have followed many studies investigating the processes which influence patterns of variation in the field (see Krahulcová et al. 2000 for a review). Specifically these studies described (1) local differences in patterns of variation among species and (2) local differences in the ability of given species combinations to hybridise. Differences among populations included the number of taxa present, the range of ploidy levels and reproductive systems; each of which contribute to determining the outcome of hybridisation.

In order to classify taxonomically such complex populations, it is obviously necessary to understand their evolutionary history. This is why we began our population studies of *Hieracium* populations in the Krkonoše mountains, part of the larger Sudeten range. The Krkonoše Mts are famous for their diversity of *Pilosella* types. Our first contribution (Krahulcová & Krahulec 1999) covered data for 13 species, many of which were polymorphic for both of the characteristics studied, i.e. chromosome number and reproductive systems. Since then, we have continued our studies, covering the whole spectrum of taxa and several more populations. Our results are presented below. In addition, the morphological characters of two species recorded as new in the Czech Republic (*H. fuscoatrum*, *H. tubulascens*), are described. The history of classification of some natural interspecific hybrids (*H. fuscoatrum*, *H. blyttianum*) is discussed in more detail.

Material and methods

Plants studied

The plants were collected during the summer of 1998–1999, and transplanted into the experimental garden at Průhonice; then their chromosome numbers and reproductive mode was determined. Their herbarium specimens are preserved in the collection of the herbarium of the Institute of Botany at Průhonice (PRA).

Chromosome numbers and breeding systems

The chromosome numbers are based on somatic mitoses in root tips of potted plants. Root tips were pre-treated with a saturated solution of α-bromnaphtalene or para-dichlorbenzene for 3 hours at room temperature, rinsed in water and fixed in cold acetic acid-ethanol (1:3) overnight. The fixed material was stored in 70% ethanol at 4°C until required. The maceration was carried out in 1N HCl at 60°C for 7 min. The root tips were then rinsed in water and the cut meristems were squashed in a drop of lacto-propionic orcein (Dyer 1963). Only temporary slides were made.

The study of reproductive system was based on the comparison of seed-set of open pollinated plants with those whose capitulum was cut just before the flowering (for more details of this method see Gadella 1987, Richards 1997, and Krahulcová & Krahulec 1999).

Results and discussion to particular species

Chromosome numbers and reproductive systems in taxa not treated yet

1. *Hieracium fuscoatrum* Nägeli et Peter

Nägeli et Peter, Hier. Mitt.-Eur. 1: 315, 1885.

H. aurantiacum – H. caespitosum

2n = 4x = 36, apomictic.

L o c a l i t y : **1.** Horní Malá Úpa, Pomezní Boudy: ruderal place at the parking place S of "Padolská bouda" chalet, 950 m a.s.l., 50°44'10"N, 15°48'10"E. Coll. F. Krahulec 26. 6. 1997. 2n = 36 (4 plants), apomictic (2 plants).

Both the chromosome number and the reproductive system in *H. fuscoatrum* are reported here for the first time. Neither ploidy level nor reproduction mode differ from both putative parents. It is difficult to say, however, which of the two facultatively apomictic putative parents served as a seed parent in this case. In spite of the past detailed research into the *Hieracium* flora in the Krkonoše Mts, the occurrence of *H. fuscoatrum* has never been reported from this area. The first record of this hybridogenous species, at a locality near Pomezní Boudy, was made in 1979 (Krahulec et al. 1997: tab. 19, rel. 120). The species still occurs there, and until now was the only known locality. The morphology of the hybrid plant is intermediate between the parents. As this species is reported here for the first time from both the Sudeten Mts and the Czech Republic, we add its brief description based on plants collected in the field as well, as on plants cultivated in the garden.

Plants 23–45 cm high, with usually short stolons; stems densely hairy; basal leaves elliptic to oblanceolate, obtuse to subacute to (the inner ones) acute at apex, densely covered by simple eglandular hairs, with no stellate hairs (except of very few ones on margins and below on the midrib), cauline leaves narrowly oblanceolate to oblong; inflorescences compact, peduncles with very few eglandular hairs, numerous glandular hairs and dense stellate hairs; involucres 7–9 mm long, involucral bracts with scattered simple eglandular hairs, scattered glandular hairs and scattered stellate hairs; styles deep yellow with dark scales. It can be easily distinguished from both *H. caespitosum* and *H. aurantiacum* by clearly intermediate color of flowers, which are ± orange, sometimes turning reddish (especially on dry material) (Fig. 1.).

Hieracium fuscoatrum was described on the basis of garden hybrid (Nägeli & Peter 1885). Later on, naturally occurring plants were found. Zahn (1922–1930) recognized in central Europe (in the sense of that monograph, i.e. including Balcan countries) subsp. *fuscoatrum* and subsp. *silvicoliforme* Zahn in Engler. The former is recorded from the Tatra Mts (the Western Carpathians) and from the Ukrainian Eastern Carpathians, the other from Macedonia. Relations to similar taxa described from northern Europe (*H. semionegense* Norrl., *H. rubrionegense* Norrl.) are moot points. Similarly, position of plants collected in the Čornohora Mts (Ukrainian Eastern Carpathians, cf. Zahn 1922–1930, also the specimens collected by J. Chrtek jun.) remains unproven.

2. *Hieracium blyttianum* Fr.

Fries, Uppsala Univ. Årsskr. (Nat.-Mat.) 1862: 21, 1862.

H. aurantiacum – *H. lactucella*

2n = 4x = 36, apomictic.

L o c a l i t i e s : **1.** Horní Malá Úpa, Pomezní Boudy: the meadow in the grassland area "Mokré jámy", ca. 250 m NEE of the sharp bend on the road to Czech – Poland border crossing, 1000–1010 m a.s.l., 50°44'20"N, 15°48'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 36 (10 plants), apomictic (3 plants). **2.** Horní Malá Úpa, Pomezní Boudy: the meadow along the woodland edge in the lower part of the ski-lift "Hybnerka", ca. 1.3 km SWW of the Czech – Poland border crossing, 1020 m a.s.l., 50°44'30"N, 15°48'40"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 36 (2 plants), apomictic (1 plant). **3.** Dolní Malá Úpa, Rennerovy Boudy settlement: the grassy place along the road margin above the "Moravanka" chalet in the

northern periphery of the settlement, 1050 m a.s.l., 50°43'50"N, 15°49'10"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36 (2 plants), apomictic (1 plant).

Two references on chromosome number in *H. blyttianum* have been published. The first one by Skalińska (1967), who recorded a tetraploid plant [corresponding to *H. blyttianum* subsp. *pyrrhanthes* (Nägeli et Peter) Zahn] in an isolated locality in the Bieszczady Mts, Poland. According to morphology, this plant showed a more pronounced similarity to *H. aurantiacum* than to *H. lactucella*, which was explained by an assumed prevalence of chromosome sets of the former species (Skalińska 1967). In addition, another plant (a hexaploid, 2n = 54), has been recorded in the Tatra Mts, Poland (Skalińska 1967), probably being of the same hybrid origin. The pentaploid *H. aurantiacum* and diploid *H. lactucella*, growing in a close vicinity of this hybrid, have been considered as its putative parents. The fertilization of an unreduced embryo sac of the pentaploid *H. aurantiacum* by reduced haploid pollen of *H. lactucella* has likely been the mode of origin of this hybrid (Skalińska 1967).

The second karyological reference on *H. blyttianum* comes from Bavarian plants, Germany (Schuhwerk & Lippert 1997). However, both spontaneous hybrids between *H. lactucella* and *H. aurantiacum* reported here are included to *H. fuscum* Vill. (described by D. Villars, G. Lauth et A. Nestler, Précis. Voy. Bot. 19, 1812), i.e. the species corresponding to *H. aurantiacum* > *H. lactucella* according to Zahn's formula (Zahn 1922–1930). The first hybrid, representing the morphotype somewhat closer to *H. lactucella* (= *H. blyttianum*), was a tetraploid (2n = 36). The second plant, morphologically closer to *H. aurantiacum* (= *H. fuscum*) was a pentaploid (2n = 45). Both cytotypes (and morphotypes) have been recorded at different localities (Schuhwerk & Lippert 1997).

The tetraploid level found in this hybridogenous species in the Krkonoše Mts, however, does not correspond to a product of simple hybridization between the putative parents, i.e. the diploid *H. lactucella* and the tetraploid *H. aurantiacum*. The former parent is known as diploid only (throughout its range), the latter occurs as tetraploid in many localities in the Krkonoše Mts, except for a rare pentaploid cytotype recorded at two localities (see below and Krahulcová & Krahulec 1999). The experimental hybridization between diploid *H. lactucella* and tetraploid *H. aurantiacum* led to triploid progeny (Krahulcová & Krahulec unpubl.). The majority of F_1 hybrids produced seeds being open pollinated. The ability of these triploids to produce tetraploid offspring corresponding to *H. blyttianum* (e.g. via unreduced gametes or backcrossing) may be a possible solution. In both cases however, the triploid spontaneous hybrids have had to take part (at least sometimes) in a sexual cross. Moreover, the ability of triploids to form euploid gametes is assumed.

The classification of naturally occurring types between *H. aurantiacum* and *H. lactucella* should promote considerable discussion. There are two taxa usually recognized at the species level, i.e. *H. blyttianum* Fr. (= *H. pyrrhanthes* Nägeli et Peter) and *H. fuscum* Vill. The former was described from Norway, the latter from the Alps. Nägeli & Peter (1885) treated *H. blyttianum* (ut *H. pyrrhanthes*) as an intermediate type between *H. aurantiacum* and *H. lactucella*, and *H. fuscum* as an intermediate type between *H. aurantiacum* and *H. niphobium* Nägeli et Peter (*H. niphostribes* Peter). In contrast, Zahn (1921–1923, 1922–1930) adopted the name *H. blyttianum* for the plants more closely related (similar) to *H. lactucella* and the latter name for those more resembling *H. aurantiacum*. Differences between target species include (cf. e.g. Zahn 1922–1930) leaf shape (leaves rather obovate and obtuse at apex in *H. blyttianum*, and at least the inner

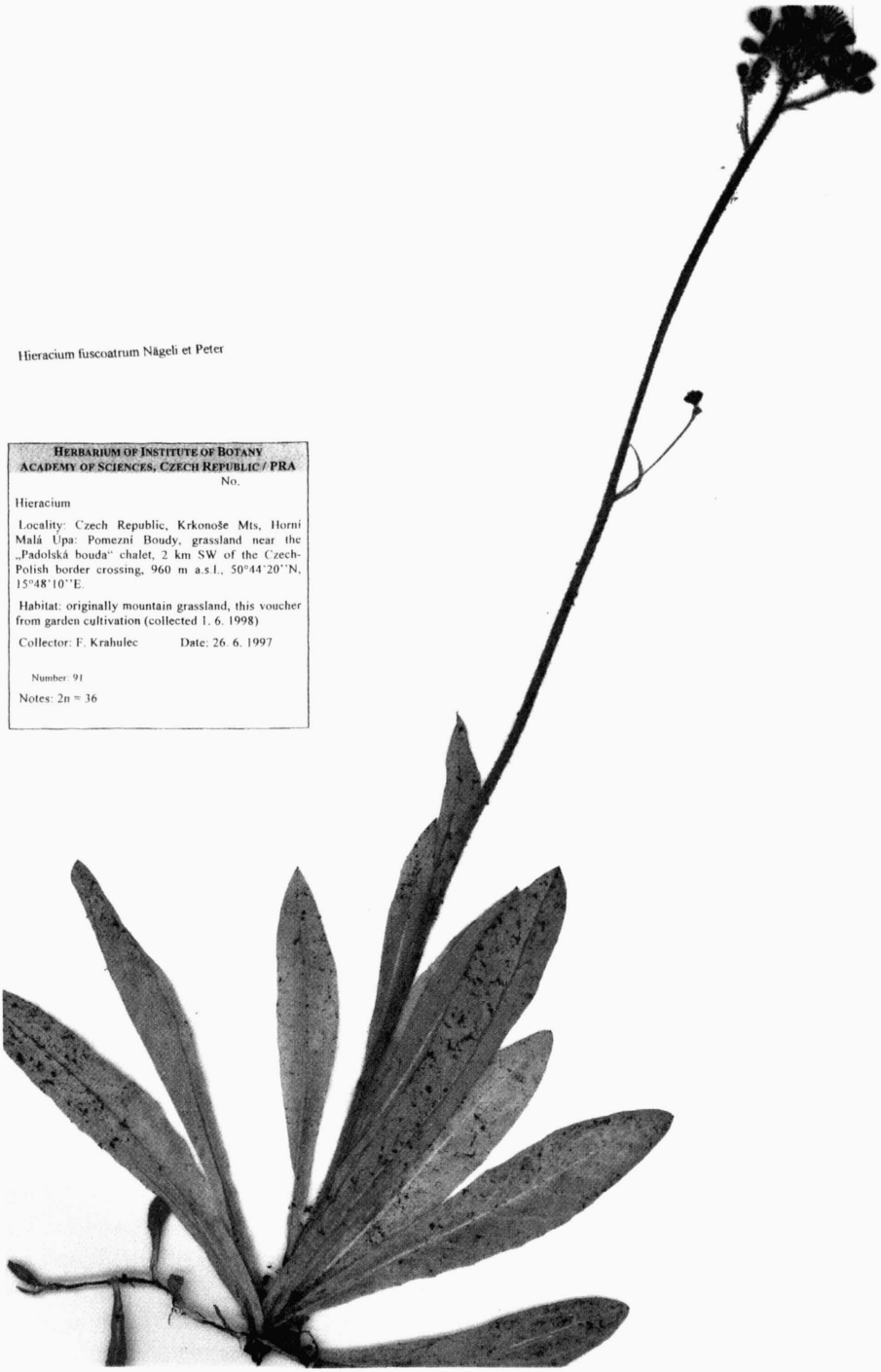

Fig. 1. – *Hieracium fuscoatrum* Nägeli et Peter

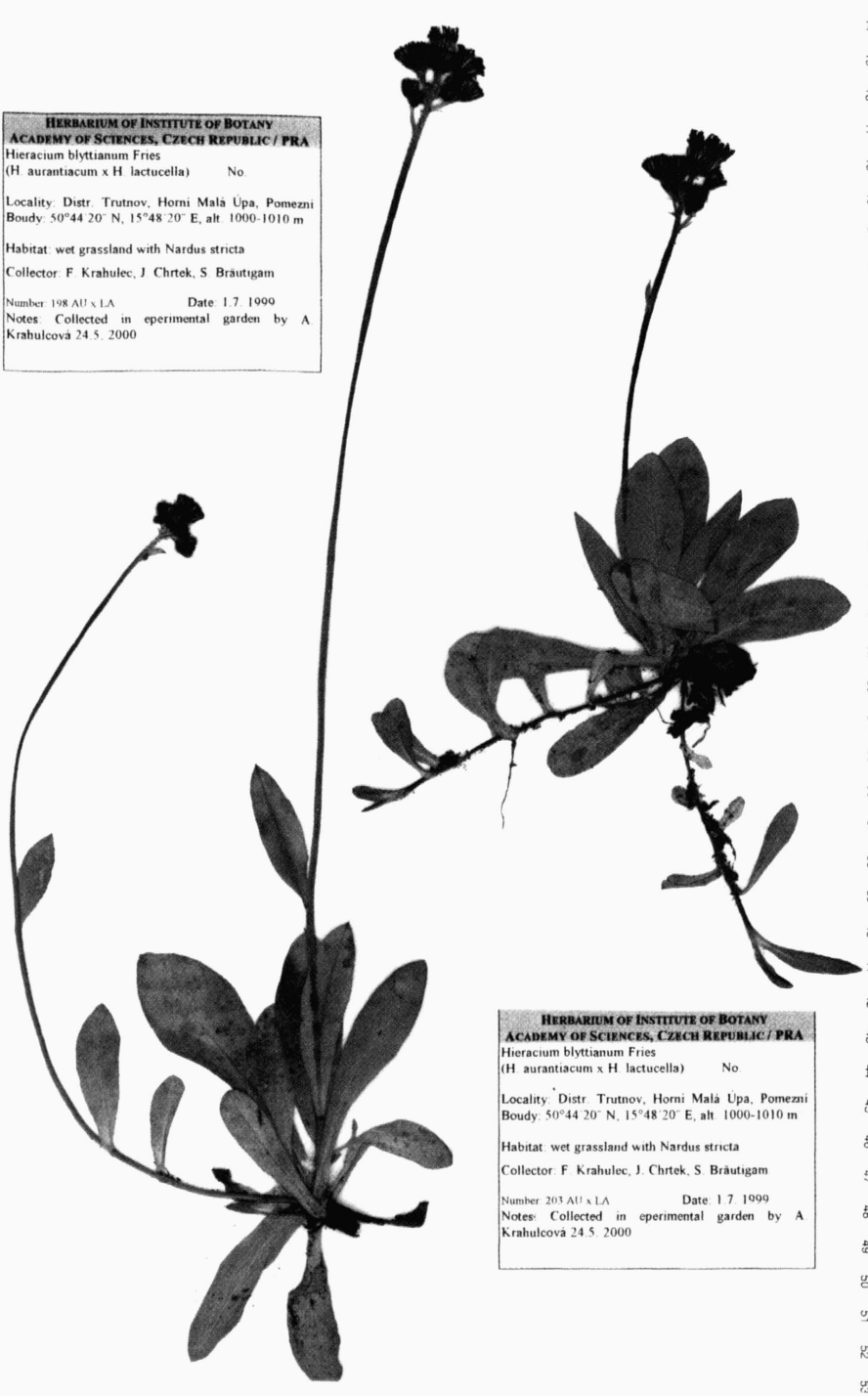

Fig. 2. – *Hieracium blyttianum* Fr.

rosette leaves lanceolate and acute in *H. f.*), length of stolons (usually long in *H. b.*, very short to more or less long in *H. f.*), character of indumentum (*H. f.* more densely hairy), length of involucres (larger in *H. f.*). *H. fuscum* is restricted to the Alps, the Jura Mts. and the Romanian Carpathians, *H. blyttianum* occurs in the Alps, the Sudeten Mts., the Carpathians, in Scandinavia and NW Russia. Schuhwerk (1997) treated *H. blyttianum* and *H. fuscum* as conspecific. Schuhwerk & Lippert (1997) found *H. fuscum* s. str. pentaploid and "*H. blyttianum*" (unified here taxonomically with *H. fuscum*) tetraploid (see above).

The first published record concerning types possessing an intermediate morphology between *H. aurantiacum* and *H. lactucella* in the Krkonoše Mts appeared in 1880. Uechtritz (1880) examined plants collected by F. Pax in the settlement of Pomezní Boudy (Grenzbauden), ca. 1000 m alt., determined originally by Pax as *H. aurantiacum*. In Uechtritz's opinion, the given plants with nearly glabrous and glaucous leaves might be evaluated either as a new species or as a hybrid *H. aurantiacum* × *H. suecicum* Fr. (*floribundum – lactucella*). Later on, Peter (1881) described *H.* ×*latibracteum*, based on the same plant. Supposed parent species are *H. aurantiacum* and *H. lactucella* (ut *auricula*), i.e. not *H. suecicum* as suggested by Uechtritz.

Further studies threw more light on understanding of this group in the Krkonoše Mts. During the revision of herbarium specimens collected by G. Schneider, Uechtritz (1885) designated one plant originated from "Goderwiese" in settlement of Pomezní Boudy (collected 1883) as *H. aurantiacum* × *H. auricula*. He also reevaluated the systematic position of a plant previously placed between *H. aurantiacum* and *H. suecicum* (see above) – the plants are now suggested as *H. aurantiacum* × *H. iseranum*. To sum up, two taxa were recognized then, i.e. (1) "*H. latibracteum*", usually without stolons, mostly with 3–6 cauline leaves, compact inflorescences, involucral bracts with only very narrow pale margin and with ± numerous simple eglandular hairs, and (2) type collected by G. Schneider with ± long stolones, lax inflorescence, involucral bract with pale margin and only few simple eglandular hairs.

A year later, Uechtritz (1886) commented on another plant collected by G. Schneider in the Pomezní Boudy settlement and near the Schlingelbaude chalet (now called Polana on the Polish side of the mountains). The plant from the former locality more closely resembled *H. lactucella*. It was not more than 10 cm high, the stem beared only one leaf and two flowering heads. The effort of Silesian botanists was crowned by Schneider's treatment of *Hieracium* (Schneider 1888–1895). He followed generally the former concept and recognized two types at subspecific level, i.e. subsp. *goderianum* G. Schneider (*H. aurantiacum* × *H. lactucella*) and subsp. *latibracteum* (*H. aurantiacum* × *H. suecicum*), the former based on the plants discussed above from "Goderwiese" and "Schlingelbaude". Distinguishing characters are generally in agreement with those given by Uechtritz (see above), important is the shape of inflorescens (compact in *latibracteum*, lax in *goderianum*), indumentum of basal leaves (few stellate hairs on leaf margin and below on the midrib in *latibracteum*, no stellate hairs in *goderianum*).

Later on Zahn (cf. e.g. 1922–1930) united both types under the name *H. blyttianum* subsp. *latibracteum*. Plants collected during the last decade by the present authors in the Krkonoše Mts. (deposited in PRA) correspond mostly to the "*latibracteum*" type in the narrow sense.

Plants occurring within the Krkonoše Mts are morphologically (Fig. 2) as well as karyologically homogeneous at all known localities. The habitat conditions at all localities studied are also similar, especially with respect to soil moisture. This species occurs on wet meadows and on a former path, being overgrown by different species of wet meadows.

3. *Hieracium bauhini* Besser

Besser, Prim. Fl. Galic. 2: 149, 1809.

2n = 5x = 45 with a long marker chromosome, apomictic.

Locality: **1**. Dolní Malá Úpa: beside the road ca. 0.7 km S of the church, 910 m a.s.l., 50°43'00"N, 15°48'40"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 45 with marker chromosome, apomictic (1 plant).

This species shows diversity in ploidy levels, although the pentaploid level seems to prevail among chromosome counts already published. Three ploidy levels (tetraploid, pentaploid and hexaploid) have been reported in *H. bauhini* from three different localities (one ploidy level at each) in Bavaria, Germany (Schuhwerk & Lippert 1997). A total of 20 pentaploid plants of *H. bauhini*, examined by means of flow-cytometry, have been recorded at a locality in Saxonia, Germany (Bräutigam & Bräutigam 1996). The pentaploid apomictic *H. bauhini* is known from Belgium and from the Netherlands (Gadella 1984, under the name of "*H. praealtum* Vill. ex Gochnat subsp. *bauhinii* (Besser) Petunnikov in Syreistschikov"). The pentaploid *H. bauhini* has also been reported from Slovakia (Uhríková 1970), while the tetraploid cytotype is recorded from Greece (under the name of "*H. praealtum* subsp. *bauhinii*" – Papanicolaou 1984).

The plant examined here is likely a recent introduction, only one specimen recorded from a freshly opened road margin. It corresponds morphologically to *H. bauhini* in its narrower circumscription. The plant is stoloniferous, stolons being only connected with rosette leaves, and peduncles are densely tomentose.

4. *H. onegense* (Norrl.) Norrl.

Norrlin, in T. Sael., Kihlm. et Hjelt, Herb. Mus. Fenn., ed. 2, 1: 118, 1889

Syn.: *Hieracium caespitosum* Dumort. subsp. *brevipilum* (Nägeli et Peter) P. D. Sell;
H. pratense Tausch subsp. *silvicolum* Zahn

2n = 2x = 18, sexual.

Locality: **1**. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 870 m a.s.l., 50°41'20"N, 15°47'50"E. Coll. F. Krahulec and A. Krahulcová 21.–23. 6. 1998. 2n = 18, sexual (2 plants).

The diploid *H. onegense* is known from other areas: from Poland under the name of *H. pratense* subsp. *silvicolum* Zahn (Skalińska & Kubień 1972). In addition, it is reported under the name *H. caespitosum* subsp. *brevipilum* from Balkan Peninsula: northern Greece (Schuhwerk & Lippert 1998) and Bulgaria – the Vitosha Mts and the Central Rhodope Mts (Vladimirov 2000).

This taxon has an eastern distribution (e.g. Zahn 1922–1930, Schljakov 1989), and its occurrence in the Krkonoše Mts is near its western distribution limit. It has already been reported from the Krkonoše Mts by Schneider (1888–1895: 32), mainly from the Silesian part of the mountain range: Jagniatków (Ober-Agnetendorf), Krzaczyne (Buschvorwerk), with only one locality on the Czech side: Labský důl (Elbegrund). On the contrary, the

other authors respecting Zahn's view did not report it (Šourek 1969, Dostál 1948–1950, 1989).

This species differs from related *H. caespitosum* by dense and short hairs (about 1 mm) on the stem, by underground stolones and yellow-green and broadly ovate leaves (Fig. 3).

5. *Hieracium tubulascens* Norrl.

Norrlin, Herb. Pl. Fenn. I. Nr. 78 et Adnot. I. 135, 1889.

H. glomeratum – *H. lactucella*

2n = 4x = 36 with a long marker chromosome, apomictic.

Locality: 1. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 870 m a.s.l., 50°41'20"N, 15°47'50"E. Coll. F. Krahulec and A. Krahulcová 21.–23. 6. 1998. 2n = 36 with marker chromosome, apomictic (1 plant).

This is the first reference on ploidy level and reproductive system in *H. tubulascens*.

During detailed population sampling, only one specimen has been collected resembling *H. glomeratum*. This plant does not match any taxon recorded from the Krkonoše Mts. It differs from *H. glomeratum* having less numerous simple eglandular hairs on stem and leaves (leaves at upper surface smooth, as at *H. floribundum* and *H. lactucella*), basal leaves obtuse at apex and usually no stellate hairs at the upper leaf surface. It differs from *H. floribundum* first of all by shorter simple eglandular hairs, and by basal leaves more resembling *H. lactucella* (markedly obtuse at apex). In our opinion, the plant is a hybrid *H. glomeratum* × *H. lactucella*. Chromosome numbers of both putative parents and of the hybrid, co-occurring at the locality, further support this proposed origin: *H. glomeratum* occurs there predominantly as the pentaploid (less frequently also as the tetraploid), *H. lactucella* as the diploid. Pentaploid *H. glomeratum* forms triploid pollen (besides diploid and aneuploid ones – unpubl. results), so the tetraploid progeny may be a result of a simple hybridization event.

The plant resembles (but is not fully identical with!) *H. tubulascens* Norrl. This hybridogenous species was described and is known from Scandinavia. Gerstlauer and Zahn (in Zahn 1922–1930) described *H. t.* subsp. *aestivae* from Bavaria (Bayern: Bayerischer Wald, am Arber bei Sommerau). Soják (1971) considered the occurrence of *H. tubulascens* in Czechoslovakia as uncertain. For that reason, our report is the first one from the area of the Czech Republic supported by existing herbarium specimen.

No similar plant(s) has been recorded (or reported by other authors) in this mountain range. Of similar hybrids, the following two have been reported from the Krkonoše Mts: *H. dubium* L. (*H. cymosum* – *H. floribundum*) by Zahn (1922–1930) and *H. suecicum* Fr. (*H. floribundum* – *H. lactucella*) by Schneider (1888–1895).

We give a brief description of this plant: Stem 72 cm high, with scattered very short simple eglandular hairs and scattered stellate hairs, at the base purplish, with numerous 0.8–1.2 mm long simple eglandular hairs, in the upper part with scattered glandular hairs; leaves at upper surface nearly glabrous, only with a few hairs towards the margin, at the lower surface with scattered simple eglandular hairs and scattered stellate hairs, basal leaves (narrowly) oblanceolate, obtuse at apex, cauline leaves 3, narrowly oblanceolate to oblong acute; inflorescence compact, peduncles with scattered 0.8–1.3 mm long simple

eglandular hairs, scattered to numerous glandular hairs and dense stellate hairs; involucres 6.5–7.5 mm long, dark greyish–green, phyllaries with scattered simple eglandular and glandular hairs, and with scattered, towards the base numerous stellate hairs; styles yellowish (Fig. 4).

Supplementary data on species already published in Krahulcová & Krahulec (1999)

1. *Hieracium pilosella* L.

2n = 4x = 36, sexual.

Localities: **1**. Pec pod Sněžkou: the grassland area "Velká Pláň" in the northern part of the village, 830 m a.s.l., 50°41'50"N, 15°43'50"E. Coll. F. Krahulec 18. 6. 1999. 2n = 36 (6 plants), sexual (4 plants). **2**. Horní Malá Úpa, Pomezní Boudy: the meadow beside the road opposite to bus stop, ca. 160 m S of "Padolská bouda" chalet, 950 m a.s.l., 50°44'10"N, 15°48'00"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 36, sexual (2 plants). **3**. Pec pod Sněžkou, Velká Úpa: the eastern part of the grassland area "Přední Výsluní" close to woodland edge, ca. 1.3 km SEE of the church, 890 m a.s.l., 50°41'20"N, 15°47'30"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36, sexual (1 plant). **4**. Špindlerův Mlýn: in the meadow beside the touring path between "Petrova bouda" and "Moravská bouda" chalets, ca. 100 m NE of "Moravská bouda" chalet, 1240 m a.s.l., 50°46'10"N, 15°36'30"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 2. 7. 1999. 2n = 36, sexual (1 plant). **5**. Benecko: in the lawn in the central part of the village ca. 0.4 km W of the parking place, 800 m a.s.l., 50°40'00"N, 15°33'00"E. Coll. F. Krahulec and S. Bräutigam 2. 7. 1999. 2n = 36, sexual (1 plant). **6**. Benecko: the upper part of the meadow below "Jindrova skála" hill (the southern slope) in the southwestern periphery of the village, 770 m a.s.l., 50°39'50"N, 15°32'40"E. Coll. F. Krahulec and S. Bräutigam 2. 7. 1999. 2n = 36, sexual (1 plant).

The occurrence of tetraploid sexual *H. pilosella* in the Krkonoše Mts is confirmed, based on data from 16 plants from 8 localities (including those reported already in Krahulcová & Krahulec 1999). In addition, several pentaploid apomictic accessions closely resembling *H. pilosella* were found at the locality near Janovy Boudy, Velká Úpa. These plants occur at a disturbed site in a hybrid swarm, together with tetraploid sexual *H. pilosella* and tetraploid hybrids (probably between *H. pilosella* and *H. glomeratum* and *H. pilosella* and *H. piloselliflorum*). Their study will continue, especially with respect to morphology making possible the proper determination.

2. *Hieracium lactucella* Wallr.

2n = 2x = 18

Locality: **1**. Pec pod Sněžkou: the grassland area "Velká Pláň" in the northern part of the village, 830 m a.s.l., 50°41'50"N, 15°43'50"E. Coll. F. Krahulec 23. 9. 1999. 2n = 18 (2 plants).

3. *Hieracium caespitosum* Dumort.

2n = 4x = 36 with a long marker chromosome, apomictic.

Localities: **1**. Pec pod Sněžkou: in the meadow near the schoolhouse in the central part of the village, ca. 100 m NNW of the bus station, 780 m a.s.l., 50°41'40"N, 15°44'00"E. Coll. F. Krahulec 18. 6. 1999. 2n = 36 with marker chromosome, apomictic (1 plant). **2**. Horní Malá Úpa, Pomezní Boudy: the meadow beside the road opposite to bus stop, ca. 160 m S of "Padolská bouda" chalet, 950 m a.s.l., 50°44'10"N, 15°48'00"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 36 with marker chromosome, apomictic (1 plant).

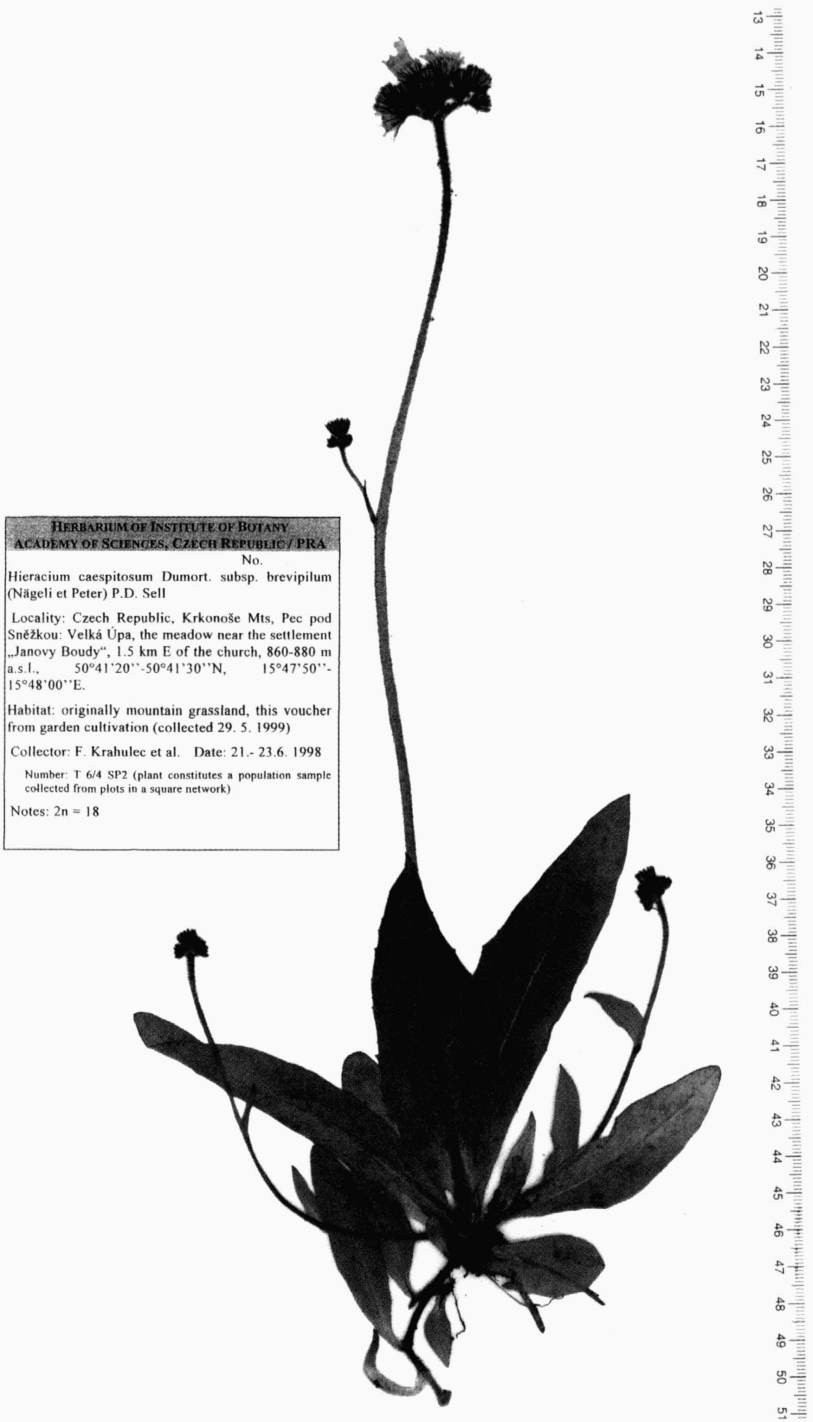

Fig. 3. – *Hieracium onegense* (Norrl.) Norrl.

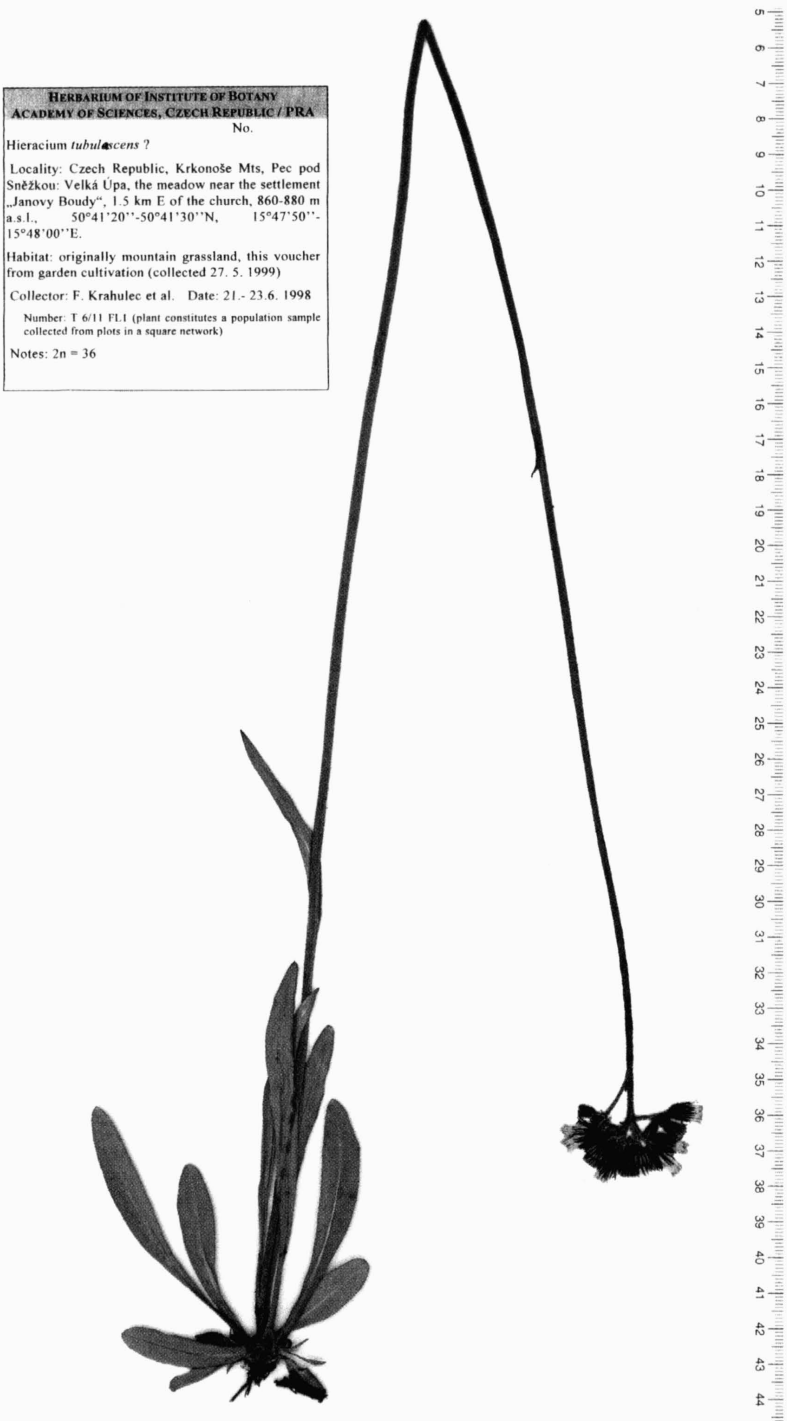

Fig. 4. – *Hieracium tubulascens* Norrl.

The apomictic reproduction was also recorded in a tetraploid plant (2n = 36) collected on Hnědý vrch (loc. no. 1 in Krahulcová & Krahulec 1999: 223).

4. *Hieracium aurantiacum* L.

2n = 4x = 36, apomictic.

Localities: **1**. Pec pod Sněžkou: Velká Úpa, grassland near the chalet "U Pašáka", at the hiking path above the Úpa river, 760 m a.s.l., 50°41'30"N, 15°44'40"E. Coll. F. Krahulec 18. 6. 1999. 2n = 36 (1 plant). **2**. Pec pod Sněžkou: the grassland "Velká Pláň" in the northern part of the village, 850 m a.s.l., 50°41'50"N, 15°43'40"E. Coll. F. Krahulec 18. 6. 1999. 2n = 36 (2 plants). **3**. Dolní Malá Úpa, Rennerovy Boudy settlement: the grassy place along the road margin above the "Moravanka" chalet in the northern periphery of the settlement, 1050 m a.s.l., 50°43'50"N, 15°49'10"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36 (1 plant). **4**. Dolní Malá Úpa: the meadow beside the road ca. 1 km S of the church, 880 m a.s.l., 50°42'50"N, 15°48'50"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36, apomictic (1 plant).

2n = 5x = 45, apomictic.

Localities: **1**. Pec pod Sněžkou: Velká Úpa, grassland near the chalet "Marienka", at the hiking path above the Úpa river, 720 m a.s.l., 50°41'20"N, 15°45'30"E. Coll. F. Krahulec 23. 6. 1998. 2n = 45 (1 plant). **2**. Pec pod Sněžkou: grassland in the settlement "Zadní Rennerovky", ca. 0.75 km SW of the chalet "Na Rozcestí", 1240 m a.s.l., 50°42'00"N, 15°40'00"E. Coll. F. Krahulec 3. 8. 1999. 2n = 45, apomictic (1 plant).

In addition, apomictic reproduction has been subsequently recorded in tetraploid plant from Horní Mísečky (loc. no. 1 in Krahulcová & Krahulec 1999: 224).

The literature on ploidy variation in the polyploid complex of *H. aurantiacum* have already been discussed (Krahulcová & Krahulec 1999). Based on our data, the tetraploid cytotype prevails in the Krkonoše Mts, and the pentaploids are rare.

5. *Hieracium schultesii* F. W. Schultz

H. pilosella – *H. lactucella*

2n = 4x = 36 (35 + fragment), apomictic.

Locality: **1**. Pec pod Sněžkou: the grassland area "Velká Pláň" in the northern part of the village, 830 m a.s.l., 50°41'50"N, 15°43'50"E. Coll. F. Krahulec 18. 6. 1999. 2n = 36 (2 plants); 2n = 35 + fragment, apomictic (1 plant).

In addition to a single tetraploid sexual plant already reported from the meadow near the settlement "Janovy Boudy" (loc. no. 2 in Krahulcová & Krahulec 1999: 225), two apomictic tetraploid accessions (2n = 36) were later recorded here as well. The tetraploid plant already reported from a disturbed place near "Padolská bouda" chalet (loc. no. 3 in Krahulcová & Krahulec 1999: 225) was found to be sexual.

This species, considered as a hybrid between two sexual putative parents, *H. lactucella* and *H. pilosella* (e.g. Sell & West 1975, Gadella 1992), is comprised of both sexual and apomictic accessions in the area studied (the tetraploids sexual or apomictic, a pentaploid apomictic – see also Krahulcová & Krahulec 1999). This fact suggests a more complicated evolutionary history than a simple cross between two sexual types, because all plants resulting from artificial crosses between *H. lactucella* and *H. pilosella* were triploid and sterile (unpublished results). One gene is responsible for inheritance of apomixis within

H. subgen. *Pilosella* (Bicknell et al. 2000); for that reason, an apomictic parent was probably involved in the origin of *H. schultesii* (we consider the mutation or the new rise of this gene as highly improbable). Till now, no apomictic clone of *H. pilosella* has been found within the Krkonoše Mts.

6. *Hieracium glomeratum* Froel.

H. caespitosum – H. cymosum

2n = 5x = 45 with a long marker chromosome, apomictic.

Localities: **1**. Dolní Malá Úpa: along the road ca. 0.7 km S of the church, 910 m a.s.l., 50°43'00"N, 15°48'40"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 45 with marker chromosome, apomictic (1 plant). **2**. Špindlerův Mlýn: "Slezské sedlo" saddle, a disturbed place beside the road along the Czech – Poland border ca. 1250 m NW of "Špindlerova bouda" chalet, 1180 m a.s.l., 50°45'55"N, 15°37'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 2. 7. 1999. 2n = 45 with marker chromosome (1 plant). **3**. Špindlerův Mlýn, "Davidovy Boudy" settlement: a disturbed place at the road margin close to "Davidova bouda" chalet, ca. 3.5 km N of the church in the town of Špindlerův Mlýn, 1020 m a.s.l., 50°45'30"N, 15°36'10"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 2. 7. 1999. 2n = 45 with marker chromosome (1 plant).

7. *Hieracium floribundum* Wimm. et Grab.

H. caespitosum > H. lactucella

2n = 2x = 18, sexual.

Locality: **1**. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 870 m a.s.l., 50°41'20"N, 15°47'40"E. Coll. F. Krahulec and A. Krahulcová 21. – 23. 6. 1998. 2n = 18 (6 plants), sexual (2 plants).

The diploid sexual *H. floribundum* is here reported for the first time. This species is considered as hybridogenous, originated from the cross between *H. lactucella* and *H. caespitosum* (incl. *H. onegense)* (Zahn 1922–1930, Skalińska 1967). As both the diploid putative parents were recorded at the same locality (see above and Krahulcová & Krahulec 1999), their spontaneous hybridization maintaining the diploid level may explain the origin of diploid *H. floribundum* here. This possibility is now under study by means of crossing experiments.

2n = 4x = 36 with a long marker chromosome, apomictic.

Localities: **1**. Horní Malá Úpa, Pomezní Boudy: the meadow in the grassland area "Mokré jámy", ca. 250 m NEE of the sharp bend on the road to Czech – Poland border, 1000 m a.s.l., 50°44'20"N, 15°48'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 36 with marker chromosome, apomictic (1 plant). **2**. Horní Malá Úpa, Pomezní Boudy: the grassy place beside the road opposite to ski-lift "Hybnerka", ca. 1.3 km SWW of the Czech – Poland border, 1010 m a.s.l., 50°44'30"N, 15°48'40"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 36 with marker chromosome, apomictic (1 plant). **3**. Špindlerův Mlýn: in the meadow beside the road along the Czech – Poland border, ca. 250 m E of "Petrova bouda" chalet, 1250 m a.s.l., 50°46'20"N, 15°37'00"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 2. 7. 1999. 2n = 36 with marker chromosome, apomictic (1 plant). This plant represents an intermediate morphotype between *H. floribundum* and *H. caespitosum*. **4**. Pec pod Sněžkou: Velká Úpa, a meadow along the ski-lift to Portášovy Boudy (the southern slope), ca. 50 m E of "Danielka" chalet, 1 km SSE of the church, 900 m a.s.l., 50°41'50"N, 15°46'10"E. Coll. F. Krahulec, A. Krahulcová and J. Chrtek 29. 6. 2000. 2n = 36 with marker chromosome (1 plant).

8. *Hieracium iseranum* Uechtr.

H. floribundum > *H. pilosella*

2n = 5x = 45, apomictic.

Locality: **1**. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 870 m a.s.l., 50°41'20"N, 15°47'40"E. Coll. F. Krahulec and A. Krahulcová 21. – 23. 6. 1998. 2n = 45, apomictic (1 plant).

In the course of a population study, only a single pentaploid accession of *H. iseranum* was recorded at this locality in contrast to many tetraploids (total of 81 tetraploid accessions). No marker chromosome has been found in the pentaploid chromosome set. On the other hand, it was recorded in 80 tetraploid accessions collected in this locality, as well as in a tetraploid *H. iseranum* originated from other localities in the Krkonoše Mts (Krahulcová & Krahulec 1999: 228).

9. *Hieracium apatelium* Nägeli et Peter

H. floribundum – *H. pilosella*

2n = 4x = 36, sexual or apomictic, 2n = 5x = 45, apomictic.

Total of 13 tetraploid (2n = 36) accessions were recorded in the population near the settlement of "Janovy Boudy" (loc. no. 2 in Krahulcová & Krahulec 1999: 228), comprised of 3 sexual and 10 apomictic plants. In addition, one pentaploid apomictic accession of this species was recorded here.

10. Hieracium piloselliflorum Nägeli et Peter

H. floribundum < *H. pilosella*

2n = 4x = 36, sexual or apomictic.

Localities: **1**. Dolní Malá Úpa: the meadow beside the road ca. 0.5 km S of the church, 950 m a.s.l., 50°43'20"N, 15°48'40"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36 (2 plants), apomictic (1 plant). **2**. Dolní Malá Úpa: the meadow beside the road ca. 1 km S of the church, 880 m a.s.l., 50°42'50"N, 15°48'50"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36 (2 plants), sexual (1 plant). **3**. Pec pod Sněžkou: Velká Úpa, a disturbed grassy place between the playground and the road in the settlement "Janovy Boudy", 1.2 km E of the church, 910 m a.s.l., 50°41'30"N, 15°47'30"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 36 (1 plant). **4**. Špindlerův Mlýn: "Slezské sedlo" saddle, in the meadow beside the hiking path along the Czech – Poland border ca. 0.8 km NWW of "Špindlerova bouda" chalet, 1200 m a.s.l., 50°45'50"N, 15°37'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 2. 7. 1999. 2n = 36 (1 plant).

2n = 5x = 45, apomictic.

Localities: **1**. Horní Malá Úpa, Pomezní Boudy: the grassy places beside the road opposite to the ski-lift "Hybnerka" and in the lower part of the ski-lift, ca. 1.3 km SWW of the Czech – Poland border crossing, 1010–1020 m a.s.l., 50°44'30"N, 15°48'40"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 45 (3 plants), apomictic (2 plants). **2**. Dolní Malá Úpa, Rennerovy Boudy settlement: the ski-piste in the eastern part of the grassland area, 1060 m a.s.l., 50°43'40"N, 15°49'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek

1. 7. 1999. 2n = 45, apomictic (1 plant). **3**. Dolní Malá Úpa: the meadow beside the road ca. 1 km S of the church, 880 m a.s.l., 50°42'50"N, 15°48'50"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 45, apomictic (1 plant). **4**. Špindlerův Mlýn: in the meadow at "Novopacká bouda" chalet ca. 0.8–0.9 km SW of Czech – Poland border, 1190–1200 m a.s.l., 50°46'00"N, 15°36'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 2. 7. 1999. 2n = 45 (2 plants), apomictic (1 plant). **5**. Benecko: the upper part of the meadow below "Jindrova skála" hill (the southern slope) in the southwestern periphery of the village, 770 m a.s.l., 50°39'50"N, 15°32'40"E. Coll. F. Krahulec and S. Bräutigam 2. 7. 1999. 2n = 45, apomictic (1 plant).

2n = 6x = 54, apomictic.

Localities: **1**. Dolní Malá Úpa, Rennerovy Boudy settlement: the ski-piste in the eastern part of the grassland area, 1060 m a.s.l., 50°43'40"N, 15°49'20"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 54, apomictic (1 plant). **2**. Dolní Malá Úpa: the meadow beside the road ca. 1 km S of the church, 880 m a.s.l., 50°42'50"N, 15°48'50"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 1. 7. 1999. 2n = 54, apomictic (1 plant).

A population sample collected in the meadow near the settlement "Janovy Boudy" (loc. no. 2 in Krahulcová & Krahulec 1999: 229) was examined in detail with respect to ploidy level and reproductive system. A total of 22 tetraploid (2n = 36), 32 pentaploid (2n = 45) and 3 hypopentaploid (2n = 44) accessions were recorded. Whereas only apomicts were found among pentaploid (21 plants examined) and hypopentaploid accessions (1 plant examined), both the sexual (7 plants examined) and the apomictic plants (12 plants examined) were recorded among the tetraploids. Apomictic reproduction was also confirmed in a pentaploid plant collected near the former "Obří bouda" chalet (loc. no. 1 in Krahulcová & Krahulec 1999: 229)

11. *Hieracium stoloniflorum* Waldst. et Kit.

H. aurantiacum < *H. pilosella*

2n = 5x = 45, the reproductive system under study.

Locality: **1**. Horní Malá Úpa, Pomezní Boudy: the meadow beside the road opposite to bus stop, ca. 160 m S of "Padolská bouda" chalet, 950 m a.s.l., 50°44'10"N, 15°48'00"E. Coll. F. Krahulec, S. Bräutigam and J. Chrtek 30. 6. 1999. 2n = 45 (1 plant).

Two hexaploid plants (2n = 54) collected in two localities have been reported from the Krkonoše Mts (Krahulcová & Krahulec 1999). The study of additional plants from this mountain area showed a diversity in ploidy level (both the pentaploid and the hexaploid cytotypes occur here). A total of three hexaploid accessions were collected in the meadow near "Janovy Boudy" settlement (loc. no. 2 in Krahulcová & Krahulec 1999: 229), all proved to be apomictic. For the ploidy level variation reported from other parts of the distribution area see Krahulcová & Krahulec (1999).

12. *Hieracium rubrum* Peter

H. flagellare – *H. aurantiacum*

2n = 6x = 54, apomictic.

Locality: **1**. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 870 m a.s.l., 50°41'20"N, 15°47'40"E. Coll. F. Krahulec and A. Krahulcová 21. – 23. 6. 1998. 2n = 54, apomictic (1 plant).

The hexaploid level is in agreement with previously published data from other localities (Krahulcová & Krahulec 1999: 230).

General discussion

The present and previous papers (Krahulcová & Krahulec 1999) give an overview of chromosome numbers and reproductive systems for all members of *Hieracium* subgen. *Pilosella* which are at present known from the Krkonoše Mts. This fact allows us to evaluate the richness of this subgenus in the Krkonoše Mts with respect to species diversity in chromosome numbers and reproductive systems. In our opinion, these two factors are responsible for the high species richness characteristic of this mountain range. The species set has the following structure with respect to their ploidy level:

Diploid: *H. lactucella, H. onegense (H. caespitosum* subsp. *brevipilum), H. floribundum*
Tetraploid: *H. pilosella, H. caespitosum, H. aurantiacum, H. pilosselliflorum, H. apatelium, H. iseranum, H. floribundum, H. glomeratum, H. schultesii, H. blyttianum, H. fuscoatrum, H. tubulascens;*
Pentaploid: *H. aurantiacum, H. bauhini, H. pilosselliflorum, H. apatelium, H. iseranum, H. glomeratum, H. stoloniflorum, H. schultesii*;
Hexaploid: *H. pilosselliflorum, H. apatelium, H. rubrum, H. stoloniflorum, H. macrostolonum.*

With respect to reproductive system, the following species were found to be fully sexual: *H. lactucella, H. pilosella, H. onegense, H. floribundum* (diploid). The tetraploid cytotypes of some other species were recorded as both sexual and apomictic within the area studied: *H. pilosselliflorum, H. apatelium*, and *H. schultesii*. All other species (and cytotypes with higher ploidy levels than tetraploids) were found as apomictic. All of them might be rarely sexual, because apospory does not result in obligate apomixis (for the review see Krahulcová et al. 2000). In addition, all cytotypes may serve as pollen donors.

In the area studied, the following basic species (in the sense of authors from central Europe) occur: *H. lactucella, H. pilosella, H. caespitosum, H. onegense, H. bauhini* and *H. aurantiacum*. Except of *H. bauhini*, which is not regular member of the flora of the range studied, all other species are involved in the hybridogeneous types. In our opinion, the high number of basic species (regularly 5) and also the high number of sexual types (7!) are the important factors responsible for the richness of all other types occurring in the field. The share of hybridogenous taxa originated within the Krkonoše Mts remains unknow. It is also unknown if the process of active evolution of new types is still going on. Isozyme studies show that there is a high variation in the number of genotypes among the particular taxa: some of them are represented by many genotypes, some by single ones (Krahulec et al. ms., and unpublished data). This suggests that at least some of the genotypes originated locally. The discovery of *H. fuscoatrum* at Pomezní Boudy (Grenzbauden) suggests its recent origin there, as this locality has been studied many times over the last 130 years. In addition, the prevailing local origin of hybridogenous species may be supported by absence of those hybridogenous species having other parents which do not occur within this mountain range. The only exception is *H. glomeratum*; its putative parent, *H. cymosum*, is not present in the mountains now.

Some questions remain unexplained: for example, the low frequency of aneuploids, the absence of triploids, or absence of hybrids with *H. aurantiacum* in the western part of the mountain range. We hope a deeper understanding into the processes going at the population level may help us to understand the processes responsible for the observed taxonomic pattern.

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Souhrn

Tato práce je druhou studií pojednávající o chromosomových počtech a reprodukčních systémech jestřábníků (*Hieracium* subgen. *Pilosella*) vyskytujících se v Krkonoších. Výsledky je možno shrnout takto: a) v Krkonoších dosud nestudované druhy: *H. fuscoatrum* Nägeli et Peter (2n = 36, apomiktický), *H. blyttianum* Fr. (2n = 36, apomiktický), *H. tubulascens* Norrl. (2n = 36, apomiktický), *H. bauhini* Besser (2n = 45, apomiktický), *H. onegense* (Norrl.) Norrl. (*H. caespitosum* Dumort. subsp. *brevipilum* (Nägeli et Peter) P. D. Sell) (2n = 18, sexuální); b) nové cytotypy zjištěné v Krkonoších: *H. floribundum* Wimm. et Grab. (2n = 18, sexuální), *H. apatelium* Nägeli et Peter (2n = 45, apomiktický), *H. iseranum* Uechtr. (2n = 45, apomiktický), *H. aurantiacum* L. (2n = 45), *H. stoloniflorum* Waldst. et Kit. (2n = 45); c) doplňková data ke dříve zjištěným počtům: *H. pilosella* L. (2n = 36, sexuální), *H. lactucella* Wallr. (2n = 18), *H. caespitosum* Dumort. (2n = 36, apomiktický), *H. aurantiacum* L. (2n = 36, apomiktický), *H. schultesii* F.W. Schultz (2n = 36, apomiktický), *H. glomeratum* Froel. (2n = 45, apomiktický), *H. floribundum* Wimm. et Grab. (2n = 36, apomiktický), *H. piloselliflorum* Nägeli et Peter (2n = 36, sexuální i apomiktický, 2n = 45, apomiktický, 2n = 54, apomiktický). Počty chromosomů byly poprvé zjištěny pro *H. fuscoatrum* a *H. tubulascens*, nové počty jsou uvedeny pro *H. floribundum, H. apatelium* a *H. iseranum*. Významný je nález diploidního sexuálního typu druhu *H. floribundum*, který byl dosud znám pouze v apomiktické triploidní nebo tetraploidní formě. Přítomnost velkého marker chromosomu v karyotypu byla nově zaznamenána u *H. bauhini* a *H. tubulascens*.

Jako nové druhy pro území České republiky a i pro celé Krkonoše (včetně polské části) jsou poprvé uvedeny *H. fuscoatrum* a *H. tubulascens*.

V závěrečné diskusi jsou rozebrány příčiny velkého druhového bohatství jestřábníků podrodu *Pilosella* v Krkonoších. K těmto příčinám nepochybně patří vysoký počet základních druhů (4) a též vysoký počet druhů se sexuálním rozmnožováním (7). Tyto skutečnosti umožňují vznik vysokého počtu hybridogenních druhů. Pro většinu z nich se dá předpokládat, že vznikly přímo na území Krkonoš.

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