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

Počty chromozómů a reproduktivní systémy vybraných zástupců jestřábníků (*Hieracium* subgen. *Pilosella*) Krkonoš

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Dedicated to František Procházka on the occasion of his 60th birthday

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Chromosome numbers and reproductive systems are given for the following taxa of *Hieracium* subgen. *Pilosella* occurring in the Krkonoše Mts: *H. pilosella* L. (2n = 36, sexual), *H. lactucella* Wallr. (2n = 18, sexual), *H. caespitosum* Dumort. (2n = 36, the mode of reproduction unknown), *H. aurantiacum* L. (2n = 36, apomictic), *H. schultesii* F.W. Schultz (2n = 36, sexual; 2n = 45, apomictic), *H. macrostolonum* G. Schneider (2n = 54, the mode of reproduction unknown), *H. glomeratum* Froel. (2n = 36, 45, both apomictic), *H. floribundum* Wimm. et Grab. (2n = 36, apomictic), *H. iseranum* Uechtr. (2n = 36, apomictic), *H. apatelium* Nägeli et Peter (2n = 36, both sexual and apomictic; 2n = 54, apomictic), *H. piloselliflorum* Nägeli et Peter (2n = 36, the mode of reproduction unknown; 2n = 45, 44, apomictic; 2n = 54, apomictic), *H. stoloniflorum* Waldst. et Kit. (2n = 54, apomictic), *H. rubrum* Peter (2n = 54, apomictic). Chromosome numbers are reported for the first time for *H. apatelium, H. iseranum,* and *H. piloselliflorum*, a new chromosome number was determined for *H. macrostolonum* and *H. schultesii*. The group of species (*H. caespitosum, H. glomeratum, H. floribundum, H. iseranum*) has been found to have a single long marker chromosome in the karyotype; this fact supports the view of their relationship. The mode of reproduction is here examined for the first time in polyploid hybridogenous species *H. iseranum, H. apatelium, H. piloselliflorum, H. stoloniflorum, H. rubrum* and *H. schultesii* from nature; the apomictic reproduction of tetraploid *H. floribundum* and of pentaploid *H. glomeratum* is also a new information. The variation of *Hieracium* subgen. *Pilosella* in the Krkonoše Mts is discussed in connection with the presence of at least four sexual types and diversity of reproductive systems. The occurrence of *H. stoloniflorum* in the Krkonoše Mts is dealt with.

K e y w o r d s : *Hieracium* subgen. *Pilosella*, chromosome numbers, reproductive systems, Krkonoše Mts, Czech Republic

Introduction

The genus *Hieracium* belongs to one of the most taxonomically intractable group of temperate flora. The subgenus *Pilosella* (sometimes considered as a separate genus) is characterized by the following features:

1. the occurrence of several ploidy levels (based on x = 9) in approximately half of the species (Schuhwerk 1996), with a diverse mode of reproduction: diploids are sexual (i. e. amphimictic), tetraploids and hexaploids are both sexual and apomictic,

pentaploids and heptaploids are apomictic, while triploids of hybridogenous origin are as a rule apomictic or sterile (Skalińska 1967, Gadella 1987, 1991a, b);
2. common hybridization between species is connected with the rise of both sexually and apomictically reproducing hybrids (Gadella 1982, 1987, 1992);
3. the aposporic type of apomixis (Rosenberg 1906, 1907, Pogan & Wcisło 1989) and the ability of apomicts to produce fertile pollen, which makes their further hybridization possible (Skalińska 1971a, Gadella 1982, 1987). In addition, several representatives of this subgenus have been proven to be facultative apomicts, being able to take part in hybridization also as seed parent, owing to fertilization of either reduced or unreduced egg cells (Skalińska 1973, 1976, Gadella 1982, 1988).
4. all types have more or less clonal growth, allowing them quick spread and survival even without seed production (e. g. Turesson & Turesson 1960, Gadella 1987, 1991a, b).

The area of the Krkonoše Mts (Riesengebirge in German, Karkonoszy in Polish) is famous with respect to the occurrence of many types (Schneider 1889–1890), supposed to be of hybridogenous origin. Many taxa have been described from this area (e. g. *H. rubrum* Peter, *H. rubripilosella* G. Schneider, *H. piloselliflorum* Nägeli et Peter, *H. sudetorum* (Peter) Weiss, *H. macrostolonum* G. Schneider), or the localities from this mountain range were included within a set of localities given in original description (*H. iseranum* Uechtr., *H. apatelium* Nägeli et Peter). The montane meadows in the eastern part of this mountain range are especially famous for richness of *Hieracium* flora (e. g. Fiek 1881, Schneider 1889–1890, Zahn 1930). The reasons for the high richness of the *Hieracium* flora of this region is unknown. One of the reasons could be related to the co-occurrence of several sexual types, which were at least in the past able to hybridize and to produce many hybridogenous taxa. To answer this question we started to study the populations of *Hieracium* subgen. *Pilosella*; their chromosome numbers and reproductive systems are of special interest, because they influence the ability to hybridize.

Plants used for study

The plants were collected in the field in June and July, during the flower period. They were transplanted to the lowland experimental garden in Průhonice, where the pollination experiments were carried out in subsequent flowering seasons. All localities (collecting sites) given below are situated in the Krkonoše Mts in north-eastern Bohemia; they are ordered from west to east. Their coordinates are determined with the accuracy to ten seconds. Because the area studied is mentioned many times in classic papers on *Hieracium* (e. g. Schneider 1889–1890, Zahn 1930), German names of all localities are also given in brackets. The voucher specimens deposited in the Institute of Botany in Průhonice are based on material cultivated in the garden.

The taxonomic concept follows an intermediate approach common for the plants of the Sudeten Mts; the taxa are designated as species in the case of both basic species (Hauptarten) and species of hybridogenous origin (Zwischenarten). However, we are aware of the fact that the latter category involves repeating old apomictic types as well as the products of recent hybridization. Even some of the sexual types of corresponding morphology are included here. Each species with supposed hybridogenous origin is given a

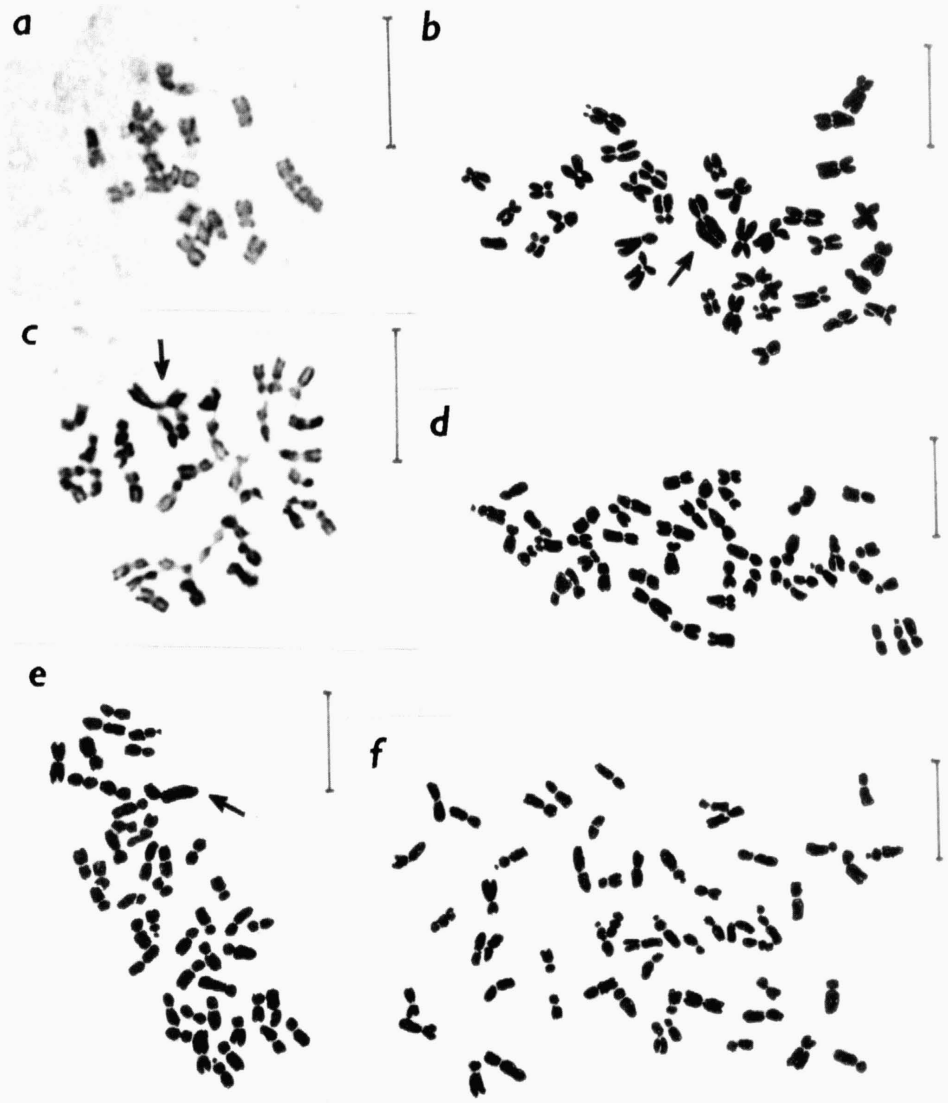
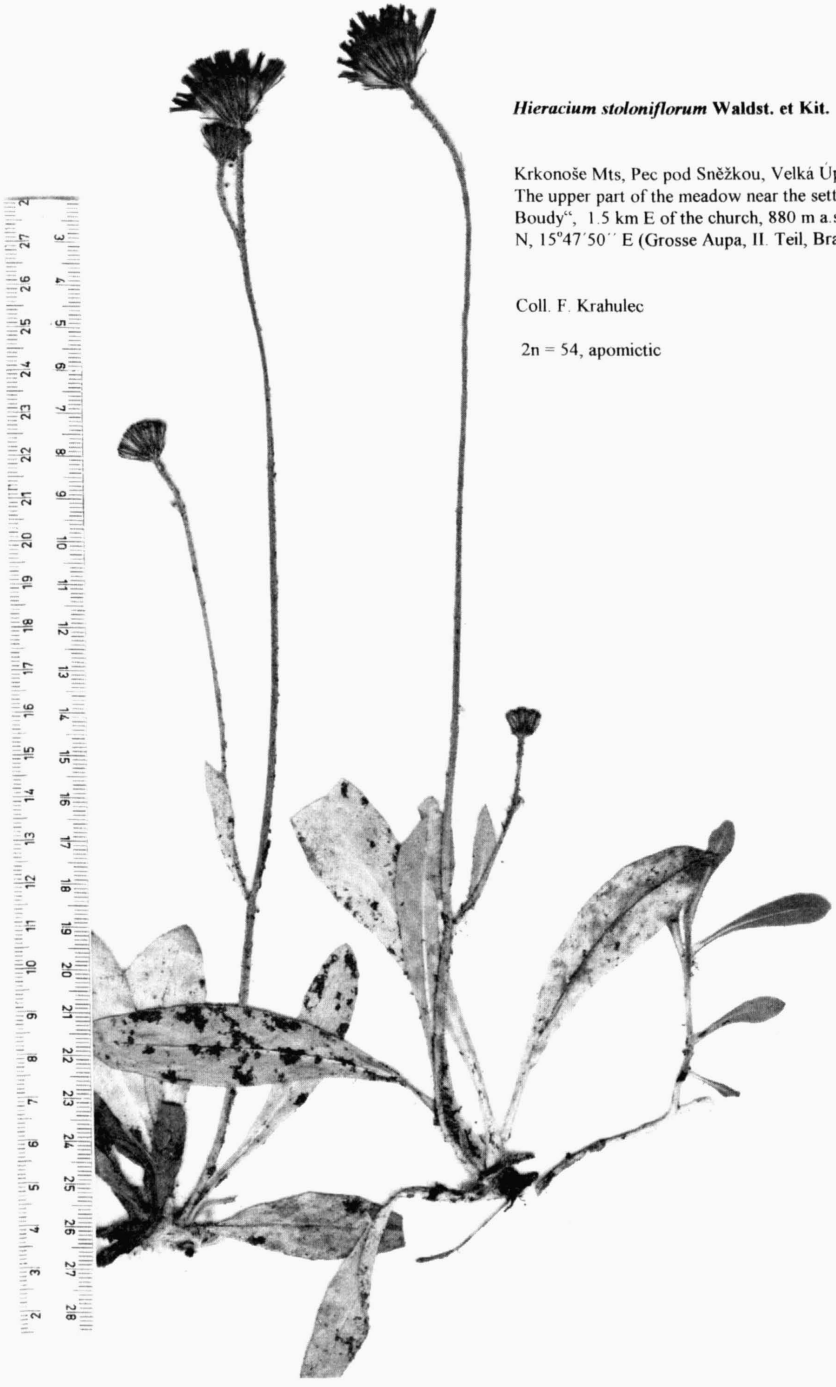


Fig. 1. – Somatic metaphases (a, c – microphotographs; b, d, e, f – drawings) in six species of *Hieracium* subgen. *Pilosella* – a: *Hieracium lactucella* Wallr., 2n = 18; b: *Hieracium floribundum* Wimm. et Grab., 2n = 36; c: *Hieracium iseranum* Uechtr., 2n = 36; d: *Hieracium piloselliflorum* Nägeli et Peter, 2n = 45; e: *Hieracium glomeratum* Froel., 2n = 45; f: *Hieracium rubrum* Peter, 2n = 54. The long marker chromosome (arrowed) is noticable in *H. floribundum* (b), *H. iseranum* (c) and *H. glomeratum* (e). The first five species (a – e) originated in the locality near Janovy boudy (for its detailed description see in text e. g. to *H. lactucella*, loc. 1); *H. rubrum* (f) was collected at Pomezní Boudy (loc. 3 in the text). [Scale bars = 10 mm].



***Hieracium stoloniflorum* Waldst. et Kit.**

Krkonoše Mts, Pec pod Sněžkou, Velká Úpa.
The upper part of the meadow near the settlement „Janovy Boudy", 1.5 km E of the church, 880 m a.s.l., 50°41´30´´ N, 15°47´50´´ E (Grosse Aupa, II. Teil, Braunboden).

Coll. F. Krahulec 26. 6. 1997.

2n = 54, apomictic

Fig. 2. – *Hieracium stoloniflorum*.

formula indicating its position between the basic species according to morphological characters; certainly, it might (but need not) indicate their origin. Most species were determined with the help of participants of the International Workshops on *Hieracium* Taxonomy in 1997 and 1998, namely of F. Schuhwerk (München) and S. Bräutigam (Görlitz). A part of the material was collected directly during common excursions; these plants are indicated by abbreviation HWE at the names of collectors.

Cytological techniques

The chromosome counts are based on somatic mitoses in root-tips of potted plants, cultivated in the garden. Root-tips were pretreated with a saturated solutions of α-bromonaphtalene or para-dichlorbenzene for 3 hours at room temperature, rinsed in water and fixed in cold acetic-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 the reproductive systems

The mode of reproduction was determined following the procedure used by Gadella (1987). The capitula of each plant examined were treated as follows: a) they were left to open-pollinate (all species studied were grown together and most of them flowered simultaneously during 5–6 weeks in May and June); b) the unopened capitula before anthesis (in the stage, when the colour of outer florets is clearly evident) were emasculated and isolated in nylon mesh bags. The emasculation was carried out by cutting off the whole upper half of the capitulum by a razor blade. The seeds were counted usually in five open-pollinated and five emasculated heads of each plant except for cases where the number of flowering heads per plant was not adequate, or where the developing seeds were damaged by insects. For this reason, the pollination experiments were carried out in two or three flowering seasons, to get satisfactory data for all plants studied. The comparison between the seed-set in open-pollinated versus emasculated heads makes it possible to determine the amphimictic (seeds develope in open-pollinated heads only) and apomictic reproduction (seeds develope after both types of pollination treatment). The sterile plants do not develope seeds at all. A difference between seed-set in the open-pollinated versus emasculated heads of the same plant might (but need not) indicate a significant participation in sexual reproduction (in so called amphi-apomictic types), which can be proved by hybridization experiments. Such detailed comparison was not performed in this study; we refer the cytotype to be apomictic if well developed seeds were present in its emasculated heads.

Results and discussion to particular species

1. *Hieracium pilosella* L.

Linnaeus, Sp. Pl. 800, 1753.

2n = 4x = 36, sexual.

Localities:

1. Vítkovice: Horní Mísečky, along the road (road margin) ca 0.5 km NNW of the settlement, 1070 m a. s. l., 50°44'20"N, 15°33'50" E (Schüsselbauden). Coll. F. Krahulec and A. Krahulcová, HWE 15. 7. 1997. 2n = 36, sexual (1 plant).
2. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860 m a. s. l., 50°41'20" N, 15°48'00" E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995. 2n = 36, sexual (3 plants).

This most thoroughly cytologically examined species of the subgen. *Pilosella* displays a considerable variability in chromosome numbers. Five ploidy levels (2x, 4x, 5x, 6x and 7x) occur in natural populations in Europe; in addition, the higher levels (9x and 10x) were found in plants obtained from experimental hybridization between cytotypes (Gadella 1982, 1987). Triploids are known as interspecific hybrids only (Gadella 1991b). Both the tetraploids and pentaploids are most widespread in Europe, the sexual tetraploids being more common in the lowlands of Western and Central Europe, while the apomictic pentaploids are more frequent in Northern Europe and at higher altitudes in the mountains (Gadella 1987). The rare occurrence of sexual diploids in the French and Italian Alps has a relict character (Gadella 1972, 1984). The hexaploids were found mainly in the Alps (Italy, France, Switzerland), but they were also discovered to be scattered in the lowlands. Heptaploids are rare in Europe, being found only in Sweden and in the Netherlands. For the details concerning the distribution of particular cytotypes in Europe and their reproductive systems see Gadella (1972, 1984) and Pogan & Wcisło (1989); for the distribution map of cytotypes Gadella (1972: 364 and 1991a: 458). Although the particular cytotypes of *H. pilosella* with different mode of reproduction (namely the sexual tetraploids and the apomictic pentaploids) may grow in close proximity, they occur only rarely intermingled within one population (Gadella 1987).

Chromosome numbers in this polymorphic species from the Krkonoše Mts were unknown hitherto. The nearest locality (about 90 km distant from the Krkonoše Mts), from where this species has already been studied karyologically, is situated in the southeastern part of the Sudeten Mts in Poland; the tetraploids (2n = 36) are reported from there (Skalińska, Pogan et al. 1971). Our specimens collected in two localities in the Krkonoše Mts have the same chromosome number and proved to be sexual. This corresponds to references concerning the reproductive system in *H. pilosella*: the tetraploids are usually sexual, except for rare hybrids with apomictic cytotypes (e. g. Gadella 1984, Pogan & Wcisło 1995), and self-incompatible (Gadella 1984). On the other hand, all cytotypes (including the tetraploids) occurring in the New Zealand are apomictic (Chapman pers. commun.). Our finding of tetraploids in the Krkonoše Mts (at altitudes 860 m and 1070 m) is rather contradictory to conclusions of Gadella (1987), who reports the tetraploids occurring mainly in lowlands and pentaploids at higher altitudes in the Central Europe.

2. *Hieracium lactucella* Wallr.

Wallroth, Sched. Crit. 1: 408, 1822. [Syn.: *H. auricula* auct.]

2n = 2x = 18 (Fig. 1a), 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, 860 m a. s. l., 50°41'20"N, 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995. 2n = 18 (4 plants), sexual (3 plants).

The diploid chromosome number (2n = 18) and sexual mode of reproduction are recorded for plants from different parts of the distribution area of this species, e. g. from Sweden, Austria (Turesson & Turesson 1960), Poland (Skalińska 1967), France, the Netherlands and Switzerland (Gadella 1984). Based on pollination experiments, *H. lactucella* is self-incompatible (Gadella 1984). The recent report by Schuhwerk & Lippert (1997) from Germany-Bavaria confirms the diploid level in *H. lactucella* as well. As this species hybridizes easily (e. g. Ostenfeld 1910, Gadella 1987), the strange triploid plants reported from Corse by Contandriopoulos (1957, 1962) might be of hybrid origin.

3. *Hieracium caespitosum* Dumort.

Dumortier, Florulae Belg. Prodr. 62, 1827. [Syn.: *Hieracium pratense* Tausch]

2n = 4x = 36 with a long marker chromosome, the reproductive system not examined hitherto.

Locality:

1. Pec pod Sněžkou, the lower part of the meadow on Hnědý vrch, 1.5 km SW of the centre of Pec, near the chalet "Banka", 910 m a. s. l., 50°41'20"N, 15°43'10"E (Grosse Aupa, III. Teil, Braunberg). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 36 with marker chromosome (1 plant).

Four ploidy levels (2x, 3x, 4x and 5x) are known within this species, most of the data referring to natural populations in Poland (Skalińska 1967, Skalińska et al. 1968, Skalińska & Kubień 1972). Tetraploids prevail in this country, triploids and pentaploids were rarely found. Some authors distinguished the diploid cytotype in this area as a separate subspecies *H. pratense* subsp. *silvicolum* Zahn (= *H. onegense* (Norrl.) Norrl., viz. Skalińska & Kubień 1972), which tends to occur in the eastern part of the distribution area of the species. Another diploid type, reported under the name of *H. caespitosum* subsp. *brevipilum* (Nägeli & Peter) P. D. Sell, was recently found in northern Greece (Schuhwerk & Lippert 1998). The other karyological data refer to the occurrence of pentaploids in Sweden (Turesson & Turesson 1963, the plants under the name of *H. subdimorphum* Norrl.) and in Germany-Saxonia (Bräutigam & Bräutigam 1996); the tetraploids are reported from Austria, the Netherlands (Gadella 1984) and also from Germany-Bavaria (Schuhwerk & Lippert 1997). Both the tetraploids and pentaploids were found in New Zealand (Jenkins & Jong 1997), where *H. caespitosum* occurs as an alien species. The presence of remarkable single long chromosome, resembling the marker chromosome observed by us in the plant from the Krkonoše Mts, is pointed out by these authors in the pentaploid cytotype (2n = 45) from New Zealand (Jenkins & Jong 1997).

Concerning the reproductive system, the diploid subsp. *silvicolum* reproduces sexually while the tetraploid cytotype is a facultative apomict (Skalińska 1967, Skalińska & Kubień 1972, Gadella 1984). The pentaploid plants from Sweden mentioned above displayed amphi-apomictic reproduction (Turesson & Turesson 1963), i. e. they were facultative apomicts.

4. *Hieracium aurantiacum* L.

Linnaeus, Sp. Pl. 801, 1753.

2n = 4x = 36, apomictic.

Localities:

1. Vítkovice: Horní Mísečky, disturbed places near the chalet "Cáchovna", 1060 m a. s. l., 50°44'10"N, 15°34'10"E (Schüsselbauden). Coll. F. Krahulec and A. Krahulcová , HWE 15. 7. 1997. 2n = 36 (1 plant).
2. Pec pod Sněžkou, the lower part of the meadow on Hnědý vrch, 1.5 km SW of the centre of Pec, near the chalet "Banka", 910–920 m a. s. l., 50°41'20"N, 15°43'10"E (Grosse Aupa, III. Teil, Braunberg). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 36 (2 plants), apomictic (1 plant).
3. Pec pod Sněžkou: Velká Úpa, road margin in the southern part of the "Hlušiny" ca. 1 km S of the church, 930 m a. s. l., 50°40'50"N, 15°46'30"E (Grosse Aupa, I. Teil, Totenboden). Coll. F. Krahulec 20. 6. 1998. 2n = 36 (1 plant).
4. Pec pod Sněžkou: Velká Úpa, the eastern part of the area "Prostřední Výsluní", road margin on the woodland edge 1 km ENE of the church, 900 m a. s. l., 50°41'40"N, 15°47'10"E (Grosse Aupa, II. Teil). Coll. F. Krahulec and A. Krahulcová, HWE 15. 7. 1997. 2n = 36, apomictic (1 plant).
5. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860 m a. s. l., 50°41'20"N, 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995. 2n = 36 (4 plants), apomictic (2 plants).
6. Horní Malá Úpa, Pomezní Boudy, grassland near the "Padolská bouda" chalet, 2 km SW of the Czech-Polish border crossing, 960 m a. s. l., 50°44'20"N, 15°48'10"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 36 (1 plant).
7. 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 (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 36 (1 plant).

Five ploidy levels (from triploid to heptaploid) comprise the polyploid complex of *H. aurantiacum*. All the cytotypes are reported to occur in natural populations in Poland (Skalińska 1967, 1970, Skalińska et al. 1968), but the triploid *H. aurantiacum* was found only once. Tetraploids and pentaploids are most frequent in Poland: both the cytotypes occur separately in the Western Carpathians, in the Bieszczady Mts (Eastern Carpathians) tetraploids prevail; only pentaploids were found in the Tatra Mts. Both the hexaploids and heptaploids have a local importance only. The prevailing tetraploid plants beside pentaploids and hexaploids are reported from Hautes-Alpes in France (Delcourt 1977). Tetraploids also prevail among karyological references concerning the other parts of the distribution area of *H. aurantiacum* (Schuhwerk 1996, Schuhwerk & Lippert 1997), including New Zealand, where this species has been introduced probably from the British Isles (Jenkins & Jong 1997). As can be suggested from our data, only this tetraploid cytotype likely occurs in the Krkonoše Mts as well. Ploidy levels higher than 7x can be achieved in this species by experimental hybridization, but these cytotypes probably do not survive in nature (Skalińska 1973, 1976).

The amphimictic types (i. e. obligatory sexuals) are unknown in this polyploid complex: the facultative apomixis is a common mode of reproduction in all cytotypes (e. g. Ostenfeld 1906, Skalińska 1971a, b, 1973). The participation of sexuality in seed reproduction is especially pronounced in those cytotypes having even chromosome numbers.

5. *Hieracium schultesii* F. W. Schultz

F. W. Schultz, Arch. Fl. Fr. Allem. 35, 1842.
H. lactucella – H. pilosella

2n = 4x = 36, amphimictic; 2n = 5x = 45, apomictic.

Localities:

1. Vítkovice: Horní Mísečky, disturbed grassland near the chalet "Cáchovna", 1060 m a. s. l., 50°44'10"N, 15°34'10"E (Schüsselbauden). Coll. F. Krahulec and A. Krahulcová, HWE 15. 7. 1997. 2n = 45, apomictic (1 plant).
2. Pec pod Sněžkou: Velká Úpa, central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860 m a. s. l., 50°41'20"N, 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 26. 6. 1997. 2n = 36, sexual (1 plant).
3. Horní Malá Úpa: Pomezní Boudy, disturbed place at the parking place S of "Padolská bouda" chalet, 950 m a. s. l., 50°44'10"N, 15°48'10"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 36 (1 plant).

This species links together some morphological characters of *H. pilosella* and *H. lactucella* (Zahn 1930) and it is considered as a spontaneous hybrid between these species (e. g. Sell & West 1975). The chromosome numbers published hitherto in *H. schultesii* correspond indeed to the triploid level (2n = 27), i. e. to a simple hybrid between the tetraploid *H. pilosella* and diploid *H. lactucella*. These data refer to plants from Corse, where the endemic subsp. *soleirolianum* Arv.-Touv. & Briq. occurs (Contandriopoulos 1957, 1962), and to plants from Germany-Bavaria (Schuhwerk & Lippert 1997).

According to first results of our study, *H. schultesii* appears to be divided in the Krkonoše Mts into two ploidy levels (tetraploid and pentaploid). The origin of these cytotypes based on simple hybridization between parental amphimictic species is difficult to explain. In the case of tetraploid *H. schultesii*, an unreduced gamete of diploid *H. lactucella* might be considered. Similarly, after joining the unreduced gamete of tetraploid *H. pilosella* and the haploid one of *H. lactucella* a pentaploid hybrid could arise. However, both types of hybrids should differ from each other in the proportion of characters inherited from the parents, depending on different proportion of parental genomes. A synthesis of this species by experimental hybridization between *H. lactucella* and *H. pilosella* was performed by Gadella (1992): both the triploid and pentaploid hybrids were sterile, while a tetraploid sexual *H. schultesii* was obtained as a result of hybridization between both sexual hexaploid *H. pilosella* and diploid *H. lactucella*. Such an origin for the tetraploid *H. schultesii* in the Krkonoše Mts might also be possible, but its hexaploid putative parent *H. pilosella* has not been found. The mode of reproduction in plants in the Krkonoše Mts appears to be different in the tetraploid (sexual) and pentaploid (apomictic) cytotypes of *H. schultesii*, a similar difference to the reproductive system between the tetraploid and the pentaploid cytotype of *H. pilosella* (e. g. Gadella 1987). More plants from the Krkonoše Mts are needed to continue the study of their chromosome number and reproduction.

6. *Hieracium macrostolonum* G. Schneider

G. Schneider, Das Riesengebirge in Wort u. Bild 9(4): 147, 1889. [Syn.: *H. cernuiforme* (Nägeli et Peter) Zahn]
H. caespitosum < *H. pilosella*

2n = 54

Locality:

1. Horní Malá Úpa: Pomezní Boudy, along the local road ca. 1.5 km SW of the Czech-Polish border crossing, 1000 m a. s. l., 50°44'20"N, 15°48'50"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 54 (1 plant).

This species represents one of the intermediate types between *H. caespitosum* and *H. pilosella* (Zahn 1930). Schuhwerk & Lippert (1997) examined the chromosome number in *H. macrostolonum* (under the name of *H. cernuiforme*) for the first time in Germany-Bavaria and they report a tetraploid (2n = 36). Because the tetraploid *H. caespitosum* was found growing together in the same population with two other intermediate species between *H. caespitosum* and *H. pilosella (H. prussicum* Nägeli et Peter and *H. flagellare* Willd.), the authors point out the possible recent hybridization events in this population. The plant from the Krkonoše Mts examined by us was a hexaploid (2n = 54), i. e. a higher ploidy than we found in either *H. pilosella* or *H. caespitosum* from this mountain area (2n = 36). The unreduced gametes can participate in hybridization, resulting in new forms with increasing ploidy levels within the polyploid complex of *H. aurantiacum* (Skalińska 1976); an analogous process might lead to hexaploid *H. macrostolonum* in the Krkonoše Mts. However, more representatives of this species from this area are needed to study. This taxon of hybridogenous origin has been described from this locality, which increases the importance of the chromosome number recorded.

7. *Hieracium glomeratum* Froel.

Froelich in DC. Prodr. 7, 1: 207, 1838. [Syn.: *H. ambiguum* Ehrh., nom. nud.]
H. caespitosum – H. cymosum

2n = 4x = 36 with a long marker chromosome, apomictic; 2n = 5x = 45 with a long marker chromosome (Fig. 1e), apomictic.

Localities:

1. Pec pod Sněžkou: Velká Úpa, meadow in the area of "Zadní Výsluní", beside the local road 0.7 km NW of the church, 810 m a. s. l., 50°41'40"N, 15°46'10"E (Grosse Aupa, II. Teil). Coll. F. Krahulec 20. 6. 1995. 2n = 45 with marker chromosome, apomictic (1 plant).
2. Pec pod Sněžkou: Velká Úpa, the central and upper part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860–880 m a. s. l., 50°41'20" – 50°41'30"N, 15°47'50" – 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995. 2n = 36 with marker chromosome (2 plants), 2n = 45 with marker chromosome, apomictic (4 plants).
3. Horní Malá Úpa: Pomezní Boudy, grassland near the "Padolská bouda" chalet, 2 km SW of the Czech-Polish border crossing, 960 m a. s. l., 50°44'20"N, 15°48'10"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 36 with marker chromosome, apomictic (1 plant).

The tetraploid chromosome number (2n = 36) prevails among poor references to this species. Three morphotypes from Sweden, classified by Turesson & Turesson (1963) as sepa-

rate species, were found to be tetraploid (the plants under the name of *H. tenerescens* Norrl., *H. umbelliflorum* Nägeli et Peter and *H. vacillans* Norrl.); the corrections in their taxonomic classification (i. e. their incorporation into *H. glomeratum*) are here accepted according to Schuhwerk (1996). The amphi-apomictic reproduction is reported in the first of these tetraploid "species" (Turesson & Turesson 1963). In addition, the pentaploid cytotype is reported in *H. vacillans* mentioned above as well (Turesson & Turesson 1963). The tetraploid chromosome number 2n = 36 was later found in plants classified as *H. glomeratum* subsp. *dubium* (L.) Nägeli et Peter, which originated from Germany-Bavaria and from the Czech Republic-Bohemia (Schuhwerk & Lippert 1997). We found both the tetraploid and pentaploid cytotypes in the Krkonoše Mts, growing together in one meadow (loc. 2). The apomictic reproduction reported here (concerning especially the pentaploid cytotype of *H. glomeratum*) completes the information about the mode of reproduction in this species.

8. *Hieracium floribundum* Wimm. et Grab.

Wimmer et Grabowski, Fl. Siles. 2(2): 204, 1829.
H. caespitosum > *H. lactucella*

2n = 4x = 36 with a long marker chromosome (Fig. 1b), apomictic.

Localities:

1. Pec pod Sněžkou, the upper part of the meadow on Hnědý vrch, 1.5 km SW of the centre of Pec, near the chalet "Lucký", 970 m a. s. l., 50°41'20"N, 15°43'00"E (Grosse Aupa, III. Teil, Braunberg). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 36 with marker chromosome, apomictic (1 plant).
2. Pec pod Sněžkou: Velká Úpa, the central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860–865 m a. s. l., 50°41'20"N, 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995 and 26. 6. 1997. 2n = 36 with marker chromosome, apomictic (5 plants).

Hieracium floribundum represents an intermediate species between *H. caespitosum* and *H. lactucella* with prevailing characters of the former species (Zahn 1930). The first karyological studies carried out on *H. floribundum* in Poland in the Eastern Carpathians revealed the triploid level (2n = 27), which corresponds to a hybrid between tetraploid *H. caespitosum* and diploid *H. lactucella* (Skalińska 1967). The prevailing characters of the former parent could be explained by the presence of two genomes of *H. caespitosum* in the hybrid (Skalińska 1967). Nevertheless, the tetraploid *H. floribundum* was later found in the Far East (Probatova et al. 1989) and in Germany-Bavaria, the latter reference concerning the typical subspecies *floribundum* (Schuhwerk & Lippert 1997). Thinking about the origin of the tetraploid cytotype (including also the plants from the Krkonoše Mts), the participation of unreduced gametes or backcrossing could be taken into consideration (the apomictic representatives of the subgenus *Pilosella* can serve as good pollen donors – e. g. Skalińska 1971a, Gadella 1982, 1987). While the facultative apomixis was found in triploid *H. floribundum* (Skalińska 1968), the apomictic reproduction of the tetraploid cytotype is here reported for the first time.

9. *Hieracium iseranum* Uechtr.

Uechtritz in Fiek, Fl. Schles. 261, 1881.
H. floribundum > *H. pilosella*

2n = 4x = 36 usually with a long marker chromosome (Fig. 1c), apomictic.

Localities:

1. Pec pod Sněžkou, disturbed place at the local road ca. 250 m NNE of "Výrovka" chalet, 1390 m a. s. l., 50°43'10"N, 15°41'00"E (2.25 km NW von der Richterbauden). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 36 with marker chromosome, apomictic (1 plant).
2. Pec pod Sněžkou, disturbed place along the hiking path, ca. 0.5 km ENE of "Luční bouda" chalet, 1410 m a. s. l., 50°44'10"N, 15°42'20"E (Wiesenbaude). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 36 with marker chromosome (1 plant).
3. Pec pod Sněžkou, the lower part of the meadow on the Hnědý vrch, 1.5 km SW of the centre of Pec, near the chalet "Banka", 910 m a. s. l., 50°41'20"N, 15°43'10"E (Grosse Aupa, III. Teil, Braunberg). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 36 with marker chromosome, apomictic (1 plant).
4. Pec pod Sněžkou: Velká Úpa, meadow in the eastern part of the area of "Prostřední Výsluní", 1 km ENE of the church, 910–920 m a. s. l., 50°41'40"N, 15°47'10"E (Grosse Aupa, II. Teil). Coll. F. Krahulec 20. 6. 1995. 2n = 36 with marker chromosome (3 plants).
5. Pec pod Sněžkou: Velká Úpa, the central and upper part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860–880 m a. s. l., 50°41'20" – 50°41'30"N, 15°47'50" – 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995. 2n = 36 with marker chromosome (5 plants), apomictic (4 plants); 2n = 36 without marker chromosome, apomictic (1 plant).

Neither the chromosome number, nor the mode of reproduction has been known in this species.

10. *Hieracium apatelium* Nägeli et Peter

Nägeli et Peter, Die Hieracien Mittel-Europas 1: 706, 1885.
H. floribundum – H. pilosella

2n = 4x = 36, both the apomictic and amphimictic types; 2n = 6x = 54, apomictic.

Localities:

1. Pec pod Sněžkou: Velká Úpa, the meadow on "Zadní Výsluní", along the local road 0.7 km NW of the church, 810 m a. s. l., 50°41'40"N, 15°46'10"E (Grosse Aupa, II.Teil). Coll. F. Krahulec 20. 6. 1995. 2n = 36 (5 plants), apomictic (2 plants).
2. Pec pod Sněžkou: Velká Úpa, the central part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860 m a. s. l., 50°41'20"N, 15°48'00"E (Grosse Aupa, Braunboden). Coll. F. Krahulec 20. 6. 1995. 2n = 36 (3 plants), sexual (1 plant).
3. Horní Malá Úpa, the meadow in the Pomezní Boudy, along the local road ca. 1.5 km SW of the Czech-Polish border crossing, 1000 m a. s. l., 50°44'20"N, 15°48'50"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 54, apomictic (1 plant).

The chromosome numbers as well as the mode of reproduction in *H. apatelium* are here reported for the first time.

11. *Hieracium piloselliflorum* Nägeli et Peter

Nägeli et Peter, Die Hieracien Mittel-Europas 1: 707, 1885.
H. floribundum < *H. pilosella*

2n = 4x = 36, the reproductive system not examined hitherto; 2n = 5x = 45 (44) (Fig. 1d), apomictic; 2n = 6x = 54, apomictic.

Localities:

1. Pec pod Sněžkou: ca. 0.2 km W of the former "Obří bouda" chalet, along the hiking path to "Luční bouda" chalet, 1350 m a. s. l., 50°44'20"N, 15°43'40"E (Riesenbaude). Coll. F. Krahulec and A. Krahulcová, HWE 16. 7. 1997. 2n = 45 (1 plant).
2. Pec pod Sněžkou: Velká Úpa, central and upper part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 860–880 m a. s. l., 50°41'20" – 50°41'30"N, 15°47'50" – 15°48'00"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 20. 6. 1995 and 26. 6. 1997, F. Krahulec and A. Krahulcová 22. 6. 1998. 2n = 36 (2 plants); 2n = 45 (7 plants), apomictic (3 plants); 2n = 44 (2 plants).
3. Horní Malá Úpa: Pomezní Boudy, along the local road ca. 1.5 km SW of the Czech-Polish border crossing, 1000 m a. s. l., 50°44'20"N, 15°48'50"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 54, apomictic (2 plants).

The differentiation into three ploidy levels (4x, 5x and 6x) was revealed in this species, whose chromosome number was previously unknown. Aneuploidy is extremely rare in the whole subgenus *Pilosella* in Europe (e. g. Bräutigam & Bräutigam 1996), but not rare in New Zealand, where this taxonomic group has been introduced. For example, a hypopentaploid *H. pilosella* (2n = 42, 43, 44) occurs there (Chapman, pers. commun.). A similar hypopentaploid cytotype of *H. piloselliflorum* (2n = 44) was twice found by us in the years 1997 and 1998 in the meadow near "Janovy Boudy" settlement (loc. no. 2). We do not know, if both these aneuploid plants examined belong to the same clone. The mode of reproduction of the both pentaploid and hexaploid cytotypes was proved to be apomictic, the tetraploids are under study in this respect.

12. *Hieracium stoloniflorum* Waldst. et Kit.

Waldstein et Kitaibel, Pl. Rar. Hung. 3:303, 1812.
H. aurantiacum < *H. pilosella*

2n = 6x = 54, apomictic.

Localities:

1. Pec pod Sněžkou: Velká Úpa, grassland in the centre, ca. 0.5 km WNW of the church, 700 m a. s. l., 50°41'30"N, 15°46'10"E (Grosse Aupa, II. Teil). Coll. F. Krahulec 23. 6. 1997. 2n = 54 (1 plant).
2. Pec pod Sněžkou: Velká Úpa, the upper part of the meadow near the settlement "Janovy Boudy", 1.5 km E of the church, 880 m a. s. l., 50°41'30"N, 15°47'50"E (Grosse Aupa, II. Teil, Braunboden). Coll. F. Krahulec 26. 6. 1997. 2n = 54, apomictic (1 plant).

This species represents a product of spontaneous hybridization between *H. pilosella* and *H. aurantiacum*; the hybrids possess a considerable variation in morphology, probably due to backcrossing (Sell & West 1975). Four ploidy levels are known in *H. stoloniflorum*: the triploids (2n = 27) are given from Germany-Bavaria (Schuhwerk & Lippert 1997), the tetraploids (2n = 36) from Germany-Saxonia (Bräutigam & Bräutigam 1996), the

pentaploids (2n = 45) as a garden weed from Scotland (Jenkins & Jong 1997) and the hexaploids (2n = 54) from Germany-Bavaria (Schuhwerk & Lippert 1997) and also from New Zealand, where *H. stoloniflorum* occurs as an alien plant (Jenkins & Jong 1997). In addition, a single reference to aneuploidy (2n = 46) is given (Finch ined. in Moore 1982). The reproductive system has not been studied in this species untill now. The plants from the Krkonoše Mts proved to be hexaploid and apomictic.

H. stoloniflorum has been given from the area of the Krkonoše Mts for the first time by Schneider (1889–1890). He described this species from two localities, Grenzbauden (Pomezní Boudy) and Schlingelbaude (now Polana SW of Karpacz in Poland). However, the occurrence of this species in the Krkonoše Mts has not been accepted by Zahn (e. g. 1930) and books based on his concept (e. g. Dostál 1989). According to our observations in the field, the occurrence of a red-orange taxon with two or three capitula, smaller than *H. rubrum* and corresponding to *H. stoloniflorum*, cannot be neglected (Fig. 2).

13. *Hieracium rubrum* Peter

Peter, Flora 64 (N. R. 39): 126, 1881.
H. flagellare – H. aurantiacum

2n = 6x = 54 (Fig. 1f), apomictic.

Localities:

1. Pec pod Sněžkou: Velká Úpa, the meadow in the eastern part of the meadow area "Prostřední Výsluní", on the slope above the local road 1 km ENE of the church, 910–920 m a. s. l., 50°41'40"N, 15°E47'10"E (Grosse Aupa, II. Teil). Coll. F. Krahulec 20. 6. 1995. 2n = 54 (3 plants), apomictic (2 plants).
2. Horní Malá Úpa: Pomezní Boudy, disturbed place at the parking place S of "Padolská bouda" chalet, 950 m a. s. l., 50°44'10"N, 15°48'10"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 54, apomictic (1 plant).
3. Horní Malá Úpa: Pomezní Boudy, meadow along the local road ca. 1.5 km SW of the Czech-Polish border crossing, 1000 m a. s. l., 50°44'20"N, 15°48'50"E (Grenzbauden). Coll. F. Krahulec 26. 6. 1997. 2n = 54 (4 plants), apomictic (3 plants).

The hexaploid chromosome number found in *H. rubrum* is in agreement with a single reference by Schuhwerk & Lippert (1997), concerning plants from Germany-Bavaria. This species is considered as a spontaneous hybrid between *H. aurantiacum* and *H. flagellare* Willd. (Sell & West 1975). It appears to be apomictic in the Krkonoše Mts.

General discussion and conclusions

Several features can be referred to the whole group of species studied in the Krkonoše Mts. It appears that all members of the subgenus *Pilosella* in this area are comprised of four ploidy levels, namely diploids, tetraploids, pentaploids and hexaploids. The tetraploid species (or cytotypes respectively) appear to prevail among the plants studied. No triploids were found, although the triploid spontaneous interspecific hybrids between sexual diploids and sexual or apomictic tetraploids are reported in the literature, some of them resulting in a new hybridogenous species (e. g. *H. floribundum* – Skalińska 1967, *H. schultesii* – Sell & West 1975). The only diploid species recorded in the Krkonoše Mts is *H. lactucella*, which is not rare here (Schneider 1889–1890, Šourek 1969, Krahulec et al. 1997); there-

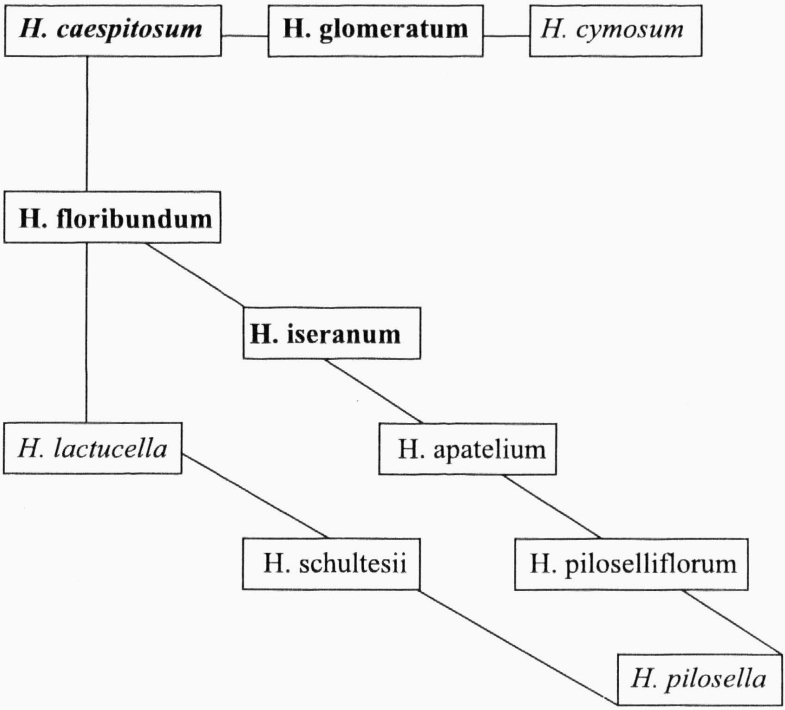


Fig. 3. – The relationship among selected species of *Hieracium* subgen. *Pilosella* forming an apomictic complex. All the species represented schematically occur in the Krkonoše Mts; except for *H. cymosum*, they all were a subject of the present study. The basic species (Hauptarten) are given in italics, the hybridogenous species in usual typeface. The species, characterized by a long marker chromosome in the karyotype, are given in bold. Note that the position of hybridogenous types between *H. pilosella* and *H. floribundum* is based on morphological affinity and does not necessarily reflect their origin.

fore the possibility of hybridization between this sexual species and some of the tetraploid species (they are common in the Krkonoše Mts) can be supposed. However, we do not know anything about the conditions for successful establishment of triploid hybrids under competition with surrounding vegetation. Four of the species examined display polymorphism in ploidy levels: in addition to the tetraploid cytotype within each of them the pentaploid and/or hexaploid cytotype exists (*H. apatelium* – tetraploid and hexaploid, *H. glomeratum* – tetraploid and pentaploid, *H. piloselliflorum* – tetraploid, pentaploid and hexaploid and *H. schultesii* – tetraploid and pentaploid).

This study revealed four sexual species in the Krkonoše Mts: the diploid *H. lactucella*, the tetraploid *H. pilosella* and the tetraploid cytotype of *H. schultesii* and of *H. apatelium*. The last tetraploid, however, occurs here as the sexual and apomictic form respectively. The rest of species and cytotypes, in which the reproductive system was examined, appears to be (at least facultatively) apomictic: a part of tetraploids and all pentaploid and hexaploid cytotypes examined belong here.

Our find of a long marker chromosome in the chromosome set of several species (Fig. 1) has an important aspect. This group is formed by *H. caespitosum* and hybridogenous taxa with involvement of this species (Fig. 3). The same marker chromosome has been reported in *H. caespitosum* introduced to the New Zealand (Jenkins & Jong 1997). Thus, the subsequent transfer of this abnormal chromosome by gametes taking part in hybridization is probable. The series involves the following four species occurring in the Krkonoše Mts and characterized by this chromosomal marker: *H. glomeratum*, *H. caespitosum*, *H. floribundum* and *H. iseranum* (Fig. 3). This chromosome was found no more in the last two hybridogenous species of this series, nearest to *H. pilosella* (*H. apatelium* and *H. pilosselliflorum* – Fig. 3).

Some of the species recorded in the Krkonoše Mts have undoubtedly arisen through hybridization. However the high ploidy levels recorded in some of these species are indicative of more than simple hybridization. This is because their ploidy levels are higher than the putative parental species. At least two processes could be considered in the rise of these taxa: the participation of unreduced gametes in the zygote formation and/or backcrossing. By that way crossing of the same species can produce polymorphic progeny with respect to their chromosome number (and morphology). The backcrossing could be possible due to partial sexuality of hybrids (facultative apomicts) and/or to their fertile pollen. The ability to produce the highly polyploid "additional hybrids" due to unreduced gametes has already been proved in hybridization experiments, e. g. in *H. aurantiacum* (Skalińska 1971a, b, 1973), *H. pilosella* (Gadella 1988, 1991b, 1992) and in *H. caespitosum* (Chapman & Bicknell 1999).

With respect to the polymorphism found within *H. apatelium* and *H. pilosselliflorum*, we should mention that older authors (e. g. Schneider 1889–1890) have already distinguished several (micro)species or subspecies within them: two within *H. apatelium* (spp. *apatelium, confinium*), four within *H. pilosselliflorum* (subsp. *striiferum, pilosselliflorum, aupaense, paxii*). We do not know if the particular cytotypes could directly be related to these taxa because of the limited number of plants examined.

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Souhrn

Práce přináší první poznatky ze současného studia jestřábníků podrodu *Pilosella* v Krkonoších. Zejména východní Krkonoše jsou známé velkou diverzitou této skupiny, která může mít vztah k přítomnosti většího množství sexuálních typů umožňujících větší rozsah hybridizace. U následujících druhů byl zjištěn počet chromozómů a reproduktivní systém: *H. pilosella* L. (2n = 36, sexuální), *H. lactucella* Wallr. (2n = 18, sexuální), *H. caespitosum* Dumort. (2n = 36, reproduktivní systém dosud nezjištěn), *H. aurantiacum* L. (2n = 36, apomiktický), *H. schultesii* F. W. Schultz (2n = 36, sexuální; 2n = 45, apomiktický), *H. macrostolonum* G. Schneider (2n = 54, reproduktivní systém dosud nezjištěn), *H. glomeratum* Froel. (2n = 36, 45, oba typy apomiktické), *H. floribundum*

Wimm. et Grab. (2n = 36, apomiktický), *H. iseranum* Uechtr. (2n = 36, apomiktický), *H. apatelium* Nägeli et Peter (2n = 36, apomiktický i sexuální typ; 2n = 54, apomiktický), *H. pilosselliflorum* Nägeli et Peter (2n = 36, reproduktivní systém dosud nezjištěn; 2n = 45, 44, apomiktický; 2n = 54, apomiktický), *H. stoloniflorum* Waldst. et Kit. (2n = 54, apomiktický), *H. rubrum* Peter (2n = 54, apomiktický). Pro *H. apatelium, H. iseranum* a *H. pilosselliflorum* nebyl dosud počet chromozómů známý, pro *H. macrostolonum* a *H. schultesii* byly zjištěny nové počty. Zde uvedené chromozómové počty některých z těchto druhů jsou významnější o to více, že byly zjištěny z oblasti, odkud byly tyto taxony popsány. U *H. caespitosum* a skupiny hybridogenních druhů (*H. glomeratum, H. floribundum, H. iseranum*), kde je předpokládán podíl tohoto druhu, byl nalezen význačný velký nepárový signální chromozóm (t.j. "marker" chromozóm); podle literatury byl podobný chromozóm již dříve pozorován u (zavlečených) novozélandských populací *H. caespitosum*. Reproduktivní systémy jsou zde poprvé studovány u hybridogenních druhů *H. iseranum, H. apatelium, H. pilosselliflorum, H. stoloniflorum, H. rubrum* a *H. schultesii* z přírody; apomixe u tetraploidního *H. floribundum* a pentaploidního *H. glomeratum* je zde rovněž zmíněna poprvé. Práce uvádí celkem čtyři sexuální druhy (resp. cytotypy), které byly nalezeny v Krkonoších: diploidní *H. lactucella* a tetraploidní *H. pilosella, H. apatelium* a *H. schultesii*. Velká diverzita jak v množství cytotypů, tak jejich reproduktivních systémů může být výsledkem dvou procesů, které se mohou vzájemně kombinovat: tvorby gamet s jiným než redukovaným počtem chromozómů a zpětné hybridizace, která je i u apomiktických typů umožněna fertilitou pylu. V práci je potvrzen výskyt *H. stoloniflorum* v Krkonoších udávaný již v minulém století; tento údaj však později z literatury vymizel.

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