Preslia, Praha, 76: 223–243, 2004

The Sudetic group of *Hieracium* subgen. *Pilosella* from the Krkonoše Mts: a synthetic view

Jestřábníky *Hieracium* subgen. *Pilosella* v Krkonoších: souhrnný pohled

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Dedicated to the memory of Emil Hadač

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Krahulec F., Krahulcová A., Fehrer J., Bräutigam S., Plačková I. & Chrtek J. jun (2004): The Sudetic group of *Hieracium* subgen. *Pilosella* in the Krkonoše Mts: a synthetic view. – Preslia 76: 223–243.

The present paper summarizes the results of research of *Hieracium* subgen. *Pilosella* done by using different methods. The apomictic complex of *Hieracium* subgen. *Pilosella* found in the Krkonoše Mts, consists of the following basic species: *H. lactucella* (2x, sexual), *H. onegense* (2x, sexual), *H. pilosella* (4x, sexual), *H. caespitosum* (4x, apomictic) and *H. aurantiacum* (4x and 5x, apomictic). These species are considered to be the parents of a further set of mostly apomictic hybridogenous types. The ploidy level, breeding system, isozyme phenotypes, chloroplast haplotypes and geographic distribution of this whole complex was analysed. The different hybridogenous types have different frequencies in the field and differ in the frequency of isozyme phenotypes (a conservative estimate of the number of genotypes). Most have uniform chloroplast haplotypes, but some haplotypes could have originated from reciprocal crosses. The comparison of chloroplast haplotypes suggests that apomictic species were not only pollen donors, but also contributed seed and gave rise to several hybridogenous types, illustrating the importance of the residual sexuality of apomicts in this group. *H. pilosella* is a central species in this group and is connected with other parental species, *H. floribundum, H. lactucella* and *H. aurantiacum* by a set of hybridogenous species that have a similar genetic structure. Some of the distinct hybridogenous types within the complex are of multiple origin. In contrast, crosses between the same parental types may generate diverse progenies, which can often be classified as distinct taxa. All taxa recorded in the past are surveyed and discussed with respect to present knowledge. We suggest that the taxonomy and origin of particular entities of this and other such complexes is best resolved using information from morphological, genetical, cytological and ecological studies.

Keywords: *Asteraceae*, breeding systems, chloroplast haplotypes, chromosome numbers, Czech Republic, *Hieracium* subgen. *Pilosella*, isozyme phenotypes, Krkonoše Mts, residual sexuality

Introduction

The genus *Hieracium* is one of the most complicated in the vascular flora. Complexity within the subgen. *Pilosella* is due to several phenomena (Krahulcová et al. 2000): (1) Frequent hybridization, often accompanied by an increase in ploidy level. As existing hybrids can undergo further hybridization with additional parental species, more than two species may be involved in hybrid formation. (2) Polyploidy. Especially in the subgenus *Pilosella*, polyploidy is connected with participation of unreduced gametes in crosses and thus with the origin of addition hybrids, resulting in progeny with ploidy levels exceeding those of the parents. (3) Aposporous apomixis. The subgenus *Pilosella* possesses aposporous apomixis characterized by a high degree of sexuality. Therefore, apospory is mostly a facultative trait. Apomixis enables the different products of hybridization to be perpetuated and potentially spread over large area. Some hybrids are excellent colonizers, especially in New Zealand and North America. (4) Combination with other types of reproduction. Members of subgenus *Pilosella* reproduce vegetatively (by clonal growth) by means of above- or underground stolons. Although the sexual types are allogamous, autogamy also occurs stimulated by foreign pollen (mentor effect).

All these factors strongly influence the complex population structure of the species in the subgenus *Pilosella*. The reflection of this complex pattern in taxonomic treatments is obviously diverse. Different solutions were accepted in different parts of Europe, based on traditions established in the 19th century. Over the last decades it became evident that further development is dependent upon (i) evaluation of the importance of particular factors underlying the complex patterns of variation and (ii) knowledge of the genetic population structure in the field. There are several centres of diversity of *Pilosellae* in Europe, which differ in basic species involved in hybridization, as well as in the products generated by these crosses.

During the last six years we have focused on the species of *Hieracium* subgen. *Pilosella* occurring in the western part of the Sudetes' mountain range, i.e. in the Krkonoše Mts (Karkonosze, Riesengebirge). This area was chosen for several reasons. It was known to be rich in species of *Pilosellae* with many hybridogenous types described from this area and became an important source of material for studies contributing to the understanding of the whole group (see Peter 1881, Nägeli & Peter 1885, Uechtritz 1880, 1885, 1886, Schneider 1888–1895).

For the results of our investigations on chromosome numbers and breeding systems see Krahulcová & Krahulec (1999, 2000), Krahulcová et al. (1999, 2001). Results of the molecular study can be found in Fehrer et al. (2004).

Study area

The Krkonoše Mts form the western part of the Sudeten Mts range and have an altitude ranging from 400 to 1600 meters. They are situated on the border between Poland and the Czech Republic (Fig. 1). The range of the Krkonoše Mts is in a WNW–ESE direction and the main ridge is about 40 km long. Geologically, the Krkonoše Mts are formed of granite in the west and mostly metamorphic rocks, gneiss and mica-schist, in the east. On the periphery of the mountains, there are small areas of limestone, erlan and quartzite. Generally, more acidic and coarse-grained rocks are situated at higher altitudes. The climatic conditions are closely correlated with altitude, July being the warmest and wettest month of the year. The average yearly temperature varies between 5 and 0.2° C and precipitation between 700 and 1240 mm.

The highest parts of the mountains reach above the timberline, which is situated at an altitude of approximately 1250 metres. Most *Pillosellae* occur in secondary grassland in

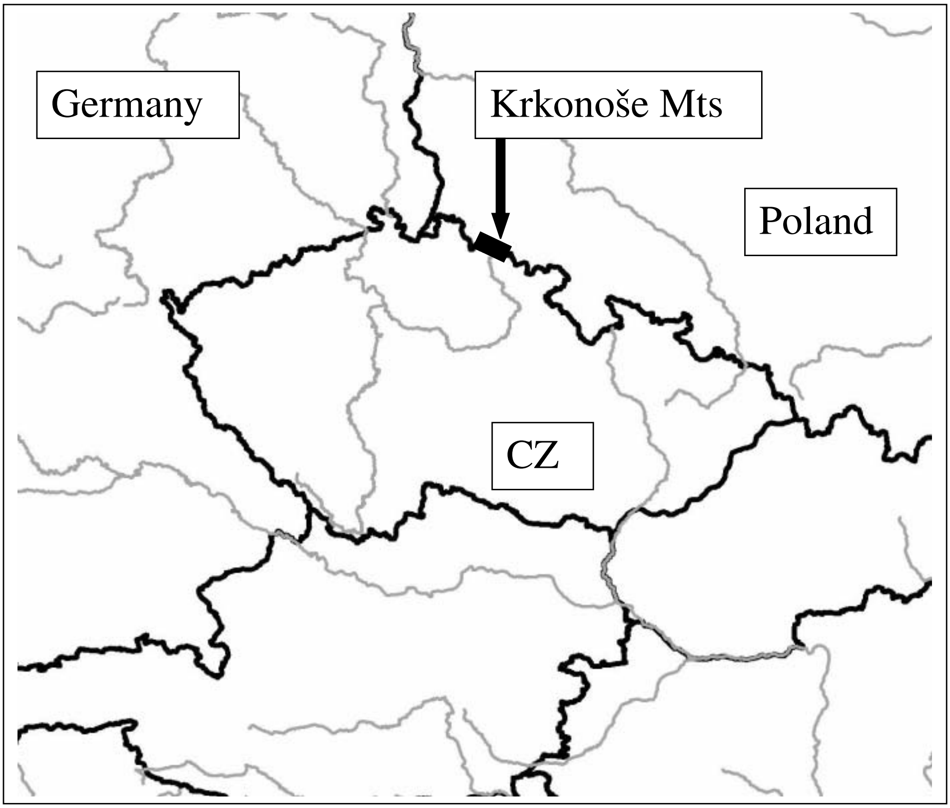

Fig. 1. – Location of the study area.

the forest (montane) zone. These montane meadows were established during the 16th and 17th century following colonization of the area. At the beginning, the main aim of the colonizers was tree felling, but later the inhabitants started cultivating the soil, including levelling of the ground, grazing cattle and mowing the newly formed grasslands. Permanent settlements were established at higher altitudes of up to 1450 m. Several settlements were situated near the forest line, at altitudes between 1200–1300 m. This facilitated an upward and downward migration of plant species. All these activities resulted in a highly diverse flora in the montane meadows in this mountain range (Krahulec et al. 1997). Fertilization of grasslands was relatively rare and limited to the vicinity of mountain chalets. This traditional land use was interrupted after World War II, when most of the inhabitants were shifted to Germany. The traditional agricultural regime survived in some places, slowly disappearing in the beginning of the 1990s along with the next period of social-economic change. At present, these grasslands are used for sporting activities (skiing) and their productive function is unimportant. With the cessation of fertilization, the nutrient status of the grasslands declined (oligotrophication), enhanced by acid precipitation. Many of these meadows were abandoned recently, some are still cut and mulched in order to prevent the establishment of trees and maintain a flat surface for skiing. The whole area is part of the Krkonoše National Park, which was established in 1963.

At present, road margins and other disturbed habitats are more important sites for *Pilosellae* than cut grasslands, which are only temporary habitats whose colonization depends on availability of seed. Grasslands with *Pilosellae* are classified mostly as *Nardo-Agrostion tenuis* Sillinger 1933 (order *Nardetalia*) or as *Polygono-Trisetion* Braun-Blanquet et Tüxen ex Marschall 1947 (order *Arrhenatheretalia*). The papers by Krahulec (1990) and Krahulec et al. (1997) give details of their phytosociology.

Taxonomic concept

We accept the modified concept of Central European authors based on Nägeli & Peter (1885) and Zahn (1922–1930). In agreement with them we distinguish basic species (Hauptarten) and intermediate species (Zwischenarten), which we consider to be of hybridogenous origin. We consider *H. onegense* (*H. caespitosum* subsp. *brevipilum*) as a separate basic species, because it is morphologically and chorologically distinct from *H. caespitosum* s.str. At present we do not distinguish further subunits such as grex or subspecies (see general discussion at the end of this paper). In our opinion, a taxonomic concept should be based on a broad insight into population structure, especially at the genetic level. The extremely narrow species concept adopted by Scandinavian and Russian authors studying East European *Pilosellae* (Schljakov 1989) is not based on such a system. Additionally, we do not accept the concept used e.g. by Sell & West (1976) for hybridogenous species. Tichomirov (2000) has recently used a broad approach and fused together such types as *H. caespitosum* and *H. floribundum.* Tyler (2001) also lumped basic and hybridogenous types together.

We distinguish hybridogenous species that originated from crosses between two distinct parental species, and are more closely related to the first or to the second parent: in our case the hybridogenous species *H. iseranum* and *H. piloselliflorum* or *H. rubrum* and *H. stoloniflorum*. Their differences in morphology, ecology, population structure and karyology support our decision.

Species belonging to other complexes, such as *H. bauhini* and *H. piloselloides*, which occur in the area mainly at low and only occasionally at high altitudes are not discussed. Furthermore, they are not involved in the hybridization of interest to this study, probably because of the period of short time they have existed in area.

The apomictic complex

A characteristic feature of the subgenus *Pilosella* is that it forms local complexes dependent on the basic species and (probably) rare hybridization events in the past. The Sudetic group is a complex of hybridogenous species specific to the western part of the Sudetes, the Krkonoše Mts. For simplicity, we divide it into two parts, or species groups; their putative relationships are based on previous analyses of morphological characters and hybridization experiments carried out as early as the 1880s and summarized by Nägeli & Peter (1885). The crosses performed by us support the previous results. Additionally, further explanations for some morphotypes were found. The first group (Fig. 2), consisting of yellow flowering species, is formed from the following basic species: *H. pilosella, H. lactucella, H. onegense* and *H. caespitosum. H. cymosum* occurs outside the study area.

Nevertheless, it was involved in the formation of one common hybridogenous type (*H. glomeratum*) and its descendants (*H. scandinavicum, H. tubulascens*). The second group of mostly orange flowering hybridogenous species consists of the following basic types: *H. lactucella, H. pilosella, H. caespitosum*, and *H. aurantiacum* (Fig. 3).

Material and Methods

Sampling and cultivation

Plants were collected in the field in an attempt to find all the morphological variation present in the different parts of the study area. Each type was collected several times to determine the range of variation it shows (numbers of plants analyzed are given in Table 1). In addition, at several localities, all the rosettes were collected within a 5 × 5 m quadrate. The most extensive sampling was done at the Janovy Boudy settlement, where more than 200 specimens were collected and analyzed with respect to their chromosome number and breeding systems. Isozyme phenotypes were also determined for a subset of the plants.

All plants collected in the field were transported to the experimental garden at the Institute of Botany, Průhonice. For some plants, herbarium specimens were collected directly in the field, and each plant grown in the garden is also documented by herbarium specimens. All these specimens are preserved in the herbaria of the Staatliches Museum für Naturkunde Görlitz (GLM) and/or the Institute of Botany at Průhonice (PRA).

Karyology

The chromosome numbers were counted in root-tip meristems of cultivated plants (see Krahulcová & Krahulec 1999) of more than 400 specimens.

Breeding systems

The breeding system of particular plants was determined by comparing the seed set of open pollinated capitula with that of emasculated (cut) capitula (see Richards 1997: 412, Gadella 1984, 1987, Krahulcová & Krahulec 1999).

Hybridization

Hybridization experiments were carried out in the experimental garden at Průhonice. The main aim of these experiments was to compare the phenotypes of artificial hybrids with those of putative hybrids in the field and estimate how easily particular species could hybridize. Chromosome numbers were counted, especially in the progeny of heteroploid crosses (Krahulcová & Krahulec 2000). The breeding system of a subset of the progeny was also determined. The detailed results will be published later. In the present paper they are used to support arguments in the discussion.

Isozyme analysis

Electrophoresis was performed on crude protein extracts of leaf material. Tissue was ground in ice-cold Tris-HCl extraction buffer: 0.1 M Tris-HCl pH 8.0; 70 mM 2-mercaptoethanol, 26 mM sodium metabisulfite, 11 mM ascorbic acid, 4% polyvinylpyrrolidone. Roughly 60 mg of fresh leaf material was homogenized with Dowex.Cl (1-X8) on ice in 0.7 ml of extraction buffer. Extracts were centrifuged for 10 min at 13,000 rpm and clear supernatants were stored at –75 °C.

All enzyme systems were investigated on polyacrylamide gels (8% acrylamide, discontinuous tris-glycine buffer system, pH 8,3). The staining procedures followed Vallejos (1983) – LAP (Fast Black K), AAT (+ Fast Violet B) and Wendel & Weeden (1989) – 6-PGDH, SHDH, EST-colorimetric (b-naphthyl phosphate, Fast Blue BB), SOD, PGM (NADP) with modifications.

Because only few enzyme systems (loci) of a subset of the plants collected were analyzed the number of isozyme phenotypes found is a conservative estimate of the number of genotypes (clones).

Chloroplast haplotypes

PCR-RFLPs and sequencing of the *trn*T-*trn*F and the *trn*T-*trn*L intergenic spacers were done as described previously (Fehrer et al. 2004). Additionally, a further distinction of subtypes within the two major haplotype groups became possible using high resolution agarose, which detected a diagnostic 5 bp-deletion within haplotype I in a restriction digest with *Eco*R I.

Results

The frequency of individual members of the complex

The individual taxa of the sudetic *Pilosella* apomictic complex differ in abundance in the field. In general, all the basic species are common in the study area, except *H. onegense*, which was re-discovered after more than 100 years and is known from a small population consisting of not more than 10 plants at a single locality (see Schneider 1889–1895, Krahulcová et al. 2001). There are pronounced differences in frequency of the hybridogenous types. They may be divided into three groups in this respect:

1. Widespread and abundant. The following types belong to this group: *H. glomeratum*, *H. floribundum*, *H. iseranum*, *H. piloselliflorum* (incl. *H. apatelium*), *H. schultesii*, *H. rubrum*, *H. blyttianum*, *H. stoloniflorum*. They were reported from this area by many authors as early as in the 19th century.
2. Hybridogenous types established at one locality: *H. scandinavicum, H. fuscoatrum*. They were found during the last decades, e.g. *H. fuscoatrum* in 1979 and established within 20 years (Krahulec et al. 1997, Krahulcová et al. 2001).
3. Very rare hybridogenous types known from one locality and a limited number of specimens: *H. tubulascens, H. lactucella* × *H. onegense*. These types were found during detailed research carried out at the population level (Krahulcová et al. 2001).

Karyology

The details of the ploidy levels and chromosome numbers for these areas were published previously (Krahulcová & Krahulec 1999, Krahulcová et al. 2001). Additional results are summarized in Figs 2 & 3, and Table 1. The individual members of the complex differ greatly in number and frequency of cytotypes. Some of the species are represented by

Table 1. – Survey of *Hieracium* subgen. *Pilosella* species studied in the Krkonoše population: chromosome numbers (2n), breeding system (sexual or apomictic) and haplotype (number of plants/number of populations in brackets). "Haplotype" refers to one or the other major chloroplast haplotype groups described by Fehrer et al. (2004). Those given in brackets refer to other individual plants than those tested for isozyme patterns and breeding system, but belonging to the same clone. (a), (r) and (c) are subtypes characteristic of *aurantiacum*, *rubrum* and *cymosum*, respectively. n.d. = not determined. In the columns "number of isozyme phenotypes", the number of different phenotypes observed and the total number of plants studied (in brackets) are given for both locality and region. The most species-rich population close to Janovy Boudy (F. Krahulec et al., unpubl.) represents here the "locality level" of variation. The "region level" (Krkonoše Mts) column indicates the number of isozyme phenotypes detected, related to the number of populations studied (in brackets). Only the enzyme systems used for identification of different phenotypes (clones) are given in the last column. If no variation was found, no system is given.

Species	Chromosome nos (2n)	Breeding system	Haplotype	Number of isozyme phenotypes		Enzyme systems
				Janovy Boudy	Krkonoše Mts	
H. lactucella Wallr.	18 (12/3)	sex (3/1)	I (2/2)	2 (9)	3 (2)	PGM
H. pilosella L.	36 (27/10)	sex (23/8)	II (5/2)	19 (27)		6-PGDH, LAP, SHDH, EST, PGM
H. caespitosum Dumort.	36 (6/6)	apo (3/3)	(II) (2/2)		1 (3)	
H. onegense (Norrl.) Norrl.	18 (2/1)	sex (2/1)	II (1/1)	1 (2)		
H. cymosum L. subsp. *cymigerum* (Reichenb.) Peter	45 (1/1)		II c (1/1)			
H. floribundum Wimm. et Grab.	36 (15/9)	apo (8/5)	(I)	1 (7)	2 (5)	6-PGDH, LAP, EST
H. glomeratum Froel.	36 (2/2)	apo (2/2)	II			
	45 (9/6)	apo (6/3)	(II) (2/2)	1 (4)	3 (5)	LAP, SHDH, PGM
	45,44 (mosaic) (1/1)		n.d.			
	45 + fragment (1/1)		n.d.			
	46 (1/1)		II (1/1)			
H. iseranum (Uechtr.) Zahn	36 (89/8)	apo (7/4)	I (4/3)	1 (25)	3 (4)	LAP, EST, PGM
	35 + fragment (1/1)		n.d.			
	45 (1/1)	apo (1/1)	n.d.			
H. piloselliflorum Nägeli et Peter	36 (55/9)	sex (11/2)	I (2/1)	3 (3)		EST, PGM
		apo (25/3)	II (2/1)	7 (16)		EST, PGM, SOD, LAP, SHDH
	36 (1/1)	n.d.				
	44 (3/1)	apo (?)	n.d.			
	45 (45/8)	apo (3/6)	II (3/1)	3 (6)		LAP, SHDH, EST, PGM
	45 (1/1)	n.d.	I (1/1)			
	54 (5/3)	apo (3/2)	(II) (3/1)			
H. schultesii F. W. Schultz	36 (3/2)	sex (2/2)	II (1/1)			
		apo (2/1)	II (1/1)			
	35 + fragment (1/1)	apo (1/1)	I (1/1)			
	45 (1/1)	apo (1/1)	II (1/1)			
H. tubulascens Norrl.	36 (1/1)	apo (1/1)	I (1/1)			
H. aurantiacum L.	36 (19/12)	apo (6/5)	I (a) (4/3)		2 (10)	LAP
	45 (5/3)	apo (1/1)	I (a, r) (2/2)		1 (3)	
	63 (1/1)	n.d.	I (r) (1/1)			
H. stoloniflorum Waldst. et Kit.	45 (1/1)	apo(1/1)	II (2/2)			
	54 (5/2)	apo (3/1)	I r (2/2)			
H. rubrum Peter	54 (12/7)	apo (8/5)	(I (r))(5/4)		2 (7)	AAT, LAP, PGM
H. fuscoatrum Nägeli et Peter	36 (4/1)	apo (2/1)	II (1/1)			
H. scandinavicum Dahlst.	36 (6/2)	apo (3/2)	I (1/1)			
H. blyttianum Fr.	36 (14/3)	apo (5/3)	I (3/1)			
H. lactucella × *H. onegense*	18 (6/1)	sex (2/1)	I (1/1)	1 (6)		

many populations of one cytotype and rare populations of another (e.g. *H. aurantiacum, H. floribundum*); others by occurrence of rare cytotypes (as individuals) within the populations (hexaploid *H. piloselliflorum*, heptaploid *H. aurantiacum*). The general pattern is not distinct in some species (e.g. *H. schultesii*). Almost 500 plants were studied by using flow cytometry and direct chromosome counting but no triploids were detected in the field. In four cases, counting of chromosomes led to the discovery of aneuploid plants. At two localities, the number 2n = 35+fragment was found instead of the eutetraploid number (2n = 36) for *H. schultesii* and *H. iseranum*. In the third case the hypopentaploid number 2n = 44 was found three times in *H. piloselliflorum* plants growing in the same part of a meadow (Krahulcová & Krahulec 1999) which probably belonged to the same clone. One clone of *H. glomeratum* with 2n = 46 was found.

Within the karyotype of several species a single long 'marker chromosome' was regularly observed (Krahulcová & Krahulec 1999). It occurs only in the taller polyploid species of the yellow members of the apomictic complex. In the study area, it is completely absent in all smaller forms. This marker chromosome occurs in a single copy, independent of the ploidy level, in apomictic tetraploid and pentaploid members of the complex. Its distribution among the species is given in Figs 2 & 3.

Breeding systems

The breeding systems and chromosome numbers were published (Krahulcová & Krahulec 1999, Krahulcová et al. 2001). They are summarized in Figs 2 & 3, and Table 1. The diploids (*H. lactucella, H. onegense*) and their diploid hybrid (named as *H. floribundum* – Krahulcová et al. 2001) are obligately sexual. The tetraploid *H. pilosella* is also obligately sexual. Both sexual and apomictic tetraploid *H. piloselliflorum* and *H. schultesii* are present. All other types are (facultative) apomicts.

Clone determination by isozyme analysis

Isozyme phenotypes (banding pattern) were used to determine the spatial scale at which different degrees of variation occur within a particular species (Table 1). The species differ both in the number of clones (phenotypes) and in the geographic scale of the detected variation. The apomictic species strongly differ from each other in this respect: at one extreme, *H. piloselliflorum* usually has several phenotypes at the same locality and at the other *H. floribundum* is almost uniform over the whole mountain range. Variation in *H. floribundum* phenotypes is found in the Jizerské hory Mts, which are connected to the Krkonoše Mts. Two clones were detected, one of which is identical to the phenotype found in the Krkonoše Mts. On the other hand, the interclonal variation in *H. piloselliflorum* was detected at a single locality, where both sexual and apomictic types occurred. In this species, even apomicts of the same cytotype (tetraploid or pentaploid) varied genetically. Essentially the same results were obtained using multilocus DNA fingerprinting on a subset of the species complex on a larger geographic scale (Fehrer et al. 2004).

The high number of phenotypes detected in *H. pilosella* and *H. piloselliflorum* is surprising, as we supposed clonal growth to be the prevailing reproductive mode, especially within micro-localities in the same meadow. Our results show that the importance of reproduction by seed was obviously underestimated.

Chloroplast haplotypes

Due to maternal inheritance, the cpDNA haplotypes indicate the maternal plants of putative hybrids. In general, there are two basic haplotype groups within subgenus *Pilosella*, with small differences within these two groups, some of which are detectable by RFLP and are partly characteristic for particular species, e.g. *H. cymosum* subsp. *cymigerum* or *H. rubrum*. These findings are presented in Table 1 (see also Fehrer et al. 2004). The distribution of these haplotype groups in the taxa of the apomictic complex is given in Figs 2 & 3. Most of the species are monomorphic in basic haplotype group. Exceptions are *H. piloselliflorum*, *H. schultesii* and *H. stoloniflorum* that show independent origin by reciprocal crosses. Haplotype surprisingly often reveals that an apomictic rather than sexual species was the seed parent of common hybridogenous species, e.g. *H. glomeratum*, *H. iseranum*, *H. rubrum.*

Discussion

Structure of the complex

The complex consists of entities of different origin and history. The old hybridogenous species, fully established in the field, form distinctive entities even in terms of their ecology. Some were documented in the field more than a century ago at the same site. *H. rubrum*, *H. glomeratum*, *H. floribundum*, *H. iseranum* and *H. piloselliflorum* belong to this group. *H. blyttianum* differs from its parental species (*H. lactucella* and *H. aurantiacum*) by occurring only in wet grassland, mostly in the absence of both parents. On the other hand, there are types that most likely originated recently and are already spreading: *H. fuscoatrum* has at present a wider distribution than 25 years ago when it was discovered (Krahulcová et al. 2001). There is one large population of *H. scandinavicum* and some rare isolated individuals. Some species are products of recent hybridization, whose future is currently unpredictable (e.g. *H. tubulascens*, pentaploid *H. stoloniflorum*).

In both groups of the complex (Figs 2, 3), *H. pilosella* plays a special role, different from other basic species. The hybridogenous species derived from *H. pilosella* (*H. piloselliflorum, H. schultesii* and *H. stoloniflorum*) and closely resembling it in morphology (Figs 2, 3), have the highest polymorphism with respect to the diversity of cytotypes, breeding systems and haplotypes. They were produced repeatedly by reciprocal hybridization. Their backcrosses may lead to gene flow towards the sexual type, e.g. tetraploid *H. pilosella*. This is true especially for *H. piloselliflorum*, which is very common and has many isozyme phenotypes within the pentaploids, and both apomictic and sexual tetraploids, even at a single locality (Table 1, Krahulec et al., in prep.). This is influenced by the tetraploid level of *H. pilosella*. The morphology of *H. pilosella* suggests no distinct border between this species and *H. piloselliflorum* and *H. schultesii*. Conversely, both other basic sexual species (*H. lactucella*, *H. onegense*) are diploid and there is no effective gene flow towards them: the triploid block is evidently enhanced by the absence of triploids in our study area (no triploid was detected among almost 500 plants examined). In addition, the diploid hybrid, corresponding morphologically to *H. floribundum*, is so rare that it does not play any role in hybridization, despite the fact it is sexual.

Probability of origin of hybridogenous species

The number of isozyme phenotypes can be used as a conservative estimate of the number of clones and their probability of being a product of sexual reproduction (recombination). The hybridogenous types differ in number of genotypes. The establishment of a new hybridogenous type depends on internal (genetic, physiological) and external (e.g., availability of pollinators, probability of seedling establishment) factors. Its survival depends on suitable habitats that persist for a long time and on further spread. In the past, such habitats were certainly more frequent than at present. Recently, a considerable portion of the artificial grassland was, or is being abandoned, and the degraded and oligotrophic meadows are almost *Hieracium* free (except for *H. lachenalii* and *H. laevigatum*, both belonging to subgen. *Hieracium*). There are reasons for this (see the phytosociological tables in Krahulec et al. 1997). Abandoned meadows are especially bad for seedling establishment. Therefore, most species dependent on the establishment of seedling decrease. *H. rubrum* seems to be one of the best adapted species in this respect, as it does occur in many abandoned meadows. Meadows that are continuously managed display the highest species richness. Meadows were regularly cut in the past and at least part of each was grazed in summer and autumn. Grazing increases the probability of seedling establishment, even of grazed species. The high species richness in the past meant species lived close together, which increased the probability of hybridization.

The genetic factors include the compatibility of individuals, which differs markedly, especially at the interspecific level. The availability of particular cytotypes is also important. Surprisingly, we did not find any triploid plants, despite species-rich localities with *H. lactucella*, a relatively common diploid species (*H. onegense* was found only once), being studied in detail. The study of haplotypes showed that the residual sexuality of apomictic species is important (Fehrer et al. 2004). Some of the hybrids between sexual and apomictic species are apomictic, as are their seed parents (in parentheses): *H. rubrum* (*H. aurantiacum*), *H. iseranum* (*H. floribundum*), *H. glomeratum* (*H. caespitosum*) and *H. stoloniflorum* (*H. rubrum*). There are also hybrids between two apomicts, such as *H. fuscoatrum* (*H. caespitosum* as seed parent) or *H. scandinavicum* (*H. floribundum* as seed parent). It seems that the apomictic nature of potential parents has no direct influence on hybridization. Additionally, hybridization may be an especially important speciation mechanism in facultatively apomictic addition hybrids (e.g. all hexaploids and higher ploidy levels).

Some of the hybrids cannot be products of simple direct hybridization, because no combination of reduced and/or unreduced gametes would yield the observed cytotypes. For example, the pentaploid *H. piloselliflorum* cannot be derived directly from a simple cross between the tetraploid *H. iseranum* (or *H. floribundum*) and *H. pilosella*.

Remarks on individual species

Basic species

Hieracium aurantiacum L. There are three cytotypes of this species within the study area, of which the tetraploid is the most common. The pentaploid cytotype was found at three localities, two of which are at higher altitudes. These plants were taller than tetraploids and had more stem leaves. The heptaploid cytotype has been found only once. With respect to haplotype, both the tetraploids and pentaploids of *H. aurantiacum* are group I type, slightly modified (showing a diagnostic five bp-deletion). On the other hand, the heptaploid plant is characterized by a typical haplotype I, without deletion but instead showing the subtype typical of *H. rubrum*. This fact suggests the heptaploid could have originated from a backcross between *H. rubrum* (maternal plant – reduced triploid egg cell) and *H. aurantiacum* (unreduced tetraploid sperm cell). In terms of morphology, this plant cannot be easily distinguished from *H. aurantiacum.*

Hieracium caespitosum Dumort. is considered to be a basic species. It shows almost no variation (a single tetraploid clone prevails over a large area) and it is apomictic. These features resemble the situation in some of the hybridogenous species, e.g. *H. floribundum* and *H. iseranum*. *H. caespitosum* is rather difficult to distinguish from *H. glomeratum,* having fewer stellate hairs on upper leaf surface than *H. glomeratum*. Tichomirov (2000) considers *H. caespitosum* a hybridogenous species, which originated from a cross between *H. onegense* and *H. lactucella* (both diploids).

Hieracium cymosum L. subsp. *cymigerum* (Reichenb.) Peter. The location of only one recent population is known from the Krkonoše Mts, foothills in the west (on the western side of the village of Víchovská Lhota). It grows there together with *H. glomeratum* and *H. pilosella.* It has the same pentaploid chromosome number and apomictic breeding system as those found in other localities, especially in N Bohemia (Šimek 2001, Fehrer et al. 2004).

The following species are not discussed separately: *H. pilosella* L. and *H. lactucella* Wallr. are sexual species, tetraploid and diploid, respectively. They show little morphological variation. *H. onegense* (Norrl.) Norrl. is discussed in detail by Krahulcová et al. (2001).

Intermediate species

Hieracium blyttianum Fr. is discussed in a separate paper (Krahulcová et al. 2001). The populations are morphologically similar, as are the DNA fingerprints.

Hieracium floribundum Wimm. et Grab. is invariably tetraploid and apomictic in the Krkonoše Mts and tetra- or pentaploid in the Jizerské hory Mts (Rotreklová et al. 2002 and unpubl.). There is little variation in isozyme phenotypes, and almost none in the Krkonoše Mts (except for a single unique individual). In the area of the Jizerské hory Mts, there are two isozyme phenotypes (one of them corresponding to that found in the Krkonoše Mts). The previously published diploid number for *H. floribundum* (Krahulcová et al. 2001) most likely is that of recent hybrid between *H. onegense* and *H. lactucella.* This is supported by the co-occurrence of both putative parental species and the experimentally produced hybrids have the same morphology.

Hieracium fuscoatrum Nägeli et Peter is discussed by Krahulcová et al. (2001).

Hieracium glomeratum Froel. This species is one of the commonest, occurring in meadows, disturbed places alongside roads and paths, and on piles of stones and old walls. In the area studied, tetraploids are rarer than pentaploids, the latter being represented by several clones. In fact, this species is more variable than *H. caespitosum*, one of its putative parents, and they are not easily distinguished morphologically (see above). This type is certainly not of recent origin; *H. cymosum*, one of its putative parents, is not present in the study area (and not even in its vicinity, see Šimek 2001 for details). One fact emerged from the hybridization experiments, this species hybridizes rather easily with some others like

H. lactucella and *H. pilosella.* Although they frequently grow together hybrids are very rare in the field (see also *H. tubulascens* and *H. scandinavicum* below).

Hieracium iseranum Uechtritz is morphologically very uniform and tetraploid throughout the whole study area. Several pentaploid specimens are recorded from other areas (Erzgebirge, S. Bräutigam). There was some variation among populations in isozyme phenotypes within the study area (three clones in total) but not at the locality level. *H. floribundum* and *H. pilosella* are generally considered to be the parents and haplotyping indicates that the apomictic *H. floribundum* was the mother plant. This is in full agreement with results from experimental hybridization. In contrast, when *H. pilosella* was used as the mother plant no progeny were obtained.

Hieracium macrostolonum G. Schneider is described from the Krkonoše Mts (Schneider 1888–1895). We recorded a corresponding type in the field, which proved to be hexaploid (Krahulcová & Krahulec 1999). However, according to the isozyme phenotype, this plant belongs to a particular clone of hexaploid *H. piloselliflorum* found at the same locality. Because of this, the present occurrence of this species in the field is unknown.

Hieracium piloselliflorum Nägeli et Peter (incl. *H. apatelium*), which fills the morphological space between *H. iseranum* and *H. pilosella* (Fig. 2), is morphologically highly variable and exists in several cytotypes (tetra-, penta- and hexaploids). The tetraploids are sexual or apomictic, the other ploidy levels apomictic. Particularly among the tetraploids, there are many genotypes (detected by fingerprinting or by isozyme analysis). The different haplotypes of *H. piloselliflorum* indicate that both parental species, *H. iseranum* and *H. pilosella*, acted as seed parents. The cross between *H. pilosella* (as a seed parent) and *H. iseranum* (both tetraploids) produced progeny corresponding morphologically to *H. piloselliflorum*. In addition, a similar morphotype corresponding to *H. piloselliflorum*, but pentaploid, was also obtained in the progeny of a cross between *H. rubrum* and *H. pilosella* (produced by fusion of reduced gametes of both species). Evidently, the situation in the field results from repeated crossing events, backcrosses and successive crosses between products of previous hybridizations. In spite of their morphological similarity, the types observed in the field could be of different origin (with respect to parental combinations). It is obvious that any classification of this complex system is likely to be difficult or even impossible. For that reason, we consider the solution suggested by Bräutigam & Schuhwerk (2002) as reasonable and pragmatic: lump all these types under *H. piloselliflorum*.

Hieracium rubrum Peter is a hybridogenous species. Nägeli and Peter (1885) considered *H. aurantiacum* and *H. pilosella* to be its parents. At the same time Schneider (1888–1895) and later Zahn (1922–1930) assumed *H. aurantiacum* and *H. flagellare* (*H. caespitosum–H. pilosella*) were the parents. Based on our hybridization experiments, the hexaploid *H. rubrum* is a hybrid between two tetraploids, *H. aurantiacum* (seed parent) and *H. pilosella*. It is highly likely that it is a so-called "addition hybrid" (Gadella 1988) formed by the fusion of an unreduced egg cell of *H. aurantiacum* and a reduced sperm cell of *H. pilosella*. The following support this view: (i) *H. rubrum* is close to *H. aurantiacum*, not in an intermediate position, possibly the effect of the prevailing genome of *H. aurantiacum* in the hybrid; (ii) *H. rubrum* segregates within the progeny in a similar way to *H. aurantiacum* (Mendel 1869, Christoff 1942, A. Krahulcová et al., unpubl.); (iii) in the subgen. *Pilosella*, unreduced eggs participate more readily in hybridization than unreduced sperm cells (Gadella 1988, Papoušková 2002, Krahulcová et al. 2004). However, there is evidently no relationship between *H. rubrum* and the most abun-

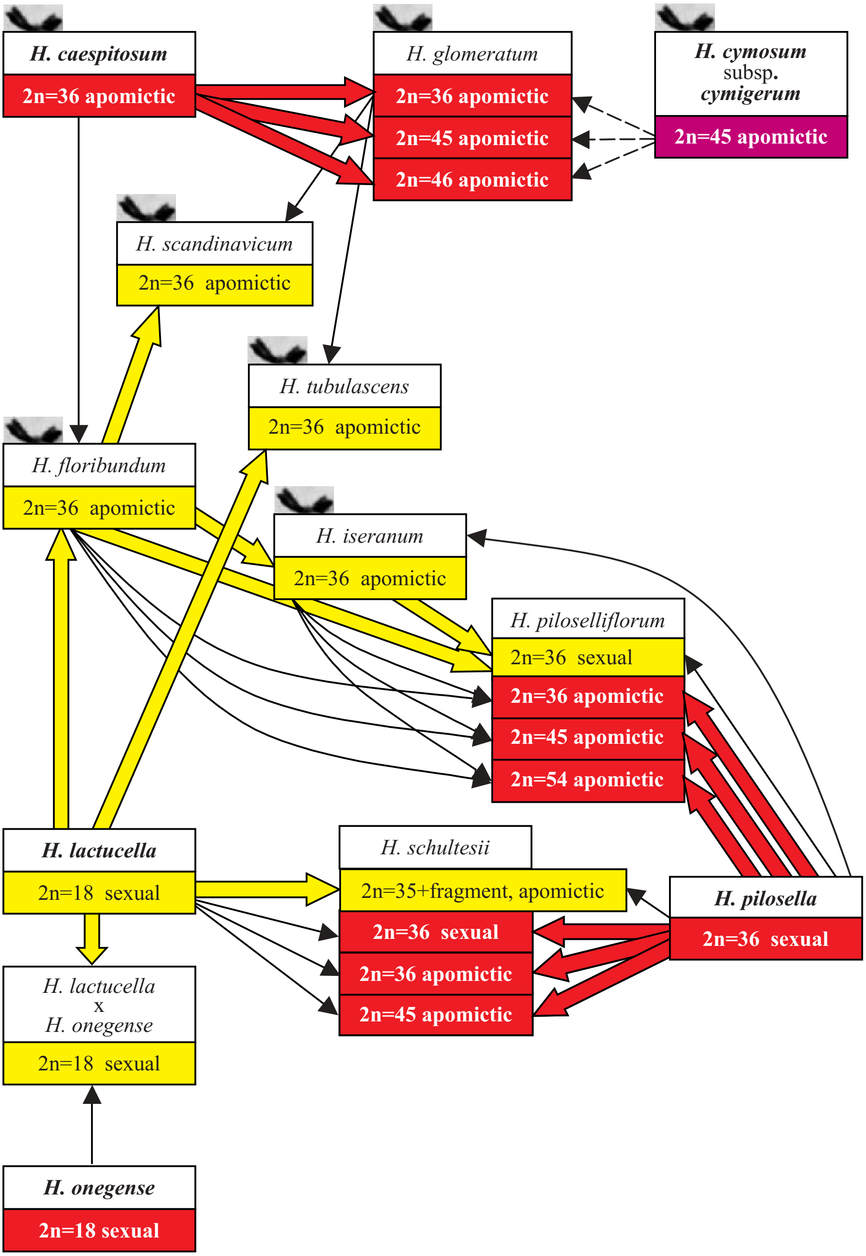

Fig. 2. – The relationships of particular taxa within the "yellow part" of the agamic complex. For every taxon, cytotypes and breeding systems are given. Arrows indicate the hypothetical origin of hybridogenous (intermediate) species. Different colours of cytotype blocks and block arrows correspond to the basic chloroplast haplotype groups (yellow – group I, red – group II, purple – *cymosum* subtype) indicating maternal origin. Black arrows refer to the inferred pollen donors. In the case of *H. floribundum* – *H. iseranum* – *H. piloselliflorum*, several possibilities are shown. The presence of a single big marker chromosome in the chromosome set is indicated above the respective species' boxes. The separation between this figure and the next was done to activate a better overview. Some of the basic species (in boldface) are involved in both complexes.

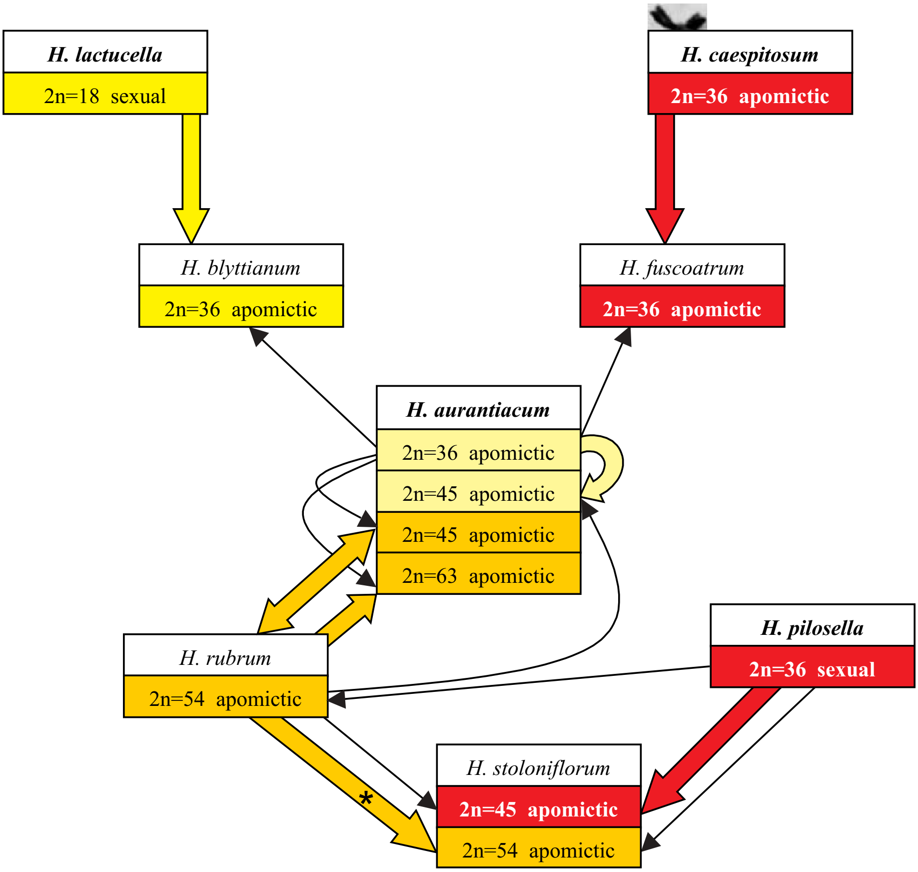

Fig. 3. – The relationships of particular taxa within the “orange part” of the agamic complex. For explanation see Fig. 2. Subtypes of the major chloroplast haplotype group I (see also Table 1) are presented in different shades of yellow. * indicates the possibility of the origin of *H. stoloniflorum* from *H. rubrum* alone (for details see text).

dant tetraploid types of *H. aurantiacum* currently present in the Krkonoše Mts. A part of pentaploid as well as tetraploid *H. aurantiacum* from this area have a small modification of the haplotype (deletion of 5 bp), and the *H. rubrum* and one clone of *H. aurantiacum* haplotypes lack this deletion and show an additional substitution; the latter creates a diagnostic restriction site. Isozyme phenotypes showed some variation. Repeated origin could be the most parsimonious explanation.

The same hexaploid level is recorded in this morphotype of *H. rubrum* from other regions, e.g. from the Alps (Schuhwerk & Lippert 1997) and Šumava Mts (A. Krahulcová et al., unpubl.). This suggests multiple origins, but a stabilized constitution with respect to the contribution of the parental genomes. In the Šumava Mts, where this morphotype of *H. rubrum* is a recent hybrid, its haplotype corresponds to that of *H. aurantiacum* (F. Krahulec et al., unpubl.), which supports our view.

Hieracium schultesii F. W. Schultz in our study area is not simply a triploid hybrid between *H. lactucella* and *H. pilosella* as in other areas (e.g. Schuhwerk & Lippert 1997, unpubl.). The types morphologically corresponding to *H. schultesii* in our study area are tetraploid or pentaploid and the tetraploids are sexual or apomictic. The chloroplast haplotype of two tetraploid plants analyzed (apomictic and sexual) indicates *H. pilosella* is the seed parent. Another tetraploid plant (2n = 35 + fragment) has *H. lactucella* haplotype. The situation in our study area is complicated because there is no clear limit between *H. schultesii* and *H. piloselliflorum*. The artificially produced hybrids between *H. lactucella* and both tetra- and pentaploid *H. piloselliflorum* indicate that at least some of the existing morphological types corresponding to *H. schultesii* arose in this way and smoothed out the boundaries between hybridogenous types.

Hieracium stoloniflorum Waldst. et Kit. is more complicated genetically than *H. rubrum*. This morphotype consists of two cytotypes and also displays different chloroplast haplotypes. The small clone of the pentaploid cytotype in the Krkonoše Mts (Krahulcová et al. 2001) is probably a product of backcrossing between hexaploid *H. rubrum* and tetraploid *H. pilosella* as the seed parent. Both putative parents occurred in close proximity at the same locality. The corresponding morphotype was obtained following artificial hybridization of these parental species and a reciprocal cross. The tetraploid plants found in the Šumava Mts (A. Krahulcová et al., unpubl.) possibly originated from a direct cross between the two tetraploid parents, *H. pilosella* and *H. aurantiacum*. The hexaploid plants found in the Krkonoše (Krahulcová & Krahulec 1999) might theoretically have been produced by hexaploid *H. rubrum* alone, by autogamy or a cross between *H. rubrum* clones. In experimental crosses between *H. rubrum* (as seed parent) and *H. pilosella* the *stoloniflorum* morphotype was obtained several times and was an heptaploid (7x) resulting from the fertilization of a reduced egg cell of *H. rubrum* by an unreduced sperm cell of *H. pilosella*. However, such heptaploids are unknown in the field.

Hieracium tubulascens Norrl. and *H. scandinavicum* Dahlst. are closely related to each other (Fig. 2). They differ only in proportions of parental genomes. *H. tubulascens* is possibly a hybrid between *H. lactucella* and *H. glomeratum* (*H. cymosum–H. caespitosum*), and *H. scandinavicum* between *H. floribundum* (*H. lactucella–H. caespitosum*) and *H. glomeratum*. We recorded *H. tubulascens* only once, a single specimen during systematic sampling of the richest population in the Krkonoše Mts. We classified this type as *H. tubulascens*, because it was the same as the artificial hybrid between these two species (for details see Krahulcová et al. 2001). Many individuals of *H. scandinavicum* were discovered by S. Hrňáková at one locality but not studied in detail. At a second locality, we found only one specimen of *H. scandinavicum.*

Taxonomic implications

It is evident that individual members of this apomictic complex are not fully comparable. Even the basic species are very different. Fully sexual species such as *H. lactucella, H. pilosella, H. onegense*, and partially also *H. cymosum* (which is found outside the study area) (Fehrer et al. 2004, Šimek 2001), have clear positions and taxonomic classifications. They behave like other sexual species in that populations are usually made up of many genotypes. The other two basic species are different. The facultatively apomictic *H. aurantiacum* has three cytotypes, the most common is tetraploid with at least two isozyme phenotypes, i.e. there are probably two genotypes in this area (Table 1). One of these genotypes is widespread in the Krkonoše, Erzgebirge and Šumava Mts. The other facultatively apomictic basic species, *H. caespitosum,* is even more homogeneous. Even

Table 2. – Survey of taxa reported from the Krkonoše Mts by Zahn (1922–1930) and Schneider (1888–1895). The taxa considered as species in the present paper are given in bold.

Zahn 1922–1930		Schneider 1888–1895
Species collectiva	Subspecies	
3. ***H. pilosella***	2. *impexum*	***H. pilosella***:
		grex *Trichophorum*: subsp. *trichophorum*
		grex *Latiusculum*: subsp. *amauroleucum*
		grex *Melanops*: subsp. *submelanops*
	72. *coalescens*	grex *Vulgare*: subspp. *parviflorum*, *trichocephalum*, *vulgare*, *hilmae*, *angustius*, *stenophyllum*, *indivisum*
	93. *pernigrescens*	grex *Subvirescens*: subspp. *chaetocaulon*, *subvirescens*, *nigrescens*, *virescens*
	128. *latiusculum*	grex *Brevipes*: subsp. *brevipes*
	153. *stenophyllum*	grex *Minuticeps*: subsp. *minuticeps*
	183. *microsphaera*	grex *Niveum*: subsp. *niveum*
11. ***H. auricula***[1]	12. *magnum*	H. auricula[1]: subspp. *melaneilema*, *auricula*, *acutisquamum*, *amaureilema*, *magnum*, *magnauricula*
		H. semiauricula
16. ***H. schultesii*** (*auricula–pilosella*)	3. *megalophyllum*	*H. auriculiforme* subsp. *megalophyllum*
	4. *schultziorum*	*H. schultesii*
	40. *typicum*	
34. ***H. aurantiacum***	5. *typicum*	*H. aurantiacum* subsp. *aurantiacum*
	6. *carpathicola*	subsp. *carpathicola*, subsp. *porphyranthes*
	7. *melinoides*	
	9. *hinterhuberi*	
42. ***H. blyttianum*** (*aurantiacum–auricula*)	4. *latibracteum*	*H. pyrrhanthes* (*aurantiacum-auricula*) (= **H. blyttianum**) subsp. *Goderianum*, *latibracteatum*
		H. stoloniflorum (*H. aurantiacum* × *pilosella*)
		H. rubripilosella (*H. pilosella*>*aurantiacum*)
43. *H. cernuatum* (*blyttianum–pilosella*)	2. *rubripilosella*	
49. ***H. rubrum*** (*aurantiacum*>*flagellare*)		*H. rubrum*
50. ***H. pratense***[2]	1. *sudetorum*	*H. pratense* subspp. *pratense* (incl. *brevipilum*), *sudetorum*, *dimorphum*
		H. prussicum (*pratense* × *pilosella*)
52. *H. flagellare* (*caespitosum–pilosella*)	17. *glatzense*	*H. flagellare* subspp. *flagellare*, *glatzense*, *tatrense*
	18. *tatrense*	
54. *H. cernuiforme* (*caespitosum* <*pilosella*)	7. *macrostolonum*	*H. macrostolonum*
55. *H. flagellariforme* (*flagellare–auricula*)	2. *euflagellariforme*	*H. flagellariforme*
56. ***H. floribundum*** (*caespitosum*>*auricula*)	5. *eufloribundum*	***H. floribundum*** grex. *Floribundum*: subsp. *floribundum*
	10. *teplitzense*	grex *Teplitzense*: subsp. *teplitzense*
	16. *suecicum*	grex *Erubescens*: subspp. *atramentarium*, *erubescens*
		H. suecicum (*floribundum* × *auricula*)
57. *H. longiscapum* (*caespitosum–auricula*)	11. *spathophyllum*	*H. spathophyllum* subsp. *diatentum*, *incertum*, *semiauricula*
59. ***H. iseranum*** (*floribundum*>*pilosella*)		*H. nigriceps* subsp. ***iseranum***
	1. *anguinescens*	
	4. *floridum*	
	10. *euiseranum*	
	14. *confinium*	*H. confinium*
	16. *atramentarioides*	

60. *H. apatelium* (*floribundum–pilosella*)		*H. apatelium*
	2. *bregense*	
	6. *pratigenum*	subsp. *pratigenum*
	8. *striiforme*	
	9. *aupaense*	
61. ***H. piloselliflorum*** (*floribundum<pilosella*)		*H. piloselliflorum* subsp. *striiferum*, *piloselliflorum*
	1. *eupiloselliflorum*	*aupaense*, *paxii*
63. ***H. cymosum***		*H. cymosum* subsp. *cymigerum*, *pulveratum*,
H. vaillantii	1. *pulveratum*	*suomense*, *suprafastigiatum*
67. *H. laaschii* (*cymosum<pilosella*)	26. *neogracile*	*H. canum* (*cymosum* × *pilosella*)
70. *H. sciadophorum* (*cymosum–auricula*)	1. *ignotum*	
82. ***H. ambiguum***[3] (*caespitosum–cymosum*)	1. *cymigeriforme*	*H. glomeratum* subsp. *cymigeriforme*
83. ***H. dubium***[4] (*cymosum–floribundum*)	1. *schweidnitzense*	
98. ***H. bauhinii***		*H. florentinum*
		grex *Obscurum*: subsp. *obscurum*, *Berninae*
		grex *Praealtum*: subsp. *praealtum*, *hirsuticeps*
		grex *Poliocladum* : *poliocladum*
		grex *Cuneense*: *basiphyllum*
C. magyaricum	5. *megalomastix*	grex *Megalomastix*: subsp. *megalomastix*
	13. *tephrops*	grex *Magyaricum*: subsp. *filiferum*
	19. *filiferum*	
H. bauhinii		grex *Bauhinii*: subspp. *arvorum*, *transgressum*
D. eubauhinii	29. *arvorum*	
	35. *viscidulum*	
		H. brachiatum (*florentinum seu magyaricum* × *pilosella*)
124. *H. atramentarium* (*piloselloides>aurantiacum*)	1. *euatramentarium*	
	2. *chryptochristum*	
		H. subhyperboreum (*florentinum>pyrrhanthes*)
137. *H. zizianum* (*piloselloides–cymosum*)	1. *subfarinosum*	*H. zizianum* subspp. *petasodes*, *leptophyllum*
	18. *leptophyllum*	
		H. arvicola (*florentinum-pratense*)

[1] *H. lactucella*, [2] *H. caespitosum*, [3] *H. glomeratum*, [4] *H. scandinavicum*

the more abundant of the *H. caespitosum* cytotypes (tetraploid) is a single clone distributed over a wide geographical area (Fehrer et al. 2004). The degree of variability in particular hybridogenous members of the apomictic complex differs. Some species have an invariable ploidy level and consist locally of a few isozyme phenotypes on the Krkonoše mountain range (*H. rubrum, H. iseranum*). In other species, there are many cytotypes, different breeding systems and many isozyme phenotypes (genotypes) within one locality (*H. piloselliflorum*). This makes it difficult to apply strict criteria to their taxonomic evaluation (see also discussion in Fehrer et al. 2004).

Types found in the past but unknown at present

The area of the Krkonoše Mts was studied in detail towards the end of the 19th century. A full list of taxa reported by Schneider (1888–1895) and Zahn (1922–1930) is given in

Table 2. For most species many subspecies are given (e.g. for *H. iseranum, H. aurantiacum,* etc.). This is rather strange, especially for those types for which restricted variation was found in this study. At least for some taxa, it is likely that the variation at the individual level (within members of a single clone) was evaluated as being taxonomically important. Conversely, it seems probable that in other species more types occurred here in former times, unfortunately many herbarium specimens were destroyed at the end of WW II in Breslau (Wrocław). Taxonomy of some of the types recorded in the past is currently evaluated differently. *H. aurantiacum* subsp. *carpaticola*, which was reported from the area of Pomezní Boudy (Grenzbauden), may serve as an example. At present, this morphological type is classified as *H. fuscoatrum*, because chloroplast haplotype and morphology indicate that *H. caespitosum* is one of the parents. However, the definite identification of old data is impossible without herbarium specimens.

However, it is very difficult to claim that the decrease in the number of taxa is real. It may be related to major changes in land use during the second half of the 20th century. This is highly probable for the group related to *H. bauhinii*, which occurs at present only in the foothills of the mountains. This species was found only once at higher altitudes (Krahulcová et al. 2001). In contrast, some taxa are currently rather rich in genotypes in the field and it is difficult to establish more closely related groups and draw correlations with the subspecies described earlier. The present richness of forms of *H. piloselliflorum* is certainly larger than the number of subspecies described for this species and for *H. apatelium*, which is also now included in this species. Below we present several examples of taxa that are currently unknown from the study area:

Hieracium rubripilosella G. Schneider. Schneider (1888–1895) described this species as a red flowering *H. pilosella*. We have no indication of present occurrence of a corresponding type in the field and can only speculate about its nature. It should be noted that we obtained a morphologically similar type from crosses between *H. rubrum* and *H. pilosella*. Part of the progeny of these crosses originated as addition hybrids, by the fusion of an unreduced egg cell of *H. rubrum* and reduced sperm cell of *H. pilosella.* The resulting octoploid plants were morphologically very homogeneous, resembling *H. pilosella* but with red inflorescences.

Hieracium flagellare Willd. (*H. caespitosum–H. pilosella*). Although many types of this hybridogenous species were found in the study area during the 19th century, it seems to be absent at present.

Hieracium flagellariforme G. Schneid. (*H. flagellare-H. lactucella*), found in the Krkonoše Mts by Schneider (1888–1895), was not recorded.

Many subspecies of *H. caespitosum* and *H. floribundum* were reported from this region. *H. caespitosum* subsp. *sudetorum* (accepted as species in the narrower concept of e.g. Schljakov 1989) was described from the Krkonoše Mts by Peter (as *H. collinum* subsp. *sudetorum*). As both species showed almost no variation in the Krkonoše Mts (see also Fehrer et al. 2004) there is no evidence for the existence of separate entities. Individuals with red-striped ligullae are regularly found and represent individual variation within one clone.

It seems likely that the evolution and extinction of types is ongoing and occurs over a relatively short time-scale (from an evolutionary perspective). These processes are strongly dependent upon land use and the presence, formation and loss of suitable habitats.

General conclusions

The results of the study of the individual species suggest that they are little comparable with respect to their variation. Thus, the species level is presently applied to very distinct biological categories. For sexual species, the species category is fully comparable with that used in other groups, characterized by many genotypes within a species and clear limits between most species. However, there are some basic species, mainly apomictic, which are represented by a limited number of genotypes only. The position of hybridogenous species is more complicated. For practical purposes, it is impossible to distinguish each genotype as an independent species. Some of the morphological species are represented by both sexual and apomictic strains originating repeatedly from reciprocal crosses, as is documented e.g. for *H. piloselliflorum* (Fehrer et al. 2004). This species is an example of multiple origins by different pathways. In contrast, we found limited genetic variation within some taxa formerly reported as having many variants (subspecies) in the study area. It is possible that the variants mainly represented individual variation.

Acknowledgements

We thank the Deutsche Forschungsgemeinschaft (grant Fe512/1-1 to J. F.) and Grant Agency of the Academy of Sciences of the Czech Republic (grants no. A6005803 and IAA6005203 to A. K. and F. K.). The work was supported by the institutional research concept no. AV0Z6005908 and project no. KSK6005114, both funded by the Academy of Sciences of the Czech Republic. The field research was supported by the administration of the Krkonoše National Park, who allowed us to perform detailed studies in the area. We also acknowledge the help of Karin Kottová, Mária Loncová, Eva Morávková, Lída Mikovcová, Věra Rydlová and Jan Štěpánek, who helped us in the field, cared for plants in the garden and worked in the laboratory. Gary Houliston (Fairbanks, Alaska) is acknowledged for many comments and language correction, Tony Dixon (Norwich) for final language editing. Many participants of the annual *Hieracium* workshops are acknowledged for stimulating discussions, especially Franz Schuhwerk (Munich) for his invaluable discussions about plant identification.

Souhrn

Apomiktický komplex jestřábníků (*Hieracium* subgen. *Pilosella*) v Krkonoších vznikl křížením těchto základních druhů: *H. lactucella* (2x, sexuální), *H. onegense* (2x, sexuální), *H. pilosella* (4x, sexuální), *H. caespitosum* (4x, 5x, apomiktický) a *H. aurantiacum* (4x, 5x, apomiktický). Strukturu komplexu jsme analyzovali z následujících hledisek: stupně ploidie, způsob rozmnožování (fakultativní apomixe nebo úplná sexualita), isozymové fenotypy odrážející genetickou homogenitu jednotlivých typů, způsob vzniku hybridogenních taxonů (analýzou matroklinně děděné chloroplastové DNA, tzv. haplotypů) a frekvence výskytu. Souhrn údajů pro všechny druhy je uveden v tab. 1. Jednotlivé hybridogenní druhy se liší jak frekvencí výskytu, tak různorodostí isozymových fenotypů, tj. odhadem minimálního počtu genotypů (klonů). Většina z nich má uniformní chloroplastový haplotyp, společný s jedním z rodičovských druhů. Některé hybridogenní druhy však sdílejí oba haplotypy předpokládaných rodičovských druhů, což ukazuje na jejich vznik reciprokým křížením. Z porovnání haplotypů vyplývá, že apomiktické typy byly často mateřskými rostlinami při hybridizaci a vzniku nových hybridogenních typů. Tato skutečnost ukazuje na velký význam zbytkové sexuality při evoluci celé skupiny. *H. pilosella* považujeme za centrální druh celého komplexu: hybridogenními typy je spojen s *H. lactucella, H. floribundum a H. aurantiacum* (obr. 2, 3). Tyto soubory hybridogenních typů mají obdobnou genetickou strukturu. Některé druhy vznikly opakovaně, různým způsobem. Naopak křížením stejných rodičů je možno získat variabilní potomstvo, které je klasifikováno jako odlišné hybridogenní druhy. Tab. 2 uvádí přehled všech taxonů udávaných v dřívějších zpracováních této skupiny jestřábníků v pracích Schneidera (Schneider 1888–1895) a Zahna (Zahn (1922–1930); tyto taxony jsou krátce diskutovány. V některých případech šlo nepochybně pouze o taxonomicky nevýznamnou individuální variabilitu, další taxony se již v přírodě nevyskytují, některé další případy považujeme za nejasné, které není možno řešit kvůli absenci dokladového materiálu. Použití velkého množství metodických přístupů na populační úrovni doporučujeme jako možnou cestu k řešení komplikovaných vztahů v této taxonomické skupině.

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Received 24 May 2004
Revision received 8 July 2004
Accepted 12 July 2004