The structure of the agamic complex of *Hieracium* subgen. *Pilosella* in the Šumava Mts and its comparison with other regions in Central Europe

Jestřábníky *Hieracium* subgen. *Pilosella* na Šumavě: struktura agamického komplexu a srovnání s dalšími středoevropskými regiony

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Dedicated to the memory of the late František Procházka (1939-2004), who stimulated and supported our work

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We studied the agamic complex of *Hieracium* subgen. *Pilosella* in the Šumava/Böhmerwald, the borderland between the Czech Republic and Germany. Their DNA ploidy levels/chromosome numbers, breeding systems, chloroplast haplotypes as well as the clonal structure of apomicts were determined. The complex consists of the following basic and intermediate species and recent hybrids. Basic species: *H. aurantiacum* L. (tetraploid and pentaploid, both apomictic), *H. caespitosum* Dumort. (tetraploid, apomictic), *H. lactucella* Wallr. (diploid, sexual), *H. pilosella* L. (tetraploid, sexual); intermediate species: *H. floribundum* Wimm. et Grab. (tetraploid, apomictic), *H. glomeratum* Froel. (tetraploid and pentaploid, both apomictic), *H. scandinavicum* Dahlst. (tetraploid, apomictic); recent hybrids: *H. floribundum* × *H. pilosella* (partly corresponding to *H. piloselliflorum* – tetraploid and hexaploid; tetraploid sexual or apomictic), *H. glomeratum* × *H.pilosella* (aneuploid, $2n = 38$), *H. aurantiacum* × *H. floribundum* (tetraploid, almost sterile or apomictic), *H. lactucella* × *H. pilosella* (*H. schultesii*, triploid sterile, tetraploid sexual), *H. aurantiacum* × *H. pilosella* (*H. stoloniflorum*, tetraploid, sexual), *H. aurantiacum* > *H. pilosella* (*H. rubrum*, hexaploid). The hexaploid hybrids between *H. pilosella* and *H. floribundum* or *H. aurantiacum* produced mainly polyhaploid progeny. Two trihaploid plants were found growing in the neighbourhood of their putative hexaploid maternal parent *H. rubrum*, which is the first record of polyhaploids of this subgenus in the field. Comparison with other mountain ranges (especially the Krušné hory/Erzgebirge, and Krkonoše) with an almost identical composition of basic species, revealed that the structure of the agamic complexes differ.

Keywords: apomixis, chloroplast haplotype, chromosome number, cytotype, DNA fingerprinting, hybridization, polyhaploids, polyploidy, reproduction

Introduction

The genus *Hieracium* is one of the most complicated genera in the temperate flora. Both the European subgenera, *Hieracium* and *Pilosella*, consist of (many) morphologically defined species and intermediate types of hybridogenous origin. Diversity within the subgen. *Pilosella* is due to many factors (reviewed by Krahulcová et al. 2000, Fehrer et al. 2007b). Most important are (i) variation in breeding systems (facultative apomixis with strongly different degrees of manifestation, haploid parthenogenesis, allogamy, induced autogamy, clonal growth), and (ii) frequent hybridization and occurrence of polyploidy. Field studies indicate that populations comprise many types that are of hybrid origin, some with local and others with a wide distribution (Krahulec et al. 2004b, Fehrer et al. 2005).

The taxonomic treatment of this subgenus varies in different parts of Europe; for a recent evaluation of approaches and species concepts see Schuhwerk (2002) and Krahulec & Krahulcová (2006), for the Nordic countries Tyler (2001, 2005). In Central Europe, the approach of Nägeli & Peter (1885) is followed in most of the broad monographs and local floras (Zahn 1922-1930, Nyárády 1965, Gottschlich 1998, Schuhwerk & Fischer 2003, Bräutigam & Schuhwerk 2002, 2005, Chrtek 2004), or modified as in Bräutigam & Greuter (2007). All these authors distinguish basic species and intermediate species, the latter being most probably of hybridogenous origin. Sell & West (1976) used basic species and all hybridogenous types with the same combination of parents lumped together. The main problem that emerged when this concept was applied is how to classify many local pecularities, which appear within both basic and intermediate species. Many of the intermediate species consist of recent hybrids as well as old hybridogenous biotypes of the same origin (parentage), but with different distributions, ecological behaviour and sometimes also morphology. For this reason we use the neutral word "type" for all these pecularities, which sometimes are of the same origin and genotype composition, and sometimes of the same morphotype. Recently, we developed a complex approach based on studies of whole populations, not just selected types, in order to elucidate the processes underlying the variation (Krahulec et al. 2004b, Fehrer et al. 2005, 2007b). The population structure of the whole species complex was studied with respect to cytotypes, breeding systems, distribution of genotypes (isozyme phenotypes or DNA fingerprints) and distribution of chloroplast haplotypes (maternal origin) within morphologically defined species. This approach was applied in a detailed study of the populations occurring in the Krkonoše Mts which are part of the Sudetes mountain range (summarized in Krahulec et al. 2004b) and the results compared with those for adjacent regions (Jizerské hory Mts, Lausitz and parts of the Erzgebirge Mts; Fehrer et al. 2005). The resulting patterns were rather complex within the whole agamic group. *Pilosella* populations in the study area are mostly formed by basic and stabilized hybridogenous species and recent hybrids are uncommon. More than half of the types of hybrid origin have more than one ploidy level and there are pronounced differences in the number of genotypes (estimated as isozyme or multilocus DNA phenotypes). Basic species have mostly only one chloroplast haplotype which allowed us to identify the parents of hybridogenous types in many cases.

Several questions remained, for example (i) do the same set of basic species form the same pattern of hybrids within an agamic complex under different ecogeographic conditions, (ii) do the basic and hybridogenous species in other regions show the same pattern of distribution of chloroplast haplotypes, and (iii) do the same morphologically defined apomictic taxa have similar patterns and distributions of genotypes?

For this reason we did a similar study in the Šumava Mts, a mountain range isolated from the formerly studied area by a distance of about 250 km. It is a region with a comparable pattern of forest and grassland resulting from past human activities, which experienced similar socio-economic changes after the 2nd WW, and comparable environmental conditions: similar climate and a generally acidic substrate. On the other hand, the Sudetes had a different florogenesis, being more closely connected with the Carpathians, whereas the Šumava has more affinities with the Alps (Hendrych 1987). During this research, which was strongly encouraged by the late František Procházka, we found during joint excursions in 2001 and 2002 several hybridogenous types that were new for his Flora of the Šumava/Böhmerwald (Procházka 2004). František Procházka provided support by organizing field excursions and drawing our attention to some localities with diverse *Hieracium* populations. In addition, Zdeněk Skála showed us some interesting localities and supplied a collection of plants from the *H. aurantiacum–H. floribundum* swarm.

Study area

The mountain range studied is named Šumava in Czech, Böhmerwald in German (Bayerischer Wald is the official German name for that part of the range situated in Bavaria). It is formed by several parallel ridges with some broad valleys at relatively high altitudes (above 700 m). The highest point (Großer Arber, 1456 m) is situated on the Bavarian side of the border. Except for the highest point, the mountains were fully forested in the past; the only areas with scattered trees (mostly spruce) were the slopes above glacial lakes (Sofron & Štěpán 1971). Large peat bogs are common and the largest are of late glacial age (Svobodová et al. 2001).

The bedrock mostly consists of acidic, medium to finely coarse granit, gneisses and granodiorite (Kodym 1963). Base rich rocks are almost absent, with some limestone only in the foothills. The area was deforested and colonized very early; e.g., there was a big settlement at Studenec (a Celtic one?) rather close to the main ridge, at an altitude of 980 m more than 2000 years ago (Sklenář et al. 1993). Later on, there were villages even at altitudes above 1000 m. They were surrounded by deforested land, which was used as arable land at lower altitudes and pastures and grasslands (for hay production) at higher altitudes. These grasslands and pastures were suitable habitats for many species (incl. *Hieracium* subgen. *Pilosella*), which spread into these deforested areas. After the 2nd WW, most of the inhabitants were relocated to Germany, and the density of permanent settlements decreased, especially at higher altitudes. Many of the former villages do not exist any longer because of the construction of the border defences along the “iron curtain”. The treeless character of part of the current landscape was maintained by the military training areas, which ceased after the political changes at the beginning of the 1990s. These socio-economic changes strongly influenced land use and the habitats for *Pilosella* populations. They survived in cut or grazed grasslands and occur commonly in irregularly disturbed places, e.g., those areas of woodland clear felled and used for military exercises and road margins, etc.

State of knowledge about *Hieracium* subgen. *Pilosella* in the Šumava Mts

For the Czech part of this mountain range, relatively little data exists on the distribution of individual species and hybrid types. Peter (1886) described the occurrence of several species and hybrids on the Bavarian and Czech sides of the mountains. Data from the small Austrian part of the mountains are rare and unsuitable for incorporation into this paper.

Floristic novelties of *Pilosella* in the Czech part of the Šumava were recently described by Procházka and colleagues (Hadinec et al. 2003, 2004, Procházka 2004). First reports of chromosome numbers or ploidy levels are in Rotreklová et al. (2002), Krahulec & Krahulcová (2006) and Krahulec et al. (2004a). The Bavarian part of the range was studied by Schuhwerk & Lippert (1991), who paid most attention to foothill areas.

Methods

Collection and treatment of the plant material

The main period of this study was 2001–2003, from the second half of June until the beginning of July. We collected flowering specimens of the basic and hybridogenous types of the subgen. *Pilosella* in the field; living plants were transplanted to the experimental garden of the Institute of Botany at Průhonice. As soon as possible after collection, we isolated DNA and determined chromosome number or measured DNA ploidy level using flow cytometry. Usually during the following season, the breeding system was studied. Herbarium specimens were prepared at the time of collection from plants in the field and from material cultivated in the experimental garden. These specimens are deposited in the herbarium of the Institute of Botany (PRA). A small number of plants died during our investigation and for these there are no herbarium specimens, as they were rejected because of potential misidentification in the field. After preliminary field determination all plants were re-determined by comparison with voucher specimens; in the case of inconsistent results from molecular or cytological analyses, the plants were studied in detail again by S. Bräutigam. All the localities of the plants used in this study are given in Appendix 1.

Determination of chromosome number, DNA ploidy level and mode of reproduction

Chromosome numbers were counted in root-tip meristems of cultivated plants as described by Krahulcová & Krahulec (1999). DNA ploidy level was determined using flow cytometry, following the method of Krahulcová et al. (2004). Plants with known chromosome numbers served as internal standards.

The reproductive mode was determined by comparing the seed production of open pollinated and cut (emasculated) capitula (cf. Krahulcová & Krahulec 1999). In addition, the mode of reproduction of hexaploid hybrids was determined by crossing them with a tetraploid sexual *H. pilosella* as the pollen parent, followed by flow cytometric determination of the ploidy level categories of the progeny (Krahulcová et al. 2004). This procedure identified the way the progeny were produced (i.e., by apomixis, haploid parthenogenesis, or different sexual processes).

Molecular analyses

DNA was isolated from fresh material by the method of Štorchová et al. (2000). For analysis of chloroplast haplotypes, restriction patterns of the amplified *trn*T-*trn*L intergenic spacer were used to distinguish between two major haplotype groups (*Pilosella* I, II) and several subtypes within each group (Krahulec et al. 2004b, Fehrer et al. 2005, 2007b). PCR amplifications were done as described in Fehrer et al. (2007a). About 50–100 ng of amplified product were digested overnight with 20 units of *Eco*RI according to the manufacturer's instructions (Fermentas), and separated on 2.5% agarose gels (Serva) to discriminate between the major haplotype groups and the subgroup specific for *H. cymosum*. For further discrimination between the ordinary haplotype of *Pilosella* I and a subtype occurring in some *H. aurantiacum* accessions, which differ by a 5 bp-deletion (Fehrer et al. 2007b), restriction digests were repeated for plants with *Pilosella* I pattern, and the products separated on 3% high resolution agarose (USB/Amersham) in TTE buffer (containing 28.7 mM taurine instead of boric acid because of glycerol tolerance).

The clonal structure was at first qualitatively inferred from cytotypes and cpDNA haplotypes (differences in either indicate separate genotypes). For apomicts not differing in both features, multilocus DNA fingerprinting was applied in order to distinguish further clones. DNA fingerprinting was done by conventional Southern hybridization (i) with the human minisatellite probe 33.15 directly labeled with alkaline phosphatase and (ii) with a digoxigenin-labelled $(GATA)_5$ microsatellite probe; the CDP-Star™ chemiluminescent reagent was used for detection (for details see Fehrer et al. 2005 and Wilson et al. 2006). Both methods produce individual- or clone-specific patterns that can be qualitatively assigned to particular genotypes.

Results

Species composition and chromosome number/ploidy level

Altogether 123 plants (accessions) were studied for ploidy level or chromosome number (Appendix 1, Fig. 1). The *Hieracium* subgen. *Pilosella* population on the Šumava mountain range consists of four basic species: *H. pilosella* (tetraploid), *H. lactucella* (diploid), *H. caespitosum* (tetraploid), and *H. aurantiacum* (usually tetraploid, rarely pentaploid). A few the intermediate species are already established hybridogenous species: *H. floribundum* (tetraploid), *H. glomeratum* (tetraploid and pentaploid) and *H. scandinavicum* (tetraploid). The rest are recent hybrids, usually confined to one or two localities (except *H. piloselliflorum*), often forming a small stand and mostly co-occurring with their putative parents: *H. aurantiacum* × *H. pilosella* (tetraploids morphologically corresponding to *H. stoloniflorum*, hexaploids to *H. rubrum*), *H. aurantiacum* × *H. floribundum* (tetraploid), *H. floribundum* × *H. pilosella* (mostly tetraploid, once hexaploid, both cytotypes corresponding in morphology to *H. piloselliflorum*), *H. lactucella* × *H. pilosella* (triploid, once tetraploid, both corresponding to *H. schultesii*) and *H. glomeratum* × *H. pilosella* (one aneuploid accession, $2n = 38$).

The presence of a single long marker chromosome (Krahulcová & Krahulec 1999) was observed in the karyotypes of all tall yellow-flowering types with a branched stem: *H. caespitosum*, *H. glomeratum*, *H. floribundum* and *H. scandinavicum*, and in addition in the hexaploid accession of *H. piloselliflorum*, which probably originated from a recent cross between *H. floribundum* × *H. pilosella* (see also Fig. 1).

Chloroplast haplotypes

The chloroplast haplotypes found were the same as in the previously investigated areas (Krahulec et al. 2004b, Fehrer et al. 2005), but their distribution among the species differed in some cases (Fig. 1).

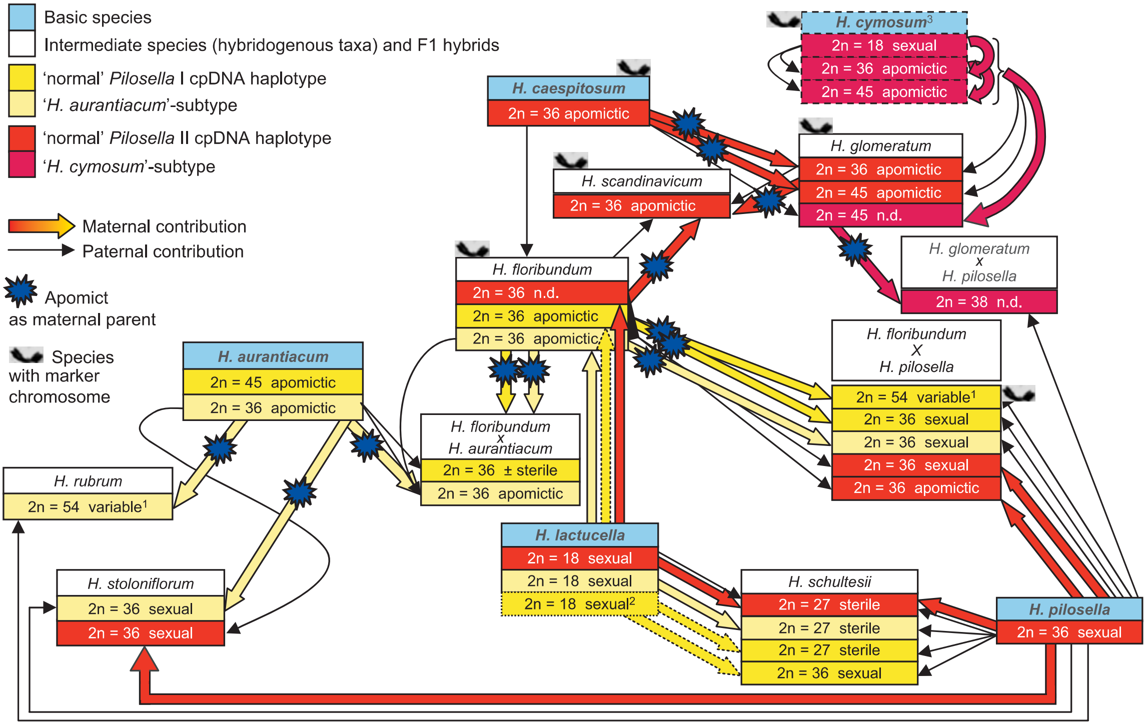

Fig. 1. – Scheme of the agamic complex
[1] apomictic, polyhaploid and various sexual offspring, see text
[2] existence assumed, as no plants of this haplotype have been found in the Šumava Mts
[3] *H. cymosum* does not occur in the Šumava Mts., see text
n.d. not determined

Basic species: *H. caespitosum* and *H. pilosella* have a type II haplotype. In *H. aurantiacum*, the *Pilosella* type I was present in the characteristic 'aurantiacum' modification, but also in the normal variant I. *Hieracium lactucella* had type II and the 'aurantiacum' variant of type I. The normal *Pilosella* type I of this species is also postulated to occur in the Šumava Mts as hybrids between *H. lactucella* and *H. pilosella* are recorded there and should have contributed to some accessions of *H. floribundum* (see Fig. 1). The number of field samples of *H. lactucella* was apparently not sufficient to detect this type. When collecting samples, this diploid was not considered to be problematic and therefore few samples of it were collected, but the high diversity of haplotypes in the small sample indicates that more variation exists in *H. lactucella* in this region than expected.

In the three hybridogenous species, *Pilosella* type I with both subtypes (normal, aurantiacum) and additionally *Pilosella* II cpDNA were represented in *H. floribundum*. *Hieracium glomeratum* had the major *Pilosella* type II with two subtypes: tetraploids the normal subtype and pentaploids the 'cymosum' plus normal subtypes. *Hieracium scandinavicum* had the normal subtype of the major type II. Recent hybrids had the cpDNA haplotypes of their putative parents suggesting multiple origin, in most cases even by reciprocal crosses.

Modes of reproduction

Among the four basic species, *H. pilosella* and *H. lactucella* were sexual, and *H. caespitosum* and *H. aurantiacum* facultatively apomictic. All stabilized hybridogenous types (*H. glomeratum*, *H. floribundum*, *H. scandinavicum*) were apomicts. Triploid hybrids (at least three different clones of *H. schultesii*) were sterile. Tetraploid hybrids were sexual, almost sterile or apomictic: those with at least one sexual parent mostly sexual (*H. stoloniflorum* of reciprocal origin, at least three different types of *H. piloselliflorum*, one accession of *H. schultesii*). At least two clones of *H. aurantiacum* × *H. floribundum* were almost sterile; one accession of each *H. aurantiacum* × *H. floribundum* and *H. piloselliflorum* apomictic.

The emasculation test indicated that the hexaploid types (two clones of *H. rubrum*, one of *H. piloselliflorum*) are apomictic (i.e., they produced seed autonomously after decapitation) and produced overall little seed. Analysis of the progeny (cultivated seedlings) showed that all three clones produced a high proportion of parthenogenetically derived polyhaploids. When these hybrids were pollinated using tetraploid sexual *H. pilosella* (which is a backcross, because *H. pilosella* was one of the parental species in each hexaploid biotype), a high proportion of trihaploids and/or of pentaploid hybrids were detected in the progeny. The proportion of true apomictic (hexaploid) progeny varied greatly among the three accessions. The proportions of particular ploidy levels, which indicate the respective origin of the progeny, are given in Figs 2 and 3. This untypical breeding system is labelled 'variable' in Fig. 1.

Clonal structure

The clonal structure of particular apomictic taxa occurring at different localities or taxa with different chloroplast haplotypes at the same locality were studied. Details are given in Table 1 and Appendix 1.

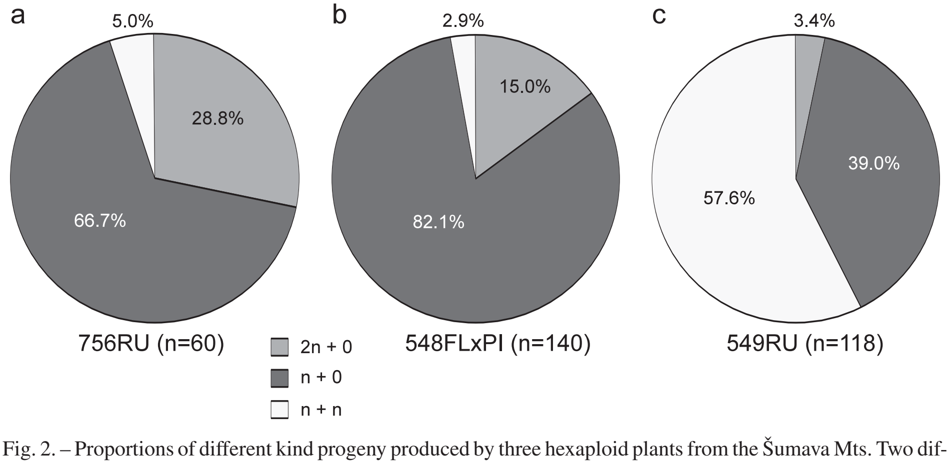

Fig. 2. – Proportions of different kind progeny produced by three hexaploid plants from the Šumava Mts. Two different *H. rubrum* genotypes (756, 549) and a hybrid between *H. floribundum* and *H. pilosella* (548) were investigated. 2n + 0 – apomictic progeny; n + 0 – progeny from haploid parthenogenesis; n + n – hybrid progeny.

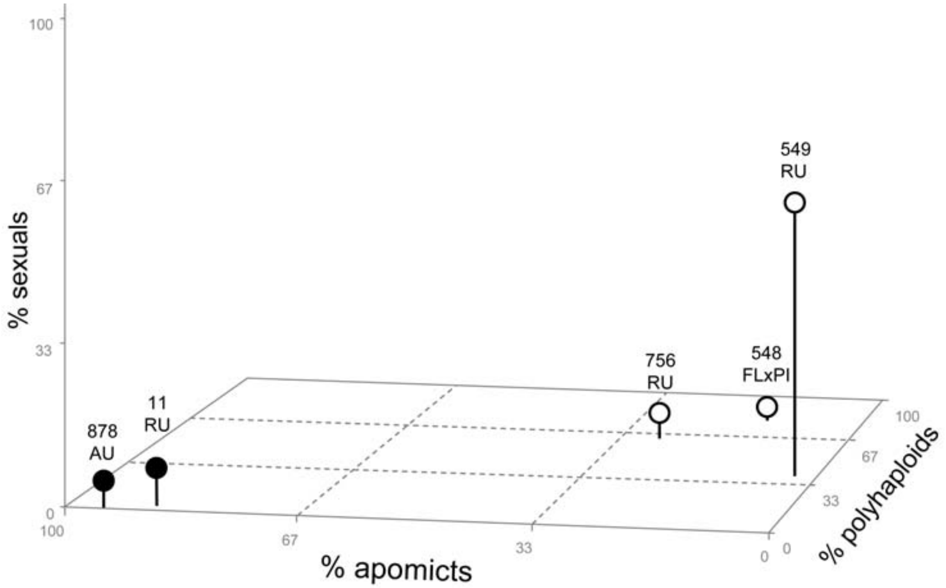

Fig. 3. – Diagram showing the position of two stabilized apomicts, *H. aurantiacum* (878AU, Šumava) and *H. rubrum* (11 RU, Krkonoše), and three unstabilized hybrids from the Šumava (756RU, 549RU, 548FLxPI) in three-dimensional space reflecting the proportions of apomictic, sexual and polyhaploid progeny after experimental crossing with *H. pilosella* as a pollen donor; some autogamous progeny could not be distinguished from true apomictic progeny by flow cytometry.

Table 1. – Clonal structure of selected apomictic species and hybrids of *Hieracium* from the Šumava Mts. For the source data see Appendix 1.

Species	Number of plants studied	Minimum number of clones
H. aurantiacum (5x)	3	1
H. aurantiacum (4x)	16	1
H. scandinavicum	10	3
H. glomeratum (5x, ‘cymosum’ haplotype II)	6	1
H. glomeratum (5x, normal haplotype II)	2	1
H. glomeratum (4x)	3	1
H. floribundum (normal haplotype I)	9	3
H. floribundum (‘aurantiacum’ haplotype I)	11	1
H. floribundum (haplotype II)	1	1
H. aurantiacum × *H. floribundum* (normal haplotype I)	5	4
H. aurantiacum × *H. floribundum* (‘aurantiacum’ haplotype I)	1	1
H. caespitosum	4	1
H. rubrum	3	2

Two different clones, with distinct ploidy levels and chloroplast haplotypes, exist in *Hieracium aurantiacum*. The tetraploid clone with the 'aurantiacum' haplotype was the most frequent and occurred at seven localities. The pentaploid type was found only at one locality and differed from the tetraploid in haplotype, having the normal haplotype I. *Hieracium caespitosum* consisted of a single clone. Two accessions of *H. rubrum*, collected at the same place in different years, belonged to the same genotype; another plant from a different locality belongs to a different genotype (Appendix), which suggests that it had an independent origin. The striking differences in the relative proportions of the respective offspring produced by the two genotypes of *H. rubrum* is surprising. Both clones very probably contain an identical genome of a particular genotype of tetraploid *H. aurantiacum* and differ only in the paternal contribution (diploid pollen) from sexual *H. pilosella* (Fig. 2a, c). *Hieracium floribundum* is comprised of several different, widespread as well as local genotypes. Three of them occurred among the individuals with 'normal' haplotype I. They are very similar. It cannot be excluded that some of them, especially those with a local distribution, could result from (back)crosses with *H. scandinavicum*. All the *H. floribundum* plants with the 'aurantiacum' haplotype belonged to the same widespread clone. *Hieracium glomeratum* should consist of at least three different genotypes according to the ploidy levels and haplotypes. One tetraploid genotype from Gerlova Huť (FL×GL C in Appendix 1) was found in plants assigned to either *H. glomeratum* or *H. scandinavicum*. Finally, the plants with this genotype were classified as *H. scandinavicum*. One pentaploid genotype of *H. glomeratum* was widespread and found in all plants with the 'cymosum' haplotype. When the rest of individuals were subjected to DNA fingerprinting, plants with different cyto- or haplotype were found to be identical. When these cultivated accessions were checked, it turned out that the respective pots had been colonized by a different *H. glomeratum* genotype. As DNA was re-isolated for these analyses in order to obtain sufficiently high concentrations for fingerprinting, the results from fingerprinting obviously did not refer to the same plants and were therefore discarded. *Hieracium scandinavicum*, apart from the clone that might correspond to tetraploid *H. glomeratum* (see above), consisted of two further genotypes. For the hybrid *H. floribundum* × *H. aurantiacum*, each individual represented a different genotype, four of them even occurring at the same locality.

Difficulty of determination in the Šumava region, and remarks on selected species and hybrids

As mentioned above, *H. floribundum* is connected with *H. glomeratum* by a number of morphotypes, named here as *H. scandinavicum*. There are several other determination problems: the recent hybrid between *H. glomeratum* and *H. pilosella* was initially determined as a hybrid between *H. lactucella* and *H. pilosella*; its identity was questioned because of the presence of haplotype II subtype 'cymosum', which is present only in pentaploid *H. glomeratum* in this region. The co-occurrence of both putative parents (*H. glomeratum* and *H. pilosella*) at this locality together with the hybrid confirms the final determination. Another difficulty is connected with the fact that sexual products of *H. aurantiacum* segregate with respect to flower colour: it varies from yellow to red-orange, sometimes also yellow-and-orange. Yellow products of hybridization between *H. aurantiacum* (and also of *H. rubrum*) and *H. pilosella* correspond morphologically to *H. piloselliflorum*. There is another problem, which was encountered during our work in the Krkonoše Mts. The number of different intraspecific taxa reported by previous authors is high for both sexual and apomictic types. It is not easy to correlate these taxa with the clones (genotypes) we detected. On the other hand, identification at the clonal level allowed us to solve some taxonomic problems unequivocally (Fehrer et al. 2005). In the Šumava, we fortunately did not meet the situation common in the Krkonoše where the number of infraspecific taxa is several times higher than number of clones we determined (e.g. *H. floribundum*, *H. caespitosum*, *H. aurantiacum*).

Basic species

Hieracium aurantiacum L. – Most accessions of this species are extremely homogeneous: tetraploids correspond fully to subsp. *aurantiacum* and pentaploids to subsp. *auropurpureum* Zahn. On the basis of a recent study on the variation in genome size in the subgenus *Pilosella* (Suda et al. 2007), we hypothesize that pentaploids could be products of a backcross between hexaploid *H. rubrum* and tetraploid *H. aurantiacum*. The nuclear DNA content of the respective species and cytotypes fit this hypothesis. For individual species, the following Cx-values (monoploid genome size) were found: *H. rubrum* 1.84 pg, pentaploid *H. aurantiacum* 1.90 pg and tetraploid *H. aurantiacum* 1.95 pg. Further support for this hypothesis comes from the distribution of their chloroplast haplotypes in the Krkonoše Mts, where the pentaploid *H. aurantiacum* and hexaploid *H. rubrum* have the same ‘rubrum’ subtype, different from that found in the tetraploid *H. aurantiacum*. Last but not least, the pentaploid plants have a more open inflorescence than the tetraploid plants (see also Zahn 1922–1930 for the description of subspecies *auropurpureum*), which suggests past hybridization with a species having a branched inflorescence. On the other hand, the density of stellate hairs in the pentaploid *H. aurantiacum* is not greater than in tetraploid cytotype, although one of the putative parents, *H. rubrum*, is distinct from *H. aurantiacum* in this character.

Hieracium caespitosum Dumort. – The plants analysed all belong to the same clone in all the regions investigated so far, even those introduced into Pacific North America (Wilson et al. 2006). Taxonomically, they correspond to *H. c.* subsp. *caespitosum* (Fehrer et al. 2005).

Hieracium lactucella Wallr. – Peter (1886) has four infraspecific taxa, but their correlation with the haplotype groups detected by us is unclear. Some morphological variation occurs within this species as it is a fully sexual type, but we do not evaluate the variants as different taxa.

Hieracium pilosella L. – Peter (1886) has eight infraspecific taxa. Again, their correlation with known ploidy levels is impossible, and the existing morphological variation in the study area is due to the obligate sexual reproduction of the dominant tetraploid cytotype. We do not evaluate the variants as different taxa.

Intermediate hybridogenous species

Hieracium floribundum Wimm. et Grab. – It is variable with respect to clonal structure and haplotypes. Peter (1886) cites three taxa: ‘*H. floribundum* α. *genuinum*’, which corresponds to the most common type, and two other taxa, *H.* (*f.*) *atramentarium* Nägeli et Peter and *H.* (*f.*) *atrocroceum* Peter could be related to some types with introgression of *H. aurantiacum*. However, the recent hybrids between *H. floribundum* and *H. aurantiacum*, at least those in the Šumava region, were found to be apomictic or almost sterile and are treated as primary hybrids of these parents (see Appendix).

Hieracium glomeratum Froel. – In the study area, it is variable with respect to ploidy levels and haplotypes. This fact suggests repeated origin. Peter (1886) gives two infraspecific taxa, viz. *H.* (*g.*) *subambiguum* Nägeli et Peter and *H.* (*g.*) *cymigeriforme* Nägeli et Peter. The latter corresponds to the widespread clone occurring in the Krkonoše Mts, the Jizerské hory and Upper Lusatia. As the Šumava types do not clearly correspond to any given subspecies and the existing variation in that area is not large, we do not distinguish subspecies there.

Hieracium scandinavicum Dahlst. – It is represented in the study area by stabilized types, which probably consist of backcrosses with both parental taxa (*H. floribundum*, *H. glomeratum*). Consequently, it is not homogeneous morphologically, filling the morphological space between both parents, as indicated by the three clones in the 10 plants analysed (Table 1, Appendix 1). To this species belong data under *H. dubium* L. s.l. published by Schuhwerk & Lippert (1991: 371).

Recent hybrids

Hieracium aurantiacum × *H. floribundum* (*H.* ×*dorei* Lepage) – We analysed six plants, at least five of them being distinct clones. This suggests independent origin at different localities as well as within one locality (see Appendix). Backcrosses and repeated crosses seem to be improbable due to apomixis and/or semisterility of the hybrids in the Šumava region. A remarkable variation in flower colour recorded especially in the population at Hadí vrch could correspond to repeated independent origin of the individual hybrids, as *H. aurantiacum* also segregates in this respect (Christoff 1942).

Hieracium aurantiacum × *H. pilosella* – Within the study area, there is no type with the features of a stabilized hybrid. Three collections that correspond morphologically to *H. stoloniflorum* Waldst. et Kit. are evidently primary n + n hybrids; they are tetraploid and sexual (the breeding system was studied in all accessions collected in the field). They arose independently from reciprocal crosses. Two other collections corresponding to *H. rubrum* are hexaploid 2n + n hybrids; they also arose independently at two different localities; their breeding system is variable, i.e., they produce both parthenogenetically derived progeny and hybrids (Figs. 2 and 3). This hybrid was found in this mountain range in the past. It is documented in the herbarium in Munich by a specimen with the following label: "*H. stoloniflorum* (= *aurantiacum* × *pilosella*) Wb: bei Fürstenhut [Knížecí Pláně] (Böhmen) 1/2 Std. v. d. bayer. Grenze. [Bohemia, half an hour from the Bavarian border] 4. Aug. [19]09 leg. F. Vollmann. Blüte, die auf dem Transporte leider verloren ging, purpurn! Sonst ganz wie *pilosella*. Unter den Eltern. z1. [Capitulum was unfortunately lost during transport, purple/red! Otherwise entirely like *pilosella*. Among the parents. z1.]"

Hieracium floribundum × *H. pilosella* L. – Several accessions corresponding to this parental combination were found; the tetraploid plants corresponding morphologically to *H. piloselliflorum* Nägeli et Peter were evidently n + n hybrids. According to their marked variation in chloroplast-haplotypes and breeding systems, they arose independently at the respective localities. None of them behave as a stabilized type at the landscape scale. One hexaploid accession (no. 548) was morphologically different (similar to plants known as *H. iseranum* Uechtr. or *H. apatelium* Nägeli et Peter from the Sudetes); with respect to its morphology (taller individual with more capitula) it was probably a 2n + n hybrid; its breeding system was variable (see above and Figs 2 and 3). The assumed origin of this hexaploid hybrid is also supported by genome size data (Suda et al. 2007), which fit a 2n (*H. floribundum*) + n (*H. pilosella*) hybridization.

Hieracium glomeratum × *H. pilosella* – This type was found only once in the field and initially determined as a *pilosella-lactucella* hybrid, but because of its ‘cymosum’ haplotype and aneuploid chromosome number (2n = 38), it was finally determined as a hybrid between pentaploid *H. glomeratum* and tetraploid *H. pilosella* (both parents occur at the respective locality). Later on, Procházka (2004) collected two further samples, which fully correspond to the hybrid combination described as *H. macranthelum* Nägeli et Peter.

Hieracium lactucella × *H. pilosella* (*H. schultesii* F. W. Schultz) – These hybrids were collected several times at several localities. They also originated several times, and are sterile and triploid or sexual and tetraploid. They do not form stabilized types in this area.

Discussion

Structure of the *Hieracium* subgen. *Pilosella* complex in the Šumava is given in Fig. 1. Here we discuss its comparison with other mountain regions.

Species and cytotype composition

The set of basic species is the same as in the previous studies except for *H. onegense*, which is at its western distribution limit in the Krkonoše and absent in the Šumava Mts. Also, the structure with respect to cytotypes of the basic species is similar in the Šumava and the Krkonoše/Erzgebirge: *H. aurantiacum* is tetra– or pentaploid in both regions, *H. lactucella* diploid, and *H. caespitosum* tetraploid. An additional pentaploid clone of *H. caespitosum* occurs in the Erzgebirge and is apparently introgressed by *H. cymosum* (Fehrer et al. 2005). It may correspond to the pentaploid plants from the Šumava with the same chloroplast haplotype identified as *H. glomeratum*. *Hieracium pilosella* is tetraploid and sexual in both regions, but recently, a pentaploid type was found at one locality in the Šumava area (Františkov between Kvilda and Borová Lada, Urfus 2006, Mráz et al. 2008).

Two hybridogenous species (*H. glomeratum*, *H. floribundum*) are also common in other mountain ranges in Central Europe. The hybridogenous species resulting from hybridization between these two, *H. scandinavicum*, is common in the Šumava, but rare in the other regions (Krahulec et al. 2004b, Chrtek 2004). Its rarity in Germany is reflected by the fact that it is not recorded by Bräutigam & Schuhwerk (2002) and Gottschlich (1998). In the newest edition of Rothmaler’s Flora, it is reported from the Bayerischer Wald (Bräutigam & Schuhwerk 2005), i.e., from the German part of the Šumava mountain range. For Austria, there is only a passing remark about it in Schuhwerk & Fischer (2003). In the Šumava Mts, *H. scandinavicum* originated repeatedly and probably backcrossed with both parents as is indicated by the broad range of morphotypes in the field. Consequently, the taxonomic delimitation between *H. scandinavicum* and *H. glomeratum* or between *H. scandinavicum* and *H. floribundum* is difficult in the Šumava region. Molecular analyses also show that DNA fingerprints of these three taxa are more similar than usual for apomictic *Pilosella* clones.

In contrast to the Krkonoše, Erzgebirge and Jizerské hory, the stabilized hybridogenous taxon *H. iseranum* is not present in the Šumava although both putative parents, *H. floribundum* and *H. pilosella*, occur there. While they hybridize in the Šumava, they produce there a broad range of morphotypes classified as *H. piloselliflorum*. In the

Krkonoše, this species is one of the most common taxa and originates there recurrently from the crosses between *H. iseranum* and *H. pilosella*. In both regions, *H. piloselliflorum* is not stabilized, but consists mostly of recent hybrids. With respect to the few individuals that were found at only three localities in the Šumava, its variation with respect to mode of reproduction, cyto- and haplotypes is rather high. Another hybridogenous species, *H. blyttianum* (*H. aurantiacum* × *H. lactucella*), is present in the Krkonoše, but not found in the Šumava Mts despite co-occurring parental species. While *H. schultesii* and *H. rubrum* behave as stabilized hybridogenous types in the Krkonoše, they behave as recent hybrids in the Šumava Mts (see discussion below).

The recent hybrids present in the Šumava are rather diverse and differ from those recorded in the Krkonoše. In spite of the fact that several pairs of prospective parental species (*H. aurantiacum*–*H. floribundum*, *H. glomeratum*–*H. pilosella*) are common in these regions, we did not find any hybrids between them. Only the hybrid between *H. glomeratum* and *H. pilosella* is recorded for the Ještědské pohoří (Czech Republic) and Oberlausitz (Germany) (Petřík et al. 2003). However, it is rare compared to the common occurrence of both parental species and the ease which with they cross under experimental conditions (Krahulcová & Krahulec 2001).

Morphotypes assigned to *H. stoloniflorum* in the Krkonoše and Šumava Mts are of different origin, which is reflected in their ploidy levels. In both regions, there are recent hybrids, not stabilized types. In the Šumava, *H. stoloniflorum* is a primary sexual hybrid between two tetraploid parents, *H. aurantiacum* (apomictic) and *H. pilosella* (sexual). It has been found three times (see Appendix 1), two accessions of which originated from reciprocal crosses. In contrast, in the Krkonoše, the apomictic pentaploid *H. stoloniflorum* is a product of a backcross of *H. rubrum* to *H. pilosella* while the origin of apomictic hexaploids is unclear.

H. schultesii, consisting of recent hybrids resulting from reciprocal crosses between *H. lactucella* and *H. pilosella*, formed sexual tetraploids in both regions, but predominantly triploid sterile hybrids in the Šumava and tetra- and pentaploid apomicts in the Krkonoše.

Clonal structure

The clonal structure of several species is similar to that found in the Krkonoše Mts. *Hieracium caespitosum* and *H. aurantiacum* have widespread clones in both regions. Their tetraploid clones are identical in both mountain ranges suggesting that these 'species' may actually consist of single genotype, at least in Central Europe. *Hieracium floribundum* is a mix of local and widespread genotypes in both regions: two clones in the Krkonoše/Jizerské hory, four in the Erzgebirge, and four in the Šumava. *Hieracium glomeratum* is composed of one widespread and one local clone in the Krkonoše/Jizerské hory, a single different one in the Erzgebirge and at least three others in the Šumava. *Hieracium scandinavicum* in the Šumava Mts has a similar pattern, with three different genotypes, but it does not occur or is very rare in the other regions (see above). These stabilized species of hybrid origin form recurrently, either infrequently or only a small selection of genotypes survive in the field. In contrast to these, all the recent hybrids studied originated many times. For example, in the hybrid *H. aurantiacum* × *H. floribundum*, each plant is a different clone, and tetraploid *H. piloselliflorum* is made up of a mixture of chloroplast haplotypes and reproductive modes, each corresponding to at least one genotype.

Chloroplast haplotypes

In the Krkonoše Mts (Krahulec et al. 2004b), the nearby Jizerské hory and Erzgebirge (Fehrer et al. 2005), there is only one major haplotype in each basic species, but some variation in Krušné hory/Erzgebirge, where there are two different subtypes of *H. lactucella*. In this respect, the situation in the Šumava is different: in two of the basic species, *H. lactucella* and *H. aurantiacum*, there are three and two haplotypes, respectively. For *H. lactucella*, this is the first report of a basic species with haplotypes of different major groups, which are supposed to have originated in different glacial refugia (Fehrer et al. 2007b). This fact is reflected in a more complicated structure of both, hybridogenous species and primary hybrids, both with a correspondingly higher number of haplotypes (e.g., *H. floribundum* and its hybrids with *H. aurantiacum*). Several haplotypes per species also indicate a repeated origin of these types, which influence the haplotype occurrence in hybrids of higher order, of which hybridogenous species were the parents. Unfortunately, this fact does not allow us to use chloroplast haplotypes as unequivocal evidence for inferring the origin of hybrids as in previous studies.

It is unknown which pattern is more common within the subgenus *Pilosella* in Europe: the pattern found in the Krkonoše Mts or that in the Šumava Mts. Future research should study these systems in different parts of Europe.

The distribution of chloroplast haplotypes confounds the explanation and interpretation of the underlying pattern and processes. The presence of the ‘aurantiacum’ cp-haplotype in *H. floribundum* could be caused by two different processes: (i) origin from repeated hybridization events between the basic species *H. caespitosum* and *H. lactucella* (with all three haplotypes present in *H. floribundum*, see Fig. 1) or (ii) as a result of hybridization and subsequent introgression (haplotype capture) between *H. floribundum* and *H. aurantiacum*. To answer such questions, species- or rather ancestor-specific molecular markers would have to be developed to trace the original lineages of the hybridogenous species. Knowledge of the haplotype patterns at a broader scale can also elucidate whether the situation observed is specific for this mountain range or not.

Breeding systems

Breeding systems of basic and hybridogenous species corresponded to those recorded in the Krkonoše Mts: *H. lactucella* and *H. pilosella* were sexual (except one apomictic pentaploid population, Urfus 2006, Mráz et al. 2008) and all others apomictic. The situation in recent hybrids was more complicated: triploid *H. schultesii* was sterile and three of the hybrids between *H. aurantiacum* and *H. floribundum* were almost sterile. Some other recent hybrids were either sexual or apomictic. The discovery of hexaploids with a “variable” breeding system opens up a new perspective because such plants (which the decapitation test seemed to indicate were apomictic) are unknown. Recently, we recorded such biotypes also among the progeny of experimentally obtained hybrid hexaploid plants, which also produce a different proportion of apomicts, polyhaploids and sexually produced hybrids. For one hexaploid *H. rubrum* genotype from Šumava (756 RU), a part of its hexaploid progeny, which we originally considered as a product of apomixis, were found to have resulted from autogamy (the progeny was hexaploid, but yellow-flowering because of segregation). Autogamy in subgen. *Pilosella* can be stimulated by the presence of foreign pollen on the style (mentor effect, Krahulcová et al. 1999). In this case, all reproductive pathways known within the subgenus *Pilosella* were recorded in a single plant: apomixis, haploid parthenogenesis, autogamy, allogamy and clonal growth by means of stolons. This example demonstrates the enormous complexity of their breeding systems. The fully sexual and almost fully apomictic plants are situated at opposite ends of the scale, more precisely the two apices of a triangle; the third possibility is the prevailing production of polyhaploids. There are plants that show different proportions of these three types of reproduction, all accompanied by clonal growth. A three-dimensional graph (Fig. 3) shows the position of the plants found in this study compared to two "good" apomicts, viz. *H. rubrum* (11 RU) from the Krkonoše Mts and *H. aurantiacum* (878AU) from the Šumava Mts.

From the data presented here, it is evident that recent hybrids are not equivalent to stabilized hybridogenous types. Addition (2n + n) hybrids with variable breeding system are in fact "bad" apomicts and should be treated as hybrids. In the case of the Šumava Mts, hexaploid *H. aurantiacum* × *H. pilosella* is of 'rubrum' morphotype, but it is different from a "good" apomict, *H. rubrum*, described from Krkonoše, which can be true endemic of this region, in spite of the occurrence of 'rubrum' morphotypes in other regions. These findings contradict the recent discussion in Krahulec (2006). However, the differences found here can help to understand apomictic taxa and enable their protection in areas where they behave as hybridogenous species (cf. Gregor & Matzke-Hajek 2002); no special conservation treatment is needed in areas where they are products of recent hybridization. To confirm whether our finding is of general validity, studies in other areas are needed.

Do polyhaploid plants occur in the field?

There are no records of *Hieracium* polyhaploid plants occurring in the field. It is easy to detect a polyhaploid plant, if the ploidy level of its mother plant is known. However, there is no test to prove unequivocally that a plant occurring in the field is of polyhaploid origin. The general belief is that polyhaploids are poor plants, which cannot survive under field conditions. This, for example, is the case for the polyhaploids of stabilized types originating from *H. rubrum* in the Krkonoše (trihaploids produced during experiments – Krahulcová et al. 2004). Trihaploids produced by recent hexaploid hybrids from the Šumava grew normally and behaved like other standard plants when cultivated in a garden. After realizing this, many sterile rosettes occurring in the vicinity of one hexaploid plant were collected in the field (549 RU), as they are known to produce a high proportion of polyhaploids under experimental conditions. Using flow cytometry, we detected two different triploid plants among the 63 sterile rosettes collected, which we suppose to be trihaploids. Using DNA fingerprints revealed that the genotypes of the two triploids were identical. Therefore, vegetative multiplication of trihaploids is possible in the field. Figure 4 shows two triploid plants: one is a trihaploid plant obtained under experimental conditions from the maternal accession 549 RU, the second is a supposed trihaploid found close to this accession in the field. Supporting this interpretation for this area, only one diploid plant, *H. lactucella*, occurs which has a very distinct morphology. It could theoretically produce triploids by hybridising with tetra- or pentaploids of other species, but the triploid plant we found in the field did not show any of the morphological characters of *H. lactucella*.

Fig. 4. – Photographs of two triploids: The plant on the left is a putative trihaploid found in the vicinity of a plant of hexaploid *H. rubrum* (549RU) in the field at Slučí Tah; the plant on the right is a trihaploid progeny of the same plant grown in an experimental garden. The yellow colour reflects segregation: *H. rubrum* is of hybrid origin.

The role of apomictic species in the formation of an agamic complex

The study in the Krkonoše, Jizerské hory and Krušné hory/Erzgebirge Mts revealed to our great surprise that about half of all the hybridogenous species and recent hybrids had an apomictic type as a maternal parent (Krahulec et al. 2004b, Fehrer et al. 2005). The same is true for the Šumava Mts. Figure 1 shows all cases where an apomict served as the egg donor in the hybridization events. From this it is evident that the degree of residual sexuality of apomicts is an important factor when estimating the probability of hybrids being produced. This characteristic is largely unknown for apomicts in general although facultative apomixis is known in other plant groups. It is also evident that the level of residual sexuality differs amongs different clones even within the same ‘species’; this makes the situation even more complicated.

There is yet another question connected with the sexual reproduction, that occurs occasionally even in apomicts along with haploid parthenogenesis and true apomixis. Several times we have indicated that because of residual sexuality and common hybridization, inferring chromosome numbers of maternal plants from chromosome counts of their seedling progeny is uncertain (e.g., Krahulcová et al. 2000). This is strongly supported by the fact that some recent hybrids, considered to be apomicts because they produce seed autonomously (parthenogenetically) in emasculated inflorescences, produce mainly polyhaploid seeds or hybrids after pollination. Such “apomictic” hybrids are also reported in this paper (see Results – breeding systems). Thus, the determination of chromosome numbers of germinated seeds or seedlings of facultative apomicts could cause problems if it is assumed that the progeny are true to type, i.e., strictly apomictic. Therefore, published data based on seedlings, not mature plants from the field, need to be evaluated with great caution. In Fehrer et al. (2007b), we propose a set of guidelines for avoiding pitfalls when investigating the population structure of agamic complexes.

The reasons for the differences in agamic complexes distributed in several Central European mountain regions

In spite of the fact that both regions, Šumava and Krkonoše Mts, have an almost identical set of basic species, the structure of the agamic complexes differ. One of the reasons for this is certainly the probability of hybridogenous species like *H. iseranum*, *H. blyttianum*, or *H. rubrum* developing. All of them occur in the Krkonoše Mts, but only an equivalent of *H. rubrum* occurs in the Šumava Mts; however, the latter produces few truly apomictic progeny and therefore does not spread, and both clones occur only locally. On the other hand, only one population of *H. scandinavicum* is known from the Krkonoše, but in the Šumava area it is one of the most common hybridogenous types; its clonal structure indicates it originated at least three times (Appendix 1).

The origin of some hybridogenous species is unlikely to be recent. For example, *Hieracium rubrum* in the Krkonoše has a chloroplast haplotype, which differs from the haplotype of its putative parent (tetraploid *H. aurantiacum*) currently growing in this area (Krahulec et al. 2004b, Fehrer et al. 2005), but corresponds to that of pentaploid *H. aurantiacum*. On the other hand, recent hybridization seems to play a larger role in the Šumava Mts than in the Krkonoše area. Hybridization occurs only in some localities in the Šumava Mts. What is common to these localities is recent disturbance, which probably increased the probability of establishment of novel genotypes. But as such places also occur in the Krkonoše the higher proportion of recent hybrids in the Šumava Mts remains unexplained. The higher number could theoretically result from increased combination possibilities due to the greater abundance of clones (genotypes) of several putative parental species. This could increase the probability of successful hybridization, in which different degrees of residual sexuality of apomicts may lead to a higher probability of sexual events between compatible genotypes. However, this remains a theoretical possibility at the moment. For example in *H. floribundum*, despite the occurrence of multiple genotypes in the Krušné hory and Šumava Mts and the presence of the same single genotype of *H. aurantiacum* in both regions, hybrids between these two apomicts only occur in the latter mountain range. Many factors should be taken into account, including chance effects. This topic has not received much attention, but may serve to identify and explain the hybridization hot spots producing the new types, which are scattered throughout Europe.

Comparison with the situation in the German part of the mountain range

A comparison with the situation on the Bavarian side of the mountains is difficult because there the *Pilosella* populations are mainly only investigated floristically and less so morphologically. Therefore, we mostly list the occurring types along with brief comments (Appendix 2). For the development of large *Pilosella* populations, the conditions on the Bavarian side of the mountains are less favourable than on the Bohemian side, for two reasons:

First, on the Bavarian side, wide plateaus are mostly missing; from the border crest, the mountains mostly have steep woody slopes down to elevations below 800 m. The little agriculturally productive land on the crest was used as pastures (so called "Schachten"), but not for mowing. Second, land use and landscape histories strongly differ from those on the Bohemian side; the decolonization and emigration to the cities in the early 20th century resulted mostly in a reafforestation of the open country previously used for agriculture. The remaining ground was exploited much more extensively than on the Bohemian side, most of all it was fertilized. Not only immediate fertilization, but also lateral nitrogen transfer left little suitable space for the development of the mostly weakly competitive *Pilosella* plants, let alone for the formation of large populations. Thus, on the Bavarian side of the Böhmerwald, they are for the most part plants of the wayside, roadside and embankments.

A part of the population also spread from the north side of the ridge of the Bayerischer Wald (= Böhmerwald) to the south side, situated close to the Danube river. On the southwest facing slopes, these species came into contact with species in the foothills, like *H. piloselloides* or *H. cymosum*. These populations, apparently were still large in the thirties of the 20th century, but are now extinct (Schuhwerk & Lippert 2002); in the present-day pastures *H. pilosella* occurs only infrequently along the edges.

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Souhrn

Na české straně Šumavy jsme studovali složení agamického komplexu jestřábníků podrodu *Pilosella*. Určili jsme jejich ploidii (podle obsahu DNA, pomocí průtokové cytometrie) či počet chromosomů, reprodukční způsob a chloroplastový haplotyp. Celý komplex se skládá z těchto základních druhů: *H. aurantiacum* L. (tetraploidní či pentaploidní, vždy apomiktické rozmnožování), *H. caespitosum* Dumort. (tetraploidní, apomiktické), *H. lactucella* Wallr. (diploidní, sexuální), *H. pilosella* L. (tetraploidní, sexuální). Dále byly studovány tyto intermedierní (hybridogenní druhy): *H. floribundum* Wimm. & Grab. (tetraploidní, apomiktické), *H. glomeratum* Froel. (tetraploidní či pentaploidní, obě ploidie apomiktické), *H. scandinavicum* Dahlst. (tetraploidní, apomiktické). V přírodě byla dále nalezena celá řada recentních hybridů: *H. floribundum* × *H. pilosella* (částečně morfologicky odpovídající *H. piloselliflorum* – tetraploid sexuální či apomiktický, hexaploid s nově definovaným proměnlivým reprodukčním systémem), *H. glomeratum* × *H. pilosella* (aneuploid, 2n=38), *H. aurantiacum* × *H. floribundum* (tetraploidní, téměř sterilní či apomiktické), *H. lactucella* × *H. pilosella* (*H. schultesii*, triploid sterilní, tetraploid sexuální), *H. aurantiacum* × *H. pilosella* (morfotyp *H. stoloniflorum* tetraploidní, sexuální), *H. aurantiacum* > *H. pilosella* (morfotyp *H. rubrum*, hexaploidní, proměnlivý reprodukční systém). Nově rozlišený proměnlivý reprodukční systém nalezený u hexaploidních hybridů je charakterizován poměrně malým podílem čistě apomiktického potomstva a různým podílem polyhaploidů (až 80 %) a hybridů. V terénu byly nalezeny dvě trihaploidní rostliny v těsné blízkosti mateřského klonu *H. rubrum*; zřejmě se jedná o první nález polyhaploidních jestřábníků v přírodě. V práci je provedeno i srovnání s bavorskou stranou pohoří. Srovnání s ostatními dosud studovanými pohořími ukázalo, že navzdory téměř identické sestavě základních druhů je struktura agamického komplexu odlišná. Odlišné je i zastoupení chloroplastových haplotypů u základních druhů.

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Appendix 1. – Hybridogenous complex of *Hieracium* subgen. *Pilosella* in the Šumava Mts. List of plants studied. Abbreviations of collectors: FK – F. Krahulec; FP – F. Procházka; SB – S. Bräutigam; FS – F. Schuhwerk; JC – J. Chrtek. (M) specifies the occurrence of the marker chromosome. n.d. = not determined.

Accession	Locality	Latitude N	Longitude E	Altitude	2n/ ploidy	Reproductive mode	Haplotype group (subtype)	Fingerprint genotype of apomicts
H. pilosella L.								
733 PI	Jelení Vrchy: FK, SB, FP & FS 2002	48°56.981'	13°47.182'	820 m	4x	sexual	II (normal)	
734 PI	Jelení Vrchy: FK, SB, FP & FS 2002	48°56.981'	13°47.182'	820 m	4x	sexual	n.d.	
739 PI	Jelení Vrchy: FK, SB, FP & FS 2002	48°48.902'	13°52.756'	892 m	4x	sexual	n.d.	
882 PI	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	sexual	II (normal)	
771 PI	Zhůří near Kašperské Hory: FK, FP, SB, FS & JC 2002	49°05'25"	13°33'00"	1140 m	4x	sexual	II (normal)	
888 PI	Filipova Huť: FK 2003	49°01.401'	13°30.664'	1058 m	4x	n.d.	II (normal)	
891 PI	Slučí Tah: FK 2003	49°09.182'	13°21.003'	876 m	4x	n.d.	II (normal)	
900 PI	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	n.d.	II (normal)	
903 PI	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	n.d.	II (normal)	
543 PI	Hadí vrch near Hartmanice: FP & FK 2001	49°11.090'	13°20.744'	958 m	36	sexual	II (normal)	
765 PI	Strašín: FK, FP, SB, FS & JC 2002	49°10.984'	13°37.794'	586 m	4x	n.d.	II (normal)	
768 PI	Nové Hutě: FK, FP, SB, FS & JC 2002	49°02.189'	13°38.531'	1014 m	4x	sexual	II (normal)	
764/2 PI	Horská Kvilda: FK, FP, SB, FS & JC 2002	49°03’36.7"	13°33’37.9"	1130 m	4x	sexual	n.d.	
268 PI	Stožec: FK 1999	48°51'30"	13°49'20"	780 m	36	sexual	n.d.	
H. lactucella Wallr.								
865 LA	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	2x	n.d.	II (normal)	
864 LA	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	2x	n.d.	I (aurantiacum)	
889 LA	Filipova Huť: FK 2003	49°01.401'	13°30.664'	1058 m	2x	n.d.	II (normal)	
269 LA	Kvilda: FK 1999	49°00'40"	13°34'40"	1050 m	18	n.d.	n.d.	
272 LA	„Novohůrecké rašeliniště“ peatbog: FK 1999	49°10'00"	13°20'00"	920 m	18	n.d.	n.d.	
H. caespitosum Dumort.								
881 CE	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	n.d.	II (normal)	CE A
760 CE	Zhůří near Kašperské Hory: FK, FP, SB, FS & JC 2002	49°05'25"	13°33'00"	1140 m	4x	apomictic	II (normal)	CE A
757 CE	Slučí Tah: FK, FP, SB, FS & JC 2002	49°09.182'	13°21.003'	876 m	4x	n.d.	II (normal)	CE A
748 CE	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	n.d.	n.d.	
H. aurantiacum L.								
759 AU	Zhůří near Kašperské Hory: FK, FP, SB, FS & JC 2002	49°05'10"	13°33'50"	1160 m	5x	n.d.	I (normal)	AU B

Accession	Locality	Latitude N	Longitude E	Altitude	2n/ ploidy	Reproductive mode	Haplotype group (subtype)	Fingerprint genotype of apomicts
769 AU	Zhůří near Kašperské Hory: FK, FP, SB, FS & JC 2002	49°05'10"	13°33'20"	1120 m	5x	apomictic	I (normal)	AU B
880 AU	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	5x	n.d.	I (normal)	AU B
883 AU	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	n.d.	I (aurantiacum)	AU A
884 AU	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	apomictic	I (aurantiacum)	AU A
878 AU	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	apomictic	I (aurantiacum)	AU A
533 AU	Zhůří near Kašperské Hory: FP & FK 2001	49°05'10"	13°33'20"	1120 m	36	n.d.	I (aurantiacum)	AU A
887 AU	Filipova Huť: FK 2003	49°01.401'	13°30.664'	1058 m	4x	n.d.	I (aurantiacum)	AU A
893 AU	Slučí Tah: FK 2003	49°09.182'	13°21.003'	876 m	4x	apomictic	I (aurantiacum)	AU A
895 AU	Slučí Tah: FK 2003	49°09.182'	13°21.003'	876 m	4x	apomictic	I (aurantiacum)	AU A
550 AU	Slučí Tah: FP & FK 2001	49°09.182'	13°21.003'	876 m	36	apomictic	I (aurantiacum)	AU A
901 AU	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	n.d.	I (aurantiacum)	AU A
902 AU	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	apomictic	I (aurantiacum)	AU A
905 AU	Zhůří near Železná Ruda: FK 2003	49°10'45"	13°20'10"	930 m	4x	n.d.	I (aurantiacum)	AU A
537 AU	Gerlova Huť: FP & FK 2001	49°09'54"	13°16'44"	950 m	36	apomictic	I (aurantiacum)	AU A
911 AU	Gerlova Huť: FK 2003	49°09'54"	13°16'44"	950 m	4x	n.d.	I (aurantiacum)	AU A
252 AU	Gerlova Huť: FP 1999	49°09'54"	13°16'44"	950 m	36	n.d.	n.d.	
547 AU	Hadí vrch near Hartmanice: FP & FK 2001	49°11.090'	13°20.744'	958 m	36	n.d.	I (aurantiacum)	AU A
546a AU	Hadí vrch near Hartmanice: FP & FK 2001	49°11.090'	13°20.744'	958 m	36	n.d.	I (aurantiacum)	AU A
753 AU	at the confluence of “Roklanský potok” and “Javoří potok” brooks: FK, FP, SB, FS & JC 2002	49°02.208'	13°22.552'	1026 m	4x	n.d.	I (aurantiacum)	AU A
H. aurantiacum > *H. pilosella* (*H. rubrum* Peter)								
549 RU	Slučí Tah: FP & FK 2001	49°09.182'	13°21.003'	876 m	54	apomictic[1]	I (aurantiacum)	RU A
897 RU	Slučí Tah: FK 2003	49°09.182'	13°21.003'	876 m	6x	n.d.	I (aurantiacum)	RU A
756 RU	Zhůří near Železná Ruda: FK, FP, SB, FS & JC 2002	49°10'50"	13°20'20"	950 m	6x	apomictic[1]	I (aurantiacum)	RU B
H.aurantiacum × *H. pilosella* (*H. stoloniflorum* Waldst. et Kit.)								
534 SF	Zhůří near Kašperské Hory: FP & FK 2001	49°05'10"	13°33'20"	1120 m	36	sexual	I (aurantiacum)	
755 SF	Zhůří near Železná Ruda: FK, FP, SB, FS & JC 2002	49°10'50"	13°20'20"	950 m	4x	sexual	II (normal)	
1324 SF	Hadí vrch near Hartmanice: FK & A. Krahulcová 2007	49°11.090'	13°20.744'	958 m	4x	sexual		

Accession	Locality	Latitude N	Longitude E	Altitude	2n/ ploidy	Reproductive mode	Haplotype group (subtype)	Fingerprint genotype of apomicts
H. floribundum Wimm. et Grab.								
532 FL	Zhůří near Kašperské Hory: FP & FK 2001	49°05'10"	13°33'50"	1160 m	36 (M)	n.d.	n.d.	
538 FL	Gerlova Huť: FP & FK 2001	49°09'54"	13°16'44"	950 m	36 (M)	n.d.	II (normal)	
539 FL	Gerlova Huť: FP & FK 2001	49°09'54"	13°16'44"	950 m	36 (M)	n.d.	I (normal)	FL A
912 FL	Gerlova Huť: FK 2003	49°09'54"	13°16'44"	950 m	4x	n.d.	I (normal)	FL A
750 FL	Gerlova Huť: FK, FP, SB, FS & JC 2002	49°09'54"	13°16'44"	950 m	4x	n.d.		FL A
866 FL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (aurantiacum)	FL D
868 FL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (aurantiacum)	
869 FL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (aurantiacum)	
870 FL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (aurantiacum)	
871 FL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (aurantiacum)	
867 FL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (normal)	FL C
535 FL	Zhůří near Kašperské Hory: FP & FK 2001	49°04'50"	13°33'10"	1140 m	36 (M)	apomictic	I (normal)	FL A
877 FL	Zhůří near Kašperské Hory: FK 2003	49°04'50"	13°33'10"	1140 m	4x	n.d.	I (aurantiacum)	FL D
879 FL	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	n.d.	I (aurantiacum)	FL D
885 FL	Zhůří near Kašperské Hory: FK 2003	49°05'10"	13°33'20"	1120 m	4x	n.d.	I (aurantiacum)	
553 FL	Slučí Tah: FP & FK 2001	49°09.182'	13°21.003'	876 m	36 (M)	n.d.	n.d.	
554 FL	Slučí Tah: FP & FK 2001	49°09.182'	13°21.003'	876 m	36 (M)	n.d.	I (normal)	
894 FL	Slučí Tah: FK 2003	49°09.182'	13°21.003'	876 m	36 (M)	n.d.	I (aurantiacum)	
898 FL	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	n.d.	I (normal)	FL A
899 FL	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	apomictic	I (normal)	FL B
747 FL	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	apomictic	I (normal)	FL B
557 FL	Keply: FP & FK 2001	49°11'35"	13°21'00"	960 m	36 (M)	apomictic	I (aurantiacum)	FL D
558 FL	Keply: FP & FK 2001	49°11'35"	13°21'00"	960 m	36 (M)	apomictic	I (aurantiacum)	FL D
559 FL	Keply: FP & FK 2001	49°11'35"	13°21'00"	960 m	36 (M)	n.d.	n.d.	
250 FL	Stará Hůrka near the lake of Laka: FP 1999	49°07'30"	13°19'48"	1005 m	36 (M)	n.d.	I (normal)	
H.aurantiacum × *H.floribundum*								
546 FL×AU	Hadí vrch near Hartmanice: FP & FK 2001	49°11.090'	13°20.744'	958 m	36	n.d.	I (normal)	
740 FL×AU	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	almost sterile	I (normal)	FL×AU A

Accession	Locality	Latitude N	Longitude E	Altitude	2n/ ploidy	Reproductive mode	Haplotype group (subtype)	Fingerprint genotype of apomicts
741 FL×AU	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	almost sterile	I (normal)	FL×AU B
745 FL×AU	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	almost sterile	I (normal)	FL×AU C
545 FL>AU	Hadí vrch near Hartmanice: FP & FK 2001	49°11.090'	13°20.744'	958 m	36	n.d.	I (normal)	FL×AU D
251 FL×AU	Stará Hůrka near the lake of Laka: FP 1999	49°07'30"	13°19'48"	1005 m	36	apomictic	I (aurantiacum)	FL×AU E
H. glomeratum Froel.								
861 GL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	5x	n.d.	II (cymosum)	GL A
863/1 GL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	5x	n.d.	II (cymosum)	
875 GL	Zhůří near Kašperské Hory: FK 2003	49°04'50"	13°33'20"	1140 m	5x	n.d.	II (cymosum)	GL A
876 GL	Zhůří near Kašperské Hory: FK 2003	49°04'50"	13°33'20"	1140 m	5x	n.d.	II (cymosum)	GL A
770 GL	Zhůří near Kašperské Hory: FK, FP, SB, FS & JC 2002	49°05'25"	13°33'00"	1140 m	5x	apomictic	II (normal)	
890 GL	Filipova Huť: FK 2003	49°01.401'	13°30.664'	1058 m	5x	n.d.	II (cymosum)	GL A
886 GL	Filipova Huť: FK 2003	49°01.401'	13°30.664'	1058 m	5x	n.d.	II (cymosum)	GL A
758 GL	Slučí Tah: FK, FP, SB, FS & JC 2002	49°09.182'	13°21.003'	876 m	4x	n.d.	II (normal)	
541 GL	Gerlova Huť: FP & FK 2001	49°09'54"	13°16'44"	950 m	36 (M)	n.d.	n.d.	
556 GL	Keply: FP & FK 2001	49°11'35"	13°21'00"	960 m	36 (M)	n.d.	II (normal)	
767 GL	Nové Hutě: FK, FP, SB, FS & JC 2002	49°02.189'	13°38.531'	1014 m	5x	n.d.	II (normal)	
H.floribundum × *H. pilosella* (mostly corresponding to *H. piloselliflorum* Nägeli et Peter)								
873 PF	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	sexual	II (normal)	
736 PF	Jelení Vrchy: FK, SB, FP & FS 2002	48°48.902'	13°52.756'	892 m	4x	sexual	I (aurantiacum)	
737 PF	Jelení Vrchy: FK, SB, FP & FS 2002	48°48.902'	13°52.756'	892 m	4x	n.d.	n.d.	
872 PF	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	I (aurantiacum)	
772 PF	Zhůří near Kašperské Hory: FK, FP, SB, FS & JC 2002	49°05'10"	13°33'20"	1120 m	4x	apomictic	II (normal)	
552 PF	Slučí Tah: FP & FK 2001	49°09.182'	13°21.003'	876 m	36	sexual	I (aurantiacum)	
892 PF	Slučí Tah: FK 2003	49°09.182'	13°21.003'	876 m	4x	n.d.	I (aurantiacum)	
752 PF	Slučí Tah: FK, FP, SB, FS & JC 2002	49°09.182'	13°21.003'	876 m	4x	sexual	I (normal)	
904 PF	Zhůří near Železná Ruda: FK 2003	49°10'50"	13°20'20"	950 m	4x	sexual	I (normal)	
764/1 PF	Horská Kvilda: FK, FP, SB, FS & JC 2002	49°03.367'	13°33.379'	1130 m	4x	n.d.	I (aurantiacum)	
742 PF	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	sexual	I (normal)	
743 FL×PI	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	54 (M)	apomictic[1]	I (normal)	

Accession	Locality	Latitude N	Longitude E	Altitude	2n/ ploidy	Reproduc-tive mode	Haplotype group (subtype)	Fingerprint genotype of apomicts
744 PF	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	n.d.	I (aurantiacum)	
746 PF	Hadí vrch near Hartmanice: FK, FP, SB, FS & JC 2002	49°11.090'	13°20.744'	958 m	4x	sexual	I (normal)	
544 PF	Hadí vrch near Hartmanice: FK & FP 2001	49°11.090'	13°20.744'	958 m	36	n.d.	n.d.	
751 PF	Stará Hůrka near the lake of Laka: FK, FP, SB, FS & JC 2002	49°07'30"	13°19'48"	1005 m	4x	sexual	I (normal)	
H.lactucella × *H. pilosella* (*H. schultesii* F. W. Schultz)								
735 SC	Jelení Vrchy: FK, SB, FP & FS 2002	48°48.902'	13°52.756'	892 m	3x	sterile	II (normal)	
738 SC	Jelení Vrchy: FK, SB, FP & FS 2002	48°48.902'	13°52.756'	892 m	4x	sexual	I (normal)	
761 SC	Horská Kvilda: FK, FP, SB, FS & JC 2002	49°03.367'	13°33.379'	1130 m	3x	sterile	I (aurantiacum)	
762 SC	Horská Kvilda: FK, FP, SB, FS & JC 2002	49°03.367'	13°33.379'	1130 m	3x	sterile	I (normal)	
763 SC	Horská Kvilda: FK, FP, SB, FS & JC 2002	49°03.367'	13°33.379'	1130 m	3x	sterile	I (aurantiacum)	
H. scandinavicum Dahlst.								
862 FL×GL	Jelení Vrchy: FK 2003	48°48.902'	13°52.756'	892 m	4x	n.d.	II (normal)	FL×GL B
531 FL×GL	Zhůří near Kašperské Hory: FP & FK 2001	49°05'10"	13°33'50"	1160 m	36 (M)	apomictic	II (normal)	FL×GL A
542 FL×GL	Gerlova Huť: FP & FK 2001	49°09'54"	13°16'44"	950 m	36 (M)	n.d.	II (normal)	FL×GL C
253 FL×GL	Gerlova Huť: FP 1999	49°09'54"	13°16'44"	950 m	36 (M)	n.d.	n.d.	
910 FL×GL	Gerlova Huť: FK 2003	49°09'54"	13°16'44"	950 m	4x	n.d.	II (normal)	FL×GL C
913 FL×GL	Gerlova Huť: FK 2003	49°09'54"	13°16'44"	950 m	4x	apomictic	II (normal)	FL×GL C
914 FLxGL	Gerlova Huť: FK 2003	49°09'54"	13°16'44"	950 m	4x	n.d.	II (normal)	FL×GL C
749 FL×GL	Gerlova Huť: FK, FP, SB, FS & JC 2002	49°09'54"	13°16'44"	950 m	4x	n.d.	II (normal)	FL×GL C
766 FL×GL	Churáňov: FK, FP, SB, FS & JC 2002	49°04.117'	13°36.931'	1120 m	4x	apomictic	II (normal)	FL×GL A
556a FL×GL	Keply: FP & FK 2001 (herbarium specimen only)	49°11'35"	13°21'00"	960 m	n.d.	n.d.	n.d.	
H. glomeratum × *H. pilosella*								
754 PI×GL	Filipova Huť: FK, FP, SB, FS & JC 2002	49°01.401'	13°30.664'	1058 m	38	n.d.	II (cymosum)	

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[1] breeding system that combines apomixis with prominent residual sexuality

Appendix 2. – Taxa occurring on the Bavarian side (for distribution patterns compare also Schönfelder & Bresinsky 1990 and BIB 2007). Ploidy levels are indicated, however, only a few populations have been analysed cytologically from this area. The order follows the section "Remarks on selected species and hybrids".

H. aurantiacum – Tetraploid. Frequent, but rarely forming large populations (e.g., Brennes saddle at the Arber); uniform, belongs to subsp. *aurantiacum*; subsp. *auropurpureum* is absent. The species is not considered as indigenous in this area (Schönfelder & Bresinsky 1990).

H. caespitosum – Relatively rare; the majority of specimens are collected before 1950. Highly variable, many specimens show a tendency to *H. glomeratum* in the structure of the indumentum.

H. lactucella – Frequent, moderately variable.

H. pilosella – Frequent, highly variable.

H. floribundum – Tetraploid (2 counts), pentaploid (1 count from the foothills of the south facing ridge). Frequent. In culture morphologically different types (e.g., *H. piloselloides*-like, corresponding to subsp. *atricroceum* Peter?) develop into typical subsp. *floribundum*. Zahn (1922–1930) distinguishes *H. longiscapum* (closer to *H. lactucella*) as subsp. *spathophyllum* from three localities.

H. glomeratum – Tetraploid (south facing ridge), pentaploid (foothills of the south facing ridge). Frequent, but rarely in large populations (e.g., Brennes saddle at the Arber), which are often only short-lived; highly variable.

H. scandinavicum – Tetraploid (2 counts). Rare. Includes *H. arvicola* subsp. *bohemicum* Vollm. (*H. arvicola* subsp. *lusenicum* Zahn, nom. illeg.). Possibly also includes *H. tubulascens* subsp. *aestivae*, described by Zahn from this area (type lost).

H. aurantiacum × *H. pilosella* – One collection by Gaggermeier 1996 from near Oberhaiderberg belongs morphologically to *H. rubrum*.

H. floribundum × *H. pilosella* – One collection by Diewald from the Nationalpark Bayerischer Wald, morphologically corresponds to *H. iseranum*, a recent hybrid.

H. lactucella × *H. pilosella* – Rare, morphologically very diverse.

Types known only from the south facing ridge

H. arvicola Nägeli et Peter – A part of the specimens collected as *H. floribundum* subsp. *atricroceum* between 1921 and 1941 in the area Deggendorf-Metten-Rusel belong morphologically to this species. All populations seem to be extinct.

H. glomeratum × *H. piloselloides* – Rare, leg. Gerstlauer.

H. glomeratum × *H. pilosella* – Rare, apparently a recent hybrid, leg. Mergenthaler 1985, Gerstlauer 1941; some are called "*H. poliodermum* Dahlst., (i.e., *H. dubium* > *H. pilosella*), possibly a new (but undescribed) subspecies of *H. macranthelum*."