

Abstracts

A chloroplast DNA phylogeny of *Hieracium* subgen. *Pilosella* and its relationship to the other subgenera and to *Andryala*

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Chloroplast DNA (*cpDNA*) is usually maternally transmitted in angiosperms giving evidence for e.g. seed dispersal and the direction of hybridizations. We confirmed maternal transmission in subgen. *Pilosella* for selected experimental hybrids from reciprocal crosses whose parental species could be distinguished by their chloroplast DNA. Thus, a *cpDNA* phylogeny will not in first place yield a phylogeny of the species, but rather one of their maternal lineages. The chloroplast genome consists of a single circular chromosome, is therefore haploid – the type of chloroplast DNA found in a species is therefore referred to as its haplotype – and does not undergo recombination, i.e., it is transmitted unchanged except for mutations accumulating over time and separately from the nuclear genome. This leads to the situation that the *cpDNA* haplotype can still be recognized after repeated backcrosses even if most of the genome of the species transmitting it is diluted out more or less completely, i.e., leaving no trace of the earlier hybridization in the species' morphology or in its nuclear genome. This outcome is called “chloroplast capture”, because a species might harbour the *cpDNA* of a foreign species without any obvious signs of it in its morphology. Such processes are the reason why the *cpDNA* often rather shows a geographic distribution than reflecting species' boundaries. Especially in a hybridogenous complex like *Pilosella*, we therefore expected a mixture of different *cpDNA* haplotypes within species as well as some geographical pattern in their distribution.

Based on previous analyses, a part of the chloroplast genome showing a relatively high variability in *Hieracium* s.l. – the *trnT-trnL* intergenic spacer – was chosen for sequencing. We found two distinct species groups in subgen. *Pilosella* exhibiting one or another major type of *cpDNA* and rather little variability within each of the two groups. Contrary to expectation, at first, no geographic structure at all was found – species with one or the other haplotype were regularly growing intermingled and evidently hybridized without exchanging their *cpDNA* in most cases. This was even true for intermediate species that were probably of hybridogenous origin. Even if they originated several times, the majority of those analyzed always showed the same type of *cpDNA* (e.g., *H. glomeratum*, *H. floribundum*, *H. iseranum*) indicating unidirectional hybridizations the reason of which is unknown. Furthermore, in several cases we found the facultative apomict serving as mother plant in hybridizations and the sexual parent providing pollen

rather than vice versa (e.g., in *H. glomeratum*, *H. iseranum*, *H. piloselliflorum*) indicating that residual sexuality in facultative apomicts might play a larger role than previously thought. The two *Pilosella* haplotype groups were even better separated than one of them could be distinguished from *Hieracium* s.str. and *Chionoracium* taxa. Thus, the separation of *Pilosella* haplotype groups which did not correspond to any morphological characters must have predated the speciation of the (sub)genus. However, it seemed to reflect some geographical/historic as well as ecological characteristics on a broader geographic scale: One of the haplotype groups (showing ancestral features in their sequences) is more restricted to western Europe and never leaves the original forest areal except at high altitudes. The previously missing geographic pattern can be understood as a consequence of our initial concentration on a small investigation area which lies in the overlap zone of both haplotype groups.

Andryala turned out to be an ingroup rather than an outgroup taxon. Its *cpDNA* was unequivocally derived from the second *Pilosella* haplotype (with more eastern distribution and derived sequence features) showing an extremely close relationship between *Pilosella* and *Andryala* which is also supported by morphological characters (achene structure, flower colour etc.) and a similar DNA content in contrast to both *Hieracium* s.str. and *Chionoracium*. The latter two could hardly be distinguished by their *cpDNA*. *Hieracium* s.l. and *Andryala* together formed a monophyletic group which was well separated from any other presumably related genera. *Hieracium hololeion* MAXIM. proved to belong to the outgroup taxa and should be referred to as *Hololeion maximowiczii* KITAMURA.

Gall-forming insects associated with *Hieracium*

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Several hawkweed species of Eurasian origin have been introduced into North America and New Zealand. Especially stoloniferous *Hieracium* spp. from the subgenus *Pilosella*, became weeds on pastures, in clear-cut areas and in nature reserves. Since traditional management efforts are often not cost-effective or non-selective, a programme to develop biological control was initiated by consortia in North America and New Zealand. During surveys for phytophagous insects associated with hawkweeds in Europe, four gall-forming insects were chosen for further investigations, i.e. three galls wasps, all of them *Aulacidea* spp., and a gall midge, *Macrolabis pilosellae*. *Aulacidea subterminalis* galls the stolon tips of *H. pilosella* and *H. aurantiacum*, *Aulacidea pilosellae* produces small galls on the midrib of leaves and stolons of several weedy *Hieracium* spp., including the target weeds *H. caespitosum* and *H. pilosella*, and *Aulacidea hieracii* galls the flower stems of several *Hieracium* spp. Since *A. hieracii* adults emerged from different looking hawkweed galls originating from the Ukraine, we plan to verify whether they differ in their host range. The multivoltine gall midge *Macrolabis pilosellae* had already been field-released in New Zealand to control *H. pilosella*, *H. caespitosum* and *H. praealtum*.

Attack by *M. pilosellae* results in fewer leaves and flower heads and shorter stolons. If it proves to be specific enough for release in North America it would have the potential to not only control *H. pilosella* but also a number of other weedy *Hieracium* spp., e.g. *H. caespitosum*, *H. piloselloides*, and *H. glomeratum*.

Experiments are being carried out to evaluate their host range within the genus and their suitability as potential biological control agents in North America where native *Hieracium* spp. in the subgenera *Hieracium* and *Stenotheca* occur. Therefore native North American hawkweed species are the main focus during host-specificity investigations.

Distribution and genetic variation in *Hieracium cyathis* (LEY) W. R. LINTON

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The genus *Hieracium* is probably the major contributor to the plant red data books in north and central Europe. In the British Isles alone more than 400 species of *Hieracium* have been recorded, and about 80 of them are rare and restricted to single or very few localities. Efforts have been made to protect *Hieracia* taxa in Wales, but identification, surveying and monitoring these rare plants is still complicated. Small populations are usually morphologically uniform, but interpopulation variability is more difficult to interpret. Genetic studies can help to identify and characterise critical microspecies and therefore to produce a reliable conservation plan according to the results.

Hieracium cyathis (Ley) W. R. Linton, Chalice Hawkweed, is a rare, endemic plant, known from a few limestone cliffs in South Wales and the Mendips in South-west England. It occurs on natural rocks and on quarry faces, usually on steep or nearly vertical rocks, and also in open calcareous grassland and on screes where it tends to be grazed and flowers poorly. Although it has been reported that English and Welsh populations differ in size, morphological examination of specimens from both countries shows that there is an overlapping distribution of characters.

In this work we have used AFLPs to study the genetic variation of this species. Leaf samples from 30 plants from natural populations were collected into silica gel and DNA was extracted from 0.2 g of dried leaf material using a modified 2× CTAB method. DNA was purified using QIAquick minicolumns (QIAGEN) following the manufacturer's protocols. AFLP reactions were performed using the standard protocols in the AFLP Plant Mapping Kit of ABI (Applied Biosystems, Inc.). Two primer pairs were chosen (EcoR1-ACC, Mse1-GAC; EcoR1-ACA, Mse1-GAC) for this study. The DNA fragments were detected on an ABI 377 automated DNA sequencer using ABI GeneScan 2.02 and GenoTyper 1.1 software (Applied Biosystems, Inc.). AFLP fragments ranging from 100 to 500 bp (base pairs) were scored as either present (1) or absent (0), but

localities of the samples were revealed until the binary matrix was completed. The data matrix was analysed using the neighbor joining (NJ) algorithms in PAUP 4.0 based on mean character difference. Although most species of *Hieracium* are apomictic, the pattern of AFLPs shows that there is genetic variation within and between populations. The presence of genetic variation has been recorded in several British microspecies. Although genetic variability apomictic taxa is lower than in sexual species, whether the source of variation is due to somatic mutation or recombination is not yet clear.

First record on recent natural hybridization in the genus *Hieracium* s. str.

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Hieracium s. str. belongs to the richest plant genera of the world. Most of the karyologically so far analyzed (micro)species are tri- or tetraploid with apomictic formation of seeds. The diploid taxa are very rare and they reproduce exclusively sexually. For some of them the strict allogamy was proved. Polyploid taxa, at least the most of them, are believed to be allopolyploid. There are some indirect proves supporting the hybridogeneous origin of polyploid taxa: (i) morphology - taxa possess the combined characters from two (or more) putative parent species; (ii) presence of fixed heterozygosity (evidence from allozyme markers); (iii) breakdown of normal chromosome pairing during microsporogenesis (univalents are often recorded), disturbance of microsporogenesis results in heterogeneous sized pollen or even in male sterility; (iv) and finally, the diplosporic apomixis can be characterized as an "escape from sterility", generally, the sterility is a frequent phenomenon accompanying the hybridization.

While the natural hybridization is quite common event at present in the closely related genus of *Pilosella*, there are no reliable data on recent hybridization in the genus *Hieracium* s. str. so far.

Probably the first recent *Hieracium* hybrid at all was found during botanical expedition in the Munții Rodnei (Romanian Eastern Carpathians) in 2001. The single plant was found by the tourist path from the village Borșa to Mt. Pietrosul Mare at the 1350 m a. s. l. in spruce zone. The plant had an intermediate appearance of the two morphologically very distant species – *Hieracium alpinum* L. and *Hieracium transsilvanicum* HEUFF. The hybrid plant was accompanied on the locality by plants of both parent species, but the former one occurred as 3 individual plants only and ca 300 m away from the hybrid site. While *H. transsilvanicum* is a typical representative of spruce (and fir-beech) forests of the Eastern and Southern Carpathians, *H. alpinum* normally

occurs in the alpine and very rarely in subalpine belts only. The presence of 3 individuals of *H. alpinum* on the borders of tourist path may be simply explicated by close proximity of the alpine belt and by the fact that locality was strongly disturbed (and cleared) by the forest machines during cutting. Thus the biotop was suitable for incidental occurring of *H. alpinum* at very unusual altitude.

From the reason of probably the first hybrid in genus, this plant was transferred to the Botanical garden of P.J. Šafárik University in Košice for cultivation and further studies. Karyological analysis revealed the diploid chromosome number ($2n=18$). Both parent species are diploid in the Eastern and Southern Carpathians (Romania and Ukraine; CHRTEK 1996, 1997, MRÁZ 2001 and unpubl.). 3 unopened flowers from one head of hybrid were tested for pollen production, but no pollen has been found. The hybrid plant was crossed with one plant of the parent species *H. transsilvanicum*. All seeds obtained from hybrid plant were completely empty and whitish. So, besides several morphological characters, also the ploidy level and male and female sterility underlines the hybridogeneous origin of this plant. Moreover, the morphological intermediate characters present in hybrid plant from the field were confirmed in hybrid progeny from the series of experimental crosses between *H. alpinum* and *H. transsilvanicum*. The progeny from these crosses, however produced pollen, but the seed production (from further hybridization, free pollination or from isolation experiments) was near 1% (near sterile) (MRÁZ & PAULE, unpubl.).

Furthermore, we compared allozyme patterns of hybrid plant and its putative parents (plants of *H. alpinum* and *H. transsilvanicum* collected in the vicinity of the hybrid). Four allozyme systems were analyzed, i.e. ADH (Alcoholdehydrogenase), LAP (Leucinaminopeptidase), PGM (Phosphoglucomutase), and SKD (Shikimate dehydrogenase). Only two loci, Skd, and Lap-1, showed allelically interpretable variation, for the others only allozyme patterns were compared. The results partially support the hypothesis about hybrid origin of the target plant.

Trichome characteristics in the tribe *Lactuceae*, with emphasis on the subtribe *Hieraciinae*

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The presence or absence of trichomes with a particular morphology and structure are frequently helpful taxonomic markers. On the level of genus or even above, the trichomes are however used more sporadically than in lower ranks – species or subspecies. Sometimes, it is difficult to decide, only on the basis of structure, which trichomes are homologous and which are not. The trichomes may be used as an accessory character to other morphological, micromorphological, palynological and molecular data. Classifications of the tribe Lactuceae have differed considerably in the genera that are

included in particular subtribes. The nature of indumentum has never been studied in detail in this tribe. The goals of the present work are as follows: (i) description and classification of trichome diversity within Lactuceae, (ii) attempting to find affinities between genera on the basis of presence and absence of similar trichome types.

Initially, we recognize 5 major trichomes types, some of them are composed of several subtypes: A. simple eglandular multiseriate trichomes; B. simple eglandular uniseriate trichomes; C. glandular trichomes; D. uniseriate trichomes with very elongated apical cells with comparison of the size of the stalk cells and E. very long uniseriate filamentous trichomes with fewer-more equally elongated cells. Types A. and B. usually give the "hairy" look of the plant, while the D. and E. types lanate or tomentous.

Preliminary results of our study show that the subtribe Hieraciinae is composed of the following genera: *Andryala*, *Hieracium*, *Hispidella* and *Pilosella*. This group of genera may be characterized as a "hairy" subtribe having the A., C., and D. trichome types. The D2 subtype ("stellate") is a unique subtype for these taxa in contrast to the rest of the genera analysed so far. This subtype is composed of a uniseriate stalk with short cells and with one or two very long multibranching apical cells. Interestingly, *Pilosella* and *Andryala* have the branches of apical cells more regularly arranged than in the genus *Hieracium*. The heterogeneous genus *Tolpis*, which is traditionally put with the above-mentioned genera in one group, differs from Hieraciinae according to our studies in the respect that no *Tolpis* species has the glandular trichomes (C.) and simple eglandular multiseriate trichomes (A.). On the other hand some *Tolpis* members possess the B. type - simple eglandular uniseriate trichomes. The exclusion of this genus from Hieraciinae is strongly supported also by DNA data.

Experimental hybridization in the genus *Hieracium* s.str.

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The genus *Hieracium* L. belongs to the most intricate plant genera. At the same time it is one of the taxonomically most complicated and species-rich genera of the plant kingdom. The present variation within the genus is probably the result of immense reticulate evolution in the past, when new taxa may have arisen in hybridogeneous swarms. Most of these new polyploid taxa were stabilized by the apomictic mode of reproduction. A large number of morphologically closely related taxa resulted from these processes. They are, however, distinguishable by means of detailed morphological studies, by secondary metabolites or molecular markers.

At present, natural hybridization within the genus is probably highly restricted (MRÁZ et CHRTEK 2003). Why does this process seem to be limited at present, if many taxa probably arose via hybridization in the past? Which factors influence the rarity of natural

hybridizations nowadays? Does competition (preference) between pollen of the same taxon and pollen from another taxon play an important role? Is the transport of apomictic gene(s)/factors from pollen-producing polyploids to progeny arising from hybridization with sexual diploid taxa possible? We know almost nothing about the possible scenario of speciation within this genus.

In 2000 we started a large series of crosses between different species of the genus *Hieracium* s. str. of various ploidy level occurring in the Carpathians (Slovakia, Ukraine and Romania). Two main experiments were carried out: crosses (i) among diploid sexual species (*H. alpinum*, *H. hryniawiense*, *H. pojoritense*, *H. transilvanicum*, *H. umbellatum*), and (ii) between diploid (preferably as seed parents) and polyploid (tri- or tetraploid) species (*H. sect. Alpina*, *H. sabaudum*, *H. valdepilosum* s.l.). At that time we obtained the results mainly from crosses between diploid species. Most of the F1 plants, as results of crossing experiments, were true hybrids. However, in some crosses the clearly matroclinal plants arising from self-pollination were detected. This is the first record of autogamy in the genus *Hieracium* s. str.

The following experiments were carried out with hybrid offspring (F1 generation) in the following years to search for its reproduction mode: (i) hand crosses with parental species (back-cross) or with other taxa, or between hybrids themselves; (ii) open pollination; (iii) emasculation in the case of triploid hybrid from crosses between diploid and tetraploid; (iv) isolation of flower heads by nylon bags.

Complete sterility was recorded (i) in one living triploid hybrid which arose from the cross between diploid *H. pojoritense* (mother plant) and tetraploid *H. valdepilosum* s.l. (pollen donor) by all types of the above-mentioned experiments, and (ii) in various diploid hybrids (from diploid–diploid crosses) by isolation experiments with nylon bags. Interestingly, the apomictic mode of reproduction was not transferred to one triploid hybrid plant (see above) from apomictically reproducing *H. valdepilosum* s.l., but a distant relation of the parental species would cause this. Near complete sterility was observed in the diploid hybrids by hand and open pollination. Only 0–5.4% of all seeds (per mother/seed plant) were well developed and only 0–2.7% germinated (per mother/seed plant). Altogether 5 plants survived. It seems that the diploid interspecific hybrids play no role as mother plants at present because of complete disturbance of megasporogenesis. On the other hand they would contribute to the microevolution within a genus as pollen donors producing pollen of a homogeneous size, although the offspring from the crosses, where the hybrids served as pollen plants, are not evaluated yet.

Cytogeography of *Pilosella officinarum* F.W. SCHULTZ et SCH. BIP. in the Western Carpathians (a preliminary study)

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The genus *Pilosella* HILL, often considered as a subgenus of the widely accepted genus *Hieracium* (*Hieracium* subgen. *Pilosella*), differs from *Hieracium* s. str. by several morphological characteristics, type of apomixis, lower DNA content in the nucleus at the same ploidy level, smaller pollen at the same ploidy level, quantity of several secondary metabolites and also by its different ecological demands. The proportion of polyploid levels among genera also differs. Most frequent are tetra- and pentaploids, less frequent are di-, tri- and hexaploids. Higher ploidy levels (to decaploids) are also produced under experimental hybridizations. In contrast to *Hieracium* s. str., natural hybridization is a common phenomenon in *Pilosella*, and probably contributes most to the large variability of cytotypes.

The "classical" example of coexistence of several ploidy levels within the same taxon is *Pilosella officinarum*. In Western Europe, tetraploids are most frequent. The situation is different particularly in the Western Carpathians. While the tetraploid cytotype prevails in the western part of this mountain range, pentaploids and hexaploids are almost the only cytotypes in the central and eastern parts. The tetraploids were found here only sporadically. Moreover, it seems that hexaploids are mainly confined to warmer biotops and regions (e.g. in southern parts of Slovakia) in contrast to pentaploids.

Some less common *Hieracium* taxa new to flora of Serbia and Montenegro

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The extensive analysis of floristic data on *Hieracia* accumulated during last several years in Serbia and Montenegro yielded 14 new taxa (mainly on the species level) for the flora of this country (including 4 new species for Balkans):

- H. cardiobasis* (Zahn) Juxip (Serbia & Montenegro, several localities),
- H. dacicum* Uechtr. (E Serbia, Stara Planina Mts.) [subsp. *zlatuiae* E. I. Nyárády & Zahn],
- H. djimilense* subsp. *brachytrichophyes* O. Behr, E. Behr & Zahn (Serbia, Kosovo, Šar Planina Mts.),
- H. gandogeri* (Zahn) Zahn (E Serbia, Stara Planina Mts.),
- H. knafii* (Čelak.) Juxip (SE Serbia, several localities),
- H. maculatum* Sm. [s.l.] (C & W Serbia, several localities),
- H. naegelianiforme* (O. Behr, E. Behr & Zahn) Niketić stat. et comb. nov. (Serbia, Kosovo, Šar Planina Mts.),
- H. oroglaucum* O. Behr, E. Behr & Zahn (Montenegro, Prokletije Mts. [= North Albanian Alps]),
- H. paxianum* E. I. Nyárády [s.l.] (Montenegro, Prokletije Mts.),
- H. pseudotranssilvanicum* Zahn (E Serbia, Stara Planina Mts.),
- H. tubulare* (Zahn) E. I. Nyárády (Serbia & Montenegro, several localities),
- H. wiesbaurianum* Uechtr. ex Baenitz (Serbia, Kosovo, canyon of Sušica river) [subsp. *subcinereum* (Arvet-Touvet) Zahn],

H. willdenowianum (Zahn) P. D. Sell & C. West (Serbia, Kosovo, Prokletije Mts.),
H. zanoagae Pax (SE Serbia, Milevska Planina Mts.).

H. paxianum represents the first taxon for Balkans derived from sect. *Alpina*. It seems that *H. naegelianiforme* and *H. oroglaucum* are derived from the same section, too.

Furthermore, three taxa were found to be new to the flora of Serbia:

H. bifidum Kit. subsp. *sinuosifrons* (Almq.) Zahn (E Serbia, Tupižnica Mts.),
H. mirificissimum [s.l.] Rohlena & Zahn (C Serbia, Kopaonik),
H. rigidum Hartman (E Serbia, Stara Planina Mts.).

Following taxa were discovered to be new for Montenegro:

H. bupleuroides C. C. Gmelin subsp. *malacosericeum* Rech. fil. & Zahn (Maganik Mts.),
H. juranum Fries subsp. *juranum* (Durmitor Mts.),
H. schmidtii Tausch [aggr.] (Montenegro, Bjelasica Mts.) [*H. brunelliforme* Arvet-Touvet].

Most of identifications were confirmed in the relevant herbaria (W, BP, B, SOB). A few of mentioned taxa were only doubtfully recorded earlier on the very border of the country.

A complete set of this collection is kept in the General Herbarium of Balkan Peninsula, Natural History Museum Belgrade (BEO). Plants were chiefly collected by the author, but include some specimens which Bojan Zlatković gave to BEO.

***Hieracium snowdoniense*, Snowdonia hawkweed, rediscovered in Wales**

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Hieracium snowdoniense. P. D. SELL & C. WEST (Asteraceae), Snowdonia Hawkweed, is a rare endemic plant only known in Snowdonia, Wales. It has been recorded from about seven sites historically. Only one plant was found during field surveys in 2000 and 2002. It may have declined due to over-grazing and acid rain deposition affecting soils. It is 'Critically Endangered' under the IUCN threat criteria. Seed has been collected and it is being cultivated at the National Botanic Garden of Wales.

The project "The Hawkweeds of Sweden"

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Hieraciology has a long tradition in Sweden with excellent authors such as Fries, Dahlstedt and Johansson. Altogether more than 1500 species of *Hieracium* (excluding *Pilosella*) are known from the country. However, during the last 50 years no botanist has been interested in this group and almost all of the old knowledge has been forgotten. The project "The Hawkweeds of Sweden" is financed by the Swedish Species Initiative and has four main aims: 1) To produce modern and easily accessible identification-guides and descriptions to all Swedish taxa of *Hieracium* s. str., 2) to reanalyse the nomenclature of these taxa and stabilize the usage in accordance with the current Code, 3) to map the distribution of all taxa as carefully as possible, analyse the distributional patterns biogeographically in a framework of models of historic dispersal, and identify taxa currently in risk of extinction, 4) to investigate the structure and levels of genetic variation within and among taxa to get a better basic understanding of their mode of evolution and speciation. Circumscribed in this way, the current project is gargantuan. Therefore, the scope is initially restricted to taxa belonging to *H.* sect. *Hieracium* and *H.* sect. *Vulgata* and these taxa are treated province by province beginning in southernmost Sweden. This far, the species of 8 (out of 29) provinces have been treated monographically, a preliminary nomenclatural check-list of all Swedish taxa has been prepared and studies of molecular genetic variation have been initiated.

DNA C-values of selected *Hieracium* species from Bulgaria

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DNA content of the chromosome set of twelve species of the genus *Hieracium* s.l. have been determined by Feulgen DNA image cytometry using the Cell Imaging and Retrieval System (CIRES, Kontron, Munich). *Pisum sativum* (2C=8.84 pg) was used as internal standard. Nine of the species (subgenus *Hieracium* – *H. intybaceum*, *H. kittanae*, *H. sparsum*, *H. transsilvanicum*, *H. umbellatum*; subgenus *Pilosella* – *H. caespitosum*, *H. hoppeanum*, *H. lactucella*) are diploid – $2n=18$. The other three species are polyploid (subg. *Hieracium* – *H. bifidum*, $2n=3x=27$; *H. pannosum*, $2n=3x=27$; subg. *Pilosella* – *H. pavichii*, $2n=4x=36$). All taxa originate from Bulgarian accessions with the exception of *H. lactucella* and *H. intybaceum* which are from the Alps.

The DNA 2C-values vary in the diploid taxa of the subg. *Hieracium* from 7.34 pg (*H. intybaceum*) to 8.25 pg (*H. umbellatum*) whereas in the subg. *Pilosella* - from 3.55 pg (*H.*

hoppeanum) to 4.15 pg (*H. caespitosum*). Variation among taxa with the same ploidy level within each of the two subgenera is relatively low, e.g. for the diploids in the subg. *Hieracium* it is up to 1.12-fold, while in the subg. *Pilosella* - up to 1.17-fold. However, the diploid species of subg. *Hieracium* have about twice (1.76- to 2.32-fold) higher 2C-values compared with the taxa from the subg. *Pilosella*. The latter fact shows the significant differences in the content and structure of the chromosomes of the two subgenera and could explain partly why intersubgeneric hybrids have never been found in nature.

The triploids *H. bifidum* and *H. pannosum* in the subg. *Hieracium* have distinctly higher C-values than the diploids, but *H. bifidum* at least has somewhat less DNA than expected from the DNA values found in the diploids.

The results confirmed the reliability of using the DNA C-values for the determination of the ploidy level in *Hieracium* s.l.

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Native and Exotic *Hieracium* species in North America

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Approximately 60 species of *Hieracium* occur in North America north of Mexico. Among these are about 42 native species and 18 species introduced from Eurasia. These species represent three subgenera: *Pilosella*, *Hieracium* and *Stenotheca*. The introduced subgenus *Pilosella* is represented by *H. pilosella*, *H. caespitosum*., *H. floribundum*, *H. piloselloides*, *H. glomeratum*, *H. aurantiacum*, and *H. flagellare*. The subgenus *Hieracium* is represented by 3 native species (*H. umbellatum*, *H. canadense* and *H. groenlandicum*) and 8 exotic species (*H. acuminatum*, *H. atratum*, *H. maculatum*, *H. saubaudum*, *H. murorum*, *H. laevigatum*, *H. vulgatum* and *H. lachenalii*). All 42 species in the subgenus *Stenotheca* are native to North America. Exotic species of *Pilosella* are serious weed problems throughout eastern and western United States and Canada. Introduced species of subgenus *Hieracium* are not as invasive as those in subgenus *Pilosella*. Species in subgenus *Stenotheca* differ genetically from members of other subgenera; all are sexually reproducing diploids. Apomixis and polyploidy are common in the other subgenera. *Stenotheca* species occur in all 50 states and all 10 Canadian provinces. They are found in a wide range of habitats including desert mountains, steppe, interior dry forest, prairie scrub, mountain forests and coastal floodplain. Most range from 750-1550 m in elevation in the northern states and Canada, but southern species can be found up to 2600 m in the desert southwest. Current taxonomic studies are described. The distribution and ecology of each subgenus and species group are described. Management of the invasive, exotic species is discussed.

On the embryology of *Hieracium kittanae*, a new species from Bulgaria

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Hieracium kittanae is a recently discovered, new to science, diploid ($2n=18$) species. It is restricted to a few gorges in the Central Rhodope Mountains, South Bulgaria. It occurs in crevices of limestone rock in shady to sunny places with high atmospheric humidity and morphologically resembles, to some extent, taxa from the *H. glaucinum* and *H. schmidtii* groups. It, otherwise, is very distinct and without close relatives in the Rhodope and neighbouring mountains.

Morphological variation and the castration experiments carried out in the Experimental garden of the Institute of Botany in Sofia suggested sexual means of reproduction of the species. This corresponds to the diploid chromosome number of the taxon and has been confirmed by embryological studies.

The anthers are tetrasporangiate. The anther wall is four-layered consisting of epidermis, an ephemeral middle layer, fibrous endothecium (not clearly expressed) and glandular tapetum. The latter transforms into ameboid false periplasmodium after one-nucleate pollen stage. The microsporogenesis results predominantly in tetrahedral and a small number of other types of tetrads in the anthers. The mature pollen is 3-celled, morphologically uniform and fertile to a high degree.

In the ovule one archesporial cell is formed hypodermally. In single ovules the archesporogenesis runs with formation of 1-2 parietal cells, which is a new embryological feature for *Asteraceae*. Usually, the archesporial cell directly functions as a megaspore mother cell and after the meiosis a linear megaspore tetrad is formed.

The development of the embryo sac (ES) runs according to monosporic *Polygonum*-type and only sporadically after *Allium* (bisporic)-type. In the mature ES the synergids are the most plastic elements varying in shape and often haustorizing to a significant degree. The legitimate embryo and endosperm are formed after a porogamous double fertilization.

The embryological studies show that the species is strongly amphimictic and combines both more primitive and evolutionary advanced embryological features.