

## MENTOR EFFECTS IN THE GENUS *HIERACIUM* S.STR. (*COMPOSITAE*, *LACTUCEAE*)

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**Abstract:** Self-incompatibility was demonstrated in the diploid taxa *Hieracium alpinum* and *H. umbellatum* using isolation experiments. However, self-incompatibility was broken down in diploid *H. alpinum* under the influence of foreign pollen from another species of this genus (mentor effects) during a series of crossing experiments. Interestingly, failure of the SI system was also recorded in diploid *H. alpinum* in an intergeneric cross with the representative of the closely related genus of *Pilosella*. This is the first record of autogamy in the genus *Hieracium* s.str. The possible evolutionary significance of this phenomenon is discussed.

**Keywords:** *Asteraceae*, Autogamy, Chromosome numbers, Hybridization, Self-incompatibility

### INTRODUCTION

Self-incompatibility (SI) is the inability of a fertile hermaphrodite seed-plant to produce zygotes after self pollination (autogamy). It is an effective mechanism that encourages obligate outbreeding and enhances genetic diversity (e.g. RICHARDS 1997, CRUZ-GARCIA & MCCLURE 2001). However, there are several natural conditions under which an otherwise normally functional SI system may fail, such as delayed pollination, high temperature and mixture of self and heterospecific pollen (so-called mentor effects) (RICHARDS 1997). Mentor effects have been recorded from several genera of *Asteraceae* with sporophytic SI, e.g. *Helianthus* (DESROCHERS & RIESEBERG 1998), *Pilosella* (KRAHULCOVÁ et al. 1999), and *Taraxacum* (e.g. MENKEN et al. 1989, TAS & VAN DIJK 1999). Examples from other families include *Lotus corniculatus* (MIRI & BUBAR 1966), *Paspalum notatum* (BURTON & HANNA 1992) and other taxa cited by DE NETTANCOURT (2001) with references therein.

Although many species have been described in *Hieracium* s.str., we know far too little about the mechanisms of speciation that caused such immense diversity. Many experimental studies have been performed in order to clarify the evolutionary processes leading to the recent variation in the closely related genus *Pilosella*, often treated as subgenus *Pilosella* of *Hieracium* (for review see KRAHULCOVÁ et al. 2000). Sexual diploid species in the genus *Hieracium* s.str. are very rare; triploid and tetraploid taxa are much more common (MERXMÜLLER 1975, SCHUHWERK 1996, SCHUHWERK & LIPPERT 1998). For polyploids, the apomictic mode of reproduction (diplospory of the *Antennaria* type) was established by embryological experiments (e.g. BERGMAN 1941, SKAWIŃSKA 1963). Diploid taxa are considered as obligatory sexuals with regular mega- and microsporogenesis (GUSTAFSSON 1947). Until now, probably only one species at the diploid level (*H. alpinum*, from the

Ukrainian Eastern Carpathians) has been tested for self-incompatibility (CHRTEK 1997). Isolated capitula did not produce any viable seeds and the diploid *Hieracium alpinum* was considered as strictly self-incompatible under field conditions, requiring cross-pollination for seed production.

## MATERIAL AND METHODS

In 2000 I started a large series of crosses between different species of the genus *Hieracium* s.str. of various ploidy levels occurring in the Carpathians (Slovakia, Ukraine and Romania). The plants used in hybridization experiments were grown and cross-pollinated in the lowland experimental garden under field conditions and also in a semi-open greenhouse (protection against rain) in the Botanical Garden of P.J. Šafárik University in Košice. Two main experiments were carried out: crosses (i) among diploid species, and (ii) between diploid (preferably as seed parents) and polyploid (tetraploid and triploid) species. All inflorescences of each parent involved in hybridization were isolated in nylon bags before anthesis (before opening of the first outer ligular flowers). At the stage of stigma receptivity, when the bifurcate stigmas protruded from the flowers, both parental capitula were rubbed together to enable transport of pollen to stigmas. Pollination was usually repeated 2–5 times per week for each pair of capitula. The pollinated capitula were isolated until the harvest of mature seeds. The progeny from cross-pollination was evaluated by means of morphology, because the parental species involved in the crosses could be easily distinguished by their morphological characters. For two diploid taxa (*H. alpinum* and *H. umbellatum*) an isolation experiment (by nylon bags) was done to confirm or exclude the presence of a self-incompatibility system.

For parental species the chromosome numbers were stated on mitotic metaphases prepared by method of MURÍN (1960). The ploidy level and chromosome number of each particular parent is given in Table 1 and in Appendix. From among the studied parental plants the diploid chromosome number was published previously only for *Pilosella lactucella* (ROTREKLOVÁ et al. 2002). Other chromosome numbers represent new counts.

## RESULTS

### Self-incompatibility

For one plant of diploid *Hieracium alpinum* (cultivation number 1018 / 1 isolated capitulum) and diploid *H. umbellatum* (cultivation number UMB12JP / 5 isolated capitula) self-incompatibility was demonstrated. All seeds from the isolated capitula were small, white and completely empty, whereas some portion of full seeds was obtained from cross pollination.

### Breakdown of SI system

Most of the F1 plants, as results of crossing experiments, were true hybrids (see Table 1). However, in some crosses clearly matroclinal plants arising from self-pollination were detected. This is the first record of autogamy in the genus *Hieracium* s.str.

In the crosses between diploid *H. alpinum* (mother seed plant, cultivation number 649) × *H. transsilvanicum* (diploid pollen donor, cultivation number 1064), altogether 4 mother-like

Table 1. Summarized results of hybridization experiments. Abbreviations used: ALP – *Hieracium alpinum* L., HRY – *H. hryniawiense* WOL., sect. *Alpina* – *H.* sp. (probably yet unnamed taxon of sect. *Alpina*), LAC – *Pilosella lactucella* (WALLR.) P.D. SELL et C. WEST, POJ – *H. pojoritense* WOL., UMB – *H. umbellatum* L., TRANS – *H. transsilvanicum* HEUFF., VAL s.l. – *H. valdepilosum* s.l. Ploidy level is given in parentheses after the cultivation number of each plant used in hybridization.

mother (seed) plant	Parents		no. of total evaluated plants	Progeny	
	father (pollen) plant			no. of matroclinal plants	proportion of autogamously arisen progeny (%)
ALP (649, 2x)	TRANS (1064, 2x)		21	4	19
ALP (661, 2x)	LAC (763, 2x)		14	14	100
ALP (664, 2x)	sect. <i>Alpina</i> (827, 3x)		17	17	100
HRY (699, 2x)	ALP (639, 2x)		54	0	0
HRY (701, 2x)	VAL s.l. (374, 4x)		2	0	0
POJ (776, 2x)	VAL s.l. (374, 4x)		1	0	0
TRANS (1064, 2x)	ALP (649, 2x)		10	0	0
TRANS (1067, 2x)	UMB (736, 2x)		8	0	0
TRANS (1067, 2x)	POJ (776, 2x)		13	0	0

plants arising by autogamy (cultivation numbers X5/12, X5/13, X5/14, X5/21) and 17 true hybrids were detected. Interestingly, all hybrid plants flowered in the first year of cultivation, contrary to the selfed progeny. The reciprocal crosses between the same parental plants did not bring any autogamous progeny, but did produce true hybrids, all flowering in the first year of cultivation.

The ability of diploid *H. alpinum* to produce an F1 generation by selfing was also confirmed in the crosses between diploid *H. alpinum* (mother plant, cultivation number 664) and an unnamed triploid taxon from *Hieracium* sect. *Alpina* (pollen donor, cultivation number 827). Contrary to the above-mentioned case, all progeny (17 plants, arising from this experiment) were evaluated as matroclinal plants. Three plants from selfing at the seedling stage were morphologically deviant: three true cotyledons on one seedling; very deeply cut lamina of one cotyledon in two seedlings. Normally, the leaf lamina of cotyledons in the genus *Hieracium* is entire.

Additionally to the crosses within the genus *Hieracium*, crosses between some representatives of *Hieracium* and *Pilosella* were undertaken. So far only the results from the crosses between diploid *Hieracium alpinum* (cultivation number 661) and diploid *Pilosella lactucella* (cultivation number 763) are available. All F1 mature progeny, 14 plants, obtained from one capitulum of *H. alpinum* (mother plant) have originated from autogamous events. It is noteworthy that 2 seedlings arising in this cross were complete albinos and they died after 3 weeks of cultivation. No plant from the F1 generation flowered in the first year of cultivation, as in previous experiments. No viable seeds were produced in the reciprocal cross combination of the same parental plants (*P. lactucella* as seed parent, *H. alpinum* as pollen donor). The lack of hybrids between the representatives of the closely related *Pilosella* and *Hieracium* underlines the differences between these two genera. No true hybrid between representatives of these genera (often treated as subgenera within large genus *Hieracium* s.l.) has been found in the field up to now.

## DISCUSSION

Different proportions of offspring arising by selfing have been recorded in different SI incompatible taxonomic groups. High selfing rates were detected in diploid-triploid crosses in the genus *Taraxacum*. Almost 90% of the viable offspring were diploids with the same isozyme phenotype as mother plants (TAS & VAN DIJK 1999). High inbreeding in some crosses between diploid taxa of two taxonomically distant sections of *Taraxacum* was found by MENKEN et al. (1989). The total proportion of autogamously derived progeny, however, was lower in the genus *Pilosella*, varying between 6.2% (or 7.6% in those crosses in which mother-like offspring occurred) in sexual diploid *Pilosella lactucella* and 13% (or 25% in those crosses in which mother like offspring occurred) in sexual tetraploid *Pilosella officinarum* (KRAHULCOVÁ et al. 1999). GADELLA (1987, 1992) did not record any matroclinal offspring in his experimental hybridization in this genus. A lower proportion of matroclinal plants (5.1%) was obtained in interspecific crosses between strictly allogamous diploid species of *Helianthus* (DESROCHERS & RIESEBERG 1998). It seems that the selfing rate depends not only on the taxonomic position of the taxa used in crosses, but also on the particular combination of parental species or even individuals, and on environmental conditions (e.g. DESROCHERS & RIESEBERG 1998, KRAHULCOVÁ et al. 1999, MENKEN et al. 1989). Although the adaptive significance of the failure of the SI system is not clear, the breakdown of self-incompatibility could play an important role in reproductive isolation and hybrid speciation mainly in hybrid zones where mixed pollen loads are common. The breakdown of the SI system in *Hieracium* could be one of several causes, why natural primary hybrids in this genus are extremely rare. Until now, only one recent, truly hybrid plant of the genus is known from the field (MRÁZ et al. 2003).

**Acknowledgement:** I am grateful to C.A. Stace (Leicester) and F. Krahulec (Průhonice) for critical comments on the manuscript and linguistic revision, to J. Paule (Košice) for providing of the chromosome count of *Hieracium alpinum* (no. 639), and to E. Sasáková (Košice) for valuable help in the experimental garden. This research was supported by the Grant Agency of Ministry of the Education and Slovak Academy of Sciences of the Slovak Republic (VEGA 2/3041/23) and by the Grant project of the University P.J. Šafárik, Faculty of Sciences (VVGs).

## REFERENCES

- BERGMAN B. (1941): Studies on the embryo sac mother cell and its development in *Hieracium* subg. *Archieracium*. *Svensk Bot. Tidskr.* 35: 1–42.
- BURTON G.W. & HANNA W.W. (1992): Using apomictic tetraploids to make a self-incompatible diploid pensacola bahiagrass clone set seed. *J. Heredity* 83: 305–306.
- CHRTEK J. (1997): Taxonomy of the *Hieracium alpinum* group in the Sudeten Mts., the West and the Ukrainian East Carpathians. *Folia Geobot. Phytotax.* 32: 69–97.
- CRUZ-GARCIA F. & MCCLURE B. A. (2001): Sexual incompatibility. In: BHOJWANI S.S. & SOH W.Y. (eds.), *Current trends in embryology of angiosperms*, Kluwer Academic Publishers, Dordrecht, 167–196.
- DE NETTANCOURT D. (2001): *Incompatibility and incongruity in wild and cultivated plants*. Springer, Berlin.
- DESROCHERS A.M. & RIESEBERG L.H. (1998): Mentor effects in wild species of *Helianthus* (*Asteraceae*). *Amer. J. Bot.* 85: 770–775.
- GADELLA TH.W.J. (1987): Sexual tetraploid and apomictic pentaploid populations of *Hieracium pilosella* (*Compositae*). *Pl. Syst. Evol.* 157: 219–245.
- GADELLA TH.W. J. (1992): Notes on some triple and inter-sectional hybrids in *Hieracium* L. subgenus *Pilosella* (HILL) S.F. GRAY. *Proc. Kon. Ned. Akad. Wetensch.* 95: 51–63.

- GUSTAFSSON Å. (1947): Apomixis in higher plants II. The causal aspect of apomixis. *Acta Univ. Lund. N. F. Adv.* 43 (2): 69–179.
- KRAHULCOVÁ A., CHRTEK J. & KRAHULEC F. (1999): Autogamy in *Hieracium* subgen. *Pilosella*. *Folia Geobot.* 34: 373–376.
- KRAHULCOVÁ A., KRAHULEC F. & CHAPMAN H.M. (2000): Variation in *Hieracium* subgen. *Pilosella* (*Asteraceae*): What do we know about its sources? *Folia Geobot.* 35: 319–338.
- MENKEN S.B.J., MORITA T., WARDENAAR E.C.P. & BOERSMA A. (1989): Genetic interpretation of enzyme variation in sexual and agamosperous taxa of *Taraxacum* sections *Vulgaria* and *Mongolica*. *Genetica* 78: 111–119.
- MERXMÜLLER H. (1975): Diploide Hieracien. *Anales Inst. Bot. Cavanilles* 32: 189–196.
- MIRI R.K. & BUBAR J.S. (1966): Self-incompatibility as an out-crossing mechanism in birds-foot trefoil (*Lotus corniculatus*). *Canad. J. Pl. Sci.* 46: 411–418.
- MURÍN A. (1960): Substitution of cellophane for glass covers to facilitate preparation of permanent squashes and smears. *Stain Technol.* 35: 351–353.
- MRÁZ P., CHRTEK J. & PLAČKOVÁ I. (2003): First record on recent natural hybridization in the genus *Hieracium* s.str. In: *Hieracium workshop, Křivoklát, Czech Republic, 28 May – 1 June, 2003*, Institute of Botany, AS CR & Protected Landscape area “Křivoklátsko” [sine pag.].
- RICHARDS A. J. (1997): *Plant breeding systems*. Ed 2. Chapman and Hall, London etc.
- ROTRÉKLOVÁ O., KRAHULCOVÁ A., VAŇKOVÁ D., PECKERT T. & MRÁZ P. (2002): Chromosome numbers and breeding systems in some species of *Hieracium* subgen. *Pilosella* from Central Europe. *Preslia* 74: 27–44.
- SCHUHWERK F. (1996): Published chromosome counts in *Hieracium*.  
<http://www.botanik.biologie.uni-muenchen.de/botsamml/projects/chrzlit.html>.
- SCHUHWERK F. & LIPPERT W. (1998): Chromosomenzahlen von *Hieracium* (*Compositae, Lactuceae*) Teil 2. *Sendtnera* 5: 269–286.
- SKAWIŃSKA R. (1963): Apomixis in *Hieracium alpinum* L. *Acta Biol. Cracov.* 5 (1962): 7–14.
- TAS I.C.Q. & VAN DIJK P. (1999): Crosses between sexual and apomictic dandelions (*Taraxacum*). I. Inheritance of apomixis. *Heredity* 83: 707–714.

Received 17 June 2003, revision received and accepted 11 August 2003

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**APPENDIX**

List of the localities of taxa used in the crosses, or used in the tests for SI system (numbers of particular plants, accompanied by chromosome number, are given in brackets after each locality; \* – counted by J. PAULE):

*Hieracium alpinum* L. – Ukraine, Svydovets' Mts.: Mt. Ungaryas'ka, N rocky slopes with *Alnus viridis*, 1705 m a.s.l., 48°18' N, 24°06' E, coll. P. MRÁZ and V. JURKOVIČOVÁ, 7 August 1999 (no. 639, 2n=18\*). – Ukraine, Svydovets' Mts.: on the ridge between Mt. Stih and Mt. Blyznytsya, 1750–1850 m a.s.l., 48°14' N, 24°14' E, coll. P. MRÁZ and V. JURKOVIČOVÁ, 10 August 1999 (no. 649, 2n=18). – Ukraine, Svydovets' Mts.: Tatulska polonina ridge, saddle below Mt. Tatul, 1760 m a.s.l., 48°16'30" N, 24°12' E, coll. P. MRÁZ and V. JURKOVIČOVÁ, 10 August 1999 (nos. 661, 664, 2n=18). – Romania, Mții Retezatului Mts.: on the ridge between Mt. Bârlea and Mt. Seșele Mari, 2300 m a.s.l., 45°20' N, 22°22' E, coll. P. MRÁZ, 8 July 2001 (1018, 2n=18).

*Hieracium hrynawiense* WOL. – Ukraine, Svydovets' Mts.: Gereshas'ka glacial cirque, below Mt. Dogyas'ka, rocky slopes, 1750 m a.s.l., 48°18' N, 24°10' E, coll. P. MRÁZ and V. JURKOVIČOVÁ, 7 August 1999 (no. 701, 2n=18).

*Hieracium pojoritense* WOL. – Romania, Mții Bistriței Mts.: Tulgeș, Mt. Pietra Runcului, calcareous rocks, 1150–1200 m a.s.l., coll. P. MRÁZ and V. JURKOVIČOVÁ, 17 July 2000 (no. 776, 2n=18).

*Hieracium* sect. *Alpina* – Romania, Mții Bistriței Mts.: Mt. Bogolini in the massive of Mt. Pietrosul Brostenilor, 1650–1700 m a.s.l., coll. P. MRÁZ, 20 July 2000 (no. 827, 2n=27)

*Hieracium transsilvanicum* HEUFF. – Romania, Mții Rodnei Mts.: Mt. Pietrosul Mare, N slopes, spruce forest by the path Borșa – Stația Meteo, 1300–1400 m a.s.l., 47°39' N, 24°39' E, coll. P. MRÁZ, 5 July 2001 (nos. 1064, 1067, 2n=18).

*Hieracium umbellatum* L. – Slovakia, Volovské vrchy Mts.: Prakovce, meadow below the ski lift, 390 m a.s.l., 48°48'45" N, 20°54'33" E, May 2000, coll. P. MRÁZ (no. 736, UMB 12JP – the plant from seed collected on this locality, 2n=18).

*Hieracium valdepilosum* s.l. – Slovakia, Veľká Fatra Mts., Malá Ramžiná valley, southern slope below the elevation 1497 m a.s.l., ca. 1 km WSW of Mt. Krížna (1574), 1340 m a.s.l., 48°52'34" N, 19°04'02" E, coll. P. MRÁZ, 12 July 1997 (no. 374, 2n=36).

*Pilosella lactucella* (WALLR.) P.D. SELL et C. WEST (syn. *Hieracium lactucella* WALLR.) – Slovakia, Volovské vrchy Mts.: Krivé sedlo saddle between Mt. Ramzová and Mt. Biele Skaly, 1110 m a.s.l., 48°43'50" N, 20°38'08" E, coll. P. MRÁZ and V. JURKOVIČOVÁ, 14 June 2000 (no. 763, 2n=18, originally published in ROTREKLOVÁ et al. 2002).