# Species relationships, biogeography, population structure and reproduction in an agamic complex: *Hieracium* subgen. *Pilosella*


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http://www.ibot.cas.cz/hieracium/studygroup/


### *Hieracium* subgen. *Pilosella*

A group of about 200 Eurasian hawkweed species, some of them invasive.

### Basic species

About 25 species of *Hieracium* subgen. *Pilosella* with unique morphological features, some of them comprising diploid plants.

### Intermediate species (hybridogenous taxa)

About 180 *Pilosella* species with character combinations of two or more basic species. Hybrid origin supposed. Most of them polyploid, many with apomictic mode of reproduction.

## Glossary

**Apomixis (apomictic, agamic)**
Reproductive mode that produces seeds true to maternal type without fertilization. Enables spread of clonal lineages by seed dispersal (easy colonization of new habitats). Apomicts usually produce fertile pollen.

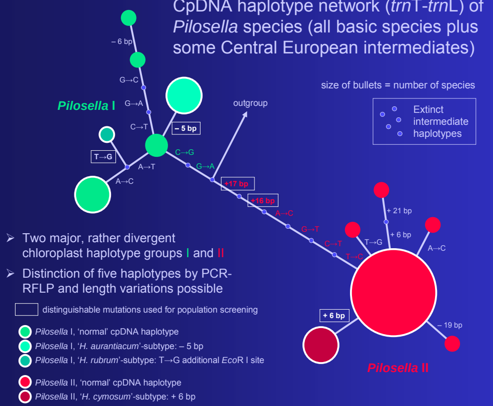
**Facultative apomicts (facultative sexuals)**
Plants reproducing predominantly by apomixis, but can be sexual occasionally, e.g., produce seeds after hybridization.

**Polyhaploids**
Plants produced by meiotically reduced maternal gametes without fertilization. While this means haploidization in case of a diploid mother, the offspring is more than haploid if the mother was polyploid.
Example: A hexaploid mother produces trihaploid (= triploid) offspring (in contrast to a triploid hybrid that has two parents).

**Addition hybrids**
Hybrids with higher ploidy than the sum of their parents' reduced (n+n) chromosome sets due to a combination of reduced and unreduced (n+2n, 2n+n) or only unreduced (2n+2n) gametes.

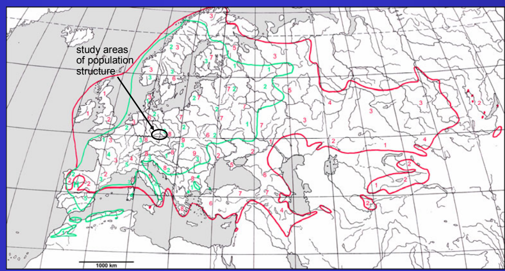
## Chloroplast DNA divergence, phylogeography and introgression history at species level

CpDNA haplotype network (*trn*T-*trn*L) of *Pilosella* species (all basic species plus some Central European intermediates)




- Two major, rather divergent chloroplast haplotype groups I and II
- Distinction of five haplotypes by PCR-RFLP and length variations possible

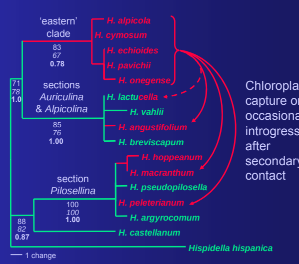
Geographic distribution of species according to cp haplotype




Species numbers in different regions are indicated (green: *Pilosella* I, red: *Pilosella* II, green H: *Hispidella*)

- Species numbers, distribution, degree of endemism and ecological constraints (no *Pilosella* I-type species in steppic habitats) suggest differentiation of cpDNA and speciation of major lineages in different glacial refuges (Iberian, SE European). CpDNA divergence provides a useful tool for the study of population structure in the large recent overlap zone formed after secondary contact. Reproductive isolation between species with different cpDNA haplotypes is absent.

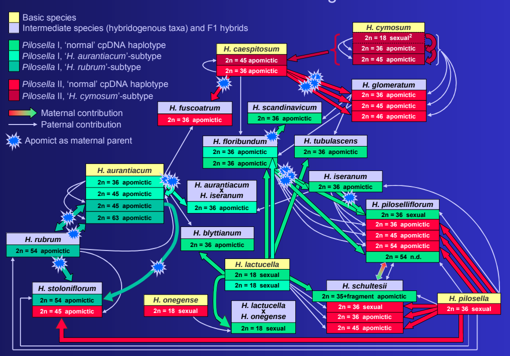
ITS tree of diploid basic species with distribution of major cpDNA haplotypes




Maximum parsimony tree
bootstrap values in parsimony analysis
*bootstrap values in maximum likelihood analysis*
**posterior probabilities in Bayesian analysis**

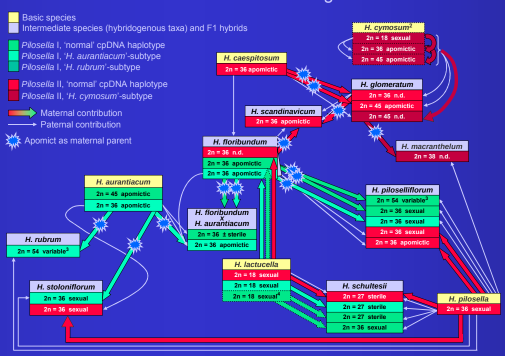
## Population structure of sexuals and apomicts in two Central European mountain ranges

Northern mountain range[1]




[1] along the northern border of the Czech Republic with Germany and Poland
[2] Diploid *H. cymosum* does not occur in the mountains, but in their vicinity

Southern mountain range[1]

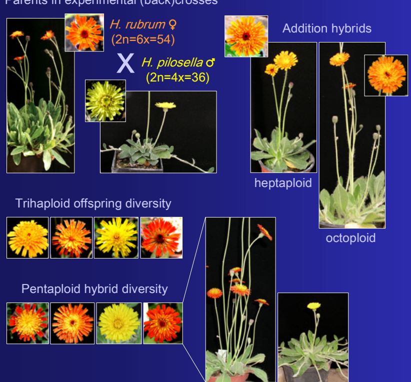


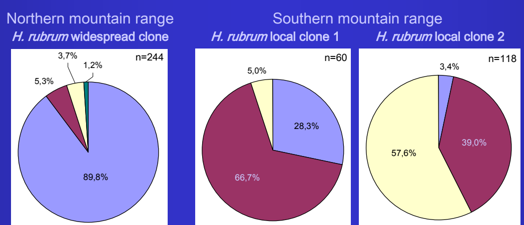

[1] along the southern border of the Czech Republic with Germany and Austria
[2] *H. cymosum* does not occur at all in this mountain range, but in its vicinity
[3] apomictic, polyhaploid, and various sexual offspring (see also below)
[4] existence assumed, but no plants of this haplotype found yet in this mountain range

- Despite an almost identical set of basic species and stabilized intermediate species in both areas, composition of hybridogenous species and F1 hybrids, their cytotypes, reproductive modes and cpDNA subtypes partly differ.
- Hybrid phenotypes assigned to the same species name / parental combination are mostly indistinguishable morphologically, irrespective of these differences.
- Species are similar with respect to major chloroplast haplotype groups (either *Pilosella* I, or *Pilosella* II, or mixed).
- In both regions, a high proportion of hybridogenous species with sexual and apomictic parents had the apomict as maternal parent (residual sexuality) in contrast to a comparably low frequency of such hybrid progeny in experiments.

## Different progeny proportions of stabilized and recent hybrid genotypes in one species

Parents in experimental (back)crosses




Offspring produced by…
…apomixis (hexaploid)
…haploid parthenogenesis (triploid / trihaploid / polyhaploid)
…hybridization, meiosis in both parents (reduced gametes): pentaploid hybrids
…hybridization, meiosis in one parent (reduced & unreduced gametes): addition hybrids (heptaploid, octoploid)

- Hybrid genotypes that form stable populations produce mainly offspring by apomixis and thus have a high chance to become established hybridogenous species. This is supposed to be the main process of apomictic species formation in *Pilosella*.
- Due to their residual (facultative) sexuality (additional to pollen fertility), clonal lineages can be maintained without becoming dead ends of evolution.
- Hybrid genotypes that do not form stable populations behave differently from each other and produce considerably less progeny by apomixis than do stabilized types. Instead, they produce a high proportion of polyhaploids and/or hybrids, which represent further raw material for selection.
- Unreduced gametes (esp. male ones) are rare, but drive the process of polyploidization.