REVIEW

How apomictic taxa are treated in current taxonomy: A review

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DOI https://doi.org/10.12705/665.3

Abstract Gametophytic apomixis (asexual seed formation without syngamy of female and male gametes) is a highly interesting mechanism for researchers in plant biotechnology, genetics, evolutionary biology, and taxonomy. Apomixis evolved repeatedly and independently in the evolution of multiple genera. It is an effective reproduction barrier and, consequently, conserved apomictic genotypes may become overrepresented in nature. Apomictic plants may easily colonize free niches with only one or a few individuals and outcompete outcrossing plants. In spite of the indisputable pros of asexual reproduction, apomixis also has several cons. One of the most commonly mentioned is the accumulation of deleterious mutations in asexual lineages and decreased genetic variation. However, apomicts in general can be genetically highly diverse. The most common sources of this variation are the accumulation of mutations, hybridization with sexual plants, and facultative apomixis. Facultative apomicts are highly variable in their level of residual sexuality, which increases their genotypic and phenotypic variation. Even in the case of obligate apomicts, gene flow is possible due to functional male meiosis and the production of viable pollen grains by apomicts. Apomixis occurs in plant genera in which hybridization together with polyploidization play an important role in diversification and causes severe problems in taxonomy. How to accommodate apomictic taxa in taxonomic treatments, and understanding what should and what should not be referred to as a species are intriguing questions. This review aims to provide an overview of the main characteristics of "apomictic genera" and the approaches used to treat apomictic taxa within these genera. To achieve this aim, the review was divided into several parts. Firstly, the distinctive features of apomictic reproduction and apomictic taxa are described together with issues related to the taxonomic evaluation of apomictic taxa. The second part discusses approaches in the known apomictic genera, and the final part presents the authors' view on important points, which need to be taken into account in the classification of apomictic taxa.

Keywords apomixis; hybridization; polyploids; speciation; species concepts; taxonomy

■ APOMIXIS

Apomixis was first defined by Winkler (1908: 300–301) as follows: "Als Apomixis endlich bezeichnen wir den Ersatz der geschlechtlichen Fortpflanzung durch einen anderen, ungeschlechtlichen, nicht mit Kern- und Zellverschmelzung verbundenen Vermehrungsprozeß" (Finally, as apomixis, we refer to the replacement of sexual reproduction by another asexual process without fusion of nucleus and cell). The etymology is Greek and means "away from mixing". Winkler's definition of apomixis is very wide and may include different types of asexual reproduction (including also vegetative reproduction). However, in the recent understanding of apomixis it is defined as a uniparental asexual mode of seed formation without fertilization of an ovule by a sperm cell (Asker & Jerling, 1992). In this definition apomixis is synonymous with the term *agamospermy*, i.e., clonal reproduction through seeds (Richards, 1997). In apomictic individuals, an embryo develops from an unfertilized single gamete without the participation of another gamete (for review see Ozias-Akins & Van Dijk, 2007; Talent, 2009 or Tucker & Koltunow, 2009). Although apomixis-like reproduction has also been described in lower plants (mosses and ferns; Asker & Jerling, 1992), the definition of apomixis as "asexual seed formation" restricts its use only to gymnosperms and angiosperms. Apomixis is rare in gymnosperms (Asker & Jerling, 1992), and a very rare case of paternal apomixis was reported for *Cupressus dupreziana* A.Camus (Pichot & al., 2000). However, for the purposes of this review, apomixis will be confined only to the flowering plants – angiosperms.

There are several types and modifications of apomixis. Major groups include sporophytic apomixis or adventitious embryony (formation of the embryo is initiated from somatic cells of nucellus or integument tissue outside the megagametophyte) and gametophytic apomixis (the embryo develops directly from the megagametophyte cells). Adventitious embryony very often occurs together with normal sexual reproduction, and besides reduced embryo sacs several additional embryonic sacs develop, thus more than one embryo can be present within

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Received: 20 Feb 2017 | returned for (first) revision: 25 Apr 2017 | (last) revision received: 14 Jun 2017 | accepted: 14 Jun 2017 || publication date(s): online fast track, 5 Oct 2017; in print and online issues, 24 Oct 2017 || Published online "open-access" under the terms of the Creative Commons Attribution 4.0 (CC-BY 4.0) License || © International Association for Plant Taxonomy (IAPT) 2017

the same seed. Adventitious embryony is common in tropical plants and many tropical fruit trees are known for the presence of adventitious embryony (*Citrus* L., *Eugenia* L., *Garcinia* L., *Mangifera* L., etc.). Although adventitious embryony is common in nature (Hojsgaard & al., 2014b), in this review we focused only on the gametophytic type of apomixis.

Gametophytic apomixis has two major developmental pathways: apospory, in which an embryo arises from aposporous initials (somatic cells outside the megaspore mother cell), and diplospory, which is characterized by an embryo developing directly from an unreduced megaspore or megaspore mother cell (see Koltunow, 1993). These types of apomixis have numerous modifications of developmental pathways among groups of plants (e.g., Asker & Jerling, 1992). Despite variation in development as well as the expression of apomixis, its genetic consequences are always the same – the progeny have a maternal genotype. The developmental pathway of apomixis requires at least two steps: (i) avoidance of meiotically reduced megagametophytes and the formation of unreduced female gametophytes instead (i.e., apomeiosis) and (ii) omission of syngamy and parthenogenic development of the embryo (Koltunow, 1993).

Apomicts have been widely considered to represent an "evolutionary dead end" due to the lack of adaptive variation (Maynard-Smith, 1978). However, the large diversity observed in populations of apomicts has swayed opinions away from such a doomsday scenario (Battjes & al., 1992; Chapman & al., 2000; Paun & al., 2006a; Paule & al., 2011). Asexual plants have other sources of genetic variation besides genetic recombination during meiosis. These sources include the accumulation of mutations, chromosome rearrangements (Richards, 1996), recombination during restitutional meiosis (Van Baarlen & al., 2000), polytopic origin from genetically divergent ancestors (e.g., *Antennaria rosea* agg. – Bayer, 2006; *Boechera ×divaricarpa* (A.Nelson) Á.Löve & D.Löve – Dobeš & al., 2004; *Potentilla alpicola* agg. – Paule & al., 2012), transposon activity (e.g., Ferreira de Carvalho & al., 2016), and heritable epigenetic variation (e.g., Wilschut & al., 2016). The majority of apomictic taxa retain functional male meiosis (even obligate apomicts) and produce viable pollen at a low ratio. Therefore, apomicts may serve as pollen donors in crosses with sexual plants (e.g., Tas & Van Dijk, 1999; Krahulec & al., 2004; Mártonfiová, 2006). The majority of apomictic taxa maintain facultative sex and obligate apomixis is relatively rare among flowering plants. Plants with the aposporic type of apomixis tend to be facultative apomicts and form both non-reduced and reduced megagametophytes. Even within one individual and one inflorescence, both reduced and unreduced ovules can be found (Asker & Jerling, 1992; Koltunow, 1993).

Some asexually reproducing animals have been shown to be evolutionarily very old, e.g., bdelloid rotifers and darwinulid ostracods have persisted for tens of millions years (Judson & Normark, 1996; Welch & al., 2009), but information about the age of asexually reproducing plants is scarce. The only relevant age estimate for asexual plants is for *Ranunculus carpaticola × cassubicifolius*, for which the divergence of the investigated apomictic genotypes from its closest sexual relatives was estimated to be around 80,000 years ago (Pellino & al., 2013).

■ CHARACTERISTIC FEATURES OF APOMICTS

Several evolutionary features are linked with apomictic reproduction. The most prominent is that gametophytic apomixis is tightly linked to hybridization and polyploidization (Asker & Jerling, 1992; Carman, 1997; Whitton & al., 2008a). Hybridization seems to be the main factor responsible for triggering the apomictic developmental pathway (e.g., Delgado & al., 2014; Hojsgaard & al., 2014a), due to the conflicts in gene expression (Carman, 1997), and subsequent polyploidization stabilizes apomictic over disturbed sexual reproduction, e.g., allowing deviation in paternal to maternal genome contribution during seed formation (Hojsgaard & al., 2014a). Most apomictic taxa are found within genera with extensive reticulate evolution and frequent polyploidization, especially species belonging to the Asteraceae, Poaceae, and Rosaceae (Carman, 1997; Richards, 2003; Whitton & al., 2008a; Talent, 2009). However, apomicts exist in all major clades of flowering plants, and the number of new records of families containing apomictic taxa continues to increase (Hojsgaard & al., 2014b). Apomixis causes the formation of reproductively isolated individual genotypes and clonal reproduction combined with a reproduction barrier may lead to overrepresentation of the clonal genotype in a short time. Moreover, if the apomictic lineage is morphologically stable over time and space, it might resemble a true species. However, in regions where sexual plants and apomicts meet the formation of hybrid swarms is expected. In general, apomictic groups represent a complex reticulate network of sexual species, stable widespread apomictic lineages and their hybrids restricted to their place of origin. Clonal copying of individual genotypes maintains the morphological uniformity of each clonal lineage. Apomictic taxa show extremely narrow morphological variation, which often falls within the broad morphological variation of their sexual relatives. Nevertheless, apomicts are not without variation, as discussed above, and the view pertaining to uniclonal apomictic taxa has gradually changed. Facultative sexuality may greatly enrich genotypic and phenotypic variation as shown for North American *Amelanchier* species (e.g., Campbell & Wright, 1996), *Pilosella* (e.g., Krahulcová & al., 2009), the *Ranunculus cassubicus* complex (e.g., Hörandl & al., 2009), *Rubus* subg. *Rubus* (e.g., Davis, 1958; Nybom, 1995; Sochor & al., 2015), and *Sorbus* (e.g., Lepší & al., 2015). Whereas "obligate" apomicts often form discrete morphological lineages, facultative apomicts show morphological gradients in which putative parental species can be traced (Krahulec & al., 2004; Fehrer & al., 2005).

■ SPECIES CONCEPTS

There has been a long-standing scientific and philosophical discussion about one of the main questions in biology: "What represents a species and how do we recognize species?", and this question is especially important in connection to asexually reproducing taxa (e.g., Weber, 1996; Dickinson, 1998, 1999; Hörandl, 1998; Stace, 1998; Mayden, 1997, 1999, 2002;

Haveman, 2013). Many species concepts have been proposed from the time of Darwin to define the basic unit of biodiversity in nature. Currently there are more than 20+ species concepts (e.g., Mayden, 1999; Haveman, 2013) commonly used, but not all of them allow for the recognition of apomictic taxa as distinct species (but see fig. 1 in Mayden, 1999; table 1 in Haveman, 2013). It is likely the discussion about species and species concepts will never end, because opinions of different scientists working with different aims with different organismal groups, using different experimental approaches and different types of data, substantially differ in many points resulting from the different observations they made, and consequently their preferences for the most appropriate concept differ.

Mayden (1997, 2002) has stated several points to ponder regarding the issue of species concepts. The main is the need for "consilience on species concepts", which can be achieved by adopting a hierarchical view of species concepts. An important prerequisite for broad consilience is the recognition and differentiation of species concepts as primary (theoretical, non-operational) and secondary (operational). The primary species concept should serve as a universal concept answering the basic question: "What is/are species?", while the secondary species concepts answer the question: "How to recognize a species?" (Mayden, 1999). There should be only one universal primary species concept (Mayden considered the *evolutionary species concept* – ESC in the sense of Wiley & Mayden, 2000, as such a universal concept), while there can be more secondary concepts. Secondary concepts differ more or less in the strict definition of what represents a species and the boundaries among them. Secondary concepts are operational concepts, and they are accommodated to different cases observed in nature, and as such, they are always restrictive in some way. Acceptance of the hierarchy of species concepts with one primary and many secondary concepts may help to solve the issue of definition of species, especially in the case of apomictic taxa.

In genera with a frequent occurrence of apomixis, infrageneric groups were often created and taxa were/are grouped into informal categories such as species aggregates, complexes, or sections, within which particular apomictic clones/lineages are described based on their distinctive morphology (Table 1). This approach is not always suitable and sometimes several different non-monophyletic clonal lineages were/are grouped under one name (*Boechera holboellii* (Hornem.) Á.Löve & D.Löve – Rushworth & al., 2011; *Ranunculus auricomus* complex – Hörandl & al., 2009), or this approach leads to the generation of separate names for each apomictic clone that differs only slightly from another morphologically similar taxon (e.g., Weber, 1996). When apomicts hybridise freely with sexual taxa or other facultatively apomictic taxa, and backcross with them, they form a great number of novel hybrid genotypes and phenotypes that may only be locally distributed (e.g., *Pilosella* L. – Krahulec & al., 2004; *Potentilla alpicola* La Soie – Paule & al., 2012; *Rubus* L. – Weber, 1996). The naming of such apomictic lineages leads to a more intricate taxonomy. The separation of exclusively sexual taxa within apomictic complexes and their treatment under the *biological species concept* helps to purge complicated taxonomy in genera with a frequent occurrence of apomictic taxa. This approach is used in many European and North American apomictic genera, for example, in *Crepis* L. (Stebbins & Babcock, 1939), *Rubus* (Weber, 1996), and *Taraxacum* Wigg. (Kirschner & Štěpánek, 1996), among others. However, the *biological species concept* in the sense of Mayr (1942), which defines species as "groups of interbreeding natural populations reproductively isolated from other such groups", is not applicable to asexual groups (e.g., Hörandl, 1998; Dickinson, 1999; and references therein) because of the lack of gene flow within and among populations. Apomictic taxa can be recognized under different concepts, e.g., *agamospecies concept* (Stuessy, 1990) or *phylogenetic species concept* (Eldredge & Cracraft, 1980; Cracraft, 1983; McKitrick & Zink, 1988). However, following Mayden's recommendation and applying the ESC which defines species as "… an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and historical tendencies" (Wiley & Mayden, 2000), then both sexual and asexual taxa can be recognized as separate species under one concept.

Thus, what is the problem with apomictic taxa? There are several problems associated with apomictic taxa, but the three issues listed by Haveman (2013) are the most prominent and often hamper the recognition of apomictic taxa as distinct species: "1) apomictic species are impossible by definition; 2) apomictic species do not resemble amphimictic outbreeders; and 3) apomictic species are not coherent". As these three points are discussed in detail in Haveman (2013), we here reduce our arguments only to short statements about each point: 1) many of the existing species concepts allow the recognition of apomictic taxa as separate species (e.g., see table 1 in Haveman, 2013); 2) many of the apomictic taxa are not uniclonal and harbour a considerable amount of genetic diversity; 3) asexual reproduction itself and/or a particular diversification process leading to the formation of a particular taxon can be seen as a coherent force.

Besides the above-mentioned species concepts two taxonomic ranks/concepts are commonly used for apomictic taxa, namely the categories of *macrospecies* = *species aggregate*/*species complex*/*species group* and *microspecies*, although these categories are not officially recognized nor accepted by the *International Code of Nomenclature for algae, fungi and plants* (McNeill & al., 2012). The *microspecies* category is used to refer to a particular morphologically/genetically homogeneous apomictic taxon/lineage within a large and variable species complex (sometimes also referred to as *agamospecies*) consisting of several/numerous morphologically/ecologically/karyologically/genetically discernible entities/taxa. *Microspecies* are characterized by morphological constancy maintained by the apomictic mode of reproduction. The category of microspecies is represented, e.g., in *Taraxacum* with numerous validly described apomictic morphotypes. However, the fact that the rank of microspecies is not accepted by the *Code* does not mean that apomictic taxa (commonly referred to as *microspecies* or *agamospecies*) are not scientifically recognized species or have not been validly described.

The term *microspecies* should point to rather small but objectively present diagnostic morphological characters/features. In contrast to *microspecies*, the rank/concept of *macrospecies* represents a group of taxa very similar in morphology and unclear boundaries between them, where distinguishable entities are not recognized as separate species and are rather bulked under one large and polymorphic taxon/species. This roughly corresponds to what is called a species complex or species aggregate in apomictic genera.

■ TAXONOMIC CONCEPTS IN MAJOR APOMICTIC GENERA

The following text provides an overview of the approaches used in some extensively studied genera in which apomictic reproduction has caused problems with the taxonomic treatment of apomictic taxa. For each listed genus a brief description of the genus with information about the type of gametophytic apomixis is provided. For *Pilosella* and *Taraxacum*, we provide more detailed information, because these genera are the focus of the authors' primary research interests.

Poaceae

Apomixis has been recorded in approximately 41 genera with both major types of gametophytic apomixis: apospory and diplospory (e.g., Kellogg, 1990; Asker & Jerling, 1992; Carman, 1997). The most species diverse subfamilies (Chloridoideae, Panicoideae, Pooideae) also contain the greatest number of apomictic genera (e.g., fig. 1 in Ortiz & al., 2013). An extreme example of the occurrence of apomixis in the grass family is the existence of the compilospecies *Bothriochloa bladhii* (Retz.) S.T.Blake (synonym *B. intermedia* (R.Br.) A.Camus) connecting the three genera *Bothriochloa-Capillipedium-Dichanthium* (De Wet & Harlan, 1970). ("A compilospecies is genetically aggressive, plundering related species of their heredities, and in some cases it may completely assimilate a species, causing it to become extinct", Harlan & De Wet, 1963: 499). Apomixis in grasses is mainly facultative, although near-obligate apomictic taxa have also been identified (e.g., Clausen, 1961; Asker & Jerling, 1992; Kelley & al., 2009; Durand & al., 2000). Facultative apomixis allows for gene flow between different genotypes and mating systems (e.g., Clausen, 1961; Kellogg, 1987; Renno & al., 2001), and the extent of sexually and asexually produced progeny is highly variable within individuals or populations (e.g., Clausen, 1961; Kellogg, 1987; Matzk & al., 2005; Hojsgaard & al., 2008; Kaushal & al., 2008). Moreover, the number of developed reduced and unreduced (aposporous) embryo sacs can be influenced by ecological factors such as day length or air temperature (e.g., Kellogg, 1987; Asker & Jerling, 1992; and references therein). Apomictic taxa are polyploid cytotypes of morphological species, which often also contain diploid cytotypes represented by sexual outcrossers (e.g., Müntzing & Müntzing, 1971; Schmelzer, 1997; Akiyama & al., 2011; Sartor & al., 2013). Apomixis itself does not lead to the formation of morphologically discrete units in grasses, but in the presence of gene flow, it leads to increased genotypic and morphological variation of facultative apomictic taxa. Many genera form polyploid complexes with many intermediate forms, which were often described as separate species. The extent of the differences (whether genetic, phenotypic, or cytotypic) depends on the species life history and the pattern of geographic distribution of apomictic and sexual cytotypes

Table 1. Basic information about the most common genera with high numbers of apomictic taxa (described in this review) and taxonomic rank used for apomictic taxa.

Family	Genus	Ploidy level of sexual cytotype	Ploidy level of apomictic cytotype	Origin of apomictic cytotypes	Criterion for species recognition	Taxonomic category or rank used for apomictic taxa	Example
Poaceae	*Paspalum* L.	2*x*	3*x* and higher ploidy levels	prevailingly autopolyploid	morphology, cytology	conspecific with 2*x* cytotype	*P. simplex* Morong[a]
	Poa L.	2*x*, 4*x*, 6*x*, also higher ploidy levels	3*x* and higher ploidy levels	autopolyploid, allopolyploid also possible	morphology, distribution	distinct species	*P. riphaea* (Asch. & Graebn.) Fritsch[b]
						conspecific with 2*x* cytotype	*P. nemoralis* L.[c]
Ranunculaceae	*Ranunculus* L.	2*x*, 4*x*	4*x*	autopolyploid	morphology, cytology, genetics	conspecific with 2*x* cytotype or subspecies	*R. kuepferi* Greuter & Burdet[d]
			6*x*	allopolyploid		nothotaxa (hybrids with defined parental taxa)	*R. carpaticola* Soó × *R. cassubicifolius* W.Koch[e]
Brassicaceae	*Boechera* Á.Löve & D.Löve	2*x*	2*x*, 3*x*	autopolyploid	morphology, distribution, cytology, parentage, genetics	conspecific with 2*x* cytotype	*B. holboellii* (Hornem.) Á.Löve & D.Löve[f]
			3*x*	allopolyploid		distinct species	*B. pauciflora* (Nutt.) Windham & Al-Shehbaz[g]

Table 1. Continued.

Family	Genus	Ploidy level of sexual cytotype	Ploidy level of apomictic cytotype	Origin of apomictic cytotypes	Criterion for species recognition	Taxonomic category or rank used for apomictic taxa	Example
Rosaceae	*Alchemilla* L. s.str.	?	high polyploids	presumably allopolyploid	morphology, cytology	species, agamospecies, species aggregates	*A. vulgaris* agg.[h]
	Amelanchier Medik.	2*x*	(3*x*), 4*x*	(autopolyploid?) allopolyploid	morphology, cytology, distribution	microspecies	*A. spicata* K.Koch[i]
	Crataegus L.	2*x*	3*x*, 4*x*	3*x*-auto-/allopolyploid, 4*x*-backcross of 3*x* with one of its parents, partly autopolyploid	morphology, cytology, distribution, genetics	conspecific with 2*x* cytotype, species complex	*C. suksdorfii* (Sarg.) Kruschke/*C. gaylussacia* A.Heller[j]
			4*x*	allopolyploid		microspecies, agamospecies complex	*C. douglasii* Lindl.[j]
	Potentilla L.	2*x*, 4*x*	6*x*	most probably allopolyploid	morphology, cytology, distribution	conspecific with 2*x* cytotype	*P. argentea* L.[k]
			5*x*, 6*x*, 7*x*	most probably allopolyploid		species aggregates	*P. collina* agg.
			6*x*	unknown		distinct species	*P. alsatica* T.Gregor[l]
	Rubus L. subg. *Rubus*	2*x*	3*x*, 4*x*, 5*x*, 6*x*	allopolyploid	morphology, distribution	(micro)species	*R. bifrons* Vest
	Sorbus L.	2*x*	4*x*,	autopolyploid	morphology, cytology, distribution	microspecies/ species	*S. rupicola* (Syme) Hedl.[m]
			3*x*, 4*x*	allopolyploid			*S. moravica* M.Lepší & P.Lepší[n]
Asteraceae	*Antennaria* Gaertn.	2*x*, 4*x*	higher ploidy levels	autopolyploid	morphology, genetics	conspecific with 2*x* cytotype, subspecies	*A. fresiana* (Trautv.) E.Ekman subsp. *fresiana*[o]
				allopolyploid		species, species complex	*A. parlinii* Fernald[o]
	Crepis sect. *Psilochenia* (Nutt.) Babc.	2*x*	3*x* and higher ploidy levels	autopolyploid	morphology, distribution	conspecific with 2*x* cytotype	*C. acuminata* Nutt.[p]
				allopolyploid		species aggregate	*C. barbigera* Leiberg[p]
	Erigeron L.	2*x*	3*x*, 4*x*, 5*x*	autopolyploid?	morphology, distribution	conspecific with 2*x* cytotype	*E. strigosus* Muhl. ex Willd.[q]
	Hieracium L. s.str.	2*x*	3*x*, 4*x*, 5*x*	allopolyploid	morphology, distribution, genetics	microspecies	*H. nigrescens* Willd.[r]
	Pilosella Vaill.	2*x**, 4*x*, 6*x*, rarely 3*x*, aneuploids	3*x*, 4*x*, 5*x*, 6*x*, also higher ploidy levels	autopolyploid, allopolyploid	morphology, cytology, distribution, reproduction mode	(micro)species, species aggregates, subspecies	*P. officinarum* Vaill.[s] *P. bauhinii* (Schult.) Arv.-Touv.[t]
	Taraxacum F.H.Wigg.	2*x*, 4*x*	3*x*, 4*x*, 5*x*, rarely higher ploidy levels	presumably allopolyploid	morphology, distribution	microspecies	*T. albidum* Dahlst.[u]

Cytotypes in parentheses are less common. ? – in case of *Alchemilla* s.str. fully sexual cytotypes are not known; * – sexual reproduction is not tightly linked to diploids; polyploids also reproduce sexually, but this is highly variable and dependent on distribution area.

a – Urbani & al., 2002/Ortiz & al., 2013; b – Hoták & al., 2013; c – Kelley & al., 2009; d – Huber, 1988/Cosendai & al., 2011; e – Hörandl & al., 2009; f – Al-Shehbaz & Windham 2010; g – Windham & Al-Shehbaz 2007a; h – Fröhner, 1995; i – Burgess & al., 2014/Campbell & al., 2014; j – Dickinson & al., 2008/Lo & al., 2010/Phipps, 2015; k – Paule & al., 2011; l – Gregor, 2004; m – Robertson & al., 2004b; n – Lepší & al., 2015; o – Bayer, 2006; p – Bogler, 2007/Sears & Whitton, 2016; q – Nesom, 2015; r – Chrtek & al., 2007; s – Mráz & al., 2008; t – Rosenbaumová & Krahulec, 2015; u – Morita, 1994.

(e.g., Renno & al., 1995; Kharrat-Souissi & al., 2011; Sartor & al., 2013). Several studies investigated the morphological differences between apomictic and sexual cytotypes/populations, but the results were generally similar with a continuous overlap of the investigated morphological traits (e.g., see Kellog, 1990 and references therein). This finding indicates the presence of individuals with increased morphological/genetic/ecological variation and a large amount of intermediates connecting a particular species complex. It has become widely accepted that in genera containing a large number of widespread variable hybrid complexes stabilized by facultative apomixis their local differentiation is not sufficient for species recognition. Apomictic cytotypes are rarely recognized as separate species and are rather combined into one "agamic complex" or "multiploid species", i.e., they are treated as a single species (e.g., Kellogg, 1990; Renno & al., 1995; Hojsgaard & al., 2008; Ortiz & al., 2013). For some apomictic complexes (e.g., *Poa pratensis* L.) particular cytotypes (also apomictic) are recognized as a subspecies or species, but this varies among local Floras. The approach of recognizing "multiploid" rather than many separate species is well established e.g., in *Paspalum* L., and partly also in *Poa* L.

***Paspalum* L. (paspalum, bahiagrasses, crowngrasses, dallis grasses). —** *Paspalum* is species-rich and one of the largest genera in Poaceae (ca. 350–370 species) (Rua & al., 2010; Ortiz & al., 2013). The distribution range includes nearly the entire world, although only a few species are cosmopolitan. The main areas of distribution include North and South America. Tropical South America is viewed as the centre of origin for the genus (Rua & al., 2010; Ortiz & al., 2013; and references therein). The genus is of great agronomic value as forage grass and because of the high potential of exploitation of apomictic reproduction in the production of apomictic crops. Recently the systematics of the genus has undergone changes, and new species formerly described under different genera have been transferred and accommodated in *Paspalum* (Hojsgaard & al., 2008; Rua & al., 2010; Ortiz & al., 2013). The infrageneric classification of the genus is not unambiguous, and still awaits large studies investigating the genus in its entire range. Traditionally the genus is divided into four subgenera (Rua & al., 2010; Ortiz & al., 2013). Pseudogamous apospory is the prevailing type of apomixis within the genus, although diplospory has been described in several species (see table 1 in Ortiz & al., 2013 and references therein; table 1 in Galdeano & al., 2016). As other apomictic genera, *Paspalum* also represents a polyploid species complex which originated via inter- and intraspecific crosses, thus apomictic taxa are both auto- and allopolyploids (Quarin, 1992; Hojsgaard & al., 2008; Ortiz & al., 2013). The best-known and investigated species complexes are *P. simplex* Morong and *P. notatum* Flüggé, which consist of both diploid sexual and autopolyploid apomictic taxa (Urbani & al., 2002; Rua & al., 2010). Investigations of natural populations showed a high level of variation in cytotype composition, reproduction mode, and genetic variation (Urbani & al., 2002; Sartor & al., 2013). A sympatric population of sexual and apomictic cytotypes contains a greater level of genetic variation than ploidy-uniform populations (Urbani & al., 2002; Sartor & al., 2011), which highlighted hybridization as a process increasing the genetic variation of apomictic cytotypes and creating new apomictic lineages (Quarin, 1992). Most *Paspalum* species represent multiploid species, containing diploid sexual and polyploid (from 3*x* to 6*x*) apomictic cytotypes (Urbani & al., 2002; Ortiz & al., 2013; Galdeano & al., 2016). Apomictic cytotypes of *Paspalum* taxa are not distinguished as separate species, but are treated as one multiploid species together with diploid sexuals (Ortiz & al., 2013).

***Poa* L. (meadow-grass, bluegrass, tussock). —** Apomixis has been detected in a number of *Poa* species (e.g., Kelley & al., 2009; Gregor, 2013). As mentioned above, particular apomictic cytotypes are recognized as subspecies or species. One such example is the *Poa glauca* Vahl s.l. complex. Several stenoendemic apomictic types are distinguished as separate species (e.g., *P. babiogorensis* Bernátová & al. – Bernátová & al., 1999, *P. margillicola* Bernátová & Májovský – Bernátová & Májovský, 1997, *P. riphaea* (Asch. & Graebn.) Fritsch – Hoták & al., 2013, and *P. sejuncta* Bernátová & al.) in Central Europe. Such an approach, however, is absent in other complexes with known apomixis including the *P. compressa* agg., *P. nemoralis* agg., *P. nervosa* agg., and *P. palustris* agg., as well as in other genera (e.g., *Bothriochloa* Kuntze, *Nardus* L.).

Ranunculaceae

Ranunculaceae consists of ~2500 species (Stevens, 2001–), and the occurrence of gametophytic apomixis is limited to *Ranunculus* (subfam. Ranunculoideae).

***Ranunculus* L. (buttercup, goldilocks). —** *Ranunculus* is a cosmopolitan genus with members that can be found in all major biomes from the tropics to the Mediterranean to arctic regions (Emadzade & al., 2011). The genus shows different ploidy levels, and polyploid cytotypes represent evolutionarily derived taxa. The genus is classified into 17 sections (Hörandl & Emadzade, 2012), while apomictic reproduction is present only in two of them in three species complexes: *R. kuepferi* Greuter & Burdet and *R. parnassiifolius* L. (both of sect. *Aconitifolii* Tutin), and *R. auricomus* (sect. *Auricomus* Schur), which suggests the independent origin of apomixis within each species complex (Hörandl & Emadzade, 2012). Apomixis includes facultative pseudogamous apospory restricted to polyploids – mainly the 4*x*, 5*x*, and 6*x* cytotypes (Nogler, 1984; Hörandl & al., 2009; Cosendai & al., 2011). The most-studied apomictic species complex with reticulate relationships is the *R. auricomus* species complex (Ericsson, 1992; Hörandl, 1998; Paun & al., 2006b; Hörandl & al., 2009) comprising roughly 800 apomictic microspecies (Hörandl & Raab-Straube, 2015), which are traditionally grouped into four morphological groups (auricomus, cassubicus, fallax, monophyllus). However, these morphogroups were designed just as informal groups (Ericsson, 1992; Hörandl & Gutermann, 1998). In contrast to the hundreds of described apomictic microspecies, only four sexual species belonging to the *R. auricomus* complex are known (*R. carpaticola* Soó, *R. cassubicifolius* W.Koch, *R. marsicus* Guss. & Ten., *R. notabilis* Hörandl & Gutermann) (Hörandl & Paun, 2007). The whole complex probably originated by hybridization of three of the four sexual species: *R. notabilis* (auricomus morphotype) × *R. carpaticola/cassubicifolius* (cassubicus morphotype). Intensive research has shed more light on the relationships within the complex and the hybrid origin of two apomictic taxa has recently been described. The hexaploid apomictic *R. carpaticola* × *cassubicifolius* from the cassubicus morphogroup originated through hybridization between two sexual taxa (most likely the tetraploid *R. cassubicifolius* and the diploid *R. carpaticola*; see Paun & al., 2006b). Hybridization between these two parental species gave rise to a group of hybrid polyploid apomictic lineages (Paun & al., 2006b). To classify this group of apomictic taxa, the category of nothotaxa (hybrid derivatives of defined sexual taxa) was suggested by Hörandl & al. (2009). *Ranunculus variabilis* Hörandl & Gutermann is another widespread apomictic taxon from the auricomus morphogroup for which an origin through hybridization was proposed. Experimental hybridization between *R. carpaticola/cassubicifolius* × *R. notabilis* resulted in progeny very much resembling *R. variabilis* in morphology (Hodač & al., 2014). Although the experimental hybrids were mostly sexual, some of them showed spontaneous apospory (Hodač & al., 2014; Hojsgaard & al., 2014a), which supports the "rescue" function of apomixis in allopolyploids – the escape from sterility due to conflicts in the gene expression of different genomes (Carman, 1997).

Another well-studied species, *R. kuepferi*, represents a polyploid set (set of 2*x*, 3*x*, 4*x*, 5*x*) in which diploids are sexual (with rare facultative apomixis – Schinkel & al., 2016), whereas apomicts are (auto)tetraploids (Burnier & al., 2009; Cosendai & al., 2011). In this case, the taxonomic treatment of apomictic cytotypes is not uniform. Huber (1988) distinguished two subspecies: *R. kuepferi* subsp. *kuepferi* (including the diploid cytotype) and *R. kuepferi* subsp. *orientalis* W.Huber (including polyploid cytotypes: tri-, tetra- and pentaploids). This division follows the concept of treating autopolyploids without diagnostic characters as subspecies. This division of *R. kuepferi* into two subspecies is also followed by Burnier & al. (2009). In contrast to this classification, Cosendai & al. (2011) did not treat apomicts as separate taxa but as apomictic polyploid cytotypes within the species, because of lack of diagnostic characters (Cosendai & al., 2013; Schinkel & al., 2016).

The third taxon, *R. parnassiifolius*, is similar to the preceding species, divided into three subspecies: *R. parnassiifolius* L. subsp. *parnassiifolius* and *R. parnassiifolius* subsp. *favargeri* P.Küpfer comprise a mixture of di- and tetraploids, while apomictic tetraploids are treated as the separate *R. parnassiifolius* subsp. *heterocarpus* P.Küpfer (Cires & al., 2012).

Brassicaceae

Brassicaceae is a monophyletic group with well-known genome/karyotype evolution (Mandáková & Lysák, 2008; Schubert & Lysák, 2011). The rare occurrence of diplosporous apomixis in a single genus (*Boechera*) is related to supernumerary chromosomes (Sharbel & al., 2004, 2005; but see Mandáková & al., 2015).

Boechera **Á.Löve & D.Löve (Boechera rockcress). —** *Boechera* represents the only case of apomixis in the family. The genus includes ca. 110 species distributed mainly in the western U.S.A., Greenland, and the Russian Far East (Alexander & al., 2013). Apomixis within this genus is meiotic diplospory (Ozias-Akins & Van Dijk, 2007). *Boechera* represents the only well-documented example of apomixis at the diploid level (Dobeš & al., 2007; Kantama & al., 2007). Except for diploids, triploids as well as aneuploids are apomictic (Kantama & al., 2007). Tetraploids and higher ploidy levels are infrequent in the genus (Dobeš & al., 2007). Intensive research showed that apomictic individuals retain a high level of sexuality and hybridize with obligate sexuals, establishing new asexual lineages (e.g., Schranz & al., 2005). The asexual mode of reproduction in *Boechera* is thought to have ancient origin and is associated with hybridization (Sharbel & al., 2009, 2010; Beck & al., 2012; Kiefer & Koch, 2012). However, recent research has revealed evidence that apomixis is more likely caused by genetic factors causing production of unreduced gametes and not by hybridization itself (Lovell & al., 2013). Apomictic triploids may be considered as true hybrids that originated from crosses between sexual and apomictic diploids, but apomictic diploids more likely originate from intraspecific crosses (Lovell & al., 2013). Evolutionary relationships within the genus are highly complex due to reticulate hybridization and apomixis (e.g., Rushworth & al., 2011; Kiefer & Koch, 2012; Alexander & al., 2013). Interspecific hybridization is very common and sexual species tend to hybridize whenever they come in contact with each other. Apomictic hybrids can also backcross with sexual individuals (Windham & Al-Shehbaz, 2006, 2007a, b; Beck & al., 2012).

The former taxonomic treatment was complicated and not appropriate due to the mixing of different sexual and asexual (alloploid) species based on their superficial similarity (e.g., Mulligan, 1995). For a long time, species of *Boechera* were thus considered to be highly variable in both morphology and reproduction (e.g., *B. divaricarpa* or *B. holboellii* formerly were used as trash cans for many different apomictic morphotypes, and have recently been split into several separate taxa; see, e.g., Windham & Al-Shehbaz, 2006; Rushworth & al., 2011 and references therein), resulting in species practically indistinguishable from each other. Following the taxonomic work of Windham & Al-Shehbaz (2006, 2007a, b), 71 diploid sexual species and 38 apomictic hybrids are currently recognized in *Flora of North America* (Al-Shehbaz & Windham, 2010). This taxonomic treatment is based on the distinction of species resulting from primary divergent evolution (diploid species) from such originating through secondary, reticulate evolution (Windham & Al-Shehbaz, 2006). To avoid misidentification and retain a sustainable taxonomy, sexual and allopolyploid apomictic taxa, for which putative diploid progenitor species were proposed, are recognized on the basis of their morphology, cytology, and geographic distribution as separate species. Apomictic taxa of autopolyploid origin are not treated separately but rather with their diploid parental species (Windham & Al-Shehbaz, 2006, 2007a, b).

Rosaceae

The prevailing type of apomixis in Rosaceae is apospory, but diplospory has been documented as well (Muniyama & Phipps, 1984). Apomixis apparently originated independently in several phylogenetic groups (e.g., Dobeš & al., 2015). Within subfam. Rosoideae different modifications of apospory are known in *Rubus* (tribe Rubeae), *Potentilla*, and *Alchemilla* (tribe Potentilleae). In subfam. Amygdaloideae, apospory is known in several genera of tribe Maleae (syn.: Pyreae). It is a putatively evolutionarily young and monophyletic group, in which reticulate evolution played a major role in diversification. Apomixis is especially known in genera with weak barriers to interspecific hybridization (and intergeneric hybridization). All genera with documented apomixis are considered to be taxonomically very complex. The number of described species varies considerably, and genera like *Cotoneaster* Medik., *Crataegus* L., and *Sorbus* s.l. (especially hybrids between the (sub)genera *Aria* (Pers.) Host and *Torminalis* Medik.) contain many hybrids and microspecies, whereas, e.g., *Amelanchier* Medik. or *Malus* Mill. represent smaller groups. A number of genera (*Aronia* Medik., *Cydonia* Mill., *Pyracantha* M.Roem., etc.) consisting of only a few diploid species can form apomictic intergeneric hybrids (e.g., ×*Sorbaronia mitschurinii* (A.K.Skvortsov & Maitul.) Sennikov – Sennikov & Phipps, 2013).

***Alchemilla* L. (lady's mantle). —** *Alchemilla*, with more than 1000 described species, is widespread mainly in the mountainous areas of the Old World, with most species being found in Europe, the Middle East, and in the mountains of eastern Africa, but a few species are also native to other parts of the world (Japan, Srí Lanka, Greenland) (Fröhner, 1995; Sepp & Paal, 1998; Gehrke & al., 2008). There are different opinions on the classification of the genus (e.g., Rothmaler, 1935, 1937; Fröhner, 1995; Notov & Kusnetzova, 2004; Gehrke & al., 2008 and references therein). In the traditional understanding the genus is paraphyletic, which is caused by a group of approximately 70 African species forming a separate Afromilla clade (Gehrke & al., 2008). Recent phylogenetic work (Gehrke & al., 2008) favours the acceptance of the genus in a wide sense with four clades or subgenera (Eualchemilla clade [*Alchemilla* s.str.], Aphanes clade, Lachemilla clade, Afromilla clade). *Alchemilla* s.str. represents a species-rich group of Eurasian taxa, however with unresolved relationships and complex taxonomy. The relationships within *Alchemilla* s.str. are not clear for several reasons: the presence of apomixis, absence of sexual taxa, high polyploidy, presence of many transitional forms, and hybridization. The majority of European taxa (around 300 described species) reproduce almost exclusively via apomixis (apomixis is of the apospory type with autonomous endosperm development; Strasburger, 1905), and only a few European species are capable of sexual reproduction (e.g., *A. pentaphyllea* L. and several taxa of the *A. hoppeana* agg.). Elevated polyploidy (the lowest chromosome counts for Central European taxa is $2n = 96$ while the highest is $2n = 152$ for *A. fissa* Günther & Schummel; the highest number of chromosomes in the genus was observed in *A. faeroensis* (Lange) Buser $2n = 182–224$ – Fröhner, 1995) causes non-functional male meiosis, and many taxa do not produce viable pollen or produce pollen of very poor quality (Fröhner, 1995). European taxa are of long-standing hybrid origin and identification of the parents is quite problematic because only a few of the extant taxa reproduce sexually (Fröhner, 1995; Sepp & Paal, 1998; Gehrke & al., 2008). The evidence of past hybridization, responsible for the complex patterns in morphological variation, are also seen in the frequent presence of aneuploids. Despite the lack of current hybridization, because of the presence of nearly obligate apomictic reproduction, non-functional female/male meiosis, and high poly-/aneuploidy and hybrid origin, taxon identification and classification is difficult and demanding (Sepp & Paal, 1998; Sepp & al., 2000). However, according to cytoembryological observations (e.g., Izmailov, 1994), some taxa are facultative rather than obligate apomicts and retain the capability for occasional hybridization.

The current classification of *Alchemilla* s.str. (or the Eualchemilla clade) went through several modifications (e.g., Rothmaler, 1935; Plocek, 1982; but see Gehrke & al., 2008 and references therein), and the most recent provided by Fröhner (1995) is based on the work of Rothmaler (1937). Fröhner's (1995) classification of the Eurasian taxa is based on morphological and cytological observations. He recognized four so-called "Hauptgruppen" or main sections which are interconnected through nine "Merkmalskomplexe" or intermediate sections. Sepp & Paal (1998) and Notov & Kusnetzova (2004) proposed some changes in Fröhner's system of sections.

Many apomictic agamospecies or microspecies were described as separate species as if they were sexual species, because of the assumptions that they are obligate apomicts, have distinctive morphological characters, and have different distribution areas and ecological niches (Fröhner, 1995; Sepp & Paal, 1998). However, recent morphological, molecular, and ecological investigations found that many of these microspecies are practically indistinguishable (e.g., *A. acutiloba* Opiz vs. *A. micans* Buser – Sepp & al., 2000), because there is continuous morphological variation between the species and only a few species have distinctive, well-preserved characteristics (e.g., *A. plicata* Buser or *A. semilunaris* Alechin – Sepp & Paal, 1998) (Sepp & Paal, 1998, 2000; Sepp & al., 2000; Pihu & al., 2009). This makes the species classification doubtful, whereas higher taxonomic ranks (such as sections, series, or agamospecies groups) are better defined using both morphology and genetics (Sepp & Paal, 1998, 2000; Sepp & al., 2000). For the classification of apomictic taxa Sepp & al. (2000: 119) suggested the following: "The treatment of agamospecies as a morphologically distinct group of plants in a population, and species as a unit joining several agamospecies is not generally accepted, but the new evidence favours this point of view."

***Amelanchier* Medik. (shadbush, serviceberry). —** This genus contains 33 species (Phipps & al., 1990; Robertson & al., 1991; but see Campbell & al., 2014) and representatives of the genus are medium-sized shrubs or small trees that are distributed in the North Temperate Zone. The genus is species diverse and taxonomically complex especially in North America (NE U.S.A., SE Canada) (Campbell & Doucette, 2015). The apomictic taxa are polyploids, mainly tetraploids (triploids are also apomictic, but retain a higher degree of sexuality), with pseudogamous apospory (Campbell & al., 1991; Burgess & al., 2014). Apomixis is facultative and apomictic individuals possess a high degree of sexuality. Diploid sexual species are self-incompatible, whereas the facultatively apomictic taxa are self-compatible (Campbell & Wright, 1996; Burgess & al., 2014). Frequent hybridization among the North American taxa resulted in a complex network of hybrids and hybrid swarms (Campbell & Wright, 1996). The problem with evaluating apomictic and hybrid taxa stems from the lack of differentiation between populations of apomictic taxa, hybridization among the taxa, and the morphological similarity of diploids and polyploids (Campbell & Wright, 1996; Campbell & al., 2014; Burgess & al., 2015). Diploid sexual taxa (in North America there are nine diploid species and all include polyploids; Burgess & al., 2014) represent more or less discrete units and fulfil the definition of a distinct species under a broad range of species concepts (Burgess & al., 2015). Polyploid apomictic taxa that are morphologically differentiated are treated as microspecies. However, there is the question what to do with many lineages of only local distribution, which cannot be recognized as distinct taxa. To keep the taxonomy of the genus at a reasonable level, widespread polyploid apomictic taxa are rather grouped into species complexes (including several similar morphotypes) (Campbell & Wright, 1996; Campbell & al., 1997, 2014; Burgess & al., 2014).

***Crataegus* L. (hawthorn). —** *Crataegus* is a large genus distributed in the Northern Hemisphere and well known for its taxonomic complexity (Talent & Dickinson, 2007). The number of species varies considerably: more than 2000 species were described (The Plant List, 2013), but the number of accepted names is around 140–200 (Phipps & al., 1990). The genus is the most species diverse (ca. 100 species) in temperate parts of the New World (from Canada to Central America), while around 60 species were identified from the Old World (Lo & al., 2009). The taxonomy is complicated due to the presence of polyploidy, gametophytic apomixis, and extensive hybridization. Frequent hybridization and high morphological variation as well as polyploidy, apomixis, and a formerly used species concept that was too narrow, led to uncritical species description in the second part of the 19th century in North America (Dickinson, 1999). The Old World species are usually morphologically well-defined diploids, but common polyploidy and a high degree of hybridization blur clear species boundaries and the complex structure of populations still awaits elucidation. The situation with the New World species (especially the eastern North American species) is similar, but more complicated (Talent & Dickinson, 2005; Dickinson & al., 2008). Within the genus there are sexual self-incompatible diploids and facultatively asexual self-compatible taxa (mostly triploids and tetraploids) (Dickinson & al., 2008). Apomixis within the genus is apospory with pseudogamous endosperm development (Campbell & al., 1991). In the current taxonomic treatment the genus is divided into ca. 14 sections and 40 series (Phipps & al., 2003). Polyploidization (both allo- and autopolyploidization), together with common hybridization and backcrossing as well as apomixis, is responsible for the complex intrinsic relationships among particular taxa (Lo & al., 2010). Allopolyploid species (sect. *Douglasianae* Loud. ser. *Douglasianae* (Loud.) Poletiko) have wider distribution ranges than sexual diploid species and autopolyploid triploid species (Coughlan & al., 2014). Morphology and geographic distribution were the basis for the recognition of species within the genus, but many recognized species represented a mixture of cytotypes (Dickinson & al., 2007). To simplify the taxonomy, a partially relaxed biological and morphological species concept is used today. Species are assigned into two species categories. Morphologically well-differentiated sexual diploids and/or tetraploids (which form a species series) are recognized as distinct species. Polyploid facultative apomictic taxa, of supposed hybrid origin, are assigned into a second group and are treated at the infraspecific level as microspecies or taxa within agamic complexes or a species series (Dickinson & al., 2007, 2008). Such agamic complexes comprise a set of morphologically similar apomictic taxa.

In Europe, the systematics of *Crataegus* is very complex. Major microevolutionary processes are similar to the processes in North America (i.e., hybridization and facultative apomixis). Yet, unlike American microspecies with morphological characteristics correlating with their distribution range, it seems that hybridization strongly prevails in European *Crataegus*, resulting in a morphological continuum among major species. Additionally, apomixis fixes morphotypes only at a regional scale, although widespread apomictic taxa also exist (Christensen, 1992). The answer to the question of whether apomictic taxa of European *Crataegus* are taxonomically well-founded or negligible requires further study of the occurrence of apomixis in populations, the composition (proportion of sex/apo cytotypes) of populations, and the stability of apomictic hybrids.

***Potentilla* L. (cinquefoil). —** *Potentilla* consists of both diploid sexual (tetraploids are sexual as well, e.g., *P. crantzii* (Crantz) Fritsch – Paule & al., 2015; *P. puberula* Krašan – Dobeš & al., 2013a) and polyploid apomictic taxa (e.g., Asker, 1985a, b). Observation of putative diploid apomixis in *P. argentea* L. was shown to be erroneous (Holm & Ghatnekar, 1996; Holm & al., 1997). Near obligate pseudogamous apospory has been detected (Håkansson, 1946), and the genus shows large variation in reproductive modes among species as well as within species (e.g., Dobeš & al., 2013b). Hybridization, polyploidization, and recurrent introgression are considered to be the main diversification forces strengthened by the stabilizing effect of apomictic reproduction (Dobeš & Paule, 2010). Within this genus, at least 16 apomictic taxa were recognized (Dobeš & al., 2013a, 2015; and references therein). Several species comprise a series of polyploid taxa, which are (according to some authors) referred to as microspecies, subspecies, or variants (which originated through interspecific or intercytotype hybridization, polyploidization, and backcrosses of sexual and apomictic lineages) (e.g., Müntzing, 1958; Asker, 1977, 1985b; Tomasz & Kołodziejek, 2008). Recent molecular studies of the *P. argentea* (Paule & al., 2011) and *P. collina* groups (Paule & al., 2012) showed that apomictic taxa within these groups originated by multiple hybridization and introgression. Widespread apomictic lineages (e.g., hexaploid *P. argentea*) contain low genotypic diversity at the intrapopulation level, and genotypes were population-specific (Paule & al., 2011). The presence of locally distributed apomictic lineages (with specific genotypes) might reflect their polytopic origin from different parental combinations (Paule & al., 2012). Although homogenous lineages can be observed within apomictic cinquefoils, backcrosses and the lack of morphological delimitation of the taxa does not allow for a comprehensive taxonomic concept for the genus. The current trend in the taxonomy of the genus is not uniform. In widespread taxa such as *P. argentea*, *P. verna* L. etc., apomictic cytotypes/lineages are not treated as taxa distinct from the sexuals (Kurtto & al., 2004). However, on a local scale polyploid hybrid taxa with limited distribution (e.g., from the *P. collina* agg.) are recognized as separate microspecies (e.g., Gregor, 2008; Tomasz & Kołodziejek, 2008).

***Rubus* L. (brambles). —** *Rubus* is another taxonomically complicated genus in which apomixis has affected diversification. The genus is traditionally classified into several subgenera, but only one – subg. *Rubus* – represents a group with predominantly asexually reproducing species (Alice & Campbell, 1999). Subgenus *Rubus* has only four exclusively sexual species in Europe (*R. canescens* DC., *R. incanescens* (DC.) Bertol., *R. sanctus* Schreb., *R. ulmifolius* Schott) and another four sexual species (*R. bollei* Focke, *R. moschus* Juzz., *R. palmensis* A.Hansen, *R. serrae* Soldano) which occur in Macaronesia and the Caucasus (Sochor & al., 2015). The remaining European species (748 species of subg. *Rubus*) are facultative apomictic polyploids (Kurtto & al., 2010). Pseudogamous apospory with highly varying levels of facultative sexual development of both reduced and unreduced embryos provides an enormous potential for hybridization and formation of novel apomictic lineages (Nybom, 1995; Šarhanová & al., 2012). Polyploidization as well as interspecific and intercytotype hybridization gave rise to a species series with different compositions of cytotypes and varying levels of facultative sexuality and clonal reproduction (Sochor & al., 2015). Patchy distribution of different series and cytotypes caused extensive hybridization and led to different parental lineages at the local scale. Hybrid lineages are stabilized by apomictic reproduction but an occasional switch to sexual reproduction may lead to the establishment of new local apomictic genotypes. Moreover, various ecological factors may influence the level of sexuality and apomixis (Šarhanová & al., 2012), and may lead to the establishment of an intricate network of different hybrids/lineages. However, apomictic reproduction can stabilize genotypes that can be homogenous and have discrete morphological characteristics. Such genotypes can also be recognized by taxonomists in the field (Davis, 1958; Ryde, 2011; Trávniček & Žíla, 2011; Haveman, 2013; Király & al., 2015). Taxonomic treatment of the apomictic species involved several approaches (for a review, see Weber, 1996). Weber (1996) suggested a species concept called the *pragmatic species concept* as an appropriate taxonomic approach to apomictic brambles. As main criterion of species delimitation, he chose the scale of geographical distribution (diameter of the distribution area). He suggested four categories of taxa: (1) apomicts with a very wide distribution range spanning (250–)500–1000 km (e.g., *R. nessensis* Hall, *R. plicatus* Weihe & Nees); (2) regionally distributed lineages with a distribution spanning 50–250 km (e.g., *R. austromoravicus* Holub, *R. bohemiicola* Holub & Palek ex Holub); (3) locally distributed lineages with a distribution diameter ≤20 km and (4) individual lineages represented by a single bush spread by runners only in a very restricted area. The taxa from the first two categories are treated as taxonomic species in local Floras, while taxa from the last two categories are not. This system is suitable for describing evolutionarily relevant asexual taxa and for avoiding taxonomic conflicts resulting from the description of supernumerary species. This concept helped to purge the taxonomy of an enormous number of local species described in the 19th and 20th centuries and reduced the number of true species in the flora to a reasonable number. Although the *Weberian concept* is generally accepted by *Rubus* taxonomists, it also encountered criticism for not being scientific, and for omitting stabilized apomictic lineages with local distribution from local floras (for the criticism and arguments against the Weberian concept, see Hörandl, 1998; Ryde, 2011; Haveman & De Ronde, 2013).

***Sorbus* L. (whitebeam, rowan, service tree, mountain-ash). —** *Sorbus* has a worldwide distribution, but it is especially species-rich in the Eurasian region. While sexual reproduction is a characteristic of diploid species, pseudogamous apospory is the typical mode of reproduction of polyploid taxa (e.g., Liljefors, 1953). An often cited case of diploid apomixis (Jankun & Kovanda, 1988) turned out to be erroneous (Vít & al., 2012). The level of apomictic reproduction varies among different taxa with some near-obligate apomicts to facultative apomicts (e.g., Robertson & al., 2004a; Bílá, 2015). In Europe, at least five primary diploid sexual species (*S. aria* (L.) Crantz, *S. aucuparia* L., *S. chamaemespilus* (L.) Crantz, *S. domestica* L., *S. torminalis* (L.) Crantz) are recognized at the subgeneric or generic level, including *Aria*, *Chamaemespilus* Medik., *Cormus* Spach, *Sorbus*, and *Torminaria* Opiz (Nelson-Jones & al., 2002; Campbell & al., 2007; Potter & al., 2007; Lepší & al., 2015). Hybridization among diploid species and backcrosses of hybrids with their parents led to the formation of apomictic hybrids (e.g., Nelson-Jones & al., 2002; Robertson & al., 2004b, 2010; Lepší & al., 2008, 2009, 2015). The taxonomy of apomictic rowans is based on the morphospecies concept coupled with distributional data. New apomictic species are described based on unique morphology coupled with karyological, cytometric, and genotypic data (e.g., Robertson & al., 2004b, 2010; Lepší & al., 2008, 2009, 2015; Vít & al., 2012). While sexual species have broad morphological variation, apomictic taxa show very narrow morphological and genotypic variation (e.g., Robertson & al., 2004b; Vít & al., 2012; Bílá, 2015), and are traditionally recognized as microspecies. Moreover, apomictic taxa have restricted distributions and are often stenoendemic (e.g., Bernátová & Májovský, 2003; Robertson & al., 2004a; Lepší & al., 2015). Only a limited number of apomictic species have a wide distribution overlapping with the distribution of their sexual parents (e.g., *S. danubialis* (Jáv.) Prodan, *S. intermedia* (Ehrh.) Pers., *Sorbus latifolia* (Lam.) Pers., *S. mougeottii* Soy.-Will. & Godr., *S. pannonica* Kárpáti).

Asteraceae

Asteraceae is one of the largest plant families in the world, and it is also the plant family with the third-largest number of apomictic taxa. Recent classification accepts 12 subfamilies (Stevens, 2001–), but most of the apomicts are present in two subfamilies, Asteroideae and Cichorioideae. Both diplospory and apospory is present in both subfamilies. Genera containing apomictic taxa belong to different evolutionary lineages, suggesting the independent and repeated evolutionary origin of apomixis.

***Antennaria* Gaertn. (pussytoes, ladies' tobacco). —** This genus comprises 45 species distributed in the temperate and arctic/alpine regions of North America, Mexico, South America, and Eurasia (Bayer & Stebbins, 1987; Bayer, 1990; Bayer & al., 1996). Two main evolutionary lineages, Leontipes and Catipes, are presently recognized within the genus and comprise six commonly recognized clades altogether (Bayer, 1990; Bayer & al., 1996). Taxa belonging to the Leontipes lineage are mostly diploid with rare autotetraploids that reproduce sexually. Members of the Catipes lineage are highly variable in cytology and in reproductive characteristics. They form a polyploid sexual-apomictic series, from diploids to decaploids, that reproduce sexually (diploids, tetraploids) and also asexually by vegetative growth and by gametophytic apomixis (e.g., Bayer & Stebbins, 1987, 1993; Bayer, 1990; Bayer & al., 1996). Within the genus dioecy has evolved to different levels that depend on the evolutionary position of a particular taxon (Bayer, 1990). For apomictic taxa, only pistillate-female plants are known. Members of the Catipes lineage have the widest distribution area in the genus (Bayer, 1990). Five main polyploid sexual-apomictic complexes are recognized within the genus that represent evolutionarily young groups: *A. alpina* (L.) Gaertn., *A. howellii* Greene, *A. parlinii* Fernald, *A. parvifolia* Nutt., and *A. rosea* Green (Bayer, 1990). These polyploid complexes have evolved via multiple hybridizations among several sexual members of the Catipes lineage. Thus, these taxa have their origins from different genetic backgrounds, and contain different portions of genome from different parental taxa, resulting in a highly heterogenic mix of genomes of several sexual progenitors. This resulted in a highly complex morphology with large phenotypic variation; e.g., *A. parlinii* combines genomes of three diploid progenitors, while the *A. alpina* complex consists of the genomes of six progenitors (for more details, see Bayer, 2006).

Previously, the taxonomic treatment of the genus was quite complicated and contained more than 350 names for taxa described at the beginning of the 20th century. Botanists described many apomictic morphotypes as separate species but did not take into account the real value of morphological characteristics for distinguishing them (Bayer & Stebbins, 1993). The present concept of the genus is based on the recognition of sexual diploids+autopolyploid taxa and their separation from polyploid hybrid derivatives. Diploid species are easy to recognize in terms of morphology, genetics, and are also well-differentiated from each other. Autopolyploid taxa, which are morphologically identical with sexual diploids, regardless of their reproduction mode (sexual or apomictic), are treated as conspecific with sexual diploids. All hybrid (allopolyploid) taxa (sexual or apomictic) are recognized as separate species and/or subspecies because they do not fit any recognized diploid sexual taxa but combine the genomes of several different sexual taxa (Bayer, 2006). This approach follows the suggestions of Bayer & Stebbins (1982) and is presently used for treating the genus in *Flora of North America* (Bayer, 2006).

***Crepis* L. (hawksbeard). —** There are around 200 species recognised in *Crepis* (Enke & Gemeinholzer, 2008), that inhabit a range of habitats throughout the Northern Hemisphere with some species occurring in East, South, and West Africa, the Canary Islands, and Madeira (Enke, 2008). Apomictic reproduction in the form of autonomous apospory, as described by Stebbins & Jenkins (1939), has been observed and documented only in the North American and some Asian species thus far (Sears, 2011). There are ten species native to the flora of North America, which are characterized by the unique base chromosome number $x = 11$, which distinguishes them from the introduced *Crepis* species found on the American continent (Bogler, 2007; Sears & Whitton, 2016). These ten species represent the monophyletic sect. *Psilochenia* (Nutt.) Babc. (Babcock, 1947; Sears & Whitton, 2016). One of the ten species (*C. runcinata* Torr. & A.Gray) is distinct from the remaining nine species because only diploids are known (Babcock & Stebbins, 1938; Bogler, 2007). The remaining nine species form the so-called "*Crepis* agamic complex" sensu Babcock & Stebbins (1938), known for its complex morphology and taxonomic difficulty, and caused by the divergent reproductive strategies of the diploid and polyploid species, as well as hybridization as pointed out by Babcock & Stebbins (1938). Diploid species are self-incompatible outcrossers, while polyploid species reproduce apomictically. Seven species (*C. acuminata* Nutt., *C. atribarba* A.Heller, *C. bakeri* Greene, *C. modocensis* Greene, *C. monticola* Coville, *C. occidentalis* Nutt., *C. pleurocarpa* A.Gray) represent groups of different taxa of different ploidy levels grouped based on morphological similarity around morphologically distinct self-incompatible diploid species (Sears & Whitton, 2016). Babcock & Stebbins (1938) called these seven species "primary species". With respect to origin, two types of polyploids – autopolyploids and allopolyploids – are recognized among the North American hawksbeards (Bogler, 2007; Sears & Whitton, 2016). Autopolyploid apomicts derived from one of the diploid primary species are assigned to a particular diploid species under the informal rank "*forma apomictica*" or are treated as subspecies (Babcock & Stebbins, 1938; Bogler, 2007). Two other species, *C. barbigera* Leiberg and *C. intermedia* A.Gray, comprise only polyploid apomictic individuals or populations grouped together based on morphology and are labelled as agamospecies or agamic complexes (Babcock & Stebbins, 1938; Bogler, 2007, but see Sears & Whitton, 2016 for comments on *C. intermedia*). These groups of agamospecies have an allopolyploid origin and combine the morphological characteristics of two or more sexual species (Whitton & al., 2008a, b).

Babcock & Stebbins (1938) were aware that lumping diploid sexual species together with polyploid apomicts does not reflect true phylogenetic relationships. To solve this issue, they designed a category below the species level, known as "*forma apomictica*", for the polyploid apomictic taxa. By creating the "*formae apomicticae*" category Babcock & Stebbins avoided the naming of each polyploid apomictic taxon and kept the number of recognized taxa at a reasonable level. However, it needs to be stressed that the category "*formae apomicticae*" has been clearly designated as an informal category.

***Erigeron* L. (fleabane). —** *Erigeron* is a widespread genus with more than 400 species occurring in North and South America as well as in Eurasia (Nesom, 1989). Phylogenetic relationships within the genus are complex, and the taxonomic treatment of the genus is based on its division into 20 sections (Noyes, 2000). Diplosporous apomixis with autonomous endosperm development (Gustafsson, 1946) has been documented for eight taxa belonging to five sections (Nesom, 1989; Noyes, 2000, 2007). A molecular phylogeny based on nuclear ITS sequences indicates that apomixis has arisen independently at least three times within the genus (Noyes, 2000), although a single origin and subsequent spread of apomixis through hybridization cannot be fully excluded (Noyes, 2000, 2007). In the present taxonomic treatment of the genus apomictic taxa are not recognised as separate species, but are treated as conspecific with sexual diploid species (Noyes, 2007; Nesom, 2015). Thus, all apomictic taxa (except *E. annuus* Pers. for which only the triploid cytotype has been recorded) represent polyploid cytotypes (mostly triploid and/or tetraploid and pentaploid) of diploid sexually reproducing species (Noyes, 2006, 2007; Nesom, 2015). The species are described mainly based on morphological and distributional criteria.

***Hieracium* L. s.str. (hawkweed). —** Here, we consider *Hieracium* in its narrow sense, excl. *Pilosella*. This is in agreement with the treatment of the genus in most but not all recent regional Floras and databases. These two genera differ in several morphological characters and also in evolutionary trends (e.g., Fehrer & al., 2007, 2009).

Hieracium: leaves with lobes and teeth, pappus hairs in 2 rows, achenes more than 2.5 mm long; diploids with restricted distribution, hybridization rare; polyploids apomictic, without residual sexuality; apomixis of diplosporous type.

Pilosella: leaves subentire, pappus hairs in 1 row; achenes less than 2.5 mm long; hybridization very common, apomicts with residual sexuality; apomixis of aposporous type.

Hieracium belongs to the largest genera of vascular plants. The number of recognized species depends strongly on the species concept and evaluation of apomicts and ranges from 500 to 1000. The genus is formed by two subgenera: subg. *Hieracium* and subg. *Chionoracium* Dumort. (e.g., Fehrer & al., 2007). The second is distributed in both North and South America and contains diploid sexual species. On the other hand, subg. *Hieracium* contains mainly polyploid apomicts, which are more common than diploid sexual species. Diploid sexual species (about 20) occur mainly in southern Europe and the only diploid sexual species having a broader distribution throughout Europe is *H. umbellatum* L. (e.g., Schuhwerk, 2002; Chrtek & al., 2004). The species richness of the genus is formed by a large amount of polyploid taxa, mainly triploids and tetraploids, which are apomictic (diplospory – Bergman, 1941; Skawińska, 1963). Among these taxa no residual sexuality is known, thus apomictic taxa are considered to be obligate apomicts. Due to the present allopatric distribution of diploid species, a strong mentor effect (Mráz, 2003a), and nearly obligate asexuality of polyploids, ancient rather than recent interspecific hybridization along with introgression, accompanied by subsequent polyploidization are considered to be main processes resulting in the great diversity of the genus (e.g., Fehrer & al., 2009; but see Mráz & al., 2005, 2011; Mráz & Paule, 2006). Only a limited number of species are known to consist of both diploid and polyploid cytotypes, e.g., *H. alpinum* L., *H. prenanthoides* Vill. or *H. racemosum* Willd. (e.g., Selvi & Fiorini, 1996; Fehrer & al., 2009; Mráz & al., 2009).

There are two concepts in the taxonomy of *Hieracium*. The first concept (often named as the German concept or "broad species concept") distinguishes basic species defined by a set of morphological characters and intermediate species combining the morphological characters of two or more basic species. These intermediate species are not recent hybrids because of the absence of sexuality among the polyploid taxa. Both basic and intermediate species are known for great richness of morphological forms and are usually considered as subspecies. This concept has been developed by Zahn (1921–1923, 1930–1935, 1936–1938) and was followed by botanists in Central and southern Europe (e.g., Nyárády, 1965; Gottschlich, 2009). Species are described in a broad sense and represent *species groups*. The second concept has its tradition in northwest Europe, and is used mainly in Great Britain, Scandinavia, and Russia (e.g., Sell & Murrell, 2006; Tyler, 2006, 2011; Rich & al., 2008; Ronikier & Szeląg, 2008; Stace 2010). Under this concept each different morphological line represents a separate (micro)species, which are often grouped into broadly defined sections, species groups or aggregates (for more details and comparison of these two concepts see, e.g., Tyler, 2006; Tyler & Jönsson, 2013). This concept is partially based on work of Dahlstedt (1893, 1894) and Johansson (1927, 1929).

Recent investigations and critical evaluation of particular taxa in several groups across Europe led researchers to consider individual apomictic lines as morphologically clearly defined units referred to as microspecies, which are grouped into informal species groups. This approach was used for several groups of mountain and alpine species (e.g., Mráz, 2002, 2003b; Szeląg, 2003; Chrtek, 2004; Chrtek & al. 2007; Ronikier & Szeląg, 2008). An attempt at joining the two approaches, the "German" and the "Scandinavian" one, was made by Tyler (2006) who proposed that only microspecies should be considered as the main evolutionary units, but for practical purposes, to deal with the immense species richness of the genus, morphologically similar taxa should be grouped under informal categories (sections) within which species aggregates, grouping more or less similar/evolutionary related taxa, were created. Within other groups, not studied yet, species with mostly unevaluated subspecies are present. Thus because of low morphological and genetic variation, as well as lack of recent hybridization (due to the presence of only a few diploid sexual species with rather isolated distribution; but see, e.g., Tyler & Jönsson, 2013), morphologically well-defined taxa are described as separate (micro)species. This approach fully agrees with suggestions made by Schuhwerk (2002: 197, points 2 and 3) or Sennikov (2003). However, in Euro+Med PlantBase (Greuter, 2006–) a concept of "wide species" with many subspecies was accepted.

***Pilosella* Vaill. (mouse-ear hawkweed). —** This genus has its native distribution area in Europe, western Siberia, and the mountains of NW Africa. Secondary areas of distribution are regions with a mild climate on other continents, including North and South America, Australia, New Zealand, Japan, and continental eastern Asia (Fehrer & al., 2007). Apomixis in *Pilosella* is autonomous apospory in which both the embryo and endosperm develop autonomously without fertilization. The genus is characterized by a large variation in ploidy levels. Ploidy levels in nature range from diploids to octoploids, and even higher ploidy levels were found in hybridization experiments (Krahulcová & al., 2000). There is no clear pattern in the relationship between ploidy level and reproduction mode. The only exceptions are diploids, which are sexual. Many species form polyploid series combining different reproduction modes. For example, populations of *P. officinarum* Vaill. are tetraploid, pentaploid, and hexaploid, and individual plants were found to be heptaploid and octoploid. Tetraploids are usually sexual, rarely apomictic, and pentaploids are apomictic and rarely sexual. Hexaploids are both apomictic and sexual depending on their distribution area (Mráz & al., 2008).

Most of the hexa-, hepta-, and octoploid hybrids of *Pilosella* that have been analysed to date have variable reproductive modes, especially hybrids between apomictic and sexual parents. Their sexual reproduction is combined with apomixis and haploid parthenogenesis in different proportions among different individuals. Facultative apomictic individuals retain a high level of residual sexuality and may participate in sexual reproduction as maternal plants (Krahulec & al., 2004, 2008; Fehrer & al., 2005, 2007; Krahulcová & al., 2009, 2014).

Several taxonomic solutions were used to classify the broad morphological variation within this genus (for more details, see Krahulec & Krahulcová, 2006).

(1) One approach originated on the European continent and was summarized by Nägeli & Peter (1885). It was followed and further developed by Zahn (1921–1923, 1922–1930). In general, this approach is followed in most national Floras in Central Europe, for example, Nyárády (1965), Gottschlich (1998), Mirek & al. (2002), Schuhwerk & Fischer (2003), Chrtek (2004), Bräutigam & Schuhwerk (2005), and Bräutigam (2011). In this approach basic species are distinguished from intermediate species (based on experimental crosses performed by Nägeli), with the latter being labelled by a formula that indicates the origin and the quantitative influence of the species' parents. In addition, there is a rich structure of infraspecific taxa treated as *grex* (group of subspecies), subspecies, and varieties. Recently, some authors have stressed (e.g., Schuhwerk, 2002) that some of the hybrids are old, fully established types behaving as independent species with their own distribution area, but other hybrids are recent hybrids.

(2) The second approach was developed in Scandinavia (Sweden, Finland) and Russia and is still used by Russian authors (e.g., Schljakov, 1989). In this approach, each distinguishable entity is described as a microspecies, and little attention is paid to the possible relationships between these microspecies. The authors treat variation in both sexual and apomictic taxa in the same manner. The result is a huge number of recognized microspecies even for sexual taxa.

(3) The third approach, developed by the British authors Sell and West, was used in *Flora Europaea* (Sell & West, 1976). These authors considered the main species of the continental flora as true species. All other types were evaluated as hybrids, and those with the same parental combination were synonymized. This approach fully corresponded to the *International Code of Nomenclature for algae, fungi, and plants* (*ICN*; McNeill & al., 2012). The resulting structure is simple and understandable, even for non-specialists. The main difficulty of this approach is the fact that only hybrid types occur in some regions. These hybrids (hybridogenous species) are apomictic and behave as independent units.

(4) Tyler (2001) recently developed a fourth approach. It is based on the knowledge of Scandinavian types and on the common hybridization among *Pilosella* species (for details, see Tyler, 2001: 67; Schuhwerk, 2002). Tyler created a system involving several main species or both main and hybrid species under one species name, e.g., *P. aurantiaca* (L.) F.W.Schultz & Sch.Bip. includes all orange-flowering taxa+*P. caespitosa* (Dumort.) P.D.Sell & C.West; *P. cymosa* (L.) F.W.Schultz & Sch. Bip. includes *P. bauhinii* (Schult.) Arv.-Touv. and *P. praealta* (Gochnat) F.W.Schultz & Sch.Bip. This approach substantially reduced the number of described species, especially in Scandinavia, but complexity is still reflected at the infraspecific level (recognition of subspecies and varieties). This approach reflects the high degree of hybridization and the presence of hybridogenous species. However, this system is based on "Scandinavian experience", and species which often hybridize in Scandinavia but not in other regions, are lumped together. In other regions (e.g., Bulgaria), hybridogenous species are almost absent and only recent hybrids of different species are common (e.g., Krahulcová & al., 2016). If we use this approach consistently, it would be necessary to develop different systems for different regions according to the frequency of hybridization. The frequency of hybridization is evidently influenced by the degree of sexuality in populations (including the presence of sexual types), the compatibility of co-occurring cytotypes, the availability of suitable habitats, and random events in the past. The parental (both hybridogenous) species *P. floribunda* (Wimm. & Grab.) Fr. and *P. glomerata* (Froel.) Fr. can serve as an example. We conducted studies in two mountain regions, the Krkonoše Mts. (Krahulec & al., 2004) and the Šumava Mts. (Krahulec & al., 2008). In the first region, these species were isolated and easily determinable. Only one population contained the hybrid species *P. scandinavica* (Dahlst.) Schljakov (*P. floribunda* × *P. glomerata*) (Krahulec & al., 2004). In the second region, it was difficult to find a border between *P. glomerata* and *P. floribunda*, because there were many repeatedly formed hybrids (corresponding to *P. scandinavica*). For these reasons, we do not consider Tyler's approach to be suitable or universal (e.g., Schuhwerk, 2002). Haveman's (2013: 265) opinion on the

congruency of the approaches developed by Tyler (2001) and Krahulcová & al. (2009) does not appear to be justified.

The most accepted approach, used at the present time in Europe, is based on the combination of the 1st and 3rd approaches described above. This combined approach focuses on the basic species, which are recognized by both approaches. Intermediate species are accepted by this approach if they are stabilized and, unlike recent hybrids, behave independently compared to their parents. This more synthetic approach substantially reduced the number of infraspecific taxa. It has already been accepted in some recent Floras (e.g., Bräutigam, 2011) as well as in the Euro+Med flora database (Bräutigam & Greuter, 2007). However, there are several weak points that may cause problems. The most important one is that the same morphotype can represent a stabilised hybrid species in one region and a recent unstabilised hybrid in another region (see Krahulcová & al., 2012). The other problem is caused by the fact that the same morphological type can originate in different ways (e.g., Urfus & al., 2014).

The final point complicating taxonomic evaluation is that some hybrids form swarms consisting of apomictic, sexual, and semisterile to sterile types. Some of these types could be easily distinguishable, but whether they can be removed from the hybrid swarm and distinguished as separate taxa regardless of other members of the hybrid swarm has yet to be determined. It is evident that many of the taxa described in the past belong to this type. Considering them as different species might be acceptable, provided that such types are allopatric and easily distinguishable. However, if they are members of a hybrid swarm, it is problematic to distinguish them as separate taxa. Examples of this problem can be seen in several species (e.g., Krahulec & al., 2004; Krahulcová & al., 2012)

During our work on *Pilosella* populations we primarily studied mechanisms generating variation. The results are summarized in the following points, which should be considered when formulating taxonomic concept for this complicated group.

(1) Hybrids are repeatedly formed in nature with different frequencies depending on the compatibility of the (cyto)types growing together.

(2) The products of hybridizations are not uniform. In hybridizations, apomicts produce more variable progeny than sexuals with respect to ploidy levels (e.g., Krahulcová & al., 2004) and also to reproduction mode (e.g., Krahulcová & al., 2011; Rosenbaumová & al., 2012), because the frequency of their residual sexuality is on the order of 10^{-2} to 10^{-1} and different combinations of reduced (n) and unreduced ($2n$) gametes are involved in the formation of progeny (Krahulcová & al., 2004, 2009, 2014; Rosenbaumová & Krahulec, 2015).

(3) Schuhwerk (2002) reported that both recent hybrids and hybrid species can be found in the field. They may have the same origin and same morphology but often differ in reproduction mode. Long-standing hybrid species are mostly apomictic, but recent hybrids can be sterile or semisterile or can have variable reproduction modes that combine apomixis, sexuality, semisterility, and haploid parthenogenesis in different proportions (e.g., Krahulcová & al., 2012).

(4) Almost every species, both basic and hybrid, is represented by several cytotypes, and often with apomictic and sexual reproduction on the same ploidy level. Exceptions are rare and mostly diploid sexual species such as *P. lactucella* (Wallr.) P.D.Sell & C.West.

(5) In spite of more than a century of extensive research, there seems to exist unknown mechanisms of reproduction that generate variation. Krahulec & al. (2011) described an autonomous "polyploid–polyhaploid–new polyploid" cycle that was discovered under experimental conditions. In this fashion, entirely new morphotypes and genotypes might be produced, especially polyploids of hybrid origin.

In general, apomicts mostly behave similar to sexual plants due to their residual sexuality. For that reason their variation cannot be evaluated in the same way as in genera without residual sexuality; they are more similar to other sexual plants, otherwise a vast number of taxa would have to be accepted.

***Taraxacum* Wigg. (dandelion). —** *Taraxacum* is a cosmopolitan genus that colonizes a wide range of ecological niches ranging from ruderal places to mineral-rich fens to xerothermic or steppe to alpine and arctic habitats. The success of the genus stems from the peculiar system in which dandelions combine different life strategies for their survival. Dandelions combine three different systems of reproduction, including two sexual (outcrossing, selfing) and one asexual system (autonomous diplospory) (Kirschner & Štěpánek, 1994). The mode of reproduction is ploidy-specific. Diploids and very rarely tetraploids (Kirschner & Štěpánek, 1998) are sexual, while all polyploids are apomictic (Kirschner & Štěpánek, 1994). In Europe, apomictic taxa prevail, whereas sexual species are restricted to much smaller areas. However, a few widely distributed sexual species are known, for example, *Taraxacum bessarabicum* (Hornem.) Hand.-Mazz., *T. erythrospermum* Besser, and *T. linearisquameum* Soest (Den Nijs & al., 1990; Kirschner & al., 1994; Vašut, 2003).

The evolutionary history of the genus is hazy because of strong reticulate evolution, a low level of morphological differentiation, and common polyploidy. Phylogenetic analyses did not resolve the phylogeny of the genus, but confirmed some links between evolutionarily ancestral and divergent taxa (e.g., Wittzell, 1999; Záveská-Drábková & al., 2009; Kirschner & al., 2015). In contrast to facultative apomicts in other genera, dandelions are considered to be (nearly) obligate apomicts (Richards, 1973). However, there is no doubt that apomictic dandelions participate in gene flow among ploidy levels in regions of sympatry with sexuals. This gene flow is most likely bidirectional, specifically sex♀ × apo♂ or apo♀ × sex♂ (Richards, 1970; Shibaike & al., 2002; Verduijn & al., 2004; Mártonfiová, 2006; Mitsuyuki & al., 2014; Majeský & al., 2015), although there is little evidence for the second possibility (e.g., Van Baarlen & al., 2000).

The present taxonomic treatment of the genus is based on groups of ecologically, morphologically, karyologically, and evolutionarily similar taxa that are grouped under sections. The section is the key infrageneric category for sorting the large diversity of *Taraxacum* species (Kirschner & Štěpánek, 1994). The concept of sections was established by the Swedish botanist Gustav H. Dahlstedt (1921) and the Austrian botanist Heinrich von Handel-Mazzetti (1907), and was followed by other taraxacologists (e.g., Kirschner, Marciniuk, Marklund, Railonsala, Richards, Štěpánek, Trávniček, Van Soest, and many others), although their species concepts differ. Dahlstedt and Handel-Mazzetti used different approaches how to treat the high number of apomictic taxa. While Handel-Mazzetti developed a concept with broadly defined species which include many different and unrelated taxa, Dahlstedt favoured a rather narrow species definition. It is interesting to note that Dahlstedt (1893, 1894) developed a similar concept also for *Hieracium* s.str. (see above), which is, however, not widely accepted among hieraciologists. Differences in the opinions of Handel-Mazzetti and Dahlstedt on the taxonomy of dandelions could originate from their different observations. While in northern Europe only apomictic (and well-distinguishable) taxa occur, in southern and Central Europe both mating systems coexist sympatrically (e.g., Kirschner & Štěpánek, 1994; Den Nijs & Menken, 1994; Uhlemann, 2001), which results in the presence of a large number of unique (often undeterminable) morphotypes. The genus consists of more than 60 sections worldwide (Kirschner & Štěpánek, 1996; Uhlemann & al., 2004). A section contains one or a few diploid sexual taxa and a number of morphologically distinct apomictic polyploids (for which more than 3000 names have been published). However, there are several sections which contain only sexual or only asexual taxa (Kirschner & Štěpánek, 1996). Sexual taxa are described as species with a wide distribution (but restricted in comparison to apomicts) and with large phenotypic and genotypic variation (Kirschner & Štěpánek, 1998; Uhlemann & al., 2004). Polyploid apomictic taxa are recognized based on their distinctive morphology and are traditionally classified as *microspecies*. In Euro+Med PlantBase genus treatment follows the approach described above, i.e., division on sections containing sexual and apomictic taxa into separate species (Kirschner & al., 2007–). Some botanists, however, prefer to refer to *broad species*/*species aggregates* (e.g., *T. laevigatum* agg., *T. officinale* agg., *T. palustre* agg.) as the equivalent of sections, e.g., *T. officinale* agg. = *T.* sect. *Taraxacum* F.H.Wigg. (former sect. *Ruderalia* Kirschner & al.); *T. laevigatum* agg. = *T.* sect. *Erythrosperma* (H.Lindb.) Dahlst.; *T. palustre* agg. = *T.* sect. *Palustria* (H.Lindb.) Dahlst.). This practice, however, is not correct, as used taxon names do not always represent the types, based on which sections were described and defined, and thus should not be used instead of a sectional name (e.g., Richards, 1985; Kirschner & Štěpánek, 1987, 2011).

Microspecies refers to morphologically homogenous narrow units with (to some extant) a defined distribution and clonal reproduction. Morphometric (Šuvada & al., 2012; Dudáš & al., 2013) and molecular studies (Mes & al., 2002; Reisch, 2004; Majeský & al., 2012, 2015; Kirschner & al., 2016) showed that it is possible to define apomictic dandelions based on morphology, which agrees with the genetic delimitation of apomictic microspecies. Clonal reproduction provides enough isolation from hybridization "trips" in fully apomictic populations, although accidental sexuality cannot be excluded (e.g., the loss of one or more chromosomes or the occasional production of reduced ovules). The recognition of apomictic *Taraxacum* microspecies as distinct taxa can be a proper way to describe the phenotypic and ecological unit of the microevolutionary processes in the genus. This practice can be supported by the fact that trained taxonomists involved in *Taraxacum* research are able to recognize and name distinct microspecies consistently (see Kirschner & al., 2016). In regions where sexuals occur, microspecies consist of a few genetically similar apomictic lineages and thus can show greater morphological variation than in regions without occurence of sexuals (Kirschner & Štěpánek, 1994; Majeský & al., 2015). However, it is necessary to take into consideration the real value of the apomictic morphotypes. Indefinite description of new microspecies that are based on limited knowledge of reproduction behaviour, morphological and genetic homogeneity, or relationships to sexual species have to be strictly avoided. If the taxonomy of apomictic dandelions has to be considered a serious science, then species described from insufficiently characterized plants should be excluded from Floras, especially in regions where sexual species co-occur and the probability of the formation of new apomictic lineages is high.

■ CONCLUSIONS

Taxonomy is a way to group taxa according to explicitly stated criteria and principles (e.g., species concepts). From the time of Linné and Darwin the key category in the description of biodiversity became the species. *Species* as a term is frequently used in science, nature conservation, and legislation, though interpretation of the term may strongly differ depending on where it is used, who uses it, and for which purpose (e.g., Dickinson, 1999; Mayden, 1997, 1999, 2002). Uncertainty exists also in the interpretation of the term species: evolutionary entity versus taxonomic category. However, the term *species* should refer to a biological entity objectively present in nature, objectively discernible based on the presence of objectively observable features (Mayden, 1999, 2002). The question of finding an appropriate way to recognize individual entities as distinct species, and thus finding a universal species concept equally applicable to all of the diverse cases discussed above, is a big challenge (see, e.g., Dickinson, 1998, 1999; Hörandl, 1998; Stace, 1998; Weber, 1996; Mayden, 1997, 1999, 2002). This is especially true if we expect such a concept to reflect the basic evolutionary unit within diverse plant groups. The diversity of apomictic plant groups is enormous, and particular cases of speciation processes are equally diverse. Today, concepts used for the delimitation of apomictic taxa are based on morphological, distributional, and evolutionary characteristics, and try to define taxa with respect to specific processes that play important roles in the diversification of particular genera (e.g., hybridization and subsequent isolation, hybridization followed by backcrossing, repeated hybridization) (Table 1). Taking into consideration different evolutionary histories, different backgrounds, and the different mechanisms that accompany the existence and diversification of apomictic genera, which are often not known, it is hardly possible to encompass all these situations with one approach.

The biosystematics of apomicts (especially with respect to the genera discussed in this review) in past decades has emphasized the correlation between morphology and other important characteristics. We consider the following criteria to be very important in the systematics of apomictic taxa.

(1) Origin of the taxon: Hybridization and polyploidization is a common phenomenon in the evolution of plants and also in apomictic taxa. Regarding the evolutionary origin of apomictic taxa it is important to know if they arose from interspecific crosses (through allopolyploidization) and thus combine the genomes of two or more species, or if they originated via autopolyploidization. However, this can be a particularly difficult task in some genera, especially when the parental taxa are not known, inhabit only remote areas, or are extinct. Distinguishing allopolyploid taxa as separate species, although apomictic, is more appropriate than distinguishing autopolyploids that rather should be treated as conspecific taxa (as done, e.g., in *Antennaria* – Bayer & Stebbins, 1982; *Boechera* – Windham & Al-Shehbaz, 2006, 2007a, b; *Crepis* – Babcock & Stebbins, 1938).

(2) Single origin: If several similar morphotypes show high genotypic variation and in fact are of multiple (polyphyletic) origin, then it is better to consider them as independently evolved types and not one highly polymorphic taxon.

(3) Stability of apomixis: The apomictic mode should be confirmed (e.g., by flow cytometric seed screen, castration or cytoembryological methods), and the proportion of apomictically vs. sexually formed seeds has to be well documented, especially in facultative apomicts (e.g., Dobeš & al., 2013b; Krahulcová & al., 2014; Schinkel & al., 2016). The degree of residual sexuality remains questionable with regard to the stability of facultative apomictic taxa. A high level of sexuality causes morphological instability of the taxon across generations and in large distribution ranges and can hamper unambiguous taxon recognition.

(4) Distribution range: Genera greatly vary in the dispersability of seeds, and different chorological criteria should be applied to different cases. However, distinction of so-called unique types (recently established hybrids) from single localities should be strictly avoided in any genus. Some might argue that such hybrids are part of the local flora and are young species, but this approach is especially problematic in regions where apomicts and sexual plants occur sympatrically, and might lead to tens or hundreds of new unilocal "species".

(5) Correlation of the above-discussed criteria with the observed stability of morphological traits of particular taxa is particularly important.

In the taxonomy of apomicts, there should be a unifying rule that strongly stresses the importance of understanding the biosystematic background of the apomictic groups that are studied. Maybe the most appropriate approach would be the recognition of primary and secondary species concepts (in the sense of Mayden, 1997), which in turn would allow the usage of more approaches with differing notions of what represents the basic species entity within a particular plant genus. We believe a clear interpretation of an evolutionary unit, which is objectively present in apomictic complexes and recognizable in nature, is important. A standard unit facilitates orientation within a particular genus and also better communication among specialists. On the other hand, for practical purposes it is essential to develop the systematics of apomicts so that it is easy to understand by non-specialists. Therefore, maintaining infrageneric groups (e.g., collective groups, aggregates, species complexes, sections, and nothotaxa) might be crucial for communication among non-specialists, especially in species-rich genera such as, *Pilosella*, *Ranuculus*, *Rubus*, *Sorbus*, or *Taraxacum*.

■ ACKNOWLEDGEMENTS

We thank to J. Paule and T. Gregor (Senckenberg Research Institute and Natural History Museum, Frankfurt) for reading the manuscript and providing suggestive comments. We also thank two anonymous referees for their constructive comments on earlier versions of this manuscript. This work was supported by the European Social Fund, The Education for Competitiveness Operational Programme [CZ.1.07/2.3.00/30.0004 to LM].

■ LITERATURE CITED

Akiyama, Y., Goel, S., Conner, J.A., Hanna, W.W., Yamada-Akiyama, H. & Ozias-Akins, P. 2011. Evolution of the apomixis transmitting chromosome in *Pennisetum*. *B. M. C. Evol. Biol.* 11: 289. https://doi.org/10.1186/1471-2148-11-289

Alexander, P.J., Windham, M.D., Beck, J.B., Al-Shehbaz, I.A., Allphin, L. & Bailey, C.D. 2013. Molecular phylogenetics and taxonomy of the genus *Boechera* and related genera (Brassicaceae: Boechereae). *Syst. Bot.* 38: 192–209. https://doi.org/10.1600/036364413X661917

Alice, A.L. & Campbell, C.S. 1999. Phylogeny of *Rubus* (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. *Amer. J. Bot.* 86: 81–97. https://doi.org/10.2307/2656957

Al-Shehbaz, I.A. & Windham, M.D. 2010. *Boechera*. Pp. 348–412 in: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 7. New York, Oxford: Oxford University Press

Asker, S. 1977. Pseudogamy, hybridization and evolution in *Potentilla*. *Hereditas* 87: 179–184. https://doi.org/10.1111/j.1601-5223.1978.tb01260.x

Asker, S. 1985a. Chromosome studies in *Potentilla*. *Hereditas* 102: 289–292. https://doi.org/10.1111/j.1601-5223.1985.tb00628.x

Asker, S. 1985b. Polymorphism of *Potentilla tabernaemontani* and related taxa on Gotland. *Hereditas* 102: 39–45. https://doi.org/10.1111/j.1601-5223.1985.tb00463.x

Asker, S.E. & Jerling, L. 1992. *Apomixis in plants*. Boca Raton: CRC Press.

Babcock, E.B. 1947. *The genus Crepis*, part 1, *The taxonomy, phylogeny, distribution and evolution of Crepis.* Berkeley: University of California Press.

Babcock, E.B. & Stebbins, G.L. 1938. *The American species of Crepis: Their interrelationships and distribution as affected by polyploidy and apomixis.* Washington: Carnegie Institution of Washington.

Battjes, J., Menken, S.B.J. & Den Nijs, J.C.M. 1992. Clonal diversity in some microspecies of *Taraxacum* sect. *Palustria* (Lindb. fil.) Dahlst. from Czechoslovakia. *Bot. Jahrb. Syst.* 114: 315–328.

Bayer, R.J. 1990. A phylogenetic reconstruction of *Antennaria* (Asteraceae: Inuleae). *Canad. J. Bot.* 68: 1389–1397. https://doi.org/10.1139/b90-177

Bayer, R.J. 2006. *Antennaria*. Pp. 388–415 in: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 19. New York, Oxford: Oxford University Press.

Bayer, R.J. & Stebbins, L.G. 1982. A revised classification of *Antennaria* (Asteraceae: Inuleae) of the eastern United States. *Syst. Bot.* 7: 300–313. https://doi.org/10.2307/2418391

Bayer, R.J. & Stebbins, L.G. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). *Syst. Bot.* 12: 305–319. https://doi.org/10.2307/2419326

Bayer, R.J. & Stebbins, L.G. 1993. A synopsis with keys for the genus *Antennaria* (Asteraceae: Inuleae: Gnaphalieae) of North America. *Canad. J. Bot.* 71: 1589–1604. https://doi.org/10.1139/b93-194

Bayer, R.J., Soltis, D.E. & Soltis, P.S. 1996. Phylogenetic inferences in *Antennaria* (Asteraceae: Gnaphalieae: Cassiniinae) based on sequences from nuclear ribosomal DNA internal transcribed spacers (ITS). *Amer. J. Bot.* 83: 516–527. https://doi.org/10.2307/2446220

Beck, J.B., Alexander, P.J., Allphin, L., Al-Shehbaz, I.A., Rushworth, C., Balley, D.S. & Windham, M.D. 2012. Does hybridization drive the transition to asexuality in diploid *Boechera*? *Evolution* 66: 985–995. https://doi.org/10.1111/j.1558-5646.2011.01507.x

Bergman, B. 1941. Studies on the embryo sac mother cell and its development in *Hieracium* subg. *Archieracium*. *Svensk Bot. Tidskr.* 35: 1–42.

Bernátová, D. & Májovský, J. 1997. The *Poa glauca* group in Western Carpathians I: *Poa margilicola* sp. nova. *Biológia (Bratislava)* 52: 27–31.

Bernátová, D. & Májovský, J. 2003. New endemic hybridogenous species of the genus *Sorbus* in the Western Carpathians. *Biológia (Bratislava)* 58: 781–790.

Bernátová, D., Májovský, J. & Obuch, J. 1999. The *Poa glauca* group in the Western Carpathians II: *Poa sejuncta* sp. nova and *P. babiogorensis* sp. nova. *Biológia (Bratislava)* 54: 37–41.

Bílá, J. 2015. *Sources of Sorbus aria agg. variation.* Dissertation, Charles University, Prague, Czech Republic.

Bogler, D.J. 2007. *Crepis*. Pp. 222–239 in: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 19. New York, Oxford: Oxford University Press.

Bräutigam, S. 2011. *Pilosella* Vaill. [*Hieracium* L. subgen. *Pilosella* (Vaill.) Gray] – Mausohrhabichtskraut, Habichtskraut. Pp. 817–829 in: Jäger, E. (ed.), *Exkursionsflora von Deutschland: Gefässpflanzen; Grundband*, ed. 20. Heidelberg: Spektrum Akademischer Verlag.

Bräutigam, S. & Greuter, W. 2007. A new treatment of *Pilosella* for the Euro-Mediterranean flora (Notulae ad floram euro-mediterraneam pertinentes No. 24). *Willdenowia* 37: 123–137. https://doi.org/10.3372/wi.37.37106

Bräutigam, S. & Schuhwerk, F. 2005. *Hieracium* L. Habichtskraut. Pp. 709–734 in: Jäger, E.J. & Werner, K. (eds.), *Exkursionsflora von Deutschland: Gefässpflanzen; Kritischer Band*, ed. 10. Heidelberg: Spektrum Akademischer Verlag.

Burgess, M.B., Cushman, K.R., Doucette, E.T., Talent, N., Frye, C.T. & Campbell, C.S. 2014. Effects of apomixis and polyploidy on diversification and geographic distribution in *Amelanchier* (Rosaceae). *Amer. J. Bot.* 101: 1375–1387. https://doi.org/10.3732/ajb.1400113

Burgess, M.B., Cushman, K.R., Doucette, E.T., Frye, C.T. & Campbell, C.S. 2015. Understanding diploid diversity: A first step in unraveling polyploid, apomictic complexity in *Amelanchier*. *Amer. J. Bot.* 102: 1–17. https://doi.org/10.3732/ajb.1500330

Burnier, J., Buerki, S., Arrigo, N., Küpfer, P. & Alvarez, N. 2009. Genetic structure and evolution of Alpine polyploid complexes: *Ranunculus kuepferi* (Ranunculaceae) as a case study. *Molec. Ecol.* 18: 3730–3744. https://doi.org/10.1111/j.1365-294X.2009.04281.x

Campbell, C.S. & Wright, W.A. 1996. Apomixis, hybridization and taxonomic complexity in Eastern North American *Amelanchier* (Rosaceae). *Folia Geobot. Phytotax.* 31: 345–354. https://doi.org/10.1007/BF02815379

Campbell, C.S., Green, C.W. & Dickinson, T.A. 1991. Reproductive biology in subfam. Maloideae (Rosaceae). *Syst. Bot.* 16: 333–349. https://doi.org/10.2307/2419284

Campbell, C.S., Wojcichowski, M.F., Baldwin, B.G., Alice, L.A. & Donoghue, M.J. 1997. Persistent nuclear ribosomal DNA sequence polymorphism in the *Amelanchier* agamic complex (Rosaceae). *Molec. Biol. Evol.* 14: 81–90. https://doi.org/10.1093/oxfordjournals.molbev.a025705

Campbell, C.S., Evans, R.C., Morgan, D.R., Dickinson, T.A. & Arsenault, M.P. 2007. Phylogeny of subtribe Pyrinae (formely the Maloideae, Rosaceae): Limited resolution of complex evolutionary history. *Pl. Syst. Evol.* 266: 119–145. https://doi.org/10.1007/s00606-007-0545-y

Campbell, C.S., Burgess, M.B., Cushman, K.R., Doucette, E.T., Dibble, A.C. & Frye, C.T. 2014. *Amelanchier*. Pp. 646–661 in: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 9. New York: Oxford University Press.

Campbell, C.S. & Doucette, E. 2015. *Amelanchier*: Systematics and evolution. http://amelanchier.umaine-biology.net/ (accessed 20 Sep 2015).

Carman, J.G. 1997. Asynchronous expression of duplicate genes in angiosperms may cause apomixis, bispory, tetraspory, and polyembryony. *Bot. J. Linn. Soc.* 61: 51–94. https://doi.org/10.1111/j.1095-8312.1997.tb01778.x

Chapman, H.M., Parh, D. & Oraguzie, N. 2000. Genetic structure and colonizing success of a clonal, weedy species, *Pilosella officinarum* (Asteraceae). *Heredity* 84: 401–409. https://doi.org/10.1046/j.1365-2540.2000.00657.x

Christensen, K. 1992. Revision of *Crataegus* sect. *Crataegus* and nothosect. *Crataeguineae* (Rosaceae-Maloideae) in the Old World. *Syst. Bot. Monogr.* 35: 1–199. https://doi.org/10.2307/25027810

Chrtek, J. 2004. *Hieracium* L. – jestřábník. Pp. 540–701 in: Slavík, B. & Štěpánková, J. (eds.), *Květena České republiky* [Flora of the Czech Republic], vol. 7. Prague: Academia.

Chrtek, J., Mráz, P. & Severa, M. 2004. Chromosome numbers in selected species of *Hieracium* s.str. (*Hieracium* subgen. *Hieracium*) in the Western Carpathians. *Preslia* 76: 119–139.

Chrtek, J., Tonková, M., Mráz, P., Marhold, K., Plačková, I., Krahulcová, A. & Kirschner, J. 2007. Morphological and allozyme diversity in the *Hieracium nigrescens* group (Compositae) in the Sudety Mountains and the western Carpathians. *Bot. J. Linn. Soc.* 153: 287–300. https://doi.org/10.1111/j.1095-8339.2007.00606.x

Cires, E., Cuesta, C., Vargas, P. & Fernández Prieto, J.A. 2012. Unravelling the evolutionary history of the polyploid complex *Ranunculus parnassiifolius* (Ranunculaceae). *Biol. J. Linn. Soc.* 107: 477–493. https://doi.org/10.1111/j.1095-8312.2012.01968.x

Clausen, J. 1961. Introgression facilitated by apomixis in polyploid Poas. *Euphytica* 10: 87–94. https://doi.org/10.1007/BF00037208

Cosendai, A.-C., Rodewald, J. & Hörandl, E. 2011. Origin and distribution of autopolyploids via apomixis in the alpine species *Ranunculus kuepferi* (Ranunculaceae): *Taxon* 60: 355–364.

Cosendai, A.-C., Wagner, J., Ladinig, U., Rosche, C. & Hörandl, E. 2013. Geographical parthenogenesis and population genetic structure in the alpine species *Ranunculus kuepferi* (Ranunculaceae). *Heredity* 110: 560–569. https://doi.org/10.1038/hdy.2013.1

Coughlan, J.M., Stefanović, S. & Dickinson, T.A. 2014. Relative resource allocation to dispersal and competition demonstrates the putative role of hybridity in geographical parthenogenesis. *J. Biogeogr.* 41: 1603–1613. https://doi.org/10.1111/jbi.12316

Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187 in: Johnson, R.F. (ed.), *Current ornithology*, vol. 1. New York: Plenum. https://doi.org/10.1007/978-1-4615-6781-3_6

Dahlstedt, H. 1893. Bidrag till sydöstra Sveriges (Smålands, Östergötlands och Gotlands) Hieraciumflora II. *Kongl. Svenska Vetensk. Acad. Handl.*, N.F., 25(3): 1–201.

Dahlstedt, H. 1894. Bidrag till sydöstra Sveriges (Smålands, Östergötlands och Gotlands) Hieraciumflora III. *Kongl. Svenska Vetensk. Acad. Handl.*, N.F., 26(3): 1–266.

Dahlstedt, H. 1921. De svenska arterna av släktet *Taraxacum*. I. *Erythrosperma*. II. *Obliqua*. *Acta Fl. Sueciae* 1: 1–160.

Davis, W.H. 1958. Apomixis, hybridization and speciation in *Rubus*. *Castanea* 23: 52–55.

De Wet, J.M.J. & Harlan, J.R. 1970. Apomixis, polyploidy and speciation in Dichanthium. *Evolution* 24: 270–277. https://doi.org/10.1111/j.1558-5646.1970.tb01760.x

Delgado, L., Galdeano, F., Sartor, M.E., Quarin, C.L., Espinoza, F. & Ortiz, J.P.A. 2014. Analysis of variation for apomictic reproduction in diploid *Paspalum rufum*. *Ann. Bot. (Oxford)* 113: 1211–1218. https://doi.org/10.1093/aob/mcu056

Den Nijs, J.C.M. & Menken, S.B.J. 1994. Breeding systems and evolution in *Taraxacum*. *Evol. Trend Pl.* 8: 11–20.

Den Nijs, H.C.M., Kirschner, J., Štěpánek, J. & Van der Hulst, A. 1990. Distribution of diploid plants of *Taraxacum* sect. *Ruderalia* in east-Central Europe, with special reference to Czechoslovakia. *Pl. Syst. Evol.* 170: 71–84.

Dickinson, T.A. 1998. Taxonomy of agamic complexes in plants: A role for metapopulation thinking. *Folia Geobot.* 33: 327–332. https://doi.org/10.1007/BF03216208

Dickinson, T.A. 1999. Species concepts in agamic complexes. Pp. 319–339 in: Van Raamsdonk, L.W.D. & Den Nijs J.C.M. (eds.), *Evolution in man-made habitats: Proceedings of the VIIth International Symposium of the International Organization of Plant Biosystematists*, 10–15 August 1998, Amsterdam, The Netherlands. Amsterdam: Hugo de Vries Laboratory.

Dickinson, T.A., Lo, E.Y.Y. & Talent, N. 2007. Polyploidy, reproductive biology and Rosaceae: Understanding evolution and making classification. *Pl. Syst. Evol.* 266: 59–78. https://doi.org/10.1007/s00606-007-0541-2

Dickinson, T.A., Lo, E.Y.Y., Talent, N. & Love, R.M. 2008. Black-fruited hawthorns of western North America – one or more agamic complexes? *Botany* 86: 846–865. https://doi.org/10.1139/B08-072

Dobeš, C. & Paule, J. 2010. A comprehensive chloroplast DNA-based phylogeny of the genus *Potentilla* (Rosaceae): Implication for its geographic origin, phylogeography and generic circumscription. *Molec. Phylogen. Evol.* 56: 156–175. https://doi.org/10.1016/j.ympev.2010.03.005

Dobeš, C., Mitchell-Olds, T. & Koch, M. 2004. Intraspecific diversification in North American *Boechera stricta* (= *Arabis drummondii*), *Boechera ×divaricarpa*, and *Boechera holboellii* (Brassicaceae) inferred from nuclear and chloroplast molecular markers — An integrative approach. *Amer. J. Bot.* 91: 2007–2101. https://doi.org/10.3732/ajb.91.12.2087

Dobeš, C., Sharbel, T.F. & Koch, M. 2007. Towards understanding the dynamics of hybridization and apomixis in the evolution of the genus *Boechera* (Brassicaceae). *Syst. Biodivers.* 5: 321–331. https://doi.org/10.1017/S1477200007002423

Dobeš, C., Milosevic, A., Prohaska, D., Schneffknecht, S., Sharbel, T.F. & Hülber, K. 2013a. Reproductive differentiation into sexual and apomictic polyploid cytotypes in *Potentilla puberula* (Potentilleae, Rosaceae). *Ann. Bot. (Oxford)* 112: 1159–1168. https://doi.org/10.1093/aob/mct167

Dobeš, C., Lückl, A., Hülber, K. & Paule, J. 2013b. Prospects and limits of the flow cytometric seed screen – insights from *Potentilla* sensu lato (Potentilleae, Rosaceae). *New Phytol.* 198: 605–616. https://doi.org/10.1111/nph.12149

Dobeš, C., Lückl, A., Kausche, L., Scheffknecht, S., Prohaska, D., Sykora, C. & Paule, J. 2015. Parallel origins of apomixis in two diverged evolutionary lineages in tribe Potentilleae (Rosaceae). *Bot. J. Linn. Soc.* 177: 214–229. https://doi.org/10.1111/boj.12239

Dudáš, M., Šuvada, R., Mártonfiová, L. & Mártonfi, P. 2013. Differentiation of the taxa of the genus *Taraxacum* sect. *Erythrosperma* on the basis of morphological characters on achenes and outer bracts. *Thaiszia* 23: 147–162.

Durand, J., Garnier, L., Dajoz, I., Mousset, S. & Veuille, M. 2000. Gene flow in a facultative apomictic Poaceae, the Savanna grass *Hyparrhenia diplandra*. *Genetics* 156: 823–831.

Eldredge, N. & Cracraft, J. 1980. *Phylogenetic patterns and the evolutionary process: Method and theory in comparative biology.* New York: Columbia University Press.

Emadzade, K., Gehrke, B., Linder, H.P. & Hörandl, E. 2011. The biogeographical history of the cosmopolitan genus *Ranunculus* L. (Ranunculaceae) in the temperate to meridional zones. *Molec. Phylogen. Evol.* 58: 4–21. https://doi.org/10.1016/j.ympev.2010.11.002

Enke, N. 2008. *Phylogeny and character evolution in the genus Crepis L. (Cichorieae, Compositae).* Dissertation, Freie Universität Berlin, Berlin, Germany.

Enke, N. & Gemeinholzer, B. 2008. Babcock revisited: New insights into generic delimitation and character evolution in *Crepis* L. (Compositae: Cichorieae) from ITS and *matK* sequence data. *Taxon* 57: 756–768.

Ericsson, S. 1992. The microspecies of the *Ranunculus auricomus* complex treated at the species level. *Ann. Bot. Fenn.* 29: 123–158.

Fehrer, J., Šimek, R., Krahulcová, A., Krahulec, F., Chrtek, J., Bräutigam, E. & Bräutigam, S. 2005. Evolution, hybridization, and clonal distribution of apo- and amphimictic species of *Hieracium* subgen. *Pilosella* (Asteraceae, Lactucaceae) in a central European mountain range. Pp. 175–201 in: Bakker, F., Chatrou, L., Gravendeel, B. & Pelser, P.B. (eds.), *Plant species-level systematics: New perspectives on pattern and process*. Regnum Vegetabile 143. Ruggell, Liechtenstein: Gantner.

Fehrer, J., Krahulcová, A., Krahulec, F., Chrtek, J., Jr., Rosenbaumová, R. & Bräutigam, S. 2007. Evolutionary aspects in *Hieracium* subgenus *Pilosella*. Pp. 359–390 in: Hörandl, E., Grossniklaus, U., Van Dijk, P. & Sharbel, T. (eds.), *Apomixis: Evolution, mechanisms and perspectives*. Regnum Vegetabile 147. Rugell, Liechtenstein: Gantner.

Fehrer, J., Krak, K. & Chrtek, J., Jr. 2009. Intra-individual polymorphism in diploid and apomictic polyploid hawkweeds (*Hieracium*, Lactuceae, Asteraceae): Disentangling phylogenetic signal, reticulation, and noise. *B. M. C. Evol. Biol.* 9: 239. https://doi.org/10.1186/1471-2148-9-239

Ferreira de Carvalho, J., Oplaat, C., Pappas, N., Derks, M., Ridder, D. de & Verhoeven, J.F. 2016. Heritable gene expression differences between apomictic clone members in *Taraxacum officinale*: Insight into early stages of evolutionary divergence in asexual plants. *B. M. C. Genomics* 17: 203. https://doi.org/10.1186/s12864-016-2524-6

Fröhner, S.E. 1995. *Alchemilla*. Pp. 13–242 in: Hegi, G. (ed.), *Illustrierte Flora von Mitteleuropa*, ed. 2, vol. 4(2B). Edited by Scholz, H., Conert, H.J., Jäger, E.J., Kadereit, J.W., Schultze-Motel, W., Wagenitz, G. & Weber, H.E. Berlin: Parey.

Galdeano, F., Urbani, M.H., Sartor, M.E., Honfi, A.I., Espinoza, F. & Quarin, C.L. 2016. Relative DNA content in diploid, polyploid, and multiploid species of *Paspalum* (Poaceae) with relation to reproductive mode and taxonomy. *J. Pl. Res.* 129: 697–710. https://doi.org/10.1007/s10265-016-0813-4

Gehrke, B., Bräuchler, C., Romoleroux, K., Lundberg, M., Heubl, G. & Eriksson, T. 2008. Molecular phylogenetics of *Alchemilla*, *Aphanes* and *Lachemilla* (Rosaceae) inferred from plastid and nuclear intron and spacer DNA sequences, with comments on generic classification. *Molec. Phylogen. Evol.* 47: 1030–1044. https://doi.org/10.1016/j.ympev.2008.03.004

Gottschlich, G. 1998. *Hieracium*. Pp. 245–263 in: Wisskirchen, R. & Haeupler, H. (eds.), *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Stuttgart: Ulmer.

Gottschlich, G. 2009. Die Gattung *Hieracium* (Compositae) in der Region Abruzzen (Italien). *Stapfia* 89: 1–328.

Gregor, T. 2004. *Potentilla alsatica* T. Gregor, ein Fingerkraut der *Potentilla collina*-Gruppe aus der südlichen Oberrheinebene. *Bauhinia* 18: 5–20.

Gregor, T. 2008. Typisierungen in der *Potentilla collina*-Gruppe (*Potentilla* subrex. *Collinae* Th. Wolf). 1. Teil: Sippen ohne Zackenhaare. *Kochia* 3: 61–73.

Gregor, T. 2013. Apomicts in the vegetation of Central Europe. *Tuexenia* 33: 233–257.

Greuter, W. 2006–. Compositae (pro parte majore). In: Greuter, W. & Raab-Straube, E. von (eds.): Compositae. Euro+Med Plantbase – The information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/PTaxonDetail.asp?NameCache=Compositae&PTRefFk=7000000

Gustafsson, A. 1946. Apomixis in higher plants. *Lunds Univ. Arsskr.*, N.F., Avd. 2, 42: 1–66.

Håkansson, A. 1946. Untersuchungen über die Embryologie einiger *Potentilla*-Formen. *Lunds Univ. Arsskr.*, N.F., Avd. 2, 42(5): 1–70.

Handel-Mazzetti, H. 1907. *Monographie der Gattung Taraxacum*. Leipzig, Vienna: Deuticke. http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=849

Harlan, J.R. & De Wet, J.M.J. 1963. The compilospecies concept. *Evolution* 17: 497–501. https://doi.org/10.1111/j.1558-5646.1963.tb03307.x

Haveman, R. 2013. Freakish patterns – Species and species concepts in apomicts. *Nordic J. Bot.* 31: 257–269. https://doi.org/10.1111/j.1756-1051.2013.00158.x

Haveman, R. & De Ronde, I. 2013. The role of the Weberian reform in European *Rubus* research and the taxonomy of locally distributed species – which species should we described? *Nordic J. Bot.* 31: 145–150. https://doi.org/10.1111/j.1756-1051.2012.01558.x

Hodač, L., Scheben, A.P., Hojsgaard, D., Paun, O. & Hörandl, E. 2014. ITS polymorphisms shed light on hybrid evolution in apomictic plants: A case study on the *Ranunculus auricomus* complex. *PLoS ONE* 9(7): e103003. https://doi.org/10.1371/journal.pone.0103003

Hojsgaard, D., Schegg, E., Valls, J.F.M., Martínez, E.J. & Quarin, C.L. 2008. Sexuality, apomixis, ploidy levels, and genomic relationships among four *Paspalum* species of the subgenus *Anachyris* (Poaceae). *Flora* 203: 535–547. https://doi.org/10.1016/j.flora.2007.09.005

Hojsgaard, D., Greilhuber, J., Pellino, M., Paun, O., Sharbel, T.F. & Hörandl, E. 2014a. Emergence of apospory and bypass of meiosis via apomixis after sexual hybridisation and polyploidization. *New Phytol.* 204: 1000–1012. https://doi.org/10.1111/nph.12954

Hojsgaard, D., Klatt, S., Baier, R., Carman, J.G. & Hörandl, E. 2014b. Taxonomy and biogeography of apomixis in angiosperms and associated biodiversity characteristics. *Crit. Rev. Pl. Sci.* 33: 414–427. https://doi.org/10.1080/07352689.2014.898488

Holm, S. & Ghatnekar, L. 1996. Sexuality and no apomixis found in crossing experiments with diploid *Potentilla argentea*. *Hereditas* 125: 77–82. https://doi.org/10.1111/j.1601-5223.1996.00077.x

Holm, S., Ghatnekar, L. & Bengtsson, B.O. 1997. Selfing and outcrossing but no apomixis in two natural populations of diploid *Potentilla argentea*. *J. Evol. Biol.* 10: 343–352. https://doi.org/10.1007/s000360050028

Hörandl, E. 1998. Species concepts in agamic complexes: Applications in the *Ranunculus auricomus* complex and general perspectives. *Folia Geobot.* 33: 335–348. https://doi.org/10.1007/BF03216210

Hörandl, E. & Emadzade, K. 2012. Evolutionary classification: A case study on the diverse plant genus *Ranunculus* L. (Ranunculaceae). *Perspect. Pl. Ecol.* 14: 210–324. https://doi.org/10.1016/j.ppees.2012.04.001

Hörandl, E. & Gutermann, W. 1998. Der *Ranunculus auricomus*-Komplex in Österreich: Die *R. cassubicus*, *R. monophyllus* und *R. fallax* Sammelgruppe. *Bot. Jahrb. Syst.* 120: 545–598.

Hörandl, E. & Paun, O. 2007. Patterns and sources of genetic diversity in apomictic plants: Implications for evolutionary potentials and ecology. Pp. 169–154 in: Hörandl, E., Grossniklaus, U., Van Dijk, P.J. & Sharbel, T. (eds.), *Apomixis: Evolution, mechanisms and perspectives.* Ruggell, Liechtenstein: Gantner.

Hörandl, E. & Raab-Straube, E. von 2015. Ranunculeae. In: Euro+Med Plantbase – The information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/PTaxonDetail.asp?NameCache=Ranunculus&PTRefFk=7500000 (accessed 20 Dec 2016).

Hörandl, E., Greilhuber, J., Klímová, K., Paun, O., Temsch, E., Emadzade, K. & Hodálová, I. 2009. Reticulate evolution and taxonomic concepts in the *Ranunculus auricomus* complex (Ranunculaceae): Insight from analysis of morphological, karyological and molecular data. *Taxon* 58: 1194–1215.

Hoták, Z., Štěpánek, J., Plačková, I. & Jarolímová, V. 2013. *Poa riphaea*, an endangered stenoendemic species in the Hrubý Jeseník Mts (Eastern Sudetes). *Preslia* 85: 81–96.

Huber, W. 1988. Natürliche Bastardierungen zwischen weiss-blühenden *Ranunculus*-Arten in den Alpen. *Veröff. Geobot. Inst. E. T. H. Stiftung Rübel Zürich* 100: 1–160.

Izmailow, R. 1994. Embryo and endosperm relations at early stages of their development in *Alchemilla* subsect. *Heliodrosium* (Rosaceae). *Polish Bot. Stud.* 8: 61–67.

Jankun, A. & Kovanda, M. 1988. Apomixis at diploid level in *Sorbus eximia* (Embryological studies in *Sorbus* 3). *Preslia* 60: 193–213.

Johansson K. 1927. Enumerantur *Hieracia vulgata* Suecicae. *Ark. Bot.* 21(15): 1–98.

Johansson K. 1929. Svenska Hieracia Tridentata Fr. *Ark. Bot.* 22(12): 1–41.

Judson, O.P. & Normark, B.B. 1996. Ancient asexual scandals. *Trends Ecol. Evol.* 11: 41–46. https://doi.org/10.1016/0169-5347(96)81040-8

Kantama, L., Sharbel, T.F., Schranz, M.E., Mitchell-Olds, T., De Vries, S. & De Jong, H. 2007. Diploid apomicts of the *Boechera holboellii* complex display large-scale chromosome substitutions and aberrant chromosomes. *Proc. Natl. Acad. Sci. U.S.A.* 104: 14026–14031. https://doi.org/10.1073/pnas.0706647104

Kaushal, P., Malaviya, D.R., Roy, A.K., Pathak, S., Agrawal, A., Khare, A. & Siddiqui, S.A. 2008. Reproductive pathways of seed development in apomictic guinea grass (*Panicum maximum* Jacq.) reveal uncoupling of apomixis components. *Euphytica* 164: 81–92. https://doi.org/10.1007/s10681-008-9650-4

Kelley, A.M., Johnson, P.G., Waldron, B.L. & Peel, M.D. 2009. A survey of apomixis and ploidy levels among *Poa* L. (Poaceae) using flow cytometry. *Crop Sci.* 49: 1395–1402. https://doi.org/10.2135/cropsci2008.09.0553

Kellogg, E.A. 1987. Apomixis in the *Poa secunda* complex. *Amer. J. Bot.* 74: 1431–1437. https://doi.org/10.2307/2444319

Kellogg, E.A. 1990. Variation and species limits in agamospermous grasses. *Syst. Bot.* 15: 112–123. https://doi.org/10.2307/2419021

Kharrat-Souissi, A., Baumel, A., Torre, F., Juin, M., Siljak-Yakovlev, S., Roig, A. & Chaieb, M. 2011. New insight into the polyploid complex *Cenchrus ciliaris* L. (Poaceae) show its capacity for gene flow and recombination processes despite its apomictic nature. *Austral. J. Bot.* 59: 543–553. https://doi.org/10.1071/BT10312

Kiefer, C. & Koch, M.A. 2012. A continental-wide perspective: The genepool of nuclear encoded ribosomal DNA and single-copy gene sequences in North American *Boechera* (Brassicaceae). *PLoS ONE* 7: e36491. https://doi.org/10.1371/journal.pone.0036491

Király, G., Trávníček, B. & Žíla, V. 2015. *Rubus gayeri* and *Rubus slavonicus*, two new species of *Rubus* ser. *Micantes* (Rosaceae) from Central and South-Eastern Europe. *Phytotaxa* 195: 279–290. https://doi.org/10.11646/phytotaxa.195.4.3

Kirschner, J. & Štěpánek, J. 1987. Again on the sections in *Taraxacum* (Cichoriaceae) (Studies in *Taraxacum* 6). *Taxon* 36: 608–617. https://doi.org/10.2307/1221855

Kirschner, J. & Štěpánek, J. 1994. Clonality as a part of the evolution process in *Taraxacum*. *Folia Geobot. Phytotx.* 29: 265–275. https://doi.org/10.1007/BF02803800

Kirschner, J. & Štěpánek, J. 1996. Modes of speciation and evolution of the sections in *Taraxacum*. *Folia Geobot. Phytotx*. 31: 415–426. https://doi.org/10.1007/BF02815386

Kirschner, J. & Štěpánek, J. 1998. A revision of *Taraxacum* sect. *Piesis* (Compositae). *Folia Geobot*. 33: 391–414. https://doi.org/10.1007/BF02803642

Kirschner, J. & Štěpánek, J. 2011. Typification of *Leontodon taraxacum* L. (≡ *Taraxacum officinale* F.H.Wigg.) and the generic name *Taraxacum*: A review and a new typification proposal. *Taxon* 60: 216–220.

Kirschner, J., Štěpánek, J., Tichý, M., Krahulcová, A., Kirschnerová, L. & Pellar, L. 1994. Variation in *Taraxacum bessarabicum* and allied taxa of the section *Piesis* (Compositae): Allozyme diversity, karyotype and breeding behaviour. *Folia Geobot. Phytotax*. 29: 61–83. https://doi.org/10.1007/BF02807777

Kirschner, J., Štepánek, J. & Greuter, W. 2007–. *Taraxacum*. – In: Greuter, W. & Raab-Straube, E. von (eds.), Compositae. Euro+Med Plantbase – The information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/PTaxonDetail.asp?NameCache=Taraxacum

Kirschner, J., Záveská-Drábková, L., Štěpánek, J. & Uhlemann, I. 2015. Towards a better understanding of the *Taraxacum* evolution (Compositae-Cichorieae) on the basis of nrDNA of sexually reproducing species. *Pl. Syst. Evol.* 301: 1135–1156. https://doi.org/10.1007/s00606-014-1139-0

Kirschner, J., Oplaat, C., Verhoeven, K.J.F., Zeisek, V., Uhlemann, I., Trávníček, B., Räsänen, J., Wilschut, R.A. & Štěpánek, J. 2016. Identification of oligoclonal agamospermous microspecies: Taxonomic specialists versus microsatellites. *Preslia* 88: 1–17.

Koltunow, A.M. 1993. Apomixis: Embryo sacs and embryos formed without meiosis or fertilization in ovules. *Pl. Cell* 5: 1425–1437. https://doi.org/10.1105/tpc.5.10.1425

Krahulcová, A., Krahulec, F. & Chapman, H. 2000. Variation in *Hieracium* subgen. *Pilosella* (Asteraceae): What do we know about its sources? *Folia Geobot*. 35: 319–338. https://doi.org/10.1007/BF02803122

Krahulcová, A., Papoušková, S. & Krahulec, F. 2004. Reproduction mode in the allopolyploid facultatively apomictic hawkweed *Hieracium rubrum* (Asteraceae, *H.* subgen. *Pilosella*). *Hereditas* 141: 19–30. https://doi.org/10.1111/j.1601-5223.2004.01845.x

Krahulcová, A., Rotreklová, O., Krahulec, F., Rosenbaumová, R. & Plačková, I. 2009. Enriching ploidy level diversity: The role of apomictic and sexual biotypes of *Hieracium* subgen. *Pilosella* (Asteraceae) that coexist in polyploid populations. *Folia Geobot*. 44: 281–306. https://doi.org/10.1007/s12224-009-9041-1

Krahulcová, A., Krahulec, F. & Rosenbaumová, R. 2011. Expressivity of apomixis in $2n+n$ hybrids from an apomictic and a sexual parent: Insights into variation detected in *Pilosella* (Asteraceae: Lactuceae). *Sexual Pl. Reprod*. 24: 63–74. https://doi.org/10.1007/s00497-010-0152-x

Krahulcová, A., Raabe, U. & Krahulec, F. 2012. Prozesse innerhalb hybridisierender *Pilosella*-Populationen: *P. aurantiaca* und *P. officinarum* in Hagen (Nordrhein-Westfalen). *Kochia* 6: 123–142.

Krahulcová, A., Rotreklová, O. & Krahulec, F. 2014. The detection, rate and manifestation of residual sexuality in apomictic populations of *Pilosella* (Asteraceae, Lactuceae). *Folia Geobot*. 49: 239–258. https://doi.org/10.1007/s12224-013-9166-0

Krahulcová, A., Vladimirov, V. & Krahulec, F. 2016. The agamic complex of *Pilosella* (Asteraceae) in Bulgaria and SW Romania: variation in ploidy levels and breeding systems. Part 2. *Phytol. Balcan*. 22: 39–62.

Krahulec, F. & Krahulcová, A. 2006. Population based approaches in the study of *Pilosella* Hill (Asteraceae): A new view of its taxonomy? Pp. 15–25 in: Bailey, J. & Ellis, R.G. (eds.), *Current taxonomic research on the British & European flora*. London: BSBI.

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

Krahulec, F., Krahulcová, A., Fehrer, J., Bräutigam, S. & Schuhwerk, F. 2008. The structure of the agamic complex of *Hieracium* subgen. *Pilosella* in the Šumava Mts and its comparison with other regions in Central Europe. *Preslia* 80: 1–26.

Krahulec, F., Krahulcová, A., Rosenbaumová, R. & Plačková, I. 2011. Production of polyhaploids by facultatively apomictic *Pilosella* can result in formation of new genotypes via genome doubling. *Preslia* 83: 471–490.

Kurtto, A., Lampinen, R. & Junikka, L. (eds.) 2004. *Atlas Florae Europaeae: Distribution of vascular plants in Europe*, vol. 13, *Rosaceae (Spiraea to Fragaria, excl. Rubus)*. Helsinki: The Commitee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo.

Kurtto, A., Weber, H.E., Lampinen, R. & Sennikov, A.N. (eds.) 2010. *Atlas Florae Europaeae: Distribution of vascular plants in Europe*, vol. 15, *Rosaceae (Rubus)*. Helsinki: The Commitee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo.

Lepší, M., Vít, P., Lepší, P., Boublík, K. & Suda, J. 2008. *Sorbus milensis*, a new hybridogenous species from nortwestern Bohemia. *Preslia* 80: 229–244.

Lepší, M., Vít, P., Lepší, P., Boublík, K. & Kolář, F. 2009. *Sorbus portae-bohemicae* and *Sorbus albensis*, two new endemic apomictic species recognized based on a revision of *Sorbus bohemica*. *Preslia* 81: 63–89.

Lepší, M., Lepší, P., Koutecký, P., Bílá, J. & Vít, P. 2015. Taxonomic revision of *Sorbus* subgenus *Aria* occurring in the Czech Republic. *Preslia* 87: 109–162.

Liljefors, A. 1953. Studies on propagation, embryology and pollination in *Sorbus*. *Acta Horti. Berg.* 16: 277–329.

Lo, E.Y.Y., Stefanovič, S., Christensen, K.I. & Dickinson, T.A. 2009. Evidence for genetic association between East Asian and western North American *Crataegus* L. (Rosaceae) and rapid divergence of the eastern North American lineages based on multiple DNA sequences. *Molec. Phylogen. Evol.* 51: 157–168. https://doi.org/10.1016/j.ympev.2009.01.018

Lo, E.Y.Y., Stefanović, S. & Dickinson, T.A. 2010. Reconstructing reticulation history in a phylogenetic framework and the potential of allopatric speciation driven by polyploidy in an agamic complex in *Crataegus* (Rosaceae). *Evolution* 64: 3593–3608. https://doi.org/10.1111/j.1558-5646.2010.01063.x

Lovell, J.T., Aliyu, O.M., Mau, M., Schranz, M.E., Koch, M., Kiefer, C., Song, B.-H., Mitchell-Olds, T. & Sharbel, T.F. 2013. On the origin and evolution of apomixis in *Boechera*. *Pl. Reprod.* 26: 309–315. https://doi.org/10.1007/s00497-013-0218-7

Majeský, Ľ., Vašut, R.J., Kitner, M. & Trávníček, B. 2012. The pattern of genetic variability in apomictic clones of *Taraxacum officinale* indicates the alternation of asexual and sexual histories of apomicts. *PLoS ONE* 7(8): e41868. https://doi.org/10.1371/journal.pone.0041868

Majeský, Ľ., Vašut, R.J. & Kitner, M. 2015. Genotypic diversity of apomictic microspecies of the *Taraxacum scanicum* group (*Taraxacum* sect. *Erythrosperma*). *Pl. Syst. Evol.* 301: 2105–2124. https://doi.org/10.1007/s00606-015-1218-x

Mandáková, T. & Lysák, M.A. 2008. Chromosomal phylogeny and karyotype evolution in $x = 7$ Crucifer species (Brassicaceae). *Pl. Cell* 20: 2559–2570. https://doi.org/10.1105/tpc.108.062166

Mandáková, T., Schranz, M.E., Sharbel, T.F., De Jong, H. & Lysák, M.A. 2015. Karyotype evolution in apomictic *Boechera* and the origin of the aberrant chromosomes. *Plant J.* 82: 785–793. https://doi.org/10.1111/tpj.12849

Mártonfiová, L. 2006. Possible pathways of the gene flow in *Taraxacum* sect. *Ruderalia*. *Folia Geobot.* 41: 183–201. https://doi.org/10.1007/BF02806478

Matzk, F., Prodanovic, S., Bäumlein, H. & Schubert, I. 2005. The inheritance of apomixis in *Poa pratensis* confirms a five locus model with differences in gene expressivity and penetrance. *Pl. Cell* 17: 13–24. https://doi.org/10.1105/tpc.104.027359

Mayden, R.L. 1997. A hierarchy of species concepts: The denouement in the saga of the species problem. Pp. 381–424 in: Claridge, M.F., Dawah, H.A. & Wilson, M.R. (eds.) *Species: The units of biodiversity.* London: Chapman and Hall.

Mayden, R.L. 1999. Consilience and hierarchy of species concepts: Advances toward closure on the species puzzle. *J. Nematol.* 31: 95–116.

Mayden, R.L. 2002. On biological species, species concepts and individuation in the natural world. *Fish Fish.* 3: 171–196. https://doi.org/10.1046/j.1467-2979.2002.00086.x

Maynard Smith, J. 1978. *The evolution of sex.* Cambridge: Cambridge University Press.

Mayr, E. 1942. *Systematics and origin of species.* New York: Columbia University Press.

McKitrick, M.C. & Zink, R.M. 1988. Species concepts in ornithology. *The Condor* 90: 1–14. https://doi.org/10.2307/1368426

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud`home van Reine W.F., Smith,G.F., Wiersema, J.H. & Turland, N.J. (eds.) 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011.* Regnum Vegetabile 154. Königstein: Koeltz Scientific Books.

Mes, T.H.M., Kuperus, P., Kirschner, J., Štepánek, J., Štorchová, H., Oosterveld, P. & Den Nijs, C.M. 2002. Detection of genetically divergent clone mates in apomictic dandelions. *Molec. Ecol.* 11: 253–265. https://doi.org/10.1046/j.1365-294X.2002.01427.x

Mirek, Z., Piekoś-Mirkowa, H., Zając, A. & Zając, M. 2002. *Flowering plants and pteridophytes of Poland: A checklist.* Kraków: W. Szafer Institute of Botany, Polish Academy of Sciences.

Mitsuyuki, C., Hoya, A., Shibaike, H., Watanabe, M. & Tetsukazu, Y. 2014. Formation of a hybrid triploid angiosperm on a sexual diploid plant: Evidence from progeny tests in *Taraxacum platycarpum* Dahlst. *Pl. Syst. Evol.* 300: 863–870. https://doi.org/10.1007/s00606-013-0925-4

Morita, T. 1994. Phytogeography and speciation of *Taraxacum* (Asteraceae) in East Asia. *Korean J. Pl. Taxon.* 24: 145–155.

Mráz, P. 2002. Contribution to the knowledge of the *Hieracium rohacsense* group in the Carpathians. *Thaiszia* 12: 109–135.

Mráz, P. 2003a. Mentor effects in the genus *Hieracium* s.str. (Compositae, Lactuceae). *Folia Geobot.* 38: 345–350. https://doi.org/10.1007/BF02803204

Mráz, P. 2003b. *Hieracium piliferum* group (Asteraceae) in the West Carpathians. *Biologia (Bratislava)* 58: 29–36.

Mráz, P. & Paule, J. 2006. Experimental hybridization in the genus *Hieracium* s.str.: crosses between diploid taxa. *Preslia* 78: 1–26.

Mráz, P., Chrtek, J., Fehrer, J. & Plačková, I. 2005. Rare recent natural hybridization in the genus *Hieracium* s.str. – Evidence from morphology, allozymes and chloroplast DNA. *Pl. Syst. Evol.* 255: 177–192. https://doi.org/10.1007/s00606-005-0329-1

Mráz, P., Šingliarová, B., Urfus, T. & Krahulec, F. 2008. Cytogeography of *Pilosella officinarum* (Compositae): Altitudinal and longitudinal differences in ploidy level distribution in the Czech Republic and Slovakia and the general pattern in Europe. *Ann. Bot. (Oxford)* 101: 59–71. https://doi.org/10.1093/aob/mcm282

Mráz, P., Chrtek, J. & Šingliarová, B. 2009. Geographical parthenogenesis, genome size variation and pollen production in the arctic-alpine species *Hieracium alpinum*. *Bot. Helv.* 119: 41–51. https://doi.org/10.1007/s00035-009-0055-3

Mráz, P., Chrtek, J. & Fehrer, J. 2011. Interspecific hybridization in the genus *Hieracium* s.str. – Evidence for bidirectional gene flow and spontaneous allopolyploidization. *Pl. Syst. Evol.* 293: 237–245. https://doi.org/10.1007/s00606-011-0441-3

Mulligan, G.A. 1995. Synopsis of the genus *Arabis* (Brassicaceae) in Canada, Alaska and Greenland. *Rhodora* 97: 109–163.

Muniyamma, M. & Phipps, J.B. 1984. Studies in *Crateagus*. X. A note on the occurrence of diplospory in *Crataegus dissona* Sarg. (Maloideae, Rosaceae). *Canad. J. Genet. Cytol.* 26: 249–252. https://doi.org/10.1139/g84-039

Müntzing, A. 1958. Heteroploidy and polymorphism in some species of *Potentilla*. *Hereditas* 44: 280–329. https://doi.org/10.1111/j.1601-5223.1958.tb03483.x

Müntzing, A. & Müntzing, G. 1971. An apomictic biotype of *Poa alpina* in the Koster islands of Sweden. *Hereditas* 67: 143–144. https://doi.org/10.1111/j.1601-5223.1971.tb02366.x

Nägeli, C. & Peter, A. 1885. *Die Hieracien Mittel-Europas: Monographische Bearbeitung der Piloselloiden mit besonderer Berücksichtigung der mitteleuropäischen Sippen.* München [Munich]: Druck und Verlag von R. Oldenburg. https://archive.org/details/DieHieracienMittelEuropas

Nelson-Jones, E.B., Briggs, D. & Smith, A.G. 2002. The origin of intermediate species of genus *Sorbus*. *Theor. Appl. Genet.* 105: 953–963. https://doi.org/10.1007/s00122-002-0957-6

Nesom, G.L. 1989. Infrageneric taxonomy of New World *Erigeron* (Compositae: Astereae). *Phytologia* 67: 67–93.

Nesom, G.L. 2015 *Erigeron*. In: eFloras: http://www.efloras.org. St. Louis: Missouri Botanical Garden; Cambridge: Harvard University Herbaria. http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=112000 (accessed 10 Aug 2015).

Nogler, G.A. 1984. Genetics of apospory in apomictic *Ranunculus auricomus*: 5. Conclusion. *Bot. Helv.* 94: 411–423.

Notov, A.A. & Kusnetzova, T.V. 2004. Architectural units, axiality and their taxonomic implications in Alchemillinae. *Wulfenia* 11: 85–130. https://doi.org/10.3732/ajb.93.3.470

Noyes, R.D. 2000. Biogeographical and evolutionary insights on *Erigeron* and allies (Asteraceae) from ITS sequence data. *Plant Syst. Evol.* 220: 93–114. https://doi.org/10.1007/BF00985373

Noyes, R.D. 2006. Intraspecific nuclear ribosomal DNA divergence and reticulation in sexual diploid *Erigeron strigosus* (Asteraceae). *Amer. J. Bot.* 93: 470–479.

Noyes, R.D. 2007. Reticulation and the evolution of apomixis in *Erigeron* sect. *Phalacroloma* (Asteraceae). Pp. 337–358 in: Hörandl, E., Grossniklaus, U., Van Dijk, P. & Sharbel, T. (eds.), *Apomixis: Evolution, mechanisms and perspectives.* Regnum Vegetabile 147. Ruggell, Liechtenstein: Gantner.

Nyárády, E.I. 1965. Genul 606. *Hieracium* L. Pp. 214–370 in: Nyárády, E.I. (ed.), *Flora Republicii populare Romîne*, vol. 19. Bucharest: Editura Academiei Republicii Populare Romîne.

Nybom, H. 1995. Evaluation of interspecific crossing experiments in facultatively apomictic blackberries (*Rubus* subgen. *Rubus*) using DNA fingerprinting. *Hereditas* 122: 57–65. https://doi.org/10.1111/j.1601-5223.1995.00057.x

Ortiz, J.P., Quarin, C.L., Pessino, S.C., Acuña, C., Martínez, E.J., Espinoza, F., Hojsgaard, D.H., Sartor, M.E., Cáceres, M.E. & Pupilli, F. 2013. Harnessing apomictic reproduction in grasses: What we have learned from *Paspalum*. *Ann. Bot. (Oxford)* 112: 767–787. https://doi.org/10.1093/aob/mct152

Ozias-Akins, P. & Van Dijk, P.J. 2007. Mendelian genetics of apomixis in plants. *Annual Rev. Pl. Biol.* 41: 509–537. https://doi.org/10.1146/annurev.genet.40.110405.090511

Paule, J., Sharbel, T.F. & Dobeš, C. 2011. Apomictic and sexual lineages of the *Potentilla argentea* L. Group (Rosaceae): Cytotype and molecular genetic differentiation. *Taxon* 60: 721–732.

Paule, J., Scherbantin, A. & Dobeš, C. 2012. Implication of hybridization and cytotypic differentiation in speciation assessed by AFLP and plastid haplotypes – A case study of *Potentilla alpicola* La Soie. *B. M. C. Evol. Biol.* 12: 132. https://doi.org/10.1186/1471-2148-12-132

Paule, J., Kolář, F. & Dobeš, C. 2015. Arctic-alpine and serpentine differentation in polyploid *Potentilla crantzii*. *Preslia* 87: 195–215.

Paun, O., Greilhuber, J., Temsch, E.M. & Hörandl, E. 2006a. Patterns, sources and ecological implications of clonal diversity in apomictic *Ranunculus carpaticola* (*Ranunculus auricomus* complex, Ranunculaceae). *Molec. Ecol.* 15: 897–910. https://doi.org/10.1111/j.1365-294X.2006.02800.x

Paun, O., Stuessy, T.F. & Hörandl, E. 2006b. The role of hybridization, polyploidization and glaciations in the origin of the apomictic *Ranunculus cassubicus* complex. *New Phytol.* 171: 223–236. https://doi.org/10.1111/j.1469-8137.2006.01738.x

Pellino, M., Hojsgaard, D., Schmutzer, T., Scholz, U., Hörandl, E., Vogel, H. & Sharbel, T.F. 2013. Asexual genome evolution in the apomictic *Ranunculus auricomus* complex: Examining the effects of hybridization and mutation accumulation. *Molec. Ecol.* 22: 5908–5921. https://doi.org/10.1111/mec.12533

Phipps, J.B. 2015. *Crataegus* Linnaeus sect. *Sanguineae* (Zabel ex Rehder) C.K. Schneider, Ill. Handb. Laubholzk. 1: 771. 1906). Pp. 514–515 in: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 9. New York, Oxford: Oxford University Press.

Phipps, J.B., Robertson, K.R. & Rohrer, J.R. 1990. A checklist of the subfamily Maloideae (Rosaceae). *Canad. J. Bot.* 68: 2209–2269. https://doi.org/10.1139/b90-288

Phipps, J.B., O'Kennon, R.J. & Lance, R.W. 2003. *Hawthorns and medlars*. Portland: Timber Press.

Pichot, C., Fady, B. & Hochu, I. 2000. Lack of mother tree alleles in zymograms of *Cupressus dupreziana* and calus embryos. *Ann. Forest Sci.* 57: 17–22. https://doi.org/10.1051/forest:2000108

Pihu, S., Hoimra, J., Köster, E. & Pärtel, M. 2009. Environmentally dependent morphological variability in seven apomictic microspecies from *Alchemilla* L. (Rosaceae). *Folia Geobot.* 44: 159–176. https://doi.org/10.1007/s12224-009-9034-0

Plocek, A. 1982. Revised nomenclature of infrageneric groups of *Alchemilla* in Eurasia. *Preslia* 54: 45–53.

Potter, D., Eriksson, T., Evans, R.C., Oh, S., Smedmark, J.E.E., Morgan, D.R., Kerr, M., Robertson, K.R., Arsenault, M., Dickinson, T.A. & Campbell, C.S. 2007. Phylogeny and classification of Rosaceae. *Pl. Syst. Evol.* 266: 5–43. https://doi.org/10.1007/s00606-007-0539-9

Quarin, C.L. 1992. The nature of apomixis and its origin in Panicoid grasses. *Apomixis Newslett.* 5: 8–15.

Reisch, C. 2004. Molecular differentiation between coexisting species of *Taraxacum* sect. *Erythrosperma* (Asteraceae) from populations in south-east and west Germany. *Bot. J. Linn. Soc.* 145: 109–117. https://doi.org/10.1111/j.1095-8339.2004.00283.x

Renno, J.F., Schmelzer, G.H. & De Jong, J.H. 1995. Variation and geographic distribution of ploidy levels in *Pennisetum* section *Brevivalvula* (Poaceae) in Burkina Faso, Benin and southern Niger. *Pl. Syst. Evol.* 198: 89–100. https://doi.org/10.1007/BF00985108

Renno, J.F., Mariac, C., Poteaux, C., Bezançon, G. & Lumaret, R. 2001. Haplotype variation of cpDNA in the agamic grass complex *Pennisetum* section *Brevivalvula* (Poaceae). *Heredity* 86: 537–544. https://doi.org/10.1046/j.1365-2540.2001.00854.x

Rich, T.C.G., McDonnell, E.J. & Lledó, M.G. 2008. Conservation of Britain's biodiversity: The case of *Hieracium cyathis* (Asteraceae) and its relation to other apomictic taxa. *Bot. J. Linn. Soc.* 156: 669–680. https://doi.org/10.1111/j.1095-8339.2007.00747.x

Richards, A.J. 1970. Hybridization in *Taraxacum*. *New Phytol.* 69: 1103–1121. https://doi.org/10.1111/j.1469-8137.1970.tb02492.x

Richards, A.J. 1973. The origin of *Taraxacum* agamospecies. *Bot. J. Linn. Soc.* 66: 189–211. https://doi.org/10.1111/j.1095-8339.1973.tb02169.x

Richards, A.J. 1985. Sectional nomenclature in *Taraxacum* (Asteraceae). *Taxon* 34: 633–644. https://doi.org/10.2307/1222201

Richards, A.J. 1996. Genetic variability in obligate apomicts of the genus *Taraxacum*. *Folia Geobot. Phytotx.* 31: 405–414. https://doi.org/10.1007/BF02815385

Richards, A.J. 1997. *Plant breeding systems*, ed. 2. London: Chapman and Hall.

Richards, A.J. 2003. Apomixis in flowering plants: An overview. *Philos. Trans., Ser B.* 358: 1085–1093

Robertson, A., Newton, A.C. & Ennos, R.A. 2004a. Breeding systems and continuing evolution in the endemic *Sorbus* taxa on Arran. *Heredity.* 93: 487–495. https://doi.org/10.1038/sj.hdy.6800528

Robertson, A., Newton, A.C. & Ennos, R.A. 2004b. Multiple hybrid origins, genetic diversity and population genetic structure of two endemic *Sorbus* taxa on the Isle of Arran, Scotland. *Molec. Ecol.* 13: 123–134. https://doi.org/10.1046/j.1365-294X.2003.02025.x

Robertson, A., Rich, T.C.G., Allen, A.M, Houston, L., Roberts, C., Bridle, J.R., Harris, S.A. & Hiscock, S.J. 2010. Hybridization and polyploidy ad drivers of continuing evolution and speciation in *Sorbus*. *Molec. Ecol.* 19: 1675–1690. https://doi.org/10.1111/j.1365-294X.2010.04585.x

Robertson, K.R., Phipps, J.B., Rohrer, J.R. & Smith, P.G. 1991. A synopsis of genera in Maloideae (Rosaceae). *Syst. Bot.* 16: 376–394. https://doi.org/10.2307/2419287

Ronikier, M. & Szeląg, Z. 2008. Differentiation among disjunct populations of agamospermous species of *Hieracium* section *Cernua* (Asteraceae) in Central European subalpine habitats. *Bot. J. Linn. Soc.* 158: 93–105. https://doi.org/10.1111/j.1095-8339.2008.00879.x

Rosenbaumová, R. & Krahulec, F. 2015. Sexual reproduction as a source of ploidy level variation in the model agamic complex of *Pilosella bauhini* and *P. officinarum* (Asteraceae: Lactuceae). *Pl. Syst. Evol.* 301: 279–290. https://doi.org/10.1007/s00606-014-1072-2

Rosenbaumová, R., Krahulcová, R. & Krahulec, F. 2012. The intriguing complexity of parthenogenesis inheritance in *Pilosella rubra* (Asteraceae, Lactuceae). *Sexual Pl. Reprod.* 25: 185–196. https://doi.org/10.1007/s00497-012-0190-7

Rothmaler, W. 1935. Systematische Vorarbeiten zu einer Monographie der Gattung *Alchemilla* (L.) Scop. II. Die systematische Gliederung der Gattung. *Repert. Spec. Nov. Regni Veg.* 38: 33–36.

Rothmaler, W. 1937. Systematische Vorarbeiten zu einer Monographie der Gattung *Alchemilla* (L.) Scop. VII. Aufteilung der Gattung und Nomenklatur. *Repert. Spec. Nov. Regni Veg.* 42: 164–173. https://doi.org/10.1002/fedr.19370421106

Rua, G.H., Speranza, P.R., Vaio, M. & Arakaki, M. 2010. A phylogenetic analysis of the genus *Paspalum* (Poaceae) based on cpDNA and morphology. *Pl. Syst. Evol.* 288: 227–243. https://doi.org/10.1007/s00606-010-0327-9

Rushworth, C.A., Song, B.-H., Lee, C.R. & Mitchell-Olds, T. 2011. *Boechera*, a model system for ecological genomics. *Molec. Ecol.* 20: 4843–4857. https://doi.org/10.1111/j.1365-294X.2011.05340.x

Ryde, U. 2011. Arguments for a narrow species concept in *Rubus* sect. *Corylifolii*. *Nordic J. Bot.* 29: 708–721. https://doi.org/10.1111/j.1756-1051.2011.01203.x

Šarhanová, P., Vašut, R.J., Dančák, M., Bureš, P. & Trávniček, B. 2012. New insight into the variability of reproduction modes in European populations of *Rubus* subg. *Rubus*: How sexual are polyploid brambles? *Sexual Pl. Reprod.* 25: 319–335. https://doi.org/10.1007/s00497-012-0200-9

Sartor, M.E., Quarin, C.L., Urbani, M.H. & Espinoza, F. 2011. Ploidy levels and reproductive behavior in natural populations of five *Paspalum* species. *Pl. Syst. Evol.* 293: 31–41. https://doi.org/10.1007/s00606-011-0416-4

Sartor, M.E., Rebozzio, R.N., Quarin, C.L. & Espinoza, F. 2013. Patterns of genetic diversity in natural populations of *Paspalum* agamic complexes. *Pl. Syst. Evol.* 299: 1295–1306. https://doi.org/10.1007/s00606-013-0797-7

Schinkel, C.C.F, Kirchheimer, B., Dellinger, A.S., Klatt, S., Winkler, M., Dullinger, S. & Hörandl, E. 2016. Correlations of polyploidy and apomixis with elevation and associated environmental gradients in an alpine plant. *AoB Plants* 8: plw064. https://doi.org/10.1093/aobpla/plw064

Schlyakov, R.N. 1989. Rod 33. Yastrabinočka – *Pilosella* Hill. Pp. 300–377 in: Tsvelev, N.N. (ed.), *Flora Evropeiskoi časti SSSR*, vol. 8. Leningrad: Nauka.

Schmelzer, G.H. 1997. Review of *Pennisetum* sect. *Brevivalvula* (Poaceae). *Euphytica* 97: 1–20. https://doi.org/10.1023/A:1003077906928

Schranz, M.E., Dobeš, C., Koch, M.A. & Mitchell-Olds, T. 2005. Sexual reproduction, hybridization, apomixis, and polyploidization in the genus *Boechera* (Brassicaceae). *Amer. J. Bot.* 92: 1797–1810. https://doi.org/10.3732/ajb.92.11.1797

Schubert, I. & Lysák, M.A. 2011. Interpretation of karyotype evolution should consider chromosome structural constraints. *Trends Genet.* 27: 207–216. https://doi.org/10.1016/j.tig.2011.03.004

Schuhwerk, F. 2002. Some thoughts on the taxonomy of *Hieracium*. *Ber. Bayer. Bot. Ges.* 72: 193–198.

Schuhwerk, F. & Fischer, M.A. 2003. Bestimmungsschlüssel der Untergattung *Hieracium* subgen. *Pilosella* in Österreich und Südtirol. *Neilreichia* 2–3: 13–58.

Sears, C.J. 2011. *Systematic investigations into the North American Crepis agamic complex.* Dissertation, The University of British Columbia, Vancouver, Canada.

Sears, C.J. & Whitton, J. 2016. A re-examination of the North American *Crepis* agamic complex and comparison with the findings if Babcock and Stebbins' classic biosystematic monograph. *Amer. J. Bot.* 103: 1–11. https://doi.org/10.3732/ajb.1600057

Sell, P. & Murrel, G. 2006. *Flora of Great Britain and Ireland*, vol. 4, *Campanulaceae – Asteraceae*. Cambridge: Cambridge University Press.

Sell, P.D. & West, C. 1976. *Hieracium*. Pp. 358–410 in: Tutin, T.G., Heywood, V.H., Burges, N.A. & Valentine D.H. (eds.), *Flora Europaea*, vol. 4. Cambridge: Cambridge University Press.

Selvi, F. & Fiorini, G. 1996 Karyology of *Hieracium* L. subg. *Hieracium* (Asteraceae) from Mount Amiata (central Italy). *Caryologia* 49: 287–299. https://doi.org/10.1080/00087114.1996.10797373

Sennikov, A.N. 2003. Taxonomic concept in *Hieracium* L. s.l. (Asteraceae). *Turczaninowia* 6: 16–41.

Sennikov, A.N. & Phipps, J.B. 2013. Atlas Florae Europaeae notes, 19–22. Nomenclatural changes and taxonomic adjustments in some native and introduced species of *Malinae* (Rosaceae) in Europe. *Willdenowia* 43: 33–44. https://doi.org/10.3372/wi.43.43104

Sepp, S. & Paal, J. 1998. Taxonomic continuum of *Alchemilla* (Rosaceae) in Estonia. *Nordic J. Bot.* 18: 519–535. https://doi.org/10.1111/j.1756-1051.1998.tb01532.x

Sepp, S. & Paal, J. 2000. Patterns and relationships between and within the sections *Alchemilla* and *Ultravulgares* of the genus *Alchemilla* (Rosaceae) in Estonia. *Nordic J. Bot.* 20: 561–571. https://doi.org/10.1111/j.1756-1051.2000.tb01606.x

Sepp, S., Bobrova, V.K., Troitsky, A.K. & Glazunova, K.P. 2000. Genetic polymorphism detected with RAPD analysis and morphological variability in some microspecies of apomictic *Alchemilla*. *Ann. Bot. Fenn.* 37: 105–123.

Sharbel, T.F., Voigt, M.L., Mitchell-Olds, T., Kantama, L. & De Jong, H. 2004. Is the aneuploid chromosome in an apomictic *Boechera holboellii* a genuine B chromosome? *Cytogenet. Genome Res.* 106:173–183. https://doi.org/10.1159/000079284

Sharbel, T.F., Mitchell-Olds, T., Dobeš, C., Kantama, L. & De Jong, H. 2005. Biogeographic distribution of polyploidy and B chromosomes in the apomictic *Boechera holboellii* complex. *Cytogenet. Genome Res.* 109: 283–292. https://doi.org/10.1159/000082411

Sharbel, T.F., Voight, M.L., Corral, J.M., Thiel, T., Varshney, A., Kumlehn, J., Vogel, H. & Rotter, B. 2009. Molecular signatures of apomictic and sexual ovules in the *Boechera holboellii* complex. *Plant J.* 58: 870–882. https://doi.org/10.1111/j.1365-313X.2009.03826.x

Sharbel, T.F., Voight, M.L., Corral, J.M., Galla, G., Kumlehn, J., Klukas, C., Schreiber, F., Vogel, H. & Rotter, B. 2010. Apomictic and sexual ovules of *Boechera* display heterochronic global gene expression patterns. *Pl. Cell* 22: 655–671. https://doi.org/10.1105/tpc.109.072223

Shibaike, H., Akiyama, H., Uchiyama, S., Kasai, K. & Morita, T. 2002. Hybridization between European and Asian dandelions (*Taraxacum* section *Ruderalia* and section *Mongolica*) 2. Natural hybrids in Japan detected by chloroplast DNA marker. *J. Pl. Res.* 115: 321–328. https://doi.org/10.1007/s10265-002-0045-7

Skawińska, R. 1963. Apomixis in *Hieracium alpinum* L. *Acta Biol. Cracov., Ser. Bot.* 5: 7–14.

Sochor, M., Vašut, R.J., Sharbel, T.F. & Trávníček, B. 2015. How just a few makes a lot: Speciation via reticulation and apomixis on example of European brambles (*Rubus* subgen. *Rubus*, Rosaceae). *Molec. Phylogen. Evol.* 89: 13–27. https://doi.org/10.1016/j.ympev.2015.04.007

Stace, A. 1998. Species recognition in agamosperms: The need for a pragmatic approach. *Folia Geobot.* 33: 319–326. https://doi.org/10.1007/BF03216207

Stace, C. 2010. *New Flora of the British Isles*, ed. 3. Cambridge: Cambridge University Press.

Stebbins, G.L. & Babcock, E.B. 1939. The effect of polyploidy and apomixis on the evolution of species in *Crepis*. *J. Heredity* 30: 519–530. https://doi.org/10.1093/oxfordjournals.jhered.a104649

Stebbins, G.L. & Jenkins, J.A. 1939. Aposporic development in the North American species of *Crepis*. *Genetica* 21: 191–224. https://doi.org/10.1007/BF01508152

Stevens, P.F. 2001–. Angiosperm Phylogeny Website, version 12 July 2012 [and updated since]. http://www.mobot.org/MOBOT/research/APweb/

Strasburger, E. 1905. Die Apogamie der Eualchemillen und allgemeine Gesichtspunkte, die sich aus ihr ergeben. *Jahrb. Wiss. Bot.* 41: 88–164.

Stuessy, T.F. 1990. *Plant taxonomy: The systematic evaluation of comparative data.* New York: Columbia University Press.

Šuvada, R., Mártonfi, P. & Mártonfiová, L. 2012. Differentiation of diploid and triploid taxa within *Taraxacum* sect. *Erythrosperma* (Asteraceae) from the Pannonian region. *Folia Geobot.* 47: 69–91. https://doi.org/10.1007/s12224-011-9109-6

Szeląg, Z. 2003. A synopsis of *Hieracium* sect. Cernua (Asteraceae). *Polish Bot. J.* 48: 89–97.

Talent, N. 2009. Evolution of gametophytic apomixis in flowering plants: An alternative model from Maloid Rosaceae. *Theory Biosci.* 128: 121–138. https://doi.org/10.1007/s12064-009-0061-4

Talent, N. & Dickinson, T.A. 2005. Polyploidy in *Crataegus* and *Mespilus* (Rosaceae, Maloideae): Evolutionary inferences from flow cytometry of nuclear DNA amounts. *Canad. J. Bot.* 83: 1268–1304. https://doi.org/10.1139/b05-088

Talent, N. & Dickinson, T.A. 2007. Apomixis and hybridization in Rosaceae subtribe Pyrinae Dumort.: A new tool promises new insights. Pp. 301–316 in: Hörandl, E., Grossniklaus, U., Van Dijk, P. & Sharbel. T. (eds.), *Apomixis: Evolution, mechanisms and perspectives*. Ruggell, Liechtenstein: Ganter.

Tas, I.C.Q. & Van Dijk, P.J. 1999. Crosses between sexual and apomictic dandelions (*Taraxacum*): I. The inheritance of apomixis. *Heredity* 83: 707–714. https://doi.org/10.1046/j.1365-2540.1999.00619.x

The Plant List 2013. Version 1.1. http://www.theplantlist.org/ (accessed 22 Apr 2016).

Tomasz, I. & Kołodziejek, J. 2008. Chromosome numbers of *Potentilla* subsect. *Collinae* (Rosaceae) from Poland. *Caryologia* 61: 170–175. https://doi.org/10.1080/00087114.2008.10589626

Trávníček, B. & Žíla, V. 2011. *Rubus silvae-bohemicae*: A new species of bramble from Bohemia and Bavaria. *Preslia* 83: 99–110.

Tucker, M.R. & Koltunow, M.G. 2009. Sexual and asexual (apomictic) seed development in flowering plants: molecular, morphological and evolutionary relationships. *Funct. Pl. Biol.* 36: 490–504. https://doi.org/10.1071/FP09078

Tyler, T. 2001. The genus *Pilosella* in the Nordic countries. *Svensk. Bot. Tidskr.* 95: 39–67.

Tyler, T. 2006. Patterns of morphometric variation and a new supraspecific classification of apomictic taxa of *Hieracium* (Asteraceae) from Denmark and southern Sweden. *Pl. Syst. Evol.* 261: 39–88. https://doi.org/10.1007/s00606-006-0446-5

Tyler, T. 2011. *Hieracium* sect. *Oreadea* (Asteraceae) in Sweden: From a complete mess to a preliminary taxonomic classification. *Nordic J. Bot.* 29: 538–589. https://doi.org/10.1111/j.1756-1051.2011.01158.x

Tyler, T. & Jönsson, J. 2013. Patterns of plastid and nuclear variation among apomictic polyploids of *Hieracium*: Evolutionary processes and taxonomic implications. *Ann. Bot. (Oxford)* 111: 591–609. https://doi.org/10.1093/aob/mct019

Uhlemann, I. 2001. Distribution of reproductive systems and taxonomical concepts in the genus *Taraxacum* F.H.Wigg. (Asteraceae, Lactuceae) in Germany. *Feddes Repert.* 112: 15–35. https://doi.org/10.1002/fedr.20011120105

Uhlemann, I., Kirschner, J. & Štěpánek, J. 2004. The genus *Taraxacum* (Asteraceae) in the Southern Hemisphere. I. The section *Antarctica* Handel-Mazzetti and notes on dandelions of Australasia. *Folia Geobot*. 39: 205–220. https://doi.org/10.1007/BF02805246

Urbani, M.H., Quarin, C.L., Espinoza, F., Penteado, M.I.O. & Rodrigues, I.F. 2002. Cytogeography and reproduction of the *Paspalum simplex* polyploid complex. *Pl. Syst. Evol.* 236: 99–105. https://doi.org/10.1007/s00606-002-0237-6

Urfus, T., Krahulec, F. & Krahulcová, A. 2014. Hybridization within a *Pilosella* population: A morphometric analysis. *Folia Geobot*. 49. 223–238. https://doi.org/10.1007/s12224-013-9179-8

Van Baarlen, P., Van Dijk, P.J., Hoekstra, R.F. & De Jong, J.H. 2000. Meiotic recombination in sexual diploid and apomictic triploid dandelions (*Taraxacum officinale* L.). *Genome* 43: 827–835. https://doi.org/10.1139/g00-047

Vašut, R.J. 2003. *Taraxacum* sect. *Erythrosperma* in Moravia (Czech Republic): Taxonomic notes and the distribution of previously described species. *Preslia* 75: 311–338.

Verduijn, M.H., Van Dijk, P.J. & Van Damme, J.M.M. 2004. The role of tetraploids in the sexual-asexual cycle in dandelions (*Taraxacum*). *Heredity* 93: 390–398. https://doi.org/10.1038/sj.hdy.6800515

Vít, P., Lepší, M. & Lepší, P. 2012. There is no diploid apomict among Czech *Sorbus* species: A biosystematic revision of *S. eximia* and discovery of *S. barrandienica*. *Preslia* 84: 71–96.

Weber, H.E. 1996. Former and modern taxonomic treatment of the apomictic *Rubus* complex. *Folia Geobot. Phytotax.* 31: 373–380. https://doi.org/10.1007/BF02815381

Welch, D.B.M., Ricci, C. & Meselson, M. 2009. Bdelloid rotifers: Progress in understanding the success of an evolutionary scandal. Pp. 259–279 in: Schön, I., Martens, K. & Van Dijk, P.J. (eds.), *Lost sex: The evolutionary biology of parthenogenesis.* London: Springer.

Whitton, J., Sears, C.J., Baack, E.J. & Otto, S.P. 2008a. The dynamic nature of apomixis in the angiosperms. *Int. J. Pl. Sci.* 169: 169–182. https://doi.org/10.1086/523369

Whitton, J., Dlugosch, K.M. & Sears, C.J. 2008b. Molecular and morphological evidence for and against gene flow in sympatric apomicts of the North American *Crepis* agamic complex (Asteraceae). *Botany* 86: 877–885. https://doi.org/10.1139/B08-071

Wiley, E.O. & Mayden, R.L. 2000. The evolutionary species concept. Pp. 70–89 in: Wheeler, Q.D. & Meier, R. (eds.), *Species concepts and phylogenetic theory: A debate*. New York: Columbia University Press.

Wilschut, R.A., Oplaat, C., Snoek, L.B., Kirschner, J. & Verhoeven, K.J.F. 2016. Natural epigenetic variation contributes to heritable flowering divergence in a widespread asexual dandelion lineage. *Molec. Ecol.* 25: 1759–1768. https://doi.org/10.1111/mec.13502

Windham, M.D. & Al-Shehbaz, I.A. 2006. New and noteworthy species of *Boechera* (Brassicaceae) I: Sexual diploids. *Harvard Pap. Bot.* 11: 61–88. https://doi.org/10.3100/1043-4534(2006)11[61:NANSOB]2.0.CO;2

Windham, M.D. & Al-Shehbaz, I.A. 2007a. New and noteworthy species of *Boechera* (Brassicaceae) II: Apomictic hybrids. *Harvard Pap. Bot.* 11: 257–274. https://doi.org/10.3100/1043-4534(2007)11[257:NANSOB]2.0.CO;2

Windham, M.D. & Al-Shehbaz, I.A. 2007b. New and noteworthy species of *Boechera* (Brassicaceae) III: Additional sexual diploids and apomictic hybrids. *Harvard Pap. Bot.* 12: 235–257. https://doi.org/10.3100/1043-4534(2007)12[235:NANSOB]2.0.CO;2

Winkler, H. 1908. Über Parthenogenesis und Apogamie im Pflanzenreiche. *Progr. Rei Bot.* 2: 293–454.

Wittzell, H. 1999. Chloroplast DNA variation and reticulate evolution in sexual and apomictic sections of dandelions. *Molec. Ecol.* 8: 2023–2035. https://doi.org/10.1046/j.1365-294x.1999.00807.x

Zahn, K.H. 1921–1923. *Hieracium*. Pp. 1–864 (1921), 865–1146 (1922), 1147–1705 (1923) in: Engler, A. (ed.), *Das Pflanzenreich*, IV.280 (Heft 75–77 [1921], 79 [1922], 82 [1923]). Leipzig: Engelmann.

Zahn, K.H. 1922–1930. *Hieracium*. Pp. 1–80 (1922), 81–160 (1924), 161–400 (1929), 401–492 (1930) in: Ascherson, P. & Graebner, P. (eds.), *Synopsis der mitteleuropäischen Flora*, vol. 12(1). Leipzig: Gebrüder Bornträger.

Zahn, K.H. 1930–1935. *Hieracium* 2. Pp. 1–160 (1930), 161–480 (1931), 481–640 (1934), 641–790 (1935) in: Ascherson, P. & Graebner, P. (eds.), *Synopsis der mitteleuropäischen Flora*, vol. 12(2). Leipzig: Gebrüder Bornträger.

Zahn, K.H. 1936–1938. *Hieracium* 3. Pp. 1–320 (1936), 321–480 (1937), 481–708 (1938) in: Ascherson, P. & Graebner, P. (eds.), *Synopsis der mitteleuropäischen Flora*, vol. 12(3). Leipzig: Gebrüder Bornträger.

Záveská-Drábková, L., Kirschner, J., Štěpánek, J., Záveský, L. & Vlček, Č. 2009. Analysis of nrDNA polymorphism in closely related diploid sexual, tetraploid sexual and polyploid agamospermous species. *Pl. Syst. Evol.* 278: 67–85. https://doi.org/10.1007/s00606-008-0134-8