

Freakish patterns – species and species concepts in apomicts

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Apomict groups keep challenging taxonomists, in classifications as well as in more fundamental question about the nature of apomictic species. The latter question is not just an academic one, because the outcome influences practical decisions on biodiversity and conservation. A historical overview over the species problem shows that a period of confusion and proliferation of species concepts between 1940 and 1990 was followed by an increasing consensus at the end of the 20th century that the species category is heterogeneous. Species come in kinds, which is understandable in light of their different evolutionary histories. Recently, Wilkins stated that we do not need a generally applicable species concept, because species are not an a priori category into which all biological organisms must fit, but salient phenomena that are to be explained. Not only biparental, but also asexual organisms often form such species-as-phenomena, explained as some combination of adaptation to an ecological niche and reproductive compatibility. The above is illustrated by historical and current studies in three well-studied apomict groups, viz. *Ranunculus cassubicus* agg., *Rubus* subgen. *Rubus* and *Hieracium* (subgen. *Hieracium* and *Pilosella*). Species in the *Ranunculus cassubicus* aggregate are the few existing sexuals, which are surrounded by a hybrid swarm of only partial apomictic forms, whereas in *Rubus* subgen. *Rubus* and *Hieracium* s.s. sexuals as well as numerous apomicts form well defined species. How species should be circumscribed in *Pilosella* is yet to be clarified. Largely, the differences between these groups can be contributed to their different modes of apomixis and the associated retained sexuality. From this review it is clear that the question is not so much ‘What is a species?’, but ‘What is a species in this particular group?’ To answer this question a thorough knowledge and understanding of the biology of the genus in question is required.

The answer to the question ‘What is a species?’ is considered one of the central issues of biology as well as one of its most vexing problems (de Queiroz 1998). This so-called ‘species debate’ has resulted in an overwhelming amount of literature on the conceptualisation and delimitation of species. It was described by Hey (2001) as ‘the long-standing failure of biologists to agree on how we should identify species and how we should define the word species’. This astounding proliferation of species concepts is not only caused by the awareness that species are the fundamental biological unit (Löve 1962, Ghiselin 1974, 1997, Mayr 1996, Mayden 1999, Mayden 2002, Sites Jr and Jonathon 2004, de Queiroz 2005b), but also a result of the rapid development of modern evolutionary biology. In an attempt to review the most important species concepts, de Queiroz (1998) discusses 13 of these, and Mayden (1997) even lists 22 species concepts. A substantial number of these concepts were published in the 10 years preceding the publication of Mayden’s and de Queiroz’s papers, and after publishing these overviews several new ones have been proposed (de Pinna 1999, Levin 2000, Hausdorf 2011).

The polyploid apomictic complexes constitute a special problem in the species debate. Their classification is a challenge for evolutionary research and systematics alike.

Apomixis, a mode of asexual reproduction via seeds which are formed without recombination (Asker and Jerlings 1992), leads to the stabilization and dissemination of single genotypes (Hörandl et al. 2009). There is much controversy over the taxonomical status of these apomictic lineages and the question whether they can be regarded as species. Or, as Wiens (2007) stated it: ‘... how should asexual species be delimited? Should we even call them species?’

How apomictic lineages are treated taxonomically largely depends on the species concept adopted. Just before the boom of species concepts, Stebbins (1941, p. 535) set aside apomict complexes as ‘...anomalous or ‘freakish’ from the systematic point of view’. As previously argued by various authors (Mishler and Budd 1990, Asker and Jerlings 1992, Hörandl 1998, Haveman et al. 2002), asexually propagating organisms cannot be classified as species under what is probably the best known, most widely used, and most influential species concept, Mayr’s ‘biological species concept’ (BSC, for abbreviations of species concepts see Table 1): species are groups of (actually or potentially) interbreeding natural populations which are reproductively isolated from other such groups (Mayr 1940, 1957, 1996, de Queiroz 2005b). Ghiselin (1987), an influential advocate of the BSC, and Löve (1962) even argued that by definition

Table 1. Evaluation of status of apomict lineages under the species concepts as reviewed in Mayden 1997. + = apomicts recognised as species, – = apomicts not recognised as species; ± recognition of apomicts dependent on the used characters.

Abbreviation	Concept	Apomict recognition	Reference
ASC	agamospecies	+	Turesson 1929
BSC	biological	–	Mayr 1942
CISC	cladistic	+	Ridley 1989
CSC	cohesion	+	Templeton 1989
CpSC	composite	–	Kornet and McAllister 1993, 2005
EcSC	ecological	+	Van Valen 1976
ESC	evolutionary	+	Simpson 1951, Wiley 1978
ESU	evolutionary significant unit	–	Waples 1996
GCC	genealogical concordance	+	Avise and Ball 1990
GSC	genetic	+/–	Simpson 1943
GCD	genotypic cluster definition	+	Mallet 1995
HSC	hennigian	–	Hennig 1950
ISC	internodal	+	Kornet 1993
MSC	morphological	+	Du Rietz 1930, Shull 1923
NDSC	non-dimensional	+/–	Paterson 1993
PhSC	phenetic	+	Sneath 1976
PSC	phylogenetic	+	Rosen 1978, Eldredge and Cracraft 1980, McKittrick and Zink 1988
PtSC	polythetic	+	–
RSC	recognition	–	Paterson 1985
RCC	reproductive competition	–	Ghiselin 1974
SSC	successional chrono-	not applicable	George 1956
TSC	taxonomical	+	Blackwelder 1967

species do not exist in asexual groups. In other species concepts, asexual organisms are explicitly excluded, like in Patterson's 'recognition species concept': species are the most inclusive population of individual biparental organisms which share a common fertilization system (Paterson 1985). In contrast, the 'agamospecies species concept' (Turesson 1929) was invented solely for apomictic groups (Mayden 1997). Recently, several authors argued that the exclusion of asexual organisms, amongst them bacteria, bdelloid rotifers as well as (facultative) apomictic plants, is a serious drawback of some species concepts (Hausdorf 2011, Chambers 2012). It seems preferable to search for a definition which covers both sexual and agamic groups.

A consistent recognition of apomictic lineages as species, as practiced by some mainly highly specialised taxonomists (Erben 1993 for *Limonium*, Fröhner 1995 for *Alchemilla*, Weber 1995 for *Rubus*, Sell and Murrell 2006 for *Hieracium* and *Taraxacum*) would increase the species richness of many regions significantly, perhaps beyond practicality (Stebbins 1941, Schuhwerk 2002). According to Haveman et al. (2002), the number of plant species in the Netherlands would increase from about 1450 to about 1900 if all known apomictic lineages of *Hieracium*, *Taraxacum* and *Rubus* were accepted as species. The flora of the British Isles would even double if apomict lineages were consistently recognised as species (Richards 2003).

This abundance of apomicts and the wide distribution of apomictic groups raise the need for practicable taxonomic concepts for biodiversity research and flora writing (Hörandl et al. 2009). Because species are commonly considered the central units of biodiversity and conservation (Stebbins 1987, Cracraft 2002, Wilson 2010), the opinion on apomict lineages as species significantly influences

the estimation of species richness and hence conservation efforts (Claridge et al. 1997). Haveman et al. (2002) and Gregor and Matzke-Hajek (2002) argued that neglecting apomictic species in floras and species check-lists leads to an underestimation of threatened species in Red Lists, thus diluting species conservation efforts. This is in concordance with the view of Soltis et al. (2007) on autopolyploids and cryptic and sibling species. Therefore, although the species debate appears to be an academic one at first sight and only significant for a few initiated scientists, it has a crucial impact on very practical questions.

In this paper, I will review the philosophical and taxonomic literature concerning apomictic species groups. The main question to be answered in this paper will be: what are species within agamic complexes? I will stroll along several pathways to approach the answer of this question. In the first part of this review, I will give a short overview of the history and literature on species concepts, concentrating on the period from the 'modern synthesis' (Huxley 1942) until now, and I will identify some key moments in the development of species concepts. In the second part of this paper, I will discuss some arguments against the apomicts-as-species idea, as well as some alternatives for the classification as species. In the last section, I will review the existing taxonomic (in a broad sense) and plant systematic literature on apomicts in order to get a clearer picture of how the conclusions from the first two sections of this paper effect the species concepts in apomict groups. Hereby, I will concentrate on a few well-studied groups: *Ranunculus auricomus* agg., *Rubus* sect. *Rubus*, *Hieracium* and *Pilosella*, although the conclusions will be applicable to other groups as well.

A short history of the species problem

As was elucidated by Richards (2010), the species problem as experienced today has both its philosophical and biological roots in the understanding of Aristotelian philosophy, and the interpretation of the species ideas of early naturalists like John Ray and Carolus Linnaeus. The traditional view, which was developed by Cain, Mayr and Hull in the mid-twentieth century, claims that until the 'Origin of species' by Charles Darwin both philosophy and biology considered species as invariable natural kinds with essential features. This 'essentialism story' was adopted by many authors, but questioned from the beginning by a minority (Richards 2010, chapter 3–4 for an overview). Recently, also Richards (2010) and Wilkins (2009b, 2010) provided good arguments for the opposite view: when Aristotle and the early naturalists wrote about the essences of species, they meant essential 'functions', not essential 'properties'. Richards pointed out that Linnaeus saw species as eternally fixed in his very first publication from 1735, but only a few years later he discovered hybridization as a modus for speciation. In a letter to Albrecht von Haller in 1744, he wrote (Larson 1968 referred to by Richards 2010): 'I beg of you not to suppose it [the *Peloria*] anything else than the offspring of (*Anthirrhinum*) *Linaria*, which plant I know well. This new plant propagates itself by its own seed, and is therefore a new species, not existing from the beginning of the world; it is a new genus, never in being until now'. Therefore the 'Essentialism story' has to be qualified as 'bad history', or, as Wilkins (2009b, p. 233) has put it: 'the standard stories and assumptions from the architects of the modern synthesis are often simply incorrect'. What is clear from the historical overviews by Wilkins (2009b) and Richards (2010) is that the investigators in the pre-Darwinian period had ideas on what species are, namely 'the generation of similar form' (Wilkins 2009b, p. 232), or, as John Ray (the father of natural history in Britain) put it in 1686, 'progeny resembling their parents' (Ray 1686). This was named the 'generative notion (or conception) of species' by Wilkins (2009b, p. 195, 2010, 2011), and I will return to this later.

The common view that Charles Darwin regarded species as arbitrary constructions of taxonomists, rather than real and objective entities in nature, has been derived primarily from a number of pages in the 'Origin of species' (Kottler 1978). A comprehensive description of the ideas of Darwin when it comes to the nature of species was recently provided by Wilkins (2009b, pp. 129–164), Richards (2010, pp. 78–112), and Mallet (in press). All these authors state that Darwin was fully aware of well-defined species. However, he was more interested in 'borderline cases' (Kottler 1978), because these provided evidence for the continuous evolution of species (Mallet in press). The most important thing Darwin added to the above idea of species as those groups of organisms that resemble their parents was the theory of how species came into existence: through natural selection. Richards (2010, p. 208) paraphrases Darwin's species concept as follows: 'Species are those lineages that have passed through sufficient divergent change to become distinct and permanent'.

The most important thing for our sake – the understanding of the different species concepts – is that Darwin's evolutionary theory affected thinking of species, and the discovery of the gene and the subsequent development of population genetics, in combination with the rediscovery of the Mendelian laws, formed the powerful basis for evolutionary biology and the 'modern synthesis' (Huxley 1942). It was Dobzhansky in his classical 1935 paper who first brought intersterility into species concept definitions: 'a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both)' (Dobzhansky 1935). Better known is Mayr's version of this species concept, taught in most biology classes and textbooks, which he called the 'biological species concept' (Mayr 1942): 'Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups'. In the decennia following the articulation of the BSC, a confusing plethora of species concepts was published: Mayden (1997) counted 22 of them, Wilkins (2009b, 2011) 26, or even 27. According to Wilkins, these species concepts can be clustered into seven 'basic' species concepts: agamospecies, biospecies, ecospecies, evolutionary species, genetic species, morphospecies and taxonomic species (Wilkins 2009b, 2011). Because these concepts have been reviewed extensively by others (Cracraft 1992, Mayden 1997, Wilkins 2009b, Richards 2010), I will not discuss them in detail again.

The long standing debate on species concepts might give the idea that the 27 published species concepts are mutually exclusive, but I think that the discussion, although as heated as in the decennia before, moved towards a unification of ideas in the years around the start of the new millennium. The first step in this process was the rediscovery of the difference between primary and secondary species concepts (Mayden 1997, 1999). Already Mayr (1957) distinguished between theoretical (primary or non-operational) and operational (secondary) properties of species concepts, but this difference was ignored in later decennia (notably by Mayr himself; Cotterill 2003). Much of the controversy between biologists in the species debate finds its origin in a lack of understanding of the difference between these two levels of species concepts. Primary species concepts are those answering the question: 'What are species?', whereas secondary species concepts are those giving answer to the question: 'How do we recognise species?' The first question is an ontological one, searching for the nature of species. The second one, however, is an epistemological question, because it searches for the properties of species by which species can be identified. The first are species 'concepts', the second are species 'criteria' (Mayden 1997, de Queiroz 1998, 1999, Cotterill 2003, Richards 2010).

As concluded by several independent reviewers, of the 22 species concepts mentioned by Mayden (1997) there is only one candidate that could serve as a primary concept: Simpson's 'evolutionary species concept' (ESC) amended by Wiley (Frost and Kluge 1994, Mayden 1997, 1999, de Queiroz 1998, 1999, Cotterill 2003). According to Wiley (1978), 'a species is a single lineage of ancestral–descendant

populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate'. de Queiroz (2005a) rephrased Simpson's ESC as his 'general lineage concept' (GLC) in which 'a species is a separately evolving (segment of a) metapopulation lineage'. A lineage is specified as a population extended through time or an ancestral–descendant series of time-limited populations (de Queiroz 2005a). Although Hausdorf (2011) argued that the ESC as well as the GLC are circular in their reasoning because they include the 'population' in the concept, in Wiley's definition it can easily be replaced by 'group of individuals' without any change of meaning, just as was done by Richards (2010, p. 158).

The question remains how to detect separate lineages, and this is where the secondary species concepts or operational rules come in. Discussing this topic, Mayden (1997), and in his footsteps Cotterill (2003), fall back on the notion of 'consilience', or the unification of (disparately derived) knowledge. Much of what is called 'species' in contemporary floras can be considered hypotheses of the lineages existing in nature. According to Mayden and Cotterill, the secondary species concepts can indicate whether to accept these hypotheses: intrinsic reproductive isolation (BSC), shared specific mate recognition or fertilization systems (RSC), phenetic differences (PSC), ecological distinctiveness (EcSC), monophyly (PhSC), morphology (MSC) to name some examples (more examples in de Queiroz 2005a). Every single one of these characters can (but not necessarily does) add evidence that our hypothetical entities correspond to real entities in nature (Sites Jr and Jonathon 2004, de Queiroz 2005a).

In the last decades, many authors have stated that the species category is heterogeneous: it consists of various types of lineages bound by different processes and displaying different structures (Mishler and Brandon 1987, Stebbins 1987, Hörandl 1998, Stace 1998, Cotterill 2003, Pigliucci 2003, Wilkins 2003, 2011, de Queiroz 2005a, Ereshefsky 2010, 2011, Hausdorf 2011, Chambers 2012). An interesting view on this was published by Chambers (2012), who claims that the process of speciation is a multi-dimensional phenomenon, because it has a time dimension. Although speciation can be instant (e.g. by polyploidisation, Soltis and Soltis 1999, Soltis et al. 2007), in most cases a new species gradually 'develops' from an ancestral species, until it is 'forever different' and 'reproductively isolated'. According to Chambers (2012) the different secondary species concepts point towards different developmental stages in the evolution of a species. He proposed a two-step decision matrix for species diagnosis to account for these different stages or levels.

Quite a different view on species concepts was published by Wilkins (2009b, 2011), who seems to consider Simpson's ESC on the same level as all other species concepts. He claims, based on thorough analysis of the history of biology and the conceptualisation of species through time, that 'species has always been thought to mean the generation of similar form. That is, a living kind or sort [species, RH] is that which has a generative power to make more instances of itself' (Wilkins 2009b, p. 232). In a noteworthy, yet unpublished paper which can be found on the internet, Wilkins (2009a) rephrased it as 'A species is

any lineage of organisms that is distinct from other lineages because of differences in some shared biological property'. This is called the 'generative conception of species' by Wilkins himself. A somewhat similar species conception was proposed by Hörandl (1998), who circumscribed species as 'all organisms of an ancestral–descendent lineage which are products of the same evolutionary process, which have a constancy of progeny (upheld by a certain reproductive system) and consequently a similarity of phenotype and of ecogeographical unity'. An important notion, derived from the mentioned unpublished paper by Wilkins, which might influence future discussions, is that species are no 'explanations' in some theory, but they are salient phenomena to be 'explained' ('explicanda' more philosophically spoken): 'If species were theoretical objects, we ought to find them as a consequence of theory, not as a 'unit' that we feed into theoretical or operational processes. ... Theory does not define species. ... We do not define species, we see them' (Wilkins 2009a). In this paper he makes the important account: 'Of course, not all lineages are species – gene, haplotype and population lineages, for example – so the point at which lineages coalesce into different kinds of species is not something that we can define abstractly. Instead, a species is a phenomenon that we observe, and seek to explain with one of the 26 or so conceptions in each case' (Wilkins 2011). His final point is that we do not need a singular definition of species, because species-as-phenomena are real things to be explained, not an a priori category or rank into which every biological organism must be fitted (Wilkins 2009a in the last sentence).

Probably, the most striking and staggering conclusion from the historical analysis of species concepts is the insight that taxonomists kept describing species and kept making their classifications within their realms of specialisation in spite of the prevailing species concept or concepts: present-day batologists keep describing new *Rubus* species, as hieraciologists do with new *Hieracium* species, and bacteriologists with new bacteria species, although most of them – probably all – have been brought up with Mayr's BSC in biology classes. In my opinion, this pleads in favour of Wilkins' view of species: taxonomists describe the phenomena they encounter in nature, irrespective of theoretical objections. We cannot escape the conclusion that all the proposed species concepts have failed to account for all types of diversity we are inclined to call 'species'. This seems logical when one realises that there are many ways how these species come into being (Hörandl 1998, Wilkins 2003, 2007).

Species recognition in apomictic groups: possible objections

If the species category is an evolutionary heterogeneous amalgam of phenomena, is there any ground for the recognition of species within apomictic groups? Before entering this question, I first have to discuss some of the objections that are made against such recognition: 1) apomict species are impossible by definition, 2) apomict species do not resemble amphimictic outbreeders, and 3) apomict species show a lack of coherence.

Apomictic species are impossible by definition

The idea that apomictic species (or asexual species more general) are impossible by definition is expressed most explicitly by the defenders of the BSC, for instance Mayr himself (Mayr 1987, 1992). One of the most dedicated proponents of this species concept, Ghiselin, states in the appendix of his excellent *Metaphysics and the origin of species*: 'An asexual biological species is a contradiction in terms' (Ghiselin 1997, p. 305). This is clear in a glance: apomict species are not compatible with the BSC, because they lack interbreeding.

With this in mind, the pertinent question is how apomicts are dealt with (or better: how they could be dealt with) under the premise of the other species concepts. Table 1 gives an overview over the species concepts reviewed by Mayden (1997) and the conception of apomict species therein (see also Asker and Jerlings 1992, and Dickinson 1998a for a discussion). The 'successional species concept' (SSC) was developed for fossil species only, and is therefore not applicable to extant organisms at all. All other species concepts in Table 1 are applicable to apomicts, but several will reject apomicts as species. The species concepts under which apomictic lineages are (or can be) regarded as species, are marked with a '+', otherwise a '-' is given. To be recognised as species, the BSC, CpSC, ESU, HSC, RCC and RSC demand biparental reproduction. Clearly, apomictic lineages are rejected by default under these species concepts, but it might be less obvious that also the entire agamic complexes are to be rejected as species because biparental reproduction is lacking. Thus, common flora entries like *Rubus fruticosus*, *Hieracium murorum* or *Taraxacum officinale* may not be recognised as species when these concepts are applied strictly. Concerning the GSC, it depends largely on the author how apomictics are treated. In the original circumscription by Simpson (1943), no reference was made to the mode of reproduction, but Dobzhansky (1950) added the notion of 'most inclusive reproductive community of sexual and cross-fertilizing individuals'. The NDSC is more of an umbrella term for several species concepts, including for instance the BSC (rejecting apomicts as species) as well as the MSC (accepting apomicts as species). All other listed species concepts, over 50%, are able to accommodate apomictic lineages as species.

Mayden (1997) argues that a useful species concept should give account for all biodiversity (p. 382), and that the recognition of hybrids and apomicts are the prerequisite for any monistic (i.e. universally valid) species concept (p. 415–416). The denial of apomictic species seems problematic indeed, 'given that sex is a relatively rare property in the universal tree of life, which would mean that most biological taxa do not come in species' (Wilkins 2011). This notion is understood by other authors too (Ereshefsky 2010, Van Regenmortel 2010).

Apomictic species do not resemble amphimictic outbreeders

Sometimes it is stated in one or another way that agamosperm species ought to include multiple genotypes to be equivalent to sexually reproducing species, and that the lineages or microspecies recognised by many highly specialised taxonomists do not fulfil this requirement (Turesson

1929, Stebbins 1941, Dickinson 1998a, b). As was stressed by Stace (1998), this argument is not very convincing, since sexual outbreeders themselves are not mutually equivalent in this respect. Furthermore, studies on population genetics have shown that apomictic complexes can harbour considerable genetic diversity within and among populations, as a result of the history of descent of apomictic complexes, the influence of backcrossing with sexual relatives, hybridization between apomictic lineages and facultative sexuality, and accumulation of mutations (reviewed by Hörandl and Paun 2007). Also from a more philosophical viewpoint, this objection doesn't keep up: the demand of one or more necessary properties (like an amount of genetic variation) is the kind of essentialism that is widely rejected when discussing the nature of species (Ghiselin 1997, de Queiroz 2005a, Richards 2010, Wilkins 2010).

Apomict species are not coherent

Sex is an important feature by which species maintain their coherence. The major processes that bind the members of a sexual species together and make them evolve as populations and not as mere individuals are recombination and intraspecific gene flow (Rieseberg and Burke 2001). This strong internal cohesive process is lacking in strictly asexual lineages and this invited Chambers (2012) to heave the sigh: 'each individual must simply be considered as a species of some sort or we must stop thinking about them in this way at all' (a similar notion had already been expressed by Fisher 1958, p. 135).

However, asexual organisms actually seem to be organised in units that resemble species of biparental organisms in both morphological and functional respect (Mishler and Brandon 1987, Goodfellow et al. 1997, Cohan 2002, Hillis 2007, Hausdorf 2011), whereas one would expect that asexual organisms would form a smear or continuum of variation (Wilkins 2006, Hillis 2007). Templeton (1989) has argued that not only internal cohesive processes can hold a group of organisms together as species, but that ecological pressure or selection can play a similar role. This idea was worked out in more detail by Wilkins (2006) in a paper on the concept and causes of microbial species. According to Wilkins, species (as phenomena, both uni- and biparental) are genetic clusters in the genome space, to be explained as some combination of adaptation to an ecological niche and reproductive compatibility (cf. Van Valen 1976).

Case studies on apomict groups

The question remains how to deal with apomictic lineages. Although much effort has been made by both biologists and philosophers to find a universally applicable species definition in the last six decennia, rather recently there seems to grow some consensus that the species category is heterogeneous, and that the search for one universal species concept might be idle. This is not very surprising, considering the diversity of the living world around us and the different modes of speciation recognized (cf. Wilkins 2003, 2007). However, we don't experience the organismal world as a complete chaos of variation: the fact that organisms are organised in lineages of similar organisms that we call

species is evident to both specialists and laypersons (Hillis 2007). Wilkins (2009a) has put forward that species are no theoretical objects, but phenomenal objects: they push themselves upon the attentive observer, both in sexual and asexual groups, and they ask for an explanation. This idea has received little attention until now, although it seems a valuable notion.

How does this affect the way we treat apomictic lineages in our taxonomies? Stace (1998) advocated a utilitarian pragmatic approach in apomict taxonomy. This was based on the assumption that the precise biological meaning that once could be inferred from the term 'species' has disappeared (Stace 1998, p. 325), but I am not sure this is really the case. More than before we understand what species are, although the awareness that species come in different kinds has grown simultaneously. I am opposing to the view of Stace, who stated that species are reduced to a utilitarian role in taxonomy, as if they were not real (Rieseberg et al. 2006, Haveman and De Ronde 2012). Hörandl et al. (2009, p. 1211) interpreted Stace's pragmatic apomict taxonomy as a case-wise approach, resulting in the rejection of apomictic species in the '*cassubicus*' group within the *Ranunculus auricomus* aggregate. As pointed out already by Davis (1958), there is no general solution to the species recognition and taxonomy of all apomictic groups, because each apomictic genus presents problems a little different from the others (Gustafsson 1947). The idea that an overall prescriptive solution to the taxonomic problems posed by apomictic groups is impossible (Richards et al. 1996, Chrtek and Marhold 1998) and that a case-wise approach is necessary, concurs with the notion of a heterogeneous species category, and that species are phenomena to be explained. This is even true for 'ideal' outbreeding species. Every taxonomic treatment must rely on gained expert knowledge of traits and features that are of importance in that particular group, and all traits in the above mentioned secondary species concepts, and even more can be used as such.

In the following sections, I will exemplify this case-wise approach for three large and more or less well studied apomictic groups, viz the *Ranunculus auricomus* aggregate, *Rubus* subgen. *Rubus* and *Hieracium* (incl. *Pilosella*). However, before doing so I have to make some remarks about the classification of apomictic lineages on other than the species level, which are valid for all discussed groups, viz their recognition 1) at some infraspecific rank, or 2) as nothospecies. Although a classification at some infraspecific level might be convenient for getting a quick overview, as was argued by Schuhwerk (2002), at least in most cases it does not reflect the phylogenetic structure of the organisms concerned, which seem to be highly reticulate (Ericsson 1992, Wittzell 1999, Hörandl et al. 2009). This taxonomical practice thus leads to the grouping of lineages with different evolutionary histories under one species (Tyler 2006), which thereby becomes polyphyletic (Ericsson 1992) and consequently artificial. Because systematics is not only aiming at naming the diversity of life, but also at clarifying their relationships and building the tree of life (Cracraft 2002, Cracraft and Donoghue 2004), classifying apomictic lineages at some infraspecific level is hindering broader systematics goals.

Most apomicts are considered to be of hybrid origin (Gustafsson 1943, 1947, Grant 1971, Richards 1973, 2003, Stace 1989, p. 154, Matzke-Hajek 1997, Paun et al. 2006, Hörandl and Paun 2007, Fehrer et al. 2009, Mráz et al. 2011), and recognition of apomictic lineages as nothospecies would therefore be an option to consider. However, since most (but not all, Robertson et al. 2004) apomictic lineages are thought to be ancient hybrids for which the parental species are unknown, and most probably extinct (Weber 1995, Mráz et al. 2011), a formal treatment as nothospecies is impossible (ICBN Art. H.3.2, McNeill et al. 2007). More fundamentally, a hybrid origin is not exceptional in the plant kingdom, and it has been argued by several authors that hybridisation is an important driving force in the evolution of angiosperms (amphimicts and apomicts alike). The topic was placed on the scientific agenda by Stebbins (1959) and extensively reviewed in Grant's seminal 'Plant speciation' (Grant 1971), and Arnold's 'Natural hybridization and evolution' (Arnold 1997). More recently, Soltis and Soltis (2009) even argued that most angiosperms have a hybrid background. Considering this claim, the ancient hybrid origin of apomicts might be no exception at all, and seems no profound argument to treat them differently from other angiosperms.

Ranunculus auricomus agg.

The *Ranunculus auricomus* complex (Goldilocks) is distributed across Europe, western Siberia and Greenland, and can be found from the Arctic to the Mediterranean zone (Jalas and Suominen 1989). It forms a polyploid complex in which the (few) diploids show sexual propagation (Hörandl and Greilhuber 2002), whereas polyploids are usually aposporous apomicts (Hörandl and Greilhuber 2002, Hörandl et al. 2001, 2009).

Linnaeus (1753) described two species, *Ranunculus auricomus* and *R. cassubicus*, which represent two morphological nuclei within the complex (Hörandl 1998). Marklund (1961, 1965) classified the complex in four morphologically distinct 'main species' (*R. cassubicus*, *R. monophyllus*, *R. fallax* and *R. auricomus*), and treated the agamic lineages as subspecies under these main species. Hörandl and Gutermann (1998) treated the main species as informal 'collective groups', each of them including groups of morphologically similar apomictic lineages; the latter were distinguished as species. Within the aggregate, approximately 800 apomictic lineages have been described as species by central and north European taxonomists (Ericsson 1992, Hörandl 1998), mainly on the basis of morphology.

In his treatment of the complex for 'Flora Nordica', Ericsson (1992) argued in favour of the treatment of the individual apomictic lineages as species, as opposed to the subspecies recognized Marklund. His arguments are that the 'main species' are polyphyletic and have ill-defined limits, while the apomictic lineages are sympatric, very constant, and lack intermediate forms. Hörandl (1998) discussed the alternatives to the agamospecies concept in the *Ranunculus auricomus* aggregate, and reached the same conclusion as Ericsson. For the whole complex, she questioned monophyly, and therefore, treating the whole complex as a single species was rejected. The same holds, *mutatis mutando*, for the

collective groups. Because the parental species were unknown at that time, a classification as hybrids was impossible as well. Consequently, the *R. auricomus* complex could not be classified at all (except for the few sexual species) if the species level was to be rejected.

However, more recently, a detailed study of the *cassubicus* group on the basis of morphological, karyological, and molecular data (Hörandl et al. 2009) revealed the instability of the apomictic species due to the frequent sexuality of apomicts, increasing genetic diversity by continuous formation of new cytotypes, local hybridization and introgression. Similar morphotypes may have multiple origins, which seriously undermines the assumption that phenetically similar populations in an area also possess an historical evolutionary coherence. To reflect the evolutionary processes involved, the authors propose a separate classification of the sexual species, *R. notabilis*, and the closely related species pair *R. cassubicifolius* and *R. carpaticola*. Based on these well-defined species, the apomictic biotypes of the ‘*cassubicus*’ group can best be classified as broad nothotaxa (*R. carpaticola* × *cassubicifolius*, and *R. × hungaricus*).

This example shows how increased understanding of multiple features of a particular group leads to a better understanding of the complex evolutionary relationships within the aggregate, and how taxonomy can benefit from such understanding. In the case of the *Ranunculus auricomus* agg., multiple data lead to the conclusion that an agamospecies concept (for at least the studied group) must be rejected, although formerly it was thought to be the only possible solution for this aggregate.

Rubus subgen. Rubus

Rubus subgen. *Rubus* (blackberry) is a polyploid complex which has its main centres of diversity across Europe, North America and the mountainous areas of South America. Furthermore, it is native in Africa, western Asia, the northern part of India, in Japan and New Zealand (Weber 1995, p. 318). It is a polyploid complex in which only six extant sexual species are known in Europe: the (sub-)Mediterranean *R. ulmifolius* and *R. canescens*, the west-Mediterranean *R. incanescens*, *R. caesius* with a wide distribution across Europe, the Canarian *R. bollei*, and the Caucasian *R. moschus* (Weber 1995, p. 302). All other European species of the subgenus are (allo-)polyploids and (mostly facultative) apomicts; obligate apomixis was detected in the triploid members of the series *Discolores* (Šarhanová et al. 2012). In the recent chorological overview of the genus published in ‘Atlas flora Europaeae’ (Kurtto et al. 2010) about 700 apomicts are recognized.

Historically there have been various attempts to classify the numerous apomicts (Weber 1996, 1999, Kurtto et al. 2010, p. 28): 1) the description of each different bramble as a separate species (Müller 1859, Boulay 1865–1869, Genevier 1869), 2) as infraspecific taxa (Syme 1864), 3) as hybrid formulae (Kuntze 1867, Schipper 1925), 4) arranging and naming of each unknown plant as an infraspecific taxon in an artificial system (Sudre 1908–1913), and 5) as species with different values depending to their fertility and distribution (Focke 1877, Gustafsson 1943). From the

1970s onward, *Rubus* systematics started with a whole new approach, called the ‘Weberian reform’ by Holub (1997). This reform relies of four major pillars: 1) mapping projects over larger areas, 2) evaluation of type material, 3) visits to loci classici, and 4) the evaluation of the status of species based on their distribution areas (Haveman and De Ronde 2012). Species are distinguished almost only on the basis of morphology, so a morphologically based agamospecies concept is used. To prevent the overflow of the systematic system, the convention among European *Rubus* taxonomists is to describe only species with a distribution area over 50 km (the fourth pillar of the ‘Weberian reform’). The basis for a phenetic agamospecies concept in *Rubus* is defensible, because DNA fingerprinting has showed that the agamic lineages regarded as species do consist mainly of single clones with very limited genetic variation (Kraft and Nybom 1995, Kraft et al. 1996, Nybom 1998, Kollmann et al. 2000), contrary to the case in many other agamic genera (reviewed by Hörandl and Paun 2007). Thorough knowledge of the phenotypic variation of the apomictic lineages will therefore lead to distinguishing of these lineages properly (Ryde 2011), even in the case of biotypes with a very limited distribution. Therefore, Ryde (2011), and in his footsteps Haveman and De Ronde (2012), declined the categorical rejection of *Rubus* species with a distribution area < 50 km, as previously done by Loos (2008). However, this phenetic approach will fail in those cases where a raised percentage of sexuality is apparent, especially in the series *Hystrix* and *Glandulosi* (Haveman and De Ronde 2012). In the mountainous areas of Europe, these series form swarms of only partly stabilised apomicts from which stabilised biotypes with large enough distribution areas are actually recognised as species, like *R. guentheri* and *R. nigricatus* (Kurtto et al. 2010). However, it is unclear which percentage of these groups (classified as ‘*Rubus hirtus* agg.’, Weber 1995) consist of stabilised apomicts with only a local distribution, and what is the percentage of sexual forms and primary hybrids. In the series *Glandulosi* Šarhanová et al. (2012), using flow cytometric seed screen (FCSS), recently demonstrated predominantly sexual propagation in the western Carpathians but predominantly apomictic propagation in the southern Bohemian Massive. An approach similar to the work of Hörandl et al. (2009) in the *cassubicus* group of the *Ranunculus auricomus* aggregate may provide insight into the structure of these hybridogenic swarms, which seems a prerequisite for an adequate taxonomic treatment. Such a genetical analysis of the *R. hirtus* aggregate was advocated also by Holub (1997) and Haveman and De Ronde (2012).

Hieracium s.l.

Within *Hieracium* s.l. (hawkweed), originally four subgenera were recognised: the American subgenus *Chionoracium* (formerly *Stenotheca*, Garland 1990), the Eurasian subgenera *Hieracium* and *Pilosella*, and the African-European subgenus *Tolpis* (Zahn 1921–1923, Fehrer et al. 2005). These subgenera, nowadays often considered as genera, differ in their mode of reproduction: the species of *Tolpis* and *Chionoracium* are all outcrossing sexual diploids (as far as known), *Hieracium* s.s. species are thought to be either polyploid obligate (diplosporous) apomicts or diploid sexuals, and

subgenus *Pilosella* is characterised by a mixture of sexual and facultatively aposporous apomicts (Koltunow et al. 1995, Krahulcová et al. 2000, Chrtek et al. 2009, Crawford et al. 2010). Contemporary taxonomies exclude *Tolpis* from *Hieracium*, which is supported by molecular phylogenetic analysis (Park et al. 2001). In addition, during the last decades, generic recognition of *Pilosella* has gained increased support. If excluding '*Hieracium*' *intybaceum*, *Hieracium* as well as *Pilosella* form monophyletic groups (Chrtek et al. 2009), differing morphologically mainly in achene features (Bräutigam and Greuter 2007). I will concentrate on the (apomictic) Eurasian (sub)genera here.

Over 10 000 names have been published in *Hieracium* and *Pilosella* (Beaman 1990), making *Hieracium* s.l. one of the largest genera worldwide. *Hieracium* taxonomy is much hindered by different regional traditions, which has led to two major, fundamentally differing taxonomical schools (cf. Schuhwerk 2002). The 'Nordic' school, in which the apomictic lineages are recognized as species, which are grouped into 'circle species', 'series', 'sections' and other informal groupings, followed the work of Fries (1862), Almquist (1881), and others in the Nordic countries, Jordan (in Boreau 1857), Boreau (1857), and Arvet-Touvet (1888, 1913) in continental western Europe, and Backhouse (1856) in Britain. The 'central-European school' of hieracology is based on the work of Von Nägeli and Peter (1885), who grouped the supposed apomictic lineages of *Pilosella* as subspecies and varieties under major aggregate species. This approach was extended to *Hieracium* s.s. by Zahn (1921–1923, 1930–1935, 1936–1938), who employed a hierarchical system of principal species ('Hauptarten') and intermediate species ('Zwischenarten', displaying characters intermediate between two or more principal species), grex, subgrex, subspecies, varieties, subvarieties, formae and subformae to account for all variation. Zahn's system is highly artificial though, like the treatment of Sudre for *Rubus* (Sudre 1908–1913); the grouping of the apomictic lineages under principal and intermediate species doesn't necessarily reflect natural relationships, and, as discussed above, the grouping of apomictic lineages as subspecies under one (collective) species most likely makes the latter polyphyletic. Besides, like Sudre in his *Rubus* monograph, Zahn often aggregated (sometimes only superficially) similar forms from all over Europe into one taxon, irrespective the large gaps in distribution areas (Chrtek and Mráz 2007).

One part of the problems in the classification of hawkweeds has had its origin in the historical lack of awareness of the fundamental differences between the reproductive systems of the subgenera *Hieracium* s.s. and *Pilosella*. Recent attempts to classify both (sub)genera try to give account to this difference (Sell and West 1976, Schou 2001, Sell and Murrell 2006, Tyler 2001, 2005).

Hieracium s.s.

Most of the analysed taxa of *Hieracium* s.s. are tri- or tetraploid apomicts, while sexual diploids are rare and mostly confined to southern latitudes (Schuhwerk 2002, Chrtek et al. 2007a, Tyler and Jönsson 2009). There are several arguments to accept a narrow (micro)-species concept in *Hieracium*. To a large extent, apomixis in *Hieracium*

is obligate; although the variation in *Hieracium* s.s., like in all apomict taxa, is thought to be partly due to hybridisation events, recent hybridisation is probably very rare (Mráz et al. 2005, 2011). In contrast, from an evolutionary perspective hybridisation events must have occurred rather frequently in the past (Fehrer et al. 2009). Other causes of the immense variation within the genus might be 'pseudo-sexual' recombination among the different copies of the same chromosomes within the seed-forming individual, structural mutations, or series of point-mutations affecting single genes influencing morphological characters. The relative importance of these various processes is still largely unknown though (Tyler 2006). Most apomictic lineages are morphologically rather well defined, due to the very low genotypic variation. As shown in several studies, most apomictic lineages consist of only one or very few genotypes (Shi et al. 1996, Mráz et al. 2001, Štorchová et al. 2002, Chrtek et al. 2007b, Ronikier and Szeląg 2008). Further, morphologically distinguished (micro)-species from the Nordic countries appear to be homogeneous with respect to ploidy level (Tyler and Jönsson 2009).

Like in the *Ranunculus auricomus* aggregate and *Rubus* sect. *Glandulosi*, genetic as well as morphological variation is higher in regions and groups where sexual diploids occur (Mráz et al. 2001). Considerable genetic variation can be found in species with a wider distribution, especially when they comprise diploid as well as polyploid populations, as shown for the arctic-alpine *H. alpina* s.s. (Shi et al. 1996, Štorchová et al. 2002). However, widespread *Hieracium* species may consist of only one clone too (Shi et al. 1996, Ronikier and Szeląg 2008). Similarly, Sell and Murrell (2006, p. 221) report only very limited variation in some apomicts, whereas others appear to be distinct species when only the extremes are taken into account. Probably such species are of polytopic origin (Shi et al. 1996, Mráz et al. 2001, 2009). How to deal with this variation will be dependent on the situation. In some cases, morphological variation can provoke the recognition of a new species, for instance when morphological variation coincides with genetic variation and chorological evidence (cf. Mráz et al. 2001, Ronikier and Szeląg 2008). In cases where the variation is clinal, like in *H. alpina* s.s., the recognition of subspecies is suggested (Shi et al. 1996), but to do so, phylogenetic relationships must be clear and allow for this.

Considering all evidence, the lack of recent hybridisation and the low genetic variation, resulting in distinct lineages with only little morphological variation, are arguments to accept a narrow (micro)-species concept in *Hieracium* s.s. To define these narrow species, Tyler (2006, 2011) applied a statistically based morphometric approach with convincing results.

Pilosella

The taxonomic situation in *Pilosella* is far more complex than in *Hieracium* s.s., due to a combination of sexuality, facultative apomixis, polyploidy, and frequent hybridization (Ostenfeld 1912, Krahulcová et al. 2000, Fehrer et al. 2007). Many field populations are heterogeneous in respect to ploidy level and/or reproductive system (Krahulcová et al. 2000, 2009a, Šingliarová et al. 2011), and hybrids are

formed often, although unevenly in different mixed populations (Krahulec et al. 2008). The combination of hybridization, apomixis and clonal growth leads to the maintenance of various hybrids, having originated from backcrossing and hybridization between more than two species (Krahulcová et al. 2000), and making the classification very cumbersome. Gene-flow is considerable among all morphotypes, including the principal species (Tyler 2005, Krahulcová et al. 2009a). As a consequence, classification in *Pilosella* cannot follow the criteria applied in *Hieracium* s.s., where hybridisation and gene-flow are very rare.

Bräutigam and Greuter (2007) sketched a brief history of the classification of *Pilosella*, starting with the revision by Fries (1862), who recognised 42 species. Von Nägeli and Peter (1885) and Zahn (1921–1923) multiplied this number, by recognizing 164 and 182 species respectively. To give account for the many micro-species that were already then described, Zahn recognised a mind-boggling number of sub-species (624 in *Hieracium pilosella* L. alone!).

Several suggestions have been given to deal with this complicated situation. In the 'Flora Europaea', Sell and West (1976) aimed to recognise species comparable with normal sexual species in other genera, and these largely agreed with the narrowly circumscribed main species of Zahn (1921–1923). The Zahnian intermediate species were considered as hybrids. A very similar approach was published by Sell and Murrell (2006, p. 209), who additionally distinguished the infraspecific groups of Zahn ('grex') as subspecies. However, this system ignores well-defined taxa as meaningless hybrids (Schuhwerk 2002), and the discrimination between pure and hybrid species is hypothetical at its best. Tyler (2001, 2005) argued against such an approach where most of the morphotypes encountered in nature are classified as hybrids. He proposed a new classification scheme in which very broadly circumscribed species are recognised, and only the recent hybrids are treated as hybrids (Schou 2001, Tyler 2001). The species recognised by him include many morphotypes treated as hybrids or intermediate taxa by central European authors. Although allozyme variation in Nordic members of *Pilosella* did not reflect the proposed classification adequately (Tyler 2005), it underlined that gene flow occurs between virtually all morphotypes to such an extent that '... it may even be argued that the whole genus *Pilosella* should be regarded as a single biological species'. The main argument used to reject Tyler's solution is the loss of information resulting from the lumping of easily recognised morphotypes (Schuhwerk 2002, Bräutigam and Greuter 2007).

Whereas the putative hybrids are omitted in the treatment of the 'Flora Europaea' (Sell and West 1976), they are included in the Euro+ Med Checklist with binomials as if they were good species (Bräutigam and Greuter 2007). These hybridogenous taxa or taxon swarms are thus not treated as nothospecies, but are termed 'collective species', and they are of very unequal nature and value: they may comprise newly formed, primary hybrids only, or correspond to stable hybridogenous species, or they often include both (Bräutigam and Greuter 2007, p. 125). In a recent paper on the population structure of mixed *Pilosella* populations, Krahulcová et al. (2009a) argued that both

hybrid categories should be distinguished, because 'Evidently, the recent hybrids are repeatedly formed, even at the same locality. Because of a low production of identical progeny by (facultative) apomixis, they usually do not spread outside the place of their origin. The stabilized hybridogenous taxa, however, behave like species at least at the landscape level'. Conceptually, the approaches by Krahulcová et al. (2009a) and Tyler (2001, 2005) are congruent to a high extent. Although the treatment by Krahulcová et al. (2009a) has hardly been tested for its usability (but see Krahulcová et al. 2009b), of all proposed systems it seems to reflect the structure of the genus best. Future taxonomic treatments of *Pilosella* have to prove its tenability.

Concluding remarks

Considering their different evolutionary histories, it cannot come as surprise that species come in kinds. Even asexuals are no homogenous group in this respect, but come in all sorts (Bengtsson 2009). If one thing is clear from the species debate, it is that there are numerous ways to define species, that they all have their own merit, but that no single one seems to capture the real essence of all groups of organisms we tend to name species (Ereshefsky 2011). It was only in approximately the last two decades that more and more philosophers and biologists alike came to the conclusion that the species category is heterogeneous, after several decades of intense, not yet closed, debate. From the examples in this paper it might be clear that it is not so much the question 'what species are in general', but 'what species are in a particular group' that is relevant. Species in the *cassubicus* group in *Ranunculus auricomus* are a few sexuals, which gave rise to an only partly apomictic hybrid swarm. Species in *Rubus* subgenus *Rubus* are numerous facultative apomictic lineages differing in morphology, distribution area, and ecology, besides a very few sexual 'biological species'. Species in *Hieracium* s.s. are mostly ancient hybrids, stabilised by almost obligate apomixis; only in some regions sexual species are found. At what species may be discerned in *Pilosella*, is not yet very clear: there are sexuals, 'ancient' hybrids stabilised by apomixis, as well as large quantities of recent hybrids, and to what extent these groups form species still has to be discovered. Such an approach is not some kind of new pragmatism, let alone only a way to order the chaos in a utilitarian way, but should be founded in a thorough biological understanding of the patterns in nature that reveal themselves after hard scientific labour.

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