Folia Geobotanica 33: 335–348, 1998

SPECIES CONCEPTS IN AGAMIC COMPLEXES: APPLICATIONS IN THE *RANUNCULUS AURICOMUS* COMPLEX AND GENERAL PERSPECTIVES

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Keywords: Apomixis, Evolution, Morphology, Phylogeny, Taxonomy

Abstract: The application of different current species concepts to the predominantly apomictic *R. auricomus* complex (goldilocks) is discussed. As with other uniparental reproducing organisms, biological species concepts are hardly applicable in apomictic groups. Information on reproductive systems, phenetic and ecological differentation, and evolutionary traits favour an "agamospecies" concept. It is argued that agamic lineages in goldilocks can be treated neither as subspecific taxa, nor as hybrids.

A general viewpoint is proposed that species are stable phases within a continuous process of diversification of ancestral-descendent lineages. Constancy of progeny, similarity of phenotype, and ecogeographical niches of organisms are regarded as the most important operational criteria for grouping and ranking of species. Mode of reproduction is seen as a feature of a species – not as a criterion for its definition. Internal stability of features is regarded as more important for species definition than the features themselves.

Introduction

Despite many years of research and discussion on agamic complexes, they still challenge us to recognize taxa and to formally rank them within our hierarchical system. Generally employed species concepts are designed for application with "standard" sexual species, and treat agamic taxa as exceptional cases. Agamic complexes are regarded as a task for specialists, who are normally fully occupied in finding solutions for their special apomictic group; therefore, even between agamic complexes in different genera, (e.g., *Alchemilla* L., *Hieracium* L., *Poa pratensis* L., *Rubus* L., *Ranunculus auricomus* complex, *Taraxacum* WEBER ex F.H. WIGG.) different approaches to classifying species have been utilized. The special treatment of each agamic complex and the lack of equivalence of asexual and sexual species continue to cause troubles to define taxa for comprehensive biodiversity research, especially in floras and conservation biology. It seems worthwhile once again, therefore, to discuss general theoretical approaches to defining species in agamic complexes, and to test their practicability by examining one agamic group in detail.

The *Ranunculus auricomus* complex is a suitable example for analyzing different species concepts. As a consequence of recent progress in research within the *R. auricomus* complex, an "agamospecies concept" has been accepted both by Central and Northern European taxonomists (ERICSSON 1992, HÖRANDL & GUTERMANN 1998a,b,c,d). Approximately 750–800 microspecies have been described in the *R. auricomus* complex (goldilocks), only a handful of them reproducing sexually, and outnumbering all other 600 species in *Ranunculus* L. (in the sense of TAMURA 1995, incl. *Ficaria* HALLER, *Batrachium* (DC.) GRAY and *Casalea* ST. HIL.). Specific arguments for the agamospecies concept in goldilocks have already been discussed in HÖRANDL & GUTERMANN (1998a). Here I compare more broadly the theoretical applicability of different current species concepts in the *R. auricomus* complex (following the species concept classification of MISHLER & BUDD 1990) and demonstrate resulting logical and practical problems. I examine whether current species concepts in the *R. auricomus* complex fulfil the requirements of MAYDEN (1997; see also HULL 1997, GORNALL 1997) for theoretical significance, generality, operationality and applicability. Although the literature is overcrowded with contributions to species concepts (for recent comprehensive surveys see, e.g., STUESSY 1990, CLARIDGE et al. 1997a), I want to add the principle viewpoint of my own classification in the hope to stimulate further discussion on a more comprehensive definition of species.

Reproductive modes in *Ranunculus* and limitations of biological species concepts (BSCs)

Amphimixis, agamospermy and vegetative propagation are the main modes of reproduction in goldilocks; autogamy has not been observed yet. *Ranunculus auricomus* agamospecies are predominantly tetraploid and aposporous (pseudogamous), with parthenogenetic development of the unreduced embryo sac resulting in maternal offspring (HÄFLIGER 1943, RUTISHAUSER 1954a,b, ROUSI 1956, NOGLER 1971–1995). Apospory is controlled and inherited by an allele A- which is simultaneously a recessive lethal factor (NOGLER 1984). Therefore, agamospecies are always heterozygous in A+A- and polyploid, because diploid (dihaploid) apomicts would be unable to inherit the apospory factor by monoploid gametes (A-). On the other hand, sexual reproduction has been shown not only in diploid, but also in polyploid taxa (MASCI et al. 1994, HÖRANDL 1998, HÖRANDL et al. 1998, HÖRANDL & SVOMA, in prep.) and is to be expected to exist in the other 2-3 known diploid taxa. Vegetative propagation through rhizome divisions occurs both in sexual and apomictic populations (HÖRANDL, unpubl.).

Recombination in goldilocks may result from facultative development of reduced embryo sacs or from facultative cross-fertilization (pollen is normally reduced by meiosis and is at least partly fertile). Allozyme-isozyme studies in Italian and Austrian natural populations indicate low to no genotypic variation and therefore high constancy and stabilization of apomixis (MASCI et al. 1994, HÖRANDL et al. 1998). Increased proportions of heterozygotes within apomictic clones and fixed heterozygosity in several loci confirm the hypothesis of hybrid origin (HÖRANDL et al. 1998). Recent hybridization between diploids and tetraploids can be regarded as exceptional events (VUILLEMIN 1992, HÖRANDL et al. 1998). As sexual reproduction has been also found in tetraploid populations, polyploidization and hybridization at the tetraploid level may play an important role in speciation processes within the *R. auricomus* complex, as suggested previously by MARKLUND & ROUSI (1961).

Is it justified to classify both sexual taxa and apomictic lineages as species? Comparing goldilocks to other species of the genus, mode of reproduction is unacceptable as a general criterion for classification: apomictic taxa of *R. kuepferi* GREUTER et BURDET and *R. parnassiifolius* L. are separated geographically, but hardly distinguishable morphologically, and have been therefore treated as subspecies (HUBER 1988, KÜPFER 1975). In *R. ficaria* L., vegetatively propagating polyploids with morphological and ecological differentiation are treated variously as species, subspecies, or varieties. Sexual taxa in the genus are normally treated as species, even if only slightly morphologically distinct as in polyploid complexes (e.g. in the *R. montanus* group), and even with high tendencies to hybridization, where hybrids may be sterile to totally fertile (e.g. in *Ranunculus* subgen. *Batrachium* (DC.) A. GRAY; COOK 1966; or in *R.* sect. *Aconitifolii* s.l.; HUBER 1988). Autogamy has been reported mainly from members of subgen. *Batrachium*, but also from other species (*R. lingua* L., *R. repens* L.). High levels of self-compatibility in alpine species of Australia, New Zealand and America (PICKERING 1997) indicate that autogamy can develop under extreme environmental conditions at high altitudes. It is obvious from these examples that the mode of reproduction causes different kinds of "biological species" within the genus and sometimes within the same taxonomic species.

According to criteria embodied within the "biological species concept" (BSC; e.g. MAYR 1942, DOBZHANSKY 1970), namely reproductive isolation of interbreeding populations, species in agamic complexes species cannot be defined. These criteria, by definition, exclude asexual organisms; even the *R. auricomus* complex as a whole cannot be regarded as a species under these criteria. As exemplified in the genus *Ranunculus* and outlined in generally by GRANT (1971), random mating is an idealized condition useful as a standard of reference, but several deviations from random cross-fertilization exist in plants: vicinism (sexual, biparental), autogamy (sexual, mainly uniparental), vegetative propagation (asexual, uniparental), and agamospermy (asexual, mainly uniparental). Reproductive mode and breeding system, as the most important operational factors of the BSC, are methodologically problematic, as discussed by JONSELL (1984), and may vary under different environmental conditions even within the same taxon. Consequently, the BSC is neither universal nor fully operational, and is moreover not necessarily equivalent to evolutionary or phylogenetic units (CRACRAFT 1997). Because of these disadvantages, the BSC and related concepts primarily based on gene flow (e.g. the recognition species concept, PATERSON 1985, 1993, LAMBERT & SPENCER 1995) are not accepted as a universal or primary concept by numerous authors, and several alternative concepts have been proposed (see reviews and discussions in MAYDEN 1997, CLARIDGE et al. 1997b, MISHLER & BUDD 1990, CRACRAFT 1989).

Morphological variation in goldilocks demonstrate problems of phenetic species concepts (PhSCs) in apomictic groups

Within the *R. auricomus* complex, morphological differentiation is striking, which prompted taxonomists early to distinguish specific and subspecific taxa. *Ranunculus cassubicus* and *R. auricomus*, described in Linnaeus' Species plantarum (1753), represent two distinct morphological nuclei within the complex. Increasing knowledge of variability and also intermediate morphotypes resulted in the description of more and more species. MARKLUND (1961, 1965) proposed a concept of four morphologically distinct "main species" (*R. cassubicus* L., *R. monophyllus* OVCZ., *R. fallax* (WIMM. et GRAB.) SLOBODA, and *R. auricomus* L., s.str.) and classified distinguishable agamic lineages from Northern Europe as subspecies under one of the main species. With the increasing knowledge of agamic taxa, this concept proved unsatisfactory due to the discovery of several morphologically intermediate taxa between those "main species"; ERICSSON (1992) treated 615 former Fennoscandian subspecies as separate species and regarded the four "main species" as mere morphological grades. HÖRANDL & GUTERMANN (1998a) preferred to treat the "main species" as four provisional "collective groups", each of them including groups of morphologically similar agamospecies. Because of unclear relationships within the complex, the collective groups are admittedly artificial and upheld mainly for practical reasons; the species level is applied on agamic lineages with distinct morphological and ecogeographical features. As some taxonomists critisize the use of this "microspecies concept", it is useful to review critically some underlying concepts.

Goldilocks provide several differential characters in habit, leaf shape, flower size, torus and nutlets. The basal leaves develop in peculiar leaf "sequences" (especially in the *R. auricomus* coll. group): ternate leaves are formed first during the bud stage, followed by pedate or multisect leaves during the flowering period and finally by ternate or undivided leaves in fruiting (BORCHERS-KOLB 1983, 1985, HÖRANDL & GUTERMANN 1995, 1998a,b,c, 1999). Similar leaf sequences can be seen also in other groups of the genus, e. g. in the *R. polyanthemos* group, but with less dramatic differences in the degree of leaf division and shape. Moreover, not all leaves of a sequence can be seen within one individual; under unfavourable environmental conditions, one plant may produce arbitrarily only one or two leaves of the sequence. The result of this peculiar leaf development is that several morphologically different individuals may exist within one clone at the same time; taxonomists working from single herbarium specimens have sometimes described individuals of one clone as different species. A careful evaluation of constant characters within and between population samples can reduce the number of species. But the question remains – is the number of distinguishable species only a function of possible character combinations? The distinct ecology and distribution of most of the better-known agamospecies confirm them as natural phenomena, but the theoretical problem of the phenetic species concept remains.

When we compare goldilocks with the rest of the genus, other problems emerge. The morphological distinctness between members of the *R. auricomus* complex, e.g. between *R. cassubicifolius* W. KOCH and *R. argoviensis* W. KOCH, *R. melzeri* HÖRANDL et GUTERMANN and *R. udicola* HÖRANDL et GUTERMANN (HÖRANDL & GUTERMANN 1998c,d) can be much larger than between other good and commonly accepted sexual species of the genus (e.g. *R. aconitifolius* L. and *R. platanifolius* L.) or even between less closely related species such as *R. acris* L. and *R. polyanthemos* L. Moreover, this differentiation can be seen not only in organs with a large modificative variation (e.g. leaf shape), but also in stable characters used for classification within the genus (e.g. torus and nutlets). These stable diagnostic features separate the sexual species of the *R. auricomus* complex, following STEBBIN's (1950) recommendation for defining agamospecies. A phenetic species concept based on morphological differentiation **has** to be considered in the *Ranunculus auricomus* complex, otherwise we would ruin the phenetic concept for the genus.

It is obvious that a phenetic concept based on morphology only will be unsuccessful in apomictic groups with only few characters, e.g. in grasses, and also will not allow the comparison of agamospecies from different genera. Even in sexual plants, a strictly comparative phenetic species is imprecise among different genera or families. The more morphological differentiation at higher taxonomic levels is increasing, the more problematic are phenotypic concepts based on morphological characters.

Other phenetic data, like karyotypes and DNA content, reflect the main infrageneric relationships in *Ranunculus* (GOEPFERT 1974, D'OVIDIO & MARCHI 1990), but they are less helpful at the inter- and infraspecific level. Molecular markers, e.g. isozyme-allozyme patterns, provide more precise comparative measures of variation and have been proved to be useful as measures of relative distinctness (CRAWFORD 1983); they may also help to reveal evolutionary processes (e.g. allopolyploidy) and give estimated times of divergence of taxa.

DNA sequence variation is now regarded as one of the most reliable approaches for reconstructing phylogenetic relationships, but the main disadvantage in apomictic groups is the limited number of markers available for evolutionary young taxa, plus methodological problems connected with polyploidy (see e.g. STACE et al. 1997). Evolution of certain genomic regions may be divergent from, and not necessarily correlated with evolution of morphological characters or even with speciation itself. Molecular markers, therefore, cannot be viewed as a substitute for phenetic systems based on morphology.

The main problem of phenetic species concepts is, therefore, the lack of a theoretical background for species delimitation: however, it is still the easiest and most operational concept in practice. The danger of phenetic concepts in apomicts, as exemplified in goldilocks, is the lack of objective criteria to avoid endless splitting, which can theoretically lead to treating each single clone as a separate species. The use of phenetic concepts in apomictic groups, therefore, cannot be used in isolation; they require additional criteria and viewpoints of species.

Evolutionary and ecological traits in goldilocks – arguments for agamic lineages as the basic unit

A short review of present ecogeographical patterns and a hypothetical outline of evolutionary patterns in goldilocks may illustrate the main evolutionary traits. Most agamic lineages may have originated from sexual ancestral species as hybrids which have been stabilized by polyploidy and escaped from sterility by apospory (Fig. 1, 2). During the last glacial periods, apospory may have conferred selective advantages, whereas several sexual ancestral species of the complex may have become extinct. The occurrence of geographically separated cytodemes of the sexual species *R. cassubicifolius* (HÖRANDL et al. 1997) indicates that geographic isolation and allopatric differentiation may also play a role in speciation within this group (symbolized in Fig. 1 by separation of two lines in the sexual species).

Within the collective groups, different traits can be seen: representatives of the Central- to eastern-European *R. cassubicus* coll. group inhabit temperate deciduous forest communities alongside climax vegetation, which might have been stable for long periods. This group is the most homogeneous in morphology, distribution and habitat, but diverse in ploidy levels. The arctic-alpine *R. monophyllus* collective group might be interpreted as having split geographically during the last glacial periods in disjunct agamic lineages with some relicts in the Alps. In the mountains of southern Europe, a few presumably sexual species can be found in high montane to alpine habitats in very restricted areas, which have not necessarily resulted from the same evolutionary process as the arctic-alpine species. Members of the *R. fallax* collective group, morphologically intermediate between the *R. cassubicus*- and *R. auricomus* collective groups, inhabit warm forest communities mainly in the Pannonian area. The concentration of *R. auricomus* members with deeply divided basal leaves in western Europe, the eastern center of the *R. cassubicus* complex and the main occurrence of intermediate *R. fallax* types in the geographically intermediate Pannonian region support a hypothesis that the *R. fallax* agamospecies are products of a large hybridization zone over Central Europe; but it is also possible, however, that an eastern European ancestor with mainly undivided leaves developed into two main lines, the present *R. cassubicus* and *R. fallax* collective groups. Within the *R. auricomus* collective group we find agamospecies scattered in wet forest communities such as swamps, alluvial forests, etc., i.e. habitats that have been widespread during the postglacial periods and provided the opportunities for distribution of

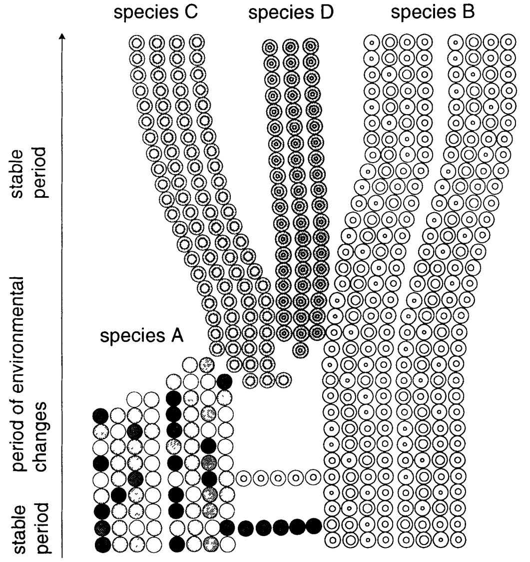

Fig. 1. Hypothetic model for the phylogeny and evolution of microspecies in *R. auricomus*, from the perspective to see species as a community of individual organisms (circles). Shading and internal circles refer to constancy and variation of genotypes (e.g., as it can be seen in electrophoretic or morphological phenotypes). In sexual species, constancy of progeny is maintained by interbreeding (here only symbolized generally as "random mating" without regard for true Mendelian ratios), in apomictic species by asexual reproduction.

the complex throughout temperate and boreal Europe. With the retreat of wet habitats, large distributional areas may have been lost or split, which could explain the present small and disjunct distribution of agamospecies specialized for wet forest habitats. On the other hand, the development of agriculture has provided new habitats for agamic lineages, mainly in meadows, where goldilocks have been enormously successful in recovering area. In Nordic countries, several agamospecies have an even stronger tendency to tolerate disturbed ruderal habitats. Most agamospecies of the *R. auricomus* collective group grow in anthropogenous habitats, show high phenotypic plasticity, a rather weak morphological differentiation compared to "forest-species" and low genetic distances between populations (HÖRANDL 1998, HÖRANDL et al. 1998), all features that suggest a recent origin. It is obvious from this hypothetical outline, that the complex as a whole, or even the collective groups, can hardly be considered products of the same evolutionary processes. Agamic lineages are likely to be of different ages, to have different evolutionary fates, and to have established in very different and specific ecological niches.

Evolutionary species concepts (ESCs) as proposed by SIMPSON (1961) and WILEY (1978) avoid the problems associated with interbreeding and hybridization and are therefore applicable also to uniparentally reproducing plants. As exemplified above, agamic lineages may represent basic evolutionary units in goldilocks, but the criteria of ESCs may be also fulfilled by single clones. The inclusion of a separate ecological niche (VAN VALEN 1976) as a criterion is helpful for grouping apomictic plants, but it does not solve the problem of ranking.

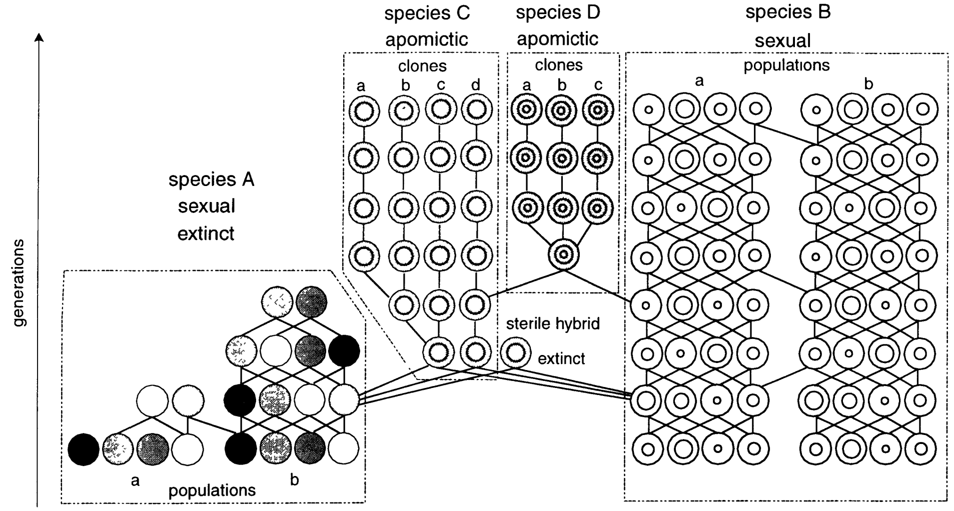

Fig. 2. Inset detail of Fig. 1, presenting different modes of internal reproductive coherence in apomictic and sexual species. In apomictic species, clones provide parallel constant progeny, but are also a historical reproductive community. Even though the "extinct sterile hybrid" is a member of the ancestral community, it is not included within one of the species, because it has become extinct after one generation.

WEBER (1981) proposed a pragmatic concept of using the absolute size of distribution areas for defining practicable species among thousands of phenetically different lineages in *Rubus*. The concept is completely dependent on prior morphological determinations, and also correlates size of distribution with evolutionary age. In goldilocks, a small distributional area may result from different factors (as outlined above) and does not necessarily reflect the age of the species nor the process of speciation. Weber's concept has, therefore, a weak theoretical background and is not universally applicable even in apomictic groups. In my opinion, it is not the absolute size of the distribution area, but the homogeneity of ecological features within a certain phytogeographical region which is useful for the definition of agamospecies. This criterion should be used as a biogeographical control of the underlying phenetic concept.

A theoretically very elaborate alternative was proposed by TEMPLETON (1989). His species are based on cohesive mechanisms (genetic and demographic exchangability), and his concept includes extremes of reproductive systems, asexuality and hybridization, where biological species concepts fail. His concept focuses on evolutionary mechanisms at the populational level, and on groups of "cohesive clones" in asexual groups. The disadvantage of his concept is that it is based mainly on processes and not on patterns. The theoretical problems of linking processes and patterns in species concepts have been already discussed by several authors (e.g. CHANDLER & GROMKO 1989, LIDÉN & OXELMAN 1989, SLUYS 1991). At a practical level, process-related concepts are very difficult to apply practically, because we rarely know details of evolutionary processes; in specific groups hence, species delimitation may be even more speculative and subjective than in pattern-related concepts.

Phylogeny in the *R. auricomus* complex and the application of phylogenetic species concepts (PSCs)

On which level can we find monophyletic groups in goldilocks? As discussed above, the whole *R. auricomus* complex may be regarded as of hybrid origin and composed of fixed agamic lineages. The striking morphological differences and the scattered distribution of the present sexual species indicate that the complex has neither a single common ancestor species nor a geographical center of origin; it is not even clear whether the present sexual species are really very closely related. For the whole complex, monophyly is questionable and therefore, treating the whole complex as a single species must be rejected. Also, at the level of collective groups or "main species", monophyly may be expected only in the rather homogeneous *R. cassubicus* coll. group; for the other three collective groups, polyphyletic origins are to be expected based on present morphological and chorological patterns. The species level cannot be applied here either, as already pointed out earlier by ERICSSON (1992).

Agamic lineages in goldilocks are fixed without remarkable degrees of hybridization and fulfil a monophyletic criterion. As lineages may arise from single individuals, endless splitting may be the consequence of a strictly applied phylogenetic species concept.

As discussed by MISHLER & BUDD (1990), phylogenetic species concepts (PSCs) are applicable both to sexual and asexual organisms. Monophyly of lineages as the main grouping component may be even more strict in agamic than in sexual organisms. Because of tokogenetic patterns (i.e. reticulate descent relationship among sexually reproducing individuals) in sexual species, some authors reject applying the term monophyletic to single species and use it only for groups of species (DAVIS 1996, 1997). Besides the theoretical problem of challenging the universality of PSCs, ranking remains the open question in agamic complexes. MISHLER & BUDD (1990) emphasize the "importance" of processes that produce and maintain lineages. As we have scant information about speciation processes in agamic lineages, this criterion will be less than helpful in practice.

The PSC of CRACRAFT (1983) puts more emphasis on diagnosibility of parent-descendent clusters of organisms. In this genealogical viewpoint we can assume that a group of clones, which are morphologically similar and have established themselves in a similar ecological and chorological niche, has a common ancestor and can be therefore classified as one species. CRACRAFT (1997) points out the advantages of his concept in conservation biology against the BSC and ESC, which may be another important argument for PSCs in apomictic plants.

Are there any alternatives to the agamospecies concept in the *R. auricomus* complex?

At least some criteria for recognition of species are partly fulfilled by groups of agamic clones in *R. auricomus*. They have distinct phenotypical, ecogeographical features and constant progeny, comparable to their sexual relatives within the complex. They fit theoretically into phylogenetic or evolutionary concepts; biological species concepts are not applicable as in other uniparental reproducing organisms. Agamic lineages of goldilocks may be classified as "microspecies" in the sense of GRANT (1971), representing comparative phenetic and ecological units within the complex. Do we really have an alternative to this concept? The *R. auricomus* complex as a whole, or even the collective groups, do not fulfil one of the criteria mentioned above – they are not natural taxa. Therefore, agamic lineages cannot be classified as forms, nor as varieties, nor as subspecies, because every subspecific taxon has to belong to a species, which does not exist above the agamic lineages. They likewise cannot be classified as hybrids, because their mode of origin and parental species are not known in most cases. Consequently, the *R. auricomus* complex **cannot be classified at all** (except the few sexual representatives) if we reject the "microspecies" level. Definition of provisional units, e.g. aggregates in the sense of EHRENDORFER (1973), or the collective groups in the sense of HÖRANDL & GUTERMANN (1998a), may provide some temporary help for research, but a system that requires an excessive and constant use of provisional units is not universal and challenges the value of taxonomy itself. Considering the wide distribution and abundance of the whole complex and similar situations in other apomictic groups, the non-classification of apomictic plants would admit a general failure of our taxonomic system.

Such a microspecies concept is necessarily more pattern-related than process-related, which has some advantages for classification. Different processes of speciation will necessarily cause different patterns. If taxonomy should both reflect evolutionary processes and provide comparative units, we would consequently need separate categories or more ranks within our system for different processes of diversification. Proposals for a parallel system (TURESSON 1929) or additional ranks for different biosystematic units (e.g. LÖVE 1961) have gained no acceptance. Perhaps this approach would have more appeal in practice if such categories were not directly connected with the present hierarchic classification system (LÖVE 1961), but were only added as additional descriptive features (e.g. as is done with growth forms). Such additional descriptors would provide at least equivalent units for comparative biosystematic studies and for statistical procedures in biodiversity research. If we maintain the present system, inequivalence of species seems inevitable. MISHLER & DONOGHUE (1982) regard species concepts as a case for pluralism; ENDLER (1989) points out conflicts resulting from different demands on species concepts, and proposes using the best fitting concept for the particular research question and the group involved.

Proposal of a comprehensive species concept

Is it really impossible to formulate a species concept applicable to all organisms? By combining the main features of current species concepts, I suggest the following: "A species consists of 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".

This perspective, starting from the organisms, is only superficially similar to the "species-as-individual" concept proposed by HULL (1976). I definitely reject viewing species as "individuals" or "superorganisms". In addition to the arguments of STUESSY (1990) and RUSE (1992) against this concept, I point out that organisms are individuals because they have an essential internal **functional** coherence of different parts (organs), which does not pertain among members of a species. The relation of an organ to an organism is definitely not the same as the relation of an organism to its species. A species may be viewed as a community of individual organisms (including previous and forthcoming generations) held together mainly by reproductive phenomena, but not as an individual itself.

The advantage of the formulation above is that it is theoretically grounded on existing natural phenomena (organisms, lineages and evolutionary processes) and it is operationally explicit through easily diagnosable elements (constancy of progeny, similarity of phenotype and ecogeographical unity). The species is seen as a diagnosable phase or segment of (temporal) constancy within a continuous diversification process of lineages. The viewpoint above includes also the main elements required for a species concept by CRACRAFT (1997) – reproductive cohesion, diagnosibility and ranking components are provided by constancy of progeny, similarity of phenotype and ecogeographical niche.

In the formulation above, emphasis is placed on the internal constancy of features within a species, rather than on the features themselves. Constancy of progeny includes both biparental and uniparental reproduction; it is not important how this constancy is acquired. In the case of biparental reproduction, individuals constitute populations which can be regarded as an organizational level that guarantees reproduction within a sexual species. Hybridization of members of one species with members of another does not affect the value of the species, as long as the species (or at least the main part of it) succeeds into bringing up its own progeny; from this viewpoint we can still define species in extensive hybridizing genera like *Salix* L., *Quercus* L., etc., which some authors even have regarded as "syngamea" (GRANT 1957) or "multispecies" (VAN VALEN 1976), because other species definitions have failed. In uniparental reproduction, constancy can be upheld even by a single individual which may constitute a clone. Normally groups of clones have a similarity of phenotype and ecogeographical unity, and hence they do have a historical reproductive coherence; so we avoid classifying each individual as a species by applying the species level to groups of phenotypically and ecologically similar clones. Primary hybrids can be easily excluded, but hybridogenous lineages may be accepted as a separate species if they succeed in reproducing and establishing themselves. In this way, mode of reproduction can be seen as a feature of a species, and not a criterion for its definition.

Internal similarity of phenotypes is a product of coherence of reproduction. In my opinion, internal similarity and constancy of characters are more important for defining species than "gaps" between them. In species with high phenotypic plasticity, e.g. *Draba* or *Salix*, the range of variability of species will always overlap with another species (even without hybridization!); it is impossible to find a "gap" or even a "borderline" between reproductively isolated and commonly accepted species, but only some "distinctness". A practical and well-known consequence of this phenomenon is, that such species can be rather easily recognized by an experienced botanist in the field, and supported by statistical data, although it seems sometimes impossible to write a workable dichotomous key. To avoid endless and impracticable splitting into microspecies in apomictic groups like goldilocks, it is much more important to stress the similarity of clones than the distinctness between them.

Ecogeographical unity (a certain ecological niche within a certain distribution area) is evidence for the successful establishment of a species and for its acceptance as an evolutionary lineage. In animals, ethological unity can be added as another important criterion for the definition of taxa (DEBEACH 1969). Ecology and distribution may also reflect the evolutionary processes from which the species resulted (e.g. allopatric speciation). Normally not the whole species, but only a part of it (some populations), is the starting point for evolution. Speciation can be explained as the development of genetic barriers between populations, and through species evolutionary progress can be maintained (FUTUYMA 1990: 248). One of the main problems for taxonomic classification is that populations cannot be referred directly to a category within our taxonomic system which therefore lacks a distinctive basic "evolutionary unit". CRACRAFT (1997) has pointed out the disadvantage of the practical use of evolutionary significant units, because they lack appropriate status within the formal taxonomic system. He stresses instead the use of phylogenetic species in practical applications, such as in conservation biology.

If within a species phenotypic and ecogeographical variation shows constant discontinuities, which are less important than the internal similarity of the species, a species may be subdivided into subspecies. A subspecies can also be viewed as a stage in the process of evolutionary divergence which has not yet reached complete isolation (GRANT 1971). In biparental reproducing species, interfertility can still be used as an important criterion to decide whether specific or subspecific rank should be applied; in uniparental reproducing taxa, subspecific units have only weak operational criteria and should therefore be avoided if the species to which they belong cannot be well defined. Autogamous lineages, which are in a way "reduced forms" of a species, sometimes fit better into a subspecific concept than apomictic lineages of hybrid origin. Species can be differentiated from higher taxa because members of genera, etc. are not reproductive communities, they have less similar phenotypes and often rather distinct ecological and geographical features. Higher taxa are groups of species linked by genealogy, but not "biological" units (in the original wide sense of the word).

From this perspective, using different features for classification in various situations would at least cause fewer logical problems, because it is not the feature itself, but its internal stability and constancy which would be the main criterion for grouping and ranking. Reproductive isolation would be permitted as a criterion for classifying sexual species, and it would be acceptable to stress more on phenotypical and ecological features in apomicts or autogamous lineages, as long as they are constant. In practice, the situation is no easier, because the main feature for delimiting species is still morphology, and the definition of "similarity" remains subjective to a high degree. Recognition of internal constancy of features requires knowledge about a broad range of variation within species, which consumes much more effort than simply locating "distinctness" between taxa. At least this perspective does force us to work as comprehensively as possible, which can only be the most desirable approach for practical work.

Acknowledgements: I am indebted to Walter Gutermann for stimulating this work, and to Franz Hadaček and Götz H. Loos for critical remarks on earlier versions of the manuscript. I wish to thank Tod F. Stuessy for literature advice, several valuable comments on the manuscript, and for correcting my English. Financial support from the Austrian Research Foundation (FWF), project no. P12156-Bio, is gratefully acknowledged.

REFERENCES

BORCHERS-KOLB E. (1983): *Ranunculus* sect. *Auricomus* in Bayern und den angrenzenden Gebieten. I. Allgemeiner Teil. *Mitt. Bot. Staatssamml. München* 19: 363–429.

BORCHERS-KOLB E. (1985): *Ranunculus* sect. *Auricomus* in Bayern und den angrenzenden Gebieten. II. Spezieller Teil. *Mitt. Bot. Staatssamml. München* 21: 49–300.

CHANDLER C.R. & GROMKO M.H. (1989): On the relationships between species concepts and speciation process. *Syst. Zool.* 38: 116–125.

CLARIDGE M.F., DAWAH H.A. & WILSON M.R. (eds.) (1997a): *Species. The units of biodiversity.* Chapman & Hall, London.

CLARIDGE M.F., DAWAH H.A. & WILSON M.R. (1997b): Practical approaches to species concepts for living organisms. In: CLARIDGE M.F., DAWAH H.A. & WILSON M.R. (eds.), *Species. The units of biodiversity,* Chapman & Hall, London, pp. 1–15.

COOK C.D.K. (1966): A monographic study of *Ranunculus* subgenus *Batrachium* (DC.) A. GRAY. *Mitt. Bot. Staatssamml. München* 6: 47–237.

CRACRAFT J. (1983): Species concept and speciation analysis. *Curr. Ornith.* 1: 159–187.

CRACRAFT J. (1989): Speciation and its ontology. In: OTTE D. & ENDLER J.A. (eds.), *Speciation and its consequences,* Sinauer Ass., Sunderland, pp. 28–59.

CRACRAFT J. (1997): Species concepts in systematics and conservation biology – an ornithological viewpoint. In: CLARIDGE M.F., DAWAH H.A. & WILSON M.R. (eds.), *Species. The units of biodiversity,* Chapman & Hall, London, pp. 325–339.

CRAWFORD D.J. (1983): Phylogenetic and systematic inferences from electrophoretic studies. In: TANKSLEY S.D. & ORTON T.J. (eds.), *Isozymes in plant genetics and breeding,* Elsevier, Amsterdam, pp. 257–287.

D'OVIDIO R. & MARCHI P. (1990): DNA content, karyotype structure analysis and karyotype symmetry in *Ranunculus* L. (*Ranunculaceae*). Italian species belonging to sections *Flammula* (WEBB) BENSON and *Micranthus* (OVCZ.) NYARADY. *Caryologia* 43: 99–115.

DAVIS J.I. (1996): Phylogenetics, molecular variation, and species concepts. *BioScience* 46: 502–511.

DAVIS J.I. (1997): Evolution, evidence and the role of species concepts in phylogenetics. *Syst. Bot.* 22: 373–403.

DE BEACH P. (1969): Uniparental, sibling and semi-species in relation to taxonomy and biological control. *Israel J. Entomol.* 4: 11–28.

DOBZHANSKY T. (1970): *Genetics of the evolutionary process.* Columbia University Press, New York.

EHRENDORFER F. (ed.) (1973): *Liste der Gefässpflanzen Mitteleuropas.* Ed. 2 (bearbeitet von W. GUTERMANN et al.). Gustav Fischer Verlag, Stuttgart.

ENDLER J.A. (1989): Conceptual and other problems in speciation. In: OTTE D. & ENDLER J.A. (eds.), *Speciation and its consequences,* Sinauer Ass., Sunderland, pp. 625–648.

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

FUTUYMA D.J. (1990): *Evolutionsbiologie.* Birkhäuser, Basel.

GOEPFERT D. (1974): Karyotypes and DNA content in species of *Ranunculus* L. and related genera. *Bot. Not.* 127: 464–489.

GORNALL R.J. (1997): Practical aspects of the species concept in plants. In: CLARIDGE M.F., DAWAH H.A. & WILSON M.R. (eds.), *Species. The units of biodiversity,* Chapman & Hall, London, pp. 171–190.

GRANT V. (1957): The plant species in theory and practice. In: MAYR E. (ed.), *The species problem,* Amer. Assoc. Adv. Sci., Washington,

GRANT V. (1971): *Plant speciation.* Columbia University Press, New York & London.

HÄFLIGER E. (1943): Zytologisch-embryologische Untersuchungen pseudogamer Ranunkeln der *Auricomus*-Gruppe. *Ber. Schweiz. Bot. Ges.* 53: 317–379.

HÖRANDL E. (1998): Isozyme variation within the apomictic *Ranunculus auricomus* complex: evidence for another sexual progenitor species in southeastern Austria. *Bot. Acta* (in press).

HÖRANDL E. & GUTERMANN W. (1995): Die Bearbeitung der *Ranunculus auricomus*-Gruppe für die "Flora von Österreich" – ein Werkstattbericht. *Fl. Austriae. Novit.* 2: 12–27.

HÖRANDL E. & GUTERMANN W. (1998a): Der *Ranunculus auricomus*-Komplex in Österreich. 1. Methodik; Gruppierung der mitteleuropäischen Sippen. *Bot. Jahrb. Syst.* 120: 1–44.

HÖRANDL E. & GUTERMANN W. (1998b): Zur Kenntnis des *Ranunculus auricomus*-Komplexes in Österreich: Die Arten der *R. phragmiteti-* und *R. indecorus*-Gruppe. *Phyton (Horn, Austria)* 37: 263–320.

HÖRANDL E. & GUTERMANN W. (1998c): Der *Ranunculus auricomus*-Komplex in Österreich. 2. Die *R. cassubicus-, R. monophyllus-* und *R. fallax*-Sammelgruppe. *Bot. Jahrb. Syst.* 120 (in press).

HÖRANDL E. & GUTERMANN W. (1998d): Der *Ranunculus auricomus*-Komplex in Österreich. 3. Die Arten der *R. latisectus-, R. puberulus-, stricticaulis-* und *R. argoviensis*-Gruppe (*R. auricomus*-Sammelgruppe). *Bot. Jahrb. Syst.* 121 (in press).

HÖRANDL E., DOBEŠ C. & LAMBROU M. (1997): Chromosomen- und Pollenuntersuchungen an österreichischen Arten des apomiktischen *Ranunculus auricomus*-Komplexes. *Bot. Helv.* 107: 195–209.

HÖRANDL E., JAKUBOWSKY G. & DOBEŠ C. (1998): Genetic variation, morphological and ecological differentiation in apomictic and sexual taxa of the *Ranunculus auricomus* complex. In: WERKER N. & VAN RENNEN G.B.A. (eds.), IOPB VIIth International Symposium "Plant Evolution in man-made habitats" August 10–15, 1988, *IOPB Newsletter Special Issue*: 44–45.

HUBER W. (1988): Natürliche Bastardierungen zwischen weißblühenden *Ranunculus*-Arten in den Alpen. *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* 100: 1–160.

HULL D.L. (1976): Are species really individuals? *Syst. Zool.* 25: 174–191.

HULL D.L. (1997): The ideal species concept – and why we can't get it. In: CLARIDGE M.F., DAWAH H.A. & WILSON M.R. (eds.), *Species. The units of biodiversity,* Chapman & Hall, London, pp. 357–380.

JONSELL B. (1984): The biological species concept reexamined. In: GRANT W.F. (ed.), *Plant biosystematics,* Academic Press Canada, Toronto, pp. 159–177.

Kupfer P. (1974): Recherches sur les liens de parent entre la flore orophile des Alpes et celle des Pyrenées. *Boissiera* 23: 1–322.

Lambert D. M. & Spencer H. G. (eds.) (1995): *Speciation and the recognition concept: theory and application.* John Hopkins University Press, Baltimore.

Lidén M. & Oxelman B. (1989): Species – patterns or process? *Taxon* 38: 228–232.

Love A. (1961): Biosystematics and classification of apomicts. *Feddes Repert.* 63: 136–148.

Marklund G. (1961): Der *Ranunculus auricomus*-Komplex in Finnland. I. Diagnosen und Fundortslisten einiger Sippen des *R. auricomus* L. coll. (s. str.). *Fl. Fenn.* 3: 1–128.

Marklund G. (1965): Der *Ranunculus auricomus*-Komplex in Finnland. II. Diagnosen und Fundortslisten einiger Sippen von *R. fallax* (W. & Gr.) Schur, *R. monophyllus* Ovcz. und *R. cassubicus* L. *Fl. Fenn.* 4: 1–104.

Marklund G. & Rousi A. (1961): Outlines of evolution in the pseudogamous *Ranunculus auricomus* group in Finland. *Evolution* 15: 510–522.

Masci S., Miho A. & Marchi P. (1994): *Ranunculus auricomus* L. aggr. (*Ranunculaceae*) in Italy. I. Sexual tetraploids on the Apennines. *Caryologia* 47: 97–108.

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

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

Mishler B.D. & Budd A.F. (1990): Species and evolution in clonal organisms – introduction. *Syst. Bot.* 15: 79–85.

Mishler B.D. & Donoghue M.J. (1982): Species concepts: a case for pluralism. *Syst. Zool.* 31: 491–503.

Nogler G.A. (1971): Genetik der Aposporie bei *Ranunculus auricomus* s. l. W. Koch: 1. Embryologie. *Ber. Schweiz. Bot. Ges.* 81: 139–179.

Nogler G.A. (1972): Genetik der Aposporie bei *Ranunculus auricomus*: 2. Endospermzytologie. *Ber. Schweiz. Bot. Ges.* 82: 54–63.

Nogler G.A. (1973): Genetik der Aposporie bei *Ranunculus auriciomus*. 3. F2-Rückkreuzungsbastarde. *Ber. Schweiz. Bot. Ges.* 83: 295–305.

Nogler G.A. (1982): How to obtain diploid apomictic *Ranunculus auricomus* plants not found in the wild state. *Ber. Schweiz. Bot. Ges.* 92: 13–22.

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

Nogler G.A. (1995): Genetics of apomixis in *Ranunculus auricomus*. 6. Epilogue. *Bot. Helv.* 105: 111–115.

Paterson H.E.H. (1985): The recognition concept of species. In: Vrba E.S. (ed.), *Species and speciation,* Transvaal Museum, Pretoria, pp. 21–29.

Paterson H.E.H. (1993): *Evolution and the recognition concept of species.* Collected writings Hugh E.H. Paterson (McEvey S. F., ed.). The John Hopkins University Press, Baltimore.

Pickering C.M. (1997): Breeding systems of Australian *Ranunculus* in the alpine region. *Nordic J. Bot.* 17: 613–620.

Rousi A. (1956): Cytotaxonomy and reproduction in the apomictic *Ranunculus auricomus* group. *Ann. Bot. Soc. Zool. -Bot. Fenn. Vanamo* 29 (2): 1–64.

Ruse M. (1992): Biological species: natural kinds, individuals, or what? In: Ereshefsky M. (ed.), *The units of evolution: esssays on the nature of species*, Massachusetts Institute of Technology, Massachusetts.

Rutishauser A. (1954a): Die Entwicklungserregung des Endosperms bei pseudogamen Ranunculusarten. *Mitt. Naturf. Ges. Schaffhausen* 25: 1–45.

Rutishauser A. (1954b): Entwicklungserregung der Eizelle bei pseudogamen Arten der Gattung *Ranunculus*. *Bull. Schweiz. Akad. Wiss.* 10: 491–512.

Simpson G.G. (1961): *Principles of animal taxonomy.* Columbia University Press, New York.

Sluys R. (1991): Species concepts, process analysis, and the hierarchy of nature. *Experientia* 47: 1162–1170.

Stace C.A., Gornall R.J. & Shi Y. (1997): Cytological and molecular variation in apomictic *Hieracium* sect. *Alpina*. Opera Botanica 132: 39–51.

Stebbins G.L. (1950): *Variation and evolution in plants.* Columbia University Press, New York.

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

TAMURA M. (1995): *Angiospermae*. Ordnung *Ranunculales*. Fam. *Ranunculaceae*. II. Systematic part. In: HIEPKO P. (ed.), *Natürliche Pflanzenfamilien, ed. 2, 17aIV,* Duncker & Humboldt, Berlin, pp. 223–519.

TEMPLETON A.R. (1989): The meaning of species and speciation: a genetic perspective. In: OTTE D. & ENDLER J.A. (eds.), *Speciation and its consequences,* Sinauer Ass., Sunderland, pp. 3-27.

TURESSON G. (1929): Zur Natur und Begrenzung der Arteinheiten. *Hereditas* 12: 323–334.

VAN VALEN L. (1976): Ecological species, multispecies, and oaks. *Taxon* 25: 233–239.

VUILLEMIN F. (1990): Index des nombres chromosomiques des Spermatophytes de la Suisse: 4. distribution des cytodmes du *Ranunculus auricomus* L. s. l. *Bot. Helv.* 100: 207–223.

VUILLEMIN F. (1992): Origine du sympatrisme des cytotypes du *Ranunculus auricomus* L. s. l.: le cas de la population Mauensee (canton de Lucerne, Suisse). *Bauhinia* 10: 85–90.

WEBER H.E. (1981): Revision der Sektion *Corylifolii* (Gattung *Rubus, Rosaceae*) in Skandinavien und im nördlichen Mitteleuropa. *Sonderb. Naturwiss. Vereins Hamburg* 4: 1–229.

WILEY E.O. (1978): The evolutionary species concept reconsidered. *Syst. Zool.* 27: 17–26.