

## A pragmatic species concept applicable to all eukaryotic organisms independent from their mode of reproduction or evolutionary history

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### Abstract

It is shown that the species concept of Ernst Mayr does not consider the evolution and modes of reproduction of eucaryotic organisms as a whole. It is only translatable into a taxonomic practice in a very special situation: sexually reproducing and sympatrically occurring organisms that do not exchange genes. Mayr's central criterion of reproductive isolation is not applicable to the pervasive cases of reticulate evolution, to numerous groups of organisms with asexual reproduction, to the frequent situations of allopatry and to classification of fossil organisms. Evaluating advantages and disadvantages of five broadly applied species concepts and integrating elements of the related concepts of Sonneborn (1957), Sokal & Crovello (1970) and De Queiroz (2007), a new synthesis, called the Pragmatic Species Concept, is presented: 'A species is a cluster of organisms which passed a threshold of evolutionary divergence. Divergence is determined by one or several operational criteria described by an adequate numerics. A single conclusive operational criterion is sufficient. Conflicts between operational criteria require an evolutionary explanation. Thresholds for each operational criterion are fixed by consensus among the experts of a discipline under the principle of avoiding over-splitting. Clusters must not be the expression of intraspecific polymorphism.' This concept is applicable to all known groups of eukaryotic organisms independent from their mode of reproduction or evolutionary history. It allows both an approach by multi-source integrative taxonomy as well as by a single discipline and is open for integrating new disciplines. The concept enables sound taxonomic decisions also in case of reticulate evolution, parthenogenesis, apomixis, allopatry, separate time horizons and reversal of strong evolutionary divergence. The complex problem could only be solved by focusing on the degree of evolutionary divergence, reproducible numeric data recording, adequate numeric analyses and the threshold principle. Recommendations of how to translate this concept into a taxonomic practice are given.

**Keywords** species concept | reticulate evolution | adaptive introgression | parthenogenetic reproduction | cryptic species | fossil species | cluster analysis

### 1. Introduction – the incomplete reality of species and a critique of Ernst Mayr's concept

The majority of currently recognized species are considered to be more real and delimitable than categories of higher rank such as genera. Yet, opinions on reality of species differ widely: some authors consider species as the only real taxonomic unit (Sudhaus & Rehfeld 1992) while

others even argue that Linnaean binary nomenclature is no longer useful in taxonomy at all (Mishler 1999, Hendry et al. 2000). Whoever is right, there is no doubt that the reality of species is frequently overestimated. There seems to exist no single trait of evolution that can be used universally to decide which groups of organisms have to be considered as the same or separate species. Taxonomists, inevitably, have to find decisions in a very complex matter and they must decide as well when evolution itself has

not found a definite decision in a divergence process or its reversal. To give classification a reasonable logic or operating procedure, taxonomists have developed species concepts from the beginning of the 20<sup>th</sup> century. Each species concept remains a theoretical construct that can hardly depict all facets of a complex reality. A species concept is reasonable if it refers to those phenomena of the real world which are significant from an evolutionary point of view and when its theoretical concept can be translated into to a sound taxonomic working routine. The endpoint of development should be a species concept applicable to all groups of extant and extinct organisms independent from their mode of reproduction or evolutionary history. This is expressed in the vision of Mallet (2013): *‘Yet a unitary definition should be possible if species are more real, objectively definable and fundamental than, say, genera or subspecies. Conversely, even if species have no greater objectivity than other taxa, unitary nominalistic guidelines for delimiting species might be adopted, perhaps after much diplomacy, via international agreement among biologists; after all, if we can adopt meters and kilograms, perhaps we could agree on units of biodiversity in a similar way.’*<sup>1</sup>

The so called ‘Biological’ Species Concept (BSC) of Mayr (1942, 1982) has been the most widely recognized species concept of the 20<sup>th</sup> century and perhaps it continues to be so among many recent zoologists. The versions of the BSC presented by Mayr himself over 40 years begin with *‘Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups’* (Mayr 1942) and end with *‘A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature’* (Mayr 1982). Throughout these 40 years Mayr insisted on his central criterion ‘reproductive isolation’. Yet, a rejection of the BSC was already expressed by Tracy Sonneborn who produced an éclat at the Annual Meeting of the American Society for the Advancement of Science in Atlanta in December 1955 (Sonneborn 1957, Schloegel 1999). Critical or rejecting voices towards the BSC continued to appear afterwards (e.g., Sokal & Crovello 1970, Donoghue 1985, Cracraft 1989). It is obvious that Mayr blinded out large segments of reproduction biology and evolutionary history of big groups of eukaryotic organisms such as protists, invertebrates or vascular plants.

An excellent review of species concepts in general and of their meaning in the practice was presented by Mallet (2013). This paper aims not on reviewing the multitude of existing concepts. It will concentrate on the development

of a new species concept and a particular critique of the BSC. This critique has the following main issues.

### 1.1. Reticulate evolution on the whole-genome and single-gene level

The BSC is not applicable to the pervasive cases of reticulate evolution – i.e., hybridogenous speciation by fusion of whole genomes or by introgressive transfer of few alleles. With 70% of hybridogenous species in some genera, vascular plants are exemplary and the known number of vertebrate and invertebrate animals involved in some form of reticulate evolution is constantly growing (e.g., Abbot et al 2013, Allendorf 1991, Arnold & Martin 2009, Bullini & Nascetti 1990, Cunha et al. 2011, Elgvin et al. 2011, Ertan 2002, Grant & Grant 1996, Hermansen et al. 2011, Mallet 2005, 2008, Mavarez et al. 2006, Phillips 1915, 1921, Schliewen & Klee 2004, Schwarz et al. 2005, Seather et al. 2007, Seifert 1999, 2006, 2010, Seifert et al. 2010, Steiner et al 2012, Streit et al. 1994). In contrast to plants, speciation by genomic fusion is rarely observed in animals. Here, the less spectacular form of reticulate evolution, interspecific transfer of only few alleles, is much more frequent and represents a serious problem for the BSC. A taxonomist considering the term ‘reproductive isolation’ in its genuine meaning of an impenetrable barrier would have to synonymize a very big portion of taxa currently considered by any taxonomist as well-separable species. Exemplary groups are ducks (Phillips 1915, 1921), redstarts (Ertan 2002) or butterflies (Mavárez et al. 2006, Kronforst 2008). In Ernst Mayr’s focal group, the birds, reproductive isolation is built up on average as late as 5 million years after phylogenetic splitting in Passeres and after 17 million years in Nonpasseres – as a rule of thumb after five million generations (Price & Bouvier 2002). This is fully comparable with the situation in other groups of vertebrates. In *Heliconius* butterflies hybrid sterility was not achieved even 30 million generations after phylogenetic separation (Kronforst 2008). F1-hybrids of the majority of related bird species are fertile in backcrosses with a heterozygous partner of a parental species giving way for introgression of heterospecific alleles into either gene pool (Ertan 2002, 2006, Elgvin et al. 2011, Hermansen et al. 2011). This principle applies to all animals with heterogametic sex and has been known for a long time as Haldane’s Rule (Haldane 1922). Adaptive introgression of certain heterospecific alleles became a normal term in evolutionary genetics of Eukaryota (Abbott et al. 2013, Arnold & Martin 2009, Mallet 2005) and whole genome analyses are beginning to tell us in a fascinating way which alleles precisely are transmitted

<sup>1</sup> All literal citations in this paper are given in italics

between species and which functional consequences they cause (e.g. The Heliconius Gene Consortium 2012, Martin et al. 2013). Despite the rarity of hybridization in animals, usually between 0.1 and 2% per mating, calculation models reveal that adaptive introgression after rare hybridization should accelerate evolution by two or three orders of magnitude faster than spontaneous mutation (Grant & Grant 1994, Seifert 2012).

### 1.2. Parthenogenetic or apomictic reproduction

The BSC is not applicable to the very many groups of parthenogenetic or apomictic organisms. Clones cannot be classified according to the criterion of reproductive isolation. A list of only the major groups of asexually reproducing organisms would need much printing space. The BSC is not applied by botanists or protozoologists and causes big difficulties in zoologists studying, e.g., Nematoda, Acari, Rotatoria or Tardigrada.

### 1.3. The allopatry problem

The BSC is not applicable to the numerous cases of allopatric distribution in which nature does not provide a test situation on reproductive isolation. Allopatric cases can only be classified by pragmatic approaches – i.e., decision rules considering thresholds being defined as an agreement between the researchers of the different disciplines. This is explained in more detail in the next sections. Conclusions on reproductive barriers between species in a natural context are only possible in sympatry or contact zones of parapatric species.

### 1.4 Differing time horizons

The BSC is not applicable if time horizons between compared entities differ – typically in classification of a series of fossil organisms from different strata. Reproductive isolation as criterion can only be applied synchronously.

What remains of the BSC? If the term ‘reproductive isolation’ is mitigated to ‘reproductive barrier’, it can be used as criterion in particular sympatric confrontations of sexually reproducing organisms. Hence, the BSC can be applied to a small segment of taxonomic reality. Yet, it is by no means universal or in agreement with the extended knowledge on evolution.

## 2. Four published species concepts - their advantages and disadvantages

It has been stated above that the development of species concepts should move towards a concept applicable to all groups of extant and extinct organisms independent from their mode of reproduction and evolutionary history. This concept should avoid all the weak points of the BSC mentioned above. Considering the published species concepts, four concepts attracted my attention: the conceptions of Sonneborn (1957), Sokal & Crovello (1970), Cracraft (1989) and De Queiroz (2007). The first concept focuses on evolutionary divergence, the second on objectivity of decision, the third emphasizes the phylogenetic Hennigian aspect and the fourth is providing a way of how to integrate different species concepts. All these concepts have in common that they do not confine to a particular discipline of research (such as genetics, ecology, ethology or morphology) and should have a broad applicability.

Sonneborn (1957), an early critic of Ernst Mayr, proposed that ‘*A species is a biological unit that passed a threshold of irreversible evolutionary divergence.*’ This is a workable species concept because a translation of ‘threshold of evolutionary divergence’ into a taxonomic working routine is possible if there is an adequate mathematic description and agreement among taxonomists on what a reasonable threshold value might be. Given this pragmatic solution, Sonneborn’s concept will have no problems with the critical points (2), (3) and (4). However, the term ‘irreversible’ is problematic. It is, at least partially, in conflict with point (1). The normality of reticulate evolution and the incredibly long time span necessary to built up reproductive isolation means that a reversal of even profound evolutionary divergence is possible. Widely divergent species having evolved in allopatry may fuse when their isolation is bypassed either by natural processes or by anthropogenic introduction. Hybridization with introduced species constitutes a constantly growing threat for species conservation – classical examples are the Nearctic Ruddy Duck, *Oxyura jamaicensis* being introduced into the range of the endangered Eurasian White-headed Duck, *Oxyura leucocephala* (Muñoz-Fuentes et al. 2007) and sticklebacks (*Gasterosteus aculeatus* complex) in British Columbia (Behm et al. 2010). The conclusion is that Sonneborn’s concept would become universal simply by deleting the term ‘irreversible’.

Sokal & Crovello (1970) did not present an explicit wording of their concept which later has been named in a rather misleading way ‘Phenetic Species Concept’. We can summarize that they considered species as clusters of individuals delimited by multivariate statistical analyses.

Multivariate statistical analysis includes diverse clustering methods, discriminant analysis or ordination and there is no other species concept imposing so explicitly the imperative to introduce mathematics into the taxonomic decision process. Another progressive trait was that they allowed in their concept ‘*all observable properties of organisms and populations in estimating similarities between pairs of Operational Taxonomic Units (OTUs)... These would include morphological, physiological, biochemical, behavioral similarity, DNA homologies, similarities in ... proteins and ecological properties, and even intercrossability...*’ (Sokal & Crovello 1970). These sentences are clearly advocating integrative taxonomy, allowing use of information from any discipline of biology provided that it can be translated into adequate numerics. The Sokal & Crovello concept would become insensitive to all the points (1) to (4) at which the BSC fails if it would include the threshold principle explained below. A frequent critique expressed by the phylogenetic systematists is also that it does not distinguish between plesiomorphies and apomorphies and, thus, could be misled by convergent evolution and adaptive radiation. I do not address this question here but will take it up again when commenting the new concept below. There is another weak point of the Sokal & Crovello concept: ‘clusters of individuals circumscribed using multivariate statistical analysis’ will also apply to different morphs of the same species. Most dangerous for the taxonomist is here a non-overlapping polymorphism expressed by fixed combinations of seemingly independent characters. This issue will be taken up again when the new concept is discussed below.

The third concept, the so-called ‘Diagnostic Species Concept’ of Cracraft (1989), considered a species as an ‘*irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent.*’ This is a reductionistic species concept focusing on phylogenetic history, trying to implement the principles of phylogenetic systematics – in particular the monophyly criterion of Hennig (1966). This idea led to inner logical inconsistencies and severe failures in practical application (Mallet 2013). I consider this concept to be of little use and perhaps even destructive because the term ‘irreducible cluster’ has produced a rather severe taxonomic inflation (Isaac et al. 2004).

The fourth concept, the ‘Unified Species Concept’ of De Queiroz (2007), reads as follows: ‘*A species is a separately evolving metapopulation lineage recognized by at least one operational criterion.*’ De Queiroz formulated only a single conceptual property (‘a separately evolving metapopulation lineage’) but left open by which operational criterion of which discipline of

research this property is recognized. He also argued that many disciplines can be used simultaneously but also a single one if it is conclusive. This flexible understanding of operational criteria is fully congruent with the view of Sokal & Crovello. Using the term metapopulation, De Queiroz wants to avoid over-splitting but in practice it is often difficult to decide which sub-populations form a metapopulation.

Assessing the status of allopatric populations is perhaps the biggest problem of taxonomy. Most of the existing species concepts fail to give a solution here. This is also the case with the concepts of Cracraft and De Queiroz and can be illustrated by the following fictitious example. Populations of a *Lasius* ant in the East Mediterranean islands of Rhodes, Crete and Cyprus each show different characters. An investigator A, who followed the concept of Cracraft, showed significant differences between them, concluded they represent three irreducible, diagnosably distinct clusters and described each of them as a different species. An investigator B, following the De Queiroz concept, agreed that there are certain differences between the three populations but he considered them of belonging to the same metapopulation because he compared it with another group of populations in the West Mediterranean. He found that divergence between the East and West Mediterranean population groups was stronger than within the groups and decided that only the West and East Mediterranean populations should belong to different species. Who is right? The splitter or the lumpers? Nobody can decide this by a stringent logic based on biological or evolutionary criteria. The example shows: terms such as ‘irreducible, diagnosably distinct cluster of common ancestry and descent’, ‘metapopulation lineage’ and ‘reproductive isolation’ do not help here. Basically the same problem occurs with allochronic populations and lines of parthenogenetic organisms - independent if they live in sympatry or allopatry. Energy-wasting disputes between taxonomists are frequently the consequence. The recommended way out of this dilemma is a pragmatism based on mutual agreement between the taxonomists. Needed is a conception setting an imperative to describe evolutionary divergence numerically and focusing on the threshold principle. This is explained below in more detail.

### 3. The Pragmatic Species Concept and its recommended translation into the taxonomic routine

The analysis of the advantages and disadvantages of the four species concepts discussed in the previous sections led to the formulation of a new species concept. I propose to name it the 'Pragmatic Species Concept' (PSC) because it is an antipode to more academic approaches by focusing on divergence between species alone instead of inferring on evolutionary processes generating these distances. This and the use of the threshold principle is the primary cause for its universal applicability. The same degree of divergence is considered to be equivalent independent if observed in sympatry, in widely separated allopatry or in allochrony. In order to avoid a complicated wording and to increase lucidity, the concept was placed in several sentences:

*'A species is a cluster of organisms which passed a threshold of evolutionary divergence. Divergence is determined by one or several operational criteria described by an adequate numerics. A single conclusive operational criterion is sufficient. Conflicts between operational criteria require an evolutionary explanation. Thresholds for each operational criterion are fixed by consensus among the experts of a discipline under the principle of avoiding over-splitting. Clusters must not be the expression of intraspecific polymorphism.'*

Comments on the wording of all elements of this concept and recommendations for its translation into a taxonomic practice are given in the following.

The reasons for accepting a part of Sonneborn's conception while deleting the term 'irreversible' are already explained in the upper section. To repeat this briefly: reversal of even strong evolutionary divergence is possible under certain natural conditions and is currently being accelerated by increasing passive introduction of species via continental and transcontinental human transport systems.

Operational criteria vary with the disciplines applied. They can be determined by any discipline contributing to assessment of evolutionary divergence. Leading disciplines in classification of species are morphology, genetics, ethology, biochemistry and ecology. New operational criteria may be inferred by future research. The presented concept needs only a single discriminative operational criterion but the ideal approach to classification is multi-source integrative taxonomy – i.e., simultaneous application of different disciplines with different operational criteria. Conflicts between operational criteria do not necessarily exclude decisions in favor of heterospecificity. Then, if practicable, the source of conflicts between operational criteria should

be considered requiring a biological or evolutionary explanation (Schlick-Steiner et al. 2010).

An operational criterion should refer in the best case to a complex character system. For example, such a criterion may be 'gaps between morphometric spaces described by twenty characters' or 'gaps between clusters of nuclear genes'. In the extreme, an operational criterion may refer to a single character. Such a criterion may be 'gaps between pubescence density on clypeus' or 'courtship song with or without crescendo'. Apart from a convincing sample size and broad geographic origin, the use of single characters requires the condition that this character is embedded in a complex character system that is an expression of nuDNA – there is no doubt that species in all their manifold biological properties are determined by nuclear genes. This condition is violated by mtDNA barcoding. Here a difference in a single triplet of mtDNA may be used as criterion to describe, e.g., masses of new species of Braconidae (Butcher et al. 2012). Turbo-taxonomy of this kind will cause lots of trouble for future taxonomists. Who can ever bring order into this chaos?

The backbone discipline of classification is morphology and it is indispensable to have a careful phenotypic investigation within the set of disciplines – at least in multi-cellular animals and higher plants. This is explained by the fact that >98% of the descriptions of published multi-cellular taxa are based on morphology. Accordingly, the link between a species under study and Linnaean nomenclature is established by evaluation of original descriptions and non-destructive morphological investigation of primary type specimens (Steiner et al. 2009, Schlick-Steiner et al. 2010).

The concept recommends the use of an adequate numeric (mathematic) evaluation system. Form and complexity of this system depend upon the level of difficulty and the discipline applied. In reply to subjectively operating taxonomists who consider numeric differential diagnoses too much time-consuming: many cases can be settled by a simple, quickly done statistics of single discriminative characters. If a taxonomist states in a verbal description that two ant species can be safely distinguished by the relative length of propodeal spines, is it then an unacceptable work to measure this single character in sufficiently sized samples and to show that there is a gap between the data of the two species? The taxonomist should make sure, or credible at least, that the proposed interspecific differences are consistent throughout the range of both species and apply with an acceptable error rate. If a taxonomist has only a single specimen of a species available (this is no exception in first descriptions and material from poorly sampled regions), he should at least provide a simple statistics describing the relation of this specimen to the known variance in the next similar

species. If this specimen is outside the 99% confidence interval, he might hypothesize heterospecificity. Given that, he has fulfilled the requirements of the first three sentences of the Pragmatic Species Concept. The next step is considering if the case might represent discrete intraspecific polymorphism instead of heterospecificity. This is difficult – often a taxonomist has no tool at hand to decide this *a priori* (but see below for the situation in eusocial organisms). Furthermore, if he has a single or very few deviating specimens, he should consider if these specimens could represent abnormalities. This requires much knowledge in developmental biology of the group of organisms under study. If both polymorphism and abnormality are considered to be unlikely, it is justified (and recommended!) describing a new species based on a single available specimen.

At the other end of difficulty scale we find cryptic species. Cryptic species were defined by Seifert (2009) as ‘two or more species which are not safely separable by primary visual or acoustic perception of an expert. This reflects the immediate sense of the word and restricts the term to the truly cryptic cases – i.e., to species not safely separable by training of innate pathways of the human cognitive system.’ This definition is rather stable in time because it considers the growth of knowledge by excluding those species called cryptic in the past but considered well-separable at the present. An example is the Common Tern (*Sterna hirundo*) and the Arctic Tern (*Sterna paradisica*) which were called hardly separable in the field some 100 years ago but are currently distinguished by trained hobby ornithologists at a quick glance. The high level of difficulty imposes the imperative of using some sort of a more complex multivariate analysis in delimiting truly cryptic species. This is done in the best case by a combination of exploratory and hypothesis driven approaches (Seifert et al. 2013).

Using thresholds is considered the only practicable way of decision finding in many disciplines of science, economy and even policy. Defining the threshold of evolutionary divergence beyond which heterospecificity may be assumed is a matter of consent among the experts of each discipline. Geneticists may have other approaches than morphologists both in algorithms and in thresholds. Quantitative analyses as they are recommended here have demonstrated the danger of over-splitting by subjective approaches (Mutanen 2005, Bose & De 2013, Seifert et al. 2014) but the quantitative taxonomists should restrain themselves. In order to avoid unreasonable over-splitting, the experts should agree on rather rigorous thresholds. The same threshold should be applied independently if species are sympatric, parapatric, allopatric or allochronous. The application of the threshold principle can be explained by recent examples from ant taxonomy.

A good remedy against over-splitting in multivariate analyses of ant worker morphology is to require that a discriminant function must confirm a minimum of 97% of the classifications proposed by explorative data analyses. In case of two parapatric and cryptic *Myrmica* species, a 100% congruence of exploratory and hypothesis-driven data analyses allowed their taxonomic separation (Seifert et al. 2014) whereas the intended taxonomic description of a new partially sympatric sibling species of *Temnothorax lichtensteini* was rejected because both systems showed only 92% of congruence (Czösz et al. 2013). Again, at least in the *Myrmica* case, there remains checking for intraspecific polymorphism. This is done in many different ways and will always require relating morphological data to information from other disciplines. In this particular *Myrmica* case, no other discipline but only spatial information was available. The conclusion in favor of heterospecificity was here that morphs, by definition provided by the same gene pool, will not occur in clean and separate parapatric populations. Taking the *Temnothorax* case, where morphology failed to indicate different species identities, it is possible that other operational criteria (e.g., investigation of nuDNA) may come to different conclusions. I remind of the above recommendation of how to solve conflicts between operational criteria (Schlick-Steiner et al. 2010).

It may be asked if it makes sense introducing into a species concept the condition that clusters must not be an expression of intraspecific polymorphism. This may refer to both sexual, transsexual and within-sex or within-caste polymorphism. This addition is a matter of formal logic and of care. Morphs belong to the same gene pool but nobody would deny that they are products of intraspecific evolutionary divergence and are fully matching the first sentences of the concept. This is the logic argument for adding the polymorphism qualification. Simultaneously it seems advisable to give an explicit warning. This is the practical argument. Most dangerous for a taxonomist is non-overlapping within-sex (or in ants within-caste) polymorphism expressed by fixed combinations of many, seemingly independent characters. Such a polymorphism feigns different species in a treachery way. Fortunately, this phenomenon seems to be rare. It is known, for instance, from only 2.2% of the 178 Central European ant species – explicitly excluding the cases of the well-known size dimorphism as for instance in the genera *Pheidole* or *Camponotus* (Seifert 1992, 2003).

It may be criticized that including intraspecific polymorphism in a species concept is a cognitive disaccord as one cannot *a priori* distinguish between heterospecificity and intraspecific polymorphism. This is true for the vast majority of organisms in which this question cannot be decided in the ‘first round’ of investigation. The

only exceptions seem to be eusocial organisms where discrete within-caste morphs can be identified a priori by comparing within-nest and population-wide distributions of morphological traits with those simulated by Mendelian inheritance models. For clearing up the polymorphism question in other organisms, we must inevitably run further rounds of investigation using other tools or disciplines – this is definitely a posteriori. However, what does this matter here? A species concept is not invalidated if an implemented criterion takes effect a priori or a posteriori relative to a point in time. Recognition of species and good taxonomy needs time. Evolutionary epistemology tells us that cognition grows up in a circling, ever widening spiral of induction and deduction, as a sequence of interaction between a priori and a posteriori hypotheses (Campbell 1974, Vollmer 1975, Oeser 1976, Riedl 1988). It is good to have a concept also reflecting the cognition process.

#### 4. Is there weakness in the Pragmatic Species Concept?

It is doubtful that a species concept can offer solutions to any thinkable case in an extremely complex system. The PSC seems to be applicable to all groups of Eukaryota independent from their mode of reproduction and evolutionary history. It seems to allow sound taxonomic decisions in case of reticulate evolution, parthenogenesis, apomixis, allopatry, separate time horizons and reversal of strong evolutionary divergence. A solution of all these problems appeared possible by focusing on the degree of evolutionary divergence and the threshold principle. The concept also addresses the problem of intraspecific polymorphism. It might also be asked if the application of the concept could extend to Prokaryota. This seems to be the case: broad fields of practical taxonomy appear to use adequate approaches in assigning microbes to species with high success in predicting pathogenicity and antibiotic sensitivity (Claridge et al. 1997).

A critique possibly being expressed by the phylogenetic systematists is that classification by the PSC could be misled by convergent evolution and adaptive radiation as it does not distinguish between plesiomorphies and apomorphies. This point may possibly be a matter of debate when higher classification is considered. Species concepts, however, are dealing with the very tips of phylogenetic trees and it is difficult to understand in which way in practice plesiomorphic and apomorphic traits can be reliably distinguished at this level – this would need looking into the past, knowing the true downward phylogeny of a whole branch. Furthermore, selecting few single traits as leading indicators in a parsimony analysis

of species identities induces a higher risk of error than using many or all studied traits without cladistic reduction. Algorithms of most multivariate analyses automatically evaluate the weight of a trait and the possible grouping of unrelated species into polyphyletic taxa should have a low risk in complex multivariate analyses if they consider numerous traits. Yet, even if such a failure occurred, we have to remember that the primary goal of species concepts is a powerful delimitation of species and not revealing their putatively correct cladistic placement. Practitioners, at least, would agree.

A problem may arise in connection with reticulate evolution. Above, we have accepted that introgression of few alleles between species is possible. This may cause conflicts with species concepts focusing on particular gene clusters – i.e., species separated by the PSC may be paraphyletic or even polyphyletic in different parts of their genomes. This conflict probably cannot be solved.

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