

# PROGRESS TOWARD A GENERAL SPECIES CONCEPT

Bernhard Hausdorf<sup>1,2</sup>

<sup>1</sup>Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

<sup>2</sup>E-mail: hausdorf@zoologie.uni-hamburg.de

Received September 15, 2010

Accepted January 3, 2011

New insights in the speciation process and the nature of “species” that accumulated in the past decade demand adjustments of the species concept. The standing of some of the most broadly accepted or most innovative species concepts in the light of the growing evidence that reproductive barriers are semipermeable to gene flow, that species can differentiate despite ongoing interbreeding, that a single species can originate polyphyletically by parallel evolution, and that uniparental organisms are organized in units that resemble species of biparental organisms is discussed. As a synthesis of ideas in existing concepts and the new insights, a generalization of the genic concept is proposed that defines species as groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact. The benefits of this differential fitness species concept are that it classifies groups that keep differentiated and keep on differentiating despite interbreeding as species, that it is not restricted to specific mutations or mechanisms causing speciation, and that it can be applied to the whole spectrum of organisms from uni- to biparentals.

**KEY WORDS:** Hybridization, introgression, speciation.

Although the “species” is one of the most important units in biology, the definition of the term is still controversial. Most biological information is given with reference to a species. There is a whole discipline, taxonomy, dedicated to the delimitation of species, which requires a species concept. Species concepts do not only define what a species is, but by defining what a species is, they also define what speciation is. Thus, research programs focusing on the conditions and factors resulting in speciation depend on the species concept. Many other biological studies depend also on the delimitation of species. For example, many ecological and behavioral studies investigate the interactions of species or the relation of species richness with abiotic and biotic factors. Most efforts in conservation biology focus on species. Even in legislation, the species is one of the most often used biological units, not only with respect to conservation, but also with regard to agricultural or medical issues. Thus, a clear definition of the term “species” is important for a broader audience than just academic biologists.

The discussion of different species concepts is not just a philosophical debate, but different species concepts may actually

result in different conclusions (Isaac et al. 2004). For example, a literature survey revealed a 49% higher count of species in studies using a phylogenetic species concept compared with studies applying nonphylogenetic concepts on the same organisms and an associated decrease in population size and range (Agapow et al. 2004).

Because of the importance of the definition of the term “species,” a plethora of species concepts has been proposed (for review see Mayden 1997; de Queiroz 1998; Harrison 1998; Coyne and Orr 2004). However, there is little agreement about the species concept so far. The endless debates about the species concept resulted in frustration and a decrease of interest in the development of the concept. Nevertheless, new insights in the speciation process and the nature of “species” that accumulated in the past decade demand adjustments of the species concept.

One of the most important new insights with regard to the species concept is that reproductive barriers are semipermeable to gene flow and that species can differentiate despite ongoing interbreeding (Harrison 1998; Rieseberg 2001; Wu 2001; Rieseberg et al. 2003; Coyne and Orr 2004; Wu and Ting 2004; Mallet 2005,

2008; Lexer and Widmer 2008). Although at least 25% of plant species and 10% of animal species are known to hybridize with other species with potential introgression of genes (Mallet 2005), most species concepts do not adequately consider gene exchange between species. The persistence of differentiated species and ongoing differentiation despite gene exchange challenge these concepts.

Further insights in the nature of “species,” which were not considered in the context of species concepts so far, were gained by studies of parallel speciation. Parallel speciation is a case of parallel evolution in which similar traits that confer reproductive isolation originate independently in separate closely related lineages resulting in a polyphyletic entity that evolves independently of the ancestral species (Schluter and Nagel 1995; Rundle et al. 2000; Johannesson 2001; Nosil et al. 2002). The traits that determine reproductive isolation may evolve as a byproduct of adaptation to different environments, but they may also originate by other processes such as independent polyploidization. Actually, most polyploid entities originated by recurrent polyploidization, often in different populations of the ancestral species (Soltis and Soltis 1999, 2000). The independently derived polyploid individuals may interbreed with each other and form coherent polyphyletic entities commonly recognized as species.

Another important finding is that uniparental organisms are actually organized in units that resemble species of biparental organisms (Holman 1987; Gevers et al. 2005; Cohan and Perry 2007; Fontaneto et al. 2007; Cohan and Koeppl 2008). The term “species” is used for all groups of organisms. Thus, the question is whether all phenomena along the continuum of reproductive systems from uni- to biparentals that are called species can be defined in a general species concept.

In the following, I will discuss the impact of these insights on some of the most broadly accepted or most innovative species concepts and I will try to develop a synthesis of existing concepts and new insights.

## *Species Concept and Species Criteria*

de Queiroz (1998) emphasized the distinction between species concept and species criteria. However, his definition of “species concept” as “idea about the kind of entity represented by the species category” is not distinct enough to be helpful. A species concept has to state the conditions that are necessary and sufficient to identify a group of individuals as a species (see also Pigliucci 2003). Based on this definition, I oppose his view that most of the earlier formulated species concepts are only species criteria. A species criterion is a condition that is necessary or sufficient to identify a group of individuals as a species. Conditions given in species concepts are species criteria. However, not all valid

criteria have to be stated directly in the species concept. Different species concepts often refer to different stages during speciation (de Queiroz 1998, 2005a,b, 2007). If a species concept specifies conditions that are generally achieved in a later stage of differentiation than the conditions of another concept, then the concepts are nested and the conditions of the former concept are sufficient criteria of the latter.

Species concepts are not right or wrong. In principle almost every species concept is usable. However, acceptance of a species concept entails an appropriate adaptation of the use of the term “species” and of species delimitation. If, for example, a species concept is adapted that does not implicate that groups of polyploid individuals should be considered as species distinct from otherwise similar diploid individuals, current classification has to be changed accordingly. Thus, species concepts should be rated the higher, the better they fit current usage of the term “species.”

## *Species Concepts*

### **LINEAGE-BASED SPECIES CONCEPTS**

de Queiroz (1998, 2005a,b, 2007) argued that all modern species concepts have a common element, namely they either explicitly or implicitly equate species with “*separately evolving (segments of) metapopulation lineages*” (de Queiroz 2005). This “general lineage concept,” which is a re-formulation of the evolutionary species concept (Simpson 1951, 1961; Wiley 1978), became popular among systematists (Wiens 2007).

To understand lineage-based species concepts, the terms “lineage” and “population” have to be defined at first. A lineage is defined as “an ancestral–descendant sequence of populations” (Simpson 1961). The term population is usually defined as a group of conspecific organisms that occupy a more or less well-defined geographical region and exhibit reproductive continuity from generation to generation (Futuyma 1998). There are several variations of this definition (Waples and Gaggiotti 2006). In any case it has to be specified which of the individuals that co-occur in an area form a population. In some definitions of “population” the more usual phrases “conspecific organisms” or “individuals of the same species” are replaced by “interbreeding individuals” (e.g., Mayr 1942, 1963; de Queiroz and Donoghue 1988). However, such a definition of population introduces the biological species concept through the back-door by including it into the definition of population. This definition was not used by de Queiroz (1998) when he introduced the general lineage concept. Rather, he emphasized that he uses population “in the general sense of an organizational level above that of the organism rather than the specific sense of a reproductive community of sexual organisms” (de Queiroz 1998). He did not specify any properties of this “organizational level above that of the organism,” leaving the exact definition of population and, thus, lineage and species unclear. The later

addition of the term metapopulation to the general lineage concept and its definition as “an inclusive population made up of a set of connected subpopulations” by de Queiroz (2005a,b) did not help to clarify the concept, rather introduced additional undefined terms. It has neither been explained how “subpopulations” are defined nor how they are “connected.”

If the usual definition of population as a group of conspecific organisms that occupy a more or less well-defined geographical region is accepted, a population (and hence, a sub- or a metapopulation) can only be delimited if we can decide which organisms are conspecific. Thus, species must be defined before populations can be delimited. It is circular to define a species as a sequence of (meta-)populations, because it is part of the definition of “population” that the organisms that form a population belong to the same species. The term “population” must not be used in definitions of “species” unless it is defined without referring to conspecific organisms. Note, that this is necessary to avoid circularity and does not indicate any doubts about the evolutionary importance of populations.

The notion of “separately evolving” units is doubtlessly the core of all modern species concepts. However, to be a useful criterion in a species concept, it has to be specified what “separately evolving” means. It is unclear how populations connected by limited gene flow should be classified. As a result of introgression, biparental taxa may not evolve separately at some loci, but do at most others (Harrison 1998; Wu 2001; Coyne and Orr 2004; Wu and Ting 2004; Mallet 2005). Moreover, coherent polyphyletic entities that originated by parallel speciation and evolve separately of the ancestral species cannot be classified as separate species by lineage-based species concepts.

Lineage-based species concepts shift the problem of defining the term “species” to the problem of defining the term “population” and result in an intricate re-formulization of the biological species concept or in circular reasoning. Furthermore, the important criterion “separately evolving” in the general lineage concept remained unclear, because it was not specified what this notion means. Thus, lineage-based species concepts present only limited progress toward a generally applicable species concept.

### BIOLOGICAL SPECIES CONCEPT

The most influential species concept is still the biological species concept that defines species as “groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr 1942, 1963; “natural populations” in this formulation can be replaced by “individuals” without change of meaning). However, two of the new findings challenge the biological species concept. The finding that reproductive barriers are semipermeable to gene flow and that species can differentiate despite ongoing interbreeding (Harrison 1998; Rieseberg 2001; Wu 2001;

Rieseberg et al. 2003; Coyne and Orr 2004; Wu and Ting 2004; Mallet 2005, 2008; Lexer and Widmer 2008) indicates that the biological species concept is not in accordance with current use of the term species. Acceptance of this concept would require lumping many well differentiated and generally accepted species that nevertheless interbreed regularly. Some authors (Orr 2001; Noor 2002; Coyne and Orr 2004) have argued for a relaxed interpretation of the biological species concept to retain it despite the new insights. However, the meaning of a species concept is that it defines the conditions under which a group of individuals should be classified as a species. If we ignore the conditions specified in a species concept, it becomes useless.

Moreover, the biological species concept has originally been formulated exclusively for biparental organisms. Acceptance of the biological species concept would entail that the term species should not be used for uniparental organisms, although growing evidence indicates that they are organised in units that resemble species of biparental organisms (Holman 1987; Gevers et al. 2005; Cohan and Perry 2007; Fontaneto et al. 2007; Cohan and Koeppel 2008). It has been suggested that a modification of the biological species concept can be applied to uniparental prokaryotes (Dykhuizen and Green 1991). This was based on the insight that prokaryotes are not simple clonal organisms, but that there is frequent gene exchange at least in some groups. However, gene exchange between prokaryotes is not limited to closely related species (Ochman et al. 2005) and, thus, an application of a modification of the biological species concept would require lumping many well-differentiated and generally accepted species. Furthermore, there are uniparental organisms without gene exchange such as parthenogenetic species, for which even a modification of the biological species concept would not be applicable.

### PHYLOGENETIC SPECIES CONCEPT

One important alternative to the biological species concept that can principally be applied also to uniparental organisms is the phylogenetic species concept. According to the diagnosable version of the phylogenetic species concept, a species is “a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind” (Eldredge and Cracraft 1980). This concept has also been recommended for prokaryotes (Staley 2006) and has recently been referred to in several DNA barcoding/ DNA taxonomy studies (e.g., Kelly et al. 2007; Sarkar et al. 2008; Monaghan et al. 2009).

However, there are problems with this concept in uni- as well as in biparentals. In uniparentals in which there is no or little gene exchange, each clone with a mutation would be classified as a separate species (Coyne and Orr 2004). In uniparentals with higher levels of gene exchange and in biparentals each substitution will

have its own particular distribution and little or no concordance might exist among the sets of individuals diagnosable with independently derived mutations except those bounded by barriers to gene flow (Avice and Ball 1990). Eldredge and Cracraft (1980) restricted the clusters of individuals that are ranked as “species” by including the condition “within which there is a parental pattern of ancestry and descent, beyond which there is not” in the concept. This condition has the function to restrict the cluster of individuals that are ranked as “species” to those that are bounded by barriers to gene flow. However, the insights that hybridization between closely related species is frequent and that species can differentiate despite ongoing interbreeding means that many currently recognized species do not show separate “parental patterns of ancestry and descent,” but that some descendants belonging to one species may have ancestors belonging to another simultaneously existing species and vice versa. Thus, these insights have similar consequences for the application of the phylogenetic species concept as for the biological species concept. Acceptance of the phylogenetic species concept would also require lumping many well-differentiated and generally accepted species that nevertheless interbreed regularly.

Moreover, polyphyletic species originating by parallel speciation will also not show a “parental patterns of ancestry and descent” separate from that of the ancestral species and would have to be lumped under the phylogenetic species concept, too.

### GENOTYPIC CLUSTER DEFINITION

Mallet (1995) recognized that the biological species concept is untenable in the face of gene flow between independently evolving units and proposed a pattern-based species concept. Adding genetics to the phenetic species concept that defines species as groups of individuals with few or no intermediates, he formulated the genotypic cluster definition according to which a species is a “*genotypic cluster that can overlap without fusing with its sibling.*”

Just as the phylogenetic species concept, this concept is in principle applicable also for uniparental organisms. However, acceptance of the genotypic cluster definition would result in the undesirable consequence that each genetically different clone will be identified as a separate species (Coyne and Orr 2004).

The prediction that species sooner or later form genotypic and phenotypic clusters can be derived from most species concepts. Thus, this is doubtlessly a useful criterion for delimiting provisional species. However, incipient species might not yet be recognizable as distinct clusters based on a random sample of genetic markers. In the case of peripatric speciation, the peripheral species will initially often form a cluster with neighboring populations of the more widespread species so that the more widespread species does not form a genotypic cluster distinct from the peripheral species. At least in their initial stages, coherent entities originating by parallel speciation from different populations of

an ancestral species cannot be recognized as separate genotypic clusters and would have to be lumped with the ancestral species under the genotypic cluster definition.

### COHESION SPECIES CONCEPT

Templeton (1989) recognized that there is a whole continuum of reproductive systems from uni- to biparentals and that any a priori restriction of the scope of a species concept with regard to reproduction mode is to some degree artificial. Furthermore, he recognized that evolutionary processes other than reproductive isolation contribute also to the formation and maintenance of coherent entities, especially in uniparentals. Templeton (1989) compiled these processes and classified these “cohesion mechanisms” into mechanisms affecting genetic exchangeability by defining the limits of spread of new genetic variants through gene flow and mechanisms affecting demographic exchangeability by defining the fundamental niche and the limits of spread of new genetic variants through genetic drift and natural selection. However, the term “cohesion mechanism” may be misleading, because most biological properties that confer cohesion did probably not arise for that purpose (Harrison 1998). Thus, cohesion is an effect, not a mechanism. Based on the “cohesion mechanisms,” Templeton (1989) formulated the cohesion species concept, according to which a species is “*the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.*”

Coyne and Orr (2004) claimed that the cohesion species concept may fail to provide a decision about the species status of two groups when the criteria of genetic and demographic exchangeability conflict, for example, if two groups of biparental individuals are genetically nonexchangeable but demographically exchangeable. This is not the case. The “and/or” between genetic and demographic exchangeability in Templeton’s (1989) formulation of the cohesion concept is a logical “or,” an inclusive disjunction. Thus, all individuals connected by any “cohesion mechanism” are classified as one species by the cohesion concept. If there are, for example, groups of biparental individuals that are genetically nonexchangeable (i.e., reproductively isolated), but demographically exchangeable, the most inclusive group includes all individuals. Thus, groups of individuals would have to be considered conspecific under the cohesion concept, if they occupy the same fundamental niche, even if they are reproductively isolated. Acceptance of the cohesion concept would require lumping many generally accepted reproductively isolated species. Moreover, the cohesion concept does not specify which kind of gene flow affects genetic exchangeability and, thus, will also result in lumping species that differentiate despite ongoing gene exchange.

### GENIC SPECIES CONCEPT

Wu (2001) developed a novel model of speciation based on a consideration of the genetic processes happening during

speciation, which explains why and what kind of gene exchange does not affect the persistence of differentiated species and the further differentiation of species. According to this model, the whole process of speciation depends primarily on the genes responsible for differential adaptation to different natural or sexual environments, the “speciation genes” (see also Wu and Ting 2004). Wu (2001) defined differential adaptation as a form of divergence in which the alternative alleles of a gene have opposite fitness effects in two groups of individuals. During the process of speciation the speciation genes may account for only a small fraction of the genome. Gene exchange is restricted at these loci, whereas gene exchange at other loci, the “marker loci,” could persist for a long period of time even after speciation. Speciation is the stage where the groups of individuals will not lose their divergence upon contact and will be able to continue to diverge. Based on this model, Wu (2001) defined species as “*groups that are differentially adapted and, upon contact, are not able to share genes controlling these adaptive characters, by direct exchanges or through intermediate hybrid populations.*” Although it was originally formulated for biparental species, this concept is in principle also applicable to uniparentals.

The genic species concept of Wu (2001) has been criticized because it exclusively focuses on differential adaptation caused by mutations in genes (Britton-Davidian 2001; Orr 2001; Rundle et al. 2001; Noor 2002). Other genetic features that may result in reproductive isolation such as chromosomal changes were classified as “special cases” by Wu (2001). However, the critics prefer to classify entities that evolve separately because they are reproductively isolated due to chromosomal changes or other nongenic mutations as separate species. Even if differential adaptation would be the most frequent process resulting in speciation, other processes that might also cause the formation of species such as genetic drift should not be excluded a priori in a species concept (Britton-Davidian 2001; Orr 2001; Rundle et al. 2001; Noor 2002).

#### DIFFERENTIAL FITNESS SPECIES CONCEPT

Compared to other species concepts, the ability of the genic species concept of Wu (2001) to specify in which cases groups of individuals can be classified as species despite gene flow between these groups represented an important conceptual advance. Thus, it is worth considering whether the two criticized restrictions of the genic species concept, that it considers only species that originated by (1) mutations in genes resulting in (2) differential adaptation, can be abolished. Wu (2001) defined differential adaptation by “opposite fitness effects” of alternative alleles. However, the features that cause speciation do not necessarily have to be alternative alleles and their fitness effects do not necessarily have to be opposite in different species, that is positive in the species that they characterize and negative in the other species. To restrict

gene flow, it is sufficient that such features, which may be heritable traits other than genes, have negative fitness effects in other species. They may be neutral in the species that they characterize. For example, a *Wolbachia* infection may be nearly neutral in the hosting species but would have a negative fitness effect in other, noninfected species. Groups of individuals become evolutionary independent only if gene flow is restricted in both directions. Thus, each group must have features that have negative fitness effects in the other species. Based on these ideas, species can be defined as *groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact.*

This differential fitness species concept considers not only mutations in genes, but any differences including, for example, chromosomal changes (White 1954; Rieseberg 2001), *Wolbachia* infections (Hurst and Schilthuisen 1998; Telschow et al. 2005; Werren et al. 2008), other selfish genetic elements such as transposable elements (Hurst and Schilthuisen 1998; Hurst and Werren 2001) or niche-specifying genes or sets of genes acquired by horizontal transfer in prokaryotes (Ochman et al. 2005; Cohan and Koeppel 2008). The differences may result from differential adaptation due to natural or sexual selection, but may also be the result of genetic drift or other often nonadaptive processes such as polyploidization or infections by symbionts. The features may be specifically adaptive for one group’s niche, but maladaptive for another’s or may be incompatible in the context of the genetic background of another group (like different *Wolbachia* infections). Such incompatibilities could result in lowered fertility or in unbalanced physiological function. As the genic species concept, the differential fitness concept allows for the exchange of genes as far as they are not important for the features that have negative fitness effects in the other species.

The differential fitness species concept differs from the biological species concept in considering that the exchange of the species-specific features may not only be restricted by reproductive isolation, but also by divergent selection. In this respect, the differential fitness species concept is closer to Darwin’s (1859) understanding of species than to the biological species concept. Darwin (1859: 485) argued “that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected.” The lack of intermediate gradations in the first differences that characterize nascent species results from the inability to exchange these features between groups and is not necessarily connected with reproductive isolation. One shortcoming of a purely phenotypic assessment of the ability to exchange potentially species-specific features is that groups of individuals characterized by different discrete polymorphisms may be taken for separate species because



of the lack of intermediate gradations. However, this does not affect the differential fitness species concept that does not focus on the lack of intermediate gradations as such, but is based on the inability to exchange species-specific features between groups. As long as groups of individuals characterized by different discrete polymorphisms are able to exchange these polymorphisms, that is the underlying genes, these groups are not considered species under the differential fitness species concept. But when this ability disappears, groups of individuals characterized by different features become species under this concept.

The differential fitness species concept can be applied to the whole spectrum of organisms from uni- to biparentals. The differential fitness species concept classifies groups as species if they are characterized by features that would have negative fitness effects in other such groups and that cannot be regularly exchanged between these groups. In biparentals these features include besides adaptations to different environments also modifications of the reproductive system that decide with which other individuals an individual can produce fertile descendants. For example, polyploidy has a negative fitness effect in a group of diploid individuals, because it would result in reproductive incompatibility. Likewise, diploidy has a negative fitness effect in a group of polyploid individuals. Thus, these groups are classified as different species under the differential fitness concept, even if they occupy the same niche. Uniparental groups characterized by features that would have negative fitness effects in other groups occupy different niches in most cases. Thus, in uniparentals species as defined by the differential fitness concept correspond usually to ecotypes, which were actually considered the equivalent of biparental species in prokaryotes (Gevers et al. 2005; Cohan and Perry 2007; Cohan and Koeppl 2008). However, mutations in different genes in different strains, each of which is selectively neutral on its own, might result in genic incompatibilities, that is, might have negative fitness effects in strains with incompatible mutations in other genes, so that such strains qualify as different species under the differential fitness concept, even if they are not ecologically differentiated. It is questionable whether neutral mutations often persist long enough in prokaryotes that such genic incompatibilities can arise or whether they are usually eliminated by periodic selection before genic incompatibilities can originate.

### *Comparison of Species Concepts*

For an easier comparison of the consequences resulting from different species concepts, some illustrative groupings and their classification under different species concepts are listed in Table 1. The general lineage concept could not be considered because of the problems discussed above.

The biological species concept differs from the other discussed concepts in that it is formulated exclusively for biparentals

and requires intrinsic reproductive isolation. The phylogenetic species concept differs from the other concepts in that it classifies groups that are only extrinsically (e.g., geographically) isolated as species. This results in considerable taxonomic inflation (Agapow et al. 2004; Isaac et al. 2004). Moreover, it classifies also diagnosable groups of uniparentals that are not characterized by features that would have negative fitness effects in other groups as species what would result in an even larger inflation in prokaryote taxonomy. Such groups might often be classified as species also using the genotypic cluster definition. With respect to the classification of other groups, the genotypic cluster definition is most similar to the differential fitness species concept. However, its outcome cannot be predicted unequivocally based on the conditions specified in Table 1, because genotypic clusters are expected to emerge under all of the specified conditions, but may come about only in later stages of differentiation. Note that genotypic clusters may arise also in only extrinsically isolated groups, but that such clusters do not qualify as species under the genotypic cluster definition, because they will fuse upon contact. The most unusual feature of the cohesion concept is that groups of biparental individuals are considered conspecific if they occupy the same fundamental niche, even if they are reproductively isolated. The conceptual advance of the genic and the differential fitness species concepts is that they do not demand complete reproductive isolation, but tolerate the exchange of features except those that are causal for the differentiation. Groups that are classified as species under the genic species concept are also considered species under the more general differential fitness species concept. The same is true for groups that are classified as species under the biological species concept, because the features that cause reproductive isolation in biparentals have negative fitness effects in other groups and cannot be regularly exchanged.

### *Species Concept and Species Delimitation*

The formulation of a species concept and the development of approaches for delimiting species are two different tasks (de Queiroz 2005b, 2007). A species concept has to be formulated in such a way that also the earliest stages after speciation are covered. Actually, the species concept defines what speciation is. The earliest stages after speciation may differ only in a few properties. After divergence differentiation of the resulting species continues so that it becomes easier to distinguish later stages.

Approaches for delimiting species should ideally be based on the conditions specified in the favored species concept. Then the delimited species should correspond exactly to the species concept. However, often properties acquired later during differentiation can be observed more easily than the few properties acquired directly at the speciation stage. Thus, delimitation

**Table 1.** Classification of groups of individuals as species (+), usually species ( $\pm$ ) or not separate species (–) by different species concepts (na, concept not applicable). BSC=biological species concept; PSC=phylogenetic species concept; GCD=genotypic cluster definition; CSC=cohesion species concept; GSC=genic species concept; DFSC=differential fitness species concept.

	BSC	PSC	GCD	CSC	GSC	DFSC
Groups of uniparentals that are characterized by features that would have negative fitness effects in other groups	na	+	$\pm$	+	+	+
Diagnosable groups that are not characterized by features that cannot be exchanged with other groups, but do not exchange genes with other groups because of geographical isolation	–	+	–	–	–	–
Diagnosable groups of uniparentals that are not characterized by features that would have negative fitness effects in other groups	na	+	$\pm$	–	–	–
Groups of biparentals that are reproductively isolated but occupy the same niche	+	+	$\pm$	–	+	+
Groups that are differentially adapted and are not able to share the genes controlling these adaptive characters, although they are interbreeding	–	–	$\pm$	–	+	+
Groups of biparentals that are reproductively isolated due to non-genic mutations or processes other than differential adaptation	+	+	$\pm$	$\pm$	–	+

approaches are often based on such properties. If an approach for delimiting species is based on properties which were acquired in later stages, the approach may result in false negatives, that is, species in early stages of speciation that are not recognized as such, but no false positives. If the properties on which an approach is based may be acquired also prior to speciation, false positives may result as well. Because methods that are not directly based on the conditions specified in a species concept will sometimes fail to delimit species boundaries properly, an eclectic approach to delimiting species is necessary (Sites and Marshall 2004).

If species delimitation should be based directly on the conditions specified in the differential fitness concept, it has to be demonstrated that groups of individuals are reciprocally characterized by features that (1) have negative fitness effects in other groups and that (2) cannot be regularly exchanged between groups upon contact. In many cases features that would have negative fitness effects in other groups, such as different beak sizes or forms in birds that allow individuals belonging to different species to use different food, differentially formed copulatory organs that impede crossing between individuals of different species, or different ploidy levels are known and are already used routinely for species delimitation. A discontinuous variation of such features usually indicates that they cannot be regularly exchanged between groups. Thus, such groups can be considered species under the differential species concept. More explicit tests of the conditions specified in the differential fitness concept will be possible only in a minority of cases in which the genetics is well understood, just as explicit tests of the conditions specified, for example, in the biological species concept have been carried out only in a minority of cases. Testing the condition that species are characterized by features that “would” have negative fitness effects in

other groups might be difficult especially in uniparental groups. However, this does not disqualify the concept as such. In principle, fitness effects of genes of other species can be tested by experimental transformation also in uniparentals.

If nothing is known about the fitness effects of features and their exchangeability, a standard approach for delimiting species is determining phenotypic or genotypic clusters (Sites and Marshall 2004; Hausdorf and Hennig 2010). This approach is justified at least in biparental species by our understanding of differentiation processes. After speciation more and more alleles become restricted to one of the descendant species, so that the individuals belonging to one species will form genotypic and phenotypic clusters sooner or later even if they were initially paraphyletic (e.g., as a result of peripatric speciation) or polyphyletic (e.g., because of parallel speciation).

#### ACKNOWLEDGMENTS

I thank R. DeBry, K. de Queiroz, D. Fairbairn, J. Mallet, D. Tautz, and an anonymous referee for discussions. I am especially grateful to F. M. Cohan for his constructive criticism that helped to improve the manuscript.

#### LITERATURE CITED

- Agapow, P.-M., O. R. P. Bininda-Emonds, K. A. Crandall, J. L. Gittleman, G. M. Mace, J. C. Marshall, and A. Purvis. 2004. The impact of species concept on biodiversity studies. *Q. Rev. Biol.* 79:161–179.
- Avise J. C., and R. M. Ball. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surv. Evol. Biol.* 7:45–67.
- Britton-Davidian, J. 2001. How do chromosomal changes fit in? *J. Evol. Biol.* 14:872–873.
- Cohan, F. M., and E. B. Perry. 2007. A systematics for discovering the fundamental units of bacterial diversity. *Curr. Biol.* 17:R373–R386.

- Cohan, F. M., and A. F. Koepfel. 2008. The origins of ecological diversity in prokaryotes. *Curr. Biol.* 18:R1024–R1034.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer, Sunderland, MA.
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.
- de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. Pp. 57–75 in D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford Univ. Press, New York, Oxford.
- . 2005a. Ernst Mayr and the modern concept of species. *Proc. Natl. Acad. Sci. USA* 102:6600–6607.
- . 2005b. Different species problems and their resolution. *BioEssays* 27:1263–1269.
- . 2007. Species concepts and species delimitation. *Syst. Biol.* 56:879–886.
- de Queiroz, K., and M. J. Donoghue. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4:317–338.
- Dykhuizen, D. E., and L. Green. 1991. Recombination in *Escherichia coli* and the definition of biological species. *J. Bacteriol.* 173:7257–7268.
- Eldredge, N., and J. Cracraft. 1980. *Phylogenetic patterns and the evolutionary process*. Columbia Univ. Press, New York.
- Fontaneto, D., E. A. Herniou, C. Boschetti, M. Caprioli, G. Melone, C. Ricci, and T. G. Barraclough. 2007. Independently evolving species in asexual bdelloid rotifers. *PLoS Biol.* 5:914–921.
- Futuyma, D. J. 1998. *Evolutionary biology*. Third Edition. Sinauer, Sunderland, MA.
- Gevers, D., F. M. Cohan, J. G. Lawrence, B. G. Spratt, T. Coenye, E. J. Feil, E. Stackebrandt, Y. Van de Peer, P. Vandamme, F. L. Thompson, et al. 2005. Re-evaluating prokaryotic species. *Nat. Rev. Microbiol.* 3:733–739.
- Harrison, R. G. 1998. Linking evolutionary pattern and process. The relevance of species concepts for the study of speciation. Pp. 19–31 in D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford Univ. Press, New York, Oxford.
- Hausdorf, B., and C. Hennig. 2010. Species delimitation using dominant and codominant multilocus markers. *Syst. Biol.* 59:491–503.
- Holman, E. W. 1987. Recognizability of sexual and asexual species of rotifers. *Syst. Zool.* 36:381–386.
- Hurst, G. D. D., and M. Schilthuizen. 1998. Selfish genetic elements and speciation. *Heredity* 80:2–8.
- Hurst, G. D. D., and J. H. Werren. 2001. The role of selfish genetic elements in eukaryotic evolution. *Nat. Rev. Genet.* 2:597–606.
- Isaac, N. J. B., J. Mallet, and G. M. Mace. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends Ecol. Evol.* 19:464–469.
- Johannesson, K. 2001. Parallel speciation: a key to sympatric divergence. *Trends Ecol. Evol.* 16:148–153.
- Kelly, R. P., I. N. Sarkar, D. J. Eernisse, and R. DeSalle. 2007. DNA barcoding using chitons (genus *Mopalia*). *Mol. Ecol. Notes* 7:177–183.
- Lexer, C., and A. Widmer. 2008. The genic view of plant speciation: recent progress and emerging questions. *Phil. Trans. R. Soc. Lond. B* 363:3023–3036.
- Mallet, J. 1995. A species definition for the Modern Synthesis. *Trends Ecol. Evol.* 10:294–299.
- . 2005. Hybridization as an invasion of the genome. *Trends Ecol. Evol.* 20:229–237.
- . 2008. Hybridization, ecological races, and the nature of species: empirical evidence for the ease of speciation. *Phil. Trans. R. Soc. Lond. B* 363:2971–2986.
- Mayden, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pp. 381–424 in M. F. Claridge, H. A. Dawah, and M. R. Wilson, eds. *Species: the units of biodiversity*. Chapman and Hall, London.
- Mayr, E. 1942. *Systematics and the origin of species*. Columbia Univ. Press, New York.
- . 1963. *Animal species and evolution*. Belknap Press, Cambridge, MA.
- Monaghan, M. T., R. Wild, M. Elliot, T. Fujisawa, M. Balke, D. J. G. Inward, D. C. Lees, R. Ranaivosolo, P. Eggleton, T. G. Barraclough, et al. 2009. Accelerated species inventory on Madagascar using coalescent-based models of species delineation. *Syst. Biol.* 58:298–311.
- Noor, M. A. F. 2002. Is the biological species concept showing its age? *Trends Ecol. Evol.* 17:153–154.
- Nosil, P., B. J. Crespi, and C. P. Sandoval. 2002. Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* 417:440–443.
- Ochman, H., E. Lerat, and V. Daubin. 2005. Examining bacterial species under the spectre of gene transfer and exchange. *Proc. Natl. Acad. Sci. USA* 102:6595–6599.
- Orr, H. A. 2001. Some doubts about (yet another) view of species. *J. Evol. Biol.* 14:870–871.
- Pigliucci, M. 2003. Species as family resemblance concepts: the (dis-)solution of the species problem? *BioEssays* 25:596–602.
- Rieseberg, L. H. 2001. Chromosomal rearrangements and speciation. *Trends Ecol. Evol.* 16:351–358.
- Rieseberg, L. H., S. A. Church, and C. L. Morjan. 2003. Integration of populations and differentiation of species. *New Phytol.* 161:59–69.
- Rundle, H. D., L. Nagel, J. W. Boughman, and D. Schluter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. *Science* 287:306–308.
- Rundle, H. D., F. Breden, C. Griswold, A. Ø. Mooers, R. A. Vos, and J. Whitton. 2001. Hybridization without guilt: gene flow and the biological species concept. *J. Evol. Biol.* 14:868–869.
- Sarkar, I. N., P. J. Planet, and R. DeSalle. 2008. CAOS software for use in character based DNA barcoding. *Mol. Ecol. Res.* 8:1256–1259.
- Schluter, D., and L. M. Nagel. 1995. Parallel speciation by natural selection. *Am. Nat.* 146:292–301.
- Simpson, G. G. 1951. The species concept. *Evolution* 5:285–298.
- . 1961. *Principles of animal taxonomy*. Columbia Univ. Press, New York.
- Sites, J. W. Jr., and J. C. Marshall. 2004. Operational criteria for delimiting species. *Annu. Rev. Ecol. Syst.* 35:199–227.
- Soltis, D. E., and P. S. Soltis. 1999. Polyploidy: recurrent formation and genome evolution. *Trends Ecol. Evol.* 14:348–352.
- Soltis, P. S., and D. E. Soltis. 2000. The role of genetic and genomic attributes in the success of polyploids. *Proc. Natl. Acad. Sci. USA* 97:7051–7057.
- Staley, J. T. 2006. The bacterial species dilemma and the genomic-phylogenetic species concept. *Phil. Trans. R. Soc. Lond. B* 361:1899–1909.
- Telschow, A., P. Hammerstein, and J. H. Werren. 2005. The effect of *Wolbachia* versus genetic incompatibilities on reinforcement and speciation. *Evolution* 59:1607–1619.
- Templeton, A. R. 1989. The meaning of species and speciation. Pp. 3–27 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, MA.
- Waples, R. S., and O. Gaggiotti. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol. Ecol.* 15:1419–1439.
- Werren, J. H., L. Baldo, and M. E. Clark. 2008. *Wolbachia*: master manipulators of invertebrate biology. *Nat. Rev. Microbiol.* 6:741–751.



- White, M. J. D. 1954. *Animal cytology and evolution*. Cambridge Univ. Press, Cambridge, UK.
- Wiens, J. J. 2007. Species delimitation: new approaches for discovering diversity. *Syst. Biol.* 56:875–878.
- Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Syst. Zool.* 27:17–26.
- Wu, C.-I. 2001. The genic view of the process of speciation. *J. Evol. Biol.* 14:851–865.
- Wu, C.-I., and C. T. Ting. 2004. Genes and speciation. *Nat. Rev. Genet.* 5:114–122.

Associate Editor: D. Fairbairn