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Department of Biological Sciences, Columbia University, New York, NY, USA

Species: the concept, category and taxon

Walter J. Bock

Abstract

The term species by itself is vague because it refers to the species concept, the species category and the species taxon, all of which are distinct although related to one another. The species concept is not primarily a part of systematics, but has always been an integral part of basic biological theory, It is based on evolutionary theory and applies only to sexually reproducing organisms. The species concept and the phyletic lineage concept are quite distinct although they are related to one another. The important aspect of the species concept is lack of gene flow between different species, and hence the defining criterion of the species is genetic isolation. The species concept is often considered as non-dimensional, both in time and space. Species possess three different major properties, namely genetic isolation, reproductive isolation and ecological isolation; these properties evolve at different times and under the effect of different causes during the speciation process. Speciation requires an external isolating barrier during the initial allopatric phase in which genetic isolation evolves and must reach 100% efficiency. The subsequent sympatric phase of speciation occurs after the disappearance of the external isolating barrier when members of the two newly evolved species can interact with one another and exert mutual selective demands on one another. Much of the reproductive and ecological isolation evolves during this secondary sympatric phase. The species category is a rank in the taxonomic hierarchy and serves as the basis on which the diversity of organisms is described; it is not the same as the species concept. The species category applied to all organisms, sexually and asexually reproducing. The species taxon is the practical application of the species category in systematics with the recognition of species taxa requiring many arbitrary decisions. No single set of rules exist by which the species category can be applied to all organisms. Recognition of species taxa in asexually reproducing organisms is based on amount of variation and gaps in the variation of phenotypic features associated with ecological attributes of these organisms as compared with similar attributes in sympatric species taxa of sexually reproducing organisms. Species taxa are multidimensional in that they exist over space–time and often have fuzzy borders. Because recognition of species taxa, including those in sexually reproducing organisms, depends on many arbitrary decisions especially when dealing with broad geographical and temporal ranges, species taxa cannot be used as the foundation for developing and testing theoretical concepts in evolutionary theory which can only be done with the non-dimensional species concept.

Key words: Species – phyletic lineage – concept – category – taxon – speciation

Introduction

Perhaps more problems exist in understanding the species concept than any other basic theoretical idea in biology in spite of excellent analyses of this concept by Mayr (1940, 1942, 1949, 1957, 1963, 1982a,b, 1986, 1987, 1988) and others. Much of this confusion apparently arises from the erroneous belief accepted by most workers that the theoretical species concept lies within the purview of systematics with some authors claiming that evolutionists have stolen the species from systematists. Further there has been attempts to develop a single species concept applicable to all organisms (Mishler and Brandon 1987) which is simply impossible. Rather, the species concept is part of basic biological theory and should not be considered the same as the species category as has been stated or implied by many workers. Recognition of species taxa depends on the definition of the species category, not on the species concept as pointed out by Mayr (1969, pp. 27–29). The species concept has changed fundamentally over time and with these changes, our ideas on species taxa have modified accordingly. From the earliest days of biological thinking until sometime after Darwin published his 'On the origin of species', the species concept was based on typological essentialism following the ideas of Plato and other early philosophers. The typological species concept is usually, but erroneously, called the morphological species concept and was applied equally to all organisms, both those reproducing sexually and asexually. Species taxa were recognized morphologically corresponding to ideas about typological essentialism. Geographic variants were treated as different species, as were many distinctive morphs within populations. As evolutionary ideas became better known, the basis of the species concept modified gradually according to understanding of evolutionary theory. By the early years of the 1940s many, but not all, workers based the species concept firmly on evolutionary theory with the biological species concept being the generally accepted one advocated by Mayr (1940, 1942), and based on earlier ideas of Jordon (1896, 1905); Poulton (1903); Rensch (1929) and others. The biological species concept applies only to sexually reproducing organisms, although most systematists do not use reproduction information when describing species taxa which are still recognized morphologically. However, morphs within populations, when recognized, are no longer considered as species and geographic variants are grouped together into broadly-based polytypic species taxa. Yet many workers continue to treat the species concept as if it was part of systematics and to believe that a single species concept exists and can be applied to all organisms, sexually and asexually reproducing. Although earlier comments may exist, Szalay and Bock (1991, p. 10) state clearly that the species concept is not a part of systematics, but rather is an integral part of evolutionary theory.

This review of the species notion will stress the necessity to distinguish between the species concept, the species category and the species taxon and that these terms should be used rather than the general term species. It will be founded on several fundamental points, namely: (a) the theoretical species concept (the non-dimensional species concept) is part of evolutionary theory and applies only to sexually reproducing organisms; (b) the species concept differs from the phyletic lineage concept; (c) recognition of species taxa in nature is part

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of systematics practice and is based on the definition of the species category and applies to all organisms, both sexually and non-sexually reproducing; (d) for sexually reproducing organisms (the multi-dimensional species notion), species taxa should be as close to the theoretical concept as possible; and (e) no single set of rules to recognize species taxa exists which can be applied equally well to all organisms.

Species versus phyletic lineages

Before it is possible to discuss the several uses of the term species, it is necessary to make a clear distinction between the species and the phyletic lineage. If the species concept is based on evolutionary theory, the first decision is which unit within this theory is to be considered the species. This problem arises because two distinctly different, but related units have been denoted as the species by number of different workers. Many workers do not make a distinction between the species concept and the phyletic lineage concept. This is especially true for philosophers of science who appear to be uniform in confusing these two concepts (see papers in Wilson 1999). One must be most careful in reading the biological and philosophical literature to determine whether the author really means 'species' or 'phyletic lineage' when the term species is used; often it is not possible to determine which of these two units was meant and to comprehend the presented analysis.

These two concepts (Fig. 1) are:

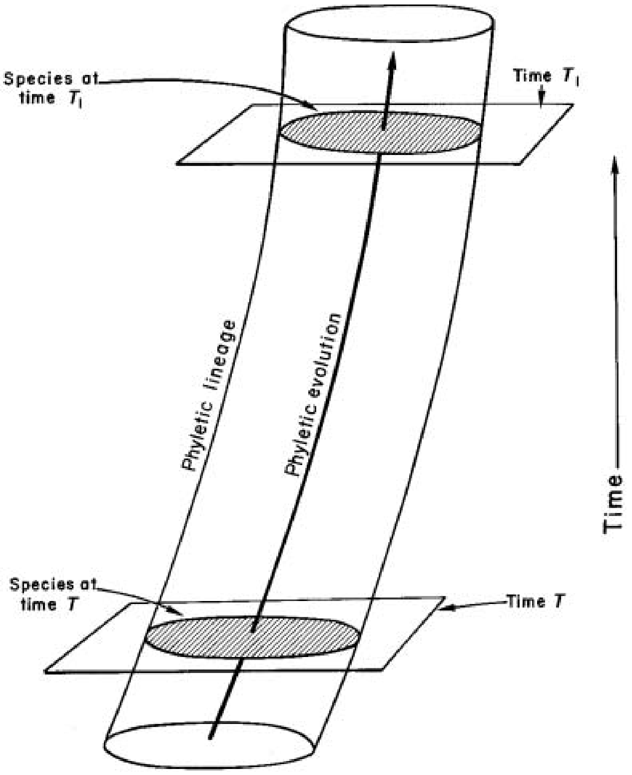

Fig. 1. Schematic model of a phyletic lineage which is the time line of a species reproducing itself; any change in the species with respect to time is phyletic evolution. A cross-section through the phyletic lineage at any time is a species. Cross-sections at different points in time are neither the same species or different species because no species boundary separates them; they are simply different cross-sections of the same phyletic lineage

(1) The species concept which is the complex of interbreeding individual organisms co-existing at one point in time which is genetically isolated from other such complexes (see below for a formal definition); and
(2) The phyletic lineage which is the time-line of the species resulting from it reproducing itself generation after generation).

Only the first of these two concepts is properly termed the species; the second is the phyletic lineage (Bock 1979, 1986, 1992). The species is a real unit existing in nature whereas the phyletic lineage represents the history of the species and cannot be said to be a real unit existing in nature. Species reproduce themselves generation after generation and can evolve. Phyletic lineages are the consequences of species having reproduced themselves and represent the history of this reproduction over time. Once a phyletic lineage has occurred, it can no longer change aside from it extending into the future so long as the species does not become extinct. Phyletic lineages no longer evolve, they are the result of past evolutionary change.

Cross-sections through a phyletic lineage represent species at the different times of these cross-sections. But regardless of how similar or dissimilar the organisms are at these different cross-sections, one cannot say whether they represent the same or different species if one assumes that evolutionary change is gradual. It is a *non-question* to ask whether these different time slices of a phyletic lineage represent the same species or different species. In theoretical considerations, limits cannot be placed on a species taxon along a phyletic lineage because any such limits would necessitate drawing a boundary between one species taxon and its successor. Such boundaries would imply an evolutionary change 'between species taxa' different from evolutionary change 'within the species taxon,' a distinction which has never been demonstrated. Therefore, if species cannot be delimited along a phyletic lineage, it is not possible to speak of the origin or the birth of a species, nor is it possible to speak of the age of a species. All existing species are of equal age, or in other terms, all species are ageless.

Species boundaries are real only in horizontal comparisons, which are between different lineages (Bock 1989), and do not exist in vertical comparisons (within a single phyletic lineage). Hence one cannot make a distinction between evolution within a species and evolution beyond the species boundary (trans-specific evolution). Evolution along a phyletic lineage never results in a new species and hence never passes a species limit regardless of the amount of phyletic evolutionary change that has taken place (Bock 1979, 1986). These misconceptions had resulted from extrapolating the valid concept of species boundaries between contemporary species taxa into the time dimension and thereby concluding that a boundary exists between an ancestral species and its descendent species.

A distinction should be made between the typological (essentialistic) species concept and the morphological species concept. The latter does not now or ever have existed as a proper theoretical species concept except as a misnomer for the typological species definition. That most species taxa are recognized on the basis of morphological criteria in immaterial to the definition of the species concept. Some workers (Mishler and Brandon 1987) have proposed a morphological species definition in the attempt to advocate a single species concept for all organisms, including asexually reproducing forms. In essence, these definitions do little more than state that the species is what a taxonomist calls a species taxon. Such recent efforts to propose morphological species concepts, regardless of the wording of the definition, represent a confusion between the theoretical definition of the species concept and guidelines for recognizing species taxa (multi-dimensional species notions). Unless authors proposing a morphological species concept also present a sweeping re-analysis of evolutionary causes and processes, including full considerations of causes and processes involved in sexual and asexual reproduction and their bearing on evolution which support their ideas on the species, morphological species concepts should be rejected out of hand.

Several species concepts – the evolutionary (Simpson 1951, 1961, p. 153; Wiley 1978, 1981), phylogenetic (Cracraft 1983, 1989; McKitrick and Zink 1988), cladistic (or Hennigian; Meier and Willman 2000), and the internodal (Kornet 1993) – are actually segments of phyletic lineages. All of these species concepts are based on the premise that different species can be distinguished from one another along a phyletic lineage which violates the basic principle of nomological evolutionary theory that evolutionary change is gradual and hence that no boundary can be drawn between successive species along a phyletic lineage (see above). Possibly it may be argued that these 'species concepts' are actually definitions of the species category or more likely of the species taxon. But in no way can they be considered species concepts under current nomological evolutionary theory. I will not discuss these species concepts further. The reader is referred to Coyne et al. (1988); Bock (1992); Wheeler and Meier (2000); Mayr (2004) and the papers cited above for additional comments.

The species concept

In the decades following Darwin, biologists struggled to ascertain the core of the species concept and finally agreed that species are groups of interbreeding individuals which possess vertical gene flow between them because of the production of offspring (Jordon 1896, 1905; Poulton 1903; Rensch 1929). The evolution of species accompanied the evolution of sexual reproduction with the evolution of limits between contemporary species restricting the range of recombinations resulting in sexual reproduction (Mayr 1949, 1959, 1988). Genetic variation in populations of sexually reproducing organisms is advantageous in allowing the production of new phenotypic traits because of the recombinations of genotypes. But too much genetic variation does have disadvantages in that too many inviable individuals will be produced and eliminated by selective demands. Species boundaries place limits on the amount of the genetic variation of each population and still allow a broad utilization of the available environmental diversity by subdividing the total range of genetic variation into discrete segments.

The boundary between species is genetic isolation or lack of (vertical) gene flow between members of different species. That is, members of a species can interbreed with one another and contribute genes to the production of offspring, but members of different species cannot do so. Or to put it in another way, members of the same species can have descendants in common, but members of different species (usually) cannot. Genetic isolation became the accepted criterion for the species concept during the evolutionary synthesis. Gene flow between species is achieved only by interbreeding (i.e. reproduction) between them. But evolutionists failed to recognize that a peculiar asymmetry exists between genetic isolation and reproductive isolation. If two species are reproductively isolated, they are also genetically isolated. But species can be genetically isolated without being reproductively isolated. Unfortunately evolutionists confused genetic isolation with reproductive isolation. They were thinking 'genetical isolation' as the basis for the species concept, but used the term 'reproductive isolation' as the defining criterion. And hence the species concept was defined in the period of the evolutionary synthesis as '*Species are groups of actually or potentially interbreeding natural populations, which are* ***reproductively*** *isolated from other such groups*' (Mayr 1942, p. 120).

Species which are reproductively isolated are genetically isolated but the reverse is not necessarily true. The horse and donkey represent two species which are genetically isolated but not reproductively isolated, at least under captive conditions if not in the wild. This confusion between genetic and reproductive isolation resulted in disagreements on aspects of speciation such as whether selective demands can increase genetic isolation from <100 to 100% after sympatry has been established between newly evolved species. Koopman (1950) did an excellent experiment as his PhD thesis under Dobzhansky in which he concluded the amount of isolation between *Drosophila pseudoobscura* and *Drosophila persimillis* could be increased with selective demands. He did indeed show that the amount of hybridization between these two species decreased during the course of the experiment, but he was dealing with increased reproductive isolation and not with genetic isolation as he thought. Because of his experimental procedure, the two species were 100% genetically isolated at the onset of the experiment, and it is not possible to improve on this degree of genetic isolation. These confusions about the species concept and the process of speciation is also shown in diverse papers in Giddings et al. (1989). One must use care in reading the literature on species because the terms genetic isolation and reproductive isolation are frequently used interchangeably. If reproductive isolation is used, it is usually in the meaning of genetic isolation.

For these reasons, I proposed a minor, but significant, modification of the biological species concept (Bock 1986, p. 33), namely that: '*A species is a group of actually or potentially interbreeding populations which are* ***genetically*** *isolated in nature from other such groups*'. This definition is actually what was meant by the original proposers of the biological species concept as can be determined from their entire analysis. Genetic isolation between species is achieved by the possession of intrinsic isolating mechanisms (IIM; see Mayr 1963, pp. 91–109; and see below).

Mayr (1963, p. 17) introduced the idea of the non-dimensional species concept (the biological species concept) which is most fundamental, but has been little appreciated by evolutionary biologists and systematists. Unfortunately Mayr did not connect the non-dimensional species concept tightly with evolutionary theory and did not contrast it sufficiently with the multi-dimensional species notion (multi-dimensional species concept as used by Mayr)[1] which is applied in systematic practice to species taxa. It cannot be stressed too strongly that further development of evolutionary theory can be achieved only with the non-dimensional species concept, not with the

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[1] Unfortunately Mayr used the term concept for both the non-dimensional and the multi-dimensional species, implying that these two notions were the same. The former is the theoretical species concept while the latter refers to the species taxon.

multi-dimensional species notion or with all recognized species taxa.

With the development of thinking about species and especially with development of understanding of genetics and nomological evolutionary theory, the species concept evolved since the early part of the 19th century so that it now applies only to sexually reproducing organisms (Mayr 1959). Remember that the species concept is part of basic biological theory which in this case is nomological evolutionary theory. The species concept is *not* primarily part of systematics contrary to the claims of many systematists. It has no meaning for asexually reproducing organisms which are not organized into interbreeding units. Species taxa corresponding to the species concept appeared in the history of life at some (reasonably short) time after the evolution of sexual reproduction, or possibly in conjunction with the evolution of sexual reproduction. The necessity for species results from the mechanisms of meiosis (the shuffling and recombination of existing genetic variation during gamete formation) and of fusion of two haploid gametes into diploid zygotes of the next generation, all of which shuffles and recombines the genetic material existing in the genotypes of parental organisms into new offspring genotypes. If too much variation exists among the genotypes of the parental organisms, then the possibility of producing too many non-viable offspring is great. Species, and hence species boundaries, provide limits to the amount of genetic variation existing within each species. The arrangement of sexually reproducing individuals into discrete species taxa permits a more efficient subdivision of the environment by sympatric species (Mayr 1949, 1986, 1988).

The current species concept (based on evolutionary theory) applies only to sexually reproducing organisms which is a major difference from the former typological species concept which was applied to all organisms. Restriction of the species concept to sexually reproducing organisms developed with a continuing analysis of evolutionary theory and genetics. The importance of sexual reproduction for evolutionary change and the fact that most organisms are sexually reproducing led to the focusing on genetic isolation as the major criterion of the species concept. This was not the only possible development of the species concept under evolutionary theory, but is the one which occurred and hence the present definition of the species concept and the current restriction of the species concept to sexually reproducing organisms.

The fact that most types of organisms are arranged into species with discrete boundaries is not an autonomic consequence of nomological evolutionary theory. There is nothing in basic evolutionary theory which necessitates the existence of the species concept and organisms arranged into clumps (species taxa) based on this concept. Rather sexual reproduction evolved with all of its advantages for evolutionary change due to the possibilities of recombinations of the parental genetic material in their offspring as well as the disadvantages of excessive non-viable offspring occurring is the amount of genetic variation became too great. As mentioned above, one of the results of the evolution of sexual reproduction in the evolutionary history of living organisms was the evolution of mechanisms by which organisms were divided into discrete species with boundaries between them to prevent exchange of genetic material between different species.

Lastly, it should be mentioned that species and speciation are not irreversible as assumed by some workers. Good species taxa may evolve and exist sympatrically for a period of time, but then may start to interbreed, exchange genetic material and finally reunite into a single species (Bock 1986)[2]. An excellent example is the towhees (*Pipilo erythrophthalmus* and *Pipilo ocaci*) found in the central Mexican highlands (Sibley 1950) which started to hybridize some hundreds of years ago and have become a single genetic-reproductive-ecological unit over most of their range. Such subsequent interbreeding and merging of formally good species depends on the nature of the intrinsic isolating mechanisms previously separated them.

The species category

Categories are the diverse levels recognized in the Linnaean hierarchy, such as species, genus, family, etc., which are used in biological classification. The species category is the basic level in this hierarchy in that all other categories are defined in terms of the species category, either directly or secondarily. Most workers have assumed that the species category is the same as the species concept and hence that the biological species concept is the species category (Mayr and Ashlock 1991, Chapter 2). Unfortunately this assumption is not valid because the species category must apply to all organisms, including asexual ones, and the biological species concept applies only to sexually reproducing organisms. A broader definition of the species category is needed. This broader definition, however, must not be in conflict with the biological species concept.

The species category can be defined as: *This is the fundamental level in the Linnaean hierarchy used to describe the diversity of biological organisms. The species category is based on the biological species concept for sexually reproducing organisms (each biological species consists of a genetic, reproductive and ecological unit) and on groups of asexual organisms (agamospecies) equivalent to the ecological unit of biological species.* This definition is somewhat awkward, but this is the consequence of the species category having to cover all organisms, both sexually and asexually reproducing, and of biological organisms being so diverse. (See below for the discussion of the genetic, reproductive and ecological units of species taxa.)

It should be noted that the definition of the species category omits mention of monophyly as is the concern of the cladistic species ‘concept’. This is because many, valid taxa at the level of the species category are not monophyletic under the general sense of that concept. Valid species taxa include tetraploid and other species taxa of plants which evolved by hybridization of two species followed by doubling of chromosome number. And if a single definition of the species category is desired, then it must exclude mention of monophyly if species taxa of hybrid origin are to be included under the species category.

Categories at all other levels in the Linnaean hierarchy are defined in terms of the species category. Hence the generic category is defined as a monophyletic taxonomic group containing one or more species. And the subspecies category as a geographic subdivision of the species category.

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[2] In such cases, members of different good species will have descendants in common as also happens in those groups of plants in which speciation occurs by hybridization between members of good species followed by doubling of the chromosomes. In all of these cases, the formally operating intrinsic isolating mechanisms for genetic isolation between these species taxa have broken down and genetic material is exchanged between members of the formally good species.

The species taxon

Introduction

As mentioned earlier, the source for much of the controversy on the species within systematics arises in the confusion from the use of the same word 'species' for the species concept, the species category and the species taxon, and from the belief of most biologists that the species concept is a part of systematic theory. A clear distinction must be made between these three species terms and especially between the species concept and the species taxon (the unit used in systematics when describing biodiversity observed in nature). And as mentioned earlier, the species concept is an integral part of evolutionary theory, not of systematic theory. The species taxon is derived from the species category, but the two are sharply distinct from one another. It must be emphasized that species taxa are not the same as species concepts, and that the species taxa recognized by systematists are at least one step removed (the species category) from the species concept regardless of the accepted species concept. Species taxa (taxonomic groups at the level of the species category) are *never defined*, but are *recognized and delimited* with a description permitting identification of other individual organisms as members of each species taxon. Recognition of species taxa – the real units in nature – is almost always based on criteria other than that used as the defining criterion for the species concept and even for the species category. Just because the paleontologist cannot ascertain whether the individual organisms present as fossils could or could not have interbred with one another, this does not provide a justified argument on which to reject the species concept defined on the basis of genetic isolation. Most species taxa are recognized on the basis of morphological characteristics which are presumed to correlate with genetic isolation. Considerable interpretation is needed in many cases in deciding on the limits of species taxa, especially when there is a considerable geographical or chronological range and variation.

Major attributes of the species

Biological species are those with sexual reproduction and possess three major attributes or can be regarded as representing three different types of units (Bock 1986, pp. 34–37; Mayr 1969, p. 26); these attributes or units are:

(I) Genetic isolation (a genetic unit) in that members of a species taxon constitute a genetic community which is genetically isolated from other species taxa. Gene flow exists among members of a species, but not from members of one species to members of another under natural conditions. The species is the largest unit in which gene flow or genetic recombinations can take place, aside from the occasional hybridization. Genetic isolation between members of different species taxa is maintained by genetic intrinsic isolating mechanisms which are phenotypic properties of the individuals of the species taxa. The set of genetic isolating mechanisms is not identical with the set of reproductive isolating mechanisms (see below) although there is a broad overlap between the two sets. Unfortunately biologists had not distinguished between the similar sets of genetic isolating and reproductive isolating mechanisms, but have treated them together under the broad heading of intrinsic isolating mechanisms.

Mayr (1963, p. 92; Table 5-1) has presented a thorough analysis and classification of genetic intrinsic isolating mechanisms, as follows:

Classification of genetic isolating mechanisms.

(1) Mechanisms that prevent interspecific crosses (premating mechanisms):

(a) potential mates do not meet (seasonal and habitat isolation),
(b) potential mates meet but do not mate (ethological isolation),
(c) copulation attempted but no transfer of sperm takes place (mechanical isolation).

(2) Mechanisms that reduce full success of interspecific crosses (postmating mechanisms):

(a) sperm transfer takes place but egg is not fertilized (gametic mortality),
(b) egg is fertilized but zygote dies (zygote mortality),
(c)* zygote produces an F_1 hybrid of reduced viability (hybrid inviability),
(d)* F_1 hybrid zygote is fully viable but partially or completely sterile, or produces deficient F_2 (hybrid sterility).

All of these intrinsic isolating mechanisms serve to prevent exchange of genetic material between members of different species taxa and therefore to achieve genetic isolation. However these intrinsic isolating mechanisms differ in other properties, most importantly in their reproductive cost which range from a very low to no reproductive cost for mechanism 1(a) to very high reproductive cost for mechanism 2(d). Moreover mechanisms 2(c) and 2(d), marked with an * which achieve genetic isolation between species taxa, do not result in reproductive isolation. Yet all of these intrinsic isolating mechanisms are cited by evolutionists as serving to maintain the distinctiveness of species taxa under the biological species concept in which the defining criterion is reproductive isolation (see discussion above). The set of intrinsic isolating mechanisms as given here are valid; it is the defining criterion of reproductive isolation in the biological species concept which is inappropriate.

(II) Reproductive isolation (a reproductive unit) in that members of a species taxon form an interbreeding community which is reproductively isolated from other species taxa. Members of one species taxon do not interbreed or attempt to interbreed with members of another species taxa under natural conditions regardless of the barriers to gene flow between these species taxa; except for the occasional hybridization. Reproductive isolation between species taxa is not the same as genetic isolation. Two species taxa could be genetically isolated without being reproductively isolated such as horses and donkeys which can reproduce, but the offspring are sterile mules. Most evolutionists have not made any distinction between genetic isolation and reproductive isolation. Interbreeding between members of different species taxon is prevented by reproductive isolating mechanisms which can be classified as follows:

(1) Mechanisms that prevent interspecific crosses (premating mechanisms):

(a) potential mates do not meet (seasonal and habitat isolation),
(b) potential mates meet but do not mate (ethological isolation),
(c) copulation attempted but no transfer of sperm takes place (mechanical isolation).

(2) Mechanisms that reduce full success of interspecific crosses (postmating mechanisms):

(a) Sperm transfer takes place but egg is not fertilized (gametic mortality),

(b) Egg is fertilized but zygote dies (zygote mortality).

This set of reproductive isolating mechanisms is a subset of the set of genetic isolating mechanisms; mechanisms 2(c) and 2(d) from the set of genetic isolating mechanisms are lacking. Because successful reproduction is usually considered to be the production of a free-living offspring, death of the zygote (fetal organism) would be counted as unsuccessful reproduction. Mechanisms based on a fertilized egg, but death of the zygote would be at the very limits of effective reproductive isolating mechanisms. I would not argue, however, with the position that mechanisms 2(a) and 2(b) should not be included in the set of reproductive isolating mechanisms.

(III) Ecological isolation (an ecological unit) in that members of a species taxon form an ecological community in which the organisms possess similar ecological requirements that differ from those possessed by members of other species taxa. Because species taxa are different ecological units means that competition between sympatric members of different species taxa will be greatly reduced or will not exist. The fact that members of a species taxon constitute an ecological unit depends on the possession of similar 'ecological' features in these organisms which differ from the 'ecological' features present in members of other species taxa. The phenotypic features resulting in ecological isolation insure that individual organisms of a species taxa are integrated whole organisms that are viable in the normal environment occupied by the species taxon. These features can be grouped together under the general heading of the adaptive features of the species taxon. Lack (1944, 1949, 1971) is one of the few biologists who stressed ecological separation between species taxa and how these features evolve during speciation.

The necessity of protecting co-adapted complexes of phenotypic features during the processes of meiosis and zygote formation during sexual reproduction led to the evolution of species (Mayr 1969, 1987, 1988). The break-up of these co-adapted complexes of phenotypic features is best shown in cases of extensive hybridization (Anderson 1949). Break-up of co-adapted, integrated organisms in the next generation following sexual reproduction is prevented by keeping individual variation within reasonable bounds in the interbreeding population, and hence in the species. Hence the genetic material of the zygote which comes from two different parents interact during ontogeny to form viable co-adapted offsprings. These are the ideas underlying the concept of the 'unity of the genotype' advocated by Mayr (1954, 1963, Chapter 10).

Claims that the species taxa under the biological species concept are reproductive and ecological units in addition to genetic units does not mean that the species concept has been also defined in terms of reproduction and ecology. No consideration had been given to the species as a reproductive unit because almost all biologists had equated genetic and reproductive isolation. Some biologists have claimed that statements that species are also ecological units (Van Valen 1976) but this does not mean that the species concept has to be defined ecologically. When defining concepts, within or outside of science, it is always best to use only one defining criterion to avoid difficulties when objects in nature corresponding to the concept lacks one of more of the defining criteria. This is indeed the case with species taxa in which not all are reproductively and/or ecologically isolated; only fully evolved species taxa possess all of there properties.

The biological species, as advocated in herein, is defined strictly in terms of genetic isolation, but species taxa have sets of properties in addition to being genetically isolated. As emphasized earlier (Bock 1986, 1992, see also Moore 1957), these different properties of species taxa evolve under the action of different evolutionary causes and may evolve at different times during the speciation process. For example, isolating mechanisms for genetic isolation never evolve under the action of selective demands for genetic isolation, but are pleiotrophic results of other evolutionary changes during the allopatric phase of speciation. These isolating mechanisms must be 100% developed by the time the two new species become sympatric. Reproductive isolating mechanisms and ecological differences may, and usually do, evolve in part under the action of selective demands for reproductive and for ecological isolation during the sympatric part of speciation.

It must be emphasized that species do not necessarily have to possess all three of these attributes. To be sympatric, species must be genetically isolated, but can still not be completely reproductively and/or ecologically isolated. Species can be considered to be fully evolved only when they are distinct in all of three attributes.

Recognition of species taxa

The fact that asexually reproducing organisms exist in many groups of organisms has no bearing on the biological or any other species concept. The criteria used to recognize species taxa, be they for sexually or asexually reproducing organisms, are generally not the defining criterion used in the species concept, but these recognition criteria are derived from the application of the species concept in classifying the spectrum of biodiversity in nature. One starts with the species category and ascertains how one recognizes species taxa in nature under certain conditions, such as whether the organisms have sexual or asexual reproduction or if the species taxa coexist in one locality or are found in different localities on the earth. If the species taxa differ in degree or if the criteria used for recognizing species taxa vary in these different studies, one must then make decisions on how to modify the criteria and which criteria to use for the recognition of all species taxa. This is done with the realization that species taxa may not be the same for all groups of organisms. What must be kept in mind is that species taxa, as all other taxa in biological classification, serve as the foundation for all other biological analyses and hence should be as similar to one another as possible.

Hence the argument that the biological species concept is wrong because it does not apply to all species taxa in all groups of organisms simply has no meaning. Contrary to the beliefs of most systematists, the value of the biological species concept or any other species concept can be decided only by a consideration of its role within evolutionary theory, not by a consideration of systematic practice.

Many workers (e.g. Mishler and Donoghue 1982; Mishler and Brandon 1987; papers in Wheeler and Meier 2000) continue to advocated same species concept of all organisms. Often when workers argue for a single species concept and/or the same criteria for species, it is not at all clear whether they refer to the species concept or to species taxa. I will assume the latter. Even when considering requirements associated with describing the earth's biodiversity, I cannot see any basis for advocating the same criteria for species taxa of all organisms aside from some rather generalized and vague statement. However species taxa are recognized, this must be based on evolutionary theory and must be related ultimately to the biological species concept and to the species taxa of the local naturalist – sympatric species taxa. If sympatric species taxa of many different major groups of animals and plants are examined, it will be discovered that the phenotypic features associated with the species as a genetic unit, as a reproductive unit and as a ecological unit vary considerably among these sympatric species taxa. Indeed, even within a restricted group such as birds, the degree of difference in these phenotypic features will vary considerably among sympatric species of different orders and even families. Thus, there does not appear to be any possibility of advocating the same criteria for recognizing species taxa in all organisms.

Rather, the most reasonable approach is to recognize allopatric and asexual species taxa on the basis of the phenotypic characteristics associated with the three units characterized by sympatric species taxa in closely related groups of organisms, e.g. birds, or mammals, or butterflies.

If one examines the biodiversity of a group of sympatric organisms – such as all vertebrates or all vascular plants living in a single geographic location, such as the New York City region or the Hamburg region – then the species taxa are easily delimited from one another especially among sexually reproducing organisms. In most cases, the species taxa of asexually reproducing organisms are also readily delimited from one another. These are the species taxa designated by Mayr (1947) as the species of the local naturalist. If the species taxa of the local naturalist are examined in the light of the biological species concept, it will be found that these species taxa in sexually reproducing organisms correspond quite closely to the defining criterion of the biological species concept (e.g. Mayr 1992). That is, these species taxa are both genetically and reproductively isolated. Further examination of these species taxa will reveal that almost all of these local species taxa, both of sexually and of asexually reproducing forms, represent distinct ecological units.

If one then examines the biodiversity of a larger area, such as the northeastern states of the USA, or western Europe, then the question of delimiting all species will not be as easy because one is be faced with geographical variation. Populations will be found which are clearly geographic variants of one another. These populations will possess distinctive sets of phenotypic features, and, in some cases, will be completely geographically separated from one another so that no intermediates (integration) from one population to the other exit. This problem of geographic variation and of geographically isolated populations increases as the biodiversity of larger and larger geographic areas are included in the analysis.

The major problems facing the working systematist is how to deal with geographic (allopatric) forms, with fossil organisms, and with asexual organisms. These are quite different questions and a general solution cannot be offered. Each of these types of species taxa will be considered separately.

Asexual organisms

One of the results of recognizing species taxa in sexually reproducing organisms is sorting out the ecological diversity into organized units based on the fact that each species is a separate ecological unit. These distinct ecological units of sexual species reflect the discontinuity of ecological conditions from which arise a discontinuity of selective demands. These selective demands result in discontinuous distribution of phenotypic features in the different species taxa. Presumably the ecological conditions and ensuing selective demands acting on asexual organisms are also discontinuous with the result that the distribution of phenotypic features of asexual organisms will also have gaps. Hence in most groups of asexual organisms, phenotypic features which are adaptations to selective demands arising from the external environment will cluster groups of individuals together with distinct gaps between these clusters. These clusters of individuals in asexual organisms correspond reasonably closely to the ecological units of species in sexually reproducing organisms. Hence the best set of criteria for recognizing species taxa in asexual organisms are adaptations to selective demands arising from the external environment of these organisms. Such asexual species taxa will be closest in meaning to the ecological aspects of sexual species taxa.

Geographic representatives

Among sexually reproducing organisms, the largest problems exist in the taxonomic treatment of geographically replacing populations. Herein are included all types of problems such as the degree and types of phenotypic differences among the geographic populations, whether any interbreeding occurs where they come into contact, etc. In the last century when the subspecies concept was being developed for geographically replacing populations, the central criteria was that interbreeding and integration was the hallmark of subspecies. This criterion is too simplistic as many isolated allopatric populations exist without any signs of interbreeding, but which are best treated as subspecies.

Basically, the major practical criterion for deciding on the taxonomic status of geographically replacing populations is the degree of phenotypic differences observed between sympatric species in the group. These phenotypic differences between sympatric species taxa are those associated with the intrinsic isolating mechanisms of the genetic and the reproductive units of the species and the adaptive features associated with the ecological units of the species. Hence the amount of phenotypic differences observed among sympatric species taxa can be used as the basis for deciding whether allopatric forms should be treated as subspecies of a broad polytypic species or as allospecies of a superspecies. Using this set of criteria for deciding the taxonomic rank of allopatric forms is in accordance with goal of any biological classification to have the taxa at any categorical level comparable. Hence one would prefer to have species taxa in a particular group such as birds of approximately the same evolutionary meaning (same amount of evolutionary change) which can be judged by the amount of phenotypic difference between the species.

If one recognized every distinguishable allopatric form as a separate species taxon, then these allopatric species taxa would have very different connotations for further biological analysis than would the sympatric species taxa. Comparative studies based on these dissimilar species taxa would suffer. Some workers (e.g. Cracraft 1983, 1989) have advocated such narrow allopatric species that every geographically distinct population would be recognized as a separate species rather than as subspecies. And in a similar fashion, use of broad species taxa would have the opposite consequence with many valid species taxa being treated as members of a very broad polytypic species.

Advocating narrow or broad species taxa does not depend on the basic species concept accepted. Haffer (1992) has shown decisively that whether a particular systematist recognized narrow or broad species taxa is independent of the species concept advocated by that worker. Hence it is invalid, for example, to claim that workers advocating a biological species concept will recognize broad species taxa and those advocating an evolutionary or a phylogenetic species concept will recognize narrow species taxa.

Species taxa of fossil organisms

The species concept applies only to horizontal comparisons, and has absolutely no meaning in vertical comparisons – that is to comparisons of organisms at different times within a single phyletic lineage. As noted, species taxa do not have a beginning, they do not have an age, and one cannot ask whether cross-sections of the same phyletic lineage at different times represent the same or different species taxa. Hence it is not valid to apply the species concept to the analysis of phyletic lineages which is a major part of paleontological analyses. Yet paleontologist are still faced with the problem of describing the diversity of organisms in the fossil record.

In describing fossils, paleontologists must deal with species taxa if for no other reasons than the strictures of zoological nomenclature. As such, they attempt to align species taxa of fossils (chronological species or palaeospecies) as closely as possible with species taxa in corresponding groups of recent organisms. The basis of these comparisons is strictly morphological and largely based on phenotypic features associated with ecological demands on the organisms. Paleontologists recognize variation within fossil species taxa and differences between fossil species taxa based on those observed + in related recent organisms. These comparisons are most difficult, and hence the fossil species taxa are even rougher approximations than those in recent organisms.

Paleontologists are faced with the description of chronological biological diversity and hence the description of vertically oriented species taxa or chronological species. Such taxa are perfectly valid within the demands of describing and arranging biological diversity within the fossil record. But great caution must be urged in using fossil species taxa in developing further biological, including evolutionary, theory because of the difficulties of knowing exactly what is represented by all fossil species taxa.

An example

I would like to examine the difficulties of recognizing species taxa, especially in geographically replacing populations, by discussing one example which is typical of many recent studies. My example is the North American Fox Sparrow, *Zonotrichia (Passerella) iliaca* which has been analyzed recently by Zink (1994). This polytypic species taxon is found throughout Canada to Alaska including the Aleutians and the west coast south to Washington State, and south in the Rocky Mountains to Colorado and in the Sierra Nevada Mountains to southern California. The many subspecies taxa of this sparrow can be combined into four major groups, the reddish *iliaca* ranging across Canada to the west coast of Alaska, the grey headed and slate-coloured *schistacea* of the Rocky Mountains, the grey headed, darker brown and thick-billed *megarhyncha* of the Pacific Coast of the USA and the western mountains in Washington State to southern California, and the dark sooty *unalaschcensis* of the Aleutian Islands, the Pacific coast of Alaska and Canada and Pacific Islands of Canada south to Vancouver Island (Anonymous 1987, p. 406; Sibley 2000, pp. 496–497, for colour illustrations of these taxa and of closely related species taxa of the Emberizinae). These geographic forms are more similar to one another morphologically than are the various species taxa of *Zonotrichia* to one another, and even more similar to one another that are some of the geographic races of the Song Sparrow, *Zonotrichia* (*Melospiza*) *melodia*. Zink accepts a phylogenetic species concept which he defines as 'minimally diagnosable clusters of individuals, or basal evolutionary groups, which may or may not be reproductively isolated' (1994, p. 106). This definition applies to subspecies and results in a complete blurring of the usual understanding of species and subspecies, as shown by the recognition of species taxa in the birds of paradise (Paradisaeidae) by Cracraft (1992) who recognized most of the subspecies in this family (see Frith and Beehler 1998) as species[3]. On the basis of his phylogenetic species definition, and in spite of hybridization between members of these major subspecies groups of the Fox Sparrow, Zink concludes that the four major geographic forms of the Fox Sparrow should be treated as different species taxa. The result is that the allopatric species taxa of the Fox Sparrow recognized by Zink represent very different evolutionary units than other congeneric species taxa of *Zonotrichia*. Comparative studies on the species taxa within the genus *Zonotrichia* would result in disparate conclusions, as would be any comparative analyses of the Paradisaeidae based on the species taxa recognized by Cracraft.

Whatever species concept or better stated whatever set of criteria for recognizing species taxa one accepts, this concept or set of recognizing criteria must be applied consistently to all organisms if species taxa are to have any meaning in describing biodiversiy or in comparative studies in biology. If Zink really believed in the species definition he advocates, then he should have placed each of the 18 recognized subspecies taxa of the Fox Sparrow in a different species taxon as these subspecies represent 'minimally diagnosable clusters of individuals' or basal units that he claims should be recognized as species taxa. Moreover, using the species definition and criteria accepted by Zink, one must conclude that various geographic populations of humans are different species taxa. That is the use of Zink's species definition and criteria for recognizing species taxa would result in placing me as a member of the western European human population in a different species taxon from the species taxon containing Kalahari Bushman population as well as in a different species taxa from many other human populations. It is simply not possible to advocate and apply a species concept and a set of recognition criteria in such a way that one recognizes four allopatric species of Fox Sparrows and a single species of humans. My reaction to placing the Kalahari Bushmen and Western Europeans in different species taxa is that such a taxonomic conclusion is completely wrong-headed and totally without any justification for any further

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[3] A number of the species of birds of paradise interbreed freely and form sizeable hybrid populations with considerable introgression between the parental forms, indicating that some of the traditionally recognized species have not yet acquired genetic isolation and may not have reached species status.

biological work. Therefore I must urge, in the strongest possible way, the rejection of any species definition and any set of criteria for recognizing species taxa which would result in such naive conclusions as placing different geographic populations of humans in different species taxa.

The process of speciation

Evolutionary change includes two different processes – phyletic evolution and speciation. Phyletic evolution takes place without any speciation, but speciation must involve phyletic evolution in at least one of the two lineages (Fig. 2). Only phyletic evolution has causes of evolutionary change – the formation of (genetically-based) phenotypic individual variation and selective demands. Speciation does not have any causes separate from those acting in phyletic evolution, but it does require a definite initial condition – an external barrier separating two populations of sexually breeding organisms so that there is no gene flow between them. External barrier must be clearly distinguished from both the genetic and the reproductive intrinsic isolating mechanisms which are phenotypic attributes of individuals of different species. The nature of this external barrier has been thoroughly discussed by Mayr (1942, 1947, 1963) and need not be repeated here. Clearly in most cases, this external barrier is a geographical–ecological barrier leading to geographic or allopatric speciation. The essential role of the external barrier was stressed by Mayr (1947) because genetic isolation must be in place before the other major attributes of species taxa (see above) can evolve fully.

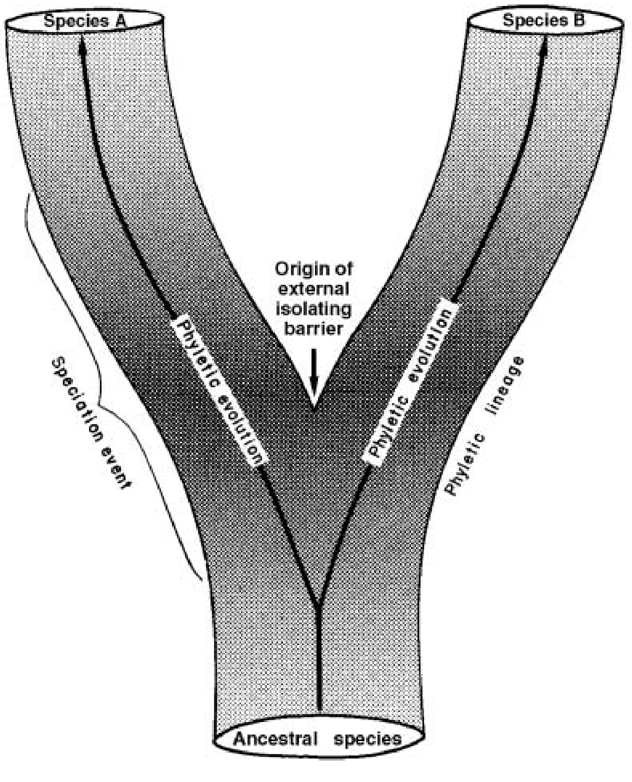

Fig. 2. Schematic model of a speciation event (splitting of a phyletic lineage into two) to show its relationship to phyletic evolution. Speciation requires the presence of an external barrier and of phyletic evolution in at least one lineage. Species A and B are distinct with a definite species boundary separating them, but neither is different from the ancestral species common to both phyletic lineages

Not all aspects of speciation will be considered herein as these have been covered by Mayr (1963 and other writings). Attention will be focused on the evolution of the evolution of the three major attributes of species and their relative timing (Fig. 3).

Evolution of the genetic intrinsic isolating mechanisms during the allopatric phase of speciation is strictly as pleiotrophic consequences of other evolutionary changes, never by the action of selective demands for these genetic intrinsic isolating mechanisms as such. Such selective demands could exist only if members of the two incipient species co-existed sympatrically, and all theoretical models show strongly that such sympatry before these isolating mechanisms were fully formed would halt the speciation process because of the resulting gene flow. Hence genetic intrinsic isolating mechanisms constitute a major class of phenotypic features

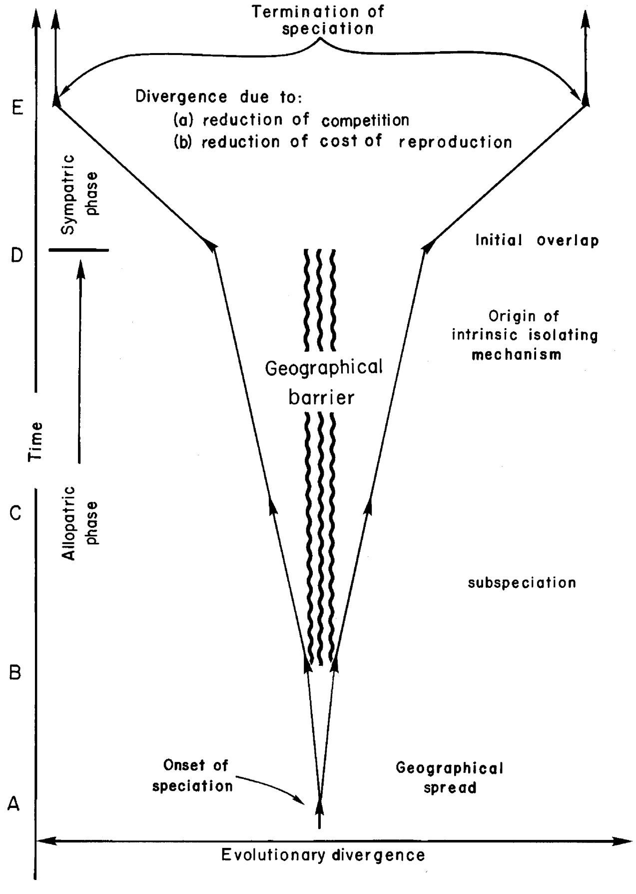

Fig. 3. Schematic model to show the divergence of the two phyletic lineages during speciation. The ancestral population (A) may have a period of subspeciation (B) before the appearance of an external barrier that separates the two lineages (C) and prevents gene flow between them. After disappearance of the external barrier (D), the two species are able to re-invade the geographic range of each other and to coexist if genetic intrinsic isolating mechanisms are fully evolved. Following is the (neo)sympatric phase of speciation (E) in which the rate of divergence usually increases sharply because of selective demands arising from exclusionary species interactions. Speciation finally comes to an end at the termination of this period of usually greater and more rapid divergence

of organisms whose evolution is never under the control of selective demands.

In the case of speciation by hybridization and subsequent polyploidy in plants, this external barrier is not required when the 2N hybrid plant is sterile and the 4N polyploid is genetically isolated from either of the parental species. That is, in this form of speciation, genetic isolation is achieved 'instantaneously' with the appearance of the 2N sterile hybrid. Hence the development of genetic isolation in speciation by hybridization-polyploidy is achieved by a single step evolutionary change. And the necessary sequence for the evolution of the diverse attributes of species taxa is maintained. The other attributes of species taxa can evolve subsequently if the process of speciation is to be completed fully.

The question still remains as to whether sympatric speciation can occur (Mayr 1993, pp. 137–138), such as has been proposed for cichlid fishes (Mayr 1984; Verheyen et al. 2003) or host specific parasitic insects (see papers in Howard and Berlocher 1998). Such speciation events (historical evolutionary explanation) may be difficult to resolve on the basis of geographical–ecological external barriers, and have been considered as examples of sympatric speciation. Still unresolved is the demonstration, as an nomological explanation, that suitable sympatric external barriers can exist for a sufficient period of time to permit the evolution of genetic intrinsic isolating mechanisms in the two sympatric populations. It is not sufficient to postulate such sympatric barriers. Their existence and operation must be shown as a nomological-deductive explanation that has been well tested with empirical objective observations before these sympatric external barriers can be invoked in a historical–narrative explanation for the evolution of complexes of sympatric species.

During the period of the Evolutionary Synthesis (1937–1948), major goals for workers interested in the species question were to identify the basic criterion for the species concept and how this property of species taxa could evolve. They fixed on genetical isolation for the defining criterion for the species concept and hence had to show how species taxa evolved intrinsic isolating mechanisms for genetic isolation given that evolution was a populational phenomenon and was gradual. Clearly this was the correct strategy as these aspects of the species concept and on the process of the speciation concept had to be solved first; their resolution was a major achievement in the evolutionary synthesis. But, having solved these problems, evolutionists believed that they had solved the entire species question. This was not to be. The speciation process is not completed at this point. There is the additional aspect of ecological relationships of species taxa. One of the few workers concerned with ecological aspects of species taxa and speciation was Lack (1944, 1949, 1971). And there was the confusion between genetic isolation and reproductive isolation which is still not appreciated by most workers. The process of speciation is not complete until reproductive isolation and ecological separation are fully evolved.

To date, almost all attention has been given to the process of speciation up to the time when the external barrier breaks down and the two new species come into direct sympatric contact. For allopatric speciation, this occurs when the geographic–ecological barrier disappears and the two species are able to expand geographically into each other's range (Fig. 3). At this point the genetic intrinsic isolating mechanisms must be 100% perfected; otherwise the two forms will start to interbreed and gene flow between them will begin. Once such gene flow starts, there does not appear to be any mechanism to stop it. Earlier arguments that selective demands can increase the efficiency of the genetic intrinsic isolating mechanisms from less than 100% (say 95%) to 100% do not have a solid theoretical foundation, and are based on the widespread confusion between genetic and reproductive intrinsic isolating mechanisms (e.g. Koopman 1950). Moore (1957) has argued convincingly against the idea that selective demands can increase the efficiency of genetic intrinsic isolating mechanisms. A secondary hybrid zone will be established and will usually increase in width. At best a narrow hybrid zone will be established as is the case of the Carrion and Hooded Crows (*Corvus corone corone* and *Corvus corone cornix*) of Europe. The width of this narrow overlap zone has been stable for several hundred years, but may have shifted in position over this time. If the genetic intrinsic isolating mechanisms are not 100% effective at this time, the process of speciation stops. The two forms are still subspecies or, at best, allospecies of a superspecies.

Following the evolution of 100% effective genetic intrinsic isolating mechanisms and establishment of true sympatry of the new species, further evolutionary changes might be required to complete the speciation process. These involve the achievement of full reproductive isolation and full ecological separation (Bock 1979). Phenotypic features associated with these two major attributes of species taxa may have started to evolve during the allopatric phase of speciation, but in most cases the largest part of the evolution of these features is during the sympatric phase of speciation under the action of mutual selective demands exerted by individuals of one species taxon on the other. These mutual selective demands are associated with exclusionary species interactions of the new species taxa (Bock 1972).

Increase in the efficiency of the reproductive intrinsic isolating mechanisms is associated with favouring those mechanisms possessing lower reproductive cost (reduction in the amount of time lost during the reproductive season by attempting to breed with individuals of another species and hence improved fitness). An examination of the list of the genetic intrinsic isolating mechanisms indicates that the reproductive cost increases from mechanism 1(a) to 2(d). Selective demands will favour phenotypic features associated with more distinctive species-specific recognition marks, courtship and other traits that permit quick recognition members of a species taxon to distinguish members of their own species from all other species and to interact and breed with members of their own species.

Increase in ecological separation is associated with all features allowing members of different species to utilize different resources of their environment and hence reduce competition, i.e. to reduce their niche overlap for resources in shorter supply. Selective demands will favour phenotypic features that decrease niche overlap and hence reduce competition between members of different species taxa.

The consequence of these evolutionary changes for greater reproductive and ecological isolation would be increased divergence between the sympatric species taxa. Although the evolution of phenotypic differences associated with these two aspects of species taxa usually start during the allopatric phase of speciation, most of their change occurs during the sympatric period because of the mutual selective demands placed by member of each species on the other. Generally, but not always, the greatest divergence between species taxa has evolved during the sympatric period of speciation. A striking case is the overlap of two species of rock nuthatches (*Sitta neumayer* and *Sitta tephronota*; Vaurie 1951) which are almost identical in their allopatric ranges, but strikingly different in their area of sympatry in Iran. The differences in bill size and in facial pattern appear to be related feeding differences (possible reduction in competition) and to species specific recognition (likely reduction in reproductive cost).

An excellent example of two not quite fully evolved species are the Blue-winged Warbler (*Vermivora pinus*) and the Golden-winged Warbler (*Vermivora chrysoptera*) of northeastern USA (Gill 1980). These species are 'almost' genetically isolated in that they can interbreed, producing fertile offspring as F1 hybrids (Brewster's Warbler) and F2 recessive offspring (Lawrence's Warbler; see Anonymous 1987, p. 354; Sibley 2000, p. 428) but these hybrids are less viable than the parental species, especially the Blue-winged Warbler), and are rapidly eliminated from the population. But these species are not ecologically separated. Rather the Blue-winged Warbler appears to be ecologically superior to the Golden-winged and is pushing the latter species northward and westward from the New York City area where they overlapped in the latter part of the 19th century.

The process of speciation is not 'instantaneous' as argued by some workers, leading to a period of 'horizontal evolution' and it does not only involve the evolution of genetic isolation. Rather it is a more complex process with full speciation including the evolution of reproductive isolation and ecological separation in addition to genetic isolation. Moreover the evolution of these three attributes of species taxa may occur at different times in the entire speciation event and they involve different evolutionary mechanisms and/or selective demands. Many of the resulting species taxa have not reached full status in that they have not completely evolved all of the attributes of species, and hence the diversity in the characteristics of recognized species taxa.

Most significant are the diverse selective demands resulting from the interactions, both arms race and exclusionary, between members of different species (Bock 1972) which are not only important during the process of speciation, but in major evolutionary changes (Bock 1979, 1986). Selective demands arising from species interactions appear to be responsible for the typical mosaic pattern (de Beer 1954) and for the rapid directional evolutionary transformation seen in most macroevolutionary changes.

Conclusions

Realization of the distinctions between the species and the phyletic lineage concepts and between the species concept, the species category and the species taxon, and the recognition of the three major attributes of species, namely genetic isolation, reproductive isolation and ecological isolation permit a better scientific and philosophical understanding of the species notion in biology. Most significant is the appreciation that species are not phyletic lineages and that equating them only leads to unacceptable conclusions on the ontology of the species concept such as species being historical individuals (Hull 1976, 1978). Discussions of pluralistic species concepts (e.g. Mishler and Donoghue 1982) are based on a failure to distinguish between the species concept and the species taxon. The plethora of species concepts, such as the evolutionary, phylogenetic, cladistic and internodal confuse the species and the phyletic lineage resulted from a failure to separate the species and phyletic lineage concepts as well as a confusion between the specoes concept and the species taxon. Ecological species concepts (Van Valen 1976) muddle the several major attributes of species and chose the wrong one as the defining criterion of the species concept. Partitioning the basic attributes of species into genetic, reproductive and ecological isolation leads to a better comprehension of the appearance of phenotypical properties of species taxa during speciation, and hence with the role of species in major evolutionary modifications.

The ideas presented in this paper will not solve all of the existing questions associated with species and the process of speciation, but a careful consideration of these points should provide considerable elucidation of outstanding problems.

Acknowledgements

It is a pleasure and honor for me to dedicate this paper to Professor Ernst Mayr on the occasion of his 100th birthday on 5 July 2004 and in recognition of his numerous contributions to our understanding of the species concept and the process of speciation.

Zusammenfassung

Die Art: ein Konzept, eine Kategorie und ein Taxon

Der Begriff 'Art' ist in sich selbst unscharf, weil er sich auf die Art als Konzept, als Kategorie und als Taxon bezieht, die alle voneinander unterschiedlich sind, wenngleich sie auch untereinander in Verbindung stehen. Das Artkonzept ist nicht primär ein Teil der Systematik, aber es ist immer ein integraler Teil der Grundlagen der theoretischen Biologie gewesen. Es basiert auf der Evolutionstheorie und ist nur bei sich sexuell reproduzierenden Organismen anwendbar. Das Artkonzept und das Konzept der phyletischen Linien sind sehr unterschiedlich, obgleich auch sie miteinander verknüpft sind. Ein wichtiger Aspekt des Artkonzepts ist der fehlende Genfluß zwischen verschiedenen Spezies und das Entscheidungskriterium ist daher die genetische Isolation. Das Artkonzept wird oft als dimensionslos, sowohl in der Zeit als auch im Raum, angesehen. Spezies haben drei verschiedene bedeutende Eigenschaften, nämlich die genetische Isolation, die reproduktive Dimension und die ökologische Isolation; diese Eigenschaften evolvieren zu verschiedenen Zeiten und unter dem Einfluß verschiedener Ursachen während des Artbildungsprozesses. Die Artbildung braucht eine externe isolierende Barriere während der anfänglichen allopatrischen Phase, in welcher die genetische Isolation entsteht und es muß die Effizienz einer hundertprozentigen Isolation gewährleisten sein. Die nachfolgende sympatrische Phase der Speziation tritt nach dem Verschwinden der externen Isolationsbarriere auf, wenn die Individuen von zwei neu evolvierten Arten miteinander interagieren und wechselseitigen selektiven Druck ausüben können. Viel an reproduktiver und ökologischer Isolation entsteht während dieser sekundären, sympatrischen Phase. Die Art als Kategorie ist eine Rangordnung in der hierarchischen Taxonomie und dient als Basis, auf der die Diversität der Organismen beschrieben werden kann; das Konzept der Kategorie ist nicht dasselbe wie das Artkonzept. Es kann aber bei allen Organismen angewendet werden, gleichgültig, ob sie sich sexuell oder asexuell reproduzieren. Die Art als Taxon entsteht aus der praktischen Anwendung des Kategoriebegriffs in der Systematik mit der Erfassung des Arten-Taxons unter Einbezug vieler willkürlicher Entscheidungen. Es gibt keinen einzigen Satz an Regeln, durch den die Art als Kategorie bei allen Organismen erfaßt werden kann. Das Erkennen eines Taxons als Spzies beruht bei sich asexuell reproduzierenden Organismen auf dem Ausmaß von Variation and der Unterbrechung der Variation von phänotypischen Eigenschaften, die wieder in Zusammenhang mit ökologischen Attributen dieser Organismen, verglichen mit ähnlichen Attributen bei sympatrischen Arten mit sexueller Reproduktion, stehen. Arten-Taxons sind vieldimensional, insofern als sie über Zeit und Raum hinweg existieren und oft

unscharfe Grenzen aufweisen. Weil das Erkennen eines Taxons als Art, auch bei sexuell reproduzierenden Organismen, vielfach auf willkürlichen Entscheidungen beruht, besonders wenn es weite geographische oder zeitliche Bereiche umfaßt, kann das Arten-Taxon nicht als Grundlage für die Entwicklung und Überprüfung von theoretischen Konzepten in der Evolutionstheorie verwendet werden, was nur mit dem dimensionslosen Spezieskonzept möglich ist.

References

Anderson, E., 1949: Introgressive hybridization. New York: John Wiley & Sons.

Anonymous, 1987: Field Guide to the Birds of North America, 2nd edn. Washington, DC: National Geographic Society.

de Beer, G., 1954: Archaeopteryx and evolution. Adv. Sci. **11,** 160–170.

Bock, W. J., 1972: Species interaction and macroevolution. In: Dobzhansky, Th.; Hecht, M. K.; Steere, W. C. (eds), Evolutionary Biology, Vol. 5. New York: Appleton, Century, Crofts, pp. 1–24.

Bock, W. J., 1979: The synthetic explanation of macroevolutionary change – a reductionist approach. Bull. Carnegie Mus. **13,** 20–69.

Bock, W. J., 1986: Species concepts, speciation, and macroevolution. In: Iwatsuki, K.; Raven, P. K.; Bock, W. J. (eds), Modern Aspects of Species. Tokyo: University of Tokyo Press, pp. 31–57.

Bock, W. J., 1989: Principles of biological comparisons. Acta Morphol. Neerl.- Scand. **26,** 17–32.

Bock, W. J., 1992: The species concept in theory and practice. Jpn J. Zool. **9,** 697–712.

Coyne, J. A.; Orr, H. A.; Futuyma, D. J., 1988: Do we really need a new species concept? Syst. Zool. **37,** 190–200.

Cracraft, J., 1983: Species concepts and speciation analysis. Current. Ornith. **1,** 159–187.

Cracraft, J., 1989: Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: Otte, D.; Endler, J. A. (eds), Speciation and Its Consequences. Sunderland, MA: Sinauer, pp. 28–59.

Cracraft, J., 1992: The species of the birds-of-paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. Cladistics **8,** 1–43.

Frith, C. B.; Beehler, B. M., 1998: The Birds of Paradise, Paradisaeidae. Oxford: Oxford University Press.

Giddings, L. V.; Kaneshiro, K. Y.; Anderson, W. W. (eds), 1989: Genetics, Speciation, and the Founder Principle. New York: Oxford University Press.

Gill, F. B., 1980: Historical aspects of hybridization between Blue-winged Warblers and Golden-winged Warblers. Auk **97,** 1–18.

Haffer, J., 1992: The history of species concepts and species limits in ornithology. Bull. Brit. Ornith. Club, Centenary vol. **112A,** 107–158.

Howard, D. J.; Berlocher, S. H., 1998: Endless Forms. Species and Speciation. New York: Oxford University Press.

Hull, D., 1976: Are species really individuals? Syst. Zool. **25,** 174–191.

Hull, D., 1978: A matter of individuality. Phil. Sci. **45,** 335–360.

Jordon, K., 1896: On mechanical selection and other problems. Novit. Zool. **3,** 426–525.

Jordon, K., 1905: Der Gegensatz zwischen geographischer und nichtgeographischer Variation. Z. wiss. Zool. **83,** 151–210.

Kornet, D. J., 1993: Permanent splits as speciation events: a formal reconstruction of the internodal species concept. J. Theor. Biol. **164,** 407–435.

Koopman, K., 1950: Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. Evolution **4,** 135–148.

Lack, D., 1944: Ecological aspects of species formation in passerine birds. Ibis **86,** 260–268.

Lack, D., 1949: The significance of ecological isolation. In: Jepsen, G. L.; Mayr, E.; Simpson, G. S. (eds), Genetics, Paleontology, and Evolution. Princeton NJ: Princeton University Press, pp. 299–308.

Lack, D., 1971: Ecological isolation in birds. Oxford: Oxford University Press.

Mayr, E., 1940: Speciation phenomena in birds. Am. Nat. **74,** 249–278.

Mayr, E., 1942: Systematics and the Origin of Species, From the Viewpoint of a Zoologist. New York: Columbia University Press.

Mayr, E., 1947: Ecological factors in speciation. Evolution **1,** 263–288.

Mayr, E., 1949: Speciation and systematics. In: Jepsen, G. L.; Mayr, E.; Simpson, G. S. (eds), Genetics, Paleontology, and Evolution. Princeton, NJ: Princeton University Press, pp. 281–298.

Mayr, E., 1954: Change of genetic environment and evolution. In: Huxley, J.; Hardy, A. C.; Ford, E. B. (eds), Evolution as a Process. London: Allen and Unwin, pp. 157–180.

Mayr, E., 1957: Species concepts and definitions. pp. 1–22 Difficulties and importance of the biological species conceptpp. 371–388. In: Mayr, E. (ed.), The Species Problem. Washington, DC: American Association Advanced Science, Publ. 50.

Mayr, E., 1959: Isolation as an evolutionary factor. Proc. Am. Phil. Soc. **103,** 221–230.

Mayr, E., 1963: Animal Species and Evolution. Cambridge, MA: Harvard University Press.

Mayr, E., 1969: Principles of Systematic Zoology. New York: McGraw-Hill.

Mayr, E., 1982a: Speciation and macroevolution. Evolution **36,** 1119–1132.

Mayr, E., 1982b: Process of speciation in animals. In: Barigozzi, C. (ed.), Mechanisms of Speciation. New York: Alan R. Liss, pp. 1–19.

Mayr, E., 1984: Evolution of fish species flocks: a commentary. In: Echelle, A. A.; Kornfield, I. (eds), Evolution of Fish Species Flocks. Orono, ME: University of Maine Press, pp. 3–11.

Mayr, E., 1986: The species as category, taxon and population. In: Roger, J.; Fischer, J. L. (eds), Histoire du concept d'espece dans les sciences de la vie. Paris: Foundation Singer-Polignac, pp. 294–311.

Mayr, E., 1987: The ontological status of species. Biol. Phil. **2,** 145–166.

Mayr, E., 1988: The why and how of species. Biol. Phil. **3,** 431–441.

Mayr, E., 1992: A local flora and the biological species concept. Am. J. Botany **79,** 222–238.

Mayr, E., 1993: Fifty years of progress in research on species and speciation. Proc. Calif. Acad. Sci. **48,** 131–140.

Mayr, E., 2004: What Makes Biology Unique? Consequences on the Autonomy of a Scientific Discipline. New York: Cambridge University Press.

Mayr, E.; Ashlock, P. D., 1991: Principles of Systematic Zoology, 2nd edn. New York: McGraw-Hill.

McKitrick, M.; Zink, R. M., 1988: Species concepts in ornithology. Condor **90,** 1–14.

Meier, R.; Willman, R., 2000: The Hennigian species concept. In: Wheeler, Q. D.; Meier, R. (eds), Species Concepts and Phylogenetic Theory. New York: Columbia University Press, pp. 30–42.

Mishler, B. D.; Brandon, R. N., 1987: Individuality, pluralism, and the phylogenetic species concept. Biol. Phil. **2,** 397–414.

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

Moore, J. A., 1957: An embryologist's view of the species concept. In: Mayr, E. (ed.), The Species Problem. Washington, DC: American Association of Advanced Sciences, Publ. 50. pp. 325–338.

Poulton, E. B., 1903: What ids a species? Proc. Ent. Soc. Lond., pp. lxxvi–cxvi.

Rensch, B., 1929: Das Prinzip geographischer Rassenkreise und das Problem der Artbildung. Berlin: Borntraeger.

Sibley, C. G., 1950: Species formation in the red-eyed towhees of Mexico. Univ. Calif. Publ. Zool. **50,** 109–194.

Sibley, D. A., 2000: The Sibley Guide to Birds. New York: Alfred A. Knopf.

Simpson, G. G., 1951: The species concept. Evolution **5,** 285–298.

Simpson, G. G., 1961: Principles of Animal Taxonomy. New York: Columbia University Press.

Szalay, F. S.; Bock, W. J., 1991: Evolutionary theory and systematics: relationships between process and patterns. Z. zool. Syst. Evol.-forsch **29,** 1–39.

Van Valen, L., 1976: Ecological species, multispecies, and oaks. Taxon **25,** 233–239.

Vaurie, C., 1951: Adaptive differences between two sympatric species of nuthatches (*Sitta*). Proc. Xth Int. Ornith. Congress, Uppsala, pp. 163–166.

Verheyen, E.; Salzburger, W.; Snocks, J.; Meyer, A., 2003: The origin of the superflock of cichlid fishes from Lake Victoria. East Afr. Sci. **300,** 325–329.

Wheeler, Q. D.; Meier, R. (eds), 2000: Species Concepts and Phylogenetic Theory. New York: Columbia University Press.

Wiley, E. O., 1978: The evolutionary species concept reconsidered. Syst. Zool. **27,** 217–226.

Wiley, E. O., 1981: Phylogenetics, the Theory and Practice of Phylogenetic Systematics. New York: J. Wiley & Sons.

Wilson, R. A. (ed.), 1999: Species. New Interdisciplinary Essays. Cambridge, MA: MIT Press.

Zink, R. M., 1994: The geography of mitochondrial DNA evolution, population structure, and hybridization in the fox sparrow (*Passerella iliaca*). Evolution **48,** 96–111.

Author's address: Walter J. Bock, Department of Biological Sciences, 1200 Amsterdam Avenue, Post Box 5521, Columbia University, New York, NY 10027, USA. E-mail: wb4@columbia.edu