

WHAT IS A SPECIES, AND WHAT IS NOT?*

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I analyze a number of widespread misconceptions concerning species. The species category, defined by a concept, denotes the rank of a species taxon in the Linnaean hierarchy. Biological species are reproducing isolated from each other, which protects the integrity of their genotypes. Degree of morphological difference is not an appropriate species definition. Unequal rates of evolution of different characters and lack of information on the mating potential of isolated populations are the major difficulties in the demarcation of species taxa.

1. What is a Species, and What is Not? As someone who has published books and papers on the biological species for more than 50 years, and who has revised and studied in detail more than 500 species of birds and many species of other groups of organisms, the reading of some recent papers on species has been a rather troubling experience. There is only one term that fits some of these authors: armchair taxonomists. Since many authors have never personally analyzed any species populations or studied species in nature, they lack any feeling for what species actually are. Darwin already knew this when, in September 1845, he wrote to Joseph Hooker: "How painfully true is your remark that no one has hardly the right to examine the question of species who has not minutely described many" (Darwin 1987, 253). These authors make a number of mistakes that have been pointed out again and again in the recent literature. Admittedly, the relevant literature is quite scattered, and some of it is perhaps rather inaccessible to a non-taxonomist. Yet, because the species concept is an important concept in the philosophy of science, every effort should be made to clarify it. It occurred to me that instead of criticizing certain recently published papers individually, it would be more constructive and helpful if I would here attempt to present, from the perspective of a practicing systematist, a concise overview of the philosophically important aspects of the problem of the 'species'. There is nothing of the sort in the literature.

The species is the principal unit of evolution and it is impossible to write about evolution, and indeed about almost any aspect of the philosophy of biology, without having a sound understanding of the meaning of biological species. A study of the history of the species problem helps to dispel some of the misconceptions (Mayr 1957, Grant 1994).

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2. Species of Organisms Are Concrete Phenomena of Nature. Some recent authors have dealt with the concept of species as if it were merely an arbitrary, man-made concept, like the concepts of reduction, demarcation, cause, derivation, prediction, progress, each of which may have almost as many definitions as there are authors who have written about them. However, the concept biological species is not like such concepts. The term ‘species’ refers to a concrete phenomenon of nature and this fact severely constrains the number and kinds of possible definitions. The word ‘species’ is, like the words ‘planet’ or ‘moon’, a technical term for a concrete phenomenon. One cannot propose a new definition of a planet as “a satellite of a sun that has its own satellite,” because this would exclude Venus, and some other planets without moons. A definition of any class of objects must be applicable to any member of this class and exclude reference to attributes not characteristic of this class. This is why any definition of the term ‘species’ must be based on a careful study of the phenomenon of nature to which this term is applied. Alas, this necessity is not appreciated by all too many of those who have recently discussed the species problem after a mere analysis of the literature.

The conclusion that there are concrete describable objects in nature which deserve to be called “species” is not unanimously accepted. There has been a widespread view that species are only arbitrary artifacts of the human mind, as some nominalists, in particular, have claimed. Their arguments were criticized by Mayr (1949a, 371).

3. Why Are There Species of Organisms? Why is the total genetic variability of nature organized in the form of discrete packages, called species? Why are there species in nature? What is their significance? The Darwinian always asks why questions because he knows that everything in living nature is the product of evolution and must have had some selective significance in order to have evolved.¹ He therefore asks: What selection forces in nature favor the origin and maintenance of species? The answer to this question becomes evident when one makes a certain thought experiment.

“It is quite possible to think of a world in which species do not exist but are replaced by a single reproductive community of individuals, each one different from every other one, and each one capable of reproducing with those other individuals that are most similar to it. Each individual would then be the center of a concentric series of circles of genetically more and more unlike individuals. What would be the consequence of the continuous uninterrupted gene flow through such a large system? In each generation certain individuals would have a selective advantage because

¹I am not aware of a single major feature of living nature of which this claim could be refuted.

they have a gene complex that is specially adapted to a particular ecological situation. However, most of these favorable combinations would be broken up by pairing with individuals with a gene complex adapted to a slightly different environment. In such a system there is no defense against the destruction of superior gene combinations except the abandonment of sexual reproduction. It is obvious that any system that prevents such unrestricted outcrossing is superior”²² (Mayr 1949b, 282). The biological species is such a system.

The biological meaning of species is thus quite apparent: “The segregation of the total genetic variability of nature into discrete packages, so called species, which are separated from each other by reproductive barriers, prevents the production of too great a number of disharmonious incompatible gene combinations. This is the basic biological meaning of species and this is the reason why there are discontinuities between sympatric species. We do know that genotypes are extremely complex epigenetic systems. There are severe limits to the amount of genetic variability that can be accommodated in a single gene pool without producing too many incompatible gene combinations” (Mayr 1969, 316). The validity of this argument is substantiated by the fact that hybrids between species, particularly in animals, are almost always of inferior viability and more extreme hybrids are usually even sterile. “Almost always” means that there are species interpreted to be the result of hybridization, particularly among plants, but except for the special case of allopolyploidy, such cases are rare.

Among the attributes members of a species share, the only ones that are of crucial significance for the species definition are those which serve the biological purpose of the species, that is, the protection of a harmonious gene pool. These attributes were named by Dobzhansky (1935) *isolating mechanisms*. It is immaterial whether or not the term isolating mechanism was well chosen, nor is it important whether one places the stress on the prevention of interbreeding with non-conspecific individuals or the facilitation (“recognition”) of breeding with conspecific individuals. The concept I have just developed is articulated in the so-called biological species definition: “*Species are groups of interbreeding natural populations that are reproductively isolated from other such groups.*” The isolating mechanism by which reproductive isolation is effected are properties of individuals. Geographic isolation therefore does not qualify as an isolating mechanism.

Reproductive Isolation. The Biological Species definition includes the statement that the populations of one species are “reproductively isolated”

²²By “superior” I meant, would be rewarded by leaving a greater number of viable descendants.

from the populations of all other species. Typologically conceived, this would mean that no individual of species A would ever hybridize with any individual of species B. Botanists soon pointed out that this did not correctly describe many situations in nature. They discovered case after case of occasional (sometimes even rather frequent) hybridization between seemingly "good" sympatric species. Anderson (1949) went so far as to claim that this was the normal situation with closely related sympatric species and that through such "introgressive hybridization," as he called it, either species would be enriched by genes from other species. Other authors minimized the frequency of such hybridization and considered parallel variation in sympatric species as the residues of ancestral polymorphisms. Recent molecular analysis has, however, confirmed the frequency of clandestine introgression. However, if the two species continue their essential integrity, they will be treated as species, in spite of the slight inefficiency of their isolating mechanisms.

There is at least one case among oaks (*Quercus*) and one among birches (*Betula*) where such introgression has apparently been going on for millions of years without leading to a fusion of the parental species. Similar cases apparently occur also in animals. After the destruction of much of the southern periphery of the habitat of the gray wolf, the area was invaded by coyotes and, owing to the fertility of the hybrids, the crossing of male wolves with female coyotes led to an introgression of alien genes into both wolf and coyote populations. The same was shown by Templeton and associates (1989, 12) for the sympatric Hawaiian species *Drosophila silvestris* and *D. heteroneura*. The fact that the mitochondria are inherited only through the females greatly facilitates the discovery of such cases of hybridization.

It is thus well established that a leakage of genes occurs among many good "reproductively isolated" species. This induced me to revise the definition of isolating mechanisms to "biological properties of individuals which prevent the interbreeding [fusion] of populations" (1970, 56). Thus, isolating mechanisms do not always prevent the occasional interbreeding of non-conspecific individuals, but they nevertheless prevent the complete fusion of such species populations. Clandestine hybridization is apparently far more common among plants than among higher animals.

Among the invalid objections to the biological species concept is the claim that it would work only if the acquisition of the isolating mechanisms was a teleological process (Paterson 1985). However, Darwin already knew that reproductive isolation between species is not acquired by teleological ad hoc selection but simply as a byproduct of the process of divergence. H. J. Muller and E. Mayr have further emphasized this point in their writings and Mayr in particular has demonstrated that indeed behavioral isolating mechanisms can be acquired through a change of

function of factors favoring sexual selection. Paterson's arguments do not in the least weaken the validity of the BSC (Mayr 1988b, Coyne et al. 1987). The contingent nature of the acquisition of isolating mechanisms is documented by their great diversity. It would seem to be merely a matter of chance what kind of device is made use of by a given incipient species to protect itself against outcrossing. It includes not only purely genetic mechanisms such as sterility factors, but the use of ecological and life history factors and (in animals) a number of behavioral devices.

The evolutionist always stresses the genetic uniqueness of every individual of a sexually reproducing population. However, the members of any species also have in common many species-specific properties. This includes, in particular, the isolating mechanisms but also many adaptations, for instance, for niche utilization, as well as certain contingent, species specific properties. If one knew the genetic basis of all the species specific characters, one might be able to give a genetic characterization of a species taxon.

The BSC is based on the recognition of properties of populations. It depends on the fact of non-interbreeding with other populations. For this reason the concept is not applicable to organisms which do not form sexual populations. The supporters of the BSC therefore agree with their critics that the BSC does not apply to asexual (uniparental) organisms. Their genotype does not require any protection because it is not threatened by destruction through outcrossing. There are a number of suggestions of how species taxa in asexual organisms can be delimited and defined, but this is outside the present discussion. However, I find that any endeavor to propose a species definition that is equally applicable to both sexually reproducing and asexual populations misses the basic characteristics of the biological species definition (the protection of harmonious gene pools).

It is important to emphasize that in the study of biological species one deals with biological populations. Some non-biologists, including some philosophers, seem to have difficulties appreciating how different biological populations are from classes of inanimate objects (Kitcher 1989, 189–194). Only a small fraction of any biological population reproduces, because not every individual in a population survives up to reproductive age and reproduces successfully. This is true on the average for only two of the total number of offspring of a parental pair in a sexually reproducing species. A mentally retarded individual may have no opportunity to reproduce but he is still a member of his population. In most marine organisms, with their high number of larvae, successful survival and reproduction is to a large extent a matter of chance, but most of the zygotes have, at the moment of their formation, an equal probability of success. Kitcher describes six situations which to him seem to cause difficulty for the concept of population as presented by me. I believe that his objections can be

answered, although it would take me too far afield to do so here. The simplest solution in most cases is to say that whatever is the product of the same gene pool belongs to the same population, together with any new immigrants.

4. The Two Meanings of the Term Species. What the scientist actually encounters in nature are populations of organisms. There is a considerable range in the size of populations, ranging from the local deme to the species taxon. The local deme is the community of potentially interbreeding individuals at a locality (see also Mayr 1963, 136), and the species taxon has been referred to by Dobzhansky as the "largest Mendelian population." The task of the biologist is to assign these populations to species. This requires two operations: (1) to develop a concept of what a species is, resulting in the definition of the species category in the Linnaean hierarchy, and (2) to apply this concept when combining populations into species taxa.

A number of recent writers on the species problem have failed to appreciate that the word 'species' is applied to these two quite different entities in nature, species taxa and the concept of the category species. As a result, their so-called species definition is nothing but a recipe for the demarcation of species taxa. This is, for instance, true for most of the recent so-called phylogenetic species definitions. It is also largely true for Templeton's (1989, 1994) cohesion species concept. A paper often quoted as a decisive refutation of the BSC (Sokal and Crovello 1970) is perhaps an extreme example of the confusion resulting from the failure to discriminate between the species as category (concept) and as taxon.

- (1) The species taxon. The word taxon refers to a concrete zoological or botanical object consisting of a classifiable population (or group of populations) of organisms. The house sparrow (*Passer domesticus*) and the potato (*Solanum tuberosum*) are species taxa. Species taxa are particulars, "individuals," biopopulations. Being particulars, they can be described and delimited against other species taxa.
- (2) The species category. Here the word 'species' indicates the rank in the Linnaean hierarchy. The species category is the class that contains all taxa of species rank. It articulates the concept of the biological species and is defined by the species definition. The principal use of the species definition is to facilitate a decision on the ranking of species level populations, that is, to answer the question about an isolated population: "Is it a full species or a subspecies?" The answer to this question has to be based on inference (the criteria on the basis of which such a decision is made are listed in the technical taxonomical literature, e.g., in Mayr and Ashlock

1991, 100–105). A complication is produced by the fact that in the Linnaean hierarchy asexual “species” are also ranked in the species category, even though they do not represent the BSC.

The literature traditionally has referred to the “species problem.” However, it is now quite clear that there are two different sets of species problems, one being the problem of how to define the species (what species concept to adopt), and the other being how to apply this concept in the demarcation of species taxa. It is necessary to discuss these two sets of problems separately.

Let me begin with a discussion of the meaning and history of the term ‘biological species’.

5. Typological Species Versus Biological Species. The biological species concept developed in the second half of the 19th century. Up to that time, from Plato and Aristotle until Linnaeus and early 19th century authors, one simply recognized “species,” *eide* (Plato), or *kinds* (Mill). Since neither the taxonomists nor the philosophers made a strict distinction between inanimate things and biological species, the species definitions they gave were rather variable and not very specific. The word ‘species’ conveyed the *idea of a class of objects, members of which shared certain defining properties*. Its definition distinguished a species from all others. Such a class is constant, it does not change in time, all deviations from the definition of the class are merely “accidents,” that is, imperfect manifestations of the essence (*eidos*). Mill in 1843 introduced the word ‘kind’ for species (and John Venn introduced ‘natural kind’ in 1866) and philosophers have since used the term natural kind occasionally for species (as defined above), particularly after B. Russell and Quine had adopted it. However, if one reads a history of the term ‘natural kind’ (Hacking 1991) one has the impression that no two authors understood quite the same thing by this term, nor did they clearly discriminate between a term for classes of inanimate objects and biological populations of organisms. There is some discussion among philosophers whether there are several types of natural kinds, but I will refrain from entering that discussion. The traditional species concept going back to Plato’s *eidos* is often referred to as the typological species concept.

The current use of the term species for inanimate objects like nuclear species or species of minerals reflects this classical concept. Up to the 19th century this was the most practical species concept also in biology. The naturalists were busy making an inventory of species in nature and the method they used for the discrimination of species was the identification procedure of downward classification (Mayr 1982, 1992a). Species were recognized by their differences, they were kinds, they were types. This

concept was usually referred to as the morphological or typological species concept.

Even though this was virtually the universal concept of species, there were a number of prophetic spirits who, in their writings, foreshadowed a different species concept, later designated as the *biological species concept* (BSC). The first among these was perhaps Buffon (Sloan 1987), but a careful search through the natural history literature would probably yield quite a few similar statements. Darwin unquestionably had adopted a biological species concept in the 1830s in his Transmutation Notebooks, even though later he largely gave it up (Kottler 1978, Mayr 1992b). Throughout the 19th century, quite a few authors proposed a species definition that was an approach to the BSC (Mayr 1957).

Late in the 19th century and in the first quarter of the 20th century, taxonomists like K. Jordan, E. Poulton, L. Plate, and E. Stresemann were among those who most clearly articulated the biological species concept, as will be shown below.

As long as the inventory taking of kinds of organisms was the primary concern of the students of species, the typological species concept was a reasonably satisfactory concept. But when species were studied more carefully, all sorts of properties were discovered that did not fit with a species concept that was strictly based on morphology. This was particularly true for behavioral and ecological properties. Most damaging was the discovery of the unreliability of morphological characters for the recognition of biological species.

Morphological difference had traditionally been the decisive criterion of species. Population A (e.g., continental North American savannah sparrows) was determined to be a different species from population B (e.g., savannah sparrows from Sable Island, Nova Scotia), if it was deemed to be sufficiently different from it by morphological characters. This definition was very useful in various clerical operations of the taxonomist such as in the cataloguing of species taxa and their arrangement in keys and in collections. However, for two reasons it was inadequate if not misleading for a study of species in nature. The first one is that, as is now realized, there are many good biological species that do not differ at all morphologically or only very slightly. Such cryptic species have been designated *sibling species*. They occur at lesser or greater frequency in almost all groups of organisms (Mayr 1948). They are apparently particularly common among protozoans. Sonneborn (1975) eventually recognized 14 sibling species under what he had originally considered a single species, *Paramecium aurelia*. Many sibling species are genetically as different from each other as morphologically highly distinct species. A second reason why a morphological species concept proved unsatisfactory is that there are often numerous different morphological types within a biological spe-

cies, either due to individual genetic variation or due to different life history categories (males, females, immatures) which are morphologically far more different from each other than are the corresponding morphological types in different species.

The morphological difference between two species fails to shed any light on the true biological significance of species, the Darwinian why question. So-called "morphological species definitions" are in principle merely operational instructions for the demarcation of species taxa. The realization of these deficiencies of the typological species concept led, in due time, to its almost complete replacement among zoologists by the so-called biological species concept (BSC).

Many of the authors who profess to adhere to the morphological species concept do not seem to realize that unconsciously they base their decisions ultimately on the reproductive community principle of the BSC. They combine drastically different phenotypes into a single species because they have observed that they were produced by the same gene pool. This was already done by Linnaeus when he synonymized the names he had given to the female mallard and the immature goshawk.

6. Insufficient or Erroneous Species Criteria.

6.1 *Characterized by its Evolutionary Potential.* Some 50 years ago the fact that species are not constant but the product of evolution and still potentially continuing to evolve was included by several authors in the species definition. For instance, in 1945 A. E. Emerson defined the biological species as follows: "a species is an evolved or evolving genetically distinctive, reproductively isolated, natural population." Indeed, nothing distinguishes a biological species better from a natural kind than its capacity to evolve. Yet, this is not a sufficient criterion. Everything else in living nature also has the capacity to evolve. Every population, every structure and organ is the product of evolution and continues to evolve, genera and higher taxa evolve, and so do faunas and floras. Most of all, the capacity for evolving is not the crucial biological criterion of a species, which is the protection of its gene pool. It is for this reason that I and most adherents of the biological species concept omit "evolving" from the species definition. Those authors who still emphasize the evolutionary aspect of the species have never made it clear what the real significance of species is.

The paleontologist Simpson attempted to make evolution the basis of a species concept: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (1961, 153). He replaced the clear-cut criterion (reproductive isolation) of the biological species concept with such undefined vague terms as "maintains its iden-

tity" (does this include geographical barriers?), "evolutionary tendencies" (what are they and how can they be determined?), and "historical fate." What population in nature can ever be classified by its "historical fate" when this is entirely in the future?

Furthermore, as I pointed out previously (Mayr 1988a, 323–324), this concept encounters three additional major difficulties: (1) it is applicable only to monotypic species and every geographical isolate would, by implication, have to be treated as a different species; (2) there are no empirical criteria by which either evolutionary tendency or historical fate can be observed in a given fossil sample (Simpson 1961, 154–160); and (3) the definition does not help in the lower or upper demarcation of chronospecies, even though the main reason why the evolutionary species concept was apparently introduced, was in order to deal with the time dimension, which is not considered in the non-dimensional biological species concept. Indeed, Simpson's definition is essentially an operational recipe for the demarcation of fossil species.

6.2 Other Unsatisfactory Species Concepts. The so-called phylogenetic species concept (Wheeler, 1996) is actually nothing more than the revival of a purely morphological species concept (Mayr 1996). The so-called ecological species concept, based on the niche occupation of a species, is for two reasons not workable. In almost all more widespread species there are local populations which differ in their niche occupation. An ecological species definition would require that these populations be called different species even though, on the basis of all other criteria, it is obvious that they are not. More fatal for the ecological species concept are the trophic species of cichlids (A. Meyer 1990) which differentiate within a single set of offspring from the same parents. Finally, there are the numerous cases (but none exhaustively analyzed) where two sympatric species seem to occupy the same niche, in conflict with Gause's rule. All this evidence shows not only how many difficulties an ecological species concept faces but also how unable it is to answer the Darwinian why? question for the existence of species.

Perhaps Templeton's (1989, 1994) cohesion species concept should be mentioned here. It attempts to combine the best components of several other species concepts but fails to escape the resulting conflicts. It emphasizes the presence of gene flow, but fails to distinguish between the internal (isolating mechanisms) and external (geographic isolation) barriers to gene flow; it stresses cohesion through gene flow, but claims also to be "applicable to taxa reproducing asexually," which have no gene flow. It attempts to characterize an evolutionary lineage, but does not indicate how to delimit such an open ended lineage at either end; and he does not state how to deal with the geographic variation of demographic-ecological attributes

in widespread polytypic species. I do not see any advantages of this concept over the BSC.

6.3 Two Origins of Species. Normally one calls a population a species when it has acquired isolating mechanisms, protecting its gene pool against its parental or a sister species. In other words, such a species is the product of the process of multiplication of species. However, the paleontologist encounters also cases where a phyletic lineage changes over time to such a degree that sooner or later it is considered to be a different species. The occurrence of the origin of such phyletic species is usually ignored when non-paleontologists speak of speciation. Phyletic evolution does not produce an additional entity, it merely modifies an existing one. Nevertheless, the changes are sometimes sufficiently pronounced so that the paleontologist gives a new species name to the modified phyletic lineage. Gingerich (1979), in particular, has called attention to the relative frequency of such cases. Such new species differ usually only in size and proportions, but not in the acquisition of any notable innovations. Such phyletic speciation must be mentioned because it is what a paleontologist usually seems to have in mind when he speaks of speciation. It is for such species that Simpson proposed the evolutionary species definition. It has been impossible so far to discover any criteria by which a phyletic species can be demarcated against ancestral and descendent "species." It is for this reason that Hennig (1966) rejects the recognition of new species without branching.

In his discussion of the origin of species, Hennig (1966) only considers the case of a phyletic lineage splitting by dichopatric speciation into two daughter species. He considers both daughter species as new species. He ignores the more frequent case where by budding from a phyletic lineage a new daughter species originates through peripatric speciation. By his definition, Hennig is forced to call the phyletic lineage after the budding point a new species, even though it has not changed at all. Hennig's species definition results also in difficulties when a phyletic lineage gradually changes into a new species, even though there has been no splitting of the lineage nor any budding. Hennig is forced to ignore such phyletic speciation no matter how conclusive the indirect (morphological) evidence for the origin of a new species may be. On the whole, whenever a biologist speaks of species, he has in mind the product of the process of multiplication of species, not the product of phyletic evolution.

6.4 Multidimensional Species Taxa. Species taxa ordinarily have an extension in space (geography) and in time. They are composed of local or temporally circumscribed populations which differ slightly from each other. Such populations, when they are considered to be conspecific, are

combined into a *polytypic species*. The major species problem in species level taxonomy is to decide which local populations to combine into polytypic species. Since this decision is based on inference, it is always somewhat uncertain. The paleontologist encounters in the time dimension the same problem which the student of the geographic variation of species encounters in the spatial dimension. During the period when the typological species concept was dominant, almost any isolated population that differed by a morphological character was called a different species. Since the rise of the biological species concept, the question is always asked whether or not such a population would interbreed with other populations differing in space or time if they would meet in nature.

The widespread use of polytypic species has several advantages for information conveyance as pointed out by Mayr and Ashlock (1991, 41). Conspecific populations that differ from each other morphologically are called subspecies. If such subspecies are part of a series of contiguous populations, they are a purely taxonomic device. However, they are incipient species if such subspecies are geographically isolated. They may in due time acquire the needed isolating mechanisms to function as well separated species. Owing to the gradualness of the process of speciation, every incipient species at one time in its cycle goes through the subspecies stage.

7. A Major Criticism of the Biological Species Concept. The biological species concept is least vulnerable to criticism in the non-dimensional situation, as I have emphasized in numerous previous papers. When two populations (in reproductive condition) meet at the same place at the same time, they either interbreed because they are conspecific or they do not do so because they are different reproductive communities (different species). In that case, their isolating mechanisms keep them apart.

A geographically isolated population also has the isolating mechanisms of the species to which it belongs, but they are, so to speak, invisible, since they do not need to be activated. In some of my earlier species definitions I said of isolated populations that they might be "potentially" reproductively isolated. If in the future any contact with a different species population was going to be established, the isolating mechanism would at once spring into action, thereby documenting their existence.

Speciation, as Darwin has shown, is normally a gradual populational phenomenon. Sudden, saltational speciation, as in the case of allopolyploidy, seems to be virtually absent in most groups of sexually reproducing organisms. Owing to the gradualness of the speciation process one should find in nature populations that are on the way to becoming separate species, but have not yet quite completed the process. Such "semi-species" are indeed found. They are documented, for instance, by the so-called zones of secondary hybridization. Here two incipient species, usually ex-

panding from a Pleistocene refuge, hybridize along a more or less long contact line, but the hybrid zone stays narrow, often less than 100 km wide, even though this contact zone may have existed for 5–10,000 years. Both of the two semi-species discriminate against introgressing genes of the other semi-species, as documented by the lowered fertility of hybrid pairs. Hybridization is too indiscriminate in the contact zone to permit a selection for isolating mechanisms, as Darwin already remarked. The effects of continuing hybridization completely override the counterselection against inferior hybrids and introgressing genes so that it does not come to any parapatric speciation. Isolating mechanisms, however, can be further improved after speciation between overlapping species has been complete (Butlin 1989; Lion and Price 1994).

During a period of geographic isolation the presence of species specific isolating mechanisms can only be inferred. Curiously, there are large numbers of taxonomists who seem to be unaware how frequent the need is for inference making in scientific theorizing. The most helpful inference on the species status of isolated populations is greater morphological difference as compared to other populations that are seemingly conspecific. To be able to use degree of morphological difference in order to be able to infer species status, one must have a "yard stick," which determines which of the isolated populations already have reached species status and which others have not. Constructing such a yard stick requires a thorough knowledge of related species and subspecies and is a rather technical procedure. It is described in Mayr and Ashlock 1991, 100–105.

What must be emphasized, because this is so often misunderstood, is that this procedure is not a falling back on a morphological species concept, but simply uses the degree of morphological difference as an indication of the underlying degree of reproductive isolation. This procedure is very much the same as that described so perceptively by G.G. Simpson (1961) for identical twins: an individual is an identical twin not because he is so similar to another individual, but rather, he is so similar to it because he is its identical (monozygotic) twin. Analogously, an individual belongs to species X not because it has the same species specific characters as other individuals of species X, but it has these species specific characteristics because, like other conspecifics, it is part of the species.

Curiously, Mahner (1994) has reversed the roles of the concept of reproductive community and species-specific characters. For a Darwinian to determine the significance of a biological process one always starts with the Darwinian why question. As far as the species is concerned, the answer clearly is protection of the gene pool through establishment of a reproductive community. The next question is how, and here the answer is isolating mechanisms and other species-specific attributes. These are indicators of species status, but do not constitute the basic meaning of 'spe-

cies'. I have pointed this out as the reason why isolation is the primary and recognition (the answer to the how question) the secondary aspect of the species (Mayr 1988b). When I used morphological inferences (Mayr 1992a) to determine which nominal species of plants in the township of Concord (Massachusetts) were good biological species, I did not shift to a morphological species concept, as Whittemore (1993) seemed to think.

8. The Ontology of the Species Taxon. A considerable clarification of the status of species taxa was achieved when it was realized by some taxonomists that species taxa are not classes but particulars or "individuals" or biopopulations, or by whatever other term you may want to characterize this difference. Much of the argument on this issue seems to be semantic, and this is not the place to deal once more with this problem. The belief that species are concrete particulars was recently rediscovered by Ghiselin and Hull, but it has actually been the view of many, if not most naturalists for more than one hundred years, as I have shown (Mayr 1988a). As early as 1866, Haeckel said "Die Art ist ein Individuum." For a detailed discussion of this conclusion, see papers by Ghiselin (1971–1972), Hull (1975), and Mayr (1987, 1988a).

One could also say that organisms that belong to sexually reproducing species have two sets of characteristics. First, those that serve as isolating mechanisms and are jointly responsible for the fact that this population of individuals constitutes a biological species, and, second, all other properties of the species. Organisms which belong to two related species usually share a large number of characteristics but this does not make them conspecific. The important thing is that they differ by a certain limited number of attributes, their *isolating mechanisms*, which prevent them from interbreeding and thus prevent the destruction of the integrity of their gene pool. To repeat, certain individuals are part of a certain species not because they have certain characteristics in common but they share these characteristics because they belong to a single reproductive community, a biological species. And this is the reason why we must rely on the biological meaning of species in articulating the BSC.

9. Difficulties in Delimiting Species Taxa. There are a number of evolutionary processes that make the delimitation of species taxa from each other and the determination of their rank often very difficult. The most important is so-called mosaic evolution. This means that certain characters may evolve much more rapidly than others. This results in a discord between the message provided by various characters. In particular, reproductive isolation and morphological difference often do not evolve in parallel with each other. This is why sibling species exist; they are reproductively isolated but morphologically indistinguishable. There is no simple

recipe by which the problem posed by mosaic evolution can be solved. The decision has to be made in each case on the basis of the totality of information as well as the usefulness of the proposed classification.

What is often the basic problem is an insufficiency of needed information. This is why the decision about the status of isolated populations has to be based on inference, it is not given directly by the available data. This is as true for populations that are geographically isolated as for stages in the evolution of a single phyletic lineage.

The basic message which emerges from this account of the numerous difficulties of the species problem is that the definition of the biological species must be based on its biological significance, which is the maintenance of the integrity of well balanced, harmonious gene pools. The actual demarcation of species taxa uses morphological, geographical, ecological, behavioral, and molecular information to infer the rank of isolated populations.

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