whether the species one is arranging originated by peripatric, parapatric, stasipatric, or sympatric separation. Indeed, we are not aware of any case where a difference in the origin of a species would have affected the proposal of a classification (except possibly in cases of hybridization).

It is evident, then, that taxonomic research at the species level—*microtaxonomy*—is rather different from the process of classifying genera and higher taxa—macrotaxonomy. This conclusion is supported by the recent history of taxonomy. For instance, the new systematics of the 1930s and 1940s involved the species level almost exclusively. Geographic variation, the recognition of polytypic species, the definition of subspecies and species, the taxonomic status of incipient species, and the role of nonmorphological characters in the delimitation of species were the principal concerns of the new systematics. Authors such as Mayr who were active in the new systematics usually did not make a substantial contribution to the classification of higher taxa. By contrast, most authors who have been most active during the flowering of macrotaxonomy from the 1960s on have made few, if any, contributions to species-level taxonomy. This statement cannot be interpreted to mean that there is no connection between the two levels. Obviously, species are the vehicle of all macroevolution. As Mayr (1963:621) stated,

> The evolutionary significance of species is quite clear: Although the evolutionist may speak of broad phenomena, such as trends, adaptations, specializations, and regressions, they are really not separable from the progression of the entities that display these trends, the species. The species are the real units of evolution, as the temporary incarnation of harmonious, well-integrated gene complexes. . . . The species, then, is the keystone of evolution.

The delimitation and proper ranking of species populations and the sorting and evaluation of characters during the construction of classifications are two very different activities. This difference is acknowledged in the recognition of two remarkably independent domains of taxonomy: microtaxonomy and macrotaxonomy. Chapters 2 through 5 are devoted to various aspects of microtaxonomy; Chapters 6 through 11, to aspects of macrotaxonomy.

CHAPTER 2

THE SPECIES CATEGORY

Deme, Speciation, Sympatric speciation, Allopatric, peripatric speciation — Sibling species (cryptic)

One of the most elementary urges of humankind is to identify things and name them. Even the most primitive peoples have names for kinds of birds, fishes, flowers, and trees. If only individual organisms existed and the diversity of nature were continuous, it would be difficult to sort them into groups and distinguish "kinds." Actually, at least in sexually reproducing higher organisms, the diversity of nature is discontinuous and consists in any local fauna of the more or less well-defined kinds of animals we call species. Around New York City, for instance, there are about 150 kinds of breeding birds. These are the species of the taxonomist. Natives in the mountains of New Guinea independently distinguish the same kinds of organisms as do specialists in the big museums of the western world (Diamond 1965). Clearly, biological species are not an arbitrary construct of the human mind.

The concept of species seems so simple that it always comes as something of a shock to a beginning taxonomist to learn how voluminous and seemingly endless the debate about the species problem has been. In zoology there is now fair agreement on the species concept, although heterodox views are still vigorously defended. For recent summaries, see Bocquet, Génermont, and Lamotte (1980), Grant (1971), Iwasuki, Raven, and Bock (1986), Mayr (1957, 1963, 1982*a*, 1987*a*, *b*), Osche (1984), Roger and Fischer (1987), Simpson (1961), Wiley (1981), and Willmann (1985).

nondimensional situation. They prefer a definition which, as Simpson has said, involves evolutionary criteria. Simpson (1961:153) therefore proposed the following definition: "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."

As has been pointed out elsewhere (Mayr 1982*a*:294), this is the definition of a phyletic lineage, not of a species. It applies equally to almost any isolated population or incipient species; it also sidesteps the crucial question of what a "unitary role" is and why phyletic lines do not interbreed with each other. What apparently most concerned Simpson was the problem of delimitation of species taxa in the time dimension, but here also his definition is of little help. When we consider a sequence of morphotypes in a single phyletic lineage, how are we to know whether these morphotypes have different unitary evolutionary roles and should thus be considered different species or whether they all have the same unitary evolutionary role and should thus be treated as *chronospecies* (Mayr 1987*a*:310–313; Reif 1984)?

The principal weakness of the so-called evolutionary species definition is that it ignores the core of the species problem—the causation and maintenance of discontinuities between contemporary species—and concentrates instead on trying to delimit species taxa in the time dimension.

Wiley (1981) attempted to improve the evolutionary species definition ("maintenance of identity" is construed as reproductive isolation), but his definition is that of a species taxon, not of the species category. Neither Simpson, Wiley, nor Hennig has solved the problem of how to deal with the relationship of descendant populations in a single lineage. Simpson arbitrarily divides the lineage into species by inferring reproductive isolation from the degree of morphological difference. By contrast, Wiley (1981:34) believes that "no presumed separate, single, evolutionary lineage may be subdivided into a series of ancestral and descendant species," a proposal that led Simpson to comment that one "could start with man and run back to a protist still in the species *Homo sapiens*." Finally, Hennig (1966*a*) arbitrarily terminated every evolutionary species when a daughter species branched off the parental lineage, ignoring the fact that a peripatric speciation event usually leaves the parental species unchanged.

FROM PHENON TO TAXON TO CATEGORY

A failure to understand the meaning of these three terms and their theoretical foundation has led some taxonomists into great confusion. It has been the cause of most attacks on the biological species concept. When an author says, "As a paleontologist I cannot employ the biological species concept because I cannot test the reproductive isolation of fossils," he or she reveals a lack of understanding. What the taxonomist observes directly are individuals, which are then sorted into phena. On the basis of certain biological concepts and information, such as an awareness of the possibility of sexual dimorphism, growth, alternation of generations, and nongenetic modifications of the phenotype, a taxonomist assigns the phena to populations, which in turn are classified into taxa. The ranking by a taxonomist of a taxon in the appropriate category (subspecies, species, or genus) is based on inferences drawn from the available data.

This methodology of basing inferences on evidence and its justification was perceptively discussed by Simpson (1961:69):

> Here it is necessary again to emphasize the distinction between definition and the evidence that the definition is met. We propose to *define* taxonomic categories in evolutionary and to the largest extent phylogenetic terms, but to use evidence that is almost entirely non-phylogenetic when taken as individual observations. In spite of considerable confusion about this distinction, even among some taxonomists, it is really not particularly difficult or esoteric. The well-known example of monozygotic ("identical") twins is explanatory and is something more than an analogy. We *define* such twins as two individuals developed from one zygote. No one has ever seen this occur in humans, but we recognize when the definition is met by *evidence* of similarities sufficient to sustain the inference. The individuals in question are not twins because they are similar but, quite the contrary, are similar because they are twins. Precisely so, individuals do not belong in the same taxon because they are similar, but they are similar because they belong to the same taxon. (Linnaeus was quite right when he said that the genus makes the characters, not vice versa, even though he did not know what makes the genus.) That statement is a central element in evolutionary taxonomy, and the alternative clearly distinguishes it from non-evolutionary taxonomy.

The reproductive isolation of a biological species—the protection of its collective gene pool against pollution by genes from other species—results in a discontinuity not only of the genotype of the species but also of its morphology and other aspects of the phenotype produced by the genotype. This is the fact on which taxonomic practice is based. Reproductive isolation cannot, of course, be observed directly in samples of preserved specimens. However, it can be inferred on the basis of various types of evidence, such as the presence of a discontinuity—a bridgeless gap—between two correlated character complexes. In living species, such inferences can be tested by means of observation and experiment.

The crucial difference between the reasoning of a typologist and that of an adherent of the biological species concept is as follows: The typologist says, "There is a clear-cut morphological difference between samples *a* and *b*; therefore, they are by definition two morphospecies, that is, sense of Plato; rather, they are entities for which there is no equivalent in the realm of inanimate objects.

Biological Species Concept

In the late eighteenth century it began to be realized that neither of the two medieval species concepts discussed in the preceding sections is applicable to biological species. An entirely new species concept began to emerge after 1750. It is augured by statements made by Buffon in his later writings (Sloan 1987), Merrem, Voigt, Walsh (1864), and many other naturalists and taxonomists of the nineteenth century. K. Jordan (1905) was the first to clearly formulate the concept in all its consequences. It combines elements of the typological and the nominalistic concepts by stating that species have independent reality and are typified by the statistics of populations of individuals. It differs from both by stressing the populational nature and genetic cohesion of the species and by pointing out that the species receives its reality from the historically evolved shared information in its gene pool.

As a result, the members of a species form a *reproductive community*. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction. A multitude of devices ensure intraspecific reproduction in all organisms. The species is also an *ecological unit* which, regardless of the individuals that constitute it, interacts as a unit with other species with which it shares its environment. The species finally is a *genetic unit* consisting of a large, intercommunicating gene pool, whereas the individual organism is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time. These three properties show that species do not conform to the typological definition of a class of objects (Mayr 1963:21). Instead, species are biological populations and have all the properties that philosophers ascribe to individuals (Chapter 3). The biological species definition which results from this theoretical species concept is as follows: *A species is a group of interbreeding natural populations that is reproductively isolated from other such groups.*

The development of the biological concept of the species was one of the earliest manifestations of the emancipation of biology from an inappropriate philosophy based on the phenomena of inanimate nature. This species concept is called biological not because it deals with biological taxa but because the definition is biological. It utilizes criteria that are meaningless in the inanimate world.

When difficulties are encountered, it is important to focus on the basic biological meaning of the species: A species is a protected gene pool. It is a Mendelian population shielded by its own devices (*isolating mechanisms*) against unsettling gene flow from other gene pools. Genes of the same gene pool form harmonious combinations because they have become coadapted by natural selection. Mixing the genes of two different species usually leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection (Mayr 1988*b*).

This makes it quite clear that *the word species in biology is a relational term: A* is a species in relation to *B* and *C* because it is reproductively isolated from them. This concept has its primary significance with respect to sympatric and synchronic populations (*nondimensional species*), and these are precisely the situations where the application of the concept poses the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other but the more biologically irrelevant this status becomes.

The biological species concept also solves the paradox caused by the conflict between the fixity of the species of the naturalist and the fluidity of the species of the evolutionist. It was this conflict that made Linnaeus deny evolution and Darwin deny the reality of species (Mayr 1957). The biological species combines the discreteness of the local species at a given time with an evolutionary potential for continuing change. The importance of the biological species concept lies in the fact that it is the concept employed in the largest number of biological disciplines, particularly ecology, physiology, and behavioral biology. In these disciplines one deals with the action of species in one locality at one time; one deals with coexisting gene pools and with the mechanisms that maintain their integrity and explain their capacity for coexistence. For all those who work with a species in a nondimensional situation, it is usually immaterial whether another population, well isolated in space or time, should be considered conspecific.

Paterson (1985) suggested that the biological species concept is faulty and should be replaced by a species recognition concept. However, Coyne, Orr, and Futuyma (1988) and Mayr (1988*b*) showed that Paterson's arguments are invalid, being largely based on misunderstandings. The unique position of species in the hierarchy of taxonomic categories has been pointed out by many authors. Taxa of the species category can be delimited against each other by operationally defined criteria, for example, interbreeding versus noninterbreeding of populations. It is the only taxonomic category for which the boundaries of the included taxa can be defined objectively.

Evolutionary Species Concept

Some authors, particularly paleontologists, are not satisfied with the biological species concept because of its strict applicability only to the

The working taxonomist sorts specimens (individuals) into phena and decides which of them belong to a single taxon of the species category. To undertake the ranking of taxa, the taxonomist must have a clear conception of the species category.

If a taxon is defined (as a morphospecies) in such a way that it coincides with the phenon, the taxonomist may facilitate the task of sorting specimens, but this activity will result in "species" that are biologically, and hence scientifically, meaningless. The objective of a scientifically sound concept of the species category is to facilitate the assembling of phena into biologically meaningful taxa on the species level. (See pp. 20–21 for a discussion of the meaning of category and taxon.)

A short survey of the history of species concepts shows how different the taxa are if one adopts either one or the other species concept.

SPECIES CONCEPTS

The taxonomic literature reports innumerable species concepts, but they fall into four groups. The first two have mainly historical significance but are still upheld by a few contemporary authors.

Typological Species Concept

According to this concept, the observed diversity of the universe reflects the existence of a limited number of underlying "universals" or types (the *eidos* of Plato). Individuals do not stand in any special relation to each other, being merely expressions of the same type. Members of a species form a class. Variation is the result of imperfect manifestations of the idea implicit in each species. This concept, which goes back to the philosophy of Plato, was the species concept of Linnaeus and his followers (Cain 1958). Because this philosophical tradition is also referred to as *essentialism*, the typological definition is also sometimes called the essentialist species concept (Mayr 1982*a*:256–263).

Various attempts at a purely numerical or mathematical definition of species are the logical equivalents of this species concept. Degree of morphological difference is the criterion of species status for the adherent of the typological species concept, for whom a different species is that which is "different." Morphological evidence is used by all taxonomists, but there is an enormous difference between basing one's species concept entirely on morphology and using morphological evidence as an inference in the application of a biological species concept (Simpson 1961:68–69).

The essentialist species concept was accepted by taxonomists almost

unanimously as late as the early post-Linnaean period. It included the acceptance of four postulates:

1 Species consist of similar individuals sharing the same essence.
2 Each species is separated from all others by a sharp discontinuity.
3 Each species is completely constant through time.
4 There are strict limits to the possible variation within any one species.

This typological species concept has been universally rejected for two practical reasons. First, individuals are frequently found in nature that are clearly conspecific with other individuals in spite of striking differences resulting from sexual dimorphism, age differences, polymorphism, and other forms of individual variation. Although often described originally as different species, they are deprived of their species status, regardless of the degree of morphological difference, as soon as they are found to be members of the same breeding population. Different phena that belong to a single population cannot be considered separate species no matter how different they are morphologically. Second, there are species in nature—*sibling species*—which differ hardly at all morphologically yet are good biological species. Degree of difference thus cannot be considered the decisive criterion in the ranking of taxa as species.

Its adherents abandon the typological species concept whenever they discover that they have named as a separate species something that is instead a conspecific phenon. The typological species concept is still defended by some writers who adhere to Thomistic philosophy. When there is a lack of biological information, a taxonomist may be forced to recognize species provisionally on the basis of strictly morphological evidence. Such species are subject to later reconsideration.

Nominalistic Species Concept

Nominalists (Occam and his followers) deny the existence of "real" universals. For them, only individuals exist while species are abstractions created by people. The nominalistic species concept was popular in France in the eighteenth century (Buffon and Lamarck in their early writings and Robinet) and has adherents to the present day (Mayr 1982*a*:264). Bessey (1908) expressed this point of view particularly well: "Nature produces individuals and nothing more . . . species have no actual existence in nature. They are mental concepts and nothing more . . . species have been invented in order that we may refer to great numbers of individuals collectively."

Any naturalist, whether a primitive native or a trained population geneticist, knows from practical experience that this is simply not true. Species of animals are not human constructs, nor are they types in the