two species." Any list of synonymies will quickly reveal how often this philosophy has led to the description of phena as species. The biological taxonomist asks, "Is the morphological difference between samples *a* and *b* of the kind one would expect to find between two reproductively isolated populations, that is, between two biological species?" In other words, the biological taxonomist uses the amount and kind of morphological difference only as an indication of reproductive isolation, only as evidence from which to draw an inference. This is a legitimate and reliable technique. Where typologists would recognize phena as (morpho) species, biologists will draw the right inferences from largely morphological evidence, and their species are usually confirmed by subsequent research. When competent taxonomic work based on morphological evidence is reexamined in the light of findings in behavior or biochemistry, it is usually confirmed in its entirety.

It is not always realized that the classification of phena is based on evidence entirely different from that which leads to the classification of species. The classification of species is based on weighted similarity, which entails the evaluation of all sorts of comparative data, morphological, physiological, or behavioral. The classification of phena is based on their relation to the gene pool of the population to which they belong. Ultimately this can be established only by their breeding behavior, which in turn can be observed in nature or studied experimentally. It does not matter whether one deals with strikingly different sexes in birds, insects, or marine invertebrates, with larval forms, or with alternating generations of parasites; breeding (or the piecing together of growth stages) is the best way to establish what phena together form a population. Sometimes molecular data also provide important clues. The experienced taxonomist knows what variation to expect within a biological species. No computer method has been found that can empirically assign phena to species. The taxonomist does this rapidly and with a high degree of precision on the basis of accumulated knowledge of the biology of the species concerned. In this taxonomic operation the classical methods still reign supreme "because they are enormously faster than the numerical methods" (Michener 1963).

DIFFICULTIES IN THE APPLICATION OF THE BIOLOGICAL SPECIES CONCEPT

The fact that difficulties sometimes arise when the biological species concept is applied to natural taxa does not mean that the concept is invalid. This has been shown by Simpson (1961:150) and Mayr (1963:21–22). Many generally accepted concepts cause similar difficulties when they have to be applied in a particular situation or to a specific sample. The concept of a tree, for instance, is not invalidated by the existence of spreading junipers, dwarf willows, giant cacti, and strangler figs. One must make a clear distinction between a concept and its application to a particular case.

The more ordinary problems of taxonomic discrimination at the species level, in particular the criteria for ranking a taxon as a species rather than a subspecies, are dealt with in Chapter 5.

The most serious difficulties in the application of the biological species concept are those caused by insufficient information, uniparental reproduction, and evolutionary intermediacy.

Insufficient Information

Individual variation in all its forms often raises doubt about whether a certain *morphotype* is a separate species or only a phenon within a variable population. Sexual dimorphism, age differences, polymorphism, and other types of variation can be unmasked as individual variations through a study of life histories and through population analysis (Chapter 5). The neontologist who normally works with preserved material is confronted by the same problems that confront the paleontologist, who also must assign phena (morphotypes) to species.

Uniparental Reproduction

Systems of reproduction in many organisms are not based on the principle of an obligatory recombination of genetic material between parental individuals during the formation of a new individual. Self-fertilizing hermaphroditism and other forms of automixis, parthenogenesis, gynogenesis, and vegetative reproduction (budding or fission) are some of the forms of uniparental reproduction. They are not infrequent among lower invertebrates, with parthenogenesis occurring even among insects and lower vertebrates up to the reptiles.

A population as defined in evolutionary biology is an interbreeding group. By this definition, an asexual biological population is a contradiction, even though the word *population* has also other uses in which a combination with *asexual* would not be contradictory. Since interbreeding is the ultimate test of conspecificity in animals and since this criterion is available only in sexually reproducing organisms, determination of categorical rank is difficult in taxa of uniparentally reproducing organisms. How should the taxonomist treat clones, pure lines, biotypes, and so-called strains or stocks of such organisms?

Such uniparental lineages are sometimes designated as *agamospecies*, binoms (Grant 1957), or paraspecies (Mayr 1987*b*). Whatever designation one chooses, one must be aware that such entities are not subdivisions of biological species (Mayr 1963:27–29) but something quite different. Ghiselin (1987) quite rightly questioned the propriety of applying the word *species* to groups of asexual clones, and we are inclined to agree with him (Mayr 1988*a*:353–355).

In some groups of animals, particularly aphids, gall wasps (Cynipidae), *Daphnia* (Crustacea), rotifers, and digenetic trematodes, a regular alternation between sexual and parthenogenetic generations may occur. In such cases neither kind of generation qualifies for separate species status, as nomenclatural recognition is not given to temporary clones. However, the parthenogenetic generations sometimes seem to fail to return to sexuality, particularly in aphids, and become permanent. When they differ from the sexual races by host plant preference or even by color genes, the suggestion that these parthenogenetic taxa should be called species deserves serious consideration.

In the case of permanently uniparentally reproducing lines, it is customary to assign species status on the basis of degree of morphological difference. There are usually well-defined morphological discontinuities among kinds of uniparentally reproducing organisms. These discontinuities are apparently produced by natural selection among the various mutants that occur in the asexual clones. It is customary to utilize the existence of such discontinuities and the amount of morphological difference among them to delimit species among uniparentally reproducing types.

Species recognition among asexual organisms is based not merely on analogy but also on the fact that each morphological entity that is separated by a gap from other similar entities seems to occupy an ecological niche of its own; each one plays its own evolutionary role. In groups such as the bdelloid rotifers, all of which reproduce by obligatory parthenogenesis, there is evidence of a definite biological meaning to the recognized morphological species.

Examples are known in which a form that is as distinct as a good species reproduces strictly parthenogenetically and no biparental species is known from which it might have branched off. Nomenclatural recognition is justified in such cases. Whenever several reproductively isolated chromosome types occur within such a "species," as in various crustaceans (e.g., *Artemia salina* Linnaeus) (White 1978), it may be convenient to distinguish them nomenclaturally. Although they are conventionally referred to as races, it is more logical to designate reproductively isolated chromosomal populations as (micro)species.

There are approximately 1000 animal species known in which the male sex is absent or nonfunctional. Such all-female species reproduce by *thelytoky*, a special term for this type of parthenogenesis. Depending on

the meiotic mechanisms, there is a trend toward either homozygosity or heterozygosity in such species. The homozygosity-generating type is rare, being restricted to a few insect groups, and there is sometimes a normally bisexually reproducing sibling species alongside the thelytokous species (White 1978). Many cases of heterozygosity-promoting thelytoky seem to be products of instantaneous speciation which results from a switch to parthenogenesis (thelytoky) in an individual that had originated as an interspecific hybrid (White 1978, Chapter 9). Existing species in this category seem to be products of relatively recent speciation events, not having been provided with sufficient time to accumulate enough individual variation to create taxonomic difficulties. This is the case with the all-female species of the lizard genus *Cnemidophorus*, which is found in the southwestern United States and Mexico. The known cases of thelytoky in salamanders and fishes are also the result of hybridization, as is one case in grasshoppers. In some special cases (e.g., *Rana esculenta, Poeciliopsis*) the male chromosomes are lost during meiosis, and fertilization by males of one of the parental species (gynogenesis, or *pseudogamy*) is needed to induce development of the egg even though the males do not contribute to the genotype of the developing zygote [kleptospecies (Dubois and Günther 1982)]. Hybridization between two distant species of animals apparently always results either in total sterility or in the abandonment of sexual reproduction (Chapter 4).

In groups with cyclical parthenogenesis, the sexual generation may be permanently lost in some species. Where this is correlated with a switch in a host species (as in the case of some aphids), it may raise doubts about species status. Hermaphrodites in most cases reproduce sexually; that is, fertilization of the eggs is effected by the spermatozoa of a different individual. However, an occasional species may practice complete self-fertilization (automixis). This results in increasing homozygosity, such as Foltz et al. (1982) found in several species (aggregates of clones) of slugs.

Evolutionary Intermediacy

The species, as manifested by a reproductive gap between populations, exists in full classical distinctness only in the nondimensional situation of a local fauna. As soon as one deals with species taxa extended in the dimensions of space (longitude and latitude) and time, the stage is set for incipient speciation. Populations may be found in these circumstances that are in the process of becoming separate species and have acquired some but not yet all of the attributes of distinct species. At what stage in this process of divergence should a diverging population be called a species? A decision is particularly difficult when the acquisition of morphological distinctness is not closely correlated with the acquisition of reproductive isolation. The various difficulties for the taxonomist that may result from evolutionary intermediacy can be summarized as follows.

1 *Acquisition of reproductive isolation without equivalent morphological change:* Reproductively isolated species without (or with very slight) morphological difference are called sibling species. Their taxonomic treatment is discussed in Chapter 5.

2 *Acquisition of strong morphological difference without reproductive isolation:* A number of genera of animals and plants are known in which morphologically very different populations interbreed at random wherever they come in contact. The typological solution of calling every morphologically distinct population a species is clearly inappropriate in such situations. Conversely, there are genera in which the isolating mechanisms between any two species break down occasionally. To consider such species conspecific would be to go to the opposite extreme. No generalized solution is possible in cases where morphological divergence and the acquisition of reproductive isolation do not coincide. The only recommendation to the specialist is to delimit species in such a way that they form biologically meaningful natural entities. The difficulty posed by the rapid morphological divergence of populations that lack reproductive isolation is well illustrated by the West Indian snail genus *Cerion* (Figure 2-1).

3 *The occasional breakdown of isolating mechanisms (hybridization):* Reproductive isolation may break down occasionally even between good species. Usually this leads only to the production of occasional hybrids, which, being either sterile or of lowered viability, do not cause any taxonomic difficulty. More rarely, there is a complete local breakdown of isolation that results in the production of an extensive hybrid swarm and more or less complete *introgression* (Mayr 1963:110–135).

Hybrid individuals are sometimes described as species before their hybrid nature is discovered. Such names lose their validity as soon as the hybridism is established (Chapter 14). Only populations are recognized as taxa, and hybrid individuals are not populations.

Situations where whole populations are formed as a result of hybridization are taxonomically more difficult. We recognize several types of natural populations that owe their origin to hybridization. The taxonomic treatment of secondary intergradation, which results from the fusion of previously isolated populations, is discussed in Chapter 5. Two other kinds of hybridism concern us here.

a *Hybrid swarms:* In certain species, the reproductive isolation that is

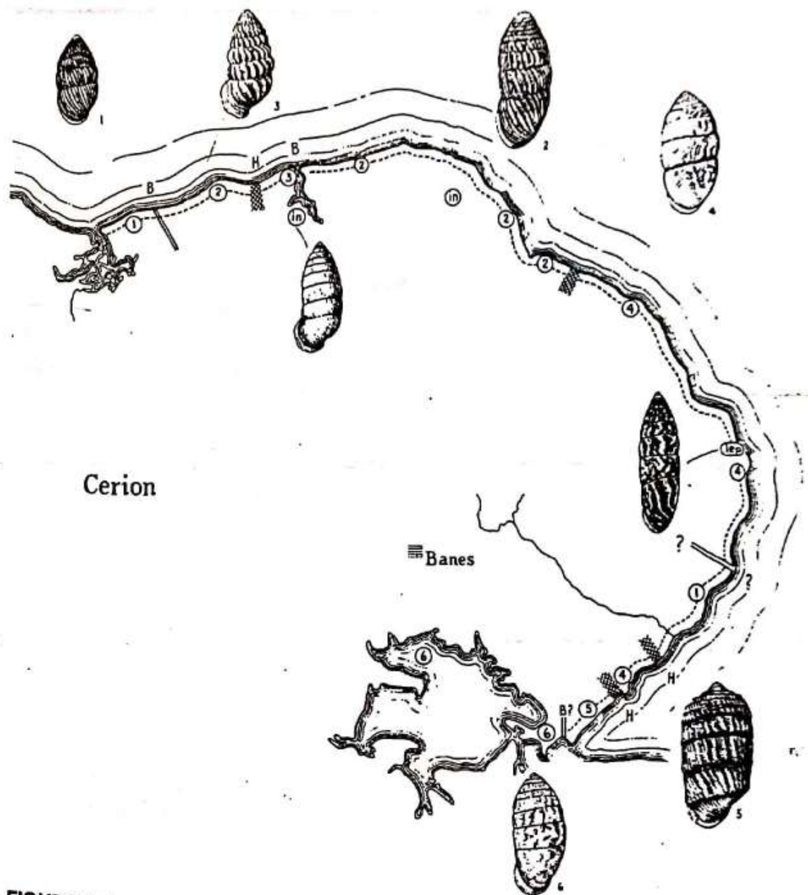

FIGURE 2-1
Irregular distribution of populations of the halophilous land snail *Cerion* in eastern Cuba. Numbers refer to different races or species. Where two populations come in contact (with the exception of *lepida*), they hybridize (H) regardless of difference. In other cases contact is prevented by a barrier (B). in = isolated populations. (*From Mayr 1963.*)

maintained over most of the area of sympatry may break down locally, resulting in the production of localized hybrid swarms. In such cases it is advisable to uphold the species status of the parental species. The example of the two Mexican towhees (*Pipilo erythrophthalmus* and *P. ocai*) provides an excellent illustration of this situation (Sibley 1954) (Figure 2-2). No taxonomic recognition is

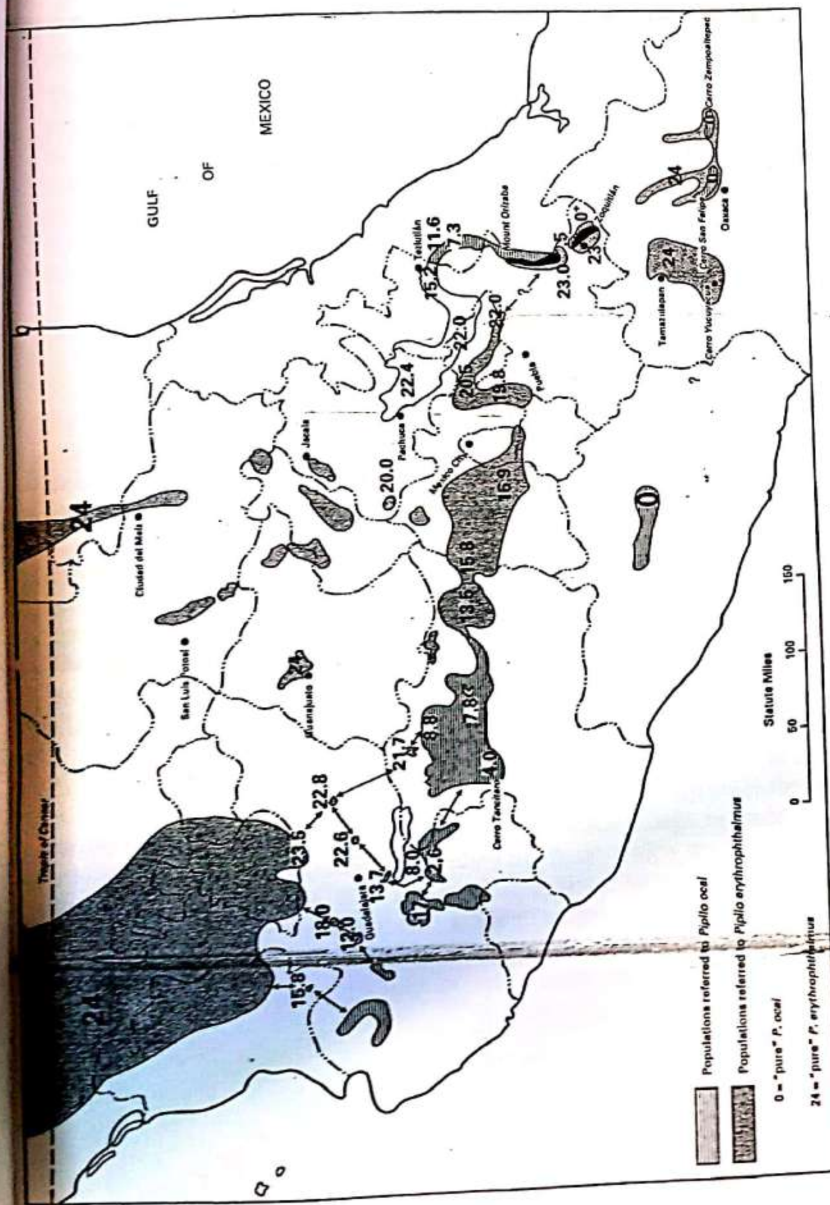

FIGURE 2-2
Sympatry and hybridization of two species of towhees (*Pipilo*) in Mexico: pure *erythrophthalmus* (24) in the north and southeast ... (0) in the south and southwest. The numbers (from 0 to 24) designate the mean character indexes of various

given to hybrid populations that result from such a local breakdown of reproductive isolation. The only possible exception would be a breakdown of isolation so complete that the two parental species fuse into a single new species. The taxonomic literature includes a number of instances that have been interpreted in this manner, but we are not aware of a single thorough analysis that would have established the fact unequivocally. For further discussion of the taxonomic aspects of hybridization, see Chapter 5.

b *Parthenogenetic species formed through hybridization:* Hybridization that results in the production of an individual with one chromosome set from parental species A and one from parental species B leads through doubling of the chromosome set to *allotetraploidy*. In plants, such individuals can immediately establish a self-fertilizing and eventually cross-fertilizing allotetraploid species. In animals, where cross-fertilization is almost always obligatory, a new allotetraploid can maintain itself only by switching to parthenogenesis (thelytoky). Such hybrid species are usually morphologically well characterized and are ordinarily recognized as valid species even after their mode of origin has been discovered.

More complex situations involve partial parthenogenesis, sometimes combined with triploidy or higher polyploidy, as is found in oligochaetes, planarians, weevils, moths (*Solenobia*) and other insects, mites, and crustaceans. Here one may find in a single "species" bisexual diploids, thelytokous diploids, and thelytokous polyploid "races" (White 1978). Even though these races may be morphologically indistinguishable, they are reproductively isolated. Most of these thelytokous races do not seem to be products of hybridization. In this case thelytoky seems to precede the origin of polyploidy.

4 *Semispecies and allospecies:* Geographic isolates occasionally have an intermediate status between subspecies and species. On the basis of some criteria, they would be considered species; on the basis of others, they would not. It is usually more convenient for the taxonomist (Chapter 5) to attach such doubtful populations as subspecies to the species with which they are most nearly allied. In other cases such isolates have evidently reached the species level but have remained members of a superspecies. Such populations may be designated as *allospecies*. Circular overlaps and other borderline cases (Mayr 1963:496–512) are other instances of evolutionary intermediacy. The method of ranking the resulting taxa has to be decided from case to case on the basis of convenience and degree of evolutionary intermediacy. Taxa intermediate between subspecies and species are often referred to as *semispecies*.

MEANING OF THE SPECIES CATEGORY

The basic role of the species definition is to function as a yardstick whenever the delimitation of a species taxon presents difficulties. Most species taxa, particularly monotypic taxa with limited variability and distribution, present no problems, but there are two sources of potential difficulties: the assembling of local phena into biological species (with the problems of polymorphism and sibling species) and the proper assignment of allopatric and allochronic populations. It is in these situations that the biological species concept facilitates the decision about which phena and populations should be considered full species and which should not.

In an analysis of the 607 species of North American birds, Mayr and Short (1970) found that the biological species concept was unable to clarify only a single case (*Pipilo*) (Figure 2-2). On the other hand, it permitted the settling of all controversies with respect to polymorphism and sibling species. In 45 cases of hybridization among species taxa, the criteria of the biological species permitted the classification of 27 cases as intraspecific and 18 cases as interspecific hybridization. Among the 607 North American species, 247 are polytypic, but only 46 of them contain populations (mostly peripheral isolates) that some authors consider full species and others (Mayr and Short included) consider subspecies. Since these populations are isolated, the biological species concept cannot be applied directly. This analysis illustrates how useful the biological species concept is in difficult situations.

In the case of populations that are isolated from each other in space or time, one can decide only by inference whether they would behave toward each other as members of the same species. Such inferences are often more robust (Chapter 5) than the outsider would suspect, but in most cases it is biologically not very important which decision is made (species or subspecies). It is the sympatric situation that is of particular importance for the ecologist and student of behavior. Furthermore, no other species definition can provide a foolproof system for the correct assignment of isolated populations or other cases of evolutionary intermediacy.