

reproductive isolation often depends on ecologic or behavioral barriers that tend to break down in captivity.

The biologic species concept has some shortcomings. Chief among them are the occasional existence of evolutionary intermediates between species and the difficulty of applying the concept when reproduction is asexual. Biologists who study groups in which asexual reproduction is the rule sometimes adopt a species concept based on phenotypic attributes, such as biochemical properties in bacteria. We focus on the biologic concept because it is thought to apply reasonably well for many of the paleontologically important groups of organisms.

The Origin of Species

If two or more populations of a species diverge to a sufficient extent genetically, they may become reproductively isolated and thus come to be distinct species. One of the principal questions in the study of the origin of species, or **speciation**, concerns the geographic relationships of the diverging populations. Do they have overlapping geographic ranges, in which case they are referred to as **sympatric**, or do they have disjunct ranges—that is, are they **allopatric**? Because gene flow can reduce distinctions between populations, and because populations living in the same broad area may be subject to largely the same forces of natural selection, it seems reasonable to presume that speciation should occur mainly between allopatric populations. In fact, this is the prevailing view among biologists, although there are many theoretical and empirical arguments in favor of sympatric speciation as well.

For allopatric speciation to take place, a population must first become geographically isolated from other populations of the species; then it must persist for some time; and finally it must attain reproductive isolation. Geographic isolates are forming all the time, as organisms disperse and found new populations geographically separated from parental populations, and as newly created geographic barriers, such as mountains, rivers, and emergent land, split populations. The resulting populations represent potential new species, but their fate is not at all assured. Many isolates become extinct, either because they start out with relatively few individuals and therefore are susceptible to fluctuations in population size, or because the environments they colonize may be unfavorable or ephemeral.

If a geographically isolated population does become established, even occasional migration of individuals between populations can lead to sufficient gene flow to prevent reproductive isolation from developing. Gene flow on a large scale is facilitated by the spatial shift of environments over time, which promotes migration as populations track the local conditions to which they are adapted. The probability that a geographically isolated population will actually become a new species is therefore generally quite low.

Our understanding of speciation comes mainly from biology rather than paleontology. Nonetheless, how species originate—that is to say, how populations become reproductively isolated and how evolutionary change is associated with this process—has important paleontological implications that we will pursue further in Chapter 7.

Discrimination of Species

It is important to distinguish between how species are defined in principle and how they are recognized in practice. Biologists rarely perform breeding experiments to determine whether two populations are part of the same species, and of course paleontologists cannot do so with fossil populations. Except for the availability of behavioral data and the widespread analysis of genetic data in biology, the approaches of biologists and paleontologists are often rather similar: One typically starts by determining whether the phenotypic difference between two populations is large relative to the variation within the populations (see Figure 3.9).

Figure 3.18 shows an example of this approach with corals from the Silurian of Arctic Canada. Here there are three clear groups that do not overlap: *Heliolites* aff. *H. luxarboreus*, *H. diligens*, and *H. tchernyshevi*. These are accepted as distinct species on morphological grounds. A fourth form, *H. sp.*, is rather similar to *H. tchernyshevi* with respect to the characters portrayed here, but it is not known from enough material to assess its variation in these characters. It is nevertheless accepted as a distinct species because it differs from the remaining species in other characters, such as the nature of the septa, or vertical plates within the corallites.

Genetic data, either in the direct form of DNA sequences or in the indirect form of proteins, have also proven invaluable in discriminating living species, and genetic analysis is now part of the standard toolkit of biologists. (See Box 3.3.) If two populations differ from each

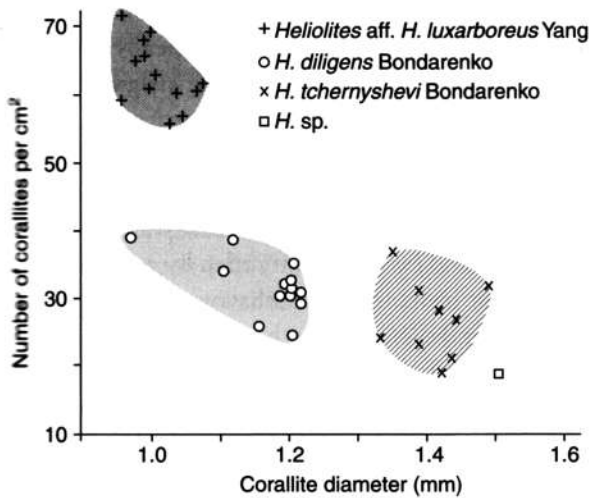


FIGURE 3.18 Morphological discrimination of species of the coral *Heliolites* from the Silurian of Arctic Canada. (From Dixon, 1989)

other by as much as two closely related species typically do, they are often regarded as belonging to distinct species. Genetic data can be used to great advantage when morphological differences are negligible or difficult to observe. As is true with morphological data, however, there is no formula that says how much genetic difference characterizes distinct species.

Morphologic and Biologic Species

In practice, both biologists and paleontologists usually apply a morphologic species concept. There are several important problems that stem from this approach.

Failing to take variation into consideration can lead to biologically unrealistic results. Figure 3.19 shows an example involving the Triassic ammonoid genus *Paranannites* from the Great Basin of the western United States. This graph plots two separate characters, the whorl width (W) and the umbilical width (U), against the shell diameter. Each point is a single specimen and each field in the graph represents a separate bivariate comparison. Within each bivariate comparison, the points form a continuous distribution. There are no obvious divisions or clusters that would serve as evidence for multiple species. Partly on these grounds, Bernhard Kummel and Grant Steele (1962) concluded that the material represents a single species, *Paranannites aspenensis*.

Thirty years before Kummel and Steele performed this analysis, J. P. Smith (1932) studied a subset of this material. In addition to *P. aspenensis*, Smith erected three other species, based mainly on differences relative to *P. aspenensis* in overall size, whorl width, and umbilical diameter, as well as on details of sculpture. Given that Smith studied the same traits as Kummel and Steele, how

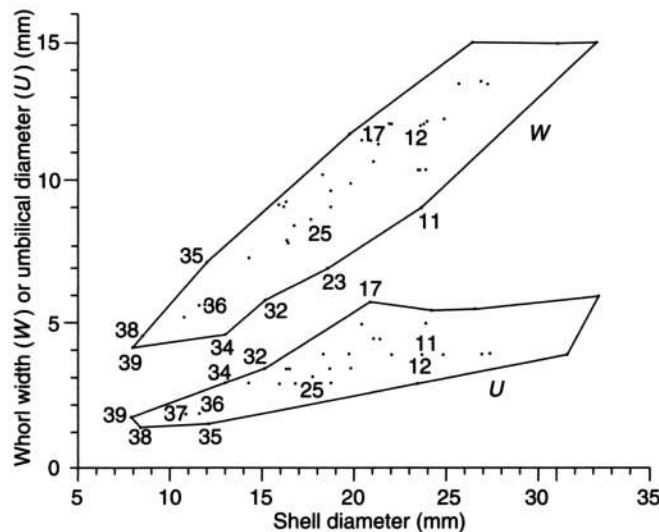


FIGURE 3.19 Biometric analysis of the ammonite species *Paranannites aspenensis* from the Triassic of the Great Basin. Two separate bivariate comparisons are shown here: whorl width (W) against shell diameter, and umbilical diameter (U) against shell diameter. Each point represents one specimen. The numbered points are type specimens that had previously been used to describe this species and three additional species. Because they show continuous variation, all the specimens are now considered to belong to a single species. The type specimens tend to fall near the extremes of the continuous distribution of form. (From Kummel & Steele, 1962)

can we account for the different numbers of species recognized by these authors? The numbered points on Figure 3.19 are Smith's type specimens—the exemplars he chose as representative of the species he described [SEE SECTION 4.1]. Most of these lie at the periphery of the scatter of points. Smith evidently focused on extreme forms and considered them to be representatives of separate species, rather than recognizing them as simply end-members of a continuum.

There are potential problems with the use of morphologic species, in both biology and paleontology, that cannot easily be overcome with more detailed assessment of morphological variation. First is the existence of **cryptic species**, also known as **sibling species**. Closely related species may be genetically and behaviorally distinct but may lack clear morphological differences. Second, species may contain numerous distinct morphological types, or **polymorphs**. The different forms within a polymorphic species are under genetic control, but they are not reproductively isolated and the genetic differences involved are generally small. Nonetheless, polymorphs are sometimes sufficiently different in form that they might be mistaken for distinct species on the basis of morphology alone. Finally, as we discussed earlier, some of the variation within species is ecophenotypic rather than heritable. Thus, two populations that belong to the same species could be mistaken for different species if they lived in environments that induced substantially different phenotypes.

There is no question that these problems exist in principle, but it is important to determine how common they are in reality. One study that explores this question involves living species of the cheilostome bryozoan genera *Steginoporella*, *Stylopoma*, and *Parasmittina* from the Caribbean Sea.

Using multivariate morphometric techniques similar to those we discussed earlier, Jeremy Jackson and Alan Cheetham (1990, 1994) analyzed a variety of skeletal measurements and found morphological clusters of specimens that were defined operationally as **morphospecies**. Once the morphospecies were established, Jackson and Cheetham sought to assess the importance of ecophenotypic variation. Embryos of known parentage were raised in environments different from those in which their parents had been raised. After rearing, the offspring were measured and assigned to prospective parents on the basis of morphological similarity. That is,

each of the offspring was assigned to the parental colony with which it was morphologically most similar. For all seven species studied, these assignments were found to be correct—matching true parentage—99 to 100 percent of the time, despite the fact that parents and offspring did not share the same environment. On the whole, morphological variation was much more strongly affected by heritability than by variation in the environment in which the embryos grew.

Jackson and Cheetham then tested for polymorphism by asking whether morphologically distinct species have consistent genetic differences. To identify genetic differences, they used the standard technique of electrophoresis, which identifies alternative forms of proteins having different mass and electrical properties. Because proteins are coded by DNA, the alternative forms of protein are used as evidence for differences in DNA sequence. In general, different forms of the same gene are referred to as **alleles**. Here the different proteins are inferred to represent different alleles. For a given kind of gene, each individual inherits one allele from its mother and one from its father. For that gene, the combination of two alleles is the individual's genotype.

Box 3.3 gives one example of how the genetic results are interpreted to test for differences between populations. When this approach was applied to the bryozoans, every pair of distinct morphospecies within a genus was found to have at least one diagnostic genetic difference. Thus, these morphospecies are likely to be true biological species rather than polymorphs within a single species. Moreover, if genetic and morphological dissimilarity between populations are compared, it is found that the magnitudes of morphological and genetic difference are well correlated (Figure 3.20). Pairs of populations that are more dissimilar morphologically also tend to be more dissimilar genetically.

Finally, Jackson and Cheetham tested for the existence of cryptic species by determining whether different populations of the same morphospecies have diagnostic genetic differences. The analysis found no cases in which two populations of the same morphospecies could be genetically distinguished with confidence. In other words, populations that could not be distinguished morphologically could not be distinguished genetically, either. Thus, there was no compelling evidence for the existence of cryptic species in these genera.

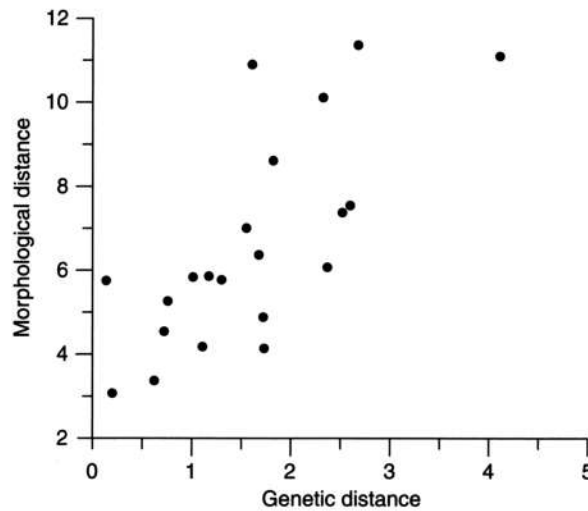


FIGURE 3.20 Comparison of morphological and genetic dissimilarity between populations of the bryozoan *Stylopoma*. Each point represents a comparison between two populations. Morphological distance is measured by a variant of the straight-line distance described in the discussion of cluster analysis in Box 3.2. Genetic distance is measured on the basis of differences in gene frequencies. (See Table 3.5 for examples of gene frequencies.) Morphological and genetic differences are positively correlated. (From Jackson & Cheetham, 1994)

Taken together, these results suggest that there is an excellent concordance between biological and morphological species in this sample of cheilostome bryozoans.

The question of concordance between morphological and biological species applies to biology as much as to paleontology. There is a special problem, however, that paleontologists must face because of the temporal dimension of the history of life. Our earlier discussion of speciation was restricted to the situation in which an evolving lineage splits into two distinct lineages. It sometimes happens that a single lineage may evolve over time to the point where it becomes morphologically quite distinct from earlier populations in the lineage, even though there has been no splitting (Figure 3.21). In cases like this, some paleontologists will divide the lineage into two or more named species. Because of the added time dimension, species such as A and B in Figure 3.21 may be referred to as **chronospecies**. Many workers today prefer, if possible, to place species boundaries at branching points and at true lineage terminations. It may be difficult to avoid erecting chronospecies, however, if the intermediate forms between A and B are not sampled.

3.4 CONCLUDING REMARKS

That there is a close correspondence between morphological and genetic species in a sample of bryozoans does not imply that the same is true for other groups of organisms, or even for other bryozoans. If these results prove to be general, however, then biologists and paleontologists are in a strong position to discriminate species on the basis of morphology. It is still too soon to assess fully the correspondence between morphospecies and biological species. Nonetheless, studies on many other groups of organisms have shown that, as in the bryozoans, morphologically defined species tend to be genetically distinct. At the same time, cryptic species are known to be common in some groups.

There is thus an asymmetry in the relationships between morphological and genetic species. If two populations are morphologically distinct, there is often a good chance that they belong to different species. But if they are morphologically indistinguishable, this need not imply that they belong to the same species. This asymmetry will be relevant when we consider the relationship between speciation and morphological evolution in Chapter 7.