Chapter 6

Systematics and Taxonomy

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1. Introduction

Biological taxonomy may seem like a simple science – biologists merely observe similarities among organisms and construct classifications according to those similarities. But biological taxonomy is not so simple. Consider an obvious type of similarity referred to as "morphological similarity": when organisms have a similar body shape and structure. Dogs have a different morphology than coyotes, and dogs and coyotes are more similar to one another than either is to foxes. Mammals come in neat morphological packages. However, morphology is an inadequate marker for classifying many organisms, especially insects, molds, fungi, and bacteria. For example, the fruit flies *Drosophila persimilis* and *Drosophila pseudoobscura* have nearly identical morphologies. It took years for biologists to determine that many organisms thought to be *Drosophila persimilis* are in fact members of a different species, *Drosophila pseudoobscura*. Matters get worse in bacteria. Some bacteriologists have thrown up their hands in classifying parasitic bacteria. The morphological differences between such bacteria grade into one another, resulting in a continuum of organisms. Bacteria are not an exceptional case. Most of life on Earth, in terms of both biomass and biodiversity, is bacterial.

Perhaps a better foundation for biological classification can be found in genetics. We live in the heady days of the Human Genome Project and other genome projects. Perhaps the organisms of one species are genetically more similar to one another than they are to organisms in other species. If this is true, then classification can be based on genetic similarity. There are, however, strong challenges to this suggestion; one being that genes are insufficient for distinguishing species. Turning to fruit flies again, there can be more genetic variation between different populations of a single fruit fly species than there is between two such species (Ferguson, 2002). In other words, two organisms in different species can be more similar to one another genetically than either is to the members of its own species.

Alternatively, one might think that species are distinguished in terms of sexual reproduction. Introductory biology texts tell us that the members of the same species can interbreed and produce viable offspring. Classification, then, should be based on the relations between organisms – in this case, interbreeding relations – rather than on similarities. Interbreeding relations do provide clean divisions among mammals and birds.

Nevertheless, the interbreeding approach to classification runs aground of a glaring biological fact: the vast majority of organisms on Earth do not reproduce by interbreeding. Most organisms reproduce asexually by cloning, self-fertilization, or by other means. So the interbreeding approach does not apply to most of life on this planet.

Which type of trait should be used for classifying organisms? This is a thorny issue. To complicate matters further, there are a number of philosophical controversies within biological taxonomy. Four of these controversies are the focus of this chapter. One controversy concerns the ontological nature of species. Are species natural kinds akin to the chemical elements whose members share theoretically significant similarities, or are they "individuals" analogous to particular organisms whose parts are connected by casual relations? Another controversy concerns the unity of science. Is there a single correct way to sort organisms into species, or are there multiple correct ways to classify the organic world? This debate pits monists against pluralists. A third philosophical controversy concerns phylogenetic inference. The majority of taxonomists would like biological classification to reflect branching on the tree of life, but how should information about organismic traits be used to infer such branching? A fourth controversy concerns the framework of biological classification, the Linnaean hierarchy. The Linnaean hierarchy was developed in the eighteenth century, well before the advent of evolutionary theory. We now live in a Darwinian age, and many biologists believe that the Linnaean hierarchy is theoretically outdated and should be replaced.

The resolution of the above philosophical issues within biological taxonomy has implications outside of taxonomy. For example, decisions concerning the nature of species affect how biological conservation should be conducted. If we consider species the basic units for assessing biodiversity, then the approach to species we choose will affect our choice of biological entities to preserve. Philosophical issues in taxonomy also affect our conception of human nature. If an account of human nature has a biological basis, then our approach to species affects what it means to be a human. Is there a genetic or other sort of biological essence to *Homo sapiens*, or is each one of us a human because we share a common evolutionary history? If the latter is true, then little can be said about what is normal or natural for humans.

Before turning to fuller discussion of these issues, some terminological clarification is in order. The terms "classification," "taxonomy," and "systematics" are often used in taxonomic discussions. It is important to be clear about their meanings. Biological taxonomy provides the principles and methods for constructing classifications. Biological taxonomy tells us how to sort organisms into species, and it provides the principles for classifying taxa into more inclusive taxa. Classifications themselves are the products of taxonomy. Biological systematics is more foundational. Systematics is the study of how organisms and taxa are related in the natural world. Ideally, the results of systematics determine the principles of taxonomy, which in turn tell us how to construct classifications of the organic world.

2. The Ontological Nature of Species

For the most part, philosophers believe that species are natural kinds. But whether species are natural kinds is controversial. Even among those philosophers who agree that species are natural kinds, there is disagreement about the nature of those kinds. This section will review two approaches to the idea that species are natural kinds as well as the thesis that species are individuals.

2.1. Species essentialism

The standard philosophical account of natural kinds assumes that the members of a kind share a common essential property or essence. This essentialist approach to natural kinds traces back to Aristotle and is found in the work of Hilary Putnam and Saul Kripke. Stated simply, kind essentialism has two main tenets: (1) All and only the members of a kind share a kind-specific essential property; and (2) a kind's essential property is causally responsible for other properties typically found among the members of that kind. The essence of the natural kind gold, for example, is gold's atomic structure, which occurs in all and only gold and is used for predicting and explaining other properties associated with pieces of gold, such as their ability to conduct electricity.

If species are essentialist kinds, what are their essences? Linnaeus thought that the essence of a plant species was its genus' fructification system and whatever traits distinguish that species from the other species in its genus. Locke thought that the essence of a species was its unique microstructure, although he did not know the nature of such microstructures. Some have speculated that the essence Locke was looking for was none other than DNA. In the past fifty years, a number of philosophers and biologists have argued that species are not natural kinds with essences (Mayr, 1959; Hull, 1965; Ghiselin, 1974; Sober, 1980; Dupré, 1981). They maintain that species essentialism is inconsistent with evolutionary theory and therefore should be abandoned. Anti-essentialists offer many arguments against species essentialism (see Ereshefsky, 2001, for a review). We will focus here on the argument that biological forces work against the existence of biological essences.

The first tenet of essentialism requires that there be a biological property in all and only the members of a particular species. Biologists have been hard-pressed to find such properties. Evolutionary biology explains why. In order for a property to be a species' essence, it must be present in *all* the members of a species. However, processes such as mutation work against a trait occurring in all members of a species. Suppose a trait is universal among the members of a species. A mutation can eliminate that trait in an organism in the next generation. If a trait fails to occur in one member of a species, then that trait is not the essence of that species. Recombination can have the same effect. Recombination does not alter DNA, but reshuffles it such that a trait universal in one generation of a species may fail to appear in a member in the next generation. In general, genetically based traits are vulnerable to the forces of mutation and recombination, which makes the universality of a trait in a species fragile.

Suppose, nevertheless, that a trait occurs in all members of a species. Essentialism also requires this trait to be *unique* to the members of the species. This constraint rules out many traits as species essences because those traits occur in other species. Evolutionary theory explains why similar traits frequently occur in different species. Organisms in closely related species inherit common genes and developmental programs from their shared ancestors. These common genetic and developmental resources cause the members of different species to be similar. Another source of similarity across taxa is parallel evolution. Similar adaptive needs cause similar traits in different species. For example, the eye of the octopus and the human eye are functionally similar, but each type of eye has a different evolutionary origin.

It is an empirical claim that evolutionary forces work against species having essences. So it is possible that a trait could occur in all and only the members of a species. But consider the stringent requirements of essentialism. A trait is the essence of a species only if it occurs in all members of that species for the entire life of that species. Furthermore, a trait is unique among the members of a species as long as it does not occur in any other organism for the *entire* history of life in the universe. If the trait occurs just once in another species, then that trait is not the essence of the species in question. Recall, also, that the second tenet of essentialism places a further requirement on essentialism. A trait might occur in all and only the members of a species, but this occurrence would be insufficient for it being a species' essence unless it also caused the other traits typically associated with that species. Given the high standards of essentialism and the confounding forces of evolution, species essentialism is probably false.

2.2. Species as individuals

If species are not natural kinds with essences, then what are they? Some philosophers and biologists believe that species are not natural kinds but individuals. The two most prominent advocates, Ghiselin (1974) and Hull (1978), contrast natural kinds and individuals in terms of space-time locality. Natural kinds, they suggest, are spatiotemporally unrestricted entities: a member of the kind gold is gold regardless of its location in space and time. The motivation for this requirement is that laws of nature refer to natural kinds and laws of nature are not restricted to particular space-time regions. If "All water boils at 100 degrees Celsius" is a law of nature, then water will boil at that temperature anywhere in space and time. In contrast to natural kinds, Ghiselin and Hull suggest that individuals are spatiotemporally restricted entities. Consider an analogy. In geology there are various kinds of rocks (granite, shale, and so on), and there are individual rocks (the granite rock in a garden). Granite, the kind, can have members across the universe, but the parts of the granite rock in the garden must be located in a restricted space-time region to be parts of that rock. Ghiselin and Hull argue that species are also spatiotemporally restricted entities, akin to the rock in the garden, hence species are individuals rather than kinds.

What is their argument for species being spatiotemporally restricted entities? Hull writes that species are units of evolution and as units of evolution species must be spatiotemporally restricted. Suppose that selection causes species to evolve. For evolution by selection to occur, the selected traits must be passed down through the generations of species. Traits are not inherited unless some causal connection exists between the members of a species. In particular, sex and reproduction require that organisms or their parts (gametes, DNA) come into contact. Evolution, thus, requires that the organisms of a species be connected genealogically. Just as the parts of an individual organism must be appropriately connected causally, so must the members of a particular species. The organisms of a species cannot be scattered throughout the universe. Hence, species are individuals.

Hull (1978) and others have drawn many implications from the thesis that species are individuals. One implication is that there is no biological essence to being a human. From an evolutionary perspective, humans are merely parts of the evolving lineage *Homo sapiens*. There is no qualitative property that all and only humans must have. Having a certain cognitive ability, social ability, even being able to communicate with language is not required for being a human. Being part of a particular evolving lineage is all that matters. Traditional accounts of human nature require that all humans have a distinctive human quality. If species are individuals, then such accounts of human nature lack a biological basis.

2.3. Species as homeostatic property cluster kinds

The debate over the ontological status of species does not end with the claim that species are individuals. A handful of philosophers argue that we should not reject the view that species are natural kinds (Boyd, 1999a; Griffiths, 1999; Wilson, 1999). The problem, they suggest, is the standard essentialist account of natural kinds. Adopt a better approach to natural kinds and species will be returned to their proper place as natural kinds. The approach to natural kinds they advocate is Boyd's Homeostatic Property Cluster (HPC) Theory. The members of an HPC kind share a cluster of similar properties, but none of these properties is essential for membership in an HPC kind. Nevertheless, these properties must be stable enough to allow for successful induction. That is, they must be stable enough to allow us to predict with better than chance probability that a member of an HPC kind will have certain properties. The members of the kind *Canis familaris* share many similar properties such that we can reasonably predict that, if an organism is a dog, it will have certain properties. According to HPC theory, the co-occurrence of properties among the members of an HPC kind is due to a kind's homeostatic mechanisms. Such homeostatic mechanisms include interbreeding, shared ancestry, and common developmental constraints.

HPC theory provides a more promising account of species as natural kinds than traditional essentialism. HPC theory allows for variation among the members of a species, and it does not require that the members of a species share a common essence. All that is required is that the members of a species share a cluster of co-occurring properties. HPC theory also recognizes the importance of genealogy. Shared ancestry and reproductive relations are homeostatic mechanisms that maintain similarities among the members of a species.

Does HPC theory provide an adequate account of species as natural kinds? Some argue that it does not (Ereshefsky & Matthen, 2005). While it is undoubtedly true that the members of a species have many similarities, it is also true that species are characterized by dissimilarities. Polymorphism – variation within a species – is an important feature of nearly every species. For example, the males and females of a species can vary dramatically, and the members of a species can vary in their life stages, as exemplified by the caterpillar and butterfly stages of a single organism. Stable polymorphism is an essential feature of nearly all species, yet HPC theory gives no account of this feature. HPC theory focuses only on explaining those similarities that exist within a species. So the first problem with HPC theory is that it provides an impoverished account of species.

A second problem with HPC theory turns on the requirement that species are lineages. Hull and others argue that from an evolutionary perspective species must be genealogical entities. HPC theory allows that species are genealogical entities, but HPC theory does not require that all species be genealogical entities (Boyd, 1999b, p.80). HPC kinds are first and foremost kinds whose members have sufficient similarity to underwrite successful predictions. Yet, as Boyd recognizes, genealogy and similarity can part company. When genealogy and similarity conflict, Boyd prefers similarity to genealogy and posits species that are not genealogical lineages. Evolutionary theory requires that all species be genealogical lineages; HPC theory does not. In sum, HPC theory is inconsistent with an evolutionary account of species. Moreover, it fails to explain the occurrence of stable polymorphism in species. The claim that species are individuals fares better on both counts. The individuality thesis is premised on the assumption that species are genealogical lineages. Furthermore, the individuality thesis provides a more robust account of the nature of species. The individuality thesis appeals to the genealogy of a species to explain the similarities *and* dissimilarities among the members of a species.

3. Taxonomic Pluralism

A common assumption in biology and philosophy is that one true classification of the organic world exists. That is, if we had a god's eye perspective, we would see that each organism belongs to a particular species, that each species belongs to a particular genus, and so on up the Linnaean hierarchy. This view, called "monism," also assumes that there is one correct definition of "species" and there is one correct method for classifying taxa into more inclusive taxa. In contrast, pluralism is the view that there are multiple correct definitions of "species" (Kitcher, 1984; Ereshefsky, 1992; Dupré, 1993). According to pluralists, there are different kinds of species and different but legitimate Linnaean classifications of the organic world.

What is the argument for taxonomic pluralism? It begins with the observation that biologists provide various definitions of the term "species" – what biologists refer to as "species concepts." The dozen or so species concepts in the current biological literature are not fringe concepts, but have widespread support among biologists. The most prominent species concepts fall into three types: interbreeding, ecological, and phylogenetic. According to interbreeding concepts, species are groups of organisms that can interbreed and produce fertile offspring. Interbreeding species are distinct gene pools, bound and maintained by sexual reproduction. Ecological species concepts also focus on the forces that maintain species. An ecological species is a lineage of organisms that live in a particular ecological niche. The selection forces in a species' niche cause a lineage to be a distinct species. Interbreeding and ecological species concepts stem from work in evolutionary biology, whereas phylogenetic species concepts are derived from the school of taxonomy called "Cladism" (see Section 4). According to cladists, organisms should be classified by their shared ancestry. Each taxon should contain all and only the descendants of a common ancestor. Such taxa are labeled "monophyletic." According to phylogenetic species concepts, species are the smallest monophyletic taxa within the Linnaean hierarchy.

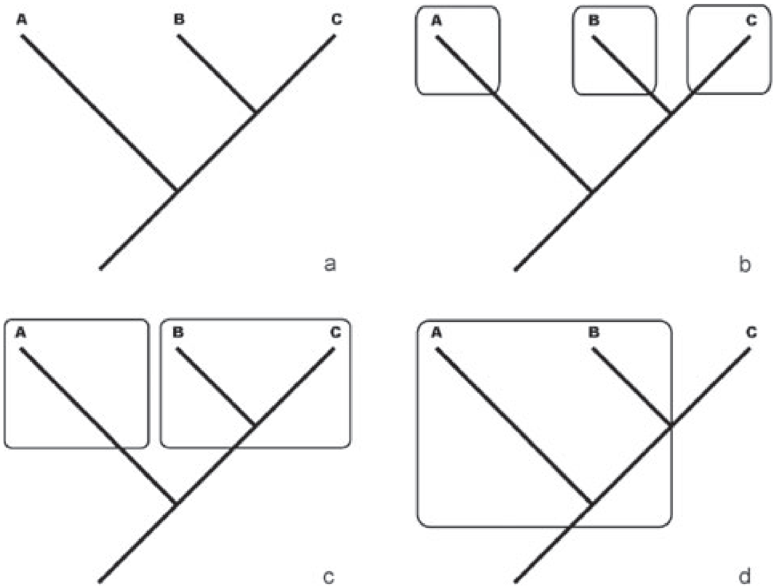

Figure 6.1 (a) A phylogenetic tree with three populations, A, B, and C. (b) The tree with three phylogenetic species, A, B, and C. (c) The tree with two ecological species, A and B + C. (d) The tree with one interbreeding species, A + B

These three approaches to species – interbreeding, ecological, and phylogenetic – assume that species are genealogical lineages. Nevertheless, these approaches highlight different types of lineages as species. As a result, they give rise to different classifications of a single group of organisms. Consider a hypothetical example, which is based on empirical studies showing that interbreeding, ecological, and phylogenetic species concepts often pick out different groups of organisms in nature (Ereshefsky, 2001). Suppose that three insect populations, A, B, C, live on the side of a mountain (Figure 6.1a), and each population forms a single basal monophyletic taxon. The organisms in B and C share a common ecological niche, while the organisms in A occupy their own distinct niche. The organisms in A and B can successfully produce fertile offspring, whereas the organisms in C reproduce asexually. Given these biological considerations, how should we classify the insects in question? According to the phylogenetic approach, there are three species: A, B, and C (Figure 6.1b). According to the ecological approach, there are two species: A and B + C (Figure 6.1c). According to the interbreeding approach, there is only one species: the species consisting of A + B (Figure 6.1d). These different approaches to species provide three different classifications of the same group of insects.

When we apply these approaches to all of life, the result is three different classifications of the organic world. Different species concepts give rise to a plurality of classifications. A monist might respond that this situation is due to our lack of biological knowledge and is merely temporary. One of the species concepts discussed, or one to be discovered, is the correct approach to species. Once biologists have settled on that correct concept, we will have a single classification of the world's organisms. However, species pluralists maintain that the case for pluralism is not our lack of information about the organic world. Quite the contrary. We have substantial information from evolutionary biology that the tree of life is segmented by various evolutionary forces into different types of species (interbreeding, ecological, phylogenetic). Taxonomic pluralism is a result of a fecundity of biological forces rather than a paucity of scientific information.

Monists offer many responses to taxonomic pluralism (Sober, 1984; Hull, 1999). We will consider two recent monist responses. De Queiroz (1999) and Mayden (2002) argue that among the species concepts found in the literature, one concept should be considered the primary species concept. They observe that, despite their differences, all species are lineages. Thus, de Queiroz and Mayden offer a lineage account of species. The lineage account of species, according to Mayden (2002, p.191), "serves as the logical and fundamental over-arching conceptualization of what scientists hope to discover in nature behaving as species. As such, this concept . . . can be argued to serve as the primary concept of diversity." De Queiroz and Mayden suggest that the various species concepts in the literature provide criteria for discovering species, but only the lineage account properly defines "species." De Queiroz and Mayden believe that although their approach to species is monistic, it captures what is correct in species pluralism. They offer a single correct species concept – the lineage account. At the same time, de Queiroz and Mayden allow that the world is populated by different types of lineages, namely, interbreeding, ecological, and phylogenetic species.

While pluralists appreciate the recognition of different types of species, they do not believe that the lineage approach to species provides a unified (monist) account of the organic world. Phylogenetic and interbreeding concepts identify different species. Consider the example of classifying insects. A phylogenetic species concept identifies three species (A, B, C), while an interbreeding species identifies one species (A + B). On Mayden and de Queiroz's lineage approach, both answers are correct. So even when one recognizes that all species are lineages, there remains a plurality of conflicting classifications. If monism is the view that there is a single correct classification of the organisms in the world, then de Queiroz and Mayden's response to pluralism fails.

A second monist response to pluralism is inspired by advances in molecular sequencing. Perhaps a single correct species concept should be based on genetic similarity. As more molecular studies are performed we may discover the distinctive genome of each species. We can then use that information to construct a single classification of the organic world. Despite its initial appeal, molecular data is not the answer to taxonomic pluralism. Molecular data provides yet another classification of the organic world. Ferguson (2002) provides examples where overall genetic similarity and the ability to interbreed do not coincide. The result is two different classifications: one that sorts organisms according to interbreeding, and another classification based on overall genetic similarity. Add to these classifications a third classification based on ecological adaptedness. Wu (2004) cites cases where a classification based on genes for ecological adaptedness fails to coincide with a classification based on overall genetic similarity. Moreover, neither of these classifications coincides with a classification based on interbreeding behavior. Bringing molecular data to the table does not reduce the number of classifications but increases their number.

A promoter of a molecular approach to classification may respond that classifications based on genetic similarity should be preferred over all other types of classifications. An argument would then need to be made for why classifications based on genetic similarity are more fundamental than classifications based on interbreeding or ecological adaptations. Some biologists doubt that such an argument is forthcoming. Molecular data faces many of the same problems that confront traditional data, in addition to its own problems (Maddison, 1997; Mayden, 2002). Furthermore, the pressing problems of biological taxonomy, such as phylogenetic inference (see Section 4), apply to molecular and nonmolecular data alike. Molecular data is not the antidote for pluralism.

4. Two Major Schools of Biological Taxonomy

We have seen that biologists disagree over the proper approach to classifying organisms into species. We now turn to the task of classifying species into genera, genera into families, and so on up the Linnaean hierarchy. As is the case with species, biologists disagree on the proper way to classify taxa into more inclusive taxa. Those differences arise from biologists subscribing to different schools of biological taxonomy, where each school provides its own principles and methods for constructing classifications.

The twentieth century saw three major schools of biological taxonomy: Evolutionary Taxonomy, Pheneticism (Numerical Taxonomy), and Cladism. Cladism is currently the most popular school among taxonomists, although many still subscribe to the tenets of Evolutionary Taxonomy. Pheneticism is no longer considered a viable taxonomic school by the vast majority of taxonomists. This section will introduce Evolutionary Taxonomy and Cladism and the philosophical issues surrounding these schools. Pheneticism will not be discussed here (for a philosophical introduction to pheneticism see Sober [1993]).

Evolutionary Taxonomy is a product of evolutionary thinking in the early twentieth century. In the 1930s, a handful of biologists developed a Mendelian framework for Darwinian evolutionary theory. The result of their work was the "evolutionary synthesis": the integration of Mendelian genetics and Darwinian theory. Theodore Dobzhansky, Ernst Mayr, and Gaylord Simpson used the insights of the evolutionary synthesis to forge the school Evolutionary Taxonomy. That school has two main tenets. First, the members of a taxon must be descendants of a common ancestor; that is, all taxa must be genealogical lineages. Second, as Mayr (1981 [1994], p.290) writes, "evolutionary taxonomists . . . aim to construct classifications that reflect both of the two major evolutionary processes, branching and divergence (cladogenesis and anagenesis)." In cladogenesis, a single lineage is split into two branches (Figure 6.2a). Suppose a population of a species becomes isolated from the rest of the species. If that population is exposed to new selection forces, it may undergo a "genetic revolution" and become a new species. In anagenesis, speciation occurs in a single lineage (Figure 6.2b). Suppose a species enters a new environment and acquires a radically new suite of adaptations. If that change is drastic enough, then the lineage has evolved into a new species.

Given that speciation can occur through either cladogenesis or anagenesis, evolutionary taxonomists believe that classifications should highlight the two types of taxa

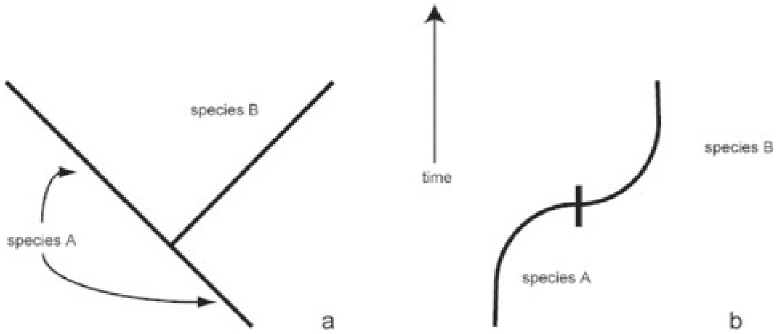

Figure 6.2 (a) Speciation by cladogenesis. (b) Speciation by anagenesis

that arise from these processes: monophyletic taxa and paraphyletic taxa. A monophyletic taxon contains an ancestor and all and only its descendants. In Figure 6.3, the group containing crocodiles and birds is monophyletic, as is the group containing lizards and snakes, and the group containing lizards, snakes, crocodiles, and birds. Monophyletic taxa are the result of cladogenesis or branching events. A paraphyletic taxon contains an ancestor and some but not all of its descendants. The group Reptilia, which contains lizards, snakes, crocodiles, but not birds, is paraphyletic. Paraphyletic taxa are the result of anagenesis. The lineage leading to birds has diverged significantly from lizards, snakes, and crocodiles, so evolutionary taxonomists exclude birds from the taxon Reptilia. In brief, evolutionary taxonomists believe that classifications should highlight only genealogical taxa, and those taxa can be either monophyletic or paraphyletic.

In the second half of the twentieth century the taxonomic school Cladism was introduced by Willi Hennig. The word "Cladism" is based on the Greek word for branch. Hennig believed that only those taxa that are the result of cladogenesis should be classified. His aim was to construct classifications that reflect common ancestry. If two taxa originate in the same branching event, then they have a common ancestor that is not shared by any other taxon. Crocodiles and birds have a common ancestor that is not shared by lizards and snakes (Figure 6.3). So a cladistic classification of those taxa places crocodiles and birds in a taxon that excludes lizards and snakes. Cladists believe that classifications should be based on common ancestry and nothing else. This view of classification has implications for the types of taxa that cladists represent in their classifications. Monophyletic taxa are defined in terms of common ancestry: a monophyletic taxon contains all and only the descendants of a common ancestor. So only monophyletic taxa are represented in cladistic classifications. Paraphyletic taxa are excluded from such classifications. A paraphyletic taxon does not contain all the descendants of a common ancestor. Because the taxon Reptilia excludes birds, this taxon does not contain all the descendents of its most recent ancestor (Figure 6.3). Thus cladists do not recognize the taxon Reptilia.

We can now see a major difference between Cladism and Evolutionary Taxonomy. Cladists only cite monophyletic taxa in their classifications because such taxa are the result of common ancestry. Evolutionary taxonomists represent both paraphyletic and

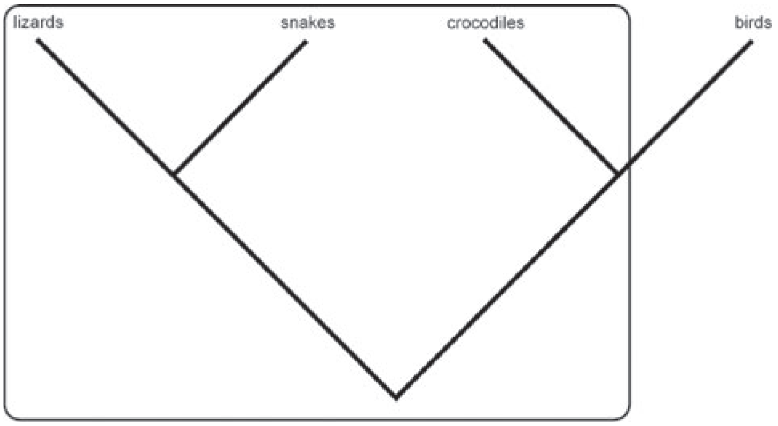

Figure 6.3 A phylogenetic tree of lizards, snakes, crocodiles, and birds

monophyletic taxa in their classifications because they believe that two types of information should be represented in classifications: common ancestry, and how much a taxon has diverged from its neighbors. This difference in taxonomic thought causes cladists and evolutionary taxonomists to construct opposing classifications. For example, evolutionary taxonomists posit the taxon Reptilia while cladists do not.

Cladists have two main complaints with Evolutionary Taxonomy (Hennig, 1966; Eldridge & Cracraft, 1980). We have already seen the first, namely that evolutionary taxonomists allow the existence of paraphyletic taxa. For cladists, such taxa are incomplete lineages: they do not contain all the descendants of a common ancestor. Cladists believe that placing crocodiles in a taxon that excludes birds ignores the unique common ancestor shared by birds and crocodiles. Another problem that cladists see with evolutionary taxonomy concerns the meaning of "significant divergence." When evolutionary taxonomists maintain that birds and reptiles have diverged significantly they cite the adaptive and phenotypic differences between those organisms. Birds, they suggest, live in a very different adaptive zone than reptiles. Furthermore, birds have significantly different traits than reptiles, such as wings and feathers. Cladists respond that the concepts of phenotypic difference and adaptive zone are ambiguous and are applied inconsistently to different types of taxa (Hennig, 1966; Eldridge & Cracraft, 1980). Cladists believe that the concepts of phenotypic diversity and adaptive zone are too malleable and reject them as grounds for classifying taxa.

Evolutionary taxonomists, for their part, think that cladists are wrong for not recognizing the existence of paraphyletic taxa (Mayr, 1981 [1994]). According to evolutionary taxonomists, paraphyletic taxa are not limited to a few marginal cases but occur throughout the organic world. Consider the case of ancestral species. Speciation frequently begins when a small population becomes isolated from the main body of a species. That "founder population" is exposed to different selection factors and becomes an incipient species. Meanwhile the main body of the old species – the ancestral species – continues to live. In Figure 6.2a, species b is the new species and species a is the ancestral species. Species a is paraphyletic because it contains some but not all of the descendants of species a's founder population: some of species a's descendants are members of species b. Cladists deny the existence of ancestral species because such species are not monophyletic. Evolutionary taxonomists respond that ancestral species abound in the world and cladists should not deny the existence of such a frequent type of phenomena.

Despite such criticisms, Cladism has become the prominent school of taxonomy. This is largely due to its precise and unambiguous methods for constructing classifications. Cladists aim to use only evidence of common ancestry to infer classifications. That evidence comes in the form of traits called "homologies." A homology occurs in two (or more) organisms and has been passed down from a common ancestor. Eyes in humans and dogs are homologous. Cladists attempt to avoid constructing classifications using traits called "homoplasies." A homoplasy is a similar trait in two (or more) organisms that has been passed down from different ancestors. Octopus eyes are similar to mammalian eyes but they evolved in different lineages. So octopus eyes and human eyes form a homoplasy and are not evidence of common ancestry. A challenge for cladists is distinguishing those similarities that are homologies from those similarities that are homoplasies. This is an important distinction for cladists because only homologies serve as evidence for cladistic classifications.

Cladists disagree over the criteria for distinguishing homologies from homoplasies (Hall, 1994). Here are two proposed criteria. According to one criterion, a homology must be a fundamental similarity rather than a superficial similarity between two traits. Bird wings and bat wings violate this criterion. They look similar on the surface, but they are supported by different digits and made of different materials. A second criterion demands that a homology be similar in both the adult form and in the embryonic stages that lead to adulthood. Barnacles and limpets have similar adult traits, such as a hard external armor and the ability to feed through a hole in that armor. However, the embryonic stages of these traits are dissimilar. So these traits are considered homoplasies.

Once a cladist determines which traits are homologies, the cladist constructs a cladogram. A cladogram represents the branching relations among a group of taxa and provides the basis for cladistic classification. The move from data concerning homologies to positing a cladogram is called "phylogenetic inference." Unfortunately the inference from putative homologies to a single cladogram is not straightforward. Cladists use dozens of traits to infer the correct cladogram for a set of taxa, and more often than not, the traits used to construct a cladogram provide conflicting evidence: some traits support one cladogram, while other traits support a different cladogram. Consider an example. Suppose that a biologist wants to classify three taxa, A, B, and C, and she has information about three traits, x, y, and z. Suppose also that each trait comes in one of two states, 0 and 1, where 0 is ancestral and 1 is derived. The distribution of traits found in the three taxa is the following:

	A	B	C
x	1	1	0
y	1	1	0
z	0	1	1

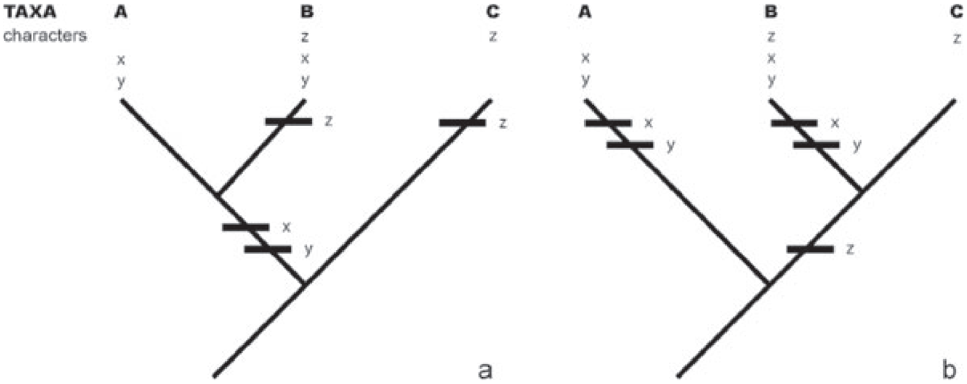

Figure 6.4 Two cladograms of the same taxa. (a) and (b) represent different evolutionary scenarios

This distribution gives rise to two conflicting cladograms (Figures 6.4a and 6.4b). According to one cladogram, A and B are more closely related to each other than either is to C (Figure 6.4a). According to the other cladogram, B and C are more closely related (Figure 6.4b). Which cladogram should a cladist posit?

Cladists agree about the source of confusion in such cases: some of the putative homologies are actually homoplasies. If the first cladogram (Figure 6.4a) is correct, then z is a homoplasy and has evolved at least twice: once in the branch leading to B and once in the branch leading to C. On the other hand, if the second cladogram (Figure 6.4b) is correct, then x and y are homoplasies. If that is the case, then x and y have each evolved at least twice: both on the branch leading to A and both on the branch leading to B. The task for cladists is to determine which of the putative homologies are homoplasies. To do this, cladists employ the principle of parsimony: choose the phylogeny that requires the minimal number of changes to arrive at a given trait distribution. In the example under consideration, the principle of parsimony counsels choosing the phylogeny represented by the first cladogram. The phylogeny captured by the first cladogram requires a minimum of four changes (they are represented by slash-marks on the cladogram), whereas the phylogeny represented by the second cladogram requires a minimum of five changes.

Cladists offer various justifications for their reliance on the principle of parsimony. Some suggest that evolution itself is parsimonious. Ridley (1986) reasons that because it is unlikely for a mutation to be selected in a species, it is even more unlikely for similar mutations to occur and to be selected in multiple species. Ridley's justification for parsimony turns on general assumptions about evolution. Other cladists argue that assumptions about evolution can justify the use of parsimony, but only on a case-by-case basis (Felsenstein, 1978). In some instances evolution is parsimonious, in others it is not, depending on local mutation rates and selection coefficients. So in some situations the use of parsimony is empirically justified, in other situations it is not.

A third group of cladists justifies the use of parsimony on more philosophical grounds. They suggest that the preference for the more parsimonious cladogram need not depend on any assumptions about evolution. Instead, we should prefer the more parsimonious cladogram because it is more falsifiable (see Farris, 1983). Cladists in this group follow Karl Popper's philosophy of science: all scientific hypotheses must be falsifiable; those hypotheses that are unfalsifiable – that cannot possibly be shown to be false with empirical evidence – are unscientific. Some cladists argue that to posit a homoplasy without empirical evidence is to posit an unfalsifiable hypothesis. The more homoplasies a cladogram requires, the greater the number of unfalsifiable hypotheses posited. Thus, the more parsimonious cladogram is preferred for the methodological reason that it is more falsifiable. (Popper might disagree with this application of his philosophy because he does not think that falsifiability comes in degrees.) Cladists have written extensively on the proper justification of parsimony. The issue is far from settled.

5. The Linnaean Hierarchy

Having discussed the philosophical issues surrounding the nature of species and the principles for classifying taxa, we now turn to the framework for constructing classifications – the Linnaean hierarchy. Although many aspects of biological taxonomy are under debate, one might hope that the Linnaean hierarchy is universally accepted. Unfortunately this is not the case. The continued use of the Linnaean hierarchy has been challenged. Some biologists and philosophers believe that the Linnaean hierarchy has outlived its usefulness and should be replaced (de Queiroz & Gauthier, 1992; Ereshefsky, 1994). Other biologists believe that the Linnaean hierarchy is still the best system available and should be retained (Forey, 2002). The debate over the Linnaean hierarchy is an important issue because much of biological theory employs the Linnaean ranks, from prey–predator relations in ecology to hypotheses concerning the tempo and mode of macroevolution.

The current Linnaean hierarchy contains 21 ranks, from subspecies to kingdom. Linnaeus posited a hierarchy of 5 ranks: variety (subspecies), species, genus, order, and class. Evolutionary taxonomists believed that Linnaeus's 5 ranks were insufficient for representing life's diversity, so they posited the 21 ranks used today. From Linnaeus's time to the advent of Cladism, taxonomists have offered various definitions of Linnaean ranks that aim to highlight a common biological factor among the taxa of a particular rank. For example, taxonomists have tried to find a biological factor that is common to families and that distinguishes families from tribes and orders. Evolutionary taxonomists and cladists have offered various suggestions for defining the higher Linnaean ranks (those ranks above the rank of species); none of those definitions has withstood criticism.

Evolutionary taxonomists have suggested that such factors as phenotypic diversity and ecological breadth indicate the rank of a taxon. The greater the phenotypic diversity within a taxon, or the greater the size of a taxon's adaptive zone, the more inclusive a taxon. For example, the adaptive zone of a tribe will be greater than the adaptive zone of a family. As discussed in the previous section, cladists consider the concepts "adaptive zone" and "phenotypic diversity" to be ambiguous and applied inconsistently across phyla. Hennig playfully asks "whether the morphological divergence between an earthworm and a lion is more or less than between a snail and a chimpanzee?" (1966, p.156). Most taxonomists now believe that the concepts of phenotypic diversity and adaptive zone are too malleable to serve as measures of a taxon's rank.

Hennig (1965) offered an alternative way of defining the higher Linnaean ranks by suggesting that taxa of the same rank originate in the same time period. Classes, for example, should be defined as all and only those taxa that originated during the Late Cretaceous. Orders would be defined as all and only those taxa that originated during a more recent time period. Hennig's suggestion for defining the higher Linnaean ranks is problematic as well. Taxa that originate in the same period often have different phylogenetic structures. Some taxa that originated during the Late Cretaceous are quite successful and contain a number of orders and genera; such taxa have extensive phylogenetic branching. Other taxa that originated during the same period are monotypic and contain only a single basal taxon; they are phylogenetic twigs. From a phylogenetic perspective, Hennig's criterion places different types of taxa under a single rank. Cladists, including later Hennig, abandoned the idea of correlating the rank of a taxon with time of origin.

Neither evolutionary taxonomists nor cladists have established a universal criterion for defining the higher Linnaean ranks. Instead, they use a patchwork of criteria for determining the ranks of such taxa. As a result, taxa of the same rank can vary dramatically. Families can vary in their age, their phylogenetic structure, their phenotypic diversity, and the breadth of their adaptive zone. Calling a taxon a "family" merely means that *within* a particular classification that taxon is more inclusive than a genus and less inclusive than a class. There is no ontological commonality among all taxa we call "families." Some have generalized this conclusion and questioned whether the higher Linnaean ranks correspond to any categories in nature (de Queiroz & Gauthier, 1992; Ereshefsky, 1994).

Thus far we have discussed the meaning of the higher Linnaean ranks, but what of the rank of species? While many taxonomists question whether there are higher Linnaean categories in nature, most continue to believe in the existence of the species category. However, species pluralism poses a threat to the claim that "species" refers to a unified category in nature. Recall that biologists offer a myriad of species concepts. Some biologists define a species as a group of organisms that successfully interbreed and produce fertile offspring. Cladists assert that a species is a group of organisms bound by a unique phylogeny. Still other biologists suggest that a species is a group of organisms that share a unique ecological niche. Each proposal highlights a different biological feature for defining "species." Species pluralists believe that each of these concepts is theoretically legitimate. Some species are groups of interbreeding organisms; others consist of asexual organisms. Some species are monophyletic, that is, good phylogenetic species; others are not. These different types of taxa that we call "species" are real, yet they lack a common significant feature.

If the above arguments concerning the Linnaean ranks are correct, then the Linnaean ranks, from species up, refer to heterogeneous collections of taxa. There is no unique and universal biological feature found in all taxa called "species," just as there is no common and distinct feature among those groups of organisms referred to as "families." This result undermines the reality of the species and other Linnaean categories. In the end, the Linnaean hierarchy may be a fictitious grid that we place on nature.

The heterogeneity of the Linnaean categories has practical implications, especially for biodiversity studies. The units biologists use for measuring biodiversity are Linnaean:

biologists count the number of species present in a location, or the number of genera or families. However, the Linnaean ranks can mask important biological differences. Suppose that we want to measure the biodiversity of a class of organisms by the number of families present. Suppose further that the comparison is between snail families and mammalian families. Snail families have much denser phylogenetic structures than mammalian families. That is, snail families contain many more species than mammalian families. If we measure biodiversity by number of families, then we are not measuring comparable units. Because some families will have many species and other families will have few species, "family" does not refer to a consistent biological unit. In general, the Linnaean ranks do not correspond to categories in nature, and they should not be employed in biodiversity studies. Instead, these studies should use parameters that capture such biological phenomena as phylogenetic structure or ecological breadth.

Thus far we have talked about the Linnaean ranks. Often when biologists talk about the Linnaean hierarchy they mean more than just the Linnaean ranks. They also have in mind the Linnaean rules of nomenclature for naming taxa. Some of these rules were introduced by Linnaeus, other rules were introduced by evolutionary taxonomists in the twentieth century. To avoid confusion, let the "Linnaean system of classification" refer to both the Linnaean hierarchy and the Linnaean rules of nomenclature.

The centerpiece of the Linnaean naming rules is the requirement that the name of a taxon should indicate a taxon's rank and classification. For species this is achieved with Linnaeus's binominal rule. The names of all species contain two parts: a generic name and a specific name. The generic name refers to a species' genus. For example, the generic name of *Homo sapiens* is *Homo*. The specific name of a species distinguishes that species from all other species in its genus. *Sapiens* is the generic name of our species. Binomial names clearly indicate which taxa are species: all and only species have binomial names, while other taxa have singular names. The generic name of a binomial indicates the classification of a species: the name *Homo* shows that our species is part of the genus *Homo*.

Similar Linnaean rules require that the names of higher taxa display a higher taxon's rank and classification. The names of most higher taxa have rank-specific endings showing the ranks of those taxa. For example, the rank of the family Hominidae is represented by the suffix *–idae*, and rank of the tribe Hominini is indicated by the suffice *–ini*. The name of a higher taxon is formed from the name of that taxon's type genus – the genus contained in that taxon. "Hominidae" and "Hominini" and are formed from the root *Homin*, which stands for the type genus *Homo*. All taxa whose names include the root *Homin* form a hierarchy of taxa containing the genus *Homo*.

Representing the ranks and classifications of taxa in their names seems like a good idea. One just needs to read a taxon's name to know that taxon's rank and classification. Since its inception, the popularity of the Linnaean system has been attributed to its practical features, such as Linnaeus's binomial rule. But some question the practicality of the Linnaean rules of nomenclature (de Queiroz & Gauthier, 1992; Ereshefsky, 1994).

Consider the activity of taxonomic revision. Such revision occurs when a taxon is assigned a new rank or given a new position in a classification. Taxonomic revision is the norm not the exception in biological taxonomy and can occur for many reasons. New DNA evidence may imply that a species should be reassigned to a different genus.

Or a shift in taxonomic theory, such as cladists eliminating paraphyletic taxa from classifications, may require changing a taxon's rank from tribe to family. Taxonomic revision causes instability in classification: new evidence or new theoretical considerations give us reason to revise our classifications. The Linnaean rules of nomenclature are also a source of instability because the names of taxa reflect the rank and classification of a taxon. As such, these rules make the job of the taxonomist harder than need be. Not only must biologists revise a taxon's classification, they must rename the taxon as well. This may not sound like much of an inconvenience, but it is. A case of taxonomic revision can involve renaming hundreds of taxa. The Linnaean rules of nomenclature themselves are a source of instability.

The Linnaean rules cause other practical problems. For instance, when taxonomists disagree on the rank of a taxon they must assign that taxon different names containing different rank-specific endings. For example, one biologist may think that a taxon is a family and another biologist may consider the same taxon to be a tribe. Following the Linnaean rules, the first biologist must name the taxon "Hominidae" while the second biologist must name it "Hominini." Even though the biologists agree they are talking about the same taxon, the Linnaean rules require the taxon to have multiple names. Another problem with the Linnaean rules of nomenclature is that they cause hasty classification. Recall that a species must be given a binomial name that includes the name of a species' genus. Often biologists do not know the genus of a newly discovered species. Yet if a biologist wants to name a new species, she must first assign that species to a genus. According to some biologists, the binomial rule often causes the assignment of a species to a genus on inadequate grounds. Thus, the binomial rule is a cause of inaccurate classification.

Supporters of the Linnaean system are well aware of the problems facing the Linnaean system of classification. But they argue that the Linnaean system is still the best system available. Detractors of the Linnaean system have constructed alternative systems of classification. The most prominent one to date is the Phylocode, which was developed by a group of cladists (Cantino et al., 2001). Supporters of the Linnaean system believe that the Phylocode is an inferior system (Forey, 2002). This judgment may be hasty because proponents of the Phylocode are just starting to develop their system. Whether biologists should continue using the Linnaean system or adopt an alternative is hotly debated by taxonomists. It is too early to predict the outcome of this debate.

One other challenge to the Linnaean hierarchy is worth mentioning. This challenge is not only to the Linnaean hierarchy, but to any system of classification that assumes life is hierarchically arranged. The Linnaean hierarchy and rival systems of classification assume that there is a single hierarchical tree of life, a tree with a single origin, and speciation events that give rise to non-overlapping lineages. Each species is a part of one and only one genus, each genus is a part of one and only one family, and so on up the hierarchy. However, recent molecular studies of bacteria challenge the assumption that life forms a single hierarchical tree (Doolittle, 1999).

Whether or not life forms a single hierarchical tree depends on how genetic information is transferred. The common assumption is that the vast majority of genes are passed down from parent to offspring. For the most part species are closed gene pools. Hybridization may occur between closely related species, but organisms in different genera and families rarely exchange genes. Bacteria and archaea (ancient bacteria), however, do not play by the same reproductive rules. Bacteria do not reproduce sexually. Bacteria can pass on their DNA, or parts of their DNA, simply by brushing up against one another. Molecular studies reveal that considerable amounts of bacterial DNA are transferred laterally among organisms of the same generation. Consequently, bacteria evolution is not one of a branching tree but of an intertwined bush. Ford Doolittle (1999, p.2124) suggests "molecular phylogeneticists will have failed to find the 'true tree,' not because their methods are inadequate or because they have chosen the wrong genes, but because the history of life cannot properly be presented as a tree."

One might question the significance of Doolittle's suggestion given that it is based on information concerning bacteria and archaea, but his suggestion should be taken very seriously. There are more types of bacteria and archaea than all other types of organisms, and the combined weight of all bacteria and archaea is greater than the combined weight of all other organisms (Tudge, 2000, p.107). We are not talking about a few isolated cases here. Molecular studies of bacteria and archaea indicate that *most* of life does not form a phylogenetic tree.

In summary, we have seen that the nature of species, the general principles of biological taxonomy, and the soundness of the Linnaean hierarchy are controversial. We now see that even the assumption that life is hierarchically arranged has been challenged. The philosophical problems facing biological taxonomy are foundational. How these problems are resolved will have widespread implications both inside and outside of biology. Biological taxonomy is rife with conceptual problems and fertile ground for philosophical analysis.

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