

SYSTEMATICS

Systematics is the science of the diversity of organisms and all relationships between them. Its core consists of taxonomy, or the science of biological classification, but systematics also includes determining evolutionary relationships (phylogeny) and determining geographic relationships (biogeography). A systematist uses the comparative approach to the diversity of life to understand all patterns and relationships that explain how life came to be the way it is. Systematics deals with such questions as these: How are species grouped into larger categories? How are classification schemes set up, and what do they mean? Systematics is more than just naming and describing new species, because species and higher taxa reflect evolution. Systematists are interested in comparing different species, deciding how they are related, and ultimately in deciphering their evolutionary history. This perspective looks at the diversity of organisms in time and space and tries to understand the large-scale patterns of nature. Systematists look at the present and past geographic distributions of organisms and try to determine how they got there. In short, systematics involves looking at the total pattern of natural diversity and trying to understand how it came to be.

Systematics provides the framework of understanding and interconnection upon which all the rest of biology and paleobiology are based. Without it, each organism is a random particle in space, and what we learn about it has no relevance to anything else in the living world. One of the most important issues on this planet today—biodiversity—is within the domain of systematics.

Taxonomy

There are many ways to classify things. Some classification schemes attempt to have a logical basis or structure to make them easier to use. For a long time, the Dewey Decimal system was the most widely used means of cataloging books, until it was replaced in many libraries by the Library of Congress system. Both try to cluster books by natural groups (such as a category for science books, which then are subdivided into physics, chemistry, biology, geology, and so on), but the Library of Congress system apparently is more flexible at handling larger numbers of books. Both natural classification schemes attempt to organize the same array of objects, but apparently one is more successful than the other.

Modern classification techniques began with the Swedish botanist Carolus Linnaeus (1707–78). His *Systema Naturae, Regnum Animale* (the system of nature, animal kingdom) was first published in 1735, and its tenth edition (1758) is now regarded as the starting point of modern systematic zoology. As thousands of new species were described since 1758, Linnaeus' original classification became outdated, but his fundamental system still is used. Each species is given a binomen (two-part name), consisting of the genus name (always italicized or underlined, and always capitalized) and the trivial name indicating the species (always italicized or underlined but never capitalized). For example, our genus is *Homo* (Latin, *human*) and our trivial name is

sapiens (Latin, *thinking*), so our species name is *Homo sapiens* (abbreviated *H. sapiens*). The trivial name can never stand by itself (as they are repeated over and over in taxonomy), but must always accompany its genus. To prevent confusion, a species name can never be used for any other organism in the same kingdom, and a genus name can only be used to name species that are closely related (there are few generic names that are reused for different animals and plants).

Genera then are grouped into higher categories, such as the family (always capitalized, but never underlined or italicized, and with the “-idae” ending in animals, the “-aceae” ending in plants), then orders, classes, divisions (for plants) or phyla (for animals), and kingdoms. For example, humans are members of the Kingdom Animalia (there are also kingdoms for plants, fungi, and single-celled organisms), the Phylum Chordata (including all other backboned animals), the Class Mammalia (mammals), the Order Primates (including lemurs, monkeys, apes, and ourselves), the Family Hominidae (including our own genus and the extinct *Australopithecus*, *Ardipithecus*, and *Paranthropus*), the genus *Homo* (including other extinct species such as *Homo habilis* and *H. erectus*), and our species *H. sapiens*.

The Linnaean classification scheme is hierarchical. Each rank is grouped into larger ranks, so that there may be several species in a genus, several genera in a family, and so on. The reason for the success of Linnaeus' scheme is this flexibility inherent in clustering groups hierarchically—there is infinite room for expansion as new species are discovered. The Latinized binomen is also very flexible and is universally recognizable in science. Universal terms are important in communication. Local vernacular names in a single language may vary greatly. For instance, in English the word “gopher” refers to both a tortoise and a burrowing rodent, and every other language uses completely different names for the same animals. But in all languages, the scientific name always is based on Latin or Greek (since these were the languages of scholars in Linnaeus' time) or on a Latinized version of other words. A scientist can pick up a publication in some unfamiliar (to most scientists) alphabet, such as Cyrillic or Hebrew or Chinese, and not recognize a word except the scientific names. These universal terms stand out and can communicate the essential content of the paper.

To Charles Darwin, clustering organisms into groups within groups to form a hierarchical, nested, branching structure of life only made sense if life had descended from common ancestry in a branching fashion. Darwin transformed the goals of classification from an arbitrary system of arranging things into pigeonholes to a system that also had evolutionary meaning. Taxonomists were trying to create natural groups that reflected evolutionary history, not just convenience. Although these goals are not contradictory, they do not always agree, either. Some taxonomists view organisms of similar descent and ecology, such as the fishes, as a formal group, “Pisces.” But in evolutionary terms, not all fish are created equal. Lungfishes, for example, are related more closely to four-legged land vertebrates (tetrapods) than they are to a shark or a tuna. In

other words, a lungfish and a cow are related more closely to each other than a lungfish and a tuna. Here we see a clear tension between ecological groupings, or evolutionary grades, such as "fish," and natural evolutionary lineages, or "clades," such as the lungfish-retrajod group (known as the Sarcopterygii). Which is better? The different priorities and goals of taxonomists has led to much debate over the proper methods of classification.

What is the proper way to classify organisms? That question had been the center of a very intense scientific debate since the 1960s. As D. Hull (1988) points out, the debate reveals almost as much about the sociology of science as it does about the science itself. In the late 1950s, there was relatively little argument, since the majority of taxonomists practiced a vaguely formulated method later called "evolutionary taxonomy," exemplified by G.G. Simpson's (1961) *Principles of Animal Taxonomy* or E. Mayr's (1966) *Principles of Systematic Zoology*. This mainstream, orthodox school of taxonomy was challenged by two upstarts in the 1960s and 1970s, "phenetics" (or numerical taxonomy) and "cladistics" (or phylogenetic taxonomy). Both schools of thought followed very different basic assumptions and used new jargon to distinguish themselves from the old style of classification. Sometimes practitioners took very extreme positions, so that they could be seen as different and not be absorbed into the mainstream as a minor variant. Later practitioners may have moderated those extremes as the controversies died down, but such positions were important in the early phases of the movements.

Phenetics

Numerical taxonomy was precipitated by several factors: the availability of the first practical computers; an increase in interest in statistical methods, and a widespread dissatisfaction with conventional taxonomy as being an intuitive, arbitrary "art" that was only valid and reproducible in the mind of the taxonomist. To get away from this subjectivity, the numerical taxonomists argued that classification should be a purely objective, statistical exercise that can be coded and deciphered by a computer. Numerical taxonomists concluded that since classifications cannot reflect both evolutionary history and degree of overall similarity, we should forget trying to make our classifications reflect historic relationships and instead base them on objective statistical similarities and differences, or overall phenetic similarity. These scientists judged a "natural" classification by how successfully it clusters groups with the most in common and how well it creates stable classification schemes that are maximally useful to scientists. Typically, this is accomplished by measuring and coding numerous anatomical features, or "characters," in each specimen or taxon (called "OTUs," or "operational taxonomic units") to create a large data matrix of OTUs versus characters. Next, a computer program sorts the data and finds clusters of OTUs that have the most characters in common. When the computer analysis is finished, a branching diagram of similarity is produced.

A few years after numerical taxonomy became popular, it went into decline. The majority of systematists never accepted the fundamental goals of phenetics. Most still wanted classification to reflect evolutionary relationships in some way, even if this was a difficult task. The most serious blows came when a number of

studies showed that the "objectivity" of phenetics was a myth. No one can code and weigh the importance of the characters in the data matrix objectively. When one systematist decides that a wing represents a single character state and another subdivides it into numerous character states, which approach is correct? Once again, the "art" of systematic judgment comes into play. Ultimately, taxonomists must decide what is a character, and that decision is filtered through their own prejudices. Even more serious were studies that showed that the same data matrix gave different results with different computer programs—occasionally even with the same computer program. If the methods were not truly objective and reproducible and, at the same time, gave up on the whole idea of evolutionary classification, then what was the advantage? If a purely phenetic classification placed unrelated animals such as whales and fish together, then what good was it?

Cladistics

The other primary reason for the decline of phenetics was competition from an even more radical school of systematics, cladistics. In many ways, cladistic methods are the opposite extreme from phenetics. Rather than abandoning the evolutionary meaning behind taxonomy, cladists argued that classification should reflect *only* evolutionary history and ignore overall phenetic similarity. Rather than throwing all the characters, unweighted, into a computer, cladists argued that not all characters are created equal. The only characters that are useful in a given problem are those that are shared evolutionary novelties, or shared derived characters ("synapomorphies," in cladistic terminology). For example, the presence of hair and mammary glands is a shared specialization of all mammals, unique to them and found nowhere else in the animal kingdom. Those characters are "synapomorphies" that help define the taxon Mammalia. Characters such as the presence of four limbs, or a backbone, would not be very useful in distinguishing mammals from other vertebrates, because they are found in reptiles, birds, and amphibians; they are shared primitive characters (they predate the origin of these various groups), or "symplesiomorphies." Taxa are recognized and defined only by their unique evolutionary novelties. Characters already found in their near relatives and ancestors are considered "primitive" and, therefore, irrelevant to the problem of the evolutionary relationships within their group.

Whether a character is primitive or derived depends upon how it is used. For example, within the Mammalia, hair and mammary glands are the primitive state; scholars cannot use them to decide the relationships of different groups of mammals. If a systematist wanted to find shared derived characters that unite monkeys, apes, and humans, he or she would use unique specializations, such as the opposable thumb and stereovision, not primitive features found in all other mammals, such as hair and mammary glands. This means that hair and mammary glands are derived characters at the level of Class Mammalia, where they can be used to distinguish between it and other related groups such as Class Reptilia; at the level of the orders and families within the Mammalia, however, these characters are primitive.

To analyze these characters, the systematist draws a branching diagram known as a "cladogram" (Figure 1). At the tip of each

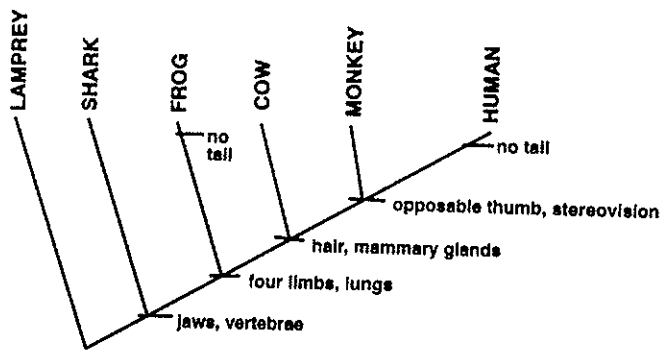


Figure 1. Cladogram showing the evolutionary relationships of some vertebrates. The unique evolutionary novelties, or "shared derived characters" ("synapomorphies"), that support these relationships are shown on the branching points (nodes) of the cladogram.

branch are the taxa, and the branching geometry shows which taxa are related more closely to each other. In Figure 1, the cladogram shows that monkeys and humans are related more closely to each other than either is to anything else in the diagram. Monkeys, humans, and cows, as mammals, are related more closely to each other than they are to any non-mammal. Frogs, cows, monkeys, and humans, as four-legged tetrapods, are related more closely to each other than they are to any non-tetrapod, such as a shark. Notice that the fork of each branch (the node) represents the common ancestor of the organisms at the tip of the branch, and the node (where lines separate) is defined by the shared derived characters that unite those taxa. For example, opposable thumbs and stereovision are derived characters that define the node uniting monkeys and humans; hair and mammary glands are derived characters that define the node Mammalia; the presence of derived characters such as four legs and lungs define the tetrapods and distinguish them from other vertebrates.

Cladogram Construction

How is a cladogram constructed? Typically, the systematist sets up a data matrix of characters and taxa, just as in phenetics. However, instead of relying on the computer to cluster these characters for overall similarity, the cladist evaluates each character and decides which state is primitive and which is derived. The best way to do this is to examine more primitive relatives, known as outgroups, and see what character state they possess. For example, hair and mammary glands are not found in mammal outgroups such as the frog, shark, or lamprey; therefore, these features are derived for the mammals. The absence of four limbs, lungs, or hands and feet instead of fins (as found in sharks and lamprey) shows that those characters are derived for tetrapods. Once the derived character states have been decided upon, then the systematist (or a computer) clusters only the derived character states to see which taxa have the most shared specializations in common and which have fewer. Ideally, this process generates a branching cladogram.

Sometimes there are several possible character states within an array of organisms. For example, the anatomy of the digestive tract of vertebrates ranges from the simple tubelike gut of some fish, to those with complex spiral intestines (as in sharks), to guts with a separate stomach and intestines (as in most vertebrates), to highly complex digestive tracts with a four-part stomach (as in ruminants, such as cows and sheep). This spectrum of morphologies forms a morphocline of character states. Although, in this case, it seems obvious which is the primitive or derived end of the morphocline, in most cases it is not so apparent. Cladists use a variety of criteria (such as outgroup comparison, or developmental transformation series) to identify the primitive and the derived characteristics in a morphocline.

Although a cladogram superficially looks like an evolutionary tree, it is not. A cladogram shows a nested pattern of evolutionary specializations within diverse taxa. It works with any three or more taxa, no matter how distant their relationships. (A family tree works only with immediate ancestors and descendants.) The nodes in a cladogram summarize the derived character states of the hypothetical common ancestor, not real ancestors. Cladists avoid naming real ancestors for several reasons. Because the fossil record is so incomplete, it is very unlikely that we actually have a true ancestor. Another problem is that ancestors have nothing but primitive character states compared to their descendants. It is impossible to tell if a potentially ancestral fossil was truly an ancestor, because it has no unique evolutionary specializations that link it with another taxon. At a more fundamental level, cladists abhor searching for ancestors because this search emphasizes primitive characters and may ignore important derived characters. In many cases, troubling long-standing phylogenetic problems were solved when the systematists stopped looking for ancestors and instead discovered a remarkable pattern of shared derived similarities that long had been neglected. Instead of ancestors and descendants, cladograms show only that two taxa are closely related sister groups. For example, monkeys and humans are sister groups, compared to cows or other non-primates.

Therefore, a cladogram is simply a branching diagram of relationships, supported by unique shared derived characters states. This arrangement makes no statements about ancestry. This minimalist approach to systematics has a major advantage: it is testable. Each cladogram is a scientific hypothesis; to test it, the systematist can look at additional character states or additional taxa (especially more outgroups). Cladists find this very appealing, because one of their central philosophical tenets is that all science must be testable. Family trees with ancestors may be more interesting, but because there is no way of testing their more complicated hypotheses and assumptions, these trees fall outside this narrow definition of science.

One of the great advantages of the cladistic method is that it provides a simple, straightforward set of rules that any systematist can follow, and each phylogenetic hypothesis can be tested immediately and rejected if better data emerge. In the old school of "evolutionary taxonomy," on the other hand, phylogenetic trees had no characters at the nodes, so they could not be tested. Trees came out of the intuition and experience of the systematist, and

since there was no way of evaluating them or seeing how they were constructed or supported, there was no way to criticize them. In a cladogram, it is apparent immediately if there are few or no derived characters to support a node. If the characters have been incorrectly coded or evaluated, that too is clear. Systematists can no longer hide behind the foggy obscurity of phylogenetic trees but have to suffer immediate criticism if their work does not hold up. A lot of early cladograms were overturned, but eventually, as fewer and fewer problems were found, the cladograms began to converge upon consistent and often surprising answers to long-standing phylogenetic problems.

Construction Difficulties

If nature were ideally cooperative, all character data matrices would give a single, unique cladogram of life, and there would be no doubts. But the real world is much more complex than this. Although life has had a single evolutionary pathway, character states have changed more than once, and in confusing ways—sometimes they have reverted back to the ancestral state. In Figure 1, for example, humans and frogs could be united by the loss of a tail. If we were basing our cladogram on just that one character, humans and frogs would be related more closely than humans and monkeys. However, many more characters support human-monkey relationships, so it is simpler (or more parsimonious) to suggest that humans and frogs independently and secondarily have lost their tails (especially since both have tails in their embryonic state). The loss of a tail is considered an evolutionary convergence. Convergence occurs when a characteristic evolves in two or more groups independently.

The criterion of simplicity, or parsimony, may not work in every case, but most problems are resolved without too many conflicts of this type. This concept is especially useful when a difficult problem appears. For example, a superficial analysis might suggest that whales, ichthyosaurs (marine reptiles), and fish share many similarities, such as fins, a paddle tail, a streamlined body, and other features related to swimming in water. But a more detailed analysis incorporating nonaquatic animals would find many more shared derived features (mostly concerning internal anatomy, which is unrelated to swimming) that overwhelmingly show that whales are mammals, ichthyosaurs are reptiles, and fish are more primitive than either. All of their phenetic similarities are due to convergence.

When cladistics burst upon the scene in the early 1970s, paleontologists were among the harshest critics. The denial of ancestors certainly alienated them, as did another extreme claim: stratigraphic order (the order in which fossils are found in rock strata) is of no relevance when deciding whether a character is primitive or derived. Most cladists felt that the stratigraphic record was too full of gaps, and that fossils were too incomplete, to ever use them reliably in determining derived character states (Schaeffer et al. 1972; Patterson 1981). This extreme position was partly a response to previous generations of paleontologists, who stacked fossils in stratigraphic order and “connected the dots” without conducting any independent anatomical analysis of the character states.

In some ways, the cladists were correct. It is true that there are many gaps in the fossil record. Some fossil species may appear earlier than their presumed ancestor. And most fossils are much less complete than living specimens for the purposes of phylogenetic analysis. As a result, since these initial debates, a number of paleontologists (Fortey and Jefferies 1982; Lazarus and Prothero 1984; Huelsenbeck 1994; Smith 1994; Hitchin and Benton 1997; Huelsenbeck and Rannala 1997) have developed methods of rigorously analyzing stratigraphic data so they can be incorporated into a cladistic analysis with some degree of testability. One such method is called “stratocladistics” (Fisher 1994; Clyde and Fisher 1997). It uses probability methods to assess the reliability of stratigraphic sequence of fossils, as well as the reliability of the character polarities.

Cladistics and Classification

Many traditional systematists agree that cladistics is an effective method for inferring phylogenetic relationships but draw the line at another issue: cladistic classification. As we mentioned earlier, some cladists argue that classification should be a strict reflection of phylogeny and nothing else. Once the branching sequence has been determined, it dictates the ranks and clustering of higher taxa. Although traditional evolutionary systematists also try to reflect phylogeny in classification, they mix in a bit of ecology and phenetic divergence as well. For example, a cladist might say that since birds are descended from theropod dinosaurs, they should be a subgroup within the Theropoda. Traditional taxonomists argue that since birds have undergone a huge evolutionary radiation (diversification and geographic spread), with their own specialized ecological niches, they deserve their own higher rank, Class Aves. A traditional classification (Figure 2) divides the vertebrates into five or more classes of equal rank: birds, mammals, reptiles, amphibians, and one or more classes of fishes. The cladistic classification is not nearly as simple, since it requires multiple ranks of taxa to reflect the fact that birds are descendants of reptiles, reptiles are lower-ranking taxon within amphibians, amphibians within lobe-finned fishes, and so on.

Figure 3 shows the cladogram of higher primates. There is little disagreement over the geometry of their relationships. Traditionally, the human-ape clade was divided into two families: the Hominidae for ourselves, and the Pongidae for all the nonhuman apes. This classification scheme reflected both the huge divergence between ourselves and the rest of the apes and also our own egotism and anthropocentrism. Such distinctions are unacceptable to a strict cladist. The Hominidae are a natural group with shared derived characters that support it (a monophyletic group), but the Pongidae becomes a “wastebasket” taxon of all the apes that don’t happen to be human. The Pongidae have some shared derived characters (such as the loss of a tail) that define them (but so do hominids). As long as Hominidae is a separate but equal family, the Pongidae is defined partially by the lack of the characters that define Hominidae. In cladistic terms, a group that does not include all its descendants is a paraphyletic group, defined by the absence of synapomorphies.

There are many such unnatural, wastebasket groups in classification schemes, such as the “invertebrates” (defined by the

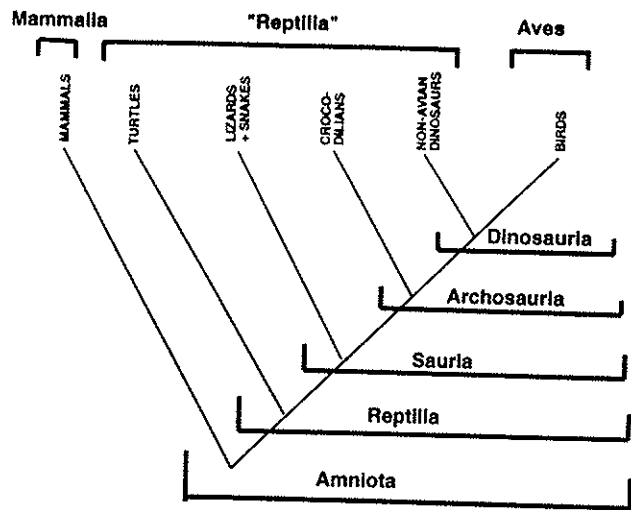


Figure 2. Different ways of classifying the same groups of organisms. *Top brackets*, traditional classifications emphasize the large morphological divergence and explosive evolutionary radiations of birds and mammals. The two are placed in their own classes, equal in rank to the rest of the amniotes, which are lumped in the paraphyletic "Reptilia." *Bottom brackets*, a cladistic classification does not permit mixing of phylogeny with other factors, such as evolutionary divergence. Instead, each group is monophyletic and defined strictly by evolutionary branching sequence. In this view, birds are a subgroup of dinosaurs, archosaurs, saurians, and reptiles.

absence of a derived character, the vertebral column) (Figure 4). If Reptilia does not include birds, then Reptilia is paraphyletic. If Amphibia does not include all higher vertebrates descended from them, then Amphibia becomes paraphyletic—and so on. In rare cases, taxa converge from very different parts of the cladogram and might be put in a group together, forming a polyphyletic group (Figure 5). These are clearly unnatural, and few systematists would defend them once their polyphyly is revealed.

Once again, this debate is not merely an argument over semantics; it represents two fundamentally different ways of looking at the world. Traditional systematists don't mind mixing a little bit of ecology or phenetics into the classification, such as when they place Class Aves in an equal rank with Class Reptilia; in such a case, the evolutionary relationship is no longer apparent in the classification. Cladists say that mixing two or more data types in the classification is confusing. How can the non-specialist recognize which groups are strictly based on phylogeny (monophyletic) and which ones mix phylogeny with ecology (paraphyletic or polyphyletic)? Traditional systematists complain that the larger, more cumbersome classification schemes demanded by cladistics are harder to learn than the simple, parallel taxa of equal rank in the old system. But cladists would argue that if the old system was a confusing and inconsistent mixture of natural and unnatural groups, why are we using it in the first place?

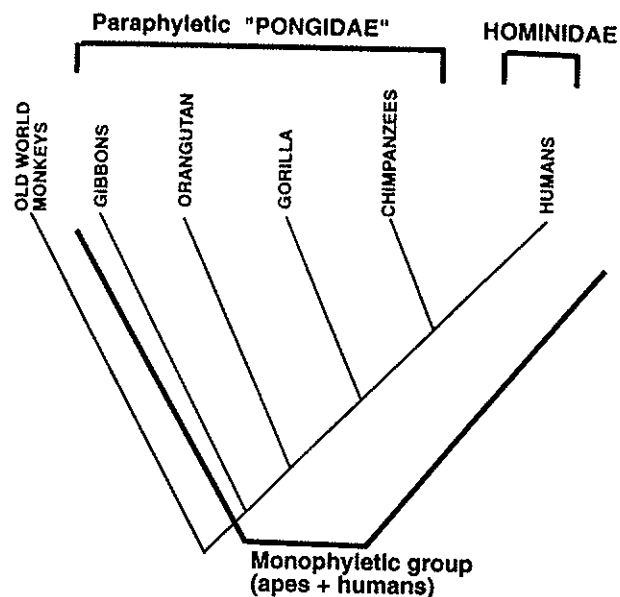


Figure 3. Traditional classifications emphasize the differences between humans and other apes by placing humans in a separate family Hominidae and placing the rest of the apes in a paraphyletic wastebasket taxon "Pongidae." To a cladist, humans must be included in the group that includes the apes. This could mean expanding the Hominidae to include all the apes, or placing the Hominidae within the Pongidae.

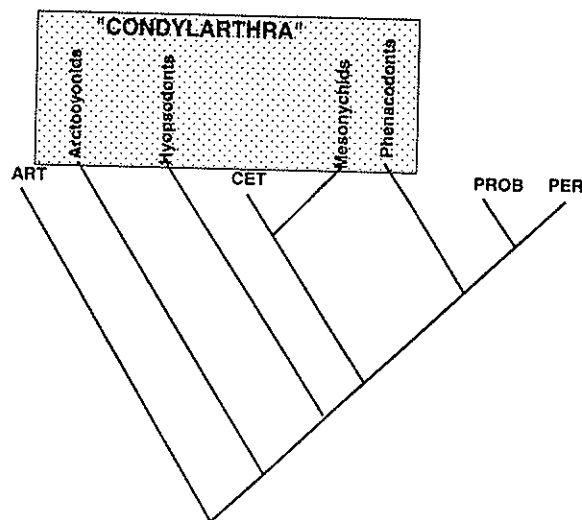


Figure 4. The taxon "Condylarthra" (shaded box) was long used as a wastebasket for all extinct hoofed mammals that clearly were not members of living orders. It is an example of a polyphyletic group, because it includes many different groups of hoofed mammals with widely different origins. These include the primitive arctocyonids and hyposodonts, the mesonychids (which are closer to whales), and the phenacodonts (which are closer to horses, rhinos, and elephants). Key: Art, artiodactyls (even-toed hoofed mammals); Cet, cetaceans (whales); Prob, proboscideans (elephants); Per, perissodactyls (odd-toed hoofed mammals).

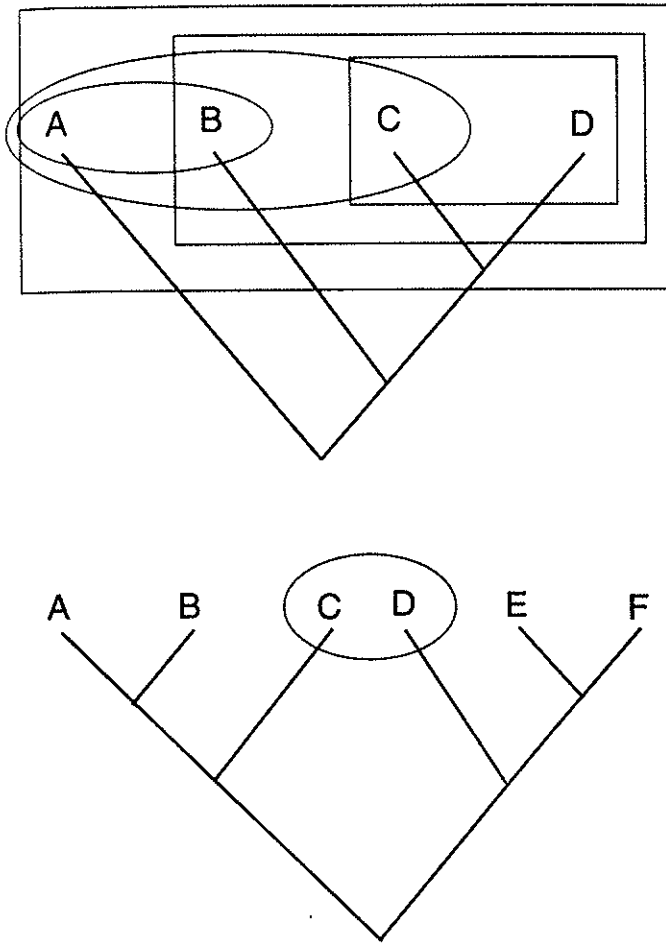


Figure 5. A “monophyletic group” includes all the descendants of a common ancestor, while a “paraphyletic group” excludes some of those descendants. *Top*, monophyletic groups, outlined by rectangles, include all descendants of a common ancestor; paraphyletic groups (in ovals) exclude at least one descendant (group D). *Bottom*, a “polyphyletic taxon” is composed of taxa from two or more unrelated lineages. In the lower figure, the grouping of C and D is polyphyletic, since these two groups are from very different lineages.

Conclusion

Although the 1960s and 1970s were marked by noisy controversies over systematics, since about the mid-1980s most systematists have followed cladistic methods in determining evolutionary relationships. The classification of organisms, however, has not changed to reflect this new systematic philosophy. Many biologists and paleontologists still prefer to use convenient but unnatural groups, such as “fishes,” “amphibians,” “reptiles,” “apes” (as conventionally defined), and have not yet abandoned these terms for those representing natural monophyletic clades, such as “gnathostomes,” “tetrapods,” “amniotes,” “archosaurs” that would replace them in a cladistic classification. In part, this resistance is owing to inertia and familiarity with the old system. Also, the current generation of biologists does not wish to surrender the convenience of

paraphyletic groups that are composite of both phylogeny and ecology for groups that do not serve their purposes as well. However, in some parts of the animal kingdom, cladistic classification is now the accepted norm, so the next generation of biologists may find the rigor of cladistic classification preferable to the established tradition and convenience of the older classification schemes (de Queiroz and Gauthier 1992, 1994).

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See also Adaptation; Diversity; Evolutionary Novelty; Evolutionary Theory; Homology; Speciation and Morphological Change

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