

Cladistics and classification

Taxonomy has always been a dual-purpose weapon; it organises knowledge and reflects relationships. These two purposes sometimes come into conflict

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Charles Darwin found one of the strongest arguments for his theory in the fact that animal and plant species fall into groups, and that these groups form a nested series, or hierarchy. Smaller groups of species, such as owls and ducks, or seals and deer, are included within successively larger groups: birds and mammals within vertebrates, vertebrates and invertebrates within animals, and so on. But hierarchical classifications were not Darwin's invention; the one we use today is derived from the work of the 18th century Swedish naturalist Carl von Linné, or Linnaeus.

Linnaeus introduced his system partly as a convenient aid to memory, a means of making comprehensible the diversity of nature. But Linnaeus also had a higher purpose than merely to catalogue nature. He believed that he was uncovering the plan of the Creator. Linnaeus and his successors recognised genera, families and other categories on the basis of similarities in structure, and believed that each group had a set of features which were its essence, or ideal plan, corresponding to something in the mind of the Creator. Comparative anatomy developed as a means of searching out these ideal plans.

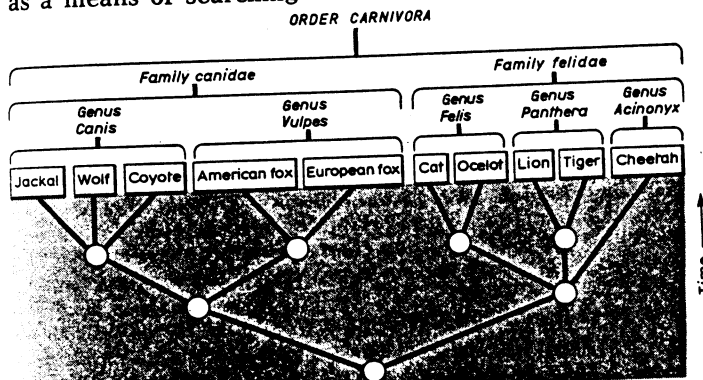


Figure 1 Classification and evolution. The boxed names are living species, and the names above show how they are classified within the Linnaean hierarchy. Species nest within genera, genera within families, and families within orders. The lower half depicts a Darwinian interpretation; the relationship is phylogenetic, the result of descent from common ancestors (open circles) more or less distant in time

By the time Darwin published *The Origin*, Linnaean hierarchical classification and classical comparative anatomy were highly developed. Darwin's contribution was to suggest, by detailed argument, that the relationship between the species of a genus, or genera of a family, is a "blood" relationship, caused by descent from a common ancestor (Figure 1). He wrote in *The Origin*: "Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation."

Darwin's expectation has not yet been fully realised. This is partly because classifications today, as in Linnaeus's time, have two purposes—to express evolutionary relationships and to act as *aides-mémoire* or simple summaries of knowledge. These two aims come into conflict because relationships of common ancestry are almost invariably more complicated than the relationships of similarity and difference on which Linnaean classification is based (Figure 2). Cladistics (from the Greek for "branch") is one method of biological classification that offers a new ap-

proach to the problem. As a method, cladistics has become both popular and controversial during the past 10 years or so; a review of the history of cladistics may explain this.

The basic principles of cladistics were set out by the German entomologist Willi Hennig in a 1950 book, but his ideas received little attention outside continental Europe until 1966, when an English translation of a much modified version was published as *Phylogenetic Systematics*.

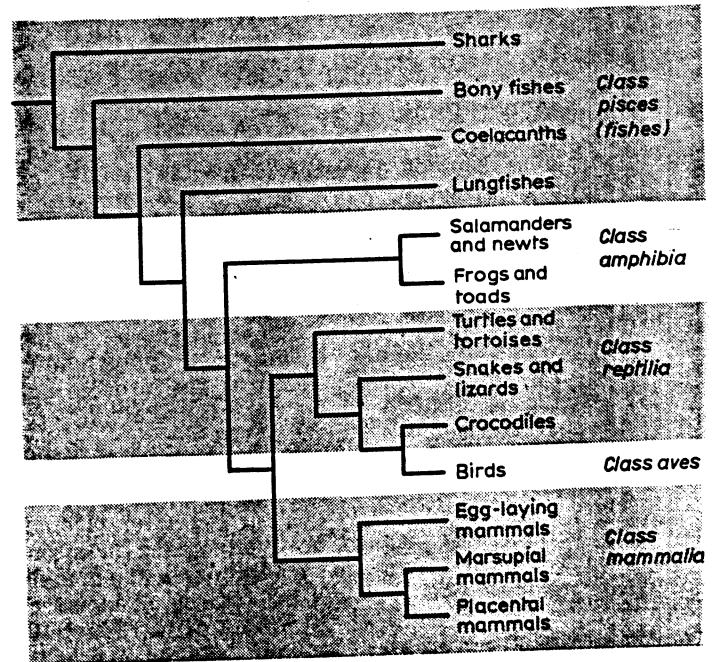


Figure 2 Tradition and ancestry. On the right are the traditional classifications of vertebrates, and on the left the ancestry of the same animals. In the genealogy, the groups are indicated by vertical bars; only two of these—amphibians and mammals—correspond to the taxonomic classes. All the other classes contain either too few members (birds), or too many (fishes)

proach to the problem. The keys to Hennig's system are his definitions of phylogenetic relationship and his discussion of how relationship is recognised. Hennig defined relationship as a branching diagram; hence "cladistics".

He saw such diagrams as evolutionary trees, and argued that relationship in his sense, that is closer common ancestry, was evinced only by shared derived characters (which he christened *synapomorphies*) inherited from that ancestor. Shared primitive characters (*symplesiomorphies*), inherited from a more remote common ancestor, are irrelevant or misleading in the search for phylogenetic relationship; for example, in Figure 3 the relationship between species C and D may be obscured or masked by features inherited by only one of them from the ancestor common to A and B (at t_1). In the same way, the teeth and long bony tail of *Archaeopteryx* are irrelevant to its relationship with birds.

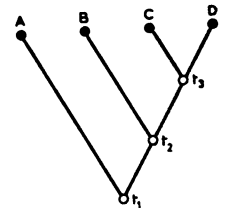


Figure 3 Hennig's definitions. Two species (C and D, for example) are more closely related to each other than to a third (A or B) if they share an ancestral species (at t_2) not shared with the third

because lizards, salamanders and fishes also have teeth and long bony tails. Feathers and a wishbone (furcula), however, are shared derived characters (synapomorphies) unique to *Archaeopteryx* and birds. Characters unique to any one group, Hennig called *autapomorphies*.

The three terms autapomorphy, synapomorphy and symplesiomorphy describe the distribution of characters relative to a particular problem: feathers are an autapomorphy of birds when one is interested in what other (featherless) groups are most closely related to birds, a synapomorphy when one is interested in the relationships of *Archaeopteryx*, and a symplesiomorphy if the problem is one of relationships within living birds.

From these ideas, Hennig derived definitions of three types of group. Monophyletic groups are those containing *all and only* the descendants of a common ancestor (ABCD, BCD or CD in Figure 3). Monophyletic groups are characterised by shared derived characters or evolutionary novelties: Mammalia and Vertebrata are examples, with their fur and backbones respectively. Para- and polyphyletic groups are those that do not contain all the descendants of a common ancestor. A paraphyletic group is left behind when one or more parts of a monophyletic group are removed because the members share *derived* characters. Paraphyletic groups are characterised by shared *primitive* characters: Reptilia and Invertebrata are examples but by their very nature share no distinguishing character. There is nothing that defines a reptile in the same way that hair defines a mammal. Polyphyletic groups are those whose defining features are inferred not to have existed in their common ancestor. Polyphyletic groups are characterised by convergent characters: a group of all winged animals (birds, bats, insects) would be an example.

One source of controversy is evident here, for cladists deny that paraphyletic groups have any place in systematics, whereas such groups are traditional and popular, especially among palaeontologists, whose "ancestral groups" are all of this type: examples of paraphyletic groups among vertebrates include Pisces (fishes), Amphibia, Reptilia, and many smaller or extinct taxa. Harvard biologist Ernst Mayr accused Hennig and his supporters of misusing well-known words such as "relationship" and "monophyly". He proposed that relationship be defined as "genes in common" or "inferred amount of shared genotype" (see Figure 5), and that monophyly be defined not in Hennig's sense, as *all* descendants of a common ancestor, but in a less restrictive sense, by immediate common ancestry alone. By this definition, all possible groupings in Figure 3 could be monophyletic. The intention of Mayr's definitions was to permit paraphyletic groups, in order to avoid a second controversial aspect of Hennig's ideas, his method of forming a classification.

For Hennig, a classification should name and rank all monophyletic groups and only those groups, and should give equal rank to "sister groups", the name he gave to species or groups that are each other's closest relatives: in Figure 3, C and D are sister groups, and B is the sister group of C+D. The motto of Hennigian systematists is "search for the sister group", because any species or group should have one species or group to which it is most closely related. Cladistic classifications are thus direct translations of phylogenetic diagrams.

Answering such critics as Mayr was one of the stimuli behind more recent developments in cladistics, leading to what has been called "transformed cladistics". As his title *Phylogenetic Systematics* implies, Hennig's work was set in an evolutionary framework. His definitions of relationship, of monophyly and paraphyly, and of symplesiomorphy and synapomorphy, were based on common ancestry and the notion of evolutionary change. Hennig's branching diagrams were evolutionary trees, with an implicit time

axis, and with forks denoting splitting of ancestral species. But it is possible to look at diagrams like Figure 3, and at the definitions Hennig associated with them, in a more general framework, one which has no evolutionary implications. Branching diagrams can be seen not as evolutionary trees, but as cladograms in which there is no time scale and the nodes imply shared characters (synapomorphies) rather than common ancestry. This distinction, between cladograms and trees, may seem like hair-splitting, but it is important. A cladogram is a summary of pattern, the pattern of character distribution, or of hierarchy in nature—what pre-Darwinians called "the natural hierarchy". An evolutionary tree is a summary of pattern with an added summary of process, the historical process of descent with modification which caused the pattern of characters. In a tree, the nodes are real ancestors (though they may not be identifiable), the forks are speciations, and the lines of the diagram are lineages of descent with modification. In a cladogram, the nodes are

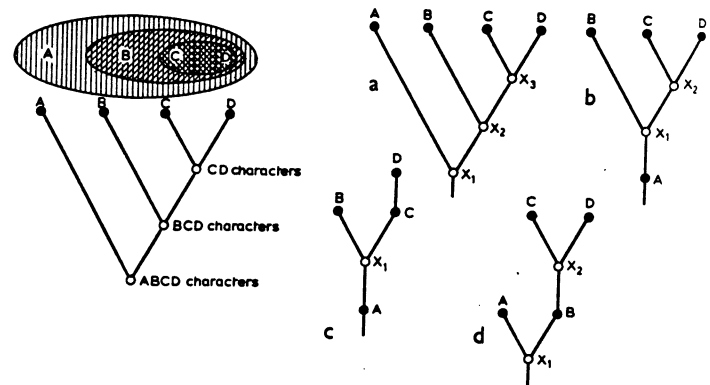


Figure 4 Cladograms and trees. A cladogram is a pattern of relationships, and is exactly equivalent to a Venn diagram of sets and subsets (left). Trees (right) carry an added implication of evolution and time. The four trees are simply representatives of the 12 possible trees one could construct from the cladogram

shared characters and the lines are immaterial—one can as well represent the pattern by a Venn diagram (Figure 4).

Thus a tree says much more than a cladogram. Tree a in Figure 4, for example, says that none of the four species is ancestral to any other, that the three ancestral species are unknown, and that speciation was dichotomous, with the unknown ancestral species becoming extinct on each occasion. The other trees offer other evolutionary stories. In short, cladograms are less restrictive, or more general, than trees, because a cladogram is equivalent to a set of evolutionary trees. And a cladogram, as a summary of pattern is not necessarily evolutionary.

But there are still evolutionary implications in the notion of advanced characters (synapomorphies) and primitive characters (symplesiomorphies). If these categories of character must be distinguished before the cladogram is constructed, then it seems necessary to understand evolution before making a classification, and there is no sense in which the cladogram is independent of evolution. But this is not so. Methods of distinguishing primitive and derived characters have been much debated, and the lack of foolproof procedures has been one of the arguments used by critics of cladistics. However, there is one apparently foolproof method: it depends not on "evolution" as we understand it, but on the usage of that word among pre-Darwinian biologists. To them, "evolution" meant the unfolding of pattern, increase in complexity, or differentiation seen in the development of individual organisms—the process of embryology rather than of descent with modification.

Embryology is the only direct evidence we have of transformation of form. We can observe that all organ-

isms begin life (in the egg, spore or seed) without certain features, that some organisms (a group) then develop those features in a general or "primitive" form, and in some smaller set of organisms (a subgroup) those features are refined into a particular or "specialised" form. This applies to a great variety of features—to structures such as the tail, limbs and brain of vertebrates, the leaves of plants, and so on, and also to features of physiology or behaviour. Such observations

were the basis of the law proposed in 1828 by the pioneering embryologist K. E. von Baer: "In development the general characters appear before the special ones." That law provides the framework of the systematic hierarchy, groups and subgroups circumscribed by recognition of general (primitive in evolutionary terms) and special (derived or advanced in evolutionary terms) characters. In this light, the synapomorphies and symplesiomorphies of phylogenetic systematics are exactly equivalent to the homologies of classical biology. Every homology characterises a group at some level in the hierarchy, and symplesiomorphy and synapomorphy are terms for homologies that stand in hierarchic relation: a symplesiomorphy (general character) makes a group, and a synapomorphy (special character) makes a subgroup. In this light, too, the rift between cladists and evolutionary systematists comes into clearer focus.

That argument centres on the kinds of group that should be recognised in classifications. Cladists demand that groups be characterised by synapomorphies (or homologies), so that they are monophyletic (or natural). Evolutionary systematists agree that cladistic analysis is the best way of approaching systematics, but in classifications they wish to take account of rate or degree of evolutionary divergence—*anagenesis*—in addition to the branching or *cladogenesis* recognised by cladists. Evolutionists regard production of classifications as a two-step process, cladistic analysis followed by analysis of divergence. For instance, when one group differs excessively from its sister group and other close relatives (*D* in Figure 5), evolutionists wish to recognise the inferred rapid divergence by raising the rank of that group. Well-known examples include man (family Hominidae) versus our sister group (chimpanzees and/or gorillas—genus *Pan* or subfamily Paninae), birds (class Aves) versus their sister

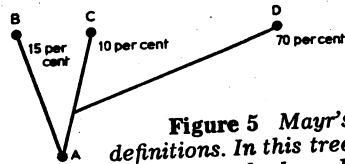


Figure 5 Mayr's definitions. In this tree the slope of the branch corresponds to the rate of evolution, and the percentages represent the degree of difference from the ancestral species A. Mayr would classify C with B because the two are more like their common ancestor. A cladist classifies C and D together because they share a common ancestor that B does not

group (crocodiles, order Crocrodilia), and land vertebrates (Tetrapoda, ranked above class) versus their sister group, lungfishes (Dipnoi, ranked below class). An inevitable consequence of the structure of the hierarchy is that when this is done the sister group of lower rank (chimps and gorillas, or crocodiles, or lungfishes) is included with others in a paraphyletic group equal in rank to the divergent group. Thus chimps and gorillas are placed in the family Pongidae, which also includes *Pongo*, the orang-utan, and sometimes also the gibbons; crocodiles are placed in the class Reptilia, which also includes lizards, snakes and turtles; and lungfishes are put in the class Osteichthyes, with other bony fishes.

A further consequence is that the cladogram reconstructed from the evolutionary classification disagrees with the cladogram based on character analysis (Figure 6). Evolutionists justify their strategy by asserting that classifications must be grounded in evolutionary theory, and by appealing to the purpose of biological classification, but it is generally agreed that the greatest virtue of a classification is predictivity, or congruence with the greatest number of characters. John Stuart Mill's doctrine is often quoted: "The ends of scientific classification are best answered, when the objects are formed into groups respecting which a greater number of general propositions can be made, and those propositions more important, than could be made respecting any other groups into which the same things could be distributed." The "objects" in biology are species, and Mill's statement implies that new information, or different types of characters, conforms better to the adopted classification than to another.

Thus evolutionists argue that new information—newly discovered or investigated characters—will conform to the groupings produced by taking anagenesis, or degree of divergence, into account. In the hominoid example, they predict that characters of chimpanzees and gorillas will be shared with orang-utans rather than with humans. During the past decade or so, newly discovered characters bearing on this example have come mostly from the molecular field, particularly amino-acid sequences of proteins and, more recently, nucleotide sequences of RNA and DNA. Without exception, these genetic details fail to meet the prediction. The best yet is a sequence of 896 nucleotides from the mitochondrial DNA of man, chimpanzee, gorilla, orang-utan and gibbon: 296 of these nucleotides differed among the five species, and whereas conventional classification predicts that chimp and gorilla should be more like orang, nucleotides unique to man, chimp and gorilla outnumber those unique to chimp, gorilla and orang more than fourfold.

Because the "predictive" defence of evolutionary classifi-

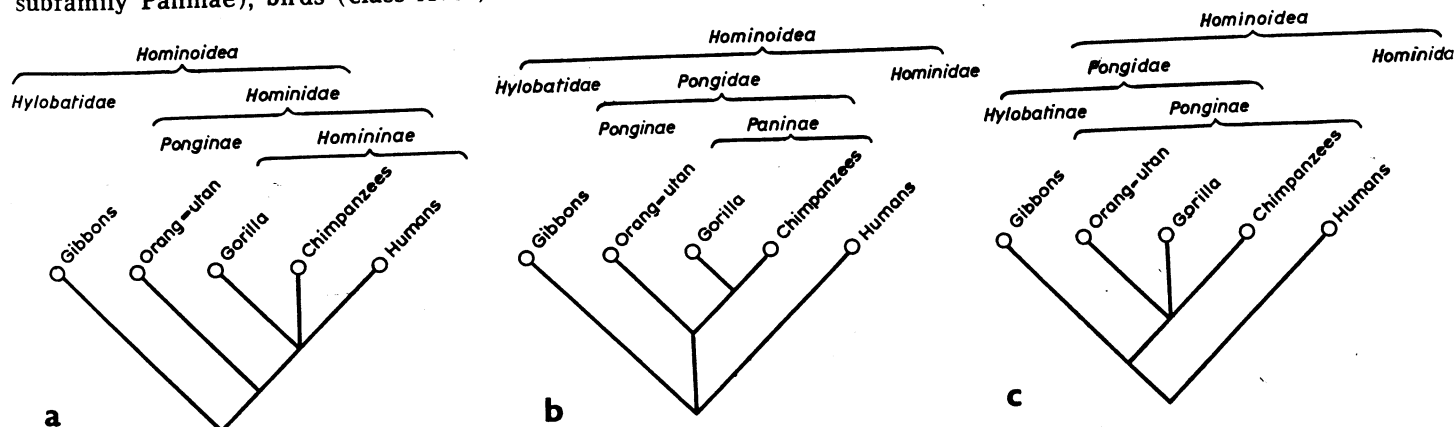
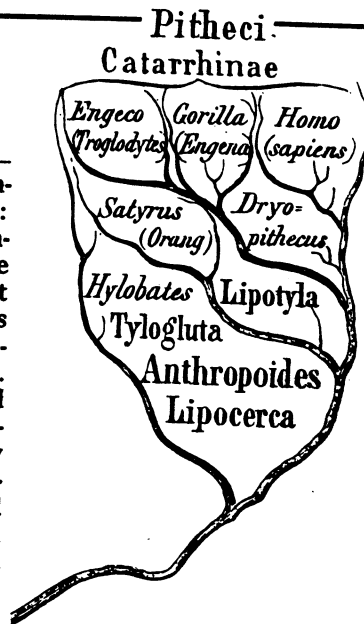


Figure 6 Cladograms and classifications of hominoids. a (left) shows the ancestry of man and the apes as currently understood, with the classification that this cladistic analysis

would support. b (middle) and c (right) show two alternative classifications in use and the different cladistic relationships these classifications imply

Figure 7 Haeckel's evolutionary tree of 1866. Engeco is chimpanzees, Hylobates gibbons. Note the similarity to Figure 6a



earlier in time than the descendant, and that the fossil record should be sufficiently complete and well-sampled for there to be no other potential ancestors. But fossils, too, present peculiar problems in analysis. They are very incomplete when compared with living organisms, so that it is generally impossible to be sure just what characters they had; they are only decipherable as organisms by comparison with living relatives, which means that they must be assigned to extant groups before they can be properly interpreted; species limits and geographic ranges of fossils are largely guesswork; and so on.

Because of all these problems, it is rare to find palaeontologists offering ancestral species, or doing so with any conviction. Instead, they usually propose "ancestral groups", as approximations to the truth, with the claim that the true ancestor, if found, would fall within the group. Extinct ancestral groups are paraphyletic, just like Reptilia and Pongidae, and have the same status as uncharacterisable artefacts, with the added complication that the included fossils may not be complete enough to say even what characters they lack. Yet these flawed artefacts play a central role in phylogenies—accounts of the evolutionary descent of lineages. This raises yet another problem, for groups cannot evolve—species are the largest units capable of change. Thus cladistics calls into question much of conventional evolutionary history.

Ancestors, either species or groups, have a place in trees but not in cladograms (Figure 4). Cladists recommend avoiding some of the problems with fossils by treating them in the same way as living species, as potential twigs of cladograms rather than stems of trees.

A further disadvantage of paraphyletic groups is that they are readily mistaken for real (monophyletic) groups. Staying with the example of man and apes, within the past few years I have seen publications by specialists dating the separation of man from apes at times that range from less than 5 to more than 75 million years ago. Any one of these dates *might* be true—we have, as yet, no foolproof way of knowing. But it is noticeable that the more remote dates are accompanied by diagrams in which the gibbons, orang-utan and African apes are shown as monophyletic (as in Figure 6b), while the middle range of dates is found with diagrams in which the orang is related to African apes (as in Figure 6c): in both instances, the specialists have treated the Pongidae as a monophyletic group. Had they recalled T. H. Huxley's words and the cladogram they imply (Figure 6a), they might have seen the implication that whatever date is assigned to the man/ape split, the chimpanzee/gorilla split will be of comparable age, and the orang-utan should diverge even earlier. It was mistaking paraphyletic groups for monophyletic groups that prompted these experts to drive the human lineage so far into the past.

The three components of the history of life are form, time and space. The biological disciplines dealing with these are systematics, which concerns the variety of form, palaeontology, concerned with that variety in time, and biogeography, concerned with that variety in space. Cladistics calls into question traditional attitudes in all three, and offers a new approach to comparative biology which has a coherent theoretical base that is not necessarily tied to evolutionary theory. As a science of pattern, cladistics holds out the possibility of a reconstruction of the history of life in space and time that does not depend on Darwinian or neo-Darwinian presuppositions. The interest of that reconstruction or cladogram is that theories of process—neo-Darwinism or any other—can be tested only against nature, and the best test will be their success in explaining past and present configurations of life. But if we are taught, as we have been, to see that pattern through the spectacles of evolutionary theory, how could the pattern ever test the theory? □

cation fails, some evolutionists have offered another: that conventional classification is preferable because it is more stable, and not subject to frequent changes as ideas on the interrelationships of species fluctuate. To stick to the hominoid example, this defence implies controversial or newly proposed notions of the interrelationships of apes and man. But as Figure 7 shows, the cladogram derived from molecular data on apes and man agrees with the first detailed evolutionary tree ever published, Ernst Haeckel's in 1866. It also agrees with T. H. Huxley's words in *Man's Place in Nature* (1863): "It is quite certain that the Ape which most nearly approaches Man, in the totality of its organisation, is either the Chimpanzee or the Gorilla." In the same work, Huxley epitomises the predictive consequence: "Whatever part of the animal fabric . . . be selected for comparison—the result would be the same—the lower Apes and the Gorilla would differ more than the Gorilla and the Man." Is stability worth more than a century of conflict with evidence?

Paraphyletic groups may seem a small price to pay for the advantages claimed for them—convenience, stability and the recognition of evolutionary advances. Yet groups such as the Pongidae and Reptilia, necessitated or permitted by evolutionary classification, have one crippling disadvantage, and unfortunate consequences. The disadvantage is that those groups are uncharacterisable: they have no characters of their own. The only statements that can be made about them are negative, that they lack the characters of the groups that have been detached (birds and mammals detached from reptiles; humans from apes). If, to quote John Stuart Mill again, we view "classification as a logical process subservient to the investigation of truth", or if, in more prosaic terms, "systematics in general consists of the search for defining characters of groups" (as Gareth Nelson and Norman Platnick put it), paraphyletic groups deny both propositions; the "truth" of human/ape relationships has been around for well over a century, and the defining characters of groups like Pongidae and Reptilia are non-existent. If those groups have no characters, they have no real existence: they are artefacts.

And those artefacts have unfortunate consequences. Historical statements that are superficially objective, like "man is descended from apes" or "birds are descended from dinosaurs", *always* invoke such groups. The concept of ancestry, as part of evolutionary theory, has so captivated systematists that they are trained to think in terms of trees, of ancestry and descent. But the only clues to relationship between species are uniquely shared characters (homologies). Such homologies may be seen as evolutionary novelties originating in the ancestor unique to those species, yet shared characters alone will not distinguish between direct ancestry and common ancestry. Two species may share a character either because one is the ancestor of the other, or because both have a common ancestor. So hypotheses of ancestry must depend on some justification beyond character distribution: for instance, that the ancestor be represented by fossils occurring