

SYSTEMATICS AND THE DARWINIAN REVOLUTION*

KEVIN DE QUEIROZ†

*Department of Zoology and Museum of Vertebrate Zoology
University of California, Berkeley*

Taxonomies of living things and the methods used to produce them changed little with the institutionalization of evolutionary thinking in biology. Instead, the relationships expressed in existing taxonomies were merely reinterpreted as the result of evolution, and evolutionary concepts were developed to justify existing methods. I argue that the delay of the Darwinian Revolution in biological taxonomy has resulted partly from a failure to distinguish between two fundamentally different ways of ordering identified by Griffiths (1974): classification and systematization. Classification consists of ordering entities into classes, groups defined by the attributes of their members; in contrast, systematization consists of ordering entities into systems, more inclusive entities whose existence depends on some natural process through which their parts are related. Evolutionary, or phylogenetic, systematics takes evolutionary descent to be the natural process of interest in biological taxonomy. I outline a general framework for a truly phylogenetic systematics and examine some of its consequences.

1. Introduction. Charles Darwin (1809–1882) is among the most influential figures in the history of Western ideas. By establishing what has been called the “fact” of evolution (for example, Gould 1982) and proposing natural selection as its mechanism, Darwin not only revolutionized biology but also changed man’s view about his own place in the universe. The impact of Darwin’s ideas has been described by many authors, among them Ruse.

The arrival of the *Origin* changed man’s world. Darwin was not the first to present a theory of “evolution”; but never before had such a theory had such convincing impact. At once it was seen to have implications far beyond biology. It struck at beliefs and behaviors from the most trivial to the most profound. (Ruse 1979, p. ix)

*Received July 1986; revised August 1986.

†I bear a tremendous intellectual debt to G. C. D. Griffiths, M. T. Ghiselin, and D. L. Hull, whose writings laid the foundation for this contribution. Other people who have strongly influenced my thinking either through conversations or their writings are R. de Queiroz, M. J. Donoghue, J. A. Gauthier, W. Hennig, E. Mayr, G. Nelson, M. A. Norell, M. J. Novacek, C. Patterson, N. I. Platnick, G. G. Simpson, E. O. Wiley, A. Wyss, and a host of other taxonomists arguing the virtues of their approaches and the drawbacks of others. M. J. Donoghue, R. Estes, J. A. Gauthier, M. T. Ghiselin, H. W. Greene, D. L. Hull, D. B. Wake, M. H. Wake, E. O. Wiley, and an anonymous referee provided valuable comments on earlier versions of the paper.

Philosophy of Science, 55 (1988) pp. 238–259.

Copyright © 1988 by the Philosophy of Science Association.

Ghiselin put it even more emphatically.

In 1859 there began what ultimately may prove to be the greatest revolution in the history of thought. *The Origin of Species*, published in November of that year, effected an immediate and cataclysmic shift in outlook, casting into doubt ideas that had seemed basic to man's conception of the entire universe. The idea of evolution, the explanation of its mechanism, and the book which had such a profound effect give to Charles Darwin a unique position in the history of ideas. (Ghiselin 1969, p. 1)

So great were the changes brought about by Darwin's ideas that they have earned the name "The Darwinian Revolution" (for example, Himelfarb 1968; Mayr 1971; Ruse 1979). Surprisingly, this revolution has only just begun in biological taxonomy, a discipline upon which one might have expected evolutionary thinking to have had a profound and immediate impact. This expectation arises from the fact that biological taxonomies depict the relationships among organisms, and the concept of relationship takes on a precise meaning under an evolutionary world view.

I have four goals in this paper: (1) to support the claim that the Darwinian Revolution has only just begun in biological taxonomy, (2) to offer an explanation for its delayed occurrence, (3) to outline a general framework the acceptance of which should bring the Darwinian Revolution in biological taxonomy to fulfillment, and (4) to describe certain changes and insights that are occurring under an implicit or explicit adoption of this framework.

2. The Influence of the Theory of Evolution on Biological Taxonomy. Biological taxonomy has been influenced by many developments since Darwin's time, from the discovery of the mechanism of inheritance, to the invention of computers for handling large quantities of data, to the refinement of methods for examining the structure of DNA and other biological molecules. During the same time, biological taxonomy has also experienced the birth, or at least the codification, of various schools, or approaches, from the new systematics of the evolutionary synthesis (for example, Huxley 1940; Mayr 1942, 1969a; Simpson 1961) to phenetics (for example, Sokal and Sneath 1963; Sneath and Sokal 1973) and cladistics (for example, Eldredge and Cracraft 1980; Wiley 1981; Nelson and Platnick 1981). The influence of some of these approaches notwithstanding, acceptance of Darwin's proposition that "community of descent is the hidden bond which naturalists have been unconsciously seeking" (1859, p. 420) has thus far had little effect on biological taxonomies or the underlying principles governing their construction. Instead, most of the developments in biological taxonomy from pre-Darwinian times to the pres-

ent represent increases in accumulated information about living things and technological advances for gathering and analyzing this information.

The opinion that biological taxonomy changed little from pre- to post-Darwinian times is widespread among biologists and historians of science. Although Darwin (1859, p. 485) recognized that an evolutionary world view clarified the meanings of taxonomic terms such as “affinity” and “relationship”, which previously had been used in a purely metaphorical sense, he did not expect evolutionary thinking to have much impact on the theory and practice of biological taxonomy.¹ This is evidenced by his statement that “systematists will be able to pursue their labors as at present” (Darwin, 1859, p. 484). Judging from the following quotes, Darwin’s prediction was upheld.

. . . the coming of evolution made surprisingly little difference to morphology [which is inseparable from classification, p. 234], . . . the same methods were consciously or unconsciously followed, the same mental attitudes taken up, after as before the publication of *The Origin of Species*. (Russell 1916, p. 247)

The job of systematists was affected hardly at all, the “natural system” sought before Darwin’s time being much the same as that posited by the theory of evolution. (Himmelfarb 1968, p. 447)

The fact is that the classification of organisms that existed before the advent of evolutionary theories has undergone surprisingly little change in the times following it. . . . The phylogenetic interpretation has been simply superimposed on the existing classification; a rejection of the former fails to do any violence to the latter. (Dobzhansky 1937, p. 305)

Stevens (1984) gives a recent statement of this position by a practicing taxonomist.

3. Why the Darwinian Revolution Never Occurred in Biological Taxonomy. Dobzhansky offered the following explanation for his observation quoted above:

. . . the only inference that can be drawn from it [the fact that taxonomy was largely unchanged by the advent of evolutionary theories] is that the classification now adopted is a natural one, reflecting the objective state of things. (Dobzhansky 1937, p. 305)

¹Stevens (1984) suggests that the success of Darwin’s ideas may have actually hampered methodological developments in phylogenetic taxonomy. Taxonomy should be genealogical, said Darwin, but he had inferred community of descent from taxonomy, so it must already have been genealogical.

I disagree. The failure of evolutionary thinking to change existing taxonomies does not necessarily reflect anything “natural” about these taxonomies, for it can be explained simply as a logical consequence of the way in which taxa traditionally have been conceived. Before developing this argument, some background information must be presented.

3.1. Taxonomy. Biological taxonomy is one of the most ancient and widely used scientific disciplines. Aristotle (384–322 B.C.) is sometimes credited with having developed the first scientific taxonomy of animals (for example, Russell 1916), but some form of biological taxonomy surely predates recorded history, for it involves as little as the recognition of groups of living things as distinct kinds and designating them with common or proper nouns. Furthermore, taxonomy has been and continues to be used by virtually every human being. Not all of us make a living as taxonomists, but we all use nouns daily that refer to different kinds of living things. Because taxonomy is ancient and its use widespread, many aspects of this discipline are taken for granted. This situation gives biological taxonomy a tremendous inertia—one great enough to have successfully resisted the Darwinian Revolution.

3.2. Classification and Systematization. I propose that the delay of the Darwinian Revolution in biological taxonomy has resulted from a failure to distinguish between two fundamentally different ways of constructing taxonomies—classification and systematization. Although this distinction was first made over ten years ago (Griffiths 1974; see also Ghiselin 1985), its significance has not been widely appreciated.

Classification is the ordering of entities (elements, individuals) into classes; a class is a group defined by a property (attribute, character) or properties shared by its members. In contrast, systematization is the ordering of entities into systems; a system is a more inclusive entity (whole) whose existence depends on some natural process through which its elements (component parts) are related. Living things, as entities, can be either classified or systematized. Griffiths (1974) uses the term ordering to include both classification and systematization.²

²The terms classification, systematics, and taxonomy currently have several usages. Some authors (for example, Wiley 1981) define systematics as the study of the relationships among living things and use taxonomy to refer to the theory and practice of ordering information about relationships into a scheme of words, or classification. Simpson (1961) and Mayr (1969a) point out that classification is used not only for the schemes of words but also for the activity of producing them; the latter is equivalent to Wiley's (1981) concept of taxonomy. Thus, one might envision a procedural progression from systematics to taxonomy/classification. Nevertheless, Griffiths (1974) points out that systematics and taxonomy are often used interchangeably, and other authors (for example, Simpson 1961) view systematics as a broader discipline that includes classification. (Simpson's proposal

3.3. *Evolution and Biological Taxonomy.* Under the definitions given in the previous section, most contemporary biological taxonomists treat taxa as if they are classes rather than systems (Griffiths 1974). This is evident in their taxonomic monographs, where it is usual to find lists of characters given as the “definitions” of taxa. If taxa are defined by characters, that is, by the attributes of their members, then these taxa are classes.³

Given that taxa are viewed as classes, biological taxonomies are classifications, and one would not expect the coming of evolutionary thinking to cause any major changes in them. Let me illustrate this proposition with an example. Reptilia is commonly defined as the group of scaly, ectothermic amniotes. Because Reptilia is defined by the attributes of its members, it is a class in the philosophical sense. But acceptance of evolution has no necessary bearing on the status of this taxon or any other that is a class concept. After all, the organisms called reptiles have scales, depend on external heat sources to elevate their body temperatures, and spend their embryonic lives floating in amniotic fluid, whether we realize that they have an evolutionary history or not. In other words, adopting an evolutionary perspective is not going to change the attributes of organisms, and because taxa are treated as if they are defined by attributes of the organisms that are their members, there is no reason to expect that adopting an evolutionary perspective would have had any effect on ex-

to define taxonomy as “the theoretical study of classification, including its bases, principles, procedures, and rules” (1961, p. 11) has not gained wide usage.)

Distinguishing between two fundamentally different ways of ordering provides a basis for redefining systematics, classification, and taxonomy. Following Griffiths (1974), I have chosen to restrict the definitions of systematics and classification so that they are modifications of the respective stems system and class. Systematics is a discipline that includes both the study of relationships and the development of schemes or words to convey these relationships. Classification similarly includes both ordering and naming components. Because taxonomies, that is, schemes of words, are used to represent interested classes as well as systems and their parts, and because such representation is inseparable from the ordering itself, taxonomy encompasses both systematics and classification.

The following table summarizes the usages adopted in this paper:

ACTIVITY	DISCIPLINE	SCHEME OF WORDS
ORDERING	TAXONOMY	TAXONOMY
CLASSIFICATION	CLASSIFICATION	CLASSIFICATION
SYSTEMATIZATION	SYSTEMATICS	SYSTEM

The term “system” refers to either a kind of taxonomy (as in “phylogenetic system”) or a whole whose parts are related through some natural process.

³In reality, biological taxa are treated as both classes and systems, for the distinction between the two concepts is not made. I focus on the class-like aspect of the taxon concept because I consider this to be responsible for the delay of the Darwinian Revolution in biological taxonomy.

isting taxonomies.⁴ Contrary to Dobzhansky's (1937) statement quoted above, the fact that evolutionary thinking had little impact on biological taxonomies does not necessarily reflect anything "natural" about these taxonomies; it is expected under the way in which taxa traditionally have been defined.

Based on the foregoing discussion, I conclude that the Darwinian Revolution has not yet occurred in biological taxonomy. The theory of evolution has not assumed a central role around which the methods and concepts of biological taxonomy are organized. Instead, existing taxonomies and the principles underlying their construction have remained largely unaltered, and evolution merely has been granted the role of an interpretation or explanation for the order already manifest in these existing taxonomies. Changes are finally beginning to occur (section 5), but in the community of biological taxonomists as a whole, evolution remains a superficial interpretation superimposed on a fundamentally nonevolutionary core. As long as this situation prevails, biological taxonomy will wait for the Darwinian Revolution.

4. Evolutionary or Phylogenetic Systematics. One way to bring the Darwinian Revolution in biological taxonomy to fruition is to begin practicing systematics. Systematics, as the discipline that orders entities according to their relationships resulting from some natural process, requires as its first task the identification of the natural process of interest. Many kinds of natural processes exist in the living world and, therefore, many possible kinds of biological systematics exist as well. But ever since Darwin, most comparative biologists have viewed evolution as the unifying concept in biology and the natural process upon which a general taxonomy of living things should be based. Therefore, although I recognize the possibility of developing other kinds of systematics, I concern myself only with evolutionary, or phylogenetic, systematics in the following discussion. In evolutionary, or phylogenetic, systematics, evolution is taken as the underlying natural process relating the basic entities that we attempt to order and thus producing the more inclusive entities that we attempt to discover.⁵

⁴Although evolutionary thinking does not change the attributes of living things, one might expect it to change the way in which these attributes are viewed. According to Platnick (1978) evolutionists must accept that tetrapod vertebrates have fins, albeit in a modified form (limbs), and that snakes have legs (Platnick 1979). While these propositions make a certain amount of sense if the phylogenetic relationships of the organisms in question are known, they are of little value when one is attempting to identify characters for determining such relationships. This is especially true in cases involving the absence of features. Without prior knowledge of phylogenetic relationships, a feature that has been lost may be indistinguishable from one that was never present.

⁵A distinction is commonly made between evolutionary (traditional, Mayrian, Simpson-

4.1. *The Axiomatization of Evolution.* Ghiselin described the initiation of phylogenetic systematics implicitly, attributing it to Charles Darwin.

The change [Darwin] made exemplifies a basic shift in attitude. Instead of finding patterns in nature and deciding that because of their conspicuousness they seem important, we discover the underlying mechanisms that impose order on natural phenomena, whether we see that order or not, and then derive the structure of our classification systems from that understanding. (1969, p. 83)

Although Ghiselin was premature in believing that this shift had already occurred, he anticipated Griffith's (1974) concept of systematics and identified evolution as the underlying natural process. Identifying evolution as the natural process underlying systematics is comparable to the common saying that systematics is "based on" evolution. Elsewhere (de Queiroz 1985), I tried to make this statement more explicit by defining phylogenetic systematics as that kind of systematics in which the relationships sought are phylogenetic relationships and, thus, evolution is taken as an *axiom* (for example, Wiley 1974; Gaffney 1979) from which systematic methods and concepts are *deduced*. Taking evolution as an axiom effectively brings this concept to the very core of systematics and requires that preexisting systematic methods and concepts be reevaluated in its light. Adopting such a perspective should bring the Darwinian Revolution in biological taxonomy to fulfillment.

4.2. *The Meaning of Evolution and Relationship in Phylogenetic Systematics.* Unfortunately, there is disagreement about the meaning of the phrase "phylogenetic relationship" (Mayr 1974, 1985). The meaning of this phrase must be clarified before my concept of phylogenetic systematics can be put into practice. Before examining the meaning of "phy-

ian, synthetic, eclectic, gradistic) and phylogenetic (Hennigian, cladistic) systematics. Both of these approaches can legitimately claim to incorporate attempts to give the concept of evolution a more important role in biological taxonomy. Notable among the developments of the synthetic approach was an attempt to redefine the species category so that its members would be evolutionary units (for example, Simpson 1961; Hull 1965; Mayr 1969b). Hennig (1965, 1966) reformulated many taxonomic concepts and methods in more precise and explicitly evolutionary terms. For this reason, I view his approach not as an alternative to traditional evolutionary methods but as a refinement of them (Wyss and de Queiroz 1984). By rejecting certain of Hennig's principles, proponents of the traditional approach have denied evolution a more central role in biological taxonomy. Furthermore, although many "cladists" accept an evolutionary basis for their brand of taxonomy, others (for example, Platnick 1979; Nelson and Platnick 1981; Patterson 1982, 1983; Nelson 1985) deny it. Because of the definition of systematics adopted here, I use the terms "phylogenetic systematics" and "evolutionary systematics" interchangeably, both referring to an approach in which evolution is accepted, in principle if not in practice, as the underlying natural process upon which systematics is based.

logenetic relationship”, however, I must examine the meaning of an even more basic term, “evolution”.

Biologists commonly distinguish between two different meanings of the phrase “theory of evolution”; it may refer simply to change, or it may refer to a particular mechanism, such as natural selection, hypothesized to be the agent of change. In any case, virtually all modern definitions of evolution stress the concept of change. But there is yet another way in which evolution is used: for the idea of descent, or common ancestry. Common ancestry rarely enters into modern definitions of evolution (Gaffney 1979 is a notable exception).

Most contemporary evolutionary biologists have accepted common ancestry as a fact and now focus their studies on the changes that have produced the diversity of living things and the mechanisms underlying these changes. For this reason, the emphasis on change in modern definitions of evolution is not surprising. Nevertheless, in the context of systematic axioms, change is of secondary importance whereas common ancestry is primary. Evolutionary change occurs only within the context of descent. One might even argue that the notion of evolutionary change is simply a consequence of accepting the proposition of common ancestry combined with the observation that living things differ.⁶ Therefore, when I refer to the axiom of evolution in systematics I mean only that *living things are related through the natural process of descent and thus its product common ancestry*.

A useful axiom upon which to base a systematics is one whose validity is not doubted. Therefore, if we truly live in a Darwinian era, the axiom of common ancestry should be readily accepted. Furthermore, because common ancestry is implicit in comparative investigations of evolutionary processes, taxonomies based on this axiom should be useful in the testing of theories about such processes (for example, Eldredge and Cracraft 1980; Wiley 1981).

Disagreements about the meaning of phylogenetic relationship are related to different uses of the term evolution. When evolution is viewed as change, the similarities and differences resulting from change or the lack thereof are sometimes said to be important components of the concept of phylogenetic relationship. Mayr (1974), for example, criticized Hennig (1966) and his followers for viewing relationship as genealogy (common ancestry) only and included genetic or phenotypic similarity along with common ancestry in his own concept of phylogenetic rela-

⁶The situation is actually more complex. Although accepting change does not necessitate accepting common ancestry, it certainly makes common ancestry more plausible. Because of the implications that each has for the other, the concepts of change and common ancestry are closely tied. In this light, perhaps the best general definition of evolution is Darwin's “descent with modification”.

tionship. To preevolutionists as well as some modern taxonomists, similarity is taken to be identical with relationship. In the context of evolutionary systematics, however, change and the similarities and differences resulting from it are of secondary importance. Although these qualities enable us to infer systematic relationships, emphasizing degrees of similarity or difference over common ancestry denies evolution a central role in taxonomy. Evolution (as change) may have produced the similarities and differences among living things, but basing taxonomies on these qualities does not automatically make them evolutionary. Taxonomies based on similarities and differences long predate the general acceptance of evolution. Furthermore, we have perfectly workable taxonomies of things that do not evolve. Thus, equating relationship with similarity grants biological taxonomies independence from the concept of evolution, leaving to this concept the role of an after the fact interpretation. In contrast, equating relationship with common ancestry makes systematics fundamentally evolutionary.

The passage from Ghiselin (1969) quoted above bears on the significance of similarity in evolutionary systematics. According to Ghiselin, the structure of our taxonomies is to be derived from the underlying process that imposes order, "*whether we see that order or not*" (1969, p. 83, emphasis added). Similarity turns out to be a red herring. If evolution is the underlying process that imposes order on our system, then common ancestry is what is important. Living things that share an exclusive common ancestry should be grouped together even if they are not very similar, and those that do not share an exclusive common ancestry should not be grouped together no matter how similar they are.

4.3. The Roles of Classification and Systematization in Biology. I have argued that existing biological taxonomies are classifications with a superficial evolutionary interpretation rather than systems based on phylogeny. I have also tried to outline a general framework for developing a truly phylogenetic systematics. Before continuing with examples of this approach, I want to state explicitly that I do not advocate rejecting classification in favor of systematization. Both activities have central and complementary roles in science in general and evolutionary biology in particular.

A common criticism of evolutionary theory is based on a confusion of classes and systems. It is sometimes stated that the theory of natural selection is not scientific because it is not predictive (Manser 1965; Barker 1969). For example, the theory of natural selection could not have predicted the evolution of elephants. Such criticisms are based on a confusion between classes, or universals, on the one hand and systems, which are individuals, or particulars, on the other (Hull 1974, 1978). Criticizing

evolutionary theory because it could not have predicted the evolution of elephants is like criticizing the law of gravity because it could not have predicted that Newton's apple would fall off its tree rather than being picked by the hungry scientist. General theories or laws of nature are statements about classes (Hull 1974, 1978; Ghiselin 1984, 1985). Taxa as phylogenetic systems are individuals (Hennig 1966; Ghiselin 1969, 1980, 1981, 1985; Griffiths 1974; Hull 1974; Patterson 1978). The notion that evolutionary theory is not predictive seemingly results from a historical tendency to treat taxa as classes defined by the traits of their members rather than individual portions of the tree of life.

The complementary roles of classification and systematization are evident in the testing of scientific theories. Predictions are derived from generalizations (theories) about classes and are tested using the individual members of these classes. For example, a theory about the temporal durations of different classes of species (for example, those composed of organisms with specialized diets versus those composed of organisms with generalized diets) would be tested using particular species. A class is useful in science when its members share one or more properties that are relevant to some theory. Class concepts such as autotroph, generalist, monophyletic group, and poikilotherm, are clearly important in biology. Nevertheless, these classes have a different ontological status than the individual systems that are their members.

The need for systematics arises from the hierarchical structure of the living world. Were organisms the only real entities in this world, there would be no need for systematics, for in most cases organisms are readily recognized as individuals (systems). In fact, individual is often treated as a synonym of organism (Ghiselin 1966, 1974; Hull 1978). But organisms are not the only real biological entities. If we accept that there are relationships among organisms, such as interbreeding or common ancestry, then there must be more inclusive systems that have organisms as their parts. These more inclusive individuals, however, are often impossible for humans to perceive directly, both because of our small size and brief temporal duration relative to those of individuals more inclusive than organisms and because of the nature of the relationships among their parts. Generally, we can identify these more inclusive individuals only by inference; this is systematics.

5. Towards a Truly Evolutionary Systematics. In this section I discuss four consequences of adopting a phylogenetic basis for biological systematics. The four examples differ in the degree to which they have been accepted by the community of biological taxonomists. I begin with the least controversial.

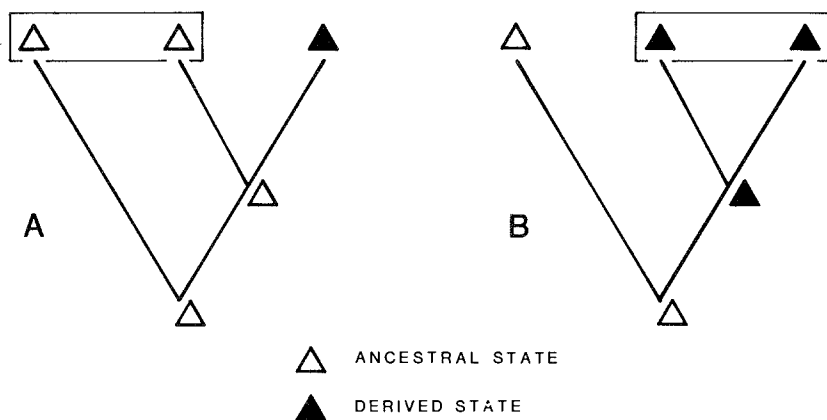


Figure 1

5.1. *The Evidence for Relationship: Synapomorphy.* One result of the axiomatization of evolution in systematics is equating the concept of relationship with common ancestry. As pointed out by Hennig (1965, 1966), this has important consequences for the way in which relationships are determined. Although classes are defined and phylogenetic relationships are inferred from observed similarities and differences among entities, only certain kinds of similarities logically provide evidence for a close common ancestry. Evolutionists have long recognized that similarities can evolve independently and that such convergences or parallelisms (homoplastic as opposed to homologous similarities) do not provide evidence of close common ancestry. Hennig (1965, 1966) pointed out that even homologous similarities (that is, ones that are shared because of inheritance from a common ancestor) do not always provide valid evidence for close phylogenetic relationship (Fig. 1). Because characters are modified during phylogeny, certain entities may be more similar in the retention of ancestral features to entities with which they share a more distant common ancestry than they are to more closely related entities that have modified characters (Fig. 1A). Hennig pointed out that among the various kinds of characters, only synapomorphies—shared, derived, homologous features—logically provide evidence of close phylogenetic relationship (Fig. 1B).

5.2. *Taxa in the Phylogenetic System.* Although Hennig's methods of phylogeny reconstruction have been widely accepted, his recommendations concerning the validity of various classes of taxa in phylogenetic taxonomies have met greater resistance. Biological taxonomists currently distinguish among three classes of taxa (Fig. 2): monophyletic, paraphy-

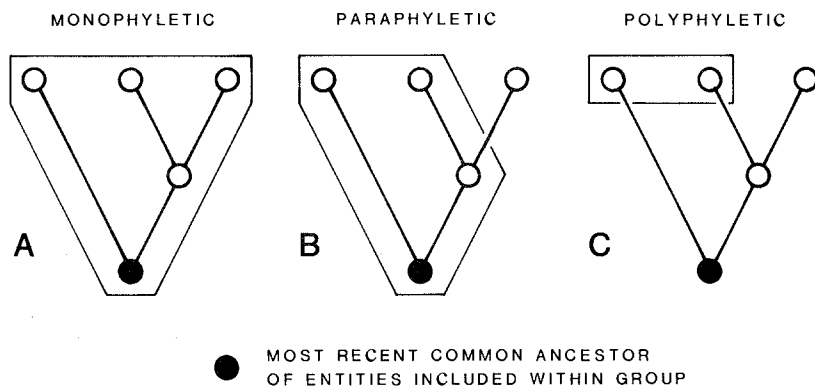


Figure 2

letic, and polyphyletic. The precise meanings of these terms vary among authors (reviewed by Wiley 1981), and I have adopted Wiley's (1981) versions of the definitions of Farris (1974) because they are straightforward and explicitly phylogenetic. A monophyletic (holophyletic) group includes a common ancestor and all of its descendants (Fig. 2A). A paraphyletic group includes a common ancestor and some but not all of its descendants (Fig. 2B). A polyphyletic group is a group in which the most recent common ancestor of the entities included within the group is not itself included within the group (Fig. 2C).

Most contemporary taxonomists who claim to practice phylogenetic taxonomy reject polyphyletic taxa, the members of which are thought to have evolved their similarities independently. Monophyletic and paraphyletic taxa are more controversial. Following Hennig, some taxonomists (so-called cladists) want to recognize only monophyletic taxa and reject paraphyletic ones. Others (so-called gradists) sometimes want to recognize monophyletic taxa but other times prefer paraphyletic ones. Thus, although many taxonomists (for example, Mayr 1974) think that birds and crocodilians shared a more recent common ancestor with one another than either did with turtles or lepidosaurs, they prefer to group crocodilians with turtles and lepidosaurs in the paraphyletic taxon *Reptilia*, which excludes birds, rather than grouping crocodilians with birds in a monophyletic taxon that excludes turtles and lepidosaurs.

The phylogenetic reality of monophyletic taxa seems unproblematic, for they are individual portions of the history of life, or complete systems of common ancestry. Although paraphyletic taxa share with monophyletic taxa the property of having a single evolutionary origin, that they fail to include some descendants of the common ancestor seriously compromises their evolutionary integrity. Paraphyletic groups are incomplete systems

of common ancestry. It is, therefore, instructive to examine justifications for recognizing paraphyletic taxa in supposedly phylogenetic taxonomies. These justifications are usually based on two kinds of arguments, (1) supposed greater overall similarity of the included entities relative to those that shared their most recent common ancestor but are not included in the taxon (for example, Ashlock 1979), or (2) supposed occupation of the same adaptive zone by the included organisms while other descendants of the same common ancestor are excluded from the taxon because they are said to have entered a new adaptive zone (for example, Mayr 1974).

The argument of similarity is simply false. Even if one could make a case for the proposition that the extant reptiles are more similar to one another than any of them is to birds, the argument of similarity inevitably breaks down when extinct forms are considered. An example is provided by *Archaeopteryx*. According to Romer, the remains of this animal “so closely resemble those of some of the smaller bipedal dinosaurs that they might well have been taken for reptiles were it not for the impressions of feathers . . .” (1966, p. 166). Similarly, Ostrom writes “In the absence of those feather impressions, I do not believe that any of the specimens of *Archaeopteryx* would ever have been recognized as avian, or even as remotely related to birds” (1976, p. 170). Nevertheless, both Romer and Ostrom considered *Archaeopteryx* to be a bird, not a reptile. Clearly similarity is not the issue. But even if the argument of similarity did not break down in practice, it still could not justify the recognition of paraphyletic taxa in phylogenetic systematics, for it is based on a false premise. Similarity is not the issue in phylogenetic systematics, the concern of which is systems whose parts are related through the underlying natural process of evolutionary descent.

The argument of similarity is sometimes stated in terms of the evolutionary process known as anagenesis, or modification within a lineage (for example, Mayr 1974). In this view, recognition of a paraphyletic taxon is justified by the claim that certain descendants of a common ancestor are not included in a taxon with its other descendants because they have undergone extensive anagenesis.⁷ This is misleading in that the real issue

⁷Mayr (1974, 1981) and Ashlock (1979) claimed that taxonomies containing only monophyletic (holophyletic) taxa neglect the dual nature of evolutionary change, in other words, that they are concerned with cladogenesis, the branching of lineages, but not with anagenesis, changes occurring within a lineage. This false accusation results from a failure to distinguish between clades (monophyletic groups) and cladogenesis (Gaffney 1979), or between cladograms and phylogenetic trees. Although the distinction was not made by earlier workers, Nelson (cited in Wiley 1979) pointed out that cladograms are more general statements than phylogenetic trees; the former depict only recency of common ancestry (or the distribution of synapomorphies), while the latter attempt to identify actual ancestors. In contrast with those of phylogenetic trees, the branchings of a cladogram do not represent cladogenetic events (Eldredge 1979). Similarly, taxonomies containing only monophyletic

is the amount of similarity or difference, which has merely been described as the result of an evolutionary process.⁸ As a variant of the argument of similarity, the argument of anagenesis is based on the same false premise: that amount of similarity, in this case stated as amount of evolutionary change, is an important consideration in evolutionary systematics. No matter how much change a lineage undergoes, it remains part of the same systems of common ancestry.

The second argument in favor of paraphyletic taxa, the argument of adaptive zone, is invariably couched in evolutionary language. This evolutionary veneer, however, merely disguises a nonevolutionary core. The term adaptive zone refers to the way of life of a group of organisms (Simpson 1953). But the way in which a group of organisms makes its living, although it can be interpreted as the result of the evolutionary process of adaptation, is not itself an evolutionary concept. Taxa based on adaptive zones are functional classes rather than phylogenetic systems. Their defining characters have merely been stated in terms of physiology, behavior, or ecology rather than morphology.

Both the argument of similarity and the argument of adaptive zone are related to the concept of the grade (for example, Huxley 1958), or level of evolutionary organization. The grade concept itself, however, is in-

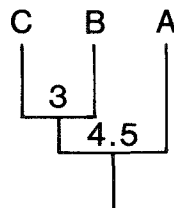
taxa are concerned directly with neither anagenesis nor cladogenesis but with recency of common ancestry.

⁸Unlike relationships of common ancestry, similarities and differences do not form a simple nested hierarchy. Griffiths (1974, citing Popper 1959) and Ghiselin (1981) give examples using a limited set of traits, but the same is also true for what has been called "overall similarity" or "phenetic relationship". For example, even though *A* may be more similar to *B* than to *C*, *B* may be more similar to *C* than to *A*. Therefore, representing phenetic relationships with tree-like branching diagrams (dendrograms) or nested hierarchies of taxa often distorts them. Phenetic relationships are more accurately represented by networks (Fig. 3). Prior to Darwin, the concept of taxonomic relationship was more or less synonymous with similarity. Stevens (1984) points out that networks were used commonly to represent taxonomic relationships in the early nineteenth century.

DIFFERENCE MATRIX

	A	B	C
A	—		
B	4	—	
C	5	3	—

DENDROGRAM



NETWORK

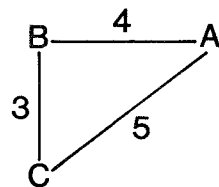


Figure 3. By averaging the *A* to *B* and *A* to *C* distances, the dendrogram, unlike the network, distorts phenetic relationships.

consistent with a basic fact of evolution. It is well known that evolution exhibits a mosaic pattern. As Mayr puts it “Every evolutionary type is a mosaic of primitive and advanced characters” (1963, p. 598), which results from unequal rates of change of different features among the descendants of a common ancestor (Mayr 1969a). The recognition of paraphyletic grades as taxa depends on emphasizing the derived traits of certain descendants (for example, birds) over those of others (for example, turtles) and, therefore, obscures the mosaic nature of evolution. The implication of paraphyletic grade taxa is that their various subgroups either did not evolve, which is simply incorrect, or that they did not evolve in an important direction, which is a subjective judgment rather than a fact of nature.⁹

The persistent recognition of paraphyletic grade taxa is perhaps the best evidence that the Darwinian Revolution has not yet occurred in biological taxonomy. Paraphyletic grades are holdovers from preevolutionary taxonomies based on the *Scala Naturae*, or great chain of being. Under this anthropocentric view, the living world was thought to be organized in a single linear hierarchy culminating in man. When taxonomies based on the *Scala Naturae* are reinterpreted in evolutionary terms, they imply in an equally anthropocentric way that evolution is a progressive process heading towards man. Those living things so unfortunate to have diverged from the lineage ultimately leading to man are relegated to some paraphyletic grade, or “level of biological improvement” (Huxley 1958, p. 27), from which the monophyletic group containing humans is said to have evolved. This is not to say that modern taxonomies are nothing more than the *Scala Naturae* interpreted in evolutionary terms. Eldredge and Cracraft (1980) point out a historical tendency to eliminate paraphyletic taxa, for example, Invertebrata and Pisces. Nevertheless, many paraphyletic taxa persist in modern taxonomies (Carroll 1984). The anthropocentrism in those taxonomies is manifest: out of the multitude of recognized paraphyletic grade taxa, not one contains *Homo sapiens*.

Grade taxa are class concepts based on defining characters (whether stated in terms of morphology or “way of life”), which, in the case of paraphyletic grades, are both ancestral and derived. Reptiles, for example, are those animals that have the derived characters of amniotes (for example, the cleidoic egg) but retain the ancestral amniote condition for those characters that have been modified in certain subgroups of amniotes (that is, mammals and birds). Retained ancestral characters, however, are uninformative about phylogenetic relationships. Furthermore, as some

⁹Similarly, the phenomenon of mosaic evolution renders inappropriate the common practice of labeling taxa as primitive or derived. Taxa possess combinations of ancestral and derived traits; only characters should be labeled primitive or derived.

reptiles shared a more recent common ancestor with birds than they did with other reptiles, the recognition of paraphyletic grade taxa obscures the actual pattern of phylogenetic relationships.

As long as taxa are viewed as classes, taxonomy will maintain independence from the concept of evolution. The identification of defining characters is central to the recognition of taxa as classes, but the presence of a character can always be interpreted as the result of some evolutionary process. Therefore, provided that the members of a taxon share one or more characters, it is logically impossible to reject any kind of grouping (monophyletic, paraphyletic, or polyphyletic) on the grounds that it is not evolutionary in this sense. Although most professed evolutionary taxonomists now reject polyphyletic taxa, they are not obligated to do so as long as they view taxa as classes. Indeed, it was not long ago that certain professed evolutionary taxonomists thought that four or five different lineages had evolved the "defining" characters of mammals independently (reviewed by Hopson and Crompton 1969), yet this did not lead to their rejection of the taxon Mammalia. Accepting evolution but leaving to it only the role of an interpretation of a taxonomy of classes does not even logically necessitate the rejection of polyphyletic groups, for convergence and parallelism are also evolutionary processes.

A third argument for the continued recognition of paraphyletic taxa was proposed by Carroll (1984), who advocated this practice partly because so many currently recognized taxa are paraphyletic. This can be viewed as an example of a general argument that considers stability to be a desirable property of a taxonomy (for example, Michener 1977). Tradition and stability are surely desirable as long as concepts are not compromised, for example, in choosing among synonymous taxon names. When these criteria are given primacy over phylogeny, however, they are implicit arguments against the Darwinian Revolution.

5.3. Definitions of Taxa in Phylogenetic Systematics. If taxa in phylogenetic systematics are not classes but individual portions of the tree of life, then they are not defined by the attributes of their component parts. How then are they defined? Phylogenetic definitions of taxa should be rooted in the concept of evolution, that is, common ancestry. Ghiselin (1985) suggests that this be done ostensibly by reference to a common ancestor and (all of) its descendants. For example, Mammalia could be defined as the most recent common ancestor of monotremes and therians (marsupials and placentals) and its descendants. Such a definition restricts Mammalia to a less inclusive group than Mammalia as conceived by most contemporary workers (T. Rowe, personal communication). If a more inclusive definition is desired, then Mammalia could be defined as all those living things that share a more recent common ancestor with mono-

tremes and therians than they do with a third taxon, which would differ depending on the desired inclusiveness of Mammalia. Although such definitions are useful only if one already knows the meanings of the terms "monotreme" and "therian", the use of words to define other words is not unique to phylogenetic definitions of taxa.

The use of phylogenetic definitions requires a knowledge of phylogenetic relationships. Some taxonomists will probably be uncomfortable with phylogenetic definitions of taxa for the reason that one can never know phylogenetic relationships with certainty. These taxonomists may prefer to define taxa with characters because the presence or absence of some character is generally less controversial than are phylogenetic relationships. In phylogenetic systematics, inferences about relationships are based on characters, and for this reason characters are said to be diagnostic rather than defining (Hull 1976; Ghiselin 1984). Because phylogenetic relationships are inferred from characters, the former must always be less certain than the latter. But this is no reason to reject phylogenetic definitions of taxa. Whoever is unwilling to accept the uncertainty of inference will simply have to refrain from systematics and be content with classification.

Using phylogenetic definitions reveals the arbitrariness of paraphyletic taxa, for they must be defined as a common ancestor and only some of its descendants, and one group of descendants can be removed as well as any other. If the justification for removal depends on the presence or absence of certain characters, whether stated in terms of morphology or "way of life", or if it depends on the amount of similarity or difference, then the justification is not based on evolution, although it can always be interpreted as the *result* of evolution.

5.4. The Species Problem and the Basic Entities of Systematics. Thus far I have been dealing with issues concerning the "higher" (that is, supraspecific) taxa. I now want to consider species. According to Dobzhansky (1976), the species problem is the oldest in biology. That it remains unsolved is evidenced by the continuing controversy over the nature of species, which can be seen in the numerous articles on this subject that have appeared in just the last few years (for example, Cracraft 1983; Kitts 1983, 1984; Willmann 1983; Bernier 1984; Holsinger 1984; Hull 1984; Kitcher 1984; Sober 1984; Vrba 1985). I do not attempt to clarify all the problems associated with species concepts. Instead, I examine the view that species are evolutionary units integrated by interbreeding, and some of the consequences that this view has for phylogenetic systematics.

Historically, the species is first a taxonomic concept. The species is the lowest mandatory categorical level in the Linnaean taxonomic hierarchy. The species is also an evolutionary concept. One outcome of the

evolutionary synthesis was an attempt to redefine the species category so that its members would be evolutionary units (Simpson 1961; Hull 1965; Mayr 1969b). Authors such as Ghiselin (1966, 1974), Hennig (1966), Hull (1974, 1976, 1978), and Wiley (1981) proposed that species be viewed as individuals, or, more specifically, integrated wholes (Ghiselin 1985), rather than as classes of similar organisms. The process conferring integration is usually identified as interbreeding, which leads to the conclusion that asexual beings do not form species (Dobzhansky 1937; Mayr 1969a; Hull 1980; Ghiselin 1985). Regardless of whether one chooses to define the term "species" with respect to interbreeding, it seems clear that asexual beings do not form larger individuals (systems) whose parts are related through this particular natural process.

That some but not all living things form supraorganismal individuals whose parts are related through interbreeding means that the pattern of common ancestry varies among different kinds of living things. This has direct relevance to phylogenetic systematics. The pattern of common ancestry sought in phylogenetic systematics is generally represented as a hierarchy of groups nested within groups, or a tree-like branching diagram (Fig. 4, left); however, when interbreeding or other forms of reticulation (for example, hybridization) are widespread, organism (and population) lineages form anastomosing networks rather than trees. In such cases, the pattern of common ancestry is more accurately represented by intersecting groups (Fig. 4, right) rather than a hierarchy of groups nested within groups. Relationships of common ancestry are accurately represented by dendrograms or nested hierarchies of taxa only when the entities being systematized form constantly diverging lineages.¹⁰ As noted by Hull (1980), the entities that form constantly diverging lineages differ for sexual and asexual beings. In asexual beings, the entities that form constantly diverging lineages exist at the level of the cell or multicellular organism. Sexual beings form more inclusive entities integrated by interbreeding. Because this mode of reproduction also results in a reticulate pattern of descent (common ancestry) among lineages of cells or multicellular organisms, the entities of sexual beings that form constantly diverging lineages exist at the level of the interbreeding community. It follows that the basic entities of phylogenetic systematics are, or should be, different for these different classes of living things. The basic elements of phylogenetic systematics should be cells or multicellular organisms for asexu-

¹⁰Lineage here refers to a single ancestor-descendant sequence (Hull 1981). The term is commonly used as a synonym of monophyletic (or even paraphyletic) group; however, although monophyletic groups originally exist as single lineages, they are often composed of multiple lineages. Lineages exist at various levels; any entities that give rise to separate entities of like kind (for example, genes, cells, multicellular organisms, populations) form lineages.

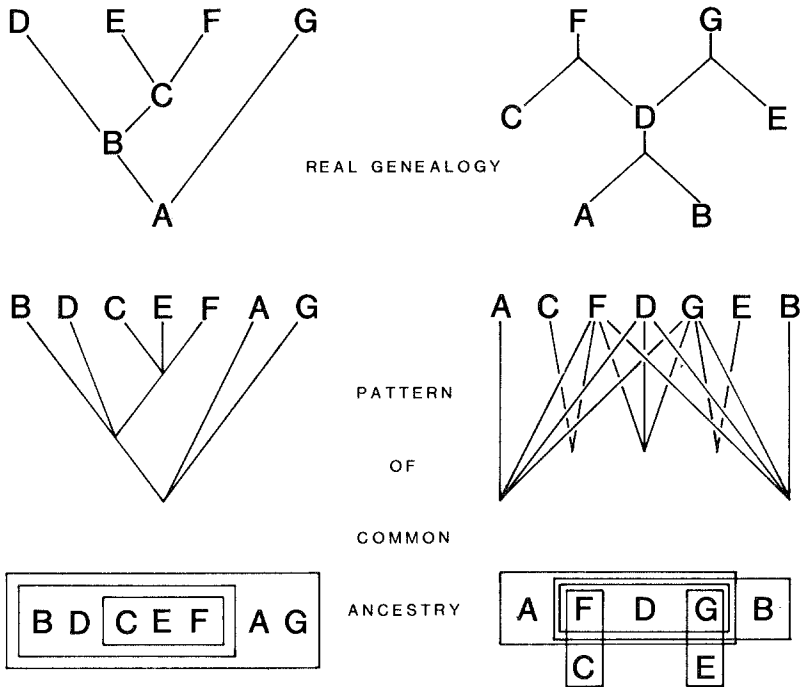


Figure 4

al beings, whereas they should be interbreeding communities of cells or of multicellular organisms for sexual beings.

Equating species with interbreeding communities would have important consequences for phylogenetic systematics. If species were viewed as evolutionary individuals integrated by interbreeding, then they would not be taxa in phylogenetic systematics; that is, they would not be systems whose existence results from the relationships of common ancestry among their parts. Instead, species would be systems whose existence depends on the natural process of interbreeding. Species of sexually reproducing beings would not be taxa in phylogenetic systematics in the same sense that organisms of asexually reproducing beings are not. Both would be basic entities among which phylogenetic relationships are sought. That such entities are often paraphyletic (Eldredge and Cracraft 1980) would not be problematic, for the requirement of monophyly applies only to taxa that are systems based on common ancestry. Furthermore, in that the species category would be based on a different underlying natural process than the category "monophyletic group", species would be qualitatively different from the "higher" taxa.

6. Conclusion. Far from being a dead field in which most of the important discoveries were made long ago, systematics is in its infancy. If a truly evolutionary systematics is to flourish, it must take the concept of evolution as an axiom rather than a superficial interpretation. This will necessitate a reevaluation of systematic concepts and the methods used to determine systematic relationships as well as the taxonomies derived from them. The beginnings of an evolutionary approach have already led to suggestions to redefine various taxonomic terms, to reject certain systematic methods, to eliminate many currently recognized taxa, and to recognize many currently unrecognized taxa. Perhaps this approach will ultimately lead to the replacement of the Linnaean taxonomic system (Griffiths 1976). In short, embracing a truly evolutionary systematics will result in drastic taxonomic changes; this is why we talk about a Darwinian Revolution.

REFERENCES

- Ashlock, P. D. (1979), "An Evolutionary Systematist's View of Classification", *Systematic Zoology* 28: 441-450.
- Barker, A. D. (1969), "An Approach to the Theory of Natural Selection", *Philosophy* 44: 271-290.
- Bernier, R. (1984), "The Species as an Individual: Facing Essentialism", *Systematic Zoology* 33: 460-469.
- Carroll, R. L. (1984), "Response to Wyss and de Queiroz", *Journal of Vertebrate Paleontology* 4: 609-612.
- Cracraft, J. (1983), "Species Concepts and Speciation Analysis", *Current Ornithology* 1: 159-187.
- Darwin, C. R. (1859), *On the Origin of Species by Means of Natural Selection*. London: John Murray.
- de Queiroz, K. (1985), "The Ontogenetic Method for Determining Character Polarity and its Relevance to Phylogenetic Systematics", *Systematic Zoology* 34: 280-299.
- Dobzhansky, T. (1937), *Genetics and the Origin of Species*. New York: Columbia University Press.
- . (1976), "Organismic and Molecular Aspects of Species Formation", in F. J. Ayala (ed.), *Molecular Evolution*. Sunderland, Mass.: Sinauer, pp. 95-105.
- Eldredge, N. (1979), "Cladism and Common Sense", in J. Cracraft and N. Eldredge (eds.), *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, pp. 165-198.
- Eldredge, N. and Cracraft, J. (1980), *Phylogenetic Patterns and the Evolutionary Process*. New York: Columbia University Press.
- Farris, J. S. (1974), "Formal Definitions of Paraphyly and Polyphyly", *Systematic Zoology* 23: 548-554.
- Gaffney, E. S. (1979), "An Introduction to the Logic of Phylogeny Reconstruction", in J. Cracraft and N. Eldredge (eds.), *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, pp. 79-111.
- Ghiselin, M. T. (1966), "On Psychologism in the Logic of Taxonomic Controversies", *Systematic Zoology* 15: 207-215.
- . (1969), *The Triumph of Darwinian Method*. Berkeley: University of California Press.
- . (1974), "A Radical Solution to the Species Problem", *Systematic Zoology* 23: 536-544.

- . (1980), "Natural Kinds and Literary Accomplishments", *The Michigan Quarterly Review* 19: 73–88.
- . (1981), "Categories, Life, and Thinking", *The Behavioral and Brain Sciences* 4: 269–313.
- . (1984), "'Definition', 'Character', and Other Equivocal Terms", *Systematic Zoology* 33: 104–110.
- . (1985), "Narrow Approaches to Phylogeny: A Review of Nine Books of Cladism", *Oxford Surveys in Evolutionary Biology* 1: 209–222.
- Gould, S. J. (1982), "Darwinism and the Expansion of Evolutionary Theory", *Science* 216: 380–387.
- Griffiths, G. C. D. (1974), "On the Foundations of Biological Systematics", *Acta Biotheoretica* 13: 85–131.
- . (1976), "The Future of Linnaean Nomenclature", *Systematic Zoology* 25: 168–173.
- Hennig, W. (1965), "Phylogenetic Systematics", *Annual Review of Entomology* 10: 97–116.
- . (1966), *Phylogenetic Systematics*. Urbana, Illinois: University of Illinois Press.
- Himmelfarb, G. (1968), *Darwin and the Darwinian Revolution*. New York: Norton.
- Holsinger, K. E. (1984), "The Nature of Biological Species", *Philosophy of Science* 51: 293–307.
- Hopson, J. A., and Crompton, A. W. (1969), "Origin of Mammals", *Evolutionary Biology* 3: 15–72.
- Hull, D. L. (1965), "The Effect of Essentialism on Taxonomy—Two Thousand Years of Stasis (II)", *The British Journal for the Philosophy of Science* 16: 1–18.
- . (1974), *Philosophy of Biological Science*. Englewood Cliffs, New Jersey: Prentice-Hall.
- . (1976), "Are Species Really Individuals?", *Systematic Zoology* 25: 174–191.
- . (1978), "A Matter of Individuality", *Philosophy of Science* 45: 335–360.
- . (1980), "Individuality and Selection", *Annual Review of Ecology and Systematics* 11: 311–332.
- . (1981), "Units of Evolution: A Metaphysical Essay", in U. J. Jensen and R. Harré (eds.), *The Philosophy of Evolution*. Brighton, Sussex: The Harvester Press, pp. 23–44.
- . (1984), "Can Kripke Alone Save Essentialism? A Reply to Kitts", *Systematic Zoology* 33: 110–112.
- Huxley, J. S. (ed.) (1940), *The New Systematics*. Oxford: Oxford University Press.
- . (1958), "Evolutionary Processes and Taxonomy with Special Reference to Grades", *Uppsala Universitets Årsskrift* 1958(6): 21–38.
- Kitcher, P. (1984), "Species", *Philosophy of Science* 51: 308–333.
- Kitts, D. B. (1983), "Can Baptism Alone Save a Species?", *Systematic Zoology* 32: 27–33.
- . (1984), "The Names of Species: A Reply to Hull", *Systematic Zoology* 33: 112–115.
- Manser, A. R. (1965), "The Concept of Evolution", *Philosophy* 40: 18–34.
- Mayr, E. (1942), *Systematics and the Origin of Species*. New York: Columbia University Press.
- . (1963), *Animal Species and Evolution*. Cambridge: Harvard University Press.
- . (1969a), *Principles of Systematic Zoology*. New York: McGraw-Hill.
- . (1969b), "The Biological Meaning of Species", *Biological Journal of the Linnean Society* 1: 311–320.
- . (1971), "The Nature of the Darwinian Revolution", *Science* 176: 981–989.
- . (1974), "Cladistic Analysis or Cladistic Classification?", *Zeitschrift für zoologische Systematik und Evolutionsforschung* 12: 94–128.
- . (1981), "Biological Classification: Toward a Synthesis of Opposing Methodologies", *Science* 214: 510–516.
- . (1985), "Darwin and the Definition of Phylogeny", *Systematic Zoology* 34: 97–98.

- Michener, C. D. (1977), "Discordant Evolution and the Classification of Allodapine Bees", *Systematic Zoology* 26: 32–56.
- Nelson, G. (1985), "Outgroups and Ontogeny", *Cladistics* 1: 29–45.
- Nelson, G. and Platnick, N. I. (1981), *Systematics and Biogeography*. New York: Columbia University Press.
- Ostrom, J. (1976), "Archaeopteryx and the Origin of Birds", *Biological Journal of the Linnean Society* 8: 91–182.
- Patterson, C. (1978), "Verifiability in Systematics", *Systematic Zoology* 27: 218–222.
- . (1982), "Morphological Characters and Homology", in K. A. Joysey and A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. London: Academic Press, pp. 21–74.
- . (1983), "How does Phylogeny Differ from Ontogeny?", in B. C. Goodwin, N. Holder and C. C. Wylie (eds.), *Development and Evolution*. Cambridge: Cambridge University Press, pp. 1–31.
- Platnick, N. I. (1978), "Gaps and Prediction in Classification", *Systematic Zoology* 27: 472–474.
- . (1979), "Philosophy and the Transformation of Cladistics", *Systematic Zoology* 28: 537–546.
- Popper, K. R. (1959), *The Logic of Scientific Discovery*. New York: Basic Books.
- Romer, A. S. (1966), *Vertebrate Paleontology*. Chicago: University of Chicago Press.
- Ruse, M. (1979), *The Darwinian Revolution*. Chicago: University of Chicago Press.
- Russell, E. S. (1916), *Form and Function*. London: John Murray.
- Simpson, G. G. (1953), *The Major Features of Evolution*. New York: Columbia University Press.
- . (1961), *Principles of Animal Taxonomy*. New York: Columbia University Press.
- Sneath, P. H. A., and Sokal, R. R. (1973), *Numerical Taxonomy*. San Francisco: Freeman.
- Sober, E. (1984), "Discussion: Sets, Species, and Evolution: Comments on Philip Kitcher's 'Species'", *Philosophy of Science* 51: 334–341.
- Sokal, R. R., and Sneath, P. H. A. (1963), *The Principles of Numerical Taxonomy*. San Francisco: Freeman.
- Stevens, P. F. (1984), "Metaphors and Typology in the Development of Botanical Systematics 1690–1960, Or the Art of Putting New Wine in Old Bottles", *Taxon* 33: 169–211.
- Vrba, E. S. (ed.) (1985), *Species and Speciation*. Pretoria: Transvaal Museum Monograph No. 4.
- Wiley, E. O. (1974), "Karl R. Popper, Systematics, and Classification: A Reply to Walter Bock and Other Evolutionary Taxonomists", *Systematic Zoology* 24: 233–243.
- . (1979), "Ancestors, Species, and Cladograms—Remarks on the Symposium", in J. Cracraft and N. Eldredge (eds.), *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, pp. 211–225.
- . (1981), *Phylogenetics*. New York: John Wiley and Sons.
- Willmann, R. (1983), "Biospecies und Phylogenetische Systematik", *Zeitschrift für zoologische Systematik und Evolutionsforschung* 21: 241–249.
- Wyss, A., and de Queiroz, K. (1984), "Phylogenetic Methods and the Early History of Amniotes", *Journal of Vertebrate Paleontology* 4: 604–608.