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**CONTEMPORARY SYSTEMATIC PHILOSOPHIES** 4001

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During the past decade, taxonomists have been engaged in a controversy over the proper methods and foundations of biological classification. Although methodologically inclined taxonomists had been discussing these issues for years, the emergence of an energetic and vocal school of taxonomists, headed by Sokal and Sneath, increased the urgency of the dispute. This phenetic school of taxonomy had its origins in a series of papers in which several workers attempted to quantify the processes and procedures used by taxonomists to classify organisms. Of special interest was the process of weighting. These early papers give the impression that the primary motivation for the movement was the desire to make taxonomy sufficiently explicit and precise to permit quantification and, hence, the utilization of computers as aids in classification (22, 23, 41, 91, 106, 107, 111, 112). The initial conclusion that these authors seemed to come to was that taxonomy, as it was then being practiced, was too vague, intuitive, and diffuse to permit quantification. Hence, the procedures and foundations of biological classification had to be changed.

The central issue in this dispute, however, has not been quantification but the extremely empirical philosophy of taxonomy which the founders of phenetic taxonomy seemed to be propounding (54, 79). The pheneticists' position on these issues is not easy to characterize because it has undergone extensive development in the last few years. The words have remained the same. Pheneticists still maintain that organisms should be classified according to overall similarity without any a priori weighting. But the intent of these words has changed. However, one thing seems fairly certain. Pheneticists believed that there was something fundamentally wrong with taxonomy as it was being practiced, especially as set out by such evolutionists as Dobzhansky, Mayr, and Simpson. Later, a third group of taxonomists, led by Hennig, Brundin, and Kiriakoff, entered the dispute, appropriating the name phylogenetic school for themselves. The evolutionists and the phylogeneticists agree that evolutionary theory must play a central role in taxonomy and that biological classification must have a systematic relation to phylogeny. They disagree only over the precise nature of this relation. For the purpose of this paper *evolutionary taxonomy* will refer to the views of the

Dobzhansky-Mayr-Simpson school and *phylogenetic taxonomy* will refer to the views of Hennig, Brundin, and Kiriakoff. Together, these two schools will be referred to as *phyleticists* in contrast to the pheneticists.

Although the emphasis of this paper will be on contemporary systematic philosophies and not on the role of quantification in taxonomy, some of the resistance which phenetic taxonomy met was due to a blanket distaste on the part of some taxonomists for mathematical techniques as such and, in particular, for the pheneticists' attempt to quantify taxonomic judgment (104, 105). When Huxley called for "more measurement" in the *New Systematics* (68), he did not have in mind the processes by which taxonomists judge affinity. It is easy to sympathize with both sides, with the biologists who were less than elated over the prospect of learning all the new, high-powered notations and techniques that were beginning to flood the literature and with the pheneticists whose work was rejected on occasion, not because the particular mathematical techniques suggested were inadequate, but because they were mathematical. Happily, this aspect of the conflict has largely abated, although pockets of resistance still remain. The question is no longer whether or not to quantify but which are the best methods for quantifying.<sup>1</sup>

Recognition should also be made of the majority of taxonomists who, though they consider themselves mildly evolutionary in outlook, feel that all such disputes over foundations and methodology are idle chatter. Taxonomy is not the kind of thing one has to talk about. One just does it. The closest approximation to a spokesman for this group is R. E. Blackwelder, but he is atypical of the majority for which he speaks since he still advocates essentialism in almost its pristine, Aristotelian form (7-13, 15, 121-123). The inadequacy of essentialism as a philosophical foundation for biological classification has been discussed so extensively that nothing more needs to be said here (63, 65, 83, 86).

Not only will this paper be limited to the philosophical aspects of the phenetic-phyletic controversy, but also, of the various issues which have been raised, it will deal with only two—the relation of phylogeny to classification and the species problem. Many of the objections raised against evolutionary taxonomy are actually criticisms of the synthetic theory of evolution, rather than of the classifications built upon it. Nor are these criticisms of recent origin. Every objection raised by the pheneticists to evolutionary theory and evolutionary taxonomy can be found in the work of earlier biologists, usually in the writings of the evolutionists themselves. The difference is that the evolutionists are optimistic about the eventual resolution of these difficulties, whereas the pheneticists, in the early years of the school, believed that they were insoluble. When viewed in the context of the development of biology during the past thirty years, phenetic taxonomy does not appear so much a recent insurrection as the culmination of long-standing grievances.

<sup>1</sup> For those interested in a review of the numerical aspects of the phenetic-phyletic controversy, I recommend Johnson (73).

Soon after the turn of the century, both taxonomy and evolutionary theory had reached a low ebb in the esteem of the rest of the scientific community. Taxonomists seemed to be engaged in a frenzy of splitting and were viewed as nit-picking, skin-sorters, more as quarrelsome old librarians than scientists. Evolutionists had indulged themselves in reconstructing phylogenies in far greater detail and scope than the data and theory warranted and were looked upon as uncritical speculators, more authors of science fiction than science. Among evolutionists themselves, there were controversies. Were the laws of macroevolution different from those of microevolution? Was there such a thing as orthogenesis and, if so, what were the mechanisms for it? At this critical period, Mendel's laws were rediscovered, but instead of clarifying the situation, the birth of modern genetics confused it even further. A whole series of prejudices, conceptual confusions, and peculiarly pernicious terminologies made it seem as if the new genetics conflicted with evolutionary theory. Adding to the intensity of the controversy was the fact that evolutionists tended to be museum and field workers, whereas geneticists were, by and large, experimentalists at home in the laboratory. It was in this setting that the synthetic theory of evolution and the New Systematics had their inception.

The initial impetus for the rebirth of evolutionary theory was Fisher's *The Genetical Theory of Natural Selection* (49), followed by similar works by Haldane (58) and Wright (130, 131). In these works it was shown that a mathematical model of evolutionary theory could be constructed in which the genetic mechanisms of Mendelian genetics meshed perfectly with the selective mechanisms of evolutionary theory. Evolutionary theory and, hence, evolutionary taxonomy had become respectable again. However, the models supplied by Fisher, Haldane, and Wright were highly restrictive and very far removed from any situation a naturalist was likely to encounter in nature. Using the techniques of idealization which had proved so successful in physics, they showed that in certain overly simple, ideal cases, natural selection working on mutations which obeyed the laws of Mendelian genetics could result in the gradual evolution and splitting of species. The task still remained of showing how the insights gained in these idealizations could be applied to real situations in nature.<sup>2</sup> The classic works on this are those by Dobzhansky (37), Mayr (80, 85, 86), Huxley (68, 69), Simpson (99, 100, 102, 103), Rensch (94, 95), Stebbins (120), Hennig (60, 61), and Remane (93). In the following discussion, the earliest works of these authorities will be cited as freely as their later works because the basic features of the synthetic theory of evolution and evolutionary taxonomy have changed very little during this period.

#### PHYLOGENY AND CLASSIFICATION

One of the most persistent problems in biology has been the quest for a

<sup>2</sup>For a more realistic, formal axiomatization of evolutionary theory, see Williams (129).

natural classification. Prior to Darwin a natural classification was one based on the essential natures of the organisms under study. Of the possible patterns that could be recognized in nature, a taxonomist would settle on one, partly because of his own peculiar psychological make-up and partly because of the scientific theories he held. Of course, another taxonomist with a different psychological make-up, perhaps holding different theoretical views, frequently recognized a different pattern. The controversies that ensued were usually settled by force of authority. The case of Cuvier and his disciples Owen and Agassiz is typical in this respect (83). There are four basic plans in the animal kingdom, no more, no less!

Evolutionary theory promised to put an end to all this dogmatic haggling. After Darwin a natural classification would be one that was genealogical. No longer would biologists have to search fruitlessly for some ideal plan but would need only to discover the genealogical relationships among the organisms being studied and record this information in their classifications. The alacrity with which many biologists adopted Darwin's suggestion stemmed in part from two illegitimate sources—an inherent vagueness in the proposal and a misconception of the relation which any system of indented, discontinuous words can have to something as continuous and complex as phylogeny. As Darwin (34) observed of Naudin's simile of a tree and classification, "He cannot, I think, have reflected much on the subject, otherwise he would see that genealogy by itself does not give classification." Nearly a century later Gilmour (56) was still forced to remark that he doubted "whether the real significance of the term 'phylogenetic relationship' is yet fully understood."

The purpose of this section will be to investigate the relationships which phylogeny can have to biological classification—assuming that phylogeny can be known with sufficient certainty. The major criticism of evolutionary taxonomy by pheneticists has been that such reconstructions are too often impossible to make. Discussion of this criticism will be postponed until the next section.

No term in taxonomy seems immune to ambiguity and misunderstanding; this includes the term *classification*. Mayr (86) has already pointed out the process-product distinction between the process of classifying and the end product of this enterprise—a classification. But even the words *a classification* are open to misunderstanding. At one extreme, a classification is nothing but a list of taxa names indented to indicate category levels. Others would also include all the characters and the taxonomic principles used to construct a classification as part of the classification. At the other extreme, some authors use the words *a classification* to refer to the entire taxonomic monograph. Unless otherwise stipulated, *a classification* in the following pages will be used in the first, restricted sense.

The simplest view of the relation of a biological classification to phylogeny is that, given a classification, one can infer the phylogeny from which it was derived. One source of this misconception is a naive yet pervasive mis-

construal of the relation between a hierarchical classification and a dendritic representation of phylogeny. According to this mistaken view, the classification of Order I sketched below

Order I

Family A

Genus 1

species a

Genus 2

species b

species c

Genus 3

species d

species e

species f

Family B

Genus 4

species g

species h

Genus 5

species i

species j

corresponds to the phylogenetic tree in Figure 1. However, Figure 1 is not a dendritic representation of a possible phylogeny. Rather it is merely a representation of the hierarchic indentations of the classification in a dendritic form. A true dendrogram of the possible phylogenetic development of the organisms involved would consist only of the species listed in the classification. One possible phylogeny from which the classification of Order I could have been derived is shown in Figure 2.

In this section we assume the phylogenetic development of the groups under discussion to be completely known. Hence, all the ancestral species are included in the classification along with extant species. In actual classifications, of course, not all ancestral species are known, but at least some are. At least sometimes, biological classifications contain reference to extinct forms. Hence, the interpretation of I in Figure 1 as the unknown stem species which gave rise to Order I, of *A* and *B* as the unknown stem species which gave rise to Families *A* and *B* respectively, and so on, cannot be carried through consistently. On occasion, at least, ancestral species will be known and will be included in the classification. The mistake is to confuse the inclusion relations in the taxonomic hierarchy with species splitting (103). An order does not split into genera nor genera into species.

A second impediment to seeing clearly the relation between phylogeny and classification has been a failure to distinguish cladistic from patristic

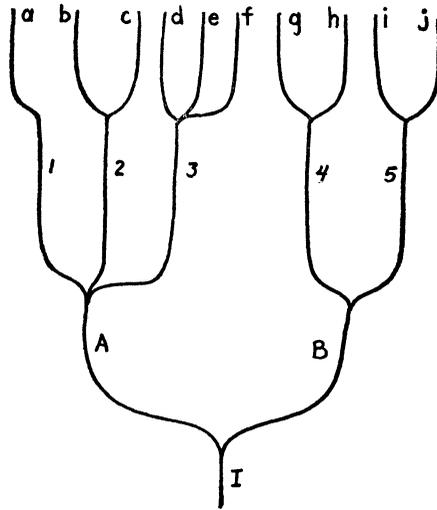


FIGURE 1. A dendritic representation of a hierarchical classification.

relations (2, 5, 23, 75, 76, 84, 89, 115, 116). The primary difference between the phylogenetic school of Hennig, Kiriakoff, and Brundin and the evolutionary school of Dobzhansky, Mayr, and Simpson is that the former want classification to reflect only cladistic affinity, whereas the latter feel that classification should also reflect such factors as degree of divergence, amount of diversification, or in general, patristic affinity.

Hennig's principles of classification are extremely straightforward (60, 61). The stem species of every single higher taxon must be included in that taxon and must be indicated as the stem species by not being included in any of the other subgroups of that taxon. Splitting is the only mechanism of species formation that is recognized. Even though a group may evolve progressively until later members are extremely divergent from their ancestors, if no splitting has taken place, all the individuals are considered members of the same species. Upon splitting, the parental species is always considered to be extinct, even though individuals may persist which are morphologically identical to members of the parent species. As far as ranking is concerned, sister groups must always be given coordinate ranks. In addition, Hennig is predisposed to Bigelow's (2-5) observation that in a truly phylogenetic classification recency of common ancestry must be considered a criterion for ranking. Taxa that evolved earlier should be given a higher taxonomic rank than those that evolved later.

The major consequences of the adoption of these principles of classification is precisely the one intended by Hennig. Given a strictly phylogenetic classification, cladistic development can be read off directly. That is, given a classification and Hennig's principles, a dendrogram could be constructed

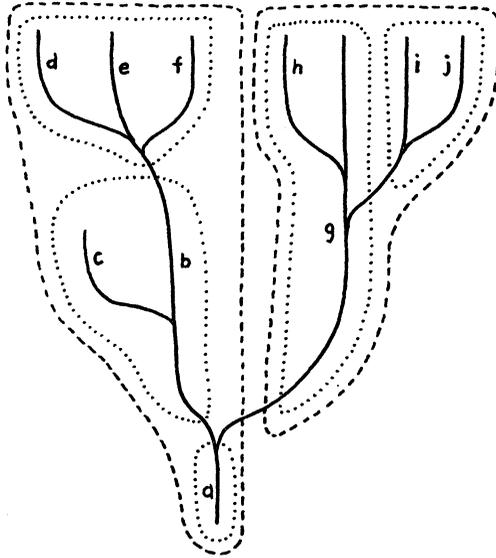


FIGURE 2. A phylogenetic tree subdivided into taxa.

which would accurately represent the cladistic relations of the groups classified. Hennig's principles of classification have something esthetically satisfying about them. They are straightforward and exceptionless. But this satisfaction is purchased at a price higher than many biologists are willing to pay. Early groups, even if they immediately became extinct without leaving descendants, would have to be recognized as separate phyla, equivalent to highly diversified, persistent groups. Hence, if it could be shown that a species split off in the Precambrian but gave rise to no other species, it nevertheless would have to be classed as a phylum. The resulting classification would be exceedingly monotypic. Our increasing ignorance as phylogeny is traced further back through the geological strata saves phylogeneticists from actually having to introduce such extreme asymmetries into their classification, but even so, enough is known so that classifications erected on the purely cladistic principles of the Hennig school would be much more asymmetrical than those now commonly accepted. Evolutionists also complain that the Hennig school is too narrow since it limits itself just to cladistic affinity. Patristic affinity is also important. Thus, for both practical and theoretical reasons, the evolutionists feel that Hennig's solution to the problem of the relation between phylogeny and classification is unacceptable.

When we turn our attention to evolutionary taxonomy, the situation is not so straightforward. The principles of evolutionary taxonomy are extremely fluid and intricate. As Simpson (103) has said, the practice of evolutionary taxonomy requires a certain flair. There is an art to taxonomy. Vagueness as to the actual relation which evolutionary classification is to

have to phylogeny can be discerned in the earliest statements on the subject. The main purpose of Dobzhansky's *Genetics and the Origin of Species* (37) was to reconcile the differences between naturalists and geneticists: to convince the naturalists that the geneticists' experimental findings in the laboratory were relevant to their work in the field and museum, and to convince the geneticists that their understanding of evolutionary theory was grossly inadequate. Dobzhansky is not a systematist and is not especially interested in the problems of systematics. The little that Dobzhansky (37) had to say about classification can be quoted in its entirety.

A knowledge of the position of an organism in an ideal natural system would permit the formation of a sufficient number of deductive propositions for its complete description. Hence, a system based on the empirically existing discontinuities in the materials to be classified, and following the hierarchical order of the discontinuous arrays, approaches most closely to the ideal natural one. Every subdivision made in such a system conveys to the student the greatest possible amount of information pertaining to the objects before him. The modern classification of organisms uses the principles on which an ideal system could be built, although it would be an exaggeration to think that the two are consubstantial.

On the other hand, since the time of Darwin and his immediate followers the term "natural classification" has meant in biology one based on the hypothetical common descent of organisms. The forms united together in a species, genus, or phylum were supposed to have descended from a single common ancestor, or from a group of very similar ancestors. The lines of separation between the systematic categories were, hence, adjusted, at least in theory, not so much to the discontinuities in the observed variations as to the branching of real or assumed phylogenetic trees. And yet the classification has continued to be based chiefly on morphological studies of the existing organisms rather than of the phylogenetic series of fossils. The logical difficulty thus incurred is circumvented with the aid of a hypothesis according to which the similarity between the organisms is a function of their descent. In other words, it is believed that one may safely base the classification on studies on the structures and functions of the organisms existing at one time level, in the assurance that if such studies are made complete enough, a picture of the phylogeny will emerge automatically. This comfortably complacent theory has received some rude shocks from certain palaeontological data that cast a grave doubt on the proposition that similarity is always a function of descent. Now, if similar organisms may, however rarely, develop from dissimilar ancestors, a phylogenetic classification must sometimes unite dissimilar, and separate similar, forms. The resulting system will be, at least in some of its parts, neither natural in the sense defined above nor convenient for practical purposes.

Fortunately, the difficulty just stated is more abstract than real. The fact is that the classification of organisms that existed before the advent of evolutionary theory has undergone surprisingly little change in the times following it, and whatever changes have been made depended only to a trifling extent on the elucidation of the actual phylogenetic relationships through palaeontological evidence. The phylogenetic interpretation has been simply superimposed on the existing classifications; a rejection of the former fails to do any violence to the latter. The subdivisions of the animal and plant kingdoms established by Linnaeus are, with few exceptions, retained in the modern classification, and this despite the enormous

number of new forms discovered since then. These new forms were either included in the Linnaean groups, or else new groups were created to accommodate them. There has been no necessity for a basic change in the classification. This fact is taken for granted by most systematists, and all too frequently overlooked by the representatives of other biological disciplines. Its connotations are worth considering. For the only inference that can be drawn from it is that the classification now adopted is not an arbitrary but a natural one, reflecting the objective state of things.<sup>3</sup>

To begin with, the position of an organism in a hierarchical classification permits the inference of numerous propositions about it only if the characters used to classify the organisms are also listed. For example, knowledge that an organism is a chordate in conjunction with the defining characters of Chordata permits the inference that at some time in its ontogenetic development it has gill slits, a dorsal, hollow nerve cord, and probably a notochord. Knowledge that it is a vertebrate in conjunction with the defining characters of Vertebrata and the fact that Vertebrata is included in Chordata permits additional inferences and so on. A claim frequently made in the recent literature is that the best classification is the one with the highest information content; that is, the one which permits the greatest number of inferences. Colless (31), for example, says:

The current conflict between the "phenetic" and "phylogenetic" approaches to taxonomy thus boils down to whether a classification should in some fashion act as a storage-and-retrieval system for information about the distribution of attributes over organisms, and thus as a theory that predicts unexamined parts of that distribution: or whether it should reflect, as closely as possible, the historical course of evolution of the organisms concerned.

What is being blurred in the preceding quotation is that a biological classification as such (whether phenetic or phyletic) permits little in the way of inferences. Only a classification in conjunction with the principles and characters used to construct it is sufficient to permit any extensive inferences about the organisms being classified. For example, given the phenon levels of a phenetic classification, it is possible to infer that members of two taxa at a particular phenon level share a certain percentage of their characteristics, but it is not possible to infer which these may be. Similarly, from an evolutionary point of view, it would be reasonable to infer that two organisms classed together at the 40 phenon level are likely to have a more recent common ancestor than two organisms which are not classed together until the 10 phenon level—if one were given just this information.<sup>4</sup> Only when the

<sup>3</sup>Dobzhansky condenses the preceding discussion to about half its length in the 3rd edition of his work and Mayr quotes the final paragraph in his *Systematics and the Origin of Species* (80).

<sup>4</sup>One of the most persistent problems in taxonomy has been the explication of the notion of "similarity" which is to be some function of descent. An analysis of this concept must be postponed until the next section.

characteristics used to partition the organisms into taxa are included can specific predictions be made about which organisms are likely to have which characters. But with the addition of such information, we are rapidly approaching the point at which the word *classification* has become expanded to include the entire monograph. Classifications in the narrow sense are incapable of storing much in the way of specific information. Rather than being storage-and-retrieval systems themselves, they serve as indexes to such storage-and-retrieval systems. The information resides in the monograph, not in the classification (128). The classification merely provides a nested set of names which can be used to refer to the relevant taxa in as felicitous a manner as possible.

A second basic misunderstanding concerning the relation between a classification and a phylogeny has contributed to the belief that phylogeny can be inferred from an evolutionary classification. One commonly meets the assertion that proximity of names in a classification implies propinquity of descent. A glance back at Figure 2 shows that this belief is mistaken. If our knowledge of phylogeny were reasonably complete, every single higher taxon would contain at least one species which would be as closely related to a species in another taxon of the same rank as it is to its closest relative in its own taxon. For example, in the classification sketched on p. 25, species *a* is twice removed from species *b* (species *b* appears two lines below species *a*) and nine places removed from species *g* (species *g* appears nine lines below species *a*)—and yet both of these species are directly descended from *a* (see Figure 2).

When stated so baldly, the claim that inferences concerning propinquity of descent can actually be made from an evolutionary classification seems incredible; yet such a view is implicit in the writings of many phyleticists. From an evolutionary classification, even in conjunction with the stated criteria of classification, implications of cladistic relations are not possible. With a reconstructed phylogeny, indefinitely many classifications are possible. With any one of these classifications, an indefinite number of phylogenies are compatible. As Mayr has observed, "Even if we had a perfect understanding of phylogeny, it would be possible to convert it into many different classifications" (86; see also 14, 62, 103). Of course, one way to falsify these claims is to expand the meaning of a *classification* to include phylogenetic dendrograms. Then, in a trivial sense, phylogeny can be inferred from an evolutionary classification.

Note that not all classifications are acceptable to an evolutionist. For example, all taxa must be "monophyletic." Each taxon can "contain only the descendants of a common ancestor." Early in the history of evolutionary theory, this meant that all the members of a taxon had to be descended from at most a single individual or pair of individuals in an immediately ancestral taxon. As the emphasis in evolutionary theory shifted from individuals to populations and species, the principle of monophyly was expanded so that descent from a single immediately ancestral species was all that was necessary for a taxon to be monophyletic. Hennig and the phylogenetic school

still retain this rather stringent notion of monophyly. Unfortunately, if this principle is adhered to, many well-known and easily recognizable taxa such as the mammals (à la Simpson) become polyphyletic. The compromise suggested by Simpson (101, 103), and Gilmour (56) before him, is that all the members of a taxon may be descended, not from a single, immediately ancestral species, but from a single, immediately ancestral taxon of the same or lower rank. (For opposing views, see 32.) Thus, since all the species which contributed to the class Mammalia were in all likelihood therapsid reptiles, Mammalia is minimally monophyletic. As reasonable as this decision seems from the point of view of retaining well-marked groups and reflecting degree of divergence, its adoption further weakens the relation between classification and phylogeny. Not all classifications are compatible with a given phylogeny, but too many to permit any precise inferences.

Numerous authors before and after Dobzhansky (37) have observed that, from their classifications alone, "it is practically impossible to tell whether zoologists of the middle decades of the nineteenth century were evolutionists or not." Evolutionists have taken this fact to imply that pre-evolutionary taxonomists had been reflecting evolution in their classifications all along, though unwittingly. Pheneticists have argued for an additional factor. Classifications, before and after the introduction of evolutionary theory, are basically phenetic. Evolutionary theory, for all intents and purposes, is irrelevant to biological classification. It has been argued in this section that a third factor is actually responsible for the similarity between pre- and post-evolutionary classifications. Hierarchical classifications, in the absence of a rigid adherence to principles of classification like those of Hennig, do not permit any extensive inferences—whether phyletic or phenetic. Hennig says that hierarchic classifications are completely adequate to indicate phylogeny because he has incorporated the requirements of hierarchic classification into his principles of classification. From a strictly phylogenetic classification (just a list of indented names of taxa) and Hennig's principles, cladistic relations can be deduced. To the extent that this is not done, to that extent the number and variety of phylogenetic inferences which can be drawn from a classification will be diminished (28, 62, 125, 126).

Thus, biologists who maintain that biological classifications should be genealogical are presented with a dilemma. If they adopted a system like Hennig's, in which cladistic development is inferable from a classification, they would have to put up with the loss of information about patristic affinities and the cumbersome classifications that would result. If they retained the more tractable classifications that result from the more pliant principles of evolutionary taxonomy, they would have to abandon the ideal that classifications imply anything very precise about phylogenetic development. Evolution and evolutionary theory would still influence evolutionary classifications, but mainly in decisions as to homologies and the basic units of classification. The way in which evolutionary theory influences estimations of homologies will be discussed in the next section. The relation between evolutionary theory and the basic units of classification will be treated in the last section.

### PHYLETIC INFERENCES AND PHENETIC TAXONOMY

In the preceding section, certain formal difficulties inherent in any attempt to establish a systematic relationship between classification and phylogeny were pointed out. The main thrust of the pheneticists' objections to evolutionary taxonomy, however, has been against permitting phylogeny to influence biological classification in the first place. The chief reasons that the pheneticists have given for excluding evolutionary considerations from biological classification are as follows: 1. We cannot make use of phylogeny in classification since, in the vast majority of cases, phylogenies are unknown (3, 4, 6, 43, 119). 2. The methods which evolutionists use to reconstruct phylogeny, when not blatantly fallacious, are not sufficiently explicit and quantitative (6, 45, 115, 119). 3. With the help of techniques being developed by the pheneticists, it eventually may be possible to reconstruct reasonably accurate phylogenies for certain groups of organisms, but since phylogeny cannot be known with sufficient certainty for all groups, it should not be used in those few cases in which we do have good reconstructions (6, 24, 115, 119). 4. Even if the necessary evidence were available for all groups and the methods of reconstructing phylogeny were reformulated to make them completely acceptable, the resulting evolutionary classification would still be a special purpose classification and inadequate for biology as a whole; a general purpose classification would still be needed (55-57, 108-110, 119).

Like other criticisms of evolutionary taxonomy, these are not new. As early as 1874, Huxley (70), hardly an enemy of evolution, can be found saying, "Valuable and important as phylogenetic speculations are, as guides to, and suggestions of, investigation, they are pure hypotheses incapable of any objective test; and there is no little danger of introducing confusion into science by mixing up such hypotheses with Taxonomy, which should be a precise and logical arrangement of verifiable facts."

There is little that a philosopher can say about the first two objections to evolutionary taxonomy. After obvious inconsistencies have been removed and warnings about the type of certainty possible in empirical science duly intoned, the controversy becomes largely an empirical matter to be decided by scientists, not philosophers (64, 66). If extensive fossil evidence for a group is necessary for reconstructing the phylogeny of that group, then the phylogenetic development of a majority of plants and animals will never be known, but many biologists think that various laws (or rules of thumb, if you prefer) can be used to reconstruct tentative phylogenies even in the absence of more direct evidence (85, 103, 124).

An interesting development in the phyletic-phenetic controversy is that some numerically minded biologists are beginning to set out formalisms for inferring phylogeny which they feel fulfill the various criteria of objectivity, etc., which more traditional methods are reputed to lack (22-24, 27, 40, 47, 48, 77, 91, 112, 118, 126). Implicit in this endeavor is the conviction that

attempts to reconstruct phylogeny even in the absence of fossil evidence are not inherently fallacious. Perhaps the practice of some evolutionists has been slipshod and certain reconstructions of the methods by which phylogenies are inferred have been mistaken, but the phyletic enterprise as such is not hopeless. For example, Colless (30) says, "I must stress at the outset that I am *not* denying that we can, and do, have available a body of reasonably credible phylogenies, which are probably fair reproductions of historical fact. I do, however, assert that some influential taxonomists have an erroneous view of the process by which such phylogenies are inferred; and, if my view is correct, such a situation clearly invites faulty inferences and sterile controversy."

Initially, phenetic and evolutionary taxonomy were treated by all those concerned as if they were in opposition to each other (84, 90, 108, 115, 116). Pheneticists argued that evolutionary classifications, based on a priori weighting, were limited in their uses because they were biased toward a single scientific theory. Phenetic classifications, on the other hand, were general purpose classifications, based on the total number of unweighted or equally weighted characters, and were equally useful to all scientists because they were biased toward no scientific theory whatsoever. Pheneticists like Cain (18-21) attributed the mistakes which early taxonomists like Aristotle, Linnaeus, and Cuvier made to their letting theoretical and philosophical beliefs affect their classifications. Evolutionists had carried on in this misbegotten tradition. To eliminate such errors, pheneticists argued that no theoretical considerations should enter into the initial stages of a purely phenetic classification. A pheneticist must classify as if he were completely ignorant of all the scientific achievements (and failures) which preceded him. Characters must be delineated, homologies established, and clusters derived without recourse to any preconceived ideas whatsoever. No character could be weighted more heavily than another because it proved to be a "good" character in previous studies (unless those studies themselves were phenetic) or because the studies were theoretically important according to current scientific theories. There must be no a priori weighting! Later, after several such purely phenetic studies had been run, certain characters would be found that tended to covary. They then could be weighted a posteriori. This a posteriori weighting would be, however, purely a function of the observed covariations of the characters being studied, not of any theoretical considerations. Finally, evolutionary interpretations could be placed on these purely phenetic classifications which would transform them into special purpose evolutionary classifications. In short, phenetic taxonomy was just look, see, code, cluster.

This initial sharp contrast between evolutionary and phenetic classification has been modified considerably in recent years. In their latest utterances, pheneticists tend to view phenetic taxonomy somewhat differently. Doubts are raised as to whether any pheneticist ever held the views described above. Purely phenetic studies are still considered necessary prelimi-

naries to scientific endeavors of any kind, including the construction of evolutionary classifications, but these phenetic studies are no longer thought of as being performed in isolation from all scientific theories—just from evolutionary theory. Homologies are not established just by observation, but are inferred via relevant genetic, embryological, physiological, and other scientific theories. Prior to any phenetic study, decisions are made as to which characters are to be considered the same, and in what sense they are to be so considered. For example, two organs which are structurally very similar in adult forms might be considered different organs because they have decidedly different embryological developments. Phenetic taxonomy is a matter of look, see, infer, code, and cluster. The resulting phenetic classifications are general purpose classifications because they have been constructed using all available knowledge, including all well-established scientific theories—except evolutionary theory. Finally, evolutionary interpretations can be placed on these phenetic classifications, but if the phenetic classification is properly constructed to begin with, it will actually be an evolutionary classification. Hence, phenetic and evolutionary classifications, when properly constructed, are equivalent to each other and are equally general purpose classifications.

It will be the purpose of this section to trace the change in phenetic taxonomy from its early, antitheory stage to its current state and to point out the fallacies in the early phenetic position which made it seem attractive and the reasons for changing it. It will be argued that purely phenetic classifications, as they were originally explicated, are impossible and that even if they were possible, they would be undesirable. To the question “Theory now or theory later?” only one answer is possible. The two processes of constructing classifications and of discovering scientific laws and formulating scientific theories must be carried on together. Neither can outstrip the other very far without engendering mutually injurious effects. The idea that an extensive and elaborate classification can be constructed in isolation from all scientific theories and then transformed only later into a theoretically significant classification is purely illusory. A priori weighting of the theoretical kind is not only desirable in taxonomy, it is necessary. The price one pays for theoretical significance is, obviously, that any change or abandonment of the theories which gave rise to the classification will necessitate corresponding changes in the classification (52, 53, 67, 68, 69).

There is less to criticize in the latest versions of the phenetic position. One still must question why, of all scientific theories, evolutionary theory must be scrupulously excluded from the process of biological classification. There may be reasons for such a rejection, but the pheneticists have not been very articulate in stating them. Most of the objections which they have raised against evolutionary theory would count equally against any scientific theory and must be interpreted as utterances stemming from their early, antitheory stage of development. Now that pheneticists are willing to accept the role of theory in science, it would be helpful if they were to spell out exactly what faults they still find with evolutionary theory. A final question

must also be asked before we turn to a detailed analysis of the evolution of phenetic taxonomy. What was all the controversy about? Except for a greater emphasis on making taxonomic practice explicit and perhaps even quantitative, how does phenetic taxonomy differ from evolutionary taxonomy? If patristic affinity is equivalent to some function of phenetics, chronistics, and cladistics, why all the acrimony? Has the phenetic-phyletic controversy been just one extended terminological confusion?

That the pheneticists actually held the early views attributed to them can easily be demonstrated. For example, as late as 1965, Sokal, Camin, Rohlf & Sneath (116) can be found saying, "Numerical taxonomists *do not disparage* interpretation or speculation or the inductive-deductive method in science. They simply feel that the process of constructing classification should be as free from such inferences as possible. . . ." (See also 18-23, 29, 30, 39, 115, 116.) According to Colless (30), phenetic taxonomy makes reference "only to the observed properties of such entities, without any reference to inferences that may be drawn *a posteriori* from the patterns displayed. Such a classification can, and, to be strictly phenetic *must*, provide nothing more than a summary of observed facts." Even in their most recent publications, pheneticists can still be found making such extremely empirical claims; for example, Sokal (114) says that taxonomy is "the grouping of like organisms based on direct observation."

The key notion in the empiricist philosophy is the claim that, ideally, a priori weighting is to be completely expunged from taxonomic practice. What pheneticists have intended by such interdictions has been extremely equivocal. At one extreme they claim that homologies must be established on the basis of pure observation (as if there were such a thing). Two instances of a character are instances of the same character if they look, smell, taste, sound, and feel the same; otherwise not. Systematics "is a pure science of relation, unconcerned with time, space, or cause" (15). All operational homologies are observational homologies.

So far no pheneticist has produced anything like a strict phenetic classification as described above. Pheneticists make reference to things like wings, antennae, anal gills, dorsal nerve cords, enzymes, and nucleotides. These are hardly pure observation terms. They presuppose all sorts of previous knowledge of a highly theoretical kind. For example, a taxonomist working on brachiopods today describes his specimens and forgets that at one time considerable effort was expended to decide whether brachiopod valves were front and back, dorsal and ventral, or right and left and that the eventual decision reached was based on various theoretical beliefs concerning their ontogenetic and phylogenetic development (35). As Sneath (108) has observed, "Many taxonomic problems start part of the way along the classificatory process, and one is apt to forget what previous knowledge is assumed."

Pheneticists take this to be a fault with traditional taxonomy rather than a characteristic of all scientific undertakings, including their own. They think that, ideally, a purely descriptive, nontheoretical classification must be

possible. The source of the persuasiveness of this view can be found in empiricist epistemology, according to which all empirical knowledge stems from sense impressions. Hence, all knowledge must be reducible to pure observation statements. Empiricists themselves have shown that such a reduction is impossible and, specifically, that scientific theories are not replaceable by sets of observation statements (59). There remains the metaphysical compulsion to believe that such a reduction must be possible, and with it, the notion of a purely phenetic classification.

At times pheneticists are a little more liberal in their interpretation of what is to count as a priori weighting. For example, Colless (29) says, "Of course, the simple act of observation of 'existing' entities involves inferences, but they are of a primitive nature and, I believe, can be clearly distinguished from those which I am concerned to exclude." But how primitive is primitive enough? What criteria does Colless have for making this distinction? And why are primitive a priori weightings acceptable but sophisticated ones illegitimate?

There is a continuum between terms that are largely observational, like white precipitate, flammable fluids, and red appendage, and those that are more theoretical, like inertia, unit charge, and selection pressure. The reason why pheneticists want classifications to be constructed using those terms nearer the observational end of the scale is all too apparent. Time and again Cain (18-21) has argued that the greatest source of error in early classifications is their reliance on scientific theories which we now know to be erroneous. Wouldn't the safest procedure be to classify neutrally? That way theories could come and go and the classification, nevertheless, remain unchanged. Such a procedure would assuredly be safe, but in the extreme it is impossible to accomplish and in moderation undesirable.

The basic fallacy underlying the phenetic position on a priori weighting is the confusion of the logical order of epistemological reconstructions with the temporal order in actual scientific investigations (50). Perhaps an analogous example from a different discipline will help to bring this fallacy into sharper focus. In the epistemological approach advocated by Sneath (108), a classification of inorganic substances must begin with purely phenetic studies in which samples are collected of a wide variety of inorganic substances, purely observational homologies established, and various clustering techniques used to group these substances into OTUs. Certain characters might then turn out to be good indicators of certain clusters and weighted more heavily for future runs. Eventually, a classification would emerge which would be equally useful for all purposes. Later, if one wished, this general purpose classification could be transformed into a special purpose classification by introducing atomic theory and weighting atomic number more heavily than all other characters put together.

The actual history of the construction of the periodic table does not, of course, read anything like this epistemological reconstruction. For example, gold was originally recognized and defined in terms of its color, malleability, weight, and so on—a characterization inadequate to distinguish gold from

various alloys. Thus, Archimedes was presented with the problem of discovering a more important characteristic of gold. He hit upon specific density. What we tend to forget is that his selection of specific density rather than a host of other characters was his acceptance of the physics of his day in which the four elements were fire, air, earth, and water! Later, as physical theory developed, atomic weight replaced specific density as the key character in distinguishing inorganic substances. In the interim a new concept of element had evolved in the context of atomic theory. Not until atomic number replaced atomic weight could elements, in this new sense, be distinguished from each other and from compounds.

The analogy to the development of evolutionary theory and the species concept is obvious. The point is that a priori considerations were, not after-the-fact interpretations, but necessary factors in every step of the formation of the periodic table. Inorganic elements are distinguished from compounds and from each other on largely theoretical grounds. Incidentally, some very rough clusters of observable characters also accompany this theoretically significant classification. Atomic number, even if considered a phenetic character, was not treated as of equal weight to all other characters. Nor was its weight established a posteriori by discovering that numerous other characters tended to covary with it. The correlation between atomic number and the overall similarity of physical elements is about on the same order of magnitude as that observed by Dobzhansky between breeding habits and the overall similarity of living organisms.

Pheneticists might reply that perhaps this is how the periodic table was constructed, but it shouldn't have been. It should have been constructed by purely phenetic means, and to be justified it must be. This contention has yet to be proven. To do so, pheneticists would have to sample all inorganic substances. They could not limit themselves to just the elements, because that would presuppose that they knew which inorganic substances were elements, a blatant instance of a priori weighting. After establishing homologies purely on the basis of observation, pheneticists would then have to erect various alternative phenetic classifications. Atomic number could hardly appear as one of these phenetic characters, since electrons are observable in only the widest sense of the word. If electrons are observable, so is evolutionary development! If one of these phenetic classifications can distinguish between elements and compounds and can order the elements as they are ordered on the periodic table, then the pheneticists will have proved their case. If recourse to atomic theory is permitted in the early stages of the investigation and atomic number weighted more heavily than all other phenetic characters put together, then phenetic taxonomy, as it was originally explicated and as it is still propounded by many, has been abandoned. If it is to be abandoned, then the original criticisms of evolutionary classifications need to be re-evaluated.

Pheneticists seem to have gradually come to realize that the notion of a theoretically neutral phenetic classification is an illusion and have modified their position accordingly. Operational homologies are established utilizing

any respectable scientific theory except evolutionary theory. The reasons given for permitting morphological, behavioral, physiological, serological, and DNA homologies, but forbidding evolutionary homologies, have all depended on repeated equivocations on the terms *phenetic character* and *operational homology*. Pheneticists claim that operational homologies are observed, whereas evolutionary homologies must be inferred. In the first place, only characters are observed. That two instances of a character are instances of the same character (i.e., that they are operationally homologous) must be inferred. Only if operational homologies are limited to observational homologies (i.e., if they both look blue then they are blue) will these inferences be made solely on the basis of observation. All other types of inferences to operational homologies will make essential reference to a particular scientific theory, and with the introduction of theory the overly simplistic notion of observational homology must be abandoned. One cannot observe that two nucleotides are operationally homologous. Both the existence of the nucleotides and which of the nucleotides are homologous must be inferred from extremely indirect evidence in the context of current biochemical theories.

Colless (30) claims that there is a "phylogenetic fallacy"—the view that "in reconstructing phylogenies, we can employ something more than the observed attributes of individual specimens, plus some concept of 'overall resemblance' and some concept of 'attribute' of a set or class of such specimens." Scientists in general, not just evolutionists, do employ something more than observed attributes and some concept of overall resemblance. This something more is scientific theory. As Colless (30) himself says, "The codon elements thus employed as attributes must, surely, be the ultimate approximation to our notion of 'unit attributes' . . ." What is or is not a codon is determined in large measure by biochemical theory. Codons are certainly not observable. In this instance, pheneticists and not phylogeneticists are guilty of reasoning fallaciously. The phenetic fallacy is the belief that in reconstructing phylogenies, we employ anything less than all the data and all the scientific theories at our disposal. For example, even a theory as far removed from biology as quantum theory is used in the process of carbon dating.

Each of the various kinds of homology has its own special problems. For example, behavioral homologies cannot be obtained very readily for extinct species, nor are the results obtained for extant species by controlled experiments in the laboratory very reliable. Thus, the argument that evolutionary homologies should not be used for any group because we cannot obtain them for all groups cannot be cogent, since, if it were, it would count against all types of homologies. Even morphological homology, the most pervasive type of homology used in classification, has limited applicability. For example, individual viruses and bacteria have few morphological characters which can be used in classifying them. The likelihood of obtaining extensive information about DNA homologies for more than an infinitesimally small percent-

age of species (and these all extant) is very slim, and yet no one would want to argue that this information should not be used when we do have it. Sokal & Camin (115) say, "Because phenetic classifications require only description, they are possible for all groups and are more likely to be obtained as a first stage in the taxonomic process." The preceding claim is true only if operational homologies are limited to observational homologies. If not, then phenetic classifications require more than description. They require the establishment of theoretically significant operational homologies.

However, the abandonment of the distinction between a priori and a posteriori weighting has certain ramifications for the notions of overall similarity and a general purpose classification. If it is admitted that the establishment of homologies presupposes various scientific theories, then the idea of a single parameter which might be termed *overall similarity* loses much of its plausibility and all classifications become special purpose classifications. As Edwards & Cavalli-Sforza (40) observed, "To say that the purpose of a classification is 'general' is, in our view, too vague to be of use in its construction." The idea of a general purpose classification is still another phenetic illusion. Pheneticists themselves have come to realize that too many parameters exist which have equal right to be termed measures of overall similarity and, hence, that there is no such thing as a general purpose classification. As the Ehrlichs (44) have said recently, "Theoretical considerations make it seem unlikely that the idea of 'overall similarity' has any validity. . . . *All* classifications are inherently special." They quickly add, however, that "no special classification is any more or less 'correct' than any other." (See also 45, 50-53, 73, 110, 115, 116.)

All actual biological classifications are mixed classifications; that is to say, they are affected to a greater or lesser degree by all current biological theories. No classification is purely evolutionary, purely embryological, and certainly, none is purely phenetic. The justifications for this irregular mixing of these various considerations in a single classification are both practical and theoretical. In the current state of these theories, evolutionary considerations could no more be untwined from all other considerations and excluded from classification than could embryological or physiological considerations. They are too interconnected. They are interconnected because the theories from which they are partially derived are themselves partially interdependent. Of course, this situation need not be permanent. These various theories may gradually become more carefully and completely formulated, and the relevant derivations more distinct. When this happens, the ideal of providing a straightforward reconstruction of the inferences involved in biological classification can be more closely approximated. We must resist at all costs the tendency to superimpose a false simplicity on the exterior of science to hide incompletely formulated theoretical foundations.

#### THE BIOLOGICAL SPECIES CONCEPT

Although Dobzhansky (36-38) first emphasized the biological species

concept, it has received its most extensive development at the hands of Ernst Mayr. From his earliest to his most recent writings, Mayr (80–83, 85–87) has set himself the task of demolishing the typological species concept and replacing it with a species concept adequate for its role in evolutionary theory. According to the typological species concept, each species is distinguished by one set of essential characteristics. The possession of each essential character is necessary for membership in the species, and the possession of all the essential characters sufficient. On this view, either a character is essential or it is not. There is nothing intermediate. If a character is essential, it is all-important. If it is accidental, then it is of no importance (63, 65).

In taxonomy, the essentialist position is known as *typology*, a word with decidedly bad connotations. In the recent literature, every school of taxonomy has been called typological at one time or another. The phylogeneticists term the evolutionists typologists because they let degree of divergence take precedence over recency of common ancestry in their classifications (75, 76). The pheneticists call both evolutionists and phylogeneticists typologists because they claim to use criteria which are rarely tested and may not actually obtain (113, 116, 117). The pheneticists in turn are called typologists because their classifications are intended to reflect overall similarity (71, 98, 103). The pheneticists reply that they are typologists but without types and of a statistical variety (113). Their opponents reply that this is not typology but nominalism (84–86)! To put a nice edge on the dispute, some taxonomists openly claim the honor of being called typologists. "Now the great object of classification everywhere is the same. It is to group the objects of study in accordance with their essential natures." (See also 13, 15, 97, 121–123, 127.)

The key feature of essentialism is the claim that natural kinds have real essences which can be defined by a set of properties which are severally necessary and jointly sufficient for membership. Hence, strictly speaking, there can be no such things as statistical typology. Biologists were always aware that the characters which they used to distinguish species did not always universally covary, as the essentialist metaphysics which they tacitly assumed entailed, but not until evolutionary theory were they forced to admit that such variation was not an accidental feature of the organic world, but intrinsic to it. After evolutionary theory was accepted, variation was acknowledged as the rule, not the exception (63, 65). Instead of ignoring it, taxonomists had to take variation into account by describing it statistically. No one specimen could possibly be typical in any but a statistical sense. Species could no longer be viewed as homogeneous groups of individuals, but as polytypic groups, often with significant subdivisions. Polythetic definitions, in terms of statistically covarying properties, replaced essentialist definitions in terms of a single character or several universally covarying characters (1, 26, 33, 63, 92).

One of the accompanying characteristics of essentialism was the gradual

insinuation of metaphysical properties and entities into taxonomy. Whenever naturalists attempted to define natural kinds in terms of observable attributes of the organisms being studied, exceptions always turned up. One way to reconcile this apparent contradiction was to dismiss all exceptions as monsters. Another way was to define the names of natural kinds in terms of unobservable attributes. However, two kinds of unobservables must be distinguished at this juncture—metaphysical entities and theoretical entities which, in the context of a particular scientific theory, are indirectly observable. The entities and attributes postulated by classical essentialists tended to be of the former type. The genetic criteria of the biological definition of species may be tested very rarely, but they are testable and, hence, are not metaphysical. What the pheneticists have in common with typologists is a belief in the existence of natural units of overall similarity. They differ in that these units can be defined only polythetically.

Recognizing the existence of variation among contemporary forms as a necessary consequence of the synthetic theory of evolution is one thing; formulating a methodology in taxonomy sufficient to handle such variation is another. The history of the biological species concept is a story of successive attempts to define species so that the resulting groups are significant units in evolution, or in Simpson's (101, 103) words, an evolutionary species is an "ancestral-descendant sequence of populations . . . evolving separately from others and with its own unitary evolutionary role and tendencies." Dobzhansky (36, 37) began by defining a species as that stage of the evolutionary process "at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding," and he emphasized the necessity of geographic isolation in species formation. "Species formation without isolation is impossible." Mayr concurred with Dobzhansky and distinguished with him between various isolating mechanisms, as such, and geographic and ecological isolation, since these latter are temporary and are readily removed. The species level is reached "when the process of speciation has become irreversible, even if some of the (component) isolating mechanisms have not yet reached perfection" (85). The classic formulation of the biological species definition is as follows:

A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.

Or it may be defined more briefly:

Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups (80).

Special attention in the preceding definition must be paid to the fact that it is populations which are said to be actually or potentially interbreeding,

reproductively isolated, and so on; not individuals. In ordinary discourse, the same terms are applied both to individuals and to groups of individuals—like populations. For example, both individuals and populations are frequently said to interbreed. In most cases, the use of two distinct senses of interbreed causes no confusion, especially since the notion of populations interbreeding is defined in terms of individuals interbreeding. Similarly, Mayr (85) says of isolating mechanisms that they are “biological properties of individuals that prevent the interbreeding of populations that are actually or potentially sympatric.” By their very nature, claims about populations interbreeding, etc., are statistical notions derived from the corresponding actions and properties of individuals. Thus, complaints that evolutionists continue to consider two groups as separate species even though members of these groups occasionally cross and produce fertile offspring are misplaced. It is the amount of crossing and the degree of viability and fertility of the offspring that matter. Complaints that values for these variables are too often difficult or impossible to specify are obviously relevant.

Since there is a definitional interdependence between species and population, charges of circularity must be allayed before we proceed further. *Species* is defined in terms of interbreeding, potential interbreeding, and reproductive isolation. Populations are included in species. Hence, populations must at least fulfill all the requirements for species. Additional requirements are added for populations. *Populations* are defined in terms of geographic distribution, ecological continuity, and genetic exchange. A population is “the total sum of conspecific individuals of a particular locality comprising a single potential interbreeding unit” (85). The members of a population must not be separated from each other by ecological or geographic barriers. They must be actually interbreeding among themselves. As a unit, they are potentially interbreeding with other such units.

Throughout his long career, Mayr has continually opposed the typological species concept and essentialism, and yet on some interpretations, the biological species concept has itself been treated typologically, as if it provided both necessary and sufficient conditions for species status. Dobzhansky (37, 82), for example, has argued that individuals which never reproduce by interbreeding can form neither populations nor species because potential interbreeding is a necessary condition for the correct application of these terms. He even goes so far as to say that the terminal populations of a *Rassenkreis*, if intersterile, are to be included in separate species, even though these populations are exchanging genes through intermediary populations! Dobzhansky seems to be confusing the importance of a particular species criterion with the importance of the species concept. The crucial issue is not whether some one character is possessed, but whether the units function in evolution as species. As Mayr (87) has said, “*Species are the real units of evolution*, they are the entities which specialize, which become adapted, or which shift their adaptation.” Do asexual “species” specialize, become adapted, split, diverge, become extinct, invade new ecological niches, com-

pete, etc.? If so, then from the point of view of evolutionary theory, they form species and criteria must be found to delimit them.

The three elements in the biological species definition are actual interbreeding, potential interbreeding, and reproductive isolation. As succinct as Mayr's shorter version of the biological species definition is, it nevertheless contains redundancies. Two or more populations are reproductively isolated from each other if, and only if, they are neither actually nor potentially interbreeding with each other. Thus, one or the other side of the equivalence could be omitted with no loss of assertive content. Species are groups of natural populations which are not reproductively isolated from each other but which are reproductively isolated from other such groups. In his most recent publication, Mayr himself omits reference to potential interbreeding in his revised version of the biological species definition: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (86).

In his new biological species definition Mayr still retains reference to interbreeding to indicate that the definition is applicable only to populations whose members reproduce by interbreeding and because successful interbreeding is the most directly observable criterion for species status. Reference to potential interbreeding is omitted because anything that can be said in terms of potential interbreeding can be said in terms of reproductive isolation. Neither morphological similarity nor time is mentioned in any of the formulations of the biological species definition. Among synchronous populations, morphological similarity and difference are of no significance, as far as species status is concerned. Questions of inferring species status aside, they function only in distinguishing phena of the same population, subspecies, sibling species, etc. [See Mayr's (86) discrimination grid.]

The omission of any temporal dimension from the biological species definition is of greater significance. The application of the biological species definition successively in time would lead to the recognition of a series of biological species with minimal temporal dimensions. What is to integrate these successive time slices into temporally extended species? The answer, as Simpson (103) pointed out earlier, is descent. If species are to be significant evolutionary units, some reference to descent eventually must be made. It is also implicit in any definition of population, since males, females, young and adults, workers and asexual castes are all to be included in the same populations. Morphological similarity won't do, because the types of individuals listed are often morphologically quite dissimilar. However, once a temporal dimension is introduced into the species concept and speciation without splitting is permitted (contra Hennig), an additional criterion must be introduced to divide gradually evolving phyletic lineages into species. The only candidate for such a criterion is degree of divergence, as indicated by morphological and physiological similarity and difference. Thus, in the discernment of biological species, morphological similarity and difference play a dual role, in most cases as the evidence by which the fulfillment of the

other criteria is inferred and in some instances as criteria themselves. By now it should be readily apparent that any adequate definition of species as evolutionary units can no more be typological in form than can any definition of any theoretically significant term in science. As Julian Huxley (68) observed quite early in the development of the synthetic theory of evolution, "Species and other taxonomic categories may be of very different types and significance in different groups; and also that there is no single criterion of species."

The objections, however, which have been made most frequently by the pheneticists against the biological species concept are not those just enumerated, but the following: 1. As important as biological species may be in evolutionary theory, such theoretical considerations should not be allowed to intrude into biological classification, both because they are theoretical and because the presence or absence of reproductive isolation can seldom be inferred with sufficient certainty. 2. There may be fairly pervasive evolutionary units in nature, but reproductive isolation does not mark them. 3. There are no pervasive evolutionary units in nature, regardless of the criteria used to discern them.

As in the case of inferring phylogeny, the commonest complaint raised by extreme empiricists in general, and the pheneticists in particular, against the biological species concept is that too often reproductive isolation cannot be inferred with sufficient certainty to warrant its intrusion into classification. As early as the *New Systematics* (68) Hogben objected that biological species could not be determined often enough, and recently Mayr (85) has said that to "determine whether or not an incipient species has reached the point of irreversibility is often impossible." The problem is not distinguishing one taxon from another but deciding when one or more taxa have reached the level of evolutionary unity and distinctness required of species. If two groups are reproductively isolated from each other, then they are included in separate species; but how often and with what degree of certainty can the presence or absence of reproductive isolation be determined?

If just the two factors space and time are taken into account, four possible situations confront the taxonomist: In the ideal case, two populations, for a while at least, are synchronous and partially overlap. Here, in principle, it is possible to confirm species status by observation. In practice, the situation is not so ideal because the making of such observations is expensive, time consuming, and difficult—not to mention that decisions have to be made regarding the frequency of crossing, the degree of viability and fertility of the offspring, etc. In most cases, even under such optimal conditions, taxonomists depend heavily on inferences from morphological similarity to aid them in their decisions. In cases of synchronic but allopatric populations, the presence or absence of reproductive isolation must be inferred. The advantage here is that on occasion such inferences can be checked, both indirectly by fertility tests in the laboratory and directly, if the populations happen to meet in nature. Usually of course, species status is inferred via

morphological similarity and difference. When two populations are separated by appreciable durations of time, inferences of species status are even more circumstantial and can never be checked by any of the more direct means. "Hence, while the definition of the BSC [biological species concept] does not involve phenetics, the actual determination of a biological species always will do so, even in the optimal case" (117).

Pheneticists have objected both to the failure of evolutionists to give phenetics its just due in the application of the biological species concept and to the deficiencies of phenetic similarity as an indicator of reproductive isolation. Since phenetics plays such a predominant role in species determination anyway and since inferences from phenetic similarity to interbreeding status are very shaky at best, they ask why one should not abandon oneself to phenetic taxonomy right from the start. The problem in replying to this question is in deciding precisely what phenetic taxonomy is. By a rigid interpretation, phenetic taxonomy, as it was originally set out, is something radically new, but by this interpretation it can be shown that there can be no such thing as phenetic taxonomy. By a more reasonable interpretation, phenetic taxonomy loses its originality, since it becomes by and large what traditional taxonomists have been doing all along. The jargon of phenetic taxonomy is different, and greater emphasis is placed on mathematical techniques of evaluation, but with such an interpretation phenetic taxonomy is not very revolutionary.

Sokal & Crovello (117) complain that since the words *potential interbreeding* have "never really been defined, let alone defined operationally, . . . it appears to us that the only possible answer one could get from the question whether or not two samples are potentially interbreeding is 'don't know.'" In the first place, potential interbreeding has been defined. If two populations are kept from interbreeding only by geographical or ecological barriers, then they are potentially interbreeding; otherwise not. It is another story, of course, whether or not ecologists and population biologists are in a position to make reasonable inferences on these matters. Sometimes, however, detailed analyses of particular situations have been provided and biologists are in a position to say more than "don't know." With equal justification, an evolutionist could say that since the words *phenetic similarity* have never really been defined, let alone defined operationally, the only possible answer one could get from the question whether or not two samples are phenetically similar is "don't know." Of course, for specific studies, when the OTUs, characters, and clustering method are specified, more specific decisions can be made, but the same is true for potential interbreeding claims. In both disciplines loose and specific questions can be asked.

As unflattering as the appellation may sound, *phenetic* has been a weasel word in phenetic taxonomy. Its meaning changes as the occasion demands. When the principles of other schools of taxonomy are being criticized, it is given a strict interpretation. Phenetic taxonomy is look, see, code, cluster. A methodologically sophisticated ignoramus could do it. But when the pheneti-

cists turn to the elaboration of the methods and procedures of phenetic taxonomy, it takes on a whole spectrum of more significant meanings, heedless of the fact that under these various interpretations the original criticisms of other taxonomic schools lose much of their decisiveness.

For example, in the flow chart designed by Sokal & Crovello (117) for the recognition of biological species, they begin by grouping individuals into rough-and-ready samples. "In the initial stages of the study it may be that sufficient estimations of phenetic similarity can be determined by visual inspection of the specimens." But they go on to admit that such groupings are not the result of mindless look-see. "Knowledge of the biology of the organisms involved may be invoked." Throughout this flow chart, *phenetically homogenous sets* must include all stages in the life cycle of the organism, various castes in social insects, males and females, etc., regardless of the polymorphisms involved (11, 16, 85, 88, 95, 96). They see this as a practical difficulty, when it is plainly a theoretical difficulty. The admission of such theoretical considerations in the initial stages of a phenetic study means that the pheneticists themselves are practicing a priori weighting, a practice which they have roundly condemned in others. Decisions to include males and females in the same taxon do not stem from earlier phenetic clustering but from previously accepted biological theories. Evolutionists emphasize reproductive isolation because they feel that it is of extreme importance in the phylogenetic development of species. They don't want to see evolutionary units broken up and scattered throughout the nomenclatural system. Similarly, biologists emphasize cellular continuity as a criterion for individuality because they feel that it is of extreme importance in the embryological development of the individual. They don't want to see embryological units broken up and scattered throughout the nomenclatural system. The theory of the individual, as Hennig calls it, may be so fundamental that it has become commonplace, but a biological theory does not cease to be a theory just because it has been around for a long time. As was argued earlier in the section on inferring phylogeny, pheneticists themselves admit theoretical (i.e., a priori) considerations in the initial stages of their studies—as well they should. The point in making this observation is not that pheneticists should be more rigorous in purging their procedures of such theoretical considerations—which are absolutely necessary—but that pheneticists should recognize them for what they are and modify their criticisms of evolutionary taxonomy accordingly.

What is a phenetic property, a phenetic classification, phenetic similarity? If a phenetic property is to be some minimal attribute analyzed in the absence of all scientific theories, regardless of how rudimentary, such characters will certainly be useless in any attempt to construct a scientifically meaningful classification. Arguments have even been set out that, in principle, such an analysis is impossible. If a phenetic property is to be some minimal unit analyzed in the context of some but not all scientific theories (and, in particular, not of evolutionary theory), then the criteria for deciding

which scientific theories are legitimate and which illegitimate must be stated explicitly and defended. If some scientific theories are to be admitted even at the initial stages of a phenetic study, then the criticisms of comparable admissions of evolutionary theory must be re-evaluated. The establishment of evolutionary homologies on the basis of evolutionary theory may still be illegitimate, but not just because it is a scientific theory entering into the initial stages of a taxonomic study.

Sokal & Crovello (117) say that phenetic taxonomy is closely related to what Blackwelder calls practical taxonomy—"the straight-forward description of the patterns of variation in nature for the purpose of ordering knowledge." As efforts of the pheneticists have ably proved, there are indefinitely many ways of describing the patterns of variation in nature, and in each way there are indefinitely many patterns to be recognized. The problem is not so much that there is nothing which might be called overall phenetic similarity, but that there are too many things which might answer to this title. The question is whether or not some of these possible ways of ordering knowledge are perhaps more significant than others. The whole course of science attests to the reply that there are some preferable orderings—those which are most compatible with current scientific theories.

Evolutionists claim that their classifications, though they may be constructed in part by intuitive means, are objective, real, nonarbitrary, and so on, because they reflect something which really exists in nature. Pheneticists reply that character covariation also really exists in nature. As might be expected, this sort of exchange has done little to clarify the issues. The difference between evolutionary and phenetic taxonomy in this respect is that evolutionists have biologically significant reasons for making one decision rather than another while, by a strict interpretation, pheneticists do not. On purely phenetic criteria, any group of organisms can be arranged in indefinitely many OTUs with coefficients of similarity ranging from zero to unity. In contrast, evolutionists contend that biological species are important units in nature, more important than numerous other units which might be discernible. They are functioning as evolutionary units in evolution. Hence, from the point of view of evolutionary theory, there is good reason to pay special attention to these units and not to others.

If science were a theoretically neutral exercise, all decisions would be on a par. There would be no difference between the claims that it rains a lot in San Francisco and that all bodies attract each other with a force equal to the product of their masses divided by the square of their distances. As soon as scientific theory is allowed to intrude, certain alternatives are closed, certain decisions are preferable. This is the important sense of natural which has lurked behind the distinction between natural and artificial classifications from the beginning.

In the absence of any scientific theory, the only difference between a natural and an artificial classification is the number of characters used. A natural classification is constructed using a large number of characters, while

an artificial classification is constructed using only a few (22, 55–57, 78, 115, 128). Biologists have tended to object to this characterization because it seemed to leave something out, but they have not been too articulate in describing this something. They have argued that a natural biological classification is one based on biologically relevant attributes—as many as possible. An artificial classification is one based on biologically irrelevant attributes—regardless of how many. The controversy has surrounded the sense in which attributes can be biologically relevant or irrelevant.

Taxonomists have tended to term an attribute relevant or taxonomically useful if it has served to cluster organisms into reasonably discrete groups. Thus, for future runs on a group, it would be given greater weight a posteriori. Pheneticists are in full agreement with this usage. But taxonomists also wish to extend their taxonomically useful attributes to cover additional, unstudied groups. This is the a priori weighting to which the pheneticists raised such vocal objections. The justification for such an extension, when it is justified, rests on the second and more important sense of biologically relevant. Certain concepts are central to biological theories; others are not. For example, canalization, geographic isolation, crossing over, epistatic interaction, and gene flow are important concepts in contemporary biological theory. Hence, a classification in which they were central would be natural in the above sense. Of course, gene flow is not used to define the name of a particular taxon, but it does serve two other functions. It plays an important part in the definition of species, and this definition, in turn, determines which taxa are classed at the species level and which are not. In addition, it might play a part in justifying the claim that an attribute which was taxonomically useful in group *A* should also prove to be taxonomically useful in group *B*. To the extent that such claims are justified, they must be backed up by appropriate scientific laws.

An empiricist might object that all attributes of organisms are equally real. This is certainly true. The broken setae of an insect are as real as a mutation which permits it to produce double the number of offspring, but they hardly are equally important. Just as physical elements are classified on the basis of their atomic number—an attribute selected because of its theoretical significance—evolutionary elements are classified on the basis of their reproductive habits and for the same reasons. Evolutionists contend that if all the data were available, a high percentage of organisms which reproduce by interbreeding could be grouped for long periods of their duration into phylogenetically significant units by the biological species definition.

The pheneticists have attacked this contention on two fronts. First, they have argued that biological species, like phenetic species, are arbitrary units and, second, that biological species, even if they could be determined, would not form pervasive, significant units in evolution. At the heart of the first criticism is the evaluative term *arbitrary*. Claiming to use *arbitrary* in Simpson's sense, Sokal & Crovello (117) say, "Our study of the opera-

tions necessary to delimit a biological species revealed considerable arbitrariness in the application of the concept. This is in direct conflict with the claim of nonarbitrariness by proponents of the BSC. . . . The degree of sterility required in any given cross, the number of fertile crosses between members of populations, not to mention the necessarily arbitrary decisions proper to the hidden phenetic components of the BSC, make this concept no less arbitrary than a purely phenetic species concept, and perhaps even more so, since phenetics is one of its components."

Simpson's definition of *arbitrary* is hardly relevant to the issues at hand. According to Simpson (101, 103), when there is a criterion of classification and a classification, groups in this classification are nonarbitrary to the extent that they have actually been classified according to the criterion. For example, if species *A* is defined in terms of property *f*, then the species is nonarbitrary if all of its members have *f*; otherwise, it is not. Simpson's definition is extraneous to this discussion since it assumes precisely what is at issue.

What then do Sokal & Crovello mean by *arbitrary*? Since they repeatedly designate decisions in phenetic taxonomy as arbitrary and since they are advocates of phenetic taxonomy, one might reasonably infer that they do not take it to be a term of condemnation. Yet in one place they talk of arbitrariness as being a drawback to various species definitions. *Arbitrary* is used in ordinary discourse in a host of different senses, and the pheneticists, in a manner not confined to themselves, seem to switch casually from one to another in their criticisms of evolutionary taxonomy. At one extreme, a decision is arbitrary if more than one choice is possible. This is unfortunate because in science more than one reasonable decision is always possible. Hence, all scientific decisions become arbitrary, and the term ceases to make a distinction. For example, should physicists retain Euclidean geometry and complicate their physical laws, or should they retain the simplicity of their laws and treat space as non-Euclidean? Either choice is possible, but physicists' decision for the latter is hardly arbitrary.

A more reasonable use of *arbitrary* is in the division of continua into segments. Biologists of all persuasions commonly admit that whenever an even gradation exists, any classificatory decision automatically becomes arbitrary (17, 103, 119). Here there are not just two or a few possible choices, but many, perhaps infinitely many. Hidden in this line of reasoning is the essentialist prejudice that the only distinctions that exist are sharp distinctions. Unless there is a complete, abrupt break in the distribution of the characters being used for classification, no meaningful decisions can be made. This prejudice was one of the primary motives for philosophers' refusing to countenance even the possibility of evolution by gradual variation and for many philosophers' and biologists' opting for evolution by saltation (65). But this prejudice runs counter to both the very nature of modern science and the methods being introduced by the pheneticists. Various statistical means exist for clustering elements, even when at least one element ex-

ists at every point in the distributional space. For example, there are reasons for dividing a bimodal curve at some points rather than at others. Darwin argued that species as well as varieties intergraded insensibly. He concluded, therefore, that they were equally arbitrary. Owing to the mathematical and philosophical prejudices of his day, Darwin's conclusion is understandable. There is no excuse for similar prejudices still persisting (25, 72).

All decisions in phenetic taxonomy are hardly arbitrary in any meaningful sense. If they were, then all the techniques of phenetic taxonomy could be replaced by the single expedient of flipping a coin. Similarly, all decisions as to the degree of crossing, the number of fertile offspring and their viability, etc., sufficient to assure the presence or absence of reproductive isolation are hardly arbitrary in any meaningful sense of the term. From all indications, various thresholds exist in the empirical world. The temperature of water can be varied continuously, but it does not follow thereby that the attendant physical phenomena also vary continuously. At the boiling point, at the freezing point, and near absolute zero, a change of a single degree is accompanied by extremely discontinuous changes in the attendant physical phenomena. Similarly, for example, Simpson refers to quantum evolution, the burst of proliferation that follows a population managing to make its way through an adaptive valley to invade a new ecological niche (88, 101, 103; see also Lewontin, this volume).

There seems to be no question that such significant thresholds exist in evolution. Recently, however, pheneticists have contended that the biological species concept does not mark such a threshold (42, 45, 115). Of all the criticisms leveled at evolutionary taxonomy in the last ten years, this is the most serious. Most of the other criticisms have been largely methodological, resting uneasily on certain dubious philosophical positions, but this criticism is empirical. In a recent study by Ehrlich & Raven (46), evidence was adduced to show that selection is so overwhelmingly important in speciation that the occasional effects of gene flow can safely be ignored in the general evolutionary picture. If this contention is borne out by additional investigation, then the role of the biological definition of species will have been fatally undermined and the synthetic theory of evolution will have to be modified accordingly.

Sokal & Crovello (117), concurring with the position of Ehrlich & Raven, observe that "possibly concepts such as the BSC are more of a burden than a help in understanding evolution." They go on to conclude, however, that "the phenetic species as normally described and whose definition may be improved by numerical taxonomy is the desirable appropriate concept to be associated with the category, species, while the local population may be the most useful unit for evolutionary study." If it can be shown that biological species are not significant units in evolution, then from the point of view of evolutionary taxonomy, the role of the biological species has been fatally undermined. It does not follow, therefore, that the phenetic species, as normally described, should automatically replace them in biological

classification, if for no other reason than that no description has been provided yet for the phenetic species. Instead, there are literally an infinite number of phenetic units, all of which have an equal right, on the principles of numerical taxonomy, to be called species.

### CONCLUSION

Numerous distinctions have been drawn in the preceding pages, but little notice has been taken of the most important distinction underlying the phenetic-phyletic controversy—the difference between explicit and implicit or intuitive taxonomy. Simpson (103) has argued that taxonomy, like many other sciences, is a combination of science and art. For example, tempering vertical with horizontal classification, dividing a gradually evolving lineage into species, deciding how much interbreeding is permissible before two populations are included in the same species, the assignment of category rank above the species level, choices between alternative ways of classifying the same phylogeny, balancing splitting and lumping tendencies, and the inductive inferences by which phylogenies are inferred are all to some extent part of the art of taxonomy. The question is whether the intuitive element in taxonomy should be decreased and, if so, at what cost.

It has been assumed in this paper that decreasing the amount of art in taxonomy is desirable. Taxonomists can be trained to produce quite excellent classifications without being able to enunciate the principles by which they are classifying, just as pigeons can be trained to use the first-order functional calculus in logic. Human beings can be trained to be quite efficient classifying machines. They can scan complex and subtle data and produce estimates of similarity with an accuracy which far exceeds the capacity of current techniques of multivariate analysis. Taxonomists as classifying machines, however, have several undesirable qualities. Although taxonomists, once trained, tend to produce consistent, accurate classifications, the programs by which they are producing these classifications are unknown to other taxonomists and vary from worker to worker. In addition, just when a taxonomist is reaching the peak of his abilities, he tends to die. Only recently one of the most accomplished taxonomists passed away and with her, all the experience which she had accumulated during decades of doing taxonomy.

The resistance to making taxonomic practice and procedures explicit seems to have stemmed from two sources: one, an obscurantist obsession with the ultimate mystery of the human intellect; the other, a concern over how much theoretical significance one must sacrifice in order to make biological classification explicit. With respect to the first reservation, Kaplan (74) has distinguished between reconstructed logic and logic-in-use. Frequently, during the course of development of formal and empirical science, empirical scientists use certain modes of inference which are beyond the current formal reconstructions. There is the tendency to dismiss these modes of inference by attributing them to genius, imagination, and unanalyzable, for-

tuitous guesswork. Kaplan (74) views the intuition of great scientists, not as lucky guesswork, but as currently unreconstructed logic-in-use. Intuition is any logic-in-use which is preconscious and outside the inference schemata for which we have readily available reconstructions. "We speak of intuition, in short, when neither we nor the discoverer himself knows quite how he arrived at his discoveries, while the frequency or pattern of their occurrence makes us reluctant to ascribe them merely to chance."

The second reservation which taxonomists have had about making taxonomy less intuitive and more explicit is less subtle, but equally important. In the early days of phenetic taxonomy, pheneticists seemed willing to dismiss the theoretical side of biological classification, since it seemed to make straightforward reconstructions extremely difficult, if not impossible. They tended to conflate the complexity of taxonomic inferences with taxonomists being muddle-headed. Certainly some of the complexity of traditional taxonomy may well have been due just to sloppy thinking, but instead of this evaluation being the immediate, initial response, it should have been the last resort. Traditional taxonomists and computer taxonomists are going to have to adapt to each other, but this adaptation cannot be purchased at the expense of the purposes of scientific investigation. These ends are better characterized by the words *theoretical significance* than by *usefulness*. An extremely accurate scientific theory of great scope will certainly be useful, but there are many things which are useful, though of little theoretical significance.

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#### LITERATURE CITED

1. Beckner, M. 1959. *The Biological Way of Thought*. New York: Columbia Univ. Press. 200 pp.
2. Bigelow, R. S. 1956. Monophyletic classification and evolution. *Syst. Zool.* 5:145-46
3. Bigelow, R. S. 1958. Classification and phylogeny. *Syst. Zool.* 7:49-59
4. Bigelow, R. S. 1959. Similarity, ancestry, and scientific principles. *Syst. Zool.* 8:165-68
5. Bigelow, R. S. 1961. Higher categories and phylogeny. *Syst. Zool.* 10:86-91
6. Birch, L. C., Ehrlich, P. R. 1967. Evolutionary history and population biology. *Nature* 214:349-52
7. Blackwelder, R. E. 1959. The present status of systematic zoology. *Syst. Zool.* 8:69-75
8. Blackwelder, R. E. 1959. The functions and limitations of classification. *Syst. Zool.* 8:202-11
9. Blackwelder, R. E. 1962. Animal taxonomy and the new systematics. *Surv. Biol. Progr.* 4:1-57
10. Blackwelder, R. E. 1964. Phyletic and phenetic *versus* omniscpective classification. In *Phenetic and Phylogenetic Classification*, ed. V. H. Heywood, J. McNeill, 17-28. London: Systematics Assoc. 164 pp.
11. Blackwelder, R. E. 1967. A critique of numerical taxonomy. *Syst. Zool.* 16:64-72
12. Blackwelder, R. E. 1967. *Taxonomy*. New York: Wiley. 698 pp.
13. Blackwelder, R. E., Boyden, A. 1952. The nature of systematics. *Syst. Zool.* 1:26-33

14. Bock, W. J. 1963. Evolution and phylogeny in morphologically uniform groups. *Am. Natur.* 97:265-85
15. Borgmeier, T. 1957. Basic questions of systematics. *Syst. Zool.* 6:53-69
16. Boyce, A. J. The value of some methods of numerical taxonomy with reference to hominoid classification. See Ref. 10, 47-65.
17. Burma, B. H. 1949. The species concept: a semantic review. *Evolution* 3:369-70
18. Cain, A. J. 1958. Logic and memory in Linnaeus's system of taxonomy. *Proc. Linn. Soc. London* 169: 144-63
19. Cain, A. J. 1959. Deductive and inductive methods in Post-Linnaean taxonomy. *Proc. Linn. Soc. London* 170:185-217
20. Cain, A. J. 1959. Taxonomic concepts. *Ibis* 101:302-18
21. Cain, A. J. 1962. Zoological classification. *Aslib Proc.* 14:226-30
22. Cain, A. J., Harrison, G. A. 1958. An analysis of the taxonomist's judgment of affinity. *Proc. Zool. Soc. London* 131:85-98
23. Cain, A. J., Harrison, G. A. 1960. Phyletic weighting. *Proc. Zool. Soc. London* 135:1-31
24. Camin, J. H., Sokal, R. R. 1965. A method for deducing branching sequences in phylogeny. *Evolution* 19:311-26
25. Cargile, J. 1969. The sorites paradox. *Brit. J. Phil. Sci.* 20:193-202
26. Carmichael, J. W., George, J. A., Julius, R. S. 1968. Finding natural clusters. *Syst. Zool.* 17:144-50
27. Cavalli-Sforza, L. L., Edwards, A. W. F. 1967. Phylogenetic analysis: models and estimation procedures. *Evolution* 21:550-70
28. Clark, R. B. 1956. Species and systematics. *Syst. Zool.* 5:1-10
29. Colless, D. H. 1967. An examination of certain concepts in phenetic taxonomy. *Syst. Zool.* 16:6-27
30. Colless, D. H. 1967. The phylogenetic fallacy. *Syst. Zool.* 16:289-95
31. Colless, D. H. 1970. The relationship of evolutionary theory to phenetic taxonomy. *Evolution*
32. Crowson, R. A. 1965. Classification, statistics and phylogeny. *Syst. Zool.* 14:144-48
33. Daly, H. V. 1961. Phenetic classification and typology. *Syst. Zool.* 10: 176-79
34. Darwin, F. 1959. *The Life and Letters of Charles Darwin*. New York: Basic Books. 2 vols. 558 pp. & 562 pp.
35. Dexter, R. W. 1966. Historical aspects of studies on the Brachiopoda by E. E. Morse. *Syst. Zool.* 15:241-43
36. Dobzhansky, T. 1935. A critique of the species concept in biology. *Phil. Sci.* 2:344-55
37. Dobzhansky, T. 1937. *Genetics and the Origin of Species*. New York: Columbia Univ. Press. 364 pp.
38. Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. *Am. Natur.* 74:312-21
39. DuPraw, E. J. 1964. Non-Linnaean taxonomy. *Nature* 202:849-52
40. Edwards, A. W. F., Cavalli-Sforza, L. L. Reconstruction of evolutionary trees. See Ref. 10, 67-76.
41. Ehrlich, P. R. 1958. Problems of higher classification. *Syst. Zool.* 7:180-84
42. Ehrlich, P. R. 1961. Has the biological species concept outlived its usefulness? *Syst. Zool.* 10:167-76
43. Ehrlich, P. R. 1964. Some axioms of taxonomy. *Syst. Zool.* 13:109-23
44. Ehrlich, P. R., Ehrlich, A. H. 1967. The phenetic relationships of the butterflies. *Syst. Zool.* 16:301-27
45. Ehrlich, P. R., Holm, R. W. 1962. Patterns and populations. *Science* 137:652-57
46. Ehrlich, P. R., Raven, P. H. 1969. Differentiation of populations. *Science* 165:1228-31
47. Farris, J. S. 1967. The meaning of relationship and taxonomic procedure. *Syst. Zool.* 16:44-51
48. Farris, J. S. 1968. Categorical rank and evolutionary taxa in numerical taxonomy. *Syst. Zool.* 17:151-59
49. Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon. 272 pp.
50. Ghiselin, M. T. 1966. On psychologism in the logic of taxonomic principles. *Syst. Zool.* 15:207-15
51. Ghiselin, M. T. 1967. Further remarks on logical errors in systematic theory. *Syst. Zool.* 16:347-48
52. Ghiselin, M. T. 1969. *The Triumph of the Darwinian Method*. Berkeley: Univ. California Press. 287 pp.

53. Ghiselin, M. T. 1969. The principles and concepts of systematic biology. In *Systematic Biology. Publ. 1962 Nat. Acad. Sci.*, ed. C. G. Sibley, 45-55. 632 pp.
54. Gilmartein, A. J. 1967. Numerical taxonomy—an eclectic viewpoint. *Taxon* 16:8-12
55. Gilmour, J. S. L. 1937. A taxonomic problem. *Nature* 139:1040-47
56. Gilmour, J. S. L. 1940. Taxonomy and philosophy. In *The New Systematics*, ed. J. Huxley, 461-74. London: Oxford Univ. Press, 583 pp.
57. Gilmour, J. S. L., Walters, S. M. 1964. Philosophy and classification. *Vistas Bot.* 4:1-22
58. Haldane, J. B. S. 1932. *The Causes of Evolution*. London: Harpers. 234 pp.
59. Hempel, C. G. 1965. *Aspects of Scientific Explanation*. New York: Free Press. 505 pp.
60. Hennig, W. 1950. *Grundsüge einer Theorie der phylogenetischen Systematik*. Berlin: Deut. Zentralverlag. 370 pp.
61. Hennig, W. 1966. *Phylogenetic Systematics*. Chicago: Univ. Illinois Press. 263 pp.
62. Hull, D. L. 1964. Consistency and monophyly. *Syst. Zool.* 13:1-11
63. Hull, D. L. 1965. The effect of essentialism on taxonomy. *Brit. J. Phil. Sci.* 15:314-26, 16:1-18
64. Hull, D. L. 1967. Certainty and circularity in evolutionary taxonomy. *Evolution* 2:174-89
65. Hull, D. L. 1967. The metaphysics of evolution. *Brit. J. Hist. Sci.* 3:309-37
66. Hull, D. L. 1968. The operational imperative—sense and nonsense in operationism. *Syst. Zool.* 16:438-57
67. Hull, D. L. 1969. The natural system and the species problem. In *Systematic Biology. Publ. 1962 Nat. Acad. Sci.*, ed. C. G. Sibley, 56-61. 632 pp.
68. Huxley, J. Ed. 1940. *The New Systematics*. London: Oxford Univ. Press. 583 pp.
69. Huxley, J. 1942. *Evolution: the Modern Synthesis*. London: Allen & Unwin. 645 pp.
70. Huxley, T. H. 1874. On the classification of the animal kingdom. *Nature* 11:101-2
71. Inger, R. R. 1958. Comments on the definition of genera. *Evolution* 12:370-84
72. James, M. T. 1963. Numerical vs. phylogenetic taxonomy. *Syst. Zool.* 12:91-93
73. Johnson, L. A. S. 1968. Rainbow's end: the quest for an optimal taxonomy. *Proc. Linn. Soc. N.S.W.* 93:8-45
74. Kaplan, A. 1964. *The Conduct of Inquiry*. San Francisco: Chandler. 428 pp.
75. Kiriakoff, S. G. 1959. Phylogenetic systematics versus typology. *Syst. Zool.* 8:117-18
76. Kiriakoff, S. G. 1965. Cladism and phylogeny. *Syst. Zool.* 15:91-93
77. Kluge, A. G., Farris, J. S. 1969. Quantitative phyletics and the evolution of Anurans. *Syst. Zool.* 18:1-32
78. Lorch, J. 1961. The natural system in biology. *Phil. Sci.* 28:282-95
79. Mackin, J. H. 1963. Rational and empirical methods of investigation in geology. In *The Fabric of Geology*, ed. C. C. Albritton, 135-63. New York: Addison-Wesley. 372 pp.
80. Mayr, E. 1942. *Systematics and the Origin of Species*. New York: Columbia Univ. Press. 334 pp.
81. Mayr, E. 1949. The species concept. *Evolution* 3:371-72
82. Mayr, E. 1957. *The Species Problem*. AAAS Publ. N. 50. Washington. 338 pp.
83. Mayr, E. 1959. Agassiz, Darwin, and evolution. *Harvard Libr. Bull.* 13:165-94
84. Mayr, E. 1965. Numerical phenetics and taxonomic theory. *Syst. Zool.* 14:73-97
85. Mayr, E. 1965. *Animal Species and Evolution*. Cambridge: Harvard Univ. Press. 797 pp.
86. Mayr, E. 1969. *Principles of Systematic Zoology*. New York: McGraw-Hill. 428 pp.
87. Mayr, E. 1969. The biological meaning of species. *Biol. J. Linn. Soc.* 1:311-20
88. Meglertsch, P. A. 1954. On the nature of the species. *Syst. Zool.* 3:49-65
89. Michener, C. D. 1957. Some bases for higher categories in classification. *Syst. Zool.* 6:160-73
90. Michener, C. D. 1963. Some future developments in taxonomy. *Syst. Zool.* 12:151-72

91. Michener, C. D., Sokal, R. R. 1957. A quantitative approach to a problem in classification. *Evolution* 11:130-62
92. Minkoff, E. C. 1964. The present state of numerical taxonomy. *Syst. Zool.* 13:98-100
93. Remane, A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Leipzig: Geest & Portig. 364 pp.
94. Rensch, B. 1929. *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung*. Berlin: Borntraeger
95. Rensch, B. 1947. *Neure Probleme der Abstammungslehre*. Stuttgart: Enke. 407 pp.
96. Rohlf, F. J. 1963. The consequence of larval and adult classification in *Aedes*. *Syst. Zool.* 12:97-117
97. Sattler, R. 1963. Methodological problems in taxonomy. *Syst. Zool.* 13:19-27
98. Sattler, R. 1963. Phenetic contra phyletic systems. *Syst. Zool.* 12:94-95
99. Simpson, G. G. 1944. *Tempo and Mode in Evolution*. New York: Columbia Univ. Press. 434 pp.
100. Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Natur. Hist.* 85:1-350
101. Simpson, G. G. 1951. The species concept. *Evolution* 5:285-98
102. Simpson, G. G. 1953. *The Major Features of Evolution*. New York: Columbia Univ. Press. 434 pp.
103. Simpson, G. G. 1961. *Principles of Animal Taxonomy*. New York: Columbia Univ. Press. 247 pp.
104. Simpson, G. G. 1964. Numerical taxonomy and biological classification. *Science* 144:712-13
105. Simpson, G. G., Roe, A., Lewontin, R. C. 1960. *Quantitative Zoology*. New York: Harcourt, Brace & World. 440 pp.
106. Sneath, P. H. A. 1957. The application of computers to taxonomy. *J. Gen. Microbiol.* 17:201-26
107. Sneath, P. H. A. 1958. Some aspects of Adansonian classification and of the taxonomic theory of correlated features. *Ann. Microbiol. Enzimol.* 8:261-68
108. Sneath, P. H. A. 1961. Recent developments in theoretical and quantitative taxonomy. *Syst. Zool.* 10:118-39
109. Sneath, P. H. A. Introduction. See Ref. 10, 43-45.
110. Sneath, P. H. A. 1968. International conference on numerical taxonomy. *Syst. Zool.* 17:88-92
111. Sokal, R. R. 1959. Comments on quantitative systematics. *Evolution* 13:420-23
112. Sokal, R. R. 1961. Distance as a measure of taxonomic similarity. *Syst. Zool.* 10:70-79
113. Sokal, R. R. 1962. Typology and empiricism in taxonomy. *J. Theor. Biol.* 3:230-67
114. Sokal, R. R. 1969. Review of Mayr's *Principles of Systematic Zoology*. *Quart. Rev. Biol.* 44:209-11
115. Sokal, R. R., Camin, J. H. 1965. The two taxonomies: areas of agreement and conflict. *Syst. Zool.* 14:176-95
116. Sokal, R. R., Camin, J. H., Rohlf, F. J., Sneath, P. H. A. 1965. Numerical taxonomy: some points of view. *Syst. Zool.* 14:237-43
117. Sokal, R. R., Crovello, T. J. 1970. The biological species concept: a critical evaluation. *Am. Natur.* 104:127-53
118. Sokal, R. R., Michener, C. D. 1958. A statistical method for evaluating systematic relationships. *Univ. Kansas Sci. Bull.* 38:1409-38
119. Sokal, R. R., Sneath, P. H. A. 1963. *The Principles of Numerical Taxonomy*. San Francisco: Freeman. 359 pp.
120. Stebbins, G. L. 1950. *Variation and Evolution in Plants*. New York: Columbia Univ. Press. 643 pp.
121. Thompson, W. R. 1952. The philosophical foundations of systematics. *Can. Entomol.* 84:1-16
122. Thompson, W. R. 1960. Systematics: the ideal and the reality. *Studio Entomol.* 3:493-99
123. Thompson, W. R. 1962. Evolution and Taxonomy. *Studio Entomol.* 5:549-70
124. Thorne, R. F. 1963. Some problems and guiding principles of Angiosperm phylogeny. *Am. Natur.* 97:287-305
125. Throckmorton, L. H. 1965. Similarity versus relationship in *Drosophila*. *Syst. Zool.* 14:221-36
126. Throckmorton, L. H. 1968. Concordance and discordance of taxo-

127. Trol, W. 1944. Urbild und Ursache in der Biologie. *Bot. Arch.* 45: 396-416
128. Warburton, F. E. 1967. The purposes of classification. *Syst. Zool.* 16:241-45
129. Williams, M. B. 1970. Deducing the consequences of evolution: a mathematical model. *J. Theor. Biol.*
130. Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159
131. Wright, S. 1931. Statistical theory of evolution. *Am. Statist. J.* March suppl., 201-8