

PHILOSOPHICAL FOUNDATIONS OF CLASSICAL EVOLUTIONARY CLASSIFICATION

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Abstract

Bock, W. J. (*Department of Biological Sciences, Columbia University, New York, New York, 10027*) 1974. *Philosophical foundations of classical evolutionary classification*. *Syst. Zool.* 22:375–392.—The primary objective of biological classification is to provide the foundation of all comparative studies in biology. These studies require consideration of two factors, namely: (a) the degree of genetic similarity between organisms; and (b) the phylogenetic sequence of events in their history. Classical evolutionary classification provides the best approach to classification, based on Popper's criterion of content, because it attempts to maximize simultaneously both of these semi-independent variables. Evolutionary classification is based on the evolution of organisms, not just their phylogeny. Application of the Popperian philosophy of the demarcation and methodology of science to classification suggests that a major task is the development of severe tests of falsification by which classifications can be tried. Although phenetic methods appear to be the best means of recognizing taxa and deducing classifications, cladistic methods appear to provide the best tests in attempts to disprove these statements of relationships. The best approach to definitions in this historical science is a theoretical one in which the defining criteria and the recognizing criteria may differ. Comparisons, which are closely akin to definitions, must be based on evolutionary theory. Homology is the primary principle in comparative biology with the possibility that all other principles of comparison are reducible to homology. The defining criterion of homology is phylogeny and the only recognizing criterion of homology is similarities of all sorts between features. Any approach to classification that excludes homology and its recognizing criterion of similarity as a primary step in deducing relationships is invalid. Use of falsifying tests suggests that relative weighting of characters may have greatly reduced importance in taxonomic methods. Lastly, the formal classification and the phylogenetic diagram of a group of organisms are not different, but redundant images of each other. Both are essential parts of the conclusions of any study of biological relationships. [Philosophy; Evolutionary classifications; Definitions; Comparisons; Homology.]

INTRODUCTION

Classification of living organisms dates back into antiquity, having its roots in the development of language and the first attempts to convey information from one person to another. The earliest organized efforts to classify animals and plants predates the beginnings of oral and written histories. Scientific classification is among the oldest of biological disciplines and has developed slowly under a variety of philosophical foundations, all of which share the central theme of comprehending order among the vast diversity of biological organisms. A well-established field of biological systematics existed in the first half of the last century, complete with a definite philosophy, a firm methodology and excellent results in the form of widely

accepted classifications that accommodated readily the numerous new species of living and fossil organisms being described daily. The major deficiency in this early nineteenth century systematics was a satisfying philosophical and scientific foundation. Biology was being swept along slowly in the transition from the ancient idea that everything is static and fixed to the newer concepts that change is occurring everywhere in the universe and that the observed world around us is a result of this ever continuing modification. A search for mechanisms underlying biological change and for an explanation of the particular type of order among organisms discovered by systematists were among the major motivations behind the formulation of the theory of organic evolution by Darwin. With the rapid, wide-

spread acceptance of the Darwinian theory of evolution by biologists, this new concept became the philosophical basis for classification. The notion that a group of organisms are related because of their evolution from a common ancestor became the fundamental criterion underlying biological comparison and classification. All major modern approaches to biological classification are evolutionary because they are based on the Darwinian theory of evolution and accept the criterion of descent from a common ancestor as the basis for relationship. Simple as this latter statement may be, it is subject to several interpretations which have given rise to widely differing approaches to classification. Analysis of these varying interpretations of common descent as the hallmark of relationship has been a central theme of classificatory theory.

The approaches to biological classification arising from the varied interpretations of common descent can be grouped under three headings which characterize the major modern schools of systematics. The purpose of this essay is to appraise the philosophical foundation of only one of these approaches—that of classical evolutionary classification—not to contrast critically or evaluate all three. In view of their common origins in Darwinian evolution, brief demarcation of each school is essential to insure clarity of discussion and meaning. These schools of systematic theory are:

A) *Phenetics*: This approach is often, but erroneously, synonymized with numerical taxonomy which is a methodology often used in phenetics but has broader usefulness. Phenetics is based on the concept that relationship between organisms is ascertained by their overall degree of similarity. Greater similarity indicates closer relationship and a smaller amount of evolutionary change from the common ancestor. Implicit in this approach is the assumption that the degree of difference between organisms is proportional to the amount of evolutionary change since their common ancestor and hence to their degree of relationship.

Various phenetic methodologies, such as numerical taxonomy (Sokal and Sneath, 1963), are largely concerned with the development of techniques by which the degree of similarity (or difference) between organisms can best be measured. Arguments as to whether phenetists measure genetical or phenotypical similarity or whether they compare “overall” or “over-some” similarity are of little significance.

Degree of similarity between organisms is an important factor in ascertaining relationships and in establishing classifications; phenetists are correct in stressing its importance. Most significant is that in pure phenetics, the only variable used in constructing classifications is similarity between organisms. No phyletic information is used (Colless, 1967), this being considered by phenetists as “the phylogenetic fallacy.” Although I believe that this fallacy is invalid (Bock, 1969 b), I agree with phenetists that phyletic information must be excluded from their approach to classification. As soon as any phyletic information is admitted into phenetics, then no basis exists to exclude any phyletic information, with the result that the philosophical foundation of phenetics has been modified radically, and little would separate phenetics from classical evolutionary classification. Such problems exist with the development of techniques such as phenetic cladistics which have emerged from pure phenetics without a careful restatement of its philosophical base.

B) *Cladistics*: The term “cladistics,” referring to branching, is less ambiguous and indeed more descriptive than the term “phylogenetic systematics” (Hennig, 1966) which is preferred by most proponents of this approach to classification. Relationship among organisms, in cladistics, is based upon joint possession of derived features (= apomorphous or advanced characters). Species which share derived features are related, and hierarchies of taxonomic groups are established on hierarchies of derived characters. Thus relationships between organisms are strictly determined by

phylogenetic branching and may be regarded as genealogical or kinship relationships.

Cladistics is based strictly upon joint possession of derived features and excludes absolutely any evaluation of similarity from the determination of relationships and construction of classification. Thus, Hennig states clearly (1966:10) that "Genealogic relationships are, however, something entirely different from 'similarity,'" and (p. 12) "The second error in the idea of a logical and historical primacy of nonphylogenetic (e.g., typological) systematics stems from the assumption that in biological systematics the primary relationships between living entities are similarity relationships (especially those of structural morphology), and that the elements of systematic work should be individuals, if not even species." Rejection of similarity as a factor in classification is repeated in his third and fourth points (Hennig, 1966: 23) summarizing the reasons for favoring cladistics as a general reference system for biological systematics.

The importance of phyletic information in classification is correctly emphasized by cladists. Not only is this an important variable in any general reference system in biology, but the best (= most severe) tests for disproving taxonomic statements are based upon phyletic information. And, as stated above for phenetics, pure cladistics is based upon consideration of only phylogenetic relationships judged by common possession of derived features. Inclusion of similarity in a cladistic approach to classification would erase the difference from evolutionary classification and cannot be done, as recognized by its proponents, without abandoning the philosophical foundation of cladistics. (Rejection of similarity as an important factor in the determination of relationships and establishment of classification results in a serious internal flaw in cladistic philosophy and methodology as shown below in the discussion of homology.)

C) *Classical evolutionary classification:*

The name for this third approach to biological classification is awkward and somewhat misleading in that it carries the implication that this is the only approach based on organic evolution. This is not the case, and once again it should be emphasized that all major approaches to classification are based on Darwinian evolution. Evolutionary classification is an eclectic approach in that it combines the important elements from phenetics and cladistics, but "eclecticism" is a poor name because it is not descriptive of the basic conceptualization of this approach to classification.

Evolutionary classification is based upon a simultaneous evaluation of the two variables used singly by phenetists and cladists to ascertain relationships between organisms, namely:

- 1) Evaluation of the amount (degree) of genetical similarity between organisms as judged by the degree of their phenotypical similarity. Greater phenotypical similarity implies greater genetical similarity and hence closer relationship. Greater similarity between species is indicative of a smaller amount of evolutionary modification of each species from their common ancestor and hence possession of a greater shared amount of genetical material.

- 2) Evaluation of the sequence of events in the evolution of each species from the common ancestor, with the events arranged in phylogenetic order. This includes proper sequential arrangement of the origin and modifications of features and of the branching sequences of each lineage. Common possession of derived features in different organisms implies common ancestry with hierarchies of phylogenetically arranged derived features used to establish taxonomic hierarchies of groups.

A general correlation exists between the degree of similarity between organisms and the phylogenetic recency of their common ancestor, but this is not an exact correlation. Otherwise we would not have the controversy that exists today between different schools of taxonomic thought. The degree of similarity and the phylogenetic sequence

of events must be regarded as two semi-independent variables (i.e., only partly correlated with one another) with the degree of independence varying from group to group and from time to time within any particular group. In evolutionary classification, relationship between organisms, as expressed in formal taxa, attempts to maximize simultaneously both semi-independent variables of degree of similarity and phylogenetic sequence of events. No reason exists why biological classification must be based on only one variable and why it cannot be based on two (or more) variables, be they semi-independent or completely independent. A major problem is that the independence of these variables varies in peculiar ways; hence, taxonomists are forced to make difficult decisions based upon evaluation of many factors. The same decisions will not be reached by all taxonomists and hence the charge of subjectivity leveled at evolutionary classification by proponents of other approaches. Such a charge may be true, and I will not argue it, but simply want to emphasize that this subjectivity is a consequence of basing classification on the simultaneous evaluation of two semi-independent variables rather than just one of the two. The resulting classification based on this eclectic approach may be "subjective" in the sense that not all taxonomists will automatically reach the same conclusion, but it has the advantage, as will be argued below, of providing a more realistic picture of the complexities of the biological world.

I prefer the descriptive adjective "classical" before evolutionary classification because I believe that this approach to biological classification had its roots in systematic studies long before Darwin and continued after 1859 with a change in its philosophical foundation and basic theory as the major school of classification. During its development, more attention was given to practical considerations—the description and classification of organic diversity—than to the clarification of philosophical foundations and the precise recording of

methodologies. A careful reading of the literature of classical evolutionary classification and consideration of the general acceptance of the classification of animals and plants—how well they endured and were able to accommodate new biological discoveries—testifies to the existence of a viable philosophy and a sound methodology. Most evolutionary taxonomists knew what they were doing and why, even in the absence of a clear statement of philosophy and methods. This lack of attention to the philosophical basis of a science is not unique to biological classification and is not necessarily a serious deterrent to rapid progress as shown by Reichenbach (1968: 114) for physics during the nineteenth century.

A firm philosophical foundation for classical evolutionary classification has existed for many decades, but has not been expounded as clearly as it deserves. The purpose of this essay is to outline briefly (a) the basis for judging which approach to biological classification provides the best general reference system and (b) the philosophical foundation for classical evolutionary classification.

At the onset, I would like to acknowledge my debt to Ernst Mayr and George G. Simpson who have done more to clarify the philosophical foundations and methodologies of classical evolutionary classification than any other living taxonomist. Almost all of the ideas expressed in this essay can be found readily in the writings of these taxonomists, such as in their "Principles of animal taxonomy" (Simpson, 1961) and "Principles of systematic zoology" (Mayr, 1969). Hopefully this paper will serve as a guide to the more extensive discussions of the philosophy and principles of classification by Mayr and Simpson.

BASIS OF BIOLOGICAL CLASSIFICATION

Foremost, in discussions of the varied approaches to biological classification, is the question—which of the possible schemes provides the best classification? This may be expressed in terms of "a general refer-

ence system" (Hennig, 1966:9) which expresses well one of the essential purposes of biological classification. Needless to say, proponents of each school of systematics believe that their approach provides the best classification and provide arguments supporting their position. Unfortunately, claims about the best classification or general reference system are vague unless firm criteria are established first on which to judge different classifications, as has been emphasized by Warburton (1967). A set of criteria must be stated clearly, even if not universally accepted, before different classifications can be judged best relative to one another.

The most fundamental attribute of biological classification is that it must be useful. It must order and summarize biological information, must be heuristic, and must provide the basis for future studies. If a classification does not meet these minimal utilitarian requirements, it should be rejected forthwith.

Several sets of criteria have been suggested as a basis on which to judge the best system of classification. One widely accepted criterion is that of greatest predictability of unknown characters in known organisms or in newly discovered species (Warburton, 1967). Thus the best classification is based on the greatest concurrence of characters in organisms which should permit the most accurate prediction of unknown characters. This criterion embraces an extremely important attribute of classification, one that is of prime concern to a large majority of biologists when using classification as a basis of their research. Maximum prediction of unknown features represents the general goal of phenetic approaches and of many evolutionary taxonomic approaches to classification.

A second criterion on which to judge the best classification is the most accurate representation of the phylogenetic history of organisms. This is the basis of considering classification as the general reference system in biology by cladists. Phylogenetic

history means precisely the exact pattern and sequence of branching of phyletic lineages. This criterion, which is the goal of cladistic approaches and, in part, of evolutionary approaches to classification, is a significant aspect of classification but one of considerably less important *direct* use to biologists when employing classification in their research. The phylogenetic criterion is of prime concern in the analysis of the evolutionary history, including mechanisms, of individual features and organ systems and in many biogeographic studies.

Other criteria have been suggested such as that classification should be the most accurate representation of the evolution of organisms, or that classification should be a natural, realistic or holistic system. These other criteria either can be reduced (e.g., the evolutionary criteria) to either one or a combination of the two criteria mentioned above, or are (e.g., the natural system) so vague that judgement of the best classification is impossible.

The several criteria, namely maximum predictability and phylogenetic history, commonly suggested for evaluating the best classification are important attributes of any system of relating organisms. Yet, they are subordinate components of a more fundamental basis of biological classification which should serve as the criterion for evaluating the best system of classifying organisms.

The primary objective of biological classification is to provide the foundation for all comparative studies in biology—with the best classification being the one that permits the most useful comparative investigations. Although this statement appears as vague as claims that classifications should be natural, criteria can be established for judging the most useful comparative studies in biology.

If one accepts the primary objective of biological classification, to be the foundation for all comparative studies, then one must accept the notion that only one system of classification is possible and that this system must be the most optimal one

for all comparisons. If biologists wish to achieve a unified science with a common set of explanations for all biological phenomena, then the results of all comparative biological studies must conform with each other—they must be interconnected or comparable—otherwise each biologist would not be able to comprehend and use the results obtained by other biologists. To be sure, some particular system of classification may serve as the best foundation for a particular or specialized comparative study, but the results will be of less general usefulness. Thus I reject the notion that different approaches to classification are equally useful and that many different schemes of classification for a group of organisms are possible and a worker can choose the one best suited for a particular study. Such a notion would simply increase the chaos in biology instead of ascertaining the existing order in biological diversity for which systematists have assumed primary responsibility.

Comparative studies of biological organisms can be based upon a number of different philosophical foundations. Non-scientific philosophies (e.g., ideal typology) can be rejected using the criterion for demarcation of science advocated by Popper. Yet it may not be possible to judge which of the scientifically valid foundations of comparison are correct or wrong, and it is probably unreasonable to attempt to do so. However, it is possible to distinguish between these different philosophical bases for comparison and to choose the best one on using another set of criteria which have been summarized by Popper (1968b:217) as:

“This criterion of relative potential satisfactoriness (which I formulated some time ago, and which, incidentally, allows us to grade theories according to their degree of relative potential satisfactoriness) is extremely simple and intuitive. It characterizes as preferable the theory which tells us more; that is to say, the theory which contains the greater amount of empirical information or *content*;

which is logically stronger; which has the greater explanatory and predictive power; and which can therefore be *more severely* tested by comparing predicted facts with observations. In short, we prefer an interesting, daring, and highly informative theory to a trivial one.

All these properties which, it thus appears we desire in a theory can be shown to amount to one and the same thing: to a higher degree of empirical *content* or of testability.”

The scientific theory that best meets these criteria as the foundation for all biological comparison is the Darwinian theory of organic evolution.

All attributes of living organisms, their form and functions, their similarities and differences, and their correlations and pattern of distribution, depend on the past evolutionary history of these organisms, not simply on their phylogeny (see Bock and von Wahlert, 1963, for a distinction between evolution and phylogeny). Hence, comparative study of biological attributes must be based on a full consideration of their evolution, including all evolutionary mechanisms and phenomena that have contributed to the development of the present condition of these features. If biological generalizations are attempts to summarize the results of organic evolution, then such an eclectic approach is necessary because these generalizations are dependent upon the system of comparison used to formulate them.

Comparative biological studies include several general types of questions which are interwoven extensively with each other. One common question is the similarity of attributes of members of a taxonomic group which bears on the degree of common genetical material, and hence the number of phenotypical features possessed in common. This is associated with the correlation of characters and the question of whether all members of a taxon will possess a new attribute discovered in one of them. A biologist is often concerned with the question of how many species, and which

ones, should be examined before having confidence in the generality of a newly discovered attribute. An experimental biologist or medical researcher must know whether he can extrapolate the results of a study done on one species to another on which he cannot experiment, and what are the chances of being correct. Many phyletic questions are important, such as whether many of the similarities between mammals and birds exist because of their common ancestry in reptiles or are the result of both groups being warm-blooded; or whether attributes found in living amphibians can be assumed to be similar to those present in the earliest tetrapods? Decisions on many such questions may involve large cost factors in terms of money and time, and the results may be of utmost importance in terms of medical practice or agriculture. Thus the decision on the philosophical foundation of biological comparison and classification is not merely of theoretical interest to a small handful of systematists, but is of extreme practical importance to everyone, biologist and nonbiologist alike.

Classification, as the foundation for comparative studies in biology, must include two factors, namely: (a) degree of genetical similarity as ascertained by the degree of similarity of phenotypical features shared in common; and (b) the phylogenetic sequence of events, including branching of lineages, in the history of the organisms as ascertained by the shared possession of derived features among other methods. The best classification is the one that maximizes simultaneously both of these semi-independent variables, not just one of them. Classical evolutionary classification is the approach, in my opinion, that achieves this simultaneous maximization of both variables, and hence provides the best system of classification for all comparative studies in biology.

Two points must be emphasized. First, that I do not claim that classical evolutionary classification is the correct approach to biological classification and that

phenetics and cladistics are wrong. Rather, I claim that using the criterion of a higher degree of empirical content or of testability, evolutionary classification provides the best foundation for all biological comparisons. Second, that this criterion for the best classification is the most essential distinction between classical evolutionary classification on the one hand and phenetics and cladistics on the other. After completing this manuscript and reviewing it in preparation for the symposium discussion, I realized that most, if not all, of the remaining comments on the philosophical foundations of evolutionary classification apply equally well to cladistics and phenetics. That is, the basic ideas of cladistics and phenetics could be reduced to the concepts to be presented below although they may not be so expressed by the proponents of either school of classification. Nor will all advocates of cladistics or phenetics agree with the positions I adopt, such as how definitions should be presented or the central role of homology.

PHILOSOPHY OF SCIENCE

Biological classification is a science, and as such should be treated within some philosophical framework of the criteria of scientific theories and methodologies. Herein, I accept the philosophical approach to science advocated by Karl Popper in his "The logic of scientific discovery" (1968a) and later in his "Conjectures and refutations" (1968b) and "Objective knowledge" (1972). And I would advocate that the theory and particularly the methodology of biological classification should be formulated according to the Popperian philosophy of science.

Popper's basic philosophy of empirical science may be summarized in two points. First, that inductive methods in science are not valid. Rather that science may "be described as the theory of *the deductive method of testing*, or as the view that a hypothesis can only be empirically *tested*—and only *after* it has been advanced." (Popper, 1968a:30). Second, that the

demarcation of empirical science from other areas of human thought which requires criteria that separate science from metaphysics but do not exclude from the domain of empirical science statements that cannot be verified. Thus Popper accepts as the criterion for demarcation of science the concept that scientific theories are capable of being disproven, not proven or confirmed. He states (Popper, 1968a:40-41):

“But I shall certainly admit a system as empirical or scientific only if it is capable of being tested by experience. These considerations suggest that not the *verifiability* but the *falsifiability* of a system is to be taken as a criterion of demarcation. In other words: I *shall not* require of a scientific system that it shall be capable of being singled out, once and for all, in a positive sense; but I *shall* require that its logical form shall be such that it can be singled out, by means of empirical tests, in a negative sense: *it must be possible for an empirical scientific system to be refuted by experience.*”

Thus, a classification, a phylogeny, a conclusion about homologous features or any other statement about relationships between organisms are scientific theories susceptible to testing in the attempt to disprove them by empirical observations. Numerous statements in the systematic literature that the available evidence proves some particular relationship or, in a more sophisticated sense, that affinities between organisms can be demonstrated with varying degrees of probabilities are invalid and suggest a fuzzy comprehension of scientific philosophy and methodology.

After a scientific theory, e.g., a particular classification, has been tested repeatedly with critical or severe tests and has repeatedly failed to be disproven, then one can have confidence in that theory. More precisely, one says that the theory has been corroborated. The term “corroboration” is preferred over that of “confirmation” (Popper, 1968b:57) because of the misuse of the latter term and its confusion with

“verification.” A theory that has withstood many attempts to disprove it with severe tests possesses a high degree of corroboration. These are not highly probable theories as Popper emphasizes (1968b:58), namely that: “Although we seek theories with a high degree of corroboration, as *scientists we do not seek highly probable theories but explanations: that is to say, powerful and improbable theories.*”

Thus, scientific theories cannot be proven or verified, but can only acquire a high degree of corroboration after repeated failures to falsify them. This is clearly seen in any statement about relationships. Biologists may have great confidence in some highly corroborated classification—until someone disproves it in a severe test using newly discovered evidence.

Popper’s philosophical approach to science is not new; he served the important role of stating these ideas in a clear, concise fashion and generalizing them into a unified philosophy of science. Ghiselin’s discussion (1969a) of the hypothetico-deductive method as used by Darwin is a somewhat specialized analysis of the general philosophy stated by Popper. The “method of reciprocal illumination” advocated by Hennig (1966:21) is a similar but more specialized expression of the same concepts. Unfortunately, the Popperian philosophy of science has not been broadly applied to classification even tacitly. Indeed, it is surprising how few systematists are aware of these ideas; Mayr, and Ghiselin (1969a, b) are among the rare exceptions. It is my belief that the theory and methodology of biological classification must be formulated in terms of the Popperian philosophy of science before a truly valid foundation can be established.

Evolutionary classification can be expressed in Popperian concepts—and quite easily, I believe, because of the earlier analyses of Mayr, Simpson and others. Space does not permit further elaboration of details, but a general analysis of the theory of evolutionary classification convinces me that it is consistent with Popper’s basic ideas.

A greater problem lies in the methodology and especially in the tests used in the attempts to falsify taxonomic statements. Less has been done in this area of evolutionary classification and it should therefore be an interesting area for future research. Several promising areas of investigation can be pointed out.

First is the establishment of which statements about affinities are valid scientific ones and what type of tests can be used in falsification attempts. In recent years, several authors have argued that statements about sister group relationships are testable, but statements about ancestral-descendent relationships are not testable. Clearly both types of statements are scientific in that they are capable of testing and falsification by empirical evidence. But the type of tests and the difficulty involved in attempts to falsify these two types of statements are quite dissimilar.

Second is that severe tests for disproving systematic statements must be developed. Not all types of empirical observations provide tests of equal severity, and the sorts of tests that may have been developed in the attempt to verify taxonomic statements are generally radically different from those that serve to falsify these assertions. Some tests are available, as for example the consistency test advocated by Wilson (1965, 1967; see Bock, 1969b), the use of paradaptations (Bock, 1967, 1969a), and the use of phyletic sequences of derived features.

It is interesting to note that phenetic approaches appear to provide the best methods to formulate taxa and classifications, but that cladistic methods appear to provide the most severe tests by which to attempt to disprove these taxonomic statements.

Third is that a change in style of taxonomic papers may be useful. Instead of presenting the classification to be advocated at the end of the paper among the conclusions, it might be better placed in the introduction. The factual evidence can then be presented in a series of tests designed to attempt the falsification of the

particular classification already advocated. The fact that an author will not successfully disprove a new classification advocated in the same publication does not argue against this sequence of presentation. The advantage to be gained is that the reader knows what statements are available for disproof, what tests will be attempted and hence why certain empirical evidence is being presented.

I believe that if attention is given to these methodological problems, that some major gains can be achieved in biological classification.

DEFINITIONS

The philosophy of definition of words is one of the most difficult subjects in philosophy and one in which I find myself a real novice. A few points of importance to biological classification can be made.

The paramountcy of consistent usage of words cannot be overstressed. Workers in any field of inquiry are constrained to maintain long established definitions and usages of words. Otherwise exchange of ideas becomes difficult if not impossible. Numerous needless controversies have arisen over the past decade largely because of redefinition of long established terms such as "monophyly" by cladists; I shall use these terms in the sense that they have always had in evolutionary classification. If the need arises to express new concepts in the development of any scholarly pursuit, then new words must be coined. The importance of maintaining consistent usage of words in discussing classificatory theory and methodology is as urgent as the need to maintain usage in scientific names for taxa for which elaborate codes and international commissions have been established.

No philosophy of definitions or of the meaning of words is inherently wrong or correct. The major impression I have from reading a number of articles in this area is the ease with which philosophers can uncover flaws in any general scheme of definition. As such, I reject the notion that only operational definitions are valid in

science. Operationalism may be a valid approach to definition, although the telling critique of operationalism by Hempel (1952, 1965) should be considered carefully before adopting this approach. It is my opinion that operational definitions are poorly suited in a historical biological science such as classification. Thus I prefer not to use operational definitions. Moreover, it must be emphasized that the failure to define classificatory words operationally does not mean that these words cannot be defined.

The approach to definition that I favor may be called "theoretical definition" in which the formal definition of the word is the concept and the word, so defined, stands for the concept. Hence, the word "species" is defined, for example, using the biological species concept. Other categories, such as genus, family and so forth, can be equally well defined. The only distinction between the definition for species and those for the higher categories is that the species definition can be associated with a definite biological phenomenon, namely lack of gene exchange. Other words, such as "phylogeny" and "homology," can be equally well defined in noncircular fashion. These definitions, in contrast to operational definitions, do not necessarily tell us how to recognize objects in nature to which the word can be applied.

A clear distinction must be made between the word defined and the objects in nature to which the word is applied. In classification, this distinction exists between the word "homology" and particular homologues that must be recognized. The same distinction exists between categories and various taxa that exist at different categorical ranks. Categories such as species, genus, and family have been clearly and succinctly defined. Numerous difficulties still exist in the methods by which taxa of different categorical ranks are recognized and distinguished from one another, but these difficulties do not detract from the formal definitions.

Words are defined, but then working

methods must be developed by which objects in nature are recognized and the defined words are applied to them. These recognizing methods are analogous to the operations in an operational definition, but are separate from the definition and do not limit its application within a rigid set of bounds. The words, especially in a historical science, are often defined in terms of one set of ideas or concepts and applied to objects in nature using another set of recognizing criteria. Thus the "species" may be defined in terms of reproductive isolation, but species taxa are generally recognized by means of morphological criteria (Mayr, 1963). Likewise the criteria for definition and those for recognition differ for "homology" and for "phylogeny." It is not necessary that the criteria used to apply the term to objects in nature be the same as the criteria in the definition. The two sets of criteria must be interconnected and the use of a particular set of recognizing criteria must be justified. Moreover, no assurance exists that words will always be applied correctly to objects in nature using any particular set of recognizing criteria. Species may be incorrectly described and false homologies are often recognized. Such errors testify to the difficulty, and the interest, of the science, but do not detract from the validity of this approach to definition.

A final word must be said about categories and taxa as the distinction between these is still confused by some taxonomists. Categories, such as species, genus and family, are words and hence are defined. Good, clear definitions exist for all categories, although only the species definition can be affixed to a definite biological phenomenon. Taxa are groups of organisms and hence are real objects in nature which are recognized, delimited, described and named. Taxa are never defined. Names are never defined. And it is not correct to speak of one's concept of a taxon such as one's concept of the Dinosauria. These taxa exist in nature, and they are first recognized, hopefully correctly, and then de-

scribed and named. It may be valid to say that we lack definite, clear and rigid criteria with which to recognize and delimit taxa at various categorial levels, and that effort should be put into this phase of systematic work. But this is an entirely different matter from definition of these categories. Unless this distinction is maintained clearly, systematics will return to the confusion that characterized much of the theoretical taxonomic discussions of the 1940's and 1950's.

PRINCIPLES OF COMPARISON

The philosophy of comparison is closely akin to that of definition and is another difficult subject. Nevertheless, comparative studies have always been an important part of biology, and a bit more can be said than about definition. I do, however, object strongly to the notion of "the comparative method" used in a vague sense and to a sharp distinction between "comparative biology" and "functional biology." Both approaches are and must be used in all areas of biological inquiry. Moreover, the principles and methodology of the comparative method, together with the sorts of interpretations that may be reached validly, must be stated clearly. I shall comment only on a few of the cardinal principles.

Any comparison made between objects in nature must be based on some definite philosophical foundation; the notion that "pure comparisons" can be made is simply invalid. Many different philosophies may exist, both scientific and nonscientific, but again none of the scientifically valid ones may be definitely shown to be correct or wrong. Because the results of any comparative study are dependent upon the philosophical basis accepted, the choice of this foundation is crucial. Herein, I will use again the criterion advocated by Popper of higher degree of empirical content or of testability as the basis on which to choose a philosophical basis for comparison.

A commonly offered suggestion is that all comparisons, whether of living organisms or of inanimate objects, are the same and

use the same philosophical foundation; this assumption is used in many phenetic approaches to classification. I reject this suggestion on the grounds that it is not of the greatest use. Comparisons of organisms made under this philosophy do not have the greatest possible content. Moreover, comparisons in all areas of science are not made on the same philosophical basis. Chemical elements are compared on the basis of the periodic table. Rocks and minerals may be compared on the basis of their composition and origin, but they may also be compared on the basis of coloration which would be less useful in petrology. Stars are frequently compared on the basis of their mass and brightness or temperature.

The best philosophical basis for biological comparison, in terms of greatest content, is organic evolution. The rationale for this decision is, as stated above, the notion that all attributes of organisms are the result of their past evolutionary history. Thus, the most meaningful comparisons are those made using a set of principles and methodologies based on the theory of organic evolution. This is the philosophy used, albeit often tacitly, by evolutionary systematists since Darwin. Much interesting work still remains to be done in formulating and further clarifying the principles of biological comparison based on evolutionary theory. Some of these principles may be mentioned briefly.

1) The concept of homology is central to all biological comparison and will be discussed separately.

2) Not all comparisons between pairs of species are the same and not all interpretations can be applied equally to all comparisons. A distinction must be made between horizontal and vertical comparisons (Bock, 1967, 1969a). Horizontal comparisons are those between members of different phyletic lineages. Vertical comparisons are those between members of the same phyletic lineage. Care must be exercised in stating that all biological comparisons are between pairs of species because a vertical comparison is made be-

tween different time segments of the same phyletic lineage and, as such, cannot be regarded as a comparison between different species. A phyletic lineage is formed by the consequence of a single species descending through time (Bock, 1973). A cross-section of a phyletic lineage at any point in time is a species, but it is not valid to consider cross-sections of the same phyletic lineage at different times as different species.

It must be noted that one often does not know whether comparisons (actual or theoretical) are vertical or horizontal because the particular phyletic lineages are unknown when the comparisons are made. Rather, the differing types of interpretations reached on the basis of these comparisons may permit the conclusion of whether the comparison was horizontal or vertical, and hence whether one is dealing with members of the same or of differing phyletic lineages. Actual comparisons between all Recent species are, by definition, horizontal because these species are all members of different phyletic lineages.

Some of the differing interpretations of horizontal versus vertical comparisons have been discussed in my earlier papers (Bock, 1959, 1967, 1969a; Bock and de W. Miller, 1959). Differences observed in vertical comparisons are frequently adaptive in terms of the selection forces operating during the evolutionary changes. Differences observed in horizontal comparisons are frequently irrelevant with regard to these selection forces. This conclusion has led to the notion of multiple evolutionary pathways (Bock, 1959) and to the concept of paradaptation (Bock, 1967) which are closely related to the idea of chance versus design in evolution (Mayr, 1962). The concept of paradaptation provides the basis of a valuable test of relationships (Bock, 1969a).

3) The origin and radiation of taxa does not involve random evolutionary change in the attributes of the group. Rather, only some features are modified and these changes are constrained within limits set

by the genotypic and phenotypic characteristics of the group. Thus the attributes present in members of any taxon should be similar and should be strongly correlated with one another. This pattern of similarities and correlation between features has been the foundation of phenetic methods that predate Darwin. In recent years, many valuable methods have been developed to analyze these phenetic correlations (e.g., Sokal and Sneath, 1963).

4) In addition to evolutionary change being constrained within narrow limits during the radiation of any taxon, these modifications occur in a definite sequence. Any evolutionary modification is dependent to a large extent on the preceding changes. These sequential events can frequently be reconstructed providing valuable comparative information that cannot be ascertained in phenetic comparisons (e.g., Hennig, 1966). These phylogenetic comparative methods had their origins in evolutionary theory; indeed, Darwin showed the extreme value of establishing "pseudophylogenies" as a comparative method. These methods have been established on a firmer footing with the rise of evolutionary morphology during the last two decades.

HOMOLOGY

Homology is, without question, the most important principle in all comparative biology. Moreover, it is possible that homology is the only method of comparing attributes of different species and that all other methods of comparison are reducible to homology. I do not wish to defend this position in this essay, but would like to express the opinion that any comparative method in conflict with the concept of homology is strongly subject to question and scrutiny.

A widely accepted definition of "homology," and the one I advocate, may be stated as follows (Bock, 1969a, c): "A feature (or condition of a feature) in one organism is homologous to a feature (or condition of a feature) in another organism if the two features (or conditions) can be traced phylogenetically to the same feature

or condition in the immediate common ancestor of both organisms.” Thus “homology” is defined in terms of “phylogeny,” and “phylogeny” can be defined in terms of “evolution” (Bock and von Wahlert, 1963). This definition is noncircular and is not an operational definition.

Homology is not an intrinsic property of a feature, such as its mass or color, but is a relationship depending upon the existence of corresponding features in other organisms. Because homology is a relational concept and because the degree of relationship varies, one must always state the nature or condition of a particular set of homologues. That is, any statement about the homology of features in different organisms must include a conditional phrase describing the nature of the relationship. Thus it is erroneous to say that the skull of a horse is homologous, or to say that the humerus of the gorilla is homologous to the humerus of the chimpanzee. Rather, one must say that the wing of birds and the wing of bats are homologous *as the forelimb of tetrapods*, or that avian wings and chiropteran wings are not homologous as aerodynamic planes. The conditional phrase describes the nature of the feature in the common ancestor from which the homologous features stemmed phylogenetically.

Hierarchies of homologues can be established by restricting the conditional phrase more and more, and ascertaining whether the features are still homologous. These hierarchies can be inclusive, nonoverlapping ones, or they can be sequential ones, or a combination of both. The inclusive, nonoverlapping hierarchies of homologues, thus established, correspond to ever closer relationships of the organisms in a phenetic sense. The sequential hierarchies, if arranged according to the presumed phylogenetic series of events, correspond to the sequence of derived features in a cladistic sense.

The use of conditional phrases in homology demonstrates that no distinction exists between characters and character states. The latter are simply characteristics which

may be homologous with a more restrictive conditional phrase.

The phylogenetic definition of homology is a nonoperational one and does not provide the methodology by which homologues are recognized. The recognizing criteria used in ascertaining homologues are similarities of all sorts (Bock, 1969a:415–416), be they of appearance, material composition, positional relationship with other features, embryological or whatever. Moreover, similarity between features is the only criterion by which homologues can be recognized. Here I must emphasize that the defining criterion for homology is phylogeny, but the recognizing criterion for homology is similarity. I do not advocate a definition for homology based on similarity.

The rationale for using similarity as the recognizing criterion of homology is simple. If features in different organisms are considered to be homologues, then these features were the same, and self-identical, in the common ancestor. During the course of the separate evolutions of the phyletic lineages leading to these organisms, the homologous features in each lineage underwent some, and usually different, changes. But those attributes of these homologous features that did not modify during the evolution from the common ancestor would still be the same. Hence shared similarities can be interpreted to be ancestral similarities and unchanged since the self-identical condition in the common ancestor, and hence provide the evidence on which to judge the homology of features in different organisms. To be sure, similarities can arise via other evolutionary mechanisms, such as independent origin, parallelism and convergence (see Throckmorton, 1965, for an interesting analysis of these complicating factors), which make classification the difficult and interesting subject it is, but do not affect the statement that similarity between features is the only method for recognizing homologues.

Unfortunately, the methods by which homologues are recognized and distinguished from nonhomologous features have

low resolving power (Bock, 1963, 1969a). Thus, numerous errors will be made in decisions on homologous features, especially in judging many nonhomologues to be true homologues. These errors cause problems in actual systematic studies, but they present no difficulties for theoretical considerations of the concept of homology. Systematists have been far too concerned about making errors in recognizing homologues. Little can be done because the available methodology possesses such low resolving power and no other methods exist. Decisions on homologues must be made and the probable errors may be recognized once classifications with a high degree of corroboration have been achieved.

The sequence of study and decision must be carefully observed to avoid the trap of circular reasoning. The first step is a comparative study of features in different organisms. Decisions on homologues, including the conditional phrases, are made on the basis of observed similarities regardless of the number of errors made. The patterns formed by the homologues, including the inclusive, nonoverlapping hierarchies and the sequential hierarchies of conditional phrases, are used to deduce the phylogeny and the classification of the organisms. Needless to say the numerous errors in recognizing homologues causes great difficulties at this step. And, hence, the basic principle has been developed of basing classifications on many characters.

Two general approaches have been developed to overcome the difficulty arising from the low resolving power of methods to recognize homologues and the many resulting erroneous homologues. These are:

1) The use of an extremely large number of characters in deducing a classification as advocated by the numerical taxonomists who recognized this problem clearly. They argue, perhaps tacitly, that many of the homologues used in classification are wrong, but the use of a large number of characters will provide sufficient correct homologues, even if they are unknown, on which to base a classification. Even if only ten percent of the homologues are correct,

a valid foundation on which to deduce classifications can be obtained if several hundred features are used. This approach is based on the assumption that the "noise" generated by the incorrect homologues will cancel out and not affect the final conclusions; this assumption appears to be generally valid.

2) The careful study of each feature and rejection of those in which the possibility of error in the judgement of homology is high. The features used in deducing a classification are reduced to a much smaller number, but each feature is one in which the taxonomist has more confidence in the initial decision on homology. This approach has been used extensively in evolutionary classification under the notion of "weighing of characters." Much of what has been done in weighing of characters is not justified, but I believe that some of the newer methods developed in evolutionary morphology will permit homologies to be recognized on firmer reasons. My preference is for this approach mainly because it permits many interesting morphological and evolutionary studies along with the taxonomic analyses. But I believe that both approaches, if properly used, provide equally valid bases to deduce classifications.

No information derived from the presumed relationships of a group of organisms can be used to recognize homologues. This includes any information from their classification, phylogeny or possible intermediate position of taxa. Use of such information would result in circular reasoning if these homologues were used to test the presumed relationships of these organisms. Thus it should be noted (Bock, 1969a:416) that one of Remane's major criteria for homology (1956:58) and all of his supporting criteria depend on earlier conclusions about relationships and should not be used. Theoretical analyses of comparative methods (e.g., Bock, 1963, 1969a) in which "false homologies" are discussed on the basis of classifications with a high degree of corroboration must be done with care because the "false homologies" may

not be incorrect at all and may represent the critical test disproving the classification.

All statements about homologous features and phylogenies are scientific theories, and hence may be disproven, but never verified. At best they can acquire a high degree of corroboration, after which systematists have such confidence in them that they rarely bother to test them.

All comparative methods in biology depend, I believe, on homology. The length of time involved in the comparative study of features, deciding homologies and deducing classifications is of no importance. The initial sorting of specimens into species and grouping of these species into taxa of higher rank may be done extremely rapidly on the basis of superficial examination. Likewise, the recognition of new species and their assignment to the correct higher taxa may be done very rapidly by an experienced taxonomist. But the procedure followed, no matter how fast it is done, is to make a large number of decisions about homologues complete with conditional phrases based on recognizing criteria of similarity and then to use these homologues to deduce relationships. The speed at which the human mind can operate should not be underestimated, even compared to modern high-speed computers. But this speed should not be misinterpreted as some other procedure used in classification. Taxonomists do not establish taxa and systems of classification by some method other than homology and then test them by studying homologies. (One can, of course, establish classifications by some stochastic method and then test them, but few taxonomists would be interested in this approach.) Classifications are deduced on the basis of previously established homologues, no matter how rapidly done, which then serve as falsification tests for the classification. More severe falsification tests can be undertaken by careful study of certain features, which is the meaning of statements that taxa are established first and then tested by studying homologues. In such tests, one must always decide which homologues are "best," that is, in which

homologues does one have the greatest confidence.

The statement that all valid methods of classification must be reducible to the concept of homology, or at least not be in conflict with it, suggests a serious internal conflict in cladistics as formulated by Hennig (1966). To my knowledge, no later proponents of cladism have rectified this contradiction. The conflict stems from the above assertion that all comparative methods are based on the concept of homology—that homologues must be recognized before further work is possible—and that the only criteria for recognizing homologues are similarities of all sorts. This must be coupled with the notion that homology is a relative concept and that all statements about homologues must contain a conditional clause giving the nature of the homology.

Hennig (1966:10; 12; 23; and 88) states clearly that similarity is not a factor used in judging relationships; no possibility exists to interpret his statements otherwise. Relationships are based on common possession of derived homologous features. Yet, he (1966:93–94) accepts Remane's (1956) definition and methodology of homology although this part of Hennig's book is rather confused. Remane's methods of recognizing homologues are basically the same as those outlined above; they depend on similarities. Thus it is not possible to reject similarity between features as a factor in deducing classification and to base classification on homologous features which is a primary requirement of any approach to biological classification. This contradiction is a serious one, and unless it can be resolved by cladists, I believe that it eliminates the distinction claimed by cladists between their approach to classification and that of evolutionary taxonomists.

As a conclusion, I would like to offer the opinion that any approach to biological classification that excludes homology and its recognizing criterion of similarity as a primary step in deducing relationships is invalid.

WEIGHING AND TESTING

The concepts of weighing of characters and testing of classifications appear to have little to do with one another, but development of proper tests of falsification have considerable bearing on the importance of weighing of characters. The whole subject of relative weight of taxonomic characters is riddled with difficulties, has been weakly defended against major challenges, and yet has emerged unscathed. Satisfying arguments supporting the notion of weighing characters are hard to find, but really devastating arguments against this idea do not exist.

Only a slight experience with actual taxonomic problems is needed to realize that different features possess varying degrees of usefulness for classification, and that some form of weighing characters is useful. The alternative is not to weigh characters and to use very large numbers, as done in some forms of phenetic analyses. Although the basic assumptions of nonweighing approaches are valid, no one has really solved two problems. The first is the assumption that the noise of the large number of "poor" characters really cancels out without affecting the classification. Second is whether the efforts of measuring, recording and otherwise handling the large number of characters needed in nonweighing approaches are justified by the results obtained.

The major objection against weighing of characters is that few workers ever suggest what they mean by better characters or outline the procedures used to weigh them. Opponents to weighing are probably justified in claims that most weighing is done a posteriori after the classification had been established.

Nevertheless, if one accepts the validity of evolutionary phenomena of independent origin and convergence of features, and realizes that many decisions about homologues are wrong, then it must follow that some features are better clues to relationships and should be given more weight. This can be done even if one cannot state clearly why more weight is given to some

features. Such a procedure is not satisfying though to many workers.

The major concern is that circular reasoning must be avoided in assigning relative weight. Features must be weighed before the taxa are recognized or the classification deduced. Thus arguments that features unique to a group should be given more weight are invalid. So are conclusions that conservative features be weighed more unless independent evaluation of conservative characters can be given. High correlation with other features is probably not a valid criterion for assigning great weight because this decision is dependent upon prior recognition of taxonomic groups.

Some valid criteria do exist for judging relative value of taxonomic characters. Perhaps the best and most widely used is the complexity of the feature. A complex attribute with many interconnected parts is usually given more taxonomic weight than a simpler one because the possibility of independent evolutionary origins of a complex feature with many similar parts is less than the chances of independent evolution of simple features. The evolutionary origin of a new feature or major change in an existing feature is usually given greater weight than the loss of a feature, again because the chances of independent loss of a feature is greater than the independent origin of similar features. Most of the successful applications of character weighing have used criteria such as these, but problems arise again when features of similar complexity suggest conflicting classification.

The whole notion of character weighing may be of considerably less importance to classification than believed earlier once the full implications of the Popperian philosophy are applied to taxonomy. If classifications and phylogenies are deduced statements available for disproof by empirical testing, a very different approach to taxonomic features can be used in which relative weight may have no role. If some empirical evidence disproves a statement of relationship, then it matters little whether the features are of great value or

of little value taxonomically. More essential is the development of severe or critical tests which can provide a strong basis of falsification. Such tests, as Wilson's consistency tests, do exist, as mentioned above, but more effort is needed to develop and evaluate them.

It should be obvious to working systematists, that such tests will be no better than the characters used in them. And application of falsification tests will soon result in the situation of two severe tests using different features with conflicting results. Such situations will lead right back to evaluation of characters and hence arguments of weighing. Before we worry about completing the circle, I believe that serious attempts should be made to develop a good series of falsification tests, apply them and assess the results before pursuing further arguments on weighing.

CLASSIFICATION AND PHYLOGENY

The only question that I would like to investigate is whether the phylogeny of a group and the formal classification for that group must be absolutely concurrent. The principle that the formal classification should reflect the evolution of a group does not mean that a one to one relationship must exist between the classification and the phylogeny of the group. Nor is such a relationship necessary. The basic principle of evolutionary classification, and I believe most biological classification since Darwin, is that classification reflects the evolution, not just the phylogeny, of the group. And under the concepts of evolutionary classification, in which the formal classification is an attempt to maximize simultaneously the two semi-independent variables of genetic similarity and phylogenetic sequence, a one to one correlation between the classification and the phylogeny of the group is impossible.

Thus it is not possible to provide simple rules of how to derive the classification from the phylogeny of a group, or of how to regain the same phylogeny from the classification.

Because in evolutionary classification, the phylogeny and the formal classification are not different but redundant images of each other, neither one by itself is sufficient. To be most useful, the results of any study of the relationships within a group of organisms must include a formal classification and a phylogenetic diagram in its conclusions. Both are needed to provide the maximum information about relationships required by other biologists for their comparative studies.

CONCLUSION

In conclusion, I believe that a firm philosophical foundation exists for classical evolutionary classification and can be expressed in the form of a set of principles. And I believe that classical evolutionary classification is the best approach to biological classification which must provide the foundation for all comparative studies in biology. Classical evolutionary classification is based on the Popperian philosophy of scientific demarcation and methodology and on the modern synthesis of Darwinian evolution—namely that classification of organisms is based on their entire evolutionary history not just on their phylogeny or on their degree of similarity. In this eclectic approach, relationship between organisms, as expressed in formal taxa, attempts to maximize simultaneously the two semi-independent variables of degree of similarity and of phylogenetic sequence of events. The resulting classification may be subjective in that each taxonomist will not necessarily reach the same conclusions, but it provides the most realistic picture of the complexities of biological diversity.

Lastly, although the focus of this essay is on the philosophical foundation of biological classification and on theoretical considerations of methodology, the major plea should not be for emphasis in this phase of systematics but for more detailed systematic analyses of plant and animal groups. Historical study of the improvement in the classification of any taxon

suggests that the major reason for improved comprehension of the systematic relationships between these organisms has been a more thorough, detailed study of their characteristics, not the application of new or different philosophical approaches to classification. Continued success and survival of classification as a biological science will depend on the abilities of systematists to produce improved classifications that serve as the basis for all comparative studies in biology.

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