THE RELATIONSHIPS OF THE HIGHER TAXA OF BIRDS: PROBLEMS IN PHYLOGENETIC REASONING

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It will be the thesis of this paper that the relationships of the higher taxa of birds (here, subfamilies and higher) are very poorly understood and consequently that our classifications reflect this lack of knowledge. Indeed, the disparity between what many ornithologists might interpret from the classifications that have been published and the reality of avian phylogeny is so great that our classifications can scarcely be called "phylogenetic." I want to discuss the reasons for this situation and will attempt to show that avoidance of certain kinds of phylogenetic reasoning should help to improve our understanding of avian relationships. A major purpose of this paper, then, is to review the theories and methods used within avian systematics. To my knowledge this has not been attempted previously, and such an examination will hopefully prove useful since there now seems to be a renewed interest in morphological and systematic work in ornithology.

At the outset I want to emphasize that this paper is concerned with the study of phylogeny and not with the theory or methodologies used to construct classifications. I consider the problems of classification to be secondary to those of phylogeny, because a proper understanding of the latter is a prerequisite for the study of numerous evolutionary phenomena (see below). A given theory of phylogeny need not have a close correspondence with any specific theory of classification. Of course, classification cannot be divorced entirely from phylogeny since the former depends (at least in most taxonomic philosophies today) on knowledge of the latter, but I believe the central issues confronting avian systematics lie within the domain of phylogenetic inquiry rather than that of classification per se. Hence, I will restrict this discussion to the theories and methodologies used to determine relationships within the higher taxa of birds.

In the following pages I will use the term "relationship" in the sense of recency of common ancestry (genealogy). Thus, two taxa are more closely related to each other than to a third if they share a common ancestor that is not at the same time an ancestor of the third taxon. The term "relationship" defined in this way will be devoid of the notion of degrees of morphological resemblance or divergence. A more detailed treatment of this approach to relationships will be presented below.

RELATIONSHIPS OF THE HIGHER TAXA: STATEMENT OF THE PROBLEM

It probably is a general impression among many ornithologists, including some systematists, that the phylogenetic relationships of avian families are fairly well understood. This conclusion might follow from the various major classifications (but less so from their accompanying discussions) such as Mayr and Amadon (1951), Wetmore (1960), or Storer (1960b, 1971), none of which is drastically different from the other. Moreover, the most widely accepted classification, that of Wetmore (1930, 1951, 1960), has not changed significantly in three decades. However, as Stresemann (1959:274) notes, the considerable number of detailed systematic studies "have made it apparent that the relationship of certain species or groups of species is far less unequivocably established than one would conclude from a study of currently adopted systems, the authors of which attempt to present a simplified phylogenetic tree of birds."

A paradox seemingly exists within the current state of systematic knowledge. On the one hand, our classifications suggest a stable system, one in which our ideas about relationships seem to be either rather firmly established, or alternatively, one in which we have little confidence in the systematic work on the higher taxa; in either case, we have the appearance of a system which embodies a seemingly unlimited amount of inertia. On the other hand, the large number of systematic papers appears to tell us that the classifications need a major revision, that they may reflect conservatism of opinion rather than reality.

Part of the problem, I think, is that systematists have emphasized "classification" to the detriment of determining phylogeny; that is,

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we have not been interested in the construction of specific scientific hypotheses such as which family might share a most recent common origin with another family but rather in more general problems such as to what family or to what order this or that taxon might conveniently be placed. The desire to have a "stable" or "orderly" classification is understandable but, in our quest for this stability, classification has become the proverbial cart to the phylogenetic horse.

As was implied above, many of the morphological studies attempting to resolve the relationships of "problem taxa" have not been well received or adopted by the majority of systematists. Dissatisfaction with these studies is leading either to a state of near apathy in which it is assumed we can only "subjectively" determine relationships (Stresemann 1959) or, to the use of techniques by some workers that appear to them to hold almost unlimited promise in resolving relationships (e.g., Sibley 1960, 1970) but which, in fact, seem to promulgate the same theoretical and methodological problems as the work they criticize.

Still, the question must be asked why many morphological investigations, whether of molecules, muscle, or bone, fail to arouse widespread support. Is it because the workers have not produced detailed comparative studies? I do not think this is the case. We have steadily accumulated comparative data but they seem to be leading us nowhere in determining avian relationships. Rather, I suspect that we have failed to consider in detail the theoretical and methodological background with which to analyze the data that have been collected. Obviously, the theoretical framework used by a given investigator influences strongly the manner in which he gathers and interprets his data. Unfortunately, there has been little direct discussion as to the working methods employed by different avian systematists. In my opinion, an interchange of theoretical ideas may enhance the value of future morphological work, and I hope that this paper can contribute to such a discussion. In a sense, the paper is presented with the idea of challenging the status quo but also, and more importantly, with the desire of finding some methods that will give us the answers to our questions about avian relationships.

DETERMINATION OF PHYLOGENETIC RELATIONSHIPS

Before discussing the approaches that have been used by various ornithologists to determine phylogenetic relationships, it is necessary to present the viewpoint advocated here. Such a procedure will then provide a basis on which the discussion of previous work can be compared and evaluated. In principle, I am supporting many of the ideas formalized by Hennig (1966) and commonly termed cladistics or phylogenetic systematics. I am not claiming unqualified acceptance of all of his theories or methods, but I do believe that his system contains those methods offering the best chance of determining phylogenies within the higher categories of birds, and that his system is more objective than those in current use. For these reasons his work deserves close attention by avian systematists.

A discussion of the methodology involved in determining phylogenetic relationships (as (defined in the introduction) starts with several basic assumptions. Through the phylogeny of a higher taxon (e.g., the class Aves), every monophyletic assemblage of species (i.e., orders, families, genera) evolves certain character-states that are unique to that lineage. Thus, these character-states have been *derived* within these lineages after branching from their ancestor, and if we can recognize such character-states, then we will have a basis on which to define monophyletic assemblages. (In a very real sense, knowledge of the mere existence of these monophyletic lineages is dependent by definition on the recognition of derived characters.) However, the recognition of derived character-states is frequently difficult, and systematists have constructed a number of methodologies for their recognition (see below).

It is basic to cladistic theory that phylogenetic branching involves dichotomies (Hennig 1966). Theoretically, this should be accepted as a generality by most workers, especially when their concern is the higher categories. The supposed exceptions at the species level are few in number and lack detailed substantiation, thus the arguments raised by various critics fail to undermine the hypothesis of dichotomous branching (Darlington 1970). Even at the species level it is very improbable that populations which are postulated to have become isolated more or less at the same time will all attain species-level differentiation simultaneously. Hennig (1966: 211) correctly notes that "the impossibility of determining with certainty the sequence of dichotomous cleavages in a group never means that all the species arose simultaneously (by radiation) from one stem species." The use of cladistic theory does not guarantee that workers will be able to determine dichotomous relationships at all taxonomic levels. Indeed, I suspect that it will be difficult, if not impossible, to determine dichotomous intergeneric and interspecific relationships of many avian families, especially passerines.

When a species divides into two separate lineages, we can term these lineages "sister-groups" (Hennig 1966). Likewise, when we trace the evolutionary trends of homologous features in these sister-groups, we see that one lineage will possess a more or less primitive character-state of that feature whereas the other lineage will have a relatively derived character-state. If we repeat this procedure for a number of characters, we will discover that each lineage possesses both primitive and derived characters. It becomes obvious that if derived character-states can be identified, then monophyletic lineages can be constructed. It is equally obvious that taxa which share primitive character-states—i.e., those inherited from a distant ancestor—cannot be united on the basis of those characters. Figure 1A summarizes these conclusions. Each of the lineages, A–G, is defined as monophyletic because they each possess a suite of derived characters which have their primitive counterpart in the coordinate sister-group. If figure 1A is assumed to represent the true phylogeny, then a character analysis which yields the phylogeny of figure 1B would be incorrect (in this case the characters of suite 2, assumed to unite F and D/E, are in fact not derived). Thus, this theoretical system provides a straightforward method for invalidating a proposed phylogeny, and the invalidation is not based on ambiguous arguments about which groups share a greater number of "more important characters." Phylogenies can be refuted by (a) showing that a given suite of characters used to define the lineages are either primitive or of multiple origins, and (b) arguing for a different set of derived characters which yields a different phylogenetic hypothesis. If one is working with higher categories of birds, it should be possible to detect multiple origins of character-states if a sufficient number of characters are analyzed. If character 1 argues for a relationship between taxa A and B, and other characters (also seemingly derived) support a closer affinity between B and C, then one might suspect character convergence in character 1, depending upon the number of contradictory characters and the clarity of their evolutionary trends.

As I will try to support in a subsequent section, this theoretical model seems to be the best one available for determining relationships in a relatively unambiguous fashion, with a reasonable degree of confidence, and with a minimum of subjective decision making; the other approaches are either reducible to this in principle or they have a greater chance of producing erroneous phylogenies.

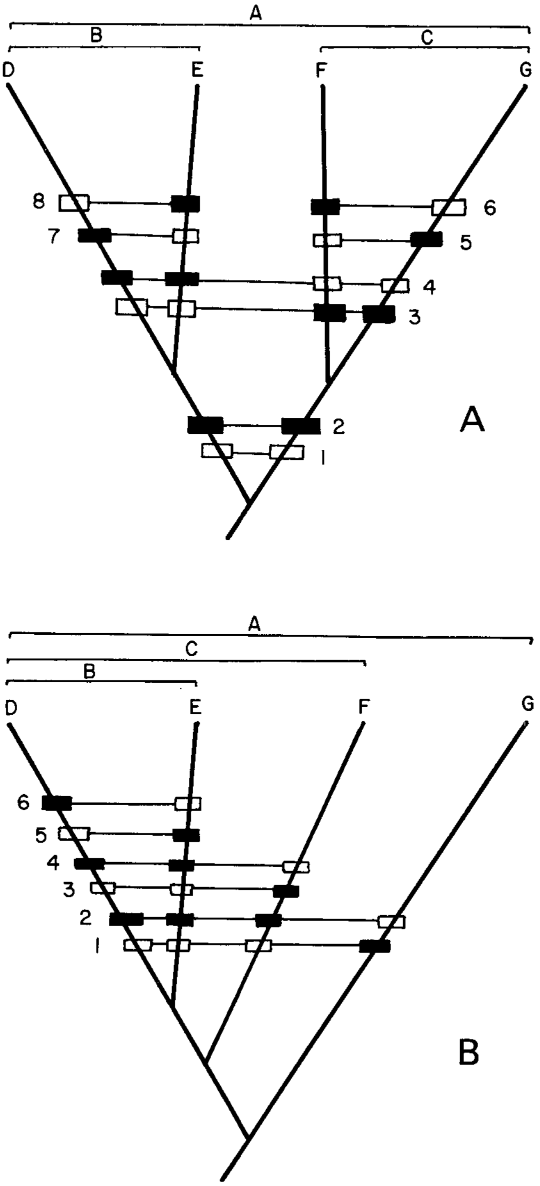

FIGURE 1. A, Dendrogram of a phylogeny assumed to be true. Dark rectangles represent derived character-states; open rectangles represent corresponding primitive character-states of same characters. Taxon B is defined monophyletic by character-state suite 4, taxon C by suite 3, and so forth. B. Phylogeny of taxa A–G arrived at by incorrect analysis of character-state suites 1–4. See text.

Accepting the above theoretical framework as valid for determining phylogenies, we must now consider the critical problem of developing methods capable of recognizing primitive and derived character-states. This problem has been discussed in detail by numerous workers (e.g., Maslin 1952; Simpson 1961; Hennig 1966; Mayr 1969; Crowson 1970; Kluge 1971) and need not be belabored here. Possibly without exception, these and other systematists agree that comparative analysis of the distribution of character-states is the best method (and parsimony the criterion) for recognizing the primitive condition. Thus, "a condition which occurs in related forms outside the group [under investigation] is probably primitive within it" (Crowson 1970: 106; see also the extended discussion in Hennig 1966:88ff). It is essential that a worker specify the hierarchical level for which he considers the character to be primitive or derived, because these latter characteristics are relative to taxa of different levels. For example, whereas the possession of feathers is a derived character *for* the class Aves, it is a primitive character *within* the group.

Obviously, it will not be possible to determine relationships within a given taxon unless a character analysis of closely related taxa is also made. On this basis alone many systematic papers in the avian literature are questionable for they provide little or no comparative basis on which to arrive at reliable judgments of primitiveness. The problem of deciding which "closely related taxa" to compare is frequently real and sometimes subjective. When the argument for considering particular taxa as close relatives is weak, then it is clear that one should make as broad a comparative study as possible before deciding what character-states are primitive.

A comparative analysis such as advocated above permits the recognition of evolutionary trends and also the direction of those trends. To my knowledge there exist no objective criteria with which to recognize the direction of trends outside of a comparative analysis.

Another method used to discern primitive character-states is the occurrence of these character-states at different levels in time. Primitive characters are generally expected to occur earlier in time. Whereas this may be and is frequently true, numerous exceptions can be found mainly because of the incompleteness of the fossil record. Differential extinction of species possessing derived character-states and/or uneven paleontological sampling can result in primitive character-states appearing later in time than derived character-states. The direction of these trends can be established only by a comparative analysis, and if the latter does not reveal trends, then time occurrence data should be avoided or interpreted with considerable caution. The congruence of evolutionary trends and stratigraphic sequences is not always reliable, and comparative analysis is our only independent means of checking this reliability.

A final method of recognizing a primitive character-state might be the use of developmental studies. For example, if we are attempting to determine the primitive-derived sequence of two bones which have apparently fused in some taxa, and we find in those taxa with a single adult bone that two were present in an early stage of development, we may be on firm ground in postulating the latter as the primitive condition. Although this method often can provide important data concerning character sequences, the amount of work will be too time-consuming for most systematic studies.

The recognition of the primitive condition is sometimes very easy, sometimes impossible. Usually it involves detailed comparative study. Occasionally, characters will be found that show an apparent derived condition in two taxa thought to be unrelated. Usually such multiple origins of derived characters may be detected by the study of numerous other characters which clearly define the taxa in question. Furthermore, derived characters can be lost or modified to a secondarily primitive condition. It is also possible that two sister-groups will each diverge so much from their common ancestor that relative degrees of primitiveness cannot be recognized for some characters. These problems merely indicate that this aspect of phylogenetic analysis requires detailed work and the realization that definitive answers are not always possible (see the workers cited above for extended discussions of these problems). In general, if it is not possible to tell primitive-derived sequences using distribution patterns of the character-states, it will usually be advisable to abandon the use of that character and thus not weaken phylogenetic hypotheses. It is my belief that if one is considering the relationships of the higher taxa of birds (especially nonpasserines where divergence is greater), an adequate number of characters (skeletal, myological, etc.) will almost always be available, and therefore rejection of some characters will not be a serious problem.

The theory and practical application of the above phylogenetic procedure are discussed in great detail by Hennig (1966), Brundin (1966), and Crowson (1970). The central issue which they raise is that affinities of two taxa can be demonstrated only by the use of shared derived character-states and that primitive similarities contain no phylogenetic information.

RELATIONSHIPS OF THE HIGHER TAXA: EXAMINATION OF PREVIOUS METHODOLOGY

It will be the purpose of this section to reexamine and analyze some past and present approaches advocated or used to determine phylogenetic relationships in birds. I will attempt to show that many of these approaches are more likely to lead to erroneous conclusions or produce relatively useless and ambiguous statements about relationships than is the method discussed above. It should be understood that this criticism is formulated from the preceding theoretical remarks.

GENERAL OVERALL RESEMBLANCE

That most ornithologists, past and present, have based or do base the relationships of birds on some notion of general overall resemblance can hardly be questioned. Nearly all of the 19th and 20th century morphologists have followed this approach. A characteristic statement, for example, would be that taxa A and B resemble each other more than either does C, therefore A and B are more closely related. Such an approach often leads to the vague and ambiguous conclusion that taxon A is intermediate in structure between B and C and therefore is related to both. Imprecise statements such as this abound in the systematic literature. With few exceptions, avian paleontologists use the overall resemblance argument for relationships. General overall resemblance has provided the foundation for a number of well-known classifications and is, I believe, the basis for the differences one sometimes sees in them (e.g., Mayr and Amadon 1951; Verheyen 1960; Wetmore 1960). Most, if not all, of the statements concerning relationships proposed by the molecular systematists (e.g., Sibley 1960, 1970; Sibley et al. 1969; Hendrickson 1969; to name only a few) have general overall resemblance as their principal working method. [The concept of general overall resemblance applies to those studies that "weight" their taxonomic characters as well as to those that consider their characters of equal weight (e.g., Schnell 1970a, 1970b). In terms of their basic approach, "weighting" seems to be of little importance to most ornithologists, especially since it is rarely discussed and procedures for weighting are not mentioned.]

The concept of overall resemblance, while having provided ornithology with the general outlines of avian relationships, has been one of the major causes for the ambiguity and conflict that I discussed in a previous section. This follows from the fact that such an approach has a large component of subjective decision-making and is easily susceptible to errors, stemming not so much from observation but from interpretation. Overall resemblance also provides no objective basis on which to judge the validity of the conclusions produced by this method. Cladistic methodology, while certainly not devoid of all subjectivity, uses a more critical and less subjective character analysis than does that of overall resemblance.

The primary reason for rejecting the concept of overall resemblance as a working method in avian systematics is that we never know whether the similarities being used to argue relationships are primitive or derived. Too often they are primitive and thus lead to incorrect conclusions. A classic example is the interfamilial relationships of the Galliformes. On the basis of overall resemblance several opinions have gained wide acceptance: (1) the Cracidae and Megapodiidae are more closely related to each other than to the other galliforms (e.g., Holman 1964; Wetmore 1960); and (2) the Eocene family Gallinuloididae is more closely related to the Cracidae than to the Phasianidae (Tordoff and MacDonald 1957; Wetmore 1960; Brodkorb 1964). Recently, Lester L. Short and I undertook a study of the interfamilial relationships of the fossil and recent galliforms, and we based our phylogeny on a detailed analysis of primitive and derived character sequences (see fig. 2). Although this study will be published elsewhere, certain results can be mentioned here for they provide an example of how the use of overall resemblance has led to erroneous conclusions. In figure 2 we see that the suites of characters used to unite the megapodiids and cracids and the gallinuloidids and cracids (suites 10 and 11, respectively) consist of primitive characters which are devoid of phylogenetic information since they were inherited from their common ancestor (character suite 1). Some primitive characters included in both suites 10 and 11 are the absence of an intermetacarpal process on the carpometacarpus and a shallow internal notch of the sternum. Holman (1964) lists numerous other similarities between cracids and megapodiids, and in nearly every case he himself claims they are primitive within the galliforms. Study of the skeletal anatomy of galliforms does indeed

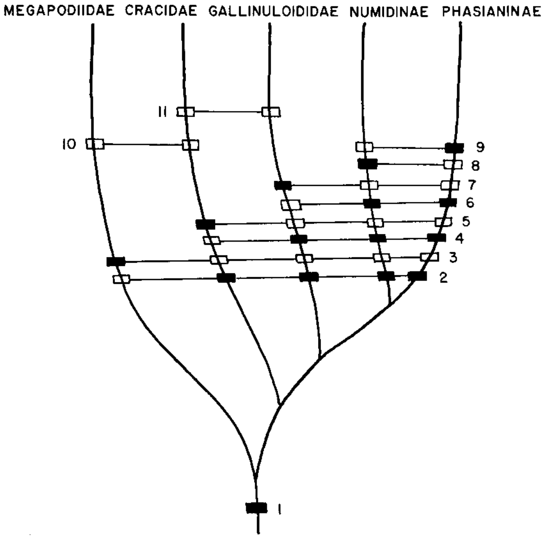

FIGURE 2. A phylogeny of the Galliformes based on an analysis of primitive-derived character-states. Note that suites of character-states 10 and 11 considered by some authors to unite Megapodiidae with Cracidae and Gallinuloididae with Cracidae are primitive and thus devoid of phylogenetic information. Dark rectangles represent derived character-states; open rectangles represent corresponding primitive character-states of same characters. See text.

reveal that the Megapodiidae and Cracidae share a large number of striking features, but in the absence of a character analysis based on valid systematic theory one cannot draw phylogenetic conclusions from these similarities.

A previous study of the relationships of some fossil gruiform families (Cracraft 1968) used general overall resemblance as a working method, and the affinities of some of these families were misinterpreted. A more recent investigation using primitive-derived sequences has shown, for example, that the Bathornithidae are not more closely related to the Cariamidae (Wetmore 1960; Cracraft 1968) but rather to other fossil gruiform families such as the Idiornithidae and (somewhat more distantly) the Geranoididae (Cracraft 1972).

The influence of the concept of overall resemblance cannot be overestimated even to this day, since most systematic papers of the last decade or so have employed this theoretical framework (e.g., Cottam 1957; Johnsgard 1960, 1964; Ligon 1967; Maclean 1967; Cracraft 1967; Hudson et al. 1969; Stegmann 1969; to name a few). Any of these papers may be correct in their conclusions, but until the results are verified by a character analysis, we do not know whether the relationships they advocated are based on primitive or derived similarities.

Because of the above argument, I suggest that the concept of overall resemblance be dropped from avian systematics. I would recommend using it only when a detailed character analysis has failed to yield primitive-derived sequences of the character-states. If overall resemblance is used in such a case, it should be made explicitly clear that the similarities used to define groups may be primitive and not derived. I suspect that reliance on overall resemblance should be unnecessary in any sophisticated systematic study involving a reasonable number of characters. The use of overall resemblance may be inevitable in some paleontological studies where fragmentary material can often make a character analysis very difficult.

USE OF CONSERVATIVE CHARACTERS

A number of systematists have argued that conservative characters, i.e., those which have evolved slowly and changed relatively little, are to be preferred in trying to discern phylogeny (e.g., Farris 1966). Compared to the concept of general overall resemblance, application of the theory of conservative characters has received scant attention from ornithologists. A notable recent example is Jehl's (1968) study of downy plumage patterns in the Charadriiformes. Conservatism of taxonomic characters is also a strong influence on the thinking of molecular systematists (Sibley 1967:12, 1970:19).

Those people who support the use of conservative characters have, in my opinion, overlooked certain aspects of character analysis. Many of these conservative, slowly evolving characters are present in the group under study and do indeed help these workers to recognize subordinate taxa (e.g., families within an order), but these characters do not necessarily indicate phylogenetic affinity between these taxa because they may be primitive for the group as a whole. Indeed, primitive characters are by definition relatively conservative. Constancy (i.e., conservatism) of a character throughout a group is of no significance unless one can show that this is a derived constancy and not primitive. Farris' suggestion (1966) that the relative taxonomic value of a character is proportional (or somehow related) to the degree of conservatism shows a lack of understanding of how characters are used and evaluated to define monophyletic groups.

In general, the use of conservative characters is unnecessary in phylogenetic studies since conservatism becomes irrelevant once a primitive-derived character analysis has been completed. Whereas the notion of conservatism is of no help in inferring phylogenies, it may be of some value in interpreting various evolutionary phenomena once phylogenetic relationships are known.

THE PROBLEM OF ADAPTIVE AND FUNCTIONAL SIGNIFICANCE OF TAXONOMIC CHARACTERS

It has long been thought by many systematists that the more significant a character is adaptively or functionally, the less important it is taxonomically. Bock (1967) quite rightly criticized the reasoning behind this conclusion. Still some ornithologists continue to imply that "adaptive" characters are questionable for taxonomic studies. What is probably meant in most of these cases is that characters which undergo rather rapid evolutionary changes are of little taxonomic value; this is close to the idea that if a character or character-state has a high probability of multiple origins, it becomes relatively useless as an indicator of phylogenetic relationships. In essence, this is attacking the problem in the wrong manner. It would be best to undertake a primitive-derived character analysis, determine the relationships, and then discuss such factors as multiple origins of characters (see below).

The concept of multiple origins or unique occurrence leads us to a discussion of the role of functional analysis in determining the reliability of taxonomic characters (see Bock 1960). Unfortunately, there has been too great an emphasis on functional analysis as the philosopher's stone of phylogenetic studies (e.g., Cain 1959), and it has led to a misunderstanding as to what role functional analysis should play in the study of phylogeny (see Bock 1969a and Zusi 1971, for a discussion of systematics and functional analysis). This misunderstanding has also led some workers to criticize the conclusions of others who have neglected to provide a functional analysis (see, for example, Bock's 1960, 1963, critiques of Tordoff 1954, and McDowell 1948, respectively); a critique centered upon methods of comparison rather than the absence of functional analysis would have been more appropriate.

One of the major uses of functional analysis is said to be in determining the relative probability of unique occurrence of taxonomic characters (Bock 1969a:443–444); other workers who have discussed this problem (Wilson 1965) do not consider functional analysis. It is difficult for me to see just how functional analysis can do this in the absence of a comparative study, which is the only context in which this method would have any theoretical validity; moreover, a comparative study will yield information about unique occurrence. Multiple origins of characters can only be known *after* a phylogeny has been determined on other characters. Functional analysis does not provide any objective criteria for determining the probability of unique origin, and I do not know of a single example in which multiple origins cannot be recognized from conventional comparative study. Likewise, I do not know of a single example in which unique origin (or multiple origins) has been demonstrated by functional analysis in the absence of comparative data.

The above *does not imply*, of course, that functional analysis has no role in the study of phylogeny nor does it imply that those workers using functional analysis disregard comparative data. If one includes the study of evolutionary mechanisms and the explanation of adaptive trends in the realm of phylogenetic study, then functional analysis is of paramount importance. Functional analysis can be helpful in defining characters themselves. In general, the more functionally interrelated features are, the less valid it is to treat them as separate characters in order not to bias one's argument. Nevertheless, we should eliminate the notion that functional analysis is essential for the determination of phylogenetic relationships. This hinders nonfunctional comparative studies, leads to undue criticism of many systematists who do not feel compelled to include functional analysis, and perhaps causes some anxiety in those investigators who have not included such analyses.

THE THEORY OF HOMOLOGY

I do not intend to dwell upon the theory of homology for it has been discussed by numerous authors. While many workers accept the definition of homology as pertaining to structures that can be traced back to the same structure in the common ancestor, a number of workers question the usefulness of the theoretical construct in explaining historical phenomena (e.g., Nelson 1970:378–379). The differences between the ideas expressed here and those contained in the concept of homology as advocated by some evolutionary systematists (Simpson 1961; Bock 1969a, 1969b) may not be significant. One of the reasons why the use of derived characters is less ambiguous than the usual notion of homology is that the former is not tied so closely with the problem of levels of monophyly (Simpson 1961). Bock's statement (1969b:72) "A hierarchical series of homologies can be established by repetitive determinations using ever-increasingly narrower and more precise conditional phrases" appears to be the necessary approach if one is to argue relationships using homologies. Yet I am unaware of any study in which the branching sequences of a higher taxon of birds (or within any other class of vertebrates) have been determined using a hierarchy of well-argued homologies.

Followers of the phylogenetics of Hennig do not use the concept of homology in the same sense as do evolutionary systematists, because the former workers do not believe it is possible to trace structures back to the corresponding structure in an ancestor (they believe actual identification or observation of ancestors is impossible; see below). Rather, phylogeneticists are interested in primitive-derived sequences of the structures they are studying. Phylogeneticists recognize the importance of comparing the "same" (i.e., homologous) structures in making primitive-derived analyses, but the ability to identify these characters as "homologous" is almost never a problem. The criteria used to discern primitive-derived character sequences are less ambiguous and laborious than those criteria normally used to establish the hierarchy of homologies. The latter are founded on some criterion of overall resemblance, and statements almost always must be subjective and/or ambiguous, e.g., "these features are so similar in these taxa that they could have come about only by origin from a common ancestor . . . therefore they are homologous . . . therefore they indicate affinity. . . ." The concept of primitive-derived sequences avoids this form of argument by using methods that are not strictly dependent upon a measure of overall similarity.

THE CONCEPT OF PARADAPTATION

According to Bock (1967:67), "Those aspects of a feature that are dependent upon, resulting from, or under the control of chance-based evolutionary mechanisms may be termed *paradaptive* (from 'para' and 'adaptive'), meaning 'besides adaptive' in the sense that these aspects are not dependent upon selection and hence cannot be judged in the range of adaptive to nonadaptive. *Paradaptive aspects* of a feature are dependent only upon the accidental evolutionary mechanisms. . . ." Seemingly in contradiction, Bock (1969a:441) also notes that paradaptive aspects are those differences that arise between phyletic lines and "are either adaptive or nonadaptive, according to whether they are selected or rejected by selection."

Bock argues that because paradaptive aspects involve comparisons between lineages (i.e., horizontal comparisons), the distinction between monophyletic assemblages is that they possess different paradaptive aspects of taxonomic characters (Bock 1969a:441). Thus, all we need to do is develop some measure of the probability of multiple origins of these paradaptive aspects and we will have a criterion to judge the value of taxonomic characters. Those paradaptations with a higher probability of unique origin would have a greater taxonomic value.

I believe the concept of paradaptation is unnecessary for the determination of taxonomic value of characters and can lead to erroneous conclusions. In support of this statement we can examine Bock's example of the arrangement of the toes in perching birds (1969a:444): "The arrangements of the toes for perching feet in birds appear to be restricted to the anisodactyl, syndactyl, heterodactyl, and zygodactyl types (Bock and Miller 1959). If the ancestral condition of three anterior toes and a short, elevated posterior hallux is considered, then the probability that any of these four paradaptive toe arrangements will arise only once is about 0.25." From this he concludes: "the arrangement of the toes is a feature with little taxonomic value." Using this reasoning, it should be possible to eliminate nearly all taxonomic characters that have been proposed in avian systematics. For example, how many basic patterns (i.e., "paradaptive aspects") are there for jaw muscles, leg muscles, number of primaries, bill structure, egg-white proteins, and so forth? Can it be claimed that for any character in which there are four basic arrangements (not to speak of more than four), the probability of unique occurrence is about 0.25 and therefore that these arrangements are of little taxonomic value? One could postulate, on the other hand, that the heterodactyl foot of trogons is of great taxonomic value. It is clearly a derived character that helps demonstrate that the trogons are a monophyletic group. Zygodactylism cannot be used to claim relationship *between genera* of the Piciformes, Psittaciformes, or Cuculidae, but it can be used to define the monophyletic nature of these higher taxa if it can be shown that this toe arrangement is derived for each group. It is difficult to imagine any meaningful way in which the probability of unique origin can be estimated prior to the determination of a phylogeny.

I therefore suggest that the concept of paradaptation not be used to evaluate taxonomic characters.

THE ARGUMENT OF CONVERGENCE

There are several notable examples of ornithologists arguing against a particular relationship of taxa by claiming that the organisms are convergent and not really related; this I call the argument of convergence. The "convergence" of the ratites is a case in point (McDowell 1948). A more striking example (at least it is cited more often) is the argument that the loons, grebes, *Hesperornis*, and other divers are convergent and therefore not related. The argument has its basis in Stolpe's paper (1935) on the hindlimb and has been accepted by numerous workers (e.g., Mayr and Amadon 1951; Storer 1956, 1958, 1960a, 1971; Stresemann 1959; Wetmore 1960). A re-evaluation of this problem raises doubts about the validity of this type of phylogenetic argumentation. I want to discuss briefly these methods, but a detailed systematic analysis of the taxa involved will be presented at a later date (Cracraft, unpubl.).

A strong argument can be made that most of the shared morphological (principally osteological) features of loons, grebes, and their fossil allies are derived within the class Aves and therefore one must conclude that these taxa evolved from a common ancestor. The features that many call convergent are actually derived and indicate monophyly. Stolpe (1935) did not present a valid argument for concluding convergence in the diving birds. In his paper he merely showed that there are differences among these taxa, and from this he concluded nonrelationship and convergence.

We may ask whether it is acceptable to refute a given relationship by the argument of convergence. In none of the papers cited above is there (1) a primitive-derived character analysis, or (2) any evidence presented that convincingly argues a relationship of one of these groups to a separate lineage of birds. The last point is critical because, by definition, a judgment of convergence must be based on an a priori assumption of relationship. The fact that two taxa (e.g., loons and grebes) might show a number of morphological differences cannot serve as an argument for nonrelationship. The latter can only be proposed once a relationship has been demonstrated between one of these taxa and a third taxon.

I therefore suggest that arguments of convergence not be used to refute or support phylogenetic inferences. Rather, this approach should be replaced by an argument based on derived character sequences.

DISCUSSION

THE STUDY OF PHYLOGENY

All workers agree that phylogeny involves the branching of lineages and the subsequent divergence of these lineages. To most the study of phylogeny also includes a discussion of functional differences between and within lineages, differences in evolutionary rates, aspects of adaptive radiation, etc. Despite the considerable agreement among the students of phylogeny, honest differences of opinion are present; it is important to attempt a resolution of this discord. Because many ornithologists may not be aware of the conflicts between the different workers, I want to present a brief discussion of some of these views. Hopefully, each reader will examine and evaluate these views impartially, especially with regard to what they might do for the study of avian phylogeny.

For our purposes, we will discuss the differences between the followers of Hennig (1966), sometimes termed "cladists" (genealogists or phylogeneticists) because they emphasize the importance of phyletic branching or cladogenesis, and those of Simpson (1961), Mayr (1965, 1969), and others, who place a great emphasis on divergence and similarity ("evolutionary taxonomists"). I do not plan to review all of the literature. Rather, it seems appropriate to compare the views of Mayr (1965), whose stimulating work has greatly influenced avian systematics and who has given probably the most detailed and articulate criticism of the cladists, with those of Hennig. [Darlington (1970) has also presented a critique of Hennig and his followers, but his discussion raises no serious theoretical objections to cladism that were not treated earlier by Mayr.] It will be necessary to examine Mayr's views in terms of my own experience in studying the higher taxa of birds, thus I will not claim to support or defend all of the cladists' thinking. I am more interested in developing a system that will help us understand the history of avian taxa rather than debating every detail and exception of cladistics.

The conflicts between the cladists and evolutionary taxonomists begin with the meaning

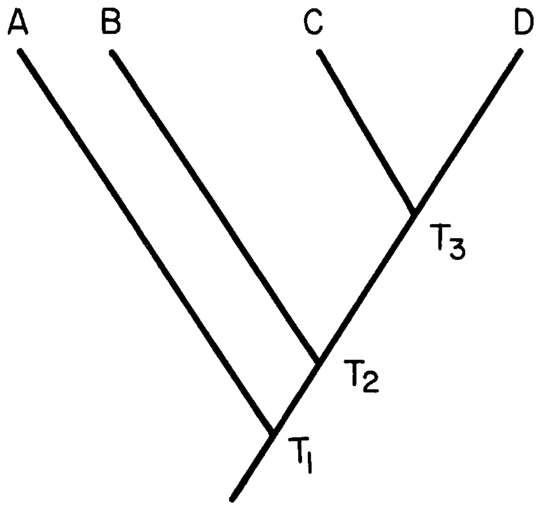

FIGURE 3. Hypothetical dendrogram. Little morphological divergence has taken place between times T_1 and T_2 compared to that between T_2 and T_3. See text.

of relationship. (I am not interested here in the definition per se but in the applicability of this definition to the study of phylogeny. We can argue *ad nauseum* about definitions without realizing that it is the implications of the definition that are of paramount importance.) The differences in viewpoint can be illustrated using figure 3, which we can consider to represent a true phylogeny of an order of birds with four families (this example is slightly modified from Mayr 1965). We will assume that there has been little morphological divergence between times T_1 and T_2 (i.e., little divergence between taxa A and B) but a greater amount of divergence between T_2 and T_3. Cladistics would define phylogenetic relationship in terms of the branching sequence, i.e., B is more closely related to C/D than to A because B and C/D share a more recent common ancestry that is not at the same time an ancestor of A. According to Mayr (1965:79), "If there was very little evolutionary change between T_1 and T_2, and a great deal of evolutionary change between T_2 and T_3, then *obviously* [emphasis mine] B is more closely related to A than it is to C/D. The argument of the cladist fails to recognize that the term *relationship* has two different meanings, genetic relationship and genealogical relationship." Mayr continues (p. 79) that "it is no longer legitimate to express relationship in terms of genealogy." This example indicates that there is a *difference in definition* between the two schools, and no amount of rhetoric can obscure this point. Thus, each systematist must ask himself which definition has the greater consistency, greater objectivity, and greater usefulness in representing the relationships of birds and in explaining the phenomenon of phylogeny. In my viewpoint the answer is the definition of the cladists. My reasons are as follows:

1. Because we assumed the phylogeny of figure 3 as given, the relationships recognized by cladists will always remain the same as long as the branching sequence remains the same. This is not true for the evolutionary taxonomist whose decisions about relationships will change with differences in divergence. How much divergence does there have to be between T_1 and T_2 before B is considered more closely related to C/D than to A? Is it not possible for two or more evolutionary taxonomists to disagree on the interpretation of the amount of divergence and therefore have contrary opinions as to the closest relative of B? What kinds of objective criteria are to be used? The viewpoint of the evolutionary taxonomist is ambiguous and subjective. On the other hand, any number of cladists would always agree on how to express relationship given the same branching sequence regardless of the degrees of divergence. Science, it seems to me, should choose the objective over the subjective, the unambiguous over the ambiguous; students of phylogeny should do no less.

2. In terms of practicality, a cladistic definition of relationship is preferable. Suppose we assume the taxa in figure 3 to be the following (which I believe to be most probably the actual phylogeny): A, Megapodiidae; B, Cracidae; C, Gallinuoididae; and D, Phasianidae (*sensu lato*). Any statements about relationships by a cladist (i.e., B is more closely related to C/D than to A) tell us information about the branching sequences of the taxa. A statement by the evolutionary taxonomist to the effect that B is closer to A would tell us A and B are most similar (at least in his opinion), which in turn may lead others to infer that A and B also had a more recent common ancestry (which is not true in this example). Thus, using the definition of the evolutionary taxonomists may lead to incorrect assumptions about ancestry; that of the cladist cannot imply incorrect information about common ancestry nor does it imply anything about similarity.

Mayr (1965), Bock (1968), and Darlington (1970) make a point of emphasizing that cladists ignore differential rates of evolution or assume equal rates. Thus, according to Mayr

(1965:80), "The most serious weakness of both the straight cladistic and straight phenetic approach is that they completely disregard the frequent occurrence of exceedingly different evolutionary rates." This viewpoint of the evolutionary taxonomists is clearly incorrect as it pertains to cladistic analysis. Although he does not discuss evolutionary rates in detail, Hennig (1966:88) rejects the possibility of equal rates and recognizes "the proven fact that there are differences in the rate of evolution." In my opinion, cladists probably pay more attention to differential rates than does the evolutionary taxonomist, because the entire system of the former rests on the use of primitive and derived character-states, which are by definition reflections of different rates of evolution. This is less true of evolutionary taxonomists, whose system is founded principally on overall similarity. An important point often ignored (or not understood) by evolutionary taxonomists in their work or in their criticism of cladistics is that evolutionary rates are only meaningful *after* the branching sequences of taxa are known. The study of evolutionary rates depends on a cladistic approach to phylogeny rather than on one of overall resemblance.

Mayr (1965:79) believes "genetic similarity" should be the dominant theme of phylogeny, and in his opinion "When a biologist speaks of phylogenetic relationship, he means relationship in gene content rather than cladistic genealogy." This concept of "genetic relatedness" has been adopted by Sibley (1970:21) in his discussion of passerine relationships. Sibley has carried the term much further than what Mayr would probably want and even speaks of the genetic relatedness of families rather than of gene pools of species. This use of "genetic relatedness" is even more curious when one considers that Sibley studied only five or six genes (assuming one gene, one protein) at most, using techniques which he himself admits tell us nothing about the actual structure of the genes (see Cracraft 1971). But even on a theoretical level "genetic similarity" has its problems since any statement comparing genetic relatedness of organisms must of necessity be inferred from some measure of overall resemblance. Mayr (1965:85–86) rejects a close correspondence between genotype and phenotype (at least in any exact, predictable manner), yet he still uses this principle as a basis for his whole system. As any ornithologist will realize, the practical use of "genetic relatedness" within the higher (or lower) taxa of birds is highly questionable (except on a purely theoretical level) and simply a hoped for, but still mythical, picture of reality.

The central problem of phylogeny is not the interpretation of dendrograms (or cladograms) but their construction. Evolutionary taxonomists would give us a dendrogram in which origin from a common ancestor is subservient to degrees of similarity. Their philosophy and working methods are usually inadequate to recognize cladistic relationships. Certainly within birds, the sister-group relationships of the families are very poorly known despite decades of evolutionary taxonomy. Avian systematists should be concerned with the history of birds. This should begin with the determination of cladistic relationships and then proceed to a study of divergence and associated phenomena.

THE IMPORTANCE OF PHYLOGENY

The importance of knowing the phylogenetic relationships of the avian taxa is obvious. Once phylogenetic relationships have been determined, the interpretation of numerous historical events will become much more significant. The examples of convergence, multiple origins of characters, and evolutionary rates have been discussed already. Several other aspects can be mentioned.

The use of cladistic relationships has more predictive value in the study of biogeography than does evolutionary taxonomy (Nelson 1969). Returning to figure 3, if we consider the cracids to be more closely related to the megapodes than to the gallinuoidids-phasianids as evolutionary taxonomists have proposed, then our statements as to the place of origin and probable paths of dispersal will be different from those postulated by a cladist. Perhaps the major problem of the endless discussions concerning the biogeographical affinities of the African and Australasian avifaunas is that the phylogenetic affinities (sister-group relationships) of the organisms are so poorly understood. One of the strongest arguments for cladistics and against the emphasis of similarity by the evolutionary taxonomists is that the historical biogeography of animals—their patterns of origin and dispersal—is not a reflection of morphological resemblance. On the other hand, these factors do reflect or have a close relationship to the cladistic affinities of the taxa. Meaningful explanations of biogeographical events are impossible given incorrect cladistic relationships. Darlington (1970:10–17) has criticized the biogeographic reasoning of several cladists, particularly Brundin (1966). In my opinion, much of this criticism misses the point because "a biogeographic analysis implies, logically follows from, and at best can be no more reliable than, a prior phyletic analysis" (Nelson 1969:246). Darlington (1970:8–9) believes that most taxonomists use the same methods as the cladists in determining relationships. Although I cannot speak for other specialties, this is unequivocally not true in ornithology. Avian phylogeny and classification have their basis in the concept of overall resemblance, which some of us reject as an unreliable approach to phyletic relationships. I would therefore predict that much of the biogeographic analysis of passerine distribution will be fruitless until cladistic relationships have been resolved in more detail. It is frustrating and somewhat futile to compare the avifaunas of the southern continents unless one knows the relationships of the taxa involved.

Another, minor predictive aspect of cladism would be the possible explanation of relationships and distribution patterns of parasites, especially Mallophaga. Many of the peculiar distribution patterns of Mallophaga, which have led to needless speculation about avian relationships, might disappear if the cladistic relationships of the hosts were known.

THE ROLE OF PALEONTOLOGY

The present state of avian paleontology is very poorly understood by ornithologists as well as by other vertebrate systematists. Unfortunately, a re-evaluation of much of the earlier work has only begun and many undescribed forms remain unstudied. A significant number of the described species, especially those from the early Tertiary, are incorrectly placed as to family, sometimes even to order. However, the avian fossil record is not as poor as some would believe, and in certain cases phyletic lines can be drawn (e.g., Cracraft 1972). On the basis of my work in paleontology I have come to several general conclusions regarding the fossil record of birds and the role it should play in avian phylogeny. These conclusions are not restricted to birds and in fact may be derived theoretically using any group of organisms (see Schaeffer et al. 1972 for an excellent discussion of the theory and working methods of paleontology).

First, the working methods of paleontology are exactly the same as those of neontology. The methods of comparison and interpretation are identical and should not be influenced by the time dimension. Of course, the nature of the paleontological material makes analysis more difficult.

Second, it is impossible to make definitive statements about the systematic position of fossils until one has an understanding of the relationships of the recent groups. Once branching sequences are determined for recent groups, then fossil taxa can be incorporated.

Third, it is pointless either to look for ancestors or to consider fossils to be ancestors. Ancestral-descendant relationships are unknowable and unprovable; no criteria exist for recognizing a particular fossil as an ancestor. Statements can be made about cladistic relationships, and this provides a basis for intelligible evolutionary interpretations. For example, I believe (Cracraft 1972) that the Eocene Eogruidae and the Oligocene Ergilornithidae share a most recent common ancestry within the order Gruiformes. The eogruids are clearly more primitive in a large number of characters and are probably near the ancestry of the ergilornithids. But how can one know whether the eogruids are really the ancestors? It is possible to discuss all the relevant evolutionary events without resorting to proposing the eogruids as *the* ancestral group.

Naturally the loss of the idea that fossils *are* ancestors (in the sense that they can be recognized as ancestors) will be difficult for some. But in doing so we will increase the precision of the working methods in paleontology and eliminate a considerable number of irresponsible statements, which have not necessarily come from the paleontologists themselves, but from those who interpret and apply their results.

FROM PHYLOGENY TO CLASSIFICATION

The emphasis of this paper is phylogeny, not classification. As do most systematists, I believe phylogeny should precede classification —that is, if the classification is to be called "phylogenetic." The strongest differences between the cladists and evolutionary taxonomists are perhaps those involving the translation of phylogeny into classification. I do not wish to enter the controversy in this paper. Rather than discuss theory at this time, I would prefer to see possible methods of classification debated after the phylogenetic relationships of various orders of birds are known. Preliminary findings within some orders suggest that a purely cladistic classification involving dichotomies is feasible and very satisfactory and should not disturb the sensibilities of most ornithologists.

CONCLUSIONS

It is hoped that the contents of this paper will help to improve and promote the study of phylogeny in the class Aves, and I have tried to raise and discuss some issues which focus on this improvement. The crux of the problem, it seems to me, is that the notion of general overall resemblance is unreliable and should be replaced by the method of character analysis of primitive-derived sequences. I have tried to give my reasons for this conclusion, the reasons being based on actual application to several orders of birds.

Every avian systematist, including myself, would freely admit that the method of overall resemblance has provided us with the skeletal framework of avian relationships. Thus, most of the families are probably correctly placed as to order. But relationships of families within orders are very poorly known, and it is at this level that cladistic analysis will be superior to overall resemblance. I have great optimism that with careful analysis of characters we will be able to resolve the phylogenetic relationships of avian families, particularly nonpasseriforms where divergence is greatest, in the near future. I believe that the incessant speculation that has characterized the study of avian phylogeny and classification will be eliminated only with the adoption of the cladistic approach. Can we afford to continue as we have?

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