

vote still would have been for the Basel sequence. Sibley grew up with the Wetmore sequence and feels more comfortable with it. However, this is a matter of sentiment and not supported by the evidence.

It should be quite obvious from these comments that the new classification of birds by Sibley et al. is a most useful working hypothesis. Indeed the authors themselves have referred to it as a progress report. However, it would be a great mistake to consider it the last word. Sibley et al. have the enormous merit of providing an opportunity to analyze and test the position of every single order, family, or subfamily of birds, and thus to establish the basis for what might eventually be a generally acceptable classification of all birds. In addition to further morphological research and the study of fossils, there are numerous other molecular methods that can be employed to test the hypotheses. They will either confirm or falsify their proposals. A new era for the study of avian classification has begun. Even though one might perhaps claim that no other individual in the last 100 years has made as great a contribution to our knowledge of the relationship of birds as Sibley, it would be a complete misconception of the nature of science to believe that the work of any one scientist must be accepted as the last word in any area of science. Science advances, as Popper has so rightly said, by conjecture and refutation.

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Response to E. Mayr

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In his Commentary Ernst Mayr supports several aspects of the Sibley, Ahlquist, and Monroe classification (1988). Professor Mayr and I have exchanged letters about the classification and some of his earlier questions have been resolved, but his Commentary contains points on which we still disagree. My comments address some of these.

It is important to question the implication that departures from the "standard avian classifications used by most authors" is somehow wrong. There have been at least 50 different classifications of birds published since that of Linnaeus. Even a cursory study of past classifications will reveal that only a few were founded on more than one, or a few, morphological characters. Others were based on tradition, intuition, or a selection of previous ideas. Fürbringer (1888) wrote two large volumes on avian morphology, but his clas-

sification was not fully accepted by his contemporaries, including his friend Hans Gadow. Gadow (1892, 1893) alone analyzed a large number (40) of characters using a kind of numerical taxonomic system. Wetmore and Miller (1926) assembled an eclectic classification for which they took "Gadow's work as a basis and . . . incorporated in it various changes that have been made by later workers. . . . When doubt seems to attach to any suggestion we have followed the older classification." Wetmore (1930, and later versions to 1960) followed the same procedure when he produced his classification of the birds of the world. Thus, the Wetmore classification, in wide use for the past 63 years, is mainly the work of Gadow, nearly a century old.

Mayr and Amadon (1951) based their classification on various sources, and included "few changes . . . from the now well-established sequence of Wetmore (1934, followed by Peters)." Mayr and Amadon (1951), and the "Basel sequence" (Mayr and Greenway 1956) advocated the "crows last" arrangement for the oscines, but Stresemann (1934) followed Wetmore (1930) and placed the nine-primaried oscines last. When Mayr

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became the editor of the Peters' Check-list, he replaced the Wetmore sequence with the Basel sequence for the oscine volumes. Wetmore (1957) criticized the Basel sequence and noted the condition of the humeral fossa, of which more below. Amadon (1957), Delacour and Vaurie (1957), and others followed the general lines of Wetmore's classification, but also introduced differences. Thus, there have been no "standard avian classifications," unless Wetmore's (or Gadow's) is so designated.

Mayr suggests that before changes are made in existing classifications, the proposed changes must be "clearly proven." It is fair to ask, were the classifications of Wetmore, which we have used for so long, "clearly proven" to be correct? If so, how? I know of no critique of any of the five versions of Wetmore's classification. However, standards have changed and it is time to implement a more rigorous criterion. The problem still is, how? Congruence with tradition is comforting, but tradition may also be wrong.

We did not advocate the *adoption* of the classification, we merely presented it. We do not recommend that any collections be rearranged. Some collections may still be in the sequence of the "Catalogue of Birds in the British Museum" or Sharpe's "Handlist." Leave them that way, for that is not the significance of a classification. Ideally, a classification reflects the phylogeny of the group, and that is what we tried to achieve. Presently there is little or nothing against which to "test" our classification except congruence with traditional arrangements. As we noted, and Mayr agrees, the DNA-based clusters of species ranked as families and orders are highly congruent with those of Wetmore and others, although the categorical ranks may differ. It is mainly at the levels where the orders are linked to one another that our classification departs from previous attempts. Stresemann (1959) discussed the problems of determining the relationships among the higher categories and the placement of "odd" taxa. He concluded that in the "absence of trustworthy information on the relationship of the highest categories of birds to each other it becomes strictly a matter of convention how to group them into orders." We have tried to substitute measurements for conventions. Whether we have succeeded or failed will require a better method of measurement, not merely complaints that we have violated convention.

Mayr prefers a classification based on a combination of phylogeny and degree of "specialization"—the clades and grades approach. We believe these two dimensions are incompatible. In combination they produce classifications in which genetically closely related species with different morphological specializations are often placed in different higher categories. Instead, we agree with the cladists on this point, namely, *only the phylogeny* is a reasonable basis for a classification. Raikow's (1985) approach expresses our philosophy of classification, and we share his

criticisms of the so-called "evolutionary" procedure that Mayr and many others prefer. Thus, classification raises the question: *is it based on a reasonable approach to the one and only true phylogeny?* We believe that our classification "represents progress toward that elusive goal" but we can't prove that it does, nor can anyone disprove it at the present time.

We too are puzzled by the DNA evidence of the relationships of the pelecaniforms and some other groups. We can't be certain whether the DNA comparisons always tell us the "truth," or whether some unknown factor, perhaps different rates of genomic evolution, accounts for the departures from expectations. These questions will not be answered by polemics, only by better quantitative, objective data.

Mayr notes criticisms of our data and methods. I call attention to a study by Caccone and Powell (1989) who repeated our hominoid experiments (Sibley and Ahlquist 1987) and obtained the same phylogenetic tree and virtually identical genetic distance values, although their technique differed from ours in some respects. Their results corroborate our hominoid study and, indirectly, validate the "corrections" we used to compensate for the experimental errors in our DNA hybridization method. In the future I propose to use procedures similar to those of Caccone and Powell.

The differences in average genomic rates of evolution among birds do not seem to be large enough to cause major problems, but we do not know exactly how large they are. However, this matters little because we used a measure of "genetic distance" as the criterion for the classification. Thus, the positions of groups are relative to their genetic distances from one another, including the effects of different average rates of DNA evolution. This approach may be flawed, but it has a logical basis. Every classification should have a basis for its structure, even if it is only intuition or "experience," as is true for most of the extant classifications.

The location of the branching points in our classification may differ from those of the true phylogeny, but it is also possible that we are closer than any previous attempt. That is enough to claim progress, which is all we claimed. If perfection is demanded, we may have to wait a while.

The "Neutral Theory" provides the basis for the molecular clock concept and, because ca. 90% of the genomes of higher organisms is composed of non-coding DNA, the differences in average genomic rates are due to factors that determine the rate of acquisition and drift of selectively neutral alleles, as proposed by Kimura (1983). The large amount of non-coding DNA is composed, in part, of introns, flanking sequences, and other regions that are not transcribed into messenger RNA. Another part may contain ca. 5% of the different sequences that are present as repeats and may constitute ca. 40% of total DNA by volume. (In the DNA hybridization method most of the repeated sequences are removed.) Another small

percentage apparently is composed of selectively neutral alleles that form a store of variability. These variants increase the probability that some members of a population will, by chance, possess a constellation of alleles that will "fit" the demands of the new environment when a selective bottleneck occurs. Within limits, this system "preadapts" a population to an unknowable future based on past experience. This idea is supported by experimental evidence from bacterial enzymes by Hartl et al. (1985) and espoused by Kimura (pers. comm.). The mechanism for the storage of variability is the result of natural selection for a system that increases the probability of the survival of lineages. Those lineages that lacked such a mechanism are long extinct, thus allelic variants are present for many genes in nearly all organisms. Contrary to Mayr, I think it is probable that virtually all of the DNA has some effect on the fitness of individuals and lineages or both over time. The fact is, we know too little about this subject to be confident of any opinion.

Mayr believes that the genes that code for proteins and determine the phenotype should be given more weight than those that produce no detectable product. I disagree. It is the selectively neutral genes that produce whatever "clock" effect there is, and the non-coding DNA is just as important in its way as the part that is coding for proteins at the present time. Without most of the non-coding DNA, the organism could not exist.

Mayr seems to assume, although I doubt he believes it, that there is a simple relationship between what the eye sees and the amount of genetic difference between species. The examples Mayr cites of the New World quails, hoopoes, trogons, kingfishers, and kinglets all have *some* basis in morphology, as well as in DNA distances. The morphological differences of the alcsids from the gulls reflect the adaptive differences between them, which strike our eyes as large. Mayr's preference for a classification that reflects such specializations in categorical ranking is only that, a preference, not necessarily a better way to construct a classification. I disagree with this approach and prefer to use the degrees of genetic difference as evidence of phylogenetic relationships. The human eye is *not* an accurate instrument with which to measure the similarities and differences in genetic relationships. Nor do I agree that because a group differs widely in morphology from other groups that it therefore "merits" recognition as a different "family" or other higher taxon. It must also pass the test of phylogenetic difference or similarity measured on some objective scale. Our DNA measures, flawed though they may be, are the first to come close to meeting this test for the classification of a major group of organisms.

Any pair of sister taxa may be rotated 180° on their common axis, thus it makes no difference whether the tinamous or the ratites are listed first. We followed tradition in listing the ratites first because there is no objective way to do otherwise. The tinamous are not

the ancestors of the ratites; they only shared an unknown and long-dead common ancestor. It is irrelevant which of these two groups, or any similar pairs, is listed first. If one wishes, the Passeriformes could be listed in a different position by rotating them on their common axis with their sister taxon at delta T₉₀H 21.6 in figure 4 of our classification (1988). The best reason for not doing so is tradition, which is a powerful factor in all classifications. For some, it is the most important "character."

In his Response, Monroe (see following) discussed the "crows last" question raised by Mayr. Ahlquist and I, with help from graduate students at Yale, examined the humeral (or tricipital) fossa in one or more species of the oscine families recognized in our classification and in that of Wetmore (1960). We found ca. 90% congruence between the single fossa condition and our Corvida, and between the double fossa condition and our Passerida. Olson (1987) also commented on this correlation. There is a random relationship between these conditions and the classifications of Wetmore, Mayr and Amadon, and the Basel sequence. Mayr suggests that the Corvida gave rise to the Passerida, but these groups are sister taxa, therefore they shared a most recent common ancestor and neither gave rise to the other; they are the results of a speciation event in the past. Because the single fossa condition occurs in the suboscines and the Corvida, it seems reasonable to assume that a single fossa was the primitive condition in the common ancestor and retained by the Corvida, and that the derived condition is the double fossa that evolved in the ancestor of the Passerida after the split. We used this as the basis for listing the Corvida first.

The reason the "Basel Committee" chose the classification with the crows last had little to do with phylogeny. As Mayr and Greenway (1956) recorded, the committee was formed to "recommend to the editors of ornithological journals a standardized sequence of the families of Passerine birds." This approach seems to indicate that the members of the committee had despaired of ever solving the problem by any rational means, so they chose to substitute authoritarianism "in view of the fact that there are no decisive arguments available in favor of any of the previously proposed sequences." Presumably, including "crows-last."

I appreciate the positive things that Professor Mayr wrote about our efforts to reconstruct the avian phylogeny and to construct a classification based on that phylogeny, and I agree with some of his criticisms. We presented the classification as "the basis for new questions and new hypotheses" and we hope it will be so used. With improved laboratory methods and procedures for data analysis, it will be possible to extract more information from the avian genome and to reexamine the departures from traditional ideas of avian relationships that we found. *Turnix*, by the way, was long placed with the galliforms, with several

other groups as suggested allies. It was first assigned to the "Ralliformes" by Fürbringer (1888), an arrangement not accepted by Gadow (1892: 244), but adopted by Wetmore and Miller (1926) and Wetmore (1930), who placed the Turnicidae with the rails in the Gruiformes. Also, it is only captive *Turnix* that begin to breed at "three to five months"—does any one know the age at first breeding for wild buttonquail?

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Response to E. Mayr

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Although Mayr is sharply critical of some aspects of the classification, I was generally pleased with his comments on the merits of the system. With respect to the DNA-DNA hybridization technique, he and I have been in much the same boat: our training and experience in the field of systematics were without much of the necessary background and knowledge in this field or in the techniques, at least initially, to appreciate fully the value of such studies to systematics. It is only recently that I have become involved in this classification project, and then only in the

aspect of providing a measure of expertise in classification and nomenclature techniques. I was not involved directly in any of the laboratory studies and certainly am not cognizant of all the techniques involved in achieving this classification. I am, however, totally convinced that the biochemical/genetic approach (and specifically DNA-DNA hybridization) is the most effective to understand the real relationships of birds, and avoids most of the pitfalls of other approaches (especially those that are morphological in nature). I sense from Mayr's comments that he feels much the same way as I did initially with the results of this technique. Many of the items not only made beautiful sense (e.g. the Corvida-Passerida evolutionary picture), but also have been supported subse-

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