

To determine if the character set used by Cherry et al. (1978, 1982) and Wyles et al. contained biases of the kind discussed above, we investigated the relative contribution of each character to the morphological distance metric, *H*. The metric comprises eight mensural characters including head width, head length, shank length, forearm length, and the like. Two of these eight characters (head length and forearm length) together account for more than 73% of the overall *H* value measured between the hummingbird and the albatross. These same characters account for an average of less than 36% of the *H* value in six interordinal comparisons of mammals and only 19% of the overall *H* value in four reptile comparisons. In birds, head length and forearm length are directly related to bill length and wing length, and it is well known that these are highly labile traits that vary conspicuously with diet and flight habits. Because the *H* metric contains two variables that are powerful discriminators among birds at all taxonomic levels, the metric would appear to be particularly sensitive to within-bird morphological differentiation. We suspect, therefore, that the *H* values measured between birds at all taxonomic levels (see Wyles et al., 1983 Table 2) are inflated relative to those of other vertebrate groups. Although Cherry et al. (1978 Footnote 13) mention that their approach "... ignores problems of allometry. . .," it is *precisely* such problems (i.e., different patterns of allometric change in different vertebrate classes) that cause the *H* statistic to be inappropriate for interclass comparisons.

We believe that the major problem is not the use of an *H* metric itself, but the application of one particular *H* metric to interclass comparisons among vertebrates. More basically, the question "Are the anatomical differences among birds as great or greater than those among mammals?" is unanswerable unless one specifies the particular anatomical feature of interest. For certain features, such as head length and forearm length, birds are probably more diverse than mammals, as represented by primates, carnivorans, and rodents; for a vast number

of other anatomical features, the question remains unanswered. Because the conclusions of Wyles et al. concerning bird versus mammal morphological diversity, rates of evolutionary change, and "behavioral drive" are entirely dependent on the validity of *H*, we feel that these conclusions are, at present, premature.

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MORPHOLOGICAL DISTANCE: AN ENCOUNTER BETWEEN TWO PERSPECTIVES IN EVOLUTIONARY BIOLOGY

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Hafner et al. (1984) question the adequacy of our data, as well as our way of measuring degree of organismal difference (i.e., morphological distance). They go on to conclude on biological grounds that morphological distances within one group of

animals cannot be compared to those within another group. We give direct answers to some of the technical points raised by Hafner et al. and then suggest that their negative conclusion be examined from two different perspectives on how to approach

problems in evolutionary biology. We are also preparing a manuscript for submission to *Evolution* that will present additional data on the body shapes of birds, mammals, and amphibians. In addition, it will explore the questions of how many traits need to be measured to obtain a global estimate of degree of difference in body plan, how many body parts need to be represented and how long the traits should be. That manuscript will allow some of the points raised by Hafner et al. (1984) to be addressed in more detail.

Diversity and Distance.—Possibly indicative of a difference in perspective, is our critics' repeated use of the term *diversity*. The papers they criticize (Cherry et al., 1978, 1982; Wyles et al., 1983) do not deal with diversity but only with degree of difference or morphological *distance*. Diversity is a complex term that includes the number of extant lineages as well as the degree of morphological difference between the tips of those lineages. Morphological distance, by contrast, is a pairwise measure that does not depend on the number of lineages compared. To illustrate this point, let us consider first a diverse taxonomic group consisting of five species, A_1 – A_5 , descended from species A, as shown in Figure 1; species B is an outside reference. We assume for simplicity that the rate of morphological change has been uniform with time along all lineages, that rate being one distance unit per unit of time (see Fig. 1). Accordingly, the degree of difference between B and any of the five species, A_1 – A_5 , is 4 units. If, however, A gave rise to only one surviving species, A_1 , the distance between B and A_1 would still be 4 units. The number of descendants of A has no effect on the degree of difference between a descendant and an outside reference species; nor does it affect the mean pairwise distance between the descendants of A (if A left more than one descendant). Since we feel that the usage of Hafner et al. (1984) obscures the distinction between the complex concept of diversity and the relatively simple concept of morphological distance, we shall assume in this rebuttal that their term "diversity" means "distance."

In this context, we respond to their criticism that we measured too few orders of mammals to support the view that the anatomical differences among bird orders are no smaller than those among mammals of comparable taxonomic rank (i.e., orders within an infraclass, see Cherry et al., 1982). We sympathize with the desire to see measurements on representatives of more than three mammalian orders, but stress that each of the orders represents a different cohort of placental mammals (Simpson, 1945). Measurements on four additional orders had already been made when the Wyles et al. (1983) paper was being written, and these were used in preparing Table 4 of that paper. We intend to present those additional measurements in the manuscript referred to above.

Orders and Classes.—By focusing attention on interordinal distances, Hafner et al. (1984) lose sight of the finding that at every level tested in the taxo-

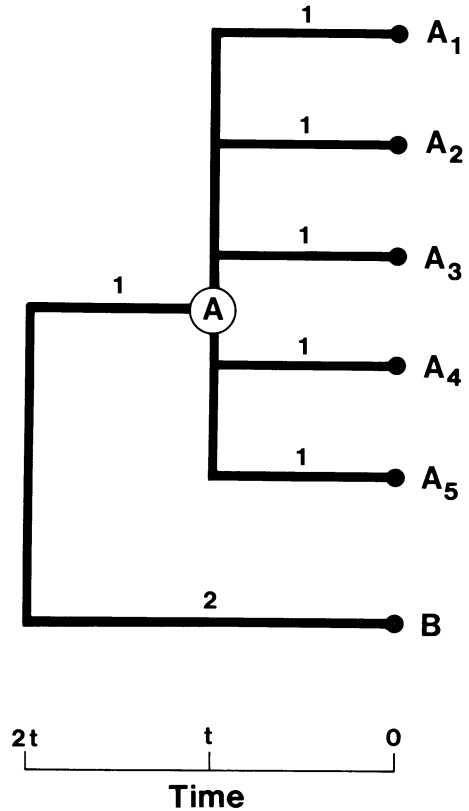


FIG. 1. Tree showing amounts of morphological change along lineages leading to six species (A_1 – A_5 , B).

nomic hierarchy, from subspecies to order, the mean distances among birds are as big as those among amphibians, reptiles, and mammals of comparable taxonomic rank (Wyles et al., 1983). Their focus on distances between higher taxonomic groups is unfortunate because those distances are subject to the saturation (or multiple-hit) problem, as becomes evident upon plotting morphological distance (H) against time of divergence between taxa. The line of best fit between H and *time* bends and approaches a plateau when the H values exceed 20. This saturation phenomenon invalidates the use of morphological distances between orders and between classes for comparisons of rates of evolution. To compare rates of morphological divergence within one class to those within another class, which was the chief goal of the Wyles et al. (1983) study, it is essential to avoid the saturation zone by working with intra- or inter-generic distances. This practice is exemplified by the rate studies of Cherry et al. (1982), Wyles et al. (1983), and Larson et al. (1984). The conclusions of those studies do not depend on the magnitude of interordinal or inter-class distances.

Another reason for being cautious about interpreting large morphological distances is that the variability in morphological distance rises with rank in the taxonomic hierarchy (Cherry et al., 1982). As is clear from the height of the standard error bars in Figure 2 of Cherry et al. (1982), a particular interordinal pair of species, like the albatross and hummingbird, might easily exhibit an H value greater than the mean value for interclass comparisons. Our comment about the albatross-hummingbird difference was made in the light of this knowledge. We did not conclude from the H values that these two birds are more different morphologically than is a cat from a seal, because it would have been short-sighted to overinterpret such single comparisons. We simply observed that the H values gave no support to Romer's (1966) assertion that cats are more different from seals than albatrosses are from hummingbirds (Wyles et al., 1983).

Focusing further on interordinal and interclass distances, Hafner et al. (1984) try to discredit our regression analysis of morphological distance versus taxonomic distance by stating that two adjacent means in the regression are not significantly different. It is widely known that the significance of a regression is not jeopardized by two or more adjacent groups of data having overlapping values. Hence it is not unreasonable for interordinal distances to overlap with interclass values, especially when, in the present case, the means in question conform to the regression trend of positive correlation between taxonomic distance and morphological distance.

Bias and Discrimination.—Hafner et al. (1984) imply that a small set of traits will favor discrimination among species within one taxonomic group over that in another group. This implied criticism of our metric (H), which is based on only eight traits, appears to ignore the facts that a) these quantitative, linear traits are from all major parts of the body, b) our goal is not to discriminate but to estimate distance (Cherry et al., 1982) and c) we have presented extensive empirical evidence for a strong correlation ($r = .8$) between H and distance in the taxonomic hierarchy (Cherry et al. 1978, 1982; Wyles et al., 1983). From these facts, we infer that no evolutionary change in any body part is likely to occur without ultimately affecting one or more of those eight traits.

In an attempt to show that the H metric discriminates better among birds than among other vertebrates, our critics draw attention to the fact that 73% of the morphological distance between a hummingbird and an albatross is due to differences in two traits (head and forearm length) and then assert that these two traits are more variable among birds in general than in mammals or reptiles. As will become clear when we publish the measurements made by Wyles et al. (1983) on more than 200 bird taxa, however, these two traits contribute only 33.5% to the mean H value for interbird comparisons. The corresponding figure for mammals, 33.1%, is not significantly different. This result points to the dan-

ger of putting too much emphasis on a result obtained with a particular pair of species.

Allometry.—Our initial goal is to obtain a quantitative estimate of how different any two species are at the organismal level, particularly in body shape. How that difference was brought about is a separate problem. Ultimately, it will be of great interest to find out how many mutations were required. Some of the body shape difference may be the result of mutations that changed the length of the growth period without altering the relative rates of growth of the various parts of the body. In other cases the converse may obtain. It will be a long time before the genetic basis of anatomical differences is known for a large number of pairs of vertebrate taxa (Edelman, 1984). In the mean time, one must avoid confusing the need for a quantitative description of the degrees of organismal difference with the need for explanations of those differences.

Two Perspectives in Evolutionary Biology.—It appears to us that the Hafner et al. (1984) criticism is a manifestation of the "populationist" perspective, which has dominated systematic and evolutionary biology since the 1940's. It focuses on the *tips* of the evolutionary tree and on the uniqueness of every trait, individual, population and species (Mayr, 1976). In contrast, we have been influenced by what might be termed the "distance" perspective, which entered evolutionary biology more than 20 years ago as biochemists began to compare proteins from species belonging to different *branches* of the tree (Zuckermandl and Pauling, 1962; Margoliash, 1963; Wilson and Kaplan, 1964; Wilson et al., 1964).¹

The "populationist" perspective's emphasis on uniqueness engenders respect for the generalisation referred to by Hafner et al. (1984): The set of characters that best discriminates among members of one taxonomic group is unique to that group. Such a perspective makes one wary of comparing the degree of difference between a pair of species in one taxonomic group with that in another taxonomic group. Molecular evolutionists, by contrast, have long been comfortable with the practice of using the same yardstick (i.e., number of substitutions) to examine and compare evolution in vastly dif-

¹ Because "populationists" work within species or between closely related species, many of the differences they encounter are the result of changes in the relative frequencies of alleles that pre-existed in the ancestral population. Molecular evolutionists, by contrast, are usually concerned with long-term evolution, which depends on new mutations. The difference between the albumins of two species that diverged 20 million years ago is mainly the result of mutations that were not present in a common ancestral population. Since population-thinking is less relevant to the analysis of such cases, it is not surprising that another perspective developed among molecular evolutionists.

ferent taxonomic groups. The criticism of our work by Hafner et al. (1984) has made us realize what a deep gulf there is between these two perspectives and how important it is to explore that gulf on another occasion.

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