

Essay-review of Sibley and Ahlquist's Phylogeny and Classification of Birds: A Study in Molecular Evolution.

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Essay-Review of Sibley and Ahlquist's *Phylogeny and Classification of Birds: A Study in Molecular Evolution*

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Phylogeny and Classification of Birds: A Study in Molecular Evolution.—Charles G. Sibley and Jon E. Ahlquist. 1990 [1991]. New Haven, Connecticut, Yale University Press. xxiv + 976 pp., 385 text figures. ISBN 0-300-04085-7. \$100.00.—In different hands at different times, an individual book may serve a variety of purposes. A text used by one person for religious inspiration may be used by another as nothing more than an

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example of prose style. A reader today probably would not turn to Homer for information about Greek history, but it was a belief in the historical truth of the “Iliad” that led Schliemann to discover the city of Troy. Sometimes a book takes on a role so far removed from its intended one that it surprises us. I once saw a volume of Xenophon used, quite successfully, as a wedge to keep a ceiling light fixture from rattling.

The first purpose of a book of science is to provide a representation of the world that can be judged true or false. But science books can serve as many different purposes as works of history or literature, and this is worth remembering as we consider “Phylogeny and Classification of Birds” by Charles Sibley and Jon Ahlquist. It is worth remembering because it is in fulfilling its scientific purpose that this book is least successful, and professional systematists are likely to be disappointed by it. The value the book does have will be realized in unexpected contexts: among those who have up to now given little thought to phylogeny and its importance, and among the young.

“Phylogeny and Classification of Birds” is a compilation of Sibley and Ahlquist’s DNA hybridization studies of avian systematics, studies that have been conducted over the last 20 years. The book is divided into two parts. The first part consists of 17 chapters that review the history of bird classification, the principles of classification, and the methods of comparative molecular biology. The second part goes through the major groups of birds, reviews the history of the classification of each group, and then presents the authors’ own phylogenetic conclusions. The second part concludes

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with a chapter on historical biogeography. Grouped at the end of the volume are more than 300 DNA melting profiles and about 30 evolutionary trees, the last of which is the famous “tapestry,” a multipart diagram that is almost 5 m long when fully assembled.

Being largely a compilation and synthesis of Sibley and Ahlquist’s earlier DNA hybridization work, this book is in the unenviable position of having had its methods and results widely criticized even before the volume appeared (Lanyon 1985; Templeton 1985; Ruvolo and Smith 1986; Cracraft 1987; Felsenstein 1987; Houde 1987; Sheldon 1987; Lewin 1988a, b; Bledsoe and Sheldon 1989; Marks et al. 1989; Sarich et al. 1989; Sheldon and Bledsoe 1989; Springer and Krajewski 1989; Bledsoe and Raikow 1990). The authors acknowledge some of this criticism, although they do not cite all of it (the papers of Templeton, Ruvolo and Smith, Cracraft, Houde, and Bledsoe and Raikow are not mentioned, nor is the news article by Lewin), and they do not respond very strongly to the criticism that they do acknowledge. But the criticism has apparently been felt; anyone who was exposed to the authors’ earlier claims for their method, and the uncritical praise of early reviewers (Diamond 1983, Gould 1985), will recognize in the Preface (p. xvii) a considerable admission: “Our data are not perfect and we did not subject them to every available statistical analysis; that we should have done many things better is undeniable, but hindsight is always crystal clear.”

The DNA hybridization techniques the authors used will by now be familiar to many. If the double-stranded DNA of an organism is put into solution and warmed, the two strands will gradually come apart. If

instead of starting with “homologous” double-stranded DNA, we join together single strands from two different species, and then melt this “hybrid” or “heterologous” DNA, we will find that it melts at a slightly lower temperature than does the homologous DNA of either of the component species. This is because the DNA strands of the two different species do not match one another perfectly, and so the hybrid helices can be more easily shaken apart. The difference in melting temperature between homologous and heterologous DNAs can be taken as a measure of the overall genetic “distance” between the two species being compared. The smaller the genetic distance, the more recently the species are assumed to have diverged from one another. From a table of such distances, calculated for a variety of taxa, it is possible to build up an evolutionary tree.

As simple as this procedure may sound, it is in fact fraught with practical and theoretical complexity. {page 991} Some of this complexity was uncovered by the authors themselves, and to the extent that they had not originally taken it into account, the discovery of this complexity has led them to undermine their own work. This is in a sense a mark of success, because it means that we now understand DNA structure and evolution better than we did before. While the range of the criticism leveled against Sibley and Ahlquist’s procedures is such that it cannot be summarized in this short space, most of their critics have focused on two areas that can be mentioned: the choice and calculation of an appropriate distance statistic, and the techniques used to construct evolutionary trees from the calculated distances.

Double-stranded DNA does not melt at a particular temperature, but rather dissociates gradually over a temperature range. The difference in melting temperature between homologous and heterologous DNAs is therefore not a difference between two points, but between two curves, and this difference can be calculated in a variety of ways. The most common difference measures used are the T_{50H} statistic and the T_{mode} statistic. The trees published in "Phylogeny and Classification of Birds" are all based on T_{50H} values, but Sarich et al. (1989) have argued that this statistic can magnify small differences spuriously, and that its useful range is narrower than Sibley and Ahlquist claim (on this latter point see also Sheldon and Bledsoe 1989). Furthermore, Sibley and Ahlquist "corrected" some of the raw values obtained in their experiments before they calculated T_{50H} values (Lewin 1988a, b). They defend these corrections in this volume (pp. 150–164), but even if this practice is legitimate, the corrections introduce an additional measure of uncertainty into their calculations of genetic distance. Sibley and Ahlquist regularly resolve branches that are only a fraction of a degree apart, but the work of their critics suggests that such resolutions are unlikely to be reliable.

Once one has chosen a distance statistic and calculated a table of distance values, the next step is to construct an evolutionary tree from the calculated distances. In their earlier publications, Sibley and Ahlquist assumed that there was a uniform average rate of DNA evolution in all lineages. They assumed that they were gathering data from a molecular clock. Under such an assumption, a phenetic clustering algorithm

such as UPGMA will produce a correct evolutionary tree, and that is in fact how the final tapestry (Figs. 357–385) was assembled. In this volume, however, the authors concede that their earlier assumption of a uniform average rate of DNA evolution was not correct. One very interesting factor that appears to influence the rate of DNA evolution is generation time: genetic distance “accumulates” more rapidly in taxa with short generation times than it does in taxa with long generation times. Sibley and Ahlquist believe this accounts for the anomaly of *Turnix*, a rapid breeder, which is exceptionally distant in genetic terms from all other avian taxa.

We now know that the rate of DNA evolution is not uniform across lineages, so the structure of the tapestry (first presented publicly at the XIX International Ornithological Congress in 1986) must be regarded with considerable skepticism. The authors provide in this volume a collection of new trees constructed according to the Fitch-Margoliash algorithm, an algorithm that does not assume equal rates of change in all lineages, and many of these trees differ in branching structure from the tapestry (compare for example the position of *Colinus* in Figs. 334 and 360, or the position of *Anseranas* in Figs. 328 and 357). In many cases these new trees are based on pooled data from entire clades, a practice that might have been legitimate if the assumption of equal rates of evolution had been true, but that now seems inadvisable. An annoying editorial lapse must be noted here: the Fitch-Margoliash trees are accompanied by tables of branch lengths, but the internal nodes of these trees are not labeled. This means that although it is possible to determine from a table that the branch between node 2 and node 5 on a

particular tree has a length of 2.24, it is difficult to determine from that tree which node is number 2 and which node is number 5.

The conclusion one is driven to is that the phylogenies presented here are uncertain to a degree that is itself uncertain. No one expects perfection, but in most phylogenetic studies today serious readers can get a feeling for how much confidence they should place in the result. Here that is not possible. We are shown distance measures calculated from raw data (perhaps corrected, perhaps not; we don't know); these distance measures are pooled in many cases, thereby concealing their actual variation (which is of unknown extent); trees are calculated from these distance measures, but these trees are not compared with trees calculated from other distance statistics, nor are we shown a consensus of the trees that could be calculated if we allowed for an error of, say, 0.5° in the $T_{50}H$ values. The phylogenies presented here will have value in suggesting appropriate outgroups for future phylogenetic studies, but no one should use them as a basis for studies of avian evolution without carefully taking into account their many weaknesses.

Turning from the DNA hybridization work, there is much in this book still to be examined. The early chapters review the general literature on molecular systematics, DNA structure, and genome organization. These chapters will be appreciated by all of us who have not kept up with the literature on molecular evolution as well as we should have. As extensive as these reviews are, however, they are short on critical analysis and synthesis, and are somewhat unsatisfying. We learn a great many details—Glaus et al. studied mtDNA in galliforms;

Awise and many others studied mtDNAs in various vertebrates; Awise and [{page 992}](#) Nelson studied mtDNA in *Ammodrammus maritimus*; Ovenden et al. studied mtDNA in *Platycercus*; Ball et al. studied mtDNA in Red-winged Blackbirds; Anderson et al. studied mtDNA in humans (p. 102)—but if we seek an overall synthesis or general interpretation of these myriad studies we will not find it. I had the sense that I was reading a collection of note cards that had been strung together, one after another. The bibliographic value of these lists is undeniable, but there are better ways of organizing an annotated bibliography. Because authors' names generally are not listed in the Index, the reader who wishes to know, for example, whether Ovenden's work is commented upon anywhere else in the volume will be out of luck.

Woven together with the biochemical reviews and the phylogenetic results in this book is another item of value: the most comprehensive review of the systematic literature on birds ever published. Detailed histories of passerine and nonpasserine classification are provided, and still more detailed discussions accompany the systematic treatments of each family or order. As with the biochemical reviews, the usefulness of these compilations is great, and I have already had occasion to consult them several times myself. Their style will be familiar to readers of Sibley and Ahlquist's earlier egg-white protein monographs (Sibley 1970, Sibley and Ahlquist 1972). But in point of fact, more than the style will be familiar, because the greater part of the text of the historical reviews in "Phylogeny and Classification of Birds" is copied directly from these earlier monographs. Sometimes this copying is word for word, and sometimes minor stylistic changes are

made, as from “can be important in the phyletic understanding of such groups” (Sibley and Ahlquist 1972: 28) to “can be important in understanding the phylogeny of such groups” (p. 220). These reviews contain new information, but more often than not this new information is simply tacked onto the beginning or end of a copied passage, rather than worked into the text. The only acknowledgement that this great quantity of material has been copied from the authors’ earlier work is a single sentence in the Preface (p. xvii) stating that “Most of these reviews [from their earlier egg-white protein monographs] are included in this book.” While I suppose that strictly speaking there is nothing wrong with copying extensively from one’s own work, it doesn’t strike me as a particularly noble practice. Readers who are under the impression that “Phylogeny and Classification of Birds” is a new work are simply mistaken: half of it is 20 years old.

But what of the quality of these systematic reviews, independent of their age? As with the biochemical reviews, they are long on detail and short on interpretation. The authors may fairly claim that they are not historians, and that these reviews are not intended to be professional works in the history of science. But if this is so, then they should have been more careful with the occasional commentary they do provide. For example, in speaking of the quinarian approach to systematics, common in the 1820s and 1830s, they declare that “this excursion into self-delusion was discredited long before Darwin provided a solid basis for systematics” (p. 185, copied from Sibley and Ahlquist 1972: 5). The quinarian approach was wrong, of course, and it was eventually rejected. But for a period of time it was seriously defended in the professional

literature by able writers; no less a systematist than T.H. Huxley experimented with it (Winsor 1976); and while it is true that Darwin never accepted the quinarian position, it was hardly rejected “long before” Darwin, inasmuch as Darwin discussed it extensively in his notebooks and was at pains to understand how evolution might produce the sorts of systematic patterns that the quinarians believed they saw (Ospovat 1981: 101–113). The knowledgeable reader can skip over remarks about “excursions into self-delusion,” but the novice should be aware that comments such as these make professional historians wince.

There is one interpretive theme that does run through all of the historical reviews in this volume, and an examination of it will help us to understand why the authors went astray in a number of areas. That theme is the failure of morphology to solve systematic problems, and the inherent superiority of genetic information. In the last 30 years systematics has been through a good deal of turmoil, and a reader who has not followed these controversies closely might assume that “Phylogeny and Classification of Birds” is an outgrowth of that turmoil. But this is not the case. Technically, this book is a product of 1980s molecular biology, but conceptually it is a product of 1950s systematics, and the “failure of morphology” theme is one of the indelible stamps of its origin. The systematics of the 1950s was highly successful at the species level, but it was poorly developed in its understanding of phylogeny. The inane remarks of Stresemann (1959), quoted with approval by Sibley and Ahlquist (pp. 235–236), show this clearly. In the 1950s the important distinction between classification and

phylogeny reconstruction was imperfectly made, and it was not understood that “homology” is composed of two distinct similarity relations, namely primitive or ancestral homology, and derived homology. Ignorance of these distinctions undergirds the “failure of morphology” theme, and allows the authors to claim that “only homologous similarities may be used to reconstruct phylogeny” (p. 4), when in fact homology (inherited similarity) tells us almost nothing about phylogeny; only derived homology is informative, even in DNA hybridization studies (Springer and Krajewski 1989). The “failure of morphology” theme assumes that theory enters into systematics hardly at all: all that matters is data, and everyone interprets data in the same way. We can see this assumption at work in the historical reviews, where the divergent [page 993](#) methods and goals of systematists over 150 years are almost completely ignored. All past authors are treated as though they were doing the same thing—“classifying birds”—when in fact some were classifying (according to a variety of principles), some were reconstructing phylogeny (also according to a variety of principles), some were doing both, and some didn’t think long enough to know what they were doing (see O’Hara 1991 for an indication of the complexity of systematic history). That older systematics was weak in its methods rather than its data is clearly shown by the approximate congruence between Sibley and Ahlquist’s DNA hybridization results and contemporary morphological cladistic studies (Raikow 1987, Bledsoe and Raikow 1990). Such congruence was acknowledged with approval by Sibley et al. (1988: 413–414), but its implications for the “failure of morphology” theme are nowhere explored.

Systematists have generated quite a bit of hot air in the last 30 years, but they have also gained many important insights into their discipline. Unfortunately, none of those insights are reflected in this volume.

What role will this book play, now and in the future? In spite of its many weaknesses, can it be redeemed? It can be, I think, if we change our notion of its proper audience.

Professional systematists will use it primarily as a bibliographic reference, and as a rough starting point for future phylogenetic analyses. For these reasons alone it should find a place on the shelves of every university, museum, and public library of any size, and in the personal collections of all who are interested in avian evolution. But if we consider “Phylogeny and Classification of Birds” to be a book only for professional systematists, we will unnecessarily restrict its usefulness. The greatest value of this book will come not from its systematic conclusions, but simply from its scope, and that value will be realized among readers—especially young readers—who have heretofore given little thought to the importance of evolutionary history. What this book does very successfully is present the *idea* of phylogeny, the *idea* of the history of life, in a way that it has rarely been presented before. Many of us will have had some particular book that inspired us when we were young, and that showed us the possibility of a scholarly career. For me, it was Mayr’s “Principles of Systematic Zoology,” which I had more or less memorized by the time I was 15; for a colleague of mine it was Romer’s “Vertebrate Paleontology.” These books were important to us not because of any particular facts they taught us; they were important because they mapped out whole new worlds of knowledge that we could expand into and

endlessly rechart for ourselves. “Phylogeny and Classification of Birds” is just the sort of book that can serve that purpose for a whole generation of young scholars. Anyone who wants to do something positive for systematics should photocopy the long string of figures that make up Sibley and Ahlquist’s tapestry, tape them together, and hang the result along a wall in a high school science laboratory or a college corridor. (Keep in mind as you do this that for \$100 the publisher should have provided you with a fold-out chart.) That one diagram, however inaccurate it may be from the viewpoint of a professional systematist, will convey to the mind the idea of the tree of life more forcefully than any other diagram I know; an idea that no checklist or collection of smaller trees can convey. Colleagues who are not accustomed to “[tree thinking](#)” may come to see from that diagram how far more interesting all of the phenomena of biology are—whether of behavior, ecology, physiology, biochemistry, biogeography, or anatomy—when they are considered in the context of history. And some stray, odd student might even be sufficiently inspired by that image to make of systematics a career.

A hundred years ago, Richard Bowdler Sharpe published another “tapestry” of bird phylogeny, one that he had displayed at the II International Ornithological Congress in Budapest (Sharpe 1891; reproduced in O’Hara 1991). Sibley and Ahlquist’s phylogeny is in many ways a direct descendant of that earlier tree. Sharpe’s diagram had the misfortune of appearing toward the end of the early Darwinian period—toward the end of phylogeny’s golden age—and after it appeared systematists began to turn away from the larger questions of evolutionary history, and

toward the smaller and more tractable problems of species and geographical variation. "Phylogeny and Classification of Birds," in contrast, appears at the beginning of a new age of phylogeny, an age filled with excitement for all of us in systematics. To the extent that this book leads more people to understand and share in that excitement, it will be considered a success. —ROBERT J. O'HARA

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