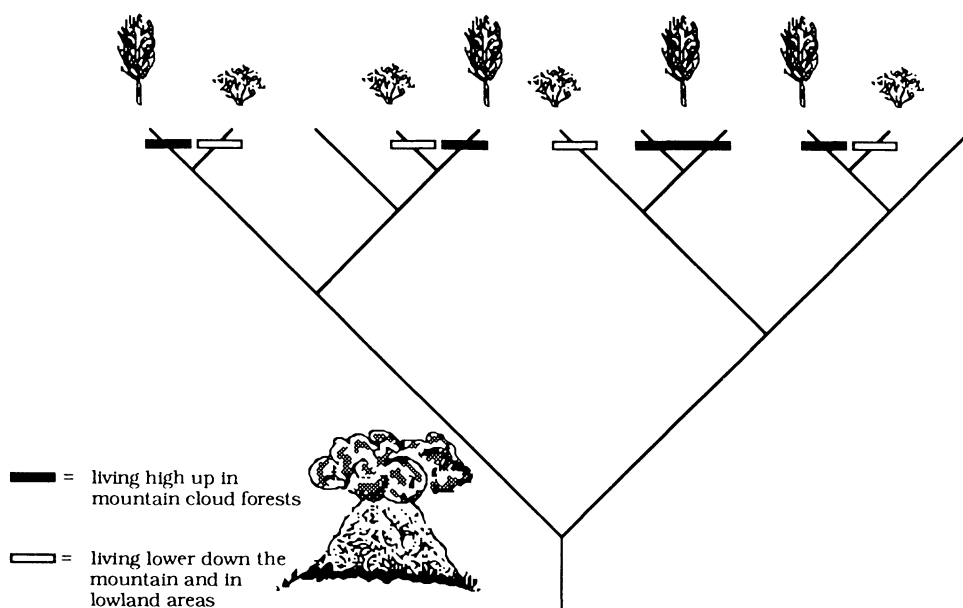




"Habitat distribution of the tree species of the genus *Montanoa* and their shrubby sister groups. Tree forms only live high in the mountain cloud forests, while the shrub forms are located lower down the mountain sides and into lowland areas." [From *Phylogeny, Ecology, and Behavior*]

speciation event occurred. For example, if two sister taxa (that is, species more closely related to each other than either is to any other) co-occur, then sympatric speciation is implicated, whereas the sympatry of non-sister taxa suggests some other mode of speciation followed by dispersal. Similarly, if the ranges of sister taxa abut, then parapatric speciation is supported, whereas disjunct ranges of sister taxa indicate allopatric speciation. On the basis of this reasoning, the authors endorse a recent analysis that concluded that a surprisingly high 8 to 14 percent of speciation events among a set of vertebrates were sympatric. Certainly, phylogenetic information will bring geographic data into sharper focus, but the reliability of the underlying assumption that the size and location of a species's range are a good indicator of its mode of speciation is suspect. Would one really expect the range of a species that arose by means of peripatric speciation (that is, in a small and isolated peripheral population) to remain restricted forever? Do sympatric sister species indicate sympatric speciation, or might they simply represent species that evolved allopatrically and subsequently expanded into sympatry? Conversely, recent paleoecological studies indicate that species that belonged to the same community in the Pleistocene no longer occur together. Consequently, sister species that are allopatric today could have arisen by sympatric speciation. Although phylogenetic information can render particular scenarios unlikely, within-species studies of speciation in action are the best bet for en-

lightening us about the underlying processes.

A more general concern is the absence of discussion of the underlying tenets of the cladistic philosophy, which is particularly distressing because this book is geared toward workers new to phylogenetics. Given that Brooks and McLennan's method invokes a double dose of parsimony, first in the construction of the phylogenetic tree and then in the optimization of character evolution upon it, the lack of any substantive discussion of the theoretical justification or potential consequences of the reliance upon parsimony is surprising. Indeed, theoretical analyses have made clear that parsimony often will fail to provide the correct phylogenetic tree; the real question is, how far off will it be? Even if the tree is correct, parallelism and reversal in the evolution of characters of interest are likely to be more common than character optimization based on parsimony would suggest. Further, no one has assessed the overall effect of such serial applications of parsimony. Character optimizations that are slightly less parsimonious on the favored tree may be overwhelmingly more parsimonious on slightly less favored trees. These and a host of other questions (for example, what about alternative methods for reconstructing phylogenies and optimizing characters?) need to be addressed before parsimony methodology can be accepted as the best means for incorporating history into comparative biology.

Two promising avenues to extend phylogenetic approaches beyond the mere formulation of historical scenarios are discussed in

the concluding chapter. First is the use of recently proposed statistical methods to test whether particular patterns, be they evolutionary correlation of characters, congruence of taxon and area cladograms, or species-richness of a clade, are more unusual than one would expect from chance. Second is the reciprocal illumination produced between historical and contemporary studies. Brooks and McLennan are at their best when they point out crucial experimental studies suggested by phylogenetic patterns. Conversely, relationships exhibited by extant taxa (such as biomechanical linkages or correlations between phenotypic and ecological features) can be investigated phylogenetically to determine whether they are obligatory and how they arose.

Brooks and McLennan have clearly demonstrated the large contribution historical contingency makes to present-day pattern; failure to consider this historical legacy will critically hinder attempts to understand the diversification of life and will doom many studies to overestimate the power of contemporary processes. Brooks and McLennan's parsimony approach is only one of a number of recently proposed phylogenetic comparative methods, however; new approaches are appearing willy-nilly. Brooks and McLennan have made a strong case for the incorporation of phylogenetic information into studies of all aspects of biological diversity, but only time will tell to what extent the cladistic approach they espouse will be accepted as the method of choice for conducting such studies.

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The Birds Reclassified

Phylogeny and Classification of Birds. A Study in Molecular Evolution. CHARLES G. SIBLEY and JON E. AHLQUIST. Yale University Press, New Haven, CT, 1991. xxiv, 976 pp., illus. \$100.

Until recently the definition of the relationships among the higher categories of birds (subfamilies, families, and orders) had changed remarkably little since the classification proposed by Hans Gadow a century ago. Ornithologists have debated such issues as whether flamingos are actually modified ducks and whether the seemingly smart ("advanced") crows should be listed last in the linear classification, but the age-old arrangement of taxa based on overall (sometimes clearly convergent) morphological similarity has persisted without substantial

change. Now Charles Sibley and his colleague Jon Ahlquist are challenging ornithological traditions with a radical new phylogeny and classification based on DNA-DNA hybridization.

The roots of their work go back 30 years to the dawn of modern biochemical systematics when Sibley first compared egg-white proteins. In those days, molecular approaches showed unlimited promise by virtue of their objectivity and freedom from selection and convergence. That promise was enhanced by subsequent theoretical advances such as proposals of a molecular clock and neutral accumulation of mutations. In the early '70s, when the proteins had failed to produce resolution of relationships among the higher groups of birds, Sibley and Ahlquist turned to DNA-DNA hybridization to measure genetic similarity. They adapted the technique, which had been developed by Roy Britten and others in the '60s and early '70s, to mass-produce hybrids for the comparison of large numbers of taxa. They assembled thousands of DNA samples from birds around the world representing species from all but three families, and they produced more than 25,000 bird DNA hybrids in an unprecedented effort to revise an entire class of organisms by a single molecular technique.

This book is the culmination of their pioneering efforts, which helped to ignite the explosive growth in molecular systematics in the '80s. It is an encyclopedic work that offers: (i) a modern and comprehensive statement of higher-category relationships among the birds of the world; (ii) a demonstration of the powers and limitations of single-copy nuclear DNA (scnDNA) hybridization methodology as practiced by the authors; and (iii) an evaluation of lineage-dependent rates of DNA evolution.

The volume is divided into three sections. The first comprises 14 short chapters on molecular genetics, phylogeny, and classifications as they pertain to comparative scnDNA hybridization studies plus 3 chapters on materials, methods, and data analysis. The second section is a 500-page encyclopedia of the systematics of major groups of birds, which emphasizes age-old taxonomic problems and includes summaries of all pertinent literature and discussions of Sibley and Ahlquist's results. This section is an extraordinary compendium of the literature on ornithological systematics; its bibliography alone belongs on every ornithologist's shelf. The text contains a host of taxonomic changes, many published previously, including the realignment of relationships among the passerine birds of Australia

and New Guinea. The presentation is clear and forceful. The accumulation and summary of information are a master effort by a distinguished pair of ornithologists. The third section of the book comprises 307 figures of selected samples of raw data depicted as hybrid dissociation curves, 28 computer-generated phylogenetic trees constructed from subsets of the taxonomic comparisons, and then the finale—"The Tapestry." The Tapestry is a giant phylogeny representing the higher categories of the birds of the world and spanning 30 interconnected figures. First displayed as a 50-foot-long poster at the International Ornithological Congress in 1986, it summarizes all of Sibley and Ahlquist's measurements and is the basis for their new classification. It also provides the structure for a large companion volume, *Distribution and Taxonomy of Birds of the World* by Sibley and Burt L. Monroe, Jr. (Yale University Press; 1135 pp., illus. \$125), which details the names, habitats, and distributions of all living species of birds.

Much as we admire Sibley and Ahlquist's vision in perceiving the potential power of DNA hybridization and their energy in compiling such a huge data set and literature review, we are equally disappointed by the many analytical shortcomings in their book. Because they failed to improve their experimental design and methods of data analysis over a 10- to 15-year period, they have been surpassed by much of the field of systematics, which relentlessly sets new and increasingly stringent standards. Cladistic ideologues will reject on first principle the notion that distance data, such as those produced by DNA hybridization, can be clustered into hierarchies reflecting genealogy, but for purposes of this review we accept that DNA hybridization works (on the congruence of results of various methods see for example Bledsoe and Raikow, *J. Mol. Evol.* **30**, 247 [1990]) and simply consider how well Sibley and Ahlquist analyze their data.

The distance statistic used by Sibley and Ahlquist is ΔT_{50H} —a measure that incorporates an index of hybrid dissociation (median melting temperature, T_m) as well as a factor reflecting the extent of hybrid formation. The success of their entire venture depends upon the utility of T_{50H} . This index permits the extrapolation of genetic distances that are too large for the usual hybrid melting indexes, T_m and mode. Without T_{50H} , for example, Sibley and Ahlquist could not postulate the interordinal relationships of such diverged groups as pigeons, woodpeckers, and ducks. But T_{50H} has fallen on hard times and lately has been the object of much criticism, particularly because it carries a large error and depends

on additional assumptions concerning genome characteristics and rates of evolution. This is one instance when Sibley and Ahlquist recognize criticism, and they parry it quite well. In addition, the accuracy of long T_{50H} extrapolation has been dramatically corroborated by the primate sequence data of Morris Goodman and colleagues at Wayne State. But Sibley and Ahlquist have modified an unspecified number of their T_{50H} values, and the effect of these changes is unknown. Although the authors discuss the principles behind them, the alterations are *a posteriori* and subjective. The reader cannot decipher how "corrections" affect a given data set or conclusion. This is a nagging problem because there are actually two overlapping kinds of data manipulation to worry about, those that clean up the data by aligning distances and those that attempt to accommodate variable rates of DNA evolution in phylogenetic tree construction.

Accommodation of variable rates of DNA evolution is the issue that in the end poisons the analyses of the data, the construction of the Tapestry, and ultimately the new classification. Current systematic standards require the construction of trees from a complete matrix of pairwise distance comparisons by an algorithm that fits a tree to the matrix distances. In light of the discovery of variable rates of evolution in different lineages, the fitting algorithm must not assume a molecular clock. When Sibley and Ahlquist began their DNA-hybridization research, it was common practice to construct trees by simple pair-grouping methods such as UPGMA, which assume constant rates of evolution. This assumption was reasonable in the heyday of the molecular clock. Indeed, Sibley and Ahlquist's early hominoid and passerine data appeared to support a "uniform average rate of DNA evolution." Thus they first compared an assortment of birds and then followed the more interesting paths with further comparisons. This approach led to many discoveries, but resulted ultimately in a series of disjunct and incomplete comparisons. When Sibley and Ahlquist tackled the enormous task of evaluating relationships among the nonpasserine birds, they encountered a new and devastating problem—variable distances due to unequal rates of evolution. Instead of starting over (who could blame them?), they tried to correct matrices for rate discrepancies and to apply a modern tree-building algorithm to subsets of the data to produce small trees for comparative purposes. But these patchwork efforts do not succeed well. The incomplete set of comparisons, combined with distances perturbed by variable rates of evolution, make it impossible to reconstruct the Tapestry objectively.

Sibley and Ahlquist's rate corrections were based on a series of three-taxon relative rate tests applied to all major groups. When rate discrepancies were discovered, the authors lengthened or shortened branches in the Tapestry accordingly. Also implicit in their corrections is the notion that rate is inversely correlated with generation time. This generation-time effect is discussed in various parts of the book, and there is a table that summarizes the range of breeding ages in some groups of birds, but nowhere do Sibley and Ahlquist quantify the relationship between generation time and rates. They simply invoke generation time to explain curious differences in rates.

The small trees Sibley and Ahlquist produce from data subsets were generated by the FITCH program of J. Felsenstein's PHYLIP computer package. These trees often differ from the Tapestry and display the branch-length variability inherent when rates of evolution differ. The authors acknowledge differences between the small trees and the Tapestry, but only rarely (as in their placement of the ducks and galliforms relative to the ratites) do they opt for the more objective FITCH-tree hierarchy. Admittedly, the FITCH trees are drawn from a small subset of data; nevertheless, they provide undistorted representations of the data and tree topologies. For example, in the order Anseriformes, the Tapestry and the classification portray the Australian magpie-goose (*Anseranas*) as the sister taxon to the screamers. Yet, the FITCH trees and also an independent set of DNA-hybridization data (Madsen *et al.*, *Auk* 105, 452 [1988]) cited by Sibley and Ahlquist indicate instead that *Anseranas* is the sister taxon of ducks and geese.

Perhaps the most graphic illustration of the issues and problems of data analysis and tree-building is to be seen in the discussion of relationships among the ratites (ostrich, emu, cassowary, rhea, and kiwi). This is the only distinct group of birds for which Sibley and Ahlquist have the data required for a rigorous phylogenetic analysis, a complete set of pairwise comparisons. The Tapestry and the classification indicate that there are two main groups, one comprising ostrich and rhea and the other kiwis, emu, and cassowaries. Data published by Sibley and Ahlquist in 1981 and the uncorrected ΔT_{50H} values presented in the current volume show that the ostrich is the sister group of all other ratites including rhea, or, more conservatively, that the branching hierarchy among ostrich, rhea, and the Australo-New Zealand species is unresolved (figures 325 and 326). Further, these data indicate that the DNA of different groups of ratites evolved at different rates (figures 18 through 24 and 325). The authors state in the text that the position of rhea is uncertain. Why

then do they group it with ostrich in the Tapestry? The net result is that their classification is not always the best representation of the data. Because there are no unresolved nodes in the Tapestry to portray many uncertainties, ornithologists interested in the DNA-hybridization phylogeny will not know which phylogenetic proposals to trust.

Phylogeny and Classification of Birds is a milestone in ornithology by virtue of its herculean scope and its pioneering methodology. Several of the phylogenetic proposals are worthy of acclaim, particularly the discovery of the Australian passerine endemism. We commend Sibley and Ahlquist for trying more seriously than any predecessor to change the status quo. By insisting on a molecular approach that was in principle free of subjectivity, they set more stringent standards for phylogeny reconstruction and initially quashed authority and experience as the basis of successful systematic analysis. Their own analyses of the data, however, then fall victim to the new standards of analytical and theoretical rigor. As a result this work is a paradigm of how the idealized promise of molecular systematics of the '60s has been compromised by the predictable discoveries of its limitations.

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Extinct New Zealanders

Prodigious Birds. Moas and Moa-Hunting in Prehistoric New Zealand. ATHOLL ANDERSON. Cambridge University Press, New York, 1990. xviii, 238 pp., illus. \$79.50.

Poking fun at ornithology, an arrogant ecologist once told me that there were three kinds of birds: large ones, small ones, and owls. After reading Atholl Anderson's book I would now add moas (Polynesian for "chicken" or "domestic fowl"). These diverse, flightless New Zealand herbivores (some apparently folivores) were as representative of New Zealand's past as sheep are of her present, and their study spans the entire spectrum of biology, from molecular evolution and systematics to plant evolution, biological anthropology, and even cryptozoology. In addition, and perhaps most important, they are the most dramatic symbol of the devastation inflicted by the Polynesians in their trek through the South Pacific; no longer will there be the image of the "noble savage" living in harmony with the environment.

Prodigious Birds is the first truly comprehensive review of the biology of these fascinating birds since the work of Archey and,



"A large moa snared and speared." It has been suggested that moas were hunted in mass drives, but "moas in general were probably more wary, mobile and aggressive" than such scenarios presume. "Individual or small-group hunting of small numbers of moas at a time, indirectly by using snares or directly with the assistance of dogs, seem the most likely methods." [From *Prodigious Birds*; C. Higham, *The Maoris* (Cambridge University Press, 1981)]

especially, Oliver published in 1941 and 1949 respectively. Interestingly, the book has appeared at about the same time as a volume of the *New Zealand Journal of Ecology* (vol. 12, 1989) devoted entirely to moa biology, in which Anderson himself has a contribution. Together, these works form a new framework for the study of New Zealand's extinct giants.

Anderson's book has a pleasing introduction interweaving the discovery of the first fossil moas in the 1830s, the great public interest in them that has endured to the present, and questions about their history, particularly the idea, discredited by Anderson, that moas survived in Europeanized Fiordland.

The remainder of the book is logically divided into two major sections. Part 1 contains chapters on the discovery, systematics, origins and development, and morphology and behavior of moas and on Maori traditions bearing on them. The chapter on systematics is introduced by a historical overview and brings us up to the present. The number of moa species has ranged from a high of some 28 proposed by Oliver in the 1940s to the 13 realistically pulled from statistical analyses by Joel Cracraft in the 1970s. The chapter on origins and development takes a difficult topic and presents all sides fairly. The main question is whether moas form part of a monophyletic, flightless, ratite lineage and were drifters on floating continents or whether they arrived much later as the volant ancestral forms. Anderson astutely concludes that all we can say is that they were palaeognathous birds descended from volant ancestors.