

REWEAVING THE TAPESTRY: WHAT CAN WE LEARN FROM SIBLEY AND AHLQUIST (1990)?

JOHN HARSHMAN

*Committee on Evolutionary Biology, University of Chicago,
1101 East 57th St., Chicago, Illinois 60637, USA*

ABSTRACT.—Sibley and Ahlquist's phylogeny of the birds ("The Tapestry") has drawn both praise and criticism. Two major criticisms are that trees were based on incomplete distance matrices and that their tree-building algorithm (UPGMA) was inappropriate. Their 1990 book answered critics by including several complete matrices analyzed by the Fitch-Margoliash algorithm. Matrices were constructed by combining species into composite taxa, which requires additional (possibly defensible) assumptions and introduces additional (probably random) error. Three problems remain: (1) The algorithm used does not always find the best-fit topology, depending on taxon order. (2) The error variance of the data does not fit the assumptions of the Fitch-Margoliash algorithm. The assumptions of the algorithms of Fitch and Margoliash and of Cavalli-Sforza and Edwards are limiting cases that bracket the truth. (3) Even a matrix with no phylogenetic content has a best-fit topology; some test of the strength of support for branches on a tree is required. To address these problems, I analyzed: (1) each matrix several times with different orderings of taxa and with user-defined trees; (2) each matrix with both algorithms; (3) upper-right and lower-left halves of each matrix separately, performed a complete set of single-taxon jackknifings, and created a jackknife strict consensus of all best-fit trees using both algorithms. Based on these analyses, 97 of 173 interior branches (56%) on the FITCH trees published by Sibley and Ahlquist (1990) were still present in my consensus trees. Many trees remained nearly intact; others collapsed into polytomies. I found that 11 of 97 remaining branches (11%) contradict the Tapestry. I conclude that the data in Sibley and Ahlquist (1990), properly analyzed, have a strong phylogenetic signal. Received 22 July 1992, accepted 25 November 1992.

THE RECENT BOOK by Sibley and Ahlquist (1990), *Phylogeny and Classification of Birds*, has already had a major influence on avian systematics and on studies that make use of phylogenies. The result of 15 years of work with DNA-DNA hybridization, the book's phylogeny (Sibley and Ahlquist 1990:figs. 353-385, commonly known as "The Tapestry") is unprecedented: an almost completely resolved tree relating nearly all families and many lower-level taxa. However, for reasons briefly discussed below, the Tapestry is seriously flawed as a representation of Sibley and Ahlquist's data. In this paper, I try to answer two questions: (1) What is the most appropriate way to analyze Sibley and Ahlquist's data? (2) What phylogenetic signals (if any) do the data contain?

THE TAPESTRY

Even before publication, the Tapestry had been criticized on two main grounds: use of incomplete data matrices, and reliance on the assumption of a constant molecular clock (Cra-craft 1987, Houde 1987). The Tapestry was pro-

duced by a modification of the clustering algorithm UPGMA (Sneath and Sokal 1973). Some of the modifications were explained by Sibley and Ahlquist (1981); others were briefly mentioned by Sibley and Ahlquist (1990), but not sufficiently explained. The Tapestry itself cannot easily be evaluated, since many of the data used to construct it, as well as the details of the algorithm used, have not yet been published.

However, in their book, Sibley and Ahlquist (1990) responded to criticisms with a modified analysis of some of their data, and this can be evaluated. I restrict my consideration here to Sibley and Ahlquist's (1990, and earlier references cited therein) analyses of distance data. I do not consider here problems involved in converting radiation counts into distance measures, and the phylogenetic interpretability of such measures; these have been discussed by Cracraft (1987), Houde (1987), Sarich et. al (1989), Sheldon and Bledsoe (1989), Springer and Krajewski (1989), Schmid and Marks (1990) and Mindell (1992).

Incomplete data matrices.—The Tapestry contains 1,118 taxa (species and genera). According

to Sibley and Ahlquist (1990), 26,554 comparisons were used to construct it. However, the number of comparisons needed for a full data matrix (one comparison for each pair of taxa) is 624,403; thus, Sibley and Ahlquist have only a maximum of 4% of the needed comparisons for UPGMA (see Lanyon 1992).

To address this problem, Sibley and Ahlquist turned incomplete matrices into complete matrices using composite taxa (Fig. 1). The cost of this approach is an increase in error. In addition to experimental error (from individual distance measurements), there is a second error component due to different rates of evolution within composite taxa. However, there is no expectation that this additional error will be systematic. Further error is introduced if composite taxa assumed to be monophyletic are not.

The molecular clock.—UPGMA assumes a constant molecular clock. Sibley and Ahlquist's own data show that this assumption is false, at least frequently enough to be unwarranted as an *a priori* assumption in analysis. For example, although they incorporated in the Tapestry an unspecified number of attempted rate corrections for some taxa, their own FITCH analyses (below) show a number of tree topologies that contradict the Tapestry, for which the simplest explanation is difference in evolutionary rates among taxa.

To avoid the invalid assumption of constant evolutionary rates, one should use a tree-building algorithm that makes no rate assumptions. Sibley and Ahlquist (1990) used the Fitch-Margoliash (1967) algorithm as implemented in FITCH, a program included in the PHYLIP package (Felsenstein 1989).

SIBLEY AND AHLQUIST'S FITCH ANALYSES

Sibley and Ahlquist (1990:figs. 325–352) published and analyzed 24 complete (composite) data matrices, representing selected portions of the Tapestry, using FITCH, and these trees should be preferred to the Tapestry in cases of conflict. However, there are still three problems with Sibley and Ahlquist's (1990) FITCH analyses, which I address below.

Best fit.—The FITCH algorithm does not guarantee finding the best-fit topology. Since the testing of every possible topology, given more than a few taxa, takes prohibitive amounts of computer time, the algorithm relies on various

heuristics to reduce the number of trees examined. The initial tree is assembled by adding taxa one at a time in a set order, and this influences the subsequent analysis. Both topology and goodness of fit of the best-fit tree found by the algorithm can depend on the ordering of taxa, particularly if the data are "noisy."

Performing several FITCH runs with different orderings of taxa improves the chance of finding the best-fit tree by eliminating the bias caused by initial tree construction. Global branch swapping (FITCH option G) increases the number of topologies examined per run. Finally, testing the data with user-defined topologies (FITCH option U) finds the best-fit branch lengths for particular topologies (not guaranteed with other options), and may be necessary to discriminate among topologies with small differences in fit.

Data consistency.—Any data matrix, even one composed of random noise with no phylogenetic implications, produces a best-fit tree. Some test of data consistency, or the strength of support for each of the tree's branches, is needed before we draw any phylogenetic conclusions.

One way to test for consistency is to partition the data and determine if subsets give a tree compatible with the one produced by the full matrix. One partition is to divide the lower-left half-matrix, all distances of the form (A,B), from the upper-right half-matrix (B,A); since (A,B) should equal (B,A), the two halves should generate the same tree. Another method is jackknifing (Lanyon 1985a), in which one produces as many matrices as there are taxa, with each having one taxon removed; since relationships among the remaining taxa do not depend on the omitted taxon, all trees should be consistent with each other.

Another possible test of data consistency, bootstrapping, is not possible to perform, since the published data lack both the standard deviation, needed for the method of Marshall (1991), and the individual distance measures averaged to produce each cell's value, needed for the method of Krajewski and Dickerman (1990). Although I did not do so, Faith and Cranston's (1991) topology-dependent permutation tail probability (T-PTP) test could be performed on the published data, with slight modifications to account for the difference between discrete character parsimony trees and best-fit distance trees (i.e. substituting goodness of fit for tree length). The FITCH algorithm would also have

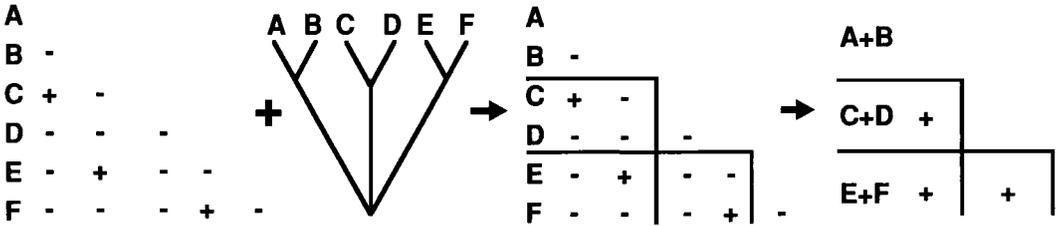


Fig. 1. Way to obtain complete matrix from incomplete matrix. For six species A-F in matrix at left only 3 of necessary 15 comparisons were made: (A,C), (B,E), and (D,F). If relationships among taxa are assumed as shown in tree, taxa and matrix cells can be grouped, producing composite taxa A+B, C+D, and E+F. Distance (A,C) is reinterpreted as (A+B,C+D), etc., producing a complete matrix at level of composite taxa.

to be changed slightly to allow for the partially constrained tree topologies required by T-PTP.

Measure of fit.—One assumption of the algorithm of Fitch and Margoliash (1967) is that the magnitude of error is proportional to distance. However the error of DNA-DNA hybridization measures probably does not vary with distance. This is certainly true for ΔT_m (Bledsoe 1987, Sheldon 1987, Springer and Kirsch 1991) and is probably true for ΔT_{50H} , although no rigorous test has been performed (see Sibley and Ahlquist 1990:table 15 and fig. 15). The appropriate algorithm is that of Cavalli-Sforza and Edwards (1967). The two components of error in composite distances—experimental error and difference in true evolutionary branch length among included taxa—complicate error assessment. The simplest possible case of a composite taxon is shown in Figure 2, and more complex composite taxa should be similar. In Figure 2, the distance between composite taxon A+B and taxon C is the mean of distances (A,C) and (B,C). The constant magnitude of experimental error is shown by the bar. Trees show true evolutionary distances. In tree 2a, A and B evolved at nearly equal rates; in tree 2b, although rates differ substantially, the time since their divergence is short. In both cases, distances (A,C) and (B,C) are similar, and the additional error introduced by composite taxa is small. As this error component approaches zero, the assumptions of the Cavalli-Sforza and Edwards algorithm are approached. In tree 2c, which shows differing rates and a long period since divergence of A and B, distances (A,C) and (B,C) are dissimilar, and the additional error is large. The expectation is that this error component will increase with distance. As the magnitude of this component increases relative to experimental

error, the assumptions of the Fitch-Margoliash algorithm are approached.

It is impossible to decide between the assumptions of the Fitch-Margoliash and Cavalli-Sforza and Edwards algorithms without knowing the true tree topology and branch lengths. Since the two algorithms are limiting cases, neither is likely to be quite correct. One solution is to use both algorithms and to accept only portions of the topology on which they agree.

Unfilled cells.—There is a fourth potential problem that I did not address. When only one comparison of a reciprocal pair was available, Sibley and Ahlquist (1990:150) filled the empty cell with its reciprocal—i.e. when there was a measured distance (A,B) but no measured distance (B,A), the value for (A,B) was used in the cell (B,A). This practice gave slightly greater weight than warranted to those repeated distances. However, I could not correct the problem since the authors did not specify which cells were so filled. The effect on trees was undoubtedly small and probably did not extend

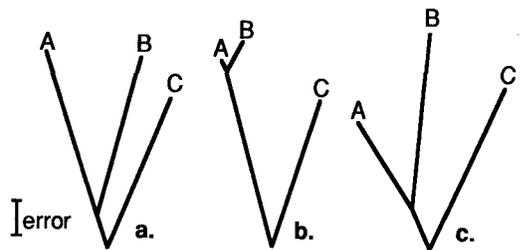


Fig. 2. Demonstration of error component due to composite taxa. If composite taxa have (a) equal evolutionary rates or (b) short branch lengths, the error component is small. (c) If taxa have different rates and long branch lengths, the error component is large. See text for further explanation.

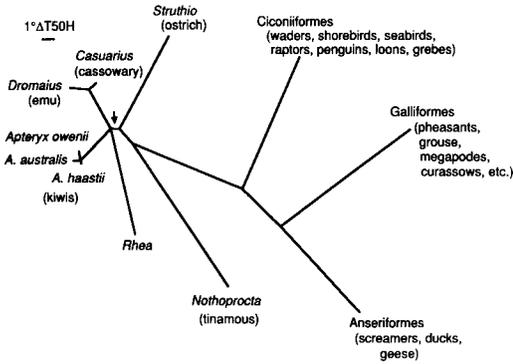


Fig. 3. Ratites.

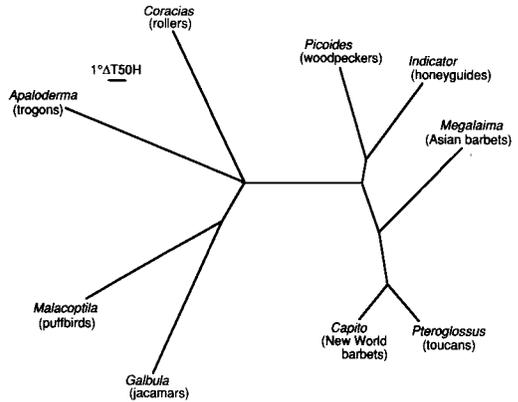


Fig. 5. Piciformes.

to changes in topology, although I am unable to test this assertion.

METHODS

I analyzed 22 of the 24 matrices in Sibley and Ahlquist (1990), incorporating the solutions described above. I divided each matrix into lower-left and upper-right half-matrices (some were already half-matrices), and created a full set of matrices, each missing one taxon, for jackknifing. I analyzed each (and the complete matrix) with both the Fitch-Margoliash and Cavalli-Sforza and Edwards algorithms using global branch swapping; I ran each algorithm five times with different random orderings of taxa. I placed each distinct topology discovered (and some variations of these topologies) into a common pool, and then tested each matrix (with both algorithms) against all topologies with the FITCH U option, choosing the single best-fit tree in each case. Finally, I combined all best-fit trees into a semistrict-jackknife-consensus tree.

RESULTS AND DISCUSSION

The semistrict-jackknife-consensus trees from my analysis are shown in Figures 3 through 24. A consensus loses information as a price of intelligibility (e.g. there are three possible resolutions for a trichotomy, but only two contradictory trees are needed to create one; higher-level polytomies lose even more information). Of 173 interior branches in Sibley and Ahlquist's (1990) 22 Fitch-Margoliash trees, 97 (56%) survived the analysis. Of 76 branches that collapsed, 11 did so because of conflict with the Cavalli-Sforza and Edwards trees, 66 because of conflict with lower-left or upper-right half-matrix trees, and 52 because of conflict with jackknife trees (some branches collapsed for more than one reason). Of surviving branches, 11 (11%) contradict the Tapestry.

In all trees shown, branch lengths are as in Sibley and Ahlquist's (1990) published FITCH

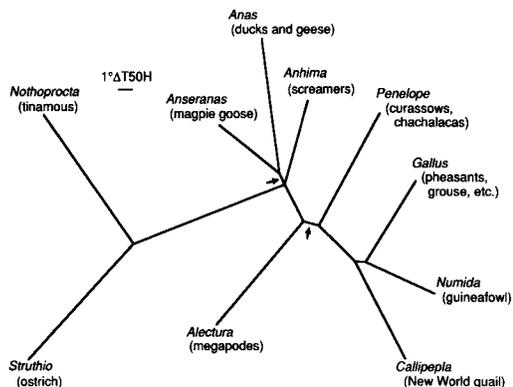


Fig. 4. Galliformes and Anseriformes.

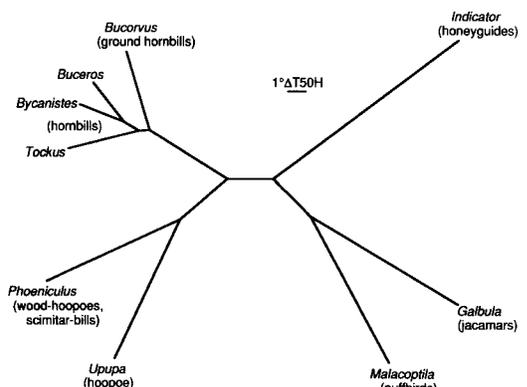


Fig. 6. Bucerotiformes and Upupiformes.

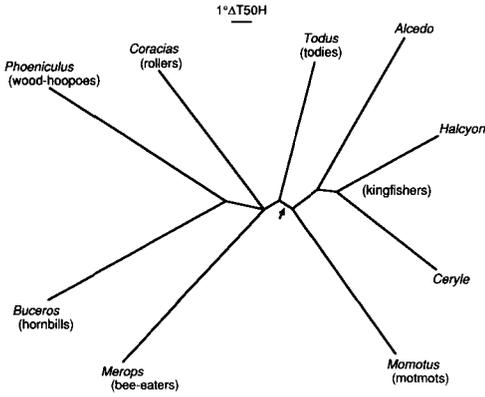


Fig. 7. Coraciiformes.

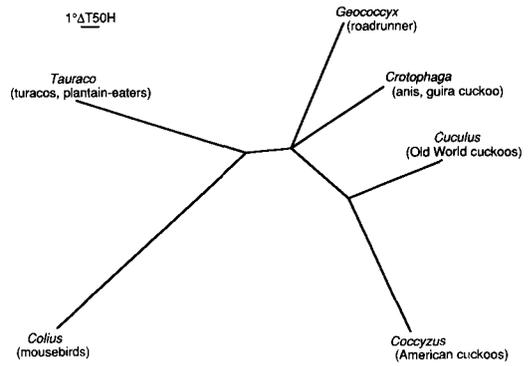


Fig. 9. Cuculiformes.

trees, and are generally similar to branch lengths in other best-fit trees used to produce the consensus. In these trees, angles between branches are not meaningful. Branches that contradict the Tapestry are indicated with arrows.

Importance of different parts of analyses.—Of the three suggested problems, only the absence of a test of data consistency was important in practice. Most branch collapses resulted from incompatibility of lower-left or upper-right half-matrices (suggesting large reciprocal distance differences) or different jackknife matrices. There were few disagreements between trees generated by the two algorithms. Failure to find the best-fit tree was not a major problem. None of my full-matrix, Fitch-Margoliash trees had a different topology than Sibley and Ahlquist's FITCH tree, although some had slightly different branch lengths and slightly better fit. However, multiple runs and testing of user-defined trees both resulted in changed topologies in a

few of the half-matrix and jackknife analyses, particularly with the largest data sets.

Interpretation and truth.—In interpreting phylogenetic trees, it is appropriate to take a conservative position. The results I present include any topology that was stable under the manipulations performed, and which thus can be inferred to be strongly supported by the data. One explanation for the existence of a strong pattern in the data is phylogeny, but others are possible, as is true for any data set, molecular or otherwise.

Branches that did not collapse are more stable and more strongly supported by the data than branches that did collapse, but there is no guarantee either that only "false" branches collapsed or that only "true" branches survived. The methods I used are unable to produce confidence intervals or other statistical measures (Felsenstein 1988). One useful question, however, is whether a matrix known to be without

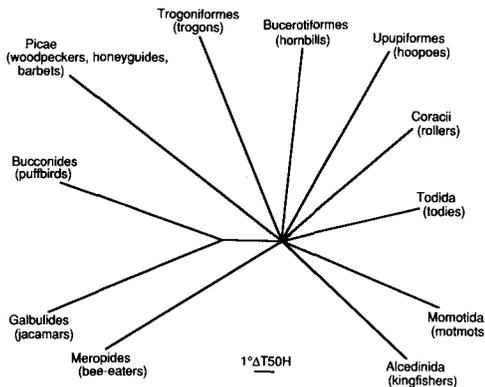


Fig. 8. Coraciae.

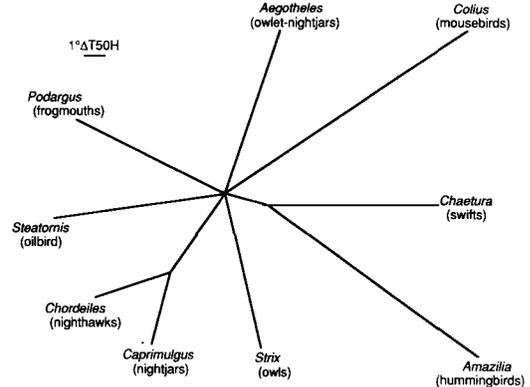


Fig. 10. Strigiformes.

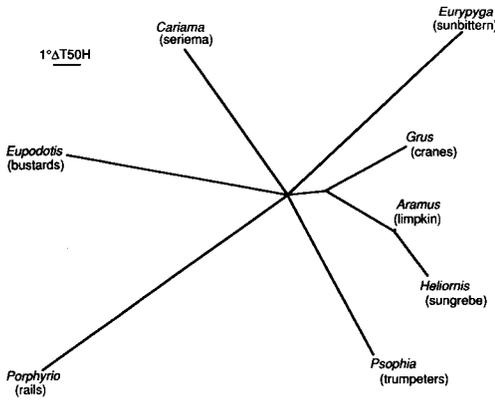


Fig. 11. Gruiformes.

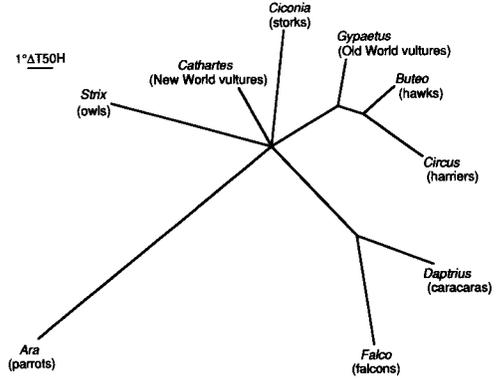


Fig. 13. Falconiformes.

phylogenetic content would show any stability in my analysis.

I produced random data matrices by scrambling the order of cells in some of Sibley and Ahlquist's (1990) matrices (but keeping reciprocal cells together). This produced a matrix with the same distribution of distances as the original, but one that certainly has no phylogenetic meaning. I performed one randomization each on four representative matrices, and analyzed them. Two of the four resulting consensus trees (for Ratites and Corvoidea) had no surviving branches, but two (Sylvioidea and Bucerotiformes + Upupiformes) had one and three surviving branches, respectively. A more

extensive analysis might help illuminate the reasons for this (chance or some nonphylogenetic regularity of the data), but it is clear that branch survival is no guarantee of phylogenetic meaning.

Obviously, the true phylogeny can only be estimated, never known for certain, and is best corroborated by congruence with trees produced from other data sets, providing that the nodes of those trees have been tested for strength of support, and that the assumptions underlying the methods used to gather and analyze the data have been examined for alternative explanations (other than phylogeny) of the trees generated.

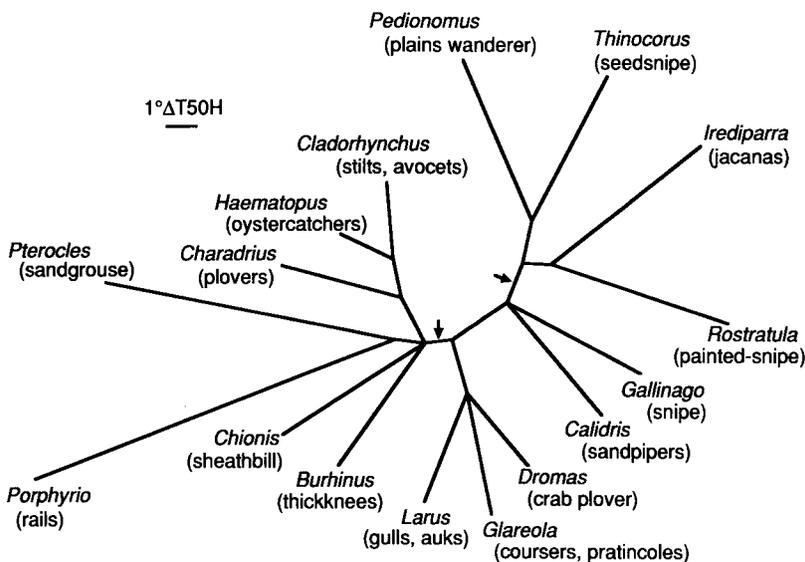


Fig. 12. Charadriiformes.

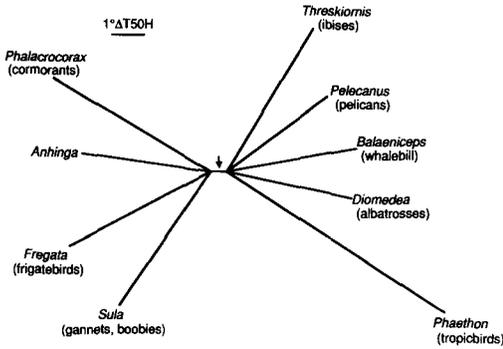


Fig. 14. Pelecaniformes.

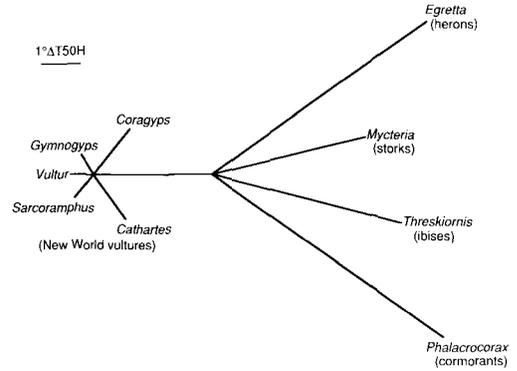


Fig. 15. Cathartidae.

Composite taxa.—One complication of the error introduced by composite taxa is that it is possible to arrive at the wrong phylogeny, even given perfect data. That is, one can construct a “true” phylogenetic tree for hypothetical taxa, abstract a composite data matrix from some of the intertaxon distances using correct hypotheses of monophyly, and emerge with a matrix which is a perfect fit to a tree that disagrees with the “true” tree. However, this requires a careful choice of branch lengths and is not easy to arrange on purpose. It is difficult to imagine a mechanism that would cause such an effect in real data.

Unrooted trees.—All trees produced by FITCH are unrooted, despite the implication by Sibley and Ahlquist (1990) that some of their FITCH trees were rooted. I have tried to draw my trees to give no impression of a root. To place a root, which can be anywhere on any branch, one needs to designate an outgroup or reintroduce a molecular clock. The root may also be usefully constrained by assuming monophyly of some subset of the tree’s taxa. Even without a root, a tree contains useful information in that many potential relationships are precluded.

FEATURES OF INDIVIDUAL TREES

Below I have included comments specific to some of the trees that were produced. Taxon names follow Sibley and Ahlquist’s (1990) FITCH trees. See Sibley and Ahlquist (1990:figs. 325–352) for an explanation of taxon composition.

Ratites (Fig. 3).—This data set is excellent, and only two branches collapsed, perhaps partly because none of the ratites are composite taxa. Assuming ratite monophyly, *Struthio* is the sis-

ter group of the remaining ratites (contra the Tapestry), which is novel. Fitting both topology and branch lengths into any simple reconstruction of the breakup of Gondwanaland would be difficult.

Galliformes and Anseriformes (Fig. 4).—Assuming monophyly of the Anseriformes, *Anseranas* is the sister group of the Anatidae (contra the Tapestry). This result apparently demonstrates the mutual “attraction” of short terminal branches in algorithms, such as UPGMA, that assume a clock, since the Tapestry makes *Anhima* the sister group of *Anseranas*. Also unlike the Tapestry, megapodes and cracids do not form a clade. This disagreement also may result from the attraction of short branches.

Piciformes (Fig. 5).—Given any rooting, the paraphyly of barbets is supported, in agreement with the Tapestry and other recent molecular studies (Lanyon and Hall 1994). The status of puffbirds and jacamars as either piciforms or coraciiforms cannot be resolved. If trogons are

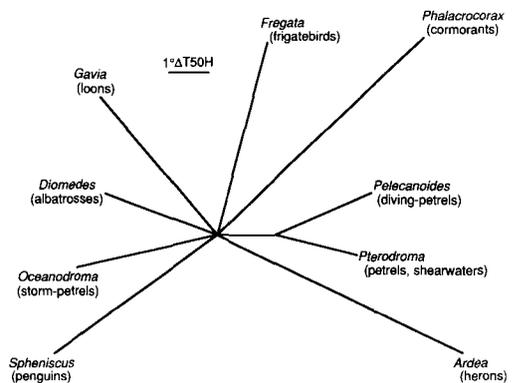


Fig. 16. Procellariiformes.

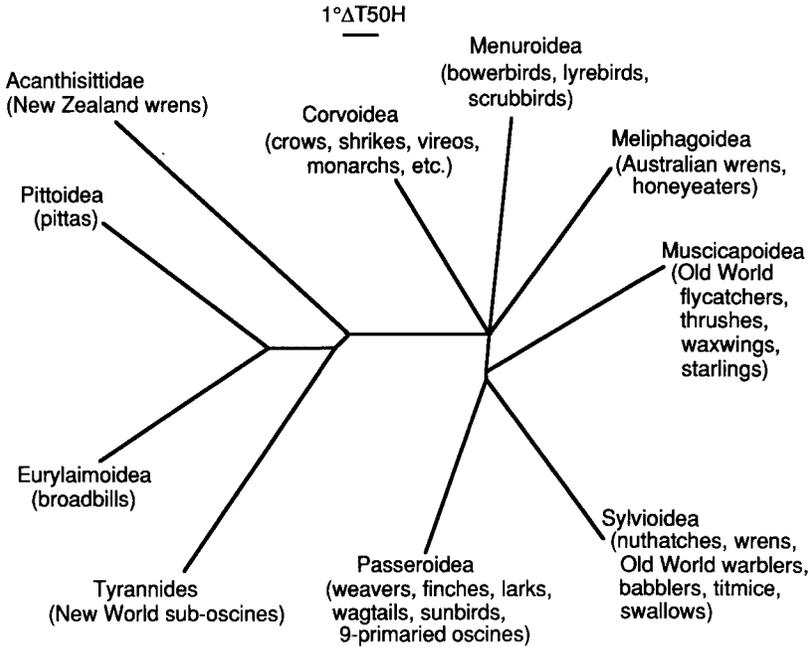


Fig. 17. Passeriformes.

taken as the outgroup, there is a basal trichotomy, and any other rooting merely assumes the answer.

Coraciae (Fig. 8).—Only one internal branch survived, indicating that the data set had major inconsistencies. Surprisingly, two other trees (Figs. 6 and 7) are among the best, with one or

no collapsed branches, despite the fact that they collectively share most of their taxa and much of their data with Figure 8. A partial explanation is that fewer taxa in Figures 6 and 7 are composites, and that species within composites are more closely related than in Figure 8. Composite taxa increase error, thus reducing resolution.

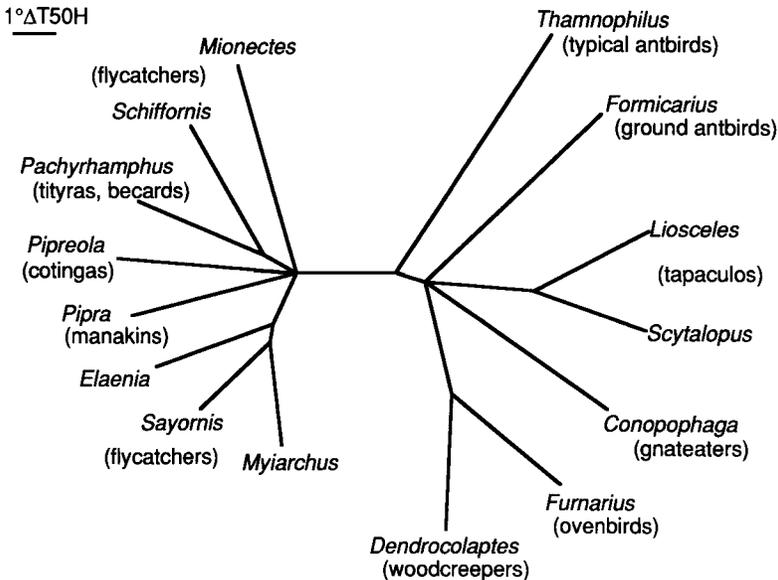


Fig. 18. Tyrannides.

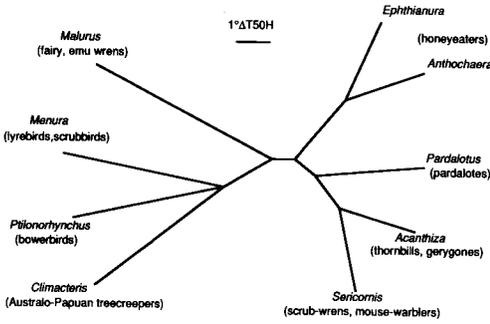


Fig. 19. Menuroidea and Meliphagoidea.

Gruiformes (Fig. 11).—Given most rootings, limpkins (*Aramus*) and sungrebes (*Heliornis*) are sister taxa. The extremely short branch leading to the Limpkin (0.02°C) is almost certainly an artifact. The Fitch-Margoliash algorithm produced very short branches in all replicates, while the Cavalli-Sforza and Edwards algorithm produced branches closer to 1°C in length. In general, branch lengths were less stable (thus less reliable) than topologies in my analyses.

Passeriformes (Fig. 17).—This tree's topology is consistent with the Tapestry. If oscine monophyly is assumed, the monophyly of Sibley and Ahlquist's (1990) Passerida is supported, but Corvida is not. Monophyly of Passerida and resolution of relationships among its included superfamilies, Passeroidea, Muscipoidea, and Sylvioidea, provide a weak argument for monophyly of each of the three superfamilies, since

mistaken assignments of species to composite taxa to which they did not belong would increase error and make branches less stable. Although the entire tree would be affected, branches closest to the incorrectly formed composite taxon would be affected most. In general, resolution of an interior branch on any of my trees is some evidence that species whose distances affect the fit of that branch were assigned to the correct composite taxa.

Tyrannides (Fig. 18).—The lack of resolution on the left side of the tree may be due to the nonmonophyly of some of the composite taxa; Sibley and Ahlquist's (1990) assignments are controversial (Lanyon 1985b). With any rooting, this tree supports the paraphyly of antbirds, a controversial claim of the Tapestry.

Corvoidea (Fig. 20).—The poor resolution of this tree may be due partly to nonmonophyly of some of the composite taxa and/or very short branch lengths. Three of the four surviving internal branches contradict the Tapestry. The sister-group relationship of vireos and whistlers (given most rootings) is a novel and interesting disjunct distribution.

Muscipoidea (Fig. 21).—Monophyly of the superfamily is not supported, since the branch uniting the waxwings and their relatives to the remaining taxa has collapsed. Thrush monophyly also is not confirmed. However, given most rootings, the relationship of the mockingbirds and starlings, one of Sibley and Ahlquist's (1990) most heralded results, is supported.

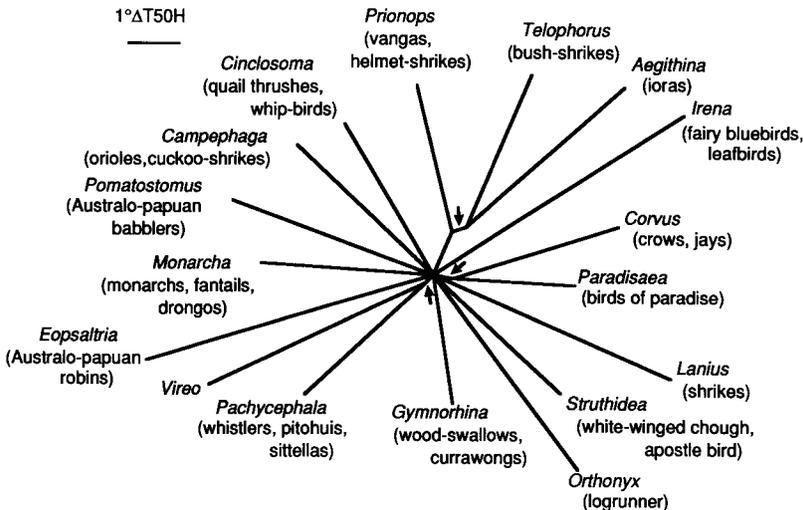


Fig. 20. Corvoidea.

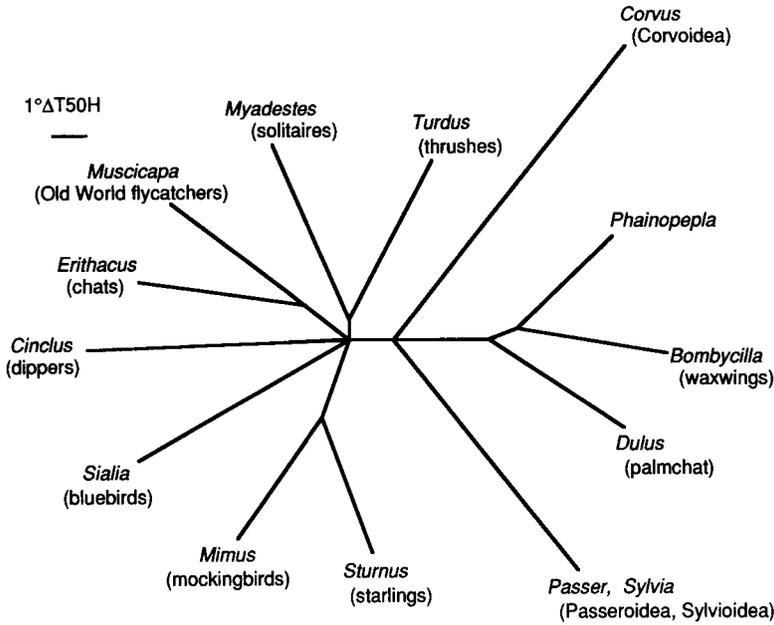


Fig. 21. Muscicapoidae.

Sylvioidea (Fig. 22).—Some very short branches on this tree (0.3° and 0.4°C) are resolved. The polytomy at the right is an example of how consensus can discard useful information. For example, in all trees found, the portion containing the polytomy can be represented as a ladder from *Aegithalos* to *Sylvia* + *Cincloramphus*

with seven branches in between. In all trees *Zosterops* is on the fifth (counting from *Aegithalos*), sixth, or seventh branch, and *Regulus* is on the first, second, or third branch. The data can be said to strongly support the claim that *Zosterops* is closer to *Sylvia* than is *Regulus*. The tree is consistent with the Tapestry.

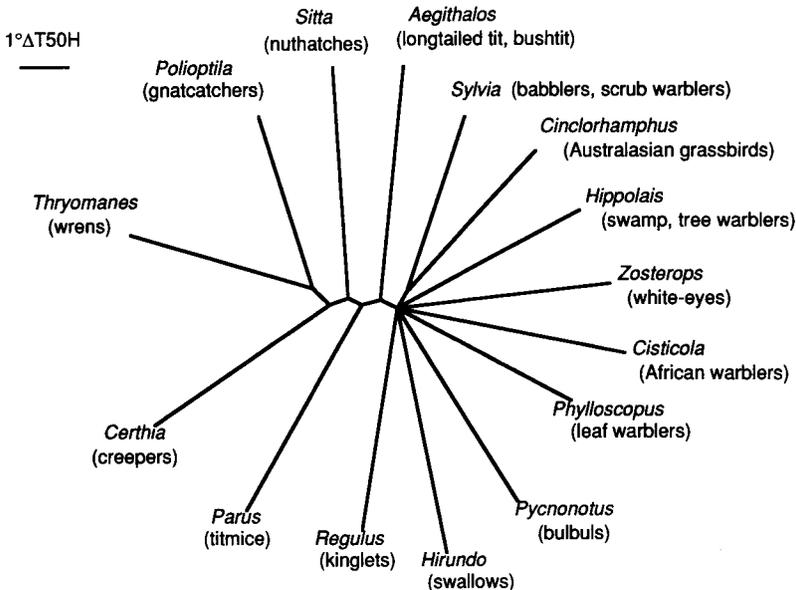


Fig. 22. Sylvioidea.

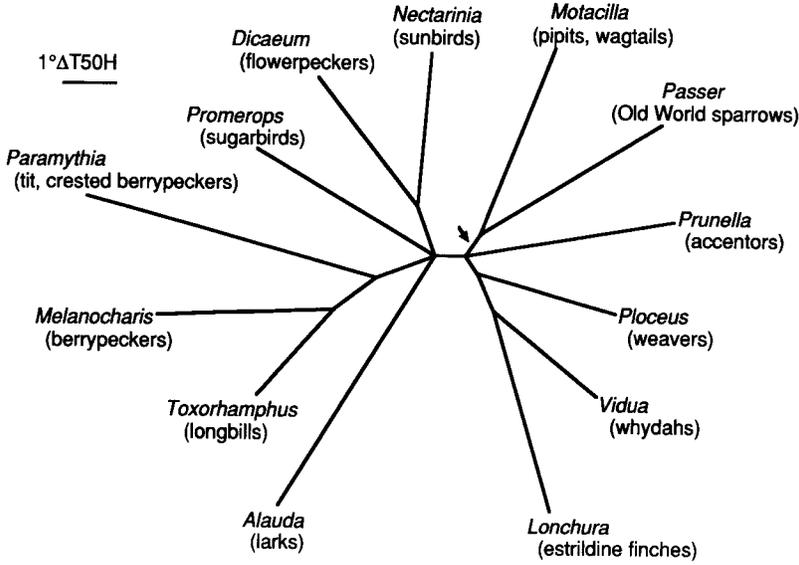


Fig. 23. Passeroidea.

Fringillidae (Fig. 24).—This tree is very well resolved, including some branches of 0.2° and 0.3°C. The tree is consistent with the Tapestry. Regardless of rooting, *Peucedramus* is shown not to be a warbler. Assumption of a molecular clock to root the tree, which may be supported by the data for this group (Bledsoe 1987), would make *Peucedramus* the sister group of the other nine-

primaried oscines. Cardinalini, given most rootings, is suggested to be the sister group of Icterini.

CONCLUSION

Such high resolution (56% of interior branches did not collapse) is surprising, considering

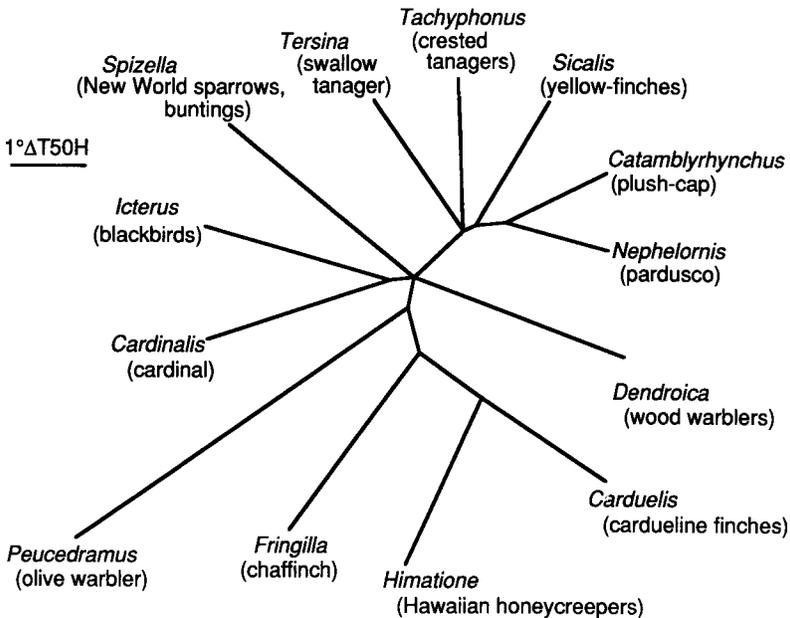


Fig. 24. Fringillidae.

the assumptions required in using composite taxa. Although many interior branches are consistent with the Tapestry, others (11%) are not. In cases of conflict, the analyses presented here should be preferred, since they better represent Sibley and Ahlquist's (1990) published data. These trees should also be preferred to Sibley and Ahlquist's (1990) published FITCH trees, from which they differ only in being less resolved. More powerful methods of analysis might produce greater resolution given the same data, but these trees should be preferred until such analyses are performed.

The success of matrices constructed from composite taxa in producing robust phylogenetic hypotheses is encouraging. It seems likely that Sibley and Ahlquist's unpublished data could be used to construct additional composite matrices, that, if properly analyzed, will have even more of value to say about avian phylogeny.

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