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A RECONSIDERATION OF SONGBIRD PHYLOGENY, WITH EMPHASIS ON THE EVOLUTION OF TITMICE AND THEIR SYLVIOID RELATIVES

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Abstract.—The phylogeny of oscine passerines was estimated by comparing 27 species using DNA–DNA hybridization. In the process, the finer structure of the "sylvioids" was examined (1) to assess the phylogenetic proposals of Sibley and Ahlquist (1990, Phylogeny and classification of birds, Yale Univ. Press, New Haven, Connecticut) and (2) to develop a framework for studies of sylvioid historical ecology. Many of Sibley and Ahlquist's phylogenetic proposals were supported, including their division of the oscines into two clades: corvids and passerids. However, their division of the passerids into three clades, Muscicapoidea, Sylvioidea, and Passeroidea, was not supported; neither their Sylvioidea nor their Passeroidea is monophyletic. The improved picture of oscine phylogeny presented here permits a more rigorous historical analysis of convergence, adaptation, phylogenetic constraint, and other evolutionary phenomena. For example, the sister group of the seed-caching Paridae is the Remizidae (including the verdin, *Auriparus*), not the nuthatches (Sittidae), which also cache seeds. Thus, seed caching arose separately in the Paridae and Sittidae and is likely to be a key innovation for these groups, i.e., an adaptation responsible for their diversification. Similar cases of convergence and thus potential opportunities for eco-phylogenetic study are common throughout the passerines. Unfortunately, such study is hampered by the difficulty of resolving passerine phylogeny, which is characterized by many short internodes. [Character mapping; DNA hybridization; historical ecology; Passeriformes; phylogeny; Sylvioidea.]

The Passeriformes is a monophyletic group that contains more than half of the world's species of birds. The reasons for the relative abundance and diversity of this enormous taxon have been the subject of recent debate (e.g., Raikow, 1986, 1988; Fitzpatrick, 1988; Slowinski and Guyer, 1989; Baptista and Trail, 1992). At issue is whether passerines have diversified as a result of key innovations, i.e., whether the increase in the size of the group is causally linked to a specific character or characters (Liem, 1973; Heard and Hauser, 1995). At face value, the key innovation hypothesis seems unlikely because this group is defined by just a few synapomorphies, which involve features of the palate, spermatozoa, forelimb and hind limb muscles, and feet (Raikow, 1982), and none of these is remarkable. But passerines also differ in certain continuous traits. They have a metabolic rate that tends to be higher than other birds of comparable size, and they have relatively large brains and superior learning abilities, especially with respect to vocalizations.

Unfortunately, it is impossible to determine if key innovation is responsible for passerine radiation. To do so requires that passerines be contrasted via the comparative method with other groups having the same putative innovations (e.g., Raikow, 1986; Sheldon and Whittingham, 1997). But the Passeriformes is unique; no other bird group of similar diversity or habits exists with which to compare it. As a result, we can only speculate that the passerine radiation is a result of a combination of characteristics acting in novel environments (Fitzpatrick, 1988; Kochmer and Wagner, 1988; Vermeij, 1988; Baptista and Trail, 1992). The combined characteristics include small size, short generation time, high metabolism, insectivory, diurnal hab-

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its, and especially profound behavioral plasticity and experimental learning abilities. The novel environments in which these characters acted are thought to have evolved in concert with the diversification of flowering plants and associated insects (Beecher, 1953; Regal, 1975; Fitzpatrick, 1988) during the Oligocene and Miocene, when passerine radiation was most dramatic (Feduccia, 1995).

Although the application of the comparative method to passerines as a group may be impossible, the potential opportunities for use of the comparative method within the passerines to test hypotheses of historical ecology are remarkable (Brooks and McLennan, 1994; Sheldon and Whittingham, 1997). Not only are the ecology and behavior of passerines unusually well known, but preliminary assessments of the phylogeny suggest a high level of convergent evolution, which is grist for the mill of comparative methodology (Pagel, 1994). Recent phylogenetic estimates suggest that passerines have repeatedly and independently evolved into such ecological forms as seedeaters, salliers, thrashers, leaf gleaners, and creepers (e.g., Bledsoe, 1988; Sibley and Ahlquist, 1990). However, these preliminary estimates of relationships also indicate that it will be difficult to reconstruct the phylogeny of passerines completely, because the passerine tree is characterized by short internodes separating most major groups. Although fundamental differences in anatomy (e.g., Ames, 1971; Raikow, 1987) and molecules (Sibley and Ahlquist, 1990; Edwards et al., 1991) distinguish two main clades of passerines, the suboscines and the oscines, the identification of monophyletic groups within these two clades has been frustrated by the large number of seemingly intermediate forms. This problem was recognized over 100 years ago by Wallace (1856; see O'Hara, 1987) and has plagued avian taxonomists and phylogeneticists ever since (e.g., Mayr and Amadon, 1951; Beecher, 1953; Wetmore, 1960; Storer, 1971; Morony et al., 1975; Voous, 1985; Sibley and Ahlquist, 1990; Edwards et al., 1991; Helm-Bychowski and Cracraft, 1993).

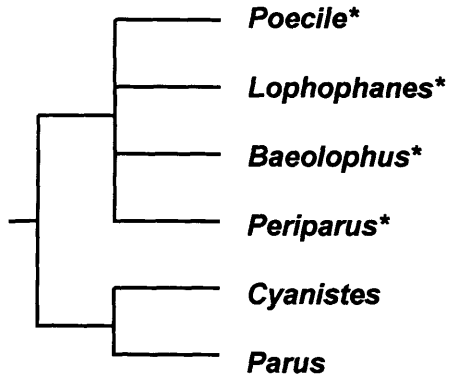

FIGURE 1. Summary of the phylogenetic relationships among *Parus* subgenera, as determined by DNA hybridization (Sheldon et al., 1992; Slikas et al., 1996). Asterisks mark seed-caching taxa. *Poecile* includes chickadees, *Lophophanes* includes Old World crested tits, *Baeolophus* includes New World titmice, *Periparus* includes coal tits, *Cyanistes* includes blue tits, and *Parus* includes great tits.

Background and Objectives

Previously, we studied two passerine families that are unusually well characterized in terms of ecology and behavior: titmice (Paridae) and swallows (Hirundinidae). These projects were intended to resolve some of the uncertainties of passerine phylogeny, while taking advantage of the opportunities for the analysis of the historical ecology of these groups. Our parid phylogeny (Gill et al., 1989; Sheldon et al., 1992; Slikas et al., 1996) revealed that the ability to cache and retrieve seeds and the specific brain physiology and behaviors associated with seed caching are restricted to one of the two main parid clades (Fig. 1). We hypothesized that seed caching is an adaptation that helped parids diversify in temperate deciduous and coniferous forests. In the swallow work (Sheldon and Winkler, 1993; Winkler and Sheldon, 1993, 1994), we found that nest structure is highly correlated with phylogeny and hypothesized that species comprising the two main clades may be phylogenetically constrained to build specific nest types.

Both of these studies, however, suffered from a poor understanding of passerine phylogeny. Without knowledge of

the close outgroups of the parids and swallows and consequently the character states at the root of the ingroup, we could not tell by parsimonious optimization which ecological, behavioral, or physiological characters had been gained or lost in the study groups. Thus, we lacked the basic phylogenetic information needed to assess whether seed caching or nest-building methods are adaptations (sensu Coddington, 1988; Baum and Larson, 1991) or key innovations (Heard and Hauser, 1995). For example, if seed caching exists in the parid sister taxon as well as some parids (Fig. 1), then caching would not be an adaptation of parids; it would simply have been lost in one parid group (assuming loss of a complicated character is easier than gain). Such a scenario is plausible because the nuthatches (Sittidae) also cache seeds and have been considered closely related to parids (Beecher, 1953; Mayr and Amadon, 1951; Wetmore, 1960). In addition, to test the hypothesis that seed caching is a key innovation in the Paridae (i.e., responsible for diversification of the caching clade) requires the comparative demonstration that seed caching is associated with diversification in other groups living in similar habitats and that it arose independently in those groups (Sheldon and Whittingham, 1997). Thus, knowledge of the phylogenetic position of parids relative to sittids and other cachers, such as crows, jays, and nutcrackers (Corvidae), is vital to our understanding of the evolution of seed caching within the Paridae. It is also vital to the investigations of other historical ecologists who are using these parid and swallow phylogenies to study morphological and ecological evolution (e.g., Moreno and Carrascal, 1993b; Carrascal et al., 1994; Suhonen et al., 1994; Cézilly and Nager, 1995).

Given this need for a broader phylogenetic perspective, we estimated in this study the phylogeny of the Sylvioidea (sensu Sibley and Ahlquist, 1990; see Fig. 2), which purportedly contains the titmice and swallows and other groups of particular interest to historical ecologists (e.g., Richman and Price, 1992; Brandl et al., 1994; Cézilly and Nager, 1995). This reconstruction required that we compare members of likely sylvioid groups and establish the monophyly of the sylvioids as a whole. To this end, we had to assess the overall phylogenetic structure of the passerines before concentrating on the sylvioids in particular.

This task would have been daunting were it not for the phylogenetic proposals of Sibley and Ahlquist (1990; hereinafter called S&A). S&A provided a framework of passerine phylogeny that we attempted simply to replicate. Although replication in itself is a valid scientific pursuit, in this case it has greater importance because of the controversy surrounding the accuracy of S&A's phylogenetic proposals (summarized by Sheldon and Bledsoe, 1993) and the common use of S&A's phylogeny in studies of avian historical ecology (e.g., Moreno and Carrascal, 1993a; Harvey and Nee, 1994; Møller and Birkhead, 1994). S&A compared over 60 "sylvioid" genera and clustered them via "modified" UPGMA into a large tree known as the Tapestry (S&A: figs. 380, 381). Although many of S&A's proposals make good biological sense, their empirical and analytical underpinnings are often shaky. S&A did not design most of their DNA hybridization comparisons to (1) account for variable rates of evolution, (2) piece together various parts of the Tapestry, or (3) test branch robustness. For example, S&A often radiolabeled one species and hybridized it to a series of other species with which it was presumably monophyletic (e.g., *Pycnonotus barbatus* to other bulbuls, S&A: fig. 380). Then they drew a branching pattern based on genetic distance from the reference (radiolabeled) species. By doing so, they assumed that the taxa were monophyletic and that short genetic distance equaled close phylogenetic relationship (and vice versa). But a short genetic distance may also result from a slow evolutionary rate. To control for this possibility requires that all of the in-

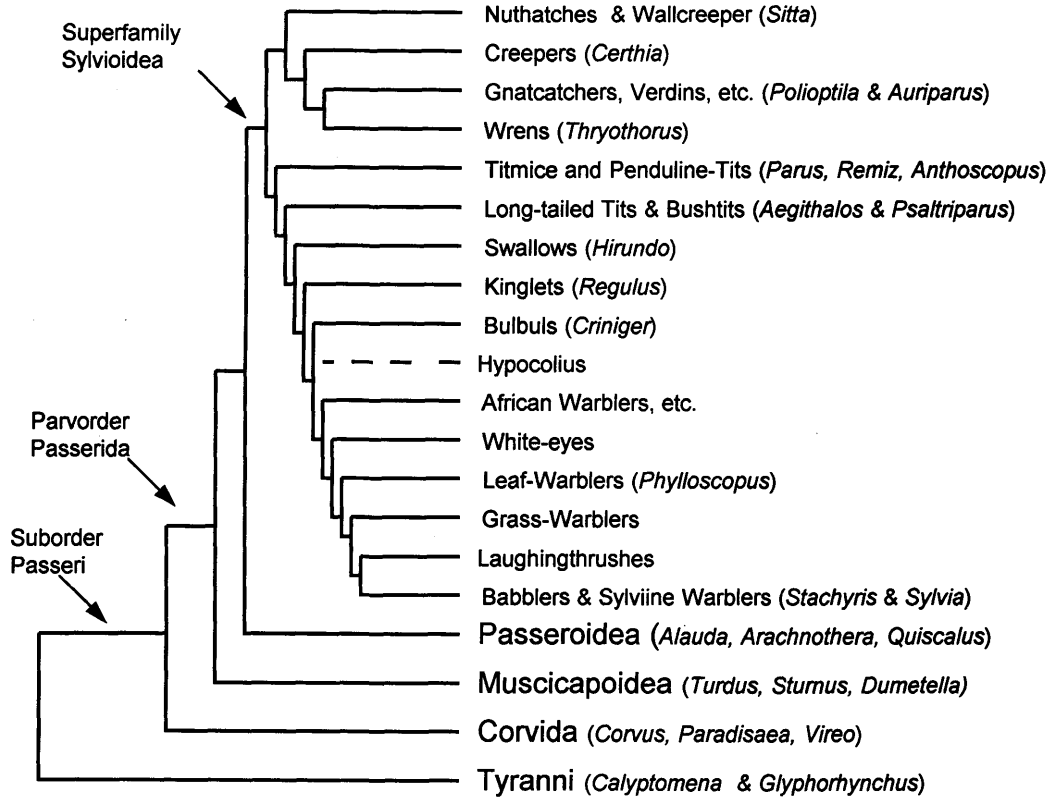

FIGURE 2. Summary of passerine phylogeny based on the Tapestry of Sibley and Ahlquist (1990: figs. 370, 380, 381). Genera that were compared in the present study are listed next to the common names of the major groups.

group taxa be compared with an outgroup taxon and that distances be fit to a branching pattern by a method that does not assume equal length of sister branches (requirements summarized by Bledsoe and Sheldon, 1990; Sheldon, 1994). Furthermore, to fit different subsections of the Tapestry together required that representatives of each clade be compared with one another, which was not done (Lanyon, 1992). Finally, because of the incomplete set of comparisons, the robustness of S&A's internodal branches could not be tested by sampling subsets of the data or taxa (e.g., by jackknifing or bootstrapping). This problem is particularly important in our study because many extremely short (and probably invalid) branches connect sylvioid and nonsylvioid taxa.

MATERIALS AND METHODS

Sylvioid Classification and Taxonomic Comparisons

Figure 2 depicts the major clades of passerine birds hypothesized by S&A and the higher level passerine classification of Sibley and Monroe (1990), which was based on S&A's phylogeny. Oscine passerines are divided into two principal clades: the parvorders Corvida and Passerida. The Passerida consists of three lineages: the superfamilies Sylvioidea, Muscicapoidea, and Passeroidea. In Figure 2, the Sylvioidea section of the tree is expanded to show the major sylvioid lineages postulated by S&A. In general, the composition of these lineages was not controversial because their phylogeny had not been studied previously. In addition, older taxonomic ar-

rangements based on morphological similarity usually placed many of the same taxa in proximate succession (e.g., Mayr and Amadon, 1951; Wetmore, 1960; Storer, 1971; Morony et al., 1975; Voous, 1985). More controversial, perhaps, is S&A's assertion that certain taxa that appear as sylvioids in traditional classifications are not closely related to sylvioids. For example, S&A found that the traditional sylvioid family Muscicapidae (Mayr and Amadon, 1951; Storer, 1971) consists of two distinct clades: one (S&A's Sylvioidea) that includes titmice, nuthatches, swallows, sylviine warblers, babblers, and wrens and another (S&A's Muscicapoidea) that includes Old World flycatchers (Muscicapinae), thrushes (Turdinae), mockingbirds (Miminae), and dippers (Cinclinae).

To assess S&A's Sylvioidea, we selected 16 species representing five major lineages of passerines as defined by S&A: Tyranni(Corvida(Muscicapoidea(Sylvioidea, Passeroidea))). The Tyranni (suboscines) is clearly an outgroup of the four oscine groups based on syringeal (Ames, 1971), myological (Raikow, 1987), and cytochrome *b* sequence (Edwards et al., 1991) data. Each of these 16 species was compared reciprocally with the others to produce a complete 16 × 16 distance matrix. In addition, 10 supplementary species that are probable sylvioids were radiolabeled and compared in one direction with each other and with the 16 species in the complete matrix to provide a phylogenetic estimate for 26 species. One species, *Paradisaea raggiana*, was used in mostly one-way comparisons with the 16 taxa in the fundamental matrix before the DNA sample was exhausted. Thus, 27 species were included in the comparisons. All species and samples are listed in Table 1, and comparisons are summarized in the Appendix.

Biochemistry and Data Analysis

To estimate phylogeny, we used DNA–DNA hybridization. This method is expected theoretically (e.g., Springer and Krajewski, 1989; Bledsoe and Sheldon, 1990; Sheldon, 1994) and has been shown empirically (Bledsoe and Raikow, 1990; Powell, 1991; Helm-Bychowski and Cracraft, 1993; Krajewski and Fetzner, 1994; Lanyon and Hall, 1994) to be highly effective for inferring phylogeny. Our biochemical protocols were based on those of S&A, Sheldon and Winkler (1993), and Slikas et al. (1996). Hybrids were formed with single-copy labels (Cot 1000) and whole DNA drivers in a ratio of about 1:10,000 and were fractionated in 2.5°C increments from 60°C to 95°C. Hybrid indexes (Tm, T50H, Tmode), normalized percent reassociation (NPR), and distances (Δ values) were calculated as described by Sheldon and Bledsoe (1989), except that Tmode was estimated by least-squares fitting of the asymmetric double-sigmoid equation of Peakfit (Jandel Scientific, 1990) instead of the modified Fermi–Dirac equation. The asymmetric double-sigmoid equation fit lower melting temperature curves better than the Fermi–Dirac equation did, although the two methods produced similar results. Entire experiments were excluded from analysis if major mechanical problems were encountered during fractionation. Individual hybrids were excluded before computing average distances if leakage during incubation was suspected, mechanical problems occurred, or possible misidentification or mixing of specimens were discovered in the course of hybrid preparation or fractionation. Because leakage during incubation causes unusually low percentage of hybridization, all oscine/oscine hybrids with <50% NPR and all oscine/suboscine hybrids with <30% NPR were excluded even if no leakage was detected. All heteroduplex hybrids that had >8.0 residual sums of squares in mode fitting were excluded, under the assumption that the poor fit stemmed from experimental problems. In the end, 121 (7%) of the hybrids were excluded.

Phylogenetic analyses were based on ΔTmode. Mean values, standard deviations, and sample sizes are provided in the Appendix. When comparing highly divergent taxa, ΔTmode provides a more linear estimate of dissimilarity (Sibley and Ahlquist, 1983; Sheldon and Bledsoe, 1989), is less affected by potential reasso-

TABLE 1. Bird species and samples compared in this study.

Name[a]	Traditional family/subfamily	Group[b]	Samples used[c]	Source locality
Aegithalos fuliginosus (white-necklaced tit)	Paridae/Aegithalinae	P/P/S	FBG2211	China
Alauda arvensis (Eurasian skylark)[d]	Alaudidae	P/P/P	5386, 5387	Greece
Criniger (Alophoixus) bres (grey-cheeked bulbul)[d]	Pycnonotidae	P/P/S	1056, 1138	Borneo
Anthoscopus minutus (southern penduline-tit)	Paridae/Remizinae	P/P/S	5471, 5472	South Africa
Arachnothera longirostra (little spiderhunter)[d]	Nectariniidae	P/P/P	1037, 1053, 1107, 1293	Borneo
Auriparus flaviceps (verdin)	Paridae/Remizinae	P/P/S	B3821	USA
Calyptomena viridis (green broadbill)[d]	Eurylaimidae	T	1054, 1190, 1233	Borneo
Certhia americana (American tree-creeper)	Certhiidae	P/P/S	4391, 4397	USA
Corvus ossifragus (fish crow)[d]	Corvidae	P/C/C	3822, 3823, 3824	USA
Dumetella carolinensis (grey catbird)	Muscicapidae/Miminae	P/P/M	3672, 3843, 3844	USA
Glyphorhynchus spirurus (wedge-billed woodcreeper)[d]	Dendrocolaptidae	T	1537, 1538, 1678, 3226	Ecuador
Hirundo rustica (barn swallow)[d]	Hirundinidae	P/P/S	3042, 3683	USA
Paradisaea raggiana (Raggiana bird-of-paradise)[e]	Paradisaeidae	P/C/C	5411	New Guinea
Parus atricapillus (black-capped chickadee)[d]	Paridae/Parinae	P/P/S	1900, 1903, 1906, FBG1849	USA
Phylloscopus collybita (common chiffchaff)	Muscicapidae/Sylviinae	P/P/S	5357, 5363	Greece
Polioptila caerulea (blue-grey gnatcatcher)	Muscicapidae/Sylviinae	P/P/S	3832	USA
Psaltriparus minimus (bushtit)	Paridae/Aegithalinae	P/P/S	5474, 5476, 5477	USA
Quiscalus quiscula (common grackle)[d]	Icteridae	P/P/P	3840, 4207	USA
Regulus satrapa (golden-crowned kinglet)	Muscicapidae/Sylviinae	P/P/S	4218, 4220	USA
Remiz pendulinus (Eurasian penduline-tit)[d]	Paridae/Remizinae	P/P/S	4381, 5361, 5368	Greece, Denmark
Sitta carolinensis (white-breasted nuthatch)[d]	Sittidae	P/P/S	3841, 4214	USA
Stachyris poliocephala (grey-headed babbler)[d]	Muscicapidae/Timaliinae	P/P/S	1077, 1097, 1164, 1182	Borneo
Sturnus vulgaris (common starling)[d]	Sturnidae	P/P/M	3689, 3690	USA
Sylvia atricapilla (blackcap)	Muscicapidae/Sylviinae	P/P/S	5358, 5371	Greece
Thryothorus ludovicianus (Carolina wren)	Muscicapidae/Troglodytinae	P/P/S	953	USA
Turdus migratorius (American robin)[d]	Muscicapidae/Turdinae	P/P/M	3661, 3663, 3664	USA
Vireo olivaceus (red-eyed vireo)[d]	Vireonidae	P/C/C	3666, 3669, 3848	USA

[a] From Sibley and Monroe (1990).

[b] Sibley and Monroe (1990) classification is abbreviated as follows. Suboscines: T = Tyranni; oscines: P/C/C = Passeri/Corvida/Corvoidea, P/P/M = Passeri/Passerida/Muscicapoidea, P/P/S = Passeri/Passerida/Sylvioidea, P/P/P = Passeri/Passerida/Passeroidea.

[c] Academy of Natural Sciences tissue collection accession numbers.

[d] Species used in the complete (fundamental) 16 × 16 matrix.

[e] *Paradisaea raggiana* was only compared with the 16 taxa in the fundamental matrix of comparisons.

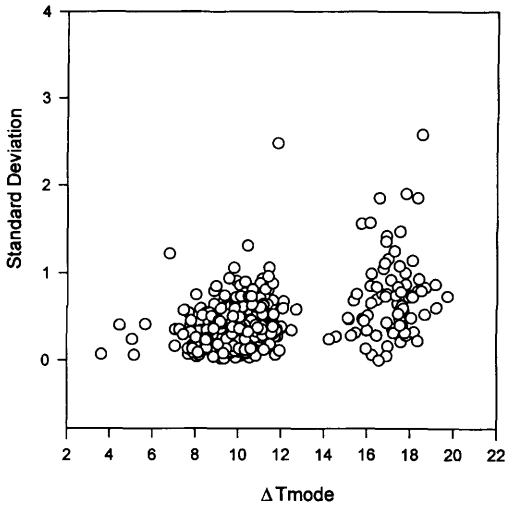

FIGURE 3. Plot of average standard deviation versus average ΔTmode for each pairwise comparison among passerine species (R = 0.433, n = 459). The right cluster consists of distances between oscines and suboscines (i.e., ingroup and outgroup species).

ciation of paralogous sequences (e.g., Sarich et al., 1989), and appears to be more precise than other distance measures (Bleiweiss and Kirsch, 1993). ΔTm was not used because it becomes highly compressed as distances increase (e.g., Sheldon and Bledsoe, 1989). ΔT50H was not used, even though it can yield remarkably good estimates of large distances (Goodman et al., 1990), because it confounds two measures, reassociation and stability (e.g., Sheldon and Bledsoe, 1989). Our final estimate of phylogeny was based on corrected ΔTmode (ΔTmode-C). Correction to ΔTmode was intended to increase the additivity of the distance values, thereby improving the adherence of the data to the additivity assumption of tree-building algorithms (Springer and Krajewski, 1989). This correction was a two-step process. First, ΔTmode was converted to percent sequence divergence (d) using the factor 1.18 determined by hybridizing known sequences of DNA (Springer et al., 1992):

$$d = 1.18(\Delta\text{Tmode}/100). \quad (1)$$

Then d was adjusted for multiple mutations at single base sites with the equation of Jukes and Cantor (1969; summarized by Swofford and Olsen, 1990), assuming a 60:40 AT:GC base pair ratio (Arthur and Straus, 1978):

$$\Delta\text{Tmode-C} = (100)(-0.74)[\ln(1 - 1.35d)]. \quad (2)$$

To fit distances to a tree-branching pattern, we relied mainly on the FITCH program of PHYLIP 3.4 (Felsenstein, 1989). Options were set so that data were fit by weighted least squares (Fitch and Margoliash, 1967). This option was used because error increased with genetic distance (Fig. 3). FITCH does not assume a molecular clock. We also estimated trees using neighbor joining and KITSCH programs; KITSCH assumes a molecular clock and neighbor joining does not. Because our matrix was missing one pairwise comparison (between *Polioptila* and *Thryothorus* because of mechanical failure), we used the lacunose distance matrix method of Lapointe and Kirsch (1995) to fill this cell.

Branch robustness was tested by bootstrapping from replicate measurements in each cell of the 16 × 16 matrix and various of its subsets (Krajewski and Dickerman, 1990; see Table 2). Trees were constructed

TABLE 2. Tests of branch stability. Types of distances and matrix size were changed to assess the effect on tree estimates.

Distance type	Analysis	Matrix size	Notes
Tmode-C	bootstrap (100[a])	16 × 16	matrix symmetrized with "symboot"
Tmode-C	bootstrap (1,000[a])	14 × 14	*Calyptomena* and *Glyphorhynchus* omitted
Tmode	jackknife	16 × 16	
Tmode-C	jackknife	16 × 16	
Tmode	jackknife	14 × 14	*Calyptomena* and *Glyphorhynchus* omitted
Tmode-C	jackknife	26 × 26	all taxa except *Paradisaea*

[a] No. bootstrap replicates.

from the bootstrap pseudomatrices with FITCH, and from these trees a 50% majority-rule consensus tree was formed with PHYLIP's CONSENSE program. We also assessed branch robustness by jackknifing taxa (Lanyon, 1985).

RESULTS

Properties of the Data

The phylogenetic estimates in this paper are based on 1,700 hybrids, consisting of 25,500 fractionation samples. For each pair of species, an average of 3.4 replicate hybrids was produced (Appendix). The average standard deviation of these replicates was 0.44, which is higher than the 0.20–0.30 values commonly encountered in intrafamilial DNA hybridization studies (Sheldon and Bledsoe, 1989; Werman et al., 1990; Sheldon and Winkler, 1993; Bleiweiss et al., 1994b; Slikas et al., 1996) but lower than the 0.90 value obtained in a recent study of relationships among orders of nonpasserines (Bleiweiss et al., 1994a). Most of our comparisons were interfamilial, and thus it is reasonable that our average replicate error should be greater than that found among intrafamilial taxa and less than that of interordinal taxa. A correlation between measurement error and distance is also evident within our study (Fig. 3). Previously, it was thought that no relationship existed between DNA-hybridization distance and error (e.g., Bledsoe, 1987; Sheldon, 1987; Werman et al., 1990), but that does not seem to be true in this case. The increase in error with distance dictates the use of weighted least squares to fit distances to branches (Fitch and Margoliash, 1967), as opposed to unweighted least squares (Cavalli-Sforza and Edwards, 1967). Weighted least squares counts short distances more heavily than long distances in computing fitting error.

To measure the degree and effects of reciprocal distance asymmetry, we computed percent nonreciprocity (Sarich and Cronin, 1976) in the uncorrected ΔTmode (16 × 16) matrix and observed the quality of branch fitting before and after symmetrization using "symboot" in the bootstrap package of Krajewski and Dickerman (1990). Percent nonreciprocity was 2.37 before and 1.54 after symmetrization. These are low (good) values of asymmetry (Springer and Kirsch, 1989; Bleiweiss et al., 1994a). Fitch–Margoliash tree fitting before and after symmetrization produced a single branching pattern with residual sums of squares of 0.27 and 0.16, respectively, which are excellent fits.

Phylogeny

The DNA-hybridization phylogeny as represented by best-fit least-squares trees is shown in Figure 4 (16 × 16 complete matrix) and Figure 5 (27 species). The robustness of branching patterns based on bootstrap, jackknife, and symmetrization analyses is shown in Figures 6 and 7. Branches that are less than ΔTmode-C 0.2 in length tend to be poorly supported and collapse in the bootstrap and jackknife consensus trees (Fig. 7).

The trees indicates a clear separation between suboscines and oscines, and the oscines divide into two well-defined monophyletic assemblages corresponding to S&A's parvorders Corvida (in this case, *Corvus* [crow], *Vireo* [vireo], and *Paradisaea* [bird-of-paradise]) and Passerida (all other oscines). Within the Passerida, several clades are evident, although relationships among these clades are not strongly indicated by the data. *Turdus* (thrush), *Sturnus* (starling), and *Dumetella* (mockingbird) form a monophyletic group corresponding to the Muscicapoidea of S&A. *Arachnothera* (sunbird) and *Quiscalus* (blackbird) appear to form a clade (at low bootstrap resolution) corresponding to S&A's Passeroidea. However, the "passeroid" *Alauda* (lark) groups with some typical sylvioids (Old World warblers, babblers, bulbuls, swallows) instead of other passeroids. S&A's sylvioids divide into three distinct clades, which intermingle with the muscicapoid and passeroid clades: (1) Old World warblers (except *Regulus*), bulbuls, babblers, and swallows; (2) parids, remizids, and *Auriparus*; and (3) nuthatches, creepers, gnatcatchers, and wrens. *Regulus* (kinglet)

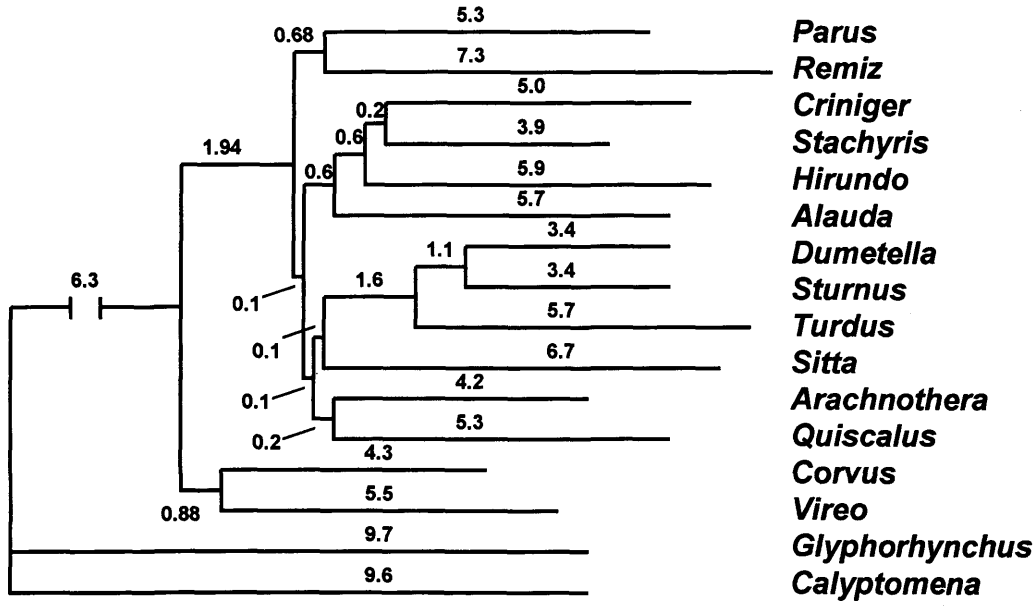

FIGURE 4. Best fit weighted least squares tree (Fitch and Margoliash, 1967) from the complete 16-taxon ΔTmode-C matrix of DNA-hybridization distances among passerines. Options: no clock assumed, no negative branches allowed, replicate measurements accounted, and *Calyptomena* as outgroup. Residual sum of squares = 1.09.

appears as the sister taxon of all other passerids.

Effects of Outgroup Selection

To test effects of outgroup choice on the stability of our phylogenetic estimate, we computed passerid trees using alternatively distant (suboscines) and close (corvids) outgroups. Using suboscines as the sole outgroup produced exactly the same passerid branching pattern as using the full 16 × 16 matrix. Using corvids as outgroup produced one branch change in our ΔTmode-C weighted least-squares tree: *Parus–Remiz* appeared as the sister group of *Criniger–Stachyris–Hirundo–Alauda* rather than sister to the entire Passerida (as in Fig. 4). However, this 0.068 branch collapsed in any event when the complete matrix was bootstrapped, thus its sensitivity to outgroup change is not particularly noteworthy. In general, outgroup choice has little effect on DNA-hybridization estimates of phylogeny (e.g., Sheldon, 1994; Slikas et al., 1996).

Rates of Evolution

The disparity in sister-taxon branch lengths evident in Figures 4 and 5 suggests that different clades have evolved at different rates. Most notably, the corvids (*Corvus, Paradisaea, Vireo*) lie on short branches relative to noncorvids, and within the Passerida, *Remiz, Hirundo, Turdus,* and *Sitta* occupy relatively long branches. To investigate patterns of rate difference, we conducted relative rate tests (Sarich and Wilson, 1967) using a variety of outgroup and ingroup combinations. Because obligate distance measures are not independent values (i.e., they depend on common reference species), we performed these tests only to illustrate trends that suggest different rates in the various clades. An ANOVA of distances from suboscines to oscines and from corvids to passerids indicated significant variation among taxa (Student–Newman–Keuls method; see Table 3). Based on distances from *Calyptomena* and

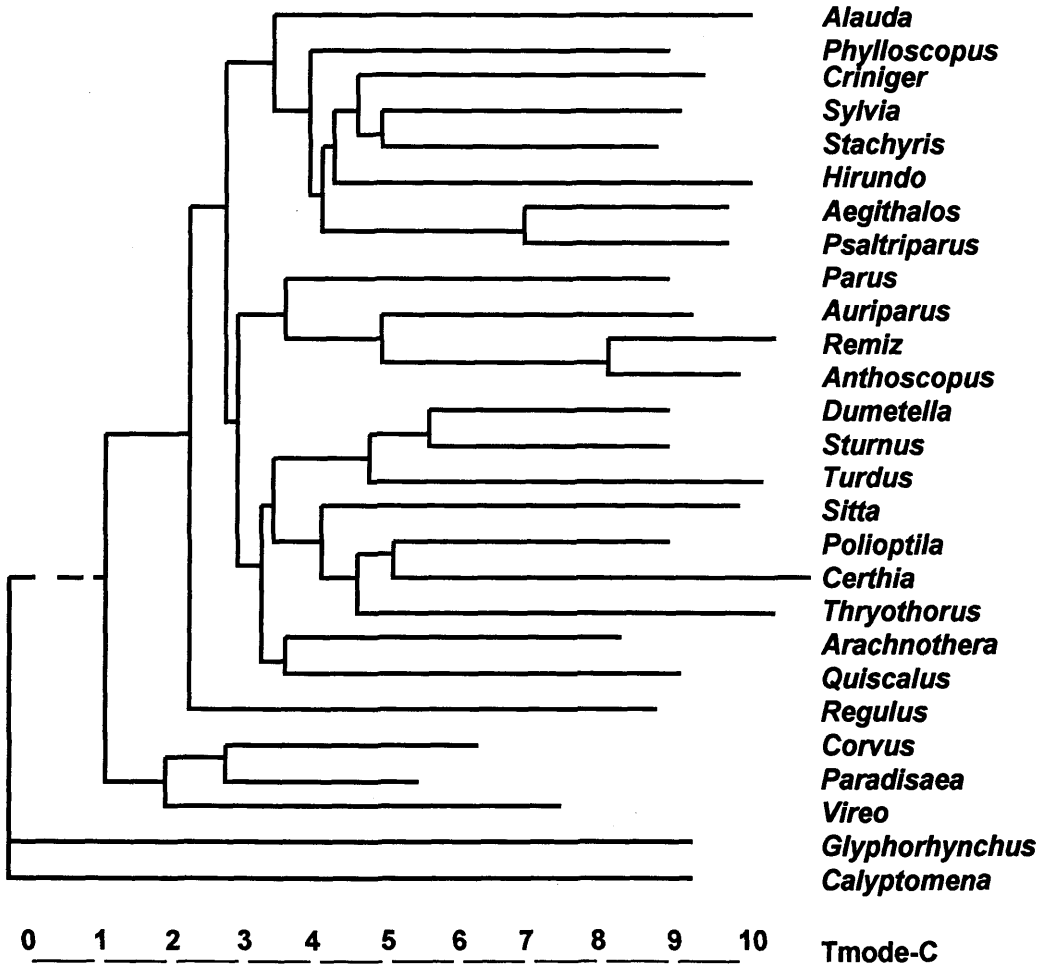

FIGURE 5. A summary weighted least squares (Fitch and Margoliash, 1967) DNA-hybridization tree for 27 passerines. This tree is primarily the best fit weighted least squares branching pattern from a 25-taxon ΔTmode-C folded matrix of DNA-hybridization distances. The position and branch length of *Paradisaea* were determined from a folded 17-taxon matrix consisting of *Paradisaea* and the 16 taxa in Figure 4. (Not enough *Paradisaea* DNA was available for comparisons with the remaining 10 species.) The branch lengths and the arrangement among *Polioptila, Certhia,* and *Thryothorus* were determined using the lacunose matrix method of Lapointe and Kirsch (1995, J. Kirsch, pers. comm.) because comparisons between *Polioptila* and *Thryothorus* failed for mechanical reasons.

Glyphorhynchus to each ingroup (oscine) species, the average distance to corvids was significantly shorter than that to passerids (*t*-test; $P < 0.05$). When distances from corvids to major passerid clades were compared, only the *Quiscalus–Arachnothera* clade appeared significantly different (shorter; *t*-test; $P < 0.05$).

DISCUSSION

Comparison with Sibley and Ahlquist (1990)

Our study supports the traditional division of the passerines into suboscines and oscines and S&A's division of the oscines into corvids and noncorvids. The corvids include not only the traditionally recognized taxa (*Corvus, Paradisaea*), but

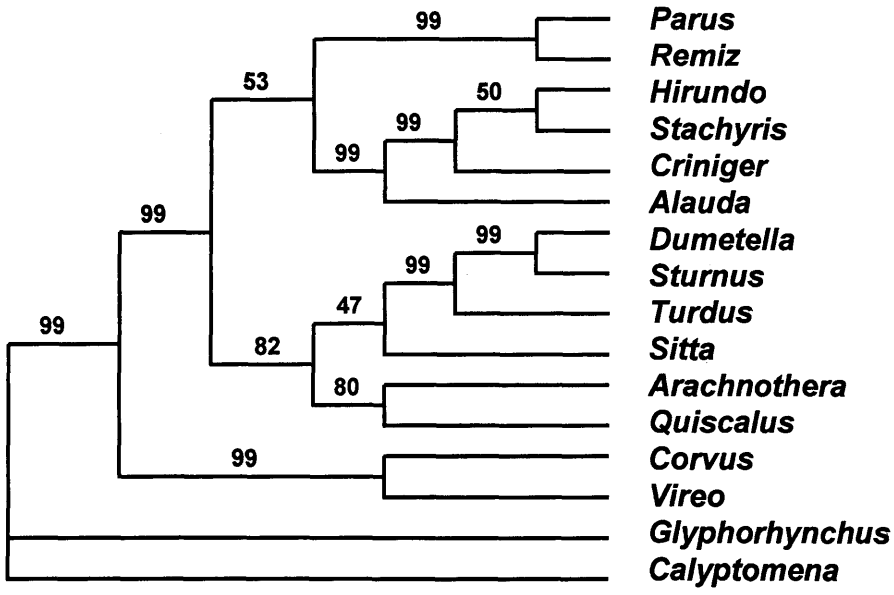

FIGURE 6. Bootstrap majority rule summary of the complete 16-taxon matrix of passerines produced from 1,000 pseudomatrices (Krajewski and Dickerman, 1990) using the PHYLIP (3.4) CONSENSE program (Felsenstein, 1989). Numbers are percentages of branch support.

also *Vireo*. Until Sibley and Ahlquist (1982) suggested its corvine affinity, *Vireo* more commonly was considered to be close to the New World nine-primaried oscines (e.g., Mayr and Amadon, 1951).

Despite congruence found at the highest levels, our study does not support the hierarchical arrangement of Passerida superfamilies proposed by S&A (Fig. 2), nor does it support the monophyly of S&A's superfamilies Sylvioidea and Passeroidea. S&A's sylvioid species divide into three clades whose positions are unresolved relative to S&A's muscicapoid (*Turdus, Dumetella, Sturnus*) and passeroid (*Arachnothera, Quiscalus*) clades. The clade that consists of nuthatches, gnatcatchers, treecreepers, and wrens, which S&A include in their Sylvioidea, in fact may be more closely related to thrushes and starlings (Muscicapoidea), but this alliance is weakly supported. The larks, represented by *Alauda*, align with typical "sylvioid" taxa rather than with the "passeroids" *Arachnothera* and *Quiscalus*. The "sylvioid" *Auriparus* belongs in the remizid–parid clade rather than in the nuthatch–creeper–gnatcatcher–wren clade. *Regulus*, which is a traditional sylvioid genus, not only is distinct from other traditional sylvioids but also is unexpectedly diverged from all the other Passerida species we examined.

Having used the same technique as S&A, why have we failed to produce a more congruent set of results? Possibly S&A's estimate of phylogeny is more accurate than ours because it relies on the comparison of more species; increasing the number of taxa would be expected to fortify short internodes (Swofford and Olsen, 1990; Lanyon, 1994). However, S&A's estimate of phylogeny is expected to contain mistakes because of the problems in their experimental design and data analysis. At the very least, many short internodes presented by S&A would probably collapse when assessed by bootstrapping and jackknifing. Also, S&A usually did not repeat hybridization measurements using different individuals of single species. Although there are practical limitations to such replications (time, cost, availability of samples), they are necessary to avoid errors caused by misidentification, sample mix-

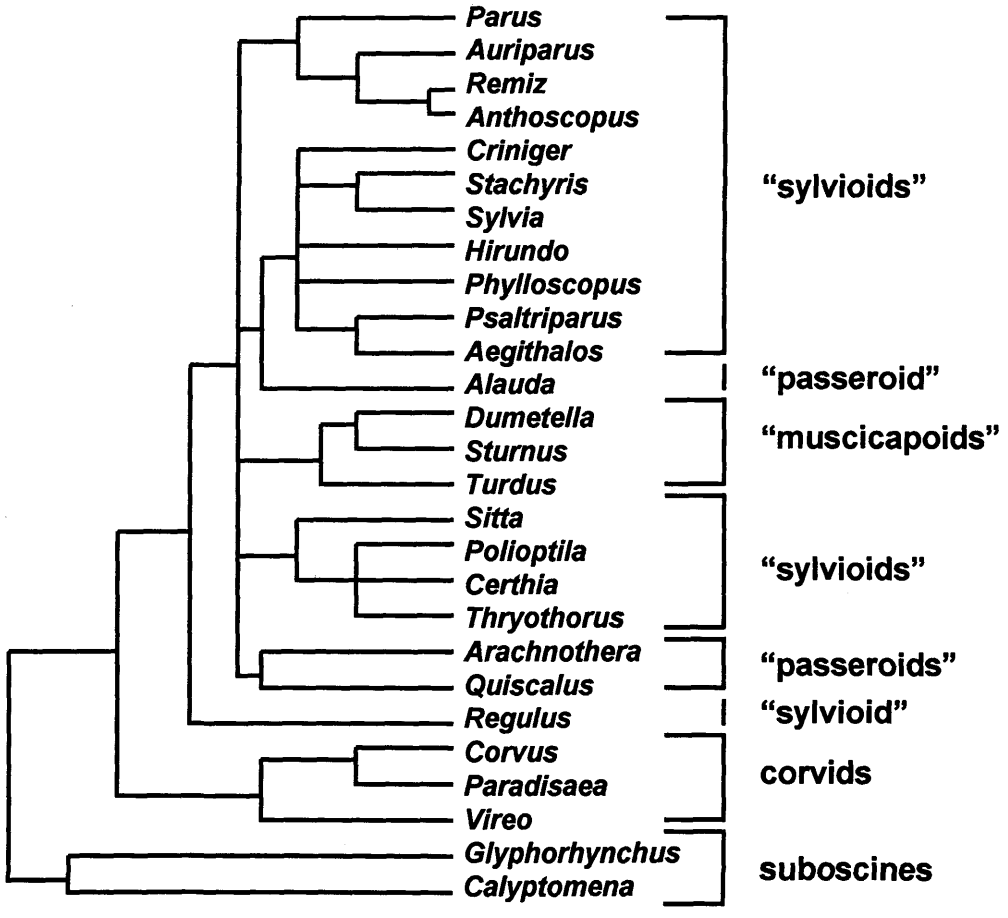

FIGURE 7. Summary tree of passerine phylogenetic relationships in which weak branches have been collapsed. Collapsed branches are those with <99% bootstrap support or those that showed inconsistency when jackknifed. One exception is the branch uniting *Arachnothera* and *Quiscalus*, which had only 80% bootstrap support but appeared consistently in jackknife tests.

TABLE 3. Relative rate tests, in which distances from avian outgroups to ingroups were compared for taxa in the 16 × 16 matrix. Rate disparity was determined by ANOVA (Student–Newman–Keuls).

Outgroup	Ingroup	$\bar{x}$	SD	n	P
Calyptomena	Corvida	16.13	0.58	10	<0.05
Calyptomena	Passerida	17.86	0.81	46	
Glyphorhynchus	Corvida	15.95	1.10	6	<0.05
Glyphorhynchus	Passerida	17.72	1.36	43	
2 Corvida species	*Arachnothera–Quiscalus* clade	9.80	0.92	22	<0.05
2 Corvida species	parid–remizid clade[a]	11.08	1.03	24	
2 Corvida species	*Sitta–Certhia* clade[b]	10.90	0.79	12	
2 Corvida species	babbler clade[c]	10.65	0.81	54	
2 Corvida species	muscicapid clade[d]	10.74	0.83	34	

[a] *Parus, Remiz,* and *Auriparus.*
[b] *Sitta, Certhia, Polioptila,* and *Thryothorus.*
[c] *Alauda, Aegithalos, Psaltriparus, Hirundo, Phylloscopus, Criniger, Stachyris,* and *Sylvia.*
[d] *Turdus, Dumetella,* and *Sturnus.*

ups, or other unrecognized laboratory problems. Laboratory mistakes leading to errors in molecular phylogenetic studies have been discovered by several investigators (Helm-Bychowski and Cracraft, 1993; Avise et al., 1995; Houde et al., 1995).

In an attempt to understand why we derived discordant results for three key taxa, *Regulus, Auriparus,* and *Alauda,* we compared our distances to those of S&A.

Kinglets.—Perhaps the most unexpected result of our study was that the kinglets (*Regulus*) appear as the sister taxon to the other passerids. Traditionally, kinglets are considered typical sylvioids, close to leaf-warblers, *Phylloscopus* (Mayr and Amadon, 1951). S&A (p. 649) separated the kinglets into their own family but retained them as sylvioids. In their comparisons, S&A (fig. 350) radiolabeled *Regulus* and provided composite distance measures in the matrix of their FITCH analysis (e.g., *Regulus–Phylloscopus* ΔT50H 8.98, 9.75; *Regulus–Sylvia* ΔT50H 9.16, 9.71). These distances are much shorter than the corresponding distances we measured; our uncorrected ΔTmodes of *Regulus–Sylvia* averaged 10.40, and those of *Phylloscopus–Regulus* averaged 10.79. This disparity caused us to wonder whether we had obtained a skewed perspective of the distances between *Regulus* and other taxa by making only one-way comparisons (i.e., omitting reciprocal measurements). However, upon reexamining the graphical raw data that S&A provided for *Regulus* (figs. 278, 285), we found that their measured distances are substantially longer than those illustrated in their figure 350 or shown in the Tapestry (fig. 380). Their actual ΔT50H values for *Regulus* to *Sylvia* and to *Phylloscopus* are closer to 11 or 12 (fig. 278), and their distance from *Sylvia* to *Regulus* is ca. ΔT50H 12.5. Thus, S&A's raw data for *Regulus* actually are consistent with ours; they indicate an unexpectedly large divergence between *Regulus* and other traditional sylvioids. Why S&A positioned *Regulus* as they did in the Tapestry is unclear.

Verdin.—The verdin (*Auriparus flaviceps*) is particularly important to our study because it forms a monophyletic group with remizids (*Remiz, Anthoscopus*) and thus is a member of the sister group of the Paridae. This finding is consistent with some traditional placements of *Auriparus* (e.g., Mayr and Amadon, 1951). S&A also placed remizids as sister of the parids, but they did not include *Auriparus* with the remizids. Instead they placed it near *Polioptila* in a large clade that includes *Polioptila, Sitta, Thryothorus,* and *Certhia.* Both S&A's and our study agree that these four taxa are part of a group distinct from parids and remizids.

S&A did not radiolabel *Auriparus* (fig. 380), and the only data they provided for this species are comparisons to radiolabeled members of the *Sitta–Polioptila–Certhia–Thryothorus* clade (figs. 266, 268, 271, 272). These data suggest that *Auriparus* is as far from *Sitta, Certhia,* and *Thryothorus* as it is from any parid or sylviid (ca. ΔT50H 10). The data of S&A (fig. 272), however, indicate that *Auriparus* is fairly close to *Polioptila* (ca. ΔT50H 6). Apparently for this reason, S&A grouped *Polioptila* and *Auriparus* together (fig. 380). Such a placement does not take into account the relatively large distances between *Auriparus* and *Sitta, Certhia,* and *Thryothorus.* S&A did not report any distances between *Auriparus* and the Remizidae or Paridae, so it is unclear whether they made these important comparisons.

We measured the following average ΔTmodes between *Auriparus* and other taxa: *Polioptila,* 9.48 (n = 3); *Certhia,* 10.65 (n = 2); *Sitta,* 10.38 (n = 4); *Thryothorus,* 10.42 (n = 4); *Parus,* 9.29 (n = 2); *Anthoscopus,* 7.78 (n = 4); and *Remiz,* 8.15 (n = 4). After *Parus* and the remizids, *Auriparus* is noticeably closer to *Polioptila* than to other members of the of the *Sitta–Polioptila–Certhia–Thryothorus* clade. Thus, an apparent evolutionary rate change is complicating reconstruction of this part of the phylogeny. If *Auriparus* is outside the *Sitta–Polioptila–Certhia–Thryothorus* lineage as we contend, then *Polioptila* has evolved more slowly than other taxa in that clade. If *Auriparus* is sister taxon to *Polioptila,* as S&A contended, then *Parus, Remiz,* and *Anthoscopus*

evolved at a rate slower than that of *Sitta, Certhia,* and *Thryothorus*. However, based on the distances above, this rate difference is not indicated by relative rate tests or other comparisons. Outgroup distances to *Polioptila* are consistently shorter than those to *Sitta, Certhia,* or *Thryothorus,* suggesting a possible rate slowdown in *Polioptila* (although the discrepancy is not statistically significant). Outgroup distances to *Parus, Remiz,* and *Anthoscopus* do not indicate a slow rate; if anything, *Remiz* and *Anthoscopus* evolved somewhat faster. These rate patterns are reflected in the branch lengths in Figures 4 and 5.

Larks.—We found larks (represented by *Alauda arvensis*) to form a monophyletic group with some typical "sylvioids," including babblers, Old World warblers, and long-tailed tits, as well as bulbuls and swallows. This finding differs substantially from S&A's (p. 665) results: "The DNA comparisons are clear and simple. The larks are the living descendents of the earliest branch of the passeroid tree at ΔT50H 10.4. The family Alaudidae is, therefore, the sister group of the other passeroid families." S&A radiolabeled *Alauda* (fig. 382) but did not present any raw data for *Alauda*-to-sylvioid comparisons or vice versa. They did show, however, hybrid melting curves for another lark, *Eremophila,* which was compared with a *Sylvia* species and two swallows (figs. 276, 295). The distances appear long (ca. ΔT50H 10–15) but are difficult to discern from these particular graphs. In the Tapestry (fig. 382), S&A placed the larks as the sister taxon of the other passeroids (at a connecting branch length of ΔT50H 0.4), and they placed the passeroids (including larks) at a branch length of ΔT50H 0.7 from the sylvioids. By DNA-hybridization standards, these are substantial internodal branch lengths (only branches below ΔTmode 0.2 collapsed in our study), but they were formulated without accounting for variable rates of evolution. Without more data, we cannot explain the discrepancy between our and S&A's positioning of larks.

In summary, our results support substantial portions of the Tapestry, i.e., the major divisions of passerine birds and the basic composition of sylvioid, passeroid, and muscicapoid clades. This support extends to S&A's placement of the remizids as sister of the parids and to their controversial assertion that starlings and mockingbirds are sister taxa (Sibley and Ahlquist, 1984). However, in other details, S&A's propositions are not corroborated, especially those concerning position of some key representative taxa (viz., *Regulus, Auriparus, Alauda*). The discrepancies between the two DNA-hybridization studies can be attributed to problems in S&A's experimental design and data analysis and interpretation, at least when adequate raw data are available for comparison.

Historical Ecology

Recent studies of seed-caching birds have demonstrated major taxonomic differences in cognitive memory. Members of Paridae (titmice), Sittidae (nuthatches), and Corvidae (crows, jays, nutcrackers) cache seeds as a means of exploiting temporary food surpluses and providing reserves for future use (Sherry, 1989; Vander Wall, 1990). Recovery of these widely dispersed, concealed seed caches requires spatial memory, which is based in the hippocampal complex of the telencephalon (Sherry et al., 1989). With two known exceptions, all chickadees and titmice regularly store seeds. The two exceptions, the subgenus *Parus* (e.g., great tit, *Parus major*) and the subgenus *Cyanistes* (e.g., blue tit, *P. caeruleus*), have significantly smaller hippocampi than other species of titmice in terms of both absolute and relative size (Krebs et al., 1989). They also differ from other parids in various aspects of their social behavior and ecology (Ekman, 1989). Parids that cache seeds, for example, tend to form small, discrete flocks, with a dominance-based membership. These flocks defend exclusive winter territories. Great tits and blue tits, however, form large, roaming, loosely aggregated winter flocks that regularly exchange members.

A main purpose of this study was to determine whether seed caching and corre-

lated brain physiology and behavior arose independently in the Paridae, Sittidae, and Corvidae. Establishing independent derivation is an important first step to testing the hypothesis that seed caching is a key innovation of the parids, i.e., an adaptation responsible for diversification. If it can be shown that whenever seed caching arises in temperate forest birds, there is marked increase in diversification of caching species, then there is good comparative evidence that seed caching is causally related to that diversity (Sheldon and Whittingham, 1997). The ability to cache seeds, for example, would be expected to increase individual fitness by providing food in winter. This increased fitness in individuals might increase the longevity of the species, which in turn would create opportunities for speciation by vicariance or dispersal. Increased longevity of species would also reduce depauperization of lineages by extinction (Allmon, 1992; Heard and Hauser, 1995).

In this study, we have corroborated S&A's contention that the Paridae and Sittidae are not sister taxa, or even particularly closely related, as is often implied in traditional classifications (e.g., Mayr and Amadon, 1951; Beecher, 1953; Wetmore, 1960). The sister taxon of the Paridae is composed of penduline-tits and verdin (*Auriparus*). These taxa are not known to cache food in the manner of parids (Vander Wall, 1990). Preliminary measurements suggest that the size of the hippocampus in *Remiz* may be similar to that in caching parids, but verification will require further study (D. F. Sherry, pers. comm.). Thus, specialized seed caching and, at least, its behavioral correlates appear to have evolved at least three times in the oscines: in the Paridae, Sittidae, and Corvidae. For *Parus*, seed caching and correlated characters are derived traits that evolved after the divergence of the subgenera *Baeolophus*, *Poecile*, *Periparus*, and *Lophophanes* from the subgenera *Cyanistes* and *Parus* (Fig. 1). We speculate that parids originated in a subtropical climate in the mid-Tertiary (Slikas et al., 1996). Subsequent development of seed caching permitted the diversification of *Baeolophus*, *Poecile*, *Periparus*, and *Lophophanes* in the coniferous forests that spread as climates cooled worldwide during the Pliocene. The nuthatches, which form an independent lineage of seed cachers that is the same approximate age as the Paridae, appear to have diversified as a result of the same environmental conditions.

Songbirds in the Bush: Problems of Phylogenetic Resolution and Classification

When subjected to bootstrapping and jackknifing tests of stability, several of the shorter branches in our tree collapse, indicating a lack of resolution among some major clades of Passerida. The branches that collapse are all less than ΔTmode 0.2 (usually <0.1). Because ΔTmode is roughly proportional to time (e.g., Britten, 1986), with some variation caused by measurement error and small rate differences, short internodal branches suggest short time intervals between the divergence of major groups. These short branches are not likely to be an artifact of taxic sampling because although adding taxa to an obligate distance data set can shorten internodes by bisection, rearrange them slightly, or fortify them by replication, it cannot lengthen them substantially. In this respect, obligate distance data differ from character data; adding taxa in character reconstructions of phylogeny can shorten, lengthen, or reposition branches by changing the number and location of synapomorphies supporting various clades. This feature of obligate distance data explains, for example, why switching between close outgroups (corvids) and distant outgroups (suboscines) had virtually no effect on the branching of passerids.

The problems we encountered in resolving relationships of major passerid groups may explain the long history of frustration in oscine phylogenetics and classification. Short times between branching events would leave little opportunity for diverging clades to acquire synapomorphies (Lanyon, 1988), and the result would be ill-defined groups. Wallace (1856) complained

that classifying passerines was unusually difficult because so many of the groups grade into one another (O'Hara, 1993), and this problem is reflected in all classifications of sylvioids produced in the subsequent 140 years. Hellmayr (1903), for example, viewed the sylvioids and Paridae from a substantially different perspective than more recent (nonphylogenetic) classifiers. His Paridae included as subfamilies the kinglets (Regulinae, including *Sylviparus*), the gnatcatchers (Polioptilinae), and the parrot-bills (Paradoxornithinae), as well as the tits (Parinae). Further, his Parinae consisted of a broad assortment of songbirds in addition to *Parus*, viz., long-tailed tits (e.g., *Aegithalos*), penduline-tits (e.g., *Remiz*), wrentit (*Chamaea*), and reedling (*Panurus*). In more recent classifications (Mayr and Amadon, 1951; Wetmore, 1960; Storer, 1971; Morony et al., 1975), the tendency has been to move each of these taxa to separate families. But the linear arrangement of these families has varied substantially, and of course none of these arrangements has been based on phylogeny. The first attempt at a phylogenetic classification was Beecher's (1953) arrangement of oscines according to primitive (simple) and derived (complex) myological traits. His approach did not produce a very satisfying tree, but it did contribute substantially to our understanding of the complexity of oscine evolution and the logic of character analysis.

Sibley and Ahlquist (1990) were the first to construct a sylvioid classification based on truly phylogenetic criteria. Unfortunately, by indicating more resolution in their Tapestry than really existed, they underplayed the uncertainty remaining in passerine phylogeny. Nevertheless, they clarified many relationships, indicated substantial convergence in this and other passerine groups, helped identify some major sources of confusion (e.g., the mixing of taxa from separate radiations in Asia and Australia), and provided a remarkable template for future phylogenetic studies.

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APPENDIX. Average ΔTmode values for comparisons among passerine taxa. Column heads are radiolabeled taxa.

	Alauda			*Arachnothera*			*Calyptomena*			*Corvus*		
	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
Alauda arvensis	0.00		6	8.90	0.31	4	17.60	0.21	3	10.84	0.22	4
Arachnothera longirostra	8.25	0.21	4	0.00		6	17.10	0.92	4	8.97	0.06	4
Calyptomena viridis	16.43	0.69	4	16.70	0.76	4	0.00		6	15.17	0.47	4
Corvus ossifragus	10.44	0.14	3	9.30	0.68	4	16.02	0.34	4	0.00		4
Criniger bres	8.57	0.17	4	8.61	0.49	4	17.69	0.57	4	10.44	0.06	4
Dumetella carolinensis	10.12	0.13	4	8.83	0.44	4	17.40	0.65	4	10.32	0.22	4
Glyphorhynchus spirurus	17.68	0.84	3	16.92	0.76	3	14.58	0.27	3	15.48	0.31	4
Hirundo rustica	9.24	0.21	4	9.26	0.16	3	17.84	0.28	4	10.82	0.19	4
Paradisaea raggiana	9.63	0.16	4				15.81	0.47	4			
Parus atricapillus	9.92	0.69	4	8.24	0.34	3	18.19	0.32	3	10.29	0.36	4
Quiscalus quiscula	9.64	0.12	4	7.95	0.32	4	17.60	0.62	4	10.08	0.31	4
Remiz pendulinus	10.74	0.30	3	9.90	0.03	2	19.16	0.87	4	11.54	0.14	4
Sitta carolinensis	10.10	0.05	3	8.71	0.55	4	18.69	0.83	4	11.01	0.15	4
Stachyris poliocephala	8.45	0.27	4	8.09	0.04	4	17.39	0.37	4	10.09	0.22	3
Sturnus vulgaris	9.45	0.24	4	8.52	0.23	4	17.32	0.74	4	10.51	0.23	4
Turdus migratorius	10.13	0.19	4	9.60	0.37	3	18.38	0.22	4	11.35	0.88	4
Vireo olivaceus	11.15	0.33	3	10.07	0.58	3	16.99	0.16	3	7.89	0.17	4
Aegithalos fuliginosus				8.70	0.16	3				10.46	0.19	4

	Parus			*Quiscalus*			*Remiz*			*Sitta*		
	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
Alauda arvensis	9.34	0.74	4	9.13	0.20	4	11.10	0.93	3	10.39	0.68	4
Arachnothera longirostra	8.44	0.45	4	7.07	0.35	3	9.56	0.29	3	8.47	0.12	3
Calyptomena viridis	17.55	0.40	4	15.88	0.45	4	16.89	1.36	4	16.76	1.05	4
Corvus ossifragus	9.91	0.68	4	9.70	0.22	4	11.76	0.06	2	10.72	0.09	3
Criniger bres	9.37	0.44	4	8.92	0.31	4	10.72	0.28	2	10.34	0.13	4
Dumetella carolinensis	9.58	0.37	4	9.21	0.26	4	11.25	0.31	3	10.02	0.51	4
Glyphorhynchus spirurus	17.42	0.84	4	16.93	0.05	2	17.55	1.47	3	16.99	1.16	3
Hirundo rustica	9.87	0.37	4	9.27	0.36	4	11.59	0.68	4	10.88	0.64	4
Paradisaea raggiana	9.47	0.46	4	8.91	0.15	4	11.40	0.28	4			
Parus atricapillus	0.00		9	9.05	0.16	4	10.40	0.73	4	10.09	0.60	7
Quiscalus quiscula	9.35	0.61	4	0.00		6	11.13	0.17	4	10.16	0.23	4
Remiz pendulinus	9.59	0.36	8	10.41	0.36	4	0.00		8	11.35	0.22	8
Sitta carolinensis	9.91	0.54	7	9.32	0.30	4	11.60	0.48	7	0.00		10
Stachyris poliocephala	8.87	0.51	4	8.88	0.31	4	10.72	0.09	4	10.10	0.22	3
Sturnus vulgaris	9.49	0.24	4	9.00	0.27	4	11.35	0.28	3	10.00	0.44	4
Turdus migratorius	10.26	0.26	4	9.97	0.26	4	12.03	0.61	4	10.37	0.48	4
Vireo olivaceus	10.88	0.37	4	10.70	0.17	4	12.72	0.58	3	11.61	0.36	3
Aegithalos fuliginosus										10.79	0.56	2

APPENDIX. Extended.

Criniger			*Dumetella*			*Glyphorhynchus*			*Hirundo*			*Paradisaea*		
$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
9.12	0.52	2	9.25		1	16.84	0.73	3	10.02	0.37	3	10.01	0.37	4
8.72	0.15	2	8.33		1	16.20	0.99	3	8.99	0.49	4	8.35	0.55	2
17.92	0.72	2	17.54	0.47	2	14.27	0.24	4	17.79	0.87	4	15.36	0.68	4
10.96	0.47	2	9.98	0.13	2	15.73	1.56	3	11.08	0.24	4	5.07	0.24	4
0.00		2	9.90	0.91	2	18.11	1.14	4	8.89	0.32	4	9.80	0.40	4
9.94	0.23	2	0.00		2	18.55	2.58	4	10.55	0.35	4	9.77	0.61	4
17.64	0.39	2	17.79	0.31	2	0.00		6	18.51	0.79	4	16.06	0.51	4
9.21	0.02	2	9.83	0.32	2	17.19	0.36	3	0.00		6	10.01	0.10	4
10.24	0.10	2	9.37	0.02	2				10.33	0.28	4	0.00		6
10.01	0.45	2	9.59	0.30	2	17.77	1.00	3	10.39	0.23	4	9.55	0.21	4
10.50		1	8.68	0.49	2	17.25	0.31	3	10.22	0.19	4	9.57	0.23	4
10.96	0.12	2	10.76	0.25	2	19.21	0.60	4	11.42	0.26	4	11.38	0.80	4
10.58	0.47	2	9.84	0.42	2	18.40	0.93	3	11.31	0.43	4	9.97	0.35	4
7.69	0.07	2	8.82		1	16.58	1.85	4	8.31	0.31	4	9.36	0.20	4
9.25	0.15	2	5.16	0.06	2	18.34	0.79	3	10.68	0.33	4	9.92	0.21	4
10.34	0.44	2	7.70	0.54	2	16.92	1.42	3	11.03	0.33	4	10.56	0.60	4
11.10	0.14	2	11.22	0.53	2	16.17	0.65	3	11.63	0.42	4	7.47	0.57	4
						18.04	0.74	4						

Stachyris			*Sturnus*			*Turdus*			*Vireo*			*Aegithalos*		
$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
8.45	0.31	2	9.69	0.58	4	11.19	0.74	4	11.85	0.27	4	9.15	0.13	4
7.07	0.16	4	8.02	0.18	4	9.14	0.27	4	9.81	0.38	4	8.69	0.54	4
16.82	1.11	3	18.07	0.48	4	18.70	0.52	3	16.15	0.85	4	17.51	1.08	4
9.61	0.13	2	10.24	0.74	4	11.01	0.41	4	7.68	0.13	4	10.44	1.31	4
6.78	1.22	3	9.86	0.53	3	10.99	0.71	4	11.34	0.63	4	8.23	0.33	4
8.24	0.59	3	5.67	0.41	3	8.15	0.42	2	11.65	0.40	4	9.72	0.43	4
16.93	0.43	3	17.57	0.78	4	19.71	0.73	4	16.44	0.84	3	17.28	1.25	4
7.26	0.35	3	10.42	0.18	4	11.28	0.50	3	11.66	0.52	4	8.92	0.16	4
8.34	0.33	3	9.91	0.35	4									
8.97	0.41	4	10.07	0.86	2	10.70	0.16	3	11.22	0.23	4	9.63	0.08	4
8.20	0.39	2	9.27	0.34	4	9.90	0.27	4	11.26	0.37	4	9.92	0.47	3
9.56	0.94	2	11.19	0.67	3	12.10	0.67	4	12.50	0.34	4	11.10	0.40	4
9.41	0.59	3	9.99	0.37	4	11.16	0.64	4	11.73	0.27	4	10.68	0.47	4
0.00		4	8.85	0.64	4	10.30	0.09	4	10.87	0.22	4	7.93	0.09	4
8.48	0.53	3	0.00		6	8.26	0.34	4	11.25	0.81	3	9.63	0.59	4
9.82	0.18	4	8.01	0.75	4	0.00		5	11.66	0.30	3	10.47	0.59	3
10.09	0.20	3	11.01	0.88	4	12.02	0.36	4	0.00		5	10.86	0.52	4
						10.72	0.18	4	11.60	0.88	3	0.00		5

APPENDIX. Continued.

	Anthoscopus			*Auriparus*			*Certhia*			*Phylloscopus*		
	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
Alauda arvensis	10.38	0.56	3	10.42	0.47	3	11.18	0.56	2	9.00	0.47	2
Arachnothera longirostra	9.05	0.43	4	8.69	0.33	3	8.85	0.79	3	8.34	0.51	3
Calyptomena viridis	17.38		1	18.35	1.85	2	17.68	0.59	2	15.51	0.76	2
Corvus ossifragus	10.81	0.24	4	10.55	0.03	2	11.84	2.48	2	10.24	0.17	2
Criniger bres	10.13	0.21	4	9.58	0.61	3	11.00	0.14	2	8.20	0.06	3
Dumetella carolinensis	10.15	0.44	3	9.82	0.65	2	10.31	0.90	3	9.47	0.52	3
Glyphorhynchus spirurus	16.92		1	17.81	1.90	2	19.56		1	16.27	0.06	2
Hirundo rustica	10.41	0.09	4	10.22	0.34	4	11.44	1.06	3	8.62	0.23	3
Paradisaea raggiana												
Parus atricapillus	8.90	0.30	3	9.29	0.25	2	10.59	0.46	4	9.90	0.64	4
Quiscalus quiscula	10.41	0.70	4	9.89	0.42	4	10.60		1	9.20	0.59	2
Remiz pendulinus	3.62	0.07	3	8.15	0.33	4	11.80	0.35	4	10.18	0.63	4
Sitta carolinensis	11.14	0.49	3	10.38	0.46	4	9.91	0.68	3	10.21	0.60	4
Stachyris poliocephala	9.71	0.30	4	10.06	0.55	2	10.84	0.05	3	7.79	0.32	4
Sturnus vulgaris	10.65	0.34	4	10.20	0.55	3	10.31	0.77	2	9.71	0.20	2
Turdus migratorius	11.03	0.21	4	10.59	0.68	4	11.17	0.62	2	9.98	0.56	2
Vireo olivaceus	12.03	0.38	4	12.10	0.59	2	11.95	0.11	2	10.63	0.36	2
Aegithalos fuliginosus	10.58	0.55	3	10.13	0.67	4	11.14	0.62	3	7.89	0.13	3
Anthoscopus minutus	0.00		4	7.78	0.40	4	11.77	0.34	3	10.35	0.26	3
Auriparus flaviceps				0.00		4	10.65	0.81	2	9.59	0.20	3
Certhia americana							0.00		4			
Phylloscopus collybita							10.61	0.65	3	0.00		4
Polioptila caerulea												
Psaltriparus minimus							10.52		1	8.95	0.85	4
Regulus satrapa							11.01	0.35	3	10.40	0.72	3
Sylvia atricapilla							11.39	0.96	2	8.55	0.34	4
Thryothorus ludovicianus	10.74	0.49	4	10.42	0.54	4	9.03	0.51	3	9.90	0.40	3

APPENDIX. Extended.

Polioptila			*Psaltriparus*			*Regulus*			*Sylvia*			*Thryothorus*		
$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
9.88	0.72	2	9.46	0.13	4	10.16	0.49	2	9.33	0.08	2	10.64	0.63	3
8.05	0.26	3	8.49	0.23	3	8.86	0.04	2	9.11	0.43	4	8.52	0.23	4
18.09	0.72	2	16.13	1.57	2	15.97	0.13	2	15.13	0.48	2	17.46	0.53	2
9.67	0.10	2	10.59	0.15	2	10.76	0.42	2	11.05		1	10.83	0.40	4
8.69	0.20	2	8.54	0.14	4	10.40	0.08	3	8.56	0.25	4	10.59	0.73	4
9.28	0.18	2	10.21	0.33	2	9.74	0.30	2	10.13		1	10.40	0.33	3
16.55		1	16.57	0.00	2	16.46	0.28	2	15.29	0.28	2	18.70		1
10.11	0.73	3	9.08	0.18	4	10.69	0.26	4	9.22	0.42	4	11.10	0.35	3
9.18	0.36	4	10.03	0.58	4	10.06	0.13	4	10.31	0.40	4	10.08	0.49	4
8.99	0.12	2	9.86	0.38	4	10.31		1	10.34	0.12	2	9.75	0.38	4
10.46	0.25	4	11.17	0.52	4	11.06	0.22	4	11.04	0.60	4	11.57	0.30	4
8.77	0.50	3	10.46	0.37	4	10.21	0.61	3	10.90	0.32	4	10.07	0.36	3
9.11	0.45	3	8.14	0.09	4	9.84	0.59	3	7.45	0.29	3	9.77	0.50	4
9.24	0.12	2	10.02	0.39	2	10.37	0.09	2	10.20	0.37	2	10.35	0.24	3
9.87	0.11	2	10.57	0.39	2	10.63	0.45	2	11.12	0.39	2	10.92	0.37	4
10.68		1	11.50	0.18	2	11.29		1	11.22	0.12	2	11.62	0.38	3
9.70		1	4.47	0.40	3	10.47	0.73	4	9.17	0.44	3	10.48	0.32	3
10.11	0.25	3	10.98	0.18	3	11.07	0.26	4	11.17	0.28	4			
9.48	0.24	3	9.98	0.48	4	10.50	0.28	4	10.10	0.40	3			
7.81	0.45	3												
9.79	1.06	3												
0.00		4												
10.19	0.43	3	0.00		4	10.57	0.26	4	8.86	0.36	4			
10.11	0.34	2				0.00		4						
9.81	0.16	3				10.79	0.26	3	0.00		4			
			10.71	0.17	4	10.51	0.17	3	10.61	0.13	3	0.00		6