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A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data

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Passerine birds comprise over half of avian diversity, but have proved difficult to classify. Despite a long history of work on this group, no comprehensive hypothesis of passerine family-level relationships was available until recent analyses of DNA–DNA hybridization data. Unfortunately, given the value of such a hypothesis in comparative studies of passerine ecology and behaviour, the DNA-hybridization results have not been well tested using independent data and analytical approaches. Therefore, we analysed nucleotide sequence variation at the nuclear RAG-1 and c-*mos* genes from 69 passerine taxa, including representatives of most currently recognized families. In contradiction to previous DNA-hybridization studies, our analyses suggest paraphyly of suboscine passerines because the suboscine New Zealand wren *Acanthisitta* was found to be sister to all other passerines. Additionally, we reconstructed the parvorder Corvida as a basal paraphyletic grade within the oscine passerines. Finally, we found strong evidence that several family-level taxa are misplaced in the hybridization results, including the Alaudidae, Irenidae, and Melanocharitidae. The hypothesis of relationships we present here suggests that the oscine passerines arose on the Australian continental plate while it was isolated by oceanic barriers and that a major northern radiation of oscines (i.e. the parvorder Passerida) originated subsequent to dispersal from the south.

Keywords: Passeriformes; 'Tapestry'; DNA–DNA hybridization; Gondwana; Wallace's line

1. INTRODUCTION

> Sibley and Ahlquist's molecular phylogeny of the birds (1990) . . . produced the unexpected but *now uncontested* conclusion that the Australian passerines are a separate radiation from other passerines (Mooers *et al.* (1994), emphasis added).

The 'perching birds' (order Passeriformes) comprise the largest order of birds and represent over half of the extant avian species diversity (59%, Sibley & Monroe 1990). Taxic diversification of the order has been accompanied by extensive morphological, life historical and behavioural diversification. The order's 45 families (Sibley & Monroe 1990) exhibit a broad range of ecological tolerances and trophic adaptations and representatives of the order occur in most terrestrial biomes. This diversity has made passerine birds useful model organisms in many studies at the single-species level, including studies of vocal communication (Catchpole 1986; West & King 1988; Payne & Payne 1993; Price 1998), mating systems (Orians 1980; Davies 1992; McDonald & Potts 1994), cooperative breeding (Woolfenden & Fitzpatrick 1984; Rabenold *et al.* 1990; Pruett-Jones & Lewis 1990; Komdeur 1994), food caching (Balda & Kamil 1989; Krebs *et al.* 1990) and migration (Berthold *et al.* 1992). Two of the most often cited cases of adaptive radiation involve passerine birds (the Hawaiian honeycreepers and the Galapagos finches, both members of the Fringillidae ((*sensu* Sibley & Monroe 1990); Raikow 1977; Lack 1947; Grant 1986; Grant & Grant 1989). In the last decade, a number of multi-species comparative studies of many of these phenomena in birds, and more specifically in passerines, have been published (e.g. Briskie & Montgomerie 1992; Promislow *et al.* 1992; Briskie *et al.* 1994; Barraclough *et al.* 1995; Poiani & Pagel 1997). Most such comparative studies rely on an explicit statement of phylogenetic relationships (and often accompanying estimates of divergence times or rates of character change; Harvey & Pagel (1991); Martins & Hansen (1996)). The analyses in these studies have, to a large degree, been contingent upon the only available comprehensive hypothesis of relationships for birds, that of Sibley & Ahlquist (1990).

Careful examination of both muscular and skeletal features has yielded important insights into aspects of passerine relationships (e.g. Ames 1971; Feduccia 1975*a*; Raikow 1978, 1987; Prum 1993). However, no comprehensive phylogenetic hypothesis of relationships among the families of passerine birds existed until the work of Sibley & Ahlquist (1985*a–d*, 1990). The hypothesis of Sibley & Ahlquist (1990), commonly referred to as the 'Tapestry', formed the basis of a complete reclassification of the class Aves as a whole and of the order Passeriformes in particular (Sibley & Monroe 1990). Their hypothesis supported many traditional notions of passerine relationships, for instance the existence of two major clades within the order: the oscines (the so-called 'songbirds', suborder Passeri; refer to Sibley & Monroe (1990) for a summary of the higher-level taxonomy) and the suboscines (suborder Tyranni). In addition, the Tapestry proposed a number of novel relationships among passerines. Most notably, they proposed a splitting of the oscine passerines into two major clades, one clade primarily a Northern Hemisphere group (the parvorder Passerida) and the other clade

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primarily an Australo–Papuan group of 'crow-like' birds (the parvorder Corvida; see also Sibley 1976; Sibley & Ahlquist 1985*a*). Unfortunately, the validity of this and other novel hypotheses embodied in the Tapestry is questionable. The analyses of Sibley & Ahlquist (1990) have been subject to a wide variety of criticisms, ranging from non-reproducibility due to unreported lineage-specific rate corrections (Mindell 1992), to sparse sampling of the complete distance matrix (Lanyon 1992). The work itself lacks internal consistency (Cracraft 1992; Lanyon 1992) and where distance matrices are presented, reanalysis often fails to reproduce the dendrograms presented (Lanyon 1992; Mindell 1992; Harshman 1994). Nevertheless, the Tapestry has become the standard hypothesis of relationships used in a large array of analyses of avian—and in particular passerine—morphological, life historical and behavioural diversity (Mooers & Cotgreave 1994), as well as in interpretation of passerine diversification (Nee *et al.* 1992; Harvey & Nee 1994; Mooers *et al.* 1994; Raikow & Bledsoe 2000; Cracraft 2001).

Several studies of higher-level passerine relationships using independent datasets have been conducted since the publication of Sibley and Ahlquist's work, including additional DNA–DNA hybridization data (Bledsoe 1988; Sheldon & Gill 1996), allozymes (Christidis & Schodde 1991, 1992; Christidis *et al.* 1993), mitochondrial DNA sequences (Edwards *et al.* 1991; Helm-Bychowski & Cracraft 1993; Christidis *et al.* 1996*a*,*b*; Groth 1998; Cibois *et al.* 1999; Pasquet *et al.* 1999; Cracraft & Feinstein 2000; Honda & Yamagishi 2000; Klicka *et al.* 2000) and, most recently, nuclear-DNA sequences (Lovette & Bermingham 2000; Ericson *et al.* 2000; Irestedt *et al.* 2001). In general, these studies have found broad congruence with Sibley and Ahlquist at the highest levels (suborders and parvorders), but significant conflicts have arisen at finer scales (superfamilies and below). However, these studies all suffer from one or more difficulties, including limited taxon sampling, limited character sampling, or a lack of resolving power due to levels of homoplasy in the data.

Though limited in taxonomic depth of sampling, the nuclear-DNA sequence data collected from passerines show a lower rate of substitution and far less homoplasy than mitochondrial DNA even for the deepest levels of comparison (Groth & Barrowclough 1999; Lovette & Bermingham 2000; Irestedt *et al.* 2001). Additionally, studies of such sequences have sometimes identified length variation, which appears phylogenetically informative and provides strong evidence for the monophyly of important clades of passerines (Ericsson *et al.* 2000). In this paper, we report the results of phylogenetic analyses of 3524 aligned bases from two nuclear gene exons in 69 species of passerine birds and three outgroups. The taxa sequenced represent nearly all passerine families recognized by Sibley & Monroe (1990) and the majority of those recognized by traditional taxonomy (e.g. Wetmore 1960). These data allow the first comprehensive tests of the monophyly of major clades of passerine birds using character-based analysis of DNA sequence data. In addition, we discuss the biogeographic implications of our preferred hypothesis relative to previous notions of passerine relationships (Sibley 1976; Sibley & Ahlquist 1985*c*, 1990).

2. MATERIAL AND METHODS

(a) *Taxon sampling*

We obtained samples from all 34 oscine passerine families recognized in Sibley & Monroe (1990) except three (the Callaeatidae, Hypocoliidae and Paramythiidae). In addition, we extensively sampled the suboscine passerines (the presumptive sister group of the oscines), including samples from 8 out of 10 Sibley & Monroe (1990) families and all major lineages within the suborder Tyranni (Sibley & Ahlquist 1990). In order to supplement this basic sampling strategy, a number of families were sampled more extensively, guided largely by subfamily designations in Sibley & Monroe (1990) and by family definitions used in traditional taxonomic treatments (e.g. Wetmore 1960; Morony *et al.* 1975). The taxa sampled in this study are summarized in Appendix A. Rather than assuming monophyly of any group within the Passeriformes, we selected three non-passerines (*Gallus*, *Apus*, *and Coracias*) as outgroups.

(b) *Collection of sequence data*

Variation at two nuclear-encoded exons, the nuclear recombination-activating gene RAG-1 (Schatz *et al.* 1989; Carlson *et al.* 1991) and the proto-oncogene c-*mos* (Schmidt *et al.* 1988; Saint *et al.* 1998), was used for phylogenetic inference. Both of these loci have previously proven useful for higher-level phylogenetic inference in birds (Cooper & Penny 1997; Groth & Barrowclough 1999; Lovette & Bermingham 2000). A large portion of the single exon of the RAG-1 locus was amplified and sequenced using standard techniques as previously described (Groth & Barrowclough 1999), using several additional primers (table 1). The RAG-1 sequences of *Gallus*, *Coracias*, *Tyrannus*, and *Passer* were obtained from GenBank (accession numbers AF143730 and AF143737–AF143739). The c-*mos* locus was amplified and sequenced using the same techniques, using primers (table 1) designed to match regions conserved in comparison with the published sequences of *Gallus* and *Homo* (Watson *et al.* 1982; Schmidt *et al.* 1988; see also Cooper and Penny 1997; Saint *et al.* 1998).

(c) *Phylogenetic analysis*

All phylogenetic analyses were performed using PAUP* v. 40b4a (Swofford 1998). The uniformity of base composition at each codon position was evaluated quantitatively via a χ^2-test of homogeneity. The correlation of sequence divergence at the two loci was evaluated qualitatively by examination of bivariate distance plots. The phylogenetic congruence between the two loci was not evaluated using the commonly employed incongruence length difference procedure (Farris *et al.* 1995), because the small size of the c-*mos* dataset made thorough searches impractical and employing search shortcuts (e.g. less thorough branch swapping) would bias the test towards rejection of the null hypothesis. For this reason, we evaluated congruence by separate analysis of the two datasets under the parsimony criterion with equal weights, estimation of nodal robustness for each using the bootstrap (Felsenstein 1985) and examination of these analyses for evidence of strongly supported conflicting hypotheses of relationship. Tree searches were heuristic, employing tree-bisection-and-reconnection (TBR) branch swapping following 50 random taxon-addition sequence replicates. Bootstrap analyses were performed with 1000 pseudoreplicates, each executed with TBR branch swapping following 10 random-addition sequence replicates. Because of the large number of equally parsimonious trees obtained, bootstrap support

Table 1. List of novel primers used in amplification and sequencing of RAG-1 and c-*mos*[a].

primer	sequence (5′–3′)	target gene
1D	GACAAACACCTCAGGAAGAAGAT	RAG-1
2I	GAGGTATATAGCCAGTGATGCTT	RAG-1
3F	CTTTAGGGGTACAGGATATGATGA	RAG-1
5D	CCAGTAGACACAATTGCAAAGAG	RAG-1
16B	GGCAGACATCACAGTTTGGGGA	RAG-1
CM1	GCCTGGTGCTCCATCGACTGGGA	c-*mos*
CM2	GGGTGATGGCAAAGGAGTAGATGTC	c-*mos*
CM3	GCCTGGGCACCATCATCATGGA	c-*mos*
CM4	GCAGGCTTCAGGTCCAAGTGCAC	c-*mos*
CM5	CCCACGCTTGGCCTGGTGCTC	c-*mos*
CM6	GATCTGCCAGAGGGTGATGGC	c-*mos*
CM7	CGGTTGGCCTGGTGCTCCAT	c-*mos*

[a] Previously published primers used were 2, 3E, 4B, 5, 6, 7, 8, 9, 10C, 11, 11B, 12B, 13, 13B, 14B, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24 (Groth & Barrowclough 1999).

for the separate analysis of the c-*mos* dataset was accomplished using a crude search protocol where trees were obtained via stepwise addition with a random-addition sequence, without branch swapping (corresponding to the 'fast-heuristic' setting in PAUP*). The combined data were analysed under the parsimony criterion as for the two datasets separately. Finally, the support or conflict of individual datasets with particular nodes recovered in the shortest parsimony trees was evaluated using the partitioned Bremer index (Baker & DeSalle 1997; Baker *et al.* 1998), calculated with the assistance of TREEROT v. 2 (Sorenson 1999).

The combined data were also analysed under the maximum-likelihood criterion. The fit of various substitution models to the data was evaluated given a neighbour-joining tree (Saitou & Nei 1987) fitted to Jukes–Cantor distances (Jukes & Cantor 1969) calculated from the data (executed using MODELTEST v. 3.04; Posada & Crandall 1998). The most appropriate model was selected by comparison of nested models of increasing complexity using the likelihood ratio statistics $-2\ln\Lambda$ compared to appropriate χ^2 null distributions (or $\bar{\chi}^2$, as appropriate, Ota *et al.* (2000); Goldman & Whelan (2000); also, incorporating a Bonferroni correction for multiple comparisons, Posada & Crandall (1998)). The standard hierarchy of tests implemented in MODELTEST (Posada & Crandall 1998) was supplemented with comparisons of the preferred model with selected parameter-enriched alternatives. Additionally, the applicability of the molecular clock to the data was tested. Parameter estimates (base composition π_i, substitution rates r_{ij}, parameter of the Γ-distribution α, and proportion of invariant sites p_{iv}) calculated on the neighbour-joining tree for selection of the preferred model were fixed in subsequent heuristic tree searches. Tree searches were performed by heuristic TBR branch swapping on an initial tree obtained via neighbour joining with Jukes–Cantor distances. Support for individual nodes in the maximum-likelihood tree estimate was estimated via the bootstrap, with searches for each of 100 pseudoreplicates using subtree pruning and regrafting (SPR) branch swapping on starting trees obtained via neighbour joining.

(d) *Biogeographic analysis*

Sibley (1976) and Sibley & Ahlquist (1985*a*, 1990) proposed the existence of a monophyletic radiation of crow-like birds (their parvorder Corvida) ancestrally endemic to the Australo–Papuan region. This proposal was tested on our hypothesis of passerine relationships. The biogeographic origin of major passerine groups (specifically the suborder Passeri and its components) was evaluated via ancestral area analysis (Bremer 1992, 1995). In accordance with its significance in avian biogeography (Wallace 1860; Mayr 1944; Keast 1981; White & Bruce 1986), Wallace's line was used to delimit the Australo–Papuan region. The ancestral area analysis was performed using regions termed cis-Wallacea (Australia, New Zealand, New Guinea and Indonesian islands found on the Australo–Papuan side of the original Wallace's Line; see Coates & Bishop 1997) and trans-Wallacea (the remainder of the globe). All families represented in the sample of taxa analysed here (including all but three Sibley & Ahlquist (1990) families) were coded for presence in the cis- and trans-Wallacean regions and the proportion of species found in each region estimated, using standard references (White & Bruce 1986; Sibley & Monroe 1990; Coates 1990; Schodde & Mason 1999) and field guides (Coates & Bishop 1997; Beehler *et al.* 1986). In cases where the assumption of monophyly for a given family was questionable, families were amalgamated to form composite higher taxa, which were biogeographically coded (these cases are explicitly noted in § 3). In this fashion, all passerine species recognized in Sibley & Monroe (1990) were effectively assigned a presence/absence value for the cis- and trans-Wallacean regions. Calculations of area gains and losses with alternative ancestral states under Camin–Sokal parsimony (Camin & Sokal 1965) were performed using MACCLADE v. 308a (Maddison & Maddison 1999).

3. RESULTS

(a) *Sequence characteristics*

Sequences obtained from the RAG-1 locus (sequences new to this study have been deposited in GenBank, under accession numbers AY056975–AY057042) varied in length from 2851 bases in *Apus* to 2884 bases in *Fringilla* (median = 2872 bp), whereas sequences of c-*mos* (deposited in GenBank under accession numbers AY056903–AY056974) varied from 598 bases in *Aegithalos* to 616 bases in *Oriolus* (median = 607 bp). The distribution of sequence lengths departing from median values did not appear to be asymmetrical for this sample of taxa (size distribution skewness values of −0.543 and 0.514 for RAG-1 and c-*mos*, respectively; Deutsch & Long 1999). One case of heterozygosity in allele length occurred in *Troglodytes*, in which one allele had a four-codon deletion

relative to the other (corresponding to positions 718–729 of the *Gallus* sequence; GenBank accession no. M58530; Carlson *et al.* 1991). Most other sequences obtained showed evidence of heterozygosity at individual nucleotide sites. At the RAG-1 locus, sequences showed polymorphism at anywhere from zero (nine sequences) to 17 sites in the sequence obtained from *Alauda*, while sequences of c-*mos* exhibited polymorphism at anywhere from zero (20 sequences) to eight sites, also in *Alauda*. The relatively high values of polymorphism observed in *Alauda* sequences prompted us to substitute another lark (*Eremopterix*) in our phylogenetic analyses, in order to validate our *Alauda* sequence (see § 3b, below).

Alignment of RAG-1 sequences was accomplished in a straightforward fashion, yielding a matrix of 2902 aligned nucleotide sites (submitted to European Molecular Biology Laboratory (EMBL), accession ALIGN_000206). Alignment of c-*mos* was not straight-forward, as one region was characterized by a series of codons very similar in primary sequence, which could not be reliably homologized. A matrix of 622 nucleotide sites was obtained (submitted to EMBL, accession ALIGN_000207), of which 36 (12 codons, positions 320–355) were excluded from analysis because of doubts about primary homology. Based on outgroup comparisons, the RAG-1 alignment implies at least 11 insertion–deletion (indel) events, including eight autapomorphic deletions, one autapomorphic insertion and two potentially informative indels. The included portion of the c-*mos* alignment exhibits no informative indel variation and there is only a single two-codon autapomorphic insertion, which can be inferred for the lineage leading to *Meliphaga*. Given these alignments, 47% of RAG-1 positions are variable across the taxa sampled here (table 2), with 24% of this variation at codon first, 15% at second, and 61% at third positions (32% of sites parsimony-informative, with a similar distribution among codon positions; results not presented). A similar pattern was found for c-*mos*, with 50% of sites variable (32% parsimony-informative; table 2), with 22, 17, and 62% of variable sites at first, second, and third codon positions respectively (again, parsimony-informative sites following essentially the same distribution; results not presented). Pairwise sequence divergences at RAG-1 varied from 0.7% (between *Thraupis* and *Cardinalis*) and 6.9% (between *Sitta* and *Gallus*; 5.2% within passerines, *Sitta* versus *Acanthisitta*), while divergences at c-*mos* varied from 0.7% (between *Ploceus* and *Passer*) to 7.1% (between *Garrulax* and *Gallus*; 6.6% within passerines, *Muscicapa* versus *Pitta*). Divergences at the two loci were highly correlated ($r = 0.784$). However, in point comparisons with both *Apus* and *Sitta*, the ratio of divergence at RAG-1 to divergence at c-*mos* showed evidence of a significant increase (result not shown), suggesting either lineage-specific substitution rate increases in RAG-1, rate decreases in c-*mos*, or both.

The pattern observed for sequence comparisons involving *Sitta* was easily explained by examination of among-taxon variation in base composition. Overall, the RAG-1 sequences analysed were slightly enriched in thymine residues and deficient in cytosine residues (31.5 and 20.3%, respectively; table 2). This overall pattern obscured a significant AT bias, which exists at codon second and third positions (62 and 54% AT, respectively), and a bias against cytosine residues at codon first positions (20%). Overall, base compositional heterogeneity at codon third positions was not significant ($\chi^2 = 114$, d.f. = 213, $p = 1.000$; as implemented in PAUP* 4.0b4). This conservative test failed to detect the substantial shift in base composition represented by the *Sitta* RAG-1 sequence. This sequence has a GC content of 54.9%, compared to an average across taxa (excluding *Sitta*) of 45.7% (s.d. = 0.02). There was some compositional variation at the GC-rich c-*mos* locus (57.0% GC overall, 70.9% at third positions, s.d. = 0.04; $\chi^2 = 158$, d.f. = 213, $p = 1.00$; table 2), but no taxa exhibit marked divergence from the norm. Thus, the pattern of pairwise divergences involving *Sitta* can be attributed to a shift from AT- to GC-richness in this lineage, possibly due to a shift of this locus between isochores (Robinson *et al.* 1997). No corresponding pattern emerged from this analysis to explain the apparent shift in divergence rates in *Apus*, and other explanations must be sought for this pattern.

(b) *Phylogenetic analysis*

Prior to a combined phylogenetic analysis of these data, they were evaluated for congruence of phylogenetic signal by evaluation of nodal robustness in separate analyses of the two gene regions. For the RAG-1 data, 38 equally parsimonious trees were obtained, whereas the c-*mos* data were consistent with nearly 60 000 equally parsimonious trees identified by the branch-swapping algorithm (table 2). Levels of homoplasy were slightly higher for the c-*mos* data (as indicated by the consistency and retention indices CI and RI, table 2). A comparison of bootstrap support for nodes inferred from separate analyses of the two loci suggested only one area of potentially significant conflict in the ingroup, in which the c-*mos* data placed *Formicarius* and *Thamnophilus* as sister taxa to the exclusion of *Furnarius* (66% of bootstrap replicates), whereas RAG-1 placed *Formicarius* and *Furnarius* as sister taxa (84% of bootstrap replicates). All other nodes receiving ⩾50% support in the c-*mos* analysis were congruent with strongly supported nodes recovered in analyses of RAG-1. The two datasets also differed in the arrangement of the out-groups with RAG-1 favouring *Coracias* as sister to the passerines, and c-*mos* favouring *Apus*. This may be attributable to rate heterogeneity in c-*mos* (see below, this section). In all cases, sequences obtained from the lark *Eremopterix* clustered with sequences of *Alauda* and the position of each of these alone, analysed with the remaining taxa, yielded identical topologies (results not shown). Results of analyses using only our sequences of *Alauda* are reported here.

Given that the observed conflict between the loci was minor, a combined analysis of the two datasets was pursued. Parsimony analysis of the two datasets combined yielded 27 equally parsimonious trees, the consensus of which was well resolved (64 of 69 possible nodes resolved; table 2; figure 1*a*). The few polytomies observed in the consensus (nodes 17, 18, and 48; figure 1*a*) were not clustered in any particular region of the tree (e.g. at the base or the tips). Our bootstrap analysis indicated large numbers of well-supported nodes, with support evenly distributed throughout the tree (figure 1*a*, Appendix B). Of 64 nodes retained in the strict consensus of equally parsimonious trees, 40 (63%) were recovered in ⩾50%, 27 (42%) in ⩾75% and 20 (31%) in ⩾90% of bootstrap

Table 2. Data characteristics and estimated substitution parameters for RAG-1, c-*mos*, and the combined data. (Maximum-likelihood parameters were all estimated on the best tree found with a TBR search under the criterion of maximum likelihood using the complete dataset (see § 2), while the number of trees, CFI, tree length and homoplasy measures are for the shortest trees under equally weighted parsimony for a given dataset.)

gene	RAG-1	c-*mos*	combined
number of bases	2902	586 (622)	3488 (3524)
number variable (%)	1357 (46.8)	286 (48.8)	1643 (47.1)
number informative (%)	923 (31.8)	188 (32.1)	1111 (31.9)
%A (1st/2nd/3rd)	0.315 (0.324/0.356/0.264)[a]	0.233 (0.262/0.307/0.113)[a]	0.3011[b]
%C (1st/2nd/3rd)	0.203 (0.200/0.191/0.218)[a]	0.255 (0.225/0.215/0.358)[a]	0.2313[b]
%G (1st/2nd/3rd)	0.242 (0.297/0.188/0.240)[a]	0.314 (0.352/0.215/0.350)[a]	0.2454[b]
%T (1st/2nd/3rd)	0.241 (0.179/0.265/0.278)[a]	0.198 (0.162/0.264/0.178)[a]	0.2221[b]
r_{AC}	1.725	1.126	1.647
r_{AG}	6.003	6.454	6.298
r_{AT}	0.911	0.591	0.878
r_{CG}	1.476	1.206	1.534
r_{CT}	10.562	10.073	10.445
α	1.416	0.656	1.058
p_{iv}	0.411	0.365	0.395
tree length (ML)	1.733	3.284	2.012
# trees (MP)	38	59 615	27
CFI[c]	61	45	64
tree length (MP)	4264	1180	5506
CI[d]	0.450 (0.372)	0.353 (0.286)	0.424 (0.349)
RI	0.464	0.459	0.452

[a] Observed base frequencies, averaged across all taxa.
[b] Maximum-likelihood estimates of the stationary base frequencies, used in maximum-likelihood analysis of the complete dataset.
[c] Consensus fork index (number of resolved nodes in consensus).
[d] Values excluding uninformative characters in parentheses.

replicates (Appendix B). Data combination did not yield any overall pattern of changes in bootstrap values for reconstructed nodes (sign test for all nodes appearing in $\geqslant$50% of bootstrap replicates for the RAG-1 data alone, $p = 0.51$, $n = 40$). Partitioned Bremer support values for the combined analysis showed that the minor conflicts between the two loci were distributed throughout the tree, with no single notably large values (except the –5 value at the root of the passerines, due to conflicting arrangement of the out-groups; Appendix B).

In addition to parsimony analysis of these data, we calculated a maximum-likelihood estimate of phylogenetic relationships. The hierarchical comparisons performed by MODELTEST yielded the Tamura–Nei model of substitution (Tamura & Nei 1993), with invariant sites and Γ-distributed rates at variable sites (TrN + I + Γ) as the most appropriate model for the combined data. However, if all transversions are allowed their own rates (the general time-reversible (GTR) model, Yang (1994)), the improvement over TrN model is highly significant ($-2\ln\Lambda = 47$, d.f. = 3, $p < 0.001$) and remains significant even when invariant sites and Γ-distributed rates are added to both models ($-2\ln\Lambda = 55$, $p < 0.001$). The molecular clock was strongly rejected ($-2\ln\Lambda = 317$, d.f. = 70, $p < 0.001$). For these reasons, the GTR + I + Γ model, without a molecular clock, was chosen as most appropriate for likelihood analysis of these data.

Heuristic searches using the preferred model, with substitution parameters estimated on a neighbour-joining tree and fixed during the searches, yielded a single most-likely tree (figure 1*b*; see table 2 for estimated parameter values). This tree was very similar in structure to the strict consensus of trees found under the parsimony criterion (CFI = 50 of 69 nodes, 78% of nodes in the parsimony strict consensus). This similarity is even more noticeable when nodal robustness is taken into account. Of 69 recoverable nodes, 46 were found in $\geqslant$50% of maximum-likelihood bootstrap pseudoreplicates, 36 in $\geqslant$75%, and 23 in $\geqslant$90%. Limiting comparisons between the parsimony and bootstrap analyses to these well-supported nodes, all but two recovered at the 50% level and all nodes found at the 75% level and higher were also recovered under the parsimony criterion. The branch length information summarized in figure 1*b* reflects the shift in base composition in the *Sitta* sequence of RAG-1, noted above as an apparent rate increase, consistent with theoretical predictions (Sueoka 1993; Takano-Shimizu 2001). No major shift is apparent in the *Apus* lineage (figure 1*b*). However, separate optimization of RAG-1 and c-*mos* data on the likelihood tree reveals a short branch leading to *Apus* for the c-*mos* sequence (result not shown). Because branch lengths in the combined analysis are, in effect, averages of predicted substitutions per site across the dataset, they reflect primarily the behaviour of the larger (RAG-1). Thus the increased ratio of RAG-1 to c-*mos* divergence observed for *Apus* is best explained by a decrease in substitution rate at the *Apus* c-*mos* locus (rather than a rate increase at the RAG-1 locus; see § 3a, above).

(c) *Biogeographic analysis*

The percentage of species on either side of Wallace's line (defined in Coates & Bishop 1997) was determined

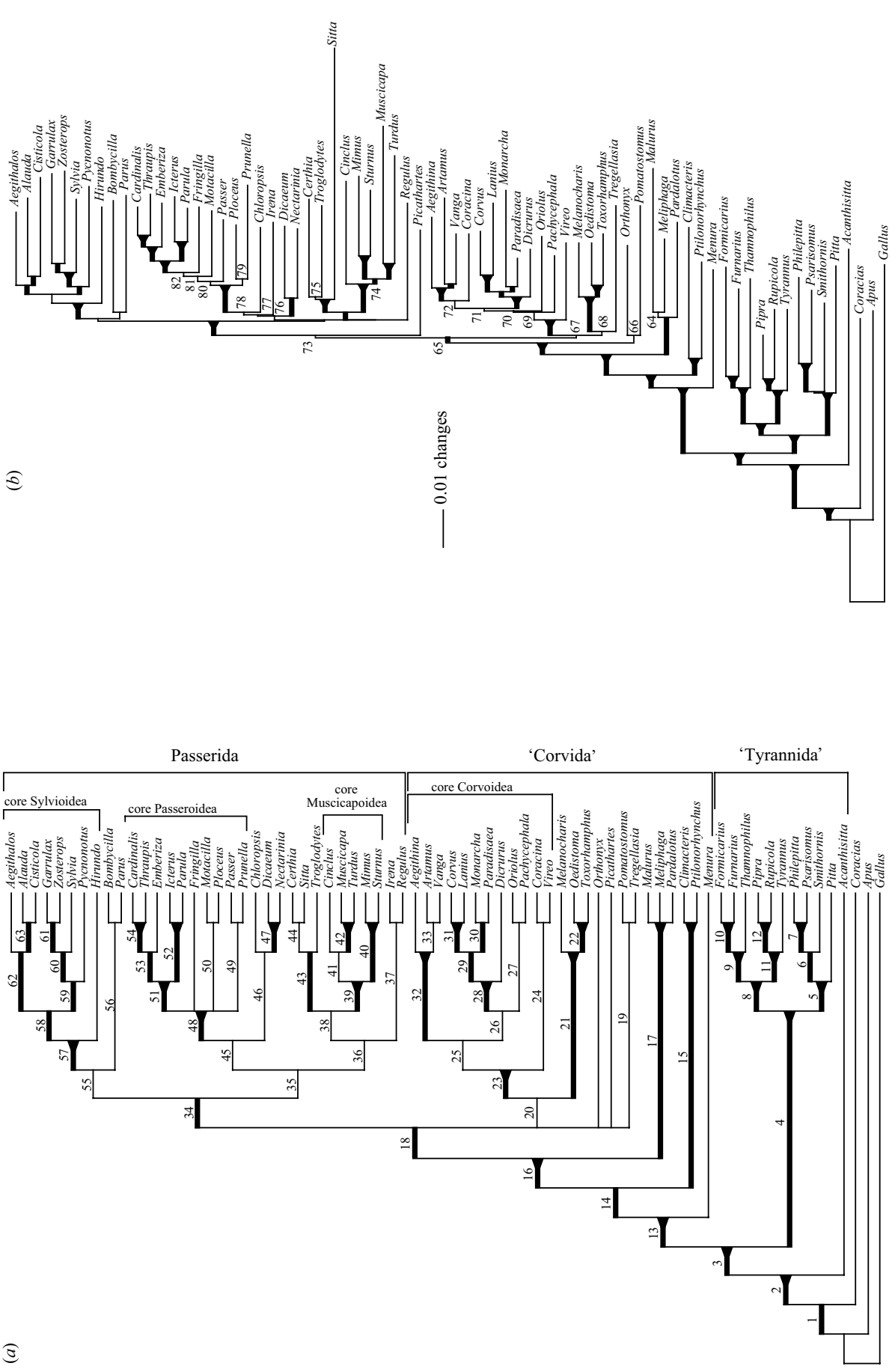

Figure 1. Trees obtained from analyses of combined passerine RAG-1 and c-*mos* data: (*a*) parsimony (strict consensus of 27 trees, L = 5506 steps) and (*b*) maximum likelihood ($-\ln\lambda = 34\,099.2$, see table 2 for parameters, branch lengths proportional to expected changes per site). The numbers on the branches refer to nodal support data in Appendix B. The proportion of bootstrap replicates in which a given node was recovered is indicated by branch thickness: a thickened branch indicates $50\% \leqslant BP < 75\%$ and a thickened branch with a terminal expansion indicates $BP \geqslant 75\%$.

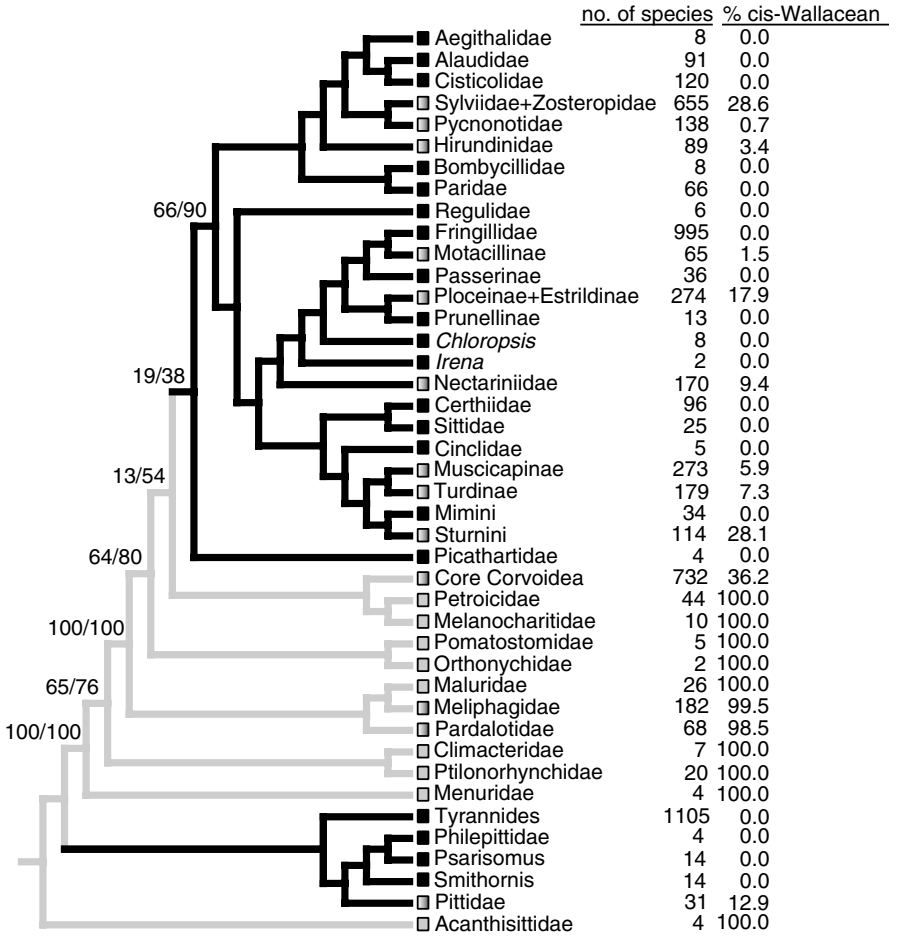

Figure 2. Distribution and biogeographic reconstruction of Passeriformes. The tree represented is the maximum-likelihood hypothesis of relationships (figure 1*b*). Numbers near basal branches indicate recovery of the indicated nodes in bootstrap analyses (parsimony/likelihood). The squares after each terminal are black if the taxon represented is entirely trans-Wallacean, grey if it is entirely cis-Wallacean and gradient-filled if the taxon is found on both sides of Wallace's line (see § 2). The most parsimonious reconstruction of the binary cis/trans character is indicated by branch shading for illustrative purposes only. Following each clade name is the number of extant species in that clade and the percentage of those species found on the Australo–Papuan side of Wallace's line (cis-Wallacean).

for all clades represented in our analysis of passerine relationships (figure 2). We took the tree inferred for these sequences under the maximum-likelihood criterion as our best point estimate of relationships among the groups represented (though we note that use of the parsimony trees yields essentially the same results). In two cases, multiple representatives from higher taxa recognized by Sibley & Ahlquist (1990) did not form monophyletic groups on this tree, when representatives from all of the component taxa within those higher taxa had not been sampled. These were the Sylviidae (represented here by sequences of *Garrulax* and *Sylvia*) and the Passeridae (represented by *Passer*, *Motacilla*, *Prunella*, and *Ploceus*). In the first case, all of the species contained within Sibley & Monroe's (1990) Sylviidae and Zosteropidae were treated and scored as a single taxon. In the second, species in the Estrildinae (not represented here) were assigned to a clade with the Ploceinae for scoring purposes, following Sibley & Ahlquist's (1990) results (see also Harshman 1994). Additionally, components of the Corvoidea that formed a strongly supported group in our analyses (the so-called 'core Corvoidea'; figure 1*a*) were scored as a single taxon. All of these composite taxa are well nested within the passerine tree and the procedure used here can have no impact on inferences regarding biogeographic patterns among basal lineages of passerines or among oscine passerines in particular.

Figure 2 summarizes the biogeographic distribution of passerine species with regard to presence on either side of Wallace's line. In particular, it provides information on endemism of higher passerine taxa in the Australo–Papuan region. These data are particularly interesting in light of the phylogenetic relationships among passerines that we have inferred. All of the basal lineages of oscine passerines are endemic or near-endemic to Australia, New Guinea and closely associated islands (cis-Wallacean). Using Bremer's approach (1992, 1995) to inferring ancestral areas for widespread clades, cis-Wallacea is reconstructed as the most likely ancestral area component for oscine passerines (table 3). The contrast between the relative likelihood of cis- and trans-Wallacean regions as components of the ancestral area for oscines is further strengthened when the Meliphagidae and Pardalotidae are assumed to be ancestrally cis-Wallacean (consistent with patterns of standing diversity and close similarity of trans-Wallacean exemplars of these families to cis-Wallacean forms). An additional, debatable assumption of ancestral limitation of the 'core Corvoidea' to cis-Wallacea further emphasizes this pattern

Table 3. Ancestral area analyses (Bremer 1992, 1995) of the oscine passerines (suborder Passeri), recognizing cis- and trans-Wallacea as potential areas of origin (see § 2 for definitions).

focal clade	ancestral area assumptions	ancestral area	gains	losses	G/L[a]
Passeri	none	cis	12	12	1.00
		trans	4	5	0.80
	families[b]	cis	12	12	1.00
		trans	2	5	0.40
	families + 'core'[c]	cis	12	12	1.00
		trans	1	5	0.20
Passerida	none	cis	7	11	0.64
		trans	1	1	1.00

[a] Ratio of inferred gains to inferred losses.
[b] Meliphagidae and Pardalotidae assumed to be ancestrally limited to cis-Wallacea (see § 3).
[c] Meliphagidae, Pardalotidae and the 'core Corvoidea' assumed to be ancestrally limited to cis-Wallacea (see § 3).

(table 3). Another striking feature of figure 2 is the large group of primarily northern (trans-Wallacean) lineages, which roughly corresponds to Sibley & Ahlquist's (1990) Passerida (see § 4). Ancestral area analysis indicates that the most probable ancestral component for this clade is the trans-Wallacean region (table 3).

4. DISCUSSION

(a) *Phylogenetic relationships within Passeriformes*

The phylogenetic hypotheses inferred here from our sample of passerine nuclear-DNA sequences support some previous notions of passerine phylogeny, contradict others and offer novel insights into relationships among passerine groups. Our taxon-sampling scheme was not specifically designed to test the monophyly of the order Passeriformes, so the fact that we do recover monophyly is not particularly meaningful. Monophyly of the Passeriformes has not been controversial (Raikow 1982; Sibley & Ahlquist 1990; but see Mindell *et al.* 1999; Johnson 2001). What has prompted some controversy is the arrangement of basal lineages within the passerines, notably among the New Zealand wrens (Acanthisittidae), other suboscines (Tyranni), the Menuridae (*Menura* and *Atrichornis*) and oscines (Passeri; Raikow 1985, 1987; Feduccia 1975*a*,*b*, 1979; Sibley 1974; Sibley *et al.* 1982; Sibley & Ahlquist 1990). Our data suggest a novel arrangement of these lineages. First, we find the New Zealand wren *Acanthisitta* to be the sister of all remaining passerine birds, with strong support for this separation in the RAG-1 and combined analyses (figure 1, Appendix B; this arrangement was also found in 52% of the equally parsimonious c-*mos* trees). *Acanthisitta* has a suboscine (suborder Tyranni) syrinx (Ames 1971), but lacks the stapedial morphology found in other suboscines (Feduccia 1975*a*) and shares a condition of the fourth digital flexor with oscine (suborder Passeri) passerines (Raikow 1987). The arrangement found with our data is congruent with syringeal and stapedial morphology, but suggests homoplasy in the digital musculature. This hypothesis was previously suggested in passing by Sibley & Ahlquist (1990, p. 582), who stated that the acanthisittids might 'be assigned to a third suborder as the sister group of the Tyranni and Passeri' (though this arrangement was not adopted in the Tapestry) and was also recovered (with weak support) in Lovette & Bermingham's (2000) maximum-likelihood analysis of variation in c-*mos*.

The placement of *Menura* as a sister group to all other oscine passerines (Passeri) was recovered in separate analyses of both the RAG-1 and c-*mos* data, as well as in the combined analyses, where it received modest support (recovered in 65% and 76% of bootstrap replicates in parsimony and likelihood analyses, respectively; Appendix B). This relationship is consistent with previous analyses that recognized *Menura*'s oscine affinities based on hind limb musculature (e.g. Raikow 1985), as well as with the distinctiveness of *Menura*'s syringeal musculature (Ames 1971), which has long been recognized by placement of the genus (and its probable sister taxon *Atrichornis*; Raikow 1985) in a separate suborder (e.g. the Menurae of Wetmore 1960). This arrangement was also recovered in analyses of allozyme data from passerines (Christidis & Schodde 1991). With regard to Sibley & Ahlquist's (1990) results, this placement of *Menura* contradicts monophyly of their parvorder Corvida, as well as their superfamily Menuroidea (which contains the Climacteridae, Menuridae and Ptilonorhynchidae), rendering both paraphyletic.

The observed paraphyly of Sibley and Ahlquist's parvorder Corvida extends beyond the placement of *Menura* as sister to all oscines. In fact, two additional nodes in the parsimony strict consensus (16 and 18; figure 1, Appendix B) and four additional nodes in the maximum-likelihood tree (16, 18, 65 and 73; figure 1, Appendix B) contradict monophyly of the Corvida. The node separating the 'Menuroidea' (represented here by *Menura*, *Ptilonorhynchus* and *Climacteris*) from the remaining oscine taxa (node 16, Appendix B) was strongly supported (found in separate analyses of RAG-1 and c-*mos*, recovered in 100% of bootstrap replicates in both parsimony and likelihood analyses) and that separating the Meliphagoidea (*Malurus*, *Meliphaga*, and *Pardalotus*) and the Menuroidea from the remaining oscines (node 18, Appendix B) had modest support (found in 64% and 80% of bootstrap replicates in parsimony and maximum-likelihood analyses, respectively). This set of relationships renders Sibley and Ahlquist's parvorder Corvida, as well as two of the superfamilies within it, paraphyletic (only the Meliphagoidea is supported by our data). Essentially, we have found the Corvida, far from being a large mono-

phyletic assemblage primarily endemic to the Australo–Papuan region (Sibley 1976; Sibley & Ahlquist 1985*a*, 1990) to be a paraphyletic basal grade within the oscines.

In contrast, Sibley & Ahlquist's (1990) conception of the parvorder Passerida is supported by our data. In figure 1, node 34 (found in 66% and 90% of bootstrap replicates in parsimony and likelihood analyses, respectively; Appendix B) unites all sampled members of the Passerida to the exclusion the 'Corvida', with two exceptions. First, the members of the family Melanocharitidae (*Melanocharis*, *Oedistoma* and *Toxorhamphus*), endemic to the highlands of New Guinea, are clearly outside of this grouping and find their closest relatives with some members of the superfamily Corvoidea (figure 1). Second, two members of the family Irenidae (*Irena* and *Chloropsis*) classified by Sibley & Ahlquist (1990) as members of the 'Corvida', are very clearly united with members of the Passerida, while another (*Aegithina*) was resolved as a member of the 'core Corvoidea' (in agreement with Sibley and Ahlquist's placement of the genus). Monophyly of the Passerida has also been supported previously by indel variation in c-*myc* (Ericson *et al.* 2000), though neither the Irenidae nor Melanocharitidae were included in that study.

We examined the number of additional steps required to fit our data to alternative phylogenetic hypotheses for the taxa we sampled. The shortest trees we could find (employing constrained heuristic searches in PAUP*, under the same conditions used in the original tree searches) that were consistent with the constraint of a monophyletic Corvida (*sensu stricto* Sibley & Ahlquist 1990), were 39 steps longer than our shortest trees overall. Allowing exclusion of the Melanocharitidae from the Passerida and inclusion of *Irena* and *Chloropsis* within the Passerida yielded trees 22 steps longer than the best parsimony trees. This latter constraint, which corrects three misplacements in the Tapestry—at least as judged by relationships in our trees—but which otherwise maintains the Corvida/Passerida distinction, was also compared with our hypothesis in a likelihood context. The difference in log-likelihood between our estimate of the maximum-likelihood tree and the best estimate we could obtain consistent with this modified notion of the Corvida, was 82.7. We compared this value with a null distribution simulated via parametric bootstrapping (the Swofford, Olson, Waddell and Hillis test; Goldman *et al.* 2000) and the test value exceeded every one of 100 replicates ($p < 0.01$). This value would presumably be even higher for the more restrictive notions of corvidan monophyly.

At a lower taxonomic level, we failed to recover monophyly of Sibley and Ahlquist's proposed division of the Passerida into three superfamilies (their Muscicapoidea, Sylvioidea and Passeroidea). We found strong support for a 'core Muscicapoidea' containing most members of the superfamily (node 39; figure 1, Appendix B), but which did not include the waxwing (*Bombycilla*). We also found strong support for a 'core Passeroidea' (node 48; figure 1, Appendix B) containing most members of the superfamily except the lark (*Alauda*), the sunbirds and flowerpeckers (Nectariniidae) and the Melanocharitidae (see above, this section). This node was also supported by an unreversed synapomorphic insertion of four amino acids in the RAG-1 gene (not coded in the analysis). The position of *Alauda* provides one of the few strongly supported contradictions to the superfamily structure proposed by Sibley & Ahlquist (1990). We found strong support for a 'core Sylvioidea' containing members of the superfamily except members of the Regulidae, Paridae, Sittidae and Certhiidae (node 57; figure 1, Appendix B), but including *Alauda*. This result was not an artifact of our sequence for this genus (see § 3) and is in agreement with Sheldon & Gill's (1996) DNA–DNA hybridization study, and Groth's (1998) mitochondrial-DNA sequence study, both of which clustered larks with sylvioids to the exclusion of other passeroids.

Finally, relationships among our samples of the Tyranni, excepting *Acanthisitta*, were perfectly congruent with those recovered by Sibley & Ahlquist (1985*b*, 1990) and largely congruent with a recent analysis of RAG-1 and c-*myc* in suboscines (Irestedt *et al.* 2001). This included both monophyly of the New and Old World suboscine groups and relationships among the New World suboscines. In addition, our study included a sample of the endemic Malagasy family Philepittidae (*Philepitta*), unavailable to Sibley & Ahlquist (1990). In agreement with morphological analyses, we found *Philepitta* to be associated with (as suggested by Olson 1971; Raikow 1987) and more specifically nested within (in agreement with Prum 1993; *contra* Raikow 1987) the Eurylaimidae (represented here by *Smithornis* and *Psarisomus*). Our analysis did not include *Calyptomena*, as did that of Irestedt *et al.* (2001), so we cannot confirm its placement relative to *Smithornis*; however, our data clearly support paraphyly of the traditional Eurylaimidae with respect to the Philepittidae.

(b) *Historical biogeographic implications*

Based upon molecular clock estimates, the order Passeriformes may have arisen as early as the late Cretaceous (Cooper & Penny 1997; Van Tuinen & Hedges 2001) and standing diversity is hypothesized to include lineages that diverged not long after its origin (77.1 ± 11.6 Myr ago; Van Tuinen & Hedges 2001). The oldest fossils attributed to the order are Gondwanan, from the Early Eocene of Australia (Boles 1995, 1997). Conversely, the earliest fossil passerines from Laurasian continents are Late Oligocene in age (Olson 1985). The timing of passerine diversification, the temporal and geographic distribution of fossils and geographic distribution of the basal passerine lineages, have all suggested a Gondwanan origin for the passerines as a whole (Feduccia & Olson 1982; Schodde 1991; Cracraft 2001; Irestedt *et al.* 2001). The relationships among passerine birds we have inferred here support this notion (and numerous previous studies) by implying deep divergences among groups now isolated on Gondwanan elements (e.g. New World suboscines in South America, the Acanthisittidae in New Zealand and the Menuridae in Australia). Here, we strengthen this argument by offering phylogenetic evidence that a now widespread and numerically dominant passerine clade, the oscine passerines, had its origin on a single Gondwanan component.

Sibley (1976) and Sibley & Ahlquist (1985*a*, 1990) postulated that Australia was colonized by one or a few oscine lineages, which founded an endemic continental radiation (the parvorder Corvida). Our phylogenetic hypothesis

suggests a different scenario. If the Passerida are nested within a grade of 'Corvidan' lineages, the most basal of which are all endemic to the Australo–Papuan region, then an Australo–Papuan origin of oscine passerines becomes parsimonious (figure 2, table 3). In this scenario, diversification of the primarily northern suborder Passerida, as well as of some 'corvidan' lineages (portions of the 'core Corvoidea'; figure 2), has resulted from dispersal and massive radiation of an ancestrally Australo–Papuan endemic clade, the oscine passerines, possibly triggered by the end of the island continent's isolation in the late Oligocene (*ca.* 25 Myr ago; Stevens 1991; Hall 1998). The fact that lineages that dispersed northward differ significantly in their standing levels of diversity is intriguing. Specifically, the Passerida are much more diverse than the sum of all 'corvidan' lineages which are northern in distribution, or have representatives in both the north and the south (figure 2). This could be attributable to the relative timing of dispersal of these lineages (e.g. an earlier dispersal of Passerida), or to differences in speciation or extinction rates related to lineage-specific characteristics (e.g. mating systems; Barraclough *et al.* 1995). Due to violation of the molecular clock, more sophisticated analyses (e.g. Huelsenbeck *et al.* 2000; Yoder & Yang 2000) of the data reported here will be necessary to clarify the timing of passerine radiations and thus begin to test these alternative hypotheses.

A variety of phenotypic characteristics of passerines have been invoked singly, or in combination, to explain their extreme diversity relative to other avian groups (Raikow 1986; Fitzpatrick 1988; Kochmer & Wagner 1988; Vermeij 1988; Baptista & Trail 1992; Barraclough *et al.* 1995; Collias 1997; Raikow & Bledsoe 2000). The analyses we have presented here suggest that extrinsic processes must be taken into account when explaining passerine diversity (see also Cotgreave & Harvey 1994; Cracraft 2001). All of the basal lineages of oscines, in addition to being Australo–Papuan in distribution, are species-poor relative to more recently derived groups (especially the Passerida, figure 2). This suggests that much of the asymmetry in species diversity is not between passerines and their non-passerine sister taxa, but between different lineages of passerines (as suggested by Raikow 1986). Based upon our biogeographic reconstructions, this asymmetry may be attributable not only to opportunistic diversification enabled by adaptation, but also to spatio-temporal limitations on diversification imposed by earth history.

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APPENDIX A

The taxa and specimens included in this study, following the higher-level passerine sequence of Sibley & Monroe (1990) and specific nomenclature of Morony *et al.* (1975). (Outgroup taxa (and samples) for this study were as follows: *Gallus gallus* (courtesy M. Zuk, University of California, Riverside), *Coracias caudata* (AMNH 22703) and *Apus affinis* (AMNH 22956).) The voucher data are in parentheses after each species. Abbreviations: AM, Australian Museum; AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; BPBM, Bernice Pauahi Bishop Museum; CSIRO, Australian National Wildlife Collection, Commonwealth Scientific and Industrial Research Organization; FMNH, Field Museum of Natural History; MVZUC, Museum of Vertebrate Zoology, University of Copenhagen; QM, Queensland Museum of Natural Environment and Cultural Heritage; ROM, Royal Ontario Museum; UKNHM, University of Kansas Natural History Museum; UWBM, University of Washington, Burke Museum; ZSSD, Zoological Society of San Diego (accession refers to a necropsied captive specimen); NA, not accessioned; DA, deaccessioned; UV, unvouchered, institutional origin of sample is given; collectors' numbers indicated in brackets.

Acanthisitta chloris (ROM UV [RIF002]), *Pitta guajara* (AMNH 22995), *Smithornis rufolateralis* (AMNH 827484), *Psarisomus dalhousiae* (AMNH 22993), *Philepitta castanea* (FMNH 345690), *Tyrannus tyrannus* (AMNH 24560), *Rupicola rupicola* (AMNH 22747), *Pipra coronata* (AMNH 9360), *Thamnophilus nigrocinereus* (AMNH 18074 DA), *Furnarius rufus* (AMNH NA [PRS1836]), *Formicarius colma* (AMNH 9343), *Climacteris picumnus* (UWBM 57695), *Menura novaehollandiae* (CSIRO 43660), *Ptilonorhynchus violaceus* (QM 3119), *Malurus melanocephalus* (AM [Lab 1109]), *Meliphaga analoga* (UKNHM UV [AM983]), *Pardalotus striatus* (AM [FB1062]), *Tregellasia leucops* (BPBM [AM819]), *Irena cyanogaster* (FMNH 350955), *Chloropsis cochinchinensis* (AMNH 22997 DA), *Orthonyx spaldingii* (CSIRO 34489), *Pomatostomus isidorei* (BPBM [AM890]), *Lanius ludovicianus* (AMNH 13207), *Vireo philadelphia* (AMNH 24546), *Pachycephala soror* (BPBM [AM804]), *Corvus corone* (AMNH 24068), *Paradisaea raggiana* (ZSSD AO48924), *Artamus leucorhynchus* (FMNH 345096), *Oriolus larvatus* (AMNH 25750), *Coracina lineata* (AMNH 23412), *Dicrurus adsimilis* (AMNH 25749), *Monarcha axillaris* (BPBM [AM838]), *Aegithina tiphia* (AMNH 22963), *Vanga curvirostris* (FMNH 352878), *Picathartes gymnocephalus* (AMNH 827716), *Bombycilla garrulus* (AMNH UV [PRS1417]), *Cinclus cinclus* (AMNH NA [PRS2328]), *Turdus falklandii* (AMNH NA [PRS1825]), *Muscicapa strophiata* (AMNH 23274), *Sturnus vulgaris* (FMNH 389606), *Mimus patagonicus* (AMNH NA [PRS1711]), *Sitta pygmaea* (FMNH 343324), *Certhia familiaris* (FMNH 351158), *Troglodytes aedon* (FMNH 343273), *Parus inornatus* (AMNH 23656), *Aegithalos*

iouschensis (AMNH 831357), *Hirundo pyrrhonota* (AMNH 23653), *Regulus calendula* (AMNH 24545), *Pycnonotus barbatus* (AMNH 24822), *Cisticola anonymus* (AMNH 832156), *Zosterops senegalensis* (FMNH 346671), *Garrulax milleti* (AMNH 833160), *Sylvia nana* (AMNH 23211), *Alauda arvensis* (AMNH NA [PRS2316]), *Dicaeum melanoxanthum* (AMNH 23295), *Nectarinia olivacea* (AMNH 831874), *Melanocharis nigra* (BPBM [AM964]), *Toxorhamphus novaeguineae* (BPBM [AM894]), *Oedistoma iliolophum* (BPBM [AM956]), *Passer montanus* (AMNH 22967), *Motacilla cinerea* (UWBM 46534), *Prunella collaris* (AMNH 831301), *Ploceus cucullatus* (AMNH 831877), *Fringilla montifringilla* (ROM UV [MKP1553]), *Emberiza schoeniclus* (MVZUC O480), *Parula americana* (AMNH UV [PRS152]), *Thraupis cyanocephala* (AMNH 24097), *Cardinalis cardinalis* (AMNH 23188), *Icterus parisorum* (AMNH 832513).

APPENDIX B

A summary of nodal support for trees obtained in combined parsimony and likelihood analyses. Nodal numbers (referring to numbering in figure 1) are followed in parentheses by the following values for that node: parsimony bootstrap (RAG-1), parsimony bootstrap (c-*mos*), parsimony bootstrap (combined analysis), maximum-likelihood bootstrap (combined analysis) and partitioned Bremer support (RAG-1/c-*mos*). Daggers indicate bootstrap values $\leqslant 10\%$. All percentages (and daggers) in plain typeface indicate presence of the node in the strict consensus of optimal trees from the corresponding analysis, whereas values in bold indicate nodes found in at least one optimal tree but not in the strict consensus and values in italics indicate nodes not occurring in any optimal tree for that analysis.

1 (83, *11*, 52, 79, 6/–5), 2 (97, 47, 99, 100, 10.1/3.9), 3 (90, **16**, 93, 80, 6/–1), 4 (96, 28, 99, 100, 12/–2), 5 (96, 53, 100, 100, 14/6), 6 (62, *40*, 60, 51, 2/0), 7 (100, 65, 100, 100, 13/2), 8 (98, †, 97, 98, 5/0), 9 (100, 90, 100, 100, 15/8), 10 (84, †, 82, 90, 4/0), 11 (100, 53, 100, 100, 16/5), 12 (92, 43, 96, 96, 6/2), 13 (100, 74, 100, 100, 25.1/6.9), 14 (44, 22, 65, 76, 3/–1), 15 (79, 52, 97, 62, 4.6/3.4), 16 (96, 14, 100, 100, 5.9/5.1), 17 (99, †, 97, 100, 8.8/2.2), 18 (73, †, 64, 80, 3.8/–1.8), 19 (†, †, 44, †, 0.4/1.6), 20 (38, †, 36, *26*, 2.4/–1.4), 21 (100, 36, 100, 100, 13.8/5.2), 22 (87, *32*, 83, 82, 4.9/–0.9), 23 (62, †, 78, 94, 5.1/–1.1), 24 (32, †, 33, *25*, 3.1/–2.1), 25 (29, †, 20, *14*, 3.1/–2.1), 26 (13, †, 12, *11*, 1.1/–0.1), 27 (31, †, 30, *17*, 0.3/0.7), 28 (73, 5, 83, 95, 5.9/–0.9), 29 (59, †, 58, 74, 2/–1), 30 (49, †, 52, 64, 2/0), 31 (87, †, 91, 99, 5/1), 32 (71, 29, 90, 94, 4.7/2.3), 33 (58, 18, 63, 62, 1.1/0.9), 34 (60, †, 66, 90, 4.6/0.4), 35 (†, †, †, 24, 0.7/0.3), 36 (†, †, †, †, 1.8/–0.8), 37 (*19*, †, 21, †, 0.5/1.5), 38 (24, †, 34, 57, 3.4/–1.4), 39 (75, †, 91, 99, 5.9/5.1), 40 (76, 83, 98, 97, 3.7/5.3), 41 (32, †, 33, *13*, 2/–1), 42 (55, 29, 90, 86, 3.7/5.3), 43 (52, †, 68, 80, 1.8/2.2), 44 (39, †, 48, *32*, 3.6/–1.6), 45 (*11*, †, 14, †, 1.9/–0.9), 46 (†, †, 26, *22*, 0.6/0.4), 47 (73, 41, 88, 91, 7.3/1.7), 48 (100, †, 99, 100, 14.1/–2.1), 49 (27, †, 34, *13*, 0.4/0.6), 50 (*14*, 39, 28, *28*, 0.4/0.6), 51 (80, **19**, 87, 99, 2.7/2.3), 52 (99, **32**, 99, 100, 5.6/1.4), 53 (72, †, 62, 81, 1.6/–0.6), 54 (98, †, 87, 87, 6.2/–1.2), 55 (15, †, †, 16, 0.4/0.6), 56 (39, †, 38, 34, 3.6/–0.6), 57 (92, †, 88, 97, 7.6/–0.6), 58 (26, †, 61, 44, 4.1/–1.1), 59 (45, †, 62, 71, 4.2/–2.2), 60 (**51**, 36, 67, 85, 0/2), 61 (68, *15*, 63, 80, 1.7/0.3), 62 (†, 21, 68, *50*, 0/4), 63 (23, 27, 73, 53, 2.9/2.1), 64 (*23*, *15*, *47*, 48, N/A), 65 (*26*, †, *13*, 54, N/A), 66 (37, †, *29*, 48, N/A), 67 (†, †, †, 26, N/A), 68 (†, †, *11*, 32, N/A), 69 (*14*, †, *16*, 25, N/A), 70 (†, †, †, †, N/A), 71 (†, †, †, 15, N/A), 72 (*12*, †, *30*, 38, N/A), 73 (*12*, †, *19*, 38, N/A), 74 (*29*, †, *30*, 62, N/A), 75 (*22*, †, *15*, 44, N/A), 76 (*22*, †, *16*, 39, N/A), 77 (†, †, *23*, 28, N/A), 78 (*16*, †, *16*, 23, N/A), 79 (*36*, †, *27*, 29, N/A), 80 (*23*, †, †, 27, N/A), 81 (*24*, †, *18*, 34, N/A), 82 (**59**, †, **49**, 46, N/A).

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