

# A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens

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Zoogeographic, palaeontological and biochemical data support a Southern Hemisphere origin for passerine birds, while accumulating molecular data suggest that most extant avian orders originated in the mid-Late Cretaceous. We obtained DNA sequence data from the nuclear *c-myc* and RAG-1 genes of the major passerine groups and here we demonstrate that the endemic New Zealand wrens (Acanthisittidae) are the sister taxon to all other extant passerines, supporting a Gondwanan origin and early radiation of passerines. We propose that (i) the acanthisittids were isolated when New Zealand separated from Gondwana (*ca.* 82–85 Myr ago), (ii) suboscines, in turn, were derived from an ancestral lineage that inhabited western Gondwana, and (iii) the ancestors of the oscines (songbirds) were subsequently isolated by the separation of Australia from Antarctica. The later spread of passerines into the Northern Hemisphere reflects the northward migration of these former Gondwanan elements.

**Keywords:** biogeography; Gondwana; New Zealand wrens; Passeriformes; phylogenetic analysis; avian systematics

## 1. INTRODUCTION

The New Zealand wrens are an enigmatic group of passerines (Raikow 1982), which appear intermediate between the oscines and suboscines, the two major groups of passerine birds (Müller 1847). The two extant taxa (rifleman, *Acanthisitta chloris* and rock wren, *Xenicus gilviventris*) are remnants of an endemic radiation that included at least seven taxa, several of which are assumed to have been flightless (Sibley *et al.* 1982; Millener 1988). Ancient DNA studies indicate that the extant and recently extinct members are genetically close, possibly as the result of a bottleneck during a marine transgression in the Oligocene period (Cooper 1994; Cooper & Cooper 1995).

The oscines and suboscines can be separated, in cladistic terms, by the derived, complex anatomy of the syrinx in oscines (Forbes 1882; Ames 1971) and the unique, bulbous columella in suboscines (Feduccia 1975). The New Zealand wrens cannot be allocated to either group, as they possess the primitive states for both of these characters. Myological data support an oscine affinity on the basis of a single character: the shared loss of the distal belly of one flexor muscle in the leg (Raikow 1987). Although DNA–DNA hybridization data indicate a sister-group relationship between New Zealand wrens and the suboscines (Sibley & Ahlquist 1990), this is not consistent with egg-white protein data (Sibley 1970). Recently, nuclear *c-mos* sequence studies failed to clarify the relationships between oscines, suboscines and New Zealand wrens (Lovette & Bermingham 2000).

Suboscine birds are currently most numerous in South and Central America (a few genera have spread to North America, probably after the formation of the Panama isthmus (*ca.* 3–5 Myr ago)) and also inhabit tropical areas of southeast Asia, Madagascar and Africa. The New World and Old World groups of suboscines are monophyletic sister lineages (Sibley & Ahlquist 1990; Irestedt *et al.* 2001).

The oscine passerines have been divided by DNA–DNA hybridization data into the major groups Corvida and Passerida (Sibley & Ahlquist 1990), with the former centred in Australasia and the latter in the Old World and North America. The monophyly of the Passerida is supported by a synapomorphic insertion of one amino acid in the nuclear *c-myc* gene sequence (Ericson *et al.* 2000), while the monophyly of Corvida remains to be verified by independent data.

DNA–DNA hybridization data (Sibley & Ahlquist 1990) also suggest that the Corvida comprises three superfamilies of which Menuroidea is basal to Meliphagoidea and Corvoidea. The first two superfamilies only inhabit the Australo–Papuan region, while several members of the Corvoidea have dispersed from this region to radiate out into other parts of the world (e.g. crows and jays, drongos, shrikes).

The Passerida is traditionally considered to include two major oscine radiations, the ‘Old World insect eaters and their relatives’ and ‘New World insect eaters and finches’ (Mayr & Greenway 1956; Voous 1985), of which the latter roughly corresponds to the superfamily Passeroidea (*sensu* Sibley & Ahlquist 1990). Within Passeroidea, the two most speciose families are the Emberizidae, centred

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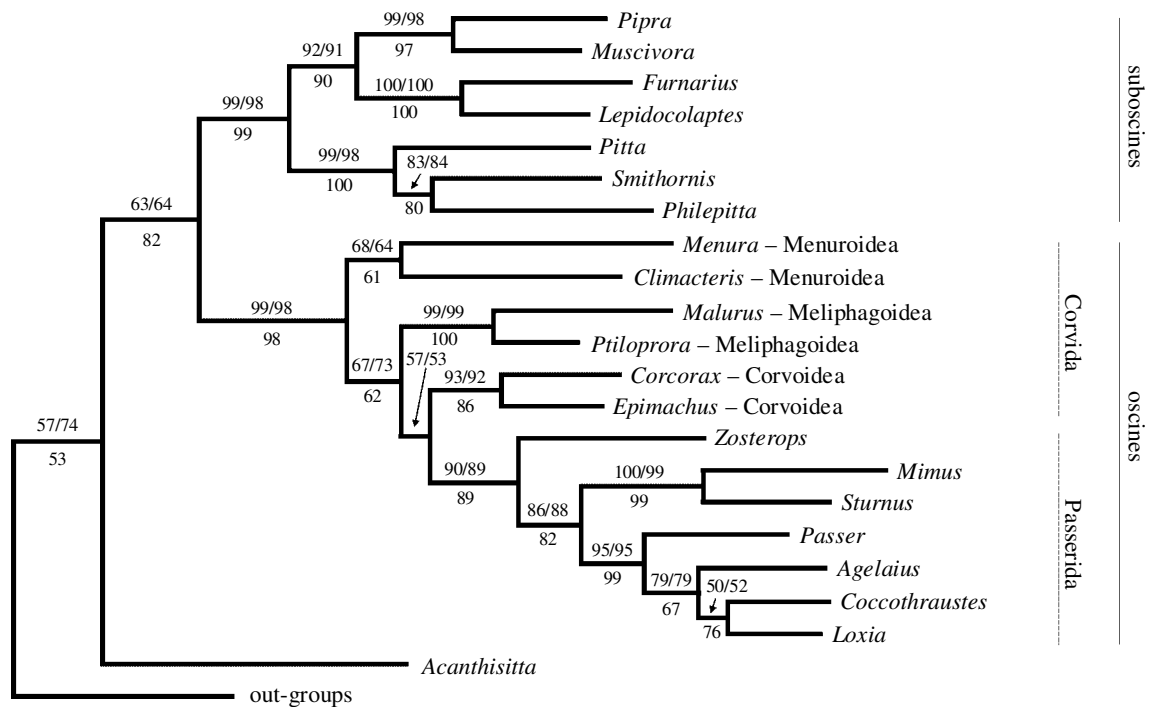


Figure 1. Phylogenetic relationships among major groups of passerine birds based on 1407 bp of nucleotide sequence data derived from two nuclear protein-coding genes, using 21 non-passerine taxa as out-groups. The tree shown is the ML tree, and is identical to one of the two most parsimonious trees found. The other most parsimonious tree differs only in the interrelationships of *Agelaius*, *Coccothraustes* and *Loxia*. The tree topology is similar to that based on DNA–DNA hybridization distances (Sibley & Ahlquist 1990), except for the basal position of the New Zealand wrens and the paraphyly of the Corvida relative to the Passerida. Branch lengths are proportional to the estimated genetic distances. Bootstrap values are given above branches for the MP analyses (1000 replicates); dataset with many non-passerine out-groups (left) and with *Amazonetta*, *Corythaixoides*, *Cuculus*, *Gallus*, *Heliomaster*, *Momotus* and *Picumnus* as out-groups (right). Bootstrap values for the ML analysis (1000 replicates) for the latter dataset are shown below the branches.

in the New World, and the Fringillidae, primarily distributed in the Old World. The emberizids and fringillids are considered to be sister taxa.

A vicariant origin for the passerines has been proposed from biogeographic and phylogenetic data, based on the break up of the Cretaceous super-continent Gondwana (Cracraft 1973, 2001). This is supported by recent molecular evidence, which suggests that extant avian orders diverged in the Early–Mid Cretaceous (Sibley & Ahlquist 1990; Hedges *et al.* 1996; Cooper & Penny 1997; Cooper *et al.* 2001; Van Tuinen & Hedges 2001). In contrast, a literal interpretation of the palaeontological record has been used to support a Tertiary origin for all modern avian orders (Feduccia 1996).

To investigate these issues, we sequenced 1428 bp (1407 bp aligned sequence) of two protein-coding nuclear genes; the proto-oncogene *c-myc* (498 bp) and the recombination-activating gene *RAG-1* (930 bp), for the rifleman (*A. chloris*) and a selection of passerine and non-passerine birds. Parsimony and maximum-likelihood (ML) analyses were used to analyse the phylogenetic relationships within the major groups of passerines and the relationships with Gondwanan biogeographic events.

## 2. MATERIAL AND METHODS

The sequences of the following in-group taxa were analysed (sample identification and GenBank accession numbers in parentheses): Acanthisittidae: *Acanthisitta chloris*

(AY037838, AY037845), Dendrocolaptidae: *Lepidocolaptes angustirostris* (NRM 937184, AF295168, AF295190), Furnariidae: *Furnarius cristatus* (NRM 966772, AF295165, AF295187), Tyrannidae: *Muscivora tyrannus* (NRM 976722, AF295182, AF295203), Pipridae: *Pipra fasciicauda* (NRM 947271, AF295175, AF295196), Pittidae: *Pitta angolensis* (ZMCU S1027, AF295176, AF295197), Eurylaimidae: *Smithornis rufolateralis* (FMNH 391675, AF295179, AF295200), Philepittidae: *Philepitta castanea* (ZMCU S458, AF295172, AF295193), Menuridae: *Menura novaehollandiae* (AM LAB1112, AF295169, AF295191), Climacteridae: *Climacteris rufa* (MV 155, AY037839, AY037846), Maluridae: *Malurus amabilis* (MV C803, AY037840, AY037847), Meliphagidae: *Ptiloprora plumbea* (MV C173, AY037841, AY037848), Corcoracidae: *Corcorax melanoramphos* (AM LAB1059, AY037842, AY037849), Paradisaeidae: *Epimachus albertsii* (MV C148, AF377278, AY037850), Zosteropidae: *Zosterops nigrorum* (ZMCU O2663, AY037843, AY037851), Mimidae: *Mimus saturinus* (NRM 966912, AF377265, AY037852), Sturnidae: *Sturnus vulgaris* (NRM 966615, AF377264, AY037853), Passeridae: *Passer montanus* (NRM 976359, AF295171, AF143738), Icteridae: *Agelaius cyanopus* (NRM 966916, AF377253, AY037854), Fringillidae: *Coccothraustes coccothraustes* (NRM 976374, AY037844, AY037855) and *Loxia curvirostra* (NRM 976546, AF377257, AY037856). Abbreviations: AM, Australian Museum, Sydney; FMNH, Field Museum of Natural History, Chicago; MV, Museum Victoria, Melbourne; NRM, Swedish Museum of Natural History, Stockholm; ZMCU, Zoological Museum of the University of Copenhagen.

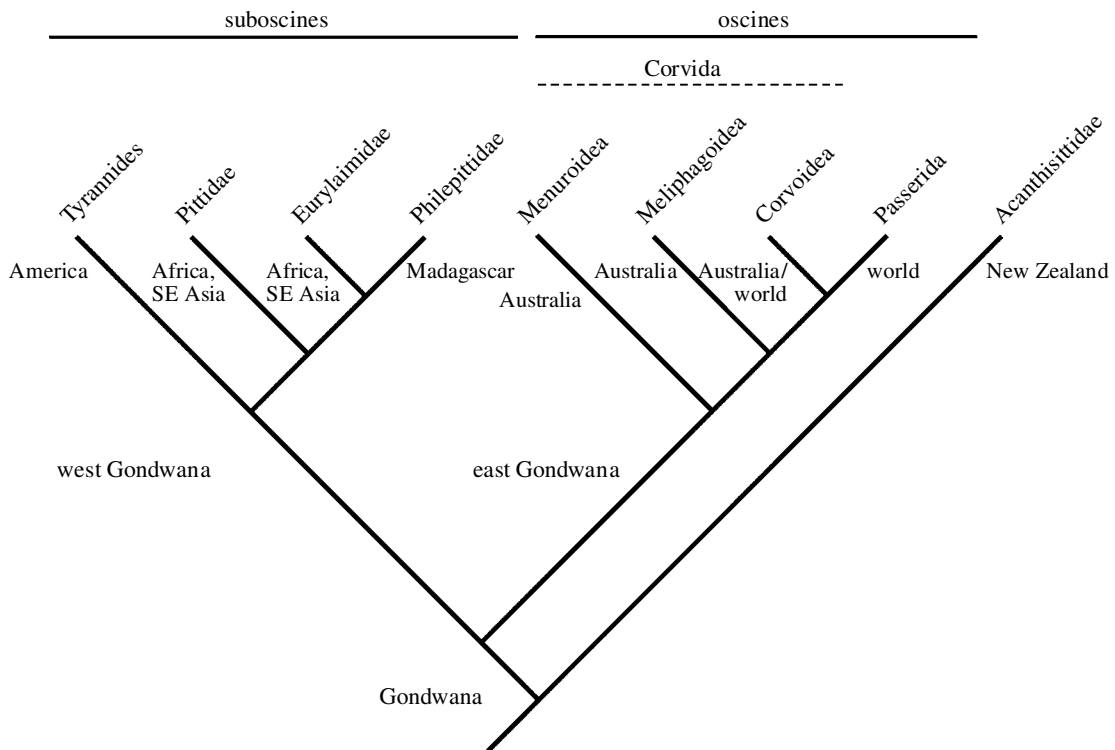


Figure 2. Cladogram of major groups of passerines based on the phylogenetic analysis presented in figure 1. Present geographical distributions of the clades are indicated on the terminal branches. Hypothetical ancestral distributions are marked on the nodes and basal branches, suggesting a Gondwanan origin of passerine birds.

To analyse the early evolutionary events within passerines it is important to locate appropriate out-groups, as alternative placements of the root to the passerine clade could support either an oscine or suboscine relationship of the New Zealand wrens. Although the sister taxon of the passerines is unknown, it is commonly believed to be found among the group of taxa referred to as the Anomalognatae (Johansson *et al.* 2001). Twenty-one species, representing 16 out of 28 families in this assemblage, were included in the analyses: Apodidae: *Apus apus*; Bucconidae: *Bucco capensis*; Caprimulgidae: *Eurostopodus macrotis*, *Podager nacunda*; Coraciidae: *Coracias caudata*; Cuculidae: *Cuculus canorus*; Galbulidae: *Galbula cyanescens*; Hemiprocnidae: *Hemiprocne longipennis*; Momotidae: *Momotus momota*; Musophagidae: *Corythaixoides leucogaster*; Nyctibiidae: *Nyctibius aethereus*; Picidae: *Dendrocopos major*, *Picumnus cirratus*; Podargidae: *Podargus strigoides*; Steatornithidae: *Steatornis caripensis*; Strigidae: *Asio flammeus*, *Glaucidium brasilianum*; Trochilidae: *Heliomaster furcifer*, *Hylocharis chrysura*, *Phaethornis pretrei*; and Trogonidae: *Harpactes diardii*. Trees were rooted with two galliform species (Megapodiidae: *Alectura lathamii*; Phasianidae: *Gallus gallus*) and one anseriform species (Anatidae: *Amazonetta brasiliensis*, AF427042, AY034411), as these two orders are thought to constitute the sister group to all other neognathous birds (Groth & Barrowclough 1999; Van Tuinen *et al.* 2000). All non-passerine sequences, except for the anatid, are already published (Irestedt *et al.* 2001; Johansson *et al.* 2001) and deposited in GenBank.

Laboratory procedures for the extraction of DNA, PCR amplification, and sequencing of the protein-coding nuclear genes *c-myc* and *RAG-1* are described elsewhere (Ericson *et al.* 2000; Irestedt *et al.* 2001).

The data were analysed using maximum parsimony (MP) and ML criteria using PAUP\* 4.0b8 (Swofford 1998). Genetic dis-

tances (uncorrected *p*-distances) were calculated using the combined dataset of 1407 bp. Unweighted MP analyses were performed using tree bisection-reconnection (TBR) branch swapping and the heuristic search option with 10 random additions of taxa. ML trees were also found using TBR branch swapping and the heuristic search option but with estimates of nucleotide substitutions, invariant sites and gamma parameters initially calculated from a neighbour-joining (NJ) tree. The general time reversible (GTR) model of nucleotide substitutions was applied with a discrete gamma model (four rate categories) and estimates of the number of invariable sites, while alternative tree topologies were statistically tested using the Shimodaira-Hasegawa test (Shimodaira & Hasegawa 1999). GTR values, invariant sites and gamma parameters were estimated independently for each of the alternative likelihood trees.

Support for the MP and ML trees was assessed using 1000 bootstrap replicates. ML bootstraps were performed using a distance matrix incorporating the previously estimated parameters for GTR, invariant sites and gamma values. As bootstrapping under the ML criterion is impractical for large datasets, a subset of the out-group taxa was used. Seven taxa (*Amazonetta*, *Cuculus*, *Gallus*, *Heliomaster*, *Momotus*, *Picumnus* and *Corythaixoides*) were randomly selected from the original 21 out-groups, based on their wide distribution across the ML tree. For comparative purposes, bootstrap values were also calculated for a MP analysis of this restricted dataset.

Molecular divergence date estimates were made from the ML tree (obtained incorporating the models described above), by quartet analysis in RHINO, a modified version of the QDATE program (Rambaut & Bromham 1998) previously used by Cooper *et al.* (2001). The RHINO program allows for rate heterogeneity in different parts of the ML tree during the estimation procedure. The geologically dated minimum age (82 Myr ago) for

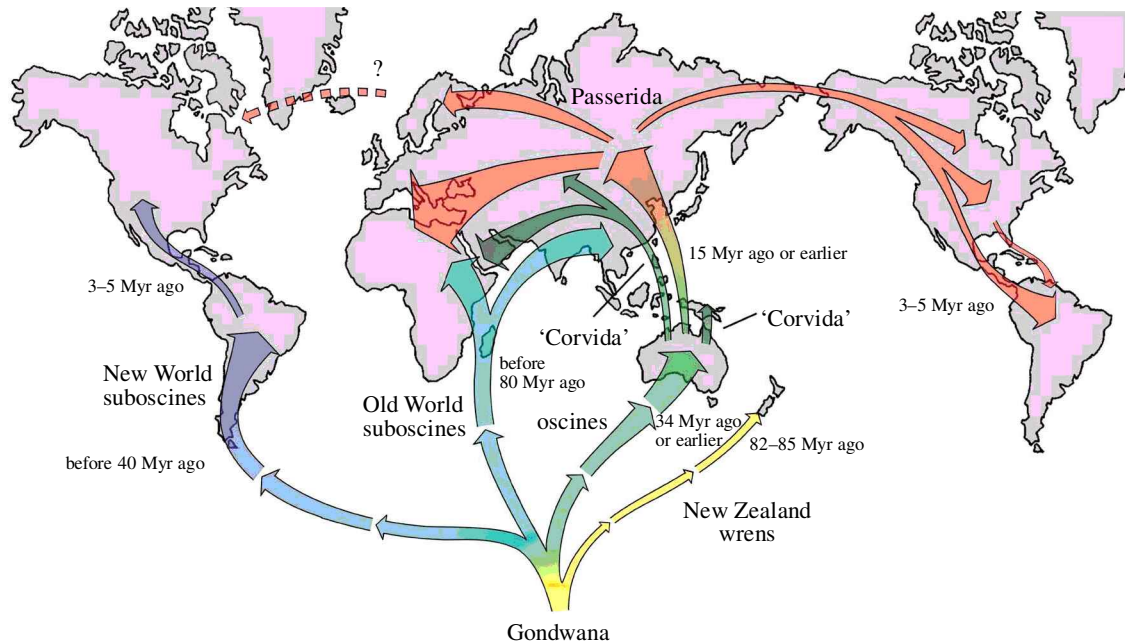


Figure 3. Suggested dispersal routes of major passerine groups from Gondwana based on phylogenetic and biogeographic data. The southern continents are shown in their current position, with Gondwana as a central southern origination point for clarity. The basal position of the New Zealand wren lineage is consistent with isolation following the separation of New Zealand from Antarctica (82–85 Myr ago). The oscines appear to have radiated in Australia and spread northwards after the collision with the southeast Asian plate, facilitating the dispersal of oscine groups throughout the world. Representatives of the speciose Passerida radiation reached the Americas, probably via the Bering Land Bridge, which has been intermittently available since the Late Cretaceous. Prior to the end of the Eocene, passerines could also have used Greenland to disperse from Europe to North America. The ancestor of the New World suboscines probably reached South America before this continent separated from Antarctica (*ca.* 40 Myr ago). The group presumably dispersed to Central and North America after the formation of the Panamanian Isthmus (3–5 Myr ago). The early separation of South America and Africa (90 Myr ago) makes it unlikely that passerines used this route for dispersal. Instead, the Old World suboscines may have spread from Gondwana to Africa/Asia via the now submerged Kerguelen Plateau (which was connected to Madagascar and the Indian plate). The citation marks for Corvida indicate the possible paraphyly of this taxon.

the separation of New Zealand from Australia/Antarctica (Cooper & Millener 1993) was used as a calibration point for the separation of the acanthisittids from the rest of the passerines. Confidence intervals were obtained using likelihood-ratio testing incorporating uncertainties in the substitution process and phylogenetic reconstruction (Rambaut & Bromham 1998).

### 3. RESULTS

The phylogenetic analyses place the suboscine and oscine passerines into separate clades, with *Acanthisitta* as their sister taxon (figure 1). This result is obtained in both ML and MP analyses irrespective of the taxa used as out-groups and the bootstrap values were also similar. The only ambiguity in the dataset concerns the internal relationships between *Agelaius*, *Coccothraustes* and *Loxia*, which resulted in two most parsimonious trees. The oscines and suboscines both form highly supported monophyletic groups separated from *Acanthisitta* by a long branch, indicating a considerable evolutionary distance. *Acanthisitta* takes a basal position both in the most parsimonious trees and in the ML tree, although constraining *Acanthisitta* to fall with either suboscines or oscines produces some trees which are only a few steps longer, or are not significantly worse (table 1).

The clades of suboscines from the New World (*Pipra*, *Muscivora*, *Furnarius* and *Lepidocolaptes*) and the Old World (*Pūta*, *Smithornis* and *Philepūta*) are both strongly

supported by the bootstrap analyses. Internal relationships in these clades agree with previous studies that used additional taxa (Irestedt *et al.* 2001).

Among the oscines, analyses recovered three clades corresponding to the superfamilies in the parvorder Corvida: Menuroidea (*Menura* and *Climacteris*), Meliphagoidea (*Ptiloprora* and *Malurus*) and Corvoidea (*Epimachus* and *Corcorax*) with Menuroidea basal. The Passerida taxa (i.e. *Zosterops*, *Mimus*, *Sturnus*, *Passer*, *Agelaius*, *Coccothraustes* and *Loxia*) form a fourth clade, which is weakly supported as the sister to the Corvoidea clade. The latter four passerida genera are members of the superfamily Passeroidea, which was also shown to be monophyletic in the analysis. Within Passeroidea, a sister-group relationship between emberizids (represented by *Agelaius*) and fringillids (*Coccothraustes* and *Loxia*) is supported by the data. The MP analysis is unable to resolve this clade, presumably due to the small genetic distances that separate these taxa (1.6–2.2%). All passerine clades are supported in the bootstrap analyses, and in most cases with large bootstrap values.

### 4. DISCUSSION

The *c-myc* and RAG-1 sequence data support the placement of the New Zealand wrens as the basal member of the passerine clade and the sister taxon to the suboscine and oscine groups (figure 1). This phylogenetic arrange-

Table 1. MP and ML analyses of alternative phylogenetic positions of the rifleman *Acanthisitta*.

Tree lengths, number of trees, and tree fit statistics (CI, confidence index; RI, retention index) are given for the MP analyses. For the ML analyses, tree fit statistics and the results of the Shimodaira–Hasegawa test of competing tree topologies are presented. The resampling estimated log-likelihoods method was used with 1000 bootstrap replicates to compute the ML trees. *p* indicates the probability of obtaining the tree topology stated under the null hypothesis of no difference between this and the ML tree. ‘all out-groups’ denotes that all 21 non-passerine taxa were used in the analyses, while ‘selected out-groups’ indicates that the *Amazonetta*, *Gallus*, *Helimaster*, *Corythaixoides*, *Corythocoides*, *Momotus*, *Cuculus* and *Picumnus* subset was used. The trees were constrained in each case as shown and GTR values, invariant sites and gamma parameters were estimated independently for each tree. diff.  $-\ln L$ , difference in log-likelihood between the ML tree and each alternative topology.

placement of <i>Acanthisitta</i>	MP					ML	
	length	no. of MP trees	CI	RI	$-\ln L$	diff. $-\ln L$	<i>p</i>
all out-groups							
basal position	1717	2	0.45	0.55	10760.6274		(best)
in suboscine clade	1718	2	0.45	0.55	10765.9658	5.3384	0.165
in oscine clade	1720	2	0.45	0.55	10767.4382	6.8108	0.092
selected out-groups							
basal position	1057	2	0.56	0.53	7381.3997		(best)
in suboscine clade	1059	4	0.56	0.53	7385.8114	4.4117	0.156
in oscine clade	1061	2	0.56	0.53	7386.2900	4.8903	0.105

Table 2. Estimated divergence times between major clades of passerines calculated from the ML tree. The calibration used the minimum geological separation of New Zealand and Australia/Antarctica at 82 Myr ago for the separation of the acanthisittid lineage from the other passerines. Confidence intervals are estimated as described elsewhere (Rambaut &amp; Bromham 1998).

calibration point <i>Acanthisitta</i> versus other passerines	suboscines versus oscines	New World suboscines versus Old World suboscines	Tyrannoidea versus Furnarioidea	Menuroidea versus rest of oscines
82	71 (78.7–62.5)	53 (62.2–43.8)	45 (55.3–36.3)	53 (61.4–44.4)

ment and the large evolutionary separation of the wrens is consistent with the early separation of New Zealand from the remnant Gondwana landmass (82–85 Myr ago), supporting a vicariant origin for passerines. Similar genetic patterns have previously been linked to vicariant speciation of other New Zealand endemic avifauna (Cooper *et al.* 2001). If the minimum age for the geological separation is used as a calibration point, the estimated divergence dates for the major clades of passerines are Late Cretaceous (table 2) with suboscines and oscines diverging at *ca.* 71 Myr ago (78.7–62.5 Myr ago), considerably before traditionally thought (e.g. Feduccia 1995, 1996).

The suboscine clade is widely distributed throughout the southern continents and southeast Asia, with the exception of the Australo–Papuan region where they are only represented by a few species of pittas, thought to have colonized the region from the north (Sibley & Ahlquist 1985). Botanical evidence shows that floral exchange between Australia/New Guinea and southeast Asia was possible through much of the Late Tertiary (Morley 1998), and this interchange may also have included avifauna. A recent immigration to Australia is consistent with the lack of suboscines in the fossil record, although passerine fossils are not rare in deposits from the Eocene onwards (Boles 1995a, 1997). The single proposed suboscine fossil from Australia, a carpometacarpus from the Miocene (5–25 Myr ago) (Boles 1995b), may not be correctly assigned to this taxon (W. Boles, personal communication). Consequently, it appears that sub-

cines were not present in Australia at the time of biogeographic contact with southeast Asia, either because they had become extinct previously, or had not inhabited the area.

If suboscines did not enter southeast Asia from Australia, it is possible that they may have spread there from Gondwana via known Late Cretaceous dispersal routes such as the Kerguelen Plateau/Indo–Madagascar, or South America/Africa (Cooper *et al.* 2001). Alternatively, the monophyletic Old and New World suboscine clades may represent independent radiations after the separation of Africa and South America (*ca.* 90 Myr ago). To resolve this issue, further sequence data is required to identify the basal taxa within each of these groups, as current morphological data are ambiguous (Prum 1993; Cracraft 2001).

The division of the oscines into the major groups Corvida and Passerida, as suggested by DNA–DNA hybridization data (Sibley & Ahlquist 1990), is not supported by the sequence data. Instead the Passerida is found to be nested within the Corvida, possibly as the sister lineage to the superfamily Corvoidea (figure 1). Besides the Corvoidea, the two corvidan groupings Menuroidea and Meliphagoidea are also recognized in the present analysis, although only a few representatives of each group were included. A sister relationship between *Menura* and *Climacteris* has also been indicated from mitochondrial-DNA sequence data (Christidis *et al.* 1996).

Christidis & Schodde (1991) speculated that suboscines

radiated in western Gondwana (South America) and oscines radiated in eastern Gondwana (proto-Australasia). Figure 1 is consistent with an eastern Gondwanan oscine radiation because the basal lineages of oscines (Menuroidea and Meliphagoidea, figure 1) are confined to the Australo-Papuan region, while the Corvoidea have basal members in the Australo-Papuan region. This phylogeographic data (figure 2) suggests that oscines originated in eastern Gondwana and only subsequently spread to the Old World (figure 3).

The present data further suggest that the Passerida derive from an ancestor that dispersed from the Australo-Papuan region to southeast Asia, before spreading further and undergoing a significant diversification. According to DNA-DNA hybridization data (Sibley & Ahlquist 1990), the superfamily Passeroidea represents a comparatively late radiation within Passerida. Our data support this scenario as only small genetic distances were observed between the representatives of Emberizidae and Fringillidae. If the emberizids radiated in the New World, as suggested by their current distribution, then the ancestor of this clade must have migrated there from the Old World. This could have been either via the Bering land connection, which has been present intermittently since the Cretaceous, or via Greenland, which provided a route until around the end of the Eocene period (Cox & Moore 2000). The emberizids are very mobile and capable of crossing moderate gaps of water. It is possible that they began to disperse from North to South America via the Caribbean Plate before the two American continents became connected (3–5 Myr ago) (cf. Burns 1998).

The nuclear data presented here are consistent with a biogeographic scenario involving Late Cretaceous geological events and are therefore in agreement with current molecular estimates for the timing of evolution within the Neornithes (Hedges *et al.* 1996; Cooper & Penny 1997; Cooper *et al.* 2001; Van Tuinen & Hedges 2001). There is an apparent anomaly between these estimates and those based on the fossil record (Feduccia 1996), which is paralleled in other birds and mammals. The time of origin of the extant avian and eutherian mammal orders, as estimated from palaeontological data (e.g. Feduccia 1996; Benton 1999), are substantially younger than those indicated by molecular clock data (e.g. Kumar & Hedges 1998). If the molecular datings are correct, the fossil record of both birds and mammals is severely biased. However, taxonomic diversification need not necessarily be followed by rapid radiations of these new groups (Cooper & Fortey 1998) and birds and mammals may have existed in low numbers in the Cretaceous. The palaeontological data also suffer from depositional and geographical biases. For example, there is a growing body of evidence suggesting that birds, along with mammals, underwent major radiations within the southern continents and may have had their origins in Gondwana (e.g. Olson 1989; Cooper & Penny 1997; Rich *et al.* 1999; Madsen *et al.* 2001). The details of these radiations are difficult to correlate with the fossil record due to the fact that very few Paleogene bird faunas are known from the Southern Hemisphere (Cooper & Penny 1997; Cooper & Fortey 1998).

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Museum, Field Museum of Natural History, Zoological Museum of Copenhagen University, Museum of Victoria and the Swedish Museum of Natural History. The authors thank Trevor Worthy for his assistance in obtaining the *Acanthisitta* sample. Samples of non-passerines were provided by museums listed in Ericson *et al.* (2000) and Irestedt *et al.* (2001). The authors also thank Thomas J. Parsons for initial methodological assistance with *c-myc* sequences, Walter E. Boles for data on Australian fossil passerines, Maria Arvidsson for assistance in the laboratory and Andrew Rambaut for assisting with the maximum-likelihood analyses. Richard Prum and Jon Fjeldså suggested improvements on an earlier draft of this paper. Funding for this project was obtained from the Swedish Natural Science Research Council (grant no. B-AA/BU 01913-304 to P.E.), Magnus Bergvalls Stiftelse, Olle och Signhild Engkvists Stiftelser, the UK NERC (to A.C. and J.J.) and the Australian Research Council (grant no. A19331979 to L.C.).

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