

Evolution, biogeography, and patterns of diversification in passerine birds

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This paper summarizes and discusses the many new insights into passerine evolution gained from an increased general interest in avian evolution among biologists, and particularly from the extensive use of DNA sequence data in phylogenetic reconstruction. The sister group relationship between the New Zealand rifleman and all other passerines, indicates the importance of the former southern supercontinent Gondwana in the earliest evolution of this group. Following the break-up of Gondwana, the ancestors of other major passerine groups became isolated in Australia (oscines), South America (New World suboscines), and possibly, the then connected Kerguelen Plateau/India/Madagascar tectonic plates (Old World suboscines). The oscines underwent a significant radiation in the Australo-Papuan region and only a few oscine lineages have spread further than to the nearby Southeast Asia. A remarkable exception is the ancestor to the vast *Passerida* radiation, which now comprises 35% of all bird species. This group obviously benefitted greatly from the increased diversity in plant seed size and morphology during the Tertiary. The lyrebirds (and possibly scrub-birds) constitute the sister group to all other oscines, which renders “*Corvida*” (*sensu* Sibley and Ahlquist 1990) paraphyletic. Sequence data suggests that *Passerida*, the other clade of oscines postulated based on the results of DNA–DNA hybridizations, is monophyletic, and that the rockfowl and rock-jumpers are the most basal members of this clade. The suboscines in the Old World (Eurylamides) and the New World (Tyrannides), respectively, are sister groups. A provisional, working classification of the passerines is presented based on the increased understanding of the major patterns of passerine evolution.

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Passerine birds are much used model-organisms in comparative studies of, for example, ecology, ecomorphology and ethology. In these studies, the interpretations often rest on the assumption that the included taxa form a monophyletic group, and that their inter-relationships are correctly understood.

Until some twenty years ago, taxonomic judgements about avian study taxa were based primarily on analyses of morphological characters. Since then, our under-

standing of the early evolution of passerine birds has gained from advances made in the field of molecular biology, or more specifically, from the extensive DNA–DNA hybridisation studies by the late Charles G. Sibley, Jon Ahlquist and their co-workers. Significant contributions to the field have been made through the increasing number of studies that employ a phylogenetic systematic methodology in the analyses of morphological and molecular data sets. Especially the

advent of methods allowing direct comparisons of nucleotide sequences between taxa, has resulted in new insights into passerine evolution. In contrast to the distance data produced by DNA–DNA hybridisations, nucleotide sequences can be homologized across taxa making the phylogenetic inferences more reliable. In addition to the steadily increasing number of studies on the systematics of extant birds, more people than ever are involved in paleornithological research. This, in turn, is partly a consequence of an increasing number of bird fossils unearthed over the last few decades. Herein we outline our current understanding of the evolutionary and phylogenetic relationships among passerine birds. We also promote the biogeographic hypothesis of a Gondwanan origin of the passerine order, and that major groups of extant passerines derive from vicariant events following from the break-up of this former supercontinent.

The earliest history of the passerines

Although the monophyly of passerines has not been seriously questioned for over hundred years, Raikow (1982) was the first to show this within a phylogenetic systematic context. Subsequently, passerine monophyly has also been corroborated by analyses of nucleotide sequence data (e.g., Johansson et al. 2001).

The age of the passerine radiation is a matter of considerable debate. Two sources of information are available. The first is the fossil record that provides minimum ages of the taxonomic groups. Until recently passerines were known to first appear in the fossil record in Late Oligocene deposits, although they did not become common until the Miocene (Olson 1988, Mourer-Chauviré 1995). The paucity of passerine fossils from the Early Tertiary led to the assumption that the group evolved later than most other modern families of birds (Feduccia 1996). Recent finds in Australia dating from the Eocene and later (Boles 1995, 1997) indicate that the passerines had a Southern Hemisphere distribution in the Early Tertiary. As most Early Tertiary deposits are from Europe, North America and Asia the fossil record of passerines may be geographically biased (Olson 1985, 1988, Cooper and Penny 1997).

Molecular studies may also provide estimates of the age of phylogenetic lineages of birds by employing a molecular clock model. From such analyses it has been suggested that several extant orders of birds, including the passerines, evolved already in the Cretaceous (Sibley and Ahlquist 1990, Hedges et al. 1996, Cooper and Penny 1997, van Tuinen and Hedges 2001, Paton et al. 2002; Fig. 1). Among other things, the molecular clock model assumes constant mutational rates in the different evolutionary lineages compared, an assumption

proven not to be universally correct. Despite this shortcoming it is questionable if the divergences from constancy will result in errors of the magnitude needed to fit the known fossil record.

The sister group of the passerines is unknown, but it is often suggested to be found among the woodpeckers and their allies (Pici; cf. Olson 1983). Analyses of morphology, DNA–DNA hybridisation data, and DNA sequences have not been able to confirm this. Nor have any alternatives been suggested. The analysis of DNA–DNA hybridisation data suggested that the order Passeriformes is basal within a clade also consisting of such differently adapted forms as cranes, gulls, raptors, boobies, and penguins (Sibley and Ahlquist 1990). As the methodological problems inherent in the DNA–DNA hybridisation analysis are especially severe when investigating very ancient lineages (as here), little confidence can be put in this result.

Analyses of mitochondrial sequence data have arrived at the unexpected conclusion that Passeriformes is paraphyletic and takes a basal position within the Class

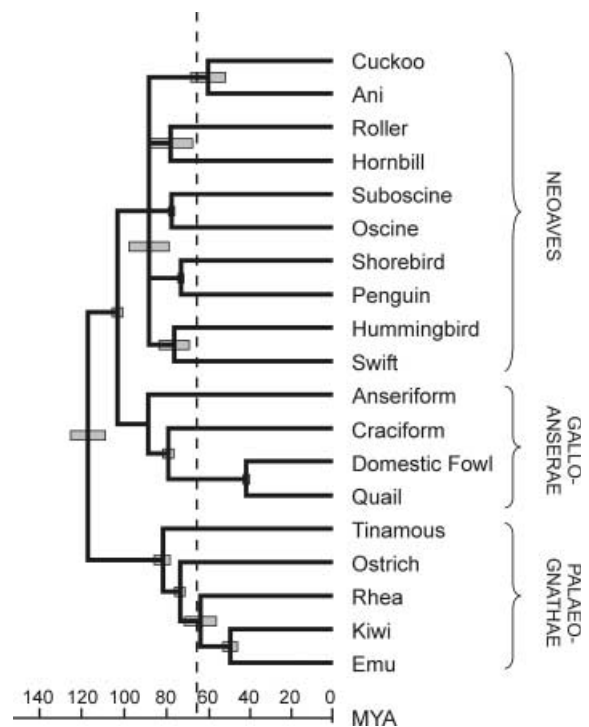


Fig. 1. Several molecular data sets (Hedges et al. 1996, Cooper and Penny 1997, van Tuinen and Hedges 2001, Paton et al. 2002) suggest that many extant orders of birds had already evolved during the Cretaceous, i.e. before 65 Mya (the hatched vertical line indicates the Cretaceous-Tertiary boundary). The figure shows a linearised tree and error bars for time of divergences calculated from three data sets (mtRNA, DNA–DNA hybridisation, and transferrin immunological distances). Modified from van Tuinen and Hedges (2001).

Aves (Mindell et al. 1997, 1999, Härlid et al. 1998, Härlid and Arnason 1999). It is probable that this unorthodox phylogenetic conclusion is incorrect owing to a combination of limited taxon sampling, a high rate of base substitutions in passerines and the use of too distantly related outgroups – crocodylians (García-Moreno and Mindell 2000). In contrast to the information obtained from the mitochondrial genome, analyses of nuclear sequence data produce results that are in better agreement with morphological data, although the sister group of the passerines remains unknown (Groth and Barrowclough 1999, van Tuinen et al. 2000, Johansson et al. 2001, García-Moreno and Mindell 2000). Thus, the passerines constitute a monophyletic group of birds whose sister group relationships among Neoaves is unresolved by the present available data.

New Zealand wrens – the first twig in the passerine tree

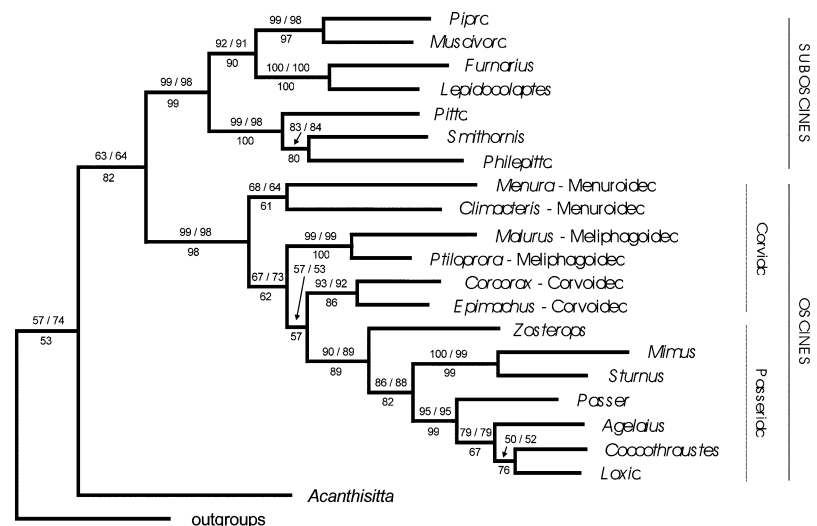
The New Zealand wrens (*Acanthisittidae*) have long constituted a taxonomic enigma as they lack the derived morphological traits used to define the two major clades of passerines, the oscines and suboscines. Systematists have regarded them as being the earliest branch in one or the other of these groupings. The systematic position of the New Zealand wrens could not be determined based on DNA–DNA hybridisation data but they were placed with the suboscines “because they are not oscines” (Sibley and Ahlquist 1990:582). The authors did suggest, however, that the New Zealand wrens possibly should be “assigned to a third suborder as the sister group of the Tyranni [suboscines] and Passeri [oscines]” (op cit.). The suggested exclusion from both the suboscine and the oscine clade has recently been supported by DNA sequence data, which

indicate that the New Zealand wrens are survivors of the earliest radiation of passerines (Barker et al. 2002, Ericson et al. 2002a) (Fig. 2). This has further raised the question of whether this is a relict family or evolved in situ since New Zealand split from Antarctica some 82–85 Mya (million years ago). In the latter case, the passerines would have existed for a considerably longer period of time than has previously been realised. Although a Gondwanan origin of the passerines has been suggested before (Feduccia and Olson 1982, Christidis and Schodde 1991, Cracraft 2001), the model for how the break-up of Gondwana relates to the diversity of extant passerines was not explicitly formulated until recently (Ericson et al. 2002a).

Hitch-hiking with continents – vicariance as an explanation of passerine evolution

The hypothesis that the New Zealand wrens had evolved more than 82 Mya suggests that vicariant events in the ancient supercontinent Gondwana may explain present passerine diversity. As will be seen, a significant part of the oscine radiation took place in the Australo-Papuan region. It has been assumed that this radiation must stem from an ancestor that reached Australia from mainland Asia as soon as the Australian plate had drifted enough northward from Antarctica to allow colonisation (Sibley and Ahlquist 1990). Based on new phylogenetic data (Barker et al. 2002, Ericson et al. 2002a), it seems plausible that this oscine ancestor already lived in Australia when this continent gradually became isolated from Antarctica at the end of Cretaceous. Likewise it can be hypothesised that the ancestor of the New World and Old World suboscines were isolated on the South American and Indian tectonic plates, respectively, when these split off from Antarctica

Fig. 2. 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 outgroups. Bootstrap values are given above branches for the maximum parsimony analyses (1000 replicates); data set with many non-passerine outgroups (left value), and with *Amazonetta*, *Corythaixoides*, *Cuculus*, *Gallus*, *Heliomaster*, *Momotus* and *Picumnus* as outgroups (right value). Bootstrap values for the maximum-likelihood analysis (1000 replicates) for the latter data set are shown below the branches. From Ericson et al. (2002a).



in the Late Cretaceous (Ericson et al. 2002a). India remained connected to Antarctica by a landbridge formed by the Kerguelen Plateau and Sri Lanka until the Late Cretaceous, possibly as late as 80 Mya (Hay et al. 1999). The significance of the Indian plate to the spread of the terrestrial, Gondwanan fauna into Laurasia in the Late Cretaceous and Early Tertiary has only recently been discovered (mammals: Krause et al. 1997, dinosaurs: Sampson et al. 1998, amphibians: Bossuyt and Milinkowitch 2001, ratite birds: Cooper et al. 2001). A study of the morphology of broadbills and asities suggests that an African taxon, *Smithornis*, may be basal to the rest (Prum 1993), but this remains to be confirmed by independent data. As of today, little is known about the evolutionary relationships and patterns of diversification of the Old World suboscines.

The fact that birds fly and easily can disperse across topographic barriers as large bodies of waters and mountain ranges may weaken the use of vicariance events to explain the current distribution of passerines. However, it should be noted that the basal members of the major clades of passerines are feeble-winged groups that are confined to the dense vegetation of tropical and subtropical forests. Groups with better flying abilities, adapted to feed in the canopy or in the air, are all derived within their respective taxonomic groups.

The subsequent spread of passerines into the Northern Hemisphere was facilitated by the northward move-

ment of the southern continents that formerly were parts of Gondwana (Fig. 3). This biogeographic scenario fits our current understanding of phylogenetic relationships of major clades of passerine birds well (see below). As yet, there is no fossil find to support it, but nor is there one contradicting it. A carpometacarpus from a Miocene deposit in Australia was tentatively identified as from a suboscine bird (Boles 1995), but this assignment may not be correct (Walter Boles in litt.). Until fossil evidence becomes available to test this scenario, the discussion will focus on the age of the passerine radiation. It may be surprising that the passerine radiation could be considerably older than the Early Tertiary. On the other hand, splitting events between certain modern bird taxa have been dated as far back as the mid-Cretaceous, based on estimates of mutational rates in various genes (Hedges et al. 1996, Cooper and Penny 1997, Cooper et al. 2001, van Tuinen and Hedges 2001, Paton et al. 2002). These studies refute the hypothesis that the diversification of all extant birds is the result of an explosive Tertiary radiation (Feduccia 1995).

Suboscine groups and their monophyly

The stapedial bone (columella) is a small ossicle located inside the ear. In suboscine birds the foot of this bone is bulb-like, unlike the condition in oscines and non-

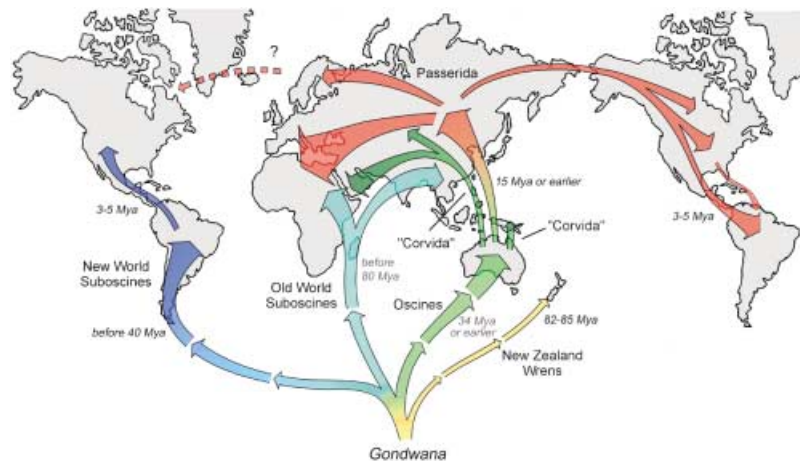


Fig. 3. Suggested dispersal routes of major passerine groups from Gondwana based on phylogenetic and biogeographic data. The southern continents are shown in their current position, with Gondwana as a central southern origination point for clarity. The basal position of the New Zealand wren lineage is consistent with isolation following the separation of New Zealand from Antarctica 82–85 Mya. 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 species-rich 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 around 40 Mya. The further dispersal of suboscines to Central and North America may have occurred in the Miocene across the Proto-Antillean plate, or after the formation of the Panamanian Isthmus. The early separation of South America and Africa (90 Mya) 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 quotation marks for Corvida indicate the paraphyly of this taxon. From Ericson et al. (2002a).

passerines, and this is the only known morphological character supporting suboscine monophyly. The suboscines typically inhabit tropical and subtropical regions in the New World, Africa and Asia (the few suboscines that occur in the Australo-Papuan region are believed to be late immigrants from Asia). Until the derived stapedal morphology was discovered in the 1970s (Feduccia 1974, 1975), the suboscines were traditionally regarded as being “primitive” in respect to the more “advanced” oscines. It was also commonly believed that they withstand competition with the oscines poorly, which would explain why suboscines are far more numerous and ecologically diverse in the New World compared to in the Old World. While the competition with the oscines supposedly has a very long history in the Old World, it has only just begun in the New World – at least if we assume that the oscines reached South America from North America after the two continents came close enough to permit dispersal of birds.

The relationships among the suboscines have been a matter of considerable taxonomic discussions. It was realised early that the suboscines could be divided into two groups based on the muscle morphology of the syrinx: a tracheophone syrinx is characterised by its more elaborate muscular system, compared with the simple haplophone syrinx. Suboscines with a tracheophone syrinx are all found in the New World and include the ovenbirds (Furnariidae), woodcreepers (Dendrocolaptidae), tapaculos (Rhinocryptidae), ground antbirds (Formicariidae), antbirds (Thamnophilidae) and gnateaters (Conopophagidae), as defined today. Many other New World suboscines, for example the tyrannids (Tyrannidae), cotingas (Cotingidae) and manakins (Pipridae), have a haplophone syrinx, as have all Madagascan, African and Asian suboscines. This observation led some systematists to suggest that especially the pittas and asities of the Old World are closely related with cotingas and tyrannids. However, it is now believed that the haplophone syrinx is plesiomorphic in passerines and of no value to reconstruct higher-level relationships among suboscines.

A systematic relationship between the tapaculos of the New World and the lyrebirds (Menuridae) of Australia was proposed based on osteology and the observation that one tapaculo genus, *Melanopareia*, lacks the typical suboscine stapedal morphology (Feduccia and Olson 1982). It was suggested that lyrebirds and tapaculos constitute the survivors of an ancient radiation of passerines that gave rise to all other modern taxa. The lyrebirds have later been conclusively shown to belong to the oscine clade (Christidis and Schodde 1991, Christidis et al. 1996, Irestedt et al. 2001, Ericson et al. 2002b), and a relationship with the tapaculos is no longer considered. The puzzling observation of the plesiomorphic stapedal morphology in *Melanopareia* remains unexplained. Although the relationships of the

tracheophones are only beginning to be clarified, nucleotide sequence data have unambiguously shown that *Melanopareia* belongs to the furnarioid clade, and is not a tapaculo (Irestedt et al. 2002).

Relationships among New World suboscines

Both DNA–DNA hybridisation and nucleotide sequence data suggest that the New World suboscines form a monophyletic group, and that it can be further divided into two clades, Furnarioidea and Tyrannoidea (Fig. 4). While the derived tracheophone syrinx in Furnarioidea provides morphological support of their monophyly, no uniquely derived morphological character is known for Tyrannoidea.

Furnarioidea traditionally (e.g., Wetmore 1960) includes the ovenbirds, woodcreepers, tapaculos, ground antbirds, antbirds and gnateaters. The taxonomic delimitations of these groups are not clear-cut, however. For example, both morphological and molecular data indicate that the woodcreepers are nested within the ovenbirds rendering the Furnariidae paraphyletic (Feduccia 1973, Irestedt et al. 2002). Furthermore, neither the ground antbirds, nor the tapaculos are recovered as monophyletic by DNA sequence data (Irestedt et al. 2002). Most interestingly, *Melanopareia* does not group with the tapaculos in the latter study, but is basal to all other furnarioids. As noted above, *Melanopareia*, together with the lyrebirds, once was suggested to be basal to all other passerines (Feduccia and Olson 1982). Although DNA sequence data do not support a rela-

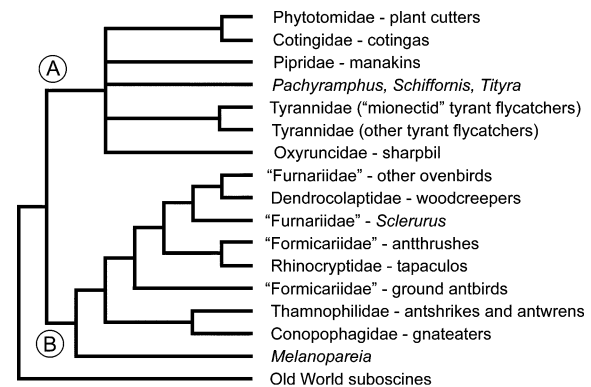


Fig. 4. Summary phylogeny for the New World suboscines. The phylogeny shows clades that received bootstrap supports exceeding 50% in the analyses of Irestedt et al. (2001, 2002) and Johansson et al. (2002). The two clades Tyrannida (A) and Furnariida (B) are recognised with high statistical support. Within Furnariida, the woodcreepers (Dendrocolaptidae) are nested within the ovenbirds (Furnariidae), and the alleged tapaculo genus *Melanopareia* does not group with the true tapaculos. Relationships within Tyrannida are less well resolved. Most importantly, the tyrant flycatchers (Tyrannidae) form a monophyletic group, contrary to what is postulated based on DNA–DNA hybridisation data.

tionship between the two, it is noteworthy that the lyrebirds are basal among the oscines (see below) while *Melanopareia* is basal to a major clade of suboscines, albeit not to all suboscines.

Tyrannoidea, the second major group of New World suboscines, forms a monophyletic clade consisting of the manakins, cotingas, tyrant flycatchers, sharpbill (*Oxyruncidae*), and plantcutters (*Phytotomidae*) (Irestedt et al. 2001, Johansson et al. 2002). The phylogenetic relationships within this clade have proven unusually difficult to entangle, indicating a rapid radiation that results in very short internodes in the evolutionary tree. One of the more unexpected results from the DNA–DNA hybridisation analysis is the suggestion that the cotingas and manakins are nested within the Tyrannidae, making that family paraphyletic (Sibley and Ahlquist 1990). Several tyrannid genera, constituting the “pipromorphine” tyrant flycatchers, were placed outside a group of the remaining tyrant flycatchers, cotingas and manakins. However, this novel systematic treatment has not been corroborated by DNA sequence data (Johansson et al. 2002). In this latter analysis all studied tyrant flycatchers, including several pipromorphine flycatchers, form a monophyletic clade with high bootstrap support. The relationships between the flycatchers and the other, mostly frugivorous tyrannoid groups are poorly resolved, however.

Suboscines in the Old World

Three families of suboscines occur in the Old World, the broadbills (*Eurylaimidae*), pittas (*Pittidae*) and asities (*Philepittidae*). The asities occur only in Madagascar, while broadbills and pittas are more widely distributed in Africa and southern Asia. Only the pittas are represented in the Australo-Papuan region to which they are supposed to have immigrated from the north. Although long a matter of discussion, the monophyly of the Old World suboscines now seems well supported based on morphology (Raikow 1987, Prum 1993) and DNA sequence data (Irestedt et al. 2001). The precise relationships among these groups are less certain though. Prum (1993) concluded, on the basis of a study of syringeal and osteological characters, that the asities are nested within the broadbill clade. This suggestion was challenged by DNA sequence data (Irestedt et al. 2001), but the latter study suffers from the limited number of broadbill representatives included. In both studies the pittas are sisters to the broadbills and asities.

The monophyly of both the Old World and New World suboscines suggests that these groups were separated long ago. There are two candidate vicariance events for this separation. One is based on the hypothesis that the suboscines once were widespread over

South America and Africa, and that the New World and Old World groups were separated when these two continents split. However, this vicariance event seems to be far too old, as the separation between South America and Africa occurred earlier than ca. 90 Mya. A more likely vicariant event is when the Kerguelen Plateau (then linked to the Indian plate) split from Antarctica in the Late Cretaceous. Subsequently, the Old World suboscines may have spread to Africa and Asia via the now submerged Kerguelen Plateau.

Paraphyly of Corvida

Sibley and Ahlquist (1990) grouped the oscines into two monophyletic clades, Corvida and Passerida, and regarded the discovery of this dichotomy as the single most unexpected and challenging result from the DNA–DNA hybridisation studies. Their Corvida includes a wide range of taxa that either are endemic to the Australo-Papuan region, or have their main diversity and centre of distribution there. In earlier classifications several of these taxa have been placed close to groups of mainly Eurasian and African taxa with similar adaptations and convergently evolved morphology, especially “flycatchers”, “thrushes” and “warblers”. The results from the DNA–DNA hybridisations implied that the Corvida radiation had taken place in the Australo-Papuan region, but that several groups subsequently dispersed to Eurasia, Africa and the Americas. Many sedentary groups of Corvida live in dense vegetation and have a limited dispersal behaviour, which explains why they have not spread far outside the Australo-Papuan region (Mayr and Diamond 2001). Other groups have been more prone to disperse and have undergone new, major radiations in Africa (shrikes, Laniidae, and bush-shrikes, *Malaconotidae*), Madagascar (vangas, *Vangidae*), Eurasia (crows and allies, *Corvidae*, and orioles, *Oriolidae*), and the New World (New World jays, *Corvidae*, and vireos, *Vireonidae*).

DNA–DNA hybridisation data (Sibley and Ahlquist 1985, 1990) further suggest that Corvida comprises three groups: Menuroidea (lyrebirds, scrub-birds, bowerbirds and treecreepers), Meliphagoidea (honeyeaters, thornbill-warblers and fairy-wrens), and Corvoidea (a large group including, for example, crows, birds-of-paradise, drongos, orioles, shrikes). No morphological or other independent characters are known to support monophyly of any of these three groups. In fact, even Corvida lacks morphological support for monophyly. In the proximal humeral head, a second pneumatic fossa has developed in a wide range of oscines (Bock 1962). This is the derived condition in passerines, and the single fossa found in many, but not all, representatives of Corvida, as well as in the suboscines and many non-passerine birds, is plesiomorphic.

Analyses of DNA sequence data refute the monophyly of *Corvida sensu* Sibley and Ahlquist (1990), and raise serious doubts about the validity of the three superfamilies recognised by these authors (Barker et al. 2002, Ericson et al. 2002a, b; Fig. 5). As inferred from morphology (Feduccia 1975, Bock and Clench 1985, Raikow 1985), the lyrebirds and scrub-birds (*Menurae*) occupy a basal position among the oscines. Although their internal phylogenetic relationships are not clarified, the bowerbirds and treecreepers (the other two members of *Menuroidea sensu* Sibley and Ahlquist 1990), also constitute early branches of the oscine tree. All other living oscines appear to form the sister group of these taxa. This also makes sense from a morphological point of view: in contrast to all other oscines the syrinxes of the lyrebirds and scrub-birds have not five, but three pairs of intrinsic muscles (Sibley 1974). Sibley and Ahlquist (1990) interpreted this as secondarily derived from the normal five-pair condition. It should be noted that also the treecreepers possess a syrinx morphology that is unique among passerines, although it differs from that of the lyrebirds and scrub-birds (Ames 1987). The syringeal morphology of the bowerbirds is of the normal oscine condition, with five pairs of intrinsic muscles (Ames 1971).

The analysis of the nucleotide sequence data recovers *Meliphagoidea sensu* Sibley and Ahlquist (1990) as monophyletic (Ericson et al. 2002b). However, this result is only tentative as *Meliphagoidea* is represented by but two representatives of honeyeaters (*Meliphagidae*) and one of the fairy-wrens (*Maluridae*) in the analysis.

The representatives of *Passerida* are nested within “*Corvida*” (the quotation marks indicate that this is not a monophyletic taxon), or more specifically, within

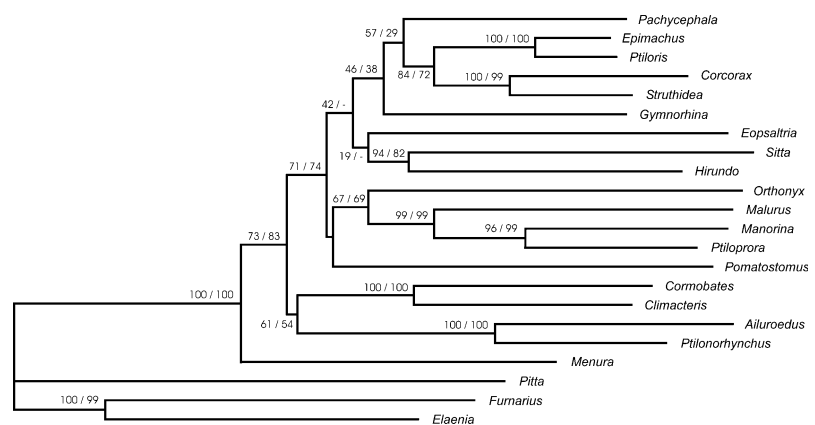
Corvoidea sensu Sibley and Ahlquist (1990). These results suggest that the earliest radiation of the oscines took place in Australia. An estimated Early Tertiary (53 Mya) date for the split between the lyrebird and all other oscines (Ericson et al. 2002a) indicates that the oscine radiation began well before Australia finally split from Antarctica in the mid Tertiary. The observed paraphyly of “*Corvida*” relative to *Passerida*, and the monophyly of the latter group (see below), also means that we should look for a specific corvid sister taxon to the entire passerid radiation. It is not obvious from the analyses of the nucleotide sequence data which this taxon is, although a preliminary analysis indicates that the Australian robins, *Eopsaltria*, may be involved.

Monophyly and early branching patterns of the *Passerida*

Although the DNA–DNA hybridisation data suggest monophyly of *Passerida*, no morphological character is known to support this. Instead, the strongest corroboration yet of monophyly of *Passerida* comes from the observation of an insertion of one amino acid in the coding region of the nuclear *c-myc* gene in all studied species of *Passerida*, but in no group outside this taxon (Ericson et al. 2000). To date, representatives of more than 90 non-passerine and almost all passerine families and subfamilies have been investigated.

If we accept the hypothesis of a monophyletic *Passerida* nested within “*Corvida*”, it follows that the *Passerida* radiation derives from a single “escapee” from Australia. Given the present-day proximity between the Australo-Papuan region and southeast Asia, it could be expected that many dispersal events from Australia

Fig. 5. Tree resulting from maximum-likelihood analysis of combined sequences obtained from the nuclear genes *c-myc*, *RAG-1* and myoglobin intron II, and the mitochondrial genes cytochrome *b* and ND2. All genes except myoglobin intron II are protein coding. Only first and second codon positions for the mitochondrial genes were included in the analyses to reduce the influence of saturation upon the results. The maximum-likelihood tree is largely congruent with the most parsimonious tree calculated from the same data set, the only differences occur in the relative positions of *Eopsaltria*, *Gymnorhina* and *Pachycephala*, whose internal relationships must be regarded as unresolved. Nodal support values are calculated from 100 replicates of the maximum-likelihood analysis (left value), and 1000 replicates of the parsimony analysis (right value). From Ericson et al. (2002b).



have resulted in radiations in the Old World as successful as the Passerida radiation. Certainly, there are examples of successful dispersals (see above), but the DNA–DNA hybridisation data suggest that most “Corvida” lineages have never spread outside the Australo-Papuan region, and even fewer outside the Australasian realm. The exchange of passerine taxa between Asia and the Australo-Papuan region has been relatively limited also in the opposite direction. Only about 42 (14% of the passerine fauna) of the species that breed on mainland Australia and Tasmania belong to the Passerida radiation. Most of these species occupy “grasslands, savannah, and arid shrub-land habitats that developed as Australia dried out in the last 20 million years” (Rowley and Russell 1997) – a clear indication that they are comparatively late arrivals to Australia.

Sibley and Ahlquist (1990) cautiously regarded the African rockfowl, *Picathartes*, and rock-jumpers, *Chaetops*, as members of their Corvida but placed them “on the boundary” between this group and Passerida. Analyses of their DNAs have shown that they do possess the insertion of one amino acid in the *c-myc* gene, postulated to be a synapomorphy of Passerida. The rockfowl and rock-jumpers thus should be viewed as members of the vast Passerida radiation in which they have a basal position, possibly being the sister group to all other Passerida.

DNA–DNA hybridisation data suggest that Passerida consists of three superfamilies, Muscicapoidea (e.g., waxwings, dippers, thrushes, Old World flycatchers, starlings, mockingbirds), Sylvioidea (e.g., nuthatches, tits, wrens, swallows, and a poorly resolved radiation of bulbuls, babblers and various warbler groups), and Passeroidea (e.g., larks, pipits and wagtails, mannikins, weavers, sparrows, finches, wood warblers, icterids, tanagers) (Sibley and Ahlquist 1990). These divisions are novel and not supported by consistently distributed morphological characters. A preliminary analysis of DNA sequence data strongly suggests Muscicapoidea and Passeroidea to be monophyletic, but not Sylvioidea (Ericson and Johansson in press; Fig. 6). Defining natural groups among babblers, bulbuls and various warbler assemblages still remains a challenge (cf. Cibois et al. 1999, 2001, Pasquet et al. 2001).

Passeroidea and the nine-primaried oscines

Passeroidea includes several radiations of granivorous birds that, in terms of number of species, are among the most successful within the entire class of birds. The ages of these radiations are currently unknown but must post-date the transition in angiosperms from the unspecialised dispersal systems, with small seeds, that pre-

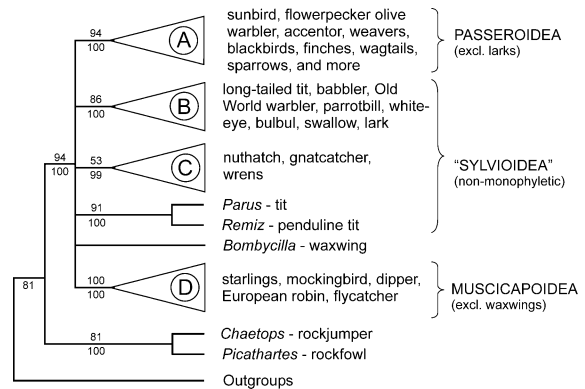


Fig. 6. Major clades of Passerida representatives recovered in an analysis of 3130 bp obtained from three nuclear and one mitochondrial gene for 48 ingroup taxa. The taxa included in each clade are indicated (in pluralis when more than one representative has been used). The African rockfowl and rock-jumper constitute the deepest split within Passerida. Relationships among the superfamilies Muscicapoidea, Passeroidea and Sylvioidea (*sensu* Sibley and Ahlquist 1990) cannot be unambiguously resolved, and monophyly of Sylvioidea could not be corroborated. From Ericson and Johansson (in press).

ailed until about the Cretaceous-Tertiary boundary (Tiffney 1984, Eriksson et al. 2000). It has been postulated that the dramatic growth in the diversity of seed and fruit features observed in the Early Tertiary could have resulted from co-evolution with birds and mammals (Wing and Tiffney 1987). Interestingly, none of the “old endemic” passerines in the Australo-Papuan region are obligate granivores, while all other major, passerine feeding adaptations have evolved here.

Several phylogenetic studies based on nucleotide sequence data have recently targeted major groups of Passeroidea (Groth 1998, Johnson and Lanyon 1999, Klicka et al. 2000, Grapputo et al. 2001, Yuri and Mindell 2002). Their focus has been mainly on the so-called New World nine-primaried oscines, a group that includes emberizid sparrows (Emberizidae), tanagers (Thraupidae), blackbirds (Icteridae) and wood-warblers (Parulidae). The emberizid sparrows also occur in other parts of the world, but the group is believed to have radiated in the New World. Likewise, the family Fringillidae is often referred to as the “Old World sparrows and finches” to acknowledge their supposed geographic origin, despite also being distributed in the New World. The fringillids are functionally nine-primaried like their New World ecological counterparts, a fact thought to indicate a close affinity between the two groups. The emberizid–fringillid relationships have long occupied systematists, and the issue was further complicated by the inclusion in the studies of certain nine-primaried taxa (e.g., vireos) that we today know are not related to the ‘true’ nine-primaried groups.

While the DNA–DNA hybridisation studies (Sibley and Ahlquist 1990) suggest monophyly of the New

World nine-primaried oscines, morphology indicates that some groups are more closely related to certain fringillid taxa (Tordoff 1954, Raikow 1978). Analyses of DNA sequences support monophyly of the assemblage of New World nine-primaried oscines, but there is little consensus on the relationships within this group (Fig. 7). The best supported hypothesis, based on both nuclear and mitochondrial genes, suggests blackbirds and wood-warblers to be sister taxa. A clade with tanagers and emberizid sparrows is positioned next outside to them, but the more precise relationships among tanagers and sparrows remain to be clarified. A surprising finding is that the genera *Calcarius* and *Plectrophenax* do not group with the emberizid sparrows, but have a position that is basal to all other New World nine-primaried oscines (Klicka et al. 2000, Grapputo et al. 2001, Ericson and Johansson in press). Thus, they “represent a previously unrecognised early radiation event and convergence upon sparrow morphology” (Klicka et al. 2000). Most likely, the earliest phases of the radiation of the New World nine-primaried oscines took place in North America whereto their ancestor had arrived either from Asia following the Beringian track, or from Europe via Greenland. Furthermore, the *Calcarius* and *Plectrophenax* sparrows are the survivors of an earlier immigration from the Old World than that of the ancestor of the other groups.

The plate tectonics of Central America is complex, but it is clear that the landbridge between North and South America (the Panamanian Isthmus) formed rather late, perhaps not before 3–5 Mya. As many New World nine-primaried representatives are strong fliers, it is highly likely that the group spread to South America long before the formation of the Panamanian Isthmus. In fact, major radiations within the group seems to have taken place in subtropical and tropical South America, perhaps as early as in the Miocene.

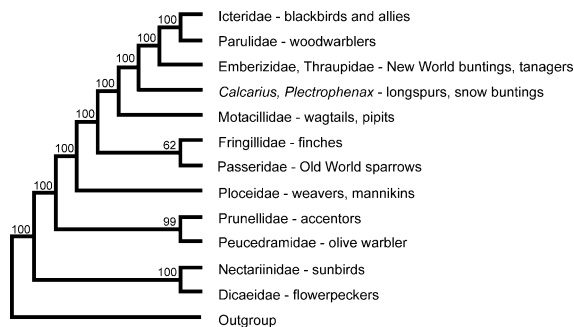


Fig. 7. Summary of phylogenetic relationships within the superfamily Passeroidea (*sensu* Sibley and Ahlquist 1990) based on an analysis of 3130 bp obtained from three nuclear and one mitochondrial gene for 25 passeroid taxa. The tree shows the topology of the maximum-likelihood tree, while nodal support values are from a Bayesian analysis. Note that no nodal supports were obtained for the relationships between the Passeridae, Fringillidae, and Motacillidae. From Ericson and Johansson (in press).

There is some uncertainty about which is the outgroup to the New World nine-primaried assemblage. The fringillid sparrows and finches, to which the Hawaiian honeycreepers (Drepanididae) belong (Beecher 1953, Raikow 1978, Groth 1998), definitely should be considered. Analysis of cytochrome *b* data suggests that the pipits and wagtails (Motacillidae) and passerids (genera *Montifringilla*, *Passer* and *Petronia*) maybe are closer than the fringillids to the group of New World nine-primaried taxa, although this arrangement did not receive bootstrap support above 50% (Groth 1998). In another analysis that includes data from two nuclear genes in addition to that from the mitochondrial cytochrome *b* gene, the motacillids, passerids and fringillids are placed as an unresolved outgroup to the New World nine-primaried oscines (Ericson and Johansson in press). A clue to the relationships of these groups may be provided by the taxonomic distribution of a unique insertion of three amino acids in the nuclear *c-myc* gene (Ericson et al. 2000). This insertion occurs in all New World nine-primaried groups, as well as in all fringillids and motacillids, but not in *Montifringilla*, *Passer* or *Petronia*. The only known exception to this pattern occurs in three species of the genus *Cacicus* (Per Ericson pers. obs.). As *Cacicus* doubtless is an icterid genus (Lanyon and Omland 1999), the lack of an insertion in these species is best interpreted as a reversal to the plesiomorphic condition. Further studies of fringillid and passerid taxa are warranted to get a more complete understanding of the evolution of the nine-primaried members of Passeroidea.

Towards a robust classification of passerines

The phylogenetic hypotheses of passerine systematics based on analyses of DNA–DNA hybridisation data

Table 1. Classification proposed by Sibley and Ahlquist (1990) based on analyses of DNA–DNA hybridisation data.

Order Passeriformes
Suborder Tyranni
Infraorder Acanthisittides (New Zealand wrens)
Infraorder Eurylaimides (Old World suboscines)
Superfamily Pittoidea
Superfamily Eurylaimoidea
Infraorder Tyrannides (New World suboscines)
Parvorder Tyrannida
Parvorder Thamnophilida
Parvorder Furnariida
Superfamily Furnarioidea
Superfamily Formicarioidea
Suborder Passeri (Oscines)
Parvorder Corvida
Superfamily Menuroidea
Superfamily Meliphagoidea
Superfamily Corvoidea
Parvorder Passerida
Superfamily Muscicapoidea
Superfamily Sylvioidea
Superfamily Passeroidea

(Sibley and Ahlquist 1990) were summarised in the classification of Sibley and Monroe (1990; see Table 1). Few analyses utilising the DNA–DNA hybridisation method have been published after 1990. Instead, most phylogenetic hypotheses formulated during the last decade rely on DNA sequence data. Until recently, these data were predominantly obtained from mitochondrial genes and more than one gene was seldom sequenced. The current trend in avian systematics is to sequence both mitochondrial and nuclear genes as this has proven to yield more robust phylogenetic estimates.

It is also an advantage if the studied genes belong to different linkage-groups and thus are independently inherited as this allows comparisons of gene-trees. The different gene-trees then yield independent estimates of the true evolutionary tree of the studied taxa, and observed congruence between the gene-trees lends confidence to the phylogenetic hypotheses. The understanding of higher-level systematics in passerines has thus grown considerably during the last few years of rapid development in this field of science. It is now possible to outline a new classification of passerines (Table 2)

Table 2. Provisional classification of major groups of passerine birds, based on analyses of nucleotide sequence data, obtained from both nuclear and mitochondrial markers. The genera listed for certain higher taxa are those that have been included in the phylogenetic analyses upon which this classification rest.

Order Passeriformes
Suborder Acanthisittia (New Zealand wrens)
Suborder Eupasserer (all other passerines)
Infraorder Suboscines
Parvorder Eurylaimides ('Old World suboscines': pittas, broadbills, asities)
Fam. Pittidae
Fam. Eurylaimidae (incl. asities, <i>Philepitta</i>)
Parvorder Tyrannides ('New World suboscines')
Furnariida
Incertae sedis
Fam. Melanopareiidae (<i>Melanopareia</i>)
Superfamily Thamnophiloidae
Fam. Thamnophilidae
Fam. Conopophagidae
Superfamily Furnarioidea
Fam. Grallariidae (with <i>Grallaria</i> , <i>Hylopezus</i> , <i>Myrmothera</i> , and <i>Grallaricula</i>)
Fam. Rhinocryptidae (tapaculos excl. <i>Melanopareia</i>)
Fam. Formicariidae (with <i>Formicarius</i> and <i>Chamaeza</i>)
Fam. Furnariidae
Subfam. Sclerurinae (with <i>Sclerurus</i>)
Subfam. Dendrocolaptinae
Subfam. Furnariinae (ovenbirds excl. <i>Sclerurus</i>)
Tyrannida
Fam. Cotingidae (incl. <i>Phytotoma</i>)
Fam. Oxyruncidae
Fam. Pipridae
Fam. Tyrannidae
Incertae sedis Tityrinae (<i>Pachyramphus</i> , <i>Schiffornis</i> , <i>Tityra</i>)
Infraorder Oscines
Parvorder Menurae (lyrebirds, scrub-birds)
Parvorder Euoscines (all other oscine passerines)
Incertae sedis (fam. Ptilonorhynchidae, fam. Climacteridae, Meliphagoidea (<i>sensu</i> Sibley and Ahlquist 1990), and Corvoidea (<i>sensu</i> Sibley and Ahlquist 1990, except <i>Picathartes</i> and <i>Chaetops</i>)
Passerida
Picathartii
Fam. Picathartidae (<i>Picathartes</i> , <i>Chaetops</i>)
Eupasserii
Superfamily Passeroidea
Fam. Nectariinidae
Fam. Dicaeidae
Fam. Prunellidae
Fam. Peucedramidae
Fam. Ploceidae
Fam. Passeridae
Fam. Fringillidae
Fam. Emberizidae
Superfamily Muscicapoidea
Fam. Muscicapidae
Fam. Turdidae
Fam. Cinclidae
Fam. Sturnidae
Fam. Mimidae
Incertae sedis all other taxa in Passerida (<i>sensu</i> Sibley and Ahlquist 1990)

that can serve as a better alternative than a classification based on DNA–DNA hybridisation data. Although this classification will be subject to many future refinements, we firmly believe that it accurately reflects the evolution of the passerines, the most species-rich group of birds in the world. As mentioned, only a handful morphological characters are useful in delimiting the different groups of passerines. The classification in Table 2 is in agreement with the taxonomic distribution of these characters (Fig. 8).

Future work in avian systematics certainly will be devoted to studying the many clusters of taxa that so far have been impossible to resolve. It can be expected that certain groups of passerines have undergone rapid adaptive radiations after, for example, having colonized new geographical areas. Rapid radiations result in short internodes between taxa and, when using DNA sequence data, the patterns of diversification in these groups can only be studied with genes that accumulate mutations at high rates. On the other hand, fast evolving genes may reach saturation if the radiations under study are very old, which seriously limits the use of sequence data in phylogenetic studies. This problem is probably the explanation of why it has been so difficult to identify the outgroup of the passerines (Johansson et al. 2001, Johansson and Ericson in press).

Passerine relationships that may be especially difficult to resolve in greater detail with DNA sequence data include parts of the inter-familial structure of Corvoidea (*sensu* Sibley and Ahlquist 1990) and the vast and obviously rapid radiation of insect-eaters in Asia

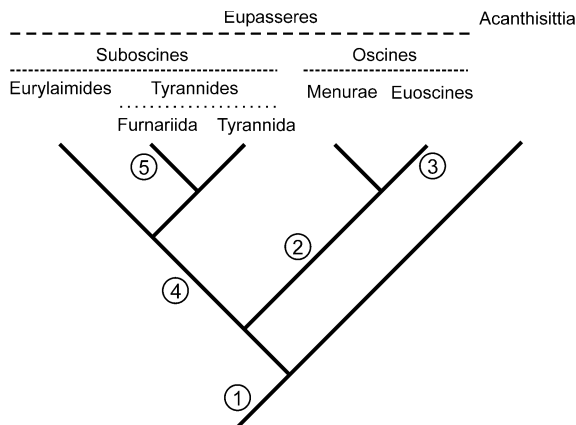


Fig. 8. Graphic representation of the provisional classification based on DNA sequence data (see Table 2). The taxonomic distribution of the morphological characters that traditionally have been used to infer relationships among basal passerines is fully consistent with this phylogenetic tree. Node 1: aegithognathous palate, “passerine” tensor propatagialis brevis, bundled spermatozoa with coiled head, enlarged hallux, and type VII deep plantar tendons (Raikow 1982). Node 2: acromyodian (oscine) syrinx (Müller 1847, Garrod 1876). Node 3: syrinx with four intrinsic muscles (Ames 1971). Node 4: stapedal bone (columella) with expanded foot (Feduccia 1975). Node 5: tracheophone syrinx (Garrod 1876, Ames 1971). From Ericson et al. (2002b).

and Africa (“flycatchers”, “thrushes”, “warblers”, and allies). These groups consist of taxa that are separated by very short internodes (delta- T_{50H} distances) in the trees based on DNA–DNA hybridisations (cf. Sibley and Ahlquist 1990). Hopefully, monophyletic subgroups of these and other especially problematic taxa can be delimited by future discoveries of rare insertion or deletion events in conservative gene regions. As molecular methods develop and become less expensive, many new genes will be scanned for such evolutionary events. In recent years it has become apparent how useful nuclear introns (non-coding regions) are when studying also rather old branching patterns (Prychitko and Moore 2000, Armstrong et al. 2001, Irestedt et al. 2002, Weibel and Moore 2002), and there is an increasing quest for identifying additional, phylogenetically informative introns.

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