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Passerine birds (Passeriformes)

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Abstract

The Order Passeriformes is the largest clade of its rank in birds, encompassing from roughly 40–100 families depending on the classification. In recent years molecular systematic data have greatly clarified interfamilial relationships, although many nodes remain poorly supported and it is clear that numerous traditional families are not monophyletic. Passeriformes is an old group, and most molecular dating studies estimate its age of origin to be late Cretaceous (100–66 million years ago, Ma) on Gondwana, with early lineages being partitioned among New Zealand, Australasia, and South America. The major lineages arose in the Paleogene (66–23 Ma) and then diversified in the Neogene (23–0 Ma).

The Passeriformes constitutes the largest order within modern birds (Neornithes) and includes the suboscines (Tyranni; Old World and New World lineages) and the Passeri (oscine songbirds). Passeriforms represent about 60% of extant avian diversity and estimates range from about 5700 biological species (1) to perhaps 15,000 or more diagnosably distinct taxa, or phylogenetic species (Fig. 1). Over the years, systematists have recognized a variable number of family-ranked taxa, from 44 to 96 (1–4). New molecular sequencing studies are discovering that a substantial number of conventional “families” are not monophyletic, and accordingly it is certain passeriform classification will be a subject of great interest in the coming years. Here, we review recent advances in passerine phylogenetics and use molecular sequence data to estimate the temporal pattern of diversification within the group.

It has been accepted for some time now that birds are divided into the paleognaths (tinamous and ratites) and neognaths (all other birds), with the latter being subdivided into the Galloanserae (duck-like and chicken-like

birds) and its closest relative, the Neoaves. Relationships within Neoaves have been controversial and difficult to resolve (5–9). Many workers have placed passeriforms close to the so-called “higher land birds,” particularly the monophyletic Piciformes and taxa of the non-monophyletic “Coraciiformes” (6–11), but some molecular analyses, including DNA hybridization (5) and whole mitochondrial genomes (12), have placed them deeper toward the base of the Neoaves and even—because of a very small taxon sample and a spurious root—at the base of all birds (13).

The monophyly of the passeriforms has never been seriously questioned (14). Morphologists of the nineteenth century used syringeal characters to establish the major oscine/suboscine divisions, and through the twentieth-century systematists (2, 15, 16) carried on the process of clustering groups of families together, primarily on the basis of overall similarity and geography and without much new character data. Although the suboscine/oscine division has been widely accepted, the placement of the New Zealand wrens (Acanthisittidae) relative to



Fig. 1 A Wood Thrush (*Hylocichla mustelina*), Family Turdidae, from North America. Credit: J. Cracraft.

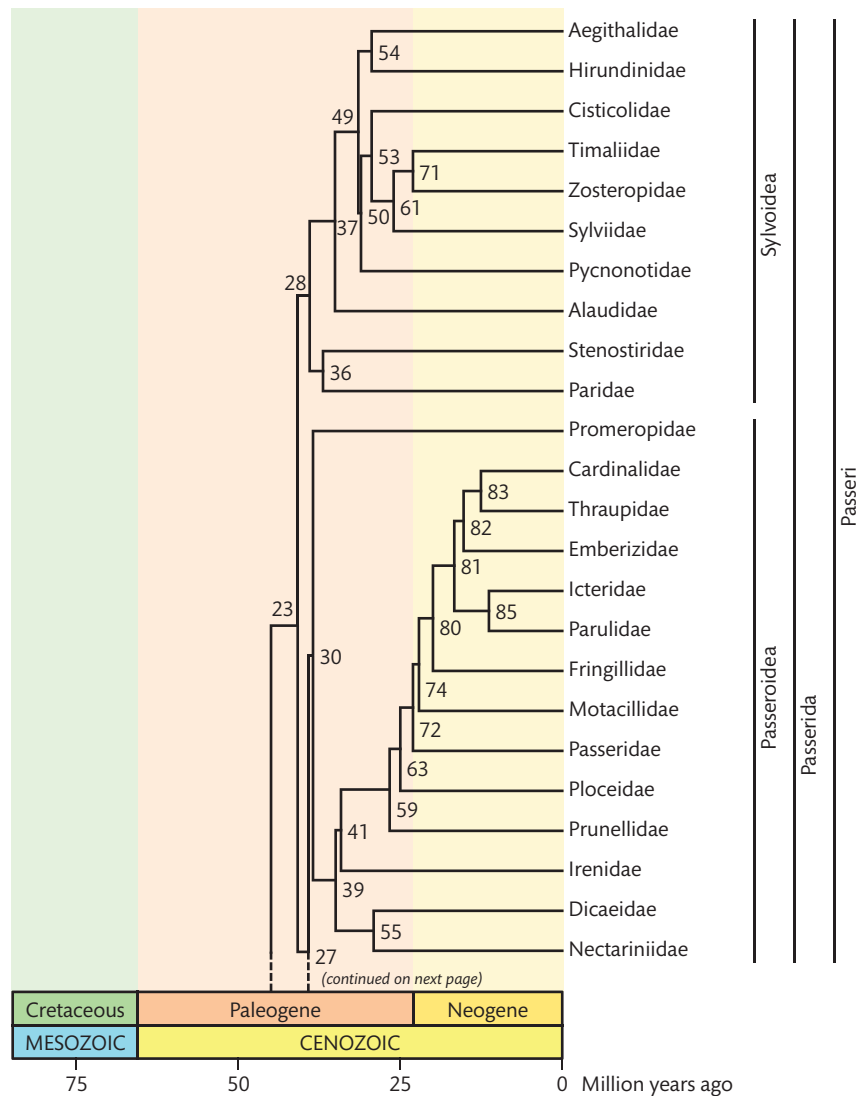


Fig. 2 Continues

those two lineages was uncertain before the emergence of molecular data (17). DNA hybridization distances (5) suggested that *Acanthisitta* was at the base of the passeriforms but that position was never tested rigorously with outgroup comparisons. Recent DNA sequencing studies, however, have strongly supported acanthisittids as the closest relatives of the suboscines + oscines (18–20). This finding has been crucial as it has provided the basis for calibrating divergence times within the passeriforms, as discussed later.

The division between the Old World suboscines (Eurylaimides) and their New World counterpart (Tyrannides + Furnariides) is well supported (18–23). With ~1200 species, the New World suboscines are the most

diverse lineage of South American birds. They are divided into two major subclades (18–20, 24), the Tyrannides (flycatchers, cotingas, and manakins; Tyranni of 17) and the Furnariides (ovenbirds, woodcreepers, antbirds, tapaculos, antpittas, and allies; Furnarii of 17 and the Furnariida + Thamnophilida of 1). Because of limited taxon sampling in currently published results, many relationships within both of these groups are subject to uncertainty.

The overwhelming taxonomic and morphological diversity of oscines (Passeri) has long presented a challenge to understanding their relationships, but in the last few years DNA sequence studies have begun to reveal the overall phylogenetic structure of this group, even though

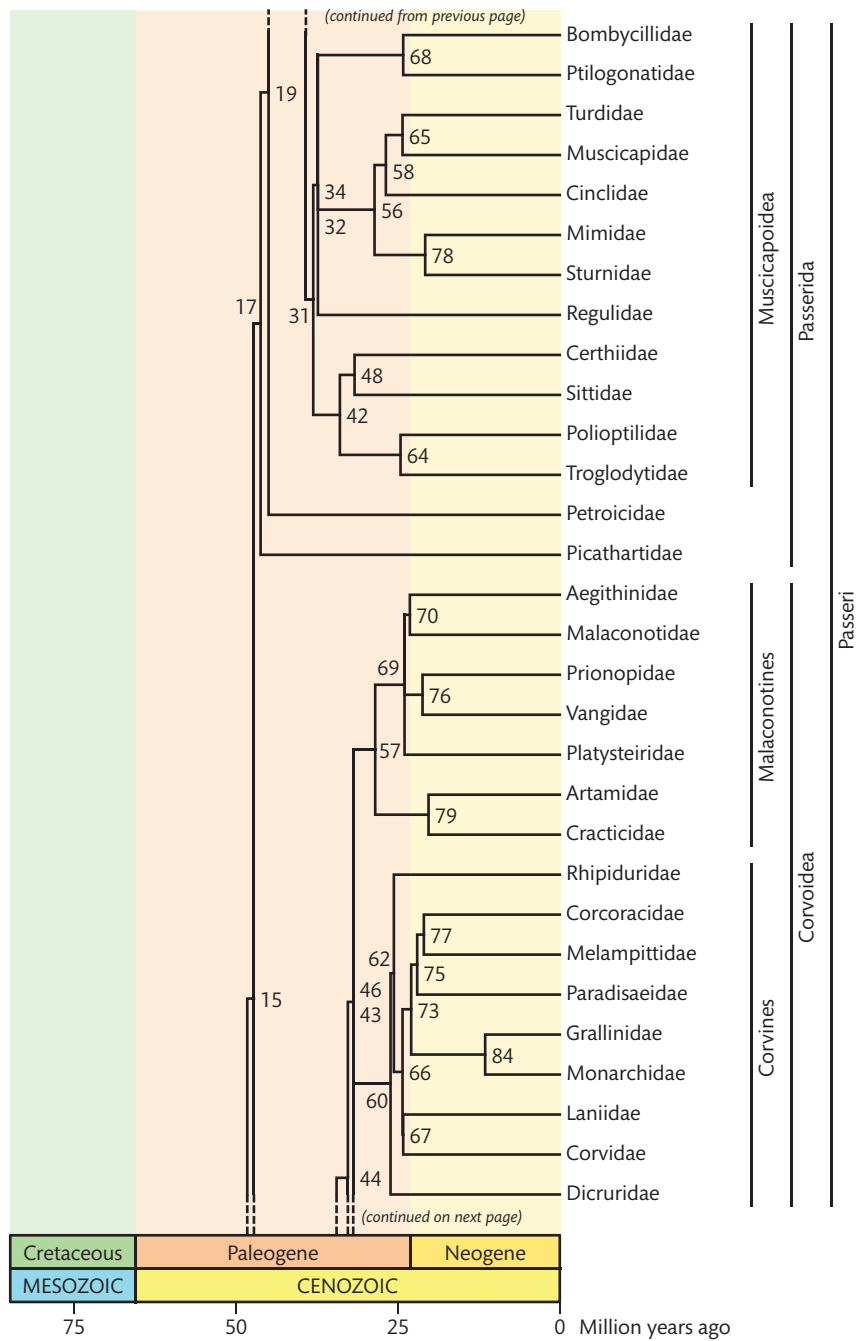


Fig. 2 Continues

there remain numerous poorly supported nodes across the tree. Sequences from *RAG1* and *RAG2* nuclear loci for a large taxon sample, including all but one passeriform family (18, 19), have established that the diverse Australasian “Corvida” that was proposed on the basis of DNA hybridization distances (5) is paraphyletic, and

that some of these lineages are, in fact, successive closest relatives of all remaining oscines. Importantly, however, a monophyletic assemblage (Corvoidea) within the “corvidans” has been found to be the closest relative of all remaining oscines (roughly speaking, Sibley and Monroe’s (1) clade Passerida). Within the latter, at least

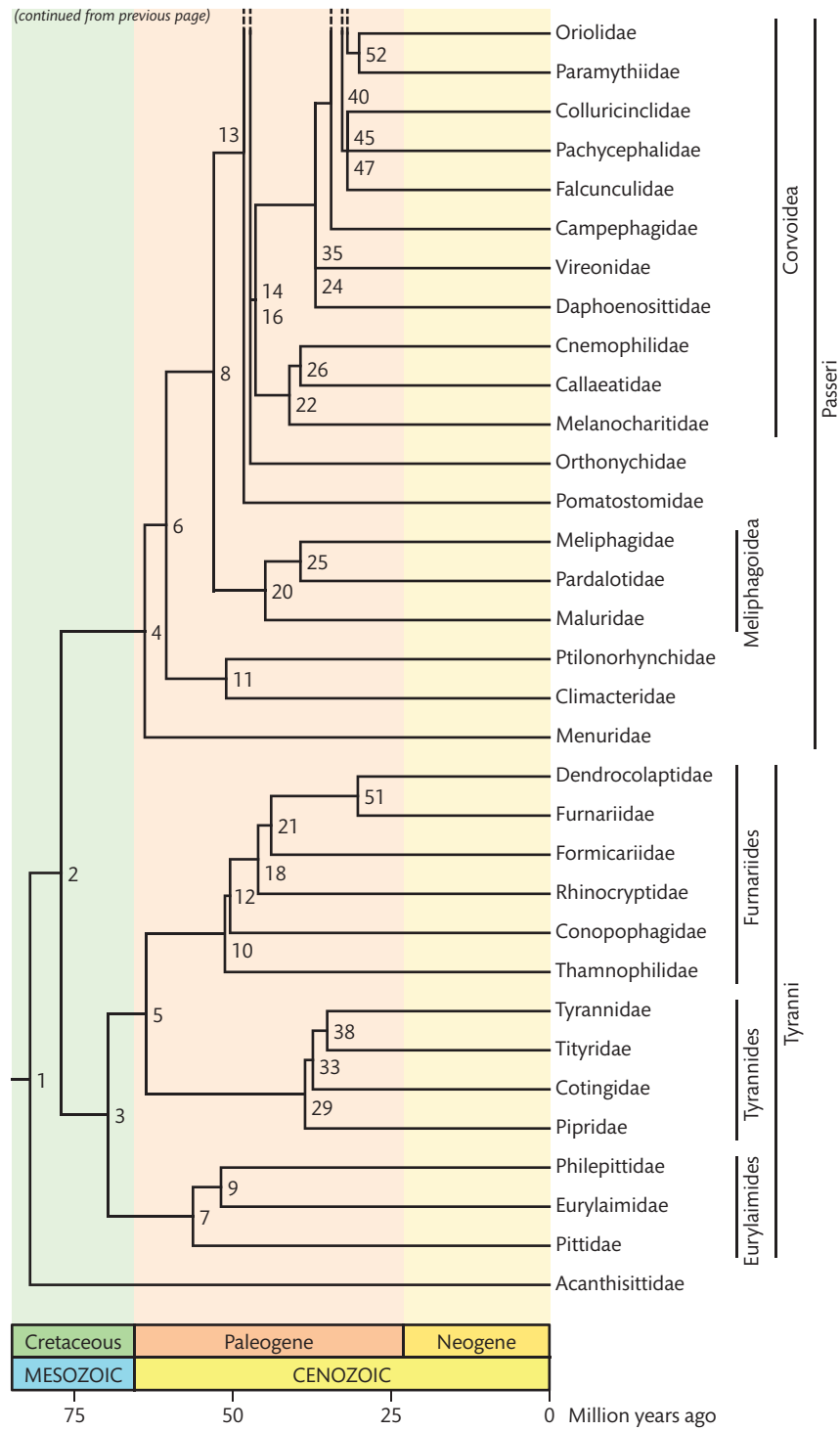


Fig. 2 A timetree of passerine birds (Passeriformes). Divergence times are shown in Table 1.

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among passerine birds (Passeriformes).

Timetree		Estimates							
Node	Time	Ref. (12)		Ref. (19)(a)		Ref. (19)(b)		Ref. (38)	
		Time	CI	Time	CI	Time	CI	Time	CI
1	82.0	95.3	107-85	82.0	-	82.0	-	82	-
2	77.1	91.8	103-81	77.4	81-73	76.8	80-72	-	-
3	69.7	-	-	70.5	78-65	68.8	73-60.9	-	-
4	63.9	-	-	64.7	70-60	63.1	67-57	-	-
5	63.7	-	-	64.6	75-55	62.7	67-56	-	-
6	60.5	-	-	61.3	72-54	59.7	66-53	-	-
7	56.3	-	-	57.3	67-47	55.2	60-47	-	-
8	53.0	-	-	54.6	67-49	51.4	60-47	-	-
9	51.9	-	-	54.4	-	49.3	-	-	-
10	51.2	-	-	53.1	-	49.3	-	-	-
11	51.0	-	-	53.4	70-48	48.5	56-42	-	-
12	50.4	-	-	52.3	-	48.5	-	-	-
13	48.3	-	-	49.7	-	46.9	-	-	-
14	47.9	46.7	54-40	48.5	63-43	47.2	55-41	46.7	54-40
15	47.2	-	-	48.5	-	45.8	-	-	-
16	46.4	-	-	47.1	62-42	45.6	62-39	-	-
17	46.2	-	-	46.7	53-42	45.7	50-40	44.5	52-41
18	46.0	-	-	47.7	-	44.2	-	-	-
19	45.0	-	-	45.3	51-39	44.6	49-39	-	-
20	44.9	-	-	45.8	58-40	44.0	52-37	-	-
21	43.9	-	-	45.6	-	42.2	-	-	-
22	41.1	-	-	42.7	-	39.5	-	-	-
23	40.8	-	-	40.7	54-15	40.8	49-36	-	-
24	39.5	-	-	40.4	45-35	38.6	42-32	-	-
25	39.3	-	-	41.1	-	37.5	-	-	-
26	39.3	-	-	41.0	-	37.6	-	-	-
27	39.2	-	-	38.2	47-14	40.2	48-35	-	-
28	39.0	-	-	38.8	54-15	39.2	54-15	37.5	42-32
29	38.6	-	-	40.5	-	36.6	-	-	-
30	38.5	-	-	38.5	53-14	38.4	53-14	38.1	43-33
31	38.1	-	-	37.9	-	38.2	-	-	-
32	37.8	-	-	37.7	51-13	37.9	50-13	-	-
33	37.4	-	-	39.2	-	35.6	-	-	-
34	37.3	-	-	37.1	-	37.5	-	-	-
35	36.9	-	-	38.5	-	35.3	-	-	-
36	36.9	-	-	36.5	-	37.2	-	-	-
37	35.1	-	-	34.9	51-13	35.2	51-13	33.8	38-29
38	35.1	-	-	36.9	-	33.2	-	-	-
39	35.0	-	-	35.1	-	34.9	-	-	-

Table 1. *Continued*

Timetree		Estimates							
Node	Time	Ref. (12)		Ref. (19)(a)		Ref. (19)(b)		Ref. (38)	
		Time	CI	Time	CI	Time	CI	Time	CI
40	34.5	-	-	36.0	-	33.0	-	-	-
41	34.2	-	-	34.2	-	34.1	-	-	-
42	34.0	-	-	34.0	41-27	33.9	38-30	-	-
43	33.4	-	-	34.9	49-28	31.9	39-26	-	-
44	32.7	-	-	34.1	-	31.3	-	-	-
45	32.5	-	-	39.3	-	25.7	-	-	-
47	31.9	-	-	33.4	-	30.4	-	-	-
46	31.9	-	-	33.2	-	30.6	-	-	-
48	31.7	-	-	32.0	-	31.3	-	-	-
49	31.5	-	-	31.0	-	32.0	-	-	-
50	31.1	-	-	30.8	48-12	31.3	48-12	-	-
51	30.3	-	-	31.7	-	28.8	-	-	-
52	30.0	-	-	31.2	-	28.7	-	-	-
53	29.4	-	-	28.7	-	30.0	-	-	-
54	29.4	-	-	29.0	-	29.7	-	-	-
55	29.1	-	-	29.3	-	28.8	-	-	-
56	28.6	-	-	27.4	-	29.7	-	-	-
57	28.5	-	-	29.2	35-23	27.7	31-21	23.1	30-21
58	26.9	-	-	25.6	-	28.1	-	-	-
59	26.6	-	-	26.0	-	27.1	-	-	-
60	26.1	-	-	26.8	-	25.4	-	-	-
61	26.0	-	-	25.4	-	26.6	-	-	-
62	25.6	-	-	26.2	-	24.9	-	-	-
63	25.0	-	-	24.3	-	25.7	-	-	-
64	24.6	-	-	24.8	-	24.4	-	-	-
65	24.3	-	-	23.0	-	25.6	-	-	-
66	24.3	-	-	24.8	-	23.7	-	-	-
67	24.2	-	-	24.5	38-19	23.9	38-17	-	-
68	24.2	-	-	24.4	-	24.0	-	-	-
69	24.0	-	-	25.1	-	22.9	-	-	-
70	23.2	-	-	24.1	-	22.2	-	-	-
71	23.1	-	-	22.5	-	23.7	-	-	-
72	23.1	-	-	22.2	-	23.9	-	-	-
73	22.9	-	-	23.4	-	22.3	-	-	-
74	22.1	-	-	21.2	-	23.0	-	-	-
75	22.0	-	-	22.4	-	21.5	-	-	-
76	21.2	-	-	22.3	-	20.1	-	-	-
77	21.0	-	-	21.3	-	20.6	-	-	-
78	20.8	-	-	20.3	26-15	21.2	26-20	-	-
79	20.3	-	-	21.5	-	19.1	-	-	-

Table 1. *Continued*

Timetree		Estimates							
Node	Time	Ref. (12)		Ref. (19)(a)		Ref. (19)(b)		Ref. (38)	
		Time	CI	Time	CI	Time	CI	Time	CI
80	20.0	-	-	18.9	-	21.0	-	-	-
81	16.7	-	-	15.5	-	17.8	-	-	-
82	15.2	-	-	14.1	-	16.3	-	-	-
83	12.6	-	-	11.6	-	13.6	-	-	-
84	11.5	-	-	10.8	-	12.2	-	-	-
85	11.3	-	-	10.3	-	12.2	-	-	-

Note: Node times in the timetree represent the mean of time estimates from the study with the most complete taxon sampling (19). Results from nonparametric rate smoothing (a) and penalized likelihood (b) analysis of the *RAG1* and *RAG2* nuclear genes are shown from ref. (19). In ref. (38), the same two genes and nonparametric rate smoothing is used to estimate divergence times.

three major groups have been delineated—Passeroidea, Muscipoidea, and Sylvioidea—but due to their short internodal distances from one another and from several problematic groups, their taxonomic boundaries and relationships are still in flux.

The largest taxon sample to date for the corvids uncovered two large clades (19). One clade, corresponding to Sibley and Ahlquist's Tribe Corvini, includes the crows and their relatives—the shrikes (Laniidae), monarch flycatchers (Monarchidae, Grallinidae), the birds of paradise (Paradisaeidae) and their relatives (Melampittidae, Corcoracidae), as well as the rhipidurine flycatchers. Their closest relative is a group of shrike-like birds with taxa in Africa (malaconotid bush shrikes, prionopid helmet shrikes, among others), Madagascar (vanga shrikes), and Southeast Asia (aegithinids, among others), all corresponding to Sibley and Ahlquist's Tribe Malaconotini. Relationships among these taxa are still unsettled (25, 26). There are a number of other corvid lineages that are more distantly related to these two groups, although their phylogenetic placement generally lacks strong support.

The *RAG1* and *RAG2* data set (19) provided an outline of sylvioid relationships based on a small “family-level” sampling, but recently the group has been sampled more broadly using *cytochrome b* and *myoglobin* intron II (27). Unfortunately, the markers used in the latter study have limitations when resolving deep branches and many nodes remain poorly resolved. Moreover, there are some significant topological incongruences in the two studies that will need further data to resolve.

The Passeroidea comprises the New World nine-primaried passerines (buntings, cardinals, warblers, tanagers, and blackbirds) as well as Old World finches, sparrows, wagtails, accentors, sunbirds and flowerpeckers, leafbirds, and sugarbirds (18, 19, 28). Within the New World passeroids *RAG1* and *RAG2* (19) and a diverse array of nuclear and mitochondrial loci (28) support a close relationship of the icterids + parulids with the thraupids + cardinalids + emberizids. These data also are in general agreement about the relationships of Old World lineages to this New World clade. Of particular significance is the finding that the closest relative of all these passeroid lineages appears to be members of an African clade including the sugarbirds (Promeropidae) and the enigmatic “babblers” *Arcanator* and *Modulatrix*.

The final major clade of Passerida, and the probable closest relative of the passeroids, is the Muscipoidea. Nuclear *RAG* gene sequences support the inclusion of the thrushes (Turdidae), muscipid flycatchers, dippers (Cinclididae), starlings (Sturnidae), mockingbirds and thrashers (Mimidae), and possibly the more distantly related waxwings and silky-flycatchers (Bombicillidae), kinglets (Regulidae), and a monophyletic lineage of wrens (Troglodytidae), gnatcatchers (Poliotilidae), nuthatches (Sittidae), and creepers (Certhiidae) (18, 19, 29). Nodes at the base of the muscipoids, however, are not well supported, hence the monophyly and relative arrangements of the major clades need further analysis.

Age estimates for Passeriformes are logically linked to our understanding of the age of modern birds as a whole and where passeriforms might fit within the avian

Tree of Life. Unfortunately, there is no clear understanding about the closest relative of passeriforms, although they probably lie with taxa traditionally classified in the “Coraciiformes” and Piciformes. Those few studies that have attempted to estimate divergence times across the avian tree have all placed the divergence of passeriforms from other orders in the late Cretaceous (8, 12, 30–33). Although there is consistency in these age estimates—that is, before the Cretaceous–Paleogene (K-P) boundary (65 Ma) and within the late Cretaceous (100–65 Ma)—the data and methods vary significantly and the taxon sampling for all these studies was not adequate for examining divergences within passerines.

There are currently no passerine fossils that are useful for internal calibration of the passeriform tree. The oldest passeriform (34) is from Australia and of early Eocene in age (~55 Ma), but its phylogenetic relationships are uncertain. As a consequence, there have been several other approaches to calibrating the passerine tree. Van Tuinen and Hedges (31) employed a distant external calibration based on a general vertebrate tree. Barker *et al.* (19) used a geological vicariance event, the separation of New Zealand (*Acanthisitta*) from Gondwana to calibrate the base of passeriforms at ~82 Ma. Pereira and Baker (12) estimated divergence times for major groups of birds using 35 complete mitochondrial genomes for 35 species of birds and 13 vertebrate outgroups, with times of splitting for the vertebrate outgroups and five nodes inside modern nonpasseriform birds being calibrated with fossils. In that study, Bayesian analysis of the data placed the origin of modern birds at 139 Ma and the separation between passeriforms and other Neoaves at 108 Ma (in their small sample, passeriforms were resolved as the closest relative of other neoavians). Within passeriforms they dated the divergence of *Acanthisitta* and other passeriforms at 95.3 Ma, although the lower CI bound included the Barker *et al.* (19) vicariance age.

The only study to estimate the entire passeriform timetree was constructed using nonparametric rate smoothing and penalized likelihood analysis (35, 36) of combined *RAG1* and *RAG2* genes, which, as noted, was calibrated with the New Zealand vicariance age of 82 Ma (19; Fig. 2). As an independent check on that calibration point, pairwise corrected distances of *cytochrome b*, converted to time using a commonly applied passerine evolutionary rate (37), yielded a divergence age for the *Acanthisitta* vs. other passerines at around 87 Ma (19), which is within the confidence interval of the whole mtDNA clock (12).

Assuming the 82 Ma calibration, the suboscines and oscines split (node 2) around 77 Ma, well before the K-P extinction event (19). Other basal splits took place just prior to the K-P boundary (Old and New World suboscines, see also 23), or more or less contemporaneously with it. Thus, the diversification into the major lineages of the New World suboscines, as well as the earliest branches within oscines, took place around the K-P boundary. A sampling of well-supported groups on the passerine timetree gives an overall picture of the temporal pattern of passerine evolution (Fig. 2).

Within the New World suboscines, there are two major clades (Fig. 2). The first is the Furnariides—including the antpittas, antbirds, and ovenbirds—which arose around 55 Ma. The other major lineage, the highly speciose Tyrannides, on the other hand, started to diversify substantially later in time, around 38–42 Ma. Numerous early lineages of oscines diversified between 65 and 50 Ma. Thus, all four primary oscine clades—corvids, muscicapoids, passeroids, and sylvioids—began radiating at roughly the same time (47–38 Ma), although the radiation of the corvids was likely initiated slightly earlier than the others. Within each of these clades some groups attained very high diversity within relatively short periods of time. The most striking is the New World passeroid radiation that began ~20 Ma and resulted in over 300 genera and 1500 species, most of which apparently diversified within the last 10–15 million years. The highly diverse groups of the Old World muscicapoids and sylvioids began radiating somewhat earlier than the New World passeroids.

There has been very little additional analysis of the oscine timetree. Several previous studies (38, 39) employed the same *RAG1* and *RAG2* data, the *Acanthisitta* calibration and rate smoothing methods as did Barker *et al.* (19), hence it is unsurprising that all three studies are consistent with respect to the timetree. Only one other study (25) dated a significant portion of the passerine tree, in this instance within malaconotine corvids. Employing two nuclear introns (*myoglobin* intron-2 and *GAPDH* intron-11) as well as sequence from the mtDNA gene *ND2*, they calibrated the suboscine–oscine split based on previous work (19, 31, 40), allowing it to vary between 77 and 71 Ma, and estimated splits within malaconotines using Bayesian methods (41). These workers found that malaconotines began radiating ~37.7 Ma using all data and ~38.9 Ma using the nuclear introns alone. These dates are significantly older, by ~9–12 Ma, than those presented in Fig. 2. In parallel with comments about the age of passerines as

a whole (see earlier), discrepancies in the estimated age of the malaconotines are likely attributable to different data sets and rate estimation methods.

Our current understanding of passerine phylogeny has led to the strong inference that passeriforms had their origin on Gondwana and that oscines in particular arose in Australasia (18–20, 40). By 47–40 Ma passeridans had reached Laurasia, and corvoids also reached the Asian mainland by about 40 Ma (Fig. 2). Both groups diversified across Laurasia and subsequently invaded the Southern Hemisphere (South America and Africa), as well as reinvaded Australia. Within corvoids, vireos reached the New World around 28–20 Ma (19, 39) and crows/jays did so ~17–14 Ma. There were multiple invasions of passeridans into the New World starting with the wrens at 34 Ma, the mimids at 22–20 Ma, and the emberizines at 22–20 Ma (19). The latter clade includes finches, warblers, blackbirds, and tanagers, which together are the dominant oscines of the New World, especially the Latin American tropics.

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