

# Out of Gondwana: the origin of passerine birds

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Two recent papers analysing nuclear DNA sequence data shed new light on the origin of perching birds (Passeriformes) and the structure of their radiation. Both papers find that the New Zealand wrens *Acanthisitta* fall at the base of the passerine radiation, implying an origin of this clade in Gondwana. Additionally, among oscine passerines (songbirds), both papers fail to support a sister group relationship between the largely Australo–Papuan Corvida and the Afro–Eurasian Passerida, as outlined in Sibley and Ahlquist’s tapestry. Rather, they converge on a phylogeny in which the Passerida is nested within the Corvida, suggesting an origin of songbirds in eastern Gondwana (Australia plus New Guinea). Finally, a Cretaceous origin of passerine birds is supported by the new data, albeit more on grounds of biogeography than of molecular clocks. The new papers solidify a synthesis of paleontological, phylogenetic and molecular data that has been growing over the past decade, and pave the way for a new generation of comparative studies of passerines.

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The higher level systematics of vertebrate clades is experiencing a renaissance, and recent data from molecules and morphology are revising our understanding of relationships within mammals and reptiles [1,2]. Now, two new papers [3,4] bring higher level relationships of the perching birds (Passeriformes) into sharper focus. Together, they place a final nail in the coffin of the old view that Australia and the rest of eastern Gondwana was the recent recipient, rather than the ancient progenitor, of the oscine songbirds, a clade comprising today >5000 species. They also brighten a phylogenetic spotlight on a clade of diminutive (and threatened) species in New Zealand, the Acanthisittidae, as the sole survivors of the sister group to all other passerines. These papers, together with a spate of recent work on higher level passerine phylogenetics [5–8], now serve as the starting point for future phylogenetic

studies and for comparative ecological and behavioral analyses of the perching bird clade, a model for diversification comprising over half of all bird species.

Until the 1970s, and throughout the 19th century heyday of description of Australia’s avifauna, ornithologists believed that the diverse Australian and New Guinea passerines were the poor last gasp of radiations that had been accumulating over eons in the Old and New Worlds. Thus, Australo–Papuan ‘robins’, ‘wrens’ and ‘treecreepers’ were thought to have been relatively recent derivatives of corresponding groups better known and already described from Eurasia and the Americas. Such a scenario was consistent with the prevailing paleobotanical view that the widespread eucalypt forest of Australia, rather than the extensive tropical rainforest that dominates eastern Australia and New Guinea today, was the ancestral habitat for animal diversification in this region [9].

## Gondwana rising

One of the first challenges to the idea of a northern origin for the Passeriformes came from paleo-ornithologists. They noted that, although extensive early Tertiary sites in North America and Europe contained many small arboreal forms, most belonged to derived nonpasseriform groups, such as the Coraciiformes, or extinct zygodactylous groups – none are passerine. Songbirds did not become common in the Northern Hemisphere record until the Middle Miocene, with the earliest unquestioned records from Upper Oligocene sites in France [10]. The absence of an early Tertiary record of passerines in the Northern Hemisphere led paleo-ornithologists to propose that these birds originated in the Southern Hemisphere, before spreading northwards [11]. However, sufficiently early Southern passerine fossils to test this idea with were not forthcoming until two small fragmentary bones were discovered in an Early Eocene deposit at Murgon, southeastern Queensland,

Australia [12]. These pushed back the known age of the Passeriformes by almost 25 million years to a time when Australia was still attached to, and just starting to split away from, eastern Antarctica.

The next revolution to the traditional ideas came from the work of Charles Sibley and Jon Ahlquist. Based first on data from egg-white proteins and then on DNA–DNA hybridization [13], they proposed that many of the Australo–Papuan songbirds (oscin passerines) formed a monophyletic group, the Corvida, that was sister to the remaining songbird groups, which comprised a monophyletic Passerida. This hypothesis can justifiably be considered the greatest achievement of Sibley’s 50-year career in avian systematics. It not only implied an autochthonous radiation of songbirds within Australia that far exceeded in scope that of the marsupials, but it also suggested that some New and Old World lineages, such as crows, jays and cuckoo-shrikes, ultimately have their roots in Australia, rather than in the neo- and paleotropics where they achieve great diversity today. Combined with recent fossil data, revised taxonomies, and paleoenvironmental reconstructions implicating rainforest as the habitat within which much of this radiation took place [9,14], the DNA hybridization data helped forge a new view of passerine diversification in which Gondwana played a leading, rather than a minor, role.

## Phylogenetics, biogeography and congruence

Both new studies [3,4] employed extensive analysis of nuclear DNA sequence data, primarily because recent analyses of mitochondrial (mt) DNA sequences for higher level relationships within birds have been controversial, showing congruence with few other studies [15]. P. Ericson *et al.* [4] sequenced parts of the *c-myc* and *RAG1* genes for a total of 1428 bp across 21 passerines, whereas Barker *et al.* [3] sequenced 3488 bp for the *c-mos* and *RAG1* genes across 69 passerines. Given the similarity of data sources and methods of analysis, it was

unsurprising that both papers strongly recovered a sister group relationship between oscines and suboscines, a result that is in strong agreement with many morphological and molecular studies. Of greater interest was that both studies recovered monophyletic New and Old World suboscine clades, corroborating the DNA hybridization work [13]. Barker *et al.*'s extensive taxon sampling – including exemplars of 31 of 34 currently recognized passerine families – is noteworthy. It enabled them to corroborate one hypothesis for the relationships of the endemic Malagasy family Philepittidae (that it is part of the broadbills, an Old World suboscine group, Eurylaimidae) and to perform an explicit parsimony analysis of ancestral biogeographical areas of passerine families implicating Gondwana as the cradle of songbird evolution.

In addition, the two new papers add a significant twist to the emerging story of passerine evolution by recovering phylogenies in which Corvida is basal to, and paraphyletic with regard to, the Passerida, which is still strongly monophyletic. Although phylogenetically less tidy than the sister group pattern proposed by Sibley and Ahlquist, the new trees favor even more strongly a Gondwanan origin for songbirds. At this level, the two papers are striking in their congruence, and allow ornithologists for the first time to implicate eastern Gondwana (Australia and New Guinea) as the birthplace for songbirds. This precision was previously not possible because, as sister groups, Passerida and Corvida had equal importance in parsimony reconstructions of ancestral areas, although the Gondwanan distribution of suboscines certainly favored a similar origin for songbirds [5]. The two papers are also highly congruent in their placement of the taxonomically enigmatic lyrebirds *Menura* spp. and the Australo-Papuan treecreepers *Climacteris* spp. at the base of the oscine radiation, albeit with slightly different relationships between these groups.

A final remarkable example of congruence between the two papers is the placement of *Acanthisitta*, an exemplar of the New Zealand wrens, at the base of the entire passerine radiation. This group possesses primitive states for several morphological traits, including the morphology of the stapes and syrinx,

which hindered clear placement as an oscine or suboscine. As in earlier work [8,13], this result was moderately strong at best; whereas the Ericson *et al.* study could not formally reject trees in which *Acanthisitta* was embedded within the passerines, the Barker *et al.* study achieved 80–93% bootstrap values for the clade comprising all passerines other than *Acanthisitta*. Noting that New Zealand was the first to break off from Gondwana around 82 million years ago (Mya), Ericson *et al.* suggest that many of the major divergences within passerines took place 71–60 Mya, somewhat earlier than the time frame for family-level radiations suggested by paleontology [16]. Although the sequence data from both studies rejected a molecular clock, Ericson *et al.* were able to employ novel rate-smoothing methods that permit divergence time estimates under these conditions. Still, their dates hinge largely on the single date supplied by the breakup of ancestral Gondwana. It would be interesting to see what this date implies about rates of nuclear DNA sequence evolution in passerines and, conversely, what the consequences of applying mammalian or other published rates would be for estimating divergences from first principles [17]. It seems probable, however, that the passerine radiation is older than was previously thought, a result that is consistent with some recent mtDNA results.

#### Digging deeper

However tenuously, a synthesis of molecular, paleontological and phylogenetic results is emerging that implicates Gondwana as the center not only of passerine evolution, but also of the diversification of the major clades of living birds in general [5]. There is but a single site in Australia (Murgon) in the Early Cretaceous–Late Oligocene time span that has produced small avian fossils, and the earliest passerine record from South America comes from the Early Miocene of Argentina [18], and that of Africa even later. Thus, the absence of relevant northern fossils at crucial ages finds agreement in the new molecular studies. Although several lines of investigation support a southern origin for the Passeriformes as well as other orders, this picture remains a broad-brush interpretation. The ability to discern the finer detail of distributional patterns

across space and time must await additional southern fossils from more early Tertiary or even Cretaceous-aged sites. Although crucial to our understanding, such new suitably aged deposits remain elusive.

For neontologists, too, much work remains. Sheldon [19] and others warned of the dangers for comparative biologists of investing too much effort in studies relying heavily on poorly resolved or contentious phylogenies. Given the attractiveness of passerines for comparative studies of a variety of behavioral, ecological and evolutionary traits, the new phylogenies will now serve as the standard tool for comparative analyses in this clade.

#### References

- Murphy, W.J. *et al.* (2001) Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* 294, 2348–2351
- Lee, M.S.Y. (2001) Molecules, morphology and the monophyly of diapsid reptiles. *Contr. Zool.* 70, 1–22
- Barker, F.K. *et al.* (2002) A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc. R. Soc. Lond. Ser. B* 269, 295–308
- Ericson, P.G.P. *et al.* (2002) A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. R. Soc. Lond. Ser. B* 269, 235–241
- Cracraft, J. (2001) Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proc. R. Soc. Lond. Ser. B* 268, 459–469
- Ericson, P.G.P. *et al.* (2000) Major divisions in oscines revealed by insertions in the nuclear gene *c-myc*: a novel gene in avian phylogenetics. *Auk* 117, 1069–1078
- Irestedt, M. *et al.* (2001) Phylogeny of the major lineages of suboscines (Passeriformes) analyzed by nuclear DNA sequence data. *J. Avian Biol.* 32, 15–25
- Lovette, I.J. and Bermingham, E. (2000) *c-mos* variation in songbirds: molecular evolution, phylogenetic implications, and comparisons with mitochondrial differentiation. *Mol. Biol. Evol.* 17, 1569–1577
- Heinsohn, R.G. *et al.* (1990) Avian cooperative breeding: old hypotheses and new directions. *Trends Ecol. Evol.* 5, 403–407
- Mourer-Chauviré, C. *et al.* (1989) Découverte de Passeriformes dans l'Oligocène supérieur de France. *C. R. Acad. Sci. II* 309, 843–849
- Olson, S.L. (1988) Aspects of global avifaunal dynamics during the Cenozoic. In *Acta XIX Congressus Internationalis Ornithologici* (Ouellet, H., ed.), pp. 2023–2029, National Museum of Natural Sciences
- Boles, W.E. (1995) The world's oldest songbird. *Nature* 374, 21–22
- Sibley, C.G. and Ahlquist, J.E. (1990) *The Phylogeny and Classification of Birds: A Study in Molecular Evolution*, Yale University Press

- 14 Schodde, R. and Mason, I.J. (1999) *The Directory of Australian Birds: A Taxonomic and Zoogeographic Atlas of the Biodiversity of Birds in Australia and its Territories*, CSIRO Publishing
- 15 Johnson, K.P. (2001) Taxon sampling and the phylogenetic position of passeriformes: evidence from 916 avian cytochrome *b* sequences. *Syst. Biol.* 50, 128–136
- 16 Feduccia, A. (1996) *The Origin and Evolution of Birds*, Yale University Press
- 17 van Tuinen, M. and Hedges, S.B. (2001) Calibration of avian molecular clocks. *Mol. Biol. Evol.* 18, 206–213
- 18 Noriega, J.I. and Chiappe, L.M. (1993) An early Miocene passeriform from Argentina. *Auk* 110, 936–938
- 19 Sheldon, F. 1997. Phylogeny in studies of bird ecology, behavior, and morphology. In *Avian Molecular Systematics and Evolution* (Mindell, D.P., ed.), pp. 279–301, Academic Press

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# Gender bias in the refereeing process?

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**Scientists are measured by their publications. Yet anonymous peer review is far from transparent. Does bias lurk within the refereeing process? Investigating the outcomes of manuscript submissions suggests that the overall process is not sexist, but differences in acceptance rates across journals according to gender of the first author give grounds for caution. Manuscripts with more authors and by native English speakers are more successful; whether this is due to bias remains to be seen.**

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Senior academics in the field of ecology and evolution are predominantly male, in spite of a gender ratio that is closer to parity among younger researchers. Clearly, this pattern is the result of a combination of factors, but a pressing question is whether gender bias is involved. Studies of grant awards [1], promotions [2] and resource allocation [3] illustrate the potential for sexual discrimination in the allocation of funding. Potentially equally important, but less scrutinized, is the process by which decisions on the publication of manuscripts are made by referees and journal editors. With the help of the editorial staff of several high impact (ISI impact factor >2) ecology and evolution primary research journals, I have examined differences in acceptance rate according to gender, nationality and the number of authors on a manuscript.

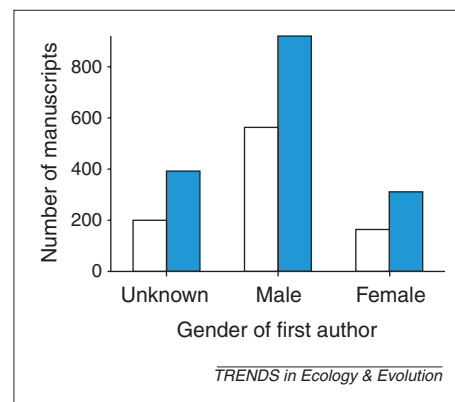
**The study**

I wrote to the editors of 24 primary research journals requesting that they record the gender, nationality, number of authors and

**Box 1. Citation rates relative to gender, number of authors and country of affiliation**

In November 2001, I examined the citation rate of 507 papers published 3–4 years previously in five leading ecology and evolution journals that generally publish authors' first names, allowing gender to be determined in most cases. Female authors do not appear more likely to use initials rather than their names: of papers where authors used initials, web searches and correspondence with co-authors revealed that 12 out of 38 were female (2 way  $\chi^2 = 2.78$ ,  $P = 0.1$ ). The number of citations for each paper was determined from the ISI citation index. There were no differences in citation rate according to gender, (Kruskal Wallis;  $\chi^2 = 3.02$ ,  $P = 0.22$ ) as would be expected if the reviewing process and citation are unbiased in relation to gender. However, there were differences in citation rate between papers according to the number of authors, with two author papers most cited and a linear decline in citation rate through 3, 1 and 4+ authors (Kruskal Wallis;  $\chi^2 = 8.26$ ,  $P = 0.041$ ). Hence, although submissions with more than four authors are the most likely to be accepted, they are the least likely to be cited. Country of affiliation of the first author has a strong effect on number of citations, even if only wealthy countries are used (see main text), with papers from non-native English speaking countries attracting fewer citations (Kruskal Wallis;  $\chi^2 = 9.17$ ,  $P = 0.002$ ).

the final decision made on their submitted manuscripts over a period of a year. Seven editors from five journals agreed to take part providing data from 2680 manuscripts on the number of authors, the gender of the first author, their country affiliation, and whether the manuscript was finally accepted or rejected. Gender was



**Fig. 1.** Acceptance of manuscripts according to gender of first author. There is no overall difference in the acceptance rate of manuscripts according to whether the first author is designated as male, female or unknown. (Open bars, accepted manuscripts; blue bars, rejected manuscripts).

designated as unknown where it was not immediately apparent from the author's first name (predominantly when only initials were provided) even if the editor actually knew the person's gender. There does not appear to be any gender difference in likelihood of choosing to use initials rather than first names (Box 1). Data were collected within the period 1997 to 2000.

Of 2680 manuscripts, 1558 had male first authors, 498 female, and 624 unknown gender, ( $\chi^2 = 751$ ,  $P < 0.001$ ). There was no difference in the proportion of manuscripts each gender submitted as a sole author (excluding unknown gender manuscripts) ( $n = 2056$ ,  $\chi^2 = 2.45$ ,  $P = 0.12$ ).

**Effect of author gender**

Combining data from all journals ( $n = 2550$  excluding those pending a decision), there is no overall difference in the acceptance rates of papers according to gender ( $\chi^2 = 4.04$ ,  $P = 0.13$ ) (Fig. 1). This pattern is the same if only single author papers are considered ( $n = 554$ ,  $\chi^2 = 1.97$ ,  $P = 0.37$ ).

Had there been a difference in acceptance rate relative to gender it would