

Evolution of terrestrial birds in three continents: biogeography and parallel radiations

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ABSTRACT

Aim To reconstruct the biogeographical history of a large clade of mainly terrestrially adapted birds (coraciiform and piciform birds, owls, diurnal raptors, New World vultures, trogons, mousebirds, cuckoo-rollers, seriemas, parrots and passerines) to test the hypothesis of its Gondwanan origin.

Location Global.

Methods The phylogenetic tree used in the analysis was a family-level tree estimated from previously published nuclear DNA sequence data. Each family for which a thorough and taxonomically well-sampled phylogenetic analysis exists was subject to an initial dispersal–vicariance analysis in order to reconstruct ancestral areas for its two most basal lineages. Both basal lineages were then used to represent the family in the subsequent reconstruction of ancestral distributions for the entire radiation.

Results The analysis showed that three reciprocally monophyletic groups of terrestrial birds have diversified in the Gondwanan land areas of Australia, South America and Africa, respectively. Although each of these three groups may also have originally included other groups, the only survivors today from the Australian radiation are the passerines and parrots, while the falcons and seriemas have survived from the South American radiation. The group of survivors from the African radiation is considerably more taxonomically diverse and includes all coraciiform and piciform birds, owls, diurnal raptors (except falcons), New World vultures, trogons, mousebirds and cuckoo-rollers.

Main conclusions The outlined evolutionary scenario with three geographically isolated clades of terrestrial birds is consistent with the available estimates of Late Cretaceous to early Palaeogene dates for these radiations. The diversifications and ecological adaptations within each of the three groups most likely took place in isolation on the different continents. Many cases of convergently evolved adaptations may be revealed through the increased understanding of the phylogenetic relationships of terrestrial birds.

Keywords

Aves, birds, convergent evolution, Cretaceous, diversification, ecological adaptation, Gondwana, niche conservatism, Palaeogene.

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INTRODUCTION

Although birds as a group have an extraordinary dispersal capability it has long been clear that major groups exhibit geographical distribution patterns that are best explained in terms of large-scale geological processes. Cracraft (1974a,b)

suggested that the biogeographical patterns in, for example, ratites, galliforms and anseriforms, bear ‘Gondwanan signatures’. This was long disputed because it assumes that several groups of Neornithes (modern birds) had already diversified in the Late Cretaceous, a time much older than the oldest fossils of these groups (Olson, 1985, 1989; Feduccia, 1999). Later,

DNA-based phylogenies were used to infer the age of major bird groups using a molecular-clock approach (e.g. Cooper & Penny, 1997; Kumar & Hedges, 1998; van Tuinen & Hedges, 2001; Ericson *et al.*, 2002, 2006; Baker *et al.*, 2007; Brown *et al.*, 2007; Slack *et al.*, 2007). Although the age estimates in these studies rarely agree completely, they invariably suggest that the earliest evolution of modern birds took place in the Cretaceous, a time when the final breaking up of the supercontinents Gondwana and Laurasia shaped much of the present-day biogeography of vertebrates (Hedges *et al.*, 1996; Bossuyt *et al.*, 2006). Fain & Houde (2004) suggested that the parallel evolution of similar ecological adaptations observed between major clades of birds was best explained by their long-term isolation in different continents. Today, it is almost

unanimously accepted that Neornithes evolved in the Cretaceous, but it is not agreed how much of the diversification of the group took place before the Palaeogene.

Two phylogenetic hypotheses based on molecular data for the large clade Neoaves, which includes 95% of all extant bird species, have been formulated by Ericson *et al.* (2006) and Hackett *et al.* (2008). The two studies are based on 5 and 19 nuclear genes, respectively, and their results are largely congruent. Both studies recover a large clade of 'landbirds' consisting of all coraciiform and piciform birds, owls, diurnal raptors, New World vultures, trogons, mousebirds, cuckoo-rollers, seriemas, parrots and passerines. This taxonomic arrangement contains several differences compared with phylogenetic hypotheses based on morphological data (e.g.

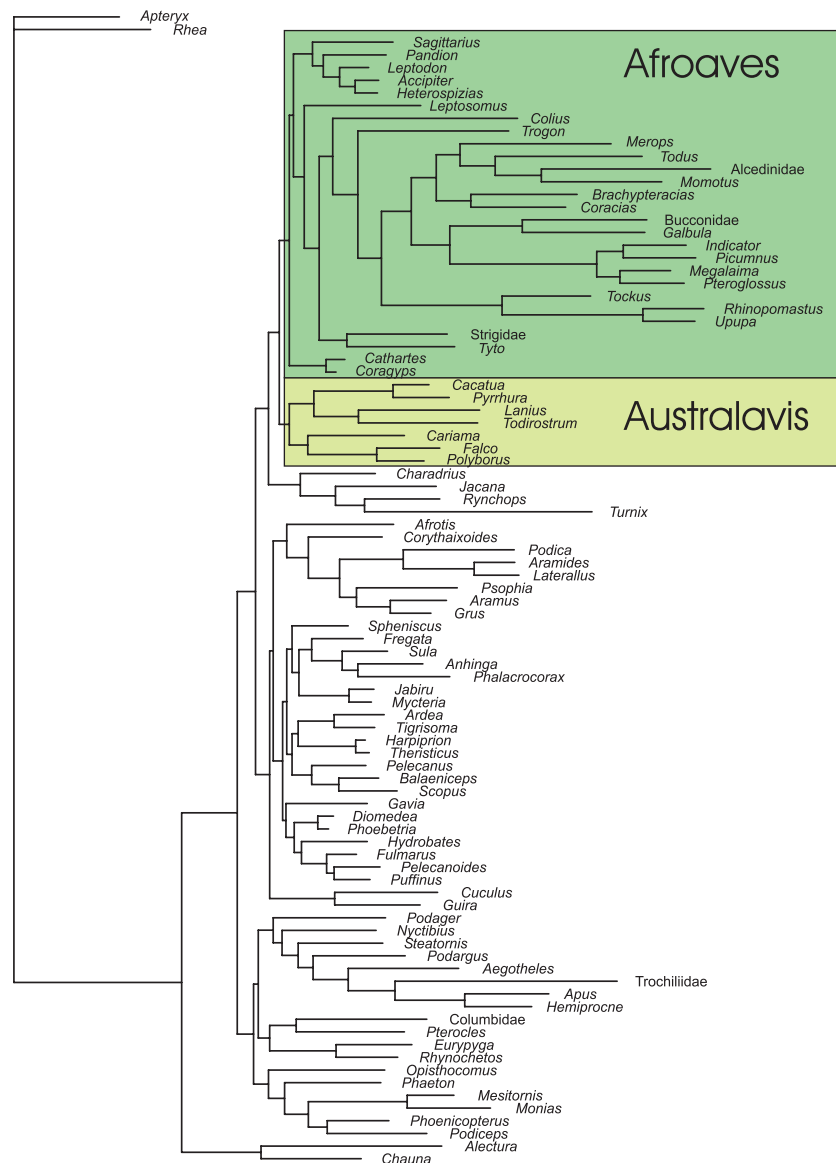


Figure 1 Best fit maximum-likelihood tree ($-\ln$ likelihood = 79,500.0718) of the combined data set of Ericson *et al.* (2006). The two clades of mainly terrestrially adapted birds are marked in green colours. The names for these clades, Afroaves and Australavis, are proposed in the text.

Livezey & Zusi, 2007). Although many landbirds also group together in the phylogeny of Livezey & Zusi (2007), the nearest counterpart to the landbird clade herein, Dendroornithes, included some groups (e.g. pigeons, sandgrouses, swifts, hummingbirds, caprimulgiforms and cuckoos) that the molecular data unambiguously place outside the 'landbird' clade. Mayr (2008) has argued that the large data matrix of 2954 morphological characters of Livezey & Zusi (2007) is burdened by a high proportion of homoplasious characters, which may lead to the outcome that unrelated taxa adapted to similar lifestyles group together. Not only does the Dendroornithes of Livezey & Zusi (2007) include taxa that molecular data suggest do not belong here, but the systematic relationships within their landbird clade also differ substantially from the molecular trees of Ericson *et al.* (2006) and Hackett *et al.* (2008). It may be argued that the morphological data provide better estimates of the avian phylogenetic tree, but I chose to use the results based on DNA sequence data for my biogeographical analysis.

The landbird clade under study thus contains all coraciiform and piciform birds, owls, diurnal raptors, New World vultures, trogons, mousebirds, cuckoo-rollers, seriemas, parrots and passerines (Fig. 1). This clade, in turn, consists of two reciprocally monophyletic subclades of which one includes the falcons, seriemas, passerines and parrots, and the other the rest. No names have been proposed for these two clades and in order to facilitate the discussion in this paper I propose the names Australavis ('southern birds') for the clade with falcons, seriemas, passerines and parrots, and Afroaves ('African birds') for the clade that consists of all coraciiform and piciform birds, owls, diurnal raptors (except falcons), New World vultures, trogons, mousebirds and cuckoo-rollers (Fig. 1).

Within Australavis the passerine-parrot clade was recovered by both Ericson *et al.* (2006), although with a posterior probability lower than 95%, and Hackett *et al.* (2008) with 77% maximum-likelihood bootstrap support. For this clade I suggest using *Cantimimus* in recognition of the ability of vocal learning in many passerines and parrots. This ability is almost unique among birds; a similar behaviour has been reported only in hummingbirds (Baptista & Schuchmann, 1990; Jarvis *et al.*, 2000; Saranathan *et al.*, 2007).

Ericson *et al.* (2006) identified a second clade in Australavis consisting of the falcons and seriemas, albeit with low posterior probability (and this clade was not recovered by Hackett *et al.*, 2008, see below). I refrain from naming this clade, and if it stands time it seems most reasonable to include *Cariamidae* in the order Falconiformes (*sensu stricto*, i.e. excluding the other diurnal raptors). The South American seriemas are the ecological equivalent of the African secretarybird. The inclusion of seriemas in Falconiformes is thus no odder than including the secretarybird in Accipitriformes (osprey, eagles, buzzards, hawks and allies), a practice accepted in avian taxonomy for many decades.

In this paper I investigate the geographical origin and dispersal history for the groups of birds included in Australavis and Afroaves. I will stress the importance of Africa for the early evolution of Afroaves as it turns out that most groups in this

clade have their origin and early radiation in the Afrotropical region. Several families still have a mainly African distribution while a few groups, such as woodpeckers and kingfishers, subsequently have dispersed across the globe.

MATERIALS AND METHODS

The ancestral areas were calculated based on a phylogeny reconstructed as described below. As the dispersal-vicariance analysis (see below) requires a fully resolved tree it was not possible to use the published 95% posterior probability consensus tree of Ericson *et al.* (2006, their fig. 1). Instead I re-analysed the original data of Ericson *et al.* (2006) with a maximum-likelihood (ML) analysis using GARLI v. 0.951 (Zwickl, 2006). The topology of the resulting tree (Fig. 1) agrees with Ericson *et al.* (2006, their fig. 1), except that it resolves several polytomies, including the basal branching order within Afroaves: the New World vultures (*Cathartes* and *Coragyps*) form the sister group to all other members of Afroaves in the maximum-likelihood tree. Within Australavis the falcons and seriemas group together, as do parrots and passerines. The Bayesian analysis of Ericson *et al.* (2006) also suggested a sister-group relationship between (falcons + seriemas) and (passerines + parrots), but the posterior probability for this dichotomy was 92% (and did thus not reach the 95% used as cut-off value in fig 1 of Ericson *et al.*, 2006).

Hackett *et al.* (2008) published a higher-level phylogeny in birds that was based on considerably more genetic data (> 52,000 bp from 200+ taxa) than in Ericson *et al.* (2006). Ideally, the two data sets should be pooled and analysed together but this proved impossible, partly due to computational limitations and partly because of differences in the taxonomic sampling. Furthermore, the 'landbird' part of the phylogenetic trees in Ericson *et al.* (2006) and Hackett *et al.* (2008) are very similar. The two phylogenies only have two topological differences that receive statistical support exceeding 70% in Hackett's *et al.*'s (2008) ML analysis. These minor differences in tree topology do not affect the reconstruction of ancestral areas as explained below.

The distributional history of Afroaves plus Australavis was reconstructed with a dispersal-vicariance analysis using DIVA v. 1.1 (Ronquist, 1997). The DIVA program requires that the maximum number of ancestral areas is determined and used as a constraint in the analysis. I set this number to 2 based on the assumption that no ancestral species occurred in more than two faunal regions. This assumption is strongly supported by data of extant species' distributions among landbirds (the osprey and peregrine falcon are among the few species that occur in three or more faunal regions today).

It may be argued that including the sister groups of the 'higher landbirds' in the biogeographical analysis would give a better estimate of the ancestral area for the entire radiation. However, the closest outgroups are the shorebird clade (Charadriiformes) and a clade of various semi-aquatic and aquatic groups of birds. Most of these taxa exhibit completely different migration (i.e. potential dispersal) patterns from the

terrestrial ingroup taxa and a set of biogeographical entities other than those used herein would be required to describe their often oceanic and coastal distributions. It is thus essentially impossible to construct a matrix of geographical distributions that is meaningful to analyse.

The current geographical distribution was used for all groups that occur in only one faunal region. For many families, their present distribution includes several continents as a result of dispersal. To increase the precision of the biogeographical reconstruction of the group, I have reconstructed the ancestral area(s) for the two most basal lineages of each family that occur today in more than two faunal regions. This could be done for all families for which a taxonomically well-sampled phylogenetic hypothesis based on molecular data has been published (true for all families except rollers and hornbills). To decrease the influence of a biased taxon sampling in these analyses, I pruned the published phylogenetic trees to include only one representative of each genus under the assumption that the genera are monophyletic. This approach is conservative in that lumping taxa may blur existing biogeographical patterns if the genus can in fact be divided into two geographically separate groups. A phylogeny at taxonomic levels lower than the genus was only used in a few cases, for example for the bee-eater genus *Merops*, for which all but two species were included in the phylogeny, and for the genus *Tyto*. For each higher-level taxon in the original phylogeny, I reconstructed ancestral areas for the two most basal lineages and included both of them in the final analysis. For example, the New Zealand wrens (Acanthisittidae) in the Australasian region is the sister group to all other passerines. The reconstructed ancestral area of the remaining passerines is likewise Australasia and these two lineages were entered into the analysis together with their respective reconstructed distribution.

By adding extra terminals to the maximum-likelihood tree, calculated as described above, the information available for the biogeographical analysis increased across the tree, as did the precision of the results. One drawback is that the addition of extra terminals that do not contain DNA data for all branches delimits the methods that can be applied to reconstruct ancestral areas. For example, it precludes the use of a model-based approach to the dispersal–vicariance analysis. Another drawback is that the method requires the use of current geographical distributions for the included taxa, while in reality fossils may prove some of these to be relictual distributions of groups that were once more widespread. Of special interest are those taxa which have a Palaeogene fossil record outside their extant distribution. These examples are rather few, however. Among the taxa included here this is true only for the seriemas, mousebirds, todies, rollers, ground rollers and New World vultures. Stem-group representatives of the South American seriemas have been described from North America and Europe. The same is true for mousebirds and todies, two groups that are now restricted to Africa and the Greater Antilles, respectively. Potentially informative fossils also exist for rollers, ground rollers and New World vultures. Most of these fossils have certainly been assigned to the correct

clade, but for some of them the precise relationships with modern groups remain to be clarified.

RESULTS

Reconstructed ancestral areas for subclades of Afroaves and Australavis

The area codings for all terminal taxa are given in Appendix S1 in Supporting Information. Discussed below is the rationale for these codings for the families that occur in more than one faunal region.

Diurnal raptors (Accipitridae)

A molecular phylogeny of Accipitridae has been published by Lerner & Mindell (2005). Their study included representatives of all genera and most species of the family, and was based on both mitochondrial and nuclear DNA. Herein I used the results of a Bayesian analysis (fig. 2 in Lerner & Mindell, 2005) as the basis for the reconstruction of ancestral states for basal nodes in their tree. The tree is simplified such that all genera not recovered as monophyletic by Lerner & Mindell were pooled and analysed as genus groups. The genus *Elanus*, which is the sister group of all other extant diurnal raptors, has an essentially global distribution, being absent only from Madagascar. The reconstructed ancestral area for the remaining species is the Afrotropics (see Fig. S1 in Appendix S2).

New world vultures (Cathartidae)

No species-level phylogeny has been published for Cathartidae. I therefore constructed a preliminary phylogeny based on a maximum-likelihood analysis of 999-bp cytochrome *b* sequences downloaded from GenBank (see Appendix S3 for accession numbers). The three species of the genus *Cathartes* form the sister group of the remaining genera. Ancestral areas of these two clades were reconstructed as the Neotropics for the *Cathartes* clade and Neotropics + Nearctic for the other genera (Fig. S2 in Appendix S2).

Trogons (Trogonidae)

The trogons occur in the tropics of the New and Old Worlds. A molecular phylogeny of Johansson & Ericson (2005) showed the African trogons (genus *Apaloderma*) to form the sister group to a clade with the reciprocally monophyletic Asian and New World trogons. The ancestral area for the latter clade was reconstructed as the Neotropics + Indomalaya (Fig. S3 in Appendix S2).

Bee-eaters (Meropidae)

Marks *et al.* (2007) published a molecular phylogeny of the bee-eaters including 23 of 25 named species. The two Indomalayan species of the genus *Nyctornis* were shown to

be the sister taxon to the genera *Meropogon* and *Merops*. I used a simplified form of their Bayesian tree based on the complete data set (Marks *et al.*, 2007; their fig. 2b) to reconstruct ancestral areas for the family. In my analysis I lumped several *Merops* species into two large groups named the *Merops boehmi* clade and the *Merops ornatus* clade. All taxa in the former clade are geographically restricted in the Afrotropics, while the latter clade includes species distributed all over the world, except in the New World. While Indomalaya is the ancestral area for the *Nyctornis* clade, Afrotropics + Australasia is reconstructed as the ancestral area for the *Meropogon/Merops* clade (Fig. S4 in Appendix S2).

Kingfishers (*Alcedinidae*)

The molecular phylogeny of Moyle (2006) was used to draw a simplified, genus-level tree (Fig. S5 in Appendix S2). Moyle (2006) found all genera studied to be monophyletic, except *Alcedo* and *Ceyx*. Although the delimitation of these two genera remains to be clarified, all studied species referred to them group in a clade that is the sister to all other kingfishers. The *Alcedo* and *Ceyx* species occur in most parts of the Old World, and no further delimitation of the ancestral area of this clade could be made. However, Indomalaya is reconstructed as the ancestral area for all other kingfishers (Fig. S5).

Barbets and toucans (*Megalaimidae*, *Lybiidae*, *Capitonidae*, *Ramphastidae*)

Ancestral areas for the two basal-most lineages of barbets and toucans were reconstructed based on the phylogeny in Moyle (2004). The tree in Fig. S6 in Appendix S2 is simplified to show only generic relationships. Note that non-monophyletic genera have been pooled. The Indomalayan genera *Caloramphus* and *Megalaima* (with *Psilopogon* nested within it) are sisters to all other barbets and toucans. The ancestral area of the latter clade is reconstructed as the Afrotropics + Neotropics.

Honeyguides (*Indicatoridae*)

No molecular phylogeny of the honeyguides has been published. All honeyguides are Afrotropical except for two presumably sister species that occur in tropical Asia. Most likely their ancestor has dispersed from Africa (Short & Horne, 2002) and in the analyses it is assumed that the family is of Afrotropical origin.

Wrynecks and woodpeckers (*Jyngidae* and *Picidae*)

The tree used to reconstruct ancestral areas for the wrynecks and woodpeckers is a composite from two recent publications with complementary taxon sampling. Both analyses agree that the wrynecks (*Jyngidae*) form the sister group to all woodpeckers (*Picidae*), and that the piculets form the sister group to

all other woodpeckers (Benz *et al.*, 2006; Fuchs *et al.*, 2007). The Antillean piculet *Nesocittes* is, however, not part of the piculet clade but sister to the remaining woodpeckers (Benz *et al.*, 2006). Fuchs *et al.* (2007) found the Indomalayan *Hemicircus* to be the most basal taxon within Picinae, but they did not include *Nesocittes*. Although the relationships between *Nesocittes* and *Hemicircus* is unresolved (Benz *et al.*, 2006; did not include *Hemicircus* in their analysis), I placed *Nesocittes* outside the Picinae (including *Hemicircus*) because of its (presumably plesiomorphic) similarities with the piculets (Fig. S7 in Appendix S2). The analysis suggests that Indomalaya is the ancestral area of the woodpeckers and also of the piculet clade. Indomalaya + Neotropics was reconstructed as the ancestral area for the remaining woodpeckers.

Barn-owls (*Tytonidae*)

The family Tytonidae consists of two genera, *Tyto* and *Phodilus*. Wink *et al.* (2004) published a phylogeny for several species and subspecies of tytonids based on mitochondrial DNA. Based on the relationships in fig. 1 of Wink *et al.* (2004) no consensus could be reached concerning the ancestral area for the tytonid clade. All major faunal regions, except the Palaearctic, were suggested to be involved (Fig. S8 in Appendix S2).

Owls (*Strigidae*)

No taxonomically exhaustive molecular phylogeny has been published for the owls. Wink *et al.* (2004) included 13 genera in an analysis based on mitochondrial DNA, and I have used their results here. The genus *Otus*, which is the sister to the other studied genera of owls, is represented in essentially all parts of the world except the Nearctic and Neotropics. The ancestral state for the remaining genera was reconstructed as the Nearctic (Fig. S9 in Appendix S2).

Passerines (*Passeriformes*)

Several studies have shown that the New Zealand wrens (family Acanthisittidae) is the sister group to all other passerines, and that the other passerines fall into two clades: oscines and suboscines (Barker *et al.*, 2002, 2004; Ericson *et al.*, 2002). Figure S10 in Appendix S2 is a simplified phylogeny for the passerine order. For both basal lineages, Australasia is inferred to be the ancestral area.

Parrots (*Psittaciformes*)

Until recently the most complete molecular phylogeny for the parrots is based on a Z-chromosomal intron sequenced for 50 species representing 47 genera (de Kloet & de Kloet, 2005). The reconstructed ancestral area for the two basal-most lineages of parrots is Australasia (Fig. S11 in Appendix S2). These calculations were based on the tree in fig. 2 of de Kloet & de Kloet

(2005), and using the groupings given in roman numerals in that figure. Wright *et al.* (2008) published a phylogeny based on analyses of 3915 bp from nuclear and mitochondrial markers. This study also suggested Australasia as the likeliest region of origin of the parrots.

Falcons and caracaras (Falconidae)

Griffiths *et al.* (2004) used 2837 bp of the nuclear *RAG-1* gene to estimate a phylogeny of all extant genera of falcons. Parsimony and maximum-likelihood analyses resulted in the same inter-generic relationships, which I used to reconstruct the ancestral areas for Falconidae (Fig. S12 in Appendix S2). The Neotropical genera *Herpetotheres* and *Micrastur* form the sister group to the other falconids. The ancestral area for the latter was reconstructed as either of the Neotropics only, Neotropics + Nearctic, or Neotropics + Australasia. The reconstructed ancestral areas for these two falconid clades were used in the higher-level analysis.

Phylogenetic hypotheses based on molecular sequence data are lacking for a few important groups included in this study, for example for hornbills (Bucerotidae) and rollers (Coraciidae). For hornbills I followed previous authors in assuming that the African ground-hornbills (genus *Bucorvus*) is the sister taxon of the other hornbills (subfamily Bucerotinae). This assumption is based on observations that the Bucerotinae are more derived in their anatomy and nesting behaviour (Kemp, 2001). The rollers have an almost world-wide distribution, lacking only in the New World. The lack of a reliable phylogeny made it impossible to hypothesize an ancestral distribution for the rollers.

Ancestral area analysis for Afroaves and Australavis

The ancestral area analysis reconstructs the Afrotropical + Nearctic + Neotropical regions as the centre of origin for Afroaves and the Australasian + Neotropical regions for Australavis (Fig. 2). The split between Afroaves and Australavis was estimated by Ericson *et al.* (2006) to have occurred in the Late Cretaceous, which is later than suggested by most other estimates for the time of origin of basal Neoavian groups (cf. van Tuinen, 2009). Nonetheless, this age, together with the postulated ancestral distributions of these clades in the Afrotropics and Australasia + Neotropics, respectively, suggests that Afroaves and Australavis have a Gondwanan origin. The two subclades of Australavis, the passerines and parrots (Cantimimus) and the falcons and seriemas (Falconiformes), respectively, also derive from ancestors distributed in southern continents: Australasia is inferred to be the ancestral area for Cantimimus and the Neotropics for Falconiformes.

The ambiguity in determining the ancestral area for Afroaves (reconstructed here as Afrotropical + Nearctic + Neotropical) is due to the basal position of the New World vultures (Cathartidae), and this is further discussed below. The dominant role of Africa as the origin for Afroaves

becomes evident above this basal node. Essentially all Afroavian clades stem from ancestors with inferred Afrotropical distributions. Groups that today have essentially global distributions, like for example raptors, woodpeckers and owls, also stem from African ancestors.

Effects of the alternative phylogenetic positions of Cathartidae within Afroaves

The Bayesian analysis of Ericson *et al.* (2006) could not resolve the relationships of the three most basal branches of Afroaves: (1) the diurnal raptors (including the osprey and secretary-bird), (2) the New World vultures, and (3) the cuckoo-rollers, owls, mousebirds and trogons as well as the coraciiform and piciform birds. In the maximum-likelihood tree (Fig. 1), however, the New World vultures are placed as sister to the other two clades and this systematic arrangement was used to reconstruct ancestral areas herein. However, the internodes are short in this part of the tree and the basal relationships obviously difficult to resolve. It is thus of interest to investigate how alternative placements of the New World vultures influence the biogeographical reconstructions.

The two alternative positions of the New World vultures in the phylogenetic tree suggested by the two analyses of large amounts of nuclear sequence data are either (1) sister to Accipitriformes (found in the analysis of Hackett *et al.*, 2008) or (2) sister to all taxa except Accipitriformes (herein, Figs 3 & 4). In both cases the ancestral area for Afroaves (including the New World vultures) is reconstructed as being the Afrotropics.

It may be questioned why we should include the New World vultures in the taxon Afroaves as they may even be the sister group to the other members included in Afroaves. In addition, they are restricted today to the New World. Besides that, the phylogenetic position of cathartids relative to other Afroaves remains poorly resolved, as the fossil record suggests that the group may not have originated in the New World: cathartid fossils are known from the middle Eocene of Europe and the late Eocene of North America (Mourer-Chauviré, 2002; Mayr, 2009). It cannot be excluded that the cathartids evolved in the Afrotropics and later dispersed via Europe to the New World, possibly using the Greenland land bridge.

Effects of alternative phylogenetic hypotheses for Neoaves

The ML tree topology published by Hackett *et al.* (2008) differs little from that used herein based on a ML analysis of the data in Ericson *et al.* (2006). The differences involve only a few taxa, and in only two cases does the alternative position receive a support value exceeding 70% in the analysis of Hackett *et al.* (2008). The first concerns the cuckoo-roller, which obtains moderate support (85%) for being placed above the mousebirds in the phylogenetic tree (the mousebirds in turn group with the owls but with no support). The other, weakly supported (73%) difference between the ML trees concerns the position of seriemas, which in the analysis of Hackett *et al.* (2008) are placed

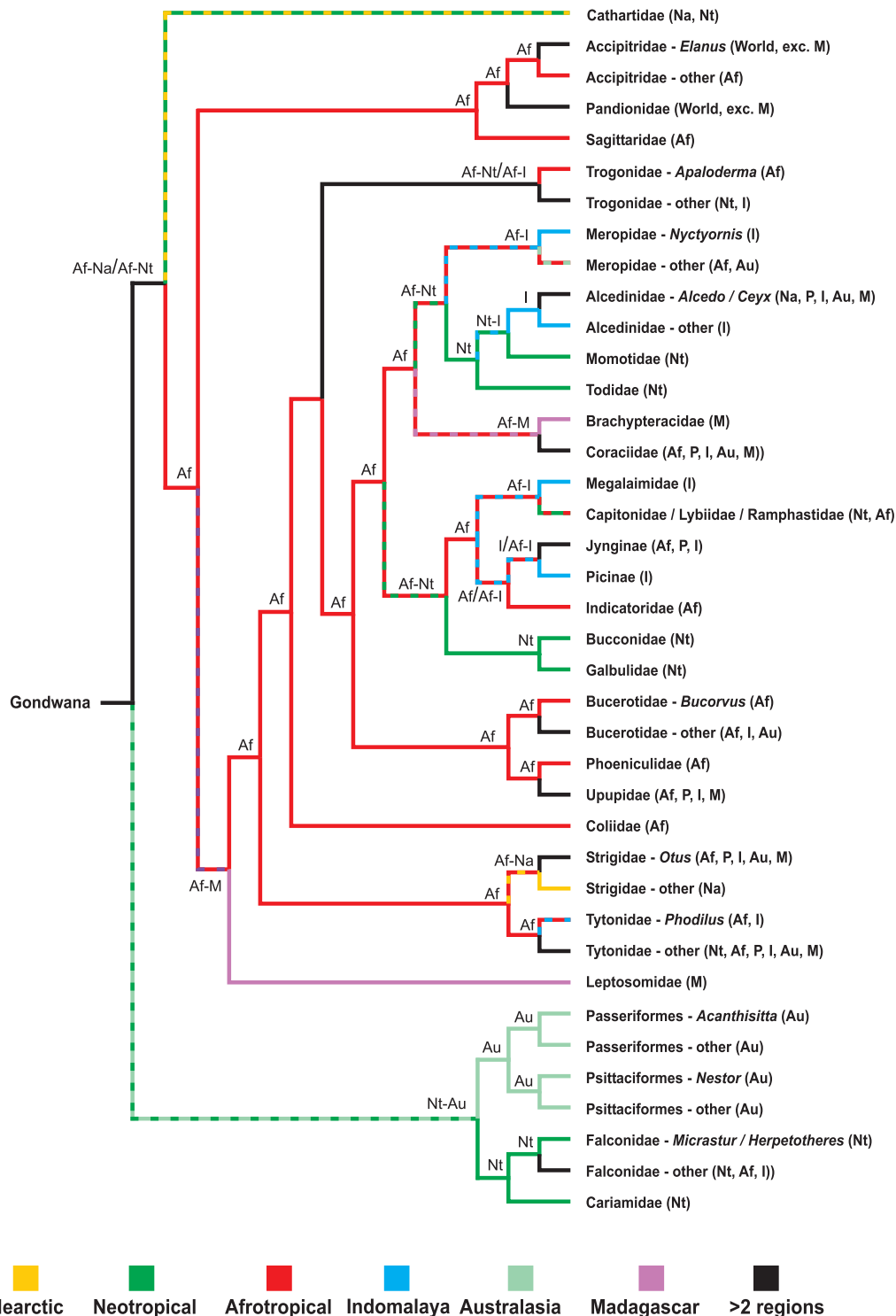


Figure 2 Ancestral area analysis for Afroaves and Australavis based on a phylogenetic tree obtained in a maximum-likelihood analysis of nuclear DNA data published by Ericson *et al.* (2006). In this tree the New World vultures form the sister group to all other taxa in Afroaves. Abbreviations of faunal regions: Na, Nearctic; Nt, Neotropics; Af, Afrotropics; P, Palearctic; I, Indomalaya; Au, Australasia; M, Madagascar.

basal to (falcons (passerines, parrots)), while being sister to the falcons in the analysis based on the data in Ericson *et al.* (2006). The only other differences involve the bee-eaters which (with no support) are placed outside the entire clade ((todies (motmots, kingfishers)) (rollers, ground rollers)) in

the analysis of Hackett *et al.*, while they are sister to (todies (motmots, kingfishers)) based on the Ericson *et al.* (2006) data.

These alternative phylogenetic hypotheses for Neoaves thus have little influence on the reconstructions of ancestral areas.

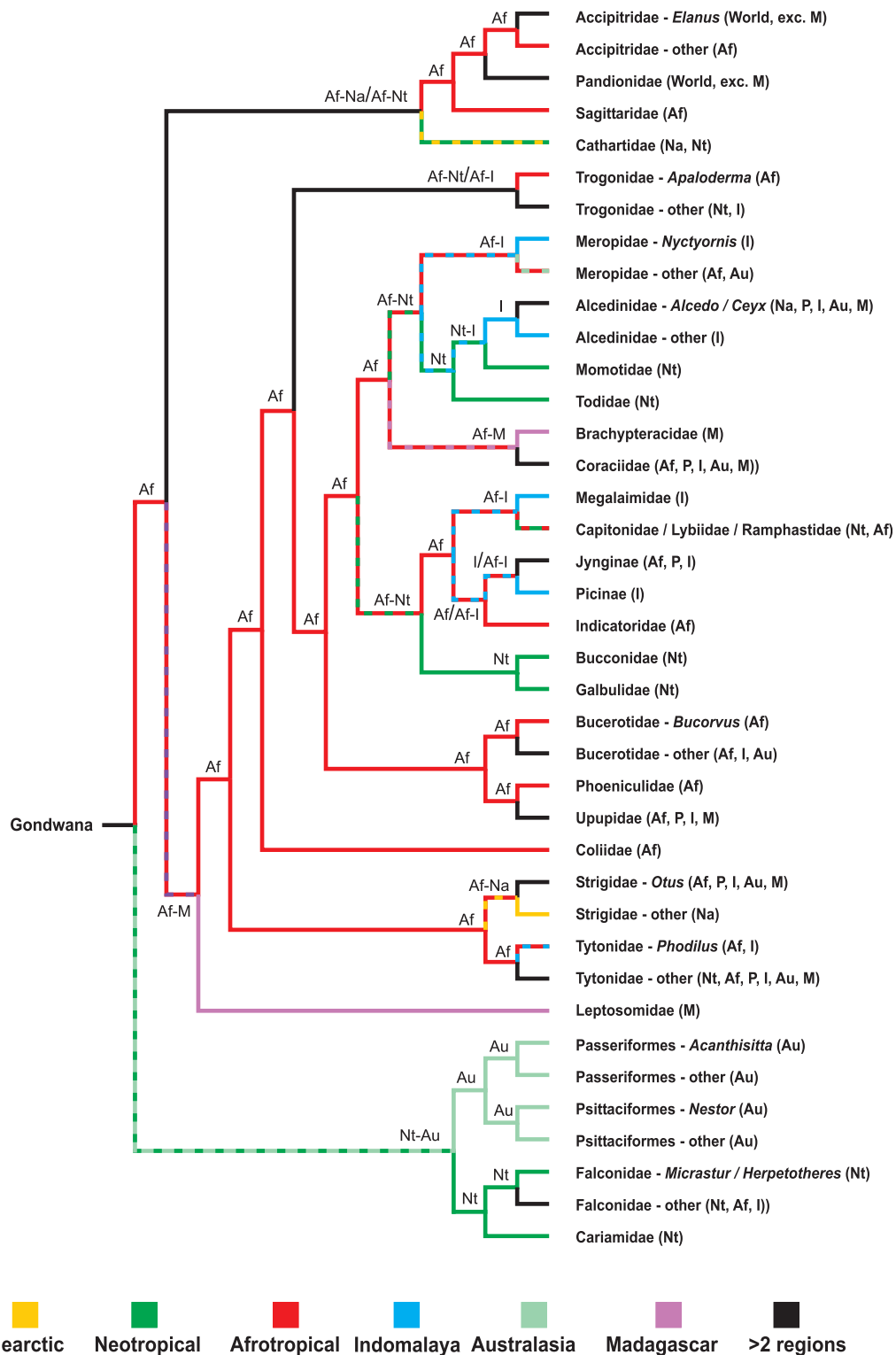


Figure 3 Same as in Fig. 2 but with the topology constrained so that the New World vultures form the sister group to the Accipitriformes. Abbreviations of faunal regions: Na, Nearctic; Nt, Neotropics; Af, Afrotropics; P, Palearctic; I, Indomalaya; Au, Australasia; M, Madagascar.

The geographical origin of Afroaves is still reconstructed as the Afrotropics, while the basal position of seriemas in Australavis shifts the origin of this clade from Australasia + South America to South America only.

DISCUSSION

The ancestral area analysis based on current geographical distributions of taxa infers two early dispersals from the

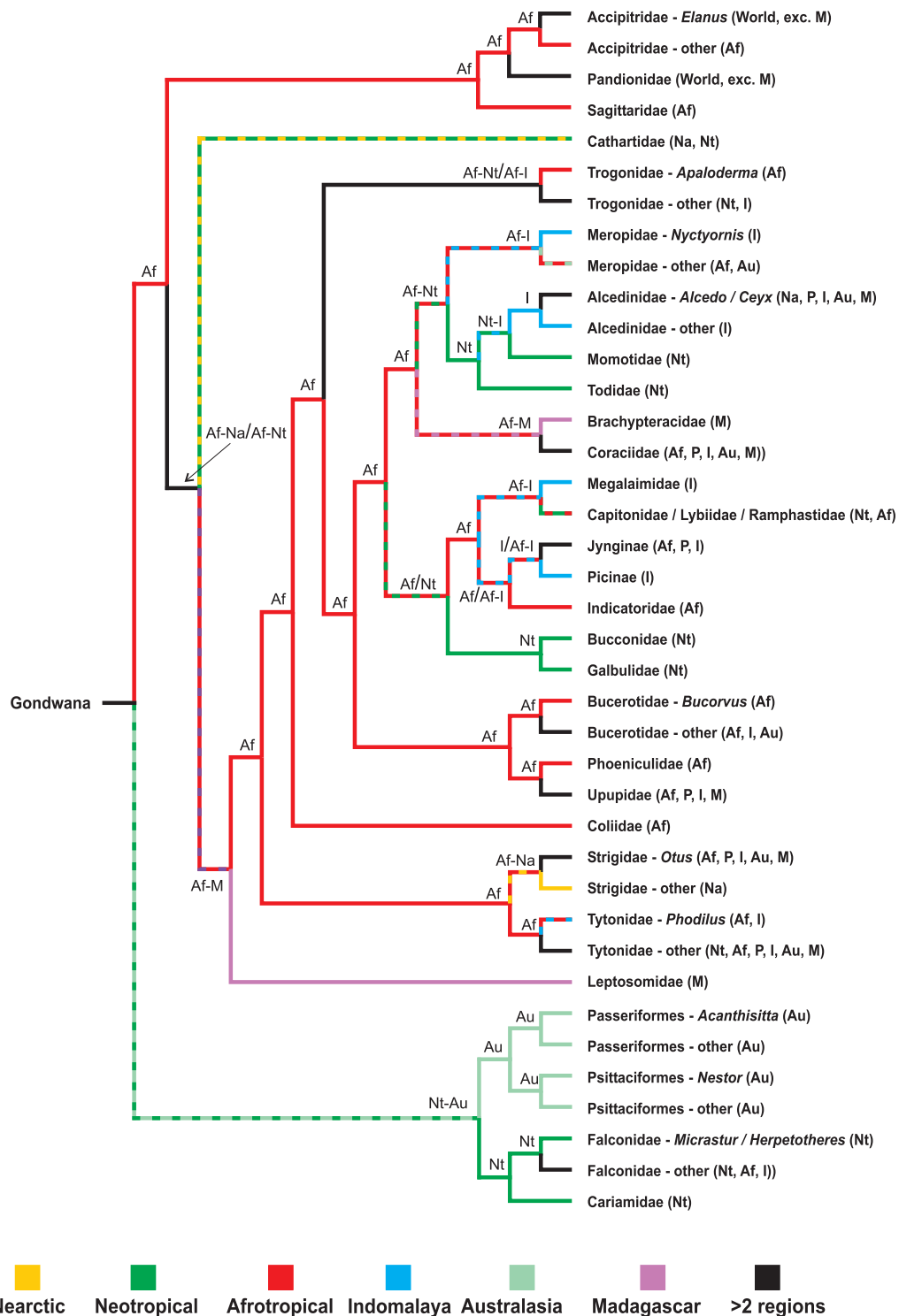


Figure 4 Same as in Fig. 2 but with the topology constrained so that the New World vultures form the sister group to all other Afroaves, except Accipitriformes. Abbreviations of faunal regions: Na, Nearctic; Nt, Neotropics; Af, Afrotropics; P, Palaearctic; I, Indomalaya; Au, Australasia; M, Madagascar.

Afrotropics to the Americas: one involving the ancestor of the clade including todies, motmots and kingfishers, and another involving the ancestor of the jacamar–puffbird clade (Galbulae). Stem group representatives of the Todidae

(*Palaeotodus*), which today is restricted to the Greater Antilles, occur in late Eocene and early Oligocene deposits of Europe and North America (Mayr, 2009). It is thus plausible that early relatives of the today–motmot–kingfisher

clade dispersed from Africa to Europe and further to North America in the Palaeogene when the continents were much closer. The climate during this so-called Palaeocene–Eocene Thermal Maximum was warmer than today, as evident from the fossil palm trees and crocodiles found in Greenland (Scotese, 2003), and land bridges between Europe and Greenland may have existed during the Palaeocene, and perhaps into the Eocene (Cox, 2000). Palaeobotanic data from Iceland suggest that North Atlantic land bridges may have occurred as late as the Miocene (*c.* 10–6 Ma), and definitely during the Oligocene (*c.* 30 Ma) (Denk *et al.*, 2011). Euro-American faunal exchange via the North Atlantic route has been reported in several terrestrial organisms, including mammals (Gingerich, 2006). It is likely that other groups of Afroaves also used this route for dispersal. For example, mousebirds, owls, rollers/ground rollers and New World vultures all have a Palaeogene fossil record in both Europe and North America.

For seriemas and falcons, which may have evolved in the Neotropics, the Greenland land bridge could have facilitated dispersal into the Old World. Indeed, the oldest stem group representatives of Cariamae (to which the extant seriemas belong), are from late Palaeocene deposits in Brazil (Mayr, 2009). There is an extensive Palaeogene record of Cariamae also in North America and Europe but the oldest of these are from the middle Eocene. Falcons have not been unambiguously identified from Palaeogene deposits.

Two groups in Afroaves restricted to Madagascar today, cuckoo-rollers and ground rollers, are both known from Palaeogene deposits in Europe and North America indicating that their present distributions are relictual (Mayr, 2009).

Parallel evolution of major ecological adaptations in different continents

It can be postulated that after the break-up of Gondwana in the Cretaceous the terrestrial avifaunas of Africa, South America and Australia were more or less isolated from each other for many millions of years. In each continent different bird groups responded to the local conditions by evolving a range of ecological adaptations. Because of a general similarity in major habitat types between the continents, several specializations evolved in parallel in different phylogenetic lineages. This becomes evident when comparing the ecological adaptations of bird groups in Afroaves with those in Australavis. Perhaps most striking are the similarities in lifestyle and behaviour between the secretarybird in Afroaves and the seriemas in Australavis. Another example of convergence in ecological adaptations is the parallel evolution of diurnal predators in the two clades, Accipitriformes in Afroaves and Falconiformes in Australavis. At an ordinal level the passerine radiation is unsurpassed in terms of the diversity in ecological adaptations. The biogeographical analysis suggests that the early passerine diversification took place in Australasia in the absence of ancestral coraciiform and piciform birds, which then were confined to the African

continent. Consequently, there are several examples of passerines occupying ecological niches similar to those occupied by coraciiforms and piciforms as rollers, bee-eaters, hoopoes, puffbirds etc.

The analysis indicates that the radiations of insectivorous and frugivorous birds within Cantiomimus in Australia and Afroaves in Africa were not paralleled within this particular clade in South America. Most likely this is because South America was already colonized by a clade of suboscine passerines, Tyrannides (New World suboscines), which included both insect eaters (e.g. tyrant flycatchers, antbirds, ovenbirds, woodcreepers) and fruit specialists (e.g. cotingas). As previously suggested (Barker *et al.*, 2002, 2004; Ericson *et al.*, 2002, 2003) this passerine lineage may have been isolated in South America at the break-up of Gondwana and diversified in isolation until the South and North American continental plates came close enough to allow dispersal.

It is reasonable to believe that the radiations of terrestrial birds in the three southern continents were originally more diversified and included more taxa than those that we know belong to these lineages today. The fossil record could shed light on this but it is unfortunately rather silent. Most parts of Australia, Africa and South America were covered by paratropical rain forests in the Late Cretaceous and early Palaeogene, which offered unfavourable conditions for the preservation of animal carcasses on land (Mayr, 2009).

Given that the three clades Cantiomimus, Afroaves and Falconiformes have long histories of diversification within different continents, but in similar habitats, it is not surprising to find examples of convergences in morphology and behaviour between them. What is perhaps more surprising is that in each of these three clades there seems to be widespread ecological niche conservatism, i.e. a failure to evolve drastically new lifestyles. It is plausible that the common ancestor of the clades Cantiomimus, Afroaves and Falconiformes was adapted to a terrestrial life, and as far as we can tell (given the incompleteness of the fossil record) all its descendants have stayed terrestrial for well over 65 million years (with the exception of a few taxa that get their food from the water, as dippers and kingfishers). A considerable plasticity of morphological and ecological adaptations is often stressed at the species level in birds, but for higher taxonomic levels this plasticity is less obvious. This seems to be true not only for the landbirds studied herein. A similar observation can be made for the 'waterbird-assemblage' (as defined in the phylogenetic analyses of Ericson *et al.*, 2006; and Hackett *et al.*, 2008). The ancestor of this large group of birds may have adapted its aquatic or semi-aquatic lifestyle as early as in the Late Cretaceous. Despite this long time of evolution it seems that very few members of this clade have a secondary evolved terrestrial lifestyle. Ecological niche conservatism above the species level is well known in other organisms, for example mammals (Hadly *et al.*, 2009; Cooper *et al.*, 2011), and it seems to be the rule also at higher taxonomic levels in birds.

ACKNOWLEDGEMENTS

I thank Marcel van Tuinen, Yanhua Qu and Jennifer Kearey for suggesting improvements to this manuscript. This research was supported by a grant (no. 621-2010-5321) from the Swedish Research Council.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Area codings used to reconstruct ancestral areas using dispersal–vicariance analysis.

Appendix S2 Ancestral analyses for each of the subclades analysed herein (Figs S1–S12).

Appendix S3 GenBank accession numbers for cytochrome *b* sequences used to establish relationships among the New World vultures (Cathartidae).

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Editor: Malte Ebach