

Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event

Joel Cracraft

Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA (jlc@amnh.org)

The fossil record has been used to support the origin and radiation of modern birds (Neornithes) in Laurasia after the Cretaceous–Tertiary mass extinction event, whereas molecular clocks have suggested a Cretaceous origin for most avian orders. These alternative views of neornithine evolution are examined using an independent set of evidence, namely phylogenetic relationships and historical biogeography. Phylogenetic relationships of basal lineages of neornithines, including ratite birds and their allies (Palaeognathae), galliforms and anseriforms (Galloanserae), as well as lineages of the more advanced Neoaves (Gruiformes, Caprimulgiformes, Passeriformes and others) demonstrate pervasive trans-Antarctic distribution patterns. The temporal history of the neornithines can be inferred from fossil taxa and the ages of vicariance events, and along with their biogeographical patterns, leads to the conclusion that neornithines arose in Gondwana prior to the Cretaceous–Tertiary extinction event.

Keywords: Neornithes; avian evolution; biogeography; Gondwana; Cretaceous–Tertiary extinction

1. INTRODUCTION

The relationships of modern birds, or Neornithes, to non-avian theropods and Mesozoic pre-neornithine avian lineages, is now well established (Chiappe 1995; Padian & Chiappe 1998; Chiappe *et al.* 1999), and there is substantial evidence that Neornithes are monophyletic (Gauthier 1986; Cracraft 1986; Cracraft & Clarke 2001). The critical uncertainties about avian evolution now centre around several core scientific problems. How are modern avian lineages interrelated? When and where did the Neornithes arise? And, what has been their temporal pattern of diversification? Putative answers to these questions have emerged from two contested hypotheses of neornithine evolution, each based on different kinds of data—palaeontological and molecular clocks.

The Tertiary radiation hypothesis (Olson 1989; Feduccia 1995, 1999) proposes that pre-neornithine lineages, including the enantiornithines and ornithurine clades (such as hesperornithiforms and ichthyornithiforms) were all exterminated at the Cretaceous–Tertiary (K–T) boundary by the Chicxulub meteoritic impact (Feduccia 1995). One, or at most a few, neornithine lineages are thought to have survived this extraterrestrial armageddon to give rise to modern orders and families of birds. The data supporting this hypothesis are entirely palaeontological, particularly the diverse unquestionably neornithine assemblages in the European and North American Palaeocene and Eocene and the paucity of a neornithine record in the Late Cretaceous (Feduccia 1999). Late Cretaceous taxa assigned to Neornithes are said to represent a gradal level of morphology termed ‘transitional shorebirds’, including the nonmonophyletic ‘Graculavidae’, which are assumed to have given rise to many of the diverse neornithine morphologies (Feduccia 1995, 1999). Acceptance of the Tertiary radiation hypothesis necessitates taking the fossil record at face value. The lack of modern groups in the Late Cretaceous is viewed as evidence for their absence, whereas the presence of diverse taxa in the Early Tertiary is interpreted as a

marker of neornithine beginnings. The fact that the preponderance of the fossils are found in North America and Europe is taken as evidence that most higher taxa of birds diversified on the Laurasian landmass and had little, if anything, to do with Gondwana (Feduccia 1995). Some of these Early Tertiary fossils have been assigned to taxa currently restricted geographically to Africa, South America or Australia, leading to the hypothesis that these groups had achieved a worldwide distribution by the Early Tertiary, and that many, even most, of the southern continent endemics we see today are merely relics of those old northern avifaunas (Mourer-Chauviré 1982; Olson 1989; Feduccia 1995, 1999). The only exceptions might include a few lineages within the galliforms, anseriforms, passeriforms, psittaciforms and columbiforms (Olson 1989).

On the other side of the debate are those who have applied a molecular-clock interpretation to genetic distances among DNA sequences of avian orders and families (Hedges *et al.* 1996; Cooper & Penny 1997; Rambaut & Bromham 1998). Using different methods, assumptions about rate constancy and clock calibrations, each of these studies concludes that nearly all modern avian orders arose in the Cretaceous, with divergence dates generally being 100 million years (Myr) ago or even older. Molecular-clock proponents suggest that the absence of fossil evidence supporting such deep divergences can be explained by the relative scarcity of Late Cretaceous fossil horizons, especially on the southern continents, and by a geographical bias on the part of palaeontologists who have primarily worked in North America and Eurasia (Cooper & Penny 1997). For those taking the fossil record at face value, on the other hand, the use of molecular clocks is misguided or, at best, the clock is seriously miscalibrated (Feduccia 1995).

Here, I examine the problem of neornithine evolution using an independent set of evidence, namely phylogenetic relationships and historical biogeography. I then use palaeontological and geological data to infer the temporal and spatial history of neornithine diversification. This

analysis implies first, that the origins of modern birds largely took place in Gondwana; second, that biogeographical mapping of phylogenetic relationships within and among many avian lineages strongly indicates the history of modern birds was influenced by the dispersal of the southern continents; and finally, therefore, many neornithine lineages arose before, and passed through, the K–T extinction event, possibly because their distribution at the time was in the Southern Hemisphere. Phylogenetic and biogeographical evidence provides a framework for evaluating the conflict between molecular clocks and the fossil record and suggests a synthesis in which these apparently disparate data sets are largely consistent with a global historical hypothesis of early neornithine evolution and Earth history.

2. NEORNITHINE PHYLOGENY AND BIOGEOGRAPHY ACROSS GONDWANALAND

Neither of the two hypotheses about neornithine evolution has emphasized sufficiently the accumulating body of diverse evidence on neornithine interrelationships, and in some instances (Feduccia 1995), they have even rejected the usefulness of contemporary phylogenetic analysis and its results. They have, moreover, dismissed the significance of conflicts among molecular, morphological and palaeontological data sets, under the assumption they are irreconcilable.

Although our knowledge of phylogenetic relationships within Neornithes is characterized by many uncertainties, molecular and morphological studies are beginning to yield congruent pictures of relationships for numerous groups, including major lineages at the base of the neornithine tree. Many of these lineages exhibit classic Gondwanan distributions (Cracraft 1973, 1976). When this biogeographical pattern is interpreted within the context of these new systematic data, powerful support emerges for the hypothesis that basal neornithine birds, as well as other more advanced lineages, originated in Gondwana and therefore must have diversified prior to the K–T mass extinction event.

(a) Basal lineages of the Neornithes

A broad array of molecular (Stapel *et al.* 1984; Caspers *et al.* 1994; Groth & Barrowclough 1999) and morphological data (Cracraft 1986; Cracraft & Clarke 2001), interpreted using modern phylogenetic methods, corroborate the division of the Neornithes into the Palaeognathae, including the tinamous and ratites, and the Neognathae, encompassing all other modern birds (figure 1). In addition, previous molecular studies using immunological distance (Ho *et al.* 1976; Prager *et al.* 1976), and more recently DNA hybridization (Sibley & Ahlquist 1990), are topologically consistent with this division even though they did not employ non-neornithine outgroups, but instead established the root by midpoint rooting or by unspecified methods. Molecular sequence evidence using fast-evolving whole mitochondrial genomes for a small sample of neornithine taxa (Mindell *et al.* 1999) produced a topology consistent with the basal relationships of figure 1, but placed the root within the neognathae. This result was almost certainly due to the long-branch attraction between the outgroup (*Alligator*) and the fast-evolving

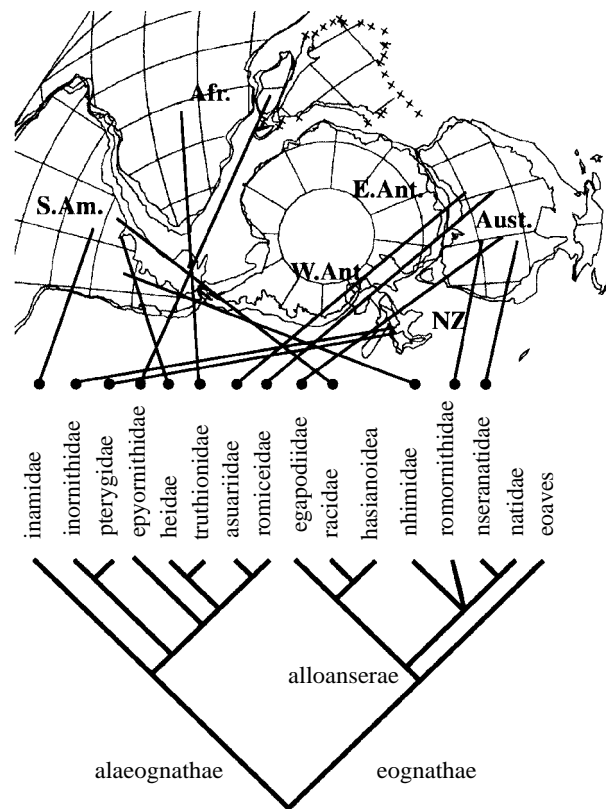


Figure 1. Relationships among the basal lineages of Neornithes, including the Palaeognathae (Cracraft 1974; Lee *et al.* 1997) and Neognathae, including the Galloanserae (Cracraft 1981, 1988; Cracraft & Clarke 2001; Livezey 1986, 1997; Groth & Barrowclough 1999), mapped on to an Early Cretaceous (120 Myr ago) reconstruction of the southern continents (modified from Smith *et al.* (1981)). The Phasianoidae, Anatidae and Neoaves have unresolved distributional patterns at this level of analysis.

songbirds, since this rooting problem disappears when using more slowly evolving nuclear genes (Groth & Barrowclough 1999) or larger taxon samples for mitochondrial sequences (Van Tuinen *et al.* 2000).

(b) Palaeognathae

As a result of accumulating molecular (Sibley & Ahlquist 1990; Lee *et al.* 1997) and morphological evidence (Cracraft 1974; Lee *et al.* 1997), a consensus has emerged that palaeognaths are monophyletic and consist of two primary lineages, the volant tinamous (Tinamidae) and their sister group, the flightless ratites (Ratitae). Relationships within the latter group, however, are unsettled because of conflicts between molecular and morphological data. Although all studies recognize a close relationship between cassowaries (Casuariidae) and emus (Dromiceidae), molecular data, whether DNA hybridization (Sibley & Ahlquist 1990) or mitochondrial DNA (mtDNA) sequences (394 bp in Cooper *et al.* (1992), 5444 bp in Lee *et al.* (1997)), group them with the kiwis (Apterygidae), and place rheas (Rheidae) and ostriches (Struthionidae) not as sister taxa but arising separately at the base of the ratite tree. Morphological data, in contrast, unite rheas and ostriches and group them with cassowaries and emus, and place the kiwis at the base of the ratites (Lee *et al.* 1997). Differences in the two results

have been postulated to be due to artefacts in the placement of the root because of rate differences in the molecular data, and a combined analysis of mtDNA sequences and morphological characters favours the morphological tree (Lee *et al.* 1997).

Inasmuch as the common ancestor of ratites is most parsimoniously interpreted as being flightless, the palaeognaths have been hypothesized (Cracraft 1974; Sibley & Ahlquist 1990) to be of Gondwanan origin and to have achieved their current distribution pattern (figure 1) via continental break-up. Doubts about this hypothesis have been raised (Olson 1985, 1989; Feduccia 1999), but they inevitably rest on an assumption of palaeognath non-monophyly, which is not supported by evidence in the form of a corroborated alternative phylogenetic hypothesis that shows palaeognath taxa independently related to different neognath groups. The monophyly and origin of palaeognaths in Gondwana have also been challenged by the supposition that fossil evidence suggests a Northern Hemisphere origin (Olson 1989; Feduccia 1999). An examination of the evidence suggests otherwise. A flightless palaeognath, *Palaeotis weigelti*, from the Middle Eocene of Europe (Houde & Haubold 1987), is thought to be related to ostriches. Although the derived features linking these taxa are few in number and possibly found in other ratites such as rheas, *Palaeotis* at most demonstrates that some ratites had a European distribution around 55 Myr ago. More interesting is the presence in the Palaeogene of North America and Europe of the so-called 'lithornithine' birds, which include perhaps eight species of supposed palaeognath-grade (Houde 1988). It appears that some of the taxa possess palaeognathous palates and are demonstrably volant (Houde 1988). Yet, because much of the material assigned to species is not comparable with the types or cannot be directly associated with other skeletal elements, the phylogenetic placement of many of the fossils close to, or within, modern palaeognath taxa has not been established adequately. Modern tinamous are palaeognathous and volant, thus the fossils minimally establish palaeognaths of a similar grade as being in the Northern Hemisphere but do not falsify the hypotheses that ratites are monophyletic, that they evolved flightlessness once, and that they were primitively Gondwanan. In fact, the oldest ratite, *Diogenornis*, is from the Palaeocene of Brazil (Alvarenga 1983).

The conclusion that palaeognaths arose in Gondwanaland does not depend on which hypothesis of ratite inter-relationships one adopts, but the implications of different phylogenetic resolutions are substantial for inferring dates of divergence among ratites as well as their intercontinental biogeographical patterns. A rhea–ostrich relationship would imply a trans-Atlantic vicariance event relatively late in ratite history, whereas if ostriches and rheas arose separately from the base of the tree, these vicariance events would be placed early in ratite history. If kiwis are closely related to cassowaries and emus, that suggests a vicariance event across or around the Tasman Sea, whereas if kiwis are basal ratites, then the vicariance event would be between West Antarctica and New Zealand. The relationships of the elephant birds (*Aepyornis*) of Madagascar lie deep in the ratite tree and are not with any group in Africa, such as ostriches (Cracraft 1974); this indicates a primary Gondwana distribution.

(c) *Galloanserae*

There is compelling evidence from immunological distances (Ho *et al.* 1976), amino-acid sequences from conservative alpha-crystallin genes (Caspers *et al.* 1997), DNA hybridization (Sibley & Ahlquist 1990), whole and partial mitochondrial gene sequences (Mindell *et al.* 1997; Van Tuinen *et al.* 2000), nuclear gene sequences (Groth & Barrowclough 1999) and morphological characters (Cracraft 1988; Dzerzhinsky 1995; Livezey 1997; Cracraft & Clarke 2001) that the Galliformes and Anseriformes are each other's closest relative (united in a group called Galloanserae) and are the basal sister group to all remaining neognaths, the Neoaves (see Cracraft & Clarke (2001), for a review).

Within the galliforms, both morphological (Cracraft 1981) and molecular data (Barrowclough & Groth 2001; Dimcheff *et al.* 2000) support the phylogenetic placement of the megapodes or moundbuilders (Megapodiidae) as the sister group to all other galliforms, and the guans and curassows (Craidae) as the closest relatives of the remaining phasianoids (figure 1). Megapodes and cracids have clear Gondwanan distributions, although a few species of megapodes have penetrated Wallacea and the western Pacific and several cracids have reached North and Central America. Phasianoids have attained a near-cosmopolitan distribution, and were present in the Northern Hemisphere at least by the beginning of the Eocene. Several fossil groups from the Early Tertiary of Europe have been viewed as being morphologically similar to cracids and megapodes (Olson 1989), but none of these fossils has been directly linked to these modern groups on the basis of derived characters.

The basal relationships of anseriforms are well understood (Livezey 1986, 1997; Ericson 1997). The screamers of South America (Anhimidae) are the sister group to the ducks, geese and swans (Anseres). Within the Anseres, the basal lineage is the Australian magpie goose (*Anseranus semipalmata*; Anseranatidae). Olson (1999) has proposed that the fossil taxon *Anatalavis* from the Laurasian Palaeogene is an anseranatid. This is based on two supposed derived characters whose precise distribution across taxa and their polarities have been variously interpreted by other workers (Livezey 1997; Ericson 1997); therefore, the presence of an anseranatid in Laurasia remains problematic. For nearly two decades the fossil taxon *Presbyornis* has been claimed to represent a 'transitional shorebird' and an evolutionary mosaic that links anseriforms, flamingos and other taxa to presumed ancestors within charadriiform shorebirds (Olson & Feduccia 1980a,b; Feduccia 1995, 1999). None of this speculative scenario has been supported by a quantitative phylogenetic analysis, and now two independent cladistic studies (Livezey 1997; Ericson 1997) confirm that *Presbyornis* is imbedded within the anseriforms as the sister group to the Anatidae. The 'transitional shorebird' hypothesis is thus decisively rejected (Livezey 1997). The phylogenetic placement of *Presbyornis* is significant because it confirms the presence of relatively advanced anseriforms in the Late Cretaceous of Antarctica (Noriega & Tambussi 1995) and the Palaeocene of North America (Olson 1994), thus implying more basal divergences within the Galloanserae and basal neornithines are at least Late Cretaceous in age.

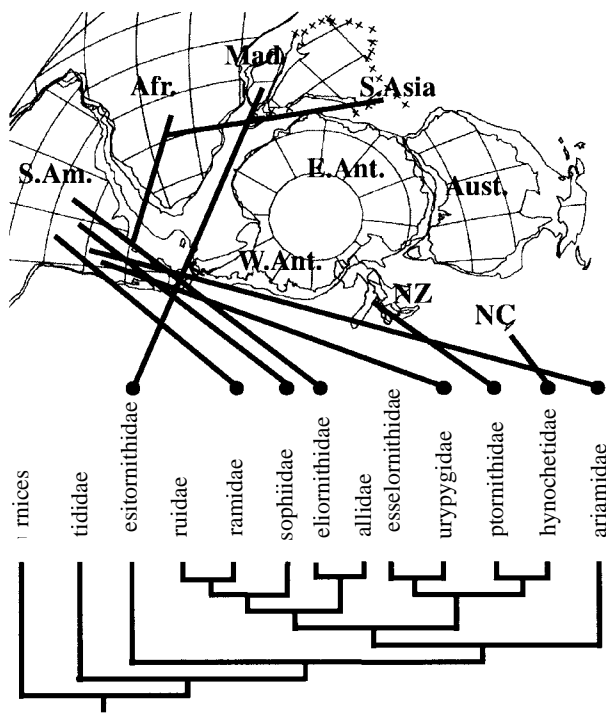


Figure 2. Relationships among the Gruiformes (Livezey 1998), mapped on to an Early Cretaceous (120 Myr ago) reconstruction of the southern continents (modified from Smith *et al.* (1981)). The Turnices, Otididae, Gruidae and Rallidae have unresolved distributional patterns at this level of analysis. The Messelornithidae are known as fossils from the Palaeogene of Europe.

(d) *Trans-Antarctic distributions within Neoaves*

Phylogenetic and biogeographical evidence for an origin of Neornithes in Gondwana can also be documented for clades within the Neoaves. Although no clear evidence exists to place a specific group at the base of the Neoaves, the observation that multiple clades exhibit trans-Antarctic relationships supports a conclusion of significant diversification among neornithines by the end of the Cretaceous. This discussion summarizes those groups for which the phylogenetic evidence supports Gondwanan (trans-Antarctic) biogeographical patterns.

The order Gruiformes has recently been the subject of a detailed phylogenetic analysis using morphological data (Livezey 1998; figure 2). This study yielded a tree substantially different from that inferred using DNA hybridization distances (Sibley & Ahlquist 1990) and partially different from that using only 366–870 bp of the mitochondrial 12S rRNA gene (Houde *et al.* 1997). The root of the hybridization tree appears to be suspect, however, and when this tree is compared with that of morphology by placing bustards (Otididae) at the root, the two topologies are more congruent. Because the morphological tree is more comprehensive empirically, it is used as the basis of this discussion. Gruiformes exhibit strong Gondwanan distribution patterns (figure 2). In particular, the flightless kagu (*Rhynochetus jubatus*) of New Caledonia has its closest relatives in two extinct flightless species (*Apterornis*) in New Zealand. *Rhynochetus* and *Apterornis*, in turn, have their closest relative in the volant

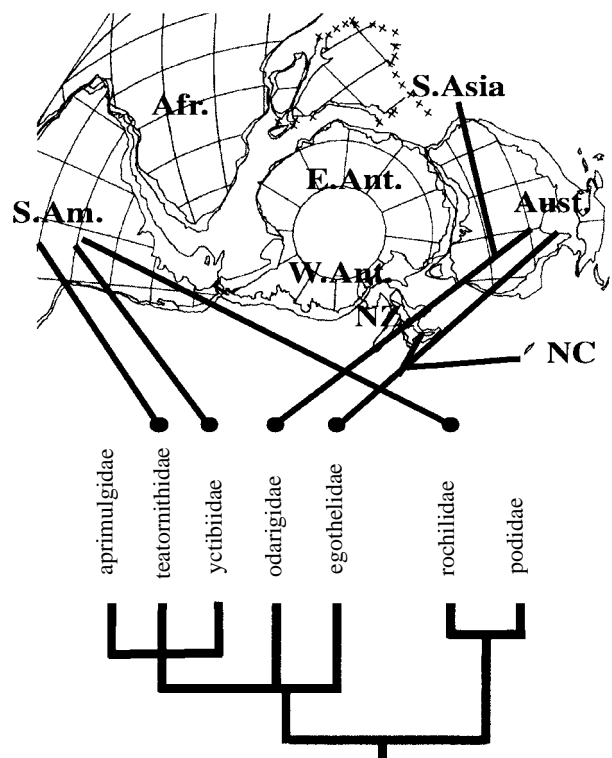


Figure 3. Relationships among the Caprimulgiformes and Apodiformes (Cracraft 1981; Sibley & Ahlquist 1990) mapped on to an Early Cretaceous (120 Myr ago) reconstruction of the southern continents (modified from Smith *et al.* (1981)). The Caprimulgidae and Apodidae have unresolved distributional patterns at this level of analysis.

sunbittern (*Eurypyga helias*) of tropical America (Cracraft 1982; Hesse 1990; Livezey 1998) and the fossil Messelornithidae of the North American and European Palaeogene (Hesse 1990; Livezey 1998). Gruiformes have an extensive Early Tertiary record in Laurasia, yet the precise relationships of these fossil taxa to Southern Hemisphere groups remain to be determined. Several European fossils have been identified as phorusrhacoids, an extinct group of predaceous gruiform birds from South America (Mourer-Chauviré 1981; Peters 1987), but the affinities of the fossils were considered problematic at the time of description. Presumed phorusrhacoids are first known from the Late Eocene of the Antarctic Peninsula (Case *et al.* 1987).

Morphological data (Cracraft 1988) suggest that the Apodiformes (hummingbirds, swifts) are close relatives of the Caprimulgiformes (nightjars and their allies). DNA hybridization distances indicate that Strigiformes (owls) are closer to caprimulgiformes, with apodiforms being the sister group of those two orders (Sibley & Ahlquist 1990). Relationships within caprimulgiformes are still in need of more study. Phylogenetic inferences based on DNA hybridization (Sibley & Ahlquist 1990) and relatively short sequences (656 bp) of the mitochondrial cytochrome *b* gene (Mariaux & Braun 1996) conflict; the source of this conflict is unknown, but it may be due to insufficient sequence data and taxon sampling. DNA hybridization data (Sibley & Ahlquist 1990) and morphology (Cracraft 1981) agree in placing steatornithids, nyctibiids and

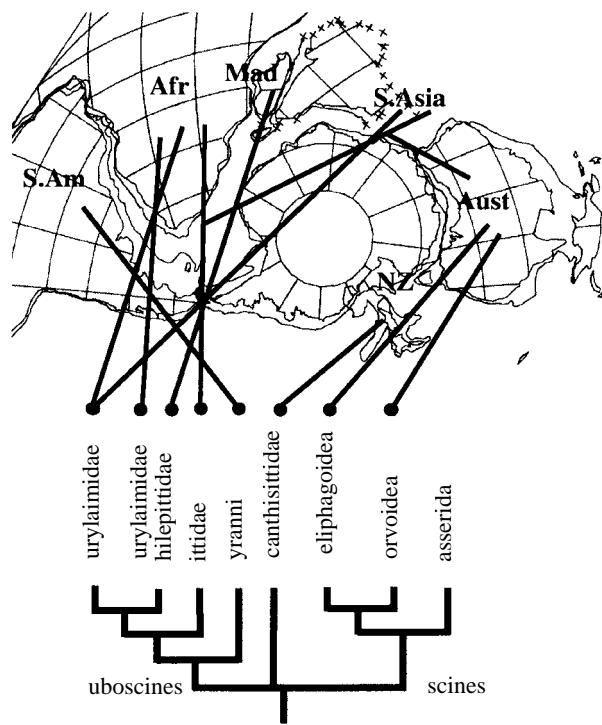


Figure 4. Relationships among the basal lineages of the Passeriformes (Raikow 1987; Sibley & Ahlquist 1990; Prum 1993; Cracraft & Feinstein 2000) mapped on to an Early Cretaceous (120 Myr ago) reconstruction of the southern continents (modified from Smith *et al.* (1981)). The Passerida have unresolved distributional patterns at this level of analysis.

caprimulgids together and this is followed here (figure 3). The relationships of aegothelids and podargids to each other (Cracraft 1981) or to the other three families (Sibley & Ahlquist 1990) are ambiguous. The most relevant observation is that an inference of trans-Antarctic biogeographical distributions among caprimulgiforms is robust to differences in relationships. This conclusion, however, is said to be challenged by the putative occurrence of all Southern Hemisphere families in the Palaeogene of Europe or North America (Olson 1989; Feduccia 1999), and thus by the suggestion that current Southern Hemisphere distributions are relict. Yet, the systematic positions of the fossil taxa are anything but secure. Records for the Australian Aegothelidae (Mourer-Chauviré 1982) and Neotropical Nyctibiidae (Mourer-Chauviré 1989) are based on fragmentary material that cannot reliably be placed phylogenetically (Mayr 1999). Proposed Palaeogene fossils of oilbirds (Steatornithidae) in North America (Olson 1987) and Europe (Mourer-Chauviré 1982; Mayr 1999) are also ambiguous phylogenetically and may not have a close relationship to the modern family (Mayr 1999). Out of the two proposed Palaeogene genera assigned to the Australasian Podargidae, one of them (*Quercypodargus*; Mourer-Chauviré 1989) is based on isolated, unassociated bones that cannot be said to be definitively caprimulgiform (Mayr 1999). The best candidate for a Palaeogene podargid is *Masillapodargus*, an articulated but crushed skeleton from the Middle Eocene of Messel (Mayr 1999) that appears to be the sister group of the two extant genera, one of which is South-East Asian in distribution.

Most modern avian diversity, over 5700 species, consists of the songbirds (Passeriformes), and phylogenetic and biogeographical patterns indicate an extensive evolutionary history in Gondwana for the order (figure 4). Relationships among the basal lineages of passeriforms are moderately well understood on the basis of molecular and morphological data (Ames 1971; Feduccia 1974, 1975; Sibley & Ahlquist 1990; Raikow 1987; Prum 1993; Cracraft & Feinstein 2000). An early divergence within passeriforms involves a trans-Antarctic relationship between the four species of New Zealand wrens (*Acanthisittidae*) and part or all of the oscine and suboscine lineages distributed elsewhere in Gondwana. Although acanthisittids are clearly passeriform, their relationships within that group are ambiguous. A single derived morphological character (Raikow 1987) suggests a relationship with oscines, whereas DNA hybridization data (Sibley & Ahlquist 1990) ambiguously place *Acanthisitta* with suboscines. Within Old World suboscines, broadbills (*Eurylaimidae*) appear to be monophyletic only if the Malagasy asities (*Philepittidae*) are included (Prum 1993). Eurylaimids and pittids are primarily tropical Asian, but have several species secondarily distributed in Africa, and in the case of the pittas, in Australasia. Along with the Tyranni, their higher-level relationships indicate a Southern Hemisphere biogeographical pattern (figure 4).

A second trans-Antarctic pattern in passeriforms is found between suboscines, which are predominantly South American (*Tyranni*; 1100 species), and the oscines (nearly 4600 species), the basal lineages of which are largely Australasian. Within suboscines, the New World Tyranni are related to pittas, broadbills and the asities of the Old World tropics. The main division within oscine songbirds is between the passeridan and the corvidan assemblages (Sibley & Ahlquist 1990). Two clades of the latter group (the *Meliphagoidea* and *Corvoidea*; figure 4) are related to each other and radiated extensively (1100 species) in Australasia, with several lineages later becoming widespread as Australia approached Asia. The sister group to the corvidan Australasian radiation, the Passerida, is the most diverse assemblage (3500 species), but their interfamilial relationships, and thus biogeographical pattern, remain unresolved. The oldest known songbird is from the Early Eocene of Australia (55 Myr ago) but its exact affinities are unknown (Boles 1995).

Other orders within Neoaves also have probable Gondwanan distributions but phylogenetic patterns are poorly understood. Penguins (*Sphenisciformes*) are restricted to the cold-water coastlines of the southern continents and have an extensive fossil record dating back to the Palaeogene of Australia, New Zealand and Antarctica (Fordyce & Jones 1990). It seems highly likely that continental break-up influenced their biogeographical history, but phylogenetic relationships among the recent and fossil taxa are not yet resolved. The same can be said for parrots (*Psittaciformes*), which have radiated extensively in South America and Australia and have a minor radiation in Africa and tropical Asia. Meagre molecular data, including DNA hybridization (Sibley & Ahlquist 1990) and mitochondrial sequences (Miyaki *et al.* 1998), are not inconsistent with the African, Australian and South American parrots each being monophyletic and with the latter two groups being sister taxa. If confirmed,

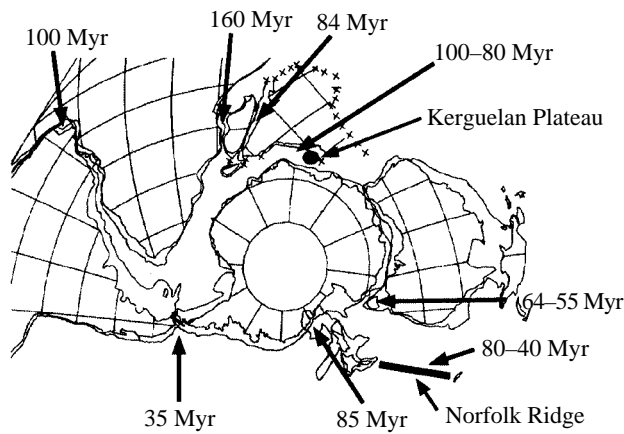


Figure 5. Estimated times of terminal land connections (vicariance) among the southern continents. Vicariance events are located on an Early Cretaceous (120 Myr ago) reconstruction of Gondwana (modified from Smith *et al.* (1981)). See § 3 for discussion.

parrots would also exhibit trans-Antarctic relationships. A Late Cretaceous dentary bone from North America has been identified as psittaciform (Stidham 1998), but this assignment is disputed (Dyke & Mayr 1999). The next earliest fossils are from the Palaeogene of Europe (Mayr & Daniels 1998) but their relationships to modern groups are unknown.

3. GONDWANAN PALAEOGEOGRAPHY: CONSTRAINTS ON THE TIMING OF AVIAN DIVERSIFICATION

Two lines of evidence are relevant for inferring the temporal pattern of neornithine diversification. First, minimum ages of lineages can be estimated when dated fossils are interpreted within the framework of a phylogenetic hypothesis, thus calibrating the ages of deeper lineages and sister taxa, including those with no fossil histories (Norell 1992). Second, ages of vicariance events derived from geological data can also be used to infer the minimum ages of lineages. Here, I review knowledge about the configuration and break-up of the southern continents to establish palaeogeographical constraints on the temporal history of neornithine diversification (figure 5).

(a) *South America/Africa*

Plume magmatism (Storey 1995; Courtillot *et al.* 1999) and sea-floor magnetic anomalies (Renne *et al.* 1992) indicate that South Atlantic rifting began by 137 Myr ago, with ocean floor being formed between 127 and 131 Myr ago at the latitude of the Paraná Basin. Of critical importance for terrestrial biogeography, however, is when final land connections might have been severed across the central South Atlantic. Most geological studies place final separation between South America and Africa along a transcurrent rift in the Late Albian about 100 Myr ago (Masclé *et al.* 1988; Szatmari & Milani 1999). This timing is consistent with ammonite (Kennedy & Cooper 1975) and echinoid (Néraudeau & Mathey 2000) faunal similarities between the northern and southern Atlantic.

(b) *Madagascar/India/East Antarctica*

Madagascar separated from the Kenya–Somali coastline and moved south-eastward, tracing the strike of the Davie Fracture Zone, in the Middle to Early Late Jurassic, 155–160 Myr ago (Rabinowitz *et al.* 1983; Coffin & Rabinowitz 1987) and attained its current position relative to Africa by 120 Myr ago (Barron 1987; Lawver *et al.* 1992). Continental extension between Greater India, on the one hand, and Australia and East Antarctica, on the other, was initiated near the time Madagascar rifted from Africa, 160 Myr ago, and the oldest magnetic anomalies off the western margin of Australia are dated to 132.5 Myr ago (Powell *et al.* 1988). The subaerial emplacement of the large Kerguelan Plateau at 114–110 Myr ago implies some separation between India and Antarctica by that time (Lawver *et al.* 1992; Hay *et al.* 1999), but precisely when India may have severed all terrestrial connections with East Antarctica is uncertain because critical events took place during the Cretaceous Quiet Zone and are not marked by magnetic anomalies. Conventional interpretations indicate southern India had separated substantially from Antarctica by 118 Myr ago (Powell *et al.* 1988; Lawver *et al.* 1992). Some reconstructions, however, while adopting similar continental positions, postulate subaerial connections between Madagascar–Seychelles–India–Sri Lanka and Antarctica via the Kerguelan Plateau well into the Late Cretaceous, 80–100 Myr ago (Hay *et al.* 1999), and this is supported by palaeontological evidence, discussed in § 4(b). Ocean crust first appeared between Madagascar and Seychelles–India at 84 Myr ago and between the latter two blocks at 64 Myr ago (Plummer & Belle 1995).

(c) *West Antarctica/New Zealand/New Caledonia*

Prior to the Late Cretaceous, the continental blocks of Campbell Plateau and Chatham Rise, New Zealand, Lord Howe Rise and the Norfolk Ridge/New Caledonia were fitted to the eastern margin of Australia and, in the south, to Marie Byrd Land and West Antarctica. These fragments dispersed to the north and east following sea-floor spreading in the Tasman and South-West Pacific basins beginning 82 Myr ago and 85 Myr ago, respectively, and land connections would have been lost at that time (Hayes & Ringis 1973; Yan & Kroenke 1993). Spreading in the Tasman Basin was relatively rapid, especially to the south, and ceased around 60 Myr ago (Weissel & Hayes 1977; Laird 1994). The north part of the Tasman Basin is younger than the south, being latest Cretaceous and Palaeogene in age (Hayes & Ringis 1973). The geology of the region east of Lord Howe Rise is still poorly understood. The Three Kings and Norfolk ridges are interpreted as an island arc system behind a west-dipping subduction zone (Ballance *et al.* 1982; Mortimer *et al.* 1998) and the Norfolk Basin as a back-arc basin (Ballance *et al.* 1982) that formed in the Early Miocene by crustal thinning and, possibly, sea-floor spreading (Mortimer *et al.* 1998). Geophysical and palaeontological data (Davey 1982; Ayress 1994; Herzer *et al.* 1997) indicate that extensive terrestrial environments existed along these continental ridges from Late Cretaceous times until perhaps the Mid-Tertiary. This would probably have permitted continuous, or at least intermittent, land connections between New Zealand and New Caledonia (Herzer *et al.* 1997).

(d) East Antarctica/Australia

The rifting history of Australia and East Antarctica is well documented (Cande & Mutter 1982; Veevers *et al.* 1990). Significant continental extension between the two blocks began at least by 160 Myr ago and sea-floor spreading was initiated at 96 Myr ago. Northward spreading of the Australian Plate was very slow until 49 Myr ago, increased slightly until 44.5 Myr ago, and since that time has increased substantially (Veevers *et al.* 1990). In the region of Tasmania and the South Tasman Rise the ridge axis is repeatedly offset southwards (Veevers *et al.* 1990) and shear motion between Antarctica and the margin of the South Tasman Rise resulted in final separation in the Early Oligocene, 33–34 Myr ago (Royer & Rollet 1997). Tasmania and the South Tasman Rise were an east-to-west barrier to marine organisms until the Middle to Late Eocene (McGowran 1973; Lawver *et al.* 1992), and land connections between East Antarctica and south-eastern Australia were likely terminated in the Palaeogene as sea levels rose (Woodburne & Case 1996).

(e) South America/Antarctica

The cordilleras of Andean South America and West Antarctica were continuous into the Palaeogene (Dalziel & Elliot 1971), thus providing continuity of the terrestrial biotas between South America and West and East Antarctica. Some connection may have persisted as late as 30–35 Myr ago when the cordillera was disrupted and formation of the Scotia Sea was initiated (Lawver *et al.* 1992).

4. DISCUSSION**(a) The timing of avian ordinal radiations**

The phylogenetic, palaeontological and palaeogeographical evidence reviewed here places constraints on our understanding of the temporal and spatial history of avian higher taxa (figure 6). When a conservative evaluation of lineage age derived from fossils is used to estimate the timing of diversification across neornithines, and when that pattern is combined with geological data on the timing of Gondwanan dispersion, many of the lineages can be inferred to be Late Cretaceous or older.

The conclusion of a substantial evolutionary history of modern birds prior to the K–T boundary is a logical consequence of interpreting lineage ages phylogenetically (Norell 1992). It is further strengthened when phylogenetic patterns are reconciled with Earth history. Fossils of Late Cretaceous age assigned to the Presbyornithidae (Noriega & Tambussi 1995), Charadriiformes (Olson & Parris 1987; Case & Tambussi 1999) and Gaviiformes (Chatterjee 1989; Olson 1992) exert a major influence on inferences about the age of deeper branch points. These fossils alone, assuming their correct age and phylogenetic placement, establish that many lineages of neornithines originated prior to the K–T boundary (figure 6). Estimated geological vicariance ages, particularly those of Africa/South America, India/Antarctica and New Zealand/Antarctica, also calibrate much of the avian tree as being Cretaceous in age (figure 6).

(b) Neornithine biogeography

The phylogenetic evidence reviewed here strongly supports the conclusion that early avian diversification

took place in Gondwana. Palaeognaths, Galloanseres and many lineages of Neoaves have clear trans-Antarctic distribution patterns. This conclusion, moreover, is generally robust to alternative hypotheses of relationship within these major groups. The involvement of so many neornithine higher taxa in Gondwana is so profound that it is likely that a Southern Hemisphere history will be implicated for additional groups of Neoaves as their relationships become more resolved. Such findings would not imply, however, that the break-up of Gondwana was causally 'responsible' (Hedges *et al.* 1996) for the diversification of modern birds. At most, continental dispersion isolated ancestors of clades that later diversified on continental land masses for a variety of other reasons.

Phylogenetic and biogeographical patterns raise many tantalizing questions. Most intriguing, perhaps, is what was the role of Greater India in the biogeographical history of birds? This continental block was a huge land-mass, much larger than peninsular India today (McKenna 1995; Patzelt *et al.* 1996), and was in tropical climates throughout the Late Cretaceous and Early Tertiary. Although the age of disjunction of India from East Antarctica is ambiguous based on geophysical evidence alone, palaeontological data provide a clearer picture. A variety of fossil vertebrates from the latest Cretaceous Maevarano Formation of Madagascar (Maastrichtian; Rogers *et al.* 2000), including theropod dinosaurs (Sampson *et al.* 1998), Gondwanatherian mammals (Krause *et al.* 1997), cichlid fishes (Farias *et al.* 1999), pelobatid frogs (Sahni *et al.* 1982), and peirosaurid (Buckley & Brochu 1999) and notosuchid crocodiles (Buckley *et al.* 2000), all have their closest relatives in the Late Cretaceous of India and/or South America, thus strongly implying a land connection between Madagascar/Greater India and East Antarctica probably via the Kerguelan Plateau (Hay *et al.* 1999) well into the Late Cretaceous (Sampson *et al.* 1998; Rogers *et al.* 2000), but prior to the 84 Myr ago separation of Madagascar/India. What are the implications for birds? At present, the Maevarano Formation has yielded only pre-neornithine taxa (Rogers *et al.* 2000), which indicates they survived until the very end of the Cretaceous. No neornithine fossils have been found as yet, but this analysis identifies three ancient endemics as being candidates for having arrived in Madagascar via India and East Antarctica: elephant birds (Aepyornithidae, figure 1); mesites (Mesitornithidae, figure 2) and the asities (Philepittidae, figure 4). Each of these has relationships to taxa on other southern continents, or also to tropical Asia (asities), and each is a member of a lineage that can be estimated to be more than 85 Myr in age as inferred from geological vicariance events.

Even though many neornithine clades had their early history in Gondwana, the expansive North American and European fossil record indicates the development of a diverse avifauna by Palaeogene times. It does not follow, however, that these fossils specify an autochthonous Laurasian origin for those lineages as opposed to their being descendants of Gondwanan groups. Only phylogenetic and biogeographical patterns can answer that question. This goes to the heart of the claim that many Palaeogene fossils are directly assignable to Southern Hemisphere families and that the latter are biogeographical

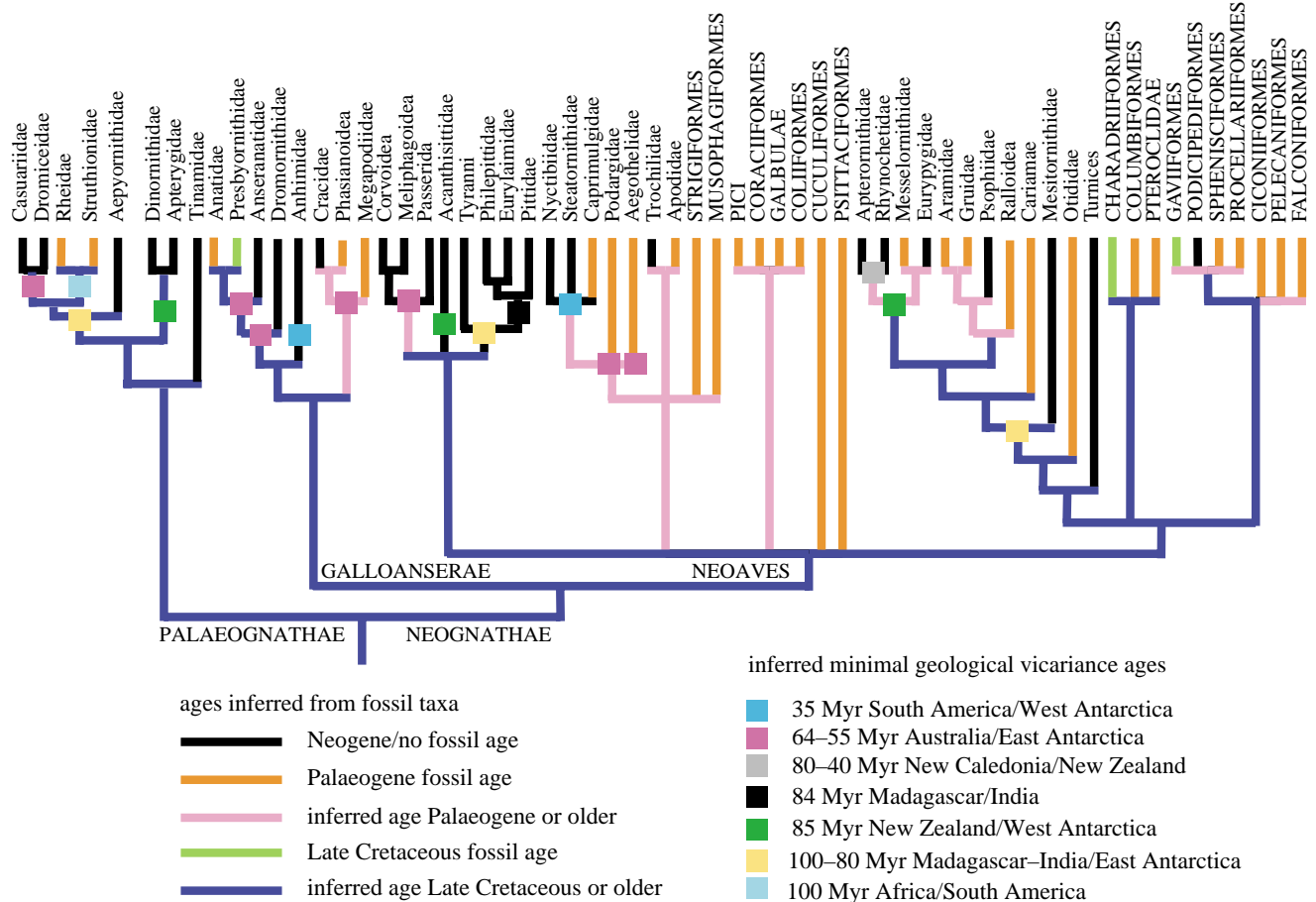


Figure 6. Empirical and estimated ages of lineages of avian higher taxa when referenced to a phylogenetic hypothesis (after figures 1–4; Cracraft 1988; Sibley & Ahlquist 1990). Ages of terminal taxa and/or lineages are based on palaeontological evidence (from citations in §2; Olson 1985; Unwin 1993). Non-terminal lineage ages are the oldest inferred from the ages of terminal taxa as determined by fossils or from palaeogeographical evidence summarized in §3 and interpreted within the framework of the postulated phylogenetic relationships (Norel 1992).

relics (Olson 1989; Mourer-Chauviré 1983, 1989; Feduccia 1995, 1999). At issue is the systematic status of the Early Tertiary fossil taxa claimed to represent extant Southern Hemisphere endemics. The ordinal affinities of many of these taxa are not in dispute, but their cladistic relationships to Southern Hemisphere forms have not been investigated sufficiently and many are assigned to families on the basis of primitive characters or non-diagnostic skeletal elements (Mayr 1999). Thus, it is dubious whether Gondwanan clades with strong trans-Antarctic patterns of relationships should be considered to be relics merely because of a Palaeogene fossil record in Laurasia. A more parsimonious hypothesis is that numerous neornithine lineages became more cosmopolitan in the Late Cretaceous or Early Tertiary and are recovered in North America and Europe as a consequence of a superior fossil record. Because phylogenetics and biogeography indicate many of these clades had southern origins, the observation that fossil taxa are nested within those lineages suggests they attained a Laurasian distribution secondarily.

(c) *Avian history and the K–T extinction event*

The molecular data used to support a Cretaceous origin of avian clades (Hedges *et al.* 1996; Cooper & Penny 1997) have little definitive to say about the overall temporal pattern of avian diversification. Each study

employed small samples of exemplar taxa of avian orders, and while the included clades may have had Cretaceous origins, the data are inadequate to examine evolutionary patterns among family-level taxa. As a consequence, additional analyses will be needed to assess the influence of the K–T extinction event on their timing of diversification.

Likewise, phylogenetic and biogeographical patterns within neornithines are inconsistent with the original formulation (Feduccia 1995) of the K–T mass extinction bottleneck hypothesis, which postulated that few clades of neornithines existed prior to the extinction event, and those that did were extirpated. The data presented here suggest that numerous lineages of neornithines were resident on the southern continents at the end of the Cretaceous, yet the hypothesis cannot be tested directly by the fossil record because of the paucity of Cretaceous fossil localities on the southern continents. Indeed, there are exceedingly few unquestioned neornithine fossil taxa from the Late Cretaceous anywhere in the world, and there is a huge diversity in the Palaeogene. Current data, therefore, are consistent with a history in which numerous lineages arose in the Late Cretaceous but did not achieve significant diversity until the Palaeogene. The hypothesis can say little about the effect of the K–T extinction event because few, if any, data are particularly informative. The palynological record across the K–T boundary on West

Antarctica does not record a marked extinction event for land vegetation (Askin 1988). If that is a general pattern, perhaps the Southern Hemisphere biota was less influenced by a northerly directed oblique impact at Chicxulub (Pierazzo & Melosh 1999) than were biotas of the Northern Hemisphere. Still, the Chicxulub bolide must have had major global environmental consequences (Toon *et al.* 1997), and avian species diversity could have been drastically reduced even in the Southern Hemisphere. Palaeontological sampling across K–T terrestrial environments, particularly on the southern continents, will be necessary to refine our understanding of this critical time in neornithine history.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.

