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Tempo and mode of modern bird evolution observed with large-scale taxonomic sampling

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Abstract
Macroevolutionists continue to disagree about the evolutionary history of birds. Their debate centers on the apparent discrepancy between molecular- and fossil-derived times of certain events. In this study we will show that there is much more agreement than discrepancy. We do it by simultaneously using both molecules (DNA hybridization and DNA sequence) and fossils to study a large set of avian taxa. Our analysis focuses on the time of origin and diversification of most of the orders and families of extant birds. Both tools show that the Cretaceous–Tertiary transition witnessed a major ordinal diversification within extant birds. Both also show a pulse of family diversification near the Eocene–Oligocene transition. Thus both of these pulses occurred close to times of mass extinction. The presented evolutionary time scale for extant birds launches testing of novel inter-disciplinary hypotheses.

Keywords: *Avian, molecular clock, divergence time, fossil record, cretaceous, tertiary*

Introduction

An accurate evolutionary timescale for modern living organisms offers several templates for future scientific research. A robust timescale places absolute dates on the divergences between major lineages and thus provides assessment of rates of biologic evolution. This timescale especially is needed for modern birds (Neornithes), a group that comprises a breadth of biologic and ecologic diversity unique among vertebrates. Revealing the evolutionary origin and rate of appearance of biologic innovations in birds leads us to a better understanding of their evolutionary history and characterization. In addition to inference of absolute divergence times (tempo), a known timescale illustrates the mode of modern bird evolution. As such, it can provide invaluable insight into past extinction patterns. For example, comparison of originations, diversifications and intermediate "ghost" time distinguishes whether neornithine diversity was formed through a single or relatively few contemporaneous radiations. Or whether divergences are more or less

continuous in time, which would indicate the gradual appearance of clades through time. Evolutionarily insightful information on the potential disparity between time of origination and diversification is gleaned from the proportion of stem age (age of initial divergence defined by the divergence between the extant group of interest and its extant sister group; (De Queiroz and Gauthier 1992) to crown age (age of initial divergence among extant taxa only, Cook et al. 2000; van Tuinen et al. 2004).

Temporal information can be gathered directly from the fossil record (Blondel and Mourer-Chauviré 1998; Dyke and van Tuinen 2004; Clarke et al. 2005; Mayr 2005) of modern birds (Neornithes), or inferred indirectly by using a molecular clock calibrated with well-constrained fossils (Dyke and van Tuinen 2004; van Tuinen and Hedges 2004). Recent molecular estimates of the origin of various bird orders (Cooper and Penny 1997; van Tuinen and Hedges 2001; Paton et al. 2002) have suggested gaps in the fossil record as large or larger than the known history of

some taxa, a pattern also present in some placental mammals (Alroy 1999; Foote et al. 1999; Brochu 2001). This incongruence has given rise to an intense debate about the usefulness of molecular clocks and the fossil record for dating deep evolutionary divergences (Benton and Ayala 2003). As yet, this debate is unresolved. One novel approach is to explore which parts of the tree reflect major incongruence between molecular and fossil estimations (Kumar and Hedges 1998).

In order to establish the true extent of temporal disparity between molecular and paleontologic data, a large number of time estimates based on both genetic and fossil data is needed. A subsequent question is whether this comparison would demonstrate a consistent trend for molecular divergence time estimates to predate the earliest known fossils (Alroy 1999; Benton 1999). Discovery of significantly older molecular estimates at every taxonomic level would suggest an unknown but pervasive molecular bias that should be understood before molecular timescales can be considered reliable and accurate. Alternatively, if fossils underestimate only the early bird history coinciding with the Late Mesozoic (proposed also for placental mammals: Kumar and Hedges 1998), a more specific bias may exist. Such bias may include fossil preservation, improper identification of stem lineages, or an undetected problem with the molecular clock assumption (i.e. extreme rate variation).

Models of possible tempo and mode

Three different models for the evolutionary mode for birds have been proposed (Cooper and Fortey 1998; Archibald and Deutschman 2001; Penny and Philips 2003). None of these models are concordant with both genetic and fossil data. To reconstruct the best possible view of modern bird evolution, data from a variety of sources must be considered. Clues on the origin and preservation of key innovations are gained from the distribution of morphological characters on the neornithine molecular tree (Mooers and Heard 1997, for review). Divergence times for major crown and stem lineages provide additional information. Given current limits of phylogenetic resolution and insights derived from molecular and fossil data, the three models of bird evolution are reviewed below within the context of macro-evolutionary patterns of origination and diversification. We highlight the importance of extinction for unraveling the patterns and processes shaping biodiversity (Raup 1995).

K–T explosion model

This model is discussed in both the paleontologic and molecular literature (Wyles et al. 1983; Feduccia 1995; Bleiweiss 1998). This type of model, regarded "short-fuse", has been applied to both neornithine and placental evolution and is based primarily on a literal interpretation of the fossil record. The bird fossil record, in large part, suggests that all modern lineages derive from a single late Cretaceous ancestor. Shortly after the Cretaceous–Tertiary (K–T) boundary (within ~10 Ma), the survivors quickly radiated into all ordinal bird lineages recognized today. Branching patterns specific to this explosive model combine short stem duration and long crown duration of modern bird orders, i.e. Cenozoic boundary origination followed soon after by the diversification of lineages surviving today (Feduccia 1996). Most biologists embracing this model equate it with near-K–T origins of all modern bird orders although superordinal divergences could extend slightly into the Cretaceous (Figure 1A,B). Recent cladistic studies have started to incorporate early Tertiary and late Mesozoic bird fossils (Ericson 1997; Livezey 1997; Dyke 2001; Stidham 2001; Clarke et al. 2005), placing some fossil lineages on derived phylogenetic branches within a small number of modern orders. This view imposes a pre-Tertiary diversification of some ordinal clades (Palaeognathae, Anseriformes, Galliformes and Gruiformes). However, an evolutionary explosion involving the remaining bird orders at or shortly after the K–T boundary remains the most plausible hypothesis based on paleontologic data alone (Dyke 2001). The K–T-explosion model has been applied foremost to ordinal diversification at the K–T boundary and is probably not relevant to the evolutionary tempo and mode of extant bird families, which are undoubtedly younger (Mayr 2005).

Alternative short fuse model

A second model has been proposed (Paton et al. 2002), as an alternative to the K–T-explosion model. This model also indicates short stem ordinal ages but differs by placing the initial diversification of living clades during the mid-late Cretaceous (Figure 1C). The available bird and mammal molecular data often are interpreted as providing evidence for this model (Alroy 1999; Benton 1999; Foote et al. 1999; Brochu 2001) Currently, few studies bear on the question of whether superordinal cladogenesis is followed immediately by crown divergence in birds or not (Cracraft 2001; van Tuinen et al. 2004). A short-fuse model does not necessarily imply a single explosive radiation encompassing all bird groups, but may be applicable to the evolution of only some major superordinal groups (e.g. Neoaves). This is an important distinction because a short-fuse model does not conflict with Cretaceous crown ages for ratites, tinamous and galloanserine birds and Tertiary ages for neoavian birds (Dyke 2001). Therefore, this model could account for multiple radiations
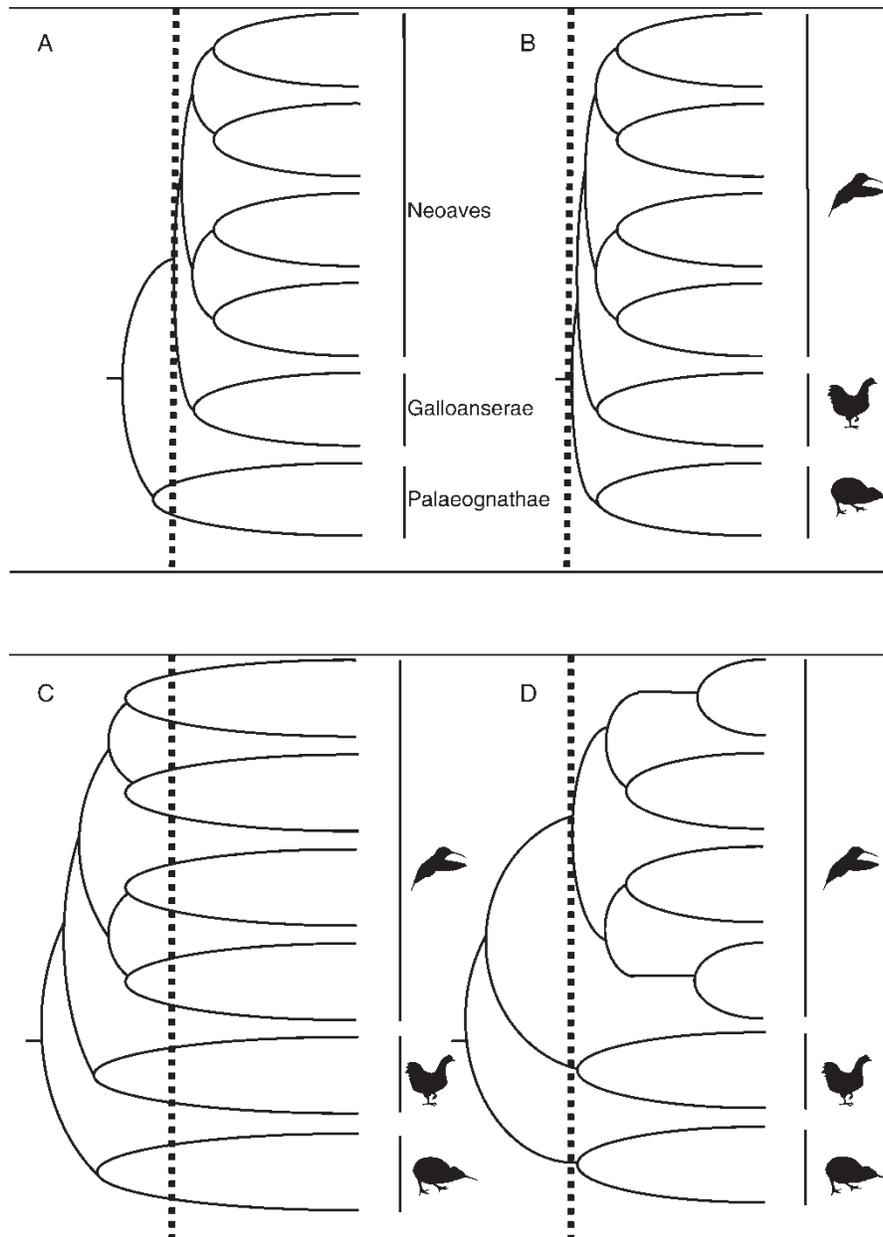
Figure 1.   Four models describing the possible relationship between time of lineage origination and diversification among and within the three modern bird superordinal clades Neoaves, Galloanserae, and Palaeognathae. Ordinal and familial clades are depicted here. (A) K–T-explosion (short-fuse) model: origin of the major orders of birds is followed soon after by diversification into families. Feduccia's (1996) model suggests that all modern birds derive from a single shorebird-like ancestor at the K–T boundary (shown as dashed line), but with the possibility that palaeognath origin extended into the Cretaceous; (B) Alternative explosive model: both origin and diversification of all modern bird orders take place very close to or at the K–T boundary; (C) Short-fuse model: the model depicted here is also an explosive model but with ordinal diversification taking place within the Cretaceous; (D) Long-fuse model: a model that combines rapid phylogenetic ordinal radiation with long Cretaceous ordinal stems. Depicted here is a K–T radiation, but a long-fuse model could hold equally well with a single or multiple pre-or post K–T radiations.

at different times within different superordinal clusters.

Long fuse model

The long fuse model implies long, "non-conspicuous" stem taxa leading up to much later diversification of extant groups (Cooper and Fortey 1998). The stem taxa may be unrecognized due to taphonomic biases in the fossil record or because of difficulties in assigning characters. It is seldom emphasized that most molecular ordinal estimates represent stem lineage divergence (of much more inclusive clades) that may not approximate diversification of extant clades. This lack of concordance between time of ordinal origination and crown age could be due to extinction

of earlier members, and molecular data alone do not provide such records of extinction. Lagtime between origination and crown radiation may be a widespread phenomenon as it is proposed also in studies on angiosperm, placental and metazoan evolution (Cooper and Fortey 1998). This type of model holds promise as a possible explanation for the dichotomy posed by the Cretaceous superordinal originations based on molecular estimates and the post-Cretaceous radiation implied by the fossil record (Figure 1D) (Cooper and Fortey 1998).

Our approach

To better address the macro-evolutionary patterns of the evolutionary tempo and mode for extant birds, broad taxonomic sampling is required with iteration between molecules and morphology. Adequate molecular sampling from each extant family is ultimately necessary because the evolutionary relevant biologic diversity among extant birds will be highest at the family level. Also, few mosaic fossils are known and early Tertiary fossils often have been diagnosed to either order or family. Presently, the data set most closely approximating the requisite broad sampling is a DNA–DNA hybridization data that includes pairwise comparison with circa 1700 of the approximately 10,000 modern species. This sampling extends across every traditional order and about two-thirds of all families (Morony et al. 1975; del Hoyo et al. 1992). We analysed this data set to provide divergence times for the major extant bird groups and enhanced it with published sequence-based divergence times. With this approach, we address the following topics:

(1) To obtain an evolutionary timescale for living birds representing family and order levels.
(2) To assess the phylogenetic distribution of temporal incongruence between molecular and fossil data through the definition of stem vs. crown clades. Towards this goal, we review the neornithine fossil record relevant to extant clades. Because of limited knowledge and molecular data on bird intraorder divergence times, we present the null hypothesis that some of the previously noted disparity (Hedges et al. 1996; Cooper and Penny 1997; Benton 1999; van Tuinen and Hedges 2001; Paton et al. 2002) between molecules and fossils is due to an implicit focus on either stem or crown clades. In fact, much of the neornithine fossil record may better reflect diversification events through recognition of morphologically distinct groups that can also include part of the stem for some unique groups.
(3) To deduce whether the temporal bias of molecular (or fossil) estimates is consistent. We investigate whether molecular divergence times reliably predate the ages presented by the oldest relevant fossils.
(4) To discriminate between origination and diversification models for the best fit with the observed temporal patterns for modern bird evolution. Other than at least one implied event (major extinction at the K–T boundary followed by adaptive radiations) and the absolute timing of events, the three scenarios on tempo and mode of bird evolution (Figure 1) differ only in their patterns of extinction and origination.

Methods

Molecular clock analyses were performed on Sibley and Ahlquist (1990) DNA–DNA hybridization data set using methods described previously (van Tuinen and Hedges 2001). Because of the lack of phylogenetic resolution above order in this data set, superordinal ages were taken from published DNA sequence studies assuming a polytomy at the base of Neoaves (Hedges et al. 1996; Haddrath and Baker 2001; van Tuinen and Hedges 2001; Paton et al. 2002; Cracraft et al. 2004).

Nodal distance estimates were converted from mean UPGMA values (from Figures 353–369 in Sibley and Ahlquist 1990) to age with a recently established (van Tuinen and Hedges 2001, 2004) rate of 0.26 (± 0.02) delta °C/Ma ($= 3.92 \pm 0.08$ Ma/delta °C). Molecular age estimates were obtained by dividing the relevant delta T_{50H} values by this rate. To avoid circular reasoning, a molecular clock cannot be calibrated with the bird fossil record if used to test the adequacy of that same record (van Tuinen and Hedges 2004). Therefore, the evolutionary rate was obtained via a two-step calibration procedure independent from the bird fossil record. Specifically, our molecular rate is based on anchoring the mean galliform–anseriform divergence (22.9 delta °C) at 89.75 Ma $\pm$ 7.0 SE. This age results from a clock analysis of 21 available nuclear genes (van Tuinen and Hedges 2001) using the reptile–mammal calibration of 310 Ma. Because both calibrations involve errors, these can be converted to a single larger error around molecular point estimates (10.3% of estimate). The propagated standard error was quantified from the square root of the sum of individual squared relative errors (van Tuinen and Hedges 2001). The quantifiable relative errors derive from phylogenetic error of the reptile–mammal calibration (3.9%: 310–298 Ma minimum age range (Benton 1997; Reisz 1997; van Tuinen and Hadly 2004) error in dating fossils relevant to that calibration (1.6%: Hess and Lippolt 1986; van Tuinen and Hadly 2004), and genetic distance estimation errors of the galliform–anseriform calibration divergence.

We obtained fossil data by reviewing the available paleoornithological literature. Our approach was conservative. We excluded fragmentary Cretaceous fossil material, and fossils were assigned preliminarily to the stem when crown characters were absent or uncertain. Because of the poor Tertiary passerine fossil record, we focused on the non-passerine neornithines. The taxonomy used follows Sibley and Monroe (1990) unless specified otherwise.

Estimation of crown and stem ages

Age estimation of an extant order or family is possible without access to data from each terminal taxon (species) as long as our sampling included the most divergent taxa in the clade. For example, to estimate the divergence time of crown Apodiformes we minimally need a representative of the two basalmost swift clades, in this case, one tree swift and one common swift. To estimate the stem age of this lineage, we minimally add one representative of its living sister group, comprising hummingbirds. On the other hand, if only one species was sampled within a family (as in all monotypic families), we can only estimate the stem age of this family. The crown of a family corresponds to the node bracketing the divergence of the basal extant genera within this family. Its stem age is based on the node that connects it with its nearest extant outgroup. Depending on the extent of interfamilial structure below the ordinal level, a stem family age may correspond to the crown age of the order to which the family belongs. This distinction of crown from stem ages is lacking in most clock studies and is an integral part of our study.

Crown and stem ages of the neornithine orders are similarly estimated. The node that encompasses the crown order corresponds to the divergence of the basal extant families within this order. The stem age of an order is determined by the node uniting it with its living sister group. This sister group can consist of a single or multiple orders. The phylogenetically resolved superordinal clades, Galloanserae (Galliformes + Anseriformes) and Palaeognathae (Ratitae + Tinamiformes), each consist of two extant orders (Figure 1). In these groups, stem ordinal ages match the crown superordinal ages. Similarly, the stem of the neognath and palaeognath clades is equated with the crown age of modern birds. The stem to modern birds includes fossils falling outside the crown group Neornithes with an older age.

Results

We explored temporal patterns with a molecular analysis encompassing all bird divergences included in the hybridization data set. Since the total taxon sampling in this data set is deficient at the species and genus level, patterns are only meaningful at the family level and higher, accounting for most non-passerine families and all orders. Analysis of the frequency distribution of all nodal ages (Figure 2A) shows that, in agreement with the fossil record, most phylogenesis of extant lineages took place in the Tertiary (60–2.8 Ma).

Despite standard errors around our age estimates that are large enough to obscure the exact times of origin and diversification for these clades, our results indicate two major Tertiary periods of lineage diversification within Neornithes: around the K–T boundary and especially covering the late Eocene into the early Oligocene (E–O). While certainly not all groups are part of this pattern, the clades that do conform delineate the majority of the recognized biologic diversity of extant non-passerine birds (65% of ordinal and 66% of familial diversifications; Table I).

More detailed analyses reveal a strong temporal correlation in diversification between the majority of living neornithines at the ordinal and at the family level, which is indicative of two major radiation events (Figure 2B). At the ordinal level, crown divergence for 13 (out of 22) orders fit around one of the two time intervals (fit is defined here as overlap of molecular estimate ± 1 SE). Of these, eight orders fit around the K–T boundary (65 ± 5 Ma), and the remaining five orders fit around the E–O boundary (33.7 ± 5 Ma). These five orders from the E–O boundary each consist of a single extant family, and in these orders the family age is thus equal to the order age (because there are not at least two families to differentiate origin from diversification). Diversification of ordinal clades Ratitae, Anseriformes, Gruiformes, Passeriformes, Coraciiformes, Caprimulgiformes and Galliformes) predate the Tertiary based on molecular estimates (mean 76.6 ± 2.0 SE Ma). Parrots and pigeons are two sparsely sampled orders, but inclusion of parrots from Africa, South America and Australasia in a cytochrome *b* data set, calibrated on a 100 Ma age for Galliformes–Psittaciformes, indicates a late Cretaceous initial parrot diversification (Miyaki et al. 1998). A recent investigation on the phylogenetic position of Dodo and Solitaire within the larger pigeon group using partial 12S rRNA and cytochrome *b* sequences (Shapiro et al. 2002) demonstrates that Columbiformes is younger and diverged close to the K–T boundary. The distribution of stem ordinal ages is highly bimodal with roughly three-fourths predating the K–T boundary (range: 65–103 Ma), and one-fourth of Tertiary origin (range: 64–39 Ma). Sibley and Ahlquist (1990) proposed combining all orders within this latter Tertiary group into a single order "Ciconiiformes". Using "Ciconiiformes" as an order, the combined stem ordinal ages ($N = 22$) show a normal distribution (range 75–103 Ma). Within this alternative distribution most stem ages cluster between 80–90 Ma (mean 85.7 ± 1.50 SE, median
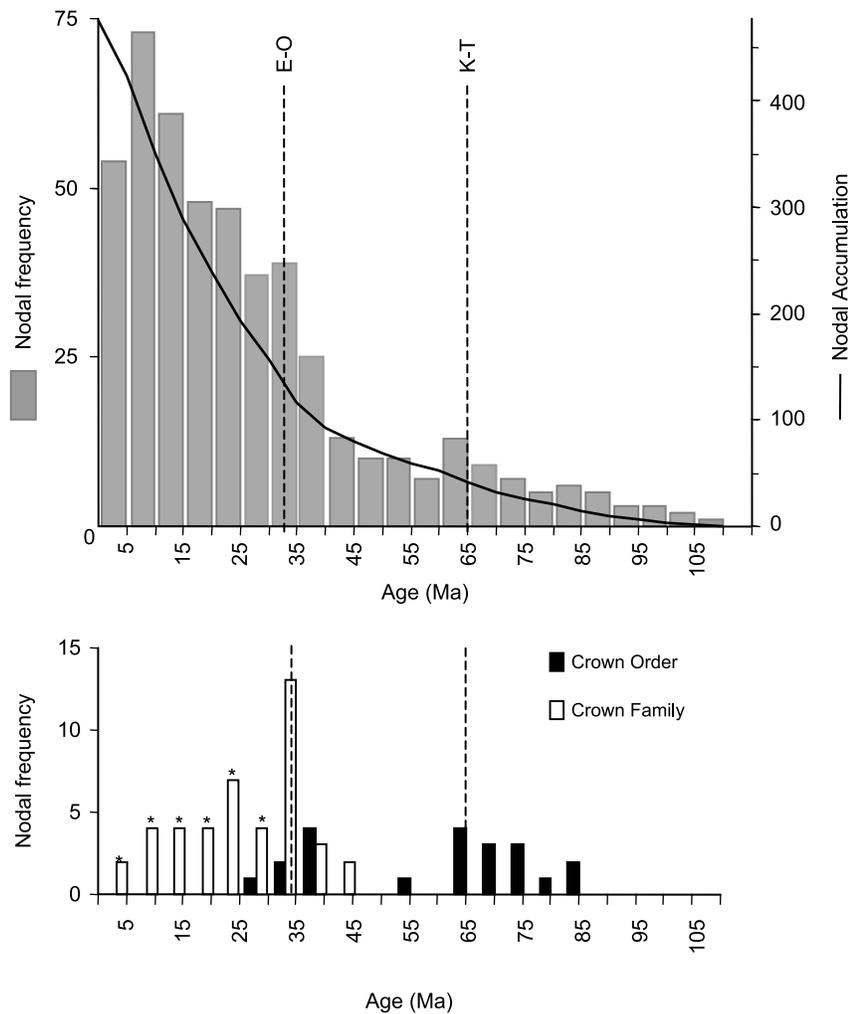
Figure 2.   Frequency distribution of number of new evolutionary dichotomous divergences, or nodes, in the neornithine tree by age. (top panel) All nodes. (bottom panel) Nodes defined by crown order (black bars) and crown family (white bar). The number of nodes was tabulated from the DNA hybridization tapestry by five million year units, and plotted together with a nodal accumulation curve against time. E–O, Eocene–Oligocene boundary; K–T, Cretaceous–Tertiary boundary. Asterisks denote units in which at least 50% of the families are aquatic (see text for discussion).

85.1, mode 81.5 Ma). Thus, analysis of the ratio of stem to crown duration agrees best with a long-fuse model (Figure 1D) for the orders that diversify near the K–T boundary. The remaining orders diversify earlier, in the Cretaceous, and display more gradual evolution and shorter fuses.

Of the 98 extant non-passerine families, 13 are monotypic (include one species), and 38 were represented inadequately for molecular dating of the crown. Of the remaining 47 families, one shows an early Paleocene divergence near the K–T boundary, 30 around the E–O boundary, three between the K–T and E–O intervals and 13 in the Oligocene or more recent (Table II). Other independent evidence supports our results (Wink and Heidrich 1999; Paton et al. 2003). Broadly sampled strigiform cytochrome *b* data suggest that the two extant crown families in this order are of similar age. The E–O crown age of Strigidae estimated here implies that

crown Tytonidae also diversified around the E–O transition. Thus, the ages of initial divergence of extant groups in many of the adequately sampled families overlap. This result suggests a major evolutionary pulse and biologic radiation at or near the E–O transition, a pattern in agreement with the fossil record. Given the current debate between clocks and fossils for assessing evolutionary ages, we emphasize this extensive congruence discovered at the family level. This congruence is especially significant given the taphonomic complications surrounding the fossil record of birds. For example, the earliest crown fossils of several families derive from only a single "lagerstätten" in the Northern Hemisphere (spanning the Eocene–Oligocene in Quercy, France: Blondel and Mourer-Chauviré 1998; Mayr and Manegold 2004). Furthermore, it is not always straightforward to place fragmentary remains on stem or within crown lineages because of either poorly

Table I. Biologic diversity and age of modern bird orders. The Sibley and Ahlquist (1990)/Sibley and Monroe (1990) nomenclature is shown together with common names. Orders in citation marks define traditional orders.

Crown divergence	Representative birds	Time of initial diversification
Palaeognathae	Ratites and Tinamous	Cretaceous
Tinamiformes	Tinamous	Cretaceous–Tertiary
Struthioniformes	Ratites	Cretaceous
Galloanserae	Gamefowl and Waterfowl	Cretaceous
Galliformes	Pheasants, quails, grouse, guineafowl	Cretaceous
Anseriformes	Ducks, geese, swans, screamers	Cretaceous
Neoaves	All other modern bird lineages	Cretaceous
Piciformes	Woodpeckers, honeyguides, barbets, toucans	Cretaceous–Tertiary
Upupiformes	Hoopoes, woodhoopoes, scimitar-bills	Cretaceous–Tertiary
Cuculiformes	Cuckoos, anis, coucals, roadrunners	Cretaceous–Tertiary
Galbuliformes	Jacamars, puffbirds	Cretaceous–Tertiary
Columbiformes	Pigeons, doves	Cretaceous–Tertiary
Apodimorphae	Swifts, hummingbirds	Cretaceous–Tertiary
"Charadriiformes"	Shorebirds, gulls, terns, auks	Cretaceous–Tertiary
"Falconiformes"	Falcons, hawks, old world vultures	Cretaceous–Tertiary
Strigiformes	Owls	Paleocene
"Pterocliformes"	Sandgrouse	Eocene–Oligocene
Trogoniformes	Trogons	Eocene–Oligocene
Coliiformes	Colies, long-tailed mousebirds	Eocene–Oligocene
"Apodiformes"	Swifts	Eocene–Oligocene
"Trochiliformes"	Hummingbirds	Eocene–Oligocene
Bucerotiformes	Hornbills	Eocene–Oligocene
"Procellariiformes"	Shearwaters, petrels, albatrosses	Eocene–Oligocene
"Ciconiiformes"	Storks, new world vultures	Eocene–Oligocene
Gruiformes	Rails, cranes, bustards, excluding buttonquails	Cretaceous
Psittaciformes	Parrots, cockatoos	Cretaceous
Caprimulgiformes	Frogmouths, oilbird, potoos, nightjars, whip-poor-wills, excluding owlet nightjars	Cretaceous
Coraciiformes	Todies, kingfishers, rollers	Cretaceous
Passeriformes	Perching "song" birds, excluding NZ wrens	Cretaceous
Ciconiiformes	Shorebirds, gulls, falcons, hawks, vultures, herons, ibises, storks, pelicans, cormorants, penguins, loons, grebes, flamingos, tropicbirds, albatrosses, petrels	Cretaceous

diagnosed groups, lack of proper morphologic characters present in the fossil species or both.

Our results reveal that the neornithine fossil record (Table II) is remarkably concordant with molecular estimates at the crown familial level (average molecular estimate = 115% of fossil estimate; Table II). Although the average molecular estimate even at this inclusive level predates the fossil record, no bias is found because several mean age estimates of families slightly postdate their earliest fossil occurrences (e.g. Pelecanidae, Ciconiidae and Strigidae). Of all molecular ages, only those for five families are in significant conflict with the fossil record. The Tertiary fossil record of these lineages previously has (Olson 1985) been described as either sparse (Burhinidae, Charadriidae) or non-existent (Bucconidae, Trochilidae and Thinocoridae). The concordance decreases with increasing age and thus taxonomic hierarchy; the gap between molecular and fossil estimates grows from 30% at the crown order level to more than 50% at the stem ordinal level. Although near-KT molecular estimates are all supported by pre-Oligocene fossils, those fossils derive typically from the exceptional middle Eocene Messel (Mayr 2005) and early-middle

Eocene Green river and London Clay deposits (Table II). Paleocene deposits producing fossil birds are rare and no reports of definitive earliest Paleocene birds exist. The middle to late Paleocene has a very sparse record (Smith and Peterson 2002; Mayr 2005) and discovery of birds in these deposits has been limited. At present, there are more bird fossils known from the latest Cretaceous (70–65 Ma) than from approximately the first half of the Paleocene (65–60 Ma).

Our analyses demonstrate that most of the discrepancy between the fossil record and our molecular age estimates remains for the lineages that extend into the Cretaceous. The Cretaceous fossil record for primitive non-crown birds is actually quite rich and reaches across a taxonomically wide scale. In contrast, few fossil clues point to the presence of modern ordinal lineages in the Cretaceous which at that time may not have had greatly diversified. Many of the earliest representatives of ordinal-level clades come from just a few exceptional fossil deposits in the Northern Hemisphere, despite the possible origin of many neornithine clades in the various parts of Gondwana (Cracraft 2001), where the fossil record is

Table II.   List of molecular and fossil divergence times with supporting literature. For comparison, stem fossil age is shown also when molecular crown age clearly predates crown fossil age. Names of ordinal groups end with -iformes, familial groups with—idae.

Divergence	Molecular age	Fossil age	Reference
Crown Tinamiformes	62.8	18	Unwin (1993); Haddrath and Baker (2001)
Crown Struthioniformes	70.4	60	Tambussi (1995)
Crown Casuariidae−Apterygidae	37.3	25	Boles (1992)
Crown Galliformes	59.4	38	Olson (1985); Mlikovski (2002)
Stem Galliformes		53−49 GRF	Lucas (1900) and Mayr (2005)
Crown Anserides	55.9	33	Mayr and Smith (2001)
Stem Anserides		66	Noriega and Tambussi (1995); Stidham (2001); Clarke et al. (2005)
Crown Anatidae	34.2	33	Mayr and Smith (2001)
Crown Piciformes	64.9	33	Mayr (2001); Mayr and Smith (2001)
Stem Piciformes		53−49 GRF	Houde and Olson (1989)
Crown Tyranni	61.9	33 Q (or 18)	Feduccia (1996)
Stem Tyranni⋆		54 (or 33)	Boles (1995); Mayr and Manegold (2004)
Crown Upupiformes	66.8	33 Q	Feduccia (1996)
Stem Upupiformes		49 M	Mayr (2000)
Crown Cuculiformes	69.1	33 Q	Olson (1985)
Stem Cuculiformes⋆		60	Baird and Vickers-Rich (1997)
Crown Cuculidae⋆	38.5	33	Weigel (1963)
Crown Coccyzidae	28.3	33 Q	Olson (1985)
Crown Todidae−Alcedinidae	64.9	38−23 Q	Mourer-Chauviré (1982)
Stem Todidae−Alcedinidae⋆		53−49 M/GRF/LC	Houde and Olson (1989); Feduccia (1996)
Crown Dacelonidae⋆	32.2	33 Q	Mourer-Chauviré (1982)
Crown Cerylidae⋆	33.4	33 Q	Mourer-Chauviré (1982)
Crown Galbuliformes⋆	68.8	53−49	Houde and Olson (1989)
Crown Bucconidae	35.4	NFR	NA
Crown Apodimorphae	67.9	49 M	Mayr and Peters (1999); Van Tuinen and Hedge (2001)
Crown Apodidae	37.3	25 M	Mayr (2005)
Crown Trochilidae	31.8	NFR	Olson (1985); Mayr (2005)
Crown Caprimulgi	70.2	53−49 GRF; M	Olson (1987); Mayr (2001a,b)
Crown Caprimulgidae	32.2	38 Q	Mourer-Chauviré (1988)
Crown Charadriides	61.3	45−33	Mourer-Chauviré (1978); Murphy et al. (2001)
Stem Charadriides		65	Brodkorb (1967); Olson and Parris (1987); Hope (2002)
Crown Jacanidae	31.4	33	Olson (1985)
Crown Burhinidae	36.1	18	Bickart (1982)
Crown Thinocoridae	31.1	NFR	NA
Crown Charadriidae	30.4	5	Olson (1985)
Crown Glareolidae−Laridae	31.8	33 Q	Mourer-Chauviré (1982)
Crown Scolopacidae	29.9	33 Q	Olson (1985)
Crown Procellariidae	31.1	23	Olson (1985)
Crown Pelecanidae/Balaeniceps	29.1	30	Rasmussen et al. (1987)
Crown Ciconiidae/Cathartidae	31.8	33	Emslie (1988)
Crown Falconidae	37.7	38−23 Q	Mourer-Chauviré (1982)
Stem Falconidae⋆		49 M	Peters (1994)
Crown Accipitridae⋆	30.7	37 Q	Mourer-Chauviré (1991)
Crown Ciconii	64.5	54−49 LC; GRF	Olson (1985)

TABLE II – continued

Divergence	Molecular age	Fossil age	Reference
Stem Ciconii		65; 60	Harrison (1985); Olson and Parris (1987)
Crown Strigidae	31.1	33 Q	Mourer-Chauviré (1987)
Stem Strigidae	53.5	58–60	Vickers-Rich and Bohaska (1976)
Crown Bucerotidae	34.2	20	Brunet (1971)
Crown Columbidae	32.2	20	Olson (1985)
Crown Cacatuidae	34.6	23	Boles (1993)
Crown non-African Psittaciforms*	36.1	38–23 Q	Mourer-Chauviré (1982)
Stem Psittaciformes		65	Stidham (1998)
Crown Pteroclidae	37.8	38–23 Q	Mourer-Chauviré (1992)
Crown Coliidae*	35.8	33 Q	Mayr (2005)
Stem Coliidae*		56	Houde and Olson (1992); Mayr and Peters (1998)
Crown Trogonidae	29.1	30	Olson (1985)
Stem Trogonidae		54 LC	Mayr (1999)
Crown Rallidae	33.7	33	Mayr and Smith (2001)

NA, not applicable; NFR, no Tertiary fossil record; LC, London Clay, England; GRF, Green River Formation; USA; M, Messel, Germany; Q, Quercy, France; Nomenclature according to Sibley and Monroe (1990). Note that crown divergences for many major modern bird clades took place near either the Cretaceous–Tertiary or Eocene–Oligocene border.
*Some fossils may require further scrutiny to verify the phylogenetic position inside the crown or stem of modern bird lineages (G. Mayr, personal communication; Mayr 2005).

poorly known. The types of habitats sampled for early neornithine fossils are another source of bias. In the latest Cretaceous and early Paleocene, the neornithine record comes almost solely from coastal deposits (near-shore marine and coastal plain). This sampling of a narrow set of habitats combined with limited continental focus has likely underestimated overall bird diversity, as it has with plants from the same period (Johnson and Ellis 2002). Despite this difference in the perspective of Cretaceous bird life, both our molecular and paleontologic data are consistent in demonstrating the absence of any crown bird family in the Cretaceous.

The limitations of the fossil record for assessing early neornithine evolution are apparent when contrasted with estimates based on molecular data. Even when taking into account large molecular errors, the 95% confidence interval of superordinal molecular estimates does not overlap with the earliest neornithine fossils (van Tuinen and Hedges 2001, 2004; Paton et al. 2002). It is likely that the initial superordinal phylogenesis within modern birds occurred in the Cretaceous but that our ability to discriminate and diagnose the fossils and the paucity of material combine to make this detection in the fossil record extremely difficult (Brochu 2001; Penny and Philips 2003). Additional clock-like data are needed to increase molecular resolution for the early bird timescale. Fortunately, existing molecular studies have strong phylogenetic resolution and extensive temporal congruence (Groth and Barrowclough 1999; van Tuinen et al. 2000; Paton et al. 2002; Cracraft et al. 2004) for most of the non-neoavian birds. Molecular clock studies most closely agree on putting the neoavian origin around 100 Ma (101.8 for mt rRNA, 101.1 for MCF Transferrin, 100.0 based on complete mt genomes, 97.0 Ma based on several nuclear genes). More variation is found around the initial split of extant birds (= stem Neognathae/stem Palaeognathae: 118.1 for mt rRNA, 128.0 for MCF Transferrin, 122.0 for complete mt genomes and 120.0 for mt 12S rRNA + nuclear c-mos). Although not directly supported by the neornithine fossil record, the range of estimated ages for the initial extant neornithine diversification is consistent with the constrained range of ages of the neornithine stem, based on the closest fossil ornithurine outgroups to Neornithes (Stidham 2001).

General patterns

Our results bearing on the tempo and mode of modern bird evolution (Figure 3) are significant in the decoupling of the origin of modern bird groups from their diversification. Our analyses indicate that the origin of extant birds occurred around 120 Ma, and was followed by the evolution of first higher-level taxa (superordinal groups) by 100 Ma. The majority of
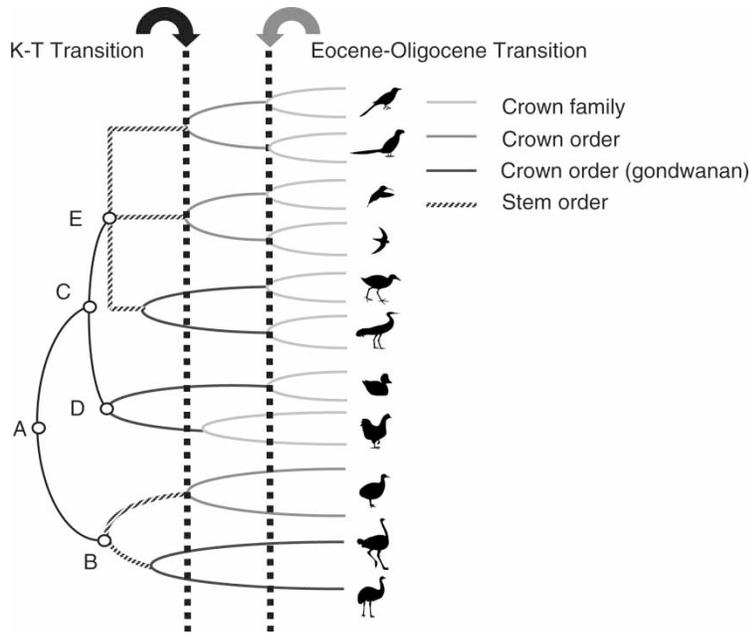
Figure 3. Generalized model of the tempo and mode of modern non-passerine bird diversity. This model illustrates our finding of the majority of modern family clades diversifying in the late Eocene or early Oligocene, diversification of some modern ordinal clades in the late Cretaceous or earliest Tertiary but with diversification of "Gondwanan" orders (illlustrated by gruiform and ratite birds) as well as all superordinal divergences taking place in the Cretaceous. Our findings suggest that extant biologic diversity observed within modern birds decreases with evolutionary age, and that taxonomically equivalent units are of similar age. Symbols from top to bottom: Cuculidae, Coccyzidae, Trochilidae, Apodidae, Rallidae, Otididae, Anatidae, Phasianidae, Tinamidae, Struthionidae/Rheidae and Casuariidae. A, Neornithes; B, Palaeognathae; C, Neognathae; D, Galloanserae; E, Neoaves.

modern orders originated around 90–80 Ma, with diversification rapidly thereafter (short-fuse) for those orders comprising all of the classic Gondwanan orders (Palaeognathae, Galloanserae, Passeriformes, Gruiformes, Caprimulgiformes, and Coraciiformes (Cracraft 2001). Diversification within most modern orders occurred later, around the K–T boundary (long-fuse), followed again later (second long-fuse) by the appearance of crown families around the Eocene–Oligocene boundary (Figure 3). The pattern of stem to crown ratios across the bird timescale is reflected by existing phylogenetic resolution of the neornithine tree. Low ratios of stem to crown duration likely decrease chances of phylogenetic resolution for both molecules and morphology while many diagnostic molecular characters are present in long stems. Thus, it is not surprising that molecular data have resolved monophyly of several traditional orders and families but have failed to resolve superordinal and enigmatic monotypic family relationships within Neoaves (Groth and Barrowclough 1999; De los Monteros 2000; van Tuinen et al. 2000, 2001; Johansson et al. 2001; Sorenson et al. 2003; Chubb 2004; Fain and Houde 2004).

The coincidence among many neornithine diversifications may point to causal relationships between climate, environmental and faunal change that need further investigation. The apparent ages of ordinal and familial diversification roughly correspond to the two largest periods of global change in the last 70 million years: the Cretaceous–Tertiary mass extinction and related environmental change (Archibald 1996) and the Eocene–Oligocene biotic change, global cooling, and glaciation (Prothero and Berggren 1992). Extinction at the K–T boundary is well-documented in the fossil record and tied to a combination of a major bolide impact at this time and increased global cooling and volcanic activity (Archibald 1996; Francis and Poole 2002; Wilf et al. 2003). The end of the Mesozoic period also saw major regression of the Western Interior Seaway in North America where our best fossil record of the terrestrial change occurs. All these factors may have contributed to the massive K–T extinctions affecting both marine and terrestrial biotas (Wilf et al. 2003). The avian fossil record shows that all non-neornithine lineages were extinct by the start of the Cenozoic (Dyke and van Tuinen 2004; Clarke et al. 2005).

The transition between the Eocene and Oligocene also coincided with major climatic changes (Zachos et al. 2001). Global cooling started in the late Eocene and peaked in the earliest Oligocene causing major vegetation shifts in north temperate regions from forest to open country (Meng and McKenna 1998). This period is marked by the first permanent icesheets and circumantarctic current in Antarctica. These factors have since controlled global thermohaline patterns and solar heat retainment (Zachos et al.

2001). The Eocene–Oligocene transition is manifested by several major extinction events in mammals and subsequent faunal turnover into new communities with marked body size and dentition changes in Europe and Asia (Prothero and Berggren 1992; Meng and McKenna 1998). However, detailed data on bird faunas are scarce and poorly documented from this time period, but such large environmental changes presumably affected birds on the same scale as mammals, and the pattern should be visible in the fossil record (Barnosky and Carrasco 2002).

Gondwanan versus Laurasian groups

Lineages that do not conform to the two-pulse model also may inform us about the mode of modern bird evolution. These exceptions can be studied from both a neontologic and paleontologic perspective. First, the neornithine fossil record provides insight into the paleoenvironmental context and paleoecologic differences among lineages that survived or were pruned by major extinction events. The fossil record of modern birds is quite poor for the Cretaceous and for the Southern Hemisphere. Nonetheless, the Paleogene and Neogene records are of some use in revealing extinction patterns in North America and Laurasia. The bird clades that became extinct in the Paleogene include lithornithids, presbyornithids, geranoidids, horusornithids, diatrymids/gastornithids, and all of the Messel endemics. Taxa that survive the Eocene–Oligocene boundary but went extinct after the Oligocene include the opisthodactylids, plotopterids and bathornithids in the Miocene, pelagornithids, ergilornithids and phororhacids in the Pliocene, and dromornithids in the Pleistocene. Many of these lineages are characterized by large size with extreme wing loading or were flightless. The majority of this neornithine paleofauna died out before the mammalian megafauna did in the Pleistocene, though there was a major Pleistocene extinction in birds (Feduccia 1996).

To further explore the significance of extrinsic events in shaping modern avian biodiversity, a detailed neontologic look at the morphology, ecology and behaviour of those modern lineages diversifying in the Cretaceous (i.e. surviving the K–T extinction), or diversifying in the Paleocene or Eocene is imperative. Figure 2a shows that the number of extant lineages starting to diversify in these time periods is limited ($N = 31$), and these lineages are unevenly distributed across few orders. The small number of those bird lineages is attributable to the result that many more orders instead demonstrate explosive evolution. In contrast, the limited early divergences offer a more gradual view of evolution (e.g. in shorebirds, and cranes and allies). Interestingly, several of the families that produce a pattern of gradual evolution in few ordinal lineages consist today of only one or two species. These species-poor families include enigmatic mostly Gondwanan species such as the Ostrich, Magpie Goose, Oilbird, Cuckoo-roller, Bearded Bee-eaters, Sunbittern, Kagu, Seriemas and Limpkin, all of which are part of modern orders that started diversifying in the Cretaceous. They also include the secretary bird (Falconiformes), Hoatzin (*incertae sedis*), Plainswanderer and Sheathbills (Charadriiformes). This intriguing result implies potential differences in rates of extinction as well as in morphologic diversification between avian histories in Gondwana and Laurasia. The trend of extant species-poor lineages dating back further than most other families is suggestive of either a difference in extinction or characteristics enhancing preferential survival in these groups, and should be investigated further.

Young age of aquatic birds

Many exceptions to the general macroevolutionary pattern of birds are located in the traditional aquatic orders and families (including ibises, penguins, flamingos, grebes and loons). None of these traditional orders and families appear to have a Cretaceous or K–T diversification, and few families exhibit diversification around the E–O boundary (Figure 2b). Although many early Tertiary bird fossils possess characteristics indicating that they were aquatic, few if any can be assigned with certainty to a modern aquatic bird group. Despite the evolution of a suite of morphologic features for aquatic habitation, modern aquatic bird groups are among the youngest of all biologically distinct groups according to molecular data. Extant aquatic orders appear not only of more recent origin based on molecular data, but also show strong relationships with each other, e.g. Procellariiformes with Sphenisciformes and Gaviiformes, Ciconiiformes with some Pelecaniformes, and Phoenicopteriformes with Podicipediformes (van Tuinen et al. 2001; Cracraft et al. 2004). Future studies are needed to better understand the evolutionary forces behind this aquatic radiation and its relatively young age (Table III). The anomaly lies either in the morphologic rate, molecular rate or both. An obvious explanation for this pattern could be rate heterogeneity, i.e. rate slowdown in the genomes of these clades compared to those of the galloanserine calibration. Future investigations should attempt to differentiate between a possible slowdown of genomic evolutionary rates in aquatic environments or, alternatively, faster rate of morphologic diversification. If a genomic slowdown in aquatic birds is real, aquatic fossils should perhaps be avoided for global calibration purposes. Furthermore, the extent of evolutionary character convergence in aquatic environments needs more study as some fossils from aquatic lineages (e.g. "Cretaceous" loons or pelecaniforms) may no longer

Table III. Traditional (water)bird families that merit family status based on morphology but show apparent low genetic variation. Some of these families also contain low species diversity. If future study should corroborate the two-pulse hypothesis, these groups could provide for fruitful inquiry into differential rates of morphologic diversity among bird groups.

Family	Common name	Crown molecular estimate
Threskiornithidae	Ibises, spoonbills	24.0
Ardeidae	Herons, bitterns	24.0
Spheniscidae	Penguins	22.81
Sulidae	Gannets, boobies	22.0
Laridae	Gulls, terns	17.7
Phaethontidae	Tropicbirds	16.8*
Podicipedidae	Grebes	14.5*
Gruidae	Cranes	13.0
Anhimidae	Screamers	12.6
Haematopodidae	Oystercatchers	9.4*
Gaviidae	Loons	8.6*
Recurvirostridae	Avocets, stilts	8.6
Phoenicopteridae	Flamingos	4.7
Fregatidae	Frigatebirds	2.8*

*Inadequately sampled.

have extant relatives. Finally, fluctuations in sea level through the Neogene have been suggested as causative agents in the formation of genetic bottlenecks in birds (Cooper and Cooper 1995) meaning that either population size and the forces of genetic drift or selection could have been heightened to produce relative differences in morphologic and molecular evolution.

Taxonomy as alternative explanation?

An increase in number of divergences towards the recent (Figure 2A) is predicted purely by the dichotomous nature of speciation (given equal extinction through time). To reveal the macroevolutionary cadence of diversification, it is critical to focus on the temporal distribution of those divergences encompassing major morphologic and ecologic innovations. From the perspective of modern diversity these evolutionary modifications within major groups are likely highest at the family and ordinal levels. Thus, our investigation is an attempt to reveal the underlying biases intrinsic to Linnean taxonomy placed in a strictly dichotomous phylogeny over time (Figure 2B). Although our macroevolutionary results appear concordant with major Cenozoic environmental events, it is possible that the two obvious pulses in modern bird evolution are a result of our focus here on crown families and orders as defined by taxonomy. Increased extinction around the K–T and E–O boundary need not be invoked as the causative factor having produced these apparent pulses of divergence if morphologic rates are homogeneous across families and orders. Although this may be a factor in causing the great similarity in age across many crown families, more age discrepancy is found at the ordinal level, considering the Cretaceous age of the Gondwanan orders. Furthermore, the small number of families

that can be traced back to the early Paleogene (Paleocene and most of Eocene) indicates that many early Tertiary lineages were pruned at the end of the Eocene. A second concern is that one may expect evolutionary pulses for families and orders because these taxonomic bounds have been defined by a small range of DNA hybridization melting temperatures. However, our dependence on age-based taxonomic definition yields lineages that are not randomly classified. Instead they agree with traditional lineations based on morphologic differentiation (Morony et al. 1975; del Hoyo et al. 1992–2002) for the majority of families and orders. Secondly, Sibley and Ahlquist (1990) for unknown reasons maintained family status for several groups with melting temperatures outside the familial melting temperature range (9–11° delta T_{50}H) in their table 14 (e.g. Anhimidae, Apterygidae, Bucconidae, Bucorvidae, Todidae and Tytonidae). These observations combined with the large spread of ordinal divergence ages (Late Cretaceous, K–T and E–O) make it unlikely that the observed temporal clustering of major diversification events is an artifact of the age-based taxonomic definition. In fact, we could argue that the similar ages of traditional families supports taxonomic definition by age or morphologic differentiation.

Molecular bias as alternative explanation?

Rate heterogeneity and non-linearity

The quantitative nature of the data presented by Sibley and Ahlquist does not allow direct testing of rate constancy and linearity across all birds. Therefore, we assumed a robust genomic clock at the taxonomic levels of interest. This assumption is supported by the close agreement between divergence times obtained here and homologous estimates

derived from narrow taxonomic comparisons based on complete mitochondrial genomes (Cooper et al. 2001; Paton et al. 2002), mitochondrial ribosomal genes, microcomplement fixation data (van Tuinen and Hedges 2001) and several bird family level DNA sequence studies (references given below). Moreover, independent DNA hybridization studies (Bleiweiss et al. 1995; van Tuinen et al. 2001), reanalysis (Harshman 1994) as well as subsequent DNA sequence studies (see below) have corroborated several key portions of the phylogeny of birds. Nevertheless, failure to correct for non-linearity could compress inferred divergence times near the root and thereby make it appear that there was an early burst of divergences rather than a more gradual pattern. For this reason, ages for the early super-ordinal nodes in this study are based instead on mitochondrial genome data corrected for multiple hits and rate heterogeneity using non-parametric rate smoothing (Paton et al. 2002) and linearized non-coding mitochondrial rRNA data (van Tuinen and Hedges 2001). Furthermore, available sequence data relevant to the early history of modern birds show a basal polytomy for Neoaves, but good resolution for the separation of galloanserines from this polytomy and palaeognaths from all other birds. Such strong resolution would not likely be found if compression of basal branches is problematic. To investigate the potential bias from forcing distance to conform to a clock, nodes available from the published FITCH trees (Figures 325–343) were also dated using the FITCH branch lengths and the same calibration, and compared to the UPGMA based ages discussed above. Although far less in taxonomic breadth, fourteen out of seventeen major nodes that can be dated agree in tempo and mode with our model. These include 7 out of 9 ordinal estimates and 7 out of 7 familial estimates. Ordinal-level ages again indicate diversification before the K–T boundary for Galliformes (85.5 Ma), Passeriformes (77.2 Ma), and Gruiformes (77.5 Ma), but not Caprimulgiformes (67.6 Ma) and Ratitae (60.2 Ma), which together with Piciformes (61.8 Ma), Charadriiformes (64.0 Ma), Upupiformes (66.1 Ma), and Cuculiformes (70.0 Ma) appeared to have diversified near the K–T boundary. The initial diversification within the procellarid, ciconiid, pelecanid, charadriid, larid-glareolid, caprimulgid, and bucerotid families again appears to have taken place in the Latest Eocene or Earliest Oligocene (35.4–28.5 Ma).

Another potential concern is the use of a relatively old calibration point. It is possible that, if saturation is a problem at this level, ages for young nodes are overestimated, and very early nodes compressed in time. However, alternative calibration on younger galliform and ratite nodes indicates little saturation for the galloanserine node (Paton et al. 2002; van Tuinen and Dyke 2004). This comparison must be interpreted carefully for several reasons, including cladistic uncertainty and circularity of the bird fossil record. Analysis of multi-locus sequences for many bird ordinal and familial taxa will be required for further testing.

Rate heterogeneity among major bird groups may introduce a second bias, since age estimates are based on clock-constrained (UPGMA) distances. If rate heterogeneity is indeed ubiquitous, ordinal and family crown and stem age estimates and evolutionary mode may perhaps be spuriously regular. It should be noted that such bias is only significant if the raw hybridization data are distorted extensively to fit the ultrametric end result. At this point, the extent of this bias can be addressed by discussing the corrections that Sibley and Ahlquist applied to their raw data, and by comparing our results with estimates based on a subsample of the taxa for which trees have been published that do not enforce the ultrametric constraints. Although perhaps less sophisticated than more recent methods that model the evolutionary rate change across branches in a tree, among-taxa rate heterogeneity was averaged out to some extent. The input distance matrix on which the UPGMA method was performed included the raw T_{50H} distances corrected for experimental and reciprocity error but also for consistent rate heterogeneity. Sibley and Ahlquist (1990) performed numerous three-taxon relative rate tests with variable outgroup taxa. A correction factor was applied when certain taxa were consistently found to evolve slower (p. 150 in Sibley and Ahlquist 1990). Rate heterogeneity was discussed in the light of demographic differences and the striking correlation between the two. Since many species of birds begin to breed at age one, few major branches would show fast rates (e.g tinamous and button-quails). Slow rates appear common in birds with delayed maturity. These groups include large seabirds and landbirds, a scenario supporting the notion of a genomic slowdown in ciconiiform lineages such as penguins, loons, tubenoses, long legged waders, and large raptors. DNA sequence data also indicate similar rate departures in tinamous, buttonquails, and some aquatic taxa, but the pattern, admittedly, is based on few loci.

Taxon sampling

Although the bird hybridization data are unique for the breadth of taxon sampling, molecular data for several key taxa are still lacking. At the ordinal level, sampling is insufficient only for Psittaciformes and Columbiformes. No data are available for 2 families, no pairwise data for 18 families, and sampling does not cover the initial divergence for another 18 families. In total, 39% of the non-passerine families had limited taxon-sampling and was not included for divergence time analysis. Additional temporal information was

drawn from available sequence studies to fill in some of those voids. When age-estimation can be performed on both DNA hybridization and sequence data, encouraging congruence often is found, as is the case with published timescales for ratites, gamefowl, storks, condors, diurnal raptors, cranes, owls, nightjars and allies, songbirds, and trogons (Edwards et al. 1991; Randi et al. 1991; Wink 1995; Krajewski and King 1996; Mariaux and Braun 1996; Wink and Heidrich 1999; De los Monteros 2000; Cooper et al. 2001; Haddrath and Baker 2001; Haring et al. 2001; van Tuinen and Hedges 2001; Barker et al. 2002; Ericson et al. 2002; Paton et al. 2002).

Lack of deep phylogenetic resolution

Limitations of the hybridization data above the ordinal level often have been mentioned (Cracraft 1987; Houde 1987), but the methodology applied here circumvents this limitation. We stress that monophyly and diagnosis of the initial divergences of most extant families and orders in the hybridization data generally agree with traditional hierarchies. When the initial branching pattern is at odds with traditional taxonomy, ages are based on the next oldest divergence. However, this correction affects only 3 of 23 orders: the Gruiformes (involving Turnicidae), Caprimulgiformes (involving Aegothelidae) and Passeriformes (involving Acanthisittidae). Thus, given the monophyly of the majority of orders and families, having restricted knowledge of interordinal relationships does not affect intraordinal diversification ages. If ordinal monophyly is in error, estimated "order" ages are likely to extend into the Cretaceous and thus are of little use in understanding the tempo and mode of the macroevolutionary relevant biologic diversity. Such might be the case for Coraciiformes, Gruiformes, and Caprimulgiformes (Mayr 2002; Cracraft et al. 2004; Fain and Houde 2004). However, alternative evolutionary reasons exist for Cretaceous origins for some of the extant orders.

Conclusions

The DNA hybridization-based timescale is compared here against the bird fossil record as a first proxy of the true evolutionary timescale of modern birds. Verification with nuclear gene sequences studies is paramount considering that no phylogenetic tree, including the hybridization-based bird phylogeny, is without problems. These data, in conjunction with additional fossil-based calibrations and the need for an expanded search for Cretaceous neornithine fossils, are necessary to infer and corroborate the ages of the true crown and stem divergences. Perhaps the greatest significance of this study is in pointing out the scientific value of having a temporal framework on a taxonomically wide scale that goes far beyond

inferring the absolute age of evolutionary divergences. Absolute evolutionary age can associate biologic divergences with the climate and paleo-environment of that time which may yield insight into extinction levels at different times and an improved biogeographic perspective. Comparison of absolute ages of diversification and origination across a broad taxonomic scale may expose gradual evolution or, as indicated here, that many major divergences occurred at similar evolutionary times. Such data encourage the proposal of novel hypotheses about the evolutionary history of modern biodiversity that can be tested only with an integrative use of paleontologic, genetic, ecologic, climatic and geologic information.

The results of this paper generate numerous specific hypotheses about the evolution of extant avian biodiversity. Available molecular data indicate that: (a) the earliest history of modern birds, including the origin of most traditional orders, lies in the Cretaceous, but that (b) the similarity in diversification times across many (but not all) major lineages creates a two-pulse radiation pattern of modern birds in the Tertiary. Specifically, these data suggest (but do not prove) that (c) two major extinction events, particularly end-Cretaceous events and Eocene–Oligocene environmental change (cooling), were important in shaping the modern day bird biologic diversity. (d) An exception to this pattern includes bird orders of southern hemispheric origin, whose initial diversification predates the K–T boundary. (e) Another exception includes several modern aquatic lineages whose history may be younger than most other lineages. It is proposed that, if corroborated, this difference is either due to (f) a potential slowdown of genomic rate in aquatic environments or that (g) extinction pressures have been different for organisms living in terrestrial and aquatic environments. The data support (h) a long-fuse model for the lineages diversifying in the Tertiary or latest Cretaceous, but (i) more gradual evolution in the Gondwanan lineages (Figure 3). Alternatively (j), some of the patterns observed and described on the evolutionary mode of modern bird biodiversity may be an artifact of their taxonomy, since constant extinction and diversification also produce broad morphologic and molecular similarities across higher taxonomic levels. To a large extent, the tempo and mode model of neornithine birds presented here is supported by similarities with placental timescales (Springer et al. 2003), which may or may not point to a causal link. Each of these hypotheses requires further testing with additional paleontologic, ecologic and molecular analyses (sensu Penny and Philips 2003).

The next few years likely will yield great advances in our understanding of the evolutionary tempo and mode of modern bird diversity. Several research groups currently are sequencing slowly evolving nuclear DNA of many major bird lineages, and

paleo-ornithologists are placing Tertiary and Mesozoic neornithine bird fossils into a cladistic framework. We anticipate continued linkages between molecules and fossils and strive to shift the debate to the more confounding Cretaceous stem lineages that preceded the crown avian biodiversity.

Acknowledgements

References

Alroy J. 1999. The fossil record of North American mammals: Evidence for a Paleocene evolutionary radiation. Syst Biol 48:107–118.

Archibald JD. 1996. Dinosaur extinction and the end of an era. What the fossils say. New York: Columbia University Press.

Archibald JD, Deutschman DH. 2001. Quantitative analysis of the timing of the origin and diversification of extant placental orders. J Mammal Evol 8:107–124.

Baird P, Vickers-Rich P. 1997. *Eutreptodactylus itaboraiensis* gen. et. sp. nov.: An early cuckoo (Aves: Cuculidae) from the late Paleocene of Brazil. Alcheringa 21:123–127.

Barker FK, Barrowclough GF, Groth JG. 2002. A phylogenetic hypothesis for passerine birds: Taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. Proc R Soc Lond B 269:295–308.

Barnosky AD, Carrasco MA. 2002. Effects of Oligo–Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. Evol Ecol Res 4:811–841.

Benton MJ. 1997. Vertebrate Paleontology. 2nd ed. London: Chapman & Hall.

Benton MJ. 1999. Early origins of modern birds and mammals: Molecules vs. morphology. Bioessays 21:1043–1052.

Benton MJ, Ayala F. 2003. Dating the tree of life. Science 5626:1698–1700.

Bickart KJ. 1982. A new thicknee, *Burhinus*, from the Miocene of Nebraska, with comments on the habitat requirements of the Burhinidae (Aves: Charadriiformes). J Vert Paleont 1:273–277.

Bleiweiss R. 1998. Fossil gap analysis supports early Tertiary origin of trophically diverse avian orders. Geology 26:323–326.

Bleiweiss R, Kirsch JAW, Shafi N. 1995. Confirmation of a portion of the Sibley–Ahlquist tapestry. Auk 112:87–97.

Blondel J, Mourer-Chauviré C. 1998. Evolution and history of the Western Palearctic avifauna. Trends Ecol Evol 13:488–492.

Boles WE. 1992. Revision of *Dromaius Gidju* Patterson and Rich 1987 from Riversleigh, northwestern Queensland, Australia, with a reassessment of its generic position. Nat Hist Mus Los Angeles County Sci Ser 36:195–208.

Boles WE. 1993. A new cockatoo (Psittaciformes: Cacatuidae) from the Tertiary of Riversleigh, northwestern Queensland and an evaluation of rostral characters in the systematics of parrots. Ibis 135:8–18.

Boles WE. 1995. The world's oldest songbird. Nature 374:21–22.

Brochu CA. 2001. Progress and future directions in archosaur phylogenetics. J Paleontol 75:1185–1201.

Brodkorb P. 1967. Catalogue of fossil birds, part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). Bull Fla State Mus Biol Sci 11:99–220.

Brunet, J. 1971. Oiseaux miocènes de Beni Mellal (Maroc); un complément à leur étude Notes. Mémoires et Service Géologique (Marocco) 31: 109–111.

Chubb AL. 2004. New nuclear evidence for the oldest divergence among neognath birds: The phylogenetic utility of ZENK (i). Mol Phylogenet Evol 30:140–151.

Clarke JA, Tambussi CP, Noriega JI, Erickson GM, Ketcham RA. 2005. Definite fossil evidence for the extant avian radiation in the Cretaceous. Nature 433:305–308.

Cook JA, Lessa EP, Hadly EA. 2000. Paleontology, phylogenetic patterns and macroevolutionary processes in subterranean rodents. In: Cameron GN, Lacey EA, Patton JL, editors. The biology of subterranean rodents: Evolutionary challenges and opportunities. Chicago: University of Chicago Press. p 332–369.

Cooper A, Cooper RA. 1995. The Oligocene bottleneck and New Zealand biota: Genetic record of a past environmental crisis. Proc R Soc Lond B 261:293–302.

Cooper A, Fortey R. 1998. Evolutionary explosions and the phylogenetic fuse. Trends Ecol Evol 13:151–156.

Cooper A, Penny D. 1997. Mass survival of birds across the K–T boundary: Molecular evidence. Science 275:1109–1113.

Cooper A, Lalueza-Fox C, Anderson S, Rambaut A, Austin J, Ward R. 2001. Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. Nature 409:704–707.

Cracraft J. 1987. DNA hybridization and avian phylogenetics. Evol Biol 21:47–96.

Cracraft J. 2001. Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event. Proc R Soc Lond B 268:459–469.

Cracraft J, Barker FK, Braun M, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, Garcia-Moreno J, Sorenson MD, Yuri T, Mindell DP. 2004. Phylogenetic relationships among modern birds (Neornithes): Toward an avian tree of life. In: Cracraft J, Donoghue M, editors. Assembling the tree of life. New York: Oxford University Press. p 469–489.

De los Monteros AE. 2000. Higher-level phylogeny of Trogoniformes. Mol Phylogenet Evol 14:20–34.

De Queiroz A, Gauthier J. 1992. Phylogenetic taxonomy. Annu Rev Ecol Syst 23:449–480.

del Hoyo J, Elliott A, Sargatal J. 1992–2002. Handbook of the birds of the world. Lynx Edicions, Barcelona (at http://www.hbw.com), Volume 1–7.

Dyke GJ. 2001. The evolutionary radiation of modern birds: Systematics and patterns of diversification. Geol J 36:305–315.

Dyke GJ, Van Tuinen M. 2004. The evolutionary radiation of modern birds (Neornithes): Reconciling molecules, morphology and the fossil record. Zool J Linn Soc 141:153–178.

Edwards SV, Arctander P, Wilson AC. 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. Proc R Soc Lond B 243:99–107.

Emslie SD. 1988. The fossil history and phylogenetic relationships of condors (Ciconiiformes: Vulturidae) in the new world. J Vert Paleont 8:212–228.

Ericson PGP. 1997. Systematic relationships of the paleogene family Presbyornithidae (Aves: Anseriformes). Zool J Linn Soc 121:429–483.

Ericson PGP, Christidis L, Cooper A, Irestedt M, Jackson J, Johansson US, Norman JA. 2002. A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. Proc R Soc Lond B 269:235–241.

Fain MG, Houde P. 2004. Parallel radiations in the primary clades of birds. Evolution 58:2558–2573.

Feduccia A. 1995. Explosive evolution in Tertiary birds and mammals. Science 267:637–638.

Feduccia A. 1996. The origin and evolution of birds. New Haven: Yale University Press.

Foote M, Hunter JP, Janis CM, Sepkoski JJ. 1999. Evolutionary and preservational constraints on origins of biologic groups: Divergence times of eutherian mammals. Science 283: 1310–1314.

Francis JE, Poole I. 2002. Cretaceous and early Tertiary climate of Antarctica: Evidence from fossil wood. Palaeogeogr Palaeoclimatol Palaeoecol 182:47–64.

Groth JG, Barrowclough GF. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. Mol Phylogenet Evol 12:115–123.

Haddrath O, Baker AJ. 2001. Complete mitochondrial DNA genome sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. Proc R Soc Lond B 268:939–945.

Haring E, Kruckenhauser L, Gamauf A, Riesing MJ, Pinsker W. 2001. The complete sequence of the mitochondrial genome of *Buteo buteo* (Aves, Accipitridae) indicates an early split in the phylogeny of raptors. Mol Biol Evol 18:1892–1904.

Harrison CJO. 1985. A Bony-toothed Bird (Odontopterygiformes) from the Palaeocene of England. Tert Res 7:23–25.

Harshman J. 1994. Reweaving the tapestry: What can we learn from Sibley and Ahlquist (1990). Auk 111:377–388.

Hedges SB, Parker PH, Sibley CG, Kumar S. 1996. Continental breakup and the ordinal diversification of birds and mammals. Nature 381:226–229.

Hess JC, Lippolt HJ. 1986. ^{40}Ar/^{39}Ar ages of tonstein and tuff sandines: New calibration points for the improvement of the upper Carboniferous time scale. Chem Geol 59:143–154.

Hope S. 2002. Above the heads of dinosaurs. In: Chiappe L, Witmer LM, editors. The Mesozoic record of Neornithes. Berkeley: University of California Press. p 339–388.

Houde P. 1987. Critical evaluation of DNA hybridization studies in avian systematics. Auk 104:17–32.

Houde P, Olson SL. 1989. Small arboreal nonpasserine birds from the early Tertiary of Western North America. Acta 19th congress international ornithogical meeting. 1: 2030–2036.

Houde P, Olson SL. 1992. A radiation of coly-like birds from the Eocene of North America (Aves: Sandcoleiformes, new order). Nat Hist Mus Los Angeles County Sci Ser 36:137–160.

Johansson US, Parsons TJ, Irestedt M, Ericson PGP. 2001. Clades within the "higher land birds", evaluated by nuclear DNA sequences. J Zool Syst Evol Res 39:37–51.

Johnson KR, Ellis B. 2002. A tropical rainforest in Colorado 1.4 million years after the Cretaceous–Tertiary boundary. Science 296:2379–2383.

Krajewski C, King DG. 1996. Molecular divergence and phylogeny: Rates and patterns of cytochrome *b* evolution in cranes. Mol Biol Evol 13:21–30.

Kumar S, Hedges SB. 1998. A molecular timescale for vertebrate evolution. Nature 392:917–920.

Livezey BC. 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis* and the interordinal relationships of waterfowl. Zool J Linn Soc 121:361–428.

Lucas FA. 1900. Characters and relations of *Gallinuloides*, a fossil gallinaceous bird from the Green river shales of Wyoming. Bull Mus Comp Zool 1900:79–84.

Mariaux J, Braun MJ. 1996. A molecular phylogenetic survey of the nightjars and allies (Caprimulgiformes) with special emphasis on the potoos (Nyctibiidae). Mol Phylogenet Evol 6:228–244.

Mayr G. 1999. A new trogon from the middle Oligocene of Céreste, France. Auk 116:427–434.

Mayr G. 2000. Tiny hoopoe-like birds from the middle Eocene of Messel (Germany). Auk 117:968–974.

Mayr G. 2001a. Comments on the osteology of *Masillapodargus longipes* Mayr 1999 and *Parafica major* Mayr 1999, caprimulgiform birds from the middle Eocene of Messel (Hessen, Germany). Neues jahrbuch geologie palaeontologie monatshefte. 2001. p 65–76.

Mayr G. 2001b. The earliest fossil record of a modern-type piciform bird from the late Oligocene of Germany. J Ornithol 142:2–6.

Mayr G. 2002. Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies). J Ornithol 143:82–97.

Mayr G. 2005. The Paleogene fossil record of birds in Europe. Biol Rev 80:1–28.

Mayr G, Manegold A. 2004. The oldest fossil songbird from the early Oligocene of Germany. Naturwissenschaften 91:173–177.

Mayr G, Peters DS. 1998. The mousebirds (Aves: Coliiformes) from the middle Eocene of Grube Messel (Hessen Germany). Senckenbergiana lethaea 78:179–197.

Mayr G, Peters DS. 1999. On the systematic position of the middle Eocene swift *Aegialornis szarskii* Peters 1985 with description of a new swift-like bird from Messel (Aves: Apodiformes). Neues jahrbuch geologie palaeontologie monatshefte. 1999. p 312–320.

Mayr G, Smith R. 2001. Duck, rails, and limicoline waders from the lowermost Oligocene of Belgium. Geobios 34:547–561.

Meng J, McKenna MC. 1998. Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. Nature 394:364–367.

Miyaki CY, Matioli SR, Burke T, Wajntal A. 1998. Parrot evolution and paleogeographical events: Mitochondrial DNA evidence. Mol Biol Evol 15:544–551.

Mlikovski J. 2002. Cenozoic birds of the world, Part 1: Europe. Prague: Ninox Press.

Mooers AO, Heard SB. 1997. Inferring evolutionary process from phylogenetic tree shape. Q Rev Biol 72:31–54.

Morony JJ, Bock WJ, Farrand J. 1975. Reference list of the birds of the world Publications of the American museum of natural history. New York: Department of Ornithology.

Mourer-Chauviré C. 1978. La pouche à phosphate de Sainte-Neboule (Lot) et sa faune de vertébrés du Ludien superieur. 6. Oiseaux. Paleovertebrata 8:217–229.

Mourer-Chauviré C. 1982. Les Oiseaux fossiles des phosphorites du Quercy (upper Eocene to lower Oligocene): Implications paleobiogeographiques. Geobios Mem Spec 6:413–426.

Mourer-Chauviré C. 1987. Les Strigiformes (Aves) des phosphorites du Quercy (France): systematique, biostratigraphie et paleobiogeography. Docum Lab Geol Lyon 99:89–135.

Mourer-Chauviré C. 1988. Le gisement du Bretou (phosporites du Quercy Tarn-et-Garonne, France) et sa fauna de vertébrés de l'Eocène supérieur. II Oiseaux. Paleontographica (A) 205:29–50.

Mourer-Chauviré C. 1991. Les Horusornithidae nov. fam Accipitriformes (Aves) a articulation intertarsienne hyperflexible de l'Eocène du Quercy. Geobios Mem Spec 13:183–192.

Mourer-Chauviré C. 1992. Un ganga primitif (Aves: Columbiformes, Pteroclidae) de très grande taille dans le paléogène des Phosphorites du Quercy (France). CR Acad Sci Ser (2A) 314:229–335.

Murphy PC, Torick LL, Bay ES, Chandler R, Evanoff E. 2001. Taphonomy, fauna, and depositional environment of the Omomys Quarry, an unusual accumulation from the Bridger Formation (Middle Eocene) of Southwestern Wyoming USA. In: Gunnell GF, editor. Eocene biodiversity; unusual occurrences and rarely sampled habitats. New York: Kluwer Academic/Plenum Publishers. p 361–402.

Noriega JI, Tambussi CP. 1995. A Late Cretaceous Presbyornithidae (Aves: Anseriformes) from Vega Island, antarctic peninsula: Paleobiogeographic implications. Ameghiniana 32:57–61.

Olson SL. 1985. The fossil record of birds. In: Farner D, editor. Avian Biology, London: Academic Press. p 80–238.

Olson SL. 1987. An early Eocene oilbird from the Green River formation of Wyoming (Caprimulgiformes: Steatornithidae). Docum Lab Geol Lyon 99:57–69.

Olson SL, Parris DC. 1987. The Cretaceous birds of New Jersey. Smithsonian Contrib Paleobiol 63:1–22.

Paton T, Haddrath O, Baker AJ. 2002. Complete mitochondrial DNA genome sequences show that modern birds are not descended from transitional shorebirds. Proc R Soc Lond B 269:839–846.

Paton TA, Baker AJ, Groth J, Barrowclough GF. 2003. RAG-1 sequences resolve phylogenetic relationships within charadriiform birds. Mol Phylogenet Evol 29:268–278.

Penny D, Philips MJ. 2003. The rise of birds and mammals: Are microevolutionary processes sufficient for macroevolution? Trends Ecol Evol 19:516–522.

Peters DS. 1994. *Messelastur gratulator* n. spec. n. gen., ein Griefvogel aus der Grube Messel (Aves: Accipitridae). Courier Forschunginstitut Senckenberg 170:3–9.

Prothero DR, Berggren WA. 1992. Eocene–Oligocene climatic and biotic evolution. Princeton: Princeton University Press.

Randi E, Fusco G, Lorenzini R, Spina F. 1991. Allozyme divergence and phylogenetic-relationships within the strigiformes. Condor 93:295–301.

Rasmussen DT, Olson SL, Simons EL. 1987. Fossil birds from the Oligocene Jebel Qatrani formation, Fayum Province, Egypt. Smithsonian Contrib Paleobiol 62:1–20.

Raup DM. 1995. The role of extinction in evolution. In: Fitch WM, Ayala FJ, editors. Tempo and mode in evolution: Genetics and paleontology 50 years after Simpson. Washington, DC: National Academy Press. p 109–124.

Reisz RR. 1997. The origin and early evolutionary history of amniotes. Trends Ecol Evol 12:218–222.

Shapiro B, Sibthorpe D, Rambaut A, Austin J, Wragg GM, Bininda-Emonds ORP, Lee PLM, Cooper A. 2002. Flight of the dodo. Science 295:1683.

Sibley CG, Ahlquist JE. 1990. Phylogeny and classification of birds: A study in molecular evolution. New Haven: Yale University Press.

Sibley CG, Monroe Jr. BL. 1990. Distribution and taxonomy of birds of the world. New Haven: Yale University Press.

Smith AB, Peterson KJ. 2002. Dating the time of origin of major clades: Molecular clocks and the fossil record. Annu Rev Earth Planet Sci 30:65–88.

Sorenson MD, Oneal E, Garcia-Moreno J, Mindell DP. 2003. More taxa, more characters: The Hoatzin problem is still unresolved. Mol Biol Evol 20:1484–1498.

Springer MS, Murphy WJ, Eizirik E, O'Brien SJ. 2003. Placental mammal diversification and the K–T boundary. Proc Natl Acad Sci USA 100:1056–1061.

Stidham TA. 1998. A lower jaw from a Cretaceous parrot. Nature 396:29–30.

Stidham, TA. 2001 The origin and ecological diversification of modern birds: Evidence from the extinct wading ducks, Presbyornithidae (Neornithes: Anseriformes). PhD thesis, University of California, Berkeley.

Tambussi CP. 1995. Fossil Rheiformes of Argentina. Courier Forschunginstitut Senckenberg 181:121–129.

Unwin DM. 1993. Aves. In: Benton MJ, editor. The fossil record. London: Chapman and Hall.

Van Tuinen M, Butvill DB, Kirsch JAW, Hedges SB. 2001. Convergence and divergence in the evolution of aquatic birds. Proc R Soc Lond B 268:1345–1350.

Van Tuinen M, Dyke GJ. 2004. Calibration of galliform molecular clocks using multiple fossils and genetic partitions. Mol Phylogenet Evol 30:74–86.

Van Tuinen M, Hadly EA. 2004. Error in estimation of rate and time inferred from the early amniote fossil record and avian molecular clocks. J Mol Evol 59:267–276.

Van Tuinen M, Hedges SB. 2001. Calibration of avian molecular clocks. Mol Biol Evol 18:206–213.

Van Tuinen M, Hedges SB. 2004. The effect of external and internal fossil calibrations on the avian evolutionary timescale. J Paleontol 78:45–50.

Van Tuinen M, Ramakrishnan U, Hadly EA. 2004. Investigating the effect of environmental change on biotic evolution: Genetic contributions, current work and future developments. Philos Trans R Soc Lond: Phys Math Eng Sci 362:2795–2820.

Van Tuinen M, Sibley CG, Hedges SB. 2000. The early history of modern birds inferred from DNA sequence of mitochondrial and nuclear ribosomal genes. Mol Biol Evol 17:451–457.

Vickers-Rich P, Bohaska DJ. 1976. The world's oldest owl: A new strigiform from the Paleocene of Southwestern Colorado. Smithsonian Contrib Paleobiol 27:87–93.

Weigel RD. 1963. Oligocene birds from Saskatchewan. Q J Fla Acad Sci 26:257–262.

Wilf P, Johnson KR, Huber BT. 2003. Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous–Paleogene boundary. Proc Natl Acad Sci USA 100:599–604.

Wink M. 1995. Phylogeny of old and new-world vultures (Aves, Accipitridae and Cathartidae) inferred from nucleotide-sequences of the mitochondrial cytochrome-*b* gene. Zeitschrift fuer Naturforschung 50:868–882.

Wink M, Heidrich P. 1999. Molecular evolution and systematics of the owls (Strigiformes). In: Konig C, Wieck F, Becking JH, editors. Owls: A guide to the owls of the world. Sussex: Pica Press. p 39–57.

Wyles JS, Kunkel JG, Wilson AC. 1983. Birds, behavior, and anatomical evolution. Proc Natl Acad Sci USA 80:4394–4397.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.