The evolutionary radiation of modern birds (Neornithes): reconciling molecules, morphology and the fossil record

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The pattern, timing and extent of the evolutionary radiation of anatomically modern birds (Neornithes) remains contentious: dramatically different timescales for this major event in vertebrate evolution have been recovered by the 'clock-like' modelling of molecular sequence data and from evidence extracted from the known fossil record. Because current synthesis would lead us to believe that fossil and nonfossil evidence conflict with regard to the neornithine timescale, especially at its base, it is high time that available data are reconciled to determine more exactly the evolutionary radiation of modern birds. In this review we highlight current understanding of the early fossil history of Neornithes in conjunction with available phylogenetic resolution for the major extant clades, as well as recent advancements in genetic methods that have constrained time estimates for major evolutionary divergences. Although the use of molecular approaches for timing the radiation of Neornithes is emphasized, the tenet of this review remains the fossil record of the major neornithine subdivisions and better-preserved taxa. Fossils allowing clear phylogenetic constraint of taxa are central to future work in the production of accurate molecular calibrations of the neornithine evolutionary timescale. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **141**, 153–177.

ADDITIONAL KEYWORDS: Aves – cladistics – Cretaceous–Tertiary (K–T) boundary – divergence – molecular clocks – phylogeny – systematics.

INTRODUCTION

THE EVOLUTION OF MODERN BIRDS

The phylogeny and evolution of modern birds (= Neornithes) have captured the interest of ornithological researchers for more than two centuries. In terms of extant groups of land vertebrates, birds are the most speciose: current classifications place the >10 000 living species within at least 23 orders (depending on author). In general, and partly because the clades of modern birds have an extensive but understudied fossil record, questions such as the origin and evolution of avian flight and the pattern of diversification of the major lineages have formed substantial research areas over the years. However, despite a recent explosion of fossil discoveries of well-preserved archaic birds from the Meso-

zoic (Chiappe, 1995; Padian & Chiappe, 1998; Chiappe & Dyke, 2002), the question of the timing and pattern of the evolutionary radiation of the modern lineages of birds remains one of the most debated areas in current vertebrate palaeontology (Dyke, 2001a; van Tuinen & Hedges, 2001). When in time did the major lineages of modern birds (including the extant orders and families) originate? How soon after their origination did major pulses of diversification occur? How many of these diversification events are still recorded by extant avian biodiversity? Are these radiations synchronous in time across orders and families, or do some of the modern lineages predate others? These are just a few of the evolutionary questions that currently remain unanswered on the basis of the available data, be it palaeontological or biochemical. Current syntheses have indicated that the fossil and nonfossil evidence are in conflict at the base of the neornithine timescale; it is therefore fundamental to reconcile these

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two highly informative data sets in order to further address the exact nature of the evolutionary radiation of modern birds.

BACKGROUND

Our modern perceptions of the evolutionary relationships between the higher taxa of Neornithes can be traced back to the 19th century (see reviews in Sibley & Ahlquist, 1990; Cracraft *et al.*, 2004). Some of the earliest anatomical descriptions of fossil birds date to the 1820s (Koenig, 1825), some time before the development of evolutionary thought in the 1850s (Darwin, 1859; Huxley, 1867). However, for much of the intervening time between the 1880s and the 1980s, the fossil record of birds was dominated by just a few heavily studied, discussed and interpreted taxa, in particular *Ichthyornis* and *Hesperornis* from the Cretaceous Inland Pierre Seaway of North America and *Archaeopteryx* from the Jurassic Solnhofen lagoons of Germany. (Padian & Chiappe, 1998; Chiappe & Dyke, 2002). Although a number of fossils of anatomically 'modern' birds were also reported during this time (e.g. Koenig, 1825; Owen, 1841), interpretation of evolutionary patterns within Neornithes was limited by the obviously very large morphological gap between these taxa and the much older (and more primitive) *Ichthyornis* and *Archaeopteryx*. As a result of the age of *Archaeopteryx*, many early workers assumed great antiquity for the extant lineages of birds: Owen (1841) considered the morphological differentiation by the earliest Eocene for taxa such as *Halcyornis* and *Lithornis* as simply too advanced to imply anything other than a Cretaceous origination for many of the modern lineages. Invariably, some early workers also linked several modern lineages directly to *Ichthyornis* or *Hesperornis* drawing evidence from the available fossil data (Wiedersheim, 1885).

Since the early 1980s, the fossil record of non-neornithine taxa from the Mesozoic, and their diagnoses by use of clear and cladistically tested osteological characters has improved dramatically (e.g. Chiappe & Witmer, 2002). More fossil birds from the Cretaceous have been discovered and described in the last 20 years than from the last two centuries combined (Chiappe, 1995; Padian & Chiappe, 1998; Chiappe & Dyke, 2002) including lineages such as Enantiornithes, entirely unknown before 1981 (Walker, 1981; Chiappe & Walker, 2002). A number of fossils now placed in the enantiornithine clade were originally described as modern birds (Brodkorb, 1976; see Chiappe & Walker, 2002). This increase in sheer fossil numbers, combined with better evolutionary understanding of the Mesozoic taxa, has tremendously advanced our understanding of modern bird evolution. Many recently described taxa have served to fill in the morphological gap

between *Archaeopteryx* and Neornithes and have documented a sequence of character change, loss and acquisition through the course of avian evolution (Norell & Clarke, 2001; Chiappe & Dyke, 2002; Clarke & Norell, 2002). Conversely, as the fossil record of birds has filled out with new discoveries, evidence has grown weaker for the unequivocal presence of modern birds in the Mesozoic and has led to speculation regarding the timing of neornithine origination and subsequent diversification. The question remains: Did modern birds enjoy great diversity prior to the Cretaceous–Tertiary (K–T) extinction event, 65 Mya? Taken at face value, the sheer number of fossil discoveries from the earliest Tertiary that have been made from the 1980s to the mid-1990s appears to indicate that the evolutionary radiation of this large clade occurred in the early stages of the Cenozoic (Wyles, Kunkel & Wilson, 1983; Olson, 1985; Feduccia, 1995, 2003). However, although palaeontological consensus has emerged in support of a post K–T radiation for the majority of Neornithes, increasing numbers of fossil specimens that are from the Mesozoic have continued to be diagnosed as modern birds; an interpretation that has received much support from molecular studies over the last 10 years (Cooper & Penny, 1997; van Tuinen & Hedges, 2001; Paton, Haddrath & Baker, 2002). This recent turn of events has created an impasse and the apparent incongruence between the bulk of the fossil record and available genetic information has caused an intense debate regarding the temporal usefulness of either data source (e.g. Cooper & Fortey, 1998; Benton, 1999; Feduccia, 2003). No recent advances have been made in untangling the causes behind this dichotomy with testable hypotheses.

AIMS

Our review highlights current understanding of the early fossil history of Neornithes in light of current phylogenetic resolution for the major extant clades and recent advancements in genetic methods that have advanced time estimates for major evolutionary divergences. The major divergences discussed here encompass the superordinal, ordinal and family levels within Neornithes and include the initial separation *between* Palaeognathae (ratite birds and tinamous) and their sister clade Neognathae (all other modern birds), *between* tinamous and ratites, *between* Galloanserae and Neoaves, as well as the origin and diversification of monophyletic orders and families (Fig. 1). In addition to discussing alternative diversification hypotheses at these three levels, we focus on the fossil record of the major neornithine subdivisions and present discussion of some of the better-preserved taxa. We emphasize that fossils are now known that have provided the basis of clear phylogenetic assess-
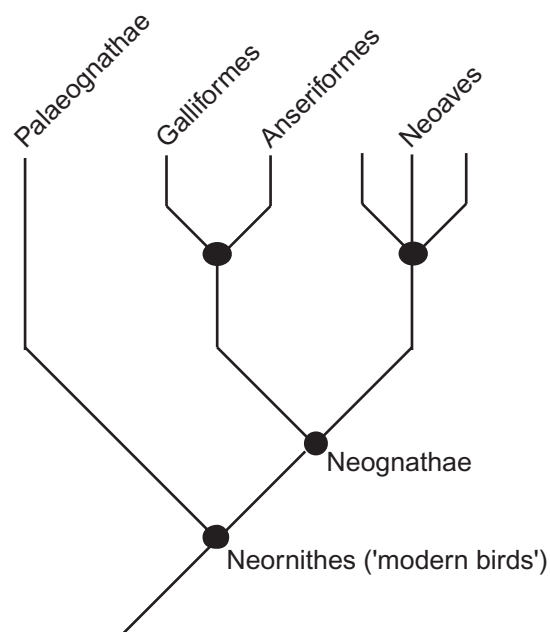
Figure 1. Summary cladogram to show the phylogenetic relationships at the base of Neornithes (based on Cracraft *et al*., 2004). Despite advances in the use of genetic data to resolve the phylogenetic relationships of birds, differences between data sets remain and have led to conflict with regard to the interrelationships of clades within Neoaves. The part of this tree to the right-hand side (relationships within Neoaves) has often been referred to as the 'neoavian comb' (Cracraft *et al*., 2004).

ments and that such phylogenetically constrained taxa could be used for future work in the production of accurate molecular calibrations. At this point, it is worth remembering that there can be just as much uncertainty surrounding the construction of trees on the basis of morphological characters as with molecular data; both data types are, however, reproducible and as such represent clearly testable hypotheses.

The fossil record provides a great deal of information (in the form of fossil skeletons, and in some cases soft anatomy) that has bearing on the early morphological history of modern birds. Many hundreds of well-preserved fossils have been discovered over the course of the last century from deposits that span at least the last 60 million years of Earth's history and these can be used to track the tempo, pattern and extent of the evolutionary diversification within and among modern bird clades (Dyke, 2001a; Chiappe & Dyke, 2002). We highlight that although divergences inferred on the basis of direct interpretation of fossils (largely Eocene in age) do post-date some genetic estimates, discrepancies between these two kinds of data may in fact be artefactual (*contra* Feduccia, 2003; see Dyke, 2003a; van Tuinen *et al*., 2003). While some

paint this debate as black and white (either the clocks or the fossils are wrong), we seek a temporal threshold beyond which consensus between fossils and molecules can be gained. In this context, one of use has argued elsewhere (M. van Tuinen, T. A. Stidham & E. A. Hadly, unpubl. data; van Tuinen & Hedges, 2004) that preliminary data indicate good temporal agreement between fossils and molecular clocks for the radiation of bird families in the mid-Tertiary, and that reasonably good agreement on earliest Tertiary diversification for most orders can be gained by use of molecular methods. Disagreement remains, however, over the depth of superordinal divergences and the character of neornithine lineages that existed in the Cretaceous. Conflict is not surprising considering the enormous scarcity of neornithine fossils that morphologically 'bridge the gap' between the monophyletic modern orders (Hope, 2002). Inconsistencies in molecular dating and calibration techniques, in the systematics and interpretation of fossil taxa used for calibration, and in differing definitions of the 'modern radiation' are all relevant to this problem.

THE SHAPE OF THE NEORNITHINE TREE

In the 1880s, Fürbringer (1888) laid the anatomical foundations for much of our current understanding of the relationships and systematics of Neornithes. The vast majority of subsequent avian classifications, up to and including those of recent times, owe much of their content to this classical study. However, despite more than a century of anatomical work on the major historical subdivisions of birds, little consensus has yet emerged regarding the specifics of neornithine phylogenetic relationships towards the tips of the tree (van Tuinen, Sibley & Hedges, 2000; Livezey & Zusi, 2001; Cracraft *et al*., 2004). In contrast, the base of the neornithine phylogeny is now well corroborated by use of both molecular and morphological information (summarized by Cracraft & Clarke, 2001). Independent evidence has reached consensus that the basal-most lineages within Neornithes comprise the Palaeognathae (ratite birds and tinamous) and its sister clade including all remaining extant taxa, the large grouping Neognathae. The Neognathae, in turn, comprise two sister clades, namely Galloanserae and Neoaves (Fig. 1). Galloanserae is the collective term used to refer to the two ordinal clades Galliformes ('landfowl' such as the pheasants, junglefowl and partridges) and Anseriformes ('waterfowl' such as the screamers, ducks and geese). However, the initial divergences within Neoaves remain completely unresolved (Cracraft *et al*., 2004). A number of the traditional orders of birds that fall within this group have often been considered monophyletic, but in some cases such assumptions based on older classifications remain largely

untested (e.g. Gruiformes, Coraciiformes). Due consideration of well-represented fossil taxa will provide additional data that may further corroborate this supposed monophyly, but there remains a conundrum: How can we know to which group a fossil under study belongs if the characters considered diagnostic to major clades within Neoaves have yet to be clearly formulated, much less tested? This is an historical problem that has plagued students of the neornithine radiation; its resolution may not yet be close at hand.

THE DEBATE: MOLECULES VERSUS MORPHOLOGY

CONTRASTING MOLECULAR DATES WITH THE FOSSIL RECORD

Estimates for the timing of neornithine diversification have been based directly on the known fossil record (e.g. Feduccia, 1980, 1995, 2003; Olson, 1985), on geologically dated events in Earth History (e.g. Cracraft, 2001), or on molecular clocks (e.g. Wilson, 1986; Cooper & Penny, 1997; van Tuinen & Hedges, 2001; Paton *et al*., 2002). It is important to note that historically the known fossil record of modern birds has been concentrated in early Tertiary (Eocene) deposits of the Northern Hemisphere (Dyke, 2001a; Cracraft, 2001; M. van Tuinen, T. A. Stidham & E. A. Hadly, unpubl. data). These remains are approximately 56–50 Myr old (Dyke, 2001a; Mayr, 2000c). However, relatively little informative fossil material has ever been collected from rocks of Palaeocene age formed in the interval between the K–T boundary and the base of the Eocene (reviewed by Dyke, 2001a; Chiappe & Dyke, 2002). Largely on the basis of the accumulated Eocene fossil record, early interpretations of the pattern of diversification (Wyles *et al*., 1983; Feduccia, 1995) suggested that the radiation of modern birds occurred in the earliest Tertiary (Feduccia, 2003). This record, in combination with limited descriptions of fragmentary neornithines from the Cretaceous often classified within 'shorebird' or 'waterbird' modern orders (i.e. Charadriiformes, Anseriformes; see Hope, 2002), led Feduccia (1995; 1999) to propose his so-called 'transitional shorebird hypothesis'. In its later incarnations (Feduccia, 2003), this hypothesis states that the modern antecedents of living birds were able to survive the severe environmental perturbations caused by the K–T event and generate an explosive pulse of evolutionary diversification in the lowermost Tertiary. Neornithine crown-groups, the ordinal clades alive today, therefore descend from a primitive 'shorebird-like' ecology and morphology (Feduccia, 1995, 1999, 2002; but see Paton *et al*., 2002). This hypothesis predicts (indeed relies upon) a limited fossil record of neornithine birds from the Cretaceous and Palae-

ocene, classified to within just a handful of the modern orders. Major clade divergences are predicted to have occurred in the Eocene or Palaeocene, not earlier than 65 million years ago (Feduccia, 1995, 1999).

On the other side of the debate, recent developments in biochemical techniques for investigating phylogenetic relationships have also produced a series of estimates for the divergences of modern birds based on the premise of a molecular clock. The majority of these studies have claimed support for a Cretaceous 'radiation', in some cases deep in time, and as such at odds with much of the fossil record (Dyke, 2001a). One of the first studies (Cooper & Penny, 1997), based on two small gene fragments (42 sequences of 12S RNA and 16 sequences of c-mos) for 16 orders of modern birds, produced estimates for 15 orders (22 lineages in total) *diverging* deep in the Cretaeous, in some cases more than 100 Mya. Based on these results, mass survival across the K–T boundary and a Cretaceous *diversification* of modern birds was suggested (Cooper & Penny, 1997). Additional molecular clock analyses based on mitochondrial coding (Paton *et al*., 2002) and noncoding genes (van Tuinen & Hedges, 2001) have supported the notion that many of the modern lineages of birds *originated* in the Cretaceous. However, it is crucial to be clear that this is a phylogenetic concept and hence these studies do not imply that completely modern pigeons, rails or owls were mingling with enantiornithine birds in the Cretaceous. 'Modern-looking' morphologies evolved as recently as the oldest divergence among crown neornithines characterized by these morphologies. If the early extinct members of modern lineages looked quite different from their living descendants, then the fossil record will better reflect *diversification* (and hence not *origination*) events. It is thus essential to ask next to what extent temporal conflict exists with respect to the major modern bird *diversification* events as understood on the basis of either fossils and genetics. Although it is generally assumed that molecular data do also point to Cretaceous diversification within orders (Feduccia, 1996; Benton, 1999), these available data still suffer greatly as a result of their limited taxon sampling (van Tuinen *et al*., 2003). To date, available molecular studies have only placed the diversification of the modern ratite birds (van Tuinen & Hedges, 2001; Paton *et al*., 2002), parrots (Miyaki *et al*., 1998), songbirds (Barker, Barrowclough & Groth, 2002), galliforms (van Tuinen & Dyke, 2004) and shorebirds (Paton *et al*., 2003) in the Cretaceous. Too few data exist to further constrain the time of radiation within remaining orders (see below), and temporal resolution of the major diversification events will be required to assess the true extent of the 'modern radiation' of birds. Once more, strong disagreement does not exist over familial and ordinal

diversification, but over the evolutionary rate of morphological adaptive shifts (between orders). Neither clocks nor fossils exclude the possibility that macroevolution can proceed at a fast pace, as exemplified in mammals by the complete morphological adjustment from an artiodactyl ancestor to a whale-like aquatic ecology within less than 10 Myr (as argued, for example, by Feduccia, 2003). But is it plausible that a whale-like morphology could have evolved from more primitive, much smaller placentals not resembling ungulates in that same evolutionary time (<10 Myr)? This is the kind of timescale available for a 'shorebird-like' ancestor to have evolved into such different morphologies as pigeon, hummingbird or ostrich (see below). Phylogenetic analysis of morphological, and molecular data do not support such an extreme rate of change, but a 'numbers game' interpretation of the fossil record does, even though transitional fossils have not been found.

HYPOTHESES FOR THE NEORNITHINE RADIATION

Although there remains little doubt in the minds of most workers that the majority of the basal clades of Neornithes *must* have a Cretaceous fossil record (but see Feduccia, 2003), this inference is currently based on little convincing fossil material (Dyke, 2001a; Chiappe & Dyke, 2002). With few exceptions, the Cretaceous fossil record of modern birds comprises incomplete and fragmentary specimens that have been subject to taxonomic speculation based on informal evaluations of the characters of modern taxa (Hope, 2002). Although the record from the Tertiary is exceptional, from a number of localities in particular, it is also strongly biased and as a result debate will remain with regard to just *how deep* the neornithine radiation can be traced *prior* to the K–T boundary (Fig. 2).

The multiple lines of evidence that have to date been brought to bear on the question of the extent of this diversification through geological time converge into three distinct hypotheses: 1. The majority of the evolutionary radiation of modern birds occurred in the lowermost Tertiary (Feduccia, 1995, 2003), few entirely 'shorebird-like' neornithine groups and perhaps palaeognaths (Feduccia, 1996) having a Cretaceous origination; this single radiation gave rise to the superordinal groups, ordinal groups and led to diversification into recognizable families within just 10 Myr (Fig. 3); 2. The basal clades of Neornithes as well as the root of the neoavian diversification occurred in the Cretaceous, and the few remaining groups towards the tip of the neornithine tree (i.e. Passeriformes, Piciformes), radiated in the Tertiary and later (e.g. Dyke, 2001a, 2003a) (Fig. 3); 3. All of the origination as well as the diversification into orders and families occurred in the Cretaceous (e.g. Cooper & Penny, 1997; Cracraft, 2001) (Fig. 3).

LIMITATIONS OF MOLECULAR CLOCK ANALYSES

The accuracy – hence usefulness – of any molecular time estimate is dependent on the fossil (or age) that is being used for calibration (Dyke, 2001a; van Tuinen & Dyke, 2004; van Tuinen & Hedges, 2004). Given cur-
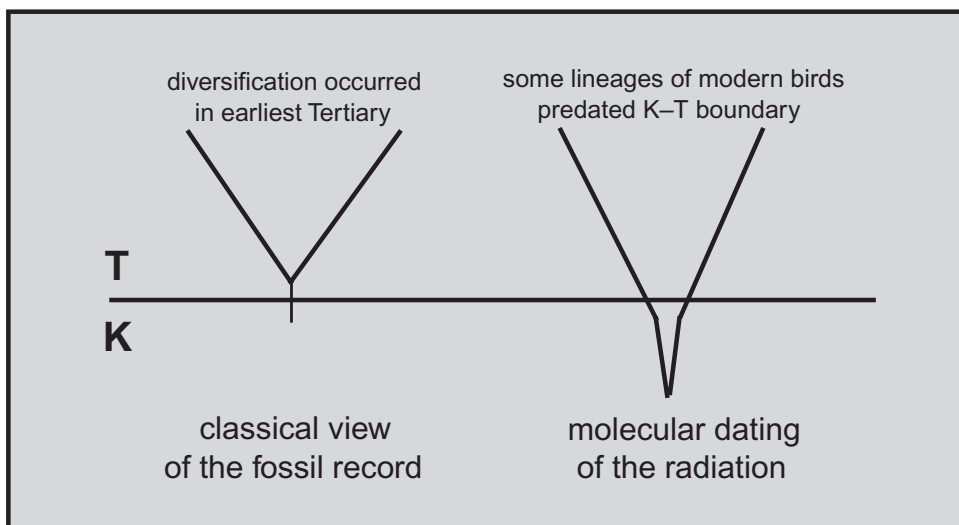

Figure 2. Cartoon to summarize the competing hypotheses for the pattern of modern bird diversification across the K–T boundary (see text for details). The lack of confirmed fossil records from the Cretaceous (K) has hindered the corroboration of alternative hypotheses (re-drawn from Dyke & Chiappe, 2003).
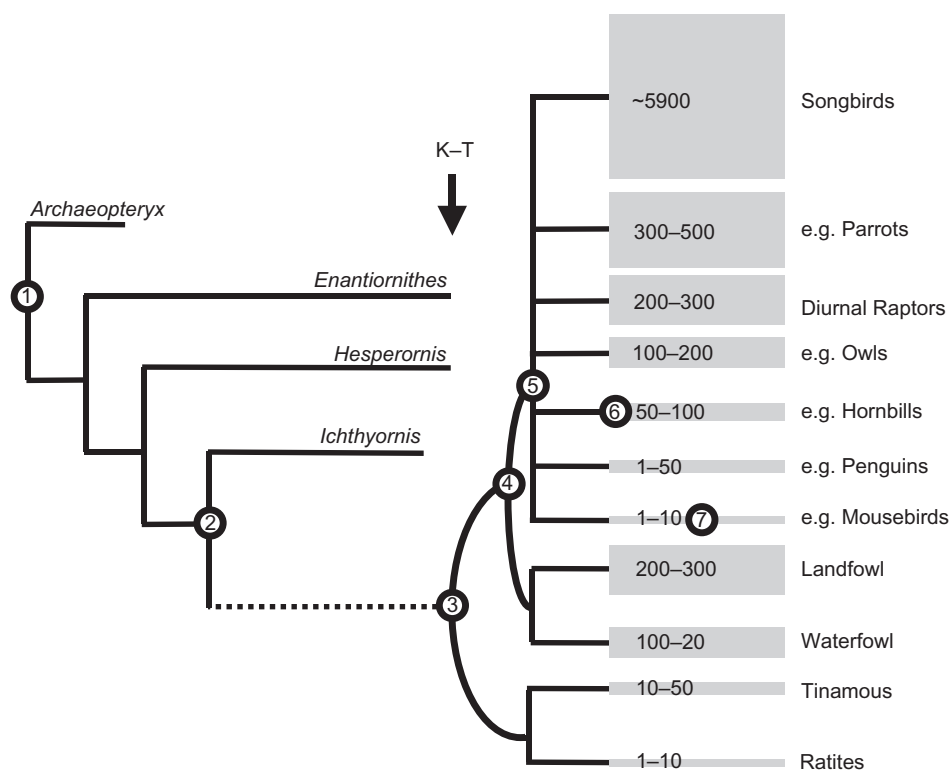
Figure 3. Seven possible definitions for the 'radiation of birds'. The true radiation of morphology observed in today's birds may have taken place as recently as points 6 or 7. Archaic ornithurines have not been found after the K–T boundary (black arrow). Although predicted from molecular clock analyses (dotted line; see text), little convincing evidence exists for neornithine fossils preceding the K–T boundary. The variation in number of species among traditional neornithine orders indicates that the 'radiation' was not equal across every major clade. Numbers refer to the following major evolutionary bird divergences: 1, diversification of Aves; 2, origin of Neornithes; 3, diversification of Neornithes; 4, origin of Neoaves; 5, origin of most orders (including 'Neoavian comb'); 6, diversification of most orders; 7, diversification of most families.

rent knowledge of the fossil record of modern birds from a phylogenetic point-of-view, studies founded on the use of internal calibrations are problematic simply because the fossils in question have in most cases yet to be adequately constrained by use of cladistic character analysis (Dyke, 2001a). The shape of the neoavian tree is simply not well enough understood at the present time on the basis of morphological characters; hence, the majority of the fossils used previously for calibration of avian molecular clocks are of uncertain phylogenetic position (even at the ordinal level). The use of fragmentary fossil material (in several cases comprising just single bones) of uncertain phylogenetic placement for internal calibration also calls into question some clock analyses (Cooper & Penny, 1997). In some cases the absolute age of fossil modern birds remains uncertain; this is true for much material collected from strata of problematic Cretaceous age, for example from North America and Antarctica (see discussion of Cretaceous-age neornithines below). Accu-

rate knowledge of the age of fossils to be used for calibration is desirable because this material needs to approximate the age of the node on which the calibration itself is to be based (i.e. the node on which the evolutionary rate is based). As discussed by a number of workers (e.g. Benton, 1999; van Tuinen & Hedges, 2004), precise temporal information may be unavailable for many fossil birds as a result of factors affecting probability of their fossilization in the first place. Examples of problematic molecular clock analyses where the assumptions of temporally and phylogenetically well-constrained fossils are not met are prevalent in the recent literature (several examples are discussed by van Tuinen & Dyke, 2004; van Tuinen & Hedges, 2004) and may be one cause for the sometimes wide range of age estimates produced for a single clade divergence. However, these limitations are likely not to be behind the discrepancy with fossils at deeper taxonomic levels, because phylogenetic misdiagnoses may cause either overestimation or underestimation of

molecular divergence times. A Cretaceous history for modern birds appears to be robust when subject to a wide variety of rate calibrations and methodologies.

THE FOSSIL RECORD

CRETACEOUS RECORDS

Although two out of the three models for neornithine diversification do suggest that the bulk of the evolutionary radiation of these birds occurred in the Cretaceous, actual, direct fossil evidence in support of these hypotheses is sparse. Only very few Cretaceous taxa that have been claimed (at one time or another) to be neornithine are actually represented by more than an isolated bone (e.g. *Gansus*, *Ambiortus*) (see Kurochkin, 1995; Dyke, 2001a; Chiappe & Dyke, 2002). The remaining handful of presumed Cretaceous neornithine fossils are either highly controversial, have not been studied in any detail, or their placement within modern birds has subsequently been rejected (Hope, 2002). Because the incompleteness of much of this material renders few characters useful for phylogenetic analysis (Clarke, 1999; Dyke & Mayr, 1999; Clarke & Chiappe, 2001; Dyke, 2001a; Hope, 2002), these fossils often cannot be evaluated within our currently limited understanding of the higher-level relationships amongst living taxa (see Cracraft & Clarke, 2001; Livezey & Zusi, 2001). As has been discussed in detail by others (Dyke, 2001a; van Tuinen & Hedges, 2004), this fossil record has nonetheless been cited (at one time or another) in support of the presence of a large variety of neornithine lineages prior to the K–T boundary, including Pelecaniformes, Psittaciformes, Charadriiformes, Galliformes, Anseriformes, Strigiformes, Gaviiformes and Procellariiformes. Speculations on the basis of this fossil record abound and interpretations have been based on some, or all, of the described Cretaceous material.

What do we know about modern birds from the Cretaceous?

In a recent compilation of the known Cretaceous modern birds, Hope (2002) has illustrated the problem inherent to this corner of the fossil record, namely that large numbers of fragmentary fossils of sometimes dubious age are proposed to occur within several of the extant orders and families. According to Hope (2002), the total number of Cretaceous fossils that can be assigned to Neornithes is around 50 specimens [see also material described by Kurochkin, Dyke & Karhu (2002) not tabulated by Hope (2002)] of which no more than six records consist of more than isolated bones (also tabulated in Dyke, 2001a and Chiappe & Dyke, 2002). This collection of incomplete specimens is considered by Hope (2002), as well as by a number of pre-

ceding authors, to perhaps document the presence of at least seven modern orders of birds by the end of the Cretaceous (not including several specimens considered Neornithes *incertae sedis*). Material compiled by Hope (2002) ranges in age from Maastrichtian to Conacian, a time span of some 15 Myr prior to the K–T boundary.

Not only is the majority of this material incomplete, but there have also been problems accurately dating many of these fossils. One well-documented example concerns the remains of fossil birds collected from the Hornerstown and Navesink Formations of New Jersey, USA. First described in detail by Olson & Parris (1987) these New Jersey birds have been the subject of much debate: Do these fossils from deposits forming part of the Cretaceous–Palaeocene Atlantic Coast of the USA testify directly to the presence of neornithine birds prior to the end of the Cretaceous? Because the stratigraphy of the New Jersey transitional greensand marls is highly complex, it remains unclear as to whether much of the bird material collected from the Hornerstown Formation in particular is actually latest Maastrichtian or earliest Palaeocene in age (see citations in Olson, 1994). Although Hope (2002) only lists records of avian material from the 'probably basal Palaeocene' Hornerstown Formation 'if the species is reported from earlier sediments' [sic], in a similar paper Parris & Hope (2002) were unable to convincingly distinguish between Cretaceous and Palaeocene records from the same rocks. As a result, evidence for the age of much of this material is equivocal even given the limited morphological information preserved on the majority of these incomplete elements.

Although this intriguing fossil record cannot be ignored, much better resolution between and within the clades of extant Neornithes must be achieved before the few characters contributed by such incomplete specimens can be convincingly evaluated (Clarke, 1999; Clarke & Chiappe, 2001; Chiappe & Dyke, 2002). Even if these fossil specimens were shown convincingly to be Palaeocene in age, they would still imply a Cretaceous age for their corresponding lineages. We do not automatically assume the misdiagnosis of every Mesozoic fossil element to Neornithes as others do (Feduccia, 2003), but the current lack of thorough cladistic analyses does downplay the utility of these fossils in constructing a conservative fossil-based timescale for modern birds. Until more complete specimens are discovered, it is safer not to consider these fossils as evidence for the undisputed presence of neornithine lineages in the Cretaceous.

Polarornis: a Cretaceous loon?

One Mesozoic fossil record, however, deserves further comment here: the recently described *Polarornis gre-*

gorii, a claimed Cretaceous loon (Gaviidae) from Antarctica (Chatterjee, 2002). Initially reported in the late 1980s (Chatterjee, 1989) and previously illustrated in a series of skeletal reconstructions (Chatterjee, 1997), *Polarornis* is known from cranial and postcranial elements collected in 1983 from a bed containing other vertebrate and invertebrate fossil material (Chatterjee, 2002). If confirmed, this is not only the oldest loon known to date from the fossil record, but also one of the most completely preserved Cretaceous fossil neornithines collected from anywhere in the world. Whatever the outcome, the fossil material pertaining to *Polarornis* (Chatterjee, 2002) appears to be exceptional, comprising a largely complete skull, four cervical vertebrae and portions of the sternum, as well as several bones of the hind limb (see illustrations in Chatterjee, 2002). Furthermore, it is likely that this fossil material does constitute a single specimen because it was collected within a single calcareous nodule, later prepared chemically (Chatterjee, 2002). However, both the age of the formation from which this specimen was collected as well as the affinities of this material within Neornithes have yet to be convincingly tested. Importantly, placing this fossil either at the stem or crown of modern loons would push back the early neornithine timescale further than any molecular studies have suggested so far (van Tuinen & Hedges, 2004).

Outstanding questions of its age notwithstanding, although *Polarornis* is a well-preserved fossil bird its specific affinities within Neornithes require further corroboration. Of the six osteological characters presented by Chatterjee (2002) to place *Polarornis* within Neognathae, five have a problematic distribution because they are seen in more primitive Mesozoic birds as well as some nonavian theropods (i.e. double-headed quadrate, carotid flanges on the cervical vertebrae, fused cranial bones and edentulous jaws). The last, the presence of a neognathous palate, will require further elucidation as this complex suite of features has been broken down into a number of characters across Neornithes and their immediate outgroups (Cracraft & Clarke, 2001). Furthermore, the relationship of *Polarornis* to extant loons (Gaviidae) remains equivocal at best on the basis of its initial description. Chatterjee (2002) presented six osteological characters as 'synapomorphies' of *Polarornis* and Gaviidae but did not test the distribution of these features by cladistic analysis among a representative sample of modern birds. The cladistic analysis presented in Chatterjee (2002) is limited at best: the placement of *Polarornis* within Neornithes is tested by use of just five terminal taxa from within the crown-clade, including the basal palaeognath *Lithornis*, Galliformes ('landfowl'), Sphenisciformes (penguins), Procellariiformes ('tube-nosed' divers) and a single extant loon. Not only are many of the supposed 'synapomorphies' presented by *Polaror-*

nis also seen in other (not included) members of Neornithes (Mayr & Clarke, 2003), but a number of other putatively closely related taxa such as Anseriformes (uncontroversially the sister-taxon of Galliformes; see above), Podicipediformes (grebes) and Pelecaniformes also were not included in the analysis. While this new specimen is certainly interesting and of clear relevance to the debate about modern bird divergences, much further work is required before the placement of *Polarornis* within Neornithes, let alone Gaviidae, can be confirmed.

EARLIEST FOSSIL RECORDS AND MOLECULAR CLOCKS

We have argued here and elsewhere (Conroy & van Tuinen, 2003; van Tuinen & Dyke, 2004) that for a neornithine fossil record to be useful, either in the establishment of the presence of a particular clade at a certain age or for use as a calibration point for molecular analyses, the following conditions have to be met: (1) the fossil must be well-dated (i.e. well-corroborated by stratigraphy, radiometric dating with limited error, or both); (2) the fossil must exhibit clear osteological characters that can be independently verified as diagnostic to the lineage in question using cladistic methods; and (3) evidence must exist that the fossil approaches the crown node it is claimed to represent.

So far, the use of molecular clocks to estimate divergence times within Neornithes has involved the use of internal and/or external fossil calibrations (reviewed in van Tuinen & Hedges, 2001, 2004). The use of an internal calibration for a molecular clock estimate is preferable; the age of the fossil will provide a time estimate closer to the true divergence time of the clade(s) in question and will therefore invoke less extrapolation and associated error (van Tuinen & Hedges, 2001, 2004). However, as we have indicated, the published fossil record of modern birds has been cited uncritically by some molecular clock workers. Consequently, we have argued that the use of external calibrations (even with more extrapolation error) has more merit in avian molecular clock studies than the use of internal but unsound calibrations (van Tuinen & Dyke, 2004; van Tuinen & Hedges, 2004).

What can actually be said on the basis of the fossil record? In this section, we demonstrate that, in many cases, the recorded 'earliest occurrences' for particular clades of Neornithes are ambiguous because the fossil material upon which they have been founded is either incomplete or extremely fragmentary. Previous compilations of the fossil record of birds have either uncritically listed published occurrences (Unwin, 1993), or have included specimens yet to be addressed within a cladistic context (Olson, 1985), and hence classified on the basis of morphological similarity alone. As such, these compilations will give a misleading picture of

the known (and informative) diversity of fossil modern birds. We list records of well-dated fossil modern birds in this section following an informal ordinal level classification that is based on Wetmore (1960) and Sibley & Ahlquist (1990), with the exception of groupings within the Palaeognathae that we have considered together. Groupings reflect recent phylogenetic work within Neornithes (Livezey & Zusi, 2001; Mayr & Clarke, 2003; Cracraft et al., 2004). Our list of fossil neornithine taxa should not be considered exhaustive as it is intended as a guide for future work making use of molecular methods for calibrating neornithine divergences (van Tuinen & Dyke, 2004). Criteria for dating many of the fossils listed here, including details of geological information for the relevant Eocene (and older) formations are given in Dyke (2001a, 2003a, 2003b).

Palaeognathae
The clade comprising the palaeognathous birds (ratites and tinamous) is the most basal divergence within modern birds (Huxley, 1867; Cracraft, 1981; Sibley & Ahlquist, 1990; Lee, Felsenstein & Cracraft, 1997; van Tuinen, Sibley & Hedges, 1998, 2000; Groth & Barrowclough, 1999; van Tuinen & Hedges, 2001; Fig. 1). In general, the fossil record of these birds is not well known from deposits older than Miocene in age (Unwin, 1993). Over the years, suggestions have been raised that a number of taxa of Mesozoic age should be placed within the palaeognathae (e.g. *Ambiortus*, *Otogornis*, *Palaeocursornis*; Kessler & Jurcsak, 1986; Kurochkin, 1995; van Tuinen, 2000; see Hope, 2002 for a review of previous inaccurate assessments), but subsequent cladistic analyses have shown that such referrals are, most likely, based on primitive characters (e.g. Chiappe, 2002).

The oldest fossils that can certainly be referred to Palaeognathae comprise a group termed the 'lithornithids' (Lithornithidae *sensu* Houde, 1988). The taxonomic history of these fossil birds is complex (Houde, 1988; Dyke, 2003a), but they are well known on the basis of a large number of specimens from lower–middle Eocene deposits of Europe and North America (Houde, 1988; Fig. 4), and have recently been noted from rocks of putative Late Cretaceous age (Parris & Hope, 2002). The lithornithids, including taxa such as *Lithornis vulturinus*, were placed within the Palaeognathae by Houde (1988) on the basis of a number of features of their skull morphology; some of these birds (e.g. *Lithornis*) have been placed as the sister-group to the extant Tinamidae by use of morphological cladistic analyses (Houde, 1988; Clarke & Norell, 2002; Dyke, 2003a; Fig. 4). However, cladistic analysis of an exceptionally well-preserved *Lithornis* including the largest data matrix to date in the context of modern palaeog-

naths instead indicates a position basal to ratites (G. J. Dyke & M. van Tuinen, unpubl. data). Either way, the certain presence of Lithornithidae in the Palaeocene pushes crown Palaeognathae into the Cretaceous, as has been suggested on the basis of some incomplete fossil bones from New Jersey (Parris & Hope, 2002)

Another well-represented and controversial fossil palaeognath, *Palaeotis weigelti* Lambrecht, is known from the Middle Eocene of Messel (Germany). Although the material pertaining to this taxon was flattened during preservation, on the basis of osteological similarity it has been suggested that *Palaeotis* is closely related to extant ratites (Houde & Haubold, 1987); cladistic analysis suggests that *Palaeotis* may be the sister-group to this clade (Dyke, 2003a; Fig. 4). A number of other fossil palaeognaths are also known from sediments older than Eocene in age, e.g. *Diogenornis* from Brazilian (Alvarenga, 1983) and *Remiornis* from French (Martin, 1992) Palaeocene deposits, but these have never been evaluated using phylogenetic methods.

Anseriformes
Although the putative fossil remains of anseriform birds have been described from a number of deposits of both certain and uncertain Mesozoic age (e.g. Olson & Parris, 1987; Olson, 1999; Hope, 2002; Parris & Hope, 2002), much of this material is incomplete and consists only of single elements (Hope, 2002). For example, the single specimen of Late Cretaceous age, *Teviornis gobiensis*, known from a Mongolian Gobi Desert site (Kurochkin et al., 2002), comprises just portions of the right wing (Fig. 5C).

If the few osteological characters referred to are not considered sufficient for the certain placement of this material within the order, then the oldest phylogenetically informative anseriform fossils are known from the Lower Eocene. The several species of *Presbyornis* from Lower Eocene rocks of North America and Europe (Feduccia, 1978; Olson, 1994; Dyke, 2001b), and *Anatalavis oxfordi* from the Lower Eocene of the London Clay (Fig. 5) are the oldest phylogenetically constrained fossil records for this order. *Presbyornis* Wetmore is known on the basis of hundreds of specimens (e.g. Wetmore, 1926; Feduccia, 1999) and has been hypothesized to be the sister taxon of the extant true ducks (Anatidae) by use of cladistic character analyses (Ericson, 1997; Livezey, 1997, 1998a; Fig. 5). *Anatalavis oxfordi* was described by Olson (1999) on the basis of an almost complete specimen (including the skull) that was collected from the very base of the Lower Eocene London Clay Formation. Although Olson (1999) placed this taxon close to the extant, and Australasian endemic, Magpie Goose (*Anseranas*) (Olson, 1999), recent consideration of this material
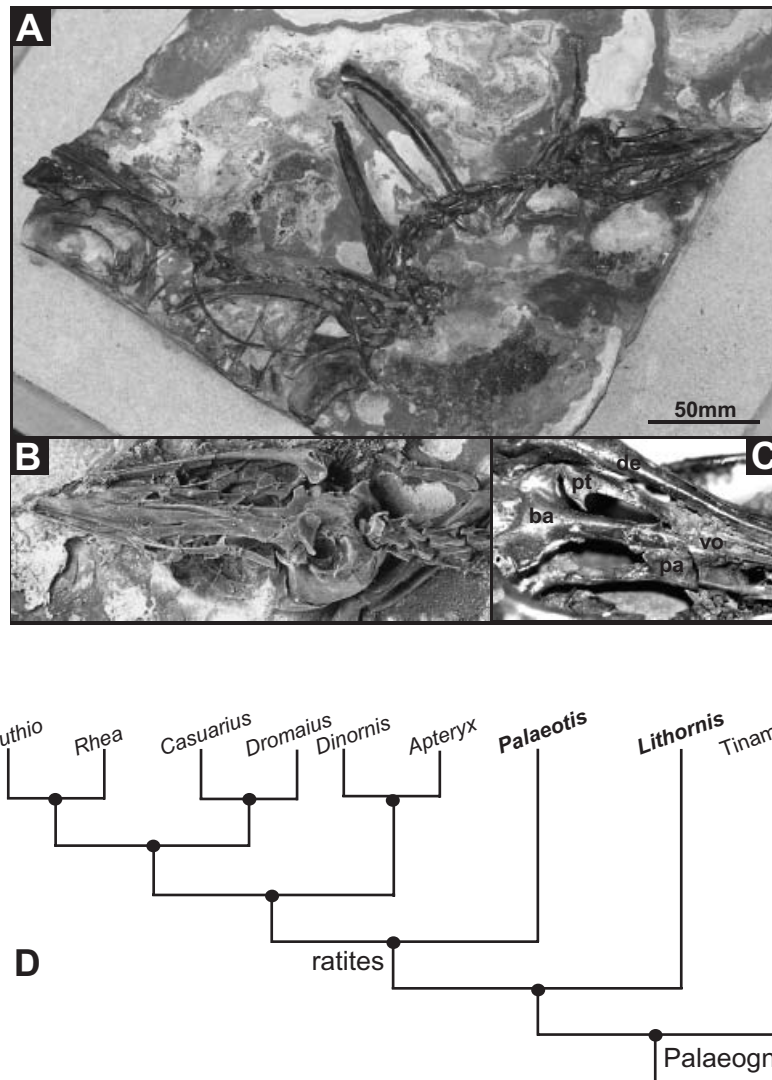
Figure 4. Phylogenetic relationships within Palaeognathae including the well-represented fossil taxa *Palaeotis* and *Lithornis* (see text for details): A, new specimen of *Lithornis* from the Palaeocene-Lower Eocene Fur Formation of Denmark (Dankræ Collections of the Geologisk Museum, Copenhagen, DK 330) encased in cement stone nodule; B, skull of DK 330 acid prepared in oblique lateral view; C, palate of *Lithornis* in ventral view (ba, basitemporal plate; de, dentary; pa, palatine; pt, pterygoid; vo, vomer); D, the phylogenetic placement of *Lithornis* and *Palaeotis* inferred from cladistic analysis of osteological characters (see G. J. Dyke & M. van Tuinen, unpubl. data for details of analysis and matrices).

within a cladistic framework suggests that it is in fact the basal member of the clade that also comprises *Presbyornis* and the Anatidae (Dyke, 2001b; Fig. 5). The recent description of the presbyornithid *Teviornis* (Kurochkin *et al.*, 2002) gives further weight to the hypothesis that divergences within Anseriformes did occur in the Cretaceous. Osteological characters and comparisons with other fossil records of these birds (Ericson, 1999) allow for the placement of this taxon in a derived position within Anseriformes (Livezey, 1997, 1998a), implying that the initial divergences of the more basal clades within this order (crown Anseri-formes, stem Anhimidae, stem Anseranatidae) at an even earlier geological time as indicated by available molecular data (M. van Tuinen, T. A. Stidham & E. A. Hadly, unpubl. data).

Galliformes
Some workers (Olson & Feduccia, 1980a, b; Ericson, 1996; Hope, 2002) have continued to debate the pairing of Galliformes with Anseriformes in the Gal-loanserae, yet this conclusion is well-supported on the basis of both morphological (including fossils) and molecular evidence at this point (see above; Fig. 1).
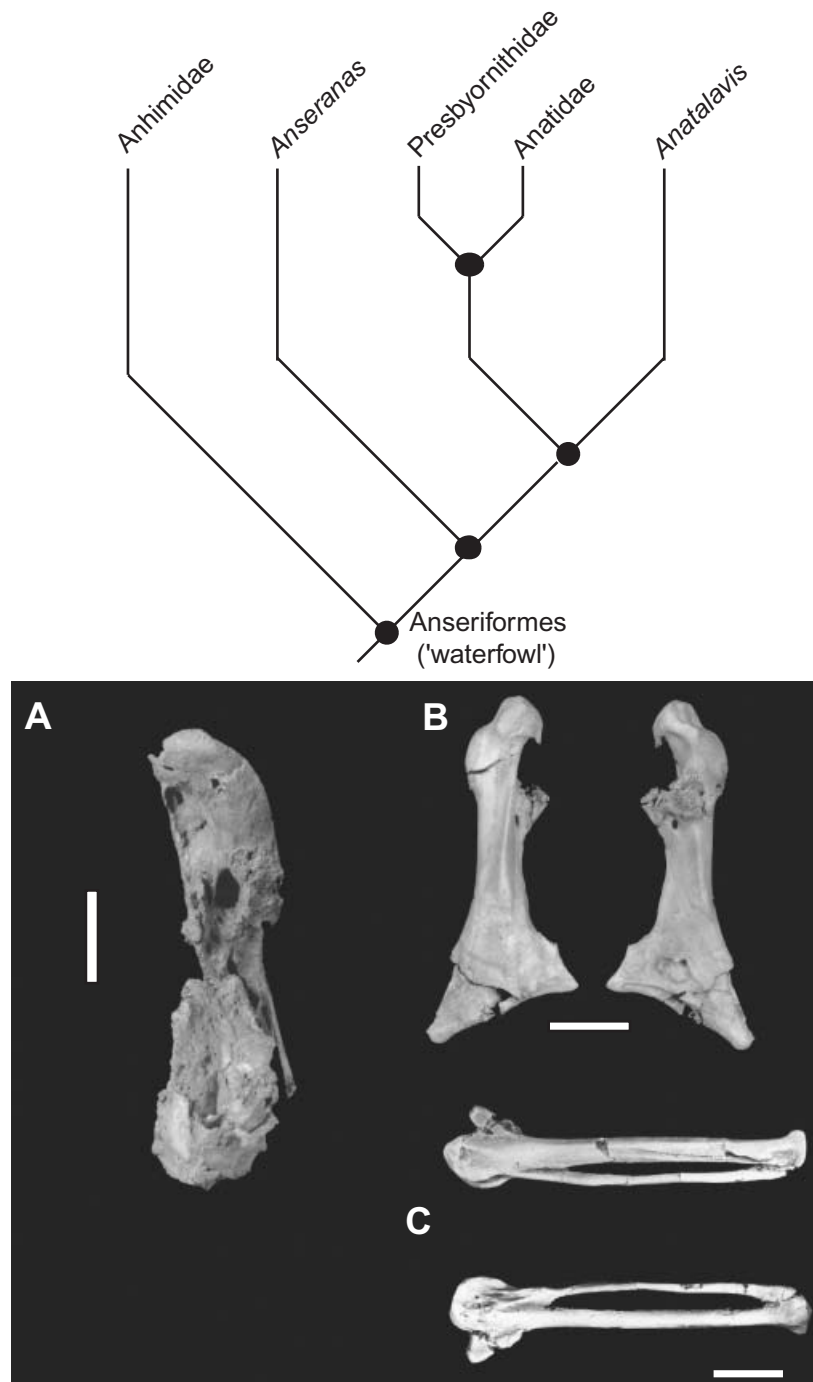
Figure 5. Cartoon depicting consensus phylogenetic relationships among Anseriformes ('waterfowl') (based on Livezey, 1997) (Presbyornithidae includes the taxa *Presbyornis* and *Teviornis*; see text for details) along with a selection of well-preserved fossil taxa: A, holotype skull of *Anatalavis oxfordi* in lateral view from the Lower Eocene London Clay Formation (The Natural History Museum, London, Palaeontology Department Collections, BMNH PAL 5922) (see Dyke, 2001b); B, holotype coracoid of BMNH PAL 5922 in dorsal and medial views) (scale bars = 10 mm); C, holotype carpometacarpus of *Teviornis gobiensis* from the Late Cretaceous Nemegt Formation of Mongolia (Palaeontological Institute of the Russian Academy of Sciences, PIN 4499–1) in dorsal and ventral views (see Kurochkin *et al.*, 2002). Scale bar = 10 mm.

Thus, a corollary of a Cretaceous age for crown Anseriformes is a Cretaceous stem age for their immediate sister-taxon, Galliformes (Fig. 1). A recent study on galliform molecular clocks using several internal calibrations also constrained crown Galliformes, including placement of the initial divergence to megapodes and cracids in the Cretaceous. We have argued that the remaining diversification of Galliformes into the more derived clades of New World Quail, Guineafowl, and phasianids most likely took place in the Tertiary (van Tuinen & Dyke, 2004).

Although fossil records of supposed galliform birds have been recorded from the Cretaceous, all of these are based on isolated, often fragmentary skeletal elements (e.g. Brodkorb, 1964; Hope, 2002). The oldest known fossil galliform that can be considered phylogenetically informative is *Gallinuloides wyomingensis* Eastman from the Lower Eocene Green River Formation of the USA (Eastman, 1900; Dyke, 2003b; Fig. 6). The holotype specimen of this taxon is complete, but not very well preserved, and has been placed within

its own family, the Gallinuloididae (Lucas, 1900). Crowe & Short (1992) have reported on the presence of another, as yet undescribed, specimen of this taxon. On the basis of a phylogenetic analysis of osteological features. Dyke (2003b) placed *Gallinuloides* basal within the large 'phasianoid' assemblage (comprising pheasants and relatives) within Galliformes (Fig. 6), not basal within the entire order as previously proposed (Eastman, 1900; Lucas, 1900; Crowe & Short, 1992), indeed assumed for molecular clock calibration purposes (Cooper & Penny, 1997). Other well-preserved fossil members of Galliformes include *Paraortygoides* from the Eocene of the UK and Germany (Fig. 6). Mayr (2000a) described *Paraortygoides messelensis*, a basal galliform bird from the Middle Eocene of Messel (Hessen, Germany) on the basis of an articulated specimen lacking the skull and presented a number of osteological characters, not only in support of galliform monophyly, but also to hypothesize the position of *Paraortygoides* near to the base of this clade. This proposal was later tested and confirmed by
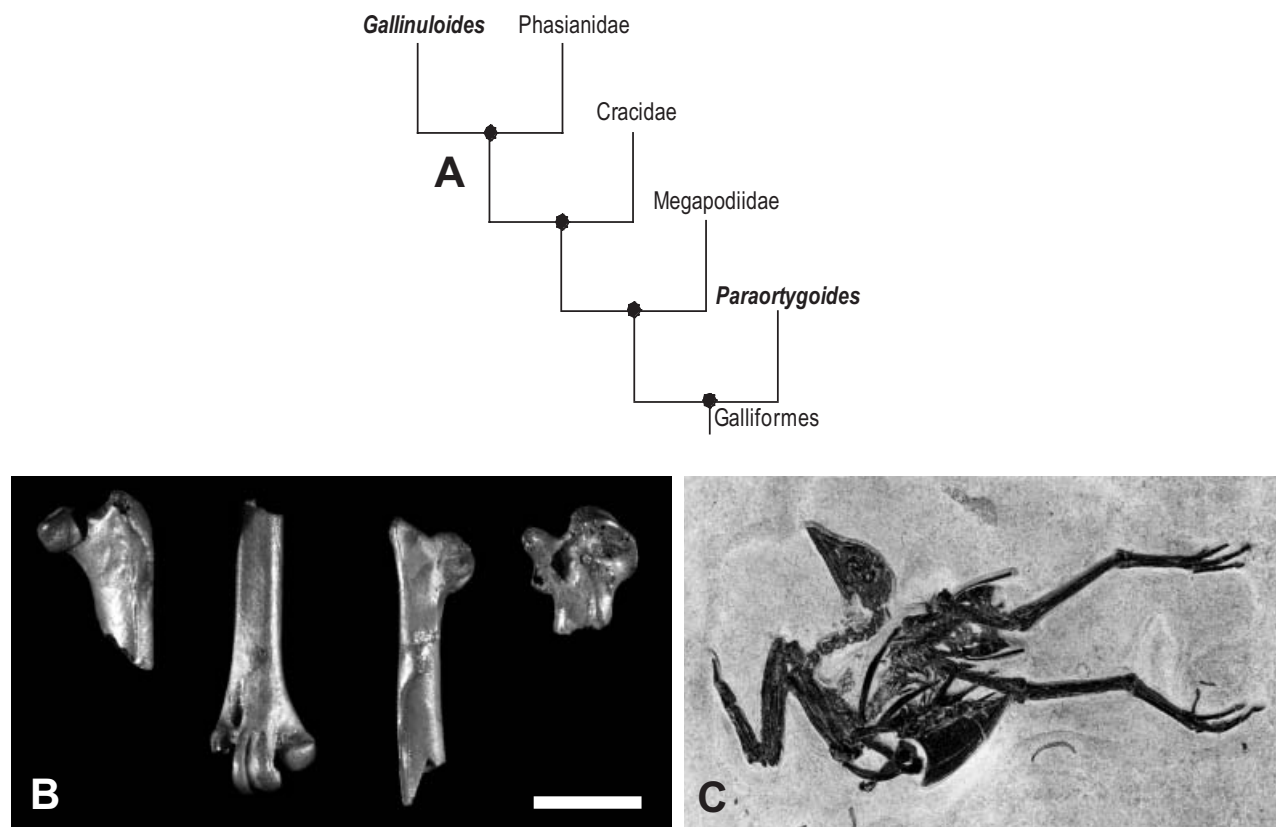

Figure 6. Cartoon to depict consensus relationships among Galliformes ('landfowl') along with some selected fossil material (based on Dyke, 2003b and Dyke *et al.*, 2003): A, hypothesis for the phylogenetic positions of the Lower Eocene (*c*. 55 Mya) taxa *Gallinuloides* and *Paraortygoides*; B, fossil elements of *Paraortygoides* from the Lower Eocene London Clay Formation of England (see Dyke & Gulas, 2002); C, holotype specimen of *Gallinuloides wyomingensis* from the Lower Eocene Green River Formation of Wyoming (North America) (Dyke, 2003b). Scale bar = 10 mm.

Dyke & Gulas (2002) as part of their description of the London Clay taxon *P. radagasti* by use of osteological cladistic analysis (Fig. 6). All of these fossil taxa have been used as the basis for molecular clock calibrations (van Tuinen & Dyke, 2004); they are well-known anatomically and have been phylogenetically constrained within Galliformes (Fig. 6).

Procellariiformes and Pelecaniformes

These birds were traditionally grouped together in the large assemblage of totipalmate swimmers (toes connected by a web; see Sibley & Ahlquist, 1990), but have more recently been divided into the two orders Pelecaniformes (e.g. Pelecanidae, Fregatidae, Sulidae and related birds) and Procellariiformes (e.g. Diomedeidae, Procellariidae, Hydrobatidae) (see Mayr, 2003a). Recent cladistic analyses of morphological features, however, suggest that the two groups are monophyletic when considered together but with the inclusion of two ciconiform taxa, *Scopus* and *Balaeniceps* (e.g. Siegel-Causey, 1997; Mayr, 2003a). Genetic data bearing on these groups show a polyphyletic origin of pelecaniformes, owing to inclusion of ciconiid, ardeid, threskiornithid, spheniscid and gaviid taxa inside this large grouping (van Tuinen, Sibley & Hedges, 2000; Cracraft *et al*., 2004). Once again, fossils from the Mesozoic have been described and referred to this group (e.g. Brodkorb, 1964; Olson & Parris, 1987; Kurochkin, 1995; Hope, 2002; Parris & Hope, 2002), but this material is all incomplete and fragmentary.

The fossil record of these birds in the Tertiary is not generally very well known, but a number of well-preserved representatives have been described from the lowermost Eocene. The best preserved specimens have been referred to the taxon *Limnofregata* described as a putative frigatebird (Fregatidae) from the Lower Eocene Green River Formation of Wyoming (Olson, 1977), but this material has yet to be considered within a cladistic framework incorporating osteology of extant taxa. Another primitive and well-preserved pelecaniform bird, *Prophaethon*, is known from the Lower Eocene London Clay Formation of the UK (Andrews, 1899; Harrison & Walker, 1976; Olson, 1985). Consideration of this taxon with respect to the phylogenetic relationships of the extant pelecaniforms suggests that it is the sister group to the traditional pelecaniforms (Dyke, 2000), but genetic results indicate that more taxon sampling is necessary to verify its exact position. *Prophaethon* remains the only fossil representative of this 'order' that has been considered in this way.

Breaking these two traditional orders down into constituent subdivisions, it is generally fair to say that 'Procellariiformes' have a poor fossil record (their characteristically 'tubular' nostrils being one possible synapomorphous feature). The Late Cretaceous and Palaeocene taxa *Tytthostonyx* (Olson & Parris, 1987) and *Eopuffinus* (Nessov, 1986), respectively, have been referred to this clade but comprise just single, incomplete bones (Hope, 2002). The earliest definitive record for this clade of Neornithes founded on more than a single skeletal element is from the early Oligocene: Mayr, Peters & Rietschel (2002) have recorded well-preserved specimens of the taxon *Diomedioides*, that has been constrained by use of clear osteological characters (Mayr *et al*., 2002).

Sphenisciformes

The available literature on fossil penguins (Sphenisciformes) is voluminous, mainly thanks to the work of G. G. Simpson (e.g. Simpson, 1946, 1975, 1979). Osteologically these birds are extremely distinctive and their fossil record is known to extend back to the middle Eocene at least, and possibly as far back as the late Palaeocene (*c*. 59 Mya) (e.g. Fordyce & Jones, 1990); currently, the earliest known specimens are known from Seymour Island, Antartica and New Zealand (Fordyce & Jones, 1990). [See Simpson (1946, 1975), Olson (1985) and Fordyce & Jones (1990) for further discussions of fossil penguins.] The systematic placement of these birds remains somewhat uncertain; some workers consider that Sphenisciformes are derived directly from within Procellariiformes (see below; Fürbringer, 1888; Simpson, 1946), whereas others have opted for an origin distinct from other clades of Neornithes (Lowe, 1933; Simpson, 1946). Molecular data support the former with close ties to loons and tubenoses (Ho *et al*., 1976; van Tuinen *et al*., 2001). In general, the fossil composition and relationships within penguins remain problematic: no single cladistic analysis comprising the extant taxa (let alone encompassing the known fossil material) has ever been conducted. The phylogenetic relationships of extant and fossil members of Sphenisciformes remains one clear area for work in the future.

Podicipediformes

Grebes (Podicipediformes) are an interesting clade of modern birds whose monophyly in the traditional sense has rarely, if ever, been doubted. Their relationships within the framework of the neoavian birds remains unresolved based on morphology (Zusi & Storer, 1969; Cracraft *et al*., 2004) but genetically form a well-resolved clade with flamingos (van Tuinen *et al*., 2001; Cracraft *et al*., 2004). Podicipediformes have a poor fossil record before the Pleistocene, the oldest known records being from the early Miocene (Svec, 1984). Consequently, the time

of modern radiation within this groups remains somewhat uncertain.

Gaviiformes

Extant loons comprise the traditional avian order Gaviiformes, one of the groups of modern birds with a putative Cretaceous fossil record (Lambrecht, 1928; Brodkorb, 1964; Olson, 1992a; Chatterjee, 1997, 2002). However, with the exception of the putative gaviiform *Polarornis* from Antarctica (see above) no single fossil referred to this clade from the Cretaceous consists of more than a single bone. Taxonomy of fossil loons has additionally borne witness to a great deal of flux of the last century; material has been moved in and out of the order on the basis of reinterpretations of few osteological features (Olson, 1992a; Hope, 2002). No good fossil material for this clade of Neornithes exists that could usefully be used for calibration purposes.

Falconiformes

There has been much historical debate over the strict monophyly of the traditional order Falconiformes (hawks, eagles, falcons and relatives) concerned with the close affinities (or lack thereof) of Cathartidae (New World vultures) and storks (see Sibley & Ahlquist, 1990 for a review). Molecular data have not yet resolved this evolutionary important question (Cracraft *et al*., 2004). However, fossils assigned to this group are numerous and include specimens from the Lower–Middle Eocene of both North America and Europe. On the basis of incomplete postcranial remains from the Lower Eocene London Clay Formation of the UK, Harrison & Walker (1977) placed the taxon *Parvigyps pracecox* close to extant Accipitridae, for example. This specimen, in addition to other incomplete fossil bones from the Lower Eocene deposits (Dyke, 2000) comprise some of these oldest putative records for this order. However, the oldest fossil material including diagnostic skull and postcranial elements is from the Middle Eocene of Messel, Germany (Peters, 1994). No cladistic analysis including both fossil and recent members of Falconiformes has ever been conducted; both the ingroup and outgroup relationships of this assemblage remain unclear.

Gruiformes

Gruiformes, the traditional order comprising sunbitterns, bustards, cranes, rails and their relatives, is another of the groupings of modern birds considered by some workers to have a Cretaceous representation. Kurochkin (1995), for example, referred the Early Cretaceous *Horezmavis eocretacea* to Gruiformes, but later

work (Hope, 2002) has suggested that some of the characters used in this assignment are also seen in more basal ornithurine (nonmodern) birds. In addition to this material, a number of other fragments from the Cretaceous and earliest Palaeocene were, at one time or another, referred within this order (Nessov, 1986, 1992; Olson & Parris, 1987; Hope, 2002). The earliest certain fossil gruiform taxon upon which phylogenetic interpretations have been founded (Livezey, 1998b) is currently the genus *Messelornis* known from the upper Palaeocene of France (Mourer-Chauviré, 1995), the Lower Eocene of North America and the Middle Eocene of Germany (Hesse, 1990). Cladistic analysis of this fossil (Livezey, 1998b) places it close to the extant sunbittern in a highly derived position. This phylogenetic result supports, albeit indirectly, a Cretaceous diversification of crown Gruiformes (Dyke, 2001a).

Charadriiformes

The traditional order Charadriiformes is one of the largest and most speciose of the nonpasserine groupings of modern birds. This clade comprises the gulls, auks, waders, sandpipers, jacanas, godwits, sheathbills, terns, plovers and related birds; collectively termed 'shorebirds', there seems to be little doubt as to the monophyly of this assemblage of related clades (Strauch, 1978; Chu, 1995; G. J. Dyke, M. van Tuinen & D. M. Waterhouse, unpubl. data; Fig. 7). Although these birds have traditionally been afforded the status of their own order (e.g. Wetmore, 1960), the molecular work of Sibley & Ahlquist (1990) placed shorebirds as a suborder within their much larger order Ciconiiformes (Charadrii).

Whatever the specific affinities of birds classified within Charadriiformes, this clade may well have one of the oldest fossil records of any of the neoavian groups based on currently published information. A number of workers have attested to the presence of 'shorebird-like' fossils in the Cretaceous, often considering them within the as yet cladistically untested assemblage 'Gravaculavidae', or 'transitional shorebirds' (see Olson, 1985; Olson & Parris, 1987; Hope, 2002; see below). Taxa referred to this grouping from Cretaceous-age rocks are, however, highly problematic as a result of their incompleteness (Hope, 2002); no single specimen comprising more than a single bone has ever been described from the Cretaceous or shown to have convincing affinities with extant Charadriiformes. A cladistic analysis of osteological characters for these birds has been completed (G. J. Dyke, M. van Tuinen & D. M. Waterhouse, unpubl. data) and a number of well-preserved taxa of early Eocene age have been described from Europe and North America (Mayr, 2000b; Fig. 7). Dating divergences within Charadriiformes is possible on the basis of well-represented fossils considered in combination with extant
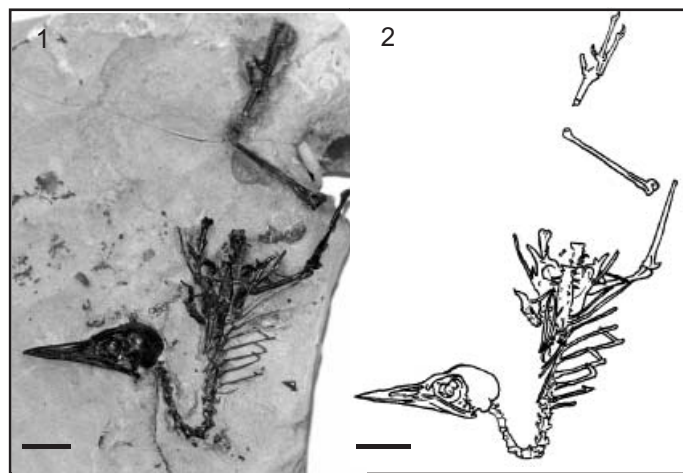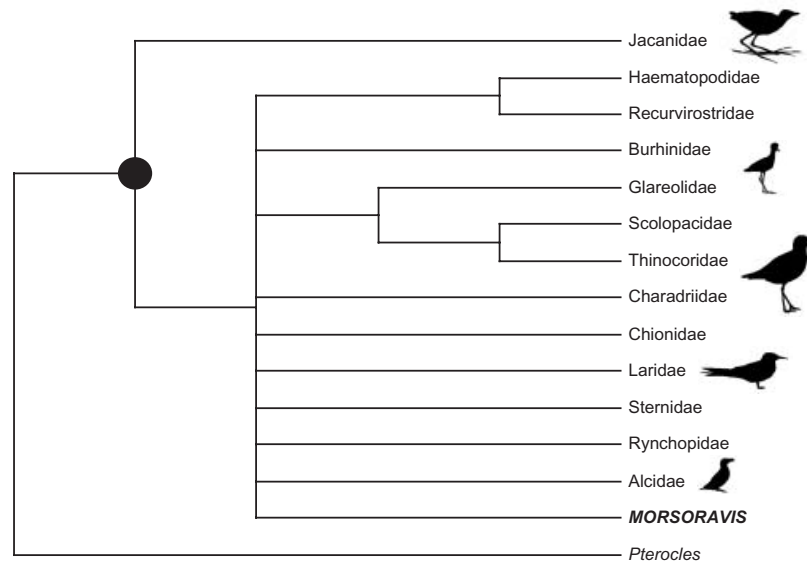
Figure 7. Cartoon to depict consensus relationships among Charadriiformes ('shorebirds') along with the holotype specimen of *Morsoravis sedile*, a new and exceptionally well-preserved fossil from Palaeocene–Lower Eocene deposits in Jutland, Denmark (1–2; G. J. Dyke, M. van Tuinen & D. M. Waterhouse, unpubl. data). The tree is based on various sources; see text for details. Scale bar = 10 mm.

taxa: basal clades within this assemblage date to at least to the basal Eocene and probably earlier (see also Paton *et al.,* 2003; Fig. 7) As highlighted by the fossil material illustrated here (Fig. 7), consideration of the fossil record and relationships of these birds represents an exciting area of current research.

Columbiformes
The avian order Columbiformes comprises extant pigeons and doves along with the extinct dodo and solitaire (Shapiro *et al*., 2002). In addition to these taxa, the problematic sandgrouse (Pteroclidae) also has been associated with Columbiformes (Cracraft, 1981;

Olson, 1985; Livezey & Zusi, 2001), either within this clade or as its immediate sister group. Some workers have suggested that Pteroclidae may represent a link between Columbiformes and their putative sister-taxon Charadriiformes (Sibley & Ahlquist, 1990). In general, this clade of modern birds has a poor fossil record in terms of numbers of specimens. The oldest certain member of Columbiformes, *Gerandia calcaria*, is from the Miocene of France (see Olson, 1985 for discussion of this and other material), although some older but problematic specimens have been described from Lower Eocene rocks. For example, Harrison & Walker (1977) described *Microena goodwini* from the

London Clay as a columbid, but this taxon is a single isolated tarsometatarsus. The time of modern radiation within this group remains unclear.

Psittaciformes

Parrots (Psittaciformes) are an example of an order of modern birds that is certainly monophyletic. An extensive literature that deals with these birds exists and on the basis of a number of features of their postcranial anatomy (in particular their feet), the monophyly of this clade has remained unchallenged for more than a century (see Sibley & Ahlquist, 1990, and Dyke & Cooper, 2000, for reviews). Although there are a number of examples of fossil parrots from the early Eocene and younger (Mourer-Chauviré, 1992; Mayr & Daniels, 1998; Dyke & Cooper, 2000) that have been considered closely related to the extant crown-group (Psittacidae), contention remains with regard to the presence of this lineage in the Cretaceous. Although Stidham (1998) described the incomplete portion of a mandible from the Cretaceous Lance Formation of North America, this fragment is inconsistent in its morphology with both extant parrots and their known Eocene fossil relatives (Dyke & Mayr, 1999; Mayr, 2002a). Molecular data are limited yet suggestive of a Cretaceous diversification among African, Australian and South American parrots (Miyaki *et al.*, 1998). Additional analyses and taxon sampling are badly needed for increased temporal resolution: calibration of the parrot clock has been based on a compromise molecular age for the parrot–galliform divergence (Miyaki *et al.*, 1998; van Tuinen & Hedges, 2004).

Coliiformes

Coliiformes is a very small clade of neornithine birds that comprises the six extant species of mousebirds and their fossil relatives. As is the case with a number of other extant clades of Neornithes, for some unknown reason Coliiformes seems to have had a much larger taxonomic distribution in the Eocene, indeed were more speciose in the past than in recent times. These birds have long been recognized as a distinctive radiation within Neornithes (Pycraft, 1907) as confirmed by the discovery in the early 1990s of a peculiar early clade of mousebirds, the Sandcoleidae (originally classified within a separate order, Sandcoleiformes) (Houde & Olson, 1992; Mayr & Peters, 1998; Peters, 1999; Dyke & Waterhouse, 2001). The two clades Coliidae and Sandcoleidae are now considered to be each other's closest relatives within a single Coliiformes grouping (Mayr & Peters, 1998), both boasting well-preserved fossil representatives from at least early Eocene and younger age rocks (Dyke & Waterhouse, 2001). Although the known Eocene taxa

have recently been evaluated in a cladistic context (Mayr & Mourer-Chauviré, 2004) so that the ingroup relationships of these enigmatic birds are now well known, no single representative of Coliiformes has ever been reported from the Cretaceous. Molecular studies including this group are currently limited; those that do exist provide little resolution perhaps due to the taxon-poor status of this modern group. Several phylogenetic hypotheses have been proposed, but none with convincing support. These include close affinities with no other living clade (Sibley & Ahlquist, 1990), parrots, and galbulid piciforms (Johansson *et al.*, 2001). Regardless of its true phylogenetic position, the mousebird clade is truly ancient. Its current fossil record provides one of the more remarkable glimpses into the early history of any modern bird lineage.

Musophagiformes

The precise composition of this neornithine order is problematic: it is certainly considered to comprise the extant turacos and relatives (Musophagidae) but possibly also the problematic hoatzin, *Opisthocomus*. Debates in the literature with regard to this latter taxon continue, largely because the hoatzin is so bizarre in many aspects of its anatomy that its placement within Neornithes remains controversial. While some workers have relegated this bird to its own monotypic order, Opisthocomiformes (Hudson & Lanzillotti, 1964), others have considered it closely related to either Galliformes (Cracraft, 1981) or Cuculiformes (Hughes, 2000; see below). Whatever the outcome of this debate, the known fossil record of these birds is poor to say the least. Some Lower Eocene fossil material from England initially described by Harrison & Walker (1977) to Musophagiformes has been shown instead to be referable to Lithornithidae by Houde (1988) (see Palaeognathae above), and specimens from the Oligocene of France also first placed within this group are instead referable to cuculids and accipitrids (Olson, 1985).

Cuculiformes

The traditional neornithine order Cuculiformes comprises the cuckoos (Cuculidae) and coucals (Centropidae), as well as possibly the enigmatic hoatzin (see above) (Hughes & Baker, 1999). Some workers have also considered that Musophagiformes should also reside within Cuculiformes; both these orders have a relatively poor fossil record in terms of described specimens. Olson (1992b) has noted the presence of Cuculiformes (the extinct Foratidae) from the lower Eocene of North America and Baird & Vickers-Rich (1997) have referred a single bone from the Palae-

ocene of Brazil to within this order (but see Mourer-Chauviré, 1999) for an alternative interpretation of this specimen). With the exception of some additional specimens from the Oligocene of North America that are possibly cuculiform, the known fossil record of these birds is almost entirely lacking. Dating the basal divergence of this order of modern birds is problematic based on available fossil evidence. Molecular clock analyses suggest a diversification time close to the K–T boundary for the cuckoos and coucals (van Tuinen & Hedges, 2001).

Strigiformes

In contrast to Cuculiformes, the fossil record of owls and their relatives (Strigiformes) is well known. Several well-preserved specimens are known from deposits of early Eocene age and younger (Olson, 1985; Mourer-Chauviré, 1987, 1994; Peters, 1992); the oldest known owl in the literature is from the Palaeocene of North America, but is founded on a single isolated bone (Vickers-Rich & Bohaska, 1976). Although Harrison & Walker (1975) placed several fossil specimens from the Late Cretaceous of Romania within Strigiformes, this material has more recently been shown to have affinities with nonavian theropod dinosaurs (Naish & Dyke, 2004). Again, cladistic analyses of the oldest owl fossils are warranted.

Caprimulgiformes

The order Caprimulgiformes traditionally comprises the oilbird, potoos, nightjars, frogmouths and their relatives, a grouping of primarily nocturnal, insect-eating birds (Sibley & Ahlquist, 1990). These birds have often been considered closely related to the Strigiformes and/or Apodiformes (see below), but their monophyly has recently been called into question (Cracraft *et al.*, 2004). Sibley & Ahlquist (1990) reduced the group to suborders within Strigiformes and Mayr (2002b) has noted that the addition of some fossil taxa to cladistic analyses of this group calls into question some of the traditional features that have been used to unite these birds as a single clade. The fossil members of Aegialornithidae, known on the basis of fossils from the Eocene and Oligocene, once thought to be closely related to Apodiformes (swifts and relatives), have been shown to have ties with some groups within Caprimulgiformes (Collins, 1976; Mayr, 2002b). On the basis of recent osteological cladistic work, some workers have argued that this traditional grouping is likely paraphyletic (Mayr, 2002b). The fossil record of these birds (at least defined subgroups within the traditional order) is, however, exceptional. Caprimulgiformes have had a long temporal presence:

their earliest representatives date from the early Eocene of North America and Europe (Olson, 1987; Mourer-Chauviré, 1998; Mayr, 1999), based on complete, articulated and, in some cases, three dimensionally preserved fossil material. The order has never been reported from the Cretaceous.

Apodiformes

Apodiformes, comprising the swifts and relatives, has formed the subject of some controversy in recent times as anatomists have debated the relationship of these birds to some clades of Caprimulgiformes (see above) and hummingbirds (Trochiliformes). The latter clade has often been subsumed in more traditional classifications (Wetmore, 1960; Cracraft, 1981). Apodiformes are, however, certainly distinct from all other modern birds on the basis of their forelimb and skull anatomy (Cracraft, 1981; Karkhu, 1988; Mayr, 2003b) and have a well-represented fossil record that extends back to at least the early Eocene. Several of the known fossil representatives of this clade have been included within osteology-based cladistic analyses (Dyke, 2001c; Mayr, 2003b), including members of the crown Apodidae (extant and fossil 'true' swifts) and extinct taxa classified within Aegialornithidae (Mayr & Peters, 1999).

Trochiliformes

As outlined above, the only serious debate regarding the placement of the highly morphologically distinctive hummingbirds (Trochiliformes) remains their relationship with Apodiformes. Do these small birds constitute the status of an order in their own right, or are they simply a subclade of Apodiformes? Opinions vary, but since the almost totally nonexistent fossil record of hummingbirds brings into question their relevance (and usefulness) to dating neornithine divergences. Probably as a result of their small size, there are no described fossil records of these birds outside subfossil deposits that have been placed within crown Trochiliformes. We also note that the available molecular data support a clade of Trochiliformes and Apodiformes (Johansson *et al.*, 2001; van Tuinen & Hedges, 2001; Cracraft *et al.*, 2004). Although unsupported by the fossil record, this clade may have started diverging close to the K–T boundary based on molecular clock evidence (van Tuinen & Hedges, 2001).

Coraciiformes

Useful discussion of the fossil record of Coraciiformes is limited because this 'order' is probably an amalgamation of clades lumped together by historical classifications. Coraciiformes (*sensu* Wetmore, 1960) is likely a paraphyletic taxon (see Livezey & Zusi, 2001). Tra-

ditionally, this grouping has been considered to include the kingfishers, todies, motmots, bee-eaters, rollers, ground rollers, hornbills and their relatives; a series of at least eight extant families of disparate birds. As a consequence, assignment of fossil material to within this order has proved an historical problem and a number of extinct clades (e.g. Geranopteridae, Sylphornithidae, Eocoraciidae) have been erected that may or may not bear relevance to the relationships of the extant taxa of 'Coraciiformes'. At this time, and until the relationships of the extant taxa comprising 'Coraciiformes' have been further elucidated on the basis of osteology and genetics, discussion of the known fossil record of these birds is of little value (see Mayr, 1998; for further discussions of the fossil representatives of these disparate birds).

Piciformes

Debate over the relationships and monophyly of Piciformes has centred around the question of whether or not the 'galbuliforms' (i.e. Bucconidae and Galbulidae) are a clade within this order (e.g. Johansson & Ericson, 2003). All the other taxa (i.e. woodpeckers, barbets and relatives) would then comprise the Pici for which monophyly has never really been in doubt. This latter grouping has been placed most often close to the songbirds (Passeriformes) (Olson, 1983; Livezey & Zusi, 2001). The fossil record of these birds extends again to the lowermost Eocene: Mayr, 1998) showed convincingly that material originally described as passerine by Harrison & Walker (1977) from Lower Eocene rocks in England could be referred to Piciformes on the basis of comparisons with exceptionally well-preserved skeletons from middle Eocene rocks in Germany. It is this German material that represents the oldest and best-preserved fossil records for these birds yet known; however, the oldest specimen preserving modern anatomical features (i.e. that can be used to date crown Piciformes) is from the Oligocene of Germany (Mayr, 2001). Some molecular data suggest a grouping of Galbulae and Pici but resolution is yet limited (Ericson, Irestedt & Johansson, 2003). If sister group taxa, the initial divergence of these two clades is clearly ancient (M. van Tuinen, T. A. Stidham & E. A. Hadly, unpubl. data).

Passeriformes

Although perching songbirds (Passeriformes) comprise by far the most diverse of the extant clades of birds (some 90% of living avian diversity by numbers of species), and form an unquestioned clade (on the basis of both morphological and molecular data), the known fossil record of this group is limited. Perhaps as a result of their small size and arboreal habitats, the oldest certain fossil record for Passeriformes is from the Oligocene; Mourer-Chauviré, Hugueney & Jonet

(1998) reported the presence of good fossil material of these birds from the Oligocene of France and they are well known in the rock record from the Miocene and younger (Feduccia, 1996).

There are no records of fossils from the Mesozoic ever having been assigned to this order. The oldest published occurrences of Passeriformes come from deposits of early Eocene age; Harrison & Walker (1977) described the taxon *Primoscens* on the basis of an incomplete carpometatacarpus from the Lower Eocene London Clay and Boles (1995, 1997) referred some material from the Lower Eocene of Riversleigh (Australia) to the order (i.e. an incomplete carpometacarpus and distal end of tibiotarsus). All of these workers cited the presence of an intermetacarpal process on the carpometatacarpus in support of their referrals, a character that is seen in a number of other groups of modern birds (including fossil and Recent Piciformes; e.g. Mayr, 1998). This incomplete material is, in fact, referrable to the piciform family Primoscenidae described on the basis of complete specimens from Messel and the London Clay by Mayr (1998). Passeriformes arguably present the largest discrepancy between fossils and molecules in terms of their time of radiation. Both molecular clock analyses (van Tuinen & Hedges, 2001; M. van Tuinen, T. A. Stidham & E. A. Hadly, unpubl. data) and biogeographical interpretations (Cracraft, 2001; Barker *et al.*, 2002) suggest a Cretaceous diversification for this large and diverse clade.

TRANSITIONAL SHOREBIRDS AND THE PHYLOGENETIC FUSE

In a series of publications over the course of the last eight years, Feduccia (1995, 2003) has expanded on the hypothesis that the fossil record of modern birds is consistent with the view that the bulk of the diversification of the modern orders and families occurred in the aftermath of the K–T event. This hypothesis has been referred to as the 'big bang' or 'explosive evolution' model and depends on a literal interpretation of the Tertiary fossil record of Neornithes (Feduccia, 1996; but see Dyke, 2003c; van Tuinen *et al.*, 2003). Feduccia (2003) has stated that 'the fossil record provides evidence that modern birds represent an explosive Tertiary radiation, following the Cretaceous–Tertiary cataclysm, and their origins are almost 50 million years younger than that predicted by molecular studies' [sic]. Accounting for published records of Neornithes from the Cretaceous, he has argued that these fossil taxa can be classified within a small number of putatively related clades termed 'transitional shorebirds' (i.e. palaeognaths, Charadriiformes, Anseriformes): 'a near total demize of archaic birds occurred at the K–T boundary, with a rapid reorgani-

zation and explosive early Tertiary evolution from a bottleneck of modern ornithurine morphological types, perhaps involving "transitional shorebirds" ' (Feduccia, 2003). However, because this hypothesis is non-phylogenetic, interpretation of the early Tertiary fossil record is problematic and vague with regard to the concept of Cretaceous 'transitional' forms (Livezey, 1997; Paton *et al.*, 2002). Extant and fossil shorebirds (i.e. representatives of the order from Lower Eocene deposits of Europe and North America; see above; Fig. 7) *per se* form a well-defined clade, classified within Charadriiformes on the basis of clear, albeit few (Chu, 1995), shared-derived osteological characters (Strauch, 1978; Mayr, 2000b; G. J. Dyke, M. van Tuinen & D. M. Waterhouse unpubl. data); Feduccia (1996) lumps a number of other birds such as ibises, flamingos, grebes, loons and gruids nominally within his 'transitional shorebird' assemblage. However, there is currently no morphological or genetic evidence for these assignments (Dyke, 2003a; van Tuinen *et al.*, 2003). As we have discussed, the uncontroversially most basal clades of neornithine birds are Palaeognathae, Anseriformes and Galliformes; although some Cretaceous records have been referred to these groups, the large and disparate clade Charadriiformes (shorebirds) is certainly a subgroup of Neoaves (Groth & Barrowclough, 1999; van Tuinen *et al.*, 2000; Paton *et al.*, 2002). Even given the phylogenetic problem with the 'transitional shorebird' hypothesis, there is currently little good character evidence bearing on the affinities of the Cretaceous neornithine fossil record. Feduccia (2003) deals with fossils described from the Cretaceous since 1995 either by ecological modification of his original concept of 'transitional shorebirds' or by noting that some other modern clades also survived the extinction as well (palaeognaths, Anseriformes; Feduccia, 2003). It is unclear as to whether he is now suggesting that ancestral character states for Neoaves are 'shorebird-like' or are to be found within other clades such as Galliformes and Anseriformes.

In addition to clear phylogenetic problems with a 'big bang' interpretation of the diversification of Neornithes, the presence of 'mosaic fossils' in the Eocene is continually cited as additional support for this hypothesis (Olson, 1985; Feduccia, 1996, 2003). Such taxa have appeared in the literature in the form of fossils such as *Presbyornis*, cited as morphologically intermediate (and therefore a link) between ducks (Anseriformes) and flamingos (Phoenicopteridae) (Olson & Feduccia, 1980a, b). Phylogenetic assessment of fossil material pertaining to this taxon has shown *Presbyornis* (and related genera) to be derived within Anseriformes close to the divergence of true ducks, Anatidae (Livezey, 1997, 1998a; Ericson, 1999; Kurochkin *et al.*, 2002). A link between such disparate avian groups as

ibises, shorebirds and ducks is not supported by the fossil record, molecular or morphological evidence (see van Tuinen *et al.*, 2001; Paton *et al.*, 2002).

From an ecological point of view, there is also no evidence for shorebird-like ecology and morphology in the earliest members of Neornithes. None of the known basal groups of Galliformes or Anseriformes approach modern shorebirds in their known attributes and few of them have been found in near-shore habitats (Hope, 2002). The primitive neornithine ecology, behaviour, and morphology are perhaps best reflected in today's tinamous: chicken-sized forest dwellers and open grassland browsers that fly with little stamina yet with tremendous power in taking off from the ground when approached by predators. Fossil evidence indicates that the ancestors to modern ratites were smaller and capable of only limited flight (*Lithornis*). The ancestral ratites, according to *Palaeotis*, suggest that they were forest dwellers (like today's cassowaries and kiwis) before becoming cursorial. The most primitive living anseriform and galliform lineages, respectively, the screamers, currassows, and megapodes, also fit this pattern and are nonaquatic (van Tuinen, 2002).

TEMPO AND MODE OF MODERN BIRD DIVERSIFICATION

One remaining issue germane to all discussions presented above is the question of how we define 'evolutionary radiation' (Fig. 3). This broad term refers to the rapid appearance of both morphological and ecological characters seen in birds alive today and as a consequence refers to the divergences of the crown group taxa. Crown group taxa form the basis for both historical classifications and recent analyses of avian relationships and diversity; characters defined and formulated on the basis of living taxa therefore are not necessarily relevant to the consideration of isolated fossil taxa unless of course such taxa are included within the cladistic analysis a priori. To date, cladistic analyses dealing with clades of extant birds have largely excluded data drawn from the fossil record; those that have included representatives from the early Tertiary (e.g. *Lithornis*, *Palaeotis*, *Presbyornis*, *Gallinuloides*, *Messelornis*; summarized in Dyke, 2001a, 2003a; Chiappe & Dyke, 2002) have been able to constrain the origin and diversification of the superordinal clades Palaeognathae, Neognathae and Neoaves, and the orders Anseriformes, Galliformes and Gruiformes to the Cretaceous (Fig. 3).

Separate to the use of actual fossil records as terminals in cladistic analyses, most molecular clock studies have gone as far as to strongly support Cretaceous originations (in terms of estimated ages) for the bulk of the modern bird orders (excluding perhaps several traditional aquatic orders; M. van Tuinen, T. A.

Stidham & E. A. Hadly, unpubl. data). The findings of these studies (calibration problems notwithstanding) are not currently incongruent with the fossil record for at least the clades Struthioniformes, Galliformes, Anseriformes and Gruiformes. However, limited genetic data exist on how soon diversification took place after origination and the early Tertiary fossil record currently provides a better representation at this level (see above). An ongoing molecular investigation of the DNA–DNA hybridization tree from Sibley & Ahlquist (1990) is in progress by one of us (M. van Tuinen, T. A. Stidham & E. A. Hadly, unpubl. data). This data set is being used to provide a first detailed look at both origination and diversification times within many major bird lineages. Preliminary findings indicate large-scale temporal consensus between fossil and molecular estimates for family diversifications, that the majority of ordinal diversification took place in the earliest Tertiary, that some orders diversified in the Mesozoic (e.g. Galliformes, Struthioniformes, Gruiformes and Passeriformes), and that all cladogenesis uniting different orders (*sensu* Sibley & Ahlquist, 1990), including the diversification of Neornithes into palaeognaths and neognaths, likely took place in the Mesozoic. Several parts of the molecular neornithine tree appear to indicate explosive radiations (i.e. initial origination followed much later by rapid diversification, with no intermediate cladogenesis preserved in modern taxa). However, other groups show more gradual evolution. This new idea that the evolution of modern birds appears to be sometimes gradual and sometimes explosive presents a viable and interesting alternative to those end-point models already proposed for the mode of bird evolution. The neornithine fossil record (at least at face value and by use of the described fossil record) supports the scenario of one, perhaps few, large biological radiations (Feduccia, 1995, 2003). Alternatively, some genetic studies have concluded that the Mesozoic age of many modern lineages supports a more gradual diversification (Paton *et al.*, 2002). That the truth may lie in between the two end-point models for diversification (i.e. fossil record vs. molecular clocks) should not come as a surprise as even within a single lineage (e.g. horses) a mixture of gradual and explosive evolution has been demonstrated (McFadden, 1992). New molecular studies drawing on taxon-rich sequence data sets for birds, in combination with more and better constrained fossil records, will allow us to move beyond the current stalemate (*contra* Feduccia, 2003).

CONCLUSIONS AND PROSPECTUS

The goal of current research must be the continued development of an accurate evolutionary timescale for modern birds, one that can accurately combine the use of fossils with molecular methods. However, in order to achieve this goal, considerably more sequence data for many more birds will be required in addition to more, better-constrained fossil discoveries. The discovery and description of well-preserved fossil taxa is not enough: much work remains to address the relationships of the existing neornithine fossil record within the context of morphological and molecular phylogenetic analyses for the extant clades of birds. We note, however, that a corollary paramount to increased research effort on both these fronts is the development of a morphological framework for Neornithes that includes fossil taxa. Well-preserved fossil taxa are known, but in many cases their precise placements within Neornithes, in general, and Neoaves, in particular, remain questionable on the basis of current morphological data.

The quality of the Tertiary fossil record of modern birds is well known, and continues to reveal an abundance of taxa that appear to display 'mosaics' of morphological characters. The importance of these taxa cannot be understated because there is no doubt that many of them will be relevant to testing the validity of many of the 'traditional' higher taxa of birds. Relatively few Late Cretaceous records of Neornithes have been described to date – those that have are based on incomplete and often fragmentary single skeletal elements – whereas remains from the lowermost Tertiary are currently much better represented. Key fossils (such as *Polarornis* from the Cretaceous) are known but their placements within the neornithine topology currently remain equivocal. An integrated approach to the relationships of Neornithes, including information from the morphology of fossils and extant birds, as well as their molecular makeup, will be required to resolve the timing of evolutionary diversification of this major vertebrate group. We note that, at this point, resolution at this level has been achieved in the case of just a few of the basalmost neornithine groups, in particular Palaeognathae, Anseriformes and Galliformes. At best, fossils present maximum or minimum age-constraints for clades. In combination with molecular clocks that may be, at best, local optima, but such taxa should be used in future alongside key events in Earth's history to place constraints on our calibration estimates.

NOTE ADDED IN PROOF

Since we wrote this review paper, two additional and important papers by Gerald Mayr have been published – a remarkable description of a new fossil hummingbird (*Eurotrochilus inexpectatus*) from the Oligocene (30 Mya) of Germany (Mayr, 2004) and a new representative of the fossil galliform *Gallinuloides wyomingensis* (Mayr & Weidig, 2004) from the Lower Eocene (55 Mya) Green River Formation of the USA. Both these new fossils have implications for neornithine divergences; they will, however, require assessment by use of cladistic methods.

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