

There are two principal kinds of evidence for dating events in evolutionary history: fossils and molecular clocks. Where both kinds of analysis can be applied to the same phylogenetic group, however, the estimated dates do not always agree. In particular, fossil data and molecular clock analyses conflict about the times when the great radiations of modern birds and mammals took place. In both instances, the molecular clock analyses locate the periods of diversification much earlier than the fossil evidence. Below, Michael J. Benton and Simon Easteal debate which kind of evidence is most likely to be correct.

Early origins of modern birds and mammals: molecules vs. morphology

Michael J. Benton

Summary

Recent claims from molecular evidence that modern orders of birds and mammals arose in the Early Cretaceous, over 100 million years (Myr) ago, are contrary to palaeontological evidence. The oldest fossils generally fall in the time range from 70–50 Myr ago, with no earlier finds. If the molecular results are correct, then the first half of the fossil record of modern birds and mammals is missing. Suggestions that this early history was played out in unexplored parts of the world, or that the early progenitors were obscure forms, are unlikely. Intense collecting over hundreds of years has failed to identify these missing fossils. Control experiments, in the form of numerous Cretaceous-age fossil localities which yield excellently preserved lizards, salamanders, birds, and mammals, fail to show the modern forms. The most likely explanation is that they simply did not exist, and that the molecular clock runs fast during major radiations. *BioEssays* 21:1043–1051, 1999. © 1999 John Wiley & Sons, Inc.

Introduction

Molecular and morphological data on evolutionary patterns have apparently conflicted a number of times. How are such conflicts to be resolved? Sometimes one side is clearly right, and the other wrong, as in the debate over human origins. In the 1960s and 1970s, based on the fossils palaeontologists believed that humans diverged from their ape relatives some 15–20 Myr ago. Evidence from protein sequences of haemoglobins and myoglobin, however, pointed to a date of divergence nearer to 5–7 Myr ago. Eventually this dispute was settled in favour of the molecular conclusions by closer studies of the fossil evidence: the apparent ancient human fossils turned out to be either fossil apes or side branches from the common evolutionary line that led to both humans

and apes. This, and subsequent debates have generally been resolved. Two major current phylogenetic questions are hotly debated, however: the origins of Metazoa (multicelled animals), and the origins of modern bird and mammal groups. In both cases, molecular evidence suggests that the point of origin is twice as old as the oldest known fossils. This implies either that half the fossil record of animals, and of modern birds and mammals, is cryptic, or that the molecular conclusions are flawed. Either way, there is a strong challenge to the integrity of molecular phylogenetic analytical techniques, or to claims by palaeontologists that the history of life can be divined from the fossil record. The question of metazoan origins has been debated already in *BioEssays*.^(1,2)

The idea of an earlier-than-expected date of radiation of modern bird and mammal groups has been suggested previously on the basis of molecular evidence.^(3,4,5) However, new more extensive studies by S. Blair Hedges and colleagues^(6,7) and by Alan Cooper and colleagues^(8,9) have certainly put the Cretaceous cat among the Cretaceous pigeons.

Funding agencies: Leverhulme; Grant number: A/182/FK; NERC; Grant number: GR9/03252.
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The new studies all indicate that modern bird and mammal orders radiated deep in the Cretaceous, at least 100 Myr ago, compared to the earliest fossils which are 70–50 Myr old. The first study⁽⁶⁾ used a number of nuclear and mitochondrial genes to compare modern bird and mammal lineages, finding a mean branching time of about 100 Myr ago, long before the widely accepted origin times in the latest Cretaceous, or, more typically, in the Paleogene, ranging from 70–50 Myr ago. Cooper and Penny⁽⁸⁾ come to similar conclusions for modern bird groups, based on mitochondrial and nuclear genes of 16 avian orders. They estimate that the 16 modern orders originated some 90–210 Myr ago, with a mode about 110–140 Myr ago, based on calibrations from eight oldest-known bird fossils from the Paleogene. Kumar and Hedges⁽⁷⁾ used 658 nuclear genes representing 207 vertebrate species to confirm the early dates of origin of modern bird and mammalian orders. In particular, they argued that at least five major mammalian groups, edentates, sciurognath rodents, hystricognath rodents, paenungulates (elephants and relatives), and archontans and ferungulates (bats, primates, carnivores, ungulates, and relatives), originated in the Early Cretaceous, over 100 Myr ago. Their molecular estimates for other branching points within vertebrate history match fossil-based estimates closely, and it is only the dates of origin of modern bird and mammal groups that show such a discrepancy between molecular and fossil dates.

These dramatic claims are one of many challenges to “traditional” morphology-based views. Past experience does not indicate which way the debate will go, whether the molecular challenge, or the status quo, will be upheld. Nonetheless, debates such as these have often been heated, and it is worth reviewing the current position.

Molecules vs. morphology: is there a real dispute?

The debate in the 1960s and 1970s over molecular and palaeontological evidence of human origins set the scene for a rumbling dispute that surfaces from time to time, and has been characterized as “molecules versus morphology”. In other words, according to some commentators, when there is conflict between molecular studies of evolutionary patterns and morphological, or palaeontological, studies, one side has to be right and the other wrong. In fact the more warlike have sometimes claimed that one method, molecular or morphological, is *always* right, and the other *always* wrong. Claims of this kind have been strongest for the hegemony of molecular evidence over morphological. Such claims range from a simple preference for molecular conclusions to statements that morphological and palaeontological studies of phylogeny should be rejected outright a priori if they conflict with molecular conclusions.⁽¹⁰⁾ It is hard to find such rejections of the value of molecular characters in phylogeny reconstruc-

tion, although many defences of the usefulness of morphological and palaeontological data on phylogeny have been made.^(11–13)

Outright rejection of morphological, or palaeontological, evidence on phylogeny is clearly unsupported by evidence or experience. Morphological characters are different and essentially independent from molecular characters, they can be assessed from extinct organisms,^(11,13) they are subject to natural selection and may pinpoint branching points in evolutionary trees, they can be assessed readily based on living or dead specimens, all the morphological characters in an organism may be assessed, there are few limits to the level of detail that can be achieved, and the characters can be assessed for population and intraspecific variation. Morphological data are, of course, far from perfect. Disputes over interpretation and character coding, and lack of congruence between competing cladograms, show that.

Experience shows that molecular evidence is also not perfect. Molecular phylogenies often conflict with each other, for example in the case of the radiation of modern placental mammal groups,^(14–21) the monophyly of rodents,^(18,20,22) the validity of Paenungulata,^(17,19,23) or the relationships of the whales.^(24,25) Indeed, molecular results may sometimes be nonsensical, such as the finding that monotremes fall squarely among placental mammals.⁽²⁶⁾ In cases of conflict and error, molecular trees suffer many of the same methodological problems as morphological, for example the choice of taxa in the ingroup, the choice of outgroup taxa, the choice and definition of characters, and the choice of algorithm. Results obtained using either technique may be confused by problems of convergence, long branch attraction, and rapid splitting of lineages (star phylogenies). In addition, special features of molecular phylogeny reconstruction cause problems: variable rates of substitution at different sites, differential rates of transitions and transversions, and multiple substitutions at sites.^(27,28) All can be corrected for, but such corrections are debated, and cannot be tested independently.

The obvious conclusion is the most exciting one, that both morphological and molecular data have unique properties, and both forms of data are equally valid in attempting to determine the true pattern of phylogeny, a view echoed by most participants at two meetings on the subject.^(29,30) If both sets of data are permitted, then biologists have at their disposal two essentially independent ways of reconstructing history. If one character type is rejected a priori, or even treated as subsidiary, then the possibility of assessing congruence between morphological and molecular trees is also rejected. The fact that morphological and molecular trees generally agree shows that cladistic and molecular methods do work. The fact that both approaches produce trees that generally agree with the order of fossils in the rocks^(31,32,33) confirms the validity of the techniques. Assessment of 206

morphological and molecular trees of mammals showed good congruence with stratigraphic data, and that neither morphological nor molecular trees were uniformly better or worse than the other.⁽³³⁾

The improbability that half the fossil record is missing

According to fossil evidence, modern bird⁽³⁴⁾ and mammal⁽³⁵⁾ orders originated mainly in the post-Cretaceous. Oldest representatives of nearly all orders date from the interval 65–50 Myr ago, in the Paleocene and early Eocene. Isolated records of older fossils have been reported, but these are few and far between, and some of them are disputed.

Among birds, numerous examples of modern orders have been reported from the Cretaceous, but most of these have been disproved (wrong identification or mis-dating). The only currently secure record is a flightless bird from the latest Cretaceous in southern France.⁽³⁶⁾ Other recent records from the Maastrichtian (latest Cretaceous) include a putative parrot from Wyoming, USA,⁽³⁷⁾ and a number of supposed shorebirds, ducks, and seabirds from New Jersey, USA.⁽³⁸⁾ The parrot record is based on a single specimen supposedly representing a parrot lower jaw, but it lacks parrot synapomorphies.⁽³⁹⁾ The diverse avifauna from New Jersey, the best evidence of Cretaceous birds, comes from the Hornerstown Formation, now re-dated as early Paleocene.⁽⁴⁰⁾ Other records of modern birds from the Cretaceous are dubious in the extreme.⁽³⁴⁾ Cooper and Fortey⁽⁹⁾ note that “unexpectedly advanced birds” have been found recently in the Early Cretaceous of Spain and China, but this is a mis-statement of the evidence: these specimens are not members of modern orders, and they lie midway between the older *Archaeopteryx* and modern birds, as was predicted from cladistic studies.⁽⁴¹⁾

There have been more reports of modern mammalian orders in the Late Cretaceous, but none of these even approaches an age of 100–120 Myr, and most of them do not stand up to close scrutiny. The great majority of modern mammalian orders definitively arose in the early Tertiary,⁽³⁵⁾ with no record of any Cretaceous fossils. David Archibald has confirmed this, in a recent report:⁽⁴²⁾ 15 of the 18 modern orders of placental mammals appeared in the first 16 Myr of the Tertiary, and two (Macroscelidea, Tubulidentata) appeared later. The only modern mammalian order with a Cretaceous origin is Insectivora (or Lipotyphla), with late Maastrichtian records from Wyoming (the geolabid *Batodon*). Other purported latest Cretaceous insectivores, such as *Otlestes* and others from Uzbekistan, are not members of the modern order (J.D. Archibald, pers. comm., 1999). Several authors^(6–9) have cited other purported Late Cretaceous records of modern mammalian groups, such as the Archonta, with a possible latest Maastrichtian record from Montana, the paromyid or dermopteran *Purgatorius*, and the Ungulata, with Campanian records from Uzbekistan and Kazakhstan

(the zhelestids).⁽⁴³⁾ Both of these are incorrect records, however, the oldest specimens of *Purgatorius* are Paleocene in age, not Cretaceous, and the zhelestids are not ungulates, but a sister group of ungulates, belonging to a wider taxon termed the Ungulatomorpha.⁽⁴³⁾

The fossil record of Cretaceous birds and mammals offers little comfort for those who believe that modern bird and mammal orders radiated more than 100 Myr ago. It is critical to be clear about what is being claimed, and to deal with a semantic point that has led to some confusion. Systematists accept the reality of clades, but of course the names and categorical ranks assigned to any clade are arbitrary. So does it matter whether zhelestids are members of the Order Artiodactyla, or the Superorder Ungulata, or the Infracohort Ungulatomorpha, or whatever? It does, but not in a strictly semantic manner. In this debate, claims are being made about the timing of branching of specific clades. It is not enough to cite generalized basal placental mammals from the Cretaceous. In support of the new molecular assertions, demonstrable members of the modern orders, displaying definitive morphological characters of those orders, must be found: not a Late Cretaceous ungulatomorph, but a Late Cretaceous artiodactyl or perissodactyl. A recent case in point is the report⁽⁴⁴⁾ that the mammal *Deltatheridium* from the Santonian-Campanian (87–73 Myr ago) of Mongolia is a close relative of marsupials. Is this evidence for the radiation of marsupials low in the Cretaceous? Of course not. *Deltatheridium* is a primitive outgroup to Marsupialia, and no member of crown-group Marsupialia has yet been found in the Cretaceous.⁽⁴⁴⁾

The fossil record looks complete enough to dispute the recent claims^(6–8) that modern bird and mammal orders radiated early in the Cretaceous. To accept these claims implies an unknown Cretaceous fossil record. This is a probabilistic argument, but it is equivalent to assessing the probability or improbability that, at some time in the future, palaeontologists ought to find Early Cretaceous parrots, penguins, elephants, and guinea pigs.

A first response has been given by Bleiweiss⁽⁴⁵⁾ who used gap analysis to show that it is most unlikely that modern bird orders had fossil records extending back into the Cretaceous, and certainly not into the Early Cretaceous. He chose three modern bird orders, the Strigiformes (owls), Caprimulgiformes (goatsuckers), and the Apodiformes (swifts, hummingbirds), and documented all known fossils in each order worldwide. The oldest known fossils in each of the three orders fell within a narrow time band in the late Paleocene and early Eocene, from 58–54.5 Myr ago. Fossils in each of the orders have been reported from some 20–30 separate horizons from the date of these oldest fossils to the present day (Fig. 1).

The technique of gap analysis used by Bleiweiss is an intuitive way to estimate possible unknown range extensions.

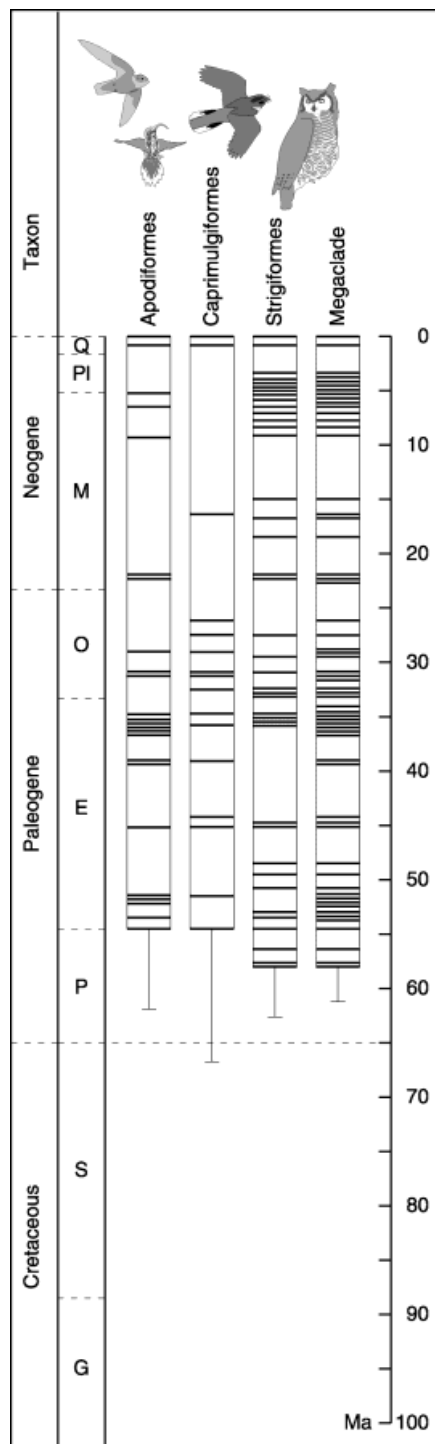


Figure 1. The known fossil record of modern bird groups gives no indication that fossil finds can be expected in the Cretaceous. Based on the distribution in time of known fossils of three modern bird orders, the apodiforms (swifts and hummingbirds), caprimulgiforms (goatsuckers), and strigiforms (owls), confidence intervals (95%) are confined mainly to the Paleogene (early Tertiary), with just one barely creeping into the latest Cretaceous. The “mega-clade” consists of all three orders summed together. The levels of known finds are indicated by horizontal bars (which may represent one find or many dozens of the same age). The more closely spaced the known finds, the shorter the confidence interval. G, Gallia; S, Senonian; P, Paleocene; E, Eocene; O, Oligocene; M, Miocene; Pl, Pliocene; Q, Quaternary. Based on data in Ref. 45.

It is based on the common-sense assumption that if fossils are known from many geological horizons within a known stratigraphic range, then it is likely that very much older (or younger) fossils will not be found. Potential range extensions, at a particular probability level, will be small. If, on the other hand, fossils are scattered sparsely through a known range, it is likely that unknown fossils may occur far below the known oldest fossil (or far above the known youngest fossil, for an extinct group). The method of gap analysis is a statistical expression of this intuitive assumption, where the probability, p , is the confidence level (say, 0.95) that a hypothetical interval added to a known range will include the true stratigraphic range,

$$P = 1 - (1 + \alpha)^{-(n-1)}$$

where α is the confidence interval expressed as a fraction of the observed stratigraphic range, and n is the number of known fossiliferous horizons.⁽⁴⁶⁾ The method was developed to deal with local rock sections, but it may be applied to global examples of this kind,⁽⁴⁷⁾ providing that the distribution of known fossiliferous horizons within the overall known range is random and independent.⁽⁴⁸⁾

In the case of birds, Bleiweiss tested for randomness, and calculated that the maximum possible range extensions, based on the known fossil records of the owls, goatsuckers, and swifts, would hardly even take these orders into the Cretaceous, let alone the Early Cretaceous. The 95% confidence intervals estimated for the base of each of the three ranges were 62 Myr for swifts, 67 Myr for goatsuckers, and 63 Myr for owls. When all three groups were combined, producing a more densely sampled composite record, the range extension, at 95% confidence, was back to only 61 Myr. The figures can be modified to test for the possibility of an earlier origin. Bleiweiss⁽⁴⁵⁾ found that the confidence level that the three orders of modern birds arose after the end of the Cretaceous is over 99%, and virtually 100% for a Late Cretaceous origin of the common ancestor of all three orders.

In opposition to these findings, it could be argued that there are fossils out there waiting to be found. It is easy to dismiss the fossil record as seriously, and unpredictably, incomplete. For example, certain groups of organisms are almost unknown as fossils, so why shouldn't large swathes of the Cretaceous vertebrate fossil record remain unsampled? This kind of argument cannot be answered conclusively. However, an argument based on effort can be made. Palaeontologists have been searching for fossils for years and, remarkably, very little has changed since 1859, when Darwin⁽⁴⁹⁾ proposed that the fossil record would show us the pattern of the history of life. By the middle of the nineteenth century, the oldest bird, *Archaeopteryx*, had been identified, and fossil mammals had been reported from the Middle Jurassic of England. Since then, numerous claims of older birds have been made, but these have not gained accep-

tance. The fossil record of mammals has been pushed back 40 Myr to the Late Triassic. No one has yet found a fossil that was wildly out of place, a Precambrian rabbit or a Silurian penguin. This stability in the record^(50,51) in the face of increasing search effort, is evidence that the broad outlines of the record are correct. This has been confirmed by comparisons of the fossil record and morphological and molecular trees^(31–33,52–54) which show good congruence in terms of branching order and in terms of cladistically implied gaps.

There is a huge premium for collectors to identify new localities or new species, and especially to find older representatives of known groups. Indeed, a find of “the oldest X” is a virtual guarantee of a paper in *Science* or *Nature*.^(36,37,43) The literature is littered with erroneous claims of Cretaceous representatives of modern avian and mammalian orders, such is the pressure to find such remains. Thus, although palaeontologists may be uncomfortable with the claims of early origins, they are hugely motivated to fill the Cretaceous gap. Thus far, they have failed to do so.

The improbability that ancestors were cryptic

One way to escape the argument of missing fossils has been the suggestion that the ancestral forms were cryptic, and so have escaped detection by palaeontologists. Cooper and Fortey⁽⁹⁾ term this phenomenon the “phylogenetic fuse”, a “comparatively obscure phase of structural innovation, which can still be detected in the genome”. This obscure phase of phylogenesis, or lineage splitting, during which the major genetic splits between clades took place, is supposed to have preceded, perhaps by many tens of millions (or in the Cambrian case, hundreds of millions) of years the more overt phase of radiation, which is detected by abundant and diverse fossils. What is not clarified is the nature of the putative obscure early phase: do Cooper and Fortey mean that organisms were absolutely rare, and yet evolving like mad, or that the organisms were soft-bodied (the implication for the Cambrian case) and hence hard to fossilize? In the present case, rarity is implied, and not that the progenitors of modern bird and mammal orders became temporarily soft-bodied.

The postulation of rare or cryptic ancestors does not really resolve anything, and is just a restatement of the problem; there is no independent evidence for the proposal that ancestors were cryptic other than the assumption that such ancestors were there and yet have not been found. The proposal fails absolutely on a probability argument: why should some 20–30 lineages, the modern bird and mammal orders reputed to have existed undetected through most of the Cretaceous, *all* uniformly have remained cryptic until they blossomed forth in abundance and with autapomorphies in place and fully displayed between 70 and 55 million years ago?

There is positive evidence against the proposal of cryptic ancestors of modern avian and mammalian orders. In cases where the molecular and morphological dates match, and for tetrapods this includes most origins other than the modern birds and mammals,⁽⁷⁾ the oldest fossils are robust and as large as typical descendants. On the other hand, Cooper and Fortey note a couple of relevant cases from the fossil record that hint at the phenomenon they propose: the early appearance of spores apparently from land plants long before land-plant fossils are known, and the report of sharks and bony fishes from the Harding Sandstone, of Ordovician age, some 50–60 Myr before abundant and more complete fossils appear in the Devonian.⁽⁵⁵⁾ In both cases, the fossils have been found, despite their apparent rarity before the major radiation. The prediction is that obscure Early Cretaceous fossils of rodents, penguins, parrots, and anteaters will in fact turn up. We wait with interest.

The improbability that ancestors were unpreservable: an experiment with a control

Cooper and Fortey⁽⁹⁾ note that “much of the Cretaceous fossil record is poor and is less likely to contain small-bodied, fragile-boned taxa . . . their habitat and limited body and population sizes may have contributed to a poor fossil record”. Hedges⁽⁶⁾ has made a similar point. If it were indeed true that the Cretaceous representatives of the modern bird and mammal orders were small and fragile, and hence unlikely to be preserved as fossils, then the apparent gap between molecular and palaeontological dates would be explained. However, there is no independent evidence for the assertion, and indeed there is a control that disproves it. This discussion has already been highlighted in reports in *Science*.^(42,56)

The experiment that refutes the suggestion that the Cretaceous terrestrial fossil record is poor is based on the observation of large numbers of tiny delicate skeletons from Cretaceous localities around the world, none of which is a member of a modern bird or mammal order. It is indeed likely that the basal members of modern avian and mammalian orders were small animals, but probably no smaller than typical lizards, insect-eating mammals, or songbirds today. Such fossils are known through the whole Cretaceous. Numerous localities in the Early and Late Cretaceous have yielded small delicate skeletons, such as the new sites in the Early Cretaceous of Spain and China and in the Late Cretaceous of Italy. These sites have yielded specimens of birds, mammals, lizards, salamanders, frogs, and fishes, many of them exquisitely preserved, and even with soft parts like feathers and skin still present. Other longer-known sites in Europe, North America, and Central Asia have yielded abundant tiny vertebrate specimens, as well as the larger dinosaurs, crocodiles, and pterosaurs. Some of the Mongolian Late Cretaceous sites have been famous for their extraordinarily diverse faunas of

small mammals and lizards for decades. Among the thousands of skeletons from all these sites, spanning the whole of Cretaceous time, and covering most continents, not a single convincing specimen assignable to a modern bird or mammal order has yet been described. The only exceptions are the incomplete remains noted above from the latest Cretaceous.

Further, global studies of the relative completeness of the Cretaceous terrestrial fossil record have confirmed that it is adequate throughout, and that it improves towards the end of the Cretaceous. The relative quality of any time interval in the fossil record may be assessed by the Simple completeness metric (SCM),

$$SCM = \frac{\textit{known}}{\textit{known} + \textit{Lazarus}}$$

where the “known” figure is the number of groups (perhaps families) represented by fossils, and the Lazarus taxa are those *known* to have been present, but not represented by fossils.⁽⁵⁷⁾ Such Lazarus taxa are known below and above the time interval in question, having apparently died, and then later come back to life. A low SCM value, produced by large numbers of Lazarus taxa, indicates a poor fossil record, while a high SCM value indicates a relatively good record.

For the Cretaceous, values for continental tetrapods in a new analysis⁽⁵⁸⁾ range from 45 to 89% (Fig. 2a), with lows at the beginning of the Cretaceous, and at the beginning of the Late Cretaceous. The highest values, of 78% and 89%, occur in the Campanian and Maastrichtian stages, the time immediately before the end of the Cretaceous. Hence, during the critical interval when modern orders of birds and mammals were coming on the scene, from 85 Myr onwards, the abundance and diversity of fossiliferous sites increases hugely, especially in North America and Central Asia, but also in southern Europe, South America, Madagascar, and India. Both mammals and birds show relatively high SCM values of 98% and 78% respectively for this time interval (Fig. 2b), although the value for birds is based on a small global sample. By this measure, both groups have considerably better fossil records through the Cretaceous than do the reptiles or amphibians. In addition, reptiles small and large have similar values of around 60%, the value for Cretaceous lizards and for Cretaceous dinosaurs. This analysis demonstrates that Cretaceous mammals and birds do not have poor fossil records, nor is there a significant difference in SCM values between small and large continental tetrapods or any indication of a drop-off of quality in the record towards the end of the Cretaceous.

The “living mastodon” argument

The fourth argument to explain the mismatch of palaeontological and molecular evidence in this case is the proposal that palaeontologists have not found the fossils yet since the modern avian and mammalian orders originated in relatively

unsampled areas on southern continents, the Gondwana area.^(8,28) However, this idea is not supported by cladistic palaeobiogeographic evidence: relationships and known geographic distributions of the modern bird and mammal orders indicate origins for many of them in the well-sampled northern hemisphere continents. Cladistic evidence indicates clearly that neognath birds and placental mammals radiated in North America and Eurasia. Endemic mammal groups in South America and Africa radiated later and independently. It is possible that six mammalian orders (Macroscelidea, Tubulidentata, Proboscidea, Sirenia, Hyracoidea, ?part of Insectivora) radiated in Africa,⁽⁵⁹⁾ but the validity of the concept of the Afrotheria has yet to be confirmed by other molecular and morphological evidence. In Australia, of course, the mammalian radiation consisted of marsupials, and placental mammals arrived only much later. On the other hand, cladistic evidence suggests that some modern bird groups did radiate in Gondwanaland.

Good-quality terrestrial deposits of Late Cretaceous age are indeed rare in Africa and Australia,⁽²⁸⁾ and it cannot be excluded that modern mammalian and avian orders originated in one or the other. However, new excavations in Late Cretaceous beds of Madagascar, part of the core of Gondwanaland, have so far produced numerous exquisitely preserved fossils, including birds, but these are of primitive type only.⁽⁶⁰⁾

The appeal to unexplored regions is interesting, but it is another negative proposal. This is exactly the doomed argument used in the 1750s to deny the possibility of extinction. American investigators at that time dug up the remains of mastodons and mammoths in Ohio, clearly quite different from the known African and Indian elephants. Some investigators argued that the American incognitum, as it was called, was not really extinct and that living mammoths and mastodons would be found in the unexplored reaches of the savage western parts of North America. We are still looking for them.

Solution: the molecular clock runs fast during times of radiation

The simplest solution to the conundrum posed by the mismatch of molecular and morphological dates of origin is that molecular clocks run at variable rates. In particular, during times of radiation, especially when ecosystems are profoundly perturbed, normal evolutionary and ecological interactions are thrown aside, and episodes of dramatic evolutionary change and niche-filling take place. This kind of dramatic change in the rate of speciation, perhaps by an order of magnitude, would surely have profound effects on the genome, including a dramatic increase in the mean molecular clock rate.^(61,62)

The molecular clock does not run at a constant rate. There is strong evidence for variation in rates between taxa (e.g.

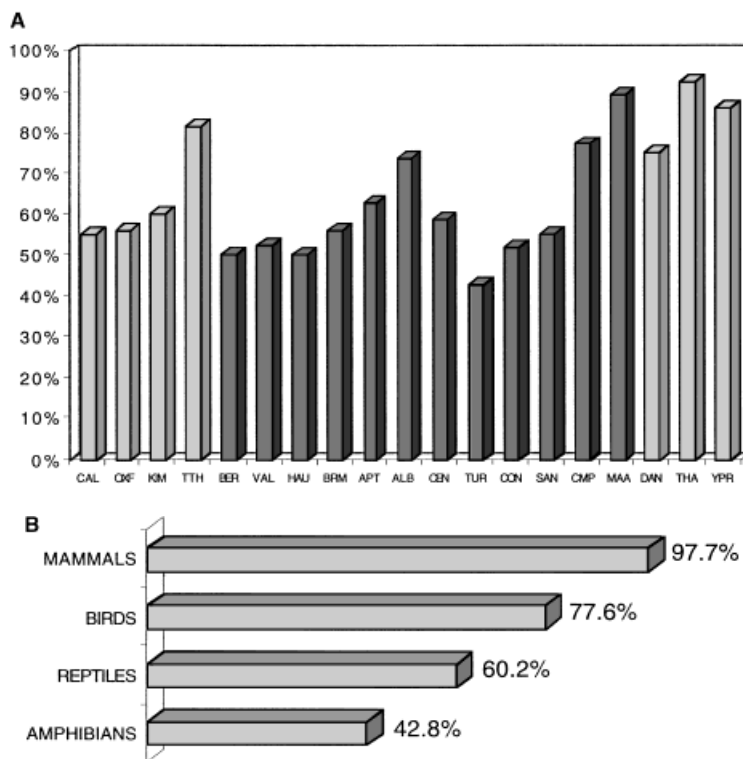


Figure 2. Measures of the relative completeness of the fossil record of continental tetrapods during the Cretaceous. **A:** Measures calculated stage-by-stage show that quality was no worse during the Cretaceous (dark columns) than in the preceding Jurassic (left) or succeeding Tertiary (right). The record was best in the mid Cretaceous, and towards the end. **B:** Mammals and birds have considerably better fossil records than do reptiles or amphibians for this interval of time. Original, courtesy of Emmanuel Fara.

between hominids and murid rodents), variation between particular sequences, and variation in relation to life history characteristics such as generation time.^(27,28,63,64) These, and other analytical problems associated with the molecular clock, are well known.^(27,28) The KT mass extinction event, 65 Myr ago, was marked by the extinction of the dinosaurs and pterosaurs, as well as numerous other groups of amphibians, lizards and snakes, birds (especially the enantiornithines), and mammals (several basal mammal and marsupial families) on land. These losses destroyed some 50% of land-dwelling species,⁽⁶⁵⁾ and clearly dramatically perturbed all groups. After the extinction, the world took some 5–10 Myr to return to normal and for diversity levels to become re-established. During that extraordinary time, from 65–55 Myr ago, it would be no surprise if rates of molecular evolution had rocketed in association with much enhanced speciation rates. High rates of the molecular clock would then give a spurious picture of a long pre-KT history for all groups so affected.

There are numerous other substantial problems to be considered before accepting date estimates founded on molecular data. As Bromham and colleagues point out,⁽²⁸⁾ current estimates of specific dates of divergence between

various clades of mammals vary enormously, and sometimes by as much as 100%. Even if the clock ticked regularly, the estimated dates differ vastly as a result of the choice of taxa, genes, alignment techniques, tree-making techniques, correction factors, and calibration points. These authors note also the weaknesses of relative rates tests, except for very long sequences, and of other methods to compare genetic distances with geological time. As they conclude, “molecular date estimates. . . should never be accepted uncritically but should be examined in the light of other sources of historical information in biology, particularly palaeontology, biogeography and phylogeny”.

Conclusions

Four clear arguments have been given against recent claims that modern orders of birds and mammals originated in the Early Cretaceous. The density of the fossil record indicates that unknown fossils are likely to extend known fossil records back only a few million years, and barely back into the Cretaceous, at 70–65 Myr old, and certainly not more than 100 Myr. The other three arguments are all negatives: that the gap between molecular and palaeontological dates is filled

with ancestral birds and mammals that were rare and cryptic, or that were too fragile to be preserved, or that lived in places that have not yet been explored.

None of these four arguments can be proved or disproved conclusively. However, probabilistic arguments can be made that all four are most unlikely as explanations of putative missing Cretaceous ancestors. And, in light of that, it is more likely that the calculated molecular dates are wrong. The most likely explanation for the discrepancy is the simplest: the molecular dates are wrong because the molecular clock does not tick regularly through geological time. During major perturbations of the biosphere when rates of evolutionary radiation increase dramatically, so too do clock rates.

The fascinating aspect of this debate is that, as fossil collecting continues, the odds on each side of the debate are heavily weighted in favour of the molecular stance. I mean this in the sense that a single new discovery, such as an unequivocal Early Cretaceous owl or artiodactyl, would provide clinching evidence for the stance of Hedges, Cooper, and others, and would destroy the conservative palaeontological position I have outlined, essentially at a stroke. Any single new discovery could never materially strengthen my position, although the accumulation of new finds within known stratigraphic ranges slowly increases the probability that the fossil record is correct. Nevertheless, I will make the wild and rash prediction that the critical fossils predicted to fill the supposed first half of the evolution of modern mammals and birds in the Cretaceous will not be found because they do not exist.

Acknowledgments

I thank David Archibald, Simon Conway Morris, Gareth Dyke, and Emmanuel Fara for helpful comments.

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