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Original Paper

The ornithologist Alfred Russel Wallace and the controversy surrounding the dinosaurian origin of birds

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Abstract

Over many years of his life, the British naturalist Alfred Russel Wallace (1823–1913) explored the tropical forests of Malaysia, collecting numerous specimens, including hundreds of birds, many of them new to science. Subsequently, Wallace published a series of papers on systematic ornithology, and discovered a new species on top of a volcano on Ternate, where he wrote, in 1858, his famous essay on natural selection. Based on this hands-on experience, and an analysis of an *Archaeopteryx* fossil, Wallace suggested that birds may have descended from dinosaurian ancestors. Here, we describe the “dinosaur-bird hypothesis” that originated with the work of Thomas H. Huxley (1825–1895). We present the strong evidence linking theropod dinosaurs to birds, and briefly outline the long and ongoing controversy around this concept. Dinosaurs preserving plumage, nesting sites and trace fossils provide overwhelming evidence for the dinosaurian origin of birds. Based on these recent findings of paleontological research, we conclude that extant birds indeed descended, with some modifications, from small, Mesozoic theropod dinosaurs. In the light of Wallace's view of bird origins, we critically evaluate recent opposing views to this idea, including Ernst Mayr's (1904–2005) arguments against the "dinosaur-bird hypothesis", and document that this famous ornithologist was not correct in his assessment of this important aspect of vertebrate evolution.

Keywords Alfred Russel Wallace – Evolution – Dinosaurs – Birds – *Archaeopteryx* – Ernst Mayr

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Introduction

Seven years after returning to his home country of England, Alfred Russel Wallace (1823–1913) published his most commercially successful book, *The Malay Archipelago* (Wallace *1869*). During his 8-year-long excursions (1854–1862) into these tropical regions of planet Earth, the British naturalist independently discovered the principle of natural selection in populations of wild animals (Wallace *1858*) and proposed a biogeographical concept that was later called "Wallace line". In addition to these contributions to evolutionary biology and biogeography, he was also an avid collector and discovered/described many new species of birds.

In one of his original papers dealing with systematic ornithology, Wallace (*1864*) provided information on the distribution and habits of parrots of the Malayan region, with the description of two new species. In another research paper on this subject, Wallace (*1865*) characterized 21 species of birds from this area, and pointed out that he had, at that time, collected a total of 212 new species of birds in the islands of the Malay Archipelago.

Another of his many original contributions to ornithology dealt with the raptorial birds of the Malay Archipelago. The author remarked, "With the exception that Vultures are entirely absent, birds of prey are tolerably plentiful in the Archipelago" (Wallace *1868*, p. 2). Interestingly, the British ornithologist attributed the occurrence of many species to geographic separation of populations. Hence, Wallace foresaw not only Ernst Mayr's (1904–2005) biological species concept (Kutschera *2003*, *2009*), but also the principle of allopatric speciation, when he suggested that "This large number (of bird species) seems to be chiefly because of the breaking up of the district into a vast number of islands" (Wallace *1868*, p. 2).

Finally, in his best- and long-seller *The Malay Archipelago*, Wallace (*1869*) devoted many pages to the distribution, behavior and taxonomy of different members of the Aves. His lucid descriptions of the exotic birds of paradise were one of the reasons for the tremendous success of this book, which is still in print today.

In this article, we discuss the opinions of Wallace concerning the evolutionary origin of birds, a class of vertebrates that he studied over many decades of his long life (Fig. 1) with reference to recent discoveries that have shed much needed light on the evolutionary history of this group of tetrapods.

Fig. 1

Drawing of the "Ternate-bird" (*Rhipidura torrida*), discovered and described by Alfred R. Wallace on the summit of the volcano, 4,000 feet above the sea, on Ternate island (adapted from Wallace *1865*)

Alfred Russel Wallace and the origin of birds

Despite the fact that Wallace collected more than 8,000 specimens of birds and described many new species (Wallace *1869*) during his travels in Southeast Asia, his writings on the evolutionary origin of birds are rather limited. His discussions of the evolutionary history of other groups are more extensive. In his popular book *Darwinism*, Wallace (*1889*) devoted chapter XIII to the “Geological evidences of evolution”. With reference to the science of geology, the author pointed out that “The theory of evolution in the organic world necessarily implies that the forms of animals and plants have, broadly speaking, progressed from a more generalized to a more specialized structure, and from simpler to more complex forms” (Wallace *1889*, p. 182). Wallace discussed the evolution of horses and other animal taxa, with reference to the corresponding work of the eminent British biologist Thomas Henry Huxley (1825–1895). In one sentence, Wallace (*1889*) also referred to the origin of birds. In his discussion of Huxley’s research on fossil crocodiles, he remarked that “Dinosaurians (are) reptiles which in some respects approach birds” (Wallace *1889*, p. 184). The author agreed with Huxley’s opinion and, on a more general note, argued that the fossil finds of his time provide “evidence of evolution; the doctrine resting upon exactly as secure a foundation as did the Copernican theory of the motions of the heavenly bodies at the time of its promulgation” (Wallace *1889*, p. 187).

In his popular book *The World of Life*, Wallace discussed several species of dinosaurs, and devoted one section to “The Earliest Birds” (Wallace *1910*). He depicted and discussed the then famous “*Archaeopteryx macrura*”, figured the skull of *A. siemensii* (Fig. 2), and noted that “The very earliest known fossil bird is from the Upper Jurassic of Bavaria, and is beautifully preserved in the fine-grained beds of lithographic stone … it is a true bird, notwithstanding its curiously elongated tail feathered on each side”. In the legend to his figure, he described this fossil as a “Lizard-Tailed Bird” (Wallace *1889*, pp. 213–215). He also explained why bird remains in the Mesozoic era are rare, but Wallace did not explicitly refer to the “dinobird-concept”, which was proposed several years before by his colleague Huxley, whom he treated with admiration and respect.

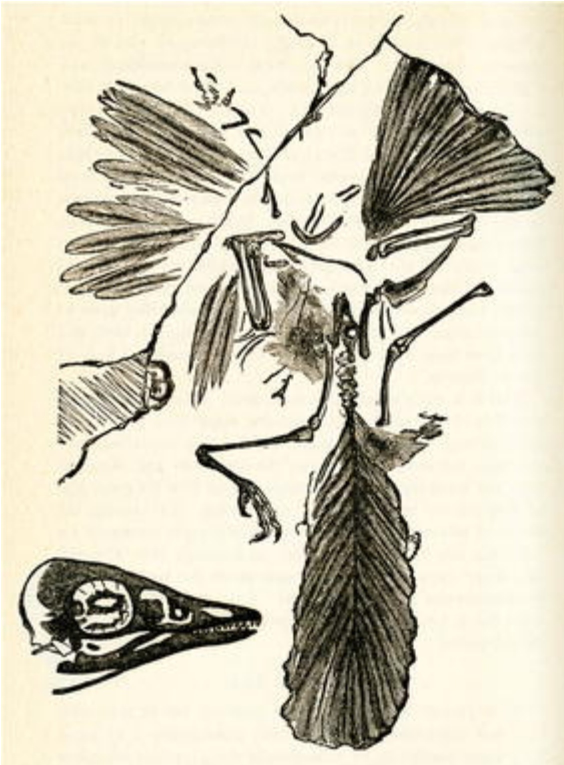

Fig. 2

Drawing of the “fossil lizard-tailed bird” (“*Archaeopteryx macrura*”—the London *Archaeopteryx*), and the skull of *Archeopteryx siemensii* (the Berlin specimen). (adapted from Wallace *1910*)

The dino-bird hypothesis: origin and evolution of a concept

The dinosaurian origin of birds, originating as an idea in the 1860s with Huxley (*1868a*, *b*, *1870*), is widely accepted today (Prum *2002*; Chiappe *2004*, *2007*, *2009*; Erickson et al. *2009*) and remains a very active and dynamic area of research. The re-emergence of the view that dinosaurs are in fact bird-like creatures is relatively recent, but first mentions of the shared anatomical characteristics between birds and (non-avian) dinosaurs, date back much further. Early pioneers of archosaur comparative anatomy, such as the German anatomist Carl Gegenbaur (1826–1903) (Hossfeld et al. *2003*), and the aforementioned zoologist Huxley, recognized these similarities (Wagner *1861*; Chiappe *2007*), which are most apparent in the skeletons of theropod dinosaurs. Thomas H. Huxley, today widely known as “Darwin’s bulldog”, was one of the most vociferous proponents of a bird-dinosaur link (Huxley *1868a*, *b*, *1870*).

While Huxley had little doubt about the dinosaurian origin of birds, some authors considered other scenarios, such as a thecodont origin as more likely (Heilmann *1926*). These views became widespread following the publication of Heilman's influential book *The Origin of Birds*, aided to no small extent by the incredibly vibrant life illustrations Heilman included in this work. By the early twentieth century, dinosaurs were no longer thought to be particularly relevant to bird origins, despite the existence of a truly astonishing fossil from Europe.

Because of the incompleteness of the fossil record, the world-famous "Urvogel" *Archaeopteryx*, from the Jurassic of Southern Germany (Bavaria), was for a long time the only key taxon and provided important insights into the morphology of a "transitional form": feathers were clearly visible in this taxon, but so were toothed jaws, well-developed claws, and a long, dinosaurian tail (Figs. 3, 4). Huxley wrote about the similarities *Archaeopteryx* shared with small predatory dinosaurs, such as *Compsognathus* (Figs. 3, 4, 5), also from the Jurassic of Germany (Huxley *1868b*). These two taxa in particular look remarkably similar in their skeletal anatomy and body shape (Figs. 2, 3, 4, 5).

Fig. 3

Photograph of the Berlin *Archaeopteryx lithographica* (or *siemensii*; see Mayr et al. *2007*). Picture courtesy of the Museum für Naturkunde, Berlin (Germany)

Fig. 4

Reconstruction of *Archaeopteryx.* Artwork by Davide Bonadonna. *Archaeopteryx lithographica*-specimens typically represent animals roughly the size of a magpie, although some were larger, about the size of a raven (see Erickson et al. *2009*)

Fig. 5

Photograph of the Munich specimen of the small predatory dinosaur *Compsognathus longipes* Wagner (*1861*), which was interpreted as a bird-like reptile. The total body length of large *Compsognathus* exceeded 1 m (the Munich specimen is considerably shorter and represents a juvenile; see Therrien and Henderson *2007*)

Considering the huge scientific importance, beautiful preservation, and rarity of *Archaeopteryx* fossils, it was probably only a question of time before doubts about the authenticity of the fossil were voiced. Claims that *Archaeopteryx* is a forgery were quickly and thoroughly proven to be false (Charig et al. *1986*), and several new specimens have been discovered (Mayr et al. *2007*); they are all referred to *A. lithographica* by some authors (Houck et al. *1990*; Senter and Robins *2003*), while others distinguish two or more species (Mayr et al. *2007*). For a long time, *Archaeopteryx* remained one of the very few physical pieces of evidence showing a mosaic of easily identifiable traditional “reptile” and “bird” characteristics.

Part of the fascination of the dinosaur-bird link undoubtedly has to do with the widespread, but superficial perception of a great difference in size and morphology between dinosaurs such as *Tyrannosaurus rex* and the vast majority of modern birds. In reality, many dinosaur skeletons show a striking similarity to the skeleton of a modern bird. This perception has sometimes hindered research exploring a possible relationship, and dinosaurs were generally thought to lack many typical avian features, such as a furcula, (proto) feathers, or an avian-style brooding behavior.

A pronounced shift in the perception of dinosaurs by the scientific community took place in the 1960s: away from a more “reptilian”, cold-blooded dinosaur (Colbert *1961*), and towards a possibly endothermic, active, and more bird-like “reptile” (Chiappe *2009*). This view was strongly espoused by a small group of dinosaur paleontologists, among them John Ostrom (1928–2005) and Robert Bakker (Bakker *1968*; Ostrom *1973*). Ostrom’s discovery of *Deinonychus antirrhopus* in particular proved very important (Ostrom *1969*). This predatory dinosaur is extremely bird-like in its anatomy (Fig. 6) and possibly even behavior, as suggested, among other things, by its appendicular anatomy (Fowler et al. *2011*) and brooding behavior (Grellet-Tinner and Makovicky *2006*). More recent finds have extended many of these features to other derived theropods, especially the group known as the maniraptoran dinosaurs (Norell et al. *1995*).

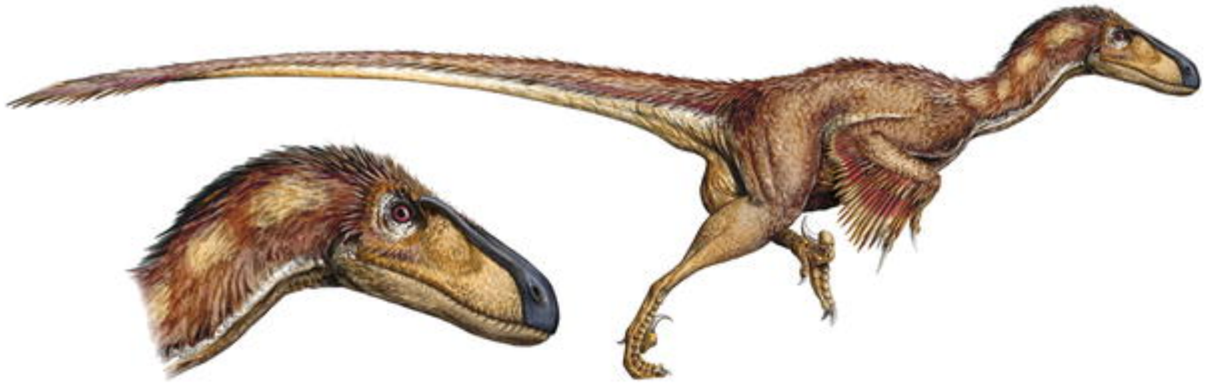

Fig. 6

Reconstruction of a feathered *Deinonychus antirrhopus*. The morphology and distribution of the plumage is based on recent paleontological discoveries from Asia. Artwork by Davide Bonadonna. Total body length of *Deinonychus*: ca. 3.3 m

Fossil evidence from Asia and beyond

Today, after an ever-increasing rate of discovery of spectacular fossils, the number of shared anatomical characters between avian and non-avian dinosaurs is overwhelming. Numerous fossil theropod skeletons (e.g., Xu and Norell *2004*; Norell and Xu *2005*), nesting sites (e.g., Norell et al. *1995*; Clark et al. *1999*; Varricchio and Jackson *2004*), ootaxa (e.g., Varricchio and Jackson *2004*; Grellet-Tinner et al. *2006*) and ichnofossils (e.g., Milner et al. *2009*) document the strong evidence for a dinosaurian origin of birds (e.g., Sereno *1999*; Chiappe and Witmer *2002*). The finds are, for the most part, from Asia (China and Mongolia). They include dinosaurs preserved in an avian sleeping posture (Xu and Norell *2004*), dinosaurs sitting on a clutch of eggs (Norell et al. *1995*; Clark et al. *1999*; Varricchio and Jackson *2004*), adopting a bird-like resting pose (Milner et al. *2009*) and outlines of fully feathered limb- or tail-sections (Xu et al. *2003*; Chiappe *2004*) (Fig. 7).

Fig. 7

A representative *Microraptor zhaoianus* fossil showing body, wing, hind limb and tail feathers. Photograph courtesy of Mick Ellison (American Museum of Natural History). *Scale bar* 5 cm

In terms of skeletal evidence, it is now well established that theropod dinosaurs share with birds a large number of key features (Fig. 8), including but not limited to: a bipedal posture, extensive pneumatisation of the skeleton (O'Connor and Claessens *2005*; Sereno et al. *2008*), the presence of a furcula, swivel-like wrist joints (semi lunate carpal), L-shaped coracoids, and fast growth (Erickson et al. *2001*). The large number of key discoveries cementing the role of predatory dinosaurs as bird ancestors led to intense debates about the origin of flight (Padian and de Ricqlès *2009*). Clearly, some forms could not fly and used feathers for display and/or insulation, but others did have the anatomical features necessary for flight (Chiappe *2004*).

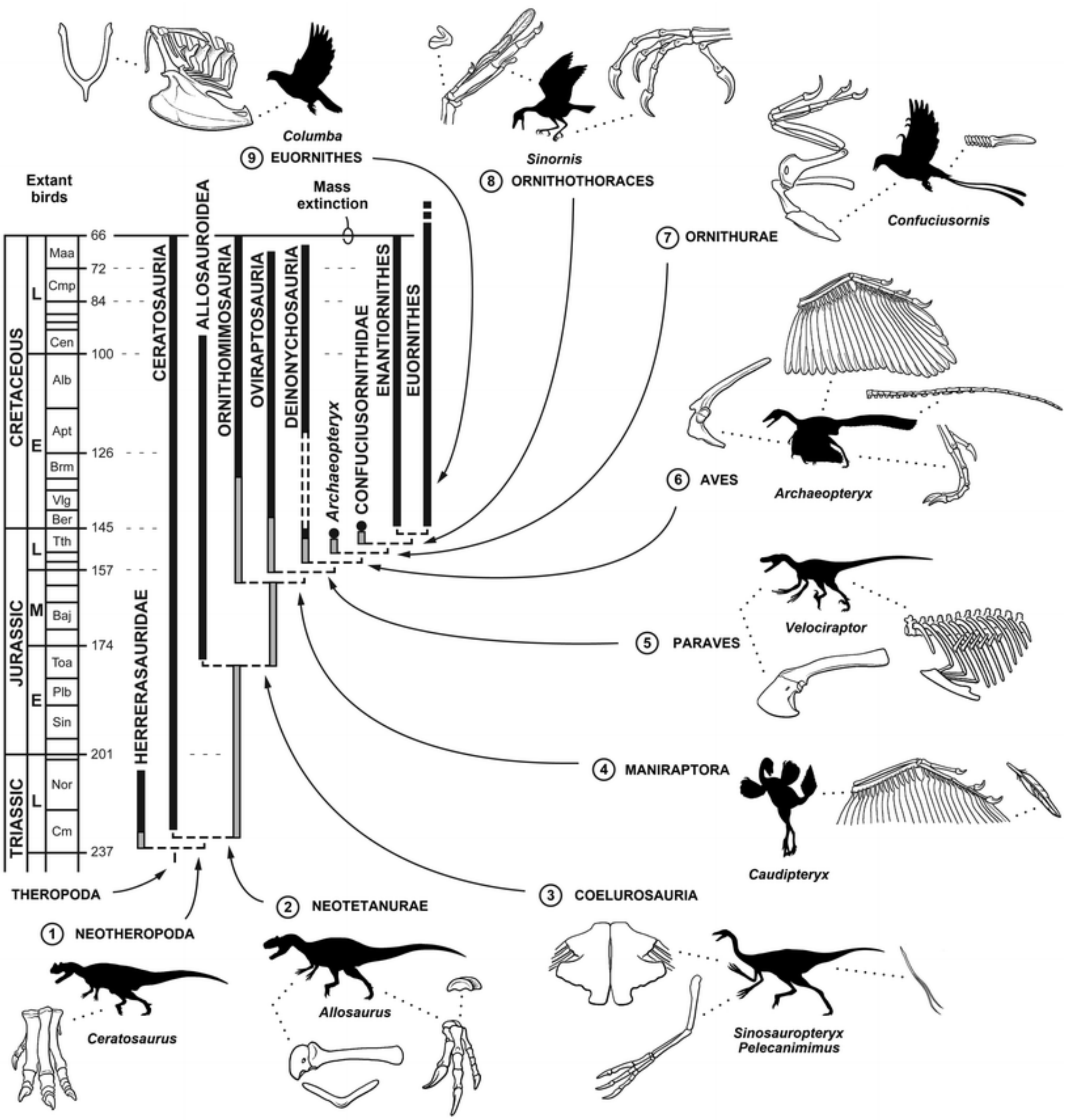

Fig. 8

Evolution of the avian skeleton from theropod dinosaurs during the Mesozoic, with representative species. The upper boundary of the timeline is marked by the Cretaceous/Paleogene mass extinction. Only one lineage (Euornithes, 9), leading to extant birds, survived the extinction event (adapted from Sereno *1999*)

Of particular interest in the evolution of flight are, in addition to *Archaeopteryx*, several new Asian taxa, including four-winged forms such as *Microraptor* (Fig. 7), a small maniraptoran from Asia (Xu et al. *2003*; Li et al. *2012*). These new specimens add important information to our understanding of leg feather morphology and evolution (Zheng et al. *2013*). The precise sequence of events leading from flightless dinosaurs to full-powered bird flight is still debated and different models have been proposed (Chiappe *2009*; Dececchi and Larsson *2011*). It is clear, however, that plumage did initially evolve for purposes unrelated to flight.

Frauds and unresolved questions

Unfortunately, research into the dinosaurian origin of birds has been temporarily overshadowed by examples of fraud, in particular, specimens that represent composite slabs, consisting of several taxa (Zhou et al. *2002*). The most famous of these fabrications has been named “*Archaeoraptor*” and, because a series of unfortunate events meant that the forgery was not detected before initial description, this provided unnecessary “ammunition” to critics of the dinosaurian origin of birds, from sceptical ornithologists to US creationists. As is the case with other “Piltdown Man” style forgeries, this unfortunate episode should not detract from the fact that in the time elapsed since the “*Archaeoraptor*” story, countless new genuine and spectacular fossils of avian and non-avian dinosaurs have come to light, in addition to the ones already known. These new finds provide a spectacular fossil sequence, rich in diversity and morphology and indicative of a complex evolutionary branching pattern.

Because of this complexity in theropod and bird evolution, some important details of taxonomic relationships remain unresolved, as competing hypotheses are currently not strong enough to rule each other out. This is relevant to the position of certain groups of theropod dinosaurs such as dromaeosaurs, troodontids, alvarezsaurids and oviraptorids for example—all of which have at one point or another been described as theropods that are particularly close to birds, and in some cases even as secondarily flightless birds (Perle et al. *1993*; Chiappe et al. *1998*; Sereno *2001*; Hwang et al. *2002*; Paul *2002*; Witmer *2002*).

More recently, evolutionary developmental biology (evo-devo) has also become an important area of debate, especially regarding digit homologies. This has traditionally been a divisive and complicated issue, but data from developmental biology now seem to show little incompatibility with the theropod origin of birds (Naish *2011*). This is also supported by recent studies based on molecular evidence (Vargas and Fallon *2005*).

Another topic discussed in avian evolution is what some researchers refer to as the "temporal paradox" (Feduccia *1999*), which, in this case, describes the temporal discrepancy between the Cretaceous age of many of the new Asian dinosaurs showing protofeathers, feathers and wings, and the appearance of the earliest known bird, *Archaeopteryx*, which is reliably dated to the Late Jurassic (~150 million years ago) (Fig. 3). This criticism has, however, little merit, since (a) maniraptoran dinosaurs are in fact known from remains that are early Jurassic in age and that consequently predate *Archaeopteryx* (e.g., Witmer *2002*; Hu et al. *2009*), (b) it has not been proposed that the Cretaceous forms are ancestral to *Archaeopteryx* or similar forms, and (c) all previously proposed alternatives are far less parsimonious (Brochu and Norell *2001*; Witmer *2002*).

The position of *Archaeopteryx* has also recently been questioned (Xu et al. *2011*), because one analysis recovered the taxon outside of Aves. This result should, however, not be regarded as a major turning point. While cladistic analyses are powerful and important tools, they can suffer from a lack of data and/or stability and results obviously also depend on definitions of groups (in this case Aves). Indeed, the phylogenetic position of *Archaeopteryx* has subsequently been reverted back to its "original" position (Lee and Worthy *2012*), emphasizing the fragility of some phylogenetic analyses, and the sometimes exaggerated importance given to them by some authors to the detriment of other approaches, such as classical comparative anatomy. This problem was the cause for several misidentifications in the past, including some concerning early birds (Naish et al. *2012*; Buffetaut *2011*).

Ernst Mayr and ongoing opposition against the dino-bird hypothesis

Unlike Alfred R. Wallace (*1889*, *1910*), some modern ornithologists have opposed the dinosaurian origin of birds. This view was also espoused by one of the most influential evolutionary biologists of the twentieth century, Ernst Mayr. This world-expert in ornithology discovered and described many species of birds (Haffer *2007*). In his popular book *What Evolution Is*, Mayr (*2001*), like some other ornithologists, appears to have underestimated, and possibly misunderstood some of the evidence linking theropod dinosaurs to birds.

Mayr (*2001*) argued that there are two distinct, plausible theories on the origin of birds, and erroneously states that the theory of the dinosaurian ancestry of birds suggests an origin from Cretaceous theropods. This is incorrect for the reasons explained above (see temporal paradox). The other theory Mayr refers to is the poorly supported thecodont origin (Witmer *2002*), which suggests that birds originated from another archosaur group in the Triassic (Martin *2004*). Mayr (*2001*) lists several, now largely discredited, lines of refutations against a dinosaurian origin of birds: differences in digit counts; differences in tooth morphology; the pectoral anatomy of late Cretaceous dinosaurs, and problems with the “ground up” model of avian flight. While a detailed refutation of the above arguments is beyond the scope of this paper and can be found elsewhere (e.g., Witmer *2002*; Chiappe *2009*), it is worth noting that some of them were surprisingly weak, even before the more recent discoveries described above made them untenable. To illustrate just one example, the argument that theropod teeth are more flattened than the simpler peg-like teeth of early birds (Mayr *2001*) ignores the fact that theropod dentition, while often relatively similar, can also vary greatly in morphology, from conical, rounded teeth in spinosaurids (Dal Sasso et al. *2005*), via the tiny, heterodont and numerous teeth of *Pelecanimimus* (Perez-Moreno et al. *1994*), to the blade-shaped teeth of carcharodontosaurids (Sereno et al. *1996*), to cite just a few examples. There is little doubt that in the face of such diversity, tooth morphology seems to be a poor choice for argument.

The view Mayr (*2001*) summarized in his popular book is in stark contrast to that expressed by the vast majority of vertebrate paleontologists, but emblematic for a relatively deep historical schism between the latter, and a substantial number of ornithologists (Feduccia *1999*). This may be in some cases a consequence of a general lack of interest, and/or expertise, in the methods used in vertebrate paleontology. As the evidence for the dinosaurian origin of birds has continuously piled up, this divide has slowly been reduced, but it has not completely disappeared (Naish *2011*). Based on currently available information and recent discoveries, the prominent ornithologist Mayr (*2001*) was not correct in his assessment of this particular aspect of evolutionary biology.

Conclusions

In two of his most influential books, Wallace (*1889*, *1910*) discussed the evolutionary origin of birds. Based on the evidence available at that time, the ornithologist Wallace pointed out that extant birds may be the descendants of extinct dinosaurs, but he did not elaborate on this topic. This "dinobird-hypothesis" was proposed for the first time by the Victorian naturalist Thomas H. Huxley, who published several original papers on this topic (Huxley *1868a*, *b*, *1870*).

Today, it is widely accepted that birds, or "avian dinosaurs", descended from, and in fact are, theropods that survived the Cretaceous/Paleogene mass extinction event 65 million years ago (Chiappe *2009*; Kutschera *2013*) (Fig. 8). Small predatory dinosaurs are the evolutionary ancestors of extant members of the Aves, a class of homoeothermic vertebrates that comprises ca. 10,000 extant species (van Tuinen *2009*). Like Wallace, Ernst Mayr was a remarkable ornithologist who discovered and described numerous species of birds (Haffer *2007*). However, in his influential book *What Evolution Is*, Mayr (*2001*) summarized evidence against Huxley's "dinobird hypothesis" in its "evolved" version (Feduccia *1999*).

In this article, we have shown that Mayr's writings do not reflect the current understanding of bird origins, and conclude that these feathered vertebrates are in fact a group of highly modified theropods that evolved during the Mesozoic from small, feathered dinosaur ancestors.

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