



COMMENTARY

Rhetoric vs. reality: A commentary on “Bird Origins Anew” by A. Feduccia

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ABSTRACT

Birds are maniraptoran theropod dinosaurs. The evidence supporting the systematic position of Avialae as a derived clade within Dinosauria is voluminous and derived from multiple independent lines of evidence. In contrast, a paucity of selectively chosen data weakly support, at best, alternative proposals regarding the origin of birds and feathers. Opponents of the theory that birds are dinosaurs have frequently based their criticisms on unorthodox interpretations of paleontological data and misrepresentation of phylogenetic systematic methods. Moreover, arguments against the nested position of Avialae in Dinosauria have often conflated the logically distinct questions of avian origins, the evolution of flight, and the phylogenetic distribution of feathers. Motivated by a Perspectives article with numerous factual inaccuracies that recently appeared in *The Auk*, we provide a review of the full complement of facts pertaining to the avian origins debate and address the misplaced criticisms raised in that opinion paper.

Keywords: evolution of flight, evolution of feathers, evolution of birds, Avialae, maniraptoran theropod dinosaurs, phylogenetic systematics

Retórica vs. Realidad: Un comentario sobre “Bird Origins Anew” por A. Feduccia, *Auk* 130:1–12

RESUMEN

Las aves son dinosaurios terópodos maniraptores. La evidencia que sustenta la posición sistemática de Avialae como un clado derivado dentro de Dinosauria es voluminosa y se deriva de múltiples líneas independientes de evidencia. En contraste, sólo escasos datos elegidos selectivamente sustentan débilmente propuestas alternativas sobre el origen de las aves y las plumas. Los opositores de la teoría de que las aves son dinosaurios frecuentemente han basado sus críticas en interpretaciones no ortodoxas de los datos paleontológicos y en la tergiversación de los métodos de la sistemática filogenética. Además, los argumentos en contra de la posición anidada de Avialae dentro de Dinosauria han confundido la distinción lógica de las preguntas sobre los orígenes de las aves, la evolución del vuelo y la distribución filogenética de las plumas. Motivados por un artículo de *Perspectivas* que apareció recientemente en *The Auk* con numerosas imprecisiones fácticas, presentamos una revisión del conjunto completo de hechos relacionados con el debate sobre el origen de las aves y abordamos las críticas equivocadas que se presentan en dicho artículo de opinión.

Palabras clave: Avialae, dinosaurios terópodos maniraptores, evolución de las aves, evolución de las plumas, evolución del vuelo, sistemática filogenética

INTRODUCTION

The evidence supporting the hypothesis that birds (i.e. Avialae sensu Gauthier and de Queiroz 2001) are derived maniraptoran theropod dinosaurs is overwhelmingly convincing in its sheer quantity and interdisciplinary breadth. Data and analytical results supporting the dinosaurian ancestry of birds and the monophyly of Avialae and Aves include examples from morphology and molecular sequence-based phylogenies, discovery of unequivocally feathered non-avian dinosaurs, studies of nesting behaviors and egg morphology shared by avian and non-avian dinosaurs, inferences regarding soft-tissue anatomy (including correlations with metabolic rates), and histological studies bearing on growth rate and genome size. In contrast to the voluminous evidence supporting the dinosaurian ancestry of birds, putative evidence supporting alternative, less parsimonious hypotheses of avian origins is practically nonexistent, largely refuted and, at best, controversial.

A recent *Perspectives in Ornithology* article characterized the debate concerning avian origins as ongoing (Feduccia 2013). This debate has been settled in the minds of all but a handful for decades and the majority of the scientific community has moved away from arguments over the origin of birds and on to other more compelling specific questions and studies regarding avian evolution. Although we find it difficult to believe that, as the article states, “a growing number of ornithologists are questioning the dinosaurian origin of birds” (Feduccia 2013:1), if true, there can be no better motivation to address the points that were deftly woven into a seemingly cogent argument. In much the same way as creationists rebooted their flawed arguments against evolution by rebranding them as “intelligent design,” the recent *Perspectives in Ornithology* article (Feduccia 2013) attempts to resurrect arguments (see Feduccia 2002, Feduccia et al. 2005) against the dinosaurian origin of birds that have been scientifically refuted (e.g., Prum 2002, 2003). Spurious conclusions are yielded by an increasingly blurry focus on an ever smaller subset of available data as well as misunderstanding of the application of contemporary, field-normative phylogenetic methods and the theoretical support for those methods.

Criticisms leveled against the hypothesis that birds are theropod dinosaurs fall into 2 broad categories: 1) selective presentation of anatomical and evolutionary data, including conflation of hypotheses regarding the origin of birds, the evolution of feathers, and the evolution of flight; and 2) methodological and theoretical issues, including flawed logic and false statements concerning phylogenetic systematics. In the interest of providing the ornithological community with a summary of the overwhelming evidence for the dinosaurian ancestry of birds, we address the points

discussed by Feduccia (2013). When the full complement of facts bearing on the origin of birds, avian flight, and feathers are considered, only a single conclusion can be reached: living birds are highly derived, extant dinosaurs.

Anatomical and Evolutionary Misinterpretations

History of the avian origins debate. Current “paleontological” and “ornithological” views on the origin of birds are not opposed. Although the avian origins debate was a fascinating episode in the history of previous centuries, those debates have little bearing on the current evidence for avian ancestry that has been amassed over the last 3 decades. Feduccia (2013) highlighted the theories of some early researchers (e.g., de Beer 1954, 1956), while ignoring others (e.g., Huxley 1867, Lowe 1935). There were many scientists from Huxley’s time onwards who supported the idea that birds were derived from dinosaurian ancestors. However, some of these hypotheses involved a diphyletic and ancient origin of birds (i.e. Lowe 1935). During the time of Huxley, workers emphasized character similarities, leading to incorrect classifications such as that considering penguins separate from other birds that were considered at that time to be allied with dinosaurs (Brown and van Tuinen 2011).

While criticizing modern classifications and advocating character similarities of his own, Feduccia claims that “the field of avian evolution seems clearly back in line with the Thomas Huxley and Percy Lowe school of thought” (Feduccia 2013:4), apparently implying that modern paleontologists advocate an ancient (Upper Paleozoic) and multiple origin hypothesis of extant birds. That viewpoint is clearly not supported by recent reviews on the subject (e.g., Chiappe and Witmer 2002, Mayr 2009, 2014, Lee et al. 2014). We submit that molecular data from extant taxa alone cannot establish the monophyly of birds relative to other Dinosauria. But the monophyly of crown Aves, the radiation of all living birds (i.e. Aves), with respect to extant Crocodylia, is overwhelmingly supported by the results of a vast array of phylogenetic analyses of molecular sequence and morphological data (e.g., Mayr and Clarke 2003, Cracraft et al. 2004, Hackett et al. 2008, Jarvis et al. 2014). Although Huxley (1867) and Lowe (1935) were correct in some aspects of their respective hypotheses on avian origins, Feduccia’s (2013:3) characterization of the paleontological and systematic communities as espousing ideas “in-line with the theories of Huxley and Lowe” is a gross misrepresentation.

Feduccia (2013) conflates the debate on avian origins with the debate regarding the evolution of flight and characterizes the ground-up theory of flight evolution as “popular among paleontologists” (Feduccia 2013:4), implying that ground-up theories have been proposed only in conformity with that paradigm (i.e. the theropod origin of birds). That assumption is fundamentally incorrect on 2

accounts: 1) epistemologically, because how avian flight originated and the evolutionary relationships of birds are not specifically linked; and 2) historically, because there are many paleontological researchers who have argued in favor of the “BMT hypothesis” (Birds are Maniraptoran Theropods) while simultaneously advocating an arboreal or gliding origin of flight (Chatterjee 1997, Xu et al. 2000, 2003, Zhang et al. 2008) that Feduccia has referred to as “trees-down.”

How and at what phylogenetic juncture flight evolved (i.e. did flight evolve first in non-avian theropods?) is a logically distinct question from the evolutionary relationships of birds (Makovicky and Dyke 2001). Inferences of phylogeny in extinct Dinosauria are based on extensive morphological character data (current theropod datasets include 850+ characters; Choiniere et al. 2010, Xu et al. 2011, Turner et al. 2012, Agnolín and Novas 2013, Godefroit et al. 2013, Brusatte et al. 2014). Contemporary systematists do not propose relationships based on plausibility of functional scenarios. Rather, the functional scenarios must conform to the constraints of anatomical data concerning the evolutionary history of a group. In other words, function does not reconstruct phylogeny; homologous characters do.

It has become clear that the “trees-up” versus “trees-down” scenario is a false dichotomy. Various studies over the past ~9 years (e.g., Heers and Dial 2012) have documented behaviors common across living birds showing that powerful aerodynamic forces can be generated in a terrestrial context using a “partial wing” linked with hind-limb-based locomotion and associated with climbing escape strategies. Additional modeling work has resulted in other proposed ways in which partial wings may function in terrestrial locomotion (Burgers and Chiappe 1999). Feduccia (2013) confuses readers by failing to differentiate passive gliding from active flying when supplying a list of vertebrates that have putatively gone through a “trees-down” scenario. Among terrestrial vertebrates, powered flight has only evolved in birds, bats, and pterosaurs and the acquisition of powered flight in these groups is arguably more complicated than an oversimplified “trees-up” or “trees-down” scenario. Moreover, gliding or even powered flight are behaviors that are impossible to observe directly in extinct animals such as pterosaurs.

Feduccia’s (2013) arguments attempt to show that birds are not nested within dinosaurs (with their supposed origins elsewhere in Reptilia among an undesignated and unknown group), yet he neglects to provide any reasonable alternative to the BMT hypothesis. This has often been the case in several of his earlier papers as pointed out by Prum (2002, 2003) among others. As in the past, more emphasis is placed on “disproving” the BMT hypothesis than identifying the closest relative to birds (Prum 2002, 2003,

Chiappe 2012). Feduccia (2013) cherry-picks potential ancestors or closest relatives of birds from a variety of selected Triassic Archosauromorpha (sensu Nesbitt 2011). Note that Feduccia (2013) refers to these taxa as “archosaurs” and “basal archosaurs,” but that Archosauria is a well-defined, more restricted clade (the most recent common ancestor of birds and crocodiles), and relationships among the near outgroup to Archosauria (i.e. “archosauromorphs”) are not entirely resolved (Nesbitt 2011). Moreover, Feduccia (2013) points out a single shared feature (partially closed acetabulum) in a basal dinosauromorph or other “early archosaurs” but never discusses the inconsistent morphologies present across the entire skeleton. For example, Feduccia (2013) refers to the Triassic taxon *Longisquama insignis* as something that may resemble the ancestor of birds, but fails to mention that this enigmatic taxon has not been recovered as part of Archosauria (Hone and Benton 2007, Nesbitt 2011). Feduccia (2013) relies on the perception of confusion regarding the taxonomy of “early archosaurs” (i.e. archosauromorpha) and their closet relatives as support for his vague hypothesis that characters of *Longisquama* (e.g., a putative “furcula,” or the ray-like integumentary structures or “parafeathers [of Feduccia 2012]” on its back) are avian. The identity of these structures are highly controversial and do not provide support for a non-dinosaurian ancestry of birds (Reisz and Sues 2000, Makovicky and Dyke 2001, Voigt et al. 2009, Buchwitz and Voigt 2012).

Feduccia (2013) further suggests that the appearance of birds in the Triassic supports an “early archosaur” view of the ancestry of birds. However, there is no evidence for the presence of birds in the Triassic. Purported Late Triassic bird tracks in Argentina described by Melchor et al. (2002) have since been shown to be Eocene in age (Melchor et al. 2013) and putative Triassic avialan taxon *Protoavis* has been shown to be a chimaera (Witmer 2001). The earliest fossil records of feathered forms remain limited to the Late Jurassic (e.g., *Archaeopteryx*, *Anchiornis*).

Protofeathers, feathers, and melanosomes. Feduccia (2013) interprets the integumentary structures of *Sino-sauropteryx* as degraded collagen fibers inside the tail based on the works of one scientist, T. Lingham-Soliar, who has argued that collagen fibers are widespread in the fossil record (Lingham-Soliar 1999, 2003a, 2003b, 2008). The discovery of the widespread preservation of melanosomes (which can be identified through scanning electron microscopy) in feathers and integument more broadly, that do not co-occur with collagenous structures (Vinther et al. 2008), provides a tractable, repeatable way to test the protofeather versus collagen nature of integumentary structures. Subsequently, subovate melanosome impressions were identified in a specimen of *Sino-sauropteryx* (IVPP 14202; Zhang et al. 2010). These structures are indistinguishable from melanosomes in extant birds and

phaeomelanin-rich melanosomes from other unequivocally feathered specimens from the Jehol Biota (Li et al. 2010, 2012). Following criticism of the identification of melanosomes in the protofeathers of *Sinosauropteryx* by Lingham-Soliar (2011), Feduccia declared that the nature of these structures as protofeathers has been “firmly refuted” (Feduccia 2013:2). Therefore, an analysis of the work of Lingham-Soliar is warranted herein.

Lingham-Soliar (2011) raises a series of alternative interpretations that can be divided into 3 categories: 1) these structures are collagen fibers that have, during decay, transformed into the observed bead-like structures that have subsequently been misinterpreted as melanosomes; 2) that the refutation of these structures as melanosomes instead of bacteria as originally posed (Wuttke 1983) is still not well founded; and 3) they could be collagen fibers, lined by melanosomes from the decayed overlying integument. The arguments of Lingham-Soliar are too complex to fully tackle here. However, it is obvious from the 3 alternatives proposed above that special pleading is indeed necessary to agree with Lingham-Soliar, and by association Feduccia (2013). Ascribing the proposed protofeathers of *Sinosauropteryx* as collagen fibers is highly untenable for a number of reasons, and is most easily refuted by observations from bird fossils collected from the same localities. The structures in question are not observed in unequivocally feathered avian specimens (e.g., *Confuciusornis*) from the Jehol Biota. If collagen fibers, which are composed of biodegradable protein, can indeed fossilize, then they would be expected to be present as disjunct, underlying structures in at least some of the soft-bodied Jehol specimens, alongside or in place of feathers. Furthermore, no fibers that might be misinterpreted as collagen have been identified in any of the hundreds of choristodere specimens found alongside *Sinosauropteryx* in coeval Chinese deposits (Makovicky and Zanno 2011).

No feathered specimen associated with unequivocal collagen fibers has been observed from the Jehol Biota, and so far the only soft tissues observed represent structures that were originally melanic (i.e. skin, feathers, eyes, liver, and the hair of mammals [see Rougier et al. 2003]). The iconic specimen of *Sinosauropteryx*, which was the first feathered non-avian dinosaur to be uncovered in the Jehol Biota (Ji and Ji 1996), represents a particularly good example of the pure melanic nature of the soft tissues found associated with vertebrates. The specimen preserves protofeathers with evidence of among feather color banding (Li et al. 2010) on the tail, as well as organic remains of the eye and liver. Although that particular specimen has not yet been made available for destructive analysis, melanosomes associated with color banding have been positively identified in other specimens of *Sinosauropteryx* (Zhang et al. 2010). Furthermore, melanosomes have been recovered in the fossil eyes of early Eocene birds

(Vinther et al. 2008) and fishes (Lindgren et al. 2012), and in livers of fossil frogs, salamanders (J. Vinther pers. obs.), and in various other dinosaurian and non-dinosaurian taxa from the Jehol Group (Li et al. 2012, 2014a). Moreover, Lingham-Soliar does not provide a feasible alternative explanation for the observed color banding along the tail of *Sinosauropteryx* (Lingham-Soliar 2011, 2012). The color banding appears in a rhythmic succession with light and dark bands spanning the length of several vertebrae, as is well illustrated in a different specimen than that figured by Lingham-Soliar (2012, figures 1, 6; IVPP V12415). Additionally, the argument that collagen fibers might be lined by melanosomes (Lingham-Soliar and Plodowski 2010) is a case of particularly special pleading. Arguments for an unfeathered *Sinosauropteryx* are not supported by the mounting evidence for the presence of integumentary structures preserving melanosomes in theropod and ornithischian dinosaurs that can be homologized with avian feathers (Li et al. 2010, 2012, Zhang et al. 2010).

Finally, the argument that protofeathers would be similar to downy feathers of chicks, which could become wet, collapse, and lose insulating capability, is a straw man. The protofeathers of taxa such as *Beipiaosaurus*, *Yutyrannus*, and *Dilong* (as well as several other theropod and ornithischian dinosaurs not from the Jehol Biota [Rauhut et al. 2012, Zelenitsky et al. 2012, Godefroit et al. 2014]) are of much more robust dimensions and quill-like morphology than the down of chicks (Xu et al. 1999, 2004, 2009a, 2009b, 2009c, 2012). As such, there are no data to support Feduccia's (2013) proposed correlations between the down of chicks and protofeathers.

Ulnar quill knobs. Quill knobs have been proposed as evidence for feathers in *Velociraptor* (Turner et al. 2007b). Although well-preserved feathers representing multiple stages of feather evolution offer more direct evidence of feathering in dinosaurs, the relationship between quill knobs and feathers, as well as their distribution in fossil and extant taxa, deserves further clarification in light of criticism (Feduccia 2013). Quill knobs provide an osteological correlate for a soft tissue structure (ligamentous attachment of feathers to bone) that does not always fossilize. Quill knobs are a prime example of a positive one-way osteological correlate (sensu Geisler and Luo 1998): the soft tissue structure, ligamentous attachments of feathers to the ulna, is always present in extant taxa that bear the osteological correlate (quill knobs), but may still be present even when that osteological correlate is absent. As such, the distribution of feathers can potentially be underestimated, but never overestimated, in the fossil record in cases where only skeletal remains are available. “Absence” of evidence for quill knobs in *Ichthyornis* (see Clarke 2004), or in other extant birds and extinct dinosaurian taxon, does not equal evidence of absence of feathers when a proper comparative context is observed.

Thus, the absence of quill knobs in both non-avian theropods and Mesozoic birds, contrary to statements by Feduccia (2013), is of no relevance to determining the evolutionary relationships of birds with other amniotes.

Dromaeosaurs, convergence, and the origin of flight.

Ever since the discovery that some paravians had long pennaceous feathers not just on the on the forelimb but also on hindlimbs, the function of these structures has been hotly debated. In some taxa (notably *Microraptor zhaoianus*; see Turner et al. 2007a, Li et al. 2012) these feathers are asymmetric and have been considered by many to be indicative of the use of the hindlimbs in volant activity (Xu et al. 2003, 2009b, Alexander et al. 2010). Others have disagreed, and everything from ground-dwelling cursor, to biplane glider, to “tetrapteryx” has been proposed as models pertaining to the evolution of avian flight (Padian and Dial 2005, Chatterjee and Templin 2007, Alexander et al. 2010). Such hindlimb feathers are known to have a wide (and ever increasing) phylogenetic distribution. Shorter leg feathers are now known in several troodontids and dromaeosaurs and even *Archaeopteryx* and enantiornithines (reviewed by Clarke 2013). While an aerodynamic function of the hindlimb feathers is debated (Padian and Dial 2005, Foth et al. 2014), that debate has no bearing on bird origins.

In analyzing the same information on microraptorine feathering, but to our knowledge not the actual specimens, Feduccia (2013:6) attempts to make the case that microraptorines are unrelated to dromaeosaurids and are in fact “derivatives of, rather than being ancestral to, the early avian radiation”; they are birds. Feduccia (2013) contradicts himself by suggesting that dromaeosaurine dinosaurs that have been systematically placed as dinosaurs based on boney evidence for nearly 80 years, suddenly become birds with the discovery of their feathers. Every time microraptorine dromaeosaurs have been analyzed using all available character data (hundreds of scored characters) phylogenetic analysis yields a placement close to birds, within Paraves, but not as “birds” (e.g., Turner et al. 2012, Xu et al. 2012, Han et al. 2014, Brusatte et al. 2014). When only unfeathered raptors such as *Velociraptor* or *Troodon* were known, Feduccia denied any relevance of those fossils to bird origins (Feduccia 1999), but now that microraptorines are known to share derived characters with this taxon, those characters are ignored and the feathers present in the specimens are interpreted as evidence that they are birds. That microraptors and birds share characters such as feathers is only more evidence in favor of the theropod ancestry of birds, not the contrary.

Only vague and unsupported assertions are provided in reference to the statement that microraptorines are “bristling” with avian characters that show they are birds and have been ignored (Feduccia 2013:6). In a flurry of seemingly contradictory ad hoc argumentation and straw

men, Feduccia (2013:6) proposes microraptorines lie outside Avialae because of a putatively closed acetabulum (not borne out by the actual specimens) but inside of Avialae because of their hand morphology that is, according to Paul’s (2002:407) arbitrary criteria, “better suited for supporting primary feathers than the hand of *Archaeopteryx*.” Furthermore, and again without providing any empirical support, Feduccia (2013) states that long feathers on the hindlimbs would be maladaptive in an animal that was cursorial. This argument is apparently intended to support the supposition that *Archaeopteryx* is not a dinosaur. Dinosaur paleontologists have described many arboreal forms, and by contrast, there are many examples both from the Mesozoic and alive today. Moreover, an analysis of microraptorines and other purportedly arboreal non-avian theropods found that microraptorines strongly cluster with terrestrial tetrapods (Dececchi and Larsson 2011).

The origin of feathers, the origin of flight, and the origin of birds have been conclusively shown to be separate evolutionary events and future discussion of these macroevolutionary changes should not conflate them. Much of the confusion inherent in Feduccia’s (2013) arguments stems from a basic misunderstanding of modern systematics, a viewpoint stemming from the earlier taxonomic philosophy that there need be a suite of “key” characters that define groups, instead of the congruence of all characters which support a specific hierarchy. For example, even though snakes, limbless lizards, caecilians, and amphisbaenians all lack limbs (i.e. morphological convergence), we nonetheless consider all of them tetrapods, as they are descended from a limbed common ancestor. A related example would be the statement that there is “no reasonable morphological definition of theropod” (Feduccia 2013:6). There is no need or empirical support for definitions of the names for taxonomic groups: arguing that just because a taxon has pennaceous feathers, it cannot be a dinosaur and must be a bird, could simply expand a proposer’s membership of “Aves” to include the small raptor dinosaurs in Dromaeosauridae and Troodontidae but have no bearing on the evolutionary relationships among taxa recovered from analysis.

Theoretical and Methodological Misunderstandings

China’s contribution to the avian origins debate.

Feduccia (2013) suggests that the Chinese fossils from the Late Jurassic–Early Cretaceous of northwestern China (Daohugou and Jehol Biotas), which have provided much of the evidentiary basis of the renaissance in the study of the origin and early evolution of birds, feathers, and flight, are “largely inaccessible in China” (Feduccia 2013:1). Far from inaccessible, China is a cosmopolitan hub for biological research across a broad swath of scientific

disciplines, and the discovery of China's diverse Mesozoic vertebrate faunas have drawn researchers from around the world to China at a much greater pace than at any time in its history. Consequently, we would suggest that these Chinese fossils actually are among the most intensely studied examples today, with many international teams having traveled to China to examine them first hand, to conduct field work in order to collect additional specimens, and to collaborate with Chinese institutions on the description of those fossils in international peer-reviewed journals (e.g., Zhou et al. 2002, Clarke et al. 2006, Lamanna et al. 2006, Xu et al. 2009a, Li et al. 2010, 2012, 2014b, Zhang et al. 2010, Gao et al. 2012, O'Connor et al. 2013, Han et al. 2014). In fact, the fossils of non-avian dinosaurs and early birds that are curated at the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing (one of many Chinese institutes curating vertebrate fossils important to this discussion) received 81 international visitors from 15 countries between January 2010 and March 2013 (this does not include visitors working on other taxa; IVPP collection use data supplied by XX and TAS). Moreover, Chinese fossils pertinent to this debate have, at times, been made available for study and displayed in museums worldwide (e.g., Yale Peabody Museum 1999, American Museum of Natural History 2001, San Diego Museum of Natural History 2005). Feduccia has himself been part of such international working groups through his collaboration with Chinese researchers on Chinese fossils (e.g., Hou et al. 1995, 1996, 1999, Lingham-Soliar et al. 2007), and a previously unpublished photograph of a Chinese specimen is included in his recent opinion paper (provided to him by Zhonghe Zhou, Director of the Institute of Vertebrate Paleontology and Paleoanthropology; Feduccia 2013, figure 5). Thus, Chinese fossils can hardly be characterized as "inaccessible" and the individual fossils that convincingly support the dinosaurian ancestry of birds have received a great deal of international scrutiny over a relatively short period of time (i.e. since their discovery <30 years ago).

Feduccia (2013:1) laments that many Chinese fossils bearing on avian origins have been only "preliminarily or superficially reported in the journals *Nature* and *Science*." While it is true that a number of important fossils key to this debate await monographic treatment, several statements seem incongruous given that Feduccia has himself been an author on such brief reports on Chinese fossils in both of those journals (Hou et al. 1995, 1996, 1999), articles that have not resulted in the detailed follow-up studies that he criticizes others for not writing. Fortunately, a number of other important specimens and/or taxa have been the focus of extensive descriptions (e.g., Chiappe et al. 1999, Turner et al. 2007a, 2012, Xu et al. 2009a). Details and lengthy analyses have often been made freely available as online supplements (e.g., Xu et al. 2009b, >100

pages of supplementary material). Moreover, the pace of discovery and description of new fossil specimens has steadily increased across a variety of journals and the appearance of in-depth papers on early birds and closely related non-avian theropods (many with feathers) is ever more frequent (Chiappe et al. 1999, 2008, 2014, Currie and Chen 2001, Clarke and Norell 2002, Hwang et al. 2002, Norell and Xu 2005, Clarke et al. 2006, Lamanna et al. 2006, Gao et al. 2012, Li et al. 2012, 2014a, O'Connor et al. 2012, 2013, Chinsamy et al. 2013). Undoubtedly, studies on the diversity of non-avian dinosaurs and early birds from the Daohugou and Jehol Biotas have resulted in a wealth of novel information about the anatomy of these animals and its relevance for understanding the origin of birds and of their flight.

Phylogenetics, hypothesis testing, and censorship.

Feduccia (2013) claims that phylogenetic systematics is a nonfunctional methodology that is incapable of producing evolutionarily realistic hypotheses and points out that many morphology-based hypotheses have been overturned by molecular data (Feduccia 2013:3). While it is true that some phylogenetic hypotheses for deep relationships within living birds have been affected and sometimes overturned by the addition of molecular sequence data, the majority of morphology-based hypotheses have been substantiated by analysis of molecular data and the combination of morphological and molecular data is a valuable strategy for inferring relationships among extant and extinct organisms (e.g., Wiens 2009, Wiens et al. 2010). Additionally, some molecular hypotheses for vertebrate relationships turn out to be unfounded, with either morphology or further molecular analysis providing more compelling alternatives (e.g., whales; Milinkovitch et al. 1993). It should also be noted that while molecular data do sometimes overturn morphology-based hypotheses, those molecular data are analyzed using the same phylogenetic systematic methods that Feduccia (2013) criticizes.

Feduccia (2013) argues that his non-phylogenetic interpretation of morphology is somehow superior to hypotheses generated using the same data but in an arguably less bias-prone and reproducible manner. Is Feduccia (2013) suggesting that we abandon generating hypotheses in a systematic way? It is hard to believe this is a viable proposal for the ornithological community. His statement regarding how "the field has taken a turn away from a standard falsificationist approach to verificationist arguments" (Feduccia 2013:3) would appear to argue in favor of using a repeatable experimental methodology such as "cladistic" inference. Additionally, Feduccia's (2013) description of the many changes in non-phylogenetic opinion through time regarding the origin of birds (e.g., Huxley, Heilmann, de Beer, Ostrom) demonstrates quite succinctly the disparity that results from hypotheses generated based on "expert opinions."

Data matrices for phylogenetic analysis of extant and extinct taxa have not only grown larger over time (in both taxa and characters), but the number of analyses that have been run on the dinosaur-to-bird transition has substantially increased over the last few decades. Multiple independent teams strive to publish the latest and most data inclusive hypotheses concerning the precise position of key taxa. If phylogenetic systematic methods are broadly recognized as field standard for generating evolutionary hypotheses concerning clades of extant birds, why would another standard be acceptable for assessing life in the past? Feduccia may perhaps garner some supporters through talking negatively about “cladists” (as was popular when he started writing on this topic 25+ years ago), but the lay reader should realize that he is taking aim at phylogenetics writ broadly. Contemporary systematic paleontologists use a variety of estimators to investigate relationships among extinct taxa (e.g., Bayesian methods, ML, and parsimony) and most do not self-identify as cladists.

As Feduccia (2013) correctly notes, alternative tests for estimating relatedness lack the rigor, falsifiability, and repeatability provided by phylogenetic systematics and other phylogenetic comparative methods. If the BMT hypothesis is incorrect, it should have lost support rather than become more strongly supported with the addition of new taxa and data over time. However, over the last 20 years the BMT hypothesis has not only become more strongly supported, but the data are now so rich and diverse (supported by morphology, behavior, genomics, metabolic studies, histology) that when considered in combination with the plethora of “intermediate” taxa now known from the fossil record, the division between what is and what is not a “bird” within Maniraptora has become blurred. Limited degrees of taxonomic uncertainty are expected if we are to theoretically “map” the point where 2 diverse lineages initially diverged by applying phylogenetic systematic methods. Given the flurry of new discoveries of taxa and characters (e.g., *Anchiornis* and *Xiaotingia*), even the avian status of *Archaeopteryx* (versus an alternative nearby placement within paravian dinosaurs) has come into question (Xu et al. 2011, Lee and Worthy 2012). Phylogenetic hypotheses are not the result of orthodoxy, but hypothesis modification and refinement resulting from the acquisition and analysis of new data. In reference to the phylogenetic results of Lee and Worthy (2012), Feduccia (2013:7) states that “[they] reinstated the iconic Urvogel to its *rightful place*” [emphasis added]. The systematic position of any taxon is determined by analysis of available data, regardless of previous hypotheses or sentimental attachment to specific hypotheses.

Although Feduccia (2013) acknowledges the utility of phylogenetic methods using molecular and biogeographic data, he contends that phylogenetic analyses based on morphological data are doomed to failure owing to missing

data, convergence, and heterochrony. Feduccia (2013) asserts that DNA-based data often reject morphological hypotheses (e.g., supposed morphological support for a loon–grebe clade) but ignores the fact that most analyses of morphology and molecules produce congruent results (e.g., Omland 1994, Jablonski and Finarelli 2009). For example, on the basis of morphological data, consensus was reached regarding the monophyly and relative placement of many major avian subclades (e.g., Paleognathae, Neognathae, Galloanseres, and Neoaves and regarding the well-nested position of passerines; reviewed in Mayr and Clarke 2003). Similarly, Feduccia (2013) asserts that massive convergence related to flightlessness should be accepted in the dinosaurs he selects to be birds with no basis in data, whereas phylogenetic analyses of large morphological character sets should be dismissed. Tellingly, this selective acceptance effectively translates to a rejection of any phylogenetic study of avian origins, which must rely on fossil data and hence on morphological characters. An extensive body of literature supports the efficacy of morphology in phylogenetic analysis (e.g., Huelsenbeck 1991, Smith 1998, Wiens 2000, 2004, Jenner 2004, Smith and Turner 2005) and those data will continue to be integral to testing evolutionary hypotheses.

Most importantly, after wholly condemning phylogenetic systematics, Feduccia (2013) characterizes two phylogenetic studies that happen to agree with his *opinion du jour* as “landmark” and “impeccably rendered” (Feduccia 2013:5, Maryańska et al. 2002, James and Pourtless 2009). Feduccia (2013) proposes that these phylogenetic results are not sufficiently cited without considering *why* these works are not highly regarded or cited by other systematists. In the case of the recent work by James and Pourtless (2009), a search of Google Scholar (<http://scholar.google.com/citations?user=QhX97JAAAAAJ&hl=en>; accessed August 30, 2013) revealed the work had been cited at least 12 times by the date Feduccia’s (2013) paper was submitted to *The Auk* (i.e. October 11, 2012). The results of James and Pourtless (2009) recover weak support for alternative hypotheses of avian origins including mostly unresolved clades comprising birds and other maniraptorans. However, those analyses are biased by egregious taxon and character sampling issues, incorrect character scorings, and illogical character state definitions that amount to rather acute data manipulation (Makovicky and Zanno 2011, Turner et al. 2012, Brusatte et al. 2014). No plausible, phylogenetically contextualized challenge to the hypothesis that birds are nested within Maniraptora exists.

One major criticism that Feduccia (2013:8) levels at phylogenetic analyses supporting a theropod origin of birds is that missing data renders the relevant matrices “risible.” Certainly, missing data can present serious challenges to phylogenetic analyses. However, the fact that fossil taxa tend to introduce missing data into analyses

should not be interpreted as a flaw of the phylogenetic method or of any given hypothesis on bird origins, but rather a statement about data quality and a consequence of taphonomy. It should also be remembered that any analysis of molecular data including taxa not sequenced for all assessed genes or partially non-overlapping gene sets contain missing data. Importantly, many modern molecular-only phylogenetic analyses, especially those using whole genome or transcriptome data, employ data matrices with a substantial fraction of missing data (e.g., Dunn et al. 2008). Therefore, missing data should not be taken as a means of bolstering support for molecular over morphological analyses of phylogeny. An expansive body of literature has been devoted to issues pertaining to missing data (Kearney 2002, Kearney and Clark 2003, Wiens 2003a, 2003b, and citations therein). Empirical and theoretical studies have shown that even taxa with highly incomplete sets of character scorings can be placed with a high degree of accuracy, and that excluding taxa that introduce missing data into an analysis a priori risks discarding information and may negatively impact the accuracy of analytical results (Wiens and Reeder 1995, Wiens 1998, 2003a, 2003b, Kearney and Clark 2003, Norell and Wheeler 2003, Wiens and Tiu 2012).

As an example of the supposed “fragility” of phylogenetic analyses of theropods, Feduccia (2013: Table 1) reprinted a portion of a data matrix from the analysis of Turner et al. (2007b), which show a high proportion of data cells that were not scored owing to the incomplete preservation of 7 fossil taxa. It is illustrative to note that removing these 7 taxa from the Turner et al. (2007b) matrix and reanalyzing the pruned dataset actually results in reduced resolution within Dromaeosauridae. *Mahakala*, *Graciliraptor*, and *Jinfengopteryx* preserve important combinations of characters that helped to unite the various subclades within Dromaeosauridae. Nevertheless, dromaeosaurids remain the sister taxon to troodontids and the birds *Archaeopteryx* and *Confuciusornis* remain deeply nested among theropod dinosaurs as the sister taxon to dromaeosaurids + troodontids even when these incompletely scored taxa are excluded from the analysis (Turner et al. 2007b). While it is true that there is a high proportion of missing entries (~54% mean per species) in the data matrix of Turner et al. (2007b), this is not unique to phylogenetic datasets that include fossils and/or use morphological characters, as noted above and illustrated in a recent molecular analysis of squamates (Pyron et al. 2013; 81% mean per species). Given the body of research indicating it is better to include species even if they are relatively incompletely sampled (be it due to incomplete skeletal preservation or incomplete molecular locus sampling), Feduccia’s (2013) focus on missing entries in a data matrix as a source of “fragility” is misplaced.

A related criticism Feduccia (2013) leveled at the Turner et al. (2007b) study is that the late geological occurrence of *Mahakala* (relative to the divergence between Deinonychosauria and Avialae) makes this taxon irrelevant to reconstructions of body size in Paraves. How this bears on bird origins is unclear. Furthermore, his criticism ignores that it is both possible and indeed typical to account for branch lengths when estimating ancestral traits using either extant or extinct species (or both; Pagel 1993, 1994, 1997, 1999, 2006, Martins 1994, Butler and King 2004, Harmon et al. 2010, Eastman et al. 2011). One can estimate the relative contributions of branch length and total phylogenetic path length when estimating ancestral values (e.g., Martins and Hansen 1997, Martins 2004, Pagel 2006), thereby making it possible to assess whether branch length *needs* to be accounted for or whether linear parsimony methods (like those utilized by Turner et al. 2007b) are appropriate. Moreover, Feduccia’s (2013) criticism is remarkable because excluding fossil taxa can increase the lengths of internal branches in a tree, and indeed many studies have demonstrated the positive impacts of including fossil taxa in ancestral state reconstructions (e.g., Polly 2001, Finarelli and Flynn 2006, Albert et al. 2009, Slater et al. 2012). If one were to accept the premise that only taxa dated to the precise age of a given node can provide information about the evolution of quantitative characters such as body mass and brain volume, then all phylogenetic comparative studies sampling only extant species would have to be considered worthless. Few comparative biologists would advocate for this paradigm, and many ornithologists would disagree with having their studies consigned to the waste bin via this line of reasoning.

Feduccia’s (2013) example of comparing *Amphioxus* and tunicates as putative ancestors of vertebrates misrepresents the concept of sister groups and evidences a profound misunderstanding of phylogeny estimation. By default, because *Amphioxus* and tunicates are living, neither can be the ancestor of vertebrates. According to genomic evidence, tunicates share a more recent common ancestor with vertebrates, but this does not make living tunicates more ancestral or the ancestor to vertebrates, nor are vertebrates the ancestor of tunicates. These taxa contain a combination of ancestral characters shared with the taxon of interest and apomorphic characters unique to that sister taxon. Estimation of ancestral character states is what evolutionary biologists seek in order to understand the origin of vertebrates. In order to ascertain the identity of these shared primitive characters, it is not essential to sample the actual ancestral species. Feduccia instead claims however, that “considering that advanced avian wings were present in the Jurassic, trying to understand the origin of avian wings and remiges by studying Late Cretaceous theropod dinosaurs seems to stretch credulity” (Feduccia 2013:2). This statement is analogous to considering all

traits found in extant species to be useless to investigating the evolution of traits in the past. For instance, is the study of mammalian reproductive tracts in monotremes and marsupials irrelevant to understanding the origin of the placental system? And what about molecular data—if only “ancestors” should be sampled then is any sort of phylogenetic hypothesis based on molecular data inherently flawed (see below)? The combination of neontological and paleontological data is critical to developing a comprehensive understanding of evolution.

It is unclear how Feduccia (2013) can value molecular data for phylogenetic reconstruction and other evolutionary investigations of bird origins yet overlook studies that indicate similar genome size in birds and non-avian dinosaurs (Organ et al. 2007). Feduccia (2013) directs the reader’s attention to a flawed ancient DNA study (Feduccia 2013:9), while ignoring recent progress in this discipline (Green et al. 2010, Krause et al. 2010, Gronau et al. 2011, Shapiro and Hofreiter 2014). In Feduccia’s words, “Cladistics is a statistical comparison of large numbers of human coded, often trivial, skeletal features, that are computer ordered in hierarchical fashion to produce a branching cladogram that, although naive, becomes the true family tree or phylogeny until a competing cladogram, using the same methodology, offers a differing phylogeny. Aside from the obvious problem of circularity (reciprocal illumination), given myriad complexities, such a simplistic approach to the exceedingly complex problem of phylogenetic reconstruction is unreasonable, especially in view of so many morphological phylogenies being negated by subsequent DNA comparisons” (Feduccia 2013:3). This appears to be a general attack on phylogenetics. We point out that in conflict with his impression of morphology-based phylogenetics, he accepts molecular phylogenies which are similarly based on relatively trivial features (i.e. single nucleotides), that are also computer aligned and coded in various fashions, and in some cases only treated with statistical modeling. In most cases, parsimony reconstruction results in similar hypotheses to those generated using likelihood or Bayesian approaches. Furthermore, to suggest that phylogenetic approaches in general lead to conflict between morphology and molecular data is inaccurate. Certainly, several important avian systematic conflicts remain (e.g., parrot–songbird relationships), but deeper cladogenetic events are not in doubt (e.g., ordinal monophyly, Paleognath–Neognath division). Conflict may exist to the extent of a modern bird lineage having been misclassified to order (e.g., buttonquails), but this is rare. No phylogenetic analysis has ever recovered any avian taxon as part of squamates or crocodiles, yet this is the level of error imputed to phylogeneticists working on bird origins by Feduccia (2013). Feduccia’s (2013) suggestion that birds are erroneously grouped among theropods because of human misinterpretation of character definition

or because of massive convergence in anatomy should, to use his words, strain credulity. Feduccia (2013) quotes Carl Sagan, who said, “Extraordinary claims require extraordinary evidence.” In the face of thousands of remarkable fossils preserving exceptional detail, capturing behavior, and 30 years of recent research on these fossils by competing labs as well as the development of phylogenetic methods that are field normative in both ornithology and paleontology, it is the proposal that birds are not dinosaurs and in fact related to mysterious and poorly known or undiscovered Triassic, tree-living, basal archosaurs that bears the burden of an extraordinary claim.

CONCLUDING REMARKS

Feduccia (2013) concludes by stating that the views he expressed “may appear new” (Feduccia 2013:10). Quite the contrary, the views expressed by Feduccia (2013) appear to us as scientifically groundless rehashing of ideas (Feduccia 1999, 2002, 2012, 2013) that have been previously and convincingly refuted (e.g., Prum 2002, 2003). Meanwhile, the hypothesis that birds are maniraptoran theropods has consistently gained support as new fossil discoveries have been described. As scientists in the 21st century, we cannot ignore or discard data that are inconvenient or do not fit into a preconceived notion. Furthermore, as systematists we should avail ourselves of the empirical tools used by *all* of our contemporaries in fields as diverse as virology, genomics, paleontology, and neontology. Many great strides in scientific knowledge have been made as the result of the analysis of “problematic” data. We strive to find hypotheses that explain all of the available data (not just those data meeting an arbitrary minimum level of completeness or triviality, to paraphrase Feduccia). Inclusiveness of data is a pillar of modern systematics (Wheeler et al. 2013). Science should not be done by committee, but should be able to bear the weight of the preponderance of evidence. Yet, it should also be open to new data changing (sometimes radically) how and which hypothesis is the best supported. Opinions and the like should stay in that category unless they can be tested or otherwise supported by data, and they should be clearly labeled as such in the published literature. Ornithologists concerned with the continued progress of our understanding of bird origins will see only further data accumulate to inform the precise affinities of Aves within theropod dinosaurs.

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LITERATURE CITED

- Albert, J. S., D. M. Johnson, and J. H. Knouft (2009). Fossils provide better estimates of ancestral body size than do extant taxa in fishes. *Acta Zoologica* 90:357–384.
- Alexander, D. E., E. Gong, L. D. Martin, D. A. Burnham, and A. R. Falk (2010). Model tests of gliding with different hindlimb configurations in the four-winged dromaeosaurid *Micro-raptor gui*. *Proceedings of the National Academy of Sciences USA* 107:2972–2976.
- Agnolín, F. L., and F. E. Novas (2013). *Avian Ancestors: A review of the Phylogenetic Relationships of the Theropods Unenlagiidae, Microraptor, Anchiornis and Scansoriopterygidae*. Springer, Dordrecht, The Netherlands.
- Brown, J., and M. van Tuinen (2011). Evolving perspectives on the antiquity of the modern avian tree. In *Living Dinosaurs: The Evolutionary History of Modern Birds* (G. J. Dyke and G. Kaiser, Editors). WileyBlackwell, Chichester, UK.
- Brusatte, S. L., G. T. Lloyd, S. C. Wang, and M. A. Norell (2014). Gradual assembly of avian body plan culminated in rapid rates of evolution across dinosaur–bird transition. *Current Biology* 24:2386–2392.
- Buchwitz, M., and S. Voigt (2012). The dorsal appendages of the Triassic reptile *Longisquama insignis*: Reconsideration of a controversial integument type. *Palaontologische Zeitschrift* 86:313–331.
- Burgers, P., and L. M. Chiappe (1999). The wing of *Archaeopteryx* as a primary thrust generator. *Nature* 399:60–62.
- Butler, M. A., and A. A. King (2004). Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *The American Naturalist* 164:683–695.
- Chatterjee, S. (1997). *The Rise of Birds*. John Hopkins University Press, Baltimore, MD, USA.
- Chatterjee, S., and R. J. Templin (2007). Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *Proceedings of the National Academy of Sciences USA* 104:1576–1580.
- Chiappe, L. M., J. Marugan-Lobon, and Z. Zhou (2008). Life history of a basal bird: Morphometrics of the early Cretaceous *Confuciusornis*. *Biology Letters* 4:719–723.
- Chiappe, L. M. (2012). The dinosaur conspiracy. *BioScience* 62:770–772.
- Chiappe, L. M., S. A. Ji, Q. Ji, and M. A. Norell (1999). Anatomy and systematics of Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of Northeastern China. *Bulletin of the American Museum of Natural History* 242:1–89.
- Chiappe, L. M., and L. M. Witmer (Editors) (2002). *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, CA, USA.
- Chiappe, L. M., B. Zhao, J. K. O'Connor, G. Chunling, X. Wang, M. Habib, J. Marugan-Lobon, Q. Meng, and X. Cheng (2014). A new specimen of the Early Cretaceous bird *Hongshanornis longicresta*: Insights into the aerodynamics and diet of a basal ornithuromorph. *PeerJ* 2:e234.
- Chinsamy, A., L. M. Chiappe, J. Marugan-Lobon, C. L. Gao, and F. J. Zhang (2013). Gender identification of the Mesozoic bird *Confuciusornis sanctus*. *Nature Communications* 4:1381.
- Choiniere, J. N., X. Xu, J. M. Clark, C. A. Forster, Y. Guo, and F. L. Han (2010). A basal alvarezsaurid theropod from the early Late Jurassic of Xinjiang, China. *Science* 327:571574.
- Clarke, J. A. (2004). Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). *Bulletin of the American Museum of Natural History* 286:1–179.
- Clarke, J. A. (2013). Feathers before flight. *Science* 340:690–692.
- Clarke, J. A., and M. A. Norell (2002). The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. *American Museum Novitates* 3387:1–46.
- Clarke, J. A., Z. Zhou, and F. Zhang (2006). Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *Journal of Anatomy* 208:287–308.
- Cracraft, J., F. K. Barker, M. Braun, J. Harshman, G. J. Dyke, J. Feinstein, S. Stanley, A. Cibois, P. Schikler, P. Beresford, J. Garcia-Moreno, et al. (2004). Phylogenetic relationships among modern birds (Neornithes): Toward an avian tree of life. In *Assembling the Tree of Life* (J. Cracraft and M. J. Donoghue, Editors). Oxford University Press, New York, NY, USA. pp. 468–489.
- Currie, P. J., and P. Chen (2001). Anatomy of *Sinosauropteryx prima* from Liaoning, northwestern China. *Canadian Journal of Earth Sciences* 38:1705–1727.
- de Beer, G. (1954). *Archaeopteryx lithographica*. A Study Based Upon the British Museum Specimen. British Museum (Natural History), London, UK.
- de Beer, G. (1956). The evolution of ratites. *Bulletin of the British Museum (Natural History)* 4:59–70.
- Dececchi, T. A., and H. C. Larsson (2011). Assessing arboreal adaptations of bird antecedents: Testing the ecological setting of the origin of the avian flight stroke. *PLOS One* 6(8): e22292. doi:10.1371/journal.pone.0022292.
- Dunn, C. W., A. Hejnol, D. Q. Matus, K. Pang, W. E. Browne, S. A. Smith, E. C. Seaver, G. W. Rouse, M. Obst, G. D. Edgecombe, M. V. Sørensen, et al. (2008). Broad taxon sampling improves resolution of the Animal Tree of Life. *Nature* 452:745–749.
- Eastman, J. M., M. E. Alfaro, P. Joyce, A. L. Hipp, and L. J. Harmon (2011). A novel comparative method for identifying shifts in the rate of character evolution on trees. *Evolution* 65:3578–3589.
- Feduccia, A. (1999). *The Origin and Evolution of Birds*, 2nd ed. Yale University Press, New Haven, CT, USA.
- Feduccia, A. (2002). Birds are dinosaurs: Simple answer to a complex problem. *The Auk* 119:1187–1201.
- Feduccia, A. (2012). *Riddle of the Feathered Dragons: Hidden Birds of China*. Yale University Press, New Haven, CT, USA.
- Feduccia, A. (2013). Bird origins anew. *The Auk* 130:1–12.
- Feduccia, A., T. Lingham-Soliar, and J. R. Hinchliffe (2005). Do feathered dinosaurs exist? Testing the hypothesis on

- neontological and paleontological evidence. *Journal of Morphology* 266:125–166.
- Finarelli, J. A., and J. J. Flynn (2006). Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): The effects of incorporating data from the fossil record. *Systematic Biology* 55:301–313.
- Foth, C., H. Tischlinger, and O. W. M. Rauhut (2014). New specimen of *Archaeopteryx* provides insights into the evolution of pennaceous feathers. *Nature* 511:79–82.
- Gao, C., L. M. Chiappe, F. Zhang, D. Pomeroy, C. Shen, A. Chinsamy, and M. O. Walsh (2012). A subadult specimen of the Early Cretaceous bird *Sapeornis chaoyangensis* and a taxonomic reassessment of sapeornithids. *Journal of Vertebrate Paleontology* 32:1103–1112.
- Gauthier, J., and K. de Queiroz (2001). Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name “Aves.” In *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom* (J. Gauthier and L. F. Gall, Editors). Yale University Peabody Museum of Natural History, New Haven, CT, USA. pp. 7–41.
- Geisler, J. H., and Z. Luo (1998). Relationships of Cetacea to terrestrial ungulates and the evolution of cranial vasculature in Cete. In *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea* (J. G. M. Thewissen, Editor). Plenum Press, New York, NY, USA.
- Godefroit, P., A. Cau, H. Dong-Yu, F. Escuillie, W. Wenhao, and G. Dyke (2013). A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* 498:359–362.
- Godefroit, P., S. M. Sinitza, D. Dhouiailly, Y. L. Bolotsky, A. V. Sizov, M. E. McNamara, M. J. Benton, and P. Spagna (2014). A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. *Science* 345:451.
- Green, R. E., J. Krause, A. W. Briggs, T. Maricic, U. Stenzel, M. Kircher, N. Patterson, H. Li, W. Zhai, M. H.-Y. Fritz, N. F. Hansen, et al. (2010). A draft sequence of the neandertal genome. *Science* 328:710–722.
- Gronau, I., M. J. Hubisz, B. Gulko, C. G. Danko, and A. Siepel (2011). Bayesian inference of ancient human demography from individual genome sequences. *Nature Genetics* 43: 1031–1034.
- Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K. Han, J. Harshman, C. J. Huddleston, et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science* 320:1763–1768.
- Han, G., L. M. Chiappe, S. Ji, M. Habib, A. H. Turner, A. Chinsamy, X. Liu, and L. Han (2014). A new raptorial dinosaur with exceptionally long feathering provides insights into dromaeosaurid flight performance. *Nature Communications* 5:4382.
- Harmon, L. J., J. B. Losos, J. Davies, R. G. Gillespie, J. L. Gittleman, W. B. Jennings, K. H. Kozak, M. A. McPeck, F. Moreno-Roark, T. J. Near, A. Purvis, et al. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64: 2385–2396.
- Heers, A. M., and K. P. Dial (2012). From extant to extinct: Locomotor ontogeny and the evolution of avian flight. *Trends in Ecology and Evolution* 27:296–305.
- Hone, D. W. E., and M. J. Benton (2007). An evaluation of the phylogenetic relationships of the pterosaurs and archosaur-omorph reptiles. *Journal of Systematic Paleontology* 5:465–469.
- Hou, L., Z. Zhou, L. D. Martin, and A. Feduccia (1995). A beaked bird from the Jurassic of China. *Nature* 377:616–618.
- Hou, L., L. D. Martin, Z. Zhou, and A. Feduccia (1996). Early adaptive radiation of birds: Evidence from fossils from Northeastern China. *Science* 274:1164–1167.
- Hou, L., L. D. Martin, Z. Zhou, A. Feduccia, and F. Zhang (1999). A diapsid skull in a new species of the primitive bird *Confuciusornis*. *Nature* 399:679–682.
- Huelsenbeck, J. P. (1991). When are fossils better than extant taxa in phylogenetic analysis? *Systematic Zoology* 40:458–469.
- Huxley, T. H. (1867). On the classification of birds: And on the taxonomic value of the modifications of certain of the cranial bones observable in the class. *Proceedings of the Zoological Society of London* 1867:415–472.
- Hwang, S., M. A. Norell, Q. Ji, and K.-Q. Gao (2002). New specimens of *Microraptor zhaoianus*. *American Museum Novitates* 3381:1–44.
- Jablonski, D., and J. A. Finarelli (2009). Congruence of morphologically-defined genera with molecular phylogenies. *Proceedings of the National Academy of Sciences USA* 106: 8262–8266.
- James, F. C., and J. A. Pourtless (2009). Cladistics and the origin of birds: A review and two new analyses. *Ornithological Monographs* 66:1–78.
- Jarvis, E. D., S. Mirarab, A. J. Aberer, B. Li, P. Houde, C. Li, S. Y. W. Ho, B. C. Faircloth, B. Nabholz, J. T. Howard, A. Suh, et al. (2014). Whole genome analyses resolve early branches in the tree of life of modern birds. *Science* 346:1320–1331.
- Jenner, R. A. (2004). Accepting partnership by submission? Morphological phylogenetics in a molecular millennium. *Systematic Biology* 53:333–342.
- Ji, Q., and S. Ji (1996). On the discovery of the earliest fossil bird in China (*Sinosauropteryx* gen. nov.) and the origin of birds. *Chinese Geology* 233:30–33.
- Kearney, M. (2002). Fragmentary taxa, missing data, and ambiguity: Mistaken assumptions and conclusions. *Systematic Biology* 51:369–381.
- Kearney, M., and J. M. Clark (2003). Problems due to missing data in phylogenetic analyses including fossils: A critical review. *Journal of Vertebrate Paleontology* 23:263–274.
- Krause, J., Q. Fu, J. M. Good, B. Viola, M. V. Shunkov, A. P. Derevianko, and S. Pääbo (2010). The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* 464:894–897.
- Lamanna, M., H. You, J. Harris, L. M. Chiappe, S. Ji, J. Lü, and Q. Ji (2006). A partial skeleton of an enantiornithine bird from the Early Cretaceous of northwestern China. *Acta Paleontologica Polonica* 51:423–434.
- Lee, M. S. Y., A. Cau, D. Naish, and G. J. Dyke (2014). Morphological clocks in paleontology, and a mid-Cretaceous origin of crown Aves. *Systematic Biology* 63:442–449.
- Lee, M. S. Y., and T. H. Worthy (2012). Likelihood reinstates *Archaeopteryx* as a primitive bird. *Biology Letters* 8:299–303.
- Li, Q., K.-Q. Gao, J. Vinther, M. D. Shawkey, J. A. Clarke, L. D’Alba, Q. Meng, D. E. G. Briggs, and R. O. Prum (2010). Plumage color patterns of an extinct dinosaur. *Science* 327:1369–1372.
- Li, Q., K.-Q. Gao, Q. Meng, J. A. Clarke, M. D. Shawkey, L. D’Alba, R. Pei, M. Ellison, M. A. Norell, and J. Vinther (2012). Reconstruction of *Microraptor* and the evolution of iridescent plumage. *Science* 335:1215–1219.

- Li, Q., J. A. Clarke, K. Gao, C. Zhou, Q. Meng, D. Li, L. D'Alba, and M. D. Shawkey (2014a). Melanosome evolution indicates a key physiological shift within feathered dinosaurs. *Nature* 507:350–353.
- Li, Q., Z. Zhou, and J. A. Clarke (2014b). A new specimen of the basal enantiornithine *Bohaiornis* from China and the inference of feeding ecology in Mesozoic birds. *Journal of Paleontology* 88:99–108.
- Lindgren, J., P. Uvdal, P. Sjövall, D. E. Nilsson, A. Engdahl, B. P. Schultz, and V. Thiel (2012). Molecular preservation of the pigment melanin in fossil melanosomes. *Nature Communications* 3:824.
- Lingham-Soliar, T. (1999). Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England. *Proceedings of the Royal Society of London, Series B* 266:2367–2373.
- Lingham-Soliar, T. (2003a). Evolution of birds: Ichthyosaur integumental fibers conform to dromaeosaur protofeathers. *Naturwissenschaften* 90:428–432.
- Lingham-Soliar, T. (2003b). The dinosaurian origin of feathers: Perspectives from dolphin (Cetacea) collagen fibers. *Naturwissenschaften* 90:563–567.
- Lingham-Soliar, T. (2008). A unique cross section through the skin of the dinosaur *Psittacosaurus* from China showing a complex fibre architecture. *Proceedings of the Royal Society of London, Series B* 275:775–780.
- Lingham-Soliar, T. (2011). The evolution of the feather: *Sinosauropteryx*, a colourful tail. *Journal of Ornithology* 152: 567–577.
- Lingham-Soliar, T. (2012). The evolution of the feather: *Sinosauropteryx*, life, death and preservation of an alleged feathered dinosaur. *Journal of Ornithology* 153:699–711.
- Lingham-Soliar, T., A. Feduccia, and X. Wang (2007). A new Chinese specimen indicates that 'protofeathers' in the Early Cretaceous theropod dinosaur *Sinosauropteryx* are degraded collagen fibres. *Proceedings of the Royal Society of London, Series B* 274:1823–1829.
- Lingham-Soliar, T., and G. Plodowdki (2010). The integument of *Psittacosaurus* from Liaoning Province, China: Taphonomy, epidermal patterns and color of a ceratopsian dinosaur. *Naturwissenschaften* 97:479–486.
- Lowe, P. R. (1935). On the relationship of Struthionines to the dinosaurs and to the rest of the avian class, with special reference to the position of *Archaeopteryx*. *Ibis* 5:398–432.
- Makovicky, P. J., and G. J. Dyke (2001). Naive falsification and the origin of birds: A commentary. In *New Perspectives on the Origin and Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom* (J. Gauthier and L. F. Gall, Editors). Yale Peabody Museum of Natural History Special Publications, New Haven, CT, USA.
- Makovicky, P. J., and L. E. Zanno (2011). Theropod diversity and the refinement of avian characteristics. In *Living Dinosaurs: The Evolutionary History Modern* (G. J. Dyke and G. Kaiser, Editors). WileyBlackwell, Chichester, UK.
- Martins, E. P. (1994). Estimating the rate of phenotypic evolution from comparative data. *The American Naturalist* 144:193–209.
- Martins, E. P. (2004). COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data. Distributed by the author at <http://compare.bio.indiana.edu/>
- Martins, E. P., and T. F. Hansen (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist* 149:646–667.
- Maryańska, T., H. Osmólska, and M. Wolsan (2002). Avialan status for Oviraptorosauria. *Acta Palaeontologica Polonica* 47:97–116.
- Mayr, G. (2009). *Paleogene Fossil Birds*. Springer-Verlag, Heidelberg, Germany.
- Mayr, G. (2014). The origins of crown group birds: Molecules and fossils. *Palaeontology* 57:231–242.
- Mayr, G., and J. A. Clarke (2003). The deep divergences of neornithine birds: A phylogenetic analysis of morphological characters. *Cladistics* 19:527–553.
- Melchor, R. N., S. De Valais, and J. F. Genise (2002). Bird-like fossil footprints from the Late Triassic. *Nature* 417:936–938.
- Melchor, R. N., R. Buchwaldt, and S. Bowring (2013). A late Eocene date for Triassic bird tracks. *Nature* 495:E1–E2.
- Milinkovitch, M. C., G. Ort, and A. Meyer (1993). Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. *Nature* 361:346–348.
- Nesbitt, S. J. (2011). The early evolution of archosaurs: Relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* 352:1–292.
- Norell, M. A., and W. C. Wheeler (2003). Missing entry replacement data analysis: A replacement approach to dealing with missing data in paleontological and total evidence data sets. *Journal of Vertebrate Paleontology* 23: 275–283.
- Norell, M. A., and X. Xu (2005). Feathered dinosaurs. *Annual Review of Earth and Planetary Science* 33:277–299.
- O'Connor, J. K., L. M. Chiappe, C. Chuong, D. J. Bottjer, and H. You (2012). Homology and potential cellular and molecular mechanisms for the development of unique feather morphologies in early birds. *Geosciences* 2:157–177.
- O'Connor, J. K., Y. Zhang, L. M. Chiappe, Q. Meng, L. Quanguo, and D. Liu (2013). A new enantiornithine from the Yixian Formation with the first enamel specialization. *Journal of Vertebrate Paleontology* 33:1–12.
- Omland, K. E. (1994). Character congruence between a molecular and a morphological phylogeny for dabbling ducks (*Anas*). *Systematic Biology* 43:369–386.
- Organ, C. L., A. M. Shedlock, A. Meade, M. Pagel, and S. V. Edwards (2007). Origin of genome size and structure in non-avian dinosaurs. *Nature* 446:180–184.
- Padian, K., and K. P. Dial (2005). Could 'four-winged' dinosaurs fly? *Nature* 421:E3.
- Pagel, M. (1993). Seeking the evolutionary regression coefficient: An analysis of what comparative methods measure. *Journal of Theoretical Biology* 64:191–205.
- Pagel, M. (1994). Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London, Series B* 255:37–45.
- Pagel, M. (1997). Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26:331–348.
- Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology* 48:612–622.

- Pagel, M. (2006). BayesTraits. v1.0. University of Reading. Available at: <http://www.evolution.rdg.ac.uk/BayesTraits.html>.
- Paul, G. S. (2002). *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*. Johns Hopkins University Press, Baltimore, MD, USA.
- Polly, P. D. (2001). Paleontology and the comparative method: Ancestral node reconstructions versus observed node values. *The American Naturalist* 57:596–609.
- Prum, R. O. (2002). Why ornithologists should care about the theropod origin of birds. *The Auk* 119:1–17.
- Prum, R. O. (2003). Are current critiques of the theropod origin of birds science? Rebuttal to Feduccia, 2002. *The Auk* 120:550–561.
- Pyron, R. A., F. T. Burbank, and J. J. Wiens (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93.
- Rauhut, O. W. M., C. Foth, H. Tischlinger, and M. A. Norell (2012). Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proceedings of the National Academy of Sciences USA* 109:11746–11751.
- Reisz, R. R., and H.-D. Sues (2000). The 'feathers' of *Longisquama*. *Nature* 408:428.
- Rougier, G. W., Q. Ji, and M. J. Novacek (2003). A new symmetrodont mammal with fur impressions from the Mesozoic of China. *Acta Geologica Sinica* 77:7–14.
- Shapiro, B., and M. Hofreiter (2014). A paleogenomic perspective on evolution and gene function: New insights from ancient DNA. *Science* 343(6169). doi:10.1126/science.1236573.
- Slater, G. J., L. J. Harmon, and M. E. Alfaro (2012). Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* 66:3931–3944.
- Smith, A. B. (1998). What does palaeontology contribute to systematics in a molecular world? *Molecular Phylogenetics and Evolution* 9:437–447.
- Smith, N. D., and A. H. Turner (2005). Morphology's role in phylogeny reconstruction: Perspectives from paleontology. *Systematic Biology* 54:166–173.
- Turner, A. H., S. H. Hwang, and M. A. Norell (2007a). A small derived theropod from Öösh, Early Cretaceous, Baykhangor Mongolia. *American Museum Novitates* 3557:1–27.
- Turner, A. H., P. J. Makovicky, and M. A. Norell (2007b). Feather quill knobs in the dinosaur *Velociraptor*. *Science* 317:1721.
- Turner, A. H., P. J. Makovicky, and M. A. Norell (2012). A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371: 1–206.
- Turner, A. H., D. Pol, J. A. Clarke, G. M. Erickson, and M. A. Norell (2007c). A basal dromaeosaurid and size evolution preceding avian flight. *Science* 317:1378–1381.
- Vinther, J., D. E. G. Briggs, R. O. Prum, and V. Saranathan (2008). The colour of fossil feathers. *Biology Letters* 4:522–525.
- Voigt, S., M. Buchwitz, J. Fisher, D. Krause, and R. Georgi (2009). Feather-like development of Triassic skin appendages. *Naturwissenschaften* 96:81–86.
- Wheeler, Q., L. Assis, and O. Rieppel (2013). Heed the father of cladistics. *Nature* 496:295–296.
- Wiens, J. J. (1998). Does adding characters with missing data increase or decrease phylogenetic accuracy? *Systematic Biology* 47:625–640.
- Wiens, J. J. (2000). *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press, Washington, DC, USA.
- Wiens, J. J. (2003a). Incomplete taxa, incomplete characters, and phylogenetic accuracy: Is there a missing data problem? *Journal of Vertebrate Paleontology* 23:297–310.
- Wiens, J. J. (2003b). Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology* 54:528–538.
- Wiens, J. J. (2004). The role of morphological data in phylogeny reconstruction. *Systematic Biology* 53:653–661.
- Wiens, J. J. (2009). Paleontology, genomics, and combined-data phylogenetics: Can molecular data improve phylogeny estimation for fossil taxa? *Systematic Biology* 58:87–99.
- Wiens, J. J., C. A. Kuczynski, T. Townsend, T. W. Reeder, D. G. Mulcahy, and J. W. Sites (2010). Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: Molecular data change the placement of fossil taxa. *Systematic Biology* 59:674–688.
- Wiens, J. J., and T. W. Reeder (1995). Combining data sets with different numbers of taxa for phylogenetic analysis. *Systematic Biology* 44:548–558.
- Wiens, J. J., and J. Tiu (2012). Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. *PLOS One* 7:e42925.
- Witmer, L. M. (2001). The role of *Protoavis* in the debate on avian origins. In *New Perspectives on the Origin and Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom* (J. Gauthier and L. F. Gall, Editors). Yale Peabody Museum of Natural History Special Publications, New Haven, CT, USA.
- Wuttke, M. (1983). Weichteil-Erhaltung durch lithifizierte Mikroorganismen bei mittel-eozänen Vertebraten aus den Ölschiefern der 'Grube Messel' bei Darmstadt. *Senckenbergiana Lethaea* 64:509–527.
- Xu, X., Z. L. Tang, and X. L. Wang (1999). A therizinosauroid dinosaur with integumentary structures from China. *Nature* 399:350–354.
- Xu, X., Z. H. Zhou, and X. L. Wang (2000). The smallest known non-avian theropod dinosaur. *Nature* 408:705–708.
- Xu, X., Z. H. Zhou, X. L. Wang, X. W. Kuang, F. C. Zhang, and X. K. Du (2003). Four-winged dinosaurs from China. *Nature* 421: 335–340.
- Xu, X., M. A. Norell, X. W. Kuang, X. L. Wang, Q. Zhao, and C. K. Jia (2004). Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431:680–684.
- Xu, X., J. M. Clark, J. Y. Mo, J. Choiniere, C. A. Forster, G. M. Erickson, D. W. E. Hone, C. Sullivan, D. A. Eberth, S. Nesbitt, Q. Zhao, et al. (2009a). A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* 459:940–944.
- Xu, X., X. T. Zheng, and H. L. You (2009b). A new feather type in a nonavian theropod and the early evolution of feathers. *Proceedings of the National Academy of Sciences USA* 106: 832–834.
- Xu, X., Q. Zhao, M. A. Norell, C. Sullivan, D. Hone, C. Erickson, X. Wang, and F. Han (2009c). A new feathered maniraptoran

- dinosaur fossil that fills a morphological gap in avian origin. *Chinese Science Bulletin* 54:430–435.
- Xu, X., H. You, K. Du, and F. Han (2011). An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475: 465–470.
- Xu, X., K. B. Wang, K. Zhang, Q. Y. Ma, L. D. Xing, C. Sullivan, D. Y. Hu, S. Q. Cheng, and S. Wang (2012). A gigantic feathered dinosaur from the Lower Cretaceous of China. *Nature* 484: 92–95.
- Zelenitsky, D. K., F. Therrien, G. M. Erickson, C. L. DeBuhr, Y. Kobayashi, D. A. Eberth, and F. Hadfield (2012). Feathered non-avian dinosaurs from North America provide insight into wing origins. *Science* 338:510.
- Zhang, F. C., Z. H. Zhou, X. Xu, X. L. Wang, and C. Sullivan (2008). A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* 455:1105–1108.
- Zhang, F. C., S. L. Kearns, P. J. Orr, M. Benton, Z. Zhou, D. Johnson, X. Xu, and X. Wang (2010). Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature* 463:1075–1078.
- Zhou, Z., J. A. Clarke, and F. Zhang (2002). *Archaeoraptor's* better half. *Nature* 420:285.