1 Theropod Diversity and the Refinement of Avian Characteristics

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Bird origins have been debated ever since Darwin published his "*Origin of Species*," and was subsequently challenged on the topic by Sir Richard Owen, who pointed out the lack of transitional fossil forms in the evolution of the highly derived avian body plan. Indeed, Owen likely carefully selected birds to make his point due to their many unique traits and physiological features such as flight, feathers, bipedality, and a remarkable respiratory system in which the lungs are connected to and ventilated by a complex system of air sacs that pneumatize the skeleton. Within two years of this debate, the discovery of the first specimens of *Archaeopteryx* provided conclusive evidence of avian evolution in the fossil record and became the focal point for research and deliberation on the topic for more than a century. While the fossils of *Archaeopteryx* provided incontrovertible evidence for a reptilian origin for birds, opinions varied as to which group of reptiles birds may have originated from.

Following the discovery of the small nonavian theropod *Compsognathus* in the same limestone deposits as *Archaeopteryx*, Huxley (1868) presciently proposed an evolutionary relationships between birds and nonavian theropods based on shared traits such as three principal, weight-bearing toes in the foot (confirmed by foot-prints), a tall ascending process of the astragalus, and hollow bones. Other contemporary evolutionary biologists such as Cope favored an evolutionary relationship between birds and ornithopod dinosaurs such as hadrosaurs, based again on a three-toed foot and a retroverted pubic shaft. While a variety of ancestors or sister taxa were proposed for birds, a broad consensus that they were related to dinosaurs prevailed until the publication of the English edition of Heilmann's (1926) "*Origin of Birds*." Heilmann's book presented a detailed study of neontological, embryological, and fossil evidence, all of which pointed to a theropod ancestry for birds. Nevertheless, based on the prevailing assumption of the time that dinosaurs ancestors had lost their clavicles, their reappearance in birds would violate Dollo's (1893) law of irreversibility. Heilmann therefore concluded that the similarities between birds and theropods were due to convergence, and that birds were derived from more basal archosaurs that still retain clavicles.

Due to the thoroughness of his book, Heilmann's (1926) hypothesis held sway for the next four decades until the discovery and description of the mid-sized dromaeosaurid theropod *Deinonychus* by Ostrom (1969). Ostrom's detailed study of the skeletal anatomy of *Deinonychus* led him to recognize derived characters shared between it and the basal bird *Archaeopteryx* (Ostrom, 1976), and to the discovery of a misidentified specimen of *Archaeopteryx* (Ostrom, 1970).

Among the new traits that Ostrom mustered to revive a theropod ancestry for birds are the presence of a half-moon-shaped wrist bone that allows the hand to adduct against the forearm as in the wing-folding mechanism of living birds, and a three-fingered hand with characteristic proportions between the three metacarpals and phalanges. Following Ostrom's work, progressively more evidence has been amassed to support this hypothesis of avian origins, as a plethora of new fossil discoveries continue to blur the morphological distinction between birds and their closest theropod relatives.

Over the past three decades, widespread adoption of cladistic methodology for establishing and testing proposed evolutionary relationships has provided the conceptual framework for deciphering the origin and evolutionary history of birds. Gauthier (1986) was the first to apply an explicit cladistic parsimony analysis of theropod relationships to the question of bird origins. In doing so, he provided the first rigorous test of the hypothesis of theropod ancestry and set the stage for evaluating the evolutionary history of avian anatomy, physiology, and behavior in a quantitative framework. Subsequent decades have seen a remarkable surge in the discovery of new theropods, including fossil stem birds, with each discovery spawning novel systematic analyses (for reviews see Weishampel et al., 2004; Norell & Xu, 2005; Benton, 2008) and further supporting the hypothesis that birds are theropod dinosaurs.

To date, profound advances have been made in teasing out the evolution of the avian body plan as well as correlated physiological features and life history parameters of modern birds. Likewise, our knowledge of these traits in modern birds and their anatomical correlates has been used to yield insight into the biology of nonavian theropod dinosaurs and to infer whether particular avian traits originated before or after the origin of the avian lineage itself. Here we provide a general overview of the stepwise acquisition of the avian body-plan throughout the theropod family tree and discuss how the physiology of modern birds is being used to reconstruct aspects of dinosaur biology.

A ROADMAP TO THE DINOSAURIAN HERITAGE OF BIRDS

Despite their radically different body plans, birds inherited a mosaic of anatomical traits from various stages of vertebrate history. A host of discoveries over the past five decades provide a detailed road map to how the highly specialized avian anatomy was assembled over the evolutionary lineage leading to birds and demonstrates that many of the traits that are considered uniquely avian among extant amniotes actually arose before the origin of birds themselves. While most of our understanding of where birds fit into the tree of life comes from study of hard tissues, dramatic new discoveries in the past decade and a half are providing unprecedented insights on the evolution of soft tissue systems (Schweitzer et al., 1999; Xu et al., 2001) aspects of physiology (Varricchio et al., 2002; Varricchio & Jackson, 2004; Organ et al., 2007), and even behavior (Norell et al., 1995; Varricchio et al., 1997; Xu & Norell, 2005).

That birds are archosaurs and the closest living relatives to crocodilians has long been inferred from shared derived traits such as a four-chambered heart and thecodont dentition. Virtually all birds possess an external mandibular fenestra, a synapomorphy of Archosauria (Benton, 1990) and fossil avians also possess an antorbital fenestra (Figure 1.1), also considered a hallmark of this clade, although in extant birds the latter opening is lost or merged with the external nares through expansion of the premaxillae and concomitant reduction of other preorbital bones. Phylogenetic analyses have identified numerous derived traits shared by birds and various hierarchically arranged subsets of archosaur diversity (Figure 1.1). A comprehensive review detailing all of these characters is beyond the scope of this chapter, so here we concentrate on a select subset of traits and evolutionary branching points that are most critical to understanding the evolution of the unique avian body plan and its derived physiological and functional correlates.
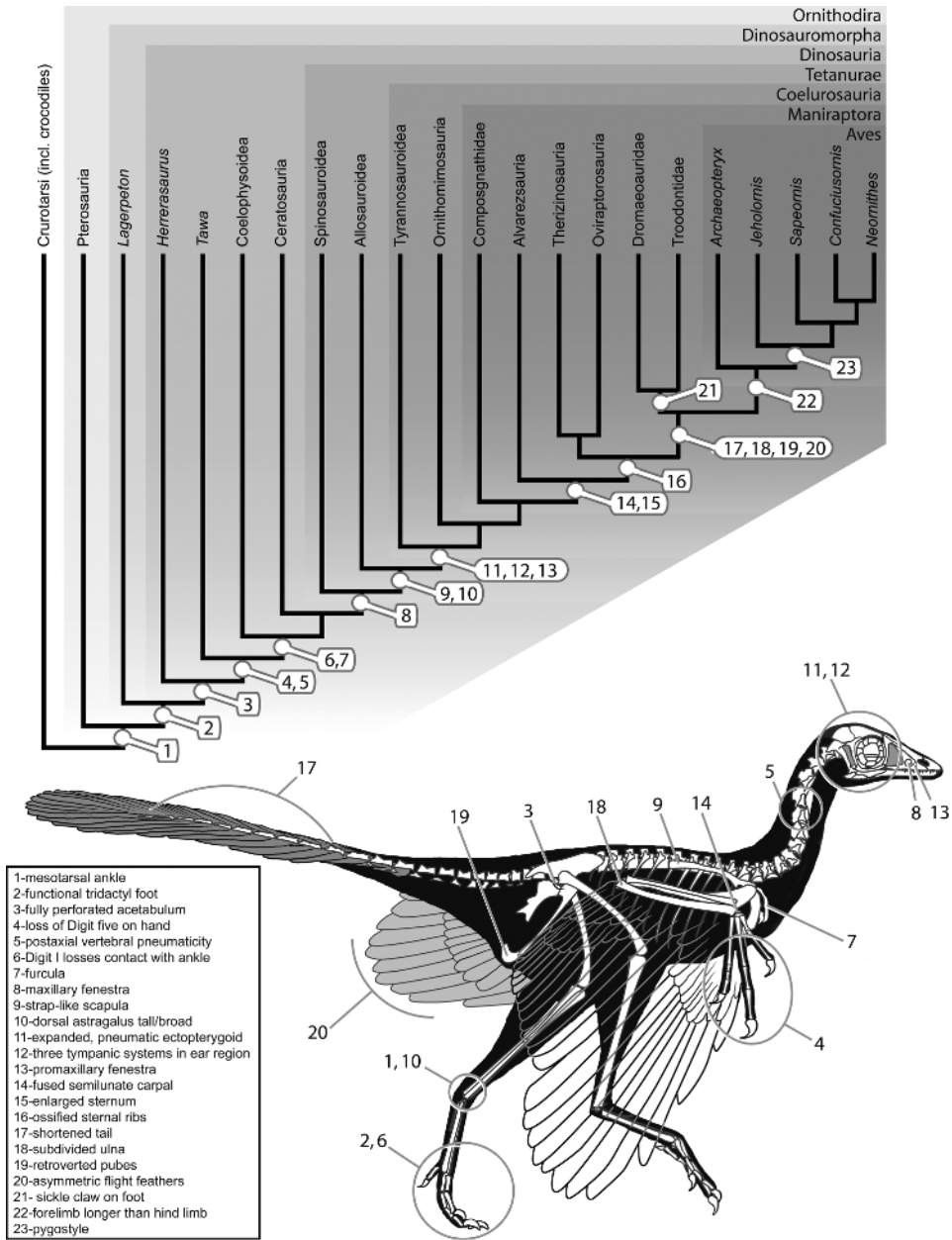
Fig. 1.1 Guide to avian evolutionary history based on a simplified evolutionary tree of Archosauria. Key traits in avian evolution are mapped onto the cladogram with their corresponding position indicated on the skeleton of *Archaeopteryx*. Note how traits are distributed throughout the skeleton revealing the mosaic assembly of avian anatomy throughout ornithodiran evolution. See text for more detailed discussion of individual traits. *Archaeopteryx* reconstruction by M. Donnelly.

The deepest division among archosaurs is between the lineages leading to the extant clades Crocodylia and Aves. Each of these branches also subtends numerous fossil clades, which were dominant faunal elements during the Mesozoic. The avian total group (= extant plus extinct diversity after the split from the lineage leading to Crocodylia) is known as Ornithodira and is characterized principally by the possession of a mesotarsal ankle joint (Figure 1.1), in which the articulation between the foot and crus occurs between the proximal and distal tarsals and approximates a roller joint, restricting foot motions to fore–aft swinging without a rotational component. Ornithodirans are also characterized by having a clearly defined femoral head that is distinctly offset from the femoral shaft. Besides birds, Ornithodira is comprised of extinct dinosaurian subclades, pterosaurs, and suite of lesser-known Triassic forms. Many of these taxa, especially those within the dinosauromorph clade, share the derived trait of being bipedal, thus freeing the forelimbs to evolve new functions including flight. Although many large, herbivorous dinosaurs later re-evolved a quadrupedal stance in concert with the evolution of large body mass, all derive from bipedal ancestors.

Dinosauromorphs, including birds, are united in their possession of three principal weight-bearing bones of the hind foot with the first and especially fifth toes at least partially reduced (Figure 1.1). Recent discoveries of dinosauriforms and basal dinosaurs from Argentina and New Mexico, USA provide new insights on the progressive nature of the reduction and loss of weight-bearing function in the first and fifth toes of the ornithodiran foot (Nesbitt *et al.*, 2009a).

Dinosauria, which comprises the bulk of known ornithodiran diversity, is characterized by a fully perforated acetabulum, in which the head of the femur fits into a medially open socket formed by the three hipbones. The head of the femur is angled almost perpendicular to the shaft allowing the hindlimbs to be brought under the body for a fully upright, parasagittal gait. Triassic dinosauromorphs such as *Lagerpeton* with partially open acetabula (Sereno & Arcucci, 1993) reveal that the acquisition of a fully open acetabulum occurred in a gradual fashion spanning several branching points at the root of the dinosaurian evolutionary tree (Figure 1.1). Counterintuitively, birds fall within the Saurischia, or "lizard-hipped" branch of dinosaur diversity, rather than the Ornithischia, the "bird-hipped" branch. Saurischians are united by their possession of hyposphen–hypantrum accessory articulations between the neural arches of the trunk vertebrae, which are also marked by lateral excavations on their neural arches presumably housing diverticula of the respiratory system. Hypantrum–hyposphen articulations were lost in a later stage of bird evolution, but some fossil birds such as *Patagopteryx* reveal that this trait was present ancestrally.

Birds form part of the theropod radiation within Saurischia. Progressive reduction of the hand toward the tridactyl condition in birds is encountered near the base of the theropod radiation. When present in basal theropods, the fourth digit is clawless and the fifth digit, known in *Eoraptor*, is reduced to a metacarpal splint devoid of knuckles (Figure 1.2). Coelophysoids and more derived theropods (Figure 1.1) display a reduction in the number of carpals to five or less, and the number of digits to four or less, although a fifth metacarpal has been tentatively identified in *Dilophosaurus* (Xu *et al.*, 2009) indicating that this process may have occurred in parallel in a number of theropod lineages. Other shared derived traits that reflect the deep theropod origins of birds include a dorsally ascending process of the astragalus, a fifth pedal digit reduced to only the metatarsal, and the wishbone. As briefly mentioned above, the presence of clavicles (whether fused or not) has been a topic of debate in avian and theropod systematics for the better part of a century (Makovicky & Currie, 1998). Because many of the earliest dinosaur discoveries were of advanced ornithopods and sauropodomorphs, taxa that have lost their clavicles, these elements were generally held to be absent in all dinosaurs, leading to the subsequent misinterpretation of theropod furculae as either interclavicles (Makovicky & Currie, 1998) or fused gastralia

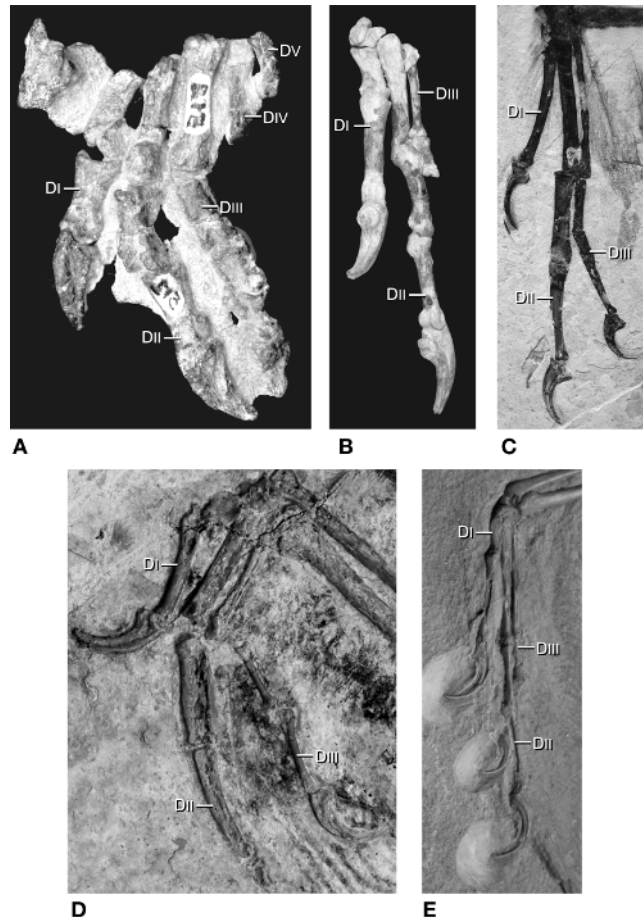**Fig. 1.2** Comparison of theropod mani showing progressive reduction and loss of digits IV and V and changes in the proportions of manus elements. *Eoraptor* (A), *Guanlong* (B), *Sinornithosaurus* (C), *Archaeopteryx* (D), and *Confuciusornis* (E). Abbreviations: DI–V, digits I–V. All specimens shown at the same scale. [This figure appears in color as Plate 1.2.]

(Chure & Madsen, 1996). Unfused clavicles are now known to occur in prosauropods (Yates & Vasconcelos, 2005) and some ceratopsians (Brown & Schlaikjer, 1940), and fused clavicles have been documented in an evergrowing list of theropod taxa, indicating that this trait is likely a synapomorphy of almost the entire clade (Smith *et al.*, 2007; Nesbitt *et al.*, 2009b). Almost all theropods with the exception of *Herrerasaurus* also exhibit some degree of pneumatization on the sides of the postaxial cervical vertebral centra, with basal forms such as *Tawa* and coelophysoids exhibiting fossae (Nesbitt *et al.*, 2009a), while more derived taxa have invasive foramina that pierce the vertebral centra invading and excavat-

ing their interiors (Britt, 1997). These pneumatic features correlate with one of the avian respiratory air-sac systems (see below). Coelophysoids and more derived theropods are characterized by a first toe in which the metatarsal is reduced and no longer contacts the ankle (Figure 1.1) – in most birds this toe is rotated on to the plantar face of the foot and allows for perching in arboreal forms.

Theropods exclusive of the basal coelophysoid radiation that spanned the Late Triassic–Early Jurassic, can be largely divided into the two major lineages, Ceratosauria and Tetanurae. Birds belong to the latter lineage, which also includes such well-known denizens as

Allosaurus, Tyrannosaurus, and *Velociraptor*. Both clades radiated throughout the Jurassic and Cretaceous giving rise to small- and large-bodied forms. Ceratosaurs are characterized by a progressive reduction of forelimb traits such as muscle attachment areas and overall robustness of the forelimbs, accompanied by a reduction of their relative size in larger taxa.

Large bodied ceratosaurs such as *Carnotaurus*, *Majungasaurus*, and *Rajasaurus* are grouped together in the clade Abelisauridae, and are characterized by very short, deep skulls adorned with surficial sculpturing and even horn-like structures in some species (Bonaparte *et al.*, 1990; Sampson *et al.*, 1998; Sereno & Brusatte, 2008), as well as heavy reduction of forelimb elements including a completely unossified wrist and loss of phalanges on most fingers (Chiappe *et al.*, 1998). These taxa have an almost exclusively Gondwanan distribution during the Cretaceous, and have been the subject of intense biogeographic debate (Sampson *et al.*, 2001; Sereno *et al.*, 2004; Sampson & Krause, 2007).

The Tetanurae have a greater known Mesozoic diversity than do the ceratosaurs, and include a wide range of both large and small taxa. Tetanuran theropods are characterized by a large suite of synapomorphies, including presence of a maxillary fenestra (Figure 1.1) rostral to the archosaurian antorbital fenestra and a fully horizontally directed femoral head. All birds exhibit this last trait, although the maxillary fenestra is only evident in *Archaeopteryx*, having been incorporated into the naris in all living and most fossil avian species. Most tetanuran taxa are members of three principal groups, the Spinosauroidea, Allosauroidea, and Coelurosauria, although membership and exact relationships among these three subclades remain debated (Sereno *et al.*, 1996; Rauhut, 2003; Smith *et al.*, 2007, 2008). Allosauroids and spinosauroids are predominantly large-bodied carnivores with body masses ranging from a few hundred kilograms to as much as seven tons in derived end-members of these clades, such as the spinosaurid *Spinosaurus* and the carcharodontosaurid allosauroid *Giganotosaurus*. Allosauroids are recovered as the sister clade to the

Coelurosauria in most cladistic analyses (Sereno *et al.*, 1996; Smith *et al.*, 2007, 2008), through their shared possession of traits such as perforated maxillary fenestra, pneumatic openings on the axial centrum, and a reduction of the ischiadic apron to form an open obturator notch rather than an enclosed fenestra. Both spinosauroids and allosauroids were globally distributed during the Late Jurassic and Early Cretaceous, but wane in diversity during the latest Cretaceous, with the coelurosaurian tyrannosaurids filling the dominant carnivore niche at least on northern landmasses.

Throughout most of the 20th century, carnivorous dinosaurs were taxonomically divided according to body size with small to medium-sized taxa grouped in Coelurosauria, and large species lumped within Carnosauria. This taxonomic scheme is artificial (Holtz, 1994) and recent work demonstrates that large body sizes evolved multiple times within Theropoda. Coelurosauria has recently been redefined (Gauthier, 1986; Sereno, 1999a) as the clade encompassing birds and all theropods closer to birds than to *Allosaurus*, and encompasses the smallest known theropods (hummingbirds) as well as some of the largest (*T. rex*), although all lineages appear to derive from small to medium-sized ancestors. Coelurosaurs are united by having a third opening, the promaxillary fenestra, within the antorbital fossa, although this is only recognizable in *Archaeopteryx* among birds as is the case with the maxillary fenestra (Figure 1.1). Other traits uniting this grouping include the presence of three tympanic pneumatic systems emanating from the middle ear (more basal taxa only possess one or two of these), an expanded and pneumatic ectopterygoid (lost in neornithine birds), and an expanded astragalar ascending process that is twice as tall as it is wide and covers almost the full width of the ankle. The manus is fully tridactyl in most Coelurosauria (Figures 1.1 and 1.2C–E), although a few basal taxa such as the basal tyrannosauroid *Guanlong* (Xu *et al.*, 2006) retain a splint-like vestige of the fourth metacarpal (Fig. 1B). The large predatory tyrannosauroids, the beaked and herbivorous

(Kobayashi *et al*., 1999, Zanno & Makovicky, 2010) ornithomimosaurs, and small compsognathids are generally considered to be basal lineages within the coelurosaur radiation, whereas birds and their closest taxa form a more exclusive clade within Coelurosauria known as Maniraptora. In the past decade, discoveries of numerous coelurosaur taxa sporting protofeathers, fully formed flight feathers (Ji *et al*., 2001), and even specialized feathers convergent on display structures in oscines (Zhang *et al*., 2008) have been made in Jurassic and Cretaceous lake-bed deposits of northeastern China. Together, these discoveries indicate that possession of plumage covering most of the body with the exception of the feet and snout likely characterizes at minimum the coelurosaurian node. The presence of hollow, fibrous integumentary structures along the dorsal midline of two ornithischian taxa and on the body of pterosaurs indicates the presence of such structures alone may be much wider among ornithodirans, though their exact homology remains unclear. Doubts have been cast regarding the presence of feather homologues in various theropods (Lingham-Soliar *et al*., 2007; Feduccia *et al*., 2005), and these have instead been interpreted as collagen fibers derived from decomposition of the skin in a specimen of the compsognathid *Sinosauropteryx*. These claims are based only on very selective comparisons between the soft tissues of feathered nonavian theropods and experimentally manipulated integument on extant reptiles and extant and extinct marine amniotes. More appropriate comparisons to either birds or reptiles from the same shale deposits that yield the feathered theropods, representing equivalent preservational conditions, were not conducted by Lingham-Soliar and colleagues, and indeed dismissed with the tautological argument that animals with feathers are by definition birds and thus need not be considered when testing for feather preservation (Fedduccia *et al*., 2005). Two recent studies (Zhang *et al*., 2010; Li *et al*., 2010) demonstrate that the preservation of nonavian coelurosaur integumentary structures matches those of unquestionable stem birds from the same rock units and that they preserve melanosomes imbedded within the keratinous matrix of the feathers themselves, thus providing not only evidence on the homology of these integumentary structures, but also on the color and appearance of these animals in life. Conversely, preservation of a body outline composed of frayed and decomposing dermal layers has never been reported in any of the hundreds of choristodere specimens collected from these shale beds, casting doubt on the conclusion that such decomposition patterns should be observed in a dinosaur as posited by Lingham-Soliar *et al*. (2007).

Maniraptorans are characterized by distinguishing traits including a half-moon shaped wrist bone that is thought to represent a fusion of the first and second distal carpal (Figure 1.1, trait 11). A pulley-like proximal surface on this element allows the hand to be flexed sideways toward the forearm, and is responsible for the wing-folding mechanism in birds. As with many other anatomical traits relevant to understanding the origins and relationships of birds, the refinement of this particular synapomorphy accrued over a range of branches in the phylogeny, and incipient versions of this structure have been recognized in more basal tetanurans such as *Allosaurus* (Sereno, 1999b). A number of novel evolutionary features in the thoracic skeleton, which are known to play a role in avian respiration (O'Connor & Claessens, 2005), further diagnose some maniraptorans. These include presence of enlarged sternal plates with extensive medial contact and distinct facets for ossified sternal ribs (Barsbold, 1983; Norell & Makovicky, 1999) (Figure 1.1, trait 16) and uncinate processes spanning the thoracic ribs (Clark *et al*., 1999).

Maniraptoran fossils that preserve integumentary structures reveal an increased complexity in both feather types and morphology over the simple filamentous structures observed in basal coelurosaurs (Xu *et al*., 2001; 2010). Xu and colleagues (2001) demonstrated a correlation between the order of appearance of progressively more complex feather types in maniraptoran evolution with their order of development in avian ontogeny, and it is clear that almost all basic feather types known in birds had evolved earlier in theropod evolution.

Several aberrant clades of theropods are included within the Maniraptora. These include the herbivorous Therizinosauria, whose theropod affinities were strongly debated due to their unusual anatomy, but which are now known to possess unquestionable theropod hallmarks such as pneumatic vertebrae, furculae, feathers, and a semilunate carpal that fuses in at least adult specimens of some taxa (Kirkland *et al.*, 2005). Another group with unusual anatomy and debated affinities are the Alvarezsauridae. Derived, small-bodied members of this group discovered in Late Cretaceous sediments of the Gobi Desert exhibit a remarkable mosaic of characters including loss of a postorbital bar, a double-headed quadrate, a keeled sternum, short but massive arms with an enlarged pollex but reduction of the other fingers, a splint-like fibula, and diminutive, supernumerary teeth (Perle *et al.*, 1993; Chiappe *et al.*, 1998). A number of these traits, such as the reduced postorbital, streptostylic quadrate, keeled sternum, and reduced fibula, are also encountered in birds more derived than *Confuciusornis*, leading to initial hypotheses that these fossil taxa represent flightless birds more derived than *Archaeopteryx*. Subsequent discoveries of more basal alvarezaurids in Argentina led to the recognition that many of the avian-like characteristics of derived alvarezsaurids evolved convergently in birds, and most recent studies agree that they represent basal maniraptorans rather than members of the avian lineage (Norell *et al.*, 2001; Novas & Pol, 2002; Senter, 2007; Zanno *et al.*, 2009).

Oviraptorosaurs represent another anatomically bizarre lineage, some members of which exhibit remarkable convergence on avian anatomy in parts of their skeleton. When analyzed in a limited context, such traits have also prompted hypotheses that this clade represents secondarily flightless birds (Maryanska *et al.*, 2002), a conclusion that is not supported in more rigorous and comprehensive phylogenetic studies incorporating a greater array of both taxa and characters. Such studies overwhelmingly posit oviraptorosaurs (often, but not always, in combination with therizinosaurs) as sister to the clade Paraves that encompasses birds and their sister taxon, the sickle-clawed Deinonychosauria. Birds and deinonychosaurs are united by numerous apomorphic features such as possessing retroverted pubes (Figure 1.1, trait 19), an expanded and flexed coracoid that repositions the humeral articulation closer to the vertebral column and imbues the scapulocoracoid with an L-shaped profile, a proximal ulna articulation subdivided into two distinct facets (Figure 1.1, trait 18), and a shortened tail with 25 or less vertebrae of which the anterior ones are short and box-like and distal ones are elongate and cylindrical (Figure 1.1, trait 17). Most paravians, including all birds, are also known to possess primary and secondary feathers with asymmetrically developed vanes on either side of the rachis (Figure 1.1, trait 20), a feature considered to be an adaptation for aerodynamic function, but the recently described *Anchiornis* exhibits symmetrical vane distribution on its primaries (Xu *et al.* 2009) as in the basal oviraptorosaur *Caudipteryx*, complicating our understanding of how many times this trait evolved.

Deinonychosauria comprises two distinct clades, the Troodontidae and Dromaeosauridae, which are united by the presence of a sickle-shaped claw on the second digit of the foot (Figures 1.1 and 1.2, trait 21), and a triangular lateral exposure of the splenial along the edge of the lower jaw. A close relationship between dromaeosaurs and birds was initially recognized by Ostrom (1976) following his discovery and description of the first relatively complete dromaeosaurid *Deinonychus* (Ostrom, 1969), but some debate persisted regarding the affinities of Troodontidae, derived members of which share characters with other coelurosaur clades and also lack some paravian synapomorphies such as a retroverted pubis. Discovery of a number of basal troodontids from the Early Cretaceous Yixian and Jiufotang Formation of China reveals that these traits are homoplastic in derived troodontids, and that Deinonychosauria is a natural grouping (Xu *et al.*, 2002). Many of the deinonychosaurs recently discovered in China and elsewhere are also significant because they represent the smallest nonavian dinosaurs yet discovered (Xu *et al.*, 2000) and are comparable in body size to

basal avian taxa such as *Archaeopteryx* and *Jeholornis* (Turner *et al.*, 2007; Xu *et al.*, 2009). Some of the small deinonychosaurs from these rock units, such as *Microraptor* and *Sinornithosaurus*, possess vaned feathers on the hindlimb as well as the forelimb (Xu *et al.*, 2001; Xu & Zhang, 2005; Ji *et al.*, 2001), along with a frond-like arrangement of the rectrices in a pattern like that of *Archaeopteryx* (Figure 1.3A). This four-winged body plan may represent a transitional step in the evolution of powered flight (Longrich, 2006; Hu *et al.*, 2009), though its optimization on the evolutionary tree is complicated by the extreme similarity between

basal members of the three principle paravian lineages and hence some phylogenetic lability between them. The earliest instance of this unique body plan is represented by *Pedopenna* (Xu & Zhang, 2005; Figure 1.3B) and *Anchiornis* (Hu *et al.*, 2009), which are Middle Jurassic in age and thus older than *Archaeopteryx*. More derived deinonychosaurian taxa evolved larger body sizes culminating in the 30 ft long *Utahraptor*.

The fossil record of Deinonychosauria was until recently largely restricted to Cretaceous deposits of the northern continents, but a slew of recent discoveries of dromaeosaurids from
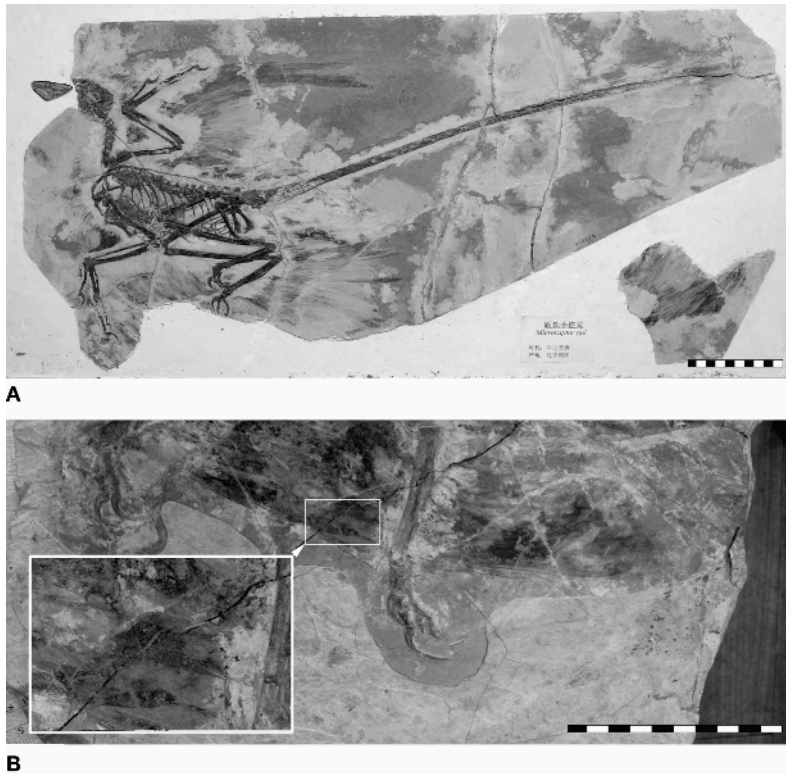

Fig. 1.3 (A) Skeleton of the dromaeosaurid *Microraptor gui* from the Yixian Formation of Liaoning, China, exhibiting vaned, asymmetric feathers on both fore- and hindlimbs. (B) Detail of hindlimb primary feathers of *Pedopenna* from the Middle Jurassic of Inner Mongolia, China. *Pedopenna* is the earliest paravian fossil to exhibit vaned feathers and a four-winged body plan. The inset shows a close-up of the aligned and parallel barbs on each vane that indicate the presence of interlocking barbules, as well as the rachis. Note the large sickle claw characteristic of deinonychosaurians (= dromaeosaurs and troodontids) on digit II of the foot. Scale bars equal 5 cm. (Photographs: P. Makovicky.) [This figure appears in color as Plate 1.3.]

Argentina (Novas & Puerta, 1997; Makovicky *et al.*, 2005; Novas & Pol, 2005) are evidence for a Gondwanan radiation of these animals. The discovery of the near-complete holotype of the Gondwanan dromaeosaurid *Buitreraptor* (Makovicky *et al.*, 2005) provided evidence to unite all of these different taxa into a single basal lineage, the Unenlagiinae, whose split from the better-known Laurasian dromaeosaurids may correlate with the break up of Pangaea. The discovery of Gondwanan dromaeosaurids also prompted a reinterpretation of the purported basal bird *Rahonavis* as member of the Unenlagiinae, demonstrating that the skeletons of basal deinonychosaurs and the earliest birds are almost indistinguishable. *Rahonavis* is characterized by hyperelongate forelimbs suggesting that such flight-related proportions may have arisen more than once in paravian evolution, with the main occurrence being characteristic of the avian lineage (Figure 1.1, trait 22).

Apart from *Archaeopteryx* and a few other species such as *Jeholornis*, most Cretaceous avian fossils exhibit rapid evolution of the avian body plan. *Sapeornis* is the most primitive bird to possess a foreshortened tail with the distalmost segments fused into a pygostyle (Figure 1.1, trait 23). Without a long tail to counterbalance the body as in typical nonavian theropods, the last common ancestor of *Confuciusornis* and more derived birds evolved a posture where the knee is permanently angled to bring the center of mass above the foot and offset the loss of a long counterbalanced tail. An ossified kneecap, which is unknown in nonavian dinosaurs, is present in *Confuciusornis* and more derived birds and serves to stabilize the bent knee. *Sapeornis* and *Confuciusornis* are also the basalmost avian taxa to exhibit a fused sternum with an incipient sternal keel for anchoring enlarged flight musculature, marking another key step in the assembly of the modern avian body plan. Both retain primitive theropod traits, however, such as a functional grasping tridactyl hand (Figure 1.2E), and *Sapeornis* and most Cretaceous birds retain dentition. Though some theropods convergently lost their teeth, the avian bill appears to have arisen at or very close to the origin of the avian crown group.

NEW INFERENCES ON SOFT TISSUE, PHYSIOLOGY, AND BEHAVIOR

The recent surge in dinosaur discoveries and research has not only yielded a better understanding of the skeletal evolution of theropods and a more nuanced understanding of the stepwise assembly of the unique avian body plan, but also provided insights into the evolution of avian physiology, reproductive biology, and even aspects of their related behaviors. Through integrative research incorporating fossil and neontological data, advances in our understanding of modern birds are being applied back in time to generate hypotheses regarding aspects of dinosaurian biology lost in the fossil record using phylogenetic history as a guide (Witmer, 1995). Here we review some recent advances in our understanding of dinosaur biology based on some of the most remarkable and informative theropod fossil discoveries made to date and new methodological approaches to the study of fossilized remains.

Metabolism and respiration

A long-standing debate regarding dinosaurian metabolic regimes has persisted for over 30 years (Chinsamy-Turan & Hillenius, 2004; Padian & Horner, 2004), since the recognition that birds are derived theropods prompted speculations that they inherited their homeothermic physiology from dinosaurian ancestors. Debates on physiological inferences made on evidence such as histological traits, the possible presence or absence of turbinals, choanal position, and basic physiological calculations have been inconclusive and marred by attempts to draw wide-ranging conclusions through oversimplified interpretations of relatively limited (and often inaccurate) data. The presence of a plumage of filamentous or downy feather homologues covering the body in a variety of coelurosaurs, including taxa that presage evolution of vaned feathers with aerodynamic functions, suggests that feathers evolved in response to selective pressures other than adaptation to aerodynamic locomotion (Norell

& Xu, 2005; Li *et al.*, 2010). Given the insulating properties of feathers and the small size and correspondingly high surface area to volume ratio of most of the nonavian theropods discovered with plumage, many authors have concluded that feather evolution may in part have been driven by a need for insulation, which in turn implies an ability to generate metabolic energy. A recent study of the histology of dinosaurs has demonstrated that theropods tend to have smaller osteocyte lacunae in their bones, indicating smaller cell sizes (Organ *et al.*, 2007). Living birds have relatively smaller cells and markedly lighter cell nuclei with far less redundant DNA compared to other amniotes. Small cell size facilitates increased basic metabolic rates due to the higher surface to volume ratio of the cells, and correlates with nuclear mass, so it is thought that birds underwent active selection for smaller nucleus size. Organ and colleagues' (2007) results robustly suggest that this selective process began much earlier in theropod history.

The high avian basal metabolic rate is in part sustained by a unique respiratory system, in which the incompressible lungs are ventilated by a complex system of interconnected air sacs. Phylogenetic continuity has been established between the pneumatic openings in the vertebral columns of theropod dinosaurs and those of birds (Britt *et al.*, 1998; O'Connor & Claessens, 2005), which are formed through ontogeny as the air sacs invade adjacent bones. Five main air sac systems are connected to the lungs either directly or through their connections to one another in birds. Of these five, the cervical, clavicular, and abdominal air sac systems invade and pneumatize vertebral, girdle, and even limb bones in birds. Skeletal pneumatic features such as openings into bones and honeycombed interior architecture correlated with these systems have been recognized in theropods, with vertebral pneumaticity related to the cervical air sacs being virtually ubiquitous in theropods (Britt *et al.*, 1998). Hard tissue correlates of the other two systems are less common, but widespread enough throughout theropod diversity to suggest that at least the last

common ancestor of ceratosaurs and tetanurans possessed abdominal air sacs (O'Connor & Claessens, 2005; Sereno *et al.*, 2008), and that most tetanurans potentially had a clavicular air sac (Makovicky *et al.*, 2005; Sereno *et al.*, 2008). It should be noted that air sacs do not always invade skeletal elements in living birds and the degree of pneumaticity is observed to correlate with life history parameters such as body size and ecological habits (O'Connor, 2009), so absence of pneumatic traces in bones of extinct theropods cannot be taken as evidence for absence of air sacs, especially if such taxa are bracketed phylogenetically by taxa with positive evidence for air sacs.

Reproductive biology

Recent discoveries of nesting or gravid maniraptoran dinosaurs from Mongolia (Norell *et al.*, 1995; Figure 1.4) and elsewhere (Varricchio *et al.*, 1997; Currie & Chen, 2001; Sato *et al.*, 2005; Grellet-Tinner & Makovicky, 2006) have yielded crucial insights into the evolution of avian reproductive biology. Examination of the histology of such specimens (Erickson *et al.*, 2007) has demonstrated that many of them are not fully grown. Assuming their association with nests is demonstrative of a parental relationship, it suggests that nonavian theropods and perhaps even the earliest birds reached reproductive maturity before attaining somatic maturity (= cessation of growth). This pattern was reinforced by a paleohistologic study of four dinosaur taxa, in which reproductive maturity was established from the presence of bony tissues interpreted as medullary bone, which in some living birds serves as a calcium reserve for generating eggshell in gravid females (Lee & Werning, 2007). The concordance between these studies indicates that nonavian theropods, including paravians, retained the primitive reptilian pattern of reproducing before attainment of somatic maturity as opposed to the modern avian reproductive cycle in which somatic maturity is decoupled from and precedes reproductive maturity (Erickson *et al.*, 2007; Lee & Werning, 2007). Given that a number of primitive avian taxa including *Archeopteryx* (Erickson *et al.*, 2009), *Confuciusornis*
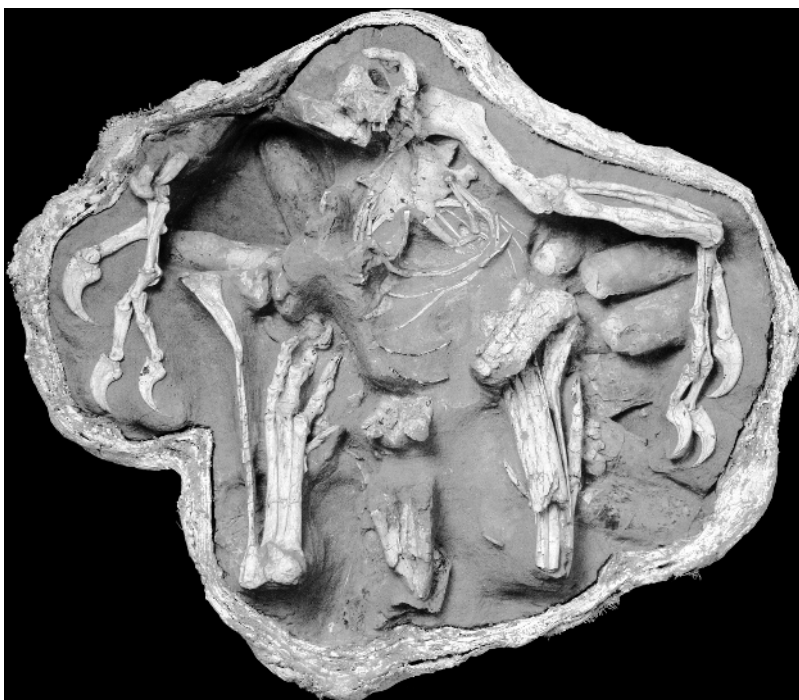
Fig. 1.4 Partial skeleton of an oviraptorosaur in brooding posture on a nest of its eggs. Egg identity has been independently confirmed through embryonic remains. Specimens such as this reveal that these dinosaurs laid eggs in pairs over protracted periods (diachronous laying), and brooded them with direct contact indicative of synchronous hatching. Such associations of eggs and sexually mature individuals are now known from multiple nonavian maniraptoran taxa. (Photograph M. Ellison/AMNH) [This figure appears in color as Plate 1.4.]

(Chiappe *et al.*, 2008), and *Patagopteryx* (Chinsamy *et al.*, 1994) reveal cyclical growth patterns and multiple age classes like nonavian dinosaurs, but unlike living birds which grow to maturity very rapidly, the decoupling between growth rate and reproductive maturity likely occurred later in avian evolution.

Living birds exhibit a relatively complex set of reproductive adaptations and behaviors relative to other reptiles (Varricchio *et al.*, 1997; Varricchio & Jackson, 2004). Although dinosaur eggs and nests have been known for well over a century, and correctly recognized since 1923, remarkable discoveries of dinosaur embryos or adults associated with nests or eggs represent intermediate stages in the evolution of the uniquely avian mode of reproduction. While most nonavian dinosaurs exhibit

clutches comparable to those of crocodilians in terms of egg numbers and individual egg volumes, at least some maniraptoran taxa have significantly larger egg volumes (Varricchio & Jackson, 2004) indicating a shift toward the derived avian condition in this important parameter. Although clutch sizes for well preserved nests of the nonavian maniraptorans *Troodon* and *Citipati* scale according to the same equations as in living birds, individual eggs are about half the volume of an extant avian egg for an animal scaled to corresponding size. The eggs of these taxa are arranged in pairs within the nest, demonstrating that nonavian theropods still retained two functional oviducts, rather than the single oviduct of extant avians (Varricchio *et al.*, 1997; Clark *et al.*, 1999; Sato *et al.*, 2005). The dimensions of the pubic canal in

basal birds such as *Archaeopteryx* and *Confuciusornis*, which retain a fused contact between the pubes distally, compares more favorably with those of nonavian theropods of similar size, rather than to the unfused and expanded pelvic canals of more derived birds. This suggests that individual egg volume was smaller in these ancestral birds than in modern taxa, and that they may have retained two functional oviducts.

The relatively large volume of nonavian maniraptoran clutches compared to body size (Varricchio & Jackson, 2004) (Figure 1.4) precludes that all eggs were retained within the female and then deposited during a single laying event. Rather these animals must have laid eggs over a protracted period of time as living birds do, a conclusion supported by analysis of the orientation of egg pairs within individual nests. Coupled with evidence for a brooding posture in individuals atop nests (Figure 1.4) (Norell *et al*., 1995; Varricchio *et al*., 1997), and for synchronous stages of embryonic development within one clutch (Varricchio *et al*., 2002), this provides compelling evidence that extinct maniraptorans exhibited synchronous hatching like their living relatives, but unlike more basal egg-laying reptiles.

Taken together, these findings demonstrate that birds inherited some components of their complex reproductive biology such as nest care/brooding, diachronous laying, and synchronous hatching from nonavian ancestors, whereas other components such as loss of one oviduct and concomitant increase in egg volume plus decoupling of somatic and sexual maturity occurred within the avian lineage itself. Much as with any of the other biological systems discussed here, avian reproduction is a mosaic of inherited traits many of which pre-date bird origins combined with others that post-date this event.

Brain evolution

Among amniotes, birds are characterized by large relative brain sizes (measured as an encephalization quotient (EQ) that takes the allometry of brain to body-mass scaling into account (Jerison, 1973)), with particularly enlarged optical lobes and cerebellum thought to be adaptations for neural control of flight. Despite popular misconceptions regarding the brain size of nonavian dinosaurs, theropods show a progressive increase in EQ throughout their evolutionary history and reconstructed EQ values from brain endocasts of various extinct maniraptorans approach those of the basal lineages of living birds (Dominguez Alonso *et al*., 2004). Detailed three-dimensional examination of the brain of *Archaeopteryx* using computed X-ray tomography (Dominguez Alonso *et al*., 2004) demonstrates that the brain of the basalmost avian taxon already possesses a bird-like architecture with a pronounced pontine flexure that displaces the hindbrain below the mid brain, and enlargements of features thought to be adaptations for enhanced neurosensory control of active flight in modern birds, such as enlarged optic lobes, a proportionately well developed cerebellum, and an enlarged inner ear with expanded semicircular canals set in a modern avian configuration. Some combination, though not all, of these traits have also been observed in nonavian coelurosaurs such as troodontids (Norell *et al*., 2009), various oviraptorosaurs (Balanoff *et al*., 2009), and ornithomimosaurs (Balanoff *et al*., 2009). Parallel trends in relative brain size evolution in birds and other maniraptoran lineages such as oviraptorosaurs have been noted, but there is little doubt that an elevated EQ and expansion of certain parts of the brain in birds was inherited from a more distant maniraptoran ancestor. Thus, with regard to the evolution of the unique avian brain, phylogeny again demonstrates how highly derived avian traits were acquired in stepwise fashion throughout theropod evolutionary history.

ARE BIRD ORIGINS STILL CONTROVERSIAL?

While widely accepted by biologists and paleontologists, the theropod ancestry of birds is not without its critics. The hypothesis has been challenged by a vocal, if small, opposition who

have pointed to a number of perceived inconsistencies in the theropod ancestry of birds. In general, their challenges fall into several categories, which include disagreements over homology of various traits and structures, the seeming 'temporal paradox' in which most nonavian maniraptorans post-date *Archaeopteryx*, and inconsistency between inferred theropod paleobiology and preferred scenarios of how some aspect of avian evolution (often involving hypothetical intermediate forms) must have progressed. Indeed, most of these challenges rely on a combination of all three categories of arguments. A number of traits shared by birds and various subsets of dinosaurs and theropods, such as a broad ascending process of the astragalus (Martin, 1991), the presence of a furcula (Feduccia &, Martin 1998), homology of the wrist and digit elements of the forelimb, and even the presence of thecodont dentition in various theropods, have been challenged (Martin & Stewart, 1999). Many of these assertions, such as whether a furcula is present in nonavian theropods or whether theropod teeth are truly thecodont are simply based on inaccurate observations such as that the interdental plates of some theropod taxa including *Archaeopteryx* (Elzanowski &

Wellnhofer, 1996) represent separate ossifications rather than being part of the dentary (Figure 1.5). Others depend on indefensible assumptions that structures be completely identical to qualify as homologues, such as Feduccia & Martin's (1998) claim that variations in interclavicular angle of the furcula between some birds and nonavian theropods represent evidence of separate evolutionary origins of these structures. Many such misconceptions have been disproven by the wealth of evidence amassed against them, but continue to be cited indefinitely by those favoring a nontheropod origin of birds.

Other challenges relating to the homology of structures such as digit and wrist identity (Burke & Fedduccia, 1997) and homology of the ascending process of the astragalus, conflate primary homology statements based on comparisons in fossils with embryological observations on a limited set of avian model taxa. For example, Martin & Stewart's (1985; see also Martin *et al.*, 1980) claim that the ascending process of the nonavian theropod astragalus is fundamentally different from the large spur of bone that emanates dorsally from the avian astragalus, because the former is termed a 'process of the astragalus' and the latter
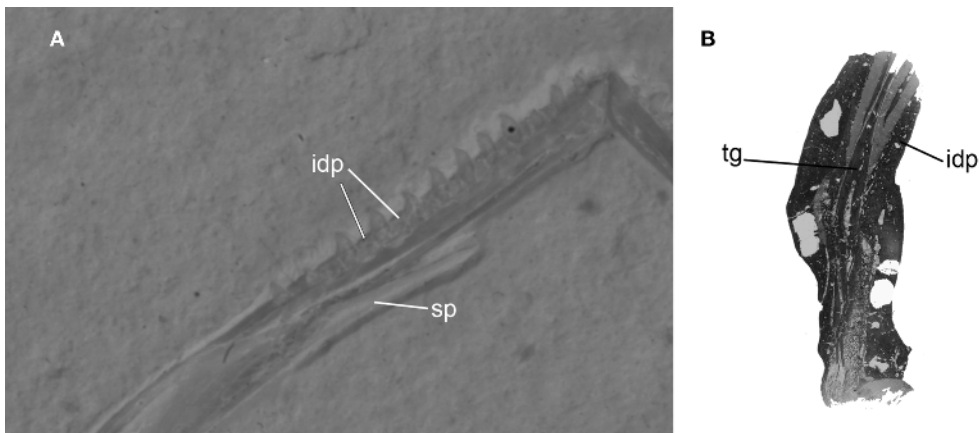

Fig. 1.5 (A) Lower jaws of the Munich specimen of *Archaeopteryx* revealing the presence of interdental plates. (B) Cross-section of the dentary of *Allosaurus* revealing continuous histological ultrastructure between the bone below the alveoli and the interdental plates and demonstrating that the latter are not separate ossifications. Abbreviations: idp, interdental plates; sp, splenial; tg, germinating tooth. Specimens not to scale. (Photographs P. Makovicky.) [This figure appears in color as Plate 1.5.]

derives from a distinct center of ossification during early embryology and is dubbed the 'pretibial bone', is based more on the polemics of how these structures are named rather than on relevant observations of their topological relationships. Since the embryology of nonavian theropods is unknown, it remains undeniable that for the life stages that can be compared across both living and fossil archosaurs, this tall, flat spur of bone that rises from the ankle along the front the tibia is present in virtually all birds and tetanurans, and is either significantly smaller or absent in more distantly related taxa (*contra* James & Pourtless, 2009).

Without question, the inconsistency between identifying avian digits by comparison to archosaur fossils versus identifying them through embryological studies of modern neornithines has been the greatest point of contention between the two opposing camps. In short, the dilemma is rooted in the fact that the tridactyl hand of *Archaeopteryx* exhibits a phalangeal formula and interelemental proportions that identify its digits as representing the first three fingers of the primitive pentadactyl amniote hand, whereas embryological studies (Burke & Feduccia, 1997; Feduccia & Nowicki, 2002; Larsson & Wagner, 2002) identify these digits as arising from the limb bud condensations that develop into digits II–IV in nonavian amniotes.

Interpreting the results of these two different methods for establishing digit identity at face value, detractors of the theropod origin of birds (Burke & Feduccia, 1997) conclude that the avian and nonavian theropod hands cannot be homologous despite the dozens of primary homologies in the shape, proportion, and number of wrist, hand, and finger bones, which they dismiss as convergence. Such a conclusion implicitly assumes a one-to-one correspondence between condensations in the developing limb bud and ossified adult structures, however, something that is untestable in fossils for which corresponding life stages are not preserved. The fundamental assumption of one-to-one correspondence has been challenged by experimental data that demonstrates considerable latent lability in the expression of chondrified digits from various primary condensations (Dahn & Fallon, 2000; Wagner, 2005), and by the recent discovery of the basal ceratosaur *Limusaurus* (Xu *et al*., 2009) which exhibits a reduced splint-like digit I and unusual phalangeal formula, demonstrating that theropod hand evolution is not as stereotypical as was once believed. With this assumption in doubt, the 'digital mismatch' can no longer be invoked to disqualify the numerous derived similarities of element shapes and proportions in hands of basal birds such as *Archaeopteryx* and other nonavian coelurosaurs. Moreover, these experimental results support novel models of how the embryology of the theropod hand evolved, most notably the Frame Shift Hypothesis (Wagner & Gauthier, 1999), which proposes a serial shift in digit identity between the embryonic primordia and chondrified digits over the course of development. Predictions of this hypothesis with respect to *Hox* gene expression patterns have been recently confirmed with chicken digit II exhibiting the digit I *Hox*-gene expression pattern of pentadactyl taxa such as mouse and alligator (Vargas *et al*., 2008). Furthermore, criticisms that a wholesale frame shift affecting all digits in a limb is not documented in any other amniote taxon have recently been muted by the confirmation of a parallel case of a frame shift in the Italian three-toed skink *Chalcides* (Wagner, 2005; Young *et al*., 2009).

Another mainstay of the opposition to the theropod ancestry of birds has been to point to a supposed 'temporal paradox' (Feduccia, 1996), namely the later occurrence in the fossil record of the coelurosaurian and maniraptoran sister clades to birds when compared to *Archaeopteryx*. While the argument as a whole is based on the mistaken assumption that taxa such as *Velociraptor* represent avian ancestors rather than sister taxa, and should therefore occur earlier in the fossil record, it has also been rendered moot by the recent discovery of several paravian taxa that pre-date *Archaeopteryx* (Xu & Zhang, 2005; Zhang *et al*., 2008; Xu *et al*., 2009).

A third persistent trend in the polemics surrounding avian origins has been the construction of scenarios circumscribing how a complex function such as avian flight or avian respiration

evolved, followed by application of these scenarios as a "test" of the fossil record. The size discrepancy between basal birds and much larger paravians such as *Velociraptor* and *Deinonychus* was long cited as evidence that flight (and implicitly birds themselves) could not have evolved from such large and earthbound animals (Feduccia, 1996), but discoveries of small maniraptoran taxa of comparable size to *Archaeopteryx* (Turner *et al.*, 2007) and with possible arboreal traits (Xu *et al.*, 2001) have erased this argument. Similar evidentiary concerns apply to other scenarios based on the incorrect projection of parameters of the anatomy and physiology of living birds onto distant fossil ancestors that have been summoned against a theropod ancestry of birds. For example, Ruben and colleagues (Ruben *et al.*, 1997) attempted to argue that theropods had a crocodylian hepatic piston pump style of breathing based on interpretation of discolorations inside the body cavity of two exceptionally preserved compsognathid specimens as defining the limits of a large liver subdividing the thoracic cavity. However, in both cases the limits of these discolorations have been demonstrated to be preservational artifacts (Currie & Chen, 2001).

With the notable exception of a recent paper by James & Pourtless (2009), none of these challenges to the bird-theropod hypothesis have been set within a modern phylogenetic context and all have relied on selectively picking certain traits, specimens, and observations while ignoring others to construct narrative, scenario-laden attacks on the theropod ancestry of birds. They contribute little to the overall understanding of how the derived avian body plan evolved and have generally offered few alternatives for avian ancestry, usually positing some vague, paraphyletic assemblage of small bodied Triassic reptiles as possible avian sister groups (Feduccia, 1996), or arguing for a close relationship between birds and crocodylomorphs based on select dental and cranial traits that have a homoplastic distribution.

James & Pourtless (2009) recently presented a detailed phylogenetic analysis to challenge the premise of whether such analyses unequivocally support a theropod ancestry for birds. While this analysis certainly represents a step forward in the debate, their effort is deeply flawed on a number of counts. For one, they based their analysis on a now outdated dataset developed to examine generic-level interrelationships of coelurosaurs (Clark *et al.*, 2002), and thus focused on traits uniting various maniraptoran genera to one another, rather than on the traits more broadly nesting birds within Theropoda. Citing many of the older challenges to synapomorphies that support the birds-as-theropods, they eliminate a number of relevant characters of the wrist, hand, and ankle while reinterpreting others to favor character interpretations put forth by proponents of a nontheropod ancestry of birds, sometimes in illogical fashion. For example James & Pourtless (2009) go to great length to defend Martin and colleagues' (1998) hypothesis that the hypocleideum of enanationithines has a distinct embryological identity from that of crown birds and proceed to redefine the relevant character definition, yet they never provide any insight on how such developmental distinctions are to be made on fully ossified structures in fossil specimens. To this decimated dataset they add a broad, but skewed, sample of more basal theropods, crocodilians, and the enigmatic and poorly preserved Triassic fossil *Longisquama,* without a correspondingly sufficient increase in character sampling to accurately test the relationships of the diversity of added taxa. Critically, they omit any basal crurotarsan taxa or other Triassic archosauriforms necessary to properly evaluate the phylogenetic affinities of either crocodylomorphs or the enigmatic Triassic fossil *Longisquama*, despite the fact that taxon sampling has been recognized as a key parameter for achieving accuracy in phylogenetic analysis (Poe, 1998; Graybeal, 1998). Remarkably, despite such manipulations, inadequate taxon and character sampling, and mistakes in data scoring (e.g. James & Pourtless' (2009) statement that interdental plates are absent in *Archeopteryx*; Figure 1.5A), the primary signal of the original data set examining the position of birds within maniraptoran dinosaurs remains largely intact, attesting to its robustness.

To date, no credible alternative to the theropod ancestry of birds enjoys much support from the fossil record. Although, new fossil discoveries offer the potential to challenge existing hypotheses of relationships, when it comes to bird origins, such discoveries have only served to further strengthen the theropod origin hypothesis through novel synapomorphies (e.g. wishbones, wrist anatomy, feathers), reduction of gaps in the fossil record, and bridging gaps in parameters such as body size. In contrast, opposing views have not been able to muster any new fossil taxa in support of alternative hypotheses (vague as these have been; Prum, 2002) in the past 25 years, relying instead on reinterpretations of a handful of fossils that are either so poorly preserved (e.g. *Longisquama*) or whose identity is so contested (e.g. *Protoavis*) that consensus on their anatomy and affinities is lacking.

CONCLUSIONS

Birds represent the most speciose and widespread clade of amniotes and are characterized by unique locomotory and physiological adaptations, which have long fascinated humans and been the focus of intense evolutionary and ecological research. To fully understand these aspects of avian biology we need to comprehend the origin of birds and their traits in a historical context. While avian origins remained unresolved for most of the first century that followed Darwin's publication of "*On the Origin of Species*", a string of discoveries of small- to medium-sized theropod dinosaurs since the 1960s has identified an inordinate number of derived characters shared with birds.

Today there is little debate over the theropod ancestry of birds. The accelerated rate of discovery and description of well-preserved Mesozoic theropods over the past decade and a half has not only strengthened this hypothesis, but has also immeasurably improved our knowledge of how avian anatomy and biology evolved.

We now know that some avian hallmarks such as the wishbone and skeletal pneumaticity have much deeper origins near the base of the theropod radiation, while others, such as feathers, evolved closer to birds but still characterize a more inclusive group of theropods. These discoveries also allow inferences on which derived physiological and behavioral traits of modern birds evolved before the avian lineage itself, and which ones came later. Paleohistological data suggest that theropods had elevated basic metabolic rates over those of living ectotherms, an inference corroborated by the presence of feather homologues in this clade, and by the growth rates approaching those of metatherian mammals and basal avian lineages (Erickson *et al.*, 2001). Nevertheless, extremely high modern avian growth rates and decoupling between somatic and reproductive maturity evolved much later within the avian lineage itself. In similar fashion, birds inherited proportionately large brain sizes from their coelurosaurian ancestors, but the evolutionary trend toward increased brain sizes continued within the avian lineage such that modern birds generally have larger encephalization quotient (EQ) values than nonavian theropods.

The continuing pace of discovery as well as technological advances in paleomolecular biology, CT scanning, and biogeochemistry hold great promise for future research surrounding the origin of birds. While our understanding of this important branching point in the tree of life has made a quantum leap in recent years, much still remains to be discovered about the earliest chapters in the evolution of birds and their biology.

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REFERENCES

Alonso PD, Milner AC, Ketcham RA, Cookson MJ, Rowe TB. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. *Nature* **430**: 666–669.

Balanoff AM, Xu X, Kobayashi Y, Matsufune Y, Norell MA. 2009. Cranial osteology of the theropod dinosaur *Incisivosaurus gauthieri* (Theropoda: Oviraptorosauria). *American Museum Novitates* **3651**: 1–35.

Barsbold R. 1983. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Joint Soviet–Mongolian Paleontological Expedition Transactions* **19**: 5–120. (In Russian)

Benton MJ. 1990. Phylogeny of the major tetrapod groups - morphological data and divergence dates. *Journal of Molecular Evolution* **30**: 409–424.

Benton MJ. 2008. How to find a dinosaur, the role of synonymy in biodiversity studies. *Paleobiology* **34**: 516–533.

Bonaparte JF, Novas FE, Coria RA. 1990. *Carnotaurus satrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum of Los Angeles County, Contributions in Science* **416**: 1–41.

Britt B. 1997. Postcranial pneumaticity. In *The Encyclopedia of Dinosaurs*, Currie PJ, Padian K (eds). San Diego: Academic Press; 590–598.

Britt BB, Makovicky PJ, Gauthier J, Bonde N. 1998. Postcranial pneumatization in *Archaeopteryx*. *Nature* **395**: 374–376.

Brown B, Schlaikjer EM. 1940. The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Sciences* **40**: 133–266.

Burke AC, Feduccia A. 1997. Developmental patterns and the identification of homologies in the avian hand. *Science* **278**: 666–668.

Chiappe LM, Norell MA, Clark JM. 1998. The skull of a relative of the stem-group bird *Mononykus*. *Nature* **392**: 275–278.

Chinsamy A, Chiappe LM, Dodson P. 1994. Growth rings in Mesozoic birds. *Nature* **368**: 196–197.

Chinsamy-Turan A, Hillenius WJ. 2004. Physiology of non-avian dinosaurs. In *The Dinosauria*, Weishampel DB, Dodson P, Osmolska H (eds). Berkeley: University of California; 643–659.

Chure DJ, Madsen JH. 1996. On the presence of furculae in some non-maniraptoran theropods. *Journal of Vertebrate Paleontology* **16**: 573–577.

Clark JM, Norell MA, Chiappe LM. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianl-like brooding position over an oviraptorid nest. *American Museum Novitates* **3265**: 1–36.

Clark JM, Norell M, Makovicky P. 2002. Cladistic approaches to the relationships of birds to other theropods. In *Mesozoic Birds: Above the Heads of Dinosaurs*, Chiappe LM, Witmer LD (eds). Berkeley: University of California Press; 31–61.

Currie PJ, Chen PJ. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences* **38**: 1705–1727.

Dahn RD, Fallon JF. 2000. Digital identity is regulated by interdigital bmp signaling. *Developmental Dynamics* **219**: 8.

Dollo LAMJ. 1893. Les lois d'Evolution. *Bulletin de la Société Belge de Géologie, de Páleontologieet d'Hydrologie, Mémoire* **7**: 164–166.

Domínguez Alonso P, Milner AC, Ketcham RA, Cookson MJ, Rowe TB. 2004. The avian nature of the brain and inner ear of Archaeopteryx. *Nature* **430**, 666–669. doi:10.1038/nature02706

Elzanowski A, Wellnhofer P. 1996. Cranial morphology of *Archaeopteryx*: Evidence from the seventh skeleton. *Journal of Vertebrate Paleontology* **16**: 81–94.

Erickson GM, Rogers KC, Yerby SA. 2001. Dinosaurian growth patterns and rapid avian growth rates. *Nature* **412**: 429–433.

Erickson GM, Curry-Rogers K, Varricchio DJ, Norell MA, Xu X. 2007. Growth patterns in brooding dinosaurs reveals the timing of sexual maturity in non-avian dinosaurs and genesis of the avian condition. *Biology Letters* **3**: 558–561.

Erickson GM, Rauhut OWM, Zhou Z, Turner AH, Inouye BD, Hu D, Norell MA. 2009. Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. *PLoS ONE* **4**(10): e7390. doi:10.1371/journal.pone.0007390

Feduccia A. 1996. *The Origin and Evolution of Birds*. New Haven: Yale University Press.

Feduccia A, Martin LD. 1998. Theropod-bird link reconsidered. *Nature* **391**: 754.

Feduccia A, Nowicki J. 2002. The hand of birds revealed by early ostrich embryos. *Naturwissenschaften* **89**: 391–393.

Feduccia A, Lingham-Soliar T, Hinchcliffe JR. 2005. Do feathered dinosaurs exist? Testing the hypothesis on

neontological and paleontological evidence. *Journal of Morphology* **266**: 125–166.

Gauthier JA. 1986. Saurischian monophyly and the origin of birds. In *The Origin of Birds and Evolution of Flight*, Padian K (ed.). San Francisco: California Academy of Sciences Memoir; 1–55.

Grellet-Tinner G, Makovicky P. 2006. A possible egg of the dromaeosaur *Deinonychus antirrhopus*: phylogenetic and biological implications: Canadian. *Journal of Earth Sciences* **43**: 705–719.

Heilman G. 1926. *The Origin of Birds*. London: Witherby; 210 pp.

Holtz TR. 1994. The phylogenetic position of the Tyrannosauridae – implications for theropod systematics. *Journal of Paleontology* **68**: 1100–1117.

Hu DY, Hou LH, Zhang LJ, Xu X. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* **461**: 640–643.

Huxley TH. 1868. On the animals which are most nearly intermediate between birds and reptiles. *Geological Magazine* **5**: 357–365.

James FC, Pourtless IV, JA. 2009. Cladistics and the origin of birds: a review and two new analyses. *Ornithological Monographs* **66**: 1–78.

Jerison HJ. 1973. *Evolution of the Brain and Intelligence*. New York, NY: Academic Press.

Ji Q, Norell MA, Gao KQ, Ji SA, Ren D. 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature* **410**: 1084–1088.

Kirkland JI, Zanno LE, Sampson SD, Clark JM, DeBlieux DD. 2005. A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. *Nature* **435**: 84–87.

Kobayashi Y, Lu JC, Dong ZM, Barsbold R, Azuma Y, Tomida Y. 1999. Palaeobiology – herbivorous diet in an ornithomimid dinosaur: *Nature* **402**: 480–481.

Larsson HCE, Wagner GP. 2002. Pentadactyl ground state of the avian wing. *Journal of Experimental Zoology* **294**: 146–151.

Lee AH, Werning S. 2008. Sexual maturity in growing dinosaurs does not fit reptilian model. *Proceedings of the National Academy of Sciences* **105**: 582–587.

Li Q, Gao K-Q, Vinther J, Shawkey MD, Clarke JA, D'Alba L, Meng Q, Briggs EEG, Prum RO. 2010. Plumage color patterns of an extinct dinosaur. *Science* **327**: 1369–1372.

Lingham-Soliar T, Feduccia A, Wang XL. 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 (Biological Sciences)* **274**: 1823–1829.

Longrich N. 2006. Structure and function of hindlimb feathers in *Archaeopteryx lithographica*. *Paleobiology* **32**: 417–431.

Makovicky PJ, Currie PJ. 1998. The presence of a furcula in tyrannosaurid theropods, its phylogenetic and functional implications. *Journal of Vertebrate Paleontology* **18**: 143–149.

Makovicky PJ, Apesteguía S, Agnolin FL. 2005. The earliest dromaeosaurid theropod from South America. *Nature* **437**: 1007–1011.

Martin LD. 1991. Mesozoic birds and the origin of birds. In *Origins of the Higher Groups of Tetrapods, Controversy and Consensus*. Schultze H-P, Trueb L (eds). Ithaca: Cornell University Press; 485–540.

Martin LD, Stewart JD. 1985. Homologies in the avian tarsus. *Nature* **315**: 159.

Martin LD, Stewart JD. 1999. Implantation and replacement of bird teeth. *Smithsonian Contributions to Paleobiology* **89**: 295–300.

Martin LD, Stewart JD, Whetstone KN. 1980. The origin of birds: structure of the tarsus and teeth. *Auk* **97**: 86–93.

Martin LD, Zhou Z, Hou L, Feduccia A. 1998. *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. *Naturwissenschaften* **85**: 286–289.

Maryanska T, Osmolska H, Wolsan M. 2002. Avialan status for Oviraptorosauria. *Acta Palaeontologica Polonica* **47**: 97–116.

Nesbitt SJ, Smith ND, Irmis RB, Turner AH, Downs AM, Norell A. 2009a. A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science* **326**: 1530–1533.

Nesbitt SJ, Turner AH, Spaulding M, Conrad JL, Norell MA. 2009b. The theropod furcula. *Journal of Morphology* **270**: 856–879.

Norell MA, Makovicky PJ. 1999. Important features of the dromaeosaurid skeleton II: Information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates* **3282**: 1–45.

Norell MA, Xu X. 2005. Feathered dinosaurs. *Annual Review of Earth and Planetary Sciences* **33**: 277–299.

Norell MA, Clark JM, Chiappe LM, Dashzeveg D. 1995. A nesting dinosaur. *Nature* **378**: 774–776.

Norell MA, Makovicky PJ, Clark JM. 2001. Relationships among Maniraptora: problems and prospects. In *New Perspectives on the Origin and Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*, Gauthier JA, Gall LF (eds). New Haven: Yale University Press; 49–68.

Norell MA, Makovicky PJ, Bever GS, Balanoff AM, Clark JM, Barsbold R, Rowe T. 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *American Museun Novitates* **3654**: 1–63.

Novas FE, Pol D. 2002. Alvarezsaurid relationships reconsidered. In *Mesozoic Birds: Above the Heads of Dinosaurs*, Chiappe LM, Witmer LM (eds). Berkeley: University of California Press; 121–124.

Novas FE, Pol D. 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature* **433**: 858–861.

Novas FE, Puerta PF. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* **387**: 390–392.

O'Connor PM. 2009. Evolution of archosaurian body plans: skeletal adaptations of an air sac-based breathing apparatus in birds and other archosaurs. *Journal of Experimental Zoology, Part A – Ecological Genetics and Physiology* **311A**: 629–646.

O'Connor PM, Claessens LP. A. M. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* **436**: 253–256.

Organ CL, Shedlock AM, Meade A, Pagel M, Edwards SV. 2007. Origin of avian genome size and structure in non-avian dinosaurs. *Nature* **446**: 180–184.

Ostrom JH. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History, Yale University Bulletin* **30**: 1–163.

Ostrom JH. 1970. *Archaeopteryx* – notice of a new specimen. *Science* **170**: 537.

Ostrom JH. 1976. *Archeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* **8**: 91–182.

Padian K, Horner JH. 2004. Dinosaur physiology. In *The Dinosauria*, Weishampel DB, Dodson P, Osmolska H (eds). Berkeley: University of California Press; 660–671.

Poe S. 1998. Sensitivity of phylogeny estimation to taxonomic sampling. *Systematic Biology* **47**: 18–31.

Perle A, Norell MA, Chiappe LM, Clark JM. 1993. Flightless Bird from the Cretaceous of Mongolia. *Nature* **362**: 623–626.

Prum RO. 2002. Why ornithologists should care about the theropod origin of birds: *Auk* **119**: 1–17.

Rauhut OWM. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**: 3–213.

Ruben JA, Jones TD, Geist NR, Hillenius WJ. 1997. Lung structure and ventilation in theropod dinosaurs and early birds. *Science* **278**: 1267–1270.

Sampson SD, Krause DW. 2007. *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar – Preface. *Society of Vertebrate Paleontology Memoir* **27**: XIII–XIV.

Sampson SD, Witmer LM, Forster CA, Krause DW, O'Connor PM, Dodson P, Ravoavy F. 1998. Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. *Science* **280**: 1048–1051.

Sampson SD, Carrano MT, Forster CA. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* **409**: 504–506.

Sato T, Cheng YN, Wu XC, Zelenitsky DK, Hsiao YF. 2005. A pair of shelled eggs inside a female dinosaur. *Science* **308**: 375–375.

Schweitzer MH, Watt JA, Avci R, Knapp L, Chiappe LM, Norell MA, Marshall M. 1999. Beta-keratin specific immunological reactivity in feather-like structures of the Cretaceous alvarezsaurid, *Shuvuuia deserti*. *Journal of Experimental Zoology* **285**: 146–157.

Senter P. 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* **5**: 429–463.

Sereno PC. 1999a. A rationale for dinosaurian taxonomy. *Journal of Vertebrate Paleontology* **19**: 788–790.

Sereno PC. 1999b. The evolution of dinosaurs. *Science* **284**: 2137–2147.

Sereno PC, Arcucci AR. 1993. Dinosaurian presursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* **13**: 385–399.

Sereno PC, Brusatte SL. 2008. Basal abelisaurid and carcharodontosaurid theropods from the lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica* **53**: 15–46.

Sereno PC, Dutheil DB, Iarochene M, Larsson HCE, Lyon GH, Magwene PM, Sidor CA, Varricchio DJ, Wilson JA. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* **272**: 986–991.

Sereno PC, Wilson JA, Conrad JL. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **271**: 1325–1330.

Sereno PC, Martinez RN, Wilson JA, Varricchio DJ, Alcober OA, Larsson HCE. 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE* **3** (9): e3303. doi:10.1371/journal.pone.0003303

Smith ND, Makovicky PJ, Hammer WR, Currie PJ. 2007. Osteology of *Cryolophosaurus ellioti* (Dinosauria:

Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society* **151**: 377–421.

Smith ND, Makovicky PJ, Agnolin FL, Ezcurra MD, Pais DF, Salisbury SW. 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **275**: 2085–2093.

Turner AH, Pol D, Clarke JA, Erickson GM, Norell MA. 2007. A basal dromaeosaurid and size evolution preceding avian flight. *Science* **317**: 1378–1381.

Vargas AO, Kohlsdorf T, Fallon JF, VandenBrooks J, Wagner GP. 2008. The evolution of HoxD-11 expression in the bird wing: insights from *Alligator mississippiensis*. *PLoS ONE* **3**(10): e3325. doi:10.1371/journal.pone.0003325

Varricchio DJ, Jackson FD. 2004. Two eggs sunny-side up: reproductive physiology in the dinosaur *Troodon formosus*. In *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*, Currie PJ, Koppelhus EB, Shugar MA, Wright JA (eds). Bloomington: Indiana University Press; 215–233.

Varricchio DJ, Jackson F, Borkowski JJ, Horner JR. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**: 247–250.

Varricchio DJ, Horner JR, Jackson FD. 2002. Embryos and eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* **22**: 564–576.

Wagner GP. 2005. The developmental evolution of avian digit homology: an update. *Theory In Biosciences* **124**: 165–183.

Wagner GP, Gauthier JA. 1999. 1, 2, 3 = 2, 3, 4: A solution to the problem of the homology of the avian hand. *Proceedings of the National Academy of Sciences, USA* **96**: 5111–5116.

Weishampel DB, Dodson P, Osmolska H. (eds). 2004. *The Dinosauria*. Berkeley: University of California Press.

Witmer LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In *Functional Morphology in Vertebrate Paleontology*, Thomason JJ (ed.). Cambridge: Cambridge University Press; 19–33.

Xu X, Norell MA. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* **431**: 838–841.

Xu X, Zhang FC. 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* **92**: 173–177.

Xu X, Zhou ZH, Wang XL. 2000. The smallest known non-avian theropod dinosaur. *Nature* **408**: 705–708.

Xu X, Zhou HH, Prum RO. 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* **410**: 200–204.

Xu X, Norell MA, Wang XL, Makovicky PJ, Wu XC. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* **415**: 780–784.

Xu X, Norell MA, Kuang XW, Wang XL, Zhao Q, Jia CK. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* **431**: 680–684.

Xu X, Clark JM, Forster CA, Norell MA, Erickson GM, Eberth DA, Jia CK, Zhao Q. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature* **439**: 715–718.

Xing X, Qi Z, Norell MA, Sullivan C, Hone DWE, Erickson GM, Wang X-L, Han F-L and Yu G. 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian evolution. *Chinese Science Bulletin* **54**: 430–435.

Xu X, Clark JM, Mo JY, Choiniere J, Forster CA, Erickson GM, Hone DWE, Sullivan C, Eberth DA, Nesbitt S, Zhao Q, Hernandez R, Jia CK, Han FL, Guo Y. 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* **459**: 940–944.

Yates AM, Vasconcelos CC. 2005. Furcula-like clavicles in the prosauropod dinosaur *Massospondylus*. *Journal of Vertebrate Paleontology* **25**: 466–468.

Young RL, Caputo V, Giovannotti M, Kohlsdorf T, Vargas AO, May GE, Wagner GP. 2009. Evolution of digit identity in the three-toed Italian skink *Chalcides chalcides*: a new case of digit identity frame shift. *Evolution and Development* **11**: 647–658.

Zanno LE, Gillette DD, Albright LB, Titus AL. 2009. A new North American therizinosaurid and the role of herbivory in 'predatory' dinosaur evolution. *Proceedings of the Royal Society of London, Series B – Biological Sciences* **276**: 3505–3511.

Zhang FC, Zhou ZH, Xu X, Wang XL, Sullivan C. 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* **455**: 1105–1108.

Zhang F, Kearns S, Orr P, Benton M, Zhou Z, Johnson D, Xu X, Wang X. 2010. Fossilized melanosomes and the colour of Cretaceous dinosaurus and birds. *Nature* **463**: 1075–1078.