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# An integrative approach to understanding bird origins

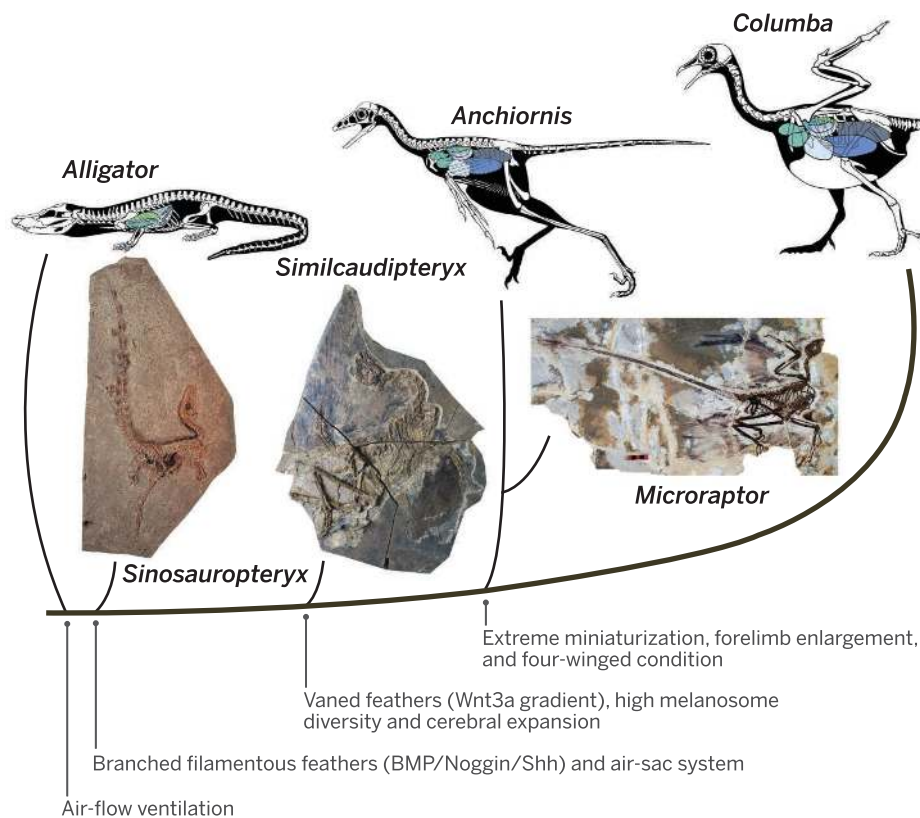
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**BACKGROUND:** The origin of birds is one of the most enduring and dramatic evolutionary debates. The hypothesis that the primarily small-sized birds are nested within a theropod dinosaur group that includes the gigantic *Tyrannosaurus rex* has been supported by strong fossil evidence, but until recently, several important issues remained unresolved, including the origins of feathers and flight, the “temporal paradox” (the coelurosaurian theropods occur too late in the fossil record to be ancestral to the Jurassic bird *Archaeopteryx*), and supposed homological incongruities (e.g., the suggested homologies of three fingers in tetanuran theropods are different from those of living birds). Recent discoveries of spectacular dinosaur fossils from China and elsewhere provide new information to address these issues.

**ADVANCES:** The discoveries of feathered dinosaur fossils from the Jurassic and Cretaceous sediments of China and elsewhere document a diverse range of feathers from monofilamentous feathers to highly complex flight feathers, which show a general evolutionary trend of increasing complexity leading to the cladogenesis of birds. The wide occurrence of foot feathers in Mesozoic theropods (i.e., short filamentous forms in relatively basal theropods and large vaned forms in derived theropods, including early birds) clarifies feather-scale relations and integumentary evolution pertinent to flight origins and also shows that bird flight likely evolved through a four-winged stage. With numerous discoveries of well-preserved dinosaur fossils over a wide range of geological periods, the morphological, functional, and temporal transition from

ground-living to flight-capable theropod dinosaurs is now one of the best-documented major evolutionary transitions. Meanwhile, studies in disciplines other than paleontology provide new insights into how bird characteristics originated and evolved—such as feathers, flight, endothermic physiology, unique strategies for reproduction and growth, and an unusual pulmonary system. The iconic features of extant birds, for the most part, evolved in a gradual and step-wise fashion throughout theropod evolution. However, new data highlight occasional bursts of morphological novelty at certain stages close to the origin of birds and an unavoidable complex, mosaic evolutionary distribution of major bird characteristics on the theropod tree. Research into bird origins provides a model of how an integration of paleontological and neontological data can be used to gain a comprehensive understanding of the complexity surrounding major evolutionary transitions and to set new research directions.

**OUTLOOK:** A refined, more robust phylogeny will be imperative to move our studies forward. A larger data set will help to increase the accuracy of phylogenetic reconstructions, but better character formulation and more accurate scorings are imperative at the current stage. In terms of character evolution, an integrative approach combining paleontological, neontological, developmental, temporal, and even paleoenvironmental data is particularly desirable. Greater examination of fossils pertaining to molecular information is also a potentially fruitful avenue for future investigation. Evolutionary scenarios for various aspects of the origin of birds have sometimes been constructed from neontological data, but any historical reconstruction must ultimately be tested using the fossil record. Consequently, dense fossil sampling along the line to modern birds and better understanding of transitional forms play key roles in such reconstructions. ■



## Evolutionary history of selected bird features inferred from multidisciplinary data.

Recent studies demonstrate that major bird characteristics have evolved in a sequential way, and many of them initiated transformation early in dinosaur evolution, with some approaching modern conditions well before the origin of birds, whereas others appear only near the origin of the crown group birds.

# An integrative approach to understanding bird origins

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Recent discoveries of spectacular dinosaur fossils overwhelmingly support the hypothesis that birds are descended from maniraptoran theropod dinosaurs, and furthermore, demonstrate that distinctive bird characteristics such as feathers, flight, endothermic physiology, unique strategies for reproduction and growth, and a novel pulmonary system originated among Mesozoic terrestrial dinosaurs. The transition from ground-living to flight-capable theropod dinosaurs now probably represents one of the best-documented major evolutionary transitions in life history. Recent studies in developmental biology and other disciplines provide additional insights into how bird characteristics originated and evolved. The iconic features of extant birds for the most part evolved in a gradual and stepwise fashion throughout archosaur evolution. However, new data also highlight occasional bursts of morphological novelty at certain stages particularly close to the origin of birds and an unavoidable complex, mosaic evolutionary distribution of major bird characteristics on the theropod tree. Research into bird origins provides a premier example of how paleontological and neontological data can interact to reveal the complexity of major innovations, to answer key evolutionary questions, and to lead to new research directions. A better understanding of bird origins requires multifaceted and integrative approaches, yet fossils necessarily provide the final test of any evolutionary model.

The origin of birds is one of the most enduring and dramatic evolutionary debates (1–3). Whether the primarily small-sized birds are nested within a theropod group including the gigantic *Tyrannosaurus rex* is of great interest to both the academic community and general public. More challenging is whether the origin of major bird characteristics can be traced among the Mesozoic terrestrial theropod dinosaurs. Recent discoveries of spectacular dinosaur fossils from China and elsewhere (Fig. 1) provide significant new information to address these issues and also prompt numerous studies in disciplines other than paleontology to explain how bird characteristics originated and evolved (4–11). Whereas these new discoveries and studies have addressed many issues on the origin of birds, they also open new research directions. A better understanding of the origin of birds requires a more integrative approach, and this is particularly true given that understanding bird origins is more about reconstructing the evolutionary patterns of major bird characteristics than just filling the gaps between birds and their theropod ancestors. In this review, we present a brief introduction to recent advances on this topic, discuss several issues that have interested both paleontologists and scientists in other fields, and finally provide our thoughts on how to proceed using an integrative approach in evolutionary biology. For the convenience of further discussion, we define the vernacular term “birds” (avians in many publications) to

correspond to Avialae, a stem-based taxon defined as the most-inclusive clade containing *Passer domesticus* but not *Dromaeosaurus albertensis* or *Troodon formosus*.

## Family tree of birds and relatives

A reliable phylogeny sets the framework for reconstructing the evolutionary sequence of major bird characters. Although birds are widely accepted to form a monophyletic group (i.e., a group composed of an ancestor and all its descendants) within the Archosauromorpha, the identity of their closest relatives has been hotly debated (1–3, 12).

The last four decades have witnessed an un-precedented accumulation of evidence supporting the hypothesis that birds are maniraptoran theropods (BMT hypothesis) (2, 3, 13), and most likely closely related to the troodontids and/or dromaeosaurs (14–23). The BMT hypothesis is supported by numerous skeletal, behavioral, and physiological resemblances between nonavian theropod dinosaurs (hereafter, theropods) and birds. These resemblances are derived from such birdlike theropods as the dromaeosaur *Deinonychus*, the troodontid *Saurornithoides*, and others (24, 25), dinosaur fossils preserving gastroliths for digestion (26), highly pneumatic theropod skeletons (27–29), dinosaur nests preserving

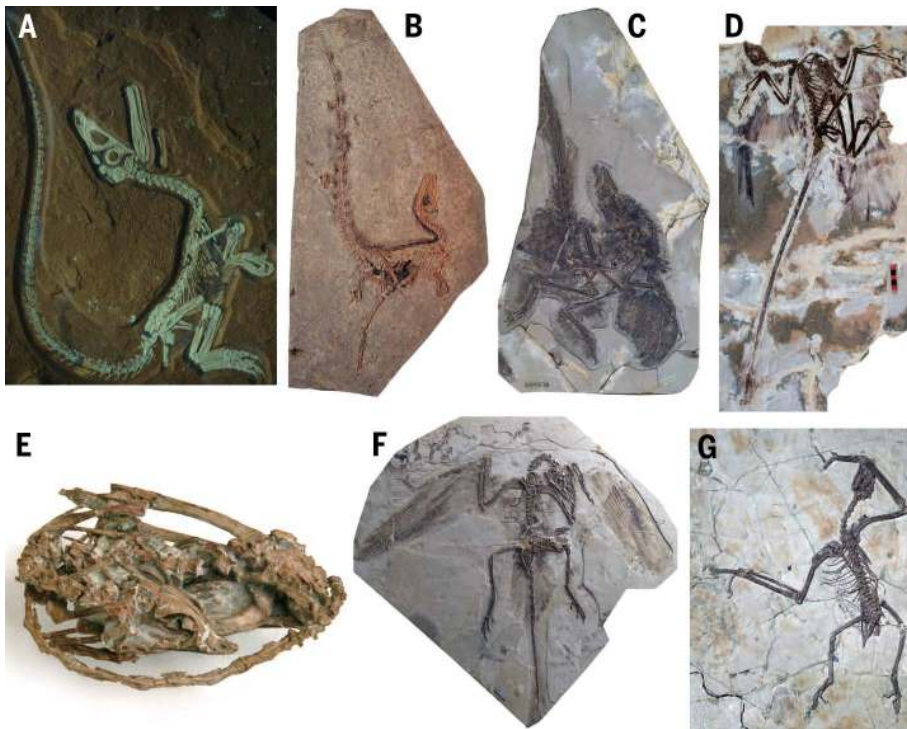
(34–36), and bone microstructures indicating fast growth rates (37), among others. Nearly all published numerical phylogenetic analyses support the BMT hypothesis (15–23, 38). Comparatively, other hypotheses on bird origin are based on a small number of similarities from certain parts of the body between birds and the proposed groups (1). One recently published numerical phylogenetic analysis places birds and other maniraptoran theropods at the base of the Archosauria rather than within the Theropoda (12), but this analysis is flawed in several aspects including a strongly biased data set used for the analysis (39).

Although birds are now widely accepted to be theropods, maniraptorans, and paravians, there is an unresolved debate on what are the most basal birds. Suggested taxa include the probably flighted *Archaeopteryx* and *Rahonavis* (40), the enigmatic scansoriopterygids (41), the four-winged *Anchiornis* and its kin (21, 42), and the Gondwanan unenlagiid theropods (38, 43). Many recent studies suggest that *Rahonavis*, other unenlagiids, and *Anchiornis* and its kin are deinonychosaur (16, 17, 22, 44, 45). Several analyses even place the iconic *Archaeopteryx* at the base of the Deinonychosauria (22), yet other studies suggest that the *Deinonychosauria* itself is paraphyletic, with the troodontids more closely related to birds than the dromaeosaurs (21) or vice versa (20). A radical suggestion is that the oviraptorosaurs are closely related to the scansoriopterygids (38, 46, 47) and, further, that they together represent the first major branching in bird evolution (46). Despite these debates, considerable consensus exists for the general branching pattern of major theropod groups (15–23, 38), here used as a framework for further discussions on bird origins (Fig. 2).

## Recently discovered transitional forms toward modern birds

Numerous recently discovered fossils of theropods and early birds have filled the morphological, functional, and temporal gaps along the line to modern birds. These discoveries have helped address several important issues repeatedly raised to challenge the BMT hypothesis (1, 48, 49), such as the origins of feathers and flight, the “temporal paradox” in the stratigraphic distribution of theropod fossils (i.e., most of the diversity of coelurosaurian theropods occurs much later in the fossil record than *Archaeopteryx* in the Late Jurassic), and the supposed homological incongruities (e.g., the suggested homologies of three fingers in tetanuran theropods are different from those of living birds).

Numerous discoveries demonstrate that many bird characteristics have their origins among theropods or a more inclusive group (Fig. 2). For example, the discoveries of Mahakala and other basal members of derived theropod groups



**Fig. 1. Selected recently discovered transitional forms of theropods and early birds.** The basal tetanuran *Scieurumimus* (A) and the basal coelurosaur *Sinosauropteryx* (B) with filamentous feathers. The deinonychosaur *Anchiornis* (C) and *Microraptor* (D) with numerous skeletal and integumentary features including large vaned feathers on hindlimbs that are also present in basal birds. (E) The troodontid *Mei* with a birdlike tuck-in sleeping posture. The basal birds *Jeholornis* with a dromaeosaur-like tail (F) and *Sapeornis* with a typical deinonychosaurian shoulder girdle (G).

suggest that extreme miniaturization and laterally movable arms necessary for flapping flight are ancestral for paravian theropods (43, 50, 51). The ceratosaur *Limusaurus*, with a highly reduced pollex, might represent a key stage in theropod hand evolution (52); the megalosaur *Scieurumimus* (Fig. 1A), the compsognathid *Sinosauropteryx* (Fig. 1B), and a few other dinosaurs—including even some ornithischians—document the appearance of primitive feathers (53–57). Other discoveries include the oviraptorosaur *Caudipteryx* (58), the deinonychosaur *Anchiornis* (Fig. 1C), *Microraptor* (Fig. 1D), and several other maniraptorans that have pennaceous (vaned) feathers (45, 57–59). The troodontid *Mei* (Fig. 1E) preserves a birdlike “tuck-in” sleeping posture (60). In contrast, a number of basal birds resemble theropods in many features. For example, new *Archaeopteryx* specimens indicate that this early bird has tetraradiate palatine, as in theropods, and probably a specialized second pedal digit as in deinonychosaur (61); *Jeholornis* (Fig. 1F) has a dromaeosaur-like long, stiff bony tail (62); and the short-tailed *Sapeornis* (Fig. 1G) has a shoulder girdle similar to those of the deinonychosaur (63).

Earlier studies demonstrate that the temporal paradox is not a real problem for the BMT hypothesis, which is in fact more consistent with the stratigraphic record than any other alternative phylogenetic hypothesis regarding the origin of birds (64). Nonetheless, recent inves-

tigations in the Jurassic have resulted in the discoveries of well-preserved fossils of several derived theropod groups, including Tyrannosauroida (65), Alvarezsauroida (23), Troodontidae (45), and possibly Therizinosauroida (66) and Oviraptorosauria (38, 41). These discoveries improve the stratigraphic fit of the theropod fossil record to the BMT hypothesis (23) and have effectively resolved the so-called temporal paradox problem by showing that many coelurosaurian groups occur earlier than *Archaeopteryx* in the fossil record (Fig. 2).

Newly discovered fossils and relevant analyses demonstrate that salient bird characteristics have a sequential and stepwise transformational pattern, with many arising early in dinosaur evolution, undergoing modifications through theropods, and finally approaching the modern condition close to the origin of the crown group birds (Fig. 2). For example, the unusually crouched hindlimb for bipedal locomotion that characterizes modern birds was acquired in stepwise fashion through much of theropod evolution (67), and both the furcula (68) and the “semilunate” carpal (69) appeared early in theropod evolution. Notably, major bird characteristics often exhibit a complex, mosaic evolutionary distribution throughout the theropod tree, and several evolutionary stages are characterized by accelerated changes (70). For example, the early evolution of paravian theropods features cerebral expansion and elaboration of

visually associated brain regions (71), forelimb enlargement (22, 67), acquisition of a crouched, knee-based hindlimb locomotor system (67), and complex pinnate feathers associated with increased melanosome diversity, which implies a key physiological shift (72). Together these features may suggest the appearance of flight capability at the base of the Paraves (22, 67).

### Transitional features in dinosaurian reproduction and growth

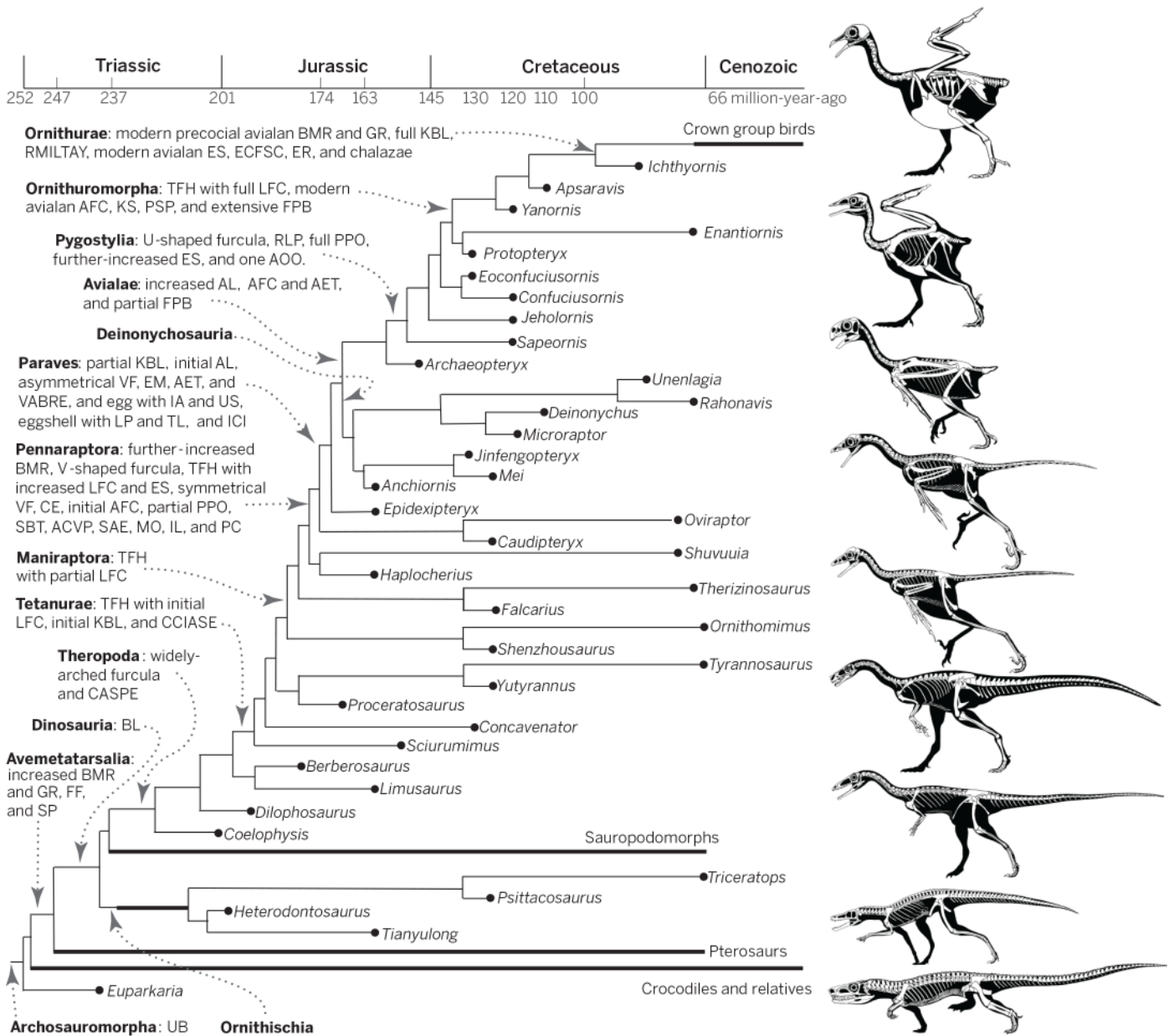
Living birds display a set of unique reproductive features unknown in other extant vertebrates. Nevertheless, based on the study of eggs, eggshell, embryos, and nesting traces, most paleontologists agree that various anatomical features including aspects of egg shape, ornamentation, microstructure, and porosity characteristic of living birds trace their origin to the maniraptoran theropods, such as oviraptorosaurs and troodontids. Currently, our understanding of reproduction in dromaeosaurs remains limited, as only one taxon is associated with any reproductive material, namely, a *Deinonychus* specimen found on top of eggs (33). These features, together with adult-egg associations, clutch configurations, and nest traces, further suggest that associated behavioral and physiological attributes may also have evolved before the origin of birds. These maniraptoran dinosaurs share with modern birds: eggs with hard calcitic shells with narrow units relative to overall shell thickness, a second structural layer of vertical prisms, sparse and narrow pores, at least some squamatic structure, and calcium absorption (“cratering”) of the mammillae by the developing embryo (34–36, 73). Egg size relative to adult size in both oviraptorosaurs and troodontids is large in comparison to the ratios for all other theropods (74). Further, these eggs greatly exceed those typical of modern reptiles of similar body mass but are less than 40% the size expected in a bird of similar adult body mass (74).

On the basis of discoveries of within-clutch egg pairing (31) and of specimens with two eggs within or in close proximity to adult skeletons (75, 76), maniraptorans have been inferred to have sequential ovulation, as in birds, but from two functional ovaries and oviducts (mono-autochronic ovulation) (31). Adult-clutch associations, some preserving brooding postures, are known for four oviraptorosaurs (30, 77), two troodontids (31, 32), a dromaeosaur (33), and one basal bird (74) providing clear evidence for parental care of eggs. The extra-large clutches of these dinosaurs exceed the mass of those for equivalent-sized extant reptiles and birds by two to fourfold (78). Such large clutch sizes are akin to those of modern birds showing paternal or maternal parental care, as opposed to those exhibiting biparental care (79). None of the clutch-associated adults ( $n = 8$ ) of nonavian maniraptorans has any osteo-histologic features associated with egg-laying females. Thus, the large clutches of oviraptorosaurs and troodontids may favor communal nesting and paternal (male-only) care for these groups (80, 81).

The eggshell and eggs of oviraptorosaurs and dromaeosaurs, where known, are two-layered, moderately porous, and only weakly asymmetric (33, 34, 36, 73), although the ornamented eggs of Alvarezsaurus have a three-layered eggshell

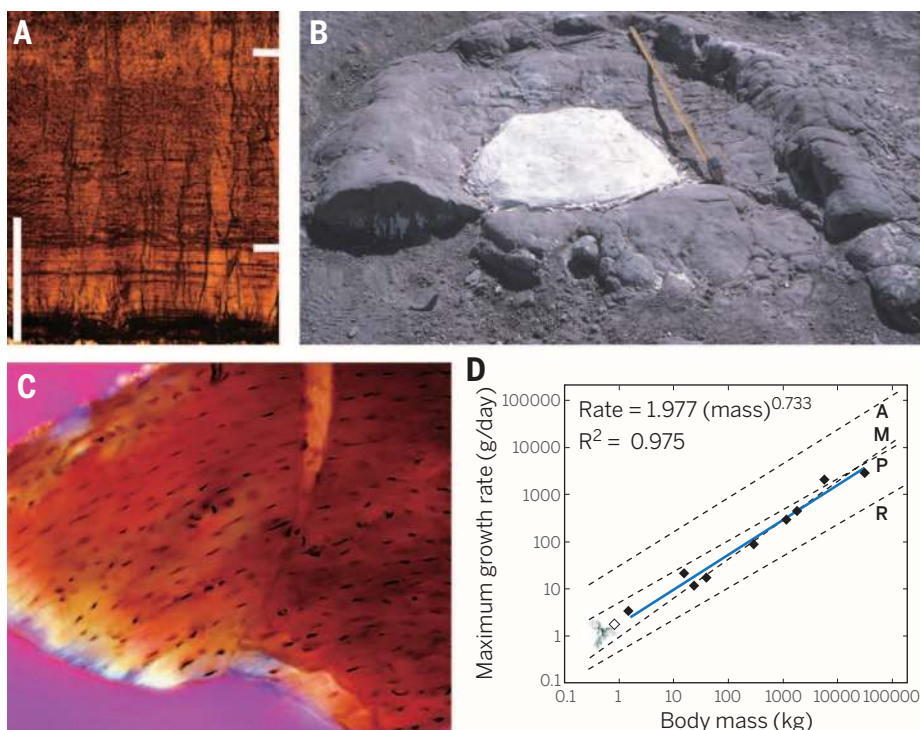
(82). In contrast, troodontids exhibit a more strongly asymmetric egg lacking ornamentation with potentially three structural shell layers and low porosity (Fig. 3A), and they are structured more like modern bird eggs than

like those of other dinosaurs (83, 84). In addition, the tighter clutch configuration, greater exposure of eggs (Fig. 3B), and avialan levels of porosity favor contact incubation in troodontids (85, 86).



**Fig. 2. Selected species on a temporally calibrated archosauromorphan phylogeny showing the evolution of major characteristics along the bird-line.** The phylogeny is a combination of two recently published analyses: The basal part of the tree is derived from (55) and the upper part from (16). Skeletal silhouettes of several archosauromorphans show the general morphological features along the bird-line within this group, and they are the basal archosauromorphan *Euparkaria*, the basal crocodylomorph *Sphenosuchus*, the basal theropod *Coelophysis*, the basal coelurosaur *Protoceratosaurus*, the basal paravian *Anchiornis*, the basal avialan *Archaeopteryx*, the basal pygostylian *Sapeornis*, the basal ornithuromorphan *Yanornis*, and the crown group bird *Columba* (bottom to top). Acronyms in the figure: ACVP, advanced costosternal ventilator pump; AET, arm elongation and thickening; AFC, arm flapping capability; AL, aerial locomotion; AOO, active ovary and oviduct; BL,

bipedal locomotion; BMR, basal metabolic rate; CASPE, cervical air sacs posterior extension; CCIASE, cranial and caudal intrathoracic air sacs elaboration; CE, cerebral expansion; ECFSC, egg clutch free of sediment cover; EM, extreme miniaturization; ER, egg rotation; ES, egg size; FF, filamentous feathers; FPB, fusion of pelvic bones; GR, growth rate; IA, increased asymmetry; ICI, improved contact incubation; IL, iterative laying; KBL, knee-based locomotion; KS, kinetic skull; LFC, laterally folding capability; LP, low porosity; MO, monoautochronic ovulation; PC, paternal care; PPO, pubis posterior orientation; PSP, plowshare-shaped pygostyle; RLP, rodlike pygostyle; RMILTAY, rapid maturity in less than a year; SAE, slightly asymmetrical egg; SBT, short bony tail; SP, skeletal pneumatization; TFH, three-fingered hand; TL, third (external) layer; UB, unidirectional breathing; US, unornamented surface; VABRE, visually associated brain regions elaboration; VF, vanned feathers.



**Fig. 3. Maniraptoran reproduction and growth.** (A) Eggshell of *Troodon* in radial thin section showing three microstructural layers (separated by white bars) as common to many extant birds. Scale bar, 0.5 mm. (B) *Troodon* nesting trace with clutch of 24 eggs preserved under white plaster jacket. Tops of the eggs were exposed within the nest structure and were incubating by an attending adult representing a transitional stage between the fully buried clutches of most nonavian dinosaurs and the sediment-free clutches typical of modern birds. Tape measure equals 1 m. (C) Histological section of an *Archaeopteryx* femur. The section, shown in polarized light microscopy, shows the characteristic long bone histology of basal-most birds composed of parallel fibrous bone matrix with negligible vascularization. Growth lines are also commonplace but are not evident in this particular specimen (Munich *Archaeopteryx*: Bayerische Staatssammlung für Palaentologie und Geologie BSPG 1999/50). The histology matches that of same-sized nonavian dinosaurs but not that of modern birds. (D) Maximal growth rates for *Archaeopteryx* compared with nonavian dinosaurs and living vertebrates. *Archaeopteryx* growth rates (skeleton) fall on the line at the lowermost bound of the nonavian dinosaur regression line (blue; individual species values are shown as black diamonds). R, typical extant reptilian growth rates, P, typical extant precocial land bird growth rates, M, typical extant marsupial growth rates, A, typical extant altricial land bird growth rates. Graphic is from (98).

Despite these similarities with modern birds, oviraptorosaurs, troodontids and even Cretaceous enantiornithine birds differ reproductively from modern birds in a few key features, including more elongate egg shape and eggs largely buried with sediment during incubation (73, 74, 87, 88). Relative egg size increases markedly from theropods to basal birds of the Mesozoic, with the latter laying eggs 50 to 70% the expected size of those in extant birds (74). Several specimens of basal birds preserve a single mass of circular objects. Although their interpretation remains debated (89), these may represent ovaries with mature ovarian follicles and suggest that basal birds had only one active ovary and oviduct as in most modern birds (90). Modern birds differ from enantiornithines in producing relatively larger eggs that are incubated in the absence of sediment (74). These features highlight the gradual acquisition of “modern” reproductive traits from Mesozoic theropods, through Mesozoic birds such as enantiornithines, and on to modern birds.

Reproductive adaptations may have implications for three other aspects of bird evolution: the development of feathers, metabolism, and flight. First, elongate forelimb and tail feathers in oviraptorosaurs parallel the brooding postures adopted by adults, and lengthening of the feathers may reflect selection for egg care (91). Reproduction in maniraptoran dinosaurs may also imply physiological similarities with birds: Egg pairs suggest a reproductive output similar to that of basal birds (74). Additionally, iterative laying, together with the complex clutch configurations and presumed synchronous hatching (83) in these theropods, further implies that both adult body and incubation temperatures were elevated over ambient conditions (92). Finally, ground nesting, the basal condition in modern birds, has been used to argue for a “ground-up” origin of flight (11). However, other factors may have initially constrained ground nesting. Through the theropod-bird transition, eggs were incubated within sediments, which

suggests that they may have lacked chalazae (31, 74) [chords of albumen present in birds that allow the embryo to maintain an upright position during egg rotation (93)]. Thus, without chalazae, arboreal maniraptoran dinosaurs may have been required to incubate eggs within sediments in order to prevent detrimental egg rotation (31), as occurs in modern crocodylians (94).

The development, growth, and physiology of theropods and basal birds have been explored using a variety of approaches. Birds are notable among living vertebrates in being endotherms, developing explosively to adult sizes in less than a year (very large forms such as ostriches are exceptions), and having exceptionally high basal metabolic rates (95). However, some osteohistological studies show that the bone histology of enantiornithine birds is nearly avascular, composed of slowly deposited parallel-fibered matrix, and having growth lines (96), which are unlike the bones of most dinosaurs (i.e., with fast-growing and highly vascularized fibro-lamellar bone with growth lines), and these studies suggest that basal birds had slowed their growth compared with their dinosaur ancestors. Furthermore, because maximal growth rates strongly correlate with metabolic rates (95), they likely had lower basal metabolic rates than dinosaurs.

Construction of mass-age growth curves showed that nonavian dinosaurs as a whole, although probably endothermic, did not have a physiology exactly like modern birds (97). They grew faster than living reptiles but somewhat slower than most precocial birds and considerably slower than altricial forms scaled to the same size. Histologic analysis shows that several derived theropods, *Archaeopteryx*, and other basal birds inherited this dinosaurian physiology and took over a year to reach somatic maturity (98) (Fig. 3, C and D). The last conclusion has been supported by further growth line evidence in other basal birds (99). The miniaturization event, once associated with the cladogenesis of birds, actually occurred in paravian theropods (50, 51, 98), and consequently, the nearly avascular bone in some basal lineages of birds and small theropods is simply a scaling effect. Modern bone types and, presumably, the remarkable elevated metabolic rates of birds—which allow growth to adult sizes in less than a year—appear to have evolved near the cladogenesis of ornithurine birds during the Cretaceous Period (37, 98, 100), although increased growth and metabolic rates occurred early in theropod evolution (Fig. 2). [Note: The pioneering studies that established dinosaur growth rates were recently criticized for insufficient sample size and other issues (101). However, a subsequent comprehensive specimen-rich analysis (102) strongly supports both the methodology and conclusions about dinosaur and basal bird growth rates and physiology.]

### Complex evolution of avialan traits

Bird morphology features many unique adaptations, and the evolution of some of these traits is so complex that a comprehensive understanding is wanting. How the theropod hand evolved

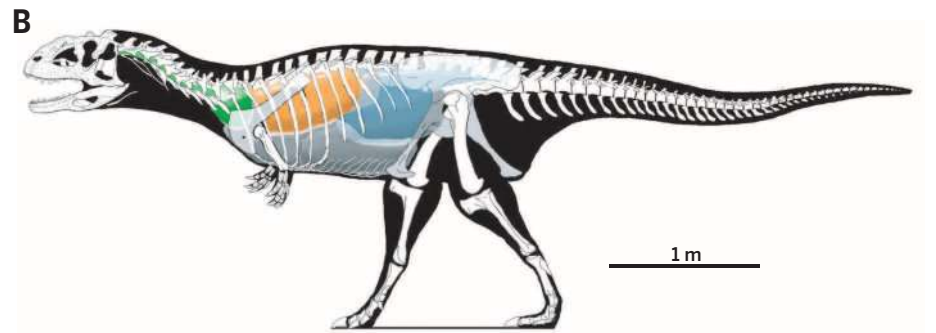
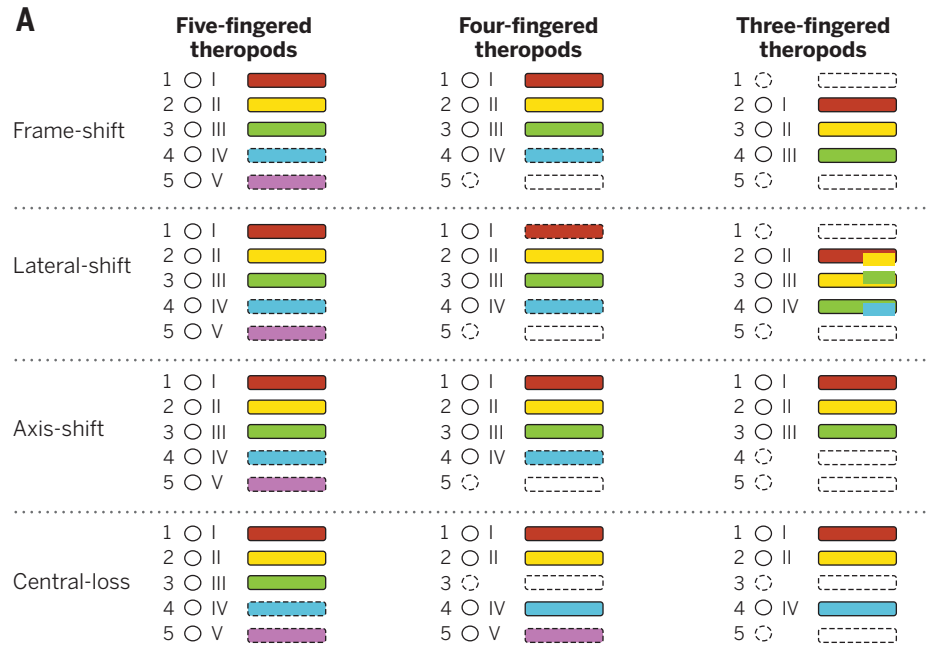
into the bird wing continues to be a hotly debated issue in evolutionary biology. Traditionally, paleontological analysis of theropod digit reductions indicated that the three-digit hand arose by unilateral loss of digits IV and V, resulting in a I, II, III digit formula (103). In contrast, the use of “positional” criteria of embryologic precursors to identify digits in modern birds revealed a digit 2, 3, 4 formula (104, 105). To resolve this paradox, it has been proposed that a homeotic transformation of digits occurred that converted the embryonic precursors to I, II, and III in the adult (frameshift hypothesis) (103). Confounding any reconciliation of evidence from these disciplines, paleontological analyses typically rely on adult morphology to infer evolutionary links, whereas developmental studies generally focus on very transient, vestigial embryonic remnants to infer homologies with adult structures that have been lost entirely during evolution. In contrast to cellular fate determination, morphological identity of a complex structure is generally not defined by any specific and unique genetic “markers,” which creates difficulty in assigning unique homologies.

Nevertheless, the analysis of expression of spatially regulated genes in the embryonic limb, which can be considered “phenotypic” criteria for digit assignment, has provided support for the frameshift hypothesis, in that certain gene expression patterns normally correlated with digit I are retained in the first digit of the chick embryo hand. In addition, recent, more comprehensive genome-wide expression profiling comparing chick embryo hand and foot digit precursors also supports a I, II, III phenotypic formula, in that the expression profiles of the first digit in both the hand and foot are remarkably similar (106). Genetic lineage tracing of *Shh*-expressing cells in the chick, which normally contribute to digits IV and V in the pentadactyl mouse, further suggests that digit IV is phenotypically absent from the chick hand (8, 107). All of the phenotypic data from chick embryos are likewise compatible with the classic paleontological interpretation of a digit I-II-III formula, if the avialan embryo “positional” evidence of digit precursors is discounted as being either misleading or incorrect. However, this requires a shift in the primary limb axis to run through digit 3 (axis shift hypothesis), both in extinct and modern tetanuran theropods (108), rather than through digit 4, as occurs in most tetrapods except urodeles (109), because the primary limb axis must, by definition, include the first digit to form in the embryo. In fact, a shortcoming of the positional data on vestigial digit condensations appearing in the embryonic hands of various avialan species is that, although a remnant of a positional fourth condensation (which could be either IV or V) is clearly posterior (lateral) to the three digits that are retained in the adult, the identification of a vestigial anterior (medial) condensation is controversial, and it is based on indistinct elements that could represent other structures [see review in (110)]. A reevaluation of digit

condensation formation in mouse embryos also suggests that some of the traditional approaches used to visualize early digit condensations may be inadequate and could miss evidence for noncontiguous digit loss (gaps between condensations). In mouse, genetic modulation of signals critical for regulating digit pattern and number across vertebrate species results in the initial loss of a central, rather than lateral, digit (111, 112). This suggests that, in principle, a I-II-IV formula is also possible (central loss hypothesis). The I-II-IV formula would explain the persistence of digit 1 and still retain the primary axis extending through digit 4, which is the accepted rule in all living tetrapods except urodeles. Note that the expression profiling data in chick (106) also revealed mixed expression features for the lateral digits, which could be construed as compatible with a I-II/III-IV avialan hand formula (or the presence of digit IV). Taken together, these developmental studies now leave

open the possibility of I-II-III, or even I-II-IV or I-III-IV formulas, for the modern avialan hand. Conversely, more recent analyses of digit morphologies in ceratosaurian and basal tetanuran theropods (52) lend some support to a II, III, IV theropod formula with secondary transformations to produce final I, II, III morphologies through multiple, partial homeotic transformations (lateral shift hypothesis).

To reconcile the paradox of digit homologies between theropods and birds, all of the proposed models (Fig. 4A) require either multiple events entailing the reduction and then reappearance of a positional digit 4 to retain the primary limb axis or require that the primary axis has undergone a novel shift in its position from digit 4 to 3. Clearly, whereas much progress has been made, a final resolution to this ongoing debate demands additional work from both paleontological and developmental perspectives (110).



**Fig. 4. The evolution of theropod hand and respiratory system. (A)** Diagrams depicting four hypotheses for the evolution of wing digits. Color shading bordered by solid line refers to fully formed digits and by dash line to reduced digits. Colored bars refer to different “morphologic” digits. Arabic numerals refer to positional embryonic digit precursors. A combination of different colors refers to a mixture of different morphological features pertaining to different phenotypes in one digit. **(B)** Reconstruction of pulmonary components [cervical air-sac system (green), lung (orange), and abdominal air-sac system (blue)] in the theropod *Majungatholus*. Graphic from (27).



A highly efficient flow-through ventilation and a high-compliance air-sac system uniquely characterize the avialan respiratory system (27). Perceived differences in the respiratory systems of theropods and other reptiles, such as crocodilians, from those of birds have been invalidly used as evidence against the BMT hypothesis (49). Nevertheless, cervical and anterior dorsal vertebrae are clearly pneumatic in nearly all theropods (29), and documentation of extensive skeletal pneumaticity in theropods such as *Majungasaurus* and *Aerosteon* (27, 28) demonstrates that a complex air-sac system and birdlike respiration evolved in birds' theropod ancestors (Fig. 4B). Furthermore, recent anatomical and physiological studies reveal that alligators (7, 113), and even monitor lizards (114), exhibit respiratory systems and unidirectional breathing akin to those of birds. These studies demonstrate that unidirectional breathing is a primitive characteristic of archosaurs or an even more inclusive group with the complex air-sac system evolving later within Archosauria. Weight savings might have driven the evolution of postcranial skeletal pneumatization in early theropods

(29), and in addition to large-bodied theropods, small maniraptoran theropods such as basal oviraptorosaurs, dromaeosaurs, and troodontids evolved the complex air-sac system similar to that of birds (28, 29).

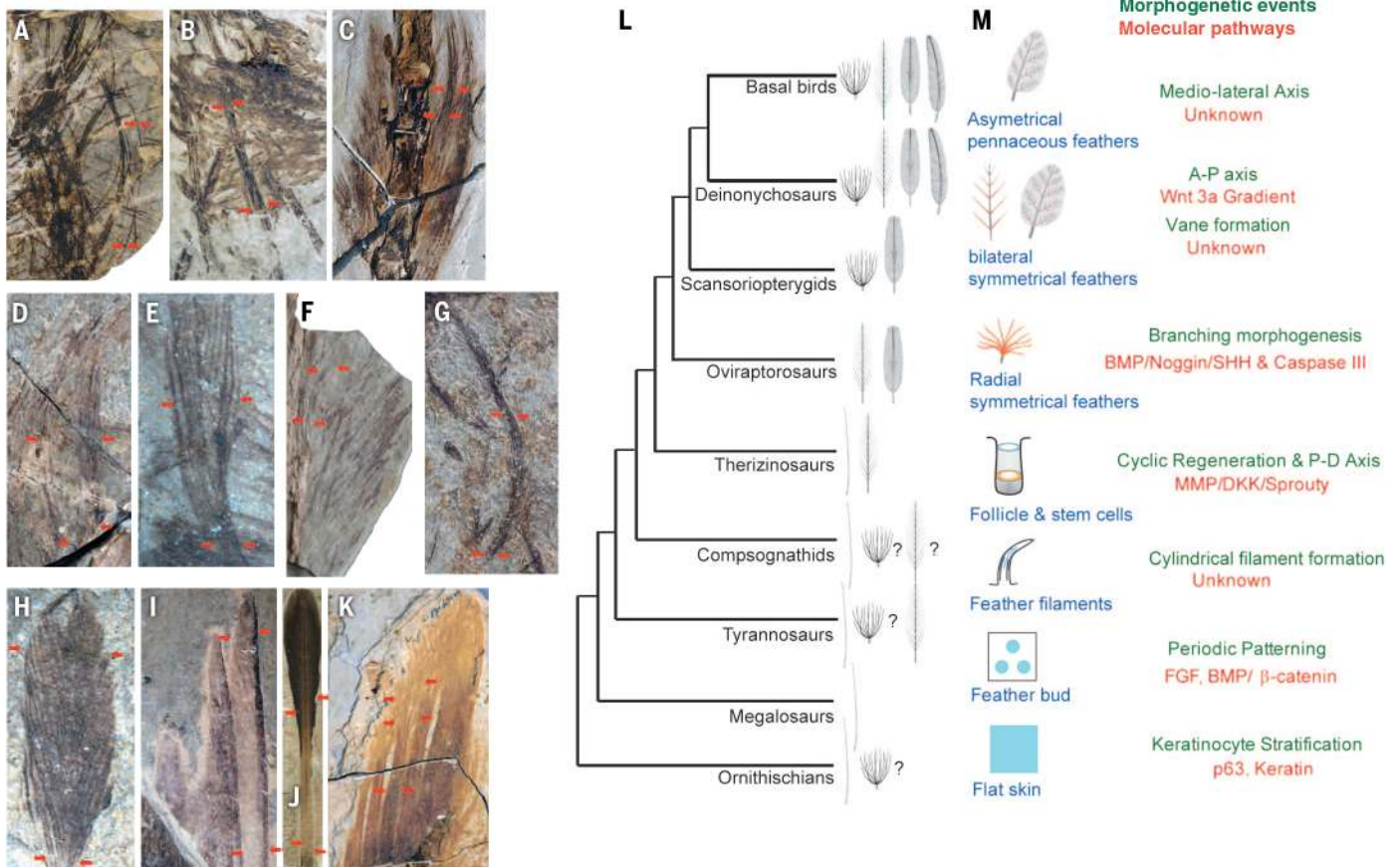
### Morphogenesis and early evolution of feathers

Feathers were once considered to be unique avialan structures. The presence of feathers is inferred in several theropods based on osteological correlates, e.g., quill knobs (115, 116) [although the presence of quill knobs in the basal tetanuran *Concavenator* has been questioned (117)] or pygostyles (118). Short filaments have been identified as feathers in the alvarezsaur *Shuvuuia* (119). Direct evidence came to light in China in 1996 with the discovery of the feathered *Sinosauropteryx* (120). Since then, numerous specimens of most theropod groups and even three ornithischian groups preserving feathers have been recovered from the Jurassic and Cretaceous beds of northeastern China (13, 21, 41, 45, 57) and from the Jurassic and Cretaceous beds of Germany, Russia, and Canada

(55, 56, 121–123). These feathers fall into several major morphotypes (Fig. 5), ranging from monofilamentous feathers to highly complex flight feathers (57). The phylogenetic distribution of these feathers largely concurs with the predictions from a developmental model of living birds (4), although some of these morphotypes are absent in living birds (57, 124).

The findings of feathers in dinosaurs prompted developmental studies over the last decade investigating the molecular mechanisms regulating feather development and regeneration in chickens (125). We can now propose the following “molecular circuits” regarding tissue morphogenesis and the evolution of modern feathers. Each molecular circuit has specific features and can be modulated to produce a diversity of morphology:

(i) Cylindrical topology and the downshift of stem cell ring. The formation of loose mesenchyme in the bud core allows a tube configuration, with basal layer facing inside. Driven by Wnt signaling, feather stem cells now are positioned near the base, forming a ring configuration (126, 127). It can remain as a tube or the



**Fig. 5. The morphogenesis and evolution of feathers in dinosaurs.** (A) Monofilamentous feathers in *Tianyulong*. (B) Broad monofilamentous feathers in *Beipiaosaurus*. (C) Radially branched feathers in *Sinosauropteryx*. (D) *Sinornithosaurus*. (E) *Anchiornis*. (F) Bilaterally branched feathers in *Dilong*. (G) *Sinornithosaurus*. (H) Wing flight feathers with symmetrical vanes in *Anchiornis*. (I) Pedal flight feathers with asymmetrical vanes in *Microaptor*. (J) Rachis-dominant tail feathers in *Confuciusornis*. (K) Proximally

ribbonlike tail feathers in *Similicaudipteryx*. (L) Phylogenetic distribution of major feather morphotypes (monofilamentous, radially branched, bilaterally branched, symmetrical flight, and asymmetrical flight feathers) among dinosaurs. (M) Major novel morphogenetic events and molecular pathways during feather evolution. These major feather morphotypes can be explained by selective usage of the five novel “molecular circuits” discussed in the text. Red arrows flank a feather.

subsequent caspase-dependent selective apoptosis can open up the tube, allowing feather vane formation (128).

(ii) Hierarchical branching and barb/barbule pattern formation. Ratio of local activators (noggin, Shh, and so on) and inhibitors (bone morphogenetic proteins) regulate the number and size of barb versus rachidial ridges (5, 129). Barb ridges, which depend on Wnt 3a gradient, can run parallel to each other to form radial symmetric feathers or angle toward the rachis to form bilateral symmetric feathers (130).

(iii) Follicle formation and regenerative cycling. During development, matrix metalloproteinase-dependent tissue invagination allows epithelia to topologically fold into a follicle (131). Follicle configuration allows protection of feather progenitors. Stem cells and dermal papilla are now clustered near the follicle base, and can undergo dickkopf Wnt-dependent cyclic regeneration (132).

(iv) Temporal regulation of stem cells along the proximal-distal axis. During feather formation, the molecular microenvironment and morphology can change along the distal (formed earlier) and proximal (formed later) through modulation of fibroblast growth factor-sprout activity (133).

(v) Organ metamorphosis and regional specific feather types. Upon regeneration, modulated by the body macroenvironments, different feather morphotypes (downy, contour, and flight feathers) can form on different body regions and in different physiological stages for optimal performance (134).

The aforementioned morphogenetic processes can be assembled selectively, in various orders, and independently to produce basic-to-more complex feather morphotypes (Fig. 5). The monofilamentous feathers seen in ornithischians (54, 56, 57) and some theropods (55, 57), two sets of morphologically different flight feathers during ontogeny in the oviraptorosaurian *Similicaudipteryx* (124), and the extensive leg feathering (particularly pedal feathering) in a number of theropods and early birds (135) imply a variety of rearrangements in the morphogenetic modules. The wide occurrence of pedal feathering in theropods and early birds (135) and an extensive distribution of scales on the bodies of both feathered theropods (e.g., *Juravenator*) and feathered ornithischians (e.g., the ceratopsian *Psittacosaurus* and the ornithomimid *Kullindadromeus*) remain particularly interesting from both developmental and evolutionary perspectives (56, 135), and will no doubt play into further discussions on feather-scale relationships.

The diverse forms of theropod feathers apparently suggest a comparable myriad of functions. Initial functions of feathers more likely include thermoregulation and communication rather than flight (57). Several different lines of data highlight the importance

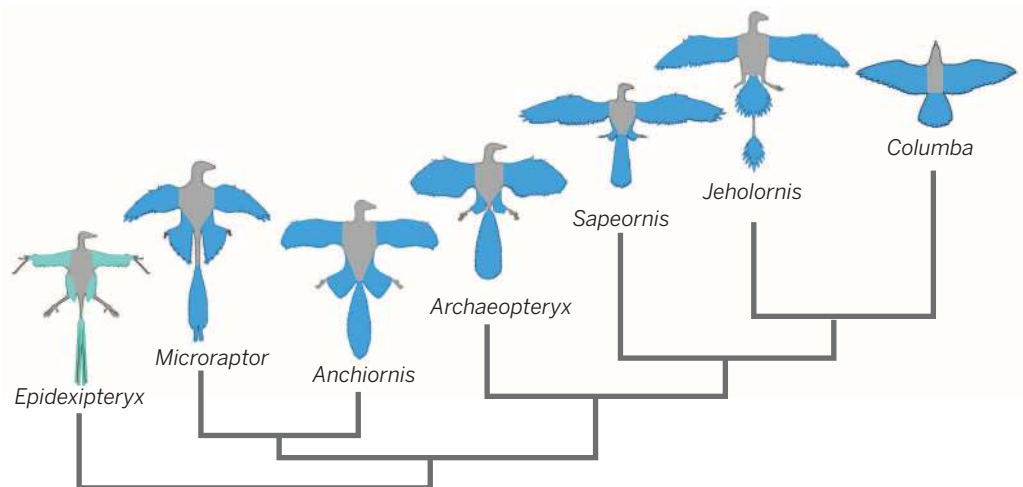
of communication in early feather evolution (41, 57, 117, 136), particularly by color patterns inferred via preserved melanosome morphologies in some theropods and early birds (136, 137), although several studies have questioned the identifications of melanosomes in specimens of feathered theropods and early birds (48, 138). One study shows an increased diversity of melanosome morphologies associated with the appearance of complex pinnate feathers during theropod evolution (72). This finding supports developmental data showing that unique topological arrangements allowing feathers to generate complex forms also permits the generation of visibly complex pigment patterns and pattern renewal during sexual maturation (139).

#### Four-winged dinosaurs and the origins of aerial behavior

Several flight-related anatomical features, such as hollow bones and the furcula, originated in early theropods; basal paravians had many hallmark features necessary for flight, including extremely small body size (50, 70); a laterally oriented, long, and robust forelimb (22, 67); an enlarged forebrain and other derived neurological adaptations (71); and large flight feathers (Figs. 1 and 2). Particularly surprising are the recent discoveries of large flight feathers forming a planar surface on the legs of some basal paravians—for example, those with asymmetrical vanes on both the tibia and metatarsus of some basal dromaeosaurs, such as *Microraptor* (59); large feathers with symmetrical vanes on both the tibia and metatarsus of the troodontid *Anchiornis* (45), the basal bird *Sapeornis*, and several other basal paravians (135); and large vaned feathers on tibiae of several basal birds including *Archaeopteryx*, confuciusornithids, and enantiornithines (135). These structures clearly would have been relevant to flight origins. The evolu-

tion of flight, nonetheless, remains highly debated, with a few recently proposed scenarios including factors as diverse as muscle hyperplasia (140) and the use of wings to assist in cursorial ascent of inclines, based on neontological observations (11). Multifactorial explanations for the origins of flight are likely, as this behavior has not been uniquely categorized; given variability in wing and tail configurations among theropods and early birds (45, 59, 135, 141, 142), flight probably had complex biomechanical origins (142, 143).

Fundamental to all hypotheses of wing evolution, however, must be consideration of those circumstances that elicited aerial behavior in ancestrally terrestrial taxa. In all extant vertebrate and invertebrate gliders, flight is associated with gravitational acceleration downward from heights and with the use in aerodynamic control of diverse body structures, including but not limited to limbs, once aloft (143). The discoveries of four-winged theropods and early birds (Fig. 6) are consistent with the gravity-assisted hypothesis for the origin of bird flight. Moreover, the concurrent presence of a large and flattened tail, along with potential use of the feathered hind legs in aerodynamic control, suggests substantial capacity for using these as rudders and for maneuvering even during the earliest stages of bird evolution (10, 144). Aerial righting reflexes, targeting movement while aloft, and controlled landings all would have been enhanced via bilaterally asymmetric motions of either wing pair. In other words, incipient and nonequilibrium flight behaviors would potentially associate with a four-winged and long-tailed arrangement in theropods and early birds (Fig. 6). There still remains disagreement as to the definitional criteria used to indicate the four-winged and long-tailed condition and as to whether large flight feathers with symmetrical



**Fig. 6. Airfoils of selected maniraptorans.** Airfoils (in blue) of the basal dromaeosaur *Microraptor*, the basal troodontid *Anchiornis*, the basal birds *Archaeopteryx*, *Sapeornis*, and *Jeholornis*, and a modern pigeon. Feathered airfoils are greater in number and are more distally positioned in early birds and their closest theropod relatives than in modern birds. The scansoriopterygid *Epidexipteryx* has stiff downlike feathers (in green) on both the forelimb and hindlimb and long ribbonlike feathers on the tail, the aerodynamic functions of which remain poorly known.

vanes in some basal paravians, including early birds, would create useful aerodynamic forces during aerial behaviors (117).

Use of the hind wings, and potentially the tail, to generate vertical force also results in a more posterior and stable position for the center of lift (10, 144) (as can be deduced from bat and pterosaur wings based on patagial connections to the hindlegs). Such a hindwing configuration contributes to static stability in gliding, whereas subsequent functional shifts to the forewings alone, with associated reductions in tail size and leg feathering (135), would have required offsetting aerodynamic control via flapping motions (145). Potential tradeoffs between increased size of the forewings and the intensity of their kinematic activation (e.g., greater frequency and amplitude of flapping) are not well understood, although robotic models of early avialan morphologies can be informative (146). Such progressive anterior specialization of the flight apparatus, with enhanced forces produced by the emerging forelimb locomotor module (145), is nonetheless derived from an ancestrally four-winged platform (Fig. 6).

## Future perspectives

Alternative phylogenetic hypotheses suggest a different evolutionary sequence of major bird characteristics and imply a different ecological origin of the group (22). Consequently a refined, more robust phylogeny will be imperative to move our studies forward. Increasing character and taxon sampling in recent theropod phylogenetic studies has, in theory, helped improve the accuracy of phylogenetic reconstructions, but better character formulation and more accurate scorings are imperative at present, pending better understanding of the morphologies of many recently discovered transitional forms.

In terms of character evolution, an integrative approach combining paleontological, neontological, developmental, geochronological, and even paleoenvironmental data is particularly desirable. A recent integrative study combining developmental, neontological, and paleontological data shows that birds evolved their highly specialized cranium mainly by pedomorphosis (147); another study using both neontological and paleontological data to reconstruct melanosome evolution suggests that feathers have changed significantly in their melanosome morphology among pennaraptoran theropods, which implies a physiological shift before the evolution of flight (72), and that concurs in association with extensive postcranial skeletal pneumaticity, which suggests the presence of birdlike endothermy (29). Similar approaches should be applied to other major structures. Certain avialan structures, such as feathers and visual system, are novel in both genetic and morphological terms. There are emerging data on how the genetic code affects the morphogenesis of these structures in developmental biology. How the genetic code and expression pattern evolved can be inferred by a detailed comparison of homologous structures in theropods, early birds and modern birds.

The construction of molecular phylogenies would enable a much better understanding of the genealogical relations among birds and their theropod relatives and the steps leading to the evolution of birds. Although once the topic of science-fiction movies, preserved organic remains have purportedly been recovered from *Tyrannosaurus* and the hadrosaur *Brachylophosaurus* (148, 149) and from even older fossils such as Early Jurassic *Lufengosaurus* specimens (150). Greater examination along these lines in fossils spanning the theropod-bird transition is a potentially fruitful avenue for future investigation.

The increasing interest in the origins of birds from developmental biology and other disciplines has enriched our understanding of this important evolutionary event (8, 10, 11), and alternative evolutionary models on various aspects of the origin of birds have sometimes been provided based on neontological data (4, 11). However, any evolutionary model must be tested using the fossil record. Consequently, dense fossil sampling along the line to birds and better understanding of the transitional forms play a key role in the discussion on this issue.

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