



Birds as dinosaurs

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Abstract The “great debate” over bird origins may never have transpired had the now-famous furcula-bearing, feathered dinosaurs from Asia surfaced when the beds in which they were interred were first discovered in the 1920s. Compelling fossil evidence is now to hand that places birds as a specialized clade within theropod dinosaurs. Major insights include a more seamless fossil record linking birds and non-avian dinosaurs, clear evidence of an early pre-avian origin for feathers and other features previously known only among birds, together with an underscoring of the importance of miniaturization for the evolution of powered flight and a broadening of the functional scenarios for how powered bird flight was first achieved [*Acta Zoologica Sinica* 50 (6): 991–1001, 2004].

Key words Dinosaurs, Birds, Flight, *Archaeopteryx*, Evolution

被视为恐龙的鸟

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摘要 尽管于 20 世纪 20 年代在亚洲地表层首次发现长有羽毛的恐龙和著名的“龙骨突位点”，关于鸟类起源的争论仍没有休止。来自化石的证据表明，鸟类在进化分支上应归于兽脚类的特殊分支。本文主要阐明完好无损的化石揭示的鸟和非鸟类恐龙的亲密关系和鸟类羽毛及鸟类出现以前的羽毛的起源证据，分析体型缩小对飞行进化的重要意义及从新的角度论述鸟类如何飞上了天 [*动物学报* 50 (6): 991–1001, 2004]。

关键词 恐龙 鸟 飞行 始祖鸟 进化

1 Introduction

1.1 Grabau's grab-bag

“These fish are often so numerous that a slab about one foot square will show from 50 to 100 individuals,” remarked Grabau in his 1928 summary of the Early Cretaceous “Jehol fauna” of northern China (p. 672). A sequence of lakebed deposits more than a thousand meters in thickness had been discovered that was literally packed with the remains of the teleost *Lycoptera*, soft-bodied invertebrates and plants (Figs. 1, 2). Now divided into two formations (Yixian and overlying Jiufotang) in Liaoning Province and adjacent areas of Inner Mongolia, the “Jehol Biota” is of world renown for the feathered dinosaurs and primitive birds that came to light during the 1990s (Chen and Fan, 1999; Chang et al., 2003; Zhou et al., 2003).

What if a feathered dinosaur had come to light in

Grabau's time? Less than a day's drive north of Beijing today, this easily accessible outcrop would surely have witnessed the same accelerated exploration that followed the first sensational finds in the 1990s. Most likely, several feathered dinosaurs and toothed birds would have been uncovered by 1925—about the time that Heilmann was finishing his influential treatise concluding that birds were not descendants of dinosaurs (Heilmann, 1926).

1.2 Heilmann's hurdle

The crux of Heilmann's argument against dinosaurian affinity involved the lack of any trace of ossified clavicles among dinosaurs then known, and the presence of co-ossified clavicles—a furcula—in *Archaeopteryx* and nearly all other birds (Witmer, 1991). For Heilmann, re-ossification of the clavicles posed an insurmountable evolutionary reversal.

Today, ossified clavicles in the form of a median furcula have been documented in most major non-a-

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Fig.1 Alternating layers of lake mud and volcanic ash compose much of the Yixian and Jiufotang Formations in western Liaoning Province and eastern Inner Mongolia that have yielded hundreds of well-preserved vertebrates, invertebrates and plants

Splitting layers by hand is typical of quarry operations like this one in the Jiufotang Formation in southeastern Inner Mongolia (near Nincheng, People's Republic of China).

vian theropod clades, including coelophysoids (Tykoski et al., 2002), spinosauroids (Lipkin and Sereno, in press), allosaurids (Chure and Madsen, 1996), therizinosaurids (Xu et al., 1999a; Zhang et al., 2001), tyrannosaurids (Makovicky and Currie, 1998; Lipkin and Sereno, in press), oviraptorosaurs (Clark et al., 1999; Zhou et al., 2000; Lü, 2002), and dromaeosaurids (Norell et al., 1997; Xu et al., 1999b; Burnham et al., 2000). The furcula, moreover, is preserved in several theropods (*Beipiaosaurus*, *Caudipteryx*, *Sinornithosaurus*) from the “Jehol fauna” in Liaoning (Xu et al., 1999a, b; Zhou et al., 2000; Xu et al., 1999b), and in two further theropods (*Oviraptor*, *Velociraptor*) from the Mongolia, the latter originally named on less complete specimens discovered in the early 1920's (Norell et al., 1997; Clark et al., 1999).

Had any of these specimens come to light when these localities were first explored, Hielmann's sole impediment to a link between dinosaurs and birds would have vanished. Furthermore, several of the



Fig.2 Hand-dug quarries like this one in the Jiufotang Formation dot the landscape in southeastern Inner Mongolia (near Nincheng, People's Republic of China)

Dug by local farmers a few years ago, this quarry descends vertically approximately 10 m and then ramifies within the most productive fossil-bearing level.

furcula-bearing Liaoning theropods (*Caudipteryx*, *Sinornithosaurus*, *Microraptor*) also preserve shafted feathers with traces of barbs in a herring-bone arrangement (see below). With dinosaurian furculae and feathers in hand by the close of the 1920's, would the modern “great debate” about bird origins ever have transpired?

1.2 “Great debate” or just bad timing?

As it happened, paleontologists would wait nearly a half-century before recovering enough fossil material to piece together the first skeleton of a maniraptoran theropod close to the origin of birds — *Deinonychus* (Ostrom, 1969). Ostrom and *Deinonychus* — without the benefit of dinosaurian furculae or feathers — rekindled Huxley's hypotheses of 1868 (also Williston, 1879) linking *Archaeopteryx* and later birds to the then recently discovered small coelurosaurian *Compsognathus*. Ostrom's papers on bird origins (Ostrom, 1973, 1976a, b) also precipitated the modern “great debate,” just as cladistic methodology was being adopted by a growing number of students in both paleontology and ornithology. During the

decade of the 1980's alone, the number of papers on bird origins exceeds the total on this subject in the preceding century (Witmer, 1991), with two opposed camps emerging: proponents of an archosaur/crocodylomorph origin (e.g., Walker, 1972; Martin, 1983; Feduccia and Wild, 1993; Jones et al., 2001; Feduccia, 2002; Olson, 2002), and those for a theropod origin (e.g., Gauthier, 1986; Holtz, 1994; Sereno, 1997, 1999; Forster et al., 1998; Padian and Chiappe, 1998; Xu et al., 1999b; Norell et al., 2001).

Witmer (2002) documented well the recent history and intensity of the debate, which he attributed to the contrasting inferences to be drawn about non-osteological features (physiology, feathers, flight), depending upon where one roots the class Aves. These issues, however, are surely better understood as manifestations of fundamental methodological differences and collegial allegiances. The most active members of the two principal camps of the debate (archosaur/crocodylomorph vs dinosaur) almost always employ mutually exclusive *phylogenetic methods* (traditional vs cladistic), and typically ally themselves with different *scientific communities* (avian vs dinosaurian paleontology). The fundamental motor of the debate is the clash between methodologies and subdisciplines.

This is well demonstrated in a pair of recent commentaries from traditional paleo-ornithologists in a journal devoted to avian biology (*The Auk*). One (Olson, 2002) was a review of a volume on bird origins in honor of John Ostrom (Gauthier and Gall, 2001), and the other (Feduccia, 2002) a response to Prum's (2002) fact-filled perspective on the accumulating phylogenetic, developmental, and reproductive evidence for the dinosaurian origin of birds. The dramatic new data bearing on the debate (summarized below) has had negligible effect on the small cadre of paleobiologists staunchly opposed to birds as derived theropods, as well as characters and parsimony as the arbiter of homology and relationships (e.g., Feduccia, 1999; Dodson, 2000). Now this opposition has seized upon incontrovertibly-feathered dromaeosaurids, like *Sinornithosaurus*, interpreting them as flightless birds after decades of denigrating Ostrom's structurally identical cousin *Deinonychus* as anything remotely resembling a bird.

The purpose of this paper is not to review such arguments; detailed reviews are available elsewhere (Padian and Chiappe, 1998; Sumida and Brochu, 2000; Prum, 2002, 2003). Under the rapidly increasing weight of evidence today, the "great debate" is fast becoming a historical footnote on the road to understanding the origins of birds, begging the question: if dinosaurian furculae and feathers were in hand

by the close of the 1920's, and a dinosaurian origin accepted then by Hielmann, traditional systematists and paleo-ornithologists, would today's "great debate" ever have transpired?

2 Observational evidence

2.1 Birdlike dinosaurs

A trove of "birdlike" dinosaurs (here meaning "basal maniraptorans") has been found in the last decade in Cretaceous rocks in Asia and North America. The most spectacular specimens include evidence of the integument and were discovered in a thick lakebed sequence in Liaoning and Inner Mongolia in China, dated radiometrically to the Early Cretaceous (ca. 130 – 110 MYA; Zhou et al., 2003). These include several basal maniraptorans such as the oviraptorosaurian *Caudipteryx* (Ji et al., 1998; Zhou et al., 2000), the troodontid *Sinovenator* (Xu et al., 2002), and the dromaeosaurids *Sinornithosaurus* (Xu et al., 1999b; Xu and Wu, 2001) and *Micro-raptor* (Hwang et al., 2002; Xu et al., 2003). Elsewhere in Asia and North America, dune and fluvial deposits have yielded nearly complete skeletons of dromaeosaurids (Fig. 4) and oviraptorids, filling in nearly all aspects of their osteology (*Velociraptor*: Barsbold and Osmólska, 1999; Norell and Makovicky, 1997, 1999; *Bambiraptor*: Burnham et al., 2000; *Oviraptor*: Clark et al., 1999).

Especially birdlike skeletal characters are revealed in the presence of uncinat processes, furculae, elongate sternal plates buttressed by squared coracoids, and elongate forelimbs with rotary wrist joints (Fig. 3). There are scores of other modifications in virtually all parts of the skeleton that establish a close relationship between non-avian theropods and birds (Sereno, 1999).

2.2 Ancient avians

The long-standing gap in the fossil record between *Archaeopteryx* and the toothed birds of the Late Cretaceous, *Ichthyornis* and the hesperornithiforms (Marsh, 1880; Martin, 1980), has now been filled with a series of basal avians slightly larger than *Archaeopteryx* in body size. Those closest to *Archaeopteryx* include *Jeholornis* from Liaoning (Zhou and Zhang, 2002a) and *Rahonavis* from Madagascar (Forster et al., 1998), both of which retain a long bony tail with moderately elongated prezygapophyses and chevrons like *Archaeopteryx* (Fig. 5). *Sapeornis*, also from Liaoning (Zhou and Zhang, 2002b), is more advanced than *Jeholornis* and *Rahonavis*, as evidenced by its shortened caudal series and terminal pygostyle. More advanced than the aforementioned avians is *Confuciusornis*, which exhibits functionally significant modifications of the wing bones and a well developed pygostyle (Hou et al., 1995, 1996) (Fig.

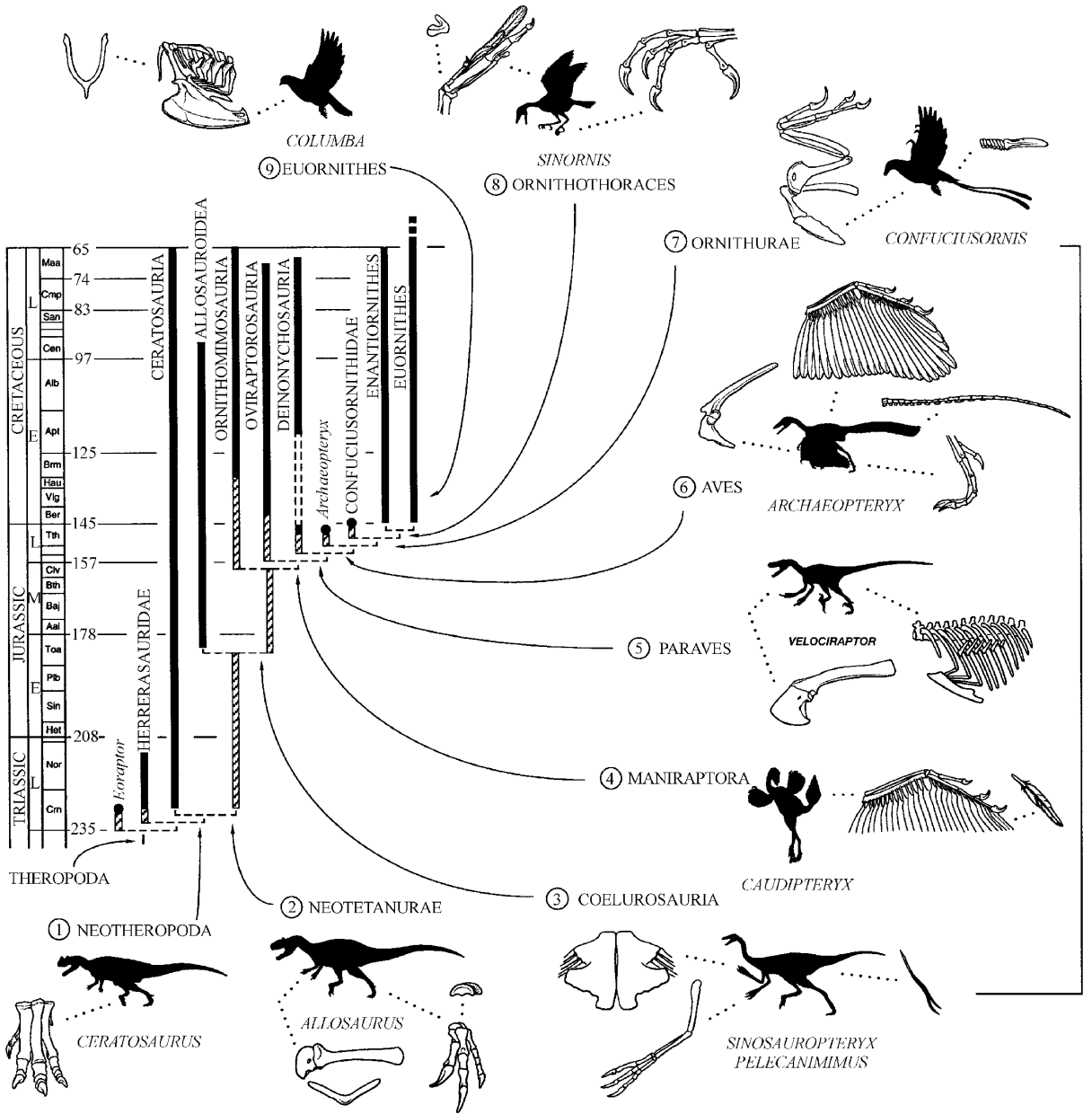


Fig. 3 Major stages in the evolution of modern avian skeletal design and function (from Sereno, 1999)

Many skeletal innovations of critical functional importance for flight arose for other purposes among early theropods, including ① the hollowing of all long bones of the skeleton (Theropoda), ② removal of pedal digit I from its role in weight support, ③ expansion of the coracoid and sternum for increased pectoral musculature, plumulaceous feathers for insulation, ④ presence of vaned feathers arranged as primaries, secondaries and rectrices for display and/or brooding, ⑤ shortening of the trunk and increased stiffness of the distal tail for balance and maneuverability. *Archaeopteryx* remains a pivotal taxon, documenting ⑥ the acquisition of basic flight and perching function before the close of the Jurassic (laterally-facing shoulder joint, split propulsion-lift wing with asymmetric feathers, reversed hallux). Key refinements of powered flight and perching in later birds include ⑦ the deep thorax with strut-shaped coracoid and pygostyle, ⑧ the triosseal canal for the tendon of the principal wing rotator (the supracoracoideus muscle), alular feathers for control of airflow at slow speeds, rectriceal fan for maneuverability and braking during landing, fully opposable hallux for advanced perching, and ⑨ the elastic furcula and deep sternal keel for massive aerobic pectoral musculature. Ornithothoracine birds diverged early into two clades: Enantiornithes (“opposite birds”), which prevailed as the predominant avians during the Cretaceous, and Euornithes (“true birds”), which underwent an explosive radiation toward the close of the Cretaceous that gave rise to all living avians (Neornithes, or “new birds”).

3). Now represented by hundreds of specimens, the toothless, crow-sized *Confuciusornis* has fast become the best known Mesozoic avian (Chiappe et al., 1999).

Although relatively obscure until recently, spar-

row-sized enantiornithine birds are now known to have dominated avifaunal diversity from mid through Late Cretaceous time (Fig. 6). Enantiornithines were first described from Argentina (Walker, 1972; Chiappe, 1996; Sereno, 2000) and later discovered in

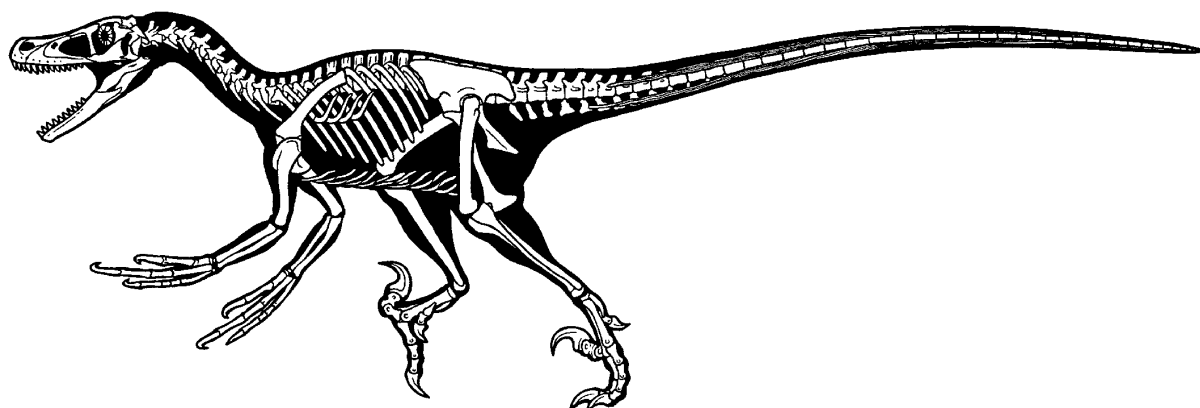


Fig. 4 Silhouette skeletal reconstruction of *Velociraptor mongoliensis* based on the holotype and many more recently discovered partial skulls and skeletons

Skeletal length approximately two meters.

the Las Hoyas beds in Spain (*Iberomesornis*: Sanz et al., 1988; Sereno, 2000; *Concornis*: Sanz et al., 1995) and Jiufotang Formation in Liaoning (*Sinornis*: Sereno et al., 1993, 2002; *Protopteryx*: Zhang and Zhou, 2000). This toothed clade of basal avians is now known from rocks around the world, although best known from lakebeds in central Spain and north-eastern China.

2.3 Filaments to asymmetric pennaceous feathers

The initial discovery of integumental “fibers” in the basal coelurosaurian *Sinosauropteryx* (Chen et al., 1998) and the more advanced therizinosaurid *Beipiaosaurus* (Xu et al., 1999a) suggested simple down-like feathers but remained controversial. The discovery of longer shafted structures with herring bone pattern fore and aft removed any doubt that basal oviraptorosaurians (*Caudipteryx*: Ji et al., 1998; Zhou et al., 2000) and dromaeosaurids (*Sinornithosaurus*: Xu et al., 1999b, 2001) pos-

sessed pennaceous feathers with barbs on the limbs and tail, and that this complex feather type, thought to be unique to birds, arose first among basal maniraptorans (Fig. 3).

The most remarkable finding is the presence of long asymmetric vanes on feathers composing primitive wings attached to the trailing edge of the fore and hind limbs of the small dromaeosaurid *Microaptor* (Xu et al., 2003). *Microaptor* appears to have been adapted to a semi-arboreal lifestyle that included gliding. If its status as a basal dromaeosaurid is confirmed (Hwang et al., 2002), this may have been the primitive lifestyle for the clade that included other terrestrial deinonychosaurians and volant birds (Paraves; Fig. 3).

2.4 Bigger brains

Compared to living reptiles, birds have dramatically larger brain volumes relative to body mass, particularly in the cerebrum (forebrain). A partial endo-

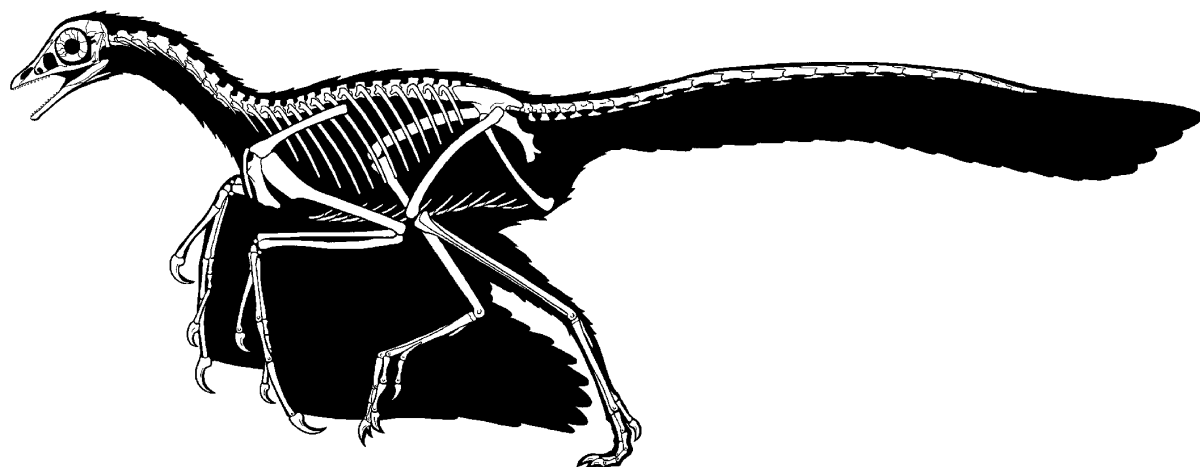


Fig. 5 Silhouette skeletal reconstruction of *Archaeopteryx lithographica*, based in particular on the Berlin and Eichstätt skeletons

Available articulated skeletal material suggests that the wrists were unable to flex at an angle less than approximately 90 degrees.



Fig. 6 Silhouette skeletal reconstruction of sparrow-sized *Sinornis santensis*, based on the holotypic specimen

Enlargements show early avian adaptations in the shoulder girdle and wrist (above) and sternum and tail (below).

cast of *Archaeopteryx* indicates that this increase was already in place to a considerable degree by the Late Jurassic (Jerison, 1973; Bühler, 1985). Forebrain enlargement has long been thought to characterize theropods closest to birds (Sues, 1978; Currie, 1985, 1995) but has been difficult to quantify for two reasons: the lack of complete endocasts from any of the most birdlike dinosaurs and the necessity to establish scaling relationships due to differences in body size.

Recent work focused on complete endocasts from two similar-sized Late Cretaceous theropods (*Carcharodontosaurus*, *Tyrannosaurus*) at different distances from birds. Their similar size allowed direct comparison of brain volumes free of scaling relationships (Larsson et al., 2000). *Tyrannosaurus*, an over-sized coelurosaurian, is phylogenetically much closer to birds than *Carcharodontosaurus*, an allosauroid; it has total endocast and cerebral volumes approximately 50% and 100% greater, respectively,

than in *Carcharodontosaurus*. The cerebrum in *Tyrannosaurus* is one-third, rather than one-quarter, of total endocast volume. Thus, brain and cerebral volumes do appear to have been increased significantly among theropods (coelurosaurians) more closely related to birds.

2.5 Invasive air spaces

The respiratory system in birds is characterized by pneumatic spaces that originate in the nasopharynx and ramify within many elements of the skull, and in air sacs from the lungs that penetrate and expand within skeletal elements. The presence of similar pneumatic structures in fossils must necessarily be inferred from bony correlates, such as smooth depressions devoid of attachment scars and openings into internal spaces.

Extensive pneumaticity of antorbital and braincase regions has occurred more than once among archosaurs but is particularly well developed in neotheropod dinosaurs and birds (Witmer, 1997).

Two systems are present, antorbital and otic, often with comparable subdivisions. Moreover, a well-developed air sac system along the axial column has arisen at least twice within dinosaurs—among basal sauropods (Wedel, 2003) and in neotheropods and their avian descendants (Britt, 1993). Air sacs in non-avian theropods open into spaces within vertebral centra via pleurocoels, and these have recently been observed in the cervical column of *Archaeopteryx* (Britt et al., 1998).

2.6 Muscle modifications

Some of the fore and hind limb musculature in birds is associated with characteristic scars or processes on limb and girdle bones which can be traced in extinct relatives. Two functionally significant sites for muscle attachment in the avian wing, for example, are the acrocoracoid process of the coracoid which anchors the chief flexor of the forearm (the biceps brachii), and the extensor tubercle on the medial aspect of metacarpal I which provides insertion for the extensor metacarpi radialis, the chief extensor of the carpometacarpus (Raikow, 1985). The emergence of each of these as distinct attachment sites that increase in relative size and shift in position among non-avian theropods and basal avians is well documented (Ostrom, 1976a).

In the pelvic girdle and hind limbs, most of the muscles are larger and the processes and scars marking their attachments provide a broader range of comparisons. The shift among non-avian theropods from predominantly tail-anchored femoral retractors to a less mobile femur with enhanced flexion at the knee joint is now a well-documented transformation series (Gatesy, 1995; Hutchinson, 2001).

2.7 Bones and body temperature

Bone histology via thin sections remains the primary means of inference concerning growth and standing metabolic rate, two physiological parameters that are substantially elevated among birds as compared to non-avian reptiles. Highly vascularized fibrolamellar bone has been shown to characterize dinosaurian embryos, juveniles and adults in a wide variety of taxa, leading to an emerging consensus that dinosaurs grew at elevated rates comparable to those in mammals and birds (Horner et al., 2001; Padian et al., 2001; Erickson et al., 2001). Some basal avians, such as enantiornithines, actually show a slightly slower growth rate with denser, less vascular bone, which may indicate precocial flight capability (Chinsamy and Elzanowski, 2001).

Oxygen isotope ratios in bone phosphate are clearly indicative of metabolic rate among extant species and also suggest that dinosaurs had elevated body temperatures and metabolic rates (Barrick and Showers, 1994). This may ultimately prove to be a

better assessment of metabolic rate than bone histology. In the meantime, the only vertebrates with growth rates as rapid as those inferred for dinosaurs from bone histology are those with elevated metabolic rates (birds, mammals). Consideration of other factors (body size, diversity, area of habitation, etc.) show that dinosaurian herbivores and carnivores grew to larger body sizes at higher species richness and within smaller areas of habitation than mammals (Farlow et al., 1995). How this was achieved remains largely unresolved.

2.8 Large paired eggs and brooding

The recent identification of ossified embryos within eggs has put to an end speculation about the identity of several egg types among non-avian dinosaurs. Eggs long held to belong to *Protoceratops* actually house embryos of the basal maniraptoran *Oviraptor* (Norell et al., 1994), and eggs have now been identified from embryos or from nests with associated adults for select ornithischians, sauropodomorphs and theropods (Horner 1999; Varricchio et al., 1997; Chiappe et al., 2001). Two important features of the eggs in basal coelurosaurs are their large size relative to body size in adults and their unique shell structure nearly identical to that in birds (Varricchio et al., 1997).

The discovery of intact dinosaur nests from several kinds of dinosaurs has led to two other remarkable finds regarding theropods. First, the eggs were laid serially in pairs in nests belonging to maniraptoran theropods (currently best known in *Oviraptor* and *Troodon*), in contrast to other dinosaurs in which a random arrangement of eggs in nests suggests that the eggs were laid at the same time. Varricchio et al. (1997) have suggested that maniraptorans maintained two functioning ovaries but that, like birds, laid only one egg from each ovary at a time. Birds have further reduced this pattern of serial clutch assembly to one egg from only one functioning ovary at a time. Secondly, the discovery of several intact *Oviraptor* skeletons crouched over nests of *Oviraptor* eggs (Dong and Currie, 1996; Clark et al., 1999) suggests that at least some basal maniraptorans brooded their eggs in a manner known elsewhere only in birds.

2.9 Diagnosing digits

Extant birds have three manual digits, the number and form of which can be traced through intermediates to *Archaeopteryx*. Like *Archaeopteryx*, basal maniraptorans (e.g., *Sinornithosaurus*, *Caudipteryx*) have three manual digits of nearly identical form, pennaceous feathers anchored on the middle digit and ulna, and a carpus shaped to form a rotary joint. This three-fingered basal maniraptoran hand and simplified carpus can likewise be traced to earlier

four- and five-fingered relatives, the latter including the basal theropods *Eoraptor* and *Herrerasaurus* (Sereno et al., 1993; Sereno, 1993). On this basis, paleontologists have long identified the manual digits in birds as I – III following Meckel (1821). Developmental biologists, on the other hand, have long identified the same digits as II – IV based on the conserved pattern of digital embryogenesis present in most extant tetrapods (Holmgren, 1955; Hinchliffe, 1985).

Recent work has unequivocally visualized the embryonic first digit in birds as a small, avascular condensation of cartilage precursors (Feduccia and Nowicki, 2002; Kundrát et al., 2002). Now all five manual digits are accounted for in the early avian limb bud, with the adult digits developing from the central three. At the same time, developmental biologists have now shown that the digital identity of the developing phalangeal series is not a stable property of condensing digital primordia, but becomes fixed during outgrowth under the influence of molecular positioning information (Dahn and Fallon, 2000). The molecular anterior-posterior positioning information involves varying concentrations of bone morphogenetic proteins which, with manipulation, can result in homeotic transformations in the phalanges, where one phalangeal series takes the form of another.

Wagner and Gauthier (1999) had earlier proposed that homeotic transfer of digital identity might have occurred within theropods—the “frame-shift” hypothesis—to explain how the very typical looking manual digits I – III of most theropods and basal birds could arise from the central three (II – IV) embryonic primordia in their extant avian descendants. Kundrát et al. (2002) noted correctly that it remains to be seen whether developmental plasticity in digital identity can be extended to the metacarpals and digital arch, as required by the frame-shift hypothesis. Then, without supporting evidence, they infer that basal birds such as *Archaeopteryx* must have undergone digital development as in extant avians and, therefore, must have descended directly from a five-fingered ancestor. Other tetrapods (many salamanders) are known to grow typical adult digits from drastically modified condensation patterns (Shubin, 1994). The nearly identical hand and feather pattern in basal maniraptorans (along with shared-derived features from every other part of the skeleton) suggests, to the contrary, that developmental biologists are just in the initial stages of understanding the molecular cues controlling digital identity in tetrapods and how these cues may be altered.

3 Major insights

3.1 “Avian” adaptations with deeper roots

Many features long held to be characteristic or unique to birds clearly have a more ancient origin among non-avian, non-volant theropods. As a consequence, they must be viewed as adaptations that originally evolved for something other than powered flight and its immediate requirements and constraints (Prum, 2002).

Skeletal features with more ancient, non-avian roots include pneumatic spaces within the axial column, uncinatate processes on the ribcage, fusion of the clavicles (a furcula), increase in size of the coracoid and sternum, a rotary wrist joint, elongation of the forelimbs and hand, bowing of the ulna, elongation and enlargement of the second manual digit, retroversion of the pubis, reduction of the caudofemoralis musculature for retraction of the femur, and shortening of the tail (Fig.3). Integumental features with more ancient non-avian roots include a body covering of plumulaceous feathers rather than scales, and pennaceous feathers with barbs projecting from the posterior aspect of the forelimb, hind limb, and tail. Reproductive and behavioral features with more ancient non-avian roots include avian-like eggshell structure, increase in relative egg size, serial egg assembly, and brooding.

3.2 Body size bottleneck

With few exceptions, non-avian dinosaurs have body masses estimated at greater than 15 kg; and several clades show long-term trends toward increasing body mass. Coelurosaurian outgroups to birds, in contrast, show a trend toward decreasing body size (Sereno, 1997). Avian flight appears to have first evolved in small-bodied species, like *Archaeopteryx*, with a body mass of less than 1 kg (Elzanowski, 2002). Clearly, powered flight evolved during a body size bottleneck, when adult body size was well below that typical for non-avian dinosaurs or the largest living volant birds (12 – 14 kg) (Pennycuik, 1989).

Early Cretaceous enantiornithines (Fig.6) were much smaller, on average, than *Archaeopteryx* (Fig.5). The perfection of avian powered flight in terms of locomotor performance (Dial, 2003a) occurred at such small body size and must have been the motor behind enantiornithine diversification during the Early Cretaceous, the first global diversification of birds.

3.3 Evolution of powered flight: multiple scenarios

Hypotheses for the evolution of powered flapping flight in birds have long been polarized. The “ground-up” scenario, originally articulated by Nopcsa (1907) and elaborated more recently (Ostrom, 1976b; Gauthier and Padian, 1985; Burgers and Chiappe, 1999; Garner et al., 1999; Earls, 2000; Gishlick, 2001), suggests that avian flight originated among non-volant

terrestrial bipeds. The opposing “trees-down” scenario, first articulated by Bock (1965, 1986) and elaborated by others (Feduccia, 1999; Geist and Feduccia, 2000), envisages gliding from an elevated perch as a necessary intermediate stage. Each scenario has been tied to competing phylogenetic hypotheses of avian origins, theropod or basal archosaur, respectively. Yet, such a one-to-one relationship between functional scenario and phylogenetic hypothesis has no intellectual basis, and clearly the former must be evaluated within the framework of the latter (Sumida and Brochu, 2000; Witmer, 2002).

Recent phylogenetic and functional work demonstrates these two points. The recent paleontological discoveries summarized above provide strong and consistent support for birds as derived theropod dinosaurs, their many attributes formerly thought unique to them originating at more basal levels within theropods. Functional scenarios consistent with this hypothesis, on the other hand, have diversified. Recent functional work, for example, suggests that flapping may have evolved to enhance hind limb traction in inclined running as a fundamental avian escape behavior, as currently employed in a wide variety of ground birds (Dial, 2003b). Likewise, the recent discovery of the small basal dromaeosaurid *Microraptor*—with arboreal adaptations and fore and hind limb wings suitable for gliding—has opened the door to several possible functional scenarios within the framework of a theropod origin of birds (Hwang et al., 2002; Xu et al., 2003).

3.4 Avian powered flight: functional modularity

Broader functional analysis of the evolution of birds as derived theropods has led to the notion of functional modularity, i. e., that locomotor function among birds is organized into three discrete functional modules (forelimbs, hind limbs, tail) with distinctive neuromuscular control (Gatesy and Dial, 1996; Dial, 2003a). The evolution of functional independence between tail and hind limb modules occurred in the transition from basal coelurosaurian theropods to basal birds. Variation in the elaboration of each of these modules, furthermore, has given rise to the diversity of avian locomotor styles, from non-volant cursors to small-bodied aerial acrobats with reduced hind limbs (Dial, 2003a).

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