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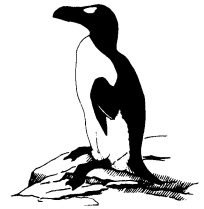
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PERSPECTIVES IN ORNITHOLOGY

ARCHAEOPTERYX 2007: QUO VADIS?

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DRAMATIC DISCOVERIES OF well-preserved avian fossils from the Early Cretaceous of China have deflected interest, somewhat, from the classic urvogel *Archaeopteryx*, the oldest known bird by at least 25 million years. *Archaeopteryx* has made a tortuous transition over the years, from a bird in the modern sense in Heilmann's (1926) classic treatise *The Origin of Birds*, to an earthbound feathered theropod that could not fly (Bakker 1975), to a theropod learning to fly from the ground up (Ostrom 1979). Today, dinosaur specialists typically view *Archaeopteryx* as a terrestrial, predatory cursor, whereas most ornithologists see an arboreal, volant, albeit primitive bird with reptilian features (Martin 1991, Tarsitano 1991, Feduccia 1999, Feduccia et al. 2005), and the urvogel has been shown to possess a sophisticated "bird brain" with neural capabilities for flight (Martin 1995, Dominguez Alonso et al. 2004). Two recent publications bring additional focus to this iconic fossil.

The recent discovery by Longrich (2006) that the Berlin *Archaeopteryx* possessed sophisticated hindlimb wings of remiges, with asymmetric vanes, curved shafts, and a self-stabilizing overlap pattern, brings this mysterious urvogel back to the focal point of interest in avian origins and the origin of flight. Among the obvious conclusions of Longrich's revelation is that the

"presence of the 'four-winged' planform in both *Archaeopteryx* and basal Dromaeosauridae indicates that their common ancestor used fore- and hindlimbs to generate lift" and that "arboreal parachuting and gliding preceded the evolution of avian flight" (Longrich 2006:425)—the arboreal theory of avian flight origins.

The conclusion that early birds had a "four-wing" planform, confirming Beebe's "Tetrapteryx" stage in the ancestry of birds, is further supported by the discovery of similar anatomical patterns in Early Cretaceous Chinese microraptors (Xu et al. 2003), enantiornithines (Zhang and Zhou 2004), and others (Longrich 2006).

In juxtaposition but starkly contrasting with Longrich (2006), Mayr et al. (2005, 2007) described a remarkable new specimen of *Archaeopteryx*, reinterpreting the anatomy to conform to the now largely discredited terrestrial theory for the origin of flight (Feduccia 1999, Long et al. 2003). Mayr et al.'s (2005:1483) claim that most of the other nine skeletal specimens of the famous urvogel are "fragmentary or poorly preserved" is easily discredited by the numerous published photographs of these specimens but, more importantly, their approach to the description of their specimen conforms to a common assumption of cladists, previously formulated by Chiappe (1997:109), that "the ancestral mode of life of birds was that of a cursorial biped. Inferences about the habits

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of *Archaeopteryx* should be made within this framework and not the reverse.”

In particular, Mayr et al. (2005) claimed that the hallux was not reversed (reversal is an unequivocal arboreal adaptation for grasping branches), as in other known birds, but had a unique position extending medially at a right angle to the other claws. This position is dubious for biomechanical reasons and would

certainly inhibit terrestrial locomotion. We are unaware of such a positioning in the *pes* of other animals, and a claim for such should be supported by the strongest evidence; Mayr et al.’s (2005) claim is not. The hallux in *Archaeopteryx* (Fig. 1) is comparable in size to that in arboreal birds and contrasts with the atrophied and non-opposable hallux of advanced deinonychosaurs (Tarsitano and Hecht 1980), in which terrestrial

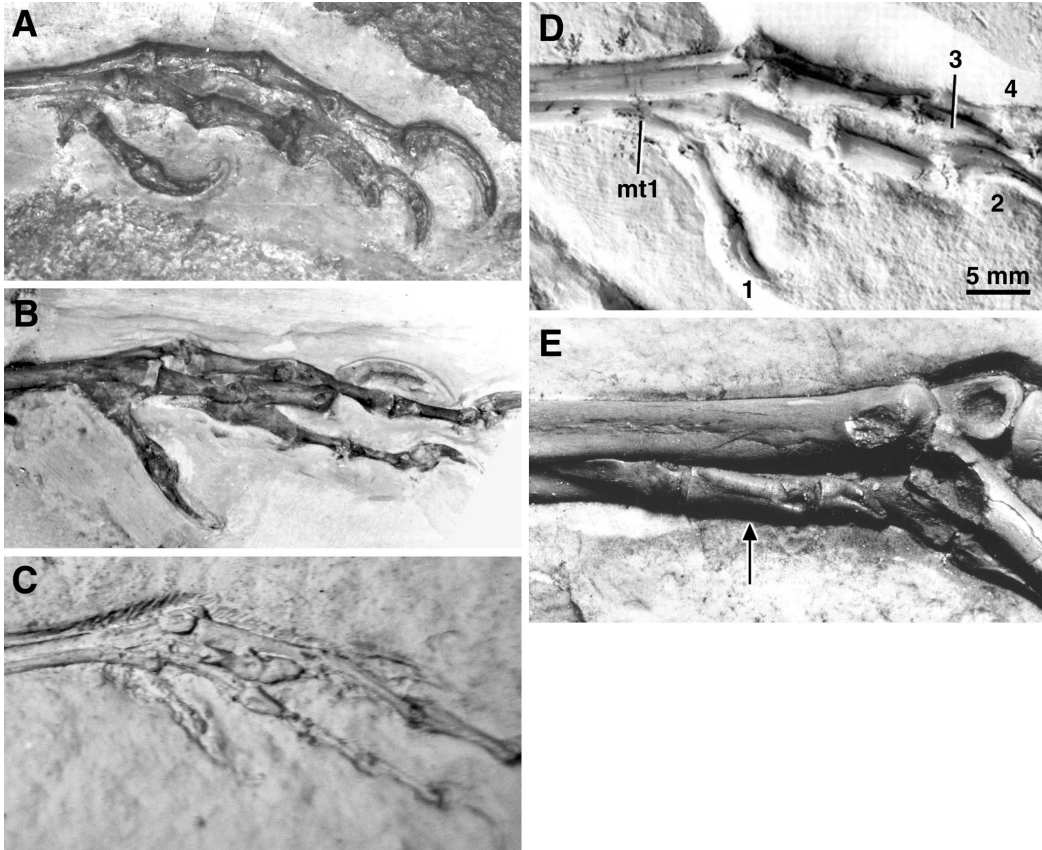


FIG. 1. Left feet of *Archaeopteryx* (scaled to the approximate same size): (A) London; (B) Berlin; (C) Eichstatt, right foot reversed; and (D) Thermopolis specimens, showing the reflexed hallux and the large size of the recurved hallucal unguis. Berlin specimen shows that the articulation of metatarsal 1 is distally located on metatarsal 2, allowing the opposability of the hallux with the other digits (photograph by S. Tarsitano). (E) *Pes* (photograph rotated for comparison) of *Compsognathus longipes*, a late Jurassic non-dromaeosaurid terrestrial theropod, showing the reduction of the hallux (arrow points to hallux and metatarsal 1); the flat hallux claw is in the typical theropod position, parallel and mesial to the tarsus, as in *Velociraptor*. (Photographs by S. Tarsitano and A. Feduccia; Thermopolis foot cropped from photograph of specimen from Mayr et al. [2005], “A well-preserved *Archaeopteryx* specimen with theropod features,” *Science* 310: 1483–1486, reprinted with permission from AAAS.) Abbreviations: mt1 = first metatarsal, 1–4 = digit numbers.

locomotion must have dominated. The hallux in Mayr et al.'s (2005) photographs opposes the other toes as it does in all other *Archaeopteryx* where the pertinent anatomy is preserved (see fig. 3D–F in Mayr et al. 2005). The metatarsal toe in their specimen is displaced so much laterally that it overlaps the anterior face of metacarpal 2. Rotated mesially, it becomes a reflexed hallux as in the London example. Mayr et al.'s (2005:1485) statement that “the absence of a fully reversed first toe indicates that *Archaeopteryx* did not have a perching foot” is totally misleading, given that the orientation of digit 1 in modern birds ranges from a high of 180° to a low of 65° in some totipalmate birds (that nest in, and are capable of perching in, trees), and many modern birds with a hallux less than fully reversed or without a hallux can perch in trees (Middleton 2001). Because the embryos of many extant birds have a mesially oriented hallux, it is difficult to imagine that any posterior reversal is associated with anything other than the perching habit. Thus, regardless of the degree of reversal of the urvogel hallux, it was an adaptation for grasping branches.

Were the hallux positioned as Mayr et al. (2005, 2007) suggested, it would have interfered with parasagittal movement of the legs, and that positioning might have been better interpreted as an adaptation for climbing tree trunks. Even Ostrom (1976) concluded that the hallux of *Archaeopteryx* was reflexed, and his specimens were similar in foot structure to the Thermopolis specimen. The remarkable sprawling legs preserved on Mayr et al.'s specimen is also shown in many specimens of *Microraptor* and may be more pertinent to the ecology of the animal, especially with the exceptional leg feathers preserved on the Berlin example (Longrich 2006).

Mayr et al. (2005, 2007) attempted to unite the deinonychosaurs and *Archaeopteryx* on the basis of both taxa having a hyperextendible (dorsiflexible) second-digit ungual claw, homologous to the well-known and characteristic sickle claw of deinonychosaurs. However, the pedal morphology is decidedly different in *Deinonychus* and *Archaeopteryx*. Ostrom (1969) illustrated that the hyperextension in *Deinonychus* of digit 2 was facilitated by an extended ventral joint surface (proximal heel) on the penultimate phalanx of the second digit, and an expanded condyle on the proximal articulation of the ungual. The condyles on the distal end of the penultimate phalanx of *Deinonychus*

are asymmetric, being larger ventrally (Fig. 2). This is reflected by an elevated (anterior) position of the ligamental pits on the distal end of the second phalanx (fig. 75 in Ostrom 1969). By contrast, the same phalanx in *Archaeopteryx* has more centrally located ligamental pits, and the condyles are longer dorsally than ventrally (Fig. 1). Mayr et al. (2005, 2007) concluded that a dorsally enlarged phalangeal condyle allows for the hyperextension of the second digit's ungual in *Archaeopteryx*. But, if *Archaeopteryx* was capable of hyperextending the second-digit ungual, it did so in a manner different from that seen in *Deinonychus* and *Velociraptor* (Fig. 1). This is emphasized by the dissimilarity of the foot of dromaeosaurs, with its hyperextendible second-toe sickle claw, to that of *Archaeopteryx*. In dromaeosaurs (Fig. 2), the mechanism is related to the extremely reduced length of the penultimate phalanx of digit 2 and as can be clearly seen, the hyperextension of the claw, is accomplished along with that of the penultimate phalanx. In addition, the basal phalanx is also reduced. By contrast, the second digit of *Archaeopteryx* shows no exceptional enlargement, but most striking is that the penultimate phalanx is elongate, as recognized by Mayr et al. (2005, 2007), thus rendering the mechanism seen in dromaeosaurs highly improbable. The hyperextension of the dromaeosaurid second digit of up to 150° or more was accomplished by extension–flexion of the two distal joints, which would have been biomechanically unlikely in *Archaeopteryx*, given the length of the penultimate phalanx. The ungual phalanx of the London specimen shows a nicely developed flexor tubercle, but this feature is consistent with climbing trunks and is characteristic of the claws of woodpeckers. Although some modest hyperextension may have been achieved in the second pedal digit of *Archaeopteryx*, it may well have been related to trunk climbing and is not likely to have been associated with predation, because the hands are “locked up” by the attachment of flight remiges. Although *Archaeopteryx* shares several characters with dromaeosaurs, the hyperextendible second-digit ungual claw is not among them and, thus, this synapomorphy is invalid and mitigates against the cladistic relationships set forth by Mayr et al. (2005, 2007).

Curvature of the claws, a definitive marker of arboreal habit not only in birds, but also expressed as phalangeal curvature in primates

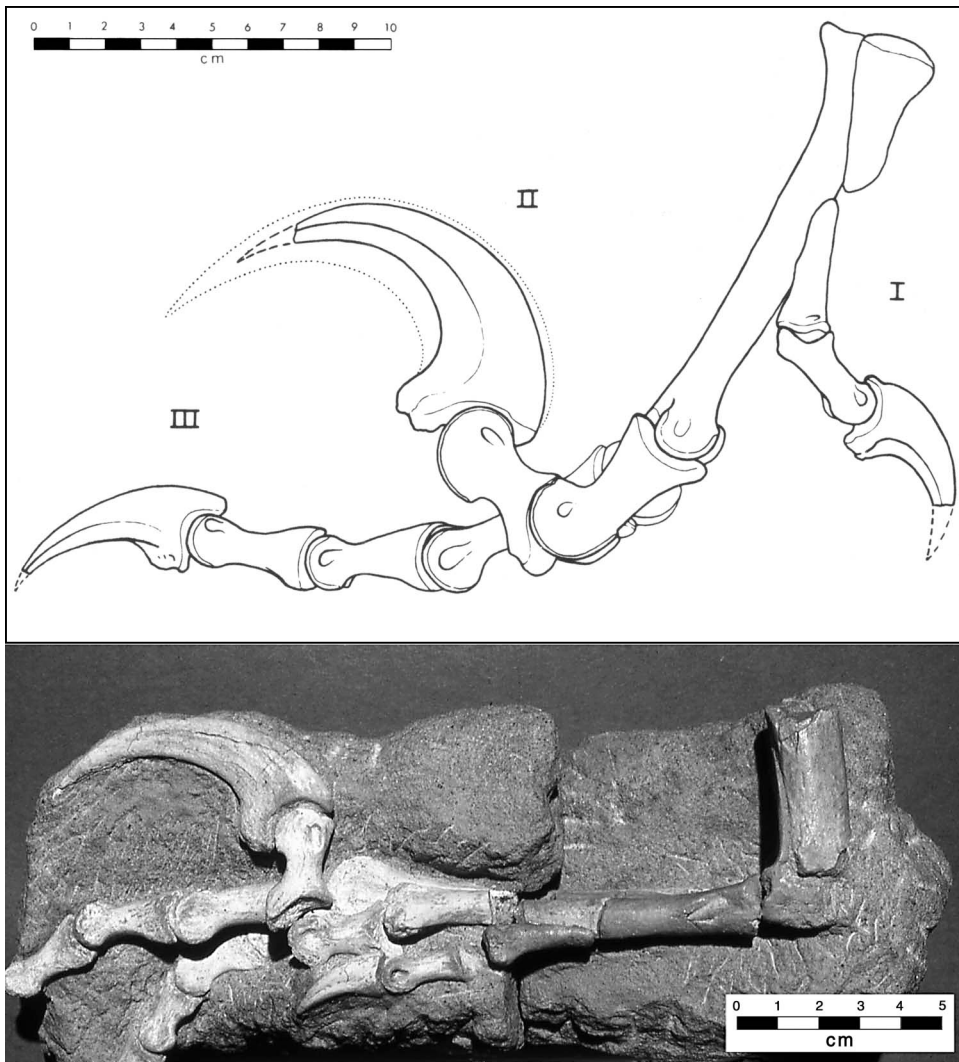


FIG. 2. Lower panel: right *pes* of *Velociraptor mongoliensis* before preparation, with sickle claw of digit 2, along with penultimate phalanx, in retracted position (H. Osmolska pers. comm.), showing: (1) the reduction of the hallux; (2) the parallel nature of the hallux in deinonychosaurs, and (3) the more proximal attachment of the metatarsal 1 on metatarsal 2, as compared with metatarsal 1 in *Archaeopteryx*. Note the ventral extension of the joint surface of the penultimate phalanx of digit 2 (not present in *Archaeopteryx*) that allows for the hyperextension (dorsiflexion) of the ungual in deinonychosaurs. Hyperextension is achieved by the extension of the ungual claw of digit 2 along with its penultimate phalanx, which is truncated, unlike that of *Archaeopteryx*. Upper panel: drawing of the *pes* of *Deinonychus* (rotated for comparison to the photograph), showing nearly identical morphology to that of *Velociraptor*. Note the incorrect position of the hallux in the drawing, presumably to make it look more birdlike. (Photograph of *Velociraptor* courtesy of H. Osmolska; *pes* of *Deinonychus*, modified and reversed to compare with the right *pes* of *Velociraptor* [modified after Ostrom 1969].)

(Feduccia 1993, Jungers et al. 1997), was ignored by Mayr et al. (2005, 2007). As noted in Feduccia (1993), the curvature of the pedal claws of *Archaeopteryx* falls within the range of living perching birds, and clearly not within the range of terrestrial birds, which have flattened claws. Likewise, the curvature of wing claws falls within the range of scansorial woodpeckers and trunk-climbing mammals (as well as fruit bats). The wing claws of all specimens, including the new Thermopolis specimen, most closely resemble those of trunk-climbing mammals and birds, not those of predators (Feduccia 1993, Griffiths 1993, Yalden 1997). It is noteworthy that all the claws of *Archaeopteryx* are like those of trunk-climbing animals and exhibit extreme lateral compression, whereas the pedal claws of cursorial theropods are flat and broad (fig. 1 in Yalden 1997). Pike and Maitland (2004) studied claw geometry in a variety of avian species and concluded that it would be difficult to assign *Archaeopteryx* to a specific locomotor category. However, they included predatory grasping birds in their analysis, which broadly overlap with perching birds in claw geometry. The claws of *Archaeopteryx* are easily distinguished from those of predatory birds, which exhibit tapering conical claws, broad at the base; those of *Archaeopteryx* are laterally compressed like those of scansorial birds and mammals. That Mayr et al. (2005, 2007) did not study the claws in detail is disappointing, because they may hold the critical evidence for a cursorial or arboreal lifestyle. Are the claws of their specimen laterally compressed, as in climbing birds and mammals, or broad as in terrestrial theropods, and are they highly recurved? It is apparent from the photographs that the pedal claws conform nicely in curvature to those of perching birds, and this is strongly supported by the presence of a highly recurved hallucal claw, which could only be a hindrance in a cursorial animal. Also unlike dromaeosaurs, all the claws of *Archaeopteryx* are recurved, not just the second-digit ungual claw. Obviously, in cursorial dromaeosaurs, the hypertrophied claw of the second digit was retracted in normal locomotion. Although we cannot discern the degree of lateral compression, it is apparent that the claws of all specimens of *Archaeopteryx* are not the broad, flat claws of a cursorial theropod.

It should be noted here that the Chinese, Early Cretaceous beaked bird *Confuciusornis*

also has been interpreted as a terrestrial predator (Padian and Chiappe 1998), but almost every aspect of its anatomy conforms to that of a fully volant, arboreal bird (Olson 2000). It has a short tarsus, like that of coraciiform birds; strongly asymmetric, pointed remiges; paired elongate tail plumes; a fully reversed hallux; and strongly recurved hallucal and front claws, nicely opposed for grasping branches. Chiappe et al. (1999:79), like most paleontologists, concluded that this early avian was "able to lift off after a short take off run," and this is exactly the mode of life that derives from the new interpretation of the Thermopolis *Archaeopteryx* specimen.

In our view, there is now little question that *Archaeopteryx* and, therefore, birds, are closely related to dromaeosaurids, particularly Chinese Lower Cretaceous microraptors, which we regard as a derived group of birds (Fig. 3), at various stages of flight and flightlessness (Martin 2004, Feduccia et al. 2005). The studies by Mayr et al. (2005, 2007) strengthen this relationship, although the diagnostic, stiffened "ramphorhynchoid" tail of dromaeosaurs is absent in *Archaeopteryx*, which is primitive in this character. Also, disappointingly, there is no mention of the fact that the Thermopolis specimen has typical Mesozoic bird, not theropod, teeth. Characters as displayed on specimens should be evaluated on their morphology, completely independent of whether or not they conform to a popular cladogram or evolutionary scenario. When thus considered, *Archaeopteryx* is clearly primitive with respect to the Chinese microraptors, a position that conforms to its temporal geological occurrence (Fig. 3). A close relationship between *Archaeopteryx* and *Microraptor* is also suggested by the presence in the latter of avian-style teeth, constricted at the base and with a closed resorption pit. Contrary to current cladograms, the microraptors are a highly derived group and are not ancestral to *Archaeopteryx*, in concordance with their temporal occurrence some 25 million years after *Archaeopteryx*.

The major problems related to the origin of birds are still unresolved, and the persistent problems of a strict theropod ancestry remain (1) the temporal paradox, (2) character mismatches (especially the digital mismatch), (3) flight from the ground up (largely falsified), and (4) the need for precise avian flight architecture to have evolved in a nonflight context.

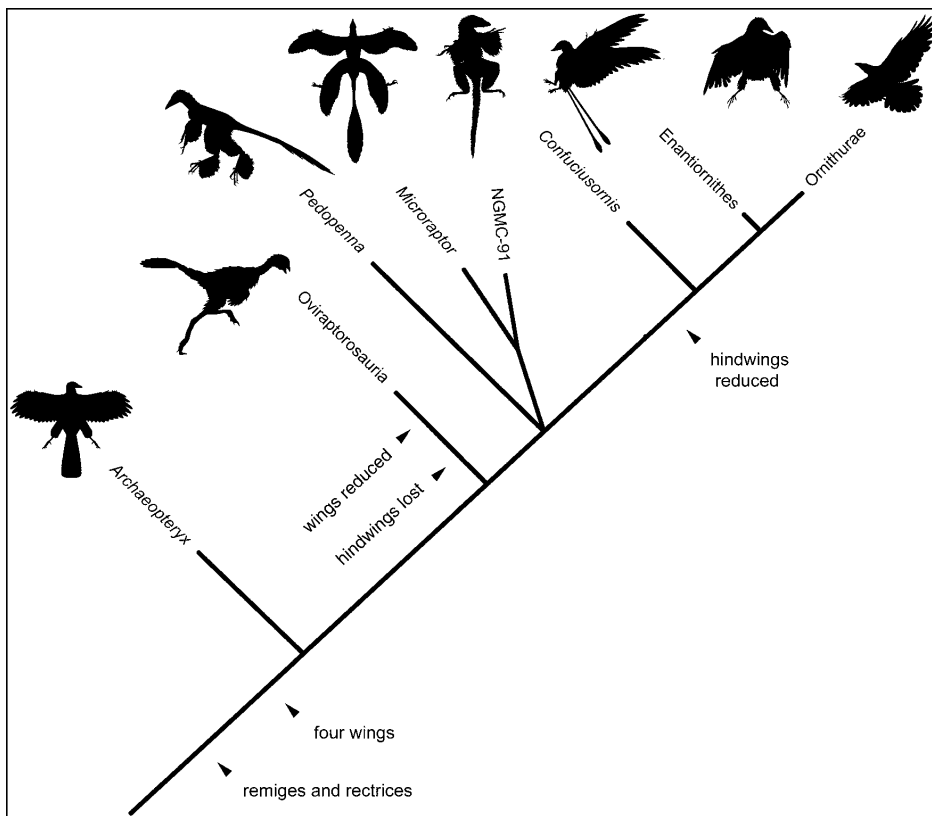


FIG. 3. Phylogeny of early birds, from Longrich (2006), following Chiappe (2002) and Xu and Zhang (2005), but modified to show the Late Jurassic *Archaeopteryx* as the basal bird, instead of derived from Early Cretaceous deinonychosaurs. Deinonychosaurs are derivatives of the early avian radiation at all stages of flight and flightlessness, and oviraptorosaurids are highly derived, secondarily flightless birds that have lost the hindwings. This new model avoids the pitfalls of the classic theropod origin of birds and redirects avian ancestry to an earlier archosaur without highly derived theropod specializations. This model conforms nicely to the temporal occurrence of taxa. According to this model, avian flight architecture evolved in an aerodynamic context, and not in earthbound theropods (modified, with permission, from Longrich [2006]).

These problems are overcome by a new interpretation of early Chinese fossils (particularly microraptors) now embraced by numerous authors (Czerkas et al. 2002, Feduccia 2002, Feduccia et al. 2005, Paul 2002, Martin 2004; and suggested as a hypothesis by Witmer [2004] and Zhou [2004]). The interpretation of microraptors as an early offshoot of the ancient avian lineage obviates the deficiencies of the theropod origin of birds. The temporal paradox is voided, because they are descendants rather than ancestors of birds. Because these "four-winged" animals are arboreal and volant, with no supra-acetabular shelf, which permits full lateral excursion of the femur,

their ancestors could not have been the obligatory bipedal theropods characterized by the Late Triassic *Herrerasaurus*, *Syntarsus*, *Coelophysis* (etc.), which also had forelimbs reduced to half the length of the hindlimbs. Such a typical theropod ancestry would require the re-elongation of already foreshortened forelimbs, as well as the acquisition of sophisticated flight architecture in an earthbound theropod. If the ancestor were an earlier, less specialized archosaur (presaging the tiny Jurassic *Epidendrosaurus* = *Scansoriopteryx* [Czerkas and Yuan 2002, Zhang et al. 2002]), the problem of character mismatches is voided, because the ancestral should be pentadactyl and

uncommitted to a hand of either digits 1-2-3 (theropodan) or 2-3-4 (avian). Finally, the discovery of "four-winged" early avians falsifies the cursorial origin of flight.

As there is no current evidence for the existence of any form of protofeather on any bird, living or fossil (Feduccia et al. 2005, T. Lingham-Soliar et al. unpubl. data), the fossil record "yields no evidence on the origin of feathers that cannot be better obtained from living birds" (Martin and Czerkas 2000: 693). The concept of "feathered dinosaurs" is further eroded (practically falsified) by the discovery of the small 151-million year old Late Jurassic compsognathid *Juravenator* (2–3 million years older than *Archaeopteryx*), which has typical dinosaurian tuberculated scaled skin but is totally devoid of feathers (Göhlich and Chiappe 2006); and the same is true for *Compsognathus corallestris* (same age) from southeastern France (Peyer 2006). To avoid the obvious conclusion that compsognathids are scaled, and identification of protofeathers in *Sinosauropteryx* in error, Xu (2006:288) surmised that "the scaled *Juravenator* would...be the starting point for feather evolution" and suggested that "feathers evolved independently or were lost in some species."

All Chinese fossils with true avian feathers are best interpreted as secondarily flightless birds (oviraptorosaurids; Lu et al. 2002, Maryanska et al. 2002) or offshoots of the early avian radiation at all stages of flight and flightlessness (microraptors; Czerkas et al. 2002, Feduccia 2002, Paul 2002, Martin 2004, Feduccia et al. 2005). According to this view, the clade Aves is defined by such salient characters as feathers, avian hand with digits 2-3-4, and a reversed hallux. The great challenge for archosaurian paleontology is to tease out the exact avian clade from early theropods with superficially similar structure.

Archaeopteryx, rosetta stone of evolution (Feduccia 1980), remains the classic urvogel.

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