



A basal archosaurian origin for birds

Larry D. MARTIN*

Museum of Natural History and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

Abstract The controversy over the origin of birds may have been resolved through the discovery of new and remarkable fossils from the Triassic of Central Asia and the Early Cretaceous of China. Flight probably originated in small, quadrupedal gliding archosaurs in the Triassic. Feathers originated for gliding rather than for insulation. The “maniraptoran dinosaurs” are actually derived from birds with at least gliding capabilities and primary feathers on the hands [Acta Zoologica Sinica 50 (6): 978–990, 2004].

Key words Birds, Origin, Archosaurs, Maniraptorans, Phylogeny

鸟类起源于基干的初龙类

Larry D. MARTIN*

Museum of Natural History and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

摘要 中亚三叠纪和中国早白垩世的新的化石发现或许可以帮助解决有关鸟类起源的争议。鸟类的飞行可能起源于三叠纪一些小型的、四脚滑翔的初龙类。羽毛的起源最初是为了滑翔而不是保温。“手盗龙类”实际上起源于鸟类，并至少发育了初级飞羽，具备滑翔的能力 [动物学报 50 (6): 978–990, 2004]。

关键词 鸟类 起源 初龙 手盗龙 系统发育

1 Introduction

Archaeopteryx was the first bird to be recognized from the Mesozoic and displayed such a remarkable combination of avian and reptilian characters that it became the archetype of a “missing link.” It was discovered in 1861, only two years after publication of Darwin’s *Origin of Species*. Little doubt remains that birds originated from reptiles, but controversy exists over the choice of reptile. Huxley (1870) was an early proponent of dinosaurs as ancestors for birds, and this was the dominant theory of avian origins until the beginning of the 20th Century (Witmer, 1991). The discovery at that time of older bipedal archosaurs provided new models lacking specializations that seemed to bar dinosaurs from direct avian ancestry. Heilmann’s (1926) book “*The Origin of Birds*” related birds to dinosaurs through a basal archosaurian stalk. Almost everybody who read his book agreed with him, and the dinosaur-bird connection was buried for over forty years until exhumed by Ostrom (1973), and used to support endothermy in dinosaurs.

The remarkable public attention garnered by dinosaurs at this time contributed to the success of a

theory relating them to birds. Ostrom (1973, 1976) used an essentially man-sized theropod *Deinonychus* as the model for his idea. He met with immediate acceptance among dinosaur paleontologists and resistance in the ornithological community (Feduccia, 1980). For nearly two decades, *Deinonychus* stood almost alone as a dinosaurian proxy for a bird ancestor, but in recent years, smaller and more bird-like theropods were discovered in the Early Cretaceous *Confuciusornis* fauna of Liaoning, China. Some of the new fossils preserve soft parts including feathers. These deposits are nearly twenty million years younger than *Archaeopteryx* (1 200 000 years old or a little older). While these deposits are much younger than the time of the origin of birds, the diversity and quality of pertinent fossils make them critical to our understanding of how birds may have originated.

2 Avian flight

The origin of avian flight is intertwined with the origin of birds. Pterosaurs and bats incorporate arms and legs into a continuous patagium and can be compared directly with living examples of gliding mammals; but in birds, the legs and wings are decoupled

with little evidence that an extensive skin patagium was ever present. Birds are accomplished bipeds, while bats and pterosaurs are basically quadrupedal. If avian flight originated in an arboreal environment, should bipedality be an expected precursor as some have suggested (Ostrom, 1979)? Were hand movements involved with capturing prey in small bipedal dinosaurs modified to supplement the thrust of the legs in running (Gishlick, 2001) and, with further modification, led to flight from the “ground-up?” Because the airfoil surface in birds is composed of feathers, this scenario presupposes that feathers had already evolved. Most supporters of a cursorial origin for flight assume that feathers originated for a function unrelated to flight (insulation, prey capture) and were later recruited for aerial propulsion. (Ostrom, 1979).

Many dinosaurs were bipedal runners balancing a teetering body on their hind legs. The back was held horizontal and the stride was exceptionally long for the length of the body (Jones, et al., 2000a). This long stride may have been the secret of dinosaurian success for nearly 180 000 000 years. Anatomical features associated with this posture—reduced forelimbs attached to a posteroventral glenoid and open acetabulum with a supra-acetabular shelf—are among the important characters defining Dinosauria (Benton, 1990). The hind legs were elongated and the feet digitigrade. The body cavity in most dinosaurs was deep and laterally compressed. Few researchers see a climber in these proportions, and proponents of a dinosaurian origin of birds mostly thought that flight originated in small bipedal dinosaurs which achieved flight speed through running (Williston, 1879; Padian, 1985). The opposing view that flight originated in small arboreal reptiles came from Williston’s former mentor, O. C. Marsh of Yale (Marsh, 1880). Both ideas have strengths and weaknesses. Small running animals lack the stride length necessary to achieve useful speeds (Rayner, 1985). The original feathers created drag slowing their bearers down, and made little adaptive sense for animals that already had too much drag and too little airspeed. Animals jumping out of trees had the opposite problem: too much airspeed and too little drag. Feathers should work for them immediately, but how were arm movements decoupled from those of the legs?

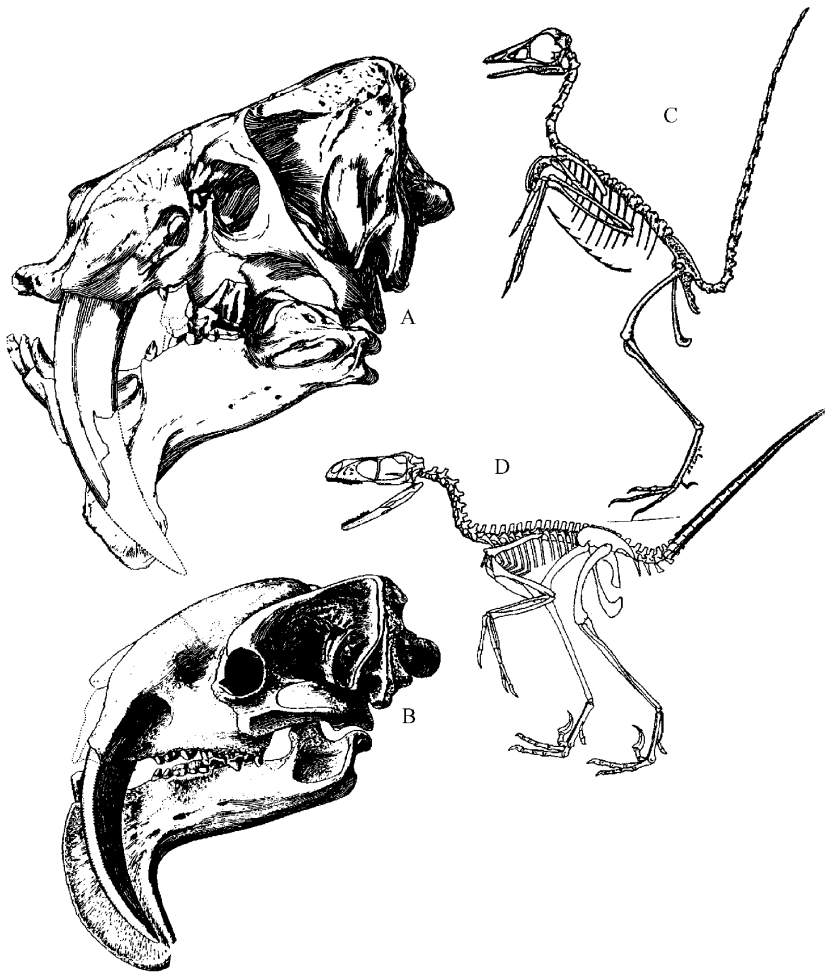
One of the most surprising features of the anatomy of *Archaeopteryx* is its poorly developed parasagittal posture. The femoral head turns forwards rather than extending perpendicular to the shaft. The pelvis has an incompletely open acetabulum, and there is no characteristic dinosaurian supra-acetabular shelf (Martin, 1991, Figs. 30–31, 34, 38–42). This results in a somewhat sprawling position for the

femur (Martin, 1991, Fig. 37) that is corrected at the knee joint, resulting in a functionally vertical leg. Modern birds have an antitrochanter on the acetabulum producing a similar divergence of the femora. This positioning permits modern birds to extend the femora forwards on either side of a broad ribcage. Their sprawl is also corrected at the knee. *Archaeopteryx* lacks basic features of both modern bird and dinosaur postures; and it is difficult to argue that it shared their peculiar backs when running, or that the common ancestor of birds and dinosaurs had already achieved such a running posture. In fact, confinement of the articular surface to the front of the acetabulum in *Archaeopteryx* results in a vertical back (Fig. 1). This posture raises the wing further from the ground permitting a more complete wing beat, a position assumed by modern birds at the point of take-off from the ground. *Archaeopteryx* appears to have been a poor runner when compared to contemporary dinosaurs. Recent analysis of phalangeal proportions (Hopson, 2001; Zhou and Farlow, 2001) shows adaptation for terrestrial locomotion at about the level of a pigeon.

Bergers and Chiappe (1999) attempted to bolster the cursorial model by proposing that power exerted by the legs could be supplemented with wing thrust. Because the wings would have to pull the animal faster than it could run, it is difficult to understand how this could work, particularly as running birds usually have small wings that are held against the body to reduce drag rather than flapped. Dial (2003) offered evidence for wing-assisted vertical running where the wing beat permits the climbing of near vertical surfaces by keeping the animal pressed to the surface rather than providing lift. This might actually provide a special case for the arboreal model where the protobird could spend time on the ground, and still run up a tree to achieve altitude for takeoff. Dial’s description seems better fitted for modern birds with their peculiar leg positioning than *Archaeopteryx*, and incompatible with the Bergers and Chiappe (1999) model. There is a strong probability that bipedal locomotion is secondary to flight in birds, and that the avian ancestor was an arboreal quadrupedal glider.

3 Dinosaurian origin of birds

No one doubts that some Cretaceous dinosaurs are remarkably similar to certain fossil birds. The question remains: how much of this similarity can be ascribed to convergent evolution and how much to direct relationship. To evaluate this question, let us compare the very bird-like maniraptoran *Bambiraptor feinbergi* with the primitive bird *Archaeopteryx* (Fig. 1: C, D). We see pronounced similarity, but



1.1 Convergence versus homology

Skull and jaws of the placental saber-tooth *Barbourofelis*. (A) compared to the very distantly related marsupial saber-tooth *Thylacosmilus* (B) Is the skeleton of the early bird *Archaeopteryx* (C) more similar to that of the birdlike “dinosaur” *Bambiraptor* (D) than the convergent saber-tooths are to one another? (A–B from Martin, 1994: Fig.7)

is it greater than that between the nimravid saber-tooth *Barbourofelis*, and the saber-toothed marsupial *Thylacosmilus* (Fig.1: A, B). These two mammals are about as distant phylogenetically as anyone has suggested for birds and dinosaurs, yet they share an extensive list of apomorphic (derived) characters. Clearly, convergence is powerful enough to confound an insufficiently critical phylogenetic analysis. A careful study of structural detail yields evidence that the saber tooth similarities were derived independently, and nobody thinks that there is an exclusive phylogenetic relationship between marsupial and placental saber-tooths. We should require a similarly rigorous study of structural detail before we accept a dinosaurian origin of birds. In particular, we should be able to offer some explanation for a “temporal paradox” and certain “anatomical barricades” that I will now address.

4 The temporal paradox

In most phylogenetic analyses (e.g., Sereno,

1999), birds are not simply closely related to dinosaurs but are actually members of the maniraptorans, the last dinosaurian clade to develop (i.e., a crown-group). Because birds are embedded within the maniraptorans, they can be regarded as living dinosaurs (Dingus and Rowe, 1998). All other major clades of saurischian dinosaurs precede the origin of birds. This creates an inconsistency in time of origin for *Protoavis*, a supposed Late Triassic bird (Chatterjee, 1995); and a similar problem exists for possible Early Jurassic “bird” tracks (Lockley et al., 1992). Even if *Protoavis* were only a dinosaur closely related to birds, all dinosaur clades preceding it must have been in existence, along with their signature characteristics, by the Late Triassic. Almost all of dinosaur evolution would have occurred in a sudden burst at about the time that dinosaurs first appear in the fossil record.

Embedding birds in the maniraptoran crown group coupled with a Late Jurassic age for *Archaeopteryx* creates a similar problem. Not only is

Archaeopteryx older than any creditable maniraptoran fossil (Feduccia, 2002), but maniraptoran diversification must be even older. This results in a hypothetical burst of evolutionary diversification in the Middle Jurassic (Serenó, 1999). Such discrete evolutionary bursts, if genuine, are more theoretically important than the question of avian origins and should be tested with evidence outside the bird/dinosaur controversy. They may also be a warning of some flaw in the cladistic analysis.

The opposing view is well articulated in the *Origin and Evolution of Birds* by Feduccia (1999). This book argues that birds are very ancient, extending into the Triassic, well before the appearance of the first dinosaurs. The ancestors of birds were cold-blooded, small and lizard-like. They lived in trees, and feathers probably evolved for flight and only later as insulation. Flight evolved from jumping from tree to tree; landing on the ground was initially an unhappy accident ('trees-down' origin of flight). Bipedality was a consequence of their arboreal lifestyle, as has been suggested for primates (Martin, 1983a, b, 1987); and the elongated foot resulted from jumping rather than terrestrial running. The 'trees-down' theory has the additional advantage of having living models for postulated evolutionary stages leading to flight (Bock, 1965, 1985).

5 Anatomical barricades

If dinosaurs are to be considered avian ancestors, several anatomical problems need to be resolved. The most serious concern the teeth and the hand. The nature of tooth implantation and replacement is critical (Wellnhofer, 1974; Martin and Stewart, 1999). These are fundamental features, and once one implantation pattern has been achieved, it is hard to understand why it would be lost and replaced by another. In birds and living crocodylians, teeth are originally implanted in a groove with sockets forming around the roots from front to back as the jaw matures. There is not enough space for the lingual tooth family, and a replacement tooth quickly migrates under the crown of its predecessor. It then finishes its development and ascends vertically. Crocodylians may show several replacement teeth stacked vertically and vertical tooth replacement is known in *Archaeopteryx* and other toothed birds (Martin and Stewart, 1999; Martin and Zhou, 1997).

Dinosaurs retain a primitive pattern of tooth replacement in which the young teeth are arranged horizontally in a lingual row. The teeth in birds or crocodiles are bordered lingually by an extension of the tooth bearing bone (premaxilla; maxilla or dentary), while dinosaur teeth are bordered by hypertrophied attachment bone (superpleurodontology; Martin

and Stewart, 1999). This suggests that the common ancestor of birds and dinosaurs did not have socketted teeth. The teeth of birds are uniform in having a short crown with a constriction near the base leading into an expanded root that usually includes an oval replacement pit. Similar teeth have not been described in dinosaurs, although dromaeosaurs were originally reported to lack interdental plates, a signature trait of dinosaurian tooth implantation. Their tooth replacement has also been claimed to be bird-like (Currie, 1987). If they had, or had had, the avian/crocodylian implantation and replacement pattern, we might argue instead that they are not dinosaurs. The common ancestor for both birds and dinosaurs would predate thecodonty in either group and lie at the base of the Archosaurian radiation.

Much of Ostrom's original evidence for a bird/dinosaur relationship was based on the wrist and hand. Wrists in the advanced maniraptorans, *Velociraptor* and *Bambiraptor*, show only two free bones, as reported by Ostrom (1969) for *Deinonychus*; but the semilunate is in the distal row as in birds (Padian and Chiappe 1998a, b) and not a proximal carpal (radiale) as reported by Ostrom (1969). In birds, the equivalent should be a distal carpal III, and this condition seems clear in *Jeholornis* and *Confuciusornis* from the Early Cretaceous of China where it only fuses to metacarpal III. In dinosaurs it should be fused distal carpals I, II. The small distal carpal IV found in birds is lost; and there is presently no evidence that the small distal carpal identified in *Deinonychus* by Padian and Chiappe (1998a, b) is distal carpal IV. There is a single proximal carpal, the radiale (ulnare of Ostrom, 1969). The metacarpals are arranged in an arch as restored by Ostrom, different from that in birds. The wrist in *Archaeopteryx* and modern birds is less derived in these respects, making maniraptorans more likely the descendants of birds than their ancestors.

The pattern of finger reduction in dinosaurs is unique and might be the best evidence for the monophyly of the group. In most other tetrapods, digit reduction proceeds from both sides inwards (perrisodactyls and artiodactyls). In dinosaurs, digit reduction is restricted to the lateral side of the hand with digits 4 – 5 reduced in the Triassic dinosaur, prosauropods and ornithischians (Feduccia, 2002). Birds clearly retain digits 2 – 4, as shown by embryological development of a five-digit hand in the ostrich (Feduccia and Nowicki, 2002) and work by Larsson and Wagner (2002) using molecular markers to identify digit condensations in the chicken embryo. As pointed out by Ostrom (1985), there are no direct data available for the pattern of digit reduction in dromaeosaurs, but an avian pattern would provide addi-

tional evidence that they are not dinosaurs. The common ancestor of advanced maniraptorans such as *Bambiraptor* and modern birds had not yet lost the ulnare or distal carpal IV. The common ancestor of birds and maniraptorians on a dinosaurian lineage must precede Triassic dinosaurs that already show the reduction of digit 4 (Fig.2).

Ostrom (1969) figured the proximal ankle (astragalus and calcaneum) of *Archaeopteryx* in several drawings and two photographs that compare the ascending process in the ankle to that of *Deinonychus*. This was one of Huxley's (1870) original features associating dinosaurs and birds, but the ascending process in birds (Martin et al., 1980) is a separate "pretibial bone." The pretibial bone is more closely united with the calcaneum than with the astragalus in most modern birds and extends up the lateral rather than medial side of the tibia. Ostrom's excellent photographs (Ostrom, 1976) clearly show that in *Archaeopteryx*, it is also a long narrow process on the

lateral side of the tibia, lying above the calcaneum and along the fibula. In the London specimen it pulled off with the calcaneum and remains on the counter slab. This position is the same as in most other birds and differs from dinosaurs.

In a *lapsus*, Ostrom (1976, Fig.29) reversed the position of the ascending process, thus making the restoration more comparable to *Deinonychus*. This error was pointed out by Martin (1983a) and Tarsitano and Hecht (1980). It was corrected by Ostrom (1985, p. 174): "I further admit to confusing the issue by illustrating this process in *Archaeopteryx* in my 1976 paper in a much more medial position than it is actually preserved in the London and Berlin specimens". All of Ostrom's illustrations in this paper differ widely from one another (Martin et al., 1980). One (Ostrom, 1976, Fig.28) is essentially identical to the condition in *Deinonychus*, showing a very reduced calcaneum and a broad ascending process from the astragalus. In fact, *Archaeopteryx* more

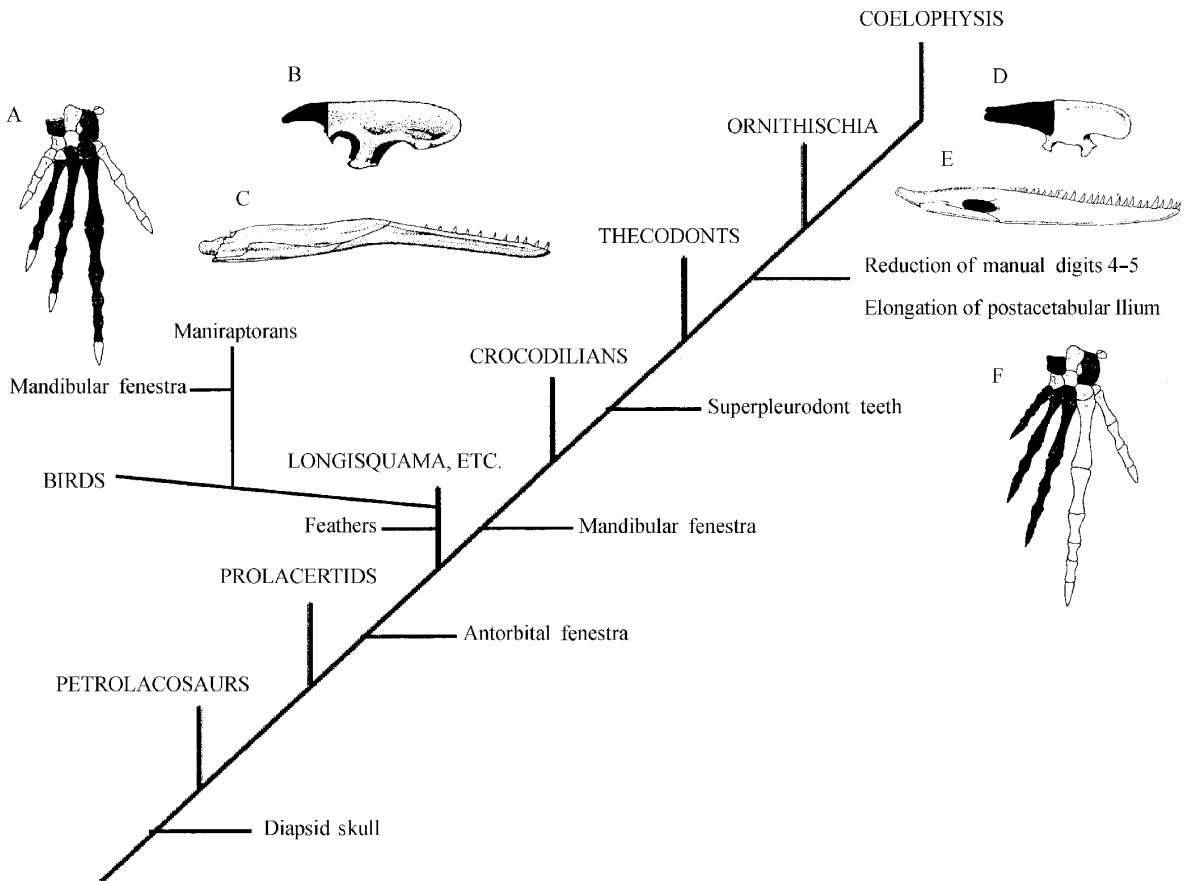


Fig.2 Diapsid reptiles and birds showing the point of first occurrence of various synapomorphies

The pattern of finger reduction (A, F) is illustrated by the hand of *Petrolacosaurus* (Reiz, 1981). A: Shaded wrist and digits preserved in birds and presumably maniraptorans. F: Those preserved in dinosaurs. The absence of the mandibular fenestra in early birds is illustrated by *Archaeopteryx* (C); it presumably would be a neomorph in maniraptorans. It is primitively present in dinosaurs, including *Coelophysis* (E, based on Colbert, 1974). The primitively short postacetabular ilium (shaded) is illustrated by *Archaeopteryx* (B) and contrasted with *Coelophysis* (D) (from Naples et al., 2002). The pattern of avian primitive structures supports a very early divergence from the line leading to dinosaurs. If maniraptorans are actually birds, their divergence would be equally early and their resemblance to dinosaurs convergent.

closely resembles carinates than ratites in this region, and is also similar to primitive ornithurines such as *Baptornis* and *Hesperornis*. In these birds, the calcaneum is large and forms the outer condyle as is usual in reptiles. In some early birds (enantiornithines) and many dinosaurs, the astragalus enlarges and the calcaneum becomes vestigial, clearly a more derived condition. We can speculate that the common ancestor of birds and dinosaurs lacked an ascending process on the ankle, and that bipedality was achieved independently.

Additional avian features that are primitive when compared to dinosaurs in general include a short post-acetabular ilium (Naples et al., 2002). The post-acetabular ilium is already elongated in the coelurosaurian dinosaur *Coelophysis* from the Triassic (Fig. 2). The absence of a mandibular fenestra in most Mesozoic birds, a condition already present in late Triassic archosaurs, including crocodylians and dinosaurs, indicates also that the basal avian stalk appeared close to the origin of archosaurs, a position consistent with evidence from tooth implantation (Fig. 2). The independent evolution of an ascending process in the ankle (pre-tibial bone in birds; ascending process of the astragalus in dinosaurs) indicates that their common ancestor predates the characteristic hind-leg posture of dinosaurs; and this is further indicated by the slightly sprawling hind-leg of *Archaeopteryx*, accompanied by partial closure of the acetabulum (Martin, 1991).

The demonstration that these features are constructed differently in dinosaurs and birds is not simply a criticism of their use in relating dinosaurs to birds. Rather we may also suppose that their common ancestor had not yet solved these particular problems. We may then go to the cladogram and constrain the point of appearance of the common ancestor (Fig. 2). The distinctly different patterns of tooth replacement and implantation, absence of a mandibular fenestra, pattern of finger reduction, short post-acetabular ilium and presence of a pre-tibial bone point clearly to a common bird/dinosaur ancestor preceding the triassic coelurosaurs *Coelophysis*, *Syntarsus*. If maniraptorians share a special ancestor with birds, it must also lie below certain cladistic points (serrated teeth, mandibular fenestrae, ossified sternum, reduced wrists, erect femora, enlarged pedal II claw and tail rods). *Archaeopteryx* has a few derived features, including a slightly shortened tail, which suggest that it is not the ancestor of maniraptorans; but any common ancestor of maniraptorans and birds looked more like it than like *Coelophysis*.

6 Feathered dinosaurs?

The origin of birds is closely coupled with the origin of feathers and related skin features. The inter-

vention of a network of skin muscles (Homberger, 2002) that can distort the follicle and thereby move the feather is such a significant part of their functional morphology that we may suppose that the evolution of feathers and the muscles that moved them was closely correlated. As soon as feathers achieved sufficient length to form a useful airfoil, they needed a mechanism to fold them out of the way. This folding utilized a sideways motion that would be impossible for an ordinary scale. In feathers, however, it is made possible by a pivot point provided by a rod-like calamus inserted deeply within a dermal pocket (follicle). Long flight feathers imply the existence of an adequately broad fold of skin to accommodate a deep follicle. In order to provide an airfoil, the feather must also be broad distally. This combination of narrow proximal and broad distal ends is the signature achievement of a feather and separates it from hair and ordinary scales. The airfoil surface of the feather develops within a tube, the feather sheath, where the barbs are folded. They unfold distally as the sheath falls away, permitting the feather tip to become much wider than the base.

The announcement of feathers in a compsognathid dinosaur *Sinosauropteryx* raised the possibility that feathers were widely distributed among dinosaurs. However, none of the above features of feathers could be confirmed in *Sinosauropteryx*. Similar structures have been found in dromaeosaurs where they are claimed to show evidence of feather structure (Xu et al., 2001) and in a pterosaur (Wang and Zhou, 2002). Such a wide phylogenetic distribution of primitive feathers or hairy coverings seems improbable. Could they be features from under the skin rather than above it e.g., collagen fibers? Fossils of superficial muscle in the marine reptile *Ichthyosaurus* (Lingham-Soliar, 1999), do duplicate many feather-like features.

Undoubted feathers (Xu et al., 2001) occur in some putative dinosaurs, including *Protarchaeopteryx*, *Microraptor* (*Archaeoraptor?*) and *Caudipteryx*. *Protarchaeopteryx* (Ji et al., 1998) has typically avian teeth, and there is no reason to doubt that it is avian. *Caudipteryx* has recently been allied with oviraptors (Sereno, 1999). Several workers have considered it a bird and so have I. The existence of long primary feathers extending from the middle finger of the hand requires a long fold of skin to accommodate the calamus. This so greatly reduces the usefulness of the hand for grasping that it must imply derivation from an arboreal flyer/glider. An arboreal stage is further supported by a reflexed hallux on the foot in all of these forms. The most recent cladistic analyses of oviraptor relationships (Lu et al., 2002; Maryanska et al., 2002) show ovirap-

tosaur as flightless birds more derived than *Archaeopteryx*. We thus have animals that are clearly dinosaurs with structures (protofeathers) that do not seem to be feathers, and animals that clearly have feathers and are also birds with primary feathers on the middle finger of the hand.

The most informative specimens are maniraptorans with obvious flight feathers coming off the arm and the hind leg (Norell et al., 2002; Czerkas et al., 2002). One of these, *Cryptovolans pauli*, (Norell et al., 2002) was described as having a rear wing, but Czerkas et al. (2002) suggested that this was too exceptional to be correctly interpreted. New material assigned to *Microraptor* (Xu et al., 2003) now confirms the existence of a rear wing and shows that the longest of the hind leg flight feathers actually come off of the foot (Fig.3)! I was fortunate to be able to examine that specimen in detail and to study a second specimen without preserved feathers but with an excellent skeleton. I also saw photographs of several other similar specimens. It seems clear that long flight feathers very similar to the primary feathers of the hand came off the *tarsometatarsus*, and that the animal had two sets of wings (Fig.3).

This is a remarkable and unexpected confirmation of the tetrapteryx stage in the origin of avian flight predicted by Beebe (1915). It is clearly a gliding adaptation, with feathers taking the place of the skin patagium found in gliding mammals. The femora are unusually long, and in order for the femur to function they must be able to extend laterally, as is the case in pterosaurs. Modifications of the proximal femur and acetabulum for this position result in an animal that could barely walk, let alone run. It must have been completely arboreal. Also supportive of this interpretation are the remarkably small toes on the foot, coupled with a reflexed hallux. The second pedal claw is enlarged but it seems unlikely that it had a predatory function; it was probably used for climbing. The tail includes stiffening rods extending anteriorly from the prezygopophyses and the chevrons. These two features imply relationship with younger forms such as *Velociraptor* and *Bambiraptor*.

The scapula-coracoid complex in the new "*Microraptor*" is arranged as in birds. There is a furcula and an ossified sternum. The pubes are reflected posteriorly, the number of caudal vertebrae is reduced, the astragalus is enlarged and the calcaneum reduced. In some respects these animals are derived compared to *Archaeopteryx* and in ways that bring them closer to terrestrial maniraptorans. They are also some twenty million years younger than *Archaeopteryx*. It is hard to see how a functional biped could have given rise to such an animal. The evolution of a hind limb wing seems to require a quadrupedal arboreal stage.

So the late Cretaceous bipedal species must be secondarily flightless, becoming more dinosaur-like than their flying (gliding) progenitors. This is remarkably similar to the pattern of evolution postulated for living ratites, and is a confirmation of the heretical hypothesis of Paul (1984, 2001, 2002). Paul solved the temporal paradox by postulating that *Velociraptor* and other maniraptorans were derived from *Archaeopteryx*-like forms. Paul's hypothesis is supported by the identification of *Microraptor* as a basal dromaeosaur (Xu et al., 2003).

In a recent cladogram (Hwang et al., 2002), oviraptorosaurs including *Caudipteryx*, an animal with genuine primary feathers coming off of the hand indicative of a flying/gliding ancestor, are coupled with a real bird *Archaeopteryx* that lies next to dromaeosaurs including *Microraptor gui*, a flying/gliding form with primary feathers (Fig.3: E)! Can we doubt that the common ancestor of these three taxa also had primary feathers or that their unusual distribution of tail feathers was already present in the common ancestor of oviraptorosaurs and dromaeosaurs? The inclusion of *Archaeopteryx* which lacks this tail structure and a mandibular fenestra seems less likely. The terrestrial maniraptorans might then be thought of as flightless birds. Their ancestor would probably have looked more like an arboreal gliding lizard than a dinosaur.

7 Basal archosaurs?

Martin (1983a) discussed *Scleromochlus* as a protobird. Padian (1984) followed von Huhne in allying it with pterosaurs, but Sereno (1991) called it a "dinosauromorph". Apparently it lies at a position near the base of the archosaur radiation and has features suitable for derivation of a flying animal (pterosaur or bird). It seems specialized for jumping, and the weak hand with short fingers would seem to exclude most arboreal activities. I gave *Scleromochlus* special consideration (Martin, 1983a) because it clearly shows the one feature that I suggested as a minimal requirement for a proto-bird. This is a conformation of the shoulder girdle that puts the arm level with the back and provides for a full range of lateral motion, with the center of mass below the arms. This is achieved through a long narrow strap-like scapula lying parallel to the vertebral column. Strap-like scapulae are known in a number of archosaurs including dinosaurs, pterosaurs and birds. However, only birds, some pterosaurs and certain basal archosaurs have scapulae parallel to the vertebral column. This position probably evolved to facilitate arm motion for climbing; in mammals it is found in primates and bats where the scapula differs, being short and broad.

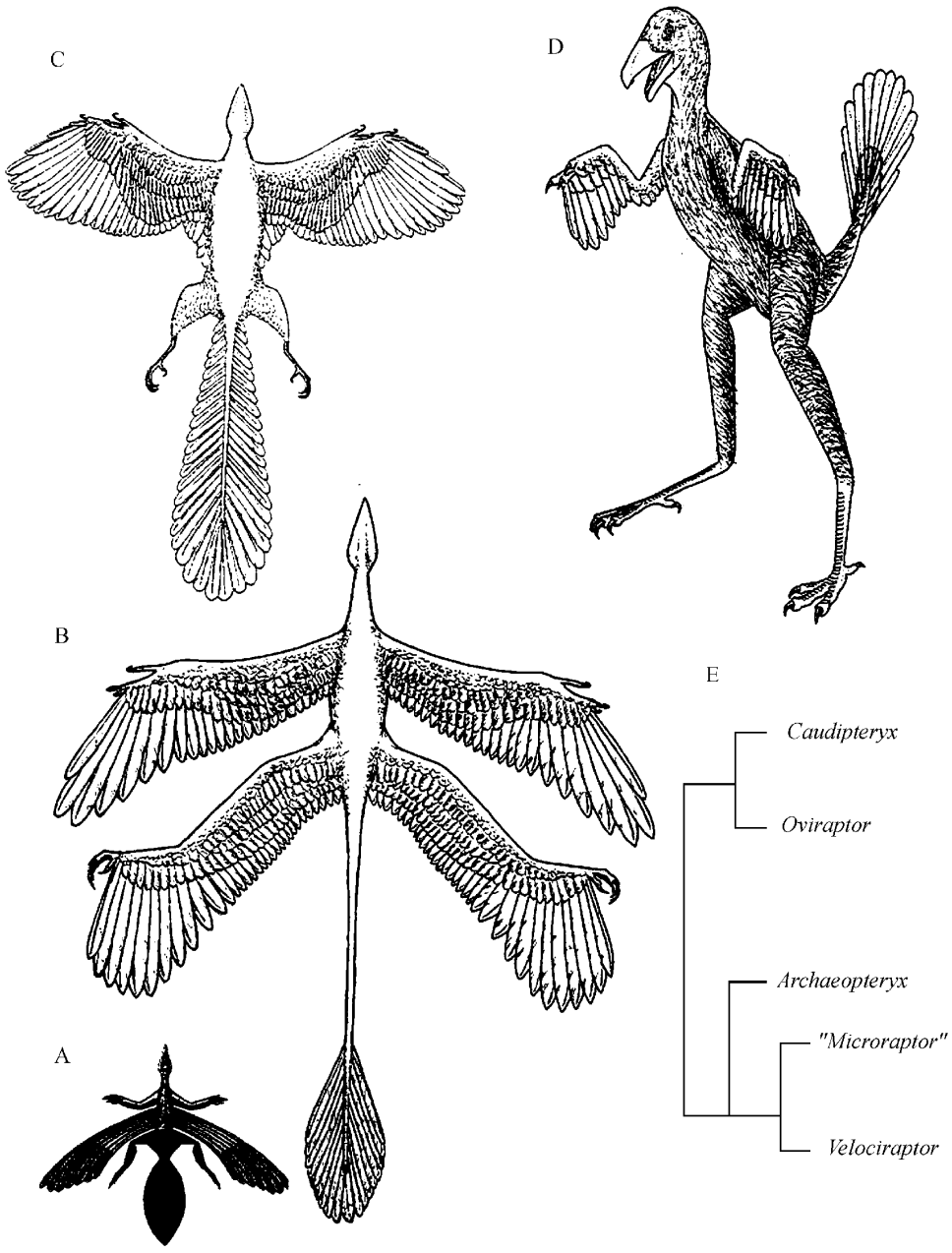


Fig. 3 Various potential stages in avian evolution

A. Thoracic wing stage (*Longisquama*): however, tail and hind legs unknown. B. Tetrapteryx stage (*Microraptor*). C. Loss of the rear wing (*Archaeopteryx*). D. Flightless runner (*Caudipteryx*). E. A simplified portion of the Hwang et al. (2002) cladogram showing that forms with primary flight feathers (*Caudipteryx*, *Archaeopteryx*, *Microraptor*) are spread across the cladogram, implying a volant common ancestor.

Long narrow scapulae are also reported for *Longisquama*, *Cosesaurus*, and *Megalancosaurus* (Sharov, 1971; Ellenberger, 1977; Geist and Feduccia, 2000). All of these genera are considered arboreal archosaurs by some authors. Ellenberger (1977) thought that he could detect impressions feathers on *Cosesaurus*. I examined that specimen and could not confirm the presence of feathers, although elongated scales may be present. It clearly has an antorbital fenestra and a furcula. The presence of a furcula seems to be characteristic of these small archosaurs, also oc-

curing in *Longisquama* and *Megalancosaurus*. *Megalancosaurus* was certainly arboreal, as both the front and hind feet show opposable toes; some consider it a glider (Geist and Feduccia, 2000).

But the most interesting of this small group of enigmatic animals is *Longisquama* from the Late Triassic of Central Asia. *Longisquama* is represented by a poorly preserved skeleton accompanied by remarkably well-preserved integumentary features described as "nonavian feathers" by Jones et al. (2000b). It has a subdivided antorbital fenestra, pointed snout,

elongate postorbital, teeth with expanded roots (?), elongated strap-like scapula, furcula, elongated penultimate phalanges, and feathers (Fig.4). The cranium is expanded and the neck attaches low on the skull. There is no mandibular fenestra although Sharov (1971) figured a small one. The teeth were described as acrodont (Sharov, 1971), but I think that they are thecodont with a bird-like waisted crown and expanded root (Martin and Stewart, 1999). The hands are very large for the size of the animal. The body is covered with elongated scales, including large flat ones extending from the trailing edge of the arm. The presence of a thoracic wing gives *Longisquama* a distinctly insect-like appearance which has probably discouraged comparison with birds (Figs.5, 6).

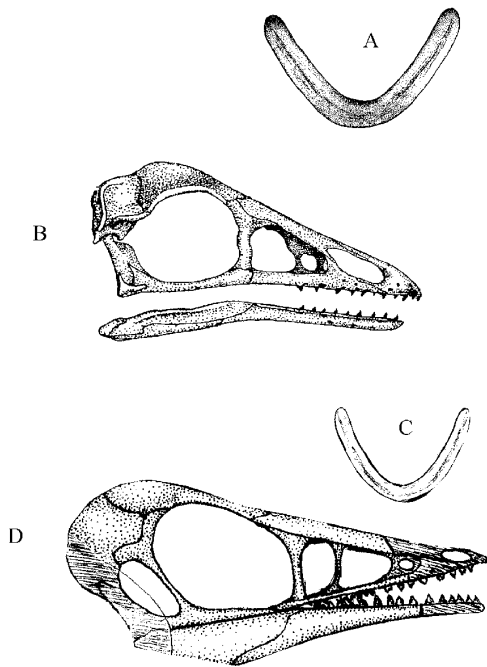


Fig.4 Furcula (A) and skull (B) of *Archaeopteryx* compared to the furcula (C) and skull (D) of *Longisquama*

Initially considered elongated scales by Sharov (hence the name *Longisquama*), and presented as a frill down the back, these structures have undergone drastic reinterpretation. First, Haubold and Buffetaut (1987) correctly recognized that they were arranged in a double row, forming a thoracic “wing” or feather “patagium”. Haubold and Buffetaut are probably wrong in the direction of folding, which actually seems to have been against the back where the “feathers” pivoted on the wide transverse processes of the dorsal vertebrae. But their interpretation of *Longisquama* as an arboreal glider is supported by subsequent investigation. Each vertebral segment has a pair of “feathers”, an arrangement not seen in modern birds but serially homologous with and fundamen-



Fig.5 Feathers of *Confuciusornis* and *Longisquama*

A: *Confuciusornis* elongated tail feather showing the lower portion in a persistent feather sheath and the distal portion with the feather unfolded. B: Composite *Longisquama* feather showing the calamus, folded barbs within the feather sheath and unfolded sheath with attached rachis and paired barbs. C: Close up showing feather sheath broken away exposing the folded barbs. D: Thoracic wing showing folding pattern.

tally identical to the arrangement of tail feathers in *Archaeopteryx*.

The feather-like structures on *Longisquama* cannot simply be elongated scales, as their tips are twice as wide as the basal portion. Scales are narrower, not wider, at the tip. Feathers have a rounded basal portion that is hollow and contains partitions (pulp caps), all of which can be seen on the structures in *Longisquama* (Jones et al., 2000b). It is almost certain that this region (like the calamus of a feather) was inserted into a follicle. Although we might expect flight feathers to have originated from scales along the edge of supporting structures, they are actually set in, on middle rather than outer fingers in birds and on the midline of the back in *Longisquama*. This type of arrangement would only make sense if they were derived from overlapping scales. Elongated scales often have a central supporting ridge. In the creation of an airfoil, sidebars (barbs) might be added to this ridge. *Longisquama*



Fig. 6 Life reconstructions of *Longisquama* showing both a resting and gliding pose

almost certainly flattened its body when gliding and may have expanded its ribs much as in the prolaceratian rib gliders. This motion of the ribs would be similar to that needed to fold and unfold the feathers of *Longisquama*, and rib musculature might have helped with that activity.

Scales are normally incapable of the kind of sideways motion needed to fold feathers. That the “feathers” of *Longisquama* were capable of this motion is demonstrated by a partially folded wing (Fig. 5). *Longisquama* is like birds too in having integumentary structures (Fig. 5), where crossbars (barbs) are folded on a rachidal ridge within a tube (the feather sheath). Upon leaving the sheath, the rachis, along with connected barb ridges, unfolds. In modern birds, the rachis and barbs emerge fused to

the sheath (Lucas and Stettenheim, 1972) but quickly separate; and as the feather matures, the sheath fragments and falls off. In a mature modern feather, the fabric of the vanes are maintained by an interlocking system of barbules and hooklets that is absent from *Longisquama* where the rachis and barbs remain fused to the unfolded sheath. Barbs towards the tip of the *Longisquama* “feather” occasionally cross over each other, demonstrating local separation of barbs from the sheath near the tip.

Evidence for a feather sheath is an important aspect of the *Longisquama* fossil. Near the base, its feather has a smooth featureless surface that flakes off to expose underlying folded barbs (Fig. 5). On occasion these also flake off, revealing a second featureless layer which indicates that the barbs were surrounded.

This is concrete proof that the feather-like structures in *Longisquama* developed within a tube. As feathers are the only integumentary structures known with this kind of development, it is reasonable to interpret these structures as feathers. The only real difference from a modern feather is the persistence of the feather sheath. Fortunately, this primitive condition was retained in the specialized elongated tail feathers found in the Early Cretaceous bird *Confuciusornis sanctis* (Fig. 5). We can thus speculate that *Longisquama* had real feathers of a primitive nature, the essential features of which are present to some degree in unquestioned birds.

Is *Longisquama* a proto-bird? I would not have thought so, but it may be more similar to the prototypic condition than we have supposed. The specialized scales on the trailing edge of the arm clearly have an airfoil structure but seem superfluous when compared to the thoracic wing. Martin (1983a) suggested that powered flight evolved for control of landing location. This may be the function of the arm airfoil, while most of the lift was provided by what amounts to a feather patagium. As the arm airfoil improved, it may have taken over the lift functions of the thoracic wing as the feather patagium shifted to the tail, as in *Archaeopteryx*, until finally lost altogether.

8 Conclusions

Gregory Paul's (1984) suggestion that some bird-like dinosaurs are actually secondarily terrestrial birds offers a compromise in a long and heated debate. He gives explanation to relationships that have been expressed in numerous cladograms placing various dinosaurs closer to modern birds than to *Archaeopteryx*. Implicit in such examples is a common ancestor similar to *Archaeopteryx*. Paul suggested (1984, 2001, 2002) that the common ancestor of maniraptorans and modern birds resembled *Archaeopteryx*, thereby solving the problem of the antiquity of *Archaeopteryx* with respect to the mostly Cretaceous maniraptoran radiation, and of numerous anatomical anomalies indicating that these special dinosaurs are too derived to be the ancestors of birds. He also provides an explanation for numerous similarities between maniraptorans and birds. In his model, flight is lost in several lineages and *Deinonychus* can be thought of as a sort of flightless bird! Most of the anatomical changes in this scenario can be duplicated in the evolution of flightless birds such as *Gastornis* from flying ancestors.

A recent study describing oviraptorosaurs as flightless birds (Maryanska et al., 2002), which is based on a detailed and sophisticated cladistic analysis, seems to epitomize the Paulian idea of avian origins. With the discovery of the new four-winged specimens

(e.g., *Cryptovolans*, *Microraptor*), I see little recourse but to accept Paul's general model. The thoracic wing of *Longisquama* and the tetrapteryx theory of Beebe both incorporate a sort of feather patagium analogous to the patagia of flying squirrels and rib-gliding reptiles, placing the origin of avian flight in the main line of gliding adaptation, much as described for it by Bock (1965, 1985).

The maniraptorans are not dinosaurs in this scheme, and their similarity to carnosaurs results from a combination of primitive character retention and parallelism. The monophyly of the Dinosauria has always been difficult to support. The peculiar reduction of the outer digits of the hand may be their most significant unifying feature, but it does not include birds and will not include maniraptorans if they are derived from birds.

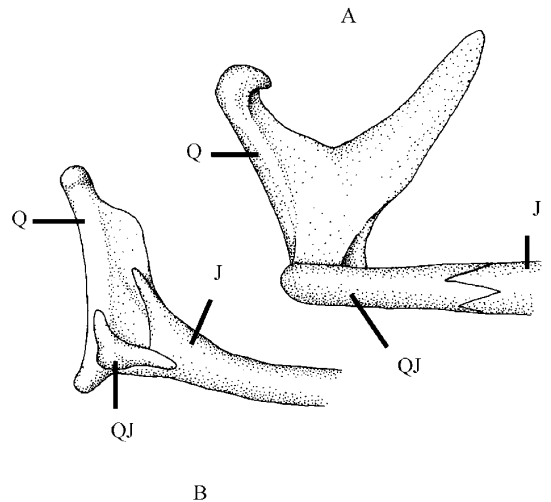


Fig. 7 Quadrate (Q), quadratojugal (QJ) and jugal (J) of the primitive ornithurine *Hesperornis* (A) compared to the sauriurine *Archaeopteryx* (B)

So we may postulate a new scheme for the early evolution of birds as follows:

1) Birds are not the youngest clade of archosaurs, but are one of the oldest, having split off before the development of a mandibular fenestra and socketed teeth.

2) The progenitors of birds were small lizard-like arboreal quadrupeds with elongated scapulae positioned on the back parallel to the vertebral column. They had furculae and elongated scales on their bodies. Bipedality evolved after flight, not before it.

3) Feathers originated for flight, and may have originally been expressed in a thoracic wing as presented in *Longisquama*. The wing on the arm originally developed to control landing and later to extend the flight path. Eventually it was able to take over flight function entirely in some lineages; but in others flight does not appear to have progressed beyond what

might be thought of as powered gliding.

4) Birds went through a tetrapteryx gliding stage; and bipedality probably evolved independently in various lineages.

5) There was a major radiation of birds in the Late Triassic or more probably the Early Jurassic. Birds divided into two fundamental lineages. One of these, the Ornithurae, gave rise to modern birds and modernized the flight apparatus at an early stage (Martin, 1983b, 1987, 1995); ornithurines with essentially modern postcranial skeletons occur in the same beds as *Microraptor* and *Confuciusornis*. Ornithurines all have rod-like quadratojugals (Fig.7).

6) The other half of the avian radiation, the Sauriurae, became extinct with the dinosaurs that they resembled. During the Jurassic, they split into several lineages including *Archaeopteryx* and the enantiornithines (Martin and Zhou, 1997). This clade is usually embedded within the maniraptorans (Fig.4), but maniraptorans may form a more exclusive clade united by the mandibular fenestra and fan-like tail feathers terminating on an elongated tail. Sauriurines all have reduced "L" shaped quadratojugals (Fig.7). Birds that may distribute with specific maniraptorans include *Confuciusornis* with *Caudipteryx* and the oviraptorosaurs. *Jeholornis* seems closer to *Microraptor* and the velociraptorines.

We thus have a surprising conclusion to our debate. The cladograms were correct in embedding some putative dinosaurs within birds, but were incorrect in their relationship to the dinosaur radiation as a whole. We can see this expressed in a recent cladogram (Hwang et al., 2002) relating *Caudipteryx*, *Archaeopteryx* and *Microraptor*. The common ancestor of such a grouping must have looked like a bird and lacked most salient dinosaurian features.

Acknowledgements I wish to thank Walter Bock and the International Ornithological Congress for the opportunity to discuss my views on avian origins, and Paul Sereno for providing an insightful and entertaining foil for my discussion. I have benefited from consultation with many workers but I am particularly grateful to Zhonghe Zhou and Lianhai Hou for sharing their new discoveries with me. The Institute for Vertebrate Palaeontology and Palaeoanthropology in Beijing has provided support and collaboration. Alan Feduccia, John Ruben, Paul Maderson, Dominique Homberger and Storrs Olsen have been especially helpful. John Chorn and Desui Miao read the manuscript and made many helpful suggestions.

References

Beebe CW, 1915. A tetrapteryx stage in the ancestry of birds. *Zoologica New York* 2 (2): 39–52.
Benton MJ, 1990. Origin and interrelationships of dinosaurs. In:

Weishampel DB, Dodson P, Osmolska H ed. *The Dinosauria*. Berkeley: Univ. California Press, 11–30.
Bergers P, Chiappe LM, 1999 The wings of *Archaeopteryx* as a primary thrust generator. *Nature* 399: 60–62.
Bock WJ, 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Syst. Zool.* 14: 272–287.
Bock WJ, 1985. The arboreal theory for the origin of birds. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P ed. *The Beginnings of Birds*. Eichstätt: Freunde des Jura-Museums, 199–207.
Chatterjee S, 1995. Protoavis, der Vogel aus der Trias. *Archaeopteryx*. Munchen 13: 15–31.
Colbert EH, 1989. The Triassic Dinosaur *Coelophysis*. Flagstaff, Arizona: Bulletin Series 57, Museum of Northern Arizona Press.
Currie PJ, 1987. Bird-like characteristics of the jaw and teeth of troodontid theropods (Dinosaurian, Saurischia). *J. Vert. Paleontol.* 7: 72–81.
Czerkas SJ, Zhang D, Li J, Li Y, 2002. Flying Dromaeosaurs. In: Czerkas SJ ed. *Feathered Dinosaurs and the Origin of Flight*. Blanding, UT: The Dinosaur Museum, 97–126.
Dial KP, 2003. Wing-assisted incline running and the evolution of flight. *Science* 299: 402–404.
Dingus L, Rowe T, 1998. *The Mistaken Extinction*. New York: WH Freeman.
Ellenberger P, 1977. Quelques Precisions Sur L' Anatomie Et La Place Systematique Tres Speciale De Cosesaurus aviceps. *Cuadernos Geologia Iberica*, Madrid 4: 169–188.
Feduccia A, 1980. *The Age of Birds*. Cambridge: Harvard Univ. Press.
Feduccia A, 1999. *The Origin and Evolution of Birds*, 2nd edn. New Haven, Conn.: Yale University Press.
Feduccia A, 2002. Birds are dinosaurs: simple answer to a complex problem. *Auk* 119 (4): 1 187–1 201.
Feduccia A, Nowicki J, 2002. The hand of birds revealed by early ostrich embryos. *Naturwissenschaften* 89: 391–393.
Geist NR, Feduccia A, 2000. Gravity-defying behaviors: identifying models for protoaves. *Amer. Zool.* 40: 664–675.
Gishlick AD, 2001. The function of the manus and forelimb of *Deinonychus antirrhopus* and its importance for the origin of avian flight. In: Gauthier J, Gall LF ed. *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in honor of John H. Ostrom*. New Haven, Conn.: Peabody Museum of Natural History, 301–318.
Haubold H, Buffetaut E, 1987. Une nouvelle interpretation de *Longisquama insignis*, reptile enigmatique du trias superior d' Asie centrale. *Compt. Rend. Acad. Sci. Paris Ser. 2A*, 305: 65–70.
Hecht MK, Tarsitano S, 1982. The paleobiology and phylogenetic position of *Archaeopteryx*. *Geobios Memoire Speciale* 6: 141–149.
Heilmann G, 1926. *The Origin of Birds*. London: Witherby Press, 210 p.
Homberger DG, 2002. The aerodynamically streamlined body shape of birds: implications for the evolution of birds, feathers, and avian flight. In: Zhou Z, Zhang F ed. *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*. Beijing: Science Press, 175–189.
Hopson JA, 2001. Ecomorphology of avian and nonavian theropod phalangeal proportions: implications for the arboreal versus terrestrial origin of bird flight. In: Gauthier J, Gall LF ed. *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in honor of John H. Ostrom*. New Haven, Conn.: Peabody Museum of Natural History, 211–235.
Huxley TH, 1870. Further evidence of the affinity between dinosaurian reptiles and birds. *Q. J. Geol. Soc.* London 26: 12–31.
Hwang SH, Norell MA, Qiang J, Kejin G, 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *Amer. Mus. Novit.* 3 381: 1–44.
Ji Q, Currie PJ, Norell MA, Ji S-A, 1998. Two feathered dinosaurs from northeastern China. *Nature* 393: 753–761.
Jones TD, Farlow JO, Ruben JA, Henderson DM, Hillenius WJ,

- 2000a. Cursoriality in bipedal archosaurs. *Nature* 406: 716–718.
- Jones TD, Ruben JA, Martin LD, Kurochkin EN, Feduccia A, Maderison PFA, Hillenius WJ, Geist NR, Alifanov V, 2000b. Non-avian feathers in a Late Triassic archosaur. *Science* 288: 2 202–2 205.
- Larsson HCE, Wagner GP, 2002. Pentadactyl ground state of the avian wing. *J. Exp. Zool.* 294: 146–151.
- Lingham-Soliar T, 1999. Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England. *Proc. R. Soc. London, Series B* 266: 2 367–2 373.
- Lockley M, Yang S, Matsukawa M, Fleming F, Lim S, 1992. The track record of Mesozoic birds: evidence and implications. *Phil. Trans. R. Soc. Lond. B*: 113–134.
- Lu J, Dong Z, Azuma Y, Barsbold R, Tomida Y, 2002. Oviraptorosaurs compared to birds. In: Zhou Z, Zhang F ed. *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*. Beijing: Science Press, 175–189.
- Lucas AS, Stettenheim PR, 1972. *Avian Anatomy: Integument*. U. S. Dept. Agriculture, Washington, DC.: Agriculture Handbook, 750 p.
- Marsh OC, 1880. *Odontornithes: A monograph on the extinct toothed birds of North America*. Washington, DC.: Department of the Army, 18: 1–201.
- Martin LD, 1983a. The origin of birds and of flight. In: Johnston RF ed. *Current Ornithol.* 1: 105–129.
- Martin LD, 1983b. The origin and early radiation of birds. In: Brush AH, Clark GA ed. *Perspectives in Ornithology*. Cambridge, Mass.: Cambridge University Press, 291–338.
- Martin LD, 1987. The beginning of the modern avian radiation. In: Mourer-Chauviré C ed. *L' Evolution des Oiseaux d' apres le Temoignage des Fossils*. Lyon: Doc. Lab. Geol. Lyon, Universite Claude-Bernard 99: 9–19.
- Martin LD, 1991. Mesozoic birds and the origins of birds. In: Schultz HP, Trub L ed. *Origins of the Higher Groups of Tetrapods, Controversy and Consensus*. Ithaca, NY: Cornell University Press, 485–540.
- Martin LD, 1994. Cenozoic climate history from a biological perspective. *TER-QUA Symposium Series, Institute for Tertiary-Quaternary Studies* 2: 39–56.
- Martin LD, 1995. The enantiornithines: terrestrial birds of the Mesozoic. In: Peters DS ed. *Acta Palaeornithologica, Proceedings of the 3rd Symposium of the Society of Avian Palaeontology and Evolution*. *Courier Forschungsinstitut Senckenberg* 181: 23–36.
- Martin LD, Stewart JD, 1999. Implantation and Replacement of Bird Teeth. In: Olson S ed. *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution*. Washington, DC.: Smithsonian Institution Press, 295–300.
- Martin LD, Stewart JD, Whetstone KN, 1980. The origin of birds: structure of the tarsus and teeth. *Auk* 97: 86–93.
- Martin LD, Zhou Z, 1997. *Archaeopteryx*-like skull in enantiornithine bird. *Nature* 389: 556.
- Maryńska T, Osmólska H, Wolsan M, 2002. Avian status for Oviraptorosauria. *Acta Palaeontol. Pol.* 47 (1): 97–116.
- Naples VL, Martin LD, Simmons J, 2002. The pelvis in early birds and dinosaurs. In: Zhou Z, Zhang F ed. *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*, Beijing. Beijing: Science Press, 175–189.
- Norell, M., Ji Q, Gao K, Yuan C, Zhao Y, Wang L, 2002. 'Modern' feathers on a non-avian dinosaur. *Nature* 416: 36–37.
- Ostrom JH, 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.* 30: 1–165.
- Ostrom JH, 1973. The ancestry of birds. *Nature* 24: 136.
- Ostrom JH, 1976. *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.* 8: 91–92.
- Ostrom JH, 1979. Bird flight: how did it begin? *American Scientist* 67: 46–56.
- Ostrom JH, 1985. The meaning of *Archaeopteryx*. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P ed. *The Beginnings of Birds*. Eichstätt: Freunde des Jura-Museums, 161–176.
- Padian K, 1984. The origins of pterosaurs. In: Reif WE, Westphal F ed. *Third Symposium on Mesozoic Terrestrial Ecosystems*. Tübingen: ATTEMPTO Verlag, 163–168.
- Padian K, 1985. The origins and aerodynamics of flight in extinct vertebrates. *Palaeontology* 28: 413–433.
- Padian K, Chiappe L, 1998a. The origin of birds and their flight. *Scientific American* 278: 38–47.
- Padian K, Chiappe LM, 1998b. The origin and early evolution of birds. *Biol. Rev.* 73: 1–42.
- Paul GS, 1984. The archosaurs, a phylogenetic study. In: Reif WE, Westphal F ed. *Third Symposium on Mesozoic Terrestrial Ecosystems*. Tübingen: ATTEMPTO Verlag, 175–180.
- Paul GS, 2001. Increasing evidence for an arboreal origin of dinosaur-avian flight, and for losses of flight in post-Ürvogel dinosaurs. *J. Vert. Paleont.* 12 (Suppl.) 3: 88A.
- Paul GS, 2002. *Dinosaurs of the Air*. Baltimore, Maryland: Johns Hopkins University Press.
- Rayner JMV, 1985. Mechanical and ecological constraints on flight evolution. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P ed. *The Beginnings of Birds*. Eichstätt: Freunde des Jura-Museums, 279–288.
- Reisz RR, 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Univ. Kansas: Museum of Natural History, No. 7*.
- Sereno PC, 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology Memoir* 2. *J. Vertebr. Paleontol.* 11 (Suppl.) to pt. 4.
- Sereno PC, 1999. The evolution of dinosaurs. *Science* 284: 2 137–2 147.
- Sharov AG, 1971. New flying reptiles from the Mesozoic deposits of Kazakhstan and Kirgizia. *Trudy Paleontol. Institut Akad. Nauk S. S. R., Moscow* 130: 104–113.
- Tarsitano SF, Hecht MK, 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zool. J. Linn. Soc. London* 69: 149–182.
- Wang X, Zhou Z, 2002. A pterodactylid pterosaur from the Jiufotang Formation of Liaoning, China. *Chin. Sci. Bull.* 47: 1 521–1 527.
- Wellnhofer P, 1974. Das funfte Skelettexemplar von *Archaeopteryx*. *Palaeontographica (A)* 147: 169–216.
- Williston SW, 1879. Are birds derived from dinosaurs? *Kansas City Rev. Sci.* 3: 457–460.
- Witmer LM, 1991. Perspectives on avian origins. In: Schultz HP, Trub L ed. *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Ithaca, NY: Cornell University Press, 427–466.
- Xu X, Zhou Z, Prum R, 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* 410: 200–204.
- Xu X, Zhou Z, Wang X, Kuang X, Zhang F, Du X, 2003. Four-winged dinosaurs from China. *Nature* 421: 335–340.
- Zhou Z, Farlow JO, 2001. Flight capability and habits of *Confuciusornis*. In: Gauthier J, Gall LF ed. *New perspectives on the origin and early evolution of birds: Proceedings of the International Symposium in honor of John H. Ostrom*. New Haven, CT: Peabody Mus. Nat. Hist. 237–254.