

# Origins of avian flight – a new perspective

Larry D. Martin

Department of Ecology and Evolutionary Biology; Museum of Natural History  
and Biodiversity Research Center, University of Kansas, Lawrence, KS 66045, USA  
e-mail: ldmartin@ku.edu

**ABSTRACT** - The discovery of a primitive bird-like dromaeosaur (*Microraptor*) with four functional wings vindicates Beebe's suggestion that birds went through a tetrapteryx stage in the origin of flight. Flight originated from an arboreal gliding ancestor and *Longisquama* may be more central to understanding how this came about than previously supposed.

**Keywords:** *Dromaeosaur, Microraptor, Longisquama, birds, flight, Upper Triassic, Lower Cretaceous*

**Les origines du vol avien – Perspectives nouvelles** - La découverte d'un dromaeosaure semblable à un oiseau primitif (*Microraptor*) avec quatre ailes fonctionnelles justifie la suggestion de Beebe selon laquelle les oiseaux sont passés par un stade tetrapteryx dans l'origine du vol. Le vol est apparu chez un ancêtre arboricole planeur, et *Longisquama* est peut être plus important qu'on l'a supposé pour comprendre les modalités de cette transition.

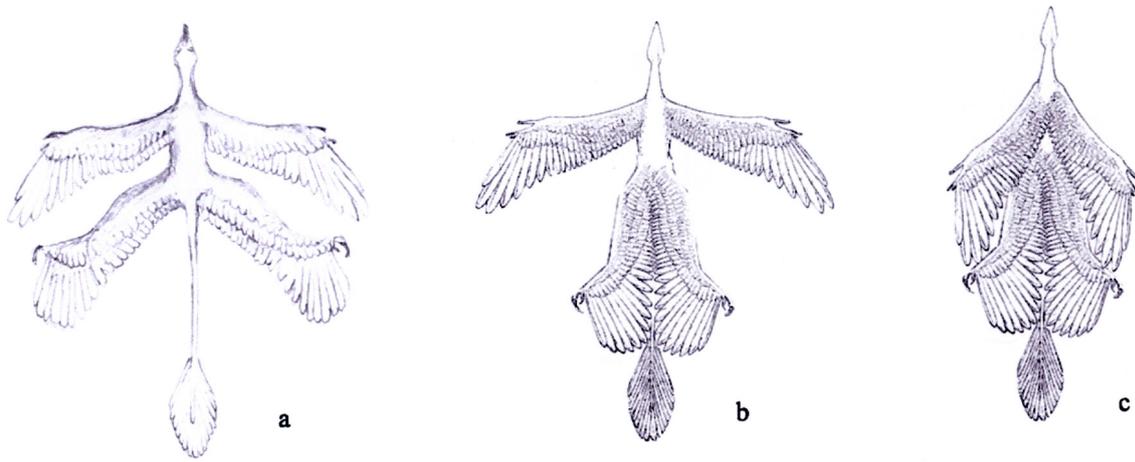
## INTRODUCTION

Much of the argument over flight origins revolves around *Archaeopteryx*, the first bird to be recognized from the Mesozoic and still the oldest known bird. *Archaeopteryx* displays a remarkable combination of avian and reptilian characters and has become the archetype of a “missing link.” It was discovered in 1861, only two years after Darwin's *Origin of Species*, but did not immediately become a major player in speculation about avian origins. In 1864, Huxley became the chief proponent of the idea that the then newly discovered bipedal dinosaurs were good ancestors for bipedal birds and this was the dominant theory until the beginning of the 20<sup>th</sup> century (Witmer, 1991). The discovery of older and more primitive bipedal archosaurs provided an alternative ancestry lacking specializations that seemed to bar dinosaurs from direct avian ancestry. Heilmann's (1926) book *The Origin of Birds* solidified the resultant position that birds are only related to dinosaurs in sharing a basal archosaurian ancestor (Martin, 2004). The dinosaur argument lay dormant for over sixty years until revived by Ostrom (1973) along with the terrestrial origin of avian flight. Ostrom did not think that all dinosaurs stood equally close to birds, and demonstrated that some advanced “theropods” were clearly more birdlike than are other dinosaurs. His observations are supported by many subsequent studies extending comparisons to late Cretaceous “maniraptorians”, like *Bambiraptor* (Burnham, 2004), which are significantly more birdlike than

the stratigraphically older *Deinonychus* studied by Ostrom (1969). In this sense the fossil record did not provide an orderly progression from terrestrial “maniraptorians” to flying birds. In fact, *Archaeopteryx*, a very typical bird in most respects, is significantly older than any credible evidence for dromaeosaurs, the dinosaurs thought to be closest to birds.

Functionally there are additional problems. All of the then known dromaeosaurs were fast running terrestrial predators with shortened arms and the scapula arranged diagonally across the chest. Modern birds develop these traits when becoming flightless, but it was hard to see how they could easily be modified in the other direction to form a flight capable wing, and indeed no flightless bird showing these modifications is known to have ever regained flight.

Dromaeosaurs are usually slender and deep bodied—decidedly unbirdlike proportions. Some had an enlarged claw on the second digit of the foot presumably as a weapon for predation, and shared with ramphorhynchoid pterosaurs a system of anteriorly projecting rods extending from the prezygopophyses and chevrons of the tail. In these respects, they are specialized as compared to *Archaeopteryx* and other birds. We can easily understand how they might be derived from primitive flying birds, as similar changes to the shoulder girdle and forelimbs also occurred in flightless birds (*Gastornis*; *Struthio*) derived from flying ancestors. It is harder to see how dromaeosaurs could resemble an avian ancestor. In particular, their highly derived body proportions would have prevented them from being very successful



**Figure 1** - Reconstruction of *Microraptor* based on Xu *et al.*, 2003 and examination of several additional specimens: a) wings out as restored in Xu *et al.*, 2003; b) hind wing posterior against the tail so that they combine to make an enlarged airfoil as in the *Archaeopteryx* tail (fig. 2c); c) front and hind wings oriented posteriorly to form a broad gliding surface.

climbers.

The best evidence for transitional forms between “maniraptorians” and more typical birds comes from the Jehol fauna of Liaoning, China (120,000,000 years old or a little older). These deposits show a diversity of animals living on or near the shorelines of Early Cretaceous lakes (Zhou *et al.*, 2003). Judging from the fossil plants and insects, the surrounding countryside was forested. The deposits preserve a combination of small terrestrial, arboreal, flying and aquatic organisms.

## ORIGIN OF FLIGHT

The origin of avian flight is one of the most interesting problems in biology. Pterosaurs and bats incorporate the arms and legs into a continuous fold of skin (patagium) and can be compared directly with living examples of gliding mammals (Bock, 1985). In birds, the legs and the wings are decoupled with little evidence showing that a full patagium was ever present, although there are distinct patagial surfaces on the wings and some birds have limited powers of flight with very little feather development (megapode chicks). Modern birds are accomplished bipeds, and differ in this respect from bats and pterosaurs although some bats show brief bursts of bipedal locomotion on the ground and we would expect pterosaurs to do the same if only to free the wings for take off. If all other examples of flight in terrestrial vertebrates are rooted in arboreal quadrupedal forms, should bipedality be an expected precursor to avian flight? It wouldn't seem likely, if flight originated in an arboreal glider as is nearly certain with bats and pterosaurs. Such animals place aerodynamic lift above the body mass and distribute it down the length of the body to ensure stability. It is hard to see how the legs could avoid being involved in the early gliding phases. The hypothesis of a dinosaurian origin of

birds is usually framed to avoid this problem. Bipedality predates flight and birds were derived from small, fast running predatory dinosaurs with sophisticated powers of hand manipulation (Padian, 1985; Gishlick, 2001). The movements involved with prey capture were modified to provide a power supplement to the legs in running 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 of flight assume that feathers originated for a nonflight function (insulation, prey capture) and were later recruited for aerial propulsion. The earliest examples might lack any traces of features giving airfoil capability. Fibrous structures lacking diagnostic feather features have been described from the Early Cretaceous Chinese deposits as feather progenitors and were found in a variety of dinosaurs and other archosaurs (pterosaurs) (Ji *et al.*, 1998; Czerkas and Ji, 2002; Mayr *et al.*, 2002; Xu *et al.*, 2001; Wang *et al.* 2002). This broad phylogenetic distribution implies that feathers evolved early in archosaur evolution and were replaced later with scales in a variety of lineages including all the dinosaurs known to be covered with scales (carnosaurs, compsognathids, sauro-pods, hadrosaurs, ceratopsians, ornithomimosaurs (Martin and Czerkas, 2000)).

These putative fiber-like feathers are arranged in a variety of patterns, but few resemble the distribution of feathers in modern birds or *Archaeopteryx*, and they often seem to form the outline of crests or flaps. Individually they appear to be solid, and without a continuous branching pattern. They often lie closely parallel to each other (Xu *et al.*, 2001). Feathers are hollow, widely spaced from each other and usually arranged in distinct “tracts”, but not long “crests”. They are normally composed of multiple branches (barbs) converging towards a central rachis. None of these

features are clearly demonstrated in the so-called protofeathers and their anatomical arrangement and distribution is often identical with muscles and ligaments (Lingham-Soliar, 1999; 2003a, b). An interpretation of some of these structures as collagen and/or muscle fibers is consistent with their anatomical distribution and better fits their tendency to divide into progressively smaller bundles of fibers. It is also likely that scales and taphonomic accidents have in some additional cases, been misinterpreted as protofeathers or even feathers. It would seem, that even on an unquestioned fossil bird, anatomical characters should be visible before we accept an identification of feathers for a fibrous haze surrounding the skeleton.

Unquestioned feathers eventually made the cover of *Nature* (Xu *et al.*, 2003) on a supposed dinosaur, *Caudipteryx*. Others concluded (Martin and Czerkas, 2001) that *Caudipteryx* was a flightless bird on the basis of an avian wing with primary flight feathers coming off the middle finger of the hand (fig. 1). Because large feathers have to have a deep follicle, they are inset from the body margin so that the main flight feathers in a bird cross the middle finger. The palm of the hand extends distally to include the third and fourth fingers, giving the avian hand its characteristic shape. A mold of this sort of hand is preserved in the Berlin *Archaeopteryx* (Martin and Lim, 2005). We can expect this form of hand in any animal with primary flight feathers and it must indicate an ancestor that could fly or glide. *Caudipteryx* was flightless but surely secondarily so, as was concluded by Jones *et al.* (2000a). Sereno (1999) arranged it cladistically as the primitive sister taxon of the oviraptors, an interesting conclusion when we consider that many of the modern revisions of the oviraptors have independently concluded that they were birds (Elzanowski, 1999; Lü *et al.*, 2002). Perhaps the most impressive study to reach that conclusion is a highly sophisticated cladistic analysis by Maryanska *et al.* (2002).

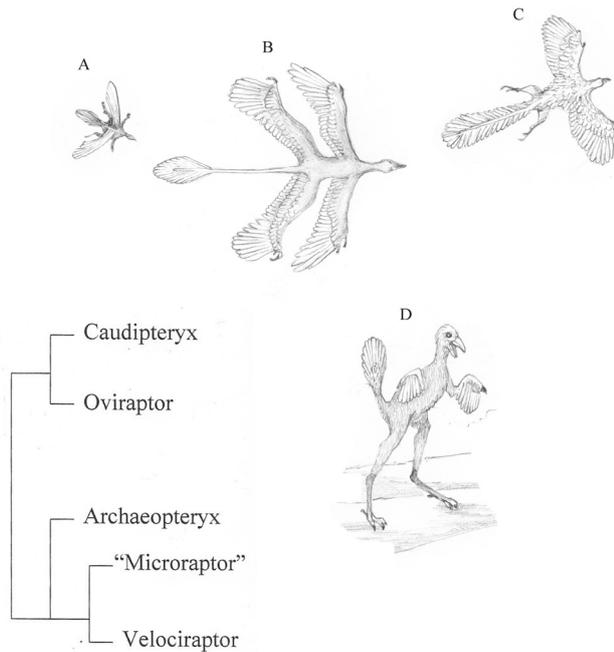
Norell *et al.* (2002) reported a dromaeosaur with genuine feathers including flight feathers on the leg. This specimen is described in more detail along with a second specimen by Czerkas *et al.* (2002) as *Cryptovolans pauli*. Neither set of authors grasped that they were viewing an animal with two sets of wings, but this was demonstrated (Xu *et al.*, 2003) with a dramatic cover article in *Nature*. I have examined the original material and some eleven more specimens. There can be no doubt that there is an anterior wing with primary flight feathers coming off the middle finger of the hand. This is accompanied by a completely birdlike, L-shaped scapulacoracoid. The wrist has three and probably all four avian bones arranged in the avian manner. The pubis is opisthopic and the acetabulum is partially closed and lacks the characteristic dorsal shelf. The femur is compressed proximally so that it can rotate horizontally to the pelvis and this is the position that it has in many of the known specimens. The hallux is reflexed and the toes are tiny when compared to the tarsometatarsus. In almost all ways it corresponds more closely to the avian skeleton

than do other dromaeosaurs. Its status as a dromaeosaur is strongly supported by an enlarged second digit claw on the foot and forward projecting elongations of the prezygopophyses and chevrons on the caudal vertebrae. Cladistically it occupies the same plesiomorphic sister-group relationship to the other dromaeosaurs that *Caudipteryx* has to the oviraptors (Hwang *et al.*, 2002). The posterior wing is similar in size and morphology to the anterior one with the longest feathers coming off the foot.

Xu *et al.* (2003) assigned their material to *Microaptor* Xu, Zhou, and Wang, 2000a. The combination of tiny toes, flight feathers on the tarsometatarsus and nature of the femur and pelvis make it almost impossible for *Microaptor* to have walked efficiently, let alone run. It must have been completely arboreal. The hind legs lack a suitable musculature to provide a wing beat and the rear wing provided passive lift, much like the expanded tail found in *Archaeopteryx*. The front wing probably did provide a wing beat, but *Microaptor* was more of a powered glider than true flyer and the recent reconstruction of it by Paul (2003) as a “biplane” seems improbable. How the hind limb wings were positioned is hard to access directly. The short, upwardly elevated femoral neck coupled with the absence of a supracetabular shelf allows the femur to be brought horizontal to the body and it may have been nearly perpendicular to the acetabulum as originally restored (fig. 1a). If the legs were brought posteriorly, they would have fitted between the body and the extended flap of feathers on the distal tail (fig. 1b), producing something like the broad tail found in *Archaeopteryx* (fig. 2). If the anterior wings were used for limited powered flight, this would be the most likely positioning. Such flight might have been mostly for orientation just before landing, if the front wings are also folded back, they form an extensive airfoil similar to the patagium in dermopterans (fig. 1c). It is hard to see how this four-wing arrangement could develop from an animal with the vertical hind leg typical of dinosaurs, and we must seriously consider that the protobird was an arboreal quadruped with a sprawling posture. It would seem that the tree-down gliding origin of flight has triumphed. The enlarged foot claw, rather than being originally a predatory structure probably began as a climbing spike that also permitted the grasping of tree limbs.

## BEEBE'S REMARKABLE IDEA

The same Evans who first recognized the teeth of *Archaeopteryx* suggested (Evans, 1881) that there were flight feathers on the thigh of *Archaeopteryx*, and that *Archaeopteryx* used its legs as well as arms for flight. Later C. William Beebe (1915) proposed that birds had gone through a tetrapteryx (four-winged) gliding stage in the origin of flight. However, elongated flight feathers on the hind wing would interfere with bipedal locomotion and the leg would have to have been able to extend nearly horizontally from the socket. Acceptance of these features implies that flight began in a



**Figure 2** – Relationship of pertinent taxa based on Hwang, *et al.*, 2002. *Microraptor* (b), *Archaeopteryx* (c) and *Caudipteryx* (d) all have avian wings, suggesting that the common ancestor of all these clades had an avian wing and was a bird. Possible stages in the origin of avian flight might include a quadrupedal, arboreal glider similar to the Triassic reptile *Longisquama* (a), leading to a tetrapteryx stage similar to *Microraptor* (b), and from there to more accomplished flyers like *Archaeopteryx* (c) or to flightless terrestrial forms like *Caudipteryx* (d).

quadrupedal animal with a sprawling posture. Heilmann thought that bipedality was an essential avian feature and a tetrapteryx stage almost unimaginable (Heilmann, 1926: 199). He also rejected the main line of evidence presented by Beebe, a developmental comparison between developing feathers on the femoral feather tract and those of the wing in the young pigeon (squab). Heilmann (1926) pointed out that this comparison was no more impressive than that with the spinal feather tract (a point that may be more interesting than he had supposed). Like Evans, Beebe (1915) suggested that the posterior leg feathers of *Archaeopteryx* were elongated, and recent studies seem to confirm that observation.

The discovery of the hind wing stimulated a search for potential flight feathers on the legs of other Mesozoic birds. Elongated leg feathers are now reported (Christiansen and Bonde, 2004) for *Archaeopteryx* (as suggested by Evans) and other Mesozoic birds (Zhang and Zhou, 2004). It would seem that Beebe (1915) may have been right after all, and birds went through a tetrapteryx-gliding phase.

### GREGORY PAUL'S HERETICAL IDEA

Since Ostrom's work on *Deinonychus*, dromaeosaurs are consistently put forth as the dinosaurian group closest to birds. As anatomical objections in the hand, ankle and teeth were raised against a dinosaurian origin of birds (Feduccia, 1980; Martin *et al.*, 1980) it was pointed out that the avian condition might still be found within the dromaeosaurs. Alone among the dinosaurs, dromaeosaurs and oviraptorosaurs show most of the complicated cranial pneumaticity found in birds. Alone among the dinosaurs they have been argued to have teeth with the characteristic waist and closed replacement pit (Currie and Zhao, 1993). Ostrom (1973) was most impressed by the shared semilunate carpal, but his recon-

struction of the *Deinonychus* wrist differed sharply from that of birds. It was composed of two bones arranged in a single row while birds were more primitive with four bones arranged in the original two rows. Ostrom's semilunate carpal was identified as a proximal carpal (radiale) in *Deinonychus*, as he thought that the distal row had been lost. Birds retain both rows and the semilunate bone is actually in the distal row. If Ostrom's observations were taken at face value, and they were for nearly two decades, no homology could exist between the dromaeosaur and avian semilunate carpals. Later work (Gishlick, 2001) shows that the two bones are arranged in proximal and distal rows with the semilunate bone in the distal row, making homology possible between it and the avian semilunate carpal. Two of the avian wrist bones are lost and the dromaeosaur wrist must be considered more derived rather than less when compared with typical birds. The presence of a furcula in dromaeosaurs is another feature bringing them close to birds (Norell and Makovicky, 1997). Finally a reflexed pubis was demonstrated in dromaeosaurs, although some workers had restored the pubis in *Archaeopteryx* as vertical, bringing that genus more in line with how the pelvis in these same dromaeosaurs had been incorrectly restored (Norell and Makovicky, 1997). The reduction of the calcaneum seen in many dromaeosaurs must also be viewed as more derived than in modern birds where it still has primitive proportions.

Gregory Paul (1984; 2001; 2002) decided to accept the known stratigraphic distribution of birds and dromaeosaurs and suggested that the Cretaceous dromaeosaurs were the descendents of older "archaeopterygiformes". The idea not only solved the temporal paradox but also brought the many derived anatomical structures found in dromaeosaurs as compared to even modern birds into line with stratigraphy. The problem with Paul's scheme is that it converts the bird-

like dromaeosaurs to birds advanced beyond *Archaeopteryx*. As such, they do not contribute more to understanding avian origins or flight than could that genus. Although Paul was a strong supporter of the dinosaurian origin of birds, most dinosaur specialists rejected his idea, and students of fossil birds who accepted that dromaeosaurs had been correctly embedded within the Dinosauria, also ignored Paul's hypothesis. Several cladograms placing various dinosaurs between *Archaeopteryx* and modern birds were discussed at the 1996 SAPE meeting in Washington D.C., and the Paulian idea, along with Olshevsky's (1994) version, was presented as a "nonstandard hypothesis" in a roundtable discussion where I made the following comment (Witmer, 1999, p. 331-332): "One of the things about this conference that I've found extremely interesting is how many of the papers that were presented today could be taken to support Gregory Paul's so-called 'nonstandard hypothesis'. I would say he's getting so much support that we can view it as a school—the 'Paulian School of Bird Origins.' The only thing I see that it lacks for a confirmation would be the discovery of a Cretaceous dinosaur with enlarged feathers...and I would really think that we would have very strong support for Paul's viewpoint."

We now come to the Paulian question. Are these advanced "dromaeosaurs" birds or dinosaurs? How do we define either birds or dinosaurs? If we seek morphological criteria, we probably can't do any better than with the hand. Dinosaurs are united by a nearly unique synapomorphy where the outer two fingers are reduced while birds retain the more normal reduction pattern (Feduccia and Nowicki, 2002) reducing digits 1 and 5. Unfortunately we cannot observe the reduction pattern directly in known dromaeosaurs, but we can look at the various cladograms and in particular Hwang *et al.* (2002). If we examine the portion including oviraptors, *Archaeopteryx*, and dromaeosaurs (fig.2), we see *Caudipteryx* as the primitive sister group to the other oviraptors. That clade is the sister group to *Archaeopteryx* plus the dromaeosaurs, and *Microraptor* is the primitive sister group to the rest of the dromaeosaurs. *Caudipteryx*, *Archaeopteryx* and *Microraptor* can all be shown to have primary feathers and an avian wing, so how can we doubt that their common ancestor also had this structure? Primary feathers and an avian wing are a good structural definition for birds and we may consider this common ancestor a bird.

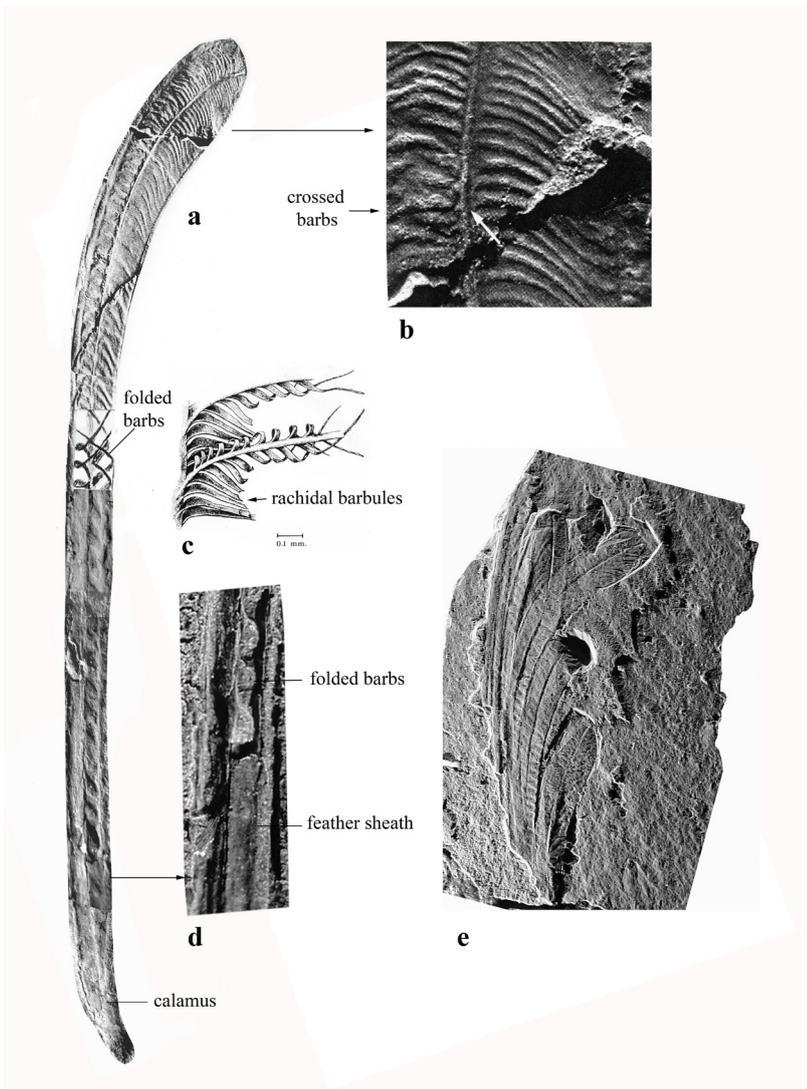
It is also clear from the cladogram that the common ancestor of the various bird lineages would have looked more like *Microraptor* than like *Deinonychus* and that many polarities based on a bipedal running ancestor are incorrectly drawn. The character of the teeth, the position of the glenoid for the arm and the lack of a supra-acetabular shelf on the pelvis in *Microraptor* do not support a dinosaurian relationship. The difference in tooth implantation and replacement suggests a very early common ancestor for birds and dinosaurs, as does the difference in digit reduction. Rather than looking at the top of the archosaur radiation, we should look at its base. Here we find several small arboreal animals with

elongate scapulae running parallel to the spine as in birds. They also have furculae, and subdivided antorbital fenestrae (Martin, 2004).

## SHAROV'S LITTLE DRAGON

While searching for fossil insects in the Late Triassic of Kyrgyzstan in Central Asia, Sharov (1971) discovered *Longisquama*, a small lizard-like animal with remarkable integumentary structures on its back. He initially described them as elongated scales (hence the name *Longisquama*) and restored them as a frill. Haubold and Buffetaut (1987) correctly recognized that they were in a double row, forming a thoracic, gliding wing. Sharov (1971) noticed that they had many feather-like features and when restudied (Jones *et al.*, 2000b; 2001) they were described as "nonavian" feathers.

The nature of their preservation is so remarkable that it deserves some comment. The surrounding matrix is a claystone that preserves fine detail. The feathers include the impression of a surrounding tube (feather sheath) that is unfolded near the tip so that it was open on that end and the clay filtered into the tube, surrounding an internal structure that is represented by an internal cast (steinkern). According to Sharov (1971), the internal structure was composed of folded branches that unfold to form paired branches near the tip and further examination confirms his interpretation. This provides proof of an integumentary structure enclosed by a tube that was open on one end. Feathers are the only integument fitting this description and this would be enough by itself to argue that these structures are feathers. Sharov and later observers were able to observe this relationship directly from portions where the smooth outer layer has broken off (fig. 3d) revealing the folded structures within. In some places, these internal structures have also been removed to show a smooth underlayer identical to that on the top, demonstrating that the folded structures were enclosed. Towards the tip the structure unfolds revealing a central axis (rachis) with paired branches (barbs). Unlike modern birds, the feather sheath does not break up and fall off as the feather unfolds but remains to make the airfoil and the rachis and barbs adhere to it. In modern birds they also originally adhere to the feather sheath, but become separated as the feather grows (Lucas and Stettenheim, 1972). In *Longisquama* this only occurs near the tip where barbs can be seen crossing each other showing that they are becoming free at that point (fig. 3b). Because the feather sheath maintains the structure of the feather, barbules and hooklets are not needed and are not present. In a modern feather the barbs are like small rachi and the barbules more like the barbs of *Longisquama* (fig. 3c) in being more flattened. When folded the barbs are nearly vertical and this is reflected in a sharp down turn of the barbs where they join the shaft in modern birds and in *Longisquama*. A persistent feather sheath is not found in modern birds and gives the feathers in *Longisquama* a scale-like appearance. Because the sheath is retained some confusion has developed over the nature of these peculiar feathers (Reiz and Sues,



**Figure 3** - Feather structure in *Longisquama*: a) composite figure with the proximal two thirds coming from photographs of the holotype specimen, and the distal one third from photographs of one of the isolated feathers. The calamus is clearly demarcated and the bulk of the vane is folded within the sheath. The folded barbs are delineated as they press against the inside of the sheath. In one region the sheath has broken away (d) revealing the internal cavity and folded barbs. Towards the tip the sheath unfolds revealing the rachis and paired barbs. At that point the feather doubles in width. A drawing of folded barbules in a modern bird is inserted into the composite photograph to show the hypothesized arrangement of barbs within the sheath. A drawing (c) of rachis, barbs and barbules modified from Lucas and Stettenheim (1972, fig. 180) shows similarity of barbs in *Longisquama* (b) to rachidal barbules. The white arrow indicates where the barbs in b swing proximally to join the rachis, as do the rachidal barbules in c. The black arrow (b) indicates barbs that have become entangled so that they cross each other. Figure 3e is the articulated *Longisquama* wing showing typical avian folding of the feathers over each other.

2000) where wrinkling of the sheath has been used to deny their feather-like nature. However even this is not unique as *Confuciusornis* and various enantiornithines have a pair of elongated tail feathers with a persistent feather sheath only unfolded near the tip. These particular feathers are paired structures coming off a caudal vertebra and are thus serially homologous to the feathers coming off the back of *Longisquama* as are the tail feathers of *Archaeopteryx*.

One of the clearest lines of evidence that the structures on *Longisquama*'s back are not scales can be found in their proportions (fig. 3a). They are constricted proximally where they form a hollow tube and it seems almost certain that this region was inserted into a deep follicle that extended across the top of the ribs to the neural spine of a single vertebra. The transverse processes are expanded to match the shape of the feather tip. Most of the following shaft is almost exactly half the width of the distal portion. Because of the way they grow, it is essentially impossible for a scale to be significantly wider distally than proximally as is characteristic of feathers. Because of their extreme length, feathers

need to be able to pivot sideways so that they can be folded. Scales cannot fold sideways because of their broad flat base and the evolution of a pivot point would be necessary before feathers could reach the extreme sizes needed for effective flight. Birds seem to have accomplished this by folding a flat scale into a tube and allowing it to unfold distally. Initially the part of the tube above the follicle (feather sheath) was an aerodynamic part of the feather as it is in *Longisquama*. The rachis and barbs began as ridges applied to the feather sheath to help it maintain its shape. The follicle and the muscle net used to move the feathers must have evolved in step with this scenario (Homerger, 2002), but another factor may have helped *Longisquama*. Small vertebrates commonly flattened their bodies when falling to slow their descent, and in some the ribs are hinged and elongated to enhance this effect. In rib gliders the elongated ribs folded posteriorly when not used for gliding and are brought forwards and upwards when needed. This movement parallels and probably assisted the wing folding/unfolding pattern in *Longisquama*. The ribcage would thereby provide extra support for the feathers when

they were in use. The fleshy tail of *Archaeopteryx* shows that enough room existed for the follicle, as it had a diameter close to that of the body of *Longisquama* and similarly sized feathers attached in about the same way.

Evidence for an avian type of sideways folding of individual feathers so that they overlap can be seen in the articulated wing (fig. 3e). In order for this to happen there must be a narrow pivot point (calamus) inserted into a deep follicle. In birds the calamus is a hollow tube divided horizontally by pulp caps representing intervals of interrupted growth. Such structure has been described for *Longisquama* (Jones *et al.*, 2000b) and is probably required for the rest of the morphology.

The origin of these structures may be inferred from the scales preserved on the rest of the *Longisquama* specimen. Sharov (1971) illustrated a thick mat of very elongated scales on the neck and ventral surface of the body. If these scales were enlarged and folded at the base, they would grossly resemble the features on the back. The evolution of feathers from elongated scales covering the body is consistent with Homberger's (2002) suggestion that streamlining was an important component of feather evolution. Additional enlarged scales occur on the trailing surface of the arm and must have had an airfoil function. This arrangement gives a possible explanation for a problem with the gliding origin of avian flight. This is the question of how the protobird developed a wing beat and still retained a gliding airfoil. In *Longisquama* the actions were decoupled with the arm wing separated from the thoracic wing. Because the thoracic wing provided almost all the lift, the airfoil on the wing must have been mostly for steering and a little forward propulsion. As the wing on the arm enlarged and begin to provide significant lift, the thoracic wing could be reduced until it was only represented by a spinal feather tract showing the same early development as the hind limb tract that impressed Beebe (1915). I have argued elsewhere (Martin, 1983), that powered flight originated not so much to extend the flight path as to control the choice of landing point. That true powered flight developed rather slowly in birds is documented by continuance of essentially powered gliding in *Microraptor*. It is possible that the tail of *Archaeopteryx* represents the last remnants of a thoracic wing system as in *Longisquama*. Unfortunately the tail is missing in the only skeleton of *Longisquama*, but some of the isolated feathers are different enough from those of the preserved wing and of a size to suggest that they might be tail feathers. If they are tail feathers, we might reasonably restore a tail similar to that in *Archaeopteryx*.

Preservation of the *Longisquama* skeleton is somewhat problematic. The pelvis and the rest of the hind end are missing, but the body and anterior skeleton is preserved although much of it is only available as an impression. The skull lacks the anterior end but enough remains to show that the snout was narrow and pointed. Sharov described the teeth as acrodont but close examination of the actual specimen show that the surface of the jaw had separated when the slab was split and it seems likely that what we have exposed

is the whole tooth rather than an unusually long crown. In that case the teeth were probably thecodont with short crowns and expanded roots. Sharov also mentioned a mandibular fenestra, but that observation is not confirmed and is probably wrong. He was correct that the skull was diapsid and there is a distinct postorbital with an elongated ventral arm. He was also correct about the presence of an antorbital fenestra (although denied by Senter, 2004), but Sharov's (1971) drawing shows it as a posterior round hole. What he drew is probably the posterior opening within a large complex triangular fenestra. The strange "crest" at the top of the cranium resulted from misidentification of the left parietal that had separated and twisted upwards as the cranium was compressed, a taphonomic arrangement often seen in fossil bird skulls (this is probably the "backward swept parietal" listed in Senter, 2004). It would appear that a rounded cranium was present. The scapula is elongated as was noted by Sharov, who used this unusual trait as a feature in his diagnosis and there is a distinct *Archaeopteryx*-like furcula. The arms are long with a slender humerus showing a distinct deltoid crest and no epicondylar foramen. The hands are remarkable for their large size being as long as the forearm. There is an opposable fifth digit on the manus making the limb-grasping hand of an arboreal animal. The penultimate digits are elongated, also suggestive of climbing ability. The skeleton posterior to the pelvis is missing but the number of preserved dorsal vertebrae corresponds to the number of thoracic feathers on the preserved wing (fig. 3e) suggesting that the back is nearly complete.

There is nothing in *Longisquama*'s morphology that is inconsistent with a protobird, and the combination of detailed feather anatomy with skeletal features that include an elongated scapula, furcula, and pointed snout is interesting. The absence of a mandibular fenestra (also noted by Senter, 2004) is intriguing as most Mesozoic birds also lack one. This would suggest that birds separated from the main archosaur line before mandibular fenestrae developed in archosaurs, a situation that parallels the teeth where the split may have preceded thecodonty (Martin and Stewart, 1999). It is clear that there was a radiation of small arboreal basal archosaurs in the Triassic with elongated scapulae, and most also have furculae. *Longisquama* is part of this radiation. It is a small, quadrupedal, arboreal glider with an avian shoulder girdle and feathers. It would seem that *Microraptor* must have had a very similar ancestor.

## CONCLUSIONS

The most likely ancestor for birds would be a small arboreal quadrupedal glider. Feathers evolved to provide a gliding plane (Feduccia, 1999) and it seems likely that they evolved from elongate scales (Maderson, 1972) similar to those seen on the body of *Longisquama* that overlapped the edges. These scales developed narrow bases forming pivot points for folding groups of feathers together. This apparently was achieved by folding the scale at its base giving the

base of the feather its characteristic shape as a hollow tube. The tube unfolds at the tip to provide the broad airfoil surface. The rachis and barbs originally were supporting ridges on the unfolded airfoil. Originally they were fused to the surface of the scale but later they separated leaving an enclosing tube, the feather sheath. After barbules and hooklets evolved to tightly hold the feather fabric together, the feather sheath lost its airfoil function and is now lost in adult feathers.

In *Longisquama* the thoracic wing occupies roughly the same region as the spinal feather tract in modern birds. It may have continued onto the tail providing lift down the entire body. Additional enlarged feathers/scales on the arm provided control and limited propulsion. As the arm feathers grew larger and began to provide lift, the spinal tract feathers were reduced, and are restricted to the tail in *Archaeopteryx*. As the hind leg feathers enlarged some of the gliding plane could shift to them and reduction of the spinal tract feathers would also become possible. This scenario permits the arm to evolve full powered flight without endangering the gliding surface, and solves one of the greatest problems for evolving avian flight from a gliding progenitor.

Lift and propulsion are mostly achieved in modern birds with the primary feathers on the hand. In the evolution of the avian hand these feathers enlarged and required a progressively deeper follicle. To accommodate this follicle, the palm extended distally to include the third and fourth digits largely immobilizing those fingers. This produces the characteristic configuration of an avian hand and any animal with such a hand might be reasonably considered a "bird." The wrist is also modified to provide rotation of the hand for flight and a hinge that permits the hand to fold, tucking the feathers against the body. In certain maniraptorians the hand and wrist lose their flight function and are further modified for terrestrial predation through the loss of half the bones in the wrist and modification and rearrangement of the metacarpals and carpals.

All birds went through a tetrapteryx gliding stage in their evolution with a hindleg wing as seen in *Microraptor*. Elongated leg feathers are seen in a number of other Mesozoic birds including *Archaeopteryx* showing that this a general feature in early birds. If we examine a recent cladogram (Hwang *et al.*, 2002) showing *Caudipteryx* as the sister taxon of oviraptorosaurs and that clade as the sister clade to dromaeosaurs and *Archaeopteryx*, we see that *Caudipteryx* has an avian hand with primary feathers as does *Archaeopteryx* and *Microraptor* (the primitive sister of the rest of the dromaeosaurs). We cannot escape the conclusion that the common ancestor of all these clades also had an avian hand with primary feathers and thus would fit our definition of a bird. Terrestrial dromaeosaurs and oviraptorosaurs are best thought of as flightless birds as suggested by Paul's hypothesis (Paul, 1984). Their more terrestrial adaptations are apomorphic not plesiomorphic to primitive birds like *Archaeopteryx*. They are thus no longer a transition between typical dinosaurs and birds and comparison with dinosaurs should

be restricted to other taxa. One thing seems certain: there is little reason now to maintain a hypothesis of flight origin from the ground up.

## ACKNOWLEDGEMENTS

I thank Z. Zhou, S. Czerkas and E. Kurochkin for access to specimens. J. Ruben, N. Geist, T. Jones and J. Hillenius provided valuable commentary and the photographs of *Longisquama*. I have benefited from conversations with Z. Zhou, D. Homberger, P. Maderson, and J. Hillenius. Figures are by M. Tanner, E. Ebert, Brian Platt, and E. Dickey. The manuscript was read by D. Burnham, who made helpful suggestions.

## REFERENCES

- Beebe, C.W. 1915. A tetrapteryx stage in the ancestry of birds. *Zoologica*, New York, 2(2) : 39-52.
- Bock, W.J. 1985. The Arboreal Theory for the Origin of Birds; pp. 199-207. In Hecht, M.K., Ostrom, J.H. & Viohl, G. *et al.*, (eds.) *The Beginnings of Birds*, Freunde des Jura-Museums, Eichstätt.
- Burnham, D. 2004. New Information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana; pp. 67-111. In Currie, P.J., Koppelhus, E.B., Shugar, M.A. & Wright, J.L. (eds.) *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Indiana University Press, Bloomington.
- Christiansen, P. & Bonde, N. 2004. Body plumage in *Archaeopteryx*: a review, and new evidence from the Berlin specimen. *Comptes Rendus Palevol*, 3 : 99-118.
- Currie, P.J. & Zhao, X. 1993. A New Troodontid (Dinosauria, Theropoda) Braincase from the Dinosaur Park Formation of Alberta. *Canadian Journal of Earth Sciences*, 30 : 2231-2247.
- Czerkas, S.A. & Ji, Q. 2002. A New Rhamphorhynchoid with a Headcrest and Complex Integumentary Structures; pp.14-41. In Czerkas, S.J. (ed.) *Feathered Dinosaurs and the Origin of Flight*, The Dinosaur Museum, Blanding.
- Czerkas, S.A., Zhang, D., Li, J. & Li Y. 2002. Flying Dromaeosaurs; pp. 97-126. In Czerkas, S.J. (ed.) *Feathered Dinosaurs and the Origin of Flight*, The Dinosaur Museum, Blanding.
- Elzanowski, A. 1999. A Comparison of the Jaw skeleton in Theropods and Birds, with a Description of the Palate in the Oviraptoridae; pp. 311-323. In Olson, S. (ed.) *Avian Paleontology at the Close of the 20<sup>th</sup> Century: Proceedings of the 4<sup>th</sup> International Meeting of the Society of Avian Paleontology and Evolution*. Smithsonian Institution Press, Washington, D.C.
- Evans, J. 1881. Reprint by Virtue & Co., London, with new introduction, of Evans (1865): On portions of a cranium

- and of a jaw, in the slab containing the fossil remains of *Archaeopteryx*. *Natural History Review*, 5 : 415-425.
- Feduccia, A. 1980. *The Age of Birds*. Harvard University Press, Cambridge.
- Feduccia, A. 1999. *The Origin and Evolution of Birds*. Yale University Press, New Haven.
- Feduccia, A. & Nowicki, J. 2002. The hand of birds revealed by early ostrich embryos. *Naturwissenschaften*, 89 : 391-393
- Gishlick, A.D. 2001. The function of the manus and forelimb of *Deinonychus antirrhopus* and its importance for the origin of avian flight; pp. 301-318. In Gauthier, J. & Gall, L.F. (eds.) *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Peabody Museum of Natural History, New Haven.
- Haubold, H. & Buffetaut, E. 1987. Une nouvelle interpretation de *Longisquama insignis*, reptile ingmatique du trias superior d'Asie centrale. *Comptes Rendus de l'Académie des Sciences de Paris*, ser. 2A, 305 : 65-70.
- Heilmann, G. 1926. *The Origin of Birds*. Witherby Press, London.
- Homberger, D.G. 2002. The aerodynamically streamlined body shape of birds: implications for the evolution of birds, feathers, and avian flight; pp. 175-189. In Zhou, Z. & Zhang, F. (eds.) *Proceedings of the 5<sup>th</sup> Symposium of the Society of Avian Paleontology and Evolution*. Science Press, Beijing.
- Hwang, S.H., Norell, M.A., Qiang, J. & Gao, K. 2002. New Specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *American Museum Novitates*, 3381 : 1-44
- Ji, Q., Currie, P.J., Norell, M.A. & Ji, S-A. 1998. Two feathered dinosaurs from northeastern China. *Nature*, 393 (25): 753-761.
- Jones, T.D., Farlow, J.O., Ruben, J.A., Henderson, D.M. & Hillenius, W.J. 2000. Cursoriality in bipedal archosaurs. *Nature*, 406 : 716-718.
- Jones, T.D., Ruben, J.A., Martin, L.D. *et al.* 2000. Non-avian feathers in a Late Triassic archosaur. *Science*, 288: 2202-2205.
- Jones, T.D., Ruben, J.A., Maderson, P.F.A. *et al.* 2001. Response to: R.O. Prum, D.M. Unwin and M.J. Benton on *Longisquama* Fossil and Feather Morphology. *Science*, 291: 1901-1902.
- Larsson, H.C.E. & Wagner, G.P. 2002. Pentadactyl ground state of the avian wing. *Journal of Experimental Zoology*, 294: 146-151.
- Lingham-Soliar, T. 1999. Rare soft tissue preservation showing fibrous structures in an ichthyosaur from the Lower Lias (Jurassic) of England. *Proceedings of the Royal Society of London*, series B, 266: 2367-2373.
- Lingham-Soliar, T. 2003a. The dinosaurian origin of feathers: perspectives from dolphin (Cetacea) collagen fibers. *Naturwissenschaften*, 90: 563-567.
- Lingham-Soliar, T. 2003b. Evolution of birds: ichthyosaur integumental fibers conform to dromaeosaur protofeathers. *Naturwissenschaften*, 90: 428-432
- Lü, J., Dong, Z., Azuma, Y., Barsbold, R. & Tomida, Y. 2002. Oviraptorosaurs Compared to Birds; pp. 175-189. In Zhou, Z. & Zhang, F. (eds.) *Proceedings of the 5<sup>th</sup> Symposium of the Society of Avian Paleontology and Evolution*, Science Press, Beijing.
- Lucas, A.M. & Stettenheim, P.R. 1972. Avian anatomy: Integument. *Agricultural Handbook No. 362 (2 vols.)*, U.S. government Printing Office, Washington, D.C.
- Maderson, P.F.A. 1972. On how an archosaurian scale might have given rise to an avian feather. *American Naturalist*, 146: 424-428.
- Martin, L.D. 1983. The origin of birds and of flight; pp. 105-129. In Johnston, R.F. (ed.) *Current Ornithology*, Plenum Press, New York.
- Martin, L.D. 1991. Mesozoic birds and the origins of birds; pp. 485-540. In Schultz, H.P. & Trueb, L. (eds.) *Origins of the Higher Groups of Tetrapods, Controversy and Consensus*, Cornell University Press, Ithaca.
- Martin, L.D. 1995. A New Skeletal Model of Archaeopteryx. *Archaeopteryx*, 13: 33-40.
- Martin, L.D. 2004. A basal archosaurian origin for birds. *Acta Zoologica Sinica*, 50 (6): 978-990.
- Martin, L.D. & Czerkas, S.A. 2000. The Fossil Record of Feather Evolution in the Mesozoic. *American Zoology*, 40: 687-694.
- Martin, L.D., Stewart, J.D. & Whetstone, K.N. 1980. The origin of birds: structure of the tarsus and teeth. *Auk*, 97: 86-93.
- Martin, L.D. & Stewart, J.D. 1999. Implantation and replacement of bird teeth; pp. 295-300. In Olson, S. (ed.) *Avian Paleontology at the Close of the 20<sup>th</sup> Century: Proceedings of the 4<sup>th</sup> International Meeting of the Society of Avian Paleontology and Evolution*, Smithsonian Institution Press, Washington, D.C.
- Maryanska, T., H. Osmolska, H. & Wolsan, M. 2002. Avian status for Oviraptorosauria. *Acta Palaeontologica Polonica*, 47 (1): 97-116
- Mayr, G, Peters, D.S., Plodowski, G. & Vogel, O. 2002. Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften*, 89: 361-365.
- Norell, M.A., Ji, Q., Gao, K., Yuan, C., Zhao, Y. & Wang, L. 2002. 'Modern' Feathers on a Non-avian Dinosaur. *Nature*, 416: 36-37.
- Norell, M.A. & Makovicky, P.J. 1997. Important Features of the Dromaeosaur Skeleton: Information from a New Specimen. *American Museum Novitates*, 3215: 1-28.
- Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin*, 30 : 1-165
- Ostrom, J.H. 1973. The ancestry of birds. *Nature*, 24: 136.
- Padian, K. 1985. The Origins and Aerodynamics of Flight in Extinct Vertebrates. *Paleontology*, 28 (3): 413-433.

- Paul, G.S. 1984. The archosaurs, a phylogenetic study; pp.175-180. In Reif, W.E. & Westphal, F. (eds.) *Third Symposium on Mesozoic Terrestrial Ecosystems*, ATTEMPTO Verlag, Tübingen.
- Paul, G.S. 2001. Increasing evidence for an arboreal origin of dinosaur-avian flight, and for losses of flight in post-Ürvogel (sic!) dinosaurs. *Journal of Vertebrate Paleontology*, 12 (Suppl. To 3): 88A
- Paul, G.S. 2002. *Dinosaurs of the Air*. John Hopkins University Press, Baltimore.
- Paul, G.S. 2003. Screaming Biplane Dromaeosaurs of the Air. *Prehistoric Times*, 60: 48-50.
- Reisz, R.R. & Sues, H. 2000. The 'feathers' of *Longisquama*. *Nature*, 408: 428.
- Senter, P. 2004. Phylogeny of Drepanosauridae (Reptilia: Diapsida). *Journal of Systematic Palaeontology*, 2 : 257-268.
- Sereno, P.C. 1999. The evolution of dinosaurs. *Science*, 284: 2137-2147.
- Sharov, A.G. 1971. New flying reptiles from the Mesozoic deposits of Kazakhstan and Kirgizia. *Trudy Paleontologeskii Institut Akademia Nauk S. S. R.*, Moscow, 130: 104-113.
- Wang, X.L., Zhou, Z., Zhang, F.C. & Xu, X. 2002. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and "hairs" from inner Mongolia, northeast China. *Chinese Science Bulletin*, 47: 226-230.
- Williston, S.W. 1879. Are Birds Derived from Dinosaurs? *Kansas City Review of Science*, 3: 357-360.
- Witmer, L.M. 1991. Perspectives on avian origins; pp. 427-466. In Schultz, H.P. & Trueb, L. (eds.) *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*, Cornell University Press, Ithaca.
- Witmer, L.M. 1999. New Aspects of Avian Origins: Roundtable Report; pp. 327-334. In Olson, S.L. (ed.) *Avian Paleontology at the Close of the 20<sup>th</sup> Century: Proceedings of the 4<sup>th</sup> International Meeting of the Society of Avian Paleontology and Evolution*, Smithsonian Institution Press, Washington, D.C.
- Xu, X., Wang, X., Zhang F. *et al.* 2000. Important Features of *Caudipteryx* – Evidence From Two Nearly Complete New Specimens. *Vertebrata Palasiatica*, 38 (4) : 241-254.
- Xu, X., Zhou, Z. & Wang, X. 2000b. The Smallest Known Non-avian Theropod Dinosaur. *Nature*. 408: 705-707.
- 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.
- Zhang, F. & Zhou, Z. 2004. Leg feathers in an Early Cretaceous bird of China. *Nature*, 431: 925.
- Zhou, Z., Barrett, P.M. & Hilton, J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, 421: 807-814.