The Fossil Record of Feather Evolution in the Mesozoic[1]

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SYNOPSIS.   The oldest known feathers from the Late Jurassic are already modern in form and microscopic detail. Because these oldest examples are assignable to an extinct branch (Sauriurae) of the basal avian dichotomy, their features must have been established at a significantly earlier date. The skin of a wide variety of dinosaurs is now known and is unlikely to represent a predecessor to a feather bearing integument. Examples of feathered dinosaurs result from erroneous identification of internal structures as part of the skin covering, and from the confusion of flightless birds from the Early Cretaceous of China with dinosaurs.

INTRODUCTION

Fossilized impressions of skin are known from several dinosaur families. The best known are from the duck-billed hadrosaurs, showing the entire animal covered with scales. The type of scalation is not squamate, or imbricated, as in many reptiles, *e.g.,* snakes, and the scutes on the feet of birds. The surface skin of dinosaurs is consistently composed of tuberculate or pebble-like scales. Collectively, these scales are not arranged in distinct parallel rows, but form a continuous rosette pattern, producing a field of small scales around larger scales. While contributing to an overall appearance of ornamentation, the larger scales also provide a tougher skin surface for greater mechanical protection, and the largest scales occur on the leading edges of the limbs.

Distinct patterns of ornamentation are known from different types of dinosaurs. Compared to hadrosaurs, the ceratopsians have proportionately larger scales, with irregular rows of flat sub-circular scales over the thighs and presumably the sides of the body. Sauropods had a more elaborate skin texture. While the exact scale pattern is not known in detail, the sides of the body of diplodocids were covered with raised studs

some of which are over ten centimeters in diameter. They do not cover dermal ossicles as in the armored scutes of crocodilians. The preservation of theropod skin is rare enough that it has been suggested that their skin structure was different from that of other dinosaurs, namely smoother and more leathery (Czerkas and Czerkas, 1997). However, examples from a variety of theropods, including: tyrannosaurs, allosaurs, and abelisaurs, have consistently shown a skin similar to that of other dinosaurs, consisting of tuberculate scales. *Carnotosaurus* is the most extensively known theropod showing skin impressions for portions of the head, neck, shoulders, torso and tail (Czerkas and Czerkas, 1997). Hadrosaurs and sauropods possess a distinct frill composed of dermal spines (Czerkas, 1992). These frills resemble those occurring in certain lizards, *e.g., Iguana,* and may be analogous to the elevated dermal spines that contribute to the paddle-like shape of a crocodilian tail. The recent discovery of typically dinosaurian pebble-like scales in the ornithimimosaur, *Pelicanimimus* demonstrates the existence of this skin type in advanced coelurosaurs and makes the description of a hair-like body covering for the compsognathid, *Sinosauropteryx* (Chen *et al.*, 1998) inconsistent with its phylogenetic position below ornithomimosaurs. This problem is resolved by the second Beijing specimen of *Sinosauropteryx* (Ackerman, 1998) in which a slab of scale impressions has been removed from the body

area. One of us (Martin) was shown this specimen as an example of cross-sections of feather quills, but that interpretation is unlikely to be correct. Feather quills are widely separated from each other and do not form a sheet of contacting rounded objects as could be seen in the fossil specimen. Although this specimen has not yet been published, it would seem to confirm a *Pelicanimimus*-like skin covering for *Sinosauropteryx* of rounded pebble scales. The occurrence of a crest or frill down the back and on the ventral surface of the tail in *Sinosauropteryx* is perfectly consistent with known frills in hadrosaurs and other dinosaurs (Czerkas, 1992).

An imbricating pattern of tuberculated scales does not provide a likely starting point for the complex musculature associated with feathers (see Homberger, 2000), and we should search for other fossil models. An interesting fossil example of elongated scales occurs in the Triassic basal archosaur, *Longisquama* (Maderson, 1972).

ARCHAEOPTERYX

The oldest evidence for feathers are still those of *Archaeopteryx* from the late Jurassic of Germany (Martin, 1983). Fortunately, all specimens of *Archaeopteryx* preserve some feathers and the condition of preservation in some provides unusual structural detail (Fig. 1). Strangely, there is still no evidence for contour feathers although an early drawing of the Berlin specimen shows them on the legs (Ostrom, 1985). This is the usual place to find fossilized contour feathers and where they were first discovered in *Confusciusornis,* the oldest existing fossil record (Early Cretaceous). Unfortunately, all traces of contour feathers were prepared off of the *Archaeopteryx* specimen (Ostrom, 1985).

The presence or absence of contour feathers may tell us very little about endothermy. The most recent (latest Cretaceous) enantiornithine birds have bone tissue indicative of ectothermy, while older Ornithurine birds have the typical bone structure of modern endothermic birds (Chinsamy *et al.*, 1998). It seems almost certain that the common ancestor of birds was an ectotherm, and that endothermy only evolved in

the Ornithurae (Hou *et al.*, 1996). The detailed characteristics of modern plummage are shared among all the birds and must have been present in the common ancestor. In a small ectotherm, feathers would interfere with basking, and might have been more important in keeping heat out of the body. This argument as presented by Regal (1975) makes sense in the Jurassic when global temperatures appear to have reached a high. At that time, the ambient temperature approached the body temperature of mammals and endothermy may have been more of a physiological expense than a benefit.

Feathers may have evolved to extend the glide path from tree to tree. The development of a bipedal posture and elongated hind limbs and feet may be related to vertical clinging and leaping from branch to tree trunk similar to the evolutionary path suggested for some primates (Martin, 1983; Feduccia, 1993). Ultimately, contour feathers would evolve as streamlining and would improve lift.

The feather morphology of *Archaeopteryx* is remarkable for its modern structure (Fig. 1). The complex structure of feathers provides good evidence that feathers arose only once in birds and that essentially all of their major features were in place before the major dichotomy of birds into the Sauriurae (*Archaeopteryx* and the enantiornithine birds) and the Ornithurae, comprising all modern birds plus the Early Cretaceous *Chaoyangia* (Hou *et al.*, 1996).

Norberg (1985) shows that the feather asymmetry and the backward curvature of the flight feathers in *Archaeopteryx* are typical of flying birds. This interpretation was questioned by Speakman and Thompson (1994). They demonstrated that vane asymmetry tends to decrease medially through the remiges and that the primary feathers are the most asymmetric. This is reasonable as primary feathers are spread during flight and have a greater opportunity to operate as individual airfoils. When one of us (Martin) tried to duplicate Speakman and Thompson's measurements on the Berlin specimen, values were obtained in the low end of the flighted birds. This is coupled with the fact that many of the so-called flightless
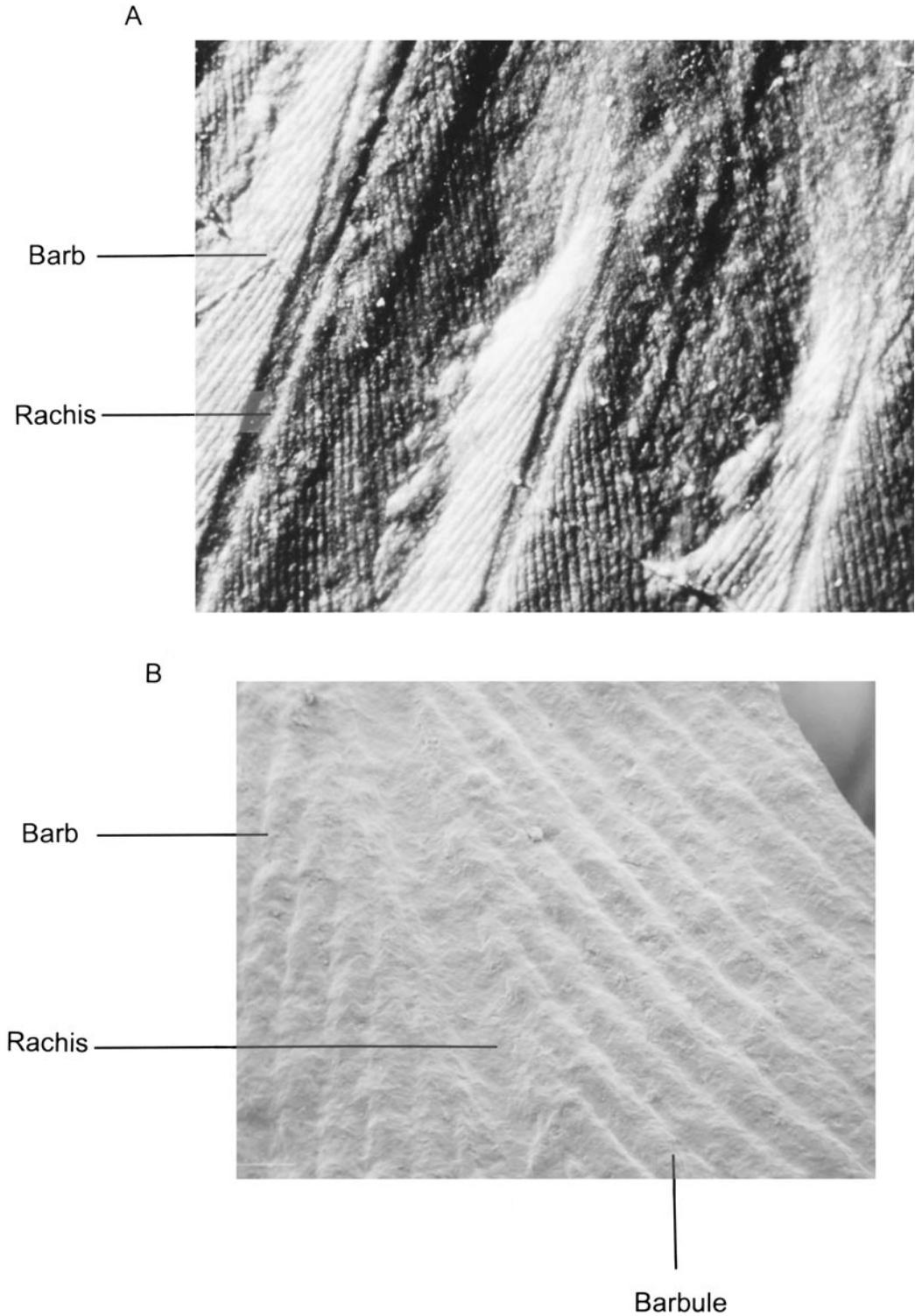
A

Barb

Rachis

B

Barb

Rachis

Barbule

FIG. 1. Details of the primary feathers of the Berlin specimen of Archaeopteryx. A. section of the counterslab showing asymmetry, rachis, and barbs. B. scanning electron microscope photograph showing a rachis, barbs, and barbules.

birds are still capable of powered flight and probably as much as suggested for *Archaeopteryx* by Fedduciа (1996), whose arguments for true powered flight in *Archaeopteryx* seem solid.

The remiges in *Archaeopteryx* are divided into secondaries and primaries exactly as they are in modern birds. Stephan (1985) identifies twelve primaries with two of them attached to the second phalanx of the middle digit. Primaries are necessary for avian flight, but render the hand useless for most other purposes, as all the fingers except the inner one are tied to feathers and, as Stephan (1985) points out, reconstructions showing free fingers on the hand of *Archaeopteryx* are incorrect and would prevent any sort of flight. The most recent example of this mistake was the reconstruction of *Confusciusornis* by Padian and Chiappe (1998) on the cover of *Scientific American* in which the fingers were left free (Feduccia *et al.*, 1998). As I have shown elsewhere (Martin, 1991), *Archaeopteryx* had an essentially modern avian wrist and could make all the motions needed for powered flight and the folding of the wing. The inability to grasp objects with its hands, coupled with enlarged and highly recurved claws, is strong evidence for the use of the hand claws as climbing spikes rather than for prey capture. This structure of the hand would be most functional on tree trunks, and the normal flight pattern was from tree trunk to tree trunk, suggesting that *Archaeopteryx* frequented dense woodlands. Feduccia (1996) points out that the wing shape is characteristic of birds that are able to maneuver through dense forests.

One of the most striking features of *Archaeopteryx* is its relatively long tail. All known modern birds have shortened the bony tail. It is interesting to note that this shortening is usually not achieved by reducing the number of tail vertebrae. Almost all of the 23 vertebrae found in the tail of *Archaeopteryx* can be identified in modern birds, although reduced in size with some added to either the sacrum or to the pygostyle. In *Archaeopteryx,* each caudal vertebra has a pair of long feathers that stick out to the side to form an air foil. A significant percentage of the total lift in *Archaeopteryx* is provided by this surface.

Archaeopteryx lacks an antitrochanter on the acetabulum of the pelvis. In fact, there is no articular surface at the back of the acetabulum, nor a supra-acetabular shelf characteristic of dinosaurs. The pelvis does have a strong articulation at the front of the acetabulum resulting in a vertical posture. In this respect it resembles a monkey (Martin, 1995) and is unsettling when compared with the horizontal backs of dinosaurs and modern birds. However, there seems to be little room for alternative postures and a vertical posture fits with the use of the clawed hands for tree trunk climbing and the origin of bipedality through vertical clinging and leaping (Martin, 1983). Without an articulation at the back of the acetabulum, the femur could not be easily swung forward, and the legs were not folded under the center of mass during flight as in modern birds. Instead, the femur and tibia would have extended posteriorly, shifting the flight center and requiring a more posterior lift surface provided by the tail (Peters and Gutmann, 1985). The tail could not be shortened in flying birds until the development of an antitrochantor so that the femur could be fixed in the forward position.

PROTARCHAEOPTERYX AND CAUDIPTERYX

Protarchaeopteryx was originally described by Ji and Ji (1997) as a bird more primitive than *Archaeopteryx,* being on a direct line to *Confusciusornis* as a descendent of *Sinosauropteryx*. It is now clear that all of these Chinese taxa are from roughly the same stratigraphic horizon and age (ten or twenty million years younger than *Archaeopteryx).* They are our best evidence for an early diversification of birds (Hou *et al.*, 1996), but are not old enough to be relevant to the question of avian origins other than making it even more unlikely that birds originated in the Late Jurassic rather than some earlier time. Their reassignment to the Dinosauria as feathered forms by Ji *et al.* (1998) stimulated further interest. There are several isolated feathers and a remarkable clump of tail feathers preserved with the skeleton of *Protarchaeopteryx.* Unfortunately, none of these are directly as-

sociated with the skeleton. Flight feathers are not preserved, but *Protarchaeopteryx* has a large hand, and given long enough feathers it might have had limited flight capabilities. The teeth are avian in character with a waisted crown and expanded roots. The maxillary teeth are actually very similar to those in *Archaeopteryx*, but the teeth in the premaxillary are elongated fangs unlike the teeth of any other bird or dinosaur. In the original description (Ji and Ji, 1997) the teeth are described as unserrated, but Ji *et al.* (1998) report them as serrated even though their figures do not show serrations and our examination of the specimen failed to find them. If any serrations exist, they are not similar to the prominent serrations of theropod dinosaurs like *Sinosauropteryx*. *Protarchaeopteryx* has a shortened tail and fibula, as well as a reflexed hallux. It is almost certainly a bird.

Caudipteryx zoui Ji *et al.* (1998) is represented by two specimens that are better prepared and preserved than the *Protarchaeopteryx* specimen. Although described as a dinosaur, no derived characters unique to dinosaurs can be certainly identified. It possesses a number of avian features, including expanded roots on the premaxillary teeth; primary feathers; a carpus with at least four bones (Ji *et al.*, 1998: Fig. 5); absence of a pubic foot; a reflexed hallux; and a shortened tail. Several of these features indicate that *Caudipteryx* is specialized beyond *Archaeopteryx* and may be closer to *Confuciusornis* (Fig. 2) including loss of teeth in the maxillary and dentary; a mandibular foramen in the mandible; enlargement of the premaxillary; reduction of the maxillary; reduction of the hyperpubic spoon; ball-shaped head on the femur; reduction of the fibula; enlargement of the astragalus at the expense of the calcaneum; and a greatly shortened tail with some evidence of pygostyle formation. According to Ji *et al.* (1998), the wing feathers attach to the middle metacarpal and the first two phalanges of the middle digit leaving only the claw free (Fig. 2). As discussed previously, this prevents the use of the hand for grasping and would be a hindrance to a terrestrial animal that uses its hands to acquire food. The feathers are well formed with a central rachis and barbs. They have an appearance often found in flightless birds with symmetrical vanes and separation of the barbs. It is hard to see how this hand makes any sense except as an inherited complex from a flighted ancestor. This is consistent with the marked reduction of the hand, foot claws, and furcula. The presence of a large number of gastroliths coupled with tooth loss is characteristic of terrestrial herbivores.

The short tail could not be used to balance the body with the back horizontal as in a theropod dinosaur, and *Caudipteryx* must have had a more upright posture, more similar to that of *Archaeopteryx.*

Caudipteryx is best considered a herbivorous flightless bird related to *Protarchaeopteryx* and *Confusciusornis.* It is more advanced than the significantly older *Archaeopteryx.* The existence of a flightless bird in the Early Cretaceous of China provides further evidence of the diversification of birds at this time, but contributes little to our understanding of the origin of birds.

CONFUSCIUSORNIS AND ENANTIORNITHINES

The most important bird from the Liaoning deposits in China is *Confuciusornis* the only bird besides *Archaeopteryx* with enlarged claws for climbing. It also has a full set of gastralia and a postorbital bone that meets the jugal. Coupled with very primitive features are some that are very derived, including the loss of all teeth and the development of a horny bill that is preserved on several specimens (Fig. 2). The bill is unusual in being turned up at the tip. It seems likely that *Confuciusornis* like *Caudipteryx* was a herbivore. The toothless upturned bill would be of little use to a predator. Unlike *Archaeopteryx,* there are deep pleurocoels in the vertebrae; the fibula is reduced; and the bony tail is short with an elongated pygostyle (Martin *et al.*, 1998). The elongated pygostyle is also characteristic of more typical enantiornithine birds, but is not found in Mesozoic Ornithurines except for *Baptornis* (Martin and Tate, 1976). In all other known Mesozoic ornithurines, the pygostyle consists of the two penultimate caudal vertebrae fused to each
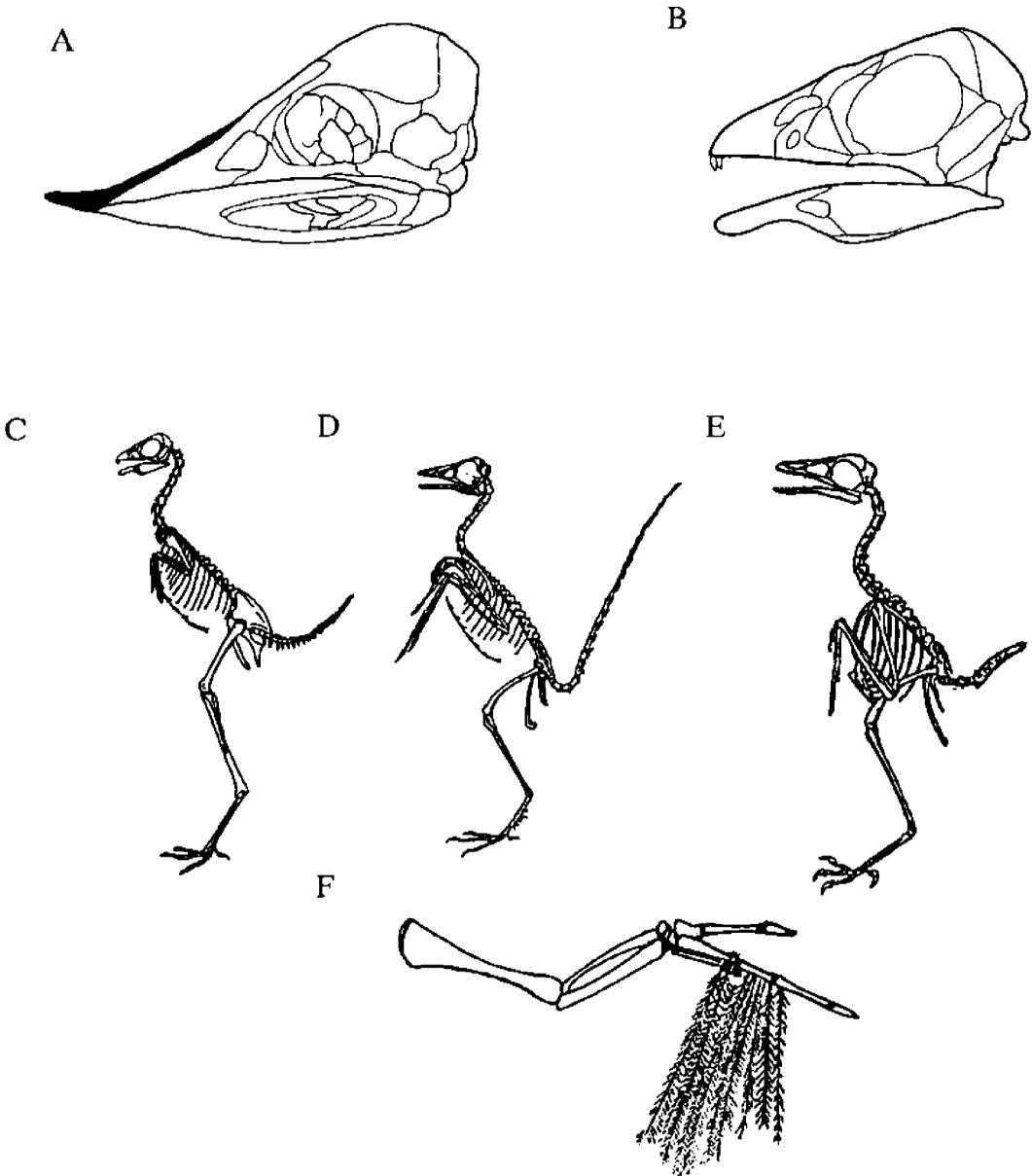
Fig. 2. A. Skull of *Confusciusornis* showing the outline of the horny bill. B. Skull of *Caudipteryx*. C–E. Restored skeletons of *Caudipteryx, Archaeopteryx,* and *Iberomesornis.* The extremely short tail of *Caudipteryx* is striking and unlike that of any dinosaur. F. Reconstruction of the arm of *Caudipteryx,* showing approximately the attachment of the primary feathers. D–E from Martin (1995).

other but not to the terminal vertebra. The terminal vertebra can be flexed dorsally, and this is related to the characteristic insertion of the tail feathers found in modern birds (Baumel *et al.*, 1990). It contrasts with the elongate and triangular pygostyle

of the enantiornithines that may contain as many as ten vertebrae. *Confusciusornis* and the enantiornithines have a pair of greatly elongated tail feathers that insert along the margins of the elongate pygostyle. In *Confusciusornis,* this seems to be a sexually di-

morphic trait that is expressed in only a small percentage of the specimens.

Enantiornithines and *Confusciusornis* also resemble each other and differ from *Archaeopteryx* in having wings with high aspect ratios. The primary feathers are asymmetrical and greatly elongated. The number of primaries does not seem to be as great as in *Archaeopteryx* but they are difficult to count. There may be as few as six or seven primaries in *Confusciusornis. Archaeopteryx* and *Confusciusornis* lack alula feathers. The enlarged inner finger may have acted as a primitive aerodynamic slot to prevent stalling at low speeds. The earliest example of an alula with feathers is on an undescribed primitive enantiornithine with an unkeeled sternum from the same Geological horizon as *Confusciusornis.*

MESOZOIC ORNITHURINE BIRDS

The Sauriurae are the most abundant and best represented birds from the Age of Dinosaurs. They are almost absent from marine sediments, but are very common in lake deposits. Most of what we know about Mesozoic feathers relate to them. The oldest ornithurine bird *Chaoyangia* occurs just above the *Confusciusornis* level and has an essentially modern skeleton, except for teeth in the premaxillary, maxillary, and dentary. The pubis is also fused and has a cup-shaped termination similar to the one in *Archaeopteryx*. Its feathers are not known, and the earliest ornithurine feathers are those assigned to *Ambiortis* from the lower Cretaceous of Russia (Feduccia, 1996). Unfortunately, these feathers are not associated with the skeletal remains and mainly show a high degree of asymmetry. Histological studies suggest that, unlike the enantiornithines, the Mesozoic ornithurines were warm-blooded like their living descendents (Chimsany, *et al.,* 1998). The feather covering of the flightless, foot-propelled divers belonging to the extinct Hesperornithiformes was unusual and may have had a hair-like appearance(Martin and Tate, 1976). The feet were covered with scuttelate and reticulate scales.

CONCLUSIONS

The oldest known feathers are modern even to the level of microscopic detail, and all the basic features of feathers must have been in place before a basic dichotomy into Sauriurae and the Ornithurae occured. This division must be older than *Archaeopteryx* (late Jurassic) and may be much earlier. The basal Ornithurae radiated into aquatic habitats beginning on the shoreline and extending into swimming and diving.

The difference between the flight mechanism of *Archaeopteryx* and modern birds has mostly to do with the triosseal pully system and the ability to flip the wings above the back, permitting a full flight stroke when the bird was on the ground. The ability to take off from a flat surface is crucial to a bird living on a shoreline or in the water, and selection for an improved flight apparatus proceeded more rapidly in the Ornithurae. If *Archaeopteryx* was on the ground and its back was horizontal, the absence of a dorsal glenoid surface would have prevented the wings from being elevated and they would have struck the ground if flapped.

The fossil record of feathers presently yields no evidence on the origin of feathers that cannot be better obtained from living birds. The known dinosaur integument provides a poor model for a feather progenitor. The so-called feathered dinosaurs, *Protarchaeopteryx* and *Caudipteryx* are flightless birds.

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