

# Feathers and 'feather-like' integumentary structures in Liaoning birds and dinosaurs

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We provide an overview of the known feather and other 'feather-like' integumentary structure types known to-date in the birds and dinosaurs from the Cretaceous rocks of Liaoning, NE China. These feather-types are classified and compared with similar structures seen in Mesozoic and extant birds. We consider that integumentary feathers and 'feather-like' structures fall within two major structural categories ('shafted' and 'non-shafted'). Comments are also made on the possible aerodynamic or insulating function of leg and tail feathers in Mesozoic birds and theropods. Copyright © 2006 John Wiley & Sons, Ltd.

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## 1. INTRODUCTION

Ornithologists have long been aware that feathers are the most complex vertebrate integuments (Lucas and Stettenheim 1972; Gill 1995; Zheng 1995). However, although various feather types and 'feather-like' integuments have been reported in dinosaurs, these external structures are still considered one of the most important characteristics of avians, conferring the ability to fly.

It has also been well documented for more than a century that hardly any known difference exists in feathers between the 10 000 or so extant taxa, and the most primitive known bird *Archaeopteryx*. In addition, the preserved feathers found to-date in other fossil birds are also generally similar to those of living birds (Figure 1). As a result, many earlier authors considered that the fossil record of birds seems to add little information to the discussion about the origin and early evolution of feathers (Rayner 1988), despite the fact that the number of known specimens has dramatically increased since the early 1990s (Fountaine *et al.* 2005).

This situation has begun to change recently with the discovery and description of a number of birds and dinosaurs from Early Cretaceous sediments in Liaoning, northeastern China (Ji and Ji 1996; Chen *et al.* 1998; Ji *et al.* 1998, 2001; Xu *et al.* 1999a, 1999b, 2000, 2001, 2003, 2004; Zhang and Zhou 2000, 2004; Zhou and Wang 2000; Zhou *et al.* 2000, 2003; Padian *et al.* 2001; Xu 2003; Xu and Zhang 2005; Figures 2–6). The traditional view of the distribution of feathers and their origin amongst the bird is facing serious challenges as a result of these new fossil discoveries. For example, it now appears that the aerodynamic flight feathers of birds originated from feathers that had no obligatory aerodynamic function: as a result, feathers *per se* can no longer be considered *the* unique feature that defines birds (see Feduccia *et al.* 2005 for an alternative view).

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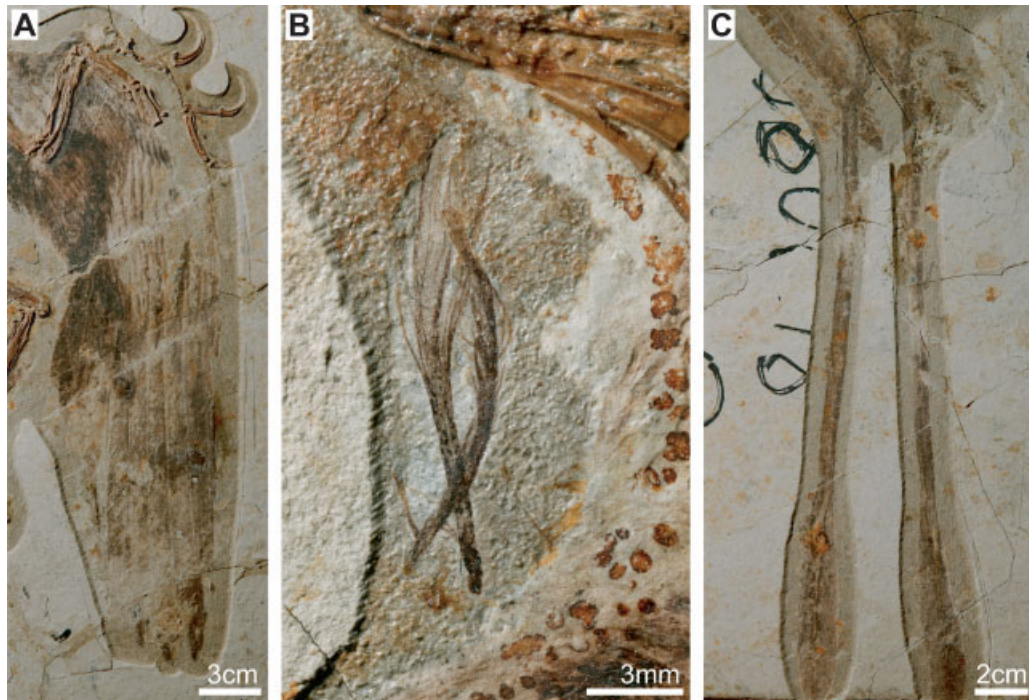


Figure 1. Three types of feathers seen in Mesozoic birds, preserved with skeletons: (A) The shafted feathers of *Confuciusornis* make up the wing in this very common Chinese bird; (B) two isolated non-shafted feathers from the enantiornithine *Protopteryx*; (C) two shafted feathers, the central tail feathers of *Confuciusornis*.

New insights from the Chinese fossil record have also strengthened the hypothesis for a dinosaurian origin for birds; anatomical features as well as information from the external integument now seem to have put this hypothesis beyond question. However, as we highlight, a number of key questions in broad-scale feather morphological evolution still remain unresolved. How, for example, can the unusual feather-types seen in the central part of the tail in *Confuciusornis* and *Protopteryx* be explained?—such differentially elongate central tail feathers are not commonly seen in living birds—and how can we classify the single ‘fibre-like’ integuments seen in *Sinosauropteryx* and the two additional types of ‘branched filaments’ seen in other non-avian theropods (*Sinornithosaurus*), in the context of avian feather evolution?

## 2. STRUCTURE AND VARIATION OF FEATHERS IN MESOZOIC BIRDS AND DINOSAURS

The shape of a feather and its internal structure determine its function. Thus, the presence, or absence, of interlocked barbules is generally considered a criterion for determining whether, or not, a feather can produce useful aerodynamic lift. Barbules hold the feather together, maintaining integrity, and forming a potential aerodynamic surface. Combined with the shape of the feather and the presence of a central feather shaft, interlocked barbules allow the avian wing to generate both lift and thrust during the wing-beat cycle. An avian flight feather typically has three ordinal branches: the barbs, barbules and barbicels. These microstructures lock together to form a unitary vane (Lucas and Stettenheim 1972), but are very hard to identify in fossils.

In living birds, feathers are classified either as contour feathers, semiplumes, down feathers, filoplumes, bristles and powder feathers (Proctor and Lynch 1993; Zheng 1995). The criteria of this classification are the functions of the

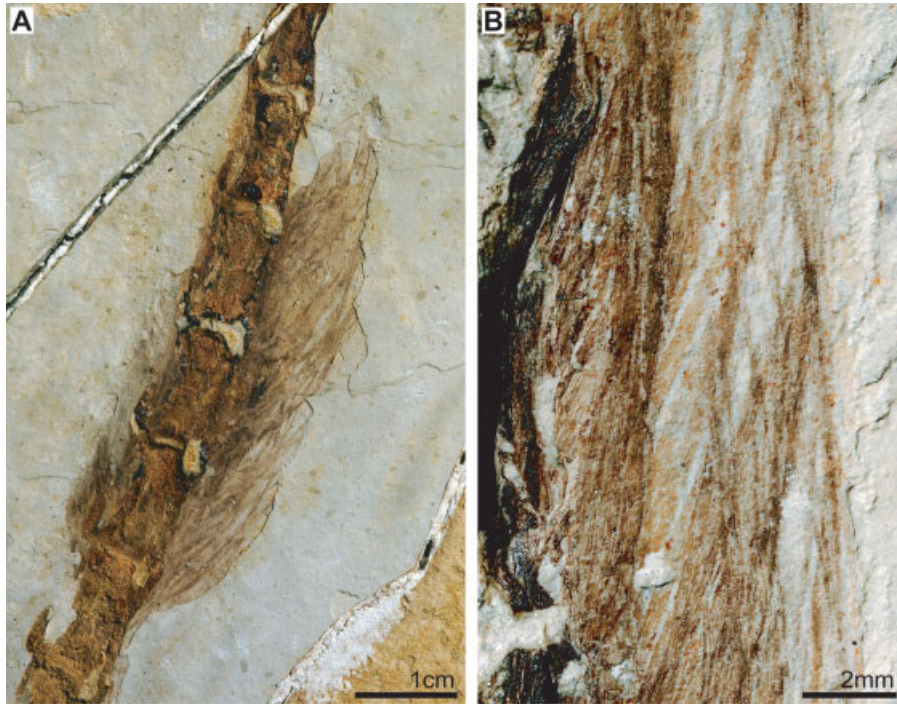


Figure 2. Integumentary structures preserved in the theropod *Sinosauropteryx* (compsognathid) closely allied to its caudal vertebrae: (A) bundle-shaped filaments roughly parallel to one another; (B) incorporated into non-shafted feathers.

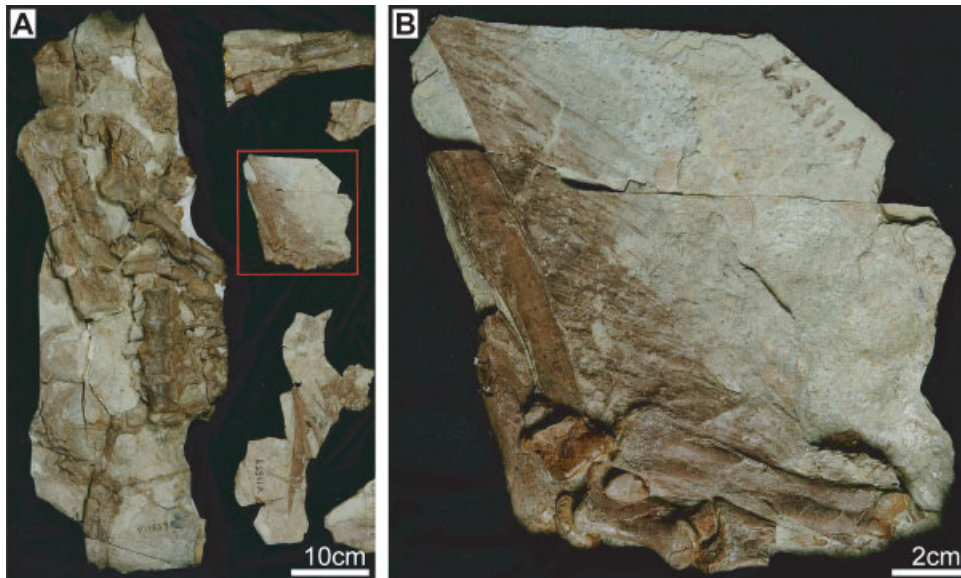


Figure 3. (A) The theropod *Beipiaosaurus* (therizinosaur) with covered filaments; (B) close-up view showing fibre-like elements associated with the skeleton that are structurally unclear (as in *Sinornithosaurus*) and which are tentatively classed as 'non-shafted' feathers.

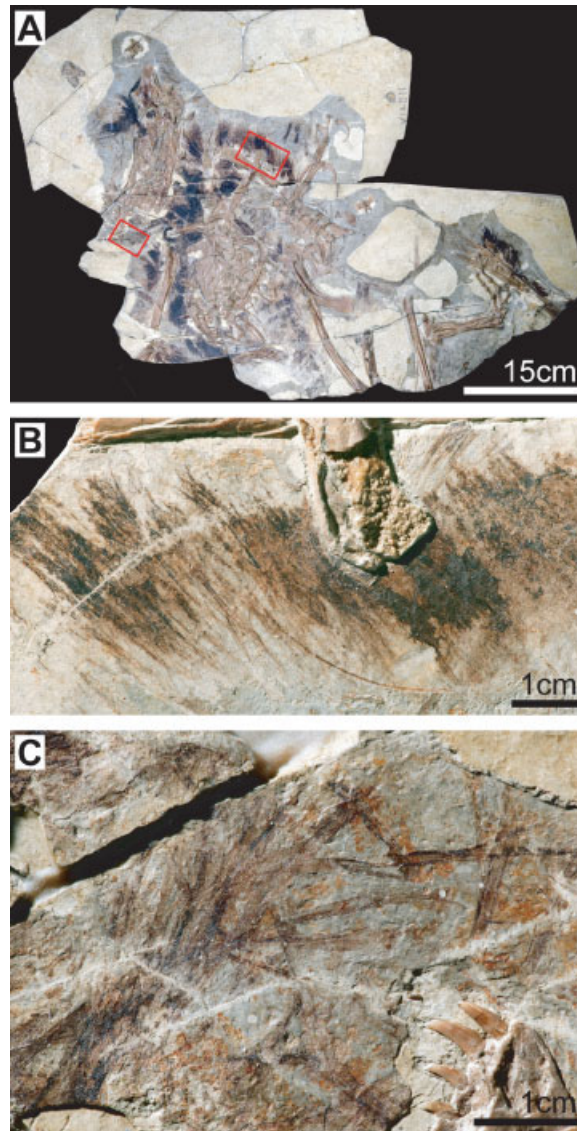


Figure 4. (A) The theropod *Sinornithosaurus* (dromaeosaur); (B) 'fibre-like' structures; (C); filaments present in bundles.

different feather types: aerodynamic, insulation, display, sensory, for example. Integumentary structures in dinosaurs, alongside novel feather structures seen in fossil birds, have never been classified in the context of modern birds.

### 2.1. Feather variation in Mesozoic birds

The feathers of Mesozoic birds were generally similar to those of extant birds (Hecht *et al.* 1985; Feduccia 1999; Zhang and Zhou 2000). In recent years many Early Cretaceous birds have been found in northern China, including: (1) basal birds such as *Jeholornis* (Zhou and Zhang 2003) and *Confuciusornis* (Hou *et al.* 1995a, 1995b; Hou 1997; Chiappe *et al.* 1999); (2) enantiornithine birds such as *Protopteryx* (Zhang and Zhou 2000), *Eoenantiornis* (Hou *et al.* 1999), *Longipteryx* (Zhang *et al.* 2001) and *Longirostravis* (Hou *et al.* 2004); and (3) ornithurine birds such as

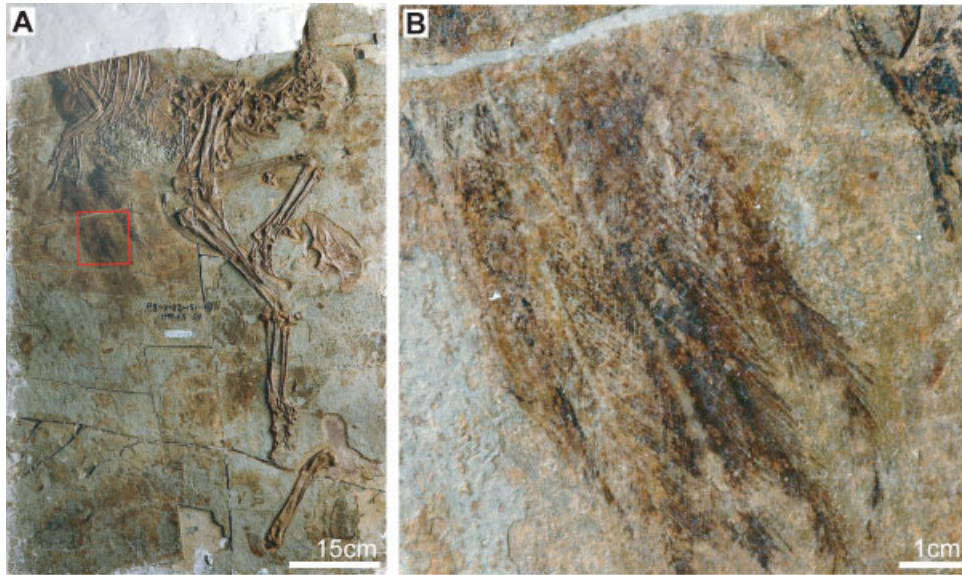


Figure 5. (A) The theropod *Caudipteryx* (oviraptorosaur); (B) close-up view of its shafted feathers. These complex integuments are very similar to the flight feathers of Mesozoic and living extant birds.

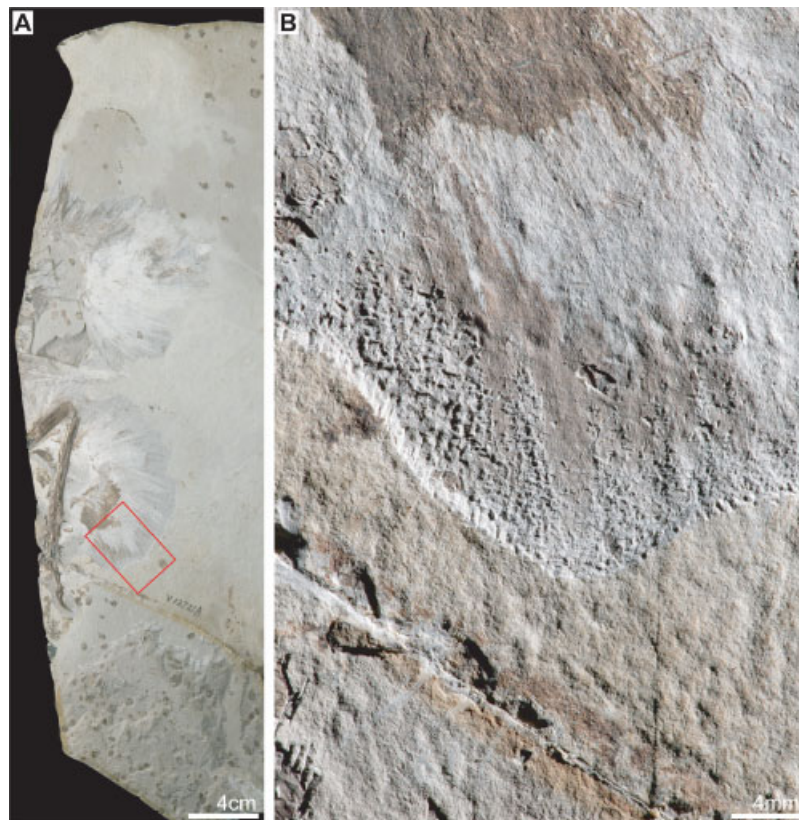


Figure 6. (A) The theropod *Pedopenna* and (B) its penna-like integument. (B) is a close-up view of the red box in (A) and shows that the neighbouring barb-like filaments are orderly and parallel. These filaments are incorporated into shafted feathers.

*Yixianornis*, *Yanornis* and *Hongshanornis* (Zhou and Zhang 2001a; Zhou and Zhang 2005). Almost all feathers known from these birds, those of the Jurassic *Archaeopteryx*, and isolated feathers from Mesozoic rocks, are similar in structure to those of living birds (Figure 1). Shafted feathers are commonly preserved in Mesozoic birds and include body contour feathers, wing feathers, alula feathers, covert feathers and tail feathers (Zhang and Zhou 2006).

However, despite the general similarity between fossil feathers and those of extant birds, one type of feather does exist that is different from that seen in extant birds: long central tail feathers, as in *Confuciusornis* and some enantiornithines (e.g. *Protopteryx*; Zhang and Zhou 2000; Zhou and Zhang 2001b; Figure 1C). These feathers have also been found isolated in the Liaoning deposits (Figure 7A). The distal part of this type of feather bears a normal rachis and vanes formed by interlocking barbs, which are branched from the central rachis. On its proximal end, however, there is a central shaft with unbranched vane on its margin; these vanes resemble elongated scales rather



Figure 7. Four different types of isolated shafted feathers from Liaoning birds: (A) supposed central tail feather, similar in morphology to those seen in *Confuciusornis* and *Protopteryx*; (B) and (C) contour feathers preserved on a slab and counterslab that possesses a shaft, barbs and barbules. The presence of these features implies aerodynamic function; (D) an obviously asymmetric feather possesses a strong and curved shaft and quill; (E) a shafted feather with a weak shaft but relatively long barbs.

than interlocked barbs. From the proximal to the distal end of the central tail feather, the vanes become progressively differentiated into barbs. Because the elongated central tail feathers in *Confuciusornis* and *Protopteryx* have a shaft, we consider these partly branched tail feathers to be true shafted feathers.

In contrast, non-shafted feathers include downy, or undifferentiated structures that lack a rachis (Zhang and Zhou 2006). This kind of integument has been found in almost all of the Chinese birds, distributed across the whole body around the head, neck and trunk (Zhang *et al.* 2003). This type is often harder to interpret because non-shafted feathers can be interlaced with others (Figure 1B).

## 2.2. Feathers or 'feather-like' integuments in dinosaurs

Many of the theropod dinosaurs that have been recovered in recent years from the Early Cretaceous deposits in Liaoning Province (northeastern China) reportedly possess feathers or 'feather-like' integumentary structures (Figures 2–6). In their preserved morphologies, some of these structures do resemble the contour feathers of birds—the feathers associated with the forelimbs, hindlimbs and tail preserved in specimens of the theropods *Caudipteryx*, *Protarchaeopteryx*, *Pedopenna* and *Microraptor gui*, for example. Structures in these dinosaurs do have most of the characteristic features of bird feathers: a rachis, barbs and more or less asymmetric vanes (Figures 5 and 6). We also consider these feathers, like those of Mesozoic birds, to be true shafted feathers (Xu *et al.* 2003; Xu and Zhang 2005).

However, some of the integumentary structures that have been reported from these Liaoning theropods are questionable in their characterisation as 'shafted feathers'—the structures reported as 'protofeathers' in *Sinornithosaurus* (Figure 4). One of the integumentary types in *Sinornithosaurus* was described as comprising 'filaments joined at their bases in series along a central filament' (Xu *et al.* 2001). However, structurally it is difficult to tell the difference between the 'central filament' and other filaments; it is also difficult to find any similarity between the 'central filament' and the rachis of contour feathers of primitive birds or some other dinosaurs such as *Caudipteryx*, *Protarchaeopteryx*, *Pedopenna* and *Microraptor gui*. In another, as yet unnamed theropod dinosaur (National Geological Museum of China, NGMC 91), some of these filaments were described as 'appear(ing) to be around a central rachis' (Ji *et al.* 2001). As in *Sinornithosaurus* (Figure 4), the 'central rachis' in NGMC 91 is difficult to identify.

Non-shafted feathers preserved in the Liaoning dinosaurs include 'down-like' feathers and 'fibre-like' integuments. In *Sinornithosaurus*, for example, a 'multiple structure' has been described such that 'filaments are joined in a basal tuft' (Xu *et al.* 2001). In the unnamed dinosaur (NGMC 91), some integuments were described as 'filaments originating from a single point and forming a radiating spray' (Ji *et al.* 2001). Both kinds of integument lack a defined central shaft and are structurally similar to the down feathers of Mesozoic and extant birds. We define them here as non-shafted (Figure 4).

In some of the Liaoning theropods there also exists a third type of integument—simple single fibre-like structures that were first identified in the compsognathid *Sinosauropteryx* (Chen *et al.* 1998; Ji *et al.* 2001). Generally, because such fibres are recognisable as different from the surrounding matrix by their colour, rather than structure (Figure 2), they are hard to identify and not well understood. Fibre-like structures such as these have been identified in the theropods *Caudipteryx*, *Sinornithosaurus*, the unnamed dinosaur NGMC 91, *Beipiaosaurus*, *Microraptor Zhaoianus* and *Dilong* (Xu 2003) (Figure 3).

Interestingly, long integumentary structures are not only present in theropod dinosaurs, but also in two individuals of the ornithischian dinosaur *Psittacosaurus* (Mayr *et al.* 2002; Feduccia *et al.* 2005). Both of these *Psittacosaurus* specimens also come from the Early Cretaceous of Liaoning—one is housed in the Senckenberg Museum in Frankfurt, Germany (Mayr *et al.* 2002), and the other in the Nanjing Institute of Geology and Paleontology (Feduccia *et al.* 2005). At least in the German specimen the sparsely preserved integumentary structures are much longer and thicker than those seen in theropod dinosaurs and are only attached to the tail region (Mayr *et al.* 2002). Structurally, they are distinct and bristle-like, unlike the blurry or foggy fibre-like filaments thus far described in theropods; their relevance to the origin of avian feathers remains unclear.

### 3. FUNCTIONS OF FEATHERS AND 'FEATHER-LIKE' INTEGUMENTS

#### 3.1. Aerodynamic function(s) of tail feathers

Compared to the asymmetric flight feathers of living birds, the central tail feathers of the Mesozoic *Confuciusornis* and *Protopteryx* seem too long and cumbersome to assist efficient flight. In the same species, these central tail feathers seem only to be present in some individuals and absent in others; this has led to hypotheses that these feathers could be indicators of sexual dimorphism in these birds (Hou *et al.* 1996; Martin *et al.* 1998), or could have been used for display (Chiappe *et al.* 1999). However, the presence of a rachis and branched and unbranched vanes in these central tail feathers do suggest some potential aerodynamic function. As is the case in flight feathers, the central rachis of these elongate tail feathers passes along their entire length and is much longer than the barbs; this is seen in dozens of specimens, either in association with a skeleton or as isolated feathers (Figure 1C, Figure 7A; Zhang *et al.* 2003). In the proximal portion of the tail feather, the unbranched vanes are obviously less rigid than that of a rachis; in some specimens the margins of the vane are folded while the rachis remains in its straight position.

#### 3.2. Leg feathers and flight

The fact that *Archaeopteryx* had leg feathers was reported many years ago (reviewed in Feduccia 1999). As a result, the so-called tetrapteryx hypothesis for the origin of avian flight was proposed by Beebe (1915) and developed by Heilmann (1927). Thus, the more recent report of leg feathers preserved in the dromaeosaurid theropod *Microraptor gui* (Xu *et al.* 2003) has resurrected the idea that these feathers may have some bearing on our understanding of the origin of flight of birds.

We know that the feathers that were attached to the tibia of the Berlin *Archaeopteryx* specimen are typical contour feathers (Feduccia 1999). Although Christiansen and Bonde (2004) argued that these feathers are 'rather long' for contour feathers, they are in fact relatively shorter than typical avian flight feathers. Others have suggested that these leg feathers may be the remnants of a functionally awkward 'hind wing' rather than an efficient aerodynamic appendage (Zhang and Zhou 2004). It is unlikely that *Archaeopteryx* was able to generate useful lift using this hind wing surface.

In the theropod *Microraptor gui* both the morphology of hind limb feathers and their distribution suggest that each leg feather could act as an airfoil, allowing passive parachuting (Xu *et al.* 2003) or even slight flapping flight. In this small dinosaur almost all of the known leg feathers are longer than the metatarsus and form a profile comparable to the forelimb wing (Martin 2004). Except for aerodynamic function, it is hard to conceive another functional interpretation for these leg feathers.

The presence of leg feathers is not limited to *Microraptor gui* and *Archaeopteryx*. Such feathers have also been recently reported in other Mesozoic birds such as *Confuciusornis* and some enantiornithines (Zhang and Zhou 2004).

We know that *Microraptor*, if capable of flapping flight, would have had to fly fast (like *Archaeopteryx*), because all known specimens lack a broad keeled sternum (Xu *et al.* 2000, 2003) and thus likely had weak supracoracoideus musculature (the wing elevator in modern birds). Only at fast speeds would wing lift have been sufficient to elevate the forelimb following the downstroke. As we have discussed, the most complex mode of flight theoretically available to this dinosaur is a tandem wing configuration with flapping forelimbs and fixed hindlimbs, requiring the latter to be held level and perpendicular to the body. This original reconstruction for *Microraptor's* wing shape (Xu *et al.* 2003) was based on Beebe's (1915) now famous and much older hypothesis of a tetrapteryx ('four-winged' or biplane) ancestral condition for avian flight. This wing configuration would have allowed *Microraptor* to fly reasonably well—extra thrust produced by the interaction of the forelimbs and hindlimbs—perhaps even more efficiently than *Archaeopteryx*. However, such a tandem wing configuration would require movement of the femoral head within the hip joint (acetabulum) to be far greater than in extant birds and estimated for other theropod dinosaurs. The femoral shaft in *Microraptor* is aligned in a plane with respect to the vertebral column, is curved, and would have conferred a swept leading edge to the hindwing. Although not theoretically impossible, a between-femora angle of 180° seems highly unlikely; such a tendon-muscle system is unknown among extant vertebrates. Furthermore, examination of the available specimens suggests that the femur lay in a near vertical position like in



other dromaeosaurids. Hip and knee joint flexure is a derived avian characteristic, seen for the first time among the much more advanced ornithurine birds. Aerodynamic theory tells us that tandem or biplane wings work most efficiently if the two wings are equal in length, or if a shorter wing is offset below and behind the forewing (as in biplane aircraft). Although the dromaeosaur forelimb is long, the forewing feathers in *Microraptor* are elongate (longer than on the leg) and the highly swept hindlimb leading edge is not compatible with a biplane arrangement.

The most likely mode of flight for a four-winged non-avian theropod is gliding. We know that these dinosaurs would have been passively stable in the air—for one, they had long tails relative to their bodies. Gliding would work best if the hindlimbs were independent yet still aerodynamically useful and would require the leading edge of the rear wing to be subparallel to the forelimb, but with all feathers aligned in the same direction. Given the conservative morphology of the theropod hindlimb and the fact that these dinosaurs were most likely able to move bipedally the most parsimonious interpretation of the hindlimbs is that they were held in a ‘bird-like’ posture—the femur, tibia and tarsals aligned subparallel to the backbone (Xu *et al.* 2003). By rotating their ankles and/or metatarsals the feathers on the tarsus would be rendered useful aerodynamically. Evidence for the leading edge of the rear wing is found in the orientation of *Microraptor*’s hindlimb feather shafts; they lie at an acute angle to the tarsus (Xu *et al.* 2003). If this were the posture in flight, these feather shafts could have lain transversely to the line of flight only if the tarsus (and thus the other bones of the hindlimb) also lies subparallel to the backbone.

### 3.3. Insulating function of non-shafted feathers

Non-shafted feathers in birds and dinosaurs include: (1) downy feathers (Mesozoic birds), (2) ‘down-like’ feathers (some dinosaurs) and (3) ambiguous ‘down-like’ integuments (or single ‘fibre-like’ filaments) (some dinosaurs). Although the function of these non-shafted feathers remains ambiguous, it is likely that they were used for insulation. In most cases, the distal parts of these single fibre-like integuments are better preserved in theropods (*Sinosauropteryx*, *Sinornithosaurus*, *Beipiaosaurus*); they are hard to distinguish from the downy feathers of extant birds and some other dinosaurs (*Caudipteryx*). In spite of a degree of controversy regarding the structure of the single fibre-like integuments in *Sinosauropteryx* (Feduccia *et al.* 2005), there seems to exist little reason to regard these features as anything other than insulatory in function.

## 4. SUMMARY

Recent discoveries in China of a number of different kinds of feathers and related complex integumentary structures have dramatically increased our fundamental knowledge about the origin of the avian feather. Fossil evidence alone, however, cannot provide an unambiguous scenario for the evolution of these features; much work remains to be done to incorporate fossil evidence from feathered dinosaurs into a clear hypothesis for the refinement of avian feathers.

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