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从新的古生物学及今生物学资料看羽毛的起源与早期演化1)

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摘要:近年来关于羽毛和羽状皮肤衍生物的研究极大促进了我们对羽毛起源与早期演化的理解。结合最新的古生物学与今生物学资料,对一些保存了皮肤衍生物的非鸟恐龙标本进行观察研究,为这个重要的进化问题提供了新见解。推测羽毛的演化在鸟类起源之前就以下列顺序完成了 5 个主要的形态发生事件:1）丝状和管状结构的出现;2）羽囊及羽枝脊形成;3）羽轴的发生;4）羽平面的形成;5）羽状羽小支的产生。这些演化事件形成了多种曾存在于各类非鸟初龙类中的羽毛形态,但这些形态在鸟类演化过程中可能退化或丢失了;这些演化事件也产生了一些近似现代羽毛或者与现代羽毛完全相同的羽毛形态。非鸟恐龙身上的羽毛有一些现代羽毛具有的独特特征,但也有一些现生鸟羽没有的特征。尽管一些基于发育学资料建立的有关鸟类羽毛起源和早期演化的模型推测羽毛的起源是一个全新的演化事件,与爬行动物的鳞片无关,我们认为用来定义现代鸟羽的特征应该是逐步演化产生的,而不是突然出现。因此,对于羽毛演化而言,一个兼具逐步变化与完全创新的模型较为合理。从目前的证据推断,最早的羽毛既不是用来飞行也不是用来保暖,各种其他假说皆有可能,其中包括展示或者散热假说。展开整合性的研究有望为羽毛的起源问题提供更多思路。

关键词:鸟类,兽脚类,恐龙,皮肤附属物,羽毛,起源与早期演化

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THE ORIGIN AND EARLY EVOLUTION OF FEATHERS: INSIGHTS FROM RECENT PALEONTOLOGICAL AND NEONTOLOGICAL DATA

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Abstract　Recent paleontological and neontological studies on feathers and feather-like integumentary structures have improved greatly our understanding of the origin and early evolution of feathers. New observations on some non-avian dinosaur specimens preserving integumentary structures, in combination with recent paleontological and neontological data, provide additional insights into this important evolutionary issue. Five major morphogenesis events are inferred to have occurred sequentially early in feather

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evolution before the origin of the Aves, and they are: 1) appearance of filamentous and tubular morphology, 2) formation of follicle and barb ridges, 3) appearance of rachis, 4) appearance of planar form, and 5) formation of pennaceous barbules. These events produce several morphotypes of feathers that are common among non-avian archosaurs but are probably lost later in avian evolution, and they also produced several morphotypes of feathers that are nearly identical or identical to those of modern birds. While feathers of non-avian dinosaurs exhibit many unique features of modern feathers, some of them also possess striking features unknown in modern feathers. Several models of evolutionary origin of feathers based on developmental data suggest that the origin of feathers is a completely innovative event and the first feathers have nothing to do with reptilian scales. We believe, however, that the defining features of modern feathers might have evolved in an incremental manner rather than in a sudden way. Consequently, an evolutionary model characteristic of both transformation and innovation is more acceptable for feather evolution. The function of the first feather is inferred to be neither related to flight nor to insulation. Display or heat dissipation, among others, remains viable hypotheses for initial function of feathers. An integrative study is promising to provide much new insights into the origin of feathers.

Key words birds, theropods, dinosaurs, integumentary appendages, feathers, origin and early evolution

1 Introduction

Feathers are the most complicated integumentary derivative of birds, and also the most characteristic feature of them. A typical feather is composed of hierarchical branches of rachis, barbs and barbules on a tubular structure called calamus, and it is either radially symmetrical or essentially in a planar form. Some feathers lack a rachis, but most feathers have a shaft (calamus of basal tubular portion and rachis of the rest solid portion) with barbs forming vanes on either side which are secondarily branched to form barbules. This basic plan shows a great diversity, and results in a wide variety of forms, which differ in: implantation (in the skin or on the skeleton), thickness and stiffness of the rachis, relative sizes of rachis and barbs, type, spacing and placement of barbs, symmetry and curvature of vanes, presence and structure of an afterfeather, and melanin pigmentation (Stettenheim, 2000). Largely corresponding to the diverse morphology, feathers also serve a diverse of functions, including physical protection, thermal regulation, locomotion, display, tactile sensation, and water repellency, among others (Stettenheim, 2000).

Mainly due to the diverse morphologies and functions of modern feathers, there is little consensus on the possible earliest morphology and initial function of feathers. Early fossil feathers also fail to provide relevant information. Feather-like structure has been claimed to be present in the Early Jurassic theropod (Kundrat, 2004), but this interpretation receives little attention due to their structure is preserved only as imprint. The Late Jurassic *Archaeopteryx* specimens preserve fine feather impressions, but they are identical in morphology to modern feathers. Similarly, other known basal birds all have feathers of fully modern form (Zhang and Zhou, 2006; Zhou and Zhang, 2006). In general, the known feathers of basal avians provide little significant information concerning the origin of feathers. Though the highly specialized tail feathers with an undifferentiated vane region on either side of the central rachis in many basal birds (Zhang and Zhou, 2000) and even in a non-avian theropod (Zhang et al., 2008b) have been suggested to represent a type of primitive feathers, their implications for understanding the origin of feathers have been questioned mainly due to their relatively late appearance in feather evolution (Prum and Brush, 2002; Xu, 2002).

Most non-avian diapsids have scaled skin. However, *Longisquama insignis*, a small diapsid reptile with uncertain systematic position, has recently been suggested to have non-avian feathers (Jones et al., 2000). Its highly specialized elongated dorsal scales have recently described as feather-like in many details and have been regarded as non-avian feathers (Jones et al., 2000). However, this interpretation has been criticized from the perspective of both preservation and morphology (Reisz and Sues, 2000; Prum, 2001; Unwin and Benton, 2001).

Understanding the evolution of structures must lie in a phylogenetic framework. Over the last few decades, a wealth of fossil evidence has been found to support the theropod hypothesis of bird origins, and numerous systematic analyses also strongly corroborate this hypothesis, suggesting that birds are nested deeply within a group of theropod dinosaurs called Coelurosauria (Gauthier, 1986; Sereno, 1999). It is therefore expected that simpler feather-like integumentary structures should be present in the closest evolutionary relatives of birds among the coelurosaurian theropods.

Over the last decade, numerous dinosaur specimens preserving soft tissue have been recovered from the Early Cretaceous Jehol Group of northern China, the lacustrine beds of uncertain Jurassic-Cretaceous age in western Liaoning, and the Jurassic Daohugou Formation of eastern Nei Mongol (Xu and Zhang, 2005; Xu and Norell, 2006; Zhang et al., 2008b; Xu et al., 2009a). In general, these findings suggest that: 1) early feathers are simple filamentous structures and have appeared at least in basal coelurosaurian theropods; 2) more complex pennaceous feathers evolved early in maniraptoran theropods and some non-avian theropods even had flight feathers with asymmetrical vanes; and 3) the original function of feathers has nothing to do with flight. The discoveries of these specimens have significantly advanced our understanding of the origin and early evolution of feathers, though admittedly still much information is needed to understand some critical stages for feather evolution.

In the present paper, we will review recent paleontological and neontological data relevant to the origin and early evolution of feathers, comment on their implications, and propose an evolutionary scenario to describe the origin and early evolution of feathers.

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2　Morphologies of non-avian dinosaurian integumentary appendage

Fossil skin is rarely preserved and it is particularly true for dinosaurs that are terrestrial animals. Nevertheless, integumentary morphologies have been known for some dinosaur taxa (Fig. 1), though in most cases only small patches of the skin impressions are preserved, which results in only incomplete knowledge of integumentary morphologies of non-avian dinosaurs. The recent discoveries of exceptionally well preserved non-avian dinosaur specimens from China have added much new information on dinosaurian integument (Norell and Xu, 2005; Xu and Norell, 2006; Zhang and Zhou, 2006), suggesting that non-avian dinosaurs are diverse in integumentary morphologies both between taxa and on different body parts (Figs. 1–3).

2.1　Integumentary appendage of non-theropod dinosaurs

Typically ornithischian dinosaurs have tuberculate, polygonal scales covering their body, and these scales are variable in size and shape on different parts of the body (Czerkas, 1997) as in other scaled reptiles (Fig. 1). However, two ornithischian taxa are also known to bear filamentous integumentary appendages.

Heterodontosaurid *Tianyulong* has recently been reported to bear filamentous integumentary structures (Zheng et al., 2009). Three patches of filamentous integumentary structures are preserved near the cervical, dorsal, and anterior caudal vertebrae in the holotype of *Tianyulong confuciusi*. The filaments are about 60 mm long and 0.4 mm wide, proportionally very large for an animal of about 70 cm in total body length. They are mono-filamentous, relatively rigid, and probably tubular (Zheng et al., 2009).

Some hadrosaurs are known to possess tuberculate, polygonal scales and dermal spines, which are suggested to be composed of purely keratinous, hypertrophied tubercles (Czerkas, 1997). Large, polygonal scales of a centimeter or more in size are reported to cover the tail of iguanodonts (Czerkas, 1997).

Ceratopsian skin is best represented by *Centrosaurus* and *Chasmosaurus*, which have large, round, flattened scales surrounded by prominent polygonal tubercles arranged in rosette patterns in their upper thigh and adjacent region of the torso (Czerkas, 1997). Unexpectedly, an exceptionally well preserved *Psittacosaurus* specimen from the Early Cretaceous Liaoning shows that this small ornithischian dinosaur has both scaly and thick filamentous integumentary structures (Mayr et al., 2002). *Psittacosaurus* has typical ornithischian scales (Fig. 1D) around nearly the whole skeleton, which are variable in shape and size, but also a row of long, rigid, and probably tubular monofilamentous integumentary appendages along the proximal half of the tail, which appear to grow on the caudal vertebrae (Mayr et al., 2002).

Among thyreophorans, the stegosaurian *Gigantspinosaurus sichuanensis* has been reported to bear small, non-overlapping polygonal scales near the shoulder region of a specimen (Fig. 1C; Peng et al., 2005).

Sauropod skin was suggested to be scaly nature (Czerkas, 1997). In a *Mamenchisaurus youngi* specimen, a patch of skin impression is preserved near the distal end of the ischium (Pi et al., 1996). It is composed of numerous polygonal scales of about 6 ~ 15 mm in diameter, proportionally extremely small for a large sauropod (Fig. 1A). Skin impression near the forelimb in a titanosaurian sauropod specimen indicates the presence of close-packed polygonal ossicles, each between one and a few centimeters in diameter (Upchurch et al., 2004). Titanosaurian embryo fossils show that the embryonic sauropods have round, non-overlapping, tubercle-like scales covering the body (Chiappe et al., 1998).

2.2 Integumentary appendage of non-avian theropod dinosaurs

Bony ossicles are present around the neck and tail of a *Ceratosaurus* specimen. Large patches of skin impressions are found in a *Carnotaurus* specimen, which are consisting of small tubercles about 5 mm in diameter, surrounding low, conical studs 40 ~ 50 mm in diameter that have no bony cores (Bonaparte et al., 1990; Czerkas, 1997). Similar skin impression is also found in *Aucasaurus* (Coria et al., 2002).

The skin of compsognathids is variable in morphology between taxa. In a basal compsognathid *Juravenator* specimen, patches of skin impression near the tail (Fig. 1B) and the hindlimb indicate that it has a scaly skin, which is composed of small tubercles similar in appearance to the small, conical and non-imbricated tubercles of many other non-avian dinosaurs (Gohlich and Chiappe, 2006). Filamentous feathers are, however, present in *Sinosauropteryx* and they are preserved dorsal to the back half of the skull and ventral to the posterior part of the mandible, dorsal to the cervical and dorsal series, over the hips and along both sides of the tail, and near the forelimbs (Fig. 2B). The filamentous feathers are mostly considerably narrower than 0.1 mm and occasionally exceed 0.3 mm in width, and range from 2 mm to over 40 mm long (Currie and Chen, 2001). They are rather coarse for such a small animal and thickest strands are much thicker than the hairs of the vast majority of small mammals (Chen et al., 1998; Currie and Chen, 2001). Although filamentous feathers of *Sinosauropteryx* are likely to be branched structures, with relatively short quills and long, filamentous barbs, it is difficult to isolate a single feather to confirm the branching structure (Chen et al., 1998; Currie and Chen, 2001). It is questionable that the somewhat scalloped distribution pattern of filaments along the tail is resulted in by a frill nature of these dark impressions (Lingham-Soliar et al., 2007), but it is interesting that such a pattern appears in several specimens.

Small patches of scaly hide consisting of typical dinosaurian tubercles are reported to be present in tyrannosaurid (Czerkas, 1997). However, filamentous feathers are preserved near the mandible and around the middle caudal vertebrae of a basal tyrannosauroid *Dilong* specimen. Those attached to the distal caudal vertebrae are more than 20 mm in length and about 0.3 mm in width. These filamentous feathers are proportionally wide for an animal of 1 ~ 2 meters long. They are branched but the pattern is difficult to discern (Xu et al., 2004).

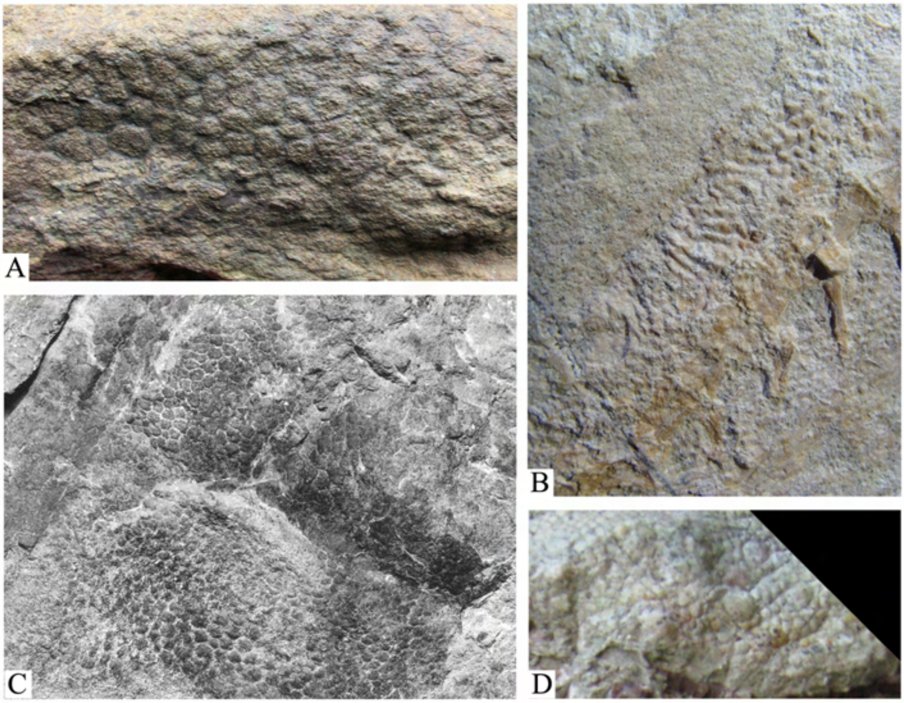

Fig. 1　Scaly integuments of several non-avian dinosaurs
A. the sauropod *Mamenchisaurus*; B. the compsognathid *Juravenator*; C. the stegosaurian *Gigantspinosaurus*; D. the ceratopsian *Psittacosaurus*

The basal ornithomimosaur *Pelicanimimus polyodon* has been reported to have filamentous integumentary structures (Pérez-Moreno et al., 1994), but this was questioned later (Xu, 2002). No other information has been published on ornithomimosaur skin, though the holotype of *Pelicanimimus polyodon* preserves even the impressions of muscle fibers.

In the Alvarezsauroidea, the only known integumentary fossil record is the extremely short, filamentous elements reported to be associated with *Shuvuuia deserti* (Schweitzer et al., 1999). The integumentary nature of these small filaments has been revealed by an immunological study that demonstrates the presence of β keratins in these filaments (Schweitzer et al., 1999).

The therizinosauroid integument is represented by two *Beipiaosaurus* specimens from the Early Cretaceous Yixian Formation (Xu et al., 1999, 2009b). Large patches of integumentary structures were found in close association with the ulna, radius, femur and tibia, as well as with pectoral elements of the holotype of *Beipiaosaurus inexpectus*. Most of the integumentary filaments near the ulna are about 50 mm long and can be up to 70 mm. They are probably tubular and branched distally. An unusual morphotype of filamentous appendages has been found in the holotype of *Beipiaosaurus inexpectus* and in a specimen referable to *Beipiaosaurus* (Xu et al., 2009b). They are composed of a single, rigid filament and are up to 150 mm long and about 2 ~ 3 mm wide, which are large for an animal of about 2 meters in total body length. These feathers are distributed on the posterior part of the skull and mandible, anterior part of the neck, over the shoulder girdle, and along the distal part of the tail.

Feather impressions are preserved on specimens of two oviraptorosaur taxa. In the holotype of *Protarchaeopteryx robusta*, plumulaceous feathers are preserved near the chest, anterior portion of the tail, and near the femur, and they are up to 27 mm long. Rectrices are preserved attached to the posterior caudal vertebrae. They are at least 132 mm long, with a basally 1.5-mm-wide rachis and symmetrical vanes which are slightly more than 5 mm wide (Ji et al., 1998). The rectrices have plumulaceous barbs basally. In *Caudipteryx*, remiges are preserved along metacarpal II, phalanx II-1, and the base of phalanx II-2 and also appear to be along the forearms. The longest remex is about 160 mm long in IVPP V 12344 with an about-150-mm-long femur. The remiges have symmetrical vanes on either side of the rachis. As in *Protarchaeopteryx*, rectrices are attached to posterior caudal vertebrae. They have symmetrical vanes (The vane of the sixth feather is 6 mm wide on either side of the rachis) and a rachis of about 0.7 mm wide. The body is covered by plumulaceous feathers of up to 14 mm long (Ji et al., 1998).

The holotype of the troodontid *Jinfengopteryx* preserves feathers around the neck, trunk, hip, upper hindlimb, tail and manus. Those near the neck, body, hip and upper legs are short and simple in morphology, similar to *Sinosauropteryx*, *Protarchaeopteryx* and some dromaeosaurids; some feathers near the manus are also not pennaceous (Ji et al., 2005). Rectrices are, however, clearly present along nearly whole length of the tail, as in *Archaeopteryx*, and they have symmetrical vanes (Ji et al., 2005). In the basal troodontid *Anchiornis huxleyi*, there are several morphotypes of feathers including pennaceous feathers. Plumulaceous feathers cover nearly the whole body except the limbs and tail. Pennaceous feathers are present along the forearm and manus, along the tibia, metatarsus, and nearly whole pedal digits, and also along the tail (Hu et al., 2009).

Fossilized feathers have been reported from a number of dromaeosaurid specimens, referable to several different taxa (Xu, 2002). The holotype of *Sinornithosaurus millenii* is a subadult individual and it preserves three different morphotypes of feathers: compound structure composed of multiple filaments joined in a basal tuft, or multiple filaments inserting on the distal end of a rachis, or multiple filaments joined at their bases in series along a central filament (Xu et al., 2001). Surprisingly, no pennaceous feathers are visible though feathers are preserved around the whole skeleton of the holotype of *Sinornithosaurus millenii*. In a smaller specimen referable to *Sinornithosaurus*, similar feathers have been reported (Ji et al., 2001), but some of them are closer in morphology to pennaceous feathers than those in the holotype of *Sinornithosaurus millenii*. In the holotype of *Microraptor zhaoianus*, feather-like structures have been reported to bear prominent rachis, but no typical pennaceous feathers are visible (Xu et al., 2000). In the holotype of *Microraptor gui*, several different morphotypes of feathers have been reported, including short plumulaceous feathers which are preserved near the skull, along the neck, and around the hip region, short pennaceous feathers which are preserved over the skull, and flight feathers that are preserved along the forearms, manus, tibia, metatarsus, and posterior half of the tail. Noteworthy is that some of the flight feathers have asymmetrical vanes (Xu et al., 2003). The longest rectrices are more than 220 mm long in the holotype of *Microraptor gui*, an individual of about 77 cm in total body length.

Scansoriopterygidae is a newly discovered theropod higher taxon which has been placed at the base of the Avialae (Zhang et al., 2008b). *Epidexipteryx hui* holotype has well-preserved feathers around nearly the whole skeleton. Two morphotypes of feathers have been identified in this specimen. Short plumulaceous feathers are similar to those of other feathered dinosaurs in having branched structures, but their nearly parallel barbs appear to arise from the edge of a membranous structure (Zhang et al., 2008b). Four long tail feathers which miss the distal ends have a central rachis and unbranched vanes, a morphology similar to highly specialized tail feathers of several basal birds (Zhang and Zhou, 2006).

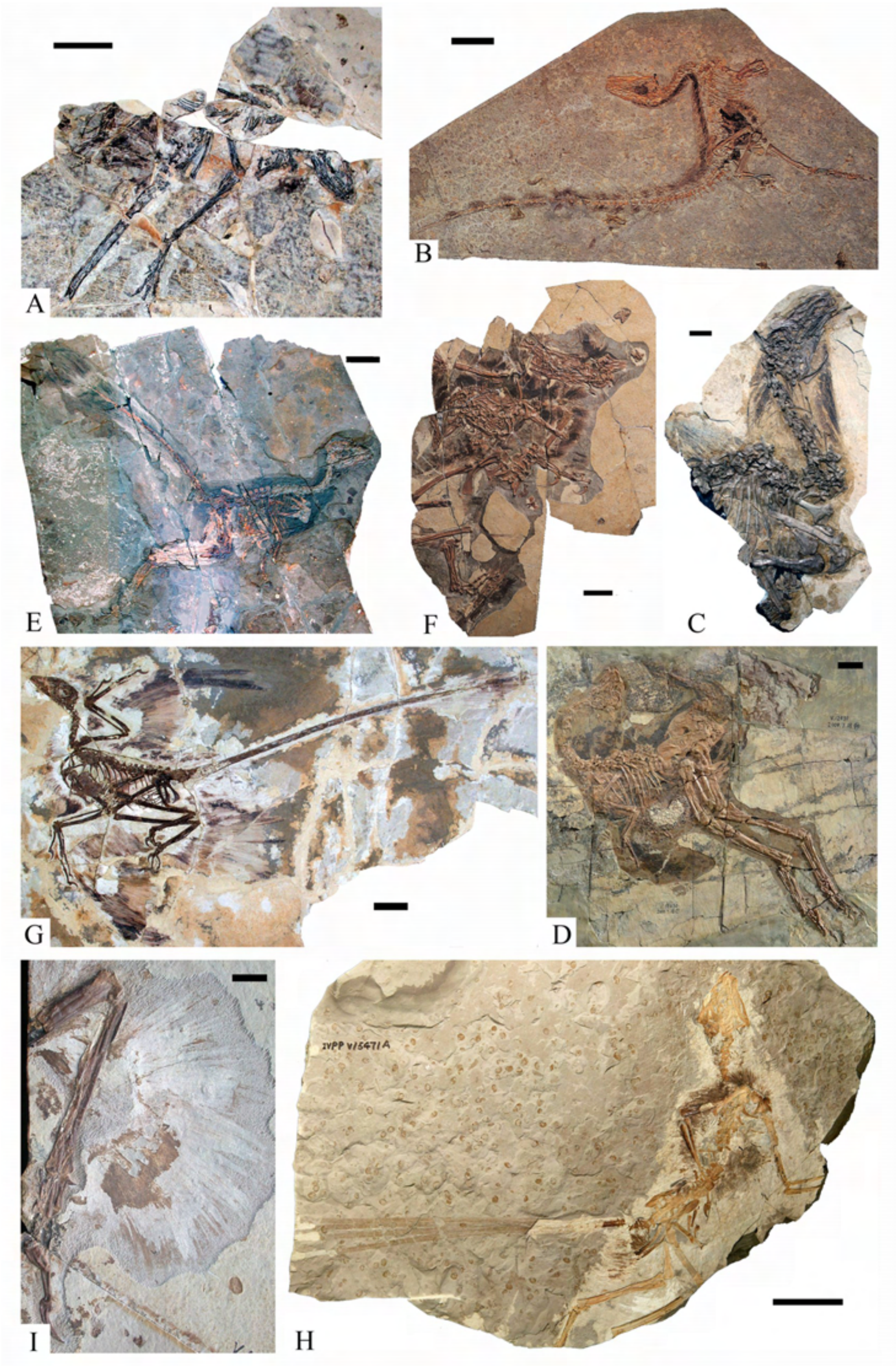

Fig. 2　Filamentous integuments of several non-avian dinosaurs

A. the heterodontosaurid *Tianyulong*; B. the compsognathid *Sinosauropteryx*; C. the therizinosauroid *Beipiaosaurus*; D. the oviraptorosaur *Caudipteryx*; E. the troodontid *Jinfengopteryx*; F. the dromaeosaurid *Sinornithosaurus*; G. the dromaeosaurid *Microraptor*; H. the scansoriopterygid *Epidexipteryx*; I. the avialan *Pedopenna*; scale bars = 5 cm in A–H and = 0.5 cm in I

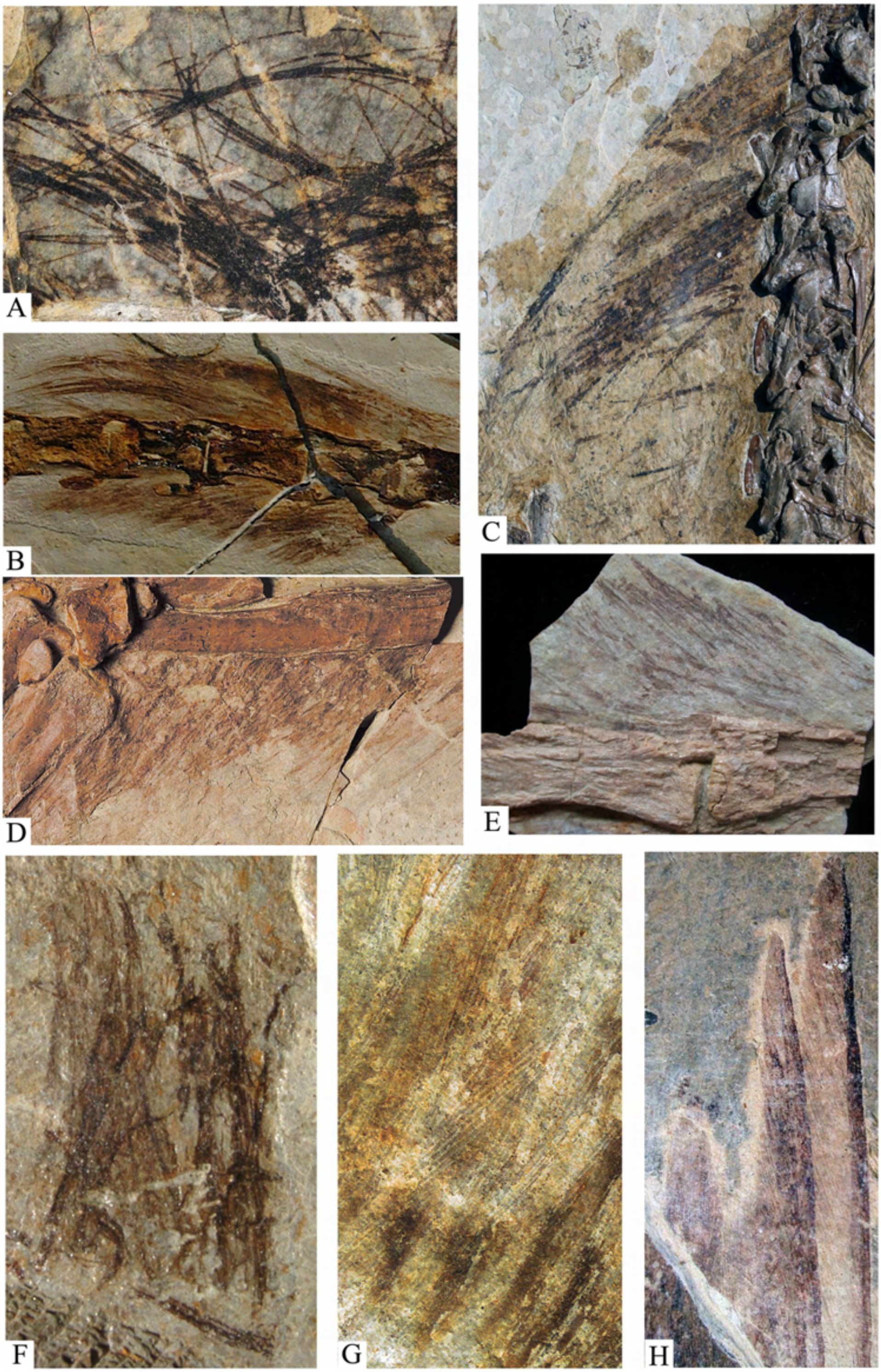

Fig. 3 Close-up of filamentous integuments
A. *Tianyulong*; B. *Sinosauropteryx*; C, D. *Beipiaosaurus*; E. *Dilong*; F. *Sinornithosaurus*; G. *Caudipteryx*; H. *Microraptor*

3 Evolutionary origin of feathers

The integumentary appendages seen in non-avian dinosaurs document a series of transitional forms from typical archosaurian scales to typical avian feathers. These paleontological data stimulate new discussions on the origin and early evolution of feathers in developmental biology (Harris et al., 2002; Yu et al., 2002; Sawyer et al., 2005) and significant advances have been made recently from the perspective of biochemistry, cellular biology, and molecular biology.

3.1 New insight from neontological data into feather origin

Feathers are composed of a subclass of β-keratins (feather type β-keratins or Φ-keratins). However, recent studies show that Φ-keratins are not unique to feathers and they are also expressed in avian scutate scales, beak, and claw and also the bristles of the wild turkey beard (Sawyer et al., 2003b), though they are slightly larger in scales than in feathers (Sawyer et al., 2000; Prum and Brush, 2002). Further more, alligator claw is also composed of Φ-keratins and alligator embryonic scales have their outer layer formed by Φ-keratins as well, suggesting that biochemical composition of feathers is similar to that of archosaurian scales (Sawyer et al., 2000, 2003a) and is not truly innovative in this respect.

At the cellular level, recent developmental studies support the homology between the embryonic epidermis of alligator, the epidermal cell populations of the scutate scales and the feathers of avian embryo (Harris et al., 2002; Sawyer et al., 2003a), though there are some differences between the cytodifferentiation of scales and feathers (avian feathers continue their epidermal cytodifferentiation at hatching compared to discarding the epidermal cell populations at hatching in archosaurian scales) (Sawyer et al., 2003a). These data indicate that first feathers might have evolved from their predecessors in an incremental manner rather than in an innovative way from the perspective of biochemistry and embryological developmental mechanism.

In the molecular level, much advances have been made on the understanding of feather morphogenesis (Chuong et al., 2003; Widelitz et al., 2003; Sawyer et al., 2005). A number of genes are involved in developing epithelial appendages (Chuong et al., 2003), and among them, *Bmp* and *Shh* genes are significant in regulating the formation and balance among the rachis and barbs of feathers (Widelitz et al., 2003). *Shh* and *Bmp* signaling is a conserved developmental signaling module in archosaur epidermal appendage development and derived patterns of *Shh*-*Bmp*2 signaling result in the novel features in feather development such as the barb ridge formation (Zou and Niswander, 1996; Harris et al., 2002). A recent study further demonstrates that the antagonistic balance between noggin and *Bmp*4 plays a key role in feather branching, with *Bmp*4 promoting rachis formation and barb fusion, and noggin enhancing rachis and barb branching (Yu et al., 2002). These studies support the transformational mode of barb to rachis and suggest that radially symmetric feather is more primitive than the bilaterally symmetric feather in terms of molecular and developmental mechanisms (Yu et al., 2002).

3.2 Major feather morphotypes in non-avian dinosaurs

A few different types of filamentous integumentary structures are known from non-avian dinosaurs and it is debated whether all these morphotypes are referable to feathers (Sawyer et al.,2003b; Xu et al., 2009b; Zheng et al., 2009). In an evolutionary context, defining feathers is a somewhat arbitrary procedure. Modern feathers are diverse in morphology and some feather morphotypes are much simpler than other morphotypes in form, but as a whole they can still be defined as complex integumentary appendages formed by hierarchical branches of rachis, barbs, and barbules which are composed of Φ-keratins and grow from a follicle. Such a structure is characteristic of a set of unique biochemical, morphological, and developmental features (Chuong et al., 2003) and is suggested to represent an evolutionary novelty (Prum, 1999).

However, complex modern feathers must have been evolved from simpler structures and their morphological and developmental complexity probably has been increased incrementally in feather evolution; it is therefore somewhat arbitrary to define structures such as feathers in an evolutionary context. Nevertheless, terminology is important in science activity and in this case a definition for feathers that can been applicable to both modern feathers and its close evolutionary predecessors is necessary for studying feather evolution and for communication and education purposes as well.

Most developmental criteria for defining modern feathers are not applicable to fossil feathers, though many of fossil feathers are inferred to be developed in similar way as modern feathers based on nearly identical or identical morphology that they shared with modern feathers. Defining feathers thus has to depend on morphological criteria in studying fossil feathers.

Several important morphological criteria for defining modern feathers include filamentous morphology produced by a proximo-distal growth mode, essentially tubular nature, presence of a follicle that has the ability to molt and regenerate, and hierarchical branches of rachis, barbs, and barbules. In an evolutionary context, these features have probably evolved in an incremental manner rather than simultaneously, as also indicated by developmental data. Among these defining features, tubular nature and filamentous morphology represent the earliest ones appearing in feather evolution and mark the origin of feathers as indicated by both paleontological and neontological data (Harris et al., 2002; Xu et al., 2009b). Feathers are thus here defined as integumentary structures that are tubular and filamentous in morphology. Follicle, hierarchical branches, and planar form are inferred to have evolved later in feather evolution. Under such a definition, eight morphotypes of feathers are identified in non-avian dinosaurs (Fig. 4).

Morphotype 1 is known from the heterodontosaurid *Tianyulong* and the ceratopsian *Psittacosaurus* (Mayr et al., 2002; Zheng et al., 2009). Its main characteristic is being monofilament and relatively great length and rigidity. A variant of this morphotype is seen in *Beipiaosaurus*, which differs from those of *Tianyulong* and *Psittacosaurus* in its relatively great width (Xu et al., 2009b). Morphotype 2 is a compound structure composed of multiple filaments joined basally. It is clearly present in *Sinornithosaurus* and *Anchiornis*, and probably also in *Sinosauropteryx* and *Beipiaosaurus*. Morphotype 3 is a distally branched filament, which is seen in the holotype of *Sinornithosaurus millenii* and probably in *Beipiaosaurus* (Xu et al., 1999). The main characteristic of this morphotype of feather is its barbs breaking off from the tip of a central filament and distally positioned short barbs. Morphotype 4 is a compound structure consisting of multiple filaments branching laterally from most of the length of a central filament. It is known in *Sinornithosaurus*, *Anchiornis*, *Caudipteryx*, *Protarchaeopteryx*, and probably *Dilong* as well (Xu et al., 2004). Morphotype 5 is only known in *Epidexipteryx*. It consists of parallel barbs arising from the edge of a membrane structure (Zhang et al., 2008b). Given its so unusual morphology, possibility of its being part of a more complete integumentary structure could not be completely excluded, particularly in consideration that morphotypes 2 and 4 display distally parallel barbs in some cases.

Two morphotypes of pennaceous feathers are known in non-avian theropods. Morphotype 6 is known in *Caudipteryx*, *Protarchaeopteryx*, *Microraptor*, and *Anchiornis*. It is a fully pennaceous feather with a prominent rachis and well organized, symmetrical vanes. While most of these pennaceous feathers have straight rachis, distal remiges of *Anchiornis* have moderately curved rachis. Morphotype 7 is only known in *Microraptor*. It is similar to morphotype 6 in general morphology, but differs in vane asymmetry and rachis curvature. Morphotype 8 is a type of highly specialized feathers known in *Epidexipteryx hui* (Zhang et al., 2008b), which have undifferentiated vanes on either side of a rachis. It is likely to be similar to tail feathers of some basal birds that have typical branched vanes close to their tips.

Morphotypes 3, 4, 6, 7 and 8 are shafted feathers and morphotypes 1, 2, and 5 are nonshafted feathers according to the category system proposed by Zhang and Zhou (2006). Some of

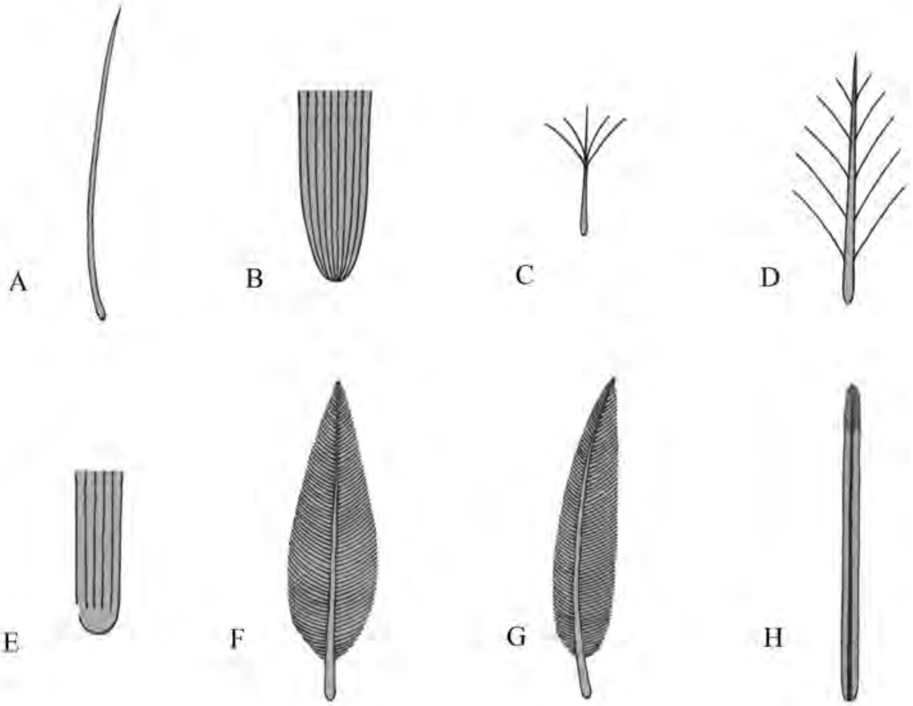

Fig. 4 Known feather morphotypes of non-avian dinosaurs

A. morphotype 1, single filament; B. morphotype 2, multiple filaments joined basally; C. morphotype 3, multiple filaments jointed basally on a central filament; D. morphotype 4, multiple filaments branching laterally from most of the length of a central filament; E. morphotype 5, multiple filaments arising from the edge of a membrane structure; F. morphotype 6, compound structure composed of a prominent rachis with symmetrical, well-organized and closed vanes on either sides; G. morphotype 7, compound structure composed of a prominent rachis with asymmetrical, well-organized and closed vanes on either side; H. morphotype 8, a prominent rachis with symmetrical, undifferentiated vanes on either side

these feather morphotypes can correspond to modern feathers, such as morphotypes 6 and 7 (and probably morphotype 8), but other morphotypes such as morphotypes 1-5 are difficult to be referred to a known modern feather category. They could be primitive feathers different from any modern feathers. Alternatively, this could be due to the fact that the available specimens do not preserve enough details or we are unable to observe some preserved morphologies. Nevertheless, the distribution of these feather morphotypes across a dinosaurian phylogeny, in combination with recent advances in neontological study on archosaurian integuments, reveals an evolutionary sequence of these structures and their possible adaptive context (Fig. 5).

3.3 Major morphogenesis events in feather evolution

Five major morphogenesis events are inferred to have occurred sequentially in feather evolution before the origin of the Aves and they are: 1) appearance of filamentous and tubular morphology, 2) formation of follicle and barb ridges, 3) appearance of rachis, 4) appearance of planar form, and 5) formation of pennaceous barbules.

Feather morphotype 1 described above might document the appearance of filamentous and tubular morphology in feather evolution. Although several studies suggest that follicle is a characteristic of the first feather (Prum, 1999; Brush, 2000), numerous studies demonstrate the formation of the embryonic feather filament prior to follicle formation (Sawyer et al., 2003a).

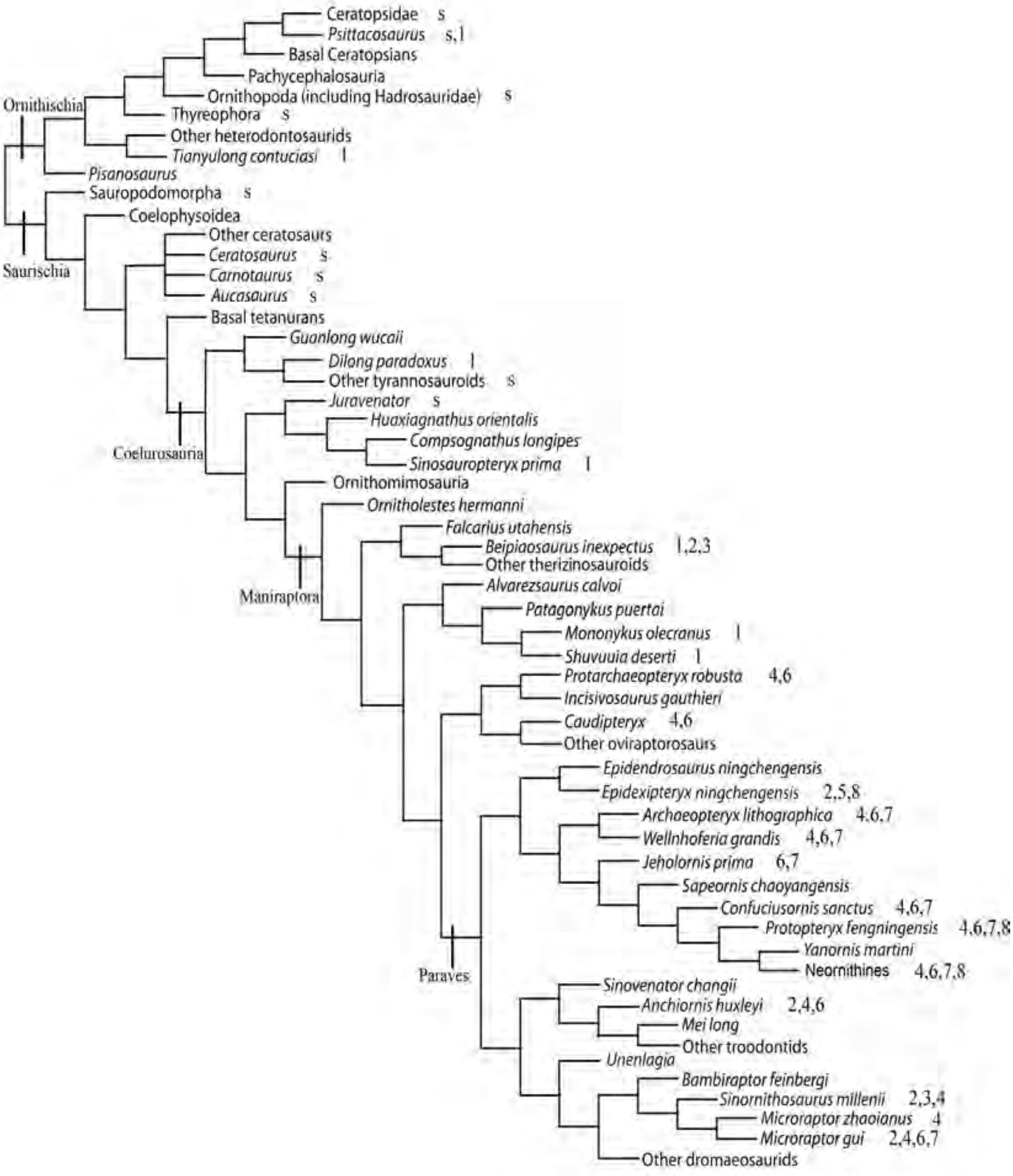

Fig. 5 Distribution of major feather morphotypes across a simplified dinosaurian phylogeny based on Sereno, 1999, Xu, 2002, and Butler et al., 2008

Numbers refer to the feather morphotypes identified in present paper and s refers to the presence of scaly integumentary structures

An embryonic feather filament is characterized by periderm, sheath, and barb ridge cell populations in crown birds, but the first feather might not be identical to the embryonic feather filament of extant birds. However, the importance of the cylindrical configuration and tubular nature, both featuring the embryonic feather filament, has been emphasized in initiating the morphogenesis of modern feathers by recent development studies (Harris et al., 2002; Prum, 2005). Given that the integumentary structures seen in some pterosaurs (Bakhurina and Unwin, 1995; Ji and Yuan, 2002; Wang et al., 2002) are filamentous and possibly tubular, feather morphotype 1 thus has a broad distribution among the Ornithodira (the clade include the Pterosauria and Dinosauria) and the first feather could have evolved at the base of the Ornithodira (Xu et al., 2009b; Zheng et al., 2009). If this is true, feathers would have a long evolutionary history of about 240 million years (Xu et al., 2009b).

Feather morphotype 2 probably documents the appearance of follicle and barb ridges. Although a series of basally jointed filaments represents a simple branching pattern, developmentally a relatively complex mechanism is probably necessary for developing such a structure. Given that follicle plays a key role in producing many innovative features in feather development (Prum, 1999; Brush, 2000) and particularly branching occurs within the follicle during the development of modern feathers, feather morphotype 2 probably indicates the presence of a follicle. On the other hand, barb ridges are developed earlier than follicle and their development initiates the formation of follicle in modern feathers. Consequently the appearance of follicle and barb-ridges might be simultaneous in feather evolution.

Barb ridges play a central role in feather development and they finally develop into hierarchical branches of rachis, barbs, and barbules (Alibardi, 2005). The filaments of feather morphotype 2 are apparently unlikely to be rachis. It remains unknown whether these filaments are just rami or complete barbs with barbules because the state of preservation does not allow either a positive identification of barbules on these filaments or a rejection of the presence of such structures. A notable feature is that the filaments in feather morphotype 2 are somewhat strap-like, a feature also characteristic of barbs in modern feathers, yet the filaments in feather morphotype 2 are apparently proportionally wider than barbs in modern feathers. Recent developmental studies demonstrate the impossibility of separate formation of barb and barbule cells and suggest that primitive feathers with only barbs but not barbules are unlikely to exist (Alibardi, 2005). If this holds true, some sort of simple, small barbules might be present in feather morphotype 2 or other primitive feathers.

Feather morphotype 3 documents the rachis formation. The rachis is formed by fusion of barb basal ends through a helical growth mode of barb ridges in modern contour feathers, but is formed in a different way in some other morphotypes of feathers, though fusion appears to be involved in the formation of all morphotypes of feathers with a rachis (Lucas and Stettenheim, 1972). Nevertheless, neontological data, at both embryological and molecular levels, support the hypothesis that barbs have appeared evolutionarily before rachis. The barb-first model is also supported by fossil feathers. Besides fossil evidence from Liaoning, Perrichot et al. (2008) reported a morphotype of feather that has a shaft consisting of incompletely fused, still distinguishable, partially superimposed barbs. Some isolated feathers from the Barremian limestones of Spain appear to have only barbs but not rachis (Sanz et al., 1988).

Feather morphotype 4 might document the appearance of planar form. Planar form of feathers basically results from the helical growth of barb ridges within the follicle. Bilaterally arranged barbs along a rachis indicate the presence of planar form, which is a critical feature for the majority of modern feathers.

Feather morphotypes 6–7 document the formation of pennaceous barbules. Although not being observed directly, pennaceous barbules are probably present in pennaceous feathers of *Caudipteryx*, *Protarchaeopteryx*, and *Anchiornis* given their well-organized vanes; barbules are visible in pennaceous feathers of *Microraptor*, but details are not clear. Given the significance of contour feathers (including flight feathers) in living birds, the appearance of pennaceous barbules and consequently of pannaceous feathers mark one of the most important events in feather evolution. The presence of pennaceous feathers in *Anchiornis* (Hu et al., 2009) suggest that this important event have occurred about 160 Ma or even earlier.

Noteworthy is the elongate ribbon-like tail feathers seen in *Epidexipteryx* and some basal birds as well, including confuciusonithids (Zhang et al., 2008a) and some enantiornithines (Zhang and Zhou, 2000). Although these highly specialized tail feathers have been suggested to represent a type of primitive feather and their discovery to support a scale plate-rachis-barbs model for feather evolution, their relatively late appearance in feather evolution, extremely limited distribution on the body, and discovery of similar tail feathers in *Confuciusornis* but which is distally branched as the normal pennaceous feathers (Chiappe et al., 1999; Zhang and Zhou, 2006) are against such a suggestion. Further more, some living birds have superficially scale-like feathers which are formed by the fusion of barbs (Prum and Brush, 2002). Developmentally suppression of Sonic hedgehog (*Shh*) can lead to a webby membrane remnant between barbs (Widelitz et al., 2003) and thus the scale-like feathers in *Epidexipteryx* and some basal birds are likely to be a similar variant of the normal pennaceous feathers produced by the same genetic change.

3.4 Feathered feet

Three non-avian dinosaurs are known to bear large pennaceous feather on their feet, including basal dromaeosaurid *Microraptor*, basal troodontid *Anchiornis*, and basal avialan *Pedopenna*. Large pennaceous feathers on lower legs also appear to be common in basal avians (they are reported in *Archaeopteryx*, *Confuciusornis*, and some enantiornithines) (Christiansen and Bonde, 2004; Zhang and Zhou, 2006). In living birds, lower legs are not extensively feathered as in most other parts of the body and normally are covered by only small feathers (but in hawks, owls, and many cuckoos, a group of large feathers called a crural flag is seen in the knee region). Some living birds (such as grouse, owls, many hawks and breeds of chickens) have feathered feet, but most extant birds lack feathers completely on their feet (Lucas and Stettenheim, 1972). The feathering of lower legs including feet is thus different between basal paravians, in which lower legs represent the third major anatomical region besides the forelimbs and tail bearing large pennaceous feathers, and most other birds, in which lower legs are among the least feathered regions of the body.

Scale formation on the avian legs including feet first requires a repression of feather development (Sawyer et al., 2005), which has been suggested to indicate that the avian scutate scales are derived from feathers (Sawyer and Knapp, 2003). Avian scutate scales share uniquely with avian feathers in having ectodermal placodes, though they differ temporally, morphologically, and functionally from those of feathers (Sawyer et al., 2005). Consequently, both paleontological and neontological data suggest that feathered feet are primitive condition for the Paraves and avian scutate scales might be derived structures, different from pedal scales of non-avian dinosaurs.

Interestingly, the phylogenetic and anatomical distribution of large pennaceous feathers shows that these structures first evolved on the distal portions of the hindlimbs as in forelimbs and tail in maniraptoran theropods (Xu et al., 2003; Hu et al., 2009), though large leg feathers are reduced and lost subsequently in avian evolution. Such a distal-first pattern is also seen in the development of flight feathers in living birds (Lucas and Stettenheim, 1972).

3.5 Feather tract evolution

Although developmentally feather morphogenesis starts from the formation of feather tract fields, it is probably not the first step evolutionarily as suggested by some developmental studies (Widelitz et al., 2003). Because feather tracts are characteristic of the presence of contour feathers, their appearance is probably associated with the evolution of contour feathers, the dominant feathers on the body of living birds. Large pennaceous feathers are seen in limbs and tail of *Caudipteryx*, *Protarchaeopteryx*, *Anchiornis*, and *Microraptor* and some short ones on the head of *Microraptor*, but there is no evidence of extensive growth of contour feathers on the body of non-avian dinosaurs. *Microraptor* is clearly covered by plumulaceous feathers on most of its body; *Epi-*

dexipteryx has more extensive covering of short, small plumulaceous feathers (Zhang et al., 2008b). Recent re-study on the Berlin *Archaeopteryx* specimen suggest that faint hair-like structures at the base of the neck may have been generated from some sort of 'proto-apteria' and longer feathers with vanes on back and legs grew from 'proto-pterylae' (Christiansen and Bonde, 2004). If this observation is true, feather tract is likely to have evolved first at the base of the Aves.

3.6 Functions of early feathers

Locomotion (including flight), thermoregulation, and display are three major functions for modern feathers and all have been previously suggested to represent the initial function of the feathers (Xu et al., 2009b). The discoveries of feathered dinosaurs from China reject the flight hypothesis (Ji et al., 1998; Xu et al., 1999). Although it is in many cases difficult to infer securely the function of fossil structures, some information is obtainable concerning the functions of early feathers and thus useful to infer the initial function of feathers.

The monofilaments in *Tianyulong* and *Psittacosaurus* (Mayr et al., 2002; Zheng et al., 2009) are apparently not related to flight functionally as they lack any aerodynamic features. They are long and rigid and are distributed on only certain parts of the body. Furthermore, their density is relatively low compared to filamentous integumentary structures of other feathered dinosaurs. Such structures could not have formed an effective insulative layer and thus the initial function of feathers is probably not related to insulation. Display and heat dissipation, among others, remain viable hypotheses for earliest function of feathers. The length, rigidity, and limited distribution on the body of the monofilaments of *Tianyulong* and *Psittacosaurus* (Mayr et al., 2002; Zheng et al., 2009) and also *Beipiaosaurus* (Xu et al., 2009b) suggest a display function for these structures. A display function has also been suggested for the elongate ribbon-like tail feathers of *Epidexipteryx* (Zhang et al., 2008b). However, the possibility of being used to dissipate heat, as seen in some lizards that have frill over their vertebral column, could not be excluded for the monofilaments of *Tianyulong* and *Psittacosaurus*, particularly if these structures are hollow inside as suggested (Mayr et al., 2002; Zheng et al., 2009).

Morphotypes 2–4 are composed of multiple filaments and interestingly these filaments are proportionally thick compared to barbs of down feathers in modern birds or hairs in extant mammals; and they are also more rigid than barbs of down feathers in birds. These structures are likely to have an insulation function as suggested by previous studies (Chen et al., 1998; Xu et al., 1999), but the above mentioned features suggest that they are not ideal structures for such a function or at least are not as effective in insulating body as down feathers of modern birds. One notable difference between the plumulaceous feathers of basal coelurosaurs such as *Sinosauropteryx* and those of derived ones such as *Microraptor* is the density. The plumulaceous feathers of the latter are more densely distributed on the body than those of the former, which implies either a functional difference or a difference in effectiveness in insulating the body.

The large pennaceous feathers seen on forelimbs and tail of *Caudipteryx* are probably not related to flight because they have no striking aerodynamic features and also because this taxon has little osteological features suggesting any aerial capability. Other functions, such as maintaining balance or producing additional thrust during running or climbing, insulating eggs, and display, are all viable hypotheses. Similar large pannaceous feathers seen in forelimbs and tail of *Protarchaeopteryx* and particularly *Anchiornis* are less clear regarding to their functions. Similar to the pennaceous feathers in *Caudipteryx*, the large pennaceous feathers in *Protarchaeopteryx* and *Anchiornis* lack striking aerodynamic features, but their bearers are osteologically fairly close to *Archaeopteryx* (for example, they have significantly elongate forelimbs) and they are possible to contribute to some sort of aerial locomotion.

Little is known about the function of large symmetrical pennaceous feathers attached to the feet of *Anchiornis* and *Pedopenna*. Because they are well organized into a coherent planar surface, they are possible to have some aerodynamic function. Modern analogy of feathers in some birds suggests a protection or insulation function for the pedal feathers of *Anchiornis* and *Pedopenna*. Another possibility is an ornamentation function, which is also inferred for feather morphotype 8. The variable morphology of metatarsal feathers in basal paravians might reflect a shift in function (from flight to ornamentation, protection or insulation) and/or relative importance in aerodynamics.

The large asymmetrical pennaceous feathers on the forelimbs, hindlimbs, and tail of *Microraptor* possess several striking aerodynamic features including strong curvature and asymmetry. For example, a distal metatarsal feather of *Microraptor* has an asymmetry ratio of more than 8, comparable to the distal primary flight feathers of some extant capable flying birds. These features strongly support the hypothesis that asymmetrical pennaceous feathers functioned in flight in *Microraptor*.

In summary, flight, insulation, and display functions are all inferred to have evolved before the origin of the Aves, but flight function is the last of the three to appear in feather evolution. Furthermore, insulation is inferred not to represent the initial function of feathers and it appears to have evolved later than a display function.

4 Conclusions

Recent paleontological and neontological data both support: 1) the first feather is a single, tubular filament; 2) barbs are structures phylogenetically appearing earlier than rachis; 3) radially symmetrical plumulaceous feathers are more primitive than bilaterally symmetrical pennaceous feathers. These conclusions represent significant advances over earlier studies on the origin and early evolution of feathers, but some debates remain regarding to various aspects of early feather evolution and a lot more critical information is needed to complete the reconstruction of evolutionary history of feathers.

The known developmental models of the origin of feathers all suggest that feathers are evolutionarily innovative structures. These studies emphasize the differences between feathers and scales, though they do demonstrate that feathers and scales share numerous similarities biochemically, genetically, at cellular level, and in early embryological development (they are thus partially homologous). Most developmental models accept simple filamentous integumentary structures of non-avian theropods as feathers and suggest them to have grown from a follicle because the latter structure plays a central role in producing unique features of modern feathers. These models suggest that the first feathers are not homologous to scales of any form. An extreme example of emphasizing the novelties of feathers is the questioning of the homologous relationships between feathers of modern birds and the simple filamentous integumentary structures of non-avian theropods (Sawyer et al., 2003b). For example, because the bristles of the wild turkey beard possess several striking defining features of modern feather such as expressing the feather-type β keratins, hollow, and branching distally, some recent developmental studies consider these features not to be the defining features of feathers any more and suggest that the simple filamentous integumentary structures of some non-avian theropods are not primitive feathers (Sawyer et al., 2003b).

An evolutionary model characteristic of both transformation and innovation for the origin and early evolution of feathers might be more acceptable (Xu, 2006). Although being proposed as evidence against the hypothesis that simple, filamentous integumentary structures are primitive feathers, the presence of some striking defining features of modern feather in the bristles of the wild turkey beard instead suggests that these features could have evolved incrementally in the predecessors of modern feathers rather than have appeared simultaneously in the first feather. The discovery of the simple, monofilamentous ornithischian integumentary structures and a pattern of increasing complexity toward the Aves for those filamentous integumentary structures in non-avian dinosaurs also provide indirect evidence supporting an incremental pattern of the evolution of feather features. A sudden appearance of a whole set of unique, complex developmental mechanisms and associated morphologies is also unlikely from the perspective of adaptation.

In future study, obtaining information on the fine details of the identified feathers in non-avian dinosaurs is important for comparing them with modern feathers and thus evaluating the exact significance of these structures. It is significant to know whether these feather morphotypes have barbules, whether they have a calamus or have a short rachis, whether a follicle is present, and how the distribution pattern of various feathers on non-avian dinosaur body, which contribute significantly to the understanding of the exact evolutionary sequence of some important features of feathers and the functional inference of some early feathers. In developmental studies, more data is needed on the mechanisms of the rachis formation in non-contour feathers and of the relationships between the formation of barb ridges and follicle. An integrative study of paleontology and neontology on feather evolution promises to shed significant new insights into this extremely intriguing evolutionary issue.

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