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Origin of feathers – perspectives from fossil evidence

ZHONGHE ZHOU AND FUCHENG ZHANG

Introduction

Feathers are probably the most complex and fascinating integuments of vertebrates. The issue of the origin of feathers has puzzled scientists for over a century. Perhaps with the appearance of civilization and culture, the fact feathers are a unique feature distinguishing birds from reptiles has become as obvious to us as the day and night. This is probably still the case for many of us, but most paleontologists would now say "wait!" and tell you a different story. The secret they believe they have discovered is that there existed feathered dinosaurs. While ornithologists and paleontologists are still hotly debating on the presence of feathers in several dinosaurs from China, an international research group comprising ornithologists, paleontologists and physiologists announced that they found feathers in a much more ancient and primitive reptile, named *Longisquama* from Kyrgyzstan. Only a few months earlier, Chinese paleontologists reported an intermediate integumentary type between reptilian scales and avian feathers in a primitive bird, named *Protopteryx*.

In the past, most of the evidence in the study of the origin of feathers has been derived from the developmental and theoretical work. Little fossil evidence has played an important role in the discussion of the hypothesis on the origin of feathers. The feathers of the oldest known bird *Archaeopteryx* are basically of modern appearance and could provide little information for the study of the early stage of

Z. Zhou, Research Professor of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. His main interest is the origin and early evolution of birds and their flight. E-mail. zhonghe@yeah.net.

F. Zhang, Associate Research Professor of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. His main interest is the early evolution of birds, feather evolution and paleohistology of birds and dinosaurs. E-mail. fuchengzhang@yeah.net

feather evolution. *Longisquama* is probably the only fossil that has shed light on the issue of the origin of feathers. This situation has significantly changed over the past several years as a result of the findings of half dozen feathered dinosaurs in China, which has in turn trigged a new round of hot debate on the issue of the origin of feathers.

In the study of the origin and evolution of feathers, there are several important aspects that have often been dealt with more details. One is about the functional explanation or selective pressures involved; in other words, one has to answer whether feathers were developed initially for flight, thermoregulation, display or other purposes. The second is related to the intermediate structures; one has to propose an evolutionary model as to how feathers with modern structures were progressively developed. Another relevant issue is perhaps about the long-standing debate of hot-bloodness (endothermy) versus cold-bloodness (ectothermy) in dinosaurs and early birds. In this paper we will focus our discussions on these issues mainly based on recent fossil discoveries, and hopefully will provide a summary of the advances in the study of the origin of feathers from the evolutionary perspectives.

Fossil discoveries and debates

1. Protofeathers in theropod dinosaurs Sinosauropteryx *and* Sinornithosaurus?

Since 1996, several small to medium sized theropod dinosaurs from the Early Cretaceous lake deposits of the Yixian Formation in western Liaoning Province, northeast China have been reported to be clothed with protofeathers. These new and surprising feathered creatures have been dated as old as approximately 125 million years from present. Among these theropods, the first described is dubbed *Sinosauropteryx*[1], generally believed to be a close relative of another famous chicken-sized theropod *Compsognathus* from the Late Jurassic marine deposit in Solnhofen, Germany. Unlike the latter, *Sinosauropteryx* has hair-like integuments, which are exclaimed by many paleontologists as the first evidence of feathers in dinosaurs. Thus, it not only lends strong support to the dinosaurian origin of birds but also has many implications for the origin of feathers. *Sinosauropteryx* is obviously a fast running theropod with no flying capability, therefore the protofeahers in this creature could not be used for flight. As a result, paleontologists quickly inferred from this fossil that feathers were probably initially developed for thermoregulation or display rather than for flight. And the flight function of feathers must be explained as an exadaptation.

Quickly after the discovery of *Sinosauropteryx*, another feathered theropod *Beipiaosaurus*[2] was described. This creature is a medium sized theropod unique to the East Asia areas in the Early Cretaceous. Paleontologists still disagree on exactly how this dinosaur is positioned in the phylogenetic trees of theropod evolution. Although *Beipiaosaurus*'s integuments are basically similar to that of *Sinosauropteryx* and it is generally believed that the integuments of both *Beipiaosaurus* and *Sinosauropteryx* lack any branched structures typical of avian feathers the discovery of more than one feathered dinosaurs seems to confirm that feathers were common in some dinosaurs.

While most paleontologists are celebrating the historical discoveries of feathered dinosaurs of which, John Ostrom, retired Yale Professor and the main proponent of the theory of the dinosaurian origin of birds[3], had dreamed for decades there are a few other paleontologists, ornithologists and physiologists who are not so much impressed. They argued in stead that the so-called protofeathers in those theropods are probably cartilaginous fibers[4]. In their opinion, except for superficial resemblances they have nothing to do with feathers of birds.

It is interesting to note that those who are most firmly against the dinosaurian origin of birds also disagree that those theropods have feathers. And reverse is true for those true believers of the dinosaurian origin of birds. For most paleontologists, especially dinosaur experts, these fossils were exactly what they had expected

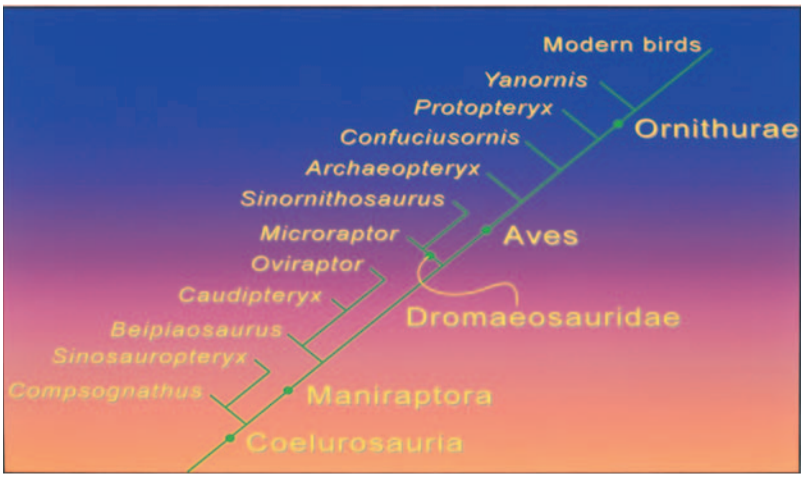

Fig. 1. *Cladogram showing the phylogenetic relationships among major groups of dinosaurs and birds.*

Fig. 2. *Protofeathers of* Sinornithosaurus, *a basal member of dromaeosaur dinosaurs that are generally believed to closest relatives of birds. The arrow points to a basal branching of feather.*

for years. But they were not completely satisfied with the evidence available. They also hope to find feathers in another group of theropods, namely Dromaeosauridae, because it is now generally accepted to be closest relatives of birds. The discovery of the *Sinornithosaurus*[5] specimen happened at the right time for two reasons: first it is a basal dromaeosaurid dinosaur with protofeathers; second, most of the dromaeosaur fossils had previously been collected from the Late Cretaceous age, and a few paleontologists argued that one major problem with the hypothesis of the dinosaurian origin of birds is that there exists time gap between the oldest bird and most of the dromaeosaurs known that were regarded to be most closely related to birds. *Sinornithosaurus* (125 millions years old) is only slightly younger than the oldest bird *Archaeopteryx* (140–150 millions years old), thus greatly reducing the gap.

Recently the integuments of *Sinornithosaurus* were restudied by a team comprising the ornithologist, paleornithologist and dinosaurologist[6]. Based on newly revealed information from the further prepared integuments of the type specimen of *Sinornithosaurus*, they concluded that their integumental appendages are compound structures composed of multiple filaments rather than simple and solitary fiber-like structures. Furthermore, they recognized for the first time in dinosaurs two types of branched structures that are unique to avian feathers in vertebrates. Among these two protofeather types, one is composed of filaments joined in a basal tuft comparable to avian natal down feathers, in which the filamentous barbs are basically fused to a calamus; the other is composed of filaments joined at the bases in series along a central shaft, which is comparable to barbs along a rachis in a pennaceous feather. In several cases they reported the noticeable central filament and secondary branches within a single appendage. With all the resemblance to modern feathers, the protofeathers of *Sinornithosaurus* are different from modern feathers at least in lacking barbules, thus preventing it from forming a closed pennaceous vane.

Most of the branched integuments of *Sinornithosaurus* are distributed along the skull, neck, forelimb, leg and tail. Since the branched structure is the most distinctive morphological feature of avian feathers, they argued that the presence of branched structures in the integumental appendages in *Sinornithosaurus* appear to corroborate that hypothesis that the integumental appendages of *Sinornithosaurus* as well as other feathered theropods are indeed homologous to the feathers of modern birds.

The study of the integuments of *Sinornithosaurus* also seems to be congruent with a developmental model of the evolutionary origin of avian feathers. According this model feathers were first developed within a hollow and cylindrical feather follicle, and then evolved through a series of evolutionary stages. In brief, feathers first evolved filamentous structure (Stage I), then basal branching (Stage II), and further a rachis with barbs (Stage III) before they evolved differentiated proximal and distal barbules, and the closed pennaceous vanes (IV) that are required for flight. The two types of branching integumental appendage in *Sinornithosaurus* are congruent with stages II and III of the developmental model. It is interesting to note that the unbranched integuments in *Sinosauropteryx* is congruent with the first stage of the aforementioned model. Since *Sinosauropteryx* is a basal coelurosaur, which is much more remotely related to birds than *Sinornithosaurus*, therefore the recognition of two types of branched integuments in *Sinornithosaurus* and unbranched integuments in *Sinosauropteryx* further support the hypothesis that feathers did first appear in dinosaurs and it had evolved into avian feathers before they were adapted for flight in birds.

2. Caudipteryx*, a dinosaur with genuine modern avian feather?*

Among the several generally called feathered dinosaurs from Liaoning, northeast China, there are two genera that are significantly different from others in several aspects. First, they have true feathers that are hardly distinguishable from modern feathers; second, their phylogenetic positions are more controversial. One of them was called *Protarchaeopteryx* because it was first recognized as a primitive bird, the second is named *Caudipteryx* after its fan-shaped tail feathers[7]. Since its publication, *Protarchaeopteryx* has been relatively less known due to poor preservation; however, *Caudipteryx* has now been represented by two species and several completely articulated specimens[8-9].

No one has doubted about the recognition of true avian feathers in these two obviously cursorial creatures. They are both larger than *Sinosauropteryx* and the oldest bird *Archaeopteryx*. Besides, it can be easily concluded that neither of them could fly as indicated by their elongated legs and relatively short forelimbs. Several new materials of *Caudipteryx* confirm that it has symmetrical feathers attached to the forelimb. It has been well known that all volant birds have asymmetric flight feathers, the loss of asymmetry is characteristic of secondarily flightless birds.

For many paleontologists, these fossils are just too good to be true because the protofeathers of *Sinornithosaurus* and others are remarkably distinguishable from those of modern birds. If unambiguous

Fig. 3. *A nearly complete skeleton and feathers of* Caudipteryx*, presumably a dinosaur with feathers nearly identical to those of modern birds.*

feathers are indeed present in dinosaurs, then it will be really difficult to reject the hypothesis of the dinosaurian origin of birds. However, a few paleontologists quickly pointed out that these two so-called feathered dinosaurs were probably not dinosaurs at all, they could be secondarily flightless birds or "Mesozoic Kiwi" [4,10]. Except for feathers, *Caudipteryx* did preserve several characters that are quite similar to birds. For instance, the manual digits are reduced into a "2-3-1" format much like in advanced birds[9].

While resembling birds in some characteristics, *Caudipteryx* also show characters typical of dinosaurs such as a ventro-anteriorly directed pubis and unfused tarsometatarsus. The phylogenetic position of a creature is not decided by a single or a few characters, but by a cladogram. Then how do we get a cladogram? Today, the phylogenetic method most paleontologists use in systematic analysis is called cladistics. The philosophy behind the method is called the principle of parsimony. In practice, they use all available anatomical characters from selected taxa, polarize them into primitive or derived (represented by 0 and 1, respectively) and put them in a data matrix, then they run a computer program to choose the most parsimonious tree that requires the fewest evolutionary steps from one taxa to others. In the case of *Caudipteryx*, most paleontologists now conclude that it is embedded in the theropod dinosaurs, and furthermore it is most closely related to a particular lineage of dinosaurs called oviraptorids[11].

The phylogenetic result of *Caudipteryx* is both exciting and difficult to explain for paleontologists because it implies that feathers with modern structures were indeed present in dinosaurs; on the other hand, the phylogenetic distribution of different feathers types in dinosaurs seem to be incongruent with the evolutionary model of the origin of feathers. In other words, *Caudipteryx* is less closely related to birds than dromaeosaurs such as *Sinornithosaurus* but it has much more advanced feathers. How do we explain this dilemma? There seem to be two alternations: one is that *Caudipteryx* is a bird, the phylogenetic position is not correct. Although the cladistic method is currently widely used by many paleontologists, it has also been strongly criticized by others, they argue that no one can provide evidence that the most parsimonious evolutionary tree must be the one that best reflects the phylogeny of organisms; the second alternative is that modern feathers had independently evolved more than once. The second alternative hypothesis will certainly be criticized by many biologists because feathers are generally accepted as the most complex integumentary derivatives in any vertebrates.

At the moment, more anatomical work of *Caudipteryx* is still going on. Until a comprehensive and commonly accepted phylogenetic conclusion about this feathered creature is accepted, it would be difficult to evaluate either of the two aforementioned hypotheses.

3. Feathers in the Triassic archosaur reptile Longisquama*?*

Longisquama was first described in 1970 as a mouse-sized archosaur reptile from the Late Triassic (220 million years from present) [12]. Archosaurs are the stem group of reptiles in the Mesozoic that had given rise to dinosaurs, crocodiles, pterosaurs and birds. The most distinctive feature of *Longisquama* is the presence of a series of elongated and paired integumental appendages or generally known as long scales along the dorsal axis. The scales are vane-like and up to 12 centimeters long. Each scale has a longitudinal ridge and some branching features on both side of the middle ridge. Ever since the discovery of *Longisquama*, it has been pictured by many paleontologists as a gliding animal, and accordingly the long scales as an experiment of scales elongation, in a sense representing a transitional stage between scales and feathers. Others have suggested in stead that the elongated scales were only for sexual display and could have nothing to do with gliding.

Recently, a paper was published in *Science* with description of its appendages in the greatest detail yet[13]. The authors not only argued that these scales resemble avian feathers in many details but also went even further: they argued that they are feathers much like modern feathers. Notably the authors proposing the radial view are also the most radial opponents of the dinosaurian origin of birds. The significance of this work to them cannot be more obvious: because feathers existed in pre-dinosaur reptiles and feathers are the most complex integumentary derivatives in vertebrates and they were unlikely developed twice, therefore birds might have come from a group of animals as primitive as *Longisquama* rather than dinosaurs. The main evidence they cited as supporting their arguments of feathers in *Longisquama* are summarized as follows: first, each of the elongated scale is composed of a central axis comparable to the rachis of avian feathers; second, distally the shaft is branched regularly from the central axis, which is comparable to the barbs of avian feathers; third and probably most importantly, the base of the integumentary appendages is also similar to the tubular or cylindrical morphology of the calamus of avian feathers, which is consistent with development within a follicle unique to feathers.

Not surprisingly, the explanation of the integuments of *Longisquama* as feathers had quickly drawn strong criticism[14]. Two groups of paleontologists[15-16] and an ornithologist[17] all bluntly dismissed the new explanation of the scales in *Longisquama*. They insisted that the so called feathers of *Longisquama* are highly modified membrane-like scales rather than feathers. The median ridge or rachis of the individual shaft is a vein-like supporting structure of the membrane, and the so-called branches or barbs are membrane corrugations. One group explicitly suggested that they were anchored in the skin or epaxial muscles. Another group argued that feathers such as the "hollow remnant of spongy air-filled pith" and "pulp cavities" are actually artifacts resulting from the sediment in which the main slab and counter slab split through the sediment that replicated the external surfaces of each scale.

For ornithologists there exist even more differences between the integumentary appendages of *Longisquama* and modern birds. They argued, for instance, feathers tend to fray at the edges but the plumes of *Longisquama* are fused and unfrayed; in proximal portions of the integumental structures of *Longisquama*, the ribs extend from the shaft backward toward the body while in avian feathers the barbs extend toward the tip. They concluded that the so-called feathers of *Longisquama* consist of membranous blade with a continuous, unfrayed ribbon-like margin with ripples radiating from a central shaft.

These criticisms were complained by the authors of the *Longisquama* paper as denying observable facts[18]. They insisted that a series of detailed, featherlike features such as follicularly shaped feather base, calamus, sheath, rachis and barbs of *Longisquama* cannot all be contributed to artifacts of preservation.

Except for the homology of feathers, paleontologists are also skeptical of its phylogenetic position. They suggested that *Longisquama* might not be an archosaur but a primitive diapsid reptile. They argued that the specimen lacks the diagnostic features of archosaurs such as the presence of an antorbital fenestra and a mandibular fenestra. The also questioned the recognition of a furcula in *Longisquama*. In response to this criticism, the authors of the *Longisquama* paper argued that an antorbital fenestra, the hallmark of the Archosauria, is clearly visible in the counterslab. And the furcula of *Longisquama* is not only present but also similar to that of *Archaeopteryx*. The senior author of this paper was lucky to have examined the specimen of *Longisquama*. Although the skull bones are admittedly not so clearly preserved the presence of a furcula can be confirmed; and the furcula, in our opinion, is actually very similar to more advanced birds such as the Early Cretaceous ornithurine birds *Ambiortus* from Mongolia, *Yanornis* and *Yixianornis* from China[19]. The presence of such an avian furcula may indicate that the previous recognition of *Longisquama* as archosaur appears justifiable, but until more evidence is supplied we see no phylogenetic connection between this creature and birds.

As in the case of *Sinornithosaurus*, we definitely have seen the most comprehensive and detailed investigation as well as exchanges of opposite views on the peculiar integumentary structures in *Longisquama*. No one would expect that these work will cease any debate; on the contrary, we believe from the limited evidence known so far the controversy over the integumentary structures of *Longisquama* as well as all feathered dinosaurs will probably continue for many years to come. Wherever *Longisquama* fits on the phylogenetic family tree of reptiles, it is an important creature from a critical geological time, when a few paleornithologists believe that major groups of reptiles such as dinosaurs, crocodiles, pterosaurs and birds first appeared.

4. Protofeathers in the Early Cretaceous bird Protopteryx*?*

Because the oldest bird *Archaeopteryx* has preserved feathers as advanced as those of modern birds it has been generally agreed that more primitive feathers must have appeared among the ancestors of birds. For most paleontologists, birds were derived from a special group of theropod dinosaurs, therefore the discoveries of protofeathers in *Sinosauropteryx*, *Beipiaosaurus*, and *Sinornithosaurus* are just what we have been waiting for decades. However, for those who disagree on the dinosaurian origin of birds, the discovery of protofeathers in a reptile more primitive than dinosaurs appears more exciting and reasonable. Unfortunately little attention has previously been paid to other early birds mainly due to poor preservation of feathers associated with skeleton in the Early Cretaceous. The recent findings of abundant and excellently preserved Early Cretaceous birds provide a lot important information about the early evolution of feathers. Among them, the most notable is the discovery of *Protopteryx*[20] from Hebei Province, northern China.

Phylogenetically, *Protopteryx* represents the most primitive known member of the avian group Enantiornithes, which comprises the prevalent continent birds in the Mesozoic. Enantiornithes are more abundant and diverse than the contemporary ornithurine birds, which had more advanced flight apparatus

Protopteryx has preserved three types of feathers: down feathers, asymmetric flight feathers and tail feathers. The barbules are not

Fig. 4. *Life reconstruction and tail feather of the Early Cretaceous bird* Protopteryx.

observable in any feathers of *Protopteryx*. The most distinctive feature of *Protopteryx* is the presence of a pair of long central tail feathers. The tail feathers are unique in that they are only branched into barbs at the distal portions; proximally the feather is narrow and strap-like, the vanes are not differentiated into barbs. The rachis is present along the full length of the tail feather. It is noteworthy that this kind of feather is also present in some *Confuciusornis* and other undescribed enantiornithine specimens.

Such a feather structure is different from all other known fossil and modern feathers. Therefore it probably represents a new "primitive" feather type that had first developed in an ancestor of birds yet unknown to us. In other words, it may represent a transitional type between elongated scales and feathers.

It must also be pointed out that in a few modern birds such as Red Bird-of-Paradise[21], the central tail looks like strips of plastics and has undifferentiated vanes that resemble the proximal tail feathers of *Protopteryx* and *Confuciusornis*. The presence of such primitive structures in birds of paradises is explained as a neotenic feature. Because *Protopteryx* is both younger and more advanced than *Archaeopteryx*, and fossil record of feathers is usually rare and incomplete, therefore it becomes a major issue as to how to distinguish primitive conditions of feathers from secondarily specialized types in a primitive bird, thus an alternative explanation of this feather type in *Protopteryx* is that it was secondary specialization from its ancestral normal feathers. However, either of the interpretations of the "protofeather" in *Protopteryx* might have some important implications for the origin and early evolution of feathers. Since it is quite commonly present in early birds, it might actually represent a stage from which elongated scales evolved into an early form of feathers.

Based on the study of the tail feathers of *Protopteryx* and *Confuciusornis* it has been suggested that modern feathers probably evolved through the following stages: 1) scale elongated, 2) appearance of central shaft or rachis, 3) differentiation of vanes into barbs, and 4) appearance of barbules and barbicels. This model is different from that derived from the evidence of feathered dinosaurs *Sinosauropteryx* and *Sinornithosaurus* as discussed earlier in this paper. The major difference between these two evolutionary models of the origin of feathers: the former hypothesizes that the rachis was formed before the vanes were differentiated into barbs; the latter suggests that barbs appeared first and then there was a rachis.

5. Endothermy, display or other functions of the first feather?

One of the major questions in the study of the origin of feathers is about the functional background or selective pressure during the process of the origin of feathers. The study of *Protopteryx* suggested that birds probably first developed the feather for aerodynamic purpose rather than for thermoregulation or other functions; however, the arguments of various stages of protofeathers in theropod dinosaurs indicate that feathers were probably initially developed for thermoregulation or sexual display, and feathers were only associated with flight in birds as an exadaptation.

For some paleontologists, the discoveries of feathered dinosaurs also provide evidence for the endothermic dinosaur hypothesis. Obviously, it is logically natural for them to accept the hypothesis that thermoregulatory function is a preadaptation for avian flight. The presence of feathers of modern appearance in *Caudipteryx* and *Protarchaeopteryx*, however, are not quite consistent with this hypothesis. Neither of these two supposedly feathered dinosaurs could fly or be related to flight, then why bother developing feathers of such complex structures? Hair-like structures would be much simple and efficient[22].

Perhaps the major difficulty for the endothermic hypothesis of feathered dinosaurs is that there is even no evidence that early birds were all endothermic. The association of feathers with endothermy inferred from modern birds is purely speculative for early birds. There is no reason to argue that hot-bloodness would automatically occur as a result of the acquisition of thermoregulatory integuments such as feathers or hairs. Endothermy is energetically expensive and requires specialized physiology. The maintenance of high constant body temperatures is not simply decided by an effective system of insulation but by efficient metabolic heat production. Highly efficient respiratory system is also vital to the maintenance of hot-bloodness.

The flight capability of early birds such as *Archaeopteryx* and *Confuciusornis* are quite limited based on their primitive flight apparatus. For instance, they all lacked an alula, an advanced flight apparatus, which is vital to the balance during slow flight and taking off. The sternum is much flatter than those of modern birds. The air sacs that make possible a continuous unidirectional, highly efficient flow of air through lungs, are not well developed in these early birds. At least in *Archaeopteryx*, the ribs lack uncinate processes that help strength the rib cage to resist the pressure of the intensive respiration during flight. Paleohistological work indicates that the metabolic rates of enantiornithine birds are probably much lower than that of

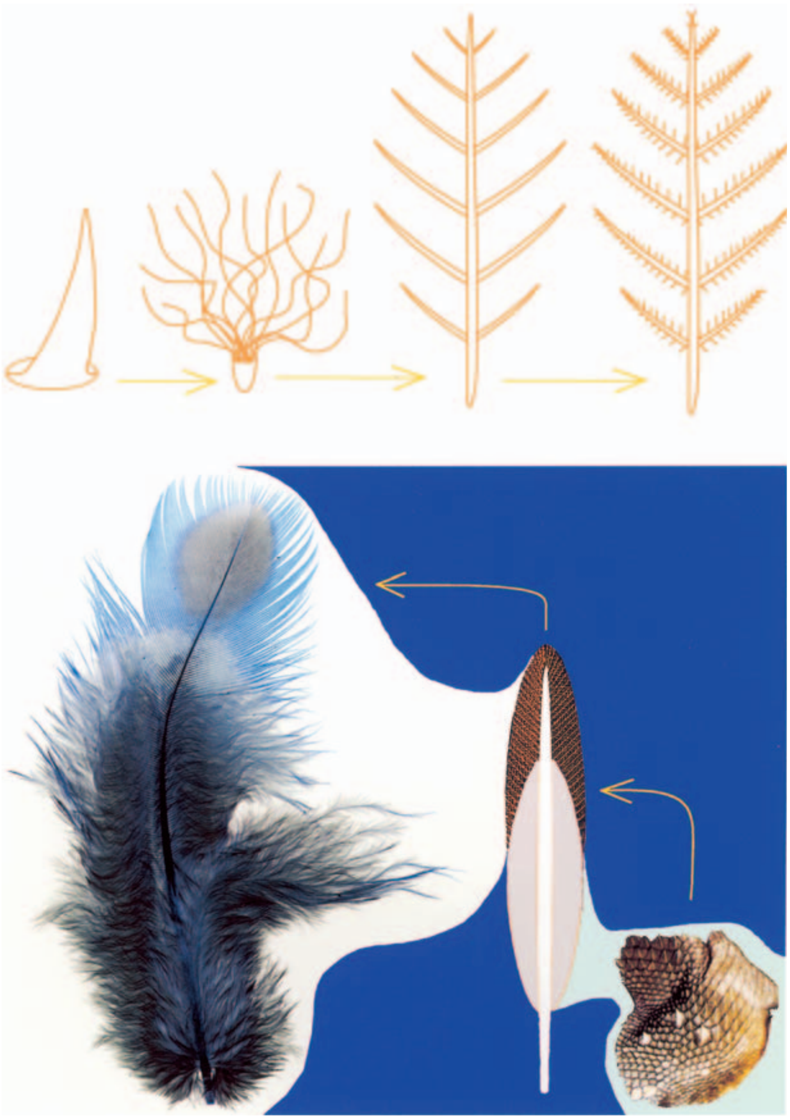

Fig. 5. *Comparison of the evolutionary models of feathers based on evidence of* Sinornithosaurus *(top) and* Protopteryx *(below), respectively.*

modern birds[23]. There is yet no solid evidence suggesting that these birds were all endothermic.

Another group of early birds, referred to the Ornithurae, is probably endothermic with little doubt. These birds have possessed the flight structures almost indistinguishable from those of modern birds[19].

They have an elongated keeled sternum with deeply concave dorsal surface. The uncinate processes form a strong rib cage as in modern birds. The air sac system is also well developed. It is generally concurred that one branch of this group gave rise to modern birds at a time roughly around the boundary between the Cretaceous and the Tertiary.

The protofeathers might have initially served for thermoregulation or sexual display as is the case of the cursorial feathered dinosaur *Sinosauropteryx* although endothermy was not achieved at that stage. However, when the immediate ancestors of birds began to climb the trees for whatever reasons (escaping from predators or for food), the protofeathers were perhaps used for different purposes before they are mainly used for flight in birds. The integuments in small sized dromaeosaurs such as *Sinornithosaurus* could possibly have been used for balance in trunk climbing or breaking the fall of an animal as it fell to the ground or of allowing the animal to steer as it fell through the air[22]. The report of the smallest adult dinosaur *Microraptor*[24] with protofeathers might shed some new light on the early evolution of feathers. This creature is about the size of the oldest birds *Archaeopteryx*, the small size as well as the foot features indicate that it could perch in the trees. While this conclusion lends strong support to the arboreal hypothesis of the origin of avian flight it may also indicate that the protofeathers were useful for balance during the climbing and jumping of these relatives of birds.

Conclusion

It is probably noteworthy that the studies of the feathered dinosaurs are still going on. Controversy over the phylogenetic position of the two dinosaurs with true and most modern avian feathers, namely *Caudipteryx* and *Protarchaeopteryx*, will not end soon. Until a commonly accepted phylogeny of these creatures is known and the recognition of the branched integumentary appendages in *Sinornithosaurus* is generally agreed it is probably immature to conclude that the mystery of the origin of avian feathers has been deciphered. In the meanwhile, hair-like structures are now being discovered and studied in several non-theropod vertebrates including several pterosaurs that show remarkable resemblance to those of feathered dinosaurs. It will certainly be wise not to jump onto any conclusion at this critical stage of discoveries. As the old saying goes, extraordinary claims require extraordinary evidence, in the case of the origin of feathers, we have obtained extraordinary evidence, but we are certainly expecting more.

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