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From Dinosaurs to Birds: Puzzles Unraveled while Evidence Building up

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Rejuvenation of dinosaurian origin of birds and its theoretical difficulties

In 1986, Prof. Jacques Gauthier from Yale University first applied cladistic systimatics to the analysis of the relationships between birds and other species in archosauria, a basal reptilian group that includes dinosaurs, pterosaurs, crocodilias and some other extinct reptilians. His analysis further confirmed that birds might have originated from a branch of small theropods close to Deinonychosauria. Encouraged by this work, the paleontological community cast intense attention to birds' dinosaurian origin theory, which was first presented by Thomas Henry Huxley over one century ago. Later on the discovery of feathered theropods in the Jehol Biota in 1996 offered much more robust evidence for this theory, and our understandings have since been significantly improved concerning how birds evolved from dinosaurs. Meanwhile, these exceptionally well-preserved specimens found in the Early Cretaceous strata of west Liaoning Province, China and its vicinity have also provided important information about the origins and early evolution of feathers and flight.

However, still some puzzles persist concerning how these reptiles evolved toward birds, where this theory encounters some difficulties. For example, a time framework for early birds' branching from theropods is still pending. Although it is well agreed that the earliest bird known to date is *Archaeopteryx* from the Late Jurassic strata in south Germany, fossil theropods, which are close relatives to birds according to this theory, are seldom found in large number in contemporary strata, especially Deinonychosauria. On the other hand, there is inconsistency between fossil evidence and developmental biological results concerning the evolution of theropod digits: fossil evidence suggests that in their evolution towards birds theropods had two degenerate digits on the outer side of their forelimbs, leaving the three digits closer to their body (Digit I, II and III) fully developed; whereas developmental biological materials show that extant birds have a vestigial digit on either side of the forelimb, leaving the three in the middle (Digit II, III and IV) fully developed and extraordinarily robust.

Time framework aside, this theory also has difficulties in explaining the true nature of the "feather-like" filamentary integuments found in fossil dinosaur specimens from Liaoning. Some scholars rebutted that these "integuments" could actually be the remains from some tissues, like fibers beneath the hypodermis of the creatures, rather than external structures or feathers. If this proved to be true, a key foundation stone on which the dinosaurian origin theory is built would fall apart; so would the congenetic relationships between avian feathers and the hairy integuments of dinosaurs.

Other open questions in this field also pose challenges to this theory, including difficulties in explaining how feathers and flight originated and evolved at the very first instance.

Thankfully, in 2009 and 2010 a series of discoveries come for rescue, unveiling spectacular episodes of this big transition in evolutionary history: from dragons to birds.

Haplocheirus sollers: new light on time framework

Alvarezsauroid, a family of theropod dinosaurs morphologically similar to birds, have been deemed to be evidence for birds' dinosaurian origin. However, their position on the evolution tree have been controversial: some scholars identified them as flightless birds rather than dinosaurs, given that the earliest specimen of this family was dated to the Late Cretaceous, or about 90 million years before the present, far later than the time when *Archaeopteryx* used to live. Arguments arose in response to this puzzle, claiming that alvarezsauroids were too young to deserve the title of ancestors of birds.

New hopes dawned when *Haplocheirus*, a new alvarezsauroid dinosaur emerged from the Late Jurassic strata in the gobi desert of the Xinjiang Uyghur Autonomous Region, China. An expedition co-led by Dr. James Clark of George Washington University and Dr. XU Xing from the CAS Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) identified this new species and named it as *Haplocheirus sollers* (a dinosaur with simple and skillful hands). Dated about 160 million years before present—about 10 to 15 million years older than *Archaeopteryx*, this ten-feet-long dragon might help clearing clouds over the time framework for birds' branching from dinosaurs.

In their paper published in the Jan 29, 2010 issue of *Science*, Mr. Jonah Choiniere and Dr. Xu's team proposed that this new species represents the earliest diverging member of Alvarezsauroidea family. Based on their analysis of the fossil and its relationships with selected theropods, the coauthors asserted that Alvarezsauroidea family should be positioned as a basal group of Maniraptora, a clade comprising birds and their closest theropod relatives, rather than flightless birds as formerly believed by some scholars.

Extending fossil record of Alvaezsauroidae backward by 63 million years, this work suggests that before *Archaeopteryx*, many species might have been living as early ancestors of the first birds, bearing composite features distinguishing them from birds and meanwhile suggesting links to the avian group. By introducing a species much older than *Archaeopteryx* to the "bird-like" theropod family, this research has solved the long-lasting puzzle about the time framework for the transition from dinosaurs to birds.

Results from quantitative analysis by the coauthors are also consistent with those from former phylogenetic analyses, strongly weakening the claim that theropods were too young to be ancestors of birds.

Haplocheirus has gained its name for its special "hands," which are closer to bird's wings compared with other known theropods. It has three digits on either hand; among them the middle one is much longer than the others. Similar to birds, this creature could swing its forelimbs laterally, just like a bird extending its wings. It had many other bird-like characters, including its hindlimbs. The first of its four toes grew laterally, and the other three frontward. This could be a transitional feature from dinosaurs to birds, given that extant birds have their first toe backwards and the other three forward.

The skeleton of *Haplocheirus sollers*, a bird-like dinosaur 10 to 15 million years older than *Archaeopteryx*, the oldest bird known to science. This discovery helps reconstruct the time framework in which dinosaurs evolved into birds, hence resolving the "Temporal Paradox" that have long been bothering advocators of dinosaurian origin of birds. (Photo: Courtesy of Dr. XU Xing)

Despite its bird-like features, *Haplocheirus* was not a bird. It could be entitled as an early ancestor of birds, but it was actually an out-and-out carnivorous dinosaur, according to Dr. Xu.

(For further information on this research, please refer to the report by Dr. Corwin Sullivan on page 89 of this issue of *BCAS*.)

Anchiornis huxleyi: A four-winged dinosaur older than *Archaeopteryx*

Aside from *Haplocheirus, Anchiornis huxleyi* is another dinosaur shedding light on the time framework for the dino-to-avian transition. As jointly reported by Dr. Xu at IVPP and Prof. HU Dongyu with Shenyang Normal University and their colleagues in the October 1st issue of *Nature* in 2009, this feathered dinosaur was dated to somewhere between 161 and 151 million years ago, at least several million years older than *Archaeopteryx*, which is 145 to 150 million years old and accepted as the oldest-known bird. It was also older than the feathered dinosaurs from the Jehol Biota by approximately 30 million years.

Unearthed from the earliest Late Jurassic Tiaojishan Formation of Jianchang County, Liaoning Province of China, this exceptionally well-preserved specimen, with its interesting age, provides paleontologists with significant clues for solving the "Temporal Paradox" on the origin of birds by filling in the blank in the temporal framework of theropod divergence, and therefore fueling new proof for the dinosaurian origin of birds.

The discovery of *Anchiornis huxleyi* has further bridged the morphological gap between Avialae, Troodontidae and Dromaeosauridae (another branch of Deinonychosauria).

Also the appearance of long pennaceous feathers on the hind legs of this small theropod further supports the hypothesis that in their transition to birds, dinosaurs might have experienced a "four-winged" period.

The most striking structure of *Anchiornis huxleyi* is its long pennaceous feathers covering the forelimbs, hindlimbs and tail. Imprints from these feathers can be clearly identified around the almost complete skeleton of the newly discovered specimen. Comparing with *Microraptor* and *Archaeopteryx*, the feathers on *Anchiornis huxleyi* were relatively smaller, with thinner rachises and symmetric vanes. Similar to *Microraptor*, which is about 30 to 40 million years younger, the pennaceous feathers on its hindlimbs formed a pair of hind wings. More interestingly, its phalanges were also covered with feathers except for the toes, a unique feature never reported in extinct species before.

An artist reconstruction of *Anchiornis*, a four-winged dinosaur several million years older than *Archaeopteryx*. (Reconstruction by ZHAO Chuang and XING Lida; Picture courtesy of Dr. Xu)

Aside from *Microraptor* and *Anchiornis*, hind wings are also found in other theropods closely related to birds, like *Pedopenna*, suggesting that the "four-winged" form is a necessary stage in avian origin. Scientists at IVPP suggested that in the subsequent stages of their avian transformation, theropods gradually reduced their hind wings, and their fore wings gained more and more weight in development, as an adaptation to avian life.

"Mud lizard" gives more clues about digit evolution

The most primitive dinosaurs in the famous theropod group (that later included *Tyrannosaurus rex*) had five "fingers." Later theropods had three, just like the birds that evolved from them. But which digits? The theropod and bird digits failed to match up if you number the digits from I to V starting with the thumb with respect to our hands. Theropods seemed to have had digits I, II and III, while birds have digits II, III and IV. Paleontologists have long been puzzled by theropods' palms: how did they change from a I-II-III mode to a II-III-IV one when approaching the dino-avian threshold? The emergence of *Limusaurus inextricabilis*, or "mud lizard," helps to clear the haze on how theropods gain bird-like wings.

Digits of *Limusaurus inextricabilis*. Its obviously reduced digit I provides new clues about how a branch of dinosaurs gradually gained bird-like palms in their evolution towards birds and inspires fresh thoughts on the evolutionary mode of their digits. (Photo: Courtesy of Dr. Xu)

A reconstruction of *Limusaurus inextricabilis*. (Courtesy of Dr. Xu)

This unique ceratosaurian species, described by Dr. Xu and his colleagues at IVPP in the June 18 issue of *Nature* in 2009, has a strongly reduced first digit (Digit I), hence inspiring new thoughts on possible modes for the transition. To explain how theropods switched from a I-II-III palm to a II-III-IV one when developing into birds, two hypotheses were widely accepted before the discovery of *Limusaurus*, one called Lateral Digit Reduction (LDR) and the other Bilateral Digit Reduction (BDR). The LDR theory proposes that in their evolution theropods might have progressively reduced the outer two digits; while the other insists that the inner- and outer-most digits might have been gradually reduced, like what is commonly seen in all other tetrapod groups, which include extant birds. However, the BDR mode lacked support from fossil evidence in dinosaurian tetrapods until the excavation of *Limusaurus*, which suggests that BDR might also have occurred in Tetanurae, a sister group of ceratosaurs.

The new species, dated about 160 million years ago, was unearthed from the Jurassic strata in northern Xinjiang, China. Aside from its greatly reduced Digit I, its particularly elongated Digit II displays a degeneration mode totally different from other early theropods. Xu and the coauthors proposed that the evolutionary mode of theropod digits might be much more complicated than previously thought. Based on closer observations and analyses of theropod claw structures, in combination with the latest paleontological and modern developmental biological materials, they brought forward a new hypothesis to explain the evolution of theropod digits. They believed that at first the outward-most digit (Digit V) was reduced, and then as a result from the changes in theropods' predatory behaviors, the inward-most one (Digit I) also gradually reduced and disappeared. In the end, as what occurred in tetanurans (including the well-known allosaurus and velociraptor), the three middle digits (the Digit II, III and IV) retained and through some homeotic transformation gained the morphology of the inward digits (Digit I, II and III). What apparently I-III digits in tetanurans might actually be digits II-IV, as previously considered by Thulborn and Hamley, whose thoughts were subsequently overlooked by the paleontological community.

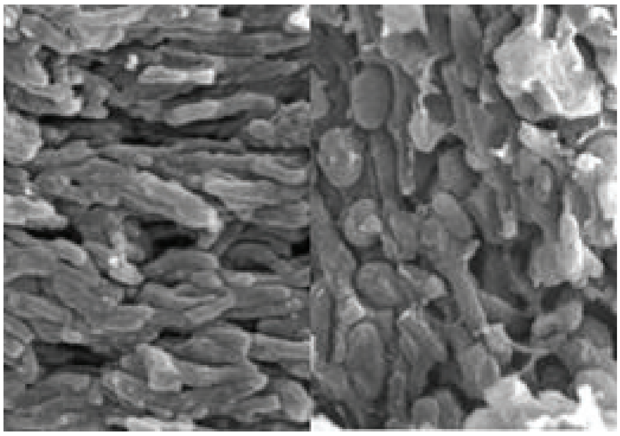
The new discovery has changed the conventional belief that tetanurans retained digits I-III and solved the discrepancy between fossil record and developmental biological evidence. Concerning the digits of *Limusaurus* and other issues on dinosaur research, Dr. Corwin Sullivan from Dr. Xu's group at IVPP has more story (see page 89 of this issue).

True colors of dinosaurs clear doubts on true nature of dinosaur feathers

The discovery of feathered dinosaurs is a big event in paleontological research and has strongly bolstered the dinosaurian origin of birds. However, doubts on the true nature of the feather-like integuments found in the fossils are meanwhile loud: some scholars argue that these integuments are actually remains from the hypodermic tissues of these extinct theropods, rather than primitive feathers.

The latest discovery by a joint research team led by Dr. ZHANG Fucheng with IVPP and Michael Benton of the University of Bristol in UK, reported in the Jan 28, 2010 issue of *Nature*, not only revealed the true colors of some dinosaurs, but might eventually settle down the dust stirred up by this debate.

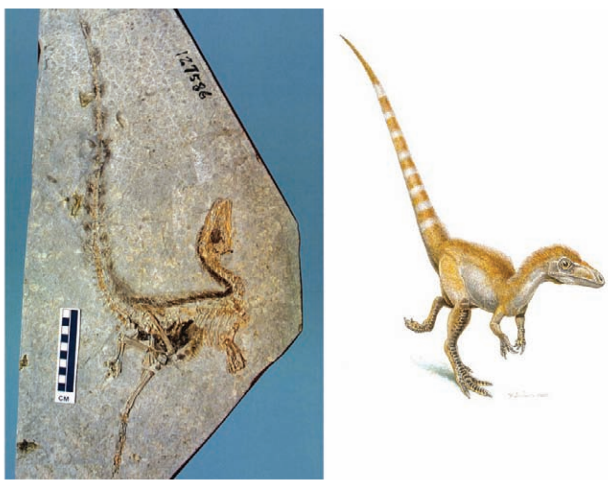
IVPP researchers found two types of melanosomes, the sausage-shaped eumelanosomes and the spherical phaeomelanosomes, in the tiny feathers or bristles on some primitive birds and feathered dinosaurs from the Jehol Biota, including two small species of theropods, *Sinosauropteryx* and *Sinornithosaurus*. Given that in extant birds melanosomes are only found in the developing feathers instead of the hypodermic fibers, this discovery hints that some theropod dinosaurs did have colorful feathers.



The eumelanosomes (left) and phaeomelanosomes (right) found in some feathered dinosaurs. This discovery strongly supports the congenetic relationship between dinosaur and avian feathers, and has cleared the clouds over the real nature of the "feather-like integuments" found in some theropods. (Photo: Courtesy of Dr. ZHANG Fucheng)

For the first time ever, scientists confirmed that the "feather-like integuments" found in some fossil dinosaurs are of the same origin as extant birds, and is really external structures derived from their skins, rather than hypodermic fibers.

Of course, this discovery directly helps reconstructing the original colors of dinosaur feathers; otherwise we would have to rely on artists' imagination to visualize these extinct creatures. On feathers of primitive birds and dinosaurs, Dr. David Hone from Dr. Xu's team at IVPP has more details (page 92 of this issue).

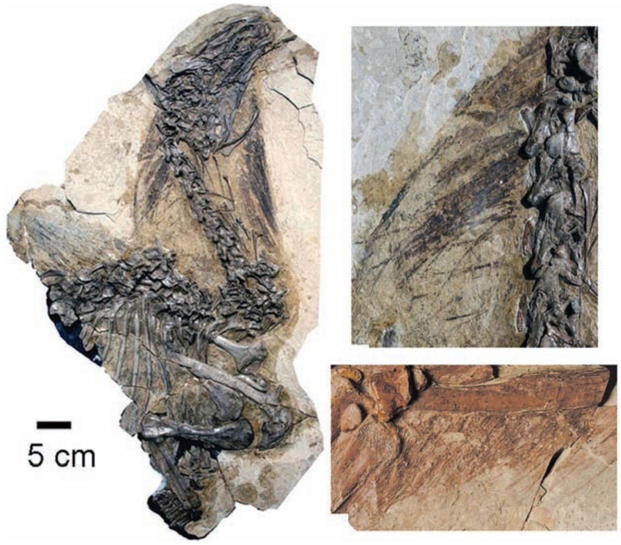


The *Sinosauropteryx* specimen (left) and a scientific reconstruction of its original colors based on the melanosomes lately found in the species. (Photo and picture: Courtesy of Dr. ZHANG Fucheng)

Exploration continues

Doubts on the existence of feathers in “furry dinosaurs” having been cleared, further exploration concerning the early evolution of feathers and the origin of flight can now start from more secure a point. New evidence from research on dinosaurs like *Beipiaosaurus* and *Similicaudipteryx* opens a new door to the future journey. In this direction scientists are seeing more and more complete a picture.

A reconstruction of *Beipiaosaurus*, the dinosaur which bears the most primitive feathers known to date. (Reconstruction by Zhao Chuang and Xing Lida; Picture courtesy of Dr. Xu.)



Beipiaosaurus specimen (left) and a close-up view of the filamentary integuments in *Beipiaosaurus* speciment (right). They represent the most primitive type of feathers so far known to science, with a very simple structure. (Photo: Courtesy of Dr. Xu)

To decipher the early evolution of feathers, paleontologists suggest that they might have developed into the pennaceous feathers as found on modern birds from a very simple type, which had only a single filament in the shape of hair. However all feather-like integuments previously found in dinosaur fossils have advanced, compound structures. The simple type of filament, theorized to have covered over feathered dinosaurs, at last came to light in Jan, 2009, as described on the *Beipiaosaurus* dinosaur by Dr. Xu and his team in the journal *Proceedings of the National Academy of Sciences*, strongly supporting the hypothesis that feathers evolved and initially diversified in non-avian theropods before the origin of birds and the evolution of flight. Forthermore, the dramatic age-related shift in plumage was noted in newly described fossils of *Similicaudipteryx* as reported in the April 29 issue of *Nature* in 2010 by Dr. Xu and his collaborators, suggesting that early birds and feathered dinosaurs experimented with a diversity of feather types and a variety of ways to use them, which only later stabilized to the more conservative system we see now with modern birds.

Dr. Hone’s report in this issue of BCAS offers more information on the latest developments of research on early evolution of feathers and, the origin of flight (see page 92).

The strikingly different flight feathers of two individuals at different ontogenetic stages of the oviraptorosaurian *Similicaudipteryx*. (Reconstruction by Xing Lida and Song Qijin; Courtesy of Dr. Xu)