On Some Examples of Missing Links – Perspectives from Fossil Evidence in China

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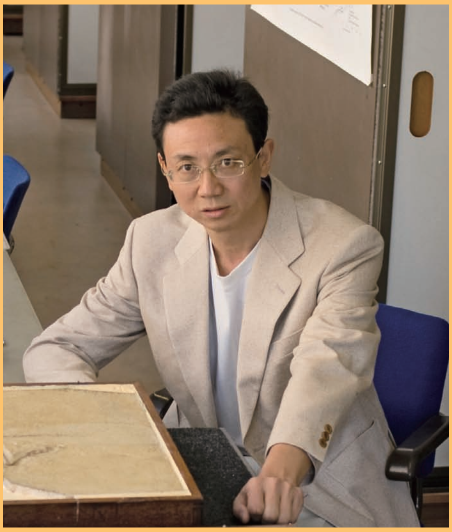

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About the Author

Zhonghe Zhou is currently the director and senior research fellow at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of the Chinese Academy of Sciences. He graduated from the Department of Geology of Nanjing University in 1986, and received his Ph.D. degree with honors at the Department of Ecology and Evolutionary Biology of the University of Kansas in 1999. He returned to China in 1999 with the support of the "Hundred Talents Project" of the Chinese Academy of Sciences.

His main research interest is on the origin and early evolution of birds, feathers, and bird flight. He is also involved in the study of Mesozoic fishes, feathered dinosaurs, pterosaurs, biostratigraphy and the evolution of the Jehol Biota, and reconstruction of the Early Cretaceous terrestrial ecosystem.

In the past 20 years, together with his colleagues, he has discovered and published over 30 new species of birds and dinosaurs from the Early Cretaceous of Northeast China, making it the most important area for the study of early avian evolution and having greatly improved our understanding of the morphological differentiation and ecological and evolutional radiation of early birds.

To date, he has authored and coauthored over 100 scientific papers including 18 in *Nature* and *Science*, and 2 in *PNAS*. He and his colleagues proposed in their 2003 *Nature* review article the idea of the Jehol Biota area as a cradle and diversification center for many biological groups. This article was featured as a Fast Moving Front article by Science Watch website in November 2008.

He has received a number of national awards including two National Natural Science Awards from the Chinese government (2000, 2007), and one for popular science publication by the Chinese government (2003). He and his research team also earned several honors from the Chinese Academy of Sciences and the Ministry of Science and Technology of China.

Representative articles

[1] Zhou Z, Zhang. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature*, 2002, 418:405-409.
[2] Zhou Z, Barrett P M, Hilton H. An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, 2003, 421:807-814.
[3] Zhou Z. The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften*, 2004, 91:455-471.
[4] Zhou Z, Zhang F. A precocial avian embryo from the Lower Cretaceous of China. *Science*, 2004, 306:653.
[5] Zhou Z, Zhang F. Discovery of a new ornithurine bird and its implication for Early Cretaceous avian radiation. *PNAS*, 2005, 102(52):18998-19002.

Abstract

Significant progress has been made in the discovery of fossil evidence of missing links since Darwin published his book *On the Origin of Species*. Among the most remarkable recently found in China are the earliest vertebrates from the Early Cambrian, the oldest and most primitive turtle from the Middle Triassic, four-winged dinosaurs that are among the closest relatives to birds from the Middle Jurassic to Early Cretaceous, and some of the most basal birds from the Early Cretaceous. These fossils represent some of the major steps in vertebrate evolution and show some key anatomical transitions. Despite the general impression of the incompleteness of fossil records, our knowledge of biological evolutionary history has been greatly enriched. Thanks to the significant progress in studies of paleontology, geochronology, and the molecular timescale, our understanding of the evolution of life on earth is now probably much better than anyone could have imagined several decades ago.

Key Words

Missing link; fossil; China

Introduction

In his *On the Origin of Species* (Darwin 1859), Darwin devoted two chapters to the discussion of fossils, but he was obviously not satisfied by the fossil record. His dissatisfaction was justifiable, for in 1850s, missing links were indeed very rare. Regardless of the impact of the punctuated equilibrium theory (Eldredge and Gould 1972) in explaining some of the gaps that Darwin worried about, after one hundred and fifty year's extensive fossil collecting, missing links are now no longer rare. Paleontologists can easily provide a list of hundreds of examples of missing links that connect various lineages of animal and plant groups. Darwin's complaints about inadequate fossil records are now largely addressed.

Radiometric dating of fossils or fossil-bearing strata was not available in Darwin's time. Today, with a refined and nearly complete geochronological framework for the entire history of biological evolution, paleontologists are able to discuss the missing links against a solid temporal background. For instance, several exact dates are now available for our understanding of the transition from dinosaurs to birds (Swisher *et al*. 1999; He *et al*. 2004; Hu *et al*. 2009). In other words, now we have more convincing examples of missing links that not only lie at the right phylogenetic position but also occurred at the right time in geological history, confirming when approximately the major transition from one biological group to another might have occurred.

Another fast growing area that has contributed greatly to our understanding of evolutionary missing links is the study of the molecular timescale and evolutionary rates. Unavailable in Darwin's time, studies of molecular timescales have now proved to be important evidence for deciphering the evolutionary history of life on Earth (Kumar and Hedges 1998). More importantly, many predictions of the time of origin for major groups based on molecular timescales are consistent with those indicated by the actual fossil record with absolute dating. One good example is that molecular timescales predicted the divergence of humans (hominids) from the chimpanzee at approximately seven million years ago, which is now confirmed by actual fossil records (Lebatard *et al*. 2008).

Many exciting fossil discoveries have been made in the past decade. Notably, many missing links have been made known from China and other areas of the world. The discoveries of various primitive angiosperms from the Lower Cretaceous of China and other areas (Sun *et al*. 1998, 2002; Leng *et al*. 2003; von Balthazar *et al*. 2008) show that Darwin's "perplexing phenomenon"and "abominable mystery" due to the sudden appearance of the angiosperms and their rapid rise to dominance in the fossil record is now explainable even for those who believe in gradual evolution. And it is no longer correct to say "that the fossil record tells us nothing about the evolution of flowering plants".

Ironically, even today, the lack of sufficient and perfect missing links or the abrupt manner in which whole groups of species suddenly appeared in certain formations have frequently been used by creationists as "fatal" objections to Darwin's evolutionary theory. For instance, the sudden appearance of nearly every major type of animal anatomy in the fossil record of just a few million years in the Early Cambrian is often cited as one such example. However, this has been shown to be due to lack of understanding of the complete biostratigraphic sequence and sufficient collecting of fossils near the boundary between the Precambrian and Cambrian (Rong *et al*. 2006). This short essay intends to show how recent progress in both paleontological and geochronological studies have provided fresh and strong support for Darwin's evolutionary theory by offering some of the most remarkable examples of missing links from fossil records in China.

1. What Are "Missing Links"?

Darwin's (1859) comment that the extinct forms of life help to fill up the wide intervals between existing genera, families, and orders cannot be disputed. Missing links can probably be diagnosed as any transitional fossils in an evolutionary context. In other words, phylogenetically, any fossil taxon linking two lineages can be regarded as a missing link. However, often only a selected few transitional fossils that are critical in the evolutionary process are considered as missing links in the literature. It is also notable that the actual species as a missing link is difficult to find in most cases, and it is more realistic to find a close relative of the actual ancestral species between two lineages.

Archaeopteryx is generally accepted as a classic example of a missing link between birds and reptiles (Mayr *et al*. 2005). Other good examples may also include *Ichthyostega* that links land vertebrates and choanate fishes, *Hyracotherium* that links horses and tapirs and rhinoceroses, and also a number of other missing links during the evolution from *Hyracotherium* towards *Equus*, such as *Mesohippus* and *Pliohippus*. And in the evolution of humans, many important missing links known to us today were completely lacking in Darwin's time. Among the most famous genera and species are probably *Australopithecus africanus* and *Homo erectus*. And a number of recent discoveries can be added to this list, including the 4.4 million years old *Ardipithecus ramidus* that is represented by a skeleton (White *et al*. 2009), *Orrorin tugenensis* (Galik *et al*. 2004) and *Sahelanthropus tchadensis* (Brunet *et al*. 2002; Lebatard *et al*. 2008) that are as old as six and seven million years, respectively. Many intermediate fossil forms have been identified as missing links leading to the evolution of whales (Thewissen *et al*. 2007). An Early Cretaceous gingko is recognized as a missing link between its Jurassic ancestor and extant gingkoes (Zhou and Zheng 2003). Equally interesting missing links may also include Cretaceous snakes with legs (Tchernov *et al*. 2000; Apesteguia and Zaher 2006) and the recently discovered *Tiktaalik roseae* that has been regarded by many as an excellent example of a missing link between fish and tetrapods (Shubin *et al*. 2006).

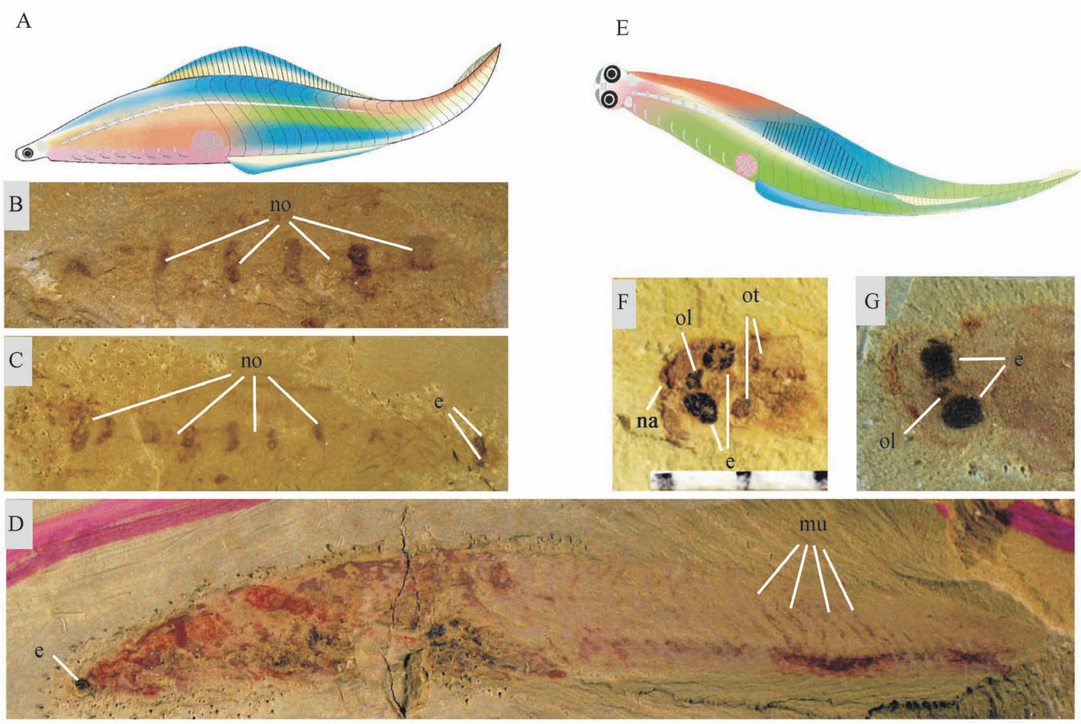
This paper is not intended to provide an overview of all the major missing links in the fossil record, but instead it will focus on some remarkable examples of recent fossil discoveries from China that will likely be accepted by most as truly significant missing links in major evolutionary transitions. Some of them have even bridged a wide gap between major biological groups. A brief introduction of these fossil taxa will be provided along with a general discussion on the transition of major features that demonstrate the actual changes as indicated by their phylogenetic positions.

2. The First Vertebrate

Vertebrata is a subphylum of the phylum Chordata. It is distinguished from others subphyla of chordates in possessing a distinctive head with a brain and developed nerve system, vertebrae and other anatomical features. Among vertebrata, Agnatha represents the most basal class, with living members such as lampreys that are probably highly derived. Therefore, we have to rely on the fossil record to better investigate the transition from invertebrates to vertebrates.

The appearance of the first vertebrate undoubtedly represents a major step in biological evolution. The Early Cambrian Chengjiang Fauna from southwest China is well known for producing many exceptionally preserved fossils of diverse metazoan groups, representing a number of extant phyla. Most notable among them is probably the report of two fish-like animals, or the oldest vertebrates, namely *Myllokunmingia* and the similar *Haikouichthys* (Shu *et al*. 1999, 2003). Phylogenetic analyses place both in the agnathans, suggesting that they represent some of the most primitive vertebrates. In particular, *Haikouichthys* is now represented by several hundred specimens, and provides much information for our understanding of the transition from invertebrates to vertebrates.

Some of the key innovations in vertebrate evolution may include the origin of the head, a complex brain, and well-developed eyes, as well as auditory and olfactory systems. *Haikouichthys* has a head with lobate extension, eyes, a small paired nasal capsule, and otic capsules, and the brain is surrounded by cartilaginous protective tissues. Like *Myllokunmingia*, *Haikouichthys* also possesses a notochord, with separate vertebral elements, putative vertebrae, which may have been made from cartilage in life. *Haikouichthys* also has a dorsal fin and a ventral fin (Fig. 1).



▲ **Fig. 1**

Photo of *Haikouichthys*. A. life reconstruction in lateral view; **B**. specimen (ELI-0001021) in lateral view, showing a notochord and cartilaginous vertebral elements; **C**. specimen (ELI-0001022) in lateral view, showing eyes, a notochord, and cartilaginous vertebral elements; **D**. specimen (ELI-0001030) in lateral view, showing the eye and "W"-shaped muscles; **E**. life reconstruction in dorsal view; **F**. head of specimen (ELI-0001003) in dorsal view, showing eyes, the olfactory capsule, nasal capsule, and possible otic capsules; **G**. head of specimen (ELI-0001013) in dorsal view, showing eyes and the olfactory capsule. Abbreviations: e, eye; mu, muscle; na, nasal capsule; no, notochord with vertebrae; ol, olfactory capsule; ot, otic capsule.

On the other hand, these earliest vertebrates also retain many ancestral features, such as a notochord. In living vertebrates, the notochord only appears in embryological stages. They also lack paired fins as seen in real fishes.

Although *Myllokunmingia* and *Haikouichthys* can be regarded as major missing links, their exact phylogenetic positions remain to be further investigated. It was proposed that the possession of eyes (and probably nasal sacs) is consistent with *Haikouichthys* being a craniate, indicating that vertebrate evolution was well advanced by the Early Cambrian (Shu *et al*. 2003). In other words, we might predict to find in the future an earlier ancestor of vertebrates that can better demonstrate the transition from invertebrates to vertebrates. However, *Myllokunmingia* and *Haikouichthys* are probably the best candidates for now.

3. The Most Primitive Turtle Is Half-Shelled

Turtles have long been held as an example of slow evolution. Turtles have a horny beak instead of teeth, and possess a composite shell with an upper carapace and a lower plastron. In other words, turtles, with an intact protective shell, have remained hardly changed in major structures since their first appearance in the Triassic, almost at the same time as dinosaurs first appeared. As a result, it is difficult to find an intermediate form in turtle evolution in its long history and the origin of the turtle body plan has often been regarded as one of the great mysteries of reptilian evolution. However, a recent remarkable discovery from the 220 million-year-old Triassic marine deposits in Guizhou Province, Southwest China, has nearly completely changed our view on this (Li *et al*. 2008). This half-shelled aquatic turtle, named *Odontochelys semistestacea*, represents not only the oldest known turtle but also the most primitive one ever discovered. In addition to the presence of teeth, it also possesses free sacral ribs and a long tail (Fig. 2). The ventral shell of *Odontochelys* is complete whereas the dorsal one is incomplete, and a series of neural carapace plates developed from the underlying vertebrae. The ribs were broadened as in a modern turtle embryo, but they did not form connecting plates, nor did any other elements of the carapace ossify (Rieppel 2009). For various reasons, it can be regarded as a perfect missing link in vertebrate evolution.

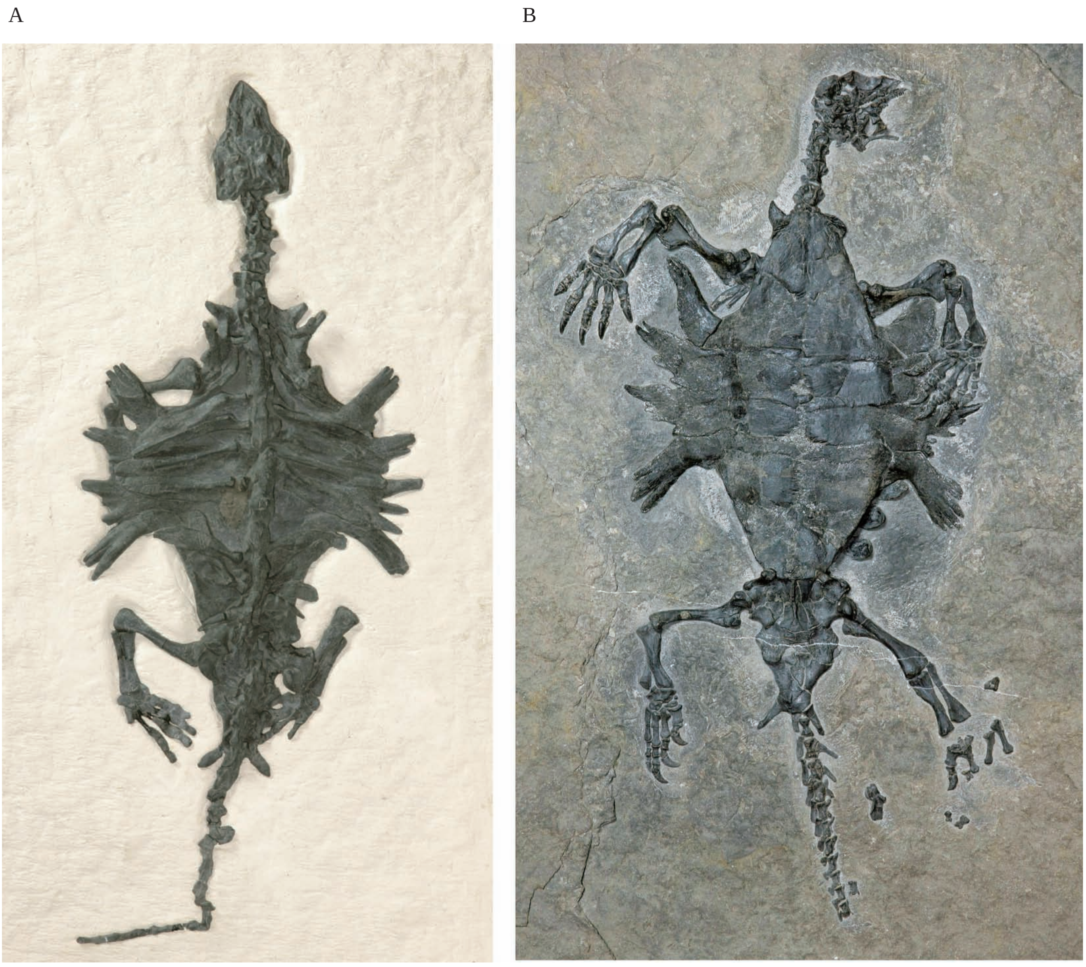
First, *Odontochelys* is clearly recognized as a turtle. Despite its primitive appearance and ancient age, it does possess several diagnostic features of turtles, such as the shell plates, which cover the belly in a nearly identical way to those of extant turtles.

Second, *Odontochelys* was equipped with teeth on the upper and lower jaws just like the ancestors of turtles, whereas all modern turtles only have beaks that bear no teeth. The second oldest turtle, *Proganochelys*, also had no teeth on the upper and lower jaws, but it retained palatal teeth (Lee 1993). The evolution of a beak and loss of teeth in turtles parallels that in avian evolution. *Archaeopteryx* and many other Mesozoic birds also retained teeth; however, all birds known from the Cenozoic have completely lost teeth.

Third, *Odontochelys* only had a partial shell covering its belly, whereas modern turtles have shells covering both the back and belly. Thus, this was an intermediate stage of shell evolution previously unknown to us. *Proganochelys*, which lived about 210 million years ago, had a fully formed shell, providing little evidence as to how the shell evolved.

Fourth, the discovery of *Odontochelys* provides important clues to understanding how the turtle shell evolved. The fossil evidence of the earliest known turtle now clearly supports the hypothesis that the belly shell evolved first and then ribs and backbone broadened to form the upper shell.

Finally, the fossil evidence and the hypothesis of processes in the origin of turtle shells seem to be consistent with the observation in the muscular and skeletal changes during the embryogenesis of modern turtles. It is shown that the modern turtles have acquired their unique body plan by passing through an *Odontochelys*-like ancestral state during embryonic development (Nagashima *et al*. 2009). This confirms that *Odontochelys* represents



▲ **Fig. 2**

Photos of *Odontochelys semistestacea*. A. specimen (IVPP V13240) in dorsal view, showing movable ribs and absence of dorsal carapace; **B**. specimen (IVPP V15639) in ventral view, showing development of a complete carapace.

an ancestral turtle instead of a specialized early side branch of turtles (Reisz and Head 2008).

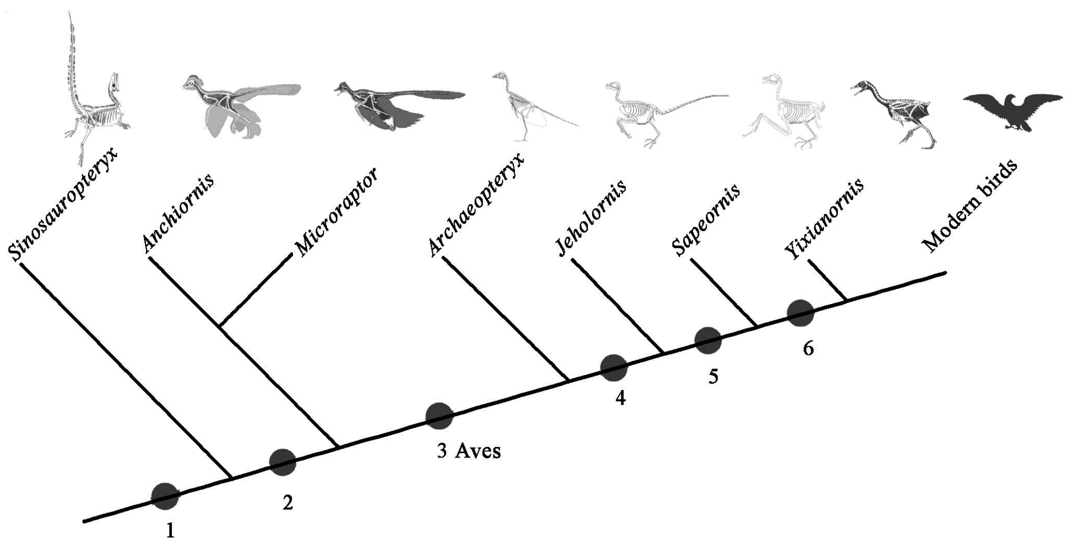
4. Four-Winged Dinosaurs

It is not widely known that it was Thomas Huxley, "Darwin's Bulldog", who made the first scientific proposal that birds were derived from dinosaurs. When we celebrate Darwin's life and great book today, let us not forget the fact that Huxley's hypothesis is widely accepted today and it is well supported by a variety of lines of evidence. Notably, the evidence has emerged from the Middle Jurassic to Early Cretaceous of China (Chen 2007; Ji *et al*. 1998; Zhang *et al*. 2008; Hu *et al*. 2009) upon the discoveries of abundant fossils or missing links between dinosaurs and birds. For example, over a dozen genera of feathered dinosaurs have been reported from China and among them, the four-winged dinosaurs are most remarkable as they provide not only the link between dinosaurs and birds but also a transition towards the flapping flight in birds.

Microraptor gui is the first reported four-winged dinosaur from the Early Cretaceous of China (Xu *et al*. 2003). Despite its age that is later than the oldest bird, this basal dromaeosaurid lies very close to birds in the phylogenetic tree (Fig. 3). In addition to a general resemblance in skeletal morphology to basalmost birds, it preserved feathers in both forelimbs and hindlimbs that are nearly identical to those of extant birds by possessing a distinctive rachis and branching barbs. Furthermore, the feather also shows an asymmetric structure as seen in flying birds. The most remarkable feature of this dinosaur is probably the preservation of long hindlimb feathers, which makes it the first recognized four-winged vertebrate. It was proposed that the four-winged stage probably represents a transition during the evolution towards true two-winged flapping flight in birds. The hindlimb feathers with aerodynamic function are either significantly reduced as in some early birds (Zhang and Zhou 2004) or lost as in more advanced birds. Although there is still debate on the model of flight of the four-winged ancestor of birds (Chatterjee and Templin 2007), the discovery of *Microraptor gui* seems to strengthen the arboreal hypothesis of the flight origin of birds.

Phylogenetic analysis clearly shows that *Microraptor* belongs to the theropod family Dromaeosauridae, one of the groups that are very close to the transition from non-avian dinosaurs to birds. Despite the presence of possible gliding capability, it lacks evidence for flapping flight, and in some details, it shows more primitive features than in *Archaeopteryx*, such as a relatively short forelimb compared to the hindlimb and the absence of the reversed hallux that is critical for a perching foot. Therefore, such a combination of derived avian and primitive dinosaurian features in *Microraptor* qualifies it as a critical missing link in the evolution of birds from dinosaurs.

The recently reported four-winged dinosaur *Anchiornis* (Xu *et al*. 2009; Hu *et al*. 2009) can



▲ **Fig. 3**

A simplified cladogram showing the transition from theropod dinosaurs to birds (modified from Zhou and Zhang 2002; Clarke *et al*. 2006, Hu *et al*. 2009). The major structural innovations leading to the evolution of modern birds are listed according to nodes 1-6: 1. protofeather with unbranched structures; 2. true branched modern feathers, three manual digits with a phalangeal formula of “2-3-4”; 3. at least partially reversed hallux, wing nearly as long as the leg; 4. sternum with lateral trabeculae, elongated coracoid; 5. a long pygostyle, two phalanges on third wing digit; 6. alula on wing, large keel on elongated sternum, a well-developed procoracoidal process on coracoid, a completely fused carpometacarpus, and a short pygostyle.

probably be regarded as a better missing link than *Microraptor gui*. In addition to the presence of four wings as in *Microraptor*, further indicating that the four-winged mode indeed represents a transitional stage in the evolution of avian flight, *Anchiornis* provides several reasons to strengthen this argument. First, phylogenetically, it belongs to troodontids, a sister group with dromaeosaurids that includes *Microraptor*, and both troodontids and dromaoesaurids are very close to the common ancestor of all birds (Hu *et al*. 2009). Second, in skeletal details, it has a forelimb with carpal morphology more similar to that of *Archaeopteryx* than other dinosaurs. And third, *Anchiornis* lived in the Middle to Late Jurassic, most likely at least five million years earlier than *Archaeopteryx*. Therefore, it is a missing link in terms of morphology, phylogeny, flight, and age. Can we expect a more perfect missing link than this in the fossil record?

5. Missing Links from Dinosaurs to Extant Birds

Archaeopteryx was discovered in 1861, only two years after Darwin's *On the Origin of Species* was published. It was regarded as a missing link because it resembles extant birds in having modern feathers and a skeleton hardly distinguishable from that of reptiles, such as the retention of teeth in the jaws, claws on the wings, and a long skeletal tail. Despite the discoveries of feathers in various non-avian dinosaurs, *Archaeopteryx* is still held by many as the ancestor of birds.

Thanks to the discoveries of over thirty avian genera from the Early Cretaceous lake deposits of Northeast China in the last two decades, our understanding of early avian evolution has been significantly enriched (Zhou *et al*. 2003; Zhou 2004; Chiappe 2007). Phylogenetic studies show that a number of taxa have been added to the list of missing links between *Archaeopteryx* and extant birds. These birds often possess a mosaic of characters, yet each may represent a step further towards to the evolution of extant birds.

Among the Early Cretaceous birds, *Jeholornis* (Zhou and Zhang 2002, 2003) is unique in possessing a long skeletal tail comprising up to 27 caudal vertebrae, more than the 23 caudal vertebrae seen in the oldest bird *Archaeopteryx*. Like *Archaeopteryx*, it retains claws on the wings and a fifth metatarsal in the foot and its distinctive chevron is recognized to be associated with the caudal vertebrae. On the other hand, *Jeholornis* is more derived than *Archaeopteryx* in having reduced teeth in the jaws, a more advanced flight apparatus such as a more elongated coracoid, a large sternum with lateral trabeculae and fenestrae, and a longer wing-to-leg proportion. Like *Archaeopteryx*, *Jeholornis* can be regarded as another link between dinosaurs and birds.

Sapeornis (Zhou and Zhang 2002, 2003) from the same deposits as *Jeholornis* represents yet another missing link between *Archaeopteryx* and extant birds. It is more advanced than *Archaeopteryx* and *Jeholornis* in having a reduced and much shortened caudal series, i.e., there are fewer than eight free caudal vertebrae anterior to a fused pygostyle (ossified from the distal caudal vertebrae). The presence of a pygostyle links them to more derived fossil and extant birds. *Sapeornis* has a synsacrum composed of more sacral vertebrae than in *Archaeopteryx* and *Jeholornis*; only two claws are retained on each wing, and the third wing digit contains only two phalanges whereas four are present in *Archaeopteryx* and *Jeholornis*. It is also easily distinguishable from *Archaeopteryx* in having a greater wing-to-leg length ratio. However, *Sapeornis* is still remote from the common ancestor of extant birds and clearly represents only an extinct taxon in early avian evolution. It retained many primitive features that distinguish it from more advanced birds. For instance, like *Archaeopteryx* and dinosaurs, it has a large postorbital process that contacts the jugal bone and forms a diapsid skull; the coracoid is short and robust and lacks a procoracoidal process; the furcula is still boomerang-shaped rather than "U"-shaped, etc.

Ornithurines represent the most advanced avian group in the Early Cretaceous. *Yixianornis* (Zhou and Zhang 2001; Clarke *et al*. 2006) is one of those from the Early Cretaceous of China. Like other more primitive birds from the Late Jurassic to the Early Cretaceous, it retains large claws on the wings, gastralia, and a pubic symphysis, all of which are absent in extant birds. Furthermore, teeth are retained in both the upper and lower jaws as in many Mesozoic birds. On the other hand, as one of the basal ornithurine birds, it also distinguishes itself from enantiornithines and other more basal birds such as *Archaeopteryx*, *Jeholornis*, and *Confuciusornis* in possessing a number of derived features that are nearly identical to those of extant birds. Most notable among them are an elongated sternum with a large keel extending along its full length, a strut-like coracoid with a well-developed procoracoidal process and a "ball and socket" articulation with the scapula, a laterally compressable "U"-shaped furcula, a laterally expanded major wing digit, completely fused carpometacarpus and tarsometatarsus, presence of an alula (bustard wing) on the alular manual digit, and long fan-shaped tail feathers. These features strongly suggest that *Yixianornis* possessed a flight capability like that of extant volant birds. Although *Yixianornis* cannot yet be regarded as the direct ancestor of extant birds, the combination of modern flight structures and the retention of some primitive features warrants it as a good example of a missing link between *Archaeopteryx* and extant birds.

6. Summary

The fossil record of evolutionary missing links has been greatly enriched since Darwin published his *On the Origin of Species*. The examples discussed in this paper are only a few selected from the long list, particularly from the discoveries in China in the last ten years.

It is probably fair to argue that Darwin's evolutionary theory was largely based on his knowledge and observation of the biology, geology, geography, and fossil evidence during the *Beagle* voyage. Fossils undoubtedly provide unique evidence of how animals and plants evolved over time. The advantage of paleontological evidence for evolution is that there existed a paleoenvironmental background over a long temporal range, so we can document the origin, macroevolution, radiation, extinction, and recovery events in the history of life, which is normally unapproachable in a modern biology laboratory or field station. Furthermore, in a strict scientific sense, you may propose as many predictions as you can to testify the evolutionary hypothesis, and Darwin's theory will always prove to be true. It must be admitted that there will never be such a thing as the perfect fossil record, yet we are lucky enough to have sufficient evidence to demonstrate the beauty of evolution by natural selection in geological history. Finally, the combined progress in molecular biology, paleontology, and geochronology have greatly stimulated our efforts in reconstructing the evolution of life on earth, which is now probably much better than anyone could have imagined several decades ago.

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References

[1] Darwin C. On the Origin of Species. London: John Murray, 1859.

[2] Eldredge N, Gould S J. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf T J M ed. Models in Paleobiology. San Francisco: Freeman, Cooper and Co, 1972, 84-115.

[3] Swisher III C C, Wang Y, Wang X, *et al*. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature*, 1999, 400:58-61.

[4] He H, Wang X, Zhou Z, *et al*. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China and its implications. *Geophy Res Let*t, 2004, 31(12):L12605.

[5] Hu D, Hou L, Zhang L, *et al*. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature*, 2009, 461:640-643.
[6] Kumar S, Hedges, S B. A molecular timescale for vertebrate evolution. *Nature*, 1998, 392:917-920.
[7] Lebatard A-E, Bourles D L, Duringer P, *et al*. Cosmogenic nuclide dating of *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali*: Mio-Pliocene hominids from Chad. *PNAS*, 2008, 105:3226-3231.
[8] Sun G, Dilcher D L, Zheng S *et al*. In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from northeast China. *Science*, 1998, 282:1692-1695.
[9] Sun G, Ji Q, Dilcher D L, *et al*. Archaefructaceae, a new basal angiosperm family. *Science*, 2002, 296:899–904.
[10] Leng Q, Friis E M. *Sinocarpus decussatus* gen. et sp. nov., a new angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China. *Plant Syst Evol*, 2003, 241:77-88.
[11] von Balthazar M, Pedersen K R, Crane P R, *et al*. Carpestella lacunata gen. et sp nov., a new basal angiosperm flower from the Early Cretaceous (Early to Middle Albian) of eastern North America. *Inter J Plant Sci*, 2008, 169(7):890-898.
[12] Rong J, Fang Z, Zhou Z, *et al*. (eds.). Originations, radiations and biodiversity changes-evidences from the Chinese fossil record. Beijing: Science Press, 2006.
[13] Mayr G, Pohl B, Peters D S. A well-preserved *Archaeopteryx* specimen with theropod features. *Science*, 2005, 310:1483-1486.
[14] White T D, Asfaw B, Beyene Y, *et al*. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science*, 2009, 326:75-86.
[15] Galik K, Senut B, Pickford M *et al*. External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. *Science*, 2004, 305(5689):1450-1453.
[16] Brunet M, Guy F, Pilbeam D, *et al*. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, 2002, 418:145-151
[17] Thewissen J G M, Cooper L N, Clementz M T, *et al*. Whales originated from aquatic artiodactyls in the Eocene epoch of India. *Nature*, 2007, 450:1190-1194.
[18] Zhou Z, Zheng S. The missing link in *Ginkgo* evolution. *Nature*, 2003, 423:821-822.
[19] Tchernov E, Rieppel O, Zaher H, *et al*. A fossil snake with limbs. *Science*, 2000, 287:2010-2012.
[20] Apesteguia S, Zaher H. A Cretaceous terrestrail snake with robust hindlimbs and a sacrum. *Nature*, 2006, 440:1037-1040.
[21] Shubin N H, Daeschler E B, Jenkins F A. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature*, 2006, 440:764-771.
[22] Shu D, Luo H, Morris C, Zhang X, *et al*. Lower Cambrian vertebrates from south China. *Nature*, 1999, 402:42-46.
[23] Shu D, Morris C, Han J, *et al*. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. *Nature*, 2003, 421:526-529
[24] Li C, Wu X, Rieppel O, *et al*. An ancestral turtle from the Late Triassic of southwestern China. *Nature*, 2008, 456:497-501.
[25] Rieppel O. 2009. How did the turtle get its shell? *Science*, 325: 154-156.
[26] Lee M S Y. The origin of the turtle body plan: bridging a famous morphological gap. *Science*, 1993, 261:1716-1720.
[27] Nagashima H, Sugahara F, Takechi M, *et al*. Evolution of the turtle body plan by the folding and creation of new muscle connections, *Science*, 2009, 325:193.
[28] Reisz R, Head J. Palaeontology: Turtle origins out to sea. *Nature*, 2008, 456:450-451.
[29] Xu X, Zhou Z, Wang X, *et al*. Four-winged dinosaurs from China. *Nature*, 2003, 421:335-340.
[30] Chen P, Dong Z, Zhen S. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature*, 1998, 391:147-152.
[31] Ji Q, Currie P J, Norell M A, *et al*. Two feathered dinosaurs from northeastern China. *Nature*, 1998, 393:753-761.
[32] Zhang, F, Zhou Z, Xu X, *et al*. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature*, 2008, 455:1105-1108.
[33] Zhang F, Zhou Z. Leg feathers in an Early Cretaceous bird of China. *Nature*, 2004, 431:925.
[34] Chatterjee S, Templin R J. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. *PNAS*, 2007, 104 (5):1576–80.
[35] Xu X, Zhao Q, Norell M, *et al*. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chinese Sci Bull*, 2009, 54:430-435.
[36] Zhou Z, Barrett, P M, Hilton J. An exceptionally preserved Lower Cretaceous ecosystem. *Nature*, 2003, 421:807-814.
[37] Zhou Z. The origin and early evolution of birds: Discoveries, disputes, and perspectives from fossil evidence. *Naturwissenschaften*, 2004, 91:455-471.
[37] Chiappe L M. 2007. Glorified dinosaurs: the origin and early evolution of birds. New Jersey: John Wiley & Sons, Inc., 2007.
[39] Zhou Z, Zhang, F. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature*, 2002, 418:405-409.
[40] Zhou Z, Zhang F. *Jeholornis* compared to *Archaeopteryx*, with a new understanding of the earliest avian evolution. *Naturwissenschaften*, 2003, 90:220-225.
[41] Zhou Z, Zhang F. Largest bird from the Early Cretaceous and its implications for the earliest avian ecological diversification. *Naturwissenschaften*, 2002, 89:34-38.
[42] Zhou Z, Zhang F. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can J Earth Sci*, 2003, 40(5):731-747.
[43] Zhou Z, Zhang F. Two new ornithurine birds from the Early Cretaceous of western Liaoning, China. *Chinese Sci Bull*, 2001, 46(15):1258-1264.
[44] Clarke J, Zhou Z, Zhang F. Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *J Anat*, 2006, 208:287-308.