

Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian origins

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The last two decades have witnessed great advances in reconstructing the transition from non-avian theropods to avians, but views in opposition to the theropod hypothesis still exist. Here we highlight one issue that is often considered to raise problems for the theropod hypothesis of avian origins, i.e. the “temporal paradox” in the stratigraphic distribution of theropod fossils — the idea that the earliest known avian is from the Late Jurassic but most other coelurosaurian groups are poorly known in the Jurassic, implying that avians arose before their supposed ancestors. However, a number of Jurassic non-avian coelurosaurian theropods have recently been discovered, thus documenting the presence of most of the major coelurosaurian groups in the Jurassic alongside, or prior to, avians. These discoveries have greatly improved the congruence between stratigraphy and phylogeny for derived theropods and, effectively, they reject the “temporal paradox” concept. Most importantly, these discoveries provide significant new information that supports the relatively basal positions of the Tyrannosauroidae and Alvarezsauroidae among the Coelurosauria. Indeed, they imply a new phylogenetic hypothesis for the interrelationships of Paraves, in which *Archaeopteryx*, the Dromaeosauridae, and the Troodontidae form a monophyletic group while the Scansoriopterygidae, other basal birds, and probably also the Oviraptorosauria, form another clade. Mapping some of the salient features onto a temporally-calibrated theropod phylogeny indicates that characteristics related to flight and arboreality evolved at the base of the Paraves, earlier than the Late Jurassic.

Jurassic, fossil record, Coelurosauria, Theropoda, avian origins

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It is widely accepted that the group Aves is nested deeply within the Theropoda, a major dinosaurian group composed of predominantly carnivorous animals [1,2]. More specifically, birds are considered to be hierarchically tetanuran theropods, coelurosaurian theropods, maniraptoran theropods, and paravian theropods (Figure 1). The currently accepted theropod phylogeny, in combination with their known fossil records, suggests that the Paraves diversified in the Jurassic and, consequently, so did the more exclusive Maniraptora and Coelurosauria [3].

The bird-like non-avian coelurosaurians were mostly small to medium-sized animals, although they also include very large members, like the famous *Tyrannosaurus rex* [4]. Previously, our knowledge of the Coelurosauria has been based on fossils recovered from Cretaceous deposits because of the poor sampling of Jurassic beds [5]. This has created an apparent discrepancy between stratigraphy and phylogeny, which has sometimes been used to argue against the theropod hypothesis of bird origins, because the earliest known bird, *Archaeopteryx*, is from the Late Jurassic [2,6]. Quantitative analyses strongly suggest that placing the Aves within the Coelurosauria is more parsimonious than placing

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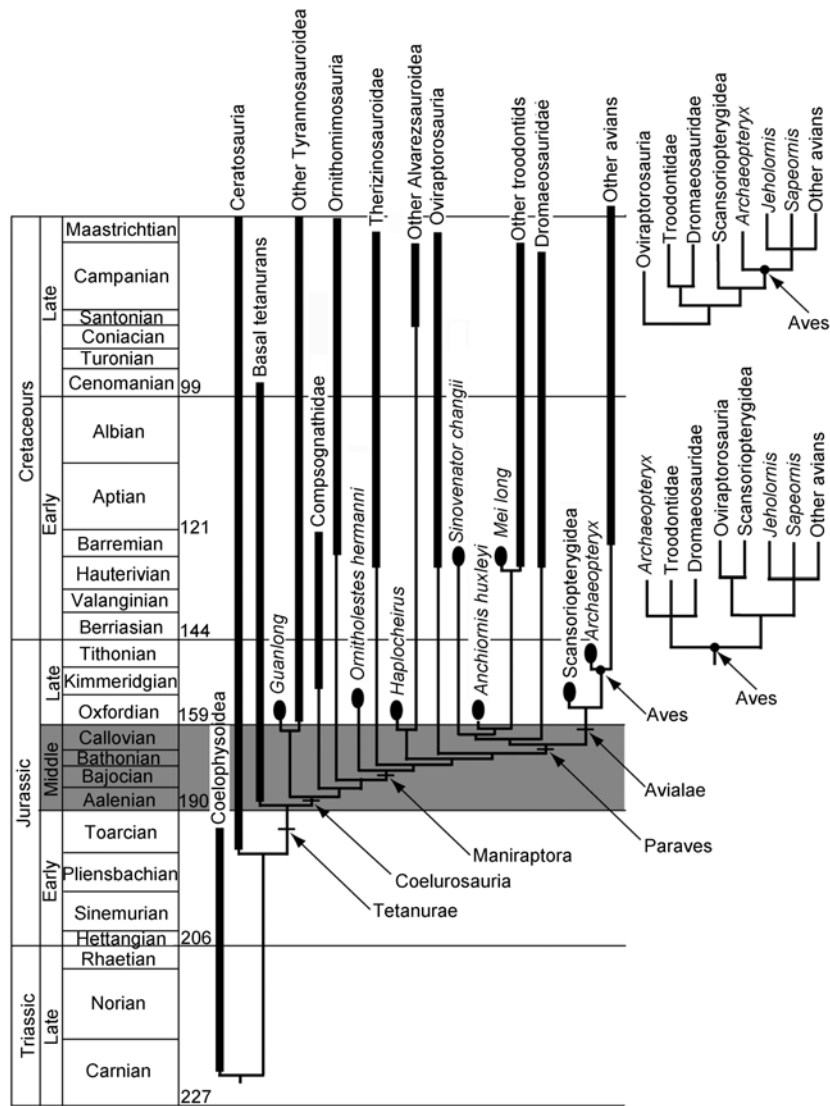


Figure 1 Temporally calibrated phylogeny of Theropoda. This evolutionary tree has been compiled and simplified from several phylogenetic analyses [3,4,8,9]. While there is a general consensus on the inter-relationships of the major theropod groups, debate exists concerning the systematic positions of several theropod groups. One of the most important topics concerns the inter-relationships among the major maniraptoran groups, which provide the basis for understanding the evolution of salient avian features. Most recent phylogenetic analyses recover a traditional monophyletic Aves (right above). However, an alternative hypothesis is implied by new information from the Jurassic maniraptorans, which suggests that several traditional non-avian theropod groups are actually basal members of the Aves (right lower), if Aves is defined as the least inclusive group including *Archaeopteryx* and extant birds. The temporal durations (solid bars) of the major theropod groups are based on well-corroborated fossil occurrences (numbers refer to the age in millions of years).

it anywhere in the Archosaurian phylogeny, which tends to invalidate the so-called temporal paradox argument against the theropod hypothesis [7]. Nevertheless, the poor fossil record of the coelurosaurians in the Jurassic has hindered our understanding of the early evolution of this group, and also of the origin of the Aves. Prospecting in Jurassic sediments and the discovery of Jurassic coelurosaurian fossils are thus very important undertakings in the field of theropod research, which promise to provide significant new information for our understanding of the early evolution of the Coelurosauria and avian origins. In this paper, we review

the known fossil records of major coelurosaurian groups and highlight our recent efforts in this regard.

1 Fossil records of major coelurosaurian groups

Besides the Aves, the major groups of the Coelurosauria include the Tyrannosauroidae, Compsoognathidae, Ornithomimosauria, Alvarezsauroidae, Therizinosauroidae, Oviraptorosauria, Troodontidae, Dromaeosauridae, and Scansoriopterygidae. The fossil records of these groups are derived

primarily from Cretaceous deposits and, until recently, the best coelurosaurian fossil records were restricted to the Late Cretaceous of Laurasia [5].

The systematic position of the Tyrannosauroida has been controversial. While most studies suggest that the Tyrannosauroida is a basal coelurosaurian group [8–10], others suggest that it is more closely related to the Aves than to other coelurosaurian groups, such as the Ornithomimosauria and Alvarezsauroida [3]. The Tyrannosauroida are best represented by fossils recovered from the Latest Cretaceous of North America, while others are known from Asia, also from this period [11]. Recent discoveries demonstrate that this group had already diversified by the Early Cretaceous [12–15] and a number of Jurassic tyrannosauroids have been reported from North America and Europe [11,16]. The earliest known is *Proceratosaurus* from the Bathonian of Europe [17]. However, nearly all of these non-Cretaceous examples are based on fragmentary specimens [11]. Our recent discoveries of two nearly complete skeletons of *Guanlong wucaii* from the Oxfordian upper section of the Shishugou Formation (Figure 2(a)) represent the best fossil record of this group in the Jurassic [18].

The first members of Compsognathidae were originally discovered from the Late Jurassic of Europe and, currently, the group is also known in the Early Cretaceous of Asia and South America [19]. While most studies place this group within the Coelurosauria, or even in the Maniraptora [9], a number of early studies suggest that the Compsognathidae lies outside the Coelurosauria [3]. The earliest known compsognathid is the Kimmeridgian *Compsognathus longipes* from Europe [20].

The Ornithomimosauria is one of two non-avian theropod groups in which the derived members are toothless and the basal taxa are toothed [21] (the other being the oviraptorosaurs). Although the ornithomimosaurians are widely accepted to be a basal group of the Coelurosauria [3,9,22–24], their fossil occurrences are mostly from the Late Cretaceous [25]. Geographically, this group is restricted to the Laurasia [21]. The earliest known indisputable ornithomimosaur is the Valanginian-Barremian *Shenzhousaurus orientalis*, a recent discovery from the famous Yixian Formation of western Liaoning Province, China [26,27].

The systematic position of the Alvarezsauroida has been highly controversial [3,23,28–30]. They are all small in size and have once been suggested to be flightless birds [28]. Previously their known fossil records are all from the Late Cretaceous [31], with the earliest known one from the Turonian of Argentina, South America [32]. Our recent expedition in the Jurassic sediments of the Junggar Basin, Xinjiang Uygur Autonomous Region, China resulted in the discovery of a nearly complete skeleton of a basal alvarezsaurid (Figure 2(b)), which extends the fossil record of this group by some 63 million years [24].

The Therizinosauroida is a group of unusual herbivorous theropod dinosaurs with a bulky body [33]. Originally

known from the Late Cretaceous of Asia, they have been recently discovered in the Early Cretaceous of both Asia and North America [34–36]. The earliest indisputable examples of this group include the Valanginian-Barremian *Beipiaosaurus* [27,34] from Liaoning, China and the Barremian *Falcarius* from North America [36]. Although the Hettangian *Eshanosaurus* has been referred to the Therizinosauroida [37], this taxon is based on a very fragmentary specimen and its suggested therizinosauroid affinity requires confirmation by additional material.

The Oviraptorosauria is best known from the Late Cretaceous of Laurasia [38]. They have been also suggested to be present in the Early Cretaceous of Australia [39] and the Late Cretaceous of South America [40], but these identifications have been questioned [40]. Recent discoveries of several basal oviraptorosaurs from the Jehol Group demonstrate that this group diversified significantly in the Early Cretaceous of Asia [41]. The earliest known unquestionable oviraptorosaur is the Valanginian-Barremian *Incisivosaurus* [27,42] from the Jehol Group of Liaoning, China.

The Dromaeosauridae is the non-avian theropod group considered by most phylogenetic analyses to be most closely related to the birds [3,8–10,43,44]. The fossil records of this group are known throughout the Cretaceous of Laurasia and Gondwana [23,45–47]. Recent discoveries of several basal dromaeosaurid taxa from the Jehol Group indicate a high diversity of this group in the Early Cretaceous [23,48]. The earliest known unquestionable dromaeosaurid is the Valanginian-Barremian *Graciliraptor* [27,49] from the Jehol Group of Liaoning, China. Some isolated teeth from the Middle Jurassic of Europe have also been referred to the group, but this identification needs further confirmation.

The Troodontidae is a group of small, lightly built non-avian theropods and represents one of the most bird-like groups (with the dromaeosaurs, they comprise the Deinonychosauria, widely regarded as the sister taxon to the Avialae). Their unequivocal fossil records were previously known only from the Cretaceous deposits of Asia and North America, although some fragmentary specimens from the Jurassic of North America have also been referred to this group [50]. Recently some exceptionally well preserved troodontid specimens have been recovered from the early Late Jurassic Tiaojishan Formation (Figure 2(c)) of western Liaoning Province, China and these specimens represent the oldest known troodontid taxon and also the earliest known unquestionably feathered species [51,52].

The Scansoriopterygidae is a newly recognized clade at the base of the Avialae, which contains only 2 genera, *Epidendrosaurus* and *Epidexipteryx* (Figure 2(d)). Both are from the Daohugou Formation of Inner Mongolia Autonomous Region, China [53,54], which also produced the basal avialan *Pedopenna* [55]. The Daohugou Formation is likely to be Middle to Late Jurassic (Bathonian-Kimmeridgian) in age [56], though this interpretation has been questioned [57].

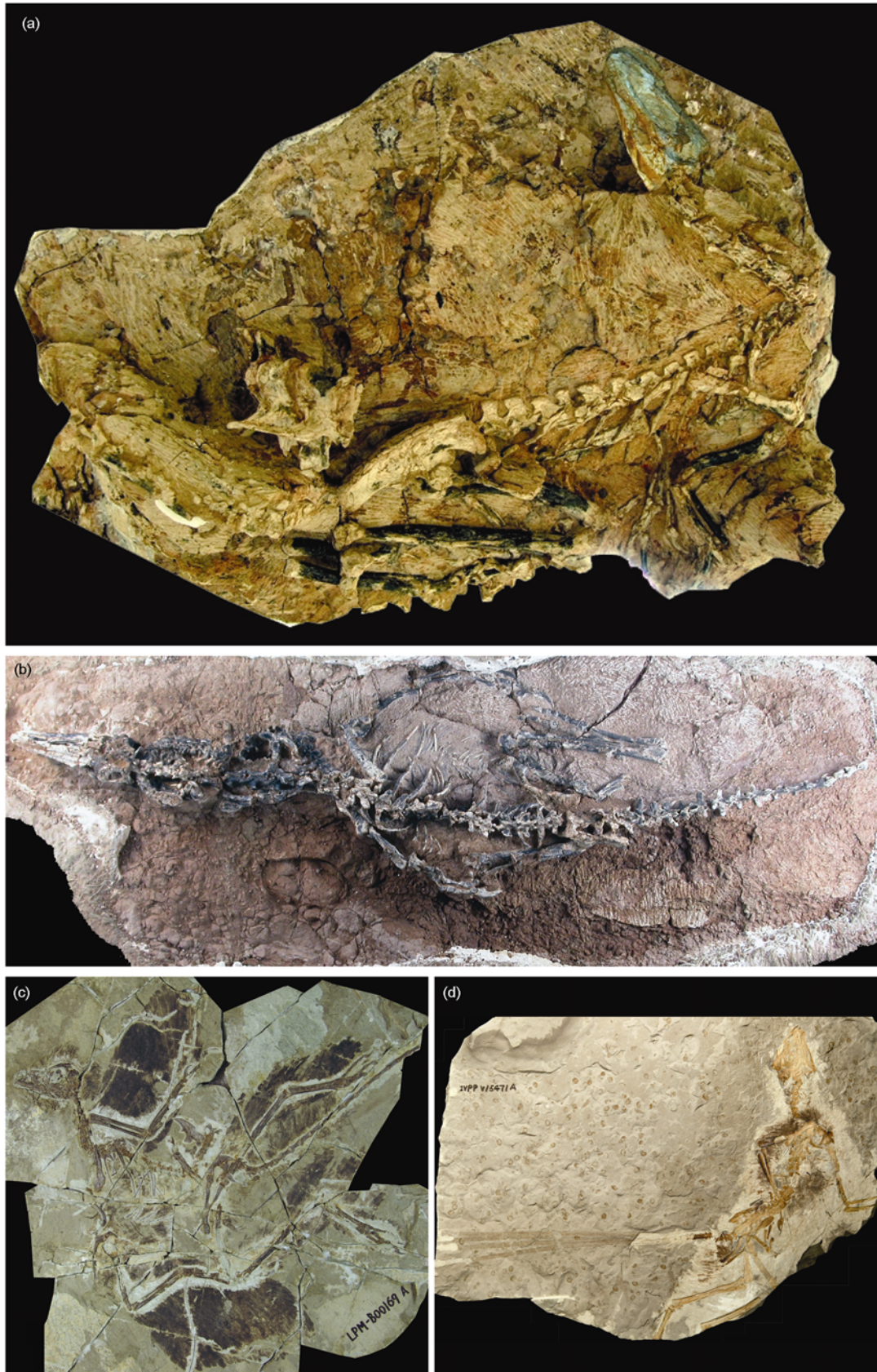


Figure 2 Selected coelurosaurian taxa from the Jurassic. (a) The basal tyrannosauroid *Guanlong*; (b) the basal alvarezsauroid *Haplocheirus*; (c) the basal troodontid *Anchiornis*; and (d) the scansoriopterygid *Epidexipteryx*.

2 Pre-*Archaeopteryx* coelurosaurians and avian origins

Until recently, our understanding of coelurosaurian evolution has been based mainly on fossils from the Upper Cretaceous of Laurasia [58]. As described above, this situation has changed considerably over last two decades, largely because of the discoveries of various coelurosaurian fossils from the Lower Cretaceous Jehol Group of China [41,59], from the Upper Cretaceous of Mongolia [10], from the Cretaceous of the southern continents [60,61], and from the Middle-Upper Jurassic of China [18,24,52,54,55], among others. Because basal members of clades often have important roles in the reconstruction of the phylogenetic trees and ancestral conditions of the corresponding groups [62], the Jurassic coelurosaurians are significant in this regard. This is particularly true given the presence of widely distributed reversals and convergences in coelurosaurian evolution (especially with respect to bird-like features) [63].

Coelurosaurian theropods from the Jurassic have long been known but, in most cases, they are based on fragmentary material [5]. In the last decade, we have recovered well-preserved specimens of several coelurosaurian taxa from the Jurassic sediments, including the basal tyrannosauroid *Guanlong* [18], the basal alvarezsauroid *Haplocheirus* [24], the basal troodontid *Anchiornis* [51,52], and the scansoriopterygids *Epidendrosaurus* [53] and *Epidexipteryx* [54]. These discoveries provide significant new information on various aspects of coelurosaurian evolution and, in particular, on avian origins.

Phylogeny is the basis for evolutionary reconstruction. A robust phylogenetic hypothesis is the pre-condition for an accurate reconstruction of the evolutionary history of the theropod-bird transition. Because of the wide distribution of reversals and convergences in coelurosaurian evolution [63], the Jurassic coelurosaurians have an important role in reconstructing theropod phylogeny. The basal tyrannosauroid *Guanlong* and the basal alvarezsauroid *Haplocheirus* exhibit many plesiomorphic features seen in other basal coelurosaurians, and even some plesiomorphic features seen in more basal tetanuran theropods, and they provide strong evidence supporting the relatively basal positions of the tyrannosauroids and alvarezsauroids among the Coelurosauria [18,24]. The basal troodontid *Anchiornis* has significantly reduced the morphological gaps among the troodontids, the dromaeosaurids, and *Archaeopteryx* and, thus, it has provided further evidence for close relationships among these taxa [51,52]. On the one hand, the troodontids, the dromaeosaurids, and *Archaeopteryx* share some derived similarities that are absent in other avialans and most other non-avian theropods, including the large promaxillary fenestra situated posterior to the anterior border of the antorbital fossa, a T-shaped lacrimal, and a coracoid with a distinct fossa on the ventral surface; on the other hand, the

scansoriopterygids *Epidendrosaurus* [53] and *Epidexipteryx* [54] are more similar to basal birds, such as *Jeholornis* and *Sapeornis* [64,65], than to *Archaeopteryx* in many of their derived features, particularly in a number of derived cranial features. Surprisingly these cranial features are also seen in the oviraptorosaurs [54]. Together, the Jurassic maniraptorans suggest a monophyletic group composed of the scansoriopterygids, all other birds except *Archaeopteryx*, and probably also the oviraptorosaurs. This would represent a sister taxon to a monophyletic group containing the troodontids, the dromaeosaurids, and *Archaeopteryx* (Figure 1). Such a phylogenetic hypothesis would have significant implications for the reconstruction of the theropod-bird transition but it has yet to be tested by quantitative phylogenetic analysis.

The Jurassic coelurosaurians are also important in reconstructing the phylogenetic and temporal distribution pattern of salient avian features. The troodontid *Anchiornis* from the Late Jurassic Tiaojishan Formation possesses flight feathers on the forelimbs, hind limbs, and tail. Its discovery further extends the fossil record of flight feathers to the Middle-Late Jurassic boundary, indicating that flight feathers first appeared before the Late Jurassic [52]. Phylogenetically, a four-winged condition is primitive for the Paraves and it evolved before the Late Jurassic. Besides *Anchiornis*, two other Jurassic non-avian paravians, *Epidendrosaurus* [53] and *Epidexipteryx* both possess long and robust arms and a number pedal features similar to those in arboreal animals [54]. These features suggest that features related to flight and arboreality evolved at the base of the Paraves earlier than the Late Jurassic.

The discoveries of many Jurassic coelurosaurians, and particularly basal paravians, provide strong evidence, supporting the hypothesis that the major coelurosaurian groups, including the Avialae, originated and diversified before the Late Jurassic. A quantitative analysis incorporating these new findings results in a much improved fit between the phylogeny and the fossil record of theropods [24]. Interestingly, a calibrated theropod phylogeny based only on well-corroborated fossil occurrences suggests that all coelurosaurian groups, including Aves, diversified rapidly in the Middle Jurassic (Figure 1). Coincidentally, and perhaps significantly, this period also witnessed drastic paleogeographical and climatic changes.

3 Conclusions

Significant advances in the theropod origins of birds have been made over the last two decades, resulting from more comprehensive phylogenetic analyses [3,9,23,44,66]; the discoveries of new specimens of both non-avian dinosaurs and basal birds that have provided significant osteological and even behavioral information [41,46,47,54,67–72]; analyses of bone and eggshell microstructure that imply the

growth strategy and physiology of non-avian dinosaurs and early birds; and even from the recovery of molecular information [73–75]. In particular, discoveries of various Jurassic non-avian coelurosaurian theropods have greatly improved the congruence between stratigraphy and phylogeny for derived theropods, and also our understanding of the phylogenetic and temporal distribution pattern of avian features [18,24,52,54]. However, there are still few known pre-*Archaeopteryx* coelurosaurs and the early evolution of the Coelurosauria is still relatively poorly understood. An accurate reconstruction of the theropod-bird transition will depend on additional discoveries from the Jurassic coelurosaurs and on their in-depth analyses.

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