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A short-armed dromaeosaurid from the Jehol Group of China with implications for early dromaeosaurid evolution

Xiaoting Zheng¹, Xing Xu^{2,*}, Hailu You³, Qi Zhao²
and Zhiming Dong²

¹Tianyu Museum of Nature, Pingyi, Shandong, 273300, China

²Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xiwai Street, Beijing 100044, China

³Geological Institute, Chinese Academy of Geological Sciences, 26 Baiwanzhuang Road, Beijing 100037, China

Recent discoveries of basal dromaeosaurids from the Early Cretaceous Jiufotang and Yixian formations of Liaoning, China, add significant new information about the transition from non-avian dinosaurs to avians. Here we report on a new dromaeosaurid, *Tianyuraptor ostromi* gen. et sp. nov., from the Early Cretaceous Yixian Formation of western Liaoning, China, based on a nearly complete skeleton. *Tianyuraptor* possesses several features only seen in other Liaoning dromaeosaurids, although to a less developed degree, and it also exhibits features unknown in Laurasian dromaeosaurids but present in the Gondwanan dromaeosaurids and basal avialans, thus reducing the morphological gap between these groups. *Tianyuraptor* possesses a comparatively small furcula and proportionally short forelimbs. This lies in stark contrast to the possible capacity for flight in the microraptorines, which have proportionally long and robust forelimbs and large furculae. The presence of such striking differences between the Early Cretaceous Jehol dromaeosaurids reveals a great diversity in morphology, locomotion and ecology early in dromaeosaurid evolution.

Keywords: Dromaeosauridae; Paraves; Theropoda; Early Cretaceous; Jehol Group

1. INTRODUCTION

Dromaeosaurids are a group of small to medium theropods with a highly specialized pedal digit II (Ostrom 1969; Norell & Makovicky 2004; Makovicky *et al.* 2005). Most phylogenetic analyses posit the Dromaeosauridae as the sister taxon to the Troodontidae, forming a monophyletic Deinonychosauria, which in turn is the sister taxon to the Avialae (Ostrom 1969; Gauthier 1986; Sereno 1999; Norell *et al.* 2001; Xu 2002; Senter *et al.* 2004; Senter 2007; Turner *et al.* 2007b), although some analyses suggest that the dromaeosaurids themselves are the closest relatives of birds (Xu *et al.* 1999; Holtz 2000). As one of the most bird-like groups, they share numerous derived similarities with birds, including small size, a feature considered critical for the origin of avian flight (Novas & Puerta 1997; Sereno 1999; Xu *et al.* 2000; Xu & Norell 2004; Turner *et al.* 2007b). Basal dromaeosaurids are all small in size and this is particularly true for Liaoning dromaeosaurids (Xu *et al.* 1999, 2000, 2003; Hwang *et al.* 2002; Xu & Wang 2004; Xu 2006). So far, five dromaeosaurid taxa have been reported from the Early Cretaceous Jehol Group of western Liaoning, China, all being shorter than 150 cm in total body length. These taxa are *Sinornithosaurus millenii* from the Yixian Formation (Xu *et al.* 1999),

Sinornithosaurus haoiana from the Yixian Formation (Liu *et al.* 2004), *Microraptor zhaoianus* from the Jiufotang Formation (Xu *et al.* 2000), *Microraptor gui* from the Jiufotang Formation (Xu *et al.* 2003), and *Graciliraptor lujiatunensis* from the Yixian Formation (Xu & Wang 2004). They share several unique features and are suggested to form a monophyletic group at the base of the dromaeosaurid phylogenetic tree (Xu 2002; Senter *et al.* 2004; Xu & Wang 2004; Turner *et al.* 2007b). Here we report the sixth dromaeosaurid taxon from the Jehol Group, which is a medium-sized taxon with an unusual combination of characters. Its discovery has implications for understanding the early evolution of the dromaeosaurid dinosaurs.

2. SYSTEMATIC PALAEOLOGY

Maniraptora Gauthier, 1986

Dromaeosauridae Matthew & Brown, 1922

Tianyuraptor ostromi gen. et sp. nov.

(a) Etymology

'Tianyu' is derived from the name of the museum that has the holotype, and 'raptor' refers to the Latin for 'robber'. The specific name is in honour of John Ostrom, who contributed greatly to the study of dromaeosaurid fossils.

(b) Holotype

A nearly complete, articulated skeleton missing only the distal end of the tail, housed in Tianyu Museum of Nature (STM1–3).

* Author for correspondence (xingxu@vip.sina.com).

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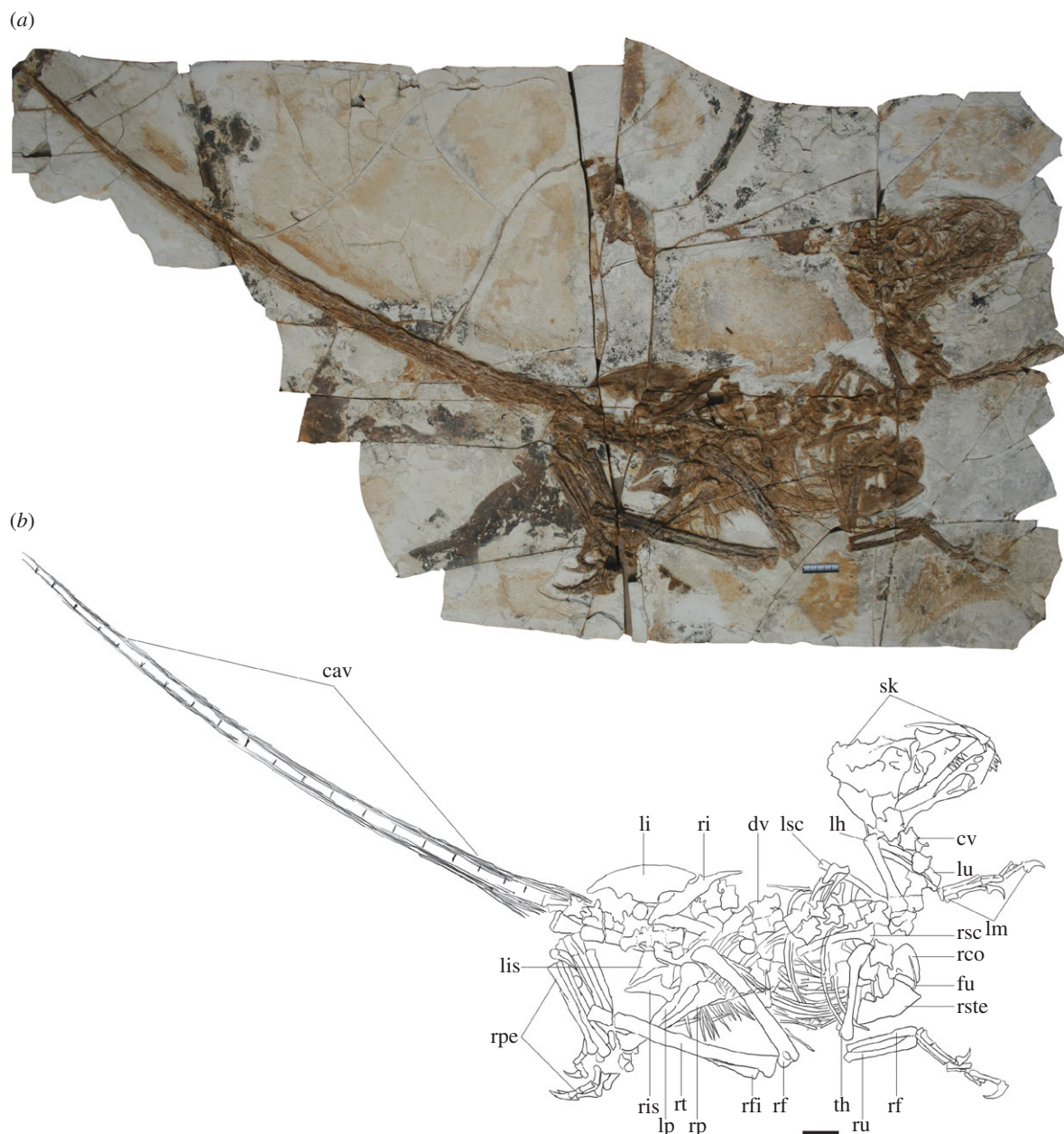


Figure 1. *Tianyuraptor ostromi* holotype. (a) Photograph and (b) line drawing of the holotype skeleton. Abbreviations: sk, skull; cv, cervical vertebrae; dv, dorsal vertebrae; cav, caudal vertebrae; rsc, right scapula; lsc, left scapula; rco, right coracoid; rste, right sternal; fu, furcula; lh, left humerus; rh, right humerus; lu, left ulna; ru, right ulna; rr, right radius; lm, left manus; rm, right manus; li, left ilium; lis, left ischium; ris, right ischium; lp, left pubis; rp, right pubis; rf, right femur; rt, right tibia; rfi, right fibula; rpe, right pes. Scale bar, 5 cm

(c) *Locality and horizon*

Dawangzhangzi, Lingyuan, western Liaoning, China; Early Cretaceous Yixian Formation (Wang *et al.* 1998; Swisher *et al.* 2002).

(d) *Diagnosis*

A medium-sized dromaeosaurid that differs from other dromaeosaurids in the following derived features: length of the middle caudal vertebrae more than twice that of the dorsal vertebrae, a small and extremely slender furcula, and an elongated hindlimb about three times as long as the dorsal series.

(e) *Description and comparison*

The holotype and only known specimen (figure 1) is thought to be a sub-adult, as indicated by a suite of

characters associated with the fusion of skeletal parts during ontogeny: the neurocentral sutures of all vertebrae are closed, the xiphiapophyses are fused, the astragalus–calcaneum complex is separated from the tibia. As with some other theropod specimens from the Jehol Group, STM1–3 has no soft tissues preserved.

The skull is proportionally large in size and is longer than the femur (figures 1*a,b* and 2*a*). The maxilla is weakly sculptured by small pits on the lateral surface of the bone at the anteroventral corner, a feature also seen in other Liaoning dromaeosaurids (Xu *et al.* 1999; Xu 2002), although, in the latter, the sculpting is much more developed. The antorbital fossa does not have a sharp border anteriorly and ventrally, unlike other Liaoning dromaeosaurids (Xu & Wu 2001) but similar to most other

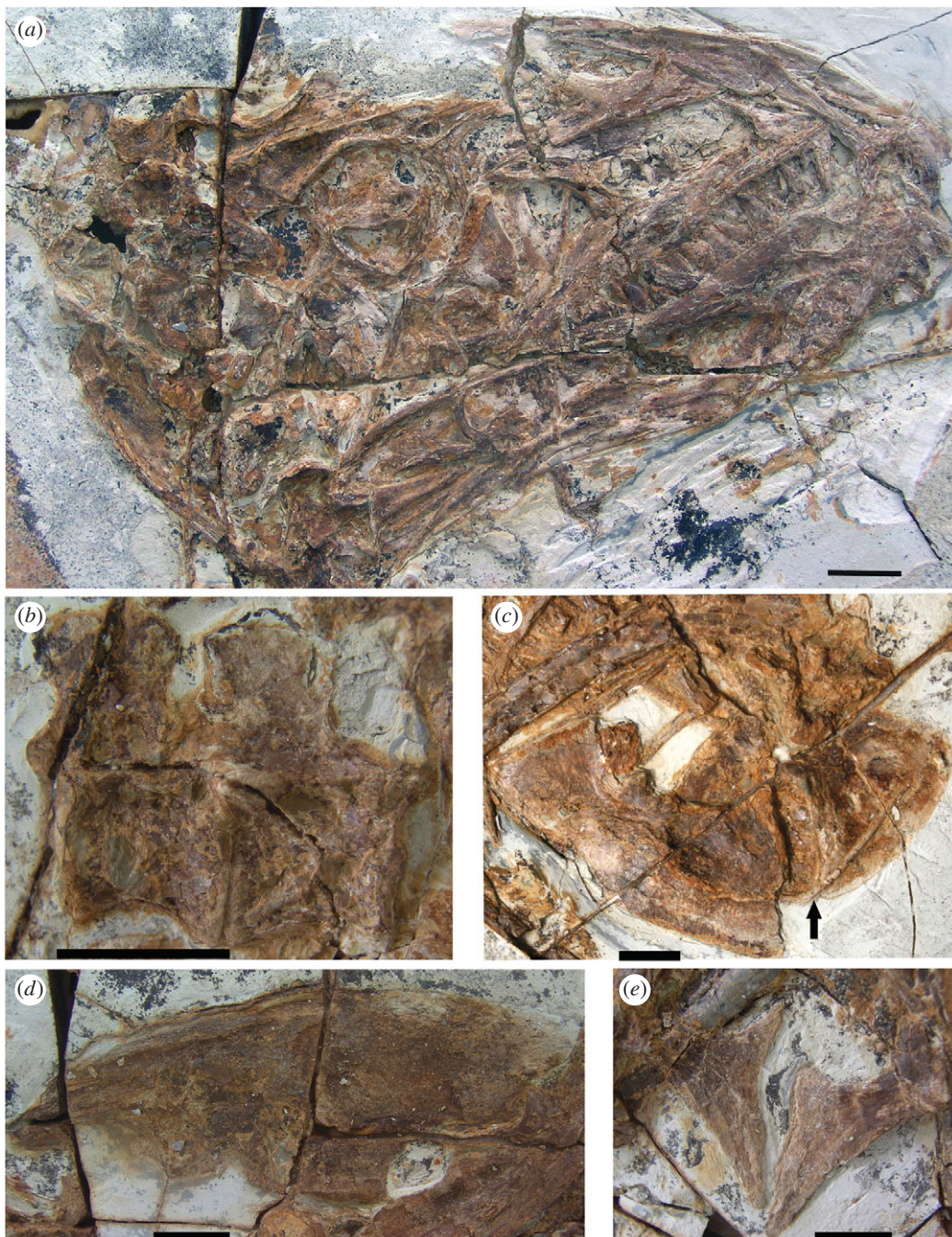


Figure 2. Selected skeletal elements of *Tianyuraptor ostromi* holotype. (a) Skull and mandible in lateral view. (b) Two posterior dorsal vertebrae in lateral view. (c) Furcula, right sternal plate, and right coracoid. Arrow indicates the reduced furcula. (d) Left ilium in medial view. (e) Right ischium in medial view. Scale bar, 2 cm

dromaeosaurids (Barsbold & Osmolska 1999; Norell *et al.* 2006). As in other Liaoning dromaeosaurids, basal troodontids and basal avialans (Xu 2002), the promaxillary fenestra is enlarged and close in size to the maxillary fenestra. The latter is located dorsally, a feature unique to Laurasian dromaeosaurids (Norell & Makovicky 2004; Senter *et al.* 2004; Turner *et al.* 2007a). The ascending process of the maxilla is well developed, and it sends a robust process extending posteriorly considerably beyond the anterior border of the antorbital fenestra. The nasal is long and slender. As in some Liaoning dromaeosaurids, the frontal process of the postorbital is slightly constricted at the base and blunt distally. The teeth are stout, proportionally short apicobasally and labiolingually. Both the mesial and distal carinae bear fine serrations, the

former significantly smaller than the latter as in many dromaeosaurids (Currie 1995; Xu 2002).

The cervical vertebrae are about the same length as the dorsal vertebrae and thus differ from the proportionally longer cervicals in other Liaoning dromaeosaurids (Hwang *et al.* 2002; Xu 2002). The posterior margin of the neural arches of the anterior cervicals appear to be located considerably posterior to the posterior margin of the centra. The neural spines of the posterior dorsal vertebrae are positioned on the posterior half of the centra and their posterior margins are obviously posterior to the inter-central articulation (figure 2b). As in other Liaoning dromaeosaurids (Senter *et al.* 2004), the tail is proportionally long (here a preserved length of 960 mm), approximately 4.8 times as long as the femur.

Twenty-five fully articulated caudal vertebrae are preserved and at most only three are estimated to be missing. The middle caudal vertebrae are more than twice the length of the posterior dorsal vertebrae. The sternal plate is proportionally short along the long axis, each plate being only slightly more than twice as long as it is wide. The sub-triangular lateral xiphoid process is extremely small in size (figure 2c).

The furcula is small in comparison to that of most other dromaeosaurids (Norell & Makovicky 1997; Xu 2002; Burnham 2004), about one-fifth of the femoral length and one-third of the scapular width, respectively. It has an interclavicle angle of about 110° and, as in *Buitreraptor* (Makovicky *et al.* 2005), the apophysis appears to be flat (figure 2c). No hypocleidium is present. The scapula is not fused to the coracoid. The former is proportionally short (88% of the humeral length) and robust (minimum blade width greater than the mid-shaft diameter of the ulna). The sub-rectangular coracoid has a prominent, laterally located tubercle and its ventral margin is obviously convex and is proportionally long (162% of the length of the lateral margin, much longer than in other Liaoning dromaeosaurids (Xu 2002)). It also differs from other Liaoning dromaeosaurids (Ji *et al.* 2001; Xu 2002) in that a large fenestra in the coracoid is absent (figure 2c).

The forelimb is very short and slender compared to the hindlimb (53% of the hindlimb length). Most other dromaeosaurids have a relatively long forelimb compared with other non-avian theropods (more than 70% of the hindlimb length in most dromaeosaurids). The humerus is only about 65 per cent of the femoral length. It has a short deltopectoral crest (29% of the humeral length) and a proximodistally long, crest-like internal tuberosity that projects proximally at about the same level as the humeral head. The ulna is considerably more slender than the humerus and it has a small olecranon process. The radius is less than half of the femoral length and distally has a distinct lateral flange as in other dromaeosaurids (Burnham 2004). The manus is short relative to the femur (86% of the femoral length), but long relative to the humerus (133% of the humeral length). The semilunate carpal is partially fused to the middle metacarpal and also slightly contacts both metacarpals I and III. The penultimate manual phalanges are significantly longer than the preceding phalanges as in most other dromaeosaurids except those from Liaoning (Ostrom 1969; Gauthier 1986; Xu 2002). However, like other Liaoning dromaeosaurids (Xu *et al.* 1999, 2003; Xu 2002; Xu & Wang 2004) it has a significantly shortened manual phalanx III-2 (about half as long as III-1).

The ilium is similar to that of other Liaoning dromaeosaurids in its relatively small size (75% of the femoral length) and its concave anterior margin with a somewhat pointed anterodorsal corner (figure 2d), but differs in having a proportionally much longer preacetabular process (taking up 63% of the whole iliac length compared to about 50–55% in other Liaoning dromaeosaurids). As in *Rahonavis* and some other dromaeosaurids (Forster *et al.* 1998; Novas 2004), the pubic peduncle is proportionally wide (23% of the iliac length and about 2.5 times as wide anteroposteriorly as deep dorsoventrally). The posterior end of the ilium is positioned ventrally, but not to the degree seen in other Liaoning

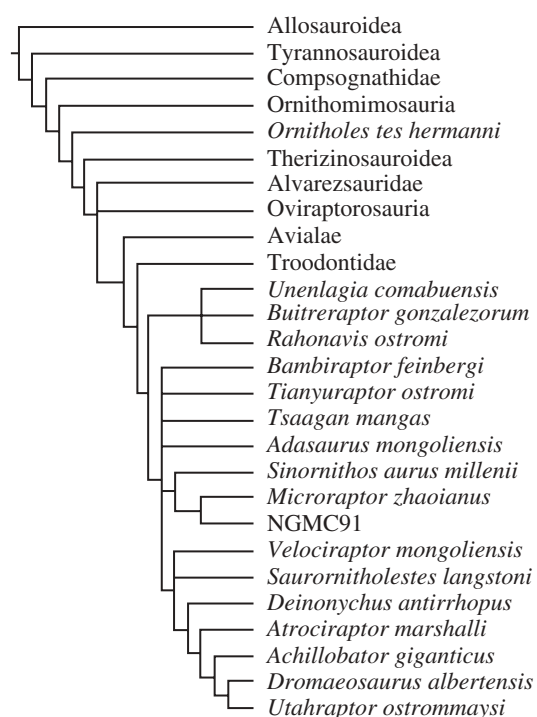


Figure 3. Simplified strict consensus of 30 most parsimonious trees (tree length = 1232; CI = 0.35; RI = 0.75) showing systematic position of *Tianyuraptor ostromi* recovered by a numerical phylogenetic analysis (see electronic supplementary material for more details).

dromaeosaurids. The pubis is straight in lateral view and it lacks a lateral projection at the mid-shaft, but it appears to be similar to that of other Liaoning dromaeosaurids in having a spatulate distal end (Xu 2002). As in other Liaoning dromaeosaurids, unenlagiines (Novas & Puerta 1997), and basal paravians (Xu 2002), the ischium is significantly shorter than the pubis in length (less than 40% of the pubic length) and as in most other derived coelurosaurians (Makovicky & Norell 2004; Norell & Makovicky 2004; Osmolska *et al.* 2004), the large, triangular obturator process is located at the mid-length of the ischium (figure 2e). The posterior margin of the ischium is strongly concave and bears no distinct posterodistal process seen in other basal paravians (Novas & Puerta 1997; Forster *et al.* 1998; Makovicky *et al.* 2005).

The hindlimb is obviously more robust than the forelimb and is proportionally very long (about three times the length of the dorsal series). The femur has a prominent trochanteric crest formed by the completely fused greater and lesser trochanters. Distally, a prominent ectocondylar tuber is located medially and proximally relative to the lateral condyle. The tibiotarsus is about 135 per cent of the femoral length, proportionally much longer than similarly sized dromaeosaurids. The metatarsus is about 70 per cent of the femoral length. Metatarsal III is considerably compressed proximally, but not to the degree seen in other Liaoning dromaeosaurids.

3. DISCUSSION

A numerical phylogenetic analysis posits *Tianyuraptor* as basal member of the Laurasian dromaeosaurids (figure 3). Synapomorphies supporting this phylogenetic

Table 1. Relative proportions of selected elements in Liaoning dromaeosaurids.

element	<i>T. ostromi</i>	<i>S. millenii</i>	<i>M. zhaoianus</i>	<i>M. gui</i>
coracoid width/length	1.62	1.20	0.98	0.95
furcula width/scapula width	0.30	1.18	1.14	1.33
arm length/leg length	0.53	0.83	0.81	0.80
humerus length/femur length	0.65	0.91	0.78	0.85
radius length/femur length	0.49	0.72	0.68	0.73
manus length/femur length	0.86	1.02	1.06	1.06
tibiotarsus length/femur length	1.33	? ^a	1.32	1.30

^aThis ratio unknown in this specimen.

hypothesis include the dorsal arch of manual ungual I and extreme elongation of the prezygapophyses and chevrons of the caudal vertebrae. *Tianyuraptor* possess several features unknown in other Laurasian dromaeosaurids, but which are seen in basal avialans and Gondwanan dromaeosaurids, that is, *Buitreraptor*, *Unenlagia*, *Rahonavis*, *Neuquenraptor* and *Austroraptor* (Novas & Puerta 1997; Forster *et al.* 1998; Makovicky *et al.* 2005; Novas & Pol 2005; Novas *et al.* 2009); these include significantly elongated iliac preacetabular process and a strongly concave ischial posterior margin, thus reducing the morphological gap between these groups.

Liaoning dromaeosaurids share several unique morphological features and are suggested to form a monophyletic Microraptorinae (Senter *et al.* 2004; Xu & Wang 2004; Makovicky *et al.* 2005; Senter 2007; Turner *et al.* 2007b). *Tianyuraptor* possesses some of these features, including a laterally sculpted maxilla, a significantly shortened manual phalanx III-2 and a spatulate pubic symphysis, but it lacks many other microraptorine features, such as a large oval fenestra in the coracoid, shortened penultimate manual phalanges with their distal end curving ventrally, the posterior end of the ilium being significantly ventral to the ischial peduncle, and a lateral projection on the mid-length of the pubic shaft. This suggests that *Tianyuraptor* might be the most basal microraptorine, which is indicated by six of the 30 resulting most parsimonious trees recovered by our analysis. A short-armed microraptorine at the base of the Microraptorinae indicates that the more derived long-armed microraptorines might have independently developed some aerial capability (Xu *et al.* 2003; Chatterjee & Templin 2007).

Alternatively, *Tianyuraptor* may be a basal member of a clade containing all other Laurasian dromaeosaurids except the Microraptorinae as indicated by the other 24 trees of the 30 recovered most parsimonious trees. Within the context of the phylogeny proposed in figure 3, the distributions of Laurasian and Gondwanan dromaeosaurids could be explained by a vicariant hypothesis (Russell 1993; Upchurch *et al.* 2002; Makovicky *et al.* 2005; Novas & Pol 2005). However, in the early evolution of the dromaeosaurids, a dispersal event from Asia to North America occurred at least as early as the middle Early Cretaceous (Xu & Norell 2006), and thus Asia could not have been isolated from other continents at this time.

Tianyuraptor and microraptorines are among the earliest known unquestionable dromaeosaurids (Burton *et al.* 2006) and both are from the Early Cretaceous

Jehol Group (Xu 2002). Although *Tianyuraptor* is larger in size than microraptorines, it has comparably elongated lower hindlimbs. In this regard, it is different from most other dromaeosaurids, which have relatively short lower legs (Currie 1997). For example, *Tianyuraptor* has a tibiotarsus/femur length ratio of greater than 1.30, while a similarly sized *Velociraptor mongoliensis* specimen exhibits a ratio of less than 1.10 (Norell & Makovicky 1999). Although sharing elongate hindlimbs, *Tianyuraptor* and microraptorines are significantly different from each other in relative lengths of the forelimb elements (table 1). The arm/leg length ratio is 0.53 in *Tianyuraptor* and is more than 0.80 in other Liaoning dromaeosaurids (Xu 2002). The forelimbs of *Tianyuraptor* are proportionally even shorter than those of some other larger dromaeosaurids (Ostrom 1969; Norell & Makovicky 1999; Novas *et al.* 2009). For example, a similarly sized *Velociraptor* specimen shows an arm/leg length ratio of about 0.75.

The striking difference between the length and robustness of the forelimb of *Tianyuraptor* and microraptorines implies a functional difference. The microraptorines have been suggested to have some aerodynamic capabilities (Xu *et al.* 2003; Chatterjee & Templin 2007), which are indicated by the long and robust forelimbs and large, asymmetrical flight feathers. The significantly shortened forelimb of *Tianyuraptor* suggests a lack of aerodynamic function, which is further supported by the transversely wide coracoid (in microraptorines and birds, the coracoid is long along the axial direction) and the small furcula (in microraptorines and birds, the furcula is much more robust; table 1). Interestingly, significant forelimb shortening has occurred independently in the much larger Gondwanan dromaeosaurid *Austroraptor cabazai* (Novas *et al.* 2009). In our analysis, some character states related to the elongation of the forelimb are optimized as synapomorphies of the Paraves, such as a long radius relative to the femur (state 2 of character 277 in our dataset). However, a short radius is optimized as an autapomorphy of several paravian taxa, such as the Troodontidae, *Tianyuraptor*, and a clade containing most Laurasian dromaeosaurids, suggesting that secondary shortening of the forelimb has occurred independently in some paravian taxa. The presence of long-armed, four-winged *Microraptor*, short-armed *Tianyuraptor*, and various intermediate forms in the Early Cretaceous Jehol Biota (Xu 2002; Xu & Norell 2006) indicates a great diversity of morphology, locomotion and ecology being present early in dromaeosaurid evolution.

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