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# 长掌义县龙(兽脚类:恐龙)及其在手盗龙类进化和热河动物群生态学研究中的意义

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**摘要**:重新研究了产于辽西义县组下部的带羽毛小型兽脚类恐龙长掌义县龙(*Yixianosaurus longimanus*)的不完整骨架。系统发育分析得出义县龙属于手盗龙类基干类群,与阿尔瓦雷斯龙(*Alvarezsaurus*)、镰刀龙类、除阿尔瓦雷斯龙之外的其他阿尔瓦雷斯龙类以及由窃蛋龙类和副鸟龙类等进步手盗龙类组成的一个类群形成多分支状态。义县龙既有原始特征,如臂指数低,第三指强壮;也有进步特征,如乌喙骨近长方形,表明在手盗龙类当中,前肢演化呈现出比以前认为的更加复杂的镶嵌现象。强壮的前肢骨骼以及厚重、弯曲而尖利的手爪表明义县龙是捕食者,尽管这一认识尚待该属种更完整化石的发现来证实。义县龙在手盗龙类系统发育中的基部位置暗示,在虚骨龙类演化的这一节点上,前肢形态的变异范围更大。在许多方面,义县龙强壮的前肢和过度增大的弯曲爪子与长臂猎龙(*Tanycolagreus*)和虚骨龙(*Coelurus*)的相似,可能代表了这些属种与基干镰刀龙类和窃蛋龙类之间的过渡形态。义县龙保存了大的片状体羽,表明这些皮肤衍生物在虚骨龙类中的起源可能比以前报道的要早。最后,强壮而伸长的前肢暗示了其生态功能与根据同一区域的其他小型兽脚类推测的不同,支持了热河生物群的小型非鸟兽脚类中存在小生境划分的观点。

**关键词**:热河生物群,恐龙,手盗龙类,指骨指数,古生态学,异速生长

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# *YIXIANOSAURUS LONGIMANUS* (THEROPODA: DINOSAURIA) AND ITS BEARING ON THE EVOLUTION OF MANIRAPTORA AND ECOLOGY OF THE JEHOL FAUNA

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**Abstract** We re-examine the partial skeleton of the enigmatic small feathered theropod *Yixianosaurus longimanus* from the Lower Yixian Formation, China. A phylogenetic analysis recovers *Yixianosaurus* as a basal maniraptoran, in a polytomy with *Alvarezsaurus*, Therizinosauria, Alvarezsauroidea excluding *Alvarezsaurus*, and a well-resolved clade of derived maniraptorans including Oviraptorosauria and Paraves. The blend in *Yixianosaurus* of primitive traits, such as a low brachial index and robust digit Ⅲ, and derived traits such as a subrectangular coracoid, suggests a more complicated mosaic of forelimb evolution within Maniraptora than previously proposed. The robust forelimb bones and massive, recurved, and

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pointed manual unguals suggest *Yixianosaurus* was predatory, although this assessment remains tentative until more complete fossils of this taxon are found. The basal maniraptoran phylogenetic position implies a larger range of forelimb morphologies at this point in coelurosaurian evolution. In many ways, the robust forelimb and hypertrophied recurved unguals are similar to those of *Tanycolagreus* and *Coelurus*, and may be morphologically transitional between these taxa and basal therizinosaurs and oviraptorosaurs. The presence of large, veined, pennaceous contour feathers on *Yixianosaurus* indicates the origin of these integumentary structures may be deeper in coelurosaur phylogeny than previously reported. Finally, the robust, elongate forelimbs suggest a different ecological role than inferred for other sympatric small theropods, and lend support to the idea of niche partitioning among the small non-avian theropods of the Jehol fauna.

**Key words** Jehol Biota, Dinosauria, Maniraptora, phalangeal index, paleoecology, allometry

## 1 Introduction

The Early Cretaceous Jehol deposits are among the most important fossil-bearing localities in the world in terms of their academic and public contribution to palaeontology (Zhou and Wang, 2010; Sullivan et al., in press). Taxa discovered in these beds have greatly expanded our understanding of the evolutionary history of mammals, pterosaurs, plants, theropod dinosaurs, and early birds (Meng et al., 2006; Xu and Norell, 2006; Wang and Zhou, 2006; Benton et al., 2008). The diversity of the fauna from these beds is greater than that seen almost any other comparable Mesozoic or early Cenozoic terrestrial-dominated Lagerstätte (Zhou and Wang, 2010), with over 1000 species of animals and plants known from the Jehol ecosystems (Benton et al., 2008). The vertebrates in these deposits represent over 40 species of early birds, 35 species of non-avian dinosaurs, and over a dozen species of mammals, including some of the earliest known crown eutherian and metatherian mammals (Zhou and Wang, 2010; Hu et al., 2010; Luo et al., 2011).

Among these dinosaurs of the Yixian Formation is the enigmatic theropod *Yixianosaurus longimanus* Xu & Wang 2003, known only from a pair of articulated pectoral girdles, feathered forelimbs, and associated ribs and gastralia fragments. Here we present a further description of the morphology of this specimen, and, for the first time, evaluate the phylogenetic relationships of *Yixianosaurus*. We also attempt to reconstruct the ecology of this small theropod and highlight its importance to the evolution of maniraptoran theropods.

The place of *Yixianosaurus* in the Jehol fauna and theropod evolution has generally been overlooked. In their original description, Xu and Wang (2003) suggested it might be a derived maniraptoran but no phylogenetic analysis was performed. Since the original description, our knowledge of Jehol theropods has grown considerably, with theropod diversity alone more than doubling to twenty-one genera (Benton et al., 2008). This fossil ecosystem is extremely well preserved and permits some analysis of potential niche partitioning between taxa (Zhou and Wang, 2010). Although incomplete, *Yixianosaurus* may add much to this analysis given its unique morphology and size.

## 2 Description

The type and only known specimen of *Yixianosaurus* is housed in the Institute of Vertebrate Paleontology and Paleoanthropology as IVPP V 12638. Xu and Wang (2003) presented a preliminary description of the specimen. We only intend to supplement their earlier description with new interpretations and a discussion of the phylogenetic and ecological implications of these morphologies, although some details overlap with the original description. The specimen is preserved in near complete articulation with the pectoral girdle and most forelimb elements in medial view and the manus in palmar view (Fig. 1,2). This represents an unusual view of the specimen compared to other two dimensionally preserved Jehol theropods, but still reveals many morphological details. Each forelimb, though articulated, is incomplete, but between the two all elements are preserved with the exception of the distal portion of the second ungual and the first phalanx of digit Ⅲ. A complete list of linear measurements used in our description and comparisons of this specimen is given in Table 1.

**Table 1　Linear measurements and ratios of *Yixianosaurus longimanus* IVPP V 12638**　(mm)

| Bone | Length/midshaft width | Maximum alternative measures | Humerus/Scapula | 1.37 |
|---|---|---|---|---|
| Scapula | 65 | | Humerus L/W | 10.35/9.47 |
| Humerus | 89/8.6 | 89/9.4 | Radius W/Ulna W | 0.72/0.83 |
| Ulna | 64/4.6 | 73/4.8 | Ulna/Humerus | 0.72/0.82 |
| Radius | 63/3.3 | 72/4.0 | Manus/Total Forelimb | 0.40/0.38 |
| Mc Ⅰ | 14.5/4.2 | | Mc Ⅰ/Mc Ⅱ | 0.40 |
| Ⅰ-1 | 34 | | Mc Ⅰ L/W | 3.5 |
| Mc Ⅱ | 36/3.4 | | Mc Ⅱ L/W | 10.6 |
| Ⅱ-1 | 26 | | Mc Ⅲ L/W | 12.1 |
| Ⅱ-2 | 38 | | PI digit Ⅱ | 1.78 |
| Mc Ⅲ | 34/2.8 | | Ⅱ-2/Mc Ⅱ | 1.06 |
| Ⅲ-1 | 9 | | PI digit Ⅲ | 1.15 |
| Ⅲ-2 | 8 | | Ⅲ-3/Ⅲ 1+2 | 1.29 |
| Ⅲ-3 | 22 | | Ⅲ-3/Ⅲ-3 | 2.44 |

Note: Alternative measurements are possible for the humerus, ulna, and radius because of differing interpretations of how the fragmentary parts overlap. A maximum interpretive measure is given based on overlapping both sides to produce the reconstruction in Fig. 2. Ratios based on maximum alternative values are given after the forward slash. Total forelimb length is the total of the humerus, ulna, metacarpal Ⅱ, and phalanges Ⅱ-1 and Ⅱ-2 lengths. Manus length is the combined length of metacarpal Ⅱ and phalanges Ⅱ-1 and Ⅱ-2. PI is the phalangeal index, defined as the sum of all non-ungual phalangeal lengths of a digit divided by the corresponding metacarpal length.

Both scapulae have suffered extensive damage, with the right scapula only preserving details of the mid-shaft. The scapular blade is elongate and strap-like with a minor distal expansion. The proximal portions of both scapulae have been twisted so their glenoid regions face anteriorly relative to the coracoid (Fig. 1). This taphonomic distortion means that the anteriorly extending acromion process identified by Xu and Wang (2003) is instead here considered to be the posteroventral surface of the scapula. No acromion is visible on either scapula, but the limited height of the coracoid suggests that it was not extensive. The scapulocoracoid suture is not fused and is directed anteriorly and slightly ventrally, suggesting the absence of a hypertrophied acromion.

The coracoids are subrectangular with a ventral process that extends posteriorly beyond the glenoid. The dorsoventral length of the coracoid is subequal to its anteroposterior length and the coracoid is not significantly elongated as seen in paravians. The glenoid region is damaged, but the morphology that can be determined indicates the glenoid faced posteroventrally. Only a small portion of the glenoid is visible, but this is due to the medial aspect of the coracoid and the glenoid may not be reduced, as in many derived maniraptorans. A large supracoracoid

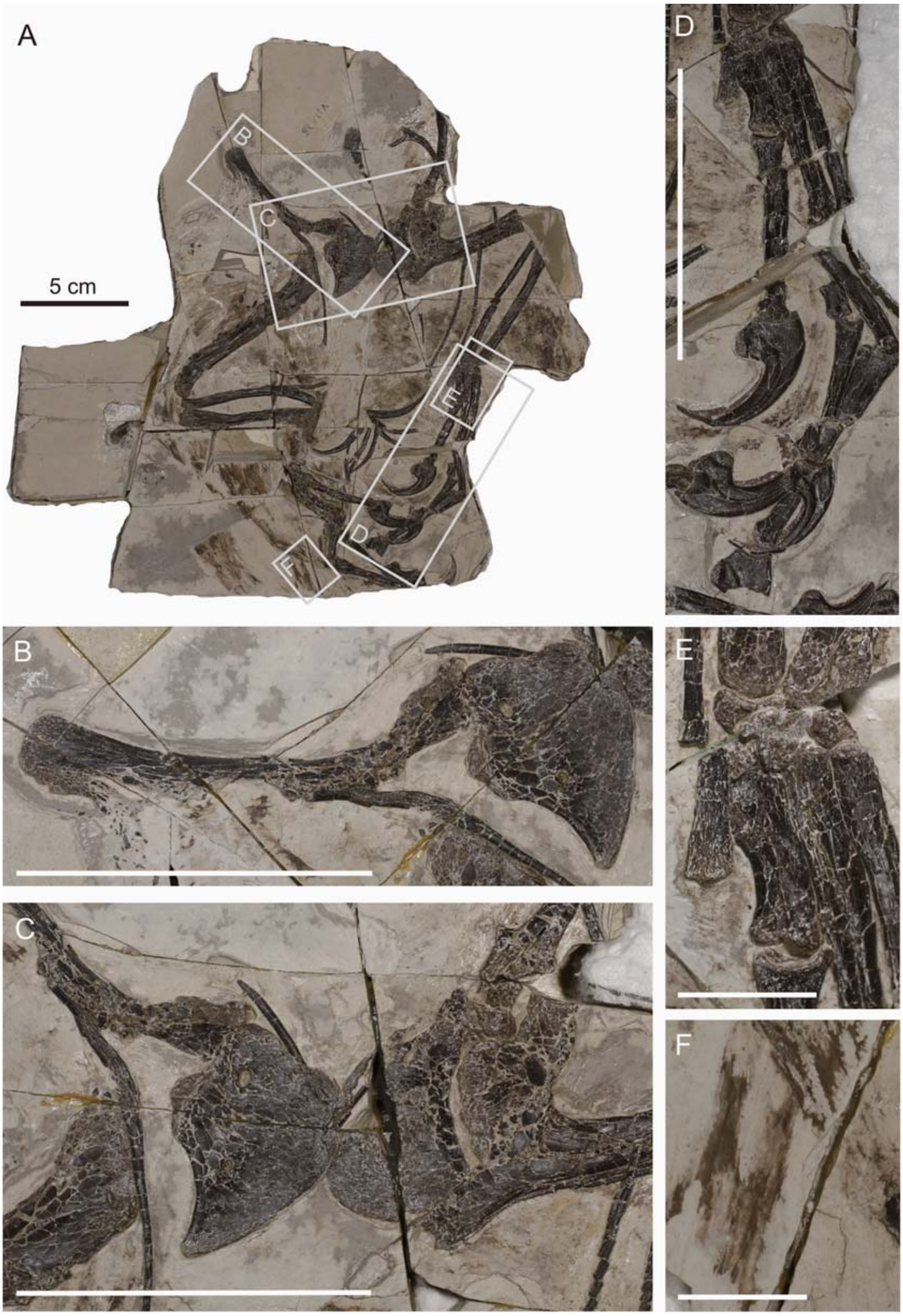

Fig. 1 Photographs of *Yixianosaurus longimanus* (IVPP V 12638)

A. complete specimen; B. left scapula and the glenoid region of the pectoral girdle to illustrate the twisted scapula and posteriorly facing glenoid; C. possible furcula and coracoids; D. right manus in palmar aspect; E. right carpals and metacarpals in palmar aspect; F. preserved feather structures; scale bars for A-D equal 5 cm and scale bars for E and F equal 1 cm foramen is present near the scapulocoracoid suture. The ventral portion of the coracoid appears to have been in approximately the same plane as its proximal portion, without an obvious medial inflection. Although this particular trait is open to interpretation because of the flattening of the specimen, there is no evidence to suggest the coracoids originally possessed a sharp, ventromedially inflected angle.

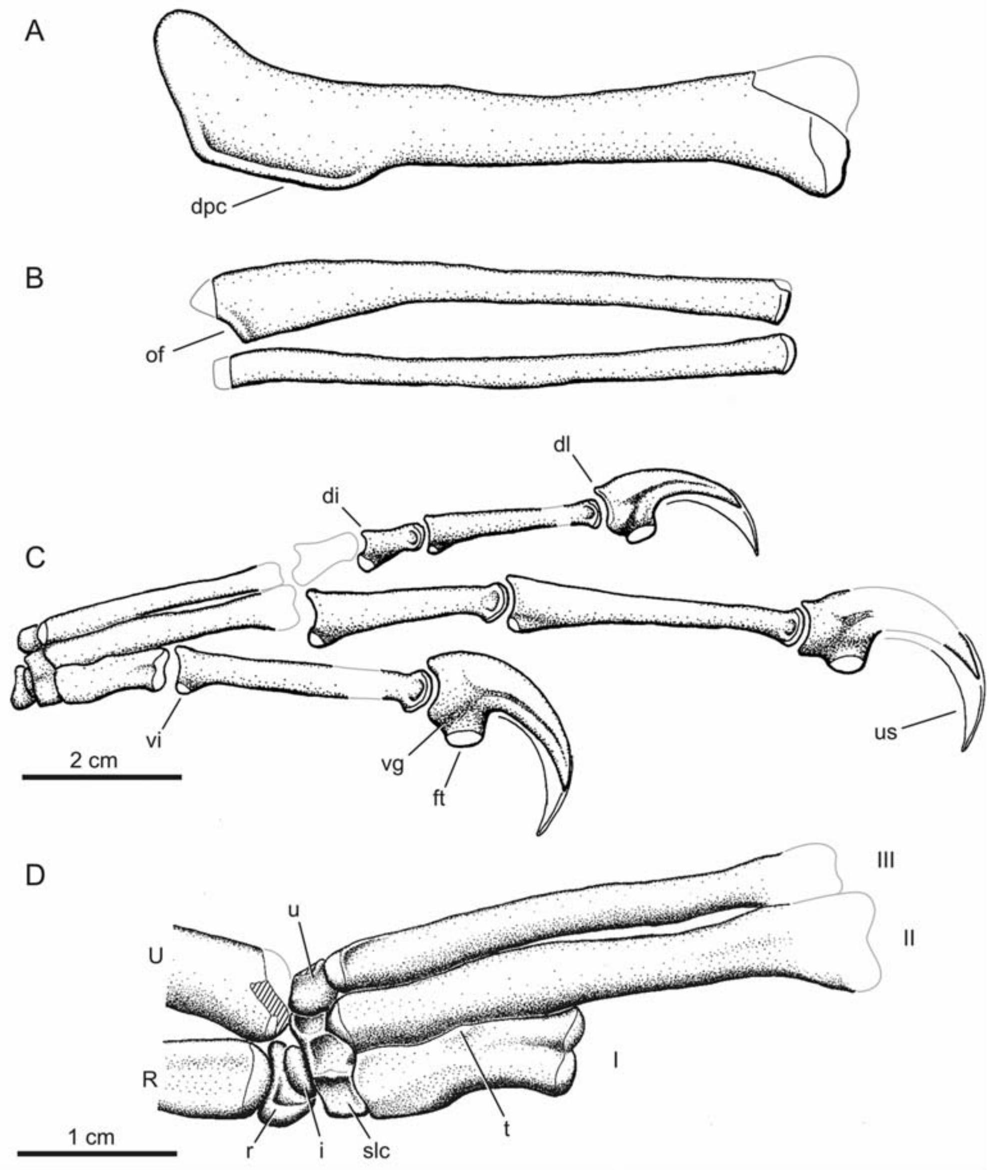

Fig. 2 Illustration of the forelimb of *Yixianosaurus longimanus*

A. humerus in anterior aspect; B. radius and ulna in medial aspect; C. manus with metacarpals in palmar aspect and phalanges in medial aspect; D. carpals and metacarpals in palmar aspect. A-C at same scale and scale bar equals 2 cm. Scale bar for D equals 1 cm. All bones are illustrated primarily from the right forelimb, but missing portions are drawn from the left forelimb when preserved there

Abbreviations: di. dorsal intercondylar tuberosity; dl. dorsal lip; dpc. deltopectoral crest; ft. flexor tubercle; i. intermedium; of. olecranon fossa; R. radius; r. radiale; slc. semilunate carpal; t. ventrolateral tab on metacarpal I; U. ulna; u. ulnare; us. ungual sheath; vg. ventral groove; vi. ventral intercondylar tuberosity

An elongate, slender bone lies on the external surface of each coracoid. The position, morphology, and orientation of these bones suggest they are the distal ends of a furcula. The distal ends are slightly sigmoidal and flattened as in the "epicleidal" region of non-avian theropod furculae (Nesbitt et al., 2009). The curved morphology and slenderness of these bones distinguish them from the relatively straight and robust gastralia preserved more posteriorly on the specimen. The distal ramus bends laterally, as in other theropod furculae (Makovicky and Currie, 1998), and superficially resembles the thin furculae present in some small-bodied theropods, such as *Coelophysis* and *Bambiraptor* (Nesbitt et al., 2009).

Both humeri are incomplete and slightly crushed. The left humerus is damaged only at the distal ulnar condyle and the proximal portion of the deltopectoral crest. The right is damaged proximally, via crushing and shearing, and is also missing its distal third. The humerus is elongate and approximately 1.4 times longer than the scapula. The humeral shaft is relatively straight, with no obvious bowing near its distal end. The internal tuberosity is large, but not hypertrophied, and rounded without a visible demarcation from the humeral head, though a rib fragment may be partially obscuring the proximalmost edge. The deltopectoral crest is long, measuring approximately 30% of the humeral length (Xu and Wang, 2003), and low. The humeral shaft is robust and its minimum width does not appear to be exaggerated by crushing in the right humerus. The approximate length to width ratio is 10.3 (Table 1). Distally, the humerus expands only moderately with the ectepicondyle preserved as a small protuberance. The orientation of the distal condyles cannot be determined.

Both antebrachia are damaged with the left missing its most proximal and distal portions and the right missing its proximal portion and part of its distal ulna. The preserved portions overlap extensively and the estimated complete lengths of the ulna and radius are 72% and 70% of humeral length, respectively. Both proximal ulnae are missing, so the olecranon process and the articular surfaces for the humerus and radius cannot be described. The ulna is thicker than the radius though both have a slight bow along their length. The radius is relatively robust compared to other maniraptorans. The right antebrachium is minimally crushed, and its dimensions indicate the mid-shaft diameter of the radius is approximately 70% that of the ulna. The left antebrachium appears to have been distorted, giving the left ulna and radius a more sigmoidal appearance. Proximally, the radius is relatively flat and probably had the circular articular surface typical of theropods. Distally, the radius is spatulate and articulates into the concave fossa of the radiale.

Only the right carpals are preserved in articulation with the manus. The left carpus is largely missing, but two elements, identified by Xu and Wang (2003) as the semilunate carpal and radiale, have been displaced to the midshaft of the left humerus. The carpus is composed of at least four individual bones (Xu and Wang, 2003). A large radiale articulates with the distal radius and semilunate carpal. The radiale is proximally concave to receive the radius and appears to be distally convex to articulate into a flat or concave proximal surface of the semilunate carpal. Ventrally, the radiale is slightly convex to articulate with a thin, oval-shaped carpal that is probably an intermedium. Although the intermedium partially covers the ventrolateral surface of the radiale, we estimate the radiale angle in *Yixianosaurus* at approximately 40° (following the methodology of Sullivan et al., 2010), indicating a flexible wrist capable of a large degree of abduction towards the ulna (Sullivan et al., 2010). In ventral aspect, the semilunate carpal is mediolaterally elongate and quadratic, and contacts nearly the entire proximal surface of metacarpal Ⅰ and at least three quarters of the proximal surface of metacarpal Ⅱ. The ventral surface of the semilunate is excavated by subequal medial and lateral fossae, separated by a ridge that is aligned with the lateral edge of metacarpal I. This ridge may be the point of fusion between distal carpals 1 and 2. A ventrolaterally facing fossa on the semilunate carpal faces a nodular carpal articulating in the proximal notch between metacarpals

Ⅱ and Ⅲ. This carpal is likely an ulnare, and probably articulated with the ventrolateral fossa of the semilunate carpal.

The manus is large and tridactyl, with the central digit the longest as in other coelurosaurs. Excluding the unguals, the manus, measured along the metacarpal and phalanges of digit Ⅱ, is 40% the length of the forelimb and 112% of the length of the humerus. Metacarpal Ⅰ is short and robust, at only 40% the length of metacarpal Ⅱ. The proximal two fifths of the ventrolateral edge of metacarpal Ⅰ bears a distinct flange that overlaps the ventromedial edge of metacarpal Ⅱ. This flange is reminiscent of a rectangular buttress, but this morphology cannot be confirmed with the metacarpals in such tight articulation. A discrete tab protrudes from the ventrolateral edge of metacarpal Ⅰ at about its midlength. Metacarpals Ⅱ and Ⅲ are subequal in length, with metacarpal Ⅲ 94% the length of metacarpal Ⅱ and 82% its midshaft width. Metacarpal Ⅲ is relatively robust with a length to mid-shaft width ratio of 12.1. Values of the same ratio for metacarpals Ⅱ and Ⅰ are 10.6 and 3.5, respectively. Metacarpal Ⅲ may have a slight bow along its length, but otherwise appears relatively straight. The proximal end of metacarpal Ⅲ is expanded to about 120% of the mid-shaft width. The proximal part of the lateral edge of metacarpal Ⅲ is tapered so that the proximal surface has a triangular outline with the apex facing laterally.

Only phalanx Ⅲ-1 is missing from the specimen. All preserved phalanges, including those of digit Ⅲ, are robust with strongly ginglymoidal articular ends and well developed collateral ligament pits suggesting strong extension and flexion capabilities (Xu and Wang, 2003). All appear to be dorsoventrally expanded, partly due to their hypertrophied dorsal and ventral intercondylar tuberosities. The ventral intercondylar tuberosity is present on all preserved phalanges and expands the proximal end of each phalanx to almost twice its mid-length dorsoventral diameter. The hypertrophied ventral intercondylar tuberosities would have limited the maximum flexion of each metacarpal-phalangeal and interphalangeal joint to approximately 90 degrees. The preserved articulated left phalanges Ⅱ-2 and Ⅱ-3 are "locked" at approximately 90 degrees with the ventral intercondylar tuberosity of the latter pressed to the ventral surface of the former. Further flexion seems impossible without dislocation.

The phalangeal index (PI = sum of non-ungual phalangeal lengths/metacarpal length) for digit Ⅱ is 1.78, and the distal phalanges on all digits elongate. This PI value is similar to those calculated for basal coelurosaurs such as *Coelurus* (1.78), *Tanycolagreus* (1.73), and *Guanlong* (1.7) (Tables 1, 4). As noted by Xu and Wang (2003), the penultimate phalanx of digit Ⅱ is extremely elongated (Ph Ⅱ-2/Mc Ⅱ = 1.06) and is the longest bone in the manus. Digit Ⅲ has a shorter PI (1.15) but phalanx Ⅲ-3 is greatly elongated relative to the proximal phalanges of the digit, being approximately 1.3 times the estimated combined length of phalanges Ⅲ-1 and 2.

All unguals are preserved and are presented in lateral aspect, but the distal portion of the ungual of digit Ⅱ is missing. The manual unguals are nearly equal in size, although that of digit Ⅲ is slightly smaller than the others. All the unguals are highly recurved and robust, and have large, proximally positioned flexor tubercles. The flexor tubercles are rugose ventrally and ventrolaterally. Each tubercle extends nearly perpendicularly from the ventral curvature of the claw and is separated from the proximal articular portion by a sulcus that is a ventral extension of the ungual groove. The ungual groove divides the claw into roughly equal extensor and palmar halves, but appears to bifurcate at the proximal body of the ungual in a Y-shape, with a dorsal shallow groove extending toward, but not completely to, the proximodorsal edge of the ungual. The groove is pinched near the base of the flexor tubercle by a swelling near the articular margin of each ungual. The unguals of digits Ⅱ and Ⅲ have obvious dorsal lips on their proximodorsal edges but this morphology is absent on the ungual of digit Ⅰ. The claw sheaths are well preserved and extend beyond the ungual's tip by approximately one third the length of the inner curvature of the ungual. The extensor edge of the claw sheath is thickened with respect to the rest of the sheath.

The specimen preserves some plumage (Xu and Wang, 2003). Feathers are preserved around each forelimb in a manner similar to that seen in birds (Xu and Wang, 2003) and non-avian maniraptorans from the same deposits. Some feathers are elongate, with the longest over 100 mm in length but distally incomplete. These feathers are significantly longer than the bones they are associated with. The long feathers of *Yixianosaurus* are not elongate broad filamentous feathers (EBFFs) (Xu et al., 2009a) because they are not unusually broad, extremely rigid, and ribbon-like. Although the structure of these feathers is not fully visible, there is a hint of a pennate branching structure in the distalmost portions of the forelimb feathers near the right manus (Fig. 1D). This branching structure, coupled with their length and position, suggests they were contour feathers.

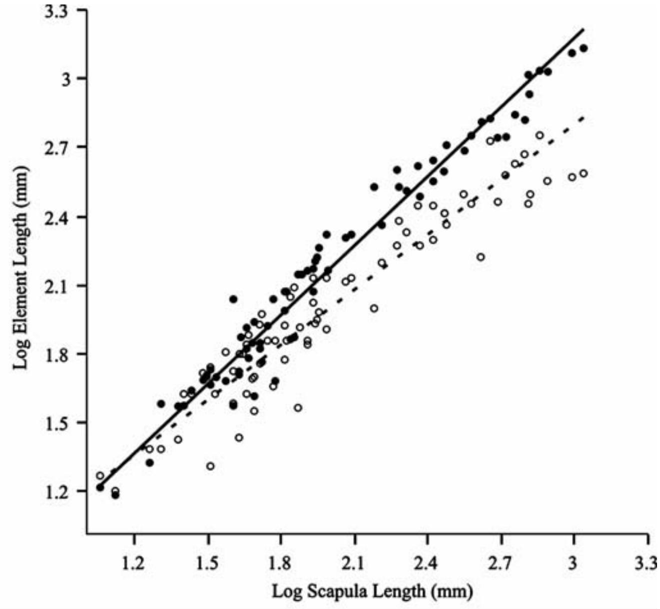

Fig. 3 Reduced major axis linear regressions for log femur length (open circles, $y = 0.98777x + 0.19527$, $r^2 = 0.9616$, $n = 58$) and log snout-vent length (closed circles, $y = 0.95766x + 0.86914$) against scapula length for theropods

**Body size** Femoral length is the most commonly used proxy to reconstruct body size in theropods, as it is suspected to correlate with both body mass and length (Fariña and Christiansen, 2004; Turner et al., 2007). Due to the limited nature of the sole *Yixianosaurus* specimen we cannot directly measure femoral length, but it can be estimated using scapular length. Regressing scapular length against femoral length in non-avian theropods and early birds yields a high correlation ($r^2 > 0.95$) and a near isometric slope (Fig. 3). There is only a modest amount of spread in the data despite the inclusion of both taxa with reduced forelimbs and volant avians, with percentage error scores of 18% for the entire dataset and 12% if only adult non-avian theropod specimens are included. These percentage error scores are comparable to those seen in the mass estimates of Fariña and Christiansen (2004). Although scapular length also has a tight correlation with arm length, this may be due to arm length also being correlated with body size (Dececchi and Larsson, in prep). Scapular length correlates significantly more strongly with femoral length than with humeral length, as indicated by significantly higher $r^2$ and partial Pearson's correlation analyses. This strong correlation between scapular and femoral lengths is present both when early birds are included and when they are excluded (Table 2).

Using the tight correlation between scapula and femur length, we derived a femoral length estimate for *Yixianosaurus* of 97 ~ 109 mm. These values yield a mass estimate of 1.3 ~ 2.0 kg using the equation of Fariña and Christiansen (2004). This body mass estimate is similar to those obtained for other Jehol theropods like *Microraptor gui*, *Sinovenator* and *Sinosauropteryx* (Turner et al., 2007). The robust forelimbs and gastralia suggest the upper bounds of the mass estimates are likely to be more realistic for *Yixianosaurus*.

**Table 2　Reduced major axis log-log regression equations and partial correlation scores of both humeral and femoral length on scapula length**

| | N | Slope | err | Intercept | err | $r^2$ | | Scapula | Humerus | Femur |
|---|---|---|---|---|---|---|---|---|---|---|
| **All taxa** | | | | | | | **All taxa** | | | |
| Scapula versus humerus | 73 | 0.79904 | 0.03073 | 0.40143 | 0.00397 | 0.895 | Scapula | — | <0.0001 | <0.0001 |
| | | | | | | | Humerus | 0.61029 | — | 0.125 |
| Scapula versus femur | 73 | 1.0043 | 0.02362 | 0.16652 | 0.00234 | 0.961 | Femur | 0.87484 | -0.18257 | — |
| **No avians or duplicates** | | | | | | | **No avians or duplicates** | | | |
| Scapula versus humerus | 43 | 0.83487 | 0.04508 | 0.047929 | 0.00024 | 0.880 | Scapula | — | 0.001 | <0.0001 |
| | | | | | | | Humerus | 0.49512 | — | 0.406 |
| Scapula versus femur | 43 | 0.91293 | 0.02214 | 0.38185 | 0.00248 | 0.976 | Femur | 0.916 | -0.13167 | — |

Note: We analysed two permutations of the dataset, the first with all specimens and the second with all avian taxa and duplicate specimens removed. This was done to ensure that neither overrepresentation by specific taxa nor the effects of the origin of flight in birds unduly influenced our results. Under both permutations scapula to femur length shows a significantly higher r value. In the left part of the table, for the all-specimen dataset $Z = 2.28$, $p < 0.05$, for the dataset without avians or duplicates $Z = 3.69$, $p < 0.001$; in the right part, all taxa $Z = 2.88$, $p < 0.001$, without avians or duplicates $Z = 4.57$, $p < 0.001$.

## 3　Phylogenetic analysis

A maximum parsimony phylogenetic analysis was performed using the discrete morphological dataset of Zanno (2010), which is derived from the Theropod Working Group (TWiG) dataset and has been augmented by Zanno to include many unique characters present in basal maniraptorans and basal therizinosaurs. Parsimony analyses used TNT (Goloboff et al., 2003) and character evolution was examined using Mesquite 2.73 (Maddison and Maddison, 2009). We scored the rectangular buttress on metacarpal Ⅰ as absent for *Yixianosaurus* to be conservative. Character scores for *Yixianosaurus* are given in Table 3. Changes to character scores for taxa in the original matrix, including changes to scorings that were previously listed as unknown, are listed in the table captions.

**Table 3　Character scores for *Yixianosaurus* using the phylogenetic matrix of Zanno (2010)**

0??????????????????????????????????????????????????????????????????????????????????????????????????
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0?0000000???????????????????????????????????????0?????

Note: Changes to the matrix were made to correct scores for two characters for some taxa based on firsthand observations and published descriptions: character 139 was changed from a ? to a 0 for *Harpymimus*, from a 0 to a 1 for *Compsognathus*, *Gallimimus*, *Huaxiagnathus*, and *Ornithomimus*, and from a ? to a 1 for *Sinovenator*; character 146 was changed from a 0 to a 1 for *Falcarius*.

The strict consensus tree of 65 most parsimonious trees retains the same general topology seen in the original analysis and positions *Yixianosaurus* in a near-basal maniraptoran polytomy with *Alvarezsaurus*, Therizinosauria, a clade of all other alvarezsauroids, and a clade of higher maniraptorans composed of Oviraptorosauria and Paraves (Fig. 4). It must be noted that although *Alvarezsaurus* falls outside a clade of other Alvarezsauroidea, we do not question the monophyly of Alvarezsauroidea. This result is probably attributable to the relatively poor scoring of only 16% of all characters for *Alvarezsaurus* in the matrix, combined with the character homoplasy added by the inclusion of *Yixianosaurus*. *Ornitholestes* is the most basal maniraptoran,

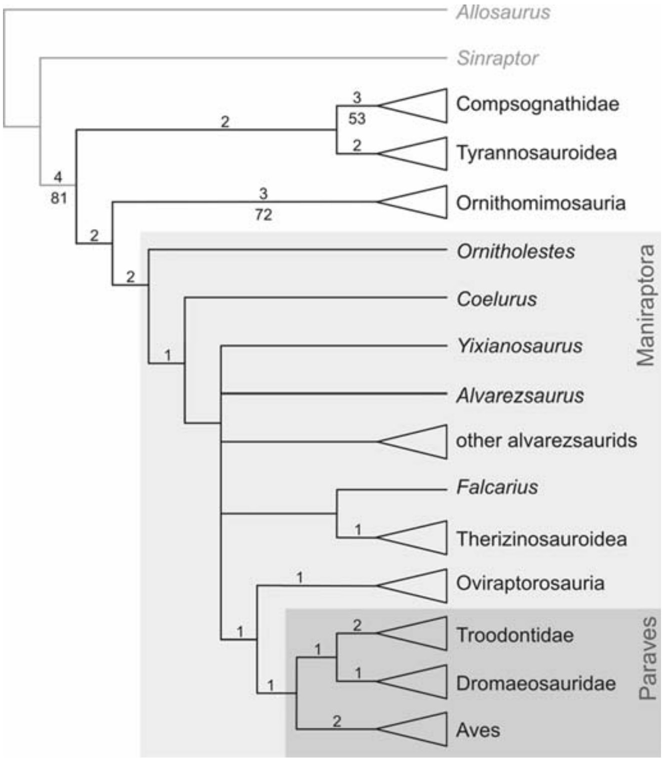

Fig. 4 Phylogenetic position of *Yixianosaurus*

The phylogeny is derived using the data matrix of Zanno (2010) with the inclusion of *Yixianosaurus* (Table 5). Only coelurosaurs and immediate sister taxa are shown. Major clades are collapsed for brevity but are otherwise similar to the phylogenetic results of Zanno (2010). The tree is a strict consensus of 65 most parsimonious trees with a tree length of 1245 steps, a CI of 0.35, and a RI of 0.69. Bremer support values are above branches and bootstrap supports are below. Note that few branches, even major clades, have high values, indicating the general instability of the topology

followed by *Coelurus* and then the near-basal polytomy described above. As in other recent phylogenetic analyses, the maniraptoran portion of the tree is very unstable, with most major nodes having Bremer support values of 1 or 2 and many with bootstrap supports of less than 50% (Choiniere et al., 2010a; Xu et al., 2011b; Zanno, 2010). An Adams consensus suggests that *Yixianosaurus* is the wildcard taxon responsible for this near-basal maniraptoran polytomy, likely because of its fragmentary nature. *Yixianosaurus* can be moved to most positions between ornithomimosaurs and paravians with only one extra step. It takes only three extra steps to make *Yixianosaurus* sister to Ornithomimosauria and three extra steps to move it to be sister to the Ornithomimosauria plus Maniraptora clade. It takes one extra step to move *Yixianosaurus* to be sister to Oviraptorosauria, four extra steps to move it to be sister to Deinonychosauria, four extra steps to move it to be sister to Dromaeosauridae, five extra steps to move it to be sister to Troodontidae, and four extra steps to move it to be sister to Aves.

In spite of the poor stability of the phylogenetic results, many characters do inform the basal maniraptoran position of *Yixianosaurus*. Three characters are present in *Yixianosaurus* that are also unambiguous synapomorphies for stem Maniraptora. First, the ulnare is triangular in proximal aspect in this clade, although this character is unknown in *Coelurus* and *Ornitholestes*. Second is the presence of a single distal carpal, composed of fused distal carpals 1 and 2, that caps metacarpals Ⅰ and Ⅱ. This character is present in all maniraptorans, with the exceptions of derived therizinosaurs (more advanced than *Alxasaurus*) and the paravian *Microraptor*, as well as the putative basal maniraptorans *Coelurus* and *Ornitholestes*. The third character supporting a maniraptoran position of *Yixianosaurus* is the well developed, medially directed internal tuberosity of the humerus.

A character that may prove useful in future analyses is the continuous arch of the articulated scapula and coracoid in anterior and posterior aspect. Although this character is plesiomorphic for Maniraptora it is lost in some derived therizinosaurs, *Caudipteryx*, and paravians.

A large number of characters that unambiguously diagnose Paraves are absent in *Yixianosaurus*. In paravians, the posterolateral surface of the coracoid just ventral to the glenoid is expanded into a subglenoid fossa and coracoid tuber. Although the lateral surface of the coracoid is not visible in *Yixianosaurus*, the posterior margin is, and it does not indicate the presence of any expansion of this region of the coracoid. An important synapomorphy of Paraves is the laterally facing glenoid that expands onto the external surface of the scapula (Xu et al., 2011b). At least in medial view, the glenoid in *Yixianosaurus* appears entirely restricted to the posterior surface of the coracoid and scapula and does not appear different from those of other non-paravian maniraptorans. The proximal surface of the ulna is divided into two distinct fossae separated by a median ridge in paravians. *Yixianosaurus*, like all other non-paravian theropods with the exception of *Coelurus*, has a single continuous articular facet instead. The final synapomorphy of Paraves not present in *Yixianosaurus* is the presence of a laterally convex metacarpal Ⅲ. Although this metacarpal does have a slight bow in *Yixianosaurus*, similar to other maniraptorans, it does not approach the strong bowing present in paravians. The robust nature of *Yixianosaurus* may obscure this character state (Fig. 1), though, and more quantitative characterization of the range of curvatures present in maniraptorans might prove useful. One character specifically supports the exclusion of *Yixianosaurus* from Deinonychosauria. The deltopectoral crest of deinonychosaurians is marked near its lateral edge with a distinct scar for the insertion of a biceps muscle but this crest is lacking in birds and most other theropods, including *Yixianosaurus*.

## 4 Comparisons to Maniraptora

Xu and Wang (2003) suggested that *Yixianosaurus* is a derived maniraptoran. No phylogenetic analysis was performed at the time and we are not aware of any published since then that has included this taxon, perhaps due to the fragmentary nature of the only known specimen of *Yixianosaurus*. We present a phylogenetic analysis above, but will also compare *Yixianosaurus* as thoroughly as possible to all major maniraptoran clades, in addition to some poorly resolved basal taxa. Many of these comparisons discuss morphologies that are not yet coded in phylogenetic analyses, so this discussion is also intended to serve as a starting point for potential new characters. Numerical comparisons for these taxa are given in Table 4.

***Ornitholestes*, *Coelurus*, and *Tanycolagreus*** Due to the uncertain affinities and limited available material, only a brief consideration of these taxa will be presented. *Ornitholestes* lacks a complete scapulocoracoid, but these bones are preserved in *Tanycolagreus* and compare well to those in *Yixianosaurus*, the only exception being that the scapula is significantly longer than the humerus in the former. The forelimb of *Yixianosaurus* resembles those of *Coelurus* and *Tanycolagreus* in overall proportions. *Coelurus* and *Tanycolagreus* share with *Yixianosaurus* the traits of having a relatively long grasping manus, comprising ~40% of the forelimb, with a reduced antebrachium and a robust humerus. The carpals are also remarkably similar between *Tanycolagreus* and *Yixianosaurus*, including the size and placement of the semilunate (Carpenter et al., 2005a). The manus of *Yixianosaurus* differs from *Coelurus* in having only three digits, as opposed to four. Unlike *Tanycolagreus*, metacarpal Ⅲ of *Yixianosaurus* is not obviously more slender than metacarpal Ⅱ, nor is it bowed. *Coelurus*, *Tanycolagreus* and *Yixianosaurus* all have similar degrees of phalangeal elongation, as evidenced by their PIs and proportions of the total forelimb (Tables 4-5), but *Yixianosaurus* has even longer distal phalanges. The unguals of *Tanycolagreus* and *Yixianosaurus* share some morphologies. The first ungual of *Tanycolagreus* has a low, dorsal “lip” and its second ungual has a swollen articular region to slightly restrict its lateral groove. This swollen proximal ungual morphology is also present in the basal coelurosaur *Zuolong* (Choiniere et al., 2010b). Although *Yixianosaurus* does not have a dorsal “lip” on its first ungual, it does have them on its second and third unguals. *Yixianosaurus* has swollen articular regions on all its unguals, instead of only its second.

**Ornithomimosauria** The forelimbs and pectoral girdles of ornithomimosaurs and *Yixianosaurus* are superficially similar. Both have humeri subequal to or longer than the scapula

**Table 4 Comparison of forelimb length indices between *Yixianosaurus longimanus* and selected theropods**

| Taxa | H/S | BI | M/H | PⅠ\|Ⅱ | Ⅱ-2/Mc | PⅠ\|Ⅲ | Ⅲ-3 /(1+2) | Ⅲ-3/1 | McⅠ /McⅡ |
|---|---|---|---|---|---|---|---|---|---|
| *Yixianosaurus* | 1.37 | 0.72<br>[0.82] | 1.12 | 1.78 | 1.06 | 1.15 | 1.29 | 2.44 | 0.40 |
| **Basal theropods** | | | | | | | | | |
| *Coelophysis* | 1.12 | 0.61 | 0.59 | 1.01 | 0.54 | 1.27 | 0.63 | 1.39 | 0.51 |
| *Herrerasaurus* | — | 0.99 | 0.77 | 1.26 | 0.64 | 1.61 | 0.51 | 0.91 | 0.76 |
| *Acrocanthosaurus* | 0.36 | 0.69 | 0.86 | 1.76 | 0.89 | 1.71 | 0.65 | 1.20 | 0.53 |
| *Allosaurus* | 0.48 | 0.85 | 1.04 | 1.57 | 0.82 | 1.36 | 0.57 | 1.04 | 0.58 |
| **Coelurosaurs** | | | | | | | | | |
| *Coelurus* | — | 0.83 | 1.27 | 1.78 | 0.92 | — | — | — | — |
| *Compsognathus* | 1.10 | 0.82 | 1.15 | 1.37 | 0.88 | — | — | — | 0.25 |
| *Huaxiagnathus* | 1.01 | 0.62 | 1.14 | 1.55 | 0.85 | 1.39 | 0.87 | 1.63 | 0.49 |
| *Juravenator* | 0.65 | 0.75 | 1.07 | 1.57 | 0.87 | 1.56 | 0.65 | 1.38 | 0.39 |
| *Scipionyx* | 1.11 | 0.73 | 1.08 | 1.67 | 0.98 | 1.40 | 1.22 | 2.31 | 0.38 |
| *Tanycolagreus* | 0.76 | 0.77 | 1.12 | 1.73 | 0.93 | 1.13 | 1.00 | 2.21 | 0.46 |
| *Sinosauropteryx* | 0.73 | 0.79 | 0.95 | 0.99 | 0.52 | 0.96 | 0.60 | 1.06 | 0.51 |
| **Tyrannosauroids** | | | | | | | | | |
| *Albertosaurus* | 0.41 | 0.54 | 0.60 | 1.19 | 0.70 | — | — | — | 0.51 |
| *Dilong* | 1.39 | — | 1.19 | 1.65 | 1.00 | — | — | — | 0.49 |
| *Guanlong* | — | 0.80 | 1.10 | 1.70 | 0.99 | — | — | — | 0.48 |
| *Gorgosaurus* | 0.37 | 0.56 | 0.73 | 1.43 | 0.85 | — | — | — | 0.49 |
| *Tyrannosaurus* * | 0.35 | 0.56 | 0.62 | 1.46 | 0.83 | — | — | — | 0.58 |
| **Ornithomimosaurs** | | | | | | | | | |
| *Archaeornithomimus* | — | 0.80 | 0.50 | 1.56 | 1.06 | — | — | — | 0.87 |
| *Deinocheirus* | 0.79 | 0.73 | 0.64 | 1.59 | 0.98 | 1.63 | 0.87 | 1.69 | 0.96 |
| *Gallimimus* | 1.18 | 0.71 | 0.51 | 1.33 | 0.87 | 1.35 | 1.09 | 2.31 | 0.85 |
| *Harpymimus* | 0.97 | 0.82 | 0.84 | 1.63 | 1.11 | 1.45 | 1.19 | 2.61 | 0.51 |
| *Ornithomimus* | 1.06 | 0.75 | 0.82 | 1.26 | 0.90 | 1.31 | 1.37 | 2.39 | 1.07 |
| *Sinornithomimus* | 1.04 | 0.69 | 0.63 | 1.46 | 1.10 | 1.33 | 1.51 | 3.09 | 0.75 |
| *Struthiomimus* | 0.89 | 0.79 | 0.76 | 1.29 | 0.86 | 1.20 | 1.21 | 2.43 | 0.86 |
| *Struthiomimus* | 0.95 | 0.71 | 0.73 | 1.40 | 1.04 | 1.30 | 1.68 | 3.71 | 0.94 |
| *Shenzhousaurus* | — | — | — | 1.78 | 1.20 | 1.60 | 1.16 | 2.26 | — |
| **Therizinosaurs** | | | | | | | | | |
| *Alxasaurus* | 0.72 | 0.71 | 0.70 | 1.37 | 0.72 | — | — | — | 0.50 |
| *Erliansaurus* | 1.22 | 0.86 | 0.73 | 0.73 | 0.39 | 0.81 | 1.06 | 2.36 | 0.49 |
| *Falcarius* | 0.88 | 0.77 | 0.96 | 1.63 | 0.91 | 1.45 | 0.79 | 1.55 | 0.45 |
| *Nothronychus* | 0.74 | 0.73 | 0.89 | 1.67 | 0.94 | — | — | — | 0.64 |

continued

| Taxa | H/S | BI | M/H | P Ⅰ \| Ⅱ | Ⅱ-2/Mc | P Ⅰ \| Ⅲ | Ⅲ-3 /(1+2) | Ⅲ-3/1 | Mc Ⅰ /Mc Ⅱ |
|---|---|---|---|---|---|---|---|---|---|
| **Oviraptorosaurs** | | | | | | | | | |
| *Caudipteryx* | 0.90 | 0.88 | 1.03 | 1.54 | 0.86 | — | — | — | 0.43 |
| *Protarchaeopteryx* | — | 0.84 | 1.56 | — | — | — | — | — | 0.39 |
| *Oviraptor* | 0.80 | 0.88 | 1.24 | 1.15 | 0.64 | 0.95 | 0.42 | 0.76 | — |
| **Troodontids** | | | | | | | | | |
| *Anchiornis* | 1.53 | 0.80 | 1.19 | 1.42 | 0.80 | 0.97 | 0.93 | 1.75 | 0.37 |
| *Jinfengopteryx* | 1.03 | 0.88 | 1.17 | 1.70 | 0.99 | — | — | 1.30 | 0.41 |
| *Sinornithoides* | — | 0.78 | 0.97 | 1.40 | 0.85 | 0.93 | 1.64 | 4.83 | 0.36 |
| *Xiaotingia* | 1.29 | 0.92 | 0.90 | 1.67 | 1.04 | 1.13 | 1.25 | 1.88 | 0.42 |
| **Dromaeosaurids** | | | | | | | | | |
| *Bambiraptor* | 1.24 | 0.89 | 0.99 | 1.18 | 0.73 | 1.01 | 1.08 | 1.52 | 0.35 |
| *Deinonychus* | 1.25 | 0.78 | 0.90 | 1.48 | 0.87 | 1.15 | 1.27 | 2.18 | — |
| *Microraptor gui* | 1.30 | 0.84 | 1.07 | 0.93 | 0.48 | — | — | — | 0.26 |
| *M. zhaoianus* | 1.46 | 0.85 | 0.97 | 0.95 | 0.52 | 0.83 | 0.73 | 1.02 | 0.25 |
| *Sinornithosaurus* | 1.58 | 0.82 | 0.97 | 1.06 | 0.56 | 0.83 | 0.85 | 1.28 | 0.32 |
| *Tianyuraptor* | 1.13 | 0.80 | 1.02 | 1.30 | 0.74 | 0.95 | 1.17 | 1.75 | 0.35 |
| **Scansoriopterygids** | | | | | | | | | |
| *Epidendrosaurus* | 1.51 | 0.88 | 0.82 | 1.65 | 1.04 | 3.41 | 0.44 | 0.85 | 0.38 |
| **Avians** | | | | | | | | | |
| *Archaeopteryx* | 1.50 | 0.87 | 1.00 | 1.24 | 0.69 | 0.93 | 1.18 | 1.92 | 0.25 |
| *Dalianraptor* | 1.73 | 0.88 | 1.23 | 1.78 | 0.83 | 1.36 | 0.76 | 2.60 | — |

Note: The maximal estimated measurement ratio values for *Yixianosaurus* are given in square brackets. BI. brachial index; H. humerus; M. manus; Mc. metacarpal; P Ⅰ | Ⅱ. phalangeal index of digit Ⅱ; P Ⅰ | Ⅲ. phalangeal index of digit Ⅲ; S. scapula. * For *Tyrannosaurus*, manual values were based on MOR 009, and all other values were based on FMNH PR 2081. Individual phalanges are denoted by digit number in Roman numerals and phalangeal position in Arabic numerals.

and long distal phalanges on digits Ⅱ and Ⅲ. Three ornithomimosaur taxa (*Harpymimus*, *Archaeornithomimus*, and *Sinornithomimus*) share with *Yixianosaurus* the unique traits of having Ph Ⅱ-2 longer than Mc Ⅱ and having Ph Ⅲ-3 longer than the combined lengths of Ph Ⅲ 1 + 2 (Xu and Wang, 2003). There is likely a fourth case within Ornithomimosauria, *Shenzhousaurus*, though the manus of the only specimen is too incomplete to confirm metacarpal Ⅱ length (Ji et al., 2003). Yet despite these similarities, the overall forelimb morphologies differ significantly. The humerus of *Yixianosaurus* possesses a large, subrectangular deltopectoral crest and a sigmoidal humeral shaft whereas those of ornithomimosaurians are characterized by straight shafts with a proximally placed and poorly developed deltopectoral crest (Makovicky et al., 2004). *Yixianosaurus* has the characteristic bowed ulna of maniraptorans, which is absent in ornithomimosaurs and more basal coelurosaurs. Ornithomimosaurians, including the basal *Pelecanimimus*, have a tightly appressed or ligamentously articulated (syndesmosis) distal radius and ulna (Pérez-Moreno et al., 1994; Nicholls and Russell, 1985) whereas *Yixianosaurus* has the general theropod condition of these elements being separate. Unlike *Yixianosaurus*, whose carpus is composed of four carpals arranged in the typical maniraptoran pattern, ornithomimosaurs have a highly apomorphic wrist possessing up to six carpals (Makovicky et al., 2004; Sullivan et al., 2010). The arrangement of the carpals and the relatively large angle of the radiale (as per Sullivan et al., 2010) of approximately 40° in *Yixianosaurus* are unlike the six carpals and low radiale angle present in ornithomimosaurs (Sullivan et al., 2010). In contrast to *Yixianosaurus* and other coelurosaurs, ornithomimosaurs are characterized by an elongate metacarpal Ⅰ relative to metacarpal Ⅱ (though *Harpymimus* does not have such an extreme elongation). The manus is relatively reduced in ornithomimosaurs, representing less than a third of the total forelimb length, with the humerus as the longest bone at around 40% or more of the length of the forelimb (Table 4). In *Yixianosaurus*, the manus is the largest component (40% of total limb), with the humerus accounting for only 36% of the limb.

Unlike in derived ornithomimosaurs, the manus in basal forms such as *Harpymimus* and *Shenzhousaurus* is more typically theropodan, with digit Ⅰ smaller than Ⅱ or Ⅲ and recurved unguals (Ji et al., 2003). Although less specialized than those of advanced ornithomimosaurs, the mani of these taxa are still substantially different from that of *Yixianosaurus*. Unlike in *Harpymimus*, the humerus of *Yixianosaurus* is significantly longer than the scapula, yet shorter than the manus. The wrist of *Harpymimus* shows the typical ornithomimosaur condition with 5 carpals and a low radiale angle (Sullivan et al., 2010). *Yixianosaurus* has a reduced metacarpal Ⅰ (40% as long as McⅡ compared to 51% in *Harpymimus*). Metacarpal Ⅲ is shorter than metacarpal Ⅱ in *Yixianosaurus*, whereas basal ornithomimosaurs have a metacarpal Ⅲ that is equal to or longer than metacarpal Ⅱ (Ji et al., 2003; Kobayashi and Barsbold, 2006). The unguals of both *Harpymimus* and *Shenzhousaurus* are gently recurved, unlike the trenchant unguals of *Yixianosaurus*, and lack a robust, proximally placed flexor tubercle. *Yixianosaurus* differs from the possible ornithomimosaur *Deinocheirus* in having a manus significantly longer than the humerus, metacarpal Ⅱ longer than metacarpal Ⅲ, PhⅡ-2 longer than metacarpal Ⅱ, and PhⅢ-3 longer than the combined lengths of PhⅢ-1 and PhⅢ-2 (Table 4). The humerus of *Deinocheirus* shows a moderate, triangular deltopectoral crest (Osmólska and Roniewicz, 1970) unlike the long quadrangular condition in *Yixianosaurus*. Although the flexor tubercles on the unguals of *Deinocheirus* are more developed than those in later ornithomimosaurs, they are not developed to the extent present in *Yixianosaurus*, nor is the claw as recurved and raptorial.

**Therizinosauria** Derived therizinosaurs have highly modified forelimbs with a hypertrophied humeral internal tuberosity separated from the head by a distinct notch, a greatly expanded distal humerus, relatively short phalanges, and exaggerated unguals (Zanno, 2010). *Yixianosaurus* has none of these states and our comparison will concentrate on the basal therizinosaurs, notably the coeval *Falcarius* and *Beipiaosaurus*. The slight distal expansion of the scapula of *Yixianosaurus*, greater contribution to the glenoid from the scapula than the coracoid, and pronounced ventral process of the coracoid are also present in *Falcarius* (Zanno, 2006). The humeri of both taxa are markedly similar in overall shape, though the lack of preserved distal condyles in *Yixianosaurus* prevents any comparison to the characteristic cranially oriented condyles of basal therizinosaurs. The deltopectoral crests are similar in extent, though that of *Yixianosaurus* is slightly less than that of *Falcarius* (30% and 33% respectively). The forearm has a similar level of robustness and the brachial indices are similar (*Falcarius* 77%, *Yixianosaurus* 72%). Both have similar intralimb proportions, though the manus is relatively longer in *Yixianosaurus*, and high phalangeal indices. The distal phalanges of digits Ⅱ and Ⅲ are relatively longer in *Yixianosaurus* than *Falcarius*. The carpus of *Yixianosaurus* is similar to that of *Falcarius* in that it has four carpals and the semilunate is mediolaterally elongate, supporting the bases of metacarpals Ⅰ and Ⅱ. The radiale angle at 40° is very close to the 39° angle measured for *Alxasaurus* (Sullivan et al., 2010). The enlarged flange at the ventrolateral base of metacarpal Ⅰ in *Yixianosaurus* may be either an example of the slightly hypertrophied edge that is common to many maniraptorans or an incipient form of the rectangular buttress that is unique to therizinosaurs. Without a disarticulated manus, however, the identity of this flange cannot be determined. *Yixianosaurus* does have a small tab protruding from the mid-length of metacarpal Ⅰ that appears similar to a tab interpreted as an autapomorphy of *Beipiaosaurus* (Zanno, 2010). The other manual autapomorphy of *Beipiaosaurus* is the presence of an elongate lateral articular surface on phalanx Ⅰ-1 (Xu et al., 1999). This surface is not visible in *Yixianosaurus*.

Similar to *Falcarius*, *Yixianosaurus* has extremely large ventral intercondylar tuberosities on all phalanges of all three digits, though they are developed to a greater extent in digit Ⅲ than in either Ⅰ or Ⅱ. This morphology is not unique to these two taxa and similar, but generally smaller, tuberosities are found on two of the three digits of the oviraptorosaurs *Hagryphus* and *Chirostenotes*, some phalanges of digits Ⅱ and Ⅲ of paravians such as *Microraptor*, and phalanx Ⅱ-2 of *Haplocheirus*. The presence of hypertrophied ventral intercondylar tuberosities on all phalanges of all digits is unusual in theropods and, currently, the only taxon comparable to *Yixianosaurus* in this respect is *Falcarius*. *Yixianosaurus* has a dorsal lip on the unguals of digits Ⅱ and Ⅲ. This feature is present in some therizinosaurs, including *Falcarius*, but is also common in oviraptorids and some dromaeosaurids (Zanno, 2006). The articular regions of all manual unguals of *Falcarius* are also swollen and the proximal portion of the lateral groove forms a deep sulcus between the flexor tubercle and the remainder of the ungual, like in *Yixianosaurus*.

These similarities, coupled with the small size of *Yixianosaurus*, its uncertain ontogenetic stage (although see Xu and Wang [2003] for evidence that it was an adult), and its co-occurrence with *Beipiaosaurus* in the same formation, suggest the possibility that *Yixianosaurus* may be a juvenile specimen of *Beipiaosaurus*. We do not favour this hypothesis based on a number of characteristics. The internal humeral tuberosity is square and confluent with the humeral head in *Yixianosaurus*, unlike in *Beipiaosaurus*, which possesses a pointed internal tuberosity that is well separated from the humeral shaft by a visible depression (Xu et al., 1999). In addition, the relative lengths of the bones of *Yixianosaurus*, including humerus > scapula, PhⅢ-3 > PhⅢ 1+2 and PhⅡ-2 > McⅡ, all differentiate this specimen from known examples of *Beipiaosaurus*. While we cannot rule out the possibility that some or all of these traits used to currently distinguish *Yixianosaurus* from *Beipiaosaurus* are ontogenetically variable, we maintain that there is sufficient evidence to retain *Yixianosaurus* as a separate taxon.

**Alvarezsauroidea** Advanced alvarezsauroids have greatly modified forelimbs that are reduced in size, extremely robust with a hypertrophied olecranon, and characterized by reduction of digits Ⅱ and Ⅲ to vestigial structures (Perle et al., 1994; Longrich and Currie, 2009; Xu et al., 2011a). These morphologies are sufficiently different from *Yixianosaurus* that further comparisons are unnecessary. The most basal alvarezsauroid, *Haplocheirus*, does not have the same degree of forelimb specialization and is the only member of this clade used here for comparison. *Yixianosaurus* lacks the following alvarezsauroid traits seen in *Haplocheirus* (Choiniere et al., 2010a): a large ectepicondyle with a rounded articular surface, a bulbous trochlear articular surface of the distal ulna, an axial furrow on PhI-1, and a greatly enlarged digit Ⅰ ungual having enclosed lateral grooves. The lateral grooves on the unguals of *Yixianosaurus* are slightly restricted near their proximal ends by the swollen articular surface of the ungual, but this morphology is not like the enclosed grooves of alvarezsauroids. Additionally, the base of metacarpal Ⅰ is not enlarged (compared to metacarpal Ⅱ) to the same degree, nor is PhI-1 as robust, as in *Haplocheirus* (Choiniere et al., 2010a).

**Oviraptorosauria** The pectoral girdle of *Yixianosaurus* resembles that of oviraptorosaurs in possessing a scapula with a modest degree of distal expansion, having an obtuse angle of contact between the scapula and the coracoid, except in *Caudipteryx* (Zhou et al., 2000), and possessing a large ventral process of the coracoid (Osmólska et al., 2004; Lü et al., 2005). Unfortunately none of these characters are diagnostic, and most of them occur in many more basal taxa such as *Tanycolagreus* and *Falcarius* (Carpenter et al., 2005a; Zanno, 2006). Oviraptorosaurs uniquely have a laterally everted acromion (Osmólska et al., 2004), but due to the state of preservation of both proximal scapulae, this character cannot be determined in *Yixianosaurus*. Several basal oviraptorosaurs are known from the Jehol beds. Two of these, *Caudipteryx* and *Similicaudipteryx*, are immediately distinguishable from *Yixianosaurus* in having a scapula-coracoid angle of 90° in addition to reduced forelimbs and a reduced digit Ⅲ (Zhou et al., 2000; Zhou and Wang, 2000; He et al., 2008). Another Jehol basal oviraptorosaur, *Protarchaeopteryx*, resembles *Yixianosaurus* in possessing an elongated arm (Ji and Ji, 1997; Ji et al., 1998), yet *Protarchaeopteryx* differs in also having an elongated ulna (brachial index = 0.84), a proportionally longer manus (46% of the forelimb compared to 40% in *Yixianosaurus*) and weakly recurved claws with distally displaced flexor tubercles. Most oviraptorosaurs have a relatively elongate metacarpal Ⅰ and a relatively short phalanx Ⅲ-3 (Gauthier, 1986); both of these traits are absent in *Yixianosaurus*. Additionally, the humerus of *Yixianosaurus* differs from those of oviraptorosaurs in possessing a deltopectoral crest whose apex is less than a third of the shaft length, whereas in oviraptorosaurs the deltopectoral crest is markedly distally expanded (Osmólska et al., 2004; Longrich et al., 2010). Some similarities are present between *Yixianosaurus* and selected oviraptorosaurs. The enlarged proximal flange and mid-length tab on the ventrolateral edge of metacarpal Ⅰ in *Yixianosaurus* compares well to similar morphologies in *Machairasaurus* (Longrich et al., 2010). These similarities suggest that an incipient rectangular buttress on metacarpal Ⅰ may have a broader phylogenetic distribution. The presence of this tab suggests that this morphology, which was originally identified as a unique autapomorphy of *Beipiaosaurus*, may in fact be more widespread throughout Maniraptora. Additionally, the bifurcating ungual groove on the lateral surface of the ungual of *Yixianosaurus* is also seen in many oviraptorosaurs, such as *Hagryphus* (Zanno and Sampson, 2005).

**Scansoriopterygidae** This clade is currently composed of two species, only one of which is known from post-hatchling material. The diagnostic characters and phylogenetic relationships of this clade are poorly resolved, given the multiple differing phylogenetic hypotheses (e.g. Zhang et al., 2008; Xu et al., 2009b; Choiniere et al., 2010a; Agnolin and Novas, 2011). Due to the early ontogenetic stage of *Epidendrosaurus* we agree with Zhang et al. (2002) that many of the intra- and interlimb ratios in this specimen are unreliable for phylogenetic purposes until its ontogenetic trajectory is known. Comparisons to *Epidexipteryx* are problematic given the lack of description of the forelimbs and the incomplete preservation of the manus. Therefore our comparison will be brief and contingent on these limitations. Of the characters Zhang et al. (2008) used to diagnose Scansoriopterygidae, only one, the relatively small flexor tubercle size, is applicable here. Unlike the non-trenchant manual claws, with their reduced flexor tubercles, *Yixianosaurus* claws are highly recurved and have enormous tubercles. Additionally, the brachial index differs significantly between these taxa, and *Yixianosaurus* does not have the extreme modifications to digit Ⅲ present in *Epidendrosaurus*. Within the extremely elongated digit Ⅲ of *Epidendrosaurus* (PI = 3.4), the longest bones are the most proximal phalanges, with the combined length of PhⅢ-1 + 2 equal to ~225% the length of PhⅢ-3. In *Yixianosaurus* this ratio is only 77%.

**Paraves** Paravian forelimbs are generally elongate and slender, although troodontids and some derived dromaeosaurids have secondarily reduced the forelimb skeleton (Turner et al., 2007; Novas et al., 2009). The paravian pectoral girdle is characterized by a scapula that is shorter than the humerus and whose distal portion is parallel-edged (Hu et al., 2009). The scapula-coracoid suture is inclined anteroventrally, perhaps in relation to an enlarged acromion (Jasinoski, 2003). The coracoid is rectangular and has a strong medial inflection, forming an

"L" shape (Hu et al., 2009). In *Yixianosaurus*, the scapula is shorter than the humerus but does have a degree of distal expansion not seen in paravians, except for *Sinornithoides* (Russell and Dong, 1993). In paravians the humerus is not always longer than the scapula: the basal troodontid *Mei long* and the derived dromaeosaurid *Linheraptor* both reverse this trait, and its presence in derived troodontids and the short-armed dromaeosaurids, such as *Mahakala* and *Austroraptor*, is uncertain. Nor is the existence of a humerus that is longer than the scapula confined to Paravians. This trait is present across a wide range of theropods, including the basal theropod *Coelophysis*, multiple compsognathids and ornithomimosaurs, and the basal tyrannosauroid *Dilong*, and has been reported in the oviraptorid *Gigantoraptor* (Xu et al., 2007). Barsbold (1983) described *Therizinosaurus* as having a scapula only 88% the length of its humerus, but we regard this with scepticism because the scapula has since been lost and this measurement cannot be verified (Zanno, pers. com.). The therizinosaur *Erliansaurus* is similarly reported to have a humerus longer than its scapula, but this specimen is missing the distalmost part of the blade and the measurement given by Xu et al. (2002) should therefore be regarded with caution. The scapula and coracoid of *Yixianosaurus* appear to form a continuous curving plane that does not have the obvious ventromedial inflection of the ventral portion of the coracoid that characterizes paravians (Norell and Makovicky, 1999), nor does it have an anteroventrally inclined scapula-coracoid suture. The glenoid of *Yixianosaurus* faces ventrally, rather than laterally as in advanced paravians (see character 259 in the matrix of Choiniere et al., 2010a).

The forelimb of *Yixianosaurus* has multiple features that suggest this taxon is unlikely to be a paravian. *Yixianosaurus* has a reduced antebrachium, with the ulna only 72% of the humeral length. In dromaeosaurids and troodontids this ratio is above 80%, except in *Sinornithoides* (78%), and tends to be even higher in basal avians. *Yixianosaurus* has a semilunate carpal capping nearly the entire proximal surfaces of metacarpals Ⅰ and Ⅱ. The semilunate of paravians, on the other hand, is centred on metacarpal Ⅱ (Xu et al., 2003; Hu et al., 2009). Additionally, *Yixianosaurus* has four well preserved carpals whereas most non-avian paravians preserve only two. Metacarpal Ⅰ is relatively long, at approximately 40% the length of metacarpal Ⅱ, which would reverse the trend among other small bodied paravians toward reduction of the former element. Unlike dromaeosaurids and avians, but similar to some basal troodontids, digit Ⅲ of *Yixianosaurus* is not obviously more gracile than digit Ⅱ, nor is metacarpal Ⅲ strongly bowed. The manual proportions are unlike those of Jehol dromaeosaurids and most troodontids in that the phalangeal indices of both digit Ⅱ and digit Ⅲ are high. *Yixianosaurus* has a long digit Ⅰ (McI + PhI-1 is 135% the length of metacarpal Ⅱ) compared to paravians, especially to coeval or similar-sized taxa. Values within paravians range from less than 100% in *Microraptor* sp. and birds (Xu et al., 2003) to 123% in *Deinonychus*, with most paravians between 105% and 120%. In *Yixianosaurus*, phalanx Ⅲ-1 is only 12% longer than Ⅲ-2, whereas in dromaeosaurids Ⅲ-1 is minimally 40% longer. As in some paravians, phalanx Ⅲ-3 is longer than the combined lengths of Ⅲ 1 + 2, though this is not true of microraptorines, *Linheraptor*, or *Anchiornis*. The same feature is also present in some non-paravian coelurosaurs, including *Erliansaurus*, *Scipionyx*, *Tanycolagreus*, and ornithomimosaurs, and is suspected to be present in *Coelurus* and *Protarchaeopteryx* (Carpenter et al., 2005b; Ji and Ji, 1997; Ji et al., 1998).

## 5 Discussion

### 5.1 Diet and significance to maniraptoran evolution

Though the skull and dentition are not preserved in *Yixianosaurus*, some inferences about the diet of this taxon can be drawn based on claw and forelimb morphology. *Yixianosaurus* has large raptorial claws on all three manual digits, with hypertrophied, proximally placed flexor tubercles. The manus is elongate with a large phalangeal index and the forelimb is robust with prominent brachial flexor attachments on the distal humerus (Fig. 1). In addition, the long, robust, manus and deep ligament pits on the phalanges suggest strong grasping capabilities, and resemble the forelimbs of predatory forms such as dromaeosaurids and basal coelurosaurs such as *Tanycolagreus* and *Coelurus* (Xu and Wang, 2003; Carpenter et al., 2005b). Although the basal therizinosaurs *Falcarius* and *Alxasaurus* also have trenchant claws with enlarged flexor tubercles, these morphologies are present mainly on digit Ⅰ and are less pronounced in the other digits (Zanno, 2006). In *Falcarius*, the flexor tubercles on the unguals of digits Ⅱ and Ⅲ are displaced distally and reduced relative to the articular facets, but this is not the case in *Yixianosaurus*. Reduction and distal displacement of the flexor tubercle has been associated with a reduction in the predatory function of the claw (Longrich et al., 2010). In oviraptorosaurs there is evidence of both herbivory and carnivory (Norell et al., 1994; Ji et al., 1998) yet many derived members of this clade retain relatively raptorial (that is, long, curved, and dorsoventrally robust) manual claws compared to those of ornithomimosaurs. However, *Yixianosaurus* has significantly more robust unguals, with much larger tubercles than are seen in many oviraptorosaurs (Barsbold, 1981; Currie and Russell, 1988; Longrich et al., 2010), and in particular the unguals of *Yixianosaurus* are very different from those of the herbivorous *Caudipteryx* (Ji et al., 1998; Zhou and Wang, 2000).

When compared to definitively carnivorous taxa, the unguals of *Yixianosaurus* are more raptorial than those of basal tyrannosauroids (e. g. *Guanlong*, IVPP V 14531) or some compsognathids (Currie and Chen, 2001; Chiappe and Göhlich, 2010). The unguals of *Yixianosaurus* are more similar to those of carnivorous basal tetanurans such as allosauroids, basal coelurosaurs such as *Tanycolagreus*, and the hypercarnivorous dromaeosaurids (Ostrom, 1969; Carpenter, 1998; Hone et al., 2010). Although we cannot exclude herbivory from the diet of *Yixianosaurus*, we propose a primarily carnivorous or only partially omnivorous life history reconstruction based on the predatory nature of the forelimb. Similarly, if we survey extant clawed vertebrates with highly recurved manual claws that are similar in form to those of *Yixianosaurus*, such as varanid lizards and felid mammals, they are more likely to be carnivorous.

Recently, Zanno et al. (2009) proposed that maniraptorans were ancestrally herbivorous, based on the known or suspected occurrence of herbivory within the ornithomimosaurs, therizinosaurs, oviraptorosaurs, troodontids and basal avialans. Because *Yixianosaurus* was recovered among the basal maniraptorans, its putative dietary regime is of significance to this debate. Based on available anatomical and ecological data and analyses, Zanno et al. (2009) considered therizinosaurs, ornithomimosaurs and oviraptorosaurs to be predominantly herbivorous. *Ornitholestes* and Alvarezsauridae were listed as "unknown" and only dromaeosaurids were considered to be exclusively carnivorous.

Despite the convincing evidence for herbivory or facultative herbivory in multiple coelurosaur lineages presented by Zanno et al. (2009) and Zanno and Makovicky (2011), both *Yixianosaurus* and the recently described basal alvarezsauroid *Haplocheirus* (Choiniere et al., 2010a) interrupt this sequence of herbivory dominating the ecology of non-dromaeosaurid maniraptorans. *Yixianosaurus* cannot be assessed according to the indicators of herbivory of Zanno et al. (2009) and Zanno and Makovicky (2011) owing to the lack of cranial material. However, based on the available elements, there is reason to conclude that *Yixianosaurus* was a carnivore (as noted above) and the phylogenetic position recovered here for the genus places it as a potential meat-eater among the herbivores. Although manual unguals and other features may be functionally adapted for other tasks, these can also be strong indicators of a carnivorous lifestyle and should not be overlooked. Future investigations should look beyond the cranium and digestive apparatus (e. g. reversed pubis) as prey capture and food processing can involve both the pes and manus.

More notably, *Haplocheirus*, recovered by Choiniere et al. (2010a) as the basalmost alvarezsauroid, has carnivorous characteristics such as recurved, serrated teeth (Choiniere et al., 2010a; DWEH, pers. obs.), which suggest that alvarezsauroids were ancestrally carnivorous if not hypercarnivorous before later adopting an insectivorous lifestyle (Senter, 2005). A number of the putatively herbivorous characters coded by Zanno and Makovicky (2011) in derived alvarezsauroids, such as reduced or absent teeth and simplified jaws with a weak bite, are also typical in myrmecophages. This indicates that some of the characters claimed to support herbivory in the derived alvarezsauroids may be alternatively interpreted as supporting the hypothesis of insectivory (considered a form of carnivory by Zanno et al., 2009), which fits both other lines of evidence in the group (Senter, 2005; Xu et al., 2010) and the carnivorous characteristics of *Haplocheirus*.

The phylogeny recovered here, with both *Yixianosaurus* and alvarezsauroids recovered in a polytomy with therizinosaurs, suggest that dietary regimes within Maniraptora may have been more complex than proposed by Zanno and Makovicky (2011). We suggest that with the integration of further characters to assess dietary preference (e. g. those of the manus and pes) and additional specimens, as well as the inclusion of taxa like *Haplocheirus*, the distribution of dietary preferences within Maniraptora will become better resolved.

## 5.2 Manual morphology and indices

The most striking aspect of *Yixianosaurus* is the proportions of the manus. In recent years, a number of new discoveries have increased the disparity in known manual morphologies within Theropoda, and in particular Maniraptora, and necessitate a re-evaluation of *Yixianosaurus* with respect to other coelurosaurs. Xu and Wang (2003) suggested that the degree of elongation of the manus reinforced a derived maniraptoran affinity of *Yixianosaurus* and that the elongation of the penultimate phalanges indicated strong grasping capabilities, something previously proposed in theropods (Currie and Chen, 2001) and other taxa (Fröbisch and Reisz, 2009). Furthermore, they interpreted the increased grasping capabilities in this and other Jehol theropods as a potential indicator of arboreality within these taxa. Although the question of arboreal behaviour is beyond the scope of this paper (see Dececchi and Larsson, 2011 for an analysis of the subject) an examination of the variation in the proportions of the manus of *Yixianosaurus* and other theropods is presented here.

Complex locomotory behaviours, like arboreality, require a suite of adaptations in the postcranial skeleton (Fröbisch and Reisz, 2009; Dececchi and Larsson, 2011). If some derived maniraptorans were grip-based climbers, they should differ in key morphologies in their forelimbs from their sister group. Since the publication of Xu and Wang (2003), a large number of new coelurosaurian, and especially maniraptoran, theropods have been discovered. Our goal here is to incorporate data from these new finds to determine if there is still a trend toward increasing manual and penultimate phalangeal lengths within non-avian theropods along the lineage that leads to birds. We will refer to *Anchiornis*, *Epidendrosaurus*, *Microraptor*, *Xiaotingia*, *Archaeopteryx* and *Yixianosaurus* as "advanced graspers" and to other non-avian theropods as "general graspers". We emphasize that this is not an easy problem to examine since claw morphology in a particular taxon may be dictated by a compromise between many functions, the most obvious of which is the probable use of the forelimbs in many predatory non-avian theropod taxa to grip prey (Carpenter, 1998; Senter and Robins, 2005). However, comparing these putative climbing taxa to taxa that are not considered to have been arboreal may be informative when examining particular traits, such as relative lengths of penultimate phalanges. We will emphasize comparisons of grasping ability between putatively arboreal and non-arboreal taxa based on both total manus and penultimate phalangeal elongation (Zhou and Zhang, 2002; Xu and Wang, 2003; Xu et al., 2011b), without making larger behavioural and ecological statements. We also examine phalangeal index (PI) values for these theropods. PI is positively associated with grasping behaviour in extant taxa (Lemlin, 1999; Hopson, 2001; Kirk et al., 2008; Fröbisch and Reisz, 2009). Relatively long fingers allow organisms to encircle small objects while maintaining a firm grip (Lemlin, 1999). This metric is different than elongation of the penultimate phalanges alone, and research on extant taxa has found PI to be more closely related to efficient grasping (Lemlin, 1999).

We measure the manus length as the combined lengths of McⅡ,PhⅡ-1 and PhⅡ-2. This digit is the longest in most tridactyl theropods and correlates well with overall manus length. The manus of *Yixianosaurus* is elongate relative to the rest of the forelimb (112% of humerus, 40% of entire forelimb). Although high, this degree of manus elongation is similar to that seen in compsognathids, basal tyrannosauroids, *Coelurus* and *Tanycolagreus*, *Falcarius*, and some advanced maniraptorans (Table 4; Figs. 4-5). The elongate manus of *Epidendrosaurus* does not show as an outlier here because its digit Ⅱ is relatively normal and only the first phalanx of digit Ⅲ is autapomorphically hypertrophied (Zhang et al., 2002). Direct comparisons between basal coelurosaurs (compsognathids, *Tanycolagreus*, *Coelurus*, and *Dilong*) and either paravians or advanced maniraptorans (oviraptorosaurs + paravians) indicate that the basal taxa have proportionately longer hands under either measure (Table 4; Figs. 4-5). This indicates that the relative length of the manus is greater in basal coelurosaurs than more advanced maniraptorans, though oviraptorine oviraptorosaurs are underrepresented in this sample and many are reported to possess an elongate manus (Longrich et al., 2010).

Penultimate phalanx lengths for digits Ⅱ and Ⅲ were compared, relative to metacarpal Ⅱ and phalanx Ⅲ-1, respectively. These metrics have been used in the past and we adopt them here. We find that although the distal phalanges of *Yixianosaurus* are elongate, their relative lengths are not significantly greater than is the case in ornithomimosaurs (Tables 4-5; Figs. 5-6). The elongate digit Ⅱ penultimate phalanx seen in *Yixianosaurus* and *Epidendrosaurus* is found to have a broad distribution within theropods (Tables 4-5). In particular, multiple species of ornithomimosaurs, the basal tyrannosauroid *Dilong*, and the troodontid *Xiaotingia* all have PhⅡ-2 longer than McⅡ, and many other taxa have values greater than 0.9 (Tables 4-5). When the digit as a whole is examined, PhⅡ-2 of *Yixianosaurus* represents 38% of the total digital length, similar to other theropods including *Compsognathus*, *Raptorex* and *Deinocheirus* and lower than in most advanced ornithomimosaurs, with the exception of *Gallimimus* (37%). There is no difference in the length of Ⅱ-2 between "advanced" and "general grasping" theropods (unequal variance T-test $t = -0.0773$, $p(\text{same}) = 0.94$). In fact, most ornithomimosaurs have significantly higher values than "advanced graspers".

A similar pattern is seen in digit Ⅲ, with ornithomimosaurs once again having relative penultimate phalangeal lengths significantly higher than other theropods, using either Ⅲ-3/Ⅲ-1 or Ⅲ-3 as a percentage of total digit length (McⅢ + Ⅲ1-3) (Tables 4-5). Although *Yixianosaurus* has an extremely high Ⅲ-3/Ⅲ-1 score (2.44), similar or greater values are present in the basal coelurosaurs *Scipionyx* and *Tanycolagreus* as well as the troodontid *Sinornithoides* and multiple ornithomimosaurs (Table 5). "Advanced graspers" do not have enlarged ratios compared to other theropods, and in fact have significantly lower values than ornithomimosaurs under both measures.

*Yixianosaurus* has an extremely high PI, among the highest of all theropods studied here. Despite their extreme penultimate phalangeal measurements, advanced ornithomimosaurs do not have high PI values, although the basal ornithomimosaurs *Shenzhousaurus* and *Harpymimus* have relatively elevated values. Among "advanced grasping" taxa, *Xiaotingia* (1.67) and *Epidendrosaurus* (1.51) have values well above the theropod average (1.41), though equal or greater

**Table 5 Phalangeal proportions for digits Ⅱ and Ⅲ in non-avian and avian theropods**

| Genera | Mc Ⅱ | Ⅱ-1 | Ⅱ-2 | PI | 2/Mc | Mc Ⅲ | Ⅲ-1 | Ⅲ-2 | Ⅲ-3 | PI | 3/(1+2) | 3/(1) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acrocanthosaurus* | 116 | 101 | 103 | 1.76 | 0.89 | 89 | 50 | 42 | 60 | 1.71 | 0.65 | 1.2 |
| *Albertosaurus* | 83 | 41 | 58 | 1.19 | 0.7 | — | — | — | — | — | — | — |
| *Allosaurus* | 125 | 94 | 102 | 1.57 | 0.82 | 105 | 50 | 41 | 52 | 1.36 | 0.57 | 1.04 |
| *Alxasaurus* | 111 | 72 | 80 | 1.37 | 0.72 | — | — | — | — | — | — | — |
| *Anchiornis* | 33.9 | 21 | 27 | 1.42 | 0.8 | 30.5 | 8.1 | 7.2 | 14.2 | 0.97 | 0.93 | 1.75 |
| *Archaeopteryx* | 28 | 15.4 | 19.4 | 1.24 | 0.69 | 24.5 | 6.4 | 4 | 12.3 | 0.93 | 1.18 | 1.92 |
| *Archaeopteryx* | 17.8 | 10.1 | 14.5 | 1.38 | 0.81 | 16.5 | 4.8 | 2.2 | 9.5 | 1 | 1.36 | 1.98 |
| *Archaeopteryx* | 25 | 12.5 | 18.5 | 1.24 | 0.74 | 23 | — | — | — | — | — | — |
| *Archaeopteryx* | 34.3 | 19 | 27 | 1.34 | 0.79 | — | 7.9 | 6.1 | 17.5 | — | 1.25 | 2.22 |
| *Archaeornithomimus* | 54 | 27 | 57 | 1.56 | 1.06 | 50 | 17 | — | 43 | — | — | 2.53 |
| *Bambiraptor* | 47.8 | 21.4 | 35 | 1.18 | 0.73 | 44.9 | 15.5 | 6.3 | 23.5 | 1.01 | 1.08 | 1.52 |
| *Caudipteryx* | 29 | 18.5 | 25 | 1.5 | 0.86 | — | — | — | — | — | — | — |
| *Caudipteryx* | 28 | 19 | 24 | 1.54 | 0.86 | — | — | — | — | — | — | — |
| *Caudipteryx* | 28 | 17 | 24 | 1.46 | 0.86 | — | — | — | — | — | — | — |
| *Coelurus* | 53 | 46 | 48.5 | 1.78 | 0.92 | — | — | — | — | — | — | — |
| *Coelophysis* | 39.2 | 18.6 | 21 | 1.01 | 0.54 | 35.9 | 12.6 | 15.4 | 17.5 | 1.27 | 0.63 | 1.39 |
| *Compsognathus* | 17.6 | 7.8 | 14.5 | 1.27 | 0.82 | — | — | — | — | — | — | — |
| *Compsognathus* | 27.3 | 13.4 | 24 | 1.37 | 0.88 | — | — | — | — | — | — | — |
| *Dalianraptor* | 23 | 22 | 19 | 1.78 | 0.83 | 22 | 5 | 12 | 13 | 1.36 | 0.76 | 2.6 |
| *Deinocheirus* | 230 | 140 | 226 | 1.59 | 0.98 | 246 | 110 | 104 | 186 | 1.63 | 0.87 | 1.69 |
| *Deinonychus* | 88.3 | 54 | 76.5 | 1.48 | 0.87 | 73.4 | 21.7 | 15.5 | 47.3 | 1.15 | 1.27 | 2.18 |
| *Deinonychus* | 93.7 | 55.3 | 78 | 1.42 | 0.83 | — | — | — | — | — | — | — |
| *Dilong* | 43 | 28 | 43 | 1.65 | 1 | — | — | — | — | — | — | — |
| *Dilophosaurus* | 105 | 70 | 63 | 1.27 | 0.6 | 115 | 41 | 44 | 45 | 1.13 | 0.53 | 1.1 |
| ek troodontid | 40 | 26 | 24 | 1.25 | 0.6 | — | — | — | — | — | — | — |
| *Epidendrosaurus* | 5.2 | 3.2 | 5.4 | 1.65 | 1.04 | 5.75 | 7.1 | 6.5 | 6 | 3.41 | 0.44 | 0.85 |
| *Epidendrosaurus* | 5.5 | 3.1 | 5.2 | 1.51 | 0.95 | — | 7.3 | 6.8 | 6.3 | — | 0.45 | 0.86 |
| *Erliansaurus* | 116 | 40 | 45 | 0.73 | 0.39 | 79 | 14 | 17 | 33 | 0.81 | 1.06 | 2.36 |
| *Falcarius* | 96 | 69 | 87 | 1.63 | 0.91 | 75 | 31 | 30 | 48 | 1.45 | 0.79 | 1.55 |
| *Guanlong* | 90.5 | 63.9 | 90* | 1.7 | 0.99 | — | — | — | — | — | — | — |
| *Gallimimus* | 115 | 53 | 100 | 1.33 | 0.87 | 105 | 32 | 36 | 74 | 1.35 | 1.09 | 2.31 |
| *Gorgosaurus* | 98 | 57 | 83 | 1.43 | 0.85 | — | — | — | — | — | — | — |
| *Hagryphus* | 122 | 95 | 99 | 1.59 | 0.81 | 8.7 | 5.4 | 4.5 | 6 | 1.83 | 0.61 | 1.11 |
| *Harpymimus* | 94 | 49 | 104 | 1.63 | 1.11 | 103 | 31 | 37 | 81 | 1.45 | 1.19 | 2.61 |
| *Herrerasaurus*# | 66 | 47 | 51 | 1.48 | 0.77 | 74 | 44 | 35 | 40 | 1.61 | 0.51 | 0.91 |
| *Huaxiagnathus* | 39.16 | 27.41 | 33.42 | 1.55 | 0.85 | 29.3 | 11.6 | 10.2 | 18.8 | 1.39 | 0.87 | 1.63 |
| *Jeholornis* | 36.7 | 17.8 | 19.2 | 1.01 | 0.52 | — | — | — | — | — | — | — |
| *Jinfengopteryx* | 21.37 | 15.26 | 21.07 | 1.7 | 0.99 | — | — | — | — | — | — | — |

continued

| Genera | McⅡ | Ⅱ-1 | Ⅱ-2 | PI | 2/Mc | McⅢ | Ⅲ-1 | Ⅲ-2 | Ⅲ-3 | PI | 3/(1+2) | 3/(1) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Jixiangornis* | 44.9 | 22.7 | 21.1 | 0.98 | 0.47 | — | — | — | — | — | — | — |
| *Juravenator* | 11.5 | 8 | 10 | 1.57 | 0.87 | 9 | 4 | 4.5 | 5.5 | 1.56 | 0.65 | 1.38 |
| *Limusaurus* | 12 | 6.2 | 4.3 | 0.88 | 0.36 | — | — | — | — | — | — | — |
| *Linheraptor* | 63 | 37 | 52 | 1.41 | 0.83 | 52 | 25 | 12 | 36 | 1.4 | 0.97 | 1.44 |
| *Microraptor* | 31.27 | 13.26 | 16.39 | 0.95 | 0.52 | 29.8 | 10.12 | 4.1 | 10.37 | 0.83 | 0.73 | 1.02 |
| *Microraptor* | 22.3 | 11.3 | 11.8 | 1.04 | 0.53 | 21 | 9.8 | — | 10.2 | — | — | 1.04 |
| *Nothronychus* | 141.2 | 102 | 133.4 | 1.67 | 0.94 | — | — | — | — | — | — | — |
| *Ornithomimus* | 100 | 36 | 90 | 1.26 | 0.9 | 98 | 31 | 23 | 74 | 1.31 | 1.37 | 2.39 |
| *Oviraptor* | 107 | 55 | 68 | 1.15 | 0.64 | 99 | 37 | 29 | 28 | 0.95 | 0.42 | 0.76 |
| *Raptorex* | 20 | 13 | 22 | 1.75 | 1.1 | — | — | — | — | — | — | — |
| *Sapeornis* | 57.1 | 30 | 27.7 | 1.01 | 0.49 | — | — | — | — | — | — | — |
| *Sapeornis* | 51.3 | 29 | 25.9 | 1.07 | 0.5 | — | — | — | — | — | — | — |
| *Sapeornis* | 52.9 | 30.6 | 26.6 | 1.08 | 0.5 | — | — | — | — | — | — | — |
| *Scipionyx* | 10.6 | 7.3 | 10.4 | 1.67 | 0.98 | 8.7 | 2.9 | 2.6 | 6.7 | 1.4 | 1.22 | 2.31 |
| *Shenzhousaurus* | 50* | 29 | 60 | 1.78 | 1.2 | 50 | 19 | 18 | 43 | 1.6 | 1.16 | 2.26 |
| *Sinornis* | 10.7 | 5.4 | 3.8 | 0.86 | 0.36 | — | — | — | — | — | — | — |
| *Sinornithoides* | 33.5 | 18.5 | 28.5 | 1.4 | 0.85 | 35 | 4.2 | 8.2 | 20.3 | 0.93 | 1.64 | 4.83 |
| *Sinornithomimus* | 54.7 | 19.9 | 59.9 | 1.46 | 1.1 | 53.8 | 13.9 | 14.6 | 42.9 | 1.33 | 1.51 | 3.09 |
| *Sinornithosaurus* | 63 | 32 | 35 | 1.06 | 0.56 | 60 | 18 | 9 | 23 | 0.83 | 0.85 | 1.28 |
| *Sinosauropteryx* | 10.2 | 4.7 | 6 | 1.05 | 0.59 | 8.3 | 3.4 | 2 | 3 | 1.01 | 0.56 | 0.88 |
| *Sinosauropteryx* | 17 | 7.9 | 8.9 | 0.99 | 0.52 | 13.8 | 4.7 | 3.6 | 5 | 0.96 | 0.6 | 1.06 |
| Compsognathid ? | 21 | 13.9 | 18.5 | 1.54 | 0.88 | — | — | — | — | — | — | — |
| *Struthiomimus* | 109 | 40 | 113 | 1.4 | 1.04 | 109 | 24 | 29 | 89 | 1.3 | 1.68 | 3.71 |
| *Struthiomimus* | 103 | 44 | 89 | 1.29 | 0.86 | 103 | 28 | 28 | 68 | 1.2 | 1.21 | 2.43 |
| *Syntarsus* | 26 | 13 | 17 | 1.15 | 0.65 | 26 | 10 | 9 | 12 | 1.19 | 0.63 | 1.2 |
| *Tanycolagreus* | 81 | 65 | 75 | 1.73 | 0.93 | 55 | 14 | 17 | 31 | 1.13 | 1 | 2.21 |
| *Tarbosaurus* | 75 | 34 | 62 | 1.28 | 0.83 | — | — | — | — | — | — | — |
| *Tianyuraptor* | 57 | 32 | 42 | 1.3 | 0.74 | 55 | 16 | 8 | 28 | 0.95 | 1.17 | 1.75 |
| *Tyrannosaurus* | 95 | 60 | 79 | 1.46 | 0.83 | — | — | — | — | — | — | — |
| *Velociraptor* | 50.8 | 31.3 | 45.8 | 1.52 | 0.9 | 45 | 17.6 | 10.1 | 32.2 | 1.33 | 1.16 | 1.83 |
| *Xiaotingia* | 24 | 15 | 25 | 1.67 | 1.04 | 24 | 8 | 4 | 15 | 1.13 | 1.25 | 1.88 |
| *Yixianornis* | 25.6 | 12.5 | 12.3 | 0.97 | 0.48 | — | — | — | — | — | — | — |
| *Yixianosaurus* | 36 | 26 | 38 | 1.78 | 1.06 | 31 | 9 | 8 | 22 | 1.15 | 1.29 | 2.44 |

Note: * estimated value; # values based on PVSJ 380, while those given for *Herrerasaurus* in Table 4 are based on the more complete but smaller PVSJ 373.

values are also present in more basal taxa such as *Coelurus* (1.78), *Tanycolagreus* (1.73), *Acrocanthosaurus* (1.76), and *Dilong* (1.65). Both *Anchiornis* (1.42) and *Archaeopteryx* (1.24~1.38) have values near the theropod median and *Microraptor* (0.95~1.04) has extremely low values.

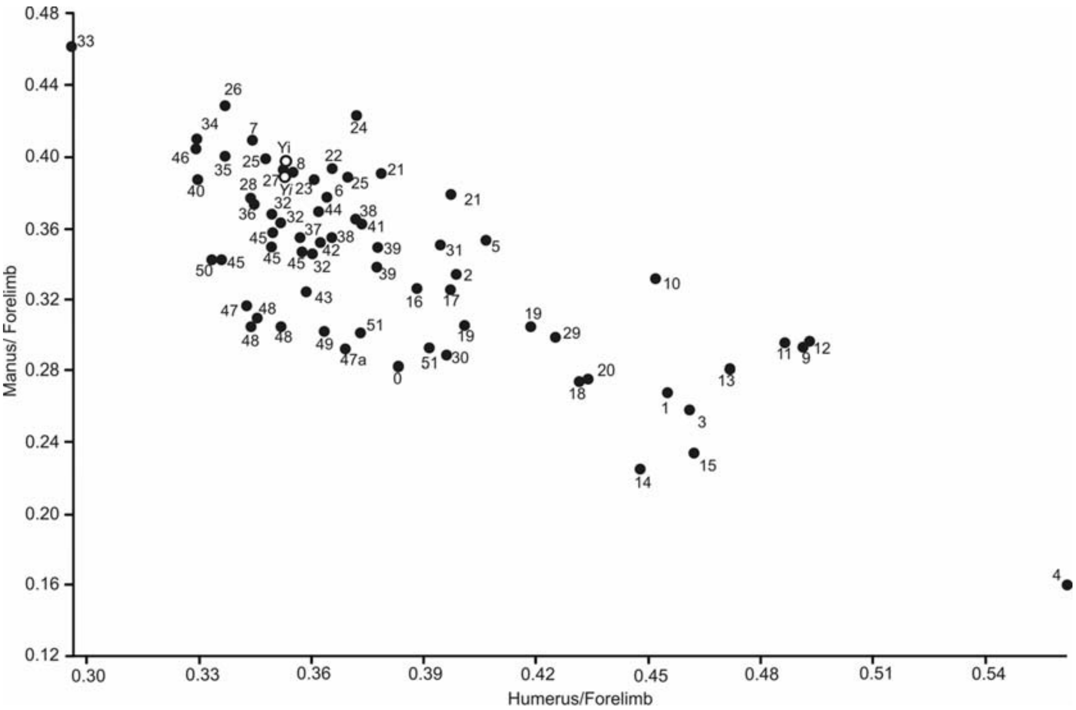

Fig. 5 Graph of the relationship between the log lengths of the humeri and mani of theropods

Manus length is the total length of Mc Ⅱ + Ph Ⅱ 1 + 2. Forelimb length is here measured as the combined lengths of the humerus, radius and manus. Here both *Raptorex* (13) and *Jixiangornis* (52) are treated as distinct genera, but see Fowler et al. (2011) and Li et al. (2010). The radius of *Dilong* was estimated based on values in *Guanlong*

Numerical abbreviations: 0. *Herrerasaurus*; 1. *Coelophysis*; 2. *Dilophosaurus*; 3. *Syntarsus*; 4. *Limusaurus*; 5. *Acrocanthosaurus*; 6. *Allosaurus*; 7. *Dilong*; 8. *Guanlong*; 9. *Albertosaurus*; 10. *Gorgosaurus*; 11. *Tyrannosaurus*; 12. *Tarbosaurus*; 13. *Raptorex*; 14. *Archaeornithomimus*; 15. *Gallimimus*; 16. *Harpymimus*; 17. *Ornithomimus*; 18. *Sinornithomimus*; 19. *Struthiomimus*; 20. *Deinocheirus*; 21. *Sinosauropteryx*; 22. *Scipionyx*; 23. *Juravenator*; 24. *Huaxiagnathus*; 25. *Compsognathus*; 26. *Coelurus*; 27. *Tanycolagreus*; 28. *Falcarius*; 29. *Alxasaurus*; 30. *Erliansaurus*; 31. *Nothronychus*; 32. *Caudipteryx*; 33. *Protarchaeopteryx*; 34. *Oviraptor*; 35. *Anchiornis*; 36. *Microraptor*; 37. *Bambiraptor*; 38. *Linheraptor*; 39. *Deinonychus*; 40. *Jinfengopteryx*; 41. *Sinornithoides*; 42. *Sinornithosaurus*; 43. *Xiaotingia*; 44. *Tianyuraptor*; 45. *Archaeopteryx*; 46. *Dalianraptor*; 47. *Jeholornis*; 48. *Sapeornis*; 49. *Sinornis*; 50. *Yixianornis*; 51. *Epidendrosaurus*; 52. *Jixiangornis*; Yi. *Yixianosaurus* [original measurements]; *Yi*. *Yixianosaurus* [maximum measurement interpretations]

These results do not support the assertion that penultimate phalangeal elongation is a strong indicator of advanced grasping ability within theropods (contra Currie and Chen, 2001). Ornithomimosaurs consistently have the highest penultimate phalangeal lengths, in either digit Ⅱ or Ⅲ, yet their hand has reduced ligament pits and poorly recurved claws with weakly developed flexor tubercles (Nicholls and Russell, 1985; Makovicky et al., 2004), traits not associated with a strong grasping manus. We find that "advanced grasping" theropods do not show a consistent or distinctive pattern of manual proportions compared to other theropods. Certain "advanced graspers", such as *Microraptor*, possess phalangeal portions suggesting they had much lower grasping capabilities than typical theropods, lower even than in large bodied basal forms such as coleophysoids or neotetanurans (Table 4). Although elongated distal phalanges may have behavioural or ecological significance within other clades (Fröbisch and Reisz, 2009) we suggest caution about using them within non-avian theropods. The elevated scores seen in ornithomimosaurs, which are suspected to be poor graspers (Nicholls and Russell, 1985; Makovicky et al., 2004) and in the second digit of *Acrocanthosaurus*, whose forelimbs could not have

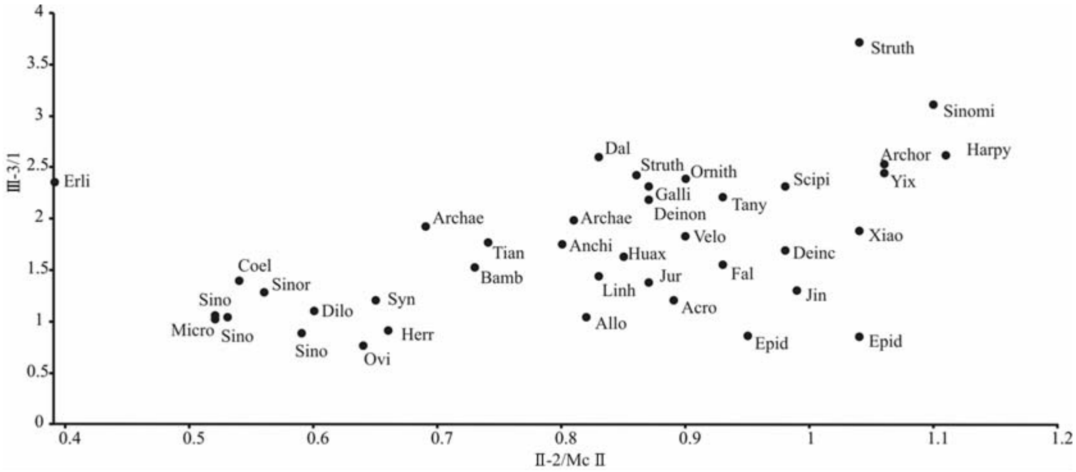

Fig. 6 Graph of relative penultimate phalanx lengths for digits Ⅱ and Ⅲ of theropods

Note that ornithomimosaurs score highest on both indices

Abbreviations: Acro. *Acrocanthosaurus*; Allo. *Allosaurus*; Anchi. *Anchiornis*; Archae. *Archaeopteryx*; Archor. *Archaeornithomimus*; Bamb. *Bambiraptor*; Coel. *Coelophysis*; Dal. *Dalianraptor*; Deinc. *Deinocheirus*; Deinon. *Deinonychus*; Dilo. *Dilophosaurus*; Epid. *Epidendrosaurus*; Erli. *Erliansaurus*; Fal. *Falcarius*; Galli. *Gallimimus*; Harpy. *Harpymimus*; Herr. *Herrerasaurus*; Huax. *Huaxiagnathus*; Jin. *Jinfengopteryx*; Jur. *Juravenator*; Linh. *Linheraptor*; Micro. *Microraptor*; Ornith. *Ornithomimus*; Ovi. *Oviraptor*; Scipi. *Scipionyx*; Sino. *Sinosauropteryx*; Sinor. *Sinornithosaurus*; Sinomi. *Sinornithomimus*; Struth. *Struthiomimus*; Syn. *Syntarsus*; Tany. *Tanycolargrues*; Tian. *Tianyuraptor*; Velo. *Velociraptor*; Xiao. *Xiaotingia*. Yix. *Yixianosaurus*

been the primary means of securing prey items (Senter and Robins, 2005), contradict the predictive relationship between this index and enhanced grip capabilities.

Despite this, we support Xu and Wang's (2003) assertion that the manus of *Yixianosaurus* is well adapted for grasping. Although individual phalangeal proportions alone may not be enough to infer grasping capability, the combination of multiple elevated phalangeal indices with other anatomical signals suggests this diagnosis. The robust nature of the digits, including digit Ⅲ, and the presence of deep collateral ligament pits and well developed ginglymoidal surfaces indicate a manus capable of a robust grip. We suggest that this suite of features more accurately reflects the potential for grasping in theropods than any single phalangeal ratio. Each index documents an adaptation that may be necessary, but in itself is not sufficient, to increase grasping function of the manus. It is the combination of characters that supports the idea that the manus of *Yixianosaurus* possessed a level of raptorial functionality similar to that seen in *Tanycolagreus*, *Coelurus*, or *Deinonychus*.

## 5.3 Ecology

The Dawangzhangzi Beds of the Yixian Formation have yielded six non-avian theropods (*Yixianosaurus*, *Sinosauropteryx*, *Tianyuraptor*, *Sinornithosaurus haoiana*, an unnamed troodontid and an unnamed dromaeosaurid (NGMC 91)), two ornithischians, and multiple birds, pterosaurs, squamates and other vertebrates (Ji et al., 2001; Xu and Norell, 2006; Zhou, 2006; Benton et al., 2008; Zheng et al., 2009). The Dawangzhangzi non-avian theropods are similar to one another in estimated body mass, with all the predatory taxa save *Tianyuraptor* between 1 and 5 kg. Sympatric predators usually have different prey preferences to partition food sources and reduce interspecific competition (Ray and Sunquist, 2001; Farrell et al., 2000; Carvalho and Gomes, 2004). Although prey choice overlap is still present in modern sympatric prey systems, some degree of prey choice partitioning may be hypothesized to have been present between the Dawangzhangzi theropods.

The small compsognathid *Sinosauropteryx* is known from multiple specimens with gut contents to have fed upon small lizards and mammals less than 50 g in size (Currie and Chen, 2001). Due to the shortened forelimbs and sub-raptorial manual claws, *Sinosauropteryx* most likely used its jaws as its primary means of prey capture.

Dromaeosaurids, with their long forelimbs, trenchant manual unguals and enlarged and recurved second pedal ungual, have been suggested to have fed on relatively larger prey items, even greater than their own body mass (Carpenter, 1998; Maxwell and Ostrom, 1995). Although the jaws of dromaeosaurids are not considered to be extremely powerful (Sakamoto, 2010; but see Gignac et al., 2010) the combination of jaws, forelimbs and hind limbs would potentially have allowed dromaeosaurids to subdue relatively large prey.

Without cranial material it is difficult to reconstruct the predatory abilities of *Yixianosaurus*, though the elongate and robust proportions of the forelimbs suggest a different mode of prey capture to contemporaneous theropods. The robustness of the forelimb of *Yixianosaurus* is best illustrated through direct comparisons to the holotype of *Microraptor gui* (IVPP V 13352), whose forelimbs are similar in length although the individual forelimb bones of *Yixianosaurus* are typically twice the diameter of their equivalents in *M. gui* (Fig. 7). This robustness is unusual in maniraptoran

Fig. 7　Comparison of the forelimbs of *Yixianosaurus longimanus* IVPP V 12638 (A) and *Microraptor gui* IVPP V 13352 (B)

Due to the extensive damage to the right humerus of *Yixianosaurus* its size and shape have been reconstructed (dotted lines) based on the more complete left humerus theropods without reduced forelimbs. The long yet robust forelimb of *Yixianosaurus* contrasts with the reduced forelimb of compsognathids and the long gracile forelimb of dromaeosaurids, and suggests a different prey capture strategy than those employed by similar-sized Jehol theropods. The difference in forelimb morphology among these three taxa suggests differential use of the arms during predation, potentially allowing for ecological separation.

### 5.4 Feathers

*Yixianosaurus* possesses elongated contour feathers on its forelimbs, which though incomplete are significantly longer than the humerus at over 100 mm in length. These integumentary structures do not resemble the typical "downy" feathers of more basal coelurosaurs (Chen et al., 1998; Xu et al., 1999, 2004) but are closer to the feathers of oviraptorosaurians and paravians (Ji et al., 1998; Xu et al., 2004). Based on our phylogenetic reconstruction and direct comparisons, the placement of *Yixianosaurus* outside advanced maniraptorans suggests that the origin of large pennaceous feathers occurred earlier within theropods than previously suggested. The presence of large non-downy feathers on the therizinosaurian *Beipiaosaurus* (Xu et al., 2009a) and filamentous feathers in the alvarezsauroid *Shuvuuia* (Schweitzer et al., 1999) hint that a complex evolution of feather structures may have been present at the base of Maniraptora, with individual lineages modifying these structures, including by reducing them. Also of interest is that although these feathers are large and similar in length to those on the forewing of *Microraptor gui* (Hone et al., 2010), they probably had little aerodynamic function because the robustness of *Yixianosaurus* suggests an animal significantly heavier than *Microraptor*. The presence of pennaceous feathers in a basal maniraptoran reinforces the hypothesis that contour feathers first developed for display purposes and were later co-opted into a locomotor role within advanced paravians (Xu et al., 2009a).

## 6 Conclusion

Reinterpretation of the small maniraptoran theropod *Yixianosaurus longimanus*, and incorporating it for the first time into a phylogenetic analysis, has provided multiple key pieces of information for our understanding of maniraptoran evolution and the ecology of the Jehol Biota. The evidence for some level of carnivory in this taxon, coupled with its placement at the base of Maniraptora, has implications for maniraptoran dietary reconstructions. The presence of large contour feathers indicates that true feathers were present earlier than previously supposed. The evidence of niche partitioning between similar-sized predatory theropods allows for a deeper understanding of the trophic interactions and the ecology of the fauna from the Dawangzhangzi Beds. Although *Yixianosaurus* is incomplete, it is highly informative for such a fragmentary specimen. It also suggests that, as more specimens and taxa are discovered in the Jehol Group, our knowledge of myriad aspects of the paleoecology and diversity within this community will only increase.

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