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The systematic position of the enigmatic theropod dinosaur *Yixianosaurus longimanus*

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Abstract *Yixianosaurus longimanus* is a small theropod from the Lower Cretaceous of western Liaoning Province, China. It was originally suggested to be a derived maniraptoran, but this interpretation was challenged by a recent study that proposed instead that *Y. longimanus* was a basal maniraptoran. Given that the systematic position of this taxon will affect our understanding of such broad issues as the evolution of the theropod forelimb and plumage, it is important to carefully evaluate both systematic hypotheses and determine which is better supported. Here we review all available morphological features in *Y. longimanus* that appear informative with regard to its systematic position. We demonstrate that this small theropod is a basal paravian and most likely a basal deinonychosaurian, a result that conforms to the original interpretation of this specimen. The hypothesis that *Y. longimanus* is a basal paravian is consistent with the probable presence of pennaceous feathers in this taxon, and avoids implying a complicated evolutionary history for the maniraptoran forelimb.

Key words Liaoning, Early Cretaceous, Maniraptora, Paraves, systematics

1 Introduction

The small theropod *Yixianosaurus longimanus* is represented only by a single specimen housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, and cataloged as IVPP V 12638. This specimen preserves both halves of the pectoral girdle, the forelimbs, several ribs and gastralia, and associated feathers (Fig. 1A). Although the known material is limited, the preserved pectoral girdle and forelimbs show many features that are potentially informative with respect to the systematic position of *Y. longimanus*, and which suggest that this species is a derived maniraptoran (Xu and Wang, 2003).

Dececchi et al. (2012) recently provided an informative redescription of *Y. longimanus*, and carried out a numerical phylogenetic analysis that recovered *Y. longimanus* as a basal maniraptoran. Based on this result and the general morphology of *Y. longimanus*, these authors further proposed that the early history of Maniraptora was characterized by both strong mosaic evolution and the presence of a high level of disparity in forelimb morphology. Most

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significantly, *Y. longimanus* probably has pennaceous feathers, and placement of this taxon as a basal maniraptoran would imply that pennaceous feathers appeared early in maniraptoran evolution (Dececchi et al., 2012). Given its broad potential impact on our understanding of the evolution of feathers and other features in theropods close to the origin of birds, the new phylogenetic hypothesis proposed by Dececchi et al. (2012) deserves careful evaluation.

In this paper, we comment on the evidence presented by Dececchi et al. (2012) to support phylogenetic placement of *Y. longimanus* near the base of Maniraptora, list phylogenetically informative features of this taxon that support an alternative placement, discuss some paleobiological implications of these features, and finally conduct a numerical analysis to rigorously test both phylogenetic hypotheses. It should be noted that we identify the three manual digits of *Y. longimanus* and other maniraptorans as II-III-IV (Xu et al., 2009a), rather than I-II-III as in many other studies (Bever et al., 2011; Tamura et al., 2011; Towers et al., 2011; Dececchi et al., 2012).

2 Comment on *Y. longimanus* as a basal maniraptoran

Dececchi et al. (2012) listed a few osteological features that they considered to support placement of *Y. longimanus* near the base of the Maniraptora. However, these features are only doubtfully present in *Y. longimanus* and/or are not clearly indicative of basal rather than derived maniraptoran affinities. We comment on each of the features below:

(1) Absence of subglenoid fossa. The subglenoid fossa seen in some theropods is a shallow depression below the glenoid and posteroventral to the coracoid tubercle on the lateral side of the coracoid. Dececchi et al. (2012) regarded this feature as absent in *Y. longimanus*, but it is not possible to determine whether the fossa is present in IVPP V 12638 because both coracoids are preserved in medial view in this specimen (Fig. 1A, B). Furthermore, the subglenoid fossa is essentially a synapomorphy of the Deinonychosauria. This structure is unquestionably known only in dromaeosaurids, troodontids, *Archaeopteryx* and *Anchiornis* (Makovicky et al., 2005; Xu et al., 2011b), despite the presence of a superficially similar feature in ornithomimosaurians (Makovicky et al., 2005). Even if a subglenoid fossa could be shown to be absent in *Y. longimanus*, this would not represent evidence excluding this species from the Paraves because basal avialans appear to lack a subglenoid fossa (Xu et al., 2011b).

(2) Absence of laterally facing glenoid that extends onto external surface of scapula. Because the glenoid regions of both scapulae of V 12638 are poorly preserved, it cannot be determined whether the glenoid fossa extends onto the external surface. Dececchi et al. (2012:121) reported that “[a]t least in medial view, the glenoid in *Yixianosaurus* appears entirely restricted to the posterior surface of the coracoid and scapula” , but it is not possible to rule out extension of the glenoid onto the lateral surface based entirely on the appearance of the scapula in medial view. Furthermore, lateral orientation of the glenoid fossa and extension of this feature onto the external surface of the scapula are not necessarily equivalent. In such

deinonychosaurians as *Mei* and *Sinovenator*, lateral orientation of the glenoid fossa results from realignment of the scapula rather than extension of the fossa. Even if Dececchi et al. (2012) are correct in their assertion that the glenoid fossa was restricted to the posterior surface of the scapula in *Y. longimanus*, this taxon may have resembled other paravians (Xu et al., 2002a; Makovicky et al., 2005; Turner et al., 2007) in having a laterally directed glenoid depending on the orientation of the scapula.

(3) Absence of median ridge dividing proximal articular surface of ulna. Such a ridge has been suggested to be a diagnostic feature for the Paraves (Sereno, 1999), but in some paravians this feature is minimally developed or even absent. In V 12638, the proximal end of the ulna is not preserved in the right forelimb and only partially preserved in the left. Furthermore, the left ulna is exposed in medial view, rendering it impossible to tell whether a sharp ridge divides the proximal end of this bone into two articular surfaces.

(4) Metacarpal IV relatively straight. A strongly bowed metacarpal IV (equivalent to metacarpal III of Dececchi et al. (2012)) is seen in *Archaeopteryx*, *Jeholornis*, enantiornithines, and dromaeosaurids, but is absent in troodontids and in some basal avialans including

Fig. 1 The holotype of *Yixianosaurus longimanus* (IVPP V 12638)
A. photograph; B. left scapulocoracoid in medial view; C. left humerus in anterior view; D. close-up of right carpal region in ventral view; scale bar equals 4.5 mm in (A), 9.5 mm in (B), 10 mm in (C), and 32 mm in (D)

scansoriopterygids, sapeornithids, and confuciusornithids (Xu et al., 2011b). In fact, the relatively straight and thick metacarpal IV of *Y. longimanus* is somewhat similar to those of *Xiaotingia* (Xu et al., 2011b) and *Anchiornis* (Hu et al., 2009b; Xu et al., 2009b), and thus does not militate against paravian affinities.

(5) Absence of scar near lateral edge of deltopectoral crest. A prominent scar on the posterolateral surface of the humerus near the distal end of the deltopectoral crest is present in a variety of deinonychosaurians including some derived dromaeosaurids and troodontids (Norell and Makovicky, 2004; Xu et al., 2011a), but this feature is not obviously developed at least in some basal troodontids such as *Sinovenator* (Xu, 2002). Furthermore, whether *Y. longimanus* has a scar near the lateral edge of the deltopectoral crest is uncertain due to the poor preservation of the specimen (Fig. 1C).

Dececchi et al. (2012) also presented several other features that they interpreted as evidence against the hypothesis that *Y. longimanus* is a paravian, including: distally expanded scapula, absence of medial inflection of ventral portion of coracoid, short ulna, large number of carpals, semilunate carpal articulating only with metacarpals II and III, relatively long manual digit II, relatively long metacarpal II, and relatively robust digit IV. However, none of these features provides convincing evidence weighing against the paravian affinities of *Y. longimanus* (Fig. 2A).

Distal expansion of the scapula is not restricted to non-paravian theropods, but in fact occurs in some paravians. In scansoriopterygids (Zhang et al., 2008) and deinonychosaurians (Xu, 2002) such as *Mei* (IVPP V 12733), the degree of distal expansion is even greater than that seen in *Y. longimanus*. Medial inflection of the ventral portion of the coracoid is not an accurate description of the modified morphology of the coracoid seen in derived theropods (Xu, 2002). Even if the feature were a valid one, its presence in *Y. longimanus* would be difficult to assess because of the manner of preservation and exposure of the coracoids in V 12638. Comparing the medial side of the coracoid of *Y. longimanus* with the equivalent surface in other paravians, such as *Sinovenator*, reveals no substantial differences (Fig. 2B).

Y. longimanus has a relatively short ulna, but the proportional length of this element appears to be within the range previously known for paravians. The ulna and radius are not completely preserved on either side of the skeleton. The better preserved right radius, which is missing the proximal end, measures about 63 mm (72% of the humeral length). A complete ulna of *Y. longimanus* is estimated to have been more than 80% as long as the humerus, as in most basal deinonychosaurians.

Dececchi et al. (2012) and Xu and Wang (2003) identified four carpals, but this is a misinterpretation. The right carpus of V 12638, which is better-preserved than the left, comprises only three bones: a radiale, a semilunate carpal, and a distal carpal that we here identify as distal carpal 4 although Dececchi et al. (2012) considered it to be an ulnare (Fig. 1D). Others have referred to the same element as “distal carpal X” in basal birds and other basal paravians (Chiappe et al., 2007). The “intermedium” identified by Dececchi et al. (2012)

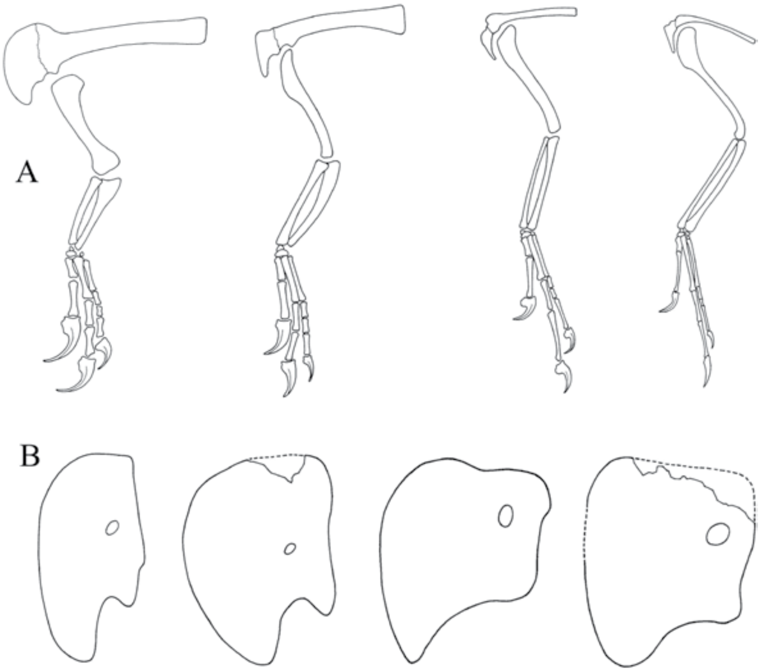

Fig. 2　Pectoral girdle and forelimbs of selected coelurosaurians
A. comparative drawings of pectoral girdle and forelimbs of the tyrannosauroid *Yutyrannus* (left), the oviraptorid *Khaan* (middle-left), the paravian *Yixianosaurus* (middle-right), and the paravian *Archaeopteryx* (right); B. comparative drawings of the coracoids of the ornithomimosaurian *Sinornithomimus* (left), the alvarezsauroid *Haplocheirus* (middle-left), the paravian *Yixianosaurus* (middle-right), and the troodontid *Sinovenator* (right); not to scale

is in fact the proximal part of the semilunate carpal, based on its proximal convexity and its position between the main part of the semilunate carpal and the surface of the radiale that normally articulates with the semilunate carpal in maniraptoran theropods. A crack extending across the entire carpal region divides the semilunate carpal into two parts (Fig. 1D), and separates a block of matrix preserving the radiale, a small part of the semilunate carpal, and the distal portions of the radius and ulna from one preserving distal carpal 4, the bulk of the semilunate carpal, and the proximal part of the manus. The blocks have been glued together in such a way that the distal one is slightly displaced laterally relative to the proximal one, and the proximally positioned broken surface of the larger part of the semilunate carpal is still visible. Correct alignment of the two blocks would result in a complete semilunate carpal identical in ventral outline to those of other basal paravians.

Dececchi et al. (2012) and Xu and Wang (2003) claimed that the semilunate carpal of *Y. longimanus* contacts only metacarpals II and III, but this statement is not convincing given that the lateral end of the semilunate carpal is obscured by distal carpal 4 (Fig. 1D). Furthermore, the shapes and positions of the semilunate carpal and distal carpal 4 suggest that the semilunate carpal contacts all three metacarpals as in derived maniraptorans (Xu, 2002).

The relatively long manual digit II and metacarpal II of *Y. longimanus*, and the relatively robust manual digit IV, do not weigh against paravian affinities given that these features are also present in *Anchiornis*, *Xiaotingia*, and at least some troodontids (Xu, 2002; Hu et al., 2009; Xu et al., 2011b).

In summary, *Y. longimanus* does not have a single morphological feature that unambiguously supports basal maniraptoran as opposed to paravian affinities. Without exception, the features adduced by Dececchi et al. (2012) as evidence that *Y. longimanus* is not a paravian are impossible to confirm as present in the only known specimen of this taxon because of preservational shortcomings and/or also known in some other paravians.

3 Morphological evidence that *Y. longimanus* is a paravian

Many features present in *Y. longimanus* support identification of this taxon as a maniraptoran, such as the bowed ulna and thin radius (contra Dececchi et al. (2012), the radius is much thinner than the ulna, based on the better-preserved right forearm). A variety of additional features suggest that *Y. longimanus* occupies a derived position within Maniraptora, as follows:

(1) Scapula short and slender. As in some paravians, the scapula is relatively slender (length/minimum width ratio about 15.0) and short (about 70% of humeral length) in *Y. longimanus* (Fig. 2A). A scapula that is considerably shorter than the humerus has been listed as a derived maniraptoran feature (Xu et al., 1999; Makovicky et al., 2005; Zanno and Makovicky, 2011), but Dececchi et al. (2012) claimed that this feature is widely distributed among theropods. Among non-paravian theropods, the scapula is significantly shorter than the humerus only in *Dilong* (Xu et al., 2004). However, the scapula of *Dilong* is very robust (length/minimum width ratio about 6.0), in contrast to that of *Y. longimanus*. Several other basal coelurosaurs have a scapula that is only slightly longer than the humerus, but in these cases the scapula is also relatively robust (length/minimum width ratio less than 10.0). The maniraptorans *Erlianosaurus* and *Gigantoraptor* and the compsognathid *Huaxiagnathus* have been suggested to have a short scapula (Dececchi et al., 2012), but the scapulae are not completely preserved in *Erlianosaurus* and *Gigantoraptor* (Xu et al., 2002b, 2007) and the measurements of *Huaxiagnathus* by Dececchi et al. (2012) are in conflict with the original description (Hwang et al., 2004). Furthermore, most reports of proportionally short scapulae in coelurosaurs have been based on measurements of juvenile specimens (Dal Sasso and Maganuco, 2011), and scapular length has been shown to be positively allometric over theropod ontogeny (Currie, 2003). Consequently, very short and slender scapular proportions are restricted to paravians among theropods, though some paravians underwent reversal to the primitive condition of having a scapula that is longer than the humerus.

(2) Coracoid elongated parallel to long axis of scapulocoracoid. As in oviraptorosaurians and paravians, the coracoid of *Y. longimanus* is elongated parallel to the long axis of the

scapulocoracoid (ratio of anteroposterior length to dorsoventral depth at the level of the scapular suture about 1.2; Fig. 2B). In other theropods, the coracoid is deeper dorsoventrally than long anteroposteriorly (Fig. 2B).

(3) Humerus robust. A robust arm is a diagnostic feature for the Paraves (Xu et al., 2011b), though in some derived deinonychosaurians the arm is secondarily slender. The robustness of the arm can be assessed based on the diameter of the humerus relative to that of the femur, but this is impossible in *Y. longimanus* because the hindlimbs are not preserved. However, the mediolateral width of the humerus is much greater than the width of the scapular blade, a condition known only among paravians.

(4) Internal tuberosity of humerus long and proximally projecting. In basal paravians, including deinonychosaurians and basal avialans such as sapeornithids and enantiornithines, the medially situated internal tuberosity of the humerus is proximodistally elongated and indeed projects farther proximally than the humeral head. In non-paravian theropods, the internal tuberosity is either small or triangular in shape, and is positioned distal to the level of the humeral head. *Y. longimanus* resembles other paravians in possessing a proximodistally long and proximally projecting internal tuberosity.

(5) Lateral process of ulna subequal to coronoid process in size. In a typical theropod ulna, the proximal articular surface of the ulna is partly on the proximal surface of the lateral process, and partly on the proximal surface of the coronoid process. In most non-paravian theropods the lateral process is much smaller than the prominent coronoid process, but in paravians the two processes are subequal in size. Although the lateral process is not visible in V 12638, it is clear that the coronoid process is relatively small, reflecting the paravian condition.

(6) 'Semilunate' distal carpal transversely wide and proximodistally thick. A transversely wide 'semilunate' distal carpal characterizes derived maniraptorans, including the Oviraptorosauria and the Paraves (Fig. 2A). The 'semilunate' distal carpal is much narrower transversely in more basal theropods, although some therizinosauroids display a unique condition in that they possess a large 'semilunate' carpal formed by two distal carpals. Also, the 'semilunate' distal carpal is proximodistally thick, due to the strong, convex proximal expansion of the element in oviraptorosaurians and paravians. In other theropods, including therizinosauroids, the 'semilunate' distal carpal is much wider transversely than thick proximodistally.

(7) Metacarpal IV long. Metacarpal IV is sub-equal in length to metacarpal III in oviraptorosaurians and paravians, rather than significantly shorter than the latter metacarpal as in more basal coelurosaurs including *Ornitholestes*, therizinosaurs, and alvarezsauroids. In *Y. longimanus* metacarpal IV is nearly as long as metacarpal III, as in derived maniraptorans and ornithomimosaurians. The latter clade represents the only known basal coelurosaurian group in which metacarpal IV is long.

(8) Manual phalanx II-1 long and slender. Manual phalanx II-1 is both slender (ratio of

maximum length to minimum dorsoventral shaft diameter about 10.0) and long (considerably longer than II-2) in *Y. longimanus*, a feature shared with oviraptorosaurians and paravians. In more basal coelurosaurs, apart from some ornithomimosaurians, manual phalanx II-1 is relatively robust and only subequal in length to phalanx II-2.

(9) Manual phalanx III-2 significantly elongated. In *Y. longimanus* manual phalanx III-2 is longer than metacarpal III, and is much longer than III-1 (III-2/III-1 length ratio more than 1.4). Such an elongated III-2 is known only in certain ornithomimosaurians, and in basal paravians such as *Anchiornis* and *Xiaotingia*. In other maniraptorans, III-2 is considerably shorter than metacarpal III, and the III-2/III-1 length ratio is much lower.

(10) Manual phalanx IV-3 long. Manual phalanx IV-3 is considerably longer than IV-1 and IV-2 combined in *Archaeopteryx*, *Xiaotingia*, *Anchiornis*, and other deinonychosaurians, but is relatively short in other theropods with the exception of ornithomimosaurians (Xu et al., 2011b). *Y. longimanus* shares the derived elongation of IV-3 with the Deinonychosauria. Dececchi et al. (2012) claimed that manual phalanx IV-3 is also longer than the combined length of IV-1 and IV-2 in *Erliansaurus*, *Scipionyx* and *Tanycolagreus*, and stated (p. 127) that this also “is suspected” to be true of *Coelurus* and *Protarchaeopteryx*. However, manual digit IV is so incompletely preserved in the known material of *Coelurus* (Carpenter et al., 2005b) that there appears to be no firm empirical basis for “suspecting” unusual elongation of phalanx IV-3 in this taxon. Similarly, the proximal phalanges of manual digit IV are not preserved in the holotype of *Tanycolagreus*, TPII 2000-09-29 (Carpenter et al., 2005a). In a manus (AMNH 587) originally considered to belong to *Ornitholestes* (Osborn, 1903), but referred to *Tanycolagreus* by *Carpenter* et al. (2005b), illustrations by Osborn (1903:figs. 2-3) suggest that phalanx IV-3 is subequal in length to IV-1 and IV-2 combined rather than significantly longer. In *Protarchaeopteryx* manual phalanx IV-3 is likewise only subequal in length to IV-1 and IV-2 combined (Ji et al., 1998). The length of manual phalanx IV-3 at least slightly exceeds that of IV-1 and IV-2 combined in *Erliansaurus* (Xu et al., 2002b) and *Scipionyx* (Dal Sasso and Maganuco, 2011), as correctly noted by Dececchi et al. (2012). However, *Y. longimanus* differs from these taxa and from most other theropods in that manual phalanx IV-3 is considerably longer than IV-4, a feature known to occur in basal paravians.

These features are known either in both oviraptorosaurians and paravians (Characters 2, 5-8), or only in paravians (Characters 1, 3, 4, 9, and 10), but are absent in other theropod groups (except that characters 7-10, most of which involve elongation of the penultimate phalanges of the manus, are also present in some ornithomimosaurians). These features, in combination with more broadly distributed maniraptoran character states present in *Y. longimanus*, strongly suggest that this species is a derived maniraptoran as originally proposed by Xu and Wang (2003) rather than a basal maniraptoran as proposed by Dececchi et al. (2012). It is noteworthy that some of the manual features seen in *Y. longimanus* are shared by both ornithomimosaurians and paravians, but absent in other theropods. These features are best explained as independently evolved in the two groups, presumably in response to analogous though not necessarily identical functional requirements.

Within the Paraves, *Y. longimanus* is more likely to be a deinonychosaurian than an avialan. *Y. longimanus* lacks avialan autapomorphies, but possesses several derived features that appear to be present only in certain deinonychosaurians. Admittedly these features are subtle, and their absence in non-deinonychosaurian taxa still needs confirmation on the basis of new, better preserved specimens and additional examination of previously described material. They include:

(11) Manual penultimate phalanges with dorsoventrally high distal condyles. The distal condyles of the manual penultimate phalanges are proximodistally short and dorsoventrally high in *Y. longimanus*, as in other deinonychosaurians including *Anchiornis*, *Xiaotingia*, and *Archaeopteryx* (Xu, 2002; Wellnhofer, 2009). In most other theropods, the distal condyles of the manual penultimate phalanges are proximodistally long and dorsoventrally low.

(12) Tips of manual unguals III and IV do not protrude far ventrally. In *Y. longimanus* manual unguals III and IV are strongly dorsally arched, so that if the proximal articular surfaces of these unguals are positioned vertically their tips do not extend far beyond the level of the flexor tubercles in the ventral direction. The same condition exists in other deinonychosaurians, including *Anchiornis*, *Xiaotingia*, and *Archaeopteryx* (Xu, 2002; Senter, 2007; Wellnhofer, 2009). In most other theropods, however, the tips of the corresponding unguals extend well ventral to the flexor tubercles.

(13) Manual ungual III with prominent flexor tubercle. The flexor tubercle of manual ungual III is prominent and subequal in height to the proximal articular facet in *Y. longimanus*, as in other deinonychosaurians including *Anchiornis*, *Xiaotingia*, and *Archaeopteryx* (Xu, 2002; Senter, 2007; Wellnhofer, 2009). In most other theropods, the flexor tubercle of this ungual is relatively small, being much lower than the proximal articular facet.

Interestingly, characters 11-13 all relate to the manual phalanges, and indeed to the unguals or their articular relationship with the penultimate phalanges. These features may indicate that the grasping function of the deinonychosaurian hand was enhanced or at least modified to some degree, relative to the condition in other theropods. In particular, the enlarged flexor tubercle on manual ungual III would have increased the moment arm of the flexor musculature that inserted on this structure, allowing for more forceful flexion. The specific functional significance of the dorsally arched unguals and proportionally high distal articular surfaces of the penultimate phalanges is difficult to determine without explicit biomechanical analysis of the manus.

It is notable that Senter (2006) investigated the ranges of motion in the hands of the dromaeosaurids *Deinonychus* and *Bambiraptor*, and found that the ability of each digit to flex towards the palmar surface of the metacarpus was relatively limited. He concluded that *Deinonychus* would not have been capable of gripping objects in only one hand, whereas *Bambiraptor* would only have been able to do so only because specialized features of digits II and IV made these digits partially opposable (Senter, 2006). However, Senter' s (2006) reconstructions of articulated hands in various postures imply that even *Deinonychus* could have flexed its fingers enough to allow one-handed grasping of objects that were large relative to the manus, and in the absence of articular cartilage it is possible that the range of flexion at some manual joints was underestimated in any case.

4 Manual grasping capability in *Y. longimanus*

Dececchi et al. (2012) presented a large data set consisting of manual measurements for a variety of theropods, and noted that *Y. longimanus* is characterized by a number of features that appear linked to strong grasping ability. The flexor tubercles of all three manual unguals are well developed, the non-ungual phalangeal portion of each digit is elongate relative to the corresponding metacarpal, and the penultimate phalanges of digits III and IV are elongate relative to metacarpal III and phalanx IV-1 respectively. While large manual flexor tubercles are characteristic of paravians (Rauhut, 2003), high values of various length ratios that are plausibly related to grasping display a complex and homoplastic distribution at least among coelurosaurian theropods and do not always occur together (Dececchi et al., 2012). Nevertheless, all of the indices considered by Dececchi et al. (2012) suggest that *Y. longimanus* was a capable grasper.

The grasping manus of *Y. longimanus* may have been used in predation, as suggested by Dececchi et al. (2012). However, grasping ability would also be useful in carrying out other types of behaviour, perhaps most notably arboreal climbing, and we disagree with Dececchi et al. (2012) that the grasping hand of *Y. longimanus* should be viewed as evidence that this species was a carnivore rather than a herbivore. Similarly, Dececchi et al. (2012) suggested that the "raptorial" proportions and large flexor tubercles of the manual unguals of *Y. longimanus*, in addition to the robustness of the forelimb and "prominent brachial flexor attachments on the distal humerus" (Dececchi et al., 2012:128), provided additional evidence of predatory habits. However, all of these features are open to alternative interpretations. Distinguishing theropod unguals adapted to arboreal climbing from those adapted to predatory grasping is a difficult problem, as both tend to be deeply curved. A widely accepted qualitative criterion (Yalden, 1985; Feduccia, 1993; Pike and Maitland, 2004) is the greater transverse compression of unguals adapted for climbing as opposed to predation, but this cannot be applied to V 12638 because none of the unguals is exposed in dorsal or ventral view. However, the sharp and abruptly tapering distal tips of the keratin sheaths of the manual unguals seen in *Y. longimanus* are if anything more compatible with the "needle-like" morphology expected in a climber than the blunter and less delicate configuration expected in a predator (Yalden, 1985; Pike and Maitland, 2004).

The forelimbs of *Y. longimanus* are indeed robustly constructed (Dececchi et al., 2012), but this condition is broadly characteristic of basal paravians rather than unique to *Y.*

longimanus (Xu et al., 2011b). The robustness of the paravian forelimb is an unusual feature that is difficult to associate with predation or any other specific behaviour, though it might be linked to the production of large muscular forces that require a heavily built skeleton to withstand. However, the exertion of such forces could be linked to climbing or to behaviours such as wing assisted incline running (Dial, 2003), stability flapping (Fowler et al., 2011), or even flight (Xu et al., 2011b), rather than to predation. Finally, the size of the attachment area on the distal part of the humerus for flexor musculature is difficult to assess in V 12638, given that the distal end is preserved only in the case of the left humerus and is exposed in medial rather than flexor view. In sum, we believe that the grasping features seen in the hand of *Y. longimanus*, like the other morphological details that can be discerned in V 12638, provide no clear basis for assessing the diet of this taxon.

5 Numerical phylogenetic analysis

Dececchi et al. (2012) conducted a numerical phylogenetic analysis in which *Y. longimanus* was added to the recently published dataset of Zanno (2010), and recovered *Y. longimanus* as a basal maniraptoran. However, examination of the scorings presented by Dececchi et al. (2012) for *Y. longimanus* reveals that these authors scored many characters that cannot be confidently assessed based on the preserved morphology of V 12638, casting doubt on the results of their analysis. For example, Dececchi et al. (2012) assigned *Y. longimanus* a score of '0' for character 1 in the matrix, defined as "Vaned feathers on forelimb symmetric (0) or asymmetric (1)" (Zanno, 2010: supplementary information), but the feathers of V 12638 are so poorly preserved that it is effectively impossible to determine whether their vanes are asymmetric or not. Dececchi et al. (2012) also scored several features pertaining to anatomical regions that are not adequately exposed in the only known specimen, such as the lateral side of the scapulocoracoid and the proximal surface of the ulna.

To re-evaluate the phylogenetic position of *Y. longimanus*, we added this taxon to Zanno's (2009) matrix (Zanno et al., 2009)1), and the resulting scorings are listed in appendex 1. We ran a phylogenetic analysis of the matrix using the TNT software package (Goloboff et al., 2008), recovering 34589 most parsimonious trees. Their strict consensus places *Y. longimanus* at the base of the Deinonychosauria, in a polytomy with the Troodontidae and a paraphyletic Dromaeosauridae (Fig. 3). The paravian status of *Y. longimanus* is thus strongly supported by the available data given that our numerical phylogenetic analysis, even without incorporating some of the previously mentioned probable paravian (e.g. character 4, above) and possible deinonychosaurian (e.g. characters 11-13) features seen in *Y. longimanus*,

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1) The data matrix of Zanno et al. (2009) is substantively identical to that of Zanno (2010), but the version of the character list presented in the former study is easier to use because it is in anatomical order. We thus added *Y. longimanus* to Zanno et al.'s (2009) matrix, rather than Zanno's (2010) matrix, in order to carry out our analysis.

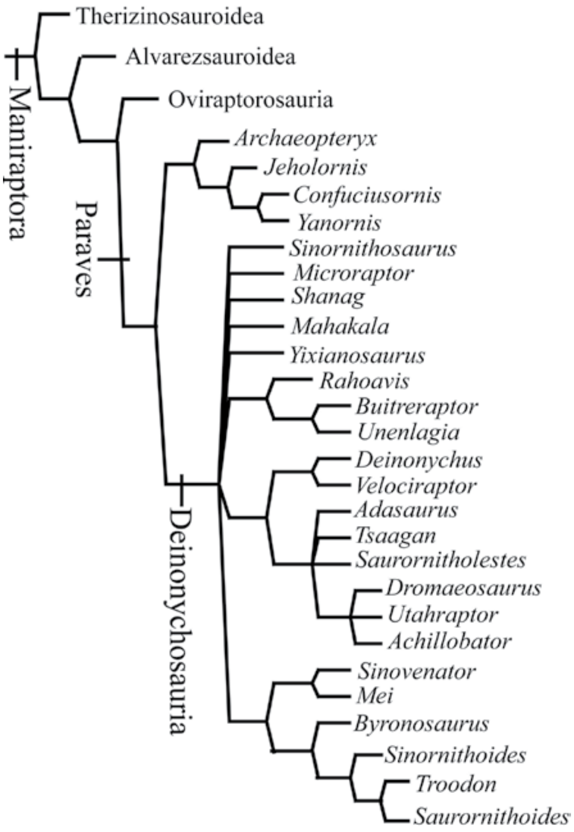

Fig. 3 A simplified version of the strict consensus of 34589 most parsimonious trees (tree length = 1233; CI = 0.35; RI = 0.70) produced by a numerical analysis of the dataset of Zanno et al. (2009) with *Yixianosaurus longimanus* added in

recovers *Y. longimanus* as a basal deinonychosaurian.

6 Conclusions

Fragmentary specimens are sometimes difficult to place securely on phylogenetic trees, but this does not appear to be the case with regard to V 12638. Only the pectoral girdle and forelimbs are preserved in this specimen, along with a few axial elements, but the forelimb is so heavily modified in paravians that *Y. longimanus* can be recognized as a member of this clade even on the basis of the single highly incomplete skeleton that is available for study.

Both character analysis and numerical phylogenetic analysis suggest that *Y. longimanus* is a basal paravian, and probably a basal deinonychosaurian. Under Dececchi et al.' s (2012) hypothesis that the taxon is a basal maniraptoran, many osteological features of *Y. longimanus* would be most parsimoniously interpreted as convergently evolved paravian-like traits. Under our systematic hypothesis, these features are reinterpreted as synapomorphies shared with at least some other paravians. This is true, for example, of the elongation of the penultimate phalanges of all three manual digits, which contributes to the grasping function of the manus.

Similarly, the pennaceous feathers seen in *Y. longimanus* would be surprising in a basal maniraptoran, given that previous reports of feathers of this type are restricted to oviraptorosaurs and deinonychosaurs among non-avialan theropods (Xu and Guo, 2009), but their presence is unremarkable under the assumption that *Y. longimanus* is a paravian. The feathers are so poorly preserved that their proportions, arrangement and degree of symmetry cannot be determined, but they hint that *Y. longimanus* may have been among the many Jehol paravians that appear to have been capable of some form of aerial locomotion. Finally, although we consider the diet of *Y. longimanus* to be uncertain, the hypothesis that this taxon was a predator (Dececchi et al., 2012) is particularly compatible with the possibility that it represents a basal member of Deinonychosauria. Carnivory is the typical deinonychosaurian condition (Xu et al., 2011b), whereas herbivory is arguably characteristic of both basal birds and basal maniraptorans (Zanno and Makovicky, 2011). Although *Y. longimanus* is poorly known, the available evidence places this taxon among Paraves and probably among Deinonychosauria, and suggests that it may have been a relatively typical basal member of the latter group.

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兽脚类恐龙长掌义县龙的系统发育位置

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摘要：长掌义县龙(*Yixianosaurus longimanus*)是发现于中国辽西下白垩统的一种小型兽脚类恐龙。最初的研究认为它代表一种进步的手盗龙类，但最近的一项研究工作质疑了这一系统发育假说，新的系统发育研究认为长掌义县龙代表一种原始的手盗龙类。鉴于长掌义县龙的系统位置会影响我们对兽脚类前肢和羽毛演化等关键问题的理解，因此需要评估哪一个系统发育假说更为可靠。本文评述了长掌义县龙所有可被用于系统发育研究的形态学特征，证明了这一小型兽脚类恐龙属于基干副鸟类，并很可能属于基干恐爪龙类。这一结论与最初的研究结果相吻合。这一系统位置也与长掌义县龙可能具片状羽毛相吻合，并且否定了手盗龙类前肢演化历史复杂的假说。

关键词：辽宁，早白垩世，手盗龙类，副鸟类，系统位置

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Appendex 1 Scorings for *Y. longimanus* using the phylogenetic matrix of Zanno et al. (2009)

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??0??01?0??11??????0??0?1?00?01
102001001110?100001???
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