



A NEW OVIRAPTORID (DINOSAURIA: THEROPODA) FROM THE UPPER CRETACEOUS OF BAYAN MANDAHU, INNER MONGOLIA

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Abstract: A new oviraptorid is described on the basis of a partial forelimb collected from the Upper Cretaceous redbeds of Bayan Mandahu, Inner Mongolia. *Machairasaurus leptonychus*, gen. et sp. nov. is diagnosed by slender, weakly curved manual unguals, reduced flexor tubercles, penultimate phalanges that are subequal in length to the preceding phalanges, and short, robust manual digits. *Machairasaurus* is found to be a member of the Ingeniinae, along with *Ingenia yanshini*, *Heyuannia huangi*, *Conchoraptor gracilis*, and *Nemegtomaia barsboldi*. *Machairasaurus* exhibits unusual proportions of the manus, suggesting that the manus was not primarily used to grasp prey. Instead, *Machairasaurus* and other oviraptorids are likely to have fed largely

on plant material. The recognition of a previously unknown oviraptorid at Bayan Mandahu provides further evidence that the Bayan Mandahu dinosaur assemblage is distinct from that found at the Djadokhta Formation exposures at Bayn Dzak, Tugriken Shireh, and Ukhaa Tolgod. Given that these localities are separated by just a few hundred kilometres and represent similar palaeoenvironments, marked differences in the fauna suggest that the Bayan Mandahu Formation of Inner Mongolia is not coeval with the known Djadokhta localities in Mongolia.

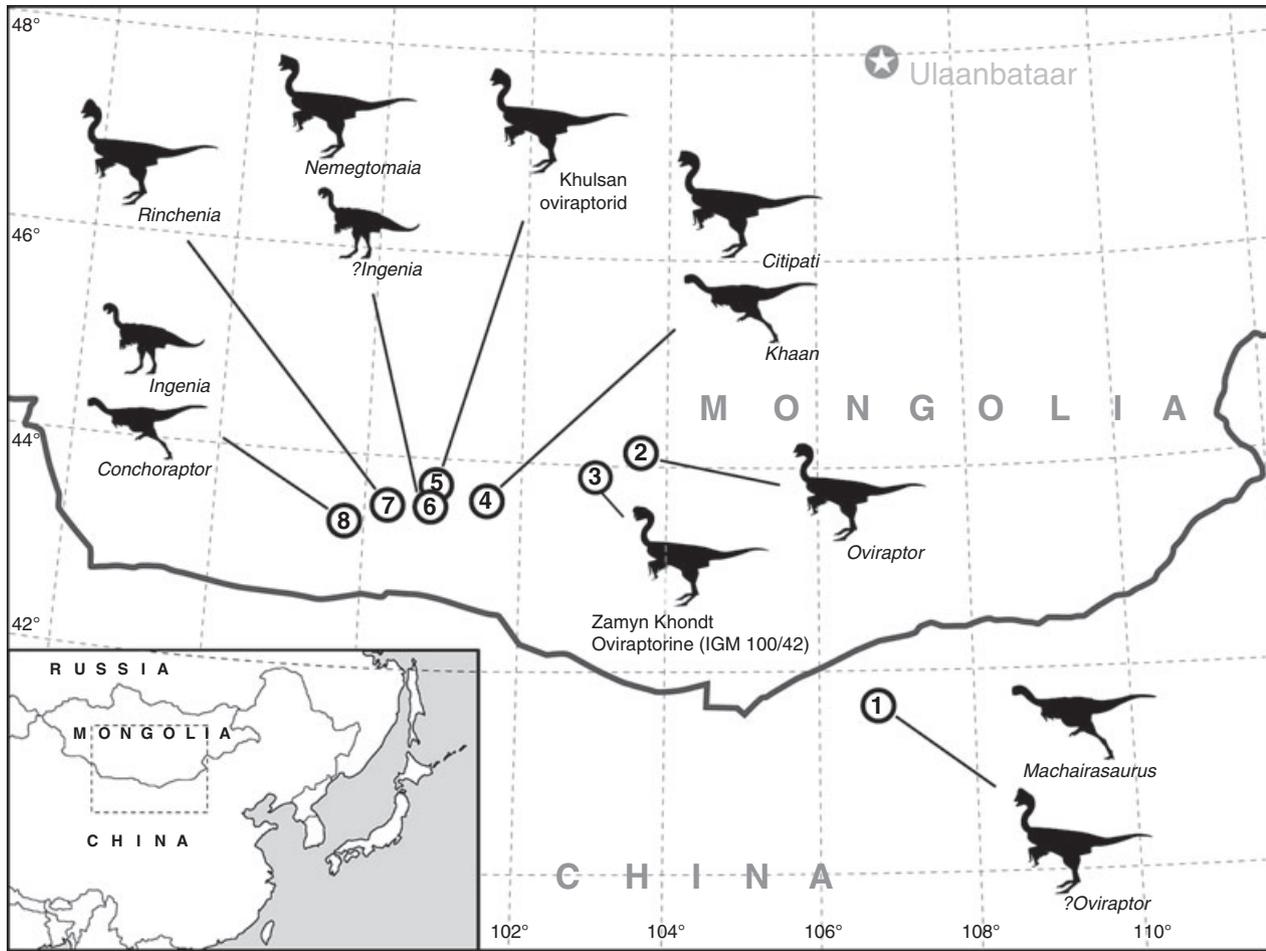
Key words: Theropoda, Oviraptoridae, Upper Cretaceous, Inner Mongolia, Bayan Mandahu Formation, Djadokhta.

OVIRAPTORIDS are small, birdlike theropods characterized by parrot-like beaks, highly pneumatized skulls and, in some instances, elaborate cranial crests. The known stratigraphic and geographical range of the group is limited. The family Oviraptoridae is known exclusively from the Upper Cretaceous of eastern Asia, and with the exception of *Heyuannia huangi* (Lü, 2002) and a Henan oviraptorid (Lü *et al.* 2008), all known oviraptorids come from the Gobi of Mongolia and China (Text-fig. 1). Despite this limited distribution, the clade is relatively diverse, and a large number of species are now known (Table 1). The oviraptorids of Mongolia have been the subject of many studies (Osborn 1924; Barsbold 1976, 1977, 1981, 1986; Norell *et al.* 1995; Clark *et al.* 2001, 2002; Lü *et al.* 2004b, 2005; Osmólska *et al.* 2004), but less is known about the oviraptorids of Inner Mongolia.

In 1988 and 1990, the Sino-Canadian dinosaur expeditions (Jerzykiewicz *et al.* 1993) collected a number of oviraptorids from the redbeds of Bayan Mandahu, Inner Mongolia. One of these specimens, IVPP V9608, has previously been described. It consists of a partial skeleton of a large oviraptorid sitting atop a clutch of eggs (Dong

and Currie 1996). Although this specimen was tentatively referred to *Oviraptor philoceratops*, the phalangeal proportions differ enough to preclude referral to this species, and the specimen is here referred to Oviraptorinae indet. Two other partial oviraptorid skeletons were collected from Bayan Mandahu, IVPP V15979 and IVPP V15980. They come from animals significantly smaller than the nesting specimen, but they have not previously been described in detail. However, recent work on the Bayan Mandahu Formation suggested that these specimens deserved to be studied in more detail.

Initial studies of the Bayan Mandahu Formation emphasized the similarities between this locality and the well-known Djadokhta Formation exposures at Bayn Dzak (the 'Flaming Cliffs') in Mongolia (Jerzykiewicz *et al.* 1993). In both sites, the beds consist of aeolian to alluvial sediments deposited in a semi-arid or arid climate. In both sites, squamates are highly diverse (Gao and Hou 1996; Gao and Norell 2000), and the dinosaur fauna consists of a few small-bodied taxa, dominated by *Protoceratops* (Brown and Schlaikjer 1940; Jerzykiewicz *et al.* 1993; Lambert *et al.* 2001). Despite these similarities, recent



TEXT-FIG. 1. Map of the Gobi Desert showing the provenance of different taxa of Oviraptoridae. 1, Bayan Mandahu, Bayan Mandahu redbeds; 2, Bayn Dzak, Djadokhta Formation; 3, Zamyn Khondt, Djadokhta Formation; 4, Ukhaa Tolgod, Djadokhta Formation; 5, Khulsan, Barun Goyot Formation; 6, Nemegt, Nemegt Formation; 7, Altan Ula, Nemegt Formation; 8, Khermin Tsav, Barun Goyot Formation.

TABLE 1. Known taxa of Oviraptoridae.

Taxon	Locality	Formation	Age	Reference
<i>Oviraptor philoceratops</i>	Bayn Dzak	Djadokhta	Campanian	Osborn, 1924
<i>Ingenia yanshini</i>	Khermin Tsav	Barun Goyot	Campanian–Maastrichtian	Barsbold, 1981
<i>Conchoraptor gracilis</i>	Khermin Tsav	Barun Goyot	Campanian–Maastrichtian	Barsbold, 1986
<i>Rinchenia mongoliensis</i>	Altan Ula	Nemegt	Maastrichtian	Barsbold 1986
<i>Citipati osmolskae</i>	Ukhaa Tolgod	Djadokhta	Campanian	Clark <i>et al.</i> , 2001
<i>Khaan mckennai</i>	Ukhaa Tolgod	Djadokhta	Campanian	Clark <i>et al.</i> , 2001
<i>Heyuannia huangi</i>	Heyuan City	Dalangshan	Maastrichtian	Lü, 2002
<i>Nemegtomaia barsboldi</i>	Nemegt	Nemegt	Maastrichtian	Lü <i>et al.</i> 2004b
? <i>Citipati</i> sp. nov.	Zamyn Khondt	Djadokhta	Campanian	Osmólska <i>et al.</i> 2004
Oviraptorinae indet.	Bayan Mandahu	Djadokhta	Campanian	Dong and Currie, 1996
Oviraptorinae sp. nov.	Khulsan	Barun Goyot	Campanian–Maastrichtian	This paper

studies have shown that many of the dinosaurs at Bayan Mandahu represent new taxa that are not known from Bayn Dzak. These include a new species of *Protoceratops*, *P. hellenikorhinus* (Lambert *et al.* 2001), a new species of

Pinacosaurus, *P. mephistocephalus* (Godefroit *et al.* 1999), and a new species of *Velociraptor*, *V. osmolskae* (Godefroit *et al.* 2008), as well as the *Bagaceratops*-like protoceratopsid *Magnirostris dodsoni* (You and Dong 2003).

In this light, we re-examined the small oviraptorids collected from Bayan Mandahu, focusing on IVPP V15979 (Text-figs 2–5). Although the specimen is very incomplete, the manus is well preserved. As the oviraptorosaurian forelimb exhibits a high degree of interspecific variation (Zanno and Sampson 2005), the forelimb alone allowed the specimen to be distinguished from all previously described members of the Oviraptoridae (Text-fig. 6) and permitted the diagnosis of a new taxon. This animal, *Machairasaurus leptonychus*, provides additional evidence that the Bayan Mandahu assemblage is distinct from the dinosaur assemblage found at Bayn Dzak and elsewhere in the Djadokhta Formation. On the basis of the dinosaur fauna, we argue that the Bayan Mandahu Formation is likely younger than the Djadokhta Formation exposures at Bayn Dzak.

GEOLOGICAL SETTING

The Bayan Mandahu redbeds are located in Nei Mongol Autonomous Region, China, along the southern edge of the Gobi Desert (Text-fig. 1). As with many other Gobi localities, no information is available concerning the absolute age of the Bayan Mandahu exposures. However, based on general similarities between the vertebrate fauna and sediments of Bayan Mandahu and the Djadokhta Formation (Jerzykiewicz *et al.* 1993), the Bayan Mandahu Formation is considered to be Late Cretaceous in age, probably Campanian (Godefroit *et al.*, 2008).

The sediments at Bayan Mandahu consist of fine sands, mudstones and caliches. These sediments are interpreted as being deposited between a mountain range and an active dune field (Eberth 1993; Jerzykiewicz *et al.* 1993), by streams, ponds and dunes. Overall, the facies closely resemble those found at Bayn Dzak (Eberth 1993; Jerzykiewicz *et al.* 1993). As with Bayn Dzak, the dinosaur fauna is species-poor and dominated by small dinosaurs, particularly *Protoceratops* (Currie and Peng 1993; Dong and Currie 1996; Lambert *et al.* 2001). A wide range of other vertebrates are also known from Bayan Mandahu, including squamates (Gao and Hou 1996; Wu *et al.* 1996), turtles (Brinkman and Peng 1996) mammals (Jerzykiewicz *et al.* 1993; Smith *et al.* 2001) and dinosaurs (Currie and Peng 1993; Dong and Currie 1996; Godefroit *et al.* 1999, 2008; Lambert *et al.* 2001), including small oviraptorids. Aquatic and semi-aquatic vertebrates, however, are poorly represented in the assemblage (Jerzykiewicz *et al.* 1993).

The climate appears to have been semi-arid or arid, as indicated by the existence of well-developed caliches and aeolian beds, as well as the rarity and low diversity of aquatic and semi-aquatic vertebrates (Jerzykiewicz *et al.* 1993). The high diversity of lizards (Gao and Hou 1996) com-

parable to that found in the modern Australian desert (Gao and Norell 2000) suggests that Bayan Mandahu may have been a hot desert, similar to the modern Australian desert or North America's Sonoran Desert. Similar interpretations have been put forward for the Djadokhta Formation (Favovskiy *et al.* 1997; Loope *et al.* 1998; Longrich in press).

Institutional abbreviations. IGM, Mongolian Institute of Geology, Ulan Bator; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

SYSTEMATIC PALAEOLOGY

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

MANIRAPTORA Gauthier, 1986

OVIRAPTOROSAURIA Barsbold, 1976

OVIRAPTORIDAE Barsbold, 1976

Genus MACHAIRASAURUS gen. nov.

Derivation of name. From Greek *machaira*, a forward-curving sword (referring to the shape of the unguals), and *saurus*, 'lizard.'

Type species. *Machairasaurus leptonychus* sp. nov.

Diagnosis. As for the type and only species.

Machairasaurus leptonychus sp. nov.

Text-figures 2–5

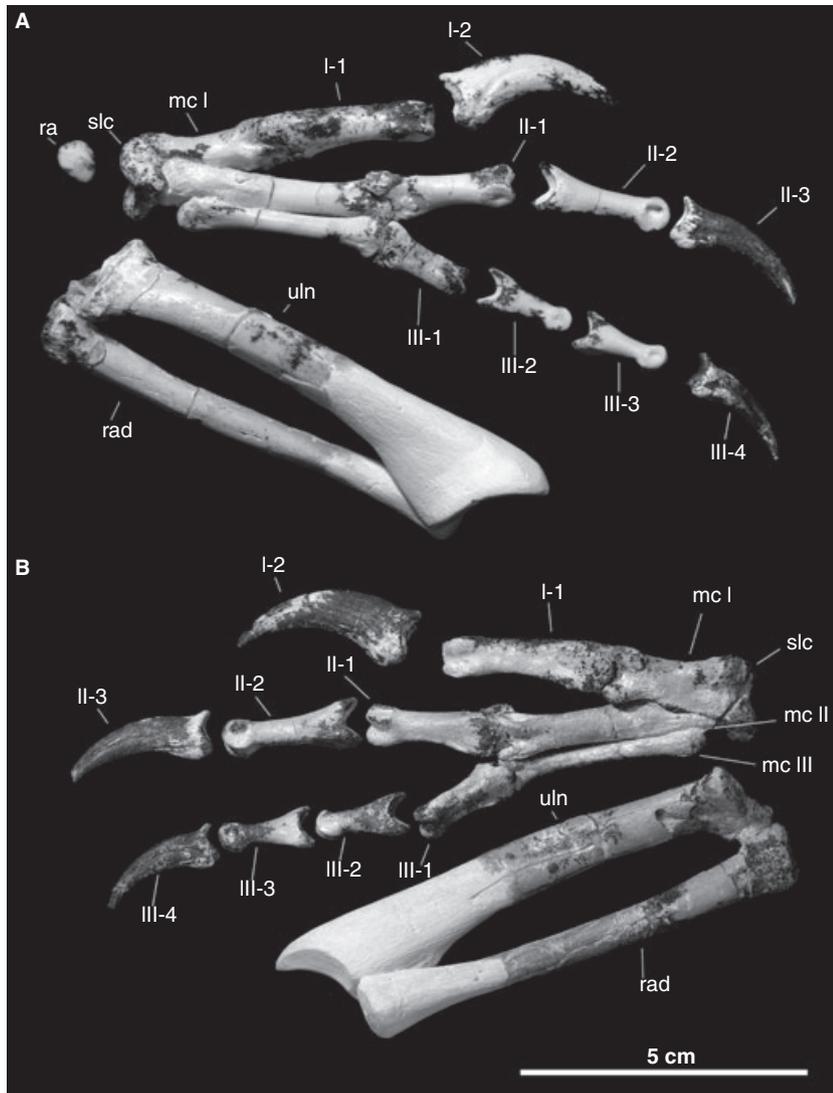
Derivation of name. From Greek *leptos*, 'slender', and *onychos*, 'claw'.

Holotype. IVPP V15979 (Text-figs 2–5), a partial skeleton including a nearly complete articulated right forearm and manus, fragments of the left manus and pedal phalanges.

Referred material. IVPP V15980, a partial skeleton including manual and pedal phalanges, fragments of left metatarsals III and IV, caudal vertebrae, dorsal ribs and chevrons. IVPP V15980 comes from the same locality as the holotype, and resembles the holotype in having short, broad pedal unguals and robust manual phalanges, and in overall size. It is tentatively referred to *Machairasaurus* on this basis. This specimen is very fragmentary and has not been prepared, and so it is not described further herein.

Horizon and type locality. Bayan Mandahu Formation, Late Cretaceous (Campanian), Bayan Mandahu, Inner Mongolia.

Diagnosis. *Machairasaurus leptonychus* is a small (c. 1.5 m long) oviraptorid. *Machairasaurus* exhibits a single



TEXT-FIG. 2. *Machairasaurus leptonychus*, gen. et sp. nov., holotype, Upper Cretaceous redbeds of Bayan Mandahu. A, dorsal view; B, ventral view. Abbreviations: mcI, metacarpal I; mcII, metacarpal II; mcIII, metacarpal III. slc, semilunate carpal (fused distal carpal I + II), uln, ulna; rad, radius. Roman numerals I, II, and III refer to phalanges I, II, and III, numbers refer to order of phalanx from proximal to distal.

autapomorphic character: manual unguals I–III elongate and bladelike in lateral view (length of claw approximately 400 per cent the height of the proximal articular surface).

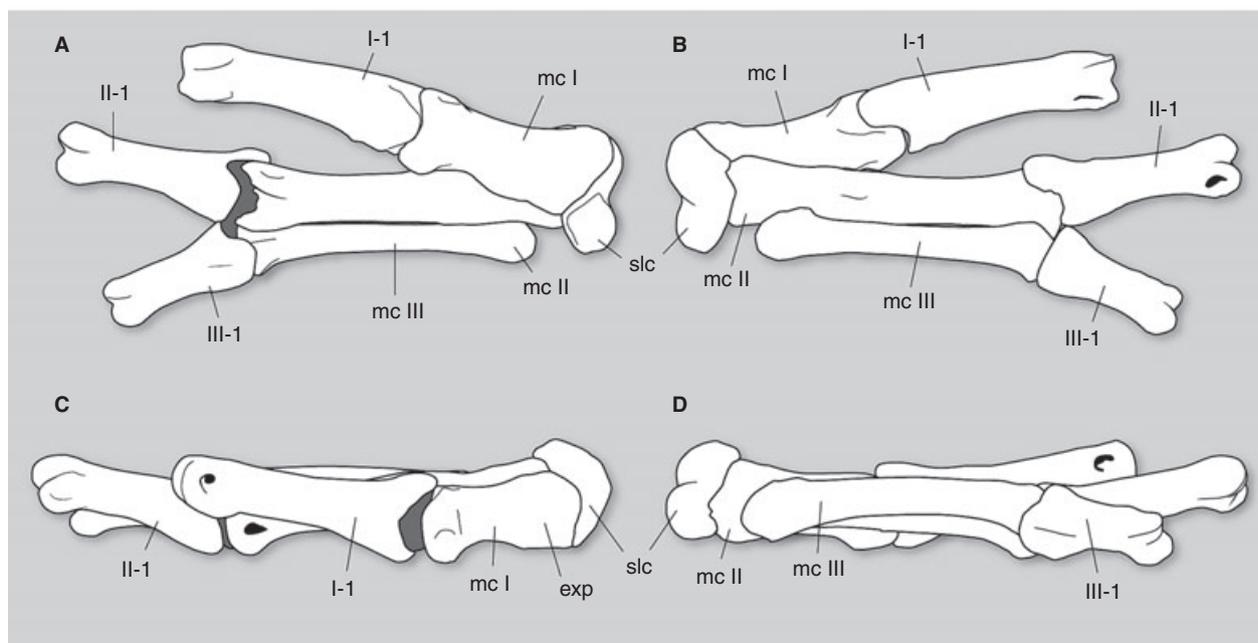
Differential diagnosis. *Machairasaurus* differs from oviraptorines in possessing the following derived characters: unguals of manual digits II and III weakly curved and bearing reduced flexor tubercles (shared with *Khaan*, *Ingenia* and *Conchoraptor*; condition unknown for *Heyuannia*). Among the Ingeniinae, *Machairasaurus* differs from *Khaan* in the following derived characters: manual phalanx II-2 that does not exceed the length of II-1; ventral flange of metacarpal I overlapping the ventral surface of metacarpal II; combined length of phalanges II-1 and II-2 does not exceed 110 per cent the length of metacarpal II, metacarpal I at least 50 per cent the length of metacarpal II (shared with *Heyuannia* and *Ingenia*, condition unknown for

Conchoraptor). *Machairasaurus* differs from *Conchoraptor* and *Khaan* in the following derived characters: phalanx III-3 does not exceed length of phalanx III-2; phalanx I-1 robust (shaft diameter at least 20 per cent of length).

Ingenia and *Heyuannia* differ from *Machairasaurus* in possessing the following derived characters: ulna straight; manual phalanx I-1 extremely robust (shaft diameter at least 25% of length); manual phalanx II-2 shorter than manual phalanx II-1; combined lengths of phalanges II-1 and II-2 do not exceed length of metacarpal II. *Nemegtomaia* differs from *Machairasaurus* in possessing an extremely robust radius.

Description

Radius and ulna. Only the distal end of the radius and ulna are preserved (Text-fig. 3). The radius is weakly



TEXT-FIG. 3. *Machairasaurus leptonychus*, gen. et sp. nov., holotype. Carpus, metacarpus, and proximal phalanges in A, ventral view; B, dorsal view; C, medial view; D, lateral view. Abbreviations: mc I, metacarpal I; mc II, metacarpal II; mc III, metacarpal III. slc, semilunate carpal.

bowed anteriorly. It is moderately robust and subcircular in section. The distal end of the radius is expanded and knob-like. The distal articular surface is subtriangular in shape and relatively flat; a shallow sulcus divides the articular surface into medial and lateral condyles.

The ulna is larger in diameter than the radius and bowed caudally. The shaft shows slight mediolateral flat-

tening. The distal end of the ulna is strongly compressed mediolaterally and dorsoventrally expanded, giving the end of the bone a spatulate shape, as is typical of maniraptorans. The hand would have pivoted around the long axis of the distal articular surface, allowing the hand to fold against the forearm, as seen in an articulated specimen of *Khaan mckennai* (IGM 100/1002).

Carpus. The radiale (Text-fig. 3) is ovoid in shape and poorly defined. The distal carpals are fused into a semilunate carpal, as in other maniraptorans, which covers the bases of metacarpals I and II. However, rather than simply capping the metacarpals, the semilunate carpal's articular facets for metacarpals I and II are angled relative to each other, such that the carpal block is tightly wedged between the two carpals in dorsal or ventral view. In dorsal view, the lateral edge of the carpal block wraps around the base of metacarpal II. In proximal view, the semilunate carpal of *Machairasaurus* is approximately as tall dorsoventrally as wide mediolaterally, and the carpal trochlea is deep and well defined.

Metacarpals. The three metacarpals are short and robust (Text-fig. 3), but metacarpal I is proportionately long, about 50 per cent the length of metacarpal II. The bone is slightly larger than metacarpal II in diameter. Proximally, the ventromedial edge of the first metacarpal bears a rugose, anteroposteriorly elongate knob. This knob occupies the same position as the flange-like extensor process found in dromaeosaurids (Ostrom 1969) and *Archaeopteryx* (Wellnhofer 2008) and is presumably homologous with the extensor process. The proximomedial edge of metacarpal I has a broad, smooth surface. This appears to be an articular surface which extends the carpal trochlea medially, as in other maniraptorans (Sereni 2001). In ventral view, the proximal end of metacarpal I bears a flange which almost completely covers the base of metacarpal II. The shaft of metacarpal I is bent such that the distal articular surface diverges from the long axis of the bone by approximately 30 degrees. The distal articular surface has a well-developed trochlea.

Metacarpal II is moderately robust, with the shaft's diameter being about 15 per cent the bone's length. The shaft is subcircular in section. In dorsal view, the shaft is slightly bowed laterally. The proximal end of metacarpal II is mediolaterally compressed, particularly ventrally. This lends the base of the bone a subtriangular section. The distal condyles are roughly subcircular in lateral view and appear to have permitted relatively extensive flexion-extension of the second digit. Prominent collateral ligament pits are present.

The shaft of metacarpal III is again moderately robust, the diameter being about 13 per cent the bone's length. The shaft is bowed laterally such that the shaft parallels the shaft of metacarpal II, and there is little space between the two. In lateral view, the shaft of metacarpal III is bowed dorsally. The shaft is subcircular in section, but the proximal end of metacarpal III is mediolaterally compressed and dorsoventrally expanded. The proximal end is broader ventrally than dorsally, giving the base of the bone a wedge shaped section. The proximal surface of metacarpal III is rounded. The third metacarpal neither

reaches the proximal end of metacarpal II, nor contacts the semilunate carpal.

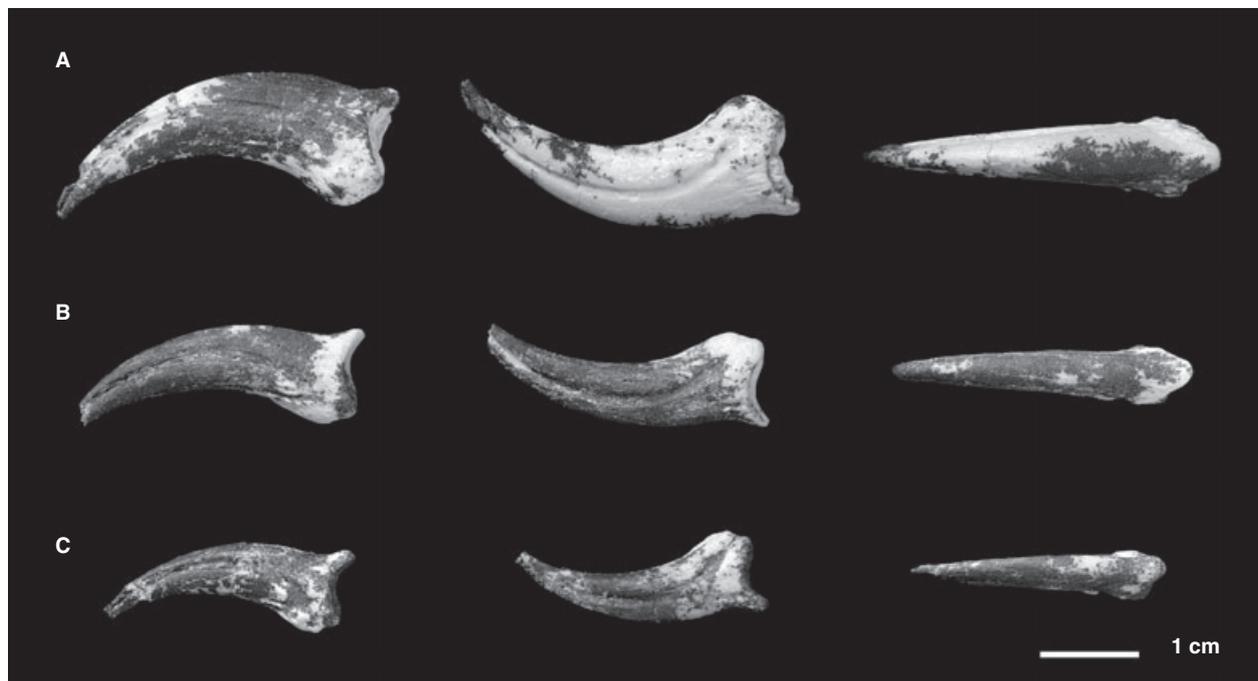
Manual phalanges. The manual phalanges are short and robust (Text-fig. 2), although not to the degree found in *Ingenia* or *Heyuannia*. Manual phalanx I-1 is short, being about 75 per cent the length of metacarpal II, and powerfully constructed, its diameter being about 20 per cent its length. The shaft is slightly bowed medially in dorsal view. In ventral view, the shaft is slightly flattened, and a pair of large rugosities is present near the base of the phalanx. In crocodylians, the tendons of the *m. flexor digitorum brevis superficialis* insert in this position (Meers 2003), suggesting that these represent the scars associated with these muscles. The area between these scars is slightly concave: presumably the underlying tendon of the *m. flexor digitorum profundus* (Meers 2003) would have passed through this groove. The proximal articular surface of I-1 is extended ventrally by a rounded heel, and dorsally by an elongated lip.

Manual ungual I is elongate, weakly curved and has a reduced flexor tubercle (Text-fig. 4A). This ungual is laterally compressed. The claw bears a simple, single groove on its lateral surface and a 'Y'-shaped groove on the medial surface. The flexor tubercle is developed as a low, mound-like rugosity. The claw's proximal articular surface extends dorsally as a well-developed tongue-like projection.

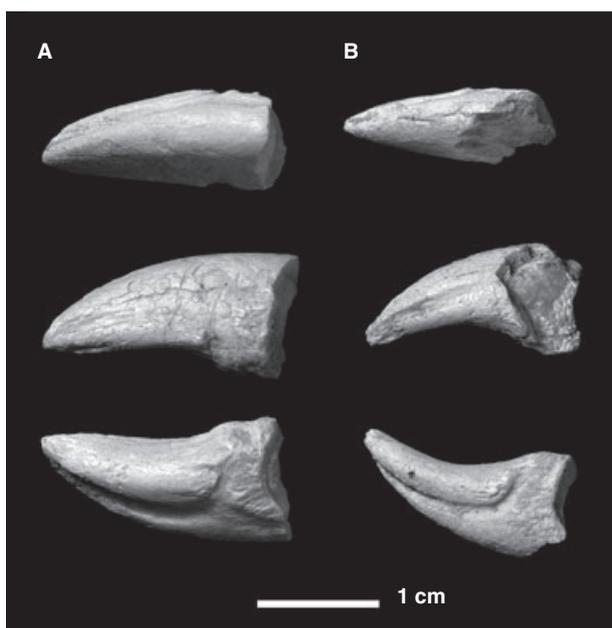
Manual phalanges II-1 and II-2 are short, each being about half the length of metacarpal II, and moderately robust. The distal articular surface of II-1 is circular in lateral view and extends onto the dorsal surface of the phalanx, where there is a pit for the proximodorsal articular 'tongue' of the following phalanx. The collateral ligament pits are very poorly developed. The proximal articular surface of II-2 is highly concave and again bears an elongate articular heel and tongue; the construction of the articular surfaces appears to have permitted hyperextension at this joint. The second manual ungual (Text-fig. 4B) is similar to the first, but smaller, proportionately more elongate, and more weakly curved. The proximodorsal lip is relatively larger, but the flexor tubercle is more weakly developed.

Manual phalanges III-1, III-2, and III-3 are short and subequal in length. The proximal articular surfaces of III-2 and III-3 are highly concave. As with digit II, the interphalangeal joints appear to have permitted hyperextension of the phalanges. The third ungual (Text-fig. 4C) resembles the ungual of digit II in shape, but is smaller.

Pedal phalanges. Several pedal phalanges are preserved with the holotype, including two unguals and fragments of non-ungual phalanges (Text-fig. 5). The pedal unguals



TEXT-FIG. 4. *Machairasaurus leptonychus*, gen. et sp. nov., holotype, manual unguals. A, manual ungual I. B, manual ungula II. C, manual ungual III. In (left to right) medial, lateral, and dorsal views.



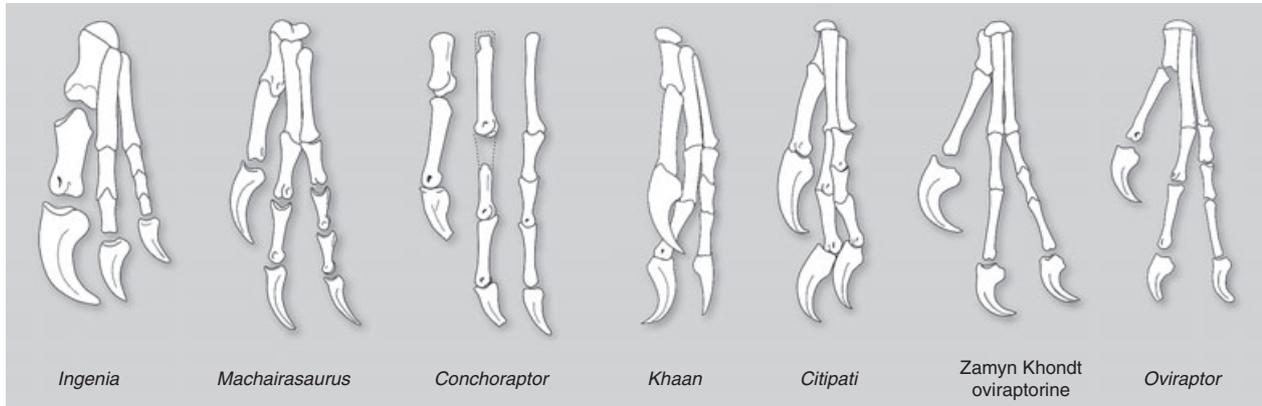
TEXT-FIG. 5. *Machairasaurus leptonychus*, gen. et sp. nov., holotype, pedal unguals. A, pedal ungual ?IV. B, pedal ungual ?II.

are relatively small, suggesting that they may represent pedal phalanges I-2 (Text-fig. 5B) and IV-5 (Text-fig. 5A). The unguals phalanges are relatively broad compared to their width, and moderately curved.

COMPARISONS

Overall, *Machairasaurus* is a relatively small animal, probably less than two metres in length. In size, it was comparable to other Ingeniinae; the Oviraptorinae are generally much larger animals. More detailed comparisons with other Oviraptoridae show that *Machairasaurus* exhibits a combination of derived and primitive characters.

The bowed ulna seen in *Machairasaurus* is a primitive character (Gauthier 1986), whereas the advanced ingeniines *Ingenia* (Osmólska *et al.* 2004) and *Heyuannia* (Lü 2002) have a straight ulna. The semilunate carpal is derived in being reduced compared to the condition in either *Deinonychus* or *Oviraptor* (Text-fig. 6). *Machairasaurus* is also more advanced than oviraptorines such as *Oviraptor* and the Zamyx Khondt oviraptorid (Osmólska *et al.* 2004) in having a relatively robust manus; here, it resembles *Ingenia*, *Heyuannia*, and *Khaan* (IGM 100/1002). In ventral view, the proximal end of metacarpal I almost completely covers the base of metacarpal II, as in *Heyuannia* (Lü *et al.* 2005) and *Ingenia* (uncatalogued IGM specimen), but in the more primitive *Khaan* (IGM 100/1127), the second metacarpal is only partly covered by metacarpal II. Metacarpal II is moderately robust compared to that of oviraptorines such as *Oviraptor* (Osborn 1924). As in *Citipati* (Clark *et al.* 1999) and *Khaan*, the base of metacarpal III does not reach the base of



TEXT-FIG. 6. The manus of different species of Oviraptoridae, showing the distinctive proportions that characterize each genus. *Machairasaurus leptonychus* differs from the other taxa in having long, slender manual unguals, moderate reduction of the nonungual phalanges, and a phalanx III-3 which is subequal in length to phalanx III-2. *Ingenia*, *Conchoraptor*, and the Zamyn Khondt oviraptorine after Osmólska *et al.* (2004); *Citipati* after Clark *et al.* (1999).

metacarpal II. The unguals exhibit less lateral compression than seen in other maniraptorans such as caenagnathids (Currie and Russell 1988) or dromaeosaurids (Ostrom 1969). As described above, the interphalangeal joints would have afforded a high degree of mobility. In the case of the joint between phalanx II-1 and II-2, the second phalanx could have been hyperextended by almost 45 degrees. This contrasts with the condition in dromaeosaurids (Gishlick 2001) and ornithomimids (Kobayashi and Barsbold 2005), where extension of this joint is highly constrained. The pedal phalanges are relatively broad compared to their width and moderately curved. In this respect, they closely resemble the pedal phalanges of *Ingenia yanshini* and *Khaan mckennai* (IGM 100/1127); the pedal phalanges of Caenagnathidae are more recurved, however (Currie and Russell 1988).

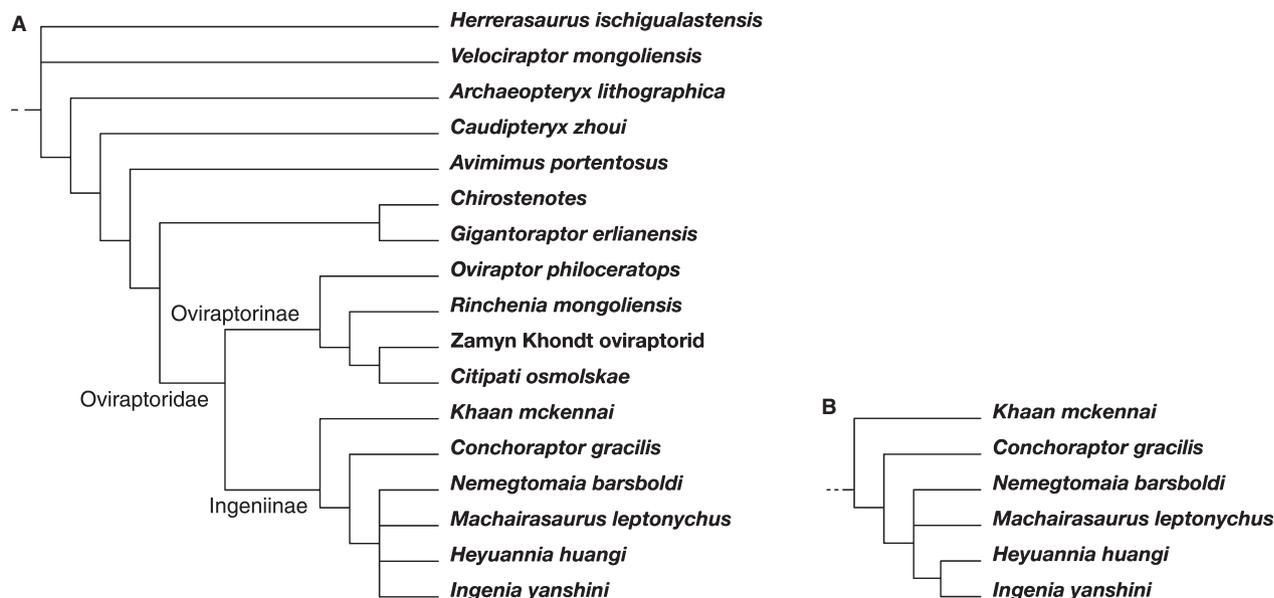
PHYLOGENETIC ANALYSIS AND SYSTEMATICS

Phylogenetic analysis was performed using a modified version of the matrix of Osmólska *et al.* (2004). The matrix was expanded by the addition of five additional taxa (*Machairasaurus leptonychus*, *Oviraptor philoceratops*, *Nemegtomaia barsboldi*, *Heyuannia huangi* and *Gigantoraptor erlianensis*) and twenty characters relating to the skull, forelimb, pelvis and hindlimb. This resulted in a matrix of 17 taxa and 181 characters (see Appendix S1). Three characters were ordered, and five characters were found to be parsimony-uninformative. Phylogenetic analysis was performed using the branch-and-bound search algorithm of PAUP* 4.0b10 (Swofford 2002), with default settings enabled. Five trees were found, with tree lengths of 289. Excluding uninformative characters, the consis-

tency index is 0.6581, the retention index is 0.7206, and the rescaled consistency index is 0.4804.

The resulting strict consensus tree generally agrees with the phylogeny found by Osmólska *et al.* (2004) in that the Oviraptoridae is divided into two clades, Ingeniinae and Oviraptorinae (Text-fig. 7A). Ingeniinae contains *Machairasaurus leptonychus*, *Khaan mckennai*, *Conchoraptor gracilis*, *Heyuannia huangi*, *Ingenia yanshini* and *Nemegtomaia barsboldi*. *Machairasaurus* appears to occupy a position between basal Ingeniinae (*Khaan* and *Conchoraptor*) and derived Ingeniinae (*Ingenia* and *Heyuannia*) (Text-fig. 7B). The Ingeniinae are characterized by small size (*c.* 1.5 m in length), short and robust forelimbs with weakly curved unguals, a short, robust metatarsus, a long, low ilium with a shallow preacetabular process, a relatively straight ischium, and (with the exception of *Nemegtomaia*) the absence of a prominent cranial crest. The presence of the cranial crest in *Nemegtomaia* raises the possibility that the evolution of this feature involved several losses or gains, or that *Nemegtomaia* may not belong to this clade.

Oviraptorinae includes *Oviraptor philoceratops*, *Citipati osmolskae*, *Rinchenia mongoliensis* and the unnamed Zamyn Khondt oviraptorid. The oviraptorines are united by a spur-like anterior process of the surangular and dorsal expansion of the frontals to create a frontal-nasal crest (although the condition of this character is not known for *Oviraptor*). All known oviraptorines are relatively large compared to the Ingeniinae, and they retain relatively long forelimbs and highly curved manual and pedal unguals, as in caenagnathids (Currie and Russell 1988). Despite their larger size, the oviraptorines are more gracile animals than the ingeniines. The Oviraptorinae probably includes two other forms. One is the large oviraptorid described from Bayan Mandahu by



TEXT-FIG. 7. Phylogeny of Oviraptoridae. Five trees were found with tree length 321, a consistency index of 0.6581, a retention index of 0.7206, and a rescaled consistency index of 0.4804. A, Strict consensus tree. B, topology of the Ingeniinae in an Adams consensus tree.

Dong and Currie (1996); its large size and the elongate manus are consistent with referral to Oviraptorinae. A second is a large oviraptorid discovered in 2007 in Barun Goyot exposures near Khulsan; it is a relatively large animal and has an enlarged nasofrontal crest, which suggest oviraptorine affinities. Both are in need of further study.

The giant oviraptorosaur *Gigantoraptor erlianensis* was found to be a basal member of the Oviraptoridae by Xu *et al.* (2007). However, the analysis presented here places *Gigantoraptor* in the Caenagnathidae. This is supported by several characters (complete fusion of the dentaries; fossa on the lateral surface of the dentary; flange on the ventral margin of the surangular). The highly derived and enigmatic *Avimimus* is here found to be the sister taxon of the clade formed by Oviraptoridae and Caenagnathidae.

PALAEOBIOLOGY OF MACHAIRASAUROS AND OTHER OVIRAPTORIDS

The Ingeniinae have a highly derived morphology that may reflect adaptation for a specialized lifestyle. In *Machairasaurus* and other members of Ingeniinae, the morphology of the hands suggests that they were adapted for some function other than prey capture. Primitively in theropods, the manus exhibits features correlated with grasping, including elongate penultimate phalanges (Sereno 1994; Hopson 2001), elongate digits, and curved

unguals with large flexor tubercles (Sereno 1994). *Machairasaurus* shows none of these features. *Ingenia* and *Heyuannia* do retain a strongly curved manual ungual I, but resemble *Machairasaurus* in having shortened digits and reduced penultimate phalanges.

The humerus is not known for *Machairasaurus* and the forearm is fragmentary, but in *Ingenia* and *Heyuannia* these elements are highly modified (Osmólska *et al.* 2004; Lü *et al.* 2005). The humerus is robust, with a broad, distally extended deltopectoral crest and large entepicondyle. The antebrachium is also heavily built and shortened relative to the humerus. Among mammals, such features are commonly found in digging animals (Hildebrand and Goslow 2001). Oddly, the enlargement of a single digit of the manus, as seen in *Ingenia* (Osmólska *et al.* 2004), *Heyuannia* (Lü *et al.* 2005) and, to a lesser degree, *Machairasaurus*, is a common feature in ant- and termite-eating taxa, such as anteaters, pangolins and the giant armadillo (Senter 2005; Longrich and Currie 2009). Obviously, the jaw morphology of ingeniines argues against an insectivorous diet, but the similarities in forelimb morphology suggest that the forelimbs might have functioned in a broadly similar fashion. Presumably, they were used for forceful scratching, tearing or, conceivably, digging. Therefore, while it seems clear that the forelimbs of *Machairasaurus* and other derived members of Ingeniinae were not primarily used for prey capture, it is less obvious precisely what they were used for, or what these animals might have fed upon.

Oviraptorids have variously been interpreted as egg predators (Osborn 1924), molluscivores (Barsbold 1977), or

herbivores (Paul 1988; Smith 1992). The presence of gastroliths in *Caudipteryx* (Ji *et al.* 1998) and large wear facets in *Incisivosaurus* (Xu *et al.* 2002) have both been cited as evidence for herbivory in these taxa, and perhaps for herbivory in Oviraptorosauria as a whole (Barrett 2005).

Examination of oviraptorid jaws suggests that they were not used for durophagy. The jaws of durophages, such as shell-crushing reptiles and mammals, tend to possess teeth with broad, sometimes molariform crushing surfaces (Hildebrand and Goslow, 2001). In contrast, the sharp edges of the oviraptorid dentary suggest the presence of a sharp-edged rhamphotheca that would be used for shearing tough food, rather than cracking hard items such as bivalves or eggs. The symphyseal shelf of the dentary may have been able to provide some crushing ability, but the relatively small area of the shelf suggests that this was not the primary function of the jaws.

Instead, the oviraptorosaurid feeding apparatus exhibits features seen in herbivorous tetrapods. Among extinct taxa, the jaws of oviraptorids most closely resemble those of the dicynodont synapsids. Cracraft (1971) first drew attention to these features in his discussion of *Caenagnathus*, but oviraptorids also show these characters (Osmólska 1976), as well as dicynodont-like features not seen in *Caenagnathus*. Oviraptorid mandibles resemble those of dicynodonts in being short, deep and edentulous. Both taxa have elongate dentary symphyses. Elongate external mandibular fenestrae occur in both groups, although they are better developed in oviraptorids. The articular-quadrate joint is highly specialized in both oviraptorosaurs and dicynodonts, with the articular joint being formed by two anteroposteriorly elongate condyles separated by an anteroposterior ridge; this joint apparently allowed the jaw to slide anteroposteriorly relative to the quadrate (Cracraft 1971). In both groups, the palate has an extensive, ventrally projecting bar formed by the pterygoids and ectopterygoids (Osmólska 1976; Osmólska *et al.* 2004). Other features, including anteroposteriorly elongate supratemporal fenestrae, a reduced contribution of the maxilla to the palate, and a short, broad premaxilla bearing prominent palatal ridges, are likewise found in both oviraptorids (Osmólska *et al.* 2004) and dicynodonts (Romer 1956; Carroll 1988; King *et al.* 1989). Among modern taxa, the oviraptorids resemble parrots (Psittacidae) and tortoises (Testudinidae) in the structure of the jaws, although the convergence is not as extensive as in the case of the dicynodonts. The blunt, tooth-like projections of the oviraptorid premaxilla, however, are quite similar to those seen in Testudinidae (NRL, pers. obs. of *Geochelone nigra*). Given the extensive morphological convergence between oviraptorids and dicynodonts, which are generally believed to be herbivorous (King *et al.* 1989; King 1996), and given the similarities shared by oviraptorids and extant herbivores such as parrots and tortoises,

it is probable that plant matter formed the bulk of the oviraptorid diet.

In this context, the frequency with which oviraptorids are found at Bayan Mandahu and other Gobi localities has important biological implications. The Sino-Canadian expeditions recovered parts of at least three oviraptorid skeletons from Bayan Mandahu (Dong and Currie 1996; this paper) as well as fragments collected from a bonebed (a partial dentary and a pair of caudal vertebrae) representing at least one more animal. This makes oviraptorids among the most common dinosaurs in the assemblage; only protoceratopsids and ankylosaurids appear to have been more common. Oviraptorids are also relatively abundant at Khermin Tsav (Osmólska *et al.* 2004) and Ukhaa Tolgod (Norell *et al.* 1995). Although Bayn Dzak has produced only a single oviraptorid skeleton, the numerous oviraptorid eggs and nests found there (Norell *et al.* 1995) suggest that oviraptorids were a significant component of the fauna. The abundance of oviraptorids in these assemblages is consistent with the pattern seen in herbivorous dinosaurs such as Ornithomimidae (Barrett, 2005), Hadrosauridae, and Ceratopsidae (Dodson 1971; Bakker 1972; Currie and Russell 2005) in North America. These animals tend to be much more abundant than carnivorous dinosaurs, simply because more energy is available at lower trophic levels.

The ecology of oviraptorids must also be considered in the light of the palaeoenvironments they inhabited. The discovery of *Machairasaurus* at Bayan Mandahu provides further evidence for an association between the oviraptorids and xeric palaeoenvironments. Most oviraptorids (in terms of either number of species or number of specimens) come from redbed exposures such as Bayan Mandahu, Bayn Dzak, Ukhaa Tolgod, and the Barun Goyot exposures at Khulsan and Khermin Tsav (Osmólska *et al.* 2004). These sediments represent semi-arid and arid environments (Jerzykiewicz and Russell 1991; Jerzykiewicz *et al.* 1993; Fastovsky *et al.* 1997; Loope *et al.* 1998). In contrast, relatively few oviraptorids have been reported from the Baynshiree, Iren Dabasu, and Nemegt Formations, which are fluvial dominated (Jerzykiewicz and Russell 1991; Itterbeeck *et al.* 2005); *Nemegtomaia* (Lü *et al.* 2004b) is one of the few exceptions. Protoceratopsids demonstrate a remarkably similar pattern (Longrich in press). These patterns suggest that oviraptorids may have specialized in exploiting xeric environments. The strong association between oviraptorids and xeric palaeoenvironments provides additional evidence against egg- or shellfish-eating in oviraptorids: it is unlikely that such harsh palaeoenvironments could have provided enough eggs to support specialist egg predators, and neither is it likely that these semi-arid and arid environments would have supported enough shellfish to support mollusc-eating dinosaurs. Instead, it seems probable that the highly specialized jaws

of the oviraptorids were important in processing the kinds of food, and xerophytic vegetation in particular, that would presumably have grown in such settings. Unfortunately, this hypothesis is currently difficult to test, given that virtually nothing is known of the flora in the Gobi redbeds.

PALAEOBIOGEOGRAPHIC AND BIOSTRATIGRAPHIC IMPLICATIONS

The recognition of *Machairasaurus* adds to a growing list of new taxa from the Bayan Mandahu assemblage (Godefroit et al. 1999, 2008; Lambert et al. 2001; You and Dong

2003). At present, none of the material found at Bayan Mandahu can be definitively referred to species known from Bayn Dzak or any of the other Djadokhta Formation localities (Table 2). The lack of overlap between the species seen at Bayan Mandahu and other Gobi localities could potentially be explained by several factors: (1) environmental differences, (2) geographical isolation, or (3) differences in the ages of the strata (Godefroit et al. 2008).

1. Environmental differences. There is strong evidence that some dinosaur taxa favoured particular habitats. For instance, in the Late Maastrichtian of western North America, *Leptoceratops* and *Ankylosaurus* tend to be

TABLE 2. The dinosaur fauna of Bayan Mandahu, Inner Mongolia, compared with faunas of Bayn Dzak and Ukhaa Tolgod.

	Bayan Mandahu (?Djadokhta)	Bayan Dzak (Djadokhta)	Tugriken Shireh (Djadokhta)	Ukhaa Tolgod (Djadokhta)	Khulsan (Barun Goyot)	Hermin Tsav (Barun Goyot)
Protoceratopsidae	<i>Protoceratops hellenikorhinus</i> <i>Magnirostris</i> (=Bagaceratops?) <i>dodsoni</i> ? <i>Udanoceratops</i>	<i>Protoceratops andrewsi</i> , <i>Bainoceratops efremovi</i>	<i>Protoceratops andrewsi</i>	<i>Protoceratops</i> sp.	<i>Bagaceratops rostdestvenskii</i>	<i>Bagaceratops rostdestvenskii</i>
Ankylosauridae	<i>Pinacosaurus mephistocephalus</i>	<i>Pinacosaurus grangeri</i>	<i>Pinacosaurus</i> sp.	<i>Pinacosaurus grangeri</i>	<i>Saichania chulsanensis</i> <i>Tarchia gigantea</i>	<i>Saichania chulsanensis</i>
Tyrannosauridae	Indeterminate tyrannosaur	Indeterminate tyrannosaur	–	–	–	–
Alvarezsauridae	–	Indeterminate alvarezsaur	? <i>Parvicursor</i> sp.	<i>Shuvuuia deserti</i>	<i>Parvicursor remotus</i> ? <i>Mononykus</i> sp.	–
Ornithomimidae	–	–	–	Indeterminate ornithomimid	–	–
Oviraptorosauria	Oviraptoridae indet. <i>Machairasaurus leptonychus</i>	<i>Oviraptor philoceratops</i>	–	<i>Citipati osmolskae</i> <i>Khaan mckennai</i>	Oviraptorinae indet. <i>Avimimus</i> cf. <i>portentosus</i>	<i>Ingenia yanshinii</i> <i>Conchoraptor gracilis</i>
Dromaeosauridae	<i>Velociraptor osmolskae</i>	<i>Velociraptor mongoliensis</i>	<i>Velociraptor mongoliensis</i> <i>Mahakala omnogovae</i>	<i>Tsaagan mangas</i>	Velociraptorinae indet.	Velociraptorinae indet.
Troodontidae	Cf. <i>Saurornithoides</i> unnamed small troodontid	<i>Saurornithoides mongoliensis</i>	–	<i>Byronosaurus jaffei</i> cf. <i>Saurornithoides</i>	–	–
Sauropoda	Indeterminate sauropod	–	–	–	Indeterminate sauropod	–
Pachycephalosauridae	–	–	–	–	<i>Tylocephale gilmorei</i>	–
Hadrosauridae	Indeterminate hadrosaur	–	–	–	–	–

Sources for Bayan Mandahu: Currie and Peng 1993; Dong and Currie 1993, 1996; Godefroit et al. 1999; Lambert et al. 2001; You and Dong 2003. Sources for Djadokhta: Osborn 1924, Gilmore 1933, Brown and Schlaikjer 1940, Tereschenko and Alifanov 2003, and Dashzeveg et al. 2005. Ukhaa Tolgod data from Chiappe et al. 1998, Norell et al. 2000, Gao and Norell 2000, Clark et al. 2001, Hill et al. 2003, Ksepka and Norell 2004, Norell and Hwang 2004, Norell et al. 2006, Godefroit et al. 2008. Khulsan and Hermin Tsav data from Weishampel et al., 2004; pers. obs.

common in the inland deposits of Alberta's Scollard Formation, but hadrosaurs are all but absent (Lehman 2001; NRL pers. obs. of TMP collections). In contrast, the hadrosaur *Edmontosaurus* is relatively common in the coastal lowland habitats of eastern Montana's Hell Creek and Wyoming's Lance Formation, while *Leptoceratops* and *Ankylosaurus* are relatively uncommon (Lehman 2001; NRL pers. obs.).

Similar patterns are seen in Asia. Fluvial-dominated systems representing mesic palaeoenvironments, including the Bayn Shireh, Iren Dabasu and Nemegt Formations, have a diverse dinosaur assemblage dominated by hadrosaurs and ornithomimids, which are joined by therizinosaurs, titanosaurs, avimimids and tyrannosaurs (Jerzykiewicz and Russell 1991; Weishampel *et al.* 2004; Itterbeeck *et al.* 2005; Longrich in press). In these settings, oviraptorids and protoceratopsids are uncommon or absent. In contrast, the xeric palaeoenvironments recorded in the Djadokhta, Bayan Mandahu and Barun Goyot Formations are species-poor, and tend to be dominated by small-bodied protoceratopsids, oviraptorids and ankylosaurids (Osborn 1924; Brown and Schlaikjer 1940; Weishampel *et al.* 2004; Dashzeveg *et al.* 2005; Longrich in press). Here, large dinosaurs tend to be relatively rare.

Environmental differences, therefore, provide one mechanism that could potentially explain the faunal differences between Bayan Mandahu and other Djadokhta Formation localities. In this scenario, differences in climate, geography, and the biota (vegetation, prey items, competitors and predators) found at Bayan Mandahu favour the survival of a different set of dinosaur species.

In practice, there are major problems with this hypothesis. First, while different parts of the Western Interior of North America do have very different dinosaur assemblages, significant overlap also occurs. The Scollard and Hell Creek formations do differ in species richness and relative abundance of taxa, but many of the Hell Creek species occur in the Scollard, and most if not all of the Scollard species appear to occur in the Hell Creek (Weishampel *et al.* 2004; NRL, pers. obs.). Second, the available evidence suggests that the palaeoenvironments of Bayan Mandahu and Bayn Dzak were quite similar (Jerzykiewicz *et al.* 1993). The sedimentary facies suggest very similar depositional environments. The vertebrate community structure is also similar in both localities: squamates are diverse, aquatic vertebrates are rare and the dinosaur fauna is species-poor and dominated by small-bodied forms, particularly protoceratopsids. For these reasons, it is unlikely that environmental differences alone could explain the distinct fauna found at Bayan Mandahu.

2. Endemism. Another possible explanation is that the dinosaurs in question had non-overlapping geographical ranges, perhaps because of some isolating mechanism

(Godefroit *et al.* 2008). In this scenario, as we move from one locality to another, we find the same ecological niches occupied by different species of dinosaur. The problem with this interpretation is that the distances between Bayan Mandahu and the Djadokhta Formation localities appear inadequate to explain the marked differences in their dinosaur assemblages, particularly in the absence of any obvious isolating mechanism that would prevent dispersal from one site to another. Animals with the size of oviraptorids, *Protoceratops* and *Pinacosaurus*, ought to have been able to easily travel between the two localities. Moving at just 5–10 km a day, an animal could travel from one site to another in a matter of weeks. It also seems unlikely that the desert could serve as an effective isolating mechanism for these animals, because they were already inhabitants of harsh, arid and semi-arid environments. Furthermore, the lizard fauna does not appear to differ markedly between the two localities (Gao and Norrell 2000), even though the lizards should have less dispersal ability than dinosaurs due to their small size. For these reasons, it seems unlikely that endemism can explain the distinctiveness of the Bayan Mandahu dinosaur fauna.

3. Faunal turnover. The final possibility is that the rocks at Bayan Mandahu and the Mongolian localities were deposited at different times, and that the differences in the dinosaur assemblages result from speciation and extinction (Godefroit *et al.* 2008; Makovicky 2008). This seems a plausible explanation in the light of increasing evidence that many of the various Gobi redbeds were deposited at different times (Kielan-Jaworowska *et al.* 2003; Dashzeveg *et al.* 2005; Makovicky 2008).

In this scenario, the overall community structure of the dinosaur fauna may have remained relatively stable for millions of years, but the individual species making up the community continually evolve and become extinct, persisting for only a few million or even a few hundred thousand years. The result of this continuous faunal turnover is that sedimentary units of different ages exhibit a similar community structure, but the species composing each assemblage differ slightly.

Recent work on North American dinosaur assemblages suggests that dinosaur species were relatively short-lived. In the Dinosaur Park Formation, three successive faunas occur in a period of less than two million years, suggesting rapid faunal turnover (Ryan and Evans 2005). Thus, even if the sediments at Bayan Mandahu were deposited just one million years after those at Bayn Dzak, such a difference in time might be sufficient to explain the differences in their faunas. The absence of substantial differences between the lizards at Bayan Mandahu and elsewhere could be explained by slower rates of evolution among the squamates. In fact, many of the lizard taxa found at Bayn Dzak and Ukhaa Tolgod occur in the

younger Barun Goyot exposures at Khulsan (Gao and Norell 2000) suggesting that this may be the case. However, it is also possible that the lizards of the various Gobi localities have been subjected to taxonomic 'lumping' and that the lizard assemblages are more distinct than they initially appear (J. Conrad, pers. comm. 2008).

We therefore suggest that faunal change over time is the most likely explanation for the distinctiveness of the Bayan Mandahu dinosaurs, given (1) that neither distance nor the existence of deserts are likely to have been effective isolating mechanisms for relatively large, desert-dwelling dinosaurs and (2) the community structure and sedimentology are broadly similar, suggesting that differences in palaeoenvironment are insufficient to explain the differences seen here. In this light, it is worth noting that, thus far, none of the oviraptorid species found at a given Gobi locality have been definitively shown to occur at another locality (Text-fig. 1).

The age the Bayan Mandahu Formation relative to other Gobi localities remains an open question. Makovicky (2008), using a cladistic approach to biostratigraphy, suggested that the Bayan Mandahu site was the oldest of the Gobi redbed deposits. However, two lines of evidence suggest that Bayan Mandahu may be younger than Bayn Dzak.

First, the Bayan Mandahu fauna combines taxa characteristic of the older Bayn Dzak assemblage, such as *Protoceratops* and *Pinacosaurus* (Godefroit *et al.* 1999; Lambert *et al.* 2001) with taxa that appear more closely related to animals found in the younger Barun Goyot assemblages, such as the *Bagaceratops*-like *Magnirostris* (You and Dong 2003) and the derived ingeniine *Machairasaurus*. This appears more consistent with the hypothesis that the Bayan Mandahu Formation lies between the older Bayan Dzak exposures and the younger Barun Goyot Formation in time.

Second, when the taxa found at Bayan Mandahu are compared with congeneric taxa in the Bayan Dzak assemblage, it is the Bayan Mandahu animals that are more derived. For instance, *Protoceratops hellenikorhinus* exhibits derived features that are absent from *P. andrewsi* (deep, abbreviated rostrum; forward-curving parietal bar; enlarged nasal ridges; large size: Lambert *et al.* 2001). Assuming equal rates of evolution on the branches leading to *P. andrewsi* and to *P. hellenikorhinus*, the more derived morphology of *P. hellenikorhinus* suggests that this lineage has been evolving for a longer time, and thus that this species would be the younger of the two sister species (or is descended from the first). A similar pattern is seen in the velociraptorines, where *Velociraptor osmolskae* exhibits derived features that are absent from *V. mongoliensis* (elongate maxillary fenestra, enlarged promaxillary fenestra: Godefroit *et al.* 2008). Again, *Pinacosaurus mephistocephalus* exhibits derived features that

are absent in *P. grangeri* (enlarged, spikelike horns on jugal and squamosal; caudal margin of external nares positioned along the midline: Godefroit *et al.* 1999). The consistently more derived or 'evolved' appearance of the Bayan Mandahu dinosaurs argues that Bayan Mandahu is younger than Bayan Dzak. Given this evidence, it is probable that Bayan Mandahu Formation is relatively young, perhaps even younger than the Ukhaa Tolgod assemblage.

Unfortunately, there are currently few chronostratigraphic data that can be used to determine the absolute age or relative age of the Bayan Mandahu Formation. The hypothesis of faunal turnover therefore appears to be a plausible explanation for the distinctive fauna seen at Bayan Mandahu (and other Gobi redbed deposits), but testing this hypothesis will require independent data concerning the age of the Cretaceous strata of Central Asia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Character descriptions and character-taxon matrix.

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