Article

A new dromaeosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China

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Abstract

We describe a new dromaeosaurid theropod from the Upper Cretaceous Wulansuhai Formation of Bayan Mandahu, Inner Mongolia. The new taxon, *Linheraptor exquisitus* **gen. et sp. nov.**, is based on an exceptionally well-preserved, nearly complete skeleton. This specimen represents the fifth dromaeosaurid taxon recovered from the Upper Cretaceous Djadokhta Formation and its laterally equivalent strata, which include the Wulansuhai Formation, and adds to the known diversity of Late Cretaceous dromaeosaurids. *Linheraptor exquisitus* closely resembles the recently reported *Tsaagan mangas*. Uniquely among dromaeosaurids, the two taxa share a large, anteriorly located maxillary fenestra and a contact between the jugal and the squamosal that excludes the postorbital from the infratemporal fenestra. These features suggest a sister-taxon relationship between *L. exquisitus* and *T. mangas*, which indicates the presence of a unique dromaeosaurid lineage in the Late Cretaceous of Asia. A number of cranial and dental features seen in *L. exquisitus* and *T. mangas*, and particularly some postcranial features of *L. exquisitus*, suggest that these two taxa are probably intermediate in systematic position between known basal and derived dromaeosaurids. The discovery of *Linheraptor exquisitus* is thus important for understanding the evolution of some salient features seen in the derived dromaeosaurids.

Key words: Dromaeosauridae, Theropoda, Upper Cretaceous, Nei Mongol, China

Introduction

Dromaeosaurids are a derived group of maniraptoran theropod dinosaurs currently known from the Cretaceous of both Laurasia and Gondwana (Norell & Makovicky 2004; Novas *et al.* 2009), although current phylogenetic hypotheses and the presence of troodontids (the sistergroup to dromaeosaurids) in older sediments predict their presence in the Jurassic (Sereno 1999; Xu *et al.* 2001; Hu *et al.* 2009). As one of the theropod groups most closely related to the Aves, dromaeosaurids are important for understanding avian origins and have been the focus of several recent studies (Norell & Makovicky 1997, 1999; Xu 2002; Senter *et al.* 2004; Makovicky *et al.* 2005; Turner *et al.* 2007b). The Upper Cretaceous Djadokhta Formation and its laterally equivalent beds in Mongolia and China have previously produced four dromaeosaurid taxa: *Velociraptor mongoliensis* Osborn, 1924; *Velociraptor osmolskae* Godefroit, Currie, Li, Shang & Dong, 2008; *Tsaagan mangas* Norell, Clark, Turner, Makovicky, Barsbold & Rowe, 2006; and *Mahakala omnogovae* Turner, Pol, Clarke, Erickson & Norell, 2007b. Here we report a fifth taxon from these beds based on a well-preserved specimen. It represents one of the few nearly complete and articulated dromaeosaurid skeletons from the Upper Cretaceous worldwide. The specimen was found in the Wulansuhai Formation of Bayan

Mandahu, Inner Mongolia, China, a lateral equivalent of the Djadokhta Formation (Jerzykiewicz *et al.* 1993). The specimen was discovered and excavated by members of the 2008 Gobi expedition, a joint project by the Institute of Vertebrate Paleontology & Paleoanthropology (IVPP) and the Long Hao Institute of Geology and Paleontology (LHIGP) aiming to improve our understanding of the dinosaurian fauna of the Late Cretaceous of Inner Mongolia.

Systematic Paleontology

Theropoda Marsh, 1881

Coelurosauria Huene, 1920

Maniraptora Gauthier, 1986

Dromaeosauridae Matthew & Brown, 1922

Linheraptor exquisitus **gen. et sp. nov.**

Etymology. The generic name refers to the animal's status as a predatory dinosaur ('raptor') from Linhe, Nei Mongol, China (area of origin); the specific name refers to the exceptional preservation of the holotype specimen.

    Holotype. IVPP V 16923**,** an articulated, nearly complete skeleton.

    Locality and Horizon. Bayan Mandahu, "The Gate" locality, Wulansuhai Formation, Campanian, Upper Cretaceous (Jerzykiewicz *et al.* 1993).

    Diagnosis. Dromaeosaurid that can be distinguished from other known dromaeosaurid taxa by the presence of the following autapomorphies: greatly enlarged maxillary fenestra sub-equal in size to external naris; several large foramina on lateral surface of jugal. Differs from other known dromaeosaurids except *Tsaagan* in the following features: large and anteriorly located maxillary fenestra; lacrimal lacking lateral flange over descending process and with relatively broad medial lamina; sharp angle between anterior and ascending processes of quadratojugal; contact between jugal and squamosal that excludes postorbital from infratemporal fenestra. Differs from *Tsaagan* in the following features: absence of osseous inner wall partly blocking antorbital fenestra; sharply rimmed ventral margin of antorbital fossa; considerably smaller angle between frontal and jugal processes of postorbital; anteroventrally curved postorbital process of squamosal; considerably shorter quadratojugal process of squamosal; dorsoventrally shorter lateral flange of quadrate; less curved and less posteriorly inclined quadrate shaft; paroccipital process more laterally oriented; angular more extended posteriorly towards glenoid fossa; considerably deeper posterior end of mandible such that glenoid fossa is approximately level with tooth row; pneumatic foramen present on axis vertebra.

    Description and comparison. The holotype specimen is probably an adult individual as indicated by the complete closure of the neurocentral sutures of all preserved vertebrae and the fusion of the tibiotarsus. Measuring approximately 1.8m in total length, *Linheraptor* is a relatively small theropod (Table 1), but is similar in size to other Asian Late Cretaceous dromaeosaurids (Norell & Makovicky 1997, 1999; Xu 2002; Norell *et al.* 2006; Turner *et al.* 2007a, 2007b).

    The skull as preserved is shallower than that of *Tsaagan*, which has a taller maxilla (Norell *et al.* 2006). However, preserved skulls of the dromaeosaurid taxon *Velociraptor mongoliensis* show considerable variation in their proportions due to preservational deformation. Thus, caution is warranted when differentiating dromaeosaurid taxa based on skull proportions alone. For comparison, the ratio of snout length to snout depth at the level of the anterior border of the antorbital fossa is about 0.2 in *Linheraptor* and 0.3 in *Tsaagan*. The skull is only slightly longer than the femur (Table 1), whereas derived dromaeosaurids such as *Deinonychus* appear to have proportionally longer skulls (Ostrom 1969). The cranial openings are similar in size, shape, and position to those of most other dromaeosaurids (Norell & Makovicky 2004): the external naris is located

relatively posteriorly, with most of its area lying posterior to the anterior extremity of the maxilla; the maximum anteroposterior diameter of the antorbital fossa is less than half the snout length; the obliquely oriented oval orbit extends further dorsally than the sub-triangular antorbital fenestra; the infratemporal fenestra is kidney-shaped; and the quadrate foramen is large.

TABLE 1. Measurements of selected elements in *Linheraptor exquisitus*, IVPP V 16923 (in millimeters; * indicates estimated measurement). Measurements are lengths except where noted.

Skull length (from snout tip to ventral end of quadrate)	225
Cervical series	320
Trunk length (first dorsal to acetabulum)	365*
Anteriormost caudal vertebra	20
A middle caudal vertebra (the longest preserved one)	30
Right scapula	160*
Right humerus	155*
Right radius	110
Metacarpal II	25
Metacarpal III	63
Metacarpal IV	52
Manual phalanx II-1	49
Manual phalanx III-1	37*
Manual phalanx III-2	52
Manual phalanx III-3	41
Manual phalanx IV-1	25
Manual phalanx IV-2	12
Manual phalanx IV-3	36*
Sternal plate length	80
Sternal plate width (each plate)	55
Right pubis	240
Right femur	230
Right tibiotarsus	255
Right metatarsal II	105
Right metatarsal III	125
Right metatarsal IV	110
Pedal phalanx II-2	25
Pedal phalanx II-3	75
Pedal phalanx III-1	50
Pedal phalanx III-2	25*
Pedal phalanx III-3	20*
Pedal phalanx III-4	45*
Pedal phalanx IV-4	22
Pedal phalanx IV-5	18

The premaxilla bears a long subnarial process that excludes the maxilla from the external naris, as in most dromaeosaurids (Barsbold & Osmólska 1999; Norell & Makovicky 2004), but in relative length this process is intermediate between the extremely long one in *Velociraptor* (Barsbold & Osmólska 1999) and the relatively

short ones in most other taxa such as *Deinonychus* (Ostrom 1969) and *Tsaagan* (Norell *et al*. 2006). An important similarity to *Tsaagan* (Norell *et al*. 2006), and a probable synapomorphy for *Linheraptor* and *Tsaagan* amongst dromaeosaurids, is that the large maxillary fenestra is anteriorly located and extends to the anterior border of the antorbital fossa. In other dromaeosaurids, including the two *Velociraptor* species (Godefroit *et al*. 2008), the maxillary fenestra is located considerably posterior to the anterior border of the antorbital fossa. However, the maxillary fenestra of *Linheraptor* is narrower and more slit-like than that of *Tsaagan*, which is relatively round. Unlike in *Tsaagan* (Norell *et al*. 2006), a small promaxillary fenestra is visible in lateral view and is located ventral to the maxillary fenestra. Comparatively, the promaxillary fenestra is larger and more dorsally located in the two *Velociraptor* species (Godefroit *et al*. 2008). Unlike in *Velociraptor* (Barsbold & Osmólska 1999), *Tsaagan*, and several other dromaeosaurids (Norell *et al*. 2006), the ventral margin of the antorbital fossa is sharply rimmed laterally. As in most other non-avian theropods, *Linheraptor* has a fully open antorbital fenestra. In *Velociraptor* and *Tsaagan* (Norell *et al*. 2006), the anterior portion of the antorbital fenestra has a small osseous medial wall; in some Liaoning deinonychosaurian specimens such as the *Mei long* holotype (Xu & Norell 2004), the antorbital fenestra has an even larger osseous floor. Unlike in *Tsaagan*, in which the nasal is only shallowly inflected, the nasal of *Linheraptor* is dorsally concave in lateral view. It bears a row of distinctive foramina close to the lateral edge as in *Deinonychus* (Ostrom 1969), *Velociraptor* (Barsbold & Osmólska 1999), and *Tsaagan* (Norell *et al*. 2006). The T-shaped lacrimal is similar to that of *Tsaagan* (Norell *et al*. 2006) in lacking a lateral flange over the descending process, and in bearing a relatively broad medial lamina that floors the posterodorsal corner of the antorbital fossa. The robust jugal bears a few relatively large foramina on its lateral surface. The postorbital process of the jugal contacts the squamosal to exclude the postorbital from the infratemporal fenestra, a feature otherwise known only in *Tsaagan* (Norell *et al*. 2006). In *Linheraptor*, the frontal and jugal processes of the postorbital are angled at slightly more than 90 degrees to each other, while in *Tsaagan* the angle between these processes is approximately 135 degrees (Norell *et al*. 2006). As in other dromaeosaurids (Norell *et al*. 2006), the quadratojugal is shaped like an inverted T, with the posterior process being much larger than the anterior process. As in *Tsaagan*, the angle between the anterior and ascending processes is smaller than 90 degrees. The quadratojugal forms the anterior and lateral borders of the quadrate foramen, which is proportionally even larger than in other dromaeosaurids except *Velociraptor* (Barsbold & Osmólska 1999). The ratio of the maximum diameter of the quadrate foramen to the height of the quadrate is 0.56 in *Linheraptor*, but significantly smaller than 0.5 in other dromaeosaurids except *Velociraptor*. The presence of a greatly enlarged and more laterally-facing foramen in *Linheraptor* and *Velociraptor* is associated with a number of features that distinguish these taxa from most other dromaeosaurids. These include proportionally longer ascending and posterior processes of the quadratojugal and a dorsoventrally shorter lateral flange of the quadrate. The posterior edge of the quadrate is less concave than in other dromaeosaurids (Norell *et al*. 2006). As in other dromaeosaurids, the squamosal has an anteroventrally oriented quadratojugal process that is inset from the lateral margin of the bone. This process is considerably shorter than that of *Tsaagan* (Norell *et al*. 2006). The postorbital process of the squamosal curves distinctly ventrally as in *Velociraptor* and *Deinonychus* (Ostrom 1969), unlike the straight postorbital process of *Tsaagan* (Norell *et al*. 2006). As in *Velociraptor* and other dromaeosaurids (Barsbold & Osmólska 1999), the paroccipital processes are posterolaterally oriented. In *Tsaagan*, the processes are pendant and are proximodistally longer (Norell *et al*. 2006), whereas in *Mahakala* they are intermediate in condition (Turner *et al*. 2007b). The braincase is currently under preparation, so it is not possible to determine if the basipterygoid processes are elongate as in *Tsaagan*.

The mandible has a slightly downturned anterior end, a feature described in some basal dromaeosaurids such as *Microraptor* (Xu 2002). It is nevertheless similar to those of other dromaeosaurids in possessing the following features: symmetric concave dorsal margin and convex ventral margin, two rows of mental foramina on the dentary, and prominent surangular crest overhanging an enlarged surangular foramen. A second surangular foramen appears to be present, a feature also seemingly present in *Tsaagan* (Norell *et al*. 2006). Relative to other dromaeosaurids, other distinctive features of the mandible of *Linheraptor* include a greater posterior extension of the angular that approaches the posterior level of the mandibular glenoid fossa,

and a considerably taller posterior end of the mandible such that the glenoid fossa is approximately level with the tooth row (in *Tsaagan* and *Dromaeosaurus* the posterior end of the mandible is shallow, and the glenoid fossa lies considerably ventral to the tooth row: Currie 1995; Norell *et al.* 2006).

Poor preservation of the dentition precludes exact counts of the premaxillary, maxillary, and dentary teeth. However, the dentary is inferred to bear about 15 teeth, a number similar to the counts recorded in *Tsaagan*, *Velociraptor*, and some other dromaeosaurids (Barsbold & Osmólska 1999; Norell *et al.* 2006). The maxillary and dentary teeth are relatively sparsely distributed. As in *Tsaagan* (Norell *et al.* 2006) and also most basal dromaeosaurids (Xu 2002), all teeth lack serrations along the anterior carina.

There are 10 cervical vertebrae including the atlas and axis. Corresponding to the S-shaped neck, the neural spines are oriented as follows along the cervical series: posteriorly in the second (axis), third and fourth cervicals; subvertically in the fifth cervical; anteriorly in the sixth through ninth cervicals; and nearly vertically again in the tenth. The neural spines of nearly all the presacral vertebrae other than the axis show little transverse expansion distally. The axis bears a large pneumatic foramen in the center of the lateral surface of the centrum, as in *Mahakala* (Turner *et al.* 2007b)*, Velociraptor* and *Deinonychus*, but not *Tsaagan* (Norell *et al.* 2006). Distinct pneumatic foramina are not visible on the lateral central surfaces of the middle and posterior cervical vertebrae, although deep lateral fossae are present. Epipophyses are well developed on the anterior cervical vertebrae, and the fifth vertebra bears an epipophysis that extends posteriorly to the level of the posterior edge of the postzygapophysis. Most cervical rib shafts, except the two most posterior ones, span nearly two cervicals. The sixth and seventh cervical ribs are the most robust, while the ninth and tenth (and possibly the eighth) are relatively short anteroposteriorly. In the middle of the cervical series, the cervical rib heads are partially fused to the corresponding vertebrae. The posterior surfaces of the dorsal ribs bear long, slender uncinate processes, which arise from the mid-shaft region in each case. The uncinate processes angle dorsally, and each process extends posteriorly beyond the posterior margin of the next rib in the series, as in *Velociraptor* (Norell & Makovicky 1999). As in most dromaeosaurids except the unenlagiines and *Mahakala* (Makovicky *et al.* 2005; Turner *et al.* 2007b), the caudal vertebrae possess extremely elongated prezygapophyses and chevrons. The middle and posterior caudal vertebrae are not significantly elongated. The longest middle caudal vertebrae are proportionally much shorter than those of basal paravians including basal dromaeosaurids (Xu 2002). They are approximately 170% as long as the most anterior caudal vertebrae, a condition similar to derived dromaeosaurids such as *Velociraptor* (Norell & Makovicky 1999). The lateral surface of each middle caudal vertebra is flat and lacks a longitudinal groove or ridge near the neurocentral suture as in some basal dromaeosaurids such as *Mahakala*, *Buitreraptor* and *Rahonavis* (Makovicky *et al.* 2005; Turner *et al.* 2007b). Distinct, strap-like transverse processes are present on at least the first 12 caudal vertebrae. In *Velociraptor*, transverse processes are present on only 11 caudal vertebrae (Norell & Makovicky 1999). Interestingly, the transition is sudden, with no vertebrae intermediate between those with distinct transverse processes and those that lack transverse processes entirely. Long, low, distinct neural spines are present back to at least the 15th caudal vertebra.

The two sternal plates are fused anteriorly but separate posteriorly. The sternal plates are transversely curved, and the midline of the entire bipartite structure forms a low carina.

The humerus is less than 70% the length of the femur. A prominent longitudinal groove is present along the posterior surface immediately distal to the deltopectoral crest, a feature shared with *Velociraptor* and *Deinonychus* (Norell & Makovicky 1999). This groove is much wider proximally than distally. The radius bears a semilunate lateral flange distally. On the basis of positional homologies, we identify the manual digits of *Linheraptor* as corresponding to the middle three digits of ancestral archosaurs, as is currently hypothesized for all maniraptorans (Xu *et al.* 2009). While the manus is in general similar to that of derived dromaeosaurids, manual phalanx IV-1 is more than twice as long as IV-2, a condition shared with basal dromaeosaurids such as *Microraptor* (Xu 2002). Although IV-1 is considerably longer than IV-2 in all dromaeosaurids (Xu 2002), IV-1 is less than twice the length of IV-2 in *Archaeopteryx* (Wellnhofer 2008) and in derived dromaeosaurids like *Deinonychus* (Ostrom 1969) and *Velociraptor* (Norell & Makovicky 1999).
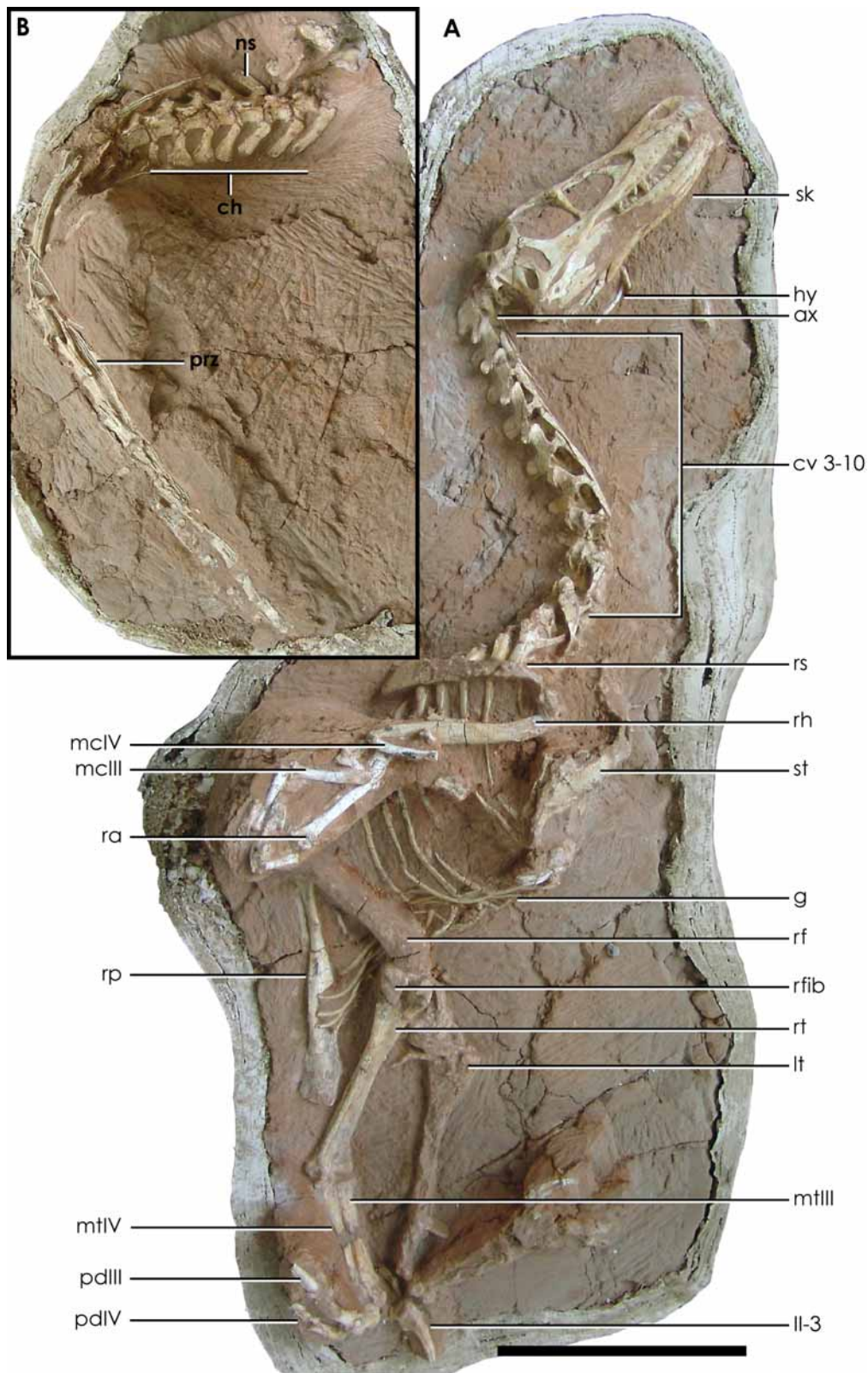
FIGURE 1. Photographs of the holotype of *Linheraptor exquisitus* (IVPP V 16923). The specimen was collected in two separate plaster-jackets: the main jacket (A) contains the majority of the skeleton; the second jacket (B) contains the partial tail. Abbreviations: II-3, pedal ungual, digit II; ax, axis; ch, chevrons; cv, cervical vertebra; g, gastralia; hy, hyoid; lt, left tibia; mc, metacarpal; mt, metatarsal; ns, neural spine; pd, pedal digit; prz, elongated prezygapophyses; ra, radius; rf, right femur; rfib, right fibula; rh, right humerus; rp, right pubis; rs, right scapula; rt, right tibia; sk, skull; st, sternum. Scale bar equals 20 cm.
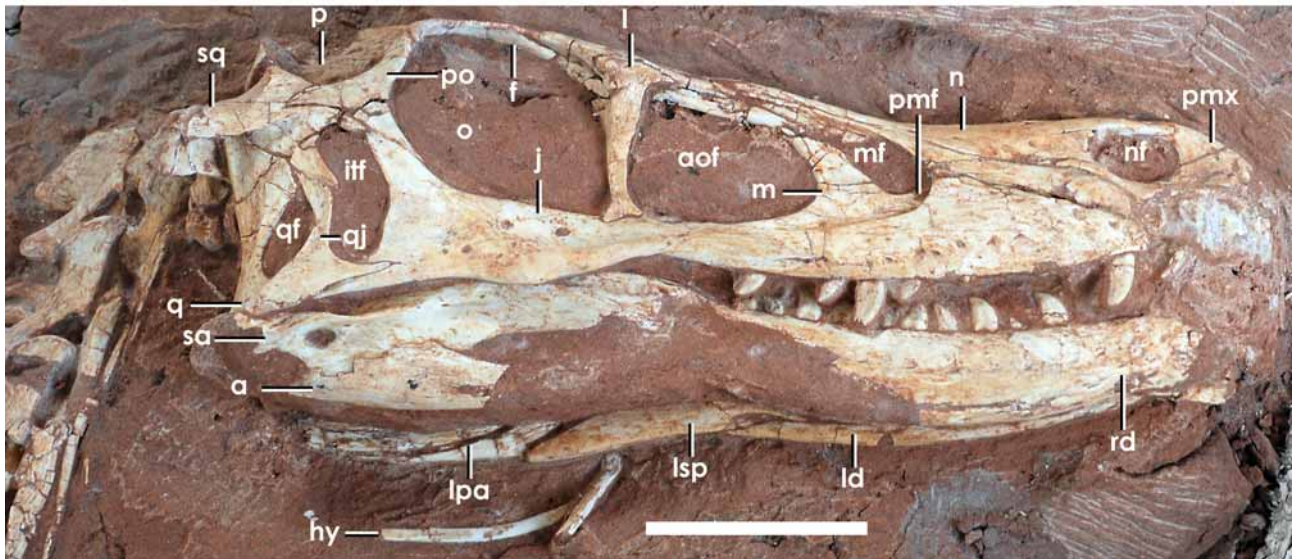
FIGURE 2. Photograph in right lateral view of the skull and mandible of the *Linheraptor exquisitus* holotype (IVPP V 16923). Abbreviations: a, angular; aof, antorbital fenestra; f, frontal; hy, hyoid; itf, infratemporal fenestra; j, jugal; l, lacrimal; ld, left dentary; lpa, left prearticular; lsp, left splenial; m, maxilla; mf, maxillary fenestra; n, nasal; nf, narial fenestra; o, orbital; p, parietal; pmf, promaxillary fenestra; pmx, premaxilla; q, quadrate; qf, quadrate foramen; qj, quadratojugal; rd, right dentary; sa, surangular; sq, squamosal. Scale bar equals 5 cm.

The posteriorly projecting pubis is longer than the femur as in some other dromaeosaurids, such as *Velociraptor* and *Deinonychus* (Ostrom 1976). This feature may characterize derived dromaeosaurids, given that basal dromaeosaurids resemble most other non-avian theropods in having a pubis shorter than the femur (Xu 2002). A longer pubis relative to the femur appears to be correlated with a full posterior rotation of the pubis in derived dromaeosaurids. The pubis is straight in lateral view, and although it lacks a distinct pubic boot, the distal quarter is anteroposteriorly enlarged relative to the shaft. Proximal to the anteroposteriorly expanded distal region, the pubic shaft forms a considerable lateral expansion as in *Velociraptor*. This condition is somewhat similar to that of basal dromaeosaurids from Liaoning (Xu 2002), in which a lateral projection occurs near the midpoint of the pubic shaft. The hindlimb has proportions intermediate between those of basal and derived dromaeosaurids (Table 1): the tibiotarsus and metatarsus are respectively 111% and 54% the length of the femur. In derived dromaeosaurids such as *Velociraptor* (Norell & Makovicky 1997, 1999), the distal segments of the hindlimb are proportionally shorter. The astragalus and calcaneum are fused to each other and appear to be co-ossified with the tibia, forming a true tibiotarsus. The tibia bears a distinct tuberosity medial to the distal end of the fibular crest, along the anteromedial margin of the shaft. The two hemicondyles of the astragalus-calcaneum complex are transversely narrow.

Discussion

Linheraptor is referable to the Dromaeosauridae based on a suite of derived features unique to the group: squamosal with lateral flange overhanging descending process; quadrate with large lateral flange; and quadrate foramen large and developed between the quadrate and quadratojugal. *Linheraptor* also has a jugal with a broad and plate-like postorbital process, and a highly modified pedal digit II with a raptorial, hypertrophied claw. These are both derived features seen in other dromaeosaurids, although they also evolved independently in certain other theropod taxa (Xu 2002). *Linheraptor* is probably a member of a derived dromaeosaurid clade based on several features present in derived dromaeosaurids but absent in basal ones such as unenlagiines and *Mahakala* (Currie 1997; Xu 2002; Makovicky *et al.* 2005; Turner *et al.* 2007b): caudal vertebrae with significantly elongated chevrons and prezygapophyses; pubis longer than femur; full opisthopubic condition; and non-arctometatarsalian foot.

Among known dromaeosaurids, *Linheraptor* is probably more closely related to *Tsaagan* than to other dromaeosaurid taxa because the two taxa share a few unique features unknown in other dromaeosaurids: large, anteriorly located maxillary fenestra; lacrimal lacking lateral flange over descending process and with relatively broad medial lamina; sharp angle between anterior and ascending processes of quadratojugal; and contact between jugal and squamosal that excludes postorbital from infratemporal fenestra. The two taxa also share a relatively long anterior projection of the maxillary body beyond the antorbital fossa (a feature also seen in *Velociraptor*) and tooth crowns lacking serrations along the anterior carina (similar to basal dromaeosaurids). Although *Linheraptor* is similar to *Velociraptor* in many features, most of these features are probably plesiomorphic. Furthermore, *Velociraptor* is probably more closely related to derived dromaeosaurids than to *Linheraptor* because *Velociraptor* and derived dromaeosaurids share a number of features. These include tooth crowns with posterior serrations that are considerably larger than anterior ones and proportionally shorter tibia and metatarsus relative to femur. These features are unlike the typical coelurosaurian condition and indicative of the uniqueness of the group (Currie 1997).

The importance of *Linheraptor*, in the context of dromaeosaurid diversity, is enhanced by the preservation in this taxon of many phylogenetically informative postcranial features that cannot be assessed in the highly incomplete *Tsaagan*. These features help to establish that *Linheraptor* and *Tsaagan*, which can be identified as close relatives on the basis of cranial features, constitute a unique dromaeosaurid lineage in the Late Cretaceous of Asia. The new character information provided by *Linheraptor* is likely to confirm that *Tsaagan* and *Linheraptor* are both intermediate in systematic position between the basal and derived dromaeosaurids, a phylogenetic hypothesis already proposed for *Tsaagan* (Norell *et al.* 2006). This phylogenetic position is supported by the presence of a lateral expansion near the midpoint of the pubic shaft, a feature probably homologous to the lateral projection seen in basal Early Cretaceous dromaeosaurids from Liaoning (Xu 2002). Additional evidence comes from the proportions of the forelimb and hindlimb. The significantly shortened manual phalanx IV-2 is proportionally intermediate between the Liaoning dromaeosaurids and other dromaeosaurids (Xu 2002). The moderately elongate lower segments of the hindlimb are intermediate between highly cursorial basal dromaeosaurids and derived dromaeosaurids with distal hindlimb elements that are relatively short compared to other non-avian coelurosaurian theropods (Currie 1997). A detailed description of *Linheraptor* and a numerical analysis of its systematic position will be given elsewhere.

References

Barsbold, R. & Osmólska, H. (1999) The skull of *Velociraptor* (Theropoda) from the late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, 44, 189–219.

Currie, P.J. (1995) New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology*, 15, 576–591.

Currie, P.J. (1997) Dromaeosauridae. *In*: Currie, P.J. & Padian, K. (Eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego, 194–195.

Gauthier, J. (1986) Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, 8, 1–55.

Godefroit, P., Currie, P.J., Li, H., Shang, C.-Y. & Dong, Z.M. (2008) A new species of *Velociraptor* (Dinosauria: Dromaeosauridae) from the Upper Cretaceous of northern China. *Journal of Vertebrate Paleontology*, 28, 432–438.

Hu, D.Y., Hou, L.-H., Zhang, L.J. & Xu, X. (2009) A pre-*Archaeopteryx* troodontid from China with long feathers on the metatarsus. *Nature*, 461, 640–643.

Huene, F. von. (1920) Bemerkungen zur Systematik und Stammesgeschichte einiger Reptilien. *Zeitschrift für Induktive Abstammungsund Vererbungslehre*, 22, 209–212

Jerzykiewicz, T., Currie, P.J., Eberth, D.A., Johnston, P.A., Koster, E.H. & Zheng, J.-J. (1993) Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. *Canadian Journal of Earth Sciences*, 30, 2180–2190.

Makovicky, P. J., Apesteguía, S. & Agnolín, F.L. (2005) The earliest dromaeosaurid theropod from South America. *Nature*, 437, 1007–1011.

Marsh, O.C. (1881) Principal characters of American Jurassic dinosaurs. Part IV. *American Journal of Science (series 3)*, 21, 417–423

Matthew, W.D. & Brown, B. (1922) The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History*, 46, 367–385.

Norell, M.A. & Makovicky, P.J. (1997) Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates*, 3215, 1–28.

Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R. & Rowe, T. (2006) A new dromaeosaurid theropod from Ukhaa Tolgod (Omnogov, Mongolia). *American Museum Novitates*, 3545, 1–51.

Norell, M.A. & Makovicky, P.J. (1999) Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates*, 3282, 1–45.

Norell, M.A. & Makovicky, P.J. (2004). Dromaeosauridae. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria* (second edition). University of California Press, Berkeley, 196–209.

Novas, F.E., Pol, D., Canale, J.I., Porfiri, J.D. & Calvo, J.O. (2009) A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society B*, 276, 1101–1107.

Osborn, H.F. (1924) Three new Theropoda, *Protoceratops* zone, central Mongolia. *American Museum Novitates*, 144, 1–12.

Ostrom, J.H. (1969) Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bulletin of the Peabody Museum of Natural History, Yale University*, 30, 1–165.

Ostrom, J.H. (1976) On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. *Breviora*, 439, 1–21.

Senter, P., Barsbold, R., Britt, B.B. & Burnham, D.A. (2004) Systematics and evolution of Dromaeosauridae (Dinosauria, Theropoda). *Bulletin of the Gunma Museum of Natural History*, 8, 1–20.

Sereno, P.C. (1999) The evolution of dinosaurs. *Science*, 284, 2137–2147.

Turner, A.H., Hwang, S.H. & Norell, M.A. (2007a) A small derived theropod from Oosh, Early Cretaceous, Baykhangor Mongolia. *American Museum Novitates*, 3557, 1–27.

Turner, A.H., Pol, D., Clarke, J.A., Erickson, G.M. & Norell, M.A. (2007b). A basal dromaeosaurid and size evolution preceding avian flight. *Science*, 317, 1378–1381.

Wellnhofer, P. (2008) *Archaeopteryx: der Urvogel von Solnhofen*. Verlag Dr. Friedrich Pfeil, München, 256 pp.

Xu, X. (2002) *Deinonychosaurian fossils from the Jehol Group of western Liaoning and the coelurosaurian evolution*. PhD thesis, Chinese Academy of Sciences, Beijing.

Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C.-k., Han, F.-l. & Guo, Y. (2009) A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature*, 459, 940–944.

Xu, X. & Norell, M.A. (2004) A new troodontid from China with avian-like sleeping posture. *Nature*, 431, 838–841.

Xu, X., Zhao, X.-J. & Clark, J.M. (2001). A new therizinosaur from the Lower Jurassic Lufeng Formation of Yunnan, China. *Journal of Vertebrate Paleontology*, 21, 477–483.