

New Oviraptorid Dinosaur (Dinosauria: Oviraptorosauria) from the Nemegt Formation of Southwestern Mongolia

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Abstract *Nemegtia barsboldi* gen. et sp. nov. here described is a new oviraptorid dinosaur from the Late Cretaceous (mid-Maastrichtian) Nemegt Formation of southwestern Mongolia. It differs from other oviraptorids in the skull having a well-developed crest, the anterior margin of which is nearly vertical, and the dorsal margin of the skull and the anterior margin of the crest form nearly 90°; the nasal process of the premaxilla being less exposed on the dorsal surface of the skull than those in other known oviraptorids; the length of the frontal being approximately one fourth that of the parietal along the midline of the skull. Phylogenetic analysis shows that *Nemegtia barsboldi* is more closely related to *Citipati osmolskae* than to any other oviraptorosaurs.

Key words: Nemegt Basin, Mongolia, Nemegt Formation, Late Cretaceous, Oviraptorosauria, *Nemegtia*.

Introduction

Oviraptorosaurs are generally regarded as non-avian theropod dinosaurs (Osborn, 1924; Barsbold, 1976, 1977, 1981, 1983, 1986, 1997; Gauthier, 1986; Smith, 1992; Sereno, 1999; Barsbold, Currie *et al.*, 2000; Barsbold, Osmólska *et al.*, 2000; Holtz, 2000, 2001; Norell *et al.*, 1994; Norell *et al.*, 1995; Norell, Clark, and Makovicky, 2001; Xu, Norell *et al.*, 2002). They are medium-sized theropods characterized by a short, deep skull with toothless jaws in derived forms, teeth present in primitive forms such as *Incisivosaurus gauthieri* (Xu, Cheng *et al.*, 2002) and *Caudipteryx zoui* (Ji *et al.*, 1998), pneumatized caudal vertebrae present in derived forms, anteriorly concave pubic shaft, and a posteriorly curved ischium present in Oviraptoridae (Barsbold and Osmólska, 1990; Barsbold, Osmólska *et al.*, 2000; Makovicky and Sues, 1998). Oviraptorosauria is here regarded to include three families: Oviraptoridae, Caenagnathi-

dae, and Caudipterygidae (Barsbold, 1976; Sternberg, 1940; Currie, 2000; Clark *et al.*, 2001; Ji *et al.*, 1998; Zhou and Wang, 2000; Zhou *et al.*, 2000).

The Oviraptorosauria are mainly distributed in Mongolia (Osborn, 1924; Barsbold, 1976, 1977, 1981, 1983, 1986, 1997; Osmólska, 1976; Norell *et al.*, 1994, 1995; Wester, 1996; Clark *et al.*, 1999, 2001, 2002), China (Dong and Currie, 1996; Ji *et al.*, 1998; Lü *et al.*, 2000; Xu, Cheng *et al.*, 2002; Lü, 2003) and North America (Sternberg, 1940; Cracraft, 1971; Currie and Russell, 1988; Sues, 1997). Additionally, oviraptorosaurs from the Southern Hemisphere have been reported (Frey and Martill, 1995; Currie *et al.*, 1996; Frankfurt and Chiappe, 1999), although validity of the taxonomic assignment is doubtful.

In the summer of 1996, an incomplete oviraptorid skeleton with a nearly complete skull was discovered in the Nemegt Formation of Nemegt Basin, southwestern Mongolia by the Mongolian

Highland International Dinosaur Project team. It was initially described by Lü *et al.* (2002) as *Ingenia* sp. The skull morphology (vertical anterior margin of the developed crest on the skull, less exposed nasal process of the premaxilla, and a process on the quadrate bearing a convex surface projecting into the cotyla on the medial surface of the quadratojugal) indicates that it is distinct from named oviraptorosaurs. It represents a new taxon from the Late Cretaceous.

Systematic Paleontology

Theropoda Marsh, 1881

Oviraptorosauria Barsbold, 1976

Family Oviraptoridae Barsbold, 1976

Nemegtia gen. nov.

Diagnosis: As for the only known species.

Etymology: *Nemegtia* refers to the fossil locality, the Nemegt Basin of southwestern Mongolia.

Nemegtia barsboldi sp. nov.

(Figs. 1, 3, 5, 6)

Ingenia sp. Lü *et al.*, 2002

Etymology: The species is named in honor of Dr. R. Barsbold, the Mongolian vertebrate paleontologist, one of the leaders of the Mongolian Highland International Dinosaur Project.

Type locality and horizon: The Nemegt locality of Gradzinski *et al.* (1968), Nemegt Basin, southern Gobi Desert, Mongolia; Nemegt Formation, mid-Maastrichtian (Jerzykiewicz and Russell, 1991) of the Upper Cretaceous.

Holotype: GIN100/2112 (formerly PC100/2112, see Lü *et al.*, 2002): an incomplete skeleton with a nearly complete skull. Specimen stored in the Paleontological Center of the Mongolian Academy of Sciences, Ulan Bator, Mongolia.

Diagnosis: An oviraptorid displaying the following derived characters. The skull with a nasopremaxillary crest, anterior margin (the nasal process of the premaxilla) nearly vertical; the

nasal process of the premaxilla, which forms part of the crest, being barely exposed in dorsal view; the anteroposterior length of the frontal is approximately one quarter of that of the parietals; a presence of prefrontal; process on the quadrate bears a convex surface projecting into the cotyla on the medial surface of the quadratojugal. Mandibular condyles of the quadrate situated rostrally to the occipital condyle.

Description

1. Skull and mandible

The skull (Fig. 1) is deep, narrow and short, and has a naso-premaxillary vertical crest. The jaws are toothless, and the articular has a medial process. These characters indicate that *Nemegtia barsboldi* is a derived oviraptorosaur.

Skull: The premaxillae, vomers and maxillae form a hard palate as in other oviraptorid dinosaurs (Fig. 1C), and the premaxillae form the main part of the crest. Both premaxillae are fused. The central palatal part of the joined premaxillae is strongly concave. There is a cleft on the central part of the palate. Anteriorly, small foramina distributed on the lateral sides of the suture between the premaxillae may represent nutrient openings. The nasal processes of the premaxillae are perpendicular to the palatal surface of the upper jaw, and extend dorsally, connecting with the nasals at the highest point of the crest (Fig. 1A), and is barely exposed in dorsal view of the skull. The crest extends posteriorly and ventrally, and forms a round arc at its highest point.

The antorbital cavity consists of a large internal antorbital fenestra posteriorly and a small maxillary fenestra (see Witmer, 1997) anteroventrally. The internal antorbital fenestra is sub-oval, and the long axis is vertical. The external surface of the maxilla is smooth, and moderately concave. Ventrally, there are two longitudinal, rounded ridges on each maxilla as in other oviraptorids. In addition to the lateral ridge, there is a longitudinal groove. Posteriorly, there is a ventrally directed tooth-like process on the palatal shelf of each maxilla as in other oviraptorids.

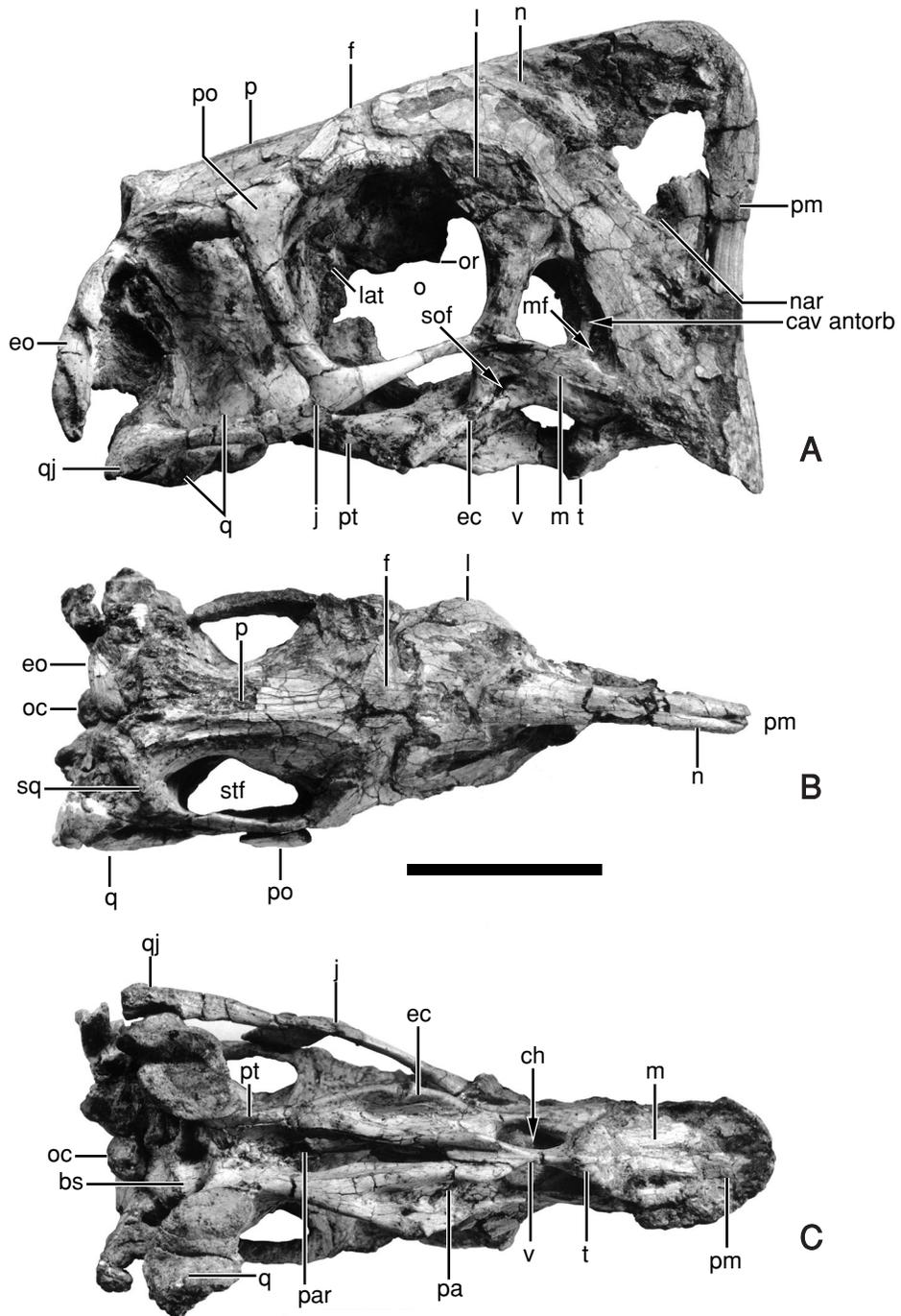


Fig. 1. The skull of *Nemegtia barsboldi* gen. et sp. nov. (GIN100/2112). In lateral (A), dorsal (B), and ventral views (C). Scale bar=5 cm. Abbreviations, as in appendix 1.

Both nasals are completely fused posteriorly with no trace of the suture. Anteriorly, the nasals are not fused, forming a “<” shaped cleft, which receives the nasal processes of the premaxillae (Fig. 1B). The dorsal portion of the lacrimal is crescent shaped in lateral view. The shaft of the lacrimal is stout, and forms the posterior margin of the antorbital cavity. There is a large lacrimal foramen in the middle of the anterior edge of the orbit. The posterodorsal part of the lacrimal is wedged between the prefrontal and frontal. The lateral surface of the lacrimal is smooth. Posterodorsal to the antorbital cavity, there is a large recessed pneumatic pocket (6 mm high, 4 mm wide), similar to that in *Citipati osmolskae* (Clark *et al.*, 2002).

Anterodorsal to the left orbit, there is a small triangular bone, which is located between the frontal and lacrimal. It should be a prefrontal, although this bone has not been reported in other oviraptorosaurs.

The jugal is a triradiate bone. The posterior part of its anterior branch is stout and plate-like. Anteriorly, it gradually becomes rod-like and then ends as a thin plate (Fig. 2), where it inserts between the maxilla, lacrimal and ectopterygoid.

The postorbital process of the jugal inclines posterodorsally, and forms almost 2/3 of the height of the postorbital bar, similar to other oviraptorosaurs (Barsbold *et al.*, 1990). The process becomes widened, and slightly twisted, and its medial surface is smooth, near the position where it contacts the descending process of the postorbital. The dorsal part of the postorbital process of the jugal is tightly attached to the posteroventral surface of the postorbital. The posterior branch of the jugal contacts the anterior process of the quadratojugal. The angle of the postorbital branch and posterior branch of the jugal is 90°, which form the anterior and ventral margins of the large lateral temporal fenestra, respectively.

The width of the frontal is much greater than its length. In lateral view, the whole central part of the frontal surface is convex, thus the transverse cross-section of the frontal is arc-shaped. The anteroposterior length of the frontal is approximately one quarter of that of the parietals. Anteriorly, the suture of the frontal and the nasal is relatively straight, while posteriorly, the suture with the parietal is convex anteriorly (Fig. 1B). There is a deep groove along the suture with the nasal. When compared with other oviraptorids,

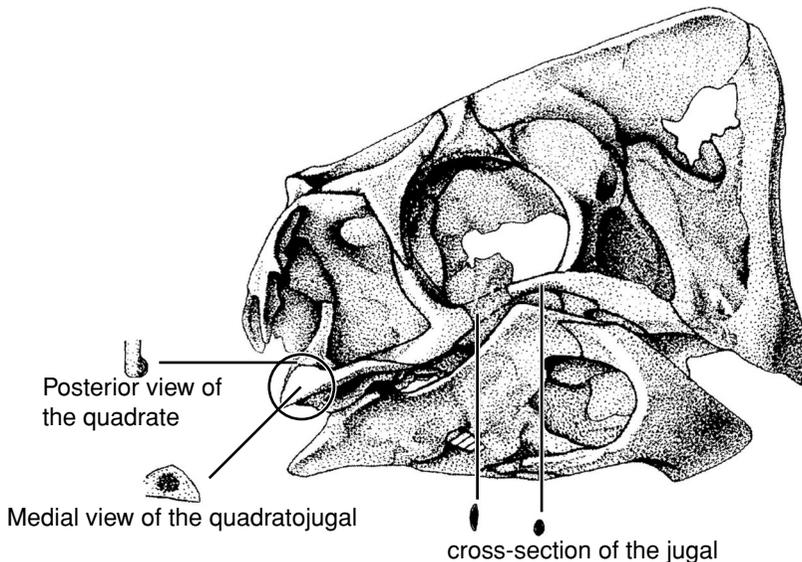


Fig. 2. Skull of *Nemegtia barsboldi* gen. et sp. nov. (GIN100/2112) showing the structure of the jugal and the relationship between the quadrate and the quadratojugal.

the frontal is very short medially and widens laterally towards orbital margin.

The parietals are fused. Their dorsal surface is smooth. A sagittal parietal ridge is present. This ridge extends anteriorly and disappears at the level of the anterior corner of the supratemporal fossa, not reaching the frontoparietal suture.

The right squamosal is almost completely preserved. It curves posteriorly. There is a notch, which holds the distal lateral head of the quadrate on the middle of the lateral margin. The anterior process of the squamosal forms the postolateral margin of the sub-oval supratemporal fossa. The long axis of the suboval supratemporal fossa points anterolaterally, making an angle with the long axis of the skull of nearly 30°.

The postorbital is a triradiate bone. The frontal process of the postorbital is upturned about 90 degrees. Its descending process occupies 2/3 of the height of the postorbital bar. The anterior surface of this process is smooth. The angle of the anteromedial process and the posterior squamosal process is greater than 90°. The frontal process covers the orbital process of the frontal. The squamosal process extends posteriorly with a sharp dorsal margin and overlies the anterior process of the squamosal. This process does not reach the posterolateral corner of the supratemporal fossa. The upper part of the postorbital bar forms most of the anterolateral margin of the supratemporal fossa.

A shallow groove separates the articular surface into two parts in the quadrate. In ventral view, the width of the mandibular articular surface of the quadrate is greater than its length. The mandibular condyles are situated rostrally to the occipital condyle. The articular surface for the quadratojugal is convex, while that on the quadratojugal for the quadrate is concave. This joint forms a mobile junction (Fig. 2), which is similar to the condition in most birds and other oviraptorosaurs (Maryanska and Osmólska, 1997). The convex quadrate and concave quadratojugal joint is reversed from the condition in other oviraptorosaurs (Maryanska and Osmólska, 1997).

In ventral view, the vomer has a sharp process, which projects ventrally. This tooth-like process is also formed in part by processes of the maxillae. The vomers are completely fused anteriorly. The posterior parts of the vomers are separated from each other by the cultriform process of the parasphenoid, which wedges rostrally between the vomers as in all oviraptorids. The middle part of the vomer is relatively long, its surface is smooth, and its dorsal part is fused with the anterior part of the cultriform process. The posterior part of the vomer is covered by the anterior part of the palatal ramus of the pterygoid. The fused part of the vomer projects ventrally, and the middle part has a round ventral surface, while its posterior part is relatively flat.

The palatine forms the posterior and lateral margins of the elliptic choana. It connects with the vomer medially, and with the maxilla anterolaterally. The posterolateral part of the palatine contacts the anteromedial side of the ectopterygoid, and its posteromedial part contacts the palatal ramus of the pterygoid.

Ventrally, the pterygoids have elongated palatal processes, which do not meet along the middle line until they contact the vomers. Each palatal process has a longitudinal groove, which divides the palatal branch of the pterygoid into two parts anteriorly: the lateral part connects with the ectopterygoid, while the medial one connects with the palatine and quadrate.

The ectopterygoid is located rostral to the pterygoid. It extends vertically, similar to other derived oviraptorids, whereas in other theropods, it extends horizontally. The posterior end of the dorsal part disappears near anterior end of the jugal. There is an opening within ectopterygoid, which is close to the maxilla. This opening may be homologous to the dorsal ectopterygoid recess of dromaeosaurids (Witmer, 1997).

The epipterygoid is present on both sides of the skull. It is a thin plate-like bone with an irregular triangular shape, whose free vertex angle projects dorsally. It tightly ties to the pterygoid branch of the quadrate. Its anterior margin is sharp and free.

The basioccipital condyle is ball-shaped, with a weak neck region. The articular surface of the occipital condyle faces posteroventrally. The anterior part of the basioccipital projects ventrally and laterally, forming the posterior part of the basal tubera. The suture of the basioccipital and basisphenoid is clear. Its middle part projects posteriorly; therefore, in the ventral view, the suture has a weak “W” shape.

The basisphenoid forms the posteroventral part of the floor of the braincase. The sutures with the pterygoid, and the parasphenoid are not clear. In ventral view, it is narrow anteriorly and broad posteriorly. The portion comprising the basal tubera is strongly developed. Its middle portion is strongly depressed, and has a large opening. This opening is probably the Vidian canal for the passage of the internal carotid artery and the palatal branch of nerve VII, which entered the pituitary fossa through the basisphenoid. The basiptyergoid process is absent, similar to other derived oviraptorosaurs (Clark *et al.*, 2002).

The tall parasphenoid process is delicate. It is shallow anteriorly and deep posteriorly. Its depth gradually lessens anteriorly, as it connects with the vomer. Its posterodorsal part extends dorsally between the epiptyergoid and pterygoid, contacting the laterosphenoid. In ventral view, it extends forward into the large space called interptyergoid vacuity. Its length is about 1/4 of that of the skull.

The laterosphenoid is a thin plate-like bone, anterior to the floor of the braincase. The orbitosphenoid is also a thin plate like bone, anterior to laterosphenoid portion of the floor of the braincase.

The suture between the exoccipital and supraoccipital is not clear, but the trend of the suture shows that both exoccipitals connect above the oval foramen magnum. Thus, they separate the supraoccipital from the foramen magnum, which is larger than the occipital condyle.

Mandible: The lower jaw is short and deep (Fig. 3). The dorsal margin of the external mandibular fenestra is formed by the surangular and the dorsal arch of the dentary. The surangular has a middle branch, which projects into the ex-

ternal mandibular fenestra, as in other oviraptorids. The ventral surface of the lower jaw is convex, and the mandibular symphysis is short. In dorsal view, the jaw slightly projects laterally in the middle part, and both branches of the lower jaw are parallel posteriorly from the level of the posterior margin of the mandibular symphysis (Fig. 3A). The dentaries have a dorsal protrusion near the posterior margin of the mandibular symphysis. The large external mandibular fenestra is located at the anterior part of the lower jaw. The coronoid process is posterior to the mandibular fenestra.

The mandibular symphysis is short and deep. No evidence shows that a coronoid is present in the present specimen. CT scanning shows that the dorsal margin of the mandibular symphysis is thin, while its lower margin (lower part) is stout, the symphysis is highly pneumatized, and the spaces are uniform in size and distribution (Figs. 4A, B). There is no bony construction between the hollow spaces of the right and left dentaries. The cross section near the mandibular symphysis shows that both sides are steep, displaying a “V” shape. It is “U” shaped in *Caenagnathus* and there is a bar of bone between the dorsal and ventral surface supporting the midline ridge on the lingual surface of the symphyseal shelf (Currie *et al.*, 1993; Figs. 4C, D). Around the anterior margin of the external mandibular fenestra, the dentaries are deflected inwards, forming a shallowly flattened surface, thus producing a thin and sharp anterior edge on the external mandibular fenestra. The ventral process of the dentary is relatively weak, and it tightly extends along the ventrolateral part of the anterior portion of the angular, and disappears at the level of the coronoid eminence. The dorsal process of the dentary is comparatively massive, and dorsally, its distal end is divided into lateral and medial prongs, with the anterior branch of the articular-surangular-coronoid complex (ASC) wedged between them. It disappears anterior to the coronoid eminence. The ventral process of the dentary extends more posteriorly than that of the dorsal process. Only the external surfaces of both processes of the dentaries are

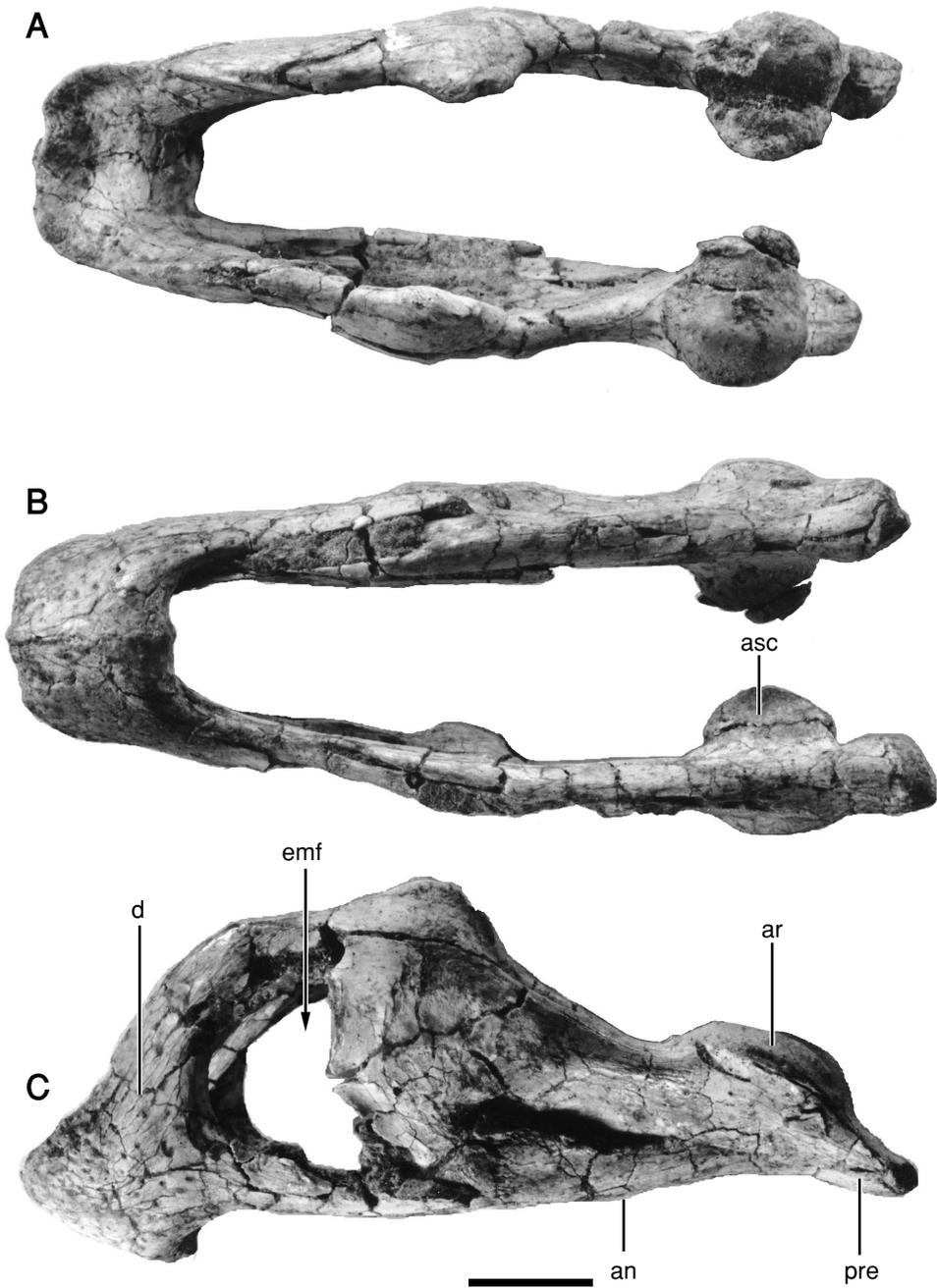


Fig. 3. Lower jaw of *Nemegtia barsboldi* gen. et sp. nov. (GIN100/2112). In dorsal (A), ventral (B), and lateral (C) views. Scale bar=2 cm. Abbreviations as in appendix 1.



Fig. 4. Comparison CT scans of the corresponding positions of the lower jaws of *Nemegtia* (GIN100/2112) and *Caenagnathus*. A, C: cross section through anterior part of the symphyseal region; B, D: cross section through the posterior portion of the symphyseal region. Scale bar=10 mm (C and D are chosen from Currie *et al.*, 1993, Fig. 7). Abbreviations as in appendix 1.

smooth. Anterior to the external mandibular fenestra and the lateral edges of the mandibular symphysis, irregular small holes are densely distributed. A row of four small foramina is symmetrically distributed on both sides of the serrated suture of the mandibular symphysis. This row of small foramina extends posterolaterally, forming a nearly 30° angle with the serrated symphyseal suture. The lateral surface of the ventral part of the mandibular symphysis is convex, and there is a process centrally.

The surangular and articular are fused in the posterior part of the lower jaw, with no clear suture between them. The fused part occupies the position, which corresponds to the position of the articular, surangular, and coronoid in other theropods. Currie *et al.* (1993) named it as the articular-surangular-coronoid complex (ASC).

There is a longitudinal rounded ridge on the articular surface. This ridge corresponds to the longitudinal sulcus on the articular surface of the quadrate condyle. The ridge separates the articular surface into two parts: a medial one, called the internal mandibular process by Sternberg (1940), is large and semicircular, and a lateral one, called the external mandibular process (Sternberg, 1940), is smaller and sub-oval. The surface of the lateral one slightly slants laterally. The lengths of both processes are nearly equal. The retroarticular process is slender, extending posteroventrally from the articular surface. Its ventral and medial surfaces are covered by the prearticular. Its lateral surface is covered by articular-surangular-coronoid complex. The angular does not cover the prearticular, and it projects posteromedially. The articular-surangular-coro-

noid complex occupies the major part, posterior to the posterior margin of the external mandibular fenestra. There is a deep, longitudinal groove on the lateral surface of the anteroventral part of the articular bone. This depression should be the insertion area for the external mandibular adductors. The coronoid process projects posteromedially.

The angular wedges anteriorly between the splenial and the ventral process of the dentary, and disappears anteriorly to the anterior margin of the external mandibular fenestra. Medially, the suture with the prearticular is clear, but, laterally, the suture with the surangular is not clear.

The prearticular is located at the ventromedial surface of the articular. It is a thin plate-like bone, which covers a part of the medial surface of the lower jaw.

The splenial is strap-like, wider anteriorly than posteriorly. It contacts the dentary anteriorly, but it does not take part in the formation of the mandibular symphysis. Its medial surface is

smooth. It becomes thin and sharp posteriorly, and disappears at the level of 1/3 length of the lower jaw from the retroarticular process.

2. Postcranial skeleton

A nearly complete cervical series, part of the dorsal vertebrae, a nearly complete sacrum, both ilia, the proximal ends of the pubis and ischium, the proximal end of the femur, parts of the humerus, and the complete right radius are preserved.

Cervical series: The cervical series (Fig. 5) includes 12 of 13 vertebrae naturally articulated (including a small part of the axis). Although sometimes, it is difficult to distinguish the posterior cervical vertebrae from the anterior dorsal vertebrae, the presence of a weak median ventral keel and a hypapophysis on the last of the naturally articulated 13 vertebrae indicate that this last vertebra should be the first dorsal vertebra. Thus, with the atlas, the number of the cervical vertebrae is 13. The measurements of the pre-

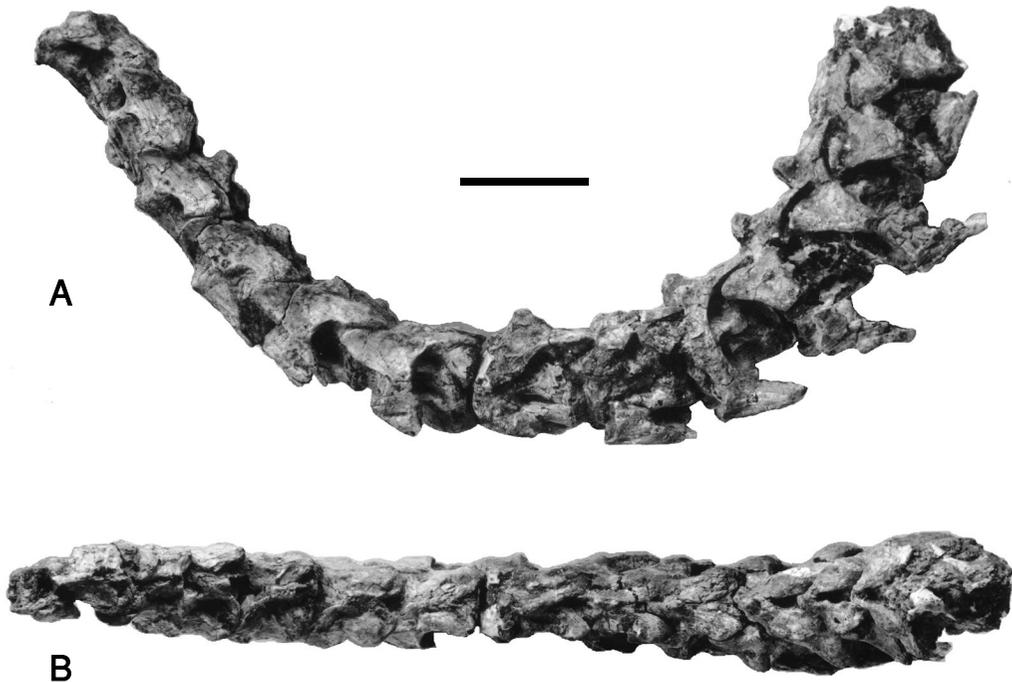


Fig. 5. The cervical vertebrae and the anterior dorsal vertebra (the last one) of *Nemegtia barsboldi* gen. et sp. nov. (GIN100/2112). In lateral view (A), and dorsal view (B). Scale bar=5 cm. Abbreviations as in appendix 1.

Table 1. The measurements of the 12 (including part of axis but not the atlas) articulated cervical vertebrae and the first dorsal vertebra (mm).

	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	D1
Length of the centrum	?	33	29	32	31	31	33	35	37	37	36	33	31
Width of the centrum	?	15	27	30.5	39	39	40	42*	42*	43	48	52	52*

“*” represents estimation, “?” missing.

served 13 vertebrae are given in Table 1.

Only the posterior part of the axis is preserved, and it is fused with the third cervical vertebra. Two postzygapophyseal facets are preserved, and the distal end of the postzygapophysis is relatively sharp. There is no epiphysis on the dorsal surfaces of postzygapophyses.

The anterior end of the 3rd cervical vertebra is almost twice as wide as the posterior end. The central part of the lateral surface is strongly depressed with a well-developed elongated pleurocoel. In the lateral view, the centrum is wedge-shaped. There is a weak epiphysis on the posterodorsal surface of the postzygapophysis. The posterior articular end of the centrum is concave.

The neural arch of the 4th cervical vertebra is obviously larger than that of the 3rd centrum, but the length of the centrum is slightly shorter than the anterior one. From the lateral view, the anterior articular end slants anterodorsally at 45°, corresponding to the posterior end of the anterior connected centrum. The anterior margin of the prezygapophysis slightly outruns the anterior margin of the centrum, whereas the posterior margin of the postzygapophysis is at the level of the posterior end.

In dorsal view, the distance between the postzygapophyses of the 5th cervical vertebra is greater than that between the prezygapophyses. The epiphysis is well developed. The anteriorly slanted spine is much lower than the previous one. The anterior margin of the prezygapophysis extends far beyond the margin of the anterior end of the centrum. The posterior margin of the postzygapophysis is located anterodorsally to the posterior articular end of the centrum. Compared with the 4th vertebra, the relative position of the neural arch on the centrum is greatly changed,

the position of the neural arch is much more forward.

The distance between the prezygapophyses and that of the postzygapophyses of the 6th cervical vertebra is nearly equal to the length of the centra, thus forming a square outline. This is different from that of other centrum in that the anterior and posterior widths are equal in dorsal view, the diapophyseal facets are larger than that of the anterior ones, but smaller than that of the posterior ones.

In dorsal view, the distance between the prezygapophyses of the 7th cervical vertebra is longer than that of the postzygapophyses. The lateral surface of the centrum is concave, with a well-developed pleurocoel on the central part. The anterior margin of the pleurocoel is sharp, its posteroventral margin is not clear. The size, position and the morphology of epiphysis are similar to that of the 6th cervical vertebra.

The neural arch of the 8th cervical vertebra is obviously smaller than those of the anterior ones. The distance between the prezygapophyses is slightly greater than that of the postzygapophyses. The epiphysis is relatively small and located anteriorly. The facet of the postzygapophysis faces posteroventrally.

In the 9th to 13th cervical vertebrae, the size of each vertebra is nearly equal. The position of pleurocoels on the lateral surface of the centra gradually moves posteriorly from the 9th centrum to the 13th centrum. It arrives at the central part of the centrum in the 12th cervical vertebra, and the pleurocoel is oval. The radius of the posterior margin of the pleurocoel is larger than those of the anterior ones, while the radius of the anterior margin of the pleurocoel is larger than the posterior one in the anterior vertebrae. There

are clear fossae posteroventral to the prezygapophyses of the 11th and the 12th cervical vertebrae. The infradiapophyseal fossa is reduced in the posterior vertebrae. There is no infraprezygapophyseal fossa. The distance between the prezygapophyses of the five vertebrae is equal to that of the postzygapophyses, but this distance is shorter than the length of the centrum. Therefore, their outlines are rectangle. The facet of the postzygapophysis faces postolaterally. The posterior part of the ventral surface of the centrum is flat and slightly expanded.

The neural spines of the cervical vertebrae are short and centered on neural arch, giving neural arches an "X" shaped appearance (Fig. 5B), as that in Caenagnathidae, *Microvenator celer*, and other oviraptorids (Makovicky and Sues, 1998). The vertebrae in the middle of the cervical series are the largest (5th, 6th and 7th). The facets of the postzygapophysis from the 3rd to 8th cervical vertebrae face posteroventrally, while those from the 9th to 13th vertebrae face posterolaterally. An infradiapophyseal fossa appears in the 11th and 12th cervical vertebrae. In dorsal view, the outline formed by the four zygapophyses in the sixth cervical is nearly square, it is rectangle (the angle formed by the right-left prezygapophysis with the centered neural arch is greater than 90°) in the 4th and 5th cervical vertebrae, but the angle is less than 90° after the seventh cervical vertebrae. There are also variations in the pleurocoels. They are relatively small in anterior vertebrae. The anterior margin of the oval pleurocoel is larger than that of the posterior margin from the 3rd to 9th cervical vertebrae, whereas the pleurocoel of the 10th is circular. From the 11th to the last cervical vertebrae, the posterior margin of the pleurocoel is larger than its anterior margin.

Almost all the cervical ribs are preserved. The axis rib is slender, rod-like and it is the longest one among the cervical ribs. It extends to the anterior end of the 4th cervical rib. The 3rd cervical rib is also rod-like, longer than the length of the 3rd centrum.

The 5th and the 6th cervical ribs are very similar. The rib head is fused with the parapophysis,

while the rib tubercle is not fused with the centrum. The rib tubercle of the 5th cervical rib is smaller than that of the 6th cervical rib.

In the 7th to 12th cervical ribs, the rib tubercle and rib head are completely fused with the diapophyses and parapophyses of the centra. The tubercle of the 13th cervical rib is clearly not fused with parapophysis, and its morphology is similar to the anterior ones.

Dorsal vertebrae: Only the anterior one and a half dorsal vertebrae, and three posterior dorsal vertebrae and two neural arches, which articulated with the sacral vertebrae, are preserved. The count of dorsal vertebrae is uncertain.

The pleurocoel in the 1st dorsal vertebra is much larger than those of cervical vertebrae. The distance between the postzygapophyses becomes shorter. There is a weak ventral keel. A clear projection on the middle part of the ventral margin of the anterior end of the vertebra represents the hypapophysis. According to Sues (1997), the presence of the hypapophysis generally appears to be restricted to the first three or four dorsal vertebrae in non-avian theropods. Compared with the cervical vertebrae, the first dorsal vertebra is short and high, and the posterior articular end is flat. The spine is triangular in anterior and posterior views. The anterior margin of the prezygapophyseal facet approaches the middle of the anterior vertebra, unlike that of the cervical vertebrae. Only the anterior part of the 2nd dorsal vertebra is preserved, and the anterior articular surface is strongly concave.

On the five preserved posterior dorsal vertebrae, only the neural arches of the anterior two posterior dorsals are preserved. The base of the transverse process is wider than on posterior vertebra. The pleurocoel in the middle two is large and circular. The neural spine is wide, thin and plate-like. Its width is nearly $2/3$ of the length of the vertebra.

The last dorsal vertebra is located medial to the anterior end of the ilium, and has a free rib, but its transverse process contacts the ilium. The ventral surface of the centrum is round. There is a large pleurocoel in the middle of the lateral sur-

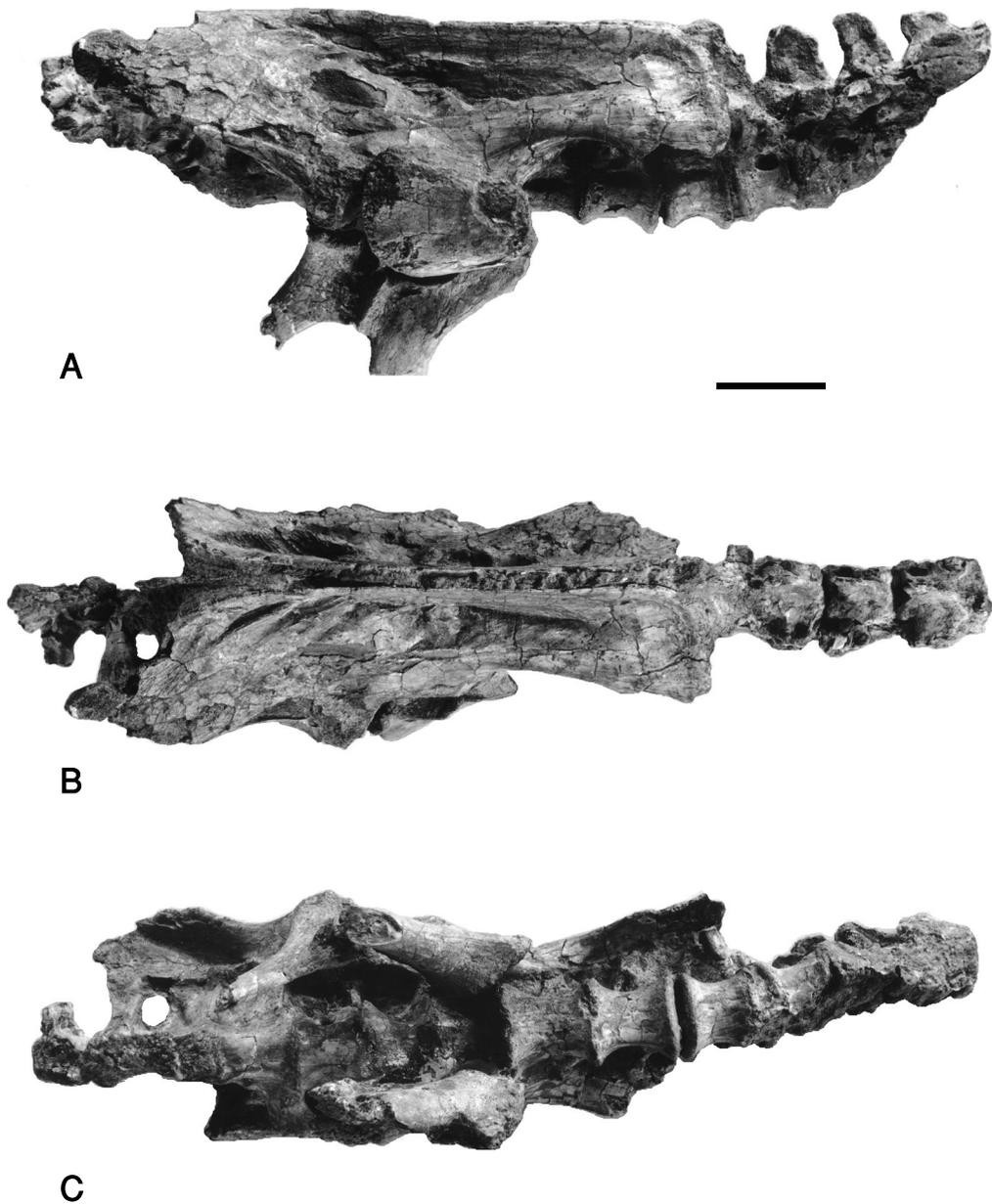


Fig. 6. Sacrum and pelvic girdle of *Nemegtia barsboldi* gen. et sp. nov. (GIN100/2112).

face of the centrum. The posterior articular end is not fused to the first sacral vertebra and the articular surface is slightly concave.

Sacral vertebrae: There are 8 sacral vertebrae (Fig. 6). The anterior six are completely preserved, the 7th sacral vertebra is partly preserved, and the 8th has preserved only a small anterior

part and its neural arch. Whether their spines are fused together or not is uncertain, due to their being covered by the matrix, but it is clear that the distal ends of the spines do not rise above the dorsal margins of the ilia. The measurements of the sacral vertebrae are given in Table 2.

The width of the anterior end of the 1st sacral

Table 2. The measurements of the sacral vertebrae (mm).

	S1	S2	S3	S4	S5	S6	S7	S8
Length of the centrum	32	33	29	29	29	32	40	?
Width of the centrum	22	23	22	20	21	21	?	?

“?” missing.

vertebra is greater than its posterior end. The anterior articular end is strongly concave. The ventral surface of the centrum is smooth. The 2nd sacral vertebra is similar to the 1st, except that the pleurocoel is elongated and enlarged, and it occupies nearly 1/2 the length of the centrum. The width of the anterior end of the 3rd centrum is larger than its posterior end, while in the 4th and 5th centra, the width of both ends is equal. There is a shallow groove on the anterior portion of the ventral surface in the 4th centrum. This is clearly different from other centra. The pleurocoel becomes smaller, and the sacral rib of the 4th vertebra is located at the same level as the ischiadic peduncle. The anterior articular end is larger than the posterior in the 6th centrum, and the contact area of the rib with the centrum is the largest among the sacrals, occupying nearly the whole length of the centrum. Only a small part of its anterior end is fused with the posterior end of the 5th centrum. The small pleurocoel is located on the mid-posterior part of the centrum. The distal end of the 7th sacral rib is divided into two parts, which contact the ilium. Posterior to where the sacral rib is fused with the sacral centrum, there are two fenestrae, which are nearly parallel to each other, and they are much larger than the anterior pleurocoels. The right sacral rib of the 8th sacral vertebra is fused with the transverse process of the centrum and is nearly rod-like. The middle of the rib shaft is relatively slender, but both ends are widened. Its distal end tightly contacts the internal surface of the ilium. The preserved part shows that the fusion with the connected centra is weaker than that of other centrum.

Caudal vertebrae: Only the neural arches of the first two caudal vertebrae are preserved. The nearly vertical facet of the prezygapophysis faces

inwards, while the postzygapophysis faces laterally.

Shoulder girdle and the fore limb: The proximal end of the left scapula is preserved. It is similar to those of other oviraptorosaurs. Distal parts of both humeri are preserved (Figs. 7A, B). The preserved portions are similar to other oviraptorosaurs, but there is a fossa on the anterior surface (Fig. 7A, fmb) occupying a similar position to the *fossa m. brachialis* (Baumel and Witmer, 1993) in modern birds. This is not observed in other oviraptorosaurs.

The right radius is completely preserved (Figs. 7C, D). It is straight, and the cross section of the shaft is oval. Both ends are slightly expanded, but the proximal is larger.

Pelvic girdle and the hind limb (Fig. 6): The preserved length of the ilium is 280 mm. In lateral view, the dorsal margin of the ilium is straight, and the depth of the preacetabular process is the same as that of the postacetabular process. The anterodorsal part of the preacetabular process is concave, while its ventral part is convex. The pubic peduncle is slender and projects downwards and its articular end is triangular. The ischiadic peduncle is relatively stout with a round articular end. Dorsally, the ilia nearly meet, but are not fused. The same condition is also found in other oviraptorosaurs, such as *Nomingia gobiensis* (Barsbold, Osmólska *et al.*, 2000).

Only the proximal part of both ischia is preserved. The process that contacts the pubis is smaller than that which articulates with the ilium. The proximal ends of both pubes are preserved.

Only the proximal end of the femur is preserved. There is a clear neck between the femoral head and the shaft of the femur. The angle of the neck and the shaft is about 90°. There is a shallow groove between the greater trochanter and

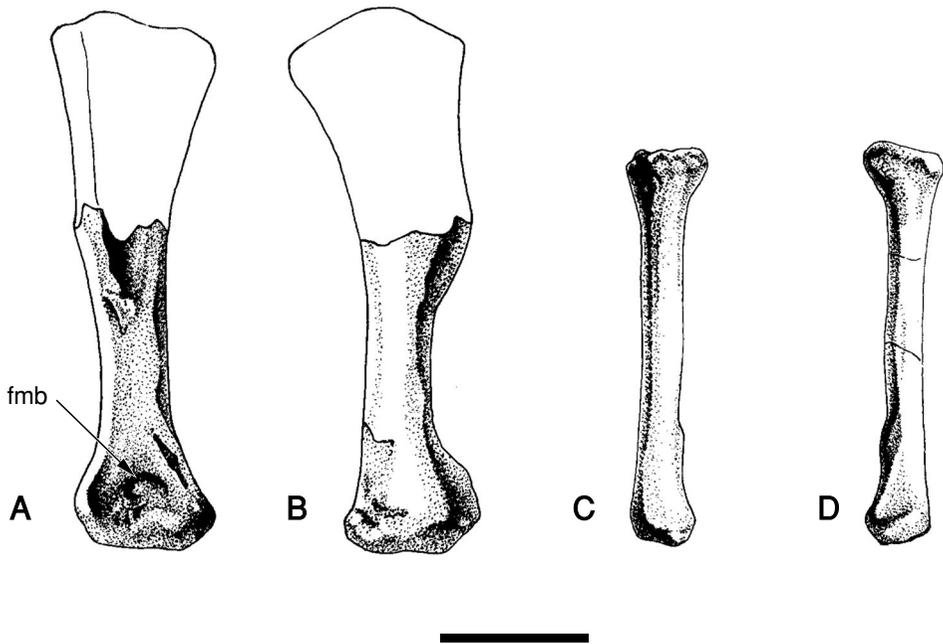


Fig. 7. The left humerus in anterior view (A) and posterior view (B) and the right radius in medial view (C) and lateral view (D) of *Nemegtia barsboldi* gen. et sp. nov. (GIN100/2112). Scale bar=4 cm. Abbreviations as in appendix 1.

the femoral head. The lesser trochanter is smaller and fingerlike. It connects tightly with the greater trochanter. The broken surface shows that many bony struts are distributed near the lateral wall of the shaft.

Comparison and Discussion

The high, narrow and short skull with toothless jaws and the medial process of the articular indicate that *Nemegtia barsboldi* is a derived oviraptorosaur (Barsbold and Osmólska, 1990; Barsbold, 1997). *Nemegtia* is different from *Oviraptor* in the skull crest. The anterior margin of the skull crest is vertical and the highest point of the crest is located between the nasals and premaxillae in *Nemegtia barsboldi*. The dorsal anterior margin of the premaxilla projects forward and the ventral anterior margin of the crest is concave posteriorly in the specimen GIN 100/42, which was described as *Oviraptor philoceratops* by Barsbold *et al.* (1990). The highest point of

the crest is located above between the lacrimals in *O. mongoliensis*, although the anterior margin of the crest is nearly vertical (Barsbold and Osmólska, 1990). Dorsally, the premaxillae are barely exposed, and the anteroposterior length of the parietal is greater than the frontal in *Nemegtia barsboldi*, but the exposed nasal process of the premaxilla is much larger than the nasals, and the lengths of the parietal and the frontal are nearly equal in *O. philoceratops* (Barsbold and Osmólska, 1990). An additional opening appearing on the wall within the antorbital cavity in *Nemegtia barsboldi* is smaller than that of the *O. philoceratops*. The posterior margin of the quadrate condyle is distinctly posterior to the anteroventral margin of the occipital condyle in *O. philoceratops*. The shape of the ilium, and the number of the sacral vertebrae are also different between *Nemegtia* and *Oviraptor*.

Nemegtia barsboldi has eight sacral vertebrae whereas *Ingenia yanshini* has six or seven. *Nemegtia barsboldi* has a distinct crest in contrast

to *Ingenia yanshini*. The ischiadic peduncle of the ilium is relatively stout, and the pubic peduncle is relatively weak in *Nemegtia barsboldi*, as opposed to the condition in *Ingenia yanshini*.

Nemegtia barsboldi is different from *Conchoraptor gracilis* in having a developed crest, while the skull has no crest in *Conchoraptor gracilis*.

Nemegtia barsboldi is different from *Citipati osmolskae*, in that the convex crest is higher than the dorsal surface of the skull, and the occiput and the quadrate are vertical, while the top of the skull crest is below the dorsal surface of the

skull, the occiput and the quadrate sloped anterodorsally in *Citipati osmolskae* (Clark *et al.*, 2001; 2002), the width and the length of the cervical vertebrae are not so different in *Nemegtia barsboldi*, but the length of the cervical vertebrae is about two times longer than their width in *Citipati osmolskae*. The phylogenetic analysis shows that *Nemegtia barsboldi* is more closely related to *Citipati osmolskae* than to any other oviraptorosaurs (Fig. 8).

Nemegtia barsboldi differs from *Khaan mckennai* (Clark *et al.*, 2001) in having both a distinct skull crest and a parietal crest, which are

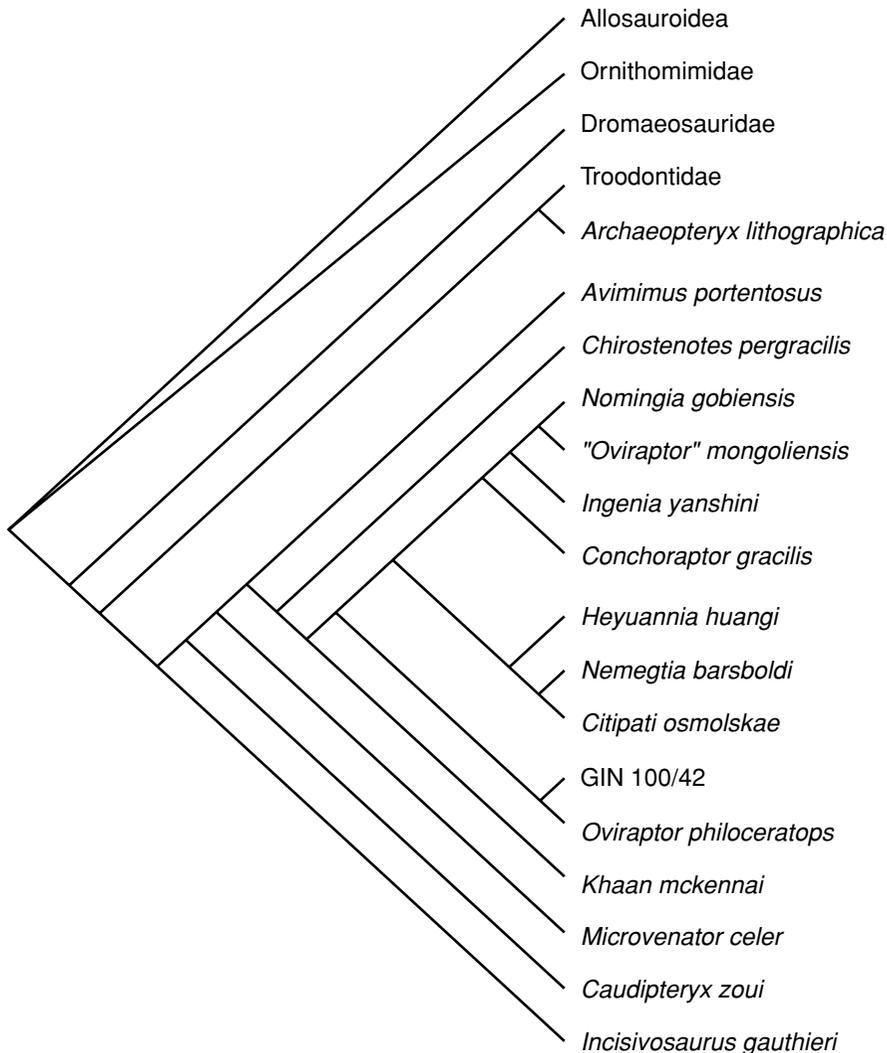


Fig. 8. One most parsimonious tree found by PAUP.

lacking in *Khaan*. The dorsal process of the premaxilla is vertical in *Nemegtia barsboldi*, but it extends posterodorsally in *Khaan mckennai*, the jugal extends further anteriorly in *Nemegtia barsboldi*, but it extends further posteriorly in *Khaan mckennai*.

Nemegtia barsboldi is different from *Nomingia gobiensis* in that having eight sacral vertebrae, compared to five in *Nomingia gobiensis*; the dorsal margin of the ilium is straight in *Nemegtia barsboldi*, but convex in *Nomingia gobiensis*; the pubic peduncle is more slender and weaker in *Nemegtia barsboldi*, compared to *Nomingia gobiensis*. *Nomingia* has a pygostyle (Barsbold, Currie *et al.*, 2000).

Nemegtia barsboldi differs *Microvenator celer* in having one pleurocoel on the cervicals and hypophysis on the ventral surface of dorsal vertebrae in *Nemegtia*, compared with two pleurocoels and no hypophysis in *Microvenator celer*; the number of sacral vertebrae is at least 8 in *Nemegtia barsboldi*, it is less than 6 in *Microvenator celer*.

Nemegtia barsboldi differs from *Caudipteryx zoui* in that *Nemegtia barsboldi* has no premaxillary teeth, while *Caudipteryx zoui* has premaxillary teeth. *Nemegtia* has a well-developed crest in the skull, but the skull of *Caudipteryx zoui* lacks a crest. Additionally, the pubic peduncle is slender and weaker than ischiadic peduncle in *Nemegtia barsboldi*, but it is stronger in *Caudipteryx zoui*.

Nemegtia barsboldi differs from *Heyuannia huangi* (Lü, 2003) in that the articular surface for the quadratojugal is convex, while it is more groove-like in *Heyuannia huangi*. *Nemegtia barsboldi* has a developed skull crest, whereas *Heyuannia huangi* does not. In the lateral view, the dorsal margin of the ilium is straight throughout its length, while it is convex in *Heyuannia huangi*.

The relative position of the external nasal opening and the antorbital cavity varies in different oviraptorosaurs. The apparent primitive state is with the dorsal margin of the external nasal opening below or near the level of the dorsal

margin of the antorbital cavity (Fig. 9), such as in *Incisivosaurus gauthieri*. In *Caudipteryx* sp. (IVPP V 12430, Zhou *et al.*, 2000), although the skull is heavily crushed, it still can be inferred that the dorsal margin of the external nasal opening is below the dorsal margin of the antorbital cavity. Derived forms have the dorsal margin of the external nasal opening above the dorsal margin of the antorbital cavity, a larger distance being more derived. This condition in *Nemegtia barsboldi* shows that *Nemegtia barsboldi* is a more derived oviraptorosaur.

The morphology of the lower jaw of *Nemegtia* shows that it is similar to those of derived oviraptorosaurs, *Oviraptor philoceratops* and *O. mongoliensis*, *Ingenia yanshini* (Barsbold *et al.*, 1990), *Citipati osmolskae* (Clark *et al.*, 2002), *Khaan mckennai* (Clark *et al.*, 2001), and *Heyuannia huangi* (Lü, 2003), in which the lower jaw is short and deep, the upper margin of the external mandibular fenestra is formed by the surangular and the dorsal branch of the dentary, the surangular has a middle branch, which projects into the external mandibular fenestra. The ventral surface of the lower jaw is convex, and the mandibular symphysis is short. This is different from that of *Caenagnathus collinsi* (Sternberg, 1940; Cracraft, 1971; Currie *et al.*, 1993), where the lower jaw is slender and shallow, the mandibular symphysis is also longer, the external mandibular fenestra is elongate with a dorsal margin, which is formed by the surangular, and the surangular had no middle branch. *Incisivosaurus gauthieri* (Xu, Cheng *et al.*, 2002) also has a longer lower jaw, similar to that of *Caenagnathus collinsi*, but it bears teeth. It may represent a primitive caenagnathid oviraptorosaur.

Eight sacral vertebrae are present in *Nemegtia barsboldi*, similar to some derived oviraptors but more than most known non-avian theropod dinosaurs. More basal theropods, such as *Compsognathus longipes* (Ostrom, 1978), and *Dilophosaurus wetherilli* (Welles, 1984) have four sacrals, five in the relatively advanced theropods-*Ceratosaurus* (Gilmore, 1920), *Al-*

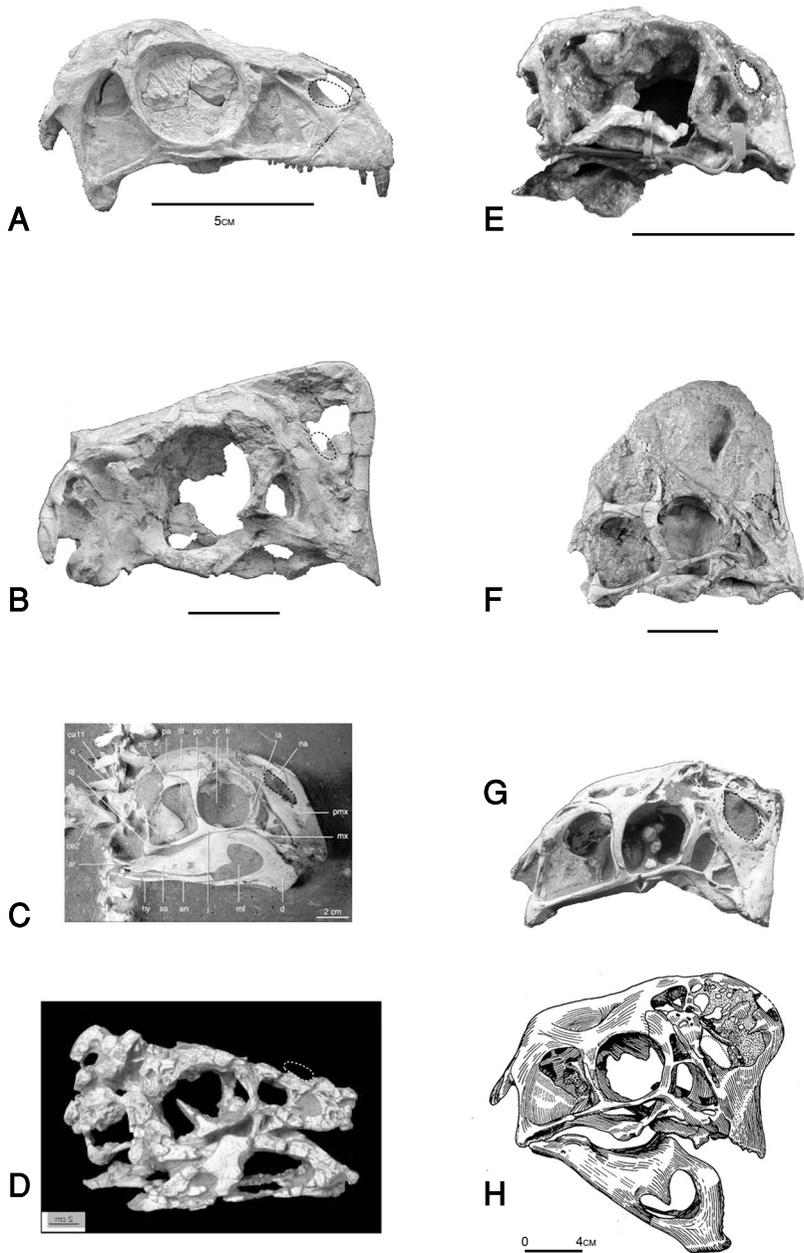


Fig. 9. Skulls of (A) *Incisivosaurus gauthieri*, (B) GIN 100/2112, (C) *Khaan mckennai* (from Clark *et al.*, 2001), (D) *Oviraptor philoceratops* (reversed, from Clark *et al.*, 2002), (E) *Conchoraptor gracilis*, (F) “*Oviraptor*” *mongoliensis*, (G) *Citipati osmolskai* (from Clark *et al.*, 2002), and (H) *Oviraptor philoceratops* (GIN 100/42) (from Barsbold, 1986). Scale bar=5 cm in A, B, E and F, 2 cm in C and D, 4 cm in H.

losaurus fragilis (Madsen, 1976), *Nomingia gobiensis* (Barsbold, Osmólska *et al.*, 2000), six or seven in *Oviraptor* (Barsbold *et al.*, 1990), and eight in *Heyuannia huangi* (Lü, 2003).

Nemegtia barsboldi independently acquired the avian characters such as the fused premaxillae, as in *Confuciusornis sanctus* (Chiappe *et al.*, 1999), toothless jaws, and the presence of nutrient openings on the premaxilla and the maxilla as in other oviraptorids.

Sharp ventrolateral margins of the premaxillae indicate that a keratinous structure probably covered the end of the rostrum, as in *Erlicosaurus andrewsi* (Clark *et al.*, 1994), ornithomimids (Norell, Makovicky, and Currie, 2001; Kobayashi and Lü, 2003), and birds. The rod-like jugal is similar to that of *Confuciusornis sanctus* and other birds (Elzanowski, 1999), the mobile condition between the quadrate and the quadratojugal is similar to the condition of most birds, and so are the increased cervical and sacral vertebral counts.

Phylogenetic Analysis

In order to determine the phylogenetic status of *Nemegtia barsboldi* among oviraptorosaurs, 20 taxa and 200 characters (107 cranial and 93 postcranial characters) (Appendices 2 and 3) are used for this analysis. All characters are equally weighted and unrooted. The character/matrix are modified from Maryanska *et al.* (2002). Five new genera of Oviraptorosauria are added to the matrix; these include *Khaan mckennai* (Clark *et al.*, 2001), *Citipati osmolskae* (Clark *et al.*, 2001, 2002), *Incisivosaurus gauthieri* (Xu, Cheng *et al.*, 2002), *Nemegtia barsboldi*, and *Heyuannia huangi* (Lü, 2003). The aim of this analysis is to determine the phylogenetic position of *Nemegtia barsboldi* among oviraptorosaurs, so the most primitive forms such as *Herrerasaurus ischigualastensis*, *Coelophysis bauri*, and the specialized forms such as Tyrannosauridae and Alvarezsauridae, which were used by Maryanska *et al.* (2002) as the outgroup in their analysis, are excluded from the present analysis. Although *Mi-*

crovenator celer and Troodontidae were excluded in Maryanska *et al.*'s analysis due to the large amount of missing data they thought (Maryanska *et al.*, 2002), taxa should not be excluded a priori from phylogenetic analysis based only on the number of preserved characters (Kearney and Clark, 2003). Therefore, in the present analysis, these taxa are still employed. Most characters are from Maryanska *et al.* (2002). New characters and their sources in appendix 2 are in bold.

Phylogenetic analysis was performed using MacClade 3.08 (Maddison and Maddison, 1992) and PAUP 4.0b (Swofford, 1998). Because of the large data set (20 taxa) and many missing character states, a Heuristic Search was used (Swofford and Begle, 1993), with branch-swapping options of the TBR swapping algorithm method. The analysis resulted in one most parsimonious tree (tree length=481; consistency index=0.5073; retention index=0.6269) (Fig. 8). This tree shows that Oviraptorosauria forms a monophyletic group. Nineteen unambiguous synapomorphies support this clade. These characters are 1(1), 9(1), 23(1), 37(1), 40(1), 41(2), 43(1), 46(1), 47(1), 55(1), 58(1), 69(1), 71(1), 76(1), 77(1), 81(1), 84(1), 86(1) and 88(1). The primitive forms, such as *Incisivosaurus gauthieri*, *Caudipteryx zoui*, *Microvenator celer*, and *Avimimus portentosus* form an ascending sequence from most basal to more derived in the tree. *Avimimus portentosus* is a basal form of Caenagnathoidea. Following Barsbold (1981; 1983), Maryanska *et al.* (2002) used GIN 100/42 (IGM 100/42) as the representative of *Oviraptor philoceratops* in their phylogenetic analysis. The present analysis shows that GIN100/42 and *Oviraptor philoceratops* are closely related. GIN100/42 either belongs to a different species of the same genus as *O. philoceratops* or the same species, the latter differs from Clark *et al.*'s judgment (Clark *et al.*, 2002). *Nemegtia barsboldi* is closely related to *Citipati osmolskae*.

Conclusion

Nemegtia barsboldi is distinguished by at least

five autapomorphies from other known oviraptorosaurs (vertical skull crest, anteroposterior length of the frontal approximately 25% of that of the parietals in dorsal view, less exposed nasal process of the premaxilla on the dorsal surface of the skull, a process on the quadrate projecting into the cotyla of the quadatojugal, mandibular condyles of the quadrate situated rostrally to the occipital condyle). Phylogenetic analysis shows that *Nemegtia barsboldi* is closer to *Citipati osmolskae* than to other oviraptorosaurs.

Acknowledgments

The authors would like to thank Drs. Louis L. Jacobs, Dale A. Winkler (SMU, USA), H. Osmólska (Poland), R. E. Molnar (USA), R. Barsbold (Mongolia), and Y. Kobayashi (Japan) for their valuable comments on the early versions of the manuscript, and to acknowledge the members of the Mongol Highland International Dinosaur Project. Special thanks go to Y. Kobayashi, who found this beautiful specimen in 1996. Thanks also go to Drs. Zhou, Z. and Xu, X. (IVPP of Chinese Academy of Sciences, Beijing, China), for access of the specimens in their care. This project is supported by Chunichi Shinbun Co. Ltd., Kyoto Kagaku Co. Ltd., Chukyo TV Broadcasting Co. Ltd., and Tokai Bank Ltd.; plus Institute for the Study of Earth and Man at Southern Methodist University, the Jurassic Foundation, and the Chang Ying-Chien Science Grant for USA-China Collaborative Field Research to Junchang Lü.

References

- Barsbold, R., 1976. [On a new Late Cretaceous family of small theropods (Oviraptoridae fam. n.) of Mongolia]. *Doklady Akademia Nauk SSSR*, **226**(3): 685–688 (in Russian).
- Barsbold, R., 1977. Kinetism and peculiarity of the jaw apparatus of oviraptors (Theropoda, Saurischia). *Transactions, Joint Soviet-Mongolia Geological Expedition*, **4**: 37–47 (in Russian).
- Barsbold, R., 1981. Toothless carnivorous dinosaurs of Mongolia. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **15**: 28–39.
- Barsbold, R., 1983. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **19**: 5–120.
- Barsbold, R., 1986. [Raubdinosaurier Oviraptoren]. In Vorobyeva, E. I. (ed). *Herpetologische Untersuchungen in der Mongolischen Volksrepublik*. Pp. 210–223. Akad. Nauk. S. S. S. R. Inst. Evolyucionnoy Morfologii i Ekologii Zhivotnykh im. A. M. Severtsova, Moskva (in Russian with German summary).
- Barsbold, R., 1997. Oviraptorosauria. In Currie, P. J. and Padian, K. (eds.). *Encyclopedia of Dinosaurs*. Pp. 505–509. Academic Press, San Diego.
- Barsbold, R., Currie, P. J., Myhrvold, N. P., Osmólska, H., Tsogtbaatar, K. & Watabe, M., 2000. A pygostyle from a non-avian theropod. *Nature*, **403**: 155–156.
- Barsbold, R., Maryanska, T. & Osmólska, H., 1990. Oviraptorosauria. In Weishampel, D. B., Dodson, P. and Osmólska, H. (eds.). *The Dinosauria*. Pp. 249–258. University of California Press, Berkeley.
- Barsbold, R. & Osmólska, H., 1999. The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, **44**(2): 189–219.
- Barsbold, R., Osmólska, H., Watabe, M., Currie, P. J. & Tsogtbaatar, K., 2000. A new oviraptorosaur (dinosaur, theropod) from Mongolia: the first dinosaur with a pygostyle. *Acta Palaeontologica Polonica*, **45**(2): 97–106.
- Baumel, J. J. & Witmer, M., 1993. Osteologia. In Baumel, J. J., King, A. S. et al. (eds.). *Handbook of avian anatomy: nomina anatomica avium*, second edition. Pp. 45–132. Cambridge, Massachusetts.
- Bonaparte, J. F., Novas, F. E. & Coria, R. A., 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions in Science Nat. History Museum Los Angeles County*, **416**: 1–42.
- Chiappe, L. M., 1996. Late Cretaceous birds of southern South America: Anatomy and systematics of enantiornithes and *Patagopteryx deferrariisi*. *Munchner Geowiss. Abh. (A)*, **30**: 203–224.
- Chiappe, L. M., 2001. Phylogenetic relationships among basal birds. In Gauthier, J. and Gall, L. F. (eds.). *New perspectives on the origin and early evolution of birds, Proceedings of the International Symposium in Honor of John H. Ostrom*. Pp. 125–139. Yale Peabody Museum.
- Chiappe, L. M., 2002. Basal bird phylogeny: Problems and solutions. In Chiappe L. M. and Witmer L. M. (eds.). *Mesozoic birds above the heads of dinosaurs*. Pp. 448–472. University of California Press, Berkeley.
- Chiappe, L. M., Ji, S-A., Ji, Q. & Norell, M. A., 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of north-eastern China. *Bulletin of the American Museum of*

- Natural History*, **242**: 1–89.
- Chiappe, L. M., Norell, M. A. & Clark, J. M., 1996. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. *Memoirs of the Queensland Museum*, **39**(3): 557–582.
- Chiappe, L. P., Norell, M. A. & Clark, J. M., 1998. The skull of a relative of the stem-group bird *Mononykus*. *Nature*, **392**: 275–278.
- Clark, J. M., Altangerel, P. & Norell, M. A., 1994. The skull of *Erlicosaurus andrewsi*, a Late Cretaceous segnosaur (Theropoda: Therizinosauridae) from Mongolia. *American Museum Novitates*, **3115**: 1–39.
- Clark, J. M., Norell, M. A. & Barsbold, R., 2001. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. *Journal of Vertebrate Paleontology*, **21**(2): 209–213.
- Clark, J. M., Norell, M. A. & Chiappe, L.M., 1999. An oviraptorid skeleton from the late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. *American Museum Novitates*, **3265**: 1–36.
- Clark, J. M., Norell, M. A. & Rowe, T., 2002. Cranial anatomy of *Citipati osmolskae* (Theropoda, Oviraptorosauria), and a reinterpretation of the holotype of *Oviraptor philoceratops*. *American Museum Novitates*, **3364**: 1–24.
- Colbert, E. H. & Russell, D. A., 1969. The small Cretaceous dinosaur *Dromaeosaurus*. *American Museum Novitates*, **2380**: 1–49.
- Cracraft, J., 1971. Caenagnathiformes: Cretaceous birds convergent in jaw mechanism to dicynodont reptiles. *Journal of Paleontology*, **45**(2): 805–809.
- Cracraft, J. 1986. The origin and early diversification of birds. *Paleobiology*, **12**: 383–399.
- Currie, P. J., 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. *Canadian Journal of Earth Sciences*, **22**: 1643–1658.
- 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., 2000. Theropods from the Cretaceous of Mongolia. In Benton, M. J., Shishkin, M. A., Unwin, D. M. and Kurochkin, E. N. (eds.). *The age of dinosaurs in Russia and Mongolia*. Pp. 434–455. Cambridge University Press, Cambridge.
- Currie, P. J., Godfrey, S. J. & Nesson, L., 1993. New caenagnathid (Dinosauria: Theropoda) specimens from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences*, **30**: 2255–2272.
- Currie, P. J. & Russell, D. A., 1988. Osteology and relationships of *Chirostenotes* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada. *Canadian Journal of Earth Sciences*, **25**: 972–986.
- Currie, P. J., Vickers-Rich, P. & Rich, T. H., 1996. Possible oviraptorosaur (Theropoda, Dinosauria) specimens from the Early Cretaceous Otway Group of Dinosaur Cove, Australia. *Alcheringa*, **20**: 73–79.
- Currie, P. J. and Zhao, X.-J., 1993a: A new carnosaur (Dinosauria: Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2037–2081.
- Currie, P. J. & Zhao, X.-J., 1993b. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences*, **30**: 2231–2247.
- Dong, Z.-M. & Currie, P. J., 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Byan Mandahu, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*, **33**: 631–636.
- Elzanowski, A., 1999. A comparison of the jaw skeleton in theropods and birds, with a description of the palate in the Oviraptoridae. In Olson, S. L. (ed.). *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution*, Washington, D.C., 4–7 June 1996. *Smithsonian Contributions to Paleobiology*, **89**: 311–323.
- Frankfurt, N. G. & Chiappe, L. M., 1999. A possible oviraptorosaur from the Late Cretaceous of northwestern Argentina. *Journal of Vertebrate Paleontology*, **19**(1): 101–105.
- Frey, E. & Martill, D. M., 1995. A possible oviraptorosaurid theropod from the Santana Formation (Lower Cretaceous, ?Albian) of Brazil. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **7**: 397–412.
- Gauthier, J., 1986. Saurischian monophyly and the origin of birds. In Padian K. (ed.). *The origin of birds and the evolution of flight*. *Memoirs of the California Academy of Sciences* 8. San Francisco, Pp. 1–55.
- Gilmore, C. W., 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *United States National Museum, Bulletin*, **110**: 1–154.
- Gradzinski, R., Kazmierczak, J. & Lefeld, J., 1968. Geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. *Palaeontologia Polonica*, **19**: 33–92.
- Holmgren, N., 1955. Studies on the phylogeny of birds. *Acta Zoologica*, **36**: 243–328.
- Holtz, T. R. Jr., 1994. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *Journal of Vertebrate Paleontology*, **14**: 101–105.

- brate Paleontology*, **14**(4): 480–519.
- Holtz, T. R. Jr., 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia*, **15**: 5–61.
- Holtz, T. R. Jr., 2001. Arctometatarsalia revised: The problem of homoplasy in reconstructing theropod phylogeny. In Gauthier, J. and Gall, L. F. (eds.). *New perspectives on the origin and Early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Pp. 99–122. Peabody Museum of Natural History, Yale University, New Haven.
- Hwang, S.-H., Norell, M. A., Ji, Q. & Gao, K.-Q., 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *American Museum Novitates*, **3381**: 1–44
- Hwang, S.-H., Norell, M. A., Ji, Q. & Gao, K.-Q., 2004. A large compognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Palaeontology*, **2**(1): 13–30.
- Jerzykiewicz, T. & Russell, D. A., 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research*, **12**: 345–377.
- Ji, Q., Currie, P. J., Norell, M. A. & Ji, S.-A., 1998. Two feathered dinosaurs from northeastern China. *Nature*, **393**: 753–761.
- Ji, Q., Ji, S.-A., You, H.-L., Zhang, J.-P., Yuan, C.-X., Ji, X.-X., Li, J.-L. & Li, Y.-X., 2002. Discovery of an avialae bird *Shenzhouraptor sinensis* gen. et sp. nov. — from China, *Geological Bulletin of China* **21**(7): 363–369.
- Ji, Q., Ji, S.-A., You, H.-L., Zhang, J.-P., Zhang, H.-B., Zhang, N.-J., Yuan, C.-X. & Ji, X.-X., 2003. An Early Cretaceous avialan bird, *Shenzhouraptor sinensis* from western Liaoning, China. *Acta Geologica Sinica*, **77**(1): 21–26.
- Kearney, M. & Clark, J. M., 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. *Journal of Vertebrate Paleontology*, **23**(2): 263–274.
- Kobayashi, Y. & Lü, J.-C., 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica*, **48**(2): 235–259.
- Lü, J.-C., 2003. A new oviraptorosaurid (Theropoda: Oviraptorosauria) from the Late Cretaceous of southern China. *Journal of Vertebrate Paleontology*, **22**(4): 871–875.
- Lü, J.-C., Dong, Z.-M., Azuma, Y., Barsbold, R. & Tomida, Y., 2002. *Oviraptorosaurs* compared to birds. In Zhou, Z.-H., and Zhang, F.-C. (eds.). *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*, Science Press, Beijing China, Pp. 175–189.
- Lü, J.-C., Huang, D. & Zhang, S., 2000. The first discovery of oviraptorosaur from Guangdong Province. *Vertebrata Palasiatica*, **38**(2): 99.
- Maddison, W. P. & Maddison, D. R., 1992. *MacClade: analysis of phylogeny and character evolution*, version 3. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Madsen, J. H. Jr., 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineral Survey, Bulletin*, **109**: 1–163.
- Makovicky, P. J. & Sues, H.-D., 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microraptor celer* from the Lower Cretaceous of Montana. *American Museum Novitates*, **3240**: 1–27.
- Marsh, O. C., 1881. Classification of the Dinosauria. *The American Journal of Science, Third series*, **23**: 81–86.
- Maryanska, T. & Osmólska, H., 1997. The quadrate of oviraptorid dinosaurs. *Acta Palaeontologica Polonica*, **42**(3): 361–371.
- Maryanska, T., Osmólska, H. & Wolsan, M., 2002. Avialan status for Oviraptorosauria. *Acta Palaeontologica Polonica*, **47**(1): 97–116.
- Molnar, R. E., 1973. The cranial morphology and mechanics of *Tyrannosaurus rex* (Reptilia: Saurischia). PhD. Diss., University of California at Los Angeles.
- Molnar, R. E., 1991. The cranial morphology of *Tyrannosaurus rex*. *Palaeontographica*, **217**(4–6): 137–176.
- Norell, M. A., Clark, J. M., Chiappe, L. M. & Dashzeveg, D., 1995. A nesting dinosaur. *Nature*, **378**: 774–776.
- Norell, M. A., Clark, J. M., Dashzeveg, D., Barsbold, R., Chiappe, L. M., Davidson, A. K., Mckenna M. C., Altanerel, P. & Novacek, M. J., 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs Dinosaur eggs. *Science*, **266**: 779–782.
- Norell, M. A., Clark, J. M. & Makovicky, P. J., 2001. Phylogenetic relationships among coelurosaurian theropods. In Gauthier, J. and Gall, L. F. (eds.). *New perspectives on the origin and Early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Pp. 49–67. Peabody Mus. Nat. Hist. Yale University, New Haven.
- Norell, M. A., Makovicky, P. J. & Currie, P. J., 2001. The beaks of ostrich dinosaurs. *Nature*, **412**: 873–874.
- Novas, F. E., 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology*, **13**: 400–423.
- Osborn, H. F., 1924. Three new theropoda, protoceratops zone, central Mongolia. *American Museum Novitates*, **144**(7): 1–12.
- Osmólska, H., 1976. New light on the skull anatomy and systematic position of *Oviraptor*. *Nature*, **262**: 683–684.
- Osmólska, H., Roniewicz, E. & Barsbold, R., 1972. A new dinosaur *Gallimimus bullatus*, n. gen. n. sp. (Or-

- nithomimidae) from the Upper Cretaceous of Mongolia. *Palaeontol. Polonica*, **27**: 103–143.
- Ostrom, J. H., 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana*, **4**: 73–118.
- Rauhut, O. W. M., 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, **69**: 1–213.
- Russell, D. A. & Dong, Z.-M., 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2107–2127.
- Sanz, J. L. & Bonaparte, J. F. 1992. *Iberomesornis romerali*, a fossil small bird articulated skeleton from the Early Cretaceous of Spain. Proceedings of the II International Symposium of Avialian Paleontology, 1988, Pp. 39–49.
- Sereno, P. C., 1999. The evolution of dinosaurs. *Science*, **284**: 2137–2147.
- Sereno, P. C., 2000. *Iberomesornis romerali* (Aves, Ornithothoraces) reevaluated as an Early Cretaceous enantiornithine. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **215**(3): 365–395.
- Sereno, P. C. & Novas, F. E., 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, **13**(4): 451–476.
- Sereno, P. C. & Rao, C.-G., 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science*, **255**: 845–848.
- Smith, D., 1992. The type specimen of *Oviraptor philoceratops*, a theropod dinosaur from the Upper Cretaceous of Mongolia. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **186**(3): 365–388.
- Sternberg, R. M., 1940. A toothless bird from the Cretaceous of Alberta. *Journal of Paleontology*, **14**(1): 81–85.
- Sues, H.-D., 1997. On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. *Journal of Vertebrate Paleontology*, **17**: 698–716.
- Swofford, D. L., 1998. *PAUP*: phylogenetic analysis using parsimony (and other methods)*. Version 4.0. Sinauer, Sunderland, Mass.
- Swofford, D. L. & Begle, D. P., 1993. *PAUP: phylogenetic analysis using parsimony. Version 3.1. User's manual*. Illinois Natural History Survey, Champaign, Illinois.
- Welles, S. P., 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica A*, **185**: 85–180.
- Wester, D., 1996. Dinosaurs of the Gobi. *National Geographic*, **190**(1): 70–89.
- Witmer, L. M., 1990. The craniofacial air sac system of Mesozoic birds (Aves). *Zoological Journal of the Linnean Society of London*, **100**: 327–378.
- Witmer, L. M., 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Society of Vertebrate Paleontology memoir 3. *Journal of Vertebrate Paleontology*, **17**: supplement to number 1.
- Xu, X., Cheng, Y.-N., Wang, X.-L. & Chang, C.-X., 2002. An unusual oviraptorosaurian dinosaur from China. *Nature*, **419**: 291–293.
- Xu, X., Norell, M. A., Wang, X.-L., Makovicky, P. J. & Wu, X.-C., 2002. A basal troodontid from the Early Cretaceous of China. *Nature*, **415**: 780–784.
- Zhou, Z.-H., & Wang, X.-L., 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, Northwest China. *Vertebrata Palasiatica*, **38**(2): 111–127.
- Zhou, Z.-H., Wang, X.-L., Zhang, F.-C., & Xu, X., 2000. Important features of *Caudipteryx*-evidence from two nearly complete new specimens. *Vertebrata Palasiatica*, **38**(4): 241–254.
- Zhou, Z.-H. & Zhang, F.-C., 2002. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature*, **418**: 405–409.

Appendix 1

Abbreviations: An: angular; ar: articular; asc: articular-surangular-coronoid complex; bs: basisphenoid; cav antorb: antorbital cavity; ch: choana; CH: chamber; d: dentary; ec: ectopterygoid; emf: external mandibular fenestra; eo: exoccipital; f: frontal; fmb: *fossa m. brachialis*; j: jugal; l: lacrimal; lat: laterosphenoid; m: maxilla; mf: maxillary fenestra; na: nasal; nar: narial opening; oc: occipital condyle; o, orbit; or: orbitosphenoid; SP: supporting pillar; p: parietal; pa: palatine; par: parasphenoid; pm: premaxilla; po: postorbital pre: prearticular; pt: pterygoid; q: quadrate; qj: quadratojugal; sof: suborbital fenestra; sq: squamosal; stf: supratemporal fenestra; t: tooth-like process formed by maxillae and vomers; v: vomer.

Appendix 2.

Characters for phylogenetic analysis of the relationships among Oviraptorosauria (modified from Maryanska *et al.*, 2002 with additional taxa and recoded and additional characters as noted in bold) and data matrix: 0=plesiomorphic character state; 1, 2, 3=derived character states; ?=missing data; p=character not applicable.

1. Preorbital skull length to basal skull length ratio: 0.6 or more (0); 0.5 or less (1).
2. Longitudinal pneumatized crest-like prominence on the skull roof: absent (0), present (1).
3. Premaxilla main body length (ventral) to height (below the naris) ratio: 1.0–1.4(0); more than 1.7(1); 0.7 or less (2).
4. **Otosphenoidal crest vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess (0) or well developed, crescent shaped, thin crest forms anterior edge of enlarged pneumatic recess (1).** This structure forms the anterior, and most distinct, border of the “lateral depression” of the middle ear region (see Currie, 1985; Currie and Zhao, 1993) of troodontids and some extant avians (Hwang *et al.*, 2004).
5. Subnarial (maxillary) process of the premaxilla: contacts the nasal, the maxilla excluded from the narial border (0); does not contact the nasal, the maxilla participates in formation of the narial border (1).
6. **Premaxillae in adult: unfused (0); fused (1) (Chiappe, 1996).**
7. Pneumatization of the premaxilla: absent (0); present (1).
8. **Basisphenoid recess present between basisphenoid and basioccipital (0) or entirely within basisphenoid (1) or absent (2) (Hwang *et al.*, 2004).**
9. Subantorbital portion of the maxilla: not inset medially (0); inset medially (1).
10. Palatal shelf of the maxilla with two longitudinal ridges and a tooth-like process: absent (0); present (1).
11. Rim around the antorbital fossa: well pronounced (0); poorly delimited (1).
12. Antorbital fossa: not bordered rostrally by the premaxilla (0); bordered rostrally by the premaxilla (1).
13. **Preorbital region of the skull in post-hatchling individuals: elongate, nasals considerably longer than frontals, maxilla at least twice the length of the premaxilla (0); shortened, nasals subequal in length to frontals or shorter, maxillary length less than twice the length of the premaxillary body (1) (Rauhut, 2003).** In the majority of theropods, the preorbital part of the skull forms an elongate snout, with maxilla and nasal being two of the longest bones of the skull roof. In the basal oviraptorosaur *Incisivosaurus gauthieri* and in *Nemegtia barsboldi*, the nasal is longer than the frontal (Xu *et al.*, 2002). In *Caudipteryx zoui* (Ji *et al.*, 1998) and most derived oviraptorosaurs, the nasal is shorter than the frontal.
14. **Maxillary process of premaxilla contacts nasal to form posterior border of nares (0) or maxillary process reduced so that maxilla participates broadly in external nares (1) or maxillary process of premaxilla extends posteriorly to separate maxilla from nasal posterior to nares (2) (Hwang *et al.*, 2004).**
15. Nasal recesses: absent (0); present (1).
16. Caudal margin of the naris: rostral to the rostral border of the antorbital fossa (0); nearly reaching or overlapping the rostral part of the antorbital fossa (1); overlapping most of the antorbital fossa (2).
17. Ventral margin of the external naris: at the level of the maxilla (0); dorsal to the maxilla (1).
18. Prefrontal: present (0); absent or fused with the lacrimal (1). In the majority of theropods, the prefrontal is large. Prefrontal may be absent in all oviraptorosaurs, including the primitive *Incisivosaurus gauthieri*.
19. Lacrimal recess: absent (0); present (1).
20. **Premaxillary symphysis acute, V-shaped (0); or rounded, U-shaped (1) (Hwang *et al.*, 2004).**
21. **Pronounced, round accessory antorbital fenestra absent (0); or present (1).** A small fenestra, variously termed the accessory antorbital fenestra or maxillary fen-

- estra, penetrates the medial wall of the antorbital fossa anterior to the antorbital fenestra in a variety of coelurosaurs and other theropods (Hwang *et al.*, 2004).
22. Parietal length to frontal length ratio: 0.6 or less (0); 1.0 or more (1).
 23. **Narial region apneumatic or poorly pneumatized (0); or with extensive pneumatic fossae, especially along posterodorsal rim of fossa (1) (Hwang *et al.*, 2004).**
 24. Sagittal crest on the parietals: absent (0); present (1).
 25. **Jugal pneumatic recess in posteroventral corner of antorbital fossa present (0); or absent (1) (Hwang *et al.*, 2004).**
 26. Infratemporal fenestra: ventrally nearly as long as high rostrally (0); shorter ventrally than (1); large, square (2); not separate from the orbit (3).
 27. Descending (prequadratic) process of the squamosal: constricting the dorsal part of the infratemporal fenestra (0); not constricting the infratemporal fenestra (1).
 28. **Jugal and quadratojugal separate (0); or quadratojugal and jugal fused and not distinguishable from one another (1) (Hwang *et al.*, 2004).**
 29. Suborbital part of the jugal: deep dorsoventrally and flattened lateromedially (0); shallow dorsoventrally or rod-shaped (1).
 30. Jugal-postorbital contact: present (0); absent (1).
 31. Quadratojugal process of the jugal in lateral view: forked (0); tapering (1); fused with the quadratojugal (2).
 32. **Quadratojugal-squamosal contact: tips of the bones widely separated (0); the contact present (1) (modified).**
 33. Ascending (squamosal) process of the quadratojugal: massive, bordering about the ventral half of the infratemporal fenestra (0); slender, bordering the ventral half or less of the infratemporal fenestra (1); slender, bordering the ventral two-thirds or more of the infratemporal fenestra (2); absent (3).
 34. Dorsal part of the quadrate: erect (0); directed backwards (1).
 35. Otic process of the quadrate: articulating only with the squamosal (0); articulating with the squamosal and the lateral wall of the braincase (1).
 36. Pneumatization of the quadrate: absent (0); present (1). In many theropods, the quadrate is a solid bone and it is not invaded by a diverticulum of the tympanic pneumatic system, but the quadrate is pneumatized by the quadrate diverticulum in most modern birds. The diverticulum enters the bone ventromedially, dorsomedially or caudally (Witmer, 1990). In dromaeosaurids (*Velociraptor mongoliensis*) and other non-avian theropods, the quadrate lacks pneumatic foramina (Colbert and Russell, 1969; Madsen, 1976; Bonaparte *et al.*, 1990; Barsbold and Osmólska, 1999). Among non-avian theropods, troodontids (Currie and Zhao, 1993b) and tyrannosaurids (Molnar, 1991) are the exception, in which the quadrate is pneumatic. A large pneumatic foramen is placed anteromedially and somewhat below the mid-height in some oviraptorids (Maryanska and Osmólska, 1997). Some birds, such as *Archaeopteryx lithographica*, *Hesperornis regalis* and *Parahesperornis alexi* (Chiappe, 1996) also lack pneumatic foramina. The quadrate diverticulum perforates the lateral surface of the quadrate in *Patagopteryx deferrariisi* (Chiappe, 1996), and a similar condition is present in *Heyuannia huangi* (Lü, 2003), but it is absent in “*Oviraptor*” *mongoliensis*. The lateral position of the entrance of the quadrate diverticulum is regarded as an autapomorphy of *Patagopteryx deferrariisi* (Chiappe, 1996), but the similar position in *Heyuannia* indicates an independent acquisition. Witmer (1990) considered the presence of quadrate pneumatici-

ty as a synapomorphy of the Carinatae [Ichthyornithiformes+Aves], but Chiappe (1996) thought that a pneumatic quadrate was present at least in the common ancestor of *Patagopteryx deferrariisi* and the Ornithurae and it might have evolved as early as at the origin of the ornithothoraces. The pneumatic quadrate in oviraptorosaurs is considered here as independently acquired.

37. Accessory process for a contact with the quadratojugal on the distal end of the quadrate: absent (0); present (1).
38. **Quadratojugal sutured to the quadrate (0); or joined through a ligamentary articulation (1) (Chiappe, 2001, 2002).** In *Archaeopteryx* and most non-avian theropod dinosaurs, the quadratojugal is sutured to the quadrate, in almost all derived oviraptorosaurs, a cotyle is present either on the quadrate (“*Oviraptor*” *mongoliensis*, GIN 100/42, and *Conchoraptor gracilis*, Maryanska *et al.*, 2002) or on the medial surface of the quadratojugal GIN 100/2112 (Lü *et al.*, 2002). *Heyuannia huangi* has a groove-like structure on the quadrate (Lü, 2003). The presence of a cotyle or a groove-like surface on the quadrate or quadratojugal is interpreted here as a ligamentary articulation between the quadrate and quadratojugal. In *Citipati osmolskae*, the quadrate is tightly sutured to the quadratojugal (Clark *et al.*, 2002). A shallow depression is present on the lateral condyle of the quadrate in *Confuciusornis sanctus* (Chiappe *et al.*, 1999), therefore it is interpreted as having a ligamentary articulation between the quadrate and quadratojugal.
39. Mandibular condyles of the quadrate situated: caudal to the occipital condyle (0); in the same vertical plane as the occipital condyle (1); rostral to the occipital condyle (2). In *Herrerasaurus ischigualastensis* (Serenó and Novas, 1993), *Allosaurus* and sinraptorids (Currie and

Zhao, 1993a), the mandibular condyle of the quadrate is caudal to the occipital condyle. In *Archaeopteryx lithographica*, *Incisivosaurus gauthieri* and *Caudipteryx* sp. (IVPP V 12430), the mandibular condyle of the quadrate is rostral to the occipital condyle. Although there are no completely three-dimensionally preserved skulls of *Caudipteryx*, the preserved skull is little disturbed in *Caudipteryx* sp. (IVPP V 12430). It shows clearly relative position between the mandibular condyles of the quadrate and the occipital condyle. In *Nemegtia barsboldi* and “*Oviraptor*” *mongoliensis* and *Heyuannia huangi*, the mandibular condyles of the quadrate are in the same vertical plane as the occipital condyle.

40. **Enlarged foramen or foramina opening laterally at the angle of the lacrimal, absent (0); or present (1) (Hwang *et al.*, 2002).**
41. Paroccipital process directed: laterad (0); lateroventrad (1), ventrad (2). In both *Herrerasaurus ischigualastensis* and *Allosaurus fragilis*, the paroccipital process is directed lateroventrally, but it is directed much more strongly so in *A. fragilis* than in *H. ischigualastensis*. The paroccipital process directed ventrad in *Incisivosaurus gauthieri*, *Chirostenotes pergracilis*, and derived oviraptorosaurs.
42. **Dorsal surface of parietals flat, lateral ridge borders supratemporal fenestra (0); or parietals dorsally convex with very low sagittal crest along midline (1); or dorsally convex with a well-developed sagittal crest (2) (Hwang *et al.*, 2004).**
43. Foramen magnum: smaller than or equal to the occipital condyle (0); larger than the occipital condyle (1).
44. Basal tubera: modestly pronounced (0); well pronounced, widely separated (1).
45. Pneumatization of the basisphenoid: weak or absent (0); extensive (1).

46. Basipterygoid process: well developed (0); strongly reduced (1); absent (2).
47. **Posterior end of dentary without posterodorsal process dorsal to mandibular fenestra (0); or with dorsal process above anterior end of mandibular fenestra (1); or with elongate dorsal process extending over most of fenestra (2) (Hwang *et al.*, 2004).**
48. Parasphenoid rostrum: horizontal or directed rostrad (0); slanting rostroventrad (1).
49. **Tibiofibular crest in the lateral condyle of femur: absent (0); present (1) (Ji *et al.*, 1998).**
50. **Parietals separate (0) or fused (1) (Hwang *et al.*, 2004).**
51. **Foramen magnum subcircular, slightly wider than tall (0); or oval, taller than wide (1) (Hwang *et al.*, 2004).**
52. Medially extended pterygoids meeting each other along the midline and ventrally underlying the basisphenoid and parasphenoid: absent (0); present (1).
53. Quadrate wing of the pterygoid: distinct from the braincase wall (0); overlapping the braincase (1).
54. Pterygoid basal process for contact with the basisphenoid: absent (0); present (1).
55. Ectopterygoid situated: lateral to the pterygoid (0); rostral to the pterygoid (1).
56. Ectopterygoid contacts with the maxilla and lacrimal: absent (0); present (1).
57. Hook-like jugal process on the ectopterygoid: present (0); absent (1).
58. Massive pterygoid-ectopterygoid longitudinal bar: absent (0); present (1).
59. Palate extending below the cheek margin: absent (0); present (1).
60. Palatine: tetra- or triradiate (0); triradiate, without a jugal process (1); developed in three planes perpendicular to each other (2). Triradiate palatine is present in *Incisivosaurus gauthieri* (Xu, Cheng *et al.*, 2002), *Citipati osmolskai* (Clark *et al.*, 2002) and GIN100\2112. So Hwang *et al.* (2004), in which IGM100\42 was coded as having a tetra- or triradiate palatine, may be wrong.
61. Pterygoid wing of the palatine situated: dorsal to the pterygoid (0); ventral to the pterygoid (1).
62. Maxillary process of the palatine: shorter than vomeral process (0); longer than the vomeral process (1).
63. Vomer: distant from the parasphenoid rostrum (0); approaching or in contact with the rostrum (1).
64. Suborbital (ectopterygoid-palatine) fenestra: well-developed (0); closed or reduced (1).
65. Pterygopalatine fenestra: absent (0); present (1).
66. Jaw joint: distant from the skull midline (0); close to the skull midline (1).
67. **Occipital condyle without constricted neck (0); or subspherical with constricted neck (1) (Hwang *et al.*, 2004).**
68. Mandibular symphysis: loose (0); tightly sutured (1); fused (2).
69. Extended symphyseal shelf at the mandibular symphysis: absent (0); present (1).
70. Downturned symphyseal portion of the dentary: absent (0); present (1).
71. U-shaped mandibular symphysis: absent (0); present (1).
72. Retroarticular process' length to total mandibular length ratio: less than 0.05 or the process absent (0); about 0.10 (1).
73. Mandible maximum height to length ratio: about 0.2(0); about 0.1 (1); 0.3–0.4(2).
74. External mandibular fenestra's height to length ratio: 0.2–0.5(0); 0.7–1.0 (1); the fenestra absent (2). In *Caenagnathus collinsi* and *Incisivosaurus gauthieri*, the ratio is less than 0.25, but in the derived oviraptorosaurs such as *Ingenia yanshini*, *Heyuannia huangi*, *Oviraptor philoceras*, "*Oviraptor*" *mongoliensis*, *Conchoraptor gracilis*, *Citipati osmolskai*, this ratio is greater than 0.25.

75. **External mandibular fenestra's length to total mandibular length ratio: 0.15–0.2(0), 0.1– or less (1); 0.21 or more (2); the fenestra absent (3) (modified).**
76. Coossification of the articular with the surangular: absent (0); present (1).
77. Mandibular rami in dorsal view: straight (0); bowed laterad at the mid-length (1).
78. **Rostradorsal margin of the dentary: straight or weakly convex (0); deeply concave (1) (modified).** In most theropods and *Oviraptor philoceratops*, the rostradorsal margin of the dentary is straight. In the basal oviraptorosaur *Incisivosaurus gauthieri*, it is slightly convex. It is deeply concave in *Oviraptor philoceratops*, *Caenagnathus collinsi*, “*Oviraptor*” *mongoliensis*, *Heyuannia huangi*, *Citipati osmolskae*, *Conchoraptor gracilis*, *Nemegtia barsboldi*, and *Ingenia yanshini*.
79. Caudal margin of the dentary: incised, producing two caudal processes (0); oblique (1). The posterior end of the dentary is strongly forked to form the anterior margin of the external mandibular fenestra in oviraptorosaurs. In several theropods, such as *Allosaurus*, dromaeosaurids, ornithomimosaurids, therizinosauroids and tyrannosaurs, and *Archaeopteryx*, the caudal margin of the dentary is oblique.
80. Long and shallow caudodorsal process of the dentary: present (0); absent (1).
81. Long and shallow caudoventral process of the dentary, extending caudad at least to the caudal border of the external mandibular fenestra: absent (0); present (1).
82. **Pronounced coronoid eminence: absent (0); present (1) (modified).** The coronoid eminence on the surangular is absent in most theropods. In *Incisivosaurus gauthieri* the coronoid eminence is weakly developed, so it is coded here as (0). The pronounced coronoid eminence is present in *Avimimus portentosus* and derived oviraptorosaurs.
83. **External mandibular fenestra oval (0); or subdivided by a spinous rostral process of the surangular (1) (Hwang *et al.*, 2002).** The external mandibular fenestra is elongate, and no spinous rostral process of the surangular is present in *Incisivosaurus gauthieri* (Xu, Cheng *et al.*, 2002) and *Caudipteryx* sp. (IVPP V 12430, pers. observation). In derived oviraptorosaurs, the external mandibular fenestra is subdivided by a spinous rostral process of the surangular.
84. Mandibular articular facet for the quadrate: formed of the surangular and articular (0); formed exclusively of the articular (1).
85. Mandibular articular facet for the quadrate: with one or two cotylae (0); convex in lateral view, transversely wide (1).
86. Articular facet for the mandibular joint positioned: below the dorsal margin of the caudal part of the mandibular ramus (0); above this margin (1).
87. Rostral part of the prearticular: deep, approaching the dorsal margin of the mandible (0); shallow, strap-like, not approaching the dorsal margin of the mandible (1).
88. Splenial: subtriangular, approaching the dorsal margin of the mandible (0); strap-like, shallow, not approaching the dorsal margin of the mandible (1).
89. Mandibular adductor fossa: rostrally delimited, occupying the caudal part of the mandible (0); large, rostrally and dorsally extended, not delimited rostrally (1).
90. **Coronoid bone: well developed (0); reduced (1) or absent (2) (modified).** The coronoid bone is present in most theropods, but it is weakly developed and strap-like in *Incisivosaurus gauthieri* (Xu *et al.*, 2002b), *Caudipteryx* sp. (IVPP V 12430; Pers. observation) and *Citipati osmolskae* (Clark *et al.*, 2002). It is also present in therizinosauroids (Clark *et al.*, 1994). It is absent in birds (*Archaeo-*

- pteryx*), ornithomimosaur (Osmólska *et al.*, 1972) and other derived oviraptorosaurs including *Nemegtia barsboldi*, *Conchoraptor gracilis*, *Ingenia* and *Oviraptor*.
91. Premaxillary teeth: present (0); absent (1). Premaxillary teeth are present in *Incisivosaurus*, *Caudipteryx*, *Archaeopteryx* and most theropods. But premaxillary teeth are absent in therizinosauroids (Clark *et al.*, 1994), derived oviraptorosaurs and advanced birds.
 92. Maxillary tooth row: extends at least to the level of the preorbital bar (0); does not reach the level of the preorbital bar (1); maxillary teeth absent (2). Maxillary teeth are present in *Incisivosaurus gauthieri*, and the majority of theropods. Maxillary teeth are absent in *Caudipteryx zoui* and derived oviraptorosaurs.
 93. Dentary teeth: present (0); absent (1). Dentary teeth are present in *Incisivosaurus gauthieri*, but absent in derived oviraptorosaurs, *Microvenator celer* (Makovicky and Sues, 1998), *Caudipteryx zoui* (Ji *et al.*, 1998), *Avimimus portentosus*, advanced ornithomimosaur and birds.
 94. Number of the cervicals (excluding the cervicodorsal): not more than 10 (0); more than 10 (1).
 95. Cranial articular facets of the centra in the anterior postaxial cervicals: not inclined or only slightly inclined (0); strongly inclined ventrocaudal, almost continuous with the ventral surface of the centra (1); ball-shaped (2).
 96. Anterior cervical centra: not extending posteriorly beyond the respective neural arches (0); extending posteriorly beyond the respective neural arches (1).
 97. Epiphyses on the postaxial cervicals: in form of a low crest or rugosity (0); prong-shaped (1). The epiphyses on the postaxial cervicals are in form of a low crest in *Microvenator celer*, a rugosity in *Coelophysis bauri*, *Avimimus portentosus*, *Archaeopteryx lithographica*, Ornithomimosauria, Therizinosauria, *Oviraptor philoceratops*, *Caudipteryx* sp., *Nemegtia barsboldi*, *Heyuannia huangi*, *Conchoraptor gracilis*, *Ingenia yanshini*. The epiphyses are only present in the third and fourth cervicals of “*Oviraptor*” *mongoliensis*. They are very developed, prong-shaped, and usually extending over the distal end of the postzygopophyses in *Herrerasaurus ischigualastensis*, *Allosaurus fragilis*, Dromaeosauridae, Troodontidae and Tyrannosauridae.
 98. Cervical ribs: loosely attached to vertebrae in adults (0); firmly attached (1).
 99. Shafts of the cervical ribs: longer than the respective centra (0); not longer than the respective centra (1).
 100. Pleurocoels or lateral excavations on the dorsal centra: absent (0); present (1).
 101. Postzygopophyses on the dorsals: not extending beyond the respective centra (0); markedly extending beyond the centra (1).
 102. Number of the vertebrae included in the sacrum in adults: not more than five (0); more than five (1) (the term sacrum is used here instead of synsacrum in Maryanska *et al.*'s original description).
 103. Sacral spine in adults: unfused (0); fused (1).
 104. Continuous sulcus along the ventral side of the mid-sacral centra: absent (0); present (1).
 105. Pleurocoels on the sacral centra: absent (0); present (1).
 106. **Scapula and coracoid separate (0), or fused into scapulacoracoid (1) (Hwang *et al.*, 2004).** The scapula and coracoid are separate in most theropods, including *Allosaurus fragilis*, *Tyrannosaurus rex*, *Deinonychus antirrhopus*, *Chirostenotes pergracilis*, and *Caudipteryx* sp. They are fused in *Velociraptor mongoliensis*, *Archaeopteryx lithographica*, *Confuciusornis sanctus*, *Ingenia yanshini*, “*Oviraptor*”

mongoliensis, *Oviraptor philoceratops*, *Conchoraptor gracilis*, and *Heyuannia huangi*. Because both character states are present in dromaeosaurids and ornithomimids, this character is coded as 0/1 in them.

- 107. Hyosphene-hypantrum articulations in trunk vertebrae present (0); or absent (1) (contrary to the code of Hwang *et al.*, 2004).** These articulations are present in *Herrerasaurus ischigualastensis* (Novas, 1993), *Allosaurus fragilis* (Madsen, 1976), *Avimimus portentosus*, *Microraptor celer*, *Chirostenotes pergracilis*, *Conchoraptor gracilis*, ornithomimids, troodontids, tyrannosaurids. They are absent in *Confuciusornis sanctus* and advanced birds. But it is not clear in *Archaeopteryx lithographica*. In “*Oviraptor*” *mongoliensis*, and *Heyuannia huangi*, these articulations are very weak, so it was coded here as absent (0).
108. Pleurocoels on the caudal centra: absent (0); present at least in the proximal part of the tail (1).
- 109. Number of caudals: more than 35 (0); 35–25 (1); fewer than 25 (2) (modified from Lü *et al.*, 2002).** Most theropods have more than 35 caudals. 22 caudals are present in *Caudipteryx* sp. (Zhou *et al.*, 2000), 24 caudals in *Nomingia gobiensis* (Barsbold, Osmólska *et al.*, 2000), about 33 in “*Oviraptor*” *mongoliensis*. There are about 26 caudals in *Microraptor zhaoianus* and 25 in *Shenzhouraptor* (= *Jeholornis*, Zhou and Zhang, 2002; Ji *et al.*, 2002; 2003).
110. Pygostyle: absent or rudimentary (fewer than three elements) (0), present (1). The last three to six caudal vertebrae fuse to form a pygostyle in modern birds (Baumel and Raikow, 1993) that support the tail feathers. A pygostyle is present in the ornithurines, hesperorniforms and ichthyornithiforms, enantiornithines (*Iberomesornis*, *Sinornis*, Sereno, 2000; Sereno and

Rao, 1992), but is absent in non-avian theropod dinosaurs, *Archaeopteryx lithographica* (Chiappe, 1996) and the basal bird *Shenzhouraptor* (Zhou and Zhang, 2002; Ji *et al.*, 2003). The presence of a pygostyle in *Nomingia gobiensis* is of great interest in the study of the relationship between birds and non-avian theropods, although it is most parsimonious to consider it a convergence (Osmólska, pers. comm., 2003). Some have even regarded the pygostyle in modern ratite and carinate birds, to be not homologous (Holmgren, 1955). The structure of pygostyle in *Nomingia gobiensis* (Barsbold, Osmólska *et al.*, 2000) and the ostrich (Holmgren, 1955) are very similar (fused dorsally in the vertebrae rather than ventrally in carinate birds). The complete distal tail of *Heyuannia huangi* shows that there is no pygostyle. It is also absent in *Caudipteryx zoui* (Ji *et al.*, 1998; Zhou *et al.*, 2000). The development of a pygostyle was regarded as a synapomorphy of the clade composed of all birds more advanced than *Archaeopteryx lithographica* (Gauthier, 1986). Cracraft (1986) considered it as synapomorphy of Ornithurae, whereas Sanz and Bonaparte (1992) considered it as synapomorphic for *Iberomesornis* plus Ornithurae. In agreement with Sanz and Bonaparte (1992), Chiappe (1996) considered it as a synapomorphy of the Ornithothoraces. The discoveries of *Jeholornis* and *Rahonavis* further supports Sanz and Buscalioni (1992) and Chiappe (1996)'s hypotheses (Chiappe, 2002).

111. Scapular caudal end: blunt and much expanded (0); tapered to a sharp point or slightly expanded (1) (modified from Chiappe, 2002).

112. Scapular and coracoid: nearly in the same plane (0); forming a distinct angle (1) at the level of the glenoid cavity (Chiappe *et al.*, 1998).

113. Distal caudal prezygapophyses: overlap-

- ping less than a half of the centrum of the preceding vertebra (0); overlapping at least a half of the preceding vertebra (1).
114. Hypapophyses in the cervicodorsal vertebral region: absent (0); small (1); prominent (2). The hypapophyses are absent in *Coelophysis bauri*, *Herrerasaurus ichigualastensis*, *Allosaurus fragilis*, *Microraptor celer*, ornithomimids, tyrannosauridae. Because it is absent in *Microraptor*, present in *Velociraptor mongoliensis*, this character is coded here as 0/1 in Dromaeosauridae. It is not prominent in *Heyuannia huangi*, *Caudipteryx* sp., and *Nemegtia barsboldi*. It is well developed in “*Oviraptor*” *mongoliensis*, *Conchoraptor gracilis*, *Chirostenotes pergracilis*, *Avimimus portentosus*, and troodontids.
115. Distal chevrons: deeper than long (0); longer than deep (1).
116. Sternum: unossified or small (0); ossified, large (1).
117. Scapula length to humerus length ratio: 0.8–1.1 (0); 1.2 or more (1); 0.7 or less (2).
118. Acromion: projecting dorsad (0); everted laterad (1); projecting cranial (2).
119. Caudovertral process on the coracoid: absent (0); short, not extending beyond the glenoid diameter (1); long, caudoventrally extending beyond the glenoid (2).
120. Orientation of the glenoid on the pectoral girdle: caudoventral (0); lateral (1).
121. Deltopectoral crest: low, with the width equal to or smaller than the shaft diameter (0); expanded, wider than the shaft diameter (1).
122. Internal tuberosity on humerus: weakly pronounced or absent (0); well pronounced but low (1); subtriangular, distinctly extended medially (2); in form of a longitudinally short, tuber-like extension, sharply delimited from the shaft and usually also from the humeral head (3).
123. Deltopectoral crest (measured from the humeral head to the apex) extending for:
- about the proximal third of the humerus length or less (0); about 40–50% of the humerus length (1).
124. Epicondyles on the humerus: absent or poorly developed (0); the ectepicondyle more prominent than the entepicondyle (1); the entepicondyle more prominent than the ectepicondyle (2); the ectepicondyle and entepicondyle about equally prominent (3).
125. Shaft of the ulna: straight (0); bowed, convex caudally (1); bowed, concave caudally (2).
126. Radius length to humerus length ratio: 0.80 or less (0); 0.85 or more (1).
127. **Distal carpals: flat, mostly separate (0); carpals I and II separate, carpal I with the proximal trochlea (1); carpals I and II fused, half-moon-shaped, with the trochlea on the proximal surface, covering metacarpals I and II (2).** The expanded semilunate (half-moon-shaped) carpal block completely caps the proximal surface of metacarpals I and II in oviraptorosaurs, dromaeosaurids and avialians. It is regarded as diagnostic of Maniraptora. The absence in ornithomimosaur and adult tyrannosaurids are treated as reversals (modified from Holtz, 2001).
128. Combined lengths of manual phalanges III-1 and III-2: greater than the length of phalanx III-3 (0); less than or equal to the length of phalanx III-3 (1).
129. Metacarpal I length to metacarpal II length ratio: 0.5 or more (0); less than 0.5 (1).
130. Proximal margin of the metacarpal I in dorsal view: straight, horizontal (0); angled due to the medial extent of the carpal trochlea (1).
131. Metacarpal II relative to metacarpal III: shorter (0); subequal (1); longer (2). In *Heyuannia huangi*, and *Ingenia yanshini*, the length of metacarpal III is shorter than that of metacarpal II; In *Conchoraptor gracilis*, the length of metacarpal III is

- longer than that of metacarpal II; In *Caudipteryx*, metacarpal II is subequal to metacarpal III.
132. Metacarpal II length to humerus length ratio: 0.4 or less (0); more than 0.4 (1).
133. Metacarpal III: unmodified (0); very slender (1).
134. Lip or nubbin on the proximodorsal edge of the manual unguals: absent (0); present (1).
135. Manus length to humerus length plus radius length ratio: 0.50–0.65 (0); more than 0.65 (1); less than 0.50 (2).
136. Manus length to femur length ratio: 0.3–0.6 (0); more than 0.7(1); less than 0.2 (2).
137. Humerus length to femur length ratio: 0.5–0.6 (0); less than 0.4 (1); 0.7 or more (2).
138. Dorsal margins of the opposite iliac blades: well separated from each other (0); close to or contacting each other along their medial sections (1).
139. Dorsal margin of the ilium along the central portion of the blade: straight (0); arched (1).
140. Preacetabular process relative to the postacetabular process (the lengths measured from center of the acetabulum): shorter or equal (0); longer (1).
141. Preacetabular process: not expanded or weakly expanded ventrally below the level of the dorsal acetabular margin (0); expanded ventrally well below the level of the dorsal acetabular margin (1).
142. Morphology of the ventral margin of the preacetabular process: the cuppedicus fossa absent, the margin transversely narrow (0); the cuppedicus fossa or wide shelf present (1); the margin flat, wide at least the base of the pubic peduncle (2).
143. Cranioventral process on the preacetabular blade: absent (0); rounded (1); hook-like (2).
144. Distal end of the postacetabular process: truncated or broadly rounded (0); narrowed or acuminate (1).
145. Supracetabular crest: well developed (0); reduced or absent (1).
- 146. Craniocaudal length of the pubic peduncle: about as long as the ischiadic peduncle (0); distinctly longer than the ischiadic peduncle (1); distinctly shorter than the ischiadic peduncle (2) (modified).**
147. Dorsoventral extension of the pubic peduncle: level with the ischiadic peduncle (0); deeper than the ischiadic peduncle (1).
148. Brevis fossa: absent or small (0); large (1).
149. Antitrochanter on the ilium: present (0); absent (1).
150. Ilium length to femur length ratio: 0.5–0.7 (0); 0.8 or more (1).
- 151. Hypocleidium on furcula absent (0); or present (1). The hypocleidium is a process extending from the ventral midline of the furcula, and is attached to the sternum by a ligament in extant birds (Hwang *et al.*, 2004).**
152. Pubic shaft: straight (0); concave cranially (1).
- 153. Pubic foot: with the cranial and caudal processes being about equally long (0); with the cranial process being longer than the caudal process (1); with the cranial process being shorter than the caudal process (2); absent (3) (state 2 is modified).**
154. Dorsoventral length of the pubic apron: longer than half total length of the pubis (0); not longer than the half of total length of the pubis (1).
155. Caudal margin of the ischiadic shaft: straight or almost straight (0); strongly concave (1).
156. Position of the obturator process on the ischium: proximal (0); at about mid-length (1); distal (2); obturator process lacking (3).
157. Distal end of the ischium: not expanded (0); expanded (1).
158. Ischium length to pubis length ratio: 0.75

- or more (0); 0.70 or less (1).
159. Posterior (greater) trochanter: weakly separated or not separated from the femoral head (0); distinctly separated from the femoral head (1).
 160. Craniocaudal extent of the posterior trochanter of femur: short (0); long (1).
 161. **Pleurocoels absent on sacral vertebrae (0); or present on anterior sacrals only (1); or present on all sacrals (2).** A pleurocoel may be present on the first sacral in *Alxasaurus elesitaiensis*, although this area is badly crushed (Russell and Dong, 1993) (Hwang *et al.*, 2004).
 162. Anterior and posterior trochanters: well separated (0); contacting (1); fused (2).
 163. Dorsal extremity of the anterior trochanter of femur: well below the posterior trochanter (0); about level with the posterior trochanter (1).
 164. Fourth trochanter of femur: well developed (0); weakly developed or absent (1).
 165. Adductor fossa and associated craniomedial crest on the distal femur: weak or absent (0); well developed (1).
 166. Strong distal projection of the fibular condyle on the femur: absent (0); present (1).
 167. Medial surface of the fibular head: flat or shallowly concave (0); with a deep fossa (1).
 168. Contacts of the distal end of the fibula with tarsus: present (0); absent (1). In most theropod dinosaurs, and *Heyuannia huangi*, the distal end of the fibula contacts the tarsus, but in *Ingenia yanshini*, this contact is absent, similar to the case in most birds.
 169. Ascending process of the astragalus: as tall as wide across the base (0); taller than wide (1).
 170. Distal tarsals: not fused with metatarsals (0); fused with metatarsals (1).
 171. Proximal coossification of metatarsals II–IV: absent (0); present (1).
 172. **Arctometatarsus: absent (0); present (1).** Because the metatarsi of some ornithomimosaur (*Garudimimus* and *Harpymimus*) are not strongly pinched as in more typical ornithomimids, this character was coded as (0,1) for Ornithomimidae by Holtz (2001) in his phylogenetic analysis. This character is coded here as (0, 1), in agreement with Holtz, instead of being coded as (1) as in Maryanska *et al.* (2002).
 173. Metatarsals II and IV: not in contact on the plantar surface (0); contacting distally (1).
 174. Metatarsal I length: more than 50% of metatarsal II length (0); less than 50% of metatarsal II length (1); metatarsal I absent (2).
 175. Metatarsal IV length relative to metatarsal II length: about equal (0); longer (1).
 176. **Epipterygoid present (0), absent (1) (new).** An epipterygoid is known in allosaurids (Madsen, 1976), ornithomimids (Barsbold, 1981), tyrannosaurids (Molnar, 1973), *Dromaeosaurus albertensis* (Currie, 1995), the derived oviraptorid *Citipati osmolskae* (Clark *et al.*, 2002) and *Nemegtia barsboldi*. It is not clear in *Incisivosaurus gauthieri*, and it is absent in “*Oviraptor*” *mongoliensis* and birds.
 177. Metatarsus length to femur length ratio: 0.4–0.6 (0); about 0.3 (1); 0.7–0.8 (2).
 178. **Thoracic vertebral count: 13–14 (0); 11–12 (1); fewer than 11 (2) (Chiappe, 2002).**
 179. Ossified uncinata processes: absent (0); present (1).
 180. Coracoid shape: short (0); elongated with trapezoidal profile (1); strut like (2).
 181. **The proximal end of metacarpal III: contacts the distal carpals (0); does not contact (1) (new).**
 182. **Metacarpals I and II fused proximally: absent (0); present (1) (new).**
 183. **Ectopterygoid with constricted opening into fossa (0); or with open ventral fossa in the main body of the element (1)**

- (Hwang *et al.*, 2004).
184. **Flange of pterygoid well developed (0); or reduced in size or absent (1) (Hwang *et al.*, 2004).**
185. **Symphyseal region of dentary broad and straight, paralleling lateral margin (0) or medially recurved slightly (1); or strongly recurved medially (2) (Hwang *et al.*, 2004).**
186. **Mandibular articulation surface as long as distal end of quadrate (0); or twice or more as long as quadrate surface, allowing anteroposterior movement of mandible (1) (Hwang *et al.*, 2004).**
187. **Maxilla toothed (0); or edentulous (1) (Hwang *et al.*, 2004).**
188. **The lower margin of the external nasal opening is below (0), or close or above (1) the level of the upper corner of the antorbital fenestra (new).** The lower margin of the external nasal opening is below the level of the upper corner of the antorbital fenestra in *Coelophysis bauri*, *Herrerasaurus ischigualastensis*, *Velociraptor mongoliensis*, troodontids, ornithomimids, Tyrannosauridae, *Allosaurus fragilis*, *Caudipteryx* sp., *Oviraptor philoceratops*, *Incisivosaurus gauthieri*, *Khaan mckennai*, and *Ingenia* (100/80). It is close in *Citipati osmolskae* (Clark *et al.*, 2002), above in *Conchoraptor gracilis* (Barsbold *et al.*, 1990), *Nemegtia barsboldi*, and “*Oviraptor*” *mongoliensis*.
189. **The quadratojugal and quadrate contact area is far from (0), or near (1) the lateral surface of the quadrate articular surface (new).**
190. **Nasals and premaxillae do not form a crest (0), or form a crest (1) (new).**
191. **External nasal opening round (0), or oval (1) (new).** In *Incisivosaurus gauthieri*, the external nasal opening is round, in *Caudipteryx* sp. and *Citipati osmolskae*, the external nasal opening is nearly round (slightly elongated). In other derived oviraptorids, such as *Conchoraptor gracilis*, “*Oviraptor*” *mongoliensis*, *Nemegtia barsboldi* and *Oviraptor philoceratops*, the external nasal openings are elongate. In majority of theropods, the external nasal openings are oval (elongate), such as in *Herrerasaurus ischigualastensis*, *Coelophysis bauri*, *Allosaurus fragilis*, ornithomimids, troodontids and dromaeosaurids.
192. **The maxillary fenestra is relatively smaller or absent (0), or larger than the antorbital fenestra (1) (new).** The maxillary fenestra is usually larger, opens laterally, and is clearly visible in lateral view (Rauhut, 2003). It is relatively smaller in *Incisivosaurus gauthieri*, *Caudipteryx dongi* and “*Oviraptor*” *mongoliensis*. It is relatively larger in *Ingenia yanshini* (GIN100/80), *Citipati osmolskae*, and *Nemegtia barsboldi*. It was thought that in caenagnathid *Chirostenotes pergracilis* (ROM 43250), there was no maxillary fenestra (Rauhut, 2003), but according to Clark *et al.* (2002, Fig. 12), a relatively larger maxillary fenestra is present in *Chirostenotes pergracilis* as in *Oviraptor philoceratops*.
193. **Large openings absent (0), or present (0) on the base of the neural arches of anterior caudal vertebrae (new).** On the anterior caudal vertebrae of *Ingenia yanshini* and “*Oviraptor*” *mongoliensis*, there are large openings on the lateral surface near the base of the neural arches, these openings are larger than the pleurocoels; In *Allosaurus fragilis*, *Heyuannia huangi*, *Conchoraptor gracilis*, and *Caudipteryx* sp., this kind of opening is absent.
194. **Large openings (fossa) present (0), or absent (1) on the neural arches of cervical vertebrae (new).** Large openings are present in the neural arches of cervical vertebrae in *Coelophysis bauri*, *Archaeopteryx lithographica*, *Avimimus portentosus*, *Microvenator celer*, *Conchoraptor gracilis*, *Heyuannia huangi*. They are

- absent in *Allosaurus fragilis*, *Herrerasaurus ischigualastensis*, *Ingenia* (GIN 100/32-02), *Caudipteryx* sp., *Nemegtia barsboldi*, and “*Oviraptor*” *mongoliensis*.
- 195. Constriction between articulated premaxillae and maxillae: absent (0), present (1). (Rauhut, 2003).** In most of theropod dinosaurs and a basal oviraptorosaur, *Incisivosaurus gauthieri*, there is no pronounced constriction, but in derived forms such as *Oviraptor philoceratops*, *Conchoraptor gracilis*, *Citipati osmolskae*, “*Oviraptor*” *mongoliensis*, and *Nemegtia barsboldi*, this constriction is distinct.
- 196. Shape of nasals: expanding posteriorly (0); of subequal width throughout their length (1). (Rauhut, 2003).** The nasals expand posteriorly in *Incisivosaurus gauthieri*, and they are very broad and widen posteriorly in *Conchoraptor*. But the nasals are of subequal width in *Oviraptor philoceratops*, *Citipati osmolskae*, “*Oviraptor*” *mongoliensis*, and *Nemegtia barsboldi*.
- 197. Postorbital part of the skull roof: as high as the orbital region (0); deflected ventrally in adult individuals (1). (Holtz, 1994).** In most dinosaurs, the parietals and the medial parts of the squamosals are approximately level with the frontals above the orbits, and their surfaces face dorsally. In *Avimimus portentosus*, *Archaeopteryx lithographica*, *Incisivosaurus gauthieri*, derived oviraptorosaurs, ornithomimosaur and troodontids, the postorbital part of the skull roof deflected ventrally, showing very developed braincase.
- 198. Number of pleurocoels in cervicals: absent (0), two, arranged horizontally (1); one (2) (modified from Rauhut, 2003).** There are no pleurocoels in *Herrerasaurus ischigualastensis* and *Caudipteryx* sp. Two pairs of pneumatic openings are present in *Coelophysis bauri*, *Microvenator celer* (Makovicky and Sues, 1998), *Ingenia* (GI 100/30), *Chirostenotes pergracilis* and *Avimimus portentosus*. Although in *Avimimus portentosus*, a second pair of opening is present in some vertebrae, it is coded here as (0), in contrast to Rauhut (2003). One pair is present in *Allosaurus fragilis*, “*Oviraptor*” *mongoliensis* and *Heyuannia huangi*.
- 199. Pleurocoels developed as: deep depressions (0); foramina (1) on cervical vertebrae (Rauhut, 2003).** Pleurocoels develop as deep depressions in *Coelophysis bauri*, *Microvenator celer*, “*Oviraptor*” *mongoliensis*, *Ingenia yanshini*; as foramina in *Archaeopteryx lithographica*, *Avimimus portentosus*, *Conchoraptor gracilis*, *Heyuannia huangi*, *Nemegtia barsboldi*, and *Allosaurus fragilis*.
- 200. Nasal fusion: absent, nasals separate (0); present, nasals fused together (1) (Holtz, 2000).**

Appendix 3

Characters and data matrix: Character state 0 is plesiomorphic; character state 1–3 are apomorphic. “–” is not comparable character state; “?” is either not preserved or unknown. [] means two character states included.

Allosauroidea

```
0000[01]000001001[01]10010100[01]11[01]000
01[02]00000011000000000000000000[01]000
010000000[01]000[01]1000000000000002[01]1
0010000001000001[01]00101002120010102000
101000002000[01]1[01][01]00[02][01]00100000
0010100000010000?00000000001101000110
```

Ornithomimidae

```
000000010000020000[01][01]00011100001110
10020[01]0[01]010[01]0[01]0010000000???01
002011000[01]000[01]10000000002[01][01][01]
00100100[01]011[01]1000001010002001002001
001000[02][01][02]1001120010111?001001000
00111110110[01][01]2101002000000[01]00011
010?10–0
```

Dromaeosauridae

00[01]000000[01]002100110100101100001100
0001001010000000000000000010[01]00000
0010001100000000000001011[01]111110[01]1
0000[01]111102[12]1[01]2021021[01]12011112
000011[01]111001002101[01]10[01]011[01]000
00100011000110000000?010010100-0

Troodontidae

002110020000010001001001?11?0?010?10?10
020[01]100001100000?00?????100000001?00
11000??0?0?0?0?1[01]0?0?110001001110110
?12?1?0?11211111011011001110?1000?03?01
10110111??11?01111?10010000[01]?00?0110?
0010-0

Archaeopteryx lithographica

00?1100?00101101100010001?01110?1?00020
?1??000?0?0?0000001?1?????0000112300011-
0000000020000??0101100??1?01110001122210
00?1121111110120110101111?100021-?-11??
?0100?0?110?101100110010000001000?101?

Avimimus portentosus

????1??0??????1?1?1?3?111213??00-1?2
111?1??1101??????????00??11??1?????10
000??10?1100011011110?102??2??0120011
1112?1??????00000?0110?001?0110??1110010
01101111120?1??01??21??0?00??111?

Caudipteryx zoui

101?100?1??1101111110001??01011200011?1
?1????1?0??0?00?????????01110002?110010
01?101?101110000000?00[01]0020000100200
00000110-10101010000011011101001111101
110?0100001000010?121010??21101000011??
0-0

Chirostenotes pergracilis

??1??00101????1??0????????????????2?1
0?12??0?0?0?????????1121011002111001101
111112?11????0?1?111111????1??1?1?????
?????11????11??1110????011101??1??1?1??
?0?101000??10??2?1??1??1??1??

Nomingia gobiensis

????????????????????????????????????
?????1????????????????????????????????
??????????0??100011001201?12-?????????
??????????11111101100011001110111111?10
01?????????0????????????????????

Microvenator celer

????????????????????????????????????
??2?1??????????????????0????????????????
?????????0??11????01????0?????1?020011????
??1?0?0?112?1100??1?0????11?011?000100?
??0?????????2??????00??10?

“Oviraptor” mongoliensis

112?0111110112121111?11112101011211111
12?11122111?01111112111101?111112120120
011111111211111001111011?010011021111
21120100??????1?011011211100011?????1
1111111?????????1?1??1121111101?111101

GIN 100/42

1120011011011012111111112101011211111
12111122111001111111211110101111212012
001111111121111101111011111?01?02110
1201201112011111110100121110000111111
0111111110?100001010?11??11211?????????
???

Conchoraptor gracilis

102?011?11011012111101111210101121111
1112111122111?011111112111101?111112120
120011111111211111011110111?10011011
1112012111200111111010002101000011111
110111111110?100001010?1?1?2111101?00
101111

Ingenia yanshini

102?011?11011?121111111121010112111111
??111?2?11??1?11121????1?11111212012001
111111112111?110011110110?1001101011121
12110020011011200100121010000111111011
11111101100001010??1????21101011110110
1

Heyuannia huangi

10??11????????????1????????10??111111?2?

1???2?1????????????????1111?12121?2?01111
 11??1??111110111?1?01001?0?1010111?11211
 112?112?10??01110211100001111011001?1111
 11001000010?011111??211?10??00??11?

12211?11??1111110010110101102101?20?110?
 ?100101?1?1000?????????????????????????
 ???
 ??????????????????????00000?001??1

Nemegtia barsboldi

1121011111010212111111111210101?2111112
 121111221?1001111111211110111111211112
 00111111112?111110111?1?01??1????1????
 ?????????????????100021?10000?11?????1?1
 11????????????0?????112111111?1111?11

Oviraptor philoceratops

112?011??011012111111111210101121111??
 ?????????0????????????????0?????????????1?
 11??1??11?????????????????1????????01??11?
 ?????00????????????0??1?????????????????
 ?????????0????10????????????

Citipati osmolskae

112101111101121211111111121010112111100
 121111221?100111111121111011111121?112
 0011111111111111??????????1?????????1?12?
 111?01?01?1101??????????????11?????????
 ??00?00?110??1??112111101??111??1

Khaan mckennai

10210?1?1?0112121111111012001011211?1111
 ?1????2?????1?????1??????11111212111????
 ?111??1?1111??01??????????0010?????????
 11?0??????0?000?10??????1??01?????????
 ???????????1??21101010????1??1

Incisivosaurus gauthieri

100?00011010021111101011010100213111102