

New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People's Republic of China

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Abstract: Troodontid specimens were recovered from three localities in China by the Sino-Canadian expeditions between 1987 and 1990. These include a Lower Cretaceous form (*Sinornithoides youngi*), which is the most complete troodontid skeleton ever found, isolated bones from the Iren Dabasu Formation (?Turonian), and partial skeletons of *Saurornithoides mongoliensis* from Djadokhta-equivalent beds (?Campanian). These, and other specimens recently described from North America, allow a better assessment of the phylogenetic position of troodontids than has been possible before. Although troodontids have autapomorphies that eliminate them from consideration as bird ancestors, they are nevertheless one of the closest avian outgroups within the Theropoda.

Résumé : Au cours des expéditions sino-canadiennes de 1987 à 1990, des spécimens de troodontidés ont été recueillis dans trois localités en Chine. Ils comprennent une forme du Crétacé inférieur (*Sinornithoides youngi*) qui représente le squelette le plus complet de troodontidé jamais trouvé, des os isolés de la Formation Iren Dabasu (? Turonien) et des squelettes partiels de *Saurornithoides mongoliensis* provenant de lits équivalents au Djadokhta (? Campanien). Ces spécimens et d'autres décrits récemment en provenance de l'Amérique du Nord permettent de mieux évaluer qu'auparavant la position phylogénétique des troodontidés. Bien que les troodontidés aient des autapomorphies qui empêchent de les considérer comme des ancêtres des oiseaux, ils sont néanmoins l'un des exogroupes aviaires les plus rapprochés parmi les Théropodes.

[Traduit par la Rédaction]

Introduction

Troodontids were amongst the first dinosaurs discovered and described, *Troodon formosus* having been established on the basis of a tooth by Leidy in 1856. The first good cranial and skeletal material of a troodontid was also one of the first Asian dinosaurs described, *Saurornithoides mongoliensis* having been collected by the Central Asiatic Expedition of 1922 (Osborn 1924). In spite of these early discoveries, troodontids remained poorly known until the relatively recent discoveries of better preserved specimens in North America and Asia (Russell and Dong 1993; Varricchio 1997; Norell et al. 2000). These once enigmatic animals are becoming so well known that even aspects of their growth (Varricchio 1993) and behavior (Varricchio et al. 1997; Ryan et al. 2000) are now evident.

There has been considerable speculation concerning the relationship of troodontids to other theropods and birds. Recent analyses favor close relationships to either ornithomimosaur (Osmólska et al. 1972; Currie 1985; Pérez-Moreno et al. 1994; Holtz 1994, 1996; Padian and Hutchinson 1997) or dromaeosaurids (Ostrom 1969; Osmólska and Barsbold 1990; Makovicky and Sues 1998; Sereno 1999). In addition,

they are one of the stronger candidates as the closest sister group to birds (Currie 1985; Forster et al. 1998).

In addition to reporting on the first records of troodontids from the Iren Dabasu Formation, characters that are useful for determining the interrelationships of troodontid genera and the phylogenetic relationships of the family itself are described. Characters that have not been described previously but which are useful for determining the systematic position of the Asian genera will also be dealt with. For more general descriptions of *Saurornithoides* and *Sinornithoides*, the reader is referred to papers by Barsbold (1974), Barsbold and Osmólska (1990), Osborn (1924), and Russell and Dong (1993).

Institutional abbreviations

AMNH, American Museum of Natural History, New York; CMN, Canadian Museum of Nature, Ottawa, Ontario; GIN, Mongolian Geological Institute, Ulaan Baatar; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MOR, Museum of the Rockies, Bozeman, Montana; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow; TMP, Royal Tyrrell Museum of

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Systematic Palaeontology

Reptilia Linnaeus 1758
Archosauromorpha Huene 1946
Dinosauria Owen 1842
Saurischia Seeley 1888
Theropoda Marsh 1881
Troodontidae Gilmore 1924

Material

AMNH 21751. Distal ends of a left and a right third metatarsals of an unknown species of troodontid. Collected in the 1920s by the third Central Asiatic Expedition from exposures of the Iren Dabasu Formation (?Santonian) near Erenhot, China.

AMNH 21772. Metatarsal of unknown species of troodontid. Collected in the 1920s from exposures of the Iren Dabasu Formation (?Santonian) near Erenhot, China.

IVPP V9612, holotype of *Sinornithoides youngi*. Nearly complete skeleton, lacking the roof of the skull and most of the cervical and dorsal vertebrae. Collected in 1988 from Lower Cretaceous exposures of the Ejinhoru Formation of the Ordos Basin, China.

IVPP V10599, sacral and caudal vertebrae, pelvis of *Saurornithoides mongoliensis*. Collected in 1988 from Djadokhta-equivalent exposures (?Campanian) at Bayan Mandahu, China.

IVPP 230790-16. Metatarsal of unknown species of troodontid. Collected in 1990 from exposures of the Iren Dabasu Formation (?Santonian) near Erenhot, China.

Description

Sinornithoides youngi

The most complete troodontid skeleton presently known is a remarkable skeleton collected from Lower Cretaceous exposures near the village of Muhuaxiao in the Ordos Basin (Russell and Dong 1993). Associated fossils are listed by Dong (1992).

The skull of IVPP V9612 is difficult to see in its present position because it is upside down and is covered by the left hand and part of the tail. The specimen was prepared from underneath, but computerized tomography (CT) scans (Chapman and Andersen 2000) reveal that most of the skull roof had been eroded away before the specimen was collected.

IVPP V9612 is not a mature specimen (long bones have the pitted surfaces characteristic of immature individuals, cervical ribs are not fused to the corresponding ribs; the scapula and coracoid have not fused; the ilium, pubis, and ischium are separate; the ends of the paired pubes are not fused), although it was apparently approaching maturity because the neural arches are indistinguishably fused to the centra in the middle and distal regions of the tail, and the astragalus and calcaneum are indistinguishably fused. *Sinornithoides* could not have been as large as either *Saurornithoides* or *Troodon*.

The skull of *Sinornithoides* is relatively shorter and deeper, and the orbits are relatively larger, than those of *Saurornithoides* (Osborn 1924; Barsbold 1974) and *Troodon* (Russell and Sequin 1982). Unfortunately, these are size- and age-related characters that show strong allometry with growth and are not satisfactory for use in diagnosing genera.

In contrast with dromaeosaurids (Currie 1995) and the majority of theropods, the maxilla separates the subnasal processes of the premaxilla and nasal. The maxilla also forms part of the margin of the external naris in *Byronosaurus* (Norell et al. 2000), *Saurornithoides* (Barsbold 1974), and *Troodon* (Russell 1969; Currie 1985). This is a derived character that developed independently in abelisaurids (Chatterjee 1978; Bonaparte et al. 1990; Sampson et al. 1998) and possibly therizinosaurids, like *Erlikosaurus* (ref). It is also present in *Archaeopteryx* (Tarsitano and Hecht 1980; Wellnhofer 1974, 1988) and other early birds (Chiappe et al. 1999).

The antorbital fossa is almost entirely occupied by two large facial fenestrae, as in *Saurornithoides* (Osborn 1924; Barsbold 1974) and *Archaeopteryx* (Wellnhofer 1974). The antorbital fenestra and the maxillary fenestra are separated by a thin pillar of bone recessed from the lateral margin of the maxilla, whereas those of *Byronosaurus* and *Saurornithoides* are anteroposteriorly wider. Furthermore, the interfenestral bar is not inset from the lateral surface of the maxilla in *Byronosaurus* (Norell et al. 2000). The maxillary fenestra is relatively larger than those of dromaeosaurids (Osborn 1924; Ostrom 1969; Sues 1977; Burnham et al. 2000) and is positioned in a more ventral position close to the ventral margin of the antorbital fossa. In contrast, the dromaeosaurid maxillary fenestra is smaller and is positioned in the upper part of the maxillary fossa. The anteroventral margin of the antorbital fossa is pierced by a small, slit-like promaxillary fenestra. As in *Byronosaurus* (Norell et al. 2000) and *Troodon*, CT scans show that the maxilla of *Sinornithoides* formed part of the extensive secondary palate.

The T-shaped, left lacrimal is complete except for much of the anterodorsal process (Fig. 1A), but has been damaged dorsally by erosion. As in *Byronosaurus*, *Saurornithoides*, and *Troodon*, there is a distinct, ventrally concave, thin shelf overhanging the anterolateral corner of the orbit. As in other troodontids, the dorsal surface of the lacrimal was strongly tilted so that the anterodorsal process was significantly lower than the process above the orbit. The preorbital bar is more slender than that of *Troodon* (Currie 1985) and is more strongly curved anteroventrally. Like its Late Cretaceous relatives, however, the preorbital bar is anteroposteriorly long dorsally, but twists ventrally to become mediolaterally wider than long. Several autapomorphies of the lacrimal distinguish *Sinornithoides* and other troodontids from dromaeosaurids and other theropods. A lacrimal duct does not pierce the preorbital bar as it does in dromaeosaurids and other theropods. What is interpreted as a possible lacrimal duct (Currie 1985) is higher on the lacrimal, crosses the lateral surface at the top of the preorbital bar, and enters a foramen in the anterodorsal process. The surface of the preorbital bar is smooth, lacking the rugose region for skin attachment found in dromaeosaurids and most other theropods. There is no evidence of a ventral slip of the prefrontal along the

dorsomedial edge of the lacrimal. The elements identified in *Troodon* as possible prefrontals by Currie (1985) are more likely neomorphs (Gauthier 1986). It is likely that the prefrontal has become indistinguishably fused to the lacrimal in the Troodontidae, as it apparently has in velociraptorines.

The incomplete right frontal (Figs. 1B–1E) preserves most of the interfrontal suture, but not the orbital rim, nor the sutures for the lacrimal, postorbital, laterosphenoid, nasal, or parietal. Nevertheless, it has the characteristic elongate shape of a troodontid (Currie 1987b). Unlike dromaeosaurids, the olfactory lobe of *Sinornithoides* was clearly elongate.

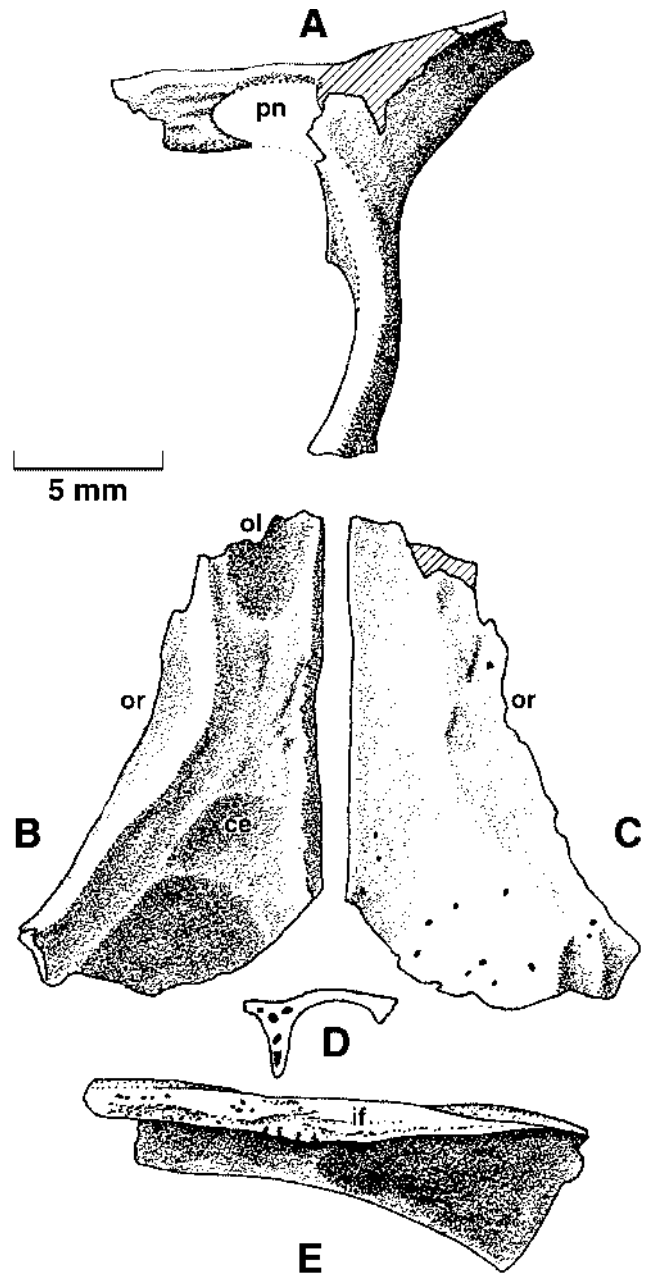
Like other troodontids, the dentary has a distinct groove (Fig. 2E), in which there is a concentration of foramina (Norell et al. 2000). In lateral view, the dentary tapers anteriorly as in other troodontids; but in ventral view, it is straight with none of the anteromedial curvature at the symphysis that is present in *Troodon* (Currie 1987a).

The teeth of *Sinornithoides* (Fig. 2) are similar to those of other troodontids (Currie et al. 1990). They are relatively small and numerous, with 18 maxillary teeth. The dentary teeth are smaller than the maxillary teeth, the longest being 2.2 mm (fore–aft base length (FABL) is 1.3) compared with 3.2 mm (with a FABL of 2.4) for the tallest maxillary tooth.

Teeth are differentiated into four regions (premaxilla, maxilla, anterior dentary, mid and posterior dentary). There is a conspicuous constriction between the crown and root of each tooth. Four premaxillary teeth are present (Fig. 2A), as in the vast majority of toothed theropods, and these have denticles on both carina (Russell and Dong 1993). The third premaxillary tooth is 2.7 mm long. The maxillary and dentary teeth only have denticles on the posterior carinae, as in many specimens of *Saurornithoides* but not *Troodon* (Currie 1987a). A significant difference from *Troodon* and *Saurornithoides* is the relatively small size of the denticles (Fig. 2C, 2D). Using denticular basal diameter (as seen in lateral or medial view) is preferable to estimating the number of denticles per 5 mm when comparing taxa with small teeth, with relatively few denticles, or with denticles that are highly variable in basal diameter. The maximum basal diameter of one serration is 0.3 mm in the maxillary teeth (Russell and Dong 1993) of *Sinornithoides*. Although the small size is in part attributable to the small size of the teeth (Farlow et al. 1991), juvenile *Troodon* teeth in the same size range have fewer denticles with larger basal diameters (Fig. 3). The higher range of variability (lower correlation coefficient in Fig. 3) in denticle size in troodontid teeth is a consequence of the greater degree of heterodonty in this family (Currie 1987a) than in other theropods. The teeth of *Byronosaurus* (Norell et al. 2000) lack denticles. In spite of the highly variable nature of troodontid denticle size, the maxillary denticles in *Sinornithoides* are relatively smaller than even the smallest dentary denticles of *Troodon* (Fig. 3). They are, however, still relatively larger than those of most other theropods (Fig. 3).

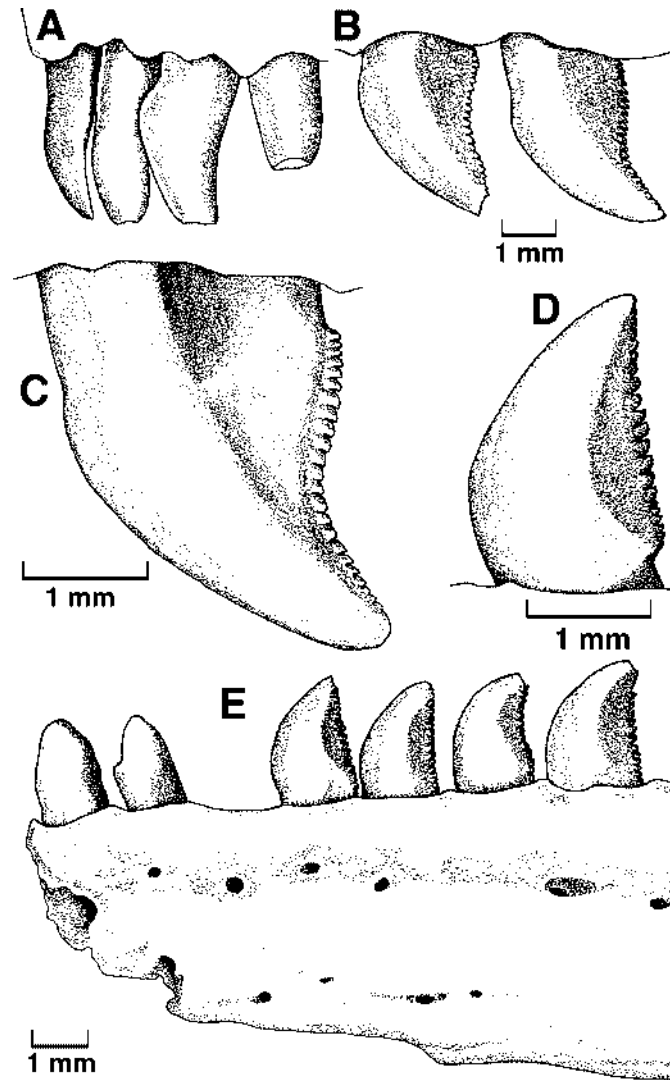
Cervical, dorsal, and sacral vertebrae are not well exposed in IVPP V9612. Two anterior (possibly the fourth and fifth) cervical vertebrae were found eroded from the skeleton. The more posterior of the two (Figs. 4A, 4B) is reasonably well preserved on the left side, retaining the zygapophyses, the parapophysis, and the base of the diapophysis. The posterior

Fig. 1. *Sinornithoides youngi*, IVPP V9612. Ventrolateral aspect of left lacrimal (A). Ventral (B), dorsal (C), anterior (D), and medial (E) views of right frontal. ce, impression for cerebral hemisphere; if, interfrontal suture; ol, depression for olfactory lobe; or, orbital margin; pn, lacrimal pneumatic recess.



zygapophyses of both anterior cervicals have short, knob-like epipophyses that are relatively smaller than those of dromaeosaurids (Ostrom 1969), but more pronounced than those of *Gallimimus* (Osmólska et al. 1972). As in dromaeosaurids and ornithomimids, the parapophyses are lower than the ventral margin of the centrum on the midline. Although the diapophysis of the possible fifth cervical is incomplete, its distal end closely approaches the parapophysis. A depression in the side of the centrum is penetrated by two foramina. The smaller, more anterior one is situated on the anterior rim of the depression (Fig. 4A)

Fig. 2. *Sinornithoides youngi* (IVPP V9612) dentition from left side of skull. (A) Premaxillary teeth (note that denticles are present but are not visible in this view). (B) Anterior maxillary teeth. (C) Maxillary tooth. (D) Dentary tooth (fourth alveolar position). (E) Anterior part of dentary showing first seven tooth positions.



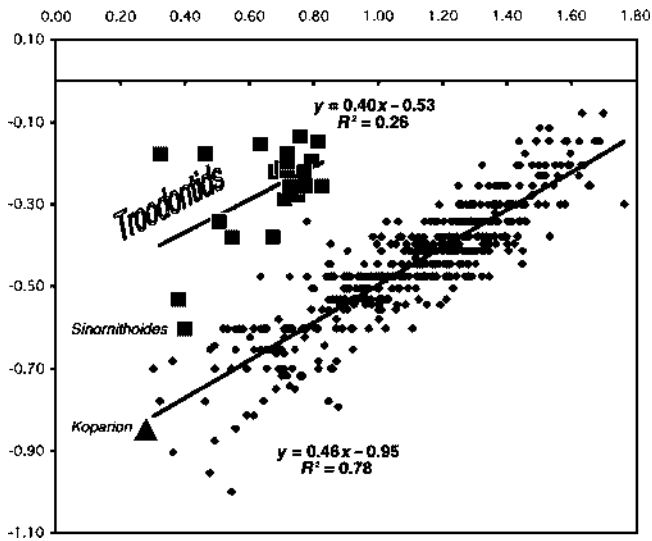
and may have been used by a blood vessel or nerve. It is separated from the larger, more posterior pneumatopore by about 0.5 mm. The lamina connecting the diapophysis to the margin of the postzygapophysis is well developed and overhangs the centrum as in *Gallimimus* (Osmólska et al. 1972). It is pierced lateroventrally by a pneumatic foramen that was connected to the air-filled interior of the neural arch. This pneumatopore is presumably equivalent to the infrapostzygapophysial fossa of other theropods (Makovicky 1997). Other pneumatic features of the neural arch are obscured by matrix.

The posterior (almost certainly the ninth and tenth) cervicals are exposed in ventral view. The cervical ribs were not fused to them. The parapophyses are low on the margin of the centrum (Fig. 4C), and the transverse processes are almost directly above them in a more anterior position than they are in most theropods. As in ornithomimids, the transverse process extends posteriorly as a thin, horizontal shelf of bone. There is at least one pleurocoel on the side of the centrum posterodorsal to the parapophysis. Medial to the

parapophysis is a distinct carotid process (Fig. 4C) as in ornithomimids (Osmólska et al. 1972), avimimids (Kurzanov 1987), and birds. The carotid processes of the posterior cervicals are separated by a deep concavity in the ventral surface of the centrum. The concave region is narrower on the last cervical than it is on the penultimate cervical. The posterior region of the centrum is ventrally convex if viewed in section.

The first dorsal vertebra has a strong and deep hypapophysis (Fig. 4D). It is not as large in the second dorsal, but it is still prominent. Hypapophyses are almost universally present in theropods, but only seldom are as powerfully developed as in *Sinornithoides*. Although *Deinonychus* has only moderately sized hypapophyses on the anterior dorsals (Ostrom 1969), they are very large on *Troodon* (Makovicky 1995) and the velociraptorine dromaeosaurid *Saurornitholestes* (MOR 660). Hypapophyses are also powerfully developed in *Avimimus* (Kurzanov 1987), but are very weak in ornithomimids (Osmólska et al. 1972). There are two pneumatopores on the exposed right

Fig. 3. Logarithmic bivariate plot of FABL (x -axis) versus basal diameter of largest posterior denticle (y -axis). Small diamonds and the lower trend line represent a variety of Jurassic and Cretaceous tetrapods. Large squares and upper trend line represent troodontids, including *Sinornithoides*. *Koparion* (large triangle) is based on a tooth from the Upper Jurassic Morrison Formation and has been assigned tentatively to the Troodontidae. Data derived in part from Chure (1994) and Farlow et al. (1991) and in part from new specimens. R^2 , correlation coefficient.



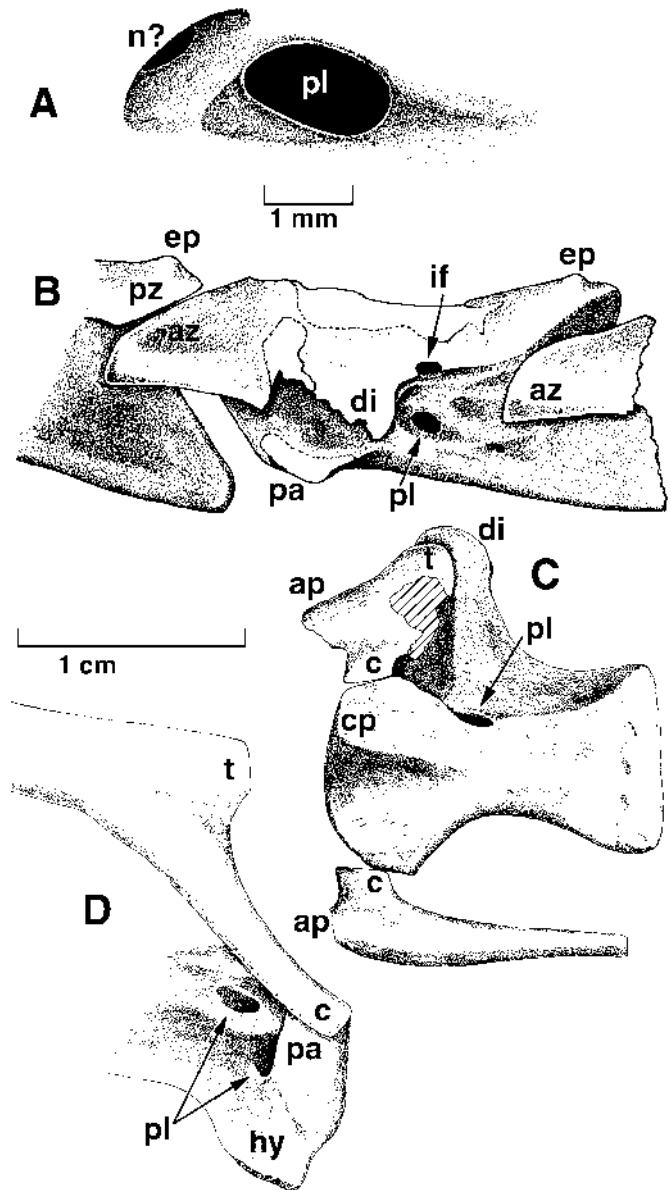
side of the vertebra (Fig. 4D). The upper opening is the infraprezygapophyseal fossa, which invades the transverse process as in *Troodon* (Makovicky 1995). The pneumatic fossa of the centrum in *Sinornithoides* is in the expected position behind the parapophysis as in *Troodon* (Varricchio 1997).

Most of the sacral vertebrae are obscured by the presence of other bones. The last sacral has a sacral rib that extends to and contacts the ilium. The first caudal vertebra, identified by its posteriorly recurved transverse process that does not contact the ilium, and by its contact with the first haemal arch, is closely associated with the last sacral, but does not appear to have been fused to it. The sacrum of *Saurornithoides junior* includes the first caudal vertebra (Barsbold 1974) for a total of six segments. The holotype of *Saurornithoides mongoliensis* (AMNH 6516) also incorporates six vertebrae, the last of which is presumably a caudosacral. This is followed by a free caudal, to which is attached the first haemal spine of AMNH 6516. The last coossified sacral of IVPP 10599 is obviously a caudosacral, because the first haemal spine attaches directly to it. It is conceivable that this specimen had seven sacrals, because it is one of the largest specimens known.

As reported by Russell and Dong (1993), almost all of the tail is preserved. There are 27 vertebrae in the holotype. The small sizes of the distal vertebrae indicate that the tail was not much longer than what has been preserved. The reduction in vertebral length is gradual in the last five complete vertebrae, from 21–18 mm. Usually the last two or three caudal vertebrae show drastic, stepped size reduction in coelurosaurs, which suggests that there were at least two or three more caudal vertebrae in the living animal. It is likely

Fig. 4. *Sinornithoides youngi*, IVPP V9612, vertebrae.

Posteroventral view of left side of centrum (A) of approximately the fourth cervical vertebra. ?Fifth cervical vertebra (B) in left lateral view, with portions of the adjacent cervicals attached. Second last cervical (9th?) along with portions of its ribs in ventral aspect (C). First dorsal (11th presacral) in right lateral view (D). ap, anterior process of cervical rib; az, anterior zygopophysis; c, capitulum; cp, carotid process; di, diapophysis; ep, epipophysis; hy, hypapophysis; if, infrapostzygapophysial fossa; n?, possible nutrient foramen; pa, parapophysis; pl, pleurocoel; pz, posterior zygopophysis; t, tuberculum.



that *Sinornithoides* had between 30 and 32 caudal segments, comparable with the numbers in ornithomimids (32–35) and oviraptorosaurs (22–32, Barsbold et al. 2000). Dromaeosaurids (36–40, Ostrom 1969), tyrannosaurids (38–39), and most other coelurosaurs had marginally longer tails.

Although well-developed transverse processes are on only the first nine caudal vertebrae, they persist as faint ridges (Fig. 5A) until at least the thirteenth caudal. The lengths of

caudal centra increase posteriorly to a maximum in the thirteenth segment, after which they decrease progressively in length.

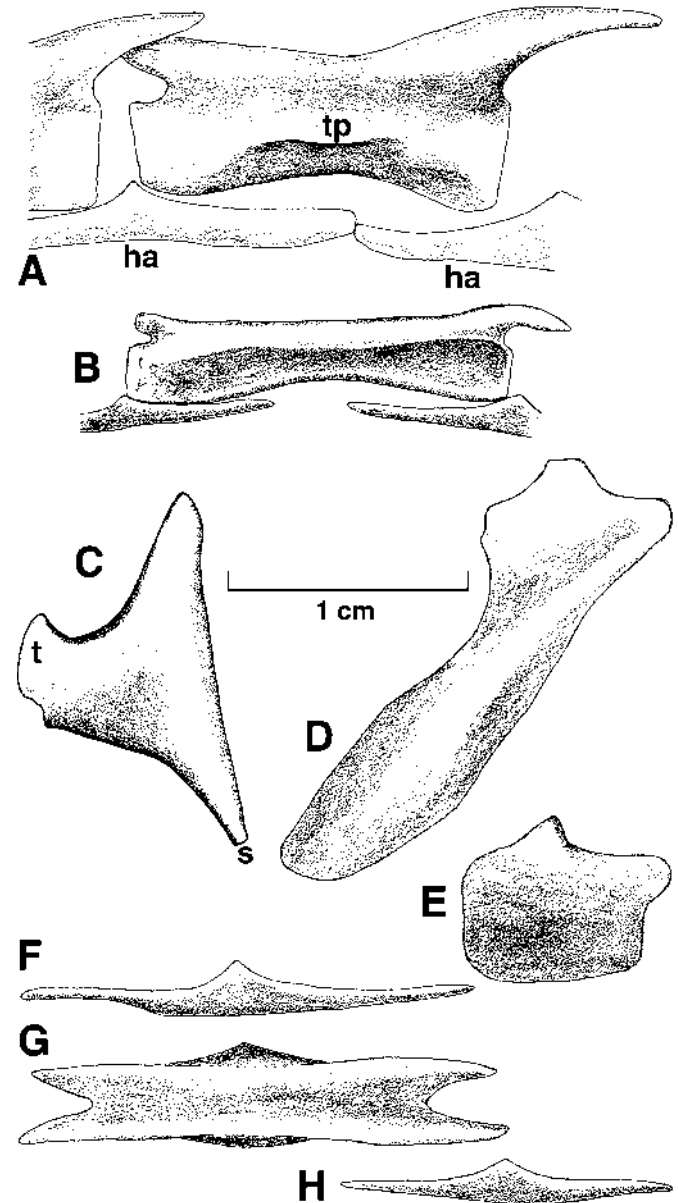
Few of the ribs are visible. The penultimate cervical ribs were evidently relatively short (Fig. 4C), but had the characteristic theropod capitulum, tuberculum, short anterolateral process, and elongate rib shaft. There is no anterolateral process on the last cervical (Fig. 5C), which is short and triangular. The first dorsal rib (Fig. 4D) shows a radical change in shape from the last cervical and was obviously a much longer rib with an elongate, slender capitulum.

Haemal arches in *Sinornithoides* are characteristic of troodontids. The first haemal spine of IVPP V9612 is attached between the first and second caudal centra. In reptiles, the haemal arches often start earlier in the tails of males than they do in females (Romer 1956; Larson 1997). The type specimen (AMNH 6516) of *Saurornithoides mongoliensis* was possibly a female, because its first haemal arch is between the second and third caudals, whereas IVPP V10599 may have been male, because the most anterior haemal contacts the first and second centra. Because the number of sacrals is the same in *Sinornithoides* as it is in *Saurornithoides*, it can be assumed from the position of the first haemal arch that the holotype of the former (IVPP V9612) may also have been a male. The shaft of the first haemal spine is inclined posteroventrally, but the distal end hooks strongly posteriorly. Measured along its longitudinal axis, it is 16 mm long. The second haemal spine (Fig. 5D) is 22 mm long and is not so strongly recurved distally. More posterior haemal spines become progressively shorter, until the sixth and seventh ones are quadrilateral in outline and longer than deep (Fig. 5E). The proximal ends of the first seven haemal arches wedge between the associated centra and wrap anteriorly and posteriorly around their ventral margins. The anterior process is longer than the posterior one. The eighth haemal arch is covered by matrix, so its nature cannot be determined at this time. The ninth and subsequent haemal arches are horizontal plates of bone (Figs. 5A, 5B, 5F–5H) that extend anteriorly and posteriorly from the intervertebral wedge. There is a longitudinal, medial, shallow trough on the ventral surface as in *Deinonychus* (Ostrom 1969) and other theropods. In lateral aspect, they taper anteriorly and posteriorly, and there is no vertical extension on the midline.

The gastralialia are nicely preserved in the holotype of *Sinornithoides* (Fig. 6). There were at least fourteen sets, each consisting of left and right lateral elements, and left and right medial elements. No pairs of gastralialia are fused, but the proximal ends of the medial ones overlap in a pattern characteristic of theropods and early birds (Claessens 1996). The lateral gastralialia are longer than their medial counterparts.

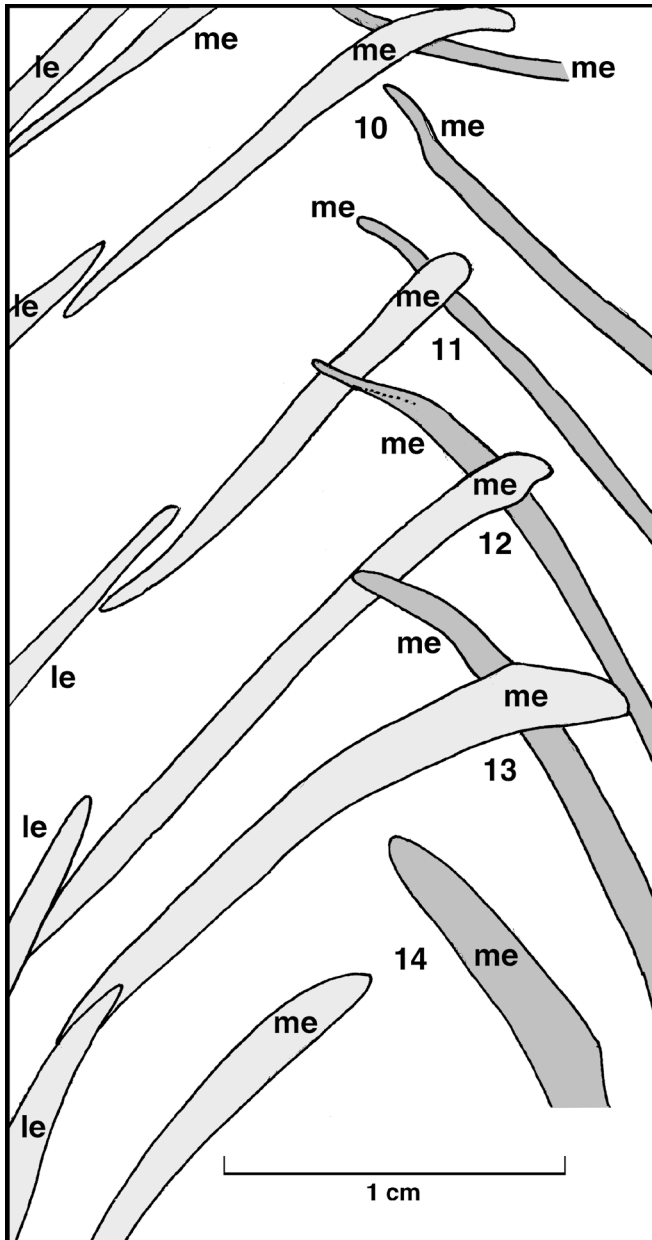
Both clavicles are preserved in position, each attached to the acromion process of the scapula (Fig. 7). It is unclear however, whether they extended ventrally far enough to contact each other. The left clavicle is 13.7 mm long, and the right is 14.3. The difference in length, and the fact that the ventral margins of both look like broken surfaces, suggests that neither is complete, and that the middle section of the furcula was displaced and lost. It is also possible that this region had not ossified because of the immaturity of the specimen. Given

Fig. 5. *Sinornithoides youngi*, IVPP V9612. Eleventh caudal vertebra (A) plus anterior region of the twelfth caudal vertebra, and the tenth and the eleventh haemal arches. Twenty-fourth caudal vertebra (B), last right cervical rib (C), the shaft of which is broken; haemal arch and spine of second caudal (D) seen from right side; right lateral view of sixth haemal arch and spine (E); lateral (F) and ventral (G) views of tenth haemal arch; lateral view of twenty-second caudal chevron (H). ha, haemal arch; s, rib shaft; t, tuberculum; tp, transverse process.



the widespread distribution of furculae in theropods (Makovicky and Currie 1998), including possibly *Troodon* (Thulborn 1984, but see Claessens 1996), the clavicles of *Sinornithoides* may have extended ventromedially to contact and form a furcula in at least mature animals. The clavicle tapers dorsally to a sharp point that attached to the everted margin of the dorsal edge of the acromion process. The broken end is 1.8 mm wide and only 0.9 mm thick. In cross section, the clavicle is concave posteromedially, and convex externally.

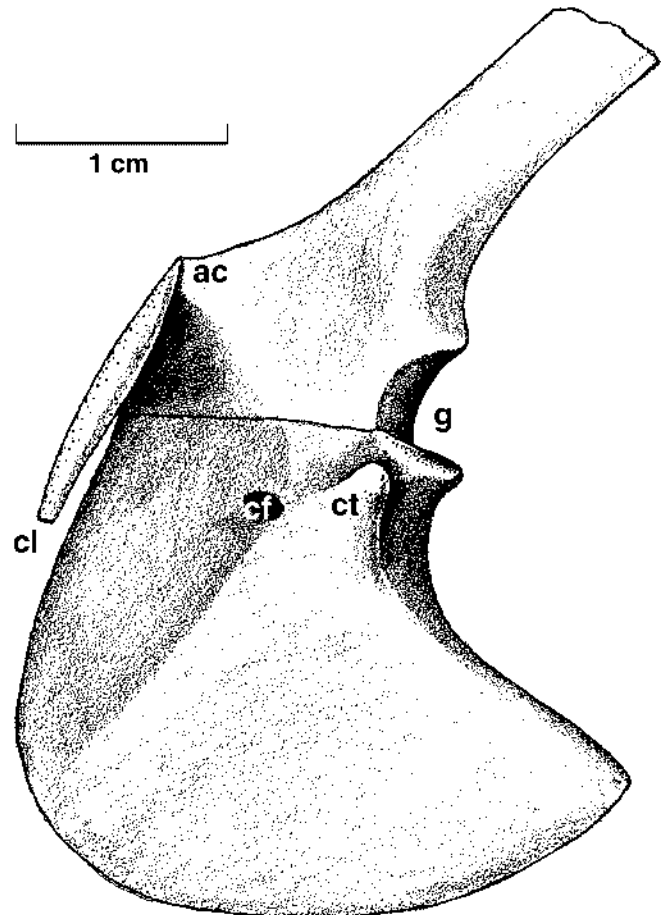
Fig. 6. *Sinornithoides youngi*, IVPP V9612. Ventral view of most posterior medial gastralia. Lightly shaded gastralia are from the right side of the body, the darker shaded ones are from the left side. Segments 11, 12, and 13 are in proper articulation, whereas others are out of alignment. le, lateral element; me, medial element.



Neither of the clavicles contacts the coracoids ventrally in this specimen.

The proximal end of the right scapula is exposed and demonstrates that the scapular blade had a long slender, strap-like profile (Fig. 7). The suture with the coracoid is unfused, although the contact appears to be tight. There is a long, rather gradual slope from the anterior margin of the shaft into the acromion process, which is small relative to the sharply divergent acromion of tyrannosaurids. It does however compare well with those of dromaeosaurids, oviraptorids, and early birds, like *Archaeopteryx*. The

Fig. 7. *Sinornithoides youngi*, IVPP V9612, left pectoral girdle elements. ac, acromion process; cf, coracoid foramen; ct, coracoid tubercle; g, glenoid.



glenoid is long (6.8 mm) but low (5.0 mm). Unlike those of dromaeosaurids (Burnham et al. 2000; Norell et al. 2000) and birds (Novas and Puerta 1997), it is not oriented as much laterally as posteriorly, but faces mostly backwards. The supraglenoid ridge is not pronounced. A ridge extends anterodorsally from the coracoid suture at the back of the glenoid to the anterodorsal margin of the acromion process. Ventral to this ridge, the lateral surface of the scapula is shallowly concave. The dorsal edge of the clavicle articulates with the high point on the anterodorsal corner of the acromion process. From this point to the posterior limit of the ridge above the glenoid, the scapula is 16 mm long. Above this, the shaft of the scapula tapers until it is only 11 mm in length. The full height of the scapula is unknown.

There is some variation between the two coracoids, although both are longer than they are tall. The right coracoid is 27.2 mm long and 25.7 mm high, whereas the same dimensions on the left coracoid (Fig. 7) are 29.3 mm and 24.9 mm. The coracoid facet of the glenoid is convex and oriented more proximally than laterally. Like other coelurosaurs, the coracoid extends far behind the coracoid facet of the glenoid. However, there is no distinct sternal process like that of *Velociraptor* (Norell and Makovicky 1999). The coracoid foramen is positioned beneath the middle

Fig. 8. *Sinornithoides youngi*, IVPP V9612. Right humerus (A) with piece of distal end (X) still attached to proximal ends of right radius and ulna. Ulna (B) and radius (C) shown in from right side but based on bones from the left side with proximal ends restored from right side. d, deltopectoral crest; R, radius; U, ulna.

of the scapulocoracoid suture and has a diameter of 1.6 mm. The coracoid tubercle ("biceps" tubercle) is pronounced, extending 6.5 mm from the coracoid foramen. Although the sternum is not ossified, the posteromedial margins of the paired coracoids form a V-shaped gap that suggests the cartilaginous sternum was about 16 mm across.

The arm is almost half as long as the leg, but is relatively short compared with the arms of dromaeosaurids and birds.

The slender, relatively straight humerus (Fig. 8A) is 60% the length of the femur. The ventrally oriented deltopectoral crest is positioned mostly in the proximal quarter of the bone with the conical apex about 2 cm from the proximal end. The internal tuberosity is poorly developed in this specimen, but this is probably a consequence of ontogeny.

The ulna (Fig. 8B) is almost 80% the length of the humerus. The shaft, which is bowed as in most maniraptorans, has a diameter 45% greater than that of the radius. The olecranon process is low, in part because of the immaturity of the specimen, and is subtriangular in section. The shaft of the radius is straight (Fig. 8C), and the distal end expands anteroposteriorly but is flattened mediolaterally.

There are only two carpals preserved in each of the left or right wrists (Fig. 9A). The radiale is a flat, disklike bone that intervenes between the radius and the semilunate carpal in the right hand. The semilunate, composed of one or more distal carpals, capped the first and second metacarpals as in most maniraptoran theropods. The transverse proximal groove seems to have articulated directly with the ulna and the radiale.

The first metacarpal (Fig. 9A) has a short, thick (5 mm), twisted shaft that is in close contact with Metacarpal II for almost half of its length. Its length is 35% that of the second, which in turn is half a millimetre longer than Metatarsal III. The second metacarpal, which is 40% the length of the humerus, is the longest of the three. The minimum shaft diameter of Metacarpal III is 1.5mm, which is about 25% thinner than the shaft of the second metacarpal. As preserved the shaft of the third metacarpal from the right side appears to be straight (Holtz 2000). However, it has clearly been crushed and damaged, but the rapid prototype (a plastic model produced from CT scan images) reveals that the left Metacarpal III is curved as in other maniraptorans. Amongst the non-ungual phalanges, I-1 is the longest and most robust. In each finger, the penultimate phalanx is longer than the anti-penultimate phalanges (Table 1). The unguals of the first two digits are almost equally strong, whereas that of the third is visibly smaller. The keratinous sheathes of the unguals were thick along the extensor margin, and these regions are preserved near the tips of at least two of the unguals (Fig. 9B). The medial surface of right ungual I-2 also seems to be covered by a thin layer of residual keratin.

The dorsal margins of both ilia have been destroyed by erosion. The pubic pedicel is longer and deeper than the ischial pedicel and is oriented ventrally. The acetabulum was

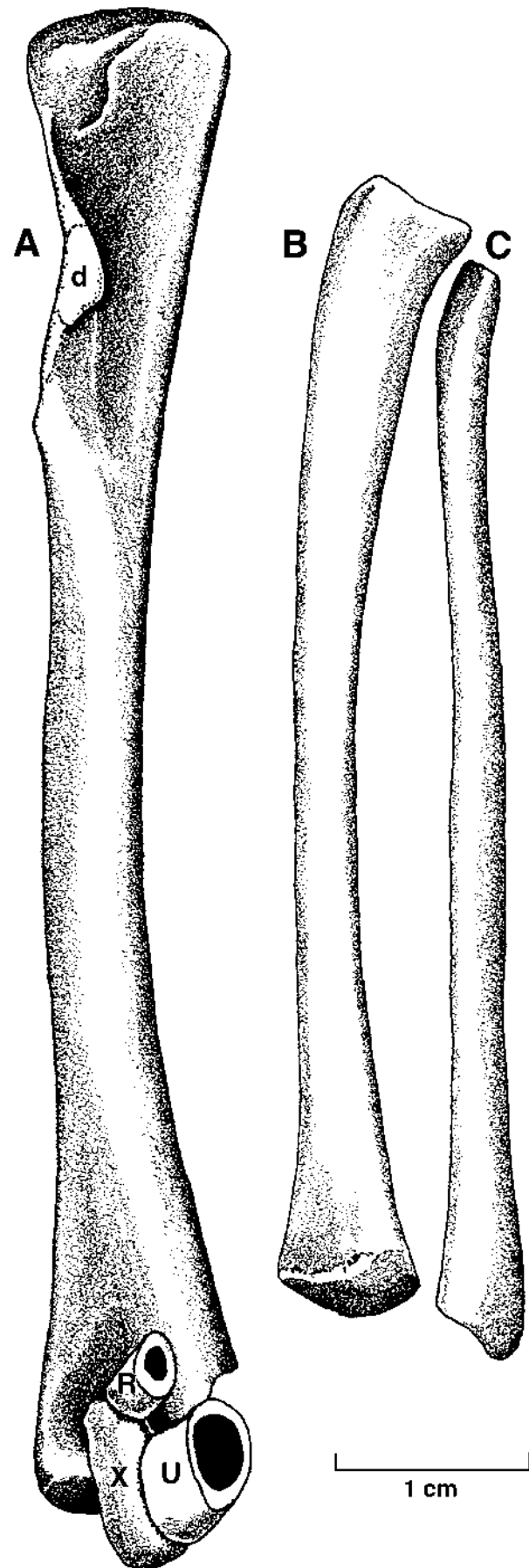
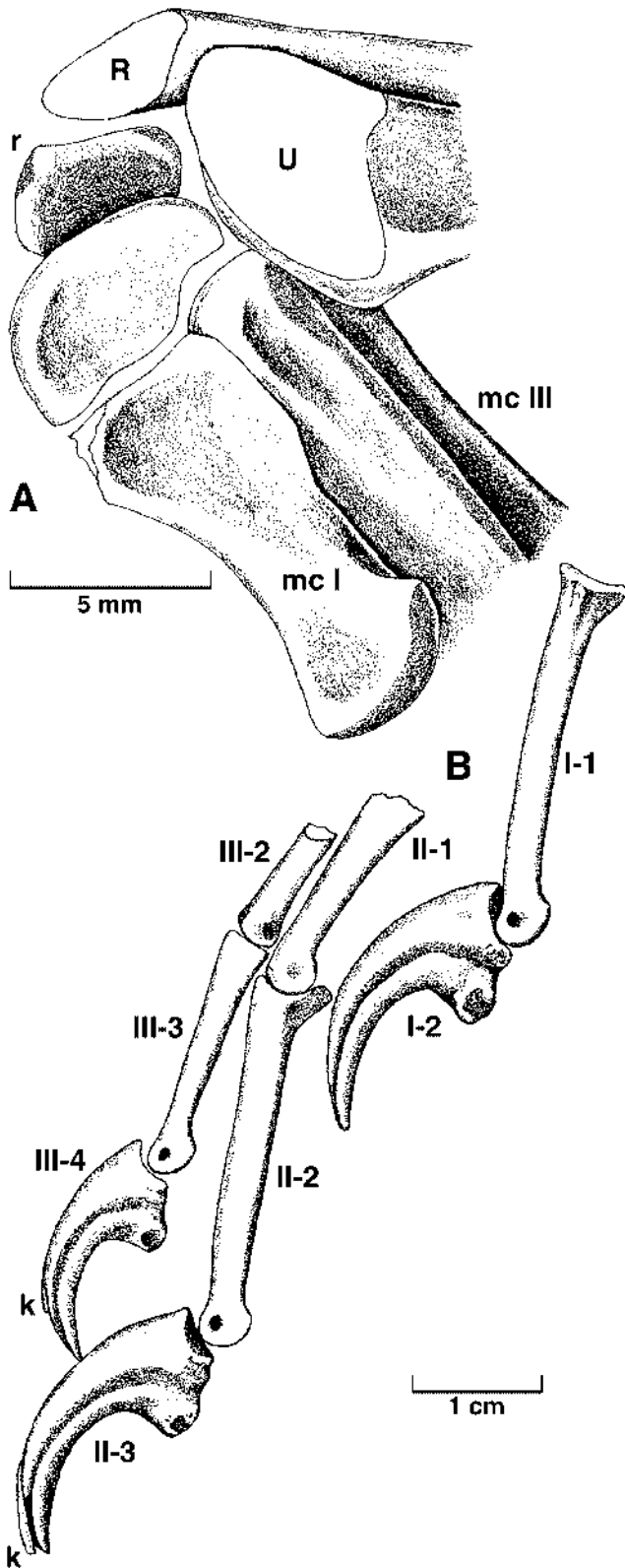


Fig. 9. *Sinornithoides youngi*, IVPP V9612. k, keratin, mc, metacarpal; R, radius; r, radiale; U, ulna.



about 19 mm long anteroposteriorly, and has a broad supraacetabular rim. The preacetabular blade (anterior to the pubic pedicel) of the right ilium is 26 mm long, whereas the

postacetabular blade of the left ilium is longer (30 mm). The ilium is therefore dolichoiliac. The anterior margin of the pubis tapers gradually into an anteroventral process. There is no evidence of the fossa for the *M. cuppedicus*. The pubis, as noted by Russell and Dong (1993), is almost double the length of the ischium. Proximally, the shaft is oval in cross-section, but a centimetre-wide flange develops more distally on the medial surface to form the pubic apron. The latter meets its equivalent from the other side in a long, unfused pubic symphysis. The pubic aprons define a shallow longitudinal trough that opens posteroventrally. As in *Deinonychus* (Ostrom 1976) and *Velociraptor* (Norell and Makovicky 1999), the paired pubes narrow distally to less than half the width at mid-shaft length. There is no evidence of a pubic boot (Russell and Dong 1993), although it may not have been ossified because of the small size and young age of this individual. The ischia expand posteroventrally into relatively flat obturator processes that apparently contacted each other but are not fused along their ventral margins.

The shaft of the femur is arched anteriorly as in other troodontids and as in dromaeosaurids and early avialians (Norell and Makovicky 1999). The lesser trochanter was proximal in position and formed part of the trochanteric crest as in other troodontids (Currie and Peng 1993). Oviraptorids are similar although the lesser trochanter is separated from the greater trochanter by a shallow incision. The trochanteric crest is not seen in dromaeosaurids or apparently *Archaeopteryx* (Norell and Makovicky 1997), but is present in *Confuciusornis* and more advanced birds (Chiappe et al. 1999). However, it should be pointed out that only a shallow notch generally separates the lesser and greater trochanters in dromaeosaurids. There is a distinct tubercle on the posterolateral margin of the femur that has been identified as the "posterior trochanter" (Currie and Peng 1993), even though it is more lateral in position than the posterior trochanters of *Deinonychus* (Ostrom 1976) or *Velociraptor* (Norell and Makovicky 1999). The posterior trochanter is at the same level and is continuous with a more lateral, distal ridge (the "lateral ridge" of Norell and Makovicky 1999), and it is bounded proximally by a depression in both troodontids and dromaeosaurids. This suggests that the posterior trochanter of dromaeosaurids is homologous with the more lateral tubercle in troodontids. There is no indication of a fourth trochanter, which is variably developed in dromaeosaurids (Norell and Makovicky 1999) and oviraptorids (personal observations, 1999–2000).

More than 40% longer than the femur, the tibia is a large straight-shafted bone with a single but well-developed cnemial crest. There is a long, well-developed crista fibularis in the proximal quarter of the tibia.

The shaft of the fibula is slender (1.7 mm, which is less than 17% the shaft width of the tibia) and is appressed closely to the surface of the tibia. The anterolateral process for the *M. iliofibularis* projects laterally with virtually no anterior orientation. Distally, the fibula twists onto the anterolateral face of the tibia to contact the tarsus, where it expands to 1.9 mm. Contrary to the initial report (Russell and Dong 1993), it is not fused to the tibia distally.

As described by Russell and Dong (1993), the astragalus and calcaneum appear to be coossified into a single, indistinguishable unit. The only other possible interpretation is that

Table 1. Lengths of Manus elements.

Digit	Metacarpal	1	2	3	4
I	11.7	29	22.5	—	—
II	33.5	18.5	28.5	22	—
III	33	4.2	8.6	20.3	17.3

Note: Ungual measurements are all straight line distances from the upper margin of the proximal articulation to the tip.

the calcaneum has been lost, although this seems less likely considering the fact that the fibula extends to contact the ankle, and there appears to be a line of fusion between the astragalus and calcaneum of *Troodon* (Russell 1969). The medial condyle is mediolaterally narrower but deeper (proximodistally and anteroposteriorly) than the lateral condyle. The two condyles, which are separated by a deep groove, are positioned almost entirely anterior to the distal end of the tibia. There is a tall ascending process on the astragalus, although its exact height is unknown, because it is largely covered by the metatarsus, which is folded against the tibia. There is a deep pit in the base of the ascending process separating it from the distal condyles. Two distal tarsals tightly cap the metatarsus, but remain as distinct bones (Fig. 10A).

As preserved, the five metatarsals of each foot are seen in posterior view (Fig. 10A). The first left metatarsal is pathologic. At mid-height the shaft is expanded by a bony callosity (Figs. 10D, 10E), larger than the distal end. The distal articulation is small, round, and twisted away from alignment of the normal central axis of the bone. The shaft of the second metatarsal becomes lateromedially thin (3.3 mm) but anteroposteriorly long (5.9 mm) at midshaft, and reaches its thinnest dimensions a third of the distance from the distal end. The proximal end of the third metatarsal separates the second and fourth ones by 5 mm on the flexor surface. The shaft of the third metatarsal thins at midshaft, as in *Tochisaurus* (Kurzanov and Osmólska 1991), *Troodon* (Wilson and Currie 1985), and other troodontids, and only a 1 mm width can be seen between the second and fourth metatarsals on the right foot (Fig. 10A) for most of its height. Although it has been reported that Metatarsals II and IV contact each other along the flexor surface in *Tochisaurus* (Kurzanov and Osmólska 1991), this does not seem to have happened in *Saurornithoides*. The fourth metatarsal is more powerfully built, with cross-sectional dimensions of 5.3 by 8.6 mm at midshaft.

Metatarsal III has the tongue-like extension of the distal articulation typical of other troodontids, although it is not as well-developed as in Late Cretaceous genera (Russell and Dong 1993). Unlike other troodontids, the tongue-like extension has a shallow concave trough separating the articular surface into medial and lateral ridges, and the proximal outline is indented in posterior view (Fig. 10F). Surprisingly, there is also a tongue-like extension of the medial articular surface of the distal end of the fourth metatarsal. Such a process is present but not as well developed in other troodontids, including *Troodon* (TMP 92.36.575) and *Saurornithoides* (Currie and Peng 1993). Its surface seems to be continuous with that of the tongue-like process of the distal articulation of the third metatarsal. It demonstrates that troodontids were able to flex their third and fourth pedal digits to a much

greater extent than all other theropods with the possible exception of dromaeosaurids.

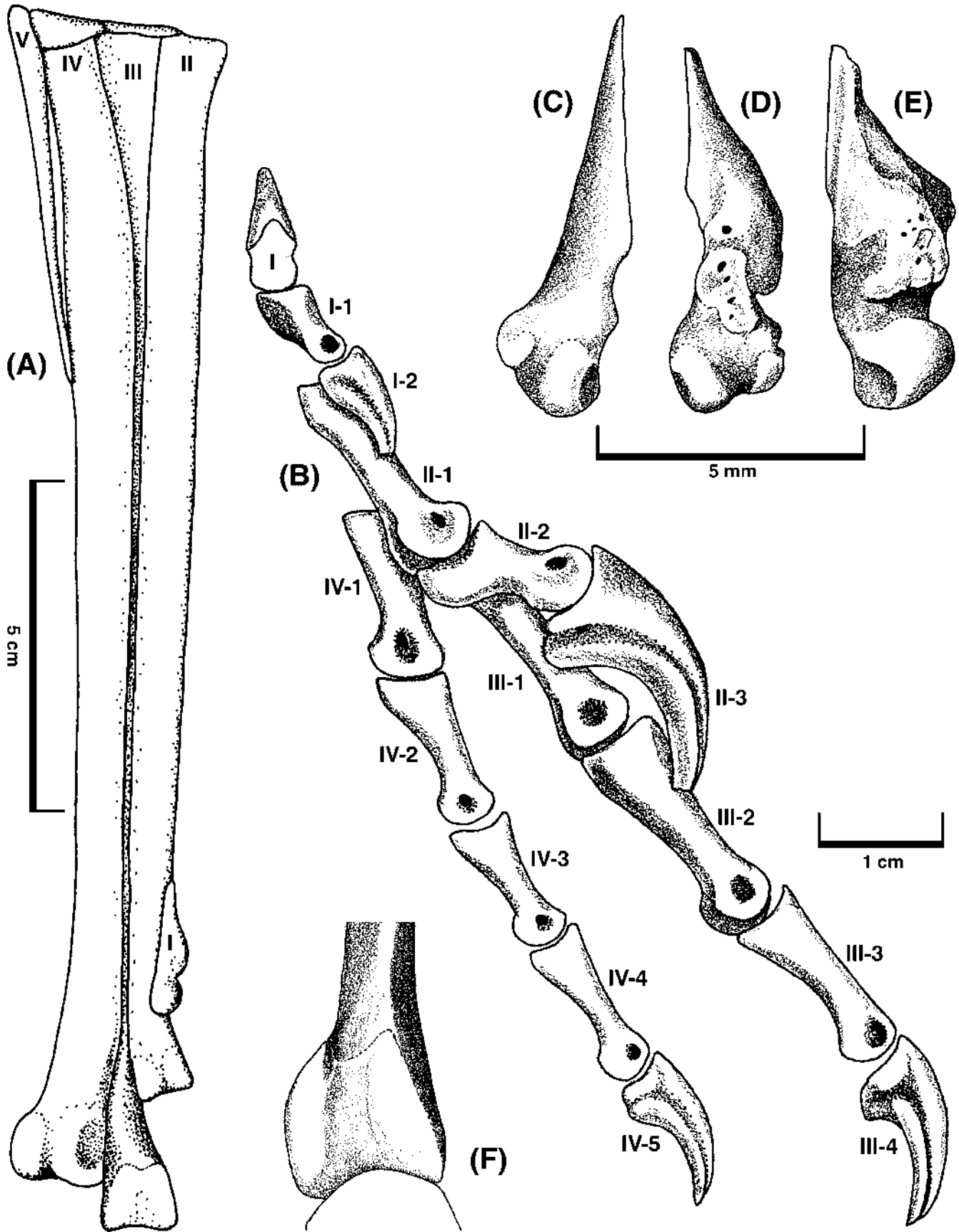
The proximal end of the splint-like fifth metatarsal protrudes above the other metatarsals and the distal tarsals, presumably to contact the astragalus and calcaneum. Compared with *Troodon* (TMP 92.36.575), where the ratio of the length of mtV:mtIII is 0.30, that of *Sinornithoides* is higher (0.38). This is apparently not a juvenile characteristic, because the ratio is only 0.20 in a juvenile specimen of *Saurornithoides* (Currie and Peng 1993). The fifth metatarsal is 3.2 mm wide at the proximal end, but rapidly tapers to only 1.3 mm at midshaft and to a point distally. As in other troodontids (Currie and Peng 1993), it is gently arched posteriorly and only contacts the fourth metatarsal with its proximal and distal ends.

As in other troodontids, the first digit is positioned equally on the medial and posterior surfaces close to the end of the second metatarsal. It is relatively short, only about a quarter of the length of the third digit. As in most coelurosaurs, other than dromaeosaurids and tyrannosaurids, it is even shorter than the first phalanx of the third digit. There is a typical troodontid raptorial second digit (Currie and Peng 1993), in which the first phalanx is longer than the second and is almost as long as the third. The second phalanx has a proximoventral extension (heel) that is characteristic of all troodontids. In both articulated feet, the second digit is raised so that it angles about 145 degrees from the longitudinal axis of the first phalanx (Fig. 10B). Although this suggests that the raptorial claw was normally raised off the ground, the angle is less than in other troodontids and dromaeosaurids, where it is often less than 90 degrees (Currie and Peng 1993). It is possible that the raptorial function of this claw had not evolved as far from the ancestral condition. The unguis is more strongly curved than the unguis of the other digits (Fig. 10B) and is similar in development to all other troodontids, except *Borogovia*. The fourth digit is almost 90% the length of the third, emphasizing the important role of the fourth digit in locomotion.

Troodontid material from Iren Dabasu

Isolated bones (AMNH 21751, AMNH 21772, IVPP 230790-16) from Iren Dabasu show that the fauna included a troodontid of about the same size as *Saurornithoides mongoliensis*. AMNH 21772 is the proximal end of a second metatarsal. It is identified as a troodontid on the basis of its contact surface for the fourth metatarsal, its size, and especially its lateromedial compression. The tongue-like posterior extension of the distal articular surface for phalanx III-1 is highly characteristic of advanced troodontids (Wilson and Currie 1985) and is clearly seen in both third metatarsal fragments numbered AMNH 21751. These two distal ends

Fig. 10. *Sinornithoides youngi*, IVPP V9612. Posterior view of left metatarsus (A), left pedal digits (B) in medial aspect, right metatarsal I in ventral view (C), left metatarsal I in ventral (D) and medial (E) aspects, and posterior view of the distal end of left metatarsal III (F).



of third metatarsals are about the same size and represent left and right elements. Although they may represent the same individual, the two fossils are different colours, which suggests they may not have been found together. As previously stated, *Sinornithoides* has the distinctive troodontid, tongue-like extension of the distal articulation of the third metatarsal. However, it retains a shallow longitudinal groove, which is presumably a remnant of the deep groove separating the two articulating ridges that extend from the distal articulation in non-troodontid theropods. In contrast, the tongue-like extensions of the third metatarsals from Iren Dabasu are flat like those of *Troodon* (Wilson and Currie 1985), *Borogovia* (Osmólska 1987; Osmólska and Barsbold 1990), and *Tochisaurus* (Kurzanov and Osmólska 1991). Curiously, the only described specimen of *Saurornithoides* with the distal end of the third metatarsal (Currie and Peng 1993) lacks the tongue-like articular surface, presumably because it is a juvenile. The Iren Dabasu troodontid, therefore, cannot be identified further without additional material, although it does seem to be an advanced representative of the family.

Discussion

Holtz et al. (2000) discuss the possibility that troodontids are herbivorous, because the size of their serrations scale with herbivorous dinosaurs rather than other carnivores. In spite of their arguments to the contrary, troodontids clearly have anatomy consistent with carnivorous, not herbivorous, habits. Furthermore, the structure of individual denticles (Currie 1987a; Currie et al. 1990) is not significantly different from that of other theropods. They are distally curved towards the tip of the tooth, sharply pointed, have razor-sharp enamel ridges between successive denticles, and have blood grooves at the base. These characters are not found in the herbivorous dinosaur serrations, which are overall simpler cones. Furthermore, the discovery of troodontid teeth with juvenile hadrosaurs (Ryan et al. 2000) is suggestive of a predator-prey association.

Norell et al. (2000) recently examined the interrelationships of troodontids and determined that the Late Cretaceous *Byronosaurus*, *Troodon*, and *Saurornithoides* form a clade, which has *Sinornithoides* as a sister taxon. An unnamed Early Cretaceous troodontid species (GIN 100/44, Barsbold et al. 1987) seems to be the sister taxon of all of these genera. *Borogovia* (Osmólska 1987), *Koparion* (Chure 1994), and *Tochisaurus* (Kurzanov and Osmólska 1991) were not included in their study because of problems associated with the incompleteness of the only known specimens. Their analysis was thorough, and the new information on *Sinornithoides* does not offer any substantial changes to our understanding of the interrelationships of the Troodontidae. However, there is sufficient confusion about the systematic relationships of troodontids to ornithomimids, dromaeosaurids, birds, and other theropods (Russell and Dong 1993; Sereno 1997) to merit further analysis. In recent years, troodontids have been allied most frequently with either ornithomimids (Thulborn 1984; Currie 1985; Pérez-Moreno et al. 1994; Holtz 1994, 1996) or dromaeosaurids (Russell 1969; Ostrom 1969; Gauthier 1986; Osmólska and Barsbold 1990; Makovicky and Sues 1998). Holtz (2000) found it equally parsimonious

to include troodontids as either a paravian maniraptoran (related to dromaeosaurids and birds) or a bullatosaurian arctometatarsalian (related to ornithomimosaurs). Troodontids have also been considered by some (Currie 1985, 1987a; Forster et al. 1998) as the closest sister group to birds, although most workers (including Holtz 2000) feel that dromaeosaurids are closer to birds than troodontids.

The holotype of *Sinornithoides youngi* is the single best troodontid specimen known. This Lower Cretaceous form has all of the autapomorphies expected of the family Troodontidae, although some of these features are not as fully developed as in Late Cretaceous troodontids. For example, the serrations on teeth are enlarged in comparison with those of most other theropods, but not to the degree that they are in *Troodon* or *Saurornithoides*. Troodontidae can be defined by many autapomorphic characters that suggest they had a long independent history that preceded the Early Cretaceous. These include the distinctive teeth with their large serrations and constrictions between crown and root, the loss of interdental plates in the dentary, the implantation of the posterior dentary teeth in a paradental groove rather than sockets, the trochanteric crest of the femur, fusion of the astragalus and calcaneum, the relatively short and mediolaterally compressed shaft of Metatarsal II, and the tongue-like extension of the distal articular surface of the third metatarsal.

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