A juvenile specimen of *Saurornithoides mongoliensis* from the Upper Cretaceous of northern China

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A hind limb of *Saurornithoides mongoliensis* from the Djadokhta Formation equivalent beds (Upper Cretaceous) of Bayan Mandahu (People's Republic of China) provides more information on the anatomy of the leg of this species than any other known specimen. Although it shares apomorphies of all troodontid theropods, the metatarsus is relatively longer and more derived than that of *Troodon* itself. The specimen is of an immature individual, less than half the size of the holotype. The degree of ossification suggests that troodontids were well developed at birth and that parental care was probably unnecessary.

Un membre postérieur de *Saurornithoides mongoliensis*, trouvé dans les strates équivalentes à la Formation de Djadokhta (Crétacé supérieur) de Bayan Mandahu (République populaire de Chine), fournit des enseignements nouveaux sur l'anatomie du membre postérieur de cette espèce qui ne sont pas révélés par aucun autre spécimen connu. Bien qu'il présente en commun les apomorphies de tous les théropodes troodontidés, cependant le métatarse est relativement plus long et plus évolué que celui du *Troodon* lui-même. Le spécimen représente un individu immature, de taille inférieure à la moité de celle de l'holotype. Le degré d'ossification suggère que les troodontidés étaient bien développés dès leur naissance, et que, probablement, ils n'avaient pas besoin de recevoir des soins de leurs parents.

[Traduit par la rédaction]

在中国内蒙古巴彦满达呼与 Djadokhta 组同时代的晚白垩世地层中所发现的 Saurornithoides mongoliensis 一后肢比目前所知的任何其他标本都提供了更多有关该种腿部解剖的信息。尽管这枚标本具有兽脚类中所有似鸟龙类的近裔性状，它的跖骨比似鸟龙（Troodon）的更长更进步。这具标本属于未成年个体，只有正型标本的一半大小。它的骨化程度说明似鸟龙类在出生时就已经发育完全，不需要父母的照管。

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Задняя конечность Saurornithoides mongoliensis из подобных пластов верхнемеловой формации Джадокта, Баян Мандаху (Китай) дает большую информацию об анатомии задней конечности представителей этого вида, чем имеющаяся для других известных экземпляров. Хотя у него такие же апоморфии как у всех терапод - троодонтид, его плюсна сравнительно длиннее и более выражена чем у Troodon. Данный экземпляр принадлежал неполовозрелой особи, по размерам более чем в два раза меньшей, чем голотип. Степень окостенения показывает, что троодонтиды при рождении были хорошо развиты и, вероятно, не нуждались в родительском уходе.

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Introduction

In 1924, Osborn described the first specimen of *Saurornithoides mongoliensis* (AMNH 6516), which was a poorly preserved but relatively complete skull collected from the Djadokhta Formation of Mongolia. Although postcranial material was found with this specimen (Osborn 1924; Russell 1969), it has never been properly described.

Barsbold (1974) established a second species of *Saurornithoides*, *Saurornithoides junior*, from the Nemegt Formation of Mongolia. The specimen includes a nearly complete skull and some postcranial elements, including the proximal end of a metatarsus. The metatarsus of *Saurornithoides* shares with *Troodon* a number of specializations (Russell 1969; Barsbold

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1974; Wilson and Currie 1985; Currie 1987) that are only found in troodontids. Three additional species of troodontids have been discovered in Mongolia, but are known from partial skeletons only (Osmólska 1987; Barsbold et al. 1987; Kurzanov and Osmólska 1991). The most complete troodontid discovered and described to date is from the Lower Cretaceous of China (Russell and Dong 1993).

Troodontids are unusual theropods that in some features are more like birds than dinosaurs, and study of these animals may provide indirect evidence of the ancestry of birds (Currie 1985, 1987).

In 1988, the Dinosaur Project (China – Canada – Alberta – Ex Terra) sent an expedition to the vicinity of Bayan Mandahu (Inner Mongolia, People's Republic of China, 41°45′N, 106°45′E). The extensive exposures in this region are correlative with the Djadokhta Formation of Mongolia (Jerzykiewicz et al. 1989), the type section of which is located at Bayn Dzak (Shabarakh Usu), approximately 300 km to the northwest. During the course of the expedition, the articulated remains of an incomplete hind limb of *Saurornithoides* were collected from the Nigerndeg bone bed (site 36). The left leg represents a small individual, considerably less than half the mature size of *Saurornithoides mongoliensis*, and includes elements that have not previously been described for *Saurornithoides*. In spite of the size difference and incomplete nature of troodontid specimens, it is most reasonable to refer IVPP V10597 to *Saurornithoides mongoliensis*.

Systematic palaeontology

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

Abbreviations

AMNH, American Museum of Natural History, New York; CMN, Canadian Museum of Nature, Ottawa; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MOR, Museum of the Rockies, Bozeman; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow; SPS, Stratigraphy and Paleontology Section of the Geological Institute, Mongolian Academy of Sciences, Ulan Bator; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Material

IVPP V10597, left hind limb (Fig. 1) including femur, partial tibia, partial fibula, astragalus, distal tarsals III and IV, metatarsals I, II, III, IV, and V, phalanges I-1, II-1, II-2, II-3, III-1, III-2, III-3, IV-1, IV-2, IV-3, IV-4, and IV-5.

Description

The width of the metatarsus of IVPP V10597 is 11.1 mm proximally, about 20% that of *Saurornithoides junior* (Barsbold 1974), and the astragalus is 10.6 mm wide, about 18% of the same dimension in *Troodon formosus* (Russell 1969). IVPP V9612 (Russell and Dong 1993) represents a new taxon with an astragalus that is almost double the width of IVPP V10597, although the length of metatarsal III is only about 4% greater. *Troodon formosus* was about 2.8 m long (Russell and Sequin 1982), whereas the length of IVPP V9612 is 1.1 m (Russell and Dong 1993). Comparison with these specimens suggests that IVPP V10597 would have been between 0.5 and 0.7 m long when it was alive.

The femur of IVPP V10597 (Figs. 1*a*, 1*b*, 1*c*, 1*d*, 1*n*) is 86.5 mm long, and the shaft diameter is 7.0 mm, compared with a shaft diameter of 20.5 mm in the type of *Saurornithoides mongoliensis*. The femur of IVPP V9612 is estimated to have been 140 mm long (Russell and Dong 1993), 62% larger than the specimen from Bayan Mandahu. The femur of IVPP V10597 is hollow, the intervening space having been infilled with silica. At midshaft, the hollow has a cross-sectional diameter of 5.0 mm. The head of the femur is well set off from the shaft of the bone. Troodontid femora are easily distinguished from other theropods. Although the lesser trochanter has been damaged in IVPP V10597, it is still evident that the base of this process was close to the proximal end of the bone as in dromaeosaurids (Currie and Russell 1988). The degree of separation cannot be determined in this specimen, but in other troodontids (MOR 430, PIN 2549-100) there is no notch between the lesser and greater trochanters. Unlike dromaeosaurids, the continuous plate of bone formed by these trochanters is almost perpendicular (Fig. 1*n*) to the axis of the head. The distinct, saddle-shaped articular surface is outlined laterally by a raised rim (similar to the crista trochanteris of birds) formed by the greater trochanter, and probably the lesser trochanter as well. There is a distinct but low posterior trochanter (Figs. 1*b*, 1*d*) for insertion of the ischiofemoralis muscle. Analysis of limb movement suggests the leg was held directly beneath the body, but swung outward to clear the belly as it moved forward and to compensate for any rotation of the hips. The curvature of the shaft is quite strong in comparison with velociraptorines (Ostrom 1976) and *Chirostenotes* (Currie and Russell 1988). The distal condyles have been damaged and little can be said about them. A strong process on the anteromedial surface of the distal end of the femur (Figs. 1*a*, 1*c*) has no equivalent in other theropods and may have marked the insertion of one of the joint ligaments or may simply be pathologic.

A section of the shaft of the tibia was not recovered from the excavation in spite of repeated screening of the surrounding matrix. Even so, the preserved length of the tibia (90 mm) exceeds the length of the femur by 4%. Russell (1969) estimated the lengths of the femur and tibia (198 mm and 243 mm, respectively) of AMNH 6516 and concluded that the tibia should be 20–25% longer than the femur in *Saurornithoides*. The ratio of femur to tibia is about 1.4 in IVPP V9612 (Russell and Dong 1993). Based on this, the missing section of shaft of IVPP V10597 would have been at least 15 mm long, making the tibia at least 105 mm long. Much of the surface of the proximal end of the tibia has flaked off, so it is difficult to see any significant features other than the cnemial crest, the articulation for the proximal head of the fibula, and part of the crista fibularis. The preserved width of the proximal end is 15 mm, three times the minimum diameter of the shaft. The distal end is better preserved (Figs. 1*e*, 1*f*, 1*g*, 1*h*) and has a maximum transverse width of 10.2 mm.

The proximal and distal ends of the fibula were recovered, and a quartz endocast of a short section of the shaft, but none of these pieces show any distinctive characteristics.

The astragalus of IVPP V10597 represents the first specimen of *Saurornithoides* discovered with a complete, well-preserved ascending process (Figs. 1*e*, 1*g*, 1*h*, 1*m*, 1*o*). This

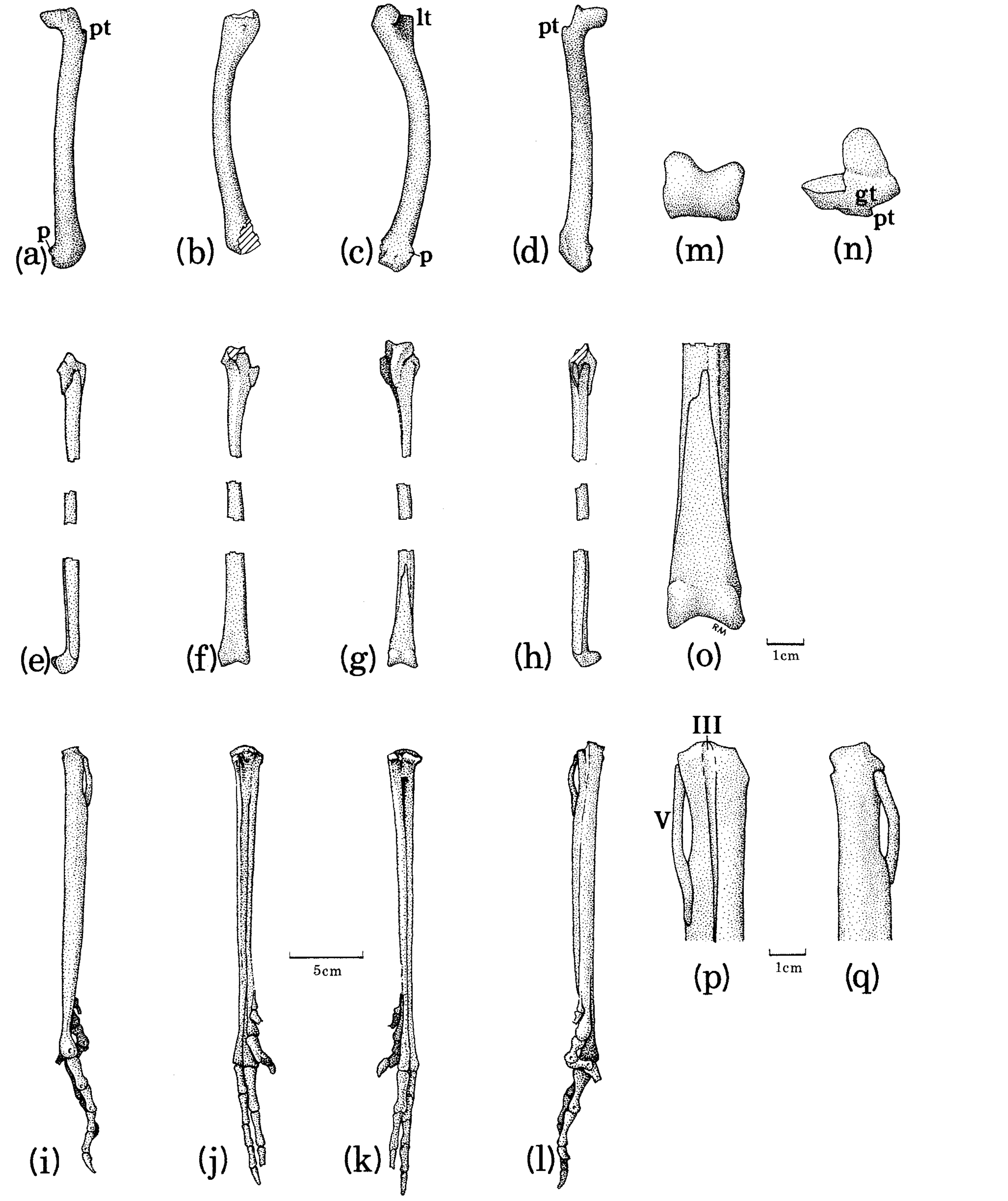

FIG. 1. *Saurornithoides mongoliensis*, IVPP V10597, left hind limb. Femur in (*a*) anterior, (*b*) lateral, (*c*) medial, (*d*) posterior, and (*n*) proximal views. Tibia and astragalus in (*e*) lateral, (*f*) posterior, (*g*, *o*) anterior, (*h*) medial, and (*m*) distal aspects. Tarsometatarsus and phalanges in (*i*, *q*) lateral, (*j*, *p*) posterior, (*k*) anterior, and (*l*) medial views. gt, greater trochanter; lt, lesser trochanter; *p*, unknown process; pt, posterior trochanter; III, V, third and fifth metatarsals.

process is very high and makes up most of the 36.2 mm proximodistal length of the astragalus, covering more than 30% of the estimated length of the tibia. The condylar portion of the astragalus covers the entire distal end of the tibia, but does not extend onto the posterior surface. In this and other respects, it is identical to described specimens of *Saurornithoides junior* (Barsbold 1974) and *Troodon formosus* (Russell 1969). There would have been only limited contact with the fibula. The lateral condyle of the astragalus is higher (7.5 mm) proximodistally than the medial condyle (5.9 mm), but is transversely narrower. There is no deep emargination or pit between the ascending process and the articular condyles (Fig. 1*o*) as there is in some theropods (Welles and Long 1974).

There is no sign of a separate calcaneum, and the shape of the astragalus (Fig. 1*o*) suggests that there was none. It has been suggested (Russell 1969; Barsbold 1974) that these elements are coossified in troodontids, but if this is the case, then it must have happened very early in ontogeny. It is more likely, especially considering the slender nature of the distal end of the fibula (Russell and Dong 1993), that the calcaneum was lost.

The third and fourth distal tarsals are still attached to the proximal end of the metatarsus but details are difficult to make out. However, in position and size they appear to be indistinguishable from the distal tarsals of dromaeosaurids (Ostrom 1969) and elmisaurids (Currie 1990). The fourth distal tarsal sits over the fourth metatarsal, and the third contacts both the second and third metatarsals. Their proximal surfaces articulate perfectly with the distal condyles of the astragalus.

The first metatarsal consists of only a distal segment 4 mm long, most of which is a ball-like condyle (Figs. 1*j*, 1*l*). The distal end of the first metatarsal is located 18 mm from the distal end of metatarsal III and is positioned on the posteromedial edge of metatarsal II.

The second metatarsal, like those of *Troodon* (Wilson and Currie 1985) and *Tochisaurus* (Kurzanov and Osmólska 1991), is reduced from the condition seen in other theropods and is compressed mediolaterally into a plate of bone that is only 1 mm thick for most of its 94 mm length. Proximally, the second metatarsal is 6.0 mm anteroposteriorly, thins to 4.0 mm, expands to 5.0 mm at a third of the length from the proximal end, and then thins progressively again until the shaft is only 2.5 mm near the distal head. The distal articular surface of metatarsal II is much smaller than it is in either the third or fourth metatarsals. This compares well with *Troodon* (Russell 1969; Wilson and Currie 1985), but is quite different from *Borogovia* from the Nemegt Formation of Mongolia (Osmólska 1987).

The third metatarsal is the longest element (107 mm) in the metatarsus, which is about 24% longer than the femur and about the same length as that estimated for the tibia. It is squeezed out by the second and fourth metatarsals throughout most of the midshaft region. This same phenomena was noted in *Troodon* (Wilson and Currie 1985) and *Tochisaurus* (Kurzanov and Osmólska 1991). Only the proximal 22 mm of the midshaft region of metatarsal III can be seen (Fig. 1*p*) and 25 mm of the distal end (Fig. 1*k*), and the diameter of the shaft must be very small to be so thoroughly obscured. The distal end of the third metatarsal expands to a maximum mediolateral width of 4.0 mm to support the largest phalanx of the foot. The posterior tongue-like extension of the articular surface that is characteristic of the posterior surface in *Troodon* (Russell 1969), *Borogovia* (Osmólska 1987), and IVPP V9612 (Russell and Dong 1993) is not present in this specimen, probably because of its immaturity. However, this tongue-like extension is present in MOR 430, a specimen that is only 25% larger than IVPP V10597.

The fourth metatarsal is the strongest element in the metatarsus, which is a synapomorphy of troodontids. The distal head of the fourth is almost at the same level as the third (Fig. 1*k*). At 105 mm, it is longer than the second metatarsal. The medial surface is slightly convex where it contacts the third metatarsal. The shaft is mediolaterally compressed in this specimen. In contrast, the fourth metatarsal of *Troodon formosus* is almost as long anteroposteriorly in section as it is wide (Wilson and Currie 1985). The anteroposterior length of the fourth in IVPP V10597 is greatest just distal to the end of the fifth metatarsal (Figs. 1*i*, 1*l*) where it is 8.0 mm long, after which it tapers to 3.5 mm just proximal to the distal head.

The fifth metatarsal is a short (21.5 mm), thin, slightly curved slip of bone that has remained in its proper position in the metatarsus. This is the one of the few theropods known that shows how the fifth articulates with the fourth. This bone is positioned posterolateral to the fourth and curves away from the shaft of the larger bone. Distally it overlaps the medial surface of the posterolateral longitudinal ridge of the fourth (Figs. 1*p*, 1*q*).

Only the proximal head of the first phalanx of the first digit is preserved, but it shows that this toe was oriented anteromedially, as suggested by Russell and Sequin (1982), rather than facing posteriorly as it does in birds. I-1 is a small, slender phalanx.

The first phalanx of the second digit is long (10.5 mm) and relatively slender. It is followed by the distinctive but shorter (8.4 mm, maximum length) II-2, which in medial view is held at nearly right angles to the first phalanx (Fig. 1*l*). The proximal articular surface is oriented posterodorsally rather than proximally. It was this joint between II-1 and II-2 that allowed the maximum rotation of the ungual. The distal articular surface is lateromedially compressed and would allow only minimal rotation of the ungual. The tip of the ungual for digit II was not found, but the base is quite deep, indicating a strong element. The ungual was strongly curved, in contrast with that of *Borogovia* (Osmólska 1987).

Phalanx III-1 is 14.5 mm in length. The next phalanx, III-2, is also a large element (length = 12.0 mm). The third phalanx is incomplete and the fourth unknown. A conservative estimate of the total length of the third digit would be 44 mm.

All of the fourth digit is preserved, giving a total length of 47.5 mm (IV-1 = 11.0 mm, IV-2 = 10.5 , IV-3 = 9.0, IV-4 = 9.0, IV-5 = 8.0). As in CMN 8539 (Sternberg 1932), the fourth digit was probably almost as long as the third. The phalanges of this digit have typical ginglymoid articular surfaces, as in *Troodon* but in contrast with *Borogovia* (Osmólska 1987). The ungual is sharply pointed but relatively short and was better adapted for running rather than use as a weapon.

Discussion

The metatarsus of IVPP V10597 (Fig. 2*a*) differs from that of the type specimen of *Saurornithoides mongoliensis* in overall size and length relative to femur (Russell 1969). However Russell (1969) assumed that the metatarsus of *Saurornithoides* had the same proportions as that of *Troodon*, and the lengths of the femur and tibia were estimates. As in the tyrannosaurids (Russell 1970), the metatarsus probably grew with negative allometry when compared to femoral or tibial length, which suggests that the great length of the metatarsus of IVPP V10597 may be accounted for in part by its immaturity.

Although IVPP V10597 is small, the proximal articular surface on the femur is well defined and all bones are well formed. The bones have remained in articulation, and there are no significant gaps for cartilage between the bones. These features are often interpreted as indicators of maturity, which

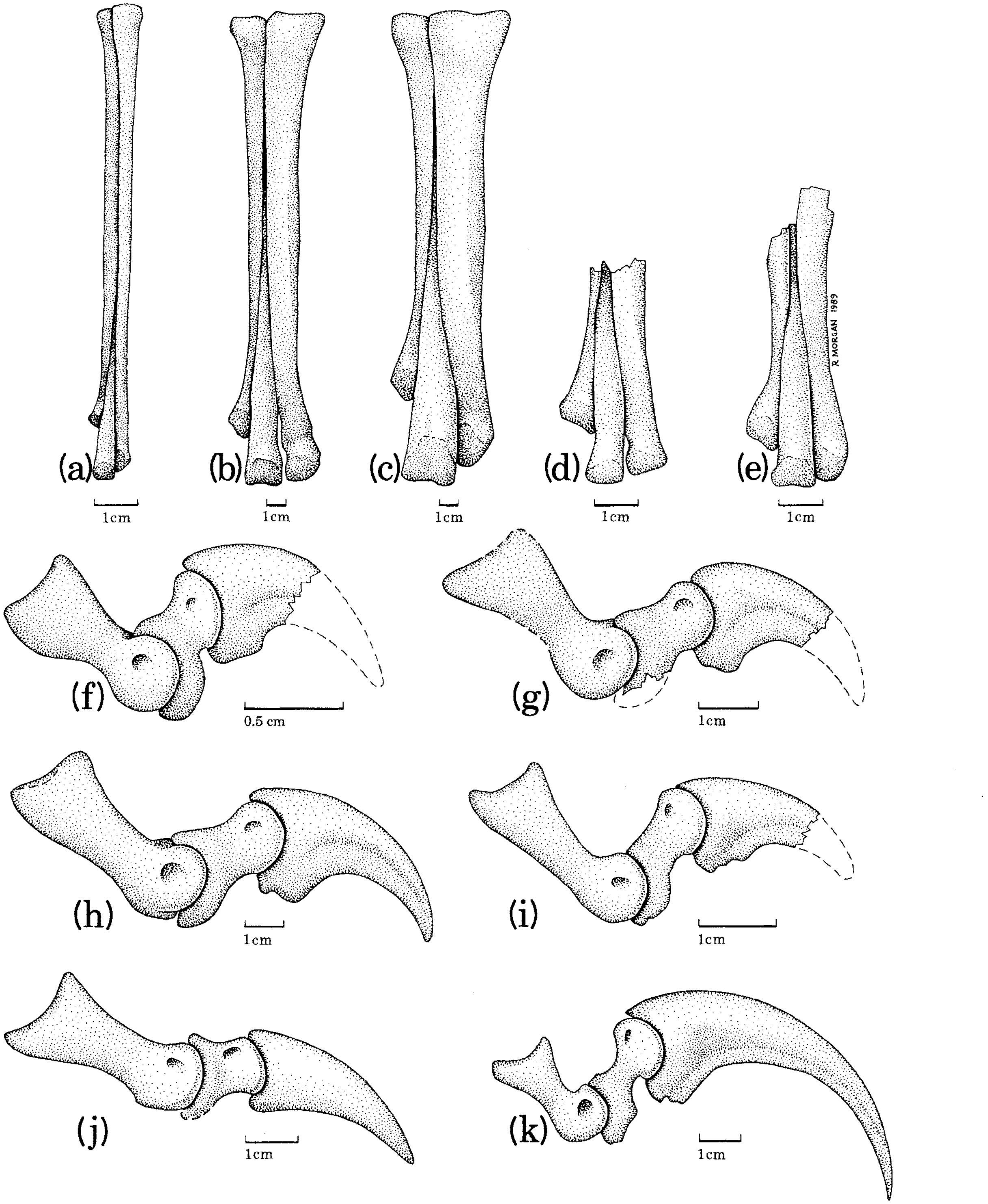

FIG. 2. (*a–e*) Anterior views of the left metatarsals II, III and IV of troodontids; and medial views (*f–j*) of the second digit of troodontids and a (*k*) dromaeosaurid. (*a*) *Saurornithoides mongoliensis*, IVPP V10597; (*b*) *Tochisaurus nemegtensis* (after Kurzanov 1987); (*c*) *Troodon formosus* (after Wilson and Currie 1985); (*d*) Troodontidae indet. (after Barsbold et al. 1987); (*e*) *Borogovia gracilicrus* (after Osmólska 1987); (*f*) *Saurornithoides mongoliensis*, IVPP V10597; (*g*) *Saurornithoides mongoliensis*, AMNH 6516; (*h*) *Troodon formosus*, NMC 1650 (right side, image reversed); (*i*) Troodontidae indet., SPS 100/44 (III-3 from right side, image reversed); (*j*) *Borogovia gracilicrus* (after Osmólska 1987); (*k*) *Saurornitholestes langstoni*, RTMP 88.121.39 (II-1, II-3) and RTMP 80.16.1318 (II-2, right side, image reversed).

would suggest that the specimen might represent a new, small species of Troodontidae. However, precocious development of the skeleton has been noted in embryonic hypsilophodonts (Horner and Weishampel 1988), where the controlling factor was speculated to be the requirement for juveniles to perform similar activities as their adult counterparts. A juvenile specimen of *Troodon formosus* (MOR 430) clearly demonstrates that the articular surfaces were well-formed in very young individuals of that species. Therefore, degree of ossification cannot be used in these theropods as a means of showing degree of maturity, and size or proportional differences alone cannot be used to diagnose troodontid species.

Wilson and Currie (1985) emphasized the unusual, derived characteristics of the metatarsus of *Troodon formosus* and speculated on the functional morphology of the foot. It can be shown now that the metatarsus of *Saurornithoides mongoliensis* is almost identical to that of the North American species.

Barsbold et al. (1987) have described a new troodontid from the Lower Cretaceous Dzunbainskaya Suite of Mongolia, the metatarsus (Fig. 2*d*) of which is not significantly different from those of Late Cretaceous troodontids. *Borogovia* (Osmólska 1987) from the Upper Cretaceous Nemegt Formation is based on a gracile, highly derived foot with a reduced third digit that sets it apart from all other troodontids.

As in *Troodon* (Fig. 2*c*) and *Tochisaurus* (Fig. 2*b*), the foot of *Saurornithoides* is clearly didactylous, the inner two toes being held off the ground, and incapable of assisting in the support of the animals weight. However, *Saurornithoides* differs from *Troodon* in that the third metatarsal seems to be even more reduced and derived. In contrast, the skull appears to be less derived (Currie 1985).

The raptorial second digit is often used as evidence of the close relationship between troodontids and dromaeosaurids. However, there are fundamental differences in the relative proportions of the phalanges in the second digits of troodontids (Figs. 2*f*–2*j*) and dromaeosaurids (Fig. 2*k*). Phalanx II-1 is always longer than II-2 and is close to the length of II-3 (the ungual). In contrast, the third (ungual) phalanx is the longest one in a dromaeosaurid second pedal digit, whereas II-1 and II-2 are almost the same length. This suggests, but does not prove, that the raptorial second digit may have arisen independently in the two families. Other differences in the hind limb are more striking. In the hind limb, troodontids differ from dromaeosaurids in many significant ways: the greater trochanter (and possibly the lesser) extend dorsally beyond the upper margin of the femoral head to form a bird-like crista trochanteris; in proximal aspect, the femoral head is almost perpendicular to the lateral surface of the femur; there is a tall ascending process of the astragalus; the calcaneum has been lost as a distinct element; a troodontid metatarsus is at least three quarters the length of the femur, whereas that of a dromaeosaurid is about half; the second metatarsal is laterally compressed and is significantly smaller in all dimensions from the fourth; the proximal end of the third metatarsal is compressed and the flexor surface of the proximal end was covered by the second and fourth metatarsals, which contact each other; the distal articulation of the third metatarsal extends posteroproximally into a distinctive "tongue"; and the fourth metatarsal is almost as long as the third, and is the most robust bone in the metatarsus. In the elongation of the metatarsus and the reduction of the proximal end of the third metatarsal, troodontids are closer to ornithomimids and tyrannosaurids than they are to dromaeosaurids.

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