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PHILIP J. CURRIE

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The first records of *Elmisaurus* (Saurischia, Theropoda) from North America

PHILIP J. CURRIE

Tyrrell Museum of Palaeontology, Drumheller, Alta., Canada T0J 0Y0

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The discovery of a fused tarsometatarsus in the Upper Cretaceous (Campanian) strata of Dinosaur Provincial Park shows that *Elmisaurus*, previously known only from Mongolia, also lived in North America. Reexamination of the type specimen of "*Ornithomimus*" *elegans* (Parks 1933) confirms the identification and provides a species name. *Elmisaurus elegans* is more gracile than *Elmisaurus rarus*, has a weaker longitudinal ridge on the fourth metatarsal, and has a pair of distal processes on metatarsals II and IV. Although six theropod families had representatives in both North America and Asia during Cretaceous times, the degree of genetic similarity is poorly understood. Analysis of the *Elmisaurus* material suggests that faunal interchange was still underway during the Late Cretaceous.

La découverte d'un tarsométatarsaire fusionné dans les strates du Crétacé supérieur (Campanien) du Parc provincial des Dinosauriens, montre que *Elmisaurus*, connu antérieurement uniquement en Mongolie, vivait également en Amérique du Nord. Le réexamen de ce spécimen-type de « *Ornithomimus* » *elegans* (Parks 1933) confirme l'identification et fournit un nom d'espèce. *Elmisaurus elegans* est plus gracile que *Elmisaurus rarus*, il possède une crête longitudinale moins saillante sur le quatrième métatarsien et il a une paire d'apophyses distales sur les métatarses II et IV. En dépit de six familles de théropodes représentées en Amérique du Nord et en Asie durant la période du Crétacé, le degré de similitude génétique reste mal compris. L'étude du matériel de *Elmisaurus* suggère un interchange faunique toujours actif durant le Crétacé tardif.

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Introduction

Chirostenotes pergracilis was described on the basis of a pair of articulated hands collected from the Judith River Formation of Alberta (Gilmore 1924). An articulated foot from the same region and formation was given the name *Macrophalangia canadensis* (Sternberg 1932), but from time to time people have wondered if *Chirostenotes* and *Macrophalangia* were the same species of animal (Colbert and Russell 1969; Osmolska 1981). Parks (1933) put another metatarsus from the Judith River Formation on record as *Ornithomimus elegans*, but this was subsequently synonymized with *Macrophalangia canadensis* (Russell 1972).

In 1979, a partial skeleton of a theropod was collected in Dinosaur Provincial Park (Currie and Russell 1988). The associated remains demonstrated conclusively that *Chirostenotes* and *Macrophalangia* are synonymous and that the former name has priority. Currie and Russell (1988) also suggested that *Chirostenotes* may be the senior synonym of *Caenagnathus*.

A new genus and species of Asian theropod—*Elmisaurus rarus*—was described by Osmolska (1981). Although the hand is very similar to that of *Chirostenotes*, the foot is distinctive in having a fused tarsometatarsus. The suture between the proximal ends of the second and fourth metatarsals is identifiable, but specimens of *Elmisaurus* are in a more advanced state of fusion than any *Chirostenotes* specimen. The size and degree of fusion indicate that *Elmisaurus* was a smaller animal than *Chirostenotes* at maturity. Osmolska (1981) defined a new family—the Elmisauridae—to include *Elmisaurus* and *Chirostenotes*.

Although it is tempting to refer *Elmisaurus* to the genus

Chirostenotes, the discovery of a new specimen in Dinosaur Provincial Park indicates that they are distinct genera. Re-examination of the type specimen of *Ornithomimus elegans* and an undescribed specimen in the collections of the Royal Ontario Museum confirms the presence of *Elmisaurus* in the Campanian of Alberta.

Systematic palaeontology

CLASS Reptilia Linnaeus 1758

DIVISION Archosauromorpha Huene 1946

ORDER Saurischia Seeley 1888

SUBORDER Theropoda Marsh 1881

FAMILY Elmisauridae Osmolska 1981

Elmisaurus elegans (Parks 1933) new comb.

Holotype

ROM 781, collected along Little Sandhill Creek (Dinosaur Provincial Park, Alberta) in 1926. Complete left metatarsals II and IV and the incomplete remains of distal tarsal III, distal tarsal IV, and metatarsal III. Originally described as *Ornithomimus elegans*.

Referred specimens

TMP 82.39.4, collected in Dinosaur Provincial Park (lsd. 2, sec. 4, tp. 21, rge. 11, W 4th mer.) by Linda Strong-Watson in 1982. Proximal end of right tarsometatarsus.

ROM 37163, collected sometime between 1920 and 1954 by a University of Toronto – Royal Ontario Museum expedition to the badlands (now in Dinosaur Provincial Park).

Abbreviations

NMC, National Museum of Natural Sciences, National

Museums of Canada, Ottawa; ROM, Royal Ontario Museum, Toronto; TMP, Tyrrell Museum of Palaeontology, Drumheller; ZPAL, Zakład Paleobiologii, Polska Akademia Nauk, Warszawa, Poland.

Stratigraphy

Judith River Formation (Campanian, Upper Cretaceous).

Diagnosis

More gracile than either *Elmisaurus rarus* or *Chirostenotes pergracilis*. In dorsal view, the posteromedial corner of the tarsometatarsus is more deeply emarginated than that of *Elmisaurus rarus*. The longitudinal, ridge-like posterolateral margin of metatarsal IV is not as powerfully developed proximally as that of *Elmisaurus rarus*. Close to the distal articular surfaces, small processes of metatarsals II and IV overlap metatarsal III.

Description

TMP 82.39.4 (Figs. 1a–1e) is the proximal end of a fused right tarsometatarsus that was collected from bonebed 87 in Dinosaur Provincial Park. Fusion is virtually complete, and with the exception of a faint line that may indicate the point of anteroproximal contact between metatarsals II and IV (Fig. 1c), all sutural surfaces have been resorbed. This is not the case with *Chirostenotes* (Currie and Russell 1988), where tarsals and metatarsals have remained distinct elements. Specimens identified as *Chirostenotes* are larger than TMP 82.39.4 (Table 1), so it is highly unlikely that the latter is a juvenile of *Chirostenotes*. *Elmisaurus rarus* from Mongolia (Osmolska 1981) is marginally bigger than TMP 82.39.4 and is also characterized by fusion of the tarsometatarsus. However, there is still a distinct line of fusion between the second and fourth metatarsals in the two described specimens of tarsometatarsi from Mongolia (ZPAL MgD-I/172, MgD-I/20).

Although individual bones cannot be distinguished, evidence from other theropod genera (especially undescribed specimens of dromaeosaurids in the collections of the Tyrrell Museum of Palaeontology) and the surface contours of this specimen show that the fused tarsometatarsus is composed of distal tarsals III and IV and metatarsals II–IV. In overall shape and morphology, TMP 82.39.4 is almost identical to *Elmisaurus rarus* (Fig. 1). The only other animals that could be confused with the Alberta specimen on the basis of the fused tarsometatarsus are *Avimimus* (Kurzanov 1981, 1983, 1987) and *Avisaurus* (Brett-Surman and Paul 1985). However, these are smaller animals than *Elmisaurus*, the ratio of the proximal width of the tarsometatarsus to its anteroposterior proximal length (Osmolska 1981, Zpal MgD-I/85; Kurzanov 1981) is higher than what is found in either *Elmisaurus rarus* (Osmolska 1981) or the new specimen, and there are fundamental anatomical differences. *Avisaurus*, like enantiornithine birds and many theropods, is less derived than *Elmisaurus* in that the third metatarsal is not pinched proximally. The tarsometatarsus of *Avimimus*, like that of *Elmisaurus*, has a prominent proximolateral projection. It is more derived, however, in that fusion also incorporates the fifth metatarsal, while the shaft of metatarsal III is more reduced.

The proximal end of TMP 82.39.4 is roughly rectangular in outline (Figs. 1b, 1h). In dorsal view, a notch on the anterior margin marks the ontogenetic division between metatarsals II and IV. The posteromedial corner of the proximal surface is deeply emarginated in a manner that is distinct from that of *Elmisaurus rarus* (Fig. 1i). The posterolateral edge was

damaged but formed the base of a distinctive posterodorsal process such as is found in *Elmisaurus rarus* (Fig. 1). The broken surfaces reveal that the tarsals are composed mostly of spongy bone (Fig. 1d). The intertarsal joint was inclined laterally at an angle about 85° from the longitudinal axis of the metatarsus.

Metatarsals II, III, and IV are hollow bones (Fig. 1a). The second metatarsal is almost round in section, but it is flattened medially as in *Elmisaurus rarus*. The second metatarsal is smaller in diameter proximally than the fourth. As in *Chirostenotes pergracilis* and *Elmisaurus rarus*, the proximal ends of the second and fourth metatarsals meet anteriorly for 15.5 mm, thereby excluding the third from the anterior surface of the metatarsus.

The preserved portion of metatarsal III is triangular in section, in contrast with *Chirostenotes pergracilis*, where it is diamond shaped (Currie and Russell 1988). Like *Elmisaurus rarus*, the proximal end of the third metatarsal is considerably smaller in diameter than its neighbours and is inset from the anterior and posterior surfaces of the metatarsus. A blood vessel passed between the third and fourth metatarsals distal to the fused area, as in *Elmisaurus rarus* (Osmolska 1981). This blood vessel was almost certainly present in all theropods, but its position is emphasized in *Elmisaurus* by the fusion of the tarsometatarsus.

Discovery of the specimen TMP 82.39.4 prompted a reexamination of ROM 781 (Fig. 2), the holotype of *Ornithomimus elegans* (Parks 1933). Although this specimen does not initially appear to have a fused tarsometatarsus, fusion was well underway when the animal died. Distal tarsals III and IV had coossified and fused to metatarsals II, III, and IV (Figs. 2k–2m). Although metatarsals II and IV had separated in the specimen, as had the distal end of metatarsal III, this separation was caused by breakage. Part of distal tarsal III is fused to the head of metatarsal IV (Fig. 2l), but fragments of distal tarsal III have remained attached to the heads of metatarsals II and III. The broken surfaces show that the sutural surfaces between distal tarsal III and metatarsal III had been resorbed and that the cancellous tissue in these bones is continuous. The proximal end of metatarsal III has remained in close contact with metatarsal II and was in the process of being fused to it when the animal died.

It can be concluded then that ROM 781 is a coossified tarsometatarsus. It is slightly larger than TMP 82.39.4 (Table 1) but is not as well fused, showing that degree and ontogenetic timing of fusion may have been somewhat variable. H. Osmolska (oral communication, 1987) indicated that degree of fusion is also variable in *Elmisaurus rarus*.

The type specimen of "*Ornithomimus*" *elegans* compares very closely with *Elmisaurus rarus* in a number of diagnostic features in addition to coossification. Distal tarsal IV (Figs. 2f, 2l, 2m) is a small bone with a prominent posterodorsal process. Metatarsals II and III are more intimately associated than III is with IV. In contrast with *Chirostenotes pergracilis*, the proximal end of metatarsal III is triangular in section, with the acute angle facing forward. The proximal end of metatarsal III is excluded from the anterior margin of the tarsometatarsus by a flat, triangular contact between metatarsals II and IV (Figs. 2c, 2g). A blood vessel passed between metatarsals III and IV, and the ventral boundary of the opening is defined by a small medial process on the fourth metatarsal (Fig. 2f).

There has been some distortion in the shafts of metatarsals

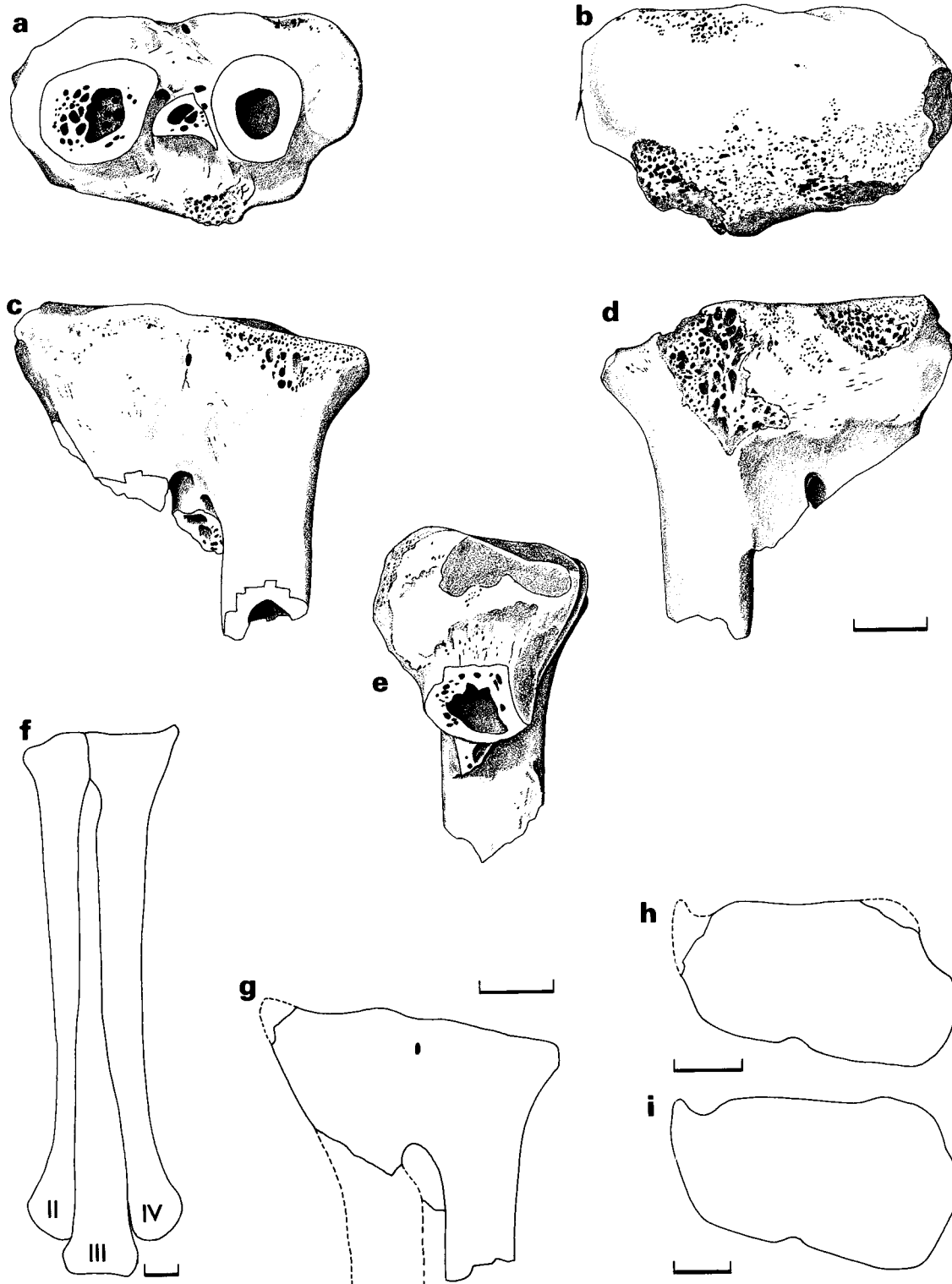


FIG. 1. Tarsometatarsus of *Elmisaurus*. TMP 82.39.4 (right side), *Elmisaurus elegans*, in (a) ventral, (b) dorsal, (c) anterior-extensor, (d) posterior-flexor, and (e) right lateral views. *Elmisaurus rarus* tarsometatarsus in (f) anterior and (i) dorsal aspects (after Osmolska 1981). Partial reconstruction of TMP 82.39.4 in (g) anterior and (h) dorsal views. All scales, 1 cm.

II and IV, so they do not articulate properly with metatarsal III in ROM 781 (Parks 1933, Pl. VI). However, the shafts still show a suite of unique characteristics that are shared with *Elmisaurus rarus*. There are strong longitudinal ridges forming the posteromedial edge of metatarsal II and the postero-

lateral margin of metatarsal IV. Because of these ridges, the posterior margin of the metatarsus is more deeply emarginated (Figs. 2*p*, 2*q*) than it is in other small theropods (Ostrom 1969; Wilson and Currie 1985). The distal ends of the shafts of the second and fourth metatarsals bow distinctively out-

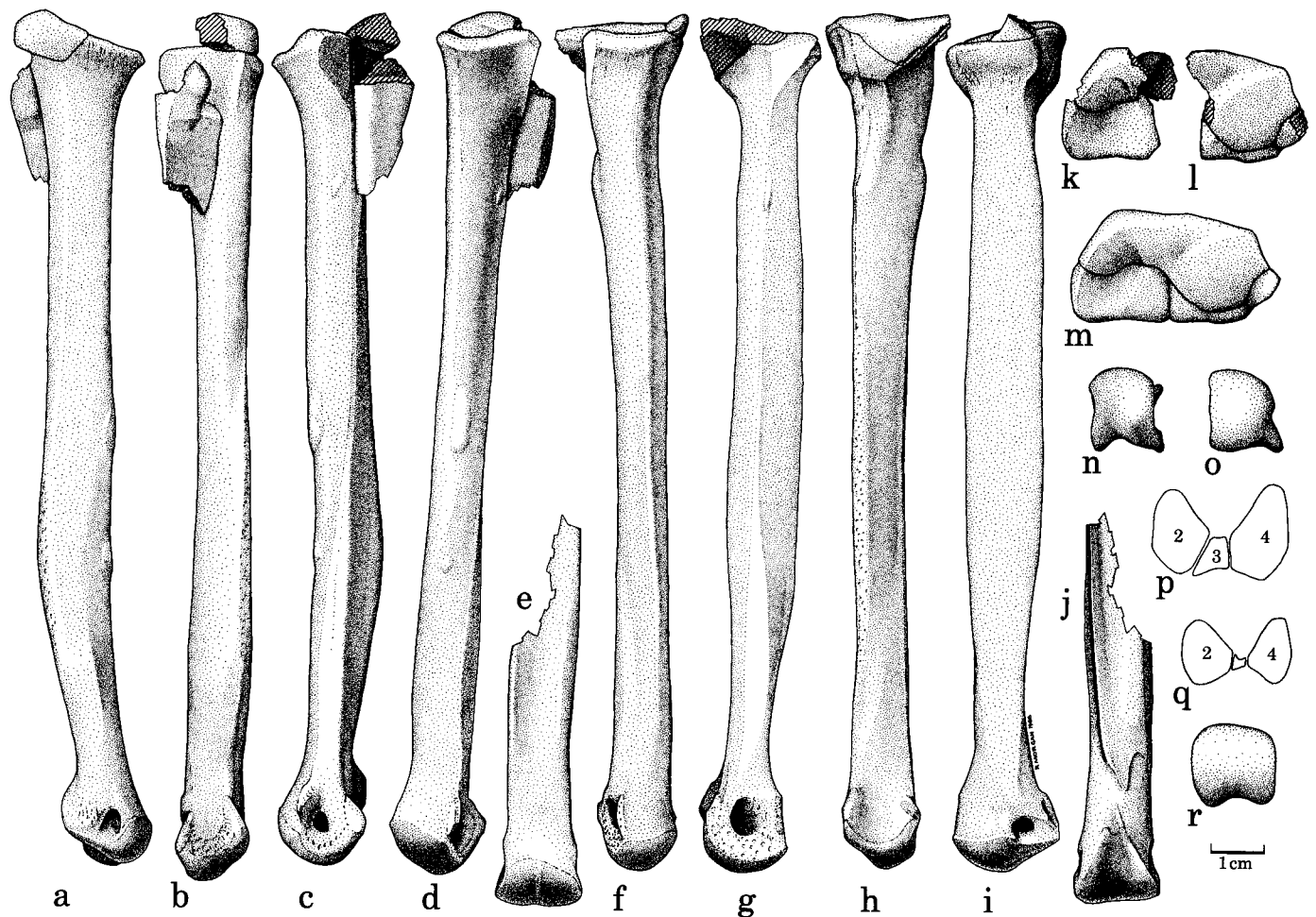


FIG. 2. Left tarsometatarsus of *Elmisaurus elegans*. Metatarsal II of ROM 781 (a) medial, (b) posterior, (c) lateral, (d), anterior, (k) proximal, and (n) distal views. Metatarsal III of ROM 781 in (e) anterior, (j) posterior, and (r) distal views. Metatarsal IV of ROM 781 in (f) anterior, (g) medial, (h) posterior, (i) lateral, (l) proximal, and (o) distal aspects. (m) Restoration of proximal view of fused tarsometatarsus. Cross sections of metatarsals II, III, and IV about one third the length from the distal end for (p) *Elmisaurus elegans* and (q) *Elmisaurus rarus*. Scale, 1 cm.

TABLE 1. Comparison of metatarsal size in known Elmisauridae

Specimen No.	1	2	mtII	mtIII	mtIV	II/III	IV/III	II/IV	Identification
TMP 82.39.4	37	22	—	—	—	—	—	—	<i>Elmisaurus elegans</i>
ROM 781	39	23	155	161	157	0.96	0.98	0.99	<i>Elmisaurus elegans</i>
ROM 37163	—	—	137e	—	—	—	—	—	<i>Elmisaurus elegans</i>
MGD-I/172*	—	—	147	157	147	0.94	0.94	1.00	<i>Elmisaurus rarus</i>
MDG-I/20*	55	—	—	—	—	—	—	—	<i>Elmisaurus rarus</i>
TMP 79.20.1	48e	27e	181	207	186	0.87	0.90	0.97	<i>Chirostenotes pergracilis</i>
NMC 8538	51e	—	205	230	212	0.89	0.92	0.97	<i>Chirostenotes pergracilis</i>
NMC 9570	—	39	258	—	—	—	—	—	<i>Chirostenotes cf. pergracilis</i>

NOTES: mediolateral width of metatarsus; 2, anteroposterior length of proximal end of metatarsus. All measurements in millimetres; e, estimate.

*After Osmolska (1981).

wards and anteriorly from the longitudinal centre of the metatarsus. Although metatarsals II and IV are subequal in length, the articulation between metatarsals II and III extends slightly more distally than that between III and IV.

ROM 781 is more gracile than the metatarsus of *Elmisaurus rarus*. The ratio of maximum shaft diameter to metatarsal (II and IV only) length is 0.09 in ROM 781 and 0.12 in *Elmi-*

saurus rarus. The posterolateral, longitudinal ridge of metatarsal IV in *Elmisaurus rarus* originates more proximally than in ROM 781 and is better developed. A small but distinct anterolateral process on metatarsal II and a similar anteromedial process on IV extend out over the distal end of metatarsal three.

A third specimen, ROM 37163, is the shaft and distal end

of a left metatarsal II. It is smaller than ROM 781 (Table 1), and sutural and articular surfaces are not as well defined, which suggests that it is not as mature. The shaft is straight, confirming that there is some distortion in ROM 781.

Discussion

TMP 82.39.4 is a fused tarsometatarsus that compares closely with *Elmisaurus rarus* in size and morphology. It is distinct from *Elmisaurus rarus* in the greater degree of fusion at an equivalent size (although this character can be somewhat variable in elmsaurids), in metatarsal II having a more slender shaft, and in being emarginated along the posteromedial margin in proximal view.

ROM 781 is more complete than TMP 82.39.4 and shows other features that are diagnostic for *Elmisaurus*. Metatarsals II and IV are subequal in length, and the distal end of each curves anteriorly and mediolaterally away from the longitudinal axis of the metatarsus. Ridges along the backs of the second and fourth metatarsals are well developed, so the metatarsus is deeply emarginated in cross section.

TMP 82.39.4 is slightly smaller than ROM 781, the type specimen of "*Ornithomimus*" *elegans*. Russell (1972) referred this species to *Macrophalangia*, an identification that was accepted by Currie and Russell (1988). However, reexamination of ROM 781 shows that the specimen is actually a fused tarsometatarsus that has been subsequently broken. Although it is slightly larger than TMP 82.39.4, the degree of fusion is not as pronounced. Nevertheless, the two specimens are the same in all essential characteristics and should be referred to the same species. A third specimen, ROM 37163, is the distal end of metatarsal II from a smaller, less mature individual than TMP 82.39.4 and ROM 781.

There are small but significant differences between the tarsometatarsi of Alberta and Mongolia that support distinction at least at the species level. The Alberta form is more gracile and has at least three osteological characteristics (shape of proximal articular surface, lesser development of the longitudinal posterolateral ridge on metatarsal IV, and the presence of small rugosities on the distal ends of the second and fourth metatarsals that slightly overlap the third) that distinguish it from *Elmisaurus rarus*. Therefore, it is highly likely that ROM 781, TMP 82.39.4, and ROM 37163 represent a distinct species of *Elmisaurus*—*Elmisaurus elegans*. There are many similarities in the Late Cretaceous theropod faunas of central Asia and North America (Currie, in press a), but the presence of distinct species of *Elmisaurus* suggests genetic separation between the Judith River Formation of Alberta and the Nemegt Formation. It is unknown whether speciation was caused by geographic, temporal, or ecological separation.

Chirostenotes pergracilis is a well established species based on axial, manual, pelvic, hind limb, and pedal elements (Currie and Russell 1988). Manual and pedal elements compare closely with those of *Elmisaurus* but are distinctive in their larger size (Table 1) and in the lack of fusion in the tarsometatarsus. It is best to consider *Chirostenotes* as a distinct genus within the family Elmsauridae (Currie, in press b).

Unlike with birds, fusion of the tarsometatarsus is limited to the proximal end, and the distal ends of the metatarsals are free.

A coossified tarsometatarsus from Mongolia described but not named by Osmolska (1981) has now been assigned to *Avimimus* (H. Osmolska, oral communication, 1987). Avimimids are an enigmatic group of small theropods that show

strong similarities to birds (Kurzanov 1981, 1983, 1987). Differences between *Chirostenotes* and *Avimimus* in the vertebrae, pelvis, and hind limbs suggest that elmsaurids and avimimids are not closely related. The fused tarsometatarsus is similar in length to that of *Elmisaurus* but is more compact, incorporates a splint-like fifth metatarsal, has a more reduced metatarsal III, and is not as emarginated posteriorly.

Coossified metatarsals of *Ceratosaurus*, *Syntarsus*, and *Avisaurus* (Brett-Surman and Paul 1985) each have a third metatarsal that is not reduced proximally and numerous other features that easily distinguish them from Elmsaurids. These taxa are not closely related to the Elmsauridae but show that fusion of tarsal and metatarsal elements occurred in several theropod lineages independently.

Currie and Russell (1988) speculated on whether *Chirostenotes* is the senior synonym of *Caenagnathus*. However, *Caenagnathus* shows strong similarities in the lower jaw to *Oviraptor*, whereas the undescribed metatarsus of *Oviraptor* is more primitive than that of either *Chirostenotes* or *Elmisaurus* in that the third metatarsal is not pinched proximally (H. Osmolska, oral communication, 1987). A conservative classification would retain generic and familial separation of *Chirostenotes* and *Caenagnathus*.

Although all of these problems would be resolved by the discovery of better specimens, small theropods continue to be one of the rarest but most interesting faunal elements in the known Upper Cretaceous sites.

Acknowledgments

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