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COOSSIFIED TARSOMETATARSI IN THEROPOD DINOSAURS AND THEIR BEARING ON THE PROBLEM OF BIRD ORIGINS

OSMÓLSKA, H.: Coossified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins, Palaeontologia Polonica, 42, 79–95, 1981.

Limb remains of two small theropod dinosaurs from the Upper Cretaceous deposits of Mongolia display fused tarsometatarsi. Presence of fusion in the tarsometatarsus in some theropods is considered as additional evidence for the theropod origin of birds. *Elmisaurus rarus* gen. et sp. n. is described based upon a fragmentary skeleton represented by limbs. Family Elmisauridae nov. is erected to include *Elmisaurus, Chirostenotes* GILMORE and *Macrophalangia* STERNBERG.

Key words: Dinosauria, Theropoda, bird origins, Upper Cretaceous, Mongolia.

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Received: June 1979.

Streszczenie. — W pracy opisano szczątki małych dinozaurów drapieżnych z osadów górnokredowych Mongolii. Stopa tych dinozaurów wykazuje obecność zrośniętego tarsometatarsusa. Zrośnięcie to stanowi dodatkowy dowód na pochodzenie ptaków od dinozaurów drapieżnych. Opisano nowy rodzaj i gatunek dinozaura drapieżnego *Elmisaurus rarus*, który zaliczono do nowej rodziny Elmisauridae. Do rodziny tej, oprócz *Elmisaurus*, należą: *Chirostenotes* GILMORE i *Macrophalangia* STERNBERG.

Praca była finansowana przez Polską Akademię Nauk w ramach problemu międzyresortowego MR II-6.

INTRODUCTION

During the Polish-Mongolian Paleontological Expedition to Mongolia in 1970 (KIELAN-JAWOROWSKA and BARSBOLD 1972) comparatively numerous limb fragments of various small theropod dinosaurs were found in the Nemegt Formation at the northern part of the Nemegt locality (Upper Cretaceous, GRADZIŃSKI *et al.* 1977). Among others, there are 4 more or less complete metapodia in the collection of the Institute of Paleobiology in Warsaw, which display the proximal coalescence of the metatarsals and also of two distal tarsals; thus an incipient form of the avian-like tarsometatarsus is present in this species. Three of these tarsometatarsi belong to three individuals of the same species *Elimisaurus rarus* gen. et sp. n., the fourth has a quite different structure and if it were more complete it might be diagnosed as a separate genus. It is here referred to as a "theropod gen. et sp. indet". One of the *E. rarus* tarsometatarsi was associated with several pedal phalanges, a fragmentary manus of the *Chirostenotes*-type and some other skeletal elements, all pertaining to the same individual. It should be also mentioned here that still another theropod with a fused tarsometatarsus was found in the Upper Cretaceous of Mongolia by the Soviet-Mongolian Paleontological Expeditions and it is currently being investigated by Dr S. M. Kurzanov (Paleontological Institute of the USSR Academy of Sciences Moscow; Dr Kurzanov's personal information).

Coalesced theropod metatarsi have been reported before in the Triassic podokesaurid *Syntarsus* (Raath 1969) and in the Jurassic ceratosaurid *Ceratosaurus* (Marsh 1884, Gilmore 1920). In the former case, it was considered by Raath to be due to the gerontic changes while in the latter case as a possibly pathological condition (Ostrom 1976:121). Occurrence of the coossification within the metapodial region, in at least two different theropods reported from the Mongolian Upper Cretaceous, calls for a reconsideration of this distinctive morphology.

The manuscript of this paper was read critically by Dr S. M. Kurzanov, who offered some valuable comments, which is highly appreciated by the present author. Dr D. A. Russell (National Museum of Natural Sciences, Ottawa) kindly provided the casts of the *Chirostenotes* and *Macrophalangia* types, which is acknowledged with gratitude. Dr M. Brett-Surman (The Johns Hopkins University, Baltimore) most kindly corrected the English of the present paper and made valuable suggestions.

Abbreviations used:

PIN — Paleontological Museum of the USSR Academy of Sciences, Moscow;
QVM — Queen Victoria Museum, Salisbury;
USNM — United States National Museum;
YMP — Peabody Museum, Yale;
ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warszawa.

Order **Saurischia**
Suborder **Theropoda**
Infraorder **?Coelurosauria**
Family **Elmisauridae** nov.

Genera assigned: *Elmisaurus* gen. n., *Chirostenotes* Gilmore, 1924, *Macrophalangia* Sternberg, 1932.

Diagnosis. — Lightly built, medium sized theropods with very thin-walled limb bones. Manus slender, anisotridactyl with long digits; second digit the longest and strongest, with phalanges 1 and 2 equally long; the third digit distinctly thinner than others, unguals laterally compressed and curved, with a dorsoposterior "lip". Pes long and slender, functionally tridactyl and with abbreviated first digit; metatarsal III wedged between adjoining metatarsals but anteriorly visible for most of its length; third digit the longest, second and fourth digits subequal in length, unguals recurved.

Stratigraphic and geographic range. — Upper Cretaceous of North America and Asia.

Remarks. — The infraordinal assignment of the Elmisauridae is tentative as nothing is known about the skull and most of the postcranial skeleton of *Elmisaurus* and other representatives of this family. Some resemblances may be noticed to the members of the families Coelurosauridae, Dromaeosauridae, Caenagnathidae (= Oviraptoridae of Barsbold 1976*a*), Saurornithoididae and Ornithomimidae, which were recently assigned by Barsbold (1976*b*) to four separate infraorders. The anisotridactyl manus in elmisaurids represents the same functional type as these in the coelurids, dromaeosaurids and caenagnathids, although in the first two families, metacarpal I is more shortened and less slender than in *Elmisaurus* and probably also in *Chirostenotes*. It may be added here that the Lower Cretaceous *Microvenator celer* Ostrom (Ostrom 1970:73, pl. 12N) of the Coeluridae displays a comparable long and slender metacarpal I. On the other hand, the manus in the ornithomimids, which is almost isotridactyl and with a strongly elongated metacarpal I, is quite different from the manus in the elmisaurids.

The pes in the elmisaurids, displaying the relatively slender metatarsus and wedged metatarsal III is somewhat similar to the pes in the saurornithoidids and ornithomimids, but in the former family the metatarsal III is hidden posteriorly almost completely by the metatarsal IV, and the second digit is highly specialized. (RUSSELL 1969: fig. 14). This is not the case in *Macrophalangia* and also not in *Elmisaurus*. Wedging of metatarsal III is much more advanced in the ornithomimids[1] than in the elmisaurids and the first digit is lacking in the ornithomimids, while still present in the elmisaurids. The structure of the pes in the dromaeosaurids and caenagnathids is entirely incomparable to this morphology in the elmisaurids, because it displays a short and stout metatarsus with an unwedged metatarsal III.

It follows from the above comparisons that a relationship with the Ornithomimosauria BARSBOLD, 1976 is least probable, while a relationship with the Coelurosauria HUENE, 1914 — is most probable, althought the final decision must be pending until more data on the elmisaurids are available. The combination of the coelurid, probably synapomorphic, character (structure of the manus) with a definitely non-coelurid character (structure of metatarsus) warrants the establishment of a new family.

Chirostenotes GILMORE, 1924 and *Macrophalangia* STERNBERG, 1932 cannot be easily allocated in any known family (see also: GILMORE 1924, STERNBERG 1932, RUSSELL 1972). However, they display very close similarities to *Elmisaurus* (p. 88) and for this reason they are assigned to the Elmisauridae. OSTROM (1969) considered *Chirostenotes* as best allied with the Dromaeosauridae, but association of the *Chirostenotes*-like manus with the definitely non-dromaeosaurid-like pes in *Elmisaurus rarus* makes this assignment rather improbable. It cannot be excluded that *Macrophalangia*, *Chirostenotes* and *Elmisaurus* will appear synonyms in the future.

Genus *Elmisaurus* gen. n.

Type species: *Elmisaurus rarus* sp. n.
Derivation of the name: *elmyi* which is Mongolian for pes — the type species is based upon the pes.

Diagnosis. — Manus *Chirostenotes*-like with metacarpal I more than half the length of metacarpal II; two distal tarsals 3 and 4 coossified with each other and with metatarsus. Tarsal 4 with and upward process at lateral margin; cross-section of metatarsus semilunal. Metatarsals II, III and IV fused proximally.

Genus monotypic. — Geographic and stratigraphic range as for the type species.

Elmisaurus rarus sp. n.
(pl. 20:1, 2; pl. 21:1-3; figs. 1-4)

Type specimen: left tarsometatarsus, ZPAL Mg-D-I/172: pl. 21:1.
Type locality: Northern Nemegt, Nemegt Basin, Gobi Desert, Mongolian People's Republic.
Type horizon: Nemegt Formation, Upper Cretaceous (Upper Campanian or Lower Maastrichtian).
Derivation of the name: *rarus* (Lat.) — rare.

Diagnosis. — Metatarsal III visible anteriorly for about 90% of its entire length; length/width ratio of metatarsus 0.18; metacarpal I about 2/3 the length of phalanx 1 in this digit, digit III markedly thinner than digits I and II both of which are equally thick; ventroposterior portions of the manus phalanges distinctly thickened at the proximal surfaces.

[1] Since this paper was submitted to publication Dr. R. BARSBOLD informed me, that an ornithomimid specimen was found in Mongolia which displays a weakly advanced, four-digital pes.

Table 1

Measurements of the manus and pes elements in *E. rarus* (mm)

	ZPAL MgD-I/		
	172	98	20
Metacarpal I			
length	—	45	—
proximal transverse width	—	14	—
distal transverse width	—	12	—
Metacarpal II			
length	—	—	—
proximal transverse width	—	—	—
distal transverse width	—	13	—
Phalanges			
I-1 length	—	65	—
proximal transverse width	—	13	—
distal transverse width	—	10	—
II-1 length	—	66	—
proximal transverse width	—	14	—
distal transverse width	—	12	—
II-2 length	—	66	—
proximal transverse width	—	12	—
distal transverse width	—	10	—
III-1 length	—	30	—
proximal transverse width	—	5	—
distal transverse width	—	6	—
III-2 length	—	30	—
proximal transverse width	—	6	—
distal transverse width	—	7	—
III-3 length	—	43	—
proximal transverse width	—	7	—
distal transverse width	—	6	—
Ungual (?I-2) length	—	44	—
Tarsometatarsus			
maximal length	163	—	—
proximal transverse width	46	—	55
medial transverse width	28	—	—
distal transverse width	46	44e	—
Metatarsal II			
length	147	—	—
proximal transverse width	22	—	27
distal transverse width	15	17	—
Metatarsal III			
length (seen anteriorly)	141	—	—
length (seen posteriorly)	157	—	—
proximal transverse width (posteriorly)	11	—	14
distal transverse width	22	23	—
Metatarsal IV			
length	147	—	—
proximal transverse width	25	—	31
distal transverse width	17	17	—
Phalanges			
I-1 length	—	26	—
proximal transverse width	—	0·9	—
distal transverse width	—	0·9	—
II-1 length	—	44	—
proximal transverse width	—	18	—
distal transverse width	—	15	—
II-2 length	—	33	—
proximal transverse width	—	14	—
III-1 length	—	43	—
proximal transverse width	—	22	—
distal transverse width	—	16	—
III-2 length	—	32	—
proximal transverse width	—	17	—
distal transverse width	—	15	—
III-3 proximal transverse width	—	14	—

Material. — Holotype ZPAL MgD-I/172 — complete left tarsometatarsus (lacking Mt I); referred: ZPAL MgD-I/98 — right pes including distal portion of the metatarsus, phalanx I_1, phalanx II_1 and damaged phalanx II_2, phalanges III_1, III_2, and proximal portion of the phalanx III_3, two undetermined fragmentary phalanges IV, two fragmentary unguals (II and IV?); right manus including metacarpal I and distal portion of the metacarpal II, phalanx I_1, phalanges II_1, II_2, phalanges III_1, III_2, III_3, a complete ungual probably of the digit I and proximal portion of another ungual (II?); undeterminable fragments of long bones of limbs, pertaining to the same individual; ZPAL MgD-I/20 — proximal portion of the right tarsometatarsus.

All from the northern part of Nemegt locality, Nemegt Formation.

DESCRIPTION

Manus. The manus is slender with the first digit the shortest, the second digit the longest and the third digit the thinest (pl. 20: 1; figs. 1, 2). Except for the unguals, all phalanges of digits I and II are subequal in the length (table 1).

Metacarpus. Metacarpal I is slender and its length equals two thirds of the length of phalanx I_1; its shaft is triangular in cross-section. The proximal articular surface is triangular, concave anteromedially and from its medial corner a massive flange extends downwards, which is posteromedially directed and has well finished articular surface. The elongated posterolateral corner of the proximal surface forms another posterior flange (fig. $1A_2$). The distal surface is slightly twisted in relation to the proximal one; it has a subquadrangular shape and is very wide with a weakly concave groove (somewhat deeper toward the palmar side) and might permit some mobility of digit I in the transverse plane, but only in the extended position (see below). The lateral side of metacarpal I is proximally flattened for a close, immobile contact

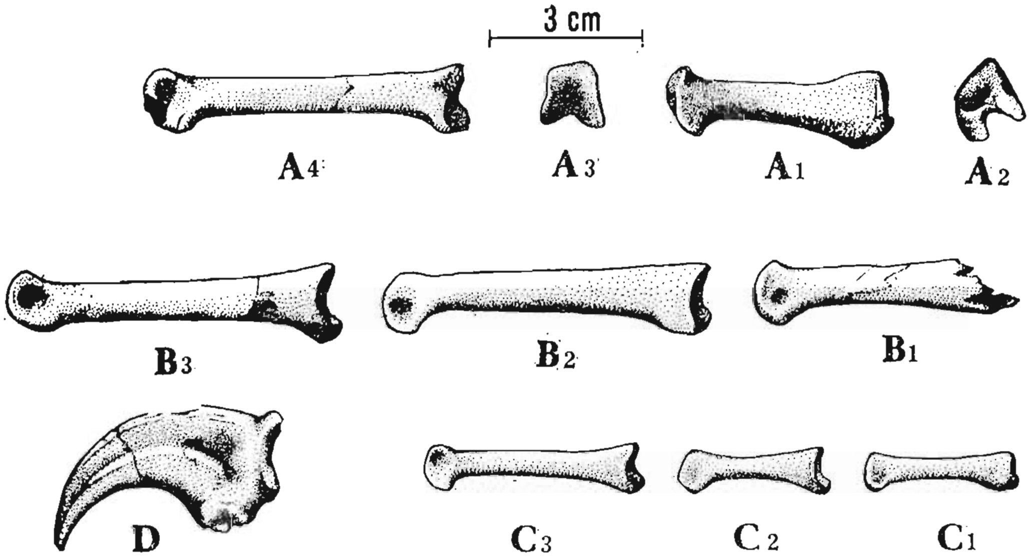


Fig. 1

Elmisaurus rarus gen. et sp. n., digits of the right manus in medial view (except A_2, A_3 and D), ZPAL MgD-I/98; *A* digit I: *1* metacarpal I, *2* proximal articular surface of metacarpal I, *3* distal articular surface of metacarpal I *4* phalanx I_1; *B* digit II: *1* distal portion of metacarpal II, *2* phalanx II_1, *3* phalanx II_2; *C* digit III: *1* phalanx III_1, *2* phalanx III_2, *3* phalanx III_3; *D* ungual of digit I (?) in lateral view.

6*

with the metacarpal II; the palmar surface is concave proximally, because of the presence of the medial and lateral flanges mentioned above. There is no medial fossa for the collateral ligament, which is on the lateral side and is relatively deep. The preserved distal portion of metacarpal II is 53 mm long, and the shaft is flattened dorsally. The distal articular surface is almost symmetric and broadly grooved. The medial condyle is somewhat larger. Both condyles are separated dorsally by a short but deep furrow which is absent in the metacarpal I.

Digit I. This digit comprises 2 phalanges and diverges somewhat medially due to the twist of the distal articular surface of the metacarpal I. Phalanx I_1 is very long and slender, its shaft is slightly bowed laterally and is somewhat compressed transversely in cross-section; the dorsal edge of the proximal surface is damaged medially. As preserved, the articular ridge on the proximal articular surface is almost absent. Ventrally, there is a strong tuber-like thickening on the proximal articular surface, which extends onto the palmar side of the phalanx

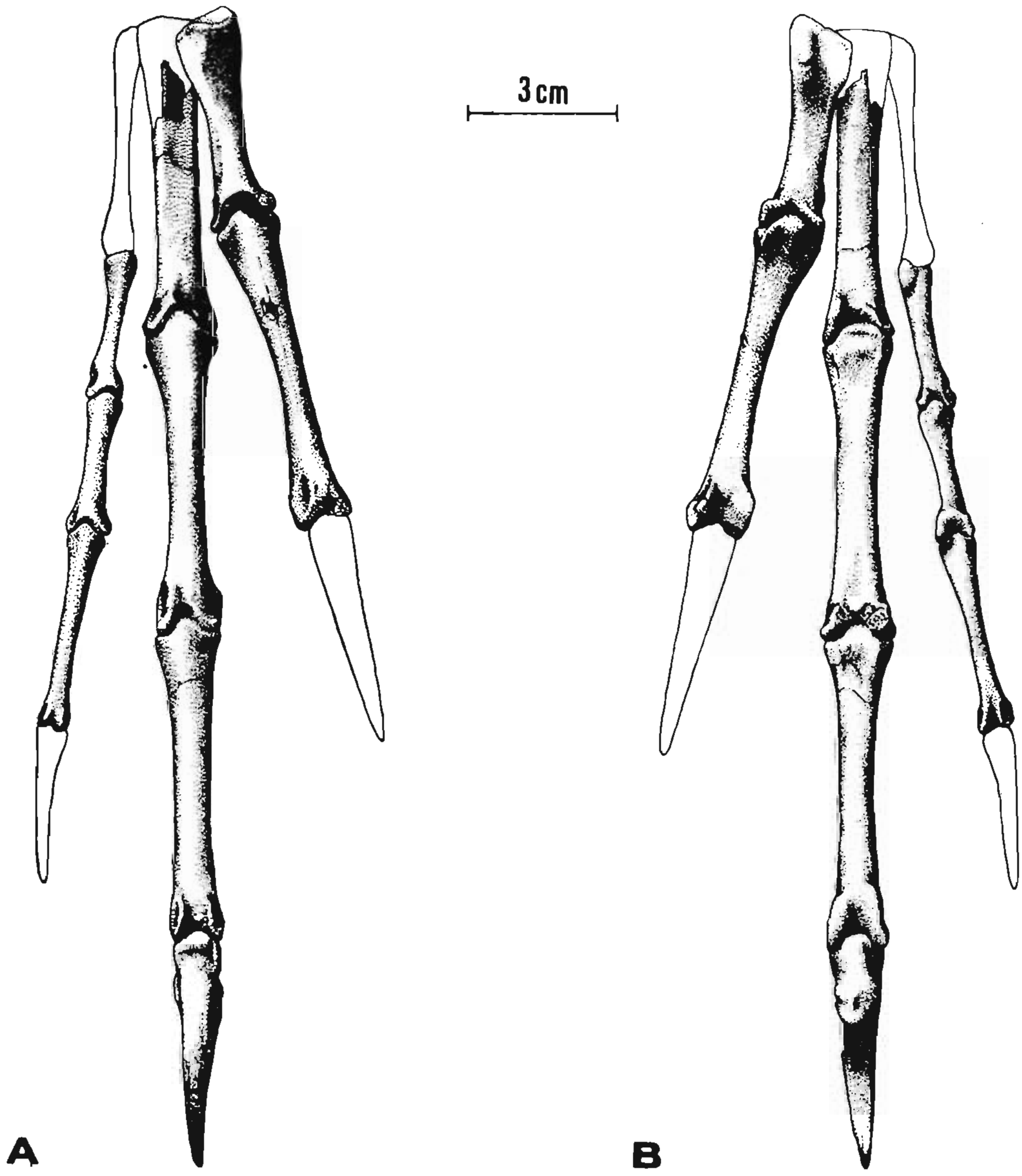


Fig. 2

Elmisaurus rarus, reconstruction of right manus based upon specimen ZPAL MgD-I/98; *A* dorsal view, *B* palmar view forming a kind of a low flexor tuber. This thickening might effectively restrict any medial or lateral movement of the digit in the flexed position; the foveae ligamentosae are very deep. The ungual probably pertaining to the digit I is strongly curved, compressed laterally, relatively short, it bears a distinct longitudinal sulcus. There is present, posterodorsally, a characteristic "lip" (extensor crest) above the articular surface. The ventral edge of the ungual is rounded and blunt, the flexor tuber is prominent and the articular surface is very indistinctly divided, and only so ventrally.

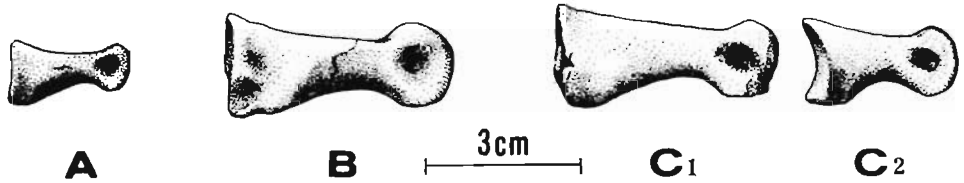


Fig. 3

Elmisaurus rarus, phalanges of right pes in lateral view, ZPAL MgD-I/98; *A* phalanx I_1, *B* phalanx II_1, C_1 phalanx III_1, C_2 phalanx III_2.

Digit II. The phalanges II_1, II_2 are equally long. Phalanx II_1 is the somewhat thicker of the two. It has a broad proximal articular surface divided slightly and asymmetrically by a low, indistinct ridge. The thickening, similar to this in phalanx I_1 only wider, is developed in the ventral part of the proximal articular surface. A furrow separates the distal condyles on the dorsal face of the phalanx; and this furrow is slightly wider than this on metacarpal II. The distal articular surface is shallow and almost symmetrically grooved; the medial fovea ligamentosa of this phalanx is shallower than the opposite one. Phalanx II_2 displays the proximal articular surface which is higher than wide and has a very prominent ventral thickening. The tuber on the palmar face of the phalanx, at the proximal surface, is also prominent and extends into a short longitudinal ridge laterally. The distal articular surface is more distinctly grooved than these of other phalanges, but also here the groove separates the condyles symmetrically. The foveae ligamentosae are very deep.

Digit III. This digit is very thin and its 3 preserved phalanges are strongly compressed transversely. Phalanx III_1 is the thinnest; its proximal articular surface is very indistinctly grooved and the foveae ligamentosae are extremely shallow. The articular surfaces of phalanx III_2 are divided weakly and symmetrically. Posteroventrally the phalanx is elongated and thickened forming the tuber. The foveae ligamentosae are indistinct. Phalanx III_3 is longer than each of two preceding ones and has more distinctly divided articular surfaces. Its lateral fovea is very deep, while the medial one much shallower.

Pes. The pes is incompletely known, but it seems that digit III was the longest and strongest (figs. 3, 4). The pes is tetradactyl with the first digit greatly shortened, not reaching the ground. It is impossible to state whether the first digit was reversed, as only phalanx I_1 has been found, and on metatarsal II there is no trace of the appositional surface for metatarsal I.

Tarsometatarsus. The most striking character of the pes is the presence of a complete, traceless fusion of the two distal tarsals (3+4) and of the fusion of these coalesced tarsals with the metatarsus. They cover somewhat more than the posterior half of the proximal articular surface. The demarcation line between these tarsals and the metatarsus is distinct although faint. The anterior borders of these tarsals are relatively well visible against the articular surface of the metatarsus (fig. 4C). Posterolaterally tarsal 4 has a process projecting proximally which is difficult to interpret as nothing comparable has so far been reported in other theropods. The proximal part of the metatarsus also displays a fusion of the metatarsals II, III and IV; the fusion between metatarsals II and III being more advanced. More distally, the metatarsals are closely appressed to each other but not fused, and at the distal ends, they separate. In the anterior (dorsal) view (pl. 21:1a, fig. 4A), metatarsal III narrows uniformely toward the proximal end and is visible for about nine tenths of its length. From about half its length, it sinks gradually between metatarsals II and IV which are higher at this point. The distal articular surface of metatarsal III is wider than these of the adjoining metatarsals and is distinctly delimited from the dorsal surface of the shaft. It is nearly subrectangular, symmetrical, and not grooved. The distal articular surfaces of metatarsals II and IV are smaller and rounded with that of metatarsal II facing distinctly medial. Close to the proximal end of the tarsometatarsus is a distinct, tripartite, rough protuberance which occupies the dorsolateral slope of metatarsal II, the dorsal surface of metatarsal III and the dorsomedial slope of metatarsal IV. It might be interpreted as the attachment site of the strong *m. extensor digitorum longus*. In posterior (plantar) view (pl. 21: 1b, fig. 4B) the tarsometatarsus is deeply concave, especially along its medial portion, with metatarsals II and IV being transversely compressed and forming the medial and lateral flanges on the sides of the depression, the bottom of which is formed of the flat, plantar surface of the narrow metatarsal III. The posteriorly directed edges of the flanges of metatarsal II and IV are rough; the metatarsal III is narrowest at the middle. At the proximal end it is completely coalesced with metatarsal II. The fusion with metatarsal IV is somewhat weaker. Just below the proximal end, a small slit is present between metatarsals III and IV, which is accompanied by a groove on metatarsal IV. It pierces the tarsometatarsus and opens on its anterior face just above the attachment site mentioned above. It probably served as a vessel or nerve canal. Another slit, although narrower, is present somewhat below and between metatarsals II and III, but it does not appear to conduct a vessel or nerve. The distal articular surface of metatarsal III, as seen posteriorly, is deeply depressed medially. A similar, deep, but narrower depression is developed on the posterior face of the articular surface of metatarsal II and a short furrow extends from this depression distally which disappears on reaching the extremity of the articular surface, without invading its anterior face. The posterior face of the articular head of metatarsal IV is only weakly depressed. The medial condyle of metatarsal II and the lateral condyle of metatarsal IV are stronger, whereas those of metatarsal III are symmetrically developed. Both ligamental fossae on metatarsal III are very deep, while on metatarsal II the lateral one, and the medial one on metatarsal IV are deeper than the opposite ones. The distal articular surfaces of all three metatarsals described above are well finished except for their posterior faces which are rough. Metatarsal V has not been found with any tarsometatarsus of *Elmisaurus*, however, there is a weakly pronounced triangular surface on the posterior face of the metatarsus lying proximally, which might indicate that a splint of bone was attached there.

Digit I. Phalanx I_1 is slender and slightly bowed laterally. It has a rounded, centrally depressed, proximal articular surface. The distal articular surface is well developed, slightly asymmetrical with the lateral condyle larger and with deep ligamental fossae.

Digit II. Phalanx II_1 is comparatively slender. Its proximal articular surface is centrally depressed, the end is flat and rough on the ventral side. On the lateral side, it bears two small depressions, the more ventral one being deeper. The distal articular surface is broad, symmetrically and widely grooved. The lateral condyle is higher along its laterodorsal edge. The dorsal face of the articular surface is distinctly asymmetrical extending toward the lateral side. Centromedially and proximally to it lies a depression. The medial fovea ligamentosa is deeper and extending dorsoposteriorly from it, a shallow sulcus is present. Phalanx II_2 has a damaged shaft as well as a damaged distal articular surface on the medial side. Its length is three-quarters that of phalanx II_1. Its proximal end is flat ventrally and its proximal articular surface forms and almost isosceles triangle symmetrically divided by an indistinct ridge.

Digit III. Phalanx III_1 is as long as phalanx II_1, but thicker. Proximally, the articular surface is subrectangular, flat, and rough ventrally. The distal articular surface is very broad, symmetrically and widely grooved. Proximally to the well delimited dorsal face of the distal

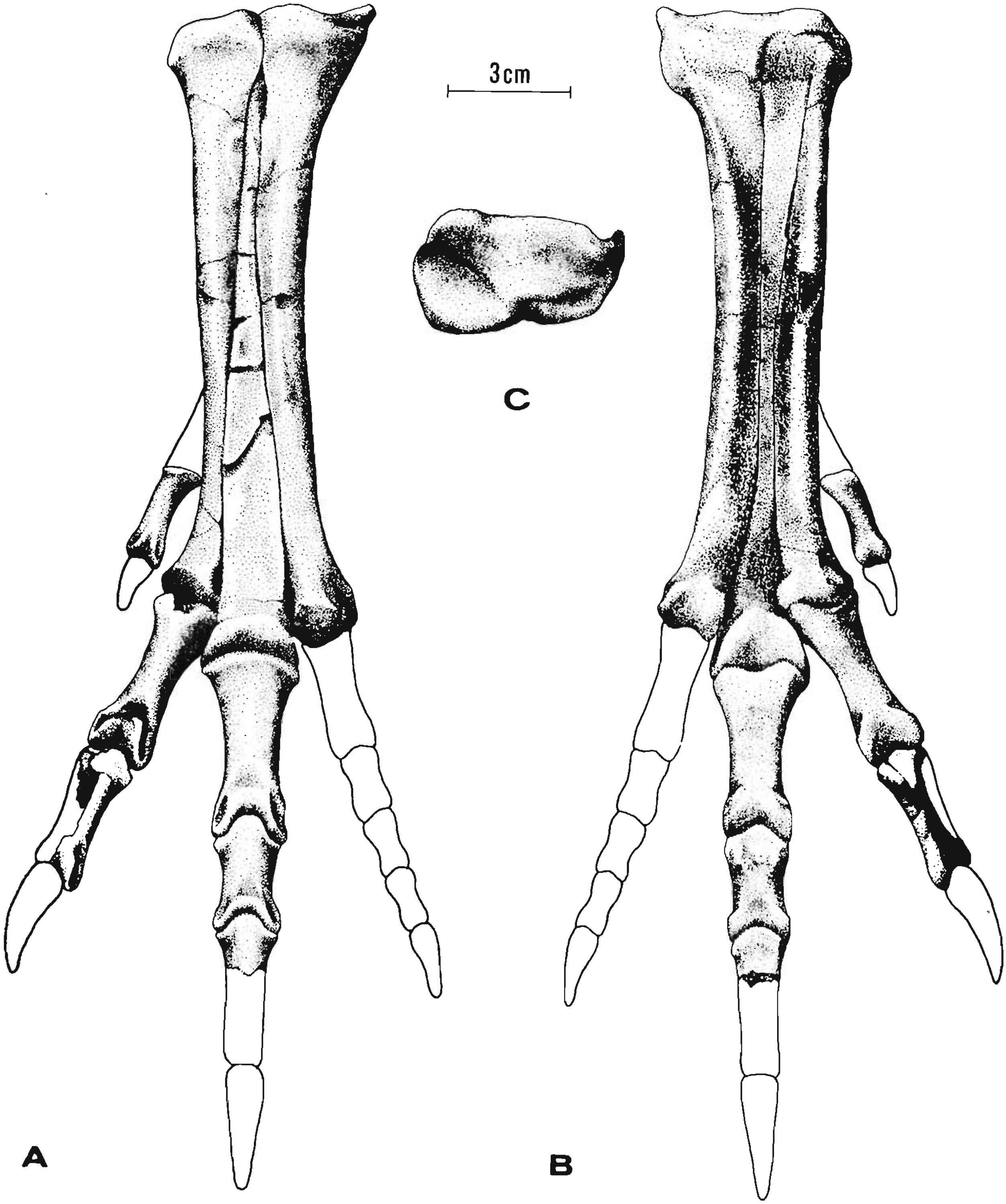


Fig. 4

Elmisaurus rarus, reconstruction of left pes based upon specimens: ZPAL MgD-I/172 (tarsometatarsus) and ZPAL MgD-I/98 (digits, reversed from right side); *A* dorsal view, *B* plantar view, *C* proximal articular surface of tarsometatarsus.

articular surface is a depression. The foveae ligamentosae are deep on either side. Phalanx III_2 is about a quarter shorter than phalanx III_1. Its proximal articular surface is very indistinctly divided. The proximal end is posteriorly elongated on the dorsal side. The rough and flat portion on the ventral side is narrow. A depression located proximally to the dorsal face of the distal articular surface is very shallow. The preserved proximal portion of phalanx III_3 is similar to that of the preceding phalanx.

Unguals. The preserved proximal portions of two unguals indicate that they pertain to the marginal toes of the right pes, the second and the fourth. Each of them seems to be too large to represent the ungual of the first toe. These unguals were probably weakly curved and their ventral edges are blunt and rounded. The ungual, which most probably belongs to the second digit judging from its articular surface, has a very weakly developed flexor tuber. The other, possibly of the fourth digit, is almost devoid of the tuber.

As the shapes of articular surfaces of the pedal phalanges in *Elmisaurus* indicate, the flexory movements of the digits were very limited. The extensory movements, however, might have been quite extensive.

Discussion. — *Elmisaurus rarus* gen. et sp. n. in the structure of manus is very similar to *Chirostenotes pergracilis* GILMORE, 1924. As far as can be judged from what has been preserved in both species, the only difference concerns the shape of the unguals which are more slender in *Ch. pergracilis*. In the structure of the pes, *E. rarus* resembles *Macrophalangia canadensis* STERNBERG, 1932. Both have a third metatarsal which is incipiently wedged, metatarsals II and IV that are almost equally long and a first digit which is shortened. There are also, however, some distinct differences. The metatarsus in *E. rarus* is more slender (table 2), proximally fused, with the proximal ends of metatarsals II and IV attaching to each other anteriorly and hiding the proximal end of metatarsal III. This is not the case in *M. canadensis*, in which metatarsal III is visible anteriorly up to its extreme proximal end. The digits in *E. rarus* seem to be relatively shorter, especially digit I which is more advanced in its reduction. Phalanx I_1 is only somewhat more than a half the length of phalanx II_1, while it is three quarters of that length in *M. canadensis*. Within digit III, the phalanx III_2 is relatively longer in *E. rarus* than in *M. canadensis*.

Table 2

Width to length ratios of the metatarsi in some theropods and in *Archaeopteryx lithographica*

Ornithomimus edmontonicus ROM 851	0·09
Gallimimus bullatus ZPAL MgD-I/94, GPS 100/11	0·11–0·12
Stenonychosaurus inaequalis NMC 8339	0·15 (1)
Macrophalangia canadensis NMC 8538	0·21 e
Elmisaurus rarus ZPAL MgD-I/172	0·18
Syntarsus rhodesiensis QVM/1	0·23 (2)
Deinonychus antirrhopus YMP 5205	0·31 (3)
Velociraptor sp. ZPAL MgD-I/97	0·31
Archaeopteryx lithographica (Maxberg specimen)	0·19 (4)

(1) counted from the reconstruction in RUSSELL (1969: fig. 13)
(2) counted from figure in RAATH (1969: fig. 6a)
(3) counted from figure in OSTROM (1969: fig. 73)
(4) counted from figure in OSTROM (1976: fig. 4c)

The state of preservation in the metatarsus of *M. canadensis* does not allow a statement of whether the posterior (plantar) face of the metatarsus in this species is also as concave as it is in *E. rarus*. It does appear, however, that it is somewhat concave, not flat as it is in *Velociraptor* (undescribed referred material in ZPAL collection) or in *Deinonychus*.

Because the manus of *E. rarus* is almost identical with that of *Ch. pergracilis* and the pes of *E. rarus* similar to that of *M. canadensis*, it is possible that *Ch. pergracilis* and *M. canadensis* may be conspecific. COLBERT and RUSSELL (1969) were the first to suggest this, and the Mongolian findings give new support to this suggestion. Until further direct evidence to the conspecifity of these two Canadian forms is found, however, it is reasonable to consider them separate but within the same family Elmisauridae.

Among other non-carnosaurian Upper Cretaceous theropods, which are similar to *E. rarus* and combine the wedged metatarsal III and the presence of digit I, the species of *Saurornithoides* and *Stenonychosaurus* should be mentioned. The pes structure in the former genus is poorly known but it can be noticed that *E. rarus* differs from the *Saurornithoides* species in this respect as follows:

1) when seen posteriorly, metatarsus IV occupies only about a half of the entire proximal width of the metatarsus in *E. rarus*, while it occupies more than two thirds the width in *S. junior* (BARSBOLD 1974: fig. 5b);

2) phalanges II_1 and III_1 are equally long in *E. rarus* while phalanx III_1 is longer in *S. mongoliensis* (RUSSELL 1969: table VII).

Stenonychosaurus inaequalis STERNBERG, 1932, as reconstructed by RUSSELL (1969: fig. 13), may be distinguished by a disparity in the length of metatarsals II and IV, these being almost equally long in *E. rarus*. There is a peculiar posteroproximal extension of the distal articular surface of metatarsal III in *S. inaequalis* which is lacking in *E. rarus*. Metatarsal III in posterior view contributes less to the width of the metatarsus in *S. inaequalis* than it does in *E. rarus*. Additionally, the species of *Saurornithoides* and *Stenonychosaurus* have highly specialized, shortened digit II in the pes, which is not the case in *E. rarus*.

Neither of the so far described theropods (except probably *Macrophalangia canadensis*, comp. above) has the peculiar posteriorly concave metatarsus which is so striking in *E. rarus* and which results in the semilunar cross-section of the metatarsus in the latter species. Also, the upward process of the lateral distal tarsal 4 is an unusual character of *E. rarus* not found in any theropod dinosaur (*Syntarsus*?; comp. RAATH 1969: fig. 6a).

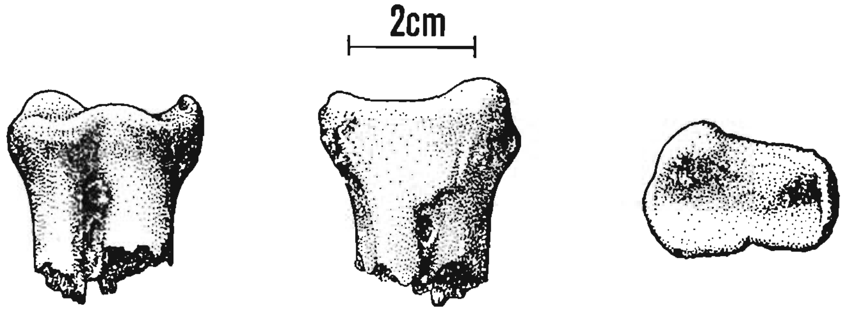
Infraorder and family uncertain

Theropod gen. et sp. indet.

(pl. 20:3; 21:4; fig. 5)

Material. — A proximal portion of tarsometatarsus ZPAL MgD-I/85, from the Nemegt Formation, the northern part of Nemegt locality, Nemegt Basin, Gobi Desert, Mongolian People's Republic.

Description. — The distal tarsals, probably 2 in number, are completely fused with each other and with the metatarsus, leaving almost no demarcation line, thus producing a single surface for articulation with the astragalus + calcaneum. This articular surface of the tarsometatarsus displays laterally and medially two shallow depressions. A prominent boss is developed posteriorly to the medial depression (above the metatarsal II) and the lateroposterior edge of the articular surface forms a ridge-like elevation. The proximal ends of the metatarsals, as preserved, are completely fused with each other and the line of the fusion is very weakly visible in anterior view, dividing the proximal end of the tarsometatarsus into two equally broad portions. Metatarsal III is very thin proximally and visible only some distance below the proximal articular surface of the tarsometatarsus. In posterior view, a broad, flat medial wing of metatarsal IV overlaps proximally the lateral portion of metatarsal II, thus occupying two thirds of the proximal width of the tarsometatarsus. Some distance below, where metatarsal III is more prominent, metatarsal IV contributes only to about a half of the entire width of the tarsometatarsus.



A B C

Fig. 5

Theropod gen. et sp. indet., proximal portion of left tarsometatarsus, ZPAL MgD-I/85; *A* dorsal view, *B* plantar view, *C* articular surface.

Remarks. — The above described fragment of the tarsometatarsus displays a much stronger fusion of its elements than in the case of *E. rarus*. The posterior (plantar) faces of both compared tarsometatarsi are quite different, not only in the mutual proportions of the contributing bones, but also in the lack of the upward process on tarsal 4, which is a distinctive feature in *E. rarus*. The latter species lacks posteriorly the medial wing of metatarsal IV. A somewhat comparable proximal end of a metatarsus was described and figured as *Saurornithoides junior* by Barsbold (1974: fig. 5). In the latter species, a discrepancy in the width of metatarsals II and IV is distinct in anterior view. As seen posteriorly, metatarsal III in *S. junior* reaches distal tarsal 3, which is not the case in the fragment of the tarsometatarsus described here. Additionally, the fusion of the metatarsus and the tarsals are lacking in *S. junior*.

CONCLUSIONS

The coossification of the metapodials has been generally considered as an exclusive bird character. Nevertheless, ankylosed metatarsals have been described in some dinosaurs (table 3; fig. 6). Marsh (1884), and later Gilmore (1920), described ankylosed metatarsals in the Upper Jurassic *Ceratosaurus nasicornis* Marsh (Ceratosauridae). Since then, a fused tarsometatarsus was reported by Raath (1969) in the Upper Triassic *Syntarsus rhodesiensis* Raath (Podokesauridae). In both cases, the fusion was stated to be in a single specimens, thus it was considered as probably due to a pathologic condition (*Ceratosaurus*; see Ostrom 1976:121) or to advanced individual age of the animal (*Syntarsus*; see Raath 1969:22). The partial fusion within the tarsometatarsus in *E. rarus* can be considered neither as a pathologic nor as a gerontic feature, because it was found in two individuals of this species (ZPAL MgD-I/172, 20: pl. 20:2; pl. 21:1) which markedly differ in size. Additionally, the taxonomically undeterminable, fragmentary tarsometatarsus (ZPAL MgD-I/85; pl. 20:3; pl. 21:4) described above, as well as the recent finding by members of the Joint Soviet-Mongolian Paleontological Expeditions of a long, completely fused tarsometarsus (Dr S. M. Kurzanov's personal information) show further evidence that the fusion of the distal tarsals and of metatarsals into a tarsometatarsus was not an exceptional phenomenon in the theropods. In view of these facts, it seems most probable that the fusion of the metapodium in *Syntarsus*, and perhaps also in *Ceratosaurus*, was the normal character in these dinosaurs.

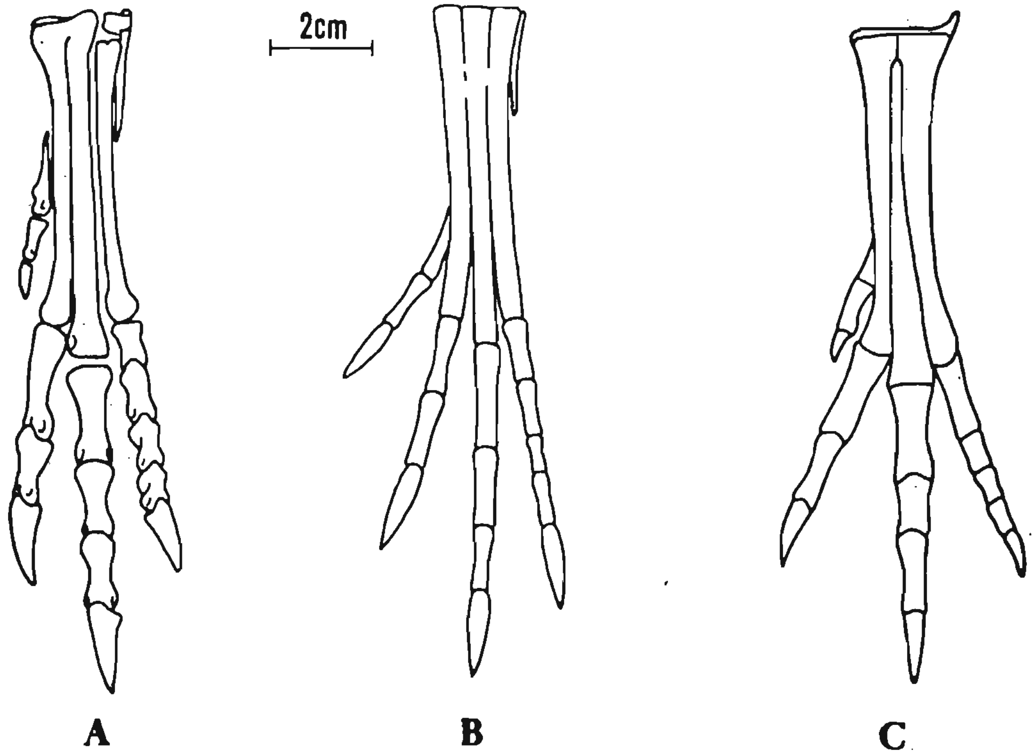


Fig. 6

Pes in: *A Syntarsus rhodesiensis, B Archaeopteryx litographica, C Elmisaurus rarus.* Not to scale. *A* after RAATH 1969, *B* after OSTROM 1976, *C* original.

It follows that formation of the tarsometatarsus is not an exclusive avian character and that the tendency toward the fusion was a common character to some theropod dinosaurs and birds. This speaks very much in favour of OSTROM's hypothesis (1973, 1975) concerning the theropod origin of *Archaeopteryx*, and consequently of birds. This hypothesis was challanged by HECHT (1976) and WALKER (1977). Both these authors considered, as one of the weak points in OSTROM's hypothesis, the dissimilarity of the pelves in *Archaeopteryx* and in the coelurosaurians (*sensu* OSTROM 1976: 181). However, recent findings in the Upper Cretaceous of Mongolia by BARSBOLD (1977, 1979) make this objection immaterial: a representative of the Dromaeosauridae — *Adasaurus (nomen nudum)*, the pelvis of which was illustrated by BARSBOLD (1977: fig. 1:8) — clearly displays a posteriorly directed pubis, hardly differing from the reconstruction of the *Archaeopteryx* pelvis presented by WALKER (1977: fig. 13).

The list of "avian" characters of the coelurosaurians (*sensu* OSTROM, *l. c.*) has been further supplemented since OSTROM's papers on the origins of birds were published. These characters are: the presence of a V-shaped bone in the shoulder girdle in *Oviraptor* (BARSBOLD 1976) which may be compared with the bird furcula, the strong pneumatisation of skull bones, and shortening of the oflactory lobes in *Oviraptor* (OSMÓLSKA 1976). The fusion within the tarsometatarsus in *Elmisaurus* and in the theropod gen. et sp. indet. described above should also be added to this list.

Table 3

Fused tarsometatarsi in theropod dinosaurs as compared with *Archaeopteryx lithographica*

Taxon/coll. number of specimen	Distal tarsals	Metatarsals	Stratigraphic age	Familial assignment
1. *Syntarsus rhodesiensis* QVM QG/1	2 and 3 — fused with each other and with Mts II, III; 4 — free;	II and III — fused proximally; IV — free;	Upper Triassic	Podokesauridae
2. *Ceratosaurus nasicornis* USNM 4735	only one preserved, free;	II, III, IV — fused medially; pathology caused by healed injury (?);	Upper Jurassic	Ceratosauridae
3. *Elmisaurus rarus* ZPAL MgD-I/172;/20	3 and 4 — fused with each other and with Mts II, III, IV;	II, III, IV — fused proximally; fusion between II and III stronger than between III and IV;	Upper Cretaceous	Elmisauridae fam. n.
4. Theropod gen. et sp. indet. ZPAL MgD-I/85	3 and 4 — fused with each other and with Mts. II, III, IV;	II and IV — fused proximally; III — fused with II and IV, but not reaching proximal articular surface;	Upper Cretaceous	?
5. *Archaeopteryx lithographica* Maxberg specimen	one or two fused with each other and possibly with Mts. III and IV;	II, III, IV — fused proximally;	Upper Jurassic	Archaeopterygidae

The formation of the tarsometatarsus in theropods mentioned here is reminiscent of this in *Archaeopteryx* (HELLER 1960), where it was considered by OSTROM (1976: 121) as the only avian character of the metatarsus. According to the reconstructions of *Archaeopteryx* by WELLNHOFER (1974), and OSTROM (1976), metatarsal III is not wedged proximally between the adjoining metatarsals in *Archaeopteryx*; thus, in this respect, the *Archaeopteryx* foot is closer to the Upper Triassic podokesaurid *Syntarsus* and to the Cretaceous dromaeosaurids than to those in the saurornithoidids and the elmisaurids, despite of the bird-like fusion of the tarsometatarsus occurring occasionally in this latter family.

In summary, the tendency toward a more or less complete fusion within the metapodium existed in different theropod lines of the coelurosaurian clade and it was evident as early as the Late Triassic. Thus, it was not avian but theropod acquisition, which may have been inherited, developed and further perfected in birds on a broader scale.

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EXPLANATION OF THE PLATES 20 AND 21

PLATE 20

Elmisaurus rarus gen. et sp. n.

Upper Cretaceous, Nemegt Formation, N Nemegt, Nemegt Basin, Gobi Desert, Mongolia

1a. Fragmentary right manus in dorsal view; ZPAL MgD-I/98.
1b. The same in palmar view.
2a. Proximal portion of the right tarsometatarsus in anterior view; ZPAL MgD-I/20.
2b. The same in plantar view.

Theropod gen. et sp. indet.

Upper Cretaceous, Nemegt Formation, N Nemegt, Nemegt Basin, Gobi Desert, Mongolia

3a. Proximal portion of the left tarsometatarsus in anterior view; ZPAL MgD-I/85.
3b. The same in plantar view.

All stereo-photographs, × 0·5

PLATE 21

Elmisaurus rarus gen. et sp. n.

Upper Cretaceous, Nemegt Formation, N. Nemegt, Nemegt Basin, Mongolia

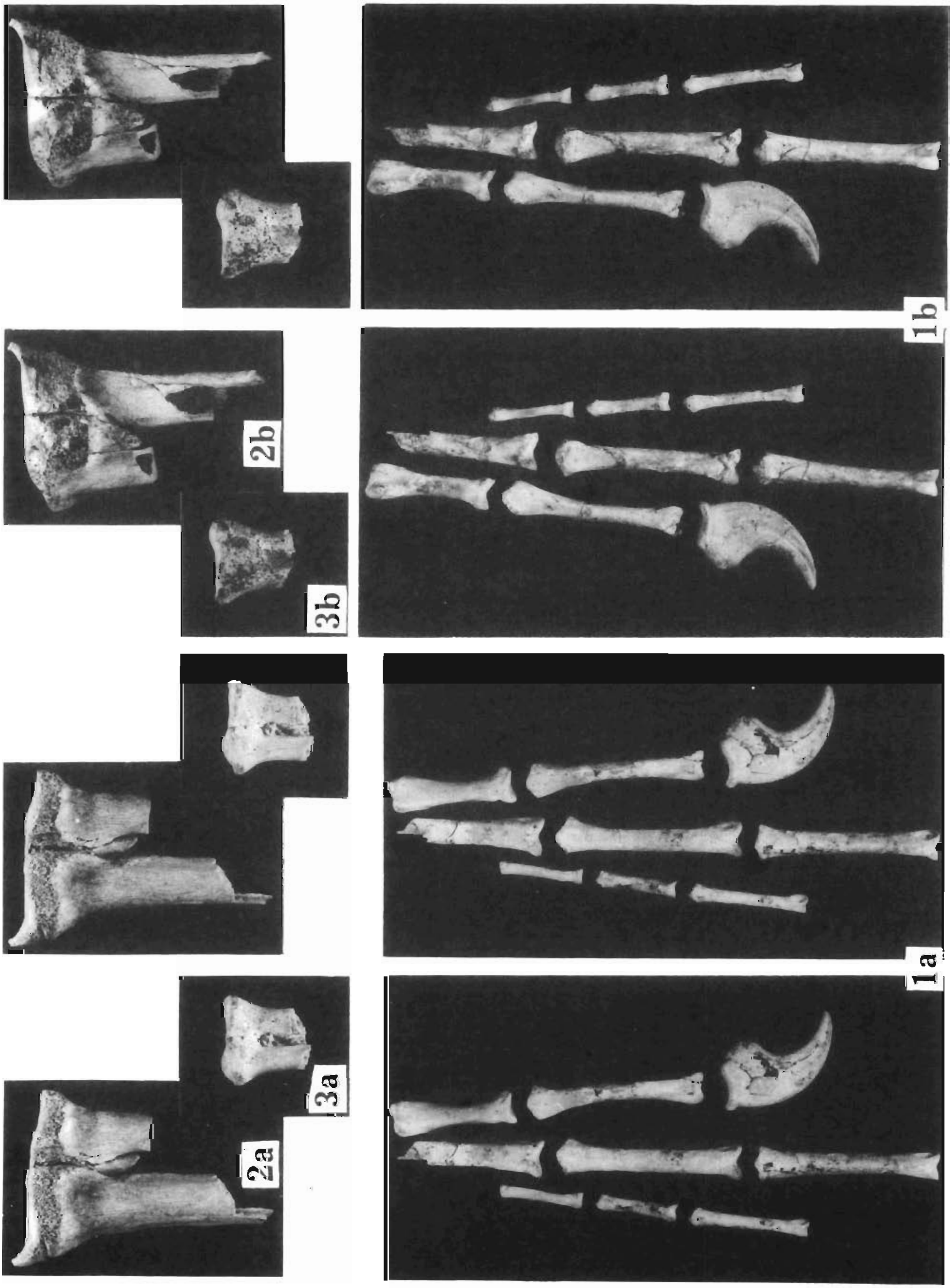
1a. Left tarsometatarsus in anterior view; ZPAL MgD-I/172, holotype.
1b. The same in plantar view.
2. Proximal articular surface of the right tarsometatarsus; ZPAL MgD-I/20.
3a. Fragmentary right pes in anterior view; ZPAL MgD-I/98.
3b. The same in plantar view.

Theropod gen. et sp. indet.

Upper Cretaceous, Nemegt Formation, N Nemegt, Nemegt Basin, Gobi Desert; Mongolia

4. Proximal articular surface of the left tarsometatarsus; ZPAL MgD-I/85, × 1.

All stereo-photographs, × 0·5, except for 4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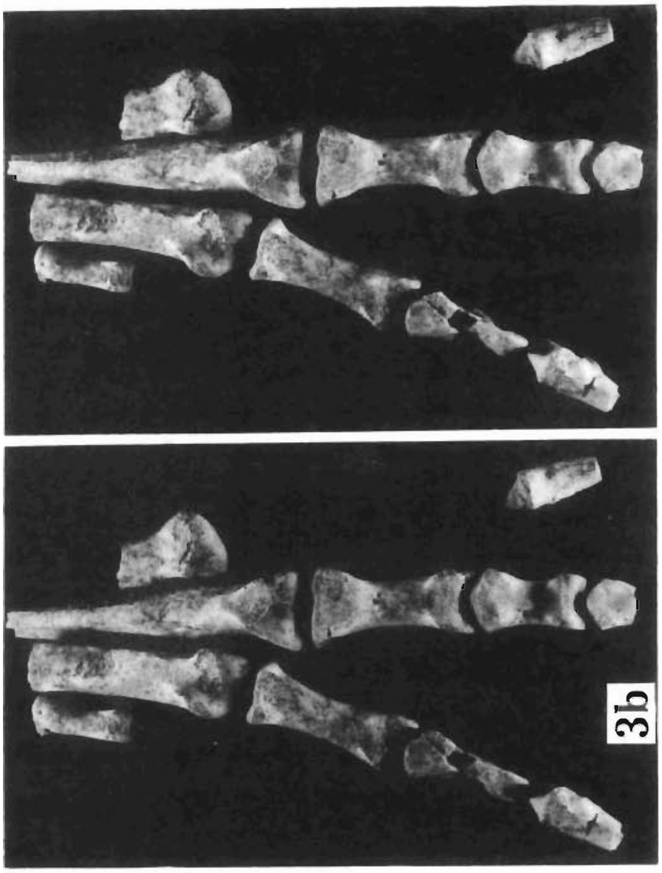
1a
3a
2a


1b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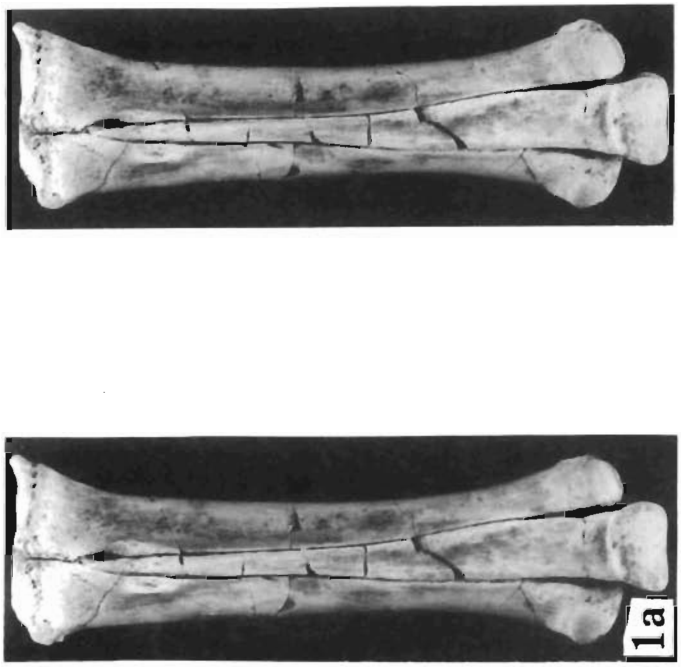
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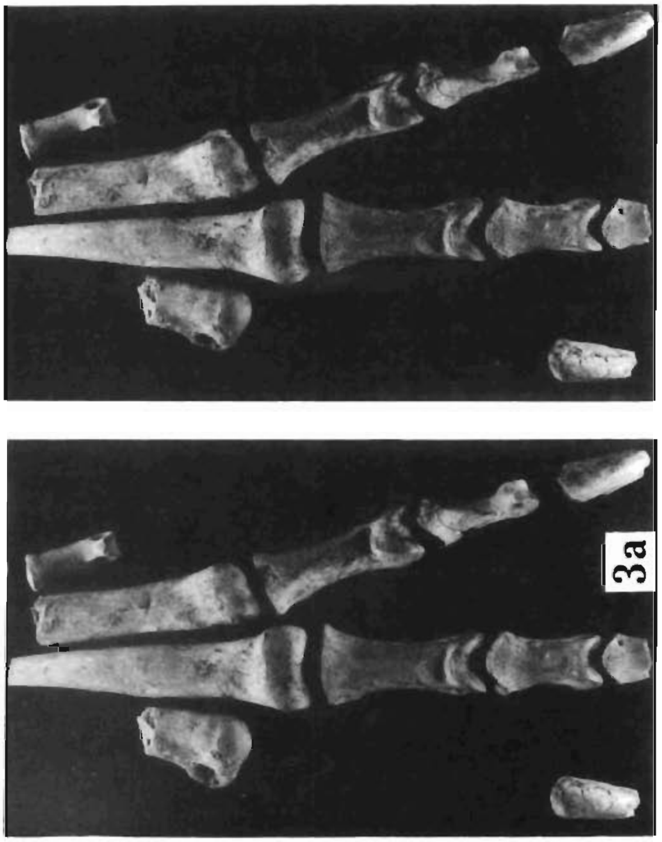
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