New elmisaurine specimens from North America and their relationship to the Mongolian *Elmisaurus rarus*

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New specimens from Canada confirm the presence of elmisaurines in North America and shed light on the relationship of *Leptorhynchos elegans* to Mongolian forms. These specimens have hindlimb elements previously unknown from elmisaurines in the Dinosaur Park Formation, including tibiae and pedal phalanges. Metatarsal anatomy is sufficiently different to merit a generic distinction from *Elmisaurus rarus*, and both can be distinguished from *Caenagnathus collinsi* and *Chirostenotes pergracilis*. Differences between these taxa include body size, degree of coossification of the tarsometatarsus, and development of cruciate ridges of the metatarsal III. Histological analysis confirms that these differences are not correlated with ontogenetic age of the specimens. The results support the informal separation of caenagnathids based on metatarsal structure, and allow comments on paleobiological differences between caenagnathids and oviraptorids.

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Introduction

The first caenagnathid remains discovered in North America were a pair of hands described by Gilmore (1924). Although Gilmore suggested that they were ornithomimid in nature, Osborn (1924) noticed that they were similar to those of *Oviraptor philoceratops* Osborn, 1924. More unusual "ornithomimid-like" material was identified by Sternberg (1932) and Parks (1933). Sternberg (1940) described an edentulous mandible he attributed to Aves, as a new order "Caenagnathiformes". Only much later (Osmólska 1976) would it be established that all of these fossils are oviraptorosaurian. Osmólska (1981) then described *Elmisaurus rarus* Osmólska, 1981, based on three specimens collected by the Polish-Mongolian Paleontological Expedition in 1970. She noted that there were similarities between *Chirostenotes pergracilis* Gilmore, 1924 and *Macrophalangia canadensis* Sternberg, 1932 and suggested that they might be synonymous. She also speculated that *Elmisaurus rarus* was closely related but distinct from *Chirostenotes pergracilis*, based on the fusion of the metatarsals. Currie and Russell (1988) demonstrated that *Chirostenotes* and *Macrophalangia* were, in fact, synonymous, based on a skeleton with a ma-

nus and pes. Currie (1989), prompted by the discovery of a fused proximal metatarsus in Dinosaur Provincial Park, reexamined the material described by Parks (1933) and expanded the range of elmisaurines to North America. Further work by Currie et al. (1993) and Sues (1997) established that *Chirostenotes pergracilis* was closely related to *Caenagnathus collinsi* (Sternberg, 1940), but distinct from the Mongolian *Elmisaurus rarus*.

Many specimens have been collected in Dinosaur Provincial Park (Alberta, Canada) that are almost indistinguishable anatomically from the Mongolian *Elmisaurus rarus*, although the North American tarsometatarsi are more gracile. They were referred to as *Elmisaurus elegans* (Parks, 1933) by Currie (1989, 1990, 1997). Sues (1997) subsumed "*Elmisaurus*" *elegans* into *Chirostenotes*, as a separate species, *Chirostenotes elegans*, and included material from "*Caenagnathus sternbergi*" in this species. Varricchio (2001) described MOR 752, a partial left foot from the Hell Creek Formation of Montana, and referred it to *Elmisaurus elegans*, rejecting the synonymy of Sues (1997). Sullivan et al. (2011) reevaluated ROM 43250 and placed it in its own genus, *Epichirostenotes* Sullivan, Jasinski, and Van Tomme 2011. They did not comment on the status of the "*Elmisaurus*" *elegans* material from

Dinosaur Provincial Park, but did note that the synonymy with *Chirostenotes* by Sues (1997) was tenuous. Questions remain, therefore, regarding whether *Elmisaurus* is present in North America, and the relationship between *Chirostenotes* and *Elmisaurus*.

Recently, Longrich et al. (2013) suggested that "*Elmisaurus*" *elegans* material was sufficiently distinct from *Elmisaurus rarus* to erect a new genus, *Leptorhynchos*. A reevaluation of undescribed material from the Dinosaur Park and Frenchman Formations, presented here, confirms this suspicion. Although there are enough differences between *Elmisaurus rarus* and "*Elmisaurus*" *elegans* to justify the establishment of a new genus for the latter, Longrich et al. (2013) made ROM 781 (a tarsometatarsus that has none of the characters included in the diagnosis) the holotype. It is questionable whether the tarsometatarsus of the holotype can be associated with the dentaries that were used to establish the diagnosis. Furthermore, Longrich et al. (2013) used the smaller sizes of the mandibles to associate them with ROM 781, but some elmisaurine metatarsi are comparable in size to *Chirostenotes* (Table 1). Although it is conceivable that *Leptorhynchos* may be a nomen dubium, this name was not replaced in this paper with another generic name that would add to the confusion that has already existed for more than half a century. All specimens that have been previously referred to the species "*Ornithomimus*" *elegans* (Parks 1933), "*Elmisaurus*" *elegans* (Currie 1989, 1990, 1997; Varricchio 2001), and "*Chirostenotes*" *elegans* (Sues 1997) will be referred to as *Leptorhynchos elegans* (Parks, 1933), in this paper. However, it is possible that a new generic name may be necessary should a skeleton be discovered with a dentary and metatarsus showing that the association made by Longrich et al. (2013) is incorrect.

Institutional abbreviations.—MOR, Museum of the Rockies, Bozeman, Montana, USA; MPC-D, Mongolian Paleontological Center, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; RSM, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting

Most elmisaurine material from North America comes from the (Upper Campanian) Dinosaur Park Formation of Alberta. The Dinosaur Park Formation is characterized by sandstone and mudstone rocks, but the sedimentological provenance of the specimens described here is not known. Other formations that have produced elmisaurine material are the Hell Creek Formation (Upper Maastrichtian) of Montana and the Frenchman Formation (Upper Maastrichtian) of Saskatchewan.

Table 1. Measurements (in mm) of elmisaurine and caenagnathine metatarsi from Campanian–Maastrichtian of Canada. *, width refers to transverse (mediolateral) breadth, and depth refers to anteroposterior thickness; e, estimated; MT, metatarsal; P, pathological.

Taxon	*Leptorhynchos elegans*				*Chirostenotes pergracilis*		*Elmisaurus rarus*	
Specimen	TMP 1982.016.0006	TMP 1993.036.0181	TMP 1996.012.0141	TMP 2000.012.0008	CMN 8538	TMP 1979.020.0001	MPC-D 102/006	MPC-D 102/007
Length of tarsometatarsus	178	250e	150e	185e	230e	207e	182.7	170e
Transverse width of proximal tarsometatarsus	48.5	50	35.7	–	56	–	58.5	–
Length of MT II	152.4	221	130e	164.8	205	181	171.9	159.3
Length of MT III	172.2	–	–	185.3	230	207	182.7	–
Length of MT IV	160.5	220	135e	–	212	186	175.7	161.9
Length of MT V	44.3	–	-	–	60	–	69.5	–
Minimum shaft width* of MT II	8.4	P	12.1	11.0	–	–	11.7	10.8
Maximum shaft width of MT III	12.5	–	-	14.1	35	–	17.1	13.6
Minimum shaft width of MT IV	11.4	P	11.6	–	–	–	9.3	10.5
Condyle width of MT II	13.6	18.7	13.7	16.6	–	–	16.6	16.9
Condyle width of MT III	16.2	–	–	19.8	–	–	23.3	19.4
Condyle width of MT IV	15e	17.0	15.3	–	–	–	17.1	19.0
Condyle depth* of MT II	16.5	–	15.1	16.4	–	–	22.9	19.2
Condyle depth of MT III	15.9	–	–	18.0	–	–	22.9	19.1
Condyle depth of MT IV	14e	–	15.3	–	–	–	22.0	15.5
Proximal width of MT II	20.3	23.2	16.3	18.8	–	–	26.0	23.6
Proximal width of MT III	–	–	–	5.9	–	–	13.7	–
Proximal width of MT IV	19.8	25.5	18.6	–	–	–	23.7	24.1
Proximal depth of MT II	14.6	–	17.2	30.2	–	–	36.6	27.9
Proximal depth of MT III	–	–	–	17.44	–	–	23.0	–
Proximal depth of MT IV	15.5	–	17.0	–	–	–	32.8	24.1

Material and methods

There are more than a dozen North American specimens that are currently referable to Elmisaurinae. All of the material is excellently preserved, but it varies in terms of crushing and completeness. Much of the material represents isolated single or compound elements (i.e., fused tarsometatarsi), but one specimen (TMP 2000.012.0008) includes multiple associated elements. Most of the specimens are partial tarsometatarsi that include more than one metatarsal, but some include additional skeletal elements. In specimens where the proximal part of the tarsometatarsus is present, it invariably shows fusion between distal tarsals III and IV, which in turn are coossified with metatarsals II, III, IV, and sometimes V. Distal tarsal IV has a hook-like posterodorsal process that contacts and fuses with metatarsal V, although this is broken on some specimens. In all of these respects, the North American metatarsi are nearly indistinguishable from the Mongolian *Elmisaurus rarus* (Osmólska 1981; Currie et al. 2016).

UALVP 55585 was stabilized via resin impregnation using Buehler EpoThinlow-viscosity resin and hardener under a vacuum. A thin section was prepared petrographically to a thickness of 230 μm and polished using CeO_2 powder. The section was examined and photographed in detail on a Nikon Eclipse E600POL trinocular polarizing microscope with an attached Nikon DXM 1200F digital camera. A scan of the whole slide was taken with a Nikon Super Coolscan 5000 ED. All specimens were documented through observation, photographs, and measurements. Histological measurements were taken using ImageJ 1.40g. Other measurements were taken with digital calipers or with measuring tape if greater than 150 mm.

Systematic paleontology

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Oviraptorosauria Barsbold, 1976

Caenagnathoidea Sternberg, 1940

Caenagnathidae Sternberg, 1940

Elmisaurinae Osmólska, 1981

Leptorhynchos Longrich, Clark, Barnes, and Millar 2013

Type species: *Leptorhynchos gaddisi* Longrich, Clark, Barnes, and Millar 2013; Aguja Formation (Campanian), Terlingua, Texas.

Leptorhynchos elegans (Parks, 1933)

Figs. 1–7, 9–10.

Holotype: ROM 781, partial tarsometatarsus; complete left metatarsals II and IV and partial metatarsal III, partial distal tarsal III and partial distal tarsal IV.

Type locality: Dinosaur Provincial Park (Little Sandhill Creek), Canada.

Type horizon: Dinosaur Park Formation (Campanian).

Material.—Specimens from Hell Creek Formation (Upper Maastrichtian): MOR 752, a partial left foot including a fragment of the astragalus, a partial metatarsal II, an unidentified metatarsal fragment, the distal end of phalanx II-1, phalanx II-2, and complete digits III and IV (MOR locality HC-147, sec. 32, T16N, R56E, Dawson County Montana, USA); TMP 1996.005.0012, distal end of metatarsal III (near Jordan, Montana, USA.

Specimens from Dinosaur Park Formation (Campanian), Dinosaur Provincial Park, Canada: ROM 37163, distal portion of left metatarsal II (collected between 1920 and 1954 by a joint University of Toronto—Royal Ontario Museum expedition); TMP 1982.016.0006, complete right tarsometatarsus (coossified), including metatarsal V (Wolf Coulee, legal subdivision 12, section 13, township 20, range 10, west of the 4th Meridian); TMP 1982.039.0004, proximal end of right tarsometatarsus (legal subdivision 2, section 4, township 21, range 11, west of the 4th Meridian); TMP 1984.163.0036, distal end of metatarsal III (legal subdivision 12, section 3, township 22, range 10, west of the 4th Meridian); TMP 1986.036.0186, distal end of metatarsal III (UTM 12U; E 471,850, N 5,624,260, WGS84); TMP 1988.036.0104, distal half of metatarsal II (UTM 12U 0455600; 5628640); TMP 1993.036.0181, partial tarsometatarsus including fused distal tarsals, and metatarsals II and IV (legal subdivision 12, section 33, township 20, range 11, west of the 4th Meridian); TMP 1993.036.0630, distal end of metatarsal III (TMP Locality L0418, Bonebed BB112); TMP 1994.012.0880, left tibia (300 m East of BB042, 10 m higher in section); TMP 1996.012.0141, left tarsometatarsus, including fused distal tarsals and proximal ends of metatarsals II, III, and IV, most of the shafts of metatarsals II and IV, and distal ends of metatarsals II and IV (bonebed BB047, TMP Locality L0047, section 31, township 20, range 11, west of the 4th Meridian); TMP 2000.012.0008, partial right foot including metatarsals II and III, phalanges II-1, III-1, III-2, III-3, and IV-? 3 (Iddelsleigh region, UTM 12U; E 473,277, N 5,623,497, WGS84); TMP 2005.049.0190, right metatarsal III (UTM 12U; E 459,250, N 5,629,544, WGS84); UALVP 55585, distal shaft of metatarsal III used for thin-sectioning (BB038A).

Description.—TMP 1994.012.0880: A crushed left tibia (Fig. 1) is similar to those of *Elmisaurus rarus* (Currie et al. 2016), but there are some differences. The tibia is 280 mm long, shorter than that of MPC-D 102/007 (*Elmisaurus elegans*), but still more gracile than those of oviraptorids. The cnemial crest is laterally deflected, with a deep incisura tibialis separating it from the fibular condyle. The fibular crest has a rugose posterolateral surface, with a shallow groove for the interosseum tibiofibular ligament. There is a foramen at the distal base of this groove, as in *Elmisaurus rarus, Ingenia yanshini* Barsbold, 1981, and *Khaan mckennai* Clark, Norell, and Barsbold, 2000 (Balanoff and Norell 2012). The ante-
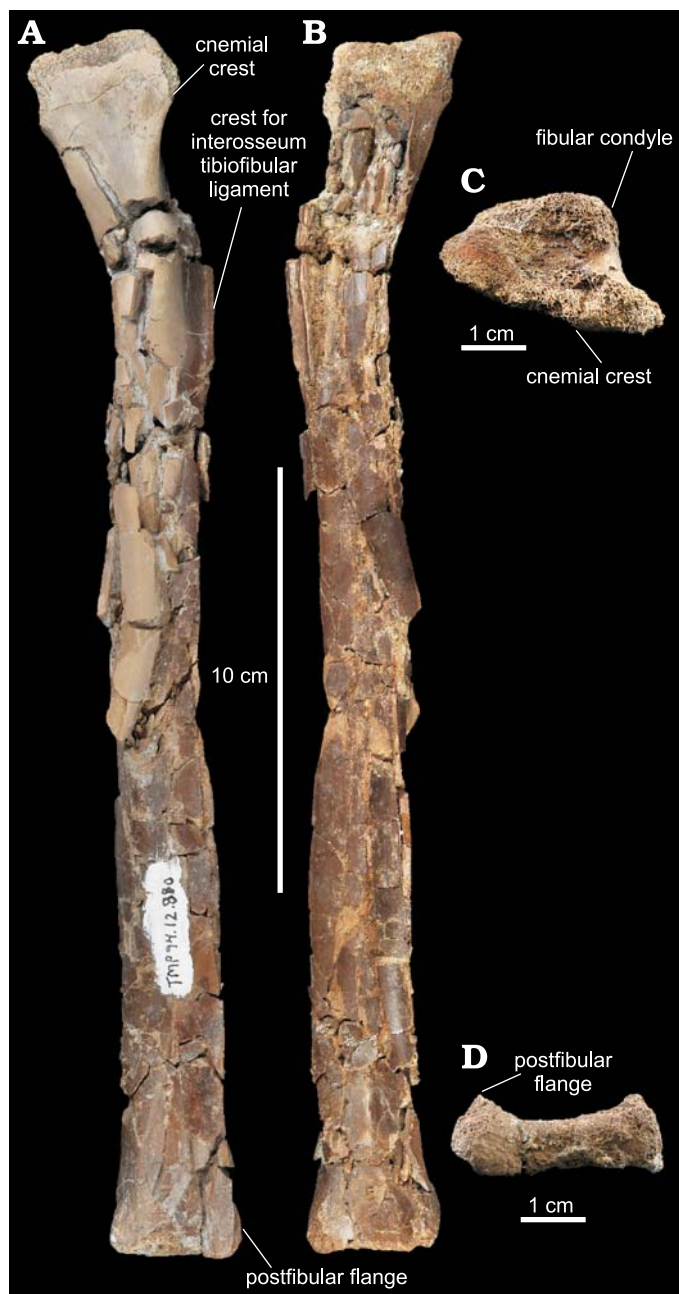
Fig. 1. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) (TMP 1994.012.0880) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. Left tibia in anterior (**A**), posterior (**B**), proximal (**C**), and distal (**D**) views.

rior surface of the shaft is flat, and the posterior surface is curved, resulting in a semi-circular shaft in cross section. The distal condyles are worn, especially the lateral (fibular) condyle, which nevertheless has a prominent postfibular flange (Fig. 1A, D). The contact with the ascending process of the astragalus is slightly concave mediolaterally.

ROM 781: The holotype for *Leptorhynchos elegans* (Fig. 3C), has been described in detail (Parks 1933; Currie 1989), so only salient details will be noted here. The metatarsus is small but well fused, leading Currie (1989) to infer that it was a mature specimen of a small taxon. The meta-

tarsus approaches arctometatarsalian form, with metatarsal III pinched between metatarsals II and IV. Only the most proximal part of metatarsal III is obscured in anterior view by the contact of metatarsi II and IV. The posterior (palmar) surface of metatarsal III has two longitudinal (cruciate) ridges that extend most of the height of the bone and are separated by a longitudinal sulcus. The distal articular end extends onto the posterior surface as a pair of ridges. The medial one becomes less pronounced proximally until it crosses the back of the metatarsal to become continuous with the lateral cruciate ridge. The lateral ridge from the distal articulation crosses to the medial side to meet the ventral end of the medial cruciate ridge. The intersecting "X" shape (Fig. 4) is more distinct in *Leptorhynchos elegans* than in *Elmisaurus rarus*, but this distinctive feature is not present in *Chirostenotes* (TMP 1979.020.0001). It is also absent in all of the oviraptorids examined in the collections of the Mongolian Paleontological Center (GFF, PJC personal observations). These ridges, and the medial and lateral facets they demarcate, indicate a closer association between metatarsals II and III than between metatarsals III and IV. There is a prominent faceted posteromedial ridge on metatarsal II, which gives the metatarsus a posteriorly concave outline in cross section (Fig. 2); the distal part of this ridge likely contacted metatarsal I. This posteromedial ridge is absent in *Caenagnathus collinsi* (Funston et al. 2015) and is poorly developed in *Chirostenotes pergracilis* (Currie and Russell 1988). Metatarsal IV of ROM 781 has a rugose posterolateral ridge, and a sharp anteromedial ridge. The latter ridge is variably present in other elmisaurine specimens from the Dinosaur Park Formation. Distal tarsal IV is fused to the proximal surface of metatarsal IV, and its lateral margin is attenuated into a posterodorsal hook-like process. In all respects the tarsometatarsus of ROM 781 is nearly identical to *Elmisaurus rarus* (MPC-D 102/006, ZPAL MgD-I/127). It differs in that the proximal ends of metatarsals II and IV do not coossify as extensively posteriorly, and that the distal part of metatarsal III of ROM 781 does not have the prominent horizontal sulcus seen in MPC-D 102/006 above the distal articulation.

ROM 37163: Metatarsal II assigned by Currie (1989) to *Elmisaurus elegans*, is slightly smaller than ROM 781 but nearly identical otherwise. In place of the medial rugosity on metatarsal II of ROM 781, ROM 37163 has a
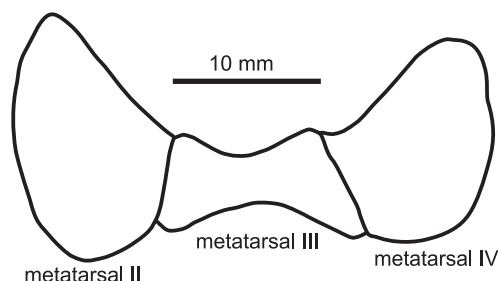

Fig. 2. Cross section demonstrating the deep plantar concavity of the tarsometatarsus of elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) (ROM 781) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada.
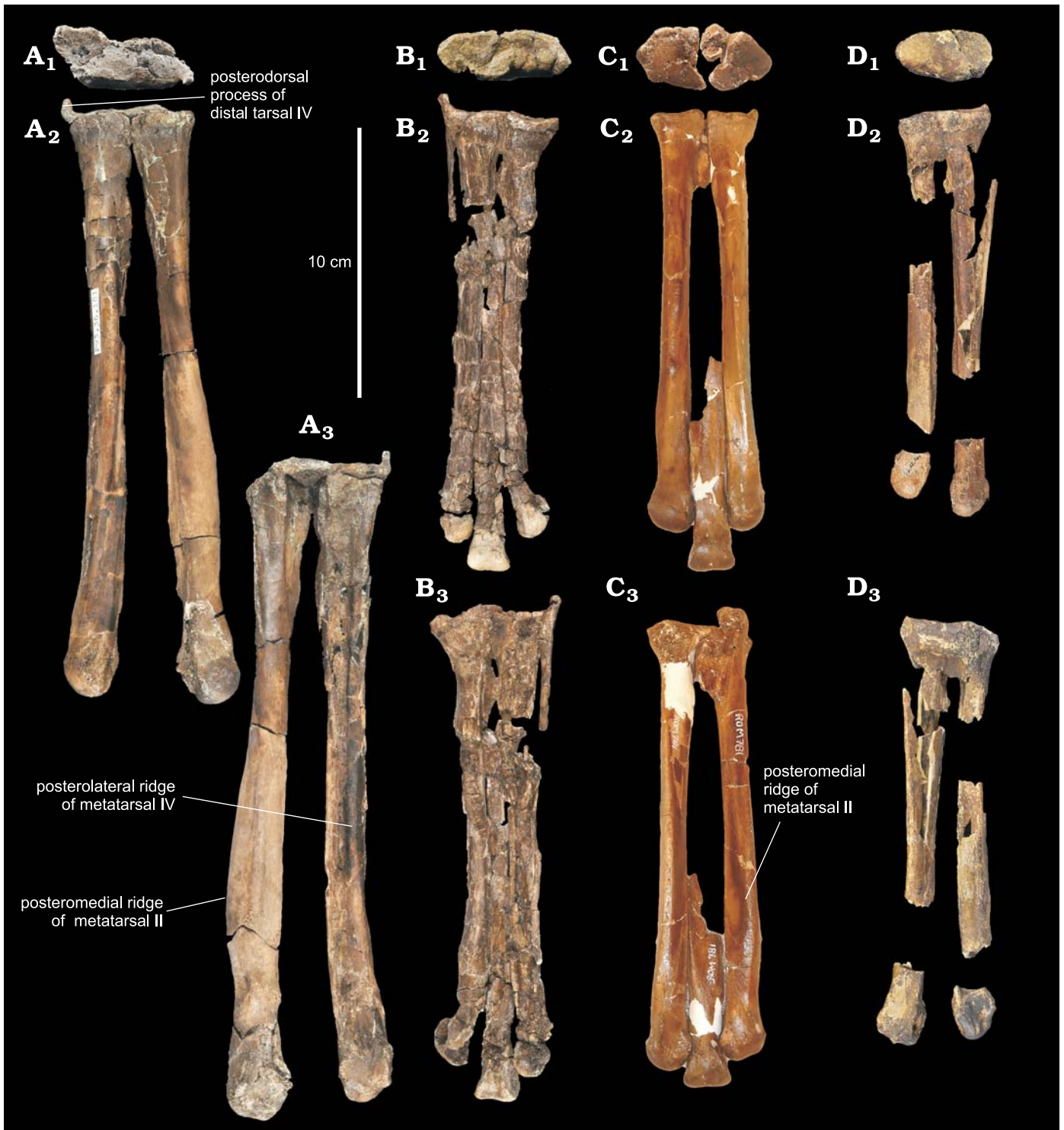
Fig. 3. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. **A**. TMP 1993.036.0181. **B**. TMP 1982.016.0006. **C**. ROM 781. **D**. TMP 1996.012.0141. Tarsometatarsi in proximal (A_1–D_1), anterior (A_2–D_2), and posterior (A_3–D_3) views.

small flange of bone in the same position. This suggests that this is the insertion for the M. tibialis cranialis, which may become stronger and more pronounced with age. In addition, the medial condylar fossa is shallower in ROM 37163 than ROM 781, likely a result of muscle development in older specimens. The posteromedial ridge is strong, as in other elmisaurines, but unlike *Caenagnathus collinsi* and *Chirostenotes pergracilis*. The development of this ridge helps to distinguish elmisaurines from other caenagnathids.

TMP 1982.016.0006: An almost complete right tarsometatarsus that lacks metatarsal I and is somewhat crushed (Figs. 3, 5). It shows that the distinct proximal fu-
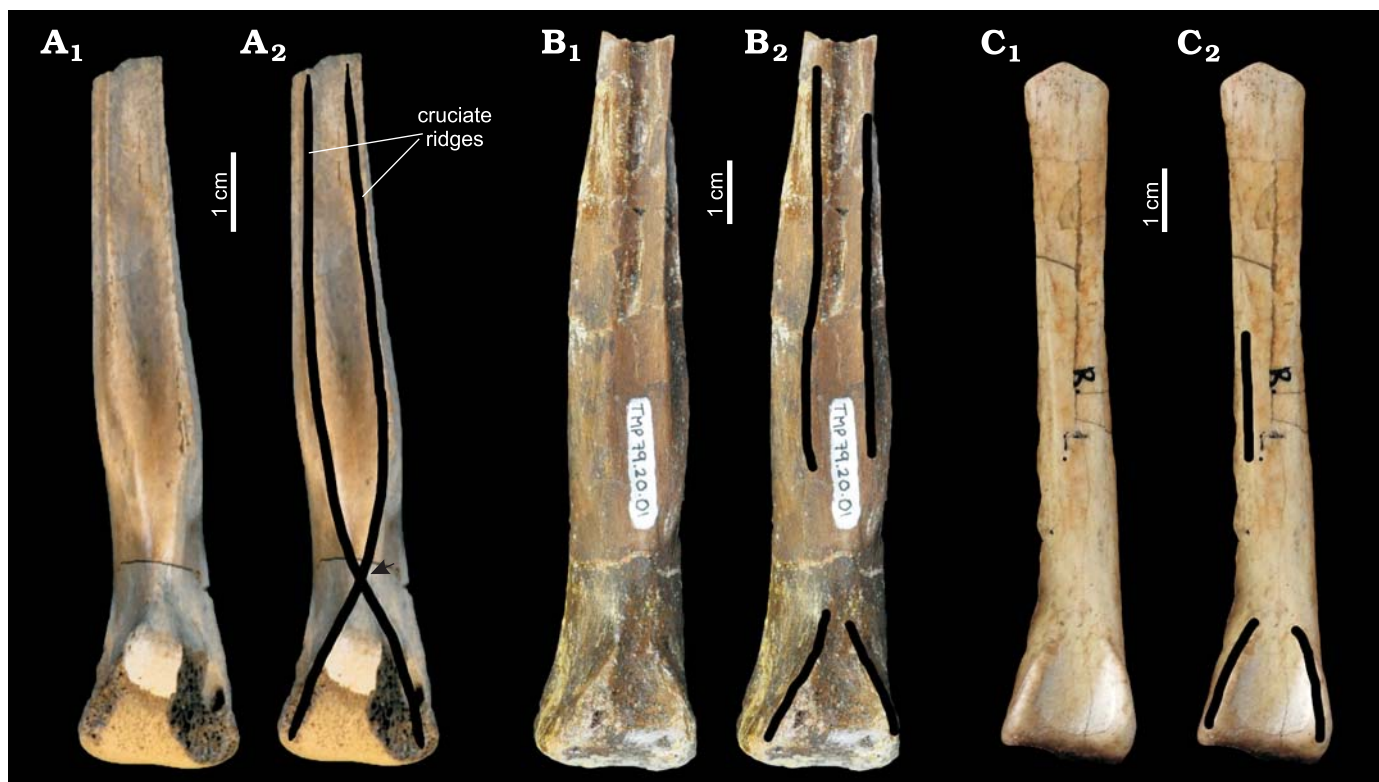
Fig. 4. Posterior surface of metatarsal III in elmisaurine dinosaurs. **A**. *Leptorhynchos elegans* (Parks, 1933) (TMP 1986.036.0186) from Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. **B**. *Chirosenotes pergracilis* Gilmore, 1924 (TMP 1979.020.0001) from Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. **C**. *Ingenia yanshini* Barsbold, 1981 (MPC-D 102/011), provenance unknown: confiscated specimen. Photographs (A_1–C_1), annotated photographs (A_2–C_2), black lines indicate longitudinal ridges; arrow indicates cruciate ridge feature of *Leptorhynchos elegans*.

sion of ROM 781 is not a result of pathology and solidifies the presence of elmisaurines in North America. The distal tarsals are fused to each other and to the proximal face of the metatarsus. Distal tarsals III and IV are fused indistinguishably and cover the proximal surfaces of metatarsals II–IV (Fig. 5A). Distal tarsal IV is arched posterodorsally into a hook-like process (Fig. 5B), which contacts and is fused to metatarsal V. In proximal view (Fig. 5A), the proximal surface of the tarsometatarsus is oval in shape, but wider transversely and narrower anteroposteriorly than in *Elmisaurus rarus*. This is due in part to the lack of the posterior protuberance caused by the coossification of the distal tarsals and metatarsals in *Elmisaurus rarus.*

Metatarsal II of TMP 1982.016.0006 is straight along most of its length (152 mm), but the distal condyle is deflected medially. The proximal end is semi-circular in proximal view, and lacks the posterior protuberance of *Caenagnathus collinsi* (Funston et al. 2015). Near the proximal end of the shaft, there is an oval slit separating etatarsals II and III, but there is no separation between metatarsi III and IV proximal to this region. In *Elmisaurus rarus* there are two holes between the metatarsi: proximally, there is a foramen between metatarsi III and IV, and distal to this point, there is a slit between metatarsi II and III. Currie et al. (2016) suggest that the proximal slit between metatarsi II and III accommodated the a. tarsalis plantaris. It is likely

that in *Leptorhynchos elegans*, the more distal slit between metatarsals II and III played the same role. This suggests that the proximal slit between metatarsal III and IV conducts another artery or vein. As in other elmisaurine specimens, *Velociraptor mongoliensis* Osborn, 1924 (Norell and Makovicky 1997), and *Confuciusornis sanctus* Hou, Zhou, Martin, and Feduccia, 1995 (Chiappe et al. 1999), there is a rugosity on both metatarsi II and IV, for the insertion of the M. tibialis cranialis, on the lateral side of the shaft just proximal to the distal condyle. The posteromedial ridge of metatarsal II bows laterally, probably to accommodate metatarsal I. There is a prominent ridge on the posterior surface of the distal condyle of metatarsal II that extends from the proximal edge of the articular surface.

As in caenagnathines and *Elmisaurus rarus*, metatarsal III of TMP 1982.016.0006 is the longest (172 mm) bone of the foot (Table 1), and the shaft is widest (12.5 mm) about a quarter of its length from the distal end. Proximally, metatarsal III is fused with distal tarsal III, although a distinct suture is still present. Metatarsal III tapers dorsally on the anterior surface, and its proximal end is covered anteriorly by the contact between metatarsals II and IV. There is a horizontal groove on the anterior surface just proximal to the distal articular surface, although it is not as well developed as in MPC-D 102/006. Metatarsal III has nearly symmetrical distal condyles. On the posterior (palmar) surface of

metatarsal III, there are two cruciate ridges that extend most of the height of the bone and are separated by a vertical sulcus that contributes to the deep longitudinal concavity of the tarsometatarsus. On the palmar surface, metatarsal III is thinnest at mid-height but expands dorsally to separate the proximal heads of metatarsals II and IV posteriorly.

The minimum shaft width of metatarsal IV (TMP 1982.016.0006) is wider (11.4 mm) than that of metatarsal II (8.4 mm) in anterior view. Metatarsal IV is straight along its entire length (160 mm). At its proximal end, it is wide (19.9 mm) and fused indistinguishably with distal tarsals III and IV. A well-developed anterior ridge ends just proximal to the distal condyle. Although the posterior (palmar) surface of metatarsal IV is damaged, it appears that it would have had a posterolateral ridge that would have accentuated the concave posterior surface of the tarsometatarsus. The distal condyle of metatarsal IV is rounded but broken.

Metatarsal V (Fig. 5B) of TMP 1982.016.0006 (Fig. 3) is relatively short (44.3 mm) and splint-like, and has an anteriorly deflected distal end. Metatarsal V is straighter along its length in elmisaurines (MPC-D 102/006, TMP 1982.016.0006) than in caenagnathines (Currie and Russell 1988) and other theropods (Currie and Peng 1993). It is fused to the hooklike posterodorsal process of distal tarsal IV, and closely associated but not fused with metatarsal IV proximally.

TMP 1982.039.0004: A fused proximal tarsometatarsus described by Currie (1989). The proximal ends of those metatarsi have coossified and are fused with the distal tarsals. Distal tarsal IV has a hook-like posterodorsal process that would have contacted and fused with metatarsal V. Currie (1989) notes that the shape of the proximal face of the tarsometatarsus has a posteromedial emargination that is not seen in *Elmisaurus rarus*. This emargination is present to a lesser degree in other specimens of *Leptorhynchos elegans* (TMP 1993.036.0181; TMP 1996.012.0141), but it may serve to distinguish *Leptorhynchos* from *Elmisaurus*. This feature is not present in TMP 1982.016.0006, probably because of post-mortem crushing. Posteriorly, between metatarsals III and IV, there is a rounded hole, which probably accommodated the a. tarsalis plantaris. The second slit between metatarsals II and III, which are completely fused, cannot be seen, but it may have been situated more distally.

TMP 1993.036.0181: A pathological partial metatarsus, including metatarsals II and IV and the coossified distal tarsals III and IV (Figs. 3, 6). It is the largest elmisaurine tarsometatarus recovered from Alberta (Table 1), comparable in size with "*Macrophalangia canadensis*" (CMN 8538). Metatarsal II is 221 mm in length, and if the proportions are similar between TMP 1982.016.0006 and TMP 1993.036.0181, the total length of the tarsometatarsus would exceed 250 mm. The shaft of metatarsal II is mediolaterally expanded by a large tuberosity of twisted bone (Fig. 6B, C). Two holes pierce the distal shaft near the tuberosity, one on the medial side oblique to the shaft, and one on the lateral side parallel with the long axis of the shaft. Metatarsal IV is 221 mm long and appears unaffected by the pathology. Distal tarsal III covers
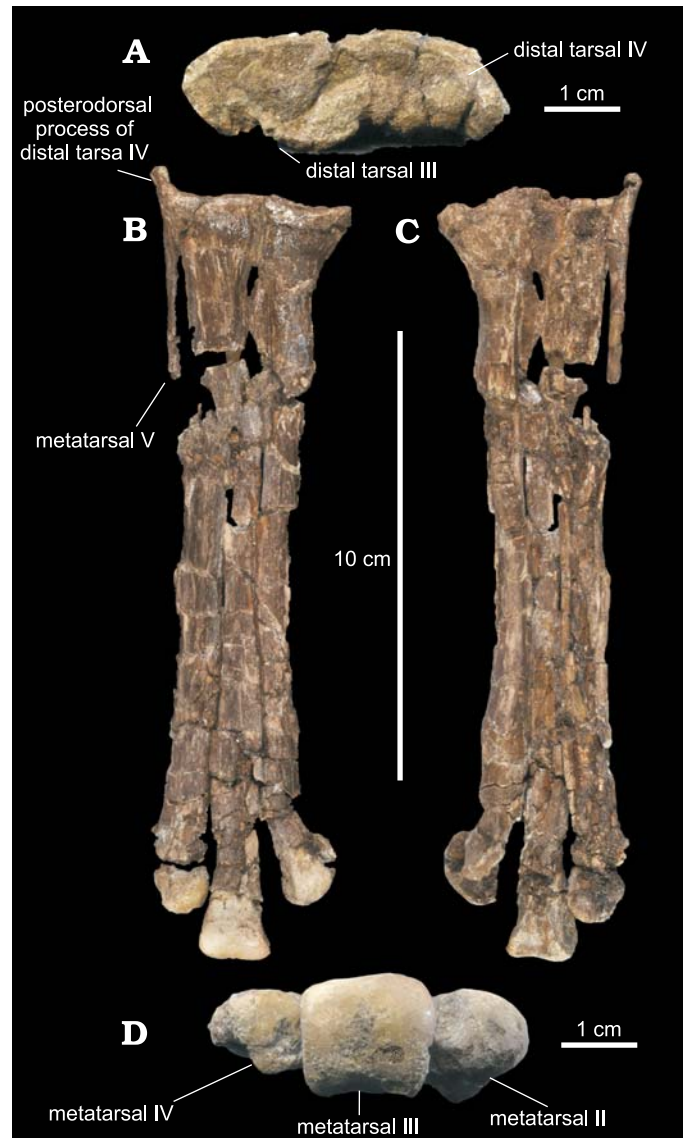

Fig. 5. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) (TMP 1982.016.0006) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. Right tarsometatarsus in proximal (**A**), anterior (**B**), posterior (**C**), and distal (**D**) views.

metatarsals II and IV (Fig. 6A) and is fused to both, although there is a suture between distal tarsal III and metatarsal II. Distal tarsal IV has the posterodorsal process typical of elmisaurines, although metatarsal V is missing, so it is unclear if they were fused. The proximal tarsometatarsus is 50 mm wide transversely, narrower than "*Macrophalangia*" despite the greater lengths of the metatarsi.

The proximal end of metatarsal II is coossified with metatarsal IV but not metatarsal III, as indicated by the clean bone surface on the facet for metatarsal III. The shaft of metatarsal II is pathologically deformed, but the posteromedial ridge is still discernable. The distal condyle is rounded and faces ventrolaterally. The shaft of metatarsal IV has a prominent anterior ridge, separated from the facet for metatarsal III by a groove. The distal condyle faces laterally, and there is a poorly developed scar for the insertion of
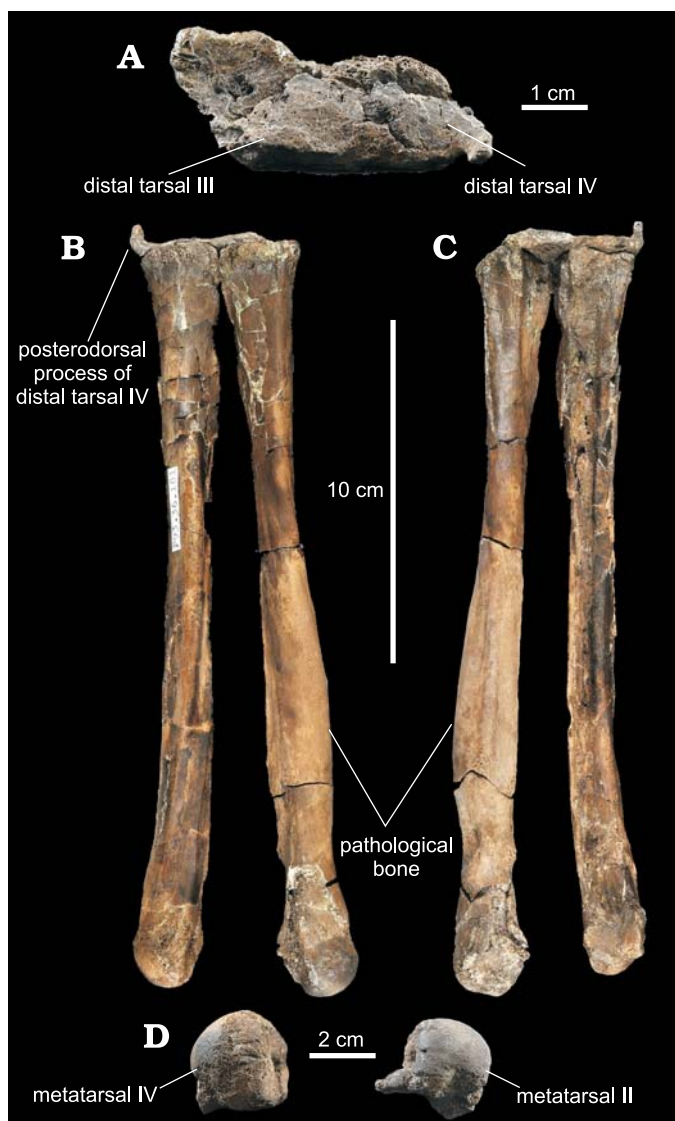
Fig. 6. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) (TMP 1993.036.0181) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. Right tarsometatarsus in proximal (**A**), anterior (**B**), posterior (**C**), and distal (**D**) views.

the M. tibialis cranialis. The proximal end of metatarsal IV (TMP 1993.036.0181) is separated from metatarsal II posteriorly by the wedge-shaped proximal end of metatarsal III, which is missing. These bones apparently had not coossified or fused, as the edge between metatarsals II and IV is natural, despite the great size (>250 mm) of the tarsometatarsus.

TMP 1996.012.0141: Another partial tarsometatarsus (Fig. 3), includes distal tarsals III and IV and metatarsals II, III, IV. The distal tarsals are fused without visible sutures to metatarsals II, III, and IV, and the posterodorsal process of distal tarsal IV is present but worn. Most of the shafts of metatarsals II and IV are preserved, as well as the distal condyles of each. Metatarsal II is fused to distal tarsal III and proximally to metatarsals III and IV, and there is a suture between metatarsals II and III. The shaft of metatarsal II has a well-developed and rugose posteromedial ridge, and a

distinct facet for metatarsal III extends onto the anterior face of the shaft. The distal condyle is rounded and bulbous, and has a distinct lateral rugosity proximal to the distal condyle for M. tibialis cranialis with a medial rugosity opposite it.

Metatarsal III of TMP 1996.012.0141 is preserved only proximally, where it is appressed between metatarsals II and IV, to which it is fused. It is triangular in cross section, but the anterior wedge does not separate metatarsals II and IV anteriorly, as it does in *Elmisaurus rarus*.

Metatarsal IV of TMP 1996.012.0141 is fused indistinguishably with metatarsals II and IV and distal tarsals III and IV at its proximal end. There is a strong anteromedial ridge on the shaft, and a well-developed posterolateral ridge. The shaft is teardrop-shaped in cross section as a result. The distal condyle is gnarled and rugose, with a prominent medial rugosity for M. tibialis cranialis.

TMP 2000.012.0008: A partial foot (Fig. 7), provides information on the pedal anatomy of *Leptorhynchos elegans* that was formerly unknown. The specimen includes partial distal tarsals III and IV, metatarsals II and III, and seven pedal phalanges, including two pedal unguals. As in *Elmisaurus rarus*, distal tarsals III and IV are fused to the proximal ends of metatarsals II and III. Metatarsals II and III are preserved in articulation, although there is a small gap between their shafts that would not have been present in life. The proximal end of metatarsal II is roughly trapezoidal in anterior view where it contacted metatarsal IV in life, and tapers distally in medial view. The facet on metatarsal II for the contact with the expanded distal half of metatarsal III invades the anterior surface of metatarsal II, creating a sharp ridge. A small, triangular sheet of bone adheres to the proximal end of metatarsal II on the medial surface; it also contacts metatarsal III, and possibly distal tarsal III. The identification of this fragment is unknown, and it presumably does not belong in this position. The posteromedial ridge of metatarsal II is well defined and has a flat, rugose facet (Fig. 7B, D). The insertion for the M. tibialis cranialis is visible just proximal to the distal condyle of metatarsal II, as in other elmisaurines. The distal end of metatarsal II is medially inflected to a greater degree than other specimens, but faces ventromedially.

Metatarsal III of TMP 2000.012.0008 is preserved in its entirety, including the proximal end, which tends to break off in isolated specimens. In lateral view, the proximal end of metatarsal III tapers distally, whereas in anterior view it expands distally. Metatarsal III is inclined longitudinally so that its anterior surface is posterior to the anterior surface of metatarsal II for the proximal two thirds of its length, but is anterior to the distal end of metatarsal II (Fig. 7D). Unlike other elmisaurine specimens, the posteromedial ridge of metatarsal III (the medial cruciate ridge) is poorly developed. Instead of a horizontal sulcus on the anterior surface of the bone proximal to the distal condyle, the flat surface of the shaft has two small rugosities marking the insertion of the M. tibialis cranialis. The distal condyle of metatarsal III is symmetrical.
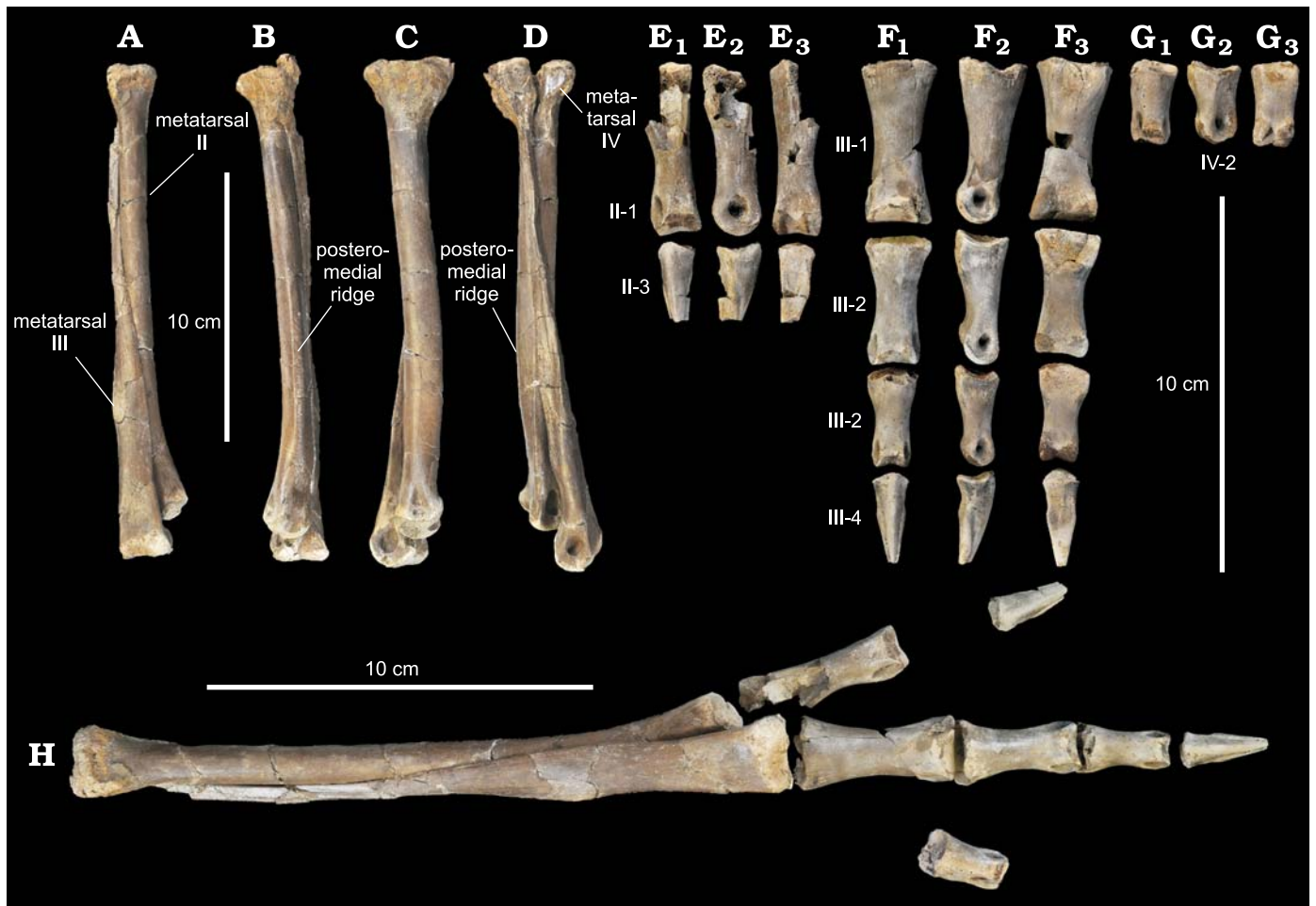
Fig. 7. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) (TMP 2000.012.0008) from Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. Partial foot, articulated metatarsals II and III in anterior (**A**), posterior (**B**), medial (**C**), and lateral (**D**) views. Pedal phalanges of digits II (**E**), III (**F**), and IV (**G**) in dorsal (E_1–G_1), lateral (E_2–G_2), and ventral (E_3–G_3) views. Reconstruction of foot in anterior view (**H**).

The phalanges preserved with TMP 2000.012.0008 (Fig. 7E–G) appear to represent at least a portion of each digit. The distal condyles of all of the phalanges are relatively smaller than those of *Chirostenotes pergracilis* (CMN 1149, CMN 8538) and do not extend dorsally above the margin of the shaft. Digit two (Fig. 7E) has one proximal phalanx and the ungual phalanx, but lacks II-2. Phalanx II-1 is elongate and asymmetrical, with a single ventral ridge and a depression above the distal condyles. The proximal end is damaged, but the bone is longer than III-1. The ungual phalanx (II-3) is long and flat, with a pentagonal proximal articular surface. On the ventral surface there is a fossa bisected by a median protuberance for attachment of the flexor ligaments. The ungual is deflected medially, but the tip is missing.

The third pedal digit of TMP 2000.012.0008 (Fig. 7F) is complete, with four phalanges including a small ungual III-4. Phalanx III-1 is the largest preserved, and is symmetrical mediolaterally. The dorsal surface is flat, although there is a depression proximal to the distal condyles. The proximal articular surface is deeply concave and oval, although the proximal surface extends ventromedially and ventrolaterally (reflecting ridges on the ventral surface of the bone).

Phalanx III-2 is nearly identical in shape and morphology to III-1, except that it is smaller, and the proximal articular surface is semicircular in cross section and lacks the ventromedial and ventrolateral extensions. Pedal III-3 is elongate and symmetrical, but lacks the dorsal depression proximal to the distal condyles. The proximal articular surface is kidney-shaped, with a shallow ventral invagination. The ungual (III-4) is similar to but smaller than II-3, but is not medially deflected. It is long and straight and has a similar ligamentous fossa and protuberance on the ventral surface.

The fourth digit of TMP 2000.012.0008 (Fig. 7G) is represented by a single phalanx. It is neither IV-1 nor IV-4 based on morphology, and the ratio of its length (22.3 mm) to the rest of the phalanges suggests it is IV-2. The proximal end is symmetrical, and the distal end is asymmetrical, with almost no shaft in between.

MOR 752: Varricchio (2001) described a partial foot (MOR 752) from the Hell Creek Formation that he referred to "*Elmisaurus*" *elegans*. The morphology of the foot has been well described, and it shares several features with *Leptorhynchos elegans* from Alberta. Left metatarsal II is about 135 mm long, but the medial side of the proximal end
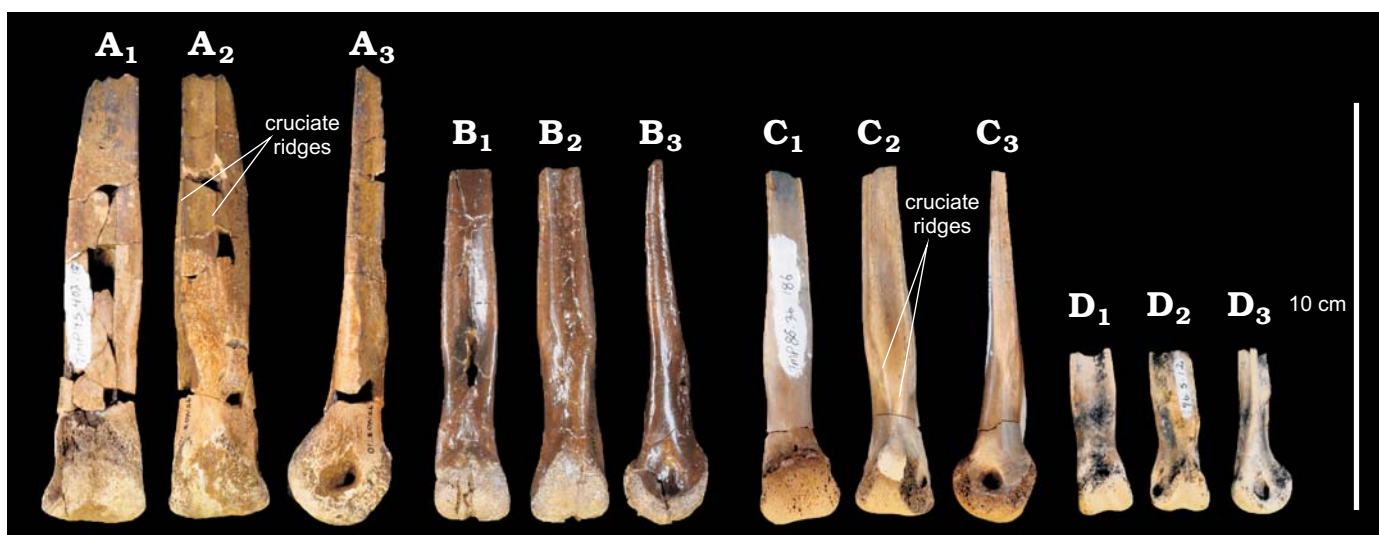
Fig. 8. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. **A**. TMP 1995.403.0010. **B**. TMP 1984.163.0036. **C**. TMP 1986.036.0186. **D**. TMP 1996.5.12. Isolated metatarsals III in anterior (A_1–D_1), posterior (A_2–D_2), and lateral (A_3–D_3) views.

is missing, so its fusion to the rest of the tarsometatarsus cannot be evaluated. The lateral side of the shaft has a facet for metatarsal III and suggests that metatarsal II excluded the third from the anterior surface proximally. Above the distal condyle, there is a rugose knob for M. tibialis cranialis, as in *Leptorhynchos elegans* and *Elmisaurus rarus*. The posteromedial ridge of metatarsal II is not as well developed as in other elmisaurine specimens, but this may be explained by the small size of the specimen. Interestingly, Varricchio (2001) notes that the penultimate phalanges of the third and fourth digits are longer than those immediately proximal to them. This is untrue for *Leptorhynchos elegans* from the Dinosaur Park Formation, as demonstrated by TMP 2000.012.0008, where the penultimate phalanx of the third digit is shorter than the one immediately proximal to it. Varricchio (2001) suggests that the elongation of the penultimate phalanges is an adaptation for a grasping foot, which is therefore less developed in the *Leptorhynchos elegans* from Alberta. Although it is possible that this is evidence against the referral of MOR 752 to *Leptorhynchos elegans*, it is more conservative to include it until it can be definitively separated.

Isolated elmisaur metatarsals: Six isolated metatarsal IIIs (Fig. 8) and one isolated metatarsal II attributable to *Leptorhynchos elegans* have been recovered from North America. Metatarsals III (TMP 1984.163.0036, TMP 1986.036.0186, TMP 1993.036.0630, TMP 1996.005.0012, TMP 2005.049.0190, and UALVP 55585) all include the distal portions of the shafts. Invariably, the shaft is flat anteroposteriorly, and expands mediolaterally towards the distal end. The posterior surface has two cruciate ridges (medial and lateral), which are continuous with the lateral and medial postcondylar ridges (Fig. 4). In each case, the crossing of these ridges forms a chiasmata, distinctive enough to identify them as elmisaurine. Where the distal condyle is present,

it is invariably thicker anteroposteriorly than wide mediolaterally, a feature that distinguishes *Leptorhynchos elegans* from *Elmisaurus rarus* and *Chirostenotes pergracilis*.

One of these metatarsals, UALVP 55585 (Fig. 9), was thin-sectioned to determine its histological age. The specimen represents the distal portion of the shaft, which is anteriorly concave and has well-developed, paired cruciate ridges (Fig. 9C). The minimum transverse shaft width is 11.4 mm, which is intermediate in size compared to other isolated elmisaurine metatarsals III.

The thin-sectioned metatarsal III (Fig. 9D) shows an average relative bone wall thickness (RBT) of 40% of the diameter; however, cortical thickness varies from 0.088 mm at the anterior cortex to 0.267 mm in the anterolateral corners of the cross-section. The cortex exhibits roughly equal quantities of primary fibrolamellar and secondarily remodeled Haversian bone; however, they are not distributed evenly throughout the cortex. The highest proportion of Haversian bone occurs in the thicker anteromedial and anterolateral corners of the cortex. Blood vessel canals in the primary bone show predominantly longitudinal orientations. There is a thin (0.016 mm) region along the periosteal surface of the medial cortex consisting of more highly vascularized primary woven-fibered bone with simple longitudinal blood vessel canals. No cyclical growth marks were observed anywhere in the cortex, including an external fundamental system. An inner circumferential layer, composed of avascular parallel-fibered bone, is present lining the entire wall of the medullary cavity, although it is variable in thickness.

Isolated metatarsal II (TMP 1988.036.0104) has several characters that distinguish it as *Leptorhynchos elegans*. Unfortunately only the distal half is preserved, so it is unclear if the proximal end was fused to the other metatarsals. The facet for metatarsal III invades the anterior face of the shaft, as in other elmisaurines, and there is a distinct
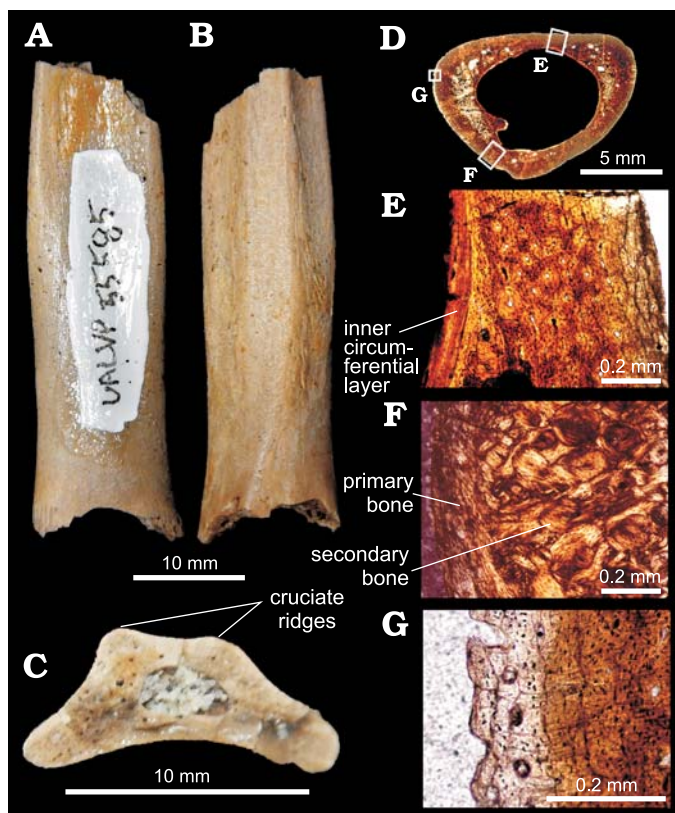
Fig. 9. Elmisaurine dinosaur *Leptorhynchos elegans* (Parks, 1933) (UALVP 55585) from the Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. Metatarsal III in anterior (**A**), posterior (**B**), and cross-sectional (**C**) views. **D**. Full petrographic thin section in proximal cross-sectional view (anterior is up). **E–G**. Details of D. **E**. Thin anterior cortex showing development of the inner circumferential layer. **F**. Posterior cortex showing extent of secondary bone relative to primary bone. **G**. Anteromedial corner showing localized development of highly vascularized periosteal bone. Images in plane-polarized light (D, E, G) and 90° cross-polarized light (F).

lateral rugosity for M. tibialis cranialis, a feature absent in *Chirostenotes*. The distal shaft is deflected anteriorly, and there is a large, well-developed posteromedial ridge with a rugose apex. The strong development of the posteromedial ridge and the rugosity for M. tibialis cranialis are features that appear to be present only in elmisaurines, so they can be used to identify metatarsals II of the group.

Stratigraphic and geographic range.—Upper Campanian Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada, to Upper Maastrichtian Hell Creek Formation, Montana, USA.

Leptorhynchos sp.

Fig. 10

Material.—RSM P2600.1, partial skeleton including? scapula, partial proximal tibia, distal end of left tibia, proximal end of fibula, right astragalocalcaneum, partial left astragalocalcaneum, distal end of metatarsal II, and distal end of metatarsal III. Frenchman Formation (Maastrichtian), Chambery Coulee, Frenchman River Valley, Saskatchewan,

Canada. RSM P2161.1, complete left metatarsal II. Upper Maastrichtian Frenchman Formation, Grasslands National Park, Canada. Collected by Kevin Conlin in 1989.

Description.—The Frenchman Formation material is referable to elmisaurines and is likely congeneric with *Leptorhynchos elegans*. The partial skeleton (RSM P2600.1) is composed mostly of hindlimb elements, including the distal end of a left tibia and some of the metatarsals (Fig. 10). The distal end of the tibia is similar in shape to *Leptorhynchos elegans* from Alberta, but is relatively wider where it contacts the astragalus and calcaneum, which are fused. The astragalocalcaneum lacks a horizontal groove distal to the ascending process and extends far onto the posterior surface of the tibia (Fig. 10A$_2$, A$_4$). The distal condyle of metatarsal II faces ventromedially, and there is a rugosity for M. tibialis cranialis proximal to the condyle. The shaft of metatarsal III is broader transversely than the distal condyle and is anteriorly concave. The posterior surface has two cruciate ridges, as in *Leptorhynchos elegans* and *Elmisaurus rarus*. The facets for the contacts with metatarsals II and IV appear asymmetrical, as in other elmisaurines, and suggest a closer association between metatarsals II and III than metatarsals II and IV. The distal condyle is as mediolaterally wide as it is anteroposteriorly deep, whereas in *Leptorhynchos elegans* from Alberta, it is deeper than wide.

Metatarsal II (RSM P2161.1) from the left foot was recovered from Grasslands National Park in Saskatchewan. The proximal end has a flat posterior surface for the contact with distal tarsal III, which does not appear to have coossified in this individual. The proximal end lacks the posterior process of *Caenagnathus collinsi*, and is nearly identical in shape to *Leptorhynchos elegans* (TMP 1982.016.0006). The shaft, however, is straight and not deflected medially at its distal end, unlike *Leptorhynchos elegans*. There is a large posteromedial ridge on the shaft, as in *Leptorhynchos elegans* and *Elmisaurus rarus*.

Discussion

The inclusion of *Leptorhynchos elegans* in Caenagnathidae is supported by its metatarsal structure, especially the distinctive metatarsal III. Metatarsal III is proximally pinched between metatarsals II and IV, but is visible along its length in anterior view, excluding the proximal end. Metatarsal III is also anteroposteriorly flat, a feature that distinguishes caenagnathids from other oviraptorosaurs, dromaeosaurids, ornithomimids, and tyrannosaurids (GFF personal observation). The tibiae of *Elmisaurus rarus* and *Leptorhynchos elegans* are similar in shape and proportions to those of *Chirostenotes pergracilis* (Currie and Russell 1988), and all three have metapodials more than half as long as the tibia. In oviraptorids, like *Ingenia* (MPC-D 100/030; MPC-D 102/011), the tibiae are shorter and more robust, and the metatarsus is less than half as long as the tibia. Although no

Fig. 10. Elmisaurine dinosaur *Leptorhynchos* sp. from Upper Maastrichtian Frenchman Formation, Saskatchewan, Canada. **A**. RSM P2600.1, distal portion of left tibia and astragalocalcaneum in posterior (A_1), lateral (A_2), and medial (A_3) views; distal portion of right second metatarsal in anterior (A_4) and posterior (A_5) views; distal portion of third metatarsal in anterior (A_6), posterior (A_7), and distal (A_8) views. **B**. RSM P2161.1, left second metatarsal in anterior (B_1), medial (B_2), posterior (B_3), lateral (B_4), distal (B_5), and proximal (B_6) views.

manual material for *Leptorhynchos elegans* has been recovered, the closely related *Elmisaurus rarus* has manual and pedal proportions close to *Chirostenotes pergracilis*, and the unguals are nearly indistinguishable.

Based on metatarsal structure, Caenagnathidae can be divided into two informal groups: elmisaurines (Osmólska 1981) and caenagnathines (Longrich et al. 2013). Elmisaurines currently include only *Elmisaurus rarus* and *Leptorhynchos elegans*, although it is likely that *Caenagnathasia martinsoni* and *Leptorhynchos gaddisi* are representatives as well. Additional postcranial material of *Caenagnathasia martinsoni* and *Leptorhynchos gaddisi* could verify their status in the group. Caenagnathines appear to form the majority of caenagnathids, and include at least *Caenagnathus collinsi* and *Chirostenotes pergracilis*.

Though the monophyly of these groups has yet to be demonstrated phylogenetically, there are a number of features that separate them. Cladistic work is ongoing to evaluate the taxonomic implications of these differences, and will be presented elsewhere (GFF and PJC unpublished material). The most consistent feature distinguishing elmisaurines and caenagnathines is the coossification of the distal tarsals and the proximal metatarsus in the former. Although the coossification is more extensive in *Elmisaurus rarus*, producing a posterior protuberance (Osmólska 1981; Currie et al. 2016), the proximal metatarsus of *Leptorhynchos elegans* is consistently fused to the distal tarsals. The posterodorsal hook of distal tarsal IV in *Elmisaurus rarus* and *Leptorhynchos elegans* is unique among theropods. Furthermore, although presence of the posterodorsal hook of distal tarsal IV cannot be ascertained in *Chirostenotes pergracilis*, in *Elmisaurus rarus* and *Leptorhynchos elegans*, it fuses to metatarsal V. Combined with the curvature of its shaft, the dissociation of metatarsal V from the rest of the metatarsus in *Chirostenotes pergracilis* (TMP 1979.020.0001 and CMN 8538) suggests that it did not fuse to distal tarsal IV. The metatarsi of elmisaurines are also distinct from caenagnathines proportionally. Whereas most oviraptorosaurs have broad, flat metatarsi, in elmisaurines the metatarsi are elongate, so the average tarsometatarsus length is 6.25 times the minimum transverse width of the metatarsus. Caenagnathines have similarly elongate metatarsi, but the average length is only 4.55 times the minimum transverse width of the metatarsus, shorter than elmisaurines. Despite this, both groups have relatively longer tarsometatarsi (3.57 times as long as wide) than those of oviraptorids. In terms of isolated metatarsi, *Leptorhynchos elegans* can be distinguished from *Chirostenotes pergracilis* based on several features. In *Leptorhynchos elegans*, the shaft of metatarsal II has a well-developed posteromedial ridge that extends posteriorly beyond the extent of the distal condyle. The lateral facet for metatarsal III wraps around onto the anterior surface of the shaft, and distal to this there is a rugosity for M. tibialis cranialis. The posterior surface of metatarsal III has two cruciate ridges, instead of one longitudinal ridge. The anterior surface often bears a longitudinal sulcus in ad-

dition to the one on the posterior surface. The distal condyle is deeper than wide, which is the opposite of *Elmisaurus rarus* and *Chirostenotes pergracilis*. The development of the rugosity for M. tibialis cranialis is variable, but proximal to the distal condyle there is always at least one rugose area. Metatarsal IV has a large posterolateral ridge. There is also often an anteromedial ridge on the anterior surface, although its development is variable. Neither of these ridges is present in *Chirostenotes pergracilis* to the same extent as *Leptorhynchos elegans*. Similar to metatarsals II and III, there is a rugose knob proximal to the distal condyle on metatarsal IV.

Within elmisaurines, there are a number of features that distinguish *Elmisaurus rarus* from *Leptorhynchos elegans*. As pointed out by Longrich et al. (2013), these taxa merit distinction at the generic level. The North American *Leptorhynchos elegans* tarsometatarsi are longer than those of *Elmisaurus rarus* but are more gracile. The posterior extension of the proximal metatarsus is larger in *Elmisaurus rarus*, due to the more extensive coossification of the distal tarsals to the back of the metatarsus. The distal condyles of metatarsal III in *Leptorhynchos elegans* are deeper anteroposteriorly than wide mediolaterally, which is the opposite in *Elmisaurus rarus*. On metatarsal III of *Elmisaurus rarus*, there is rugosity on the distal base of the lateral cruciate ridge, and a small longitudinal ridge that bisects the longitudinal sulcus between the cruciate ridges proximally. Both of these features are absent in *Leptorhynchos elegans*. The most conspicuous difference in the tarsometatarsi of *Elmisaurus* and *Leptorhynchos* is that in *Elmisaurus*, the shaft of metatarsal II is straight distally, and the distal third of the shaft of metatarsal IV curves laterally. The opposite is true in *Leptorhynchos*, where the distal third of the shaft of metatarsal II curves medially but metatarsal IV is straight along its length. The divergence of the metatarsals in both taxa is to accommodate metatarsal III, which is transversely wide distally.

The specimens from the Hell Creek Formation and Frenchman Formation, both Maastrichtian in age, extend the temporal range of elmisaurines in North America. Recently described caenagnathine material from the Frenchman Formation (Bell et al. 2015) established the presence of large caenagnathines in Saskatchewan, but this is the first record of elmisaurine material there. Interestingly, elmisaurines have not yet been recovered from the Horseshoe Canyon Formation, which straddles the Campanian-Maastrichtian boundary and has produced caenagnathine material. This could suggest that elmisaurines preferred only upland environments, whereas caenagnathines occupied both upland and nearshore environments. The presence of both elmisaurines and caenagnathines in the Dinosaur Park, Hell Creek, and Frenchman Formations, however, suggests that they shared similar environments. Alternatively, some "caenagnathine" material from the Horseshoe Canyon Formation may be, in fact, elmisaurine. Despite the excellent preservation of ROM 43250 (*Epichirostenotes curriei*) and TMP

1993.051.0001, neither preserves the tarsometatarsus. The similar manual proportions of *Elmisaurus rarus* in Mongolia and *Chirostenotes pergracilis* in Canada may indicate that elmisaurines and caenagnathines are difficult to distinguish without tarsometatarsi.

Histological sectioning of UALVP 55585 provides some insight on the physiology of caenagnathids. Varricchio (1993) examined three metatarsal III samples for the similarly sized, contemporaneous theropod *Troodon formosus* Leidy, 1856, which he estimated to have reached adult size in 3–5 years. The degree of secondary remodeling in the elmisaurine examined here (UALVP 55585) most closely resembles the subadult or adult *Troodon* metatarsal III; however, the absence of cyclical growth marks is distinctive. In *Troodon*, Haversian substitution began in the cortex well before adult body size was attained (Varricchio 1993). The high degree of remodeling in *Troodon* and UALVP 55585 is unusual among theropods, and more similar to the conditions in sauropods and mammals (Scheyer et al. 2010).

The lack of cyclical growth marks makes it impossible to assess the precise age at death of UALVP 55585 (Fig. 9). The extent of secondary remodeling in the cortex and the presence of an inner circumferential layer, however, suggests that the individual was not a juvenile at the time of death. Nevertheless, the absence of an external fundamental system suggests this was not a skeletally mature adult. The deposition of relatively well-vascularized woven-fibered bone along the medial periosteal surface indicates a localized increase in the deposition rate of bone, possibly in response to ontogenetic load changes or interaction with the adjacent metatarsal.

The new specimens allow us to comment on the paleobiology of elmisaurines. Based on *Elmisaurus rarus* (Currie et al. 2016), the tibia is elongate relative to the femur, which suggests cursorial adaptations. With the long gracile tarsometatarsi in both *Elmisaurus rarus* and *Leptorhynchos elegans*, the distal hindlimb of an elmisaurine would have been more than double the length of the femur. The manus is well adapted for grasping, with long phalanges and robust flexor tubercles on the unguals. The combination of these features suggests that elmisaurines engaged in at least some predation. Although the assignment of mandibles to *Leptorhynchos elegans* by Longrich et al. (2013) is tenuous, some dietary comments can be made. Funston and Currie (2014) suggested that the deep beaks of caenagnathids were suitable for shearing plants and flesh, and the upturned mandibles assigned to *Leptorhynchos* would certainly agree with this interpretation. The relatively short dentaries of *Leptorhynchos elegans* compared to *Anzu wyliei* and *Caenagnathus collinsi* suggest dietary differences. Shorter dentaries allow for a stronger bite but less efficient bite, and the sharply upturned anterior occlusal margin may have facilitated the processing of meat. Combined with clear cursorial adaptations in the hindlimbs, this suggests that elmisaurines may have emphasized predation more than shallow-beaked caenagnathids. Unequivocal

elmisaurine mandibular material is required to verify this hypothesis. This is supported, however, by the presence of *Caenagnathasia martinsoni* Currie, Godfrey, and Nessov, 1993 in Asia (Currie et al. 1993), where only elmisaurines, not caenagnathines, have been recovered. In either case, the adaptations of the postcrania agree with the omnivorous adaptations of caenagnathid mandibles.

Compared to oviraptorids, caenagnathids show a suite of features that likely indicate paleobiological differences. For example, oviraptorids, like *Ingenia* (MPC-D 100/030) and *Khaan* (MPC-D 100/1127), have short hindlimbs with wide metapodials, but caenagnathids have elongate hindlimbs with arcometatarsalian metapodials. In other theropods, like ornithomimids and tyrannosaurs, the arctometatarsalian condition is developed in conjunction with increased agility, for evasion or predation (Snively et al. 2004). This suggests that caenagnathids were better adapted for running than oviraptorids, perhaps because they were more predatory. Adaptations of the mandible are congruent with increased predation in caenagnathids. In oviraptorids, the high coronoid arch of the dentary and surangular forms a bony "cheek" that aids in shearing food and restricts the size of food items (Smith 1992). Caenagnathids have much less prominent coronoid eminences, resulting in a wider gape to accommodate larger food items. The z-shaped overlapping dentary-surangular suture in caenagnathids (Currie et al. 1993; Funston and Currie 2014) probably allowed some degree of mandibular kinesis, which may have helped accommodate larger food items. The upturned anterior occlusal margin of the dentary in caenagnathids would allow them to rip flesh easily. Oviraptorids have small and simple lingual surfaces on the dentaries, which suggests the dentaries played little role in food processing. In contrast, the complex lingual surface of the dentaries of caenagnathids (Currie et al. 1994; Funston and Currie 2014) suggests that they processed food primarily in the mouth. Smith (1992) noted that oviraptorids were closest in lever mechanics to ceratopsian dinosaurs and suggested that this indicated a primarily herbivorous diet. Overall, it seems reasonable to suggest that skeletal differences between oviraptorids and caenagnathids are the result of dietary differences.

Conclusions

The new specimens conclusively support the presence of elmisaurines in North America, and further indicate that *Elmisaurus rarus* and *Leptorhynchos elegans* form an informal group within Caenagnathidae. These taxa are distinguished from caenagnathines by the fusion of the distal tarsals with each other and the proximal metatarsus, and by their smaller body size at maturity. Histological analysis reveals that the distinctive morphology of elmisaurines is not a result of juvenile ages. The new material suggests cursorial adaptations, which are congruent with the omnivorous diet proposed by earlier studies.

Acknowledgements

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