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A king-sized theropod coprolite

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Fossil faeces (coprolites) provide unique trophic perspectives on ancient ecosystems. Yet, although thousands of coprolites have been discovered, specimens that can be unequivocally attributed to carnivorous dinosaurs are almost unknown. A few fossil faeces have been ascribed to herbivorous dinosaurs[1–3], but it is more difficult to identify coprolites produced by theropods because other carnivorous taxa coexisted with dinosaurs and most faeces are taxonomically ambiguous. Thus sizeable (up to 20 cm long and 10 cm wide) phosphatic coprolites from Belgium[4] and India[5,6] that have been attributed to dinosaurs might have been produced by contemporaneous crocodylians[7] or fish. But there is no ambiguity about the theropod origin of the Cretaceous coprolite we report here. This specimen is more than twice as large as any previously reported carnivore coprolite, and its great size and temporal and geographic context indicate that it was produced by a tyrannosaur, most likely *Tyrannosaurus rex*. The specimen contains a high proportion (30–50%) of bone fragments, and is rare tangible evidence of theropod diet and digestive processes.

The specimen (SMNH P2609.1) was discovered as an elongate mass weathering out of the fluvial Maastrichtian Frenchman Formation in Southwestern Saskatchewan, roughly 35 km southeast of the town of Eastend. The fractured mass was distinguished by its indurated nature and numerous inclusions of comminuted bone. The main portion of the mass was found *in situ* in a bentonitic mudstone, though numerous fragments had eroded downslope. No fossil bones were found in association with the coprolite, but fossils of a number of large vertebrates have been recovered from the Frenchman Formation[8].

The main body of the specimen is roughly 44 cm long, 13 cm high and 16 cm wide (Fig. 1). The density of the material (approximately 2.94 g ml^{-1}) and the weight of all portions (over 7.1 kg) indicate that the present volume of the mass is ~2.4 litres, though it is likely that the original faecal mass was larger before it was subjected to compaction, attrition, and/or desiccation. Broken surfaces of the specimen expose numerous dark brown macroscopic bone fragments ranging from 2 to 34 mm in length. These pieces are suspended in a microcrystalline ground mass and are generally aligned in a consistent direction. The ground mass also contains sand-sized bone clasts (Fig. 2). Most of the included bone appears to be similar in type, with highly vascularized cortical bone tissue up to 14-mm thick in a fibrolamellar pattern. All of the observed bone is primary, and no lines of arrested growth were detected.

Bulk chemical analyses using X-ray fluorescence (Table 1) reveal marked differences between the specimen and the Frenchman Formation mudstone. The bone-bearing specimen contains high concentrations of phosphorus and calcium, and lower concentrations of aluminium and silicon, relative to the host sediment. Microprobe analyses of specific areas of the specimen indicate that the bone fragments and coprolitic ground mass have similar compositions, though the ground mass contains more silicon and aluminium (Table 2). X-ray powder-diffraction analyses indicate that carbonate fluorapatite is the predominant phosphate mineral in both the bone and the ground mass.

Several factors confirm that this specimen is a coprolite. The most diagnostic feature is a phosphatic composition, which is characteristic of carnivore coprolites[9]. As phosphorus normally constitutes only about 0.1% of the Earth's crustal rocks[10], concentrated phosphate deposits usually indicate biotic accumulations, and the overall configuration of the mass is consistent with the irregular faecal deposits produced by very large animals. The matrix-supported distribution of bone fragments argues against the possibility that the mass represents regurgitated material or fluvially aggregated bone debris.

The tremendous size of the specimen indicates that the faecal mass was produced by a large theropod. The largest theropod found in the Frenchman Formation is *Tyrannosaurus*, with an estimated body weight of 5,400 to 6,300 kg (ref. 11). Although other theropods, crocodylomorphs, and a chelonian (*Dromaeosaurus*, *Saurornitholestes*, *Troodon*, *Richardoestesia*, *Chirostenotes*, an ornithomimid, *Leidyosuchus*, *Champsosaurus*, and *Aspideretes*) have also been recovered from the Frenchman Formation[8], these smaller carnivorous taxa probably weighed <100 kg (ref. 12), and it

Figure 1 Large, bone-bearing theropod coprolite with some of the broken pieces that had eroded downslope. This specimen was found in Chamberry Coulee in the Frenchman River Valley, roughly 11.5 m below the Cretaceous/Tertiary boundary. Scale bar, 10 cm.

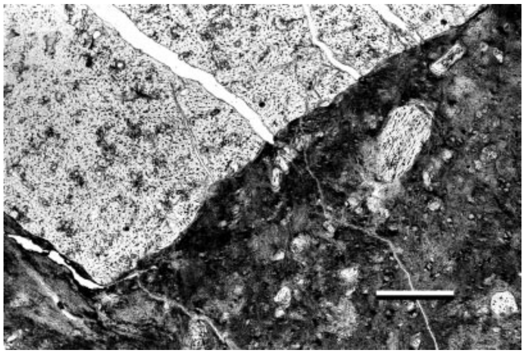

Figure 2 Photomicrograph of a thin section of the theropod coprolite, showing sand- to pebble-sized bone clasts within a microcrystalline phosphatic ground mass. The elemental composition of the ground mass is similar to that of the bone fragments, indicating that it is probably largely composed of reprecipitated bone apatite infiltrated by clay minerals from the host sediment (Table 1). The large bone fragment in the upper left portion of the image exhibits a fibrolamellar pattern, with osteocyte lacunae concentrically arranged around the vascular canals. Probe measurements of the interior of bone lacunae revealed that many of these channels are at least partially empty, whereas others exhibit variable element distributions, with generally lower concentrations of calcium and phosphorus, and higher silicon and aluminium levels (Table 2). Scale bar, 400 μm.

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is unlikely that they could have produced large quantities of faeces. The mass could have been produced by a different species of tyrannosaur, but no others have been recognized in the Frenchman Formation.

The stomach acids and proteolytic enzymes of large extant carnivores digest bone to varying degrees[13–16]. Tangible evidence of this process is apparent in areas of the theropod coprolite where aligned and rounded bone pieces represent the degraded remains of large bone fragments (Fig. 3). The contents of carnivore coprolites might reflect animal physiology, because the extent of bone digestion can be indicative of gut-residence time[17]. Carnivore feeding activity is usually variable, however, and stomach acidity and gut-residence time can be altered by non-physiological factors such as frequency of meals[15]. Even so, the high percentage of incompletely digested bone in this specimen is interesting because it is inconsistent with the general prediction that large theropods digested most consumed bone[18] in the manner of extant crocodilians[14].

The chemistry of the coprolite reflects several factors. A large percentage of the phosphate of the ground mass was probably derived from dissolved bone apatite, but other dietary residues would have contributed additional phosphorus, as microorganisms and animal soft tissues contain significant concentrations of this element. Postdepositional phosphate precipitation may have been triggered by bacterial enzymes[19] after burial of the faecal mass. Although the chemistry of this diagenetic phosphate is similar to that of the included bone, the increased amounts of silicon and aluminium and small differences in amounts of other elements indicate contributions from the host sediment. Thus, although the overall phosphatic composition of the coprolite reflects a carnivorous diet, minor chemical differences in the bone and ground mass seem to reveal more about diagenesis than about diet.

Histological and morphological analyses of the included bone fragments give clues to the identity of the ingested animal. Dinosaurs are the only Late Cretaceous animals that regularly produced thick fibrolamellar cortical bone[20]. The absence of secondary osteons indicates that the bone was ontogenetically juvenile, so the ingested animal appears to have been a subadult dinosaur. Although bone histology is not species-specific, the absence of arrested growth lines may indicate an ornithischian dinosaur. Lines of arrested growth have been observed in several theropods[21] but have not been observed in the long bones of *Triceratops* and *Edmontosaurus* (G.M.E., unpublished observation), the most common dinosaurs found in the Frenchman Formation. Other ornithischians from the formation include *Torosaurus*, *Thescelosaurus* and an ankylosaur[8].

The thickness of the cortical bone indicates that the fragments may be derived from appendicular bone or ceratopsian frill. If the fragments were derived from long-bone diaphyses, estimates of the weight[22] of the consumed animal might range from ~200 kg (for a bipedal dinosaur) to 750 kg (for a quadrupedal dinosaur). The pronounced fragmentation and angularity of the consumed bone indicate that it was fractured before ingestion—apparently by biting during feeding. Although extant birds (avian dinosaurs) often use a horny gizzard and/or ingested grit for food maceration[23], such mechanisms could not have been solely responsible for the degree of comminution seen in the coprolite. Furthermore, significant trituration would have resulted in well rounded bone clasts, and there is no evidence for the use of gastroliths by non-avian theropods.

The coprolitic evidence for extensive bite-induced bone fragmentation is surprising in view of modern reptilian feeding habits. Extant reptiles have poor dental occlusion and generally swallow

Table 1 X-ray-fluorescence data of the weight percentage of oxides found in bulk powdered samples of the coprolite and host sediment

	Coprolite	Host sediment
SiO_2	7.93	70.2
Al_2O_3	2.43	18.1
TiO_2	0.128	0.794
FeO	0.95	6.02
MnO	0.151	0.018
CaO	44.6	0.97
MgO	0.16	1.42
K_2O	0.27	2.22
Na_2O_2	0.28	1.08
P_2O_5	26.5	0.70
Total	83.5	100.9

The clay-rich sediment reflects the low phosphorus concentration of most inorganic rocks, whereas the coprolite is largely composed of biotically concentrated phosphorus and calcium.

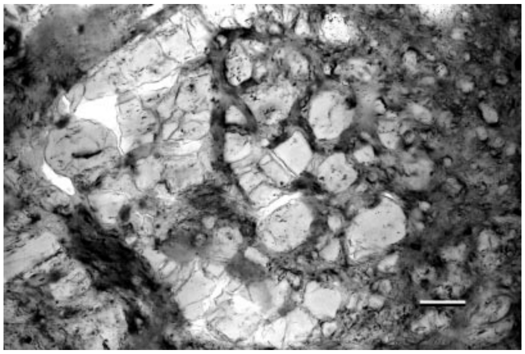

Figure 3 Photomicrograph of a thin section of the theropod coprolite, showing associated bone fragments that indicate digestive degradation. Digestive acids and enzymes probably infiltrated the interior of the bone through vascular canals. Scale bar, 100 μm.

Table 2 Microprobe data indicating weight percentage of oxides, fluorine and chlorine in different regions of the coprolite

	Bone fragments $n = 60$ points		Ground mass $n = 60$ points		Bone lacunae $n = 27$ points	
	Mean	s.d.	Mean	s.d.	Mean	s.d.
SiO_2	0.038	0.102	4.03	1.42	29.5	13.2
Al_2O_3	0.094	0.046	1.71	0.516	13.6	5.80
FeO	0.484	0.034	0.730	0.101	3.24	1.39
MnO	0.230	0.026	0.144	0.018	0.068	0.046
MgO	0.103	0.018	0.210	0.030	1.02	0.47
CaO	51.5	0.290	48.9	1.09	20.2	13.5
SrO	0.157	0.030	0.117	0.024	0.036	0.040
Na_2O	0.335	0.046	0.237	0.032	0.184	0.056
K_2O	0.025	0.010	0.163	0.044	0.312	0.110
SO_3	0.142	0.055	0.285	0.029	0.157	0.080
P_2O_5	35.7	0.466	32.6	0.859	13.4	9.37
F	2.95	0.074	2.62	0.117	0.943	0.750
Cl	NA	–	NA	–	0.108	0.090
Total	90.5	0.582	90.7	0.584	82.4	4.96

The compositions of the bone and ground mass are similar, though the ground mass appears to contain more contributions from the host sediment. Of 67 probe measurements of lacunae, 40 registered low element totals, indicating that the vascular canals were incompletely filled. These channels would have acted as conduits for digestive fluids and for postdepositional contaminants. Data listed above are from the 27 lacunae that registered element totals over 70%. NA, no analyses done.

large pieces of prey whole[14,24]. Such observations of modern feeding behaviours have led to speculation that extinct theropods did little bone-crushing[18,25] and wasted a significant proportion of the food available from carcasses[26]. Tyrannosaur teeth appear to be stout enough to damage bone[27], however, and analyses of bite marks on *Triceratops* and *Edmontosaurus* bones indicate that *Tyrannosaurus* pulverized bones during feeding[28] and probably consumed bone fragments[29].

Although a single coprolite cannot be construed as representative of diet, this rare example of fossilized dietary residues helps to refine our understanding of theropod feeding behaviour by providing physical evidence that a tyrannosaur crushed, consumed, and incompletely digested large quantities of bone when feeding on a subadult dinosaur. It also presents a new search image for future discoveries of theropod faeces that will help us to elucidate the food habits of these giant meat-eaters. ☐

Methods

Bulk chemical analyses of the coprolite and host sediment (Table 1) were made on a Rigaku 3370 spectrometer by the staff of the GeoAnalytical Laboratories, Washington State University, using described procedures[30].

Mineralogical compositions of the bone and ground mass were examined with a Phillips V2.0 diffractometer at the University of California, Santa Barbara (scanning from 2–80° θ). Elemental analyses of these components (Table 2) were made on a JEOL 8900 microprobe at the US Geological Survey, Menlo Park. A 15 kV, 20 nA beam defocused to produce a spot size of 15 μm was used to analyse bone and ground mass; a 10 nA current was used for lacunae analyses. Natural minerals (Wilberforce apatite, Tiburon albite, strontianite, barite, San Carlos olivine, and sodalite) and synthetic materials (faylite, Mn_2O_3, An100, and GSC glass) were used as standards.

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Genetics underlying inbreeding depression in *Mimulus* with contrasting mating systems

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The importance of inbreeding depression in theoretical considerations of mating-system evolution[1–5] and its potential impact on the persistence of small populations[6] has renewed interest in the genetic basis of this phenomenon. Inbreeding increases homozygosity. This can produce inbreeding depression for two different reasons: first, deleterious recessive or partially recessive alleles that are masked at heterozygous loci by dominant alleles become fully expressed in homozygotes; and second, alleles may interact in an overdominant manner, such that the fitness of either type of homozygote is lower than that of heterozygotes. These two mechanisms produce different long-term effects in populations experiencing increased levels of inbreeding. Inbreeding depression resulting from deleterious alleles can be removed by selection, but inbreeding depression produced by overdominance cannot be removed without lowering the mean fitness of the population[1–5]. Using a North Carolina 3 breeding programme[7], the most powerful quantitative genetics technique available[8–10], we show here that deleterious recessive alleles are mainly responsible for inbreeding depression in two closely related annual plants, the primarily selfing *Mimulus micranthus* and the mixed-mating *M. guttatus*. Estimates indicate that deleterious alleles in *M. micranthus* are more nearly additive than they are in *M. guttatus*.

The genetic basis of inbreeding depression (or its converse, heterosis) has been examined primarily in crop plants. There is evidence for both dominance-based[11–13] and overdominance-based[13–16] inbreeding depression. However, the relative importance of dominance-based versus overdominance-based inbreeding depression in natural plant populations is largely unknown. Studies of *Eichhornia paniculata*[17] (Pontederiaceae) and two *Amsinckia* species[18] (Boraginaceae) have found indirect evidence for dominance-based inbreeding depression.

The genus *Mimulus* (Scrophulariaceae) has been the focus of many studies aimed at understanding the processes responsible for the evolution of plant mating systems[19–24]. *Mimulus guttatus*, the common monkey flower, has large, bee-pollinated flowers, and measured outcrossing rates for three populations, including one used in this study, ranged from 0.68–0.80 (ref. 25). *Mimulus micranthus* is a