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POSSIBLE EVIDENCE OF GREGARIOUS BEHAVIOR IN TYRANNOSAURIDS

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ABSTRACT: In 1910, a collecting party from the American Museum of Natural History led by Barnum Brown floated down the Red Deer River of Alberta. In the Horseshoe Canyon Formation (Edmonton Group, Campanian-Maastrichtian, Upper Cretaceous) close to the mouth of Big Valley Creek, they excavated semi-articulated skeletons of several individuals of *Albertosaurus sarcophagus* OSBORN, 1905 from a single quarry. Other than the tyrannosaurids, only two hadrosaur phalanges were recovered. Eight articulated feet with associated limb bones were given catalogue numbers, as was an articulated string of twenty-five caudal vertebrae. The remaining tyrannosaurid fossils that could not be associated with any of these specimens or with each other were all assigned a single number. Brown's other discoveries of well-preserved dinosaur skeletons in southern Alberta overshadowed the tyrannosaurid find, and the specimens were largely forgotten. However, it is the best evidence that exists to suggest that tyrannosaurids may have been gregarious animals. The almost complete lack of herbivore bones from the excavation suggests that this was probably not a predator trap, such as has been postulated for the *Allosaurus* MARSH, 1877 accumulation at the Cleveland-Lloyd Quarry near Price, Utah. Comparative measurements indicate that juvenile tyrannosaurids were probably almost as fast at running as ornithomimids. This suggests a division of labor amongst a hunting pack of tyrannosaurids.

INTRODUCTION

On August 10, 1910, Barnum Brown and Peter Kaisen discovered what they at first determined to be an articulated skeleton of the tyrannosaurid *Albertosaurus sarcophagus*. They had been floating by boat down the Red Deer River of the province of Alberta in Canada, and had been prospecting in the badlands near what is now Dry Island Buffalo Jump Provincial Park, across the river from the mouth of Big Valley Creek. Both men were seasoned collectors from the American Museum of Natural History (New York), and were aware of the *Albertosaurus* fossils that had been collected in the same region more than twenty years earlier (OSBORN, 1905). The bones were found in a very hard sandstone about twelve meters above river level. The hard rock separated cleanly from the bones, which are well preserved. After working on the site for less than a day, they realized that the articulated limb bones they were collecting represented several individuals. The three square meter excavation continued until September 1, during which time they excavated some skull bones, two dentaries with teeth, vertebrae, and many front and hind limb bones (unpublished information in Barnum Brown's "Annual Report for the Year 1910: Expedition to the Laramie Cretaceous of Montana and Alberta", which is on file in the Department of Vertebrate Paleontology, American Museum of Natural History). The excavation took two weeks to complete (a maximum of 29 man-days were invested by Brown, Kaisen and Davenport), and eight boxes of fossils were shipped back to New York.

Brown recognized that they had collected five partial or complete legs of *Albertosaurus*, plus limb bones that he identified as ornithomimid, and two hadrosaur phalanges. Preparation of the bones initially classified as ornithomimids revealed that they were actually from juvenile *Albertosaurus*. Each of the articulated specimens was given its own catalogue number (TABLE I). Most of the unassociated tyrannosaur bones were catalogued as AMNH 5218, and this collection consisted of two nearly complete dentaries, 14 vertebrae, two chevrons, one scapula, one coracoid, two humeri, a pair of pubes, two femora, three tibiae, half a fibula, two astragali, one calcaneum, a pair of associated metatarsals (II-III), six isolated metatarsals, 42 phalanges, and seven unguals. The two hadrosaur phalanges were also given this number. Although no quarry map was made, no detailed notes were written, and only one photograph of the quarry was taken from a distance, it is clear that both articulated and disarticulated specimens were being recov-

TABLE I
The minimum number of individuals from the AMNH *Albertosaurus* quarry was established by comparative measurements of identified elements. AMNH 5228, 5234 and 5235 are all close in size, but each has a right metatarsal IV to show that they came from different individuals. More than fifty *Albertosaurus* bones (mostly pedal phalanges) catalogued as AMNH 5218 were examined and assigned by size to the individuals represented by the articulated feet. Two bones (both III-3) found under that catalogue number represent two additional individuals (numbers 1 and 9), one very small and one very large. One articulated metatarsus from the quarry (AMNH 5230) could not be found for examination and measurement. Femur and total body length estimates were made from regression analysis of skeletons of *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus* and *Tyrannosaurus* skeletons.

INDIVIDUAL	SPECIMEN NUMBER	ELEMENTS	SIZE (AND ELEMENT) (mm)	ESTIMATE OF FEMUR LENGTH (mm)	ESTIMATE OF BODY LENGTH (m)
1	5218	III-3	42 (III-3)	500	4.1
2	5229 5218	mt IV III-2,-3	394 (mt IV)	601	5.1
3	5233 5218	mt II, III, IV, II-1, III-1 I-1, III-3, IV-1, IV-3, IV-4	426 (mt IV)	703	6.0
4	5234 5218	astralagus, mt II, III, IV, III-1, IV-1 humerus, II-1, III-2, III-3, IV-3	452 (mt IV)	791	6.8
5	5228 5218	mt III, IV II-2, IV-3	465 (mt IV)	800	6.9
6	5235 5218	femur, ungual, mt II, III, IV humerus, I-1, II-1, III-2	486 (mt IV)	850	7.3
7	5231 5218	astralagus, 2 tarsals, mt II, IV, II-1, II-2, IV-2 femur, tibia, II-1, II-2, III-1, IV-1, IV-2	510 (mt IV)	877	7.6
8	5232 5226 5227 5218	2 tarsals, mt II, III, IV, V 25 caudals tibia, fibula, astralagus I-1, III-1, IV-1	521 (mt IV)	935	8.1
9	5218	III-3	99 (III-3)	1000	8.7

ered. Articulated metatarsals with associated limb bones were the most common elements excavated. It is not known whether Brown and Kaisen were collecting everything they found, or were collecting only those elements that could be used to determine how many individuals were represented in the quarry. If the former, then there must have been some kind of taphonomic filter that favoured the preservation of hind limb bones over all else. It is impossible to know what such a filter may have been. Alternatively, it is possible that the party was collecting only the most useful bones. Peter Kaisen estimated in his field notes of August 13, 1910, two weeks before they finished the excavation, that it would take three weeks to finish the work. This suggests all of the bones in the quarry were not collected.

Brown occasionally referred to this bonebed (BROWN, 1914), but he never published anything on it. RUSSELL & CHAMNEY (1967) commented on the association, but were unable to relocate the quarry (Russell, pers. comm., 1997). Because of the height of the bonebed above the river, they knew it was from Member B of what was then known as the Edmonton Formation. This formation has now been elevated to group status, and the relevent rocks are from the upper part of the Horseshoe Canyon Formation (GIBSON, 1977). The site was also briefly mentioned by FARLOW (1976), along with other evidence for packing behavior in theropods.

In 1996, I decided to investigate further by examining specimens, field notes, field photographs, and letters that Brown wrote while he was in the field. The site was relocated in 1997 by a joint expedition of the Royal Tyrrell Museum of Palaeontology and the Dinamation International Society. Examination of the spoil piles around the original quarry confirmed that Brown was being selective in his choice of specimens collected. The bonebed, which extends deep into the hill, is now being quarried by staff of the Tyrrell Museum.

RESULTS

The specimens (Fig. 1) collected from the *Albertosaurus* quarry include at least seven articulated sets of metatarsals, several of which are associated with phalanges and other limb bones (TABLE I). Additional metatarsals catalogued as AMNH 5218 and AMNH 5230 had not been located by the time this paper was written, and could therefore not be considered in this census. These may represent the same individuals, or might have come from one or two additional animals. Of the seven groups of articulated metatarsals, three represent animals of about the same size. Because each of these three includes a right metatarsal IV, they clearly came from three different animals. The remaining sets of metatarsals are different enough in size and proportions to demonstrate the presence of four more individuals.

All other elements collected from the quarry were sorted by size and were assigned whenever possible to the seven individuals (TABLE I) using data from articulated tyrannosaur skeletons. One pedal phalanx (III-3) was found to indicate the presence of an *Albertosaurus* smaller than the first seven, whereas another pedal III-3 was clearly from a larger, more massive individual. Therefore, the quarry has yielded the remains of at least nine tyrannosaur specimens. Comparison of the bones with articulated skeletons of *Albertosaurus sarcophagus* (ROM 807, TMP 81.10.1, TMP 85.64.1, TMP 85.98.1 and TMP 86.205.1) suggests that all individuals, with one possible exception, should be assigned to this species. The exception is the large pedal phalanx III-3, which is massive enough to possibly be *Daspletosaurus* RUSSELL, 1970, the only other large tyrannosaurid presently recognised in the Horseshoe Canyon Formation.

The smaller sets of metatarsals (individuals 1 and 2) are slender and more elongate than the larger ones (Fig. 1). Because of their size and proportions, Brown originally believed that they were from or-

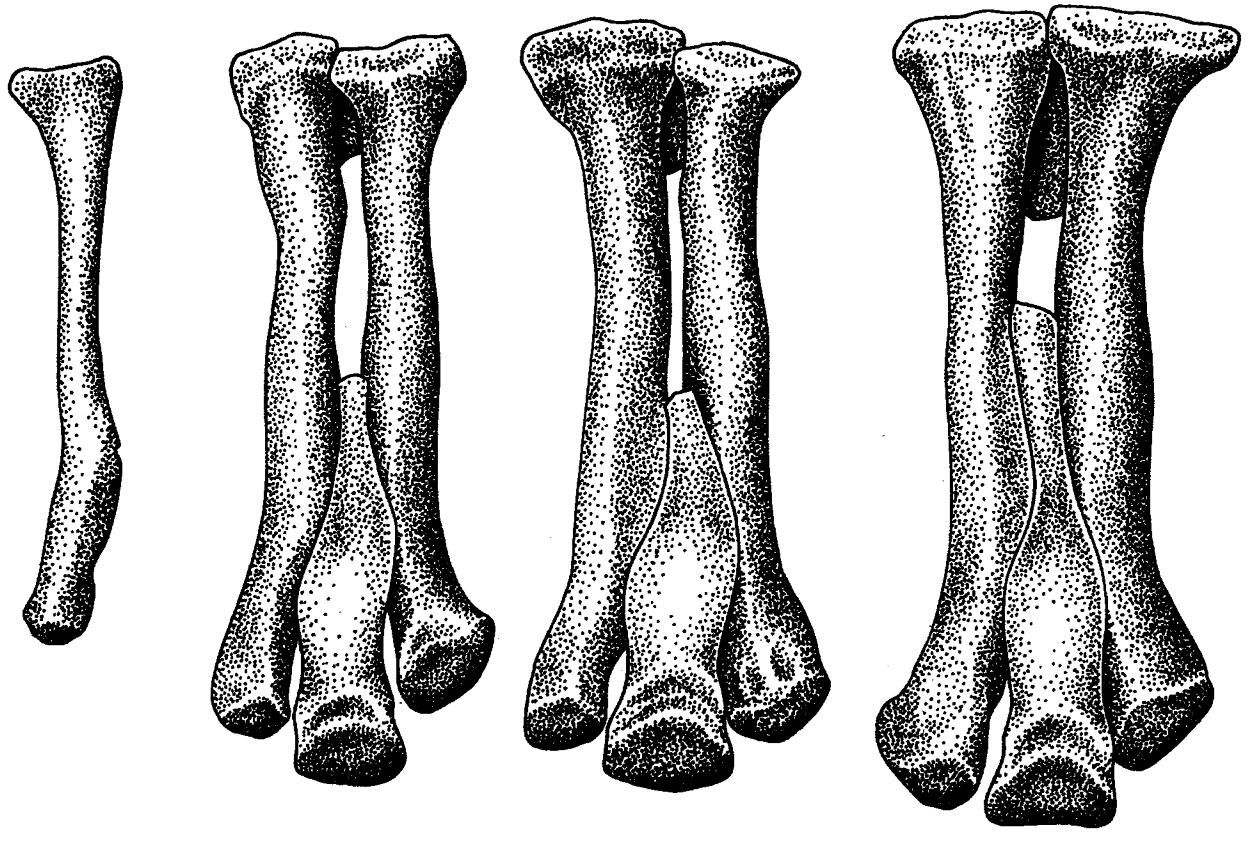

Fig. 1 - *Albertosaurus sarcophagus* OSBORN 1905 metatarsals (right) collected by Barnum Brown in the Horseshoe Canyon Formation of Alberta, Canada. From left to right, AMNH 5229 (individual 2 of TABLE I), AMNH 5233 (individual 3), AMNH 5234 (individual 4), and AMNH 5232 (individual 8). See TABLE I for measurements.

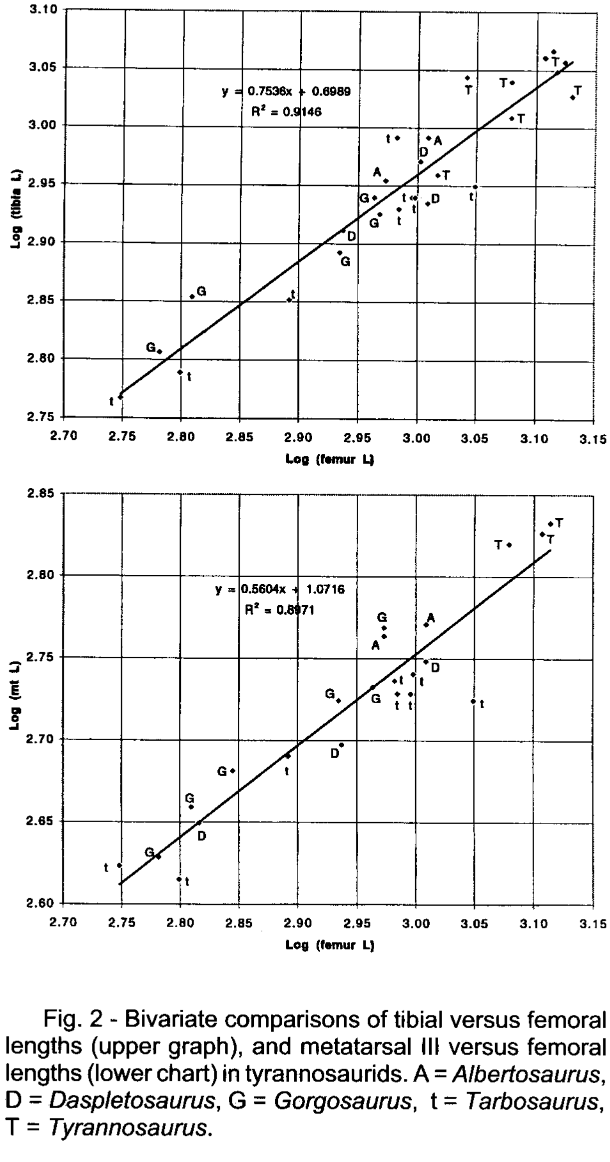

Fig. 2 - Bivariate comparisons of tibial versus femoral lengths (upper graph), and metatarsal III versus femoral lengths (lower chart) in tyrannosaurids. A = *Albertosaurus*, D = *Daspletosaurus*, G = *Gorgosaurus*, t = *Tarbosaurus*, T = *Tyrannosaurus*.

nithomimids. However, anatomical details led him to re-identify them as tyrannosaur once they were prepared. Regression analysis of hind limb elements clearly supports this result. In tyrannosaurids, the tibia shows negative allometry (compared with the femur) during growth (Russell, 1970; Gatesy, 1991; Holtz, 1994), but not to the same degree as the metatarsus (Fig. 2).

DISCUSSION AND CONCLUSIONS

The discovery of nine or more tyrannosaurids, at least eight of which are the same species, in a single quarry can be interpreted in many ways. Given the fact that twenty species of dinosaurs are known from the Horseshoe Canyon Formation (Appendix I), and that the number of individuals of *Albertosaurus sarcophagus* made up less than ten percent of the dinosaur fauna, it is highly unlikely that the nine individuals ended up in the same place as a result of chance. The bonebed was apparently not very thick, and the similarity in degree of disarticulation of most of the skeletons indicates that all of the animals died around the same time and shared the same taphonomic history of burial. The almost complete lack of bones of herbivorous dinosaurs, and the absence of tooth marks or other evidence of predation suggests that the site was probably not a predator trap. The most parsimonious interpretation is that the tyrannosaurids were part of a group that died together. Because it is difficult to imagine why they would have collected into a group immediately before death, they were probably living together for a period of time before they died. There is not enough information available about the excavation to speculate what caused their death, but disease, drought, drowning and suffocation are some of the causes proposed for similar catastrophic death assemblages of herbivorous dinosaurs (Currie & Dodson, 1984; Varricchio & Horner, 1992; Coria, 1994; Sampson, 1995).

Brown's *Albertosaurus* bonebed is not the only report of theropod bonebed concentrations. During Late Triassic and Early Jurassic times, *Coelophysis* Cope, 1889 (Colbert, 1989) and *Syntarsus* Raath, 1969 (Raath, 1990) are two examples of theropods that died *en masse*, whereas trackway sites (Ostrom, 1972) suggest that these animals may have actually been moving in packs. The *Coelophysis* bonebed has most recently been interpreted as species-selectivity in drought conditions (Schwartz & Gillette, 1994). The Upper Jurassic Cleveland-Lloyd quarry, which has produced evidence of more than seventy specimens of *Allosaurus fragilis*, has been interpreted as a predator trap (Madsen, 1976; Miller, Horrocks & Madsen, 1996) for both individuals and packs of this species (Richmond & Morris, 1996). Skeletal evidence points towards pack hunting behavior in the small dromaeosaurid theropod *Deinonychus* Ostrom, 1969 (Ostrom, 1969; Maxwell & Ostrom, 1995). There are many examples of Jurassic and Cretaceous trackway sites that show theropods moving in groups (Lockley, 1991; Mossman & Sarjeant, 1983). The Late Cretaceous theropod *Troodon* Leidy, 1856 may have been a pack animal (Varricchio & Currie, 1991). For tyrannosaurids, however, only one record of multiple individuals has been reported to date. When the large *Tyrannosaurus rex* Osborn, 1905 known as "Sue" was excavated, parts of three other tyrannosaur skeletons (an adult, a juvenile, and a "baby") were collected from the same quarry (Larson, 1995).

Another fact revealed by the metatarsals from Brown's *Albertosaurus* quarry (Fig. 1), and by comparative analysis of tyrannosaur measurements, is

TABLE II
Limb proportions in tyrannosaurids and ornithomimids, arranged in order of femur length (millimeters).

SPECIES	SPECIMEN	F	Mt	T/F
Gallimimus	IGM 100/10	192	0.82	1.14
Gallimimus	ZPAL D-I/94	270	0.81	
Ornithomimus	NMC 8636	310		1.47
Gallimimus	ZPAL D-I/1	360	0.78	
Struthiomimus	AMNH 5385	370		1.10
Dromiceiomimus	AMNH 5201	387		1.13
Struthiomimus	ROM 1790	390	0.77	1.05
Dromiceiomimus	ROM 797	390	0.76	1.21
Gallimimus	IGM 100/52	400	0.71	1.00
Ornithomimus	TMP 95.110.1	425	0.78	1.09
Struthiomimus	NMC 930	430		1.30
Gallimimus	IGM 100/30	435	0.69	1.03
Ornithomimus	ROM 851	435	0.71	1.09
Dromiceiomimus	ROM 852	440	0.84	1.18
Struthiomimus	AMNH 5339	480	0.77	1.13
Struthiomimus	AMNH 5257	512	0.72	1.08
Tarbosaurus	PIN 552-2	560	0.75	1.04
Gorgosaurus	AMNH 5423	605	0.70	1.06
Tarbosaurus	940823-Bgt-1	630	0.65	0.98
Gallimimus	ZPAL D-I/8	635	0.80	
Gorgosaurus	TMP 91.36.500	645	0.71	1.11
Daspletosaurus	NMC 11315	655	0.68	
Gallimimus	IGM 100/11	665	0.80	1.05
Alectrosaurus	AMNH 6554	685c	0.70	1.07
Gorgosaurus	AMNH 5664	700	0.69	
Albertosaurus	AMNH 5233	703c	0.65	
Tarbosaurus	IGM 100/61	780	0.63	0.91
Albertosaurus	TMP 86.64.1	782c	0.61	0.96
Albertosaurus	AMNH 5234	791c	0.59	
Dryptosaurus	ANSP 9995	813		0.96
Albertosaurus	AMNH 5235	850c	0.61	
Gorgosaurus	USNM 12814	860	0.62	0.91
Daspletosaurus	MOR 590	865	0.58	0.94
Albertosaurus	AMNH 5227	898c		0.94
Gorgosaurus	TMP 94.12.602	920	0.59	0.95
Gorgosaurus	NMC 350	930		0.91
Albertosaurus	AMNH 5232	935c	0.58	
Albertosaurus	TMP 81.10.1	940	0.62	0.96
Gorgosaurus	NMC 11593	940	0.62	
Tarbosaurus	IGM 100/63	960	0.57	1.02
Tarbosaurus	PIN 551-2	965	0.55	0.88
Gorgosaurus	AMNH 5432	967c	0.59	0.94
Tarbosaurus	IGM 107/3	990	0.54	0.88
Tarbosaurus	PIN 552-1	995	0.55	0.87
Daspletosaurus	AMNH 5438	1005		0.93
Daspletosaurus	TMP 85.62.1	1020	0.55	0.84
Albertosaurus	ROM 807	1020	0.58	0.96
Tyrannosaurus	USNM 6183	1040		0.88
Tyrannosaurus	MOR 009	1100		1.00
Tarbosaurus	IGM 107/2	1120	0.47	0.79
Tyrannosaurus	TMP 81.6.1	1200		0.85
Tyrannosaurus	TMP 81.12.1	1200	0.55	0.91
Tyrannosaurus	MOR 555	1280	0.52	0.90
Tyrannosaurus	CM 9380 (AMNH973)	1300c	0.52	0.90
Tyrannosaurus	AMNH 5027	1310		0.85
Tyrannosaurus	BHI 2033 (Sue)	1330		0.86
Tyrannosaurus	BHI 3033 (Stan)	1350		0.79

c - calculated on the basis of regression analysis of tyrannosaurid limb elements; **F** - femur; **Mt** - (metatarsal III)/(femur length); **T/F** - (tibia length)/(femur length).

that juvenile tyrannosaurids have hind limb proportions (HOLTZ, 1994) similar to those of ornithomimids (TABLE II). For individuals with a femur length between 500 and 700 mm, the average ratio of tibia to femur is 1.05 in tyrannosaurids, and 1.06 in ornithomimids. The same comparison for metatarsal III is 0.70 in tyrannosaurids and 0.77 in ornithomimids. The tibia/femur and metatarsus/femur ratios for carnosaurs and ceratosaurs in this size range are 0.95 and 0.50 respectively, and these were clearly much slower animals. It is widely accepted that limb proportions indicate ornithomimids were capable of running rapidly (RUSSELL, 1972). In fact, they are often compared with ostriches, which can attain speeds of up to 70 km.h^{-1}. Although proportions are similar in the hind legs of an ornithomimid and an ostrich, the femur is held in a more horizontal position in the extant animal, and it lacks the long tail. The biomechanical effects of these differences on speed have not been analyzed. Nevertheless, the relative proportions of limb elements and their slender proportions suggest that juvenile tyrannosaurids were almost as fast as equivalent sized ornithomimids, which in turn were probably faster than any other known dinosaurs.

The implications of this are extremely interesting. First, it is apparent that juvenile tyrannosaurids were probably faster runners than both their own parents and most other theropods of the same general size. In part this probably increased their chances of survival. Furthermore, juvenile tyrannosaurids, like ornithomimids and troodontids, were unquestionably faster than any of the herbivores that lived during Late Cretaceous times, regardless of what their absolute speeds were. Limb proportions also suggest that even the largest tyrannosaurid was capable of moving faster than any equivalent-sized, contemporary herbivore. If tyrannosaurids were packing animals, it is also possible that they practiced a division of labor, just as lions, wolves, or many other modern carnivores do. The faster, more agile juveniles may have been responsible for driving potential prey towards the larger, more powerful adult tyrannosaurids.

The evidence for packs of tyrannosaurids argues against these animals being obligatory scavengers (HORNER & LESSEM, 1993). They were clearly opportunists that took advantage of eating the carcasses of other animals when they were available (CURRIE & DODSON, 1984). However, it is doubtful that a single tyrannosaur could have found enough meat to scavenge to keep it alive. For a pack of tyrannosaurids to find enough dead animals is even less likely. Any mature tyrannosaur would have been large enough, fast enough, and strong enough to bring down any contemporary herbivore. Packing behavior would have improved this advantage, reducing the chance of injury to any individual tyrannosaur.

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ABBREVIATIONS

AMNH - American Museum of Natural History, New York, USA; FMNH - Field Museum of Natural History, Chicago, USA; IGM - Institute of Geology, Mongolia, Ulaan Baatar, Mongolia; NMC - Canadian Museum of Nature, Ottawa, Canada; PIN - Paleontological Institute, Moscow, Russia; MOR - Museum of the Rockies, Bozeman, USA; ROM - Royal Ontario Museum, Toronto, Canada; TMP - Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; USNM - United States National Museum, Smithsonian Institute, Washington, USA; ZPAL - Palaeozoological Institute of the Polish Academy of Sciences, Warsaw, Poland.

APPENDIX I

DINOSAURS OF THE HORSESHOE CANYON FORMATION NEAR DRUMHELLER, ALBERTA, CANADA

Theropoda

Albertosaurus sarcophagus OSBORN, 1905

Aublysodon sp.

Chirostenotes pergracilis GILMORE, 1924

Daspletosaurus n.sp

Dromaeosaurus sp.

Dromiceiomimus brevitertius (PARKS, 1926)

Ornithomimus edmontonticus STERNBERG, 1933

Struthiomimus altus OSBORN, 1917

Troodon formosus LEIDY, 1856

Velociraptorinae n. gen., n. sp.

Hadrosauridae

Edmontosaurus regalis LAMBE, 1917

Hypacrosaurus altispinus BROWN, 1913

Saurolophus osborni BROWN, 1912

Ankylosauria

Edmontonia longiceps STERNBERG, 1928

Euoplocephalus tutus LAMBE, 1910

Panoplosaurus sp.

Pachycephalosauria

Stegoceras edmontonense (BROWN & SCHLAIKJER, 1943)

Neoceratopsia

Anchiceratops ornatus BROWN, 1914

Arrhinoceratops brachyops PARKS, 1925

Pachyrhinosaurus canadensis STERNBERG, 1950

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