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Mass death of a herd of Ceratopsian dinosaurs

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Although Alberta is well known as one of the richest sources of articulated dinosaur skeletons (BELAND & RUSSELL, 1978), few people realize that bonebeds are common in Upper Cretaceous strata throughout the province. Since 1980, staff of the Tyrrell Museum of Palaeontology have discovered, sampled and documented 90 bonebeds, the largest covering an area of more than one square kilometer, in Dinosaur Provincial Park near Brooks, Alberta. As these bonebeds represent an interaction of biological and geological factors quite distinct from those that result in the preservation of single skeletons, they form an independent means of sampling the paleoecology of the Judith River (Oldman) Formation. The faunal compositions of most bonebeds correlate well with the percent composition of articulated specimens, and the remains of hadrosaurs usually outnumber those of ceratopsians by 50%. Less than 10% of bonebeds tend to be dominated by single genera of ceratopsian dinosaurs. Monospecific domination of such bone accumulations is presently known in Alberta only for ceratopsians, but is widespread (STERNBERG, 1970; LANGSTON, 1975). Some of the bonebeds may turn out to be dominated by a single species of hadrosaurs, but there is no evidence to confirm this at this time.

Evidence suggests that most major groups of dinosaurs included gregarious species (OSTROM, 1972). Evidence of herding behaviour among ceratopsians however, has been circumstantial. The discovery of associated skeletons of Protoceratops of Mongolia (BROWN & SCHLAIKJER, 1940) and of a small group of Leptoceratops in Alberta (STERNBERG, 1951) could be attributed to habitat preference. Studies of cranial morphology (FARLOW & DODSON, 1975) suggest complex behaviour in a hierarchy establishment for some genera. However, bonebeds in Alberta could represent the first good evidence that ceratopsians were gregarious, herding animals.

In Dinosaur Provincial Park, bonebeds of Centrosaurus (Quarry 143), cf. Monoclonius (Bonebed 30) and Styracosaurus (Bonebed 42) are found less than two kilometres apart. Another accumulation of Styracosaurus remains (STERNBERG, 1970) and at least two more Centrosaurus accumulations occur elsewhere in the Park. A Chasmosaurus bonebed has been discovered in the Judith River Formation along the South Saskatchewan River north of Medicine Hat (A. LINDOE, personal communication). Centrosaurus, Chasmosaurus, Monoclonius and Styracosaurus were contemporaneous in life (Fig. 1), and segregation of their remains into distinct

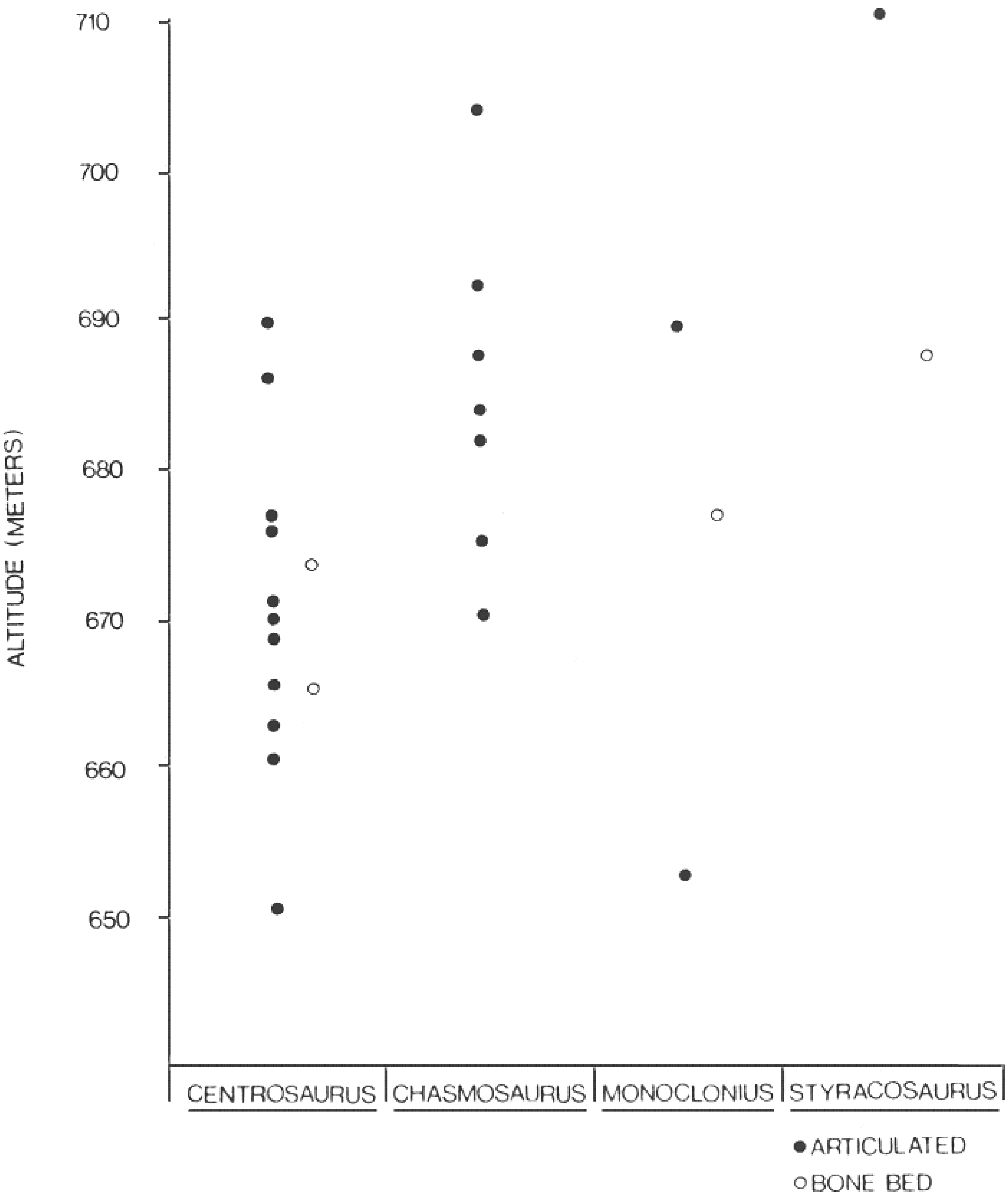

Figure 1. Stratigraphic distribution of four genera of Ceratopsia in the Judith River (Campanian) strata of Dinosaur Provincial Park, Alberta.

bonebed accumulations may indicate that they moved in herds, or that the genera occupied specific habitats. The proximity of the bonebeds, the thinness of bone-bearing levels, the more widespread occurrence of articulated ceratopsian remains and the fact that these large animals when alive would have been capable of covering large areas in search of food may argue against the latter hypothesis, but detailed taphonomic studies of each type of ceratopsian bonebed are necessary to determine possible differences in depositional environments.

In 1979, a field party of of the Tyrrell Museum of Palaeontology opened Quarry 143, a bonebed covering more than 3,000 square metres. By the end of the 1983 field season, less than 15% of the excavation had been completed. Bones were systematically uncovered, identified, mapped and measured. Approximately 10% of the specimens are catalogued and excavated. Of the more than 1100 bones catalogued, 84% can be attributed to ceratopsians, 5% to theropods, 4% to hadrosaurs and the balance to fish, amphibians, small reptiles and mammals. This census is strongly biased against ceratopsians, because only reasonably complete ceratopsian bones were collected, whereas every identifiable non-ceratopsian specimen was recovered. Forty-three braincases from mature ceratopsians and seven right orbital horn cores from juvenile individuals establish a minimum count of 50 individuals. Diagnostic cranial elements indicate that most of the ceratopsian bones belong to at least 36 individuals of Centrosaurus. A partial skull of Eoceratops (TMP P79.11.147) was collected from Quarry 143. Because it represents the only articulated remains ever found in the quarry, it is not unreasonable to assume that it was not exposed to the elements before burial as long as the Centrosaurus remains. A water-worn fragment of a parietal crest (TMP P81.18.231) may represent Chasmosaurus.

In most areas of the Quarry, approximately twenty bones per square metre were uncovered, but in places the count exceeds sixty. The bonebed is less than 10 cm thick. It does not follow a planar surface, but varies more than 1.5 metres in altitude. The bonebed is in a major channel sandstone seven metres thick, and appears to follow the topography of an ancient channel bottom. Bones uncovered in the lower levels of the bonebed that have been excavated show some indication of current alignment (Fig. 2), with the mode at 100° - 120° and a secondary concentration at nearly right angles to this, resulting in an observed mean of 89° (N=160). Another indication of current alignment is provided by intact vertebrae with NW - SE orientation; in a small sample of 14 specimens, centra lie upstream with twice the frequency with which they lie downstream. Excavation on the higher level of the bonebed has just started, and early indications suggest less evidence of current sorting than the lower levels. The disarticulation of the skeletal elements is almost total. The average size of 284 skeletal elements preserved in one section of the quarry is 173 mm in length and the model size class is 50 to 100 mm. The elements have passed through a strong

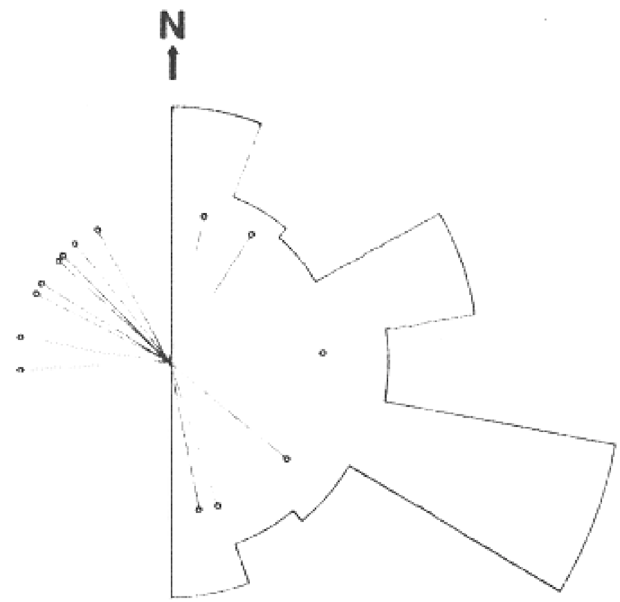

Figure 2. Orientation of bones in one section of Quarry 143. The outline represents a sample of 160 bones with an observed mean of 89°. The polarities of 14 ceratopsian vertebrae are shown, the circles representing the centra and the lines neural spines. Eight vertebrae have heavy ends (centra) oriented upstream and four downstream.

post-mortem filter - most bones are fractured at both ends. Broken surfaces are fresh or rounded. Water worn fragments are common, particularly in the smallest size class. Most of these bone clasts that can be identified are not ceratopsian remains. Many bones, including complex braincases, are well preserved and show little evidence of preburial abrasion. Some bones have fresh textures, whereas others have dull, somewhat weathered surfaces; one never finds deeply weathered textures such as those reported by BEHRENSMEYER (1978).
Anatomically, the deposit consists of 50% rib fragments, 20% vertebrae, 15% skull parts, 10% limb bone and a small quantity of foot and girdle elements. The dominance of ribs and vertebrae indicates clearly that this is not a current-winnowed, transported assemblage (VOORHIES, 1969; BEHRENSMEYER, 1975) The lower levels of the bonebed are depauperate in podial and girdle elements, and seem to be enriched in ribs relative to vertebrae, in comparison with the proportion of skeletal elements found in a Centrosaurus skeleton. The characteristic stages of carcass decomposition among dinosaurs from this region have been documented (DODSON, 1971). At an early stage of decomposition, the extremities - manus, pes and tip of the tail - are lost. A hypothetical, partially decomposed Centrosaurus lacking podials and two-thirds of the tail would have anatomical representation of similar proportions to those found in Quarry 143. The actual bonebed census indicates that the cranial and limb material approach the expected proportions, vertebrae are under-represented (as is frequently the case in fossil deposits) and ribs resolutely remain over-represented. Ribs, however, are highly fragmented, and thus are overcounted.

Large numbers of orbital horn cores have been collected from the bonebed; they fall into three distinct size classes. Two very young (as determined by degree of ossification and size) individuals have orbital horn cores 20 mm in length. Five individuals represent the next size class, and have horn cores double the length of the smallest animals. The remaining horn cores form a graded size series between 60 and 100 mm long. The discrete size classes may reflect the age structure of the herd at time of death. Growth rings in tree stumps, champsosaur bones and other organisms indicate that the climate of southern Alberta experienced seasonal fluctuations during Campanian times (DODSON, 1971). We assume that in an environment affected by annual fluctuations of temperature and /or humidity that the young would be born during seasonally optimal conditions for their survival. It seems reasonable to assume that Centrosaurus young would hatch at the same time every year. If the smallest animals represented in Quarry 143 are less than a year old, the next size class would represent animals that are a year older than the smallest ones. The next year of life would see a lower rate of growth, but it would be still high enough to segregate the second size class from the larger animals by a distinct gap. In the third and subsequent years, the growth rate would be slow enough for the cumulative annual size increases to be masked by individual variation. The size distribution of the orbital horn cores of the known sample (50 individuals) fits this model. No attempt has been made yet to see if the size distribution of other skeletal elements agree, primarily because no other elements with a large enough sample are diagnostic for the species. The model will undergo further testing as additional specimens are recovered in upcoming field seasons.

A synthesis may be attempted, drawing upon the recorded observations. Given the striking and spectacular dominance of a single species of animal, it is difficult to avoid the conclusion that a herd of Centrosaurus encountered misfortune; the demographic structure is consistent with catastrophic rather than attritional mortality (VOORHIES, 1969). The nature of the catastrophe is, however, unknown. We believe that a herd of well defended animals this large could not be over-come by predator ambush. Natural deaths en masse of thousands of large herding mammals such as Bison, Connochaetes and Equus (McHUGH, 1972; SCHALLER, 1973) are well documented, so there is nothing remarkable about the ceratopsian bonebeds if these animals travelled in herds.

Following the death of the herd, the carcasses, exposed on a point bar, were subject to thorough scavenging by large and small theropods. Much of the bone is tooth marked, and the breakage of ribs and limb bones could have been caused by the large theropods. Next to the ceratopsian remains, carnivore teeth, shed during feeding, are the most common elements recovered from Quarry 143. Trampling by other dinosaurs fractured still green bones, and buried them in the soft sediments. During continued exposure, skulls disarticulated and fell apart along the sutures, and all ligaments and tendons holding bone to bone disintegrated. Exposed vertebrae and limbs weathered and their surfaces dulled; elements forced into the sediment remained fresh. When flowing water returned, part of the bone accumulation was undercut and current aligned as a lag deposit. Small cylindrical caudal vertebrae, and podial elements rolled away, but most bones in the assemblage moved a modest distance in the bed load. Areas not undercut by the moving water remained at a higher level, were not current aligned, and were not thinned out. Bone pebbles and other faunal elements were washed into the assemblage from upstream. Some bones were buried quickly in the channel bottom; others remained with ends exposed to be rounded off by the abrasive flow. Finally, all were buried.

Work will continue in Quarry 143 in Dinosaur Provincial Park until at least half of the bonebed has been excavated. Detailed morphological studies will give us a better understanding of most skeletal elements of Centrosaurus because of the disarticulated nature of the specimens. The amount of material will permit study of allometric growth, and age and individual variation in a single, sympatric species of horned dinosaur. It is evident already that all characteristics used to distinguish species of Centrosaurus can be found in specimens from this bonebed. If Quarry 143 represents a mass death of a ceratopsian herd and young of these dinosaurs were born on an annual cycle, then growth rates can be calculated for the first few years of life. Herd structure then may disclose information on behaviour, ecology and physiology of horned dinosaurs.

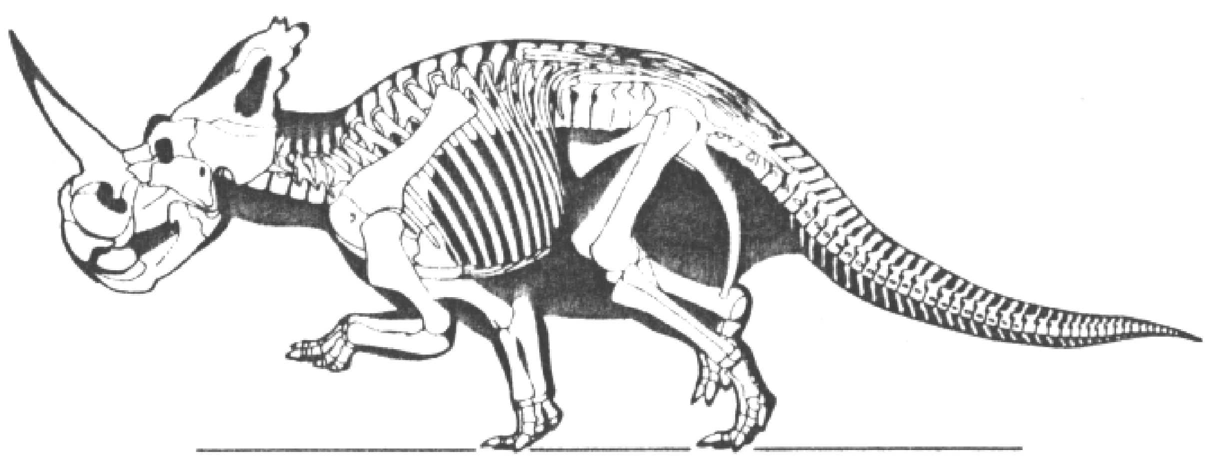

Figure 3. Reconstruction of the skeleton of Centrosaurus nasicornis, based on a specimen in the American Museum of Natural History (AMNH 5351). The femur is 740 mm.

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