

The Taphonomy of a *Centrosaurus* (Ornithischia: Certopsidae) Bone Bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with Comments on Cranial Ontogeny

MICHAEL J. RYAN and ANTHONY P. RUSSELL

Vertebrate Morphology and Palaeontology Research Group, Department of Biological Sciences, University of Calgary, Calgary Alberta T2N 1N4, Canada

DAVID A. EBERTH and PHILIP J. CURRIE

Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller Alberta T0J 0Y0, Canada

PALAIOS, 2001, V. 16, p. 482–506

Bone bed 43 is one of at least eight paucispecific Centrosaurus bone beds located in the Dinosaur Park Formation (Upper Campanian) in Dinosaur Provincial Park, Alberta, Canada. It long has been used as a case example for evidence of herding and social behavior in dinosaurs, but a detailed analysis of the site has not been presented until this study. The bone bed is dominated by the disarticulated, mostly fragmentary and slightly abraded remains of Centrosaurus apertus, with minor occurrences of other taxa, notably teeth from the large tyrannosaurid Albertosaurus libratus. Fossils occur in a stacked to amalgamated succession of lag deposits, deposited and reworked at the erosional base of a paleochannel. The most parsimonious scenario suggests that Centrosaurus material represents part of a large aggregation of animals (possibly numbering in the thousands) that died by drowning on the alluvial plain. Disarticulation occurred at a point upriver from the bone-bed site. Scavenging by theropods, primarily Albertosaurus, at or near the original site of death is suggested by the high number of shed theropod teeth. A subsequent event prior to fossilisation moved the material to its present location removing many juvenile-sized and hydrodynamically light elements from the original death assemblage. Evidence for distinct size classes amongst the preserved elements is not supported by the data, but the size range of elements preserved are representative of living individuals that would have ranged from small juveniles to mature adults. The large data base of specimens from bone bed 43 allows for the illustration of the ontogenetic changes that occurred in the diagnostic cranial elements of Centrosaurus.

INTRODUCTION

The Judith River (Belly River) Group (Fig. 1) of Alberta yields one of the most abundant and taxonomically diverse collections of Upper Cretaceous vertebrate remains in the world, including at least 35 dinosaur species (Braman et al., 1995). The large collections of these dinosaurs made over the past century, and housed around the world, largely have shaped our view of the Late Cretaceous dinosaur fauna of the Northern Hemisphere. The monophyletic

Ceratopsia (the horned dinosaurs) is one of the best represented dinosaur clades, consisting of many genera, known from complete or nearly complete skeletons. The Ceratopsia comprises the small-bodied, basal, Psittacosauridae, confined to Asia, and the Neoceratopsia, generally divided into the Protoceratopsidae (possibly paraphyletic, Chinnery and Weishampel, 1998) and the Ceratopsidae. Ceratopsids are large-bodied, ornithischian herbivores traditionally divided into two monophyletic clades: the 'long-frilled' Chasmosaurinae (Lambe, 1915), and the 'short-frilled' Centrosaurinae (Lehman, 1990). The Chasmosaurinae includes at least nine species distributed among seven genera (*Anchiceratops* Brown 1914; *Arrhinoceratops* Parks 1925; *Chasmosaurus* Lambe 1914; *Diceratops* Hatcher, Marsh and Lull 1907; *Pentaceratops* Osborn 1923; *Torosaurus* Marsh 1891; and *Triceratops* Marsh 1889). The Centrosaurinae contains at least six genera (*Achelosaurus* Sampson 1995; *Avaceratops* Dodson 1986; *Centrosaurus* Lambe 1904; *Einiotaurus* Sampson 1995; *Pachyrhinosaurus* Sternberg 1950; and *Styracosaurus* Lambe 1913), all of which are currently monospecific. Two centrosaurine genera, *Brachyceratops* Gilmore 1914, and *Monoclonius* Cope 1876, recently have been declared *nomina dubia* (Sampson et al., 1997).

The remains of ceratopsids in Alberta are common, and are found as isolated elements, teeth in microsites, as well as articulated and associated specimens as constituents of paucispecific bone beds. A fossil vertebrate-bone bed can be defined as a stratigraphically and geographically constrained bed or facies that predictably yields specimens from more than one individual whenever it is worked. The fossils typically are concentrated along bedding planes and/or erosional surfaces. Within the Campanian-aged Judith River Group (79.0–74.5 MA) only centrosaurs are preserved in bone beds. At least 20 *Centrosaurus* bone beds are known from along the Red Deer and South Saskatchewan rivers, while two *Styracosaurus* bone beds are known and confined to the Red Deer River valley badlands in and around Dinosaur Provincial Park. In the Maastriichtian, the chasmosaurine *Anchiceratops* is known from one bone bed in the Horseshoe Canyon Formation, while *Pachyrhinosaurus* has been identified from bone beds in the Horseshoe Canyon (Langston, 1975), St. Mary River (Dodson and Currie, 1990), and Wapiti formations (Tanke,

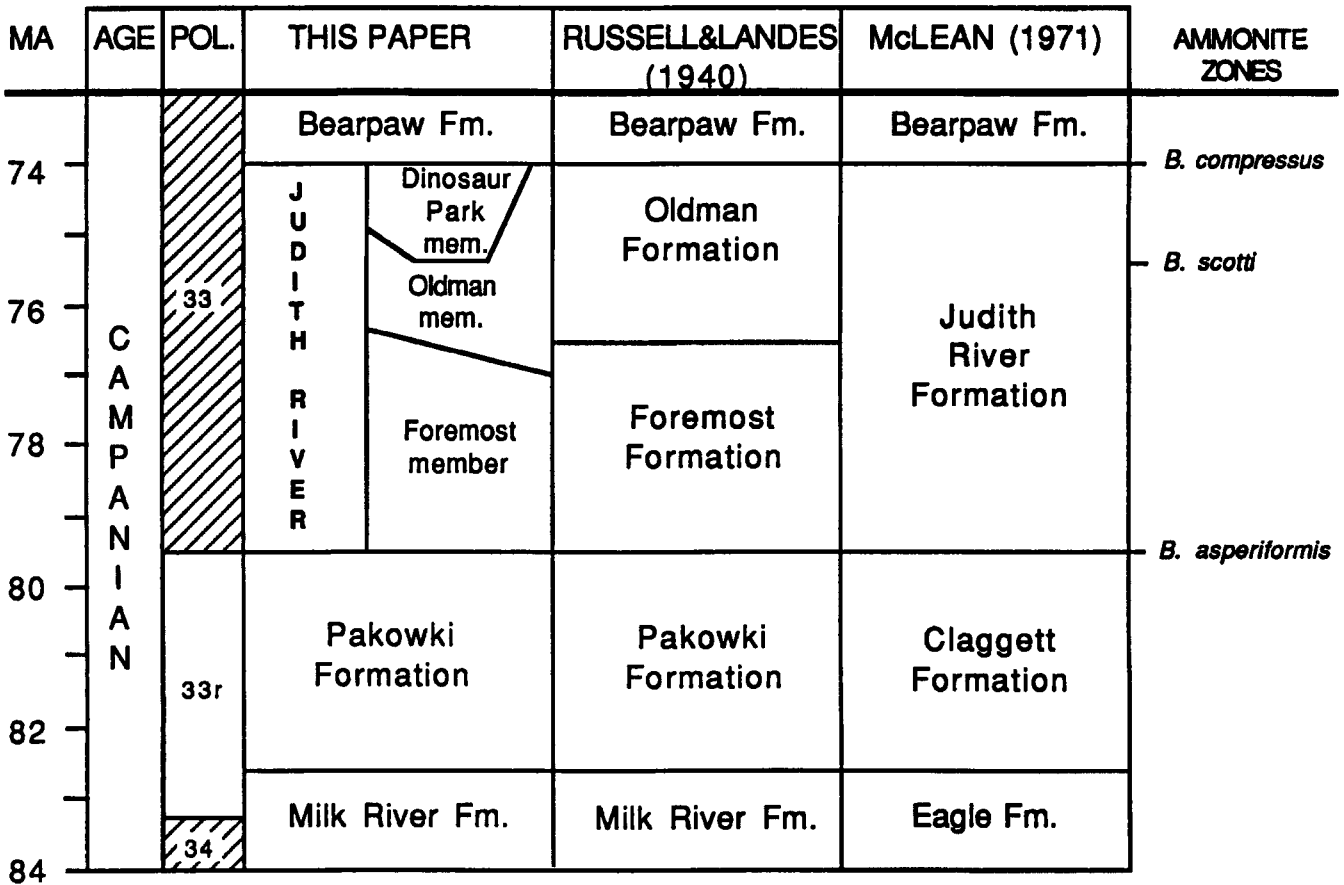


FIGURE 1—Geologic Column for southern Alberta. (After Bramen et al., 1995)

1988) of Alberta, as well as from the Prince Creek Formation of the Alaskan North Slope (T. Fiorillo, pers. comm.).

Ceratopsids are defined largely by their cranial morphology, specifically the size and shape of the parietal, and the nasal and the postorbital horns. The ceratopsid material described herein from bone bed 43 (BB 43) has been referred to *Centrosaurus* by Currie and Dodson (1984). The convoluted taxonomic history of *Centrosaurus* and *Monoclonius* has been reviewed thoroughly by Dodson (1990) who concluded that only one species of *Centrosaurus* (*C. apertus*) is valid. The genus is distinguished by a long nasal horn, relatively short orbital horns, and is diagnosed (Lambe, 1904, 1910) by two sets of hook-like processes that originate near the midline of the thick posterior parietal bar (although one member of the second hook pair may variably be missing).

In the 19th and 20th centuries, dinosaur paleontology has focused on the collection of complete skulls and whole skeletons, with disarticulated bone assemblages (bone beds) largely being ignored, as they have been deemed to lack easily collectable, display-quality specimens. Since the 1960s, the science of taphonomy has blossomed, with numerous mass assemblages of invertebrates, vertebrates, and plant localities being studied intensively (see DiMichele and Hook, 1992; Behrensmeyer and Hook, 1992; Wing and Sues, 1992 for numerous references). In Canada, the modern era of taphonomic research on dinosaurs began with Dodson's (1971) research in DPP on di-

nosaur bone beds and quarries. Additionally, he developed hypothetical decomposition sequences for dinosaurs under various conditions, and made inferences about their association with different paleocommunities. Significant taphonomic work on dinosaur bone beds in the northern hemisphere include those of Lawton (1977), Horner and Makeela (1979), Dodson et al. (1980), Horner (1982), Lehman (1982, 1989), Currie and Dodson (1984), Visser (1986), Norman (1987), Fiorillo (1991a), Rogers (1991), Varricchio and Horner (1992), and Varricchio (1995).

A preliminary discussion of BB 43 was published by Currie and Dodson (1984) who concluded that the centrosaurine remains preserved therein represented a catastrophic mass death assemblage of *Centrosaurus*. Rogers (1991), examining bone beds of *Achelosaurus* and *Einiosaurius* from the Two Medicine Formation, Montana, and Visser (1986), working on a *Styracosaurus* bone bed from the Dinosaur Park Formation, Alberta, also recognised their localities as representing catastrophic assemblages, with all the preserved remains coming from centrosaurines that died at or near the site of burial within a relatively short period of time. Other significant works on bone beds containing large amounts of ceratopsid material include those of Langston, Jr. (1975; *Pachyrhinosaurus*, St. Mary Formation), Lehman (1989; *Chasmosaurus mariscalensis*, Ajuga Formation), Ryan (1992; *Centrosaurus*, DPP), and Wolfe and Kirkland (1998; *Zuniceratops* (a basal neoceratopsid), Moreno Hill Formation). Work is cur-

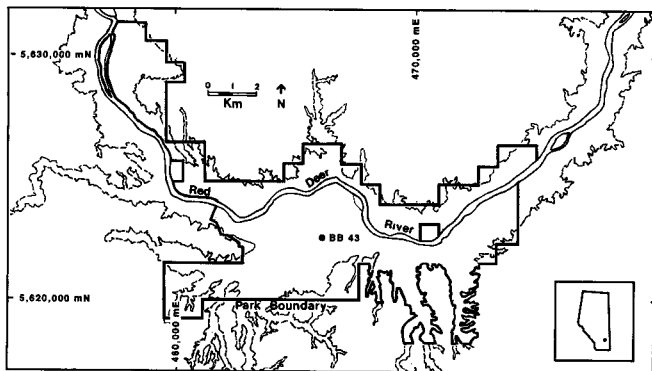


FIGURE 2—Locality map of bone bed 43 (quarry 143) in Dinosaur Provincial Park, Alberta. UTM coordinates are 456920 N, 5622350 E (S 5, T 21, R 11, W of 4).

rently in progress on the taphonomy and systematics of a putative new species of *Pachyrhinosaurus* recovered from a paucispecific bone bed in Grande Prairie, Alberta.

MATERIALS AND METHODS

Location

BB 43 (Fig. 2) is located about 48 km north of Brooks, Alberta, within the core area of the 75 km² of badlands that comprise the UNESCO World Heritage site of DPP. UTM coordinates are 456920 N, 5622350 E (map datum NAD 27), (S 5, T 21, R 11, W of 4).

Methods

The *Centrosaurus* BB 43 (also known as quarry 143) was noted early on by paleontologists in the DPP Region. In a photograph dated 1915, an unknown member of Charles H. Sternberg's field crew photographed portions of BB 43. In 1921, C. M. Sternberg excavated the type specimen of *Daspletosaurus torosus* from the upper Oldman Formation just below the western margin of BB 43, and could not have failed to recognize the dense accumulation of ceratopsid bones in the area. After the bone bed was 'rediscovered' by Park staff in 1979, systematic grid excavations were begun in that year by staff and volunteers of the Provincial Museum of Alberta, and later continued by many of the same staff working for the Royal Tyrrell Museum of Palaeontology (Currie, 1981, 1982). These excavations continued, with the exception of 1990, until 1991. Each year a new area of excavation was opened or a previous years' excavation was continued. Between 1984 and 1989 seven excavations, containing 144 1m² grids, were opened, with 72 grids being completely excavated (all fossil material removed; see Figures 3 and 4 for locations). The excavations ranged in size from 4 m² to 35 m², and were situated along, at, or near the margin of the bone bed exposure, and at several points between. All quarries were worked using standard excavation techniques. All specimens were mapped with respect to location and orientation. Material collected included all non-ceratopsid remains, regardless of condition, any complete ceratopsid element, all ceratopsid skull material regardless of condition, and any other ceratopsid element from

which significant morphological or taphonomic data could be gathered. The ubiquitous rib and vertebral fragments, as well as heavily abraded bone chips, usually were not collected. Morphologic and taphonomic data were collected in the field and cross-referenced after preparation. Prepared elements were measured for all relevant linear dimensions, following the methods of Lehman (1982) and Dodson (1990). Orientation data were collected in the field using a Brunton Compass for all collected specimens. Additional orientation and length measurements were made directly from the original quarry maps using a Steadtler Navigational Protractor (# 999-5). The stratigraphically highest and lowest specimens in each grid were measured relative to a 0m field datum and later converted to elevation above sea level (m ASL). Microvertebrate screen-washing was not conducted in BB 43, but removed rock matrix was crumbled systematically and examined for small fossil inclusions. Other than heavily abraded bone chips, few significant fossils were encountered. A complete data set, including a list of all catalogued elements, their linear dimensions, a description of their taphonomic features, orientation data, and complete maps for all quarries are on file at the Royal Tyrrell Museum of Palaeontology.

During the summer of 1989, sixty-two points at the bone-bearing layer at the base of the *Centrosaurus* bone-bed lithosome were identified and surveyed, using a Wild T2 theodolite with a telescopic level on a GST20 tripod (see Fig. 3 for the location of these survey points). In 1996, a stratigraphic section was measured from the lower contact of the Dinosaur Park Formation upwards through the bone-bed lithosome on the western margin of the exposures hosting the bone bed (Fig. 5).

Analysis of BB 43 material in this study is confined to the specimens catalogued between 1979 and 1989 ($n = 1576$), and to the data contained in the maps produced from 1984 to 1989. The latter restriction has been implemented because the senior author was involved in each of these years' excavations, but not previously. The excavations included in this study are as follows: 1984 (1 × 11 m; Fig. 3A, 6); 1985 (2 × 11 m; Fig. 3A, 6); 1986 East (Fig. 3B); 1986 West (Fig. 4); 1987 (Fig. 3C); 1988 (3 × 3; Fig. 3); 1989 North (1 × 4 m; Fig. 3D); and 1989 South (2 × 2 m; Fig. 3E). The 1984 and 1985 excavations abutted each other, and their data were combined. The excavation in 1988 was designed to provide the Park's staff with a permanent display to be used for interpretative tours and, as such, all grids were uncovered but not completely excavated. The excavation map for 1984 and 1985 is reproduced in Figure 6 as being representative of a typical excavation.

LOCAL GEOLOGY

The Judith River Group (Fig. 1) comprises an eastward-thinning, non-marine-to-paralic clastic wedge that was deposited along the western margin of the Western Interior Basin during mid- to late Campanian times (McLean, 1971; Eberth and Hamblin, 1993). The Judith River Group crops out intermittently for more than 1000 km, from central Alberta and Saskatchewan in the north, to south-central Montana in the south. The Group thickens to the west and northwest, passing into the non-marine Belly River, Brazeau, and Wapiti formations (Eberth, 1990). In Montana, the Group passes westward into the

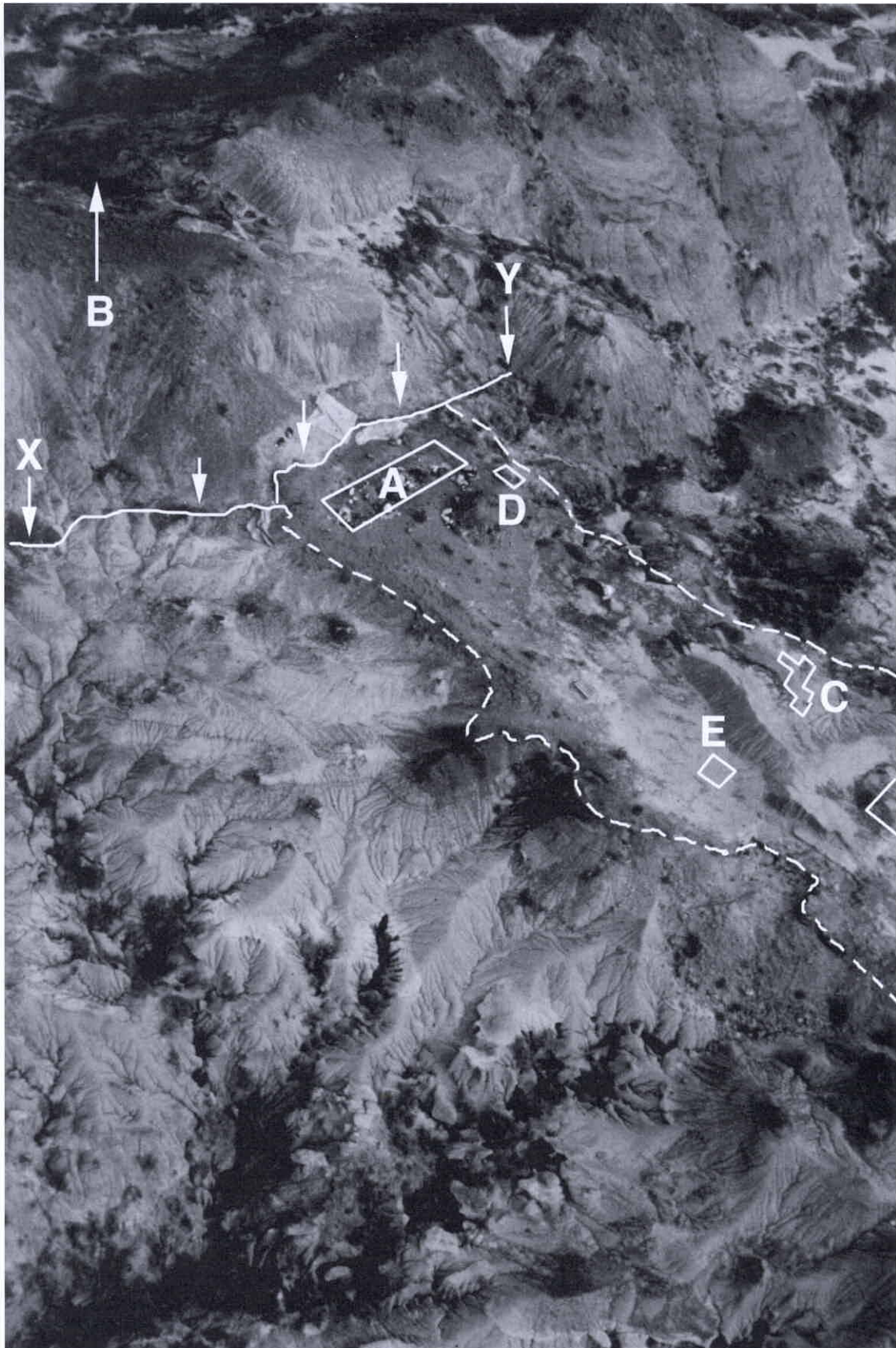


FIGURE 3—Aerial view of the western two-thirds of bone bed 43, August 1985, showing quarries. (A) 1984 and 1985 quarries; (B) 1986 (east) (obscured by exposure); (C) 1987 quarry; (D) 1989 quarry (north); (E) 1989 quarry (south). Thirty nine survey points were run between X and Y and used to reconstruct the palaeochannel (Fig. 7). Arrows between X and Y indicate the cross-sectional exposure of the palaeochannel.

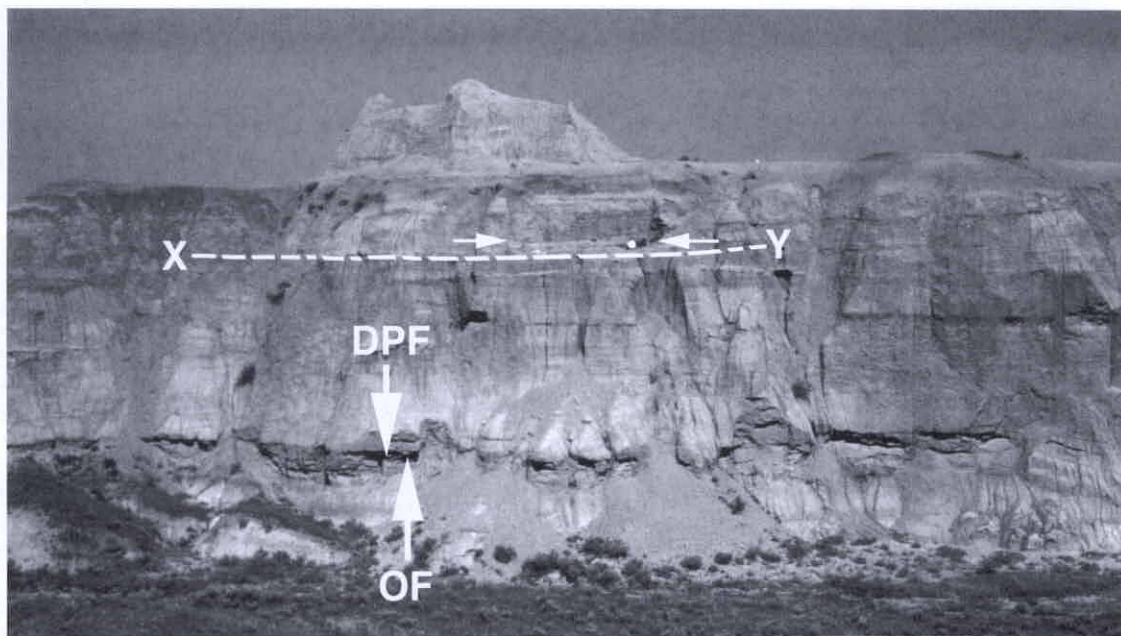


FIGURE 4—View of 1985 quarry (west) marking the eastern erosion truncation of bone bed 43. The quarry lies approximately 10 meters above the contact of the Dinosaur Park and Oldman formations and lies between the horizontal arrows. The bone bed paleochannel is marked to its visible margins at X and Y. Abbreviations: DPF = Dinosaur Park Formation; OF = Oldman Formation. The sandstone structure above the bone bed is the 'citadel' referred to in field notes.

thick, continental sediments of the Two Medicine Formation (Eberth and Hamblin, 1993). The Judith River Group is divided into three formations; in ascending stratigraphic order these are the Foremost, Oldman, and Dinosaur Park formations. Within DPP, bedrock exposures range in thickness from 60–100 m, and in ascending order include the uppermost Oldman Formation, the complete Dinosaur Park Formation, and the basal 25 m of the Bearpaw Formation (in the eastern part of the park).

The area, which is now DPP, was located on the eastern edge of the broad, low-gradient coastal plain along the western shoreline of the Western Interior Seaway. BB 43 is preserved within the fluvial sandstones of the Dinosaur Park Formation about 20 m above its base. The formation comprises alluvial, estuarine, and paralic facies, bounded at its base by a regional disconformity, and is overlain sharply by the shales of the Bearpaw Formation. The regional disconformity crops out throughout much of the Judith River Group in Canada, and represents an erosional surface of negligible geologic time that is time-transgressive north to south (Eberth and Hamblin, 1993). The Dinosaur Park Formation comprises strata of Late Campanian age (Judithian of the North American Land Mammal 'Age' System). Radiometric Ar 40/Ar 39 dates of bentonites provide an age of 76.43 ± 0.28 Ma from just below the formation, and 75.14 ± 0.16 Ma from above its' base (Eberth and Hamblin, 1993). The formation represents a low-to-high sinuosity, alluvial-to-tidally-influenced, fluvial-to-estuarine system composed of deep (up to 25 m), wide (hundreds of meters) channels (Koster et al., 1987; Wood 1989; Eberth and Hamblin, 1993). Mean annual discharges were from 60 to 360 m³/s and could have reached 460 to 1390 m³/s under flood conditions (Wood, 1985). The mean paleocurrent direction of the Dinosaur Park Formation is

east-southeast, suggesting an origin in the north-central Cordillera (Eberth, 1990; Eberth and Hamblin, 1993).

Modern and Ancient Setting of Bone Bed 43

The preserved outcrop of the fossil-producing horizon covers approximately 13,000m² and is roughly 100 × 130 m as determined by a compass and pace method of mapping. The surface topography (Fig. 3) is roughly planar, but both the eastern and western margins are covered by overburden. In these directions the depositional edges of the bone bed and its host facies are well preserved. The southern and northern edges are truncated erosionally along modern cliff faces. To the southeast the bone bed is overlain by tall sandstone peak (Fig. 4) referred to in field notes as "the citadel."

BB 43 occurs at the base of the uppermost sandstone body, interpreted here as a paleochannel-fill, in an amalgamated lithosome that comprises three, stacked sandstone bodies (Fig. 5, 12.3–16.8m). Each sandstone body is bounded below by a locally-erosive surface that is overlain by a variably-developed decm-thick lag consisting of intraformational mudstone and ironstone clasts, fossil wood, and vertebrate fossils. Lag deposits fine upward into fine-grained sandstones that are organized into decm-scale and thinning-upward sets of trough cross-bedding. Where preserved, the uppermost portion of each sandstone consists of ripple-laminated-to-massive, very-fine sandstone and siltstone. BB 43 is distributed broadly and in association with the lag deposit that defines the base of the uppermost sandstone body (Fig. 5, 15.5m).

Strike-parallel cross-sections through the basal erosional surface and associated fossiliferous lag deposit in the BB 43 sandstone reveal two deeply erosional areas (Fig. 7,

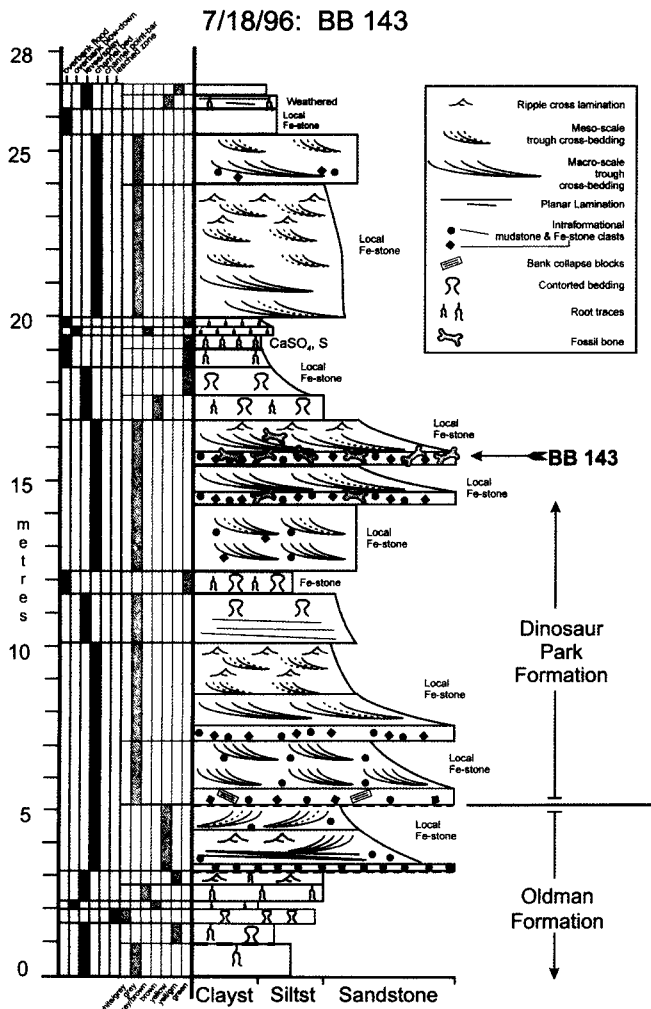


FIGURE 5—Stratigraphic column through the bone bed 43 lithosome (see Fig. 4 for location of section).

points 19–30 and 34–38), and one area where fossils are concentrated in two discrete, stacked lags (Fig. 7, points 30–34). Iron-stained, mudstone drapes occur locally along vaguely-developed m-scale inclined surfaces in the eastern-most portion of the sandstone (Fig. 7, points 30–42). Inclined surfaces do not continue into the lowest portions of the sandstone fill. The entire succession fines up conformably into massive to locally-shaley siltstone with locally-developed vertical root traces. The exposed strike-parallel cross-section along the southern cliff face reveals a broadly U-shaped basal erosional surface and overlying fossiliferous lag (Fig. 4), with very-low-angle inclined surfaces dipping westward (to the left in Fig. 4) toward the thickest portion of the sandstone body. Bones are concentrated most densely in the lowest (deepest) portions of the sandstone.

RESULTS

Taxonomic Composition of Bone Bed 43

Based on all catalogued material (n = 1576), the bone bed has yielded 80.4% (n = 1280) ceratopsid fossils (excluding rib fragments and uncatalogued, unidentified bone fragments; Table 1). The actual percentage of ceratopsids in the bone bed is much higher, given that not all ceratopsid fossils were collected, and that all other vertebrate fossils were. The minimum number of individual (MNI) putative *Centrosaurus apertus* collected from the excavations is 57 (Table 2), based on the total number of braincases and loose occipital condyles, all of which are from adult-sized animals. None of the condyles could be associated with the braincases; hence, the combined total was used for assessing the MNI. All diagnostic parietal fragments (14) are referable to *C. apertus*. The only ceratopsid material identified as non-*Centrosaurus* is a partial *Chasmosaurus* skull (TMP 79.11.147). The articulated nature of this specimen and its extremely abraided (Stage 3; Table 4) condition suggests a separate taphonomic history when compared to the *Centrosaurus* material. The only other articulated specimen from BB 43 is a partial series of distal caudals recovered with a skin impression.

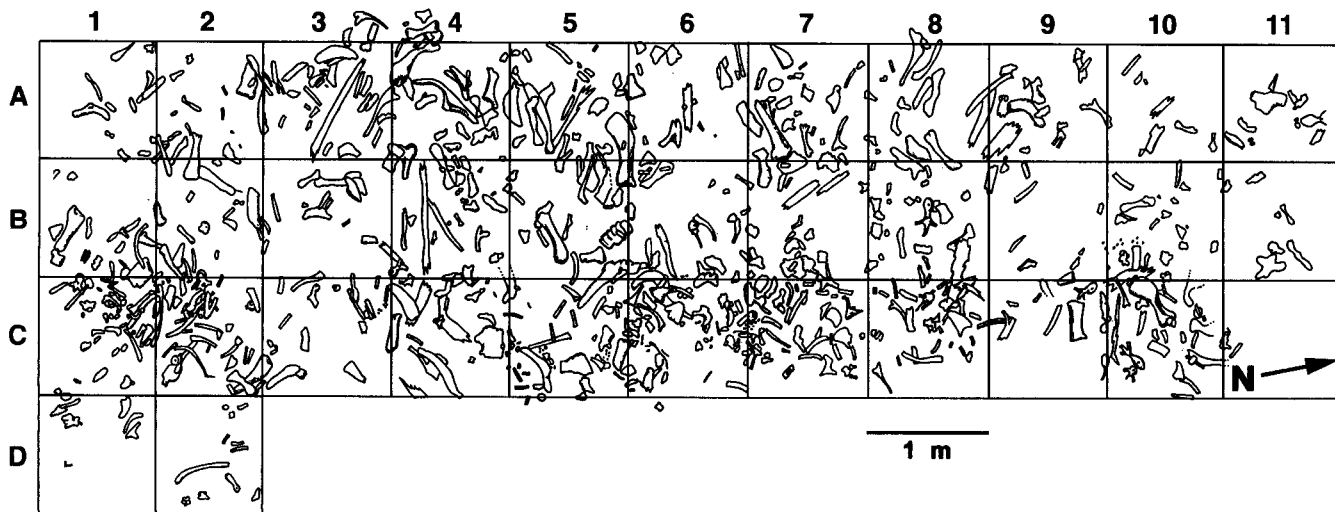


FIGURE 6—Map of quarry from 1984 and 1985 (A in Fig. 3).

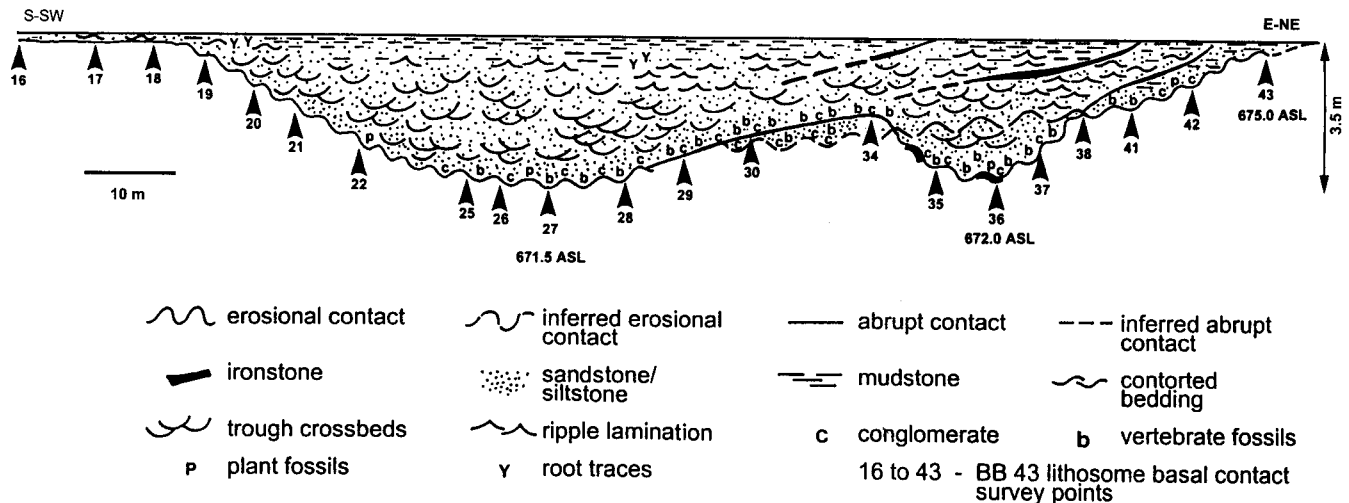


FIGURE 7—Cross-section from S-SW to E-NE through the western margin of the bone bed 43. Numbers indicate survey stations.

The remaining 19.1% ($n = 296$) catalogued material is divided between large and small theropods (6.6%) and other non-theropod vertebrate remains (12.5%). The latter are composed of hadrosaur (80; mostly teeth), *Myledaphus* teeth (37), *Champsosaurus* (25; mostly rib fragments), ankylosaur (18; mostly scutes), turtle shell fragments (18), crocodile teeth (9), fish scales (6), indeterminate amphibian vertebrae (3), and one each lizard and mammal tooth.

The theropod material comprises 105 specimens, of which 82 (78%) are teeth, which are distributed amongst taxa as follows: 44 *Albertosaurus*, 22 theropod indet. fragments (but probably from *Albertosaurus*), 6 *Saurornitholestes*, 5 *Aublysodon*, 3 *Dromaeosaurus*, and one each *Daspletosaurus* and *Troodon*. The 23 non-tooth fossils consist of 14 ornithomimid fragments and nine theropod indet. bone fragments.

Data from the quarry maps show that the most abundant type of material uncovered was unidentifiable bone fragments (typically <50 mm — 910; 43.6%), with c.f. *Centrosaurus* rib fragments (605; 29.0%), identified *Centrosaurus* material (535; 25.6%), and other non-ceratopsid vertebrates (36; 1.7%) making up the remainder of the mapped material.

Skeletal Representation

Except for the partial ceratopsid tail collected in 1987, all ceratopsid elements from BB 43 were disarticulated, frequently broken, and disassociated. Fused elements commonly present include adult-sized braincases and the supraorbitals (the fusion of the frontal, lacrimal, palpebral, prefrontal and postorbital) of adult-sized ceratopsids. Individual supraorbital elements from juvenile and sub-adult ceratopsids were recovered infrequently, as were sub-adult sized basioccipitals. No other non-fused braincase elements were identified. Notably, no complete or partial skulls were recovered, suggesting both that the skulls did not fuse, even in old individuals, and that the ceratopsid material had ample time for even the soft tissue connections between tightly associated elements to decompose. Elements from every region of the ceratopsid skeleton are present in BB 43, although no carpals, tar-

sals, scleral ossicles, or palatal elements can be identified with confidence. This likely is due to the difficulty in identifying these poorly described and relatively non-descript elements in the case of the three former, while the delicate nature of the palatal elements may have lead to their being broken up into difficult to identify smaller fragments. There was no preferential preservation of elements from either side of the body.

Table 3 indicates the average length, range, and number of elements for all of the BB 43 quarries excavated between 1984–1989. For completely excavated 1m² grids from these quarries, the number of specimens ranges from 7 to 133, with an average of 30.0 specimens per grid. Fossil material in the quarries ranged in length from <5 mm (bone chips and tooth fragments) to 2500 mm (for wood impressions, the major non-vertebrate component of BB 43). The average length of specimens per quarry ranges from 105.7 mm (1989) to 201.5 mm (1987), with an overall average of 151.0 mm for all completely excavated grids (Table 3).

Relative Age Profile of the *Centrosaurus* Bone Bed Material

Currie and Dodson's (1984) conclusion that the centrosaurine material in BB 43 resulted from the mass death of a large number of animals was based, in part, on their recognition of discrete size classes, as well as the taphonomic condition of the material. The size and taphonomic criteria used in examining the same material for this study is outlined below.

As has been noted by Varricchio (1995) and others, determining the chronological age of dinosaur fossils is not currently possible. The typical criteria used for mammalian material (tooth eruption patterns, counts of tooth annuli, crown height and wear patterns, and degree of epiphyseal fusion) cannot be applied to reptiles. Instead, the material under examination must be aged in a relative sense using as criteria, (1) surficial bone texture, (2) the size of the element, and, (3) degree of ontogenetic development.

TABLE 1—Taxa catalogued from bone bed 43 between 1979–1989.

Taxa	Total for catalogued material from bone bed 43 (n = 1279)
Chondrichthyes	
Holocephali	
Chimaeriformes	
Chimaeridae	
<i>Myledaphus</i>	37
Osteichthyes idet.	6
Amphibia idet.	3
Reptilia	
Anapsida	
Testudinata	
Chelonia	
Cryptodira idet.	18
Diapsida	
Choristodera	
Chamosauridae	
<i>Chamososaurus</i>	25
Archosauria	
Crocodylia	
Crocodylidae	
<i>Brachyuranochampsia</i>	9
Saurischia	
Theropoda	
Carnosauria	
Tyrannosauridae	
Tyrannosaurinae	
<i>Albertosaurus libratus</i>	44
<i>Daspletosaurus torosus</i>	1
Aublysodontinae	
<i>Aublysodon mirandus</i>	5
Tyrannosaurid idet.	23
Ornithomimosauria	
Ornithomimid idet.	14
Coelurosauria	
Maniraptora	
Dromaeosauridae	
<i>Dromaeosaurus albertensis</i>	3
<i>Saurornitholestes langstoni</i>	6
Troodontidae	
<i>Troodon formosus</i>	1
Ornithopoda	
Hadrosauridae	
hadrosaurid idet.	80
Ornithischia	
Ceratopsia	
Ceratopsidea	
Centrosaurinae	
<i>Centrosaurus apertus</i>	1,256
Chasmosaurinae	
<i>Chasmosaurus</i> sp.	1
Mammalia	
Theria	
Metatheria	
Marsupialia	
Marsupial(?) idet.	1

TABLE 2—c.f. *Centrosaurus* elements catalogued from bone bed 43 between 1979–1989.

Region of body	Element	# In one adult <i>Centrosaurus</i>	Total catalogued
Cranial	Jugal	2	33
	Maxilla	2	15
	Nasal	1	40
	Parietal	1	68
	Prementary	1	28
	Premaxilla	2	15
	Other skull elements	8	5
	Quadrate	2	20
	Rostral	2	9
	Squamosal	2	48
Braincase	Unidentified skull elements	—	29
	Braincase (fused)	1	37
	Occipital condyle	—	20
Orbital Region	Supraorbital	1	79
	Lacrimal	—	1
	Orbital horn core fragments	—	15
	Palpebral	—	4
	Postorbital	—	9
Mandible	Prefrontal	—	3
	Dentary	2	74
	Other mandibular elements	10	38
Axial	Teeth*	—	112
	Vertebrae	70	156
	Ribs (including fragments)	42	109
	Chevron	25	1
	Tendons	—	3
Appendicular			
	Pectoral Girdle		
	Coracoid	2	2
	Scapula	2	11
	Sternal plates	2	4
	Humerus	2	16
	Radius	2	4
	Ulna	2	13
Pelvic Girdle	Ilium	2	24
	Ischia	2	22
	Pubis	2	10
	Femur	2	10
	Fibula	2	12
	Tibia	2	16
	Unidentified limb elements	—	19
	Metapodials	56	52
	Phalanges	—	19
	Unidentified bone fragments		
Total		288*	1,279

* Total number of elements in one complete adult *Centrosaurus* excludes teeth, tendons, sclerotic plates, and assumes the elements of the braincase and supraorbital are fused.

Bone Texture

Ryan (1992) and Sampson et al. (1997) noted that the flat bones of the centrosaurine skull (medial surface of the jugal, nasal, squamosal and postorbital [jugal contact], and the ventral surface of the parietal) exhibit one of three distinct surface textures that can be associated reliably with the stage of ontogenetic development (see Sampson et al., 1997, for a complete discussion of this argument). These bone textures are:

Long-grain texture (Fig. 8C, 9D): characterised by multi-

TABLE 3—Summary of abundance and lengths of mapped specimens from excavated grids in bone bed 43, 1984–1989. * indicates incompletely excavated grids included in data. All grids 1 × 1 m.

Education year & grids n = # mapped specimens	# Of specimens/ grids n = # grids	Average length of specimens (mm) n = # measured specimens	Specimen length range (mm)
1984 19 grids n = 387	20.4 n = 19	169.3 n = 385	5–940
1985 10 grids n = 416	41.6 n = 10	139.2 n = 406	5–630
1984–85 29 grids n = 803	27.7 n = 29	155.0 n = 791	5–940
1986 east 8 grids n = 524	65.6 n = 8	117.9 n = 436	10–590
1986 west 10 grids n = 258	23.5 n = 11	185.1 n = 239	20–810
1987 13 grids n = 278	22.3 n = 15	201.5 n = 253	15–900
1988 15 grids* n = 204	13.6 n = 15	161.7 n = 188	5–2,500
1989 4 grids n = 127	31.8 n = 4	113.8 n = 116	10–524
1989 south 4 grids n = 157	31.4 n = 5	105.7 n = 135	7–600

ple, parallel, fine striations (up to 20 per cm) running in the direction of bone growth (typically the long axis). This texture is indicative of bone undergoing rapid growth and remodelling at the time of death, and is seen in juvenile centrosaurines whose skulls have not developed, or are only starting to develop, their diagnostic ornamentations.

Mottled texture (Fig. 9D) appears as a fine pitting as the long-grain striations are disrupted by the inception of the typical adult texture. This represents a transitional stage between long-grain and adult textures, and is found on elements that are at or near their adult size, with the bone taking on its final adult size and form (e.g., incipient hooks forming on *Centrosaurus* or spikes on *Styracosaurus*).

The adult texture is characterized by a variably smooth to highly textured surface of any fully grown adult bone that also lacks the distinctive long-grain striations or fine pitting of the long-grained or mottled textures. Adult texture can vary between elements, but, when identified on the appropriate skull element, these elements have fully developed diagnostic adult ornamentation, and no trace of long-grain or mottled texture is present.

Size

The material from BB 43 was allocated to one of three size groupings—juvenile, sub-adult, and adult—based on comparison with the museum specimens listed below. These groupings do not directly imply chronological age, but can be used in the broad sense of identifying the probable relative age of the animal that an element came from in the same way that extant animals can be determined to be 'young' or 'old' based on upon their size.

The published illustrations and measurements of the

skeleton of *Centrosaurus apertus* YPM (Yale Peabody Museum) 2015 (Lull, 1933) were used as the size basis for adult specimens. YPM 2015 is presumed to be a fully grown adult, based on the thickness of the posterior parietal bar, and the well-developed parietal hooks. Element sizes listed for this specimen fall within the upper size range for similar elements collected from centrosaurines in the Campanian-aged deposits of Alberta and Montana. Measurements of *Brachyceratops montanensis* (USNM 7951—a partial skull, and USNM 7952—a partial post-cranial skeleton) were used for determining features associated with sub-adult specimens. Additionally, the measurements, illustrations, and photographs provided by Gilmore (1914, 1917, 1922) for *Brachyceratops* were used. USNM 7951 has a thin posterior parietal bar lacking ornamentation, making it a putative sub-adult (Sternberg, 1940; Sampson et al., 1997). Generally, sub-adult material was considered to be between one-half and two-thirds the size of equivalent adult specimens. Material classified as juvenile on the basis of size, was so recognized if it was 20% smaller than *B. montanensis* material. TMP 82.16.11, a cf. *Monoclonius* (Dodson and Currie, 1988), consisting of a complete but partially crushed frill (parietal and squamosals) with an associated laterosphenoid, also was used to help determine the features of juvenile material. Additionally, most of the types and referred centrosaurine skulls and their associated post-cranial material in the collections of the American Museum of Natural History (AMNH), Academy of Natural Sciences, Philadelphia, Canadian Museum of Nature (NMC), Museum of the Rockies, Royal Ontario Museum, Royal Tyrrell Museum of Palaeontology (TMP), and the United States National Museum (USNM) were examined to help determine the size grouping of elements. If the inferred size grouping for a bone was uncertain, the specimen was placed in the smaller of the two possible categories. The criteria used for placement were as follows:

- Juvenile—A bone that is less than one-half the size of that of a typical adult specimen.
- Sub-adult—A bone between one-half and two-thirds the size of that of a typical adult specimen.
- Adult—A bone that is approximately the size of that of a typical adult specimen.

Ontogenetic Development

In the course of examining the centrosaurine material from BB 43, as well as other Campanian-aged centrosaurine material housed in other North American collections, it became apparent that it is possible to distinguish the putative age of individual skull elements and skulls based on their degree of ontogenetic development. Although the post-cranial skeletons of ceratopsids appear to be highly conservative, the nasals, parietal and postorbital elements of each taxon undergoes significant ontogenetic change, concordant with the size and surface bone texture of the element. The large sample sizes of various elements obtained from different centrosaurine bone beds have made it possible to recognise the ontogenetic trajectory of most centrosaurines. Using these data, Sampson et al. (1997) demonstrated that for centrosaurine ceratopsids for which significant bone bed material is known (*Achelosaurus*, *Centrosaurus*, *Einosaurus* and *Pachyrhinosaurus*), each cen-

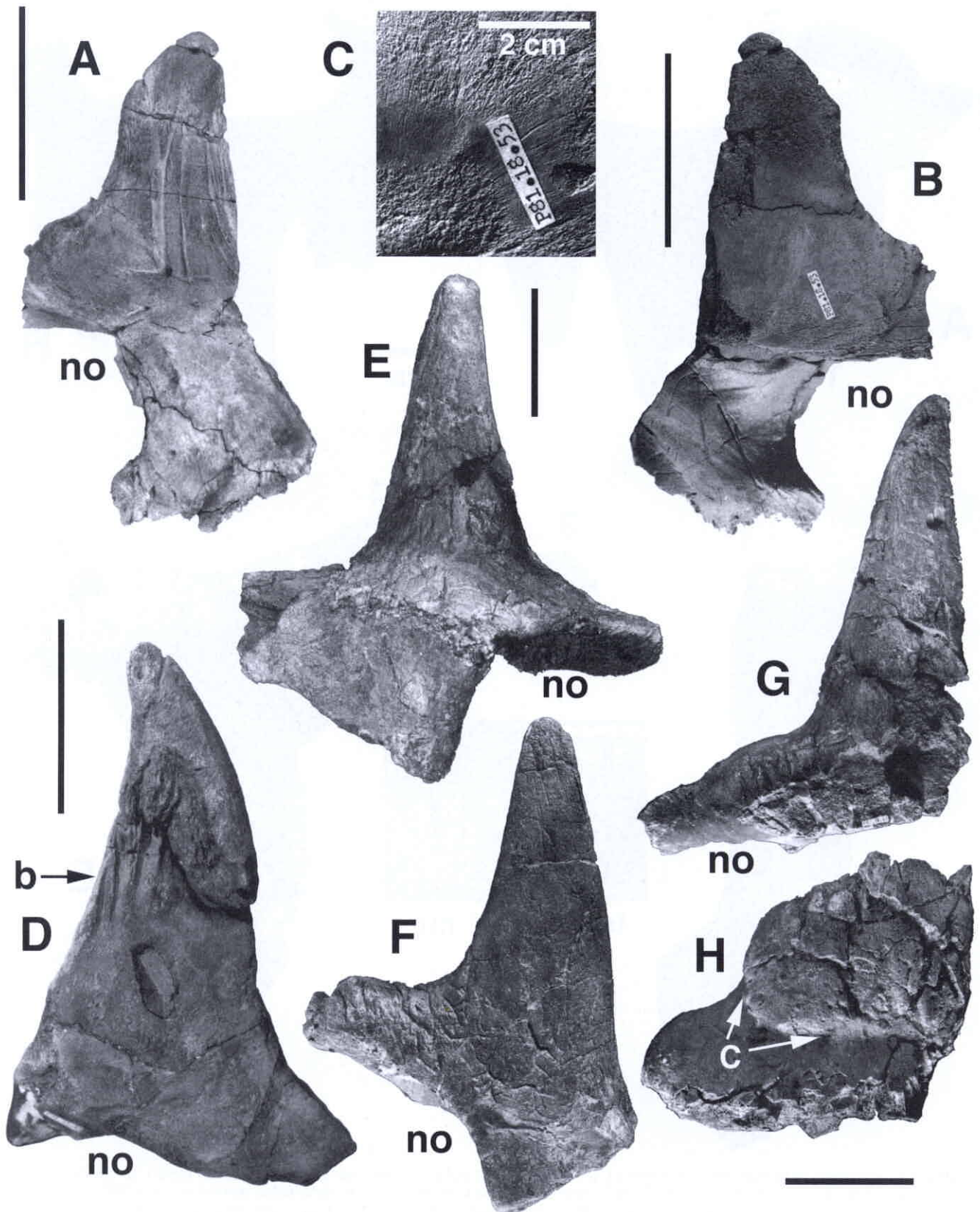


FIGURE 8—*Centrosaurus* nasals from bone bed 43. (A-C) TMP 81.18.53, left nasal in (A) lateral view and (B) medial view. (C) is a close up of juvenile bone texture from (B). (D) TMP 79.11.83, medial view of left nasal with partially fused right nasal at apex. Note bevelling of medial surface below fused elements. (E) TMP 87.18.39, fused nasals in right lateral view. (F) TMP 82.18.67, fused nasals in left lateral view. (G) TMP 82.18.44, fused nasals in left lateral view. Nasal horn is broken above base. Note constriction due to bone overgrowth at base. Abbreviations: b = bevelling; c = constriction; no = narial opening. Scale bar = 10 cm unless labelled.

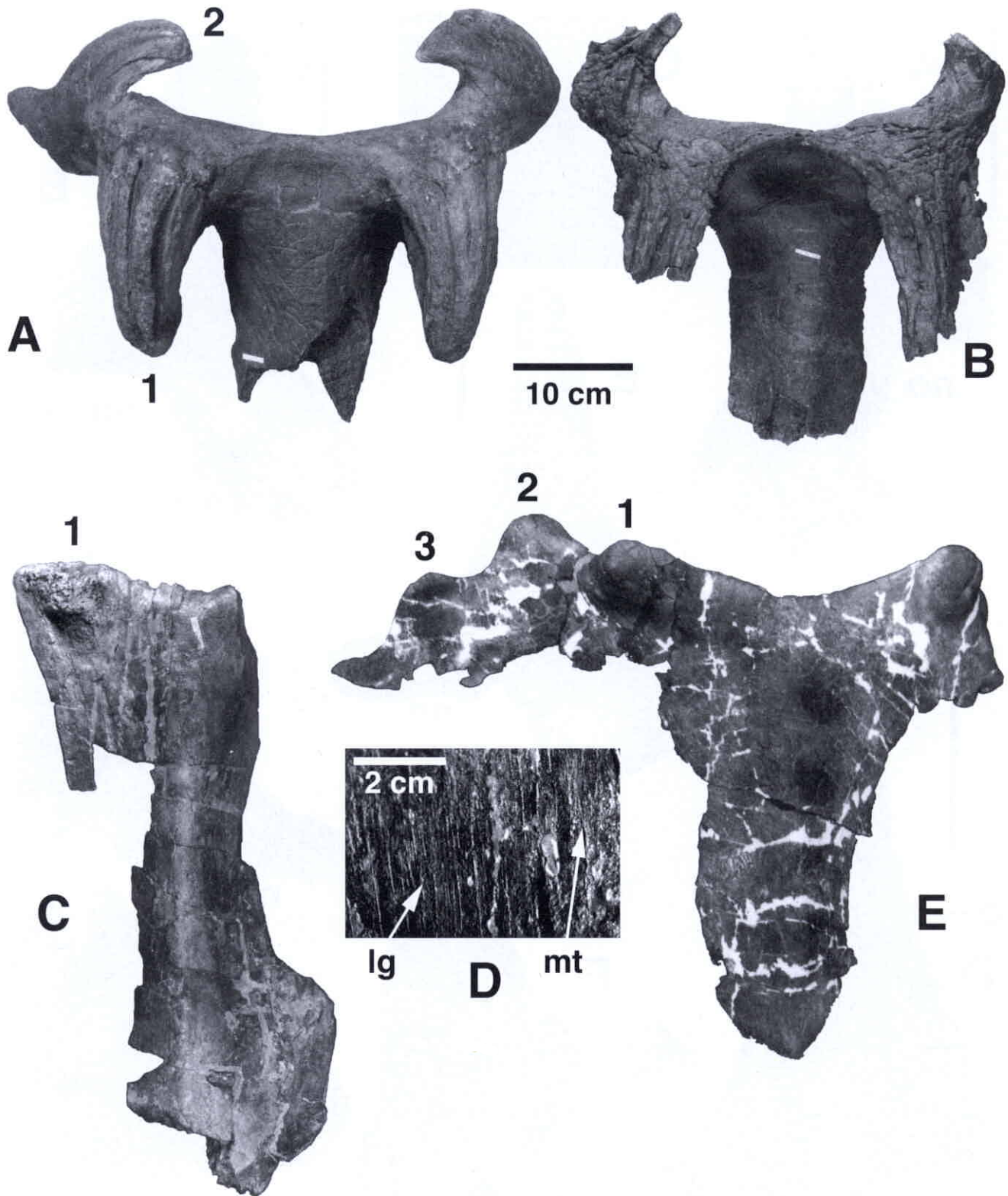


FIGURE 9—*Centrosaurus* parietals from bone bed 43. (A) TMP 82.18.79 (adult), dorsal view. (B) TMP 82.18.277 (adult), dorsal view. (C) TMP 80.18.260 (juvenile), dorsal view. (D) TMP 80.18.260, close up of juvenile bone texture on distoventral parietal bar. (E) TMP 79.11.76 (sub-adult). 1–4 = marginal processes, numbered from medial to lateral (see text). Abbreviations: lg = long-grain texture; mt = mottled texture. Scale bars for A, B, C, and E = 10 cm.

troosaurine starts life as a juvenile with a skull that includes: (1) an unfused, short-based, laterally compressed nasal horn, that points directly up or recurves slightly at its apex; (2) a parietal with thin lateral and posterior margins, lacking fused epoccipitals or parietal ornamentation (hooks or spikes), and; (3) a postorbital unfused to any other element of the adult supraorbital (frontal, lacrimal, palpebral, and prefrontal) expressing a short, roughly pyramid-shaped horn over the orbit. Elements attributed to juveniles, whether present in isolation in a bone bed, or present on a skull, exhibit long-grain bone texture. As the centrosaurine obtained adult size, and probably with the onset of sexual maturity: the nasals fused along the midline and expanded, often procurving; the parietal thickened along each of its margins, progressively fusing epoccipitals from the posterior midline forward; and the epoccipital-covered outgrowths of the parietal developed into the diagnostic ornamentation of the taxon. During this transition, the elements of the supraorbital region fused. Individual elements or skulls with diagnostic cranial ornamentation are noticeably larger than elements or skulls undergoing ontogenetic modification, and the latter always show mottled bone texture, or mottled bone texture overlying the long-grained bone texture of smaller elements. This transitional, sub-adult, stage was probably brief, with the nasals, parietals, and orbital horns rapidly taking on their adult morphology and adult bone texture. Material previously referable to *Brachyceratops* and *Monoclonius*, including articulated skulls and the holotype specimens, are recognized now as juvenile specimens of indeterminate mature taxa and, as such, have been declared *nomina dubia* (Sampson et al., 1997).

Of the 463 catalogued specimens from BB 43 for which bone texture could be determined (Table 4), the majority (92.9%) exhibits adult texture, 1.3% has mottled texture, and 5.8% have long grain texture. Six hundred and fifty-eight could be sorted reliably by size and/or degree of ontogenetic development: 88.6% are "adult," 7.0% are "sub-adults," and 4.4% are "juveniles." Using these criteria, just under 90% of the animals preserved in BB 43 were mature adults, with juveniles making up no more than 5% of the specimens.

Intraspecific Variation in Specimens from Bone Bed 43

Bone beds containing large numbers of individual elements derived from animals presumed to be from a genetically circumscribed population have the potential to illustrate the natural morphological variation associated with each element (Sampson and Ryan, 1997). The variation seen in the important diagnostic elements (nasal, parietal, and post/supraorbital) for *Centrosaurus* recovered from BB 43 are examined here.

Nasal

In juvenile centrosaurs, the opposing, unfused nasals are compressed laterally, with the horn developed as a low, sub-triangular, short based, dorsal projection with its apex recurved (e.g., TMP 81.18.53, Fig. 8A and B). The medial surface of an unfused juvenile nasal has long-grained bone texture (TMP 81.18.53, Fig. 8C), with the growth lines radiating anterodorsally from the posterior

TABLE 4—Summary of frequencies of bone features of *Centrosaurus* material from bone bed 43. See text for explanation of conditions and stages.

Bone features	Condition/ stage	Total	% Of total
Bone texture n = 463	long-grain	27	5.8
	mottled	6	1.3
	adult	430	92.9
Size n = 658	juvenile	29	4.4
	sub-adult	46	7.0
	adult	583	88.6
Fragment n = 656	1	177	30.0
	2	479	70.0
Breakage n = 615	0	80	13.0
	1	60	9.8
	2	89	14.4
Fracture n = 646 (excluding CF)	3	386	62.8
	Spiral	13	2.0
	Compression	33	5.1
	Longitudinal	26	4.0
Abrasion n = 653	Unfractured	54	8.4
	Indeterminate	520	80.5
	Collection	15	—
	0	87	13.3
Weathering n = 567	1	456	69.8
	2	108	16.5
	3	2	0.4
	0	483	85.2
	1	56	9.9
	2	26	4.6
	3	2	0.3

base of the horn. TMP 79.11.83 (Fig. 8D) illustrates a maturing specimen undergoing fusion. The opposing surfaces fuse through mutual interdigitation and progresses from the apex to base of the horn (also seen in TMP 80.18.310, 81.18.10, and 82.18.164). An identical pattern is expressed in *Centrosaurus* nasals from other localities (e.g., TMP 66.33.17 from the Dinosaur Park Formation of Hilda, Alberta). On mature specimens, the horn is tall, robust, usually at least slightly compressed, and tapers to a blunt tip (e.g., TMP 87.18.39, Fig. 8E; TMP 82.18.67, Fig. 8F; TMP 83.18.44, Fig. 8G). Isolated nasals from BB 43, and complete skulls from elsewhere in the formation, show that large adult nasal horns usually are fused completely, with the tip directed either straight up perpendicular to its base or, more usually, having its tip gently to strongly procurved. Nasal horns from BB 43 range in size from those of small juveniles (TMP 81.18.53, Fig. 8A and B; 105.0 in height) to old adults (TMP 82.18.44, Fig. 8F, the tallest, most complete horn at 280.0 mm in height, as measured from the posterior base to the tip along the posterior surface of the horn). In adult *Centrosaurus*, the line of fusion of the horn is obliterated completely and only can be seen on the ventral roof of the nares. Rostral and caudal to the horn, the nasal fuses only after the fusion of the horn is complete. Even in the largest specimens, the rostral nasal suture is still visible (e.g., TMP 87.18.20, and 82.18.44).

Adult nasal horns exhibit the greatest degree of variation in their robustness (compressed vs ovoid in cross section) and in the degree to which the tip procurves; however these two features do not seem to be correlated when bone bed material is compared with the nasals of articulated

skulls. BB 43 is dominated by robust, straight horns, few of which are more than slightly procurved at their tips.

Sternberg (1938) noted a constriction at the base of some *Centrosaurus* nasal horns, which he believed could be used to distinguish *Centrosaurus* from *Monoclonius*. TMP 79.11.166 (Fig. 8H) exhibits this constriction (as do other specimens), but it is more pronounced on the right side, and, like the overall robustness of the horn, appears to represent natural variation within the *Centrosaurus* material from BB 43.

Parietal

The diagnostic centrosaurine frill ornamentation is expressed on the lateral and posterior margins of the fused parietal (Sternberg, 1927). This fusion probably occurred early in ontogeny, as unfused parietals have never been found in ceratopsids (Dodson and Currie, 1990). In centrosaurines, the parietal ornamentation develops from epoccipitals that fuse along the parietal margin. These modified epoccipitals are numbered sequentially outward from the parietal midline (Fig. 9). In *Centrosaurus*, the first two pairs of processes are developed as hooks close to the midline parietal bar (Fig. 9A-C, E). The first pair of hooks, which can procurve over most of the length the parietal fenestra of articulated skulls, can variably have one of the pair undeveloped (e.g., *C. apertus* (NMC 971; AMNH 8795) in what appears to be natural variation for the genus.

Based on material from paucispecific bone beds of *Acheilosaurus*, *Centrosaurus*, *Einosaurus*, and *Pachyrhinosaurus* (as reported by Sampson et al., 1997), a *Styracosaurus* bone bed from the Dinosaur Park Formation of Alberta (Ryan, unpublished), and bone bed material from two new, undescribed cf. centrosaurine ceratopsids from the Oldman Formation of Alberta (Ryan, unpublished), all juvenile centrosaurines appear to have indistinguishable parietals (e.g., TMP 79.11.76 Fig. 9E and TMP 80.18.260; Fig. 9C). Juvenile parietals have a short midline length, are thin along all margins, lack any fused epoccipitals or other ornamentation, and express long-grain bone texture (e.g., ventral surface of TMP 80.18.260; Fig. 9D). As outlined by Sampson et al. (1997), these features are modified through ontogeny: the parietal increases in absolute size; the posterior, and to a lesser extent, the lateral, margins thicken; epoccipitals fuse from posterior to anterior along these margins, and eventually express a taxon specific morphology; the most cranial lateral processes imbricate relative to each other when viewed on edge; and, finally, the bone texture takes on its typical adult appearance.

All of the 87 catalogued parietals from BB 43 are partial specimens. The fragmental remains typically consist of isolated anterior midline bars, lateral margins, or short segments of the posterior bar. Small, complete juvenile parietals are not known from BB 43, but numerous fragments of thin-edged parietals with long grained bone texture were collected. The smallest complete parietal known from a ceratopsid in Canada was described by Dodson and Currie (1988). Originally referred to *Monoclonius*, this specimen probably can be referred to *Centrosaurus* based on its stratigraphic position.

Fourteen diagnostic adult parietal fragments allow for the identification of the ceratopsid in BB 43 as *Centrosau-*

rus apertus. TMP 80.18.260 (Fig. 9C) and 79.11.76 (Fig. 9E) are parietals showing the initial development of the first pair of parietal hooks as outgrowths of the posterior parietal bar. Both specimens possess a mixture of the long-grained and mottled texture indicative of the extensive remodelling the bone was undergoing as the hooks developed.

TMP 82.18.79 (Fig. 9A) is a typical example of a diagnostic *C. apertus* parietal from BB 43. The first pair of hooks procurve forward and lie at an angle roughly parallel to the midline bar. Both hooks are of roughly the same length, with their distal tips eroded away. Preserved length of the right is 213.6 mm; left = 210.2 mm. The surfaces of each are deeply fluted parallel to their longitudinal axis. There are several small fossae scattered over the surfaces that have anteriorly-directed grooves leading away from them. The second pair of hooks are convex along their superior margin and recurve towards the midline in the plane of the frill. Their distal tips also are broken or eroded, but in life, when covered by a keratinous sheath, may have approached the midline. As with the first pair of hooks, their surfaces are grooved deeply and show some small, slightly abraded fossae. The forward growth of the first pair of hooks frequently results in the posterior-most margin of the midline bar being curled forward in many specimens. In such cases, the last 50 mm or so of the bar is "pulled up" to form a shallow-to-deep, cup-like depression between the first pair of hooks.

The remainder of the dorsal surface of TMP 82.18.79 is rugose, contrasting sharply with the smooth ventral surface. The maximum thickness of the midline bar is 44.6 mm, while its lateral margins are extremely thin, indicating that these preserved margins were close to the edges of the parietal fenestrae. TMP. 82.18.277 (Fig. 9B) is a partial parietal similar in size and shape to TMP 82.18.79, with the exception that the preserved hooks have a 'withered' appearance. The hooks have a very rugose texture and are deeply fluted along their length. Some other *Centrosaurus* parietals (e.g., AMNH 5377; NMC 348—the holotype of *C. apertus*) have a similar hook morphology. Whether this is due to diagenetic or taphonomic processes is unknown, but this morphology does tend to be associated with skulls that have undergone post-mortem distortion. It is also possible that it is a natural feature of these skulls and may suggest a form of dimorphism.

TMP 80.18.260 (Fig. 9C) is the most complete midline bar from BB 43, with a total preserved length of 455 mm and an estimated midline length of 420 mm. It is from a centrosaur that was beginning to mature and develop parietal ornamentation at the time of its death, as evidenced by the thickened posterior margin possessing a mixture of long grain and mottled texture on its ventral surface (Fig. 9D), and showing the initial development of the first right hook as an incipient outgrowth of the parietal. It has six, low, midline bumps. These are present in variable numbers on all centrosaurine parietals and are observed best by viewing the parietal in profile. In the adult-sized parietal of the undescribed putative new *Pachyrhinosaurus* species from Grande Prairie, Alberta, one or more of these midline bumps develop into short, parietal spikes.

Orbital Horn Core

As noted by Gilmore (1914) and Brown and Schlaikjer (1940), the orbital horn core (Fig. 10A-J; 11A-D) of *Centro-*

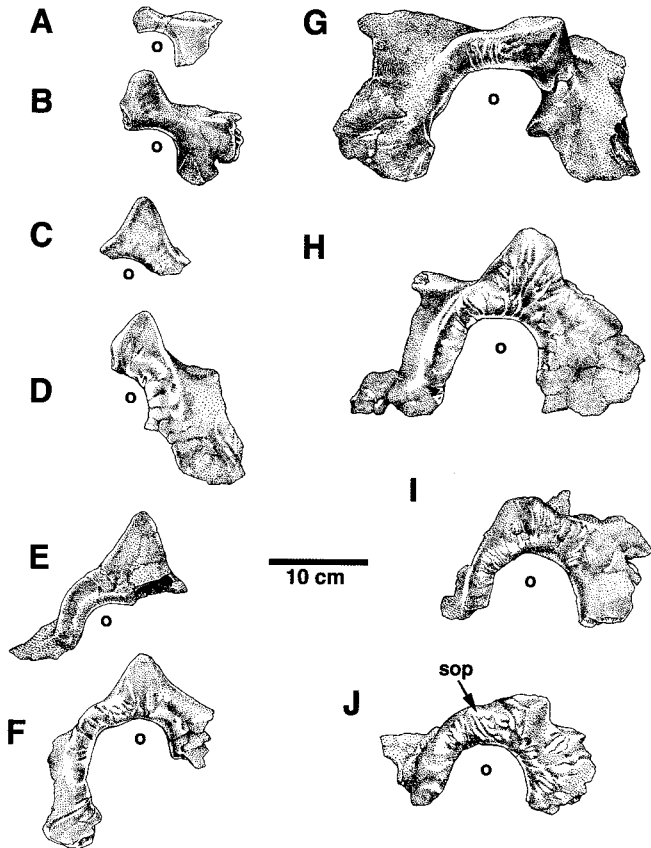


FIGURE 10—*Centrosaurus* postorbitals and supraorbitals from bone bed 43 in lateral view. A–J represents an inferred growth series with A and B being unfused postorbitals from juveniles; C–I being fused supraorbitals representing young sub-adults to old adults; and J representing the oldest adult with a large supraorbital ‘resorption’ pit. (A) TMP 79.11.157, left postorbital. (B) TMP 79.11.20, left postorbital. (C) TMP 80.18.315, left orbital horn broken off of supraorbital. (D) TMP 79.11.31, right supraorbital. (E) TMP 79.11.163, left supraorbital. (F) TMP 80.18.16, left supraorbital. (G) TMP 80.18.83, left supraorbital. (H) TMP 79.11.89, right supraorbital (*image reversed*). (I) TMP 80.18.221, right (*imaged reversed*) supraorbital. (J) TMP 79.11.80, right (*imaged reversed*) supraorbital. Abbreviations: o = orbit; sop = supraorbital pit. Scale bar = 10 cm. A is modified from Sampson et al. (1997).

saurus is a direct out growth of the postorbital and not a separate ossification. The incipient horn clearly can be seen on TMP 79.11.157 (Fig. 10A), 82.18.16, and 82.18.139, the smallest postorbitals recovered from BB 43. These horns have heights above the rim of the orbit of 10.6 mm, 10.0 mm, and 12.4 mm, respectively. At this stage, the horn in *Centrosaurus* is a laterally compressed, low, rounded prominence with a broad base. The lateral surface is flat and confluent with the orbital rim from which it grows, while the medial surface is rounded and slopes down from the tip to the open frontal suture. The smallest known centrosaurine postorbital (roughly 20% smaller than TMP 82.18.139) is TMP 80.16.1694, also from the Dinosaur Park Formation of Dinosaur Provincial Park. This specimen probably came from a very young, possibly hatchling-sized, animal, indicating that centrosaurines began their free-living existence with at least a rudimentary orbital horn core. As the animal grew, the postorbital

fused with the remaining abutting elements to form the element known as the supraorbital. Of these elements, the palpebral variably may not fuse, even in the largest articulated skulls. Nine unfused postorbitals were recovered from BB 43, each of which is at least 50% larger than TMP 82.18.139. These have an orbital horn that is roughly pyramid-shaped (e.g., TMP 79.11.20 Fig. 10B). The lateral surface is still flat and the medial surface is concave. The antero- and posterolateral margins are well-defined and end at the sharp tip. Unlike the longer orbital horns of some chasmosaurines, the horn of *Centrosaurus* is solid through its basal core and throughout its length. Horns that are not remodelled (described below) have their longitudinal axis perpendicular to the base. Therefore, the horn on an articulated skull points directly up or is angled slightly caudally.

On large, fused supraorbitals, the horns can appear as either of two, probably related, morphologies: (1) inflated, and (2) remodelled (= development of supraorbital pits). In the former, the horn (e.g., TMP 80.18.221; Fig. 10I) frequently exhibits a great increase in robustness, losing its pyramidal shape and sharply defined tip as the medial surface and lateral margin “swell.” The medial and, to a lesser extent, the lateral surface become very rugose, developing deep, vascular-like grooves running parallel to the long axis of the horn. This inflation of the horn appears to precede development of supraorbital pits in the second “remodelled” morphology.

As noted by Sampson et al. (1997), the supraorbital pits (Fig. 11A–D) developed on the orbital horns of putative mature or old centrosaurines have been suggested to occur due to the resorption of bone, but the process and reason for this are unknown. Pitting, or small depressions suggestive of pit development, is first seen near the tip (TMP 79.11.58; Fig. 11A) or just medial to it (TMP 80.18.322; Fig. 11B). TMP 79.11.40 (Fig. 11C) and TMP 79.11.142 (Fig. 11D) show supraorbital horns in which the horn tips are clad with larger (>10 mm) pits. Pitting is never seen on unfused postorbitals, indicating that this feature only develops in older, mature animals. In some specimens (e.g., TMP 79.11.44) the horn is destroyed completely, leaving in its place a rugose orbital rim. The development of the supraorbital pits appears to be variable. For example, the skull of *Centrosaurus* NMC 348 has a low, rounded horn on the right side with 4 supraorbital pits, while the left side is unmodified. This may indicate that the timing of the development of pits is not synchronous. Other centrosaurines, including *Einosaurus* and the holotype of *Styracosaurus albertensis* (NMC 344), also show the development of supraorbital pits. Unfortunately, the lack of unfused *Styracosaurus* postorbitals does not allow for an interpretation on whether *Styracosaurus* ever had even an incipient postorbital horn.

Figure 10 illustrates the ontogenetic development of a *Centrosaurus* supraorbital horn. TMP 79.11.157 is a small unfused postorbital with a small horn projecting above its orbital rim. As the animal grew, the horn became more robust (TMP 79.11.20, Fig. 10B) and increased in height with the increasing overall size of the element. At some point in its growth, possibly at sexual maturity, the postorbital fused to its surrounding elements. At this stage the supraorbital horn is a sharply defined pyramidal structure (TMP 80.18.315, Fig. 10C; TMP 79.11.31, Fig. 10D;

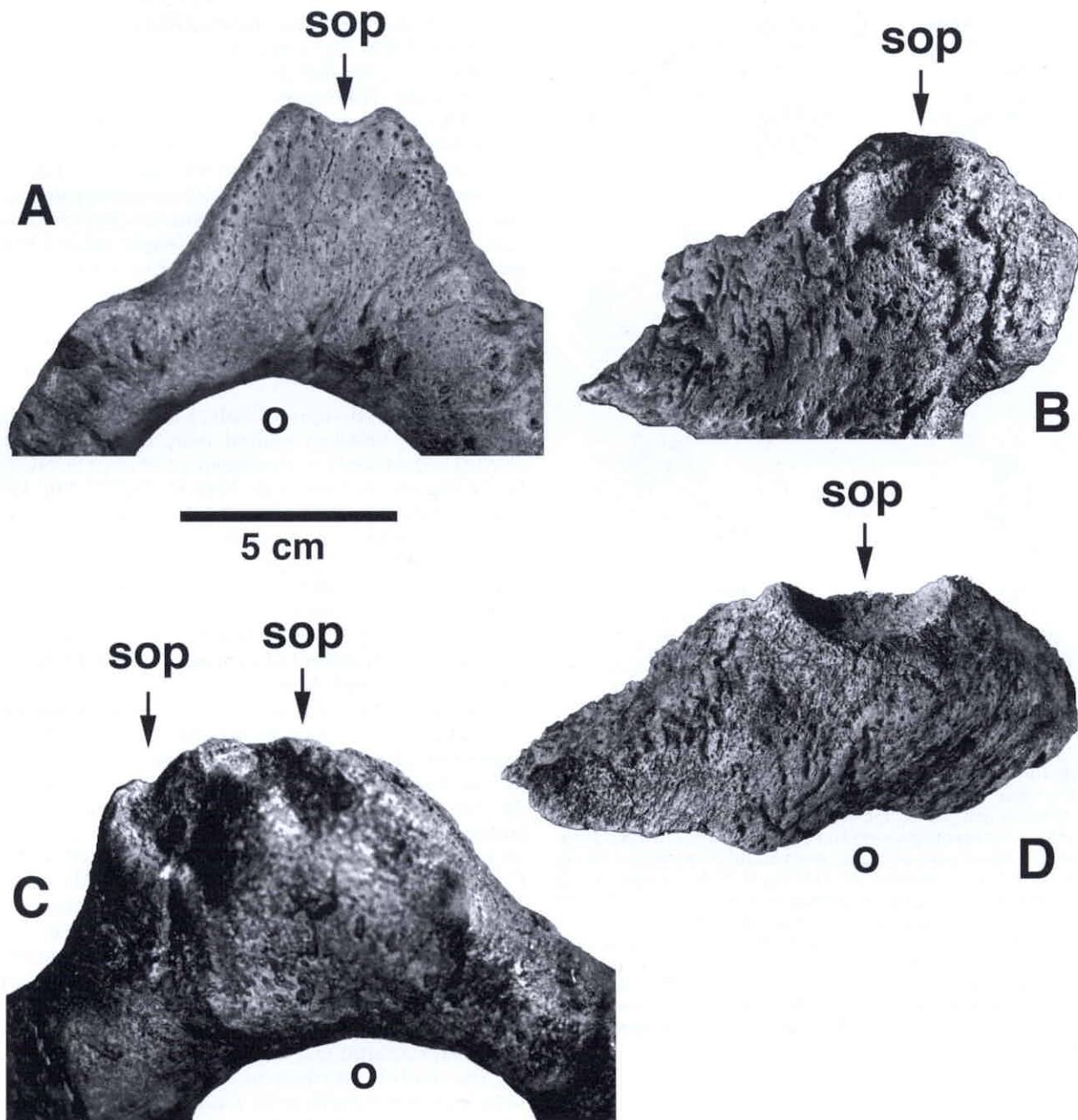


FIGURE 11—Adult supraorbital horns showing supraorbital pits. (A) TMP 79.11.58, left supraorbital in lateral view. (B) TMP 80.18.322, fragmentary right supraorbital in oblique dorsomedial view. (C) TMP 79.11.40, right supraorbital in oblique dorsolateral view. (D) TMP 79.11.142, fragmentary left supraorbital in oblique dorsolateral view. Abbreviations: o = orbit; sop = supraorbital pit.

TMP 79.11.163, Fig. 10E; and TMP 80.18.16, Fig. 10F). As the animal further matured, the supraorbital horn inflated and developed longitudinal grooves along its medial side, as the entire element developed a more rugose texture (TMP 80.18.87, Fig. 10G; TMP 79.11.89, Fig. 10H). At this point, the inflated shape of the horn tends to obscure its original shape and the tip appears blunted (TMP 80.18.221, Fig. 10I). A transverse channel may appear along the medial surface at this stage. Finally, and probably indicative of advancing age, one or more supraorbital pits appear on the surface of the horn, reducing its height (TMP 79.11.80, Fig. 10J). The horn may continue to be eroded by the pits until no evidence of it is left. Inferences

made concerning centrosaurine supraorbital horn height should be undertaken with caution, as this horn actually decreased in height with age after full height had been attained.

Taphonomic Modifications

Prior to fossilization, the remains of dead animals can be subjected to a variety of modifying forces, which may alter their physical structure and/or move them from where they died. Scavengers may disarticulate a carcass and move the pieces while consuming soft tissues, breaking or marking bones in the process. Remains can be modified by

exposure to the elements, or, if contained in a flowing water system, be abraded by entrained sediment. The effects of these taphonomic agents have been examined for a variety of fossil assemblages (e.g., Behrensmeier, 1975; Fiorillo, 1988, 1991a) and the criteria for evaluating their presence in BB 43 is outlined here. The most extreme expression of each taphonomic category that covers more than 10% of the preserved specimen has been recorded.

Breakage and Fracturing

The material collected from BB 43 is notable in that most of it is fragmentary, being primarily composed of portions of large (i.e., >200 mm) adult-sized elements. Even the most complete specimens are usually missing small chips or chunks of bone. However, smaller, complete elements, typically < 100mm (e.g., podials) show the least amount of breakage and no fracturing. Of 656 specimens examined (Table 4), 479 (70%) are more than 10% incomplete. Over 60% of these 479 specimens have both proximal and distal ends missing or show more than minor breakage. Neither end of any bone in any class was broken preferentially.

Identification of the types of fractures present on the fossils was based on the work of Haynes (1983). Although his work focused primarily on long bones, other elements were included where appropriate. Fracture patterns identified are:

Collection fracture—A break on the fossil obviously made during the collection or preparation of the specimen.

Longitudinal fracture—A break parallel to the long bone shaft. These usually are attributable to desiccation cracks, but the material from this site with these fractures lack any of the other attributes suggestive of prolonged weathering. They are considered here to be a form of 'compression' fracture.

Spiral fracture (green-fracture)—On a long bone this is a fracture at an angle other than perpendicular to the shaft. These fractures are equated with breakage prior to fossilization. They may be incomplete and end part way around the shaft at a longitudinal fracture. Morlan (1980) observed that fresh ("green") breaks can be distinguished from breaks in aged bones by (1) the presence of relatively smooth fracture surfaces, or (2) the presence of acute or obtuse angles where the fracture surface intersects the outer surface of the shaft.

Transverse/compression fracture—A fracture on the surface of a specimen giving the impression that an object has been crushed. The fracture pattern can include multiple "stepped" cracks parallel to each other, or single or multiple concentric cracks. These usually are attributable to sediment deformation, but also may indicate trampling.

Indeterminate fracture—The break on the fossil can not be placed reliably in one of the above categories.

Unfractured—No discernible fracture on a fossil element.

Of 656 examined specimens, 81% had fractures of indeterminate origin or attributable to collection (Table 4). Only 2% could confidently be assigned as green fractures, while 5% have definite compression-style fractures; 8% were classified as being unfractured. Of the 71 catalogued major limb bones, 18.3% bear spiral fractures, all of which are believed to be fresh "green" fractures.

The high percentage of broken and fractured material from BB 43 suggests that it was modified actively by some external force. Much of the damage may have occurred during transport to its final resting spot, although breakage by trampling at the point of disarticulation can not be ruled out. If the material was carried in a high energy flow as the sedimentology indicates, then much of the material may have tumbled end over end and, consequently, been broken on contact with the substrate or other entrained material. Smaller and lighter elements would tend to bounce off the river bottom helping to explain why these specimens show fewer breaks.

The 13 green fractures are seen primarily on long limb elements and may be attributable to trampling of the material before it was transported and deposited in its present location, a scenario recognized in other fossil localities (Fiorillo, 1984). The small number of elements bearing green fractures may not be unusual for an animal the size of *Centrosaurus*, even if trampling of the original material was heavy. Haynes (1983) noted that non-brittle elements tend to resist breakage better than small elements. He examined 565 long bones of bison and moose (animals in the size range of *Centrosaurus*) in northern Canada and found that only 11% of these bones had spiral fractures. He determined that bones were not fractured by trampling unless they were either first weathered and degreased, or had their epiphysal ends gnawed off by carnivores. However, for smaller animals (e.g., deer or caribou), over 50% of their long bones may be spirally fractured by trampling. Additionally, trampling and dust-wallowing by bison resulted in the crushing and splintering of ribs, vertebrae and scapulae, the disarticulation and breakage of some skull and post-cranial material, and the breakage of teeth from their sockets (Haynes, 1983). Similar actions may have been responsible for at least some of the breakage and fractures seen on fossils from BB 43. Alternatively, the potentially large number of centrosaurs that composed the original death assemblage could explain the low number of trample-related fractures. With so many carcasses present, not all were trampled, and of those that were, many may have been pushed into the underlying soft substrate without having elements fractured.

Bone marked by theropod teeth was encountered rarely in the bone bed (only 17 specimens, comprising <0.02% of the catalogued ceratopsid material, excluding teeth). Tooth marked elements (many illustrated in Jacobsen, 1995) include an indeterminate ornithischian tendon (TMP 81.18.4), a femur (TMP 80.18.249), an ilium (TMP 81.18.100), ischia (TMP 81.18.52, 81.18.156), quadrates (TMP 80.18.312, 83.18.48, 86.18.11), ribs (TMP 81.18.14, 82.18.56, 82.18.93, 83.18.144), a scapula (TMP 79.11.30), vertebrae (TMP 80.18.24, 80.18.271), and cf. ceratopsid indeterminate bone fragments (TMP 89.18.135, 89.18.142). The low number of tooth-marked bone may not be unusual for a dinosaur assemblage. Fiorillo (1991b) surveyed bone-bed assemblages and noted that tooth marks on dinosaur bones are rare, being found on only between 0–4.0% of specimens. This contrasts with modern and fossil mammal assemblages that can have up to 37.5% tooth-marked bones (Fiorillo, 1991b). Unlike modern mammals, which are known to actively gnaw bone, archosauromorphs have not been reported to process carcasses in this manner.

Most of the catalogued material does not show signifi-

cant deformation or compression-style fractures. This is to be expected given the coarse-grained sandstone in which the material lies and which surrounds it. Fossil material preserved in sandstones tends to show little or no evidence of sediment compaction when compared to fossil material preserved in finer-grained mud- or siltstones.

Abrasion

The abrasion stages reported in this study are modified from the stages developed by Fiorillo (1988) who, in turn, based his work, in part, on that of Hunt (1978). Fiorillo (1988) incorporated the sedimentological terminology for grain rounding when describing bone abrasion, with the caveat that bones, with their varying densities due to internal structure and composition, do not necessarily break down in the same manner as minerals. Elements from BB 43 were identified as belonging to one of the following stages:

Stage 0—The fossil has a pristine surface and is unabraded; comparable to the “very angular to angular” sedimentological category.

Stage 1—Broken edges of the fossil are rounded; surface may be polished; comparable to the “subangular” sedimentological category.

Stage 2—Broken and unbroken edges of the fossil are well rounded. Surface is well-polished but original texture is still discernible. All processes are rounded but recognizable as to their original structure; comparable to the “subrounded” sedimentological category.

Stage 3—All edges of the fossil are extremely well-rounded. Processes are recognizable as protrusions on the bone, but would not be recognizable if they were not still attached to the bone. Preserved surface is well-polished; comparable to the “rounded” category in sedimentology.

The majority of the catalogued specimens exhibit stage 1 abrasion (69.8% of 653 elements examined). Approximately one half of the mapped material only could be classified as unidentified bone fragments (< 50 mm) or bone chips (< 10 mm; Table 2). Most of this material is very well abraded (Stage 3) and cannot be identified as anything other than vertebrate bone fragments. These data suggest that the larger centrosaur elements and the smaller bone fragments and chips have had different histories prior to becoming entombed in the bone bed. The former are associated in time, probably originating from a single event, and were submerged, but exposed to entrained sediments long enough to polish surfaces and round off broken edges. The unidentifiable material probably represents material that had been present in the local fluvial systems for a long period of time, and potentially were reworked many times. This well abraded, unidentifiable material is typical of that found in vertebrate microfossil assemblages from both in-channel intraclast deposits and siltstone/sandstone crevasse splay deposits throughout Dinosaur Park (Brinkman, 1990; Eberth, 1990), and are a common component of large vertebrate bone beds. The “background” occurrence of well abraded, unidentifiable bone fragments in BB 43 is also typical of that seen in the other

Centrosaurus bone beds throughout the Dinosaur Park Formation of Alberta.

Behrensmeyer (1990) noted that fresh, unbroken bone is very resistant to water-borne sediment abrasion. She states that exposure to poorly-sorted sand for up to 35 hours in a tumbling machine is necessary to produce significant abrasion on fresh bones. Stationary bones, however, can be heavily abraded without significant transport when sand blasted by water or wind-borne sediment (Behrensmeyer, 1990). Trample marks (*sensu* Behrensmeyer et al., 1986; Fiorillo, 1987) are seen on elements with ‘polished’ surfaces (class 1 abrasion). However, given that only a small number of specimens exhibit breaks that can be attributed to trampling, the “trample marks” may have been caused by some other event, possibly as the result of sediments flowing over and scouring the bone, or by scouring as the bone was dragged by traction along the river bed.

Weathering

The first quantification of weathering stages is attributable to Behrensmeyer (1978) when she outlined six progressively more extreme stages, based on observations of recent mammal bones lying on various dry surfaces in Amboseli National Park, Kenya. As these stages are based, in part, on the diminishing amounts of grease and soft tissue remaining on the bones over time, which can not be evaluated for fossil material, the following modification of the four weathering stages of Fiorillo (1988) who, as in this study, also was dealing with material deposited in a fluvial system have been used. Each stage of weathering refers to modification of an element as it desiccates, flakes, cracks, and finally splinters into small fragments.

Stage 0—Fossil surface shows no sign of cracking or flaking due to weathering.

Stage 1—Fossil surface shows cracking parallel or sub-parallel to the fiber structure of the bone. Ends of long bones may or may not be cracked or eroded away.

Stage 2—Fossil has parallel or sub-parallel cracks that are starting to penetrate into the marrow cavities of long bones. Surface is usually flaking away from these cracks. Ends of long bones are deeply eroded or ends may be missing, with sandstone infilling the head of the shaft.

Stage 3—Large chunks of outer laminated bone have flaked away. Preserved surface is highly cracked and flaking. Heads of the long bones have broken or eroded away.

Of 567 catalogued and identified specimens examined (Table 4), over 85% are assignable to stage 0 (unweathered). The remaining 15% of the *Centrosaurus* bones all show some minor or moderate weathering (stages 1–2). Differential weathering seen on the opposing sides of some elements probably is attributable to modern weathering of one partially exposed side. In Behrensmeyer’s (1978) classification, stage 0 is indicative of less than a year elapsing since the time of death if the material was fully exposed on a dry, open soil surface. All sedimentological indications indicate the Dinosaur Park Formation of Dinosaur Park preserves a warm, humid environment not prone to prolonged dry spells; hence, Behrensmeyer’s weathering clas-

sification is not completely consistent with the environment in which BB 43 was formed. However, the lack of any identifiable bacterial or fungal degradation, or insect borings on any of the BB 43 material suggests that it was buried rapidly after death.

Orientation of Elements

Following the work of Toots (1965) and Voorhies (1969), recent taphonomic analyses of fossil assemblages preserved in fluvial systems (e.g., Varricchio, 1995) frequently use the vector orientation of fossils to aid in determining the direction of paleocurrent. Orientation data ($n = 519$) for material from BB 43 for material greater than 100 mm in length were converted to rose diagrams using Rockware software. Preferred modal [each mode = 15°] directions were determined using the non-parametric Chi-square goodness of fit test for circular data. This test was used rather than the parametric Raleigh test (Davis, 1986) because if the latter is used and rejected, the assumption is that the sampled population is unimodal. If the fossil vectors are actually sampled from a bi- or multimodal distribution, then the Raleigh test will give misleading results. The actual preferred direction(s) for any set of directional data was calculated using the equation (Gaile and Burt, 1980):

$$\text{Preferred direction} = L + \frac{F_o - F_a}{(2F_o) - F_b} \cdot h$$

where, L = lower limit of modal class, F_o = frequency of the modal class, F_a = frequency of the preceding modal class, F_b = frequency of the following modal class, h = length (in degrees) of the class interval.

Each quarry for which sufficient data were available showed a single preferred direction, ranging from 49.3° to 93.8°. Currie and Dodson (1984) observed that the centra of complete vertebrae in BB 43 were oriented downstream more frequently than they were oriented upstream, and this was noted in this study as well. Paleocurrent directions for DPP have been reported as 84.7° for the mean of 218 cross-strata measurements (Dodson, 1971); 84° for 63 cross-beds contained within 121 Type 1 inclined heterolithic stratified channel sequences (Koster et al., 1987); and 99° "for abundant sets of trough cross-beds" (Koster et al., 1987:37). The preferred directions obtained for fossil material from excavations within BB 43 are in general agreement with the published data for DPP, and suggest that the material preserved here was current-aligned before burial, in roughly the general direction of current flow.

Plunge measurements were taken infrequently in BB 43 because the majority of the material was lying flat relative to the substrate. Of 72 recorded plunges, only 42 exceeded 20°. These plunges were scattered randomly amongst the quarries, and only three elements approximated a 90° plunge. Such steeply angled bones have been inferred to indicate trampling of material by ungulate herds in modern (Haynes, 1983) and fossil (Hill and Walker, 1972; Fiorillo, 1988) mammal assemblages, and by scavenging theropods prior to fossilization in dinosaur bone assemblages (Fiorillo, 1991b; Rogers, 1991). As the steeply angled bones were not in contact with any other bone or leaning against some other preserved feature in

the bone bed, they may represent random trampling of the material after they were deposited in their present location, or they may simply have been the result of chance inclination of the bones as they came to rest on the substrate.

Voorhies Transportation Groups Analysis

The transportation of modern, disarticulated vertebrate elements by water has been studied under a number of conditions: in flumes (Voorhies, 1969; Dodson, 1973; Boaz and Behrensmeier, 1976; Blob, 1997), in settling tanks (Behrensmeier, 1975; Korth, 1979), and in natural channels (Frey et al., 1975; Behrensmeier, 1982). Transportation of a skeletal element in flowing water is determined by a combination of factors, including its size, three-dimensional shape, density, and degree of disarticulation, as well as the velocity of the water (Behrensmeier, 1975; Blob, 1997). Disarticulation and decomposition are controlled by factors such as pH, P_{O_2} , salinity, bioturbation, and water velocity (Dodson, 1973). In examining the hydraulic characteristics of fossil bone elements, Behrensmeier (1975) found that factors complicating analysis included pre-transport weathering and pore saturation once in transport.

Voorhies (1969) showed that disarticulated bones can form distinctive dispersal groups (now referred to as Voorhies groups) when sorted under the influence of increasingly greater current velocities. A group 1 assemblage (Table 5) consists of bones of relatively low mass (vertebrae, phalanges, etc.) that are affected by slight currents, and are the first to be transported by saltation or flotation. An assemblage consisting mostly of these bones is considered to be a transported assemblage. A group 2 assemblage contains elements (mostly limbs) that are removed gradually from a deposit, primarily by traction, and is considered a mixed assemblage. Elements in a group 3 assemblage (the remainder of the skeleton) tend to resist transport and remain behind as a lag deposit in water currents that have removed the bones comprising the first two groups.

Although Voorhies (1969) worked with bones from coyotes and sheep (<100 kg), Behrensmeier (1975) demonstrated that these dispersal patterns tend to hold true for mammals as large as hippopotami that approximate the size of *Centrosaurus*. Dodson (1973) showed that similar patterns also were exhibited by frog, toad, and mouse bones, although some elements dispersed much differently than predicted from the results obtained for the larger animals. Blob (1997) demonstrated that for small animals, such as soft-shelled turtles, the overall shape of the element also plays an important role in dispersal patterns. In evaluating the chasmosaurine ceratopsid, *Chasmosaurus mariscalensis*, from the Aguja Formation of Big Bend National Park, Texas, Lehman (1982:57) stated that its elements "...dispersed under transport like the bones of large mammals." Following Lehman's assumptions, the catalogued material from BB 43 has been placed into its appropriate Voorhies category (Table 5). Unlike the material dealt with by Lehman (1982) and previous workers, the skulls in BB 43 were disarticulated completely and the elements disassociated. In the present study, skulls are represented by the total of isolated braincases and occipi-

TABLE 5—Composition of Voorhies transportation groups for a *Centrosaurus* skeleton (after Lehman, 1982) and data from bone bed 43. (a) The number of elements (284) in a complete adult *Centrosaurus* is based on the following assumptions: braincase is not disarticulated; nasals fused; supraorbital fused (includes frontal, lacrimal, palpebral, postorbital, and prefrontal). Elements excluded from count are: epoccipitals, sclerotic plates, tendons and teeth as they can not be reliably estimated from a single individual. Intercoronoids and prearticulars are fused to the dentary. The unidentified limb material has been divided by their proportion in the body and included in the limb and divided across the element counts. (1) = Total of braincases and free occipital condyles; (2) = Dentary bone only; (3) = Teeth not included.

Voorhies Group I	Total in one centrosaur	Total from BB 43	Voorhies Group II	Total in centrosaur	Total from BB 43	Voorhies Group III	Total in centrosaur	Total from BB 43
Cervical vertebrae	11	16.3	Dorsal vertebrae	12	16.7	Sacrum	1	3
Caudal vertebrae	46	64	Ribs	42	74	Iliia	2	12
Metapodials	28	24	Pubes	2	1	Femora	2	10
Phalanges	56	5	Fibulae	2	11.5	Tibiae	2	6
Ischia	2	23	Radii	2	11.5	Scapulae	2	8
			Ulnae	2	13.5	Humeri	2	14.5
			Coracoids	2	0	Skull (1)	1	10
			Predentaries	1	3	Dentaries (2)	2	12
						Teeth (3)	—	—
Total	143	132.3		65	131.2		14	96.5
% of skeleton (a)	65.0			29.0			6.0	
% of 3 Voorhies classes		36.8			36.4			26.8

tal condyles. The dentary was taken to equal the ramus of Voorhies (1969) and mandible of Lehman (1982). All other skull elements, except the prementary, were excluded in the present effort to replicate the methodologies of these previous workers.

Analysis of the data indicates that the recovered material from BB 43 approximates the ratio of 1:1:1 for each group. Because each Voorhies group is not represented by the same number of elements, it is important to compare the observed percentages from the assemblage to the proportions of elements from the animal under consideration that could be found in each group (Fiorillo, 1991a). When the observed percentages in each transport group are compared to the expected percentages, as represented by a complete centrosaur skeleton (Table 5, bottom two rows), it is evident that group 1 is under-represented by about 50% (36.8% observed vs 65% expected); group 2 is slightly over represented (36.4% vs 29%); and group 3 is greatly over represented (26.8% vs 6%). Clearly the material present in the bone bed was stripped largely of its smaller, lighter elements and constitutes a lag-style deposit.

DISCUSSION

Formation of the BB 43 Lithosome

The bone bed 43 sand body easily is interpreted as a paleochannel-fill, with a bankfull depth of at least 3.5 m, based on its overall lenticular, cross-sectional geometry, presence of a basal erosive surface with an associated intraformational and fossil lag, fining- and thinning-upward sets of sandstone, and overlying rooted siltstone. All of these features are consistent with incision and initial vertical aggradation associated with a maximum to waning flood phase. The presence of inclined surfaces that do not extend down into the lower 1/3 of the sandstone fill are consistent with other Dinosaur Park Formation channels that exhibit similar inclined heterolithic stratification, and are interpreted as lateral accretion surfaces (Koster et al., 1987; Thomas et al., 1987; Wood, 1989).

The co-occurrence of multiple, basal erosional scours,

thick deposits of cross-bedded sandstone, and inclined surfaces restricted to the upper portions of the sandstone body, suggest that the paleochannel experienced a multiple flood-event history with significant variations in discharge, channel sinuosity, and rates and style of sedimentation. Similar patterns have been observed for other Dinosaur Park Formation paleochannels by Koster et al. (1987) and (Eberth, 1996). The point bar origin for the *Centrosaurus* material in BB 43, previously suggested by Currie and Dodson (1984) and Wood et al. (1988), is not supported by the sedimentologic or taphonomic evidence. The fossil material occurs only above the basal contact and does not occur in the overlying sandstone or on the ironstone laminae (i.e., it can not be traced up presumed point bar surfaces).

The bone bed 43 host sandstone originated as a small paleochannel approximately 4m deep and 50–60m wide (Fig. 7, points 34–43; bankfull channel width calculated using 2/3 rule of Ethridge and Schumm, 1978). It initially underwent a phase of scour, emplacement of the lag deposit, vertical aggradation of the sands, and subsequently a phase of lateral accretion. Following channel migration of approximately 25m to the SW, a subsequent erosional event carved a new basal erosional surface in the center of the paleochannel and emplaced the fossiliferous basal lag that forms the heart of the bone bed (points 22–34). This event broadened the channel and probably reworked upstream portions of the original basal lag. As during the first flooding phase, the channel subsequently underwent a transition to a higher-sinuosity form with a width of 100m and a bankfull depth of 4.5–5m. A phase of channel abandonment and subsequent vertical aggradation occurred after the paleochannel had shifted no more than 25 m to the SW. The interval between points 29 and 35 demonstrates the presence of two stacked lag deposits. This may reflect either a temporally separate flooding event similar to, but occurring between, the times of those described above, or a multi-pulse flooding event associated with the second flooding event described above. Such multi-stacked-to-amalgamated basal lags are common within the Dinosaur Park Formation paleochannels.

The sedimentological evidence and taphonomic interpretations presented here indicate that the bonebed 43 fossil assemblage was reworked from an, as yet, unknown upstream position and facies. Although the initial and subsequent emplacement of the bones was rapid (taking place during the waning flood phase), the depositional context indicates a multi-phase reworking history for all of the fossils.

The taphonomic signatures of the *Centrosaurus* elements in BB 43 also support the above interpretation of the formation of the bone bed. The predominance of Voorhies group II large vertebrate skeletal elements at the basal erosional contact, and the relative lack of smaller elements, suggests that BB 43 represents a channel-lag assemblage (*sensu* Behrensmeyer, 1988) associated with the erosional event that emplaced the centrosaur material. The large number of broken and fragmented elements suggest that the elements were broken during the high energy event that carried them to their present resting place. The presence of fining-upward, trough cross-bedded structures, as well as the presence of current-aligned bones, suggests that the channel was subject to successive, fluctuating or episodic current flow before the material was entombed completely. However, the almost complete lack of weathering (desiccation cracks) on any of the catalogued material and the minimal abrasion on most specimens indicate that the centrosaur elements were in a moist environment prior to being incorporated rapidly into the bone bed.

Smith (1972) reported in modern environments that recent mudstone pebbles of different mud/clay composition were destroyed during transport over distances ranging from tens to hundreds of meters. Assuming that the numerous mudstone intraclasts found in the bone bed were formed during the same flooding event that picked up the ceratopsid material from its penultimate resting place, it is probable that the original site of death was no further away than the source of the mudclasts and was probably within the present day confines of DPP.

Ceratopsid Material in Bone Bed 43 and Its Origin

BB 43 is a paucispecific *Centrosaurus apertus* bone bed. All diagnostic ceratopsid skull material is referable to this taxon. The only exception to this is a partially articulated *Chasmosaurus* skull with a significantly different taphonomic signature from any other large element in the bone bed, suggesting that it had a different origin from the *Centrosaurus* material. The only other centrosaurine ceratopsid in the Dinosaur Park Formation, *Styracosaurus albertensis*, can be removed from consideration because recent work (Ryan et al., 1998) has shown that the two taxa are isolated stratigraphically in the park; *C. apertus* is not found more than 25 m above the base of the Dinosaur Park Formation and *S. albertensis* is not found below this level.

The 1576 catalogued elements from BB 43 are 80.4% ceratopsid, but this sample is biased in that not every ceratopsid element was collected, while every non-ceratopsid element was. A census of the less biased quarry map tabulations suggest that the composition of the bone bed is 93.1% ceratopsid, 3.5% theropod material (mostly teeth), and 3.4% other non-ceratopsid vertebrate (dominated by hadrosaurs). The present assemblage went through a

strong post-mortem filter, removing many skeletal elements, possibly including a large number of juvenile and sub-adult specimens. These inferences, and the highly fragmented nature of the material, makes it difficult to draw any conclusions about the existence of size classes or demographic structure of the original accumulation of *Centrosaurus* from which the bone material was derived. It is known that the assemblage includes both small juveniles and old adults, and potentially included hatchling-sized animals. The large number of *Albertosaurus* and other theropod teeth, and the presence of *Centrosaurus* bones that are tooth-marked suggests that the post-mortem filter included scavenging by theropods.

The minimum number of centrosaurs present in the excavated portion of the bone bed is 57, based on braincases and free (broken) occipital condyles. This number of centrosaurs would have generated an expected total of 16188 elements, had none been lost (based on a total of 284 elements in an adult centrosaur, excluding teeth and assuming the braincases are fused). 2050 *Centrosaurus* elements were mapped from the completely excavated grids (Table 2). If the unidentifiable bone fragments and chips, and incomplete ribs are excluded from this total, the number of observed *Centrosaurus* elements is 535. Thus, only 18.8% of the potentially obtainable material from at least 220 *Centrosaurus* was actually recovered from these excavations. This suggests that at up to 80% of the original post mortem *Centrosaurus* assemblage is missing from BB 43. Much of this material probably was washed away prior to, or during, the event that formed the BB 43 lithosome. If *Centrosaurus* material is distributed evenly throughout the preserved, but mostly unexcavated, bone bed (13000 m²; admittedly an unlikely probability), then the upper estimated number of centrosaurs forming the pre-transport death assemblage may have numbered 40,000 or more. A more likely estimate might be 10% of this upper limit, or 4000 ceratopsids—still an impressive number. Of note is another *Centrosaurus* bone bed (#128) located approximately 400 m NW of BB 43 and at approximately the same elevation (672.0 m ASL). This site may represent an upriver accumulation of the same centrosaur material in BB 43. If these two sites are part of the same bone bed then the original number of dead centrosaurs may have numbered in the tens of thousands.

The data presented in this study support a catastrophic death for the original *Centrosaurus* assemblage. The low diversity assemblage with an almost uniform taphonomic signature suggests that a large group of one species was killed in one place at the same time, then disarticulated and transported to their final resting place very quickly, probably in under a few years. The similar abrasion and breakage patterns for all the material suggest that it underwent the same modification processes at approximately the same time, and that the material was not accumulated attritionally over a long period of time.

Kurten (1952) points out that while mass deaths do occur, they are fairly rare. Behrensmeyer (1975) suggests that it is the exception (drowning) that usually produces a fossil, while "normal" life habits leave little or no fossil evidence. Given the rarity of fossilization, it would seem likely that the record of a mass death would best be preserved if it was tied to a specific instance that increased the chances of fossilization, such as in a mass death by drown-

ing. Catastrophic death assemblages resulting from floods that killed all or portions of herds of early mammals have been invoked by Loomis (1910:*Stenomylus*), Schlosser (1921:*Hipparion*), Kurten (1952:*Hipparion*), and Turnbull and Martill (1988:cf. *Mesatirhinus*). Mass deaths of large segments of herds of modern mammals in flash floods and at water holes have been well-documented for *Bison* and *Equus* (McHugh, 1972) and *Connochaetes* (Schaller, 1972, 1973). In northern Quebec more than 10000 *Rangifer* drowned while trying to cross a river in 1985, and it is possible to visualize similar groupings of dinosaurs perishing in a like fashion.

Although the cause of death for the centrosaurs can never be known conclusively, evidence for agents such as disease or drought is not present. Although it is difficult to determine the health of the centrosaurs at the time of their death, only four pathological bones were recovered from BB 43, possibly indicating that population was not environmentally stressed at the time of death. A drought-induced origin has been suggested for other Late Cretaceous dinosaur bone beds from the Western Interior of North America (e.g., Rogers, 1991; Varricchio and Horner, 1992), but it is not a plausible explanation for BB 43. There is no sedimentological support (e.g., presence of caliches) for periods of prolonged drought either in the BB 43, or anywhere else in the Dinosaur Park Formation of Dinosaur Park, although this does not mean that droughts did not occur. Additionally, the assemblage is not associated with a facies indicative of ponded water around which a drought-stricken group of centrosaurs might have gathered, nor does it resemble that proposed for a drought-induced assemblage. That is, a high percentage of juvenile-sized specimens concentrated in an area with extensive caliche beds (Rogers, 1991). Given the numerous stacked channels present in the Dinosaur Park Formation and the high probability of seasonal storms flooding the coastline of the Western Interior Seaway, a catastrophic death by drowning for the centrosaurs preserved in BB 43 is a likely scenario.

The BB 43 pattern of preservation is repeated in the additional more than two dozen, *Centrosaurus* bone beds known from the Dinosaur Park Formation of southern Alberta. All of these bone beds are confined to the lower 25 m of the formation, and no paucispecific bone beds are known for other taxa. Notable by their absence are hadrosaur bone beds, a group that otherwise numerically dominates the formation in articulated skeletons, isolated elements, and specimens from vertebrate microsites. The large number of *Centrosaurus* bone beds and the lack of paucispecific bone beds of other taxa have implications for the interpretation of dinosaur behavior, and the possible direction and timing of migration routes. Whether Campanian-aged centrosaurine ceratopsids "migrated" is open to debate. Currie (1989) suggested that *Pachyrhinosaurus*, known from material in southern Alberta and Alaska, participated in annual north-south migrations. However, it is now known that the deposits containing these fossils are not contemporaneous, and probably contain different species. Also, centrosaurines from the Campanian are highly confined geographically suggesting that migration for these animals was limited, possibly from areas near the margin of the Western Interior Seaway to areas inland (Brinkman et al., 1998).

Where defined as "aggregations," "collections," "herds," or "packs," it seems clear that centrosaurs associated in large groups for at least part of the year. It is possible that hadrosaurs did not express this behavior in the Dinosaur Provincial Park area, or if they did, they did not do it when the chances of dying and being preserved in large numbers occurred.

Morphological Variation of Ceratopsid Material in Bone Bed 43 and Its Implications

BB 43 provides excellent documentation of the morphological variation present in one population of *Centrosaurus*. Although variation is often difficult to quantify, especially for putative fossil populations (see discussion in Sampson and Ryan, 1997), qualitative description of the diagnostic ceratopsid elements from the bone bed (even when fragmentary), universally recognizes the material as being from *Centrosaurus*. The site documents the ontogenetic development of the genus for each of the key diagnostic ceratopsid elements (nasal, parietal, and postorbital) and provides the best data set available for understanding the ontogenetic development of centrosaurine ceratopsids (Sampson et al., 1997) and neoceratopsids, in general. Centrosaurine ceratopsids began life with a generalized, non-ornamented skull lacking the diagnostic features of the nasal, orbital region, and frill that developed with the attainment of adult size.

Although sexual dimorphism has been inferred for basal neoceratopsians (Kursanov, 1972; Dodson, 1976) and ceratopsids (Dodson, 1990; Lehman, 1990; Happ and Morrow, 1996), the material preserved in this bone bed does not show or suggest sexual dimorphism for this population. Dodson (1990) suggested that individual *Centrosaurus* skulls could be identified as male or female based on minor variations of the proportions of the skulls or some individual elements. The recognition of ontogenetic variability within *Centrosaurus*, and the variability present in adults elements, suggests that sexual dimorphism within *Centrosaurus* will be difficult to establish. Further, Dodson suggested that one skull (*C. nasicornis* AMNH 5351) represents the female of *Styracosaurus albertensis*. This is highly unlikely given the apparent stratigraphic separation of the two taxa within the Dinosaur Park Formation.

Evaluation of Size Classes in BB 43 Material

Preliminary examination of orbital horn cores from BB 43 collected before 1983 suggested that there were three distinct size classes amongst the ceratopsid bones (Currie and Dodson, 1984). Three very small horn cores had been recovered, five twice this size, and the remaining forty-two reported at that time were a minimum of 50% larger than those in the second group. Currie and Dodson (1984) suggested that the first group of horn cores may be representative of centrosaurs less than a year old, the next representing a size class equivalent to yearlings, and the remainder being equivalent to adults. They reasoned that the centrosaurs doubled their size in the first year of life, giving discrete "hatchling" and "yearling" size classes. But beyond the second year, individual variation masked any differences in discrete size classes that might have been present. Their conclusions were not unreasonable given

their data set and the contemporary knowledge of reptilian growth rates based on the work of McIhenny (1935) and Neill (1971). These studies showed that alligators more than double their hatchling weight each year for the first six to eight years of life, after which they grow more slowly. There is a difference in the rate of growth of males and females after the first 10 years or so, with males reaching a total length of roughly double that of the females. Webb and Messel (1978) found that hatchling *Crocodylus porosus* of less than a year of age formed a discrete size class, but that the members of subsequent year classes could not be distinguished from each other.

A survey of all the supraorbitals and the isolated post-orbital bones collected up to the end of the 1989 field season clearly reveals a range of sizes that would include small juveniles to mature adults. The three smallest post-orbitals form a discrete size class, being >50% smaller than the next largest postorbital, and probably can be referred to individuals born in the year that they died. However, with the addition of more specimens, Currie and Dodson's (1984) intermediate size class is no longer recognizable as a discrete cluster in comparison to the largest, and oldest, size class (unpublished analysis conducted using Cluster and Principal Component Analysis program, SYSTAT 5.0 Statistics package, run on an IBM PC). This is due, in part, to the frequent resorption of the supra-orbital horn seen in the morphologically largest specimens. Indeed the largest, most massive supraorbitals have the shortest horns (0.0 mm for the two largest specimens). Unfortunately, due to the fragmentary nature of most of the material from BB 43, other elements could not be analyzed for the presence of discrete size classes. Thus, the presence of discrete size classes, and the suggested putative age structure of the preserved *Centrosaurus* remains as suggested by Currie and Dodson (1984), lack corroboration. Other *Centrosaurus* bone beds along the South Saskatchewan River of southern Alberta, however, have yielded elements of sufficient quality and quantity to enable further testing of this hypothesis in the future.

Although discrete size classes for post/supraorbitals could not be established, three developmental stages can be identified. These are:

Stage 1—The postorbital is not fused to any other supra-orbital element. Its horn is laterally compressed, with a rounded tip in the smallest specimens. In larger specimens the horn is: roughly pyramidal in shape with a sharply defined apex; it is gracile in morphology; and has non-rugose bone texture laterally and dorsally, and long-grain texture on the medial surface.

Stage 2—The postorbital is fused to the remaining supra-orbital elements and the horn core, although more robust, has not been modified significantly (no resorption pits or other reduction of horn height; lateral and dorsal surface rugosities may or may not be present), and bears long-grain or mottled bone texture on the medial surface.

Stage 3—Supra-orbital elements are fused, the horn is modified significantly by one or more resorption pits (no trace of the horn is visible in some specimens; e.g., TMP 80.18.138).

SUMMARY

(1) BB 43 is a paucispecific *Centrosaurus* bone bed preserved as a lag deposit resting on the erosional surface of a paleochannel comprising three stacked fining- and thinning-upward sets of sandstone. After the initial scour- and fill-event that emplaced the lag deposit, the paleochannel experienced several flood-events. One of these flood events carved a second erosional surface in the center of the paleochannel, forming the major portion of the bone bed and reworking upstream portions of the original basal lag.

(2) The material in BB 43 was reworked from an upstream assemblage that probably was transported only a short distance to its current resting place. After death of the original assemblage, taphonomic indicators suggest that disarticulation (including scavenging by theropods), transportation to the present resting site, and entombment in the sediments of the bone bed lithosome was rapid, probably occurring in several years or less.

(3) Although the cause of death can not be determined conclusively, the originally proposed scenario of a catastrophic death for part of a large group of *Centrosaurus* drowning on the flooded margin of the Western Interior Seaway is the most parsimonious explanation.

(4) Analysis of the *Centrosaurus* material does not support the presence of discrete size classes (juvenile, sub-adult, and adult) as originally proposed by Currie and Dodson (1984). However, this may be due to the problem of obtaining the appropriate data for testing from the highly fragmented and fluviially-winnowed assemblage which is biased towards the preservation of robust adult-sized elements, and portions thereof. Some elements (e.g., post-orbitals) show that the assemblage preserved *Centrosaurus* elements derived from individuals ranging in size from very small juvenile- to mature, adult-sized animals.

(5) Data from this study illustrate the ontogeny of the diagnostic cranial elements of *Centrosaurus* (nasal, post-orbital, parietal, and epoccipitals) and has important implications for recognising the sub-adult states of skull elements from other centrosaurs. Juvenile-sized cranial elements of *Centrosaurus* and other centrosaurine ceratopsids have a generalized juvenile morphology common to all centrosaurines. Hence, care must be taken when making taxonomic identifications of juvenile- to sub-adult-sized elements.

ACKNOWLEDGEMENTS

Thanks are due to all the staff and volunteers of the Royal Tyrrell Museum of Palaeontology, too numerous to name individually, who have worked in BB 43, assisted in the preparation of fossils from this site, or who otherwise have supported (and continue to support) research into the numerous ceratopsid bone beds in Alberta. Special thanks to Darren Tanke for all the work he has put into this locality, and for graciously sharing his knowledge and thoughts on ceratopsids. Steve Kwasnowski assisted with the stratigraphic survey of BB 43 and prepared the original version of Figure 7. Donna Sloan prepared the original version of Figure 2 and assisted with photography. Chad Kerychuk of Digital Dream Machine (Edmonton, AB) assisted with the layout of Figures 3, 4, 8, 9, and 11. The thoughtful comments of two anonymous reviewers im-

proved the quality of this paper. This research was funded partially through an NSERC Operating Grant to A.P. Russell. M.J. Ryan gratefully acknowledges financial assistance from the Dinosaur Natural History Association (for travel), and a research travel grant from the American Museum of Natural History.

REFERENCES

- BEHRENSMEYER, A.K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya: *Bulletin of the Museum of Comparative Zoology, Harvard University*, v. 146, p. 474–578.
- BEHRENSMEYER, A.K., 1978, Taphonomic and ecological information from bone weathering: *Paleobiology*, v. 4, p. 150–162.
- BEHRENSMEYER, A.K., 1982, Time resolution in fluvial vertebrate assemblages: *Paleobiology*, v. 8, p. 211–227.
- BEHRENSMEYER, A.K., 1988, Vertebrate preservation, in fluvial channels: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 183–199.
- BEHRENSMEYER, A.K., 1990, Bones: in BRIGGS, D.E.G., and CROWTHER, P.R., eds., *Palaeobiology*: Blackwell Scientific Publications, Oxford, p. 232–235.
- BEHRENSMEYER, A.K., and HOOKS, R.W., 1992, Paleoenvironmental contexts and taphonomic modes: in BEHRENSMEYER, A.K., DAMUTH, J.D., DiMICHELE, W.A., POTTS, R., SUES, H.-D., and WING, S.L., eds., *Terrestrial Ecosystems through Time: The University of Chicago Press, Chicago*, p. 15–136.
- BEHRENSMEYER, A.K., GORDON, K.D., and YANAGI, G.T., 1986, Trampling as a cause of bone surface damage and pseudo-cutmarks: *Nature*, v. 319, p. 768–771.
- BLOB, R.W., 1997, Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: Implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates: *PALAIOS*, v. 12, p. 151–164.
- BOAZ, N.T., and BEHRENSMEYER, A.K., 1976, Hominid taphonomy: Transport of human skeletal parts in an artificial fluvial environment: *American Journal of Physical Anthropology*, v. 45, p. 53–60.
- BRAMAN, D.R., JOHNSTON, P.A., and HAGLUND, W.M., 1995, Canadian Paleontology Conference Field Trip Guidebook No. 4: Upper Cretaceous Paleontology, Stratigraphy and Depositional Environments at Dinosaur Park and Drumheller, Alberta: Canadian Paleontology Conference V, Drumheller '95, Royal Tyrrell Museum of Paleontology, 29 September–2 October, 1995, 119 p.
- BRINKMAN, D.B., 1990, Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park: Evidence from vertebrate microfossil localities: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 78, p. 37–54.
- BRINKMAN, D.B., RYAN, M.J., and EBERTH, D.A., 1998, The palaeogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the Upper Judith River Group of Western Canada: *PALAIOS*, v.13, p. 160–169.
- BROWN, B., 1914, *Anchiceratops*, a new genus of horned dinosaur from the Edmonton Cretaceous of Alberta. With discussion of the origin of the ceratopsian crest and the brain casts of *Anchiceratops* and *Trachodon*: *Bulletin of the American Museum of Natural History*, v. 33, p. 539–548.
- BROWN, B., and SCHLAIKJER, E.M., 1940, The structure and relationships of *Protoceratops*: *Annals of the New York Academy of Sciences*, v. 40, p. 133–266.
- CHINNERY, B.J., and WEISHAMPPEL, D.B., 1998, *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsidae) and relationships among Asian and North American basal neoceratopsians: *Journal of Vertebrate Paleontology*, v. 18, p. 569–585.
- COPE, E.D., 1876, Description of some vertebrate remains from the Fort Union beds of Montana: *Proceedings of the Academy of Natural Sciences, Philadelphia*, v. 28, p. 248–261.
- CURRIE, P.J., 1981, Hunting dinosaurs in Alberta's huge bonebed: *Canadian Geographical Journal*, v. 101, p. 32–39.
- CURRIE, P.J., 1982, Dinosaur Provincial Park: Geological Association of Canada, Palaeontological Division, Field Trip Guidebook: Geological Association of Canada, Toronto, Ontario, 11 p.
- CURRIE, P.J., 1982, Long distance dinosaurs: *Natural History*, v. 6, p. 60–65.
- CURRIE, P.J., and DODSON, P., 1984, Mass death of a herd of ceratopsian dinosaurs: in REIF, W.E., and WESTPHAL, F., eds., *Third Symposium on Mesozoic Terrestrial Ecosystems, Tubingen, Short Papers*, p. 61–66.
- DAVIS, J.C., 1986, *Statistics and Data Analysis in Geology*: John Wiley & Sons, Inc., New York, 646 p.
- DiMICHELE, W.A., and HOOK, R.W., 1992, Palaeozoic Terrestrial Ecosystems: in BEHRENSMEYER, A.K., DAMUTH, J.D., DiMICHELE, W.A., POTTS, R., SUES, H.-D., and WING, S.L., eds., *Terrestrial Ecosystems Through Time: University of Chicago Press, Chicago*, p. 205–325.
- DODSON, P., 1971, Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 10, p. 21–74.
- DODSON, P., 1973, The significance of small bones in paleoecological interpretation: *University of Wyoming, Contributions to Geology*, v. 12, p. 15–19.
- DODSON, P., 1976, Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*: *Journal of Paleontology*, v. 50, p. 929–940.
- DODSON, P., 1986, *Avaceratops lammersi*: A new ceratopsid from the Judith River Formation of Montana: *Proceedings of the Academy of Natural Sciences, Philadelphia*, v. 138, p. 305–317.
- DODSON, P., 1990, On the status of the ceratopsids *Monoclonius* and *Centrosaurus*: in CURRIE, P.J., and CARPENTER, K., eds., *Dinosaur Systematics: Approaches and Perspectives*: Cambridge University Press, Cambridge, p. 231–243.
- DODSON, P., and CURRIE, P.J., 1988, The smallest ceratopsid skull—Judith River Formation of Alberta: *Canadian Journal of Earth Sciences*, v. 25, p. 926–930.
- DODSON, P., and CURRIE, P.J., 1990, Neoceratopsia: in WEISHAMPPEL, D.B., DODSON, P., and OSMOLSKA, H., eds., *The Dinosauria*: University of California Press, Berkeley, p. 593–618.
- DODSON, P., BEHRENSMEYER, A.K., BAKKER, R.T., and MCINTOSH, M.S., 1980, Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation: *Paleobiology*, v. 6, p. 208–232.
- EBERTH, D.A., 1990, Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 78, p. 1–36.
- EBERTH, D.A., 1996, Origin and significance of mud-filled incised valleys (Upper Cretaceous) in southern Alberta, Canada: *Sedimentology*, v. 43, p. 459–477.
- EBERTH, D.A., and HAMBLIN, A.P., 1993, Tectonic, stratigraphic, and sedimentological significance of a regional disconformity in the upper Judith River Formation (Belly River Wedge) of southern Alberta, Saskatchewan and northern Montana: *Canadian Journal of Earth Sciences*, v. 30, p. 174–200.
- ETHRIDGE, F.G. and SCHUMM, S. A., 1978, Reconstructing paleochannel morphologic and flow characteristics: Methodology, limitations and assessment: in MAILL, A.D., ed., *Fluvial sedimentology: Memoir of the Canadian Society of Petroleum Geologists*, v. 5, p. 703–721.
- FIORILLO, A.R., 1984, An introduction to the identification of trample marks: *Current Research, University of Maine*, v. 1, p. 47–48.
- FIORILLO, A.R., 1987, Trample marks: Caution from the Cretaceous: *Current Research in the Pleistocene, University of Maine*, v. 4, p. 76–78.
- FIORILLO, A.R., 1988, Taphonomy of Hazard Homestead Quarry (Ogalla Group), Hitchcock County, Nebraska: *Contributions to Geology, University of Wyoming*, v. 26, p. 7–97.
- FIORILLO, A.R., 1991a, Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, U.S.A.: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 81, p. 281–311.
- FIORILLO, A.R., 1991b, Prey bone utilization by predatory dinosaurs: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 88, p. 157–166.
- FREY, R.W., VOORHIES, M.R., and HOWARD, J.D., 1975, Fossil and re-

- cent skeletal remains in Georgia estuaries: *Senckenbergiana Maritima*, v. 7, p. 257–295.
- GAILE, G.L., and BURT, J.E., 1980, Directional Statistics. Concepts and Techniques in Modern Geology 25: Geo Abstracts, University of East Anglia, Norwich, England, 29 p.
- GILMORE, C.W., 1914, A new ceratopsian dinosaur from the Upper Cretaceous of Montana, with a note on *Hypacrosaurus*: Smithsonian Miscellaneous Collections, v. 63, p. 1–10.
- GILMORE, C.W., 1917, *Brachyceratops*, a ceratopsian dinosaur from the Two Medicine Formation of Montana: United States Geological Survey Professional Paper No. 103, p. 1–45.
- GILMORE, C.W., 1922, The smallest known horned dinosaur, *Brachyceratops*: United States National Museum Proceedings, v. 61, p. 1–4.
- HAPP, J.W., and MORROW, C.M., 1996, Separation of *Triceratops* (Dinosauria: Ceratopsidae) into two allopatric species by cranial morphology: *Journal of Vertebrate Paleontology*, v. 16 (abstracts), p. 40A.
- HATCHER, J.B., MARSH, O.C., and LULL, R.S., 1907, The Ceratopsia: United States Geological Survey Monograph No. 49, 300 p.
- HAYNES, G., 1983, Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages: *American Antiquity*, v. 48, p. 102–114.
- HILL, A., and WALKER, A., 1972, Procedures in vertebrate taphonomy: Notes on a Uganda Miocene fossil locality: *Journal of the Geological Society of London*, v. 128, p. 399–406.
- HORNER, J.R., 1982, Evidence of colonial nesting and 'site fidelity' among ornithischian dinosaurs: *Nature*, v. 297, p. 675–676.
- HORNER, J.R., and MAKELA, R., 1979, Nest of juveniles provides evidence of family structure among dinosaurs: *Nature*, v. 282, p. 296–298.
- HUNT, R.M., Jr., 1978, Depositional setting of a Miocene mammal assemblage, Sioux County, Nebraska (U.S.A.): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 24, p. 1–52.
- JACOBSEN, A.R., 1995, Predatory behaviour of carnivorous dinosaurs: Ecological interpretations based on tooth marked dinosaur bones and wear patterns of theropod teeth: Unpublished M.S. Thesis, University of Copenhagen, Copenhagen, 79 p.
- KORTH, W.A., 1979, Taphonomy of microvertebrate fossil assemblages: *Annals of the Carnegie Museum*, v. 48, p. 235–285.
- KOSTER, E.H., CURRIE, P.J., EBERTH, D., BRINKMAN, D., JOHNSON, P., and BRAMAN, D., 1987, Sedimentology and Palaeontology of the Upper Cretaceous Judith River/Bearpaw Formations at Dinosaur Provincial Park, Alberta, Field Trip #10: Geological Association of Canada, Mineralogical Association of Canada, Joint Annual Meeting, Saskatoon, Saskatchewan, 130 p.
- KURTEN, B., 1952, The Chinese *Hipparion* fauna. A quantitative survey, with comments on the ecology of the machair rodents and hyaenids and the taxonomy of the gazelles: *Societas Scientiarum Fennica, Commentationes Biologicae*, v. 13, p. 1–82.
- KURZANOV, S.M., 1972, Sexual dimorphism in protoceratopsids: *Paleontological Zhurnal*, v. 1972, p. 91–97 (In Russian).
- LAMBE, L.M., 1904, On the squamoso-parietal crest of two species of horned dinosaurs from the Cretaceous of Alberta: *Ottawa Naturalist*, v. 18, p. 81–84.
- LAMBE, L.M., 1910, Note on the parietal crest of *Centrosaurus apertus* and a proposed new name for *Stereocephalus tutus*: *Ottawa Naturalist*, v. 24, p. 149–151.
- LAMBE, L.M., 1913, A new genus and species from the Belly River Formation of Alberta: *Ottawa Naturalist*, v. 27, p. 109–116.
- LAMBE, L.M., 1914, On *Gryposaurus notabilis*, a new genus and species of trachodont dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Chasmosaurus belli*: *Ottawa Naturalist*, v. 27, p. 145–155.
- LAMBE, L.M., 1915, On *Eoceratops canadensis*, gen. nov., with remarks on other genera of Cretaceous horned dinosaurs: *Geological Survey of Canada, Museum Bulletin*, v. 12, p. 1–49.
- LANGSTON, W.L., Jr., 1975, The ceratopsian dinosaurs and associated lower vertebrates from the St. Mary River Formation (Maestrichtian) at Scabby Butte, southern Alberta: *Canadian Journal of Earth Sciences*, v. 12, p. 1576–1608.
- LAWTON, R., 1977, Taphonomy of the dinosaur quarry, Dinosaur National Monument: *Contributions to Geology*, University of Wyoming, v. 15, p. 119–126.
- LEHMAN, T.M., 1982, A ceratopsian bone bed from the Aguja Formation (Upper Cretaceous) Big Bend National Park, Texas: Unpublished M.S. Thesis, University of Texas at Austin, 210 p.
- LEHMAN, T.M., 1989, *Chasmosaurus mariscalensis*, sp. nov., a new ceratopsian dinosaur from Texas: *Journal of Vertebrate Paleontology*, v. 9, p. 137–162.
- LEHMAN, T.M., 1990, The ceratopsian subfamily Chasmosaurinae: Sexual dimorphism and systematics: in CURRIE, P.J., and CARPENTER, K., eds., *Dinosaur Systematics: Approaches and Perspectives*: Cambridge University Press, Cambridge, p. 211–229.
- LOOMIS, F.M., 1910, Osteology and Affinities of the genus *Stenonyx*: *American Journal of Science*, v. 29, p. 297–321.
- LULL, R.S., 1933, A revision of the Ceratopsia: *Memoirs of the Peabody Museum of Natural History* No. 3, p. 1–175.
- MARSH, O.C., 1889, Notice of gigantic horned Dinosauria from the Cretaceous: *American Journal of Science*, v. 38, p. 173–175.
- MARSH, O.C., 1891, The gigantic Ceratopsidae, or horned dinosaurs, of North America: *American Journal of Science*, v. 41, p. 167–177.
- McHUGH, T., 1972, *The Time of the Buffalo*: University of Nebraska Press, Lincoln, 339 p.
- McILHENNY, E.A., 1935, The alligator's life history: *Society for the Study of Amphibians and Reptiles*, 125 p.
- McLEAN, J.R., 1971, Stratigraphy of the Upper Cretaceous Judith River Formation in the Canadian Great Plains: Saskatchewan Research Council, Geology Division, Report No. 11, 96 p.
- MORLAN, R.E., 1980, Taphonomy and archeology in the Upper Pleistocene of the Northern Yukon Territory: a glimpse of the peopling of the New World: National Museum of Man, Mercury Series, Archaeological Survey of Canada, Ottawa Paper No. 94, 49 p.
- NEILL, W.T., 1971, The last of the ruling reptiles: Alligators, crocodiles and their kin: Columbia University Press, New York, 486 p.
- NORMAN, D.B., 1987, A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany: *Proceedings of the Royal Society of London B*, v. 230, p. 215–255.
- OSBORN, H.F., 1923, Two Lower Cretaceous dinosaurs from Mongolia: *American Museum Novitates* No. 95, p. 1–10.
- PARKS, W.A., 1925, *Arrhinoceratops brachyops*, a new genus and species of Ceratopsia from the Edmonton Formation of Alberta: *University of Toronto Studies (Geology Series)* No. 19, p. 5–15.
- PARRISH, J.M., PARRISH, J.T., HUTCHINSON, J.H., and SPICER, R.A., 1987, Late Cretaceous vertebrate fossils from the North Slope of Alaska and implications for dinosaur ecology: *PALAIOS*, v. 2, p. 377–389.
- ROGERS, R.R., 1991, Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of Northwestern Montana: Evidence for drought-related mortality: *PALAIOS*, v. 5, p. 394–413.
- RYAN, M.J., 1992, The taphonomy of a Centrosaurus (Reptilia: Ornithischia) bone bed (Campanian), Dinosaur Provincial Park, Alberta, Canada: Unpublished M.S. Thesis, University of Calgary, Alberta, 526 p.
- RYAN, M.J., EBERTH, D.A., BRINKMAN, D.A., and RUSSELL, A.P., 1998, A sub-adult *Styracosaurus* (Ornithischia) from the Dinosaur Park Formation (Late Campanian), Alberta: Canada. *Journal of Vertebrate Paleontology*, v. 18 (supplement), p. 72A.
- SAMPSON, S.D., 1995, Two new horned dinosaurs from the upper Cretaceous Two Medicine Formation of Montana, with a phylogenetic analysis of the Centrosaurinae (Ornithischia: Ceratopsidae): *Journal of Vertebrate Paleontology*, v. 15, p. 743–760.
- SAMPSON, S.D., and RYAN, M.J., 1997, Individual Variation: in CURRIE, P.J., and PADIAN, K., eds. *The Encyclopedia of Dinosaurs*: Academic Press, San Diego, p. 773–780.
- SAMPSON, S.D., RYAN, M.J., and TANKE, D.H., 1997, Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): Taphonomic and Behavioral Phylogenetic implications: *Zoological Journal of the Linnean Society*, v. 121, p. 293–337.
- SCHALLER, G.B., 1972, *The Serengeti Lion*: University of Chicago Press, Chicago, 480 p.
- SCHALLER, G.B., 1973, *Golden Shadows, Flying Hooves*: Alfred A. Knopf, New York, 287 p.
- SCHLOSSER, H., 1921, Die hipparionen fauna von Veles in Mazedonien: *Abhandlungen Bayerische Akademie Wissenschaften*, v. 29, p. 1–79.

- SMITH, N.D., 1972, Flume experiments on the durability of mud clasts: *Journal of Sedimentary Petrology*, v. 42, p. 378–383.
- STERNBERG, C.M., 1927, Homologies of certain bones of the ceratopsian skull: *Transactions of the Royal Society of Canada*, v. 21, p. 135–143.
- STERNBERG, C.M., 1938, *Monoclonius* from southeastern Alberta compared with *Centrosaurus*: *Journal of Paleontology*, v. 12, p. 284–286.
- STERNBERG, C.M., 1940, Ceratopsidae from Alberta: *Journal of Paleontology*, v. 14, p. 468–480.
- STERNBERG, C.M., 1950, *Pachyrhinosaurus canadensis*, representing a new family of Ceratopsia: *Bulletin of the National Museum of Canada*, v. 118, p. 109–120.
- TANKE, D.H., 1988, Ontogeny and dimorphism in *Pachyrhinosaurus* (Reptilia: Ceratopsidae), Pipestone Creek, N.W. Alberta, Canada: *Journal of Vertebrate Paleontology*, v. 8, (abstracts), p. 41A.
- TOOTS, H., 1965, Sequence of disarticulation in mammalian skeletons: *Contributions to Geology, University of Wyoming*, v. 4, p. 37–39.
- TURNBULL, W.D., and MARTILL, D.M., 1988, Taphonomy and preservation of a monospecific titanotheres assemblage from the Washakie Formation (Late Eocene), southern Wyoming. An ecological accident in the fossil record: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 91–108.
- VARRICCHIO, D.J., 1995, Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 114, p. 297–323.
- VARRICCHIO, D.J., and HORNER, J.R., 1992, Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: Taphonomic and biological implications: *Canadian Journal of Earth Sciences*, v. 30, p. 997–1006.
- VISSER, J., 1986, Sedimentology and taphonomy of a *Styracosaurus* bonebed in the Late Cretaceous Judith River Formation, Dinosaur Provincial Park, Alberta: Unpublished M.S. Thesis, University of Calgary, Alberta, 150 p.
- VOORHIES, M.R., 1969, Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska: University of Wyoming, *Contributions to Geology, Special Paper No. 1*, p. 1–69.
- WEBB, G.J.W., and MESSEL, H., 1978, Morphometric analysis of *Crocodylus porosus* from the North Coast of Arnhem land, Northern Australia: *Australian Journal of Zoology*, v. 26, p. 1–28.
- WING, S.L., and SUES, H.-D., 1992, Mesozoic Terrestrial Ecosystems: in BEHRENSMEYER, A.K., DAMUTH, J.D., DiMICHELE, W.A., POTTS, R., SUES, H.-D., and WING, S.L., eds., *Terrestrial Ecosystems through Time: The University of Chicago Press, Chicago*, p. 327–416.
- WOLFE, D.G., and KIRKLAND, J.I., 1998, *Zuniceratops christopheri* n. gen. & n. sp., a ceratopsian dinosaur from the Moreno Hill Formation (Cretaceous, Turonian) of west-central New Mexico: in LUCAS, S.G., KIRKLAND, J.I., and JACOBS, J.W., eds., *Lower and Middle Cretaceous Terrestrial Ecosystems: New Mexico Museum of Natural History and Science Bulletin No. 14*, p. 303–317.
- WOOD, J.M., 1985, Sedimentology of the Late Cretaceous Judith River Formation, "Cathedral" area, Dinosaur Provincial Park, Alberta: Unpublished M.S. Thesis, University of Calgary, Alberta, 215 p.
- WOOD, J.M., 1989, Alluvial architecture of the Upper Cretaceous Judith River Formation, Dinosaur Provincial Park, Alberta, Canada: *Bulletin of Canadian Petroleum Geology*, v. 37, p. 169–181.
- WOOD, J.M., THOMAS, R.G., and VISSER, J., 1988, Fluvial processes and vertebrate taphonomy: the Upper Cretaceous Judith River Formation, south-central Dinosaur Provincial Park, Alberta, Canada: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 66, p. 127–143.

ACCEPTED MAY 11, 2001

