

The Ceratopsian Dinosaurs and Associated Lower Vertebrates from the St. Mary River Formation (Maestrichtian) at Scabby Butte, Southern Alberta

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Scabby Butte, a limited exposure of late Cretaceous sediments in southern Alberta, Canada, is an important source for the large ceratopsian dinosaur *Pachyrhinosaurus* Sternberg. New cranial material confirms this taxon's place among short-faced ceratopsids, and circumstantial evidence suggests that it possessed a spiked frill reminiscent of *Styracosaurus*. Postcranial bones associated with *Pachyrhinosaurus* skulls in a bonebed deposit probably belong to the genus and indicate a massive body approaching *Triceratops* dimensions. Another ceratopsian, *Anchiceratops*, is sparsely represented.

All classes of gnathostomes, except birds, are represented by fragmentary material at Scabby Butte. Of 21 lower vertebrate taxa, fourteen are new to the St. Mary River Formation (*Squatirhina*, *Squatina*, *Amia*, *Belonostomus*, *Paralbula*, *Platacodon*, *Opisthotriton*, *Boremys*, *Plioplatecarpus*, a tyrannosaur, a coelurosaur, an ornithomimid, *Troödon*, *Edmontosaurus*, *Edmontonia*).

Scabby Butte, un affleurement de sédiments Crétacé inférieur au sud-est de l'Alberta, Canada, est une source importante des grands dinosauriens ceratopsiens *Pachyrhinosaurus* Sternberg. De nouveaux matériaux craniens confirment leur classification taxonomique en cératopsides à petites faces, et des évidences secondaires suggèrent qu'ils possédaient un reste de la colerette dentelée de *Styracosaurus*. Des os craniens associés aux débris de *Pachyrhinosaurus*, dans un dépôt riche en os, indiquent un animal massif s'approchant des dimensions de *Triceratops*. Un autre ceratopsien, *Anchiceratops*, est également rarement représenté.

Toutes les classes de gnathostomes, sauf les oiseaux, sont représentées par des fragments de matériel osseux à Scabby Butte. Des 21 taxonomies d'invertébrés inférieurs, 14 sont nouvelles pour la Formation St-Mary River (*Squatirhina*, *Squatina*, *Amia*, *Belonostomus*, *Paralbula*, *Platacodon*, *Opisthotriton*, *Boremys*, *Plioplatecarpus*, un tyrannosaure, un coelurosaure, un ornithomimidé, *Troödon*, *Edmontosaurus*, *Edmontonia*). [Traduit par le journal]

Introduction

After a century of spectacular paleontological revelations in the Mesozoic fossil fields of North America, the finding of a genuinely new kind of dinosaur is a novel event. Such was the discovery of the large battering-ram ceratopsian *Pachyrhinosaurus*, reported by C. M. Sternberg in 1950. One of Sternberg's three specimens was recovered from Upper Cretaceous rocks of the St. Mary River Formation at an isolated patch of badlands known as Scabby Butte, about 17 miles (~27 km) north-northwest of Lethbridge, Alberta. Subsequent work at Scabby Butte by L. S. Russell, R. L. Fowler, and by parties from the National Museum of Natural Sciences under my supervision have brought to light a considerable array of fossil vertebrates. The mammals have already been described by Sloan and Russell (1974), but the non-mammalian taxa

have not been dealt with in detail. The material, all of which is housed at the National Museum of Natural Sciences in Ottawa, provides additional information about *Pachyrhinosaurus*, which is still but poorly known. And, although no new genera are recognized, eleven taxa are new to the St. Mary River Formation. This paper is a supplement to another report (Langston 1975), to which the reader is referred for a review of the occurrence, history of collecting, geological matters, and detailed locality data at Scabby Butte, and a paleoecological interpretation of the deposit.

Non-Mammalian Vertebrates from Scabby Butte

The non-mammalian vertebrates from Scabby Butte are summarized below (for a list of the mammals, see Sloan and Russell 1974).

Class ELASMOBRANCHII

Order Isuriformes

Orectolobidae

Squatirhina americana Estes

Order Squatinoidei

Squatinidae

Squatina Risso, sp. indet.

Order Rajiformes

Dasyatidae

Myledaphus bipartitus Cope

Class OSTEICHTHYES

Order Amiiiformes

Amiidae

Amia cf. *A. fragosa* (Jordan)

Order Aspidorhynchiformes

Aspidorhynchidae

Belonostomus cf. *B. longirostris* (Lambe)

Order Lepisosteiformes

Lepisosteidae

Lepisosteus Lacépède, sp. indet.

Order Elopiformes

Phyllodontidae

Paralbula casei Estes

Order Perciformes

Sciaenidae

Platacodon cf. *P. nanus* Marsh

Class AMPHIBIA

Order Urodela

Batrachosauroididae

Opisthotriton Auffenberg, sp. indet.

Class REPTILIA

Order Testudines

Trionychidae

Aspideretes Hay, sp. indet.

Baenidae

Boremys Lambe, sp. indet.

Order Eosuchia

Champsosauridae

Champsosaurus Cope, sp. indet.

Order Squamata

Mosasauridae

Plioplatecarpus Dollo, sp. indet.

Order Crocodylia

Crocodylidae

Leidyosuchus Lambe, sp. indet.

Crocodylia, gen. and sp. indet.

Order Saurischia

Tyrannosauridae, gen. and sp. indet.

?Coeluridae, gen. and sp. indet.

Ornithomimidae, gen. and sp. indet.

Troödontidae

Troödon Leidy, sp. indet.

Order Ornithischia

Hadrosauridae

Edmontosaurus Lambe, sp. indet.

Ceratopsidae

Pachyrhinosaurus canadensis Sternberg*Anchiceratops* Brown, sp. indet.

Nodosauridae

Edmontonia cf. *E. longiceps* Sternberg

These taxa have come from six sites within the general Scabby Butte locality area. The sites are discussed in greater detail in another paper (Langston 1975), but they are summarized here for the convenience of readers lacking access to the study cited. All sites occur in tp. 11, rge. 22, west of the fourth meridian.

Site 1—About 100 ft (~31 m) north of the south line, SE 1/4, SE 1/4, sec. 19. This is the site from which the first *Pachyrhinosaurus* skull material was obtained in 1945 and 1946 (Sternberg 1950).

Site 2—On the westerly escarpment in SE 1/4, SE 1/4, sec. 19. This is the main quarry excavated in 1955 and 1957.

Site 3—On an erosional bench on a westward promontory near the northeast corner of NE 1/4, NW 1/4, sec. 18. This is a 'shell bed' about halfway up the escarpment. It provided most of the small vertebrate remains, including fish and mammal teeth. A mosasaur vertebra was also found here.

Site 4—South-facing escarpment near south line of NW 1/4, NE 1/4, sec. 18. A mosasaur skeleton was found here. The occurrence is at about the same stratigraphic level as the shell bed at Site 3 and about 200 yards (~180 m) E.S.E. of it. Not improbably, the mosasaur vertebra at Site 3 was derived from this skeleton.

Site 5—Northwest escarpment in NW 1/4, sec. 18, about 20 ft (~6 m) below upper prairie level. This locality is stratigraphically higher than the others. It provided a few bones of a large hadrosaur—besides the mosasaur at Site 4,

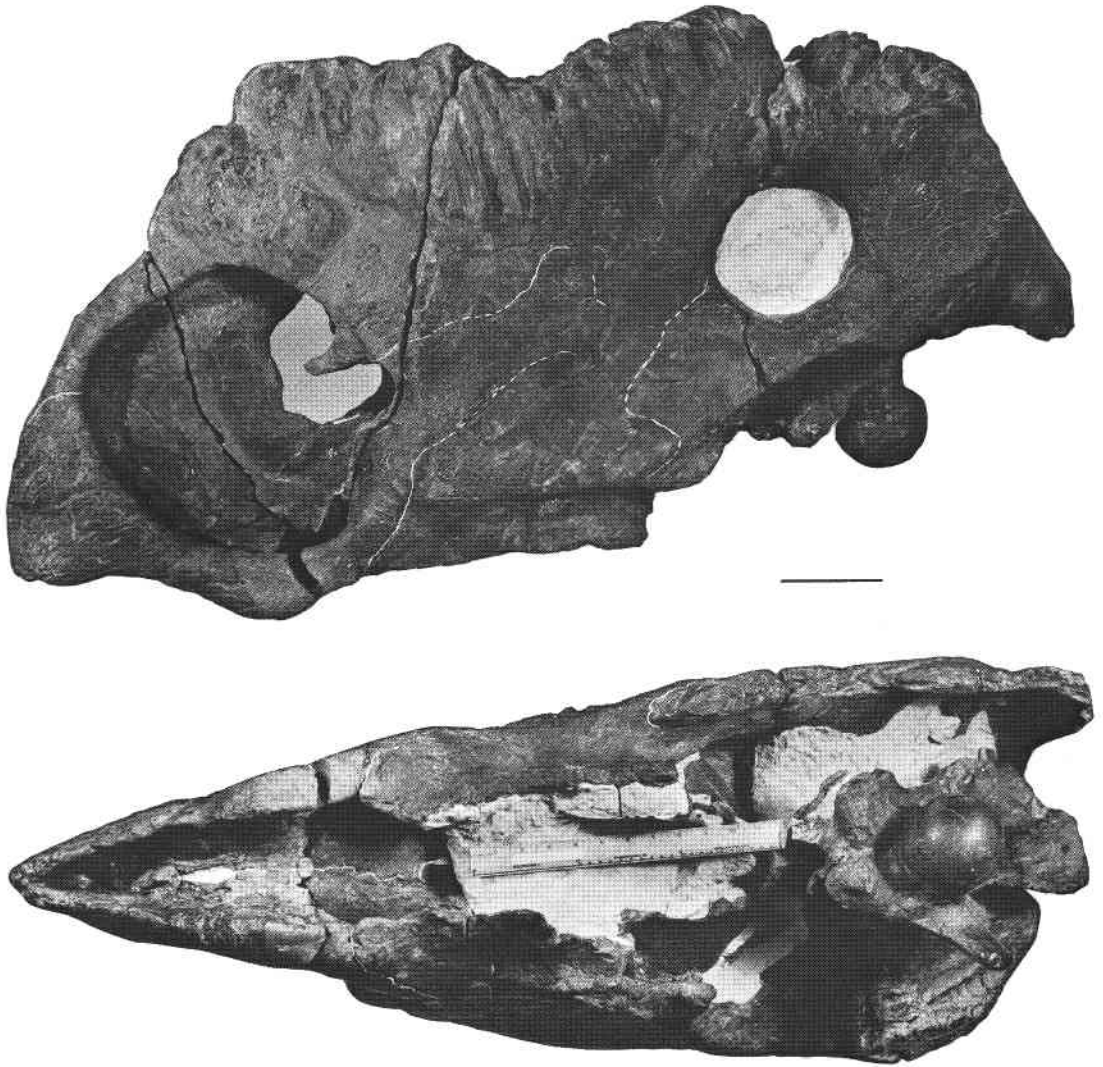


PLATE I. *Pachyrhinosaurus canadensis* Sternberg. NMC 9485, skull lacking cheek and frill. Above, left lateral view; below, palatal aspect. Scale equals 10 cm.

the only positively associated material of one individual yet found in the Scabby Butte area.

Site 6—This locality includes Scabby Butte badlands as a whole. The number is applied to all surface finds. Specimens so designated have been transported unknown distances from their sources.

Ceratopsian Dinosaurs from Scabby Butte

Because *Pachyrhinosaurus* is, in terms of its morphological contribution to the present study,

the most significant element in the Scabby Butte vertebrate assemblage, I am departing from customary systematic procedures to deal with it and certain associated ceratopsians before turning to other forms.

Pachyrhinosaurus Sternberg, 1950
P. canadensis Sternberg, 1950

Four skulls of *Pachyrhinosaurus* have been discussed previously in the literature (Sternberg 1950; Langston 1967, 1968). The holotype of

PLATE II

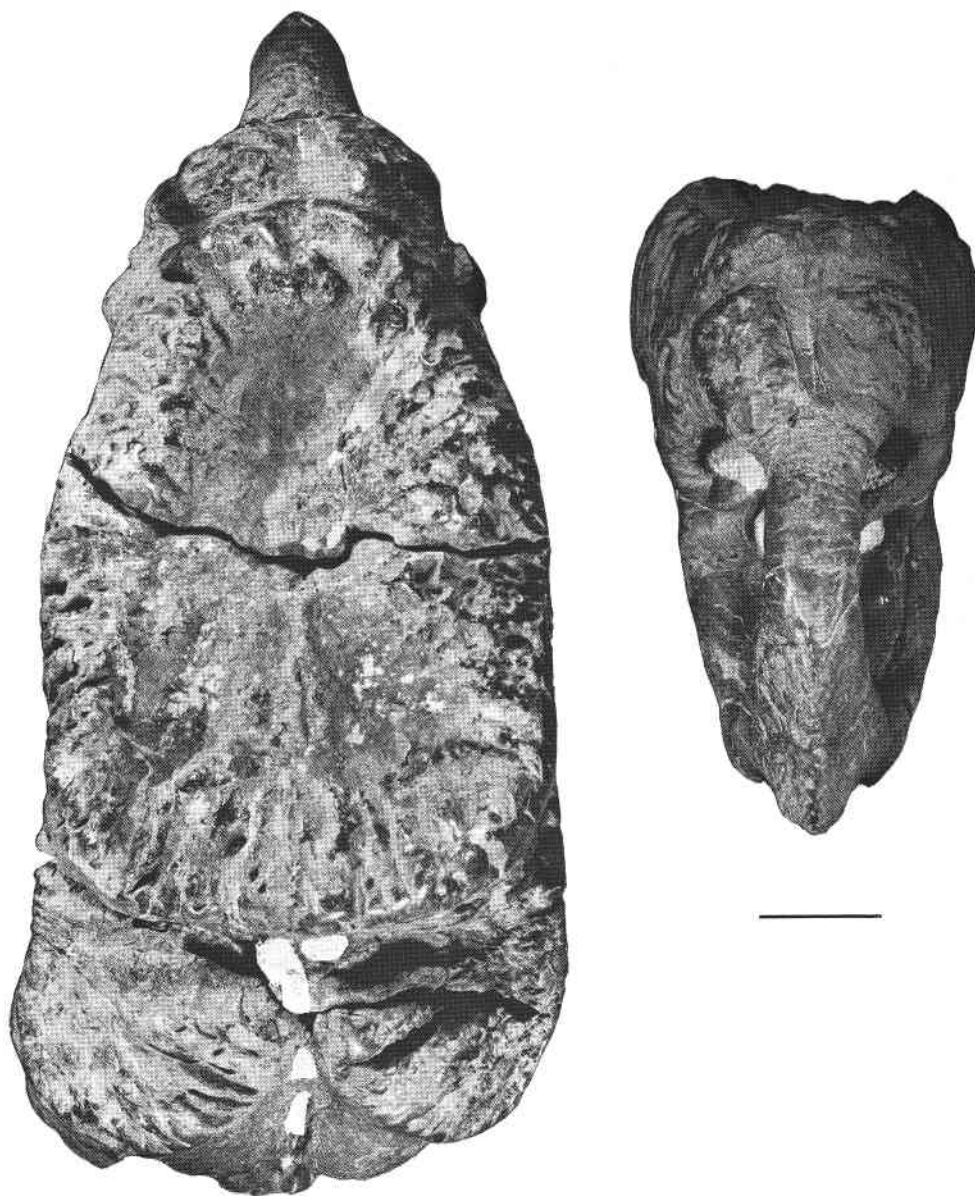


PLATE II. *Pachyrhinosaurus canadensis* Sternberg. NMC 9485, skull lacking cheek and frill. Left, superior aspect; right, anterior aspect. In anterior view, relative width of the nasofrontal boss is diminished by parallax. Scale equals 10 cm.

P. canadensis Sternberg (NMC 8867) is fairly complete, but is flattened laterally to only a fraction of its normal width; a paratype specimen (NMC 8866) comprises only the central part of the cranium and some of the mandible. These specimens are from Lower Edmonton/St. Mary

River rocks on Little Bow River in southern Alberta, some 10 miles (~16 km) from Scabby Butte. A relatively good skull displayed in the Drumheller Museum is from the Lower Edmonton on the Red Deer River near Drumheller (Langston 1967, 1968). The fourth (and first-

discovered) specimen (NMC 8860) is an incomplete rostrum and nasofrontal boss from Scabby Butte. Although these specimens provide some idea of the cranial morphology of *Pachyrhinosaurus*, points of uncertainty and puzzlement remain. The cranial frill is scarcely known, and the braincase and palatal structures have not been described in detail.

Ceratopsian remains occur at Scabby Butte in numbers second only to the ubiquitous hadrosaurs. *Pachyrhinosaurus* is by far the best represented genus. Positive identification of this taxon from the uniquely thickened bone of the cranial boss is easy; resisting erosion, fragments of the massive bosses are common surface finds throughout the badlands. To date, no less than fourteen occurrences of fairly large pieces have been noted, and uncounted smaller but recognizable fragments have been seen in the field. The important cranial material from Scabby Butte is tabulated below:

NMC No.	Description	Site
8860	Nasofrontal boss, part of rostrum, and fragments, possibly composite	1
9485	Skull, lacking cheek bones and frill	2
10663	Skull, lacking cheek bones, frill, and one side of face	2
10664	Right lacrimal	2
10646	Left quadratojugal and part of attached jugal	2
9610	Left quadrate	2
9594	Incomplete left squamosal	2
10665;	Skull fragments of uncertain	2
10666	position	
10667	Tooth	2
10643	Right dentary	2
10629	Left surangular	2
10645	Fragmentary skull and lower jaw	6
21863;	Fragmentary cranial bosses	6
21864;	and other skull parts	
10669		

The new material may be best discussed with emphasis on features not hitherto reported.

Skull—In some respects, NMC 9485 is the best *Pachyrhinosaurus* skull yet recovered. It was found in the course of excavating Site 2, lying on its left side, and little crushed. The only weathering experienced by this skull occurred

before burial when the relatively weak cheek plates and frill were broken off. Parts of a jugal and quadratojugal, quadrate, and squamosal found nearby in the quarry were probably derived from this skull (Fig. 1). The second skull (NMC 10663) from Site 2 was badly weathered and extensively fractured, with most of the external surface destroyed; but what remains is uncrushed and the rostrum and braincase are well preserved. Other specimens from Scabby Butte are fragmentary and will be mentioned only as they elucidate features not seen in the better-preserved material.

All known *Pachyrhinosaurus* skulls are large, but meaningful measurements are difficult to obtain owing to irregular topography, absence of sutures, and (in most instances) poor preservation. A schematic system of mensuration, used previously for the Drumheller skull and augmented here (Table 1) assists comparisons, but errors of 5 to 10% in some dimensions are probable. Most measurements from the best specimens vary by no more than 20%, but the variations are not constant and, I believe, may be as much a result of imprecision as of differing skull proportions.

Skull NMC 9485 agrees well in gross morphology with the previously described specimens. Although sutures are mostly indistinct, their positions can sometimes be inferred with more confidence than in any other specimen. (Huene's 1950 reconstruction of sutures in *P. canadensis*, based on an interpretation of Sternberg's photographs, is wholly fanciful). This skull confirms my earlier interpretation of the *Pachyrhinosaurus* rostrum (Langston 1967), showing it to contain a wide, short, and uncomplicated narial aperture of centrosaur form. On the left side of the skull there is a remarkably long and massive process which, twisting slightly, projects, finger-like, forward into the naris for some 8 cm (Pls. I, II). Similar processes were present in the Drumheller skull. Composed wholly of the nasal bones, their function is unknown, but they may have supported the vestibulum from below and in some way separated this structure from ramifications of the cavum nasi proprium. The external nares thus probably opened superior to the processes. Usually broken off in fossils, the processes are variably developed in the short-faced ceratopsians, but are not present in long-faced taxa.

NMC 9485 reveals for the first time the nature

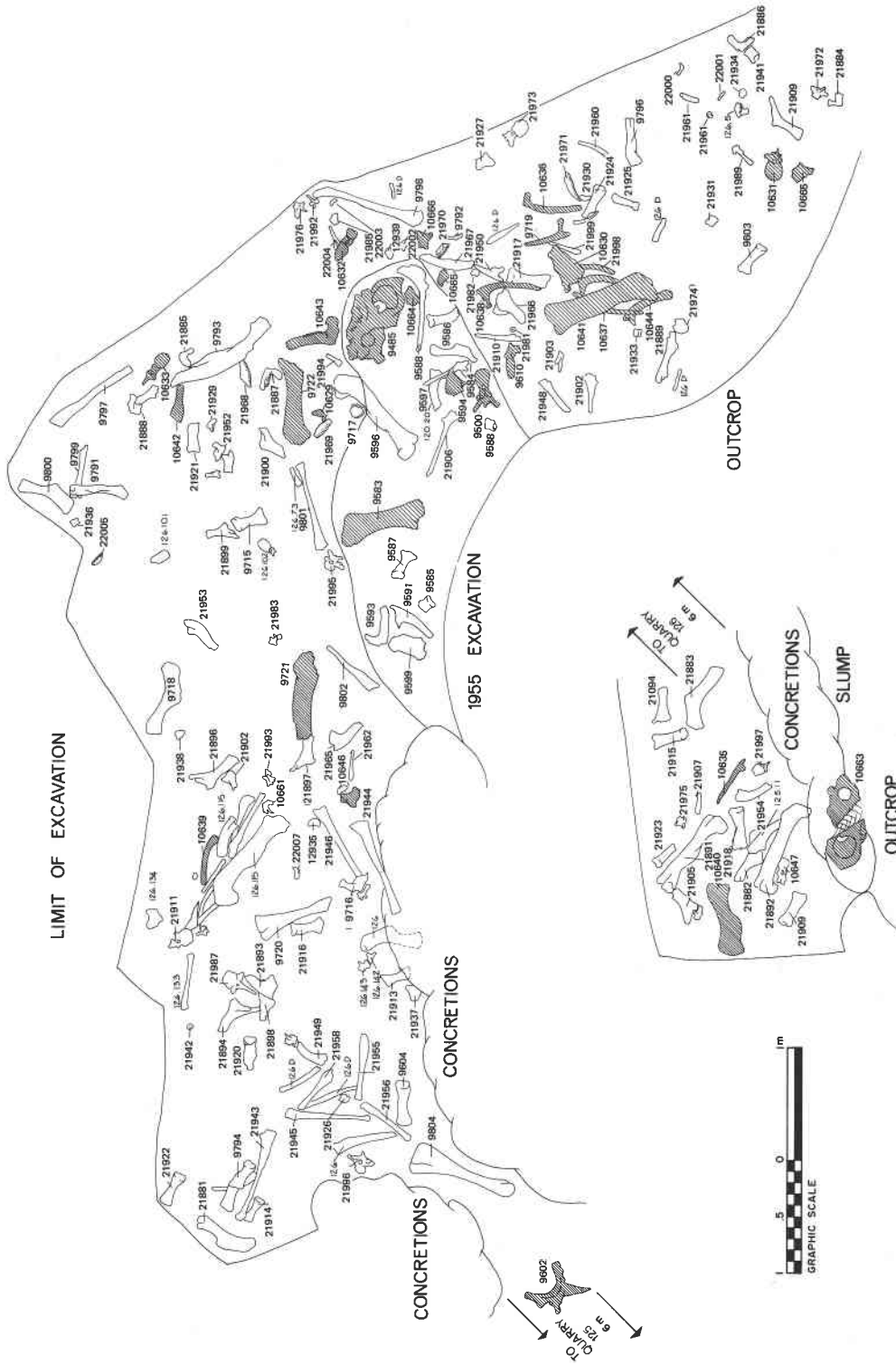


FIG. 1. Quarry diagram of Scabby Butte Site 2 (NMC locality P-5510). Shaded specimens are ceratopsian bones, all others are hadrosaurian. Numbers in boldface are National Museum of Natural Sciences (NMC) designations; others are field numbers.

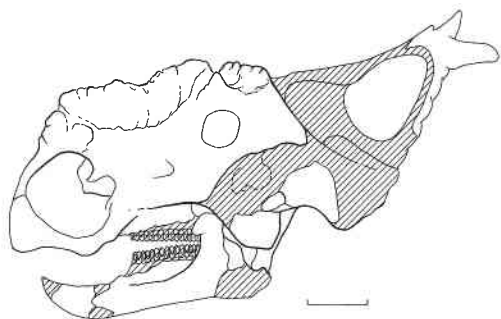


FIG. 2. Reconstruction of *Pachyrhinosaurus canadensis* skull based on material from Scabby Butte (unshaded). All parts except the parietal frill and the predepratory were probably derived from one individual. Frill is largely conjectural; see text for further explanation. Scale: 40 cm \pm .

of the massive excrescence behind the rostrum. The supranarial bridge, composed of premaxillae and nasals, is formed much as in *Centrosaurus* and *Styracosaurus*, but is relatively thicker and wider than in these less robust genera. The bridge thickens rapidly toward the part of the snout roofed by the nasal bones. Here a large, flattened tumescent bulge occurs on either side of a wide but shallow mid-longitudinal sulcus (Pls. I, II). Relatively massive in the paratype of *P. canadensis*, and least developed in the holotype, remnants of these bilateral 'supranasal' bosses are visible in all skulls. The broadly convex superior surfaces of the bosses, facing mainly forward and laterad, are sculptured in the same way as the superior surface of the huge nasofrontal boss. Their shape varies even on opposite sides of the same skull: in NMC 9485 the right boss is roughly circular in plan and is separated from a similar but smaller elevation in front by a wide sulcus, which curves upward out of the narial aperture. The opposite boss is triangular in plan owing to the coalescence of the two parts and disappearance of the sulcus between them. The bosses are evidently outgrowths of the underlying nasal bones and not osteoscutes fused to the skull. The left boss in NMC 9485 has principle diameters of approximately 9.5 and 14 cm.

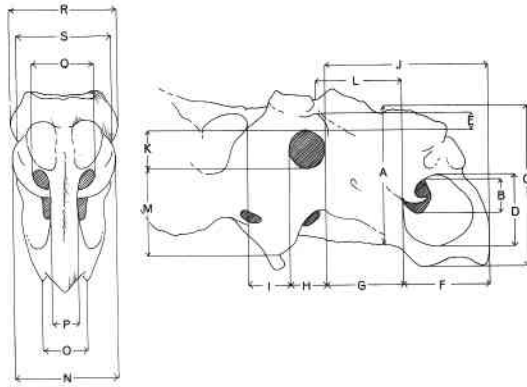
Just behind the supranasal boss is the 'fist-sized' knob noted by Sternberg (1950, p. 111) in the holotype of *P. canadensis*. This flattened, hemispherical elevation is about a third as large as the adjacent boss and is separated from it by a groove (Pls. I, II). Conditions in the Drum-

heller skull suggest that these objects are osteoscutes—usually, but not always, fused to the underlying bones (Langston 1967). A subcircular crater similar to one described in that specimen occurs on the right side of NMC 8860, but unlike the Drumheller specimen where the elevated rim surrounds a smooth depression, the crater-like facet in NMC 8860 contains a concave-sided, irregularly pyramidal elevation whose blunt apex projects a little above the crater's rim. Another, still smaller, elevation occurs postero-ventral to the osteoscuta in NMC 9485 and NMC 8860; these are not very high, but they are roughened somewhat more than the surrounding area. In NMC 8860 there is a distinct button-shaped rugosity having an irregularly constricted base and expanded summit with dimensions of 42 and 39 mm.

The nasofrontal boss of NMC 9485 is the best example of this structure yet found (Pls. I, II). Its general form and relationships to the skull are as described in the Drumheller specimen, but there the edges and superior surface of the boss have been damaged and fail to give a complete idea of its shape. Viewed from above, the boss is sub-triangular in plan, with rounded corners and slightly convex sides and base. Its top is 54 cm long and has a greatest width of about 34.5 cm. But at varying distances below its top, the boss is expanded laterally so that at about midlength its greatest transverse diameter is 39.5 cm. This is the widest part of the skull in front of the orbits, and hence no part of the face is visible from above (Pl. II). The superior surface of the boss is concave, comprising three shallow excavations within the large central depression. One excavation 5.7 cm deep occurs anteriorly and is separated from two bilateral and shallower depressions behind a low ridge. The posterior basins are divided sagittally by a broad and low longitudinal ridge. Although I had earlier believed that the nasofrontal boss was composed mainly of nasal bones, with prefrontals and frontals contributing relatively little, these ridges may coincide with sutures (not seen) and would thus suggest that more than half of the mass is composed of prefrontals united in the midline. If this is so, little if any frontal bone appears in the superior surfaces of the boss, these elements having been 'overgrown' by exostosis of the prefrontals and postorbitals.

Postorbital bosses seem better developed in

TABLE 1. Comparative measurements (in centimeters) of *Pachyrhinosaurus* skulls (for system of measurements refer to accompanying diagram)



Measurements	NMC 8867	NMC 9485	NMC 8866	Drumheller specimen	Key to Measurements
A	56.0	53.0	57.0	61.8	A. Vertical diameter, average top of boss to ventral edge of maxilla.
B	16.0	14.4	14.5	17.2	B. Vertical diameter of naris visible in lateral aspect.
C	—	56.0	—	68.0	C. Maximum vertical diameter of skull.
D	—	29.5	—	34.0	D. Vertical diameter of narial aperture.
E	11.5±	9.5±	—	10.0	E. Distance from top of orbit to tip of supraorbital horn.
F	—	43.0	—	44.0	F. Length, tip of rostrum to posterior edge of naris.
G	31.0	30.2	—	30.0	G. Length, posterior edge of naris to anterior edge of orbit.
H	13.5	14.7	—	13.6	H. Width of orbit.
I	17.0	18.0	—	15.4	I. Length, posterior edge of orbit to edge of supra-temporal fenestra.
J	—	73.2	—	87.6	J. Length, tip of rostrum to anterior edge of orbit.
K	14.0	14.6	—	18.0	K. Height of orbit.
L	40.0	42.0	—	34.0	L. Length, posterior edge of naris to posterior margin of nasofrontal boss.
M	33.5	—	—	—	M. Height, bottom of orbit to ventral edge of jugal.
N	—	31.0	36.0±	26.5	N. Greatest transverse diameter at expansions behind nares.
O	—	13.3	—	14.0	O. Transverse diameter across lowest flanges of premaxillae.
P	—	8.4	—	7.0	P. Least transverse diameter of narial bridge.
Q	—	19.5	—	19.0	Q. Greatest transverse diameter of narial aperture.
R	—	39.0	41.0	35.0	R. Greatest width of nasofrontal boss.
S	—	36.0	—	33.0	S. Least transverse diameter of face between orbits and nares.

NMC 9485 than in the Drumheller skull. Situated posterodorsal to the orbits, they resemble large, flattened sponges appressed to the sides of the skull. A shallow annular sulcus at the base of each boss separates its vertically grooved sides from more conventionally sculptured bone below. The structures were apparently formed in the same way as the nasofrontal boss (see Langston 1967, p. 176), but are of course

much smaller and do not exhibit any concavity on top. Although NMC 9485 has suffered some damage in the area between the postorbital and the nasofrontal bosses, it is evident that the former must have extended forward to impinge against the latter as in the Drumheller skull. As there, no fusion between exostoses from different growth centers seems to have occurred. Of the transverse tunnel beneath the postorbital exos-

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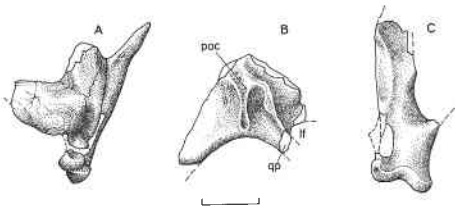


FIG. 3. *Pachyrhinosaurus canadensis* Sternberg. A. NMC 10646, left quadratojugal and incomplete jugal, lateral view, attached to quadrate NMC 9610; B. NMC 9594, incomplete left squamosal, medial surface; C. NMC 9610, incomplete left quadrate, anterior view. Scale: 10 cm. Abbreviations: *lf*, edge of lateral temporal fenestra; *poc*, groove for articulation with the paroccipital process; *qp*, quadrate ramus of squamosal (broken).

tosis described in the Drumheller specimen, only a wide, transverse trough remains in NMC 9485, its roof having been destroyed.

The location of the postorbital bosses suggests that they are formed mainly or entirely of postorbital bone. However, a fortuitous fracture passing diagonally through the center of the right boss in NMC 9485 exposes some sutures within the substance of the bone. A contact between postorbital and frontal extends dorsally and probably emerges onto the superior surface of the boss, but its precise path upward is indistinct. The frontal bone thus forms the medial part of each boss (as well as an undetermined amount of the cranial surface surrounding the postfrontal fontanelle, in centrosaur fashion).

Supraorbital horns seem to have been as variable in *Pachyrhinosaurus* as in other ceratopsians. Cornua described in the Drumheller skull are better developed than in other specimens, but what appears to be the broken base of a small supraorbital horn is present on the left side of the holotype of *P. canadensis*. The damaged base of the right horn can be seen in NMC 9485, but on the left side at the same place there is a shallow excavation divided into two small basins. Such excavations, varying in size, shape, and arrangement, occur on postorbital bones of several short-faced ceratopsids; in the famous skull of *Styracosaurus albertensis* (NMC 344), similar excavations are present above the orbits in place of supraorbital horns, whereas in some *Centrosaurus* skulls the pits may be present on one side and absent on the other. They may even occur on the sides or at the top of cornua. One may ask if they are a result of pathological (?fungal) corrosion and without genetic basis.

Development of the orbital rim also seems to have been variable in *Pachyrhinosaurus*, but the so-called "antorbital buttress" commonly present in other large ceratopsians never occurs. A palpebral bone (superorbital of authors) cannot be defined but is probably present, integrated as usual in the orbital rim.

The quadratojugal with an incomplete jugal attached (NMC 10646) articulates exactly with the quadrate NMC 9610 (Fig. 3a). When re-assembled, the jugal is broadly exposed in lateral aspect. The bone is thick at its posteroventral corner, and its deeply sculptured lateral surface projects a little to the side. There is no indication that an epijugal was present. In the holotype of *P. canadensis*, the lateral surface immediately anterodorsal to the thickened corner and edge of the jugal is depressed, and this seems to be a natural condition in which the bone thins rapidly toward the depression. Much of the corresponding area is missing in the Scabby Butte specimens, but what remains gives no indication of this sort of depression, and the thickness of the jugal does not vary much. The quadratojugal is of the sort found in the short-faced ceratopsids and seems completely unlike the bone in *Triceratops*. Although incomplete dorsally, it could not have entered the lateral temporal fenestra as it does characteristically in that genus. The specimen has a greatest transverse diameter of 4.6 cm. The ventromedian part of the bone curves downward to ensheath the lateral edge of the quadrate.

The squamosal NMC 9594 (Fig. 3b) is represented by only the ventrolateral flange; contact surfaces for adjacent roofing bones have been lost and abrasion has removed all trace of surface sculpture. The characteristic brevity of the flange in *Pachyrhinosaurus* is strikingly illustrated by the preserved part, which is almost exactly the same size as the corresponding area in a skull of *Centrosaurus recurvatus* (NMC 8797) that was perhaps no more than half the size of the *Pachyrhinosaurus* skulls from Site 2. The anteroventral edge of the squamosal is broadly arched, resulting in a very shallow 'otic notch'. The anteroventrally directed quadrate process is much stouter than in the *Centrosaurus* skull, reflecting a relatively stronger suspensorium in *Pachyrhinosaurus*. The posterodorsal corner of the lateral temporal fenestra is preserved, showing that the opening was relatively small. On the medial side, the complex of ridges and grooves

for articulation with the occiput and the quadrate are arranged about as in *Centrosaurus*, but seem more strongly defined. The parallel ridge and groove that articulated with the lateral end of the paroccipital process is curved anteriorly as in *Centrosaurus* and not straight as in the squamosal of *Eoceratops* (= *Monoclonius*) *canadensis* figured by Lambe (1904, Pl. 2).

The quadrate NMC 9610 (Fig. 3a, c) is of the short-faced ceratopsid construction and not at all like the bone in *Triceratops*. It seems unusually stout, however; with a height exceeding 30 cm and a transverse diameter across the condyles of 10 cm, it is close to the measurements for large *Triceratops*. There is no trace of a quadrate foramen, the lateral edge of the bone providing an unbroken sutural surface for the quadratojugal. There was apparently a wide pterygoid flange, but most of this has been destroyed. The preserved edge of the pterygoid surface shows a sharply depressed semiovate border. This notch is well developed in the quadrate of *Monoclonius lowei* Sternberg (NMC 8790), but is absent in a *Centrosaurus longirostris* quadrate at hand. There was no pit here to receive a process of the pterygoid, as occurs in the quadrate of *T. flabellatus* (see Hatcher *et al.* 1907, Fig. 17). The lateral condyle is larger than the medial one, but does not extend so far ventrally. Longitudinal axes of both condyles are nearly parallel, with their planes passing obliquely anteromedially. The outer condyle has a hemispherical articular surface that is separated from the dorsal ramus of the quadrate by a deep longitudinal sulcus. The posterior surface of the quadrate mesad to the condyle contains a circular depression. The medial condyle also has a well rounded, hemispherical articular face, but most of this occurs on the medial side of the bone. The articular surface turns onto the posteromedial side of the quadrate, and the area so formed is larger than in any other ceratopsian. The saddle-shaped bridge between the condyles is relatively flat anteroposteriorly, but is of course concave transversely.

Both sides of the face are well preserved in NMC 9485. The lateral ridge on the maxilla that continues posteriorly onto the jugal is thick and massive, but sharp. Above this the antorbital region is broadly concave laterally and relatively featureless, except for the presence of a well defined antorbital fenestra with principle diameters of 60 and 25 mm (Pl. I). This opening

is present in all specimens from Scabby Butte in which the critical area is preserved. Sternberg failed to find a fenestra in his Little Bow River specimens, but further preparation of the holotype of *P. canadensis* suggests that it was present there. I am certain, however, that the Drumheller skull lacks the fenestra on the right side (the left side of the face was not preserved). Possibly the supposed absence of an antorbital fenestra in some examples of *Pachyrhinosaurus* may constitute a valid specific character if it can be correlated in some way with geographic distribution, but until confirmation is forthcoming, it seems better to regard the absence of the opening in the Drumheller skull as a pathologic or gerontic aberration in that individual.

In the Drumheller skull, the postfrontal fontanelle remains open as far forward as the posterior base of the nasofrontal boss, thus separating the postorbital bosses. In NMC 9485 the bosses are joined intermittently in the midline above the fontanelle. Sternberg (1950, p. 111) expressed some puzzlement about a large opening in the skull roof of the holotype NMC 8867. Although possibly related to the fontanelle, it seems more likely that the condition is artificial, resulting from the loss of the postorbital boss and some underlying bone from the exposed side of the specimen. (Conditions on the other side are undetermined). Whether the opening is accidental or pathologic is uncertain, but damage after death seems more probable in view of the weakening of the frill base that would have resulted from destruction of so large an area of living bone.

Palatal structures are partly visible in NMC 9485 (Pl. I). Pterygoids are largely missing, palatines are hidden in matrix, and except in cross-section, only the tip of the vomerine rostrum is exposed. The right maxilla has suffered some damage, and all teeth are lost. As noted in the Drumheller skull, the uncrushed palate is remarkably narrow: the greatest transverse diameter between the maxillae was only about 70 mm in NMC 9485. Surprisingly, the vault is narrowest (some 60 mm) posteriorly. As in other ceratopsians, the maxillae have horizontal shelves anteriorly which, meeting in the midline for a distance of about 13 cm, form a short, hard palate beneath the anterior third of the narial aperture. Posteriorly, the maxillae bound the forward ends of the choanae. Anteriorly, the maxillary flanges lap along the underside of the

conjoined premaxillae. The maxillary tooth row was at least 27 cm long.

The premaxillae are separated in the palatal roof by a median foramen 1.7 cm wide and 5.4 cm long. Similar foramina are rarely reported in ceratopsids, but a skull of *Centrosaurus* described by Sternberg (1940) has an even larger one, and I suspect they were normally present. Their function is not clear. Association with Jakobsen's organ seems improbable because of their unpaired condition and wide separation from the choanae. (Absence of the septomaxilla in ornithischians may imply reduction of the nasovomerine gland). Probably the opening is homologous with the incisive foramen of eusuchian crocodylians, which serves no known function.

Ceratopsians generally have a number of paired foramina in the anterior palatal roof; at least two pairs occur in the premaxillae of NMC 9485. They are probably homologous with the variably situated foramina along the lingual side of the tooth row in crocodylians, and, as there, transmitted efferent vessels and twigs of the maxillary nerves into the lining of the mouth. The premaxillary roof of the rostrum curves upward anteriorly to make contact with the rostral bone near (or inside) a deep conical excavation at the apex of the palate. Similar conditions are figured in *Triceratops* (for example, see Hatcher *et al.* 1907, Pl. 46). The excavation suggests the presence in life of a long and sharp prementary sheath.

Where exposed in cross-section near the anterior ends of the choanae, the vomerine rostrum is rectangular, showing no tendency toward the vertical expansion noted in the Drumheller skull. The vomer descends to the level of the hard palate anteriorly, where it is inserted between the palatal flanges of the maxillae for a distance of 3.5 cm.

Transverse fractures through NMC 9485 reveal something of the internal structure of the facial region (Fig. 4). A large triangular canal occurs at about the level of the maxillary-premaxillary contact (Fig. 4a-a'). Although surrounded mainly by the premaxillae, it is floored by the maxillae at this place. Matrix filling the canal has not been removed, but it is clear that the passage connects the floor of the narial aperture with the so-called incisive foramen. The vertical partition within the narial aperture is thicker than in any other ceratopsids. This

plate-like structure is usually termed nasal septum in ceratopsians, but it is composed of dermal bones and lays in front of the nasal capsules; it is not, therefore, homologous with the septum nasii *sensu stricto* of reptiles and might better be termed the narial septum, which it in fact is.

Diagonal sections in slightly different planes reveal a wide central vacuity largely enclosed by maxillae, premaxillae, and nasal bones and incompletely floored by the narrow vomerine rostrum (Fig. 4b-b'; c-c'). Since it occurs too far forward to have been associated with the pterygoid musculature, this great void was probably occupied in life by bulky nasal structures, perhaps analogous with the complicated membranous sinuses and recesses of crocodylians (see Parsons 1970). Inwardly expanded flanges of the premaxillae partly divide the space horizontally into an inferior and a considerably larger, superior cavity. Possibly the inferior cavity may have accommodated the nasopharyngeal duct, whereas the greater space above, enclosed mainly by premaxillae and nasals, could have lodged the cavum nasi proprium and its various conchal formations, supported by capsular cartilages. No channels for the nasal tracts appear on the deep surfaces of the nasal bones, and there is no septum nasii.

The thickness of the bones involved in the nasofrontal boss at level b-b' varies from 7 cm at the midline to about 12 cm through the thickest part of the boss. Corresponding measurements in *Centrosaurus* would be only a few millimetres. The lateral walls of the face are greatly thickened, with the nasals at the plane of fracture having a least transverse diameter of 7 cm. On either side, a canal passes transversely through the nasal bone, that on the right side opening laterally into the groove at the base of the nasofrontal boss. The left canal opens farther down on the side of the face. Irregularly disposed foramina appear on the sides of the nasal bones in some other ceratopsians and probably represent passages for blood vessels.

The cross-sections also show that the premaxillae curve upward posteriorly on the side of the face, passing just beneath the finger-like narial processes of the nasal bones as in *Centrosaurus*. It is unknown if they extend so far posteriorly as the lacrimal. What appears to be a separate element (presumably paired) lies across the midline subjacent to the thickened nasals, and probably represents forwardly-

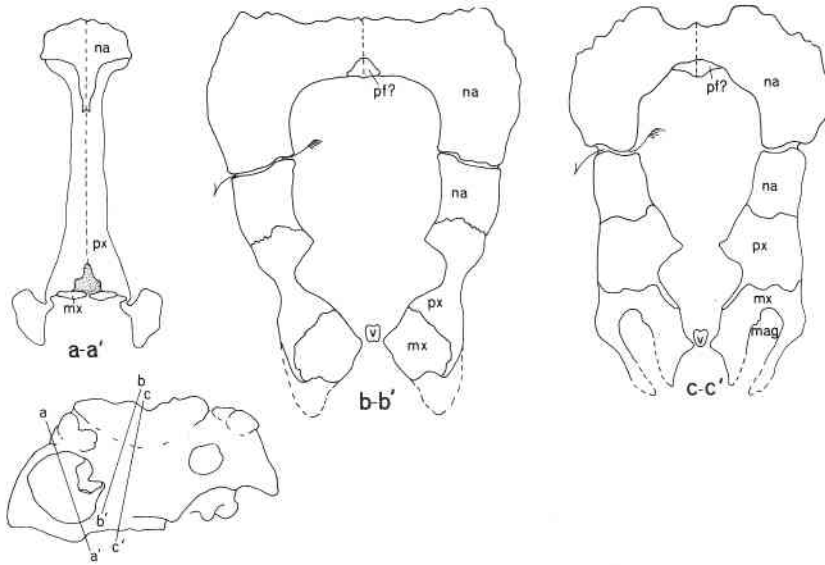


FIG. 4. *Pachyrhinosaurus canadensis* Sternberg. NMC 9485, semidiagrammatic composite sections through facial region at planes indicated. Abbreviations: *mag*, dental magazine; *mx*, maxilla; *na*, nasal; *pf?*, ?prefrontal; *px*, premaxilla; *v*, vomer; arrow, passages through facial wall.

projecting tips of coalesced prefrontals. (Fig. 4b-b').

The braincase in NMC 9485 is asymmetrical, but whether because of post-mortem effects or deformity is uncertain. The great mass and complexity of the skull as a whole suggests that unequal growth may be responsible. Viewed from behind (Fig. 5), the braincase and associated structures appear characteristically ceratopsid. The huge occipital condyle is 95 mm wide and 92 mm high. The condylar 'neck' is relatively short and thick, with a transverse diameter of 92 mm. Massive basioccipital tubera seem more pendulous than in *Triceratops*, are placed close together, and are separated distally by only a shallow V-shaped median notch. Interestingly, they are small in relation to the condyle: tubera of a *Chasmosaurus* cranium at hand are as large, although the condyle is smaller. The tubera are ensheathed anterodorsally by broad posteroventrally expanded flanges, presumably of basisphenoidal origin. These flanges thicken in front of the tubera, forming stout basipterygoid processes which appear to have been relatively longer than in the *Chasmosaurus* skull. The processes are separated ventrally by the usual long median sulcus whose sides converge forwardly, eventually to disappear into the base of the basisphenoid rostrum (Pl. I).

Paraoccipital processes are poorly preserved in NMC 9485. A massive nuchal crest rises into the supraoccipital region where a thin median ridge with a rounded and transversely expanded summit extends upward to meet the median parietal bar of the frill. There has been much debate concerning the identity of various structures and the extent of different bones in this part of the ceratopsian cranium (see, for example, Gilmore 1919; Lull 1933), and I am not convinced that even now all homologies have been identified. Viewed from above, the supraoccipital bone describes a wedge-shaped figure with concave sides. Anteriorly, it contains a forwardly directed median trough that leads into the post-frontal fontanelle, a condition frequently noted in ceratopsians but apparently never adequately explained.

It is impossible to define the limits of any of the braincase elements appearing in lateral aspect (Fig. 6); all sutures having been ankylosed, the bones can only be described by reference to the regions they normally occupy in other reptile skulls. The otic region is expanded laterally and forms a thick semilunar ridge. This passes from the anterior surface of the paraoccipital process in a gentle curve, up along the edge of the laterosphenoid. Below this ridge the lateral surface of the braincase appears relatively broader

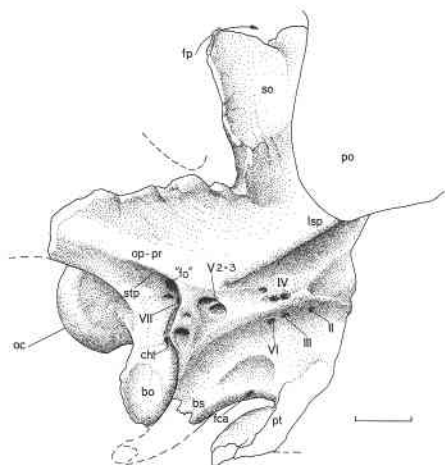


FIG. 5. *Pachyrhinosaurus canadensis* Sternberg. NMC 9485, braincase, lateral aspect. Scale: 5 cm. (Drawn from photograph.) Abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *ch*, path of the chorda tympani; *fca*, foramen for internal carotid artery; "fo", fenestra ovalis of authors; *fp*, longitudinal channel in top of supraoccipital which leads into the postfrontal fontanelle; *lsp*, laterosphenoid; *oc*, occipital condyle; *op-pr*, opisthotic + prootic; *po*, area hidden by postorbital; *pt*, pterygoid; *so*, supraoccipital; *stp*, stapedial groove; *II-V*, exits for cranial nerves.

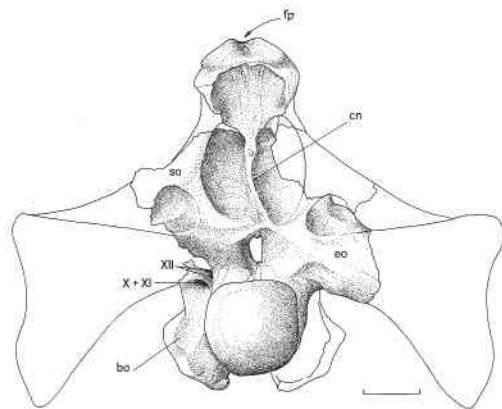


FIG. 6. *Pachyrhinosaurus canadensis* Sternberg. NMC 9485, braincase, posterior aspect. Scale: 5 cm. (Drawn from photograph.) Abbreviations: *cn*, nuchal crest; *eo*, exoccipital; *X-XII*, exits for cranial nerves; other abbreviations as in Fig. 5.

than in *Chasmosaurus* or *Triceratops*, owing partly at least to the smaller size of most of the cranial foramina punctuating the braincase walls. Lateral ridges between the large posterior foramina are not strongly developed; instead, the whole side of the braincase is thickened. The anterodorsal process of the laterosphenoid is

unusually massive and appears to be partly fused with the roofing bones. Since this was the last entracranial articulation to solidify in large ceratopsians, it is clear that NMC 9485 was an adult individual.

Authors have experienced great difficulties in interpreting the braincase foramina in large ceratopsians, not only because most sutures within the massive crania are almost always obliterated, but also because the paths of nerves and blood vessels that would normally pass directly through the braincase walls in animals with thinner bones sometimes coalesce within the thickened ceratopsian cranial walls with the result that fewer openings exit from the braincase than enter it from the endocranial cavity. Only external openings are visible in the *Pachyrhinosaurus* material. Although the braincase of *Triceratops* has been extensively interpreted (Hay 1909; Gilmore 1919), and description of the brains of *Anchiceratops* (Brown 1914a) and *Protoceratops* (Brown and Schlaikjer 1940) exist, there appears to be no useful account of a braincase from a short-faced ceratopsid in the literature, nor do I have a specimen for comparison (an incomplete chasmosaur braincase has been used for comparative purposes in the following discussion).

The vertically oval foramen magnum is 37 mm high and 22 mm wide, thus appearing small in comparison with the condyle. At its opening it is apparently surrounded by the exoccipitals as in ceratopsids generally.

Besides the foramen magnum, the most readily recognized cranial foramina in ceratopsians are two or three openings near the base of the condylar neck, behind the plane of the paroccipital processes. Hay (1909) identified two of these in *Triceratops* as exits for cranial nerves IX-XI (jugular foramen) and the passage for a vein, the third as the hypoglossal foramen (XII). In *Pachyrhinosaurus* only two large foramina emerge laterally from the exoccipital area at the base of the condylar neck. The smaller, more dorsal one is believed to be hypoglossal. The other foramen occurs just below and a little anterior to this. It is oval, with diameters of 9 and 11 mm. Deep within this opening is a horizontal partition, which divides it into two parts. In the *Chasmosaurus* braincase at hand three small passages leave the hindbrain space in series near the floor of the braincase. The largest, posterior, and presumably hypoglossal, foramen passes directly through the thick cranial wall to emerge

at the base of the condylar neck, as in the *Pachyrhinosaurus* skull. The other two passages unite into a common tunnel within the cranial wall. This passage then communicates anteroproximally with the long, narrow slit representing the persistent metotic fissure. Endocranial casts and probing in this specimen suggest that tubular structures entering the metotic fissure from different places within the endocranium emerged partly through the more anterior of the two so-called hypoglossal foramina (the jugular foramen of Hay) and partly through the opening that is usually termed the fenestra ovalis in ceratopsians. One interpretation of this arrangement would have all branches of the hypoglossal nerve exiting through a single posterior foramen, with nerves IX-XI emerging from the jugular foramen nearby. However, it seems more likely that the three serially aligned foramina in the *Chasmosaurus* endocranium carried separate branches of the twelfth nerve, and that two anterior branches, joining with the tenth and eleventh nerves from the metotic fissure, exited with these through a common passage behind the plane of the transverse occipital plate. The ninth cranial nerve, on the other hand, (possibly accompanied by the tenth), remained in the bony metotic fissure, eventually emerging via the large 'fenestra ovalis' of authors. (I have shown (Langston 1960) that the glossopharyngeal nerve probably passes close to the fenestra ovalis in a hadrosaur.) Possibly the perilymphatic duct was also associated with the large lateral opening as well. This opening occurs in *Pachyrhinosaurus* in about the same position as the so-called fenestra ovalis of *Triceratops* (Hay 1909, Pl. I). It is vertically oval with diameters of 29 and 9 mm. The corresponding opening in the *Chasmosaurus* cranium is funnel-shaped, being widest laterally. Not only does it communicate directly with the metotic fissure, but the cavum capsularis opens into it via the true fenestra ovalis deep within the braincase wall; the fenestra ovalis is not visible in lateral aspect, but what I suppose to be a stapedial groove passes out of the large opening and extends a short distance laterally across the anteroventral surface of the paroccipital process in NMC 9485, and from its anteroventral corner a sulcus possibly marking the route of the stapedial artery may be followed along the basioccipital-basisphenoid contact. Hence the large ceratopsid fenestra ovalis of authors is, distally, much more

than just the oval window, comprising in addition the jugular foramen and possibly the foramen rotundum.

The exit for the facial nerve, generally small in ceratopsians, appears unusually so in *Pachyrhinosaurus*. The foramen with a diameter of 3 mm occurs a short distance in front of the lower corner of the 'fenestra ovalis' in NMC 9485. Except for the problematical route of the chorda tympani, no indication of the paths of this nerve's branches appear on the lateral walls of the braincase. The largest of the lateral cranial foramina lies 9 mm anterior to the facialis and, as in other ceratopsians, is believed to have transmitted the maxillary and mandibular rami of the trigeminal nerve. In large ceratopsids the ophthalmic ramus turned forward within the braincase wall to emerge some distance antero-dorsal to the main trigeminal foramen. This opening is not definable in NMC 9485, but a number of small openings occur in the area where it should be expected.

Small foramina, presumably for nerves VI and III, exit laterally about as figured in *Triceratops* (Hay 1909, Pl. I) below the thick 'antotic buttress'. The fourth nerve is believed to have emerged higher up on the side of this buttress. The optic foramen is only a little smaller than the trigeminal. It lies anterior to and in line with exits VI and III.

The only other cranial foramen that can be identified in the specimen transmitted the internal carotid artery. This landmark enters the basicranium lateral to the sharp ventral edge of the basisphenoid. The area nearby is crushed on the right side (the left side is not exposed), and it is impossible to state whether there is a sulcus leading into the foramen. The opening is, however, relatively and absolutely smaller than in the *Chasmosaurus* skull or in *Triceratops*. It is also situated much lower down on the side of the cranium.

Mandible—The Scabby Butte collection contains an anterior end of a dentary bone and an associated prementary that were found with parts of a skull (NMC 10645) about a quarter of a mile (~400 m) from Site 2. This was an isolated occurrence, and there is no reason to suppose that the fragments do not belong to one individual. The dentary fragment containing the bottoms of the first twelve alveolar grooves agrees with a more complete dentary from Site 2

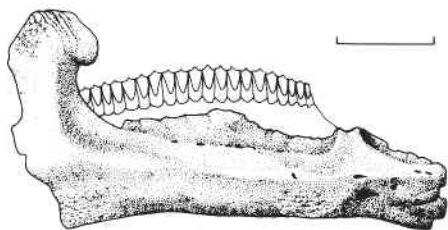


FIG. 7. *Pachyrhinosaurus canadensis* Sternberg. NMC 10645, right dentary, lateral aspect. Scale: 10 cm.

(NMC 10643). The Site 2 specimen (Fig. 7) was found close to the skull NMC 9485 and seems to correspond with it in length; it may well have belonged to the same individual. Its dorsal edge has been destroyed, and the dental magazine is lost, and, as preserved, the bone appears relatively more slender than the dentary in the paratype of *P. canadensis* (NMC 8866). But both jaws are relatively deeper than any ceratopsian jaws compared—a *Styracosaurus* dentary (NMC 344) which is 44.1 cm long, is 19.2 cm high at the coronoid process, whereas NMC 10643, which is about 48 cm long, has a coronoid process 24 cm high.

The coronoid process is expanded dorsally into the usual hook. This is 10 cm long. At mid-height the process is reduced to an anteroposterior diameter of 6.1 cm, and here is 4.7 cm wide. The pseudotemporalis fossa, between the coronoid process and the horizontal ramus of the dentary, seems disproportionately wide.

Although the complete length of the dental magazine is not determinable, it was probably similar to that of the *Styracosaurus* specimen and hence relatively abbreviated. As there, the dental battery was separated from the prementary by a relatively short diastema. This part of the jaw is unexpectedly constricted dorsoventrally, with a vertical diameter of only 9.8 cm as compared to 13.5 cm in the *Styracosaurus* dentary.

The characteristic longitudinal ridge on the lateral side of the dentary seems unusually strong and extends from the base of the coronoid process anteriorly for the full length of the bone. The depressed area above the ridge is relatively deep and sharply defined. The usual foramina appear on the lateral surface of the dentary.

The incomplete left surangular (NMC 10629) from Site 2 is of a size appropriate to the right dentary just described. Correlated with the elevated coronoid process, the ascending ramus is relatively higher and narrower than in *Styraco-*

saurus; although more massive, it seems to have about the same proportions as the surangular in the holotype of *Centrosaurus longirostris* Sternberg (NMC 8795). The small excavation that received part of the lateral quadrate condyle is distorted but would apparently have accommodated the quadrate described above. An interesting divergence from the pattern seen in *Styracosaurus* and *Centrosaurus* occurs at the posteromedian edge of the ascending ramus. In those genera, this edge is thin and sharp and curves broadly mesad to pass underneath the anterolateral corner of the articular bone. The corresponding edge in NMC 10629 is thick and is emarginated by a wide notch over which the posterior adductor muscle probably passed on its way to the adductor fossa (see Ostrom 1964). This edge is broken off in the paratype of *P. canadensis*.

The prementary bone of *Pachyrhinosaurus* has not been reported before. The incomplete and distorted element found with NMC 10645 seems massive and relatively deep, but by itself would be difficult to distinguish from prementaries of other large ceratopsids. As preserved, the greatest height is 12.2 cm, but the complete bone was at least a little higher than this.

The conclusion that the *Pachyrhinosaurus* jaw was in life a most powerful organ, even among ceratopsians (see Ostrom 1964), seems inescapable.

Pachyostosis—Surely the most striking quality of *Pachyrhinosaurus* is the degree to which the cranial bones have become thickened. The only other tetrapods displaying remotely similar conditions are certain therapsid reptiles, the pachycephalosaurid dinosaurs, and, among mammals, the musk oxen. Thickening of the skull bones in *Pachyrhinosaurus* is of two fundamental kinds, according to the classification of pachyostoses proposed by Kaiser (1960). Contrary to Kaiser's belief that the hypertrophy in the cranial bosses was what he terms a true pachyostosis, these structures display features of his "Pseudo-Pachyostose". Exemplified by some pareiasaurs and therapsids (Kaiser 1960, Pl. 19, Figs. 6, 7), pseudopachyostosis involves thickening of bones by expansion of the spongiosa, in contrast to pachyostosis *s.s.*, in which there is hypertrophy of compacta, often at the expense of spongiosa. On the other hand, the dense and greatly thickened facial bones of *Pachyrhinosaurus* display a true pachyostosis. Examination of possible

gradation between the two conditions would be interesting, as their development may be functionally related.

Postcranial Material Ascribed to Pachyrhinosaurus—The *Pachyrhinosaurus* census at Scabby Butte based on cranial material probably exceeds twenty individuals. It is curious that with so many skulls here and on the Little Bow River, no postcranial bones have been assigned to the genus. Circumstantial evidence now suggests that several large ceratopsian axial and appendicular elements from Site 2 pertain to *Pachyrhinosaurus*:

- (a) they were closely associated with two *Pachyrhinosaurus* skulls in a restricted space that contained otherwise mainly remains of hadrosaurs (see Fig. 1);
- (b) *Pachyrhinosaurus* individuals recognized from skull parts are by far the most abundant ceratopsians at Scabby Butte—not counting specimens at Site 2, they outnumber all other ceratopsians in the area by a ratio of at least four to one;
- (c) except for two problematic frill fragments, all cranial material from Site 2 clearly belongs to *Pachyrhinosaurus*;
- (d) except for one dorsal vertebra, all postcranial bones seem larger and more massive than usual in ceratopsians of pre-Lancian age, a condition consistent with the relatively large size of the *Pachyrhinosaurus* skull; and
- (e) the condylar cup of a ceratopsian cervical 'bar' from Site 2, though crushed, would have accommodated the condyle of either of the associated skulls.

Postcranial bones from Site 2 assigned to *Pachyrhinosaurus* are: NMC 9600, 10630-10633, vertebrae; NMC 9719, 10635-10639, dorsal ribs; NMC 9721, right scapula; NMC 9722, left scapula; NMC 10640, right humerus; NMC 10641, right femur; NMC 9583, right tibia; NMC 10642, distal end of fibula.

To judge from their size alone, the femur and tibia may have belonged to one individual; the scapulae are so precisely 'mirror images' that it seems certain they are from one animal. The position of the bones in the quarry further supports this conclusion.

The postcranial osteology of two quite different large ceratopsians, *Triceratops* and *Centrosaurus*,

has been monographed by Hatcher *et al.* (1907) and Lull (1933), respectively. Postcranial bones from Site 2 seem closer to *Centrosaurus*, differing mainly in their larger size and massiveness. The condition of the bones from Scabby Butte does not justify lengthy descriptions; their appearance can be best portrayed by comparing them iconographically with corresponding elements of a related taxon. Closely similar postcranially to *Centrosaurus* is *Styracosaurus*, which is represented in the National Museums of Canada by the almost complete skeleton of *S. albertensis* Lambe (NMC 344). Although the skull of this specimen has been described (Lambe 1913), the postcranial skeleton that was collected at a later time by a party from the Royal Ontario Museum has never been described or figured. (The skeleton originally at Toronto was reunited with the skull in Ottawa through an exchange of specimens in 1957, and has been mounted recently for display.) I shall take this opportunity to illustrate some of the *Styracosaurus* bones by way of comparison with presumed *Pachyrhinosaurus* elements from Site 2 (Figs. 8-11).

All bones are crushed and distorted to some degree, and not one is complete. For this reason, measurements are of very little use. What is important is that these bones, while resembling the corresponding *Styracosaurus* elements, are relatively much more massive (the humerus is a possible exception) with thickened shafts reminiscent of *Triceratops*. Femur and tibia are, respectively, 93 and 70 cm long as preserved, and have mid-shaft circumferences of 47 and 39 cm. They thus enter the range for these measurements in *Triceratops*, suggesting a body of comparable bulk though not necessarily of similar proportions. The ratio of tibia length to femur was probably close to 0.75 and comparable with this ratio in *Centrosaurus* and *Styracosaurus* rather than in *Triceratops*, where the femur tends to be relatively longer. The vertebrae are relatively heavier, their centra broader, and (in the coalesced cervicals) the neural spines lower, than in other large ceratopsians. No doubt such differences are related to the size of the head.

Systematic Position—Although a few differences between the known *Pachyrhinosaurus* skulls have been noted, I believe these can be attributed to individual variation, and, as advocated earlier (Langston 1968), all specimens may

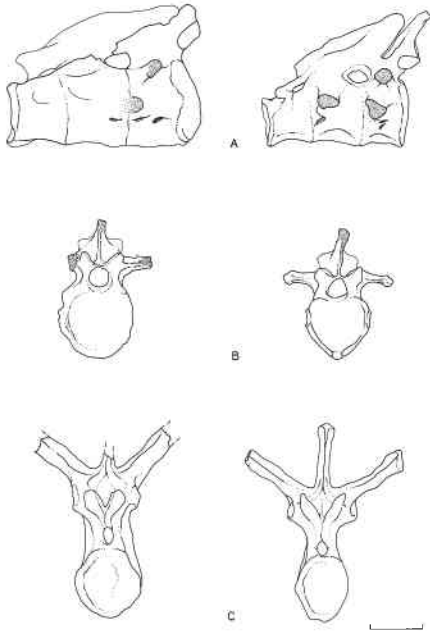


FIG. 8. Vertebrae referred to *Pachyrhinosaurus canadensis* Sternberg (left) compared with corresponding vertebrae of *Styracosaurus albertensis* Lambe, NMC 344 (right). A. coalesced cervicals I-III, NMC 10630, lateral aspect; B. presumed fifth cervical, NMC 10631, anterior aspect; C. presumed fourth thoracic, NMC 9500; anterior aspect. Scale: 10 cm.

be assigned to Sternberg's species, *P. canadensis*. That the skulls are very similar is shown graphically in Fig. 12a.

This study has revealed no reasons for altering conclusions previously expressed (Langston 1967) about the systematic position of *Pachyrhinosaurus* within the Ceratopsidae; on the contrary, the additional material from Scabby Butte seems to confirm a relationship with the short-faced ceratopsids. Additional support for this conclusion may be anticipated from comparisons of braincases, when a detailed description of a short-faced ceratopsian braincase becomes available. The foregoing comparisons between the *Pachyrhinosaurus* braincase and that of *Triceratops* and *Chasmosaurus*, both long-faced forms, reveal numerous differences, and it would be instructive to learn if these differences are shared with *Styracosaurus* and *Centrosaurus*. The reconstruction of the *Pachyrhinosaurus* skull now offered appears strikingly similar to the skull of *Centrosaurus* (Fig. 12b). Most of the differences in outline and proportions seem related to the development of the *Pachyrhino-*

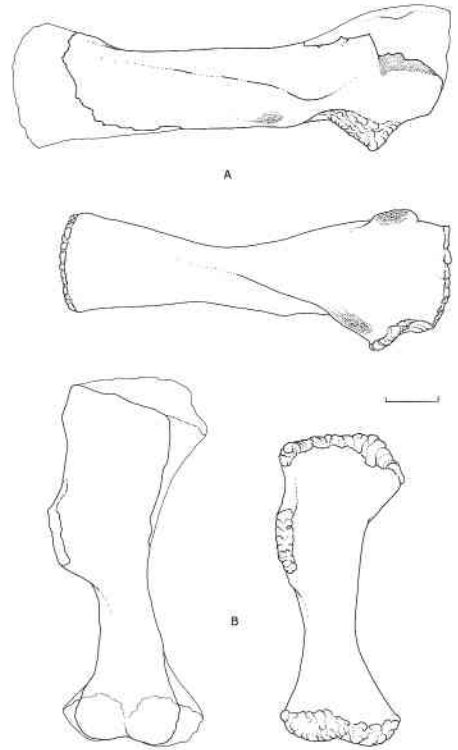


FIG. 9. Bones referred to *Pachyrhinosaurus canadensis* Sternberg compared with corresponding elements of *Styracosaurus albertensis* Lambe, NMC 344. A. right scapula, NMC 9722 (above), lateral aspect; B. right humerus, NMC 10649 (left), ventral aspect. Scale: 10 cm.

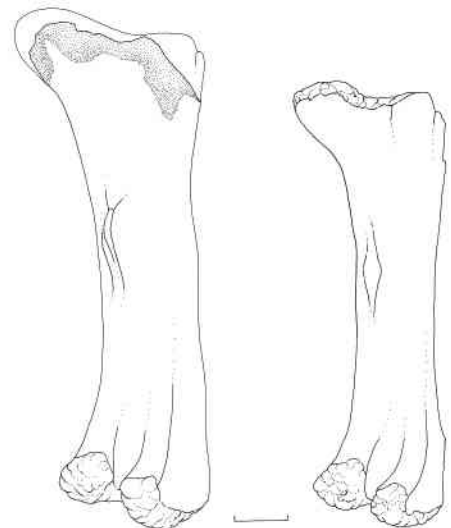


FIG. 10. Right femur referred to *Pachyrhinosaurus canadensis* Sternberg, NMC 10641, compared with corresponding bone of *Styracosaurus albertensis* Lambe, NMC 344 (right), ventral aspect. Scale: 10 cm.

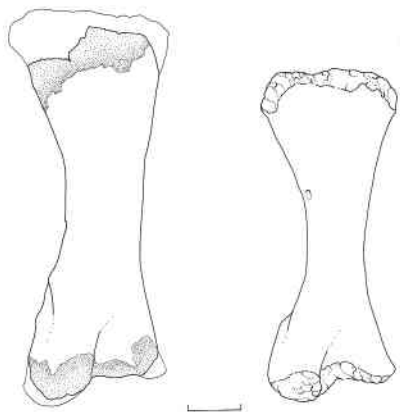


FIG. 11. Right tibia referred to *Pachyrhinosaurus canadensis* Sternberg, NMC 9583, compared with corresponding bone of *Styracosaurus albertensis* Lambe, NMC 344 (right), dorsal aspect. Both bones have been twisted somewhat by crushing, and the presumed *Pachyrhinosaurus* tibia has been greatly flattened. Scale: 10 cm.

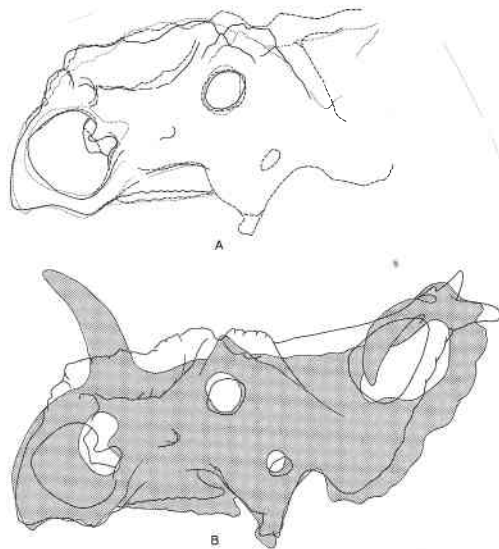


FIG. 12. *Pachyrhinosaurus* skulls compared. A. Outlines of three skulls referred to *P. canadensis* Sternberg: continuous line, NMC 9485, from Scabby Butte; broken line, NMC 8867 (holotype), from Little Bow River; dotted line, skull in the Drumheller Museum, from Red Deer River near Munson, Alberta. Drawings to same scale (shortest distance between orbit and naris equals unity.) B. Outline of reconstructed *Pachyrhinosaurus* skull superimposed on a drawing of a skull of *Centrosaurus flexus* (shaded). Drawings scaled to obtain best fit. *Centrosaurus* modified after Lull.

saurus cranial bosses and slightly different frill construction. A comparison with the skull of *Styracosaurus* might prove even closer than with *Centrosaurus*, but no good reconstruction of *Styracosaurus* exists—the skull of *S. parksi* is fragmentary and extensively reconstructed after *Centrosaurus*, and the holotype skull of *S. albertensis* has been crushed dorsoventrally, distorting the very features of the rostrum and frill that would be most illuminating.

Thus, though sometimes assigned to its own family (Sternberg 1950) or subfamily (Huene 1950), *Pachyrhinosaurus* belongs among the short-faced ceratopsids with *Centrosaurus* (= *Monoclonius* of authors), *Monoclonius* (*sensu* Sternberg, 1940), and *Styracosaurus*.

In 1967 I emphasized the importance of similar narial architecture in this group as contrasted with that of so-called long-faced ceratopsids, with which group I included *Triceratops*, following Sternberg (1940). This is not the place to discuss the broad question of ceratopsian classification, but the assignment of *Triceratops* to the long-faced group apparently needs clarification. This assignment has been questioned implicitly, most recently by Steel (1969), who prefers to group ceratopsids according to the relative lengths of the frills and squamosal bones. In this scheme, *Triceratops* would seem to belong with those forms which Sternberg and I have referred to as short-faced. Although neither the frill nor the squamosal of *Triceratops*

is comparable in relative length to these parts in such taxa as *Chasmosaurus* or *Torosaurus*, neither are they so abbreviated as in the short-faced ceratopsids, *Centrosaurus* and *Styracosaurus*. The fact that the squamosal contacts the parietal throughout in *Triceratops* and *Centrosaurus*, but does not do so in the so-called long-frilled (and long-faced) taxa is explained by the additional fact that the wide intraparietal fenestrae are absent in *Triceratops*. I believe there is a strong case for considering the pre-Lancian *Arrhinoceratops brachyops* (with a long squamosal) ancestral to *Triceratops*. If it is, then the *Triceratops* squamosal has become a little abbreviated, possibly in connection with closure of the intraparietal fenestrae and great thickening of the frill bones. So different is *Triceratops* from other ceratopsids (especially those here termed short-faced) that it seems as reasonable to view it as a long-frilled derivative improving its jaw mechanics by paralleling the short-frilled ceratopsids, as it would be to regard it (as Ostrom does, 1966) as the culmination of frill-shortening within a short-frilled phylum.

Anchiceratops Brown
Anchiceratops sp.

Positive evidence of *Anchiceratops* at Scabby Butte is provided by a piece of frill bone (NMC 9829) found at the southeast corner of the badlands. This bone bears a large epoccipital and has a maximum thickness of 2.5 cm. Its ventral surface is traversed by deep and sharply defined vascular sulci, which radiate toward the edge of the bone and branch distally. The dorsal surface contains fewer and less well marked grooves. Two of the ventral sulci enter the epoccipital bone through a pair of foramina at its base. Presumably these continue within the bone, for passages can be seen in section at the broken side of the epoccipital. Such passages within epoccipitals are characteristic of *Anchiceratops* (Langston 1959). The epoccipital is almost equilateral and is thicker in the center of its base than the adjacent frill bone.

Vascular grooves occur on the frills of most ceratopsians and are apparently somewhat variable within species. *Triceratops*, *Arrhinoceratops*, and *Anchiceratops* generally show the most heavily sculptured surfaces. But *Arrhinoceratops* and *Torosaurus* do not have large triangular epoccipitals, and the surface sulci of *Triceratops* are less regularly disposed than those of *Anchiceratops*. *Triceratops* epoccipitals seem to attach to facets along the edges of the frill and are not large cap-like osteoderms fused to epoccipital processes of the frill bones as in *Anchiceratops*. Although its size agrees better with *A. longirostris* Sternberg than with *A. ornatus* Brown, the position of this fragment in the frill is unknown, and there is no basis for specific assignment.

Two sections of ceratopsian horns have been found at Scabby Butte. The larger one (NMC 10645) was obtained on the surface several hundred metres southeast of Site 2. It is 8.6 cm long, has a greatest proximal (?anteroposterior) diameter of 10.8 cm, a distal diameter of 8.4 cm, and an oval transverse section. The horn was gently curved, but I am uncertain in which direction. A cavity occurs in the base of the specimen, and, lacking any trace of a 'median' suture, it is most likely a brow horn. Generic identification of this fragment by itself would be impossible, but since it occurred in beds containing the hornless *Pachyrhinosaurus* and the long-horned *Anchiceratops*, it may reasonably be referred to the latter genus.

The second horn fragment (NMC 9590) is similarly assigned. It is from a more distal part of the core, but was obtained close to Site 2, and there is no indication that it is part of the other specimen. The section is 6.6 cm in diameter at its proximal end and tapers to a diameter of 4.7 cm in a length of 8.1 cm. It is round in transverse section, straight, and solid.

A mid-dorsal vertebra (NMC 10647) found at Site 2 is smaller than the supposed dorsals of *Pachyrhinosaurus* from this quarry and may pertain to *Anchiceratops*. It is, however, generically unidentifiable. Although its presence in the *Pachyrhinosaurus* quarry may inject a degree of doubt into the assignment of the Site 2 postcranial elements to *Pachyrhinosaurus*, its small size clearly removes any possibility that the other bones might belong to the same individual as this vertebra.

Ceratopsian Frills

Parts of two ceratopsian frills of unusual form were found at Site 2. Both specimens are of the same sort, though they differ considerably in form and probably represent two individuals. The better specimen (NMC 9602) is believed to be part of the right parietal (Fig. 13). Viewed from above, it is reminiscent of the parietal of *Styracosaurus*, for it bears at its edge a huge posterolaterally (or laterally) directed spike. Just medial to this spike is a smaller, hooked process suggestive of the medially turned 'hooks' on *Centrosaurus* frills (see Lambe 1904, Pl. I). The large spike has a preserved length of 23 cm, but some of the tip is missing. It is essentially straight, curving only a little toward the side distally. The base has an oval section 12.5 cm wide and 7.4 cm high. Most of the spike appears to have been accidentally flattened dorsoventrally and, in its normal condition, would probably have maintained these proportions throughout most of its length. The surface is roughened, and several wide, roughly parallel grooves extend unbranched almost the full length of the process. Firmly fused to the edge of the frill, the base is expanded in such a way as to suggest that this spike is of osteodermal origin and not an outgrowth of the parietal bone. It is uncertain if the hooked process is completely preserved; what is seen may be only a thick splinter adhering to the edge of the frill after the major part of another large spike had been broken away. It may also be a discrete structure

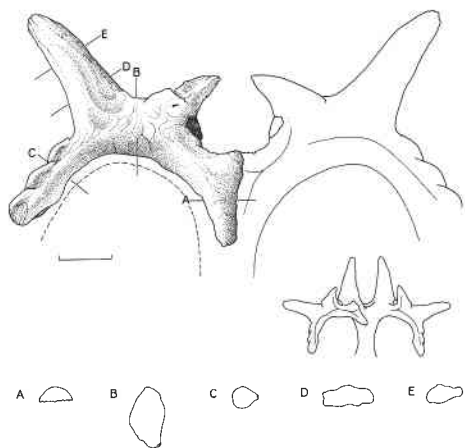


FIG. 13. Ceratopsian frill, NMC 9602, from Site 2, tentatively referred to *Pachyrhinosaurus*, anterior aspect. Two possible orientations of this specimen are shown as explained in the text. A-E, sections through frill at points indicated. Scale: 10 cm.

narrowly separated at its base from a larger process, now lost. Thickening of the frill beneath the spikes is comparable to that seen in *Centrosaurus* adjacent to the frill hooks. This is the thickest part of the frill and has an oval cross-section with a maximum diameter of 6.9 cm. The thickened region contains a huge sinus surrounded by broken edges. This opening is about 15.7 cm wide and 5 cm high and is partly divided into four subequal pockets by two broad intersecting ridges within. If the interparietal bar is correctly identified, the cavity extends across the midline of the skull and was bilaterally asymmetrical. The bony floor beneath the cavity is expanded downward, and its ventral (*i.e.*, exterior) surface is deeply sculptured. I have not seen such an opening in any other ceratopsian frill. That the cavity was not of pathological origin seems clear from the fact that its lining is mostly smooth and shows no evidence of necrotic erosion. One might suppose that voids developed at the bases of frill spikes, thereby lightening a rather weakly supported frill structure. But a fracture close to the base of the large preserved spike shows only a slight increase in cancellous bone and nothing resembling the finished surfaces within the sinus. The edge of the frill remains thick laterally along the side of the parietal, but nevertheless seems relatively weak in view of the heavy structure that it had to support. Anterior to the spike, the edge of the frill carries three broad lateral undulations

representing epoccipital processes. These are oval and arranged so that their long axes cross the edge of the frill obliquely, rising posteriorly. They are separated by wide and similarly oriented (oblique) notches in the edge of the frill. Epoccipital bones do not seem to be present. The parietal thins rapidly toward the edge of the intraparietal fenestra, but no edges of this opening are preserved. As usual in ceratopsian frill bones, the surface is deeply marked by irregular grooves that are more numerous and deeper on the underside than above. Two possible arrangements of this specimen in the frill are suggested in Fig. 13.

At first glance the second frill (NMC 10644) appears quite different. It bears no spikes, and whereas the edge of the first specimen is broadly curved, the second is almost straight (Fig. 14). But both bones have the same unusual epoccipital development, similar thickening of the edges, and rapid thinning of the parietal bone medial to this. Furthermore, NMC 10644 contains a large sinus with an internal ridge somewhat similar to that in NMC 9602. This specimen may therefore represent the same part of the frill as NMC 9602, with the spike replaced by an epoccipital process. This differs from other processes, being twice as long and having its principle axis parallel to that of the frill instead of obliquely inclined.

These specimens appear to represent frills of similar size, so the differences noted are aberrant, perhaps attributable to individual (?sexual) variation. In this connection, the variability in the development of the forwardly hooked pro-

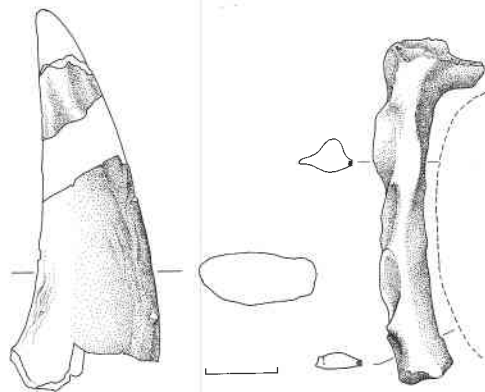


FIG. 14. A supposed frill spike of a ceratopsian, possibly *Pachyrhinosaurus*, NMC 8863 (left). Portion of ?parietal frill, possibly *Pachyrhinosaurus*, NMC 10644 (right), anterior aspect. Scale: 10 cm.

cesses on the *Centrosaurus* frill may be recalled (see, for example, Brown 1914b). It is interesting, though probably of no great significance, that the big spike on NMC 9602 resembles the forward process on the left side of the frill in Lambe's type of *Centrosaurus apertus* (NMC 971)—which was originally mistaken for a nasal horn (Lambe 1904; 1910).

A puzzling horn-like bone (NMC 8863) was collected by C. M. Sternberg at Scabby Butte in 1946. In lateral outline (Fig. 14) it resembles the curved nasal horns of some centrosaurs, but it is heavier and longer than in any known species. Unlike nasal horn cores, the surface texture appears to be asymmetrical, with longitudinal sulci better developed on one side than the other. A section is missing, and something has been lost from the tip, but the complete bone must have been in the neighborhood of 55 cm long. It is flattened, with proximal diameters of 18.5 cm and 7.5 cm, but does not appear to be distorted. The shape is suggestive of the frill spike on NMC 9602; at the base there is the merest suggestion of a smooth surface reminiscent of the finished lining of the sinus in the parietal bars described above.

The form and arrangement of the spikes in NMC 9602 can be compared with the frill of *Styracosaurus ovatus* Gilmore from the Two Medicine Formation of Montana (Gilmore 1930, Pl. 10, Fig. 2). However, the Scabby Butte specimen is less massive, and a medial pair of spikes (if present) may have been differently oriented than those of *S. ovatus*. The single spike of NMC 9602 was relatively shorter than the similarly placed spike in *S. ovatus*, but the supposed spike NMC 8863 is almost twice as large as the largest one in the Two Medicine specimen. Gilmore's material includes a separate fragment bearing a smaller spike, which he believed belonged considerably farther forward than the larger spikes. The attached part of the frill in this specimen is more massive than any part of the frill anterior to the spike in NMC 9602, and I find no evidence of another spike in this specimen. The resemblance between NMC 9602 and the frill of *S. albertensis* is less obvious, but there is a fundamental similarity in the general shape of the bone and the arrangement of the lateral epoccipital processes. If under my alternative interpretation (Fig. 13) the Scabby Butte frill possessed long medial spikes, these may have been oriented more as in *S. albertensis* than in *S. ovatus*.

Because of their occurrence in the same restricted area with skulls in *Pachyrhinosaurus*, whose frill is largely unknown, the question naturally arises: can these unusual frills belong to that genus? What evidence there is, is circumstantial, but it seems convincing that:

- (1) the frill of *Pachyrhinosaurus* was fenestrated, as are these frills;
- (2) *Pachyrhinosaurus* had a remarkably short squamosal, implying unusual architecture for the frill as a whole;
- (3) a short squamosal is associated with a spiked frill in *Styracosaurus*;
- (4) the frill resembles the frills of *Styracosaurus* and *Centrosaurus* more than any other ceratopsians, and *Pachyrhinosaurus* is clearly related to these genera;
- (5) NMC 9602 was found about midway between the two *Pachyrhinosaurus* skulls at Site 2, and NMC 10644 was only a few feet removed from skull NMC 9485;
- (6) although Site 2 may contain remains of another ceratopsian, *Anchiceratops*, the frill in this genus is entirely different from these specimens; and
- (7) NMC 8860, the fragmentary skull collected by Sternberg at Scabby Butte, includes a small piece of bone some 87 mm long that seems to agree with the bone comprising the presumed lateral bars of the frills from Site 2.

There is, on the other hand, no direct evidence that these frills (or, for that matter, the frill of *S. ovatus*) belong to *Styracosaurus*. I suspect that they pertain to *Pachyrhinosaurus* and offer the accompanying reconstruction (Fig. 15) with some confidence.

Non-Ceratopsian Vertebrates from Scabby Butte

Curiously, non-ceratopsian bones are very rare at Scabby Butte outside the Site 2 bonebed. Fish and amphibian remains occur in quantity only in the bonebed at Site 3, but every taxon recognized at Scabby Butte is represented at that locality. Hadrosaurs are abundant at Site 2 but nowhere else. The poor representation of some common Edmonton (= Horseshoe Canyon) forms—for example, *Champsosaurus*, hadrosaurs, carnosaurs, and ankylosaurs—is noteworthy. The unique occurrence of a mosasaur at Site 4 is to be further dealt with by D. A. Russell in another publication.

As stratigraphic distances at Scabby Butte are small, horizons will not be indicated in the

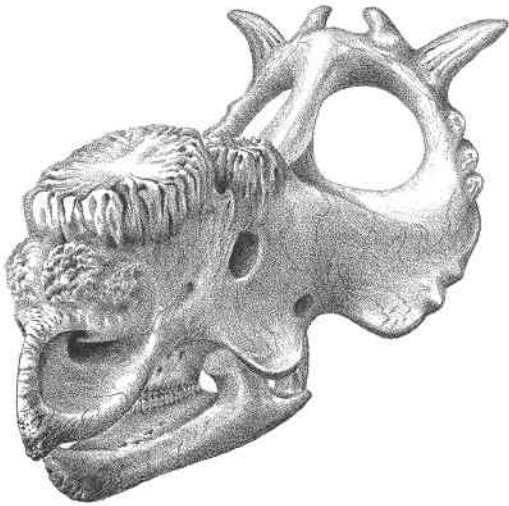


FIG. 15. Artist's reconstruction of the skull and jaw of *Pachyrhinosaurus* based on all available material. Incorporation of the spiked frill is problematic, as explained in the text.

following descriptions. The relative stratigraphic positions of the sites are given elsewhere (Langston 1975).

Class ELASMOBRANCHII
Order ISURIFORMES
Family ORECTOLOBIDAE
Squatirhina Casier

Squatirhina americana Estes

Material—NMC 21869, 17 teeth; NMC 21876, seven teeth; NMC 71868, a symphyseal tooth.

Locality—Site 3.

Remarks—Estes (1964) was the first to recognize *Squatirhina* in North America. His specimens, assigned to a new species, *S. americana*, were all from one Lancian locality. Teeth numbered NMC 21869 differ from Estes' specimens most notably in the construction of the root, in which the median sulcus (= central root canal of Estes) is relatively narrow or undeveloped beneath the internal protuberance. They are also a little smaller, with maximum root diameters ranging from 0.8 to 1.6 mm (compared with 1.5 to 2.0 mm for the Lance specimens). Crown height varies from 0.9 to 1.6 mm.

Casier (1947) described the teeth of *Squatirhina lonzeensis* as having a crown of squatinoid form and a divided rhinobatoid root. But he pointed out that the external part of the median sulcus is still very wide and suggested that this condition is intermediate between squatinoids and rhinobatoids (in which the sulcus is narrow

throughout its length). There is no mediointernal foramen (Casier's terminology) in *Squatirhina*; the squatinoid mediointernal canal having been exposed through bifurcation of the root. *Squatirhina* species subsequently described by Arambourg (1952)—*S. casieri*, *S. numidica*, *S. dartevellei*, *S. aegyptiacus* (Stromer)—and *S. americana* Estes share this characteristic root construction.

Seven teeth (NMC 21876), otherwise indistinguishable from NMC 21869, have an undivided (= squatinoid) root (Fig. 16c). The sulcus is nevertheless as wide externally as in the other teeth; however, it disappears mediointernally into a canal, which opens at the apex of the internal protuberance through a mediointernal foramen. The conspicuous notch visible in the roots of *S. americana* teeth (Estes 1964, Fig. 6a, b) is lacking. Also conforming to squatinoid architecture is a large lateroventral foramen situated in a wide depression on either side of the prominent internal protuberance. There are, in addition, a variable number of smaller foramina issuing from the roots in hybodont fashion in the teeth with squatinoid roots. In those teeth where the median sulcus is poorly developed, the bases of the roots are grooved, suggesting the exposure of internal canaliculi through incomplete formation of the basal plate. The occurrence of two root forms in this sample suggests a degree of dimorphism not hitherto recognized in *Squatirhina*. Whether the variation occurs within a single dentition topographically and/or ontogenetically, or was a matter of intraspecific variability, is a question that must await the discovery of better samples.

NMC 21868 (Fig. 16d) resembles the so-called symphyseal teeth of *Lonchidion selachos* Estes. Patterson (1966) noted that no teeth of this type occur among several hundred *Lonchidion* teeth from the British Wealden and Purbeck. Except for the size of the sample, an exactly contrary situation exists at Scabby Butte, where no characteristic *Lonchidion* teeth have been found. Patterson (1966, p. 331) concluded, "... it seems ... probable that the teeth described by Estes belong to a squatinid or orectolobid, perhaps to his species *Squatirhina americana* or a related form." The assemblage from Scabby Butte supports Patterson's view, with which Estes now agrees in part (Estes *et al.* 1969; personal communication, 1973). Placement of this sort of tooth in *Squatirhina* seems more appropriate for the time being at least than

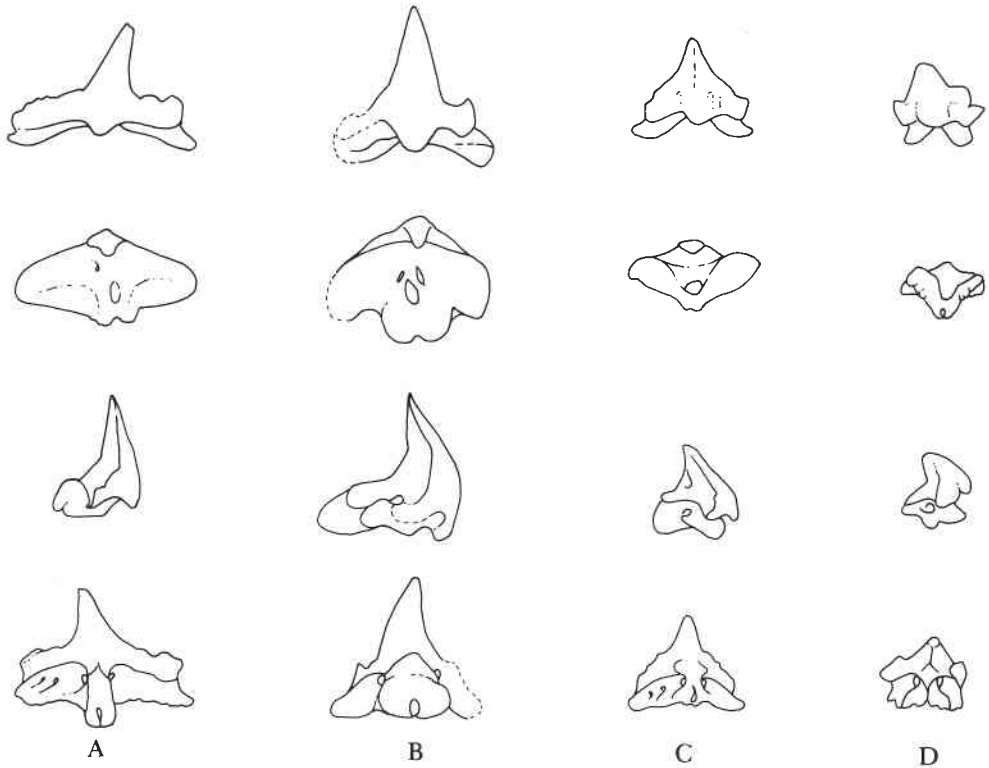


FIG. 16. Isuriform and squatinoid elasmobranch teeth from Scabby Butte Site 3. Top to bottom: labial, basal, medial, and lingual views. A. *Squatina* sp., NMC 21875; B. NMC 21877, root damaged; C. *Squatirhina americana* Estes, NMC 21876, with squatinoid root; D. a symphyseal tooth of the sort assigned to *Lonchidion selachos* by Estes, but here placed tentatively in *Squatirhina*. Scale: 2 mm.

assignment to *Squatina*, which, in its living representatives, lacks symphyseal dentition.

Fox (1972) listed *Lonchidion* sp. from the Upper Milk River Formation of southern Alberta, but did not state whether the reference was based on so-called symphyseal teeth or the characteristic type of dentition. *Squatirhina* is not recorded elsewhere in the western Canadian Cretaceous.

Order SQUATINOIDEI

Family SQUATINIDAE

Squatina Risso

Squatina spp.

Material—NMC 21875, a tooth; NMC 21877, eight teeth.

Locality—Site 3.

Remarks—NMC 21875 (Fig. 16a), except for its slightly bent central cusp and the presence of small secondary cusps, is reminiscent of the teeth of *S. cranei* (Woodward 1912, Pl. 47,

Figs. 7–12) and *S. prima* (Arambourg 1952, Pl. 27, Figs. 1–16). The anterior and posterior cusps (denticles of White and Frost 1931) have their sharp cutting edges a little bent over in the oral direction.

Teeth numbered NMC 21877 (all broken) display general features of Squatinoidei, but whether they pertain to the same form as NMC 21875 is uncertain. These teeth (Fig. 16b) have long, straight or slightly bent central cusps arising near the middle of a widely expanded base. The roots are thicker than in NMC 21875 and show a tendency to subdivide into three lobate branches. The wide external depression (Casier's terminology) occupies nearly all of the ventral surface of the root, and in all but one specimen there is a large central foramen in about the center of the root, and a median canal of variable length. Both internal and external lateral canals are also present and better developed than usual in *Squatina* (comparable with

Squatirhina). The central canal opens in a small mediointernal foramen at the tip of a prominent and thickened internal protuberance and is visible in occlusal aspect. One tooth lacks the enclosed canal, thus resembling *Squatirhina*. Also in *Squatirhina* fashion, the central cusp has a ventrolabial process, but the cusp itself is longer and more fang-like than in *S. americana*. The vitreous cap of the central cusp extends well out onto the ventrolabial process in these teeth. On either side of the crown the sharp edges of the central cusp develop low secondary cuspsules with weakly crenulated cutting edges. The usual number of such cuspsules is two, but as many as four may be present. They are better developed in NMC 21877 teeth than in NMC 21875, a condition reflected in the thickening and trilobate development of the roots not present in NMC 21875.

The impracticability of distinguishing species on the basis of dental characters in *Squatina* has been noted repeatedly by authors, and I make no attempt to do so here. There may even be some uncertainty about assigning teeth numbered NMC 21877 to the genus, but NMC 21875 almost surely belongs there. Secondary cusps, not reported in *Squatina*, are, however, variably developed in species of *Squatirhina*, and the present specimens may indicate comparable variability in *Squatina*. *Squatina* is represented by several existing species in continental waters (Bigelow and Schroeder 1948). Its presence in a brackish or fresh water deposit should not be surprising in view of increasing evidence that elasmobranchs are more euryhaline in habits than once supposed (for example, see Thorson 1971). The taxon does not seem to have been encountered previously in the Cretaceous of western Canada.

Order RAJIFORMES
Family DASYATIDAE

Myledaphus Cope
Myledaphus bipartitus Cope

Material—NMC 10672, several hundred teeth; NMC 10673, about thirty dermal scales.

Locality—Widespread at Scabby Butte, but most abundant at Site 3.

Remarks—This ray, ubiquitous in late Cretaceous fresh-water deposits of the northern plains, is the only vertebrate besides *Pachyrhinosaurus* widely distributed at Scabby Butte. As in Edmonton deposits elsewhere in Alberta, it is represented by a wide variety of tooth forms; all of

the shapes described by Estes (1964, Figs. 7, 8) are represented. A great number of specimens were obtained at Site 3.

A number of presumed dasyatid dermal scales were found at Site 3. If they belong to *Myledaphus*, their small number in the deposit as compared to the abundant teeth suggests that *Myledaphus* was a relatively 'naked' ray; an articulated but incomplete ray skeleton from Oldman beds, possibly *Myledaphus*, shows no scales at all (Langston 1970).

The scales (Pl. III) consist of a dentinal basal plate or root with sharply defined stellate ridges and a relatively simple crown capped by vitreous tissue. The number of ridges increases away from the crown, dichotomizing as in existing dasatids or arising independently between primary ridges as in the potamotrygons (Garman 1913). The ventral surface of the root contains small, randomly arranged foramina. In conical scales there is often a larger, centrally located opening, but there is no suggestion of a basal division as in *Myledaphus* teeth. Other foramina occur in the troughs between the edges on the sides of the roots. Two forms are distinguishable. One, of relatively small size and occurring in smaller numbers, is toadstool-shaped with a slender, stalk-like root and an expanded, flat, button-shaped crown. The other scales have an expanded basal plate whose ridges, radiating outward below, produce a strongly pectinate edge around the basal plate. The ridges converge upward and mostly disappear below the crown, but a few (from two to about seven) are sometimes reflected in the crown. Such crowns are moderately to sharply hooked (?) backward. Although dasyatid affinities are suspected, it is well to recall that other elasmobranchs are present in the Site 3 material and, "La séparation des boucles en différents types n'implique pas que chaque type correspond à une espèce déterminée; il se peut en effet qu'une même espèce possède différents types . . . et que des espèces différentes portent des boucles identiques." (Cappetta 1970, p. 116).

The largest teeth are wider than long, some examples having diameters as great as 9.0 and 7.0 mm, respectively. The smallest teeth are almost microscopic. The largest scales have basal diameters of about 3.0 mm and heights up to 2.2 mm. The largest of the toadstool-shaped scales are no more than 0.7 mm in crown diameter and 0.6 mm high; the smallest are scarcely visible without a lens.

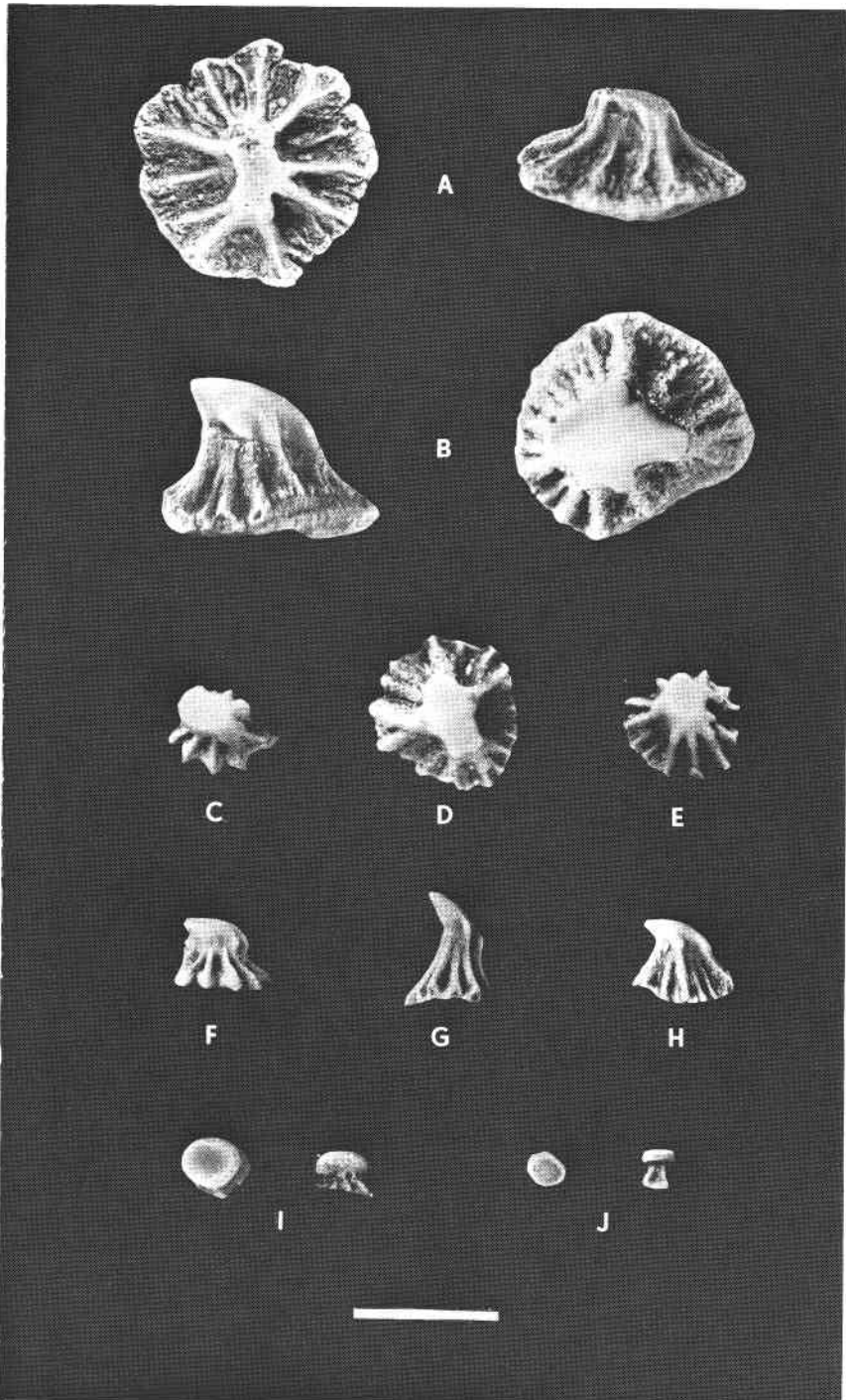


PLATE III. Dasyatid scales, presumably *Myledaphus bipartitus* Cope. NMC 10673, illustrating range of variability. A, top and side views of a large scale with worn crown; B, a similar but unworn scale; C-E, top, and F-H, side views of six different scales; I-J, top and side views of small toadstool-shaped scales. Scale equals 2 mm.

Class OSTEICHTHYES

Order AMIIFORMES

Family AMIIDAE

Amia Linneus*Amia* cf. *A. fragosa* (Jordan)

Material—NMC 10677, teeth, scales, and a few bones, not necessarily one individual.

Locality—Site 3.

Remarks—Estes and Berberian (1969) and Boreske (1974) have recently reviewed the case for synonymy of the North American late Cretaceous and early Tertiary fishes *Kindleia* Jordan and *Stylomyleodon* Russell. They concur with Janot (1967) that both should be placed in *Amia*. Of *Amia* remains at Site 3, teeth are most abundant. These include both sharp and blunt styloform types. Fragments of ossified scales and cranial plates are also present. A caudal vertebra with diameters of 8.5 mm and 9 mm is 4 mm long. It is damaged ventrally, but the attachment areas for the neural arch can be seen dorsally. The chordal foramen is closed, but whether smoothly covered or plugged by ossified notochord is not clear. Nothing in this material is useful for specific determination, but the caudal vertebra resembles *A. calva*. Boreske (1974) listed *A. fragosa* from the Edmonton beds, but his *Amia* cf. *uintaensis* is recorded from a number of late Cretaceous horizons in North America. Amiids are reported from the Upper Milk River (Fox 1972) and Oldman Formations (Estes 1964), and from various Lancean deposits of western Canada (L. S. Russell 1964).

Order ASPIDORHYNCHIFORMES

Family ASPIDORHYNCHIDAE

Belonostomus Agassiz*Belonostomus* cf. *B. longirostris* (Lambe)

Material—NMC 21863, a number of jaw fragments and scraps of ganoid scales.

Locality—Site 3.

Remarks—Estes (1964) has demonstrated the synonymy of *Belonostomus* Agassiz (= *Diphiodus* Lambe). Clearly recognizable as *Belonostomus* is a short segment of a cranial rostrum 3.0 mm long, which contained in this distance two large lateral teeth on each side. Tiny marginal teeth were present, but are not preserved. It is apparently undivided in the midline and is semicircular in cross-section (width 2.3 mm, height 1.8 mm). It displays an acute longitudinal groove on the oral side, but there is no trace of the dorsal keel reported in *B. longirostris* by Estes (1964). The outer surface is devoid of

ganoine. A post-rostral fragment in this group of specimens is, however, coated with ganoine. Among his Lance material, Estes found smaller rostra tended to lack ganoine, whereas the larger ones were heavily coated. He concluded that this variation was most likely a size or sex difference. The outer surface of the specimen is covered by fine subparallel longitudinal ridges and striae as in *B. longirostris*. This species is the only Maestrichtian *Belonostomus* reported by Estes from North America; its presence in Campanian rocks of western Canada has been noted in the Upper Milk River beds (Fox 1972) and the Oldman Formation (Lambe 1902). The oldest occurrence of the genus in North America is, however, of Coniacian age (Bardack 1968).

Order LEPISOSTEIFORMES

Family LEPISOSTEIDAE

Lepisosteus Lacépède*Lepisosteus* sp.

Material—NMC 10678, three scales; NMC 10679, isolated teeth and miscellaneous fragments.

Locality—Sites 2 (NMC 10678) and 3 (NMC 10679).

Remarks—Two complete scales were recovered at Site 2; in addition to scales and teeth, a few fragments of dermal skull bones were found at Site 3. All individuals were relatively small, but the material is otherwise uninformative.

Order ELOPIFORMES

Family PHYLLODONTIDAE

Paralbula Blake*Paralbula casei* Estes

Material—NMC 21867, about a hundred shed teeth.

Locality—Site 3.

Remarks—Phyllodont teeth are the second most abundant vertebrate fossil (after *Myledaphus*) at Site 3. Curiously, although about a hundred of these characteristic button-shaped teeth were recovered, no trace of basibranchial or parasphenoid tooth plates was found. The condition of the teeth varies from unworn to extremely worn, and the only explanation for their isolated presence in the deposit appears to be that, as in the living drumfish *Archosargus* (not a phyllodont), paralbuid teeth were not firmly attached to the bones and tended to fall out after death. Rounded teeth vary in diameter from 0.5 to 3.5 mm.

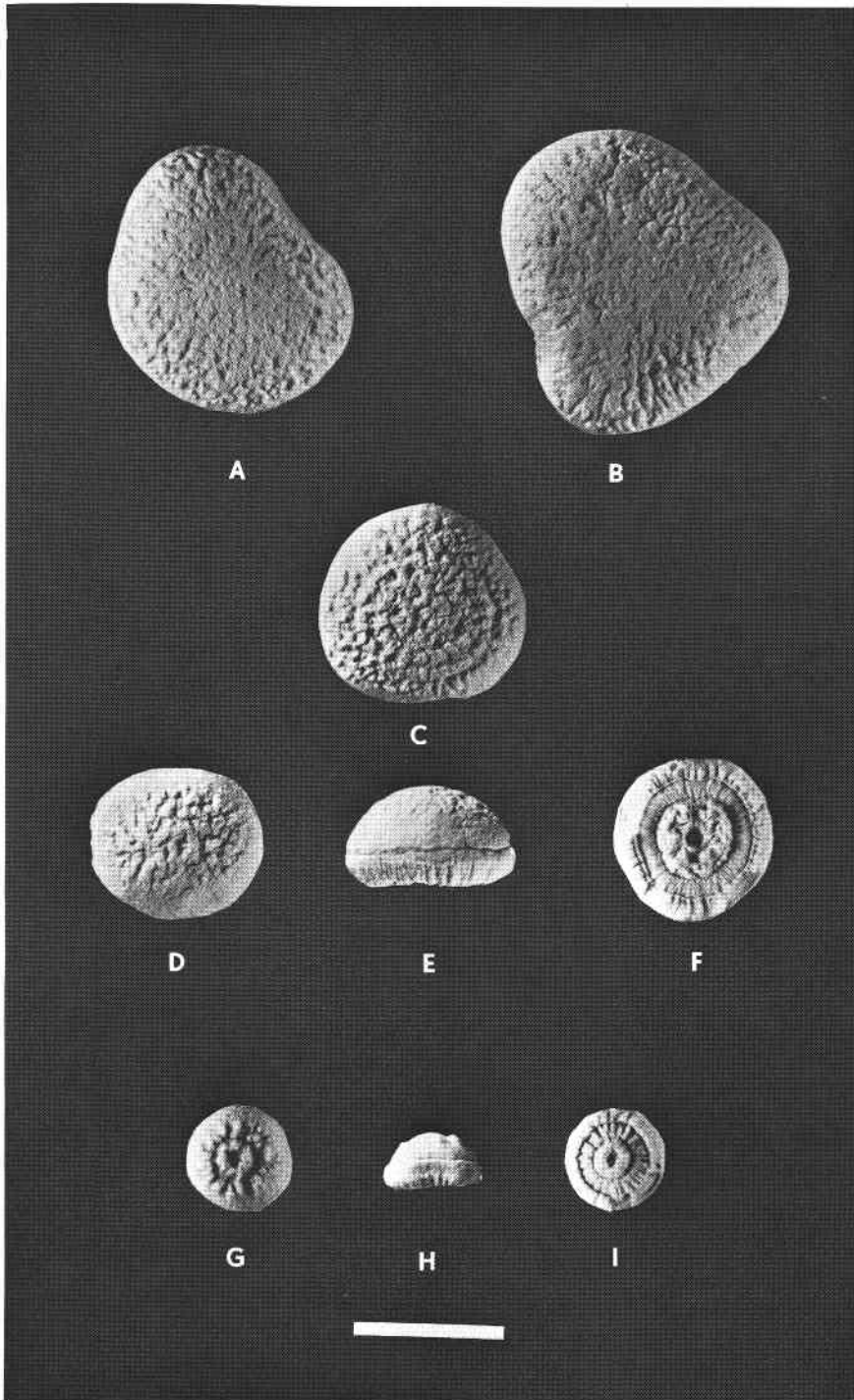


PLATE IV. *Parabula casei* Estes. NMC 21867, assorted teeth from Site 3, illustrating range of variation in shape, surface details, size, and root construction. A-D, G, occlusal surface; E, H, lateral view; F, I, basal aspect. D-F and G-I are three views of two teeth. Scale equals 2 mm.

Most of the specimens are hemispherical, but a few, mainly the larger ones, are irregular in plan, varying from oval to bean-shaped or even triangular (Pl. IV). Unworn crowns have finely crenulated occlusal surfaces in which the delicate wrinkling varies from a symmetrical, concentric, or radiating pattern to a completely random arrangement. Many teeth are encircled at the base by a low cingulum. Larger teeth tend to be depressed, whereas smaller, presumably peripheral ones, are often bulbous. Larger and less worn teeth may contain large pulp cavities surrounded by a concentric laminar structure. Smaller teeth, lacking pulp cavities, often have instead a small conical elevation near the center of the attachment surface and both concentric and radiating structures.

Estes (1969a) reported *A. casei* from the Oldman Formation in southeastern Alberta and Fox (1972) listed cf. *P. casei* from the Upper Milk Formation. This species was evidently fairly widespread, ranging from Campanian in North America to Ypresian (early Eocene) in England. Although present in the Maestrichtian of New Jersey, this is the first post-Campanian record from western Canada.

Order PERCIFORMES
Family SCIAENIDAE
Platacodon Marsh

Platacodon cf. *P. nanus* Marsh

Material—NMC 21874, three pharyngeal teeth.

Locality—Site 3.

Remarks—Originally described as mammalian (Marsh 1889), tiny teeth of this perciform fish have been reported previously in Canada from the Milk River beds (Fox 1972) and in the United States from the Lance and Hell Creek (Estes and Berberian 1970). It is new to the St. Mary River Formation.

Class AMPHIBIA
Order URODELA
Family BATRACHOSAUROIDIDAE
Opisthotriton Auffenberg

Opisthotriton sp.

Material—NMC 21865, jaw fragment; NMC 21866, several vertebral centra.

Locality—Site 3.

Remarks—*Opisthotriton* is the only amphibian so far recognized at Scabby Butte. The material is fragmentary, the vertebrae being represented in every case by half-centra from which all apophyses have been lost. However, the com-

bination of strong basapophyses (now broken off) and flattened, mostly bone-filled anterior condyles is unmistakable. The largest centrum has a transverse diameter of 2.25 mm, but most specimens are 2 mm in diameter or less. They are thus a little smaller than the holotype of *O. kayi* Auffenberg (a mid-trunk vertebra) or the specimens described by Estes (1964).

This urodele is of relatively rare occurrence in western Canada as compared with the much larger cryptobranch *Scapherpeton tectum* Cope. Reported previously from the early Campanian Upper Milk River beds (Fox 1972), Lance and Paleocene (Auffenberg 1961; Estes 1964, 1969b), this is the first record from Maestrichtian rocks in Canada.

Class REPTILIA
Order TESTUDINES
Suborder CRYPTODIRA
Family TRIONYCHIDAE
Aspideretes Hay
Aspideretes sp.

Material—NMC 10659, a corocoid and several shell fragments.

Locality—Site 6 (surface finds).

Remarks—The swamp turtles so common in the dinosaur beds of western Canada are represented at Scabby Butte by only a few water-worn fragments of bones and shell plates bearing 'trionyhid' sculpture. Specific determination of this material is impossible.

Family BAENIDAE
Boremys Lambe
Boremys sp.

Material—NMC 10660, small piece of a marginal plate; NMC 10658, a humerus.

Locality—Site 6 (surface finds).

Remarks—The coarsely marked fragment of shell is reminiscent of *Boremys* material, which is common on Oldman beds but is as yet unreported from the Edmonton (Gaffney 1972). The humerus is placed here with reservation; it is not *Aspideretes*.

Order EOSUCHIA
Family CHAMPSOSAURIDAE
Champsosaurus Cope
Champsosaurus sp.

Material—NMC 10654, 10680, a small number of teeth and fragmentary bones, including vertebral centra.

Locality—Sites 2, 3, and 6.

Remarks—This ubiquitous aquatic reptile is

unusually scarce throughout the Scabby Butte badlands. This is surprising because as a rule its characteristic spool-shaped vertebral centra are among the most abundant vertebrate fossils in the Oldman and lower Edmonton deposits, especially in small bonebeds, where they are usually associated with *Myledaphus*, *Lepisosteus*, sturgeons, bow-fins, and salamanders (L. S. Russell 1956). Most of the champsosaur bones from Scabby Butte are from the bonebed at Site 3. Present are two dorsal, one sacral, and three caudal centra, and the ends of a few ribs and limb bones (all numbered NMC 10654). To judge from the size of the centra, at least three individuals are represented, and these are well within the size range of the usual Oldman and Edmonton specimens. Most of the specimens, however, are smaller than usual.

In his review of the North American champsosaurs, L. S. Russell (1956) concluded that of thirteen described species, perhaps no more than five are definable and, "... distinctions based on form and proportions of the vertebrae have little practical value..." (p. 2). Erickson (1972) concurred in general with this view. Thus specific assignment of the Scabby Butte champsosaurs is presently impossible.

Order SQUAMATA
Family MOSASAURIDAE

Plioplatecarpus Dollo
Plioplatecarpus sp.

Material—NMC 21853, incomplete but partly articulated skeleton; NMC 21830, a distal caudal vertebra.

Locality—Sites 3 (NMC 21830) and 4 (NMC 21853).

Remarks—These specimens are under study by D. A. Russell. Their occurrence in presumed fresh-water deposits at Scabby Butte was surprising, but the specimen may represent an individual stranded in an estuary during a brief and otherwise unrecorded local episode of marine flooding (Langston 1975).

Order CROCODYLIA
Family CROCODYLIDAE

Leidyosuchus Lambe
Leidyosuchus sp.

Material—NMC 10656, several teeth.

Locality—Site 3.

Remarks—Except for shed teeth, crocodylian remains are not very common in the Upper Cretaceous fresh water deposits of western

Canada. Neither is there much systematic variety, known genera numbering only two or three. Traditionally, lacking evidence to the contrary, most finds are referred to *Leidyosuchus* Lambe, and several of the teeth from Scabby Butte may be so treated.

Genus indeterminate

Material—NMC 10676, eight teeth.

Locality—Site 3.

Remarks—Eight teeth differ from *Leidyosuchus* in having distinctly crenulated and relatively long and slender crowns, a little constricted at the base. Two of these teeth are sharply bent at midheight. Their general form is that generally expected in slender-snouted crocodylians. No really longirostrine taxa have been recorded from skeletal material in the western Canadian Cretaceous, and these teeth are unlike those of *Leidyosuchus multidentatus*, a moderately slender-snouted early Tertiary species. Neither do they resemble teeth of the long-snouted *Thoracosaurus*, which occurs in the famous Bug Creek fauna in Montana (Estes and Berberian 1970). It is possible that they are not crocodylian.

Order SAURISCHIA

Family TYRANNOSAURIDAE

Genus indeterminate

Material—NMC 9589, 9723, 10650, 10651, 10652, 10675, shed teeth.

Locality—Sites 2 (NMC 9589, 9723, 10650, 10651, 10652) and 3 (NMC 10675).

Remarks—As usual in the late Mesozoic bonebeds, shed carnosaur teeth occur at Sites 2 and 3, but no recognizable bones of this group were found at Scabby Butte. All parts of the dental series except 'incisors' are represented. Most of the teeth bear pronounced wear facets, and those in which crowns are complete show evidence of root resorption. Some of the Scabby Butte teeth are very large and heavy: NMC 9589, 9723, 10650, and 10651 are apparently close to the upper limits found in *Albertosaurus libratus* (Lambe), and a worn tooth, NMC 10652, which is 102 mm long, is larger than any specimen in the National Museum assigned to *Albertosaurus* or *Daspletosaurus*. Both of these large pre-Lancian tyrannosaurs are known from Oldman and lower Edmonton deposits (D. A. Russell 1970). I am unaware of any practical means of distinguishing large isolated carnosaur teeth at the generic level, but if size is significant, most

of the Scabby Butte specimens are more likely to have belonged to *Albertosaurus* than to *Daspletosaurus*.

Family ?COELURIDAE

Genus indeterminate

Material—NMC 10674, mid-part of a tooth.

Locality—Site 3.

Remarks—Tiny serrated reptile teeth have been known for over a century from the Upper Cretaceous of western North America. D. A. Russell (1969) has recently reviewed *Stenonychosaurus* Sternberg, concluding that, while distinct, it is closely related to *Saurornithoides* Osborn. Estes (1964) reported a form comparable to *Saurornithoides* from the Lance. Teeth of *Saurornithoides* are very coarsely serrated (denticulated is more descriptive) along the posterior edge, but are so poorly preserved that the presence of anterior serrations cannot be determined (D. A. Russell 1969). An incomplete small dentary from the Oldman Formation, referred to *Troödon formosus* Leidy by L. S. Russell (1948), is believed by D. A. Russell to belong to *Stenonychosaurus*. A tooth in this jaw is said to possess weak anterior serrations (L. S. Russell 1948). If, therefore, *Stenonychosaurus* and *Saurornithoides* are as closely related as other parts of the skeletons seem to suggest, the teeth of *Saurornithoides* may be expected to possess serrations along both edges.

Although Estes found no differences between the teeth of *Saurornithoides* and the compared tooth from the Lance, the latter has no serrations on the leading edge. The tiny tooth from Scabby Butte is strongly bent and flat-sided and is clearly similar to the cf. *Saurornithoides* tooth of Estes in general shape and proportions. The serrations on the posterior edge, though coarse for a tooth of this size, are nevertheless finer than those of Estes' specimen, there being about four in 1 mm. The leading edge is smooth.

I believe the Scabby Butte specimen may belong to an animal similar to the one from the Lance, but I am less confident than Estes about comparing either tooth to *Saurornithoides*. They may in fact represent yet another unnamed tiny theropod. I see no compelling reason to place them in the family Troödontidae with *Saurornithoides*, although assignment in the Coeluridae is scarcely more satisfactory.

Family ORNITHOMIMIDAE

Genus indeterminate

Material—NMC 10653, distal end of left metatarsal IV.

Locality—near Scabby Butte Site 3, in section 18 (surface find).

Remarks—D. A. Russell (1972) recognized three genera of 'ostrich dinosaurs' from the pre-Lancian Cretaceous of western Canada: *Ornithomimus*, *Struthiomimus*, and *Dromiceiomimus*. All have representatives in the Edmonton beds, but *Dromiceiomimus* is the most abundant at these levels. Comparisons between Scabby Butte specimens and several ornithomimid metatarsals—for example, the holotype of *Struthiomimus* (= *Ornithomimus*) *altus* (Lambe) in the National Museum collections—reveal no obvious differences except for the relatively larger dimensions of NMC 10653.

Family TROÖDONTIDAE

Troödon Leidy

Troödon sp.

Material—NMC 10649, an incomplete tooth.

Locality—Site 2.

Remarks—What remains of this tooth is indistinguishable from several teeth in the National Museum collections assigned to *Troödon* by Sternberg (1945). These differ from others in the same collection, and from the holotype of *T. formosus* Leidy, in their relatively weaker marginal denticulations which, nevertheless, seem large for the size of the teeth. It is possible that they pertain to *Stenonychosaurus*, which may be a junior synonym of *Troödon*, according to D. A. Russell (1969).

Order ORNITHISCHIA

Family HADROSAURIDAE

Edmontosaurus Lambe

Edmontosaurus sp.

Material—NMC 21968–69, 21971, 22005, maxillae; NMC 9716, 9803, 21884–88, dentaries; NMC 10661, squamosal; NMC 22000–1, 22007, surangulars; NMC 9598, 9717, 21972–97, 22006, 22010, vertebrae; NMC 21998–99 and unnumbered, ribs; NMC 21949–54, scapulae; NMC 9591–93, 21963–67, ilia; NMC 21893–21905, pubes; NMC 9588, 9597, 21906–12, ischia; NMC 9584, 9718, 9795, 9800, 21881–83, humeri; NMC 21958, ulnae; NMC 21955–56, radii; NMC 21959–62, metacarpals; NMC 9791, 9793, 9796, 21890–92, femora; NMC 9720, 9804, 21889, tibiae; NMC 9797–99, 9801–02, 21943–48, fibulae; NMC 21927–28, 21937, 22002, astragali; NMC 21942, 22008, calcanea; NMC 9586–

87, 9603-04, 9715, 9794, 21913-25, metatarsals; NMC 9585, 9595, 21926, 21920-36, 21938-40, phalanges.

Localities—NMC 22010, Site 5; all others, Site 3.

Remarks—D. A. Russell (1967) noted that hadrosaurs comprise more than half of all dinosaurs collected from pre-Lancian rocks in western Canada, and I suspect that the proportion of duck-billed dinosaurs encountered in the field must be even larger. The proportion of hadrosaurs is about 85% at Site 2, but otherwise they are notably scarce in the Scabby Butte area. The seven or so individuals represented at Site 2 range in size from that of the little *Cheneosaurus*, an Edmonton 'genus' probably comprising juvenile individuals of some large lambeosaurine, up to animals almost as big as small representatives of *Edmontosaurus*. Little diagnostic material was found, but two ischia—one small, the other large (NMC 9597, 9588)—are of the long, slender hadrosaurine kind. Several humeri of differing lengths have slender shafts, a usual but not universal attribute of this subfamily. Most illuminating is the incomplete squamosal (NMC 10661). It retains the quadrate fossa, a complete quadrate process, and part of the postorbital and paroccipital articulations, but the transverse ramus, and hence all evidence of the significant relationships to the parietal, is lost. Although hadrosaur squamosals have received little attention from systematists, attempts to identify the present specimen suggest that they may provide useful characters for generic differentiation. NMC 10661 is clearly of the kind found in hadrosaurines of the *Edmontosaurus-Anatosaurus* group. Lull and Wright (1942, p. 56) stated that the zig-zag suture between postorbital and squamosal is "quite variable in form", but among several *Edmontosaurus* squamosals in the National Museums of Canada I find that two groups can be distinguished from the pattern of this contact. Specimens assigned to *E. regalis* on other grounds have a relatively uncomplicated suture and the postorbital overlaps the squamosal as far back as the center of the quadrate fossa, making the squamosal appear short in lateral aspect. The group containing *E. edmontoni* has a distinctly bifurcate suture in which a lateral process of the postorbital is separated from a broader, medial one by a strong forwardly directed wedge of the squamosal. The postorbital

overlaps the squamosal less in animals with this sutural pattern, and the squamosal appears longer. The squamosal from Scabby Butte is very similar to that in the holotype of *Edmontosaurus* (= *Thespesius*) *edmontoni* (Gilmore) (NMC 8399) and of *Anatosaurus* (= *Thespesius*) *saskatchewanensis* (Sternberg) (NMC 8509). But the genus *Anatosaurus* is unknown earlier than the Lancian stage, whereas *Edmontosaurus*, its possible ancestor, is confined to lower parts of the Edmonton sequence and equivalents.

What evidence there is thus seems to favor assignment of the Scabby Butte hadrosaurs to the genus *Edmontosaurus*. *Edmontosaurus edmontoni* was evidently consistently smaller than *E. regalis*, and none of the Scabby Butte animals was quite so large as the described *E. edmontoni* specimens.

Several ribs and dorsal vertebrae of a large hadrosaur (NMC 22010) were obtained at Site 5. The vertebrae have thick, upright neural spines of moderate length. It is unlikely therefore that the specimen represents *Hypacrosaurus*, the common lower Edmonton lambeosaurine. There is no evidence of this hadrosaurian in the Scabby Butte assemblage.

Family NODOSAURIDAE

Edmontonia Sternberg

Edmontonia cf. *E. longiceps* Sternberg

Material—NMC 21864, a broken tooth.

Locality—Site 3.

Remarks—This small tooth has a thickened but not greatly roughened cingulum. Not enough is preserved for positive identification, but it seems to agree best with *E. longiceps* Sternberg among the nodosaurs (see L. S. Russell 1940).

Vertebrate Remains of Undetermined Affinity

As usual in any large and varied collection of fossil vertebrates, the Scabby Butte assemblage contains a number of specimens that cannot be placed in a particular systematic pigeonhole. Among these are a coprolite (NMC 21872), an otolith (NMC 21873), and several unnumbered fragments, both large and small.

Three small osteoscutes (NMC 21870) appearing as flattened, wrinkled granules are suggestive of sturgeon scutes and would thus be the only evidence of the Acipenseriformes in the collection. They are, however, "not characteristic enough for identification" (R. Estes, personal communication, 1973). A few small, rounded,

and highly polished black pebbles (NMC 21871) are so anomalous in the fine-grained sediment at Site 3 that they must be either recent intrusions or, more probably, gastroliths. The largest pebble has a diameter of 11 mm, but most are considerably smaller. So similar are they generally in size and shape to teeth of *Parabulba* that once introduced into the depositional environment, these two sorts of objects probably behaved in similar fashion.

Acknowledgments

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All specimens referred to by number in the text are in the National Museum of Natural Sciences (NMC).

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