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LATEST CRETACEOUS OCCURRENCE OF NODOSAURID ANKYLOSAURS (DINOSAURIA, ORNITHISCHIA) IN WESTERN NORTH AMERICA AND THE GRADUAL EXTINCTION OF THE DINOSAURS

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ABSTRACT—The presence of nodosaurid ankylosaurs in the Lance, Hell Creek, and Laramie formations of western North America is confirmed, thereby extending the geochronological range of this family into the Maastrichtian (Lancian). The material includes a cervical spine and a skull referable to *Edmontonia* sp., and numerous teeth, plates and a basioccipital, which are questionably assigned to *Edmontonia* sp.

Comparison of the amount of nodosaurid material known from the Judith River Formation (Campanian) with that from the Lancian deposits indicates a substantial decrease in the relative abundance of nodosaurids in the Maastrichtian. Furthermore, the stratigraphic distribution of these nodosaurs is apparently limited to the lower part of the Lancian deposits, suggesting that they became extinct before the end of the Cretaceous. If true, this would support the hypothesis that the dinosaur extinction at the end of the Maastrichtian was gradual, not catastrophic.

INTRODUCTION

Nodosaurid ankylosaurs first appear in Europe by the Middle Callovian (Middle Jurassic) (Galton, 1983, 1984) and by the Neocomian (earliest Cretaceous) in North America (Carpenter and Bakker, manuscript). The timing of their extinction, however, is uncertain. Coombs (1978) places it at the end of the Campanian or earliest Maastrichtian, and Galton (1984) at the end of the Campanian. Russell (1982), on the other hand, places their extinction at the end of the Maastrichtian, although no data are given. We conclude, however, on the basis of new data, that the Nodosauridae became extinct well before the end of the Maastrichtian, possibly by mid-Maastrichtian. These new data are based on various specimens collected from Montana, South Dakota, Wyoming, and Colorado (Fig. 1).

Abbreviations—AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences; DMNH = Denver Museum of Natural History; GI SPS = Geological Institute Section of Paleontology and Stratigraphy, the Academy of Sciences of the Mongolian People's Republic; NMC = National Museums of Canada, Museum of Natural History; ROM = Royal Ontario Museum; TMP = Tyrrell Museum of Palaeontology; UCM = University of Colorado Museum; UCMP = University of California, Museum of Paleontology; USNM = United States National Museum of Natural History; UW = University of Wyoming; ZPAL = Zaklad Paleobiologii of the Polish Academy of Sciences.

SYSTEMATIC PALEONTOLOGY

Class ARCHOSAURIA
Order ORNITHISCHIA
Suborder ANKYLOSAURIA
Family NODOSAURIDAE

EDMONTONIA sp.

Referred Material—DMNH 468, complete skull (lacking lower jaws) and associated plates; lower Hell Creek Formation, Corson County, South Dakota. USNM 5793, lateral body spine; Lance Formation, Niobrara County, Wyoming.

Description

The skull (DMNH 468) is dorsoventrally crushed and slightly damaged in the left orbital-squamosal region (Fig. 2A, B). Most of the cranial sutures are obliterated, but as Brown and Schlaikjer (1940) noted for *Protoceratops,* this alone is not necessarily indicative of old age. The dermal plates of the dorsal surface are also fused together, with the sutures between the plates preserved as shallow grooves. Similar fusion of the cranium is seen in the mounted *Edmontonia* on display at the American Museum of Natural History (see Matthew, 1922; Carpenter, in prep).

No teeth are preserved, and postburial compression has made it difficult to determine the original number of alveoli. At least six alveoli are seen on the left maxilla and ten on the right. Compression has also bent

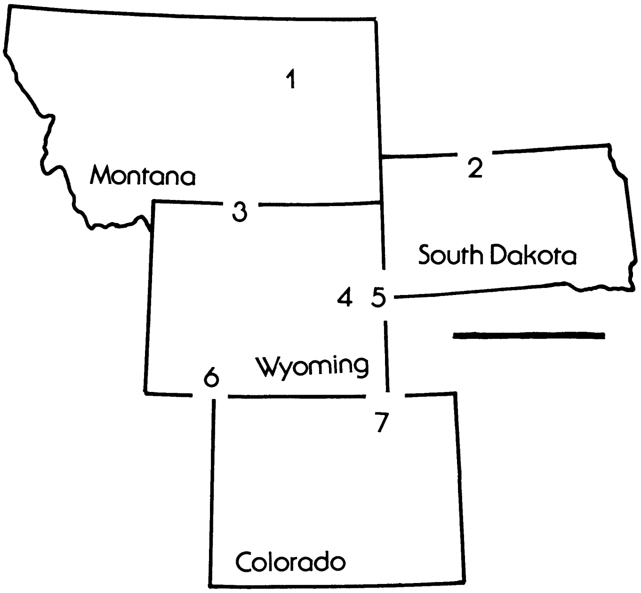

FIGURE 1. Geographical distribution of Maastrichtian nodosaurid material. Locality numbers correspond to those given to Table 3. Heavy bar below South Dakota = 200 miles.

TABLE 1. Measurements (in cm) for DMNH 468, *Edmontonia* sp.

Greatest skull length (premaxilla–supraoccipital)	49.6
Greatest skull width behind orbits	34.6
Width across anterior edge of beak	13.3
Greatest width of beak behind external nares	19.5
Width across paroccipital process	26.8
Quadrate length (estimate)	16.2
Quadrate width across right articular condyle	5.7
Quadrate width across left articular condyle	5.2
Greatest external quadrate to quadrate width	25.6
Greatest length of right orbit (crushed)	9.0
Greatest width of foramen magnum	3.6
Greatest height of foramen magnum	4.2
Width of occipital condyle	6.9
Minimum distance between external nares	7.9
Greatest length of lateral temporal fossa (estimate)	12.0

the occipital condyle forward onto the basioccipital and has pulled the pterygoids apart at the midline.

The skull is referred to *Edmontonia* because of the absence of the lumpy (colloform) cranial armor that characterizes *Panoplosaurus,* and because the vomer is keeled rather than grooved (Carpenter, in prep.). Skull measurements are given in Table 1.

The lower jaws are absent and were apparently separated from the skull prior to burial. Several uncatalogued armor plates were found in the DMNH collection with the skull, but it is not certain if they were collected with the skull (D. Lindsey, pers. comm.). The plates are oval and keeled, and are of the type found in the mid-dorsal region of *Edmontonia* (Carpenter, in prep.) suggesting that they were, indeed, found with the skull.

A large anterolateral spine of *Edmontonia* is also known. This spine (USNM 5793) was previously identified as possibly from the distal tail of *Triceratops* (Hatcher et al., 1907, fig. 74, 1–3). Gilmore (1914), however, compared the spine to those of *Hoplitosaurus,* and, on the basis of Nopcsa's (1905) reconstruction of *Polacanthus,* suggested the spine was from the mid-dorsal region near the sacrum. Comparisons with AMNH 5665 ("*Palaeoscincus*" specimen of Matthew, 1922; Carpenter, in prep.), indicate the spine is the first lateral cervical spine. The spine is slightly smaller than the comparable spine of AMNH 5665, and is about the same size as one in USNM 11868 (see Fig. 3A–G).

EDMONTONIA? sp.

Referred Material—DMNH uncatalogued, four teeth; Hell Creek Formation, Corson County, South Dakota. UCM 42663, tooth, lacking enamel; UCM Loc. 79016; Lance Formation, Niobrara County, Wyoming. UCM 48369, three teeth lacking enamel; UCM Loc. 80004, "Lance" Formation, Park County, Wyoming. UCMP 120002, tooth, lacking enamel; UCMP Loc. V-72208, Hell Creek Formation, Garfield County, Montana. UW 14095, 14096, two teeth, lacking enamel; UW Loc. V-79032, Lance Formation, Sweetwater County, Wyoming. UCM 7572, basiocipital; Laramie Formation, Weld County, Colorado.

Description

Most of the teeth are worn, have incomplete roots, and a few even lack enamel, suggesting all are shed teeth. The teeth are identified as nodosaurid rather than ankylosaurid because of the basal cingulum on one side of the crown. This cingulum, however, is not well developed on teeth lacking enamel, indicating that it is formed primarily by a ridge of enamel. In anky-

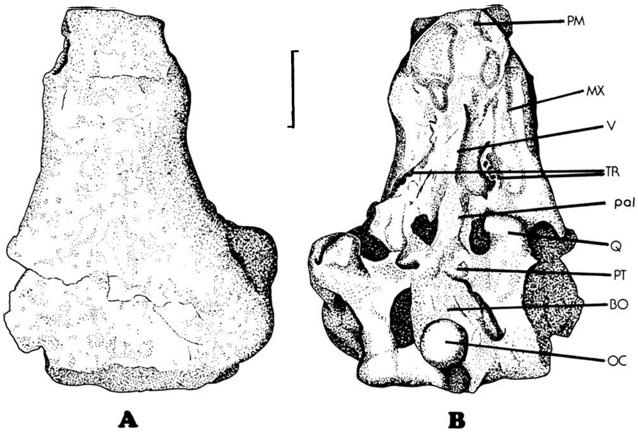

FIGURE 2. Skull of *Edmontonia* sp. (DMNH 468) in **A**, dorsal, and **B**, ventral views. Abbreviations: **BO** = basioccipital; **MX** = maxilla; **OC** = occipital condyle; **PAL** = palatine; **PM** = premaxilla; **PT** = pterygoid; **Q** = quadrate; **TR** = tooth rows; **V** = vomer. Bar = 10 cm.

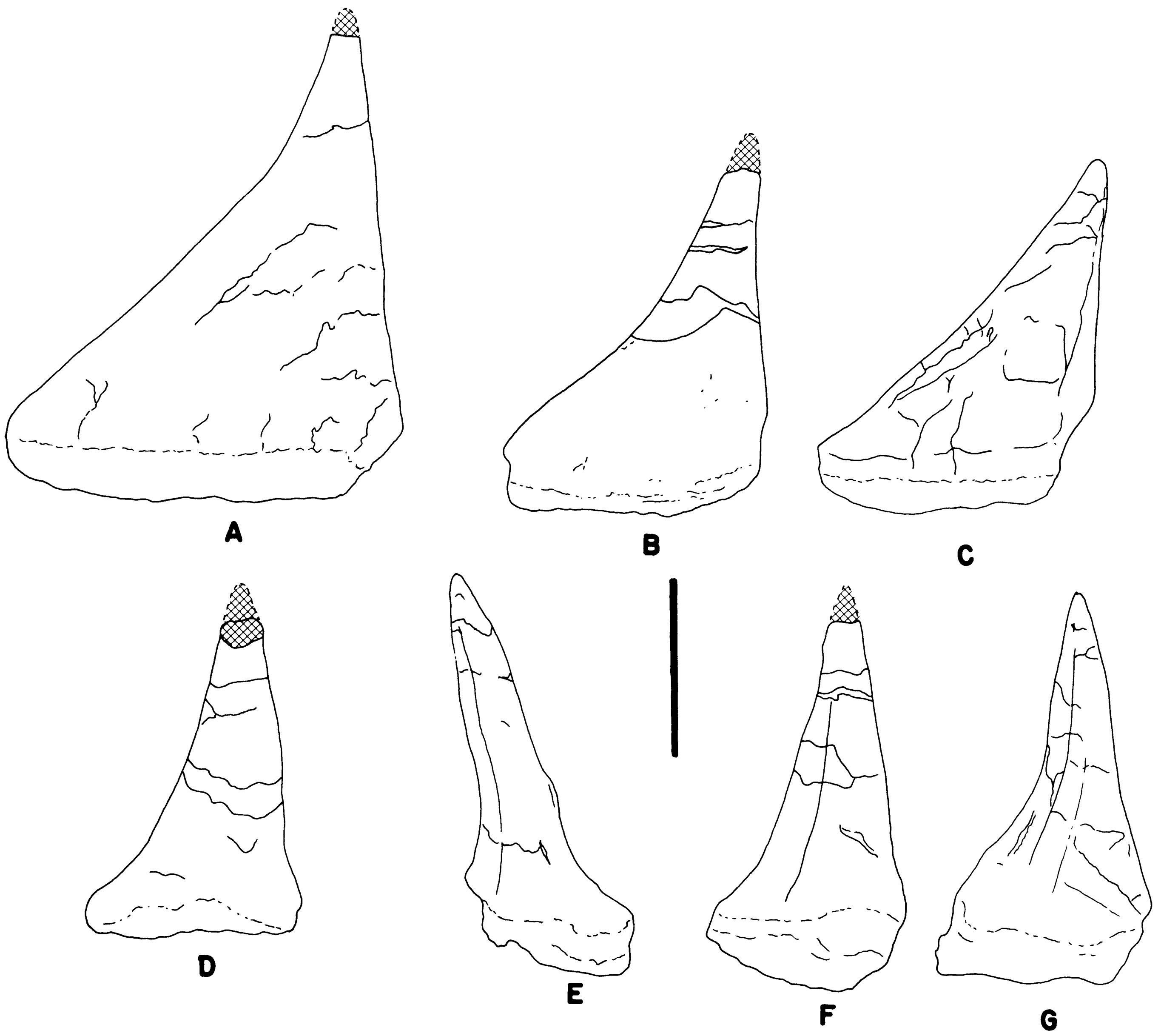

FIGURE 3. First anterolateral cervical spines. AMNH 5665 in **A**, lateral view; USNM 5793 in **B**, lateral, **D**, posterior, and **F**, anterior views; USNM 11868 in **C**, lateral, **E**, posterior, and **G**, anterior views. Bar = 10 cm.

losaurids, the teeth have a greatly swollen base and never a cingulum (Fig. 4A–P).

The basioccipital has a well developed condyle attached to a short neck and is directed obliquely downward as is characteristic of the Ankylosauria (Fig. 5A, B). The length of this condylar neck is longer than seen in *Ankylosaurus,* but is similar to that seen in the nodosaurid *Edmontonia* (compare Fig. 5A, D, and F). Other nodosaurid characteristics of the basioccipital include failure of the exoccipitals to contribute to the dorsolateral corners of the occipital condyle and the spherical shape of the occipital condyle (72 mm wide × 73 mm tall).

There seems to be a high positive correlation (0.98) between condyle width and skull length for three *Edmontonia* specimens for which measurements are available. From this, it is estimated that the basioccipital belonged to an individual having a skull length of 506 mm, making it the largest nodosaurid known if this estimate is correct.

Discussion—*Edmontonia* was described by Sternberg (1928) on the basis of a partial skeleton, including skull, from the Horseshoe Canyon Formation (= Lower Edmonton Formation) of Alberta. Coombs (1978), however, synonymized it with *Panoplosaurus,* based on a specimen described earlier by Lambe (1919). There

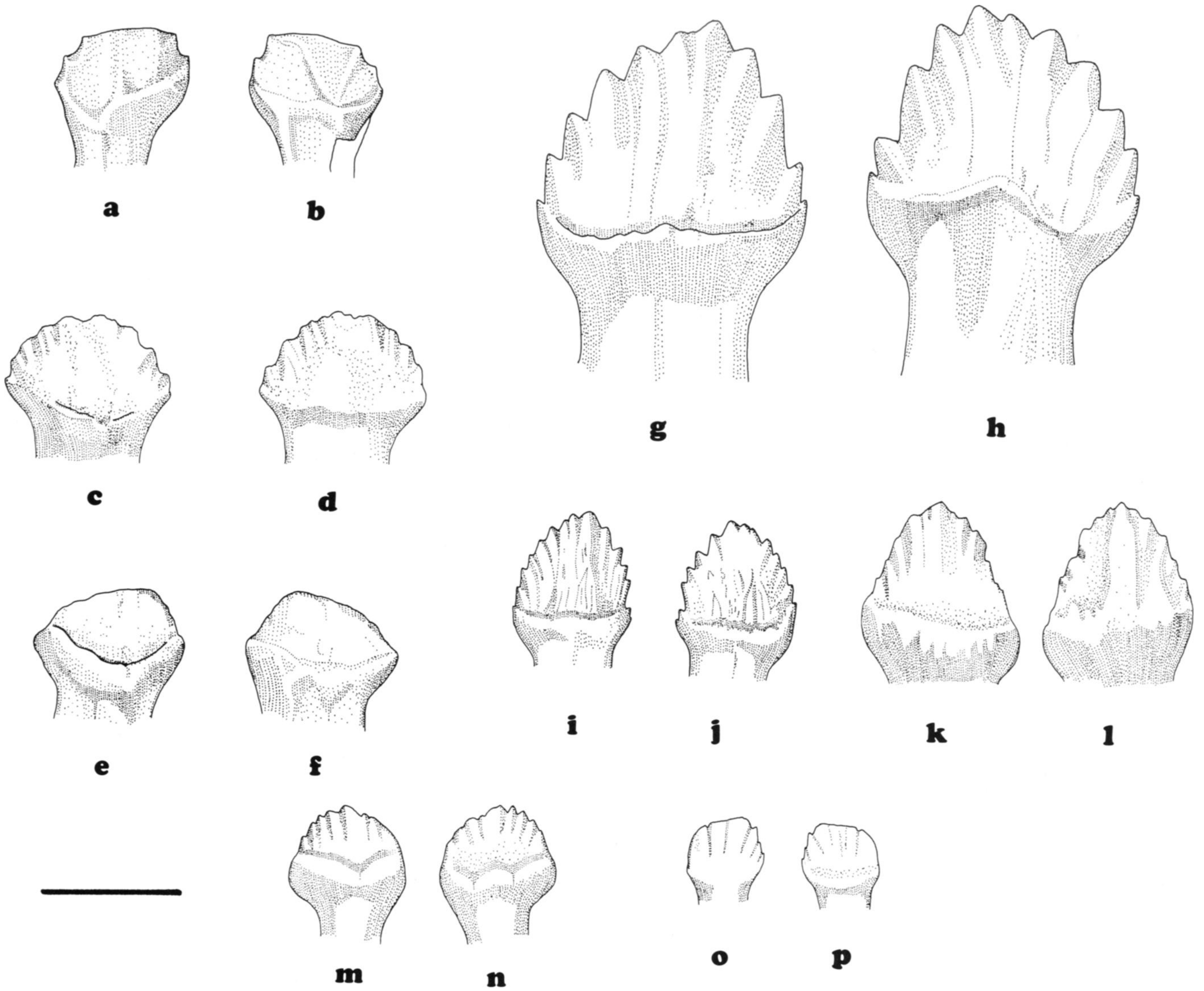

FIGURE 4. Isolated nodosaurid teeth from the Lance Formation, Wyoming, and a comparison of nodosaurid and ankylosaurid teeth. **A**, **B**, and **C**, **D**, enamelous nodosaurid teeth (UCM 48369) from Locality 3; **E**, **F**, nodosaurid tooth (UW 14095) from Locality 6; **G**, **H**, large, unworn *Edmontonia longiceps* tooth associated with Matthew's "*Palaeoscincus*" specimen (AMNH 5665); **I**, **J**, unworn *Euoplocephalus tutus* tooth (AMNH 5337); **K**, **L**, unworn *Ankylosaurus magniventris* tooth (AMNH 5214); **M**, **N**, unworn *Saichania chulsanensis* tooth (GI SPS 100/151; modified from Maryánska, 1977); **O**, **P**, worn *Pinacosaurus grangeri* tooth (ZPAL MgD-II/1; modified from Maryánska, 1977). Bar = 10 mm.

are enough morphological differences between the two genera, however, to regard each as distinct (Carpenter, in prep.). As discussed above, the new skull is assignable to *Edmontonia* and is estimated to be the largest complete skull known for that genus (Table 2). The basioccipital is assigned questionably to *Edmontonia* because the occipital condyle neck is constricted more than seems to occur in *Panoplosaurus* and is similar to that in *Edmontonia.*

The teeth from the Lance and Hell Creek formations are questionably referred to *Edmontonia* because this seems to be the only nodosaurid genus present in these formations. Previously (Carpenter, 1983), these teeth and the skull were incorrectly referred to *Palaeoscincus. Palaeoscincus* is considered a *nomen dubium,* a point that will be discussed further in a review of North American Late Cretaceous nodosaurids (Carpenter, in prep.).

EDMONTONIA AS A TEST OF CATASTROPHIC EXTINCTION

After almost a hundred years of study, the vertebrate faunas of the Lance and Hell Creek formations of the western United States are the best kown of any of their age in the world. Much of the early history of this

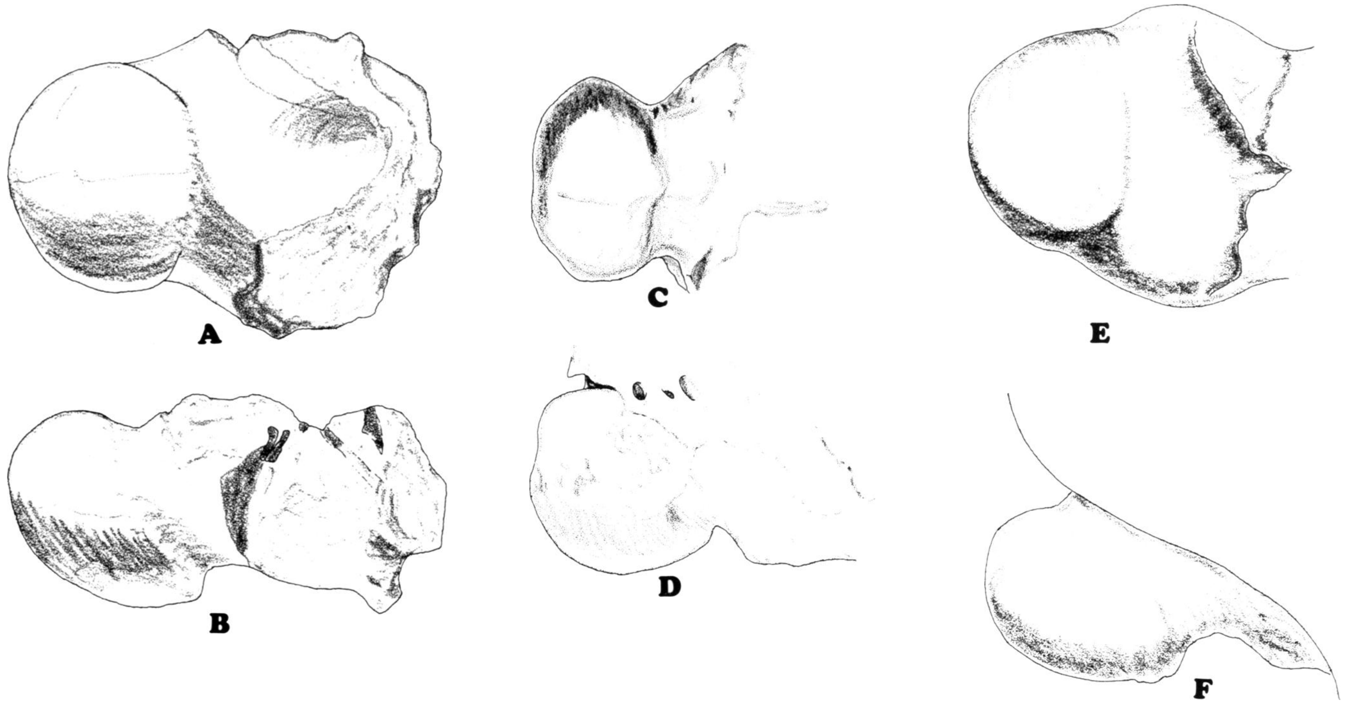

FIGURE 5. Comparison of the basioccipital of ?*Edmontonia* sp., *Ankylosaurus magniventris,* and *Edmontonia longiceps.* ?*Edmontonia* sp. (UCM 7572) in **A**, ventral and **B**, lateral views; *Ankylosaurus magniventris* (AMNH 5214) in **C**, ventral and **D**, lateral views; *Edmontonia longiceps* (AMNH 5665) in **E**, ventral and **F**, lateral views. In **E** the basioccipital tubercles partially hide the large depression in the basioccipital.

collecting, as well as summaries of the faunas, is given by Estes (1964), Russell (1964), Estes et al. (1969), Clemens et al. (1979), Archibald (1981), and Breithaupt (1982).

These faunas have long played an important role in vertebrate paleontology, for they mark the end of the "Age of Dinosaurs". The cause or causes of this extinction have long been a source of debate (early views summarized by Jepsen, 1964; Cloudsley-Thompson, 1978). This debate has been renewed recently with the discovery of iridium concentrations at the Cretaceous–Tertiary boundary (Russell, 1979). The possible asteroid impact as a source for this iridium, and its implication for a catastrophic extinction at the end of the Cretaceous, was first presented by Alvarez et al. (1980). Many of the arguments for and against this hypothesis appear in Silver and Schultz (1982), and are summarized by Van Valen (1984), who remained unconvinced.

Central to many of the catastrophic extinction hypotheses is the apparent sudden extinction of the dinosaurs at the end of the Cretaceous. The argument has basically been that if dinosaur species X occurs within the Hell Creek or Lance formations (late Maastrichtian), but is absent in the overlying Fort Union Formation (Paleocene), species X became extinct at the Cretaceous–Paleocene boundary (e.g. Russell, 1982, 1984). To test this hypothesis two questions need to be asked: what is the stratigraphic distribution of species X in the Lance and Hell Creek formations? Is there any change in relative abundance of species X throughout its stratigraphic range, possibly indicative of a gradual extinction? The discovery of nodosaurid material of known provenance in the Hell Creek, Lance, and Laramie formations permitted us to consider these questions and thereby test the catastrophic extinction model.

Dinosaurs shed many teeth throughout their life, and the relative abundance of teeth should therefore give an indication of the relative abundance of a particular taxon, even if skeletal remains are rare. This permits us to rank dinosaurs from microvertebrate sites solely on the relative abundance of their teeth. By this we mean that species X is more abundant than species Y, which in turn is more abundant than species Z. Minimum numbers of individuals are not implied because not all dinosaurs have the same number of functional

TABLE 2. Length and width measurements for *Edmontonia* skulls.

	AMNH 5665	DMNH 468	NMC 8531	USNM 11868
Length (cm)	43	49.6	49	47
Width (cm)	43	34.6	29	34
Quadrate length (cm)	17	16	11.8	15

TABLE 3. Stratigraphic distribution of Maastrichtian *Edmontonia* specimens.

	County/state	Material	Stratigraphic position (thickness of formation)
1	Garfield County, Montana	teeth	base of Hell Creek Fm. (167 m)
2	Corson County, South Dakota	skull, armor	lower 10 m of Hell Creek Fm. (175 m)
3	Park County, Wyoming	teeth	120 m below unconformity with Fort Union Fm. (up to 426 m)
4	Niobrara County, Wyoming	spine	low in Lance Fm. (762 m)
5	Niobrara County, Wyoming	teeth	low in Lance Fm. and lower 5 m (762 m)
6	Sweetwater County, Wyoming	teeth	30 m below unconformity with Fort Union Fm. (up to 222 m)
7	Weld County, Colorado	basioccipital	Laramie Fm. (91 m)

teeth, and because replacement rates for the teeth of different species are unknown. For example, a hadrosaur has more functional teeth at any given moment than a nodosaur, and thus has the potential of contributing a far greater number of teeth to the fossil record. However, neither animal is sessile, and teeth shed by replacement should be spread more or less randomly throughout the animal's feeding range. For species with higher population levels (hadrosaurs and ceratopsians) as determined by skeletal remains, the number of fossil teeth found is correspondingly higher.

We have tested our hypothesis by comparing the relative abundance of isolated nodosaurid teeth with skeletal material in Campanian and Maastrichtian vertebrate collections at AMNH, NMC, ROM, TMP, UCMP, and USNM. As expected, isolated teeth are several orders of magnitude more common in Campanian sediments (mostly Judith River Formation), than in Maastrichtian sediments (Lance and Hell Creek formations). That this decrease is not the result of an ecological shift in *Edmontonia* is indicated by the apparent absence of any morphological difference between the Lancian and Judithian material (Carpenter, in prep.), and that the Judith River, Hell Creek, and Lance formations represent similar environments on a coastal plain. We therefore conclude that the scarcity of teeth and skeletal material of nodosaurids in the Lance and Hell Creek formations reflect a real and substantial decrease in population levels of nodosaurids during the Lancian.

We should not assume that because nodosaurids (*Edmontonia*) are present in Lancian sediments they persisted to the end of the Cretaceous. The stratigraphic distribution of the material discussed above is restricted to the lower Lance and Hell Creek formations, and to the Laramie Formation, which is laterally equivalent to the lower Lance. This distribution is significant because most vertebrate collections have been made in the upper half of the Lance and Hell Creek formations (Clemens et al., 1979). Although we are aware of the dangers of using last occurrences, we believe that the absence of nodosaurids stratigraphically high in Lancian deposits is real and not an artifact of collecting. For example, of 526 UCMP localities sampling the Hell Creek Formation in eastern Montana, only a single nodosaurid tooth is known from a locality (UCMP 77208) that is stratigraphically low. This implies that nodosaurids became extinct well before the end of the Cretaceous.

CONCLUSION

With the discovery of nodosaurid material from the Lance, Hell Creek, and Laramie formations, the stratigraphic distribution of the Nodosauridae has been extended from the Campanian to Maastrichtian. All of the material is referable to *Edmontonia* sp., a genus previously known only from the Judith River (= Oldman) and Horseshoe Canyon (= Edmonton) formations of Alberta, and the Two Medicine Formation of Montana.

The relative abundance of nodosaurids in the Upper Cretaceous of North America indicates that they reached their greatest abundance during the Campanian. After this, they declined in relative abundance, and apparently became extinct during the Maastrichtian, but well before the end of the Cretaceous. The data suggest that this extinction occurred in the first half of the Lancian. We predict that careful analysis of macro- and microvertebrate localities in the Lance and Hell Creek formations will show a stratigraphic decrease in the relative abundance of various other dinosaur species towards the Cretaceous–Tertiary boundary. In addition, we predict that the diversity of dinosaur species near the boundary will prove to be drastically reduced. This latter hypothesis is supported by the fact that in UCMP collections, thirteen dinosaur localities within three meters of the Z coal (which Z coal was not always known) produced only an unidentifiable small theropod, *Paronychodon,* an hadrosaur, a ceratopsian, *Thescelosaurus,* and *Tyrannosaurus.* Most, but not all of the specimens were teeth. In ranked abundance from the most abundant to the most rare are ceratopsian, hadrosaur, small theropod, *Tyrannosaurus, Paronychodon,* and *Thescelosaurus* (one specimen). Additional work will probably increase this diversity and change the relative abundance rank of some taxa. Nevertheless, we believe the diversity and relative abundance of many dinosaurs will not approach that seen in the lower part of the Hell Creek Formation.

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