

- Suppl. 348, 1 (1970); R. Y. Moore, *Exp. Neurol.* 49, 617 (1975); T. Ebendahl, L. Olson, A. Seiger, K.-O. Hedlund, *Nature (London)* 286, 25 (1980).
12. W. D. Matthew and A. W. Sandrock, *Soc. Neurosci. Abstr.* 11, 1254 (1985).
 13. C. Sachs, *Acta Physiol. Scand. Suppl.* 341, 1 (1970); in *6-OHDA and Catecholamine Neurons*, T. Malmfors and H. Thoenen, Eds. (North-Holland, Amsterdam, 1971).
 14. P. J. Finn *et al.*, *J. Neurocytol.* 15, 169 (1986); R. A. Murphy *et al.*, *Dev. Biol.* 114, 369 (1986).
 15. R. W. Gundersen, *J. Neurosci. Res.* 13, 199 (1985); A. W. Sandrock, W. D. Matthew, *Brain Res.*, in press.
 16. The level of norepinephrine uptake by explanted irides is an accurate measure of the density of its sympathetic innervation if it is assayed when the uptake rate is constant. Therefore, the rate of uptake of 0.1 μ M [3 H]norepinephrine into irides was determined. The level of norepinephrine uptake was linear for incubation periods up to 40 minutes. Thus, we assayed irideal norepinephrine uptake during a 30-minute incubation period to maximize the signal while remaining within the linear portion of the curve.
 17. J. C. de la Torre and J. W. Surgeon, *Histochemistry* 49, 81 (1976).
 18. Hybridomas were maintained in logarithmic growth in L15-CO₂ medium supplemented with 0.6% glucose, 2 mM glutamine, penicillin (100 U/ml), streptomycin (100 U/ml), and 10% fetal calf serum, until the time of transplantation. The cells were washed twice with serum-free L15 medium and resuspended in a small volume of serum-free medium (supplemented with the same concentrations of glucose, glutamine, and antibiotics) at a final concentration of 10⁷ to 10⁸ cells per milliliter. Male albino Sprague-Dawley rats weighing 175 to 225 g were each anesthetized with halothane U.S.P. (Halocarbon Labs.) and placed under a dissecting microscope. After a corneal reflex could no longer be elicited, a clean 10- μ l glass syringe equipped with a 33-gauge needle (Hamilton) was used to puncture both corneas. For each eye, the extruded aqueous humor was wiped from each eye, and the same syringe was filled to capacity with a suspension of the appropriate hybridoma cells. Approximately 10⁵ hybridomas were injected into the anterior chamber of one eye through the original puncture wound in about 5 μ l, immediately followed by the injection of about 0.5 μ l of air (the air bubble in the anterior chamber lodges in the puncture wound and prevents the cell suspension from leaking out of the eye). One eye received experimental hybridoma cells—those secreting a function-blocking monoclonal antibody (either INO or RN3B3)—while the contralateral eye received control hybridomas (RN1A2). One week after hybridoma injection, the rats were anesthetized with halothane and both eyes were examined under a dissecting microscope for signs of tissue damage, as well as for the presence of characteristic clumps of growing hybridoma cells. Only those rats with apparently normal eyes containing visible clumps of hybridoma cells in the anterior chambers of both eyes were retained for sympathectomy. Each rat was injected intraperitoneally with 6-OHDA · HCl (100 mg/kg, Sigma) freshly dissolved in 0.05% ascorbic acid, 0.9% NaCl. Only those rats that exhibited marked ptosis of the eyelids on the next day were considered adequately sympathectomized and retained for further study.
 19. Expert assistance was provided by J. Gagliardi and M. LaFratta. We thank many colleagues for helpful discussions, especially E. Furshpan, S. Landis, P. Patterson, and D. Potter. Supported by research grant NS02253 from the National Institutes of Health, and aided by a McKnight Foundation Scholars Award, an Alfred P. Sloan Foundation Fellowship, and Basil O'Connor Starter Research Grant 5-523 from the March of Dimes Birth Defects Foundation. A.W.S. is the recipient of Public Health Service, National Research Service Award 2T 32 GM07753-07 from the National Institute of General Medical Sciences. In all cases, procedures performed on animals and the care of animals were in accordance with the guidelines of Harvard Medical School.

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Dinosaurs on the North Slope, Alaska: High Latitude, Latest Cretaceous Environments

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Abundant skeletal remains demonstrate that lambeosaurine hadrosaurid, tyrannosaurid, and troodontid dinosaurs lived on the Alaskan North Slope during late Campanian–early Maestrichtian time (about 66 to 76 million years ago) in a deltaic environment dominated by herbaceous vegetation. The high ground terrestrial plant community was a mild- to cold-temperate forest composed of coniferous and broad leaf trees. The high paleolatitude (about 70° to 85° North) implies extreme seasonal variation in solar insolation, temperature, and herbivore food supply. Great distances of migration to contemporaneous evergreen floras and the presence of both juvenile and adult hadrosaurs suggest that they remained at high latitudes year-round. This challenges the hypothesis that short-term periods of darkness and temperature decrease resulting from a bolide impact caused dinosaurian extinction.

CLOSELY RELATED LATE CRETACEOUS (about 66 to 76 million years before the present) terrestrial vertebrates found in mid-latitudes of North America and Asia suggest that Alaska was part of an intercontinental route of dispersal and supported diverse faunas (1). Until recently, dinosaurian footprints and skin impressions were the only published records of Alaskan Late Cretaceous terrestrial vertebrates (2). The first discovery of dinosaurian bones in Alaska was made in 1961 by the late R. L. Liscomb at a site on the Colville River. The significance of his discovery went unnoticed until 1984 when Liscomb's collection was sent to C. A. Repenning, who recognized that the collection documented an exceptionally high latitude occurrence of dinosaurs and forwarded the material to W. Langston, Jr., for further study (3).

Dinosaur-bearing sediments crop out in bluffs (Fig. 1) along the Colville River (4, 5) and are part of the type section of the upper Kogosukruk Tongue, Prince Creek Formation, upper Colville Group (6). This unit is composed of delta plain silts, channel sands, local stringers of coal, beds of tephra, and nearshore marine sands and silts (7). Skeletal remains of dinosaurs are preserved at six known stratigraphic levels and within three distinct fault blocks (Fig. 2). The precise stratigraphic relationships of strata between these fault blocks are not known (8).

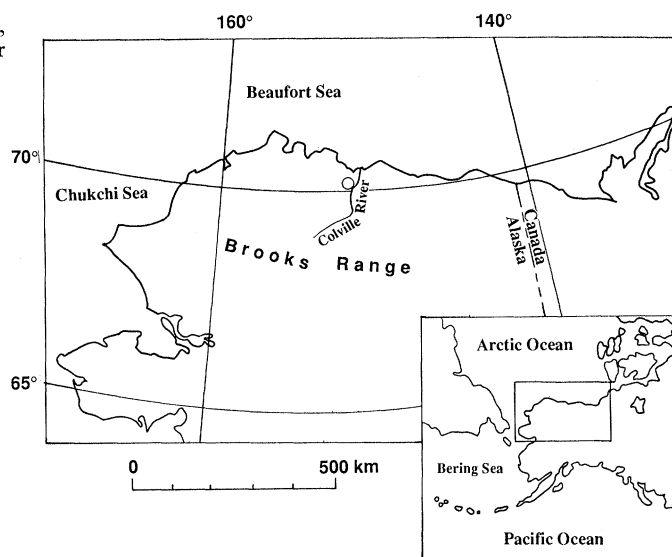
The bone bed discovered by Liscomb ranges from 0.5 to 1.0 m in thickness. The

disarticulated dinosaur bones are remarkably well preserved, and, except for post-depositional breakage, are not distorted. The bones are stained dark brown to brownish black, with rare permineralization. They are size-sorted, with the largest elements and densest concentration near the base of the bed. The matrix is a dark brown, carbonaceous siltstone containing scattered calcareous concretions; both lithologies contain large amounts of plant debris and roots, but rare fossil wood. Total organic carbon content of the siltstone is high and dominated by terrestrial carbon sources (9). The bone bed shows an abrupt lateral facies change northward into a lighter colored siltstone that contains no bones and has markedly less plant debris. Three other bone-bearing horizons consist of similar carbonaceous, dark brown siltstones with concretions, these three organic-rich beds and the Liscomb bone bed are thought to represent soils (8). The remaining two bone-bearing horizons are in sand and represent fluvial channel lag deposits (8). All of the bone beds are laterally discontinuous, ranging from 25 m to more than 100 m in horizontal extent (8).

Most identifiable vertebrate fossils are remains of lambeosaurine hadrosaurids (holow-crested duck-bill dinosaurs). No skeletal elements diagnostic at the genus or species level have been recovered. Some bones are parts of the skeletons of individuals as large as an adult *Parasaurolophus* or *Corythosaurus* (about 9 to 10 m in length); others represent individuals one-half to one-third the size and show morphological traits of juvenile individuals. Carnivorous or scavenging dinosaurs are represented by isolated teeth of a tyrannosaurid and *Troodon*. In lower latitudes the known stratigraphic ranges of these dinosaurs fall within the Upper Cretaceous. To date, remains of other kinds of vertebrates have not been found; we have yet to determine whether the absence of

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Fig. 1. North Slope, Alaska, showing the Colville River locality (circle).



non-dinosaurian vertebrates reflects the composition of the fauna, a taphonomic bias, or an artifact of the initial collections.

Charophytes and nonmarine ostracodes are relatively common in association with the bone-bearing strata. Most of the charophytes are a species of *Microchara*, a genus common in Late Cretaceous to lower Eocene sediments of the Western Interior and northern Europe; a few specimens are referable to *Mesochara*, a genus restricted to the Cretaceous (10). Ostracode taxa include *Bisulcocypridea* spp., common in Late Cretaceous to lower Eocene sediments of North America (11, 12), *Cypridea* sp., found in Jurassic to Cretaceous sediments worldwide (12), and ?*Candonopsis*.

An abundant, low diversity arenaceous foraminifer assemblage occurs in the siltstone immediately below the Liscomb bone bed (Fig. 2); rare arenaceous foraminifers occur just above. The foraminifer assemblage includes *Verneulinoides fischeri*, *Trochammina albertensis*, small globular forms referred to *T. cf. T. albertensis*, *T. diagonis*, *Reophax texanus*, and *Ammomarginulina* sp., and correlates with faunas from the Upper Cretaceous Sentinel Hill Member, Schrader Bluff Formation of northern Alaska, primarily of late Campanian age (13). Correlative assemblages from well-dated sequences in Alberta, Saskatchewan, and Manitoba range from late Campanian to early Maestrichtian in age (14).

Fossil pollen and spores from the Liscomb bone bed and from six samples between 1.8 m below and 7.5 m above it contain numerous Late Cretaceous pollen types, including *Porosipollis porosus*, *Senipites drumhellerensis*, *Callistopollenites* spp., *Aquilapollenites rectus*, *A. delicatus*, *A. laticarpus*, *Cranwellia* sp., and several "oculata" types; the latter include *Wodehouseia edmontonicola*,

Azonia cribrata, and *A. pulchella*. The known biostratigraphic ranges of these taxa (15) suggest that the age of the bone bed is most likely early Maestrichtian.

In summary, the available biostratigraphic evidence supports the interpretation that the dinosaur-bearing beds are of Late Cretaceous age, most likely late Campanian to early Maestrichtian.

A freshwater, low energy fluvial environment, which probably includes small ponds or oxbows, is indicated from the ostracode and charophyte assemblages. The presence of arenaceous foraminifers suggests a direct connection of the fluvial system with marine waters and confirms the close proximity of the early Arctic Ocean. The foraminifers indicate very low salinities, approaching freshwater conditions, and are interpreted as representing marginal marine paleoenvironments consisting of salt marsh or brackish water interdistributary embayments adjacent to a broad, flat delta plain.

The palynomorphs and megaflores indicate that low ground on the delta plain was dominated by an herbaceous ground cover consisting predominantly of *Equisetites* and ferns, with a smaller, but diverse, component of herbaceous angiosperms. The rivers, ponds, and oxbows contained a low diversity assemblage of emergent and subaquatic vegetation. High ground on the delta plain probably included small stands of deciduous coniferous trees (mostly forms related to *Metasequoia*). Upstream from the lower delta plain, the megaflores were dominated by deciduous gymnosperms and represent a mild- to cold-temperate deciduous forest. This vegetation was dominant from Alaska to as far south as the latitude of northern Montana (16), which marks the northernmost contemporaneous evergreen vegetation. The deciduousness probably can be

attributed to the absence of, or greatly reduced, winter light (16). Preliminary estimates based on megaflores suggest that the Maestrichtian North Slope was characterized by annual temperatures that ranged from a warmest month mean of 10° to 12°C to a coldest month mean of 2° to 4°C (16). The occurrence of frost was therefore likely, but periods of weeks or months of subfreezing conditions are doubtful. Estimates of mean annual temperature as cold as 2° to 6°C with a coldest mean month of -11°C have been proposed (17), but the nonmarine microfauna and mollusks are incompatible with these temperatures.

Estimates of paleolatitude for this area during Cretaceous time are as much as 15° farther north than present, ranging from 70° to 85°N, on the basis of paleomagnetic data and tectonic reconstructions (18), suggesting that the dinosaurs and associated organisms lived as much as 18° north of the Maestrichtian Arctic Circle. Weeks, or more probably months, of total darkness occurred on a seasonal basis at these latitudes.

The deciduous nature of most of the endemic flora would result in an annual period of stress for herbivorous hadrosaurids, during which they had to cope with a greatly decreased food supply either by seasonal migration (19) or by overwintering at reduced levels of activity. The presence of young hadrosaurids suggests year-round residency rather than migrations over great distances. Subaquatic rhizome-mat vegetation, branches of woody ground cover vege-

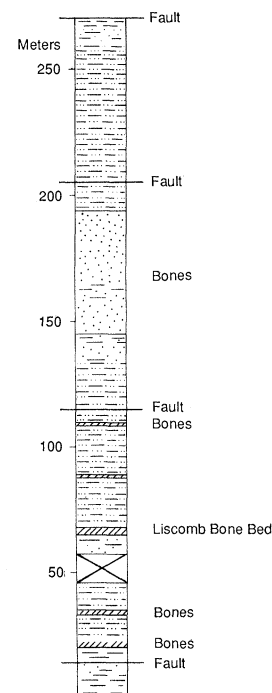


Fig. 2. Schematic stratigraphic column showing six bone-bearing horizons in deltaic silts and channel sands of the upper Kogosukruk Tongue.

tation, and perhaps some evergreen conifers could have provided a source of food during the winter. Many of the palynomorph taxa represent plants of unknown affinity that may also have provided a year-round source of food for the hadrosaurids. Hadrosaurs had well-developed dentitions capable of coping with diverse feeding habits to accommodate available forage (20). Their wide muzzles with upper and low horny rhamphothecae (pads) might have been useful in stripping off leaves from branches or shrubs or in rooting up and pulling off pieces of rhizome mats. The massive dental battery could accommodate large amounts of tooth wear, a consequence of eating subaquatic rhizome mats full of silt, mud, and abrasive, silica-rich *Equisetites* vegetation.

Current hypotheses suggesting an extra-terrestrial cause of the extinction of dinosaurs, such as an asteroid's impact (21), invoke lethal effects that include a period of darkness lasting a few weeks or months and a great decrease in ambient temperature. If the North Slope dinosaurs were not migratory, their occurrence at high northern, Late Cretaceous latitudes provides direct evidence of the ability of some species to tolerate up to several months of darkness and to cope with cold air temperatures. Thus, some of the proposed effects of impacts of an asteroid or comets, increased volcanism, or related hypotheses may not have been the direct cause of the demise of the dinosaurs.

REFERENCES AND NOTES

1. D. B. Weishampel, in preparation; A. R. Milner and D. B. Norman, in *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, W.-E. Reif and F. Westphal, Eds. (ATTEMPTO Verlag, Tübingen, 1984), pp. 145–150.
2. H. Roehler and G. Stricker, *J. Alaska Geol. Soc.* **4**, 35 (1984).
3. K. Davies, *J. Paleontol.* **61**, 198 (1987).
4. Liscomb's site was relocated in 1984 and 1986 by E.M.B., L.D.C., and T.A.A., who collected additional vertebrate fossils and sediments that have yielded microfossil assemblages. In 1985, a field party under W.A.C. made extensive collections of vertebrate fossils. Locality data are on file at the U.S. Geological Survey (Reston, VA; Denver, CO; and Menlo Park, CA); the Museum of Paleontology, University of California, Berkeley; and the Museum, University of Alaska, Fairbanks. The National Museum of Natural History, Washington, DC, will be the final repository of the collections. Some of the 1985 collections are curated in the Museum, University of Alaska, Fairbanks.
5. W. A. Clemens and C. W. Allison, *Abstr. Programs Geol. Soc. Am.* **17**, 548 (1985).
6. W. P. Brosge and C. L. Whittington, *U.S. Geol. Surv. Prof. Pap.* **303-H** (1966), p. 501.
7. Several tephra layers below the stratigraphically lowest dinosaur occurrence are being analyzed by means of K-Ar, ³⁹Ar-⁴⁰Ar, fission-track, and chemical characterization. One of these tephra has yielded a fission-track age of 50.9 ± 7.7 million years, now considered a minimum age [L. D. Carter et al., *U.S. Geol. Surv. Circ.* **751-B** (1971), p. B12].
8. Based on 1986 field studies by E.M.B., L.D.C., R. L. Phillips, and L. Marinovich.
9. Total organic carbon (TOC) analyses of sediments associated with the Liscomb bone bed indicate an average of 6.85% TOC for the bone bed and concretions, 1.05% TOC for the siltstone immediately above the bone bed, and 0.58% TOC for the siltstone immediately below the bone bed (analyses provided by J. T. Parrish).
10. M. Feist and N. Grambast-Fessard, *Paleobiol. Continent.* **13**, 1 (1982).
11. F. P. C. M. van Morkhoven, *Post-Palaeozoic Ostracoda* (Elsevier, Amsterdam, 1963).
12. T. D. Fouch et al., in *1979 Basin and Range Symposium*, G. W. Newman and H. D. Goode, Eds. (Rocky Mountain Association of Geologists, Denver, CO), pp. 305–312.
13. H. Tappan, *U.S. Geol. Surv. Prof. Pap.* **236-C** (1962).
14. W. G. E. Caldwell et al., *Geol. Assoc. Canada Spec. Pap.* **18** (1978), p. 495; D. H. McNeil and W. G. E. Caldwell, *Geol. Assoc. Canada Spec. Pap.* **21** (1981).
15. N. O. Frederiksen, in *Am. Assoc. Stratigr. Palynol. Program Abstr. 19th Annu. Meeting* (1986), p. 11; V. D. Wiggins, *Geosci. Man.* **15**, 51 (1976); B. D. Tschudy, *U.S. Geol. Surv. Prof. Pap.* **643-A** (1969).
16. J. A. Wolfe and G. R. Upchurch, Jr., *Palaeogeogr. Palaeoclim. Palaeoecol.*, in press; R. A. Spicer and J. T. Parrish, *Geology* **14**, 703 (1986).
17. J. T. Parrish et al., *Abstr. Programs Geol. Soc. Am.* **19**, 326 (1987).
18. W. K. Witte et al., in *North Slope Geology*, I. L. Tailleux and P. Weimer, Eds. (Society of Economic Paleontologists and Mineralogists, Tulsa, OK, in press); L. D. Carter and J. W. Hillhouse, unpublished paleomagnetic data.
19. D. I. Axelrod, *Palaeogeogr. Palaeoclim. Palaeoecol.* **45**, 105 (1984); R. T. Bakker, *Sci. Am.* **232**, 58 (April 1975); N. Hutton, in *A Cold Look at Warm-Blooded Dinosaurs*, R. D. K. Thomas and E. C. Olson, Eds. (American Association for the Advancement of Science, Washington, DC, 1980), pp. 311–350.
20. D. B. Weishampel, *Adv. Anat. Embryol. Cell Biol.* **87**, 1 (1984); R. Krausel, *Palaeont. Z.* **4**, 80 (1922).
21. L. W. Alvarez, W. Alvarez, F. Asaro, H. V. Michel, *Science* **208**, 1095 (1980); W. Alvarez, *Eos* **67**, 649 (1986).
22. We thank R. Emmons (Shell Oil Company) for his assistance in relocating the late R. L. Liscomb's field notes and collections. W. Langston, Jr., and K. Davies (University of Texas) made available their analyses of Liscomb's collection and a preprint of Davies' paper. The assistance of P. Currie (Tyrrell Museum, Drumheller, Alberta) and J. Horner (Museum of the Rockies, Bozeman, MT) with identifications and discussions of ontogenetic change in dinosaurs is gratefully acknowledged. C. A. Repenning (U.S. Geological Survey, Denver, CO) and D. Weishampel (Johns Hopkins University) provided insights on hadrosaur jaw and tooth structure and possible seasonal food sources. Fieldwork for W.A.C. during 1985 was supported by USGS grant 14-08-0001-G-1122. Funding for 1986 fieldwork for R.A.S. was provided by British Petroleum.

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Identification of a Novel Thyroid Hormone Receptor Expressed in the Mammalian Central Nervous System

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A complementary DNA clone derived from rat brain messenger RNA has been isolated on the basis of homology to the human thyroid hormone receptor gene. Expression of this complementary DNA produces a high-affinity binding protein for thyroid hormones. Sequence analysis and the mapping of this gene to a distinct human genetic locus indicate the existence of multiple human thyroid hormone receptors. Messenger RNA from this gene is expressed in a tissue-specific fashion with highest levels in the central nervous system.

THYROID HORMONES ARE INVOLVED in a complex array of developmental and physiological responses in many tissues of higher vertebrates (1). Their numerous and diverse effects include the regulation of important metabolic enzymes, hormones, and receptors (2). The actions of thyroid hormones are mediated through a nuclear receptor, which modulates the expression of specific genes in target cells (3–5). These properties are similar to the interactions of steroid hormones with their receptors and are consistent with the recent observation of structural relatedness between steroid and thyroid hormone receptors (6).

Despite the diversity of thyroid hormone action, it is generally accepted that thyroid hormone function occurs through a single high-affinity nuclear receptor. However, the

recent characterization of the thyroid hormone receptor as the cellular homolog of the *v-erbA* oncogene product (6, 7), along with the previous identification of multiple *c-erbA* genes on human chromosomes 3 and 17 (6, 8), predicts the existence of multiple thyroid hormone receptors. To examine the possibility that the mechanisms underlying the multiple thyroid hormone responses

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