

Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and a description of a new species of theropod

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ABSTRACT

Published accounts of very young or baby dinosaurs suggest that such remains are rare in the fossil record. The use of screen-washing in the Late Cretaceous Lance and Hell Creek formations in Wyoming and Montana, however, has produced small teeth and cranial elements which are identified as from baby dinosaurs. At least eleven taxa from nine localities are represented: a dromaeosaurid, an unidentifiable theropod, a tyrannosaurid, a ceratopsian, a hadrosaur, *Saurornithoides inequalis*, *Pectinodon bakkeri* new genus and species, *Aublysodon mirandus*, *Paronychodon lacustris*, *Thescelosaurus* sp., and *Ankylosaurus magniventris*. The abundance and diversity of remains of baby dinosaurs evidenced by this study suggest that they are not as rare as previously thought. Nevertheless, they are not as abundant as the remains of adults. The present global distribution of remains of baby dinosaurs and dinosaur egg shells suggests paleoenvironmental controls. The two most important controls are believed to be soil drainage and soil pH.

INTRODUCTION

The apparent scarcity of juvenile dinosaurs in the fossil record has been explained by two hypotheses. Matthew (1915) and Sternberg (1955) suggested that nurseries, where eggs were laid and the young matured, were in "upland" areas which are seldom preserved in the sedimentary record. As the dinosaurs matured, they migrated to the coastal plain and deltaic areas where sedimentation was rapid. In such areas, adult dinosaurs had a better chance of fossilization after death. Alternatively, Richmond (1965) suggested that dinosaurs had very long life spans, analogous to certain modern reptiles (e. g., tortoises). With such longevity, the annual replacement rate was on the order of one percent or less. Low replacement rates, high egg and juvenile mortality, and the vagaries of fossilization would result in the apparent underrepresentation of juvenile dinosaurs.

It is not possible to test Richmond's hypothesis because the life span, growth rate, reproductive age, and net reproductive rate of dinosaurs are unknown, despite Case's (1978) attempt. Furthermore, these factors probably differed considerably if the dinosaurs were endothermic rather than ectothermic. It is possible, however, to test the Matthew-Sternberg hypothesis. Horner and Makela (1979) reported numerous dinosaur nests and remains of baby dinosaurs from parts of the Two Medicine Formation of central Montana. This area, they maintain, is an "upland" breeding site since the shoreline of the Late Cretaceous epeiric sea was hundreds of kilometers to the east. It then becomes necessary, however, to explain the existence of baby dinosaur material used in the present study, which were recovered from the coastal plain sediments of the Lance and Hell Creek formations. A possible solution is that dinosaurs living on the coastal plains did not migrate to "upland" breeding sites, but laid their eggs on the better-drained "interfluvial" parts of the floodplains (Dodson, 1971). This implies that dinosaurs, whether of an "upland" community or a "lowland" community, laid their eggs wherever soil conditions were suitable.

An objection to the idea of dinosaurs nesting on the coastal plain is that dinosaur egg shells are much less

abundant in the Lance and Hell Creek formations than in the Two Medicine Formation (J. R. Horner, *personal communication*). Although it is possible that some dinosaurs may have been viviparous or may have laid eggs with an easily decomposed leathery shell, it is doubtful that such dinosaurs were restricted to the coastal plain environments while dinosaurs with calcareous shells were restricted to the "uplands."

In order to present an alternative hypothesis to explain the scarcity of fossilized dinosaur egg shells in the Lance and Hell Creek formations, it is necessary to examine the depositional environments represented; what taphonomic processes, if any, were operating to control the distribution of egg shells? Although detailed lithological data are not available for either the Lance or Hell Creek formations, gross sedimentological studies (such as Clemens', 1963) permit speculations about the depositional environment. The dominant lithological units in the Lance and Hell Creek formations are light to drab-colored, often calcareous, medium- to fine-grained sandstone, light to dark grey, fissile, poorly-indurated siltstone, and light brown to dark grey or even purple mudstone. Other lithological units, such as coarse sand and lithic conglomerate, are also present, but in minor amounts. Two exceptions are thin, laterally discontinuous lignites and lignitic shales or fissile siltstone. Much of the coloration, especially of the finer-grained sediments, is due to plant debris, while that of the sandstones is due to iron hydroxide (limonite and goethite) and iron oxide (hematite and possibly some magnetite). Pyrite and siderite may also color the sediments, although they often break down into iron hydroxides and iron oxides.

The dominance of drab and somber colored sediments, the abundance of disseminated plant debris and lignite, and the presence of pyrite and siderite indicate that the depositional environment was reducing (low Eh). This can be interpreted best as poorly drained, often water-logged soils with numerous marshes or backswamps. In such moist and humid environments, subaerial decomposition of leaf litter can lower the soil pH to as low as 2.8 (Richards, 1964) or 3.5 (Krauskopf, 1967), while in subaquatic environments anaerobic de-

composition can produce pH levels as low as 3.2 (see Table 1). These low pH levels are the result, especially, of the formation of carbonic and sulfuric acids (Chenery, 1954; Garrels and Christ, 1965; see Mohr and others, 1972, for a complete list of the acids produced). Volumetrically, carbonic acid is the most abundant acid produced due to the large amounts of CO₂ given off by bacterial formation and decomposition of methane. ZoBell (1964) reported that in subaqueous environments up to 85 percent of the volume of the upper sediment layer may be occupied by bacterially-produced methane, yet only a small part of this escapes decomposition by bacteria in the overlying water.

In the sediments, microbial activity decreases with depth as the free oxygen is used up and weak bacterial decomposition of organic material produces ammonia. This ammonia causes a rise in pH and a lowering of the Eh to negative values (Borchert, 1960), permitting the precipitation of various carbonate minerals. Coleman (1966) reported syngenetic carbonate nodules (calcium, manganese, magnesium, calcium-magnesium, and iron carbonates) about four meters below the surface of a modern poorly-drained swamp. The depth at which the minimum pH is reached, however, depends upon the concentration of organic material in the sediment; the less the concentration, the deeper the minimum pH curve (Borchert, 1960).

It was probably in the upper few centimeters or meters of the sediment where minimum pH levels are at-

tained and that destruction (by decalcification) of dinosaur egg shells and bones occurred. Partial and complete decalcification of bone has been reported in some Iron Age human bodies recovered from peat bogs in northern Europe. The best example is the Damendorf Man, of whom only the skin and leather belt and shoes are preserved, the entire skeleton having been removed by decalcification (Glob, 1971). Eyre (1964) reports that many of the northern peat bogs drop below pH 4.

To verify the hypothesis that acids produced by the decomposition of plant debris is enough to destroy calcareous egg shells as well as bone, I placed chicken egg shell fragments in a semi-closed container of water (to maintain anaerobic conditions and minimize water loss) and shed leaf debris (cottonwood, *Populus deltoides*, and peach, *Prunus persica*). After sixty days at room temperature, the pH had dropped from 7 to 6.6. Examination of the egg shells under a microscope revealed that dissolution had begun, especially at the corners of the broken edges. Thus, it would appear that severe pH levels are not needed for the dissolution of calcareous egg shells. However, it is not known if the pH had dropped below 6.6 at any time during the sixty days since daily and hourly pH readings were not made. Further tests using different leaf litter, especially of trees and shrubs similar to those living during the Late Cretaceous, are needed with close monitoring of pH levels.

Table 1 lists pH values for some modern tropical and subtropical environments similar to those believed

TABLE 1. PH VALUES FROM SOME MODERN TROPICAL AND SUBTROPICAL ENVIRONMENTS.

pH ¹	Environment/Location	Reference
2.8-6.1 (S)	forest, Borneo	Richards, 1964
2.7-6.1 (S)	forest, Bangha	Richards, 1964
3.2-4.9 (S)	peat swamp, Malaya	Parberry and Venkatchalam, 1964
3.5-4.9 (W)	blackwater, Malacca	Johnston, 1968
3.6-4.3 (S)	evergreen hardwood swamp, Florida	Monk, 1966
3.6-5.2 (W)	Congo tributaries, Africa	Marlier, 1973
3.6-5.4 (S)	cypress heads, Florida	Monk and Brown, 1965
3.8-6.8 (S)	deciduous hardwood swamp, Florida	Monk, 1966
4-5.4 (W)	Rio Negro River, Brazil	Williams, 1968
< 4.5 (S)	mangrove swamp, Malaya	Johnston, 1968
4.5-4.8 (S)	tree island in swamp, Florida	Loveless, 1959
5.1-5.3 (S)	black gum swamp, Louisiana	Hall and Penfound, 1939b
5.3 (W)	Rio Branco River, Brazil	Williams, 1968
5.3-6 (S)	cypress-gum swamp, Alabama	Hall and Penfound, 1943
5.4-6 (S)	bur reed marsh, Alabama	Hall and Penfound, 1943
5-5.5 (W)	blackwater, Malaya	Johnston, 1968
6.1-6.7 (S)	cypress-gum swamp, Louisiana	Hall and Penfound, 1939a
6.5 (W)	cypress-gum swamp, Louisiana	Hall and Penfound, 1939a
6.7 (W)	stream, Malaya	Richards, 1964
6.8 (W)	Amazon River, Brazil	Williams, 1968
6.9 (W)	West Pearl River, Louisiana	Hall and Penfound, 1939a
7 (W)	mouth of the Amazon River, Brazil	Williams, 1968

¹ S = soil; W = water

BABY DINOSAURS FROM LANCE AND HELL CREEK FORMATIONS

TABLE 2. AREAS FROM WHICH DINOSAUR EGGS HAVE BEEN REPORTED.

Locality	Relative Abundance ¹	Local Sediments	Reference
China			
Hunan			
Dongting Basin	C	"red beds"	Zeng and Zhang, 1979
Tsatzejuanksu	C	?	Young, 1965
Henan			
Xiaguan Basin	C	"red beds"?	Zhao, 1979
Kiangsi			
Wuliting	VC	red mudstone	Young, 1965
Laiyang			
Hsiachiayin	C	red mudstone	Young, 1965
Hungtouyeh	C	red mudstone	Young, 1965
Nanhsiung			
Chuetien	VC	red mudstone?	Young, 1965
Hoshangkong	C	red mudstone	Young, 1965
Lashuyuan	VC	red mudstone?	Young, 1965
Nanhsiung	VC	red mudstone?	Young, 1965
Tangmienling	VC	red mudstone?	Young, 1965
Yaotun	VC	red mudstone	Young, 1965
Shinkiang			
Chiangchun	R	red mudstone	Young, 1965
Chuehrkon	R	red mudstone	Young, 1965
Shengehingkou	R	red mudstone	Young, 1965
Europe			
France			
Aix-en-Provence	VC	red and grey sandstone, siltstone, mudstone	Lapparent, 1958
Portugal			
Alfreizao	VC	"red beds"	White, 1967
Spain			
Bastus	VC	red sandstone	Lapparent, 1958
Mongolia			
Altan Ula IV	C	red sandstone and mudstone	Gradziński, 1970
Bayn Dzak	VC	red sandstone	Sochava, 1971
Bugeen Tsav	VC	red sandstone	Sochava, 1969
Kahaychin-Ula	VC	red sandstone	Sochava, 1971
Naran-Bulak	C	red sandstone	Sochava, 1971
Nemegt	VC	red sandstone	Sochava, 1969
Ologoy-Ulan Tsav	C	?	Sochava, 1971
Sheeregeen Gashoon	C	?	Sochava, 1969
Tel' Ulan Ula	C	?	Sochava, 1969
Tsagan Khushu	C	yellow sandstone, red and olive mudstone	Sochava, 1971
North America			
Montana			
Chouteau	VC	red and green mudstone	Horner and Makela, 1979
Judith River	C	brown "shale"	Sahni, 1972
Red Lodge	C	brown mudstone	Jepsen, 1931
Utah			
Castle Dale	C	sandstone and varigated mudstone	Jensen, 1970
Coalville	C	sandstone and varigated mudstone	Jensen, 1970
Wasatch Plateau	C	varigated mudstone	Jensen, 1966
Wyoming			
Lance Creek	R	yellow sandstone	unpublished, UCM and UCMP collections
Folecat Bench	R	?	Wittier, Personal communication
South America			
Argentina			
Mendoza	R	"red beds"	White, 1967
Laguna La Colorada	R	"red beds"	Bonaparte and Vince, 1979
Brazil			
Bauru	R	?	White, 1967
Peru			
Lake Umayo	R	"red beds"	Sigé, 1968
Union of Soviet Socialist Republics			
Kazakhstan			
Alxa Ningxia	C	?	Zhao and Ding, 1976
Lake Zayson	?	?	Sochava, 1971
Tayshugen River	?	?	Sochava, 1971

¹ VC - very common; C - common; R - rare

to have existed on the Late Cretaceous coastal plain. These pH values give an indication of the pH levels which may have existed and explain why dinosaur egg shells are rare in the Lance and Hell Creek formations. These low pH levels may also explain Dodson's (1971) observation that dinosaur bones are uncommon in floodplain sediments of the Oldman Formation. The same appears to be true of the Lance Formation, based upon my own observations. What little bone I have found in the floodplain sediments is usually poorly preserved, suggesting partial decalcification. As in the Oldman Formation, most of the dinosaur bone is found in the channel sandstones. This is also where most of the bones of baby dinosaurs in the Lance and Hell Creek formations used in this study were collected.

Although it would appear that soil and water pH during the Late Cretaceous was the major controlling factor in the present distribution of dinosaur bones and dinosaur eggs, it is necessary to explain the presence of fossil bones in lignite deposits, such as Geiseltal. This Eocene lignite deposit in Germany is the only one in the region in which bone is known to have been preserved. It is believed that calcareous groundwater, derived from limestone in the Muschelkalk region to the south, permeated the swamp, neutralizing the acids and enabling the bones to survive (Rolfe and Brett, 1969). This buffering of acidic environments by calcareous water may also explain why Simpson (1928) was able to collect numerous vertebrate fossils from the Eagle Coal Mine in the Fort Union Formation. The calcareous buffer was probably derived from the weathering of uplifted Paleozoic limestones nearby.

From the earlier discussion about the destruction of calcareous egg shells by decalcification, it might be expected that there would be a close correlation between the present distribution of dinosaur egg shells and the depositional environment. A literature search shows that this is exactly what occurs. Most of the eggs come from well drained, oxidized sediments such as the red beds of the Kiangsi Province of China (Young, 1965). Table 2 is a compilation of the published dinosaur egg localities and the nature of their enclosing sediments.

Although soil- and water-pH during the Late Cretaceous may have been the major controlling factor for the preservability of dinosaur eggs and bones of baby dinosaurs, juvenile dinosaurs still are not as well represented as adults. Part of this problem is that juvenile dinosaurs often have gone unrecognized because of ontogenetic changes that accompany growth. Consequently, many immature dinosaurs were treated as new taxa (Dodson, 1975). Although juvenile dinosaurs may not be as uncommon as previously thought, very young or baby dinosaurs (here defined as young with a live body weight of less than one-eighth that of an adult) are still rare. Babies have been reported for Hadrosaurinae (see Sternberg, 1955), *Bagaceratops rozhdestvenski*, *Protoceratops andrewsi*, *?P. kozlowskii* (see Maryanska and Osmolska, 1975; Sochava, 1972), cf. *Maiasaura peeblesorum* (see Horner and Makela, 1979), *Mussaurus patagonicus* (see Bonaparte and

Vince, 1979), an unidentified dinosaur (Kitching, 1979) *Psittacosaurus mongoliensis* (see Coombs, 1980), *?Tarbosaurus* sp. (R. D. Estes, *personal communication*), and *Troodon* sp. (J. R. Horner, *personal communication*).

The reasons for the scarcity of bones of baby dinosaurs may be threefold: (1) some of the small bones, because of their size and delicate construction, were easily destroyed by scavengers, preburial transportation, low environmental pH, and postburial erosion (before and after fossilization); (2) the small size of some bones makes them easy to overlook in the field (this may also apply to dinosaur egg shell fragments); or (3) without some knowledge of dinosaur osteology, small broken fragments may go unrecognized in the field or among microvertebrates collected by screen-washing.

My own observations of large samples of microvertebrate remains in the Lance and Hell Creek formations convinces me that many fragments of baby dinosaurs go unrecognized or unreported. However, the amount of material seen is still much less than expected if nurseries were on the sandy shores of rivers, on levees, or on bar scrolls adjacent to active river channels. Kraemer and Bell (1980) documented high egg and hatchling mortality among turtles due to suffocation and drowning following heavy rains or a rise in rivers. It is, therefore, doubtful that dinosaurs used river shores, levees, or bar scrolls as nurseries, because these areas were frequently submerged during flooding. It is possible that some nests were atop sandbars left on the coastal plain following the regression of the coastline represented by the Fox Hills Sandstone (this is modeled after Trail Ridge, behind which the Okefenokee Swamp is developed). Other nests may have been atop levees and bar scrolls adjacent to oxbows and far enough from the active rivers to escape submergence during flooding. But even these "islands" above the poorly drained soils and swamps probably had abundant leaf litter, and so maintained an acidic environment. Thus, the chances of calcareous egg shells and bones of baby dinosaurs escaping destruction by decalcification were slim. It probably was only when avulsion brought the river channel near the nesting site that bones and egg shell fragments could fall or be transported in that chances of preservation increased. The presence of mudball conglomerates and mudball pebbles in many of the sandstones of the Lance and Hell Creek formations suggest that the rivers also cut into the sides of old levees and bar scrolls. Bank collapse would have introduced any baby dinosaur bones or calcareous egg shells into the river where the constant flow of freshwater could protect the material from acid.

SYSTEMATIC PALEONTOLOGY

Most of the fossils discussed here were recovered by underwater washing and screening and are, consequently, small. Measurements are given in millimeters and, for teeth, were taken from crown tip to crown base (H) and across the greatest anteroposterior width of the crown (W). These measurements are given after the specimen and locality numbers.

TABLE 3. DISTRIBUTION OF LOCALITIES BY FORMATION.

LANCE FORMATION	HELL CREEK FORMATION
UCMP-V5003	UCMP-V73076
UCMP-V5620	UCMP-V73087
UCMP-V5622	UCMP-V73093
UCMP-V5711	UCMP-V75165
UCMP-V5815	

Abbreviations for institutions whose specimens were used in this study are: AMNH—American Museum of Natural History; NMC—National Museum of Natural Sciences, National Museums of Canada; PMAA P—Provincial Museum and Archives of Alberta, Paleontological Collections; ROM—Royal Ontario Museum; UCM—University of Colorado Museum; UCMP—University of California, Museum of Paleontology; UW—University of Wyoming. In addition, all locality numbers are those of the University of California (Berkeley) and are preceded by UCMP-V. Formational distributions of these localities are presented in Table 3 for easy reference. All of localities in the Lance Formation were discussed by Clemens (1963).

Order SAURISCHIA
Family DROMAEOSAURIDAE

Fig. 1

Material: Dentary fragments: UW 13684 (UCMP-V5003); and UCMP 125238 (UCMP-V73089). Teeth: UCM 39502 (UCMP-V5711) H 1.7 mm, W 2 mm; UCM 45055 (UCMP-V5620) H 2.6 mm, W 2.2 mm; UCMP 124983 (UCMP-V73087) H 2.1 mm, W 2 mm; UCMP 124984 (UCMP-V73087) H 3 mm, W 2.1 mm; and UCMP 124985 (UCMP-V73087) H 2.7 mm, W 2.1 mm.

Discussion: The two dentary fragments are much alike and are probably conspecific. UW 13684 is the more complete, measuring 15 mm long and containing the base of two teeth separated by an empty alveolus. UCMP 125238 is 6.5 mm long and contains a nearly complete tooth and a partial alveolus. In both fragments, the alveoli are longer than wide and subrectangular in shape. No interdental plates are present. The inner and outer dental parapets are nearly equal in height. On the external surface the dental foramina are anteroposteriorly elongated and terminate at faint grooves which extend ventrally from the dental border. The preserved parts of the teeth are strongly compressed laterally, and have a shallow sulcus on both sides of the root; this sulcus does not extend onto the crown. The tip of the crown is missing in UCMP 125238; however, the tooth is complete enough to show that it was posteriorly recurved, with well developed serrations on the posterior edge and faint, poorly developed ones on the anterior edge. There are 11 serrations per 2 mm on the posterior edge; those on the anterior edge cannot be counted. Reconstructed, the crown was about as long anteroposteriorly as high.

These dentary fragments are similar to *Velociraptor* in the absence of interdental plates, the subequal height of the inner and outer dental parapets, the long and narrow, subrectangular aveoli, and in the elongated external foramina (see Sues, 1977, Pl. 16). Although these dentary fragments may be those of *Velociraptor*, they are too fragmentary for positive identification. As will be shown elsewhere (Carpenter and Paul, *in preparation*), *Velociraptor* occurs in North America and may differ enough from *Dromaeosaurus* to warrant its own family.

Isolated teeth used in this study are almost as long anteroposteriorly as they are high, strongly compressed laterally, and recurved with serrations well developed along the posterior margin. Development of anterior serrations vary in strength. In these features, these teeth resemble the posterior teeth of *Velociraptor mongoliensis* (e.g., AMNH 6515). Many of the teeth in the collections show some degree of usage wear, especially at the tip.

Family SAURORNITHOIDIDAE

Saurornithoides inequalis (Sternberg, 1932),
new combination
Fig. 2a-h

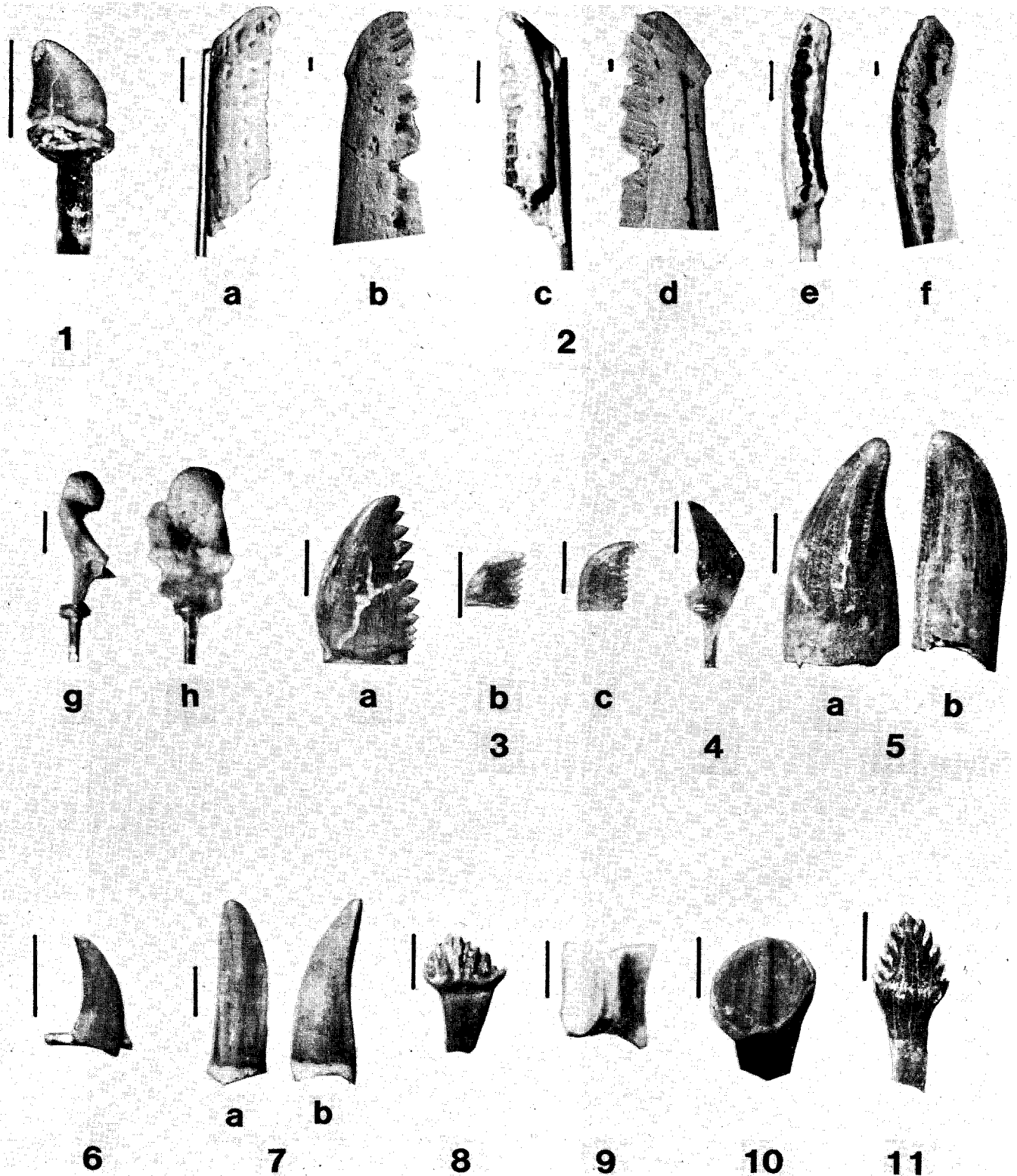
Synonomies: *Ornithomimus altus* Lambe, 1902 (in part)
Polyodontosaurus grandis Gilmore, 1932
Stenonychosaurus inequalis Sternberg, 1932
Troodon formosus Russell, 1948
Saurornithoididae Sues, 1977

Material: Partial left dentary, UCM 41666 (UCMP-V5711); and basioccipital, UCM 43218 (UCMP-V5711).

Discussion: This material probably represents one individual, because: (1) the bones were found in the same sack of matrix; (2) of the similar color of the bones; and (3) of the minute size of the bones. The dentary fragment is 11 mm long and has 13 alveoli preserved (Fig. 2a,c,e).

The dentary fragment is similar to the dentary of *Saurornithoides inequalis*, NMC 8540, differing primarily in size. Comparison of the dentaries shows the following similarities: (1) on the external surfaces (Fig. 2a,b) a shallow longitudinal groove connects the dental foramina; and (2) this groove shallows anteriorly. There are vertical flutes anteriorly which extend ventrally from the dental border, and each encloses a dental foramen. Internally (Fig. 2c,d), the inner dental parapet is lower than the outer dental parapet. A narrow, deeply incised meckelian groove extends along the ventral margin of the dentaries to a single foramen near the symphysis. Each alveolus (Fig. 2e,f) is separated by an alveolar septum; no interdental plates are present.

The only differences between the two dentaries, other than size, are the weakly developed symphysis and lack of a prominent tuberosity below the symphysis for the geniohyoideus muscle in UCM 41666 (compare c and d, Fig. 2). Both of these features reflect the extreme immaturity of the specimen, and probably does not in-



Figures 1-11. Fig. 1, Dromaeosauridae, tooth, UCM 39502. Fig. 2a-h, *Saurornithoides inequalis*: 2a, buccal view of hatchling left dentary, UCM 41666; c, lingual view; e, dorsal view; b, buccal view of left dentary, NMC 8540 (cast); d, lingual view; f, dorsal view; g, lateral view of hatchling basioccipital, UCM 43218; and h, ventral view. Fig. 3a-c, teeth of *Pectinodon bakkeri*: a, holotype, UCM 38445; b, paratype, UCM 38446; and c, paratype, UCMP 73098. Fig. 4, *Paronychodon lacustris*, tooth, UCMP 124990. Fig. 5a, b, Tyrannosauridae: a, lateral view of UCMP 119853; and b, posterior view. Fig. 6, Theropoda, tooth, UCMP 124987. Fig. 7a, b, tooth of *Aublysodon mirandus*: a, lateral view of UCMP 124406; and b, posterior view. Fig. 8, *Thescelosaurus* sp., tooth, UCMP 124973. Fig. 9, Hadrosauridae, tooth, UCM 45060. Fig. 10, Ceratopsidae, tooth, UCM 45057. Fig. 11, *Ankylosaurus magniventris*, tooth, UCMP 124399. Heavy bars to left of specimens = 2 mm.

dicating taxonomic difference. In addition, there is a peculiar dorsobuccal twist of the symphysis in UCM 41666 which would cause the first dentary tooth to project obliquely away from the jaw. It is not certain whether this was to enable the hatchling to slit through the leathery egg shell with the tooth, or whether the condition was pathological. If pathological, this may be the first reported example of a birth defect in a dinosaur.

The basioccipital (Fig. 2g,h) is similar to that figured by Russell (1969, Fig. 4), differing only in that some of the structures are underdeveloped; the dorsal neural groove is not as deep as that figured, nor are the basal tubera as prominent or as rugose. The occipital condyle, however, is well developed and separated from the main body of the basioccipital by a constricted neck. Sutural scars for the exoccipitals are present on each side of the dorsal neural groove and indicate that the exoccipitals contribute to only a small part of the occipital condyle, as in most theropods.

The minute size and underdeveloped condition of the dentary and basioccipital suggest that these bones probably are from a hatchling. The great size disparity between hatchling and adult *Saurornithoides* is illustrated by comparing tooth row lengths: the first 13 alveoli in the hatchling dentary occupies 8.5 mm, while the first 13 alveoli in ROM 1445 occupies 26.6 mm, 28 mm in NMC 8540, and 30 mm in PMAA P67.14.39. ROM 1445, NMC 8540, and PMAA P67.14.39 are almost the same size as the type *Saurornithoides mongoliensis* (AMNH 6516), and are believed to be from adults. It is not possible to measure the length of the first 13 alveoli in AMNH 6515 as the lower jaws are in occlusion (see Osborn, 1924, Fig. 3).

All the hatchling cranial material is similar to specimens referred to *Stenonychosaurus inequalis* by Russell (1969). However, as will be shown in detail later (Carpenter and Paul, *in preparation*), *Stenonychosaurus* is a junior synonym of *Saurornithoides*. This was originally suggested by Russell (1969) and again by Barsbold (1974), although neither made the synonymy official. Only one species of *Saurornithoides* (*S. inequalis*) is recognized from the Late Cretaceous of Mongolia, and one is known from the Late Cretaceous of Mongolia (*S. mongoliensis*, Barsbold, 1974, notwithstanding).

The presence of *Saurornithoides* in North America is not surprising, as similarities between the dinosaur and mammal faunas of North America and Mongolia have been the subject of comment before (e. g., Kielan-Jarowowska, 1975; Fox, 1978).

Pectinodon new genus

Diagnosis: Crowns of teeth strongly compressed laterally and recurved. Anterior margin without serrations, denticles, or sharp translucent keel; edge usually rounded, but may have low, blunt, opaque keel or ridge. Posterior margin with large serrations having translucent edges. Serrations largest in middle, and may be subequal to crown's tip in size. Posterior serrations perpendicular to vertical axis of tooth. Crown tip

directed posteriorly, almost parallel to crown base. Crown tip does not function as a piercing tip, but as first serration. First definitive serration occurs immediately below crown tip and differs from other small theropods ("dromaeosaurids") in that it is not significantly smaller than crown tip. Near tooth's base, two small serrations are crowded together. Antero-posterior length of tooth almost equal to height.

Type species: *Pectinodon bakkeri* new species

Etymology: *pectin-*, Latin for "comb"; and *-odon*, Greek for "tooth."

Pectinodon bakkeri new species

Fig. 3a-c

Synonymy: *Saurornithoides* sp. Estes, 1964 (in part).

Diagnosis: As for genus.

Material: Holotype tooth, UCM 38445 (UCMP-V5711) H 6.2 mm, W 3.7 mm. Paratype teeth: UCM 38446 (UCMP-V5711) H 1.8 mm, W 2 mm; UCMP 73098 (UCMP-V5815) H 2.8 mm, W 1.8 mm; and UCMP 125239 (UCMP-V5815) H 3.2 mm, W 2.5 mm. Referred teeth (all adults and all from UCMP-V5620): UCMP 125240-125247.

Distribution: Apparently restricted to Lance Formation of eastern Wyoming. Holotype from UCMP-V5711, Bushy Tailed Blowout, S½, sec. 20, T. 37 N., R. 64 W., Niobrara County.

Etymology: Specific name in honor of Dr. Robert T. Bakker, who has contributed considerably to the study of dinosaurs.

Discussion: The large holotype tooth (Fig. 3a) is not from a juvenile. The paratypes (figs. 3b,c), however, are small and probably are from babies. Estes (1964) referred teeth with large posterior denticulations to *Saurornithoides* sp., but later noted that this identification was incorrect (*personal communication*). Re-examination of Estes' material revealed the presence of three different kinds of small theropod teeth. One group has large posterior serrations and are clearly referable to *Pectinodon bakkeri* (e. g., Estes, 1964, Fig. 69a). Another group of teeth has smaller posterior serrations which are directed obliquely upward. The tip of the crown is oblique to the vertical axis of the tooth, but does not project posteriorly as in *Pectinodon*; the crown has a piercing tip. The first serration is significantly smaller than the crown tip. There may be poorly developed serrations on the anterior edge or a sharp translucent keel. These teeth are similar to those in the dentary of *Saurornithoides inequalis* (ROM 1445) previously referred to *Troodon formosus* by Russell (1948), and to *Saurornithoides junior* by Barsbold (1974). This group of teeth from the Lance Formation is referred to *S. inequalis*. The third group of teeth has well developed serrations on the anterior and posterior margins; however, these serrations are smaller than those in *Pectinodon* or *Saurornithoides*. As in *Saurornithoides*, the crown tip functions in piercing. Furthermore, the first serration is significantly smaller than the crown tip. In many respects, these teeth resemble those of *Velociraptor*

mongoliensis (e. g., AMNH 6515), except that the anterior serrations are not significantly smaller than the posterior serrations.

Pectinodon bakkeri is provisionally placed in the family Saurornithoididae because the crowns are strongly compressed laterally and serrations are well developed only on the posterior edge.

Family DROMAEOSAURIDAE or Family SAURORNITHOIDIDAE

Paronychodon lacustris

Fig. 4

Material: Teeth: UCM 38288 (UCMP-V5711) H 4 mm, W 1.3 mm; UCM 38459 (UCMP-V5711) H 1.7 mm, W 2.3 mm; UCM 124990 (UCMP-V73087) H 3.4 mm, W 1.7 mm; UCM 124991 (UCMP-V73087) H 4.8 mm, W 1.9 mm; and UCM 124992 (UCMP-V73087) H 4.3 mm, W 1.6 mm.

Discussion: Despite their small size, these teeth are clearly referable to *Paronychodon lacustris*. The anterior and posterior edges are vertical and parallel near the base (Fig. 4), but then curve sharply posteriorly with the two edges meeting in a pointed tip. The teeth are laterally compressed, with one side being flat and covered by long ridges parallel to the edges of the crown. These ridges cover the one side of the crown between the tip and where the tooth curves posteriorly. Serrations may or may not be present on the posterior edge; none occurs on the anterior edge.

Family TYRANNOSAURIDAE

Fig. 5a,b

Material: Tooth, UCM 119853 (UCMP-V72207) H 8 mm, W 4 mm.

Discussion: The D-shaped cross section, position of the serrations, and robustness indicate a first right maxillary tooth (Fig. 5a,b). The D-shaped cross-section gives the tooth an incisiform appearance, and is known only in the premaxillary teeth and first maxillary teeth of tyrannosaurids and in the teeth of *Aublysodon mirandus* (see below). In all other theropods, the premaxillary teeth become progressively more asymmetrical toward the front of the tooth row as the anterior serrations assume a more medial position (but this does not result in a D-shaped cross section and incisiform tooth; see Lambe, 1917 and Ostrom, 1969). UCM 119853 is so heavily worn that the anterior serrations are almost obliterated.

THEROPODA *incertae sedis*

Fig. 6

Material: Teeth: UCM 39503 (UCMP-V5711) H 3.2 mm, W 1.8 mm; UCM 45063 (UCMP-V5620) H 2.8 mm, W 1.8 mm; UCM 124986 (UCMP-V73087) H 1.6 mm, W 1.3 mm; UCM 124987 (UCMP-V73087) H 2.8 mm, W 2.2 mm; and UCM 124988 (UCMP-V73087) H 2.6 mm, W 2 mm.

Discussion: These teeth differ significantly from those discussed above, and may represent other thermo-

pod taxa. Further work on theropod teeth may permit some of these teeth to be assigned to known taxa. Most of the teeth have serrations both on the anterior and posterior edges.

Aublysodon mirandus

Fig. 7a,b

Material: Teeth: UCM 43447 (UCMP-V5711) H 7 mm, W 2.5 mm; UCM 73091 (UCMP-V5622) H 6.3 mm, W 2.2 mm; UCM 124367 (UCMP-V75165) H 6.1 mm, W 2 mm; UCM 124399 (UCMP-V5620) H 8.9 mm, W 2.6 mm; UCM 124406 (UCMP-V73087) H 6.6 mm, W 2 mm; UCM 124978 (UCMP-V73087) H 7 mm, W 2.9 mm; UCM 124980 (UCMP-V73087) H 6.2 mm, W 2.5 mm; UCM 124981 (UCMP-V73087) H 7 mm, W 2.5 mm; and UCM 124982 (UCMP-V73087) H 7 mm, W 2.4 mm. W measurements taken transversely across face of tooth near base.

Discussion: Leidy (1868) established *Aublysodon mirandus* on the basis of three incisiform teeth, D-shaped in cross section, which were collected from the Judith River Formation of Montana by Hayden. Subsequent workers, notably Cope (1876), Lambe (1902) and Osborn (1905), noted a similarity of two of the serrated teeth with the premaxillary teeth of *Deinodon* (= *Albertosaurus*), and therefore treated *Aublysodon* as a junior synonym of *Deinodon*. Lambe (1902), however, was uncertain of the third tooth, which was unserrated, and placed it tentatively with *Ornithomimus altus*. Osborn (1905) was less certain of its affinities.

Since Leidy's description, numerous additional specimens of teeth, D-shaped in cross section and lacking serrations, have been collected. Study of these teeth (Carpenter, *in preparation*) indicates that *Aublysodon mirandus* is valid in reference to Leidy's figured specimen (Leidy, 1860, Pl. 9, figs. 41-45), here designated as the lectotype.

The juvenile specimens, except for one, resemble the lectotype in their D-shaped cross section, parallel sides, and paired posterior lateral ridges that lack serrations. These lateral ridges curve toward one another near the base, but do not meet. This condition is unlike any known tyrannosaur or any theropod premaxillary tooth, in which the serrations diverge from tip to base. One tooth UCM 43447 differs from the lectotype; it has a slight left-lateral twist of the crown, giving the tooth a spatulate appearance. In all other aspects, however, this tooth is similar to those of *Aublysodon*.

Order ORNITHISCHIA

Family HYSILOPHODONTIDAE

Thescelosaurus sp.

Fig. 8

Material: Teeth: UCM 43223 (UCMP-V5711) H 1.9 mm, W 2.2 mm; UCM 124972 (UCMP-V5620) H 1.6 mm, W 2.4 mm; UCM 124973 (UCMP-V5620) H 2.2 mm, W 3 mm; UCM 124974 (UCMP-V5620) H 2 mm, W 2.5 mm; UCM 124975 (UCMP-V5620) H 2.2 mm,

W 3 mm; UCMP 124976 (UCMP-V5620) H 1.5 mm, W 2.3 mm; UCMP 124977 (UCMP-V5620) H 1.3 mm, W 2.5 mm; UCMP 124997 (UCMP-V5815) H 1.5 mm, 2 mm; and UCMP 124998 (UCMP-V5815) H 3.2 mm; 2.7 mm.

Discussion: These teeth look like minute versions of the cheek teeth figured by Sternberg (1940). The teeth are enameled on one side; this side has numerous vertical corrugations. The opposite side lacks enamel, and in many specimens shows considerable wear. The wear may produce two facets on each side of the midline, which meet at the apex as figured by Sternberg, or may produce a single facet across the entire surface. No conical premaxillary teeth are present in the collections.

Family HADROSAURIDAE

Fig. 9

Material: Teeth: UCM 45060 (UCMP-V5711) H 3.6 mm, W 3 mm; and UCM 45061 (UCMP-V5711) H 2.9 mm, W 3 mm.

Discussion: The teeth show heavy usage wear (Fig. 9); a similar condition was noted by Horner and Makela (1979) for baby hadrosaurs recovered from the Two Medicine Formation. It has been standard procedure to assign all isolated hadrosaur teeth from the Lance and Hell Creek formations to *Edmontosaurus* (= *Anatotosaurus*); however, there may be yet another genus of hadrosaur in the Lancian (M. Brett-Surman, *personal communication*).

Family CERATOPSIDAE

Fig. 10

Material: Teeth: UCM 37878 (UCMP-V5711) H 6 mm, W 3.8 mm; UCM 43526 (UCMP-V5711) H 2 mm, W 2.5 mm; UCM 45057 (UCMP-V5711) H 3.6 mm, W 3.8 mm; UCM 45058 (UCMP-V5711) H 3.5 mm, W 4.1 mm; and UCM 45059 (UCMP-V5711) H 4 mm, W 3.7 mm.

Discussion: Only UCM 45059 is heavily worn. Unworn teeth have a triangular enameled face with a vertical medial ridge (Fig. 10). Small denticles are present along the upper edge of the enameled surface. Unlike adult ceratopsian teeth, these have a single unbifurcated root, a condition Hatcher and others (1907) noted for young incipient teeth. It is doubtful that these small teeth are incipient teeth of an adult, because they are well developed and have a long root, which is unlike the short, thin-walled, open root of the adult. It is probable that the root became bifurcated as the animal matured.

Because there are two genera of ceratopsians (*Triceratops* and *Torosaurus*) in the Lance and Hell Creek formations, it is not possible to be more specific in the identification.

Family ANKYLOSAURIDAE

Ankylosaurus magniventris

Fig. 11

Material: Teeth: UCMP 120195 (UCMP-V73076)

H 3.3 mm, W 2.9 mm; and UCMP 124399 (UCMP-V5620) H 3.2 mm, W 2.7 mm.

Discussion: Teeth of *Ankylosaurus* are diagnostic, being simple, smooth cones with large denticles on the anterior and posterior edges and in having swollen bases. Other ankylosaurids, such as *Euoplocephalus* (see Coombs, 1971), *Pinacosaurus*, and *Saichania* (see Maryanska, 1977, Pl. 21, Fig. 2a,b and Pl. 29, Fig. 4a,b), have fluted or corrugated sides.

Only one of the teeth (UCMP 124399) is undamaged and unworn (Fig. 11). It looks much like the tooth figured by Brown (1908), but lacks the wear facet and faint vertical ridges on the lingual side. There are six denticles on each side of the crown, the basal denticle being the smallest.

The other tooth is heavily worn. It is identified as *Ankylosaurus* because there is a smooth enameled surface and a large medial cone with denticles on the sides. It is not possible to determine if there was a swollen base, as this area is heavily worn. The heavy wear shows, despite the small size of the teeth relative to the skull (Coombs, 1978), that ankylosaurids, at least the babies, relied upon their teeth to process food and did not crop and swallow food whole.

DISCUSSION

Only two major fossil collections from the Lance and Hell Creek formations were used in this study, one from the University of Colorado Museum and one from the University of California (Berkeley), Museum of Paleontology. Nevertheless, it appears that very young or baby dinosaurs may not be as uncommon as previously thought. Still, it is doubtful that even if all collections were used true species diversity and relative abundances of baby dinosaurs would be represented. Behrensmeyer and others (1979) have demonstrated a correlation between live body weight and preservability of the skeleton in terrestrial mammals. They found that "of the 53 species of mammals ≥ 1 kg body weight that have been recorded in . . . [Amboseli] basin over the last decade, 39 (74%) are recognized in the sample of skeletal remains . . . All species greater than 100 kg body weight are represented, but for smaller animals among the wild species, representation is inversely related to size . . ." (Behrensmeyer and others, 1979, p. 15). The reason for the under-representation of the smaller species of mammals was that the skeletons were more vulnerable to biological and physical degradation. But it is equally true that any animal less than 100 kg body weight, such as juveniles of animals which exceed 100 kg body weight as adults, are also less likely to avoid destruction. The implication of this is that skeletal material of baby dinosaurs will always be less common than skeletal material of adults, except in unusual environments.

The resistance of teeth to biological destruction (except possibly by gastric juices) and the preservational bias against animals with a body weight less than 100 kg, may explain why some, apparently small, species of

dinosaurs are only known from teeth (*e. g.*, *Paronychodon* and *Pectinodon*). This may also explain why in the Lance and Hell Creek formations most baby dinosaurs are represented by teeth and not by skeletal elements (although additional skeletal material may still be present in unsorted collections of microvertebrates).

CONCLUSION

Most of the fossils in this study show little or no transport abrasion; this would have been especially noticeable on the delicate material of *Saurornithoides* hatchlings. The unabraded condition of the fossils suggests that transportation was minimal prior to burial. Most of the teeth are laterally compressed and, lying on the stream bottom, would offer little resistance to currents. This is apparently why Dodson (1973) found that mouse incisors and jaws are not easily transported in flume tests.

The abundance of hatchling bones and teeth used in this study, their lack of abrasion, and apparent low transportability (including the material of *Saurornithoides*), suggest that nesting sites of some dinosaurs were not far from where the fossils were collected. This is supported by the occasional discovery of dinosaur egg shell fragments. These occur in channel sandstone (such as at UCMP-V5616 and UCMP-V5711 in the Lance Formation) where a constant flow of fresh water would have kept the pH from dropping to a point at which dissolution would begin.

ACKNOWLEDGMENTS

It has taken several years to produce this paper in its final form, and I thank the many readers of earlier manuscripts for their helpful, sometimes exasperating comments, suggestions, arguments, and challenges: R. T. Bakker, T. M. Bown, D. Chipps, R. D. Estes, E. Evanoff, J. R. Horner, G. Paul, P. Robinson, R. Stucky, and J. Van Couvering. I especially thank Bown and Horner for stimulating me to consider geochemical environments of the Late Cretaceous coastal plain. I thank the various people who provided specimens or casts: W. A. Clemens, University of California, Berkeley, Museum of Paleontology; P. Currie, Provincial Museum of Alberta; R. C. Fox, University of Alberta; C. R. Harington, National Museum of Canada; J. A. Lillegraven, University of Wyoming; and J. Lindsay, Royal Ontario Museum.

REFERENCES CITED

- Barsbold, R., 1974, *Saurornithoididae*, a new family of small theropod dinosaurs from central Asia and North America: Results of the Polish-Mongolian Palaeontological Expeditions, Part V, *Palaeontologia Polonica*, no. 30, p. 5-22.
- Behrensmeyer, A. K., Western, D., and Boaz, D. E. D., 1979, New perspectives in vertebrate paleoecology from a recent bone assemblage: *Paleobiology*, v. 5, p. 12-21.
- Bonaparte, J. F., and Vince, M., 1979, El hallazgo del primer nido de dinosaurios Triasicos (*Saurischia*, *Prosauropoda*), Triasico superior de Patagonia, Argentina: *Ameghiana*, v. 16, p. 173-182.
- Borchert, H., 1960, Genesis of marine sedimentary iron ores: *Institution of Mining and Metallurgy, Bulletin*, v. 64, p. 261-279.
- Brown, B., 1908, The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous: *American Museum of Natural History, Bulletin*, v. 24, p. 187-201.
- Case, T. J., 1978, Speculations on the growth rate and reproduction of some dinosaurs; *Paleobiology*, v. 4, p. 320-328.
- Chenery, E., 1954, Acid sulphate soils in central Africa: 5th International Congress of Soil Science Transactions, v. 4, p. 195.
- Clemens, W. A., 1963, Fossil mammals of the type Lance Formation, Wyoming: Part 1. Introduction and Multituberculata: *University of California, Publications in Geological Sciences*, v. 48, vi + 105 p.
- Coleman, J. M., 1966, Ecological changes in a massive fresh-water clay sequence: *Gulf Coast Association of Geological Societies, Transactions*, v. 16, p. 159-174.
- Coombs, W. P., 1971, The Ankylosauria [PhD thesis]: New York, New York, Columbia University, 487 p.
- , 1978, The families of the ornithischian dinosaur Order Ankylosauria: *Palaeontology*, v. 21, p. 143-170.
- , 1980, Juvenile ceratopsians from Mongolia—the smallest known dinosaur specimens: *Nature*, v. 283, p. 380-381.
- Cope, E. D., 1876, On some extinct reptiles and Batrachia from the Judith River and Fox Hills Beds of Montana: *Academy of Natural Sciences of Philadelphia, Proceedings*, v. 28, p. 340-359.
- Dodson, P., 1971, Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 10, p. 21-74.
- , The significance of small bones in paleoecological interpretation: *Contributions to Geology, University of Wyoming*, v. 12, p. 15-19.
- , Taxonomic implications of relative growth in lambeosaurine hadrosaurs: *Systematic Zoology*, v. 24, p. 37-54.
- Eyre, S. R., 1968, *Vegetation and soils*: London, Edward Arnold Publishers Ltd., 328 p.
- Estes, R. D., 1964, Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming: *University of California, Publications in Geological Sciences*, v. 49, 180 p.

- Fox, R. C., 1978, Upper Cretaceous terrestrial vertebrate stratigraphy of the Gobi Desert (Mongolian People's Republic) and western North America, *in* Stelck, C. R., and Chatterton, B. D. E., eds, Western and Arctic Canadian biostratigraphy: Geological Association of Canada, Special Paper 18, p. 577-594.
- Garrels, R. and Christ, C. L., 1965, Solutions, minerals, and equilibria: San Francisco, Freeman, Cooper & Company, 450 p.
- Gilmore, C. W., 1932, A new fossil lizard from the Belly River Formation of Canada: Royal Society of Canada, Transactions, v. 26, p. 117-119.
- Glob, P. V., 1971, The Bog People: Iron-Age Man preserved: New York, Ballantine Books, 144 p.
- Gradziński, R., 1970, Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert: Results of the Polish-Mongolian Palaeontological Expeditions, Part 2, Palaeontologia Polonica v. 21, p. 148-229.
- Hall, T. F., and Penfound, W. T., 1939a, A phytosociological study of a cypress-gum swamp in southeastern Louisiana: American Midland Naturalist, v. 21, p. 378-395.
- 1939b, A phytosociological study of a *Nyssa biflora* consocieties in southern Louisiana: *ibid.*, v. 21, p. 369-375.
- 1943, Cypress-gum communities in the Blue Girth Swamp near Selma, Alabama: Ecology v. 24, p. 208-217.
- Hatcher, J. B., Marsh, O. C., and Lull, R. S., 1907, The Ceratopsia: U.S. Geological Survey, Monograph 49, 198 p.
- Horner, J. R., and Makela, R., 1979, Nest of juvenile provides evidence of family structure among dinosaurs: Nature, v. 282, p. 296-298.
- Jensen, J. A., 1966, Dinosaur eggs from the Upper Cretaceous North Horn Formation of Central Utah: Brigham Young University, Geology Studies, v. 13, p. 55-67.
- 1970, Fossil eggs in the Lower Cretaceous of Utah: *ibid.*, v. 17, p. 51-65.
- Jepsen, G. L., 1931, Dinosaur egg shell fragments from Montana: Science, v. 73, p. 12-13.
- Johnston, D. S., 1968, Malayan blackwaters: *in* Misra, R., and Gopal, B., eds, Symposium on recent advances in tropical ecology: Faridat, India, Shri R. K. Jain, Today and Tomorrow's Printers and Publishers, p. 303-310.
- Kielan-Jaworowska, Z., 1975, Late Cretaceous mammals and dinosaurs from the Gobi Desert: American Scientist, v. 63, p. 150-159.
- Kitching, J., 1979, Preliminary report on a clutch of six dinosaurian eggs from the Upper Triassic Elliot Formation, northern Orange Free State: Palaeontologica Africana, v. 22, p. 41-45.
- Kraemer, J. E., and Bell, R., 1980, Rain-induced mortality of eggs and hatchlings of Loggerhead Sea Turtles (*Caretta caretta*) on the Georgia coast: Herpetologica, v. 36, p. 72-77.
- Krauskopf, K. B., 1967, Introduction to geochemistry: New York, McGraw-Hill Book Company, 721 p.
- Lambe, L. M., 1902, New genera and species from the Belly River Series (Mid-Cretaceous): Geological Survey of Canada, Contributions to Canadian Paleontology, v. 3, p. 25-81.
- 1917, The Cretaceous theropodous dinosaur *Gorgosaurus*: Geological Survey of Canada, Memoir 100, 84 p.
- Lapparent, A. F., 1958, Decouverte d'un gisement d'oeufs de Dinosauriens dans le Cretace superieur du bassin de Tremp (Province de Lerida, Espagne): Academie des Sciences, Comptes Rendus, v. 247, p. 1879-1886.
- Leidy, J., 1860, Extinct Vertebrata from the Judith River and Great Lignite Formations of Nebraska: American Philosophical Society, Transactions, new series, v. 11, p. 139-154.
- 1868, Remarks on a jaw fragment of *Megalosaurus*: Academy of Natural Sciences of Philadelphia, Proceedings, v. 20, p. 197-200.
- Loveless, C. M., 1959, A study of the vegetation in the Florida Everglades: Ecology, v. 40, p. 1-9.
- Marlier, G., 1973, Limnology of the Congo and Amazon rivers, *in* Meggers, B. J., Ayensu, E. S., and Duchworth, W. D., eds, Tropical Forest Ecosystems in Africa and South America: a comparative review: Washington, D. C., Smithsonian Institution Press, p. 223-238.
- Maryanska, T., 1977, Ankylosauridae (Dinosauria) from Mongolia: Results of the Polish-Mongolian Palaeontological Expeditions, Part 7, Palaeontologia Polonica, no. 37, p. 85-151.
- Maryanska, T., and Osmolska, H., 1975, Protoceratopsidae (Dinosauria) of Asia: *ibid.*, Part 6, no. 33, p. 132-175.
- Matthew, W. D., 1915, Climate and evolution: New York Academy of Science, Annals, v. 24, p. 171-318.
- Mohr, E., Van Baren, F., and Van Schuylenborgh, E., 1972, Tropical soils: Hague, Mouton Press, 3rd ed., 481 p.
- Monk, C., 1966, An ecological study of hardwood swamps in northcentral Florida: Ecology, v. 47, p. 649-654.
- Monk, C., and Brown, T., 1965, Ecological consideration of Cypress Heads in northcentral Florida: American Midland Naturalist, v. 74, p. 126-140.

- Osborn, H. F., 1905, *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs: American Museum of Natural History, Bulletin, v. 21, p. 259-265.
- _____, 1924, Three new Theropoda, *Protoceratops* zone, central Mongolia: American Museum Novitates, no. 144, 12 p.
- Ostrom, J. H., 1969, Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana: Peabody Museum of Natural History, Bulletin, no. 30, 165 p.
- Parberry, D., and Venkatchalam, R., 1964, Chemical analysis of South Malayan peat soil: Journal of Tropical Geography, v. 18, p. 125-133.
- Richards, P., 1964, Tropical rain forest: London, Cambridge University Press, 450 p.
- Richmond, N., 1965, Perhaps juvenile dinosaurs were always scarce: Journal of Paleontology, v. 39, p. 503-505.
- Rolfe, W., and Brett, D., 1969, Fossilization processes, in Eglington, G., and Murphy, M., eds, Organic geochemistry: methods and results: New York, Springer-Verlag, p. 213-244.
- Russell, D. A., 1969, A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta: Canadian Journal of Earth Sciences, v. 6, p. 595-612.
- Russell, L. S., 1948, The dentary of *Troodon*, a genus of theropod dinosaurs: Journal of Paleontology, v. 22, p. 625-629.
- Sahni, A., 1972, The vertebrate fauna of the Judith River Formation, Montana: American Museum of Natural History, Bulletin, v. 147, p. 323-412.
- Sigé, M., 1968, Dents de Micromammifères et fragments de coquilles d'oeufs de Dinosauriens dans la fauna de Vertébrés du Crétacé supérieur de Laguna Umayo (Andes péruviennes): Academie des Sciences, Comptes Rendus, sér. D, v. 267, p. 1495-1498.
- Simpson, G. G., 1928, A new mammalian fauna from the Fort Union Formation of southern Montana: American Museum Novitates, no. 297, 15 p.
- Sochava, A. V., 1969, Dinosaur eggs from the Upper Cretaceous of the Gobi Desert: Palaeontology Journal, v. 3, p. 517-527.
- _____, 1971, Two types of dinosaur egg shells in the Senonian dinosaurs: *ibid.*, v. 5, p. 353-361.
- _____, 1972, The skeleton of an embryo in a dinosaur egg: *ibid.*, v. 6, p. 527-530.
- Sternberg, C. M., 1932, Two new theropod dinosaurs from the Belly River Formation of Alberta: Canadian Field Naturalist, v. 46, p. 99-105.
- _____, 1940, *Thescelosaurus edmontonensis* n. sp. and classification of the Hypsilophodontidae: Journal of Paleontology, v. 14, p. 480-481.
- _____, 1955, A juvenile hadrosaur from the Oldman Formation of Alberta: National Museum of Canada, Annual Report 1953-1954, Bulletin 136, p. 120-122.
- Sues, H.-D., 1977, The skull of *Velociraptor mongoliensis*, a small Cretaceous theropod dinosaur from Mongolia: Palaontologische Zeitschrift, v. 51, p. 173-184.
- White, T., 1967, Dinosaurs at home: New York, Vantage Press, 232 p.
- Williams, P., 1968, Organic and inorganic constituents of the Amazon River: Nature, v. 218, p. 937-938.
- Young, C., 1965, Fossil eggs from Nanhsiung, Kwangtung and Kanchou, Kiangsi: Vertebrata Palasiatica, v. 9, p. 141-170.
- Zeng D., and Zhang J., 1979, On the dinosaur eggs from the western Dongting Basin, Hunan: *ibid.*, v. 17, p. 131-136.
- Zhao, Z., 1979, Discovery of the dinosaurian eggs and footprint from Neixang County, Hunan Province: *ibid.*, v. 17, p. 304-307.
- Zhao, Z., and Ding, S., 1976, Discovery of the dinosaurian egg-shells from Alxa, Ningxia and its stratigraphic significance: *ibid.*, v. 14, p. 42-44.
- ZoBell, C., 1964, Geochemical aspects of the microbial modification of carbon compounds: Advances in Organic Geochemistry, Monograph 15, Earth Science Series, p. 339-356.

NOTE ADDED IN PROOF

For completeness, it should be noted that Charles Sternberg originally presented an hypothesis on upland nurseries in 1949. In this paper he also noted that *Brachyceratops montanensis* from the Two Medicine Formation was, in reality, an immature *Monoclonius*, and that single-rooted teeth were features characteristic of immature animals. Since the composite skeleton of "*Brachyceratops*" on exhibit at the U.S. National Museum would have had a body weight less than one-eighth that of an adult *Monoclonius*, it is considered here as a baby. (Sternberg, C. M., 1949, The Edmonton fauna and description of a new *Triceratops* from the Upper Edmonton member; phylogeny of the Ceratopsidae: National Museum of Canada, Bulletin 113, p. 33-46.)

MANUSCRIPT RECEIVED MAY 11, 1981

REVISED MANUSCRIPT RECEIVED SEPTEMBER 7, 1981

MANUSCRIPT ACCEPTED SEPTEMBER 16, 1981