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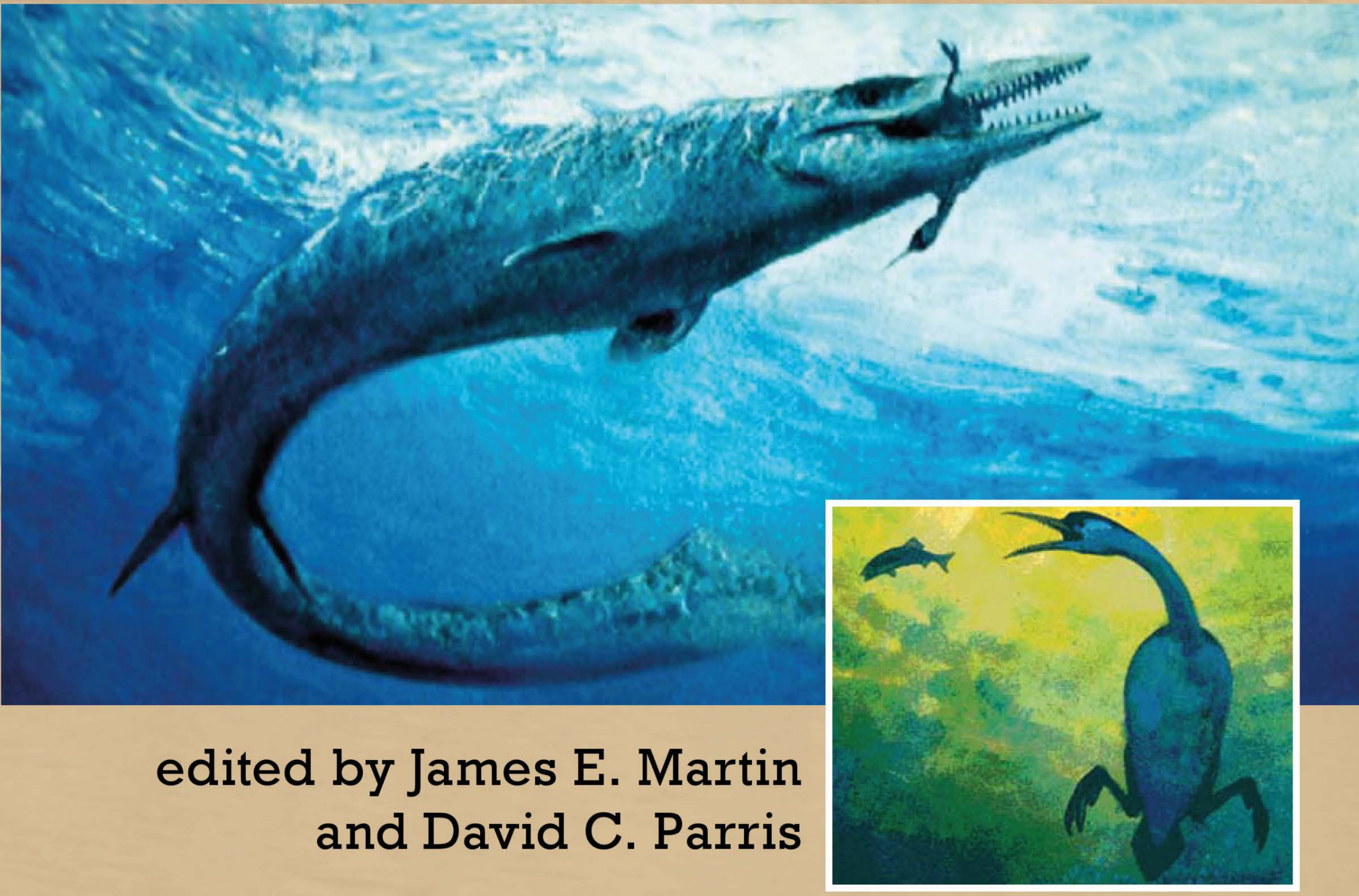
The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas



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Cover: Screened image is the Late Cretaceous Niobrara Chalk overlain by newly defined members of the Sharon Springs Formation of the Pierre Shale Group. The large reptile is that of a new species of the mosasaur (*Hainosaurus*) feeding upon a diving bird (*Hesperornis*). The illustration in the right foreground is a reconstruction of a new species of the Late Cretaceous diving bird (*Baptornis*). Both illustrations courtesy of Daniel Varner.

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Introduction to the geology and paleontology of the Late Cretaceous marine deposits of the Dakotas

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A CLASSIC AREA FOR INVESTIGATION

This volume represents a "State of the Science" assemblage of studies for the classic section of marine Cretaceous formations along the Missouri River. Two hundred years ago along that fabled route the Lewis and Clark Corps of Discovery carried out its mission, which may be said to have established public sponsorship of science in the young republic. While exploration, commerce, national and international politics, and the various visions of America were important aspects, the natural history described in the journals remains memorable and significant. A few words of tribute are certainly justified, as well as an appended commentary reviewing the ways in which that expedition began scientific investigation of our stated topic.

The excellence with which Lewis and Clark conducted their mission not only served the purposes of presidential policies but also determined much future policy making. Considering the available resources at that time and the unknown vastness they sought to explore, their enterprise could scarcely have been conducted with more competence and efficiency, including the choice of participants, regard for the safety of all, and full participation in the gathering of information. We are among only the latest of subsequent analysts, and we hold them in as much esteem as does anyone. While the general history of the expedition is the subject of current commemorations (Gilman, 2003), our perspective is primarily geological.

Geology was of obvious practical importance to an expedition interested in passages, trade routes, and military applications. President Jefferson was interested in such information, and his personal vision of America as a dominant agricultural nation also was compatible with geological knowledge. Whatever his degree of familiarity with the pioneering geological works of Europeans at that time, their grounding in engineering and agriculture was no doubt known to him.

As for paleontology, we cannot fully know what could have been anticipated, except that Jefferson's hope of finding living megafauna was not realized. However, the paleontological potential of the Louisiana tracts was eventually to yield creatures far more bizarre than any known to Jefferson, and unfortunately (or fortunately) just as extinct. While paleontology does have practical economic applications, its appeal to the general population (and even to us as practitioners) remains largely humanistic.

Although coincidental, the outbound expedition saw the marine Cretaceous section from the lower to the upper, much as a practical field geologist of today would wish its examination (Martin et al., 2004). Fortunately, Lewis and Clark also made many geological observations in the early months; they noted many points of geological interest before encountering numerous and substantial discoveries of living flora and fauna. They thus provided some reasonable observations on the Cretaceous section, despite their lack of geological training.

Late Cretaceous Stratigraphic Units

The rocks of the Cretaceous System in the Great Plains are, of course, dominantly of marine origin. Along the Missouri River the Dakota Formation (Lower Cretaceous) begins the sequence, followed by units traditionally mapped as Graneros and Greenhorn Formations. Both of the latter formations were originally described by the noted federal survey geologist G.K. Gilbert (1896) and are familiar and widespread lithostratigraphic units. The Greenhorn Formation in the Black Hills area has produced

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numerous fossils, including a new plesiosaur, described herein by B.A. Schumacher. The Carlile Formation (Turonian), also named by Gilbert (1896), overlies the Greenhorn Formation and is widespread and abundantly fossiliferous.

The Carlile Formation is overlain unconformably (Hattin, 1975) by the Niobrara Formation (Coniacian–early Campanian), which, being chalk dominated, is the signature unit of the Cretaceous System in the Western Interior (Shurr, 1984). Historically, the Niobrara's exposure in the Missouri River Trench was from the vicinity of Yankton, South Dakota, to near Fort Thompson, South Dakota (Kirby, 1932; Petsch, 1955), although now the unit is obscured by impoundments for much of that interval. Its geology and paleontology have been extensively studied by many authorities (see especially Gries and Martin, 1985; Schumacher, 1997; Martin et al., 1998).

The black marine Pierre Shale (Campanian–Maastrichtian) is exposed throughout much of the Great Plains region and may overlie the Niobrara Formation either conformably or unconformably; local unconformities are known within the Pierre Shale (Martin, 1996), and the faunas of the two formations have some similarities (Carpenter, 1990). Readily observed in elevated outcrops from Fort Randall, South Dakota, northward, the Pierre Shale dominates the river basin upstream well into North Dakota (Kirby, 1932; Petsch, 1955; Clayton et al., 1980). Many earlier studies were completed that sought to describe practical subdivisions of the formation (see especially Searight, 1937). However, the benchmark publication of Crandell (1958) established a sound basis for much of the work of the last half century. Although there have been many additional geologic and paleontologic investigations of the Pierre Formation, the intensity of studies during the past two decades has prompted the symposium of papers published here.

The Fox Hills Formation (Maastrichtian) essentially completes the marine Cretaceous sequence, although the marine Breien Member (Maastrichtian) of the overlying Hell Creek Formation deserves independent mention. Overlying and gradational with the Pierre Formation, the sandstone-dominated Fox Hills Formation is widespread at the surface in much of northwestern South Dakota (Waage, 1961, 1968; Pettyjohn, 1967) but is not found along the Missouri River unless an observer goes upstream to the vicinity of Dewey and Corson Counties (Kirby, 1932; Petsch, 1955). In North Dakota the Fox Hills Formation is at basin level in the vicinity of the confluence with the Cannonball River and upstream to near Bismarck (Clayton et al., 1980). Upstream from there, the Missouri River is predominantly within Tertiary sediments. Studies of the Fox Hills Formation and the Breien Member in North Dakota have yielded much information during recent years (Hoganson and Murphy, 2002, 2003; Becker et al., 2004).

As will be evident from the papers of this volume, the intricacies of this seemingly simple sequence are numerous, and our investigations have led us to propose new units as described herein. However, the basic sequence, as subdivided, is to some degree recognizable in the earliest works of explorers.

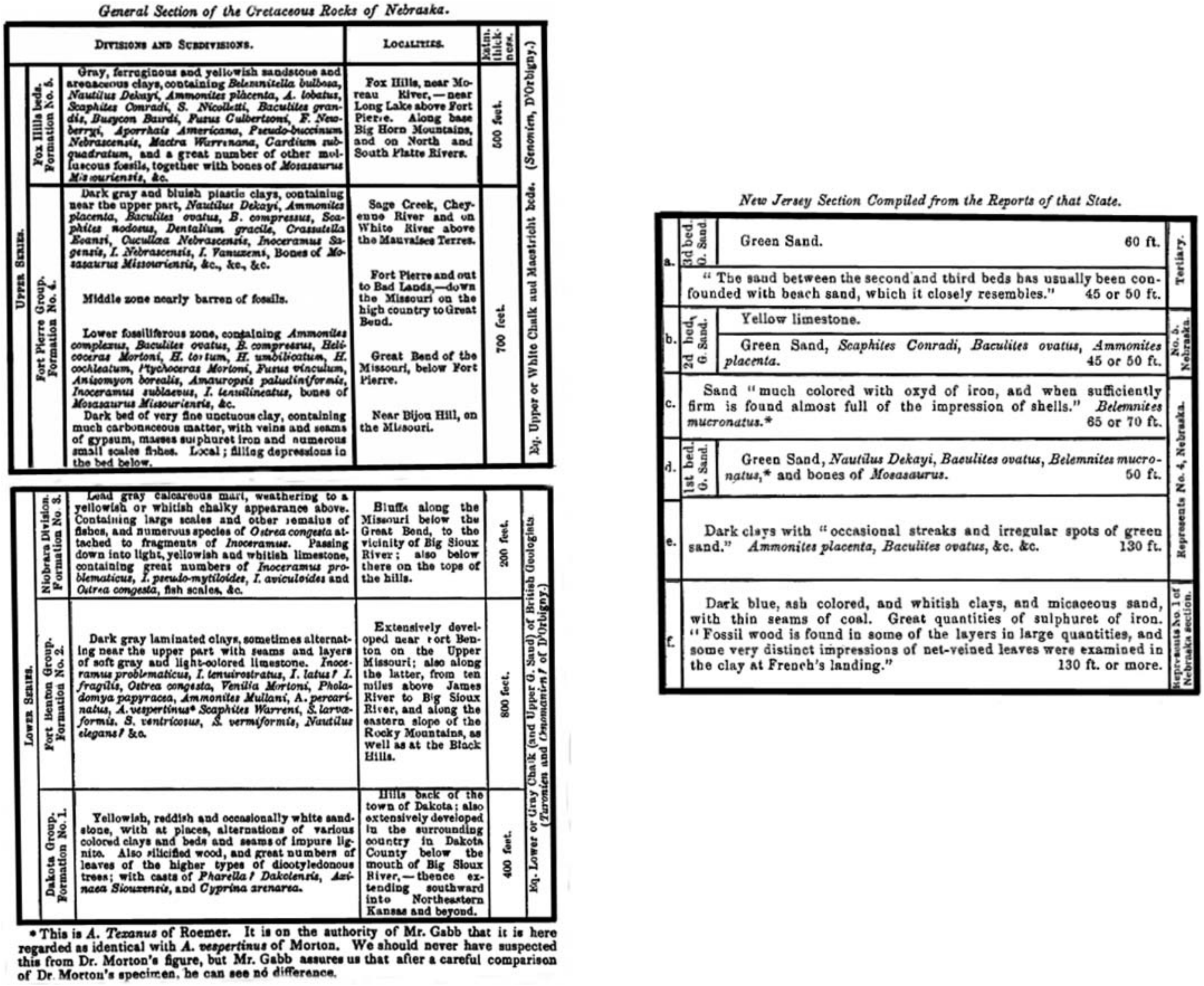
The first formal proposal of units in the Cretaceous sequence was by Meek and Hayden (1862), who described the Niobrara, Fort Pierre (Pierre), and Fox Hills Formations (Fig. 1). As these three lithostratigraphic units form the bulk of the considerations in current studies, it is appropriate to review the original concepts. Published only ~50 yr after Lewis and Clark's Corps of Discovery, the units described by Meek and Hayden are readily recognizable as the foundation of current stratigraphic nomenclature. The underlying Fort Benton Group of Meek and Hayden was later to receive formational designations from Gilbert (1896) but is readily recognizable as including the Graneros, Greenhorn, and Carlile Formations of later usage.

The description of the Niobrara Division of Meek and Hayden (1862) is of great interest, for although they appropriately picked the confluence of the Missouri and Niobrara Rivers as the type locality, their knowledge of the entire range of exposures along the Missouri River was extensive. Noting that the Niobrara "is first seen in descending the Missouri, a short distance below the Great Bend, where it rises by a gentle dip from beneath the succeeding formation (the Fort Pierre Group)," they were giving a description that could not be improved upon even now. The lithologic description is also readily recognized: "mainly of lead gray richly calcareous marl, which, where long exposed assumes a light buff or whitish color, and presents much the appearance of true chalk. Below it passes into more compact beds of soft bluish gray limestone."

Although common usage has shortened the Fort Pierre Group of Meek and Hayden (1862) into Pierre Formation (or Pierre Shale), the lithology, as they described it, is all too familiar: "The Fort Pierre Group consists of a vast accumulation of fine gray and dark colored clays in moderately distinct layers, but never presents a laminated or slaty structure like the Fort Benton Group. When wet, these clays are soft and plastic, but in drying they often crack and crumble so as to obliterate the marks of deposition in vertical exposures." In that time, prior to motorized vehicles, the conversion of the formation to "gumbo" in wet weather could still be modestly described. The bentonitic shale is a major source of the sediment that gave rise in early times to the nickname "Big Muddy" for the Missouri River.

A few more quotations make it clear that the authors were well aware of the areal extent of the surface exposures. "This formation composes all the hills on both sides of the Missouri at Fort Pierre, and much of the country between there and the Bad Lands." And later, in the same paragraph, "Above Fort Pierre, it gradually sinks beneath the Fox Hills Group in the region of Cheyenne and Moreau Rivers, but continues to be seen in the bluffs of the Missouri and other streams for some distance beyond." It would appear that with current research of this extraordinarily thick and widespread sequence, the papers published herein justify raising the Pierre once again to group status in the sense of twenty-first century usage.

With respect to the research of this current volume, we also note that the comparison to the Cretaceous of New Jersey and its paleofauna was also of great interest to Meek and Hayden. Their notation that "the beds at the Great Bend of the Missouri, are probably on a parallel with the Green Sand of New Jersey" anticipated much of the institutional collaboration that remains current



General Section of the Cretaceous Rocks of Nebraska.

Divisions and Subdivisions.			Localities.	Estm. thickness.	
Upper Series.	Fox Hills beds. Formation No. 5.	Gray, ferruginous and yellowish sandstone and arenaceous clays, containing *Belemnitella bulbosa, Nautilus Dekayi, Ammonites placenta, A. lobatus, Scaphites Conradi, S. Nicolletti, Baculites grandis, Busycon Bairdi, Fusus Culbertsoni, F. Newberryi, Aporrhais Americana, Pseudo-buccinum Nebrascensis, Mactra Warrenana, Cardium subquadratum*, and a great number of other molluscous fossils, together with bones of *Mosasaurus Missouriensis*, &c.	Fox Hills, near Moreau River, — near Long Lake above Fort Pierre. Along base Big Horn Mountains, and on North and South Platte Rivers.	500 feet.	Eq. Upper or White Chalk and Maestricht beds. (Senonien, D'Orbigny.)
	Fort Pierre Group. Formation No. 4.	Dark gray and bluish plastic clays, containing near the upper part, *Nautilus Dekayi, Ammonites placenta, Baculites ovatus, B. compressus, Scaphites nodosus, Dentalium gracile, Crassatella Evansi, Cucullæa Nebrascensis, Inoceramus Sagensis, I. Nebrascensis, I. Vanuxemi*, Bones of *Mosasaurus Missouriensis*, &c., &c., &c.	Sage Creek, Cheyenne River and on White River above the Mauvaises Terres.	700 feet.	
		Middle zone nearly barren of fossils.	Fort Pierre and out to Bad Lands,—down the Missouri on the high country to Great Bend.		
		Lower fossiliferous zone, containing *Ammonites complexus, Baculites ovatus, B. compressus, Helicoceras Mortoni, H. tortum, H. umbilicatum, H. cochleatum, Ptychoceras Mortoni, Fusus vinculum, Anisomyon borealis, Amauropsis paludiniformis, Inoceramus sublaevus, I. tenuilineatus*, bones of *Mosasaurus Missouriensis*, &c.	Great Bend of the Missouri, below Fort Pierre.		
		Dark bed of very fine unctuous clay, containing much carbonaceous matter, with veins and seams of gypsum, masses sulphuret iron and numerous small scales fishes. Local; filling depressions in the bed below.	Near Bijou Hill, on the Missouri.		
Lower Series.	Niobrara Division. Formation No. 3.	Lead gray calcareous marl, weathering to a yellowish or whitish chalky appearance above. Containing large scales and other remains of fishes, and numerous species of *Ostrea congesta* attached to fragments of *Inoceramus*. Passing down into light, yellowish and whitish limestone, containing great numbers of *Inoceramus problematicus, I. pseudo-mytiloides, I. aviculoides* and *Ostrea congesta*, fish scales, &c.	Bluffs along the Missouri below the Great Bend, to the vicinity of Big Sioux River; also below there on the tops of the hills.	200 feet.	Eq. Lower or Gray Chalk (and Upper G. Sand) of British Geologists (*Turonien* and *Cenomanien*? of D'Orbigny.)
	Fort Benton Group. Formation No. 2.	Dark gray laminated clays, sometimes alternating near the upper part with seams and layers of soft gray and light-colored limestone. *Inoceramus problematicus, I. tenuirostratus, I. latus? I. fragilis, Ostrea congesta, Venilia Mortoni, Pholadomya papyracea, Ammonites Mullani, A. percarinatus, A. vespertinus* Scaphites Warreni, S. larvæformis. S. ventricosus, S. vermiformis, Nautilus elegans?* &c.	Extensively developed near Fort Benton on the Upper Missouri; also along the latter, from ten miles above James River to Big Sioux River, and along the eastern slope of the Rocky Mountains, as well as at the Black Hills.	800 feet.	
	Dakota Group. Formation No. 1.	Yellowish, reddish and occasionally white sandstone, with at places, alternations of various colored clays and beds and seams of impure lignite. Also silicified wood, and great numbers of leaves of the higher types of dicotyledonous trees; with casts of *Pharella? Dakotensis, Axinaea Siouxensis*, and *Cyprina arenarea*.	Hills back of the town of Dakota; also extensively developed in the surrounding country in Dakota County below the mouth of Big Sioux River, — thence extending southward into Northeastern Kansas and beyond.	400 feet.	

* This is *A. Texanus* of Roemer. It is on the authority of Mr. Gabb that it is here regarded as identical with *A. vespertinus* of Morton. We should never have suspected this from Dr. Morton's figure, but Mr. Gabb assures us that after a careful comparison of Dr. Morton's specimen, he can see no difference.

New Jersey Section Compiled from the Reports of that State.

a.	3d bed. G. Sand	Green Sand.	60 ft.	Tertiary.
		" The sand between the second and third beds has usually been confounded with beach sand, which it closely resembles."	45 or 50 ft.	
b.	2d bed, G. Sand.	Yellow limestone.		No. 5. Nebraska.
		Green Sand, *Scaphites Conradi, Baculites ovatus, Ammonites placenta.*	45 or 50 ft.	
c.		Sand "much colored with oxyd of iron, and when sufficiently firm is found almost full of the impression of shells." *Belemnites mucronatus.**	65 or 70 ft.	Represents No. 4, Nebraska.
d.	1st bed. G. Sand.	Green Sand, *Nautilus Dekayi, Baculites ovatus, Belemnites mucronatus,** and bones of *Mosasaurus.*	50 ft.	
e.		Dark clays with "occasional streaks and irregular spots of green sand." *Ammonites placenta, Baculites ovatus*, &c. &c.	130 ft.	
f.		Dark blue, ash colored, and whitish clays, and micaceous sand, with thin seams of coal. Great quantities of sulphuret of iron. "Fossil wood is found in some of the layers in large quantities, and some very distinct impressions of net-veined leaves were examined in the clay at French's landing."	130 ft. or more.	Represents No. 1 of Nebraska section.

Figure 1. Original subdivision of the Cretaceous units by Meek and Hayden (1862).

today. Their correlation chart, reproduced above, represented a creditable amount of communication and scientific consensus.

The perception with which Meek and Hayden described the lower formations is also notable in their description of the Fox Hills beds. They noted the more arenaceous composition of the Fox Hills as well as the "more yellowish or ferruginous tinge." For this, the last major marine formation in the regional Cretaceous series, they again included faunal information that correlated with the Eastern Seaboard.

CONTENTS OF THIS VOLUME

As noted previously, the investigations of the past two decades have brought new understanding of the marine sequence, especially to the Pierre Shale, a hallmark formation of the Northern Plains. Detailed lithostratigraphy now enables the elevation of the recognizable units within the formation, and it is here proposed that the Pierre be raised to group status, its members to formations, and new members recognized (Martin et al., Chapter 2). Prior studies noted the existence of bentonites and touted their use as potential correlation tools and time line approximations. This potential has now been fully realized as described herein (Bertog et al., Chapter 3), and lithostratigraphy and chronostratigraphy have both benefited accordingly. The detailed measurement of lithostratigraphic sections, completed in conjunction with paleontologic prospecting, has enabled more competent mapping and paleoenvironmental analysis. The interpretation of marine water depths of sedimentation (Hanczaryk and Gallagher, Chapter 4) serves as a tool in sequence stratigraphy and other broader interpretations. The development of rare-earth-element analysis as a method in paleoenvironmental research has also come to major fruition during recent years (Patrick et al., Chapter 5).

No aspect of the Pierre Formation has been more significantly advanced by new discoveries than has the paleontology, notably in the lower and middle members. Invertebrate paleontology of the Pierre Formation has received great emphasis in previous research, notably for biostratigraphy on the basis of cephalopod assemblages and pelecypod occurrences. Fox (Chapter 6) contributes paleoecologic interpretations on the basis of invertebrate fossils of the DeGrey Member.

Vertebrate paleontology of the Pierre Formation now includes many and varied research projects, and fossil fish are abundantly represented in the record. Parris et al. (Chapter 7) examined some aspects and new discoveries of this extensive record, which enables greater understanding of North American Cretaceous ichthyofaunas.

Reptilian fossils of the Pierre Formation include some of the earliest discoveries and many long-standing questions. The taxonomy of the marine turtles, in particular the well known genus *Toxochelys,* can now be more readily studied by examination of a sufficient sampling of cranial specimens (i.e., those specimens best suited for taxonomic diagnoses). Hart Carrino (Chapter 8) has researched this genus, seeking clarification of the specific assemblage.

Plesiosaurs are relatively uncommon finds among marine reptiles, and almost every good specimen provides important information. This is certainly true of the specimen herein described by Schumacher (Chapter 9), because it provides insights for classification of plesiosaurs generally. The comparisons described by Thompson et al. (Chapter 10) reveal differences in gastrolith ingestion between North American and Antarctic specimens.

Mosasaurs are marine lizards, well represented in the Pierre Formation and included among some of the most important paleontological discoveries of recent years. However, one of the earliest specimens to be found, the type specimen of *Mosasaurus missouriensis,* continues to be of interest. The restudy of this important specimen demonstrates once again the historical (as well as scientific) importance of paleontology in the Missouri River region. The afore-mentioned use of rare-earth-element analysis in paleontological work also has been applied to this important mosasaur specimen to determine precise provenance data. This case study (Patrick et al., Chapter 11) indicates the utility of this methodology.

A few individual mosasaur specimens are so remarkably informative that they deserve individual description. So it is with the stomach contents from the best specimen ever recovered of the rare genus *Globidens* (Martin and Fox, Chapter 12), providing definitive information on the function of the spherical tooth crowns of a new species of the genus (Martin, Chapter 13). Martin (Chapter 14) also contributes new information concerning the unequivocal first occurrence of the large mosasaur *Hainosaurus* in North America, including the description of a new species. The huge size attained by some mosasaur genera and their possible initial discovery by Lewis and Clark are revealed in a specimen description by Meredith et al. (Chapter 15).

The Pierre Formation is one of the few lithologic units to yield a fair number of flying reptile specimens. These comprise a sufficient sampling to permit taphonomic analysis by Hargrave (Chapter 16), including some conclusions about the ways of life and the taphonomy of individuals of the genus *Pteranodon*.

The fossils of flightless diving birds have long been known to occur in the Pierre Shale, but most specimens are referable to long-established taxa. Thus, the description of a new species of *Baptornis* (Martin and Cordes-Person, Chapter 17) is of particular interest.

While this volume features many papers concerning the Pierre Formation and its fauna, the overlying Fox Hills Formation has yielded a substantial vertebrate fauna as well. The paleoecological interpretations are discussed by Hoganson et al. (Chapter 18).

In conclusion, this collection of papers should provide a sound impression of the status of knowledge of the marine Cretaceous of the northern Great Plains.

GEOLOGY AND PALEONTOLOGY RECORDED BY THE CORPS OF DISCOVERY

Although many annotations of the journals of Lewis and Clark exist, our objective here is only to add what we can on the basis of our own current investigations. The following are notes on the accounts of the expedition in the sections where we ourselves have field experience that provided the basis of the papers herein, primarily the Missouri River Trench between the confluences of the Platte to the Cannonball Rivers, 21 July through 18 October 1804, of the outbound expedition.

As the expedition moved upstream from the Platte confluence, the first significant geologic comments concerned the area of the Council Bluff (for the sake of consistency, our references will be made to the Thwaites [1905] edition of the journals, as republished in 1969). As noted by the editor, some doubt persists as to the exact location of the Council Bluff historic event, but there seems to be no question that the locality was marked by loess hills, self-evident to any modern observer. Clark's notation (3 August) that the "Soil of the Bluff well adapted for brick" is consistent. It is not so obvious what he meant by "Pumey stones" observed the next day, but if pumice was the supposed rock type, it would be a reasonable mistake to use that term for partially consolidated loess material or water-worn chalk (and less logical to apply it to glacial erratics).

5 August 1804. Clark commented about erosion and caving of the banks and bends of the river, and probably correctly surmised that the "Mud or Ooze" he observed was material eroded and redeposited any number of times in the flood basin.

6 August 1804. Party passed the Soldiers River Mouth. Now engineered and presumably realigned, this drainage would be the approximate position from which the expedition's first fossil find was recovered, a fish now known as *Saurocephalus lanciformis*. As noted by previous accounts (Simpson, 1942), the fossil exists but is not mentioned in the journal. Simpson's extensive discussion of the fossil has established its authenticity for any reasonable observer, and the only question left unanswered is the apparent displacement from original context.

The statement on the original field label, which is still in existence, is that the fossil was found some distance eastward from the river. To any observer throughout the region, this would mean the conspicuous outcrops of the loess hills in Harrison County, Iowa. The cavern described on the label would almost certainly be a cliff overhang rather than a cavern in the usual sense, and the obvious implication would be that an aboriginal inhabitant had left the specimen there, some distance from the Niobrara Formation that was its probable source. As Simpson noted, the label was probably written by Lewis, but the fossil could have been found by anyone in the expedition. The journal entry attributed to Clark (Ordway edition consistent) indicates that the expedition was preoccupied with stormy weather and the distraction of a presumed deserter, so the fossil find might have been subsequently labeled, and possibly misdated. This is totally speculative, of course, and the geological situation would have been essentially the same from 3 through 20 August.

11 August 1804. The Clark entry notes sandstone (possibly glacial deposits?) in the vicinity of the mound burial of Mahars (Omahas) King Black Bird, and considerable topographic relief (300 ft) on what is now the Nebraska side of the river.

12 August 1804. Clark cites "Commencement of a Bluff," with yellow and brown clay and soft sandstone (possible glacial deposits?), on the Nebraska side.

20 August 1804. The death of Sergeant Floyd occurred, and he was honored with naming of a river and bluff.

21 August 1804. The expedition passed the Big Sioux River, and mentions the occurrence of pipestone at a distance upstream in that river, related by interpreter Durrien. This accurately records the existence of catlinite beds within the Precambrian Sioux Quartzite.

22 August 1804. Clark describes a bluff with mineral deposits, one of the more complete attempts to describe a geological feature. A presumed paleontological aspect is the description of cemented shells therein. Of more immediate concern was Lewis's having experienced some degree of poisoning, presumably by taste-testing the minerals. The various minerals described were only field identifications, of course: "Alum, Copperas, Cobalt, Pyrites." Presumably, leachate was the cause of the deposition, as suggested by editorial commentary.

24 August 1804. Clark gave account of a heated bluff, footnoted in the Thwaites edition with a comment from Erwin Hinckley Barbour, and presumed to be at Ionia, Nebraska (in the Carlile Formation?). Similar phenomena are known in South Dakota, including possibly the origin of the somewhat redundant place name Burning Brule. Clark's comment about the surface material suggests that fused or encrusted material was called "Cobalt" by him. In the same log entry he refers to the White Stone River and the presence of Spirit Mound, the former name signifying the Niobrara Formation in the vicinity. Note that various entries of the following days include mention of white or yellow color.

25 August 1804. Further comments by Clark regarding Spirit Mound, whether natural or human-made. (It is, of course, a natural prominence.) There is a further note of Lewis's feeling ill from mineral tasting.

26 August 1804. Entry describes white and blue or dark earth cliff.

27 August 1804. Description of a white clay marl or chalk bluff, noting cobalt (of Clark's supposition) and "ore" embedded.

28 August 1804. White bluffs noted, and Calumet Bluff named, footnoted by Thwaites's authorities as opposite Yankton presently.

1 September 1804. More cliffs described as resembling chalk of varying color.

2 September 1804. Yellow Clay bluff noted in Bon Homme vicinity.

3 September 1804. Continuation of white banks on both sides of river.

4 September 1804. Creek called White Lime.

5 September 1804. Bluff of Blue Earth noted, with emerging springs of mineral salts.

7 September 1804. Clark describes a conical prominence, footnoted by Thwaites as "The Tower."

8 September 1804. Prominences described near Chicot Island (Fort Randall). "Countrey on the S.S. is pore & broken."

10 September 1804. The most intriguing entry from the paleontological standpoint was recorded this day and continues to confound interpretation. By Clark's account, it is 10–11 mi upriver from Fort Randall, "below this on a hill on the L.S. we found the back bone of a fish, 45 feet long tapering to the tale, Some teeth &c. those joints were separated and all petrified."

Lest anyone suspect Clark exaggerated the size or misstated it, Ordway's account is nearly identical. There is, however, no indication that any of it was collected. The site would be in what is now Gregory County, South Dakota. Although it was thoroughly discussed by Simpson (1942), some additional speculation is possible on the basis of current investigations along the river. Whether Niobrara Chalk or lower Pierre Shale was the source, it would be a zone in which tylosaurine mosasaurs could be found, fossils of that size range, with conspicuous teeth and vertebrae and superficially resembling a fish (Meredith et al., Chapter 15). Because the Corps of Discovery was investigating a river, and had no concept of an epicontinental seaway, the interpretation of a tylosaur as a huge fish would have been quite reasonable. Another likely possibility is that the "fish" may have been an elasmosaurid plesiosaur, whose large flat vertebrae could have been mistaken for those of a fish.

There is no mention of any collection of the specimen, and though it seems unlikely that they would have collected all of it, it is equally unlikely that they collected none of it, especially the teeth. It will be recalled that no mention is made of the *Saurocephalus lanciformis* specimen in the journals either. One suspects that they may have intended to collect such a huge specimen on the return trip, rather than carry or ship it, but it may have been forgotten or obscured 2 yr later, when they were undoubtedly anxious to get home. None of our extensive efforts connected with this contribution, nor any others published as of this time, have produced other information about this specimen.

12 September 1804. By Clark's account, 28 mi farther upriver from the supposed fish fossil, the terrain is described as high hills on either side, with slate and coal mixed. This would probably be the description of the lower Pierre Shale (Sharon Springs Member) by a casual observer; it certainly would not be the Niobrara Formation.

13 September 1804. Clark describes camping beneath a bluff, and commenting regarding mineralization that varies among the bluffs of each side. This may refer to sulfurous and/or gypsiferous minerals in the Pierre Formation, particularly in the Sharon Springs Member.

14 September 1804. Clark describes searching for a purported volcano, described to him by an acquaintance. Not finding any such thing, there is no further description, but it likely refers to the burning or steaming outcrop, equivalents of which were previously described. He also commented on the ease of erosion of the rock formations. He was downstream slightly from the confluence with the White River.

16 September 1804. Clark named *Corvus* Creek in honor of a magpie he collected there, noting its relationship within corvids. This foreshadowed (unwittingly) the day when the Crow Creek Reservation would become famous as a site for Cretaceous fossils, but the venerability of the tribal name, dating to this contact period, is noteworthy.

20 September 1804. At the end of the previous day's entry, Clark commented on the commencement of the Big Bend of the river, apparently well known and previously described to him. He crossed it on foot, observing the rocks with little comment. However, a casual comment in the course distances and readings mentions hard rocks along the shores, and this presumably refers to the glacial erratics that abound near the bend.

21 September 1804. A bank collapse occurred, endangering the encampment, an event unsurprising to those familiar with the banks there, lined with the Gregory Member of the Pierre Shale, which is quite unstable when wet.

22 September 1804. Hunters complained of the rough surface rocks, which were hard on moccasins. This again probably refers to the glacial erratics on the surface.

24 September 1804. Approaching the confluence of the Bad River (Teton River of the journals), and expectations of meeting the local tribes. Clark again comments on the abundance of rocks, by which he surely was referring to the erratics.

1 October 1804. Arrival at the Cheyenne River (Dog, or Chien, River of journal entries). A Frenchman resident there gave a reasonable account of conditions up that drainage to the Black Hills, both in distance and terrain.

6 October 1804. Clark described large stones in the water, washed from nearby hills. The reference seems more likely to mean erratics rather than concretions, but it is difficult to say for certain. The Pierre Shale in this area, now Walworth County, are mostly upper members and would not likely produce large concretions (such as might be seen in the Sharon Springs Member).

7 October 1804. Clark commented on the Moreau River, erroneously attributing its origin to the Black Hills area.

8 October 1804. Clark's comment on the Grand River again inaccurately attributes its origin to the Black Hills.

13 October 1804. Clark described stones in the river, resembling human and dog shapes, and speculated on their legendary origins. At this point the expedition would have been near to what is now the state line, possibly in the Fox Hills Formation.

15 October 1804. Curious hills, shaped like houses with roofs, are described by Clark. This would confirm that the Expedition, by then in what is now North Dakota, was in typical Fox Hills Formation terrain.

18 October 1804. Having reached the Cannonball River, the entry comments on the geological origin of the name of the stream. (See also Hoganson and Murphy, 2003.)

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Many of the papers presented here are the result of field investigations on tracts of the U.S. Army Corps of Engineers (which provided considerable financial support) and the Crow Creek Tribal Lands. These investigations could not have proceeded without their kindnesses. The people of Chamberlain and Oacoma, South Dakota, graciously hosted our field parties, providing constant support. The editors are also grateful to the Geological Society of America and the South Dakota Academy of Science for providing forums for public presentation of the research. E. Beitel provided technical assistance for reproduction of Figure 1.

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Revised lithostratigraphy of the lower Pierre Shale Group (Campanian) of central South Dakota, including newly designated members

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ABSTRACT

The Pierre Shale, a member of the Montana Group, is extensively exposed throughout the Northern Great Plains and is well exposed along the Missouri River Trench in central South Dakota. Currently, the Pierre Shale is of formational rank, but herein it is elevated to group status and should be termed the *Pierre Shale Group.* Most current members of the Pierre Shale should be elevated to formational rank, as they are of distinctive lithology and are mappable throughout the Missouri River area and elsewhere. The name *Montana Group* should be abandoned because of its relatively limited lithostratigraphic utility.

Extensive geological and paleontological investigations of the lower Missouri River Trench indicate that a number of previously described units should be subdivided. In particular, the lowest described unit of the Pierre Shale along the Missouri River, the Sharon Springs, exhibits three distinct disconformity-bounded lithostratigraphic units that are newly designated as members. The lowermost unit is distinguished by bentonites, and the upper two units can be observed in the type area of the Sharon Springs in western Kansas. The lowermost unit is characterized by numerous bentonite beds similar to the Ardmore bentonitic succession in the southern Black Hills, is normally disconformably superjacent to the Niobrara Formation, may be absent where degraded, and is named the *Burning Brule Member.* The overlying middle unit within the Sharon Springs consists of a siliceous shale that weathers vertically and is termed the *Boyer Bay Member,* whereas the upper unit is a bentonitic shale characterized by gypsiferous phosphatic concretions and is named the *Nicholas Creek Member.* These three units are herein regarded as new members of a hierarchically elevated Sharon Springs Formation.

Other currently recognized members of the Pierre Shale in central South Dakota should likewise be elevated to formation-rank units except for the Crow Creek Member, a relatively thin tan siltstone. Because this unit is not mappable at recognized

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scales, it should be retained as a member of the DeGrey Formation. Inclusion of the Crow Creek Member within the DeGrey Formation is based upon another sporadically occurring tan siltstone that lies stratigraphically lower, and the intervening shales are similar to those of the lower DeGrey Formation.

The Pierre Shale members should also be elevated to formational status in North Dakota, Kansas, and around the Black Hills in eastern Wyoming and western South Dakota. The elevation of units should probably be made throughout the Pierre Shale depositional area, but those decisions should be made by local investigators.

Keywords: Cretaceous, Pierre Shale Group, lithostratigraphy, new members, South Dakota.

INTRODUCTION

One of the classically known geological units in the American West is the Pierre Shale, whose type area occurs in central South Dakota (Fig. 1). Lewis and Clark visited the area in 1804 while ascending the Missouri River (see the introduction to this volume, Parris et al.), and in 1810 Nuttall noticed a pyrite-rich unit (Nuttall, 1821) that was destined to become the Sharon Springs Member of the Pierre Shale. The next major investigators were F.B. Meek, J. Hall, and F.V. Hayden, associated with the federal geological survey, although Joseph Nicollet and John Evans collected specimens from what was to become the Pierre Shale in 1839 and 1849, respectively. Meek and Hayden (1862) described the unit for exposures of interbedded black shale, bentonite, concretions, and marl along the banks of the Missouri River in the vicinity of old Fort Pierre, an early western fort established originally in 1817 and eventually named for Pierre Chouteau Jr., which was utilized principally as a trading post and later as a steamboat destination. The lithostratigraphic unit was designated as the Fort Pierre Group, the fourth of five subdivisions of the Cretaceous of the Great Plains that had previously been numerically designated (Parris et al., this volume, Chapter 1) by Hall and Meek (1855). Eldridge (1888, 1889) included the Fort Pierre Shale of formational rank in the Montana Group, a group that originally included the marine Fort Pierre Shale and the estuarine-deltaic Fox Hills Formation. Later, the name and lithostratigraphic rank of the unit was shortened to *Pierre Shale*. The Montana Group was expanded (Gill and Cobban, 1973) to include all formations from the top of the Niobrara Formation through the terrestrial Lance and Hell Creek formational equivalents (Fig. 2). Therefore, the Montana Group consists of a great range of lithologies, representing a diversity of paleoenvironments, ranging from totally marine

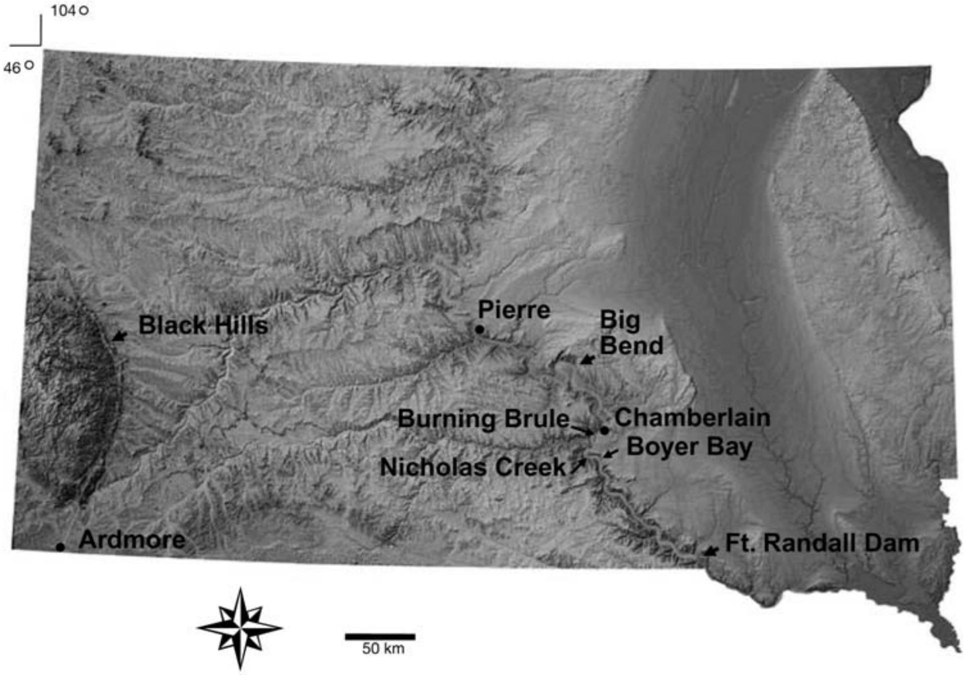

Figure 1. Index map of South Dakota. Important sites are marked along the Missouri River Trench in central South Dakota.

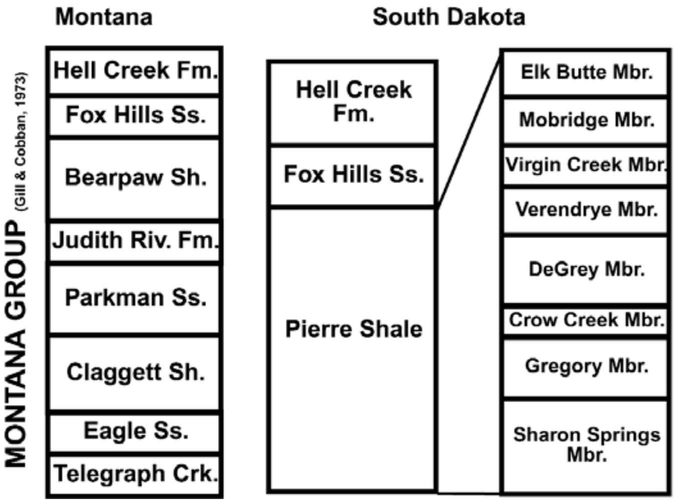

Figure 2. Original nomenclature of the Montana Group in Montana and South Dakota.

to totally terrestrial. Moreover, the group appears to include parts of two separate major transgressive-regressive marine cycles, the Claggett and Bearpaw cycles (Caldwell et al., 1993). Therefore, few uniting factors may be identified for the Montana Group, and this group term should be abandoned.

Although Meek and Hayden (1862) attempted the first subdivision of the Fort Pierre Group, Searight (1937) formally named five superposed members: Gregory, Sully, Virgin Creek, Mobridge, and Elk Creek members. The Gregory and Sully members were subsequently refined. The Sharon Springs Member, originally described in western Kansas by Elias (1931), was extended into South Dakota by Moxon et al. (1938) for the lower portion of the Gregory Member. The upper Gregory, a marl, was designated the *Crow Creek* by Gries and Rothrock (1941) and was considered a formal member of the Pierre Shale by Crandell (1950, 1952). Crandell (1950) also revised the Sully Member to include the DeGrey Member, subjacent to the Verendrye Member. No matter the nomenclature, each member-rank unit, except the Crow Creek, has been mapped by the South Dakota Geological Survey and the U.S. Geological Survey on the basis of distinct lithologies, and therefore these units qualify as formation-rank entities.

Nomenclatural problems are principally found among members of the lower Pierre that were originally considered the Gregory Member by Searight (1937). When the name *Sharon Springs* was extended into South Dakota (Moxon et al., 1938), the Gregory Member was restricted to the upper marl and sandstone, later considered the Crow Creek Member (Crandell, 1950). Gries and Rothrock (1941) noted a marl below the Crow Creek and included this marl and the intervening shale in a newly defined Gregory Member. As a result, the original Gregory Member of Searight (1937) now consists of the Sharon Springs, Gregory, and Crow Creek units.

In 1942, Gries noted an intermittent chalky bed below the Crow Creek. The intervening shale between the two tan units appears identical to the lower bentonitic portion of the DeGrey unit. This lower tan unit has been informally considered to be the Fort Thompson beds (see Hanczaryk and Gallagher, this volume).

The other major nomenclatural revision concerns Searight's (1937) Sully Member. As previously described, the basal unit of the Sully Member, a marl, is now considered the Crow Creek Member. Of the three remaining superposed lithologies of the Sully Member—the Agency, Oacoma, and Verendrye shales—only the latter remains unchanged as the Verendrye Member. In 1942, Gries indicated that the Agency and Oacoma shales were not superposed units; therefore, Crandell (1950) redefined the Agency-Oacoma interval as the DeGrey Member. As a result, as recognized in Crandell's (1950) revision, the Pierre Shale of formational rank included the Sharon Springs, Gregory, Crow Creek, DeGrey, Verendrye, Virgin Creek, Mobridge, and Elk Creek members (Crandell, 1958).

PROPOSAL AND JUSTIFICATION

Our investigation of the lower Pierre Shale during the last 15 yr, in conjunction with detailed vertebrate biostratigraphical collections, suggests that additional revision is required. A number of discrete lithologies occur within the previously designated members, and some members should be redefined on the basis of lithological consideration. These revisions will result in a nomenclature that will have more utility for detailed geological and paleontological studies. Nearly every member of the Pierre Shale has been mapped on a scale of 1 inch to 1 mile (1:62,500) on the following South Dakota and U.S. Geological Survey quadrangles: Lake Andes (Stevenson and Carlson, 1951), Bonesteel (Stevenson and Carlson, 1950), Platte (Carlson, 1950), Lucas (Baker and Carlson, 1951), Dixon (Baker, 1951), Iona (Baldwin and Baker, 1952), Chamberlain (Petsch, 1952), Stephan (Curtiss, 1951), Lower Brule (Petsch and Curtiss, 1950a), Fort George Butte (Petsch and Curtiss, 1950b), Oahe (Crandell, 1955), Canning (Crandell, 1954b), Pierre (Crandell, 1954a), Fort Bennett (Petsch and Bolin, 1950), No Heart (Stevens, 1952a), Artichoke Butte (Stevens, 1952b), Cheyenne Agency (Mickelson, 1952), Mouth of Moreau (Mickelson and Baker, 1950), Mobridge (Baker, 1952), and Pollack (Baldwin, 1951). Therefore, owing to the distinct lithologies of the various members of the Pierre Shale (Crandell, 1958) and their suitability for mapping (North American Commission on Stratigraphic Nomenclature, 1983, p. 858), most members should be raised to formational status (Fig. 3) and should include the Sharon Springs Formation, the Gregory Formation, the DeGrey Formation, the Verendrye Formation, the Virgin Creek Formation, the Mobridge Formation, and the Elk Creek Formation. Because the Crow Creek Member is thin (~3 m), it cannot be mapped like the other Pierre units and should be regarded as a member of the DeGrey Formation. Similar situations occur in western South Dakota, eastern Wyoming, and elsewhere where

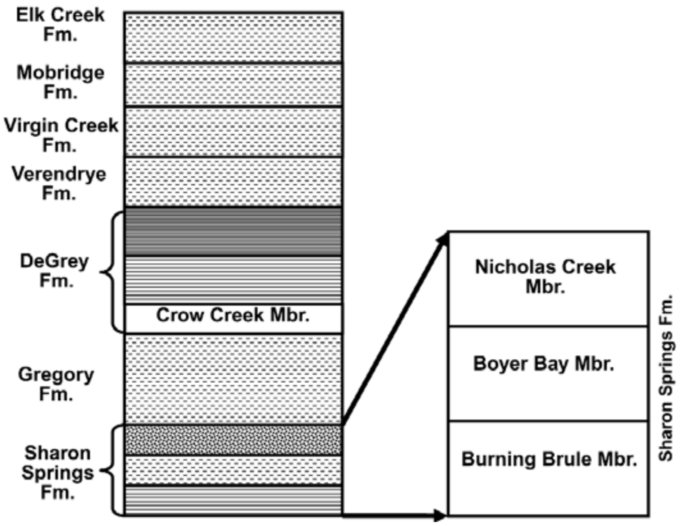

Figure 3. Nomenclature of the Pierre Shale Group as revised herein.

separate successions of members have been described, and these, too, should be elevated to formational rank. Therefore, the Pierre Shale should be raised to group rank and considered to be the Pierre Shale Group. As a consequence, the Montana Group could be raised to supergroup status (North American Commission on Stratigraphic Nomenclature, 1983, p. 859), but its relatively little lithostratigraphic utility suggests that this concept should be abandoned. Another reason for abandonment is that the base of the Montana lithostratigraphic unit has traditionally been placed at the base of the Pierre Shale. However, the similarity of marine deposition and paleofaunas between the subjacent Niobrara Formation and the Pierre Shale suggests that this boundary would not serve as that of a supergroup. On these bases, therefore, we propose abandonment of the Montana Group of Eldridge (1888, 1889).

LOWER PIERRE SHALE GROUP

The lower Pierre Shale Group is the major focus of this contribution (higher occurring units will be reviewed, and new units delineated in later contributions). This portion of the Pierre Shale Group occurs within the Missouri River Trench within South Dakota and is exposed in North Dakota, Colorado, around the Black Hills of South Dakota and Wyoming, and elsewhere. In particular, the Sharon Springs Formation has been found to include distinctive lithologies that may be considered as new members. In northeastern North Dakota this lithostratigraphic interval has been termed the *Pembina Member of the Pierre Shale* (Gill and Cobban, 1965), extending the member terminology from Canada. However, identical member subdivisions occur in North Dakota, as in South Dakota and Kansas; therefore, the Pembina Member should be considered the Sharon Springs Formation in North Dakota. Although it may be argued that the Pembina has priority by a single year (Kirk, 1930), the Pembina was described as the Pembina beds, whereas the Sharon Springs was formally designated a member. Moreover, the long historical, widespread, and common usage of the Sharon Springs terminology in the United States, coupled with the equivalent subdivisions in South Dakota and the type area in Kansas, resulted in our decision to retain the Sharon Springs name.

The Sharon Springs Member was initially designated in Logan and Wallace counties, Kansas, by Elias (1931) for black shales superposed above the Niobrara chalk. Later investigations revealed three subdivisions of the member, including a basal soft, organic-rich shale unit successively overlain by a vertically weathered organic shale and a phosphatic nodular unit (Gill et al., 1972). The soft, organic-rich shale contains relatively few bentonites and lies gradationally above the Niobrara chalk. Based upon bentonite correlations, this lower unit may be equivalent to the basal Pierre Shale unit, the Gammon Ferruginous Shale of the Black Hills area. This lower unit in Kansas is ~27.4 m thick and is disconformably overlain by the vertically weathered shale. This vertically weathered unit is of the same approximate thickness and contains layers of dense carbonate concretions near the top. The upper phosphatic shale unit conformably overlies the vertically weathered unit. The upper unit is ~3–3.5 m thick and contains as many as 10 layers of phosphatic nodules (Gill et al., 1972).

The Sharon Springs Member of Kansas was extended into the Missouri River breaks of South Dakota by Searight (*in* Moxon et al., 1938) and was later extended into the region surrounding the Black Hills (Moxon et al., 1939). Here, the lower Pierre Shale has been subdivided into the Gammon Ferruginous, Sharon Springs, and Mitten Black Shale members (see Gries and Martin, 1985, for historical review). The Sharon Springs Member around the margin of the southern Black Hills contains a basal interval, characterized by numerous bentonite beds, that has been considered informally by us as the Ardmore bentonite succession. This interval is similar to that in central South Dakota and northeastern North Dakota, and geochemical fingerprinting of bentonites confirms this correlation (see Bertog et al., this volume). The main body of the Sharon Springs Member in the Black Hills area normally lies disconformably above the bentonitic-layered unit and contains at least three layers of dense carbonate concretionary layers. This unit weathers vertically because of its highly organic, siliceous nature. A third, softer organic shale may disconformably overlie the vertically weathered unit. This softer shale has thin, interbedded bentonites and is disconformably overlain by the darker, iron-manganese shales and concretions of the Mitten Black Shale Member, named by Rubey (1930).

As previously mentioned, the Sharon Springs equivalent in northeastern North Dakota has been regarded as the Pembina Member of the Pierre Shale but should be considered as the Sharon Springs. Interestingly, three lithological subdivisions may also be recognized, although they are thicker than those exposed in central South Dakota. These subdivisions include superposed units of a lower shale characterized by bentonite layers, a middle unit of vertically weathering organic-rich shale, and an upper phosphatic nodular unit. These subdivisions may be regarded as members of the Sharon Springs Formation in North Dakota.

Three distinct lithologies at both macroscopic and microscopic scales (Martin et al., 2004; Patrick et al., 2004, and this volume) occur within the Sharon Springs Formation along the Missouri River in south-central South Dakota (Fig. 4) and northeastern North Dakota. The basal unit is characterized by numerous distinct beds of yellow-weathered bentonite. The middle unit is characterized by few thin bentonites within a fissile, highly organic, somewhat siliceous gray shale (Schultz et al., 1980) that weathers to a vertical profile (also termed *buttress-weathered* by Gill et al., 1972). The upper unit is a black bentonitic shale characterized by numerous, poorly layered, white to pink, gypsiferous, phosphatic concretions. These three units are herein considered members of the Sharon Springs Formation, and in the Missouri River Trench they represent disconformably bounded packages as well as distinct lithological entities. Therefore, the units in their type area along the Missouri River qualify as both lithostratigraphic and allostratigraphic units. The lower lithostratigraphic member is herein named the *Burning Brule Member,* the middle interval the *Boyer Bay Member,* and the upper unit the *Nicholas Creek Member,* all named from exposures south of the town of Chamberlain, South Dakota, along the banks of the Missouri River. Allomember designations could likewise be applied, utilizing the same geographic name, but the allomembers are of more localized extent than the lithostratigraphic members that occur at a minimum from Kansas to North Dakota.

Sharon Springs Formation

The Sharon Springs Member, a distinctive black, highly organic, fissile shale with numerous bentonites (Gries and Martin, 1985), originally described in Kansas and correlated into South Dakota by Searight (*in* Moxon et al., 1938), is herewith revised and elevated to lithostratigraphic formational rank.

Type section of formation. Near center of section 8, T. 12 S., R. 36 W., Logan County, Kansas, ~2 mi (3.3 km) east of McAllaster Buttes near the abandoned town of Lisbon (Gill et al., 1972).

Original author. Elias (1931); see also Gill et al. (1972).

Etymology. Named for the town of Sharon Springs in Wallace County, western Kansas.

Lithology. Black to gray, highly organic claystone with a fissile parting, commonly with concretions and numerous yellow-weathered bentonite beds, particularly near the base (Gries and Martin, 1985).

Figure 4. Section of Sharon Springs Formation near the type section of the Burning Brule Member. White bars denote contacts. The Niobrara Formation is seen in the lower part of the photograph, the Burning Brule Member contains the banded bentonites, the Boyer Bay Member weathers vertically, the Nicholas Creek Member is gray and less resistant, and the upper part of the section includes the light tan shales and marls of the lower Gregory Formation.

Age. Medial Campanian: *Baculites obtusus* through *Baculites perplexus* Ammonoid Range Biozones (Cobban, 1993; Obradovich, 1993; Grandstein et al., 1994).

Distribution. Northern Great Plains, including the Missouri River Trench of central South Dakota.

Synonymy. Pembina Member, Canada.

Boundaries. Underlain disconformably by the Niobrara Formation in some areas or conformably by the Gammon Ferruginous Formation in others.

Members. Burning Brule Member successively overlain by Boyer Bay Member and Nicholas Creek Member (newly named herein).

Description. The Sharon Springs Formation is composed of gray to black, organic-rich claystones that weather into well-parted shales. These shales are characterized by numerous bentonite layers and concretionary zones. The Sharon Springs Formation differs from other Pierre Shale Group formations in its high radioactivity, resistance to erosion, and darker color owing to very high organic content (Gill et al., 1972). In most areas, bentonite beds characterize the lower portion of the Sharon Springs Formation, including the Ardmore bentonite bed (Spivey, 1940; Bertog et al., this volume), whereas organic-rich, siliceous shale with resistant carbonate concretionary zones characterizes the middle portion of the formation. The upper portion of the formation is less resistant owing to disseminated bentonite and is characterized by phosphatic nodules.

Burning Brule Member of Sharon Springs Formation

In central South Dakota the Pierre Shale Group lies with disconformity over the Niobrara Formation, composed of chalk in its upper part. However, in western South Dakota–eastern Wyoming, the Gammon Ferruginous Formation intervenes. In both regions the basal portion of the black siliceous shale of the Sharon Springs Formation is characterized by bentonites, including the Ardmore bentonite bed of Spivey (1940), exposed in the southern Black Hills. Numerous bentonites occur near the base of the Sharon Springs that prompted Martin et al. (1996) to consider informally the entire interval around the Black Hills as the Ardmore succession, including a distinctive bentonite couplet (~0.3 m each) near the top of the interval. In central South Dakota south of the town of Chamberlain in an area known as Burning Brule (named because the organic-rich Pierre Shale caught fire and smoked for many years), 12–13 bentonites occur within an 8 m interval of black siliceous shale (a similar number occurs in about half the thickness in the Black Hills area; see Bertog et al., this volume). The type section at Burning Brule (Fig. 5) represents the thickest, most completely known succession of bentonites in central South Dakota; most other areas exhibit differential erosion of the upper contact. The bentonites vary extensively laterally, and the entire interval may be degraded. In some areas, thick bentonites split into two bentonite beds; in other areas, bentonites fade laterally. Distinctive channeling can be observed within the Burning Brule Member, and these channels may represent disconformable surfaces noted elsewhere within the Sharon Springs Formation (Martin, 1996). The base overlies a disconformable surface on which occurs a basal lag composed principally of large vertebrate remains in a clayey sand matrix.

Type section. SW¼NE¼ section 30, T. 104 N., R. 71 W., Brule County, South Dakota (Appendix 1).

Etymology. Named for the area known as Burning Brule south of the town of Chamberlain along the Missouri River, Brule County, central South Dakota.

Lithology. Black, organic-rich shale with numerous yellow-weathered bentonite interbeds; in some areas isolated concretions occur and may be associated with bentonite layers; basal lag deposits occur sporadically that are sometimes composed of vertebrate bone conglomerates.

Thickness. 0–4.5 m in type area.

Age. Medial Campanian: *Baculites obtusus* Ammonoid Range Biozone (Gill et al., 1972; Cobban, 1993; Obradovich, 1993; Grandstein et al., 1994); Ar/Ar determination from sanidine from the Ardmore succession in the Elk Basin of Wyoming yielded 80.54 ± 0.55 Ma (Obradovich, 1993); another date, also from sanidine, of the Ardmore bentonite bed near Redbird, Wyoming, revealed a date of 80.04 ± 0.4 Ma (Hicks et al., 1999).

Distribution. Central South Dakota west to the Black Hills region and into eastern North Dakota.

Equivalents. The same member occurs in the Black Hills region, where it includes the Ardmore bentonite succession, and in northeastern North Dakota, where it is also characterized by numerous bentonite layers.

Boundaries. Both the upper and lower boundaries are disconformable. In the type area the lower contact lies disconformably above the Niobrara chalk; a basal lag may be present. The upper contact with the suprajacent member is likewise disconformable, and the disconformity may have completely cut out the Burning Brule Member.

Figure 5. Type section of the Burning Brule Member of the Sharon Springs Formation. The individual is holding a grid unit that is 0.5 m on a side. The base of the grid unit lies on top of the Niobrara Formation.

Boyer Bay Member of Sharon Springs Formation

The Boyer Bay Member of the Sharon Springs Formation appears to be a widespread unit and can be identified from western Kansas through South Dakota, westward into Wyoming, and north into northeastern North Dakota. The member is characterized by highly organic-rich, siliceous shales with relatively few thin bentonites. The resistant nature of the shale results in a vertical-weathering profile (Fig. 6), and even with extensive weathering the unit retains relatively steep slopes of gray fissile shale. Bentonites in the type area of central South Dakota are thin but striking, owing to the contrast of the white or yellow bentonite with the black shale. The lowest bentonite is 1.5 cm thick, occurs ~1 m above the contact, and is distinctive because of its siliceous nature. This white bentonite has been informally termed the *porcellanite bentonite* owing to its brittle nature. Laterally, this bentonite may grade into a typical yellowish-white clay. Higher in the section, two more bentonites occur and are separated by ~1 m. The lower of the two is 2.5–3.0 cm thick, whereas the higher of the two is relatively thick, ~4.0–7.5 cm (Appendix 2).

As previously mentioned, the base of the Boyer Bay Member lies directly on the Niobrara Formation in some areas and is found to have cut down into various levels within the Burning Brule Member in other areas. In all cases where observable, the lower contact is disconformable. The upper contact is sharp but also disconformable.

Type section. NW¼SE¼ section 5, T. 102 N., R. 71 W., Brule County, South Dakota (Appendix 2).

Etymology. Named for Boyer Bay south of the town of Chamberlain in Brule County, South Dakota, where the type section occurs.

Lithology. Black to gray, highly siliceous, organic-rich shale with vertical or steep weathering profiles, with distinctive, thin white- or yellow-weathered bentonite beds.

Thickness. 6.5–9.7 m in type area.

Age. Medial Campanian: top of *Baculites obtusus* through *Baculites asperiformis* Ammonoid Range Biozones (Gill et al., 1972; Cobban, 1993; Obradovich, 1993; Grandstein et al., 1994).

Distribution. Western Kansas through South Dakota into Wyoming and north into North Dakota.

Equivalents. The same member occurs in the Black Hills region and in northeastern North Dakota, where it overlies the Ardmore bentonite succession (Burning Brule Member). This member may also extend into the type Sharon Springs area of western

Figure 6. Type area of the Boyer Bay Member of the Sharon Springs Formation. The member is characterized by vertically weathered, organic-rich shale. The individual's feet are at the basal contact.

Kansas, where it is represented by the buttress-weathering middle unit of Gill et al. (1972).

Boundaries. Both the upper and lower contacts are bounded by disconformable surfaces.

Nicholas Creek Member of Sharon Springs Formation

The uppermost member of the Sharon Springs Formation in central South Dakota is a black, bentonitic shale characterized by white to pinkish phosphatic concretions (Fig. 7). These concretionary bodies form a layer at the base of the member (Fig. 8), appearing almost as a basal lag. These relatively small (~10 cm long × 5 cm high) concretions appear to be scattered through the remainder of the member. In some areas the concretions appear to be somewhat aligned into discrete layers, but these layers are not as well developed as the basal layer of concretions. This unit can be distinguished by its soft bentonitic character in comparison with the highly resistant lower members. Nevertheless, it appears more similar to the black-gray shales of the lower members than to the brown, argillaceous units of the overlying Gregory Formation. The upper contact with the Gregory Formation is sharp and marked by a distinct color change from black to brown and a lithological change from bentonitic shale to bedded argillaceous shale.

The base of the Gregory Formation was placed by Gries and Rothrock (1941) and Crandell (1950) at the base of a 0.5-m-thick, yellowish red marl for convenience. However, the brown, bedded argillaceous shales of the Gregory Formation lie below the marl and above the black, massive Nicholas Creek Member. Therefore, the basal contact of the Gregory Formation is placed low enough to include brown argillaceous shale and bentonites (Appendix 3).

Type section. NE¼SW¼ section 11, T. 102 N., R. 72 W., Lyman County, South Dakota (Appendix 3).

Etymology. Named for Nicholas Creek, south of the town of Chamberlain, western shore of the Missouri River, Lyman County, South Dakota; the type section occurs just south of the mouth of Nicholas Creek.

Lithology. Black bentonitic shale containing numerous poorly layered to scattered white to pinkish gypsiferous, phosphatic concretions.

Thickness. 2.2–3.7 m in type area.

Age. Medial Campanian: top of *Baculites asperiformis* to top of *Baculites* sp. (smooth) Ammonoid Range Biozones (Gill et al., 1972; Cobban, 1993; Obradovich, 1993; Grandstein et al., 1994).

Distribution. Western Kansas, central South Dakota, northeastern North Dakota.

Equivalents. The Nicholas Creek Member is found in northeastern North Dakota and also extends into the type Sharon Springs area of western Kansas, where it is represented by the phosphatic nodular unit of Gill et al. (1972).

RESULTS

In view of years of geological and paleontological investigations along the Missouri Trench in central South Dakota and elsewhere, we have raised the Pierre Shale of Meek and Hayden (1862) to group status, essentially restoring the status that was originally proposed by Meek and Hayden. The Montana Group is herewith abandoned because of its relatively limited utility. The former members of the Pierre Shale (except the Crow Creek Member) are elevated to formational rank, and new members are described for distinctive lithologies within the Sharon Springs Formation. Additional members will be named for other distinctive lithologies

Figure 7. Type section of the Nicholas Creek Member of the Sharon Springs Formation. The individuals are collecting a mosasaur jaw in a plaster jacket that lies on the basal contact of the Nicholas Creek Member. Note the phosphatic concretions in poorly organized layers above this level. The upper contact is demarked by the distinct change in color and lithology. The light band across the middle of the photograph is the marl formerly utilized as the base of the Gregory Formation; note that typical Gregory deposits underlie the marl, resulting in a downward shift of the formational contact.

within the DeGrey Formation in a later contribution. However, the Crow Creek unit is retained at member status and considered a member of the DeGrey Formation. Consequently, the following listing represents the changes proposed herein:

1. The Pierre Shale of formational rank is elevated to group status and should be considered the Pierre Shale Group.
2. The Montana Group that included the Pierre Shale should be abandoned.
3. Former members of the Pierre Shale in western Kansas, central and western South Dakota, North Dakota, and southeastern Wyoming should be elevated to formational status. A similar situation may be proposed for other areas of the Pierre Shale and its equivalents, but those decisions should be made by local investigators. Within South Dakota the only previously considered member to retain its member status is the Crow Creek Member owing to its thinness, which does not allow the unit to be mapped at appropriate scales. Therefore, in central South Dakota the following superposed formations should be recognized: Sharon Springs Formation, Gregory Formation, DeGrey Formation, Verendrye Formation, Virgin Creek Formation, Mobridge Formation, and Elk Creek Formation. In western South Dakota–eastern Wyoming the following superposed formations should be recognized: Gammon Ferruginous Formation, Sharon Springs Formation, Mitten Black Shale Formation, Red Bird Silty Formation, a lower unnamed shale unit, Monument Hill Bentonitic Formation, Kara Bentonitic Formation, and an upper unnamed shale unit (see Gries and Martin, 1985). In northeastern

Figure 8. Basal phosphatic layer of the Nicholas Creek Member of the Sharon Springs Formation. Scale in centimeters.

North Dakota and into Canada, the Pembina Member should be considered the Sharon Springs Formation.

4. The Crow Creek Member, a tan siltstone, should be considered a member of the DeGrey Formation, because other, similar tan marls have been recognized in the section interbedded with typical dark gray bentonitic claystone of the lower DeGrey Formation.
5. The Sharon Springs Formation exhibits three distinct lithologies that are named as separate, disconformity-bounded members: the Burning Brule, Boyer Bay, and Nicholas Creek members.
6. The Burning Brule Member is characterized by black organic-rich shale interbedded with numerous relatively thick, yellow-weathered bentonites that appear to be correlative with the Ardmore succession to the west and the basal bentonite-rich unit in northeastern North Dakota. In central South Dakota the member disconformably overlies the Niobrara Formation, composed principally of chalk.
7. The Boyer Bay Member is another organic-rich siliceous black-gray shale but exhibits only a few very thin bentonites and retains a near-vertical weathering profile, and at places is considered a buttress-forming shale. This member, too, has a disconformable base that appears incised into different levels of the subjacent member. This unit also occurs in western Kansas, northeastern North Dakota, around the southern Black Hills, and will probably be correlated farther into Colorado, Montana, and elsewhere.

8. The Nicholas Creek Member is a bentonitic black shale characterized by white to pink gypsiferous phosphatic concretions. The concretions are normally concentrated at the base of the member and occur in poorly organized layers or scattered throughout the member. This member also occurs in western Kansas and northeastern North Dakota.
9. Other members of superposed formations will be designated in subsequent contributions, particularly those for the DeGrey Formation.

APPENDIX 1. STRATOTYPE SECTION (FIG. 5) FOR THE BURNING BRULE MEMBER, SHARON SPRINGS FORMATION (SW¼NE¼ SECTION 30, T. 104 N., R. 71 W., BRULE COUNTY, SOUTH DAKOTA)

Thickness	Description	Color codes*
<u>Boyer Bay Member</u>		
6 cm	silicified bentonite, “porcellanite” bentonite	5YR4/1
45 cm	black, vertically weathered organic-rich shale	N4
<u>Burning Brule Member</u>		
8 cm	siliceous bentonite	N3
2 cm	black silicified organic-rich shale	N3
1 cm	weathered bentonite	N3
28 cm	organic-rich shale w/scattered Fe-stained concretions	5YR4/1
9 cm	weathered bentonite	N3
23 cm	organic-rich shale	N3
15 cm	indurated ferruginous sandstone	N6
41 cm	organic-rich shale	N4
14 cm	weathered bentonite	5Y8/4
25.9 cm	organic-rich shale	N3
27.5 cm	weathered bentonite	5Y7/2
16.5 cm	organic-rich shale	N1
5 cm	indurated bentonite	5Y8/4
27 cm	organic-rich shale	N2
12.7 cm	bentonite	N9
27 cm	organic-rich shale	N2
20 cm	indurated bentonite	N7
3.5 cm	organic-rich shale	N3
4 cm	indurated bentonite	N8
7.8 cm	organic-rich shale	N5
4 cm	coarse-grained bentonite	5Y7/2
47 cm	organic-rich shale	5YR2/1
6 cm	bentonite	N6
4.3 cm	organic-rich shale	N4
28 cm	weathered bentonite	5Y8/4
14 cm	organic-rich shale	N2
3.5 cm	weathered bentonite	N6
6 cm	organic-rich shale	5YR2/1
2 cm	gypsiferous shale	5YR2/1
	Contact with Niobrara Formation	

Note: Top not preserved.
*Munsell standard colors.

APPENDIX 2: STRATOTYPE SECTION (FIG. 6) FOR THE BOYER BAY MEMBER, SHARON SPRINGS FORMATION (NW¼ SE¼ SECTION 5, T. 102 N., R. 71 W., BRULE COUNTY, SOUTH DAKOTA)

Contact with Nicholas Creek Member	
<u>Boyer Bay Member</u>	
220 cm	black organic-rich, vertically weathered shale
4 cm	yellow weathered bentonite
126 cm	black organic-rich, vertically weathered shale
2.5 cm	yellow weathered bentonite
220 cm	black organic-rich, vertically weathered shale
0.2 cm	yellow weathered bentonite
181 cm	black organic-rich, vertically weathered shale
3 cm	yellow weathered bentonite
845 cm	black organic-rich, vertically weathered shale
<u>Burning Brule Member</u>	
2.8 cm	yellow weathered bentonite
3.5 cm	black organic-rich shale
18.5 cm	bluish gray bentonite
2.5 cm	black organic-rich shale
11 cm	bluish gray bentonite
5.2 cm	black organic-rich shale
0.3 cm	bluish gray bentonite
4.6 cm	black organic-rich shale
3 cm	bluish gray bentonite
8.8 cm	black organic-rich shale
Contact with Niobrara Formation	

APPENDIX 3. STRATOTYPE SECTION (FIG. 7) FOR THE NICHOLAS CREEK MEMBER, SHARON SPRINGS FORMATION (NE¼SW¼ SECTION 11, T. 102 N., R. 72 W., LYMAN COUNTY, SOUTH DAKOTA)

Top not preserved	
<u>Gregory Formation</u>	
20 cm	reddish yellow ferruginous concretionary layer
100 cm	brownish black shale
25 cm	reddish yellow ferruginous concretionary layer
150 cm	brownish black shale
28 cm	brownish tan, Fe-stained siltstone normally present (previously considered base of Gregory Formation)
57 cm	brownish black shale
1 cm	yellow weathered bentonite
72 cm	brownish black shale
4 cm	reddish pink Fe-stained siltstone
<u>Nicholas Creek Member of Sharon Springs Formation</u>	
290 cm	bentonitic black shale with scattered cobble-sized, compressed phosphatic concretions; concretions occur also in distinct basal layer
<u>Boyer Bay Member of Sharon Springs Formation</u>	
100 cm	black organic-rich shale
Base covered by talus	

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Geochemical and mineralogical recognition of the bentonites in the lower Pierre Shale Group and their use in regional stratigraphic correlation

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ABSTRACT

The lower Pierre Shale consists primarily of the Sharon Springs Formation, which has been correlated regionally throughout Kansas, Colorado, Nebraska, Wyoming, South Dakota, and North Dakota. The unit represents distal sedimentation in a tectonically active foreland basin. Correlation of the lower Pierre Shale Group is complicated by the application of a single name, the Sharon Springs, to a wide range of facies. Bentonite correlation provides an independent framework for verifying the age equivalence of various facies of the Sharon Springs Formation. Bentonite correlation involves using a variety of unique chemical characteristics to differentiate individual beds. A combination of whole rock rare-earth-element geochemistry, phenocryst composition, biotite geochemistry, and stratigraphic position has been used to correlate bentonites of the lower Pierre Shale and equivalent units across the Western Interior of the United States.

Keywords: Pierre Shale, Sharon Springs, bentonites, stratigraphy, geochemistry.

INTRODUCTION

The Late Cretaceous Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) was deposited in a shallow marine foreland basin, distal to the Sevier orogenic belt (Kauffman, 1977) (Fig. 1). Owing to tectonic forces to the west, a shallow interior seaway was formed, which can be divided into four broad tectonic regions (DeCelles, 1994): the western foredeep, the western median trough, the eastern median hinge line, and the eastern platform. The western foredeep is adjacent to the thrust belt and is the tectonically deepest part of the basin. With mountains to the west having provided most of the sediment, the foredeep was filled with coarse siliciclastics, resulting in a coastal plain. The western median trough is the bathymetrically deepest part of the basin. Most of the coarse sediments are restricted to the western foredeep, so only fine-grained pelagic sediments were deposited in the trough. The eastern median hinge line is a result of reciprocal tectonic forces, which caused a narrow, tectonically high area. The eastern platform is a relatively stable part of the basin, distal to the tectonic forces. The transcontinental arch is a Precambrian high that separates the northern part of the seaway (South Dakota, North Dakota, Wyoming, Montana) from the southern part of the basin (Kansas, Colorado, Oklahoma, New Mexico, and Texas). Most of the tectonic activity, and the resulting tectonic belts, are restricted

Bertog, J., Huff, W., and Martin, J.E., 2007, Geochemical and mineralogical recognition of the bentonites in the lower Pierre Shale Group and their use in regional stratigraphic correlation, *in* Martin, J.E., and Parris, D.C., eds., The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas: Geological Society of America Special Paper 427, p. 23–50, doi: 10.1130/2007.2427(03). For permission to copy, contact editing@geosociety.org.

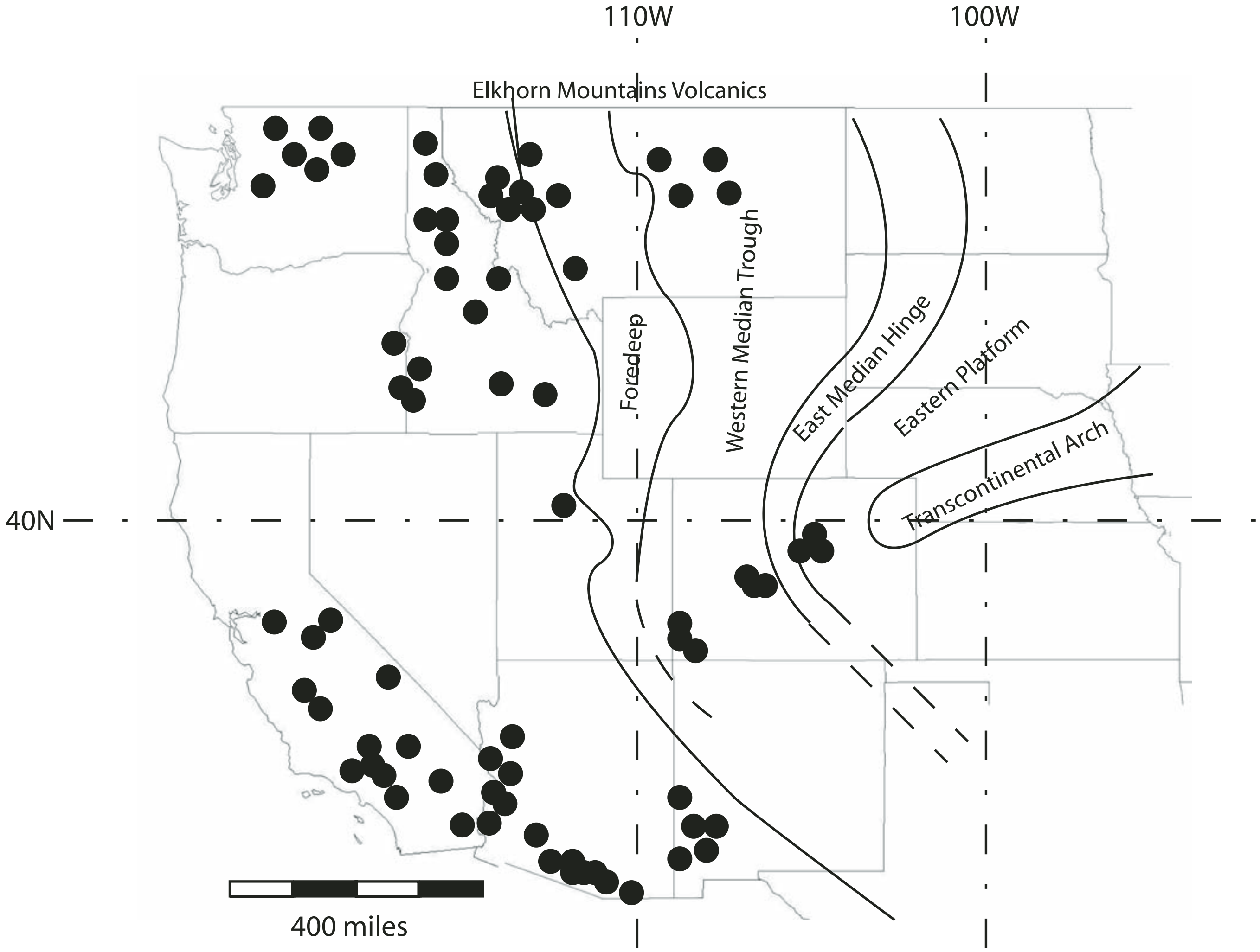


Figure 1. Map of the western United States, showing geographic features during the Campanian. Solid black circles represent volcanic centers that were active (Armstrong and Ward, 1993). In western Montana the Elkhorn Mountains volcanic complex was the most active volcanic center during deposition of the Sharon Springs Formation. Owing to tectonic forces in the west, a shallow interior seaway was formed, which can be divided into four broad tectonic regions: the western foredeep, the western median trough, the eastern median hinge line, and the eastern stable platform. The transcontinental arch separates the northern part of the basin from the southern part.

to the northern part of the basin. The Pierre Shale was deposited in the western median trough, the eastern median hinge line, and the eastern platform (Fig. 1). To the west, in the foredeep and the western part of the western median trough, coarser grained sediments were deposited as alluvial fans off the mountain belt (Kauffman and Caldwell, 1993). The Pierre Shale has been used as a "wastebasket" term that includes an extensive section of black shale above the Niobrara Formation (Hayden, 1862) (Fig. 2). In the lower Pierre Shale Group the Sharon Springs Formation has been assigned to multiple facies at the base of the formation (Fig. 2). This formation has a wide geographic distribution, having been described in Kansas (Elias, 1931; Gill et al., 1972), Colorado (Gill et al., 1975; Izett et al., 1971), Nebraska (DeGraw, 1975), Wyoming (Gill and Cobban, 1966), and South Dakota (Gries and Rothrock, 1941; Robinson et al., 1964; Robinson et al., 1959; Schultz et al., 1980; Searight, 1937; Wing, 1940) (Fig. 2). Only in the Black Hills of South Dakota and Wyoming has this unit been divided into separate members: the Gammon Ferruginous Member, Sharon Springs Member, and Mitten Black Shale Member (Gill and Cobban, 1966) (Fig. 2).

In order to understand the regional variations within this unit, the stratigraphy is being revised by elevating the Sharon Springs Member to formational status and naming individual members within the formation (Martin et al., this volume) (Fig. 2). Regional correlation among these members can be accomplished by bentonite correlation.

Bentonite correlation is useful for regional stratigraphic correlation owing to the depositional nature of bentonites. As altered volcanic ash, bentonites are deposited across facies boundaries in a geologically instantaneous time frame. Owing to magmatic history, which includes partial melting, magma mixing, and crystal fractionation, each volcanic eruption can have a unique chemical

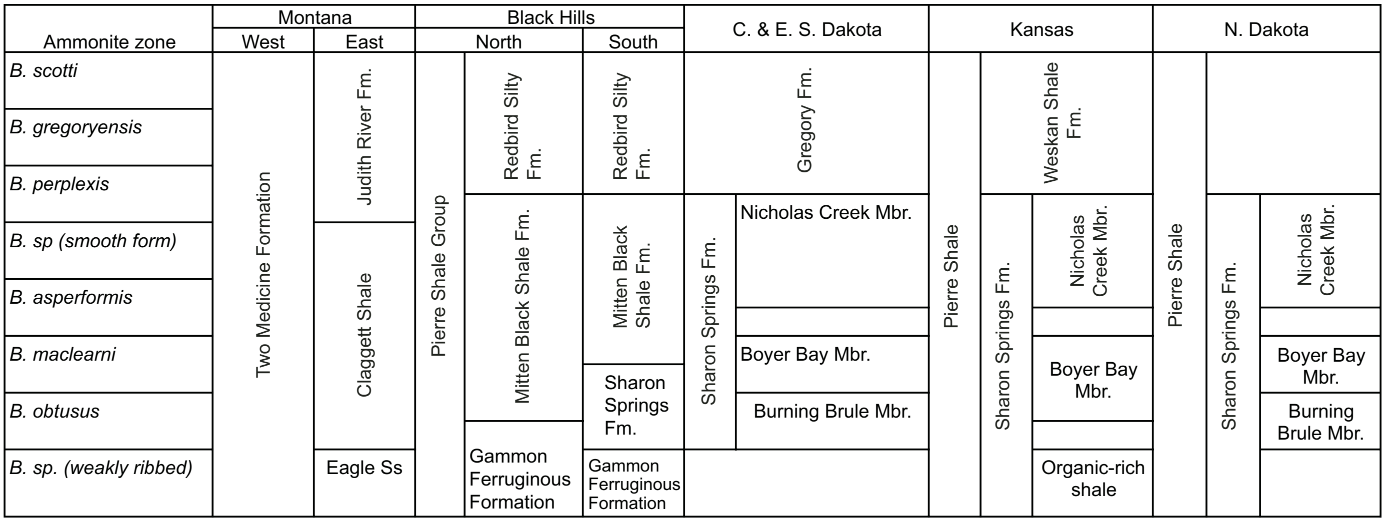


Figure 2. Generalized stratigraphy of the lower Pierre Shale, indicating terminology used in this paper.

and mineralogical signature. The geochemical and mineralogical signature is a combination of the geographic and tectonic position of the volcanic source as well as the conditions of the magma at the time of eruption, including the degree of fractionation, crustal contamination, and fluid content (Tatsumi and Eggins, 1995). Despite diagenesis, this signature is retained in the bentonites and can be used to identify bentonite beds across large areas.

A combination of stratigraphic, geochemical, and mineralogical criteria have been used to identify individual or groups of bentonites within the Sharon Springs unit. Detailed stratigraphic sections were measured in the Sharon Springs interval in the Black Hills, central South Dakota, Kansas, and North Dakota and in equivalent formations in Montana and Wyoming.

BACKGROUND

Stratigraphy of the Lower Pierre Shale Group

The stratigraphy of the lower Pierre Shale is complicated by facies changes across the region. Traditional correlation of these units has been done by ammonite zonation and the recognition of what is generally referred to as the Ardmore bentonite succession near the base of the Sharon Springs Formation in most areas (Fig. 2). Although the Sharon Springs Formation is widely recognized, the application of this name refers to different facies in different regions. The primary regions of exposure of the Sharon Springs Formation are the Black Hills of South Dakota and Wyoming, central and eastern South Dakota, western Kansas, and parts of Colorado. In North Dakota the name *Pembina Member* was applied to the equivalent facies (Fig. 2), using the Canadian terminology.

The Sharon Springs Member was first named in western Kansas from exposures of organic-rich black shale (Elias, 1931). As originally described, the member included three units: an organic-rich shale unit, a buttress-weathering shale unit, and a phosphate nodule unit (Gill et al., 1972) (Fig. 2)—the latter two units are considered the Boyer Bay and Nicholas Creek members, respectively (Martin et al., this volume). The base of the organic-rich shale unit is a gradational contact with the underlying Niobrara Formation. An iron-stained shale and intraformational conglomerate marks the boundary between the organic-rich shale and the buttress-weathering shale units. A large septarian concretion zone with abundant baculite fossils marks the contact between the buttress-weathering shale and the phosphate nodule facies. Bentonites within the Sharon Springs Formation at the type locality are thin and sparse, except in the phosphate nodule unit, where they are more abundant but still thin.

The Sharon Springs was extended to the Black Hills, where it was later subdivided into the Gammon Ferruginous Formation, the Sharon Springs Formation, and the Mitten Black Shale Formation (Gill and Cobban, 1966; Martin et al., this volume) (Fig. 2). The Gammon Ferruginous Formation is characterized by abundant siderite and limestone concretionary zones. Bentonites are common in the Gammon Ferruginous Formation and can be as thick as 0.25 m. The Sharon Springs Formation in the Black Hills is restricted to only the most organic-rich black shale. The Sharon Springs in the Black Hills is characterized by several thick bentonite beds, reaching up to 1 m in thickness. The Ardmore bentonite succession marks the base of the Sharon Springs Formation in the Black Hills (Spivey, 1940), and this succession has been used for regional correlation on the basis of stratigraphic position (Dyman et al., 1994), radiometric dating (Obradovich, 1993), and ammonite association (Gill and Cobban, 1966) from the Black Hills to Montana, Wyoming, and eastern South Dakota. The Mitten Black Shale is characterized by black shale with few thin bentonites.

In central and eastern South Dakota the Sharon Springs Member has been elevated to formational status (Martin et al., this volume). The members of the Sharon Springs Formation in this region are the Burning Brule Member, the Boyer Bay Member, and the Nicholas Creek Member (Fig. 2). The Burning Brule Member is similar to the lower Sharon Springs Formation in the Black Hills and is characterized by abundant thick bentonites and organic-rich black shale. The Boyer Bay Member is similar to the buttress-weathering shale member of western Kansas and contains two bentonites that are 0.25 m thick and sparse thin bentonites. The Nicholas Creek Member is similar to the phosphate nodule unit of western Kansas.

In North Dakota the Pembina Member is almost identical to the Sharon Springs Formation in central South Dakota, except that the Pembina Member is much thicker than the Sharon Springs Formation of central South Dakota (Gill and Cobban, 1965). The Pembina Member also includes three units: an organic-rich black shale with abundant thick bentonites, a buttress-weathering black shale, and a phosphate nodule unit (Fig. 2).

Bentonite Stratigraphy

Within the lower Pierre Shale the primary bentonites of interest have been the Ardmore bentonite succession. This thick succession of bentonites was of interest initially for its economic value and later for its use as a regional correlation tool. Spivey (1940) first described the Ardmore bentonite as the ~1-m-thick bentonite at the base of the Sharon Springs Formation of the Pierre Shale in the Black Hills of South Dakota. This bentonite was mined in the southern Black Hills and was the primary bentonite of interest. Spivey recognized the bentonite around the southern Black Hills. However, other workers subsequently pointed out that several additional bentonites are present in close stratigraphic proximity to the Ardmore bentonite (Gill and Cobban, 1966). Five to eight bentonites, averaging 15 cm thick, are present above the 1-m-thick basal bentonite. Two thin bentonites, 3 cm thick each, are also present <5 cm above the highest of the 15–cm-thick bentonites. A similar distribution of bentonites was described in the lower part of the Pierre Shale in the northern Black Hills of South Dakota (Spivey, 1940). Gill and Cobban (1966) expanded the term *Ardmore bentonite* to Redbird, Wyoming, where they included all the thick bentonites in close proximity to the 1-m-thick bentonite. The Ardmore bentonite beds are now used extensively for stratigraphic correlation and have been recognized in the Two Medicine Formation (Dyman et al., 1994) and the Gammon Ferruginous Formation (Spivey, 1940) of the Pierre Shale in South Dakota and Colorado, and the Pembina Member in North Dakota (Gill and Cobban, 1965).

Ar:Ar radiometric dating of sanidine crystals from the thick bentonite (the "Ardmore bentonite" sensu stricto) at Redbird, Wyoming, yielded an age of 80.04 ± 0.4 Ma (Hicks et al., 1999). The basal thick Ardmore bentonite was recognized in the Claggett Shale of the Elk Basin in Wyoming, where it is present within the *Baculites obtusus* ammonite range zone. Here the bentonite yielded a date of 80.54 ± 0.55 Ma using Ar:Ar in sanidine crystals (Obradovich, 1993).

Previous accounts of the Ardmore bentonite beds have not provided detailed stratigraphic information about the individual bentonites in the succession, nor have they provided independent variables for identifying the Ardmore bentonite beds. Other bentonites within the lower Pierre Shale have not been used for correlation previously. Correlation of even the thin bentonite beds can provide a high-resolution stratigraphic framework for interpreting regional facies changes (Elder, 1988; Huff et al., 1997; Kolata et al., 1996; Slaughter and Early, 1965).

Middle Campanian Volcanism

The subduction of the Farallon plate under the North American plate resulted in extensive volcanism along the western margin, with several volcanic centers (Monger, 1993). At ca. 80 Ma the western part of North America underwent a culmination of volcanic activity (Armstrong and Ward, 1993). The subducting plate is thought to have changed to a shallower angle of subduction, shifting a great deal of the volcanism inland to what is now Colorado, New Mexico, and Montana (Cross and Pilger, 1978; Dickinson, 1981) (Fig. 1). Some magmatic centers continued to be active from earlier in the Cretaceous. Calcalkaline centers were active in northern British Columbia and in Washington–southern British Columbia (Armstrong and Ward, 1993) as well as in northern Nevada (Vikre and McKee, 1985). Sierran magmatism was previously active in California and Nevada but came to an end ca. 80 Ma (Armstrong and Ward, 1993). Coinciding with the change in the subduction angle, magmatic activity in southern California and Arizona transgressed across Arizona and into New Mexico (Coney and Reynolds, 1977). Backarc magmatism was active in Colorado and Montana (Armstrong and Ward, 1993). The largest active volcanic center was the Little Elkhorn Mountains volcanic complex in western Montana (Armstrong and Ward, 1993; Robinson et al., 1968). These volcanoes produced extensive ash that was transported into the Western Interior Seaway and were the result of the complex interplay between the thickening of the crust from the Sevier orogeny and melting of the Farallon plate in the backarc setting (Christensen et al., 1994).

Four primary explosive volcanic centers can be recognized using bentonite whole-rock rare earth element (REE) analysis: a forearc, volcanic arc, backarc, and anorogenic setting (Tatsumi and Eggins, 1995). A backarc volcanic source is characterized by having a high light rare earth element (LREE) concentration and a slight negative europium anomaly, consistent with magma differentiation and continental crustal contamination. During differentiation, crystallization of plagioclase preferentially incorporates europium, resulting in a depletion of this element relative to other REE in the liquid. LREE are generally incorporated into minerals in the final phases of crystallization (quartz, potassium feldspar, muscovite). As a result, an increase in these elements indicates an incorporation of these minerals into the melt, possibly owing to partial melting of the continental crust (Tatsumi and Eggins, 1995). The volcanic arc source of volcanism is characterized by having lower LREE concentrations than the backarc setting, but the LREE are still enriched relative to the heavy rare earth elements (HREE), and a slight negative europium anomaly is present, consistent with magma differentiation. A forearc volcanic source is characterized by having a positive europium anomaly, indicating the incorporation of plagioclase into the melt. Because plagioclase preferentially incorporates europium during crystallization, melting of plagioclase will increase the europium content relative to other REE in the melt (Tatsumi and

Eggins, 1995). Plagioclase is in altered basalt of the subducting continental crust, and incorporation of plagioclase into the melt suggests melting of the subducting slab. A final volcanic source indicates an anorogenic, dacitic volcanic source that produced localized ash characterized by low Al_2O_3 concentrations, reflecting an alkaline source (Adbel-Rahman, 1996).

METHODS

To define the Ardmore bentonite beds stratigraphically and to characterize their mineralogy and geochemistry, detailed stratigraphic sections were measured in the Sharon Springs Member in the southern Black Hills, and samples of the bentonites were collected for analysis. Stratigraphic sections from equivalent units in Montana, Wyoming, South Dakota, North Dakota, Colorado, and Kansas were also measured, and bentonites were collected (Table 1) to determine the lateral extent of the Ardmore bentonite beds on the basis of composition (Fig. 3; Table 2).

Samples were collected from fresh bentonite (blue color, Elzea and Murray, 1990). For thin bentonites (<10 cm thick), one sample was collected that covered the full thickness of the bentonites. For thicker bentonites, samples were collected at even intervals throughout the thickness of the bentonite (generally 10 cm intervals). This method ensured comparison between the generally phenocryst-rich base of the bentonite and the phenocryst-poor upper parts of the bentonite. In addition, it allowed for identification of multiple volcanic events that were recorded within a single bentonite as a result of low sedimentation rates between events. In general, bentonite in the field was “clean,” free of detrital shale. However, in some samples the top of the bentonite was interbedded with shale. In these cases, care was taken to separate bentonite from shale during collection to ensure that geochemical results represented the bentonite.

Bentonite samples were disaggregated in water using trisodium phosphate and wet-sieving; material between 62.5 and 250 μm diameter was retained for further analysis. Grains were separated with bromoform, separating quartz and feldspar from biotite, ilmenite, apatite, and zircon. Isolated grains were identified using binocular microscope and petrographic microscope characteristics, and were verified with a Hitachi S-4000 scanning electron microscope equipped with Oxford energy-dispersive X-ray capabilities at the University of Cincinnati Advanced Materials Characterization Center. Relative abundances of minerals were described for each bentonite. For the light mineral fraction, 300 grains were counted using a petrographic microscope for all samples to determine the relative abundance of quartz and feldspar (Streckeisen, 1976).

TABLE 1. LOCALITIES OF BENTONITE SAMPLES FROM THE LOWER PIERRE SHALE AND EQUIVALENT UNITS

7MH	Sevenmile Hill, sec. 27, T 23 N, R 5 W, Teton County, Montana
PEM	Walhalla, sec. 13, T 163 N, R 58 W, Pembina County, North Dakota
RED	Redbird, sec. 13, T 38 N, R 62 W, Niobrara County, Wyoming
WR	Wallace Ranch, sec. 27, T 11 S, R 1 E, Fall River County, South Dakota
WsR	Wasserburger Ranch, sec. 16, T 12 S, R 4 E, Fall River County, South Dakota
BG	Buffalo Gap, sec. 31, T 7 S, R 7 E, Custer County, South Dakota
BR	Brown Ranch, sec. 30, T 2 S, R 87 E, Custer County, South Dakota
C	Missouri River, sec. 9, T 102 N, R 71 W, Brule County, South Dakota
YKT	Yankton, sec. 11, T 93 N, R 56 W, Yankton County, South Dakota
WAL	McAllaster Buttes, sec. 13, T 12 S, R 37 W, Logan County, Kansas
BUR	Burris Draw, sec. 9, T 15 S, R 32 W, Logan County, Kansas

Explosively erupted ash beds commonly show only minor variation in composition with distance from the source, indicating that whole rock analysis of immobile elements in bentonites can provide information regarding magmatic source (Heiken and Wohletz, 1992; Izett, 1981). In all, 105 samples, averaging 15 samples per locality, were analyzed for 34 elements using instrumental neutron activation analysis. Rare earth elements normalized to chondrite (Appendix 1) and plotted on chondrite-normalized graphs (after Floyd and Winchester, 1978). Chondrite values are assumed to represent primitive Earth compositions, and deviations from this composition indicate differentiation of the magma. Chondrite-normalized REE distribution of the bentonites revealed three magma sources for the bentonites of the lower Pierre Shale, discussed as follows. Multivariate discriminant function analysis separates groups of bentonites that are used to identify discrete zones across the basin.

In addition to whole rock analysis, phenocryst mineralogy and geochemistry were evaluated. Samples were wet sieved using 62.5 and 250 μm sieves. The material that was <62.5 μm was allowed to settle for 2 h so that only the clay-sized fraction, <2 μm, remained in suspension. Oriented slides were prepared using the pipette method. Samples were analyzed by powder X-ray diffraction of the samples under air-dried, glycolated, and heated conditions. Samples were run from 2 θ to 32 θ with a step size of 0.05 θ and a count time of 2 s (Moore and Reynolds, 1997).

Material that was between 62.5 and 250 μm was soaked in dilute nitric acid to break up aggregates and remove carbonates. The samples were then wet sieved again to remove any additional clay-sized particles. Phenocrysts from 62.5 to 250 μm were dried in an oven and kept for further analysis.

Bromoform, with a specific gravity of 2.84 g/cm^3, was used to separate light grains from heavy grains. Biotite has a tendency to be found in both the heavy and the light mineral fractions as a result of its density being close to that of bromoform, and any slight amount of weathering will reduce its specific gravity. Analysis of biotite in the light fraction indicated that the biotite in the light fraction was slightly altered, so only the heavy biotite was used in analysis. The heavy mineral fraction was further separated magnetically. Magnetic separation was done at 0.2, 0.4, 0.6, 0.8, and 1.0 A. The nonmagnetic fraction was further separated using methylene iodide with a specific gravity of 3.1 g/cm^3.

Selected grain mounts were thin sectioned for point count analysis (Appendix 2), and phenocrysts from other samples were mounted for scanning electron microscope (SEM) and EDS

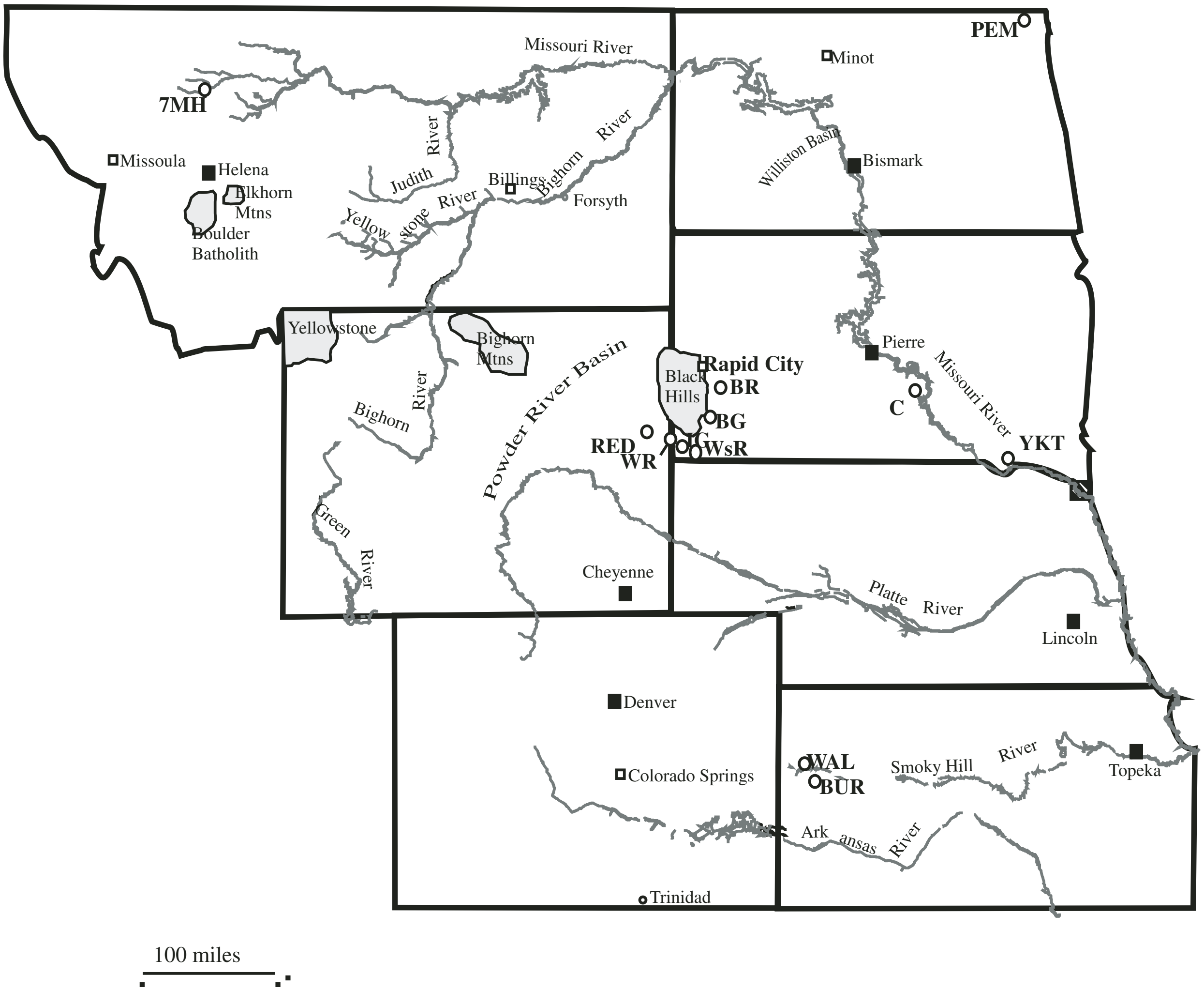


Figure 3. Localities of bentonite samples from the lower Pierre Shale and equivalent units. Refer to Table 1 for locality abbreviations.

(energy dispersive spectroscopy) analysis to verify identification of grains. The 0.4 A magnetic separation contained most of the biotite, and this fraction was mounted in epoxy and polished using 0.5 µm diamond paste for microprobe analysis. Single grains were chosen by visual inspection during microprobe analysis. The samples were put in a brass sample holder, and the grains were analyzed using an ARL SEMQ (quantitative scanning electron microscopy) microprobe equipped with wavelength dispersive crystal spectrometers and energy dispersive spectrometers (Appendix 3). The microprobe was set to 15 kV at 100 A. The standards used were magnesium olivine for magnesium on the TAP (Thallium acid phthalate 1011) crystal, magnetite for iron on the LiF (lithium floride 200) crystal, albite for silica on the PET (pentaerythritol 002) crystal and calcium on the ADP (ammonium dihydrogen phosphate 011) crystal, anorthite for aluminum on the ADP crystal and sodium on the TAP crystal, orthoclase for potassium on the PET crystal, and TiO_2 for titanium on the LiF crystal, from the University of Cincinnati Department of Geology standards database. Samples were analyzed with count times of 10 s on peak and 4 s off peak. For each sample, 10 biotite grains were analyzed, and 5 points were analyzed on each grain. This provided for analysis of both within the grain and within the sample variation so that samples could be discriminated between individual beds.

RESULTS AND DISCUSSION

Bentonite Fingerprinting

Fingerprinting bentonites can be useful for widespread correlation. Like traditional fingerprinting, bentonite fingerprinting involves finding unique characteristics that can be used to identify a layer anywhere that it is deposited. For this to be successful, the characters must be variable between volcanic eruptions, must be impervious to the depositional environment, and must be independent of diagenesis.

Individual methods of bentonite characterization may not provide a unique fingerprint. For example, REE patterns in several bentonites are similar. This is due to the control over the REE pattern by

TABLE 2. SUMMARY OF GEOCHEMICAL AND PETROGRAPHIC DATA AND BENTONITE GROUPS

WR group (interpreted source region)	Igneous rock type	Calcalkaline or alkaline	Biotite composition	Bentonite name	Samples collected
WR group 1 (backarc or anorogenic)					
	Dacite				
		Calcalkaline			
			Biotite		
				Ardmore A1A	BG 2, 3
					Pem1-5, 6, 7
					Red2-3, 4, 5
					WsR 2,3
				Ardmore A1B	BG 5
					Red2-11
					WsR 5
					C 5
					YKT 5
				Ardmore A1C	BG 6, 7
					Red2-12
					WsR 13
					C 6
				Ardmore A1D	BG 8
					Red2-13
					WsR 14
					C 7
				Ardmore A1E	BG 9
					Pem1- 13, 14
					Red2-14, 15
					C 8, 9
					WsR 15, 16, 17
				Ardmore A1F	WsR 19
		Alkaline			
			Biotite		
				Ardmore A2A	Red2-8
	Rhyolite				
		Calcalkaline			
			No biotite		
				Bentonite E	
				Bentonite G	
WR group 2 (volcanic arc)					
	Rhyolite				
		Calcalkaline			
			Biotite		
				Ardmore R2A	C 1, 2, 3, 4
					Red2-6, 7
					Pem1-8, 9, 11, 12
					BG 4
					WsR-4
					YKT 1, 2, 3, 4
				Ardmore R2B	Red2-9
			Biotite		
				Bentonite C2	BG 15
					WsR 26
					Pem1-20
					Red2-26
			No biotite		
				Ardmore R1A	Red-2-1, 2
					WsR-1
					BG-1
					Pem-3, 4
				Ardmore R1B	BG-11, 12
					Pem1-16
					Red2-16
					WsR-18
				Bentonite B	
WR group 3 (forearc)					
	Rhyolite				
		Calcalkaline			
			Biotite		
				Bentonite F2	BG 18
					WsR 32
			No biotite		
				Bentonite D	
				Bentonite F1	BG 17
					WsR 31
WR group 4 (volcanic arc)					
	Rhyolite				
		Calcalkaline			
			No biotite		
				Bentonite C1	BG 15
					Red2-24

the volcanic source region. The phenocrysts, however, will be different between layers with the same REE. This is because phenocryst composition is related to magma composition at the time of eruption. Therefore, a combination of REE with phenocryst composition and chemistry can be used to identify individual layers.

Other characteristics of bentonites, however, are less useful in fingerprinting. This is due to the ambiguous nature or the variability of the characteristics because of depositional environment and diagenesis. Most major elements and many trace elements in the volcanic glass are mobile during diagenesis and will be altered as a result of the composition of surrounding pore waters.

Whole Rock Geochemistry

Whole rock REE geochemistry is a reflection of the general magmatic character of the source volcano. In subduction zone environments, four magmatic regions are recognized: forearc, island arc, backarc, and anorogenic. Forearc volcanic sources are unusual, typically being found only in subduction zones where a young oceanic crust is subducting, resulting in the melting of the oceanic crust. This melting results in the incorporation of plagioclase into the melt. Plagioclase is a mineral that will fractionate europium, and when plagioclase melts, an increased amount of europium is found in the melt. Volcanic arc magmatism is produced by melting of the mantle wedge in the subduction zone and subsequent partial fractionation prior to eruption. This fractionation results in an increase of LREE over HREE and a decrease of europium as plagioclase crystallizes out of the melt. This pattern is typical of upper crustal rocks, and a similar signature is also seen in nonvolcanic rocks, including the shale that is typically found in association with the bentonites. The pattern seen in shale is a result of weathering of crustal and volcanic rocks. Backarc volcanism is similar to volcanic arc volcanism, except that the time of fractionation is increased owing to the thicker crust in this region. As a result, LREE are fractionated up to 1000 times chondrite values. Additionally, anorogenic magmatism can occur in the backarc region, within the continental crust. This will result in a REE pattern almost identical to that of the backarc volcanism.

Within these magmatic regions, individual volcanic sources will have slightly variable REE signatures, which can be identified using statistical discriminant function analysis. Discriminant function analysis uses multivariate functions to distinguish statistically unique groups. The bentonites separated into four groups, based on whole rock REE from Wallace Ranch (WR1–WR4) (Fig. 4). The two functions that were calculated are:

$$\text{Function 1} = 13.799 + 0.109{*}\text{La} - 0.265{*}\text{Ce} - 0.002{*}\text{Nd} + 0.632{*}\text{Sm} + 0.925{*}\text{Eu} - 1.336{*}\text{Tb} - 0.505{*}\text{Yb} - 0.194{*}\text{Lu} + 3.747{*}\text{Eu/Eu}^{*}.$$

$$\text{Function 2} = 21.399 + 0.069{*}\text{La} - 0.193{*}\text{Ce} + 0.192{*}\text{Nd} - 0.322{*}\text{Sm} + 2.58{*}\text{Eu} - 0.773{*}\text{Tb} + 1.131{*}\text{Yb} - 0.734{*}\text{Lu} + 19.857{*}\text{Eu/Eu}^{*}.$$

$^{*}\text{Eu/Eu}^{*} = [\text{Eu}/(\text{Sm}/{*}\text{Tb}){*}0.5]$. If Tb was below detection limits, Yb was used in the calculation.

Although discriminant function analysis provides a statistical means for segregating bentonite groups, it does little to provide an interpretation of the bentonite source regions. Plotting the REE

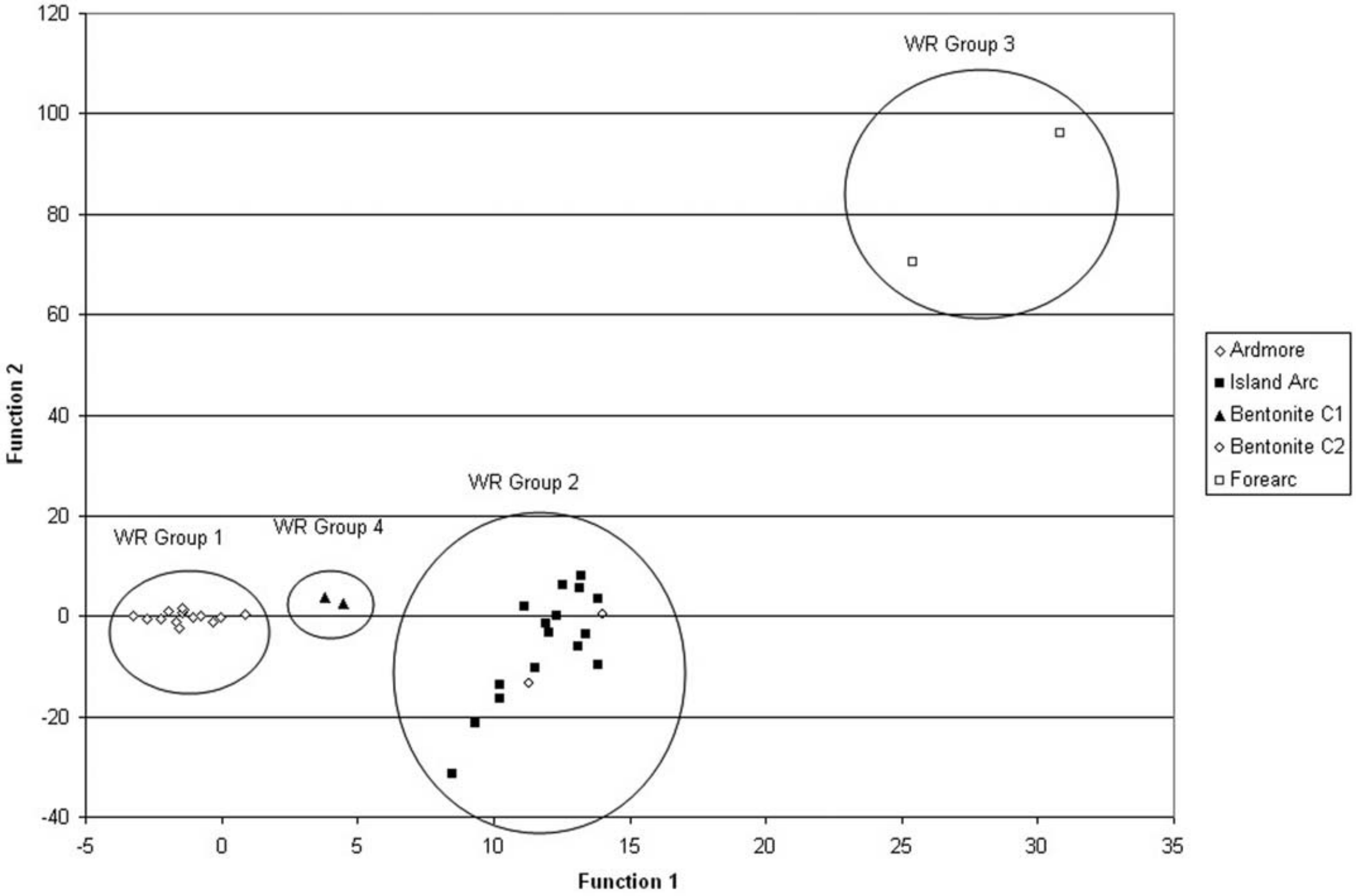


Figure 4. Discriminant function analysis combines multiple parameters to distinguish groups within a data set. Based on discriminant function analysis, two functions produced four separate groups. WR (Wallace Ranch) groups 1, 2, and 3 correlate with groups on the basis of spider diagram plots. WR group 4 plotted with group 1 on spider diagrams but was differentiated on the basis of this analysis.

results using spider diagrams, compared to known results from the four volcanic sources, reveals the source regions for the four groups distinguished using discriminant function analysis (Fig. 5).

WR groups 1 and 4 plot within the backarc or anorogenic magma sources. In these groups the LREE are enriched, with values ∼100 times chondrite values. The HREE have concentrations ∼10–20 times chondrite values. The bentonites have a slight europium anomaly. Stratigraphically, bentonites of WR group 1 are found throughout the section, and this is the most abundant group based on REE. WR group 4 is restricted to a single bentonite ∼25 cm thick that is restricted to the Black Hills region. Phenocryst mineralogy and biotite geochemistry will further differentiate these two groups. WR group 2, with a lower LREE composition than WR group 1, ∼10 times chondrite values, compares favorably with the volcanic arc compositions. WR group 3 is found in three bentonites throughout the Black Hills region and in Chamberlain, South Dakota. WR group 3 is unique in exhibiting a positive europium anomaly and very low HREE concentrations, between 1 and 5 times chondrite, such as that seen in a forearc volcanic center.

Primary volcanogenic phenocrysts are abundant in many of the bentonites in the lower Pierre Shale. These phenocrysts are sand sized, dominantly between 62.5 and 250 μm in diameter, although biotite grains >250 μm were noted in some samples. Phenocrysts are typically concentrated at the base of the bentonite beds and fine upward. Primary phenocrysts in the bentonites of the lower Pierre Shale included quartz, potassium feldspar, plagioclase, ilmenite, biotite, apatite, and zircon.

The presence and abundance of all minerals characterize the mineral suites (Table 2). Point counts of the light mineral fraction (quartz, plagioclase, and potassium feldspar) characterize the major igneous rock type for the magma source when plotted using the International Union of Geological Sciences classification (Streckeisen, 1976) (Appendix 2, Fig. 6). Igneous rock types are based generally on the degree of fractionation of magma. As a magma becomes more fractionated, the melt progresses from andesite to dacite to rhyolite. Most of the bentonites plot within the rhyolite field. Seven bentonite layers that had plotted in WR group 1 on the basis of whole rock REE analysis plotted as dacite in the phenocryst plots. Although most bentonites are within the rhyolite field, individual bentonite layers show a variation in mineralogical composition that can be used in conjunction with geochemistry for their characterization.

Biotite Geochemistry

Biotite is abundant in the bentonites of the Ardmore bentonite succession and in the two bentonite beds above the Ardmore succession in the lower Pierre Shale. Biotite phenocrysts are useful because their chemistry can be used to help interpret volcanic source magma (Adbel-Rahman, 1996). Biotite was analyzed for SiO_2, TiO_2, Al_2O_3, FeO*, MgO, CaO, Na_2O, and K_2O (Appendix 3). Concentrations of Fe^{2+}, Fe^{3+}, Mg^{2+}, and the magnesium number were calculated for all samples. The general formula for biotite is $KB_{2-3}(X,Si)_4O_{10}(O,OH,F)_2$. Biotite crystals are arranged in layers of tetrahedra-octahedra-tetrahedra, separated by interlayer cations,

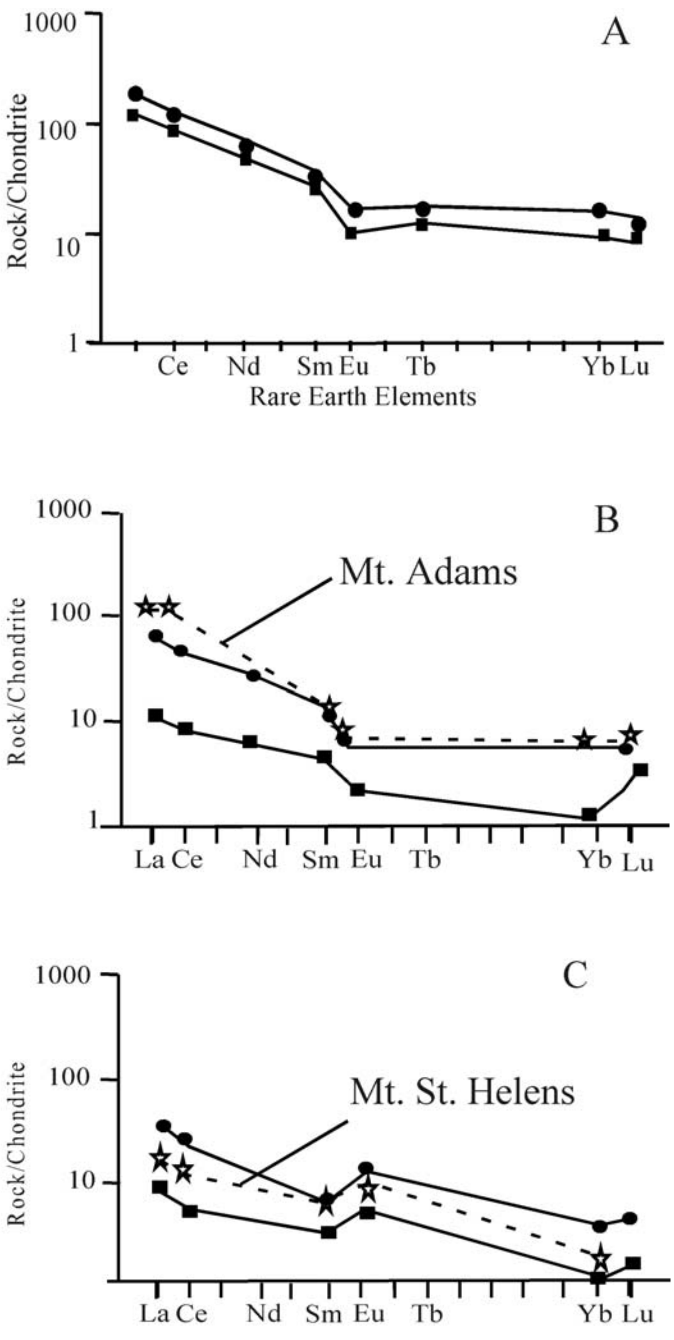
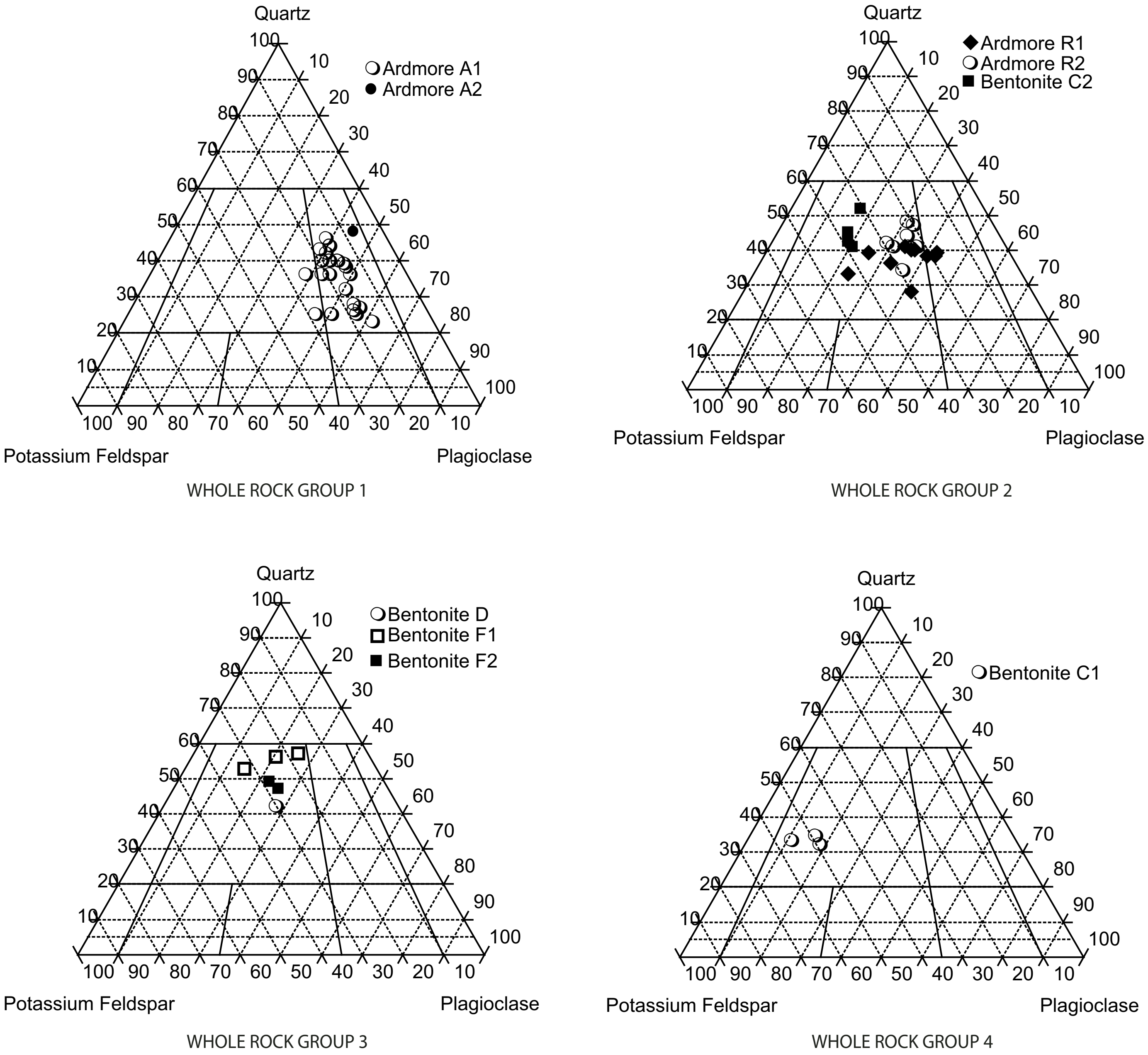


Figure 5. Whole rock REE analysis of the bentonites can be divided into three major categories on the basis of the REE distribution in spider diagrams. (A) Bentonites of WR group 1 and 4 represent a backarc setting and are enriched in REE, with a slight europium anomaly. Top and bottom lines on each graph represent the range of values for the group of bentonites. Refer to Table 2 for a list of the bentonites in this group. (B) Bentonites of WR group 2 represent an island arc setting and are similar to Mount Adams in Washington State (dashed line), with a slight enrichment of the LREE and a slight europium anomaly. (C) Bentonites of WR group 3 represent a forearc setting and are similar to eruptions from Mount Saint Helens (Washington State), with a positive europium anomaly.



WHOLE ROCK GROUP 1

WHOLE ROCK GROUP 2

WHOLE ROCK GROUP 3

WHOLE ROCK GROUP 4

Figure 6. Based on the distribution of light phenocrysts, and plotted on a QAF (quartz-alkali feldspar-potassium feldspar) diagram, bentonites can be classified as rhyolites and dacites. Bentonites of WR group 1 (see Fig. 4) are dacites, while bentonites from WR Groups 2–4 are rhyolites.

in this case potassium (Adbel-Rahman, 1996). The tetrahedra consist of $(X,Si)_2O_5$, where X is usually aluminum, but can also include Be, B, and Fe^{3+} and can replace silica by up to 50%. Most substitution occurs in the octahedral layer, B, where Al, Fe, Ti, and Mg are the primary elements that can occur. These cations in the biotite structure indicate their availability in the magma. Magnesium and iron values in biotite and amphibole are only slightly higher than the coexisting melt, so the biotite composition is a reflection of the melt composition. The magnesium number is a useful indicator of the degree of crystal fractionation, assuming a mantle-derived primary magma. Initial magma generated from the mantle has a magnesium number of ~90. In early stages of crystallization, magnesium-rich minerals such as olivine and pyroxene crystallize out, so that differentiated magmas have a lower magnesium number (Tatsumi and Eggins, 1995). Concentrations of Fe^{2+}, Fe^{3+}, Mg^{2+} and the magnesium number were calculated for all samples. The magnesium number was calculated with the equation $Mg^{2+}/(Mg^{2+} + Fe^{2+})*100$ (Tatsumi and Eggins, 1995).

Total oxide weight percentages are between 73% and 99% of the total for biotite samples. Most of the variation that accounts for the differences in weight percentages between samples was in the SiO_2 content. A small part of the biotite crystal consists of volatiles, such as water and fluorine, which account for some of the missing weight in the microprobe totals. In unaltered biotites the K_2O concentration is ~9%. K_2O values for the biotite samples were between 4.6% and 10.4%. Even in grains with low K_2O values, concentrations of other elements, particularly TiO_2, Al_2O_3, FeO*, and MgO, remained consistent within a sample, between altered and unaltered biotite.

Biotite data were plotted on bivariate and ternary plots (Figs. 7, 8). Figure 7 shows ternary plots of Al_2O_3, FeO, and MgO. This plot is based on data of known volcanic compositions from 26 separate volcanoes and 329 biotite samples representing alkaline, calcalkaline, and peraluminous magma sources (Adbel-Rahman, 1996). Al_2O_3, FeO, and MgO were used because they are interchangeable in the octahedral cation site of biotite. Alkaline magmas are iron rich, owing to crystal fractionation and the fact that iron oxides and iron-titanium oxides form late in the fractionation sequence (Adbel-Rahman, 1996). Calcalkaline magmas are relatively magnesium rich as a result of increased water content that allows iron oxides and iron-rich amphiboles to crystallize early, removing iron from the system. Peraluminous magmas are enriched in aluminum owing to partial melting of the continental crust, with abundant aluminum-rich minerals.

Most of the bentonites in the lower Pierre Shale plot within the calcalkaline field (Fig. 7). Within this field, bentonites of the Ardmore succession (WR group 1) and bentonite C2 appear to show a slight differentiation trend, with bentonite C more enriched in iron than bentonites of the Ardmore succession (bentonite C is stratigraphically higher than the Ardmore succession, supporting the idea that these bentonites are part of the same differentiation trend). A single bentonite plotted in the alkaline field (Ardmore bentonite A2A). This bentonite was found only at a single locality near Redbird, Wyoming. Alkaline volcanism is often less eruptive than calcalkaline volcanism and may explain the localized distribution of this bentonite.

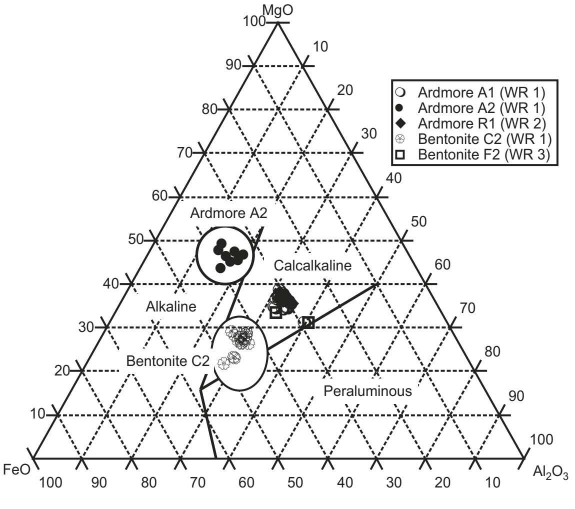


Figure 7. Plot of biotite major element composition indicates that most bentonites are calcalkaline, consistent with subduction-zone boundary volcanism. The Ardmore A2 bentonite plots within an alkaline source and can be differentiated on the basis of its low Al_2O_3 content.

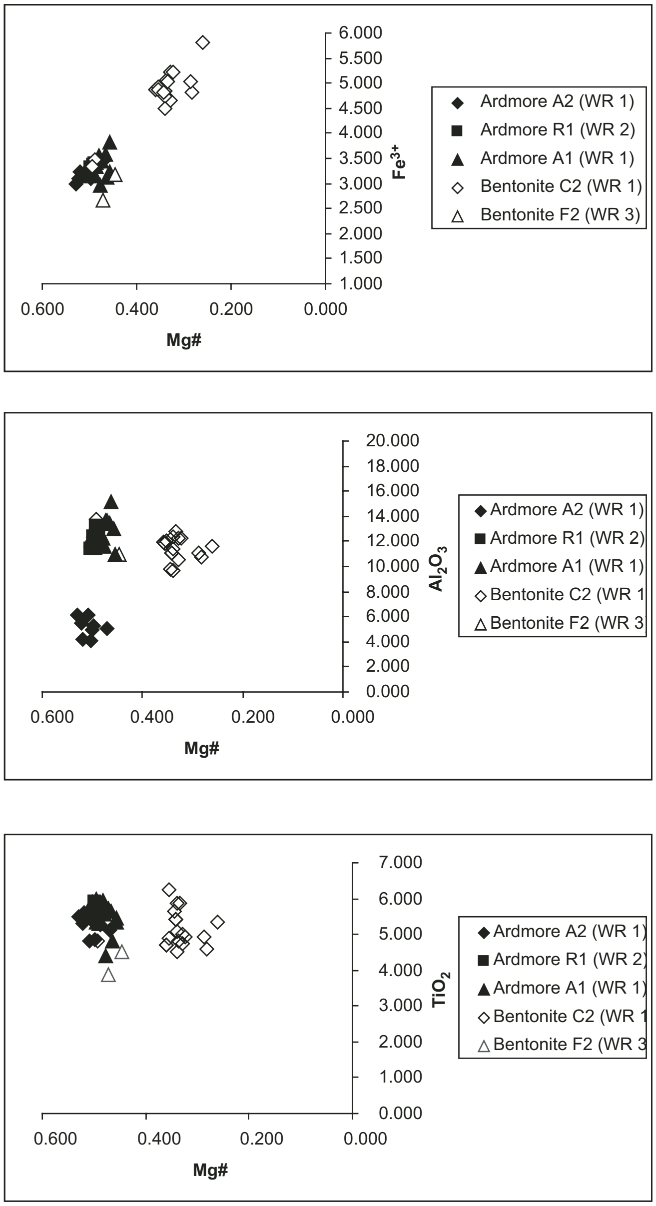


Figure 8. Bivariate plots of biotite major elements segregate bentonite C2 on the basis of lower Mg# and higher Fe^{3+}, indicating a more fractionated magma. As in the ternary diagram (Fig. 7), the Ardmore A2 bentonite has a lower Al_2O_3 content.

Bivariate plots of Al_2O_3, Fe^{3+}, and TiO_2 were plotted against magnesium number to show variations of these elements with increased differentiation. Magnesium number decreases with increased differentiation, so plots are shown with magnesium number decreasing to the right (after Tatsumi and Eggins, 1995). In a plot of Fe^{3+} against the magnesium number, bentonite C2 plotted significantly higher than bentonites of the Ardmore succession

(Fig. 8). Bentonites of the Ardmore succession showed relatively low differentiation. A similar trend is seen in the plot of magnesium number compared to TiO_2, with bentonite C2 plotting higher in magnesium number but similar in concentration of TiO_2 (Fig. 8). With the plot of Al_2O_3, a third group emerges, the alkaline bentonite. As with the ternary plot, this bentonite is segregated on the basis of its lower Al_2O_3 content in comparison with the bentonites of the Ardmore succession and bentonite C2 (Fig. 8).

Stratigraphic Correlation

Based on a combination of stratigraphy (Appendix 4), geochemistry, and mineralogy, bentonites of the lower Pierre Shale Group can be correlated regionally (Figs. 9, 10). Bentonites were identified using the characteristics previously described. This process is summarized in Table 2. First, bentonites were divided into four groups on the basis of their whole rock REE compositions. Second, within each of these four groups the bentonites were divided into dacite or rhyolite composition on the basis of their light phenocryst composition. Third, bentonites were divided into calcalkaline and alkaline (this was applicable only to WR group 1). Fourth, bentonites were divided into those with biotite phenocrysts and those without. Finally, individual bentonite layers were identified on the basis of stratigraphic position. Bentonites were given a designation code on the basis of the combination of geochemical, mineralogical, and stratigraphic characteristics. For example, bentonites within the Ardmore bentonite succession were labeled “Ardmore A1” if they were calcalkaline (1) dacites (A). Then they were labeled alphabetically by stratigraphic position. So, calcalkaline bentonites in the Ardmore succession are labeled “Ardmore A1A” to “Ardmore A1F.” Alkaline dacites in the Ardmore succession were labeled “Ardmore A2,” with an alphabetic stratigraphic indicator. So, alkaline dacites in the Ardmore are labeled “Ardmore A2A.” Because the Ardmore bentonite succession is the only named group of bentonites, the remainder of the bentonites were given alphabetic designations. Therefore, the first bentonite above the Ardmore succession is bentonite B. If bentonites have similar characteristics in the field or have close affiliations, they are grouped together. So, above bentonite B are two thick bentonites that are found commonly in close association in the field. These two bentonites are labeled together as “Bentonite C1 and C2.”

The distribution of the bentonites can be used for regional correlation of units in the lower Pierre Shale. Bentonites of the Gammon Ferruginous Formation in the Black Hills correlate with bentonites of the organic-rich shale unit in western Kansas (Figs. 9, 10). The interval is not present in central and eastern South Dakota or North Dakota. Bentonites of the Ardmore bentonite succession are present in the Black Hills, central and eastern South Dakota, and North Dakota (Figs. 9, 10). The dacitic bentonites of this interval are also present in the Two Medicine Formation in Montana (Figs. 9, 10). Bentonites above the Ardmore bentonite succession in the Black Hills are not found in other areas in the region. Bentonites of the Boyer Bay Member of the Sharon Springs Formation in central South Dakota are present in western Kansas (Figs. 9, 10). These bentonites may also correlate with bentonites in the Mitten Black Shale Formation in the Black Hills and in the buttress-weathering shale unit of the Pembina Member in North Dakota, but these sections were not included in the study.

CONCLUSIONS

Multivariate statistical analysis of bentonites, including stratigraphy, geochemistry, and phenocryst composition, can be used for interpretation of volcanic sources. Because each bentonite layer represents a unique volcanic eruption, the geochemical and mineralogical characteristics can also be used for regional correlation independent of stratigraphic properties.

Volcanic source composition was identified by a combination of whole rock REE analysis, phenocryst composition, and biotite major element geochemistry. Using these characteristics, biotites were first divided into four groups on the basis of their whole rock REE composition. Bentonites of the lower Pierre Shale represent volcanic sources that came from the forearc, volcanic arc, and backarc source regions as well as from an anorogenic volcanic source. The backarc volcanic source was the Little Elkhorn Mountains. Bentonites of the lower Pierre Shale with a backarc REE signature correlate with bentonites in the terrestrial Two Medicine Formation that have been directly correlated with the Little Elkhorn Mountains on the basis of a volcanic ignimbrite layer associated with the volcanoes. Sources of the forearc and volcanic arc bentonites were likely to have been in northern British Columbia and northern Washington–southern British Columbia. Bentonites, with the exception of the anorogenic source, were calcalkaline on the basis of biotite chemical composition. Most of the bentonites are rhyolite in composition on the basis of their phenocryst mineralogy. However, bentonites from the backarc volcanic center were dacitic and contain abundant biotite. Groups of bentonites are summarized in Table 2.

Using the geochemical characteristics summarized in Table 2 and on the basis of their stratigraphic position, 22 bentonite beds, representing 22 volcanic events, were identified and correlated from western Montana to Yankton, South Dakota, and from Pembina, North Dakota, to Weskan, Kansas.

Through bentonite correlation, stratigraphic distributions can be interpreted. The Ardmore bentonite succession is a historically important unit for regional correlation as well as for economic use. Multivariate correlation shows that this unit is a composite bentonite. In the Black Hills, where the Ardmore bentonite succession was first described, the succession includes an average of six thick bentonites, ranging in thickness from 25 to 100 cm. In the Black Hills the bentonites of the Ardmore bentonite succession show a consistent pattern: a 25 cm bentonite at the base, a 100 cm bentonite superjacent, and 4 to 7 bentonites superposed with an average thickness of 25 cm. However, in other regions, including central South Dakota, North Dakota, and western Kansas, many single bentonites from the Black Hills are divided into two or more smaller bentonites. This pattern indicates lower sedimentation rates in the Black Hills, resulting in multiple bentonites having been deposited one on top of another without intervening sedimentation.

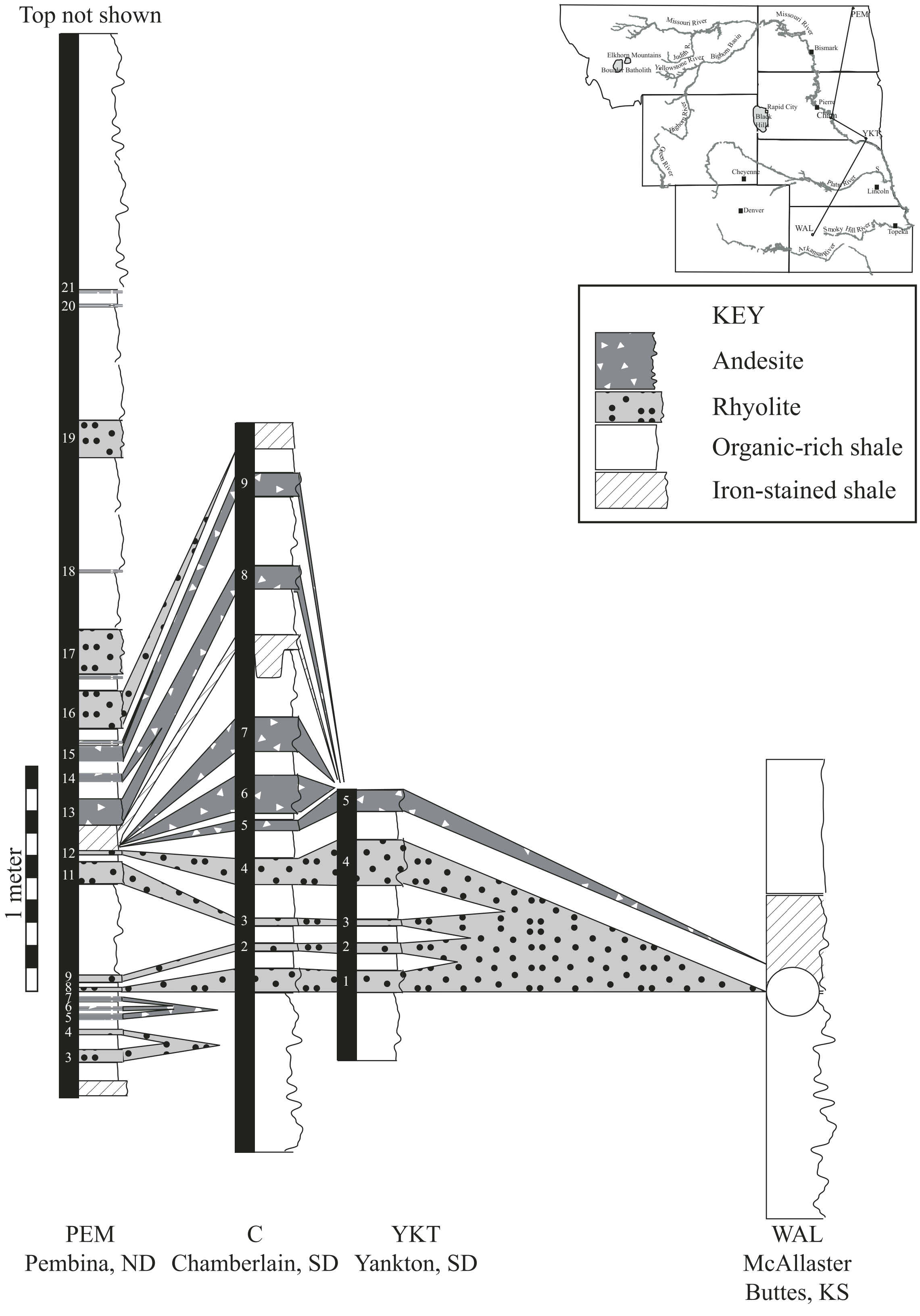


Figure 9. Stratigraphic correlation of the lower Pierre Shale from Pembina, North Dakota, to McAllaster Buttes, Kansas. Bentonite samples are numbered according to geochemical samples in the text and appendices.

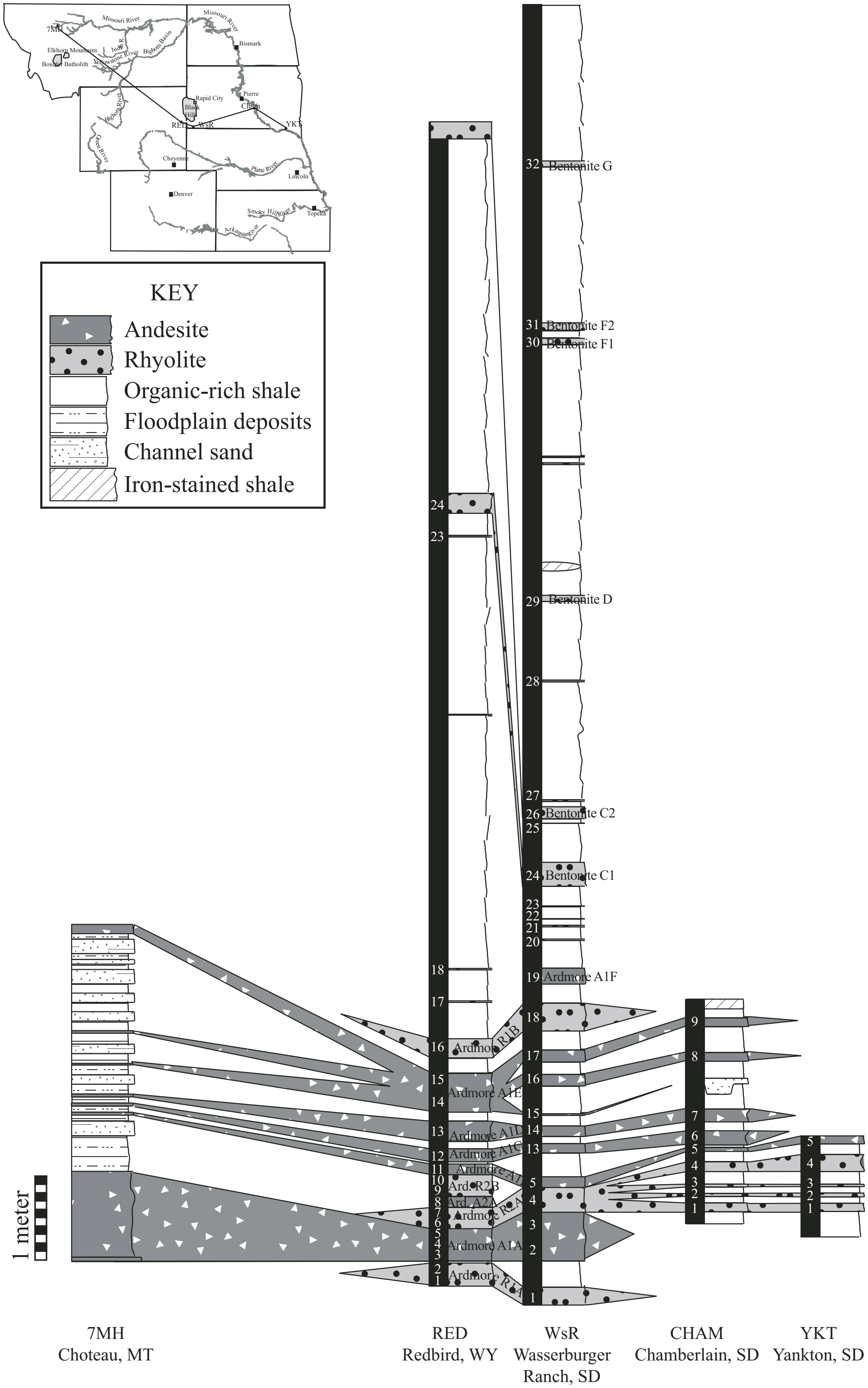


Figure 10. Stratigraphic correlation of the lower Pierre Shale and equivalents from Choteau, Montana (Two Medicine Formation), to Yankton, South Dakota. Bentonite samples are numbered according to geochemical samples in the text and appendices.

APPENDIX 1. WHOLE-ROCK RARE EARTH ELEMENT ANALYSES OF BENTONITE SAMPLES, LOWER PIERRE SHALE

	La	Ce	Nd	Sm	Eu	Tb	Yb	Lu
Chondrite:	0.367	0.957	0.711	0.231	0.087	0.058	0.248	0.0381
Buffalo Gap								
1a	182.5613	133.7513	70.32349	45.45455	25.28736	24.13793	14.51613	13.12336
1b	196.1853	143.1557	70.32349	37.22944	24.13793	17.24138	13.70968	12.59843
1c	174.3869	133.7513	70.32349	44.58874	18.3908	18.96552	15.32258	13.64829
2	73.56948	57.47126	42.19409	29.00433	17.24138	18.96552	14.91935	133.8583
3a	158.0381	112.8527	56.25879	35.06494	21.83908	15.51724	12.09677	12.07349
3b	160.7629	113.8976	70.32349	35.49784	17.24138	17.24138	12.09677	11.28609
4	144.4142	103.4483	56.25879	32.03463	14.94253	15.51724	12.09677	10.76115
5	128.0654	96.13375	56.25879	34.63203	21.83908	17.24138	16.93548	12.86089
6	168.9373	119.1223	70.32349	35.49784	18.3908	15.51724	14.1129	13.12336
7a	144.4142	105.5381	70.32349	39.82684	20.68966	18.96552	15.32258	14.69816
7b	171.6621	117.0324	56.25879	35.49784	17.24138	15.51724	14.51613	13.12336
8	166.2125	119.1223	70.32349	39.82684	20.68966	15.51724	12.90323	11.54856
9	19.07357	14.62905		8.225108	5.747126		5.241935	4.461942
10	29.97275	22.98851	14.0647	7.359307	6.896552		2.822581	4.199475
11	138.9646	96.13375	56.25879	30.30303	12.64368	12.06897	9.274194	8.39895
12	46.32153	33.43783	14.0647	11.68831	8.045977		4.83871	4.724409
16	185.2861	47.02194	14.0647	5.627706	6.896552		3.225806	3.937008
16	27.24796	18.80878		6.926407	5.747126		4.032258	5.249344
17	38.14714	26.1233	14.0647	10.38961	5.747126		6.451613	6.036745
18	62.6703	45.97701	28.1294	14.71861	5.747126		4.83871	5.249344
19	523.1608	246.604	84.38819	25.97403	20.68966		3.225806	2.624672
17	8.174387	6.269592		3.896104	5.747126		1.209677	2.362205
19	114.4414	82.54963	42.19409	25.10823	12.64368	12.06897	8.467742	7.611549
Brown Ranch								
1a	106.267	75.23511	42.19409	24.24242	12.64368	12.06897	14.1129	13.91076
1b	119.891	94.04389	42.19409	28.57143	17.24138	13.7931	13.30645	12.07349
1c	84.46866	58.5162	28.1294	19.91342	10.34483	12.06897	11.29032	10.76115
1d	144.4142	100.3135	56.25879	30.30303	16.09195	13.7931	11.29032	10.76115
1e	196.1853	125.3918	70.32349	34.19913	19.54023	13.7931	13.30645	12.33596
2	138.9646	98.22362	56.25879	29.43723	12.64368	12.06897	11.69355	11.02362
3	79.01907	53.29154	28.1294	17.74892	11.49425	8.62069	11.29032	11.28609
4	163.4877	107.628	56.25879	30.30303	16.09195	12.06897	12.5	11.28609
5	130.7902	88.81923	42.19409	27.70563	18.3908	13.7931	12.09677	12.07349
6a	87.19346	97.17868	56.25879	43.72294	22.98851	18.96552	19.35484	13.38583
6b	122.6158	86.72936	42.19409	24.67532	11.49425	12.06897	9.274194	8.39895
6c	166.2125	112.8527	56.25879	29.43723	16.09195	10.34483	9.274194	8.136483
7	152.5886	102.4033	42.19409	24.24242	9.195402	10.34483	10.48387	10.76115
8	62.6703	42.84222	14.0647	11.68831	9.195402	8.62069	10.08065	12.07349
9	24.52316	16.71891	14.0647	6.926407	4.597701		3.629032	4.461942
10	8.174387	5.22466		3.463203	4.597701		2.016129	3.412073
11	40.87193	24.03344	14.0647	6.926407	4.597701		4.032258	3.674541
12	19.07357	12.53918		5.627706	6.896552		2.822581	3.412073
13	49.04632	22.98851	14.0647	6.926407	4.597701		2.822581	4.461942
11	43.59673	29.2581	14.0647	9.090909	9.195402		5.645161	6.036745
12	29.97275	20.89864	14.0647	7.792208	6.896552		4.435484	4.461942
13	27.24796	18.80878	14.0647	8.225108	8.045977		3.225806	3.937008
14	21.79837	12.53918	0	5.627706	4.597701		2.419355	2.362205
15	343.3243	152.5601	42.19409	15.15152	11.49425		4.435484	4.199475
16	13.62398	10.44932	0	5.194805	5.747126		1.612903	1.83727
17	40.87193	25.07837	14.0647	6.493506	4.597701		2.822581	2.887139
Wallace Ranch								
1	152.5886		42.19409	24.24242	9.195402	10.34483	10.48387	10.76115
2	237.0572	127.4817	126.5823	82.25108	57.47126	41.37931	13.30645	9.973753
3	125.3406		112.5176	102.5974	58.62069	65.51724	14.91935	11.81102

(*continued*)

APPENDIX 1. WHOLE-ROCK RARE EARTH ELEMENT ANALYSES OF BENTONITE SAMPLES, LOWER PIERRE SHALE (*continued*)

Chondrite:	La 0.367	Ce 0.957	Nd 0.711	Sm 0.231	Eu 0.087	Tb 0.058	Yb 0.248	Lu 0.0381
4	182.5613		70.32349	44.15584	25.28736	22.41379	14.51613	13.91076
5	174.3869	117.0324	70.32349	36.36364	19.54023	20.68966	14.91935	13.38583
6	160.7629	111.8077	56.25879	36.79654	27.58621	18.96552	15.32258	14.69816
11	57.22071	33.43783	14.0647	9.95671	6.896552		3.225806	2.624672
10	13.62398	9.404389		7.359307	14.94253		2.822581	2.099738
9	24.52316	19.85371	14.0647	12.98701	8.045977		4.435484	3.937008
8	8.174387	8.359457		6.926407	5.747126		2.419355	2.624672
7	32.69755	19.85371		5.194805	10.34483		4.032258	4.199475
8	10.89918	11.49425		9.090909	9.195402		3.629032	4.461942
7	32.69755	21.94357		5.627706	13.7931		4.435484	4.461942
Chamberlain								
1	59.9455	39.70742	28.1294	19.48052	9.195402	8.62069	5.241935	5.249344
2	81.74387	65.83072	42.19409	39.39394	22.98851	24.13793	12.09677	12.33596
3a	182.5613	129.5716	70.32349	34.63203	14.94253	13.7931	10.08065	9.448819
3b	228.8828	155.6949	84.38819	41.99134	19.54023	15.51724	6.048387	6.299213
4	81.74387	53.29154	28.1294	12.55411	3.448276		3.225806	3.937008
5	92.64305	51.20167	28.1294	16.88312	8.045977		4.032258	4.461942
5	54.49591	35.52769	14.0647	9.52381	3.448276		2.822581	3.674541
6	21.79837	11.49425		3.463203	4.597701		0.806452	1.312336
7	21.79837	12.53918		3.030303	3.448276		0.806452	1.574803
8	79.01907	43.88715	14.0647	5.194805	0.804598			
9	10.89918	12.53918	28.1294	21.64502	13.7931		1.612903	1.83727
Wasserburger Ranch								
1a	168.9373	114.9425	56.25879	33.33333	17.24138	15.51724	11.69355	9.973753
1b	179.8365	121.2121	56.25879	34.19913	19.54023	17.24138	14.91935	14.4357
1c	163.4877	112.8527	56.25879	33.33333	14.94253	15.51724	13.30645	12.86089
1d	185.2861	128.5266	70.32349	40.25974	20.68966	20.68966	12.90323	13.12336
1e	193.4605	136.8861	70.32349	42.42424	25.28736	20.68966	13.30645	12.59843
1f	215.2589	154.6499	84.38819	43.72294	25.28736	20.68966	13.30645	12.07349
1g	128.0654	94.04389	56.25879	32.90043	19.54023	17.24138	12.09677	12.59843
1h	193.4605	134.7962	70.32349	39.39394	16.09195	17.24138	12.5	12.86089
1i	106.267	76.28004	42.19409	27.70563	14.94253	15.51724	11.69355	10.49869
1j	73.56948	52.2466	28.1294	21.21212	11.49425	12.06897	14.1129	14.4357
1k	204.3597	146.2905	84.38819	44.58874	21.83908	22.41379	15.72581	16.0105
2	152.5886	108.6729	56.25879	33.33333	19.54023	15.51724	12.5	13.12336
3	49.04632	38.66249	28.1294	18.18182	11.49425	13.7931	8.064516	7.874016
4	171.6621	120.1672	56.25879	33.76623	16.09195	13.7931	12.09677	12.59843
5	166.2125	113.8976	56.25879	33.33333	18.3908	15.51724	12.09677	12.86089
6	193.4605	141.0658	84.38819	46.32035	26.43678	22.41379	18.54839	16.53543
7	128.0654	91.95402	42.19409	27.70563	14.94253	15.51724	10.48387	9.448819
8	21.79837	17.76385	14.0647	9.95671	4.597701		4.032258	3.674541
9	21.79837	19.85371	14.0647	10.82251	4.597701		4.83871	3.937008
10	147.139	92.99896	56.25879	27.70563	12.64368	12.06897	10.08065	8.923885
11	133.515	44.93208	14.0647	9.090909	13.7931		2.016129	3.149606
11	138.9646	99.26855	56.25879	29.00433	21.83908	12.06897	10.08065	9.186352
12	51.77112	29.2581	14.0647	6.926407	9.195402		3.225806	4.199475
13	95.36785	65.83072	28.1294	18.61472	10.34483	8.62069	5.645161	5.511811
14	19.07357	13.58412		7.792208	5.747126		5.241935	4.986877
15	29.97275	15.67398		2.597403	5.747126		0.806452	1.574803
16	19.07357	13.58412		6.926407	6.896552		3.225806	3.149606
19	8.174387	6.269592		3.463203	3.448276		2.822581	2.624672
17	32.69755	20.89864		5.194805	6.896552		2.419355	3.412073
18	8.174387	6.269592		3.896104	5.747126		1.209677	2.362205
17	40.87193	26.1233	14.0647	6.493506	5.747126		4.435484	4.199475
18	10.89918	7.314525		4.329004	2.298851		1.209677	2.362205

Note: A blank indicates that concentrations were below detection limits.

APPENDIX 2. POINT COUNTS OF THE LIGHT MINERAL FRACTION OF BENTONITES, LOWER PIERRE SHALE

	Quartz	K-spar	Plagioclase		Quartz	K-spar	Plagioclase
Bentonite F1 and F2				Bentonite C1 and C2			
BG18	31	42	27	BG15	50	32	18
BR30	6	14	5	BG16	39	41	20
WsR32	29	49	22	WsR24	13	9	4
BG17	31	49	13	WsR26	38	45	17
BG18	53	90	48	Red3-99-8	56	33	10
WsR31	18	57	25	Red3-99-9	39	42	18
				Pem1-20	34	56	18
Ardmore R2				Ardmore R1			
BG04	30	42	28	BG01	31	28	41
Pem1-08	29	41	30	BG11	20	38	42
Pem1-09	23	41	36	BG12	19	39	42
PEM1-11	25	41	34	Pem1-04	36	39	25
RED2-98-06	24	44	32	Pem1-16	22	38	40
RED2-98-07	21	47	32	RED2-01	44	33	23
RED2-98-09	22	48	30	Red2-02	32	36	32
WsR04	30	34	36	RED2-98-16	25	40	35
Average	25.33	42.67	32.00	WsR01	26	41	33
StDev	3.50	2.42	2.83	WsR18	24	40	36
				Average	31.75	37.5	30.75
				StDev	8.73	3.70	5.32
Ardmore dacite 1							
Ardmore A1A				Ardmore A1D			
BG02	16	44	40	BG08	25	25	50
BG03	20	40	40	RED2-98-13	25	25	50
PEM1-05	16	46	38	WsR14	29	25	46
Pem1-06	16	44	40	Average	26.333333	25	48.666667
PEM1-07	18	40	42	StDev	2.3094011	0	2.3094011
RED2-98-03	19	43	38				
RED2-98-04	18	42	40	Ardmore A1E			
RED2-98-05	22	36	42	BG09	15	39	46
WsR02	16	40	44	Pem1-14	18	40	42
WsR03	16	40	44	Red2-98-14	15	38	47
Average	17.70	41.50	40.80	Average	16	39	45
StDev	2.11	2.88	2.15	StDev	1.7320508	1	2.6457513
Ardmore A1B				Ardmore A1E			
BG05	20	36	44	BG10	18	32	50
RED2-98-11	26	36	38	Red2-98-15	15	36	49
Average	23	36	41	Average	16.5	34	49.5
StDev	4.2426407	0	4.2426407	StDev	2.1213203	2.8284271	0.7071068
Ardmore A1C				Ardmore A1F			
BG06	19	26	55	BG13	19	25	56
BG07	18	28	54	WsR19	16	23	61
RED2-98-12	19	26	55	Average	17.5	24	58.5
WsR13	17	27	56	StDev	2.1213203	1.4142136	3.5355339
Average	18.25	26.75	55				
StDev	0.9574271	0.9574271	0.8164966				
Ardmore dacite 2							
RED2-98-08	8	48	44				

APPENDIX 3. MICROPROBE ANALYSES OF BIOTITE IN BENTONITES, LOWER PIERRE SHALE

Sample ID	SiO_2	TiO_2	Al_2O_3	FeO	MgO	CaO	Na_2O	K_2O	Fe^{2+}	Fe^{3+}	Mg	Mg#	MgO
Ardmore Samples													
Red-8	38.374	5.481	6.119	10.788	15.071	0.015	0.592	8.726	8.091	2.997	9.09	0.529	15.071
Red-8	37.15	5.319	5.438	11.101	15.083	0.015	0.666	8.955	8.326	3.084	9.097	0.522	15.083
Red-8	35.658	4.866	5.229	11.148	13.734	0.004	0.534	8.483	8.361	3.097	8.283	0.498	13.734
Red-8	32.404	4.825	6.1	11.526	14.86	0.007	0.53	8.685	8.645	3.202	8.963	0.509	14.86
Red-8	34.404	5.399	4.09	11.532	14.483	0	0.538	8.769	8.649	3.204	8.735	0.502	14.483
Red-8	34.21	5.592	4.207	11.602	15.613	0.015	0.664	9.057	8.702	3.223	9.417	0.52	15.613
Red-8	35.379	5.46	4.997	11.914	14.842	0.008	0.577	9.102	8.936	3.31	8.952	0.5	14.842
Red-8	33.436	5.125	5.031	12.492	13.754	0	0.555	8.579	9.369	3.471	8.296	0.47	13.754
BS28	35.665	5.059	12.535	12.328	14.934	0.029	0.775	8.079	9.246	3.425	9.007	0.493	14.934
BS28	34.69	5.296	12.065	11.111	14.974	0.019	0.67	7.709	8.333	3.087	9.031	0.52	14.974
BS28	35.922	5.346	12.977	12.091	15.261	0.028	0.665	8.285	9.068	3.359	9.204	0.504	15.261
BS28	33.756	5.042	11.909	11.307	14.416	0.036	0.61	7.673	8.48	3.141	8.695	0.506	14.416
BS28	32.947	4.772	11.447	11.568	14.229	0.063	0.597	7.684	8.676	3.214	8.582	0.497	14.229
BS28	34.336	5.264	12.315	11.292	14.95	0	0.666	7.974	8.469	3.137	9.017	0.516	14.95
BS28	35.564	4.723	11.822	14.053	14.248	0.013	0.701	8.191	10.54	3.904	8.593	0.449	14.248
BS28	35.656	5.244	12.157	12.291	15.134	0.013	0.625	8.313	9.218	3.415	9.128	0.498	15.134
WsR01	39.226	5.603	13.228	11.222	13.597	0.088	0.481	7.937	8.417	3.118	8.201	0.494	13.597
WsR01	35.92	5.55	11.429	11.285	14.189	0.088	0.518	7.643	8.464	3.135	8.558	0.503	14.189
WsR01	35.762	5.589	12.486	11.897	14.32	0.046	0.509	8.272	8.923	3.305	8.637	0.492	14.32
WsR01	39.63	5.917	12.364	11.918	14.681	0.035	0.51	7.87	8.939	3.311	8.855	0.498	14.681
WsR01	38.763	5.814	12.391	12.086	14.476	0.067	0.466	7.863	9.065	3.358	8.731	0.491	14.476
WsR01	36.485	5.729	12.195	12.229	14.394	0.119	0.515	7.759	9.172	3.398	8.682	0.486	14.394
WsR01	39.608	5.639	12.97	12.241	14.508	0.074	0.526	8.45	9.181	3.401	8.75	0.488	14.508
WsR02	38.242	4.391	11.663	10.643	12.044	0.148	0.539	7.602	7.982	2.957	7.264	0.476	12.044
WsR02	40.002	4.826	15.157	11.223	12.072	0.151	0.466	7.269	8.417	3.118	7.281	0.464	12.072
WsR02	36.321	5.348	12.961	11.5	14.086	0.104	0.566	8.271	8.625	3.195	8.496	0.496	14.086
WsR02	35.655	5.696	12.49	11.826	14.655	1.361	0.693	8.157	8.87	3.286	8.839	0.499	14.655
WsR02	37.673	5.966	12.851	11.958	14.666	0.051	0.607	8.406	8.969	3.322	8.846	0.497	14.666
WsR02	36.863	5.313	11.937	12.02	14.05	0.087	0.503	8.525	9.015	3.339	8.474	0.485	14.05
WsR02	38.191	5.572	12.229	12.746	14.596	0.009	0.516	8.617	9.56	3.541	8.803	0.479	14.596
WsR03	39.58	5.562	12.972	11.575	13.969	1.11	0.551	8.108	8.681	3.216	8.425	0.493	13.969
WsR03	39.096	5.903	12.032	12.062	15.245	2.125	0.561	9.026	9.047	3.351	9.195	0.504	15.245
WsR03	39.066	5.705	12.916	12.338	14.489	0.037	0.464	8.731	9.254	3.428	8.739	0.486	14.489
WsR03	39.042	5.684	12.349	12.338	14.699	0.011	0.578	8.657	9.254	3.428	8.866	0.489	14.699
WsR03	38.751	5.713	13.684	12.396	13.837	0.043	0.541	8.298	9.297	3.444	8.346	0.473	13.837
WsR03	37.908	5.954	12.492	12.42	14.382	0.049	0.532	8.683	9.315	3.451	8.674	0.482	14.382
WsR03	39.174	5.633	13.442	12.84	13.925	0.032	0.48	8.564	9.63	3.567	8.399	0.466	13.925
WsR03	37.741	5.453	13.021	13.76	14.361	0.014	0.516	8.983	10.32	3.823	8.662	0.456	14.361
WsR13	39.462	5.311	13.071	11.382	13.68	0.161	0.544	8.183	8.537	3.162	8.251	0.491	13.68
WsR13	41.843	5.49	11.453	11.444	13.924	0.404	0.508	8.119	8.583	3.179	8.398	0.495	13.924
WsR13	36.273	5.324	11.857	11.532	13.783	0.108	0.564	7.852	8.649	3.204	8.313	0.49	13.783
WsR13	39.973	5.599	12.387	11.56	14.245	0.064	0.564	8.389	8.67	3.212	8.592	0.498	14.245
WsR13	38.548	5.361	10.925	11.619	12.101	0.153	0.509	7.544	8.714	3.228	7.299	0.456	12.101
WsR13	40.773	5.579	12.192	11.732	14.731	0.064	0.659	8.442	8.799	3.259	8.885	0.502	14.731
WsR13	40.286	5.67	12.478	12.123	15.002	0.037	0.581	8.96	9.092	3.368	9.048	0.499	15.002
Bentonite C2													
Red-26	33.859	4.806	4.817	18.127	11.418	0.011	0.48	9.2	13.6	5.036	6.887	0.336	11.418
Red-26	34.166	5.331	11.598	20.916	9.152	0.039	0.519	7.697	15.69	5.811	5.52	0.26	9.152
Red-26	34.773	4.511	12.369	18.241	11.606	0.064	0.513	8.31	13.68	5.068	7	0.338	11.606
Pem1-20	44.472	4.734	10.516	16.802	10.242	0.088	0.5	8.381	12.6	4.668	6.177	0.329	10.242
Pem1-20	38.228	4.595	10.706	17.37	8.514	0.005	0.411	7.623	13.03	4.826	5.135	0.283	8.514
Pem1-20	38.25	4.699	11.96	17.5	12.18	0.02	0.442	9.002	13.13	4.862	7.346	0.359	12.18

(*continued*)

APPENDIX 3. MICROPROBE ANALYSES OF BIOTITE IN BENTONITES, LOWER PIERRE SHALE (*continued*)

Sample ID	SiO_2	TiO_2	Al_2O_3	FeO	MgO	CaO	Na_2O	K_2O	Fe^{2+}	Fe^{3+}	Mg	Mg#	MgO
Pem1-20	38.249	4.699	11.964	17.501	12.181	0.02	0.442	9.002	13.13	4.862	7.347	0.359	12.181
Pem1-20	39.12	4.905	11.862	17.761	12.169	0.019	0.479	9.018	13.32	4.934	7.34	0.355	12.169
Pem1-20	36.487	4.924	11.1	18.094	9.061	0.042	0.416	7.862	13.57	5.027	5.465	0.287	9.061
Pem1-20	39.154	5.015	12.297	18.752	11.355	0.011	0.47	9.055	14.06	5.21	6.849	0.327	11.355
Pem1-20	37.848	4.941	12.238	18.837	11.219	0.018	0.475	8.847	14.13	5.233	6.767	0.324	11.219
WsR26	38.3	5.862	11.364	17.046	10.874	0.04	0.44	7.77	12.79	4.736	6.559	0.339	10.874
WsR26	37.21	6.243	12.033	17.498	11.907	0.05	0.49	8.445	13.12	4.861	7.182	0.354	11.907
WsR26	39.96	5.434	11.07	17.388	11.169	0.09	0.49	7.954	13.04	4.831	6.736	0.341	11.169
WsR26	39.96	5.434	11.07	17.388	11.169	0.09	0.49	7.954	13.04	4.831	6.736	0.341	11.169
WsR26	37.72	5.653	9.832	17.334	11.3	0.05	0.42	8.088	13	4.816	6.815	0.344	11.3
WsR26	39.28	5.872	12.841	18.135	11.283	0.02	0.45	8.378	13.6	5.038	6.805	0.333	11.283
WsR26	39.2	5.094	9.642	16.149	10.327	0.08	0.42	7.444	12.11	4.487	6.229	0.34	10.327
Bentonite F2													
BG19	39.167	3.887	13.644	9.639	10.695	0.023	0.323	7.6	7.229	2.678	6.451	0.472	10.695
BG19	35.817	4.505	10.996	11.394	11.397	0.033	0.443	8.624	8.546	3.166	6.874	0.446	11.397

Note: Fe^{2+}, Fe^{3+}, Mg, and Mg# calculated from probe data.

APPENDIX 4. MEASURED STRATIGRAPHIC SECTIONS, LOWER PIERRE SHALE

Walhalla, North Dakota

Top not exposed

100 cm	Shale, olive black, not bentonitic	
6 cm	Bentonite, yellowish gray	98-PEM1-28
250 cm	Shale, olive black, not bentonitic	
5 cm	Bentonite, yellowish gray, dirty	98-PEM1-27
34 cm	Shale, olive black, not bentonitic	
2 cm	Bentonite, grayish orange, heavily jarosite stained	98-PEM1-26
105 cm	Shale, olive black, not bentonitic, sample taken from bottom	98-PEM1-25
2–4 cm	Bentonite, light brown, dirty	98-PEM1-24
150 cm	Clay, black, sample taken from top 5 cm	98-PEM1-23
5 cm	Bentonite, light brown, dirty, grades laterally into a cemented gypsiferous layer	98-PEM1-22a/b
140 cm	Clay, black	
1 cm	Bentonite, light brown	98-PEM1-21
5 cm	Clay, black	
1 cm	Bentonite, light brown	98-PEM1-20
46 cm	Clay, black	
17 cm	Bentonite, light brown	98-PEM1-19
47 cm	Clay, black	
1 cm	Bentonite, light brown	98-PEM1-18
23 cm	Clay, black	
12 cm	Bentonite, light brown	98-PEM1-17
1 cm	Clay, black	
1 cm	Bentonite, light brown	
5 cm	Clay, black	
17 cm	Bentonite, light brown	98-PEM1-16
5 cm	Clay, black	
0.5 cm	Bentonite, light brown	
0.5 cm	Clay, black	
7 cm	Bentonite, light brown, burrowed	98-PEM1-15
5 cm	Clay, black	
4 cm	Bentonite, yellowish gray, burrowed at top	98-PEM1-14
9 cm	Clay, black	
12 cm	Bentonite, yellowish gray, burrowed at top	98-PEM1-13
12 cm	Clay, heavily iron stained	
2 cm	Bentonite, yellowish gray	98-PEM1-12

(*continued*)

Walhalla, North Dakota

Top not exposed (continued)

3 cm	Clay, black	
10 cm	Bentonite, grayish yellow, jarosite stained	98-PEM1-11
40 cm	Shale, black, blocky, bentonitic, sample taken from lower 5 cm	98-PEM1-10
4 cm	Bentonite; top has abundant large gypsum crystals and is moderate brown and extensively burrowed	98-PEM1-9
2 cm	Clay, black, bentonitic	
2 cm	Bentonite, grayish yellow	98-PEM1-8
2 cm	Clay, black, bentonitic	
2 cm	Bentonite, shale mottled, burrowed	98-PEM1-7
2 cm	Clay, black, bentonitic	
1 cm	Bentonite, grayish yellow	98-PEM1-6
2 cm	Clay, black, bentonitic	
3 cm	Bentonite, grayish orange, limonite stained, gypsiferous, contacts sharp	98-PEM1-5
4 cm	Clay, black, blocky, bentonitic	
2 cm	Bentonite, grayish orange, limonite stained, gypsiferous, contacts sharp	98-PEM1-4
7 cm	Clay, black, blocky	
5 cm	Bentonite, grayish orange, limonite stained, gypsiferous, contacts sharp	98-PEM1-3
9 cm	Clay, black, blocky, bentonitic	98-PEM1-2
7 cm	Iron-stained clay, gypsiferous, brownish black	98-PEM1-1

Base of member

1033 cm exposed

Chamberlain, Brule County, South Dakota

(Composite Section)

Sharon Springs Member

Gray shale facies

500 cm	Gray shale
25 cm	Grayish yellow calcite-cemented bentonite
50 cm	Gray shale
25 cm	Grayish yellow calcite-cemeted bentonite
50 cm	Gray shale

Phosphate nodule facies

500 cm	Black shale with abundant gypsum-encrusted phosphate nodules

Buttress-weathering shale facies

7 cm	Gray bentonite
102 cm	Fissile gray shale, mottled, vertical weathering
3 cm	Gray bentonite
375 cm	Fissile gray shale, mottled, vertical weathering
1 cm	Peach bentonite
78 cm	Fissile gray shale, vertically weathering
4 cm	Peach bentonite
22 cm	Blocky shale

Bentonite facies

2–15 cm	Iron stained unconformity
10 cm	Brown shale
10 cm	Tan bentonite
30 cm	Black clay
10 cm	Tan bentonite
20 cm	Black clay
6–20 cm	Possible channel
18–30 cm	Black clay
15 cm	Tan bentonite
10 cm	Black clay
18 cm	Tan bentonite
2 cm	Black shale
4 cm	Tan bentonite
12 cm	Black clay
12 cm	Grayish yellow bentonite
15 cm	Black shale
3 cm	Grayish yellow bentonite
7 cm	Black clay
3 cm	Grayish yellow bentonite
8 cm	Black shale
11 cm	Grayish yellow bentonite
70 cm	Black shale

(*continued*)

McAllaster Buttes (southern side), Wallace County, Kansas

Top of Sharon Springs Member

Phosphate Unit

27 cm	Cone-in-cone concretions, dark yellowish orange (10YR6/6)	
46 cm	Shale, limonitic, bentonitic, olive black (5Y 2/1)	JB-WAL1-98-S1
0.5 cm	Bentonite, very pale orange (10YR 8.2)	JB-WAL1-98-B1
8 cm	Shale, dark yellowish brown (10YR 4/2)	
1–4 cm	Phosphate nodules, medium bluish gray	
3 cm	Shale, pale yellowish brown (10 YR 6/2)	
1 cm	Bentonite, yellowish gray (5Y 7/2)	JB-WAL1-98-B2
3.5 cm	Shale, dark yellowish brown (10YR 4/2)	
0.125 cm	Bentonite, pale yellowish gray (5Y 7/2)	
11 cm	Shale, brownish black (5YR 2/1)	
3–4 cm	Phosphate nodules, medium bluish gray	
20 cm	Shale, limonitic, fish debris, olive black (5 & 2/1)	JB-WAL1-98-S2
12 cm	Shale, dark yellowish brown	
0.25 cm	Bentonite, pale yellowish gray	
10 cm	Shale, fish debris, pale yellowish brown	
0.25 cm	Bentonite, pale yellowish gray	
16 cm	Shale, dark yellowish brown	
2 cm	Phosphate nodules, medium bluish gray	
4 cm	Shale, dark yellowish brown	
18 cm	Bentonite, grayish orange (10YR 7/4); grades laterally into cone-in-cone concretions	JB-WAL1-98-B3A/B
3–5 cm	Shale, olive black (5Y 2/1), mottled with pale yellowish brown and iron staining	JB-WAL1-98-S3
3 cm	Phosphate nodules, medium bluish gray	
7 cm	Shale, olive black (5Y 2/1), mottled with pale yellowish brown, iron staining	
8 cm	Bentonite, grayish orange, limonite and jarosite stained, gypsiferous	JB-WAL1-98-B4
30 cm	Shale, fish debris, olive black	
1 cm	Bentonite, grayish orange, limonite and jarosite stained, gypsiferous	JB-WAL1-98-B5
31 cm	Shale, dark yellowish brown	JB-WAL11-98S4
1 cm	Bentonite, grayish orange	JB-WAL1-98-B6
20 cm	Shale, grayish brown	JB-WAL1-98-S5
2 cm	Bentonite, grayish orange	JB-WAL1-98-B7
32 cm	Shale, olive black	

Buttress-weathering shale unit

60 cm	Septarian concretions, ammonites	
910 cm	Shale, pale yellowish brown, fish debris, limonite staining	JB-WAL1-98-S5->13
3 cm	Bentonite, very pale orange	JB-WAL1-98-B8

McAllaster Buttes (northern side), Wallace County, Kansas

Top not exposed

Buttress-weathering shale

60 cm	Septarian concretions, ammonites	
910 cm	Shale	
3 cm	Bentonite	JB-WAL2-98-B1
490 cm	Shale, hard dusky yellowish brown, gypsiferous, some jarosite staining and joints with jarosite staining and gypsum; top 70 cm is fissile	JB-WAL3-98-S1->S6

Dark soft shale unit(?)

45 cm	Shale, heavily iron stained, gypsiferous, dark yellowish brown, fissile	JB-WAL3-98-S7
0–20 cm	Limestone-septarian concretions, medium bluish gray, up to 1 m diameter	JB-WAL3-98-S8
100 cm	Shale, fissile, olive black, jarosite stained, gypsiferous; isolated limestone concretions 3 cm from base	JB-WAL3-98-S9
1 cm	Bentonite, heavily jarosite stained, especially top and bottom, pale yellowish brown	JB-WAL3-98-B2
65 cm	Shale, fissile, olive black, jarosite stained, gypsiferous; isolated limestone concretions 35 cm from base	JB-WAL3-98-S10
0.125 cm	Jarosite stringer	
6.5 cm	Shale, fissile, olive black, jarosite stained, gypsiferous	
1.5 cm	Bentonite, heavily jarosite stained, large selenite crystals	

Base not exposed

(*continued*)

Burris Draw, Wallace County, Kansas

Top not exposed

Dark soft shale unit

∼700 cm	Shale, covered	
1cm	Bentonite, altered to jarosite	
∼500 cm	Shale, mostly covered, gypsiferous, olive black	JB-BUR1-98-S8
15 cm	Shale, heavily iron stained, forms prominent shelf in outcrop, gypsiferous, dusky yellowish brown, fissile	JB-BUR1-98-S7
120 cm	Shale, mostly covered, olive black, gypsiferous, slightly bituminous, fissile	JB-BUR1-98-S6
2 cm	Bentonite, laminated, medium bluish gray and grayish orange, heavily jarosite stained, jarosite and limonite at top and bottom	JB-BUR1-98-B3
170 cm	Shale, olive gray, gypsiferous, no jarosite staining on bedding planes (sampled from lowest 10 cm)	JB-BUR1-98-S5
0.5 cm	Bentonite, bluish gray, jarosite stained on top and bottom	
23 cm	Shale, olive gray, heavily jarosite stained along bedding planes, fissile	JB-BUR1-98-S4
0.5 cm	Bentonite	JB-BUR1-98-B2
36 cm	Shale, slightly calcareous, grading into non-calcareous ~10 cm from top, olive black, fissile	JB-BUR1-98-S3

Niobrara–Pierre Shale contact

Wallace Ranch and Slurp Flats, Fall River County, South Dakota

Mitten Black Shale Member

Top not exposed

10 cm	Siderite concretions, tabular	
20 cm	Shale, olive black, fissile	
10 cm	Siderite concretions, tabular	
20 cm	Shale, olive black, fissile	
1 cm	Bentonite, light brown	
82 cm	Shale, olive black, fissile	
1 cm	Bentonite, light brown	
4.5 cm	Shale, olive black, fissile	
3 cm	Siderite concretions, tabular	

Sharon Springs Member

300 cm	Shale, olive black	
5 cm	Bentonite, tan	WR-18
145 cm	Shale, olive black	
2.5 cm	Bentonite, light brown	WR-17
5 cm	Shale, olive black	
3 cm	Bentonite, tan	WR-16
40 cm	Shale, olive black, fissile	
10 cm	Gypsiferous septarian concretions	
3 cm	Shale, black, hard	
16 cm	Bentonite, grayish yellow	
2 cm	Shale, black, hard	
40 cm	Bentonite, grayish yellow	WR-96-15
1 cm	Shale, black, hard	
12 cm	Bentonite, grayish yellow	WR-96-14
2 cm	Shale, black, hard	
140 cm	Bentonite, grayish yellow	WR-96-8->13
3 cm	Shale, black, hard	
24 cm	Bentonite, grayish yellow	WR-96-7

Gammon Ferruginous Member

36 cm	Shale, olive black, fissile	
1 cm	Bentonite, olive brown	WR-96-25
90 cm	Shale, olive black, fissile	
1 cm	Gypsiferous layer	
20 cm	Shale, olive black, fissile, bentonitic	
20 cm	Siderite concretionary layer	
155 cm	Shale, olive black, fissile, bentonitic	
1.5 cm	Bentonite, pinkish gray	WR-96-24
40 cm	Shale, olive black, fissile, bentonitic	
20 cm	Siderite concretionary layer	

(*continued*)

Wallace Ranch and Slurp Flats, Fall River County, South Dakota

Gammon Ferruginous Member

110 cm	Shale, olive black, fissile, bentonitic	
2 cm	Bentonite, light brown	WR-96-23
110 cm	Shale, olive black, fissile, bentonitic	
2.5 cm	Bentonite, grayish yellow	WR-96-20
22 cm	Shale, olive black, fissile, bentonitic	
19 cm	Bentonite, grayish yellow	WR-96-22
2.5 cm	Shale, olive black, fissile, bentonitic	
4.5 cm	Bentonite, grayish yellow	WR-96-21

Base not exposed

Redbird, Niobrara County, Wyoming

(Composite section)

Sharon Springs Member

Top not exposed

8 cm	Heavily limonite-stained shale	
120 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
1 cm	Bentonite, yellowish gray, heavily jarosite stained, gypsiferous	RED2-99-10
15 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.25 cm	Gypsiferous layer, large crystals	
18 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.25 cm	Gypsiferous layer, large crystals	
33 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
1 cm	Bentonite, grayish yellow, heavily jarosite stained and gypsiferous	RED2-99-9
150 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.5 cm	Bentonite, heavily jarosite stained, gypsiferous	RED2-99-8
160 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.25 cm	Iron-stained gypsiferous layer	
2 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.5 cm	Bentonite, heavily jarosite stained, gypsiferous	RED2-99-7
160 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.5 cm	Bentonite, heavily jarosite stained, gypsiferous	RED2-99-6
10 cm	Shale, olive black fresh, light olive gray weathered, gypsiferous	
0.25 cm	Gypsiferous, iron-stained zone	
8 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.5 cm	Bentonite, heavily jarosite stained and gypsiferous	RED2-99-5
48 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.5 cm	Bentonite, heavily iron stained, gypsiferous	RED2-99-4
25 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
0.5 cm	Bentonite, heavily iron stained, gypsiferous	RED2-99-3
15 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
1 cm	Bentonite, heavily jarosite stained and gypsiferous, yellowish gray	RED2-99-2
23 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
2.5 cm	Bentonite, heavily jarosite stained and gypsiferous, yellowish gray	RED2-99-1
40 cm	Shale, olive black fresh, light olive gray weathered, fissile, gypsiferous	
17 cm	Bentonite, yellowish gray, heavily jarosite stained, large gypsum crystals	RED2-98-26/RED3-99-9/10
500 cm	Shale, olive black fresh, light olive gray weathered; weathers to a gentle slope that is dominantly covered, fissile, gypsiferous	RED2-98-25
25 cm	Bentonite, yellowish gray, heavily jarosite stained, large gypsum crystals, forms a small bench at the top, marked by vegetation in outcrop	RED2-98-24/RED3-99-7/8
22 cm	Shale, olive black fresh, light olive gray weathered, weathers to a gentle slope that is dominantly covered, fissile, gypsiferous	
1 cm	Bentonite, grayish yellow, jarosite-stained contacts	RED2-98-23
195 cm	Shale, olive black fresh, light olive gray weathered, weathers to a gentle slope that is dominantly covered, fissile, gypsiferous	
0.5 cm	Bentonite, yellowish gray, indistinct	
285 cm	Shale, olive black fresh, light olive gray weathered, weathers to a gentle slope which is dominantly covered, fissile, gypsiferous	
3 cm	Bentonite, grayish yellow, jarosite stained	RED2-98-18
30 cm	Shale, black, organic-rich, fissile	RED3-99-6
3 cm	Bentonite, grayish yellow, jarosite stained at base	RED2-98-17
38 cm	Shale, black, fissile, gypsiferous, top 3 cm siliceous and hard	RED2-98-20/RED3-99-5

(*continued*)

Redbird, Niobrara County, Wyoming

(Composite section)

Sharon Springs Member

Top not exposed (continued)

18 cm	Bentonite, light bluish gray, especially at base and grayish yellow, heavily jarosite stained, coarse grained at base, fines upward, greasy	RED2-98-16
14 cm	Shale, black, organic-rich, fissile	RED3-99-4
36 cm	Bentonite, light bluish gray, greasy, jarosite stained only on fractures, coarse grained at base, fines upward	RED2-98-14/15
10 cm	Shale, top 7 cm siliceous, blocky, black, organic-rich	RED3-99-3
18 cm	Bentonite, light bluish gray, greasy, jarosite stained only on fractures, coarse grained at base, fines upward	RED2-98-13
8 cm	Siliceous shale, organic-rich, black, hard	RED3-99-2
13 cm	Bentonite, grayish yellow fresh, weathers pale yellowish orange, jarosite stained, burrowed, large gypsum crystals, coarse grained at base, fines upward	RED2-98-12
2 cm	Siliceous shale, grayish black, heavily ferruginous stained, large gypsum crystals at base and top, blocky	RED3-99-1
93 cm	Bentonite	
	lower 58 cm: dominantly grayish blue when fresh, weathers pale yellowish orange, jarosite staining, large gypsum crystals	
	58-63 cm: dark yellowish orange, large gypsum crystals	
	63-93 cm: grayish yellow fresh, weathers pale yellowish orange, jarosite staining	RED2-98-3-11
1 cm	Siliceous shale, grayish black, heavily ferruginous stained, moderate reddish orange, blocky	
24 cm	Bentonite, yellowish gray, heavily stained, moderate brown with jarosite, greasy, gypsiferous	RED2-98-1/2
200 cm	Siliceous shale, olive black, heavily ferruginous stained, moderate reddish orange, blocky, mostly covered, sampled from top 20 cm	RED2-98-19
24 m		

Gammon Ferruginous Member

10 cm	Siderite concretionary zone, platy	
200 cm	Shale, dark gray, soft hackly, mostly covered	
5 cm	Bentonite, grayish yellow, flaky, sharp contacts	RED1-98-10
13 cm	Shale, dark gray, soft hackly	
8 cm	Bentonite, grayish black, soft, hackly	RED1-98-9
13 cm	Shale, grayish black, soft hackly	
3 cm	Bentonite, flaky, non-swelling, sharp contacts, grayish yellow	RED1-98-8
19 cm	Shale, dark gray, soft, hackly, fish debris	
2 cm	Bentonite, platy, non-swelling, yellowish gray, sharp contacts	RED1-98-7
31 cm	Shale, as below, soft	RED1-98-6
0.025 cm	Ferruginous stained layer, gypsiferous	
15 cm	Shale, hackly, hard gypsiferous, grayish black	RED1-98-5
17 cm	Bentonite, lower 8 cm moderate yellow, greasy bentonite with limonite staining; top 9 cm dark yellowish orange, flaky, non-swelling, contacts are sharp	RED1-98-3/4
27 cm	Shale, hackly, abundant small gypsum crystals, ferruginous stained (dark reddish brown), dark gray fresh, yellowish gray weathered	RED1-98-2

Wasserburger Ranch, Fall River County, South Dakota

Contact with Mitten Black Shale Member

180 cm	Shale, olive black fresh, light olive gray weathered	
5 cm	Grayish yellow bentonite	WsR-96-33
180 cm	Shale, olive black fresh, light olive gray weathered	
7.5 cm	Grayish orange bentonite	WsR-96-32
7.5 cm	Shale, olive black fresh, light olive gray weathered	
5 cm	Grayish yellow bentonite	WsR-96-31
135 cm	Shale, olive black fresh, light olive gray weathered	
1 cm	Grayish yellow, iron-stained bentonite	
6 cm	Shale, olive black fresh, light olive gray weathered	
2 cm	Grayish yellow, iron-stained bentonite	
120 cm	Shale, olive black fresh, light olive gray weathered	
10 cm	Siderite concretions	
30 cm	Shale, olive black fresh, light olive gray weathered	
7.5 cm	Grayish yellow bentonite	WsR-96-29
89 cm	Ferruginous, hard black shale	
2 cm	Grayish yellow bentonite	WsR-96-28
112 cm	Ferruginous, hard black shale with eight discontinuous bentonites	
2 cm	Grayish yellow bentonite	WsR-96-27

(*continued*)

APPENDIX 4. MEASURED STRATIGRAPHIC SECTIONS, LOWER PIERRE SHALE (*continued*)

Wasserburger Ranch, Fall River County, South Dakota

Contact with Mitten Black Shale Member (continued)

5 cm	Ferruginous hard black shale	
15 cm	Grayish yellow bentonite (bentonite couplet)	WsR-96-26
3 cm	Shale, olive black fresh, light olive gray weathered	
0.5 cm	Grayish yellow bentonite	WsR-96-25
42 cm	Shale, olive black fresh, light olive gray weathered	
27 cm	Grayish yellow bentonite (bentonite couplet)	WsR-96-24
22 cm	Ferruginous hard, black shale	
0.5 cm	Discontinuous bentonite	WsR-96-23
13 cm	Ferruginous hard, black shale	
0.25 cm	Discontinuous bentonite	WsR-96-22
8 cm	Ferruginous hard, black shale	
1.5 cm	Grayish yellow bentonite	WsR-96-21
14 cm	Ferruginous hard, black shale	
1 cm	Grayish yellow bentonite	WsR-96-20
31 cm	Ferruginous hard, black shale	
18 cm	Grayish yellow bentonite, bioturbated	WsR-96-19
23.5 cm	Ferruginous hard, black shale	
33 cm	Bluish gray bentonite, grayish yellow when weathered, discontinuous shale partings	WsR-96-18
18 cm	Ferruginous hard, black shale	
14 cm	Bluish gray bentonite, grayish yellow when weathered	WsR-96-17
14 cm	Ferruginous hard, black shale	
14 cm	Grayish yellow bentonite	WsR-96-16
32 cm	Ferruginous hard, black shale	
1 cm	Grayish yellow bentonite	WsR-96-15
10 cm	Ferruginous hard, black shale	
13 cm	Grayish yellow bentonite	WsR-96-14
7 cm	Ferruginous hard, black shale	
11 cm	Grayish yellow bentonite	WsR-96-13
28 cm	Ferruginous hard, black shale	
7 cm	Grayish yellow bentonite with numerous shale partings	WsR-96-5->12
32 cm	Yellow gypsiferous bentonite	WsR-96-4
13-16 cm	Bluish gray bentonite	WsR-96-3
28-32 cm	Grayish orange bentonite, gypsiferous	WsR-96-2
32 cm	Ferruginous hard, black shale	
21 cm	Bluish gray bentonite	WsR-96-1

Buffalo Gap, Fall River County, South Dakota

Top not measured

Middle unit

50 cm	Shale, fissile, grayish black	SS-JLB-37
5 cm	Bentonite, yellowish gray	BS-JLB-29
38 cm	Shale, fissile, grayish black	SS-JLB-36
0.5 cm	Bentonite, yellowish gray	
18 cm	Shale, fissile, grayish black	SS-JLB-35
1.25 cm	Bentonite, yellowish gray	
4 cm	Shale, fissile, grayish black	SS-JLB-34
1.25 cm	Bentonite, yellowish gray	
90 cm	Shale, fissile, grayish black	SS-JLB-33 (top) SS-JLB-32 (bottom)

Ardmore bentonite unit

15 cm	Bentonite, yellowish gray	BS-JLB-28
5 cm	Shale, hard, black	SS-JLB-31
17 cm	Bentonite, yellowish gray	BS-JLB-27
3 cm	Shale, hard, black	SS-JLB-30
15 cm	Bentonite, yellowish gray	BS-JLB-26
5 cm	Shale, hard, black	SS-JLB-29
60 cm	Bentonite, grayish yellow	BS-JLB-25 (top) BS-JLB-24 (middle) BS-JLB-23 (bottom)
5 cm	Shale, hard, black	SS-JLB-28

(*continued*)

APPENDIX 4. MEASURED STRATIGRAPHIC SECTIONS, LOWER PIERRE SHALE (*continued*)

Buffalo Gap, Fall River County, South Dakota

Top not measured

Ardmore bentonite unit *(continued)*

7.5 cm	Bentonite, grayish yellow	BS-JLB-22
2.5 cm	Shale, hard, black	SS-JLB-27
7.5 cm	Bentonite, grayish yellow	BS-JLB-21
3 cm	Shale, black, hard	SS-JLB-26
3 cm	Bentonite, grayish yellow	BS-JLB-20
3 cm	Shale, black, hard	SS-JLB-25
15 cm	Bentonite, grayish yellow	BS-JLB-19
4 cm	Shale, hard, black	SS-JLB-24
33 cm	Bentonite, grayish yellow	BS-JLB-18 (top) BS-JLB-17 (bottom)
2.5 cm	Shale, hard, black	
10 cm	Bentonite, grayish yellow	BS-JLB-16
1 cm	Shale, hard, black	
5 cm	Bentonite, grayish yellow	BS-JLB-15
3 cm	Shale, hard, black	SS-JLB-22
14 cm	Bentonite, grayish yellow	BS-JLB-14
14 cm	Shale, hard, black	SS-JLB-21
0.5 cm	Bentonite, grayish yellow	
14 cm	Shale, hard, black	SS-JLB-20
15 cm	Gypsiferous concretions	
15 cm	Bentonite, grayish yellow	BS-JLB-13
18 cm	Shale, hard, black	SS-JLB-17
28 cm	Bentonite, grayish yellow	BS-JLB-12 (top) BS-JLB-11 (bottom)
8 cm	Shale, hard, black	SS-JLB-16
13 cm	Bentonite, grayish yellow	BS-JLB-10
10 cm	Shale, hard, black	SS-JLB-15
10 cm	Bentonite, grayish yellow	BS-JLB-9
28 cm	Shale, hard, black	SS-JLB-14 (top) SS-JLB-13 (bottom)
1 cm	Bentonite, grayish yellow	
1 cm	Shale, hard, black	SS-JLB-12
0.5 cm	Bentonite, grayish yellow	
2 cm	Shale, hard, black	SS-JLB-11
2 cm	Concretions	
9 cm	Bentonite, grayish yellow	BS-JLB-8
7 cm	Shale, hard, black	SS-JLB-10
13 cm	Bentonite, grayish yellow	BS-JLB-7 (top) BS-JLB-6 (bottom)
45 cm	Shale, hard, black	SS-JLB-9 (top) SS-JLB-8 (middle) SS-JLB-7 (bottom)
80 cm	Bentonite, grayish yellow	BS-JLB-5 (top 20 cm) BS-JLB-4 (2nd 20 cm) BS-JLB-3 (3rd 20 cm) BS-JLB-2 (bottom)
20 cm	Shale, hard, black	SS-JLB-5 (top) SS-JLB-4 (middle) SS-JLB-3 (bottom)
15 cm	Bentonite, grayish yellow	BS-JLB-1

Base of Sharon Springs Member

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Stratigraphy and paleoecology of the middle Pierre Shale along the Missouri River, central South Dakota

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ABSTRACT

A study of the Pierre Shale was undertaken, focusing on two measured sections along the eastern side of the Missouri River near Fort Thompson, South Dakota. The members of the Pierre Shale represented within these sections are, successively, the Gregory, Crow Creek, DeGrey, and Verendrye. Micropaleontologic samples were analyzed, with factor analysis performed to classify the assemblages. Four foraminiferal biofacies are recognized: two predominantly agglutinated, Boreal in origin, one shallower and the other deeper; one composed of calcareous benthic foraminifers, Tethyan in origin; and a fourth, which represents a mixed assemblage, transitional between the others. ^{87}Strontium/^{86}Strontium age estimation yielded 12 usable results. Samples from near the *Baculites compressus* Biozone yielded an age of ca. 72.43 ± 2 Ma. An average ^{87}Sr/^{86}Sr date of 72.41 ± 2 Ma was determined from fossil shells near a *Globidens* sp. excavation site within the upper DeGrey Member. More equivocal dates of 74.58, 74.63, and 75.09 ± 2 Ma were determined for the basal Crow Creek Member, a calcareous sandy siltstone within the upper Gregory Member, and the *B. gregoryensis* Biozone at the base of the section, respectively. Based on this study, the Gregory Member is interpreted as a highstand systems tract but as a part of the regressive pulse of the Claggett depositional cycle; the Crow Creek and DeGrey Members are the result of the Bearpaw transgression (a transgressive systems tract), and the boundary between the DeGrey and Verendrye Members is interpreted as a maximum flooding surface; and the Verendrye Member is a highstand systems tract. The distinct, calcareous sandy siltstone unit in the upper Gregory Member, herein named the *Fort Thompson Beds,* is interpreted to represent a storm-dominated deposit.

Keywords: Pierre Shale, South Dakota, ^{87}Sr/^{86}Sr ages, micropaleontology.

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INTRODUCTION

During recent years a multidisciplinary study conducted jointly by the South Dakota School of Mines and the New Jersey State Museum examined exposures of the middle Pierre Shale found along the eastern side of the Missouri River in central South Dakota (Fig. 1). The primary objective of this study was to investigate the Late Cretaceous fauna found within these Western Interior Seaway marine deposits and place these discoveries into a stratigraphic framework. Additionally, emphasis was placed on reconstructing this Late Cretaceous marine paleoenvironment. For the most part, prior studies within the area had limited themselves to particular members (Gries, 1942; Crandell, 1952; Hoff, 1960; Johnson, 1961; Lange, 1962; Bretz, 1979) or to establishing the final stratigraphic nomenclature (Gries and Rothrock, 1941; Crandell, 1950), and most of these studies took place before the advent of sequence stratigraphy. The results of many of these studies have produced disagreements. For example, Bretz (1979) assigned the Crow Creek Member to the Maastrichtian Stage on the basis of studies of the foraminifers from this member, whereas studies of the macro-invertebrates, particularly those based on ammonite biozonation (Gill and Cobban, 1966; Gradstein et al., 1994), placed the overlying, and presumably younger, DeGrey Member within the Campanian.

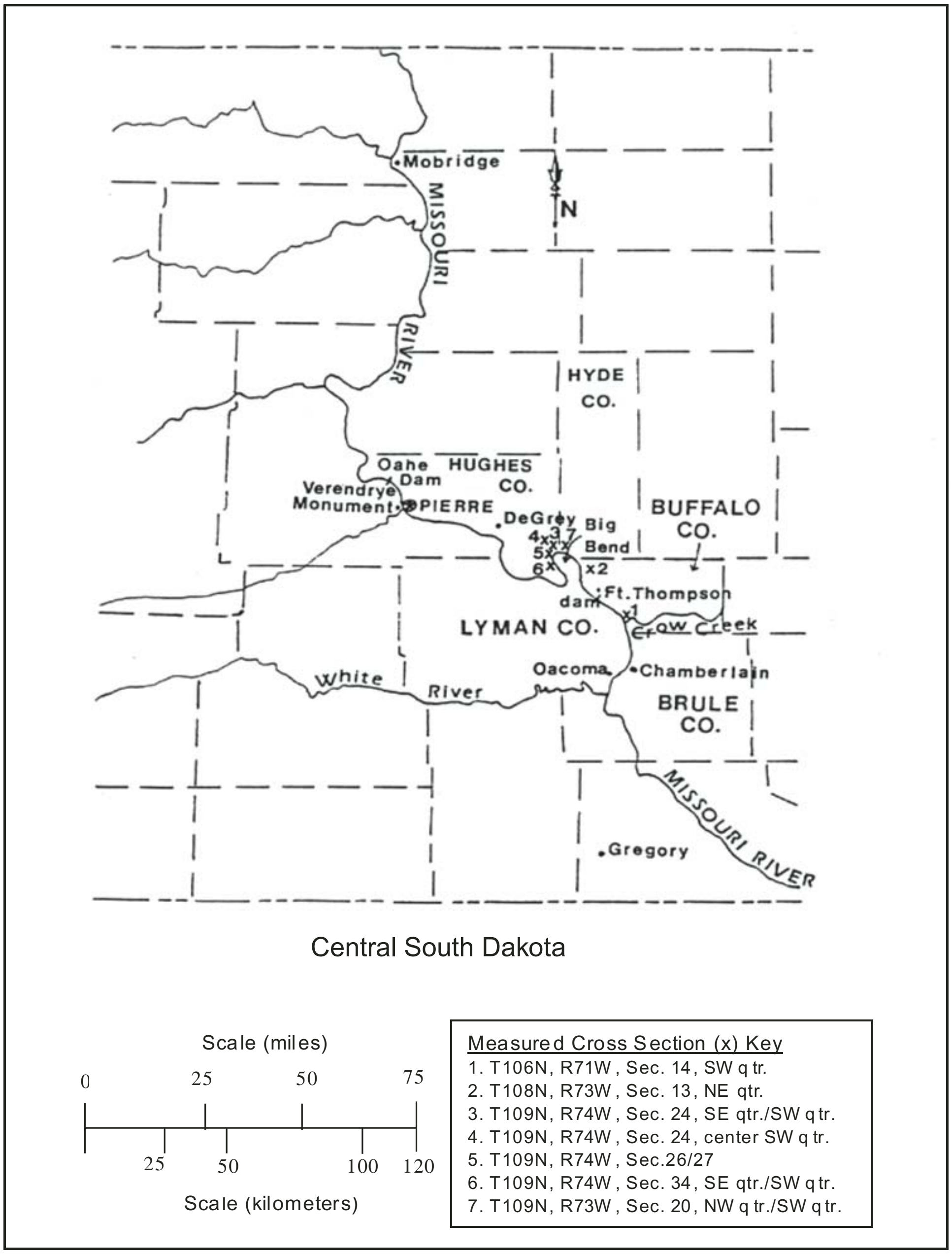

Figure 1. Map showing central South Dakota along the Missouri River with all measured cross sections within the study area indicated by an ‘x’ and a corresponding number. This paper concentrates on measured sections 2 (Fort Thompson) and 3 (North Bend). Modified from an original map by Crandell (1950).

Therefore, the objectives of this study were to determine the geologic stage of the four members of the Pierre Shale that crop out within the study area (Gregory, Crow Creek, DeGrey, and Verendrye), determine the chronostratigraphic age of several marine reptile fossils, relate the study area to a sequence stratigraphic framework, and gather data to reconstruct the paleoenvironment. In addition, Izett et al. (1993) determined that the Crow Creek Member was deposited as a result of a tsunami generated by a bolide impact some 75 Ma in what is now north-central Iowa, as evidenced by the 35-km-diameter Manson Impact Structure. Owing to the fact that the Crow Creek is prominently exposed within the study area, this study should shed further light on the origin of this lithostratigraphic unit. Furthermore, beds within the uppermost Gregory Member (Fig. 2A, B), which "closely resembles the basal Crow Creek" (Gries, 1942), were rediscovered during our field investigation and require comment with regard to their depositional origin.

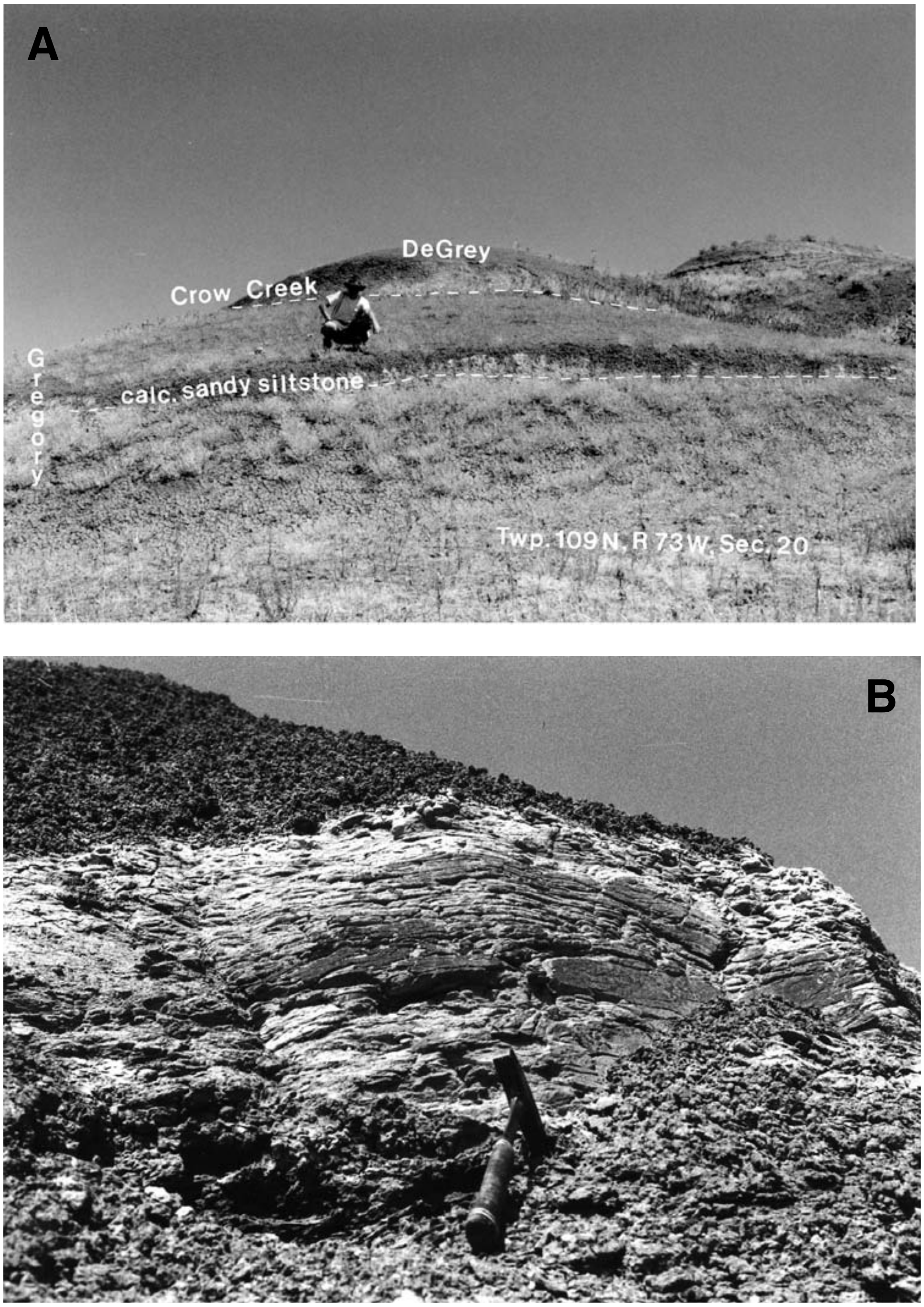

Figure 2. (A) Photograph of the relationship between the Fort Thompson beds, located ~3 m below the contact of the Gregory Member with the overlying Crow Creek Member. At this locality this relationship was viewed for >2 km. (B) Close-up of the Fort Thompson beds from the Fort Thompson measured section. These beds display the low-angle crosscutting characteristic of swaly cross-stratification (SCS).

GEOLOGIC FRAMEWORK

During the Late Cretaceous, an epicontinental seaway covered much of western North America, stretching from the Gulf of Mexico to the Arctic Ocean. Kauffman (1977) delineated this Western Interior Seaway during maximum transgression as a 3,000-mile-long (4800 km) by a minimum of a 1000-mile-wide (1600 km) strait that probably extended eastward into present-day Iowa and Minnesota. Partly from the effects of the Sevier orogeny, a foreland basin developed in which sediments were shed predominantly from the west (King, 1977) in an asymmetric wedge that thinned to the east (Dyman et al., 1994). Within this context the deposition of the fully marine Pierre Shale took place.

The Upper Cretaceous Pierre Shale along the Missouri River was first described by Meek and Hayden (1862). Many revisions of the Pierre Shale in South Dakota followed (Searight, 1937; Gries and Rothrock, 1941; Gries, 1942) before the final revision (Fig. 3) was agreed upon (Crandell, 1950). Additionally, the Pierre Shale has been known to yield a relatively diverse collection of representative Late Cretaceous marine vertebrates and invertebrates (Leidy, 1865; Cope, 1870; Williston, 1895; Wieland, 1896; Crandell, 1958; Martin and Bjork, 1987) as well as a rich and diverse assemblage of micro-invertebrates (Dix, 1957; Hoff, 1960; Johnson, 1961; Lange, 1962; Mello, 1969, 1971; Bretz, 1979).

Field Study and Sampling

The field portion of the investigation included measuring sections and gathering field samples for study to utilize several established laboratory methods. These methods included ^{87}Strontium/^{86}Strontium age estimation, statistical analysis of the micropaleontology, and thin sections of the suspect layers to look for bolide-impact–generated shocked quartz.

In addition, magnetostratigraphy and ^{40}Argon/^{39}Argon age-analysis samples were also collected. The magnetostratigraphic samples failed to yield any useful data, and the ^{40}Ar/^{39}Ar samples were abandoned owing to the absence of the currently preferred mineral, sanidine.

The two measured sections are on the eastern side of the Missouri River, the first $\sim$1 mile north of Fort Thompson, South Dakota (NE¼ sec. 13, T. 108 N., R. 73 W.), and the other just east of and overlooking the North Bend boat launch (SE¼SW¼ sec. 24, T. 109 N., R. 74 W.). The Fort Thompson section is the site of a *Globidens* mosasaur discovery (Martin, this volume, Chapter 13), and where most of the field sampling and subsequent analysis was concentrated. Sampling intervals were on the order of 3.0–1.5 m or at much closer intervals in particular areas of interest, such as at unconformities. A more detailed description of the methods used for field sampling is presented in Hanczaryk (2002).

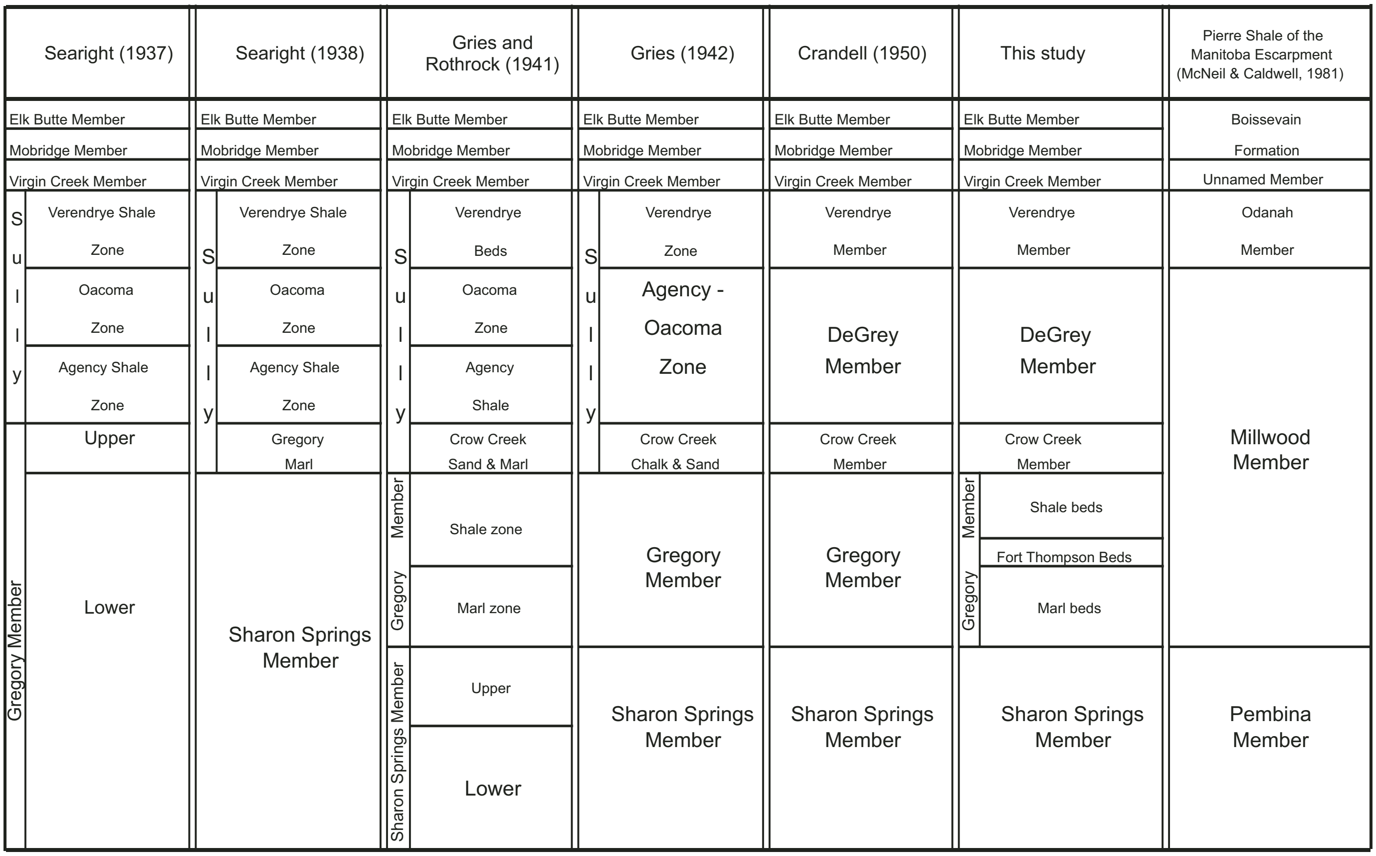

Figure 3. The stratigraphic nomenclature of the Pierre Shale in central South Dakota since 1937, with the addition of the Fort Thompson beds from this study. Figure adapted from Crandell (1950).

LITHOSTRATIGRAPHY OF THE PIERRE SHALE WITHIN THE STUDY AREA

Four members of the Pierre Shale are exposed within the study area and are, from oldest to youngest, the Gregory, Crow Creek, DeGrey, and Verendrye. Witzke et al. (1983) pointed out that much of the Pierre Shale had been removed by erosion, particularly along its eastern edge. The typical lithology of this formation is olive black (5 Y 2/1) to olive gray (5 Y 4/1) massive claystone with interbedded shales. According to Klein (1991), the dark coloration of this formation is attributed to high organic content deposited into highly anoxic marine bottom waters. Klein (1991) went on to suggest that during the Late Cretaceous, high sea levels were associated with high CO_2 levels that could have produced more equitable worldwide climates that in turn contributed to poor oceanic circulation, little mixing, and generally stagnant conditions, yielding a much higher anaerobic-dysaerobic water column than in current oceans. Numerous iron-manganese concretions are characteristic of the study area, particularly within the DeGrey Member. Several workers believe that manganese nodules formed around organic material in anoxic to suboxic conditions (Grunwald, 1964; Minoura et al., 1991), although some evidence indicates that deposition of manganese oxides or carbonates can only occur with mixing of more oxygenated waters into the anoxic-suboxic zone where manganese is concentrated (Frakes and Bolton, 1984).

The predominant source of detrital sediments in the Pierre Shale was to the west; supporting this idea are thicker and coarser terrestrial deposits found to the west in Wyoming and Colorado, fining eastward into thinner marine deposits (Kauffman, 1977). However, at various times during deposition of the Pierre Shale, a significant input of sediments came from eastern source areas, particularly from the antiformed Sioux Ridge Quartzite (Witzke et al., 1983).

Bentonite beds are ubiquitous within parts of the Pierre Shale. The bentonite beds in the Pierre Shale are composed primarily of the clay mineral montmorillonite (Tourtelot et al., 1960). In outcrop, bentonite beds have been observed to flow and expand, often appearing thicker than when deposited. The source of the ash is most probably to the west, where volcanism was frequent during the Sevier orogeny (King, 1977). In addition, thicker bentonite beds are found to the west in Wyoming and Montana, whereas much thinner beds, though still geographically widespread and measurable on the scale of centimeters, are found in the central Dakotas (Gries, 1942).

Gregory Member

The type locality of the Gregory Member is in eastern Gregory County, South Dakota, represented by exposures along the banks of the Missouri River at the former Rosebud Bridge, south of Wheeler, South Dakota (Searight, 1938; Crandell, 1950). The Gregory Member is described as containing interbedded calcareous to noncalcareous shale, marl, and limestone (Crandell, 1950; Witzke et al., 1983). In all the measured sections (Fig. 4A, B, and Fig. 5) the Gregory Member was found to be light olive gray (5 Y 6/1) claystone, locally shaly, to olive gray (5 Y 4/1) claystone, and indurated yellowish gray (5 Y 8/1) marl with several 4–10-cm-thick bentonite beds. A few concretionary layers are present, which cause more steeply inclined cliffs to form. The member thins to 1–2 m near the Sioux Ridge Quartzite and thickens to 30 m in central South Dakota (Crandell, 1950). Bretz and Johnson (1981) reported that the unit is not in southeastern South Dakota, whereas it thickens to 50 m to the central northwest and is absent near Pierre, South Dakota (Dyman et al., 1994). A part of the lower Gregory is not exposed in the section measured at Fort Thompson (Fig. 4A), where the member attains a total thickness of 23.4 m. Across the Missouri River, in nearby Lyman County, Cox (1962) reported a thickness of 36 m from a road cut along South Dakota Highway 47. Measurements taken at the base of the Fort Thompson section yielded strikes ranging from N60°E to N70°E with dips of 5°–6°NW. Slumping in the Fort Thompson section was common, particularly near the base, with large blocks of the uppermost Gregory covering in situ beds and making section measuring difficult to impossible. At the Fort Thompson measured section (Fig. 4A) the ammonite *Baculites gregoryensis* Biozone lies at the base of the section at or just below the waterline of the Missouri River.

An anomalous 1–2-m-thick calcareous sandy siltstone bed occurs within the upper Gregory Member, 2–3 m below the base of the Crow Creek Member (Fig. 2B). Gries (1942) described this unit as being “an intermittent chalky bed . . . closely resembles the basal Crow Creek.” With regard to the “intermittent” nature of this unit, a number of workers searched extensively around the various sites near the North Bend Boat Launch and could not locate these beds. However, nearby in Hyde County in the NW¼SW¼ sec. 20, T. 109 N., R. 73 W., the best continuous exposure of this unit was observed (Fig. 2A). At this locality the typically “Gregory-like” olive gray (5 Y 4/1) “popcorn” textured claystone framed this unit, and ~3 m separated it from the overlying Crow Creek sandy siltstone and marl. This well exposed outcrop was traced by walking its length for >2 km. No lateral change was observed, and no evidence indicated slumping. The lower sandy siltstone unit appears highly variegated at this outcrop. A more detailed analysis of the outcrop yielded 8 cm of moderate-yellowish-brown (10 YR 5/4) sandy siltstone at its base, overlain successively by 18 cm of moderate-yellowish-brown (10 YR 5/4) nodular, calcareous sandy siltstone; 36 cm of dark-yellowish-orange (10 YR 6/6) calcareous sandy siltstone; 3 cm of primarily grayish orange (10 YR 7/4) calcareous siltstone; and ~1 cm of yellowish gray (5 Y 7/2) sandy siltstone at the top. In contrast, the overlying Crow Creek Member is composed of <1 cm of moderate brown (5 YR 3/4) sandy siltstone at its base, overlain successively by 13 cm of massively bedded moderate brown (5 YR 3/4) calcareous siltstone and a little more than 1 m of light gray (N 7) marl with olive gray (5 Y 4/1) mottling that weathers to moderate brown (5 YR 3/4) at the top. In this section the lower anomalous sandy siltstone unit ranges in thickness from 0.66 to ~0.90 m, whereas the overlying Crow Creek Member is consistently 1.2 m thick. A chemical analysis by atomic absorption

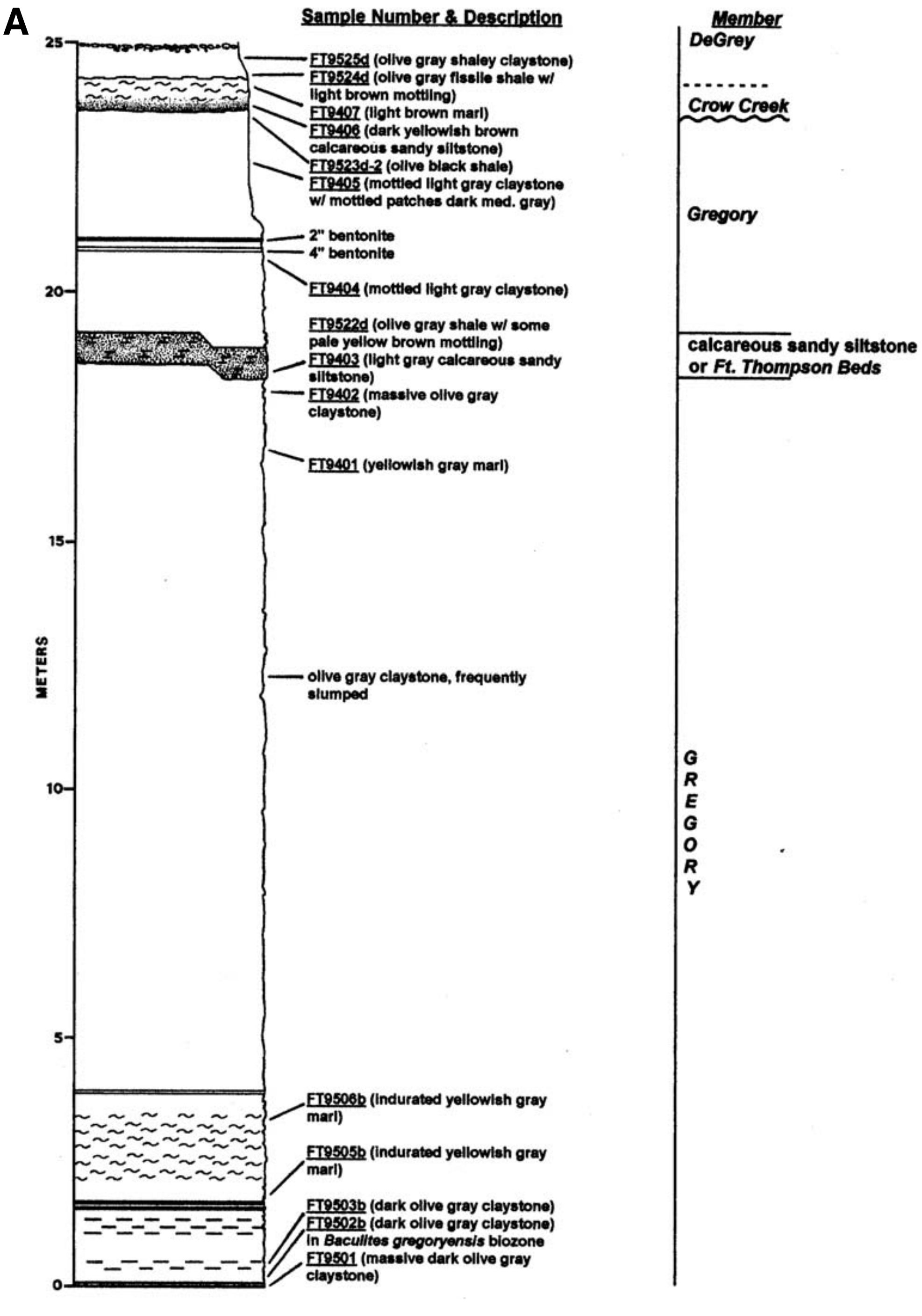

Figure 4A. (A, B) Measured section at T. 108 N., R. 73 W., Sec. 13, northeast quarter—the “Fort Thompson” section.

from the base of this unit at the Fort Thompson section yielded 59.7% $CaCO_3$ and 21.1% SiO_2.

To help distinguish the overlying Crow Creek Member from the “anomalous” and sporadic calcareous sandy siltstone unit first described by Gries (1942), and located within the upper Gregory Member, a new name is proposed, the *Fort Thompson Beds*. The North American Stratigraphic Code, Article 26, Bed(s), states: “A bed, or beds, is the smallest formal lithostratigraphic unit. . . . The designation of . . . beds as a formally named lithostratigraphic unit generally should be limited to certain distinctive beds whose recognition is particularly useful.” Owing to the potential for workers on the Pierre Shale to mistake this unit for the lithologically similar Crow Creek Member, the name *Fort Thompson Beds* is formally proposed here. These marker beds are exposed along the eastern badlands formed by the Missouri River in outcrops around the town of Fort Thompson, South Dakota.

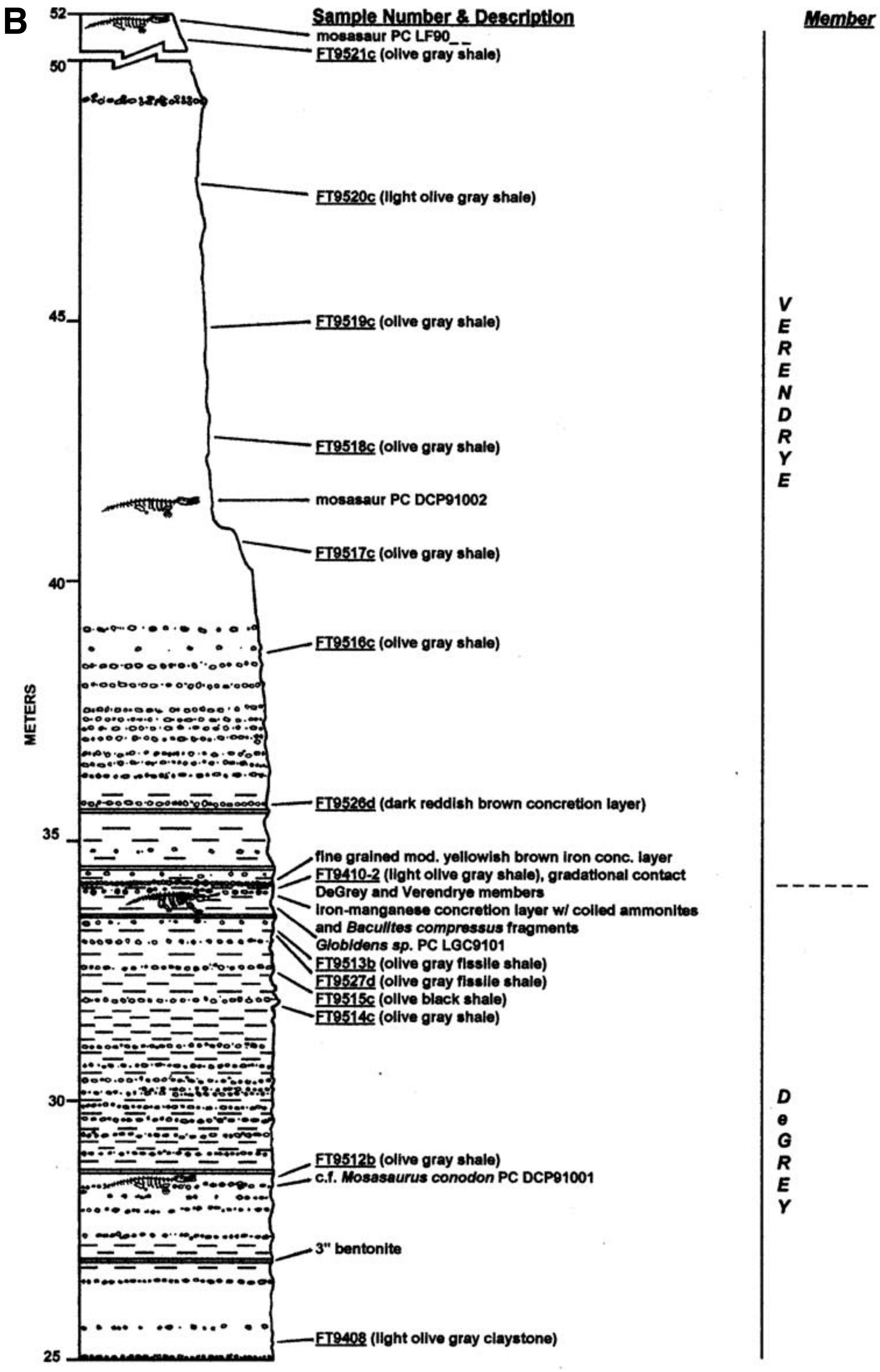

Figure 4B (*continued*)

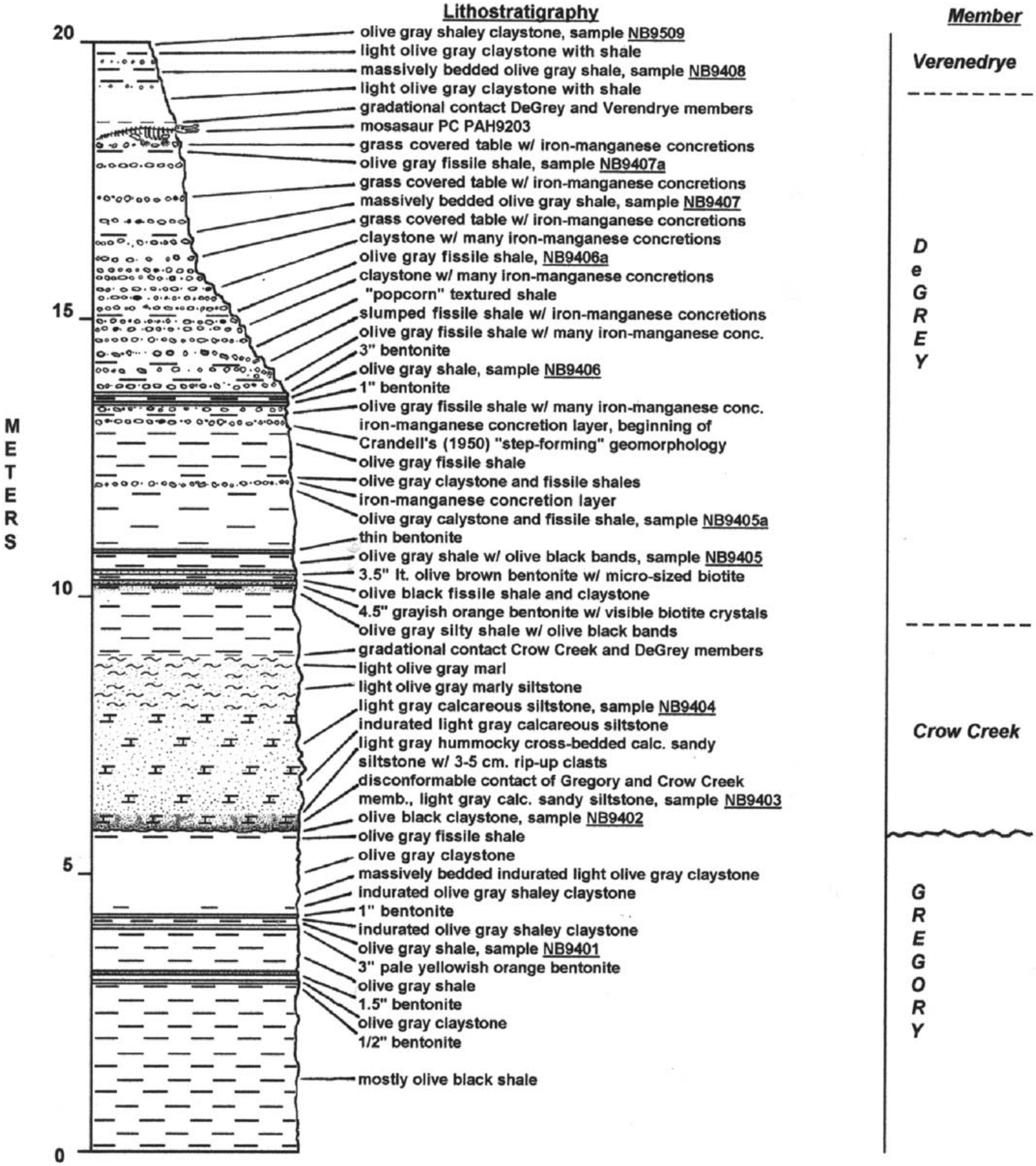

Figure 5. Measured section at T. 109 N., R. 74 W., southeast quarter of the southeast quarter—the "North Bend" section.

Bretz and Johnson (1981) characterized the contact between the Gregory and Crow Creek Members as an unconformity. Within our study area the lithologic change is also found to be abrupt. Crandell (1952) also reported a faunal change across the contact, from relatively deep marine below to shallow marine above. Witzke et al. (1983) believed that the Gregory Member was deposited as a result of the regressive pulse of the Claggett depositional cycle. Bretz and Johnson (1981) reported shale clasts "with Gregory characteristics" within the Crow Creek Member in southeastern Yankton County. Shale rip-up clasts ranging in size from 3 to 5 cm occur within the base of the Crow Creek Member in the SE¼SW¼ sec. 24, T. 109 N., R. 74 W., at North Bend (Fig. 5).

Crow Creek Member

The Crow Creek is probably the most distinctive member within the Pierre Shale. This unit is exposed in outcrop in southeastern and central South Dakota and northeastern Nebraska (Witzke et al., 1983). According to Gries (1942), the type locality of the Crow Creek Member is at "exposures at or south of the mouth of the Crow Creek, Buffalo County." Crandell (1952), referring to Gries, placed the type locality "at the mouth of the Crow Creek, Buffalo County, South Dakota." The Crow Creek Member is described as a calcareous, locally sandy siltstone with overlying beds of marl and ranging in thickness from 1.45 to 3.4 m (Crandell, 1952; Crandell, 1958; Cox, 1962; Witzke et al., 1983). Schultz (1965) reported a 6 m outcrop in an interpreted incised channel in the underlying Gregory. The Crow Creek Member is generally found in outcrop ~50 km from and around the edge of Sioux Ridge (Witzke et al., 1996). Within the measured sections the Crow Creek Member ranges in thickness from ~1.2 to 3.1 m with a mode of ~1.2 m. The Crow Creek Member has been interpreted as a shallow, high-energy, transgressive deposit (Bretz, 1979; Witzke et al., 1983). Evidence cited consists of cut-and-fill stratification, the relatively coarse sediment at the base that fines upward into a marl, the predominantly $CaCO_3$ composition of these beds interpreted to have formed in shallow marine waters, the disconformable relationship between the underlying Gregory Member's noncalcareous claystones, and a foraminiferal turnover from an interpreted deep marine to shallow marine assemblage (Crandell, 1952; Bretz, 1979; Witzke et al., 1983). For the most part the Crow Creek Member is thought to be conformable with the overlying DeGrey Member (Gries, 1942; Crandell, 1958). Within the study area this contact is observed to be unconformable, as at the Fort Thompson section, or it can change laterally within a few meters from graded to unconformable, such as at the North Bend section (Fig. 5). Bretz (1979) suggested that the variability in thickness may be due to seasonal higher energy conditions that may have removed parts of the Crow Creek Member. This might explain the variability in thickness within the study area. The color of the Crow Creek Member was found commonly to be variegated, ranging from light gray (N 6) that weathers to light gray (N 7), in places with olive gray (5 Y 4/1) mottling, to moderate brown (5 YR 3/4), brownish gray (5 YR 4/1), moderate yellowish brown (10 YR 3/4), and dark yellowish brown (10 YR 4/2). Within the study area the basal Crow Creek Member is characterized as a fine-bedded, moderate brown (5 YR 3/4) calcareous silty sandstone of ~8–9 cm thick that weathers in outcrop to numerous thin "shingles" that litter the surface. Above this is ~0.05 to just over 1 m of moderate yellowish brown (10 YR 5/4) siltstone that grades into dark yellowish orange (10 YR 6/6) marl.

The Crow Creek Member is thought to represent the transgressive phase of the Bearpaw depositional cycle (Crandell, 1950; Bretz, 1979; Witzke et al., 1983). An explanation favored by Crandell (1952) is that a localized epeirogenic event across the Transcontinental Arch in the area of Sioux Ridge uplifted this region and that the Crow Creek Member is composed of reworked older sand deposits such as the Codell Sandstone Member of the Carlile Shale. This idea was revived in part by Witzke et al. (1983) and Shurr et al. (1994) to explain the Crow Creek Member with respect to sequence stratigraphy.

In recent years, debate has intensified with regard to the nature of the Crow Creek Member, a calcareous, fine-grained sandstone to siltstone overlain by marl, bracketed by the more typical shale and claystone of the Pierre Shale. This member is found only in southeastern and central South Dakota and northeastern Nebraska in exposures around the structurally high Sioux Ridge Quartzite (Bretz and Johnson, 1981; Witzke et al., 1983). Izett et al. (1993, 1998) interpreted this member to be a tsunamtite deposited as the result of a bolide impact. The source for this tsunami was thought to be the 35-km-wide complex crater, first identified geophysically, near the town of Manson in northwest-central Iowa. Izett et al. (1993, 1998) suggested that the Crow Creek Member is akin to the tsunamtite exposed along the Brazos River in Texas that was produced by the later ca. 65 Ma Cretaceous–Tertiary (K–T) impact event. As evidence, Izett et al. (1998) identified shocked mineral grains they described as ubiquitously distributed at the base of the Crow Creek Member. They also estimated the age of the Manson Impact Structure of Iowa, utilizing Ar^{40}/Ar^{39} age analysis of well samples taken near Manson, Iowa, to be between 73.8 ± 0.1 and 74.1 ± 0.1 Ma, and, from Ar^{40}/Ar^{39} analysis of sanidine crystals found within bentonite layers bracketing the Crow Creek, they estimated the age of this unit to range from 73.8 ± 0.3 to 74.5 ± 0.1 Ma, essentially making them coincident. This contrasts with previous interpretations that concluded that the Crow Creek Member was the result of the transgressive pulse of the Bearpaw depositional cycle (Crandell, 1950; Bretz, 1979; Witzke et al., 1983). Witzke et al. (1996) rejected Izett et al.'s interpretation, arguing instead that the shocked mineral grains are reworked.

DeGrey Member

The type locality of the DeGrey Member was the DeGrey post office (Crandell, 1950). In most places the noncalcareous DeGrey Member conformably overlies the calcareous Crow Creek Member (Gries, 1942; Crandell, 1958). Crandell (1950, 1958) described the DeGrey as 38.1 m of light olive gray (5 Y 6/1), moderately siliceous, dusky red concretion-covered shale and claystone overlain by 9–23 m of less siliceous light olive gray shale and bentonites. The DeGrey Member has been found to range in thickness from

2.5 m in northern Potter County (Cox, 1962) to 49.0 m near Pierre, South Dakota (Crandell, 1950). Toward Chamberlain, South Dakota, it was reported to be ~12 m thick (Crandell, 1950; Cox, 1962). In this study the DeGrey Member was found to measure 10.1 m in thickness at the Fort Thompson section (Fig. 4), 9.5 m at the North Bend section (Fig. 5), ~8.2 m in secs. 26 and 27, T. 109 N., R. 74 W., and 12.7 m at section 34, T.109N, R.74W, SE qtr. of SW qtr. site (also referred to as the "Archelon Hill" site). Crandell (1950) described the DeGrey Member as being "step-forming" and contrasted it with the overlying conformable Verendrye by the DeGrey's "abundant iron-manganese concretions." The iron-manganese concretionary beds range from very dusky purple (5 P 2/2) to grayish black (10 YR 4/2). The concretion layers are highly fossiliferous, containing many white prismatic inoceramid fragments, oyster steinkerns, and ammonites. Crandell (1958) also stated that he found a 4–6 in. bentonite bed ~3 m above the base of the DeGrey Member with 0.1–1.0 mm biotite phenocrysts and sand-sized plagioclase grains. In the study area this bentonite bed is at the North Bend section (Fig. 5) and just south of Business Route I-90 in Chamberlain, South Dakota. The biotite crystals are thought to be unaltered phenocrysts within the volcanic ash (Crandell, 1958).

We were informed by the U.S. Army Corps of Engineers, and local DeGrey area residents Dick and Gladyss Meleen, that because of the construction of the Big Bend Dam down river, the post office where the basal portion of the type DeGrey was located is now submerged beneath the Missouri River. At least part of the DeGrey Member is still exposed in the hills beside the Meleen Ranch in the NW¼ sec. 6, T. 109 N., R. 75 W.

Verendrye Member

The type locality of the Verendrye Member is the Verendrye Monument at Fort Pierre, Stanley County, South Dakota (Searight, 1937; Crandell, 1950). Crandell (1950) reported that the thickness of the Verendrye Member at its type locality is 46 m. The Verendrye Member conformably overlies the DeGrey Member, the nature of the contact being gradational (Gries, 1942; Crandell, 1950). Crandell (1950) noted that the shales and claystones of the Verendrye Member become a sticky "gumbo" when wet. Color tends to vary from light olive gray (5 Y 5/2) to brownish gray (5 YR 4/1), weathering into chip-shaped pieces (Crandell, 1958). Cox (1962) also noted the brown coloring near the Crow Creek Dam. Crandell (1958) and Cox (1962) reported abundant iron-manganese concretions. Near Pierre the basal part of the Verendrye Member is marked by fragments of the ammonite *Baculites compressus* Say (Crandell, 1950). Throughout the study area the base of the Verendrye Member is commonly marked by a change to a steeper slope. This is probably due to a change in the "step" producing concretions from massive and very common to noticeably less massive and not quite so common. Within the measured sections the Verendrye is light olive gray (5 Y 6/1), "popcorn" textured (desiccated gumbo) claystone and light olive gray (5 Y 6/1) to olive gray (5 Y 4/1) fissile shale. The shaly material tends to weather to small flaky chips, typically olive gray (5 Y 4/1) to dark olive gray (5 Y 2/1). The claystone weathers to a "popcorn" texture that is yellowish gray (5 Y 8/1).

PREVIOUSLY ESTABLISHED BIOSTRATIGRAPHY, CHRONOSTRATIGRAPHY, AND MAGNETOSTRATIGRAPHY OF THE PIERRE SHALE WITHIN THE STUDY AREA

The base of the studied section at Fort Thompson is anchored by the *Baculites gregoryensis* Biozone within the Gregory Member (Fig. 4A). Cobban (1993) placed this biozone in the upper part of the middle Campanian, and Obradovich (1993) equated this zone with the *B. reduncus* Biozone. Although Obradovich (1993) was unable to date this biozone directly on the basis of $^{40}Ar/^{39}Ar$ dating of bentonite beds within surrounding biozones, he constrained the *B. gregoryensis–B. reduncus* Biozone to between 75.89 ± 0.72 Ma (originally the *Didymoceras nebrascense* Biozone, subsequently reidentified by Obradovich as *B. scotti*) and 80.54 ± 0.55 Ma (*B. obtusus* Biozone). Based on Obradovich's (1993) $^{40}Ar/^{39}Ar$ dating of biozones from the Western Interior Seaway, Gradstein et al. (1994) placed the age of the *B. reduncus* (= *B. gregoryensis*) Biozone to be ca. 77.0 Ma. Gradstein et al. (1994) stated that "direct calibration between ammonites and polarity exists for the middle Campanian through lower Maastrichtian"; they placed this biozone firmly within the normal polarity portion of Chron C33 (Fig. 6). This study was able to determine paleomagnetically that samples from within and near this biozone exhibited normal polarity, but owing to determining a predominantly northeast declination, and not finding any reversals, was unable to reject the null hypothesis, that a modern overprinting had been detected. Gradstein et al. (1994) showed two small reversals between Chrons C33 and the directly overlying C32. It is still possible that these reversals are not within the study area because of truncation or were missed because of the sampling interval.

All of the Western Interior biozones between *B. gregoryensis* and *B. compressus* are missing at both Fort Thompson and North Bend, as well as at several other measured sections within the study area. It is not uncommon that ammonite biozones across the Western Interior are ephemeral (Cobban, 1996, personal commun.). However, the *B. compressus* Biozone is clearly present within the study area (Fig. 4B). Obradovich (1993) and Gradstein et al. (1994), following Cobban (1993), placed this biozone within the middle upper Campanian. Magnetostratigraphically, Gradstein et al. (1994) placed the *B. compressus* Biozone in a normal polarity portion of Chron C32.

Although the *B. scotti* and *D. nebrascense* Biozones are absent from the study area, the top of the *B. scotti* zone–base of the *D. nebrascense* zone is now considered the demarcation between the middle and upper Campanian (Gill and Cobban, 1966; Obradovich, 1993; Gradstein et al., 1994). Bretz (1979) determined a Maastrichtian Age for the Crow Creek on the basis of the foraminifers; this is in contrast to this study, in which the foraminiferal assemblage encountered was determined to be mid-

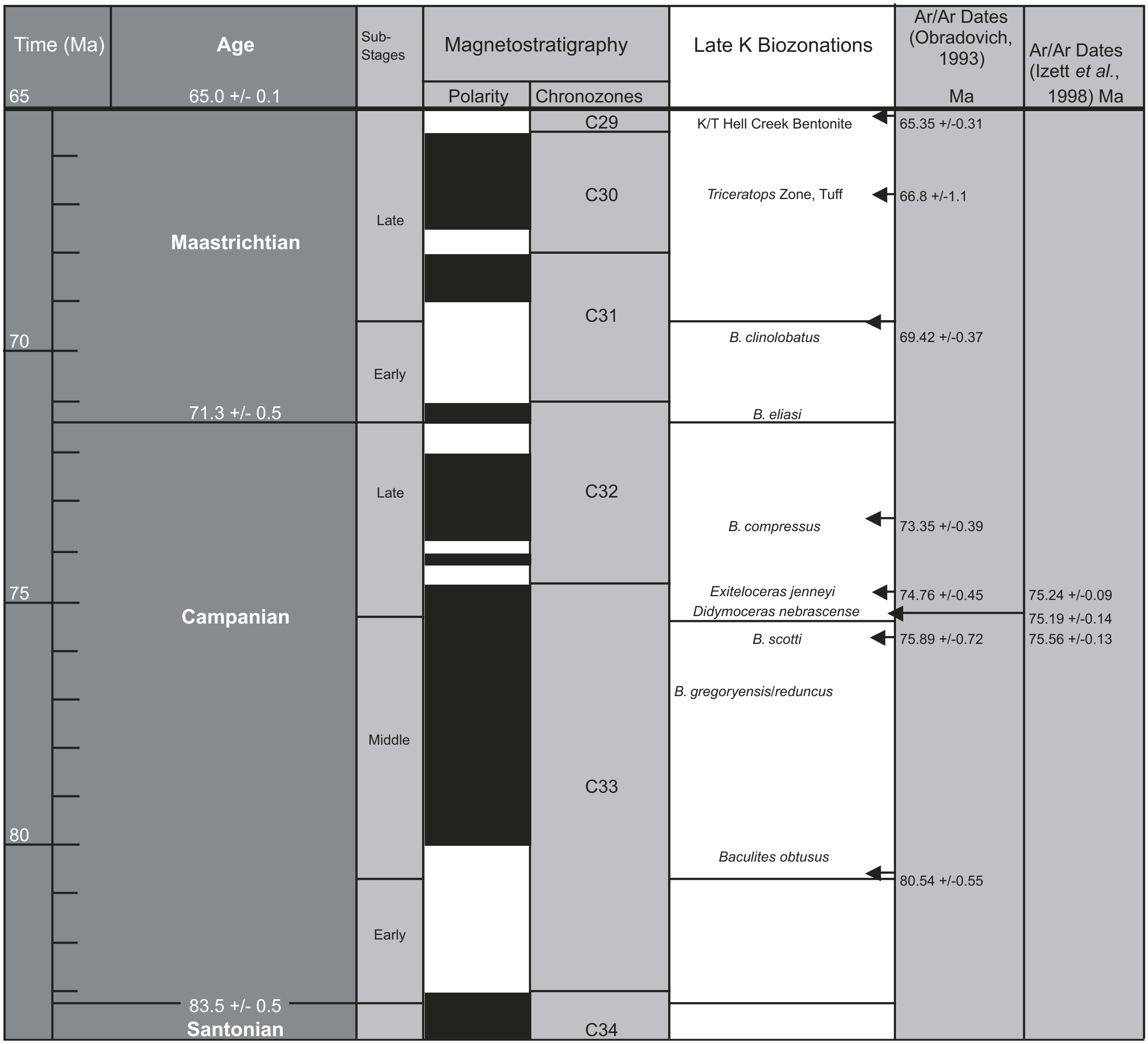

Figure 6. Late Cretaceous magnetic polarity time scale with major North American biozones and corresponding ^{39}Ar/^{40}Ar dates. ^{39}Ar/^{40}Ar dates from Izett et al. (1998) are converted relative to Hornblende Mhhb-1 of 540.4 Ma to stay consistent with Obradovich (1993). Modified from Gradstein et al. (1994), with additional information from Cande and Kent (1995).

dle Campanian and does not contain important Maastrichtian components such as the diagnostically upper Campanian–lower Maastrichtian planktonic foraminiferal elements like the appearance of keeled specimens such as *Rugotruncana* (Frerichs and Gaskill, 1988) and the return of the triserial *Guembeletria cretacea* Cushman. In addition, most Western Interior Seaway workers now accept the appearance of the ammonite *B. eliasi* as the boundary between the Campanian and Maastrichtian (Cobban, 1993; Obradovich, 1993; Gradstein et al., 1994; Izett et al., 1998). This biozone does not occur except somewhere within the Virgin Creek Member of the Pierre Shale, a unit stratigraphically above the units in this study.

RESULTS

Chronostratigraphic Results

^{87}Sr/^{86}Sr age estimation was performed using standard ion exchange and ion exchange columns as described in Oslick et al. (1994). Strontium isotope analyses were done using a VG Sector mass spectrometer. Although the ^{87}Sr/^{86}Sr relative age analysis is much less precise than the ^{40}Ar/^{39}Ar absolute age method, ^{87}Sr/^{86}Sr has one advantage over the ^{40}Ar/^{39}Ar method in that it can date fossilized skeletal material versus a related marker bed and can be particularly useful if index fossils are present. A total of 19 ^{87}Sr/^{86}Sr age estimations were performed on calcareous foraminiferal tests, inoceramid or oyster shells, and a single mosasaur tooth (Table 1). Of these, 11 yielded acceptable results, with internal errors ranging from 4×10^{-6} to 38×10^{-6} (Fig. 7). Six samples gave no result; the "whole tooth" mosasaur sample was omitted because it yielded an internal precision error of 50×10^{-6}. Using the Miller et al. (2004) regression formula and the Sugarman et al. (1995) conservative ±2 Ma age range, starting at the base of the section, samples taken within the *Baculites gregoryensis* Biozone yielded ages with a mean of 75.09 (Fig. 8) versus an approximate 77.0 Ma age (Gradstein et al., 1994), based on the ^{40}Ar/^{39}Ar analysis by Obradovich (1993). The Crow Creek Member yielded an age of 74.58 Ma; a calcareous sandy siltstone layer sporadically found exposed ~5.0 m below the base of the Crow Creek gave an age of 74.63 Ma. This value is relatively younger than the ages determined by Obradovich (1993) for the *Baculites scotti* Biozone in the uppermost Gregory Member of 75.89 ± 0.72 Ma or Izett et al.'s (1998) ^{40}Ar/^{39}Ar age of 75.44 ± 0.27 Ma for the Lower Agency Bentonite 3 m above the base of the DeGrey, but it still overlaps these values with the Sugarman et al. (1995) error value of ±2 Ma. Finally, two ^{87}Sr/^{86}Sr age estimates from oyster shells found at the *Globidens* site and inoceramid shells found 0.5 m below the *Baculites compressus* Biozone yielded ages of 72.41 Ma and 72.43 Ma, respectively. These values are relatively close to Obradovich's (1993) ^{40}Ar/^{39}Ar age of 73.35 ± 0.39 Ma for the *B. compressus* Biozone.

Micropaleontologic Assemblages Derived from Factor Analysis

Twenty-five individual samples from the Fort Thompson section were analyzed for their micropaleontologic content, revealing 77 species of calcareous benthic foraminifers, 62 species of agglutinated benthic foraminifers, 20 species of planktonic foraminifers, and 8 species of radiolarians. R-mode factor analysis was performed with Systat version 5.21 for Macintosh on the benthic and planktonic foraminifers of 24 of the samples (sample FT9521c contained only 10 benthic foraminiferal specimens, too little for statistical factor analysis). Factor analysis on just benthic foraminifers and benthic foraminifers with radiolarians was also attempted, yielding equivocal results. Four and five factors were analyzed on the "all foraminifers" database with four factors (or biofacies) yielding the best fit (Fig. 9). Twelve micropaleontologic samples from the North Bend section were also prepared. Visual inspection with an optical binocular microscope showed these samples to be equivalent to the Fort Thompson samples at the same corresponding stratigraphic zones.

Biofacies 1 (variance explained of 18.6%) is composed predominantly of *Glomispira corona* Cushman and Jarvis, *Ammodiscus cretaceous* (Reuss), *A. angustus* (Freidburg), *Haplophragmoides collyra* Nauss, plus the planktonic species *Archeoglobigerina blowi* Pessagno. This assemblage was identified by McNeil and Caldwell (1981) and named the *Glomispira corona* Foraminiferal Zone; this biozone occurs in Campanian deposits in Canada and is correlated with the *Baculites obtusus* through *Baculites gregoryensis* Ammonite Biozones. It is also similar to Kuhnt et al.'s (1989) "Biofacies B" found in the lower to middle Campanian Deep Sea Drilling Project (DSDP) Holes

TABLE 1. FORT THOMPSON Sr/Sr AGE DATA

Date run	Sample	Depth (m)	Specimen type	Individual ^{87}Sr/^{86}Sr	Error (±)
10/16/1997	FT9102-1	41.35	mosasaur tooth (whole)	0.707830	0.000056
10/16/1997	FT9102-2D	41.35	mosasaur tooth—dentine	didn't work	
10/16/1997	FT9102-2E	41.35	mosasuar tooth—enamel	didn't work	
Mar-96	FT9513b	33.84	innoceramid	0.707707	0.000004
Mar-96	FT9527d-1	33.23	oyster shell	0.707704	0.000006
5/24/1996	FT9527d-2	33.23	oyster shell	0.707713	0.000023
Mar-96	FT9406-1	23.43	calc. forams	didn't work	
10/16/1997	FT9406-2	23.43	calc. forams	0.707640	0.000052
5/24/1996	FT9523d	23.34	calc. forams	didn't work	
Mar-96	FT9403	18.13	calc. forams	0.707639	0.000026
5/24/1996	FT9401	16.43	calc. forams	didn't work	
Mar-96	FT9505b	1.53	calc. forams	didn't work	
5/24/1996	FT9504b	0.24	calc. forams	0.707662	0.000025
Mar-96	FT9503b-1	0.1	*B. gregoryensis*	0.707684	0.000006
5/24/1996	FT9503b-2	0.1	*B. gregoryensis*	0.707606	0.000025
10/16/1997	FT9503b-3	0.1	*B. gregoryensis*	0.707680	0.000007
Mar-96	FT9502b-1	0.02	*B. gregoryensis*	0.707624	0.000011
5/24/1996	FT9502b-2	0.02	*B. gregoryensis*	0.707698	0.000025
10/16/1997	FT9502b-3	0.02	*B. gregoryensis*	0.707687	0.000038

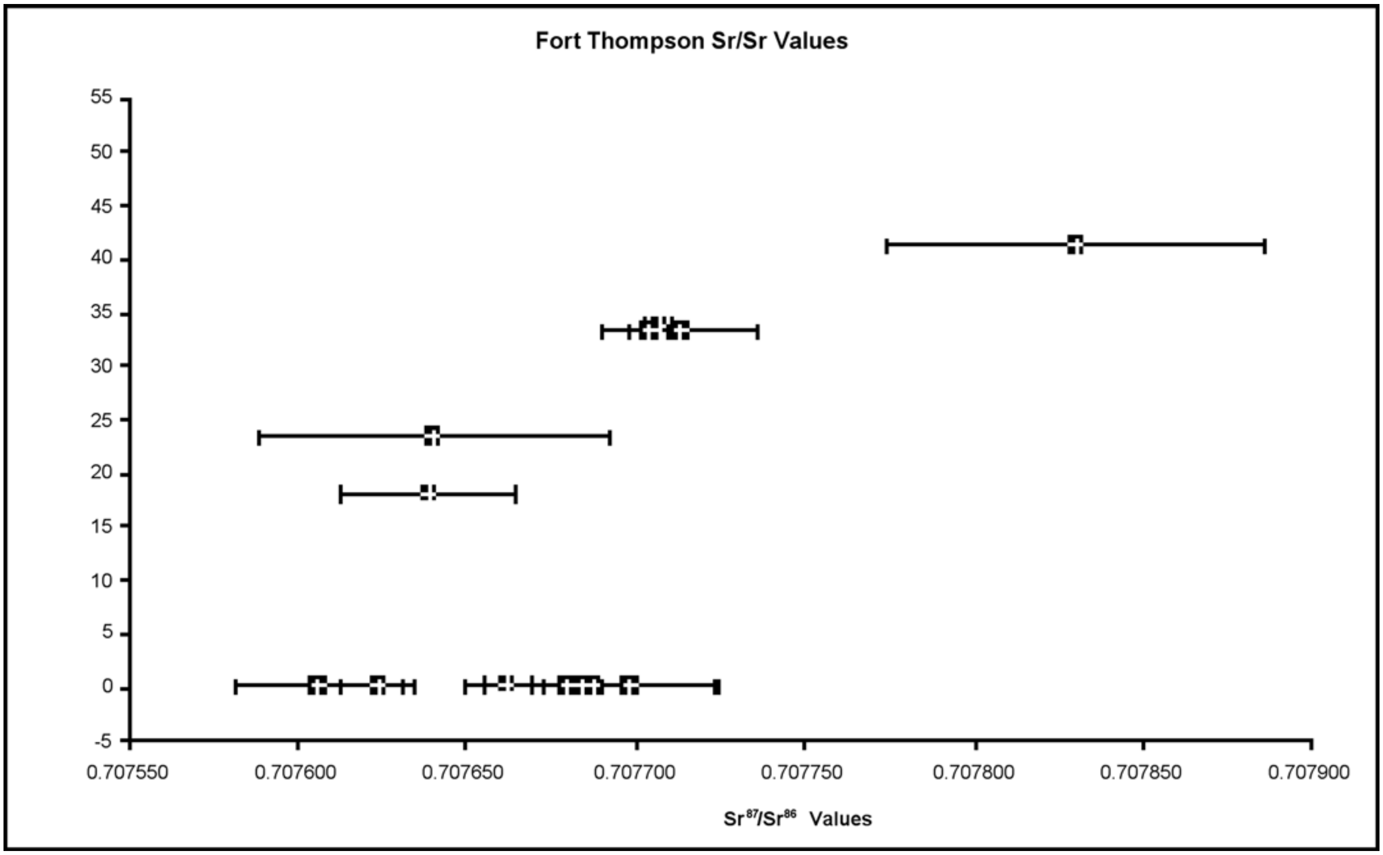

Figure 7. Plot of $^{87}Sr/^{86}Sr$ values from this study versus section thickness (in meters) with the corresponding strontium precision errors for each value as determined by the mass spectrometer.

603B and 641A in the North Atlantic. Essentially it is a low diversity, agglutinated foraminiferal assemblage. These predominantly agglutinated foraminiferal assemblages have been interpreted as having lived in cooler and more corrosive (lower pH) Boreal-derived waters (Douglas, 1972; Eicher and Diner, 1985; Wall, 1997; Watkins et al., 1997). Hoff (1960) reported that *Glomispira corona* requires a minimum water depth of 200 m. Koutsoukos and Hart (1990), in a study of Late Cretaceous marine deposits in Brazil, identified a similar Santonian through Maastrichtian assemblage living in dysaerobic to quasi-anaerobic conditions, with an oligotrophic nutrient level. Biofacies 1 within the study area lies within most of the Gregory Member (Fig. 10).

Biofacies 2 (variance explained of 16.6%) is composed of *Neobulimina canadensis* Cushman and Wickenden, *Eouvigerina aspera* (Marsson), *Gavelinella* sp., *Cibicides harperi* (Sandidge), plus numerous planktonics, mostly the species *Heterohelix globulosa* (Ehrenberg) and *Globigerinelloides prariehillensis* (Pessagno). This biofacies is mostly a calcareous foraminiferal assemblage with relatively high biodiversity that has been interpreted to be Tethyan in origin, from southern, less corrosive (higher pH), warmer waters (Douglas, 1972; Eicher and Diner, 1985). West et al. (1997) noted that the genus *Neobulimina* can be directly correlated with carbonate content and is an indicator of warmer normal-marine water masses that entered the Western Interior Seaway, presumably from the south. Leckie (1987) also noted that the presence of the biserial *Heterohelix* and high numbers of *Globigerinelloides* spp. are characteristic components of what he named “Late Cretaceous Epicontinental Sea Fauna.” Koutsoukos and Hart (1990) assigned the gavelinellids to the middle to outer shelf during the Campanian–Maastrichtian. They estimate the range of water depths occupied by these genera to have been between 100 and 200 m, suggesting that this assemblage represents a relatively shallow, warm-water biofacies. Within the study area, Biofacies 2 is restricted to the Fort Thompson Beds, which crop out ~5 m below the contact of the Gregory Member with the Crow Creek Member.

Biofacies 3 (variance explained of 13.8%) consists of *Osangularia navarroanna* (Cushman), *Saccammina placenta* (Grzybowski), *Spirolectommina* sp., *Neobulimina canadensis* Cushman and Wickenden, plus numerous radiolarians dominated by the species *Dictymitra multicostata* Zittel. Koutsoukos and Hart (1990) recognized this assemblage, with the genus *Osangularia* as a major component of the middle to outer shelf during the Campanian and Maastrichtian. It is interpreted as an aerobic assemblage that tolerated mesotrophic to oligotrophic nutrient levels, and it lived in water depths of >200 m but probably <500 m. Koutsoukos and

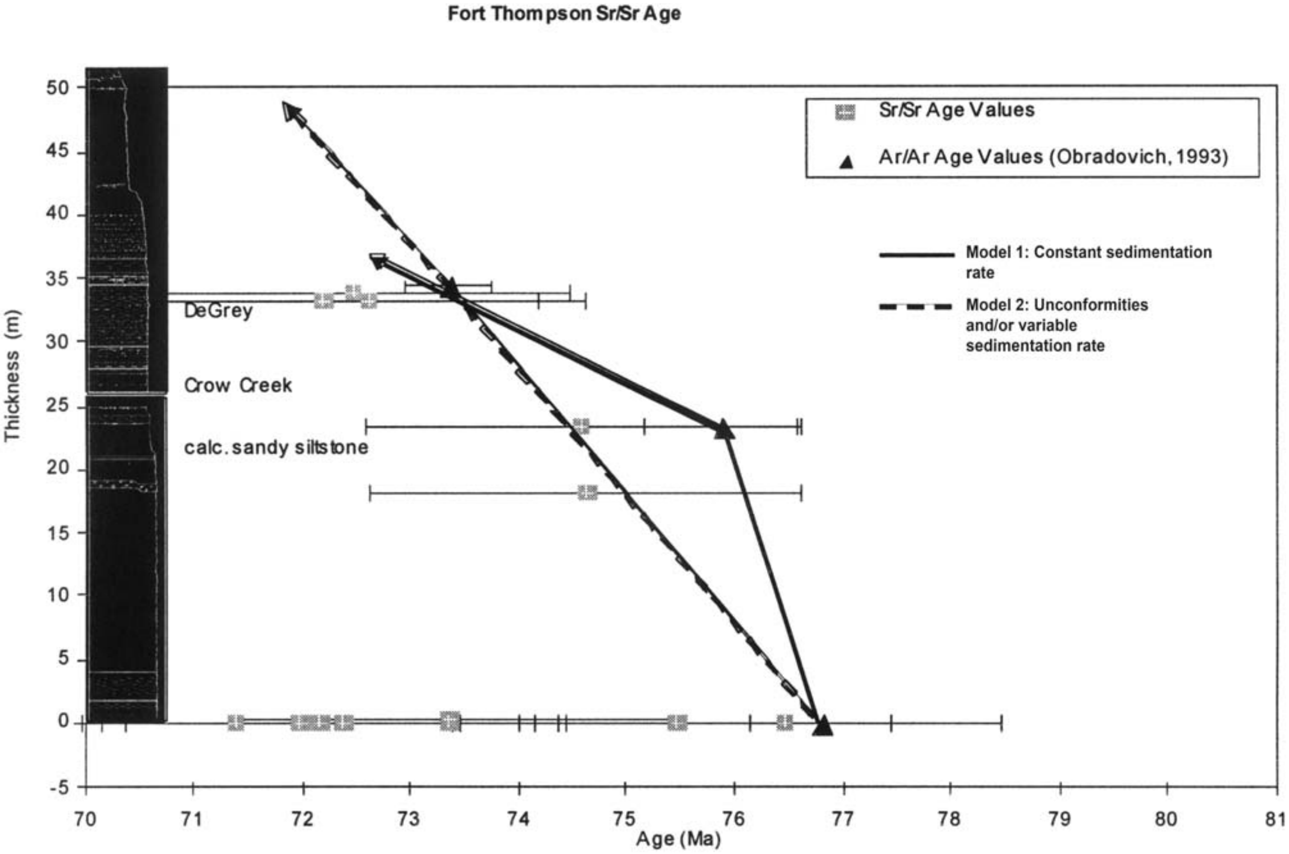
Fort Thompson Sr/Sr Age

Figure 8. Plot of ^{87}Sr/^{86}Sr relative age values from this study versus section thickness (in meters) compared with ^{39}Ar/^{40}Ar absolute age values from Obradovich (1993). All ^{87}Sr/^{86}Sr age values have an assumed conservative error of ±2 m.y.

Hart (1990) recognized the saccamminids as having lived in water depths starting at 200 m. Biofacies 3 most likely represents an intermediate depth assemblage between Biofacies 2 (shallowest, Tethyan origin) and Biofacies 4 (deepest, Boreal origin). It is found within the study area throughout most of the DeGrey Member to the basal Verendrye Member.

Biofacies 4 (variance explained of 16.6%) is composed primarily of *Bathysiphon brosgei* Tappan, *Silicosigmilina futabaensis* Asano, *Milliammina* sp., *Ammodiscus cretaceous* (Reuss), and numerous radiolarians dominated by the species *Dictymitra multicostata* Zittel. Koutsoukos and Hart (1990) described the Bathysiphonidae and Ammodisdidae as living along the middle to lower slope at water depths estimated to have started at 500 m in the Santonian through the Maastrichtian, requiring an oligotrophic nutrient level and a dysaerobic to quasi-anaerobic oxygen level. Biofacies 4 is interpreted to represent the deepest marine assemblage within the study area. It occurs at the base of the DeGrey Member and a few meters above the base of the Verendrye Member and is continuous to the top of the measured section at Fort Thompson.

Patrick et al. (2004) independently took the sea-level curve derived from these foraminiferal assemblages and compared them to their relative-depth curve on the basis of rare earth elements from the mixing of oxygenated and anoxic seawaters, and found the two curves to be in very close agreement. Patrick et al. (2004) also compared these two sea-level curves to the Haq et al. (1987) sea-level curve and still found good agreement among all these studies.

Three thin sections were prepared from three suspect stratigraphic zones to look for bolide-generated shocked quartz: the basal Crow Creek, the uppermost Gregory, and the calcareous sandy siltstone layer (field sample no. FT9403), or named herein the *Fort Thompson Beds*. The "anomalous" nature of this last unit—the fact that it is bounded unconformably and displays bedding features that appear to have formed under higher energy conditions than those typical for the Pierre Shale—may make it a better candidate for a tsunamtite than the Crow Creek Member. Because the rock is sedimentary, the vacuum impregnation method was used to prepare all three thin sections. A sodium cobaltinitrite stain was employed to identify the minerals. In all three samples, shocked quartz was not identified (Hanczaryk et al., 1999). Although three thin sections are hardly statistically significant, the results are reported for the record.

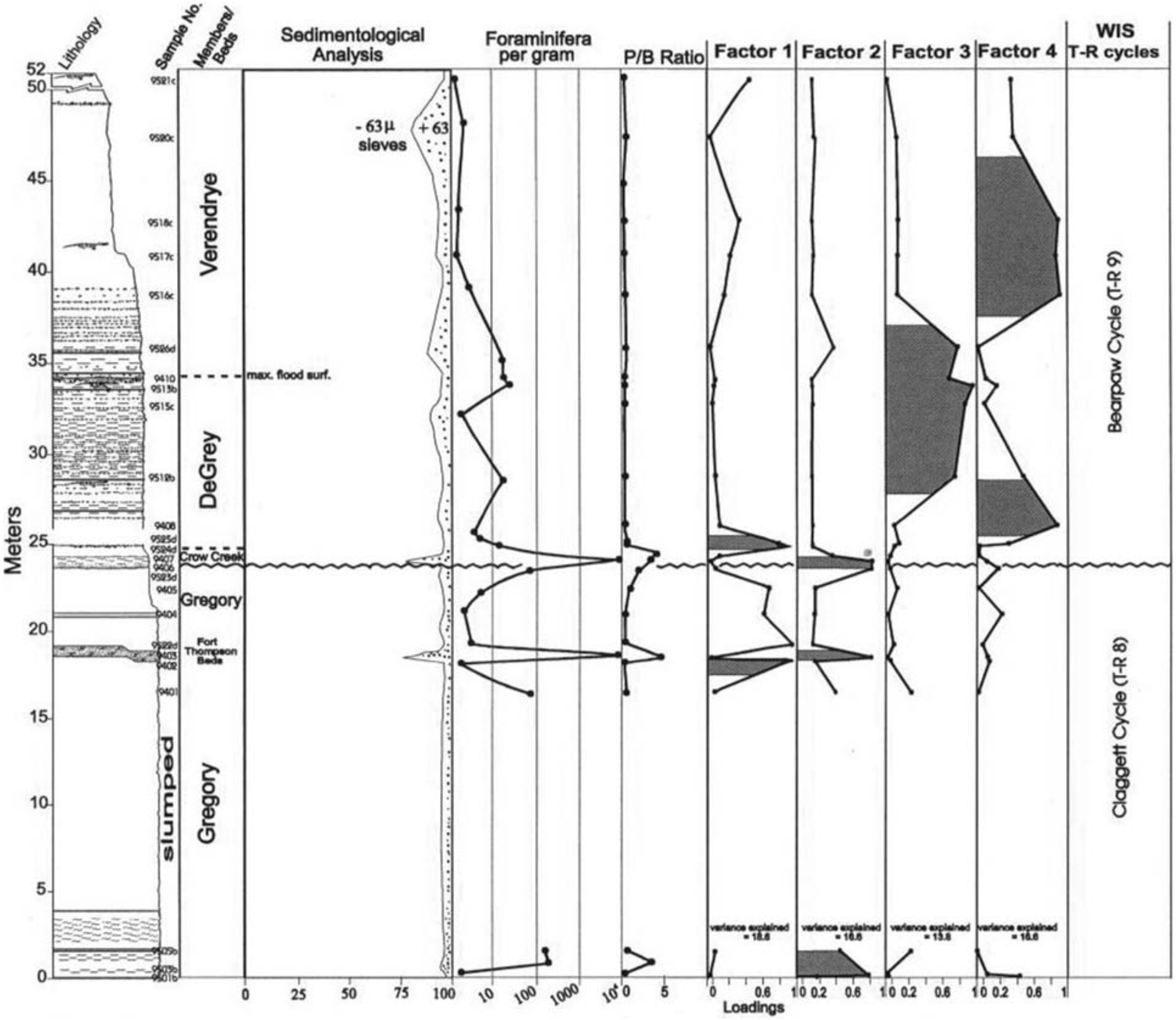

Figure 9. Fort Thompson section, Pierre Shale. Species graph of factor analysis results; factors (biofacies) 1, 2, 3, and 4. Shaded areas indicate where the results for each respective biofacies are equal to or greater than 0.5. WIS—Western Interior Seaway.

CONCLUSIONS

1. The Pierre Shale exposures within the area studied were deposited into the Western Interior Seaway during the Campanian Age of the Late Cretaceous (Kauffman, 1977; Witzke et al., 1983; Izett et al., 1998). The Gregory Member is within the middle Campanian Stage, using the Gradstein et al. (1994) time scale. The Crow Creek, DeGrey, and Verendrye Members are within the upper Campanian. The Campanian–Maastrichtian boundary established for the Western Interior Seaway is the *Baculites eliasi* Biozone (Obradovich, 1993) within the overlying (but absent here) Virgin Creek Member (Witzke et al., 1996). Therefore, the Maastrichtian Stage is not represented within the study area. This also agrees with Cobban's (1993) biozonation scheme for the Late Cretaceous stages within the Western Interior Seaway.
2. A new lithostratigraphic name, the *Fort Thompson Beds,* is proposed to distinguish the "anomalous" and sporadic calcareous sandy siltstone unit, first described by Gries (1942) and found within the upper Gregory Member from the closely overlying, lithologically similar Crow Creek Member.
3. Based on the $^{87}Sr/^{86}Sr$ results from this study, the age of the *Baculites gregoryensis* Biozone, at the base of the study area and within the Gregory Member, is estimated at 75.09 ± 2 Ma and is relatively close to the Gradstein et al. (1994) interpolated date, based on Obradovich's (1993) $^{40}Ar/^{39}Ar$ date of 77.0 Ma. The Crow Creek Member yielded an age of 74.58 Ma, and the calcareous sandy siltstone layer

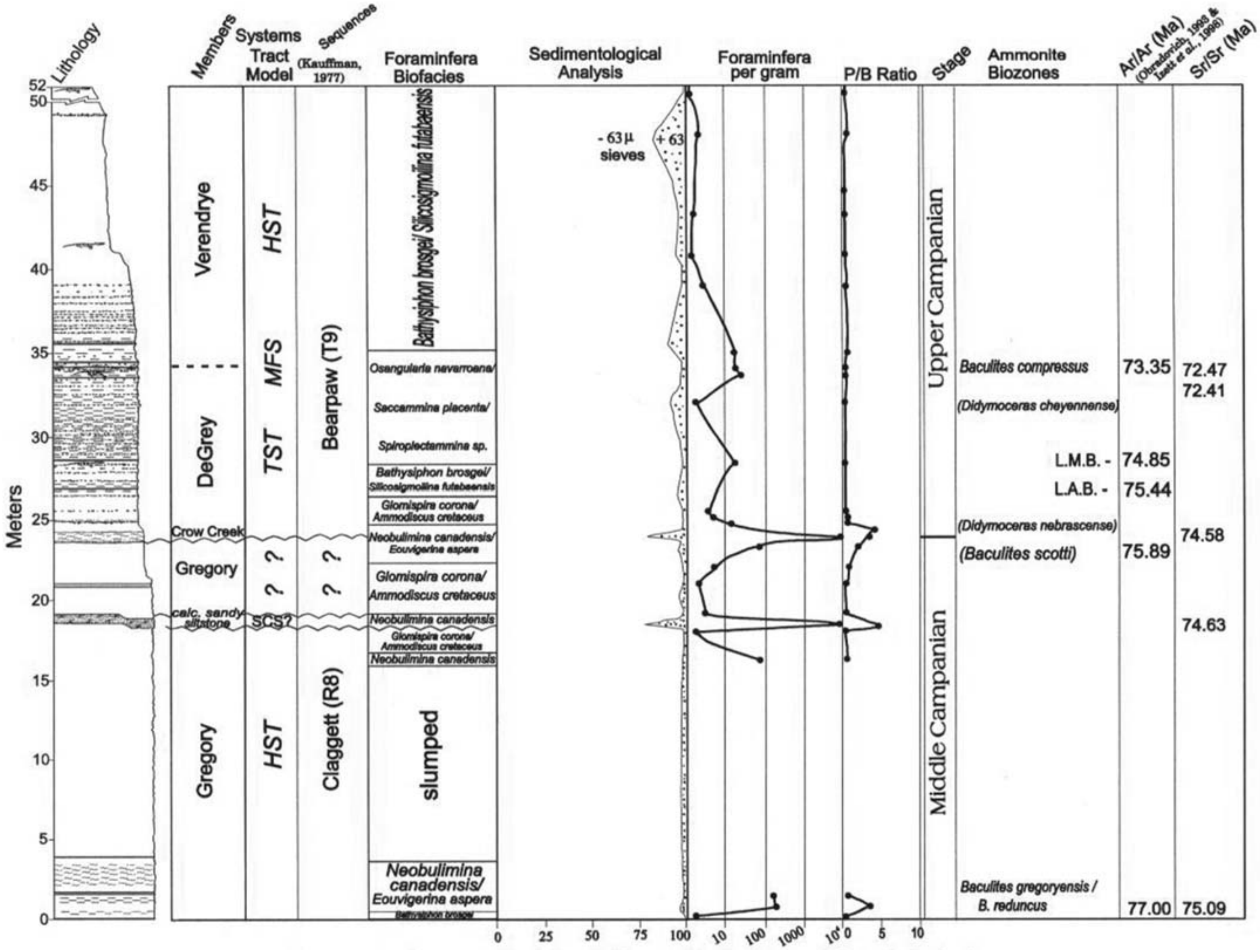

Figure 10. Summation of data for the Pierre Shale at the Fort Thompson, South Dakota, measured section.

(Fort Thompson Beds) yielded an age of 74.63 Ma. These ages contrast slightly with the ages determined by Obradovich (1993) for the *Baculites scotti* Biozone of 75.89 ± 0.72 Ma or with Izett et al.'s (1998) ^{40}Ar/^{39}Ar age for the Lower Agency Bentonite of 75.44 ± 0.27 Ma, but overlap these values with the conservative error value of ±2 Ma. Lastly, the two ^{87}Sr/^{86}Sr age estimates from oyster shells found at the *Globidens* site and inoceramid shells found 0.5 m below the *Baculites compressus* Biozone yielded ages of 72.41 Ma and 72.43 Ma, respectively, compared with Obradovich's (1993) ^{40}Ar/^{39}Ar age for the *B. compressus* Biozone of 73.35 ± 0.39 Ma.

4. Four foraminiferal biofacies are recognized. Biofacies 1 is predominantly agglutinated, Boreal in origin, and indicative of cooler, more corrosive (lower pH), less oxygenated marine conditions and relatively shallow water depths (~100 m). Biofaces 2, composed of calcareous benthic foraminifers, associated with numerous planktonic foraminifers, Tethyan in origin, and indicative of warmer, more oxygenated waters, developed in the shallowest environment (100 m or less). Biofacies 3 is interpreted as a mixed assemblage, intermediate in depth (100–200 m) between Biofacies 2 and 4. Biofacies 4 is mostly agglutinated, Boreal in origin and indicative of cooler, more corrosive (lower pH), less oxygenated marine conditions and the greatest water depths within the study area (a minimum of 200 m or more). These water depths contrast with Kauffman's (1985) and Fox's (1996 and this volume) estimates, based on invertebrate macrofossils, of ~100 m maximum depth for the eastern part of the seaway. One possible explanation for this discrepancy is that a large part of the paleo–water depth data is derived

from deposits within the open Atlantic Ocean, where water depths on the basis of foraminiferal assemblages may be applicable; but in the more restricted Western Interior Seaway the foraminiferal and radiolarian assemblages may have been controlled by other factors such as climate. An alternative explanation may be that a tectonic component could have contributed to greater water depths locally (Mitrovica et al., 1989; Shurr et al., 1994).

5. With regard to placing the study area into a sequence stratigraphic framework, and based largely on the depth interpretation of the foraminiferal assemblages, most of the Gregory Member is interpreted to be a highstand systems tract (HST), part of the transgressive pulse of the Claggett depositional cycle (R8 of Kauffman, 1977). The overlying Crow Creek through DeGrey Members are interpreted as a transgressive systems tract (TST) in response to the Bearpaw depositional cycle (T9 of Kauffman, 1977). The Verendrye Member is interpreted as an HST with a maximum flooding surface (MFS) developed approximately at or near the DeGrey–Verendrye boundary (Hanczaryk et al., 1996). The observed large number of articulated marine reptiles found at or near this horizon, coupled with a high concentration of microfossils and a well-developed macro-invertebrate zone, is suggestive of a condensed section as a result of maximum flooding. This observation is in agreement with Witzke et al.'s (1996) placement of an MFS. The newly named Fort Thompson Beds, found within the upper Gregory Member, are interpreted to be swaly cross-stratification, characterized by Leckie and Walker (1982) as a storm-dominated deposit. Based on the work of Witzke et al. (1996) in developing a Western Interior Seaway sea-level curve, this information was correlated with ^{87}Sr/^{86}Sr age estimates from Sugarman et al. (1995) of Late Cretaceous New Jersey deposits, with additional information from Olsson (1991), Gallagher (1993), Gradstein et al. (1994), and Cande and Kent (1995), to conclude that the unconformity that separates the Gregory Member from the Crow Creek Member correlates with the Haq UZA-4.4 Onlap Cycle (Haq et al., 1987) and corresponds to the unconformity that separates the Englishtown Sand from the Marshalltown (clayey glauconite) Formation in New Jersey (Hanczaryk, 2002). This also agrees well with Kennedy et al.'s (1995) biozonation and correlation of the New Jersey Late Cretaceous coastal plain deposits with the Western Interior Seaway.
6. All of the studied area is interpreted as a fully marine paleoenvironment. The preponderance of olive gray shales indicates that during most of the deposition of the Pierre Shale within the study area, dysaerobic to anoxic conditions most likely occurred (Klein, 1991). This is borne out in the foraminiferal and radiolarian assemblages. The Crow Creek Member and the Fort Thompson Beds seem to have been the exceptions, in which a relatively shallow-marine, oxygenated, carbonate-dominated depositional environment with warmer conditions are indicated to have existed. The upper DeGrey is interpreted as being dominated by Boreal marine influx, the Crow Creek Member by Tethyan, and the Gregory Member as switching back and forth between the two marine conditions.
7. The Crow Creek Member is interpreted to have resulted from the transgression of the Bearpaw Sea and not from a tsunamtite as the result of a bolide impact near what is now Manson, Iowa, as Izett et al. (1993, 1998) concluded. This decision is based on this study's micropaleontologic samples, interpretation of the measured field sections with regard to sequence stratigraphy and correlations with established sea-level curves, limited thin sections that yielded no shocked quartz, and the arguments against a Manson Impact Structure–generated tsunami by Hammond et al. (1995) and Witzke et al. (1996).

   Although the herein named Fort Thompson Beds are interpreted as storm-generated deposits, a closer, more geographically widespread look at this "anomalous" unit should be conducted. Applying a date of 74.1 ± 0.1 Ma, as reported by Izett et al. (1998), to the Manson Impact Structure in comparison with an ^{87}Sr/^{86}Sr date of 74.63 ± 2 Ma derived for the Fort Thompson Beds essentially makes them coeval.

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Rare earth element (REE) analysis of fossil vertebrates from the Upper Cretaceous Pierre Shale Group for the purposes of paleobathymetric interpretations of the Western Interior Seaway

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ABSTRACT

Biogenic apatite crystals in living organisms contain relatively high concentrations of carbonate, sodium, and other species, making the crystallite relatively soluble and reactive. During fossilization, apatite composition changes from a metastable carbonate hydroxylapatite to a thermodynamically more stable fluorapatite. Calcium, sodium, carbonate, and hydroxyl are replaced by fluoride, REE, and trace elements during diagenesis. The total REE concentrations in osteological material are generally <20 ppm; in fossil bones, however, the concentrations may be >1000–10,000 ppm. More than 95% of REE in fossil bone is incorporated during diagenesis. The fossilization process occurs within a few thousand years, and thus the chemical composition of the fossils records the composition of early diagenetic fluids. Apatite becomes a "flight recorder" for the environment of early diagenesis and can be used to interpret the condition of the paleoenvironment.

REE were analyzed from marine reptile (Mosasauridae) bones collected from five superposed formations (Sharon Springs, Gregory, Crow Creek, DeGrey, and Verendrye) of the Upper Cretaceous Pierre Shale Group at localities along the Missouri River in central South Dakota. Fossil vertebrates from each lithostratigraphic unit sampled of the Pierre Shale Group have different REE signatures. Fossils from the Sharon Springs Formation have distinctive REE signatures that may be further subdivided into three superposed members that correspond with the upper, middle, and lower Sharon Springs Formation. REE signatures are distinctive from each stratigraphic unit; therefore, fossils eroded from their stratigraphic context may be assigned to their proper depositional unit on the basis of REE signature comparisons.

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Differences in REE compositions of fossil bones among lithostratigraphic subdivisions appear to have resulted from differential mixing of oxygenated and anoxic seawaters. If differences in mixing are interpreted as depth differences, the lower Sharon Springs member was deposited in deep, anoxic water; water depths decreased for the middle and upper Sharon Springs, and the overlying Gregory and Crow Creek units were deposited in even more shallow water. Finally, the overlying DeGrey and Verendrye Formations were deposited in progressively deeper marine waters, but not as deep as for the lower Sharon Springs. These interpretations are generally consistent with those based on faunal diversity and eustatic sea level curves.

Keywords: rare earth elements, Pierre Shale, stratigraphy, paleoenvironments, paleobathymetry.

INTRODUCTION

REE concentrations and neodymium (Nd) isotopes in fossil bones and teeth, conodonts, and fish scales have been used to infer paleoredox conditions in marine waters (Wright et al., 1987), detect reworking of fossils (e.g., Trueman and Benton, 1997; Trueman, 1996, 1999; Staron et al.,2001), and accomplish or test paleoenvironmental, paleoceanographic, and paleogeographic interpretations (Grandjean et al., 1987, 1988; Grandjean-Lécuyer et al., 1993; Girard and Albarède, 1996; Reynard et al., 1999; Picard et al., 2002; Wright et al., 2002; and literature review in Trueman and Tuross, 2002). Wilde et al. (1996), Girard and Albarède (1996), Laenen et al. (1997), Baturin and Yushina (1998), Picard et al. (2002), and others have used REE in shales or phosphorites to determine sea-level variations or relative water depths.

The REE concentrations in modern bones and teeth are generally <20 ppm (Wright et al., 1984; Chenery et al., 1996; Staron et al., 2001; Patrick et al., 2001). REE in fossil bones may, however, be >1000–10,000 ppm (e.g., Arrhenius et al., 1957) (Table 1). Therefore, virtually all of the REE in fossil bone is incorporated into bone postmortem. Because most REE are introduced postmortem, REE signatures in fossils do not reflect the diet, trophic level, or phylogenetic position of the organism. REE and other trace elements are incorporated shortly after deposition (Millard and Hedges, 1995, 1996; Patrick et al., 2001; Trueman and Tuross, 2002) during early diagenetic recrystallization of the bone apatite. After incorporation into the osteological material, the REE signature in fossils is thermodynamically stable and serves as a record of depositional or early diagenetic conditions (Henderson et al., 1983; Wright et al., 1987; Trueman, 1999). REE signatures in fossils from different stratigraphic units may differ, providing unique fingerprints of variations in their depositional or diagenetic environments. REE signatures in bones deposited in marine settings reflect the composition of the water masses; therefore, inferences can potentially be drawn about paleoenvironmental conditions, including relative sea level variations and sources of marine waters in this part of the Western Interior Seaway.

FACTORS INFLUENCING REE SIGNATURES IN FOSSILS

Apatite crystals in living organisms are very small (Lowenstam and Weiner, 1989; Weiner and Traub, 1992), and their lattices have low degrees of crystallinity (Person et al., 1995) and contain relatively high concentrations of carbonate, sodium, and other species. Therefore, extant biogenic apatite crystallites are relatively soluble and reactive. During fossilization the crystallites of biogenic apatite recrystallize (Brophy and Hatch, 1962; Person et al., 1995). REE and most other trace elements are adsorbed from solution onto the biogenic apatite crystal surfaces (Tuross et al., 1989a, 1989b) and then are incorporated into the fossilizing material (Trueman, 1999; Armstrong et al., 2001). For REE, this process is largely accomplished within a few thousand years (Trueman, 1999; Trueman and Tuross, 2002; Patrick et al., 2001). The incorporation of REE, fluoride, and other trace elements, and the growth of larger, more crystalline apatite, decrease the solubility, specific surface area, and reactivity of the resulting fossilized material. Most studies (see discussion in Trueman, 1999; Armstrong et al., 2001) have suggested that once REE are incorporated into the bone, they are retained and provide a stable signal that reflects the depositional or early diagenetic environment.

Exceptions occur only when the fossil material is dissolved and reprecipitated or recrystallized during high-grade metamorphism (Armstrong et al., 2001), parameters that do not appear within these Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) sediments. Much research has been concentrated on the mechanism by which REE are incorporated into bone, much of which has been summarized by Reynard et al. (1999), Trueman (1999), and Trueman and Tuross (2002).

Henderson et al. (1983) suggested that values of distribution coefficients for all of the REE, except perhaps for cerium, are similar (see also Trueman, 1999; Trueman and Tuross, 2002). If the REE sorption coefficients are also large, REE would be essentially removed from solution, and ratios of REE in fossil materials, as well as REE signatures, should be similar to the average composition of the early diagenetic fluids from which they were obtained (Kemp and Trueman, 2003). Thus, as suggested by Henderson

TABLE 1. RARE EARTH ELEMENT CONCENTRATIONS IN CORTICAL BONE (ppm) OF MOSASAUR FOSSILS FROM SELECTED UNITS OF THE PIERRE SHALE

Sample	Unit	Specimen	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu
72	Burning Brule	Tylosaurinae	93.9	183	31.5	189.6	46.5	10.5	41.3	4.89	25.1	3.95	9.15	1.07	7.34	0.91
56	Burning Brule	?Tylosaurinae	138.9	230.4	36.1	198.5	47.6	11	41.3	4.78	24	3.69	8.54	1.04	6.69	0.79
58	Burning Brule	Tylosaurinae	79.9	132.6	42.4	344.9	94.9	18.3	47.4	8.9	50.2	8.07	24.6	2.88	16.4	2.04
110	Burning Brule	Tylosaurinae	41	129.5	14.4	57.2	13.1	2.58	9.46	1.51	8.52	1.34	3.9	0.48	2.49	0.31
111	Burning Brule	Tylosaurinae	60.6	170.8	32.2	125.2	25	4.09	18.03	2.57	11.5	1.57	4.09	0.47	2.55	0.3
112	Burning Brule	Tylosaurinae	33.3	51.6	6.72	25.6	3.53	0.74	3.36	0.43	2.46	0.46	1.21	0.14	0.73	0.1
79	Boyer Bay	Tylosaurinae	81.8	183	23.3	82.7	16.5	3.25	13.7	2.14	12.6	2.33	7.61	1.04	6.25	0.95
65	Boyer Bay	Mosasauridae	100.6	196.1	33.7	189.6	47.6	11.3	44.3	5.36	27.6	4.24	9.36	1.09	12.8	1.12
102	Boyer Bay	Tylosaurinae	270.9	438.9	77.2	274	53.4	12.4	48.5	7.93	44.7	8.07	25.2	3.38	18.9	2.56
105	Boyer Bay	Tylosaurinae	210.3	780.5	44.4	64.2	8.46	1.67	14.7	1.35	7.25	1.44	5.77	0.89	6.25	1.12
53	Nicholas Creek	Tylosaurinae	121	132.6	17.7	154.1	35.3	7.45	37.7	5.49	42.7	9.93	32.5	4.89	34.3	5.36
61	Nicholas Creek	Not identified	45	49.2	9.5	36.1	7.54	2.1	9.04	1.7	10.2	2.44	7.44	1.12	7.17	1.15
101	Nicholas Creek	Tylosaurinae	89.7	135.6	15.4	109.1	19.8	5.15	27.9	3.8	25.1	5.98	20	3.15	23.2	3.88
115	Nicholas Creek	Mosasauridae	65	87.6	13.7	82.7	28	6.19	15	3.71	30.2	5.85	16.3	2.62	14.99	1.99
116	Nicholas Creek	Tylosaurinae	132.7	178.8	21.3	95	20.8	5.78	32.1	5.01	35.5	8.45	27	3.79	23.75	3.54
62	Nicholas Creek	Tylosaurinae	48.2	43.9	1.65	6.57	1.37	0.58	3.6	0.31	2.19	0.48	1.87	0.24	1.46	0.31
64	Gregory	Mosasauridae	492.9	504	46.5	194	32.9	11.3	73.5	12.3	107.2	32.1	117.9	18.6	124.7	22.3
4	Gregory	Mosasauridae	247	230.4	28.7	116.9	24.4	5.39	44.3	9.99	72.5	23.8	100.3	17.3	133.6	23.4
207	Gregory	Mosasauridae	142.2	132.6	18.5	72.1	16.1	3.82	28.6	5.75	56.3	19.8	85.4	15.5	124.7	22.3
59	Crow Creek	Mosasauridae	470.7	817.3	22.8	73.7	13.7	7.45	40.4	3.63	25.7	7.71	28.3	4.67	30.6	5.36
60	DeGrey	Mosasauridae	170.9	270.6	17.7	68.8	15	4.19	23.8	3.38	25.7	6.56	21.5	3.08	18.4	3.3
201	DeGrey	Mosasauridae	62.1	126.6	12.5	48.7	10.9	2.25	13.4	2.18	14.5	3.21	10	1.44	9.24	1.38
202	DeGrey	Mosasauridae	220.2	220	26.8	104.2	18.9	3.91	28.6	5.01	33.1	8.65	29.6	4.46	30.6	5
203	DeGrey	Mosasauridae	215.2	356.8	45.5	185.2	41.4	9.37	49.7	8.7	53.7	11.94	38.1	6.15	47.4	7.57
204	DeGrey	Mosasauridae	205.5	356.8	46.5	185.2	37.8	7.28	41.3	6.45	38.1	8.26	25.2	3.79	27.9	4.35
205	DeGrey	Mosasauridae	74.6	105.3	13.4	53.4	11.7	2.35	15	2.04	16.2	3.95	13.5	2.18	15.3	2.56
206	DeGrey	Mosasauridae	81.8	107.7	13.4	53.4	11.4	2.35	15	3.09	17	3.95	13.9	2.13	15.7	2.56
1	Verendrye	*Plioplatecarpus*	**	215	31.5	128.2	28	6.19	35.2	5.36	36.3	7.89	23	3.23	20.2	3.23
2	Verendrye	*Plioplatecarpus*	**	55.3	8.08	32.9	7.37	1.71	9.46	1.51	10	2.22	6.63	0.97	5.97	0.97
3	Verendrye	*Plioplatecarpus*	**	159.4	21.8	84.7	17.7	4.28	24.9	3.89	26.3	6.27	19.1	2.81	17.6	2.88
5	Verendrye	*Plioplatecarpus*	**	42.9	5.86	23.3	4.65	1.13	6.55	1.02	6.92	1.65	5.03	0.71	4.53	0.76
48	Verendrye	*Plioplatecarpus*	126.7	89.6	13.4	54.7	11.7	2.7	15	2.34	15.5	3.44	10.3	1.48	9.24	1.51
49	Verendrye	*Plioplatecarpus*	56.6	19.6	2.62	10.4	2.08	0.53	3.06	0.47	3.31	0.79	2.41	0.35	2.17	0.38
21	Verendrye	*Plioplatecarpus*	**	50.4	7.54	28	6.27	1.49	8.24	1.32	8.72	1.94	5.77	0.83	5.2	0.87
36	Verendrye	*Plioplatecarpus*	258.7	419.2	53.4	222.7	48.7	11.3	61.1	8.9	61.7	13.4	39.9	5.74	36	5.61
33	Verendrye	*Plioplatecarpus*	215.2	356.8	46.5	194	41.4	9.37	52	7.58	51.3	11.4	34.8	4.89	30.6	4.77
34	Verendrye	*Plioplatecarpus*	183.1	290	37	168.9	35.3	8.35	46.3	6.75	47.9	10.4	31.7	4.56	30.6	4.67
35	Verendrye	*Plioplatecarpus*	210.3	318	39.6	165.1	34.5	8.16	46.3	6.91	49	10.9	33.2	4.77	31.3	4.89
68	Verendrye	*Plioplatecarpus*	277.2	409.6	43.4	369.6	68.8	17.9	101.4	13.2	91.3	21.7	71	10.9	103.7	14.8

**Not measured.

et al. (1983), Elderfield and Pagett (1986), Trueman (1999), Trueman and Tuross (2002), Kemp and Trueman (2003), and others, in regions of slow deposition the REE signatures of fossils are likely to preserve the signatures of the early diagenetic waters.

The source of REE incorporated in bone has also been a topic of extensive discussion. Some workers have emphasized that REE incorporated into biogenic apatite must be transported by and introduced into the fossil directly from marine or pore fluids (Henderson et al., 1983; Wright et al., 1987; Williams, 1988; Trueman, 1996; Trueman and Benton, 1997; Williams et al., 1997). For example, Trueman (1996) showed that REE signatures in fossils are usually different from those of the surrounding sediments. However, because of the low REE concentrations in surface and pore waters (e.g., Sholkovitz et al., 1989; Byrne and Sholkovitz, 1996; Johannesson and Xiaoping, 1997; German et al., 1995) and the high degree of REE enrichment in apatite, very large volumes of pore fluids would be required to provide the REE. Thus, other researchers (e.g., Reynard et al., 1999) have proposed that REE are preconcentrated by particulates and then released and assimilated into the bone, without significant fractionation, from immediately surrounding sediments. Such preconcentrating sources may be important, not only because they potentially reduce the amount of water required but also because hydrous ferric oxides (HFO) and coatings on suspended particulates are preferentially LREE enriched (Piepgras and Jacobsen, 1992; Sholkovitz et al., 1994) and phosphates may be middle REE (MREE) enriched (Hannigan and Sholkovitz, 2001) in comparison with oxic seawater. Therefore, preferential reaction or dissolution of one of these fractions could affect the REE concentrations in solutions or pore waters and the ultimate nature of the REE signature in the fossil.

Concentrations and signatures of REE have been measured in a variety of marine and terrestrial natural waters (e.g., Byrne and Sholkovitz, 1996; Johannesson and Xiaoping, 1997; Piepgras and Jacobsen, 1992). The aqueous properties of the REE change systematically across the series. For example, a systematic increase in the strength of REE-carbonate ion complexes occurs from light to heavy REE (Haas et al., 1995). Such systematic changes lead to fractionation between the REE in natural waters. Much of the variability of REE in natural waters may be explained by (1) composition of source rocks and materials providing REE to solution; (2) sorption and incorporation of light REE (LREE) in hydrous ferric oxides (HFO) and organic matter, and coatings on clays, tests of planktonic organisms, and other materials; (3) an increased tendency of heavy REE (HREE) to form aqueous complexes, particularly with carbonate in basic and alkaline waters; and (4) redox reactions affecting Ce and Eu (Wright et al., 1987; German et al., 1991; Sholkovitz et al., 1994; Byrne and Sholkovitz, 1996; Johannesson and Xiaoping, 1997; Bau and Dulski, 1996). These factors produce REE signatures in natural waters that range from light to middle to heavy REE enriched. Such variations in REE signatures may be visualized generally using a triangular or ternary diagram (Patrick et al., 2001, 2004; Patrick and Wegleitner, 2005) (Figs. 1 and 2).

Figure 1 shows a ternary diagram with North American Shale Composite (NASC) normalized (Gromet et al., 1984) Yb, Gd, and

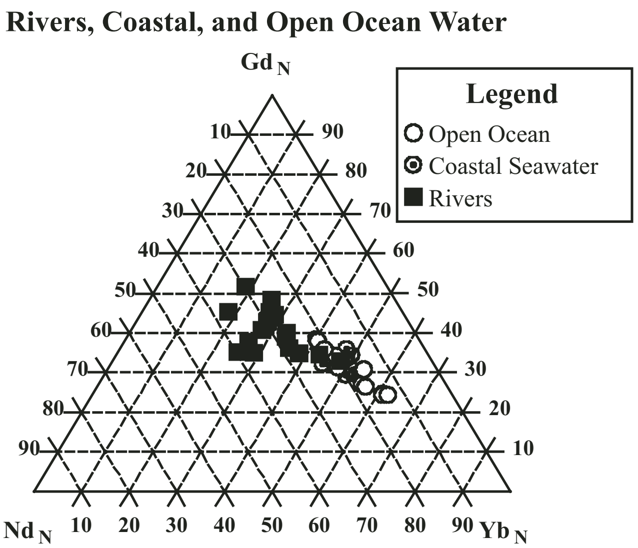

Figure 1. Ternary diagram of NASC-normalized values of Nd (a light rare earth, LREE), Gd (a middle rare earth, MREE), and Yb (a heavy rare earth, HREE) of REE signatures from selected natural waters. Ocean water masses (open circles) differ slightly in REE composition; Arctic and North Atlantic waters plot toward the top of the ocean data symbols, whereas Antarctic Deep Waters plot at the bottom. Relative standard deviations for Nd, Gd, and Yb were generally <2%. Therefore, the average uncertainty in the ratio values and symbol placement for Figure 1 is <~±0.036, slightly larger than the average symbol diameter. Data from Westerlund and Ohman (1992).

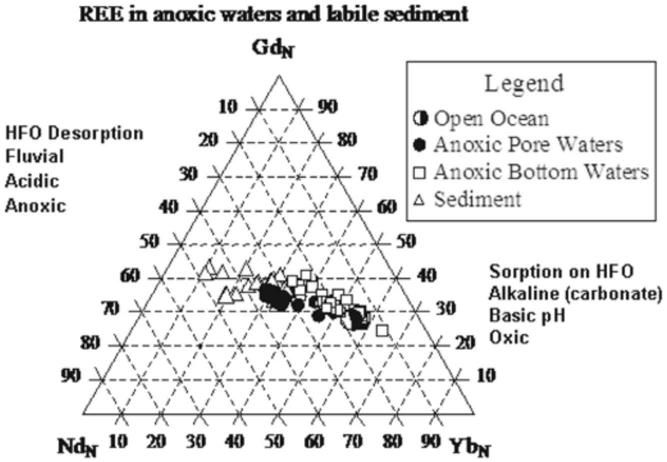

Figure 2. Nd_N-Gd_N-Yb_N ternary diagram of REE signatures from surface ocean water, anoxic marine pore waters, and anoxic or suboxic ocean bottom waters as well as suspended sediments and exchangeable carbonate and hydrous ferric oxide (HFO) fractions of Pierre Shale sediments. Anoxic or suboxic bottom-water or pore-water data generally plot on a line between the labile REE content of sediments (open triangles) and marine surface water, suggesting that their compositions result from the mixing of REE from these two reservoirs.

Nd (Yb_N, Gd_N, and Nd_N) at the vertices. Yb is representative of HREE, Gd of MREE, and Nd of LREE. Nd, Gd, and Yb are even numbered elements and therefore have higher concentrations according to the Oddo-Harkins effect, and thus produce generally more reliable analytical data (assuming proper correction for isobaric overlaps in quadrupole inductively-coupled-plasma mass spectroscopy [ICP-MS]). The LREE Ce and La were not used, because Ce is subject to the effects of oxidation and reduction, and La commonly has slightly different chemical variations than the other REE. Other REE combinations were tested, particularly substituting Pr for Nd, but these substitutions do not greatly alter the patterns.

The combination of Nd, Gd, and Yb is most useful for comparisons with previous research, and particularly for comparisons with the extensive research on dissolved REE. The ternary diagram allows the basic shape of the REE pattern to be represented. NASC-normalized samples that plot in the middle of the diagram (33% Yb_N, 33% Gd_N, and 33% Nd_N) have equal amounts of these elements and will have flat, shale-like REE patterns. Samples plotting toward Yb will be enriched in HREE, and signatures will have a positive slope; those plotting near Nd are enriched in LREE, with a negative slope; and those plotting near Gd are enriched in MREE and have a bell shape. This combination allows the interpretation of paleoenvironments.

REE concentrations in seawater are very low and are strongly HREE enriched (Piepgras and Jacobsen, 1992; Byrne and Sholkovitz, 1996). Thus, REE signatures of waters from various oceans (open circles of Fig. 1) plot toward the Yb end of the ternary diagram. The HREE enrichment is due to enhanced solubility of HREE in relatively high pH and alkaline seawater, produced by preferential HREE carbonate complexing, and sorption of LREE by HFO and tests of planktonic organisms (Piepgras and Jacobsen, 1992). Deep ocean waters tend to plot more toward the Nd-Gd end of the diagram as a result of release of LREE by dissolving tests and other particulates in deeper waters. In contrast, river waters (e.g., Elderfield et al., 1990) are relatively enriched in MREE and LREE, and often exhibit bell-shaped signatures. Such patterns may develop owing to decreased sorption of MREE on iron oxides or weathering of phosphate minerals (Hannigan and Sholkovitz, 2001). These data plot toward the upper left of the triangular diagram (Fig. 1). Some rivers (and groundwaters) plot near or within the range of seawater data; such rivers often drain limestone-rich terrains (Johannesson and Xiaoping, 1997; Stetzenbach et al., 2001), which tend to have REE signatures similar to those of seawater. REE signatures in estuaries (not plotted in Fig. 1) are variable and intermediate between river waters and seawaters (Hoyle et al., 1984; Elderfield et al., 1990; Sholkovitz and Szymezak, 2000). Coastal seawaters tend to have somewhat higher REE concentrations than does open ocean seawater (Elderfield et al., 1990). Their signatures are somewhat variable, but, except in the area of estuaries, dissolved REE tends to plot in the same area as do open ocean waters.

Figure 2 represents REE signatures for surface seawater (North Pacific; Piepgras and Jacobsen, 1992), anoxic or suboxic marine and pore waters, and the labile fractions of suspended sediments and REE components of exchangeable and HFO fractions of Pierre Shale Group (Frey, unpublished data, using the method of Tessier et al., 1979). Although most open marine waters and coastal seawaters have similar REE signatures (Fig. 1), anoxic or suboxic marine bottom or pore waters are more LREE and MREE enriched (German and Elderfield, 1989; Sholkovitz et al., 1992) and tend to plot more toward the upper left of Figure 2. Further, with increasing depth in the anoxic water column, the REE solution composition generally evolves toward increasing LREE and MREE enrichment (e.g., see data of DeBaar et al., 1988; Sholkovitz et al., 1992). In the triangular diagram the anoxic waters generally plot between the North Pacific surface seawater sample and REE values for labile fractions in sediments (Piepgras and Jacobsen, 1992; Frey, unpublished data). This tends to confirm that hydrous ferric oxides, phosphates, and coatings are the primary sources of the LREE and MREE as proposed by Sholkovitz et al. (1992, 1994), Bau et al. (1997), and Byrne and Sholkovitz (1996). Figure 2 indicates that the REE signatures of anoxic or dysoxic bottom marine waters and anoxic pore waters are similarly enriched in LREE and MREE. In this diagram the bottom waters may be slightly more MREE (Gd) enriched than pore waters. The flux of REE from the anoxic pore waters into the deep marine waters undoubtedly contributes greatly, at least in some instances, to their REE composition. In such cases REE ratios in anoxic marine and sedimentary pore waters may not be significantly different. The REE signature and position of water samples plotted in the ternary diagram appear most strongly influenced by pH, redox, concentration of complexing species such as carbonate, and reactions of phases such as HFO, which may preferentially sorb and incorporate or release various REE. It is unlikely that REE compositions of the Western Interior Seaway or other Cretaceous waters are precisely the same as these modern examples; however, if processes controlling REE concentrations remain the same, the relative shifts in water composition should be maintained.

STRATIGRAPHY OF THE PIERRE SHALE GROUP

Mosasaur samples were obtained from the Pierre Shale Group in an area between Chamberlain and Pierre, South Dakota, at localities along the northeastern bank of the Missouri River in Brule, Buffalo, Hughes, and Hyde Counties (Fig. 3). More specific locality data for some specimens is given in Patrick et al. (2002). The Pierre Shale, one of the earliest described lithologic units of the Western Interior, was deposited during the Late Cretaceous (Campanian and Maastrichtian Stages) and is primarily a sequence of organic-rich black and gray shales and interbedded bentonites, most of which formed under relatively anoxic marine conditions (Crandell, 1952; Gill and Cobban, 1961, 1973).

Rocks of this age were deposited in the north-south–trending, epicontinental Western Interior Seaway, which extended from the Canadian Arctic to the Gulf of Mexico. Originally named the Fort Pierre Group (Meek and Hayden, 1862), the Pierre Shale Group is

Figure 3. Location of field area. The field area (in dashed box in the inset outline South Dakota map) lies generally along the northeastern bank of the Missouri River, between Chamberlain and Pierre, South Dakota in Brule, Buffalo, Hughes, and Hyde counties. The base map of South Dakota county boundaries is from the U.S. Census Bureau.

extensively exposed in South Dakota. Within central South Dakota, members recognized by Crandell (1958) have gained general acceptance (e.g., Hanczaryk, 2002). Of the eight members were recognized by Crandell (1958) and now elevated to formational status (Martin et al., this volume), only the five lower formations—the Sharon Springs, Gregory, Crow Creek, DeGrey, and Verendrye—are pertinent to this investigation. All are widespread within the region, and the Sharon Springs has been recognized throughout the Northern Plains. A stratigraphic column summarizing the subdivisions of the Campanian Pierre Shale in central South Dakota, with representative *Baculites* biozones, is shown in Figure 4.

The Sharon Springs Formation has been described in numerous reports, not only in central South Dakota but also in the vicinity of the Black Hills and elsewhere. This formation consists largely of dark fissile shale, which weathers blue gray, and contains many bentonite beds and abundant pyrite and gypsum derived from recent weathering of pyrite. Biotite chemistry in the bentonites suggests that the volcanic source differentiated to a more rhyolitic composition toward the top of the formation (Bertog and Huff, 1999; Bertog et al., this volume). Vertebrate and invertebrate fossils are abundant throughout the formation, including mosasaurs, plesiosaurs, diving birds, large fish, and baculites. Within the present study area the thickness of the Sharon Springs Formation ranges from ~10 to 30 m (see also Crandell, 1958). Three superposed lithostratigraphic units have been noted (Martin, 1996; Turner et al., 2001) and are termed lower, middle, and upper Sharon Springs (although they are formally named as members by Martin et al., this volume). The Sharon Springs Formation contains moderately abundant iron phosphate (vivianite) nodules.

The Gregory Formation is ~23 m thick in the Fort Thompson section (Hanczaryk, 2002; Hanczaryk and Gallagher, this volume) and consists primarily of gray claystone and marl with a few bentonites. Much of the bentonitic content appears to have been redeposited and dispersed, which accounts for its characteristic “popcorn” weathering surface. Vivianite nodules have not been found in this formation from this studied area. The unit has yielded significant numbers of invertebrates (*Baculites gregoryensis*) and a few vertebrate fossils. The upper beds of the Gregory Formation also contain a fauna of radiolarians, including the genera *Dictyomitra* and *Tricolapsa* (Crandell, 1952).

The Crow Creek Member of the DeGrey Formation is 1.2 m thick in the Fort Thompson section but seldom exceeds 1 m in the study area. The Crow Creek is a calcareous siltstone, locally sandy, which is distinguishable from the other units by a light gray to yellow brown color and by supporting a distinctive vegetative cover. The member has produced few vertebrate fossils, and only

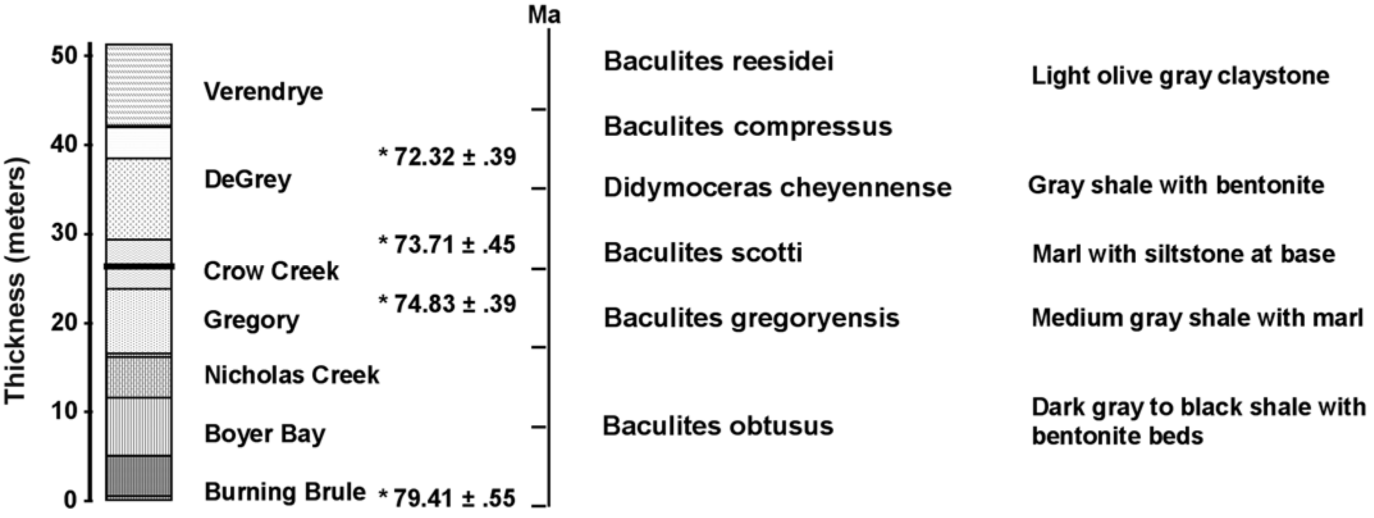

Figure 4. Stratigraphy of the Upper Cretaceous (Campanian) Pierre Shale Group in central South Dakota. *—represents ^{40}Ar/^{39}Ar dating of the DeGrey and Ardmore members (O’Bradovich, 1993).

a single in situ mosasaur sample from this member was available for REE analysis; however, the lowest part of the Crow Creek does contain both pelagic and planktonic foraminifers and a few radiolarians (Crandell, 1952).

The upper DeGrey Formation is 10.1 m thick in the Fort Thompson section; the lower 3 m consists of gray shale, interspersed with abundant iron-manganese concretions. The formation has yielded numerous vertebrate and invertebrate fossils. Pelagic foraminifers and radiolarians are also present (Crandell, 1952). The upper part of the formation is less conspicuously concretionary and is mostly silver-gray shale with some bentonites.

The Verendrye Formation consists primarily of silver-gray shale within the study area, but only the lower 17 m is exposed in the Fort Thompson section. Vertebrate and invertebrate fossils are common. Within the primary study area a number of marker units are recognizable, giving additional accuracy to lithostratigraphic measurements. The relatively thin Crow Creek Member of the DeGrey Formation itself is one such stratum. Although not of such limited thickness, the iron-manganese concretionary levels of the upper DeGrey Formation are readily recognized. A thin but persistent red stratum near the DeGrey–Verendrye contact provides a reliable reference datum throughout the study area. In addition, a recognizable terrace-forming concretionary stratum occurs ~20 m above the DeGrey–Verendrye contact. Because a complete section of the Verendrye Formation is not exposed in the study area, these marker beds are of considerable stratigraphic value.

Geochronological determinations of the Campanian Sharon Springs–Verendrye section indicate that the interval spans ~9 m.y., ranging from 80 to 71 Ma (Gill et al., 1972; Gill and Cobban, 1973; Hanczaryk, 2002). In places the lower part of the Crow Creek Member contains shocked quartz and feldspar grains that may have originated from the 74.1 ± 0.1 Ma Manson Impact Structure (Izett et al., 1998). The total thickness (Fig. 4) of this part of the Pierre Shale Group in central South Dakota, from the base of the Sharon Springs to the top of the Verendrye Formation, is ~55 m (Hanczaryk, 2002; Hanczaryk et al., 1999). In central South Dakota the 17-m-thick Verendrye Formation is incomplete and has been truncated by an unconformity. In other areas of central South Dakota where the Verendrye is conformable with the overlying Virgin Creek Formation, the thickness of the Verendrye is ~46 m. Similarly, the complete Sharon Springs section is probably ~30 m in thickness. Therefore, the maximum total thickness of the section is ~110 m, suggesting an average depositional rate of ~1.2 cm/1000 yr. Gill and Cobban (1973) previously had calculated a rate of deposition for this general area of <~1.9 cm/1000 yr.

METHODS

Sample preparation techniques follow those in Patrick (2002), Patrick et al. (2004), and Staron et al. (2001). Large, intact bone specimens were sampled by drilling, using a Dremel variable speed electric drill. Between samples the drill was cleaned with trace-metal-grade dilute (2%) nitric acid or trace-metal-grade acetone and rinsed in distilled water. Cortical bone samples were immersed in water and then in a dilute acetic acid solution in an ultrasonic bath to remove matrix and secondary carbonate. Other matrix and secondary minerals were removed by handpicking. Samples were rinsed with distilled water and dried. Selected samples were analyzed using X-ray diffraction, revealing essentially pure biogenic apatite with only minor amounts of other crystalline phases. Cleaned bone fragments were mechanically crushed in an acid-washed mortar and pestle. Approximately 0.2 g of powder was weighed for each sample. Each sample was dissolved in ~2 mL Ultrex-grade HNO_3 and diluted to 100 mL. Where only smaller masses of bone were available, the initial solution was diluted to smaller volumes to preserve the mass/volume ratio. Samples were diluted to appropriate levels with 2% ultrapure HNO_3. Initial samples were analyzed using a Finnigan MAT Element/1 high-resolution magnetic sector inductively-coupled-plasma mass spectrometer (ICP-MS) at Rutgers University. The Hawaiian Basalt (BHVO) was used as a standard reference material; precision and accuracy were better than ±4% relative to certified values. Analytical procedures followed those in Field and Sherrell (1998). New samples and remeasured samples were analyzed using a Hewlett-Packard HP4500 ICP-MS at the South Dakota School of Mines and Technology (quadrupole used; correction for isobaric overlaps). Duplicate samples were run for comparison between the two machines, and results were within experimental error. Results have been corrected for isobaric interferences where necessary. The coefficient of variation for most REE is <±5% of the analyzed value. Analytical results presented in Figures 1, 2, and 5–10 have been normalized relative to NASC (Gromet et al., 1984). In all, 16 samples were analyzed from the Sharon Springs Formation, 3 from the Gregory Formation, 7 from the DeGrey Formation, and 12 from the Verendrye Formation. The Crow Creek Member of the DeGrey Formation is generally unfossiliferous, and only a single specimen was available for analysis.

RESULTS

Results of REE analyses of fossil bones are given in Table 1. REE signatures of fossils within individual units are similar. For example, Figure 5 shows REE signatures (normalized concentration versus atomic number) in mosasaur fossils collected from the Verendrye Formation from several sites. However, fossils from other stratigraphic units yield different REE signatures (Fig. 6). REE signatures in bones from the studied units vary from LREE and MREE enriched in the lower Sharon Springs to HREE enriched in the Gregory Formation. REE signatures in fossils are generally different from those of the bulk surrounding sediments obtained by HF dissolution, which are generally similar to bulk shale (NASC).

To confirm the visual impression (Fig. 6), REE data for fossils from the lower, middle, and upper Sharon Springs and Verendrye Formations were analyzed by discriminant analysis using NCSS statistical software (Hintze, 1997). Discriminant analysis is a statistical technique (Davis, 1986) that finds the linear

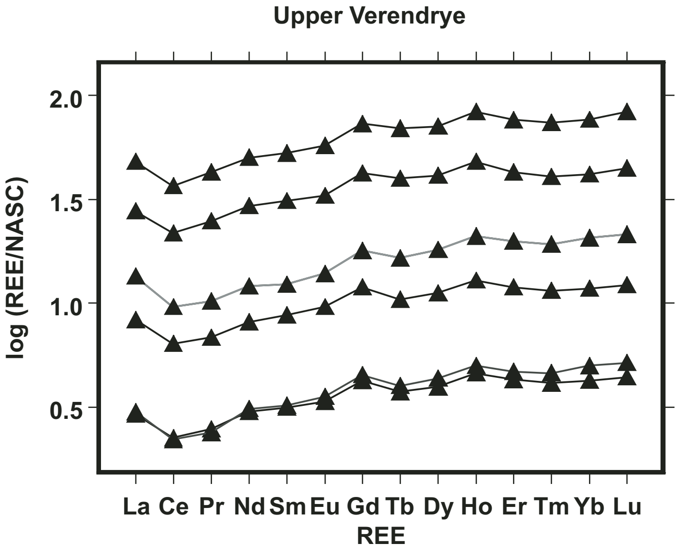

Figure 5. NASC-normalized REE signatures in fossils from the upper part of the Verendrye Formation of the Pierre Shale. Although REE concentrations vary in different fossils, possibly because of variation in osteological material, REE signatures or patterns remain the same. Fossils in this diagram were collected over an area of >250 km^2 in central South Dakota. Within each studied unit of the Pierre Shale is evidence of lateral extent (Table 1).

combination of variables (REE ratios) that produce the maximum or optimal separation between defined groups. In the case of REE analysis, discriminant analysis allows the best statistical method to determine specific groupings or units. Canonical correlation is an additional procedure for assessing the relationship between the REE ratios. Canonical analysis is used when trying to classify an unknown sample; the assignment of the unit can be determined by the best-fit parameters.

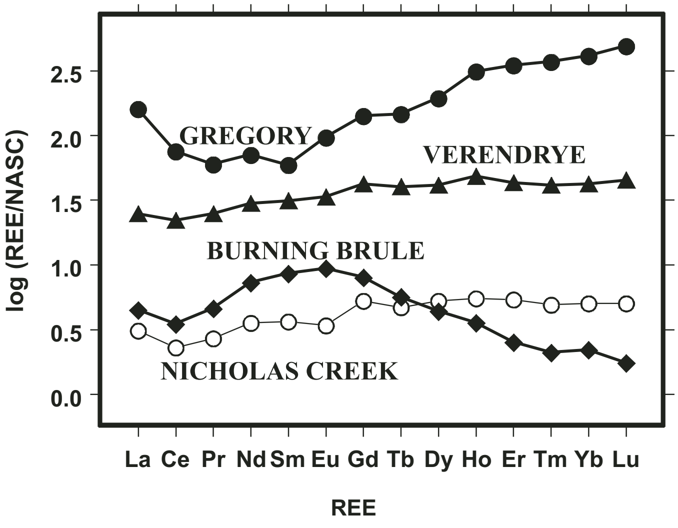

Figure 6. NASC-normalized REE signature in mosasaur fossils from selected units of the Pierre Shale Group. REE signatures in fossils from different lithostratigraphic subdivisions vary visibly. REE content is in parts per million (Table 1).

Discriminant analysis was conducted using NASC-normalized REE ratios (e.g., Nd/Yb). Elemental ratios were used, rather than concentrations, to remove the effect of differences in REE concentrations between different types of osteological materials and different localities. Discriminant analysis was conducted using stepwise regression to select the best parameters. The Sm/Dy, Tb/Er, Tb/Yb, and Sm/Yb ratios were most important for accurate classification of these units. Classification error was reduced by >90%. Canonical variant scores for these four units (Fig. 7) indicate that samples from the three Sharon Springs units and the Verendrye Formation can be statistically distinguished from one another.

Verendrye mosasaur fossils were collected at three different localities over a ~250 km^2 area of central South Dakota. Therefore, at least in some marine environments, REE signatures (Fig. 5) may have significant lateral extent. The differences within and between units can be illustrated by plotting ratios of various REE as a function of stratigraphy. Dy_N/Yb_N ratios in bones from the various units are shown in Figure 8.

These data show that Dy_N/Yb_N ratios differ from one unit to another and indicate that different unitscan be distinguished on the basis of REE signatures and ratios. The Verendrye Formation has a uniform Dy_N/Yb_N ratio throughout, whereas the Sharon Springs displays significant REE variations. The Sharon Springs Formation can be further subdivided into three parts on the basis of REE signatures. The subdivisions generally coincide with previously identified units by the second author of upper, middle, and lower Sharon Springs: Burning Brule, Boyer Bay, and Nicholas Creek Members, respectively (see Martin et al., this volume). REE data for fossils from the various units lie near a straight line between the Gregory Formation and lower Sharon Springs member (Burning Brule Member) (Fig. 9). This indicates that, as a first approximation, REE data can be explained by mixing or evolution between a Yb-rich (HREE) end member near the Gregory Formation and a relatively

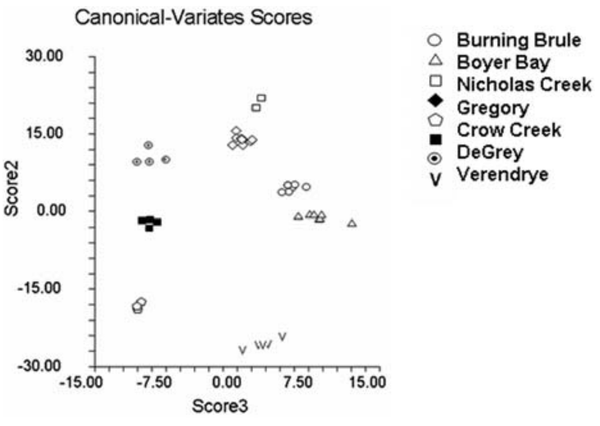

Figure 7. Canonical variate scores for mosasaur fossils from lithologic units of the Pierre Shale Group. Vertebrate fossils can be distinguished statistically on the basis of REE ratios.

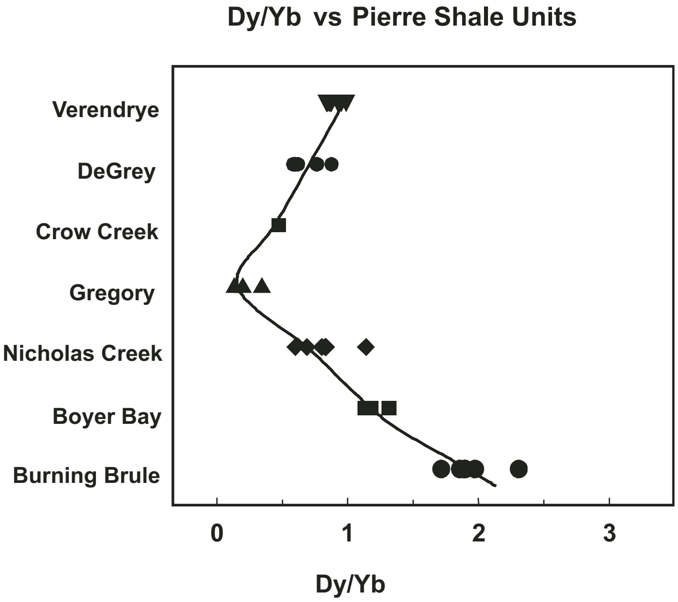

Figure 8. Shale-normalized Dy/Yb (Dy_N/Yb_N) in fossils from selected units of the Pierre Shale Group.

Nd- and Gd-rich (LREE and MREE) end member near the lower Sharon Springs. This conclusion was tested using a computer mixing model. This mixing model showed that most of the signature variations observed could be simulated using a simple two-component mixing model having those end members. The amount of variation in REE signatures in the Pierre is as great as that in some terrestrial units (Trueman, 1999). This is somewhat surprising; many previous workers (e.g., Trueman, 1999) had assumed that marine diagenetic environments had limited chemical variability and thus small variations in REE signatures in comparison with terrestrial environments. REE signatures for the fossils are generally different from those of the surrounding Pierre shale, which are generally flat and plot toward the center of the diagram. The REE variations in the fossils should be related to variations in REE compositions of marine waters. The interpretation that these REE signatures represent mixing between two end members suggests that the HREE- and MREE-enriched (hat-shaped) patterns represent a continuum and could have been derived from different water compositions by a single process. This interpretation is different from some previous studies in which the different patterns were thought to have resulted from different processes (e.g., Reynard et al., 1999). However, a number of previous studies have made paleoenvironmental interpretations on the basis of similarities between REE signatures in fossils and those of modern waters (e.g., Armstrong et al., 2001; Picard et al., 2002).

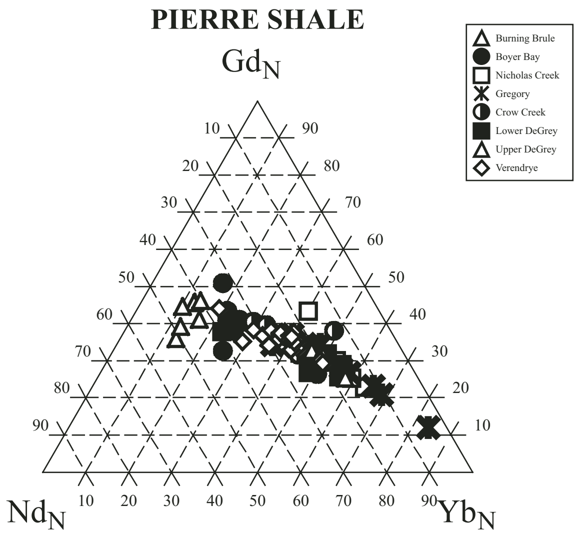

Figure 9. Ternary diagram of NASC-normalized values of Yb (HREE), Gd (MREE), and Nd (LREE) in fossils from the Pierre Shale Group. Mosasaur samples plot along a straight line (from Burning Brule to Gregory), which may result from mixing or evolution between two end-member waters, one enriched in MREE and LREE, and the other enriched in HREE. Oxygenated seawater may represent the HREE-enriched water, and deep, anoxic bottom water the MREE– and LREE–enriched end members. The average uncertainty in the ratio values and symbol placement for Figure 9 is slightly smaller than the average symbol diameter.

DISCUSSION AND PALEOENVIRONMENTAL INTERPRETATION

Differences in REE signatures in vertebrate fossils from the various members (Fig. 6) can be explained in terms of variations in REE concentrations in marine or pore waters, such as those shown in Figures 1 and 2. Previous research (Henderson et al., 1983; Trueman and Tuross, 2002) suggests that REE patterns in fossils will be very similar, though perhaps not identical, to those of waters from which the REE were obtained. Therefore, REE mixing or evolution trends in the Pierre Shale fossils, such as those shown in Figure 9, should be produced by similar trends in water composition, such as those shown in Figures 1 and 2. If the average sedimentation rate in the Pierre Shale Group is ~1.2 cm/1000 yr, and the period of REE uptake was only a few thousands of years, then the fossil would not be deeply buried during REE uptake. Although pore waters near the sediment-water interface may be different from marine bottom waters (Elderfield and Pagett, 1986; Elderfield and Sholkovitz, 1987), the slow sedimentation rate suggests that REE signatures probably most closely reflect the composition of ocean bottom waters rather than that of pore waters (Kemp and Trueman, 2003). However, as previously noted, the REE content of bottom waters may be significantly modified by any upward flux of REE from the sediment-water interface or sediment pores. Differences in REE signatures in fossils from different stratigraphic units of the Pierre Shale Group might be explained either by (1) mixing between LREE-MREE–enriched estuarine-river water (upper left in Fig. 1) and HREE-enriched oxic open marine water (lower right in Fig. 1) end members, or (2) mixing between LREE-MREE–enriched anoxic water (toward the upper left in Fig. 2) and HREE-enriched oxic open marine water (Fig. 2). There is no lithological evidence that the Pierre Shale Group in central South Dakota was deposited in an estuarine environment. As previously indicated, the Pierre Shale Group consists of laterally extensive organic-rich, largely unbioturbated black and gray shales, siltstones, and bentonites. This suggests deposition in suboxic or anoxic conditions, with low deposition rates relatively remote from estuaries.

Paleogeographic reconstructions of the Late Cretaceous mid-continental seaway (e.g., Gill and Cobban, 1961, 1973) suggest that the shorelines were far to the east and west of the study area. The fact that REE signatures of fossils from individual units are similar, even over extended distances, also suggests that the environment was fairly uniform, rather than a spatially variable environment, with mixing of REE from rivers and seawater, which might be expected in estuaries. Therefore, the main trend observed in Figure 9 appears to be most consistent with incorporation of REE from mixtures between oxygenated open seawater and anoxic or suboxic marine water masses. This would be consistent with paleoceanographic reconstructions, suggesting that the Western Interior Seaway was at least intermittently or seasonally stratified, perhaps from salinity or temperature differences, with oxygenated waters overlying dysoxic or anoxic water masses (Glancy et al., 1993; Slingerland et al., 1996; Schroeder-Adams et al., 2001; Fisher and Arthur, 2002). Thus, REE signatures in fossils from the lower Sharon Springs Formation, which are relatively enriched in MREE (Figs. 6 and 10), are more similar to signatures in anoxic or seasonally anoxic marine waters (Fig. 2) (DeBaar et al., 1988; German et al., 1991; Bau et al., 1997). This also seems consistent with the nature of the black, pyrite-rich shale of the lower Sharon Springs. In contrast, REE signatures in fossils from the Gregory Formation are highly HREE (Yb) enriched (Figs. 6 and 9). Such signatures are more similar to those of open seawater, with little input from anoxic or suboxic environments. REE signatures in the overlying Crow Creek, DeGrey, and Verendrye units became progressively more MREE and LREE enriched (Fig. 9), indicating progressively greater mixing with anoxic waters. Chemical reaction modeling, using PHREEQC (Parkhurst and Appelo, 1999), of seawater, organic matter, dissolved oxygen, goethite and hydrous ferric oxide, and biogenic apatite shows that formation of nodular vivianite, which is common in the lower parts of the Sharon Springs Formation, requires reducing conditions, consistent with extensive decomposition of organic matter in a stagnant environment, with reductive dissolution of goethite or HFO. This implies that relatively large amounts of LREE-enriched REE could be put into solution, from which REE could be adsorbed and retained by recrystallization of biogenic apatite.

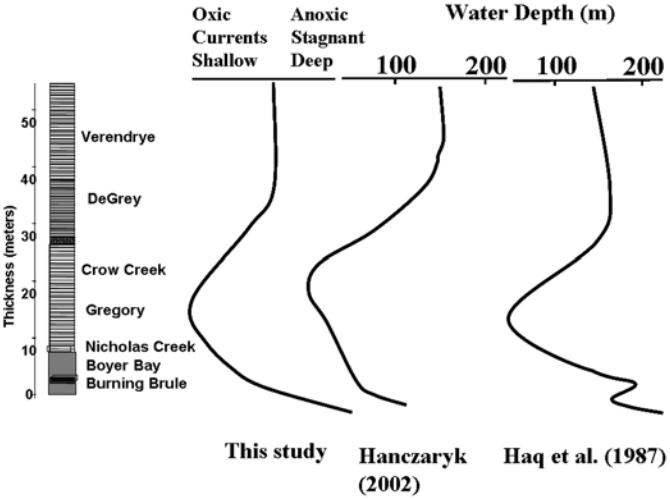

Figure 10. Comparison of variation in relative water depth during deposition of the Pierre Shale Group in the present study with that of Hanczaryk (2002) and the eustatic sea-level curve of Haq et al. (1987).

Such changes in mixing between oxic and anoxic or dysoxic marine waters in one locality might occur in several ways: (1) changes in water depth, (2) changes in organic productivity, and (3) changes in vertical stratification owing to a freshwater lid or changes in upwelling or intensity of wind-driven marine currents. Although changes in marine currents, wind, storms, or organic productivity cannot be ruled out, many researchers have proposed eustatic or relative changes in sea level during this period (Crandell, 1952; Gill and Cobban, 1961, 1973; Schultz et al., 1980; Haq et al., 1987; Stoffer et al., 1998; Hanczaryk et al., 1999). If the data are interpreted primarily in terms of changes in relative water depth, then the lower Sharon Springs fossils were deposited in relatively deep water. REE patterns in the middle and upper Sharon Springs suggest shallowing, and fossils in the overlying Gregory Formation may have been deposited in relatively shallow water. Overlying units were then deposited in progressively deeper marine environments, but not as deep as the Sharon Springs Formation (Fig. 9).

Picard et al. (2002) also suggested that increased Dy_N/Yb_N ratios in fossil fish and reptile teeth corresponded with increasing paleodepth. Data from the Pierre Shale Group (Fig. 6) are consistent with this interpretation. These results are generally consistent with paleoenvironmental interpretations by Crandell (1952), Gill and Cobban (1961, 1973), Schultz et al. (1980), and Hanczaryk (2002), and sea level variations proposed by Haq et al. (1987). Hanczaryk (2002) interpreted biofacies in formations of the Pierre Shale as indicating shallow depths, perhaps 100 m, for the Gregory, depths <100 m in the Crow Creek, 100+ m for the lower DeGrey, 200 m for the upper DeGrey, and 200 m for the DeGrey–Verendrye boundary (Fig. 10).

Gill and Cobban (1961, 1973) proposed that the Sharon Springs was deposited at the peak of a major transgression (Claggett transgression). Thus, most of those sediments were probably deposited in deep water (Schultz et al., 1980). Gill and Cobban (1961, 1973) proposed that the overlying Gregory Formation and Crow Creek Member of the DeGrey Formation were deposited during a regressive (shallowing) episode, the Judith River regression. Crandell (1952) proposed that sedimentological and micropaleontological changes indicated that the Crow Creek Member was deposited in shallow water and the upper DeGrey and Gregory Formations were deposited in slightly deeper waters. Gill and Cobban (1961, 1973) suggested that the upper DeGrey and Verendrye Formations were then deposited during a period of progressive deepening, the Bear Paw transgression. Haq et al. (1987) proposed a general long-term eustatic shallowing between 80 and 71 Ma (Verendrye), with a short-term, abrupt shallowing at ca. 75 Ma, generally consistent with HREE-enriched Gregory and Crow Creek fossils (Fig. 10). Differences between our results and the eustatic sea level curve of Haq et al. (1987) may have resulted from effects of tectonic uplift or subsidence in the Western Interior region. It should also be recognized that it is probably not possible, with the relatively few data points sampled and the limitations on stratigraphic control within units of the Pierre Shale Group, to accurately and fully portray the actual paleoenvironmental trends and their timings.

CONCLUSIONS

REE signatures in fossil mosasaur bones from selected units of the Pierre Shale Group in central South Dakota vary stratigraphically but are virtually identical within individual units over a relatively wide geographic area. Differences in REE signatures in fossils from various units can be distinguished by statistical methods, such as discriminant analysis, and can be used to identify bones from individual units. The slow depositional rate of the Pierre Shale Group suggests that REE signatures in the fossils were acquired from marine bottom waters and can be used to interpret paleoenvironments. Ternary diagrams represent the basic shape of the REE signature and facilitate comparisons of REE ratios in fossils with modern waters for interpretation of depositional or early diagenetic conditions. Ternary diagrams show that REE data for units of the Pierre Shale lie along a two-component mixing line. This line is interpreted as most consistent with mixing of HREE-enriched oxygenated marine waters with MREE- and LREE-enriched anoxic or suboxic marine water. If the REE trends are interpreted as being related to ocean depth, then the lower, middle, and upper Sharon Springs members (see Martin et al., this volume, for revised nomenclature) were deposited in different water depths; the lowest member of the Sharon Springs was deposited in relatively deep, anoxic water, whereas the middle and upper Sharon Springs members were deposited in progressively shallower, more oxygenated marine waters, consistent with progressive regression. The overlying Gregory and Crow Creek units were apparently deposited in shallow, possibly coastal, waters. The overlying formations (DeGrey and Verendrye) were deposited in progressively deeper water. These results are generally consistent with previous paleoenvironmental conclusions, based on analyses of biofacies and sedimentology and eustatic sea level curves (Gill and Cobban, 1961, 1973; Haq et al., 1987; Hanczaryk et al., 1999).

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Mollusks from the late Campanian upper DeGrey Formation of the Pierre Shale Group, Missouri River Valley, central South Dakota

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ABSTRACT

The Missouri River and its tributaries in central South Dakota have eroded into the Pierre Shale, exposing a vertical sequence of late Campanian strata, from older to younger: the Crow Creek Member of the DeGrey Formation, upper DeGrey Formation, and Verendrye Formation, deposited during the transgressive phase of the Bearpaw cyclothem.

The DeGrey Formation (*Baculites compressus* Ammonite Range Zone) is predominantly gray bentonitic shale with interbeds of thin and relatively pure cream-colored bentonite and bioturbated, fossiliferous black manganese-iron carbonate concretions. Fossils are molds, casts, and fragmented shell material from a diverse epifauna of marine bivalve mollusks dominated by byssate, cemented, and unattached inoceramids, and ostreids. Inoceramids include *Inoceramus convexus* Hall and Meek, *I. perplexus* Whitfield, *I. pertenuis* Meek and Hayden, *I. proximus* Tuomey, *I. sagensis* Whitfield, *I. tenuilineatus* Hall and Meek, *Platyceramus vanuxemi* (Meek and Hayden), and *Endocostea barabini* (Morton). The larger specimens are commonly encrusted with the oyster *Pseudoperna congesta* (Conrad). *Ostrea patina* Meek and Hayden, a solitary oyster, is also present. External casts of articulated valves of *Pholadomya hodgii* Meek, a burrower-borer, are abundant as are those of *Pteria (Pseudopteria) sublevis* Whitfield, *P. linguaeformis* (Evans and Shumard), and *P.* sp. B. *Anomia subtrigonalis* Meek and Hayden and *A. oblique* Meek and Hayden complete the bivalve fauna. Less abundant are the gastropods *Anisomyon borealis* Morton, *A. shumardi* Meek and Hayden, *Ampullina? paludinaeformis* Sohl, and *Acmaea occidentalis* (Hall and Meek). The Late Campanian ammonite index fossils *Baculites compressus* Say, and *Jeletzkytes nodosus* (Owen) and *J. brevis* (Meek), are abundant.

Bivalves of the DeGrey Formation lived on a low-energy substrate where bentonite-rich clay was accumulating. Abundant epifauna and extensive bioturbation of the manganese-iron carbonate concretions suggest aerobic conditions. Adjacent deeper, anoxic basin waters periodically transported iron and manganese upward into the oxic zone, where it was precipitated with carbonate. The fragmentary nature of most of the bivalve shells, disruption of the sediment, and abundance of possible coprolitic material suggest predation by sediment-probing and shell-crushing predators.

Keywords: Cretaceous, mollusks, Pierre Shale, South Dakota.

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INTRODUCTION

The southeast-flowing Missouri River has cut a valley ~100–120 m deep and 1.5–2.5 km wide into the Missouri Plateau section of the Great Plains Province in central South Dakota (Fig. 1). Along the valley walls of the Missouri River and its tributaries is a belt of rugged topography locally known as "the breaks" in which are exposed the formations of the Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature). One of these members, the late Campanian DeGrey Formation, forms a conspicuous dark band ~45 m above the river that can be traced around the hills and ridges near the river (Fig. 2). The black color is from oxidized manganese-iron carbonate concretions.

Stratigraphy

The upper DeGrey Formation lies between the Crow Creek Member of DeGrey and Verendrye Formation (Fig. 3) in the ammonite range zones *Didymoceras cheyennense–Baculites compressus*. Member contacts are easy to pick because the basal beds of the overlying Verendrye Formation are alternating bands of silver-gray flaky shale and dark gummy shale, and the underlying Crow Creek Member of the DeGrey Formation is light-gray to yellow-brown siltstone (Fig. 4).

In the area of study, the thickness of the upper DeGrey Formation varies from ~12 to 17 m. The lower 1.5 m (and in some places considerably more) is a light- to dark-gray siliceous shale with few fossils or concretions, grading upward into 10–14 m of light- to dark-gray bentonitic shale interbedded with very thin and relatively pure tan bentonite layers and beds of dark brown to black manganese-iron carbonate concretions. In places three prominent bentonite marker zones (Fig. 5) are called the "lower micaceous bentonite," the "big bentonite bed," and the "upper micaceous bentonite." These bentonite zones were originally named and described by Rothrock (1943). Paleogeographic maps published by Cobban et al. (1994) show the approximate shoreline configuration during the time of the *Baculites compressus* Range Zone (Fig. 6).

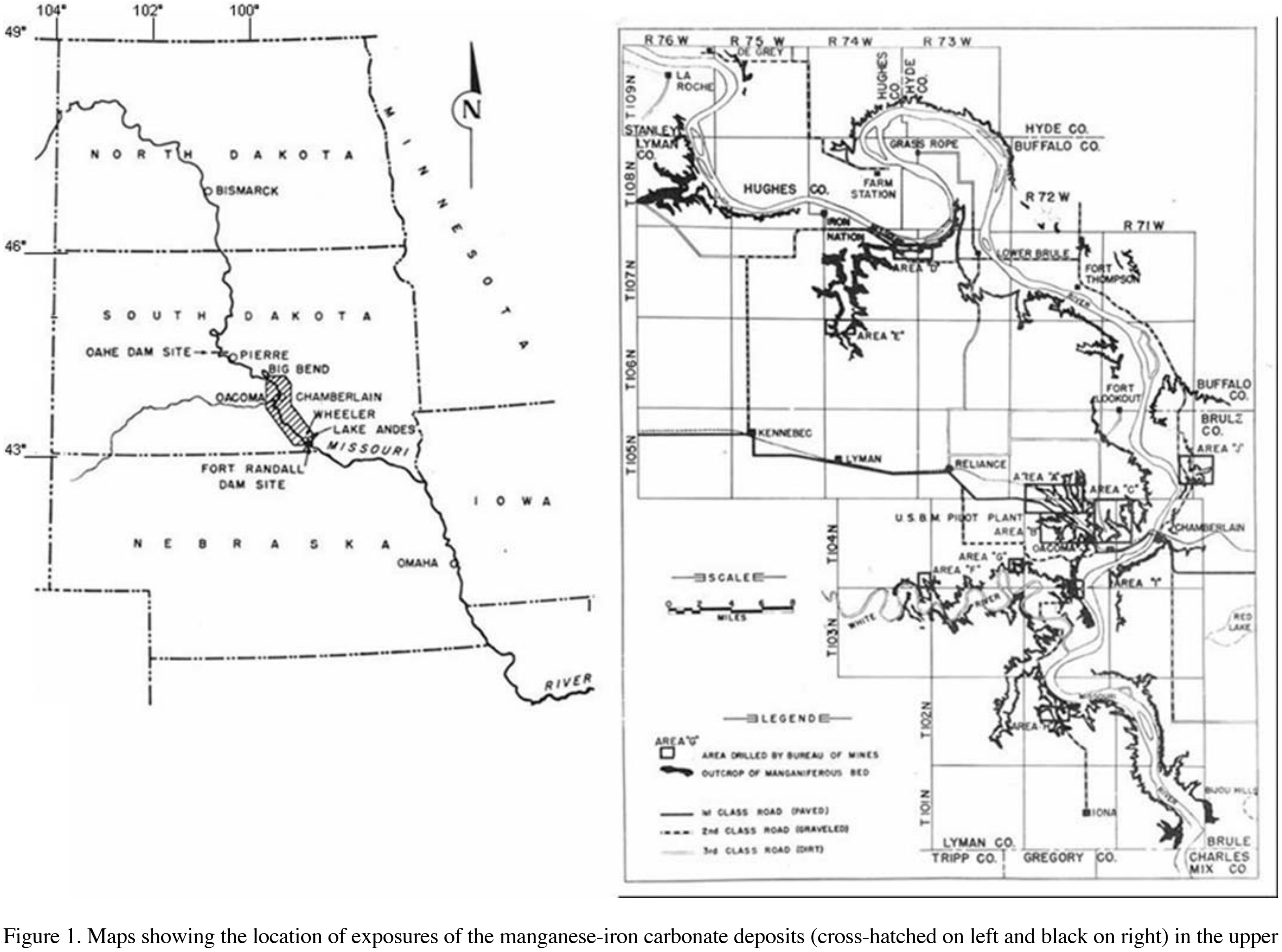


Figure 1. Maps showing the location of exposures of the manganese-iron carbonate deposits (cross-hatched on left and black on right) in the upper DeGrey Formation of the Pierre Shale. Modified slightly from Pesonen et al. (1949). U.S.B.M.—U.S. Bureau of Mines.

Figure 2. Photograph showing typical exposures of the black upper DeGrey Formation of the Pierre Shale along the breaks of the Missouri River, central South Dakota. Outcrop shown is in Buffalo County, ~4 km north of Chamberlain.

Manganese-Iron Carbonate Concretions

Manganese-iron carbonate concretions occur in single, more or less continuous layers commonly 2.5–5 cm thick, and sporadically as nodules 5–7.5 cm thick and 7.5–20 cm in diameter (Fig. 7). They are disk-shaped to egg-shaped and lie with their long dimensions parallel to the bedding. Shale intervals between concretion layers range from 2.5 cm to 1.5 m thick but commonly are 13–36 cm thick.

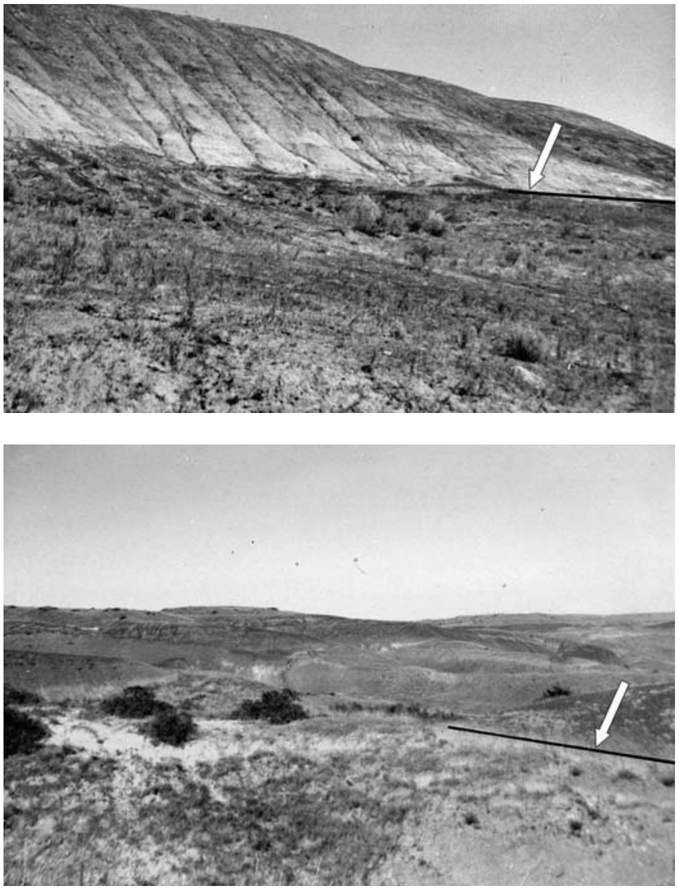


Figure 4. Photo on the top shows the upper contact of the upper DeGrey Formation with the overlying Verendrye Formation in sec. 1, T. 107 N., R. 75 W., Lyman County. The photo on the bottom shows the unconformable basal contact of the upper DeGrey Formation with the underlying Crow Creek Member of the DeGrey Formation in sec. 22, T. 103 N., R. 71 W., Lyman County.

Fossil Occurrence

Marine mollusks are abundant in the manganese-iron carbonate concretions. These fossils, which are the primary focus of this chapter, are preserved as molds, casts, and fragmented shell material. Fossils were collected from 24 localities throughout the area (Fig. 8). Also from this area, paleontologists have discovered bones from six separate taxa of mosasaurs (J.E. Martin, 2004, personal commun.), among other numerous vertebrate taxa. A sample number was assigned to each locality, and specimens were identified by comparing them to those in published reports and to specimens at the University of South Dakota Department of Earth Sciences and Physics. Complete information on localities and faunal lists is given in the Appendix at the end of this chapter.

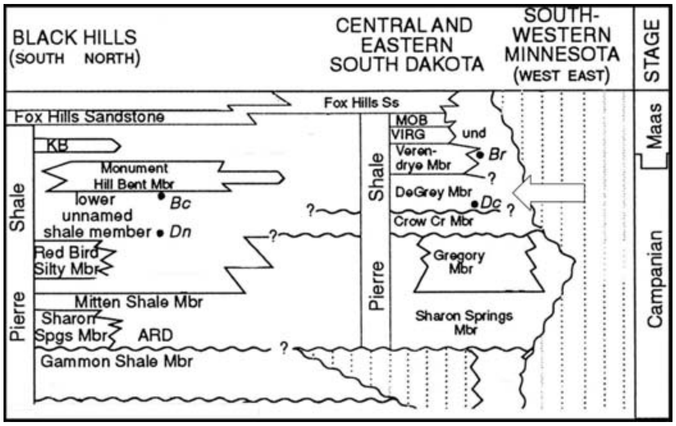


Figure 3. Diagram showing comparison of Cretaceous formations from the Black Hills to central and eastern South Dakota. Dn—*Didymoceras nebrascense;* Dc—*Didymoceras cheyennense;* Bc—*Baculites compressus;* Br—*Baculites reesidei;* VIRG—Virgin Creek Formation of Pierre Shale; MOB—Mobridge Formation of Pierre Shale; Maas—Maastrichtian. Modified from Dyman et al. (1994).

EPIFAUNAL BIVALVES

Inoceramids

Inoceramids, the dominant bivalve group in Cretaceous rocks of the central Western Interior, exhibit broad environmental

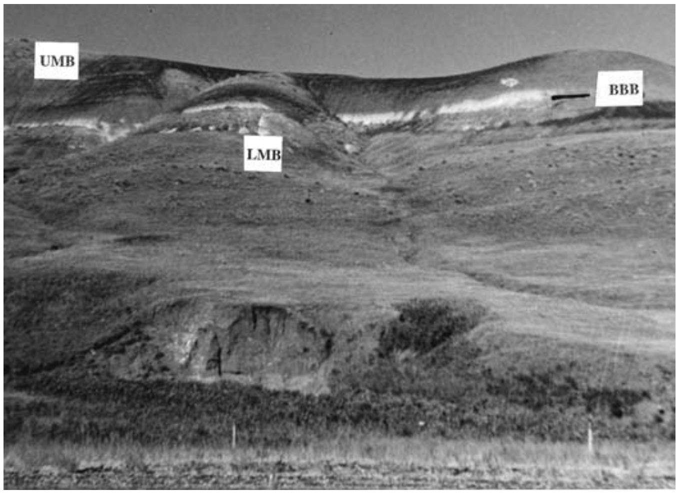


Figure 5. Three bentonite-rich intervals in the upper DeGrey Formation were named by Rothrock (1943). The outcrop shown here is in sec. 25, T. 104 N., R. 72 W., Lyman County. Near the base of the iron-manganese–rich upper part of the DeGrey is a biotitic bentonite called the "lower micaceous bentonite" (LMB). It becomes sporadic south of Lower Brule. Above this bentonite is a bentonitic interval called the "big bentonite bed" (BBB), and above it is the "upper micaceous bentonite" interval (UMB), 1.5–2.0 m below the top of the DeGrey.

tolerance (Kauffman, 1967). This is also the case in the upper DeGrey Formation, with eight species identified as follows: *Endocostea barabini, Inoceramus convexus, I. perplexus, I. pertenuis, I. proximus, I. sagensis, I. tenuilineatus,* and *Platyceramus vanuxemi*. They are from the inoceramid range zones shown in Figure 9. Note also the ammonite range zones.

Inoceramids, collectively, were subdivided by Kauffman (1967) into five morphotypes on the basis of shell shape, size, convexity, thickness, and adaptive features developed on the shell. Two of the morphotypes have been recognized in the upper DeGrey Formation. One of them, the *Inoceramus perplexus* lineage, has shells that are usually <15 cm long, slightly convex, with subequivalve shape (Fig. 10). This form, among the most abundant inoceramids in the central Western Interior and in the upper DeGrey Formation, lay weakly attached by a byssus or was free on the substrate. These bivalves were most abundant in quiet water below wave base in clay and calcareous clay substrates (Kauffman, 1967).

The second morphotype in the upper DeGrey Formation is that of large, thin-shelled, flat inoceramids with a convex early growth stage (Fig. 11). This morphotype, which is rarely articulated in the upper DeGrey Formation, is also well adapted to clay-mud environments (Kauffman, 1967), its broad and flat shell having supported it on a soft to firm mud substrate.

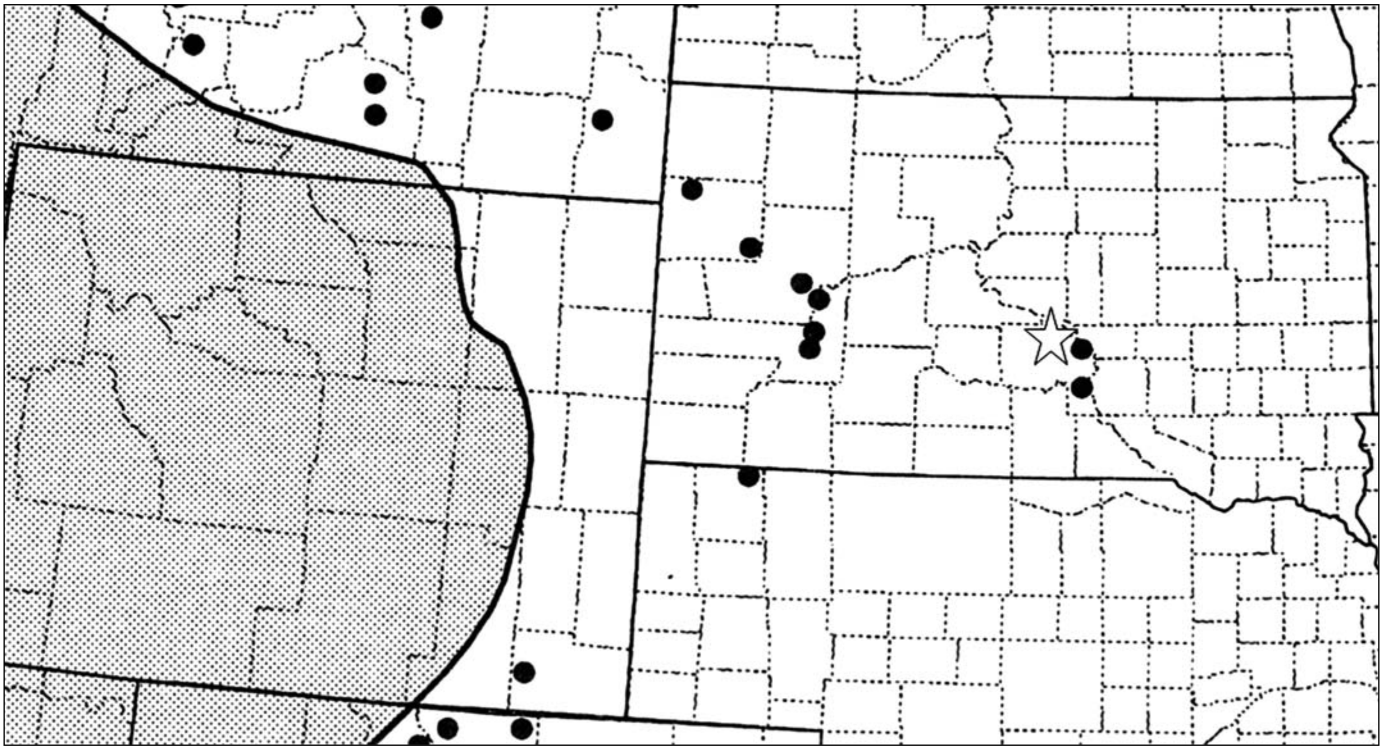


Figure 6. Map showing the western shoreline of the Cretaceous seaway (in Montana, Wyoming, and Colorado) during the time of the *Baculites compressus* Range Zone. The white area to the east of the gray area is the seaway, and the white star marks the study area. Solid black circles indicate fossil localities for this zone. From Cobban et al. (1994).

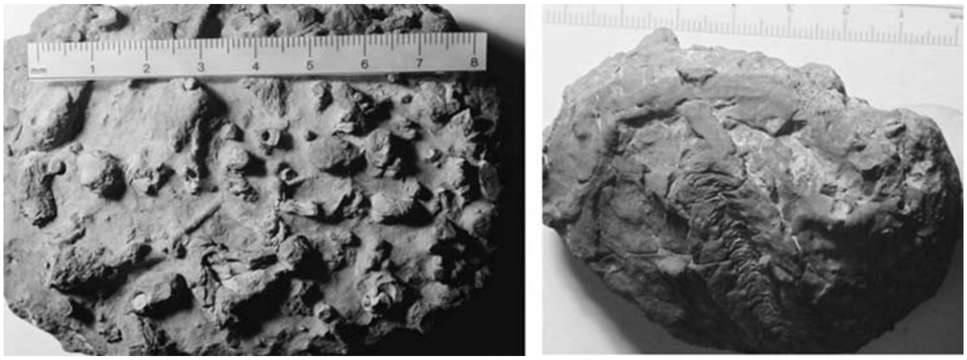


Figure 7. Bioturbated manganese-iron carbonate concretions from the upper DeGrey Formation of the Pierre Shale, central South Dakota. Scale marked in millimeters.

A preponderance of inoceramid shell material in the upper DeGrey Formation is broken into fragments that show, in cross section, the characteristic prismatic layers of the shells. Likely causes for the fragmentation may have been periodic storms that affected the bottom and/or predation by shell-crushing mosasaurs such as *Globidens* (see Martin and Fox, this volume; Martin, this volume, Chapter 13), fish, and perhaps other animals.

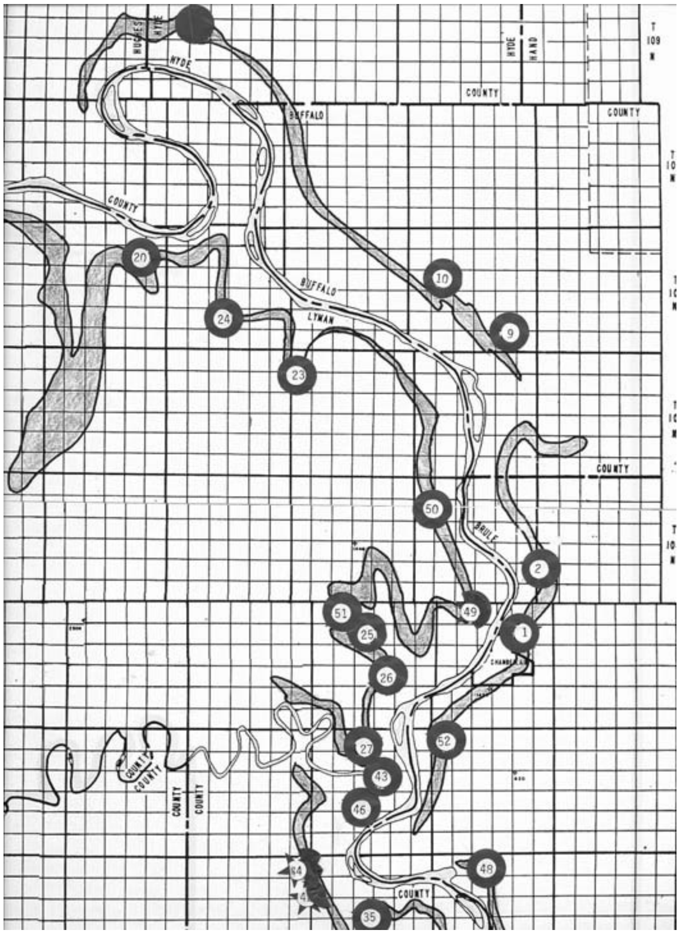


Figure 8. Map showing distribution of fossil localities. The elongated gray areas represent the outcrop pattern of the upper DeGrey Formation. Circles show 21 of the 24 collecting localities. The other three are off the map. The faunal lists for these localities are in the Appendix.

Inoceramid biozone fossils *Endocostea barabini, Inoceramus convexus,* and *Platyceramus? vanuxemi* (Kauffman et al., 1993) are shown in Figure 12, as is *Inoceramus proximus*.

Ostreidae

Oysters, usually articulated, are another important epifaunal component of the upper DeGrey Formation. *Ostrea patina* is a widely distributed solitary form (Fig. 13) that is most abundant in silty shales (Kauffman, 1967). In contrast to *O. patina, Pseudoperna congesta* is a small encrusting form that is usually attached to objects such as inoceramid shells (Fig. 14).

Pterids and Anomids

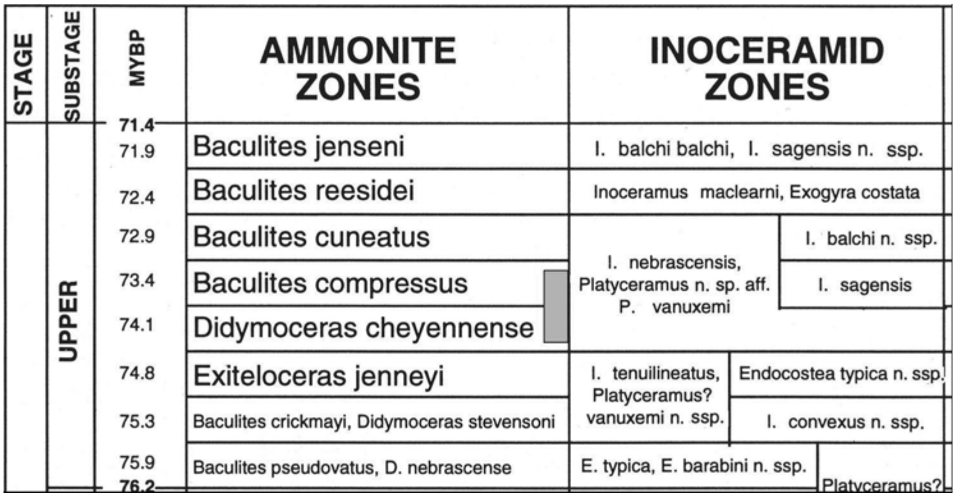
Pteria linguaeformis, P. sublevis, and *P.* sp. B are abundant (Fig. 15) in the upper DeGrey Formation, as are *Anomia subtrigonalis* and *A. obliqua* (Fig. 16). Articulated shells are typical, and most are adults. Modern species of *Pteria* and *Anomia* are widespread in nearshore to middle-shelf environments.

EPIFAUNAL GASTROPODS

Gastropods are usually most abundant and diverse in shallow-shelf and nearshore habitats and less diverse in deeper water (Kauffman, 1967). Gastropods are neither diverse nor abundant in the upper DeGrey Formation. *Anisomyon shumardi, A. borealis, Ampullina paludinaeformis,* and *Acmaea occidentalis,* the only gastropod species identified from the upper DeGrey Formation, are shown in Figure 17.

INFAUNAL BIVALVES

Pholadomya hodgei is the only infaunal bivalve from the upper DeGrey Formation; the taxon is abundant and well preserved as external casts of articulated shells composed of manganese-iron carbonate (Fig. 18). Most of the specimens are at the adult stage of ontogeny.



STAGE	SUBSTAGE	MYBP	AMMONITE ZONES	INOCERAMID ZONES	
		71.4			
	UPPER	71.9	Baculites jenseni	I. balchi balchi, I. sagensis n. ssp.	
		72.4	Baculites reesidei	Inoceramus maclearni, Exogyra costata	
		72.9	Baculites cuneatus	I. nebrascensis, Platyceramus n. sp. aff. P. vanuxemi	I. balchi n. ssp.
		73.4	Baculites compressus		I. sagensis
		74.1	Didymoceras cheyennense		
		74.8	Exiteloceras jenneyi	I. tenuilineatus, Platyceramus? vanuxemi n. ssp.	Endocostea typica n. ssp.
		75.3	Baculites crickmayi, Didymoceras stevensoni		I. convexus n. ssp.
		75.9	Baculites pseudovatus, D. nebrascense	E. typica, E. barabini n. ssp.	Platyceramus?
		76.2			

Figure 9. Late Cretaceous ammonite and inoceramid range zones for the Western Interior Cretaceous. The gray box marks the zonal interval of the upper DeGrey Formation of the Pierre Shale. Modified from Kauffman et al. (1993). MYBP—million years before present.

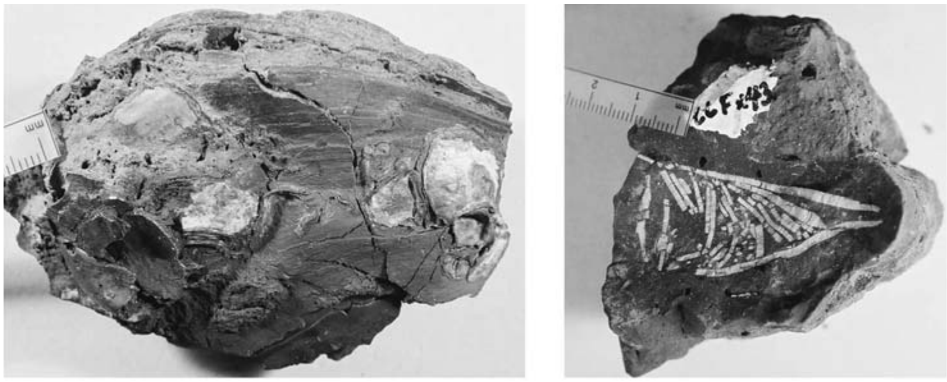


Figure 10. *Inoceramus perplexus* shell morphotype of thin, relatively flat shells that were often broken by bioturbation, predation, and occasional storms.

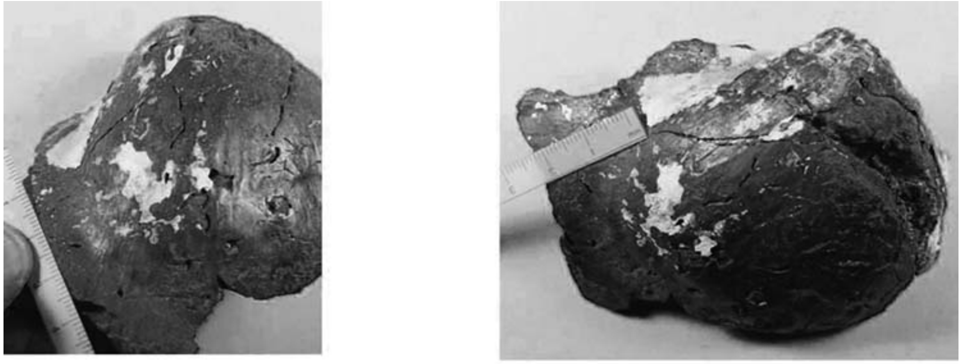


Figure 11. *Inoceramus pertenuis* (top row) and *Inoceramus tenuilineatus* (bottom row, and a biozonal index fossil) exhibit a morphotype that is large, thin shelled, and flat, but with a convex early stage. The beak and umbo of the shell are very convex, but the flat part of the shell is not preserved in these photos.

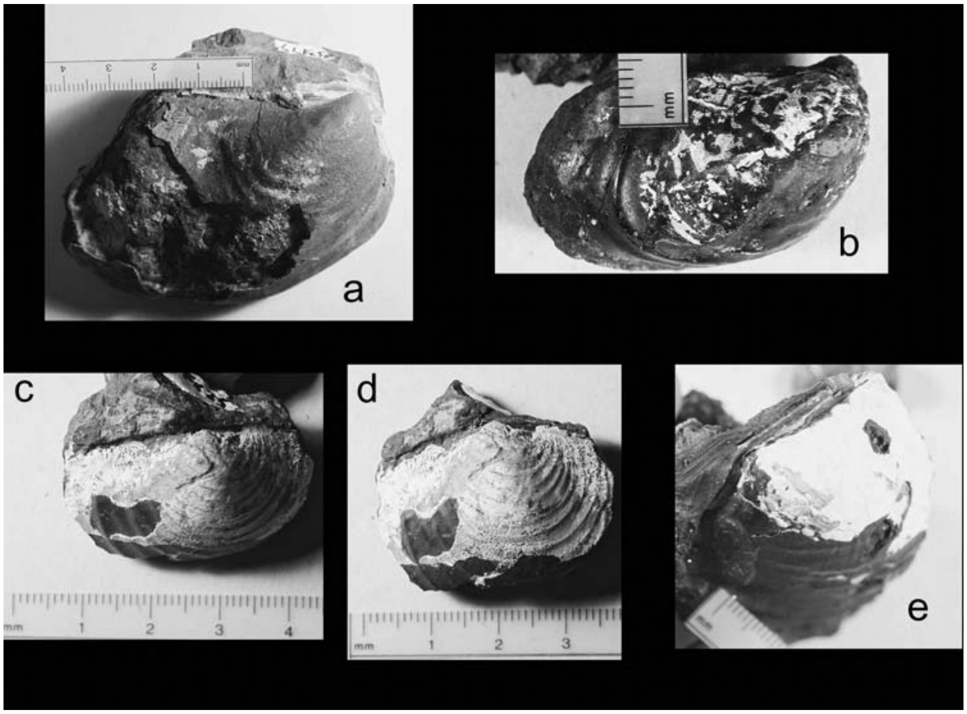


Figure 12. *Endocostea barabini* (a), *Inoceramus convexus* (b), *Platyceramus? vanuxemi* (c, d), and *Inoceramus proximus* (e). Specimens a, b, c, and d are inoceramid biozone fossils (see Fig. 9).

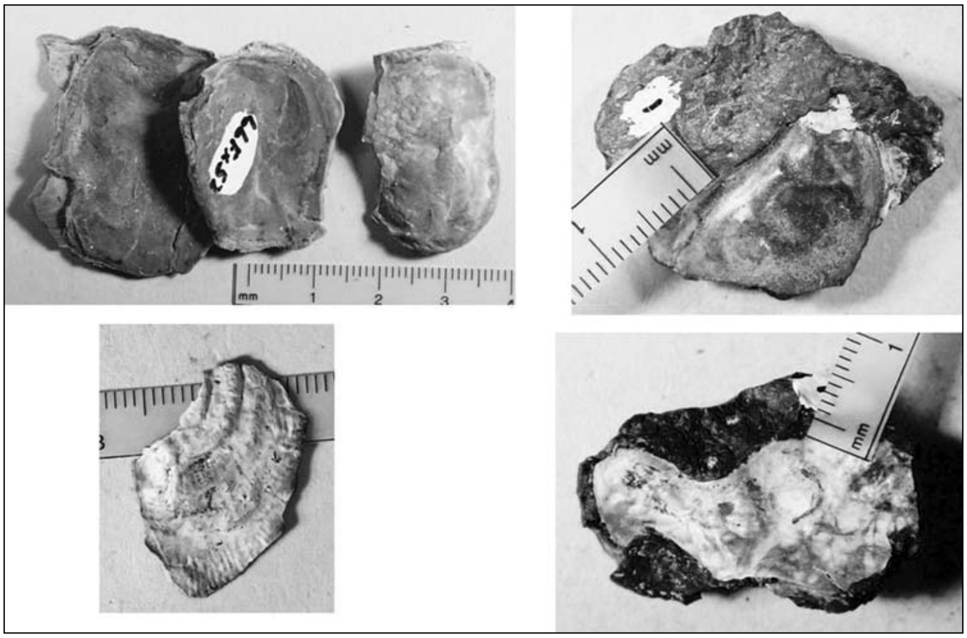


Figure 13. *Ostrea patina,* a species that lived as isolated individuals rather than in closely crowded conditions.

CEPHALOPODS

Cephalopods, although less abundant than bivalves, are important biostratigraphic zonal fossils. *Baculites compressus* and *Didymoceras nebrascense* are the zonal index fossils of the upper DeGrey Formation (Fig. 9). *Jeletzkytes nodosus* and the nautiloid *Eutrephoceras* are present in moderate abundance. Examples are shown in Figure 19.

MANGANESE-IRON CARBONATE CONCRETIONS

During the time of deposition of the upper DeGrey through the middle Verendrye Formations, the late Campanian sea was getting deeper as interpreted from rare earth element analyses (Fig. 20) by Patrick et al. (2004). This interpretation is consistent with the model of the oxic stratified basin margin for manganese-iron carbonate deposition (Fig. 21) proposed by Arthur (1979) and Force and Cannon

Figure 14. *Pseudoperna congesta,* attached to articulated inoceramid shells of the relatively flat, thin-shelled *Inoceramus perplexus* shell morphotype.

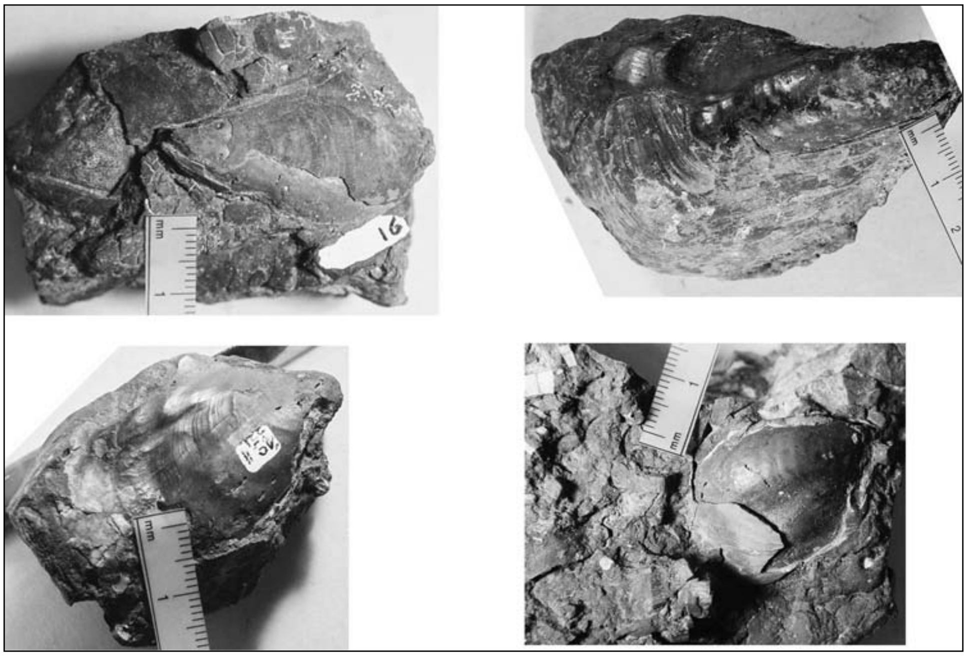


Figure 15. *Pteria sublevis* (top row) and *Pteria* sp. B (bottom row).

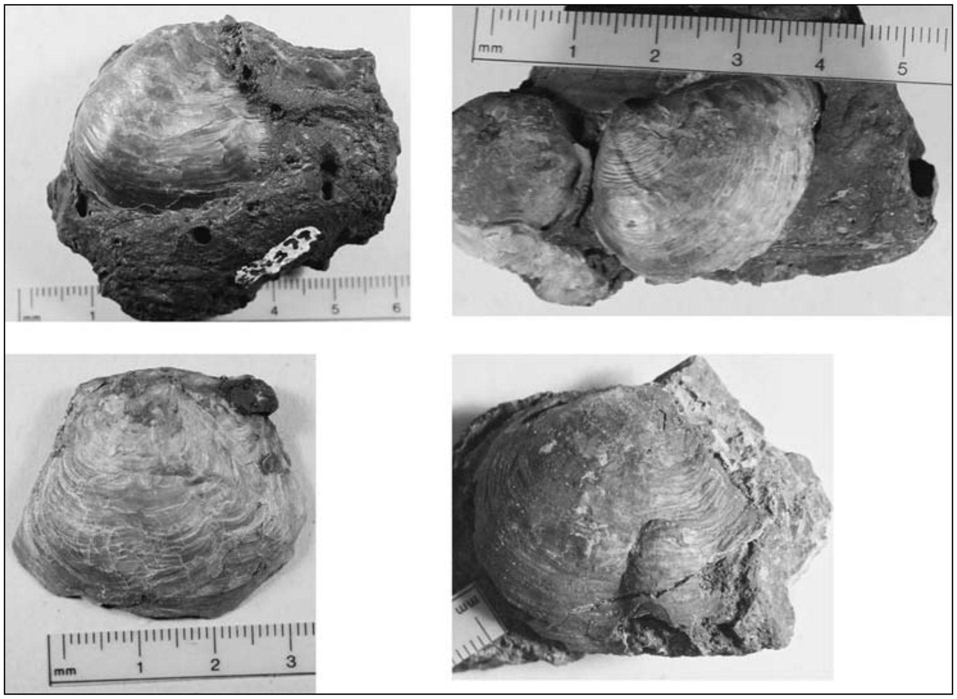


Figure 16. *Anomia subtrigonalis* (top row) and *Anomia obliqua* (bottom row).

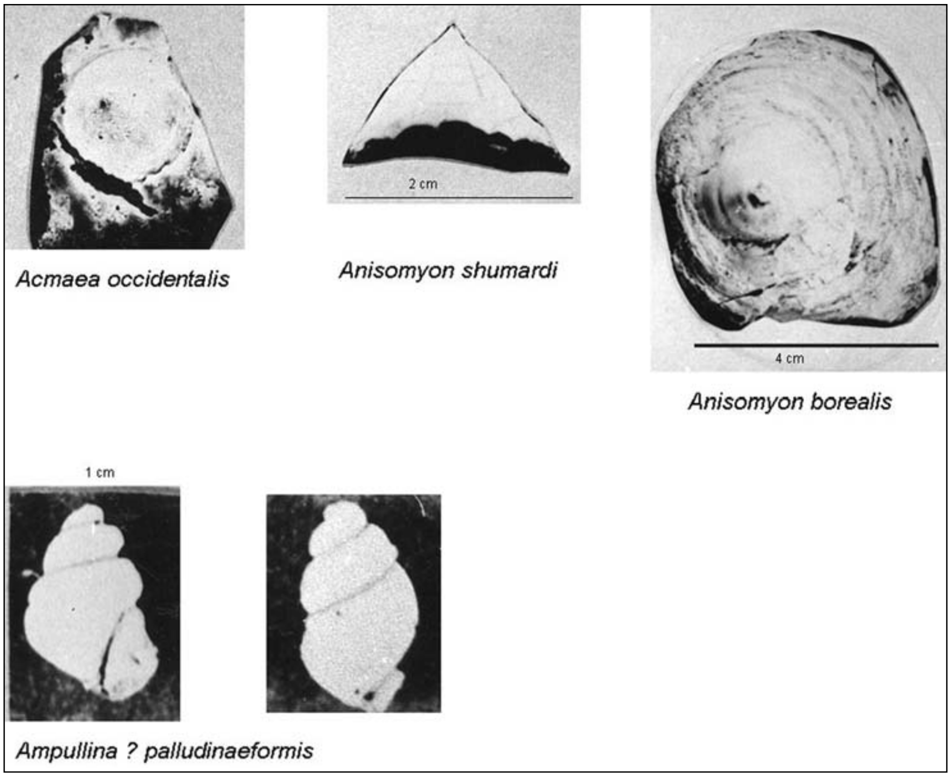


Figure 17. Gastropods *Acmaea occidentalis, Anisomyon shumardi, Anisomyon borealis,* and *Ampullina ?palludinaeformis* from the upper DeGrey Formation (from Fox, 1966).

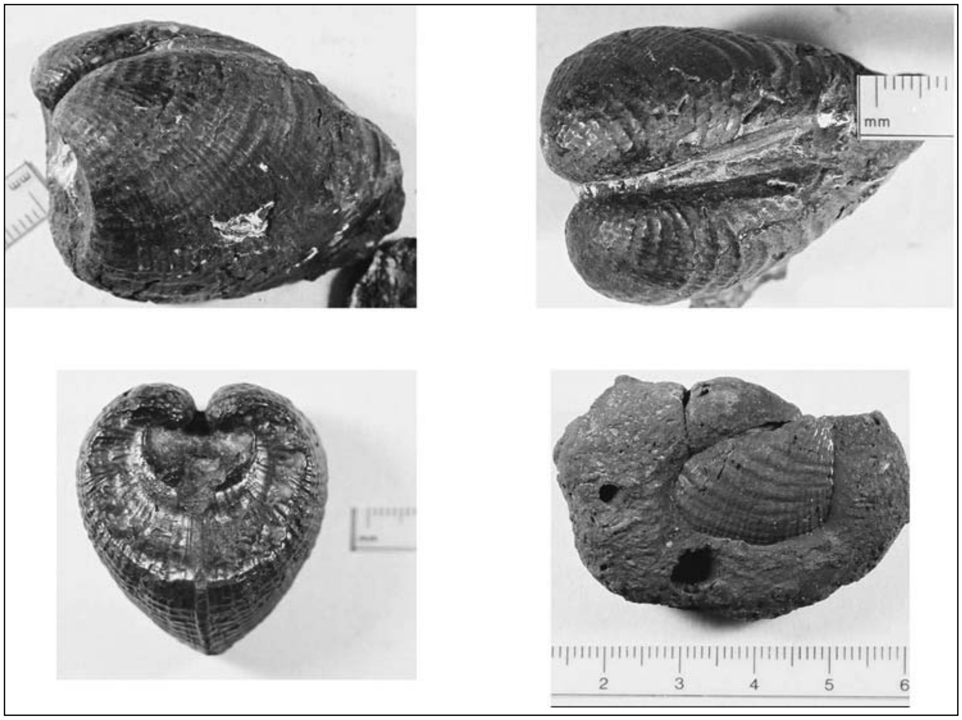


Figure 18. External casts of *Pholadomya hodgei,* preserved as manganese-iron carbonate concretions.

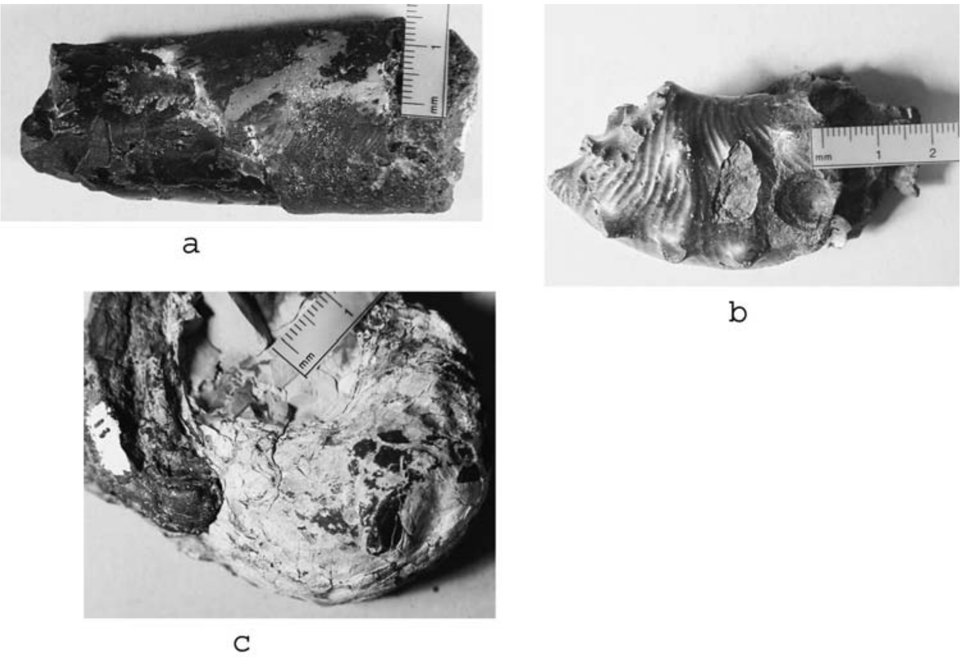


Figure 19. Cephalopods from the upper DeGrey Formation: a, *Baculites* sp.; b, *Jeletzkytes brevis;* c, *Eutrephoceras* sp. Note the impression of a gastropod *(Acmaea)* on *J. brevis* (b) just below the end of the scale. Because this is an external cast of *J. brevis, Acmaea* may have sought shelter inside the empty ammonite shell or was foraging on algae growing on the dead shell. Its external mold was later fossilized by the precipitation of manganese-iron carbonate.

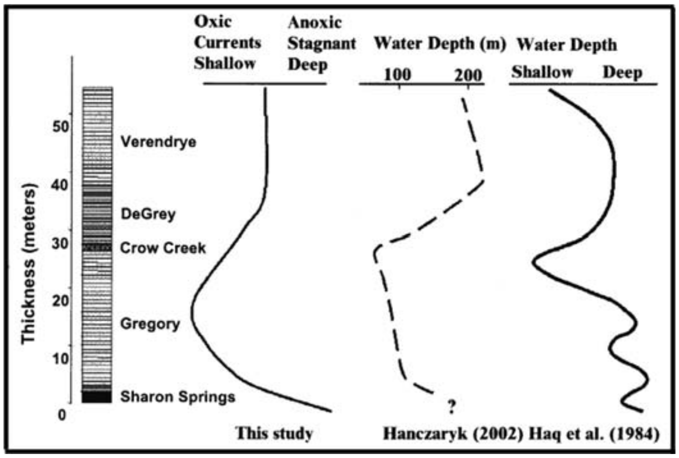


Figure 20. Water-depth curve showing deepening upward of the Pierre seaway from the Crow Creek Member upward through the upper DeGrey Formation (from Patrick et al., 2004). “This study” in the figure refers to the study of Patrick et al. (2004).

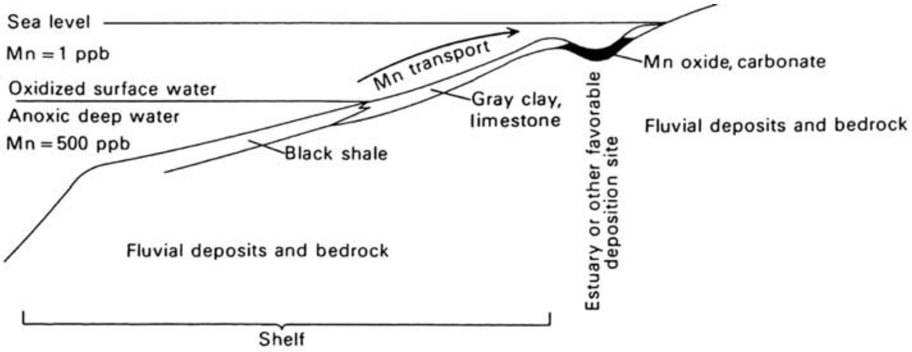


Figure 21. Oxic depositional model for stratified basin-margin manganese (after Force and Cannon, 1988).

(1988). This model infers manganese-iron carbonate precipitation on a relatively shallow oxygenated basin margin, adjacent to deeper anoxic basin waters which provided the iron and manganese that is transported upward and precipitated with carbonates.

SUMMARY AND CONCLUSIONS

Manganese-iron carbonate–bearing strata of the upper Campanian upper DeGrey Formation of the Pierre Shale contain molds, casts, and fragments of marine invertebrates and vertebrates. Mollusks, collected from 24 localities along the Missouri River Valley in central South Dakota, occur as molds and casts of black manganese-iron composition with sporadic preservation of some fragmental shell material.

Bivalves of the upper DeGrey Formation lived on a low-energy substrate where fine-grained bentonite-rich clay was accumulating. Abundant epifauna and extensive bioturbation of the manganese-iron carbonate concretions suggest aerobic conditions. Adjacent deeper anoxic basin waters periodically transported iron and manganese upward into the oxic zone, where it was precipitated with carbonate. The fragmentary nature of most of the bivalve shells, disruption of the sediment, and abundance of possible coprolitic material suggest predation by sediment probing and shell-crushing predators.

These invertebrates, along with rare earth element analyses of mosasaur bones in the upper DeGrey through middle Verendrye Formations by Patrick et al. (2004), indicate a progressively deepening marine sequence (<100 m to ~200 m).

APPENDIX. SAMPLE LOCALITIES AND FAUNA COLLECTED FROM THE UPPER DEGREY FORMATION

Sample number	Location	Distance below top of upper DeGrey Formation (m)	Fauna
1	SE NE sec. 10, T 104 N, R 71 W	3 to 7	*Pteria sublevis*
2a 2	NE SE sec. 25, T 105 N, R 71W	7	*Pteria (Endocostea)* sp. *Inoceramus perplexus* *Inoceramus proximus* *Platyceramus vanuxemi*
2b	NE SE sec. 25, T 105 N, R 71 W	8	*Ostrea patina* *Pseudoperna congesta* *Pteria linguaeformis* *Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia obliqua*
2c	NE SE sec. 25, T 105 N, R 71 W	10 to 14	*Pteria (Endocostea)* sp. *Inoceramus barabini*
9	SE SE sec. 36, T 106 N, R 71 W	3	*Pteria (Endocostea)* sp. *Inoceramus barabini*
10	SE SE sec. 8, T 107 N, R 72 W	2	*Jeletzkytes nodosus* *Baculites* cf. *B. compressus*
17	NE SW sec. 15, T 108 N, R 76 W	3 to 5	*Pseudoperna congesta* *Pteria linguaeformis* *Pteria sublevis* *Anomia obliqua* *Inoceramus perplexus* *Inoceramus sagensis* *Jeletzkytes nodosus*
18	SW SW sec. 23, T 108 N, R 76 W	3 to 5	*Pteria sublevis* *Anomia obliqua* *Anomia subtrigonalis* *Inoceramus pertenuis* *Baculites* cf. *B. compressus*
20	NE NE sec. 11, T 107 N, R 74 W	7	*Pteria linguaeformis* *Pteria sublevis* *Pteria (Endocostea)* sp. *Inoceramus convexus*

(*continued*)

APPENDIX. SAMPLE LOCALITIES AND FAUNA COLLECTED FROM THE UPPER DEGREY FORMATION (*continued*)

Sample number	Location	Distance below top of upper DeGrey Formation (m)	Fauna
23	SE NW sec. 27, T 107 N, R 73 W	3	*Ostrea patina* *Pteria sublevis* *Pteria (Endocostea)* sp. *Inoceramus proximus* *Inoceramus sagensis* *Platyceramus vanuxemi* *Baculites* sp.
25	NE NW sec. 9, T 104 N, R 72 W	0 to 3	*Pholadomya hodgei* *Pseudoperna congesta* *Anomia obliqua* *Anomia subtrigonalis* *Inoceramus barabini*
26	SE SE sec. 22, T 104 N, R 72 W	3 to 7	*Anisomyon borealis* *Pseudoperna congesta* *Pholadomya hodgei* *Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia subtrigonalis* *Anomia obliqua* *Inoceramus barabini* *Inoceramus perplexus* *Inoceramus proximus* *Inoceramus sagensis* *Platyceramus vanuxemi* *Jeletzkytes nodosus*
27	NW NW sec. 3, T 103 N, R 72 W	2	*Anomia subtrigonalis* *Anomia obliqua* *Endocostea barabini*
34	NE NE sec. 2, T 102 N, R 73 W	6 to 10	*Pholadomya hodgei* *Anomia obliqua* *Inoceramus perplexus*
35	NE SW sec. 16, T 102 N, R 72 W	3 to 5	*Pholadomya hodgei* *Pteria linguaeformis* *Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia obliqua* *Inoceramus convexus* *Inoceramus perplexus* *Inoceramus sagensis* *Platyceramus vanuxemi*
35a	NE SW sec. 16, T 102 N, R 72 W	5 to 7	*Pseudoperna congesta* *Anomia subtrigonalis* *Anomia obliqua*
37	NE SE sec. 26, T 99 N, R 70 W	8	*Platyceramus vanuxemi*
42	SE SE sec. 12, R 102 N, R 73 W	2	*Anomia obliqua*

(*continued*)

APPENDIX. SAMPLE LOCALITIES AND FAUNA COLLECTED FROM THE UPPER DEGREY FORMATION (*continued*)

Sample number	Location	Distance below top of upper DeGrey Formation (m)	Fauna
43	NE NE sec. 14, T 103 N, R 72 W	3	*Ostrea patina* *Pseudoperna congesta* *Pholadomya hodgei* *Pteria linguaeformis* *Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia subtrigonalis* *Anomia obliqua* *Endocostea barabini* *Inoceramus convexus* *Inoceramus perplexus* *Inoceramus sagensis* *Inoceramus tenuilineatus*
44	SE SE sec. 18, T 100 N, R 71 W	3 to 5	*Endocostea barabini*
44a	SE SE sec. 18, T 100 N, R 71 W	8	*Pteria sublevis* *Inoceramus proximus*
45	NE NE sec. 11, T 101 N, R 71 W	3 to 7	*Pteria sublevis* *Anomia obliqua*
46	NE NW sec. 21, T 103 N, R 72 W	2 to 3	*Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia subtrigonalis* *Anomia obliqua* *Endocostea barabini* *Inoceramus convexus* *Inoceramus pertenuis* *Baculites* cf. *B. compressus*
48	NW NW sec. 4, T 102 N, R 71 W	2 to 5	*Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia obliqua* *Inoceramus convexus* *Inoceramus tenuilineatus* *Platyceramus vanuxemi* *Jeletzkytes nodosus* *Baculites* cf. *B. compressus*
49	NW NE sec. 4, T 104 N, R 71 W	0 to 3	*Pseudoperna congesta* *Pteria (Endocostea)* sp. *Inoceramus convexus* *Inoceramus perplexus* *Baculites* cf. *B. compressus*
50	SE SW sec. 7, T 105 N, R 71 W	2 to 3	*Pholadomya hodgei* *Pteria sublevis* *Pteria (Endocostea)* sp. *Anomia obliqua* *Endocostea barabini* *Inoceramus convexus*

(*continued*)

APPENDIX. SAMPLE LOCALITIES AND FAUNA COLLECTED FROM THE UPPER DEGREY FORMATION (*continued*)

Sample number	Location	Distance below top of upper DeGrey Formation (m)	Fauna
			Inoceramus perplexus *Inoceramus proximus* *Inoceramus sagensis* *Inoceramus tenuilineatus* *Platyceramus vanuxemi* *Jeletzkytes nodosus* *Baculites* cf. *B. compressus*
51	NW SW sec. 5, T 104 N, R 72 W	0 to 3	*Ostrea patina* *Pholadomya hodgei* *Anomia obliqua* *Inoceramus perplexus* *Inoceramus pertenuis* *Inoceramus proximus* *Baculites* cf. *B. compressus*
52	NW NW sec. 6, T 103 N, R 71 W	2 to 5	*Pseudoperna congesta* *Anomia obliqua* *Inoceramus perplexus*

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Fossil fish from the Pierre Shale Group (Late Cretaceous): Clarifying the biostratigraphic record

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ABSTRACT

The osteichthyan paleofauna of the upper Pierre Shale Group has yielded range extensions for taxa known from its Sharon Springs Formation and the underlying Niobrara Formation, notably with the genera *Protosphyraena* and *Pachyrhizodus.* Links are now more apparent with Campanian and Maastrichtian (Late Cretaceous) paleofaunas from the Atlantic and Gulf Coasts of the United States, as with *Cylindracanthus* and *Enchodus.* Common elements are to be expected, considering the similarities in their geologic ages and environments of deposition.

Keywords: biostratigraphy, Cretaceous, Osteichthyes, Pierre Shale Group, South Dakota.

INTRODUCTION

Epicontinental marine Cretaceous sediments contain notable treasures of vertebrate fossils, famous since they were first discovered. That the American Great Plains paradoxically contribute so significantly to knowledge of ancient marine life has added to the popular fascination with this splendid record. Osteichthyan fossils from the chalk-dominated formations, abundant and generally well preserved, have been the subject of many noteworthy paleontological works and are featured in many museum exhibits (Stewart, 1900; Hay, 1903; Bump, 1926; Witzke, 1981; Schumacher, 1997; Martin et al., 1998; Everhart, 2005).

The clastic upper marine units of the Cretaceous System have yielded many specimens of fossil fish and remain on the frontier of discoveries. As noted in the review papers of Carpenter (1990, 2003), the Sharon Springs Formation of the Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) includes fossils of taxa also known from, or closely related to, those of the underlying Niobrara Formation. Whereas many selachian taxa have widespread distributions, this similarity is also reflected in the osteichthyan species recorded for the Pierre Shale Group in South Dakota (Martin and Bjork, 1987), primarily from the Sharon Springs Formation. The species *Enchodus shumardi* presumably was an exception, the type specimen being subsequently attributed to the Niobrara Formation (Martin et al., 1998). As of the benchmark summary work of Russell (1988), however, no fish species had been identified from the upper formations of the Pierre Shale Group in the Missouri River section, and only fragmentary remains had been reported. It is with great satisfaction that we can now report substantial new information, garnered from recent field work along the Missouri River, which supplements advances previously made in the Atlantic and Gulf Coastal Plains.

In recent decades much attention has been focused on the problems of fish classification at the higher levels (see especially Greenwood et al., 1966; Patterson and Rosen, 1977; Lauder and Liem, 1983; Bjerring, 1985; Maisey, 1991; Jamieson, 1991; Arra-

Parris, D.C., Grandstaff, B.S., and Gallagher, W.B., 2007, Fossil fish from the Pierre Shale Group (Late Cretaceous): Clarifying the biostratigraphic record, *in* Martin, J.E., and Parris, D.C., eds., The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas: Geological Society of America Special Paper 427, p. 99–109, doi: 10.1130/2007.2427(07). For permission to copy, contact editing@geosociety.org.

tia, 1996, 1997; Stiassny et al., 1996). It is not our intention to address such major issues but instead to document new geographic and stratigraphic records and range extensions, which may ultimately assist taxonomists by providing temporal and zoogeographic perspectives on the Cretaceous Western Interior Seaway.

Museum Abbreviations Used in This Study

AMNH: American Museum of Natural History, New York, New York; **KU:** University of Kansas Natural History Museum, Lawrence, Kansas; **NJSM:** New Jersey State Museum, Trenton, New Jersey; **SDSM:** Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota; **USNM:** United States National Museum, Smithsonian Institution, Washington, DC; **YPM:** Yale Peabody Museum, Yale University, New Haven, Connecticut; and **YPM/PU:** Princeton University collections, now at Yale Peabody Museum.

STRATIGRAPHIC CONSIDERATIONS

The traditional lithostratigraphic units of Crandell (1958) are revised (Fig. 1) in this volume, and field practice of the last few years has resulted in recognition of additional key beds and sequences, refining the lithostratigraphy to some degree (Martin et al., this volume). These new units will be cited herein as appropriate.

SYSTEMATIC PALEONTOLOGY

Class Osteichthyes
    Order Acipenseriformes?
        Family *Incertae sedis*
            Genus *Cylindracanthus* Leidy 1856a

Species noted herein. *Cylindracanthus ornatus* Leidy 1856a (type species), *C. rectus* Agassiz 1843, *C. acus* Cope 1870.

Specimen. SDSM 30638, a rostral spine, previously referred (Parris et al., 2001), Verendrye Formation of Pierre Shale Group, Hyde County, South Dakota. Precise zone is 2 m above a persistent iron-stained bed. Derived from SDSM locality V9544.

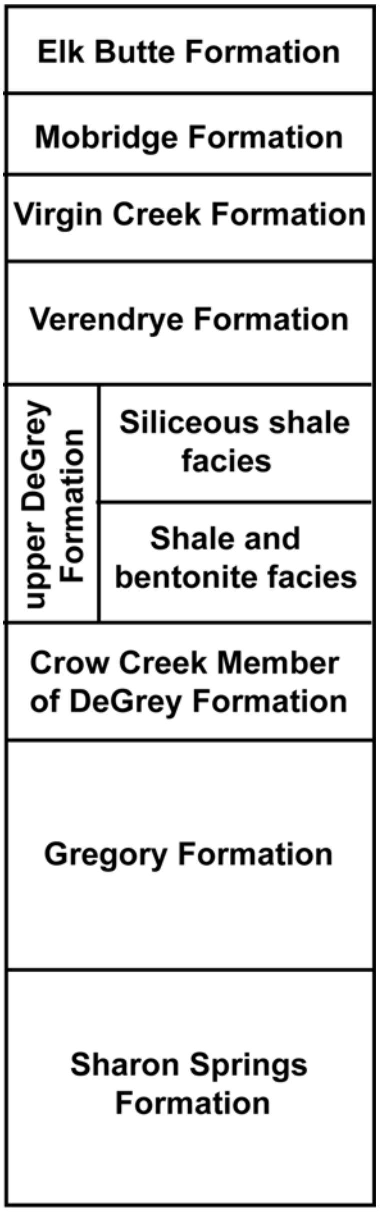

Figure 1. Stratigraphic column of Pierre Shale Group, modified from Crandell (1958), see Martin et al. (this volume).

Discussion. The discovery of *Cylindracanthus* in the Pierre Shale Group was previously noted and discussed in detail (Parris et al., 2001), and only a few additional remarks are needed here. We favor comparison of the genus to acipenseriform fishes over the traditional reference to billfishes (Table 1). The potential affinities as an acipenseriform genus have not been further commented upon by other authors, to our knowledge. Whether or not that hypothesis is correct, it seems sufficient to remove *Cylindracanthus* from the ranks of form taxa and now to place it taxonomically within regular phylogenetic lists of osteichthyans.

In addition, it should now be noted that the genus is of substantial value as a biostratigraphic indicator, because the changes in the degree to which dental vestiges are preserved exhibit a consistent trend from Cretaceous to Eocene, so far as we can observe (Parris et al., 2001). The proposed lineage would place *C. ornatus* as ancestral to *C. rectus,* with gradual reduction in the remnant dentition and tooth bases. A separate lineage would include *C. acus*.

Few specimens discovered during the last two decades of collecting in the Pierre Shale Group have clarified the taxonomic record as much as this one. In addition, it strongly demonstrates the value of comparisons between the paleofaunas of the epicontinental Western Interior Seaway deposits and those of the Atlantic and Gulf Coasts. *Cylindracanthus* had never before been recorded from the Western Interior.

TABLE 1. COMPARATIVE FEATURES OF MAJOR TAXONOMIC GROUPS IN COMPARISON WITH *CYLINDRACANTHUS*

	Cylindracanthus	Acipenseriformes	Billfishes
First appearance	Cretaceous	Cretaceous	Cenozoic
Tissue type	?Mainly cartilage	Cartilaginous	Bony
Rostrum anterior to mouth?	Yes	Yes	Yes
Tooth shape	Slender recurved cones	Slender recurved cones	Small, absent in adults
Tooth distribution	Paired single rows	Single rows	Shagreen of teeth
Rostrum shape	Cylindrical, bony	Cylindrical "vomer" + dermal elements	Triangular or half-cylinder premaxilla
Rostrum symmetry	Bilateral	Bilateral	Bilateral

Order Pachycormiformes
Family Pachycormidae
Genus *Protosphyraena* Leidy 1856d

Species noted herein. (Also see Stewart, 1988.) *Protosphyraena nitida* Cope 1872b (type species), *P. gladius* Cope 1873, *P. perniciosa* Cope 1874, *P. tenuis* Loomis 1900.

Discussion. The last major review of this genus by Stewart (1988) did much to emphasize the stratigraphic potential of the genus, while also noting the imperfect knowledge of its anatomy and the dearth of records from all but a few geographic areas. Many more specimens have since been collected, and much has been learned (Carpenter, 2003) so that further review is desirable. We confine our comments here to information based on our investigations along the Missouri River section of the Pierre Shale Group, and some related matters. This effectively confines the scope of our work to the species *Protosphyraena gladius*.

Protosphyraena gladius Cope 1873

Specimen. SDSM 66288, major portion of pectoral fin from a concretionary layer in the DeGrey Formation of the Pierre Shale Group, Hyde County, South Dakota. Derived from SDSM locality V9324.

Description. Although recovered in numerous pieces, SDSM 66288 exhibits all known anatomical features of the species *P. gladius,* without the necessity of sectioning it. The distinctive wedge of ossification, with its texture perpendicular to the edge, is readily observed (Fig. 2A). This feature appears as a change in the direction of bone texture, as noted by Stewart (1988), the grain being parallel to the rays of the fin farther caudad. The leading edge of the fin is coarsely serrate (Fig. 2B). Within each serration, the edge thins where it arches caudally, and thickens slightly to form a supporting rib where it extends cranially. The base of the fin is preserved in SDSM 66288, and the medial and lateral sides are widely separated there (Fig. 2C). The fin rays at the fin base are expanded in the mediolateral direction, but they become essentially round in cross section only ~20 cm distal to the base of the fin. There the rays are still separated from each other by an intervening poorly organized, wedge-shaped tissue core. The rays show multiple laminae (possibly growth lines) in cross section. As the fin cross section narrows distally the poorly organized tissue core area continues to be present. In more distal parts of the fin the width of this core is more uniform between the cranial and caudal edges of the fin (Fig. 2D); only in the proximal 30 cm is the tissue core markedly wider on the caudal side of the fin. The rays at the tip of the fin are relatively more fine, each being narrower in the anterior-posterior dimension than are the rays in the proximal part of the fin. The estimated restored length of the fin would exceed 50 cm.

Discussion. As noted previously, *Protosphyraena gladius* differs from *P. nitida, P. perniciosa,* and *P. tenuis* in its pectoral fin structure, having an ossification with a perpendicular textural fabric that forms the cranial (leading) edge of the fin. According to Stewart (1988), *P. gladius* is readily recognized even from fragmentary fin specimens because of its distinctive anatomy, which is visible in cross sections of the fin. The question of whether *P. gladius* may differ enough from other species of *Protosphyraena* to belong to another genus has not yet been fully resolved. Its distribution can now be given as extending from the late Coniacian to the late Campanian of North America, where it is found in the Eastern Seaboard, Gulf Coast, and Western Interior. Its geologic range is longer and lasts later than the range of any other species of the genus.

The major significance of SDSM 66288 is geographic and stratigraphic, as it falls within a major gap in the range of this species. Specimens under detailed study elsewhere include the first to be reported from the Eastern Seaboard (NJSM 14668 and NJSM 15140), from upper Campanian–lower Maastrichtian sediments. These eastern *P. gladius* specimens lived far later than any previously reported. This specimen (SDSM 66288), the first to be reported from the Campanian of South Dakota, comes from a zone well above any *P. gladius* previously reported from the Pierre Shale Group. It is presumed to be later in age than any *P. gladius* previously reported from the Demopolis Formation (Stewart, 1988) and thus provides a plausible link to the specimens still later in age from the Eastern Seaboard.

Despite the great stratigraphic range now demonstrable for *Protosphyraena gladius,* its anatomy as currently known remains consistent in all the referred material. It differs from other species of the genus only by the ossified wedge of tissue forming the core of the pectoral fin. From the standpoint of functional anatomy,

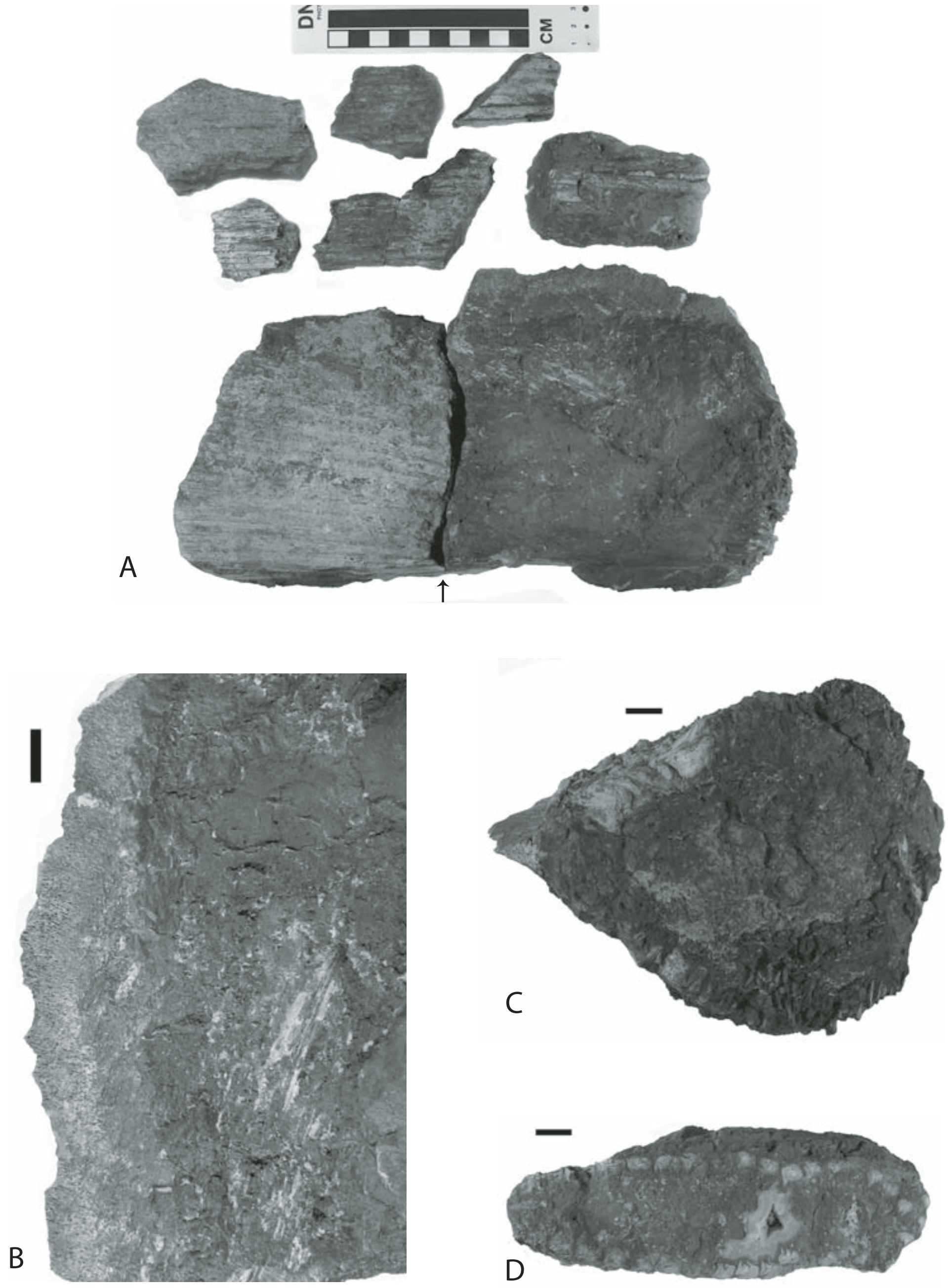

Figure 2. *Protosphyraena gladius,* fin, SDSM 66288. (A) Several of the larger fragments of SDSM 66288. Arrow indicates location of cross section in D. (B) Close-up view of the anterior edge ossification. (C) Proximal view of the fin base. (D) View of the fin in cross section at the arrow in A. Scale bars in B, C, and D are 1 cm.

this feature probably reflects an adaptation to larger size, requiring greater fin strength. In our opinion, this alone would not justify separate generic identification.

Order Ichthyodectiformes
Family Ichthyodectidae
Genus *Xiphactinus* Leidy 1870

Species noted herein. *Xiphactinus audax* Leidy 1870 (type species), *X. vetus* Leidy 1856b.

Specimen. SDSM 75551. Major part of skeleton, with complete articulated caudal fin (Fig. 3). Middle part of Sharon Springs Formation of Pierre Shale Group, Lyman County, South Dakota. Derived from SDSM locality V2002-30.

Discussion. Best known from the Niobrara Formation (Bump, 1926; Bardack, 1965; Stewart, 1990; Martin et al., 1998), this species has long been known to occur in the Sharon Springs Formation of the Pierre Shale Group as well, the youngest zone from which it is currently known (Martin et al., 1996; Schwimmer et al.,

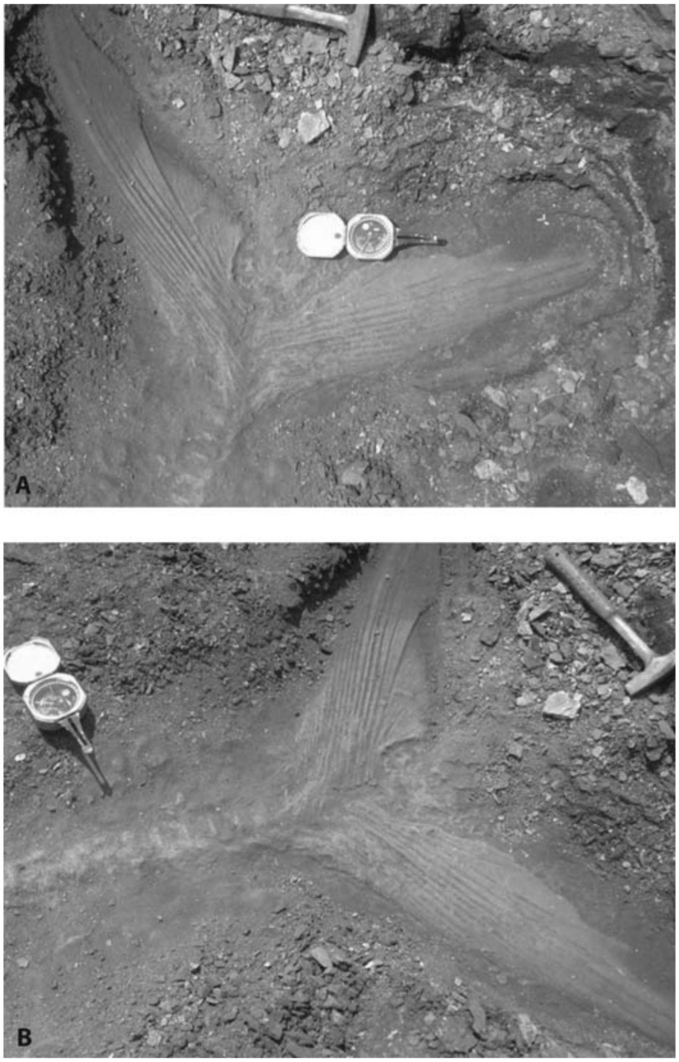

Figure 3. *Xiphactinus audax* (SDSM 75551) tail in the outcrop. Note the deeply excavated caudal margin of the tail fin skeleton, and large extent of tail fin rays relative to the diameter of the vertebrae.

1997; Carpenter, 2003). The specimen referred herein, SDSM 75551, is from the zone proposed as the Boyer Bay Member (Martin et al., this volume). It is one of the highest (thus latest) zones from which this taxon has been reported and correlates with the *Baculites mclearni* Biozone. The caudal portion of the skeleton and the caudal fin are remarkably well preserved. This is perhaps the best specimen yet known for this part of the body (Fig. 3).

The substantial number of specimens of this species and the precise determination of the Pierre Shale zones from which it is known enable a clearer perspective on its biostratigraphy relative to *Xiphactinus vetus*. It is thus appropriate to further record and clarify records of the latter species. Despite the lack of Western Interior records of *X. vetus,* it may well be found to occur there when more Maastrichtian specimens are recovered.

Xiphactinus vetus Leidy 1856b

Specimen. YPM/PU 21822, maxillary fragment from the dredge spoil piles of the Chesapeake and Delaware Canal, New Castle County, Delaware.

Description. YPM/PU 21822 is one of the best specimens of *X. vetus,* a maxillary fragment with 13 alveoli and 8 partial teeth (Fig. 4). All teeth are broken but reveal enough characteristics, notably lateral compression and facets, to make the identification certain. Found by Richard Heintz in 1976, it has matrix remnants attributable to the Marshalltown Formation and thus is correlative with the Ellisdale Local Fauna, where other specimens of this species have been found.

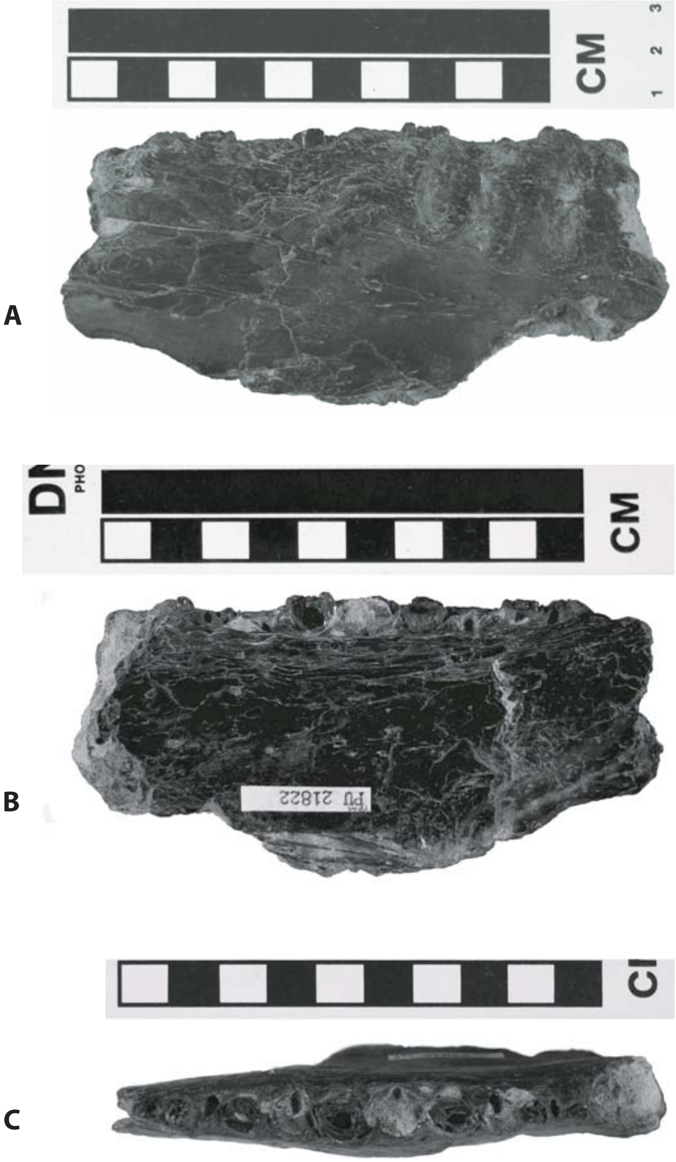

Figure 4. *Xiphactinus vetus* maxilla, YPM/PU 21822, from the Chesapeake and Delaware Canal in Delaware. (A) Labial view. (B) Lingual view. (C) Occlusal view.

Discussion. As noted by Schwimmer et al. (1997), *Xiphactinus vetus* has consistently been found in zones younger than those that yield *X. audax*. The latter species is the only one of the genus known from the Western Interior, whereas *X. vetus* is the only species known from the Atlantic Coastal Plain. It should be noted that both species have been reported from the Gulf Coastal Plain (Schwimmer et al., 1997). There is a significant interval between the uppermost zone that has yielded *X. audax* and the lowermost that has yielded *X. vetus,* approximating the time duration of 10 Western Interior ammonite zones (*B. mclearni* to *B. cuneatus*). Our extensive prospecting of Missouri River and Atlantic Coastal Plain localities has not yielded any specimens that contradict this observation. However, it may be anticipated that future collecting of specimens throughout North America will narrow this gap in the record. Whether *Xiphactinus audax–X. vetus* will prove to be a continuous lineage remains to be determined.

We note the following additional and corrected information for nomenclatural and stratigraphic clarification. The locality of the type material of *Xiphactinus vetus* should be given as Burlington County, New Jersey. Specimens from the Ellisdale Site (Campanian) are from Upper Freehold Township, Monmouth County, New Jersey. Specimens attributed to Big Brook are from Marlboro Township (and possibly Colts Neck Township), Monmouth County, New Jersey. Specimens from the Chesapeake and Delaware Canal are from New Castle County, Delaware.

Order Elopiformes
Family Crossognathidae
Genus *Apsopelix* Cope 1871
Apsopelix sp. cf. *A. anglicus* Dixon 1850

Specimen. SDSM 77482, a three-dimensional body mold, representing about the cranial one-third of an individual from the concretionary portion of the upper DeGrey Formation of the Pierre Shale Group, North Bend area, Hughes County, South Dakota. Derived from SDSM locality V9312.

Description. SDSM 77482 exhibits the following characteristics that are consistent with *Apsopelix* (Teller-Marshall and Bardack, 1978). The body is fusiform and has a head in which the length and depth are approximately equal, so far as can be observed, since the rostralmost portion is broken. In right lateral view (Fig. 5) the conspicuous circumorbital plate measures ~20 mm, whereas the total length of the head is ~60 mm. The sclerotic ring is completely co-ossified. The lower jaw articulation is beneath the rostral third of the orbit. The preopercular is expanded ventrally and has radiating ridges on the expansion surface. There appear to be 12 rows of cycloid scales on the right side of the body. In addition to these observations, which match the description by Teller-Marshall and Bardack (1978), the three-dimensional preservation of a major part of the body in a concretion seems to be characteristic of the species *Apsopelix anglicus*. This preservation further confirms the zone, which is surely an iron manganese concretion zone in the upper DeGrey Formation of the Pierre Shale Group.

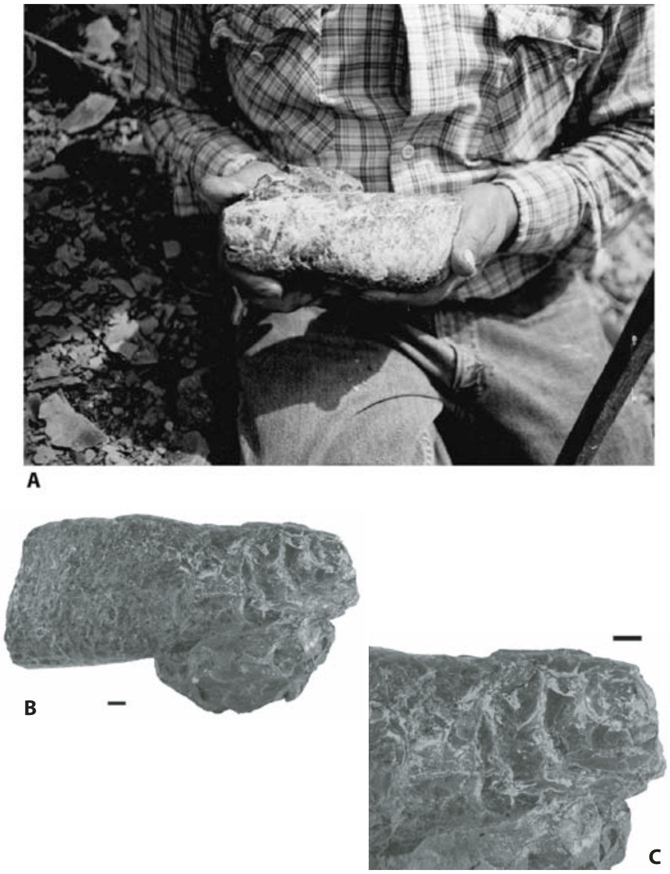

Figure 5. *Apsopelix* specimen, SDSM 77482. (A) Lee Azure holding the specimen in the field just after he discovered it. (B) Prepared specimen in lateral view, cranial to the right. (C) Close-up view of the head, showing the large orbit and sclerotic bones. Scale bars in B and C are 1 cm.

Detailed study of this specimen has not yet been attempted, but the exposed surface parts are so well preserved that further preparation and possible instrumental analysis of the interior would be highly desirable, and almost certainly most informative.

Discussion. *Apsopelix* has been reported previously from the Pierre Shale Group (Carpenter, 2003), but presumably only from the Sharon Springs Formation, which has a particularly good record of fossil fishes. However, an additional perplexing record is supplied by a Smithsonian specimen (USNM 16725) cited as being from Chamberlain, South Dakota (Teller-Marshall and Bardack, 1978), and said to be of an uncertain zone and location. Although rock units from the Niobrara Formation up through the Verendrye Formation of the Pierre Shale Group are present in the vicinity of Chamberlain, the DeGrey Formation is a prominent unit within the city itself. Yet another specimen, SDSM 77474, is on exhibit at the Museum of Geology, South Dakota School of Mines and Technology. Its precise locality and zone also are not known. This specimen is said to have been collected at Oacoma (Lyman County, South Dakota, SDSM V5370) and donated by Samuel Bice. It too appears to confirm the presence of *Apsopelix* in the DeGrey Formation, as the adherent matrix appears to be from an iron manganese concretion zone of the upper DeGrey Formation.

Family Pachyrhizodontidae
Genus *Pachyrhizodus* Agassiz 1850
Pachyrhizodus sp. indet.

Specimen. SDSM 77481, part of dentary with two teeth (Fig. 6) and seven other bone fragments, including a part of the caudal vertebral complex. From the DeGrey Formation of the Pierre Shale Group, West Bend area, Hughes County, South Dakota. Derived from SDSM locality V2001–14.

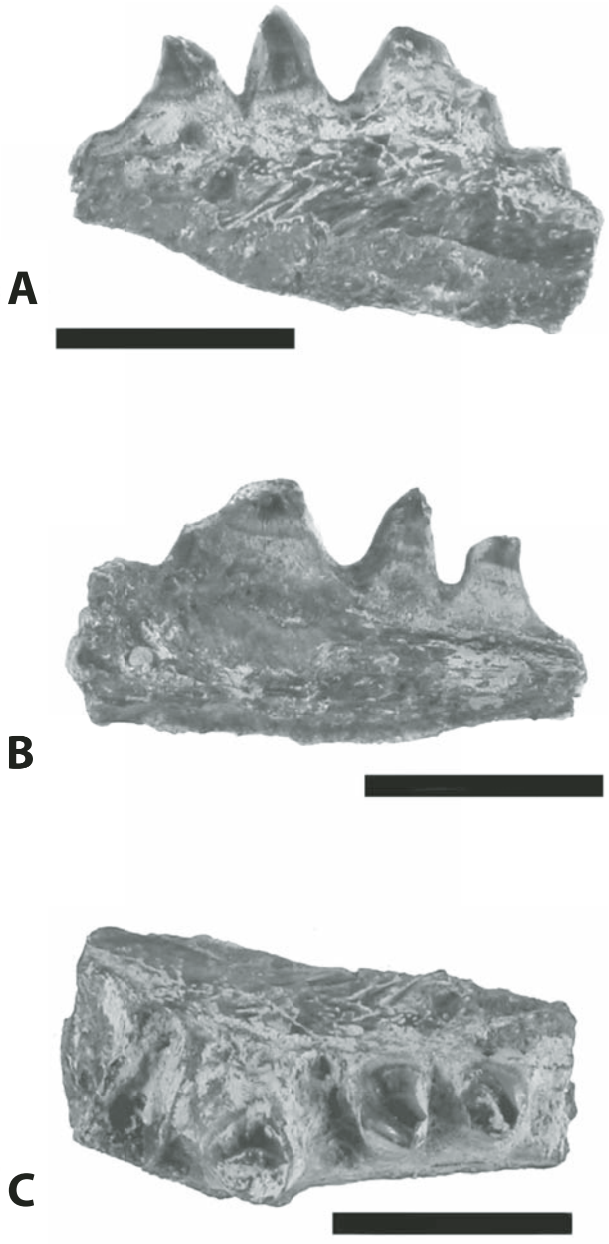

Figure 6. *Pachyrhizodus* sp., SDSM 77481. (A) Lingual view. (B) Labial view. (C) Occlusal view. Scale bars are 1 cm.

Discussion. This fragmentary specimen gives little anatomical information but is readily referred to *Pachyrhizodus* because of the distinctive robust teeth and their pleurodont arrangement on the dentary fragment, as described by Loomis (1900). The presence of the genus in the upper DeGrey Formation of the Pierre Shale Group represents a range extension well into the Campanian.

Order Aulopiformes
Family Enchodontidae
Genus *Enchodus* Agassiz 1835 (included within Agassiz 1843)

Species noted herein. *Enchodus petrosus* Cope 1874, *E. gladiolus* Cope 1872a, *E. shumardi* Leidy 1856c, *E. dirus* Leidy 1857, *E. ferox* Leidy 1855.

Discussion. Abundantly represented in marine faunas of the Late Cretaceous, *Enchodus* has long been a challenge to taxonomists in view of the seemingly overwhelming task of reviewing all significant specimens of a common cosmopolitan genus. Nonetheless, the past few decades have brought some significant efforts toward understanding its systematics. The review of Goody (1976) was notable for its detailed anatomical descriptions. Goody (1976) relied by necessity on whatever geographic and stratigraphic data had been included with historic specimens collected over a long time period, during which geographic and stratigraphic concepts changed markedly. Many species had been attributed to the Late Cretaceous of the Western Interior as a result. Corrections to historical misinterpretations of geographic and stratigraphic information followed (Grandstaff and Parris, 1990; Martin et al., 1998). The anatomical analysis of Goody (1976) reduced the number of invalid species (junior synonyms). Further substantial clarifications were added by Martin et al. (1998).

Cladistic-numerical analyses of Fielitz (1996, 1997, 1999), Fishman et al. (1995), and Schein (2004) have added further insights. The reviews of Chalifa (1989, 1996) confronted the plethora of species (while naming yet others) and suggested a simplified approach: the assumption that specimens from a single zone and locality were likely to belong to one species population. However, the presence of two distinct anatomical trends in the genus was also established, which would suggest that sympatric species could be a possibility.

We propose that the best approach to further analysis is to follow the population study method suggested by Chalifa (1996) for assemblages of recently collected specimens that have precise data. A summary of significant characteristics (Table 2) shows that the five generally recognized North American species, disregarding stratigraphic considerations, can be divided into two distinct species groups: the *E. petrosus-ferox* and the *E. gladiolus-dirus* groupings. With the added clarification that *E. shumardi* is confined to the Niobrara Formation, we presume it to represent the basal underived ancestral species. Whereas some specimens from the Niobrara Formation show characteristics of *E. petrosus* and *E. gladiolus,* it seems likely that speciation had not proceeded

TABLE 2. *ENCHODUS* TOOTH AND SKULL MORPHOLOGY

Character	*E. petrosus*	*E. ferox*	*E. gladiolus*	*E. shumardi*	*E. dirus*
Maxillary teeth present?	No		Yes		
Tooth striations	Smooth outer, coarsely striated inner	No inner or outer striations	Finely striated inner and outer	Prob. striated	Striated
Postapical barb present?	No	No inner or outer striations	Yes (partial pt. cutting edge)	Yes (true barb)	Yes (partial pt. cutting edge)
Tooth serrations	Smooth outer, coarsely striated inner	Present (very faint)	Smooth	Prob. smooth	
Palatine tooth symmetrical?	Asymmetrical	Asymmetrical; very straight	Symmetrical	Symmetrical	Symmetrical
Number/position of palatine tooth edges	Anterior and lateral	Two full-length (anterior and posterior)	Anterior only, full length	One, anterior	One, anterior
General tooth form	Palatine: long and straight Premax: small cones	Slightly concave posterior and med.; relatively stout base	Long and slender, slightly sigmoidal	Straight and needle-like	Sigmoidal, dentary teeth, curved but not sigmoidal
Position of maxillary groove	Extends to just behind tooth base	Extends above or anterior to tooth base	Extends to well behind tooth base	Ends just behind tooth base	Ends approximately halfway along palatine bone
Depth/length of palatine bone	Depth ~½ length	Bone depth ⅓ to ½ length	Depth ≤ ¼ length	Depth/length = 0.26–0.32	Depth/length = 0.40–0.55
Depth palatine bone/length of tooth	Depth just over ½ tooth length	Bone depth ~½ tooth length	Depth about ⅓ to ½ tooth length	Depth/tooth = 0.40–0.51	Depth/tooth = 0.50–0.61
Length palatine tooth/length palatine bone	Tooth length >¾ length of palatine bone	Tooth 80–100% of bone length	Tooth length just over ½ palatine	Tooth/bone length = 0.62–0.64	Tooth length/bone length = 0.73–0.95
Length mandible/coronoid depth	Length < 4 × depth		Length < 4 × depth		Length > 4 × depth
Dermal skull ornamentation		?Radiating ridges	Mainly smooth: premaxilla ornamented by ridges, no enamel beading	Thin with tubercular ornamentation	
Further remarks	Dentary ornamented by longitudinal ridges beaded with enamel	Dentary smooth except for deep groove near occlusal margin	Dentary ornamented by longitudinal ridges; no enamel beading	Small size	Large size, no dentary ornamentation

Note: Modified from Goody (1976), with modifications from Grandstaff and Parris (1990).

to any great degree at that time and that the Niobrara specimens represent one basal population.

The new collections that we have assembled from the Niobrara Formation and Pierre Shale Group, especially those from the Sharon Springs Formation, offer the opportunity to add the evidence of field collecting and biostratigraphy to earlier analyses of *Enchodus,* at least for the marine Cretaceous sequence of the Western Interior. The species *E. petrosus* is dominant within the Sharon Springs assemblage, as noted by Goody (1976) in his revision of the species. The species *E. gladiolus,* generally recognized as valid, occurs in the Sharon Springs Formation as well. If more complete specimens of *E. gladiolus* can be found that substantiate the hypothesis that it differs in body proportions from *E. petrosus,* that would seem to confirm the contention by Chalifa (1996) regarding two separate lineages. In such a case, sympatry would be more reasonable than the other possible explanation that the two forms represent gender dimorphs.

Goody (1976) attributed several species to the Maastrichtian of the Middle Atlantic States (Navesink Formation and equivalents), namely *E. petrosus, E. gladiolus, E. dirus,* and *E. ferox*. In recent decades, stratigraphically precise collections from the Hornerstown Formation of New Jersey have shown only *E. ferox* to be present. The record of *Enchodus* from the Atlantic coastal area thus seems to be consistent with the biostratigraphic spectrum hypothesized here, the records being primarily Maastrichtian. The Gulf Coast records presumably will also fit this scheme, there being nothing in the findings of Schein (2004) to the contrary (Fig. 7).

Although biostratigraphic studies of so common a form as *Enchodus* can be challenging, it now seems that anatomical, numerical, and field collecting analyses are producing relatively consistent results. The ancestral *E. shumardi,* with a symmetrical cross section of the palatine fang and a true apical barb, is succeeded by two lineages. The *E. gladiolus-dirus* lineage, which retained the symmetrical cross section of the palatine fang, has lost the true apical barb. The *E. petrosus-ferox* lineage has also lost the true apical barb but has an asymmetrical palatine fang cross section. The last-surviving *Enchodus* in North America is *E. ferox,* with fine serrations on the palatine fang (Fig. 8).

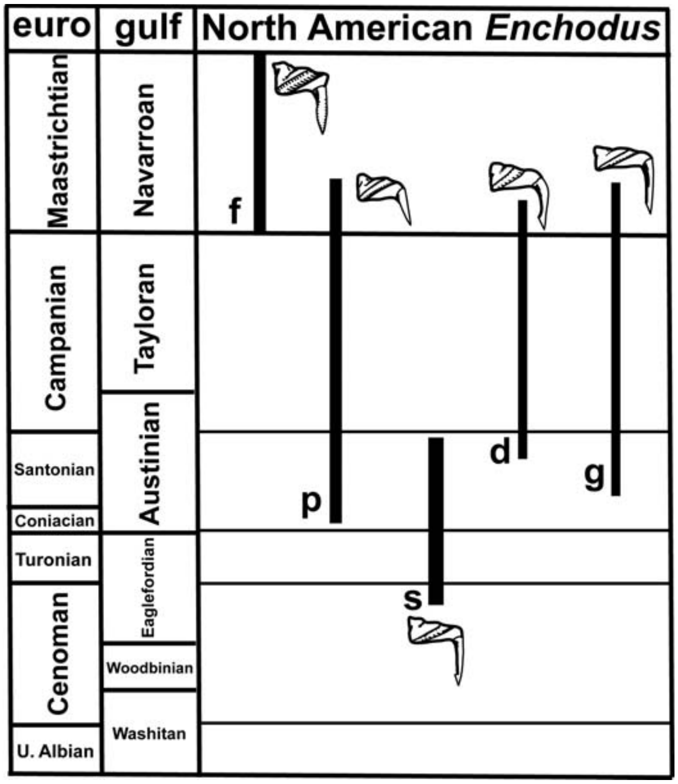

Figure 7. Stratigraphic ranges of the North American species of *Enchodus*. Abbreviations: d—*E. dirus;* f—*E. ferox;* g—*E. gladius;* p—*E. petrosus;* s—*E. shumardi;* euro—Europe; gulf—Gulf Coast; Cenoman—Cenomanian.

CONCLUSIONS

The osteichthyan collections from the upper zones of the Pierre Shale Group have yielded range extensions of taxa from the underlying Niobrara Formation and the Sharon Springs Formation of the Pierre Shale Group. Geographic range extensions into the Western Interior Seaway are confirmed for *Cylindracanthus* and *Protosphyraena*. Stratigraphic range extensions into the Campanian are found for *Protosphyraena, Xiphactinus audax, Apsopelix,* and *Pachyrhizodus*. Our studies in the Western Interior and on the Eastern Seaboard have also led to a clarification of the stratigraphic ranges of the five North American species of *Enchodus*.

Study of the upper Pierre Shale Group provides further linkages between the Campanian and Maastrichtian taxa of the Western Interior Cretaceous and those of the Atlantic and Gulf Coast Cretaceous. This is to be expected, considering the similar ages and paleoecology of these strata. Diligent prospecting will undoubtedly continue to add new detailed records.

ACKNOWLEDGMENTS

The field expeditions of the last two decades have been a partnership between the South Dakota School of Mines and Technology and the New Jersey State Museum. They were inspired by a common interest in Cretaceous marine fossils, strengthened by the knowledge that South Dakota and New Jersey fossil records would have much in common and that investigations in either area would benefit knowledge of both. In no aspect has that proved to be more true than in the studies of fossil osteichthyans. The abundant specimens thus far collected from South Dakota eventually will yield far more information than the selected items presented here, and the continuing success of field work is promising. Beginning with expeditions in the periphery of the Black Hills, and continuing in the Missouri River Trench, the collections provide new insight into the Cretaceous ichthyofauna. We here credit our numerous students and participants collectively; many individual discoveries are more fully documented in the catalogued specimen files.

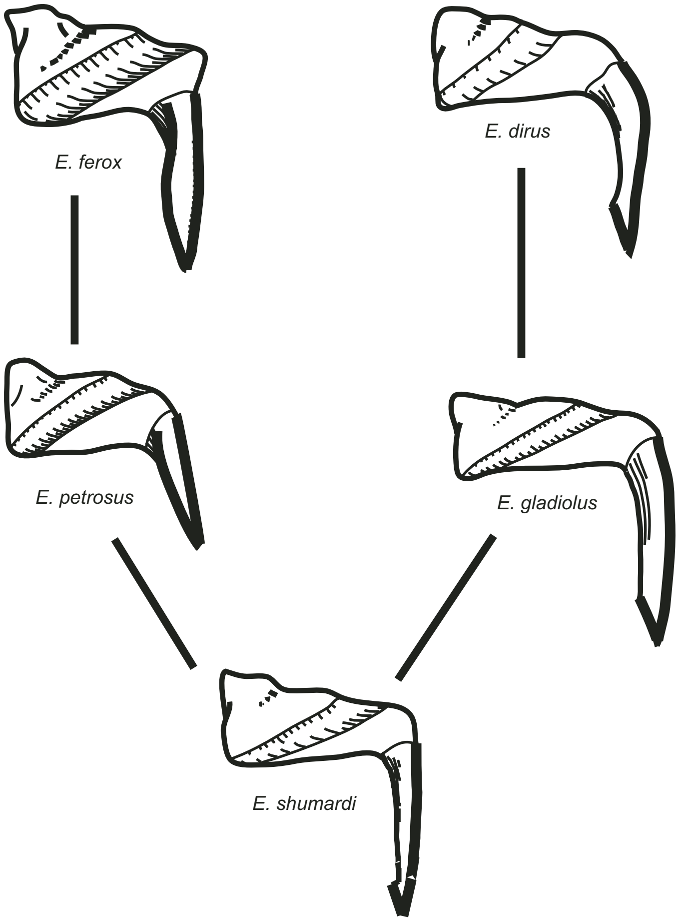

Figure 8. Schematic view of palatine morphologies in North American *Enchodus* species. Cutting edges of the fang are indicated by heavier lines. Note the true apical barb on the fang of *E. shumardi*. Straight lines indicate probable lineages.

We are grateful to the Crow Creek Nation for its support, assistance, and encouragement, a partnership that continues to be of mutual benefit. The U.S. Army Corps of Engineers has been equally supportive with permits and assistance. The South Dakota citizens of Chamberlain, Brule County, and Oacoma, Lyman County, have been gracious hosts and have offered constant support. We are also grateful to the Dane and Thomas Conger family for assistance to our research in the early days of this project.

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Special memorial honors are due Lee Azure of the Crow Creek Tribe, a tireless fossil hunter and a dedicated supporter of our efforts. Among the many fossils he found is the *Apsopelix* specimen described herein.

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Taxonomic comparison and stratigraphic distribution of Toxochelys *(Testudines: Cheloniidae) of South Dakota*

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ABSTRACT

The Campanian Pierre Shale Group contains a diverse assemblage of marine reptiles, including the sea turtle *Toxochelys.* Twenty-one specimens from South Dakota include cranial or mandibular material useful for taxonomic and stratigraphic analyses. Twenty of the toxochelyids were collected from three formations of the lower to middle Campanian Pierre Shale in western South Dakota: 1 from the basal Gammon Ferruginous Formation, 15 from the overlying Sharon Springs Formation, and 4 from the Mitten Black Shale Formation. Examination of the specimens suggests identification as *Toxochelys* sp. cf. *T. browni.* These toxochelyids reveal previously undescribed characters and are defined by snout emargination, a hooked beak of the mandible, and labial and lingual ridges of the dentary.

One toxochelyid was recovered from the DeGrey Formation of the upper Campanian Pierre Shale Group in central South Dakota and is identified as *Toxochelys* sp. A. This toxochelyid is distinguished by a smooth snout without emargination, a posterolateral margin of the pterygoid that extends to the base of the condylus mandibularis, and absence of the depressor mandibulae muscle attachment site.

Qualitative and quantitative stratigraphic analyses of the South Dakota toxochelyids indicate that *Toxochelys* sp. cf. *T. browni* could serve as the basis for a biostratigraphic local range taxon zone, spanning the time from the late early Campanian to the middle Campanian, between 81 and 78 Ma.

Keywords: *Toxochelys,* Pierre Shale, biostratigraphy, Cheloniidae.

INTRODUCTION

During the Late Cretaceous, South Dakota lay beneath an extensive sea that filled the Western Interior of North America. Sediments deposited within the Western Interior Sea and its abundance of life are recorded within the Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature). *Toxochelys* (Cope, 1873) is a primitive cheloniid sea turtle that inhabited the Western Interior Sea, first appearing in the late Coniacian Smoky Hill Member of the Niobrara Formation of Kansas. Fossil evidence suggests that *Toxochelys* became extinct during the final regression of the Western Interior Sea, with its last documented appearance in the early Maastrichtian Ripley Formation of Tennessee.

The Museum of Geology at the South Dakota School of Mines and Technology (SDSM) houses 21 *Toxochelys* specimens

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that include cranial or mandibular material. Each specimen is accompanied by contextual data, including stratigraphic position within the Pierre Shale, allowing for analysis of toxochelyids in a temporal sequence.

The purposes of this study are to document the temporal and geographic record and to assess the utility of *Toxochelys* as a biostratigraphic range taxon. This goal will be accomplished by establishing the taxonomic placement of the toxochelyids housed at the Museum of Geology, recognizing morphological changes and trends of the crania and mandible, and correlating these changes with the Pierre Shale and biostratigraphic range zones of the Western Interior Seaway.

Methods

The qualitative analysis was performed by describing and comparing the osteology of the SDSM toxochelyids with *Toxochelys latiremis*. The quantitative analysis compared 49 cranial and mandibular measurements among the 21 toxochelyids at the Museum of Geology and 7 specimens identified as *T. latiremis*. Measurements were obtained using a set of digital calipers. Because access to the *T. latiremis* specimens was not possible, the measurements were obtained from photographs in Zangerl (1953).

Each data set was compared using logarithmic scales on a standard XY scatter graph. Stratigraphy was incorporated into the quantitative analysis by separating the SDSM toxochelyids and *T. latiremis* specimens according to the stratigraphic occurrence, with different symbols. The distributions of the data plots were analyzed for both distribution and linear relationships. A close distribution of plots indicated similar size proportions, and broader distribution was interpreted as greater differences in the size proportions of the compared features. Linear relationships were compared using the slopes of calculated linear trend lines. The slopes of each trend line were used to compare the rate of change for the compared values. A slope value of 1 indicates an isometric relation in which the growth of Y increases at the same rate as the growth of X. When the slope value is not equal to 1, the relation is said to be allometric. A slope value of >1 indicates that Y increases at a quicker rate than X, and conversely. Similar or equal slopes were interpreted as comparable rates of change. Dissimilar slopes indicated different rates of change, which could be attributed to sexual dimorphism, ontogeny, clines, or speciation.

Institutional Abbreviations

AMNH: American Museum of Natural History; **KU:** University of Kansas Museum of Natural History; **SDSM:** South Dakota School of Mines and Technology; **USNM:** United States National Museum; **YPM:** Yale Peabody Museum.

PIERRE SHALE STRATIGRAPHY OF THE SOUTHERN BLACK HILLS

Rubey (1930) was the first to formally describe and subdivide the Pierre Shale in western South Dakota around the Black Hills when he described the Gammon Ferruginous, Mitten Black Shale, and Monument Hill Bentonitic Members. Gill and Cobban (1966) described seven members of the Pierre Shale section at Red Bird in eastern Wyoming that have been elevated to formations (see Martin et al., this volume). Of these, only the Gammon Ferruginous Formation, the Sharon Springs Formation, and the Mitten Black Shale Formation produced the specimens described herein.

In western South Dakota the Gammon Ferruginous Formation is the basal unit of the Pierre Shale. Its contact with the underlying Niobrara chalk may be either conformable or unconformable (Gill and Cobban, 1966; Gries and Martin, 1985). The Gammon is black to black-gray, hard, fissile, noncalcareous shale that contains many layers of bentonite. Near Hot Springs, South Dakota, the unit is 33 m thick but thins westward to 9 m at Red Bird (Gill and Cobban, 1966). The Gammon Ferruginous Formation is truncated by a disconformity that separates it from the overlying Sharon Springs Member.

Deposits around the Black Hills, later identified as the Sharon Springs Formation, were first described by Darton (1902). He described the basal unit of the Pierre as 45 m of black and splintery shale with septarian limestone and cone-in-cone concretions. Wherry (1917) described the nonswelling bentonite layers and used them to correlate stratigraphic sections around the southern Black Hills. Searight (1938) recognized the broader coverage of the Sharon Springs described by Elias (1931) in western Kansas and extended it to central South Dakota. Moxon et al. (1939) further extended the range to include the sections previously described by Darton in the southern Black Hills.

In western South Dakota the Sharon Springs Formation is rarely preserved in its entirety owing to intra-formational disconformities (Martin, 1996). An undulating disconformity truncates the unit and separates it from the overlying formation.

The Mitten Black Shale Formation was named from 44 m of blue-black shale exposed along Mitten Prong of Crook County, Wyoming (Gries and Martin, 1985). A thin bed of phosphatic *Baculites* and bone hash occurs at the base, marking an unconformity. Iron manganese and cone-in-cone concretions are found throughout this upper unit (Martin et al., 1996), and rust colored limestone concretions occur in its upper portion.

PIERRE SHALE GROUP STRATIGRAPHY OF CENTRAL SOUTH DAKOTA

Toxochelyids have been recovered from four formations of the Pierre Shale in central South Dakota: the Sharon Springs Formation, the Gregory Formation, the DeGrey Formation, and the Verendrye Formation. Only the DeGrey Formation has yielded toxochelyids with associated cranial material.

At the base of the Pierre Shale Group in central South Dakota, directly overlying the Niobrara disconformably, is the Sharon Springs Formation. Three disconformity-bound subdivisions have been described (Martin et al., this volume). The basal portion, the Burning Brule Member (Martin et al., this volume), consists of dark-gray to black, fissile, bituminous shale that contains several layers of bentonite. The middle portion, the Boyer

Bay Member, is less siliceous than the lower. The upper unit, the Nicholas Creek Member, is more bentonitic than the middle and contains phosphatic concretions. The three subdivisions are also characterized by differing rare-earth-element signatures (Patrick et al., 2004). The Sharon Springs Formation is disconformably bound by the superjacent Gregory Formation.

The Gregory Formation (Martin et al., this volume) consists of dark-gray claystone, shale, and marlstone containing calcareous and ferruginous concretions. In central South Dakota the Gregory can be up to 38 m thick (Gries, 1996). Bentonite is more abundant and the marlstone less so than in eastern South Dakota.

The Crow Creek Member of the DeGrey Formation is a thin unit, averaging 3 m in thickness near the Missouri River (Gries, 1996). This formation is composed of calcareous shale, sandstone, and marlstone. Its light-gray color visibly distinguishes it from the darker overlying and underlying units.

The upper DeGrey Member is divided into two facies. The upper, a shale and bentonite facies, was formally designated as the Oacoma Shale (Searight, 1937), but now it is considered a part of the DeGrey Formation (Crandell, 1950). The upper unit is dominated by claystone and shale, and contains abundant black manganese concretions. Thicknesses have been measured up to 41 m (Gries, 1996). The lower siliceous shale facies, formerly referred to as the Agency Shale, is light gray, weathers to flakes, and can be as thick as 38 m in the Missouri River area (Gries, 1996).

The Verendrye Formation (Martin et al., this volume) is a light- to dark-olive-gray claystone containing abundant siderite nodules and less common large calcareous concretions. In central South Dakota the Verendrye has an average thickness between 42 and 48 m (Gries, 1996). No toxochelyids have been recovered from higher up in the Pierre section in central South Dakota.

PREVIOUS BIOSTRATIGRAPHIC SURVEYS OF THE PIERRE SHALE

Numerous biostratigraphic studies have been performed on the faunas and deposits from the Western Interior Seaway. These studies have proven more successful in areas of the western and northern Western Interior Basin than in the eastern and southern regions (Caldwell et al., 1993; Obradovich, 1993). The ammonite and inoceramid faunas typical for biostratigraphic correlations were less common in the south and eastern regions, possibly because they were intolerant of the anoxic conditions in the deeper regions; of the mixing of oceanic waters from the north and the south within the continental basin, creating unfavorable chemistry; or because of the calcareous-rich sediments derived from the low-lying eastern shoreline.

Kauffman et al. (1993) combined radiometric dates (Obradovich, 1993) and the standard ammonite-inoceramid bivalve biozones with a composite of range zones of other molluskan taxa common in the Western Interior Basin (Fig. 1). This updated biostratigraphic scheme incorporated taxa that are found in ammonite-poor units, such as abundant, rapidly evolving bivalves that inhabited the anoxic ocean floor of the deeper depths of the Western Interior Sea. The anoxic taxa ranges were correlated with the range zones of recently identified taxa that occur both in oxygen-rich nearshore and anoxic offshore facies.

Others have used vertebrates of the Western Interior Seaway for biostratigraphic correlation. Martin et al. (1996) presented the stratigraphic ranges of several mosasaur taxa. The combined ranges suggest that a bipartite biozonation occurred within the Western Interior Sea: the *Tylosaurus-Clidastes* Taxon Range Zone, spanning the upper Coniacian to the middle Campanian of western South Dakota and Kansas, and the *Mosasaurus-Prognathodon* Taxon Range Zone, from the upper Campanian through the Maastrichtian of north-central South Dakota. Maloney (1996) presented a stratigraphic review regarding the general biostratigraphy of the North American marine chelonians of the Late Cretaceous. Chelonians appeared along the Gulf Coast during the early Cenomanian, with *Desmatochelys*. In the Western Interior Sea, chelonians appeared in the late Coniacian, with *Protostega, Archelon,* and *Toxochelys*. The protostegids and toxochelyids of the Western Interior Sea disappeared, respectively, in the late Campanian and the early Maastrichtian (Hirayama, 1997). Along the Atlantic Coast, chelonians appeared later, during the middle Campanian, with *Osteopygis*. Most of the Gulf Coast and Atlantic chelonians disappeared during the Maastrichtian, but *Dollochelys* and *Osteopygis* survived into the Tertiary (Maloney, 1996; Hirayama, 1997).

SYSTEMATIC HISTORY

The genus *Toxochelys* was first described by Cope in 1873 from a specimen of *Toxochelys latiremis* that was collected by Benjamin Franklin Mudge from the Niobrara chalk in Kansas (Cope, 1875). *Toxochelys browni* was originally named *Porthochelys browni* by Hay (1905) and placed in the Family Toxochelyidae. The type specimen was recovered from the Sharon Springs Formation of the Pierre Shale Group, 30 km southeast of Edgemont, South Dakota. Hay noted the close resemblance between *P. browni* and *Toxochelys latiremis,* the genotype of *Toxochelys,* but added that the size and proportions between the two turtle genera varied enough to place them in separate genera (Hay, 1905).

In his memoir of the Toxochelyidae, Zangerl (1953) recognized the similarity between *P. browni* and *T. latiremis* and relocated *P. browni* into the genus *Toxochelys*. The emargination of the snout region, postcranial characters, and the greater size of *T. browni* were defined as characters that distinguish *T. browni* from *T. latiremis*. Zangerl further noted that the two species were stratigraphically distinct from each other, *T. latiremis* having occurred in the older Niobrara Formation and *T. browni* in the younger Pierre Shale; he suggested that *T. browni* was a direct descendant of *T. latiremis* (Zangerl, 1953).

Toxochelys browni was synonymized with *Toxochelys latiremis* by Nicholls (1988), who justified the synonymy by accepting size as a reasonable variation within a species, attributing it to temporal factors. Nicholls further explained that the offset premaxilla is a “variable character” but stated that it is “never” present in *T. latiremis* turtles from the Niobrara. Nicholls further explained that the stratigraphic distinction, *T. browni* from the

Period	Stages		^{40}Ar/^{39}Ar ages (Ma)	Ammonite zones	Inoceramid Zones	Mosasaur Biostratigraphic Range Zones	Toxochelyid Biostratigraphic Local Range Zone	Red Bird Section, WY		Missouri River area, SD
Late Cretaceous	Maastrichtian	early		*Sphenodiscus*		*Mosasaurus-Prognathodon* taxon range zone		Fox Hills Sandstone		
			69.4	*Baculites clinolobatus*				Upper unnamed shale formation	Pierre Shale	Mobridge Formation
				Baculites grandis						
				Baculites baculus *Baculites eliasi*						
			71.3					Kara Bentonitic Formation		Virgin Creek Formation
	Campanian	late	71.9	*Baculites jenseni* *Baculites ressidei* *Baculites cuneatus*	*Inoceramus balchi balchi*			Lower unnamed shale formation		Verendrye Formation
					Inoceramus maclraeni					
					Inoceramus nebrascensis *Platyceramus vanuxami*					
			73.3	*Baculites compressus* *Didymoceras cheyennense* *Exiteloceras jenneyi* *Didymoceras stevensoni* *Didymoceras nebrascense*						
			74.7		*Inoceramus tenullineatus* *Platyceramus vanuxami* *n. ssp.*					DeGrey Formation
										Crow Creek Formation
			75.9		*Endocostea typica*					Gregory Formation
		middle	76.9	*Baculites scotti* *Baculites gregoryensis*	*I. saskatchewanensis* *I. buguntaensis* *I. subleavis*	*Tylosaurus-Clidastes* taxon range zone		Red Bird Silty Formation		
				Baculites perplexus *(late form)* *Baculites gilberti* *Baculites perplexus* *(early form)*	*Inoceraum regularis* *Inoceramus subcompressus*					Sharon Springs Formation
			78.5					Mitten Black Shale Formation		
				Baculites sp. (smooth) *Baculites asperiformis* *Baculites mclearni* *Baculites obtusus*			*Toxochelys sp.* cf. *T. browni* taxon range zone			
			80.5		*Inoceramus azerbaidjanensis*			Sharon Springs Formation		
		early		*Baculites sp.* *(weakly ribbed)* *Baculites sp. (smooth)* *Scaphites hippocrepis III* *Scaphites hippocrepis II* *Scaphites hippocrepis I*	*Inoceramus sp*. aff. *I. vancouverensis*			Gammon Ferruginous Formation		
			81.2 82.4		*Cordiceramus cordiformis* *Endocostea baltica*			Niobrara Formation		Niobrara Formation

Figure 1. Correlation of biostratigraphic range zones of the Pierre Shale sections at Red Bird, Wyoming, and the Missouri River area (from Gill and Cobban, 1973; Kauffman et al., 1993; Obradovich, 1993; Martin et al., 1996).

Pierre Shale and *T. latiremis* from the Niobrara Formation, is not valid because identifications had been performed without much inspection of the morphological characters. Furthermore, stratigraphic distinction may not be legitimate because the "Near fork of Smoky Hill River" cited by Cope (1875) as the Niobrara chalk locality for the type specimen of *T. latiremis* occurs in an area where the Pierre Shale crops out as well. Additionally, black shale and gypsum remain adhered to the specimen, suggesting that the type *T. latiremis* specimen is from the Pierre Shale rather than from the Niobrara (Nicholls, 1988).

Zangerl (1953) recognized four other species of *Toxochelys: T. atlantica* (Wieland) from the late Maastrichtian Hornerstown Formation of New Jersey, *T. moorevillensis* Zangerl from the early Campanian Mooreville Chalk of Alabama, *T. barberi* (Schmidt) from the early Campanian Marlbrook Marl of Alabama, and *T. weeksi* Collins from the early Maastrichtian Ripley Formation of Tennessee. *T. atlantica* was later referred to *Dollochelys* by Zangerl and remains questionably associated with that genus (Parris et al, 1986). Specimens of *T. barberi* and *T. weeksi* consist only of shell material. Nicholls examined these specimens and found that the features Zangerl used to define the two species were either age-dependent or preserved too poorly for recognition; therefore, these species, like *T. browni,* were referred to as junior synonyms of *T. latiremis* (Nicholls, 1988). Reexamination of *T. moorevillensis* by Nicholls (1988) concluded that enough distinction occurs to allow it to remain distinct from *T. latiremis.* The lingual ridge of the mandible and transverse concavity of the triturating surface were two of the characters used to distinguish *T. moorevillensis* from *T. latiremis.* Distinct characters of the mandible and triturating surfaces occur on *Toxochelys,* collected from the Pierre Shale and used in this study and which are discussed in the description of new specimens.

Nicholls (1988) concluded that only two valid species of the *Toxochelys* may be recognized, *Toxochelys latiremis,* from the Coniacian to the Maastrichtian, and *T. moorevillensis,* from the early Campanian.

NEW MATERIAL OF *TOXOCHELYS*—QUALITATIVE DESCRIPTION

The 21 toxochelyids that include the cranium or mandible from South Dakota are compared with *Toxochelys latiremis,* and significant morphological differences are described (Fig. 2). Ter-

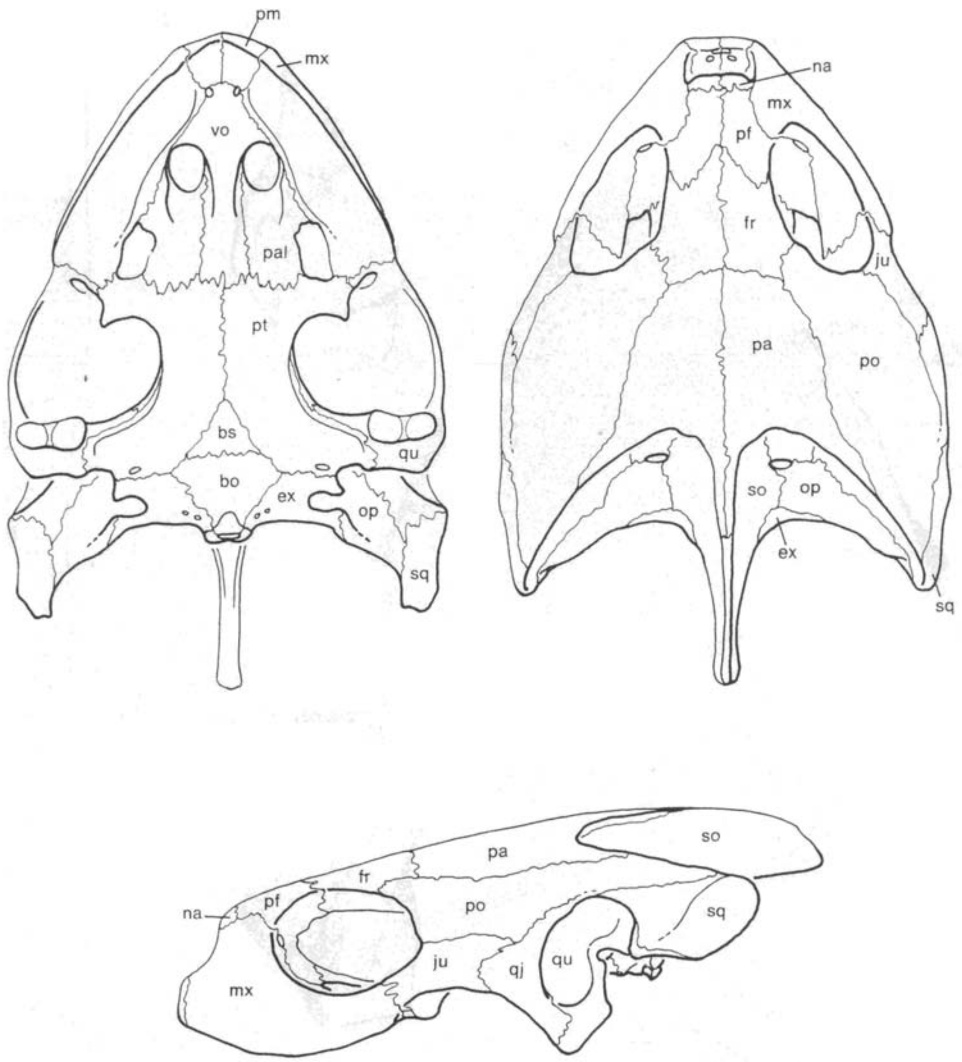


Figure 2. Nomenclature based on the reconstruction of *Toxochelys latiremis: bo*—basioccipital; *bs*—basisphenoid; *ex*—exoccipital; *fr*—frontal; *ju*—jugal; *mx*—maxilla; *na*—nasal; *op*—opisthotic; *pa*—parietal; *pal*—palatine; *pf*—prefrontal; *pm*—premaxilla; *po*—postorbital; *pt*—pterygoid; *qj*—quadratojugal; *qu*—quadrate; *sq*—squamosal; *so*—supraoccipital; *vo*—vomer. From Gaffney (1979).

minology is based on the standardized nomenclature established by Gaffney (1972).

Dermal Roofing Elements

The nasals are small rectangular paired bones that lie along the midline of the skull and meet with the maxillae laterally and the prefrontals posteriorly. The anterior margin of the nasals comprises the superior border of the nares.

The prefrontals are arc-shaped paired bones that lie along the skull midline, directly posterior to the nasals. The prefrontals are united along the midline for the anterior two-thirds of their length and diverge to enclose the anterior end of the frontals. Together, the prefrontals form a V-shape. Anterolaterally, the prefrontals meet with the ascending process of the maxilla with a long, curved suture. The lateral-most edges of the prefrontals constitute the anteromedial margins of the orbits. The posterior margins of the prefrontals interlock with the frontals by a W-shaped suture. On all specimens, with the exception of SDSM 71722 from the Sharon Springs Formation, the prefrontals appear swollen and rise dorsally to >1 cm above the frontals (Fig. 3A). On SDSM 71722, the prefrontals lie along the same plane as the frontals. On SDSM 425 from the Mitten Black Shale Formation, one-half of the anterior frontal rises up near the same level as the swollen prefrontals.

The frontals lie along the midline and extend back approximately to the same extent as the posterior margin of the orbits. The frontals are bounded by the prefrontals anteriorly with an interlocking W-shaped suture. Posterior to the frontals are the parietals, which meet along a nearly straight suture that is oriented nearly 90° to the midline in *Toxochelys latiremis* but is oriented so that it points lateroposteriorly on the SDSM toxochelyids (Fig. 3B). However, this difference may be a factor of differential preservation. Posterolaterally, the frontals meet with the postorbitals with an acutely angled suture that originates at the lateral-most extent of the frontal-parietal suture and extends anterolaterally to the posteromedial margin of the orbit.

The parietals meet along the midline. Each bone is longer than wide, with long, thin processes that extend posterolaterally

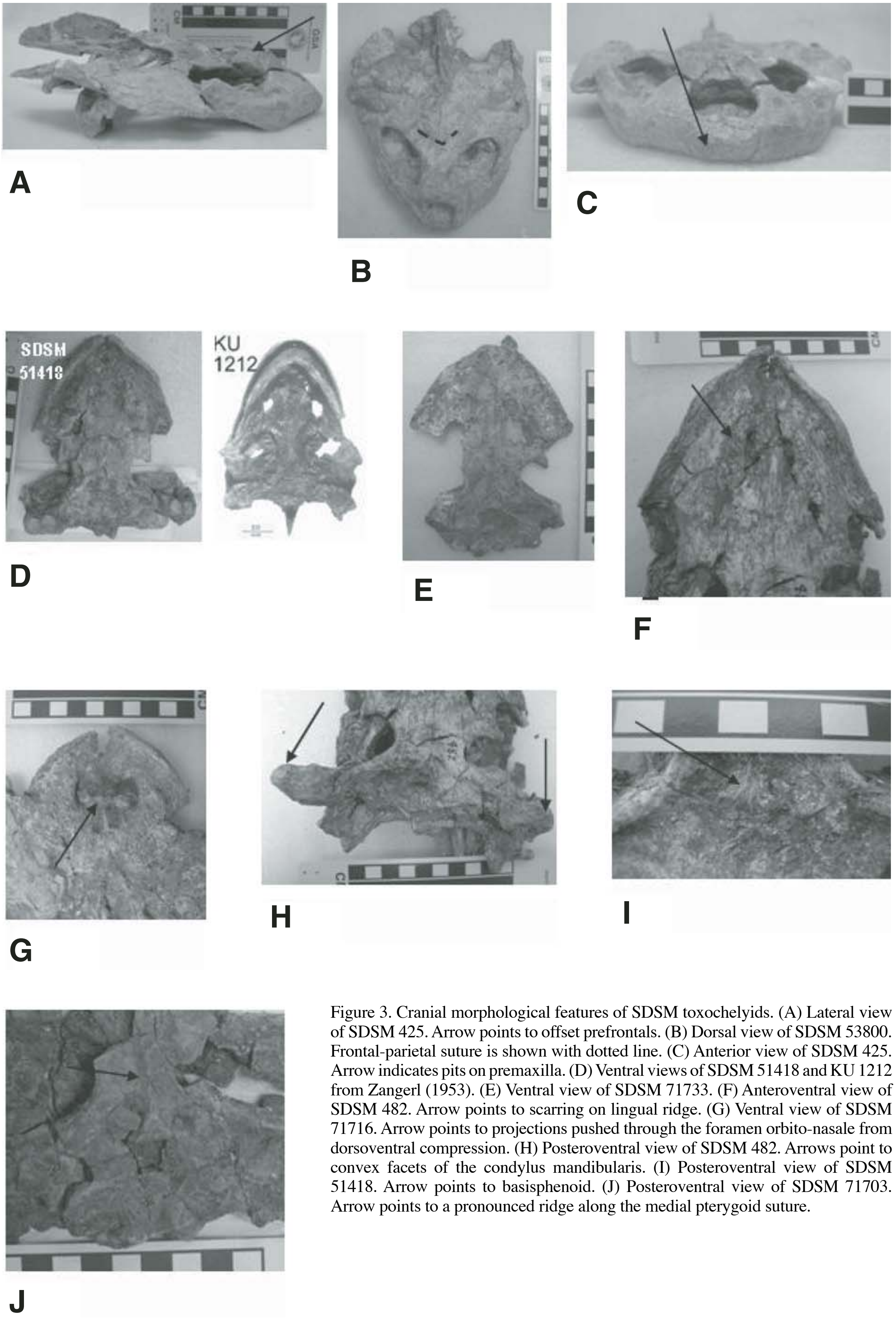


Figure 3. Cranial morphological features of SDSM toxochelyids. (A) Lateral view of SDSM 425. Arrow points to offset prefrontals. (B) Dorsal view of SDSM 53800. Frontal-parietal suture is shown with dotted line. (C) Anterior view of SDSM 425. Arrow indicates pits on premaxilla. (D) Ventral views of SDSM 51418 and KU 1212 from Zangerl (1953). (E) Ventral view of SDSM 71733. (F) Anteroventral view of SDSM 482. Arrow points to scarring on lingual ridge. (G) Ventral view of SDSM 71716. Arrow points to projections pushed through the foramen orbito-nasale from dorsoventral compression. (H) Posteroventral view of SDSM 482. Arrows point to convex facets of the condylus mandibularis. (I) Posteroventral view of SDSM 51418. Arrow points to basisphenoid. (J) Posteroventral view of SDSM 71703. Arrow points to a pronounced ridge along the medial pterygoid suture.

from the lateral margin and directly posterior from the medial margin, constituting the medial anterior portion of the supraoccipital crest. These projections and anteriorly oriented midsection constitute the anterior margins of the temporal emarginations. The parietals are bounded by the frontals anteriorly, the postorbitals laterally, and the supraoccipital posteriorly.

The postorbitals are large, elliptical paired bones that are medially separated by the parietals. Along with the parietals, the postorbitals form the temporal roof. The anterior edge forms the posterior-superior margin of the orbit. Anteromedially, the postorbitals meet with the frontals; anterolaterally and ventrally, the postorbitals meet with the jugal. Lateroventral to the postorbitals are the quadratojugals. The posterior portion of the postorbitals is nearly triangular and extends to the posterior limits of the dorsal skull roof, forming the middle portions of the lateral temporal emarginations. The laterodorsal and posteriormost tips of the postorbitals meet with the squamosals.

The jugals lie on the lateral edges of the skull, along the lateral margins of the orbits, and form part of the zygomatic arch. The jugal is bounded anteriorly by the maxilla and posteriorly by the quadratojugal; laterodorsally, the jugal adjoins the postorbital. The jugal is convex dorsally but is concave on its ventral surface. Along the ventral margin of the jugal a slight emargination of the cheek area begins and continues posteriorly. The posterior portion of the jugal ascends slightly to receive the processus coronoideus of the lower jaw.

The quadratojugals lie along the lateral portion of the skull, directly posterior to the jugals. The quadratojugal forms the posterior limit of the cheek emargination. Anterodorsally, the quadratojugal borders the postorbital; posterodorsally, the quadratojugal contacts the squamosal. The posterolateral margin is semicircular, meeting with the quadrate.

The squamosals form lateral, posteriorly projecting conical crests that lie parallel to the medial supraoccipital crest. The squamosal crests form as a result of the temporal emarginations. Along the medial side of the crests the squamosal is bounded by the processus paraoccipitalis of the opisthotic. The anterior portion of the squamosal extends along the lateral margin of the skull, bounded by the postorbital dorsally, the quadratojugal anterodorsally, and the quadrate ventrally.

Palatal Elements

The premaxillae lie along the anterior edge of the skull (Fig. 3C). The lateral surface is rugose, pitted, and best observed on SDSM 425 from the Mitten Black Shale Formation and SDSM 71693 from the DeGrey Formation. The premaxilla meets with the maxilla laterally along a relatively long suture. The dorsal surface forms the floor and the anteroinferior margin of the nares. On the ventral surface the premaxilla posteriorly contacts the vomer. Along the midline a depression receives the beak of the lower jaw. Lateral to the depression the premaxilla descends sharply to join the triturating surface of the maxilla. Along the anterolateral margins the premaxilla forms the labial ridge, which is continuous with the maxillary labial ridge. An emargination of the labial ridge occurs on most of the SDSM toxochelyids (Fig. 3D). This feature was described as one of the key morphological differences between *Toxochelys latiremis* and *Toxochelys browni* by Zangerl (1953) but was described as a variable character when *T. browni* was synonymized with *T. latiremis* (Nicholls, 1988). On *T. latiremis* the labial ridge, maxilla, and premaxilla are continuous and form a smooth, elliptical snout. On the geologically younger *Toxochelys browni* the snout region is slightly offset from the rest of the skull, creating a sigmoidally shaped emargination. This offset begins slightly posterior to the premaxilla-maxilla suture, with the labial ridge turning sharply inward, and then returning to the anteriorly directed position. From the lateral perspective, the change in snout shape can be observed by a change in vertical elevation as well. On *Toxochelys latiremis* the labial ridge extends anteriorly along a nearly consistent elevation. However, in *Toxochelys browni* the premaxilla and anterior-most portion of the maxilla rises above the elevation of the remaining maxilla. The degree of emargination of the snout varies among the SDSM toxochelyids but occurs in all of the examined specimens with the exception of SDSM 71693 from the DeGrey Formation. The snout region of this skull resembles those of *Toxochelys latiremis,* where the snout region is smooth with no indication of emargination. On SDSM 71722 from the Sharon Springs Formation, emargination is questionable, because the left premaxilla and anterior maxilla are absent and the degree of deformation of the snout makes the shape difficult to interpret. On SDSM 71733 from the Gammon Ferruginous Formation the premaxillae are fractured and set apart from the maxillae, so the degree of emargination is uncertain (Fig. 3E).

The maxillae are rugose, pitted paired bones that form the anterolateral edges of the skull. On the SDSM toxochelyids the length of the maxilla is equivalent to the width. On *Toxochelys latiremis* the maxillae are much longer than wide. The maxillae are bound by the premaxillae anteriorly. The anterodorsal portion of the maxilla forms an ascending process between the nares and orbits and connects with the nasal and prefrontal. Posterior to these junctions the maxilla creates the long anterolateral margins of the orbits, broadening posteriorly until meeting with the jugal. Medially, the maxilla connects with the vomer and palatines. Posteromedially, the maxilla meets with the anterior hook of the processus pterygoideus externus, together forming the lateral and posterior margins of the foramen palatinum posterius. On the ventral surface the maxilla forms a long, convex, toothless triturating surface. Along the lateral margins of this surface is the alveolar process, which descends from the main body of the maxilla to form a sharp labial ridge. The maxilla is bordered medially by a lower lingual ridge that originates at the maxilla-vomer suture and extends posteriorly along the maxilla-palatine suture to the posterior limit of the maxilla at the fossa subtemporalis. Short, subparallel linear scars mark the lingual ridge on specimens SDSM 482 and SDSM 4610 from the Sharon Springs Formation and SDSM 425 from the Mitten Black Shale Formation (Fig. 3F). These scars may be from either the attachment of muscles or the overlying keratin beak, the rhamphotheca.

The vomer is a single bone situated along the midline of the cranium. The anteroventral region is concave and shaped like the head of a mushroom, with the anterior portion positioned directly behind the premaxillae. The foramen praepalatinum occurs along the premaxilla-vomer suture. Anterodorsally, the vomer forms the floor of the nares. The lateral portions of the mushroom-shaped anterior region connect with the maxillae along the labial ridge. The posterolateral margin of the anterior region is bounded by the foramen orbito-nasale and the palatines. Along the midline the vomer extends posteriorly as a long, low-lying ridge, separating the palatines. The posteriormost margin of the vomer extension meets with the straight anterior margin of the pterygoids.

The palatines are elongate bones on the ventral aspect of the cranium and lie between the maxillae. The palatines are separated medially and bordered anteriorly by the vomer. The pterygoids lie posterior to the palatines. Three pairs of foramina exist on the palatines: the apertura narium interna, the foramen orbito-nasale, and the foramen palatinum posterius, listed from anterior to posterior, as well as in increasing size. The foramen orbito-nasale is in the anterior portion of the palatine, along both the anterior and anteromedial palatine-vomer and lateral palatine-maxilla sutures. In all specimens examined, with the exception of SDSM 4613 from the Sharon Springs Formation, posteromedial-oriented projections originate from within the orbito-nasale foramina and are usually distinct from the lateral margins of the foramina, as seen in SDSM 6710 from the Sharon Springs Formation. However, on SDSM 52143 from the Sharon Springs Formation the projections connect laterally to the labial ridge of the maxilla. On SDSM 53800 from the Sharon Springs Formation the projections extend posteriorly from the foramina, curve laterally to meet with the labial ridge, and extend medially around the anterior margin of the foramina. The C-shaped ridge almost entirely cups the foramen, with the exception of the medial margin, where it meets with the vomer. These projections observed on SDSM 71716 from the Sharon Springs Formation meet medially and form a vertically oriented ridge that separates the anterior region of the palatine from the posterior. The ridge on SDSM 71716 descends farther than in the other specimens, to nearly the same level as the lingual and labial ridges (Fig. 3G). Although the degree to which the process descends may be a product of preservation, the continuation along the midline to the lingual ridge may not be. On SDSM 71716 the vertical process divides the palatines and places the foramen palatinum posterius posterior to the fossa orbitalis.

The foramen palatinum posterius lies within the posterolateral portion of the palatine. This foramen is bounded posteriorly by the pterygoid and laterally by the maxilla. The shape of the foramen varies from circular, as seen in SDSM 71733 from the Gammon Ferruginous Formation, to oval, as in SDSM 53800 from the Sharon Springs Formation. Intermediate forms also occur, such as in SDSM 425 from the Mitten Black Shale Formation and SDSM 51418 from the Sharon Springs Formation. Changes in shape are most likely a product of differential compression that occurred during preservation.

The quadrate is slightly inclined posteriorly, and along its anterior margin it meets with the quadratojugal, creating the superior margin of the cavum tympani. The quadrate meets with the squamosal posterodorsally, along a broad, subcircular margin. The medial portion of the quadrate meets with the opisthotic posteroventrally and the prootic anteroventrally, forming the processus trochlearis oticum. An elongate ridge, the processus epipterygoideus, extends anteriorly from the medial extent of the quadrate, forming a long suture with the pterygoid that extends along the posteromedial portion of the fossa temporalis inferior. The anterior part of the quadrate descends from the ventral portion of the cavum tympani to form the processus articularis. The articulating surface of the condylus mandibularis is divided into two subcircular facets by a parasagittal groove that extends superiorly along the posterior face of the processus articularis. The facets are oriented anteroventrally to meet with the area articularis mandibularis of the articular. The mandibular facets vary from concave to flat to slightly convex. In specimens exhibiting flat or convex condyles, they occurred on the lateral facet, and the medial facet was observed to be concave. This condition occurs in SDSM 482, SDSM 4610, SDSM 52143, and SDSM 53800, all collected from the Sharon Springs Formation (Fig. 3H). On the quadrates of SDSM 54348 from the Sharon Springs Formation, SDSM 425 from the Mitten Black Shale Formation, and SDSM 71697 from the DeGrey Formation, both facets remained completely concave.

The pterygoids meet along the medial line of the ventral cranium, posterior to the palatines. The pterygoid is shaped like an oblong C, with the anterolateral portion bordering with the maxilla and jugal. The processus pterygoideus externus is a posteriorly oriented hooklike process that extends around the anteromedial edge of, and slightly invades, the fossa temporalis inferior. The process has a lateral, vertical plate that may help guide or buttress against the lower jaw. The process is believed to be homologous to the transverse pterygoid flange found in captorhinomorphs and other reptiles (Gaffney, 1979). Along its nearly straight anterior margin the pterygoid forms the posterior border of the foramen palatinum posterius, meets with the palatine, and along the medial anterior margin meets with the vomer. The lateral edge meets with the processus epipterygoideus and forms the medial, curved margin of the fossa temporalis inferior. The medial margins of the pterygoids diverge posteriorly, enclosing the basisphenoid and basioccipital. Closely posterior to the junction of the pterygoid, basisphenoid, and basioccipital, the pterygoid changes its parasagittal orientation and curves to become perpendicular to the midline. Along the straight posterior margin, the pterygoid is bounded by the exoccipital. At the lateral extremes of the curved process the pterygoid joins the quadrate at the base of the processus articularis. A ridge along the midline of SDSM 482, SDSM 54348, and SDSM 4610 from the Sharon Springs Formation, and SDSM 425 from the Mitten Black Shale Formation, extends anteriorly from the apex of the basisphenoid to the vomer. On the other specimens in this study the vomer and basisphenoid descend from the skull as slight ridges but are separated by the flat, plate-like pterygoids. The extent to which the ridge descends varies from being restricted posteriorly, as in SDSM 54348, to being swollen in the anterior portion of the pterygoid, as seen in SDSM 53800 also from the Sharon Springs Formation. On SDSM 482 the ridge extends almost entirely along the midline, with an exception where the ridge recesses, at which the ventral plate of the pterygoid becomes most constricted.

Braincase Elements

The supraoccipital is a single midline bone, forming the dorsal margin of the foramen magnum, and extending posteriorly to create a supraoccipital crest. The supraoccipital crest is composed of three supraoccipital plates that meet along a midline. In cross section the supraoccipital crest resembles an inverted Y. The crest is fragile and is commonly incomplete or broken off at the foramen magnum. Of the six specimens with complete supraoccipital crests, lengths varied from 3.48 cm for SDSM 53800 to 6.51 cm for SDSM 52143, both recovered from the Sharon Springs Formation. Crest lengths added an average of 25% to the complete length of the skull. The supraoccipital contacts the posteromedial margins of the parietal along the temporal emarginations. Along the ventral surface the supraoccipital meets with and separates the prootics anteriorly and the opisthotics and exoccipitals posteriorly. The exoccipitals form the lateral and ventral margins of the foramen magnum and the lateral two-thirds of the occipital condyle. Separating the exoccipitals ventromedially is the basioccipital, which constitutes the remaining third of the occipital condyle. Anteroventrally, the exoccipital meets the pterygoid along a nearly straight suture. The exoccipital is bordered anterodorsally and ventrolaterally by the opisthotic. Along the exoccipital-opisthotic suture is a sharp, medially directed infolding that forms a lateral process on the exoccipital that extends over the opisthotic.

The basioccipital is a subtriangular medial bone that lies along the posterior midline of the ventral portion of the cranium, with the apex pointing posteriorly and contributing to the ventral third of the occipital condyle, separating the exoccipitals. The anterolateral margins of the basioccipital contact the pterygoids for a short distance. The anterior border meets with the posterior margin of the basisphenoid. The basioccipital is broad and concave, with all of the margins descending into ridges. The degree of concavity varies between specimens, but all specimens are united by having the sharpest concavity anteriorly where the basioccipital joins the basisphenoid.

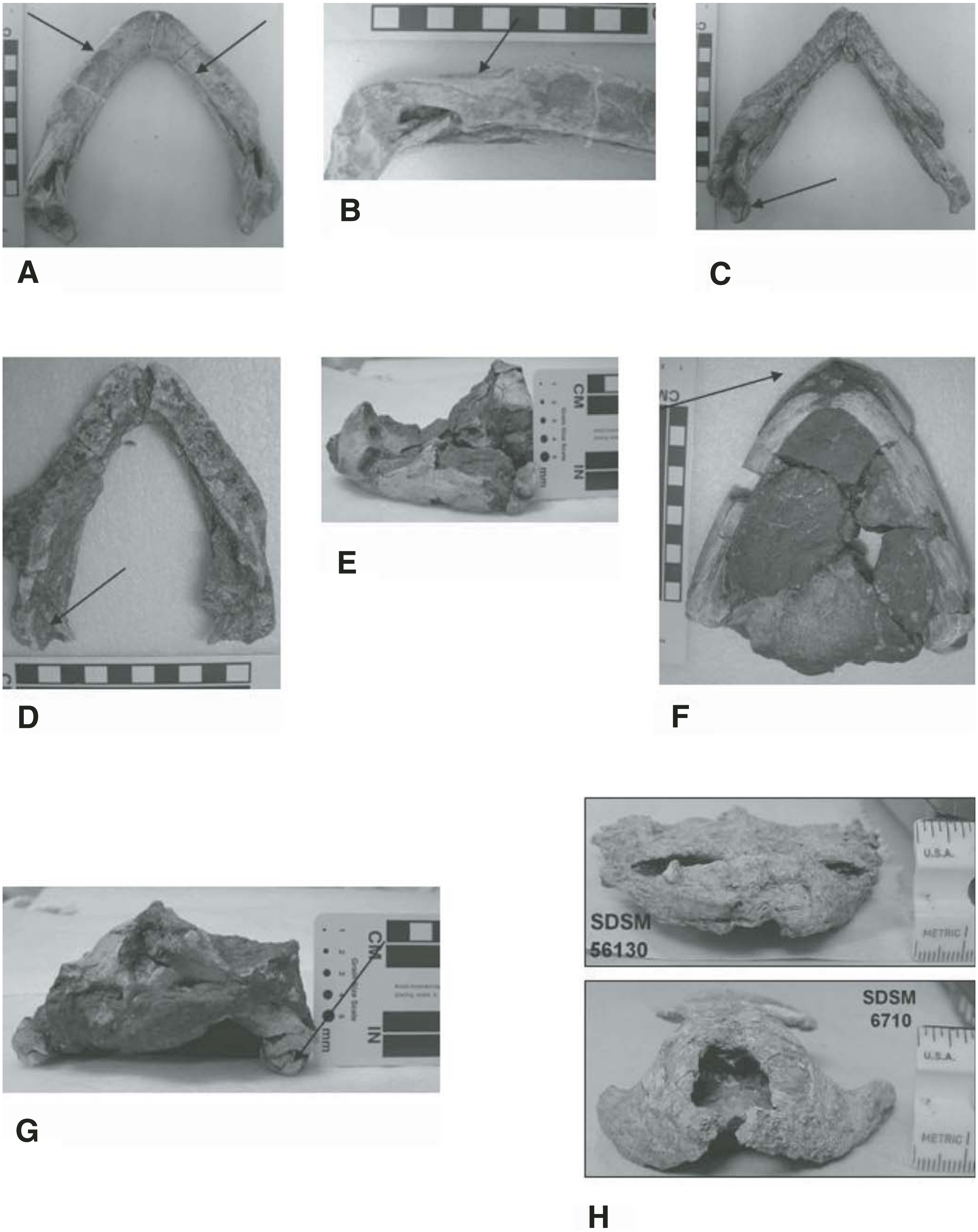
The prootics are paired, each bordered anterodorsally by the processus inferior parietalis. Posterodorsally, the prootic meets with the supraoccipital. The opisthotic lies directly posterior to the prootic, which contributes with the quadrate in forming the processus trochlearis oticum. This process changes the movement of the main adductor tendon from horizontal to nearly vertical. This structure is seen in both cryptodires and pleurodires, but it is not homologous because the functionally equivalent structure in pleurodires occurs on the pterygoid (Gaffney, 1979).

The opisthotics are posterior to the prootics. Dorsomedial to and separating the opisthotic pair is the supraoccipital. The opisthotic is bounded by the exoccipital posteromedially, with the exoccipital-opisthotic suture creating a ridge separating the overlapping exoccipital from the more internally positioned opisthotic. Anterolaterally, the opisthotic meets the quadrate near the base of the processus articularis. The opisthotic borders the squamosal medially via a long posterolateral suture that extends parallel to the posteriorly projecting squamosal process.

The basisphenoid is an unpaired triangular bone that lies along the ventral midline. The apex of the triangle extends anteriorly and separates the posterior regions of the pterygoids. The posterior region of the basisphenoid forms the base of the triangle, and the entire posterior border contacts the medial portion of the basioccipital. Dorsolaterally, the basisphenoid is bounded by the prootic. Along the anterior margin of the basisphenoid on SDSM 482 and 51418, both from the Sharon Springs Formation, several ridges radiate posteriorly from the apex. On SDSM 482 the ridges are on a concave surface, but on SDSM 51418 the surface is convex (Fig. 3I). On SDSM 53800, 4610, 54348, and 71716 from the Sharon Springs Formation, and SDSM 425 from the Mitten Black Shale Formation, the center of the basisphenoid is concave and smooth. On these specimens the triangular boundaries form ridges along the sutures with the adjacent pterygoids and basioccipital. On SDSM 71703 from the Mitten Black Shale Formation the basisphenoid is slightly convex. The lateral ridges of the basisphenoid-pterygoid suture meet at the apex and merge to form an anteriorly directed sagittal ridge that extends between the posterior regions of the pterygoids. On SDSM 71733 from the Gammon Ferruginous Formation, and SDSM 482, 4610, 53800, and 54348 from the Sharon Springs Formation, and SDSM 425 and 71703 from the Mitten Black Shale Formation, the ridge is prominent (Fig. 3J). However, the ridge is not pronounced on SDSM 51418, 52143, and 71721 from the Sharon Springs Formation. The varied forms of the basisphenoid are not related to size or stratigraphic position but rather to ontogeny. Because ossification of the cheloniid basisphenoid occurred at different stages of development (Gaffney, 1979), the variation of the basisphenoid observed among the SDSM toxochelyids is interpreted as representing various stages of ontogeny.

Lower Jaw Elements

The dentaries constitute most of the lower jaw and meet anteriorly along the mandibular symphysis. Anteriorly, a sharp beak elongates the mandibular symphysis. When the mouth is closed the beak resides in a depression along the midline between the premaxillae. The mandible morphology in specimens examined differs from that described for *Toxochelys latiremis*. The anterior mandible of *Toxochelys latiremis* is flat and does not form a sharp beak. As a result of the flat mandible, the mandibular symphysis is short (Williston, 1898; Zangerl, 1953; Nicholls, 1988). This difference in the shape of the jaw and length of the mandibular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symphysis are related to the difference in snout shape of *T. latiremis* and the SDSM toxochelyids. Zangerl (1953) used the offset premaxillary region, as exhibited in the SDSM toxochelyids, as the defining cranial character for *Toxochelys browni* but mentioned no difference on the mandible. However, the parallel change of the anterior dentary with the emargination of the snout confirms that the shape change is a morphological difference and not a product of preservation.

Another difference among *Toxochelys latiremis* and the SDSM toxochelyids is that on the latter the dentary is anteroposteriorly concave between the beak and the coronoid to receive the overlapping convex labial ridge of the maxilla. Along the concavity the triturating surface of the dentary expands posteriorly and extends the entire width of each dentary. On *Toxochelys latiremis* the triturating surface is narrow and flat, without ridges bordering the mandible (Williston, 1898; Zangerl, 1953; Nicholls, 1988). However, on the SDSM toxochelyids, labial and lingual ridges extend the lateral and medial lengths of the wide triturating surface (Fig. 4A). Ridge heights vary, with the ridges being most prominent on SDSM 53800 from the Sharon Springs Formation and SDSM 425 from the Mitten Black Shale Formation. Dorsoventral crushing of the mandible may be the cause of the reduced ridges on other specimens. Lingual ridges also occur on *Toxochelys moorevillensis* but differ in that the ridges meet medially and extend anteriorly along the mandibular symphysis, separating the mandible into left and right halves (Zangerl, 1953; Nicholls, 1988).

Along the medial surface of the dentary is a longitudinal trough, the remnant of the sulcus cartilaginis meckelii. Distortion has altered the extent to which the groove has been preserved. The sulcus cartilaginis meckelii is deeper and taller on SDSM 482 from the Sharon Springs Formation but almost nonexistent on SDSM 4614 and 52143 from the Sharon Springs Formation. Posteriorly, the sulcus cartilaginis meckelii meets with the triangular fossa meckelii, directly anterior to the foramen intermandibularis medius. On SDSM 482, the transition from the groove into the fossa is gradual and smooth, but on SDSM 425 from the Mitten Black Shale Formation the transition is sharp, with the narrow groove leading into the tall, broad fossa.

A shallow depression occurs on the posterolateral face of the dentary ventral to the processus coronoideus. This concavity marks the attachment area for the adductor mandibulae externus pars superficialis muscle (Gaffney, 1979). On SDSM 53800 and 54348 from the Sharon Springs Formation and SDSM 425 from the Mitten Black Shale Formation the depression is bordered ventrally by a narrow shelf-like process (Fig. 4B). The process occurs on specimens with deeper concavities and may have formed as a result of lateral compression applied to the dentary, where the relatively gracile coronoid is compressed inward, but the robust dentary remains largely unaffected. On SDSM 482, 4614, and 51418 from the Sharon Springs Formation, SDSM 71703 from the Mitten Black Shale Formation, and SDSM 71693 from the DeGrey Formation, the depression is very shallow and the dentary surface smooth below the coronoid. Engorgement by mineral impregnation has distorted the dentary and masked this feature on SDSM 52143, SDSM 71721, and SDSM 71722, all from the Sharon Springs Formation.

The angular is a long bone located posterior to the dentary. Anteriorly, it lies along the medial aspect of the lower jaw but descends posteriorly and wraps around to the lateral face. The angular is bounded dorsomedially by the dentary and prearticular. Posterodorsal to the angular are the articular and the surangular. As a result of dorsoventral crushing, the ventral margin of the angular is wide, almost as much as observed on the triturating surface of the dentary. On SDSM 482 from the Sharon Springs Formation the jaw is not so compressed, so the ventral edge of the angular remains narrow.

The surangular is located on the posterodorsal margin of the lower jaw, connecting with the coronoid anterodorsally, the angular posteroventrally, and the articular medially. The medial surface of the surangular constitutes the lateral border of the upper opening of the fossa meckelii. On SDSM 425, collected from the Mitten Black Shale Formation, the anteroposteriorly oriented teardrop shape of the foramen nervi auriculotemporalis is on the lateral face of the surangular, directly anterior to the lateral edge of the mandibular articulating area of the articular. This foramen is obscured by distortion on the other specimens.

The coronoid is along the dorsal margin of the jaw, posterior to the triturating surface of the dentary, and meets with the dentary anterolaterally and the subangular posteriorly. The posteromedial margin of the coronoid meets with the prearticular and contributes to the upper opening of the fossa meckelii. The processus coronoideus forms the most superior portion of the jaw and rises sharply from and posterior to the triturating surface of the dentary. The process is an attachment site for part of the adductor mandibulae externus pars superficialis muscle and the main external adductor tendon. When the jaw is closed, the processus coronoideus fits into the fossa subtemporalis beneath the lateral portion of the postorbital. On SDSM 4614 and 51418 from the Sharon Springs Formation the process is reduced but is well developed on the remaining specimens.

The articular is the posterior margin of the lower jaw, contacting the surangular laterally, the prearticular medially, and the

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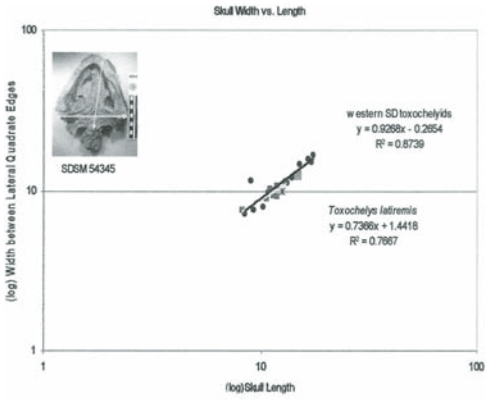
Figure 4. Lower jaw features of SDSM toxochelyids and morphology of SDSM 71693. (A) Dorsal view of mandible of SDSM 425. Arrows point to labial and lingual ridges. (B) Dorsal view of left jaw of SDSM 425. Arrow points to shelf beneath the adductor mandibulae externus pars superficialis muscle attachment site. (C) Dorsal view of mandible of SDSM 482. Arrow points to hooklike depressor mandibulae muscle attachment site. (D) Dorsal view of mandible of SDSM 51418. Arrow points to exposed canalis chorda tympani mandibularis. (E) Lateral view of SDSM 71693. (F) Ventral view of SDSM 71693. Arrow points to smooth snout lacking emargination. (G) Occipital view of SDSM 71693. Arrow points to articular with absence of attachment site for the depressor mandibulae muscle. (H) Comparison of dorsoventral compression of SDSM 56130 and SDSM 6710.

- ✱ DeGrey Formation
- ▲ Mitten Black Shale Formation
- ● Sharon Springs Formation
- ✻ Gammon Ferruginous Formation
- ■ Niobrara Formation
- — Linear (Niobrara Formation)
- — Linear (Western South Dakota toxochelyids)



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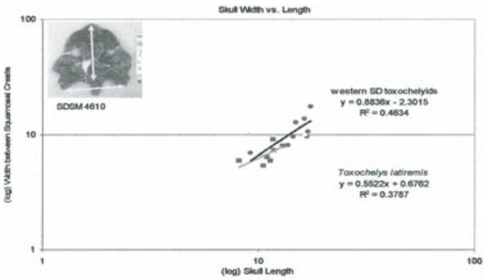

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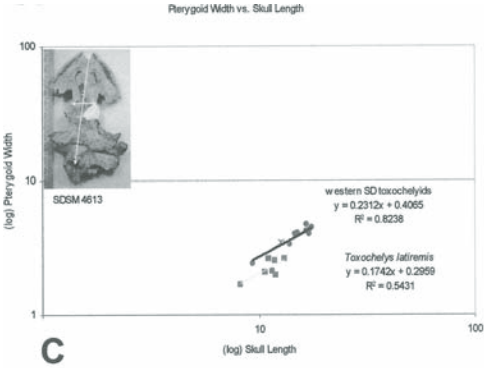

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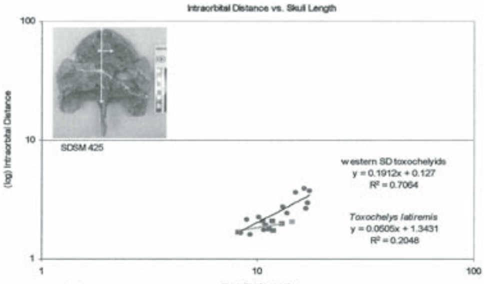

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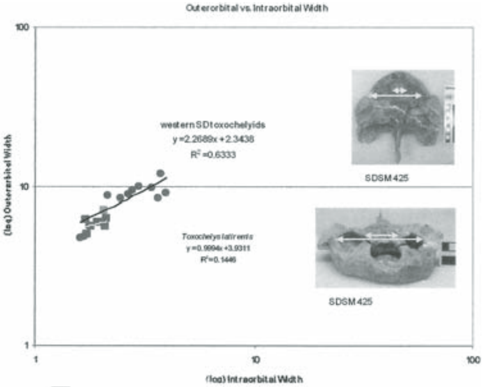

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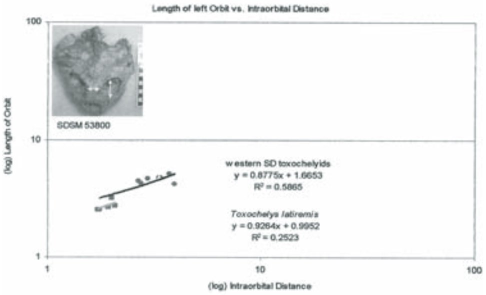

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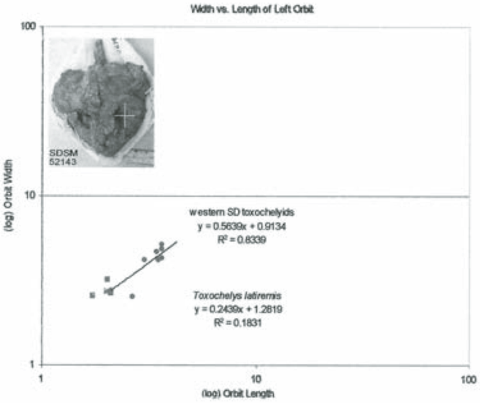

G

angular ventrally. The articular forms the posterior margin of the fossa meckelii. The dorsal portion of the articular forms the area articularis mandibularis, the surface that articulates with the condylus mandibularis of the quadrate. Similar to its cranial counterpart, the articulating surface consists of two subcircular concave facets. The facets of the lower jaw are separated by a parasagittal ridge, allowing the two articulating surfaces to interlock. The extreme posterior portion of the articular is a concave surface that is an attachment site for the depressor mandibulae muscle. The attachment site is a broad, scooplike process that extends posteromedially from the medial articulating facet of the area articularis mandibularis. On SDSM 482 from the Sharon Springs Formation, this process is preserved on the left articular and is more hooklike than scooplike (Fig. 4C). On SDSM 71693 from the DeGrey Formation, no such process occurs.

The prearticular is along the medial face of the dentary and meets with the coronoid anteromedially, the articular posteromedially, and the angular ventrally. The prearticular forms the medial wall of the fossa meckelii as well as the thin, gracile medial border of the upper opening of the fossa meckelii. On many specimens, compression caused this medial border to fracture. Directly anterior to the dorsal prearticular-articular suture is the foramen posterius chorda tympani. This foramen opens anteriorly into the canalis chorda tympani mandibularis and extends into the upper opening of the fossa meckelii. The canal is best preserved in SDSM 425 from the Mitten Black Shale Formation but is not distinct from the upper opening of the fossa meckelii on many others, such as SDSM 71713 from the Sharon Springs Formation. The posterior extension of the canal can be observed on SDSM 4613 and 51418 from the Sharon Springs Formation, because the section of the articular that normally covers the posterior part of the canal was either removed or not preserved (Fig. 4D).

SDSM 71693

The specimen recovered from the DeGrey Formation of central South Dakota, SDSM 71693, is composed of an articulated cranium and mandible. Most of the temporal roof and orbital area was not preserved, but because of preservation in a concretion, the remainder of the skull exhibits exceptional preservation. Gypsum impregnation obscures the surface texture on specimens from the lower Pierre Shale, but on SDSM 71693 the premaxilla, maxilla, and dentary exhibit pits and scarring from various muscle and rhamphotheca attachments, and nerve and blood vessel foramina are obvious (Fig. 4E).

The anterior region of the snout is smooth, with no indication of emargination (Fig. 4F), although a slight vertical change occurs on the labial ridge adjacent to the premaxilla-maxilla suture. Another difference is the extent in which the pterygoid meets with the quadrate. On the crania of *Toxochelys latiremis* and the SDSM toxochelyids from the lower Pierre Shale, the posterior pterygoid margin extends laterally to the superior portion of the processus articularis of the quadrate. On SDSM 71693 the pterygoid margin is more extensive, meeting with the condylus mandibularis at the inferior portion of the processus articularis.

The anterolateral margins of the dentary on SDSM 71693 reflect that of the snout, creating a smooth outline, unlike the dentaries of the other SDSM toxochelyids that mirror the emargination of the snout. Comparisons with the dorsal aspect of the jaw cannot be made because of its articulation with the cranium. On the lateral face of the dentary is the anterior portion of the attachment for the adductor mandibulae externus pars superficialis muscle. The attachment for the depressor mandibulae muscle, represented by a posterior extension of the articular on the other SDSM toxochelyids, is absent from both articulars on SDSM 71693 (Fig. 4G). Whereas the articular expands posteriorly beyond the area of articularis mandibularis on the other SDSM toxochelyids, on SDSM 71693 the articular abruptly ends, its posterior edge smooth with the posterior face of the condylus mandibularis of the quadrate. Both articulating joints are exposed on SDSM 71693, and both have smooth posterior surfaces, indicating that the extensions of the articulars were never present on this specimen.

NEW MATERIAL OF *TOXOCHELYS*—QUANTITATIVE ANALYSIS

The toxochelyids have been compared by examining the distribution and linear relationship of the data plots and slopes of calculated average linear trend lines. SDSM 71693 from the DeGrey Formation has been excluded from the calculated linear trend lines because of its distinct morphology. Each of the specimens was affected by postmortem crushing and mineral impregnation that greatly affected the actual size and dimensions of the cranium and mandible (Fig. 4H). The quantitative analysis was performed to demonstrate the consistent differences that remained despite the deformation. Specimen measurements are listed in the Appendix.

Skull Width versus Length

Apparent differences in skull shape occur between the SDSM toxochelyid group and *Toxochelys latiremis*. The difference was quantified by comparing the length of the skull, measured from the snout to the posterior limit of the occipital condyle, with various widths. In the first comparison, the skull length was compared with the width between the lateral margins of the quadrates (Fig. 5A). The overlapping distribution of data plots

Figure 5. Relationships between characters of SDSM toxochelyids. (A) Relationship of cranial width across quadrates vs. cranial length. (B) Relationship of cranial width between squamosal crests vs. cranial length. (C) Relationship of pterygoid width vs. skull length. (D) Relationship of intraorbital distance vs. cranial length. (E) Relationship of outer orbital vs. intraorbital width. (F) Relationship of orbital height vs. intraorbital distance. (G) Relationship of orbital width vs. orbital length.

indicates that the size proportions of the compared measurements are similar, except that SDSM 71716 from the Sharon Springs Formation has one of the shortest skull lengths (8.99 cm). Dorsoventral compression affected the specimen so much that it is only a few centimeters thick, resulting in a width (11.45 cm) comparable to specimens of lengths between 13 and 14 cm.

The compared values for all of the specimens form a linear relationship, with size increasing in a stratigraphic sequence. A closer analysis utilizing the calculated linear trend lines, which can be interpreted as the change in shape as a function of the change in size, indicates that the slope values differ slightly, suggesting subparallel development. In this comparison, both groups have slope values <1, indicating negative allometry, with the skull length increasing more rapidly than skull width. For the *T. latiremis* specimens, a slope of 0.74 indicates that the differential rate of change is slightly greater than in the western South Dakota toxochelyid group; *T. latiremis* had a narrower cranium than that of the lower Pierre Shale toxochelyids.

The second width and length comparison involved the distance between the two posteriorly projecting squamosal crests (Fig. 5B). A slightly broader distance is exhibited between the distribution of data points, suggesting a slightly greater difference in size proportions than in Figure 5A. Two of the significantly deformed SDSM toxochelyids lie distinct from the others. SDSM 51418 from the Sharon Springs Formation exhibits a temporal roof that is more flattened on the right side, causing the right squamosal crest to be inflected medially, decreasing the distance between the crests. The resulting proportion of the width to skull length resembles that of *T. latiremis,* hence its position almost along the trend line of *T. latiremis*. The other specimen, SDSM 56130, is another example of extreme dorsoventral crushing that caused the skull to lengthen rather than to broaden.

The data plots do not form a clear linear relationship, as in the previous comparison, but do tend to increase in size with time. The slope values for shape change of both groups are <1, indicating that skull length increases more quickly than skull width. This feature is greater in *T. latiremis* as shown by having a slope value 0.33 lower than the SDSM toxochelyids. The slope value of the SDSM group trend line suggests that the skull length increases 1.1 times faster than the distance between the squamosal crests. For *T. latiremis* the length increases almost twice as fast as the width.

The most constricted part of the pterygoid was used for the third skull width value (Fig. 5C). The distribution of the data plotted into two groups, forming nearly parallel trend lines, indicating subparallel rates in change for the measured values, but a greater difference in size proportion than in the previous two comparisons. The slope values for both trend lines are <1, illustrating that skull length increases more rapidly than the width of the pterygoid. Shape development between the two groups is comparable, both near 0.2, implying that length increases 5 times more quickly than width. One anomaly of the SDSM toxochelyid group, SDSM 56130 from the Sharon Springs Formation, plots closer to the *T. latiremis* group. SDSM 56130 is one of the specimens that has undergone more severe dorsoventral crushing. Resulting elongation of the skull caused the pterygoid to become narrower, explaining why the specimen plots more closely to *T. latiremis*.

The fourth comparison with the skull length was made with the intraorbital distance (Fig. 5D). The distribution of each group is closer than in the previous comparisons with the plots of *T. latiremis* overlapping with the smaller SDSM specimens collected from the Sharon Springs Formation. Despite the overlap, the general trend of the plots indicates that size increases with time, with the exception of SDSM 71693. This specimen plots intermediate between *T. latiremis* and the other Pierre Shale toxochelyids. Furthermore, the position of SDSM 71693 along the linear trendline for *T. latiremis* shows that its size proportion is more similar to that of *T. latiremis*.

Slope values of the calculated average trend lines are both strongly negatively allometric, having a difference of 0.14. However, the SDSM toxochelyid group slope is 0.19, indicating that the length increases at a rate 5 times greater than the intraorbital distance. For *T. latiremis* a slope of 0.05 implies that the rate of change for the length is 20 times faster than the rate of change for the width. This relationship is reflected by the broader crania of the Pierre Shale toxochelyids.

Sensory Apparatus Measurements

Orbital size was compared between *Toxochelys latiremis* and the Pierre Shale specimens. First, the distance between the lateral margins of the orbits was compared against the inner distance (Fig. 5E). The plot distribution shows similar proportions, with the SDSM toxochelyids and *T. latiremis* assembling into a single line. SDSM 56130 and 56135, both from the Sharon Springs Formation, plot distinctly. Both were elongated, rather than expanded laterally by extreme dorsoventral crushing. Lateral expansion from crushing is normally accompanied by a widening of the intraorbital margin, whereas elongated deformation usually has a narrowing effect. This caused the two SDSM toxochelyids to plot far from the remaining toxochelyids, and even below *T. latiremis*. The positions of the plots for the two groups appear to form one group, but a great difference occurs between the rates of measured size change. In *T. latiremis* the rate of change is isometric, with a slope value of 0.99. In the SDSM toxochelyids, the rate is positively allometric, with the distance between the lateral margins of the orbits increasing 2.27 times more rapidly than that between the medial orbital margins. SDSM 71693 from the DeGrey Formation plots directly on the average linear trend line for the SDSM toxochelyids from western South Dakota. However, its size plots more closely to *T. latiremis,* deviating again from the general trend observed in the remaining measured specimens that size increases with time.

Another orbital comparison was made between the length of the left orbit and the intraorbital width (Fig. 5F). All of the data plots appear to form a single line, but a slight difference in size proportion is observed. Anomalously, SDSM 6710, collected from the Sharon Springs Formation, falls within the *T. latiremis* range. The average linear trend lines for each group plot separately but are nearly parallel, both having slope values near 0.9.

For the measured toxochelyids the intraorbital distance increases at a rate slightly quicker than the length of the left orbit.

The final orbital comparison occurred between the widths and lengths of the left orbit (Fig. 5G). The size proportions plotted in similar manner to the previous comparison. Overlap occurred again, with SDSM toxochelyids breaching the far gap between the distributions and plotting close to the *T. latiremis* specimens. Plots representing size proportions of the width and length of the left orbit for SDSM 6710 and SDSM 482 plotted away from the other SDSM toxochelyids. Both exhibit differential distortion, where left lateral compression occurred in addition to the dorsoventral crushing, resulting in a relatively smaller left orbital width.

Slope values indicating shape change of the width and height of the left orbit for both groups were negatively allometric. Both groups show that the length of the orbits increases more rapidly than the width. The SDSM toxochelyids have lengths increasing almost twice as fast as the width. The rate change is greater for *T. latiremis,* with the length increasing 4 times as fast. This is expressed morphologically as longer, narrower orbits, as observed on *T. latiremis*.

Maxillary Dimensions

Both Hay (1905) and Zangerl (1953) noted unusual constricting of the premaxilla in relation to the maxilla in *Toxochelys browni*. This condition has never been described for *T. latiremis* (Nicholls, 1988). To quantify the difference in snout emargination, a comparison of the cranial width, using the midpoint of the maxillae and the cranial width at the premaxilla-maxilla suture, is shown in Figure 6A. The size proportions cluster in a broadly distributed group. SDSM 6710 from the Sharon Springs Formation

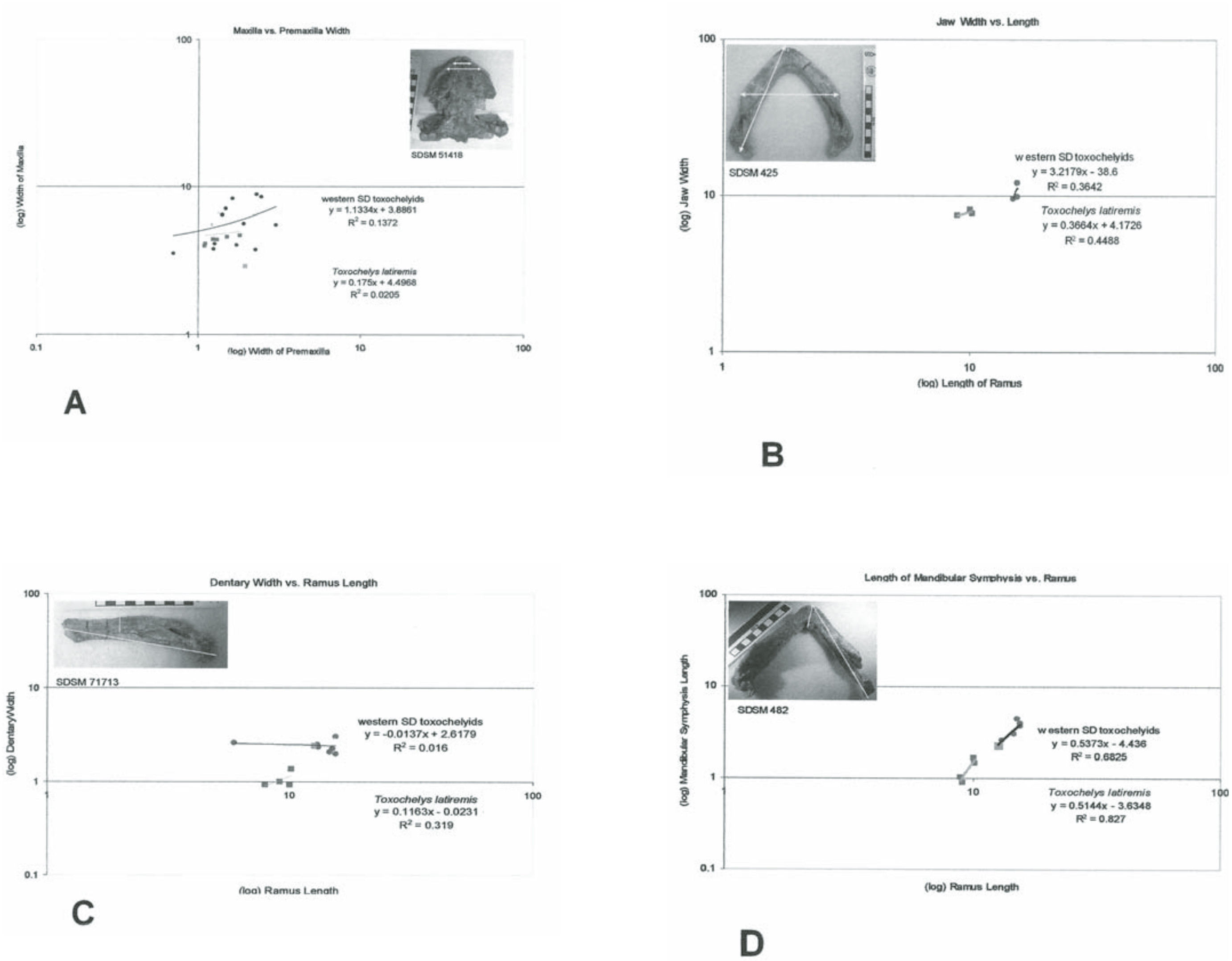

Figure 6. Relationships between characters of SDSM toxochelyids. (A) Relationship of maxillary width vs. premaxillary width. (B) Relationship of the distance between coronoid processes vs. ramus length. (C) Relationship of dentary width vs. ramus length. (D) Relationship of depth of mandibular symphysis vs. ramus length.

plots outside of the general distribution because of its very narrow premaxillae, a result of differential preservation. SDSM 71693 from the DeGrey Formation also plots outside of the distribution. This specimen is unique among the SDSM toxochelyids in that it does not exhibit snout emargination at all, instead having a smooth snout like that of *T. latiremis* (Fig. 7).

Despite the single cluster, a difference in slope value occurs between the shape changes. For the SDSM toxochelyids, positive allometry is exhibited by the width of the maxillae increasing more rapidly than the width of the premaxillae. *T. latiremis* yielded a negative allometric slope, indicating that the width across the premaxilla-maxilla suture increases 5 times more quickly than the maxillae width. This is observed morphologically by the smooth curvature of the snout without emargination.

Lower Jaw

The sample size for the lower jaw is considerably smaller. Three measurements were used for comparison against the ramus length. The first compared the distance between each processus coronoideus with length (Fig. 6B). Only four of the SDSM toxochelyids and three *Toxochelys latiremis* were complete enough to be used in this comparison. Results indicated very different proportions as well as very different rates of change for the measured components. In *T. latiremis* the length increases faster than the width of the jaw, having a slope of 0.36. For the SDSM toxochelyids the shape is strongly positively allometric, the width between the coronoids increasing 3 times more rapidly than the length of the ramus. This is consistent with the results from the skull width versus length comparisons.

Next, the width of the dentary was compared with the length of the ramus (Fig. 6C). The sample size was larger, with 9 in the SDSM toxochelyid group and 4 for *T. latiremis*. The SDSM toxochelyids and *T. latiremis* group measurements plot into two distinct clusters, with the exception of SDSM 53800 from the Sharon Springs Formation. This may be a factor of preservation, with the triturating surface having been compressed and subsequently broadened. This jaw was found in association with, but not articulated with, the cranium. Therefore, differential compression could have occurred between the two, explaining why SDSM 53800 does not appear anomalous in the cranial comparisons.

The slope value of the linear trend lines for both groups is near zero, indicating that the width of the mandible does not change significantly in relation to the rate of change in the ramus length. The slight shape change for the SDSM toxochelyids indicates that as the ramus lengthens, the width slightly decreases; the inverse occurs in *T. latiremis*.

The third comparison is the length of the mandibular symphysis against the length of the ramus (Fig. 6D). The groups separated into two clusters and yielded a strong linear relationship with size increasing with time. SDSM 71693 from the DeGrey Formation plots between the two groups instead of in stratigraphic order. Calculated rates of shape change were nearly equal between the two groups, each with the negative allometric slope value near 0.5. For both groups, the rate the mandibular symphysis lengthens is half as quick as the rate of the ramus.

DISCUSSION

Taxonomic Identification of the SDSM Toxochelyids

Both the qualitative and quantitative analyses indicate that the SDSM toxochelyids are distinct from *T. latiremis*. Several osteological variations and analytical disparities occur among the SDSM toxochelyids, but many are a result of differential preservation. A few characters were observed that are interpreted as morphologic differences.

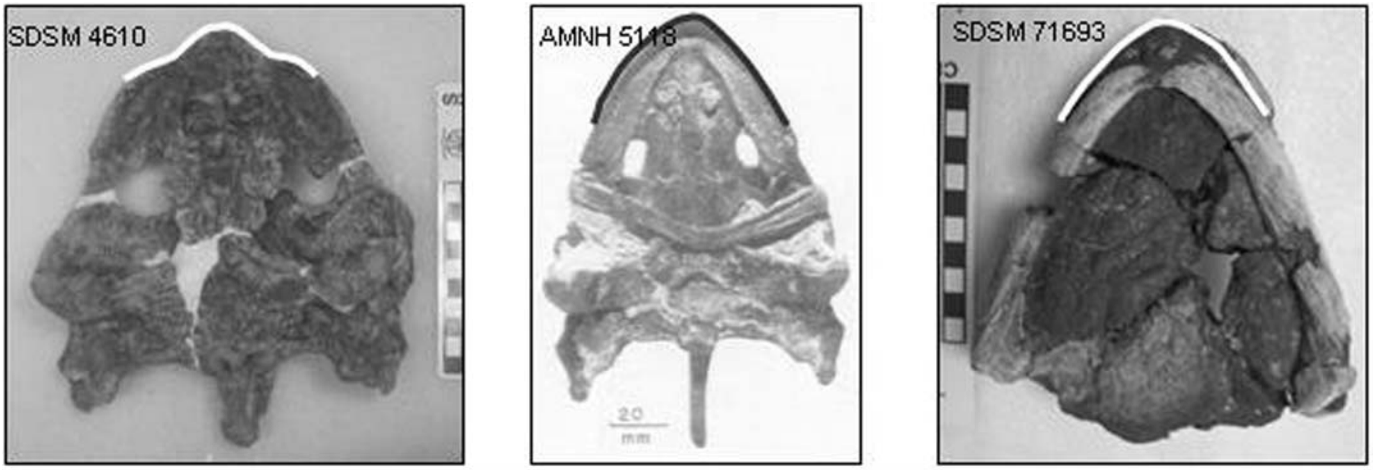

Figure 7. Comparisons of the snout of SDSM toxochelyids vs. *Toxochelys latiremis*. SDSM 4610 from the Sharon Springs Formation exhibits snout emargination. This feature does not occur in SDSM 71693 from the younger DeGrey Formation, or *Toxochelys latiremis* as represented by AMNH 5118 from Zangerl (1953).

Emargination of the snout is the most distinct character among the SDSM toxochelyids, occurring in almost all of the Pierre Shale toxochelyids. Snout emargination has been suggested as a variable character of *T. latiremis* (Nicholls, 1988) and could be the result of sexual dimorphism or ontogeny. If this were the case, smooth-snouted toxochelyids would occur along with the emarginated-snout toxochelyids. However, the two types show no overlap, with the potential exception of the type specimen of *T. latiremis,* whose stratigraphic formation of origin remains under question.

The snout region of the SDSM toxochelyids, as well as those previously referred to *T. browni,* compares very well with several types of extant turtles that inhabit both fresh-water and marine habitats. In the extant turtles, snout shape is not a function of sexual dimorphism or ontogeny but rather a direct function of the food type. Kinosternids are fresh-water musk turtles that are opportunistic omnivores, feeding on fish, worms, clams, and snails, whereas the Hawksbill, *Eretmochelys imbricate,* is an example of a marine turtle that also has an offset beaked premaxilla region. Hawksbill turtles are largely carnivorous, feeding on a variety of organisms, such as mollusks, crustaceans, small fish, and jellyfish. Not only do these turtles use their beaks for crushing and prying open shelled organisms, but they also use their narrow and beaked snouts to reach into the crevices of rocks and coral reefs to obtain prey. Extant fresh-water and marine turtles that do not have the offset snout or beak tend to subsist on a less diverse diet that includes more plant material. The wider beak is usually used to scoop material from the floor of the body of water or to shear plant material (Wyneken, 2001). Based on the comparison with extant turtles, and assuming that shape is directly related to function, the appearance of the smooth-snouted SDSM 71693 from the DeGrey Formation indicates that another sea turtle, with a diet differing from the emarginated-snout toxochelyids, existed in the Western Interior Sea.

Further distinction was observed on the mandible of the SDSM toxochelyids, mirroring the shape change observed on the snout. The mandible is anteroposteriorly convex, narrows anteriorly, and forms a hooked beak along the mandibular symphysis. The corresponding shape changes of the mandible and snout refute speculation that the emargination is a result of preservation. On the SDSM toxochelyids, labial and lingual ridges occur along the margins of the triturating surface of the mandible. The mandible of *Toxochelys latiremis* is described as smooth, without ridges. *T. moorevillensis,* from the Campanian Mooreville Chalk of Alabama, has a sagittal ridge along the mandibular symphysis that diverges and continues down the lingual margins of the mandible. Although ridges of the SDSM toxochelyids are not entirely like those of *T. moorevillensis,* the mandibles compare more favorably than with *T. latiremis.*

The qualitative mandibular distinction between the SDSM toxochelyids and *T. latiremis* is supported by the quantitative analysis. Quantitative cranial comparisons often yielded similar distribution patterns and average trend lines that suggest subparallel development between the two groups, reflecting the general cranial similarity between the two. However, despite the relatively small sample size, the quantitative analyses utilizing the mandible consistently plotted into two distinct groups, those collected from the Pierre Shale and *T. latiremis* from the Niobrara Formation. These results indicate that a difference in the general shape of the mandible occurs as well.

Although observable morphological differences are limited in number, the degree of difference is great enough to distinguish the SDSM toxochelyids from *Toxochelys latiremis*. The SDSM toxochelyids recovered from the lower Pierre Shale of western South Dakota compare best with the morphological description of *Toxochelys browni,* currently considered a junior synonym of *T. latiremis*. The defining characters in 20 of 21 new specimens, which can be related to function, suggest that *T. browni* may be distinct enough to be recognized as its own species. Until formal recognition can be established, the 20 SDSM toxochelyids are identified as *Toxochelys* sp. cf. *T. browni*.

SDSM 71693 from the middle Pierre Shale of central South Dakota possesses osteological characters that make its taxonomic placement difficult to discern. The shape of the snout suggests that SDSM 71693 is comparable to *T. latiremis,* but the posterolateral extension of the pterygoid and lack of the attachment area for the depressor mandibulae muscle indicates a distinction from *T. latiremis*. These three observations also suggest that SDSM 71693 varies a great deal from the definition of *T. browni* and the remaining SDSM toxochelyids. Analysis of the quantitative data indicated varied results in associating SDSM 71693 with either compared group. However, SDSM 71693 consistently deviated from the general trend of the specimens by plotting intermediate between the SDSM toxochelyids and *T. latiremis,* rather than in stratigraphic succession. Because of its distinction from and intermediate nature between *T. latiremis* and *Toxochelys* sp. cf. *T. browni,* SDSM 71693 is referred to as *Toxochelys* sp. A.

Temporal and Geographic Record

This unique toxochelyid collection allows for a stratigraphically ordered analysis to test whether or not characters that distinguish *T. latiremis* from *Toxochelys* sp. cf. *T. browni* are stratigraphically related and thus support an ancestor-descendant relationship. The *Toxochelys* sp. cf. *T. browni* specimens were all collected from the basal three formations of the Pierre Shale in western South Dakota and are united by the following characters: emargination of the snout, an anteroposteriorly convex mandible with a narrow and hooked beak, labial and lingual ridges of the mandible, and a greater size. The quantitative analysis indicates that size proportions and rates at which characters change vary between the two groups but are similar enough to imply an ancestor-descendant relationship.

Osteological variations on the geographically and stratigraphically distinct *Toxochelys* sp. A, SDSM 71693, distinguish it from both *T. latiremis* and *Toxochelys* sp. cf. *T. browni*. Although the origin of *Toxochelys* sp. A is unclear, the smooth snout shape, coupled with cranial and mandibular differences, suggests that SDSM 76193 represents a previously undescribed lineage of *Toxochelys latiremis*.

Toxochelys latiremis appears in the late Coniacian Smoky Hill Member of the Niobrara chalk. A descendant of *T. latiremis, Toxochelys* sp. cf. *T. browni* appeared ca. 81 Ma, distinguished from *T. latiremis* by snout emargination and a sharply beaked mandible with anteriorly narrowing, ridge-bounded triturating surfaces. *Toxochelys* sp. cf. *T. brown* persisted in the Western Interior Sea of South Dakota until 75 Ma, with the appearance of a toxochelyid lacking emargination. SDSM 71693, referred to as *Toxochelys* sp. A, occurs in the DeGrey Formation and may represent a separate lineage of *Toxochelys latiremis*. Additional specimens of *Toxochelys* sp. A are needed to clarify its systematic placement and origin.

The occurrence of *Toxochelys* sp. cf. *T. browni* as the only toxochelyid recovered from the lower Pierre Shale of South Dakota suggests that the taxon could serve as the basis for a biostratigraphic local taxon range zone, spanning the interval from the upper lower Campanian Gammon Ferruginous Formation, shortly before 81 Ma, to the middle Campanian Mitten Black Shale Formation, ca. 78 Ma (Fig. 1). Morphological variation among *Toxochelys* sp. cf. *T. browni* does not occur at a level at which further subdivision of this zone can be made.

CONCLUSIONS

The *Toxochelys* collection at the South Dakota School of Mines and Technology was examined for temporally dependent morphological characters that would allow for biostratigraphic zonation. This was performed by describing and comparing cranial and mandibular material, quantitatively analyzing characters to observe how the SDSM toxochelyids and *T. latiremis* compare in regard to size proportion and rates of change, and comparing the changes with the stratigraphic record.

Sections of the Pierre Shale in central and western South Dakota were prospected equally and produced approximately the same number of localities. Nevertheless, a disparity occurred in the amount, type, and age of material. Sites in western South Dakota yielded 20 specimens from the basal three formations of the Pierre Shale, with the majority originating in the Sharon Springs Formation. Cranial material occurred only with one specimen from the DeGrey Formation of central South Dakota. This disparity may be due to the difference in environments that existed in the Western Interior Sea during the Campanian, suggesting that toxochelyids preferred the deeper marine habitat found along the western part of South Dakota.

Analysis of the examined specimens in stratigraphic order indicates that at ca. 81 Ma *Toxochelys latiremis* of the Niobrara Formation evolved, and the descendant, *Toxochelys* sp. cf. *T. browni* of the Pierre Shale appeared, the latter distinguished by an emargination of the snout, a beaked mandible, and labial and lingual ridges lining the dentary. *Toxochelys* sp. A occurred 74 Ma and is distinguished from *Toxochelys* sp. cf. *T. browni* by a lack of snout emargination and depressor mandibulae muscle attachment site of the articular, and a more extensive pterygoid-quadrate contact. *Toxochelys* sp. cf. *T. browni* and *Toxochelys* sp. A most likely represent separate lineages that descended from a common ancestor, *Toxochelys latiremis*.

The results of the stratigraphic analysis indicate that *Toxochelys* sp. cf. *T. browni* may serve as the basis for a biostratigraphic local range taxon zone, spanning an interval from the late early Campanian to the middle Campanian, between 81 and 78 Ma.

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MEASUREMENT DATA

Abbreviations of Institutions

AMNH=American Museum of Natural History$^+$
USNM=United States National Museum$^+$
KU=University of Kansas Museum of Natural History$^+$
YPM=Yale Peabody Museum$^+$
SDSM=South Dakota School of Mines and Technology

$^+$Measurements were obtained from photographs taken from Zangerl, 1953

*Incomplete specimen, measurements were estimated; when possible, taken to the skull midline and doubled

n/a=Character on specimen was absent or not measured

Lith. Unit	Specimen Number	Skull Length from snout to Occipital Condyle (cm)	Snout to end of supraoccipital crest (cm)	Length from snout to vomer-pterygoid suture (cm)	Length of maxilla (cm)	Length from snout to basisphenoid-basioccipital suture (cm)	Skull Width across quadrates (cm)	Intraorbital distance (cm)	Outerorbital distance (cm)	Widest outerorbital distance (cm)	Greatest left orbital length (cm)	Greatest right orbital length (cm)	Greatest left orbital width (cm)	Greatest right orbital width (cm)	Greatest diagonal left orbital distance (cm)	Greatest diagonal right orbital distance (cm)	Distance between squamosal crests (cm)	Distance between cheeks (cm)	Nasal width (cm)	Nasal height (cm)
DeGrey Formation	SDSM 71693	14.6	n/a	7.56	n/a	n/a	12.5	2.06	7.05	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.36	2.03
Mitten Black Shale Formation	SDSM 71703	16.42	n/a	7.66	8.92	12.91	15.59	2.99	10.94	n/a	4.74	5.14	4.23	3.91	n/a	n/a	10.1*	13.52	1.58	n/a
	SDSM 71705	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 71706	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 425	17.42	23.69	7.94	9.22	13.59	15.99	3.34	11.25	14.02	4.74	4.57	3.21	3.70	5.33	4.79	14.81	17.64	2.70	2.41
Sharon Springs Formation	SDSM 71713	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 71716	8.99	n/a	6.46	6.64	9.63	11.45	2.14	8.61	n/a	4.2	4.52	3.02	3.2	n/a	n/a	n/a	10.01	3.5	2.62
	SDSM 53800	17.12	20.04	8.18	10.00	13.24	15.96	2.96	9.85	10.12	4.72	4.85	3.43	3.08	4.86	5.74	10.55	14.14	2.33	2.32
	SDSM 71721	14.59	n/a	7.10	n/a	11.67	12.60	3.41	9.74	n/a	4.29	4.26	3.62	3.22	n/a	n/a	9.64	11.58	2.56	2.59
	SDSM 71722	13.18	n/a	7.04	n/a	n/a	11.15	2.76	9.28	n/a	n/a	n/a	1.82	4.18	n/a	n/a	n/a	10.55	2.46	2.18
	SDSM 51418	13.82	n/a	6.31	8.18	10.52	11.98	2.45	8.38	n/a	4.85	4.03	3.61	1.24	n/a	n/a	8.03	8.48	2.15	1.24
	SDSM 56130	9.28	7.57	4.69	5.34	7.50	7.63	1.61	4.80	5.64	1.00	1.35	1.45	1.54	2.81	2.49	6.94*	5.44	1.38	.8*
	SDSM 52143	16.46	22.92	8.14	9.50	13.44	15.66	3.95	9.04	9.07	4.23	4.12	3.49	2.04	4.48	4.23	13.76	12.55	1.85	1.95
	SDSM 56135	8.40	n/a	4.19	5.74	n/a	7.16	1.67	4.84	n/a	n/a	n/a	1.78	1.87	2.58	2.32	n/a	5.79	1.85	1.76
	SDSM 6710	10.80	n/a	4.48	5.15	n/a	9.80	1.77	5.62	n/a	2.54	2.69	2.65	2.14	n/a	n/a	n/a	6.50	1.22	1.47
	SDSM 482	15.04	21.39	8.44	9.22	12.89	14.64	3.63	8.35*	9.4*	2.77	4.18	2.1*	4.62	4.61	5.17	14.6*	n/a	2.74	1.55
	SDSM 4610	17.51	22.25	8.90	9.72	13.91	16.71	3.73	11.90	15.09	5.16	5.16	3.62	4.22	5.24	5.19	17.40	19.06	2.54	2.82
	SDSM 4613	10.19	11.35	4.74	4.83	8.31	8.00	2.24	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.03	1.04
	SDSM 4614	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 54348	16.90	22.23	8.27	8.56	13.56	15.14	2.67	8.88	9.34	4.48	4.93	2.34	3.42	5.48	5.02	9.53	11.95	2.75	2.75
Gammon	SDSM 71733	12.56	n/a	4.64	5.32	n/a	9.87	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	8.61	3.2	2.85
Niobrara Formation	YPM 3602	8.19	12.05	4.35	5.20	7.05	7.60	1.69	6.2*	n/a	n/a	2.70	n/a	2.20	n/a	2.80	5.85	5.00	1.33	1.15
	USNM 11560	13.04	n/a	6.10	6.80	10.20	11.40	2.00	6.00	n/a	3.20	3.20	2.02	2.18	3.90	3.70	8.00	n/a	2.20	1.18
	KU 1212	11.85	13.62	5.33	6.59	9.63	9.27	1.73	5.05	n/a	2.56	2.35	1.73	2.09	2.38	2.35	7.27*	8.91	1.73	1.42
	AMNH 5118	11.82	15.05	5.50	6.36	9.41	10.71	2.09	5.64	n/a	2.73	3.00	2.00	1.64	3.64	3.55	9.09	8.91	1.78	1.38
	YPM 3604	11.00	14.27	5.64	6.00	9.09	10.30	1.93	6.00	n/a	2.67	3.67	2.10	1.67	3.93	2.80	6.33	8.47	1.67	1.47
	AMNH 1497	11.40	14.40	5.36	6.18	9.63	9.33	1.80	5.6*	n/a	n/a	2.47	n/a	1.93	n/a	3.23	5.87	7.33*	1.27	1.17
	YPM 3609	10.64	11.62	5.07	5.87	8.13	8.89	2.10	6.36*	n/a	n/a	2.80	n/a	1.84	n/a	3.82	5.36	7.09*	1.73	1.25

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*Incomplete specimen, measurements were estimated; when possible, taken to the skull midline and doubled

n/a=Character on specimen was absent or not measured

Lith. Unit	Specimen Number	Inner quadrate distance (cm)	Width of left quadrate (cm)	Width of right quadrate (cm)	Width of Occitpital condyle (cm)	Length from OC to end of crest (cm)	Distance between lateral sides of orbital-nasal foramina (cm)	Distance between medial sides of orbital-nasal foramina (cm)	Distance between lateral sides of Posterior palatal foramina (cm)	Distance between medial sides of Posterior palatal foramina (cm)	Longest length of left Posterior palatal foramina (cm)	Longest length of right Posterior palatal foramina (cm)	Distance between external pterygoid processes (cm)	Width of constricted pterygoid (cm)	Maxillary width at mid-maxilla (cm)	Width of premaxillary beak on ventral side (cm)	Maxilla width across pmx-max suture (cm)
DeGrey Formation	SDSM 71693	8.8	2.14	2.1	1.66	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.92	1.94	2.27
Mitten Black Shale Formation	SDSM 71703	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	4.22	5.58	2.46	3.68
	SDSM 71705	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 71706	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 425	9.77	3.00	2.95	1.95	6.37	3.49	0.09	6.66	4.56	1.59	1.66	n/a	3.99	8.12	2.04	3.53
Sharon Springs Formation	SDSM 71713	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 71716	n/a	n/a	n/a	n/a	n/a	2.7	1.1	4.5	3.78	n/a	n/a	n/a	2.48	4.05	1.72	2.05
	SDSM 53800	9.77	2.75	2.63	1.84	3.48	2.82	0.61	n/a	n/a	n/a	n/a	8.05	4.36	8.29	1.62	3.52
	SDSM 71721	n/a	n/a	n/a	1.95	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	3.99	7.10	1.47	2.48
	SDSM 71722	n/a	n/a	n/a	n/a	n/a	1.42	0.57	2.72	0.7	n/a	n/a	n/a	n/a	5.52	3	3.9
	SDSM 51418	7.66	2.14	2.31	1.66	n/a	2.55	0.91	5.12	3.12	n/a	1.30	6.51	3.37	3.77	2.25	2.33
	SDSM 56130	n/a	n/a	n/a	n/a	1.06	1.36	0.81	n/a	n/a	n/a	n/a	n/a	1.47	n/a	1.08	n/a
	SDSM 52143	9.61	3.09	2.96	1.83	6.51	n/a	n/a	5.79	4.43	1.35	0.72	n/a	4.73	6.44	1.40	2.85
	SDSM 56135	n/a	n/a	n/a	n/a	n/a	n/a	0.06	n/a	n/a	n/a	n/a	n/a	n/a	4.13	1.26	1.92
	SDSM 6710	n/a	n/a	n/a	n/a	n/a	1.62	0.04	n/a	n/a	n/a	n/a	n/a	n/a	3.56	0.70	1.84
	SDSM 482	9.16	2.72	2.89	1.67	5.27	2.34	1.45	4.77	3.85	1.21	1.56	8.23	4.09	5.63	1.90	2.74
	SDSM 4610	10.53	2.89	3.15	1.87	4.41	4.19	0.10	7.68	5.73	n/a	n/a	8.79	4.50	8.83	2.28	3.88
	SDSM 4613	5.20	n/a	0.86	1.29	n/a	1.91	5.39	3.73	2.41	n/a	n/a	n/a	2.19	3.81	1.24	1.97
	SDSM 4614	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 54348	10.31	2.64	2.22	2.15	5.37	n/a	n/a	n/a	3.99	n/a	1.99	n/a	4.02	8.50	2.43	n/a
Gammon	SDSM 71733	n/a	n/a	n/a	n/a	n/a	2.01	0.65	5.07	3.22	n/a	0.95	6.01	3.44	5.54	1.21	3.9
Niobrara Formation	YPM 3602	5.2*	n/a	1.30	1.25	2.65	n/a	n/a	n/a	n/a	n/a	n/a	n/a	1.68	4.40	1.30	1.80
	USNM 11560	8.02	1.84	1.82	1.44	n/a	n/a	n/a	n/a	n/a	n/a	n/a	6.20	2.60	4.70	1.80	3.10
	KU 1212	6.45	1.42	1.49	1.36	1.64	n/a	n/a	n/a	n/a	n/a	n/a	3.82	2.00	6.60	1.33	3.50
	AMNH 5118	6.91	1.80	2.00	1.27	3.31	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.55	4.89	1.58	3.09
	YPM 3604	6.73	1.60	1.60	1.13	3.47	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.60	4.67	1.23	2.80
	AMNH 1497	6.13	1.48	1.47	0.67	3.27	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.13	4.13	1.10	2.40
	YPM 3609	5.73	1.65	1.45	1.27	1.36	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2.09	4.00	1.09	2.45

MEASUREMENT DATA

Abbreviations of Institutions

AMNH=American Museum of Natural History^{+}
KU=University of Kansas Museum of Natural History^{+}
SDSM=South Dakota School of Mines and Technology
USNM=United States National Museum^{+}
YPM=Yale Peabody Museum^{+}

$^{+}$Measurements were obtained from photographs taken from Zangerl, 1953

*Incomplete specimen, measurements were estimated; when possible, taken to the skull midline and doubled

n/a=Character on specimen was absent or not measured

Lith. Unit	Specimen Number	Height of Premaxilla (cm)	Depth of pmx pit (cm)	Angle of Cranial Mandible	Length of mandibular symphysis (cm)	Length of Ramus (cm)	Width of dentary (cm)	Length of right articular (cm)	Length of left articular (cm)	Width of right articular (cm)	Width of left articular (cm)	Distance between coronoid processes (cm)	Height of coronoid process (cm)	Length of right uppper meckelian fossa (cm)	Length of left upper meckelian fossa (cm)
DeGrey Formation	SDSM 71693	1.44	n/a	88	2.31	12.6	2.41	1.94	1.95	1.18	0.66	n/a	n/a	n/a	n/a
Mitten Black Shale Formation	SDSM 71703	1.84	1.23	104	n/a	n/a	2.78	n/a	n/a	n/a	n/a	n/a	4.28	n/a	n/a
	SDSM 71705	n/a	n/a	n/a	1.89	n/a	1.15	n/a	n/a	n/a	n/a	n/a	1.38	n/a	n/a
	SDSM 71706	n/a	n/a	n/a	1.61	n/a	1.34	n/a	n/a	n/a	n/a	n/a	1.58	n/a	n/a
	SDSM 425	1.63	1.13	90.00	3.39	15.37	2.76	3.94	3.90	2.61	2.47	11.50	2.94	2.28	2.38
Sharon Springs Formation	SDSM 71713	n/a	n/a	n/a	2.92	n/a	2.56	2.88	n/a	2.86	n/a	n/a	3.86	2.71	n/a
	SDSM 71716	0.96	0.66	112	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 53800	1.89	1.47	88.00	2.99	5.91	2.59	3.25	n/a	2.19	n/a	11.51	2.86	n/a	n/a
	SDSM 71721	0.96	0.40	88.00	n/a	13.00	2.48	n/a	2.40	n/a	2.17	n/a	3.04	n/a	2.02
	SDSM 71722	1.54	0.9	87	3.96	15.46	3.01	n/a	n/a	n/a	n/a	9.8	3.8	n/a	n/a
	SDSM 51418	1.68	1.30	97.00	2.45	n/a	1.98	2.15	2.18	1.01	0.95	8.60	2.01	n/a	n/a
	SDSM 56130	n/a	n/a	79.00	1.41	6.79	1.18	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 52143	3.02	1.74	96.00	4.50	14.98	2.25	n/a	n/a	n/a	n/a	9.50	4.39	n/a	n/a
	SDSM 56135	0.61	n/a	62.00	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 6710	0.00	n/a	95.00	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 482	1.89	1.66	90.00	3.71	15.47	1.98	3.24	n/a	1.32	n/a	11.99	3.72	n/a	2.97
	SDSM 4610	1.64	1.19	96.00	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SDSM 4613	0.78	n/a	87.00	n/a	n/a	1.09	n/a	n/a	n/a	n/a	n/a	1.31	1.62	n/a
	SDSM 4614	n/a	n/a	n/a	2.06	13.41	1.21	2.79	n/a	2.09	n/a	n/a	n/a	2.20	n/a
	SDSM 54348	n/a	n/a	97.00	3.06	14.59	2.07	3.00	3.56	1.59	n/a	n/a	2.38	n/a	n/a
Gammon	SDSM 71733	1.09	n/a	94	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Niobrara Formation	YPM 3602	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	USNM 11560	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	KU 1212	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	AMNH 5118	n/a	n/a	n/a	1.47	10.16	1.37	2.09	2.00	1.82	1.88	7.25	n/a	n/a	n/a
	YPM 3604	n/a	n/a	n/a	1.67	10.00	0.93	2.40	2.40	1.67	1.40	8.13	n/a	n/a	n/a
	AMNH 1497	n/a	n/a	n/a	1.40	7.93*	0.93	n/a	n/a	n/a	n/a	6.73	n/a	n/a	n/a
	YPM 3609	n/a	n/a	n/a	0.91	9.09	1.00	1.73	n/a	1.35	n/a	n/a	n/a	n/a	n/a

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A new polycotylid plesiosaur (Reptilia; Sauropterygia) from the Greenhorn Limestone (Upper Cretaceous; lower upper Cenomanian), Black Hills, South Dakota

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ABSTRACT

A plesiosaur skeleton from the base of the Greenhorn Limestone (lower upper Cenomanian), western South Dakota, represents a new taxon tentatively referred to the Polycotylidae. The specimen possesses a number of features in common with the Polycotylidae, including an exceptionally elongate muzzle and mandibular symphysis, lack of a parietal foramen, homodont dentition, and faint striae only on the medial side of teeth. However, the palate and limb morphologies differ with respect to Polycotylidae as currently known. The pterygoids are united along their midline anterior to the parasphenoid, lacking an anterior interpterygoid vacuity. The preserved parasphenoid is relatively robust, possesses a strong ventral keel, and is sutured to the dorsal surface of the pterygoids. The paddles possess many plesiomorphic features, including only relatively minor postero-distal expansion of the propodials, epipodials that are longer than wide, a distinct antebrachial foramen, and relatively elongate phalanges. Derived features make it a plausible representative sister taxon to Polycotylidae, a prospect that is complemented by its stratigraphic position. This hypothesis is hampered by the palate morphology, which suggests a separate lineage of short-necked plesiosaurs far removed from genera classically assigned to Polycotylidae *(Dolichorhynchops, Polycotylus, Trinacromerum).* Nevertheless, the specimen represents the persistence of plesiomorphic limb traits and possession of a closed palate within an early polycotylid lineage until at least the early late Cenomanian in the Midcontinent of North America.

Keywords: Greenhorn, Cenomanian, Cretaceous, polycotylid, plesiosaur.

INTRODUCTION

In 1934, Charles C. Haas and his son, Arthur, collected the partial skeleton of a plesiosaur from the base of the Greenhorn Limestone in the northern Black Hills area of South Dakota (Fig. 1). They prepared major parts of the skeleton, including the skull, cervical vertebrae, and the left front and rear paddles. Mr. Haas consulted all of the scientific literature of the day and delved deeply into learning about and interpreting his find. He pronounced the skeleton "a curious mix of fish, reptile, and bird," and put together a detailed documentary but failed to find an American museum willing to purchase the specimen. A few years later he donated the specimen to the Adams Memorial Museum in Deadwood, South Dakota. The specimen was first identified by S.C. Simms, director of the Field Museum (Chicago) at that time, as *Trinacromerum bentonianum.* Upon first examining the specimen I determined it to be a new taxon based purely upon plesiomorphic features of the paddles (Schumacher, 1997). The

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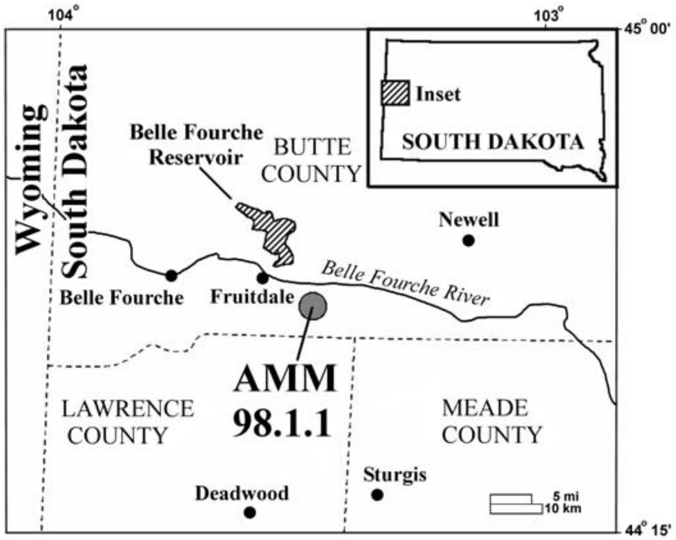

Figure 1. Location map of *Pahasapasaurus haasi* excavation site in western South Dakota.

unexpected nature of the palate was not known until later preparation of the skull's ventral surface (Schumacher, 1999). In the late 1990s the skull, anterior cervicals, and left paddles underwent further preparation for removal of aged shellac, and the remainder of the axial skeleton was removed from the original sugar sack and paste field wrappings employed by Mr. Haas. In recent years the Adams Memorial Museum has built an interpretive display around the fully prepared specimen (Fig. 2), and the skeleton is easily accessible for research purposes.

Institutional Abbreviations

AMM: Adams Memorial Museum, Deadwood, South Dakota; **AMNH:** American Museum of Natural History, New York; **FHSM:** Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas; **FMNH:** Field Museum of Natural History, Chicago, Illinois; **KUVP:** Museum of Natural History, University of Kansas, Lawrence; **BMNH:** The Natural History Museum, London; **SDSM:** Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota; **USNM:** U.S. National Museum, Washington DC; **YPM:** Yale Peabody Museum, New Haven, Connecticut.

Anatomical Abbreviations

ac, acoustic chamber; bo, basioccipital; bs, basisphenoid; cf, carotid foramina; d, dentary; ec, ectopterygoid; fr, frontal; mx, maxilla; nc, infilling of internal narial chamber; oc, occipital condyle; oe, opisthotic-exoccipital; pa, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; ptf, pterygoid facet of basioccipital; so, supraoccipital; v, vomer; vf, vomeronasal fenestra.

Measurements

The following criteria are used for data presented in Tables 1 and 2. Snout length is quantified as the distance from the tip of the premaxilla to the anterior end of the parasphenoid, divided by total skull length. Measurements of limb elements are expressed as maximum length divided by maximum width. Direct comparison of similar phalanges from different individuals is usually not possible, because few articulated and undisturbed paddles exist. Thus, phalangeal proportions are reported as an average of proximal phalanges in digits 2 through 4 from an individual paddle. It is noteworthy that overall phalanx length increases slightly and regularly from digits 1 to 5. The leading and trailing digits of the paddles (digits 1 and 5) contain phalanges with the shortest and the longest length/width ratios, respectively, and were excluded. Phalanx length is a significant and useful character in that gross proportion remains the same in individual specimens. For instance, if the proximal phalanges are relatively short, so are the more distal ones. These observations hold true in forelimbs and hind limbs.

SYSTEMATIC PALEONTOLOGY

Plesiosauria de Blainville, 1835
Polycotylidae Williston, 1908
Pahasapasaurus, gen. nov.

Genotype. *Pahasapasaurus haasi.*

Type species. *Pahasapasaurus haasi,* sp. nov.

Stratigraphic occurrence. Field notes of C. Haas state that the specimen originated in the "sharkstooth sandstone, Graneros Formation along Maloney Creek, Butte County, South Dakota." Cobban (1951) reassigned this bed as the base of the Greenhorn Formation, Gries and Martin (1985) referred the unit to the Greenhorn Limestone, and VonLoh and Bell (1998) assigned this as the basal Orman Lake Member of the Greenhorn Formation. At the time Mr. Haas collected the specimen, he had the foresight to retain associated materials from the excavation pit. In the Black Hills and throughout the Western Interior the base of the Greenhorn is marked by characteristic calcarenite (as defined by Folk, 1974) layers, which are rich in shark teeth and other particulate vertebrate material (Hattin, 1975). One slab of calcarenite matrix retained with the specimen bears an impression of the ammonite *Dunveganoceras pondi* (early late Cenomanian). Numerous teeth of sharks and bony fish were encountered during preparation of the unopened blocks, including *Squalicorax falcatus, Cretodus* sp., *Cretolamna appendiculata, Ptychodus occidentalis, Pachyrhizodus* sp., *Protosphyraena* sp., and *Enchodus* sp. Examination of the enclosing matrix, identification of associated fossil materials, and photographs taken at the excavation site in 1934 (Fig. 3) conclusively demonstrate that the specimen originated at the base of the Greenhorn Limestone.

Age. Late Cretaceous, early late Cenomanian.

Figure 2. *Pahasapasaurus haasi* skeleton during exhibit preparation. Left paddles are displayed on right side of specimen, and both paddles are positioned too far forward in order to fit within display case. Vertebral column terminates (left) with poorly preserved posterior trunk vertebrae. Note the visibly elongate neck, even though the front paddle is positioned next to posterior cervicals.

Type locality. Along Maloney Creek, just south of the Belle Fourche River, roughly 6 mi (8 km) southeast of Fruitdale, T. 8 N., R. 4 E., Butte County, South Dakota.

Etymology. Paha Sapa, Sioux Indian words meaning Black Hills.

Diagnosis. As for type and only species.

Pahasapasaurus haasi, sp. nov.
(Figs. 2–7)

Holotype. AMM 98.1.1, *Pahasapasaurus haasi,* gen. *et* sp. nov., including a partial skull, portions of left front and rear paddles, poorly preserved vertebral column and rib portions. Casts of the skull and front paddle are housed at SDSM.

Etymology. Named in honor of Charles C. Haas, who discovered, collected, and initially prepared and researched the specimen.

Diagnosis. A relatively large (~6 m in length), "long-beaked" plesiosaur possessing derived cranial features characteristic of polycotylids, a palate configuration unique among polycotylids, and plesiomorphic paddle morphologies. Diagnostic characters include anterior interpterygoid vacuity absent; pterygoids united along midline anterior to parasphenoid; parasphenoid relatively robust element, possessing prominent ventral keel and sutured to dorsal surface of pterygoids; pineal foramen absent; temporal fenestra elongate (as in *Trinacromerum*); symphysis elongate and including the splenial, encompassing the first 12 dentary teeth; teeth faintly striate on medial face; homodont dentition; teeth relatively robust; humerus sigmoidally curved; propodials bearing three distal facets and only a minor degree of posterodistal expansion; epipodials longer than wide, bearing distinct antebrachial foramen; phalanges rounded and elongate.

Description. The specimen includes a partial skull (Fig. 4) lacking the posterior portion of the suspensorium and palate. The squamosals, quadrates, jugals, and posterior portion of the pterygoids are the chief components missing; however, most of the basicranium is present. The posterior halves of the lower jaw are affixed to the skull by a hard, concretionary matrix and were left in this position for fear that their removal would jeopardize the integrity of attached pieces. In the future, it would be advisable to remove the lower jaw portions, allowing for a more accurate tooth count and an examination of the midpoint of the palate. The muzzle and symphyseal portion of the lower jaw are separate from the cranium and mandible along a vertical fracture. The sun-bleached condition of the basioccipital and first five cervical vertebrae

TABLE 1. RELATIVE PROPORTIONS OF SHORT-NECKED PLESIOSAUR CRANIA

	a	b	c	d	e	f
Pahasapasaurus haasi						
AMM 98.1.1	33.3	~90	37%	62.5	~87	72%
Liopleurodon ferox						
R. 3536	30.5	154.0	20%	–	–	–
R. 2680	–	–	–	67.2	109.6	61%
Brachauchenius lucasi						
FHSM VP321	41.0	172.5	24%	–	–	–
USNM 4989	–	–	–	56.3	90.0	63%
Peloneustes philarcus						
R. 3318	21.4	67.6	32%	–	–	–
R. 3803	20.4	70.3	29%	51.5	76.2	68%
Trinacromerum bentonianum						
KUVP 5070	33.5	74.5	45%	–	–	–
YPM 1129	25.2	67.2	37.5%	–	–	–
Dolichorhynchops osborni						
KUVP 1300	23.7	59.0	40%	39.4	53.5	74%
FHSM VP404	26.1	56.6	46%	37.5	51.0	73%
KUVP 40001	46.6	94.2	49%	67	90	74%
AMNH 5834	32.1	74.3	43%	54.3	69.3	78%
Polycotylus latipinnis						
SDSM 23020	46.5	98.0	47%	63.5	87.0	73%

Note: Length measurements are in centimeters; a—symphyseal length; b—lower jaw length; c—% length symphysis (a/b); d—snout length; e—skull length; f—% length snout (d/e).

indicates that these elements were exposed upon discovery. Details of the vertebral column are difficult to discern owing to deterioration and crushing prior to fossilization. Minimally, 21 cervical centra are present, but the posterior portion of the cervical series is heavily damaged, and a more accurate count is not possible. Most of the trunk vertebrae are present but in a very poor state of preservation. Small girdle fragments and numerous sections of ribs are better preserved but poorly represented. Most of the left front paddle is preserved, but it lacks the fifth digit and distal phalanges. Although the proximal podials and phalanges are articulated correctly, some mixing of phalanges is likely within the digits. Large portions of the left femur and proximal podials of the left paddle are well preserved but shattered and are missing numerous pieces. The overall length from the tip of the snout to the end of the preserved trunk series (likely extending to about the sacral area) is ~4.5 m, so the overall length of the animal was likely ~6 m. The maximum length of the humerus (45 cm) also illustrates the relatively large size of *P. haasi,* and in this respect is more similar to *Polycotylus* and *Trinacromerum* versus the smaller *Dolichorhynchops* (O'Keefe, 2004). *P. haasi* is ontogenetically mature, as indicated by its relatively large size and the lack of visible neuro-central sutures on the vertebrae.

SKULL: The skull is 75 cm in length from the tip of the premaxillae to the posterior edge of the occipital condyle. The preserved cranium is not crushed but is otherwise distorted, with the rostrum and lower jaws bent to the right, likely owing to post-burial deformation. The rostrum and anterior half of the lower jaws are well preserved, although lacking most of the teeth. As can be seen in Table 1, the snout and symphyseal lengths compare well with those of other polycotylid plesiosaurs. Several small teeth are preserved in the upper and lower jaws beneath the orbits. Of the larger teeth, only the anterior-most tooth of the left dentary is relatively complete, although portions of several others are present. The teeth exhibit distinct striae only on their medial sides. The dentition is homodont, with the size of alveoli gradually decreasing posteriorly. The premaxillae bear 6 teeth, the first 5 of which produce subtle swells on the lateral sides of the bones. The number of maxillary teeth is questionable because of poor preservation. The right maxilla bears 5 visible aveoli anteriorly and a series of 8 progressively smaller teeth extending to a point at the posterior edge of the orbit. Tooth spacing suggests room for 6 or 7 additional teeth for a total of 19 to 20 teeth

TABLE 2. LENGTH OVER WIDTH RATIOS OF LIMB ELEMENTS IN CRETACEOUS SHORT-NECKED PLESIOSAURS

	Humerus	Femur	Radius	Ulna	Tibia	Fibula	Phalanges
Pahasapasaurus haasi							
AMM 98.1.1	1.96	2.17	1.07	1.08	0.96	?	1.85
Trinacromerum bentonianum							
FHSM VP12059	1.90	1.94	0.82	0.74	0.70	0.87	1.76
USNM 10945			0.82	0.83	0.74	0.86	1.75
Dolichorhynchops osborni							
KUVP 1300	1.84	2.12	0.62	0.72	0.64	0.75	1.41
FHSM VP404	1.78	1.83	–	–	0.58	0.60	1.39
"Trinacromerum bonneri"							
KUVP 40002	1.65	1.8	0.59	0.78	0.68	0.75	1.32
Polycotylus latipinnis							
SDSM 23020	1.63	?	0.63	0.82	0.60	0.76	1.27
AMNH 1735	–	–	–	–	–	–	1.29
KUVP 5916	–	1.79	–	–	0.66	0.73	1.22

Figure 3. Arthur Haas, son of Charles, posing at the *Pahasapasaurus* dig site in 1934. At left lies the skull on its dorsal surface, with the vertebral column trending to beneath Arthur's feet.

in the right maxilla. Preservation of the lower jaw also limits the accuracy of a tooth count to ~25 in each dentary. Both the premaxillae and dentaries bear a high number of foramina on their lateral surfaces, with an especially high density of foramina at the anterior tips of both elements.

SKULL ROOF: The dorsal surface of the skull is preserved nearly to the posterior edge of the parietal and largely lacks the posterior and lateral borders of the temporal opening (squamosals, quadrates, and jugals). The midpoint of the skull roof is missing, and the configuration of various elements here is difficult to discern. Small portions of the right and left postfrontals are attached to the parietal, indicating the posterior border of the orbits. The right postorbital bar is largely missing, but the left has been flattened on the left maxilla and palatine. The orbital openings are large, rounded, and ovoid with the height less than the length. The missing region of skull roof reveals two well-defined masses of ferruginous marl that filled the internal narial chambers. The infillings are oblate spheroids possessing a botryoidal surface that were bound dorsally by missing portions of the premaxillae, maxillae, and possibly the frontals. The preserved prefrontals likely contacted the frontals posteriorly, and contact the maxillae anteriorly. The antero-dorsal margin of the orbit is solidly constructed, unlike the delicate construction of this area in other polycotylids (Carpenter, 1996; O'Keefe, 2004), and there is no preservation of the external nares. The premaxillae are preserved to just anterior to the narial infillings, and the contacts of the premaxillae with the maxillae are traceable to this point. The anterior-most portion of the parietal is missing and reveals the frontals beneath. Posteriorly, the parietal is preserved to the point at which the element deflects laterally to define the posterior walls of the temporal fenestrae. Although the parietal crest is broken along its length, most of the element is preserved and bears no evidence of a foramen.

PALATE: The vomer is slender, elongate, and extends anteriorly to between the first and second premaxillary teeth. The posterior termination of the vomer, where it presumably contacts the pterygoids and palatines at the internal nares, is masked by the midpoint of the attached lower jaw. Both of the palatines are broken and shifted medially and broadly overlap the pterygoids. The anterior half of the left palatine lies along the midline next to the right palatine, obscuring the anterior processes of the pterygoids. Ectopterygoids either are not preserved or not discernible owing to the displacement of the palatines. Unlike typical polycotylids (Carpenter, 1996; O'Keefe 2001, 2004), the pterygoids are tightly united along the midline, and an anterior interpterygoid vacuity is absent. The pterygoids do not trend anteriorly to slender rounded bars as in typical polycotylids, and the entire visible ventral surface anterior to the parasphenoid is a sheet of solid bone. On their dorsal surfaces, each pterygoid bears a ridge along the midline. This feature is not reflected on the ventral surfaces, which are subtly concave along the midline, and thus the pterygoids have the form of flattened triangles in cross section. The pterygoids are preserved to a position just beyond the posterior interpterygoid vacuity. The kidney-shaped central plates of the pterygoids that lie lateral to the posterior interpterygoid vacuity in typical polycotylids (as described by O'Keefe, 2004) are not preserved with the exception of small pieces affixed to the ventral surface of the basioccipital. The preserved parasphenoid is a relatively robust element possessing a thick ventral keel, unlike the flattened thin rod that is typical of most polycotylids. The parasphenoid is sutured to the dorsal surface of the pterygoids and exposed ventrally in a rounded notch where the united pterygoids separate posteriorly into the posterior interpterygoid vacuity. A break through the basicranium reveals paired canals interpreted as the carotid foramina. There is no apparent delineation between the basisphenoid and parasphenoid.

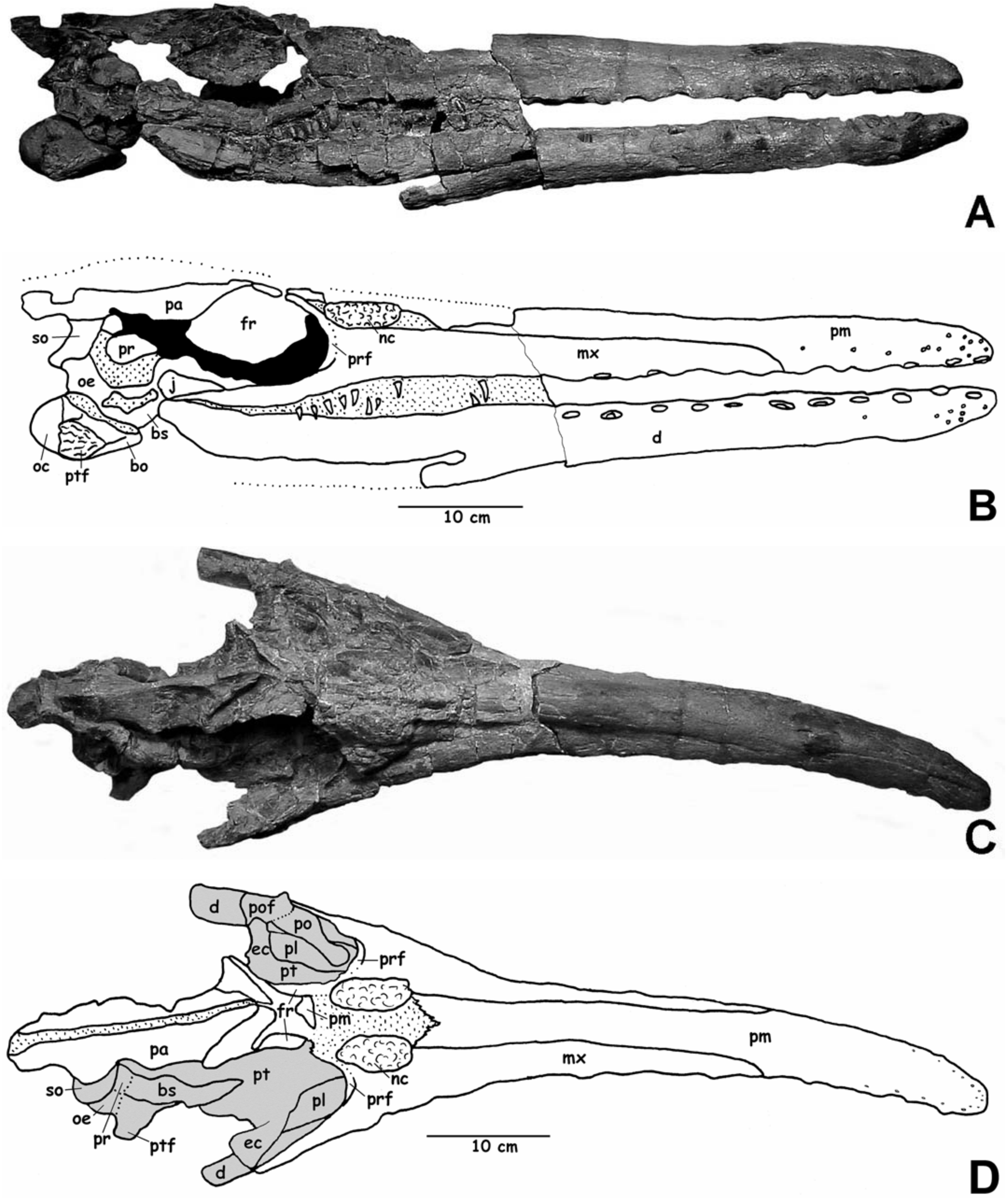

Figure 4. (*continued on the next page*) Skull, AMM 98.1.1. (A) Right lateral view. (B) Outline drawing in right lateral view. (C) Dorsal view. (D) Outline drawing in dorsal view.

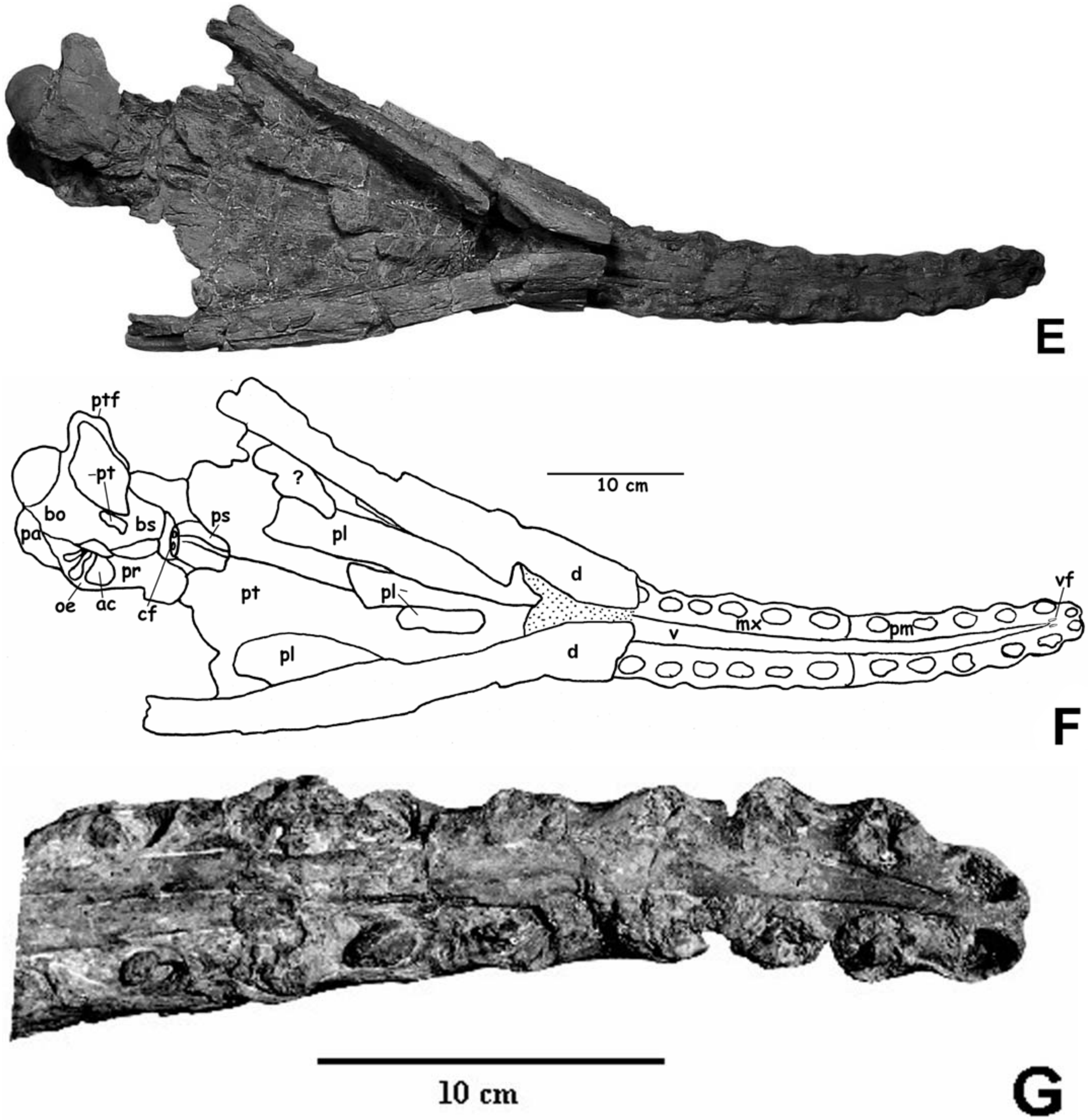

Figure 4. (*continued*) (E) Ventral view; note that anterior half of lower jaw has been removed. Skull, AMM 98.1.1. (F) Outline drawing in ventral view. (G) Symphyseal region of lower jaw in dorsal view.

MANDIBLE: The majority of both dentaries are present, although only the symphyseal portion is free from the cranium and well preserved. The mid-portion of each jaw remains in occlusion with the cranium attached by an ironstone matrix, and they are heavily weathered on their ventral surface. The posterior rami of both jaws are lacking, thus little or none of the articular, prearticular, coronoid, or surangular is preserved. Portions of the angulars and splenials are likely preserved, although poor preservation prevents distinguishing them from the dentary. The symphysis is enormously elongate (38 cm), extending nearly half the estimated total jaw length, and encompassing minimally the first 12 dentary teeth. In ventral view, a gap exists for a distance of

~5 cm beyond the fused dentaries before the point where the dentaries are inflected laterally at a greater angle. This is presumably the region occupied by an anterior projection of the splenials as figured by Williston (1908, Fig. 10) and O'Keefe (2004, Fig. 6). The continued anterior projection of the splenial into the wholly fused portion of the symphysis is not evident. Even the delineation between the right and left dentaries cannot be traced throughout their union along the ventral margin, likely owing to the late stage ontogeny of the individual. In dorsal view, what may be the anterior projections of the splenial extend to the eighth tooth position of the dentary.

RECONSTRUCTED SKULL: To assess the overall proportions of the skull in comparison with other polycotylids, and in particular to provide an accurate estimate as to the size and shape of the temporal openings, a model was sculpted of the complete skull using a plaster cast of the original as a base (Fig. 5). Teeth attributable to *Polycotylus latipinnis* in the collections of SDSM were used to complete the dentition, as large alveoli and thick tooth roots within the jaws of *Pahasapasaurus* suggest a robust tooth form. The postorbital bars extend from the existing portions of the postfrontals, and from there are sculpted to complete a smoothly rounded orbital area. The suspensorium is sculpted vertically, ending posteriorly at a position even with the occipital condyle, which coincides well with the posterior portion of the preserved parietal. The major realization from the model is the size of the temporal fenestrae, which are longer than wide as in *Trinacromerum* (Carpenter, 1996; O'Keefe, 2004). Were the suspensorium reconstructed with an anterior tilt and jaw articulation extending beyond the occipital condyle, as in *Trinacromerum* (O'Keefe, 2004), the lateral temporal bars would be longer still. On the basis of the long temporal fenestrae, the parietal crest is reconstructed as a low subtle ridge, as in *Trinacromerum* (Carpenter, 1996) and *Polycotylus* (O'Keefe, 2004), versus the high, arched crest of *Dolichorhynchops,* which has shorter temporal fenestrae. The sculpted skull is on display in the AMM along with the type specimen.

VERTEBRAE: Of the vertebrae present, only the anterior cervicals are relatively well preserved, although they are flattened (Fig. 6). Distinguishing the various components of the atlanto-axial complex is hampered by poor preservation, and whether or not the atlas centrum is exposed on the lateral sides, as in cryptocleidoids (O'Keefe, 2004), is not discernible. Despite being distorted, it can be noted that the anterior cervical vertebral centra were more or less equidimensional or perhaps slightly wider than long, but not extremely shortened as in *Polycotylus* (Storrs, 1999). The lateral walls of the anterior cervical centra are slightly concave. The articular facets are well scalloped, and the ventral surfaces bear the subcentralia foramina common to all plesiosaurs. Smaller paired foramina are also on the dorsal surface of the centra within the neural canal. The proximal heads of some cervical ribs remain attached to the vertebrae and are single headed. The remainder of the preserved presacral series is severely crushed and obscured by partial decomposition prior to fossilization, and accurate assessment of vertebral centra from this portion of the series is not possible.

LIMB ELEMENTS: The paddles of *P. haasi* are unique among polycotylids, as they retain many primitive characteristics (Fig. 7). The humerus measures 45 cm in maximum length, with only a relatively minor degree of postero-distal expansion (see Table 2). Three distinct facets are on the distal margin of the humerus for articulation of the epipodials, but the endochondral margin of the articular area continues around the postero-distal corner. The humerus displays the sigmoid curvature discussed by O'Keefe (2004), as weakly expressed in *Trinacromerum* and *Dolichorhynchops* and strongly present in *Polycotylus*. However, the upper portion of the shaft is crushed and appears to have skewed the angle of the humeral head posteriorly. The radius and ulna contrast markedly with those of other polycotylids, as they are relatively large elements compared to overall paddle size, are longer than wide, and enclose an elongate antebrachial foramen. The shafts of both the radius and ulna are entirely surrounded by perichondral bone, whereas typical polycotylids have endochondral bone surrounding these elements on all but the leading edge of the radius. Although not articulated with the paddle as originally on display, a supernumerary epipodial was assembled from loose fragments and seems likely to have originated from the

Figure 5. Reconstructed skull of *Pahasapasaurus haasi*.

Figure 6. From left to right: basioccipital, atlas-axis complex, and cervical vertebrae 3 through 5 in ventro-lateral view.

front paddle as shown in Figures 7a,c. The phalanges are long in comparison with those of other polycotylids and are rounded in cross section, with the shafts enveloped in perichondral bone. In all of these features, *P. haasi* retains primitive traits in its paddle morphology.

Metacarpal II of *P. haasi* also differs from that of other polycotylids. As seen in the type specimens of *T. bentonianum* (USNM 10945), *D. osborni* (KUVP 1300), and *P. latipinnis* (AMNH 1735), metapodial II in both the forelimb and hind limb is an element easily distinguishable from any other podial. The proximal border exhibits a convex v-shaped articulation that is shared between distal podial 1 and fused distal podial 2–3. Metacarpal II in *P. haasi* possesses only a very small articular area on its antero-proximal border for contact with distal carpal 1.

The hind limb has been shattered and is thus less well preserved than the forelimb. The tibia is roughly equidimensional, and the fibula appears to be longer than wide but is incompletely preserved. As with the radius and ulna, the tibia and fibula enclose a long epipodial foramen. The femur is 49 cm in maximum length, which is slightly longer than the humerus. This is typical

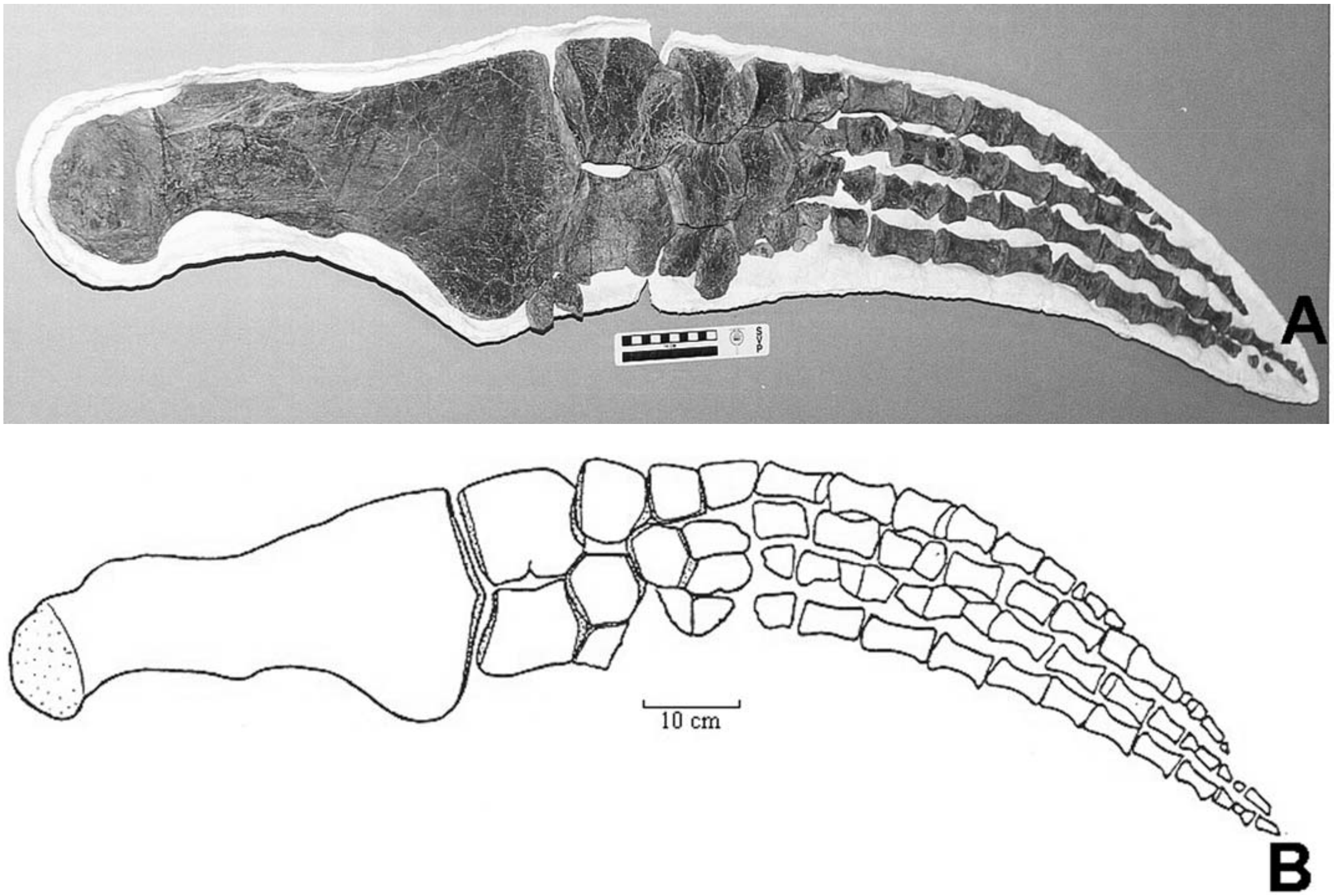

Figure 7. (*continued on the next two pages*) Left paddles, AMM 98.1.1, in ventral view. (A) Forelimb. (B) Outline drawing of forelimb.

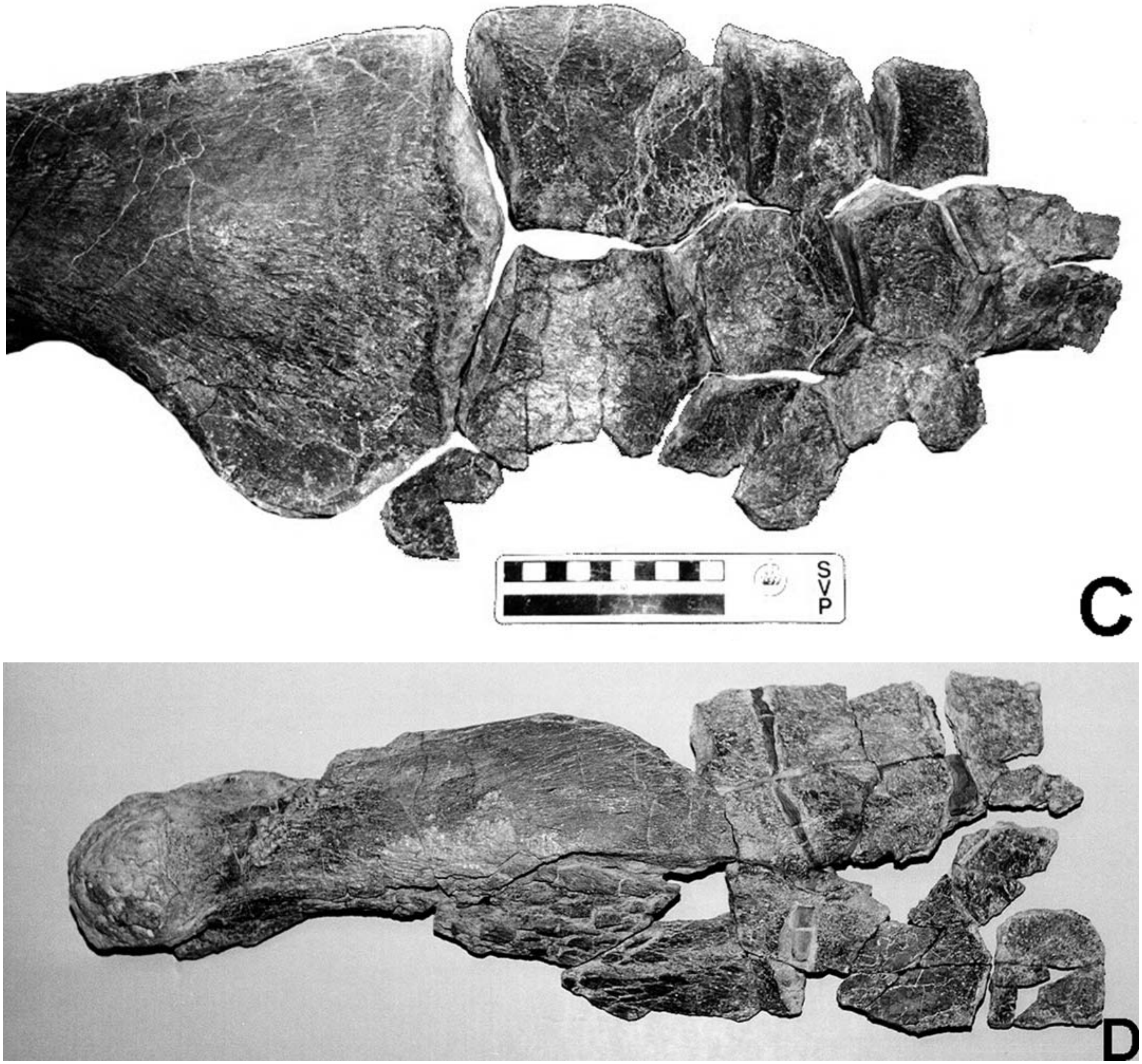

Figure 7. (*continued*) (C) Epipodials and mesopodials of forelimb. (D) Hind limb.

for polycotylids, as the femora are slightly longer but slightly less posterdistally expanded than the humeri (Table 2).

GASTROLITHS: Along with associated objects recovered from the *P. haasi* excavation pit were a number of silicic stones purported to be gastroliths. Recent literature has addressed the possibility of distinguishing true gastroliths from other polished stones based upon micro-texture and lithology (Johnston et al., 1994; Whittle and Onorato, 2000; Wings, 2004). Above all else, context is the most definitive aspect in the case for gastroliths. Stones intimately associated with fossil skeletons and occurring in offshore marine environments, where abiotic input of pebble size materials is highly unlikely, can be more confidently argued to be gastroliths. Only two of the stones originally on display with *P. haasi* are likely gastroliths. They are both ~3 cm in maximum dimension and are the only two stones coated with the shellac varnish used in the initial preparation of the skeleton. Moreover, only these two stones exhibit a rusty ferruginous rind from the enclosing bedrock. Four other larger stones are irregular in shape and are brightly colored and highly polished. It is likely that these stones were simply added to the original two gastroliths over the years to

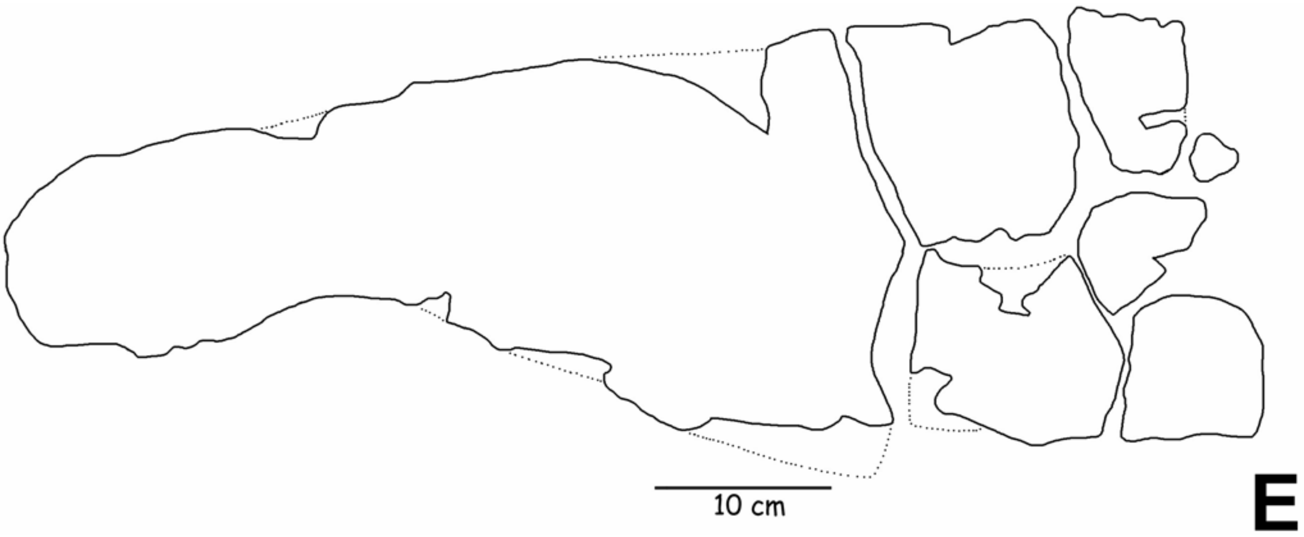

Figure 7. (*continued*) (E) Outline drawing of hind limb.

enhance the museum display. While preparing a small block containing portions of dorsal vertebrae, a third silicic stone similar to the other two was noted intimately embedded within the matrix.

This is not the first reported case of suspect gastroliths occurring with the skeleton of a short-necked plesiosaur. Other accounts include stones with the pliosaur *Peloneustes* (Andrews, 1913) and polycotylids (Martin and Kennedy, 1988; Sato and Storrs, 2000). In 1994 the author collected an association of cf. polycotylid vertebrae with small silicic stones from the Belle Fourche Shale (lower middle Cenomanian) in Rapid City, South Dakota. Although documentation exists to substantiate the use of stones by pliosaurid and polycotylid taxa, the number and sizes of the stones are much smaller than those commonly reported in association with elasmosaur skeletons (Williston, 1893; Riggs, 1939; Welles and Bump, 1949; Darby and Ojakangas, 1980; Storrs, 1993; Everhart, 2000). Also, there are significantly more polycotylid skeletons for which no association of gastroliths exists in comparison with elasmosaurid specimens. Whether the employment of gastroliths in plesiosaurs was for buoyancy (Williston, 1893) and/or as a mechanism to aid in digestion (Brown, 1904; Everhart, 2004; McHenry et al., 2005), the ecology of long-necked forms demanded the practice to a higher degree than the short-necked forms.

CLADISTIC ANALYSIS

Pahasapasaurus was scored and included in the data matrix of O'Keefe (2004) using PAUP*4.0 (Swofford, 2001) and the same outgroup, parsimony parameters, and branch and bound algorithm employed by O'Keefe. Some characters listed as unknown for *Polycotylus* in the original matrix were scored on the basis of a nearly complete skull and skeleton (SDSM 23020). The analysis yielded seven most parsimonious trees having a tree length of 172, a consistency index excluding uninformative characters of 0.650, and a rescaled consistency index of 0.485. A strict consensus tree yields a single unresolved polytomy for the Polycotylidae (Fig. 8), and all other relationships below the Polycotylidae are similar to those derived by O'Keefe. Thus, inclusion of *P. haasi* within the Polycotylidae is supported by the O'Keefe (2004) data matrix, but all resolution within the group is lost. An Adams consensus of this tree places *Edgarosaurus* and *Pahasapasaurus* as a clade of primitive taxa below the level of the polytomy including *Dolichorhynchops, Polycotylus,* and *Trinacromerum*. In this respect these results differ from those of

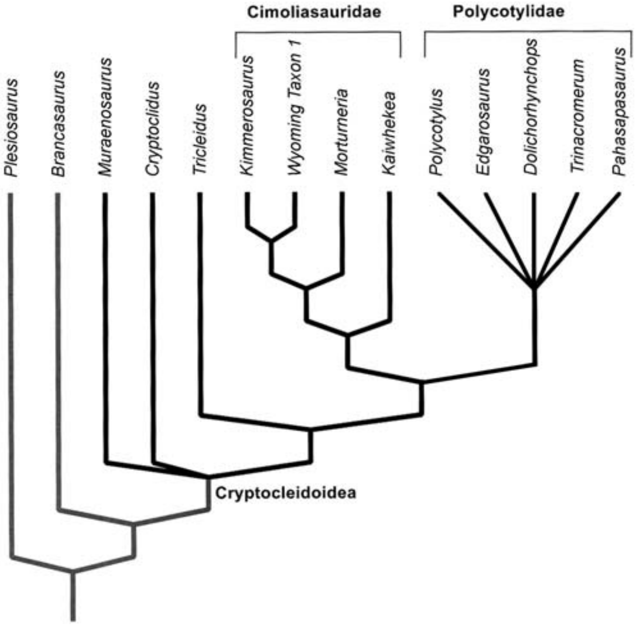

Figure 8. Cladogram of the Cryptocleidoidea (adapted from O'Keefe, 2004).

O'Keefe (2004), whose analysis consistently depicted *Polycotylus* as a sister taxon to other polycotylids.

DISCUSSION

Systematic Paleontology

Although in some respects *Pahasapasaurus* seems to be well placed within the modern definition of Polycotylidae (Carpenter, 1996; O'Keefe, 2004), it possesses characters that clash with the classical view of the clade. Historical definitions of Polycotylidae consistently included the presence of an interpterygoid vacuity and short epipodials (Williston, 1908; Welles, 1962; Carpenter, 1996). Brown (1981) noted a chronological trend for a shortening of the epipodials in Plesiosauria. Sato and Storrs (2000) and Albright et al. (2007)[1], discussed early polycotylids from Japan and Utah, respectively, and suggested that long epipodials of this specimen represent the retention of a primitive character within the Polycotylidae. The only portion of the polycotylid definition listed by O'Keefe (2004) that can be compared in *P. haasi* is the inclusion of the splenials within the symphysis. Although this character is not directly preserved in *P. haasi,* the space necessary to accommodate anterior extensions of the splenials between the dentaries is present. The O'Keefe definition does not mention short epipodials and also does not consider the nature of the pterygoids anterior to the parasphenoid. Although crucial areas of the *P. haasi* cranium are not preserved, certain fundamental characters are markedly different from any previously described polycotylid. The complete lack of an interpterygoid vacuity seems ill placed within the Polycotylidae. If one accepts the palate transformational series proposed by O'Keefe (2001, Fig. 21), the secondary closing of the interpterygoid vacuity occurred not just within the Elasmosauridae but potentially within a branch of the Polycotylidae as well. The parasphenoid of *P. haasi* is also not at all similar to polycotylids, having a more robust construction with a strong ventral keel, and terminating by suturing atop the coalesced pterygoids. Overall, the visible construction of the *P. haasi* palate looks more similar to that observed in pliosaurids such as *Peloneustes* and *Pliosaurus* (Linder, 1913). However, elasmosaurs like *Libonectes morgani* and *Callawayasaurus colombiensis* also lack an anterior interpterygoid vacuity, and they have a parasphenoid with a gracile ventral keel (Welles, 1962; Carpenter, 1997, 1999).

Tooth counts in *P. haasi* are suspect owing to preservation, and tooth counts overall seem to be a variable character within a particular taxon (Carpenter, 1996). But the presence of 6 premaxillary teeth is notable in comparison with the more usually reported number of 5 in polycotylids. Although neck length cannot be quantified, the value of minimally 21 cervical vertebrae is likely not missing a large number of the series; thus the complete cervical count of *P. haasi* is not significantly different than that of other polycotylids. Visibly (Fig. 2), the overall preserved neck length seems appreciably longer than the polycotylid *Dolichorhynchops* (Williston, 1903, plate 1), perhaps owing to less anteroposterior shortening of the cervical centra.

Several authors have pointed out that limb modifications, such as shortening and broadening of the epipodials and increased hyperphalangy, are evolutionary trends common to all plesiosaur lineages (Welles, 1943; Brown, 1981; Carpenter, 1997). In light of this, the appendicular morphology of polycotylids contains valuable phylogenetic markers for the clade. Polycotylid limb elements exhibit several key trends from the late Cenomanian to the middle Campanian in the Western Interior (Irwin and Schumacher, 2003). The paddles become more tightly knit through time, and individual elements more closely conform to each other. Podials evolve to shorter, wider elements, that unchecked would have resulted in shorter, wider appendages. The resultant loss in paddle length from podial shortening was likely accommodated by continued hyperphalangy, although testing of this hypothesis is hampered by relatively few fully articulated paddles. The foreshortening of bony elements applies throughout the paddle. For example, the podials and phalanges of *Trinacromerum* are consistently longer than those of *Dolichorhynchops* or *Polycotylus*. Likewise, the limb elements of *Pahasapasaurus* as a whole are proportionally longer than those of other polycotylids. Furthermore, this character lends some credence to the scrappy type specimen of *Polycotylus latipinnis,* which includes short, blocky phalanges (see Table 2). Postero-distal expansion of the propodials likely accommodates at least one supernumerary epipodial in *Pahasapasaurus*. More than one supernumerary in the epipodial row shows ontogenetic variability, but contrary to Carpenter (1996), I find the character to have taxonomic utility. No specimen of *Trinacromerum* that I am aware of exhibits a fourth epipodial, although there is room for a small such ossification. Specimens of *Dolichorhynchops* usually possess a small fourth epipodial in one or more of the limbs (Carpenter, 1996). Specimens of *Polycotylus* possess large, well-developed fourth metapodials (Williston, 1906), with a distinct facet for the ossification evident on the propodials (O'Keefe, 2004). These observations are apparent in comparing the length versus width ratios of propodials from the various taxa, where *Polycotylus* diplays the highest degree of postero-distal expansion (Table 2).

Phylogenetic Analysis

To this point much uncertainty remains in polycotylid phylogeny (Sato and Storrs, 2000; Druckenmiller, 2002; O'Keefe, 2004; Buchy et al., 2005; Albright et al., 2007). In just the last several years, seven new polycotylid taxa have been described, including *P. haasi* (Druckenmiller, 2002; Bardet et al., 2003; Buchy et al., 2005; Sato, 2005; Albright et al., 2007). All the newly erected taxa

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[1] As the present work was going to press, Albright et al.'s (2007) paper was published containing information highly pertinent to the content of this manuscript. Although their work could not be fully incorporated, it is noted that both *Pahasapasaurus haasi* and *Palmula quadratus* share the retention of primitive limb characters as outlined herein.

are monospecific and known from incomplete skeletons, greatly hampering the cladistic method by an abundance of unknown or uncertain character states. Given this, and after extensive testing of published and independent cladistic matrices, I concur with Buchy et al. (2005), who noted that the inclusion or removal of one or more taxa (and/or characters) can greatly modify the topology of the cladogram. I speculate that the lack of resolution within the Polycotylidae is due not only to the nature of available material but also in part to the dubious inclusion of *Edgarosaurus muddi* (Druckenmiller, 2002) within the group. This assertion is supported by the cladistic analysis of Albright et al. (2007). *E. muddi* possesses a suite of characters not in kind with the Polycotylidae, including 6 to 7 premaxillary teeth; constricted, scooplike snout and lower jaw; distinct parietal foramen; short symphysis; caniniform teeth; posterior extension of premaxilla not in contact with parietal; relatively short muzzle; suspensorium extending far posterior of the occipital condyle; and apomorphic paddle morphologies. Most of these listed characters are more commonly associated with members of the Pliosauridae.

In his phylogenetic analysis of the Cryptocleidoidea, O'Keefe (2004) included *Edgarosaurus* within his Polycotylidae, resulting in a polytomy with *Polycotylus* and other polycotylid plesiosaurs. O'Keefe (2001, 2004) further concluded that *Polycotylus* is a plausible representative sister taxon to other polycotylids based upon the presence of several primitive characters, including robust and heavily striated teeth; long and low sagittal crest; pterygoids narrowing lateral to the anterior interpterygoid vacuity; and a relatively large number of cervical vertebrae. The long and low sagittal crest is shared by *Trinacromerum* and possibly *Pahasapasaurus*. A narrowing of the pterygoid bars lateral to the anterior interpterygoid vacuity is a character that is shared by *Trinacromerum* and *Dolichorhynchops,* and differences in *Polycotylus* observed by O'Keefe (2004) are based upon an eroded pterygoid portion (FMNH 187). The apparent primitive condition of a higher cervical count could represent a reversal. *Polycotylus* shares other characters, although more derived, with *Trinacromerum* and/or *Dolichorhynchops,* including propodials (marked postero-distal expansion, sigmoid curvature of humerus); paddles (shorter podials, tightly knit phalanges with square cross sections, large supernumerary epipodials, patchy loss of perichondral bone around the margins of podials); vertebrae (short, deeply compressed lateral and ventral walls of centra); and pelvis (highly elongate ischia). In their review of plesiosaurs from the "Fort Benton" interval of Kansas, Schumacher and Everhart (2005) found that the only identifiable polycotylid known in pre-Coniacian deposits of North America is *Trinacromerum* and an unnamed polycotylid of Cenomanian age *(P. haasi)*. Thus, the known morphology and stratigraphic occurrence (early Campanian) of *Polycotylus* do not support the hypothesis that it is the sister taxon to more derived polycotylids. If *Pahasapasaurus* is accepted as a polycotylid, then the classic polycotylid palate construction and short epipodials of *Trinacromerum, Dolichorhynchops,* and *Polycotylus* indicate that they are all more closely related to each other than to *Pahasapasaurus*.

CONCLUSIONS

Pahasapasaurus haasi constitutes a new plesiosaur taxon of the Late Cretaceous Western Interior Seaway. Although most closely resembling a member of the Polycotylidae, it bears a number of features markedly different from classically known polycotylid morphology, including long epipodials and phalanges, a closed palate, and a robust parasphenoid bearing a strong ventral keel. The addition of *Pahasapasaurus* to existing cladistic analyses supports its inclusion within the Polycotylidae but destroys any resolution within the clade. *Edgarosaurus muddi* is a dubious member of the Polycotylidae owing to a suite of characters not held in kind with the group. Five new monospecific polycotylid taxa have been named in only the last few years, indicating that a great deal is still to be learned about their variation and diversity. Of North American genera ascribed to Polycotylidae, only two monospecific type specimens are from Cenomanian and older deposits *(Edgarosaurus, Pahasapasaurus)*. The three classically treated polycotylids of Turonian and younger age *(Dolichorhynchops, Polycotylus, Trinacromerum)* are better represented and somewhat better known. An improved understanding of polycotylid phylogeny and systematics will require new discoveries of poorly known pre-Turonian forms. Nevertheless, *Pahasapasaurus* indicates that a lineage of short-necked plesiosaurs with affinities to the Polycotylidae, but possessing a closed palate and plesiomorphic limbs, persisted until at least the early late Cenomanian in the Midcontinent of North America.

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Comparison of gastroliths within plesiosaurs (Elasmosauridae) from the Late Cretaceous marine deposits of Vega Island, Antarctic Peninsula, and the Missouri River area, South Dakota

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ABSTRACT

Elasmosaurid plesiosaur remains containing gastroliths have been recently recovered from the Late Cretaceous Cape Lamb Member of the Snow Hill Island Formation, Antarctic Peninsula, as well as from the Sharon Springs Formation of the Pierre Shale Group, South Dakota. The significance of the Antarctic specimens lies in the large number and relatively small size of the stones, whereas those from South Dakota and elsewhere have larger stones but relatively small numbers. All specimens compared are of relatively large elasmosaurids, and rib diameters indicate similar overall size. One testable hypothesis was whether or not the weight of the gastroliths might be similar among similarly sized individuals. However, comparisons between the gastroliths recovered from an Antarctic specimen and those recovered from the Pierre Shale show great differences in both the size and number of gastroliths. The total mass of the stones collected in the specimen from Antarctica was 3.0 kg, whereas those recovered from the South Dakota specimens totaled 2.2 kg and 8.3 kg, respectively. Perhaps not all stones originally within each plesiosaur were found, but efforts were designed to recover every stone. The number of stones recovered from the Antarctic plesiosaur was exceptionally large (2626) and appears to represent the most gastroliths recovered from a single plesiosaur. Those recovered from South Dakota elasmosaurids totaled only 124 and 253, respectively. Therefore, neither weight nor number of stones corresponds among these large individuals, perhaps mirroring the temporal or behavioral differences. Lack of correspondence among individuals furthers questions concerning the utilization of gastroliths for neutral buoyancy, ballast, or as an aid in digestion. Many parameters remain unexplored, and questions arise not only as to the utilization of the gastroliths but also as to whether physiology of the Antarctic plesiosaurs differs from those at lower latitudes.

Keywords: plesiosaurs, gastroliths, buoyancy, Antarctica.

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INTRODUCTION

During the austral summer of 1998–1999 a joint team of American and Argentine scientists recovered weathered and fragmented remains of an elasmosaurid plesiosaur and associated gastroliths. The remains are ontogenetically those of an adult, based on the large diameter (>4 cm) of recovered rib fragments. Most of the recovered quartzose gastroliths weighed <2 g, and the total weight is significantly less than that recovered from two elasmosaurids from the Late Cretaceous (Campanian) Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) in South Dakota. These plesiosaurs also yielded numerous gastroliths; however, the number and total mass of gastroliths found in both specimens from South Dakota are vastly different from those recovered from Antarctica. Therefore, little initial correlation of gastrolith function appears between plesiosaurs from South Dakota and Antarctica.

Hypotheses offered to explain gastrolith occurrences have included a role in buoyancy control, ballast, aid to digestion, relief of hunger pangs, geophagy, or a result of accidental ingestion while feeding on benthic organisms (Brown, 1904; Williston, 1893; Moodie, 1912; Darby and Ojakangas, 1980; Taylor, 1993; Everhart, 2000; Whittle and Everhart, 2000). The two primary hypotheses that dominate the debate of the physiological role of gastroliths, however, continue to be those of buoyancy control and utilization of gastroliths as a digestive aid (Brown, 1904; Darby and Ojakangas, 1980; Taylor, 1981, 1993, 1994; Everhart, 2000; Whittle and Everhart, 2000; Cicimurri and Everhart, 2001). Gastroliths in marine tetrapods, both extant and extinct, seem to be closely tied with those forms that employ “subaqueous flight,” such as sea lions, as well as the extinct plesiosaurs (Alexander, 1989; Taylor, 1981, 1993, 1994; Whittle and Everhart, 2000). Crocodilians are also known to possess gastroliths, and studies have been undertaken to better understand the role gastroliths serve in crocodilian biology (Cott, 1961; Darby and Ojakangas, 1980; Fisher, 1981; Hutton, 1987). Although some observations indicate that crocodilian gastroliths may be utilized in the digestive process, most authors suggest roles in hydrodynamic efficiency and buoyancy compensation.

Abbreviations

KUVP: University of Kansas University Museum of Natural History, Lawrence; **MLP:** Museo de La Plata, La Plata, Argentina; **NJSM:** New Jersey State Museum, Trenton; **SDSM:** South Dakota School of Mines and Technology, Museum of Geology, Rapid City.

Materials and Methods

Three primary specimens (Table 1) were used for comparison in this study: one from the Antarctic Peninsula, MLP 98-I-10–9, and two from the Missouri River Trench in central South Dakota, USA. The Antarctic specimen was weathered when found, but most of the rib cage–trunk area was preserved and removed in a series of plaster jackets. Immediately upon discovery, the numerous gastroliths were evident. No stones were found laterally, or above and below, indicating that the stones did indeed represent gastroliths. Two elasmosaurids are known from Antarctica, *Aristonectes* and another, probably assignable to *Mauisaurus* (Gasparini et al., 2003; Hiller et al., 2005; Martin and Crame, 2006; Martin and Fernández, 2007). To which elasmosaurid MLP 98-I-10–9 belongs cannot yet be positively determined. Two additional elasmosaurids that also contain numerous small gas-

TABLE 1. GASTROLITHS WITHIN LATE CRETACEOUS ELASMOSAURID PLESIOSAURS

Specimen	Total number of gastroliths	Total mass of gastroliths (kg)	Mass of largest stone (kg)	Mass of smallest stone (kg)
Styxosaurus snowii SDSM 451	253	8.249	0.580	0.008
Antarctic Elasmosauridae MLP 98-I-10–9	2626	3.021	0.046	0.00004
cf. *Styxosaurus* SDSM 77499	124	2.218	0.183	0.0005
Styxosaurus Darby and Ojakangas (1980)	197	8.840	0.662	0.005
cf. *Styxosaurus snowii* NJSM 15435	95	6.8	1.06	0.004
Elasmosauridae KUVP 1318	125	N/A	0.17	<0.001
Elasmosauridae KUVP 129744	47	13.078	1.49	0.007

troliths were observed in Antarctica by the second and third authors. Associated gastroliths were also noted with two Antarctic elasmosaurids by Chatterjee and Small (1989), indicating that MLP 98-I-10–9 is not an isolated occurrence.

One specimen from the Missouri River area of Lyman County, South Dakota, SDSM 451, was described by Welles and Bump (1949) as the type specimen of *Alzadasaurus pembertoni*. Carpenter (1999) suggested that *Alzadasaurus* is a synonym of *Styxosaurus* and that *A. pembertoni* is a synonym of *Styxosaurus snowii*. SDSM 451 is represented by a nearly complete, articulated skeleton, and the gastroliths were associated in the trunk region. Another elasmosaurid, SDSM 77499, from the Missouri River area, Charles Mix County, South Dakota, was collected by the Museum of Geology in 2003. The specimen includes the posterior portion of the neck articulated with the trunk area, and gastroliths were intimately associated in the trunk area. Because the trunk area was totally excavated, all stones were recovered that had been entombed with the carcass.

The South Dakota and Antarctic specimens were compared with other elasmosaurids from Kansas (Table 1). NJSM 15435 (Cicimurri and Everhart, 2001), KUVP 129744 (Everhart, 2000), and KUVP 1318 (Williston, 1893) were also recovered from the Sharon Springs Formation of the Pierre Shale Group. All of these specimens have associated, relatively large gastroliths. Another unnumbered specimen (Darby and Ojakangas, 1980) is represented by an elasmosaurid plesiosaur associated with gastroliths from Montana that was collected from the Campanian Bearpaw Shale.

Size comparisons among specimens are based upon similar rib sizes, and quantification of gastroliths was accomplished through counting and weighing of each stone as well as weighing all gastroliths from a single specimen to obtain total weights (Table 1). Identification of the stones as gastroliths was determined through intimate associations with skeletons, as well as through microscopic examination.

GEOLOGY

MLP 98-I-10–9, as well as other observed Antarctic specimens, occurred in the Cape Lamb Member of the Snow Hill Island Formation. The Cape Lamb Member (upper Campanian) constitutes most of the exposed area (Fig. 1) of the Cape Lamb Peninsula of Vega Island, Antarctic Peninsula (Crame et al., 1991, 2004; Marenssi and Santillana, 1998). The unit consists of massively bedded, silty sandstones to silty mudstones, which represent a transgressive-regressive cycle (Crame et al., 1991). The lithology of the unit is very important, because no concentrations of stones of any kind occur elsewhere in the unit with the exception of a conglomerate nearly 50 m above the level of the plesiosaur stones. Isolated stones are sometimes found "suspended" in the sedimentary units, but these stones are normally large and scattered vertically. The composition of the recovered gastroliths is predominantly quartzite, suggesting the notion that the origin of the stones was far from the location of the remains. This postulation is not surprising, as many plesiosaur remains have been recovered where the only known possible origin of the gastroliths is hundreds of kilometers away from the place of burial (Darby and Ojakangas, 1980; Everhart, 2000). However, the paleogeography during the Cretaceous was undoubtedly quite different from the geography of today; therefore, source postulations may be questionable.

The Pierre Shale of South Dakota represents deposition during the Late Cretaceous (Campanian) Western Interior Seaway. Numerous plesiosaur specimens have been recovered from this unit (Everhart, 2000; Martin and Kennedy, 1988; Welles, 1962; Welles and Bump, 1949), most of which occur in the Sharon Springs Formation, the lowest unit of the Pierre Shale Group, exposed along the Missouri River (see Martin et al., this volume). Although the precise level within the Sharon Springs of SDSM 451 is unknown, the level of SDSM 77499, from SDSM locality V2003–09, is at the contact between the lower bentonitic and the middle organic-rich units (Burning Brule and Boyer Bay Members, respectively, of an elevated Sharon Springs Formation in Martin et al., this volume). Gastroliths found in association with plesiosaurs in the Pierre Shale are, like those from Antarctica, usually far from any currently known source of similar lithology.

ASSOCIATED GASTROLITHS

Previous experiments in positively identifying gastroliths versus non-gastroliths have been conducted using video light-scattering instruments as well as the scanning electron microscope (Johnston et al., 1994; Whittle and Onorato, 2000). Whittle and Onorato (2000) indicated that satisfactory results could also be obtained using a simple light microscope. Comparing gastroliths to stones obtained from fluvial and marine environments showed a large difference in overall texture of the stones' surface. The gastroliths exhibited a surface that is normally smooth and even, with shallow pockmarks scattered across the surface. Antarctic gastroliths and those from SDSM 451 and SDSM 77499 exhibit similar features (Fig. 2). Therefore, the direct association of the three samples with plesiosaur carcasses and their distinctive surface texture proves that these stones are indeed gastroliths.

For comparison, the stones associated with the Antarctic specimen and South Dakota specimens were counted and weighed. The Antarctic specimen, MLP 98-I-10–9, contained 2626 gastroliths with a total mass of 3021 g. The largest stone recovered had a total mass of 46.6 g, whereas the smallest had a mass of 0.04 g. SDSM 77499, recovered from South Dakota, contained only 124 stones, with a total mass of ~2218 g. The largest stone recovered from this specimen weighed 187 g, whereas the smallest weighed 0.52 g. Welles and Bump (1949) reported 253 stones from *Alzadasaurus pembertoni* = *Styxosaurus snowii* (SDSM 451) with a total mass of 8249 g, the largest stone weighing 580 g. Darby and Ojakangas (1980) described the gastroliths recovered from a specimen of cf. *Alzadasaurus* = *Styxosaurus* and reported 197 associated gastroliths. The total weight of stones

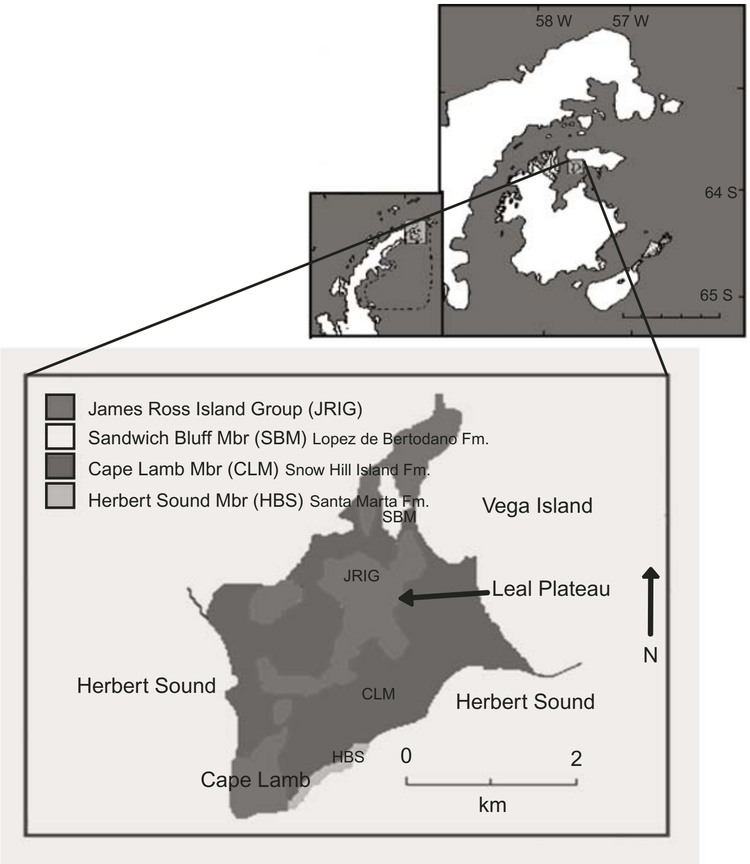
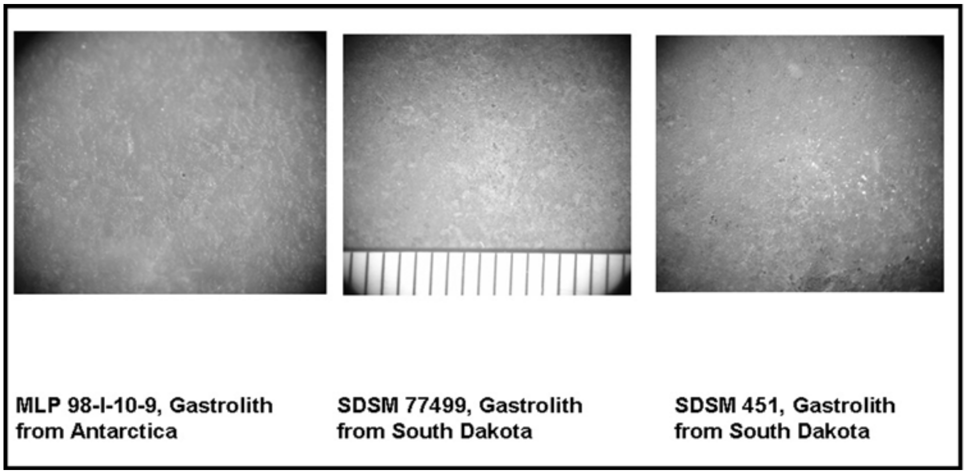


Figure 1. Diagrammatic geological map of Cape Lamb Peninsula of Vega Island in the James Ross Basin, the source of the Antarctic elasmosaurid, MLP 98-I-10–9.



MLP 98-I-10-9, Gastrolith from Antarctica

SDSM 77499, Gastrolith from South Dakota

SDSM 451, Gastrolith from South Dakota

Figure 2. Magnification (45×) of selected gastroliths exhibiting similar surface features and polish. Scale is in millimeters.

in this specimen was reported as 8840 g. The largest of these had a mass of 664 g, and the smallest 5 g. The largest mass and individual stone were found with KUVP 129744: 13.1 kg and 1.49 kg, respectively. The composition of observed stones is usually quartzite, quartz, indurated sandstone, or chert, and they are well rounded, slightly polished, and extremely smooth (Fig. 2).

DISCUSSION

An explanation for the recovery of relatively small stones may include the "bloat and float" hypothesis in which the animal dies, and gases from decomposition allow the carcass to float at the surface for a time prior to sinking and entombment (Brown, 1904; Everhart, 2000). If large stones were initially swallowed, at least some should be expected to have remained within the carcass, even if it were ruptured and a portion of the stones lost. This, however, does not seem to be the case in many instances (Brown, 1904; Everhart, 2000). The weight of the gastroliths inside the decaying soft tissues of a dead plesiosaur could have caused the tissue to fail, or alternatively, a scavenger could have released the stones during postmortem feeding. In either case, stones could be distributed far from the final resting place of the carcass. This hypothesis may explain the recovery of predominantly small stones. The small stones could have been trapped in the rugosities of the stomach lining and kept with the animal as it sank to the bottom. Nevertheless, as can be observed from Table 1, the largest gastrolith associated with the Antarctic plesiosaur is less than a quarter of the weight-size of the largest gastroliths associated with the South Dakota specimens, and the large number of gastroliths recovered suggests that no larger stones were ever ingested.

Another explanation of why such a large number of small gastroliths is associated with the Antarctic specimen in particular is that only small stones were originally swallowed. This could have been a matter of choice or availability of suitable material. Perhaps the taxon could only accommodate relatively small stones. In any case, the small stones could have settled to the ventral portion of the stomach where they could have become trapped in the rugosities of the stomach lining or between larger clasts. This, too, is consistent with the bloat and float hypothesis, as smaller stones would be less likely to be ejected, remain in the body cavity, and later be preserved. The retention of smaller stones seems to occur often in the fossil record (Martin and Kennedy, 1988; Taylor, 1993; Everhart, 2000).

The stones may also have been swallowed accidentally as the animal was feeding on benthic organisms. This is by no means a novel idea, but it may explain the large number of smaller stones in MLP 98-I-10–9 and their relatively small mass (Brown, 1904). These stones could have simply been mechanically weathered to a small size. This, however, seems highly unlikely owing to the resistant nature of quartzose clasts.

Given the relatively low mass and small size of the gastroliths in the Antarctic specimen, it is difficult to imagine their function in an efficient digestive role if the Antarctic elasmosaurids were piscivorous. Reports of broken but uncrushed bones, shells, and other remains of plesiosaur stomach contents may provide evidence that gastroliths did not completely pulverize ingested materials—contrary to the function in some dinosaurs, modern pinnipeds, and birds (Brown, 1904; Farlow, 1987; Stokes, 1987). Taylor (1993) raised the question as to why some but not all specimens possess gastroliths if they were important in digestive processes. Massare (1987) divided marine reptiles into a number of guilds on the basis of tooth morphology. According to this study, the tooth morphology of known elasmosaurids places them in a "piercing" or "general" guild, which indicates that morphology could be piercing, cutting, or smashing. The presence of principally piercing teeth could necessitate the use of a digestive aid such as gastroliths.

The alternative to gastroliths as a digestive aid is their role in buoyancy control and stability in the water column, much the same as in crocodilians (Taylor, 1993; Whittle and Everhart, 2000). However, the problem lies in the total weight of the recovered gastroliths of the Antarctic specimen in comparison with those from North America. The greatest gastrolith mass known from a plesiosaur in North America (Everhart, 2000) is 13 kg, associated with a skeleton (KUVP 129744) from the Pierre Shale of Kansas in comparison with only 2.6 kg from the large elasmosaurid from Antarctica. See Table 1 for number and weight comparisons. Although the total mass of gastroliths in all specimens considered may be low, their placement in the body may negate their lack of mass. The specimen of *Styxosaurus* described by Darby and Ojakangas (1980) was associated with 8.84 kg of stones close to the pectoral paddle. Owing to the fragmentary nature of the Antarctic specimen, the location of the recovered gastroliths can be isolated only to the trunk area. According to Taylor (1993), gastroliths may have been a mechanism to keep the lung area as a fulcrum for balance between the heavy neck and posterior body. Kept in the stomach, or possibly a gizzard, the stones would have behaved similarly to those found in a crocodile, allowing the animal to maintain its position in the water column (Darby and Ojakangas, 1980; Taylor, 1981). Following Massare's (1988) study on the swimming abilities of marine reptiles, elasmosaurid plesiosaurs may not have been fast, agile swimmers but instead ambush predators, and the gastroliths would have allowed them to more easily maintain their position in the water column (Taylor, 1981, 1994; Massare, 1988).

Subaqueous flight seems to be tied, at least partly, to the lithophagic tendencies of some taxa. Many seals and sea lions are known to swallow stones, though much speculation remains as to why (Whittle and Everhart, 2000; Taylor, 1994). Penguins have also been reported to swallow stones (Taylor, 1993). It is theorized that gastroliths provide a quick adjustment to buoyancy as an alternative to pachyostosis (Taylor, 1993, 1994). The low mass associated with the gastroliths of the Antarctic specimen lends credence to this theory, as any amount of negative buoyancy added to the animal would have decreased the depth at which it became negatively buoyant (Taylor, 1994). This would not only allow for decreased energy expenditure for staying at a particular depth but more depth control at slower speeds, as summarized by Taylor (1994).

CONCLUSIONS

The plesiosaur specimens considered in this study were found to contain varying masses and sizes of gastroliths, suggesting little correlation in function. The specimens from South Dakota are generally more similar when the sizes of stones are considered; however, a large discrepancy between their masses may be attributed to taphonomic loss. The small size and large number of gastroliths found in the Antarctic specimen is surprising, considering that the size of the Antarctic plesiosaur is within the range of the South Dakota plesiosaurs. The physiological role of these stones on the basis of these specimens is problematical. Many stones found within plesiosaurs seem too small to have performed effectively as a masticatory aid, although greater numbers of stones may have compensated in the Antarctic specimen and some abrasion may have occurred over the life of the individual. Relatively few specimens have been found with completely pulverized stomach contents, questioning the efficiency of the stones in digestion. Alternatively, small stones and small mass may have provided the appropriate weight to allow maintenance of the plesiosaur at appropriate water depths. Of course, a combination of uses is possible. No matter the utilization of the stones, the Antarctic elasmosaurids appear to have possessed the greatest number of gastroliths known among plesiosaurs. The difference in numbers may be due to temporal, behavioral, or physiological differences between the high-latitude taxa and those occurring at lower latitudes.

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Rare earth element determination of the stratigraphic position of the holotype of Mosasaurus missouriensis *(Harlan), the first named fossil reptile from the American West*

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ABSTRACT

The first marine reptile from the American West was collected long before the currently accepted lithostratigraphic nomenclature was established. The reptile, *Mosasaurus missouriensis* (Harlan), was collected from the Big Bend area of the Missouri River from what is now considered central South Dakota and taken to Germany by Prince Maximilian of Weid. Parts of the same specimen were described in 1834 and 1846, but its lithostratigraphic source could be determined only as the Late Cretaceous Pierre Shale Group, although later authors suggested its source as the Virgin Creek Formation of the Pierre Shale. Recent examination of the preservation of the holotype and associated invertebrates indicated derivation from the upper concretionary portion of the DeGrey Formation of the Pierre Shale rather than the Virgin Creek Formation. However, an independent method was sought to confirm this conclusion. Rare earth element (REE) analysis of vertebrate fossils in the Pierre Shale Group has been used successfully in interpretations of original diagenetic environments, including interpretations of paleodepth, identification of fossil provenance, paleoenvironmental interpretations, and stratigraphic correlation. REE signatures and trace element concentrations in fossil vertebrates from stratigraphic units are sufficiently distinctive to allow identification of the original unit or location in which fossilization occurred. Comparative REE analysis from numerous specimens from each unit of the lower Pierre Shale Group along the Big Bend of the Missouri River confirmed the lithostratigraphic source of the mosasaur as the upper DeGrey Formation.

Keywords: rare earth elements, Pierre Shale Group, DeGrey, fossil provenance, stratigraphy.

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INTRODUCTION

In addition to evidence of biological evolution, fossils may provide biostratigraphic, paleoenvironmental, and taphonomic information significant to interpretations of the geologic history of the enclosing lithologic units. However, if the stratigraphic context of the fossil is not known, owing to loss, destruction, or absence of precise collection records (particularly in the case of poached fossils, fossils collected as float eroded from their original stratigraphic position, or fossils in historical collections), much of this important geological information may be unknown. In some instances the style of fossil preservation may be sufficiently distinctive to allow the original stratigraphic unit or location to be identified or constrained. However, for most fossils, preservational appearance alone is not sufficiently distinctive. In other cases the distinct chemical composition of fossil materials may allow the stratigraphic source to be identified. The rare earth elements (REE) form the largest chemically coherent group in the periodic table. Although similar, the chemical properties do vary systematically within the group, allowing the REE to be fractionated during some geological processes. REE and other trace elements are introduced into vertebrate fossils during early diagenesis and provide evidence of the depositional or early diagenetic environments (Elderfield and Pagett, 1986; Wright et al., 1987; Trueman, 1999; Trueman and Tuross, 2002; Patrick et al., 2004; Martin et al., 2005). REE signatures and trace element concentrations in fossils from some stratigraphic units may be sufficiently distinctive to allow identification of the original unit or location in which fossilization occurred (Staron et al., 2001; Patrick et al., 2002). Such a situation occurred concerning a marine reptile collected in the early 1800s from what is now South Dakota.

The first reptile named from the American West was a mosasaur, *Mosasaurus missouriensis* (Harlan) 1834 (= *Mosasaurus maximiliani* Goldfuss 1845), portions of which were transported to Europe by an early explorer, Prince Maximilian of Weid, following his expedition to the American West during 1832–1834 (zu Weid, 1840–1841; reprinted as zu Weid and Bodmer, 2001). Portions of the skull and associated bones from the same specimen were described separately by Harlan (1834) and Goldfuss (1845), but have long been recognized as the same specimen (Meyer, 1845; Camp, 1942; Martin, 2004a, 2004b). Original records indicate that the fossil was collected from the upper Cretaceous Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) from the Big Bend of the Missouri River in central South Dakota (Goldfuss, 1845; Russell, 1967), but the precise locality and lithostratigraphic unit from which this historically important specimen was obtained were conjectural. Russell (1967), for example, believed that the specimen was probably derived from a concretionary zone in the upper part of the Virgin Creek Formation. However, inspection of the preservation of the mosasaur in Fe-Mn concretionary material and associated invertebrate fossils by the second author suggested another stratigraphic level within the Big Bend area of the Missouri River (Martin, 2004a, 2004b). Therefore, another independent method was sought to confirm the stratigraphic assignment. A comparison of REE data from this mosasaur with that of other mosasaur fossils from various units of the Upper Cretaceous Pierre Shale Group (Patrick et al., 2002, 2004) provided the evidence to constrain the provenance of this historically and stratigraphically important fossil.

UPPER CRETACEOUS STRATIGRAPHY OF CENTRAL SOUTH DAKOTA

The Upper Cretaceous Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) is exposed along the banks of a large meander of the Missouri River in central South Dakota, delineated in the nineteenth century as the Big Bend. This group was deposited in the north-south–trending Western Interior Seaway, which extended from the Arctic Ocean to the Gulf of Mexico. The width and depth of this epicontinental seaway changed through the Late Cretaceous as a result of eustatic sea level variations (Haq et al., 1987) and regional tectonics, leading to the deposition of sequences of carbonates, mudstones, and sandstones. Water circulation between the northern Arctic and southern Gulf waters also varied with climate and the extent of the seaway. During some intervals, stratified conditions persisted within the group, forming anoxic bottom waters and deposition of black, organic-rich shales (Fisher and Arthur, 2002; Patrick et al., 2004, Chapter 5). Active andesitic and rhyolitic volcanoes on the western margin of the seaway also contributed numerous bentonite layers, which can serve as stratigraphic markers (Kepferle, 1959; Martin et al., 1996; Martin et al., 2004).

The Pierre Shale Group, one of the earliest described lithologic units of the Western Interior, accumulated during the Late Cretaceous (Campanian and Maastrichtian stages) and is primarily an interval of organic-rich black and gray shales with interbedded bentonites and concretions, most of which were deposited under relatively anoxic marine conditions (Crandell, 1958; Gill and Cobban, 1961, 1973; Gries and Martin, 1985). The entire group appears to have represented an ideal environment for mosasaurs, the highly aquatic lizards of the Late Cretaceous. Originally named the Fort Pierre Group (Meek and Hayden, 1862), the Pierre Shale Group is extensively exposed in South Dakota. Within central South Dakota, eight superposed units recognized by Crandell (1958) and modified by Martin et al. (this volume) have gained general acceptance: the Sharon Springs Formation at the base, and successively by the Gregory Formation, Crow Creek Member of the DeGrey Formation, upper DeGrey Formation, Verendrye Formation, Virgin Creek Formation, Mobridge Formation, and Elk Butte Formation. Of these units of the Pierre Shale Group, only the Gregory, Crow Creek, DeGrey, Verendrye, and Virgin Creek occur along the Big Bend of the Missouri River. A stratigraphic column summarizing the subdivisions of the Pierre Shale in central South Dakota is shown in Figure 1.

Detailed descriptions of the various lithological units are provided by Crandell (1952, 1958), Gill and Cobban (1961, 1973), Gill et al. (1972), and Patrick et al. (2004). Most of the Pierre

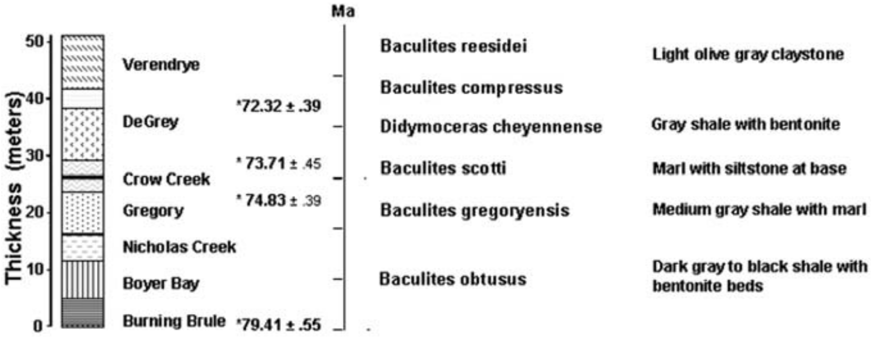

Figure 1. Stratigraphy of lithological units of the Upper Cretaceous (Campanian) Pierre Shale Group in central South Dakota. Asterisks (*) represent $^{40}Ar/^{39}Ar$ dates of the DeGrey, Gregory, and Sharon Springs Formations.

units contain widespread concretionary zones. Many varieties of concretions include calcareous, siliceous, phosphatic, and iron-manganese; vivianite nodules have not been found in the study area. The iron-manganese concretions occur in the Big Bend area from the Gregory through the Virgin Creek units, but they are particularly characteristic of the upper DeGrey Formation. The biostratigraphic zonation of the Pierre Shale for this region, based on ammonite ranges, is from the *Baculites gregoryensis* Biozone (oldest) through the *Baculites reesidei* Biozone (Fig. 1).

The Gregory Formation is ~23 m thick in the Fort Thompson section (Hanczaryk, 2002; Hanczaryk and Gallagher, this volume) and consists primarily of gray to green claystone and marl with a few bentonites. Much of the bentonitic content appears to have been redeposited and dispersed, resulting in bentonitic claystone, which accounts for its characteristic "popcorn"-weathering surface. The unit has yielded significant numbers of invertebrates (e.g., *Baculites gregoryensis*), radiolarians including the genera *Dictyomitra* and *Tricolapsa* (Crandell, 1952), and a few vertebrates.

The Crow Creek Member of the DeGrey Formation is 1.2 m thick in the Fort Thompson section and is a distinctive calcareous siltstone, locally sandy, light gray to yellow brown, supporting a distinctive vegetative cover. The member has produced few vertebrate fossils; however, the lowest part of the Crow Creek does contain both pelagic and planktonic foraminifers and a few radiolarians (Crandell, 1952).

The upper DeGrey Formation is 10.1 m thick in the Big Bend area; the lower 3 m consists of bentonitic gray shale interspersed with thin iron-manganese concretionary layers. The upper portion of the formation is conspicuously banded with concretions and is mostly silver-gray siliceous shale with interbedded bentonites. Vertebrate and invertebrate fossils are common, and pelagic foraminifers and radiolarians are also present (Crandell, 1952). The Verendrye Formation consists of gray bentonitic shale, but only the lower 17 m is exposed in the Fort Thompson section. The Virgin Creek Formation is mostly covered.

Vertebrate and invertebrate fossils are relatively abundant throughout the Big Bend area, including mosasaurs, plesiosaurs, turtles, diving birds, fish, numerous bivalves, and straight and coiled ammonites, among others. Mosasaurs are particularly abundant, with at least five species represented at the Big Bend; the two most abundantly represented mosasaur species are *Plioplatecarpus primaevus* (Russell, 1967) and *Mosasaurus missouriensis* (Martin, 2004a, 2004b). The holotype of the latter species was collected in the early nineteenth century and is the first fossil reptile described from the American West.

MATERIALS AND METHODS

The first marine reptile from the American West was collected from the Big Bend of the Missouri River and described in 1834 and again in 1845. Somehow, the snout of the mosasaur made its way from the Missouri River country to the East Coast, where Harlan described the snout as *Ichthyosaurus missouriensis*. Later in ca. 1842 he renamed the genus *Batrachiosaurus,* another rather inappropriate name. The snout had evidently been part of a skull collected by Major Benjamin O'Fallon, a friend of William Clark of Lewis and Clark fame, from the Big Bend of the Missouri, a geographic feature noted by Lewis and Clark. Following the Corps of Discovery expedition, Clark was appointed by President Thomas Jefferson to administer Indian affairs for the Missouri River area and was stationed in St. Louis. In the early 1830s, Prince Maximilian of Weid journeyed from Germany with the Swedish illustrator Karl Bodmer to document native peoples subsequent to the Lewis and Clark expeditions. In fact, the map of the Missouri region that had been made by Clark, illustrating the Big Bend, was supplied to Maximilian for his trip. Upon return to St. Louis, Maximilian was given the skull (except for the snout) and the partial postcranial skeleton of the mosasaur found by O'Fallon. The specimen was packed along with the Native American artifacts and natural history specimens and removed to Germany. In 1845, Goldfuss made a detailed description of the skeleton, noted its similarity to the famous Maastricht mosasaur *(Mosasaurus hoffmanni),* and named it *Mosasaurus maximiliani* in honor of Prince Maximilian. However, in the same year, Hermann von Meyer noted in a letter that the snout described by Harlan (1834) >10 yr earlier was a perfect fit on the cranium of the mosasaur described by Goldfuss. This fit was noted by other workers such as Charles Camp (1942), Dale Russell (1967), and J.E. Martin (2004a, 2004b). Therefore, the holotype must be considered under the taxonomic combination of *Mosasaurus missouriensis* (Harlan). The snout was lost for some years, but recently it was found in the collections at the Paris Museum of Natural History (Caldwell and Bell, 2005), and the rediscovery reiterated the well-known earlier contentions of von Meyer, Camp, and Russell.

The holotype of *Mosasaurus missouriensis* had received relatively little attention until 2004, when J.E. Martin studied the specimen in Bonn, Germany. He was given a fragment of the specimen for REE analysis. On the basis of preservation and associated invertebrate fossils, Martin had come to a conclusion concerning the lithostratigraphic source of the mosasaur; however, he did not share this conclusion with the first author (Patrick) until after she was able to ensure an unbiased geochemical determination.

The mosasaur holotype is encrusted with a ferruginous manganese concretionary material. Moreover, a number of bivalves were associated with the specimen, also taken by Prince Maximilian, and they remain with the mosasaur in Bonn. On the basis of the concretionary encrustation, Russell (1967) assumed that the holotype had been collected from the Virgin Creek Formation of the Pierre Shale Group. However, relatively little of the Virgin Creek Formation is exposed in the Big Bend area, and Russell may have been influenced in his reference because of another specimen (South Dakota School of Mines 452) he ascribed to *Mosasaurus conodon* from the Virgin Creek Formation of South Dakota. Whatever the reason for Russell's assumption, upon direct inspection the concretionary material appeared identical to the iron-manganese concretions of the upper portion of the DeGrey Formation of the Pierre Shale Group. Moreover, the bivalves, both in taxonomy *(Anomia* and *"Inoceramus")* and preservation, are identical to those from the upper DeGrey Formation. In order to prove this contention, Wingart Von Koeingwald, University of Bonn, kindly provided a bone fragment for geochemical analysis.

Earlier, comparative mosasaur samples had been obtained from the Sharon Springs, Gregory, Crow Creek, DeGrey, and Verendrye units of the Pierre Shale Group in an area between Chamberlain and Pierre, South Dakota, including the Big Bend of the Missouri River and localities to the south in Brule County (Fig. 2). Specific locality data for these specimens are given in Patrick et al. (2004). This area includes possible sites where the holotype of the Weid mosasaur was collected according to historical records.

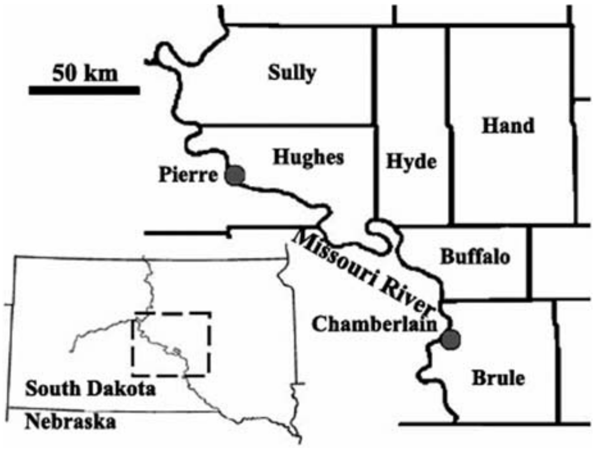

Figure 2. Location of field area (dashed box in the inset outline map of South Dakota), which lies generally along the northeastern bank of the Missouri River, between Chamberlain and Pierre, in Brule, Buffalo, Hyde, and Hughes Counties. Base map of county boundaries from U.S. Census Bureau.

Sample preparation techniques follow those in Patrick et al. (2004) and Staron et al. (2001). Large intact bone specimens were sampled by drilling, using a Dremel variable speed electric drill. Between samples the drill was cleaned with trace-metal-grade dilute (2%) nitric acid or trace-metal-grade acetone and rinsed in distilled water. Cortical bone samples were immersed in deionized water and subsequently in a dilute acetic acid solution in an ultrasonic bath to remove matrix and secondary carbonate. Other matrix and secondary minerals were removed by handpicking. Last, samples were rinsed with distilled water and dried. Selected samples were analyzed using X-ray diffraction, revealing essentially pure apatite with only minor amounts of other crystalline phases. Cleaned bone fragments were mechanically crushed in an acid-washed mortar and pestle. Approximately 0.2 g of powder was weighed for each sample. Each sample was dissolved in ~2 mL Ultrex-grade HNO_3 and diluted to 100 mL. When only smaller masses of bone were available, the initial solution was diluted to smaller volumes to preserve the mass/volume ratio. Samples were diluted to appropriate levels with 2% ultrapure HNO_3. Initial samples were analyzed using a Finnigan MAT Element/1 high-resolution magnetic sector inductively-coupled-plasma mass spectrometer (ICP-MS) at Rutgers University. The Hawaiian Basalt (BHVO) was used as a standard; precision and accuracy were better than ±4% relative to certified values. Analytical procedures followed those in Field and Sherrell (1998). Subsequent analyses were conducted using VG Plasma-Quad 3 ICP-MS. Results have been corrected for isobaric interferences where necessary. Additional samples were analyzed using a Hewlett -Packard HP4500 ICP-MS at the South Dakota School of Mines and Technology. Duplicate samples were run for comparison between the two machines, and results were within experimental error. The coefficient of variation for most REE is <±5% of the analyzed value. Analytical results have been normalized relative to the North American Shale Composite (NASC) (Gromet et al., 1984). Discriminant analysis of data was conducted using NCSS statistical software (Hintze, 1997).

Factors Influencing REE Signatures in Fossils

Extensive discussions concern sources of REE, mechanisms controlling the REE content of fossils, and the amount of fractionation of REE between fluids and osteological materials (Bernat, 1975; Wright et al., 1984, 1987; Elderfield and Pagett, 1986; Trueman, 1999; Reynard et al., 1999; Armstrong et al., 2001; Trueman and Tuross, 2002; Kemp and Trueman, 2003). Biogenic apatite crystals in living organisms are very small (Lowenstam and Weiner, 1989; Weiner and Traub, 1992), their structures have low degrees of crystallinity (Person et al., 1995), and they contain relatively high concentrations of carbonate, sodium, and other species. Therefore, biogenic apatite crystallites are relatively soluble and reactive. During fossilization the crystallites of biogenic apatite recrystallize (Brophy and Hatch, 1962; Person et al., 1995). REE and most other trace elements are adsorbed from solution onto the biogenic apatite crystal surfaces (Tuross et al., 1989a, 1989b) and incorporated into the fossilizing material during apatite crystal growth (Trueman, 1999; Armstrong et al., 2001). Henderson et al. (1983) suggested that values of distribution coefficients for all of the REE, except perhaps Ce, are similar (see also Trueman, 1999; Trueman and Tuross, 2002). Therefore, signatures and ratios of REE in fossils should be similar to the average composition of the fluids from which they were obtained, particularly if the adsorption coefficients are also large, resulting in near-quantitative removal of REE from solution (Kemp and Trueman, 2003; Reynard et al., 1999).

REE incorporation into the fossil may be largely accomplished within <10,000 yr (Trueman, 1999; Patrick et al., 2001; Trueman and Tuross, 2002), and in recent studies the incorporation has been shown to be <4000 yr (D. Patrick and J.E. Martin, 2007, current analytical data). If fossilization is rapid relative to the sediment deposition rate, the REE signature in the fossil will primarily reflect the surface water chemistry; however, if deposition is rapid, REE may be taken up primarily from sediment pore waters (Elderfield and Pagett, 1986; Kemp and Trueman, 2003). Incorporation of REE, fluorine, and other trace elements, and the growth of larger, more crystalline apatite, decrease the solubility, specific surface area, and reactivity of the resulting fossilized material. Most studies (see discussion in Trueman, 1999; Armstrong et al., 2001) have suggested that once REE are incorporated into the bone, they are retained and provide a stable signal recording the composition of waters in the depositional or early diagenetic environment. Exceptions occur only when the fossil material is dissolved and reprecipitated or recrystallized during high-grade metamorphism, processes that have not occurred in the Pierre Shale Group.

RESULTS

As previously mentioned, the holotype specimen of *Mosasaurus missouriensis* was encrusted with Fe-Mn concretionary material. This appears to have led Russell (1967) to conclude that the specimen had come from an upper concretionary zone in the Virgin Creek Formation. However, direct observation of the concretionary material led the second author to conclude that its origin was the upper concretionary portion of the DeGrey Formation, which will be renamed as a separate member in a later contribution. The associated bivalves and their preservation suggested a similar source. Finally, 15 yr of stratigraphically controlled collecting along the Missouri River indicates that *Mosasaurus missouriensis* is one of the more abundant mosasaurs from the Big Bend area and commonly is associated with Fe-Mn concretions of the upper DeGrey Formation (Martin, 2004a,2004b). Nevertheless, an independent check through REE analysis was desirable.

Previously, we had collected and analyzed many mosasaur specimens from the various lithological units of the Pierre Shale Group in the Big Bend area (Patrick et al., 2004). That work indicated that mosasaur fossils from individual units of the Pierre Shale Group have similar REE signatures over wide areas but that signatures vary significantly among superposed units, even in a restricted geographic area. Therefore, comparison with the REE data set should indicate the source of the holotype specimen. Results in parts per million are given for analyzed samples in Table 1.

Spider diagrams (Fig. 3) represent the characteristic REE signatures (normalized to the North American Shale Composite [NASC] concentration versus atomic number) of each unit of the Pierre Shale in the tested geographical area.

REE signatures of fossils within individual units are similar, whereas the concentrations seem to vary according to differences in osteological material. The greater the amount of trabecular bone in a sample, the more likely the overall REE concentrations will decrease. The variation in the REE concentration in the different osteological material can also infer the extent of alteration of the fossil material. Similarities of the REE signature in different osteological materials were also found in the same individual (Patrick et al., 2001, 2004; Martin et al., 2005). Although the REE concentrations varied according to bone material type, the REE signatures were consistent within units and varied among units. Therefore, the uniqueness of the REE signature patterns can be used to identify the units and have been shown to extend laterally >250 km^2. This wide lateral extent and consistency of the REE signature within a unit allow REE signatures to be used effectively for the determination of fossil provenance within the marine deposits of the Pierre Shale Group. The DeGrey Formation exhibits a change in lithology. Upper and lower units within the upper DeGrey Formation have been previously identified, and these differences are also confirmed in their REE signatures (Fig. 3D, E).

Figure 4 is a ternary diagram with NASC-normalized (Gromet et al., 1984) Yb, Gd, and Nd (Yb_N, Gd_N, and Nd_N) at the vertices. Yb represents a heavy REE (HREE), Gd a middle REE (MREE), and Nd a light REE (LREE). Nd, Gd, and Yb are even-numbered elements and therefore have higher concentrations, according to the Oddo-Harkins effect, and thus their analytical data are generally more reliable (assuming proper correction for isobaric overlaps in quadrupole ICP-MS).

The LREE, Ce, and La were not used because Ce is subject to effects of oxidation and reduction, and La commonly exhibits slightly different chemical variations than the other REE. Other REE combinations were tested, particularly substituting Pr for Nd, but these substitutions do not greatly alter the patterns. The combination of Nd, Gd, and Yb was found to be the most useful for comparisons through previous research, and particularly for comparisons with extensive research on dissolved REE. The ternary diagram allows the basic shape of the REE pattern to be

TABLE 1. RARE EARTH ELEMENT CONCENTRATIONS IN CORTICAL BONE (PPM) OF MOSASAUR FOSSILS FROM SELECTED UNITS OF THE PIERRE SHALE

Sample	Unit	Specimen	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu
72	Burning Brule	Tylosaurinae	93.9	183	31.5	189.6	46.5	10.5	41.3	4.89	25.1	3.95	9.15	1.07	7.34	0.91
56	Burning Brule	?Tylosaurinae	138.9	230.4	36.1	198.5	47.6	11	41.3	4.78	24	3.69	8.54	1.04	6.69	0.79
58	Burning Brule	Tylosaurinae	79.9	132.6	42.4	344.9	94.9	18.3	47.4	8.9	50.2	8.07	24.6	2.88	16.4	2.04
110	Burning Brule	Tylosaurinae	41	129.5	14.4	57.2	13.1	2.58	9.46	1.51	8.52	1.34	3.9	0.48	2.49	0.31
111	Burning Brule	Tylosaurinae	60.6	170.8	32.2	125.2	25	4.09	18.03	2.57	11.5	1.57	4.09	0.47	2.55	0.3
112	Burning Brule	Tylosaurinae	33.3	51.6	6.72	25.6	3.53	0.74	3.36	0.43	2.46	0.46	1.21	0.14	0.73	0.1
79	Boyer Bay	Tylosaurinae	81.8	183	23.3	82.7	16.5	3.25	13.7	2.14	12.6	2.33	7.61	1.04	6.25	0.95
65	Boyer Bay	Mosasauridae	100.6	196.1	33.7	189.6	47.6	11.3	44.3	5.36	27.6	4.24	9.36	1.09	12.8	1.12
102	Boyer Bay	Tylosaurinae	270.9	438.9	77.2	274	53.4	12.4	48.5	7.93	44.7	8.07	25.2	3.38	18.9	2.56
105	Boyer Bay	Tylosaurinae	210.3	780.5	44.4	64.2	8.46	1.67	14.7	1.35	7.25	1.44	5.77	0.89	6.25	1.12
53	Nicholas Creek	Tylosaurinae	121	132.6	17.7	154.1	35.3	7.45	37.7	5.49	42.7	9.93	32.5	4.89	34.3	5.36
61	Nicholas Creek	Not identified	45	49.2	9.5	36.1	7.54	2.1	9.04	1.7	10.2	2.44	7.44	1.12	7.17	1.15
101	Nicholas Creek	Tylosaurinae	89.7	135.6	15.4	109.1	19.8	5.15	27.9	3.8	25.1	5.98	20	3.15	23.2	3.88
115	Nicholas Creek	Mosasauridae	65	87.6	13.7	82.7	28	6.19	15	3.71	30.2	5.85	16.3	2.62	14.99	1.99
116	Nicholas Creek	Tylosaurinae	132.7	178.8	21.3	95	20.8	5.78	32.1	5.01	35.5	8.45	27	3.79	23.75	3.54
62	Nicholas Creek	Tylosaurinae	48.2	43.9	1.65	6.57	1.37	0.58	3.6	0.31	2.19	0.48	1.87	0.24	1.46	0.31
64	Gregory	Mosasauridae	492.9	504	46.5	194	32.9	11.3	73.5	12.3	107.2	32.1	117.9	18.6	124.7	22.3
4	Gregory	Mosasauridae	247	230.4	28.7	116.9	24.4	5.39	44.3	9.99	72.5	23.8	100.3	17.3	133.6	23.4
207	Gregory	Mosasauridae	142.2	132.6	18.5	72.1	16.1	3.82	28.6	5.75	56.3	19.8	85.4	15.5	124.7	22.3
59	Crow Creek	Mosasauridae	470.7	817.3	22.8	73.7	13.7	7.45	40.4	3.63	25.7	7.71	28.3	4.67	30.6	5.36
60	DeGrey	Mosasauridae	170.9	270.6	17.7	68.8	15	4.19	23.8	3.38	25.7	6.56	21.5	3.08	18.4	3.3
201	DeGrey	Mosasauridae	62.1	126.6	12.5	48.7	10.9	2.25	13.4	2.18	14.5	3.21	10	1.44	9.24	1.38
202	DeGrey	Mosasauridae	220.2	220	26.8	104.2	18.9	3.91	28.6	5.01	33.1	8.65	29.6	4.46	30.6	5
203	DeGrey	Mosasauridae	215.2	356.8	45.5	185.2	41.4	9.37	49.7	8.7	53.7	11.94	38.1	6.15	47.4	7.57
204	DeGrey	Mosasauridae	205.5	356.8	46.5	185.2	37.8	7.28	41.3	6.45	38.1	8.26	25.2	3.79	27.9	4.35
205	DeGrey	Mosasauridae	74.6	105.3	13.4	53.4	11.7	2.35	15	2.04	16.2	3.95	13.5	2.18	15.3	2.56
206	DeGrey	Mosasauridae	81.8	107.7	13.4	53.4	11.4	2.35	15	3.09	17	3.95	13.9	2.13	15.7	2.56
1	Verendrye	*Plioplatecarpus*	**	215	31.5	128.2	28	6.19	35.2	5.36	36.3	7.89	23	3.23	20.2	3.23
2	Verendrye	*Plioplatecarpus*	**	55.3	8.08	32.9	7.37	1.71	9.46	1.51	10	2.22	6.63	0.97	5.97	0.97
3	Verendrye	*Plioplatecarpus*	**	159.4	21.8	84.7	17.7	4.28	24.9	3.89	26.3	6.27	19.1	2.81	17.6	2.88
5	Verendrye	*Plioplatecarpus*	**	42.9	5.86	23.3	4.65	1.13	6.55	1.02	6.92	1.65	5.03	0.71	4.53	0.76
48	Verendrye	*Plioplatecarpus*	126.7	89.6	13.4	54.7	11.7	2.7	15	2.34	15.5	3.44	10.3	1.48	9.24	1.51
49	Verendrye	*Plioplatecarpus*	56.6	19.6	2.62	10.4	2.08	0.53	3.06	0.47	3.31	0.79	2.41	0.35	2.17	0.38
21	Verendrye	*Plioplatecarpus*	**	50.4	7.54	28	6.27	1.49	8.24	1.32	8.72	1.94	5.77	0.83	5.2	0.87
36	Verendrye	*Plioplatecarpus*	258.7	419.2	53.4	222.7	48.7	11.3	61.1	8.9	61.7	13.4	39.9	5.74	36	5.61
33	Verendrye	*Plioplatecarpus*	215.2	356.8	46.5	194	41.4	9.37	52	7.58	51.3	11.4	34.8	4.89	30.6	4.77
34	Verendrye	*Plioplatecarpus*	183.1	290	37	168.9	35.3	8.35	46.3	6.75	47.9	10.4	31.7	4.56	30.6	4.67
35	Verendrye	*Plioplatecarpus*	210.3	318	39.6	165.1	34.5	8.16	46.3	6.91	49	10.9	33.2	4.77	31.3	4.89
68	Verendrye	*Plioplatecarpus*	277.2	409.6	43.4	369.6	68.8	17.9	101.4	13.2	91.3	21.7	71	10.9	103.7	14.8

**Not measured.

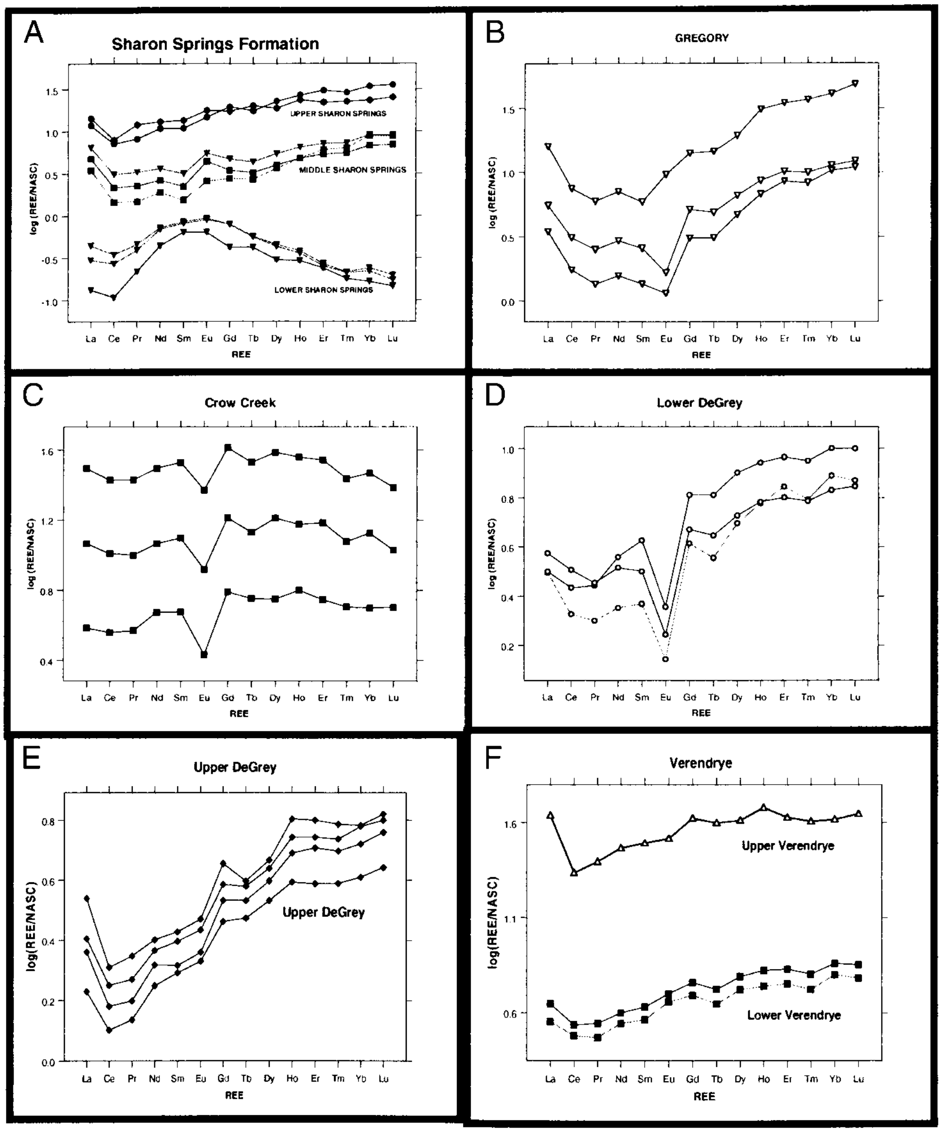

Figure 3. Set of graphs representing the rare earth element (REE) signatures in fossil vertebrates from the Pierre Shale Group. Significant variations in REE signatures upsection are noted between units and within some units such as the Sharon Springs. Within the Sharon Springs, subdivisions that were previously identified by J.E. Martin show recognizable variations in REE signatures. Similar previously identified subdivisions of the DeGrey are confirmed through REE analysis of fossil vertebrates. The average uncertainty in the laboratory analysis is always smaller than the symbol diameter. NASC—North American Shale Composite.

represented. NASC-normalized samples that plot in the middle of the diagram (33% Yb_N, 33% Gd_N, and 33% Nd_N) have equal amounts of these elements and will have flat, shalelike REE patterns. Samples plotting toward Yb will be enriched in HREE, and their signatures will have a positive slope; those plotting near Nd are enriched in LREE and will have a negative slope; and those plotting near Gd are enriched in MREE and will have a bell shape. This combination allows the interpretation of paleoenvironments, and in some cases the ratio may be sufficiently distinctive to allow identification of the original unit or location in which fossilization has occurred. Through use of a ternary diagram, elimination of most units was achieved; however, significant overlap was found between the Verendrye and DeGrey Formations, making absolute identification difficult.

To confirm the visual impression from the spider diagrams (Fig. 3) and to refine that from the ternary diagram (Fig. 4), data from each of the units were analyzed by discriminant analysis using NCSS statistical software (Hintze, 1997). Discriminant analysis is a statistical technique (Davis, 1986) that finds the linear combination of variables (REE ratios) that produce the maximum or optimal separation between defined groups. In the case of REE analysis, discriminant analysis allows the best statistical method for determining specific groupings or units. Canonical correlation is an additional procedure for assessing the relationship between the REE ratios. Canonical analysis is used when trying to classify an unknown sample; the assignment unit can be determined by the best-fit parameters.

Discriminant analysis was conducted using NASC-normalized REE ratios (e.g., Nd/Yb). Elemental ratios, rather than concentrations, were used to remove the effect of differences in REE concentrations between different types of osteological materials and different localities. Discriminant analysis was conducted using stepwise regression to select the best parameters. The Sm/Dy, Tb/Er, Tb/Yb, and Sm/Yb ratios were most important for accurate classification of these units. Classification error was reduced by >90%. Canonical variant scores for these units indicate that

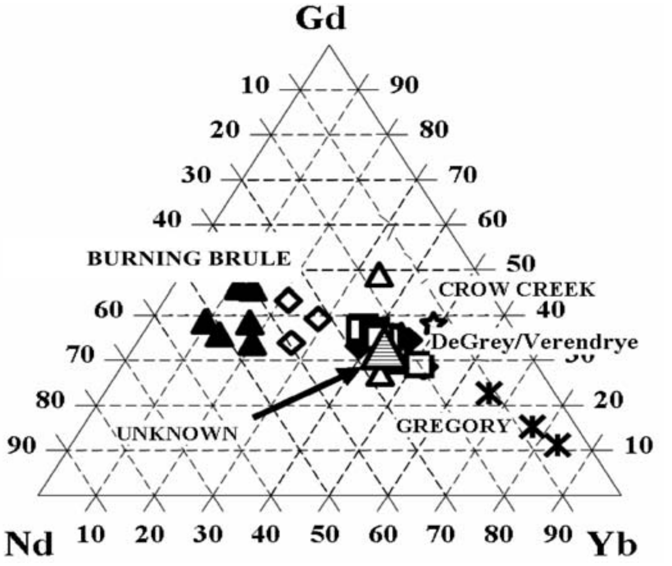

Figure 4. Ternary diagram of NASC-normalized values of Y (heavy REE, or HREE), Gd (middle REE, or MREE), and Nd (light REE, or LREE) in fossils from the Pierre Shale Group (all rights reserved, Patrick and Wegleitner, 2005). Samples plot along a straight trend line (from lower Sharon Springs to Gregory), which may result from mixing of or evolution between two end-member waters, one enriched in MREE and LREE, and the other enriched in HREE. Overlap of the Verendrye and the DeGrey Formations does not allow identification of the provenance of the unknown sample (Δ). Relative standard deviations for Nd, Gd, and Yb for analyses of samples in Table 1 were generally <2% to 3%. Therefore, the average uncertainty in the ratio values and symbol placement for this figure is <~±0.036, slightly larger than the average symbol diameter.

samples from the Pierre Shale units can be statistically distinguished from one another (Fig. 5).

The results indicate that the REE signature-ratio differences are significant enough to separate the fossils into their lithostratigraphic units. Therefore, in some marine environments, owing possibly to the homogeneity of the marine shales, distinct REE signatures may have significant lateral extent.

CONCLUSIONS

Precise stratigraphic control through detailed measurements at all sites indicated both the consistency within lithological units of REE signatures in fossil vertebrates and the variation of REE signatures between lithostratigraphic subdivisions (Fig. 3). From comparisons of all REE signatures, the closest visual match of the Weid mosasaur sample among the spider diagrams that represent various lithostratigraphic units of the Pierre Shale appears to be Figure 3E, the upper portion of the upper DeGrey Formation. Figure 6 shows that the REE signature of the Weid mosasaur sample clearly matches the DeGrey Formation of the Pierre Shale Group, and more specifically the upper portion of the upper DeGrey Formation. This is consistent with the interpretation of Martin (2004a, 2004b) that the preservation pattern of the mosasaur in Fe-Mn concretionary material and associated invertebrate fossils suggested the upper portion of the upper DeGrey Formation.

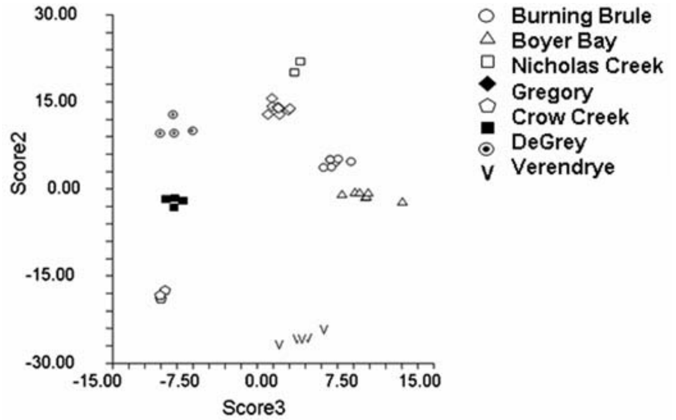

Figure 5. Canonical variate scores for mosasaur fossils from lithologic units of the Pierre Shale Group. Vertebrate fossils can be distinguished statistically on the basis of REE element ratios. Sm/Dy, Tb/Er, Tb/Yb, and Sm/Yb were most important for accurate classification of these units or optimal separation between defined groups. Classification error was reduced >95%.

Utilizing another graphical technique, the unknown sample of mosasaur was plotted (Fig. 4) in a ternary diagram (Patrick et al., 2002, 2004). This illustration narrows the provenance to two possible units in the Big Bend area. However, significant overlap exists in the ratios of the Verendrye and the DeGrey Formations owing to possible similar environments during diagenesis.

For further precision in determination the statistical analysis performed to confirm groupings of the fossils, according to litho-

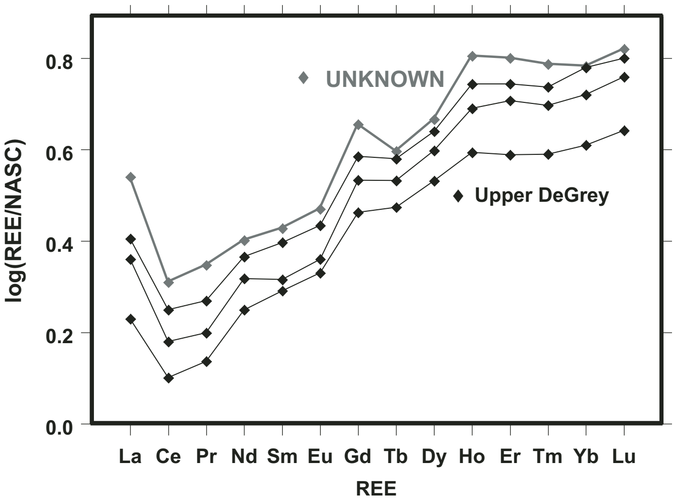

Figure 6. Weid sample (top plot), in comparison with the two plots of the upper DeGrey Formation of the Pierre Shale Group (from Fig. 3E), clearly shows a nearly identical REE signature. The average uncertainty in the laboratory analysis is invariably smaller than the symbol diameter.

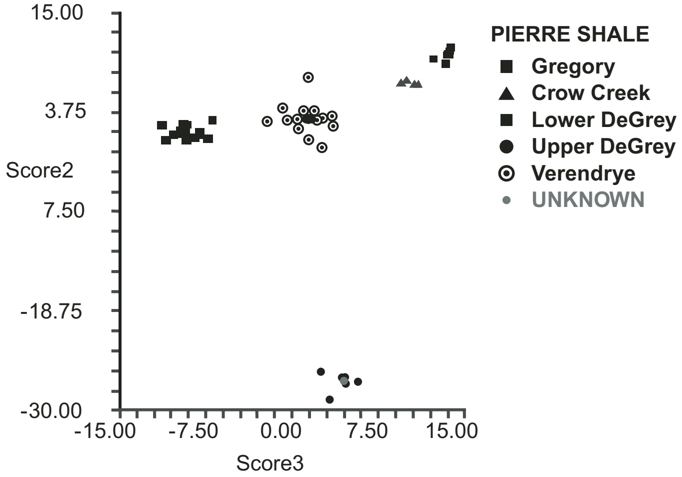

Figure 7. Canonical variate scores from the upper five lithological units of the Pierre Shale Group in the Big Bend area. The unknown Weid sample plots in the upper DeGrey Formation. Sm/Yb, Tb/Sy, Pr/Yb, and Gd/Yb ratios were most important for accurate classification of these units. Classification error was reduced by >95%.

stratigraphic subdivisions, showed a statistical difference among all of the subdivisions of the Pierre Shale Group (Fig. 5). Discriminant analysis of the upper units of the Pierre Shale Group in the Big Bend area also reflects these statistical differences (Fig. 7). Discriminant analysis was conducted to select the best parameters using stepwise regression on the upper five units of the Pierre Shale Group common in the Big Bend area. Sm/Yb, Tb/Sy, Pr/Yb, and Gd/Yb ratios were most important for accurate classification of these units. Classification error was reduced by >90%. Canonical variant scores for these units indicate that samples from the upper lithological units of the Pierre Shale can be statistically distinguished from one another. By including the Weid mosasaur, the unknown fossil plots with the other samples from the upper DeGrey Formation. Discriminant analysis grouped this fossil statistically with those of the DeGrey Formation, thus confirming the visual identification from the spider diagrams. Therefore, the provenance of this fossil could be assigned to the upper DeGrey Formation using REE analysis, which further supports the initial findings by the second author.

When the stratigraphic context of a fossil vertebrate is unknown, owing to loss, destruction, or absence of precise collection records, much of the important geological information is lost. In some instances, the style of fossil preservation may be sufficiently distinctive to allow the original stratigraphic unit or location to be identified or constrained. However, normally independent confirmation is necessary in identifying the origin or provenance of the fossil vertebrate. REE signatures and trace element concentrations in fossil vertebrates from stratigraphic units are sufficiently distinctive to allow identification of the original unit or location in which fossilization occurred. Because REE signatures differ among units, fossil bones removed from stratigraphic context can be assigned to a lithological unit on the basis of REE signature comparisons. Therefore, REE analysis offers one of the best methods for identifying fossil vertebrates of unknown origin. Precise stratigraphic control of collections of fossils and subsequent REE analysis from each distinct lithostratigraphic unit become essential in developing a database of REE signatures to enable more accurate fossil provenance assessment. This database was shown to be essential in this case study. This mosasaur sample, originally collected in the early 1800s, was known to have come from the Pierre Shale Group in central South Dakota but was not assuredly assigned to a particular lithological unit because of limited collection information. A comparison of REE data from this mosasaur with those of other fossil REE signatures from the Pierre Shale Group, accumulated within our database over the last 6 yr, provided the evidence to constrain the provenance of this historically and stratigraphically important fossil to the upper portion of the DeGrey Formation of the Pierre Shale.

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Stomach contents of Globidens, *a shell-crushing mosasaur (Squamata), from the Late Cretaceous Pierre Shale Group, Big Bend area of the Missouri River, central South Dakota*

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ABSTRACT

One of the rarest of marine reptiles is the mosasaur genus *Globidens,* characterized by a massive, bulbous dentition. The rarity of the taxon, coupled with the bulbous dentition, resulted in various theories concerning life habits. Although a consensus indicates that the dentition was adapted for crushing resistant elements, hypotheses have varied concerning prey, ranging from turtles or bivalves to scavenging. Finally, a partial skeleton of *Globidens* has been recovered from the Big Bend area of the Missouri River in central South Dakota. The specimen was discovered in the upper DeGrey Formation (upper Campanian) of the Pierre Shale Group. During analysis, bivalve fragments were found packed within the rib-cage region of the skeleton. In the field, bivalve concentrations did not occur laterally or above or below the skeleton, indicating that they were the stomach contents of the mosasaur. Associated within the stomach area are a number of bivalve taxa, including oysters and small bivalves with lamellar shells, probably of the genus *Anomia.* The most common specimens within the stomach area are bivalves that exhibit a prismatic shell microstructure typical of inoceramids. Four inoceramid shell morphotypes were recovered, including a coarse-ribbed morphotype, a fine-ribbed morphotype, one with a thickened umbo, and a large, flat, thin-shelled morphotype. Because of their position in the mosasaur, their fragmented condition, limited taxonomic diversity, and absence from surrounding sediments, the bivalves are considered stomach contents. Some smaller, complete shells of *Anomia* escaped breakage, whereas larger inoceramids were invariably crushed. Chondrichthyan teeth were found associated but are interpreted to be the result of scavenging. This specimen of *Globidens* appears to have had a preference for the large, flat, relatively thin-shelled inoceramids that contained a large, fleshy visceral mass.

Keywords: mosasaur, stomach contents, fossil bivalves, South Dakota, Cretaceous.

INTRODUCTION

One of the most unique reptiles to have swum the Late Cretaceous seas was the mosasaur *Globidens*. This mosasaur is rare, represented most commonly by isolated teeth, but even these teeth are unusual. Rather than the long, sharp, conical teeth with carinae and serrations characteristic of most carnivorous mosasaurs, the dentition of *Globidens* is characterized by blunt, brachyodont teeth with radial rugosities (Fig. 1). Occlusal wear is invariably on the apices of these robust, rounded teeth. Obviously,

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the function of the dentition was for crushing-pulverizing. Various hypotheses have been put forth concerning diet on the basis of these teeth. The hypotheses concerning the life habits of *Globidens* range from scavenging to preference for chelonians or bivalves. In 1991 a partial skeleton of *Globidens* was discovered that would provide direct evidence to confirm one of these hypotheses (Martin, 1994; Martin and Fox, 2004).

As a result of a cooperative investigation of the marine deposits of the Missouri River Trench, the specimen was located. The senior author and David Parris, New Jersey State Museum, have collaborated principally through the Field Paleontology program at the Museum of Geology, South Dakota School of Mines and Technology. One of the New Jersey students recruited by Parris, Larry Conti, found part of a mosasaur weathering from a high bluff along the Big Bend of the Missouri River in central South Dakota (Fig. 2). Armed with permission and assistance from the U.S. Army Corps of Engineers, upon whose land the specimen was discovered, along with permission and support from the Crow Creek Sioux Tribe, excavations began.

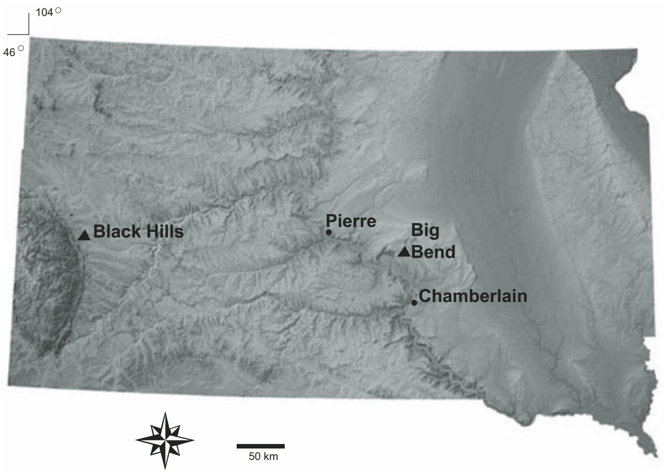

Figure 2. Location of the discovery of a skull and partial skeleton of *Globidens,* a large durophagous mosasaur from the Late Cretaceous DeGrey Formation of the Pierre Shale Group along the Big Bend of the Missouri River, central South Dakota.

Globidens is rare in South Dakota, although the type specimen of *Globidens dakotensis* was derived from the lower Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) Sharon Springs Formation (lower middle Campanian), along the eastern flank of the Black Hills Uplift (Russell, 1975). For 15 yr the School of Mines and New Jersey State Museum crews scoured the Pierre Shale around the Black Hills, resulting in no additional specimens of the durophagous mosasaur. Therefore, when the students arrived with the news that the specimen Larry Conti had discovered was that of a *Globidens,* occurring much higher in the stratigraphic section and far from the original locality of *G. dakotensis,* some time and effort went into convincing the senior author that the news was not a joke and to come and investigate the specimen. Upon examination of the excavation, not only was the specimen obviously more than half the skeleton of a *Globidens,* but the students were trenching through a coquina of bivalves in the rib-cage area. This activity was immediately halted, and efforts were undertaken to remove most of the skeleton in one large block. Moreover, efforts were expended to check if the bivalve concentration extended laterally or vertically above and below the skeleton. The bivalves were concentrated around the midsection of the mosasaur, suggesting that they were indeed gastric residues.

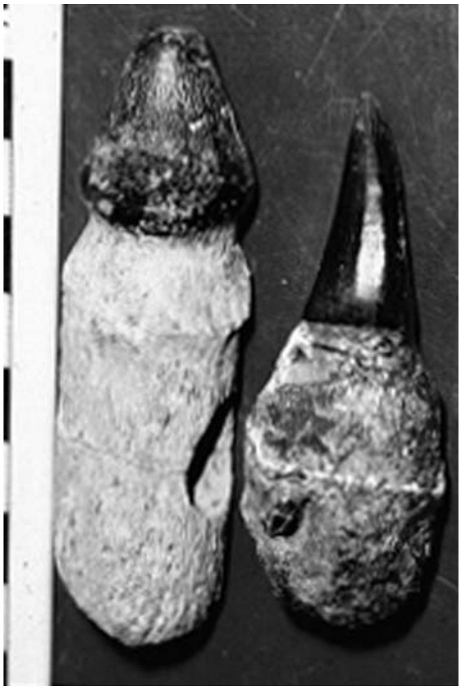

Figure 1. Comparison of an anterior tooth of *Globidens* on left with *Mosasaurus* on right, illustrating the sectorial nature of the latter. Scale in centimeters.

Every effort was made in the field and laboratory to maintain association while preparing the residues to determine diet. As a result, a huge block was removed by heavy equipment through the courtesy of the U.S. Army Corps of Engineers. In the laboratory, William Schurmann expended 5 yr while expertly preparing the specimen from its surrounding concretionary material. He secured the invertebrate specimens described herein. All macrofossils found represent the Bivalvia, the great majority of which are inoceramids. The second author identified the taxa, discussed in the following paragraphs. As expected, most bivalves had been crushed, and few specimens were intact enough for evaluating the morphology required for precise taxonomic determination.

Institutional Abbreviations

FHSM: Fort Hays State Museum, Hays, Kansas; **FMNH:** Field Museum of Natural History, Chicago, Illinois; **SDSM:** Museum of Geology, South Dakota School of Mines and Technology, Rapid City; **SMUSMP:** Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas; **USNM:** U.S. National Museum, Washington, DC.

OCCURRENCES OF *GLOBIDENS* IN NORTH AMERICA

In North America, *Globidens* is represented by two species: *Globidens alabamaensis* and *Globidens dakotensis,* both from Campanian deposits in areas of their respective namesakes, although the latter species may be slightly younger. *G. alabamaensis* was described by Gilmore (1912) on the basis of cranial elements and a vertebra (USNM 6527) from the Mooreville Chalk of the Selma Group, and *G. dakotensis* was described by Russell (1975) on the basis of a relatively complete cranium (FMNH PR 846) from the upper Sharon Springs Formation of the Pierre Shale Group. Another jaw element of *G. dakotensis* (SDSM 4612), consisting of only a partial splenial and posterior dentary with one tooth, was collected from the Sharon Springs Formation of the southern Black Hills (Russell, 1967, 1975). A lower jaw of *Globidens* (FHSM VP 13828) was found in Kansas, also from the Sharon Springs Formation (Everhart and Everhart, 1996). Most recently, a partial skull and associated postcranial elements assigned to *G. alabamaensis* were described as having been derived from the Campanian Marlbrook Marl of the Taylor Formation in Texas (Polcyn and Bell, 2005); however, a recent communication (M. Polcyn, 2006, personal commun.) suggests that the published source may be in error and that the mosasaur may have come from the Ozan Formation; therefore, a range of middle to lower upper Campanian may be more appropriate. Additional specimens of *G. alabamaensis* have been collected from the southeastern United States, including the type area, but have yet to be described. Russell (1975) assigned USNM 4993, associated coronoid, articular, and axis vertebra, and SMUSMP 62102-05, isolated teeth, from Texas and Arkansas to *Globidens dakotensis*. However, based upon the assignment of the new material from Texas to *Globidens alabamaensis* (Polcyn and Bell, 2005), these specimens may be reassigned. The partial skeleton discussed herein was derived from the upper concretionary interval of the DeGrey Formation of the Pierre Shale Group. In many regards, the skeleton (SDSM 74764) appears to be a derived, new species of *Globidens* and is characterized by its large size and relatively high-crowned dentition. The taxonomy of this specimen is outside the scope of this study and is described in another contribution (see Martin, this volume, Chapter 13).

AGE

While the *Globidens* skeleton (SDSM 74764) was being excavated, others of our colleagues were conducting geological investigations and deriving data for absolute dating. Therefore, a measured section of the site that contained the mosasaur specimen was produced (see Hanczaryk, 1998; Hanczaryk and Gallagher, this volume). Based upon their measurements, the *Globidens* specimen occurred at the top of the DeGrey Formation of the Pierre Shale Group, and specimens of *Baculites compressus* were found at the site and half a meter above. In addition, the late Campanian coiled ammonite *Jeletskytes nodosus* and the limpet *Anisomyon* were recovered from concretions and enclosing shale at the mosasaur site. The *Baculites compressus* Biozone of Cobban (1993) and the *"Inoceramus" sagensis* Biozone of Kauffman et al. (1993) were dated by Obradovich (1993) on the basis of ^{40}Ar/^{39}Ar at 73.35 ± 0.39 Ma. Hanczaryk utilized ^{87}Sr/^{86}Sr to derive a date of 72.43 ± 2.0 Ma from the *Baculites compressus* Biozone at the Big Bend. Not only was the biozone dated, but ^{87}Sr/^{86}Sr values were obtained from an oyster shell associated with the *Globidens* skeleton. Two dates for the same bivalve resulted in dates of 72.61 and 72.20, with a mean value of 72.41 ± 2.0 Ma. All absolute dates indicate that the *Globidens* skeleton was entombed during the late Campanian and therefore is the youngest *Globidens* skeleton known from North America.

MATERIALS

The partial skeleton containing the stomach contents is SDSM 74764, from SDSM locality V9837 from the Big Bend area of the Missouri River in Buffalo County, South Dakota. This area is part of the Crow Creek Sioux Indian Reservation, although the specimen was discovered on U.S. Army Corps of Engineers holdings within the reservation. Permission to collect vertebrate fossils was obtained from all concerned. The skeleton is composed of the cranium, jaws, and postcranial skeleton to the mid-dorsal region (Fig. 3); the distal portion had been eroded, but a caudal vertebra had been displaced and was found with the anterior portion of the skeleton. One pectoral girdle is relatively well preserved, and the other was eroded. The skeleton is mostly articulated, was curled, and the bivalves came principally from within the curve of the skeleton, associated with the rib cage (Fig. 4). The skull was displaced slightly, the cranium was crushed, and the jaws disarticulated. Numerous fragments of bivalves were found associated with the specimen, as were the teeth of sharks.

STOMACH CONTENTS

Unfortunately but not surprisingly, the stomach contents were crushed into small fragments. Only relatively small bivalve taxa survived the masticatory process. The area of the rib cage was packed with bivalve fragments (Figs. 3, 4). Some morphology was preserved, affording identification of the pterioids: *Anomia,* four morphotypes that exhibit the prismatic microstructure typical of the genus *"Inoceramus,"* and oysterlike remains.

Mollusca Linneaus, 1758
    Bivalvia Linneaus, 1758
        Pterioda Newell, 1965
            Inoceramidae Giebel, 1852
                "Inoceramus" sp. cf. *"I." tenuilineatus,* Hall and Meek, 1854

A few specimens were collected from the stomach region of the mosasaur that exhibit large, flat valves but with a thickened umbo area (Fig. 5A) characteristic of *"I." tenuilineatus,* which has been recorded from the Big Bend area of the Missouri River (Meek, 1876), and a species with close affinities is noted to have occurred in the late Campanian (Kauffman et al., 1993). As might be expected, the robust umbo region of the shells survived the masticatory process.

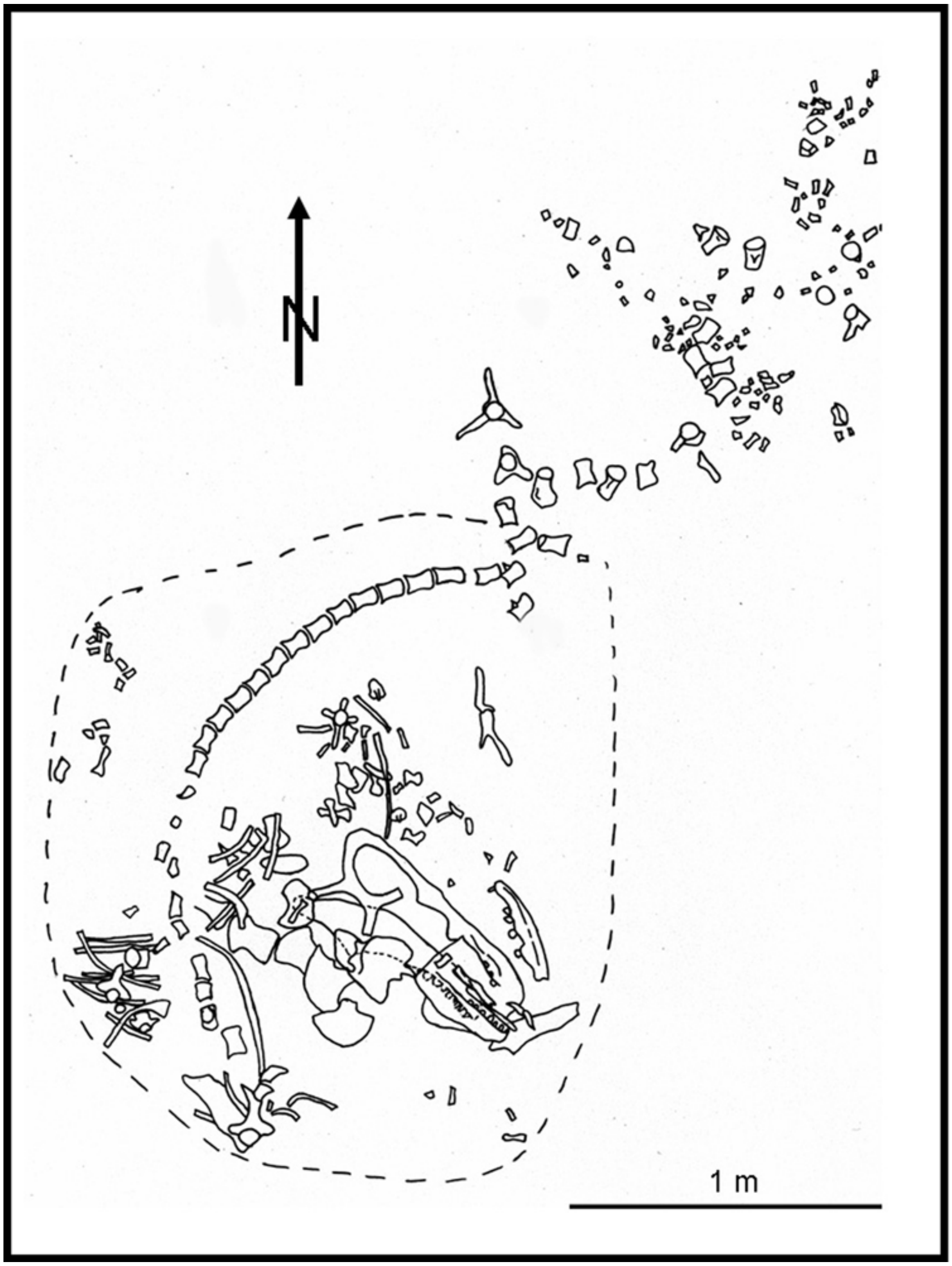

Figure 3. Drawing of skeleton, based upon field and laboratory maps. Dashed area represents area of bivalve concentration.

Inoceramidae Giebel, 1852
Coarse-ribbed genus, indet.

Fragments of a coarse-ribbed morphotype of an inoceramid bivalve were found in the rib cage (Fig. 5B). These fragments are relatively rare within the concentration, but extrapolation of size on the basis of preserved umbo areas indicates a much smaller bivalve than that described below. Similar inoceramids from the upper DeGrey Formation include *"Inoceramus" sagensis, "I." nebrascensis,* and *"I."* sp. cf. *"I." regularis;* the fragments in the stomach area may represent these taxa.

Inoceramidae Giebel, 1852
Fine-ribbed genus, indet.

One specimen found in the stomach region is relatively small, like the coarse-ribbed taxon described above, but has fine, closely spaced ribs like those of *"I." proximus*.

Inoceramidae Giebel, 1852
Thin, flat-shelled genus, indet.

Most commonly occurring within the rib cage were fragments of a large, relatively thin-shelled morphotype. This taxon was very

Figure 4. Skeleton, showing rib cage filled with bivalve fragments (the light-colored fragments distributed throughout the photograph). Scale is 15 cm.

large in diameter, and complete specimens have been found in the upper DeGrey Formation (Fig. 6), nearly 40 cm in diameter, indicating a large, fleshy body mass. The valves associated in the stomach area exhibited only wide, faint ribs in comparison with the taxon described above, and most fragments were flat or punctate. Most fragments of this morphotype were 4 cm or smaller in diameter (Fig. 5C–E), and some were found in dense, compact concretionary masses (Fig. 5F) that were up to 10 cm in diameter. Some shells were compressed into concordant layers (Fig. 5G); some were found discordant (Fig. 5H). Fragments of some valves exhibited rounded edges (Fig. 5I; Fig. 7A, B). The fragments ranged widely in thickness from 1 to 5 cm and consist of the prismatic shell layer. Although the differences in thickness may be partially explained by different thicknesses within one shell, the shear number of fragments suggests that numerous individuals of this morphotype were preserved in the stomach area of this mosasaur. Candidates for these invertebrate remains include *"Inoceramus"* sp. cf. *"I." convexus* and particularly *Platyceramus* sp. cf. *P. vanuxemi,* which also have been found in the upper DeGrey Formation.

Anomiidae Rafinesque, 1815
Anomia Linneaus, 1785
Anomia, sp. indet.

Several specimens of these small bivalves were preserved within the central body cavity of the mosasaur (Fig. 5J, K). These lamellar specimens are ~4 cm long, and many of the bivalve fragments were in this range, indicating the size after pulverization. Therefore, some smaller shells escaped breakage during the masticatory process, and the relative similar size of these and broken shells supports the contention that these sharp-edged broken fragments are remnants of stomach contents.

Ostreidae Rafinesque, 1815
Ostrea Linneaus, 1785
"Ostrea" sp. indet.

A number of fragments appear similar to the form genus, *Ostrea,* or perhaps to *Pseudoperna*. Most are relatively thin shelled in comparison with most known species of *Ostrea* or *Crassostrea* but exhibit the irregular growth typical of these benthic bivalves (Fig. 5L). Both *Ostrea inornata* and *Pseudoperna congesta* are recorded from the Big Bend area (Meek, 1876), but Kauffman et al. (1993) indicated that *Ostrea patina, Crassostrea glabra,* and *Crassostrea trogonalis* are recorded from the *Baculites compressus* Biozone.

Like *Anomia, "I."* sp. cf. *"I." tenuilineatus,* the fine-ribbed morphotype, and the coarse-ribbed inoceramid morphotype, remnants of *"Ostrea"* are relatively rare in comparison with those of the flat, thin-shelled inoceramid morphotype. Because the stomach contents are fragmented, quantitative differentiation is difficult, but the large, flat, thin-shelled inoceramids constitute ~90% of the observed fragments.

DISCUSSION

As can be observed from the preceding paragraphs, the taxonomic diversity of the bivalves within the rib-cage area is relatively low, and 90% of the valve fragments are those of the large, flat-shelled inoceramid morphotype similar to those of *Platyceramus*.

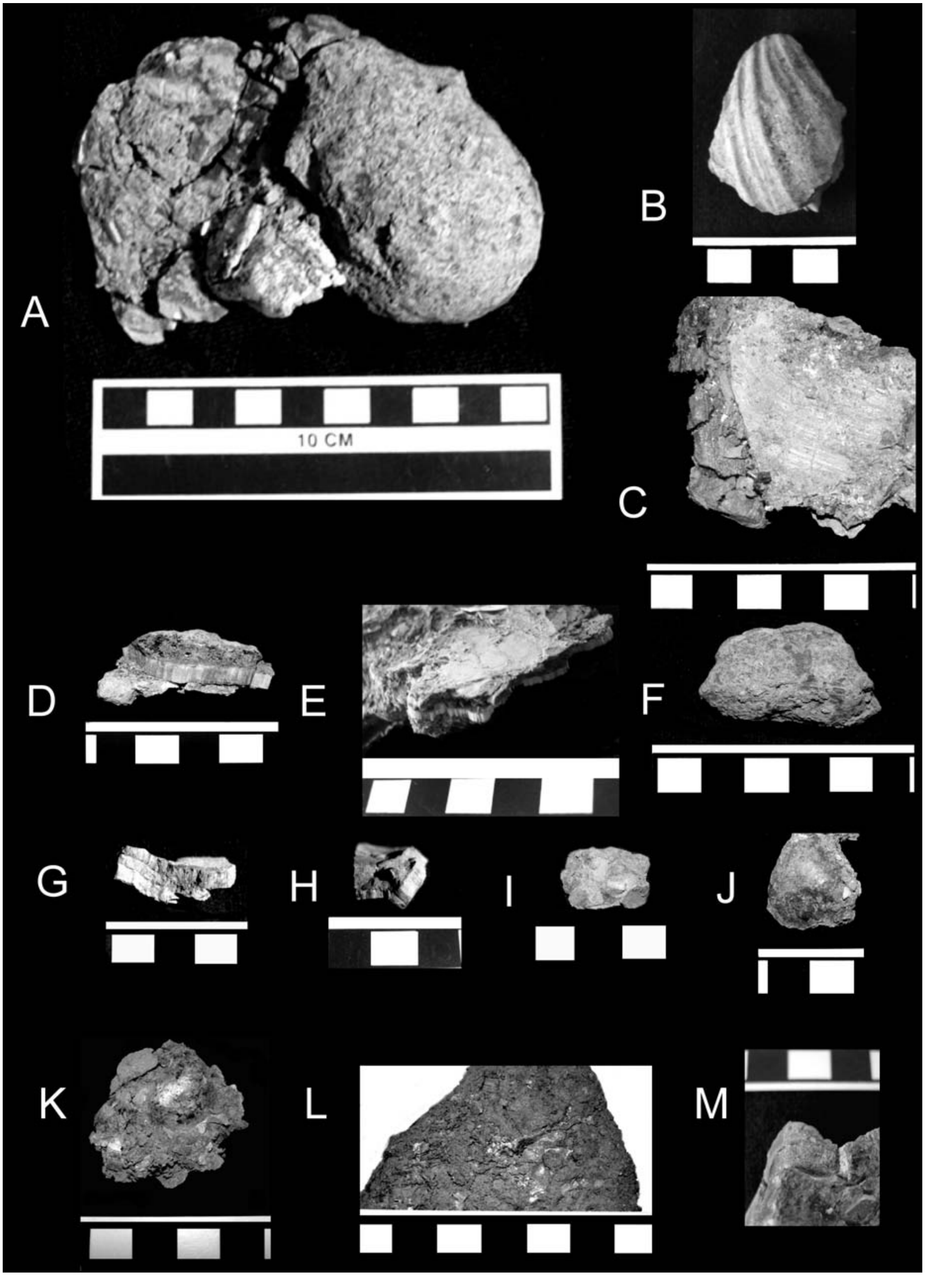

Figure 5. (A) Photograph of *"Inoceramus"* sp. cf. *"I." tenuilineatus*. (B) Fragment of coarse-ribbed inoceramid. (C) Fragment of flat-shelled inoceramid. (D) Cross section of flat-shelled inoceramid. (E) Cross section of thin, flat-shelled inoceramid. (F) Concretionary body containing bivalve fragments. (G) Flat-shelled inoceramid fragments preserved concordantly. (H) Flat-shelled inoceramid fragments preserved discordantly. (I) Inoceramid shell fragments exhibiting rounded edges. (J) Valve of *Anomia*. (K) Valve of *Anomia*. (L) Ostreid shell fragment. (M) Tooth of *Squalicorax pristodontus*. All specimens except the shark tooth (M) were found as stomach contents of the mosasaur *Globidens*.

Figure 6. Inoceramid typical of the upper DeGrey Formation of the Pierre Shale Group in the Big Bend area of the Missouri River. The pick head is 38.5 cm across.

Low diversity may be explained, because creatures are often selective in the choice of prey, and/or the final ingestion may represent a snapshot of a single, limited prey meal. In either case, low diversity may well support the contention that the fragments packed into the rib-cage area are stomach contents. Additional evidence comes in the form of the fragments themselves. Fragments range from 2 to 10 cm, but most are in the 4 to 6 cm range (Fig. 5C–E). Therefore, the relatively small size of fragments of creatures that could originally have shells nearly a third of a meter in diameter indicates breakage by mastication. Most of the edges of the broken shells were angular and unrounded, with little evidence of etching by stomach acid. However, some fragments of thick-shelled inoceramids exhibited smoother edges than the thin shells (Fig. 5I). The angular edges are due to the prismatic nature of the shells that broke apart and disaggregated. In support of this contention, microscopically, the entire stomach region was characterized by innumerable calcite prisms jumbled and jackstrawed throughout the matrix (Fig. 7A, B). Macroscopically, the prismatic shell fragments were found as isolated fragments or compacted together, stacked in layers (Fig. 5G), some concordant and some discordant (Fig. 5K). These "books" of valve fragments often occur in "concretionary bodies" (Fig. 5F). Similar occurrences of shell hash are not infrequently encountered as isolated bodies in the upper DeGrey Formation. These compact bodies full of shell fragments were difficult to explain through natural sedimentary processes until this occurrence was found. Some of these bodies may well represent coprolites (or regurgitites) of this durophagous mosasaur.

In addition to the mollusks, chondrichthyan teeth were found associated with the mosasaur skeleton. Three taxa were identified: the first, *Squalus* sp. (Fig. 7C–E), is represented by numerous small teeth; the second, *Squalicorax pristodontus* (Fig. 5M), by a few teeth; and the third by a single small tooth of *Cretalamna*. Some teeth, particularly those of *Squalus,* were found associated with the mollusk fragments (Fig. 7C–E) and might have been considered stomach contents. However, numerous mosasaur skeletons of varied taxa have been recovered from the upper DeGrey Formation of the Pierre Shale Group in the Big Bend area of the Missouri River. In every case, abundant *Squalus* teeth in particular (sometimes hundreds), are associated with each mosasaur but are not found in normal areas of shale sedimentation. A few teeth of other sharks are commonly associated, as in the case of this *Globidens* skeleton. These associations and tooth abundances indicate that these chondrichthyans were scavenging the large marine reptile carcasses, shed the teeth during the scavenging activity, and were not stomach contents. Interestingly, our investigations of numerous mosasaur skeletons from the Sharon Springs Formation lower in the stratigraphic section reveal no evidence of *Squalus* teeth. Occasionally, scattered *Squalicorax* or *Cretalamna* teeth may be found but never in abundance. When we initially found *Cretalamna* teeth associated with stomach contents of a tylosaurine mosasaur from the Sharon Springs Formation (Martin and Bjork, 1987), we assumed they were part of the stomach contents, but with experience we realized that the teeth may have been lost during scavenging. Moreover, the sudden appearance of *Squalus* in the DeGrey Formation is further evidence of a great faunal turnover, as indicated by a great change in mosasaur taxa (Martin et al., 1996). The level where this change occurs is probably demarked by the Crow Creek siltstone and an associated disconformity (see Martin et al., this volume), but vertebrates are exceedingly rare in this unit and in the underlying Gregory Formation of the Pierre Shale Group. Therefore, the vertebrate faunal change occurred sometime between deposition of the Gregory Formation and the lower DeGrey Formation of the Pierre Shale Group.

Also found associated with the mosasaur skeleton was one teleost scale (Fig. 7G). Although this fish scale may be part of the stomach contents, the single occurrence suggests that the scale was associated by chance in the marine environment.

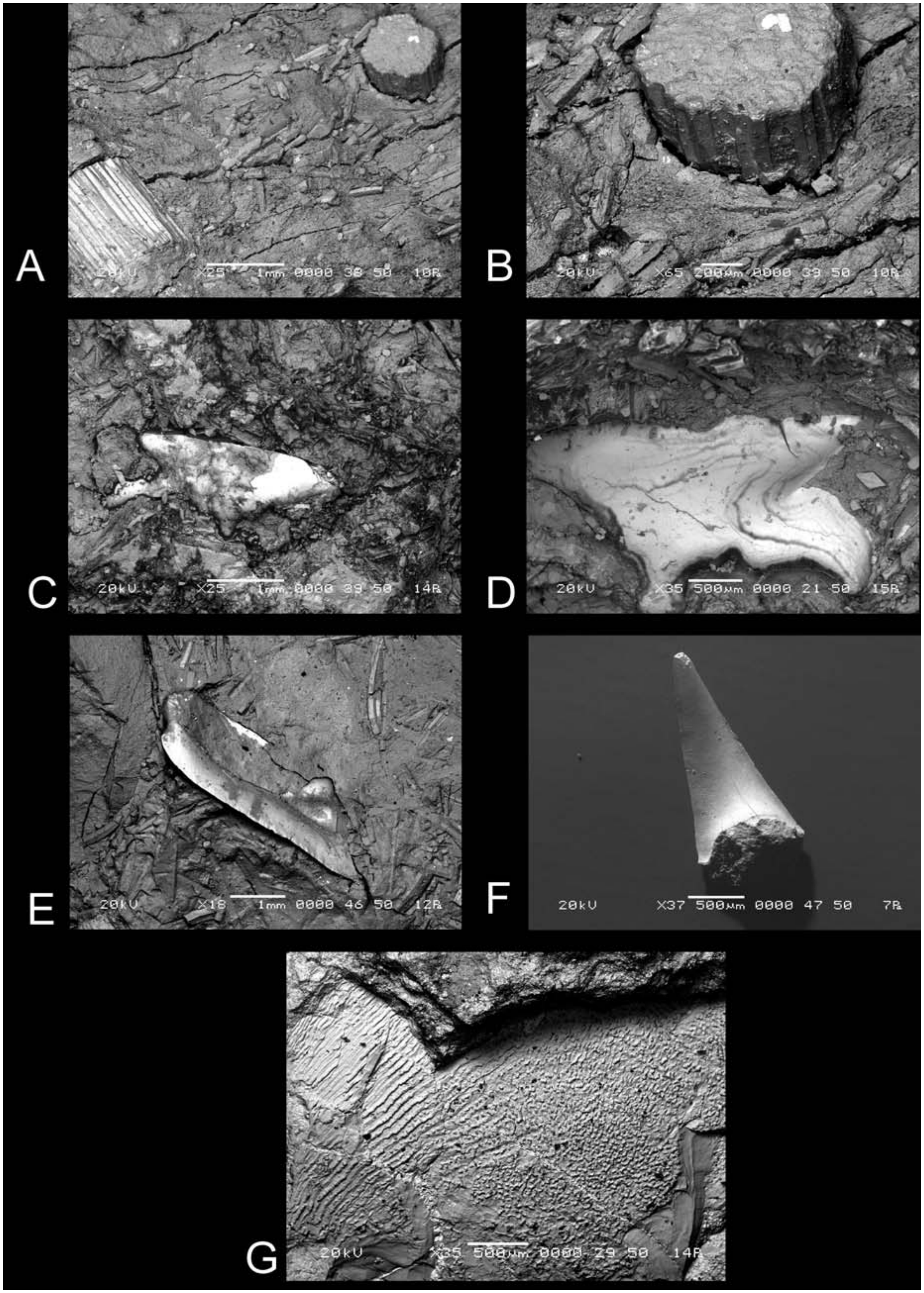

Figure 7. (A) SEM photograph of calcite prisms of inoceramid valves in the stomach region of *Globidens;* note rounded nature of inoceramid fragment. (B) Enlargement of rounded valve fragment. (C–E) SEM photographs of the teeth of the shark *Squalus,* preserved in the stomach region of *Globidens*. (F) SEM photograph of a tooth of the shark *Cretalamna,* from the stomach region. (G) SEM photograph of a teleost scale found in the stomach region of the mosasaur *Globidens*.

SUMMARY

The youngest and most complete skeleton of the durophagous mosasaur *Globidens* from North America was discovered in central South Dakota along the Big Bend of the Missouri River. The specimen occurred in the upper portion of the DeGrey Formation of the Pierre Shale Group from within the *Baculites compressus* Biozone. In addition, $^{87}Sr/^{86}Sr$ values obtained from a bivalve associated with the *Globidens* skeleton resulted in a mean value of 72.41 ± 2.0 Ma (see Hanczaryk and Gallagher, this volume), making the occurrence late Campanian.

Within the rib-cage area of the mosasaur are concentrations of six identified taxa of bivalves. Most of these specimens had been crushed during mastication into fragments ranging usually from 4 to 6 cm. Therefore, some smaller taxa, such as *Anomia,* escaped obliteration. Most of the larger shells were crushed beyond recognition at generic levels, but all resemble inoceramids and ostreids. Some fragments exhibited abrasion of the edges, but most were angular owing to the dissociation of the calcite prisms that form most of each valve. Both ribbed and nonribbed, large, flat inoceramids are found in the shell coquina, and calcite prisms are ubiquitous within the stomach area. Some valve fragments were found isolated, but many "concretionary bodies" contained books of shell fragments, some parallel and some discordant. The fragmentary, discordant shells; low taxonomic diversity; some rounding; and a lack of abundant bivalves above, below, or lateral to the skeleton indicate that these remains are stomach contents and not the result of normal sedimentation.

Three shark taxa were associated with the mosasaur skeleton, and although some teeth of *Squalus* were found in the stomach region, most teeth were found in the shale around the skeleton. Hundreds of *Squalus* teeth were recovered; a similar situation has been observed with all mosasaurs from this stratigraphic level whether or not they possessed stomach contents. Therefore, the sharks were probably scavenging the mosasaur carcass, and the teeth were shed during feeding. These teeth probably are not stomach contents, and thus far sharks cannot definitely be considered the prey of mosasaurs.

Overall, the associations with the *Globidens* skeleton indicate that this mosasaur fed upon bivalves rather than upon turtles or by scavenging carcasses. The dentition is well adapted for crushing, and apparently *Globidens* preferred bivalves, particularly the large, flat inoceramids characterized by a large, fleshy, visceral mass.

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We are greatly indebted to the U.S. Army Corps of Engineers and the various tribal chairpersons and tribal councils of the Crow Creek Sioux Tribe for permission and support of our expeditions to recover and study the fossil remains from the Big Bend area of central South Dakota. In particular, A.K. Olson, Steve Merkwin, and George Wolf, U.S. Army Corps of Engineers, arranged for heavy equipment that allowed us to maintain the integrity of this association. Carson Murdy, Bureau of Indian Affairs, also supplied required permits for our investigations. The volunteers and students of the 1991 Field Paleontology class, in association with the New Jersey State Museum, including Larry Conti, who found the specimen, are particularly commended for their efforts in recovery of the specimen. But perhaps our greatest thanks should go to William Schurmann, who has volunteered at the Museum of Geology for many years, and who single-handedly spent over 5 yr preparing this mosasaur and its associated stomach contents from extremely hard FeMn concretionary material. Dr. Mark Gabel, Black Hills State University, kindly provided the SEM photographs for Figure 7. We thank Michael Everhart, Fort Hays State Museum, Kansas, and Robert Ramsdale and David Parris of the Bureau of Natural History, New Jersey State Museum, for helpful reviews of the manuscript.

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A new species of the durophagous mosasaur Globidens *(Squamata: Mosasauridae) from the Late Cretaceous Pierre Shale Group of central South Dakota, USA*

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ABSTRACT

The most complete specimen of the unusual mosasaur *Globidens* has been discovered in central South Dakota along the Missouri River. The specimen consists of the anterior half of a skeleton, including crushed skull, pectoral girdle, partial paddle, and vertebral series. One humerus and ulna exhibit pathologies. The partial skeleton was found at the top of the DeGrey Formation (upper Campanian) of the Pierre Shale Group and is therefore the youngest skeleton from North America. The specimen exhibits apomorphies that correspond with the late occurrence and indicate a new species. Increased dental hypsodonty, lack of a posterior buttress on teeth, great size, and massive build indicate a derived intermediate species of a clade that first occurred with rounded teeth in the early Campanian in North America and Europe *(Globidens alabamaensis* and *Globidens dakotensis)* and culminated with high-crowned teeth with posterior buttresses in the Maastrichtian of Africa, the Middle East, and South America *(Globidens phosphaticus)*. Associated with the specimen are bivalves that are interpreted as stomach contents and shark teeth that are interpreted as the result of scavenging.

Keywords: mosasaur, *Globidens,* durophagous, Cretaceous, South Dakota.

INTRODUCTION

Mosasaurs were marine lizards that first appeared in the Late Cretaceous and had a relatively short duration before the terminal Cretaceous extinction. Even though short-lived, these reptiles diversified, dispersed worldwide, and have been found on every continent. Two major groups of the Mosasauridae, Subfamily Mosasaurinae and Parafamily Russellosaurina (Polcyn and Bell, 2005a), appear to have produced numerous species of mosasaurs adapted to carnivory. Nearly all these species are characterized by marginal sectorial dentitions as well as sharp teeth on the pterygoid bones. These teeth are normally high, conical to laterally compressed, and many have carinae that are serrated. A number of specimens have been found in South Dakota with stomach contents, indicating the carnivorous nature of these top-end predators (Martin and Bjork, 1987; Martin, 1994). Two tylosaurines have been found with stomach contents, one with a small mosasaurine tentatively assigned to *Clidastes,* and another with a plioplatecarpine assigned to *Platecarpus,* a teleost, and a hesperornithine bird (Martin, 1994; Martin and Bjork, 1987). A plioplatecarpine mosasaur has been found with teleosts within the stomach region (Martin, 1994). All of these specimens indicate what might be expected from the highly sectorial (piercing or slicing) teeth. In contrast, the mosasaurine, *Globidens,* is characterized by

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massive, rounded brachyodont teeth, suggesting a much different prey preference than the typical mosasaur species. Within the specimen described herein, broken, unrounded bivalves are preserved in the gastric region, demonstrating utilization of the unusual dental adaptation of this marine reptile (Martin, 1994; Martin and Fox, 2004 and this volume).

Such an unusual mosasaur expectedly would be easy to identify, and distinctive specimens have been recovered from numerous regions in the world. However, most specimens are represented by isolated teeth. Partial skeletal material is rare, and most has been discovered in North America, including the Southeast, Texas, and South Dakota. The first species described came from the Campanian Selma Group, Mooreville Chalk, of Alabama, and was named for its state of origin (*Globidens alabamaensis* Gilmore, 1912). The specimen (USNM 6527) consists of a partial skull, and a number of specimens have been since recovered, but most remain undescribed. The best known species was discovered from the middle Campanian Sharon Springs Formation of the Pierre Shale Group in South Dakota (Russell, 1975; Martin et al., this volume). The type specimen of *Globidens dakotensis* consists of a partial skull (FMNH PR 846). Another partial skull was ascribed to *G. alabamensis* and was purported to be from the lower Campanian Marlbrook Marl of the Taylor Formation of Texas (Polcyn and Bell, 2005b). However, the attribution of the specimen from the Marlbrook Marl was in error and may be from the Ozan Formation (M. Polcyn, 2006, personal commun.); therefore, a range of middle to lower upper Campanian is appropriate until the source can be positively established.

Now, the most complete skeleton of the genus (SDSM 74764) has been found in the upper Campanian DeGrey Formation of the Pierre Shale Group in central South Dakota. The specimen consists of a partial crushed skull, including a relatively complete dentition, parts of the pectoral girdles and front paddle, the anterior portion of the vertebral series, and two caudal vertebrae (Fig. 1). Most of the posterior portion of the skeleton had been eroded away, but a few elements, including caudal vertebrae, had been transported near the skull prior to burial. The skeleton was slightly curled, and the skull and pectoral girdles displaced within the curve of the vertebral column. Some elements had been displaced away from the main concentration, but most were found within a 2 m radius. The rib-cage area was filled with densely packed bivalve fragments, principally large, flat inoceramids that had a large visceral content. In addition, small, hard concretionary bodies full of shells were found within the concentration. These small bodies may represent feces that had not yet been expelled. The shell concentration was not found above or below and did not extend laterally, indicating that the shells were the remnants of ingestion. Also found associated with the skeleton were numerous shark teeth, mostly *Squalus,* that appear to represent teeth lost during scavenging of the large mosasaur carcass (Martin and Fox, this volume). The remains of this shell-crushing mosasaur exhibit distinctive morphologies that indicate a derived species in comparison with those from North America, and more similar to that described from Africa.

Globidens Distribution during the Late Cretaceous

Globidens appears to be a highly derived member of the Mosasaurinae, is most closely related to *Prognathodon,* and has been found in localities in the Middle East, Africa, Europe, South America, North America, and possibly Asia (Russell, 1975; Lingham-Soliar, 1999; Bardet et al., 2005). In North America the taxon was described originally from the upper lower–lower middle Campanian (Kiernan, 2002) Mooreville Chalk of the Selma Group in Alabama as *Globidens alabamaensis* (Gilmore, 1912) on the basis of USNM 6527. This taxon is characterized by small, rounded subspherical teeth with apical nubbins and distinct carinae, as well as the frontal with a dorsal crest and forming part of the orbital margin. The taxon has been found in Alabama, Tennessee, Mississippi, and Texas from lower to middle Campanian rocks. A second species from North America was described by Russell (1975) on the basis of a relatively complete cranium from western South Dakota (FMNH PR 846). This specimen, too, is from lower middle Campanian deposits (Cobban, 1993), having been discovered in the Sharon Springs Formation of the Pierre Shale Group. The taxon may be slightly younger than that from Alabama and exhibits a slightly larger size and subspherical teeth with apical nubbins and carinae, but the frontal is excluded from the orbital margin by contact of the prefrontal and postorbitofrontal. Another specimen of *Globidens dakotensis,* a right dentary with partial dentition, was found in the Sharon Springs Formation in Kansas (Everhart and Everhart, 1996). The specimen described herein is the third species known from North America.

From South America, *Globidens* was first noted by Price (1957) from the Late Cretaceous of Brazil. This occurrence is based upon isolated subspherical teeth with recurved apical nubbins and shallow sulci. Bardet et al. (2005) assigned these teeth to *Globidens phosphaticus,* known otherwise from Africa and the Middle East. *Globidens phosphaticus* has been characterized by heterodont teeth with tall anterior conical teeth with carinae and bulbous middle teeth with an inflated posterior surface, a recurved apical nubbin, an ovate cross section, and distinct sulci (Bardet et al., 2005).

From the Old World, numerous fragmentary specimens are known. The late Campanian occurrence from Belgium has been assigned to the North American species *G. alabamaensis* (Dollo, 1924; Russell, 1975; Lingham-Soliar, 1999), although the basis for assignment to this species is not well documented. Otherwise, the Maastrichtian *Globidens* species from Africa and the Middle East have been assigned to a new species, *Globidens phosphaticus* (Bardet et al., 2005). *G. aegyptiacus* (Zdansky, 1935), now considered to be *Igdamanosaurus aegyptiacus* (Lingham-Soliar, 1991), and *G. timorensis* (von Huene, 1935) possess massive teeth. However, in both cases these species are based upon isolated teeth, and *G. aegyptiacus* was considered a *nomen nudum* by Telles Antunes (1964) but was assigned to a separate genus, *Igdamanosaurus* (Lingham-Soliar, 1991), characterized by high, round tooth crowns with prominent striations and no basal constriction. *Globidens timorensis* may represent anterior teeth as thought by Russell (1975) or may not even be a mosasaur as pro-

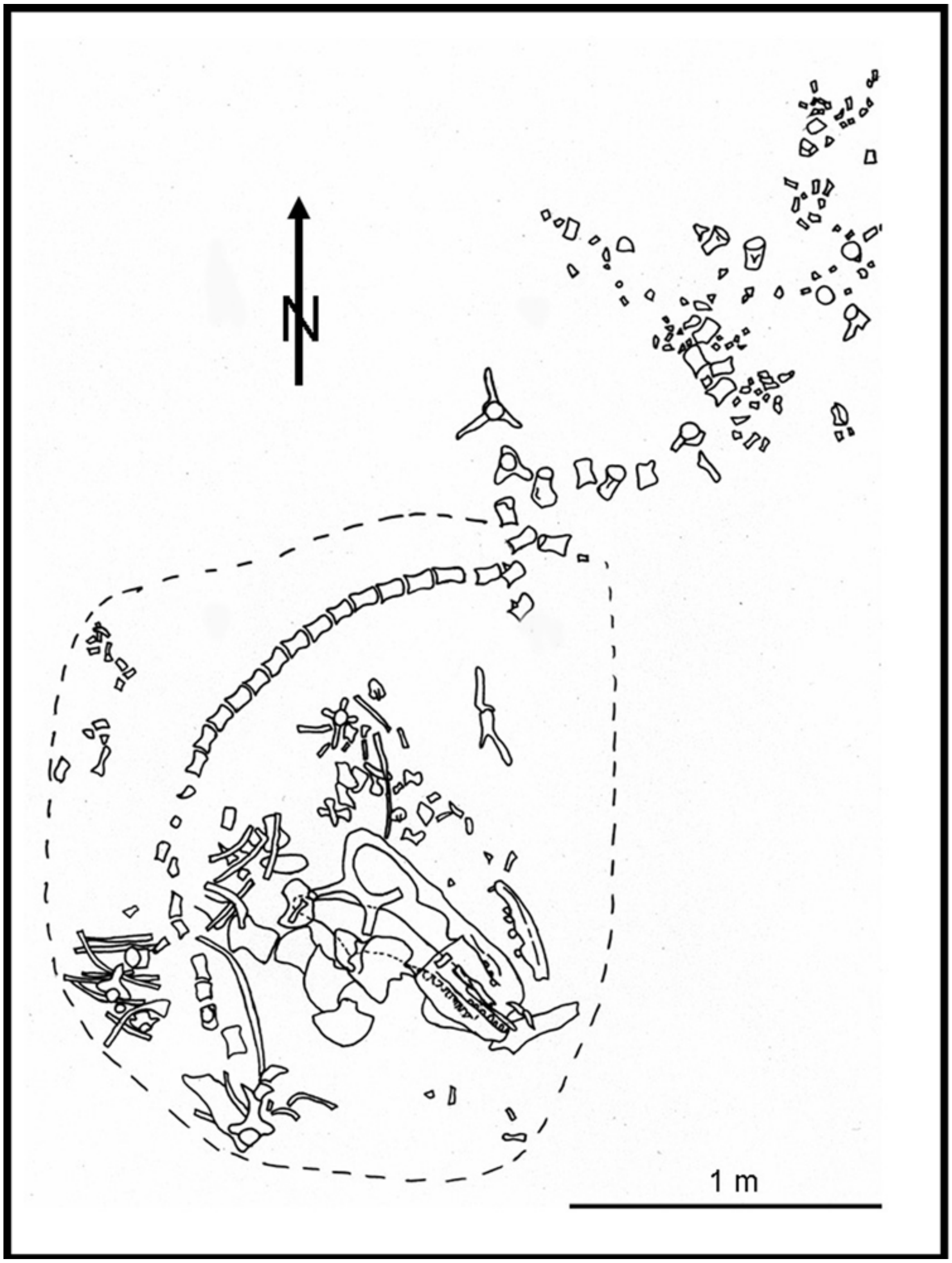


Figure 1. Drawing of skeleton, based upon field and laboratory maps. Dashed area represents area of bivalve concentration.

fessed by Lingham-Soliar (1999). In any case, these isolated teeth may not be diagnostic at a species level, and the species should be considered a *nomen vanum*. Therefore, only *G. alabamaensis, G. dakotensis, G. phosphaticus,* and the species described herein are recognized species of *Globidens*. The problem of designating species of *Globidens* on the basis of isolated teeth may be somewhat remedied by the specimen described below, which possesses a nearly complete heterodont dentition.

Institutional Abbreviations

FHSM: Fort Hays State Museum, Hays, Kansas; **FMNH:** Field Museum of Natural History, Chicago, Illinois; **KU:** University of Kansas, Lawrence; **MNHN:** Muséum national d'Histoire naturelle, Paris, France; **OCP:** Office Chérifien des Phosphates, Khouribga, Morocco; **SDSM:** Museum of Geology, South Dakota School of Mines and Technology, Rapid City; **USNM:** U.S. National Museum, Washington, DC.

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811
Mosasauridae Gervais, 1853
Mosasaurinae Gervais, 1853
Globidensini Russell, 1967
Globidens Gilmore, 1912

Type species. *Globidens alabamaensis* Gilmore, 1912 (lower Campanian, Arcola Member, Mooreville Chalk, Selma Group)

Globidens schurmanni n. sp.
Figures 1–8

Holotype. SDSM 74764, partial anterior skeleton, including cranium, jaws, cervical and trunk vertebrae partially articulated, pectoral girdles, partial anterior paddle, isolated humerus and ulna, and isolated caudal vertebrae.

Locality. SDSM locality V9837, at the Big Bend of the Missouri River, Buffalo County, South Dakota.

Age. Late Campanian.

Stratigraphic source. Uppermost DeGrey Formation of the Pierre Shale Group, 14.5 m above the top of the Crow Creek Member of the DeGrey Formation of the Pierre Shale. Specimens of *Baculites compressus, Jeletskytes nodosus,* and the limpet *Anisomyon* were associated with the mosasaur. The *Baculites compressus* Biozone of Cobban (1993) and the *"Inoceramus" sagensis* Biozone of Kauffman et al. (1993) were dated by Obradovich (1993) on the basis of ^{40}Ar/^{39}Ar at 73.35 ± 0.39 Ma. Hanczaryk and Gallagher (this volume) utilized ^{87}Sr/^{86}Sr to derive a date of 72.43 ± 2.0 Ma from the *Baculites compressus* Biozone at the Big Bend of the Missouri River in South Dakota. Not only was the biozone dated, but ^{87}Sr/^{86}Sr values were obtained from an oyster shell associated with the *Globidens* skeleton. Two dates on the same bivalve resulted in dates of 72.61 and 72.20, with a mean value of 72.41 ± 2.0 Ma. All dates indicate that the *Globidens* skeleton was entombed during the late Campanian and is therefore the youngest known *Globidens* skeleton from North America.

Etymology. Named in honor of William R. Schurmann, who spent 5 yr preparing the specimen from iron-manganese concretions and for his volunteer efforts in the Museum of Geology laboratory and the field for 20 yr. Numerous specimens have been discovered and prepared through his efforts and dedication to vertebrate paleontology.

Diagnosis. A species of *Globidens* that possesses a heterodont dentition normally without carinae and consisting of anterior high, slender teeth (particularly the first maxillary and dentary teeth); a medial tooth row interval characterized by high-crowned, symmetrical pointed teeth with no posterior buttress; and a posterior interval characterized by round, massive, brachyodont teeth that are not dorsoventrally compressed. Upper anterior teeth posteriorly inclined and recurved. Rather than the rounded teeth of North American *Globidens* species, middle portion of the tooth row exhibits a high, bell-shaped lateral profile. Middle and posterior teeth do not possess posterior buttresses. Premaxillae short and compact, with wide internarial bar. Premaxillary-maxillary suture rises vertically before trending posteriorly. Frontal anteroposteriorly short, rounded, without lateral emargination and with no medial crest.

Differentiation. *Globidens alabamaensis* described from the Campanian of southern North America and Belgium possesses subspherical posterior teeth with carinae and frontal forming part of the orbit, unlike *G. schurmanni,* which is characterized by high-crowned heterodont teeth mostly without carinae, the frontal excluded from the orbit by the prefrontal and postorbitofrontal, and the premaxillary-maxillary suture of the single known specimen described by Russell (1967) to angle posteriorly in a manner more similar to that of *Clidastes* or *Mosasaurus* rather than rising vertically. *Globidens dakotensis* from the early medial Campanian portion (Cobban, 1993) of the Western Interior Seaway of North America possesses subspherical medial and posterior teeth with carinae, a frontal with a dorsal crest, and a narrow internarial bar of the premaxillae unlike *G. schurmanni,* which has high-crowned, nearly symmetrical medial teeth without carinae, no dorsal crest on the frontal, and a wide internarial bar. *G. phosphaticus,* known from isolated teeth from Maastrichtian deposits of Africa, the Middle East, and South America, possesses high-crowned medial teeth with prominent posterior buttresses, unlike the more symmetrical teeth of *G. schurmanni*.

Globidens schurmanni is unlike *Igdamanosaurus* from Africa in possession of constricted tooth bases and lack of carinae.

Description. The holotype of *Globidens schurmanni* (SDSM 74764) is composed of the cranium, both jaws, and postcranial skeleton to the mid-dorsal region (Fig. 1), including the atlas-axis complex. The skeleton is partially articulated but was curled, with the skull displaced into the curve of the vertebral column. The cranium was crushed both dorsoventrally and laterally (Fig. 2). The rostrum was crushed dorsoventrally, and the maxillae were rotated so that the medial surfaces faced upward. The premaxillae lie between the maxillae dorsally, and the right dentary lies between the maxillae ventrally (Fig. 2). The posterior portion of the skull lies in approximate life position, but the middle portion of the cranium, including the frontal, was displaced laterally. The right jaw lies below the cranium, and the posterior portion of the jaw lies below the displaced mid-portion of the cranium. The left jaw and quadrate were disarticulated and found separated from the cranium. The basioccipital and basisphenoid are obscured. The pectoral girdle is entwined with the middle part of the cranium; the right half of the girdle and front limb are partially articulated, whereas the left scapula-coracoid is also entwined with the cranium, but most distal elements were separated. The distal portion of the skeleton had been eroded, but two caudal vertebrae had been displaced and were found with the anterior portion of the skeleton. Also found with the skeleton was a concentration of bivalves that came principally from within the curve of the skeleton and was associated with the rib cage. These bivalves represent stomach contents of the large reptile, and these, as well as

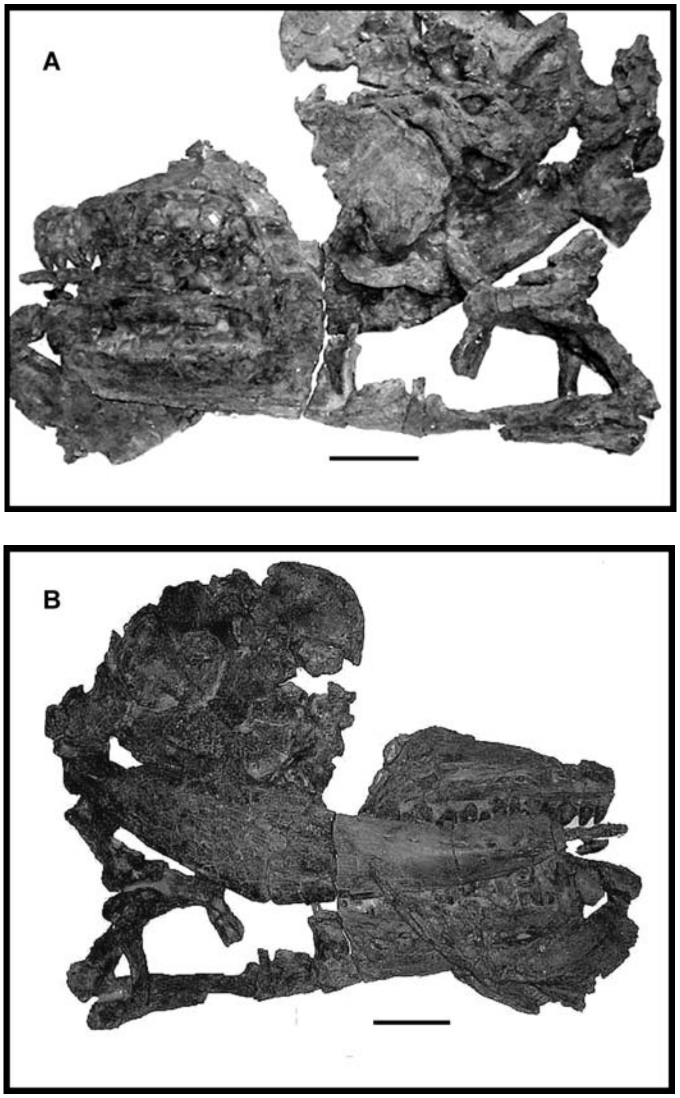


Figure 2. (A) Dorsal view of cranium of *Globidens schurmanni,* SDSM 74764, as preserved. (B) Ventral view of the skull of *Globidens schurmanni,* SDSM 74764, and the right lower jaw, which lay below the cranium. Scale is 10 cm.

chondrichthyan teeth that were shed during scavenging of the *Globidens* skeleton, are reported in another contribution (Martin and Fox, 2004, this volume).

SKULL

PREMAXILLAE: As is normal for the Mosasauridae, the premaxillae (Fig. 3A, B) are fused into a single unit. In this case the premaxillary unit is very short anteroposteriorly (~4 cm) and exhibits a relatively vertical premaxillary-maxillary suture (Fig. 3A) unlike that of *Globidens alabamaensis* as described by Russell (1967) and more similar to that of species of *Prognathodon*. The element is wide transversely (6.1 cm), wider than long. Unfortunately, the alveoli are obscured, but as in all mosasaurs, two teeth on each premaxilla are probable. The posterior alveolus is evident and relatively large, and the anterior tooth may be smaller. A similar situation appears to have occurred on the holotype of *Globidens dakotensis*. Even though the premaxillae are very short and robust, the lower jaws exhibit a short, dorsoventrally deep predental extension (Figs. 3C, 5A) similar to the condition of *Prognathodon* and tylosaurine lower jaws. However, tylosaurines possess a predental rostrum that does not occur in *Prognathodon* or *Globidens*.

The anterior portion of the premaxillae was rotated 90° and lies on its right side. However, the internarial bar remains in life position but is crushed between the maxillae, obscuring the dentition of the left maxilla. The internarial bar is relatively wide (3.25 cm) and retains its width throughout its length in comparison with that of *Globidens dakotensis*. The posterior margin appears forked to meet with the anterior prongs of the frontal. As a result, the main body of the premaxillae appears shorter, and the internarial bar remains at the same width (Fig. 3C, D), rather than narrowing medially, like that illustrated and described for *Globidens dakotensis* (Russell, 1975).

MAXILLAE: Owing to the crushed nature of the cranium, the maxillae are rotated inward and intertwined with the right dentary, internarial bar, and pterygoid (Fig. 3D). Therefore, much of the morphology is obscured, including some of the dentition, making a precise tooth count difficult. Ten teeth exposed on the left maxillae, a projection of the posterior teeth exposed on the right maxillae, and a smaller, slightly recurved isolated tooth all suggest a total tooth count of 12–13. Very large foramina for egress of the maxillary branch of the trigeminal nerve occur into two rows above the tooth rows on the lateral faces of the maxillae (Fig. 3C–E). At least 9 foramina occur on the lower row, and at least 8 on the upper row on the right maxilla. The anterior and dorsal margin of the left maxilla is better preserved (~32 cm anteroposteriorly) and possesses the premaxillary-maxillary suture. The suture (Fig. 3D) rises vertically from the tooth row and curves posteriorly to the anterior origin of the external nares to extend for a total of 9.25 cm. The end of this suture is demarked by a high, rounded dorsal process on the maxilla. The nares appear to originate above the 4th and 5th maxillary tooth of SDSM 74764 (above the 5th and 6th teeth in *Globidens alabamaensis* and *G. dakotensis*) and are wide anteriorly, narrowing posteriorly, similar to that illustrated for *Globidens dakotensis* (Russell, 1975). Posteriorly, the dorsal margin of the maxilla rises very high, higher than the anterior rounded dorsal process, to suture against the prefrontal. Even though the posterior margin rises high, higher than that illustrated for *G. dakotensis,* it probably did not eliminate the prefrontal from contact with the frontal; the prefrontal is robust and therefore probably did form part of the posterior margin of the nares as in most other mosasaurs. Elimination of the prefrontal from the narial margin is found in very long snouted mosasaurs and appears to be the result of anterior cranial elongation (Caldwell et al., 2005). The maxillary teeth are housed by an extremely robust, highly buttressed maxillary below the narial passage. The maxillae are very thick and wide transversely (Table 1; Fig. 3D, E), more than any

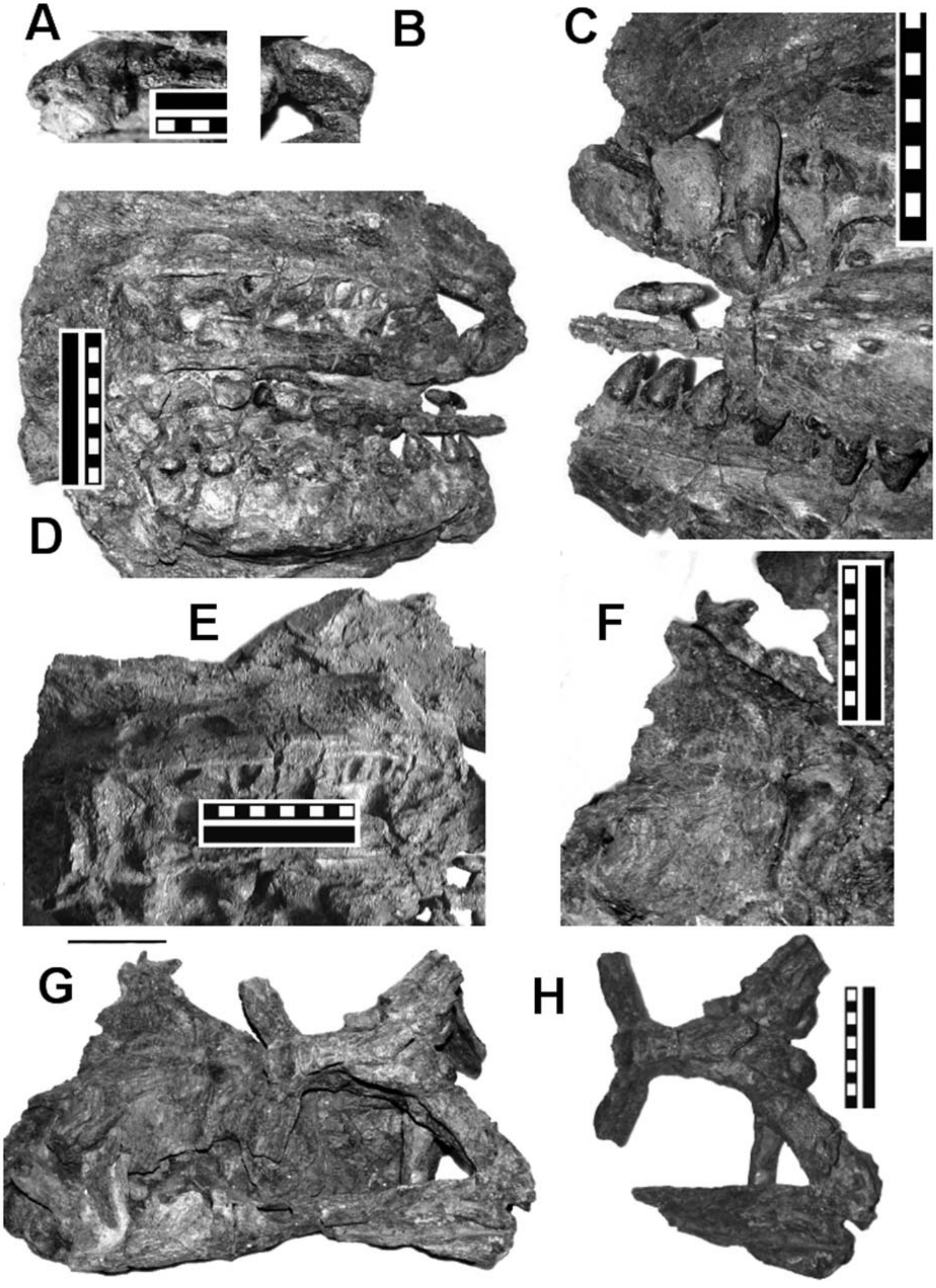


Figure 3. Cranial elements of *Globidens schurmanni* (SDSM 74764, holotype). (A) Left lateral view of premaxilla. (B) Right lateral view of premaxilla. (C) Dorsal view of close-up of anterior portion of skull. (D) Dorsal view of cranium. (E) Dorsal view of right maxilla. (F) Dorsal view of frontal. (G) Dorsal view of posterior cranium with parietal placed back into articulation. (H) Dorsal view of posterior cranium. Scales in centimeters.

TABLE 1. MEASUREMENTS (IN CENTIMETERS) OF SDSM 74764—*GLOBIDENS SCHURMANNI*

Skull measurements:	
Estimated length of cranium, premaxilla to quadratic suspensoria	~71.0
Estimated length of cranium, premaxilla to posterior end of midline parietal	~61.0
Maximum width of premaxillae	6.1
Length of external narial opening	11.5
Length of left supratemporal fenestra	18.5
Width of left supratemporal fenestra	9.45
Transverse width of parietal between fenestrae	2.28
Width of frontal across orbital area	18.0
Frontal length	~17.55
Maximum width of maxilla at 9th tooth	7.85
Width of maxilla at 3rd tooth	3.2
Maxillary tooth root depth above 9th tooth	5.15
Maximum dorsoventral depth of prefrontal	7.25
Dorsoventral depth of right dentary tip	3.59
Depth of dentary below 9th tooth	9.89
Alveolar length of left maxilla	~28.35
Quadrate height	13.38
Quadrate maximum width	10.28
Quadrate distal width	8.67
Quadrate maximum height of infrastapedial	6.14
Quadrate maximum width of suprastapedial	6.70
Quadrate minimum width across suprastapedial groove (notch)	4.30
Quadrate ala height	6.70
Quadrate ala width	3.50
Quadrate height to base of medial opening	5.00
Quadrate height to top of medial opening	9.90
Quadrate width of medial opening	2.60
Quadrate groove length below stapedial pit	2.85
Quadrate stapedial pit height	1.65
Quadrate stapedial pit width	0.70
Length of dentary from anterior end to hinge	~37.5
Length of dentary from hinge to end on articular	~36.0
Depth of right lower jaw through hinge	15.55

Dental measurements:	Anteroposterior	Transverse	Height
?Premaxillary tooth (unworn)	1.55	1.58	2.45
Right maxillary tooth ?2 (unworn)	1.53	1.93	2.20
tooth ?3 (unworn)	1.68	1.94	2.22
tooth ?4 (unworn)	2.00	—	2.30
tooth ?5 (unworn)	2.30	—	2.75
tooth ?6 (crushed)	2.68	—	—
tooth ?10 (unworn)	2.53	2.15	2.00
tooth ?11 (unworn)	2.17	1.70	1.60
Left maxillary tooth (last)	1.10	—	1.20
Right dentary tooth 1 (unworn)	1.25	—	1.95
tooth 3 (unworn)	1.33	—	2.25
tooth 4 (unworn)	1.76	—	2.35
tooth 6 (unworn)	2.42	—	2.80
tooth 7 (unworn)	2.95	—	2.75
tooth 9 (unworn)	3.20	—	3.00
tooth 10 (unworn)	2.30	—	1.82
Left dentary tooth 1 (unworn)	0.99	1.00	2.05
tooth 6 (apical wear)	2.23	2.57	2.30
tooth 7 (apical wear)	2.25	2.45	2.59
tooth 9 (apical wear)	3.08	2.82	2.66
tooth 11 (unworn)	2.57	2.52	2.13

(*continued*)

TABLE 1. MEASUREMENTS (IN CENTIMETERS) OF SDSM 74764—*GLOBIDENS SCHURMANNI* (*continued*)

Vertebral measurements of posterior centra:	Anteroposterior	Transverse	Height
Atlas intercentrum	4.35	5.13	3.75
Axis	8.1	4.85	4.45
Cervical vertebra	8.15	5.22	5.00
Anterior trunk vertebra	8.92	7.05	6.78
Trunk vertebra	7.63	6.57	6.40
Trunk vertebra	7.77	6.70	6.50
Trunk vertebra	—	6.76	6.51
Trunk vertebra	7.87	6.45	6.58
Caudal vertebra	4.9	5.28	4.73
Caudal vertebra	4.45	4.67	4.25
Girdle-limb elements:			
Right scapula—maximum transverse width			19.55
Right coracoid—maximum transverse width			20.55
Right humerus—proximodistal length			14.8
Right humerus—proximal transverse width			11.8
Right humerus—distal transverse width			14.1
Left humerus—proximodistal length			~11.0
Left humerus—proximal articular facet width			4.42
Left humerus—proximal transverse articular facet width			8.5
Left humerus—distal maximum anteroposterior width			8.8
Right radius—proximodistal length			13.6
Right radius—proximal transverse width			7.6
Right radius—distal transverse width			10.65
Left radius—proximodistal length			11.5
Left radius—proximal transverse width			8.05
Left radius—maximum width			9.9
Left radius—distal transverse width			7.7
Right ulna—proximodistal length			10.2
Right ulna—proximal width			4.3
Right ulna—proximal transverse width			~6.75
Right ulna—distal transverse width			8.14
Left ulna—proximodistal length			10.9
Left ulna—proximal anteroposterior width			6.32
Left ulna—distal anteroposterior width			3.1
Left ulna—distal transverse width			8.2
Right metacarpal V—proximodistal length			8.35
Right metacarpal V—proximal transverse width			6.92
Right metacarpal V—distal transverse width			5.75

other genus of mosasaur. The medial expansion of the maxillae indicates a trend toward medial contact, but the maxillae exhibit finished surfaces medially, so they did not meet. Nevertheless, the maxillae are expanded medially more than in any other known mosasaurid. Another unusual feature is the dorsal curve of the maxilla. The largest crushing teeth are the middle teeth on each maxilla, and the maxilla arches dorsally at this point (Table 1), probably housing longer tooth roots, forming a stronger structural arch, and/or allowing for ontogenetic growth of the expanded teeth (Estes and Williams, 1984). On the left maxillary, the resorption pits for two posterior teeth are exposed on the dorsal margin, whereas most pits are exposed on the medial side of the maxillae.

PTERYGOID: The pterygoids of SDSM 74764 are delicate in comparison with its very massive maxillae (Figs. 2, 4D). Owing to a much different feeding mechanism in comparison with typical mosasaurs and particularly of *Prognathodon,* the pterygoid teeth of *Globidens* appear to have degenerated (Russell, 1975). The element of *G. schurmanni* is long, but with thin processes. Unfortunately, the isolated specimen has the ventral aspect against the left maxilla, so the dentition is not exposed. The anterior extension, palatine process, appears very long but is probably articulated to the palatine. If so, the palatine is likewise reduced. The medial, externally directed ectopterygoid process appears long and thin, as does the posterior extension of the body of the pterygoid that normally houses the teeth. A specimen from Texas (*Globidens alabamaensis*) exhibits 10 pterygoid teeth (Polcyn and Bell, 2005b), but the teeth would have to be very small and crowded to be accommodated in the pterygoid of *G. schur-*

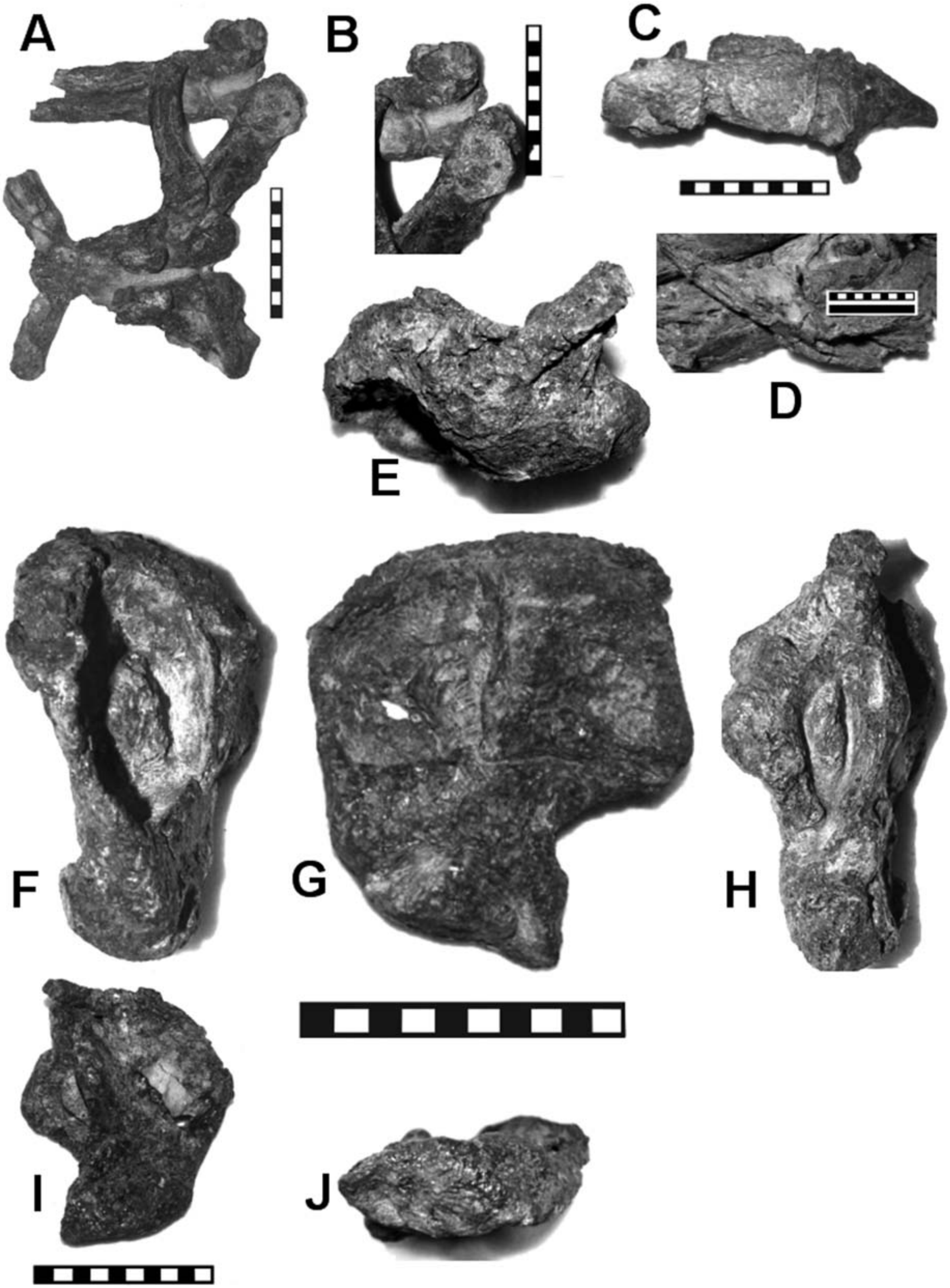


Figure 4. Cranial elements of *Globidens schurmanni* (SDSM 74764, holotype). (A) Ventral view of posterior cranium. (B) Articular surface on squamosal. (C) Lateral view of left prefrontal and postorbitofrontal. (D) Dorsal view of pterygoid. (E) Dorsal view of quadrate. (F) Lateral view of quadrate. (G) Posterior view of quadrate. (H) Medial view of quadrate. (I) Anterior view of quadrate. (J) Ventral view of quadrate. Scales in centimeters.

manni. The quadratic ramus flares widely posteriorly and laterally, as in most mosasaurs. The pterygoid is not dorsoventrally deep; therefore, large teeth with long roots like the marginal dentition are likely not present.

PREFRONTAL: The prefrontal is poorly preserved but is a very robust element (Fig. 4C). On the right side the element is crushed into the frontal, but the left prefrontal is articulated with the posterior edge of the palatine and the anterior portion of the postorbitofrontal. The prefrontal is an anteroposteriorly short, transversely wide, very thick bone. The contact with the postorbitofrontal is very wide and eliminates the frontal from any contact with the orbital opening, similar to the condition of *Globidens dakotensis,* but unlike that of *Globidens alabamaensis*. The suture is very high because the prefrontal and anterior postorbitofrontal are very deep (Table 1) and form a very robust lateral plate (Fig. 4C).

FRONTAL: The frontal (Fig. 4F, G) is extremely anteroposteriorly short but transversely wide (18 cm); only the dorsal aspect is observable. No medial crest exists (Fig. 4F, G), unlike the case for *Globidens dakotensis* (Russell, 1975) and *Globidens alabamaensis* (Russell, 1967). The dorsal surface of the frontal is smooth for its entire length, and the bone structure radiates from the posteromedial center. The interpretation of the posterior margin of the frontal is somewhat difficult but appears to have been relatively straight as in *G. dakotensis*. The lateral margins appear to be rounded, so the outline of the frontal is less triangular and less laterally emarginated than in other known mosasaurs, although the lateral corners are broken. The anterior end is birfurcate to receive the posterior prongs of the premaxillary internarial bar.

PARIETAL: The parietal is partially displaced from articulation with the frontal (Figs. 2, 3H, 4A). The anterior prongs are broken through the parietal foramen, which appears to be rather large although poorly preserved. The parietal constriction between supratemporal fenestrae is very thin (Table 1), and a slight medial furrow exists (Fig. 3H). The posterior suspensorial rami do not flare widely as in many genera of mosasaurs. The angle between the rami is only 105°. The suspensorial rami of the parietal are crushed vertically down onto the paroccipital process of the ophisthotic. Ventrally (Fig. 4A), the parietals extend far, indicating the deep nature of the cranium of *Globidens*.

POSTORBITOFRONTAL: The postorbitofrontal is massive anteriorly but thins to the narrow posterior squamosal ramus characteristic of most mosasaurs. The parietal-postorbitofrontal contact is relatively wide and acutely articulated. With a similar angle at its posterolateral corner, the supratemporal fenestra exhibits a semicircular outline with the arc internally along the margin of the parietal (Figs. 2, 3G, H). A thin process projects ventrally to articulate with the jugal.

OPHISTHOTIC-SUPRAOCCIPITAL: Most of the braincase is crushed and obscured; only the rear elements can be well distinguished. The supraoccipital is crushed into the rear of the ophisthotic and is therefore relatively indistinguishable. The opisthotic is also crushed, but some features are apparent. The paroccipital processes of the ophisthotic are relatively short, indicating the short, robust cranium of *Globidens*. The processes are sutured with the anterior process of the squamosal. Ventrally, the ophisthotics appear well separated by a ventral fissure (Fig. 4A).

SQUAMOSAL-SUPRATEMPORAL: The squamosal is a short, thick element with a very large articular surface for the dorsal margin of the quadrate (Fig. 4A, B). The anterior squamosal shaft is both wide transversely and dorsoventrally high. This shaft merges posteriorly into the body of the element, where the large, extremely convex articular surface for the quadrate occurs. In fact, the posterior margin of the articular facet has a posteroventral projection that would have restricted posterior movement of the quadrate. The squamosal is closely appressed with the supratemporal, and both elements are very dorsoventrally deep and highly buttressed to support the quadrate.

QUADRATE: The quadrate (Fig. 4E–J) is very similar to that of *Prognathodon*. The infra- and suprastapedial processes are fused, although the juncture line remains (Fig. 4F–H). The line is not horizontal but is an asymmetrical, dorsally inverted V-shape. The external leg of the V is twice as long as the medial leg. The depression on the posterior face of the suprastapedial is a large, shallow bowl (Fig. 4G). The element was anteroposteriorly compressed during fossilization, so this feature may be accentuated by preservation. The suprastapedial is extremely wide transversely, apparently more than that illustrated for *G. dakotensis,* although this, too, may be due to preservation. The medial dorsal emargination (notch) and anterior notch of the suprastapedial are large and distinct, as is characteristic of mosasaurines (Fig. 4E). The tympanic ala is circular and thick, particularly dorsally, surrounding a deeply bowled area, and the opening is relatively small (Table 1) and confined to the dorsal two-thirds of the bone (Fig. 4F). The posteroventral ascending tympanic rim is indistinct owing to the dorsal position of the ala. Internally, the opening is small, and the outline of the stapedial pit is a dorsoventrally elongate, narrow oval and lies at the anterodorsal edge of the opening (Fig. 4H). The quadrate is crushed, so the morphology of the suprastapedial ridge cannot be determined, but a groove appears below the pit that extends as far as the ventral margin of the medial opening and divides the median ridge. The median ridge is distinct dorsally but fades below the ventral margin of the medial opening. At the base of the opening a distinct groove extends posteriorly below a distinct pedestal that forms the corner of the posteromedial process of the infrastapedial process. This is very similar to the structure of *Prognathodon saturator* from the Maastrichtian of The Netherlands (Dortangs et al., 2002). The ventral articular surface (Fig. 4J) is structurally similar to that of *Prognathodon overtoni* (KU 950), with a large, rounded, medial, posteriorly projecting condyle and a smaller anteriorly projecting lateral condyle; however, the articulation appears more restricted, as mentioned for *G. dakotensis* (Russell, 1975). The ala merges with the articular surface just medial to the lateral condyle.

LOWER JAW

The right lower jaw is articulated but appressed against the ventral side of the cranium (Figs. 2, 5A). The left jaw (Fig. 5C–E)

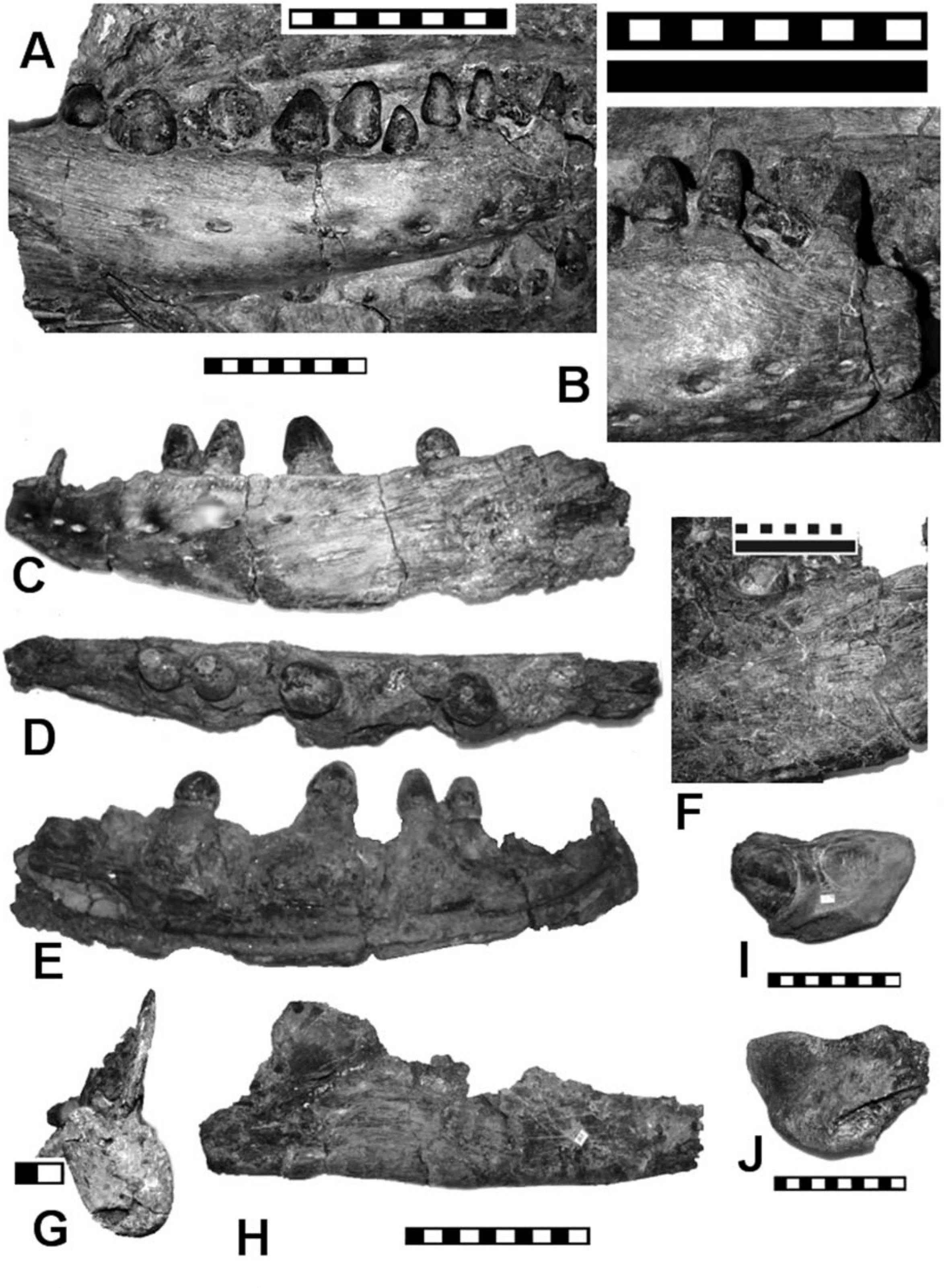


Figure 5. Lower jaw elements of *Globidens schurmanni* (SDSM 74764, holotype). (A) Lateral view of right dentary. (B) Close-up of anterior portion of right dentary. (C) Lateral view of left dentary. (D) Dorsal view of left dentary. (E) Internal view of left dentary. (F) Right coronoid and lower jaw joint. (G) Posterior view of left splenial. (H) Lateral view of left splenial. (I) Dorsal view of left retroarticular. (J) Ventral view of left retroarticular. Scales in centimeters.

is isolated, and the posterior jaw elements disarticulated and poorly preserved; a deep cut is exhibited on the retroarticular process (Fig. 5J).

DENTARY: As mentioned above, a short predental extension occurs anteriorly on the dentary, which is very deep and robust for housing the exceedingly long roots of the dentition (Fig. 5A, B). The specimen is not well preserved overall, and determination of the lower tooth count is difficult; 11 alveoli are observable, but at least 13 or 14 are more likely. The Meckelian groove is open for the length of the dentary; its anterior end curves dorsally and narrows to a point below the first tooth (Fig. 5E). Like the maxillae, the dentaries exhibit two rows of mental foramina on their lateral sides (Fig. 5A–C). At least 9 foramina occur in the dorsal row, and 6 foramina occur in the ventral row. The dentary is convex ventrally, slightly concave dorsally, and very massive.

SPLENIAL: The splenial extends along the posteroventral margin of the jaw, but little is visible from the lateral side. When articulated, the dentary and splenial compose an extremely dorsoventrally deep jaw at the distal end of the dentary (Figs. 2, 5F). Internally, the dorsal process of the splenial extends over the Meckelian canal and is very high posteriorly, gently slanting anteriorly (Fig. 5A, G, H). The left splenial is isolated and exhibits the posterior articulation with the angular. This articulation is relatively simple, with a long ridge oriented 45° to the vertical axis (Fig. 5G). A groove lying dorsal to the ridge allows a tongue and groove articulation between the splenial and angular that is relatively immovable owing to the oblique interlock. The right jaw exhibits the splenial and angular in articulation, but only the external side of the lower jaw is visible; the medial side is against the cranium.

ANGULAR: The angular of SDSM 74764 has a large dorsal flange at its anterolateral corner that extends ~6.5 cm before it descends to the ventral margin of the jaw, where it extends posteriorly to near the end of the surangular.

CORONOID: Unfortunately, the medial aspect of the coronoid is obscured, but just dorsal to the articulation of the splenial and angular a suture appears that probably represents a long medial wing of the coronoid, similar to that of *Prognathodon*. If so, the medial wing may be ventrally longer than in any other mosasaur. As such, this process, in conjunction with the oblique articulation between the angular and splenial, would essentially lock the lower jaw joint, a feature that might be expected of a durophagous creature. Laterally, the coronoid is long anteriorly and has a high posterior process (Fig. 5F), as is typical of *Prognathodon,* a closely related taxon (Bell, 1997). The dorsoventrally compressed condition of USNM 4993, a supposed coronoid of *Globidens* described by Russell (1967, p. 53), is not mirrored in SDSM 74764. A slight concave furrow for muscle insertion lies posterior to the high posterior process. The lateral descending wing of the coronoid is relatively short, with a semicircular ventral margin that merges into the parallel-sided anterior process. The anterior process is longer, but the ventral lateral wing is shorter than those respective features of *Prognathodon.*

SURANGULAR: As a result of the lateral coronoid construction, the surangular is broadly exposed between the coronoid and angular. The surangular (Fig. 2) expands posteriorly until it sutures against the articular and forms part of the glenoid facet. Much of the lateral aspect of the posterior portion of the lower jaw is formed by the surangular.

ARTICULAR: The articular (Fig. 5I, J) possesses a very wide articulation for the ventral convex surface of the quadrate, and the dorsal margin is very wide with a robust muscle scar. The retroarticular process is relatively short and wide, with the foramen for corda tympani close to the ventral margin. Interestingly, the left articular exhibits a deep cut just below the dorsal margin (Fig. 5J). Because no bone regrowth is evident, this deep gouge may represent the result of an attack or scavenging. As will be discussed, the mosasaur had paddle deformation and might therefore have been susceptible to attack.

DENTITION: The most obvious apomorphies of the taxon are exhibited by the dentition, principally because most previous diagnoses are based upon teeth morphology; some species diagnoses are based solely on isolated teeth (e.g., Bardet et al., 2005). The dentition of *Globidens schurmanni* is tripartite, with anterior, middle, and posterior divisions within both the upper and lower marginal tooth rows (Figs. 2, 5A, 6B, N). No teeth exhibit a posterior carinae (except perhaps the posteriormost upper teeth), as is characteristic of *Globidens dakotensis* or *Globidens alabamaensis,* and only the rear maxillary teeth exhibit apical nubbins (Fig. 6E, F). All teeth of *G. schurmanni* have crowns with rugose crenulations that radiate from the tip (e.g., Fig. 6A, C); the medial teeth have posterior sulci (Fig. 6K). The anterior teeth (Fig. 6A–C, G, L, M) are very high crowned (Table 1), although they cannot be considered hypsodont because they possess exceedingly long roots that may be 3 times longer than the crown. The roots are striated vertically, providing a great area for attachment within the deep sockets (Fig. 6M). A distinct constriction occurs between the enamel crowns and the distally expanded, somewhat quadrangular (in cross section) roots, resulting in a basal collar on the crowns. The crowns possess rugose, crenulated enamel radiating from the tip, are vertically elongate, conical, and taper to a point; a faint posterior sulcus is best expressed on the basal, expanded enamel collar, fading toward the crown tip. Occlusal wear is always on the tip (Fig. 6D, H, J, L). Unfortunately, the teeth were not preserved within the premaxillae. However, a number of teeth were found adjacent. One is a relatively small, well-striated, slightly recurved tooth (Fig. 6A) with a short root, approximately the same length as the crown. The premaxillae are not as deep as the maxillae or dentaries, so the extremely long roots of most teeth would be impossible to accommodate in the premaxillae. Therefore, this tooth likely represents a premaxillary tooth, perhaps the anteriormost. The anteriormost tooth is preserved within the dentaries (Figs. 5C, 6G, N) and is very high and slender, much higher crowned and thinner (Table 1) than that of *Globidens dakotensis* (FHSM VP-13828, Everhart and Everhart, 1996; Everhart, 2005) and different from any teeth illustrated for *Globidens phosphaticus* (Bardet et al., 2005). Behind this tooth in the left dentary are alveoli for four more smaller teeth (Fig. 5C–E). Most of these teeth are preserved in the right dentary (Fig. 6N); only the second tooth is missing in both lower jaws. The third tooth is also very

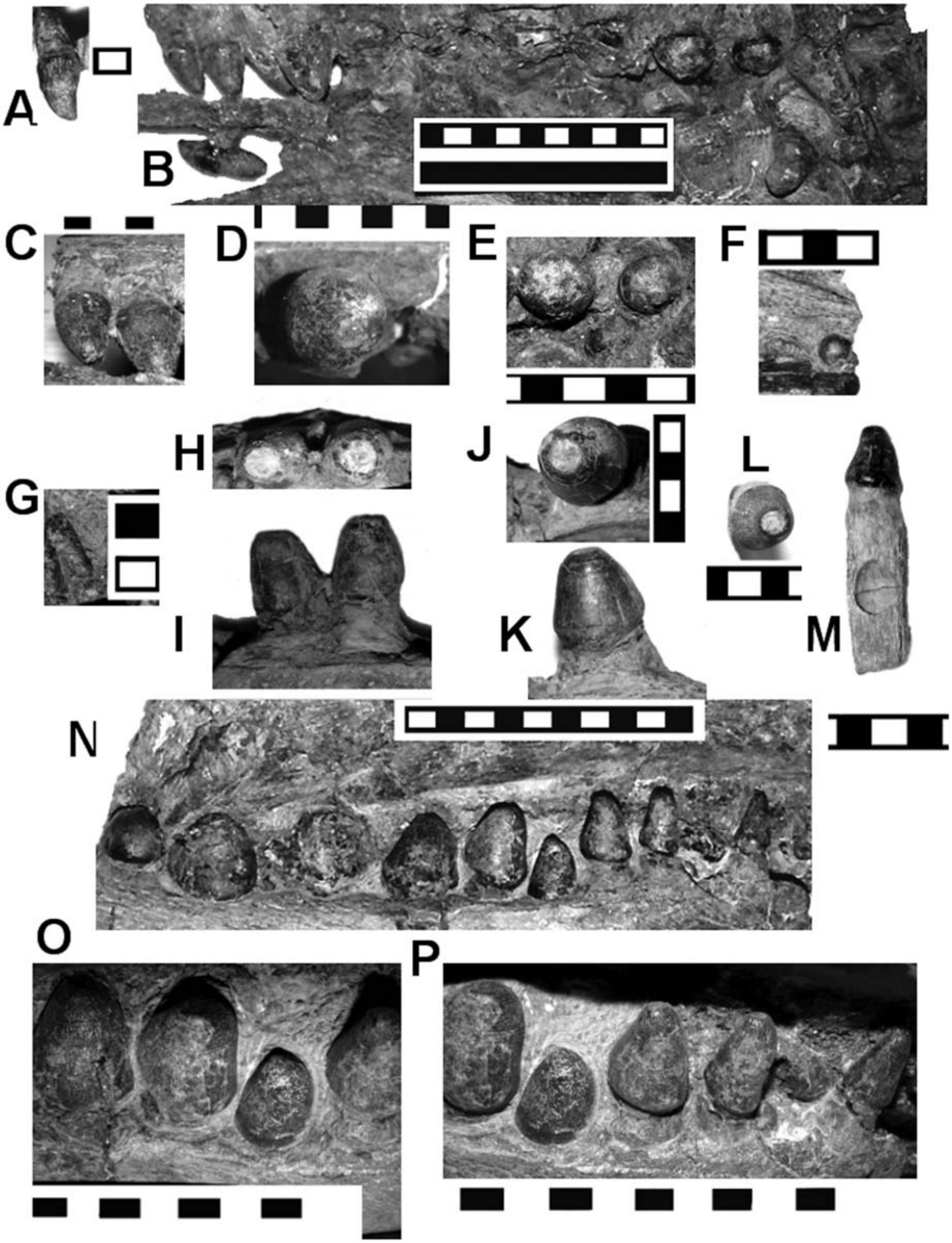


Figure 6. Dental elements of *Globidens schurmanni* (SDSM 74764, holotype). (A) Anterior ?premaxillary tooth. (B) Left upper tooth row. (C) Oblique view of anterior maxillary teeth. (D) Occlusal view of maxillary tooth from middle portion of tooth row. (E) Occlusal view of posterior maxillary teeth. (F) Occlusal view of posteriormost maxillary tooth. (G) Lateral view of anterior dentary tooth. (H) Occlusal view of 4th and 5th dentary tooth. (I) Lateral view of 4th and 5th dentary tooth. (J) Occlusal view of 9th tooth. (K) Lateral view of 9th tooth. (L) Lateral view of isolated anterior tooth. (M) Occlusal view of same isolated tooth. (N) Right lower tooth row. (O) Close-up of middle portion of lower tooth row. (P) Close-up of anterior and middle portion of lower tooth row. Scales in centimeters.

high crowned but more robust than the first. Therefore, the second would appear likewise. The three very high, slender teeth are unlike those of FHSM VP-13828, which are lower crowned and similar to the succeeding two teeth and are unlike any illustrated for *G. phosphaticus* (however, described teeth of this species are all isolated teeth, and their position within the tooth row is not known for certain). These teeth were probably utilized for food gathering rather than crushing. The fourth and fifth dentary teeth are more robust, more conical, and have a greatly expanded basal collar (Fig. 6H, I). They are much higher crowned than those of either *G. dakotensis* or *G. phosphaticus,* with the possible exception of the isolated teeth, OCP.DEK/GE 345 or MNHN Arambourg 340 (Bardet et al., 2005, Fig. 2), although the teeth of SDSM 74764 are significantly larger. Within the maxillae, at least four and perhaps five of the elongate, conical, anterior teeth occur (Fig. 6B). These are similar to those in the lower jaw, although perhaps lower crowned and broader. These teeth are sloped posteriorly, perhaps more so than the corresponding lower teeth. The last two of the anterior teeth are very robust in comparison with the lower teeth but remain relatively high crowned.

The middle portion of the tooth row is unique in that the teeth have very high crowns, are exceedingly massive (Table 1), and exhibit a relatively symmetrical bell-shape outline (Fig. 6N–P) rather than the typical spherical structure of *Globidens dakotensis* and *Globidens alabamaensis,* or the posteriorly buttressed teeth of *Globidens phosphaticus*. On *G. schurmanni* these teeth have very long roots, rounded apices, and may have up to three posterolateral sulci. These teeth, similar to those of some durophagous rays such as *Ptychodus whipplei,* were utilized to initially puncture the bivalve shells to expedite crushing. Two to three teeth occupy the medial division in both the upper and lower jaws. The two anterior teeth (Fig. 6H, I) are high and pointed in comparison with the succeeding teeth, which are more rounded but not to the degree of those of *Globidens dakotensis* or *G. alabamaensis,* and they retain a bell-shaped lateral outline. One tooth, the ninth tooth in the left dentary (Fig. 6J, K), exhibits a slight posterior expansion but not nearly to the degree as that of *Globidens phosphaticus* (Bardet et al., 2005).

The posterior portion of the dentition includes the rounded, globular teeth (Table 1) typical of *Globidens,* utilized for crushing bivalves (Fig. 6N). Three, possibly four, teeth comprise the third division. They are all round in lateral outline and decrease in size posteriorly. They are more similar to those of *G. dakotensis* and *G. alabamaensis* than to those of *G. phosphaticus,* which are more dorsoventrally compressed. Two of the posterior teeth of *G. schurmanni* exhibit apical nubbins, and one may possess a posterior carina. However, SDSM 74764 is unlike other species of *Globidens* in an overall lack of tooth carinae.

Discussion—Tooth Morphology

Because *Globidens* is commonly represented in the fossil record by isolated teeth, a great deal of attention has been concentrated on these elements. Russell (1975) described five tooth morphologies of *Globidens,* indicating that some may represent various taxonomic entities and/or positions within the tooth row. A number of species have been designated on the basis of isolated teeth, including the most recently named species, *G. phosphaticus* (Bardet et al., 2005). Once again, the tooth morphologies of Russell (1975) were an integral portion of this designation, and Bardet el al. (2005) described six tooth morphotypes considered as part of the same species. Therefore, a discussion of these morphologies appears in order, particularly owing to the relatively well preserved dentition of *G. schurmanni,* which includes tooth rows that exhibit heterodonty.

Russell (1975) designated the following tooth morphologies (of which Lingham-Soliar, 1999, recognized only two):

Type 1—crown subspherical with small, symmetrical apical nubbin, carinae, and sulci at most faintly developed;
Type 2—crown subspherical with large, recurved apical nubbin, shallow vertical grooves, crowns low in lateral profile;
Type 3—crowns conical, pointed in lateral profile and circular in horizontal cross section, apical nubbins absent; some may occupy anterior positions in jaws;
Type 4—crowns high and rounded in lateral profile, apical nubbin not well developed, anterior and posterior carinae present; and
Type 5—crowns low and rounded in lateral profile with apical nubbins, irregular horizontal cross section; some may occupy posterior position in jaws.

According to Russell (1975), type 1 includes both *G. alabamaensis* and *G. dakotensis,* type 3 includes *G. timorensis,* and types 2 through 5 include specimens assigned to *G. aegyptiacus,* now *Igdamanosaurus aegyptiacus* in part. Types 2 and 5 include *"G." fraasi,* which now is considered a species of *Carinodens* (Russell, 1975). *Globidens schurmanni* does not fit conveniently into any of the tooth morphologies described by Russell (1975), and some of the tooth morphologies are found within a single tooth row. Type 1 is not present except in the most posterior maxillary teeth of *G. schurmanni,* and in contradistinction the sulci are well developed on *G. schurmanni* (Fig. 6K). The posterior maxillary teeth of *G. schurmanni* are more similar to type 2, although those of SDSM 74764 may be higher in lateral profile. However, the anterior and medial teeth of *G. schurmanni* are unlike type 2 in being high crowned (not subspherical), having no apical nubbins, and bell shaped in lateral profile (Fig. 6N, P). Russell (1975) noted that type 3 teeth may occupy anterior jaw positions, and this appears to be the case in *G. schurmanni,* which exhibits high, conical crowns without apical nubbins. However, some of the anterior teeth of *G. schurmanni* exhibit variation from very high, slender, nearly cylindrical anteriormost dentary and maxillary teeth (Fig. 6G, P) to more conical succeeding teeth (Fig. 6N, P). The medial teeth are similar to those of type 4 but do not have carinae (Fig. 6J, O, P). The only possible posterior carinae of *G. schurmanni* may occur on rear maxillary teeth that are subspherical (Fig. 6E, F). Type 5 is unlike those of *G. schurmanni* because that species has horizontally symmetrical teeth. Therefore, *G. schurmanni* exhibits some characters of the tooth types of Russell (1975), but no single tooth type characterizes the species, which emphasizes that Russell's tooth morphologies probably represent both different positions along the tooth row and different systematical attributions.

On the basis of isolated teeth from Morocco, Bardet et al. (2005) designated six morphotypes considered to represent positions within the jaw of the same species that partially included those of Russell (1975):

Morphotype A of Bardet et al. (2005) includes teeth that exhibit high, broad, posteriorly recurved cones with a circular basal cross section and faint carinae;

Morphotype B is characterized by a high, broad, straight cone with subcircular to ovate basal cross section, apical nubbin, and carinae (these were considered to correspond with Russell's type 3; Russell, 1975, indicated that this type had no apical nubbin, but teeth of taxa included by Russell exhibit a discrete nubbin);

Morphotype C represents large, bulbous, subspherical teeth with posteriorly recurved apical nubbins, but without carinae or sulci;

Morphotype D comprises large, bulbous, high-crowned teeth but with a posterior inflation (buttress), causing a subcircular cross section, and prominent sulci but no carinae;

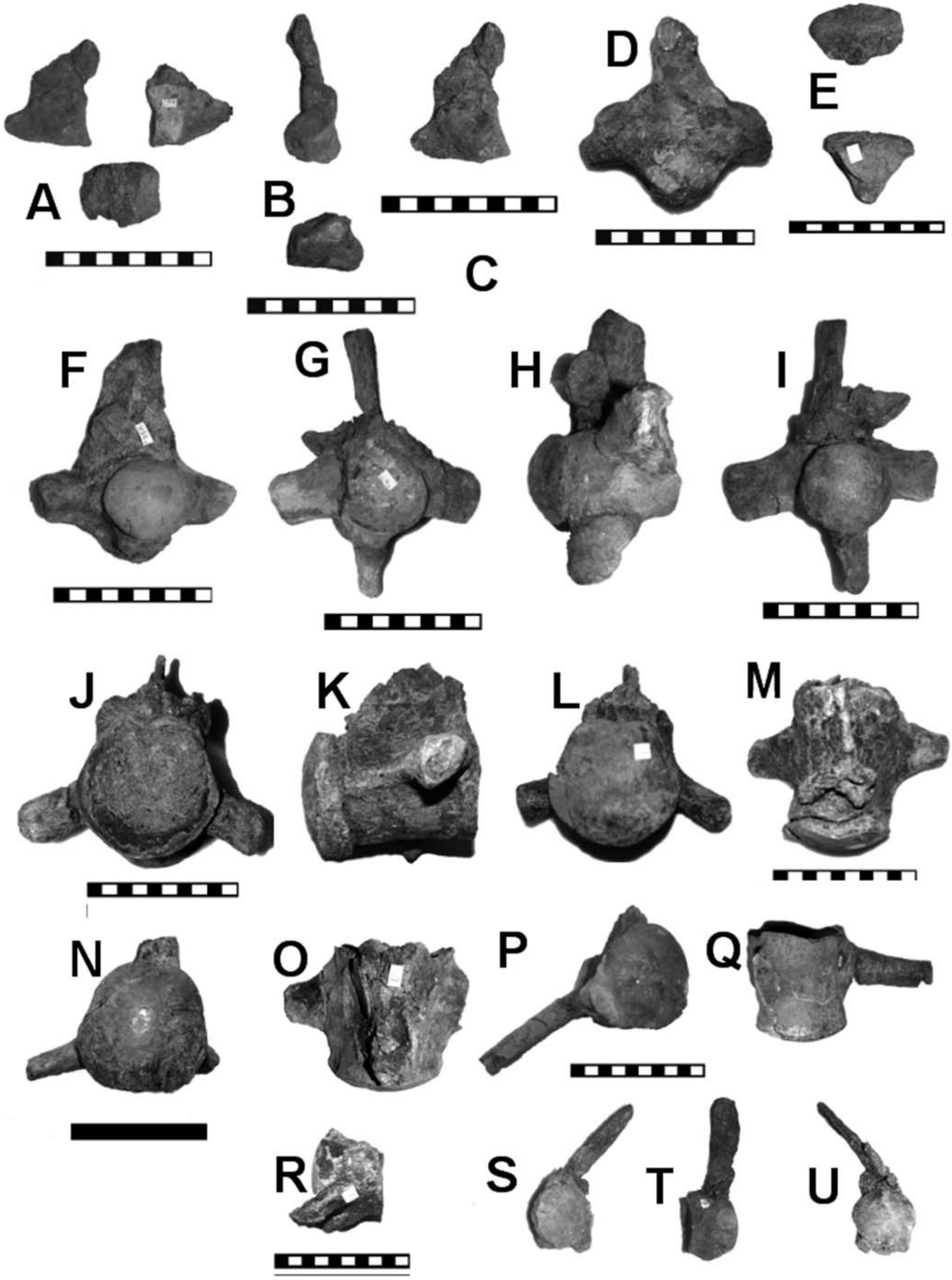
Morphotype E represents the largest teeth, bulbous, subspherical, with a strongly inflated posterior crown with a posteriorly recurved nubbin, sulci, ovate cross section, but without carinae (these were thought by Bardet et al., 2005, to correspond with type 2 of Russell, 1975, but Russell's type was relatively lower crowned and did not exhibit enlarged posterior inflation); and

Morphotype F teeth are low crowned, bulbous, with an irregular, ovate cross section, a posterior crown inflation, deep sulci, and a posteriorly recurved apical nubbin, but without carinae (as noted by Bardet et al., 2005, this morphotype appears to correspond with Russell's type 5).

Bardet et al. (2005) indicated that morphotypes A–F corresponded to succeeding positions within a tooth row, and generally their conclusions are borne out by the example of *G. schurmanni*. Morphotype A was considered to be an anterior tooth position, and this does seem to be the case as exhibited by the recurved tooth (Fig. 6A) with a short crown thought to be an anterior tooth of *G. schurmanni*. However, the cylindrical anteriormost teeth of the dentary and maxilla (Fig. 6G, P) of *G. schurmanni* do not appear to be represented in the morphotypes of Bardet et al. (2005). Morphotype B is similar to the typical anterior teeth of *G. schurmanni,* but none exhibit apical nubbins or carinae. Morphotype C is similar to the posterior maxillary teeth of *G. schurmanni,* but these are considered to be the posterior teeth of the anterior series of *G. phosphaticus* (Bardet et al., 2005). Morphotype D teeth are unique in having a posterior buttress observed in no other species. Morphotype E teeth also exhibit posterior crown inflation but are lower crowned. This morphotype is likewise unique to *G. phosphaticus*. The most posterior tooth, morphotype F, is unique in being very squat with posterior crown inflation. These differ from the posterior teeth of *G. schurmanni,* which are subspherical (Fig. 6N). Morphotypes D–F of *G. phosphaticus* differ from similar tooth positions of *G. schurmanni* because of posterior inflation. These buttresses do not occur in SDSM 74764 but could have been easily derived from these high-crowned, relatively symmetrical conical teeth.

Overall, the tooth types of Russell (1975) and Bardet et al. (2005) do not correspond directly with those of *G. schurmanni*. The morphotypes of the latter authors are indicative of positions within jaws of the same taxon, whereas those of Russell (1975) are a mixture of both tooth positions and taxonomic entities. None of the tooth types of Russell (1975) can be utilized to diagnose *G. schurmanni*. Only type 3 is similar because it may represent a generic anterior tooth. The tooth positions of Bardet et al. (2005) are more similar, but should be modified for *G. schurmanni*. Morphotype A should include not only the recurved, striated teeth but also the very high-crowned, slender, cylindrical anterior teeth. These teeth probably include the premaxillary teeth and the first tooth on the maxilla and dentary (Fig. 6A, G). Morphotype B resembles the anterior teeth succeeding the anteriormost teeth and preceding the bulbous crushing teeth (Fig. 6B, C, P), although those of *G. schurmanni* exhibit no carinae or apical nubbins. These would represent tooth positions 2 to 3 on the dentary (Fig. 6N). Morphotype C is also similar to the high-crowned, bell-shaped teeth that occupy tooth positions 2 to 5 on the dentary (Fig. 6J). These might be considered the posteriormost of the anterior teeth of *G. schurmanni*. Therefore, morphotypes B and C might be combined for *G. schurmanni*. Morphotype D represents the highest-crowned, bulbous teeth with posterior buttresses and occupies tooth positions 6 to 7 on the dentary of *G. schurmanni* (Fig. 6K, N, P). Morphotype E represents lower crowned, rounder bulbous teeth with a posterior buttress, and morphotype F represents the posteriormost teeth that are subspherical with apical nubbins, although those posteriormost teeth of *G. schurmanni* are higher crowned. Morphotype E represents tooth positions 8 perhaps to 10 on the dentary (Fig. 6N), and morphotype F represents the most posterior tooth positions on the dentary. Morphotypes E and F may be combined for *G. schurmanni*. Morphotypes C–F differ from those of *G. schurmanni* owing to the lack of posterior buttresses. Therefore, with differences noted, morphotypes A, B, D, and E may be positively identified on *G. schurmanni*. The other morphotypes may indicate greater heterodonty and autapomorphies of *G. phosphaticus*.

Based upon the various morphologies represented by isolated teeth, these teeth may be difficult to utilize for differentiation among species. Although the posterior buttresses of teeth from the middle and posterior tooth row of *G. phosphaticus* and the bell-shaped teeth of the middle tooth row of *G. schurmanni* are diagnostic, isolated teeth may not be sufficient for species designation. For example, the rear teeth of *G. alabamaensis, G. dakotensis,* and *G. schurmanni* are similar, but those from the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middle of the tooth row are much different. Therefore, more complete dentitions may exhibit a combination of features difficult to discern from isolated teeth.

AXIAL SKELETON

ATLAS-AXIS: The atlas-axis complex is preserved, although disarticulated. The atlas is surprisingly small and delicate, considering the heavy, massive skull of *Globidens schurmanni*. The atlas intercentrum lies below the neural arches and lies anterior to the axis intercentrum. The atlas intercentrum is a blocklike unit (Table 1) with two dorsal articulations and anterior and posterior articular facets (Fig. 7A, B). The ventral portion is convex. The left neural arch is complete (Fig. 7A–C) and, surprisingly, appears slightly smaller than the right arch (Fig. 7A) in which the neural tip is broken away. The neural arch is configured as is typical for mosasaurs, with an anterior facet for articulation with the occipital condyle and a facet just posterior for articulation with both the atlas and axis centra. Dorsally, a long process forms the top of the neural arch. The tip appears to have a facet that articulates with a corresponding facet on the neural process of the axis. A prominent synapophysis is oriented posterolaterally near the base of the element. The axis intercentrum (Fig. 7E) exhibits three dorsal facets: an anterior facet for the atlas intercentrum, a medial facet for the atlas centrum, and a larger, posterior interlocking articulation for the main body of the axis. The axis (Fig. 7D, F) is large, with a massive centrum, synapophyses, and neural arch. However, the neural spine is relatively short anteroposteriorly in comparison with the elongate process characteristic of some genera such as *Clidastes*. The top of the neural spine has a wrinkled, vascular surface indicating a cap of cartilage. The axis exhibits distinct zygantra posteriorly, but only the anterior, highly positioned facet for the neural arch of the atlas. The neural canal is semicircular in outline, with the flat side ventrally against the centrum. The synapophyses arise from the dorsal portion of the centrum, are anteroposteriorly as long as the body of the centrum, and are very thick dorsoventrally. The condyle of the axis is round and highly convex. A ventral facet for an articulating hypapophysis is evident.

CERVICAL VERTEBRA: An isolated cervical vertebra (Fig. 7G–I) exhibits a round, extremely concave anterior cotyle and convex posterior condyle. The centrum is relatively long (Fig. 7H), with a fused, long hypapophysis. The synapophyses are confined to the anterior half of the centrum and are dorsoventrally long. The anterior zygapophyses are broken away, and the posterior zygapophyseal area is poorly preserved with only the right postzygapophysis; the condition of the zygosphene-zygantrum cannot be ascertained. The neural spine is high, slender, and anteriorly positioned.

TRUNK-PYGAL VERTEBRAE: A number of posterior trunk or pygal vertebrae (Fig. 7J–Q) are preserved. The condyles (Fig. 7L, N) become less circular and more hexagonal, with a dorsal notch for the neural cord. The synapophyses are low on the centrum (Fig. 7J, L, N), flare widely, and become long and narrow. The neural arch is normally poorly preserved, but the neural spine does not reach the posterior margin of the centrum, covering about three-quarters of the vertebra. The neural canal becomes more triangular posteriorly.

CAUDAL VERTEBRAE: Only two posterior caudal vertebrae were preserved (Fig. 7R–U); the centra are circular (Table 1; Fig. 7S, U) and have haemal arches (chevrons) fused to the centrum (Fig. 7R). The haemals appear to be very long, slender processes. One specimen has a very high, slender neural process, and the neural arch covers the entire centrum (Fig. 7S–U). The neural canal is round.

APPENDICULAR SKELETON

The right scapula, coracoid, humerus, radius, ulna, and part of the right paddle are articulated (Fig. 8A, G). The left scapula and coracoid are articulated, and the left humerus (Fig. 8C–E), radius, and ulna (Fig. 8J–L) were found associated but separated from the scapula-coracoid. Interestingly, the left humerus and ulna exhibit extreme exostosis as the result of injury or disease (Fig. 8D, E, J, L). In either case, the distal ends of the humerus and proximal ulna display osteological overgrowth, indicating pathology that affected movement of the left front paddle.

PECTORAL GIRDLE: The scapula and coracoid are of similar size (Table 1) and are very well sutured (Fig. 8A), as is typical of mosasaurines, and the scapula is relatively symmetrical in comparison with that of most mosasaurines. The dorsal margin of the scapula is strongly convex. The coracoid is likewise symmetrical, and no anteromedial emargination exists, although the coracoid is thin and in one area on the right coracoid is actually perforated. The coracoid foramen is obvious on the right coracoid but obscured on the left. The glenoid fossa lies below the neck of the scapula-coracoid and is moderately concave. Neither the clavicles nor the interclavicle was positively identified, although long, slender elements in the pectoral region may represent these delicate elements.

Figure 7. Vertebral elements of *Globidens schurmanni* (SDSM 74764, holotype). (A) Atlas neural arches and intercentrum. (B) Anterior view of atlas neural arch and intercentrum. (C) Lateral view of atlas neural arch. (D) Anterior view of axis. (E) Dorsal and anterior view of axis intercentrum. (F) Posterior view of axis. (G) Anterior view of cervical vertebra. (H) Lateral view of cervical vertebra. (I) Posterior view of cervical vertebra. (J) Anterior view of trunk vertebra. (K) Lateral view of trunk vertebra. (L) Posterior view of trunk vertebra. (M) Dorsal view of trunk vertebra. (N) Posterior view of trunk vertebra. (O) Dorsal view of trunk vertebra. (P) Posterior view of posterior trunk vertebra. (Q) Ventral view of posterior trunk vertebra. (R) Lateral view of caudal vertebra. (S) Anterior view of posterior caudal vertebra. (T) Lateral view of posterior caudal vertebra. (U) Posterior view of posterior caudal vertebra. Scales in centimeters.

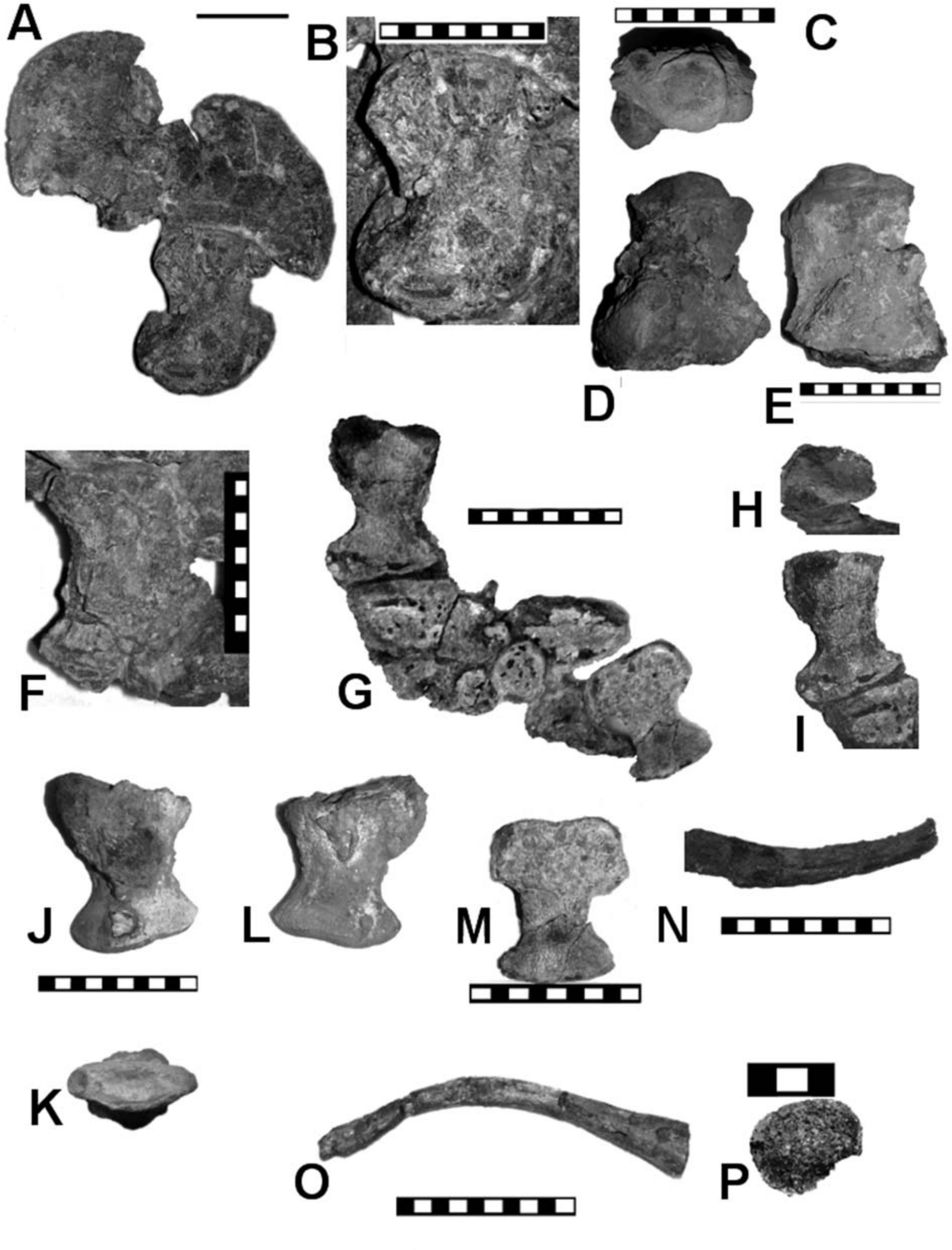

Figure 8. Pectoral girdle, paddle, and rib elements of *Globidens schurmanni* (SDSM 74764, holotype). (A) Articulated scapula, coracoid, and humerus. (B) Lateral view of right humerus. (C) Dorsal view of left humerus. (D, E) Lateral views of left humerus. (F) Lateral view of right radius. (G) Dorsal view of right ulna. (H) Lateral view of right ulna. (I, J) Lateral views of left ulna; note bone overgrowth. (K) Distal view of left ulna. (L) Articulated carpals. (M) Lateral view of metacarpal I. (N) Rib. (O) Rib. (P) Cross section of same rib. Scales in centimeters.

HUMERUS: Both humeri are preserved, but the right humerus is crushed (Fig. 8B), whereas the left humerus retains its three-dimensional form (Fig. 8C–E) but exhibits bone overgrowth distally. The humerus appears more plesiomorphic than those of other mosasaurines such as *Mosasaurus* or *Plotosaurus,* even *Clidastes*. In particular, the proximal portion is not transversely expanded but consists of a distinct, rounded head set centrally on the proximal end (Fig. 8C). On the right humerus the proximal end does appear wide transversely (Table 1), but this is the result of crushing. The postglenoid process is prominent, and a facet extends from the head toward the process. The pectoral process occurs high proximally and is capped by a distinct, rounded, convex surface. Distally, the entepicondylar process is very large (Fig. 8D) and extends to the distal margin of the humerus; the ectepicondylar process is relatively small in comparison. On the opposite side, the scar for the M. latissimus dorsi is a long, ridgelike process that trends toward the external margin (Fig. 8E).

RADIUS: The radius (Fig. 8F) is well separated from the ulna, forming a large, ovate, intervening medial opening. Proximally, the radius is broad transversely (Table 1), the medial margin is emarginated, and the distal articulation is also very wide transversely, more so than the proximal articulation. This condition is the result of lateral expansion distally, and unlike many mosasaur taxa the lateral margin is not emarginated but continuous and thin.

ULNA: Converse to the condition of the radius, the ulna is emarginated on both the medial and lateral margins, forming a waist (Fig. 8I, J, L). The proximal end is robust and expanded anteroposteriorly at the medial margin (Fig. 8H); as a result the articulation is widely ovate, much more than the proximal articulation of the radius. Distally, the ulna is thin (Fig. 8K) like the radius (Table 1). The distal ulnar articulation is concave and composed of two distinct facets and a less distinct medial articular face for the intermedium. The articulation for the ulnare is the longest and most deeply concave. The facet for the pisiform is short but massive, indicating a distinct, relatively large pisiform.

CARPALS, METACARPALS, AND PHALANGES: Overall, the configuration of the carpals and distal paddle (Fig. 8G) resembles that of *Clidastes* (Russell, 1967; Williston, 1898). However, the radiale is very broad but short dorsoventrally. The intermedium appears quite compressed, with a short interface with the radiale but with a large contact with distal carpal 2. The opposite side is broadly articulated with the ulnare, which is more rectangular than ulnares of most other mosasaur taxa. The proximal articulation of the ulnare is long, whereas the distal articulation is shorter but parallel to distal carpal 4. No obvious facet exists for the 5th metacarpal. Distal carpals 2–4 are in articulation but not well preserved. The first and second metacarpals are preserved, and the first metacarpal (Fig. 8G, M) is short (8.45 cm) and has distinctly emarginated medial and lateral sides, resulting in an hourglass shape, although articular surfaces extend distally on the proximal end. A few isolated metacarpals and carpals are associated, as are many phalanges. Many of the metacarpals and phalanges appear proximodistally elongate.

RIBS

The preserved rib fragments (Fig. 8N, O) appear relatively short and curved and exhibit a relatively thin rim of periosteal primary bone (Fig. 8P), similar to that of *Tylosaurus* (see Sheldon, 1997). Rib pachystosis was not expected in a mosasaur preying upon bivalves in relatively shallow water.

Relationships. SDSM 74764 possesses a number of characters that indicate nesting within the Mosasaurinae (Russell, 1967). Zygosphenes appear on the anterior vertebrae that possess round cotyles, and haemel arches are fused on the distal caudal vertebrae. The coracoids and scapulae are well sutured, essentially fusing the elements. The paddles retain the relatively less derived structure of mosasaurines with a relatively full complement of large carpals, a long humerus, and a wide circular foramen between the radius and ulna.

Globidens schurmanni may be considered nested within the Tribe Globidensini designated by Russell (1967), although it was shown by Russell as Globidentini in 1975. The original definition of the morphological content of the tribe includes “the highly peculiar nature of its spherical teeth and massive jaws,” which includes *G. schurmanni*. Lingham-Soliar (1999) enlarged upon the definition by including, among other characters, swollen teeth with subcircular or subrectangular cross sections, waist between root and crown, a surface covered by deep wrinkles, a single small tooth tip, and tooth bases implanted vertically. Once again, *G. schurmanni* corresponds to this revised definition.

SDSM 74764 is a species of *Globidens* owing to its short, broad, massive skull with bulbous, subspherical heterodont dentition characterized by radial rugosities originating from the tooth apices, a distinct basal tooth collar above an indentation between the crown and the root, and tooth roots significantly longer than crowns. In addition, *G. schurmanni* possesses the following combination of characters considered diagnostic of *Globidens* by Russell (1967): lateral margin of frontal convex, median dorsal surface of parietal narrow, squamosal with broad wing trending medially to contact posterolateral ramus of parietal, pterygoid reduced, suprastapedial process of quadrate fused to infrastapedial process, thick tympanic ala of quadrate, marginal teeth inflated, subcircular articulating surfaces of cervical and anterior dorsal vertebrae, atlas neural spine originating posterior to condylar facet, atlas synapophysis long and tubular, synapophyses located near center of lateral surface of axis, ventral border of synapophyses reaching nearly to the level of the ventral surface of the centrum on the axis, hypophyses of cervical vertebrae posteriorly positioned on ventral surface of centrum, and zygosphenes and zygantra on anterior presacral vertebrae.

A cladistical analysis of the lineage awaits a statistically significant sample illustrating the intraspecific range of characters. Even so, *Globidens schurmanni* does exhibit distinctive characters of the dentition. Although other features of the skeleton will become more important following the recovery of additional specimens, the dentition has been a principal basis for differentiation of species of *Globidens* (Russell, 1975; Lingham-Soliar, 1999; Bardet et al., 2005). *Globidens schurmanni* is unique in possessing a dentition with long, slender, posteriorly curved anterior teeth succeeded in the tooth row by massive, high-crowned, symmetrical teeth that are bell shaped in lateral outline. Additional characters that appear to diagnose *G. schurmanni* include a wide premaxillary narial bar, a vertical anterior premaxillary-maxillary suture, an anteroposteriorly short frontal without lateral emargination that is more rounded than that of known mosasaur frontals, and a frontal without a medial crest.

Among species of *Globidens, Globidens schurmanni* from the late Campanian appears structurally intermediate between early-medial Campanian species and the Maastrichtian species. *G. alabamaensis* and *G. dakotensis* from the earlier Campanian are characterized by a relatively simple dentition with higher crowned, conical anterior teeth succeeded by a long row of subspherical teeth. *G. schurmanni* is more derived owing to greater differentiation of the tooth row and the middle teeth becoming very high crowned. This feature is accentuated in the Maastrichtian *G. phosphaticus* by the development of a posterior buttress on the high-crowned teeth and large, deep sulci. The more derived species, *G. schurmanni* and *G. phosphaticus,* are united by high-crowned teeth, and this evolutionary advancement might be considered diagnostic of a separate genus.

DISCUSSION

Functional Morphology

The dentition of these durophagous mosasaurs has been discussed by numerous authors (e.g., Massare, 1987; Lingham-Soliar, 1999), and all agree that the skull and dentition were adapted for crushing. Some question concerned the prey of these mosasaurs, but that question was answered by SDSM 74764 in which bivalves were found in the stomach region of *Globidens schurmanni* (see Martin and Fox, this volume). In this species and *G. phosphaticus,* a greater differentiation of the tooth row occurs than in the earlier occurring *G. alabamaensis* or *G. dakotensis*. The latter species have a general bipartite distribution with an anterior tooth row composed of relatively pointed teeth and a posterior portion with robust subspherical teeth. The anterior teeth appear to be for prey acquisition, whereas the posterior teeth process the prey. The relatively homodont posterior portion is adapted for crushing the bivalve prey. *G. schurmanni* and *G. phosphaticus* are more derived with a tripartite dentition, consisting of the anterior, pointed teeth for acquisition, a middle portion of very high-crowned teeth, and a posterior massive, subspherical section. The middle section is the primary difference between the earlier occurring *G. alabamaensis* and *G. dakotensis* and the later occurring *G. schurmanni* and *G. phosphaticus*. Rather than the simple crushing dentition of the earlier group, the middle teeth of the latter two species (Fig. 5A, C) were probably adapted for the initial puncturing of shells. The greater pressure concentrated on the tips of these conical teeth would be more efficient and allow for feeding upon thicker shelled prey. Therefore, a greater efficiency would allow greater ease and speed in feeding on previously exploited prey, as well as the ability to exploit thick-shelled bivalves. Some of these thick-shelled bivalves (Kauffman et al., 1993), such as *"Inoceramus" tenuilineatus, "I." sagensis,* and/or *"I." nebrascensis,* were found in the stomach region of *G. schurmanni* (Martin and Fox, this volume). On *G. phosphaticus,* the only Maastrichtian species of *Globidens,* heterodonty appears greater than that of *G. schurmanni,* owing to the occurrence of large buttresses and sulci.

Proof for this contention may come through comparison with another vertebrate group that exhibits a similar adaptation. The principal evolution of the chondrichthyan raylike ptychodontids occurred prior to the evolution of the *Globidens* in the Late Cretaceous (Cicimurri, 1998). Many earlier occurring species possess a pavement of relatively flat, crushing teeth. Later occurring species, such as *Ptychodus whipplei* from the Turonian, exhibit teeth with a high, central, rugose cone. Of course, both low- and high-crowned morphotypes persist, indicating prey partitioning. Even so, the similarity of structure in two species suggests a polarization of the characters, and this polarization corresponds with the chronological appearance of the low-crowned teeth of both groups, followed by the higher crowned teeth.

Taphonomy-Paleopathology

A number of unusual features occur on SDSM 74764. The first includes either a pathology or injury to the left humerus and ulna (Fig. 8C–E, J, L). These two elements were some of the first elements found weathered out that indicated the presence of the skeleton. The distal portion of this paddle had been eroded away prior to discovery. The distal portion of the humerus and proximal portion of the ulna exhibit extreme exostosis, essentially fusing the two elements. Great lateral expansion and obliteration of the periosteum had occurred during precipitation of the bone overgrowth. This condition must have affected locomotion, but the degree of hindrance is conjectural. Mosasaurs are tail-propelled, and the front paddles were principally utilized in steering. How much effect on the maneuverability of the creature was caused by the deformity cannot be positively ascertained, but the condition may have made the mosasaur susceptible to attack. The mosasaur was found with numerous bivalve fragments concentrated in the stomach area (Martin and Fox, this volume), indicating that the ability to feed was not hindered. Although many specimens found during expeditions into the Pierre Shale Group are directly associated with bentonites, this specimen was not, indicating ash fall was not a direct factor in the death of the individual. A second feature of SDSM 74764 may provide more information. The left jaw is disarticulated, whereas the right remained nearly articulated, and the left retroarticular exhibits a deep cut (Fig. 5J) that does not exhibit any rehealing. The long, deep slash is too large for the *Squalus* teeth found in abundance with the mosasaur, and although rare teeth of *Squalicorax* were also found associated (see Martin and Fox, this volume), *Squalicorax* normally leaves multiple scratches during feeding-scavenging. Therefore, although sharks cannot be eliminated as a cause of death, the demise of the mosasaur cannot be positively attributed to these carnivores. Other examples of such bone modification concern interaction between mosasaurs themselves. Both predation of one mosasaur taxon by another has been documented (Martin and Bjork, 1987; Martin, 1994) as well as interspecific aggression (Bell and Martin, 1995). How the mosasaur met its fate cannot be positively determined, but sharks, another mosasaur, or another large predator appears to have killed the otherwise normally feeding and presumably relatively healthy mosasaur whose front limb mobility may have been hindered.

CONCLUSIONS

The most complete skeleton of a durophagous mosasaur has been found in the upper Campanian uppermost DeGrey Formation of the Pierre Shale Group of central South Dakota and is designated as a new species, *Globidens schurmanni*. The skull and anterior portion of the skeleton is preserved along with bivalves as stomach contents and shark teeth shed during scavenging. The left paddle exhibits exostosis owing either to disease or previous injury and may have contributed to the demise of the reptile. A distinct cut in the left retroarticular represents a tooth mark and may indicate death from attack or later scavenging, although the source of the slash cannot be positively determined.

The dentition of *G. schurmanni* is unique. Unlike that of earlier occurring species of *Globidens,* that of *G. schurmanni* is essentially tripartite with high-crowned anterior conical teeth for prey acquisition and initial puncturing, the middle of the tooth row composed of massive conical teeth for puncturing thick bivalve shells, and posterior subspherical teeth for shell processing. Species of *Globidens* from the earlier Campanian are essentially bipartite and do not exhibit the middle section of high-crowned teeth of *G. schurmanni*. *G. phosphaticus* from the Maastrichtian does possess middle high-crowned teeth but exhibits posterior buttresses on the middle and posterior teeth that do not occur on *G. schurmanni*. The high-crowned, massive medial teeth were probably utilized to initially puncture the thick bivalve shells, whereas the more posterior subspherical teeth were adapted to crush the initially broken shells. Such processed shells were found in the stomach region of *G. schurmanni*. An evolutionary succession occurs in the tooth morphologies from the bulbous posterior teeth of earlier Campanian species, through the middle high-crowned, relatively symmetrical teeth of *G. schurmanni* from the late Campanian, to the high-crowned, buttressed teeth of the Maastrichtian species. The transition from relatively flat or bulbous teeth to high-crowned teeth may be mirrored in the evolution of the durophagous ptychodontid sharks.

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A North American Hainosaurus *(Squamata: Mosasauridae) from the Late Cretaceous of southern South Dakota*

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ABSTRACT

A partial skull of a large mosasaur was discovered eroding from the upper Campanian shales of the DeGrey Formation of the Pierre Shale Group from Gregory County, South Dakota. Although the skull is not complete, sufficient characters exist to indicate that the specimen represents the first undisputed North American occurrence of the large tylosaurine mosasaur *Hainosaurus,* otherwise best known from the Maastrichtian of Europe. Diagnostic characters include relatively laterally compressed, symmetrical teeth with finely serrated carinae, an interlocking premaxillary-maxillary suture, a very large alar opening of the quadrate, a distinctly laterally deflected quadrate shaft, a nontriangular centrum outline of anterior caudal vertebrae, and, in particular, a pineal opening bordered by the frontal and parietal. Features of the quadrate indicate that the South Dakota specimen represents a new species of *Hainosaurus,* which is described herein.

Keywords: mosasaur, *Hainosaurus,* Cretaceous, South Dakota, Europe.

INTRODUCTION

During the Late Cretaceous Period, mosasaurs dominated the oceans of the world, and the longest mosasaurs known to exist during this interval were included within the Tylosaurinae. Within this subfamily, two genera, *Tylosaurus* and *Hainosaurus,* constitute a lineage of these exceedingly large carnivorous reptiles. *Tylosaurus* is well known from the upper Niobrara Formation (Santonian–lower Campanian) and the overlying Sharon Springs Formation (lower middle Campanian) of the Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) of the Western Interior Seaway of North America (Russell, 1967). *Hainosaurus* was originally described from the lower Maastrichtian Ciply phosphatic chalk deposits of southwestern Belgium (Dollo, 1885a) and has been noted from other areas in Europe, including Sweden (Lindgren, 2005), Poland (Jagt et al., 2005), southern England (Lingham-Soliar, 1993; Lindgren, 2005), and northeastern Belgium (Mulder and Mai, 1999; Kuypers et al., 1998, described as *Platecarpus,* see Lindgren, 2005); described French occurrences (Bardet, 1990) have been included within *Tylosaurus* (Lindgren, 2005). *Hainosaurus* was first described from North America by Nicholls (1988); however, later authors have shown that her species should be included with the genus *Tylosaurus*. This species, *Tylosaurus pembinensis,* was perhaps closely related to *Tylosaurus ivoensis* from the lower Campanian deposits of Sweden (Lindgren, 2005; Lindgren and Siverson, 2002).

Of the large species of tylosaurines, *Tylosaurus proriger* and *Hainosaurus bernardi* are the best known. *Tylosaurus proriger* is well known, particularly from Santonian to lower Campanian deposits within the North American Western Interior Seaway. *Hainosaurus bernardi* occurs in the upper Campanian–Maastrichtian deposits in Belgium and is known by only three specimens (Dollo, 1885a,b; Lingham-Soliar, 1992; Mulder and Mai, 1999). The type specimen is IRsNB R23C from near Mons in southern Belgium; a second specimen is IRsNB 3672 from nearby Baudour, Belgium (Lingham-Soliar, 1992), and a referred parietal is known from eastern Belgium (Mulder and Mai, 1999). The distinction between these two taxa was well documented (Russell,

Martin, J.E., 2007, A North American *Hainosaurus* (Squamata: Mosasauridae) from the Late Cretaceous of southern South Dakota, *in* Martin, J.E., and Parris, D.C., eds., The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas: Geological Society of America Special Paper 427, p. 199–207, doi: 10.1130/2007.2427(14). For permission to copy, contact editing@geosociety.org.

1967), but as additional specimens have become known the generic definitions have become less clear. *Tylosaurus proriger* is characterized by relatively smooth to faceted, asymmetrical teeth with faint striations lingually and equipped serrated carinae, normally a continuous and smooth premaxillary-maxillary suture, prominent internal suprastapedial process of the quadrate, and a pineal opening situated well within the parietal. *Hainosaurus bernardi* has relatively smooth teeth, but they are more symmetrical and more laterally compressed than are those of *Tylosaurus,* and the carinae are usually more pronounced; an interdigitating anterior portion of the premaxillary-maxillary suture is invariably present, and the pineal opening straddles the frontal-parietal suture. Because these two species are both exceedingly large and share tylosaurine characters, an ancestral-descendant relationship has been suspected (e.g., Russell, 1967). However, relatively few specimens have been described from rocks of intermediate age. Perhaps the most significant is the holotype of "*Hainosaurus*" *pembinensis* described by Nicholls (1988) from lower middle Campanian deposits of southern Manitoba, Canada. This taxon has relatively smooth, asymmetrical teeth; a smooth premaxillary-maxillary suture (Lingham-Soliar, 1992); and the pineal opening remains in the parietal. The species was considered more derived than *Tylosaurus proriger;* therefore, the species was originally considered a species of *Hainosaurus* (Nicholls, 1988). However, Lindgren (2005) argued that the taxon was a species of *Tylosaurus* on the basis of dental characters and the equivocal nature of other features, including narial length, vertebral count, femur:humerus length, and the morphology of the premaxillary-maxillary suture. As Lindgren (2005) noted, teeth of *"H." pembinensis* are not laterally compressed and symmetrical. However, the type specimen of *H. bernardi* is crushed, and at least some features may be due to preservation. The interdigitation of the premaxillary-maxillary suture has been considered an equivocal *Hainosaurus* character (Lindgren and Everhart, 2000); however, nearly all later occurring tylosaurines exhibit this character. Importantly, the position of the pineal opening is distinct between *H. bernardi* and *"H." pembinensis,* substantiating the conclusion of Lindgren (2005) that the latter is a species of *Tylosaurus*. Therefore, this feature, coupled with a possible vertebral count; bilaterally compressed, symmetrical teeth; dorsoventrally flattened, nontriangular outline of anterior caudal vertebrae; and minutely serrated pterygoid tooth carinae (Lindgren, 2005) may be considered the defining characters of *Hainosaurus*. On this basis, *"Hainosaurus" pembinensis* is now considered a derived species of *Tylosaurus* and was apparently derived from *Tylosaurus proriger.* This contention is reinforced by a cladistical analysis in a forthcoming contribution concerning another new tylosaurine specimen (Thompson, 2005) from the Sharon Springs Formation of the Pierre Shale Group in western South Dakota, a lateral equivalent of the Pembina Formation of the Pierre Shale Group in Canada. The specimen described herein, SDSM 75705, is from higher in the section (upper Campanian) and is the first described tylosaurine from North America that unequivocally exhibits a pineal opening shared by the frontal and parietal. Another North American specimen was assigned to *Hainosaurus* in abstracts (Bullard and Caldwell, 2002; Bullard, 2003), but this specimen was not yet described and characterized.

The specimen described herein was found eroded out along the bank of the Missouri River in Gregory County, South Dakota (Fig. 1), by Paul Neumiller while fishing. The skull and a few isolated vertebrae were found in a sandy concretion in the siliceous shale of the DeGrey Formation (upper Campanian) of the Pierre Shale Group (Fig. 1). The concretion had weathered and broken apart, and fragments were scattered by wave action of the river. Because the specimen was found in a high-traffic area, Neumiller gathered as many concretionary fragments with bone as he could find and hid them in the brush along the River. He contacted various entities and eventually discovered that the specimen was found on lands managed by the U.S. Army Corps of Engineers. He reported the find to the Corps and to the Museum of Geology. The Museum was also contacted by James Lindley of the Corps, owing to a long-term, cooperative scientific investigation between the agencies concerning Late Cretaceous marine vertebrates along the Missouri River. As a result, Neumiller showed the hiding place to Lindley, who brought the bones to me while I was teaching a field paleontology course in August 2005. The specimen is exquisitely preserved, and even fine detail on the bone is evident. Some elements were only partially encased by the concretionary material, and the specimen's affinities to *Hainosaurus* were immediately evident (Martin et al., 2006).

Institutional Abbreviations

IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **MB:** Museum of Natural History, Humboldt University, Berlin, Germany; **MT:** Miami Museum, Municipality of Thompson, Miami, Manitoba, Canada; **SDSM:** Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota.

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811
Mosasauridae Gervais, 1853
Russellosaurina Polcyn and Bell, 2005
Tylosaurinae Williston, 1897
Hainosaurus Dollo, 1885a

Type species. *Hainosaurus bernardi* Dollo 1885a (early Maastrichtian, Belgium)

Hainosaurus neumilleri n. sp.
Figure 2A–M; Figure 3A, B

Holotype. SDSM 75705, partial skull, paddle bones, and associated vertebrae.

Locality. SDSM locality V2005–20, along the bank of the Missouri River, Gregory County, South Dakota.

Age. Late Campanian.

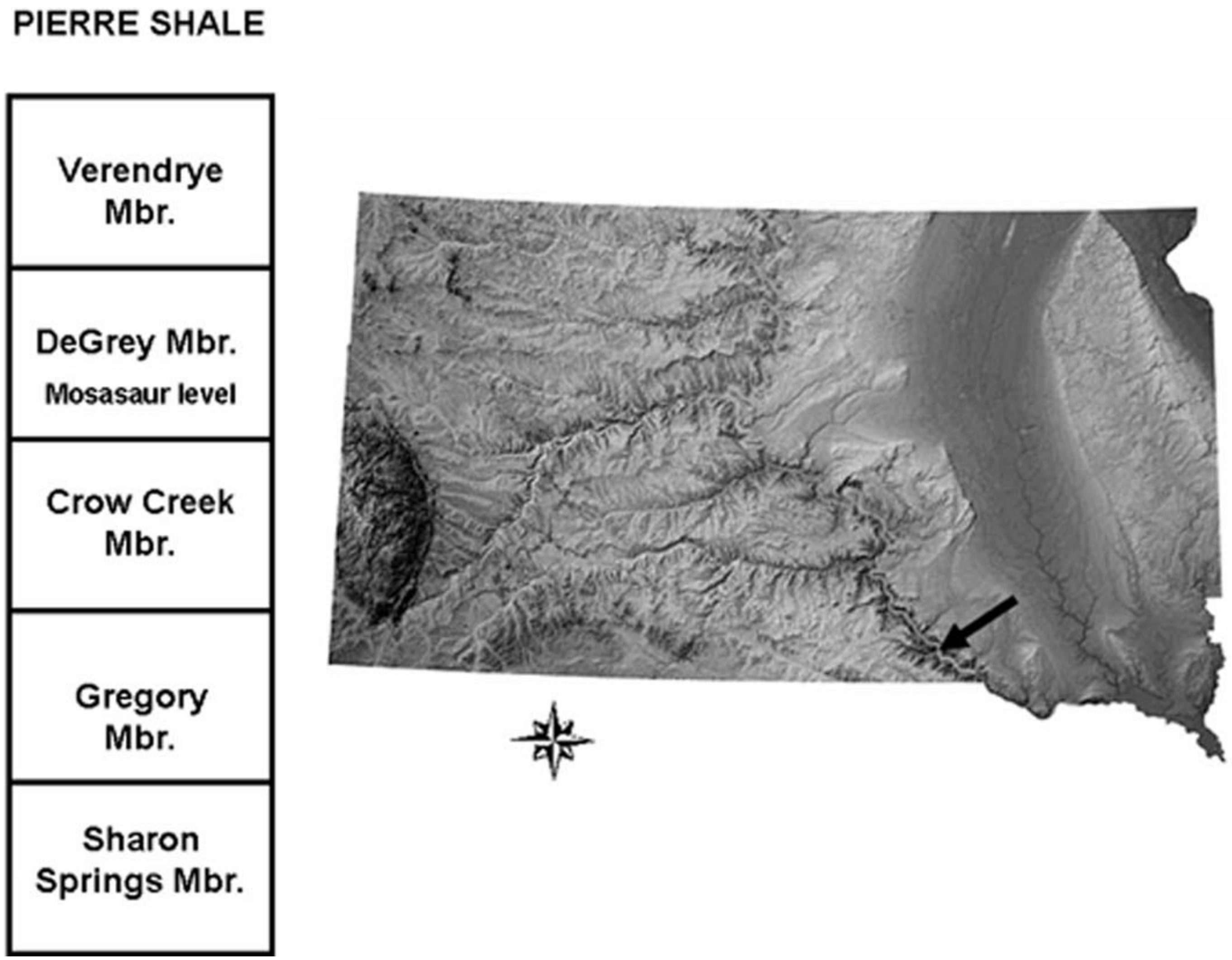

Figure 1. Geographic and stratigraphic positions of SDSM 75075, a new tylosaurine mosasaur from South Dakota. The stratigraphy illustrated indicates the formations of the Upper Cretaceous Pierre Shale Group exposed in the study area. The specimen, as indicated by the arrow, was found along the Missouri River in Gregory County, from the upper Campanian DeGrey Formation of the Pierre Shale Group.

Stratigraphic source. DeGrey Formation of the Pierre Shale Group.

Etymology. Named in honor of Paul Neumiller, who discovered the specimen and reported its occurrence to U.S. Army Corps of Engineers personnel on whose holdings the specimen was found. The scientific community commends Neumiller for his natural curiosity, kindness, and proper action to preserve the specimen for the public good.

Diagnosis. A medium-sized tylosaurine mosasaur with pineal opening shared by the frontal and parietal; interdigitating anterior premaxillary-maxillary suture; relatively wide snout; quadrate with distinct, sharp triangular ridge on the lateral margin of the infrastapedial; quadrate with large, deep, bowl-shaped excavation incorporating the stapedial pit and covering much of the medial quadrate; suprastapedial with relatively long internal process; suprastapedial deflected laterally compared with axis perpendicular to distal condyle; teeth relatively well faceted and symmetrically flattened.

Description. Unfortunately, not all of the skull was recovered. The specimen was embedded within a concretion in the siliceous shales of the DeGrey Formation, and the concretion was eroded out, broken, and dispersed by the rise and fall of the Missouri River. Many portions of the skull were recovered by Neumiller, but some important portions, such as the frontal and anterior premaxillae, were not found. Even so, diagnostic features of the skull were recovered, including the parietal and a quadrate.

PREMAXILLA: The fused premaxillae of SDSM 75705 undoubtedly possessed an elongate, predental snout as is characteristic of all tylosaurines. Moreover, all tylosaurines exhibit a great concentration of foramina around the snout, indicating a concentration of sensitive tissue. These foramina occur on the

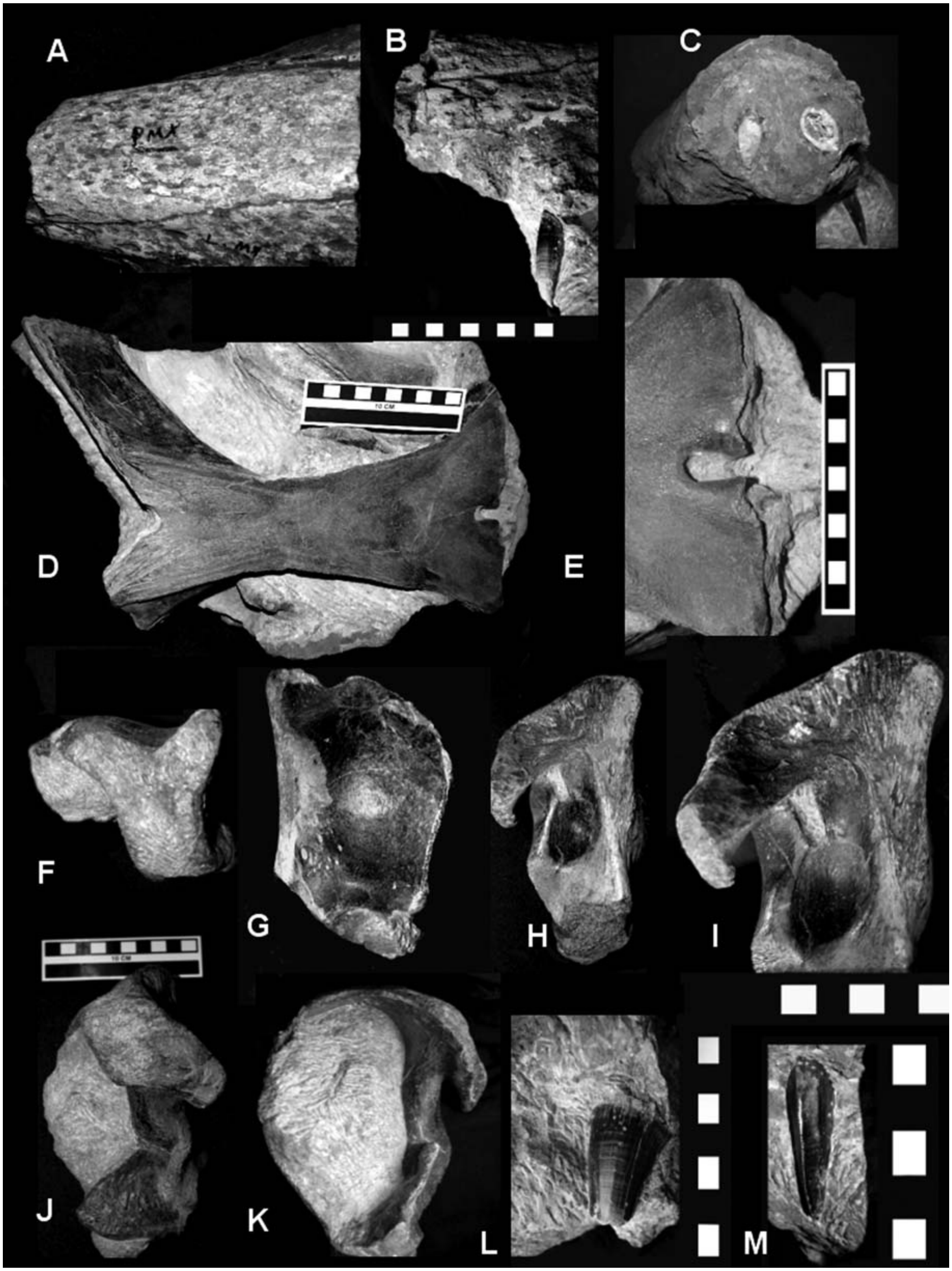

Figure 2. *Hainosaurus neumilleri* n. sp. (A) Premaxillae and maxillae, dorsal view. (B) Premaxilla-maxilla, lateral view. (C) Premaxillae, cross-sectional view and anterior view of tooth. (D) Parietal, dorsal view. (E) Parietal, anterior close-up, showing pineal opening. (F) Quadrate, dorsal view. (G) Quadrate, anterior view. (H) Quadrate, medial view. (I) Quadrate, close-up of medial view. (J) Quadrate, posterior view. (K) Quadrate, lateral view. (L) Tooth, lateral view. (M) Tooth, anterior view. Centimeter scale of B applies also to A, C; scale of J applies to F–H, K.

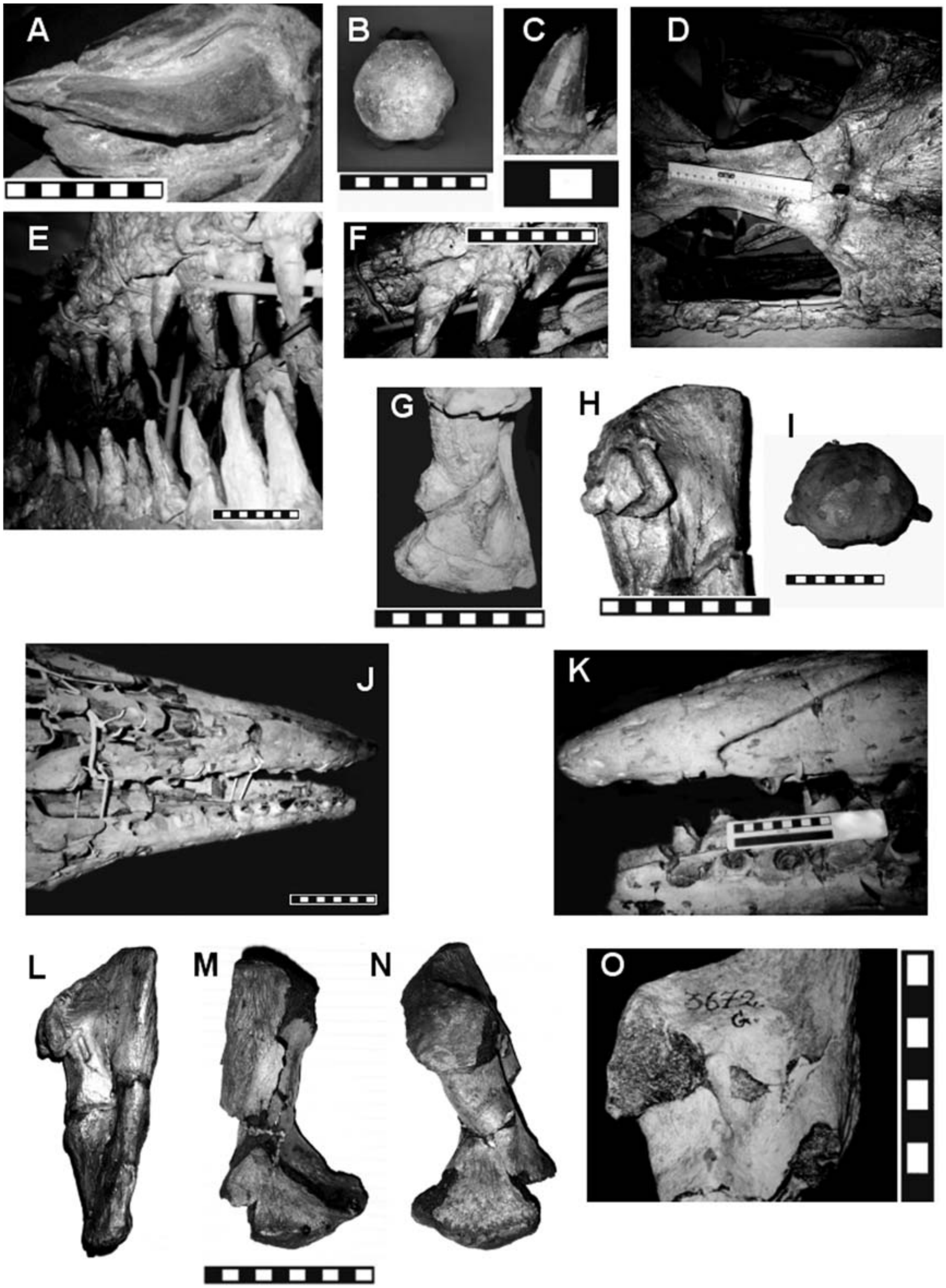

Figure 3. *Hainosaurus neumilleri* n. sp.: (A) Coronoid, ventral view. (B) Anterior caudal vertebra, posterior view. *Hainosaurus bernardi,* IRScNB R23C, holotype: (C) Maxillary tooth, lateral view. (D) Frontal-parietal, dorsal view, with pineal opening straddling suture. (E) Dentition; note lateral compression of teeth. (F) Maxillary dentition, close-up. (G) Distal quadrate, posterior view. (H) Proximal quadrate, posterior view, suprastapedial process. (I) Anterior caudal vertebra, posterior view. *Hainosaurus bernardi,* IRScNB 3672, referred specimen: (J) Anterior skull, right side; (K) Rostrum, left side. (L) Quadrate, medial view. (M) Quadrate, anterior view. (N) Quadrate, distal view. (O) Quadrate, medial view, close-up, illustrating breakage of suprastapedial process. All scales in centimeters; centimeter scale of M applies also to L, N.

remnant of the premaxillae and anterior maxillae (Fig. 2A, B). Also preserved is the important premaxillary-maxillary suture that is not a smooth line but an interdigitating suture (Fig. 2B), presumably providing greater strength to the suture on this long-snouted mosasaur. Lingham-Soliar (1992) considered this feature diagnostic of *Hainosaurus,* and indeed, all known species of *Hainosaurus* possess the feature (Fig. 3J, K). However, a tylosaurine was found from lower in the stratigraphic section in the Niobrara chalk that exhibits the feature (Lindgren and Everhart, 2000). At this level, species of *Tylosaurus* dominate. Therefore, the interdigitating suture either is a variable characteristic that rarely occurs in *Tylosaurus,* or this specimen represents a very early indication of *Hainosaurus*. The character becomes more common with time, and all known large tylosaurine mosasaurs from the upper Campanian and Maastrichtian of the Northern Hemisphere exhibit the interdigitating suture pattern.

MAXILLA: The maxillae that lie behind the suture are massive, high elements that diverge posteriorly at a relatively acute angle (Fig. 2A). Therefore, the snout does not appear as long as that of *Tylosaurus proriger* nor the type of *Hainosaurus bernardi* (IRScNB R23C); however, a referred skull of *H. bernardi* (IRScNB 3672) does not appear as elongate as the type specimen and may indicate some variability of the character. The relative snout length may be more similar to that of the tylosaurine *Taniwhasaurus* from the Campanian of New Zealand (see Caldwell et al., 2005), a taxon that includes *Lakumasaurus* (Martin and Fernández, 2005; Martin and Fernández, 2007) from the Campanian of Antarctica (Novas et al., 2002), and perhaps *Tylosaurus iembeensis* (Telles-Antunes, 1964) from Angola and which differs from *Hainosaurus* owing to well-striated teeth among other characteristics. Unfortunately, the premaxillae and maxillae of SDSM 75705 are broken anterior to the nares (Fig. 2A), so narial position and shape cannot be ascertained. Also, the posterior maxillae are not preserved, so whether or not the prefrontal is eliminated from contact with the posterior nares cannot be determined. Nevertheless, this condition is expected, as appears to be the case in all long-snouted mosasaurs (e.g., *Hainosaurus, Tylosaurus, Ectenosaurus*). The anterior maxillae are covered with indentations like those of the fused premaxillae. Some indentations appear to be preservational features, but the prominent supradental nutrient foramina are evident.

PARIETAL: An important region of the cranium of SDSM 757095 is the fused parietals (Fig. 2D, E). The most obvious feature is that the pineal opening is only partially housed in the parietal as is the case for the type specimen of *Hainosaurus bernardi,* IRScNB R23C (Fig. 3D), and a smaller parietal referred to as *Hainosaurus* sp. cf. *H. bernardi,* MB R890 (Mulder and Mai, 1999). The anterior, frontoparietal suture of *Hainosaurus neumilleri* is relatively straight. The parietal table has an elongate furrow along the sagittal plane, and the anterior portion of the skull table separating the fenestrae exhibits a large depression that appears to have been made while the bone was fresh (Fig. 2D). Whether this depression may have been involved in the cause of death or is a postmortem, prefossilization feature is uncertain. The parietal table is long, has subparallel lateral margins unlike those of *T. proriger,* and, in particular, does not have the distinct indentation at the anteromedial corner of the fenestrae as illustrated for *Tylosaurus proriger* (Russell, 1967, p. 174) or *T. pembinensis* (Nicholls, 1988, p. 1566). In this regard, the shape of the table resembles more greatly that of *H. bernardi* (Fig. 3D) with a slight medial constriction rather than a medial expansion like that of *Tylosaurus proriger* or *T. pembinensis* (see Nicholls, 1988, p. 1566). The medial constriction occurs where the parietal wings diverge posteriorly. The posterior emargination of the parietal resembles that of *Tylosaurus nepaeolicus* and *Hainosaurus bernardi* more than that of *T. proriger.* The parietal wings of the South Dakota specimen appear to flare at a greater angle than those of *Tylosaurus*.

QUADRATE: A beautifully preserved quadrate (15.1 cm high and of 10.2 cm maximum width) was found nearly in articulation with the squamosal, and this element (Fig. 2F–K) of SDSM 75705 is complete except for a small portion broken from the lateral corner of the distal articulation. The anterior surface is smooth but with a large rounded area mirroring the alar opening (Fig. 2G). Dorsally on the anterior surface is a deep, distinct emargination characteristic of tylosaurines (Fig. 2F). At the base of the anterior surface is an indentation above the condyle of the ventral margin. The ventral margin is a typical rounded condyle similar to that of *Tylosaurus*.

From the lateral perspective, the alar is well preserved and ventrally extensive, like that illustrated for *Tylosaurus pembinensis* (Nicholls, 1988, p. 1564). The posteroventral ascending tympanic rim (lateral crest) is particularly distinct and triangular (Fig. 2J, K), resembling that of a plioplatecarpine such as that illustrated by Russell (1967, p. 46) or some species of *Mosasaurus*. Such a crest occurs on some specimens of *Tylosaurus proriger* (see Russell, 1967, p. 46) but is normally not so well developed. The illustration of the quadrate of *Tylosaurus pembinensis,* MT 2, by Nicholls (1988) does not indicate such a structure, but the illustration by Lindgren (2005, p. 1161) appears to show this crest. The structure does not occur on *Hainosaurus bernardi* (Fig. 3G, N).

From the medial perspective (Fig. 2H, I), the infrastapedial process is a rounded process similar to but more prominent than that of *H. bernardi*. This process of SDSM 75705 appears less prominent than that of *Tylosaurus pembinensis* (see illustration in Lindgren, 2005, p. 1161) and *T. proriger* (see illustrations in Russell, 1967), resulting in a process intermediate in size between known species of *Tylosaurus* and *Hainosaurus*. Originating at the level of the infrastapedial process is a wide, bowl-shaped depression (Fig. 2H, I) that covers much of the medial aspect of the quadrate up to above and incorporating the stapedial pit. This deep, ovate depression (6 × 2.3 × 1.0 cm) is unlike that of previously described *Hainosaurus bernardi* or *Tylosaurus pembinensis*. Dorsally, the suprastapedial process is emarginated by an extensive dorsal notch (Fig. 2F). The stapedial pit is a long, narrow slit-like depression (Fig. 2H, I) that is angled slightly posteriorly as in other tylosaurines. The pit is separated from the suprastapedial process by a distinct crest that trends posteriorly from the suprastapedial process. The pit (1.86 × .76 cm) interrupts and terminates another, larger, very distinct ridge that forms the posterior margin of the large depression and terminates in the medial infrastapedial process. Another distinct, rounded ridge constitutes the anterior margin of the deep medial depression. This ridge extends dorsally to the base of the suprastapedial notch. Distally, the ridge extends beyond the medial depression all the way to the ventral margin.

From the posterior aspect (Fig. 2J), the suprastapedial is a prominent process and has a distinct medial extension similar to that of *Taniwhasaurus antarcticus* (see Novas et al., 2002; Martin and Fernández, 2007), *Tylosaurus pembinensis,* and some specimens of *Tylosaurus proriger.* The process of SDSM 75705 is much longer and larger than that of *Hainosaurus bernardi;* however, the type and referred specimens of *H. bernardi* both have distorted or broken suprastapedial processes (Fig. 3H, N, O). The depression on the posterior face of the suprastapedial process of SDSM 75705 is shallow. As previously mentioned, the suprastapedial notch on the dorsomedial aspect is distinct and extensive, particularly when viewed dorsally (Fig. 2F). The axis of the quadrate is not vertical but medially bent (Fig. 2J), similar to those of *Taniwhasaurus antarcticus* and *H. bernardi* (Fig. 3M, N).

Laterally, the alar opening extends all the way to the basal articulation (Fig. 2K), farther than most species of *Tylosaurus,* more similar to species of *Mosasaurus* and to *H. bernardi*. Overall, the quadrate of *Hainosaurus neumilleri* is distinct in possessing a suite of characters that include a large depression on the medial side that partially incorporates the stapedial pit, a very long medially directed suprastapedial process, a distinct triangular crestlike ridge on the lateral side of the infrastapedial, and a relatively subdued infrastapedial process on the medial aspect.

LOWER JAW: Portions of the lower jaw of SDSM 75705 are preserved, including parts of the dentary, angular, and splenial. These elements are only partially observable owing to articulation, but they appear identical to those of other tylosaurines. The coronoid was detached and lies within the left cranial fenestra; the element is similar to that of other tylosaurines in being anteroposteriorly short and possessing very short ventral processes (Fig. 3A).

DENTITION: Some teeth remain in the maxillae (Fig. 2C, L, M) of SDSM 75705. The anterior teeth, as exemplified by the broken 2nd right premaxillary tooth (~2.7 cm anteroposterior length, 1.1 cm transverse width) and the 2nd left maxillary tooth (4.3 cm high, 1.4 cm transverse width) are very laterally compressed and normally bicarinate. The carinae appear to divide the tooth into nearly equal halves, resulting in symmetrical, laterally compressed teeth (Fig. 2M), somewhat similar to those of the mosasaurine *Leiodon* and very similar to those of the holotype of *Hainosaurus bernardi*. All the teeth of SDSM 75705 exhibit facets (Fig. 2L), more similar to those of the *Hainosaurus* specimens from Sweden (Lindgren, 2005) than the somewhat smoother teeth of the holotype *Hainosaurus bernardi* (Fig. 3C), although teeth of both the type specimen, IRsNB R23C, and the referred specimen, IRsNB 3672, may exhibit faint medial striations and external facets. The anterior teeth of SDSM 75705 are laterally compressed, with finely serrated carinae, like those illustrated for *Hainosaurus* sp. from Sweden (Lindgren, 2005). The anterior carina is exceedingly sharp, and the anterior third of the tooth is very narrow, resulting in a knifelike blade (Fig. 2B, M). The 3rd maxillary tooth on the right side is just erupting, and this tooth is slightly different, somewhat more like those of *Tylosaurus* in which the internal portion of the tooth is more convex than the outer. This condition is due to its anterior position within the tooth row and also occurs in some anterior teeth of *H. bernardi;* however, most of the teeth (Fig. 3C, E, F) conform to the symmetry described by Lindgren (2005). The 4th maxillary tooth (Fig. 2L, M) on the left side of SDSM 75705 is well faceted and exhibits fine striations at the crown base, even on the lateral side. These striations do not bifurcate, and they fade 0.5 cm upward of what would be an approximately 4-cm-high crown (Fig. 2L). Interestingly, this tooth does not possess a posterior carina. However, even the holotype of *H. bernardi* exhibits a variation of this character. Most teeth are bicarinate, but the 1st right maxillary tooth has only an anterior carina. On the referred specimen from Belgium, IRsNB 3672, both the right and left 5th dentary teeth have no posterior carinae, although the 13th left dentary tooth is bicarinate.

VERTEBRAE: Associated trunk vertebrae of SDSM 75705 are relatively poorly preserved and are similar to those of species of *Tylosaurus* or *Hainosaurus,* although the anteroposterior length of the transverse processes is relatively short. One anterior caudal vertebra (7.2 cm high, 7.0 cm transversely wide) was associated (Fig. 2B) with SDSM 75705 and is subtriangular to rounded and relatively equidimensional. Lindgren (2005, p. 1162) believed that a nontriangular, dorsoventrally compressed anterior caudal was characteristic of *Hainosaurus* (Fig. 3I) in contradistinction to the triangular, high anterior caudals of *Tylosaurus*. This vertebra of SDSM 75705 appears intermediate, with a rather high vertebra but without the triangular outline.

Discussion

One of the largest reptiles to ply the seas during the end of the Cretaceous was the tylosaurine mosasaur *Hainosaurus. Hainosaurus bernardi* was originally described in 1885 from lower Maastrichtian deposits in Belgium. Other reports of *Hainosaurus* from Europe have been made (Mulder and Mai, 1999; Lindgren, 2005), but its occurrence in North America has been questioned (Lindgren, 2005). The first report of the genus in North America, *"Hainosaurus" pembinensis,* was derived from the middle Campanian Pembina Formation of the Pierre Shale Group in Canada. Later workers doubted the assignment of the Canadian taxon to *Hainosaurus,* and many authors consider the taxon as a species of the closely allied genus *Tylosaurus* (Lindgren, 2005). A number of characters have been utilized to define *Hainosaurus,* but many have been found in other taxa (Lindgren, 2005). Perhaps the most definitive character of *Hainosaurus* is that the pineal opening of this tylosaurine is shared by the frontal and parietal bones rather than being confined to the parietal. Until now, no other North American mosasaur, including the Canadian taxon, has exhibited a clearly shared pineal opening. The new specimen found in the upper Campanian DeGrey Formation of the Pierre Shale Group along the Missouri River in Gregory County, South Dakota, exhibits the pineal opening shared by the frontal and parietal bones.

The new specimen, SDSM 75705, is herein regarded as representative of the Tylosaurinae because of its very large size; long, moderately faceted teeth with internal striations and serrated carinae; suprastapedial process of the quadrate moderately large and ventromedially pointed; short ventral processes of the coronoid; large caudal vertebrae with articular surfaces for haemel arches; and concentration of numerous foramina on premaxillae and anterior maxillae. SDSM 75705 is considered a species of *Hainosaurus* owing to its symmetrical, laterally compressed dentition; strongly laterally deflected proximal portion of the quadrate; dorsoventrally long alar opening of the quadrate; a pineal opening on the suture between the fused frontals and parietals; and anterior caudals with a nontriangular, interarticular outline. In addition, an interlocking premaxillary-maxillary suture has been suggested as characteristic of *Hainosaurus*. *Hainosaurus neumilleri* differs from *Hainosaurus bernardi,* the only other species of the genus, because SDSM 75705 possesses a relatively wide rostrum; basal striations on the labial side of the tooth crown; a long ventromedially directed suprastapedial process of the quadrate that is pointed distally; a prominent infrastapedial process; a ventrolateral process that is a distinct, high, narrow ridge; and the medial side of the quadrate dominated by a large, ovate depression that incorporates the stapedial pit.

Hainosaurus neumilleri shares characters found in large *Tylosaurus* species such as *T. proriger* and *T. pembinensis*. The long, pointed suprastapedial process and prominent infrastapedial process of the quadrate are more typically considered as features of *Tylosaurus*. At least some variation in the teeth with the lingual face of some teeth being more convex than the labial, coupled with most teeth being laterally compressed, suggests an intermediate morphological position between *Tylosaurus* and *Hainosaurus*. Evidently, tylosaurine specimens during the early-medial Campanian, such as *Tylosaurus pembinensis* and *T. ivoensis,* exhibit the initial divergence of *Hainosaurus* from *Tylosaurus,* and by the late Campanian and Maastrichtian the transition had been completed, as indicated by *H. neumilleri*.

RESULTS

The first unequivocal occurrence of *Hainosaurus* in North America is represented by a new species, *Hainosaurus neumilleri*. The new species possesses a pineal opening shared by both the frontal and parietal similar to that in *Hainosaurus bernardi,* the genotypic species. A shared pineal opening is not known in any species of *Tylosaurus,* including *Tylosaurus pembinensis,* a taxon that was formerly considered a species of *Hainosaurus* (Lindgren, 2005). *Hainosaurus neumilleri* possesses other features characteristic of the genus, particularly the laterally compressed, symmetrical teeth and nontriangular intercentral outline of the anterior caudal vertebrae. However, some features of *H. neumilleri,* particularly of the quadrate, are more similar to those of species of *Tylosaurus*. Therefore, the new species of *Hainosaurus* from South Dakota appears less derived than *H. bernardi*. The polarity of characters within this phylogeny correlates with stratigraphic position: *H. neumilleri* from the upper Campanian of North America and *H. bernardi* from the upper Campanian–lower Maastrichtian of Europe.

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The largest mosasaur (Squamata: Mosasauridae) from the Missouri River area (Late Cretaceous; Pierre Shale Group) of South Dakota and its relationship to Lewis and Clark

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ABSTRACT

The Cretaceous Pierre Shale Group along the Missouri River has produced numerous mosasaur specimens since the western fossil discoveries of Lewis and Clark in 1804 that included a 45-foot "fish." Many of these marine reptile specimens represent the largest of mosasaurs, the tylosaurines. In 1990 the largest mosasaur heretofore recorded along the Missouri River was discovered near Nicholas Creek, Lyman County, central South Dakota. The specimen was recovered from a lag deposit representing an intra–Pierre Shale Group unconformity and consists of vertebrae, ribs, paddle elements, and a partial skull. The partial skeleton is referable to the subfamily Tylosaurinae, cf. *Tylosaurus* sp., based on large size, tooth structure, and long predental rostrum. Further identification must await resolution of the taxonomy of the Tylosaurinae. A lower jaw measures 1.6 m, indicating a projected body length of 11.5 m. Therefore, the large "fish" described by Lewis and Clark may have been a tylosaurine mosasaur.

Keywords: Pierre Shale Group, mosasaur, Tylosaurine, Missouri River, South Dakota.

INTRODUCTION

The Missouri River area of South Dakota is world renowned for its extensive exposures of the fossiliferous Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature). The Pierre Shale Group is an extensive marine Cretaceous lithostratigraphic unit that consists of gray to black, organic-rich shales interbedded with bentonites and concretionary zones found throughout the Northern Great Plains. The Campanian Sharon Springs Formation of the Pierre Shale Group is the oldest unit exposed in the Missouri River Trench in central South Dakota and is extremely fossiliferous. In particular, the marine reptile assemblages are well represented, including some of the largest mosasaurs, the tylosaurines. Tylosaurine material is relatively common in the lower Pierre Shale Group but becomes rare higher in the section in the Missouri River area. Relatively few specimens have been recovered from the underlying Niobrara Formation in contrast with the Niobrara Formation of Kansas (Schumacher and Martin, 1993), although this disparity is undoubtedly due to fewer scientific investigations in South Dakota (Martin et al., 1998). The tylosaurines

Meredith, R.W., Martin, J.E., and Wegleitner, P.N., 2007, The largest mosasaur (Squamata: Mosasauridae) from the Missouri River area (Late Cretaceous; Pierre Shale Group) of South Dakota and its relationship to Lewis and Clark, *in* Martin, J.E., and Parris, D.C., eds., The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas: Geological Society of America Special Paper 427, p. 209–214, doi: 10.1130/2007.2427(15). For permission to copy, contact editing@geosociety.org.

were a very successful group of large mosasaurs that existed from the Coniacian to the late Maastrichtian, with some attaining lengths of >15 m. They attained a worldwide distribution, being found in North America, Africa, Europe, New Zealand, and Antarctica. Tylosaurines were opportunistic carnivores, as indicated by their stomach contents, some of which include other mosasaurs, birds, and fish (as summarized in Martin and Bjork, 1987; Martin, 1994).

Since 1989 a systematic survey of the Late Cretaceous marine rocks of the Missouri River Trench has been undertaken through the Museum of Geology and the New Jersey State Museum in cooperation with the U.S. Army Corps of Engineers, the Crow Creek Sioux Tribe, and the Bureau of Indian Affairs to gain an understanding of the geographic, stratigraphic, and temporal distribution of fossil vertebrates. Under the direction of the second author, and in collaboration with David Parris, New Jersey State Museum, extensive collections have been made that have been tied to local stratigraphic sections. These sections are characterized by the Niobrara Formation or the Pierre Shale Group, in which interbedded bentonite layers occur. Most fossil specimens have been documented in relation to these chronostratigraphic units. Therefore, the collections represent a major contribution to understanding the evolution of the Western Interior Seaway on the basis of precise stratigraphic control. The most abundant group of marine reptiles documented in this manner is the Mosasauridae. The mosasaurs are relatively common in both the Niobrara Formation and the Pierre Shale Group and represent a major chapter in understanding the history of life in the Western Interior Seaway.

Here, we report on the largest tylosaurine mosasaur collected thus far from the Missouri River area of South Dakota (Museum of Geology, South Dakota School of Mines [SDSM] 39966). The Jim Wilkens family located the specimen in the summer of 1990 along the Missouri River at water level near the mouth of Nicholas Creek in Lyman County, South Dakota. The specimen lay in the Boyer Bay Member of the newly elevated Sharon Springs Formation (see Martin et al., this volume, for revised Pierre Shale terminology) 0.61–0.66 m below a creamy white bentonite layer just above the Niobrara Formation. Here the Boyer Bay Member of the Sharon Springs Formation unconformably overlies the Niobrara Formation, with its basal portion being a lag deposit. The lower member of the Sharon Springs Formation, the Burning Brule Member, was eroded away. Above the lag deposit, thin bentonitic layers occur throughout the remaining exposure. However, the lower Boyer Bay Member composes the section in this area, because the overlying Sharon Springs members and the remainder of the Pierre Shale Group was eroded, leaving only a small cliff at the water's edge. Unfortunately, owing to high water conditions, the specimen could not be collected completely until 2000. Most of the preserved skeleton was removed in four large plaster jackets from an area of ~10 m^2. The largest plaster jacket contained both lower jaws and miscellaneous bone fragments. The frontal, premaxillae, and postcranial material were removed in the other three large plaster jackets (Fig. 1).

Some of the skeleton was undoubtedly lost to erosion, but the specimen was already severely damaged and disarticulated before fossilization owing to the high-energy environment of deposition. Most of the recovered mosasaur bones were broken and severely abraded. The lag-deposit matrix surrounding the specimen was composed of highly rounded particulate bone from this specimen and possibly several other organisms. Clay clasts were common, as were small pebbles composed of rock and bone. Microvertebrate material was abundant but fragmentary and was predominantly unidentifiable fish material. Notable exceptions were *Squalicorax, Odontaspis,* and *Xiphactinus* teeth.

SYSTEMATIC PALEONTOLOGY

Family Mosasauridae, Gervais, 1853
Subfamily Tylosaurinae, Williston, 1895, 1897
Tylosaurinae, gen. et sp. indet.
cf. *Tylosaurus* sp. indet.

Referred specimen. SDSM 39966, partial skeleton from locality SDSM V2000–19.

Description. Portions of the anterior skull—including a nearly complete frontal and premaxilla, a nearly complete lower right jaw, a left dentary broken posterior to the 11th tooth, 4 large vertebrae, several partial to complete ribs, and phalanges—were well preserved (Fig. 2). Unlike most fossils recovered from the Sharon Springs Formation, these bones were not secondarily impregnated by gypsum.

The premaxillae are well preserved and nearly complete (Fig. 2E, F), although dorsoventrally crushed. The anterior tooth-bearing apex was found isolated from the internarial bar, which remained in partial articulation with the frontal. Foramina are abundant and distributed around the dorsal and lateral sides of the premaxilla. The dorsoventral crushing probably accounts for the broken, unerupted teeth. The long predental rostrum (11.2 cm) is characteristic of the tylosaurines (Williston, 1898; Russell, 1967). The premaxillary-maxillary suture appears to be interdigitating, rather than a smoothly rising interface. This character has been associated with *Hainosaurus* (Lingham-Soliar, 1992), but more recent work (Lindgren and Everhart, 2000) suggests it to be characteristic of all tylosaurines from the medial Campanian through late Maastrichtian (Martin, this volume, Chapter 14).

Most of the frontal is preserved although highly fractured, especially at the sutural contact with the parietal in the region of the pineal opening (Fig. 2G). As a result, the sutural contacts are not distinguishable. This is unfortunate because the frontoparietal suture is an essential character for distinguishing *Tylosaurus* from *Hainosaurus* (Russell, 1967; Martin, this volume, Chapter 14). A pineal opening within the parietal is characteristic of *Tylosaurus,* whereas an opening shared between the parietal and frontal would indicate assignment to *Hainosaurus*. Another character typical of tylosaurines is a dorsal crest on the frontal. SDSM 39966 has a crest on the anterior two-thirds of the frontal;

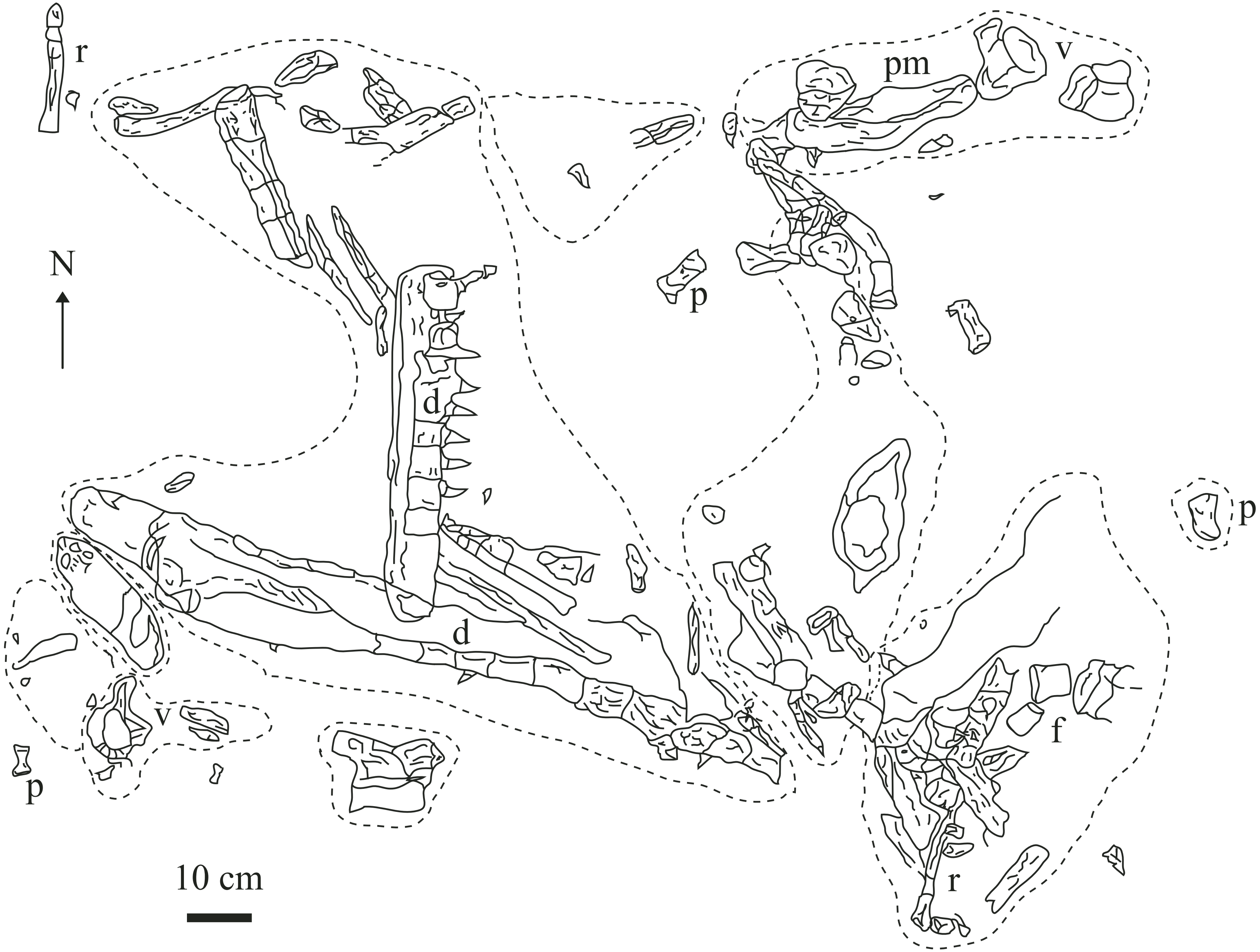
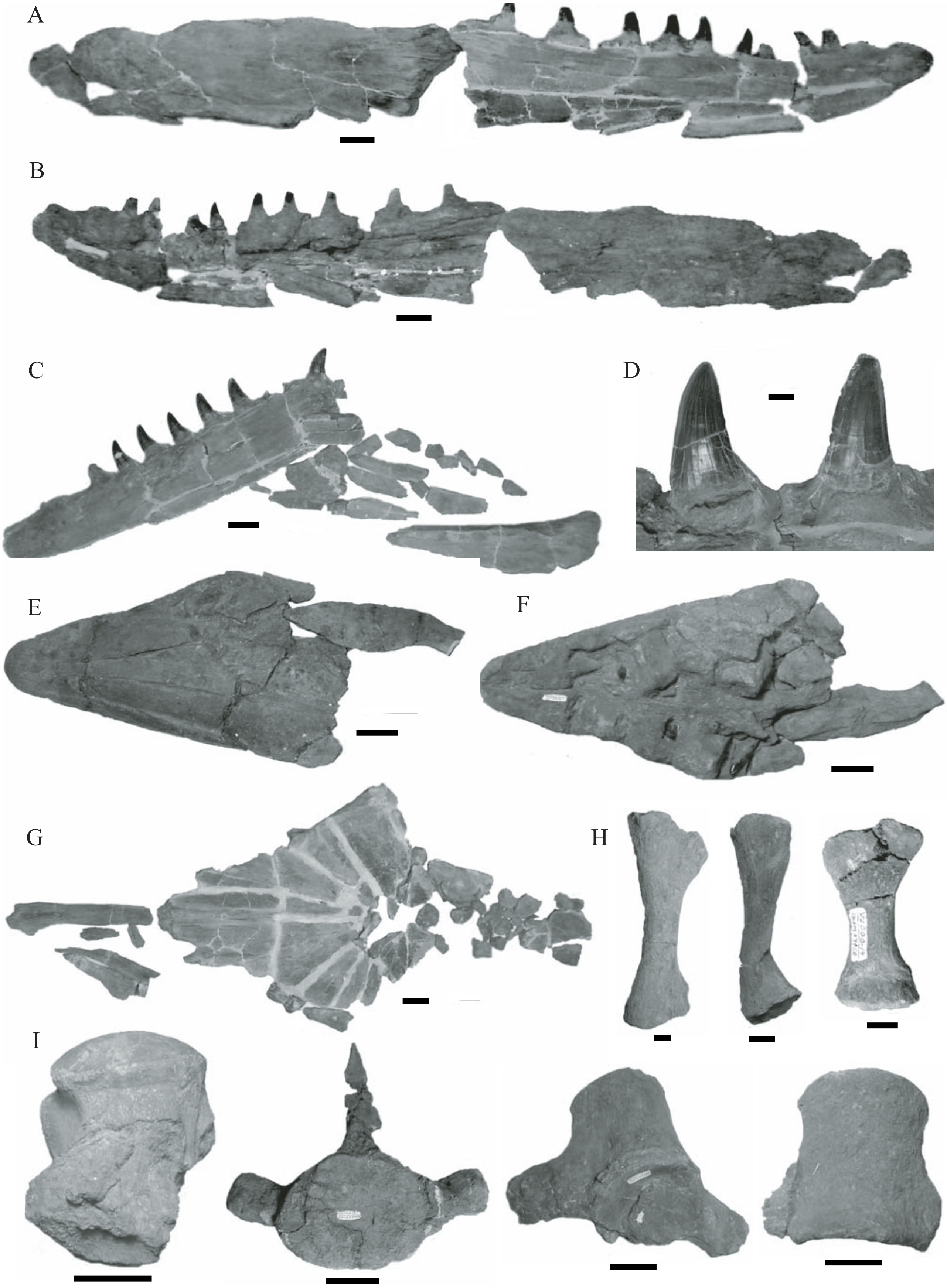


Figure 1. Field map of SDSM 39966. Dashed lines indicate plaster jackets removed. Abbreviations: pm—premaxilla; d—dentary; f—frontal; v—vertebra; p—paddle element; r—rib.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however, it appears more as a doubled crest with a medial valley. The posterior third of the midline is represented by a fissure. A fissure in a very large specimen, suggesting an adult level of ontogeny, indicates that a sagittal fissure on the parietal of mosasaurs may not represent an unfused juvenile condition. The posterior margin of the external nares is preserved on the frontal. The associated internarial bar possesses the anterior narial margin, indicating a narial length of ~30 cm.

The right lower jaw is virtually complete, with a representative portion of all seven bones (Fig. 2A, B). The splenial and angular are fragmentary, but the articular, surangular, prearticular, coronoid, and dentary are relatively complete. The total jaw length at minimum is 1.6 m, but its exact length cannot be stated with certainty because of breakage. In the right dentary, eight virtually complete teeth are preserved, although their tips are normally broken away. The following tooth positions retain teeth: 3, 4, 6–9, 11, and 13, and the tooth count in the lower jaw is 13. The left lower jaw consists of a well-preserved dentary with 7 teeth preserved, including tooth positions 4–9 and 11, but the remainder of the left jaw is broken away posterior to the 11th tooth (Fig. 2C). The symphyseal area exhibits a short predental area that is beveled medially with an oblique facet, a character of most tylosaurines and particularly well developed in *Taniwhasaurus* from New Zealand and Antarctica (Martin and Fernández, 2007). The beveled facet indicates a wide lateral flexion of the dentary during feeding.

The teeth (Fig. 2D) are well preserved, exhibiting most details. All teeth are bicarinate, and the carinae exhibit minute serrations. These carinae are not positioned on the extreme anteroposterior margins of the teeth but are normally asymmetrically positioned on the labial sides. As a result, the teeth are not symmetrical and also are not laterally compressed (although some, such as left dentary tooth 7, appear to be so as the result of postmortem crushing). Internally at the crown base, all teeth display distinct striations that fade about a third of the distance to the crown tip. Some striations also appear on the labial side of the tooth but are normally not as prominent. On this lateral face, facets dominate. Most are relatively short anteroposteriorly, so each tooth may have 8–10 facets.

Of the recovered postcranial material, most is well preserved (Fig. 2H, I) although crushed. The four trunk vertebrae, although incomplete, are very large (centra 25–30 cm in diameter), have ovate centra, and have large transverse processes that become dosoventrally thin posteriorly so that only a bladelike crest extends to the posterior condyle. Most of the rib material is fragmentary, but some is nearly complete. The metapodials and phalanges are also well preserved but provide little information with regard to generic identification.

DISCUSSION

A long predental rostrum, an interdigitating premaxillary-maxillary suture, extremely large size, and a frontal crest indicate assignment of the specimen to the Subfamily Tylosaurinae. Unfortunately, the most important elements for generic identification of tylosaurine mosasaurs are not preserved, i.e., the quadrate and parietal (Russell, 1967). However, the teeth are not well striated, indicating that the specimen could not be *Taniwhasaurus* (Martin and Fernández, 2005, 2007). Moreover, the teeth are not laterally compressed and symmetrical, suggesting that they do not represent *Hainosaurus* (Lindgren, 2005). Overall, the specimen most closely resembles *Tylosaurus proriger,* but a lack of certain diagnostic features prevents precise taxonomic assignment.

Russell (1967) provided several tylosaurine measurements, which were used by Schumacher and Martin (1993) to estimate the body length of a *Tylosaurus proriger* specimen collected from the Niobrara Formation of South Dakota along the Missouri River, south of the location of SDSM 39966. The length of the Niobrara specimen was estimated to be slightly >9.4 m. Until the discovery of the specimen described herein, it was the largest identifiable mosasaur specimen collected from the Missouri River area. Russell's (1967) measurements indicate that the dentary accounts for ~57% of the total lower jaw length. The lower jaw length in turn accounts for ~14% of the total length of the animal. Applying these estimates of body length to the new specimen suggests an individual of 11.5 m, >2 m longer than the Niobrara specimen.

The Lewis and Clark outbound expedition of 1804 to the Missouri River area of South Dakota recorded the first fossils known from this region. These early explorers found remains of a 45 ft animal and attributed them to a large fish. Unfortunately, the specimen was not collected or was lost, and verification of the identification is not possible. However, some workers (see Martin et al., 1998; Parris et al., this volume, Chapter 1) suggest that the specimen was not a fish but was instead a large marine reptile, perhaps a tylosaurine mosasaur. Cretaceous fish are well known from the Niobrara Formation–lower Pierre Shale Group deposits along the Missouri River, but none approach the 45 ft length recorded by Lewis and Clark. The largest fish known from this interval are *Xiphactinus,* but the largest are only approximately one-third of the length noted by Lewis and Clark. The large mosasaur reported here lends further support to the idea that the 45 ft "fish" of Lewis and Clark could have been a tylosaurine mosasaur. However, the possibility that the "fish" was an elasmosaurid plesiosaur cannot be discounted, even though these reptiles are much rarer along the Missouri River.

Figure 2. Preserved elements of SDSM 39966. (A) Labial view of right lower jaw. (B) Lingual view of right lower jaw. (C) Labial view of left lower dentary and jaw fragments. (D) Close-up of left lower dentary teeth. (E) Dorsal view of the anterior tooth-bearing apex of the premaxillae. (F) Ventral view of the anterior tooth-bearing apex of the premaxillae. (G) Dorsal view of the frontal and internarial bar of the premaxillae. (H) Paddle elements. (I) Vertebrae. Scale bar is 5 cm except for D and H, for which scale bar is 1 cm.

CONCLUSIONS

The specimen described herein is the largest mosasaur thus far collected from the Missouri River area of South Dakota, estimated at 11.5 m long. Precise identification of the mosasaur, SDSM 39966, is impossible at this time owing to revisions of tylosaurine taxonomy and the lack of diagnostic bones recovered. However, the specimen can be positively identified as a tylosaurine, probably *Tylosaurus,* owing to its large size, long rostrum anterior to the first premaxillary tooth, and the lack of laterally compressed, symmetrical teeth. The specimen certainly represents a tylosaurine, the largest mosasaurs to have existed. The occurrence of large mosasaurs in the Late Cretaceous Niobrara Formation–lower Pierre Shale Group section of South Dakota lends further evidence that the 45 ft fossil "fish" identified by Lewis and Clark in 1804 may have been a mosasaur, as suggested by Martin et al. (1998) and Parris et al. (this volume, Chapter 1). No fossil fish are known to have reached the size of these large marine reptiles. The only other possibility for Lewis and Clark's "fish" could be an elasmosaurid plesiosaur, but these taxa are rarer than tylosaurine mosasaurs from this portion of the Cretaceous along the Missouri River.

ACKNOWLEDGMENTS

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Pteranodon *(Reptilia: Pterosauria): Stratigraphic distribution and taphonomy in the lower Pierre Shale Group (Campanian), western South Dakota and eastern Wyoming*

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ABSTRACT

The Cretaceous Pierre Shale Group in eastern South Dakota and western Wyoming contains numerous fossils, including the flying reptile *Pteranodon,* 19 specimens of which are described herein. *Pteranodon* specimens have been found in the two lower formations of the Pierre Shale Group: 4 in the basal Gammon Ferruginous Formation, and 15 in the overlying Sharon Springs Formation. Of these specimens, 64% are associated forelimb elements. Two factors, or a combination thereof, explain the abundance of associated forelimb elements: (1) predatory preference of the muscle mass in the chest over the wing membrane, which may not have offered much nutrient to the predators; and (2) the strong wing membrane, which would have secured the wing elements while the muscle mass would have fallen away. In either case, the wing membrane may have served as a protective layer over the forelimb bones until burial. Two *Pteranodon* specimens contain vertebrae of the fish *Enchodus,* which appear to be stomach contents, the first documented *Pteranodon* stomach contents from South Dakota.

Keywords: *Pteranodon,* stratigraphy, taphonomy, Pierre Shale Group.

INTRODUCTION

Under the direction of James E. Martin, the Museum of Geology, South Dakota School of Mines and Technology (SDSM), has collected many vertebrate fossils from the Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) of western South Dakota in order to provide a biostratigraphic distribution. The Pierre Shale Group consists of dark shales that were deposited by the Western Interior Seaway that covered the middle of North America. Pterosaur specimens have been found in the lower two formations of the Campanian Pierre Shale Group, the Gammon Ferruginous and Sharon Springs Formations. No pterosaurs have yet been found in the overlying formations. An unexpected number of associated wing elements were encountered, resulting in the questioning and testing of the taphonomy to determine if a preservational bias exists, and if the bias was the result of predatory preference or anatomical constraints. Finally, fish bones were found associated with the pterosaur skeletons, suggesting their stomach contents.

The first *Pteranodon* fossil was found in 1870, and Othniel C. Marsh (1871) described a new species of American flying reptile which he named *Pteranodon,* or "toothless flier," from the Niobrara Formation in western Kansas. He based this new taxon on the lack of teeth and the presence of a crest on the back of the skull. Skeletons of this Late Cretaceous genus (from ca. 115–70 Ma) have also been reported from India, Japan, and possibly Brazil. The fossils from Brazil are fragmentary, and it is unclear whether they belong to the genus *Pteranodon* (Wellnhofer, 1991). Bennett (1994)

Hargrave, J.E., 2007, *Pteranodon* (Reptilia: Pterosauria): Stratigraphic distribution and taphonomy in the lower Pierre Shale Group (Campanian), western South Dakota and eastern Wyoming, *in* Martin, J.E., and Parris, D.C., eds., The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas: Geological Society of America Special Paper 427, p. 215–225, doi: 10.1130/2007.2427(16). For permission to copy, contact editing@geosociety.org.

concluded that the genus *Pteranodon* was endemic to the Western Interior Seaway of North America and doubted that it could fly as far as the putative worldwide distribution suggested. Numerous specimens have been found in the Pierre Shale Group, the unit that overlies the Niobrara Formation.

Geological Setting and Paleoclimate

The Pierre Shale Group is widely distributed throughout the Western Interior of the United States and represents deposition in a Cretaceous epicontinental seaway that extended from the Arctic to the Gulf of Mexico, spanning a width of as much as 1600 km (Gill and Cobban, 1973). The western border of the seaway was restricted by the Cordilleran highlands. The eastern border of the seaway is not preserved in the geologic record, but it should have extended no farther than Iowa and eastern Minnesota (Gill and Cobban, 1973).

The stratigraphic thickness of the outcrops varies with its geographic distribution. Southeast of the Black Hills the Pierre Shale Group reaches a maximum thickness of 365 m (Darton and Paige, 1925), whereas in central and southern South Dakota the thickness ranges from 150 to 300 m (Tourtelot et al., 1960). The varied thickness of the Pierre Shale Group reflects changes in thickness of its formations, with some formations absent in some localities. This study was conducted in the southwestern part of South Dakota and adjacent Wyoming.

The Late Cretaceous climate occurred under greenhouse conditions and was warmer than today (Huber et al., 2002; Schouten et al., 2003). This climate is inferred by studying isotopes from foraminiferans and nannofossils (Huber et al., 2002), Cretaceous tectonism (Poulsen et al., 2001, 2003), archaeal membrane lipids (Schouten et al., 2003), and the fauna and flora found in the strata. The nonmarine Late Cretaceous deposits are known for their variety of dinosaurs and fossil plants, and for the lack of evidence of glaciation, suggesting that the Late Cretaceous Epoch of South Dakota and Wyoming had a subtropical climate.

Volcanic activity was prevalent throughout the Mesozoic, reaching a high during the Late Cretaceous because of the tectonism of the magmatic arc on the western coast. The increase in volcanism resulted in a large number of bentonites in the rock record, such as the Ardmore succession in the Sharon Springs Formation of the Pierre Shale Group. These bentonite layers can be used to correlate the stratigraphy directly and also by using geochemistry (Bertog, 1997). The volcanics responsible for the bentonites of the Pierre Shale Group had a rhyolitic or dacitic source in Idaho or Montana (Christiansen et al., 1994; see Bertog et al., this volume).

Location of Study Area

Of the 19 *Pteranodon* specimens in the SDSM collection, 16 were found in southwestern South Dakota; the remaining 3 were found in eastern Wyoming. The South Dakota specimens were collected from the margin of the Black Hills in Pennington, Custer, and Fall River Counties. Figure 1 outlines the location of these three counties and gives the generalized geology of the area. The South Dakota localities are (1) SDSM V614: Brown Ranch locality, Pennington County; (2) SDSM V8121: *Hesperornis* locality, Custer County; (3) SDSM V491: Henderson Ranch, Fall River County; (4) SDSM V926: Slurp Flats, Fall River County; (5) SDSM

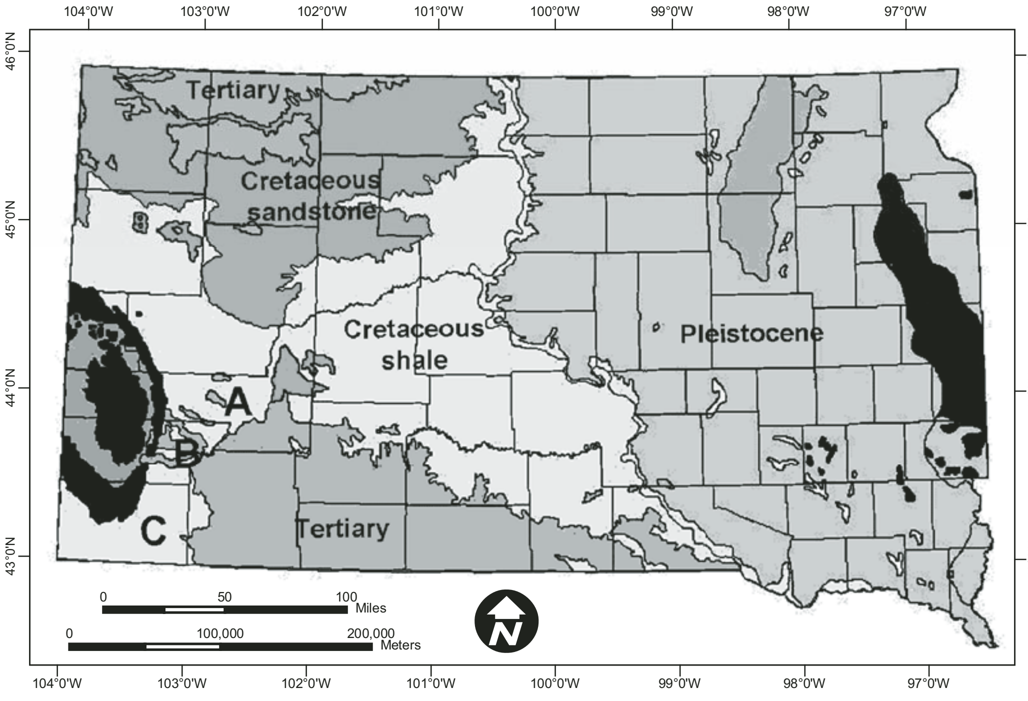

Figure 1. Generalized geologic map of South Dakota, showing counties with *Pteranodon* localities discussed in this study. A—Pennington County; B—Custer County; C—Fall River County. Modified from http://www.sdgs.usd.edu/digitalpubmaps/geomap.html.

V938: Whitley's Wash, Fall River County; (6) SDSM V8947–V8949: Conger Ranch, Fall River County; (7) SDSM V9115: Wallace Ranch locality 1, Fall River County; (8) SDSM V9116: Wallace Ranch locality 2, Fall River County; and (9) SDSM V9162: Alum Creek locality 1, Fall River County. The Wyoming specimens were collected from Mule Creek in Niobrara County near the South Dakota border.

STRATIGRAPHY

Pierre Shale Group

The Pierre Shale Group (Martin et al., this volume) is widely exposed in western South Dakota and was named by Meek and Hayden (1862) from exposures at Fort Pierre along the Missouri River. The Pierre Shale Group lies above the Niobrara Formation and below the Fox Hills Sandstone. Much of the section is composed of dark gray shales with bentonite layers (Martin et al., 1996). In the Black Hills area the group has eight formations: the basal Gammon Ferruginous, the Sharon Springs, the Mitten Black Shale, the Red Bird Silty, the lower unnamed, the Monument Hill Bentonitic, the Kara Bentonitic, and the upper unnamed. *Pteranodon* specimens have been found in the Gammon Ferruginous and Sharon Springs Formations and are the focus of this research (Fig. 2).

The Pierre Shale Group displays evidence of numerous disconformities (Martin, 1996). The bentonite layers help to determine the stratigraphic layers containing the fossils, and allow for determination of environmental and stratigraphic distribution of the *Pteranodon* fossils and their localities.

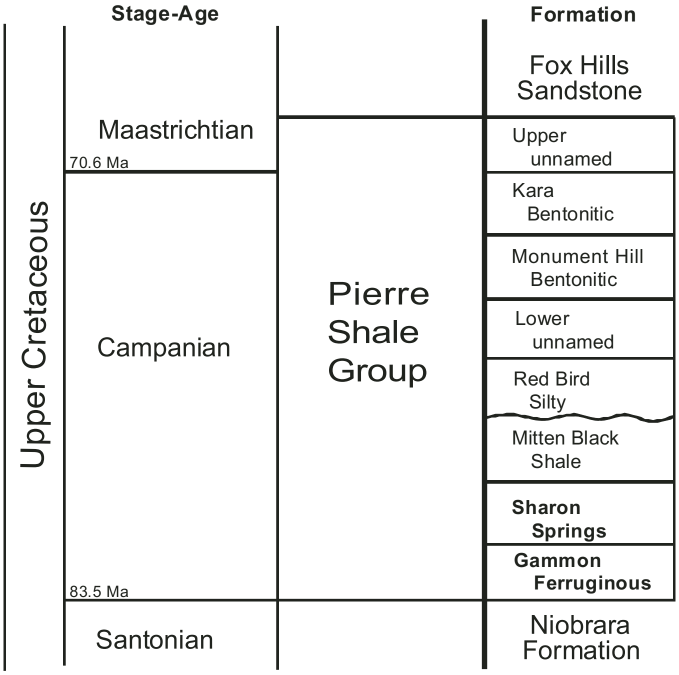

Figure 2. Stratigraphic column, showing the positions of the lower two formations of the Pierre Shale Group, which have produced *Pteranodon* fossils.

Gammon Ferruginous Formation

The basal unit of the Pierre Shale Group is the Gammon Ferruginous Formation, which is exposed in Wyoming, Montana, and South Dakota. The type locality is along Gammon Creek in Crook County, Wyoming (Agnew and Tychsen, 1965). Overall, the formation consists of dark gray mudstones and shales with some interbedded limestones and chalks, as well as numerous bentonites (Gaines, 1986). In the southern Black Hills, a 33 m measured section contained 13 bentonites, ranging from 1 to 90 cm thick (Bertog, 1997). This formation is bipartite: the lower unit is a dark gray mudstone and shale with iron concretions, and the upper unit (Fig. 3) is similar to the lower unit, except that the concretions are septarian (Gaines, 1986). The Gammon Ferruginous Formation contained 4 of the 19 pterosaur specimens of this study. The referred specimens are described in the Systematics section.

Sharon Springs Formation

Overlying the Gammon Ferruginous Formation is the Sharon Springs Formation. This formation is named from the type locality in western Logan County, Kansas, and was described as dark gray to black shales that are slightly bituminous (Gill et al., 1972).

The Sharon Springs Formation is divided into three intervals (Martin et al., 1996, 2004, this volume). Around the southern Black Hills the lowest interval is the Ardmore succession including the Ardmore bentonite, which is the basal bentonite of the formation and is usually ~3 m thick (Bertog, 1997; Bertog et al., this volume). The Ardmore succession usually consists of eight bentonites, each ~0.25 m thick (Bertog, 1997). The lithology comprises yellowish orange bentonites interbedded with shale (Martin et al., 1996). This succession is named for a quarry in Ardmore, South Dakota, and is used as a marker for Cretaceous rocks in the Great Plains (Gaines, 1986). The second unit of the formation consists of a vertically weathered shale with a thick bentonite couplet and concretionary zones. The bentonite couplets are ~0.25 m thick each and are a yellowish orange to grayish black bentonitic shale (Fig. 4). The concretionary unit is composed of gray to black shale with tan concretions (Fig. 5). The upper unit is composed of bentonite stringers (Fig. 6), composed of yellowish orange to grayish black bentonitic shale (Martin, 1996).

The overall geology of the Sharon Springs Formation is gray to black fissile shale, and the weathered rock rarely supports vegetation. The Sharon Springs Formation contains numerous fossil vertebrates, such as mosasaurs, fish, and birds (Martin et al., 1996). Invertebrate fossils are less common, because the anoxic conditions of the sea caused the dissolution of the calcareous shells and diagenesis (Gill and Cobban, 1966). However, some ammonite shells are preserved in concretions, particularly *Baculites obtusus*. Fifteen of the 19 pterosaur specimens were found in this member, and 9 have a detailed location. See referred specimens below.

Figure 3. Bentonite with associated concretions in the uppermost Gammon Ferruginous Formation of the Pierre Shale Group. White bracket indicates bentonite layer. Conger Ranch, Fall River County, South Dakota.

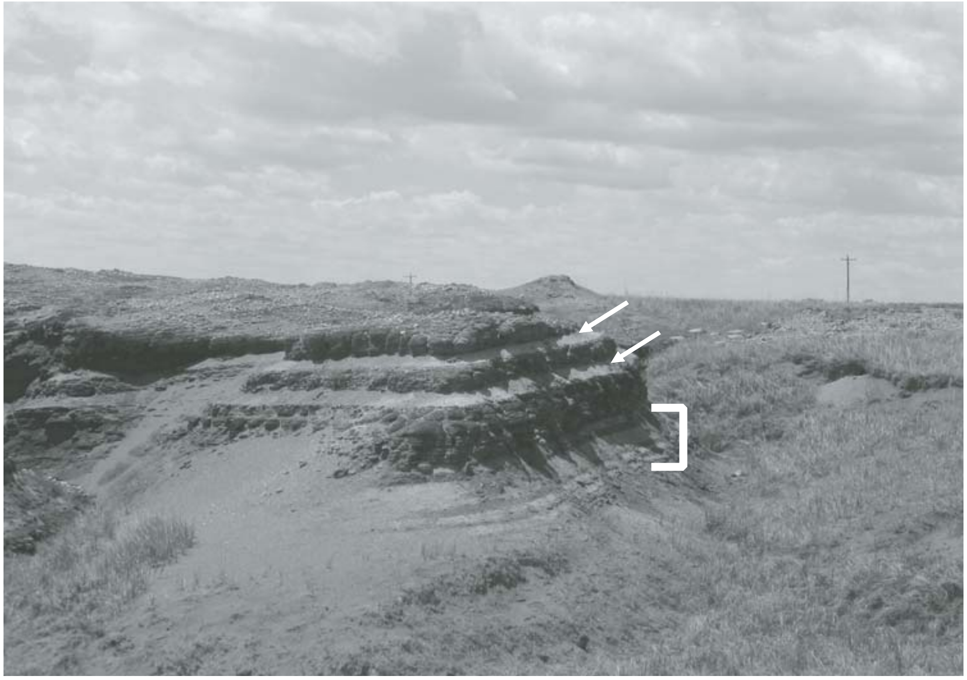

Figure 4. Bentonite couplet in the Sharon Springs Formation, shown with the white arrows. The white bracket indicates the Ardmore succession. Conger Ranch, Fall River County, South Dakota.

Figure 5. Concretionary layer in the Sharon Springs Formation. Conger Ranch, Fall River County, South Dakota.

SYSTEMATICS

Class Reptilia Linnaeus, 1758
Order Pterosauria Kaup, 1834
Suborder Pterodactyloidea Plieninger, 1901
Family Pteranodontidae Marsh, 1876
Genus *Pteranodon* Marsh, 1876
Species *Pteranodon longiceps* Marsh, 1876

Referred Specimens, Stratigraphic Occurrence, and Measurements

SDSM 497, distal metacarpal IV, and phalanges 1–3, from SDSM locality V491, in the Sharon Springs Formation; SDSM 5817, atlas-axis, anterior end of cervical vertebra, wing fragments, and the left knee joint, consisting of the interlocking distal femur and proximal tibia, from Wyoming, in the Sharon Springs Formation; SDSM 5818, posterior end of right ramus (articular surface: 19.21 mm, length: 90.64 mm, width: 12.98 mm), distal end of ulna, proximal end of ulna, left proximal carpal, left distal carpal, left distal metacarpal IV, right distal metacarpal, right proximal phalanx 1, and incomplete wing elements, from Wyoming, in the Sharon Springs Formation; SDSM 45719, a vertebra, scapula-coracoid, sternal fragment, humerus, 2 ulnae, 1 complete carpal, 3 distal carpals, a ?lateral carpal, metacarpal IV, distal metacarpal and carpal, ?metacarpal, 6 manual phalanges, femur, 5 metatarsi and fragments, pedal phalanx, ?ungual, unidentified fragments, and 2 fish vertebrae *(Enchodus),* from SDSM locality V926, 0.61–0.91 m above the Ardmore succession in the Sharon Springs Formation; SDSM 51141, the proximal end of a right femur, from SDSM locality V8121 in the Sharon Springs Formation; SDSM 54358, ulna, partial pubis, right and left femora, and right and left tibia, from Wyoming, in the Sharon Springs Formation; SDSM 56093, 5 wing fragments, from SDSM locality V9115, ~3.0–4.6 m below the Ardmore succession in the Gammon Ferruginous Formation; SDSM 56128, radius, metacarpal, metacarpal IV, 2nd and 3rd wing phalanges, and wing fragments, from SDSM locality V491 in the Sharon Springs Formation; SDSM 56224, partial dentary (articular surface: 29.93 mm, length: 238.7 mm, width: 48.8 mm), basicranium (articular surface: 15.13 mm, length: 43.1 mm, width: 59.04 mm), 11 skull fragments,

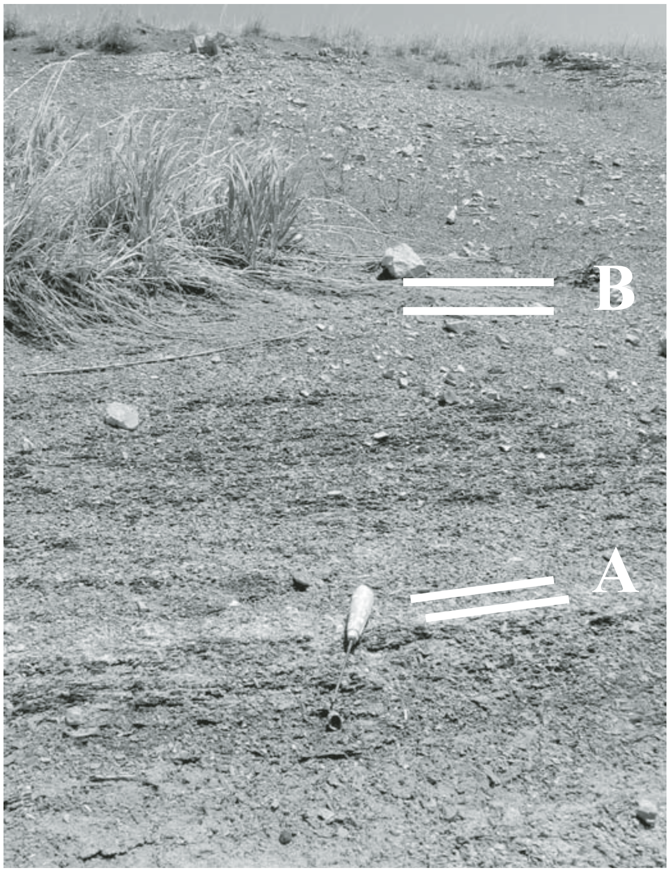

Figure 6. Bentonite stringers in the upper Sharon Springs Formation. A—lower bentonite stringer. B—upper bentonite stringer. The Mitten Black Shale Formation overlies the upper bentonite stringer. Conger Ranch, Fall River County, South Dakota.

and 4 wing fragments, from SDSM locality V938, near the 2nd stringer in the Sharon Springs Formation; SDSM 56225, 5 wing fragments, 4 with articular surfaces, from SDSM locality V938, near the 2nd stringer in the Sharon Springs Formation; SDSM 69038, a partial wing element, from SDSM locality V9115, just above the Ardmore succession in the basal Sharon Springs Formation; SDSM 69039, 5 wing fragments, from SDSM locality V9116, 0.91 m above 2nd bentonite stringer in the upper Sharon Springs Formation; SDSM 69040, a jaw fragment, ?carpal, distal phalanx, and fish vertebrae *(Enchodus),* from SDSM locality V9116, 0.76 m above 2nd bentonite stringer in the upper Sharon Springs Formation; SDSM 69041, 2 humeri, from SDSM locality V491, 7.0 m below the Ardmore succession in the Gammon Ferruginous Formation; SDSM 69042, 2 manual phalanges, from SDSM locality V614, from 0.74 m below the base of the 2nd bentonite stringer in the Sharon Springs Formation; SDSM 69043, 2 partial wing elements, from SDSM locality V9162, in the upper part of the Gammon Ferruginous Formation; SDSM 69044, a complete metacarpal IV, from SDSM locality V8947 in the concretionary layer in the Sharon Springs Formation; SDSM 69045, proximal humerus, ulna, radius, and proximal metacarpal, from SDSM locality V8949, 0.61 m below the Ardmore succession in the Gammon Ferruginous Formation; and SDSM 69046, 2 wing elements without articular surfaces, from SDSM locality V8948, ~1.83 m below the bentonite couplet in the Sharon Springs Formation.

Discussion

Most of the *Pteranodon* bones are associated wing elements and have been relatively well preserved. Although many have been crushed or flattened, most are still identifiable by their complete articular surfaces. A few of the specimens are highly gypsiferous and not well preserved. SDSM 56224 is the distal portion of the lower jaw and is well preserved. The basicranium, SDSM 56224, is also well preserved and contains the occipital condyle (Fig. 7). Two specimens, SDSM 69042 and 45719, contain associated vertebrae belonging to the fish *Enchodus*.

According to Wellnhofer (1991), there are eight species of *Pteranodon: P. longiceps* (Marsh, 1876), *P. eatoni* (Miller, 1972), *P. ingens* (Marsh, 1872), *P. marshi* (Miller, 1972), *P. occidentalis* (Marsh, 1872), *P. oregonensis* (Gilmore, 1928), *P. sternbergi* (Harksen, 1966), and *P. walkeri* (Miller, 1972). Bennett (1994) reviewed these taxa and suggested that the only valid species are *P. longiceps* and *P. sternbergi,* and that species are often determined only by comparing skull crest characteristics because the postcranials are so similar.

S.C. Bennett examined nearly all of the University of Kansas specimens of *Pteranodon* and found a significant amount of variation in size, cranial morphology, size and shape of the cranial crest, and morphology of the pelvis. From this material he generated two size classes, differentiating male and female types. The presumed males had a larger body size as well as large crests, and the females had a smaller body size and a large pelvic canal (Bennett, 1992, 1993). Bennett (1996) contended that two species exist on the basis of the orientation of the crest and the stratigraphy. *P. longiceps* had a bulbous crest that is directed up and is found in the upper part of the Smoky Hill Chalk Member of the Niobrara Formation and the Sharon Springs Formation of the Pierre Shale Group. The upper margin of the SDSM 56224 dentary (Fig. 7) is concave down, similar to examples of *P. longiceps*.

TAPHONOMY

Most *Pteranodon* bones recovered are associated wing elements. The forelimb, shoulder girdle, and sternum of most extant animals commonly remain articulated longer than other skeletal portions (Lyman, 1994). A skeletal element comparison of the SDSM specimens showed that 13 of 19 total specimens (64%) consist only of associated wing elements. Hindlimb elements represent the second highest percentage, with 10%. The remaining percentages of the pterosaur fossils include associated skull fragments found with wing bones, parts of the axial skeleton, and a partial skeleton. Two contributing factors may aid in the expla-

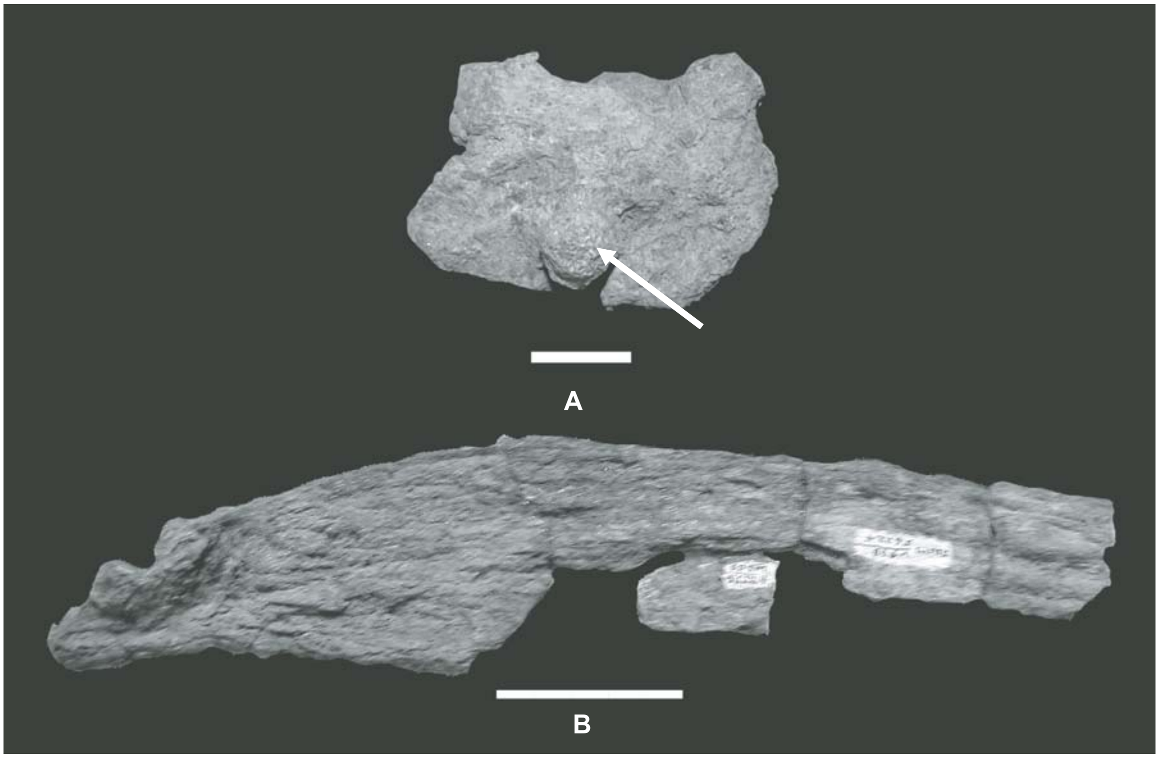

Figure 7. SDSM 56224. (A) Basicranium; white arrow shows occipital condyle; scale bar is 2 cm. (B) Dentary; scale bar is 5 cm.

nation of the abundance of wing elements in comparison with axial elements.

The first factor is the existence of a predatory preference. As in modern birds, the muscle mass of *Pteranodon* was concentrated in the chest, as a greater mass was needed for flight, and a high muscle mass throughout the wings and body would have made the reptile too heavy to fly. The wing membrane, in comparison with fleshier body parts, may not have offered as much sustenance to predators. In the effort to maximize food intake and minimize energy, predators often choose the fleshier body parts, such as the axial body, leaving the wings behind. Examples of the predatory preference factor include the wing complexes of a tern (Fig. 8A) and a penguin (Fig. 8B) from Antarctica, in which the axial and hindlimb portions were preyed upon and the wings remained intact. The other bones are free of any flesh, showing the sturdiness of the wing and the predatory preference for the axial portions. A wing covered in feathers and a wing covered in scales do not directly correlate, but the connective tissue required to stabilize the wing during flight would be required of both.

The second factor is that the wing membrane would secure the wing elements in place, whereas other elements were free to decompose and fall away. Pterosaur wing structure and function have been discussed in detail by numerous authors (Wellnhofer, 1991; Padian and Rayner, 1993; Bennett, 2000) and summarized by Chatterjee and Templin (2004). The wing membrane, or patagium, of pterosaurs was ~1 mm thick and consisted of three layers of tissue: an epidermis, a dermis with a vascular layer, and

Figure 8. Modern examples of predatory preference and strong connective tissue of wings. (A) Tern wings, showing predatory preference. James Ross Island, Antarctica. Photo courtesy of Amanda Cordes-Person, Sam Noble Oklahoma Museum of Natural History. (B) Penguin wing, showing the stability of the wing as well as predatory preference. James Ross Island, Antarctica.

muscle fibers (Martill and Unwin, 1989), adding strength to the wing (Chatterjee and Templin, 2004). In this case the patagium, which is composed of several layers including the actinofibrils (Tischlinger and Frey, 2002), apparently served as a protective layer over the bones until burial. The abundant number of individuals consisting only of associated wing elements is indicative of strong connective tissue, which was disregarded while they were preyed upon.

Although pterosaur wing elements may be more readily identified and collected, the abundance of wing elements is not a result of a collection bias. Every effort was made to thoroughly collect from the fossiliferous areas. Therefore, on the basis of this sample of individuals, a predatory preference for the axial elements, the protection of the forelimb by the patagium, and the strong connective tissue resulted in the abundance of preserved wing elements.

BEHAVIOR

The circumstances of deposition of some fossils, such as mosasaurs, a plesiosaur, and pterosaurs in the Pierre Shale, have allowed for the preservation of stomach contents. Gastric residues from a tylosaurine mosasaur were found in the Gammon Ferruginous Formation of the Pierre Shale Group (Martin and Bjork, 1987; Martin, 1994). The stomach contents included fish; *Platecarpus,* another mosasaur; *Hesperornis,* a diving bird; and possible shark remains. The mosasaur *Platecarpus* was found in a bentonite bed in the Sharon Springs Formation, and it contained fish remains. Another mosasaur, *Globidens,* contained pelecypods (Martin, 1994; Martin and Fox, this volume). A pliosaur from a bentonite bed in the Gammon Ferruginous Formation contained gastroliths and fish (Martin, 1994). An elasmosaur (NJSM 15435) was found in the Sharon Springs Formation of the Pierre Shale Group in Logan County, Kansas, containing fish fragments, including *Enchodus,* and gastroliths (Cicimurri and Everhart, 2001).

Two pterosaur specimens (SDSM 45719 and SDSM 69040) have been found in association with fish vertebrae. The vertebrae closely resemble those of the Late Cretaceous fish *Enchodus,* because they have double struts along the vertebral body as well as a projection on the dorsal side (Fig. 9). *Enchodus* is a common fish in the Sharon Springs Formation of the Pierre Shale Group, whose sediments formed on the ocean bottom. Although fish bones are abundant, these specimens may represent pterosaur stomach contents.

Relatively complete *Enchodus* skeletons are known, with the pectoral girdle well preserved. The pectoral girdle is very large for

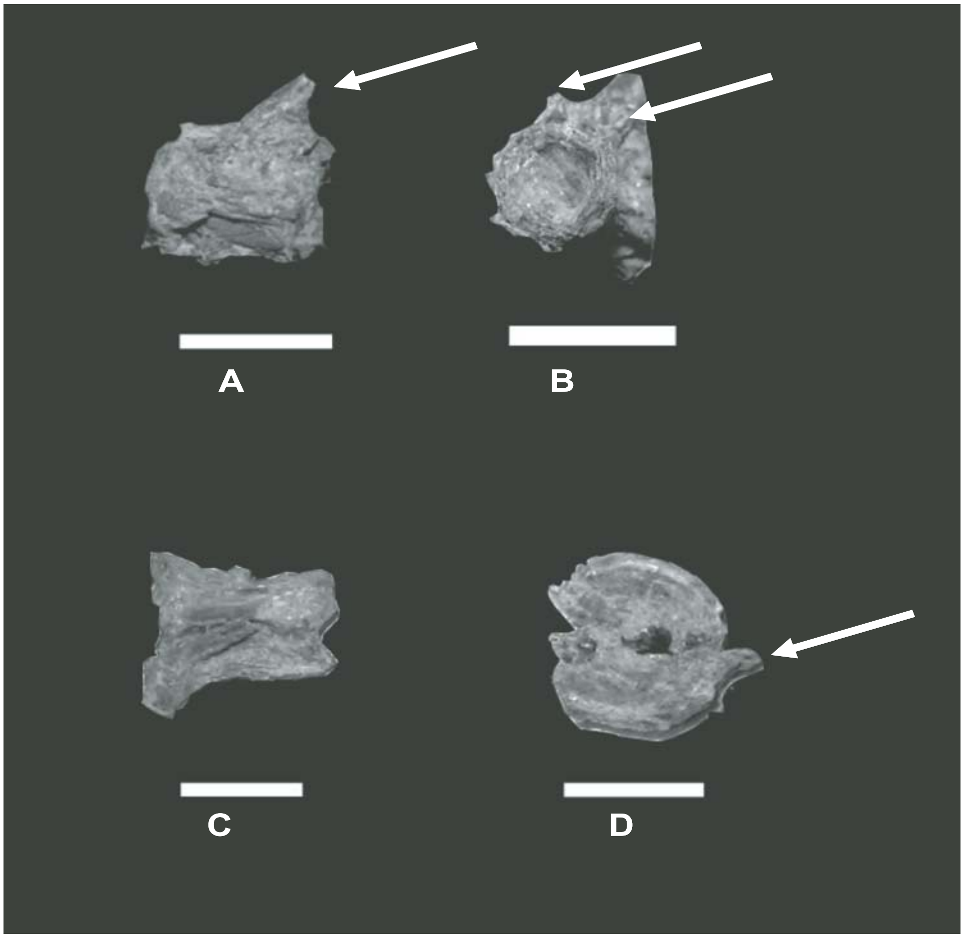

Figure 9. *Enchodus* vertebra associated with *Pteranodon* specimen. (A, B) Vertebra from SDSM 45719; single arrow points to the large projection on the dorsal side, and double arrows indicate the double struts along the vertebral body. (C, D) Vertebra from SDSM 69040; arrow points to the large projection on the dorsal side. All scale bars are 1 cm.

its body size (Fig. 10) and is interpreted as allowing the fish to jump, or "fly" from the water, as do modern flying fish (see Parris et al., this volume, Chapter 7). Therefore, one can infer that *Enchodus* was a surface swimming fish, making it easy to prey for pterosaurs.

BIOSTRATIGRAPHY

Table 1 represents a composite of the original stratigraphic locations of all pterosaur specimens at the Museum of Geology, SDSM. Detailed stratigraphic data are available for all but six specimens, and these six were collected in the 1940s and 1950s. Three are from localities in Wyoming, and the remaining three were collected in South Dakota before detailed stratigraphic notes were taken.

The lowest known stratigraphic occurrence of these *Pteranodon* specimens is in the Gammon Ferruginous Formation, 7.0 m below the Ardmore succession. The highest stratigraphic occurrence is found in the uppermost Sharon Springs Formation, 0.91 m above the second bentonite stringer. Four of the 19 specimens were within the Gammon Ferruginous Formation, and the remaining 15 were found throughout the Sharon Springs Formation.

The range of *Pteranodon* is limited to the Western Interior Seaway, the Atlantic Coast, and the Gulf Coast of North America. *Pteranodon* is found in the Sharon Springs Formation of the Pierre Shale Group in Wyoming, South Dakota, and Kansas. In Nebraska, specimens have usually been found in the Smoky Hill Chalk of the Niobrara Formation (Bennett, 1994). However, only two South Dakota specimens have been found in this unit. Fragmentary pterosaur specimens have been found on the Atlantic and Gulf Coasts, although the identification is not certain. Possible *Pteranodon* specimens have been found in the Mooreville Formation in Alabama and the Merchantville Formation in Delaware. The North American extent of *Pteranodon* parallels that of the local biostratigraphy in southwestern South Dakota (Bennett, 1994).

CONCLUSIONS

The South Dakota School of Mines pterosaur specimens are *Pteranodon longiceps* on the basis of size and cranial and morphology. The skull material in the SDSM collection, although fragmentary, represents the first *Pteranodon* skull material reported from the Pierre Shale Group of South Dakota.

All of the SDSM pterosaur specimens were collected from the lower two formations of the Campanian Pierre Shale Group. Of the 19 specimens, 4 were found in the Gammon Ferruginous Formation, and 15 in the Sharon Springs Formation. The lowest occurrence of *Pteranodon* was 7.0 m below the Ardmore succession. The highest occurrence was 0.91 m above the second bentonite stringer in the upper part of the Sharon Springs Formation.

Preferential preservation of wing elements is evident. Most of the *Pteranodon* specimens, including 64% of those from the Museum of Geology, consist of associated wing elements. The actinofibril layer of the patagium would secure the wing elements during decomposition. Predators may have chosen to eat the body parts with more muscle mass rather than the patagium. This abundance of wing elements results from a combination of a preservational bias and predatory preference.

Inferring the behavior of animals from fossils is often difficult. The lifestyles of two of the pterosaur specimens in this sample may be interpreted on the basis of direct evidence. These two specimens contain associated fish bones belonging to *Enchodus,* a common fish found in the Sharon Springs Formation. These specimens represent the first *Pteranodon* stomach contents known

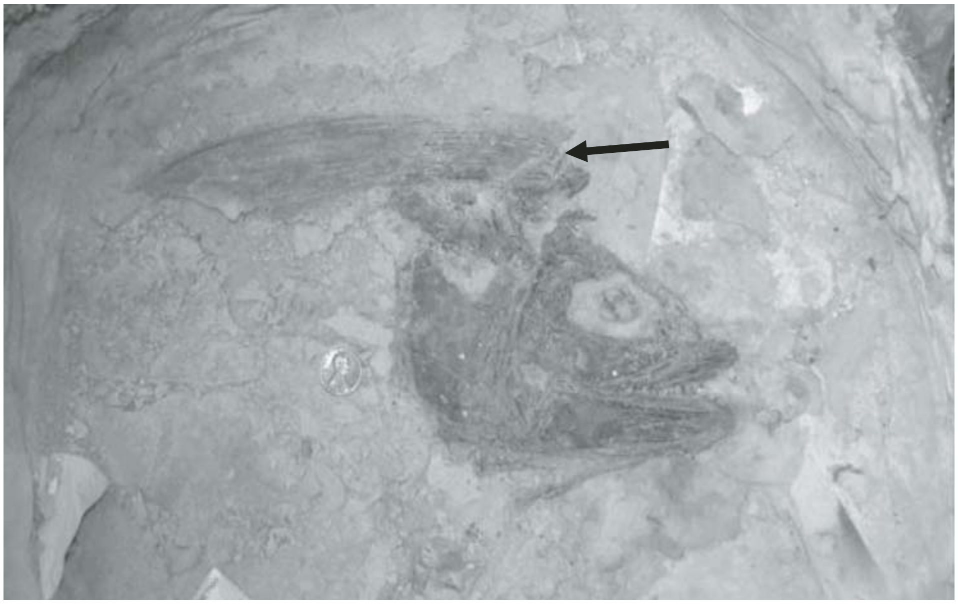

Figure 10. *Enchodus* specimen, NJSM 18777. Black arrow indicates the large pectoral appendage. Photo courtesy of David C. Parris, New Jersey State Museum (NJSM).

TABLE 1. COMPOSITE COLUMN DEMONSTRATING STRATIGRAPHIC POSITION OF *PTERANODON* SPECIMENS

	Formation	Specimen Number	Location
	Mitten Black Shale		
Sharon Springs		SDSM 69039	0.91 meters above second bentonite stringer
		SDSM 69040	0.76 meters above second bentonite stringer
	Bentonite stringers	SDSM 56224	2nd stringer of the Sharon Springs
		SDSM 56225	2nd stringer of the Sharon Springs
		SDSM 69042	0.74 meters below base of second bentonite stringer
	Concretionary layer	SDSM 69044	Concretionary layer
	Bentonite couplet	SDSM 69046	1.83 meters below bentonite couplet
		SDSM 45719	0.61–0.91 meters above Ardmore succession
	Ardmore succession	SDSM 69038	Just above Ardmore succession
	Gammon Ferriuginous	SDSM 69043	Upper part of the Gammon Ferruninous
		SDSM 69045	0.61 meters below Ardmore succession
		SDSM 56093	3.0–4.6 meters below Ardmore succession
		SDSM 69041	7.0 meters below Ardmore succession

The following specimens were collected in the 1940s–1950s and do not have detailed stratigraphic locations.

Specimen Number	Member
SDSM 497	Sharon Springs
SDSM 5817	Sharon Springs
SDSM 5818	Sharon Springs
SDSM 51111	Sharon Springs
SDSM 54358	Sharon Springs
SDSM 56128	Sharon Springs

Note: Thicknesses are not to scale.

from South Dakota. Based upon their well preserved pectoral girdle, these fish may have been "flying fish," which were near-surface fish. Hence, *Pteranodon* could have flown near the surface of the water and used its long jaws to capture the fish.

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A new species of the diving bird Baptornis *(Ornithurae: Hesperornithiformes) from the lower Pierre Shale Group (Upper Cretaceous) of southwestern South Dakota*

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ABSTRACT

Fossil birds are relatively rare in Cretaceous deposits of the Northern Great Plains, so the discovery of a large, new diving bird was unexpected. From marine deposits of the Niobrara Formation in Kansas a small diversity of birds was known, but until now the large diving bird, *Hesperornis,* was the only bird taxon known from the Pierre Shale Group of South Dakota. The new discovery, a partial skeleton of another diving bird, *Baptornis,* was secured from the Sharon Springs Formation (lower middle Campanian) of the Pierre Shale Group in Fall River County, South Dakota. The specimen is represented by vertebrae, pelvic fragments, and lower leg elements that are similar to but much more robust than *Baptornis advenus* from the subjacent Niobrara Formation. The new taxon is nearly twice the size of the Niobrara species, principally in robustness rather than in length of elements. Overall, the specimen represents the first occurrence of *Baptornis* from the Pierre Shale Group, represents a new species, and indicates a greater diversity of birds from the Pierre Shale Group than was previously known.

Keywords: *Baptornis,* Pierre Shale Group, Late Cretaceous, South Dakota, new species.

INTRODUCTION

The Cretaceous toothed diving bird *Hesperornis* is well represented in the Pierre Shale Group (see Martin et al., this volume, for stratigraphic nomenclature) of South Dakota, and in the past 25 yr stratigraphic collections produced under the direction of the first author from the Niobrara Formation and the Pierre Shale Group have produced numerous postcranial specimens. Although most of these specimens from South Dakota remain undescribed, *Hesperornis* was heretofore the only recognized bird from the Pierre Shale Group of South Dakota (Macdonald, 1951; Green, 1962; Martin and Bjork, 1987). From the subjacent Niobrara Formation in South Dakota the first *Hesperornis* was described relatively recently (Martin and Varner, 1992a), and *Ichthyornis* was recorded by Martin et al. (1998). The specimen reported here is the first occurrence of another genus of toothed diving bird, *Baptornis,* a new species from the Pierre Shale Group. The genus is yet to be discovered in the Niobrara Formation of South Dakota.

In 1991 the Museum of Geology, South Dakota School of Mines and Technology (SDSM), conducted paleontological surveys and salvage of fossiliferous Late Cretaceous marine deposits (Gries and Martin, 1985) in Fall River County, South Dakota, for the U.S. Forest Service, Nebraska National Grasslands. This contribution is the result of efforts partially funded through these

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surveys. Owing to their fossiliferous nature, the field surveys were concentrated on the lower portion of the Pierre Shale Group, including the Sharon Springs Formation. From this formation a partial postcranial skeleton of a large *Baptornis,* SDSM 68430 (Martin and Varner, 1992b), was discovered near the town of Ardmore, South Dakota (Fig. 1).

The Sharon Springs Formation of the Pierre Shale Group is a much more complex stratigraphic unit than we considered before the initiation of our surveys. Geological observations during the paleontological investigations revealed a number of disconformities within this unit in the southern Black Hills (Martin, 1996). Essentially, the Sharon Springs Formation in the Black Hills area of South Dakota and eastern Wyoming lies between the Gammon Ferruginous Formation below and the Mitten Black Shale Formation above. The base of the Sharon Springs in this area is represented by the Ardmore bentonite succession, whose name was derived from the area in which the avian skeleton was secured. This bentonite has been radiometrically dated at ca. 81 Ma (Obradovich, 1993), and this interval of bentonites has been utilized as a marker across the Northern Great Plains; a disconformity lies subjacent. A number of intra–Sharon Springs Formation unconformities exist, and the suprajacent Mitten Black Shale Formation is characterized by a basal disconformity with great differential preservation at the contact. This disconformity is normally expressed as a fossiliferous hash and can be observed to have cut down to the Ardmore bentonite succession or only into the upper part of the Sharon Springs Formation. At the top of the Sharon Springs Formation are very thin bentonite layers, informally termed by the first author as bentonite stringers (e.g., Martin et al., 1996). Normally, at least two of these stringers lie in the Sharon Springs Formation, and the bird skeleton described herein was found just above the second of these stringers. This interval of the shale has been correlated as lower middle Campanian (Cobban, 1993; Dyman et al., 1994).

Baptornis is a rear-limb-propelled diving bird in the same order, Hesperornithiformes, as the better represented genera *Hesperornis* and *Parahesperornis* (Martin and Tate, 1976; Martin, 1984). *Baptornis* is relatively rare, and until this specimen was found the taxon was known principally from the Smoky Hill Member of the Niobrara Formation of Kansas, which is the upper member of the formation, lying stratigraphically below the Pierre Shale Group. Earlier authors (Brodkorb, 1963; Martin and Tate, 1976; Galton and Martin, 2002) indicated that the specimens from the Smoky Hill Member were Coniacian in age. However, Bryant (1983) took issue with the age, and following Hattin (1979, 1982) indicated that the occurrences could also be Santonian–early Campanian (e.g., Stewart, 1990; Dyman et al., 1994). The taxon is rare even in the Niobrara Formation of Kansas, and, as stated by Martin and Tate (1976) and Martin and Bonner (1977), *Baptornis advenus* is known only from Wallace, Logan, and Gove Counties in Kansas.

Baptornis was originally described from the Niobrara Formation of Kansas (Marsh, 1877), and nearly every North American specimen has subsequently been found from this formation. However, the taxon appears to have survived into the later Cretaceous and is found in the Judith River Formation of Saskatchewan, Canada (Tokaryk and Harrington, 1993). Other baptornithids include *Pasquiaornis* from the Cenomanian of Saskatchewan, which appears to have been less well adapted for diving than the later occurring *Baptornis* (Tokaryk et al., 1997). *Neogaeornis*

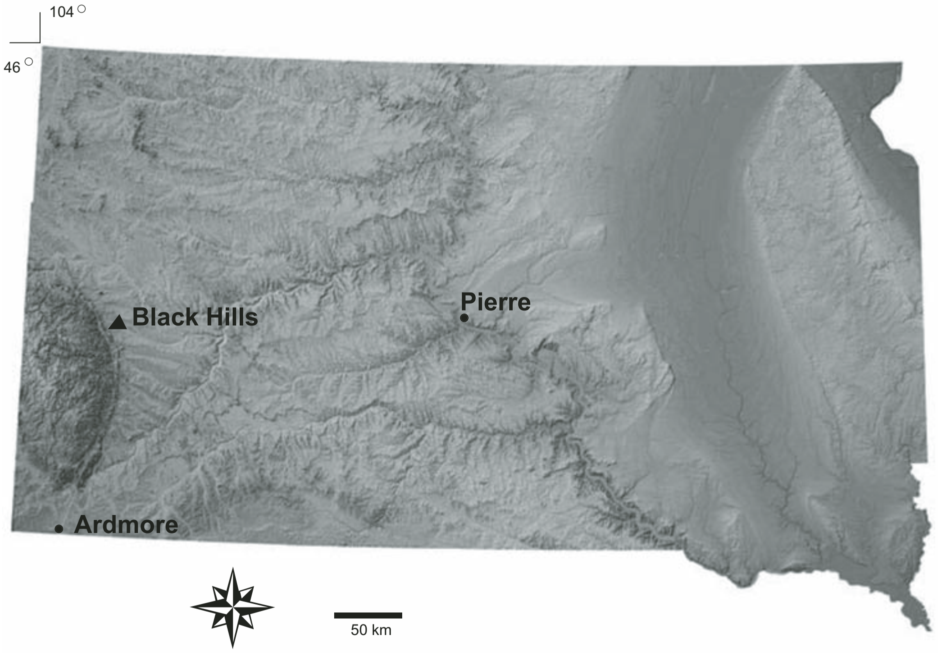

Figure 1. State of South Dakota, illustrating the town of Ardmore in the southwestern part of the state, where SDSM 68430 was derived.

from the Late Cretaceous of Chile (Lambrecht, 1929) has also been considered a member of the Baptornithidae, but the tarsometatarsus (the only material of *Neogaeornis*) is more greatly compressed, and configuration of the trochlea differs substantially from that of *Baptornis* (Olson, 1992). In any event, the tarsometatarsus of *Neogaeornis* is more greatly compressed than that of *B. advenus* or the species described herein.

The reconstruction of the new specimen and that of the only previously described species, *Baptornis advenus,* showcases reduced wing elements, a sternum without a keel, greatly expanded rear limbs, and a toothed jaw. The taxon possesses postcranial characters typical of a foot-propelled diving bird such as those of the Common Loon and the Pied-billed Grebe, particularly in possession of a proportionally small femur and elongate tibiotarsus and tarsometatarsus. The leg bones are apneumatic, the postacetabular portion of the sacrum is long and narrow, and the short, broad femur is ventrolaterally oriented with a broad, continuous patellar groove and enlarged fibular condyle. The long tibiotarsus possesses a large, laterally expanded cnemial crest. Foot-propelled diving birds are characterized by an elongation of the crest associated with shortening of the femur (Baumel, 1993). The taxon described herein exhibits all of these characters (Fig. 2). However, members of the Baptornithidae can be differentiated by a number of characters. *Pasquiaornis* exhibits a femoral trochanteric ridge close to the shaft, a proximal femur that is only slightly expanded lateromedially, an anteriorly positioned intercotylar prominence of the tarsometatarsus that overhangs the shaft, and a tarsometatarsus with the second trochlea posteriorly positioned adjacent to the base of third trochlea (Tokaryk et al., 1997). *Baptornis advenus* can be characterized by heterocelous thoracic vertebrae, a relatively slender, cranioventrally and laterally directed femur, a subcircular femoral cross section, a smooth patellar groove, a small medial femoral condyle in comparison with the lateral condyle, a tibiotarsus with the distal end inflected (shared with *Parahesperornis*), a tarsometatarsus with a proximal cap and nearly equal-sized trochleae with lateral and medial trochleae approximately the same length, a lack of crescent and peg articulation on phalanges of the 4th digit, and incipient toe rotation (Galton and Martin, 2002).

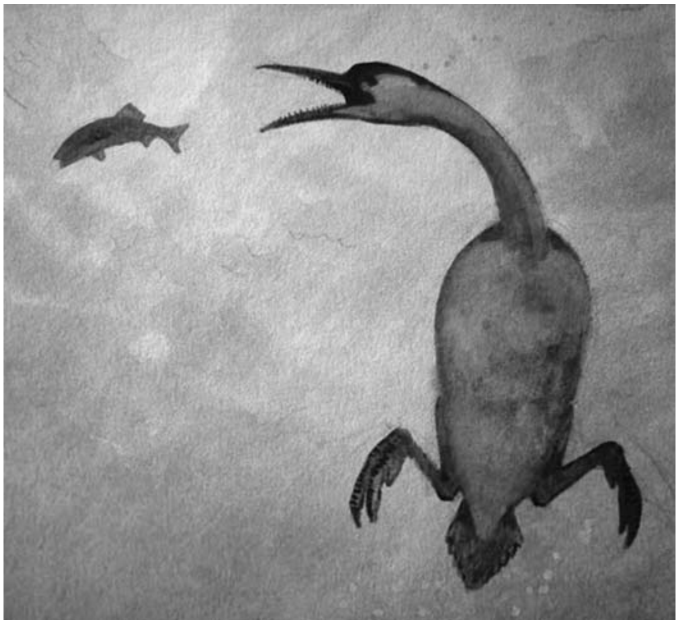

Figure 2. (*continued on the next page*) Reconstruction of *Baptornis varneri* by Daniel Varner and reconstruction of skeleton of *Baptornis advenus,* modified from Martin and Tate (1976), illustrating elements represented by SDSM 68430. Vertebral positions approximated; proximal left femur not illustrated.

Institutional Abbreviations

FMNH: Field Museum of Natural History, Chicago; **KUVP:** University of Kansas, Museum of Natural History, Lawrence; **SDSM:** Museum of Geology, South Dakota School of Mines and Technology, Rapid City; **UNSM:** University of Nebraska State Museum, Lincoln.

SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758
Ornithurae Haekel, 1866
Hesperornithiformes Furbringer, 1888
Baptornithidae American Ornithologists' Union, 1910
Baptornis Marsh, 1877
Baptornis varneri n. sp.

Holotype. SDSM 68430, *Baptornis varneri,* n. sp. (Figs. 3, 4), partial postcranial skeleton including cervical and thoracic (dorsal) vertebrae, ribs, and an almost complete right hindlimb composed of the following: posterior portions of the synsacrum-pelvis, partial femur, tibiotarsus, fibula, and tarsometatarsus.

Stratigraphic occurrence. Just above second bentonite stringer, uppermost Sharon Springs Formation of the Pierre Shale Group (see Martin et al., 1996).

Age. Early medial Campanian.

Locality. SDSM locality V9131, Fall River County, South Dakota.

Etymology. Named for Daniel Varner, who found the specimen, and for his notable contributions to paleontology in the form of artistic renderings of extinct vertebrates.

Diagnosis. A baptornithid with elongate cervical vertebrae; with head and tuberculum of ribs well separated; with antitrochanter of pelvis indistinct, open acetabulum, acetabulum with vertical sides, ischium smoothly merging with antitrochanter, ischium with indistinct anterior fossa; with femur possessing broad, smooth

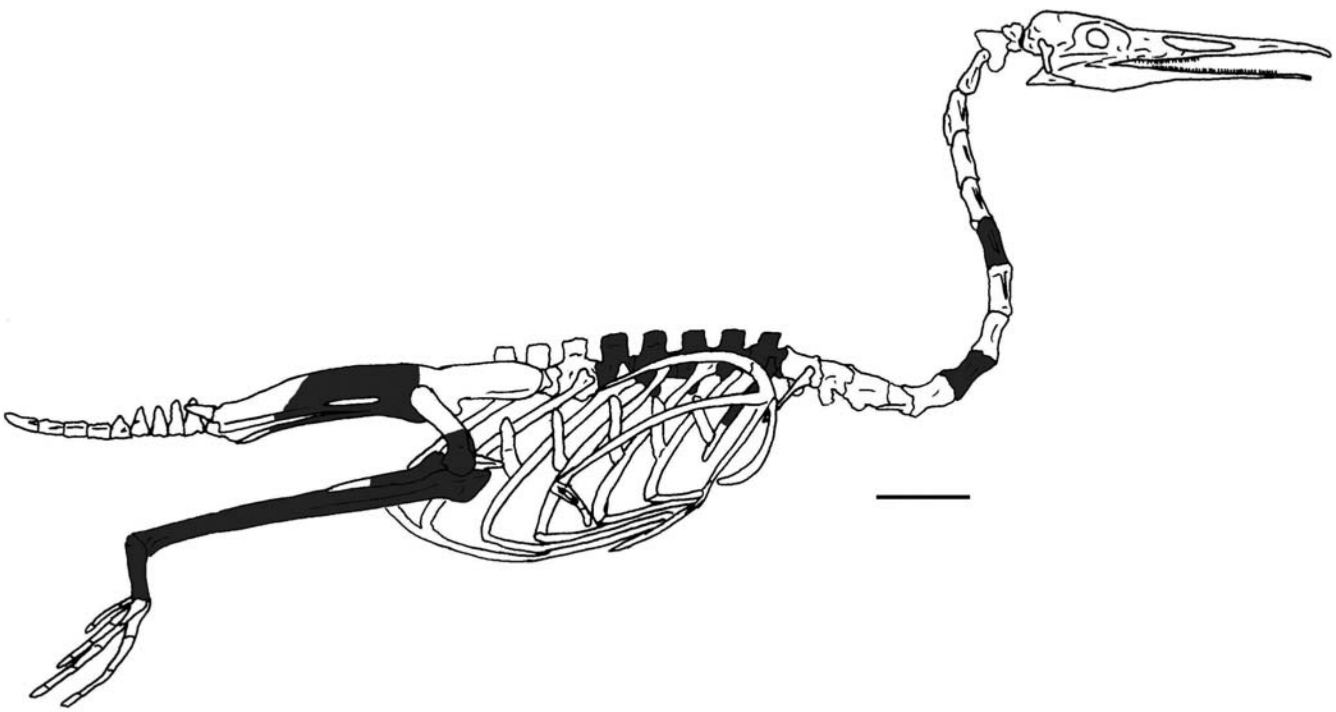

Figure 2. (*continued*)

popliteal fossa, wide and deep intercondylar fossa, prominent internal condyle; tibiotarsus with expanded proximal articulation, long straight fibular crest extending at least half the length of the shaft, and shallow, wide facet for articulation with fibula; and tarsometatarsus with proximal foramina, intertrochlear notches extending proximally to near the midpoint of shaft and with midpoint of shaft narrowing to a "waist." Some characters may be due to preservation, and others may be altered once the range of variation becomes known following the discovery of additional specimens.

Description. VERTEBRAE: A number of isolated vertebrae were associated with this skeleton. At least two anterior cervical vertebrae lacking neural processes are among their number; one is very elongate (Fig. 3A, B), more so than those of *Hesperornis,* and in comparison with those of *Hesperornis,* the specimen probably represents a vartabra from within the interval from 3 to 6 in the cervical series (see Marsh, 1880). The other cervical is most likely from the interval of cervicals 7 through 10. In neither are vertebrarterial foramina preserved, unlike the condition of *Hesperornis*. A number of isolated posterior cervicals are also represented and are provisionally assigned within the vertebral series on the basis of comparison with the known series of *Hesperornis* (Marsh, 1880). These have short centrae, no neural processes, and are shorter than the anterior cervicals. One compares most favorably with cervical 14 of *Hesperornis,* with a short neural arch, wide prezygopophyses, and roots for doubled hypapophyses. An important feature of this vertebra is a small pit on the posterior centrum similar to that illustrated for *Baptornis advenus* (Martin and Tate, 1976, p. 41) and unknown among herperornithids. A shorter vertebra may represent cervical 15, which has large hypapophyses (Fig. 3C). This vertebra also exhibits the posterior pit (?notochord remnant) on the centrum. Another vertebra resembles cervical 16 of Marsh (1880) but differs from all *Hesperornis* vertebrae in possessing a laterally long, dorsoventrally compressed anterior centrum articulation. As a result, the prezygopophyses are widely separated, and the diapophyses are anteroposteriorly short but robust. A small neural spine appears to have been present, and the costal pit is relatively low on the lateral side. A robust, but probably short hypapopyhysis appears to have been present. This vertebra, too, has a pit on the posterior centrum.

One vertebra is unusual in possessing what appear to be accessory spines (Fig. 3D, E). The vertebra is probably a distal cervical or anterior dorsal (compare with cervical 17 of Marsh, 1880). The neural arch is very wide, and a large neural process appears to have been present, based upon the broken root that extends anteroposteriorly the length of the neural arch and is relatively wide. From the wide neural arch a wide diapophysis flares laterally and slightly posteriorly. However, another set of long, narrow, spinelike processes extends directly laterally from the base of the neural arch opposite the neural canal and originates just above the dorsal corners of the centrum. No other vertebrae possess this structure, and perhaps rib fragments or uncinate processes are plastered against the vertebra. However, the symmetrical nature of these processes makes such a coincidence questionable. The vertebra also exhibits a dorsoanterior costal pit on

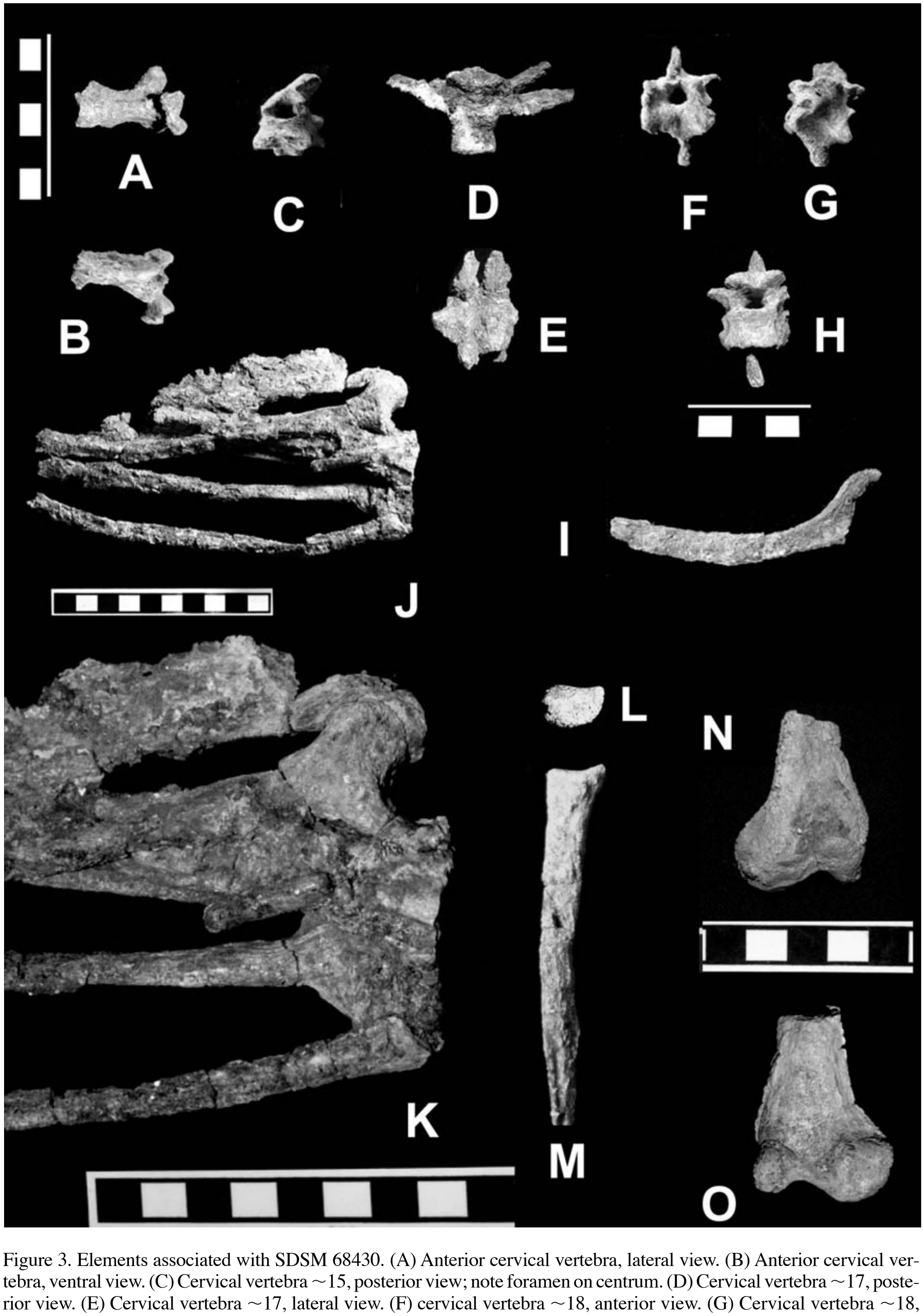

Figure 3. Elements associated with SDSM 68430. (A) Anterior cervical vertebra, lateral view. (B) Anterior cervical vertebra, ventral view. (C) Cervical vertebra ~15, posterior view; note foramen on centrum. (D) Cervical vertebra ~17, posterior view. (E) Cervical vertebra ~17, lateral view. (F) cervical vertebra ~18, anterior view. (G) Cervical vertebra ~18, lateral view. (H) Cervical vertebra ~18, posterior view. (I) Rib. (J) Pelvessynsacrum. (K) Enlargement of anterior right innominate, illustrating acetabulum, antitrochanter, and anterior portions of ischium and pubis. (L) Right fibula, dorsal view. (M) Right fibula, lateral view. (N) Right femur, anterior view of distal portion, illustrating patellar groove. (O) Right femur, posterior view of distal portion. Centimeter scale for Figure 3A–H is lateral to Figure 3A and below Figure 3H. Scale for Figure 3I, L–O is below Figure 3N.

Figure 4. Elements associated with SDSM 68430. (A) Right tibiotarsus, anterior view. (B) Right tibiotarsus, medial view. (C) Right tibiotarsus, lateral view. (D) Right tibiotarsus, posterior view. (E) Right tarsometatarsus, anterior view. (F) Right tarsometatarsus, posterior view. (G) Right tarsometatarsus, anterior view, proximal portion. (H) Right tarsometatarsus, posterior view, distal portion. Centimeter scale for Figure 4A–D is below Figure 4D.

the lateral side as well as a prominent hypapophysis. Gypsum encrustation prevents assessment of the state of the pit of the posterior centrum.

A vertebra with a prominent hypapophysis compares favorably with vertebra 18 of Marsh (1880), considered the 1st dorsal (Fig. 3F–H). The neural arch of this vertebra is as wide as the centrum and exhibits a squared dorsal outline (Fig. 3F). A long, high, narrow neural spine is preserved, as is the long ventral hypapophysis. The diapophyses are shorter, and a high anterodorsal costal pit appears similar to that on ?cervical 17 previously described. Interestingly, a pitlike depression occurs on the anterior centrum articular surface (Fig. 3F) and probably on the posterior centrum as well. Other fragmentary vertebrae have relatively short centra, suggesting posterior cervicals or anterior dorsals (thoracics), but not enough is preserved to be certain. Many of the posterior centra of these vertebrae exhibit similar pits.

Overall, the anterior vertebrae are all distinctly heterocelous and resemble those in the series known for *Hesperornis,* but the cervicals of the new species of *Baptornis* appear more elongate and resemble those of *B. advenus*. Some vertebrae of SDSM 68430 and *B. advenus* possess pits on the centra that are unknown for hesperornithids. One vertebra (Fig. 3F, E) is unusual in appearing to possess accessory posterior spines, but this feature is probably preservational.

The synsacral vertebrae are coated with gypsum, obscured by the pelvic bones, and the vertebrae anterior to the acetabulum are broken away. Therefore, little can be discerned, including the number of vertebrae.

RIBS: Two ribs of SDSM 68430 are well preserved. On one (Fig. 3I) the proximal portion is well preserved, and the tuberculum is well separated from the head, unlike the case described for *Baptornis advenus* (Martin and Tate, 1976, p. 46). However, the photograph of UNSM 20030 (Martin and Tate, 1976, p. 45) illustrates a rib in which the head appears well separated, but not perhaps to the degree of SDSM 68430 and that of the hesperornithids. In agreement with those of *Baptornis advenus,* the distal portions of the ribs are not expanded as they appear in hesperornithids.

PELVIS: The distal portions of the right and left innominates and the distal portion of the synsacrum are well preserved, but the elements are broken sharply through the acetabulum, so the anterior ilium is missing (Fig. 3J). The preserved posterior portion of the ilium is crushed and poorly preserved, particularly on the right side. The ischium and pubis are preserved on both sides and are long, thin rodlike processes. The right acetabulum is broken through, but the left is better preserved. Only shale is preserved in the acetabulum, suggesting that the acetabulum was completely open, unlike either *Baptornis advenus* or *Hesperornis*. The acetabulae also have relatively vertical sides. These characters of the acetabulum may be more similar to those of extant grebes and loons. The antitrochanter is poorly developed in this new species (Fig. 3K) in comparison with those of *Baptornis advenus* and *Hesperornis*. The anterior end of the ischium merges into the antitrochanter, and no distinct margin between the two is formed (Fig. 3K). Moreover, the fossa just anterior to the acetabulum on the anterior expansion of the ischium is very shallow relative to that of *B. advenus* or *Hesperornis*. A similar situation appears to occur with the anterior depression of the pubis, but this area is more poorly preserved than the anterior end of the ischium on SDSM 68430 (Fig. 3K). On both sides of the pelvis the ischium and pubis are well separated, contrary to the situation in most other ornithurine birds, and they appear to have curved ventrally. The latter character may be preservational, but the separation of the elements appears greater than that illustrated for *B. advenus* (Martin and Tate, 1976).

Johnsgard (1987) showed how the ratio of total pelvis length to width at the acetabulum has been used to determine the most specialized diver among diving birds of North America. The greater the ratio of total pelvis length to width at the acetabulum, the more specialized the diver. Although SDSM 68430 is broken through the acetabulum, that portion preserved suggests a similar situation to that of *B. advenus* and *Hesperornis*.

FEMUR: In SDSM 68430, several fragments of both femora are represented. Two fragments are extremely weathered and worn, so much so that many distinguishing features are no longer present. The two worn fragments are the proximal portion of the left femur and the distal portion of the right femur. Even though the proximal femoral specimen is weathered, the lateral margin of the trochanter lies closer to the axis of the shaft, similar to that of *B. advenus* and unlike *Hesperornis*. The best preserved fragment is the distal 45 mm of the right femur (Fig. 3N, O), which is much more massive and robust than that of *Baptornis advenus*. The internal condyle of the partial femur is larger than that of *Baptornis advenus,* and the intercondylar depth is greater in this new species. Martin and Tate (1976) and Martin (1984) stated that the femora of *Baptornis* and *Parahesperornis* are proportionately more elongate than those of *Hesperornis*. A similar situation occurs with SDSM 68430, but the femur of this new species is more robust than that of *Baptornis advenus*. The cross section of SDSM 68430 is subcircular (Table 1) rather than transversely elongate as in *Hesperornis*. Anteriorly, the patellar (rotular) groove (Fig. 3N) extends from the intercondylar fossa dorsally in a wide, shallow, uninterrupted groove, unlike the condition of either *Hesperornis* or *Parahesperornis*. The external condyle is a relatively low but sharp dorsoventral crest, whereas the internal condyle is characterized by a high ridge that slopes steeply laterally into the intercondylar fossa. The condyles appear more distinctly formed (Fig. 3N), particularly the medial condyle, in comparison with those of *B. advenus*. The popliteal fossa is more shallow on SDSM 68430 than on *B. advenus* or the hesperornithids (Fig. 3N). Lateral indentations on the condyles also appear shallower on SDSM 68430 than on the other fossil forms. This may be due to preservation but more likely represents an allometric feature.

Measurements of the partial femur, SDSM 68430, are compared with the measurements of three specimens of *Baptornis advenus* in Table 1. The diameter of the distal articulation was one of the most precise measurements possible, and the new species has a significantly wider distal articulation than the three known

TABLE 1. MEASUREMENTS OF *BAPTORNIS VARNERI* (SDSM 68430) IN COMPARISON WITH SPECIMENS OF *BAPTORNIS ADVENUS*

Femur

Character	**SDSM 68430**	**USNM 20030**	**FMNH 395**	**KUVP 2290**
Length	N.A.	71 mm	72 mm	75 mm
Diameter head	N.A.	10 mm	10 mm	11.5 mm
Diameter distal articulation	31.59 mm	25 mm	24 mm	26 mm
Diameter proximal end	N.A.	24.5 mm	24.5 mm	28 mm
Anteroposterior diameter midshaft	15.8 mm	11.5 mm	12 mm	12.5 mm
Transverse diameter midshaft	15.0 mm	10 mm	10.5 mm	11 mm

Tibiotarsus

Character	**SDSM 68430**	**USNM 20030**	**FMNH 395**	**KUVP 2290**
Length	206.47 mm	195 mm	194 mm	N.A.
Elevation cnemial process	15.50 mm	14 mm	13 mm	14 mm
Diameter proximal articulation	24.48 mm	18 mm	17 mm	18.5 mm
Anteroposterior diameter of shaft	11.94 mm	9 mm	8.5 mm	N.A.
Transverse diameter of shaft	15.45 mm	12 mm	11.5 mm	N.A.
Diameter of distal end	24.92 mm	19 mm	18 mm	N.A.

Fibula

Character	**SDSM 68430**	**USNM 20030**	**FMNH 395**	**KUVP 2290**
Anteroposterior diameter proximal end	8.08 mm	7 mm	6 mm	8.5 mm
Transverse diameter proximal end	13.44 mm	11 mm	9 mm	11 mm
Greatest transverse shaft diameter	∼18.0 mm	7.5 mm	7 mm	N.A.
Anteroposterior diameter at this point	∼18.0 mm	5 mm	4 mm	N.A.

Tarsometatarsus

Character	**SDSM 68430**	**USNM 20030**	**FMNH 395**	**KUVP 2290**
Length	96.13 mm	84 mm	83 mm	83 mm restored
Proximal anteroposterior diameter	10.86 mm	10 mm crushed	13.8 m	13.5 mm
Proximal width	23.90 mm	17 mm crushed	17.6 mm	18 mm
Distal anteroposterior diameter	11.85 mm	N.A.	N.A.	N.A.
Distal width	27.35 mm	15 mm	15.1 mm	16 mm
Tip of trochlea 2 to distal end	11.29 mm	11.5 mm	11.5 mm	12 mm

specimens of *Baptornis advenus,* although this feature may be somewhat allometric.

FIBULA: The proximal 79 mm of the right fibula of SDSM 68430 is preserved, including a worn, large, rectangular proximal articulation (Fig. 3L, M). The fibular head is more elongate posteriorly than that of *B. advenus,* and this element has a more robust shaft in comparison with the gracile shaft of the better known species. With regard to the fibula the anteroposterior diameter of the proximal articulation, the transverse diameter of the proximal articulation, the greatest transverse shaft diameter, and the anteroposterior diameter at this point of the new specimen are compared with the same measurements of three specimens of *Baptornis advenus* (Table 1). The new species has a more robust fibula in all measurements in comparison with that of *Baptornis advenus*.

TIBIOTARSUS: The worn but complete right tibiotarsus of SDSM 68430 (Fig. 4A–D) is elongate and apneumatic but exhibits a large medullary cavity much like that of *Hesperornis*. Proximally, the cranial cnemial crests form an equilateral triangle and appear more expanded laterally (Fig. 4A) than those of *B. advenus*. The lateral cnemial crest is low, and the groove between the two crests is broad and shallow. The entire proximal end of the tibiotarsus is more robust (Fig. 4B) than that of *B. advenus,* and the proximal expansion of the articular end relative to the shaft is even seemingly as great or greater than that of *Hesperornis*. The articular area for the fibula is worn, but it appears as a very wide, transverse groove that slopes distally (Fig. 4C), not the deep excavation of *B. advenus*. The fibular crest extends at least halfway down the shaft in comparison with that of *B. advenus,* which is confined to the proximal one-third of the tibiotarsus and does not exhibit the deep groove extending across the outer border of the shaft as in *B. advenus* (Martin and Tate, 1976). Marsh (1880) described the fibular crest of *Hesperornis* as being robustly developed and extending the proximal three-fourths of the bone. The proximal articulation areas for muscle attachment are not as deeply excavated as they are in *Hesperornis* and in modern grebes. The tendonal groove is broader and longer in this new specimen (Fig. 4A) than in *Baptornis advenus,* and the groove for the M. peroneus profundus is less distinct. In addition, the lateral condyle of SDSM 68430 is much larger transversely than the medial condyle, and the distal shaft curves more medially (Fig. 4D) than is observed in *Baptornis advenus*.

With regard to the tibiotarsus, the overall length, the elevation of the expanded cnemial process, the transverse diameter of the proximal articulation, the anteroposterior diameter and transverse diameter of the shaft, and the transverse diameter of the distal articulation of SDSM 68430 were compared with three specimens of *Baptornis advenus* (Table 1). Although the proportions between the tibiotarsi *Baptornis advenus* and the new species are similar, the new species is more robust than *Baptornis advenus* in all measurements.

TARSOMETATARSUS: An obliquely crushed and abraded right tarsometatarsus is represented in SDSM 68430 (Fig. 4E–H). Owing to crushing, the shaft is distorted laterally, the anteroproximal area of the proximal foramina is smashed, and the trochleae are successively bent posteriorly. The element is short and squat (Fig. 4E, F), much more than that of *Baptornis advenus,* even given the crushed nature of SDSM 68430. Proximally, the cotyla lateralis is smaller than the cotyla medialis, although both are worn. The intercondylar eminence is low and rounded, which may be due primarily to abrasion. Dorsally, the anteroproximal face of the shaft is deeply excavated with slitlike openings that appear to be lateral and medial proximal foramina (Fig. 4G), which are not present in *Baptornis advenus* according to Martin and Tate (1976). No calcaneal ridges appear, although two indistinct ridges occur in this area; these are most likely an artifact of preservation. Distally (Fig. 4F, H), the trochlea for the 2nd metatarsal is 11.20 mm proximal to the trochleae for metatarsals 3 and 4. The trochlea for the third metatarsal is approximately equal in length and of the same relative size as the trochlea for metatarsal 4. The intertrochlear notches extend proximally to well above the 2nd trochlea, nearly to the midpoint of the shaft (Fig. 4E), extending much farther than those of *B. advenus*. The groove between metatarsals 3 and 4 is narrow for its entire length, with only a slight widening of the distal foramen. The outer trochlea flares greatly laterally, whereas the middle trochlea is posterior to the lateral trochlea. As previously mentioned, the posterior positions of the medial trochleae are the result of oblique crushing. The neck of the outer trochlea is longer in this specimen than that of *B. advenus,* and the outer extensor groove is abbreviated, reaching approximately one-third the length of the shaft. Overall, the tarsometatarsus of this species is short, stout, and does not possess the long narrow shaft of *B. advenus*. The midpoint of the tarsometatarsal shaft of SDSM 68430 narrows, resulting in a "waisted" appearance (Fig. 4E) of the element rather than the long, thin elements of other specimens of *Baptornis*.

The overall length, proximal anteroposterior diameter, proximal width, distal anteroposterior diameter, distal width, and the measurement of the tip of the 2nd trochlea to the distal end of the new specimen were compared to three *Baptornis advenus* specimens (Table 1). The new species is overall more robust than *Baptornis advenus*.

COMPARISONS

Comparisons with previously described hesperornithiforms illustrate the differentiation of the new species. First, the species is exceedingly robust in comparison with either *Pasquiaornis* or *Baptornis advenus*. In this regard the species more closely resembles the hesperornithids, *Parahesperornis* and *Hesperornis*. However, the new species can be differentiated from the hesperornithids on the basis of the distinctive structure of the distal tarsometatarsus. The new species is characterized by the 3rd and 4th trochleae of nearly the same size and distal length, rather than exhibiting an enlarged 4th trochlea. Also, as noted by Marsh (1880), the 2nd trochlea, although proximally positioned, is of the same relative size as the other two, unlike both *Hesperornis* and *Parahesperornis*. Other characters suggest that the new species is a baptornithid, including elongate cervicals, a pit on the posterior centra articulations of anterior vertebrae, a femoral trochanter only slightly expanded laterally, a smooth uninterrupted patellar groove, a subcircular femoral shaft, and tarsometatarsus trochleae of the same approximate size, with lateral and medial trochleae of the same length.

In comparison with *Pasquiaornis,* from older rocks in Saskatchewan, the new species appears more derived and is much more robust, although the preservation of specimens is not exceptional. The proximal portion of the femur of the Pierre Shale specimen is poorly preserved because of gypsum encrustation and exposure. Therefore, the comparisons are somewhat difficult, but greater lateromedial expansion and a thicker shaft appear different. The distal end of the Pierre Shale specimen is much better preserved, exhibits a very deep intercondylar fossa, and has an internal condyle that projects posteriorly as a sharper process. Moreover, the internal condylar portion of the femur appears to project farther distally than that of *Pasquiaornis*. The intercotylar prominence of the tarsometatarsus appears to overhang the shaft as in *Pasquiaornis,* but this character in the Pierre Shale specimen is more likely owing to crushing. An important difference between the two is in the position of the 2nd trochlea. In *Pasquiaornis* the 2nd trochlea lies posteriorly and close to the base of the 3rd trochlea (Tokaryk et al., 1997). Although the 2nd trochlea is posteriorly positioned on all hesperornithiforms the degree appears greater in *Pasquiaornis,* and in the Pierre Shale specimen the 2nd trochlea is well proximal to the base of the 3rd trochlea. In contradistinction to both named species of *Pasquiaornis,* the necks of the 3rd and 4th trochleae appear at the same level.

Morphologically, *Baptornis advenus* is similar to the new species of *Baptornis*. However, *B. varneri* is much more robust and exhibits interesting differences. The massive build and other differences suggest the possibility that the Pierre Shale specimen represents a separate genus. However, with only one known specimen, such a distinction seems premature. Synapomorphies with *B. advenus* and characters that suggest close phylogenetic relationship include elongate cervical vertebrae with no evidence of vertebrarterial canals, heterocelous thoracic vertebrae, pits on posterior centra, and the similar size of all tarsometatarsal trochleae, including the 2nd, indicating less derived toe rotation. The Pierre Shale species is also similar to the Niobrara species and unlike the hesperornithids in that the cross section of the shaft of the femur is subcircular, the patellar groove extends smoothly onto the shaft, and the medial condyle is smaller relative to the lateral. Even so, the differences from *B. advenus* are striking. Perhaps the most noticeable, but difficult to convey, is the massive build of all elements, indicating a much larger, robust bird in comparison with *B. advenus*. Other differences include the head and tuberculum of the rib well separated; an indistinct antitrochanter of pelvis that merges smoothly with the ischium; a smooth anterior fossa of the ischium; a widely divergent ischium and pubis; an open acetabulum with straight margins; a lateral condyle of the femur high and distinct; a deep femoral intercondylar fossa; a shallow popliteal fossa; a proximal expansion of the tibiotarsus with the shaft curved particularly distally; a shallow facet for the fibula; a long, straight fibular crest extending at least halfway down the shaft and not curving across the outer border of the shaft; and a tarsometatarsus with a proximal foramina, expanded proximal and distal ends pinched at midshaft, resulting in an elongate hourglass outline, and intertrochlear grooves extending proximally almost to midshaft.

Many of the described specimens of *Baptornis advenus* appear to represent juvenile specimens (e.g., Martin and Bonner, 1977). Therefore, the occurrence of a large, robust individual may suggest interpretation as an adult specimen of *B. advenus*. However, some apomorphic characters suggest phylogenetic differences. For example, the antitrochanter of the pelvis is indistinct in the larger specimen but well formed in the smaller specimens of *B. advenus*. Similarly, the fossae at the anterior ends of the ischium and pubis are less distinct in the larger specimen. The popliteal fossa of the femur is shallower and poorly formed in the larger specimen, and the fibular crest of the tibiotarsus does not curve as does that of *B. advenus*. Lastly, the unusual outline of the tarsometatarsus appears difficult to derive from the long, slender element of *B. advenus*. Therefore, taken together, these characters suggest a reverse polarity from what might be expected and indicate a separate taxon, not an ontogenetic stage of *Baptornis advenus*.

SUMMARY AND CONCLUSIONS

When O.C. Marsh completed his monograph on the extinct toothed birds of North America in 1880, he had "but two specimens [of *Baptornis*] available for his study: an incomplete tarsometatarsal of one specimen, the type, and several incomplete bones of a referred specimen, including an incomplete femur and several other fragments" (Walker, 1967). Over a century later this genus is still poorly known and is described mostly from partial bones. This new species of *Baptornis* is composed of a partial skeleton, adding to our knowledge of this poorly known diving bird. The skeleton is of a large individual, but characters of the pelvis, femur, tibiotarsus, and tarsometatarsus indicate that the specimen, SDSM 68430, represents a separate taxon and not an ontogenetic stage of *Baptornis advenus*. *Baptornis varneri* was collected from the top of the middle Campanian Sharon Springs Formation of the Pierre Shale Group. As such, the specimen lies stratigraphically intermediate between the underlying Niobrara records and the later occurrence of *Baptornis* in the Judith River Formation in Saskatchewan (Tokaryk and Harrington, 1993). Keeping in mind the paucity of specimens for comparison, the new species is very robust relative to both the Niobrara and Judith River specimens. Size, coupled with numerous structural apomorphies, suggests that this taxon was well separated from *B. advenus* and may have been derived from an earlier, more plesiomorphic species such as those of *Pasquiaornis*.

In conclusion, this new specimen is nearly twice the size of *Baptornis advenus,* principally in robustness rather than in length of elements. *B. varneri* does not appear to be an ontogenetic stage of *B. advenus* and possesses derived characters that would suggest derivation from a more plesiomorphic taxon than *B. advenus*. Overall, the specimen represents the first occurrence of *Baptornis* from the Pierre Shale Group, represents a new species, and indicates a greater diversity of birds from the Pierre Shale Group than was previously known. As observed by Walker (1967), we will learn more about the Cretaceous toothed birds with further "discovery of specimens in different stratigraphic horizons, and [we will begin to understand] the wide geographic distribution of the Cretaceous birds."

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Amphibian, reptilian, and avian remains from the Fox Hills Formation (Maastrichtian): Shoreline and estuarine deposits of the Pierre Sea in south-central North Dakota

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ABSTRACT

Although vertebrate fossils, except for fish, are not common in the Maastrichtian Fox Hills Formation, amphibian, reptilian, and avian remains have been recovered at several localities in south-central North Dakota from shoreline facies of the retreating Pierre–Fox Hills seaway. This mixed fauna of aquatic, terrestrial, and marine taxa provides insight into the composition of coastal communities and habitats at the interface between the Hell Creek delta and the Western Interior Seaway. The delta-platform aquatic paleocommunity is represented by the efficient swimming salamanders *Opisthotrition kayi* and *Lisserpeton bairdi,* the carnivorous soft-shelled turtle *"Aspideretes"* sensu lato, the underwater piscivorous predator *Champsosaurus laramiensis,* and the large, predatory crocodile ?*Borealosuchus.* Terrestrial areas were inhabited by the tortoise-like *Basilemys* and the predatory dinosaurs *Tyrannosaurus* and cf. *Saurornitholestes.* Birds occupied niches in the warm-temperate to subtropical, forested delta platform and shoreline areas. These nonmarine taxa in the Fox Hills Formation indicate that the geographic range of these animals extended to shoreline areas of the Western Interior Seaway.

The toxochelyid turtle *Lophochelys* and the ambush predators *Mosasaurus dekayi* and ?*Plioplatecarpus* resided in the shallow marine and estuarine habitats. These taxa and marine fish taxa reported earlier indicate that normal marine conditions in south-central North Dakota persisted into the latest Late Cretaceous in comparison with coeval Hell Creek Formation sites more distal from the Western Interior Seaway.

Keywords: Fox Hills Formation, Dakota Isthmus, Maastrichtian, reptiles, birds, amphibians, North Dakota.

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INTRODUCTION

Poorly consolidated sedimentary rocks, primarily mudstone, siltstone, and sandstone, of the Maastrichtian Fox Hills Formation in south-central and western North Dakota, particularly those of the Missouri River Valley region, represent shoreline facies of the retreating Pierre–Fox Hills Late Cretaceous seaway in the North American Midcontinent (Gill and Cobban, 1973; Waage, 1968; Erickson, 1978, 1999) (Figs. 1 and 2). Fox Hills strata intertongue laterally and intergrade vertically with delta-platform facies complexes of the Hell Creek Formation throughout the region (Feldmann, 1972; Erickson, 1992; Peppe and Erickson, 2002; Murphy et al., 2002; Hoganson and Murphy, 2002). Progradation of the Hell Creek delta and marine fluctuation produced an isthmus (Dakota Isthmus) across the narrow seaway (Erickson, 1992, 1999) and resulted, at times, in marine tongues within the Hell Creek Formation, including the Breien Member of the Hell Creek Formation (Hoganson and Murphy, 2002) and the Cantepeta Tongue of the Hell Creek Formation (Murphy et al., 2002), or estuarine facies in the underlying and lateral coastal deposits of the Fox Hills Formation (Feldmann and Palubniak, 1975; Klett and Erickson, 1977; Bouchard et al., 2002). These relationships between the strandline and delta platform provide a physical and chronological mosaic that has long challenged stratigraphers and paleogeographers in the region (Erickson, 1992; Johnson et al., 2002; Murphy et al., 2002).

One parameter that may aid interpretation of these relationships is identification of the vertebrate fossil assemblage within the Fox Hills Formation and interpretation of the paleohabitat conditions and the faunal relationships with those of the Hell Creek Formation that they imply. Marine and brackish invertebrate faunas and biostratigraphy above the Pierre Formation are well documented (Meek, 1876; Waage, 1968; Speden, 1970; Feldmann, 1967, 1972; Erickson, 1974; Landman and Waage, 1993; Hartman and Kirkland, 2002). Studies of Hell Creek and Lance Formation nonmarine, vertebrate faunas are advanced, and the faunas are also well known (Estes, 1964; Estes et al., 1969; Greenwald, 1971; Carpenter, 1979; Archibald, 1982; Breithaupt, 1982; Hutchison and Archibald, 1986; Bryant, 1989; Archibald and Bryant, 1990; Sheehan et al., 1991, 2000; Sheehan and Fastovsky, 1992; Hoganson et al., 1994a; Murphy et al., 1995; Archibald, 1996; Hunter and Pearson, 1996; Holland, 1997; Hunter et al., 1997; Lillegraven and Eberle, 1999; Pearson et al., 2001; Pearson et al., 2002; Russell and Manabe, 2002; Holroyd and Hutchison, 2002; Hunter and Archibald, 2002; Clemens, 2002), and Hoganson and Murphy (2002) documented the mixed marine and nonmarine vertebrate fauna of the Breien Member of the Hell Creek Formation.

The earliest report of vertebrate fossils from the Fox Hills Formation in North Dakota was by Leonard (1912), who mentioned the occurrence of a large fish tooth and a *Mosasaurus* tooth (identified by C.W. Gilmore) in exposures of the formation along the Cannonball River in Sioux County. Feldmann and Palubniak (1975) illustrated a few vertebrate fossils from the Fox Hills Formation from Emmons County, North Dakota. Reptile remains from the Fox Hills Formation in North Dakota were identified by Getman (1994), Hoganson and Erickson (2004), and Hoganson et al. (1994b, 1996). Hoganson et al. (1995, 1996, 1997) and Hoganson and Erickson (2005) defined the North Dakota Fox Hills Formation fish fauna. Bouchard (1990), Cicimurri (1998), Cicimurri et al. (1999), Waage (1968), and Becker et al. (2004) listed vertebrates from the Fox Hills Formation from South Dakota.

The purpose of this report is to document the amphibian, reptilian, and avian fauna of the Fox Hills Formation in North Dakota and to establish the ecological context of the strandline deposits of the waning sea. Fossils occur as isolated skeletal parts and were recovered from nine sites in Emmons, Sioux, and Logan counties in south-central North Dakota and at one site (Getman, 1994) in Bowman County in southwestern North Dakota (Fig. 1). The only articulated specimen found was the partial skeleton of *Champsosaurus laramiensis*. These fossils provide a unique perspective on paleoecological and paleogeographic conditions at the margin of the Western Interior Seaway when it was occupied by the Pierre Sea.

Institutional Abbreviations

NDSFC: North Dakota State Fossil Collection, North Dakota Heritage Center, Bismarck; **NDGS:** North Dakota Geological Survey, Bismarck; **UND-PC:** University of North Dakota Paleontology Collection, Grand Forks, North Dakota; **SLU:** Saint Lawrence University Paleontology Collection, Canton, New York; **RF:** Rodney M. Feldmann (1975), University of North Dakota, Department of Geology, dissertation field number; **AMNH:** American Museum of Natural History, New York City.

LOCATION, STRATIGRAPHIC RELATIONSHIPS, AND AGE

Exposures of the Fox Hills Formation are restricted to isolated river cutbanks, road cuts, and butte outcrops in the Missouri River Trench area of south-central North Dakota and in the Little Missouri River Badlands in the southwestern corner of the state. It is often a challenge to determine stratigraphic placement within the formation. Lithologies exposed in the outcrops and stratigraphic position relative to formational contacts where observable, particularly with the Hell Creek Formation, provide the means for determining stratigraphic placement (Fig. 2). At some localities, in both south-central and southwestern North Dakota, the contact between the Fox Hills Formation and the Hell Creek Formation is well defined. A thin (0.3–1-m-thick), carbonaceous sandstone, siltstone, or mudstone occurs at the base of the Hell Creek Formation in both south-central and southwestern North Dakota (Murphy et al., 2002). This carbonaceous bed is underlain generally by sandstones of the Fox Hills Formation. The position of the Fox Hills Formation relative to the Cretaceous–Tertiary (K–T) boundary has also been determined in both south-central and southwestern North Dakota (Murphy et al., 2002; Hoganson and Murphy, 2002). For example, at the Stumpf Site in Morton

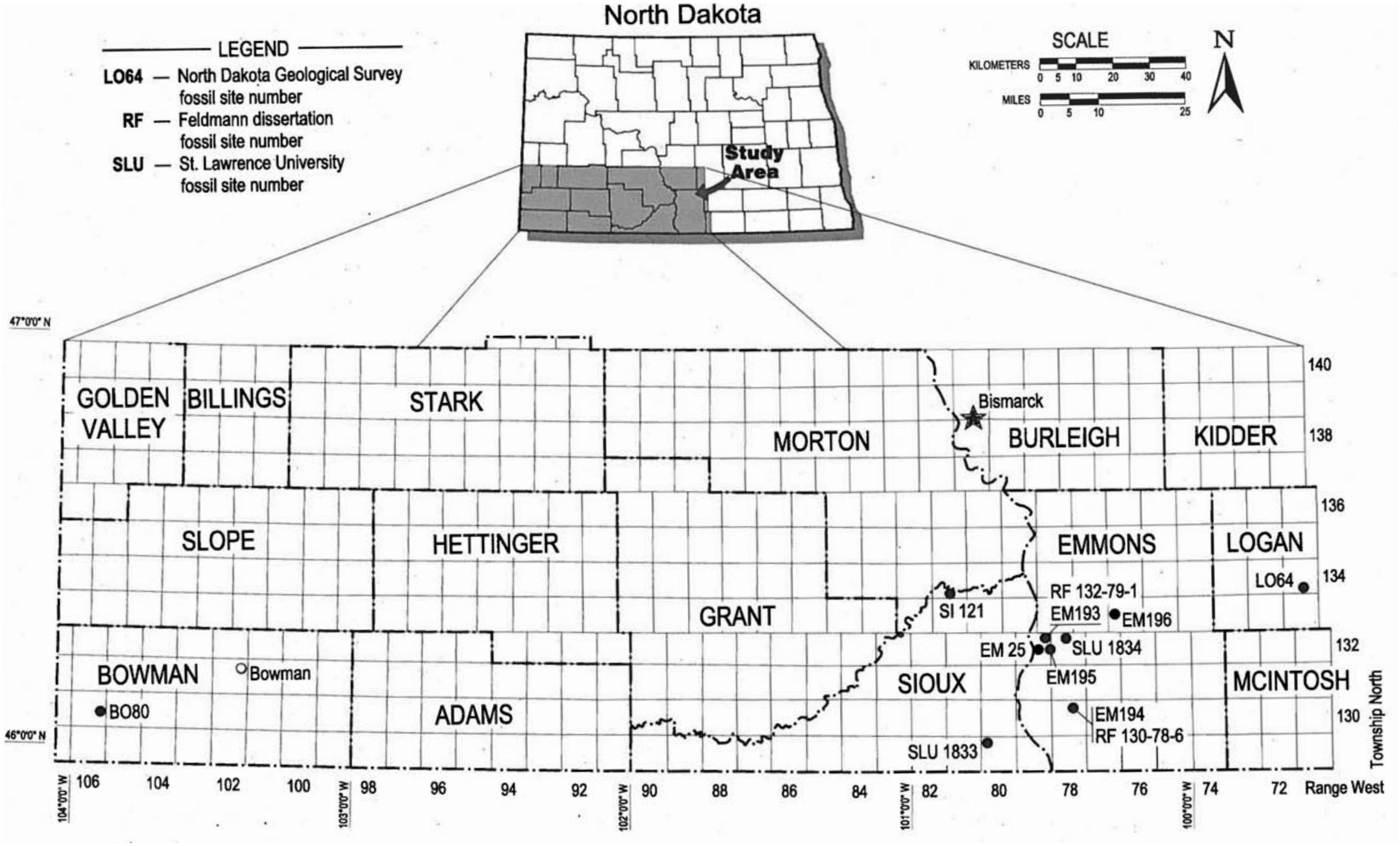


Figure 1. Map of North Dakota illustrating the locations and fossil site numbers where amphibian, reptilian, and avian fossils have been recovered from the Fox Hills Formation coastal deposits of the regressing Pierre Sea.

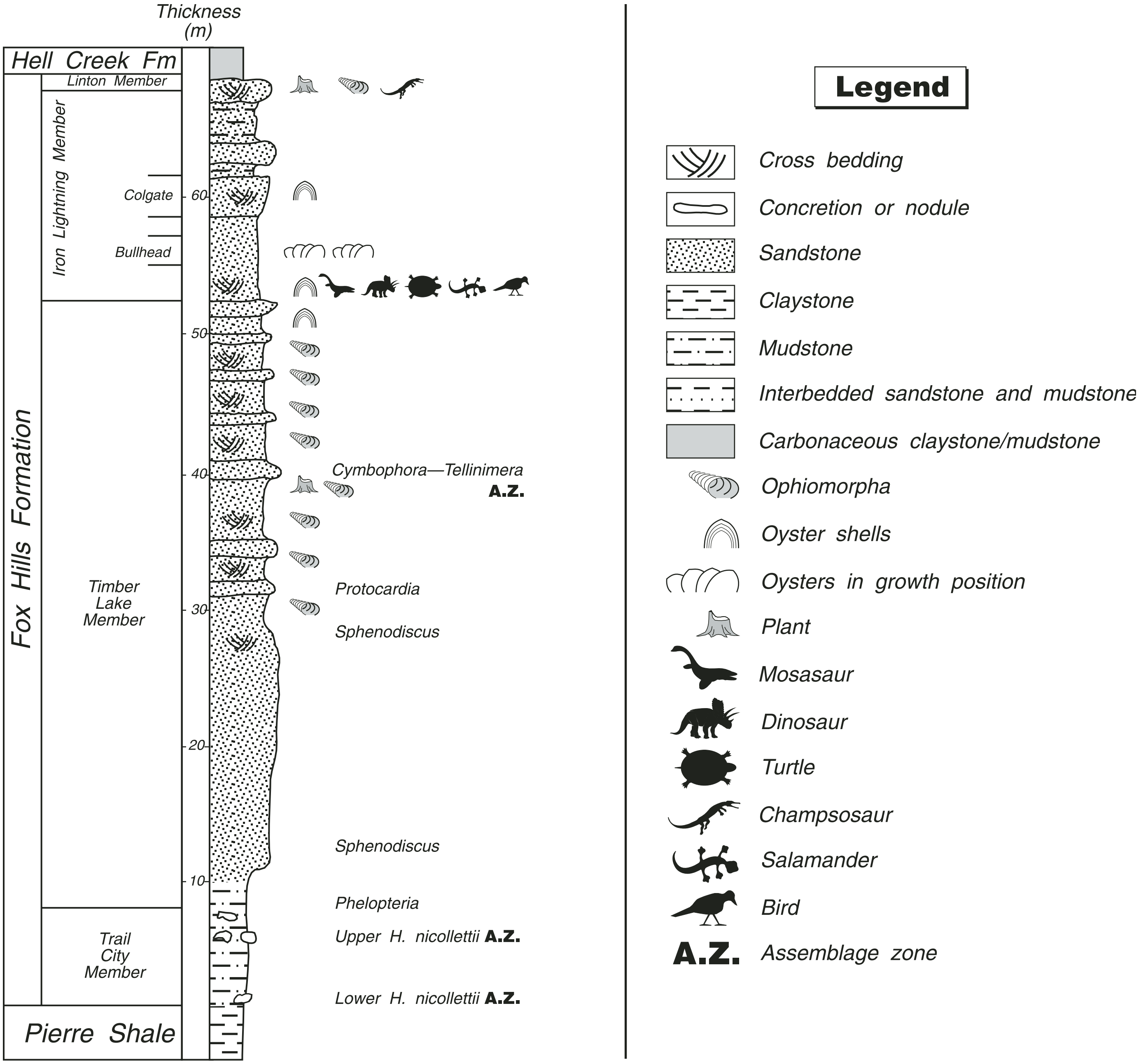


Figure 2. Diagram relating the stratigraphic nomenclature, lithologic units, and stratigraphic occurrence of amphibian, reptilian, and avian fossils in the Fox Hills Formation in North Dakota.

County, south-central North Dakota, the top of the Fox Hills Formation is ~65 m below the K–T boundary. Also, at the site, the base of the marine Breien Member of the Hell Creek Formation is 4.76 m above the top of the Fox Hills Formation (Hoganson and Murphy, 2002).

The age of the Fox Hills Formation is well established, primarily on the basis of invertebrate biochronology indicators. Deposition occurred during and perhaps after that of the *Jeletzkytes nebrascensis* Western Interior Ammonite Zone. Deposition at the time of the Western Interior *Triceratops* Zone, and a Lancian age, at least for the upper part of the formation, are implied by interfingering of the Fox Hills with the Lancian-age Hell Creek Formation.

Although indicative of age relationships, stratigraphic position does not establish age. The Fox Hills and Hell Creek Formations are, of necessity, time transgressive across the region. In the southwestern part of the study area the Fox Hills lies below the *Jeletzkytes nebrascensis* Zone. Progradation of the Sheridan Delta

(Hell Creek delta) was rapid through the late Campanian and early Maastrichtian (Gill and Cobban, 1973), but it was not geologically instantaneous, a fact that becomes more evident as stratigraphers attempt to divide the chronologic and stratigraphic records ever more thinly. Diachroneity within the complex marginal marine record, including the possibility of unconformity in Fox Hills and Hell Creek portions of the section (Erickson, 1992; Johnson et al., 2002; Peppe and Erickson, 2002), is a condition that has been proposed for relationships within and between these units by workers several times (Stanton, 1910; Calvert, 1912; Waage, 1968; Lemke, 1960) in more northerly and westerly regions of the state. Relationships in South Dakota are equally unclear (Stoffer et al., 1998; Terry et al., 2001). Knowledge of the distribution of vertebrates within this marginal marine sequence can only continue to improve chronologic resolution across its paleogeographic extent.

METHODS

Fossils examined for this study were obtained from two sources, those collected by us and those collected by R.M. Feldmann during field work in the mid-1960s at the University of North Dakota, Department of Geology. Feldmann's specimens are curated in the University of North Dakota Paleontology Collection. Feldmann's collecting and ours consisted primarily of surface gleaning. Vertebrate fossils were concentrated in a shoreline sandstone deposit at site LO64 in Logan County. At that site we conducted an excavation and collected bulk samples of the poorly consolidated fine-grained sandstone. Samples were screen washed and sieved to isolate the fossils. Specimens within this residue were removed by hand picking under magnifying glasses and microscopes. Most of that work was done by Terry Ringland, North Dakota Geological Survey paleontology laboratory assistant.

Isolated fossils were identified by comparison with described taxa in the literature. Identification confirmations were obtained when possible. Most fossil specimens examined for this study are cataloged into the North Dakota State Fossil Collection at the North Dakota Heritage Center in Bismarck, North Dakota. Some specimens are housed in the paleontology collection at Saint Lawrence University, Canton, New York, and the Feldmann specimens are in the University of North Dakota Paleontology Collection.

SYSTEMATIC PALEONTOLOGY

Class Amphibia
    Order Caudata
        Family Batrachosauroididae Auffenberg, 1958
            Opisthotriton Auffenberg, 1961
                Opisthotriton kayi Auffenberg, 1961
                Figure 3A–F

Nomenclatural summary. *Opisthotriton kayi* Auffenberg, 1961 (p. 458–463). Estes (1964) provided an extensive description and revised diagnosis of this taxon, because the specimens on which Auffenberg (1961) based his species description were eroded and fragmentary.

Holotype. Carnegie Museum Catalog of Vertebrate Fossils No. 6468.

Type locality. Lance Formation, Upper Cretaceous, Niobrara County, Wyoming.

Distribution. Laramie Formation, Colorado (Carpenter, 1979); Lance Formation (Lancian), Wyoming (Auffenberg, 1961; Estes, 1964; Whitmore and Martin, 1986); Hell Creek Formation (Lancian), Montana (Estes et al., 1969; Bryant, 1989); Fruitland Formation, New Mexico (Armstrong-Zeigler, 1978); Tullock Formation (Paleocene), Montana (Bryant, 1989); Fort Union Formation (Tiffanian), Wyoming (Estes, 1975); Tongue River Formation, Montana (Estes, 1976); Hell Creek Formation (Lancian), southwestern North Dakota (Pearson et al., 2002); Fox Hills Formation (Maastrichtian), south-central North Dakota (Hoganson and Erickson, 2004).

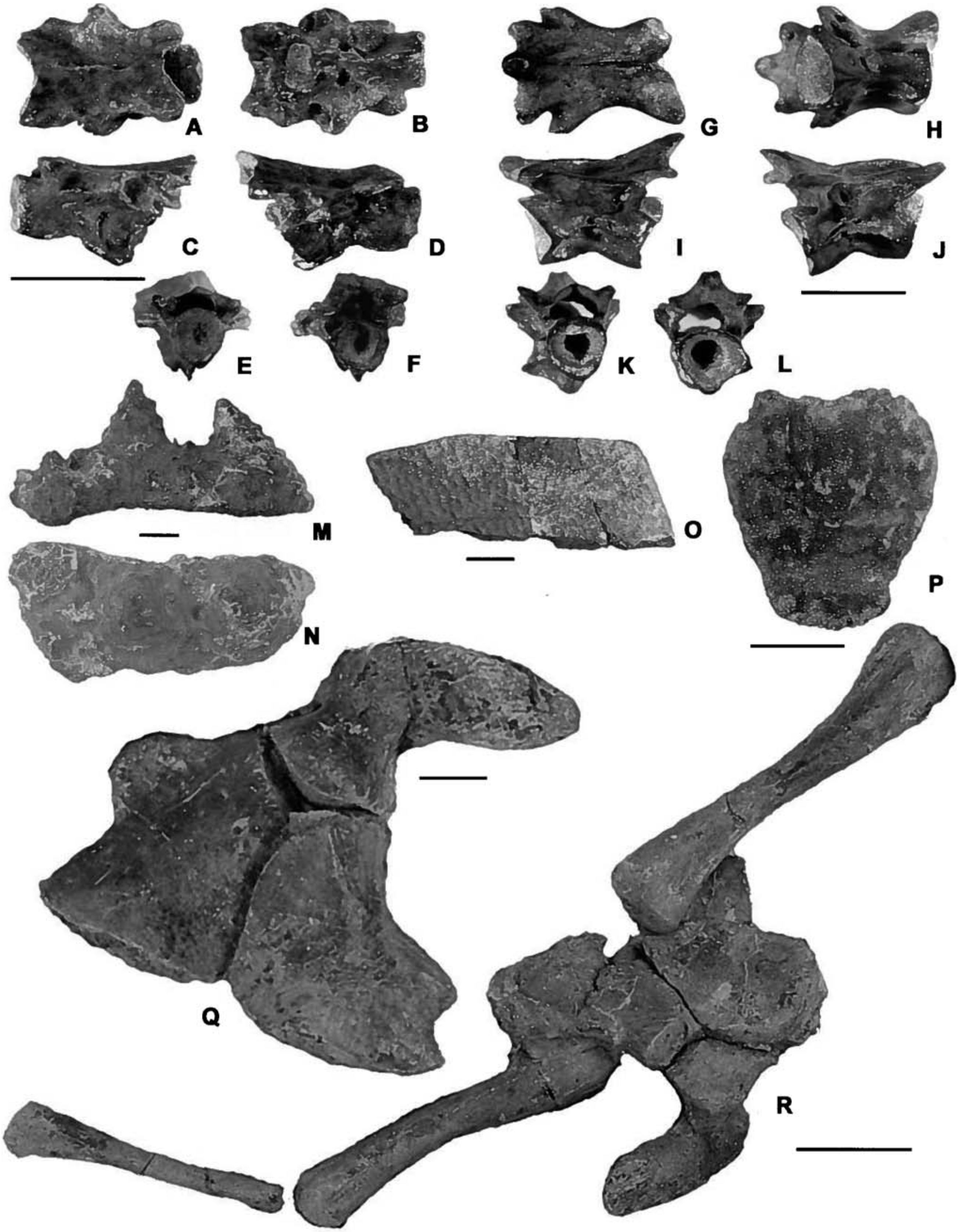
Referred specimen. Dorsal vertebra (ND 99-6.2) from NDSFC locality LO64 (Fig. 3A–F). Width, 4.83 mm; length, 6.91 mm; and height, 4.55 mm.

Description and discussion. This batrachosauroidid salamander dorsal vertebra is assignable to the species *Opisthotriton kayi,* based on comparison with Estes' (1964, p. 82) figures of an *O. kayi* dorsal vertebra and his description of dorsal vertebrae of that species summarized below. The anterior end of the centrum contains a large pit but is nearly filled with bone. The posterior cotyle is oval and hollow. The ventroposterior basapophyses are prominent and originate on the centrum at the level of the posterior border of the prezygapophysis. The basapophyses project backward and extend slightly beyond the centrum. A prominent median, concave keel is present. The neural arch is depressed and its top flattened, and a median spine is present. The zygapophyses are mostly horizontal. The transverse processes are double-headed, project from the centrum about midway along its length, and are connected by the zygapophyseal ridge with the dorsal surface of the centrum. A deep pit occurs in front and behind each transverse process.

Family Scapherpetontidae Auffenberg and Goin, 1959
    Lisserpeton Estes, 1965
        Lisserpeton bairdi Estes, 1965
        Figure 3G–L

Nomenclatural summary. *Lisserpeton bairdi* Estes, 1965 (p. 90–94).

Holotype. AMNH 8123, a complete dorsal vertebra.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Type locality. Hell Creek Formation, Bug Creek Anthills, Bug Creek, near Fort Peck Reservoir, McCone County, Montana.

Distribution. Laramie Formation, Colorado (Carpenter, 1979); Hell Creek Formation (Lancian), Montana (Estes, 1965, 1969; Bryant, 1989); Lance Formation (Lancian), Wyoming (Estes, 1965); Tullock Formation (Tiffanian), Montana (Bryant, 1989); late Paleocene (Torrejonian), Wyoming and Montana (Estes, 1965); ?Hell Creek Formation (Lancian), south-central North Dakota (Hoganson et. al., 1994a,b; Murphy et al., 1995).

Referred specimen. Dorsal vertebra (ND 99-5.1) from NDSFC locality LO64 (Fig. 3G–L). Width, 6.55 mm; length, 9.85 mm; and height, 7.35 mm.

Description and discussion. This scapherpetontid salamander dorsal vertebra is assignable to the species *Lisserpeton bairdi,* based on comparison with Estes' (1965, p. 91) figures of an *L. bairdi* dorsal vertebra and his description of dorsal vertebrae of the species summarized below. The dorsal vertebra is deeply amphicoelus. Cotylar cavities are conical, smooth, and are not bone-filled with rounded openings. The keel is central, thin, and slightly concave. Deep fossae occur on either side of the keel. The neural arch is broad and depressed medially with a single, prominent neural spine. The zygapophyses are large and tilted up at their lateral margins, with their medial edges close to the midline. The zygapophyseal ridges form a distinct edge between the side and top of the neural arch. Transverse processes are evident, as are paired rib bearers with dorsal rib bearers that emerge at the level of the dorsal surface of the neural arch.

Class Reptilia
Order Chelonia
Family Nanhsuingchelyidae Yeh, 1966
Basilemys Hay, 1902
Basilemys sp.
Figure 3M, N

Referred specimen. Ornately sculptured ossicle, probably limb armor (UND-PC 15894) from UND locality RF132-79-1 (Fig. 3M, N). Length, 42.71 mm; height, 42.78 mm.

Description and discussion. The elongate ossicular plate is formed by two fused cones. The entire surface of the plate is covered with a distinct rugose sculpture. The ossicle is similar to the *Basilemys variolosa* ossicle figured by Brinkman (2004, p. 43) from the Dinosaur Park Formation (Campanian) of Alberta. The four species of *Basilemys* recognized by Brinkman and Nicholls (1993), differentiated by the pattern of scutes on the plastron, cannot be distinguished based solely on ossicles.

Family Trionychidae (de Fitzinger, 1826)
Aspideretes Hay, 1908
"Aspideretes" sensu lato
Figure 3O

Referred specimen. Soft-shelled turtle carapace costal fragment (ND 95-5.1) from NDSFC locality EM25 (Fig. 3O). Greatest width, 70.05 mm.

Description and discussion. This carapace costal can be referred to the form genus *"Aspideretes"* based on the sculpture of the shell, which consists of shallow, closely spaced, subcircular to irregular pits that form a reticulate pattern. These pits coalesce to form a ridge and groove pattern near the margin of the shell that parallels the shell margin. This carapace sculpture is similar to the ornamentation of *Aspideretoides* illustrated by Gardner et al. (1995). The genus *Aspideretoides* was defined in that article, and the authors assigned many species from the Judith River Group and some from the Hell Creek Formation previously included in the genus *Aspideretes* to the new genus *Aspideretoides*. Unlike the Judith River Group trionychids, Lancian trionychids have not been adequately studied. We have chosen to follow Holroyd and Hutchison (2002), who opted to group *"Aspideretes"* and *Aspideretoides* from the Lance Formation in Wyoming and the Hell Creek Formation in North Dakota in the form genus *"Aspideretes"* sensu lato.

Family Toxochelyidae Baur, 1895 (emended Zangerl, 1953)
Lophochelys Zangerl, 1953
Lophochelys sp.
Figure 3P

Referred specimen. Neural (ND 99-5.2) from NDSFC locality LO64 (Fig. 3P). Width, 11.93 mm; height, 13.02 mm.

Description and discussion. This neural contains a midline ridge, and, as a result, the neural is triangular in cross-sectional view. The anterolateral sides of the hexagonally shaped neural are much shorter than the posterolateral sides, thereby resulting in a "coffin-shaped" neural. Nicholls et al. (1990) and Brinkman (2004) suggested that this neural shape is characteristic of

◄

Figure 3. Vertebrate fossils from the Fox Hills Formation. (A–F) *Opisthotriton kayi* dorsal vertebra, ND 99-6.2; scale, 0.5 cm; A, dorsal view; B, ventral view; C, left lateral view; D, right lateral view; E, anterior view; F, posterior view. (G–L) *Lisserpeton bairdi* dorsal vertebra, ND 99-5.1; scale, 0.5 cm; G, dorsal view; H, ventral view; I, left lateral view; J, right lateral view; K, anterior view; L, posterior view. (M, N) *Basilemys* ossicle, UND 15894; scale, 0.5 cm; M, lateral view; N, dorsal view. (O) *"Aspideretes"* sensu lato carapace fragment, ND 95-5.1; scale, 0.5 cm; dorsal view. (P) *Lophochelys* neural, ND 99-5.2; scale, 0.5 cm; dorsal view. (Q, R) *Champsosaurus laramiensis* semi-articulated pelvic girdle, femurs, and fibula, ND 02-17.10; Q, scale, 1.0 cm; R, scale, 4.0 cm.

Lophochelys niobrarae from the Bearpaw Formation (upper Campanian) of Alberta. Our specimen compares well with *L. niobrarae* neurals illustrated by Nicholls et al. (1990, p. 1293) and Brinkman (2004, p. 28–31) from estuarine deposits of the Bearpaw Formation and a mud-filled channel in the Lethbridge Coal Zone in Alberta. It should be noted that Hirayama (1997) synonymized *Lophochelys niobrarae* with *Toxochelys latiremis* and placed that taxon in the family Cheloniidae. Hirayama (1997) also advocated the abandonment of the genus *Lophochelys* as well as Lophochelyinae.

Order Choristodera
Family Champsosauridae Cope, 1876
Champsosaurus Cope, 1876
Champsosaurus laramiensis Brown, 1905
Figure 3Q, R

Nomenclatural summary. *Champsosaurus laramiensis* Brown, 1905 (p. 8). See Erickson (1972, p. 10–11) for synonyms, revised diagnosis, and comparison of this taxon with other *Champsosaurus* species. Katsura (2004) identified sexual dimorphism in *Champsosaurus* and proposed that *C. ambulator* is the female dimorph of *C. laramiensis*.

Holotype. AMNH 982, a nearly complete skeleton.

Type locality. Hell Creek beds, Tullock Formation, Garfield County, Montana.

Distribution. Frenchman Formation (Lancian), Saskatchewan; Hell Creek Formation (Lancian), Montana; Tullock Formation (Paleocene), Montana; and Puerco Formation (Puercan), New Mexico (Erickson, 1972). Tullock Formation (Paleocene), Montana (Katsura, 2004). Hell Creek Formation and Tullock Formation, Montana (Brown, 1905; Gao and Fox, 1998). *Champsosaurus laramiensis* is the only species within the genus that occurs in the Hell Creek Formation (Erickson, 1972). This species is here newly reported from the Linton Member of the Fox Hills Formation.

Referred specimen. Semi-articulated pelvic girdle, including ilia, pubes, and ischia. Both the femora and the right fibula are also present (ND 02-17.10) from NDSFC locality EM196. The length of the left femur is 101.65 mm, and the smallest breadth of the left femur diaphysis is 10.48 mm (Fig. 3R).

Description and discussion. This specimen is identified as *Champsosaurus laramiensis* for the following reasons. The skeletal elements in the pelvic structure and limb bones are gracile. The limb bones are relatively long and slender, particularly in comparison with *Champsosaurus gigas,* the ubiquitous *Champsosaurus* species in North Dakota Paleocene strata. The femoral internal trochanter is high on the shaft and connects with the articular surface of the proximal head, forming a bridge on the ventral surface, as shown by Katsura (2004, p. 248). This character was used by Erickson (1972, p. 1981) to separate *C. laramiensis* from *C. ambulator,* but Katsura (2004) suggested that *C. ambulator* is the female dimorph of *C. laramiensis*. The elongate and "squared off" blade of the ilium compares well with the diagram of ilia from *C. laramiensis* in Erickson (1972, p. 67) and also suggests that the Fox Hills specimen was an older juvenile or subadult.

Order Squamata
Family Mosasauridae Gervais, 1853
Mosasaurus Conybeare, 1822
Mosasaurus dekayi Bronn, 1838
Figure 4A–C

Nomenclatural summary. *Mosasaurus dekayi* Bronn 1838. Russell (1967) described and discussed this taxon in his review of American mosasaurs.

Holotype. The type specimen was not located, but Russell (1967) noted that the type consists only of the crown of a tooth.

Type locality. According to DeKay (1830, p. 135), from the foot of Neversink Hills, Sandy Hook, Monmouth County, New Jersey (Russell, 1967, p. 138).

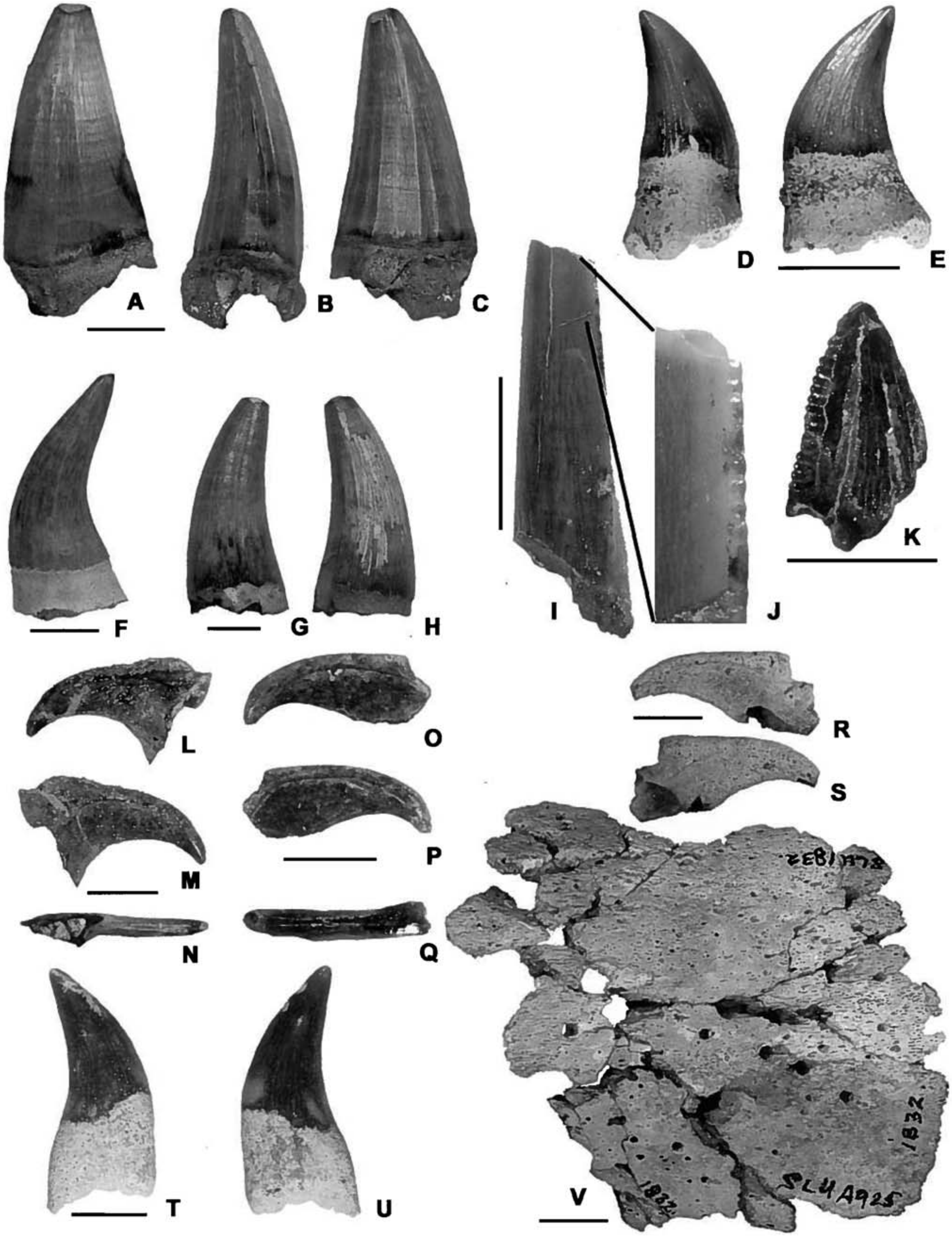
Distribution. Navesink Formation (Maastrichtian) and younger Cretaceous strata, New Jersey (Russell, 1967, p. 138). Fox Hills Formation (Maastrichtian), North Dakota (Hoganson et al., 1994a,b, 1996; Hoganson and Erickson, 2004). Pierre Formation (Campanian–Maastrichtian), South Dakota (Bell et al., 1994; although see Burrows, 2005).

Referred specimen. Tooth (UND-PC 15895) from UND locality RF132-79-1. Height, 40.98 mm; greatest width, 19.07 mm.

Description and discussion. The very large, robust, marginal mosasaurid tooth has both tooth faces distinctly faceted. The tooth is symmetrically bicarinate and laterally compressed, and

→

Figure 4. Vertebrate fossils from the Fox Hills Formation. (A–C) *Mosasaurus dekayi* tooth, UND 15895; scale, 1.0 cm. (D, E) ?*Plioplatecarpus* tooth, ND 95-13.55; scale, 0.5 cm. (F) ?*Plioplatecarpus* tooth, ND 95-3.1; scale, 0.5 cm. (G, H) ?*Borealosuchus* tooth, UND 15897; scale, 0.5 cm. (I, J) *Tyrannosaurus* tooth fragment, UND 15898; I, tooth fragment; scale, 1.0 cm; J, enlarged to show tooth denticles. (K) cf. *Saurornitholestes* tooth fragment, ND 95-13.56; scale, 0.25 cm. (L–N) ?Aves claw, ND 99-6.4; scale, 0.25 cm. (O–Q) ?Aves claw, ND 95-13.59; scale, 0.25 cm. (R, S) ?Aves claw, ND 95-13.58; scale, 0.25 cm. (T, U) ?Aves tooth, ND 95-13.57; scale, 0.25 cm. (V) Unidentified reptile bone, SLU 1832; scale, 2.0 cm.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SLU A925
1832
1832

the labial face is much less convex than the lingual face. The tooth is triangular in cross section. The labial face is divided into 4 facets, and the lingual face is divided into 10 facets. Characteristics of this tooth match those of *Mosasaurus dekayi* given by Russell (1967, p. 38). The combination of the tooth's being very robust and possessing well-developed and numerous facets on both tooth faces separates this species from other *Mosasaurus* species. This specimen was illustrated and discussed by Getman (1994).

Plioplatecarpus Dollo, 1882
?*Plioplatecarpus* sp.
Figure 4D–F

Referred specimens. Tooth (ND 95-13.55) from NDSFC locality LO64 (height, 10.38 mm; greatest width, 6.41 mm). Tooth (ND 95-3.1) from NDSFC locality SI121 (height, 19.32 mm; greatest width, 9.71 mm). Broken tooth (ND 95-4.1) from NDSFC locality BO80 (height, 13.9 mm; greatest width, 6.69 mm). Tooth (ND 99-6.3) from NDSFC locality LO64 (height, 20.25 mm; greatest width, 10.18 mm). Tooth (ND 95-2.1) from NDSFC locality SI121 (height, 18.50 mm; greatest width, 6.41 mm). Broken and eroded tooth (UND-PC 15896) from UND locality RF130-78-6 (height, 15.10 mm; greatest width, 7.17 mm).

Description and discussion. The teeth are conical but slightly compressed laterally (subcircular in cross section) and are slender, elongate, and lingually recurved. They are bicarinate and have tightly spaced striae on the lingual face and are mostly smooth or indistinctly faceted on the labial face. Striae are most distinct on the lower half of the lingual face. The lingual face is less convex than the labial face. All teeth are probably from marginal positions except for ND 95-13.55, which may be a pterygoid tooth because it is not as elongate as the others (Fig. 4D, E). Genera within the Plioplatecarpini, including *Platecarpus, Ectenosaurus,* and *Plioplatecarpus,* have bicarinate, vertically striated, and medially recurved teeth (Russell, 1967, 1993; Bell, 1997). We provisionally place our specimens in *Plioplatecarpus* because of their Maastrichtian age.

Order Crocodylia
Family Crocodylidae Gmelin, 1788
Borealosuchus Brochu, 1997
?*Borealosuchus* sp.
Figure 4G, H

Referred specimens. Tooth (UND-PC 15897) from UND locality RF132-79-1 (height, 28.37 mm; greatest width, 12.99 mm) (Fig. 4G, H). Tooth fragment with root (ND 95-8.1) from NDSFC locality EM194 (height, 32.36 mm; greatest width, 9.11 mm).

Description and discussion. Large, conical, slightly curved, smooth crocodylian teeth, probably from the anterior based on their height (Fig. 4G, H). The tooth is bicarinate, and anterior and posterior carinae extend from the base to the apex of the tooth. It is identical in size and shape to those of *Leidyosuchus* (= *Borealosuchus*) *formidabilis* from the Paleocene Bullion Creek Formation, found at the Wannagan Creek quarry in North Dakota (Erickson, 1976). Brochu (1997) synonymized most *Leidyosuchus* taxa, including the two taxa that occur in North Dakota, *L. sternbergi* and *L. formidabilis,* within his newly created genus *Borealosuchus*. Brochu (1997) pointed out that most crocodyliform teeth are similar, and consequently our teeth cannot confidently be assigned to *Borealosuchus*.

Order Saurischia
Family Dromaeosauridae Matthew and Brown, 1922
Saurornitholestes Sues, 1978
cf. *Saurornitholestes* sp.
Figure 4K

Referred specimen. Eroded tip fragment of a small theropod dinosaur tooth (ND 95-13.56) from NDSFC locality LO64. Height, 3.94 mm; greatest width, 1.95 mm.

Description and discussion. The tooth is laterally compressed with denticles that are chisel-like in form on the single preserved carina, which is from the base of the tooth. Each denticle is straight, twice as high as long, and has a slightly rounded to flat tip. Interdenticle slits are deep and narrow. Blood grooves between the bases of the denticles are indistinct. There are seven denticles per millimeter. We provisionally suggest that our tooth fragment is *Saurornitholestes* because of the shape, arrangement, and number of denticles per millimeter. Denticles of our tooth are very similar to those of *Saurornitholestes* teeth illustrated by Currie et al. (1990, p. 111, particularly Fig. 8.2q) and Sankey et al. (2002, p. 753). Sues (1978), Currie et al. (1990), and Sankey et al. (2002) noted that *Saurornitholestes* possesses seven denticles per millimeter on the anterior carina, the number on our tooth.

Family Tyrannosauridae Osborn, 1906
Tyrannosaurus Osborn, 1905
Tyrannosaurus sp.
Figure 4I, J

Referred specimen. Eroded tooth fragment from a large theropod dinosaur (UND-PC 15898) from UND locality RF132-79-1. Height, 25.55 mm; greatest width, 7.61 mm.

Description and discussion. The sliver-shaped, badly eroded, robust, laterally compressed tooth fragment is from the margin of the tooth and preserves a portion of one carina. Denticles, although worn, are preserved on the carina. There are three denticles per millimeter, and the denticles are stout and chisel shaped, with rounded tips. The denticles are wider labially-lingually than they are proximodistally. Tips of the denticles are worn, but faintly preserved ridges of enamel are present along the midlines of the denticles. Blood grooves originating between the bases of the denticles extend diagonally from the carinae. Even though this specimen is a fragment, characters match those for teeth of Tyrannosauridae given by Currie et al. (1990). We choose to place this specimen in the genus *Tyrannosaurus* because of the characters just listed and because it compares with the illustration of a portion of a *Tyrannosaurus rex* tooth by Currie et al. (1990, p. 121, Fig. 8.7A) and the *T. rex* maxillary tooth figured by Brochu (2003, p. 17, Fig. 11B).

Reptilia indet.
Figure 4V

Referred specimen. Bone fragment (SLU 1832) from NDSFC locality BO80. Length, 100.61 mm; width, 88.11 mm; greatest thickness, 11.49 mm.

Description and discussion. This is a very thin, large, platy bone, concavo-convex in cross section, with tapered, irregular margins. The bone is very porous and contains large perforations. This thin, porous bone resembles a crocodylian osteoderm, but it is yet to be identified. If it is a crocodilian osteoderm, it was from a very large animal.

Class Aves
?Aves tooth indet.
Figure 4T, U

Referred specimen. Tooth (ND 95-13.57) from NDSFC locality LO64 (Fig. 4T, U). Height, 8.11 mm; FABL (fore-aft basal length), 3.83 mm.

Description and discussion. The tooth is small, laterally compressed, smooth, and recurved posteriorly. Thin carinae, with no denticles, are present on anterior and posterior edges. Very distinct medio-lateral constriction at the base of the tooth creates a flattened oval cross section. This tooth is similar to those illustrated by Sankey et al. (2002, p. 756).

?Aves claws indet.
Figure 4L–N, O–Q, R, S

Referred specimens. Claw (ND 99-6.4) from NDSFC locality LO64 (Fig. 4L–N); length, 7.41 mm. Claw (ND 95-13.59) from NDSFC locality LO64 (Fig. 4O–Q); length, 4.93 mm. Claw (ND 95-13.58) from NDSFC locality LO64 (Fig. 4R, S); length, 5.92 mm.

Description and discussion. The claws are small, compressed laterally (flattened), and curved posteriorly. The amount of curvature varies. Deep sulci that are subparallel to the anterior margin of the claw extend from the base of the claw to the apex. A groove, also extending from the base of the claw to the apex, is incised along the posterior margin of the claw. Variation within the claws may indicate more than one taxon. The flatness of the claws, deep sulci, and the posterior groove are similar to those of Aves.

PALEOBIOGEOGRAPHIC AND PALEOECOLOGIC IMPLICATIONS

The Fox Hills amphibian, reptilian, and avian fauna known to date from North Dakota is summarized in Table 1. This fauna contains sufficient diversity to permit interpretation of the paleoecological setting of both land and sea habitats but does not contain a large enough sample size to make statistical comparisons with well-documented faunas from similar settings. Brinkman (1990) and Brinkman et al. (2004) analyzed paleoecological information from transitional formations of the Campanian Judith River Group at multiple sites in southern Alberta, Canada, permitting definition of two statistical clusters interpreted as paleocommunities in the regressive Foremost and terrestrial Oldman Formations. We are not including here discussion of our chondrichthyan or actinopterygian data (Hoganson et al., 1995, 1996) as did Brinkman et al. (2004), but the remaining Judith River vertebrate fauna shows similarities with this younger Fox Hills fauna. There are also notable differences that may be related to paleogeography or to depositional setting. In particular the marine reptiles are clearly a factor in the Fox Hills–Pierre nearshore habitat, but they are not strongly represented in the regressive Foremost Formation. Another significant distinction, although not immediately apparent from the present data, is the fact that we have yet to recover mammalian material from the Fox Hills Formation, whereas Brinkman et al. (2004) reported low numbers of several mammalian taxa even in their regressive shoreface lag deposits. The Fox Hills Formation has yielded a diverse mammalian assemblage from the Red Owl locality in western South Dakota (Wilson, 1987).

As would be expected in a dynamic shoreline-estuarine depositional setting, the amphibian, reptilian, and avian fauna of the Fox Hills Formation includes a mix of aquatic, terrestrial, and marine taxa, and taxa that inhabited the ecotone between aquatic and terrestrial habitats (e.g., crocodiles). The turtle fauna, which consists of terrestrial *(Basilemys),* fresh-water (*"Aspideretes"* sensu lato), and marine *(Lophochelys)* taxa, exemplifies the mixed nature of the assemblage. Another example of faunal mixing in a Fox Hills estuarine habitat is the occurrence of the partial skeleton of *Champsosaurus laramiensis* at site EM196, which also contains leaves from trees and other terrestrial plants (Peppe and Erickson, 2004) and remains of the marine horseshoe crab *Casterolimulus kletti* (Holland et al., 1975; Hoganson and Erickson, 2004). The marginal marine Fox Hills depositional setting was also a repository for remains of species occupying the apex of both marine and terrestrial trophic pyramids, the marine and terrestrial vagile, lone predators, mosasaurids, and tyrannosaurids. This occurrence of ecologically diverse taxa in the formation can be attributed to physical processes of mixing in a dynamic depositional

TABLE 1. LIST OF AMPHIBIAN, REPTILIAN, AND AVIAN TAXA FROM THE FOX HILLS FORMATION AND THE LOCALITIES WHERE THEY WERE FOUND

	LOCALITY AS IN FIGURE 1											
VERTEBRATE TAXON	BO80	SLU 1833	SI121	EM25	RF132-79-1	EM193	EM196	SLU 1834	EM195	EM194	RF130-78-6	LO64
Class Amphibia												
Order Uredola												
Family Batrachosauroididae												
Opisthotriton kayi												**XX**
Family Scapherpetontidae												
Lisserpeton bairdi												**XX**
Class Reptilia												
Order Chelonia												
Family Nanhsuingchelyidae												
Basilemys sp.					**XX**							
Family Trionychidae												
“Aspideretes” sensu lato				**XX**								
Family Toxochelyidae												
Lophochelys sp.												**XX**
Chelonia indet.				**XX**		**XX**			**XX**			**XX**
Order Choristodera												
Family Champsosauridae												
Champsosaurus laramiensis							**XX**					
Order Squamata												
Family Mosasauridae												
Mosasaurus dekayi					**XX**							
?*Plioplatecarpus* sp.	**XX**		**XX**								**XX**	**XX**
Mosasauridae indet.		**XX**						**XX**				
Order Crocodylia												
Family Crocodylidae												
?*Borealosuchus* sp.					**XX**					**XX**		
Order Saurischia												
Family Dromaeosauridae												
cf. *Saurornitholestes* sp.												**XX**
Family Tyrannosauridae												
Tyrannosaurus sp.					**XX**							
Reptilia sp. indet.	**XX**											
Class Aves												
?Aves tooth indet.												**XX**
?Aves claws indet.												**XX**

system and also the close proximity of coastal marine and adjacent nonmarine communities in the vicinity of the depositional sites. Some delicate skeletal elements, such as the salamander vertebrae, show little wear, which implies that the fossils were not transported far and were entombed in sediments near to where the animals died. Other fossils, including the theropod dinosaur teeth, are broken and highly abraded and must have been in the depositional system for some time before burial. The chondrichthyan and actinopterygian fauna of the Fox Hills Formation in North Dakota is also a mixed assemblage of fresh-water, brackish-water, and marine taxa (Hoganson et al., 1995, 1996).

The nonmarine component of the Fox Hills fauna consists of salamanders, *Opisthotriton kayi* and *Lisserpeton bairdi;* turtles, *Basilemys* and *"Aspideretes"* sensu lato; champsosaurids, *Champsosaurus laramiensis;* crocodiles, ?*Borealosuchus;* dinosaurs, cf. *Saurornitholestes* and *Tyrannosaurus;* and possibly birds. These taxa are all relatively commonly found in Late Cretaceous, and in some cases early Paleocene, strata in western North America (e.g., Bryant, 1989; Archibald and Bryant, 1990; Archibald, 1996). Bouchard (1990) reported *O. kayi, L. bairdi, Basilemys,* and *Borealosuchus (= Leidyosuchus)* in the Fox Hills Formation in northwestern South Dakota. *Borealosuchus (= Leidyosuchus), Basilemys,* and Tyrannosauridae were listed from the Fox Hills Formation in North Dakota (Hoganson et al., 1994b, 1996; Hoganson and Erickson, 2004). All nonmarine taxa reported from the Fox Hills Formation in this study, except *L. bairdi, "Aspideretes"* sensu lato, and *C. laramiensis,* have also been recovered from Late Cretaceous Hell Creek Formation deposits in southwestern North Dakota (Pearson et al., 2002), and *L. bairdi, "Aspideretes"* sensu lato, *Borealosuchus (= Leidyosuchus*), and Tyrannosauridae were reported from the Hell Creek Formation in south-central North Dakota (Hoganson et al., 1994a; Murphy et al., 1995). *Champsosaurus*, *Tyrannosaurus,* and Crocodylia remains have also been found in nearshore marine deposits of the Breien Member of the Hell Creek Formation in south-central North Dakota (Hoganson and Murphy, 2002). The occurrence of the nonmarine taxa reported here in the Fox Hills Formation in south-central North Dakota suggests that the geographic range of these animals extended to Fox Hills shoreline areas.

None of the marine taxa, the turtle *Lophochelys* and the mosasaurs *Mosasaurus dekayi* and ?*Plioplatecarpus* reported here occur in the Fox Hills Formation in northwestern South Dakota or the terrestrial Hell Creek deposits in western North America, although Cicimurri et al. (1999) reported the presence of an unidentified mosasaur caudal vertebra from the Fox Hills Formation in Badlands National Park, South Dakota. This indicates that normal marine conditions existed adjacent to Fox Hills deposition sites in south-central North Dakota in comparison with sites distal from the Western Interior Seaway. This is also reflected by the Fox Hills fish faunas from south-central North Dakota, which contain normal marine and nonmarine taxa (Hoganson et al., 1995, 1996). Similar conditions existed during deposition of the marine Breien Member of the Hell Creek Formation in south-central North Dakota, indicated by marine fish in a mixed nonmarine and marine fossil assemblage (Hoganson and Murphy, 2002).

By integration of information about the ecological and habitat preferences of the taxa in the Fox Hills Formation, a further understanding of the composition of the coastal communities and habitats proximal to the interface between the Western Interior Seaway and Hell Creek delta can be obtained. The Hell Creek delta aquatic fauna is represented by the salamanders *Opisthotriton kayi* and *Lisserpeton bairdi,* the soft-shelled turtle *"Aspideretes"* sensu lato, the champsosaurid *Champsosaurus laramiensis,* and the crocodylian ?*Borealosuchus*. Most salamanders are stenohaline. The taxa present here were fully aquatic in fresh water and probably lived in a riparian habitat (Estes and Berberian, 1970). Auffenberg (1961) also speculated that *O. kayi* was an efficient swimmer. Salamanders similar to *O. kayi* and *L. bairdi* exist today in the southeastern United States (Estes and Berberian, 1970).

Trionychid turtles today are aquatic carnivores that are excellent swimmers, but they usually conceal themselves by burrowing into the soft sediments in the bottoms of rivers and lakes (Hutchison and Archibald, 1986). Although the systematics of this group has not been resolved, it is assumed that *"Aspideretes"* sensu lato was a carnivore and aquatic, like most trionychids. Champsosaurs were agile, aggressive, underwater piscivorus predators that were well adapted for aquatic life (Erickson, 1972). They inhabited lakes, swamps, and ponded areas in streams. Erickson (1972) noted that the largest populations of champsosaurs inhabited coastal floodplains and swampy areas, and during the Late Cretaceous they frequented salt marshes and estuarine waters. They were apparently euryhaline and could tolerate brackish-water habitats.

Borealosuchus is considered a fresh-water taxon (Beavan and Russell, 1999). It is the most common crocodylian in Late Cretaceous and Paleocene fresh-water strata in western North America, inhabiting floodplain backswamp areas along meandering streams (Erickson, 1976). It was a predator, probably mostly ichthyophagous, that would lie in wait with eyes and nose above the water's surface like today's crocodiles (Erickson, 1976). There is evidence that turtles were also part of their diet (Erickson, 1984). One may be relatively certain that *Borealosuchus* was a top carnivore in the aquatic system behind the Fox Hills beaches.

The terrestrial community is represented by the theropod dinosaurs *Tyrannosaurus* and cf. *Saurornitholestes,* and the tortoise-like *Basilemys*. Tyrannosaurids were lone predators that roamed over large floodplain areas and had less specific habitat preferences than modern reptiles (Molnar and Farlow, 1990). Dromaeosaurids, such as cf. *Saurornitholestes,* were also predators but were of medium size, light build, and great agility (Ostrom, 1990). Ostrom (1990) observed that dromaeosaurids preferred lowland river-bank habitats. Both of these theropods were active on the shoreline areas of the Hell Creek delta. Russell (1993) noted that theropod teeth are among the most common dinosaur remains found in marine deposits. *Basilemys* was one of the few turtle genera to have become extinct by the K–T event. They were herbivorous and fully terrestrial (Hutchison and Archibald, 1986), suggesting that they were ecologically similar to living tortoises (Brinkman, 2003). It was the only terrestrial turtle genus that lived during the Late Cretaceous (Holroyd and Hutchison, 2002).

The mosasaurids *Mosasaurus dekayi* and ?*Plioplatecarpus,* and the toxochelyid turtle *Lophochelys,* were members of the marine community of the Fox Hills fauna. During the Late Cretaceous, mosasaurs were worldwide in distribution and inhabited, in abundance, subtropical coastal waters and occasionally brackish, nearshore environments (Russell, 1967). Mosasaurs were adapted for rapid bursts of speed and were ambush predators that were opportunistic feeders as well as being at the top of the marine trophic structure (Massare, 1988, 1997). Although *Plioplatecarpus* is considered a resident of open marine waters (Beavan and Russell, 1999), it also exploited estuarine and fresh-water habitats (Holmes et al., 1999). Cretaceous marine turtles are not common (Nicholls et al., 1990), and toxochelyids, medium-sized marine turtles, inhabited the Western Interior Seaway during the Late Cretaceous (Nicholls, 1988). Hirayama (1997) suggested that toxochelyids were bottom dwellers in very shallow marine waters and not good swimmers, unlike some of the large, Late Cretaceous, marine turtles. *Lophochelys* was apparently capable of entering fresh-water habitats (Brinkman, 2004), but in our samples it is found mixed with marine fossils.

CONCLUSIONS

The estuarine and shoreline areas of the Pierre Sea along its western margin in south-central North Dakota, and the aquatic and terrestrial habitats of the Hell Creek delta not far removed from the sea, were teeming with life during Fox Hills time. The remains of amphibians, reptiles, and birds from these paleocommunities are entombed in the Fox Hills strata. With a full complement of sharks, rays, and ratfish (Hoganson et al., 1995, 1996, 1997; Hoganson and Erickson, 2005), the normal marine vertebrate paleocommunity consisted of the turtle *Lophochelys* and the mosasaurs *Mosasaurus dekayi* and ?*Plioplatecarpus*. Although *Lophochelys* probably resided in the shallow marine waters, the mosasaurs were likely residents of more open marine areas and would venture into shallow marine habitats on feeding forays. It is possible, however, that the mosasaur remains in the Fox Hills Formation are from individuals that had died at sea and that after death their bloated carcasses drifted to shoreline areas. Alternatively, the living animals may have entered shallow marine areas, becoming stranded, and died, as has been observed in other paleofaunas by Sheldon (1997). Fox Hills mosasaur material does not include skeletal elements other than teeth in North Dakota, but a skull of a large (undescribed) specimen has been recovered from subtidal deposits of the formation in South Dakota. It is most likely that mosasaurs were the main ambush predators that cruised the shallow marine Fox Hills waters. Several species of sharks, many of which were the primary pursuit predators, and other predatory fish were also members of this community (Hoganson et al., 1996), which was supported by the thriving benthic marine community of the Fox Hills–Pierre Sea (Erickson, 1974; Feldmann, 1972). Rivers and streams slowly meandered across the low-relief, swampy Hell Creek delta platform near the shoreline areas in south-central North Dakota at this time. A complex of terrestrial, river and stream, pond, and swamp habitats existed on this coastal plain, and communities of aquatic and terrestrial animals and plants resided there. At that time, this part of the delta was forested (Murphy et al., 1995; Peppe and Erickson, 2004; Smrecak et al., 2005), as was the more proximal delta platform represented by Hell Creek strata on the North Dakota–Montana border (Fastovsky, 1987; Fastovsky and McSweeney, 1987) and in southwestern North Dakota (Johnson, 1992, 2002; Johnson et al., 1989; Nichols, 2002). The climate was wet and warm-temperate to subtropical, similar to forested areas of Costa Rica today (Peppe and Erickson, 2004). Fresh-water riparian stream and pond areas were inhabited by the swift-swimming salamanders *Opisthotriton kayi* and *Lisserpeton bairdi* and the carnivorous soft-shelled turtle *"Aspideretes"* sensu lato. The fish-eating *Champsosaurus laramiensis* also lived in these fresh-water habitats and brackish-water bodies on the delta margin. These aquatic areas were frequently visited by the predatory crocodile ?*Borealosuchus*. Birds, represented by claws (Fig. 4L–S) and a tooth (Fig. 4T, U) also resided in the forests, although as yet little is known about them.

The herbivorous tortoise-like turtle *Basilemys* cautiously shared the terrestrial landscape with the theropod hunters *Tyrannosaurus* and cf. *Saurornitholestes*. A variety of prey species, in the terrestrial, aquatic, and shallow marine paleocommunities, were available to these dinosaur predators on the margin of the Hell Creek delta.

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