Paludicola 5(4):125-149 June 2006

COMPARATIVE VERTEBRATE TAPHONOMY OF THE PEMBINA AND SHARON SPRINGS MEMBERS (MIDDLE CAMPANIAN) OF THE PIERRE SHALE, WESTERN INTERIOR.

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ABSTRACT

The Pembina and Sharon Springs members of the Pierre Shale are some of the most organic-rich marine shales in the central portion of the Western Interior. The shales represent the deep-water facies of the transgressive Claggett Cyclothem of the Early Middle Campanian. Both shales preserve a very rich vertebrate record of marine fossils. Theses specimens range from isolated bones shed from drifting carcasses to complete skeletons of carcasses that sank soon after death. No mass accumulation levels are present, even associated with bentonites, thus no mass deaths can be attributed to volcanic ash fallout, nor to dinoflagellate or other phytoplankton blooms ("red tide"). The accumulations are best explained as attritional in anoxic or near anoxic bottom waters. A field inventory of the Sharon Springs Member reveals that museum collections are biased toward more complete skeletons and rare specimens.

Taphonomic data is used in conjunction with wind data inferred from bentonite thickness and upwelling zones inferred from glauconite to reconstruct paleocurrents in the Claggett Seaway. The results suggest that taphonomic data provides an important source of information that should be considered in paleocurrent analyses.

INTRODUCTION

In 1988, Elizabeth (Betsy) Nicholls completed her dissertation on the marine vertebrates from the Pembina Member of the Pierre Shale from southern Manitoba, Canada. Part of this work included a brief discussion of the taphonomy of the various vertebrates, as well as an interpretation of the depositional environment of the Pembina. The Pembina is equivalent to the Sharon Springs Member of the Pierre Shale in Wyoming, Colorado and Kansas, USA (Figure 1, 2). Both are black, organic-rich shales deposited in the central portion of the Western Interior Seaway during the Claggett transgression (Kauffman, 1984). The shales suggest deposition in apparently similar anoxic environments and both members share similar vertebrate taxa as is discussed below. It seems fitting in this memorial volume that this lesser known aspect of Betsy's dissertation be complemented by my own study of the Sharon Springs Member farther south (Carpenter, 1996, see for complete inventory and specimen catalog numbers; not all specimens cited by Nicholls or by me have been cataloged because they remain unprepared).

To place the taphonomy of the Sharon Springs and Pembina in context, the depositional environment needs to be briefly described. Both members are some of the richest vertebrate bearing Cretaceous marine strata in the Western Interior. In numbers of specimens per square kilometer of outcrop, they equal and in some cases exceed the number of specimens in the Smoky Hill Chalk of the Niobrara Formation (Carpenter, 1996). The abundance of these vertebrate fossils suggest high productivity of the surface waters (more below), which in turn may have contributed to sea floor anoxia as evidenced by the high organic carbon in both shales. Total organic carbon (TOC) values in the Sharon Springs range between 3-11% (Gautier et al., 1984) making it one of the organically richest marine shale in the Western Interior. Lithologically, the Pembina and Sharon Springs are noncalcareous, dark gray to black shales that weather to silverish-black, greenish-black or brownish-black. The resistance of the shales to erosion due to their high organic content results in distinctive buttresses. Finely disseminated pyrite framboids are present in unweathered shales (Tourtelot, 1962; Schultz et al., 1980) and oxidation of this pyrite in the weathered zone produces gypsum, jarosite, ferric oxide, and hydroxide stains commonly found on the outcrop. Beds of phosphatic nodules occur, as do limestone concretions. Thin bentonites are present, especially near the base of the members. Accumulative thickness of these bentonites is up to 7.75 m (Gill and Cobban, 1973). The basal ash, the Ardmore bentonite, has produced dates of 80.54 ± 0.55 Ma by Obradovich (1993), 80.4 ± 0.45 Ma by Hicks et al. (1999; magnetic polarity C33R, Hicks et al., 1999), thus placing the Pembina and Sharon Springs in the Middle Campanian (Figure 2). The source for the ash is primarily the Elkhorn Range in western Montana (Gill and Cobban,

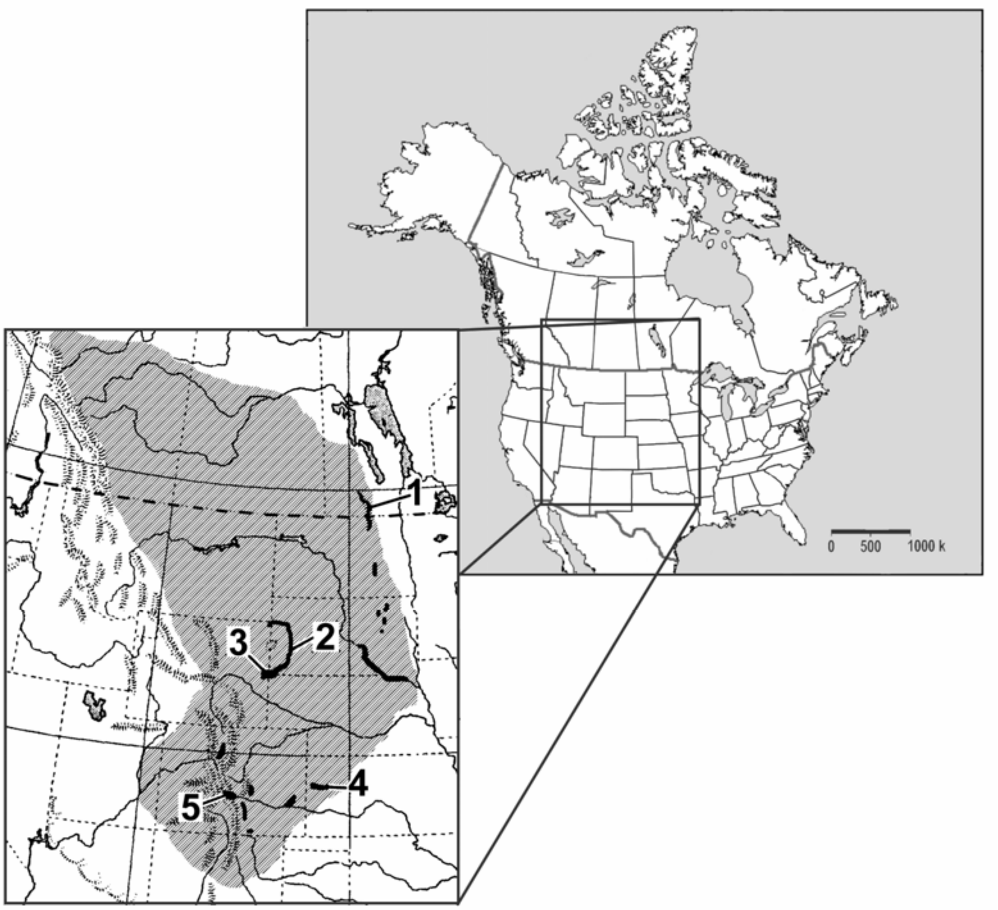

FIGURE 1.Distribution map of the Sharon Springs and Pembina Members (heavy lines) and Pierre Shale (cross-hatched) in the Western Interior. Major localities discussed in the text and figure captions: 1 - Manitoba Escarpment (Manitoba), 2 - Fairburn - Buffalo Gap (South Dakota), 3 - Edgemont-Red Bird (South Dakota - Wyoming), 4 - western Kansas, 5 - Cañon City (Colorado).

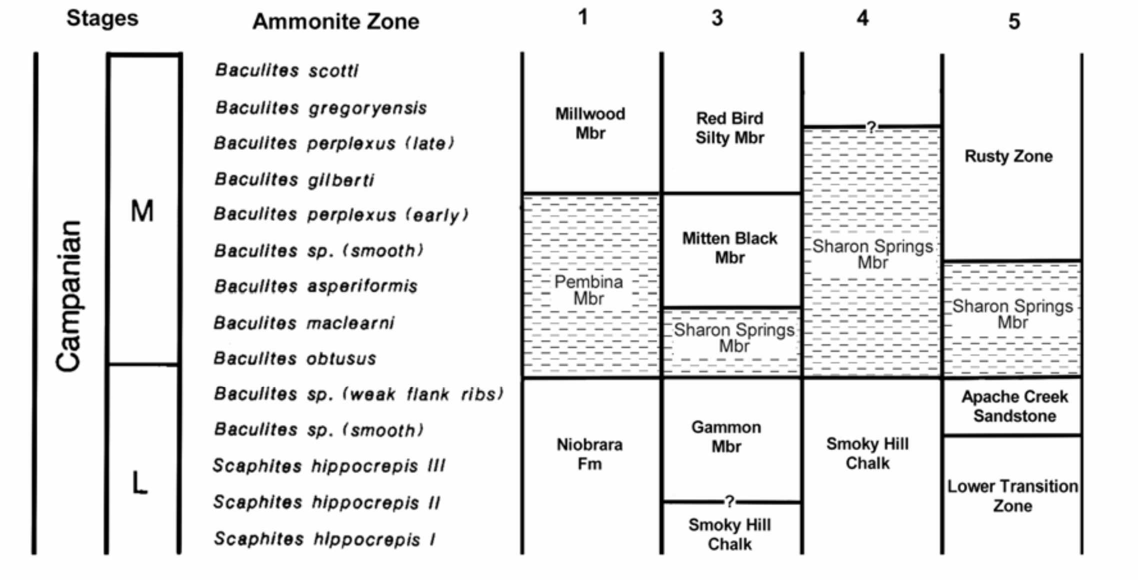

FIGURE 2. Biostratigraphy of the lower part of the Pierre Shale. Numbered columns correspond to localities in Figure 1.

1966, 1973; Rogers and Hendrix, 2000), although other sources nearer the West Coast are possible based on different bentonite composition (Bertog, 2002). The distinctiveness of the Sharon Springs and Pembina as separate members of the Pierre Shale may be disputed, but for now they are accepted as distinct.

The thickness of the Sharon Springs and Pembina varies considerably indicating different sedimentation rates in the seaway, as well as regional unconformities. In Colorado, the Sharon Springs is 13.7 m thick near Kremmling, 30 m at Cañon City and 34.5 m at Pueblo (Izett et al., 1971; Gautier et al., 1984; Scott, 1969). In western Kansas, the member is 68.6 m thick (Gill et al., 1972), whereas in Wyoming it is 37.2 m thick near Cheyenne and 38 m at Red Bird (Kiteley 1976; Gill and Cobban 1966). In South Dakota, the member is over 36 m near Hot Springs, but only 3 m near Chamberlain (Connor, 1963; Loutit et al., 1990). Sedimentation rates are estimated to have been 10 m/my at Cañon City, Colorado (Gautier et al., 1984), 64 m/my in western Kansas, and 104 m/my at Red Bird, Wyoming (Gill and Cobban, 1966). Gautier and Reddin (1983) report on sedimentation rates as low as 2 m/my in the Denver Basin, although they do not state where this was determined.

Estimates of water depth during the deposition of the Sharon Springs vary considerably, as they do for the Interior Seaway in general (Sageman and Arthur, 1994). Gill and Cobban (1966) estimated water depths as greater than 66 m based on sedimentological grounds, Mello (1971) estimated waters depths based on foraminifera as around 75 m, and Byers (1979) estimated water depths as 100 m or more. More recently, Bergstresser (1981) estimated water depths from foraminifera assemblages as middle shelf (30 - 100 m) at Cañon City, whereas depths in western Kansas were estimated to be outer shelf (100-200 m).

The production and preservation of the organically rich shales were probably due to complex interaction between inorganic and organic processes. Much of the organic carbon was probably the result of high productivity in the surface waters (Southam et al., 1982), especially in the upwelling zones (Parrish and Gautier, 1993), interstial sediment microbes (Kepkay et al., 1979), and benthic chemoautotrophic bacteria (Gallardo, 1977; Kepkay et al., 1979). In modern settings, chemoautotrophic bacteria form a very large portion of the biomass in H_2S-rich waters where they form extensive seafloor mats. Sulphate reduction in the surface of the sea floor plays an important role in the mineralization of organic carbon (Jørgensen, 1982). Once deposited on the sea floor, the preservation of the organic carbon may be due in part to its incorporation into the interlayer space of smectite (Kennedy et al., 2002), in part with its reaction with metallic ions (Degens and Mopper, 1975), and in large part to sedimentation leaving it as thin plates upon compaction of the seafloor sediments (Schultz et al., 1980).

The presence of sulfidic bottom waters in the Sharon Springs Sea has been determine by Gautier et al. (1984) from sulfur-carbon ratios and isotopically light sulfur in pyrite. These sulfidic bottom waters with a low pH may explain why calcareous foraminifera tests and steinkerns are rare in the Sharon Springs and Pembina (Mello, 1971; McNeil and Caldwell, 1981; Bergstresser, 1981; Bergstresser and Frerichs, 1982). The presence of sulfidic bottom waters, and not just anoxia, may be the cause for the absence of an epibenthic fauna in the Sharon Springs contrary to Byers (1979) and Archer and Hattin (1984). Trace fossils are not completely absent because *Skolithos* or *Chondrites* has been seen in a few concretions in Wyoming and Colorado (Figure 3), and *Chrondrites* in the Pembina where they occur beneath vertebrate specimens (Nicholls, 1988). These fossils, plus the few rare benthic invertebrate fossils show that bottom water chemistry was not consistent, but fluctuated occasionally. Benthic macro-invertebrates include several species of inoceramids (Gill and Cobban, 1966; Izett et al., 1971; Gill et al., 1972; Scott and Cobban, 1975), which are believed to have had chemosynthetic symbionts (Kauffman, 1987, 1988; MacLeod and Hoppe, 1992).

Rhythmic bedding is present in the Sharon Springs (Figure 4) and is the result of an interplay between increased primary production of organic carbon, increased organic carbon preservation under anoxic conditions and sediment accumulation rate (ROCC Group, 1986; Fischer, 1993; Kauffman and Caldwell, 1993). These cycles, also seen elsewhere in the Western Interior Cretaceous strata, undoubtedly reflect Milankovitch Cycles (ROCC Group, 1986; Fischer, 1993; Kauffman and Caldwell, 1993), although the range of cyclicity has not yet been established. The most obvious cycles may be the 20,000 year precessional because of their visual apparency (Fischer, 1993).

TAPHONOMY

Taphonomic data were recorded by both Nicholls (1988) and me (Carpenter, 1996) from surveys of museum collections and during field work. In addition, I recorded every fossil seen during field surveys in order to determine relative abundances and distribution of taxa; these results will be presented elsewhere (Carpenter, 1996), but highlights are presented below. A comparison of the faunas is summarized in Table 1. A full list of

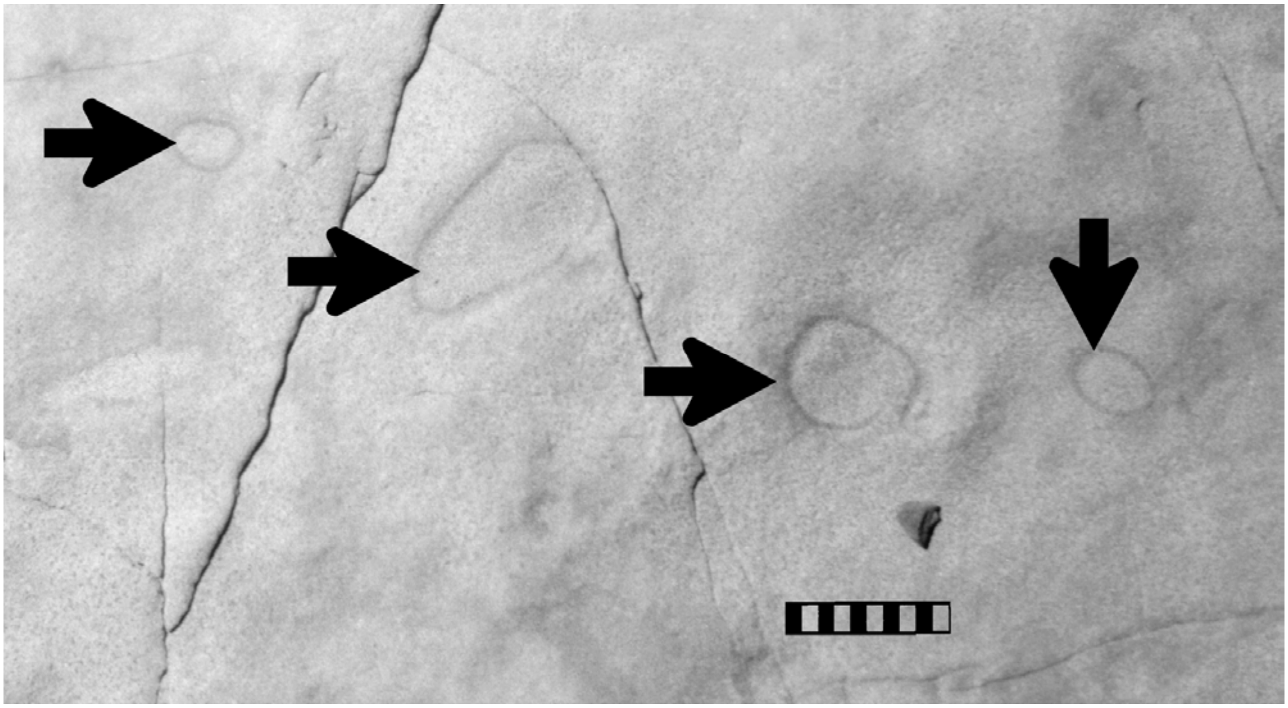

FIGURE 3. *Skolithos* or top of *Chondrites* (arrows) on a concretion in the Sharon Springs Member, Locality 5. *Chondrites* also occurs in the Pembina (Nicholls 1988). Scale in mm.

collections examined is given in Carpenter (1996). Specimens of the field inventory are mostly cataloged at the University of Colorado Museum. Institutional abbreviations used in the text: KUVP - Kansas University Vertebrate Paleontology, University of Kansas Museum of Natural History, Lawrence, KS; UCM - University of Colorado Museum, Boulder, CO.

Museum Occurrence—The sample sizes used in the taphonomic studies are large for vertebrates. Museum collections include 660 specimens from the Pembina (Nicholls, 1988), and 539 specimens from the Sharon Springs (Carpenter, 1996, 2003). The larger sample-size from the Pembina is due to the greater effort at salvage paleontology at bentonite mines. But Nicholls (1988) admitted that not all specimens were collected from the Pembina, especially if the specimen consisted of isolated bones, unless of a rare taxon. How biased the Pembina collections are is unknown. In contrast, data are available for the Sharon Springs. That the museum collections for the Sharon Springs are biased can be demonstrated by comparing the museum inventory with the multi-year field survey inventory (Figure 5), which recorded 871 specimens (Carpenter, 1996). At 77%, bony fishes are by far the most abundant specimens seen in the field, yet are only 42% of specimens in collections. In contrast, reptiles (marine reptiles + pterosaurs) make up only 20% of field specimens, but 40% of museum specimens. The most over represented specimen is the aquatic bird *Hesperornis*, which makes up only .03% of field specimens, but 13% of museum specimens. Interestingly, sharks make up 4% of both field survey and museum collections. A comparison of the biased museum collections of the Pembina and Sharon Springs specimens is presented in Figure 6. As may be seen, the Pembina collections are dominated numerically by reptiles, whereas those from the Sharon Springs are almost equally dominated by fishes and reptiles. Because the Pembina collections are knowingly biased, I am less inclined than Nicholls (1988) and Nicholls and Russell (1990) to accept the differences between the two strata as reliable.

Field Occurrence—Exposures of the Pembina Member are poor and most fossil discoveries occur in bentonite strip mines along the Manitoba Escarpment (Nicholls, 1988). In contrast, the Sharon Springs Member is well exposed in certain areas and fossils common. Specimens in both members range from isolated bones to nearly complete, articulated skeletons (Figure 7). Macerated fish remains are very common throughout both the Sharon Springs (Elias, 1931) and Pembina (Kirk, 1930), and form part of the original descriptions of these shales. The remains are of small individuals (<30 cm standard length), and some from the Sharon Springs are ascribed to an acanthomorph resembling *Sphenocephalus* and *Xenyllion* (Stewart, 1996). In contrast, articulated fish skeletons of this size are extremely rare, although *Aethocephalichthys* is known from masses of articulated

TABLE 1. Comparison of taxa from the Sharon Springs and Pembina Shales

Taxa	Sharon Springs	Pembina
Chondrichthyes		
Cretolamna appendiculata	X	X
Squalicorax kaupi	X	X
Osteichthyes		
Protosphyranea gladius	X	X
Xiphactinus audax	X	X
Ichthyodectes ctenodon	X	X
Gillicus arctuatus	X	?
Pentanogmius evolutus	X	X
Saurodon leanus	X	
Stratodus apicalis	X	X
Cimolichthyes nepaholica	X	X
Pachyrhizodus caninus	X	X
Pachyrhizodus minimus	X	X
Apteodus sp.		X
Enchodus petrosus	X	X
Enchodus gladiolus	X	
Proaurodon pygmaeus	X	
Saurocephalus lanciformis	X	
Aethocephalichthys hyainarhinos	X	
cf. *Sphenocephalus* sp.	X	
cf. *Xenyllion* sp.	X	
Chelonia		
Toxochelys latiremis	X	X
Protostega sp.		X
Mosasauridae		
Clidastes propython	X	X
Platecarpus tympanicus	X	X
Tylosaurus proriger	X	X
Hainosaurus pembinensis		X
Globidens dakotensis	X	
Plioplatecarpus cf. *P. primaevus*	X	
Plesiosauria		
Dolichorhynchops osborni	X	X
Styxosaurus snowii	X	X
Hydralmosaurus serpentinus	X	
Elasmosaurus platyurus	X	
Pterosauria		
Pteranodon n. sp.	X	
Aves		
Hesperornis regalis	X	X
Ichthyornis sp.		X

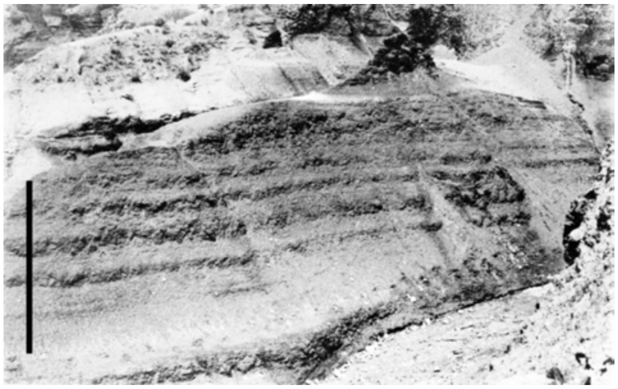

FIGURE 4. Rhythmic bedding in the Sharon Springs Member at Locality 3. Cyclic bedding is common in Cretaceous marine strata and is thought to correlate with Milankovitch Cycles. Heavy vertical bar is approximately 1 m.

scales that are laterally compressed bodies. Small fish remains are not associated with bentonite beds in either the Sharon Springs or Pembina, thereby demonstrating that volcanic ash settling through the water did not clog the gills of fish causing mass die-offs. The source of the macerated fish remains may be largely due to disaggregation of feces, because small fish bones are common in coprolites (Carpenter, 1996).

The isolated bones and skulls of larger vertebrates are most likely derived from floating carcasses. It is doubtful that scavengers played a significant role in scattering of bones on the sea floor because of the inhospitable bottom conditions precluded bottom scavengers (see above). Virtually every fish and reptile bone is represented among the solitary material, although not all taxa are represented. Schäfer (1972) reported that marine mammal carcasses buoyed by decomposition gases drift for weeks with isolated bones or small groups of bones falling to the sea floor. As it slowly falls apart, a drifting carcass can spread skeletal material over many kilometers of the sea floor, and such isolated bones are common in the Sharon Springs (e.g., Figure 7A). An isolated *Platecarpus* pelvis (UCM 70762) from Locality 3 probably represents such an occurrence. The ilium, pubis and ischium were articulated, and were evidently held together by ligaments. When found, the ischium was found protruding down through the shale suggesting that when the pelvis fell off the carcass it impacted with enough force to push the bone into the sea floor. In another example from Locality 3, an articulated string of 22 anterior caudal mosasaur caudals were found (but not collected), with several vertebrae at each end of the column scattered. Apparently, the distal end of the tail was lost first from a drifting body, then this anterior section later.

Only when decay has breached the body cavity and the gases are released do the remaining bones sink. A partial *Platecarpus* skeleton (UCM 70766) from Locality 3 may be such an example. It consists of jumbled bones scattered over about 2 m^2. Many elements were missing, but it is doubtful that this was due to erosion because so little debris was found on the surface of the soft shale. The vertebrae lay at various angles, with the neural spines of several dorsals extending down through the shale below the rest of the skeleton. The specimen lacks the skull, limbs and distal tail, parts that are lost first. The specimen appears to have been the remnant of a carcass that was mostly a jumbled bag of bones when it sank to the sea floor. It hit with enough impact to drive the neural spines into the seafloor. Headless plesiosaur skeletons from the Pembina represent such examples (Figure 8). However, not all vertebrate carcasses will float immediately upon death. Schäfer (1972) has shown that several factors determine if a carcass floats or sinks immediately upon death. These factors include fat content (whales with high fat content float, those with low sink) and whether the digestive tract was full or empty (if full, decomposition gases quickly inflate the body). Schäfer (1972) also notes that some fish species float, whereas others sink. The presence of many articulated skeletons of *Cimolichthys* and ichthyodectid skeletons suggests that possibly these two taxa tended to sink upon death (Figure 9). The relative abundance of skeletal completeness in the Sharon Springs is shown in Figure 10, where the vast majority occur as single, isolated bones. The least common are partial and complete skeletons.

All of the skeletons show some in situ disarticulation as the carcass lay on the sea floor. This disarticulation ranges from slight scatter of distal bones to more extensive separation of many or most elements. Nevertheless, the majority of the bones remain in proximity to their anatomical position (Figure 11). This wide range of disarticulation seems to imply variable, rather than continuous sedimentation, with less time between death and burial for the least disarticulated specimens. Discontinuous sedimentation for the Sharon Springs has been suggested before (Schultz, 1965; Gill And Cobban, 1966; Kennedy et al., 2002), and the same probably held true for the Pembina as well.

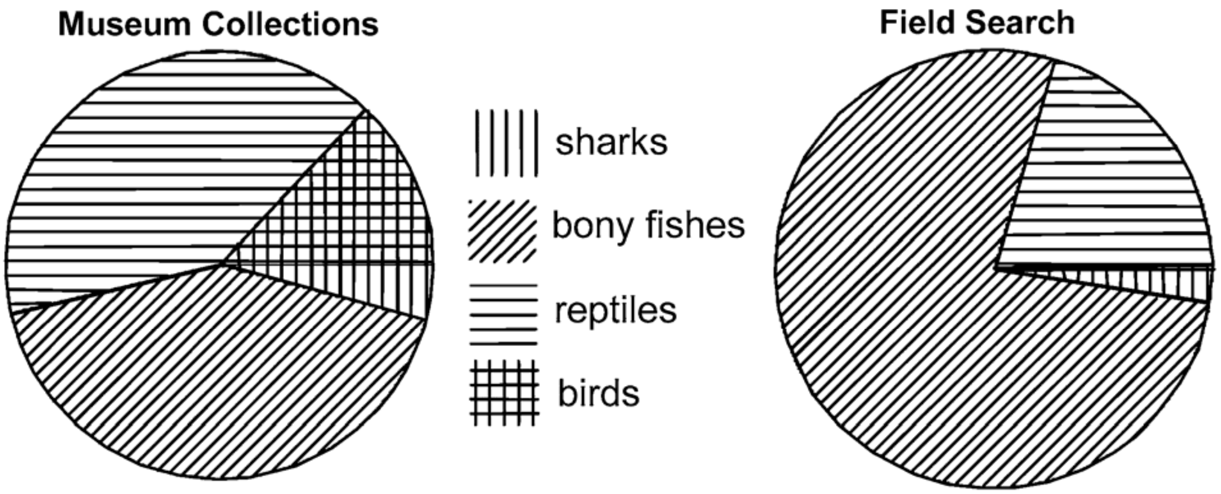

FIGURE 5. The biases of museum collections of vertebrates (n = 539) from the Sharon Springs is apparent when compared to a field inventory (n = 871) made in the same genera areas. The field inventory included isolated bones, which are rare in museum collections. Note the abundance of birds (14%) in museum collections versus their rarity in the field (.03%) In contrast, note the predominance of teleosts in the field (77%) versus 42% in collections.

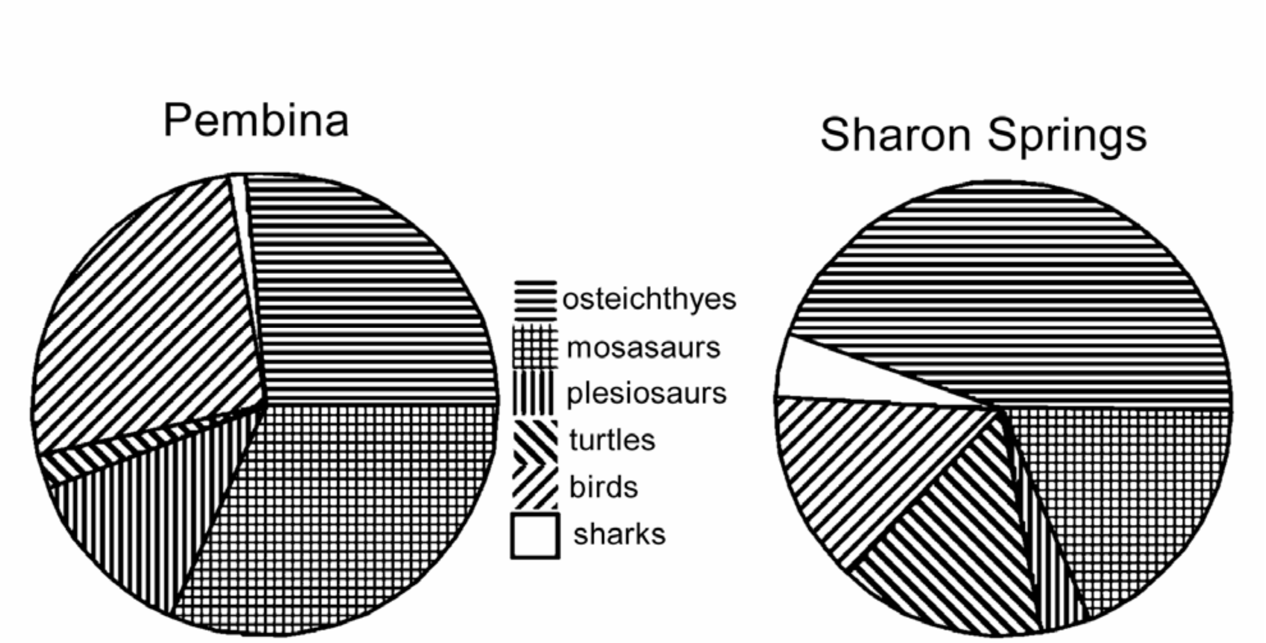

FIGURE 6. Comparison of marine vertebrates in museum collections for the Pembina (n = 660) and Sharon Springs (n = 539) Members. It is difficult to know how significant the differences are considering that both collections are biased. Pterosaurs are not included for the Sharon Springs data.

Results of Museum and Field Surveys—Some general trends are noted from the museum and field surveys.

Chondrichthyes - Shark diversity is low and specimens not very common in both the Pembina and Sharon Springs (Figure 6). At least two taxon are known, *Squalicorax kaupi* and *Cretolamna appendiculata* based on poorly preserved teeth. Calcified chondrichthian vertebral discs are more common than teeth, and often occur in articulated segments (Figure 11A). Some calcified cranial parts are known and some of these contain teeth in situ (Figure 11B); these specimens are known from the Sharon Springs, but apparently not from the Pembina (Nicholls, 1988).

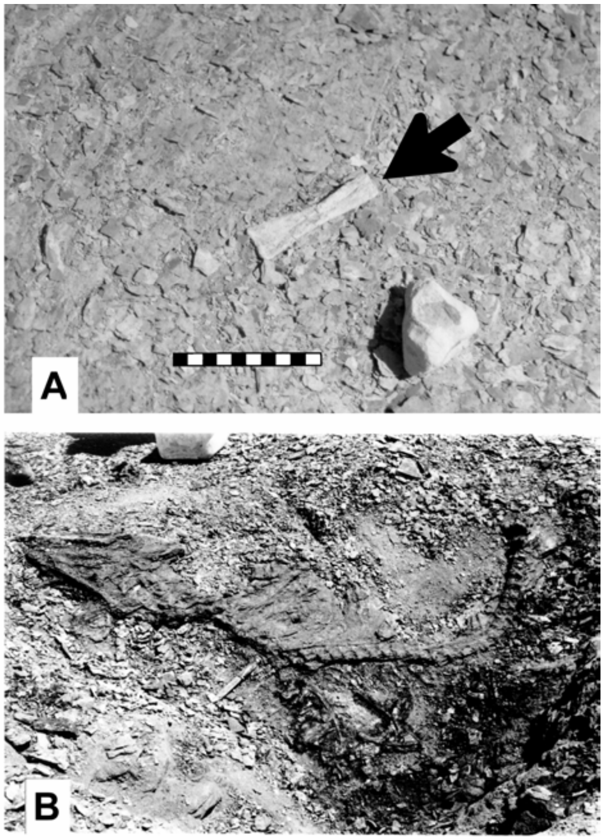

FIGURE 7. Vertebrate specimens in both the Pembina and Sharon Springs Members range from isolated bones (A) to articulated skeletons (B). A - *Toxochelys* metacarpal, Locality 3; B, *Platecarpus* skeleton, Locality 3. Scale in A in cm.

Osteichthyes - In museum collections, bony fishes are more common from the Sharon Springs than from the Pembina (Figure 6), possible due to more selective collecting in the Pembina (Nicholls, 1988). Nevertheless, museum collections as a whole do not reflect field occurrences, with fishes vastly under collected (Figure 5). As noted above, bony fishes remains range from isolated bones to complete skeletons (Figure 10). Most of the complete fishes are ichthyodectids, which must have readily sunk upon death (Figure 9). Nicholls (1988) noted little evidence of predation among the fishes, whereas this is very common among Sharon Springs specimens; this evidence is elaborated upon below. Small fish remains (<1 m) are common as isolated bones or in coprolites, but rare as whole skeletons. The few articulated specimens include *Enchodus* and *Aethocephalichthys*, the latter of which occurs as flattened bodies of scales. *Aethocephalichthys* is moderately common at Red Bird, Wyoming, where the distinctive neurocranium making up about 10% of identifiable teleosts remains. Large fish are most common as skeletons, especially the 1-2 m long *Cimolichthyes*, *Ichthyodectes* and *Gillicus*. The largest fish (>3 m), *Xiphactinus*, is not as common as in the Niobrara Formation .

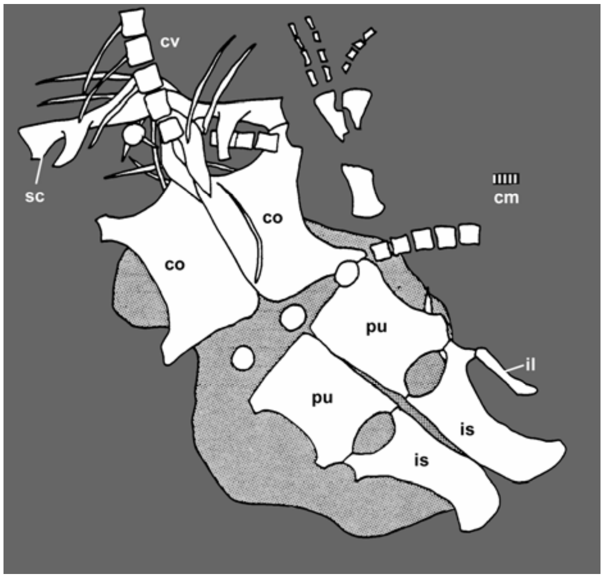

FIGURE 8. Quarry map of a headless, tail-less and limbless (except for the left forelimb) *Dolichorhynchops* skeleton, Locality 1.Stippled region is zone of gastric residue. Abbreviations: co - coracoid; cv - cervical vertebrae; il - ilium; is - ischium; pu - pubis; sc - scapula. Scale in cm. Modified from Nicholls (1988, Quarry Map 4).

Plesiosaurs - Plesiosaurs are more common in the Pembina museum collections than in those from the Sharon Springs. Most all plesiosaurs remains are collected because of their rarity, thus the difference between the Pembina and Sharon Springs museum collections is probably real. The collections contain both polycotylids and elasmosaurids, with the polycotylid *Dolichorhynchops* dominating numerically over elasmosaurs in both the Pembina (> 90%) and Sharon Springs (>80%). Most plesiosaur specimens are headless and all lack some of the distal-most phalanges. Numerous specimens consist of the thoracic section, including dorsals, ribs and girdles; one or more propodials may also be present, but usually lack the phalanges (Figure 12). Nicholls (1988) noted that girdle elements tend to remain articulated and separate from the rest of the carcass. Although this may be true, I cannot substantiate this from her figures (e.g., Figs. 8, 12), nor for specimens from the Sharon Springs. Because most skeletons lack skulls, plesiosaurs probably floated upon death and lost their heads as they drifted. Plesiosaur carcasses would have provided a large supply of food to scavengers, and the most complete skeletons probably sank once the body cavity was breached by these scavengers thereby allowing decomposition gases to vent.

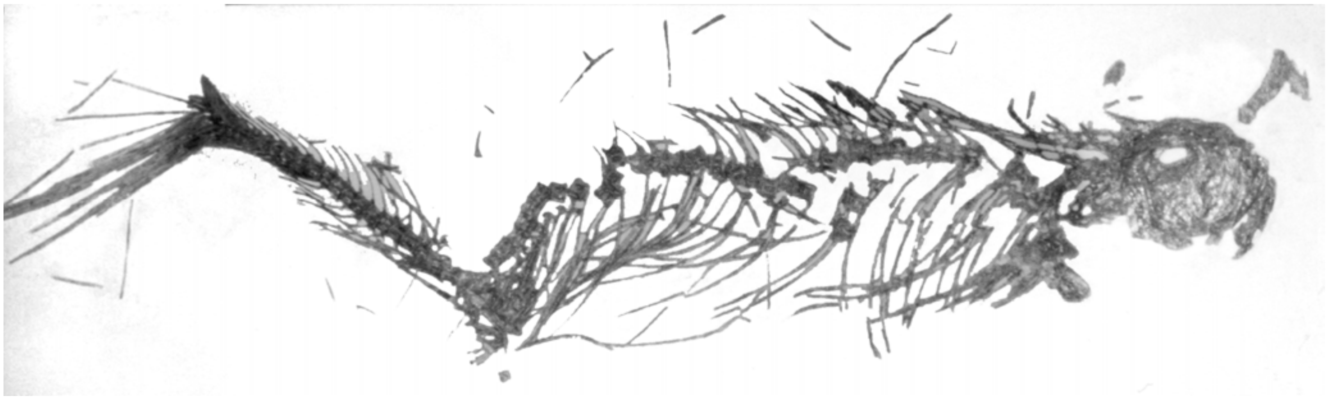

FIGURE 9. Nearly completely articulated *Gillicus* (UCM 30278), Locality 3. Slight disarticulation indicates decomposition on the sea floor prior to complete burial.

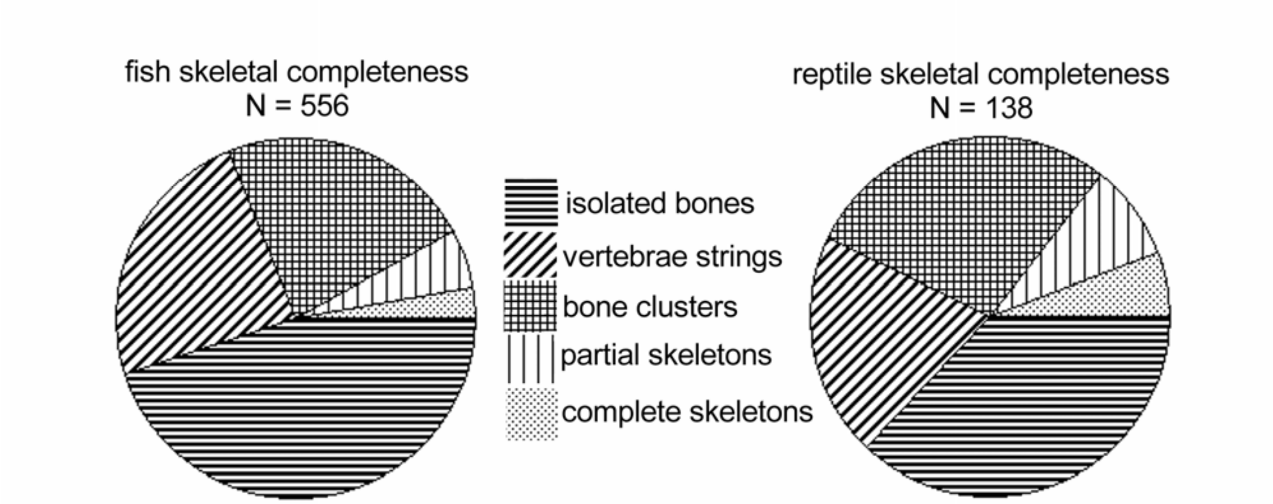

FIGURE 10. Comparison of the relative completeness of fish and reptile specimens in the Sharon Springs Member based on the field survey.

Mosasaurs - Mosasaurs are more common in the Pembina collections than from the Sharon Springs (Figure 6). Skulls are known for many specimens, although a large proportion in the Pembina appear to be disarticulated (Nicholls, 1988); this does not appear to be true of those from the Sharon Springs. Specimens range from isolated bones from drifting carcasses to nearly complete skeletons (Figure 7A); distal phalanges are usually missing even from the most complete specimens.

Turtles - Sea turtle remains consist exclusively of isolated bones or more commonly as groups of bones; no complete skeleton is known from either the Pembina or Sharon Springs. The groups of bones are usually from the same anatomical region, e.g., skull, cervicals and forelimb (Figure 14), and rarely from a mixture of different regions: skull, cervicals and hindlimb. This pattern indicates that the turtles floated upon death, with body parts separating as the carcass drifted. The turtle *Toxochelys* is moderately abundant in the Sharon Springs, but rare in the Pembina (Figure 6). *Protostega* is known from the Pembina (single specimen) and is thus the only occurrence of this taxon from the Pierre Shale.

Pterosaurs - *Pteranodon* specimens are rare in the Sharon Springs, and unknown from the Pembina. Most specimens consist of isolated bones or small clusters of bones, rarely much more (Figure 14A). The floating of the carcasses was enhanced by the highly pneumatic skeleton. A single, partial skull is known, with a short, erect crest (Figure 14B). Pterosaurs are not included in the comparison chart of Figure 6, but are in Figures 5 and 10.

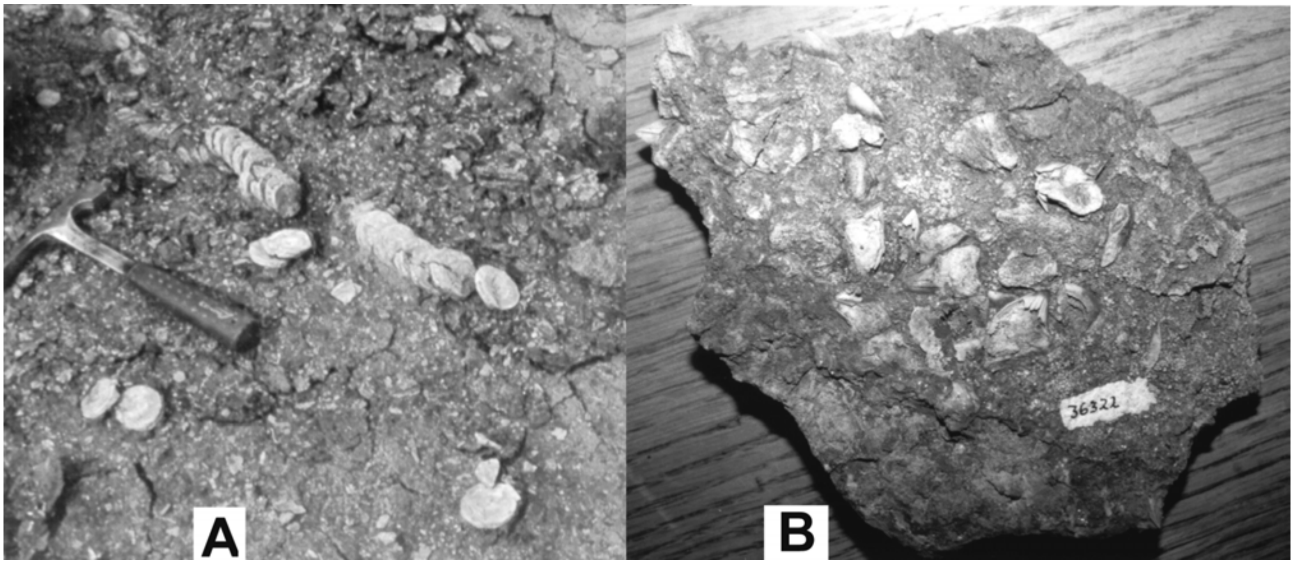

FIGURE 11. Chondricthyes remains from the Sharon Springs Member, Locality 3. (A) calcified vertebral centra, (B) *Squalicorax* teeth in situ with calcified cartilage (UCM 36322).

FIGURE 12. Quarry map of a *Dolichorhynchops* from Locality 1. The skull and most of the cervicals, caudals and podials are missing (modified from Nicholls 1988). Abbreviations: c - centrum; co - coracoid; f- femur; h - humerus; pu - pubis.

FIGURE 13. *Toxochelys* specimen (UCM 70716) in the Sharon Springs Member. The specimen consists of an upside down skull with lower jaws in occlusion, cervicals and partial left pectoral and forelimb. From Locality 3.

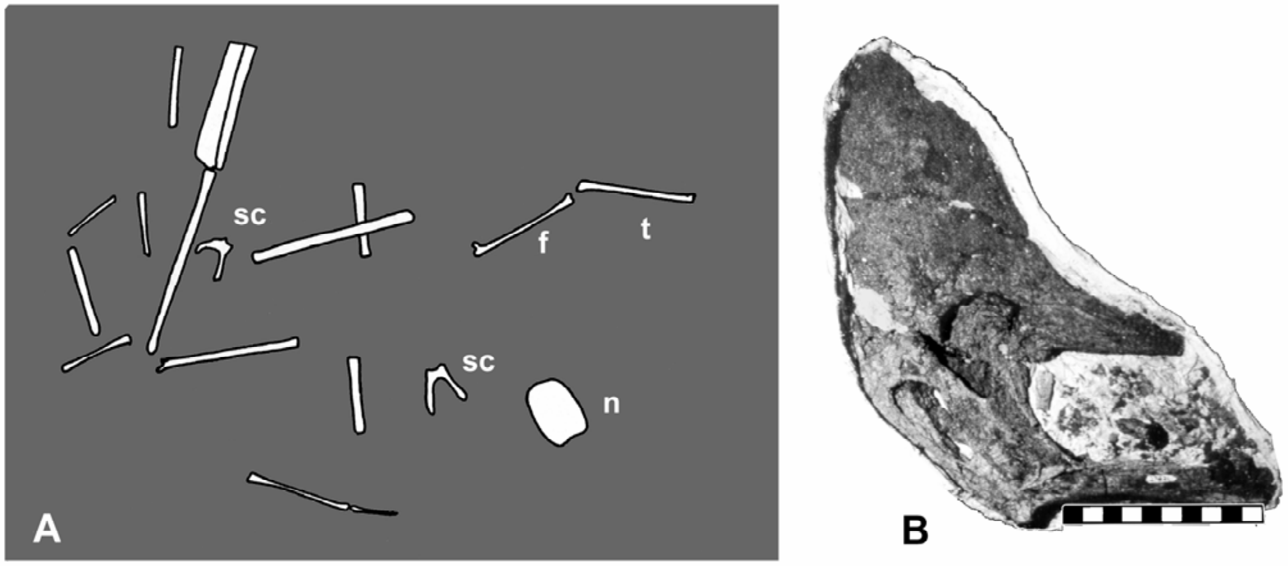

FIGURE 14. *Pteranodon* is rare in the Sharon Springs. Specimens usually consist of isolated bones or small clusters of bones, although one partial skeleton is known (A - quarry map; UCM 45062)), although one skull is known (B; KUVP 27821). Abbreviations - f - femur; n - notarium; sc - scapula-coracoid; t - tibia. Scale in B in cm.

Aves - The aquatic bird *Hesperornis* has a very unusual distribution, occurring almost exclusively along the eastern half of the Interior Seaway deposits (just east of the Black Hills, South Dakota, and Pembina Escarpment, Manitoba) . Cranial material is extremely rare, with most specimens consisting of hindlimb material, or posterior dorsals, pelvis and hindlimb. This distribution indicates that *Hesperornis* floated after death, with the posterior, non-pneumatic portions falling off. The tern-like *Ichthyornis* is known from two specimens in the Pembina and is the only occurrence from the Pierre Shale. It is not included in the chart of Figure 6, although *Hesperornis* is because it is fully aquatic. The high percentage (26%) for the Pembina collections is biased as Nicholls (1988) has noted. Nevertheless, *Hesperornis* does appear to be more abundant than in the Sharon Springs.

Other - a few dinosaur specimens are known, including the posterior half of a hadrosaur skeleton from the Sharon Springs (Figure 15). Most dinosaur specimens consist of isolated bones, mostly vertebrae. The hadrosaur was partially articulated indicating a considerable amount of soft tissue still bound the skeleton when it sank. It is not included in Figure 6.

Predation and Scavenging—Evidence for predation and scavenging occur on numerous specimens in the Sharon Springs Member; Nicholls (1988) could not substantiate this for many specimens from the Pembina Member. Much of the evidence is similar to that reported by Zangerl and Richardson (1963) from the Pennsylvanian, and includes regurgitated masses of bone or shell. Regurgitation is common among modern fish (Bowman, 1986) and reptiles (Andrews et al., 2000) as a means of removing food residues from the gut. Rejecta in the Sharon Springs is recognized by its limited extent, sharp boundaries and distinct, often phosphatic matrix surrounding bones. A mass of apparently regurgitated small, broken bivalves was found at Red Bird, Wyoming. The appearance is similar to that reported by Barthel and Janiche (1970) for a mass of aptychi.

Other evidence of predation on invertebrates include a *Platyceramus* with possible marginal damage (Figure 16). The mosasaur *Globidens*, with its bulbous teeth, from the Sharon Springs, has been suggested as a molluscivore (Russell, 1975). Interestingly, this genus has not been reported from the Smoky Hill Chalk where inoceramids are more common, possibly due to *Globidens* being a late arrival. Predation on *Baculites* is seen at Red Bird and Cañon City, Colorado, where segments of shell are common. Excavation of the shells has shown the buried end to be jaggedly truncated on many specimens, thus eliminating erosion as the cause (Figure 17). *Globidens* could certainly have preyed on these cephalopods, as could the stout-headed platecarpine mosasaurs. Thin shell fragments associated within a mosasaur (genus indet.) ribcage from Red Bird may be *Baculites* fragments. Brown (1904) reported scaphites associated with an elasmosaur from the Sharon Springs at Red Bird.

The most abundant invertebrate in the Pembina and Sharon Springs is the squid *Tusoteuthis*. Its rachis fragments are common in coprolites in the Sharon Springs and most of these are small, suggesting whole gladius <40 cm long. In at least one instance, the predator is known to have been *Cimolichthyes nepaholica*, a barracuda-like fish. This specimen from Red Bird has a 66 cm long gladius within the ribcage with the anterior end extending behind the operculum (Figure 18A; UCM 29667 and 29556). The mouth of the fish is open suggesting that the soft anatomy of the squid extended out of the mouth (Stewart and Carpenter, 1990). Another very large *Tusoteuthis* (gladius 128 cm long) from the Sharon Springs has three large punctures that have splayed the rachis rod bundles (Figure 18B, C; UCM 29668). The large size of the punctures (not crushed zones) and the great distance, 31 cm, separating two of the punctures suggests attack by a large mosasaur with a wide mouth, possibly *Tylosaurus*. Other mangled *Tusoteuthis* specimens from both the Pembina and Sharon Springs may have also be damaged by predator attack. They certainly cannot be damaged due to sediment deformation because in each case, the specimen lies along in the same plane, not across it.

Among vertebrates, predation is most commonly seen among fishes. Jumbled fish bones are common in phosphatic coprolites (Figure 19), especially in the Sharon Springs. Masses of regurgitated fish bones also occur in phosphatic sheets. Usually these masses are 20-30 cm in diameter, and composed of disarticulated fish bones. Similar masses are associated with plesiosaur skeletons in the Pembina (Figure 8; Nicholls, 1988). Phosphatic sheets from the Sharon Springs are similar to those described by Zangerl and Richardson (1963) and referred to as gastric residues from sharks. Although rare sharks are present in the Sharon Springs, regurgitation by other large predators cannot be discounted. Martin and Stewart (1982) referred to similar objects from the Pembina as coprolitic, and which Nicholls (1988) referred to as a regurgitated mass. *Enchodus* and other clupeomorph fishes have been reported associated with the stomach content of a headless elasmosaur (Cicimurri and Everhart 2001), and *Apteodus* with the stomach contents of *Dolichorhynchops* (Nicholls, 1988).

Other fish show indications of having been regurgitated before digestion. The tail of a medium-sized ichthyodectid shows all of the tail fins pulled posteriorly against each other from their more normal splayed position. The vertebrae sizes suggest an individual ~2 m

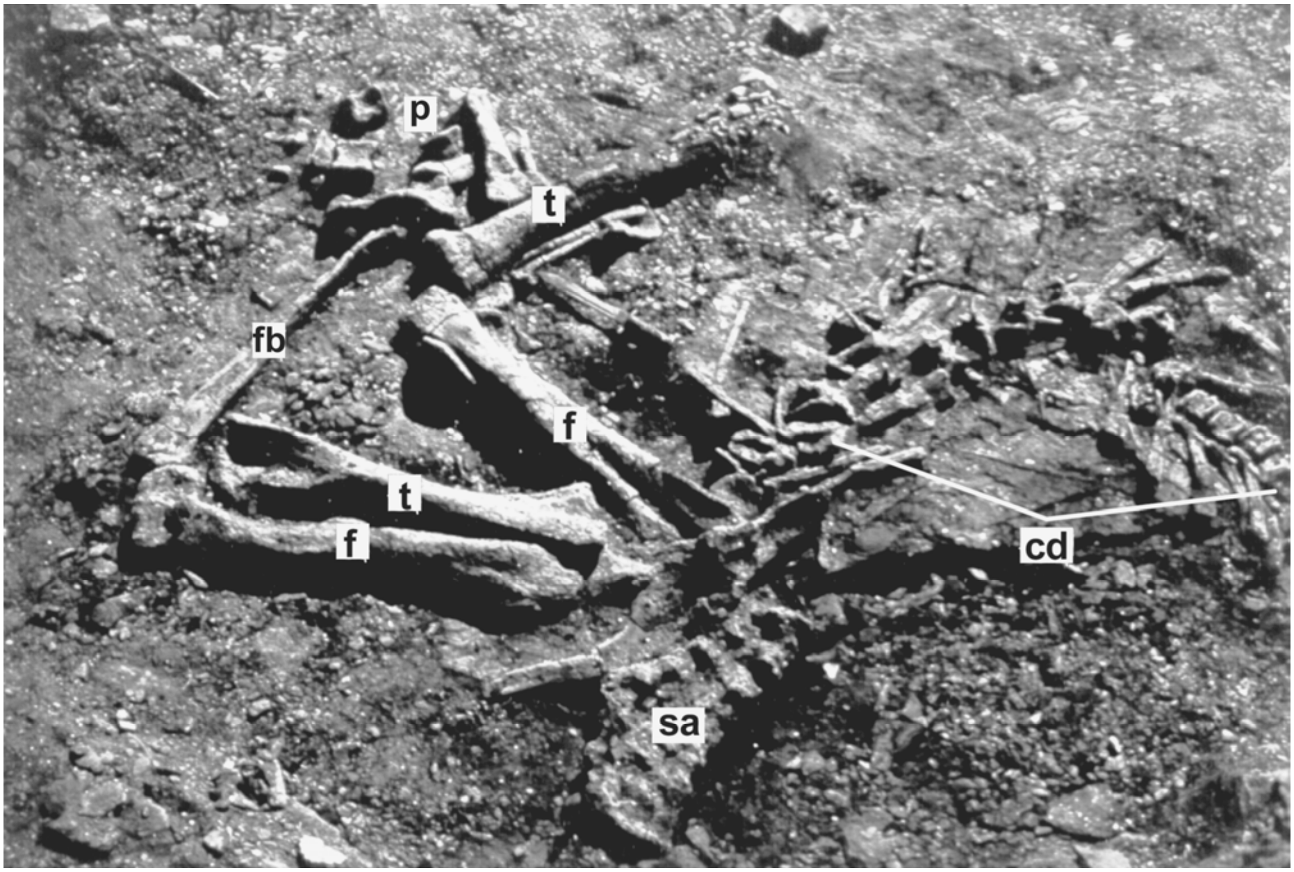

FIGURE 15. Dinosaurs constitute erratics in the Sharon Springs, as this partial hadrosaur (UCM 55033) illustrates. The specimen represents a carcass that drifted far from land before the posterior section separated and sank separately from the anterior section. The distal end of the tibia and a small portion of the right femur were exposed at the time of discovery. The ventral side of the skeleton lay on a single bedding plane indicating a firm rather than soupy sea floor. From Locality 3. Abbreviations: cd - caudals; f - femur; fb - fibula; p - pedal elements; sa - sacral vertebrae; t - tibia.

standard length. The anterior part of the body is missing (not from erosion) showing that the tail had been severed and swallowed, but then regurgitated (the specimen was deeply weathered, so was not collected; it was recorded in the field notes for 1978).

Traumatic injuries are also seen among the vertebrates, most commonly among fishes from the Sharon Springs. A nearly complete *Ichthyodectes* skeleton (UCM 70748) was bowed into a U-shape with both head and tail still encased in matrix. When excavated, the caudal fins were missing and were probably bitten off. Another specimen is more equivocal, consisting of a *Cimolichthyes* with a sharp break in the tail and the body folded over itself (see Carpenter, 1996, Figure 10A). Much more common are isolated fish tails that show severed vertebrae (Figure 20). These specimens show that the anterior, more meaty portion of the fish was eaten. Less common are the anterior portions of fish lacking the posterior portions, which were evidently eaten. One example is of a partial *Enchodus* skull (UCM 70743) that, when excavated, was found to consist only of the lower portions of the skull, the top part apparently having been bitten off jaggedly. It is possible that some of the partial skulls reported by Nicholls (1988) from the Pembina are severed remains.

The predators of these fishes are known in a few instances because fish bones have been found within the ribcages or in associations that are best explained as indicating prey. For example, Cicimurri and Everhart (2001) report on an *Enchodus* within a *Cimolichthyes*. Vertebrae, tail fin and possibly the skull of a small fish was found in the posterior abdominal region of a remarkably complete *Clidastes propython* (UCM 70777) from the Sharon Springs, and a string of ichthyodectid vertebrae was found within the ribcage, posterior to the pectoral girdle. Fish bones were found in two small coprolites associated with a *Pteranodon* sp. skeleton (UCM 45062) at Red Bird, Wyoming. Fish bones were also found in coprolites associated with a skeleton of *Toxochelys latiremis* (UCM 70738). Small fish bones and

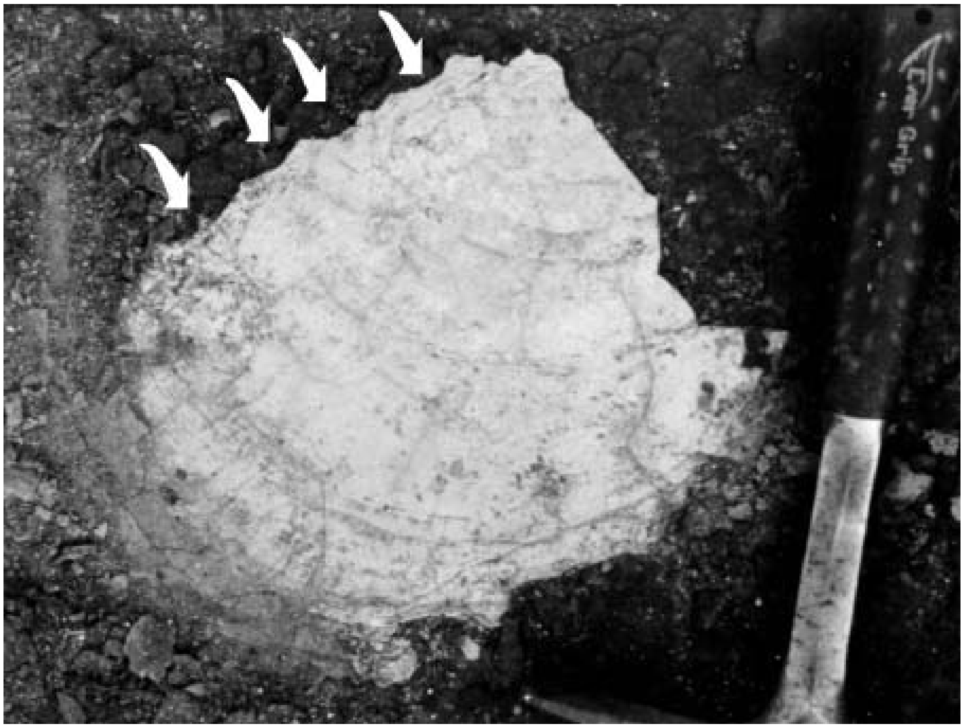

FIGURE 16. Rare specimen of *Platyceramus* from the Sharon Springs. Only a small portion of the anterior edge (lower left) was exposed at time of discovery. Note the scalloped margins (arrows) suggestive of predation by a large mouth, possibly the mosasaur *Globidens*. From Locality 3.

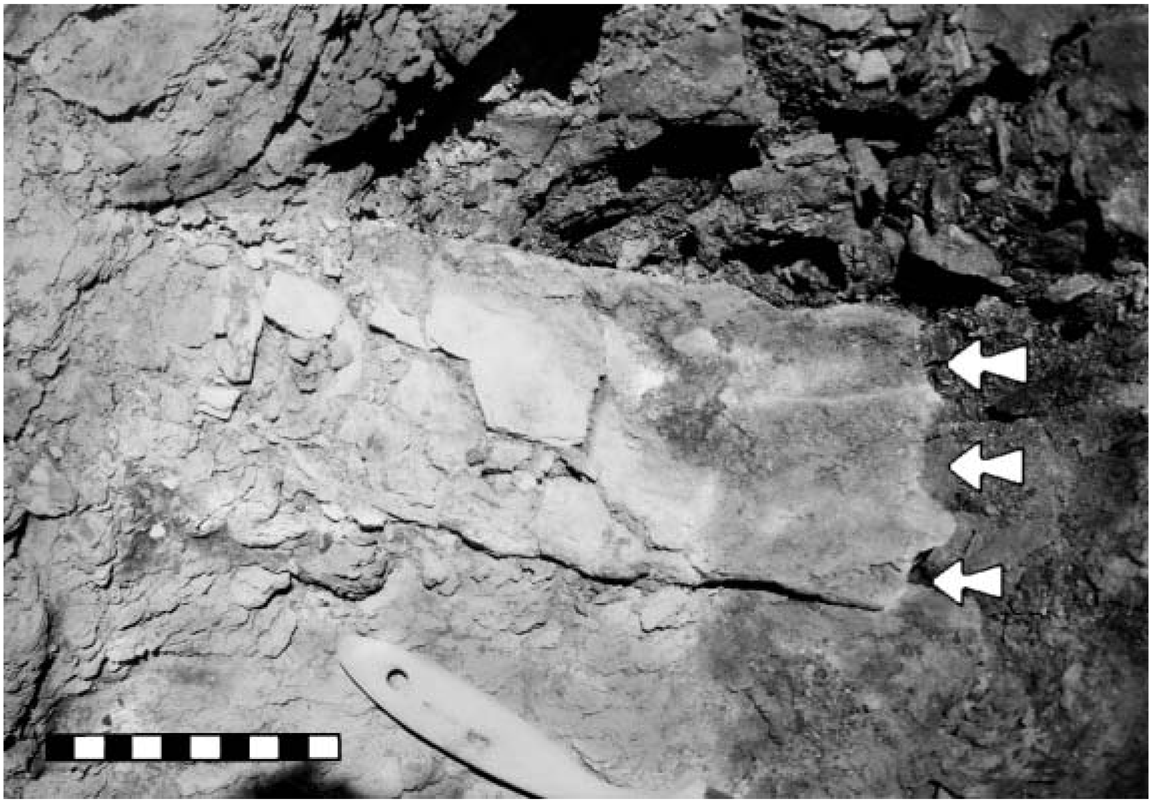

FIGURE 17. Partial, predated *Baculites mclearni*, Sharon Springs, Locality 3. Edge of probable mosasaur tooth marks at arrows. Note the lighter colored region, which was exposed, and the darker region (including tooth marks) was still buried. Therefore, the jagged edge was not due to erosion. Scale in cm. From Locality 3.

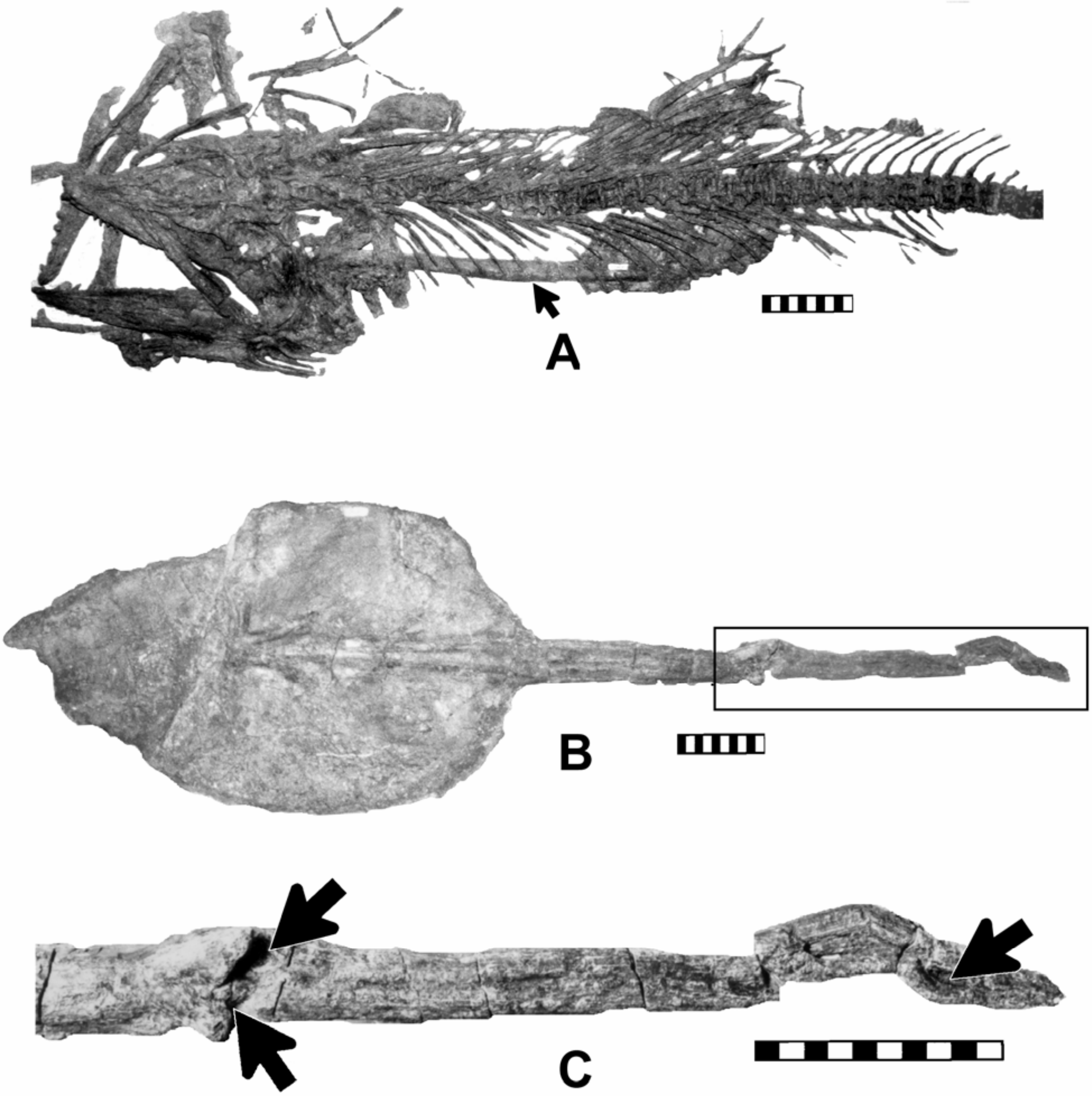

FIGURE 18. Evidence of predation on *Tusoteuthis* includes a nearly complete gladius within a *Cimolichthyes* specimen (A; UCM 29667 and 29556), and tooth punctures in the rachis of another, larger specimen (B, closeup C; UCM 29668). The rachis rod bundles are splayed apart around the tooth punctures (arrows). The large gap between the tooth punctures in C suggest a large mosasaur, possibly *Tylosaurus*. *Globidens* was probably not the predator because of punctures, rather than crushing of the rachis. Both specimens from the Sharon Springs, Locality 3. Scales in cm. From Locality 3.

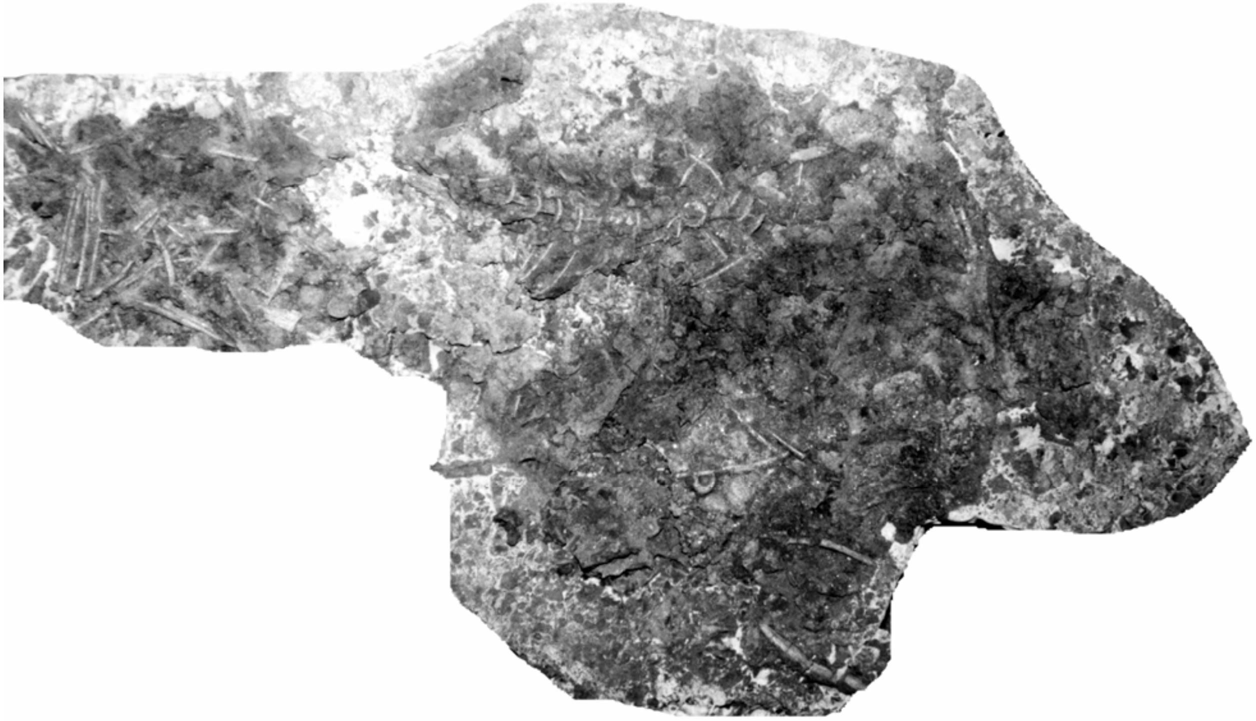

FIGURE 19. Small fish bones (*Enchodus*?) in a regurgitated mass. The ground mass incorporating the bones is highly phosphatic. From Locality 3

shell fragments, possibly from an ammonite, were found within the ribcage of a partial, unidentifiable mosasaur skeleton in a septarian concretion at Red Bird (the specimen was too fragmentary to collect). Brown (1904) reported found fish bones, and *Pteranodon* bones associated with an elasmosaur from Red Bird.

Predation on reptiles is evidenced by an incomplete juvenile polycotylid propodial (UCM 48359) from the Sharon Springs (Figure 21). The distal end is jagged and the bone crushed in a way that cannot be explained by weathering or erosion. This specimen is best interpreted as a severed limb. Predation on turtles is evidence by a juvenile skull within the abdomen region of a *Clidastes*, and possibly by some of the partial *Toxochelys* skeletons (e.g. UCM 70727, 70728). Predation on mosasaurs undoubtedly occurred as suggested by Martin and Bjork (1987), but few examples are known. One probable example is a partial, apparently sheared off caudal centrum associated with a string of mosasaur (?*Platecarpus* sp.) vertebrae from the Sharon Springs (the specimen was recorded but not collected).

WESTERN INTERIOR SEAWAY CURRENTS BASED ON TAPHONOMIC EVIDENCE

The taphonomy of the vertebrate remains discussed above not only provides evidence of vertebrate behavior, but also provides some important clues to the conditions within the Western Interior Seaway, especially bottom waters and sea floor substrate. During the field survey of the Sharon Springs, azimuth data were collected on any elongate object, including baculite shells, articulated vertebrate skeletons, strings of vertebrae, pterosaur limb bones, and logs. These data were collected because they should record current direction of the bottom waters, the presence of which has been discussed by Gill and Cobban, 1966). These data, along with bentonite and glauconite distribution maps, are used to reconstruction current and prevailing wind direction (discussed below).

Sea Floor—The condition of the sea floor of the Interior Seaway has been variously argued as firm to soupy (Kauffman and Caldwell, 1993). The hadrosaur skeleton (UCM 55033) from the Sharon Springs provides an ideal test for the various models. The preserved portion of the skeleton is mostly articulated (Figure 15)

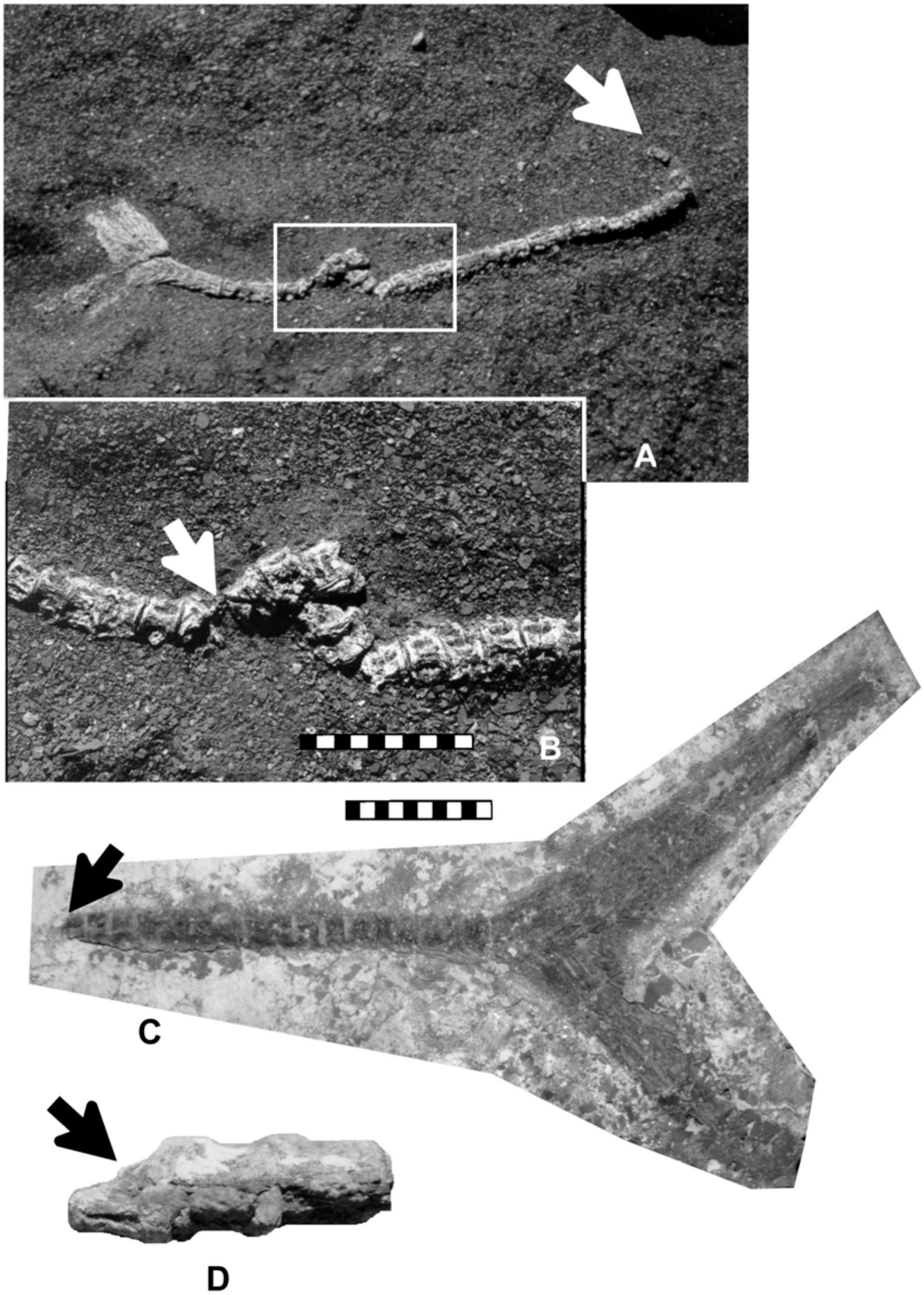

FIGURE 20. Evidence of predation on fish (ichthyodectid) is seen in the abruptly terminated vertebral column (arrow in A) and mangled vertebrae (enlargement in B). Another example includes a tail (*Cimolichthyes* UCM 70736) with truncated vertebra (C), seen in profile in (D). Scales in cm. All from Locality 3.

and lay along the same bedding plane. This skeleton demonstrates that the sea floor at that time was solid enough that the carcass did not sink appreciably on impact when it separated from the rest of the body. This means that a soupy sea floor is not the reason for the near absence of benthic invertebrates as has been hypothesized (Kauffman and Caldwell, 1993). Another example supporting a firm sea floor is the partial *Platecarpus* skeleton (UCM 70766) mentioned above in which several neural spines project down into the shale, whereas the bulk of the specimen lay on the same bedding plane. The specimen is of a carcass that floated before the rear portion separated and sank to the sea floor rapidly enough to drive some of the neural spines of the contorted vertebral column into the sediment.

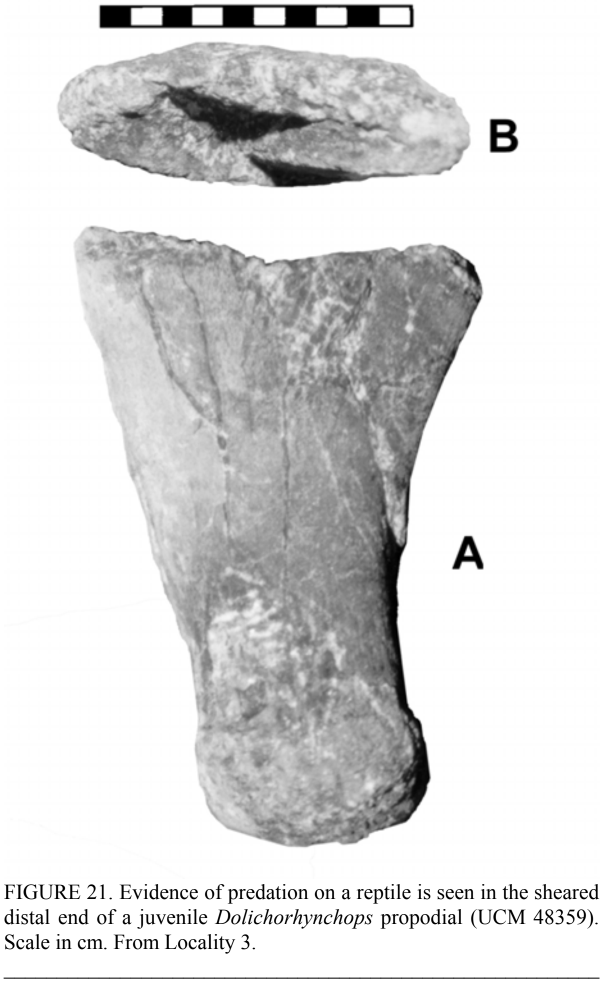

FIGURE 21. Evidence of predation on a reptile is seen in the sheared distal end of a juvenile *Dolichorhynchops* propodial (UCM 48359). Scale in cm. From Locality 3.

Bottom Waters—Articulated vertebrate skeletons in the Sharon Springs and Pembina should have provided an ideal surface for benthic organisms, such as the oyster spats on inoceramid shells from the Smoky Hill Chalk (e.g. Hattin, 1982), however none were found. This absence suggests that dyserophic or anoxic conditions extended upwards into the water column, although how high is not known. Considering that the highest surface for the hadrosaur mentioned above (lateral surface of the femur) was over 30 cm above the undersurface of the skeleton (e.g., sacrum), anoxic conditions extended at least that far. Most probably there was a gradient of decreasing oxygen content with depth (Figure 22). This undoubtedly coincided with a increase in organic carbon preservation potential as well.

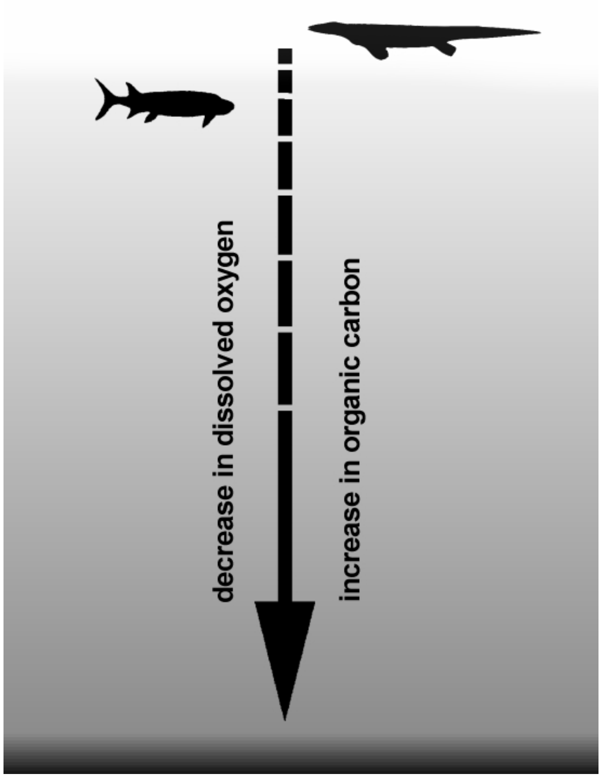

FIGURE 22. Profile of the Claggett Seaway has greater oxygen in the surface waters and less with depth. There is a increase in organic carbon with depth due to the drop off of anerobic decomposition.

Azimuth orientations of *Baculite* accumulations in the Sharon Springs are shown in Figure 23A (corrected for the Late Cretaceous paleopole position). Most of the specimens from the Sharon Springs consist of crushed, limonitic-gypsiferous shells that are found eroding from the shale (e.g. Figure 17). Because it was not always possible to determine the azimuth relative to the living chamber, the azimuth data were plotted in a mirrored 180° rose diagram. The largest baculite datum set is a combination of two groups from Red Bird, Wyoming (N = 92 and N = 66). The second largest group is from a single set at Cañon City, Colorado (N = 56), and the smallest from near Wallace, Kansas (N= 26). The Red Bird and Cañon City data sets are from areas 12-15 m^2

and from shale intervals 15-50 cm thick. The use of azimuth data from more than one bedding plane is justified because the data record the prevailing current directions, rather than a single, possibly abnormal current. The Wallace data set are from a mass accumulation of *Baculites asperiformis* in a concretion, and thus records a shorter interval of time. Scatter of the data are greatest in the Red Bird and Wallace samples, although both still show strong trends. The scatter may reflect the passage of large storms because the Cañon City data set was more protected in an embayment; here, two main axes are very distinct.

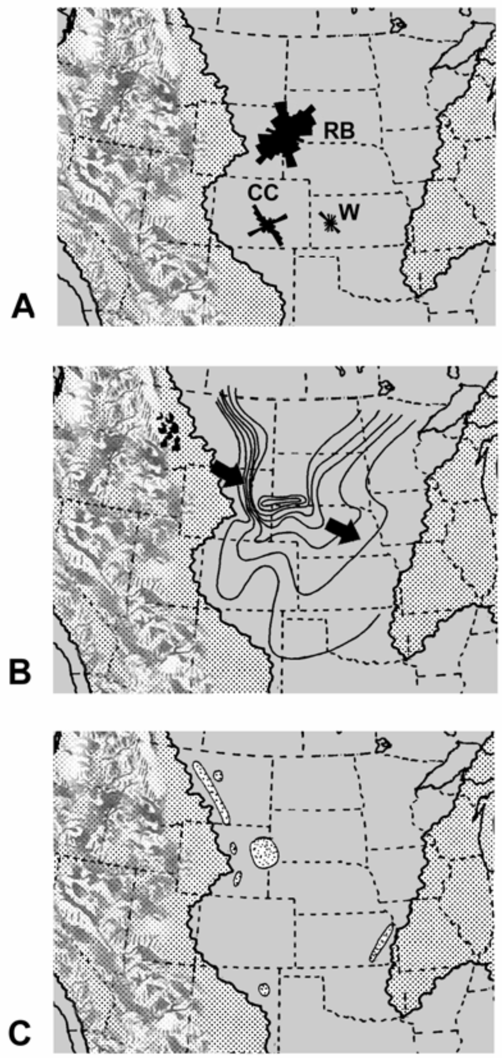

FIGURE 23. Data maps for inferring currents in the Claggett Seaway. A, Baculite orientation from Red Bird, Wyoming (RB); Cañon City, Colorado (CC); and Wallace, Kansas (W). B, isopach map of bentonite superimposed on a map of the Interior Seaway during *Baculites obtusus* zone. Inferred prevailing wind direction shown with heavy arrows (in part from Gill and Cobban 1973). C, distribution of glauconitic sands superimposed on the Interior Seaway.

Seaway Conditions—Hypothetical water circulation for the Claggett Seaway is presented in Figure 24, as well as prevailing wind direction. This interpretation is a compilation of the baculite azimuth data to show benthic paleocurrents, bentonite distribution to infer prevailing wind direction, and glauconitic sand distribution as possible upwelling zones (presented in Figure 23).

Paleowind direction is inferred from an isopach map of the bentonites (Figure 23B) deposited during the *Baculites obtusus* interval. Unlike Elder (1988) who used isopach maps for individual ashfalls during the Greenhorn Cyclothem, total ash accumulations for the entire baculite zone were used to determine the prevailing wind direction. This technique, as noted by Elder (1988), smooths out any abnormal wind patterns. The distribution shows a major ash source from the Elkhorn Mountains, but also implies another import source in the southern Canadian Rockies (see Armstrong and Ward, 1993); input from more distant sources along the West Coast is probable as well (Bertog 2002). The distribution pattern indicates a prevailing wind direction was about 310° from the west based on the paleopole position between 80-64 mya (Irving et al.,1993).

Glauconitic sand distribution imposed on the Interior Seaway show areas of probable upwelling (Figure 2C). Although controversial as to its significance, the distribution of such facies was used by Parrish and Gautier (1993) to infer upwelling along the western shore of the Sharon Springs seaway. The distribution map shows glauconitic sands deposited during Claggett time.

Water movement in the Claggett Seaway was probably affected by events immediately outside the Western Interior Sea. To the north in the Arctic Ocean Basin, Coriolis forces coupled with bathymetry caused a east to west circulation of water (Kitchell and Clark, 1982). This water would press against the northern continental masses where upwelling would occur (Kitchell and Clark, 1982). Where the land mass was missing, such as the mouth of the Interior Seaway, the water mass would flow south. Deep water production in the Arctic Basin apparently had limited or no access to the Pacific or Atlantic basins at this time (Kitchell and Clark, 1982). It is possible that the top of the bottom water exited the Arctic Basin along the Interior and Turgai seaways. The southward flow of bottom waters down the axis of the Interior Seaway is indicated by the predominance of boreal benthic foraminifera at least as far south as Cañon City, Colorado (Bergstresser, 1981). As the water moved south the volume of oxygen decreased due to decomposition of organic material. Replacement water for the Arctic Basin most likely came from the surrounding landmasses because Hay et al. (1993) observed that the northern end of the seaway lies beneath a zone of heavy precipitation. In addition, the surface waters entering the seaway were most likely brackish.

On the south end of the seaway, where evaporation was highest (Hay et al., 1993), production of deep water would occur in the Gulf of Mexico (Saltzman and Barron, 1982; Woo et al., 1992). Crowley (1991) estimates that globally, deep water production in the Cretaceous of the low latitudes amounted to 60 Sverdrups. In the Gulf of Mexico, downwelling of several Sverdrups could easily have occurred and a major part of the replacement water would have been from the Western Interior Seaway. This downwelling would have enhanced the southward flow started at the north end of the seaway. As the water flowed down the seaway, up to half of the surface waters would be pulled east across the Canadian Shield toward Greenland. A connection between the Western Interior Seaway and western Greenland is inferred at this time because of the presence of *Baculites obtusus* in both places (Birkelund, 1965), as well as other invertebrates (Williams and Stelck, 1975). Water depths in this arm are not known, but it may have been very shallow and evaporation would have been high during the "winter" resulting in dense bottom water production (Wright, 1987). Tourtelot and Rye (1969) estimate sea surface temperatures (SST) in western Greenland of about 22°C based on isotopic data. The sinking of the dense saline water would have produced a warm, low oxygen bottom current flowing southwest. The oxygen would have been rapidly used by the decomposition of organic material resulting in a southwestward flow of anoxic to dyserophic water. It is this bottom current that is recorded by the northeast-southwest axis of the baculite orientation data from Red Bird, Wyoming and Wallace, Kansas. The double axis of the baculite data, however, suggests that this density current was seasonal, shutting down during the wet "summer" season; how long of a lag occurred between these events is unknown. Wright (1987) and Parrish and Curtis (1987) predicted that seasonality was expressed by wet "summers" and dry "winters" in the Western Interior Seaway. Certainly the development of a low pressure area over the landmass east of the seaway during the "summer" would cause precipitation in the area.

Hay et al. (1993) discounted surface winds as having much affect on current direction in the Interior Seaway, although several models suggest otherwise (e.g. Parrish and Curtis, 1982; Parrish et al., 1984; Ericksen and Slingerland, 1990; Glancy et al., 1993; Parrish and Gautier, 1993). Hay et al. (1993), however, may be correct that Ekman transport was not the dominant mode of water movement. It may have enhanced the southward flow of water below 55° paleolatitude. North of 55°, Easterlies probably had little effect on surface water flow because the water was being pulled south. A further effect of the Westerly winds south of 55° north latitude would be the upwelling of the bottom waters along the western edge of the seaway as predicted by Parrish and Gautier (1993). These upwelling zones are recorded by the glauconitic sands in the Lea Park and Foreman formations, and in the Shannon and Apache Creek sandstones. Upwelling along the Sioux Ridge area of the eastern portion of the seaway (evidenced by glauconitic sands in the Split Rock Creek Formation), may be due to longshore drift enhanced by shallowing of the sea floor.

Because formation of bottom water in the northeastern part of the seaway was seasonal, upwelling was also seasonal. Most likely the link between bottom water production and upwelling lagged due to the great distance separating the two zones. The amount of bottom water produced could vary yearly depending upon the strength and duration of the wet and dry seasons. If the density of the southwestward flowing surface water was the same density as the water flowing south down the axis of the seaway, their meeting would produce a third, denser water mass (Hay et al., 1993). This water would sink below the brackish water cap produced during the wet season to become the intermediate water layer whose flow was probably south. It eventually resurfaced near the Gulf of Mexico as surface waters became more saline. This interpretation is most similar to Hay et al. (1993) Scenario III for circulation in the Interior Seaway.

CONCLUSIONS

The Sharon Springs and Pembina Members of the Pierre Shale contain a wealth of vertebrate fossils preserved in organic carbon-rich shales. Isolated bones and small groups of bones apparently originated from debris falling from drifting carcasses. As a result, a single skeleton can be distributed over a large geographical area. Less common or diverse are macro-invertebrates, although these do occur. Nektonic invertebrates, squids and baculites, are common and these often show predation marks of large vertebrates. The most common predators are the medium sized fishes *Enchodus* and *Cimolichthys* . The least common vertebrates are the largest predators, *Tylosaurus* and *Xiphactinus*, as well as the specialized predator, *Globidens*.

A new model for the Claggett Seaway combines bottom current inferred from taphonomic data, prevailing wind direction inferred from ash fall patterns, and upwelling zones inferred from glauconitic sand deposits. The resultant model involves seasonal stratification of the water column with cool, low salinity surface water during the rainy season, and warm, dense saline bottom water during the dry season; benthic water flow was predominantly south and at times may have been high enough to cause regional unconformities noted below,

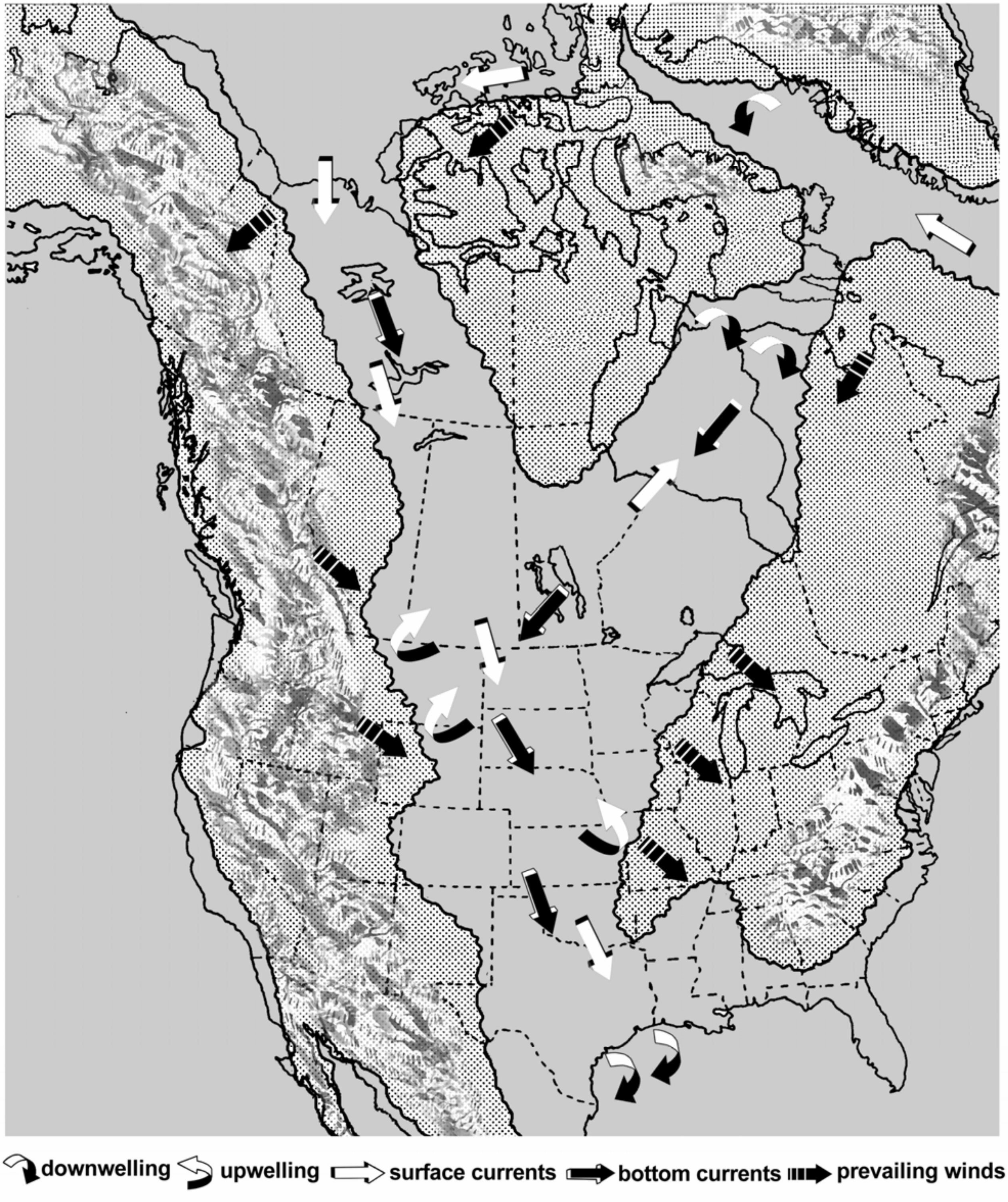

FIGURE 24. Low atmospheric, surface and deep water circulation in the Western Interior Seaway (*Baculites obtusus* zone) during the winter (high pressure zone over the Canadian Shield). During the summer, a low pressure zone over the shield would cause reverse flow of surface waters due to the freshwater flux. See text.

within and above the Pembina and Sharon Springs (DeGraw, 1975; Nicholls, 1988). This erosion may have occurred on uplifted blocks associated with lineaments reported by Shurr (1979, 1983), Shurr and Rice (1986), and Rice and Shurr (1983). Such uplifted blocks would constrict the overlying waters cause it to flow faster over the blocks thereby eroding previously deposited sediments. Nichols et al. (1994) have documented movement, as faulting, along lineaments during deposition of the Pierre Shale. Shifting of basins adjacent to uplifted blocks may explain the diachronous and sometimes laterally discontinuous occurrence of organic-rich units in the Sharon Springs noted by Izett et al. (1971), Gill et al. (1972) and Bertog (2002).

The majority of the organic carbon in the Pembina and Sharon Springs is amorphous type II (Gautier et al., 1984), hence is derived from marine plankton. This plankton in the warm, oxygenated surface waters provided a near constant supply of organic carbon to the sea floor, which in turn insured maintenance of low oxygenated or anoxic bottom waters due to decomposition (Figure 22). Chemosynthetic microbial mats probably formed on the sea floor beneath the warm, saline, sulfidic, anoxic to dyserophic bottom water.

ACKNOWLEDGMENTS

I have had the assistance of numerous individuals during my years working on the Sharon Springs. Field assistance was provided by many students and staff from the University of Colorado Museum; Drs. Peter Robinson and Judith Harris provided a great deal of encouragement and support when I started the Sharon Springs project as an undergraduate; the Meng family at Red Bird, Wyoming, graciously provided housing and field support, and more than once had to help when I was forced to abandon the collecting vehicle; Pete Bussem, Wallace Kansas, was generous with his localities and his years of expertise working the Sharon Springs in western Kansas. Dr. William Hay was generous with his expertise on paleoceanography. His paleoceanography and paleoclimatology classes helped develop the ideas on the WIS presented above. Review comments by Judy Massare and Jim Martin are appreciated, but not all their comments were accepted because I believe hypotheses (“speculation”) can play a constructive role in directing future research. The paper is dedicated to Betsy Nicholls for her work on the Pembina vertebrate fauna.

LITERATURE CITED

Andrews, P .L., M. Axelsson, C. Franklin, and S. Holmgren. 2000. The emetic reflex in a reptile (*Crocodylus porosus*). Journal of Experimental Biology 203:1625-1632.

Archer, A., and D. Hattin. 1984. Trace fossils in Upper Cretaceous argillaceous marine facies of the U.S. Western Interior. Palaeogeography, Palaeoclimatology, Palaeoecology 45:165-187.

Armstrong, R., and P. Ward. 1993. Late Triassic to Earliest Eocene magmatism in the North American Cordillera: implications for the Western Interior Basin. Pp. 49-72 in W.G.E. Caldwell, and E. Kauffman (eds.) Evolution of the Western Interior Basin, Geological Association of Canada, Special Paper 39.

Barthel, K. W., and V. Janicke. 1970. Aptychen als verdauungsrückstand in fund aus den Solnhofener Plattenkalken, unteres Unteryithon, Bayer. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1970: 65-68.

Bergstresser, T. 1981. Foraminiferal biostratigraphy and paleobathymetry of the Pierre Shale, Colorado, Kansas and Wyoming. Unpublished Ph.D. Dissertation, University of Wyoming, 337pp.

Bergstresser, T. and W. Frerichs. 1982. Planktonic foraminifera from the Upper Cretaceous Pierre Shale at Red Bird, Wyoming. Journal of Foraminifera Research 12: 353-361.

Bertog, J. L. 2002. High resolution event stratigraphic and sequence stratigraphic interpretation of the lower Pierre Shale (Campanian) with the description of the new Walhalla and Chamberlain members. Unpublished Ph .D. Thesis, University of Cincinnati, 160pp.

Birkelund, T. 1965. Ammonites from the Upper Cretaceous of West Greenland. Meddelelser om Grønland 179: 1-192.

Bowman, R. E. 1986. Effect of regurgitation on stomach content data of marine fishes. Environmental Biology of Fishes 16: 171-181.

Brown, B. 1904. Stomach stones and food of plesiosaurs. Science 20: 184-185.

Byers, C. 1979. Biogenic structures of black shale environments. Postilla 174: 1-43.

Carpenter, K. 1996. Sharon Springs Member, Pierre Shale (Lower Campanian): depositional environment and origin of it’s vertebrate fauna, with a review of North American plesiosaurs. Unpublished Ph.D. Dissertation, University of Colorado 251 p.

Carpenter, K. 2003. Vertebrate biostratigraphy of the Smoky Hill Chalk (Niobrara Formation) and the Sharon Springs Member (Pierre Shale). Pp. 421-437 in P.J. Harris (ed) Approaches to High-Resolution Stratigraphic Paleontology. Kluwer Academic Press, Dordrecht.

Cicimurri, D. J., and M. J. Everhart. 2001. An elasmosaur with stomach contents and gastroliths from the Pierre Shale (Late

Cretaceous) of Kansas. Transactions of the Kansas Academy of Science 104: 129-143.

Connor, J., 1963. Geology of the Angostura Reservoir Quadrangle, Fall River County, South Dakota. U.S. Geological Survey Bulletin 1063D: 84D-126D.

Crowley, T. 1991. Past CO_2 changes and tropical sea surface temperatures. Paleoceanography 6: 387-394.

Degens, E. T., and K. Mopper. 1975. Early diagenesis of organic matter in marine soils. Soil Science 119: 65-42.

DeGraw, H. 1975. The Pierre-Niobrara unconformity in western Nebraska. Pp. 590-606 in W.G.E. Caldwell (ed.) The Cretaceous system in the Western Interior of North America. Geological Association of Canada Special Paper 13.

Elder, W. 1988. Geometry of Upper Cretaceous bentonite beds: implications about volcanic source areas and paleowind patterns, Western Interior, United States. Geology 16: 835-838.

Elias, M. 1931. The geology of Wallace County, Kansas. Kansas Geological Survey Bulletin 18: 1-42.

Ericksen, M. and R. Slingerland. 1990. Numerical simulations of tidal and wind-driven circulation in the Cretaceous Interior Seaway of North America. Geological Society of America Bulletin 102: 1499-1516.

Fischer, A. 1993. Cyclostratigraphy of Cretaceous chalk-shale sequences. Pp. 283-295 in W. G. E. Caldwell and E. Kauffman (eds.) Evolution of the Western Interior Basin: Geological Association of Canada, Special Paper 39. Gallardo, V. 1977. Large benthic microbial communities in sulphide biota under Peru-Chile subsurface countercurrent. Nature 268: 331-332.

Gautier, D., J. Clayton, J. Leventhal, and N. Reddin. 1984. Origin and source-rock potential of the Sharon Springs Member of the Pierre Shale, Colorado and Kansas. Pp. 369-385 in J. Woodward, and F. Meissner, and J. Clayton (eds.) Hydrocarbon source rocks of the greater Rocky Mountain region. Rocky Mountain Association of Geologists, Denver.

Gautier, D. and N. Reddin. 1983. Diagenetic facies of the Sharon Springs Member of the Pierre Shale (Cretaceous), Denver Basin. Geological Society of America Abstracts 15: 580.

Gill, J. R. and W. A. Cobban. 1966, The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming. U.S. Geological Survey Professional Paper 393-A:1A-73A.

Gill, J. R. and W. A. Cobban. 1973. Stratigraphy and geologic history of the Montana Group and equivalent rocks, Montana, Wyoming, and North and South Dakota. Geological Survey Professional Paper 776: 1-37.

Gill, J. R., W. A. Cobban, and L. Schultz. 1972. Stratigraphy and composition of the Sharon Springs Member of the Pierre Shale in western Kansas. U.S. Geological Survey Professional Paper 728: 1-50.

Hattin, D. 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. Kansas Geological Survey Bulletin 225:1-108.

Fischer, A. 1993. Cyclostratigraphy of Cretaceous chalk-shale sequences. Pp. 283-295 in W. G. E. Caldwell and E. Kauffman (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Glancy, T., M. Arthur, E. Barron, and E. Kauffman. 1993. A paleoclimate model for the North American Cretaceous (Cenomanian-Turonian) epicontinental sea. Pp. 219-241 in W.G.E. Caldwell and E. Kauffman (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Hay, W., D. Eicher, and R. Diner. 1993. Physical oceanography and water masses in the Cretaceous Western Interior Seaway. Pp. 297-318 in Caldwell, W.G.E., and Kauffman, E. (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Hicks, J., J. D. Obradovich, and L. Tauxe. 1999. Magnetostratigraphy, isotopic age calibration and intercontinental correlation of the Pierre Shale, Niobrara County, Wyoming, USA. Cetaceous Research 20:1-17.

Irving, E., P. Wynne, and B. Globerman. 1993. Cretaceous paleolatitudes and overprints of North American Craton. Pp. 91-96 in W.G.E. Caldwell, and E. Kauffman (eds.). Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Izett, G., W. Cobban, and J. Gill. 1971. The Pierre Shale near Kremmling, Colorado, and its correlation to the east and the west. U.S. Geological Survey Professional Paper 684A: 1A-19A.

Jørgensen, B. 1982. Mineralization of organic matter in the sea bed - the role of sulphate reduction. Nature 296: 643-645.

Kauffman, E. G. 1984. Paleobiogeography and evolutionary response dynamic in the Cretaceous Western Interior Seaway of North America. Pp. 273-306 in G. Westermann (ed.). Jurassic-Cretaceous biochronology and paleogeography of North America. Geological Association of Canada Special Paper 27.

Kauffman, E. G. 1987. The remarkable Inoceramidae: dominant Mesozoic bivalves. Geological Society of America Abstracts 19: A286.

Kauffman, E. G. 1988. The case of the missing community: low-oxygen adapted Paleozoic and Mesozoic bivalves ("flat clams") and bacterial symbioses in typical Phanerozoic seas. Geological Society of America Abstracts 20: A48.

Kauffman, E. and W. G. E. Caldwell. 1993. The Western Interior Basin in space and time. Pp. 1-30 in W. G. E. Caldwell, and E. Kauffman (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Kennedy, M. J., D. R. Pevear, and R. J. Hill. 2002. Mineral surface control of organic carbon in black shale. Science 295:657-660.

Kepkay, P., R. Cooke, and J. Novitsky. 1979. Microbial autotrophy: a primary source of organic carbon in marine sediments. Science 204: 68-69.

Kirk, S. R. 1930. Cretaceous stratigraphy of the Manitoba Escarpment, Canada. Geological Survey of Canada, Summery Report 1929, Part B: 112-125.

Kitchell, J., and D. Clark. 1982. Late Cretaceous-Paleocene paleogeography and paleocirculation: evidence of North Polar upwelling. Palaeogeography, Palaeoclimatology, Palaeoecology 40: 135-165.

Kiteley, L. 1976. Marine shales and sandstones in the Upper Cretaceous Pierre Shale at the Francis Ranch, Laramie County, Wyoming. Mountain Geologist 13: 1-19.

Loutit, T., A. Bence, J. Smale, and J. Shane. 1990. Anatomy of an organic-rich condensed section: the Campanian Sharon Springs Member of the Pierre Shale, Powder River Basin. American Association of Petroleum Geologists Bulletin 74: 708.

MacLeod, K. G. and K. A. Hoppe. 1992. Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts. Geology 20:117-120.

Martin, J. and P. Bjork. 1987. Gastric residue associated with a mosasaur from the Late Cretaceous (Campanian) Pierre Shale in South Dakota. Dakoterra, South Dakota School of Mines, Museum of Geology: 68-72.

Martin, L., and J. D. Stewart. 1982. An ichthyornithiform bird from the Campanian of Canada. Canadian Journal of Earth Sciences 19: 324-327.

McNeil, D. H., and W. G. E. Caldwell. 1981. Cretaceous rocks and their foraminifera in the Manitoba Escarpment. Geological Association of Canada, Special Paper 21: 1-439.

Mello, J. 1971. Foraminifera from the Pierre Shale (Upper Cretaceous) at Red Bird, Wyoming. U.S. Geological Survey Professional Paper 393-C: C1-C-54.

Nicholls, E. L. 1988. Marine vertebrates of the Pembina Member of the Pierre Shale (Campanian, Upper Cretaceous) of Manitoba and their significance to the biogeography of the Western Interior Seaway. Unpublished Ph.D. Thesis, University of Calgary, 317 p.

Nicholls, E. L. and A. Russell. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79: 149-169.

Nichols, T. C., D. S. Collins, M. Jones-Cecil, and H. S. Swolfs. 1994. Faults and structure in the Pierre Shale, central South Dakota. Pp. 211-235 in G. W. Shurr, G. A. Ludvigson, and R. H. Hammond (eds.) Perspectives on the eastern margin of the Cretaceous Western Interior Basin. Geological Society of America, Special Paper 287.

Obradovich, J. 1993. A Cretaceous time scale. Pp.379-396 in W. G. E. Caldwell and E. Kauffman (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Parrish, J. and R. Curtis. 1982. Atmospheric circulation, upwelling, and organic-rich rocks in the Mesozoic and Cenozoic Eras. Palaeogeography, Palaeoclimatology, Palaeoecology 40: 31-66.

Parrish, J. and D. Gautier. 1993. Sharon Springs Member of Pierre Shale: upwelling in the Western Interior Seaway? Pp. 319-332 in W.G.E. Caldwell, and E. Kauffman (eds.) Evolution of the Western Interior Basin. Geological Association of Canada, Special Paper 39.

Parrish, J., G. Gaynor, and D. Swift. 1984. Circulation in the Cretaceous Western Interior seaway of North America. Pp. 221-231 in D. Stoot and D. Glass (eds.) The Mesozoic of Middle North America. Canadian Society of Petroleum Geologists Memoir 9.

Rice, D., and G. Shurr. 1983. Patterns of sedimentation and paleogeography across the Western Interior Seaway during time of deposition of Upper Cretaceous Eagle Sandstone and equivalent rocks, Northern Great Plains. Pp. 337-358 in M. Reynolds, and E. Dolly (eds.) Mesozoic Paleogeography of West-central United States.

Society of Economic Paleontologists and Mineralogists, Rocky Mountain Paleogeography Symposium 2.

ROCC (Research on Cretaceous Cycles) Group. 1986. Rhythmic bedding in Upper Cretaceous pelagic carbonate sequences: varying sedimentary response to climatic forcing. Geology 14:153-156.

Rogers, E. M. and M. S. Hendrix. 2000. Taphonomy of a petrified forest in the Two Medicine Formation (Campanian), northwestern Montana: implications for palinspastic restoration of the Boulder Batholith and Elkhorn Mountain Volcanics. PALAIOS 15:476-482.

Russell, D. A. 1975. A new species of *Globidens* from South Dakota, and a review of globidentine mosasaurs. Fieldiana, Geology 33: 235-256.

Sageman, B., and M. Arthur. 1994.Early Turonian paleogeographic/paleobathymetric map, Western Interior, U.S. Pp. 457-469 in M. Caputo, J. Peterson, and K. Franczyk (eds.) Mesozoic Systems of the Rocky Mountain Region, USA. C&M Press, Colorado.

Saltzman, E., and E. Barron. 1982. Deep water circulation in the Late Cretaceous: Oxygen isotope paleotemperatures from *Inoceramus* remains in D.S.P. cores. Palaeogeography, Palaeoclimatology, Palaeoecology 40: 167-181.

Schäfer, W. 1972. Ecology and Palaeoecology of Marine Environments. University of Chicago Press, 568p.

Schultz, L. G. 1965. Mineralogy and stratigraphy of the lower part of the Pierre Shale, South Dakota and Nebraska. U.S. Geological Survey Professional Paper 393-B: B1-B19.

Schultz, L., H. Tourtelot, J. Gill, and J. Boerngen. 1980. Composition and properties of the Pierre Shale and equivalent rocks, Northern Great Plains region. U.S. Geological Survey Professional Paper 1064-B: 1B-114B.

Scott, G. 1969. General and engineering geology of the northern part of Pueblo, Colorado. U.S. Geological Survey Bulletin 1262: 1-131.

Scott, G., and W. Cobban. 1975. Geologic and biostratigraphic map of the Pierre Shale in the Canon City-Florence Basin and the Twelvemile Park area, southcentral Colorado. U.S. Geological Survey Miscellaneous Investigation Series Map I-937.

Shurr, G. 1979. Upper Cretaceous tectonic activity on lineaments in western South Dakota. U.S. Geological Survey Open File Report OF79-1374: 1-24.

Shurr, G. 1983. Regional setting of Niobrara Formation in northern Great Plains. American Association of Petroleum Geologists Bulletin 68: 598-609.

Shurr, G. and D. Rice. 1986, Paleotectonic controls on deposition of Niobrara Formation, Eagle Sandstone, and equivalent rocks (Upper Cretaceous), Montana and South Dakota. Pp. 193-211 in J. Peterson (ed.) Paleotectonics and sedimentation in the Rocky Mountain Region, United States. American Association of Petroleum Geologists Memoir 41.

Southam, J., W. Peterson, and G. Brass. 1982. Dynamics of anoxia. Palaeogeography, Palaeoclimatology, Palaeoecology 40: 183-198.

Stewart, J. D. 1996. Cretaceous acanthomorphs of North America. Pp. 383-394 in G. Arratia, and G. Viohl (eds) Mesozoic Fishes - Systematics and Paleoecology. Verlag: Munchen.

Stewart, J. D., and K. Carpenter. 1990. Examples of vertebrate predation on cephalopods in the Late Cretaceous of the Western Interior. Pp. 203-207 in A. Boucot (ed.) Evolutionary Paleobiology of Behavior and Coevolution. Elsevier,

Tourtelot, H. 1962. Preliminary investigation of the geological setting and chemical composition of the Pierre Shale, Great Plains region. U.S. Geological Survey Professional Paper 390: 1-74.

Tourtelot, H. and R. Rye. 1969. Distribution of oxygen and carbon isotopes in fossils of Late Cretaceous age, Western Interior Region of North America. Geological Society of America Bulletin 80: 1903-1922.

Williams, G., and C. Stelck 1975. Speculations on the Cretaceous palaeogeography of North America. Pp. 1-20 in W.G.E. Caldwell (ed) The Cretaceous System in the Western Interior of North America. Geological Association of Canada Special Paper 13.

Woo, K.-S., T. Anderson, L. Railback, and P. Sandberg. 1992. Oxygen isotope evidence for high salinity surface seawater in the Mid-Cretaceous Gulf of Mexico: implications for warm, saline deepwater formation. Paleoceanography 7: 673-685.

Wright, E. 1987. Stratification and paleocirculation of the Late Cretaceous Western Interior Seaway of North America. Geological Society of America Bulletin 99: 480-490.

Zangerl, R., and E. Richardson. 1963.The paleoecological history of two Pennsylvanian Black Shales. Fieldiana, Geology Memoirs 4: 1-352.