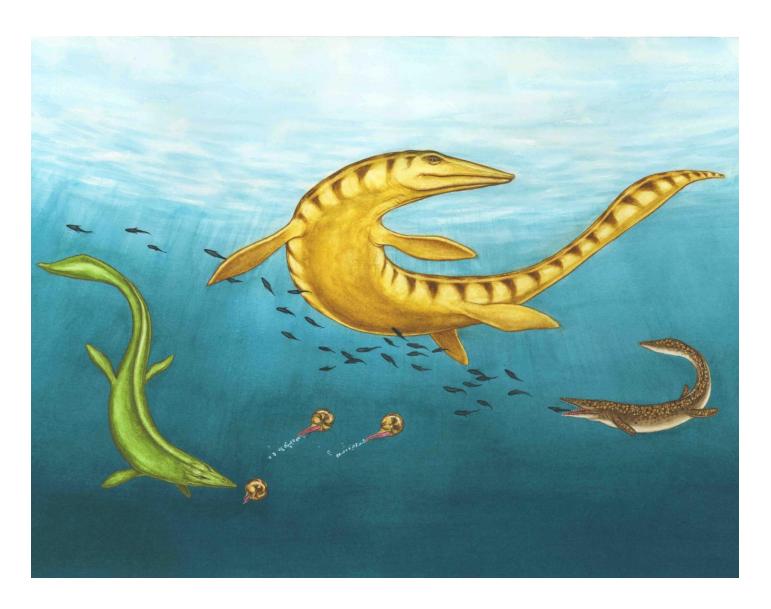


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THE CRETACEOUS

A LOVE OF FOSSILS BRINGS US TOGETHER

M.A.P.S. Digest--EXPO XXXIII Edition

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Preface

The editors wish to thank the contributors for responding to the Call for Papers in such a timely manner. The papers represent a wide range of Cretaceous related topics contributed by our members, professionals, and our guest speaker, Dr. Steven Nicklas. We would also like to thank Dr. Nicklas for delivering the keynote address.

About the Cover

The cover image illustrates the three representative mosasaurs of the Campanian (Late Cretaceous) sea that is now north-west Nebraska. The mosasaurs are (from left to right): *Platecarpus planifrons*, *Tylosaurus proriger*, and *Clidastes propython*. Original art work cover painting © 2010 Rob Sula.

Western Illinois University Western Hall Macomb, Illinois April 1, 2, 3, 2011

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John Catalani and Chris Cozart, Editors

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A stratigraphic reappraisal of the Cretaceous exposure at Black Powder Hollow, Alexander County, Illinois

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Abstract: Cretaceous deposits are very limited in Illinois, represented only by the Tuscaloosa, McNairy and Owl Creek formations in the southern-most counties, and the Baylis formation in Pike and Adams counties. A well-known exposure of the McNairy formation at Black Powder Hollow near Fayville contains lignitic siltstone, sandstone, conglomerate and gray clay. Bore-hole data suggested the Cretaceous strata lay unconformably over Silurian red marl/clay, which covered upper-Ordovician shale of the Maquoketa Group. Paleontological evidence in the form of plant macrofossils and acritarchs indicates a portion of the lower "Cretaceous" gray clay is instead reworked Maquoketa shale, requiring an update to the stratigraphic column at this site.

Introduction

During the Cretaceous Period Illinois lay at the northern end of the Mississippi Embayment (Willman and Frye, 1975). Sediments deposited in southern Illinois during this time are generally non-marine and deltaic in origin. The Tuscaloosa, McNairy and Owl Creek formations extend in a band across Alexander, Pulaski, Massac and Pope counties, Coeval sediments in Pike and Adams counties in western Illinois are transgressive near-shore deposits, almost all of which were lost to erosion.

Black Powder Hollow is located north of Fayville in Alexander County, T15S, R3W, Section 34, and is privately owned. The layers exposed there have been searched periodically over the past few decades for vertebrate and plant fossils, and more recently tested for their potential as a source of clay. Strata in the exposure are generally horizontal and show no outward evidence of folding or faulting. Figure 1 shows the exposure as it appeared in the fall of 2004.

Methodology

Measurements were made in 2000 (J. Devera, pers. comm. 2004) which allowed the development of the column shown in Figure 2. Bore hole data show a 20 to 40-foot thick layer of red clay beneath the lower gray clay. The red clay is presumed to be derived from the late-Silurian Moccasin Springs formation (J. Devera, pers. comm. 2005). Of particular importance are the upper and lower clay layers. The upper is largely a lignitic siltstone. The lower clay changes from a dense gray with Festaining and plant debris above to blue-gray with no staining below. Specimens of the upper clay were collected sufficient to fill five five-gallon buckets. Fist-sized samples of all other layers were also collected. The contents of four of the buckets of the upper clay were subjected to screen-washing in order to locate any vertebrate microfossils. Material in the remaining bucket was split and examined for macrofossils. In addition, a sample of each clay was sent to Global Geolabs for palynological processing.



Figure 1. Exposure at Black Powder Hollow in 2004.

Results

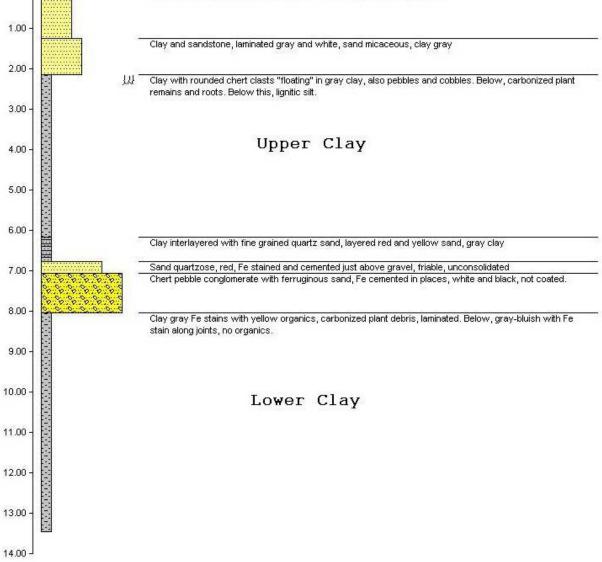
Screen washing of the upper clay revealed no vertebrate fossils of any type. Small pieces (up to 1.5 cm.) of petrified wood were common. Plant leaf and stem macrofossils were also very common. Examples are shown in Figures 3. Palynological slides showed only a very few pollen grains, shown in Figure 4. Palynological samples from the lower clay, however, contained large numbers of acritarchs. Some of these are shown in Figures 5.

Discussion

The leaf and stem fossils in the upper clay are compressions, and so delicate that they cannot have been reworked. These fossils are generally consistent with the Cretaceous floras described in Berry (1919 and 1925) from Tennessee, Mississippi, Alabama, and Georgia. Wheeler et al (1987) described dicotyledonous petrified wood from another location in Black Powder Hollow. Together with the lithology noted when the outcrop was measured, the evidence suggests the layers above the lower clay belong to the Cretaceous McNairy formation and are preserved in situ.

The lower clay that was accessible has a measured thickness of 5.5 meters. The overall thickness of this layer overlying the Moccasin Springs formation is not known. Only one sample of the lower gray clay was processed for palynological analysis. This sample contained a large and diverse acritarch flora. The acritarchs were completely consistent with those described by Wicander et al (1999) from the upper Ordovician Maquoketa shale. Since this layer is above the Silurian Moccasin Springs marl/clay, indicated by the data from bore holes, some or all of the lower gray clay is reworked material from nearby Ordovician strata. Thus, a simplified reappraisal of the stratigraphy at this site in Black Powder Hollow is shown in Figure 6.







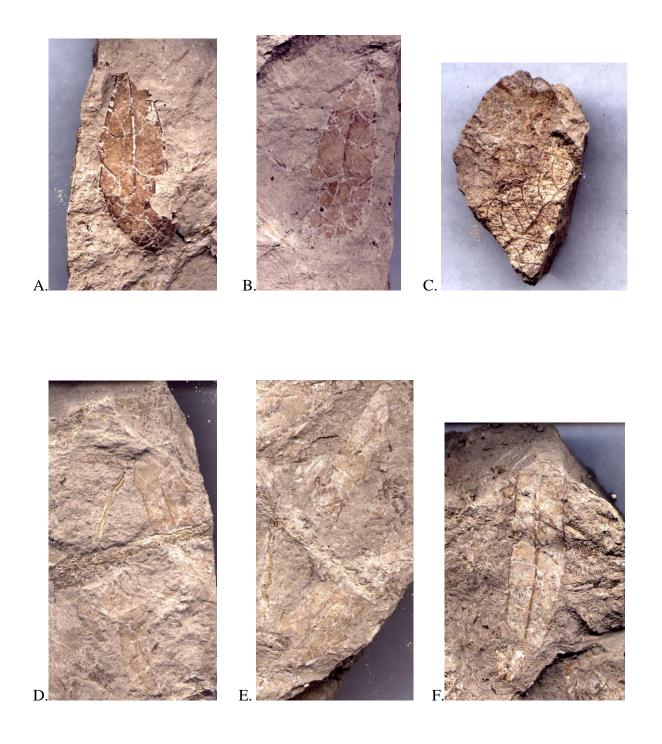


Figure 3. A, undetermined leaf; B, *Celtis* sp.; C, *Ficus*?; D and E, *Aralia problematica*; F, *Nectandra*?.

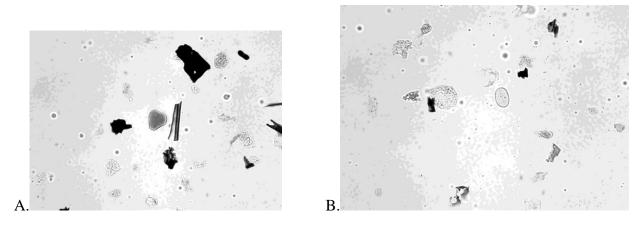


Figure 4. Two types of pollen from the upper clay.

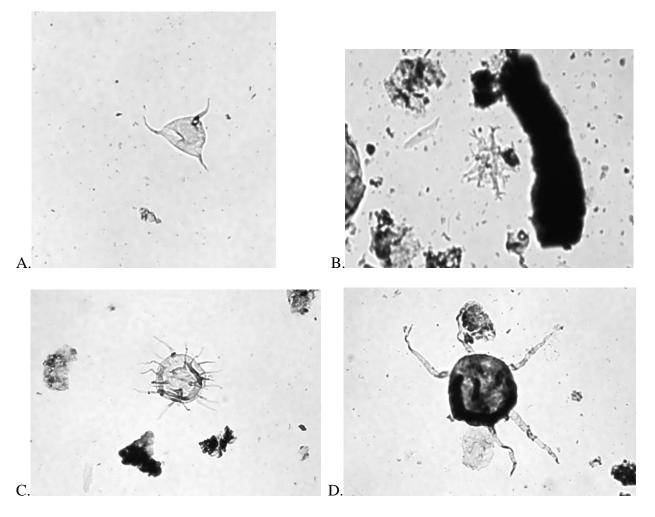


Figure 5. Acritarchs from the lower part of the lower gray clay. A, *Villosacapsula* sp.; B, *Multiplicisphaeridium* sp.; C, *Elektroriskos* sp.; D, *Orthosphaeridium* sp.

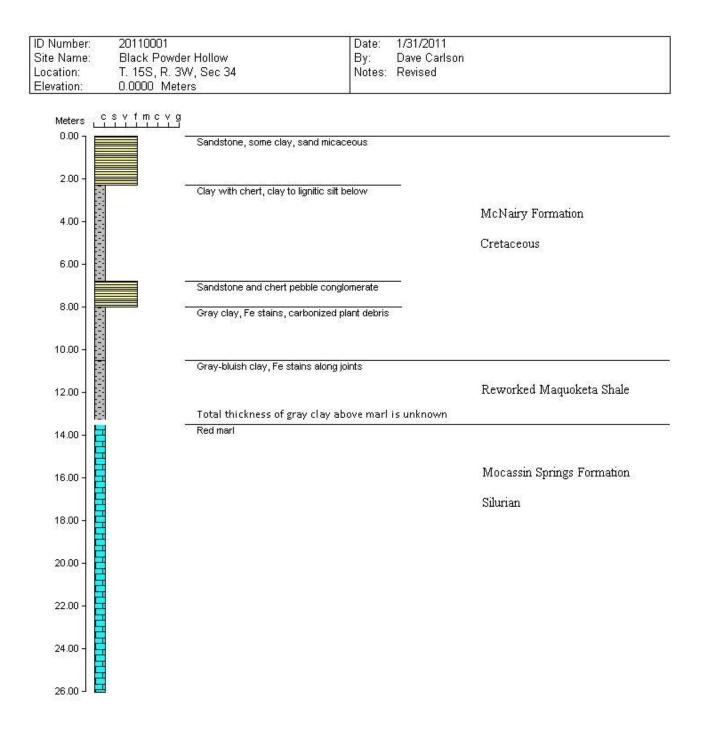


Figure 6. Revised stratigraphic column for this site in Black Powder Hollow.

The embayment area at the southern tip of Illinois is structurally complex (Kolata et al, 1981) containing many faults and grabens. It has been suggested that the area of Black Powder Hollow is part of a down-dropped block (J. Devera pers. comm. 2005). A structure like this could produce the stratigraphic ordering described here. Timing for this event is unclear but must have occurred between the late Silurian (when the Moccasin Springs formation was deposited) and the late Cretaceous (when the McNairy formation was deposited).

Acknowledgements

My thanks to Joe Devera for access to the site, the measurements and the bore hole data, Global Geolabs for processing of samples, and Reed Scherer of Northern Illinois University for the use of the microscope and camera.

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The Ardeola, Missouri Cretaceous locality

Bruce L. Stinchcomb

The great depression of 1929 had some interesting and long lasting consequences! Structures and projects initiated by governmental "alphabet soup" agencies like the CCC (Civilian Conservation Corps) and WPA (Works Project Administration) were varied, successful and enrich us in various ways even today. One of the lesser known projects of the WPA was a program to evaluate and discover potential mineral resources in various parts of the country which might assist in aiding extrication from the abysmal early "30's economic conditions---aiding or assisting local industries with the discovery and use of local resources. One of these projects was to probe for coal, lignite and clay deposits which might occur locally in southeastern Missouri and northeastern Arkansas. This was done utilizing out-of-work persons who operated hand operated augers to probe areas of suitable geology. One of these regions was the puzzling Crowley's Ridge of southeastern Missouri. Crowley's Ridge is a chain of hills (often locally rugged) which stick up abruptly from the flat lands of "swamp-east" Missouri and which ecologically and geologically are quite different from the nearby Ozarks. Clay deposits of considerable quality were already known to occur on Crowley's Ridge in Arkansas where the ridge, as in Missouri, formed a north-south hilly region in contrast with the flatlands of eastern Arkansas. Clay of two types were known to occur there, plastic clay used for brick making and other bulky ceramic objects and a non-plastic clay known as Fuller's Earth which was an excellent absorbent of liquids.. The later, of which a small market had already developed in the 1920's, was used effectively for absorption of oil which leaked from recalcitrant automobiles, especially those of Mr. Ford which had inundated the towns and cities of 1920's America. The plastic clays of Crowley's Ridge were of Eocene age, some containing well preserved fossil leaves indicative of a tropical, Caribbean climate, the Fullers Earth deposits were somewhat older, apparently (as they contained no fossils) of early Cenozoic in age.

Auguring in Missouri's part of Crowley's Ridge was overseen by geologists Dan Steward (later to discover Missouri's only known dinosaur site) and Willard Farrar (who would be killed in Germany during a WWII battle). Besides overseeing the auguring, these geologists would also explore the ridges, steep gullies and hillsides for outcrops which might yield more information as to the ridges geology. As they pursued the later, what came as a surprise in 1935 was the finding of impressions of marine fossils in a layer of brown clay or mudstone. These were marine fossils like gastropods (Turritella) and pelecypods which indicated that sometime, before Crowley's Ridge existed, the Gulf of Mexico came as far north as Missouri. What came as the real surprise, however, was that the fossils found were not from the Cenozoic Era as would have been thought from the occurrence of Eocene marine fossils on Crowley's Ridge in Arkansas but that the Missouri fossils were from the Cretaceous Period---they were fossils from the Mesozoic Era.

Prior to this discovery, Cretaceous rocks were unknown from Missouri (although some had been found to the east in southern Illinois). These fossils were found to occur in a small road cut along a steep descent to the hamlet of Ardeola, at the foot of the ridge. The layer containing the fossils was the Owl Creek Formation, originally discovered along Owl Creek near Ripley Mississippi just before the Civil War. The Owl Creek fauna is primarily a molluscan one consisting of a rich and diverse fauna which includes the fascinating ammonite *Scaphites nodosus*, an ammonite which resembles a caterpillar.

Also found near Ardeola have been the teeth, vertebrae and presumably a jaw section of a mosasaur, mosasaurs being one of the dominant marine ruling reptiles of the Cretaceous seas.

Kitty Litter

The Fuller's Earth mentioned above has become a major resource on Crowley's Ridge in Missouri—it being mined for both its oil absorbing qualities and also because it makes an excellent litter box filler much admired by cats and their owners as well as it also removes kitty odors; it's sold widely as kitty litter---every cat owner handles small portions of Crowley's Ridge when filling the litter box. In digging beneath the kitty litter layer (the Porters Creek Formation), for emplacement of a sump pump, underlying strata was recently found to have a variety of marine fossils---marine fossils representative of the Owl Creek Formation but also preserving original shell material which the fossils at Ardeola lack. What's interesting about this is that beds beneath the kitty litter layer (The Clayton Formation) are supposed to be of early Cenozoic in age---they're not supposed to contain Cretaceous fossils. Fossils in the lower portion of the Clayton Formation also appear all jumbled together occurring with large chunks of clay known as rip-up clasts. This layer looks like something threw lots of stuff together, shells, bones and rip-up clasts and left it.

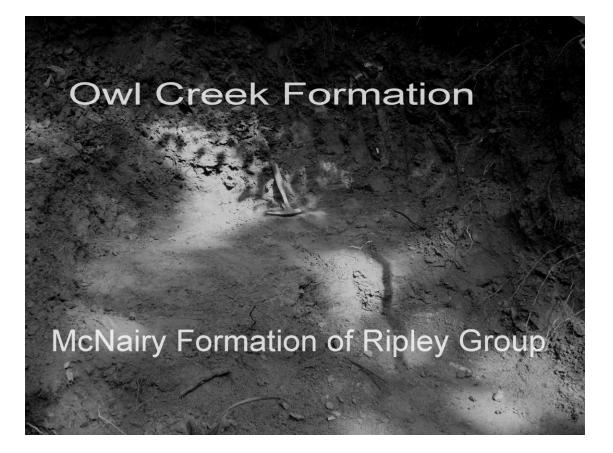
The K/T boundary

Those who have been following the saga of dinosaurs in the contemporary media know that their extinction is now suspect as being from an asteroid which impacted in the Yucatan region of Mexico some 65 million years ago. This impact, at the margin of the Gulf of Mexico, is known as the Chicxulub Crater. Accompanying this massive catastrophe was a gigantic "tidal wave", a tsunami which rolled across the Gulf of Mexico. Either the tsunami itself or the release of large mud slides, which it triggered from the continental shelf created secondary tsunami which aimed northeastward to enter the shallow embayment which later became the course of the Mississippi River. This tsunami moved northward through the embayment tearing up the sea floor, dislocating marine life and throwing all of this together to form the deposits found in the sump pump diggings and farther north exposed near Ardeola. Today the brown mudstones of the Owl Creek Formation with their very late Cretaceous fossils are overlain by the greenish Clayton Formation with its rip-up clasts, coprolites, shells and mosasaur bones. This is the tsunami zone which forms the uppermost beds of the Mesozoic Era at the head of the Gulf Embayment.

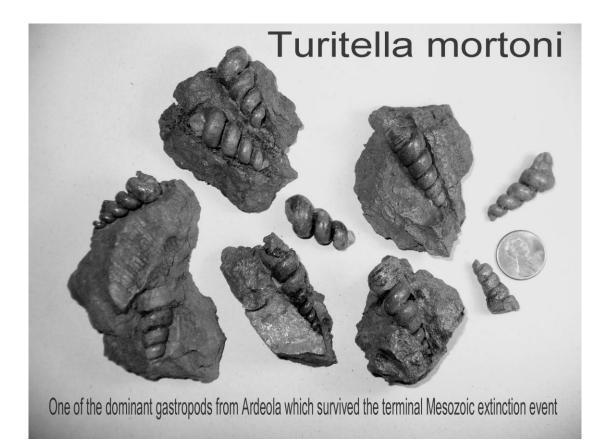


Micaceous clay layers with vertebrate tracks

Ripley Formation, Ardeola MO.









Uintacrinus, Floater or Bottom Dweller

Thomas C. Williams

Throughout time, crinoids have managed to find a way to live in as many of the sea environments as possible. Crinoids have been found on the bottom of oceans, suspended on stems of varying lengths, and as pelagic floaters. Since Marsh in 1870 found the first Uintacrinus in the Uinta Mountains in Utah, the way this crinoid has been found has raised many questions. Springer in 1901 found these crinoids as colonies with hundreds of specimens on slabs in the Niobrara Chalk. The Niobrara Chalk was deposited in the shallow intercontinental sea called the Pierre Seaway which at its height stretched from the Arctic to what is now the Caribbean. As the sea reached its height, limestone and laminated chalk made from the shells of coccoliths and foraminifera were deposited in western Kansas. Eventually the entire area was covered by the Pierre shale as the sea receded (Hess *et al.* 1999). Uintacrinus has been found world-wide in the Upper Cretaceous of North America, Europe including Russia, and Australia. This truly shows a world-wide distribution of this genus. The Niobrara chalk deposits represent a magnificent Lagerstätte deposit. *Uintacrinus* is also a true index fossil for the Santonian stage of the Cretaceous time period (Ausich and Webster 2008).

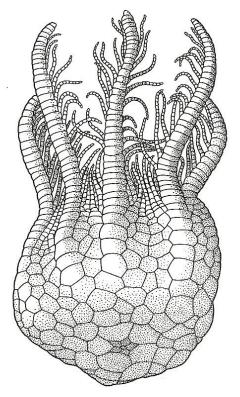


Figure 1. (Ausich and Webster 2008)

Uintacrinus (see Figure 1 at left) was classified as Subclass Articulata, Order Uintacrinda from Moore and Teichert (1978) which for a long time was thought to have arisen from an inadunate ancestor. However, more recent research has led to the possibility that camerates, cladids, disparids, and flexibles, which dominated the Paleozoic and diversified before the extinction, became totally extinct. During this diversification, an early articulate evolved, possibly from a cladid ancestor, that survived the extinction. However, the crinoids that managed to survive the Permian extinction struggled in the Triassic. A single survivor or survivors did diversify in the middle Triassic but suffered another round of extinctions. It is obvious from the end of the Permian through the Triassic that crinoids nearly went out for good; however, this was the last major blip for crinoids including the Cretaceous extinction. Extinctions in the Triassic provided new opportunities for the survivors to expand and evolve into new forms (Hess et al. 1999).

Uintacrinus, a large stemless crinoid, has been found in dense collections with as many as 25 to 50 specimens per square meter. Many slabs of this type of preservation have been recorded from Kansas, Utah, and Colorado. The substrate in which Uintacrinus has been found does not appear to

have a very high diversity of other fossils including other echinoderms. This could just be a phenomenon of fossilization, or is it the possibility of a more hostile environment favoring the types of specimens found? Stemless crinoids have been reported in the Cretaceous in other localities across the world including Texas and Oklahoma. Europe has reported over 20 different genera of stemless crinoids. Thus, stemless crinoids definitely are not something unusual for this time period (Moore 1967).

Stemless crinoids are nothing new in the fossil record and have been recorded in the Mississippian of the Carboniferous period. Forms such as *Staphylocrinus bulgeri*, *Exocrinus*, and *Agassizocrinus* are all stemless varieties of crinoids which settled into the substrate using the calyx to support them in the mud. Burdick (2011) and Chestnut and Ettensohn (1988) show a model of stemless crinoids living in the carbonate sand belt outside a lagoon in the Glen Dean formation in the Sloans Valley of Kentucky. Stemless crinoids using their calyx to support themselves were in place as a living strategy well before the Cretaceous.



Figure 2. (Ausich and Webster 2008)

The structure of *Uintacrinus* had a calyx that reached up to 7.5 centimeters composed of numerous small, well connected plates. In addition, this calyx was flexible, hence the necessity for many plates which may have enabled this crinoids' ability to change the shape of its calyx in response to its environment. A large flexible calyx was definitely a characteristic that developed to accommodate it in the Pierre seaway and other similar environments. What is interesting is that no

stems, cirri, or holdfast structures have been found with these massive deposits of specimens. Ten arms were attached to this calyx which had the potential to reach up to 125 cm, an incredible length! That brings up the question; why was the length for such long arms necessary? Pinnules near the cup could get up to 20 millimeter, but become much finer up the length of arms. The interesting arrangement of arms and pinnules with muscular articulations suggests a more advanced food collecting ability for *Uintacrinus* with the ability to move and adjust the position of its arms.

Springer found these masses in soft mud of a sea which he thought resembled something similar to the Mediterranean Sea. Masses upon masses of these crinoids piled upon each other probably helped lead these scientists to the conclusion that this was a pelagic floater and was swept into the shallow portions of the Niobrara and buried. Kirk (1911) theorized that large masses of *Uintacrinus* collected in shallow waters for spawning and Hyman thought they lived in "floating swarms" (Ausich and Webster 2008).

In contrast to the idea of floating swarms and a pelagic lifestyle, some early crinoid hunters thought from observations that this crinoid was a bottom dweller that could possibly creep along or use its arms for locomotion. Recent researchers discovered this form of locomotion is possible. Rethinking the pelagic lifestyle, Jackel described the overall structure and showed it to be too large for a pelagic lifestyle. Struve (1957) rejected the idea of this crinoid living in crowed colonies. Looking at the entire structure of the crinoids, Struve concluded that this crinoid settled on the bottom using its calyx to support itself and then out stretched its arms, which could have been up to 2 meters around, to collect its food. Uintacrinus has a large calyx probably too big to support itself as a pelagic floater (Ausich 2008). This would have required it to entrap a sufficient amount of gas in special structures near the outside wall of the calyx. Examination of the calyx of *Uintacrinus* has not revealed the existence of such structures. Therefore, this leaves the conclusion that Uintacrinus lived on the bottom of the substrate rather than on stems or floating in the open ocean.



Figure 3. (Ausich and Webster 2008)

Modern crinoids stretch out their arms in a radial manner to most effectively collect food. It is not difficult to imagine Uintacrinus out stretching its arms from the substrate to most efficiently gather food which would make the intertwining of arms difficult for gathering food. In addition, other pelagic crinoids, those that didn't use a float, are small. Other larger crinoids, such as Scyphocrinitids, had a float allowing the crinoids to drift with the current and extend down. No floats have been discovered with Uintacrinus. Further examination of how the crinoids are preserved supports that *Uintacrinus* did not float and hang its arms down into the sea. Slabs of crinoids show the arms lying sideways into the slabs which tend to support that *Uintacrinus* lived with its calyx in the mud with its arms extending upward. *Uintacrinus* may have also used some of its arms to help support itself and balance it -- why not? Now that idea might make Uintacrinus shape its arms in a bowl structure not extending them upward as much. This living style would have made it much more

stationary and kept it in place. Hess, essentially concludes, "*Uintacrinus socialis* lived gregariously on the soft bottom and was buried in life position; it colonies may have resembled dense patches of ell grass" (Hess *et al.* 1999). Another model of living suggested by Seilacher and Hauff might have drifted along the bottom as a "hemi pelagic drifter" maintaining just enough buoyancy dragging its arms as a "passive deposit feeder" (Ausich 2008). Examination of *Uintacrinus* did show inflexibility of its arms as the arms approached the calyx. This idea tends to show a limitation in the idea of a pelagic fan or extending the arms out from the bottom in bowl pattern. However, the inflexibility may have made *Uintacrinus* more able to extend its arms upwards, only making it necessary for *Uintacrinus* to find a good place to plant itself in the substrate.

Hess' ideas fit how these crinoids are found in giant masses living in colonies close together but not too close. The rich amounts of plankton allowed *Uintacrinus* to reach the size that it did with its large calyx able to provide support. The large size and the suggested ability to be flexible with its calyx would have helped keep it from sinking. With *Uintacrinus* being more sessile than the ability to move, it would have been more susceptible to rapid sedimentation or other mass mortality events allowing a colony to be buried pretty much in place -- a normal geologic event. However, imagining this crinoid bouncing along the bottom basically on its side dragging its arms is not a typical model one would expect from a crinoid. This could be explained from currents effecting how the crinoids pushed and rolled together in the same basic orientation. The weight of the calyx possibly helped to stabilize the position in the substrate perhaps using arms for support as needed. Ausich, Hess, and others in research support a benthic lifestyle where a group of crinoids settled, matured together, grew to adults, died in a mass mortality event, and were then buried. Future evidence and still many questions that shall require answers may be provided with the discovery of new specimens (Ausich and Webster 2008; Hess *et al.* 1999).

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Nautiloids v Ammonoids: Winners and Losers John A. Catalani

Introduction

To most, nautiloids and ammonoids appear very similar to each other. Members of both groups sport an external shell, a siphuncle, and suture marks that identify where the internal chamber partitions (septa) were attached to the inside of the outer shell. These sutures are visible when the external shell is absent and are used, more so with ammonoids, to determine not only genus and species but also families and are therefore critical to determining phylogeny. For the nautiloids, much less for the ammonoids, the structure of the siphuncle is used to determine taxonomic assignment and phylogeny. The most obvious difference is that nautiloids are still alive in the Pacific Ocean (*Nautilus*, *Allonautilus*) and the ammonoids (along with non-avian dinosaurs, marine reptiles, and pterosaurs) went extinct at the Cretaceous-Paleogene (K-Pg) boundary. The question is, then, why did two animal groups so similar in morphology suffer different fates at the end of the Cretaceous Period?

Classification

The classification of cephalopods has undergone many changes in recent years with some orders yet to be confirmed as valid. The following is a simplified classification that outlines the diversity of cephalopods:

Phylum MOLLUSCA **Class CEPHALOPODA** Subclass NAUTILOIDEA (external shells; 14-17 orders) Extinct nautiloids Extant Nautilus and Allonautilus Subclass BACTRITOIDEA Extinct bactritids Subclass AMMONOIDEA (external shells; 9 orders) Extinct goniatites Extinct ceratites Extinct ammonites Subclass COLEOIDEA (internal or no shells) Extinct belemnites Extant decapods (squids and cuttlefishes) Extant octopods Extant Argonauta ("Paper Nautilus")

It had been assumed that, since both the nautiloids and the ammonoids had external shells and one nautiloid genus (now split into two genera, *Nautilus* and *Allonautilus*) was still alive, *Nautilus* could serve as an analogue for ammonoid morphology, physiology, and behavior. However, it has been determined after decades of work on fossil specimens and phylogenetic analysis based on cladistics (see Fig. 1) that ammonoids are actually more closely related to coleoids (cuttlefishes, octopods, decapods) than they are to nautiloids (Jacobs and Landman 1993). Therefore, we need to look more closely at not only the similarities between ammonoids and nautiloids but also the differences between the two groups to have any hope of answering the question of why ammonoids are extinct and nautiloids are not.

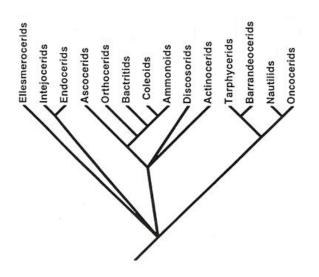


Fig. 1. This diagram illustrates the phylogenetic relationships between various segments of the Class Cephalopoda. It is important to note that the nautiloid order Ellesmerocerida gave rise to all future cephalopods and that coleoids and ammonoids are "sister taxa" quite separate from the order Nautilida that contains the extant Nautilus and Allonautilus. (Modified from Jacobs and Landman 1993, Fig. 1.)

The Shelled Cephalopods--A Comparison

Shell Morphology

Present day *Nautilus* can serve as a model for both nautiloid shell morphology and anatomy (see Fig. 2). Although the shell (conch) of *Nautilus* is coiled, the basic structure of the nautiloid shell, consisting of chambers (camerae) separated by partitions (septa) with the organic siphuncle running the length of the shell via holes (septal foramens) through each septa, is virtually identical to that of extinct forms with straight or curved shells. Neutral buoyancy was the tactical advantage that allowed the nautiloids to successfully diversify and compete with existing animals. As the animal grew, each new chamber was filled with fluid that was slowly removed by osmosis through the siphuncle and replaced with low-pressure gas giving the shell buoyancy to compensate for the increased mass of the growing animal. It is logical to assume that ammonoids, equipped with similar morphologic structures, were also able to maintain neutral buoyancy, although this assumption has been questioned.

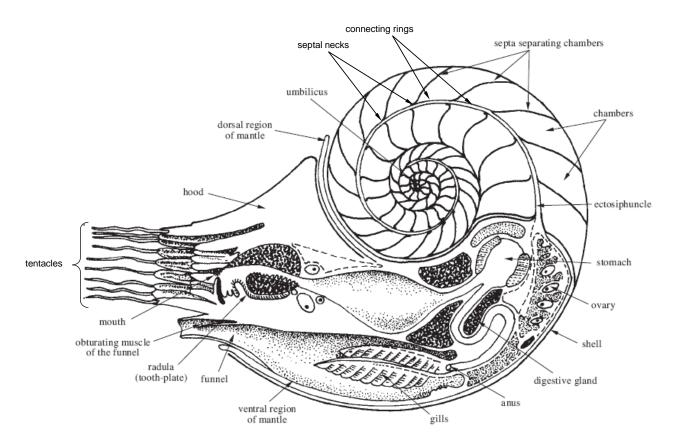


Fig. 2. Shell morphology and anatomy of *Nautilus* one of only two extant nautiloid genera. Evolution of the nautiloids through time favored an energy efficient coiled shell along with a central siphuncle and simple necks and rings.

Ammonoids had a similar-looking shell but, under closer inspection, some significant differences become apparent (see Fig. 3). The most glaring difference between nautiloids and ammonoids is the shape of the suture lines--patterns visible on internal molds (steinkerns) and formed where septa were attached to the inside of the conch. Nautiloid sutures are simple often tracing a straight line around the conch although they may display various lobes (bends in sutures away from the aperture) or saddles (bends in sutures toward the aperture).

Ammonoid sutures, however, are often intricately crenulated or frilled with complexity increasing through time. Three basic suture types are recognized each signifying a major ammonoid division (see Fig. 4). Goniatitic sutures are somewhat smooth and mostly undivided with pointed lobes and rounded saddles. Ceratitic sutures display frilling only on the lobes whereas with ammonitic sutures both the lobes and saddles are extensively frilled. Such detail on ammonite sutures is a powerful tool for determining taxonomy to the species level while the simple sutures of nautiloids are of limited help in taxonomy.

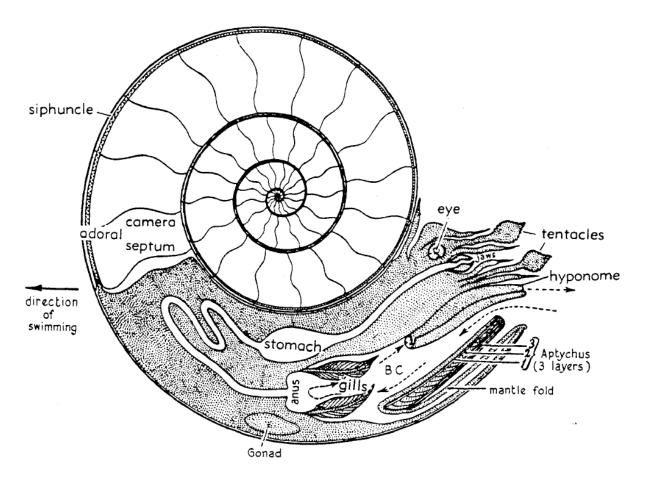


Fig. 3. Shell morphology and hypothetical anatomy of an ammonoid. (From *Treatise* Part L, fig. 124.)

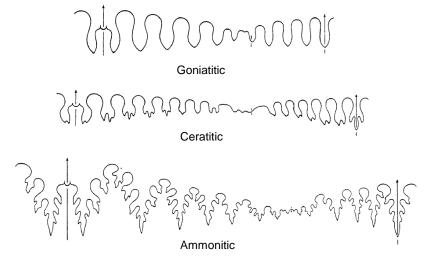


Fig. 4. Tracings of the three types of ammonoid sutures. The arrows point to the aperture. (Modified from Treatise Part L, Fig. 7.)

For nautiloids, taxonomy is most often determined by the position and structure of the siphuncle along with the shape of the septal necks and curvature of the connecting rings (see Fig. 2). The morphology of the siphuncles of nautiloids was very diverse allowing researchers to classify nautiloids both taxonomically and phylogenetically. Positions of siphuncles ranged from ventral to dorsal with ventral and central (more-or-less) locations being the most common. Through time, the siphuncle decreased in size and became more centralized as coiled shells dominated. With ammonoids, the size and position of the siphuncle displayed little variation with most siphuncles small in size and located at the ventral (outer) wall of the coiled shell (although the siphuncles of the Late Devonian order Clymeniida were located in the dorsal part of the shell).

The complexity of ammonoid sutures, indicators of septa with intricate surface topography, has been the subject of controversy since ammonoid fossils were first discovered. Many explanations for why ammonoid septa were so complex have been proposed. The most common hypothesis is that, since the flat-sided, highly compressed, thin-shelled design of many ammonoids (especially true ammonites) was much weaker than the inflated, thick-shell design of *Nautilus*, the complex folding of the septa was a method to reinforce the shell against both shrinking and implosion stresses from hydrostatic pressures "by sharing the same pressure load along a longer line" (De Blasio 2008, p. 22). Additionally, the buttressing of the shell walls by the fluted septa would have allowed the animal to conserve weight by co-evolving thinner shells and septa. This would have permitted ammonoids to grow at a faster rate and attain maturity quicker than nautiloids, an important factor in reproduction as we will see later. This argument, logical though it may seem, has been challenged on several fronts. In one study, it was found that as septa increased in complexity shell thickness remained the same (Saunders 1995). Also, it has been calculated that "any departure from a hemispherical shape actually yields higher, not lower, stresses in the septal surface" (Daniel et al. 1997, p. 470). Other plausible hypotheses include additional surfaces for muscle attachment and redistributing the biting force of durophagous (shell-crushing) predators.

In my opinion, however, the most logical explanation proposed is that folding of the septa may have aided in fluid removal during growth and fluid re-filling after a loss of shell material (Saunders 1995). In *Nautilus*, cameral fluid is removed from newly-formed chambers by osmosis and low-pressure gas is introduced into the chambers to maintain neutral buoyancy during growth. The primary structure involved in fluid removal in *Nautilus* is the siphuncle. However, since the shell is coiled, continued removal of fluid results in a loss of contact between the siphuncle and remaining fluid (termed decoupling). In *Nautilus* the surfaces of septa are layered with conchiolin (the pellicle) which soaks up and transports decoupled fluid to the siphuncle for removal. Similar structures have been detected in ammonoid fossils. The faster-growing ammonoids could have used the increased surface area of the folded septa to transport and remove fluid much more efficiently than *Nautilus*. Additionally, a loss of shell material, due to either impact with seafloor rocks or predator attack, could have been compensated for by a relative quick re-introduction of fluid to the chambers thus compensating for weight loss.

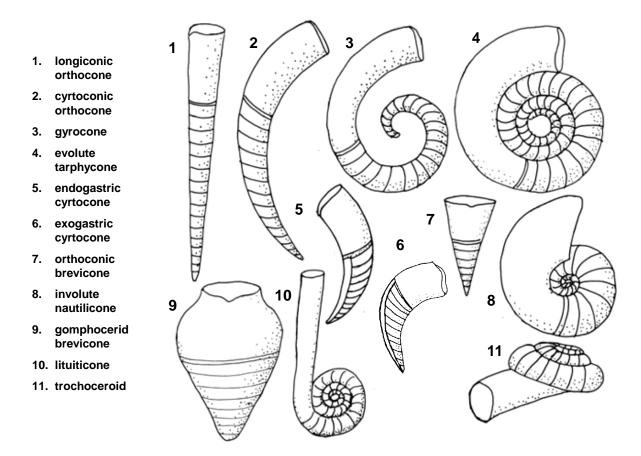


Fig. 5. Nautiloid shell shapes. (Modified from Flower, 1964, Figure 2.)

Shell form is another way in which nautiloids and ammonoids differed. Nautiloids displayed an enormous range in shell shape (see Fig. 5) ranging from straight to curved (both endogastric and exogastric) to loosely coiled to tightly coiled to flat. There were also several heteromorphic forms in which shell shape changed during ontogeny. Although ammonoid shells were mostly planispirally coiled, the coiling displayed great variation ranging from evolute through involute and from depressed to spherical to compressed shells (see Fig. 6). The real variation in ammonoid shells occurred with the Cretaceous heteromorphic ammonites. The variety and range of coiling, bending, and re-curving of the fossil shells is astounding (see Fig. 7). As we will see later, these types of shells drastically restricted both the animal's motion and its interaction with the environment.

Another aspect of shell morphology is intraspecific variation. Except for minor differences due to sexual dimorphism (see below), nautiloid shells of a single species were remarkably uniform. Ammonoid shells, on the other hand, displayed remarkable range for single species, which was only identified when massive concentrations of adult conchs were discovered (Dagys and Weitschat 1993; see Fig. 8).

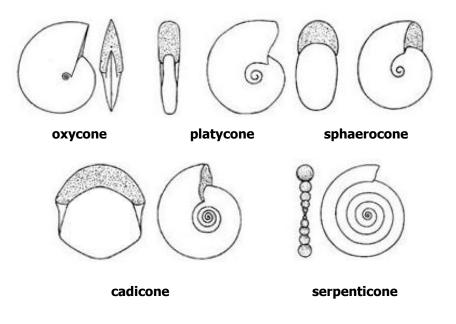


Fig. 6. A few examples of the range in coiling for ammonoid shells.

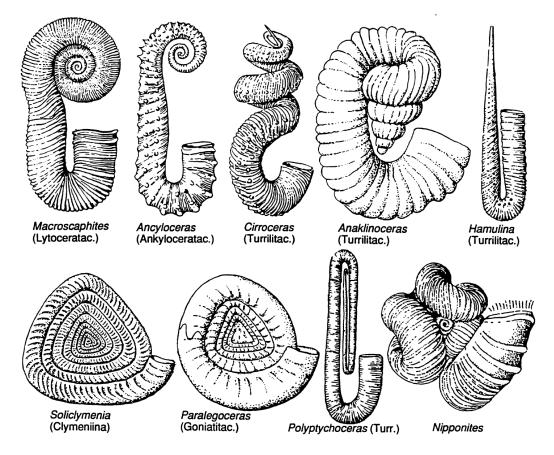


Fig. 7. Some heteromorph shell shapes. (Modified from Seilacher and Labarbera 1995, Figure 1.)

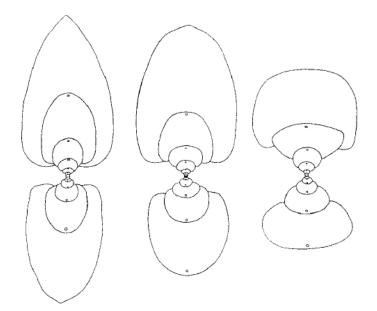


Fig. 8. Cross-sections of three morphotypes of the single ammonoid species *Czekanowskites rieberi*. (From Dagys and Weitschat 1993, Fig. 9.)

Still another morphological difference is sexual dimorphism. Adult *Nautilus* males have somewhat larger shells and broader apertures than females in part to accommodate the spadix, a reproductive organ composed of four fused tentacles. Since male and female nautiluses are otherwise remarkably similar, it is understandable that determining sexual dimorphism in fossil nautiloids is difficult at best.

Sexual dimorphism in ammonoids is both simple and complicated. The enormous difference in shell size between males and females made sex determination easier--at least once this size disparity was finally recognized. Female shells, referred to as macroconchs, can be as much as 5 times larger in size with living chambers of adult females as much as 125 times larger in volume than those of adult males, referred to as microconchs (see Fig. 9). Such a size difference, however, has also resulted in separate species or even generic designations assigned to the different sexes of the same species. It was only when the early stages of these shells were examined and found to be identical that such extreme sexual dimorphism was finally recognized. Extreme size difference exists today between female and male *Argonauta* ("paper nautilus") and to a lesser extent with coleoids in general--another similarity between ammonoids and coleoids.

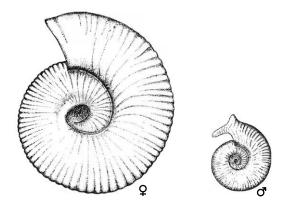


Fig. 9. Example of sexual dimorphism in ammonoids. The macroconch (female) was originally named *Bullatimorphites bullatus* and the microconch (male) was named *Schwandorfia marginata*. They are now both named *B. bullatus*. (Modified from Makowski 1962, Text-Plate XI.)

Physiology, Behavior, and Lifestyles

So far the differences between ammonoids and nautiloids appear to be superficial (suture complexity, location of siphuncle, etc.) and the similarities (fluid removal, neutral buoyancy, etc.) appear to be of overwhelming importance. However, when we begin to delve into other aspects, such as physiology and behavior, the differences between them dominate our assessment of their lifestyles and provide us with possible answers to the extinction question.

It is, of course, understandable that *Nautilus* has for decades served as a model for planispiral-type coiled ammonoids since it is the only ectocochliate (externally-shelled) cephalopod still alive. But, as stated above, modern cladistic analysis suggests that ammonoids and coleoids are sister groups and that both arose from a group of extinct cephalopods called bactritids which themselves evolved from the nautiloid order Orthocerida. This sister-group relationship is not evident in shell morphology, of course, since coleoids either have an internal shell or lack a shell entirely--a characteristic that initially prevented coleoids from being considered viable analogues for ammonoids. A much earlier split resulted in the order Oncocerida which gave rise to the Nautilida--the order that would eventually produce *Allonautilus* and *Nautilus* (see Fig. 1).

Soft anatomy is always speculative with fossil organisms (particularly extinct forms) but the phylogenetic relationships described above allow us to speculate about the number of appendages present on ammonoids and nautiloids. One fossil coleoid, named *Jeletzkya*, from the Mazon Creek Lagerstätte (Upper Carboniferous Westphalian D) in Illinois, may provide a possible answer to the evolution of cephalopod appendages--the fossil displays ten undifferentiated arms. Assuming ten arms was a primitive trait of early coleoid-type cephalopods, it would seem reasonable to assume that one pair could have been modified into tentacles thus becoming a derived feature of squids and cuttlefishes whereas two of the arms may have been lost within the octopod lineage. If true, it seems logical to further speculate that ammonoids also possessed ten arms as did the ammonoid's ancestors the bactritids and their nautiloid ancestors, the Orthocerida. Similar inferences suggest, however, that members of the Oncocerida (and their ancestors, the Tarphycerida) may have had numerous *Nautilus*-type tentacles since the Nautilida (the order that includes *Nautilus*) arose from the Oncocerida.

Since all cephalopods are marine animals, they must be able to maneuver in the water column to be successful. The swimming efficiency of ectocochliates is mostly a function of shell stability. Stability in a coiled, chambered shell is achieved when the centers of buoyancy and mass are widely separated so that not only would the force generated by the animal's "jet-propulsion" be mostly transferred into horizontal motion with a minimal amount of rocking but also would impart a restorative force to the shell should the animal experience any rotation or rocking. Separation of these two centers is greatest in coiled shells with short body chambers such as many nautiloids, including *Nautilus*, and early ammonoids. For straight shells the centers were coincident and the force was parallel to the long axis of the conch. Many ammonoids (and some early Paleozoic coiled nautiloids), however, had long, narrow living chambers that, at the extreme, approached 360° which placed the centers of buoyancy and mass very close together. In this configuration, any horizontally applied force would have resulted in a rotation of the conch instead of forward motion. Also, fossil evidence suggests that nautiloids possessed retractor muscles that were short and strong, similar to those of today's *Nautilus*, while those of ammonoids were long and weak indicating that the "jet-propulsion" method of locomotion was inefficient for many ammonoids. Other factors that limited

the swimming ability of ammonoids include constrictions of the apertures, lack of a hyponomic sinus (indentation in the aperture allowing the hyponome to direct the water jet), highly convoluted body chambers (heteromorphs), and strongly ornamented shells that caused drag. Therefore, it appears that most ammonoids were probably better adapted to vertical movements achieved by regulating the fluid in their chambers. Based on these supposed limitations, several life-styles have been proposed for ammonoids that run the gamut from benthic crawlers to planktonic floaters.

Another line of evidence that indicates many nautiloids were active in the nekto-benthic oceanic realm is shell counter-shading. Color patterns on Nautilus cover the entire shell until maturity at which time color ceases to be produced on the venter of the shell. This "two-toned" coloration (see Fig. 10), referred to as counter-shading, provides the animal with camouflage both when viewed from above--the disruptive banding on the dorsum breaks up the shell profile and blends with the substrate--and when viewed from below--the uninterrupted white of the venter blends with the bright surface waters. In fossil nautiloids, the actual coloration itself is not preserved but is represented by various patterns of pigmentation in the form of straight or zigzag lines. When present on orthocones, the patterns are confined to one side, the dorsum, which is indicative that these nautiloids engaged in active, horizontal swimming and made use of the "color" patterns as camouflage similar to *Nautilus*. When present on cyrtocones, however, these patterns often form banding that encircles the entire conch--strong evidence that these nautiloids were more-or-less confined to the ocean floor and used the banding to blend with the substrate. Nautiloids with closelyspaced septa, highly depressed shells (e.g. Gonioceras), large siphuncles, and heavy cameral deposits were also confined to the substrate while shells with no deposits and widely spaced septa (large chamber volumes) most likely floated near the surface feeding in the plankton.

"Color" patterns in ammonoids were a bit more varied than those of nautiloids. In some ammonoids the patterns were correlated with growth lines and were present on the entire conch even at maturity. Others displayed bold patterns that encircled the conch parallel to shell coiling. Still others made use of *Nautilus*-type counter-shading.



Fig. 10. *Nautilus pompilius* shell showing counter-shading (dorsal brown stripes and ventral white surface). Some orthoconic nautiloids displayed similarly positioned banding. Many ammonoids displayed similar coloration as well as other pigmentation patterns. (Photo by author.)

The way in which nautiloids and ammonoids conducted their lives has been the subject of lively debate for decades. Since fossils of nautiloids and ammonoids are rarely found in deep water sediments, it has been theorized that they were probably limited to maximum depths of around 200 meters with true ammonites restricted to relatively shallow coastal waters. We can speculate with a bit more certainty about nautiloids since there are specific morphologic features that point to certain lifestyles. For example, most straight shelled orthocones contained various ventrally-located cameral or siphonal deposits or endocones that acted as ballast to keep the shell in a more maneuverable horizontal position and minimize the "roll-over" effect. Such adaptations, along with the countershading described above, strongly suggest an active-predator type of lifestyle. On the other hand, some cyrtocones had small chamber volumes that would not have contained enough gas to induce neutral buoyancy. There are several lifestyle possibilities for these animals including total confinement to the substrate similar to snails or the ability to use the siphon to either "jump" off the substrate for a short time searching for food or hover just above the seafloor. Whatever path they followed, the continuous color-banding encircling their shells indicates that these nautiloids did not stray very far from the seafloor for any appreciable length of time. In contrast, brevicones with large chamber volumes and no deposits were better adapted to floating in the upper waters feeding on plankton life. An interesting Ordovician nautiloid was Gonioceras that, because of the large surface area and small chamber volume of its extremely depressed shell, was undoubtedly also confined to the substrate. It seems reasonable to speculate, then, that Gonioceras was an ambush predator that partially buried itself in substrate sediments waiting for prey to pass by within its reach. Extremely large endocerids were also confined to the substrate since their siphuncles occupied most of the phragmocone limiting the amount of buoyant gas. Planispirally coiled nautiloids and advanced ascocerids (nautiloids that truncated early parts of their shells) did not need ballast since the buoyant gas-filled chambers were advantageously located above the living animal.

Ammonoids did not secrete any type of mineral ballast but, since the great majority of ammonoids were planispirally coiled, there was no need to encumber the shell with needless weight. Since the swimming ability of ammonoids has been questioned, speculations on lifestyles have centered on two types of activities. First, some researchers have proposed that many were confined to the substrate living like snails on the ocean floor. Second, others have speculated that, without ballast and with thin shells, they were positively buoyant and floated near the top of the water column. Although ammonoids were probably not as adept at swimming and as maneuverable as nautiloids, the fact that they were able to effectively remove (and add, see above) fluid from their chambers indicates to me that at least ammonoids with short body chambers may have been able to carry out a lifestyle similar to Nautilus. The apertures of coiled ammonoids with body chambers extending 180° or more, however, would have been oriented vertically. Such an orientation would have challenged the animal with respect to swimming and interaction with its environment and these ammonoids may indeed have been passive planktonic floaters filtering food bits from the water. Heteromorphic shells also presented the animals with challenges. The often complex coiling and folding of the shell would have positioned the apertures in various orientations depending on the ontogenetic stage. Since many heteromorphic shells display a final bend in the body chamber as maturity was approached (see Fig. 7), these apertures would also have pointed upwards indicating that they too most likely engaged in a planktonic lifestyle. Other heteromorphs, such as Baculites, with straight shells (after an initial coiled phase) would have been oriented vertically with the aperture pointed downwards and may have floated just above the substrate searching for food (although there is a possibility that they retained cameral fluid as ballast thus assuming a horizontal orientation).

Possibly the most significant difference between nautiloids and ammonoids involves ontogeny and reproduction. After extensive field work and aquarium studies, it has been determined that the female *Nautilus* lays only about 10 relatively large (25+ mm) eggs per year in relatively warm waters and, due to a lifespan of 20-30 years, is able to breed for many years after sexual maturity is reached. The eggs hatch in about 12 months producing large offspring (20-25 mm). The fully-functional hatchlings are equipped with seven chambers and, after hatching, the juveniles descend to deeper, cooler waters where they assume adult scavenging habits. Fossil evidence indicates that extinct nautiloids experienced a similar reproductive cycle. For example, preserved morphologic features indicate that the juveniles of the Cretaceous nautiloid *Eutrephoceras* had four chambers in place upon hatching. Additionally, evidence from oxygen isotopes indicates that the eggs were laid in relatively warm water at depths of around 100-200 meters. When nautiloids, like *Nautilus*, reached sexual maturity, growth ceased and, unlike most ammonoids and coleoids, they lived for many years past maturity.

In contrast, ammonoids produced large numbers of very small eggs that hatched into 1 mmor-so embryos (which have been found fossilized) with one relatively large chamber in addition to the body chamber. The positively buoyant hatchlings most likely spent some growth-time in the plankton, as do many newly hatched squids today--an efficient method of dispersal that also, unfortunately, made them susceptible to the end-Cretaceous extinction event (see below). Many ammonoids, like most of their coleoid cousins, probably practiced a reproductive strategy involving a single communal mating event followed by post-spawning mass mortality. Several mono-specific deposits of large numbers of individuals of both sexes provide evidence for this speculation (Dagys and Weitschat 1993). However, since some coleoids experience multiple breeding episodes during life-spans of several years, it is possible that some ammonoids did the same.

So, it would appear that the physiology, soft anatomy, and behavior of ammonoids may have been more similar to present-day coleoids than to *Nautilus*. The presence of an external shell, however, presented the ammonoids with similar problems and limitations in stability, locomotion, and predator avoidance as those faced by *Nautilus* and other nautiloids. Therefore, we can gain insight into the life-style of the ammonoids by using both coleoids and *Nautilus* as analogues.

Evolution of Nautiloids and Ammonoids

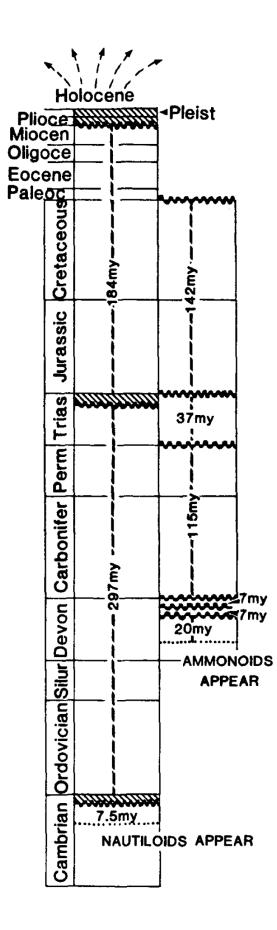
It appears that the first true cephalopod evolved from a septate monoplacophoran that developed a siphuncle. The earliest externally shelled cephalopod was the Late Cambrian nautiloid *Plectronoceras*. Extensive field work in China has revealed that Late Cambrian nautiloids diversified into 4 orders, 34 genera, and about 130 species. As shown in Fig. 11, nautiloids and ammonoids experienced several periods of stress when their taxonomic numbers were severely reduced. For nautiloids, the first of these taxonomic bottlenecks occurred near the end of the Cambrian when only one order, Ellesmerocerida, and two genera, *Clarkoceras* and *Ectenolites*, crossed the Cambrian-Ordovician boundary. This severely depleted fauna once again diversified during the Ordovician. After the Ordovician, however, nautiloids decreased both in taxonomic diversity and morphologic

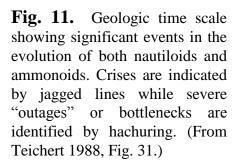
disparity. During a second bottleneck near the end of the Triassic, nautiloid diversity was reduced to one genus, *Cenoceras*, which crossed into the Jurassic allowing the nautiloids to once again diversify (although the discovery of an Early Cretaceous orthocerid indicates more survived than just *Cenoceras*).

All Late Cretaceous nautiloids were, as are *Nautilus* and *Allonautilus*, members of one order--the Nautilida. Of the nautiloids present at the end of the Cretaceous, at least three families and tenor-so genera crossed into the Paleogene. Today, nautiloids are experiencing a third bottleneck that has decreased their diversity to two genera. However, several genetic studies reveal that the separate *Nautilus* populations in the Pacific (isolated by extreme ocean depths that form barriers to migration) are genetically variable and a new diversification event may be beginning. Surprisingly, major mass extinctions at the end of the Permian and Cretaceous Periods did not appreciably affect the nautiloids.

Ammonoids appeared in the Early Devonian (see Fig. 12), as did coleoids, both having evolved from the bactritids. What sets the bactritids apart from their orthocerid ancestors and links them to the ammonoids and coleoids is their reproduction--bactritids produced large numbers of tiny eggs resulting in very small hatchlings. Of the nine ammonoid orders, four were pretty much confined to the Paleozoic. Of these, by far the most important and diverse group was the order Goniatitida, the goniatites. Although their morphologies varied, the shells of most goniatites were small, relatively smooth, and involutely coiled. In addition, it appears that, based on a deep hyponomic sinus, the goniatites were good swimmers. Another order, the Prolecanitida, was morphologically more diverse than the goniatites and gave rise to the "transitional" order Ceratitida, the ceratites, in the latest Early Permian.

Ceratites displayed a wide variety of shell coiling and ornamentation as well as more complex sutures than any ammonoid group before them. Although ceratites evolved during the Permian, the vast majority are found in Triassic rocks having survived the Permian extinction. It has recently been determined that the recovery and diversification of ammonoids in the Triassic took much less time than previously assumed (Brayard *et al.* 2009). Traditionally, the time for the recovery of the ammonoids was assumed to have been 5-10 million years or so. This recent study discovered that, during the Early Triassic, "ammonoids diversified explosively in the first million years" (p. 1118) and that "ammonoid diversity reached values equal to, if not higher than, those for the Permian" (p. 1119) in less than two million years. This Early Triassic diversification continued until the total standing ammonoid diversity was actually higher than that of both the Permian and the rest of the Triassic. In contrast, recovery of many benthic groups, such as snails and clams, was delayed until well into the Middle Triassic. Although exact details are lacking, the order Phylloceratida arose in the Early Triassic and was the only order that survived the Late Triassic extinction giving rise to all post-Triassic ammonoids.





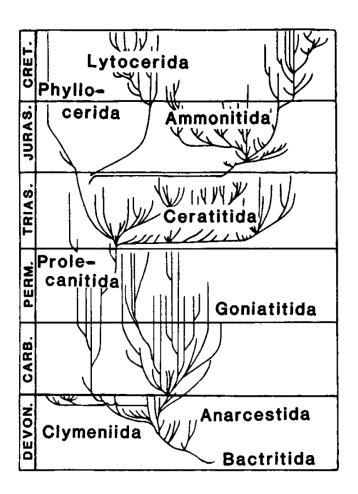


Fig. 12. A brief outline of the phylogeny of the non-heteromorph ammonoids. (From Teichert 1986, Fig. 4.)

There were four orders of ammonoids in the Jurassic and Cretaceous Periods (see Fig. 12). The Phylloceratida and the Lytoceratida were possibly the only true deep-water ammonoid groups. The third order, the Ancyloceratida, contained most of the heteromorphs. The last and the most diverse ammonoid order was the Ammonitida, true ammonites, that displayed regular coiling and, commonly, sexually-dimorphic shells. These ammonites diversified into a large number of specialized species that were limited in geographic range.

It has been argued that both the taxonomic diversity and abundance of Cretaceous ammonites declined through time and that the perceived mass extinction of the ammonites at the end of the Cretaceous was just the last gasp of a dying group. However, much of the drop in diversity had been noted for the shallow-water taxa when, in reality, many ammonites added heavy shell ornamentation and started to inhabit deeper waters in response to the increased numbers of durophagous predators. In fact, the decline in these ammonites was compensated for by the increased diversity of the heteromorphs. More recently, studies of Masstrichtian (last stage of the Cretaceous) rocks indicate fairly consistent ammonite diversity, albeit reduced from the previous stage, right to the end of the period (Ward 1997).

The ammonoids experienced crises near the end of the Devonian (actually three separate events with only two to four genera surviving each event), the end of the Permian (essentially only ceratites survived), the end of the Triassic (the only crisis affecting both nautiloids and ammonoids), and, of course, at the end of the Cretaceous when they completely disappeared (see Fig. 11).

The Extinction

When considering the demise of one group and the survival of a closely related group one must attempt to find some advantage the surviving group had over the disappearing group. Therefore, speculations on why the ammonites went extinct at the Cretaceous-Paleogene (K-Pg) boundary and the nautiloids did not, have focused on specific differences between the two groups. Many differences have been cited above and a few of these are central to possible explanations for the extinctions of the ammonites.

One explanation is centered on shell design. Nautiloids relied on the slow process of calcification to strengthen their shells. The result is a heavy coiled shell with thick outer walls as well as thick, mostly hemispherical septa perfectly designed to withstand deep-water pressures and many predators. Ammonites, on the other hand, grew quickly by secreting thinner shells and populated mostly shallow waters. Surface ornamentation and complexly folded septa would have strengthened the shell and redistributed the biting force of some predators. Unfortunately, such heavily ornamented shells were poorly designed for escaping the aggressive durophagous predators that inhabited shallow Late Cretaceous waters.

A second explanation focuses on the many short-lived and geographically-restricted ammonite species present during the Late Cretaceous. The great range of shell shapes, both coiled and heteromorph, indicates that the ammonites were ecological specialists. Unfortunately, this would have made them particularly susceptible, as are all specialized organisms, to large- or even smallscale environmental changes that occurred in the Late Cretaceous due to either the asteroid impact or the Deccan flood-basalt eruptions or both. By contrast, the nautiloids, represented by fewer, species exploited a wide range of habitats and would have been less vulnerable to such environmental changes.

The most logical explanation is based on the difference in the reproductive strategies between ammonites and nautiloids. Ammonites grew fast and many died young, perhaps within one year as many coleoids do today. As described above, to compensate for this short lifespan, thousands of extremely small eggs were laid in mass spawning events followed by post-mating adult mass mortality. The 1 mm-or-so hatchlings would have spent growth-time in the plankton since they were positively buoyant and were not able to reach neutral buoyancy for some time. This made them susceptible to the end-Cretaceous collapse of the planktonic ecosystem (Holland 1987; Gallagher 1991). It appears that the impact of an asteroid-sized body on Mexico's Yucatán Peninsula (Chicxulub crater) tapped subsurface sulfur-rich rocks resulting in prolonged acid rain and acidification of ocean surface waters. Nautiloids, on the other hand, laid only a dozen-or-so very large eggs each season that took up to a year to hatch. The fully-functional shells of the juveniles allowed them to actively negotiate the water column and swim to deep water where they would begin to assume an adult lifestyle. Therefore, even if the end-Cretaceous event killed all of the adult nautiloids and ammonites, as some believe, as well as the ammonite progeny in the plankton, the nautiloids were able to outlast the severe environmental effects of the K-Pg event because of the slow development of their eggs nestled on the ocean floor. As a result, we have been given the privilege to witness firsthand one of the most marvelously engineered animals that has ever appeared on planet Earth--the chambered Nautilus.

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Mesozoic coleoids: Fossil squids and cuttlefish By Scott McKenzie Geology Department, Mercyhurst College

Most books on fossils including the treatise do not yet deal with soft body fossils from squids or cuttlefish. There are two reasons for this, first the fossils can often be hard to interpret and secondly most are rarely seen. Over many decades of collecting fossils, I have examined several interesting soft preservation cephalopods from Mesozoic lagerstätte.

Holzmaden quarries, Germany. The Holzmaden area is in the German black Jurassic rocks which are noted for marine reptiles like ichthyosaurs, plesiosaurs and the occasional flying reptile. Squid like cephalopods are uncommon but may show fine anatomical detail. Illustration #1 shows a complete *Phragmoteuthis* with the ink sac and arms still bearing their hooks. The one in the illustration was collected long ago and was re-prepared in 1999. With Holzmaden fossils, skilled preparation exposes fine details as the fossils there seldom split out well.

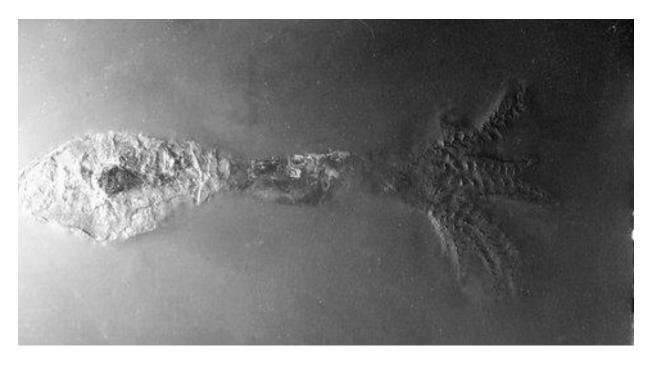


Illustration #1 *Phragmoteuthis conocauda* showing soft preservation. S. C. McKenzie specimen and photo.

Solnhofen region, Germany. The most famous lagerstätte in the world is in the White Jurassic limestones of Bavaria. Known since Roman times, the wonderful fossils of Solnhofen include several genera of squid like cephalopods with soft preservation. The common type is *Plesioteuthis* (Illustration #2). This specimen shows an exquisitely preserved ink sac. One of the oldest instances of un-altered preservation in the fossil record is ink from a Solnhofen squid. In 1903 Carnegie Museum bought the huge collection of a Belgian Barron. As there was no way to store all the fossils

in the museum, some crates were put in temporary storage in a warehouse. The warehouse caught fire and after it was extinguished, several Solnhofen fossils were stained purple from water activating the ink on a fossil squid! It has been said that an early scientific article was written with ink from one of these Jurassic squids.



Illustration #2 Plesioteuthis, ink sac, S.C. McKenzie specimen and photo.

One of the largest Mesozoic squids is *Leptoteuthis*, also from the Solnhofen region. The specimen in illustration #3 is typical. *Leptoteuthis* did not have an ink sac and had relatively short arms. Occasional examples show hooks that were inside their sucker discs for an extra strength grip.

Oxford Clay, Jurassic, England. Around 1840, railroad work exposed a stratum of exceptionally preserved squid like fossils. The locality is usually referred to as Christian Malford. The squids were fantastic, few in number and are probably unobtainable by private collectors. The exact stratum containing the coleoids has never been found again and few are in American museums. I have never encountered a specimen for sale in nearly 50 years of collecting.

Cretaceous Sub-Lithographic Limestone from Lebanon. The Lebanese quarries have been providing fine fossil fish to collectors since medieval times. In with the fish are a variety of shrimp, lobsters, clams, worms, crabs and the rare horseshoe crabs etc. The Lebanese quarries produce rare octopus as well as other squid like cephalopods. Most of the squids are marketed as octopus. The octopuses from these sites have two tiny paired "pens" or shells at the top of the head. Squids show a long pen that immediately separates them from octopus.

The squids vary in the clarity of preservation. Some are just pens, others show detail like beaks and even eyes! Some of the cephalopods offered for sale have unfortunately been painted over and are not very useful for study or anything else, except maybe throwing at stray cats. The one in the photo here (Illustration #4) is not painted.

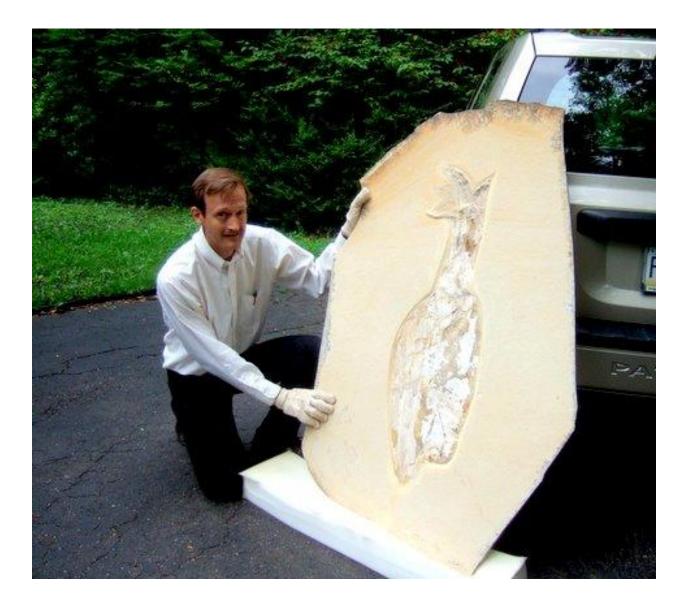


Illustration #3 Leptoteuthis gigas, with the author, S.C. McKenzie specimen and photo.

One class of cephalopod that is almost never seen as a body fossil is the cuttlefish. I have seen one specimen and a photo of another. The Quarry of Roy Noria at Hakel has been operated for fossils over several generations. They carefully save all of the fossils for their museum, for scientific study or for sale to teachers and collectors. This specimen (Illustration #5) is from the Noria quarry and is not painted.

These genera are not the only known fossil squids and other exceptional localities for them will be found in the future. Paleozoic and Cenozoic fossil coleoids exist. A few are known from Mazon Creek... they mostly look somewhat like blobs, but close examination will show hazy arms and other anatomy. Could there be others in our collections masquerading as common blobs? Who will look?



Illustration #4 *Glyphiteuthis libanotca* (Vampyropod) showing beak and soft parts. S.C. McKenzie specimen.



Illustration #5 Shows a fossil cuttlefish with soft arms, hood and body. S.C. McKenzie specimen and photo.

Turtles of the Cretaceous Period

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Introduction

The popularity, diversity, success and sudden demise of the dinosaurs of the Cretaceous Period tend to greatly overshadow the other reptile groups such as turtles that coexisted with the dinosaurs and weathered the extinction events that overtook the dinosaurs and ended the Cretaceous. A complete review of Cretaceous turtles is far beyond this short discussion, but this article will describe and illustrate some Cretaceous turtles, their habitats, and how they were related to each other and to present day forms.

Recent discoveries in the Upper Triassic of China (Ref. 1) suggest that turtles probably first evolved somewhere in Pangaea sometime in the Lower Triassic Period from one of the stem reptile groups. Archaic turtles diversified and are then found in the Upper Triassic of Europe and North America. Historically (Ref. 2), three infraorders of the order Testudines: Amphichelydia (the archaic turtles), Pleurodira and Cryptodira were recognized, but more recent work has eliminated the Amphichelydia, combining it with the Cryptodira. Pleurodires, "side-necked" turtles, cannot retract their head into the shell, where cryptodires, "hidden-necked" turtles, can retract their head into their shell by bending their neck into an S-shape. There are many views towards the classification of turtles. Modern complete classification of all chelonians is rather complex with one scheme (Ref. 3) defining nine pleurodire families and twenty-nine cryptodire families. In the Jurassic, pleurodires diversified in Gondwana and today are exclusive to the continents of the southern hemisphere and cryptodires diversified in Laurasia and today are found mainly in the northern hemisphere and worldwide in the oceans.

Cretaceous Turtles - Southern Hemisphere

At the beginning of the Cretaceous Period, Laurasia and Gondwana continued to rift, Europe first separating from North America and then Africa separating from South America. The Araripe basin of northeastern Brazil was in one of the rift valleys formed by the opening of the South Atlantic Ocean basin when South America separated from Africa. The upper Lower Cretaceous Santana formation of Albian age (105 mya) in the Araripe basin is famous for its concretions which finely preserve fish, pterosaurs and four species of turtles. These Santana turtles lived in clear, oxygenated water in a shallow embayment, estuary, near-shore or coastal marine environment. Originally two species were classified in the family Pelomedusidae (Cope, 1868), but the more common, earliest and best known fossil pleurodire, *Araripemys barretoi* (Price, 1973) while still a pelomedusid is now in its own family Araripemydidae (Price, 1973). Another pleurodire, the bothremyid *Cearachelys placidoi* (Gaffney, de Almeda Campos & Hirayama, 2001) and one marine cryptodire have also been found. Figure 1 shows a nodule containing a shell of *A. berretoi*. The small carapace is finely textured with small indentations suggesting a covering of very thin scales or skin. Complete specimens show a very long neck and broad feet suggesting these turtles had a highly aquatic life style and hunted small fish much like modern softshelled turtles. (Ref. 4)



Figure 1. Araripemys barretoi, private collection, length 15cm (6 in).

As Africa rifted from South America, it also continued to separate from Eurasia enlarging the Tethys Ocean. In freshwater deltaic and fluvial sediments from the south coast of the Tethys is found a rich and diverse vertebrate assemblage, including fish, lizards, frogs, crocodiles, dinosaurs and three families of turtles. The turtles are found in the Ifezouane formation in the Kem-Kem beds of southeastern Morocco and date from the lower Upper Cretaceous Period, early Cenomanian age (100 mya). Kem-Kem turtles have close affinities to the pleurodire fauna of the older Brazilian Santana formation with the pelomedusid *Araripemys* also being found at Kem-Kem. The pleurodire family Bothremydidae (Baur, 1891) is represented at Kem-Kem by *Galianemys whitei* (Gaffney, Tong, Meylan, 2002). *Galianemys whitei* was a large turtle as shown by the complete shell in Figure 2 and probably preferred a river or deltaic habitat as evidenced by the coarse sandstone with clay clasts in which it was found.



Figure 2. Galianemys whitei, private collection, length 54cm (21 in).

Cretaceous Turtles - Northern Hemisphere (North America)

In eastern Montana, North Dakota and South Dakota the Hell Creek formation of upper Maastrichtian age (67-65 mya) represents roughly the last two million years of the Upper Cretaceous Period prior to the global extinction event. The environment of the Hell Creek was a lush landscape of abundant rivers and open forests of small to medium height trees dominated by laurels, sycamores, magnolias and palms. The area was mid latitudinal, semi-tropical, humid with mild seasonality. The Hell Creek formation is a fluvial deposit consisting of poorly cemented, fine-grained sandstones with some siltstone and carbonaceous shale from meandering streams and rivers frequently flooding onto a broad coastal plain. This plain was situated along the western shore of the retreating, large, shallow, mid-continental Western Interior Seaway of the central North American continent on the eastern side of the rising Rocky Mountains. Many types of turtles are found in the Hell Creek and the equivalent Lance formation of Wyoming and the similar, but 10 million year older, Belly River (Judith River) Group of Alberta.

The more common turtle families of the Hell Creek include (Ref. 5) at least three genera of Baenidae (Cope, 1882) and at least two genera of Trionychidae (Fitzinger, 1826). The baenids are a group of cryptodires endemic to North America. They flourished in the Cretaceous, are common in the Hell Creek, had long digits on the front feet, streamlined shells, and long tails. All were riverine, bottom dwelling turtles, strong swimmers preferring channel habitats. The shell sutures in many adult baenids fuse into a solid mass inhibiting disarticulation and increasing their potential for preservation in the fossil record. In the Maastrichtian, eight or more baenid species are recognized from skull material, but since skulls are rare, three lineages of baenid shells can be readily recognized. The *Neurankylus* shells are large, have a finely crinkled pattern and a complete ring of marginal bones. The shells of the *Plesiobaena-Palatobaena* line lack supramarginal and neural scutes and have weak scalloping on the rear edges. The shells of the *Eubaena-Stygiochelys* line have

a nuchal scute, well developed gular scutes and strongly scalloped rear edges. Determining species within these groups is difficult and not all skulls have corresponding associated shells. Figure 3 shows a laterally crushed shell with skull and Figure 4 shows a complete, but highly fractured shell of *Plesiobaena antiqua* (Lambe, 1902).



Figure 3. Plesiobaena antiqua, private collection, length 27cm (10.5 in).



Figure 4. Plesiobaena antiqua, private collection, length 36cm (14 in).

The Turtle Graveyard locality (Ref. 6) in the Hell Creek of southwestern North Dakota has preserved large numbers of four different baenid species and two trionychid species. The environment represents an oxbow pond or shallow stream periodically drying during drought killing the turtles and then flooding, burying them with little transport. The turtle diversity, comparable to some modern southeastern North American river systems, suggests that paleoecologically the turtles specialized and partitioned the food resources in the Hell Creek environment. The skulls and jaws of these baenids would suggest that many ate mollusks, others were active carnivores and/or scavengers and some were omnivores. The baenids were very successful and dominated late Cretaceous riverine habitats in numbers and diversity with seven of nine species surviving the K/T extinction event and finally becoming extinct in the Eocene.

The Trionychidae (trionychids) or softshell turtles are a widespread group of cryptodires in Asia, Africa and North America (Ref. 7). These turtles are called softshell because they lack the horny scales or scutes of most other turtles and instead have a covering of leathery skin over the bones of the shell. The carapace and plastron are not sutured into a continuous shell as in most other turtles, but are separate and connected by strong ligaments. The underlying bone surface of the carapace and plastron is covered by lines of small pits and ridges making even a small fragment of fossil trionychid shell unmistakable. Modern trionychids are divided into two subgroups: the cyclanorbines (flapshell softshell turtles) 5 species and the trionychines (common softshell turtles) 17 species. Softshell turtles originated in Asia in the Lower Cretaceous and spread to North America in the Upper Cretaceous.

Plastomenids are either the stem or an early branch of the stem cyclanorbines. They are fossil trionychids having greater ossification of the shell, no extensive leathery edge, no protruding rib ends, and a well developed sculpturing of the carapace. Since modern cyclanorbines are only found in Asia and Africa with fossils dating only to the Miocene, and fossil plastomenids are known only from the Cretaceous-Eocene of North America, it is probable that the plastomenid/cyclanorbine - trionychine split occurred during the Cretaceous in Asia with subsequent migration of both to North America with later extinction of only the plastomenids. Plastomenids are distinguished from other trionychids by their relatively small size, domed carapace, extensively ossified shells, large eighth costal bones and extensive sculpturing of the plastron. Modern species of cyclanorbines inhabit slow-moving or stagnant rivers and marshes with sandy or muddy bottoms. This is an environment very similar to that of the Cretaceous Hell Creek and probably was also preferred by the plastomenids. The Hell Creek plastomenid *Hutchemys tetanetron* (Joyce, 2009) is shown in Figure 5.

Trionychines are the most common softshell turtle fossils of the Cretaceous. The nearly planar carapace usually has six or seven neural bones, a preneural bone in *Aspideretoides*, eight costal bones, an extensive leathery, muscular perimeter supported by elongated rib ends, and is deeply sculptured with rows of pits and ridges, especially in larger specimens. Adult trionychines are large turtles, reaching lengths of over two feet, with one Eocene fossil specimen attaining a length of over six feet. Figure 6 shows a carapace of a small specimen of *Aspideretoides foveatus* (Leidy, 1856), a common late Cretaceous trionychine species. Figure 7 shows an incomplete carapace of a large adult specimen of an *Aspideretoides*, probably also *Aspideretoides foveatus*. The modern trionychine, *Apalone spinifera* (LeSueur, 1827), is common in rivers of the southeastern US and prefers slow-moving, clean, fresh water environments such as the channels in the Okeefenokee swamp of southeast Georgia. Again, this is an environment very similar to the Cretaceous Hell Creek and was probably also preferred by *Aspideretoides*. Modern trionychines are mainly carnivorous.



Figure 5. Hutchemys tetanetron, private collection, length 12cm (4.5 in).



Figure 6. Aspideretoides foveatus, private collection, width 14cm (5.5 in).



Figure 7. Aspideretoides sp., private collection, full width of carapace est. 52cm (20.5 in).

Cretaceous Turtles - The Oceans

The extinct marine cryptodire turtle family Protostegidae became the dominant marine turtle of the Upper Cretaceous from the Albian to Turonian ages (105-90 mya), but drastically declined and became extinct in the Maastrichtian age (70 mya). The earliest protostegid turtle known is *Santanachelys gaffneyi* (Hirayama 1998) from the Santana formation of Brazil. The protostegid evolutionary trends to development of a large head, limbs modified to flippers, loss of scutes, reduction in bone mass of plastron and carapace for neutral buoyancy, and gigantism peaked in the late Campanian age (74 mya) *in Archelon ischyros* (Wieland, 1896) of the North American Interior Seaway. Protostegids probably specialized for feeding on ammonites, fish, squid and jellyfish (Ref. 8).

Confusion for largest turtle reigns between *Archelon*, a marine species, and *Stupendemys*, a terrestrial pleurodire from Venezuela. Although Stupendemys has a very thick shell and is about 7-8 feet long, the largest Archelon known measures 18 feet long, so there really is no contest for top spot. A cast of this huge *Archelon* specimen from the Campanian age found in the Pierre Shale of the southern Black Hills in South Dakota, now in the National Natural History Museum, Vienna, Austria, is shown in Figure 8. This turtle is estimated to have weighed over 4500 pounds when alive. The second largest *Archelon* known is on display at the Natural History Museum in Dallas, Texas. An excellent specimen of *Protostega gigas* (Cope, 1871) figured in many books can be seen at the Carnegie Museum in Pittsburgh, Pennsylvania.

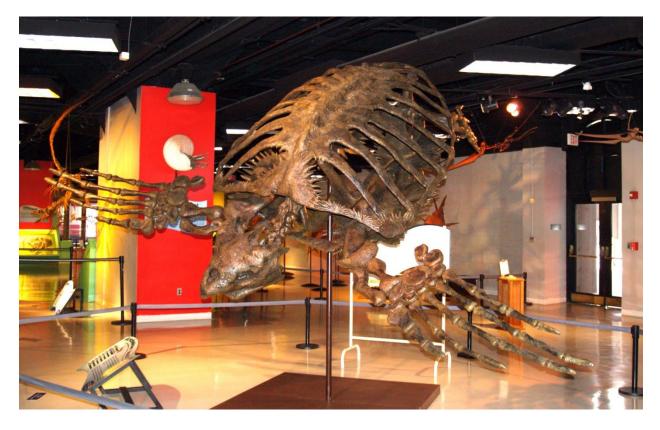


Figure 8. Archelon ischyros, cast, Richmond, VA Science Museum visiting exhibit, length 18 ft.

Cretaceous relatives of modern cryptodire cheloniid sea turtles are represented by several species of *Osteopygis* described from the Upper Cretaceous of Maryland, New Jersey, United Kingdom and North Africa. Skulls of *Lytoloma (Osteopygis) elegans* (Bergougnioux 1952) of the family Osteopygidae from Morocco, as shown in Figure 9, are commonly seen for sale. *Lytoloma* is found in the phosphate beds of the Khouribga plateau in the Ouled Abdoun basin of Morocco. These soft, yellow to orange phosphate beds which date from the latest Upper Cretaceous Maastrichtian age to the Paleocene (70-55 mya) are marine sediments deposited in the widening North Atlantic Ocean and in the Trans-Saharan Seaway. Many species of sea turtle, including *Lytoloma elegans* survived the extinction event and continued to thrive into the Paleocene.

Conclusion

This has been a brief overview of some of the turtles of the Cretaceous Period. Turtles had a major diversification and radiated throughout the world during the Cretaceous with the appearance of many of the families we have today. Turtles are tough animals that survived the K/T extinction event that ended the reign of the dinosaurs. They are still widespread throughout the world today, although many species are endangered. For more information on recent turtles, I recommend reference 7, Ernst and Barbour, "Turtles of the World" and reference 2, Prichard, "Encyclopedia of Turtles". There is no one updated reference on fossil turtles, but reference 5, Hay, "Fossil Turtles of North America" is a classic, although somewhat outdated by about a century.



Figure 9. Lytoloma (Osteopygis) elegans, private collection, length 7 inches.

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Mosasaurs of the Pierre Seaway Thomas C. Williams

During the Late Cretaceous, a short geological span of only approximately 6 or so million years, a predator evolved that would rule the sea's of the world until they became extinct approximately 65 million years ago. The word Mosasaur comes from the Latin word Mosa which is the Meuse river in Europe where the first mosasaur was discovered in a limestone quarry on the Meuse in 1764 and the Greek word sauros meaning lizard (Wikipedia). This first specimen, a partial skull was found in a quarry in Holland near the city of Maastricht. A second find drew a lot of attention to this animal and the speculation as to what it was drew a lot of incorrect conclusion that it was a whale, fish and a crocodilian. Interpretations as to what it actually was until the French scientist Georges Cuvier in 1808 confirmed Dutch scientist Adriaan Gilles Camper 1799 conclusion that this animal was a lizard. In 1822 it was given the name of *Mosasaurus* (Meuse reptile)--see Figure 1.



Figure 1. Genus *Platecarpus*

During the Late Cretaceous the world was in a changing mode geologically, however, approximately 85% of the planet was still covered by water as opposed to 71% today. During this time, the modern Atlantic Ocean was forming; Europe was beginning to look the modern continent, and the Rocky Mountains were pushing skyward. The Western Interior seaway of North America referred to as the Pierre seaway stretched as far west as Arizona and western Utah and ran north through what is today Canada to the Arctic Ocean--see Figure 2. At its largest extent the seaway was 1000 kilometers wide and as deep as 900 meters which in contrast was similar in size to the Mediterranean Sea. This area that was the Pierre seaway was once a geologic foreland basin and along with the higher sea levels of the period allowed water to flow in from the north and south. This interior sea way was subject to several periods of transgression and regression which pretty much ended in a near complete transgression at the end on the Cretaceous. Remnants of the seaway existed into the Mississippian embayment to the southern tip of Illinois. Carbonate deposits and other various forms of life confirm a warm tropical sea during the cretaceous. The higher sea levels caused marine flooding of areas enabling mosasaurs as a species to be found all over the world. Mosasaurs have been found on all continents including Antarctica and New Zealand.



Figure 2. Pierre Seaway

In North America, remnants of this interior seaway can be observed in the geologic formations throughout the former sea way which include the Pierre shale, Niobrara Chalk and the Austin in shallower waters as indicated by the presence of shallower water invertebrates in Pierre shale deposits. This does appear one significant piece of information indicating mosasaurs preferred deeper water perhaps to find larger prey. It is obvious that mosasaurs were quite capable of surviving hundreds of miles away from land in the open ocean. Recently it has been discovered that mosasaurs have been found in freshwater rivers in deposits in Hungary. Putting this together does this have some relation to size? Now did some mosasaurs find fresh water a new hunting ground where there larger cousins couldn't come. Smaller mosasaurs may have preferred shallower water to simply avoid larger mosasaurs and started migrating to near coastal and travelled up rivers as sharks do occasionally. However, these animals were once permanent land dwellers.

How mosasaurs evolved was a mystery until 2005 when an amateur fossil hunter found a fossil near Dallas Texas found a vertebra. This find turned out to be a fossil of a lizard now extinct that had evolved into one of the greatest sea predators of all time to this point. *Dallasaurus* clearly a missing link in mosasaur evolution was a three foot long lizard which was at one time a land dwelling lizard. At only three feet in length it simply would have only been on the menu for roaming predatory dinosaurs. It is theorized that *Dallasaurus* started first started taking to the water as a way of escaping those dinosaurs finding the water safer than the land. If you observe modern marine coastal lizards including komodo dragons and other monitor lizards they all swim well so this is not so hard to imagine. *Dallasaurus* appeared in the geologic record approximately 98 million years ago and at about 89 million years ago (mya) they took to the oceans for good. Within 6 million years this small marine coastal lizard evolved into many different fully aquatic species including the giant tylosaurs that approached 50 feet in length.

The Late Cretaceous seas contained a variety of mega predators that included fish, sharks and of course marine reptiles. Large marine reptiles are nothing new, the Mesozoic era was full of them with the Jurassic containing large pliosaurs like *Liopleurodon* up to 80 feet in length (Haines 2000). Sharing the Late Cretaceous sea was large fish Xiphactinus which could reach 18 feet in length and had teeth up to 3 inches long and at this size could hold prey up to 6 feet long (Everhart 2005). Sharks were also capable of reaching at least 20 feet in length, in particular Cretoxyrhina mantelli the ginsu shark which is very similar to the modern great white shark, so we have a modern day comparison. Cretoxyrhina mantelli, a lamniform shark had a world-wide distribution as demonstrated from the fossil record. A twenty-foot long predator is large by today's standards; however, for the Late Cretaceous this size while substantial is not close to the largest potential size limit. Ginsu sharks like there modern cousins fed on anything that they could catch including small mosasaurs; this has been verified by teeth marks and imbedded teeth in the bones of mosasaurs found in Kansas. What is more difficult to determine is the status of the bones, did the shark attack the mosasaur or was it already dead. It is a sure thing that sharks did both as the opportunity presented itself. The question remains, how did the Ginsu shark and other large sharks stack up against the mosasaur in terms of a top predator or was it mostly on the menu?

Reptiles included the largest variety of large predators which included: ichthyosaurs long and short neck plesiosaurs, crocodiles, turtles and of course mosasaurs. Large crocodiles up to fifty feet in length existed along the coastal areas of the Pierre Seaway. *Deinosuchus* could reach lengths of up to 33 feet weighing up to 10 tons and did attack dinosaurs when the opportunity presented itself. However, another large crocodile *Phobosuchus riograndensis* reached lengths up to 50 feet with four inch long teeth. *Phobosuchus* has been found in rocks in Texas dating 70 million years old. Crocodiles of this size while powerful are ambush predators may not have been so effective making them potential victims in the open ocean. Plesiosaurs could reach lengths up to forty feet; however, most of this length was neck with the skulls only up to two feet in length composing only 5% of *Elasmosaurus* total body length limiting what they could swallow. Plesiosaurs did have long sturdy teeth but these were primarily used for catching fish so they were capable but limited in the prey they caught.

Mosasaurs have been found in the fossil record of all sizes ranging from 9 feet Carinodens belgicus up to giant Tylosaurus proriger which did get up to 50 feet in length perhaps larger-see Figures 3 and 4. A six foot skull from the North Sulphur River in Texas possibly suggest that Tylosaurs may have gotten up to sixty feet is a possibility (Dallas Paleo Society 2001). Mosasaurus fit into Order Squamata related to modern day monitor lizards have similar body construction except for the absence of limbs for walking on land and streamlining for swimming--see Figures 1, 3 and 4. These were air breathing animals that also gave birth to live young. As shown in other parts of the fossil record webbing of the feet produced flippers that were used for steering making accurate tight turns. So where did the locomotion come, it came from the long powerful tail which contained over 100 of the approximately 130 total vertebrae. The jaw structures of mosasaurs are very similar to that of pythons both having a double hinged jaw making them capable of swallowing very large prey since they could temporarily unhinge it. Mosasaurs didn't chew their prey; their teeth were used for grasping only with the teeth pointing inward towards the mouth. Once in the grasp of a mosasaur there was only one way to go, down the hatch. A second set of double rowed pterygoid flanged teeth on the upper jaw which is today seen in pythons has helped us understand this as pythons use these extra teeth probably in the same manner. Mosasaurs only ate what they could swallow same as pythons and this may explain why some larger mosasaurs have been found uneaten and others were as known partially digested bones.

These similarities have led to the evolutionary connection between mosasaurs and pythons and in particular the reduced limbs found on pythons are clues to this evolutionary link. Both mosasaurs and pythons may have something else in common in their diet; if they can potentially swallow it they will try to eat it. Like the python that ate a very large alligator in the everglades and then burst for an unknown reason, a tylosaur was found with the remains of a sea bird, a shark, and a small mosasaur in its stomach. Like the python mosasaurs were eating machines and potentially growing as quickly as they ate, perhaps allowing mosasaurs to reach a larger size more quickly. Size may have mattered as it does with other animals if I am big enough I may be too big to swallow.

Watching the swimming motion of eels and sea snakes and their use of their paddle like tails may provide a glimpse for how they may have moved--see Figure 4. However, with the size of tail initial movement of the animal may have been much more dramatic. Large sea predators such as the great white shark use the dark coloration on the top of them for camouflage then strike upward in bursts of great power taking seals sometimes even jumping out of the water. Killer whales use their snouts to stun large prey as some fish do as well. Were these tactics used as strategy by large Mosasaurs to take prey as it has been suggested? Brains of these animals were only about the size of an index finger making more reactionary than capable of any real processing of a situation.

Fossil evidence shows that these animals fought with each other from scars left on fossil bones. These scars appear to be what is referred to as snout jousting sometimes resulting in a larger mosasaur crushing the skull of another. One basically complete specimen recovered from the Niobrara Chalk shows that the skull was crushed and the neck vertebrae snapped at a 45 degree angle and was preserved in the fossil record that way (Everhard 2005). Other specimens show damage and survival. As stated by the geologist James Hutton the present is the key to the past and there is no reason to believe that large predators of the past didn't use the same strategies.

In conclusion, mosasaurs dominated as a species world wide as recorded in the fossil record. These animals filled many potential ecological niches from being shell crackers like *Globidens alabamensis*, shallow water to the open ocean with the giant *Tylosaurus*. Predators such as *Tylosaurus* were 50 feet plus in length eating anything they could swallow. Their dominance is proven by in many cases the absence of other major predatory animals in the end such as plesiosaurs, *Cretoxyrhina mantelli*, and eventually other mosasaurs in the geologic record where lots of mosasaurs existed. Plesiosaurs and sharks may have simply moved into areas where there were fewer mosasaurs or been wiped out by a true predator, perhaps too good at what it did. Once the other large prey had been wiped out, did they turn on themselves? This is something that paleontologists are working on the proof when it comes will prove interesting! As to the final end of the mosasaurs it is a lot of theoretical ideas. Did they end exactly at the end of the Cretaceous or did they hang around for a while longer like there crocodile cousins?

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Figure 3. Tylosaurus proriger

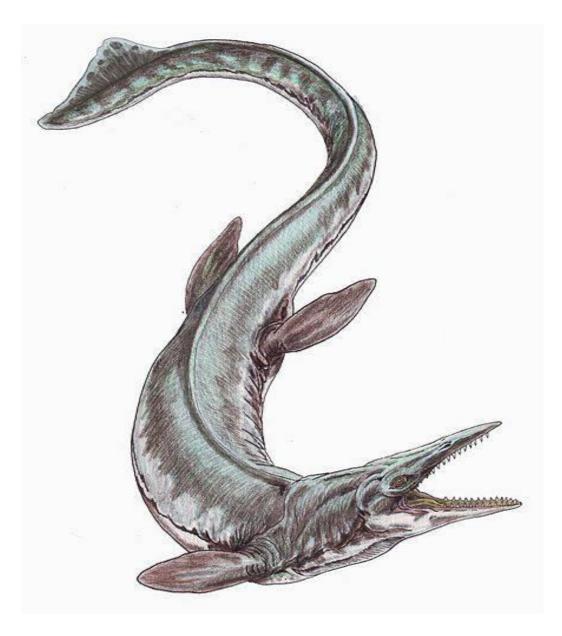


Figure 4. Reconstruction of *Tylosaurus*.

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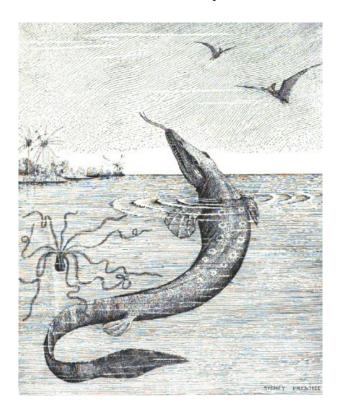
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Dragons of Kansas: The Mosasaurs of the Smokey Hill Chalk Michael T. Payne



Driving across Kansas via I-70, it would be hard to imagine that one is driving through some of the best fossil sites in the world, let alone fossil bearing formations from the age of dinosaurs. When one thinks of collecting fossils from the Mesozoic, one often thinks of locations in Montana and Utah, but finding them in Kansas?

In the Smokey Hill Valley region of western Kansas, massive exposures of chalk can be found, especially in Logan, Gove, Trego, and Ellis counties. You can often see some well worn signs along I-70 pointing to Castle Rock and Monument Rocks. These landmarks, made by the constant erosion of these chalk beds, were laid down in an ocean that split the continent in two during the latter half of the Cretaceous period. This stratum of bedrock is known as the Niobrara Formation and is divided into two members, the lower Fort Hays Limestone member and the upper Smokey Hill Chalk member. The Smoky Hill Chalk has, for over the past 140 years, produced fantastic specimens of life from the Late Cretaceous oceans that are housed in museums and universities all over the world. These include *Xiphactinus* (huge predatory fish), *Hesperornis* (large, flightless, toothed birds), plesiosaurs (giant sharks, often found with preserved soft tissue), even the occasional partial dinosaur. However, there is one group of extinct animals found here that has drawn paleontologists to the Chalk more often than any other, the mosasaurs.

Mosasaurs had been known since the first one was discovered in the Netherlands around 1780. Over the next half century, further discoveries were made in the American west. Then in 1868, a specimen of *Tylosaurus proriger* was sent to E. D. Cope that had been found in the vicinity of Monument Rocks. Over the next several years, O.C. Marsh sent a number of expeditions to the

Smoky Hill Chalk in search of these reptiles and his gamble was rewarded with over 2000 specimens being found. Other pioneers in paleontology, such as B. F. Mudge and army surgeon Dr. John Janeway, also collected in the Chalk. Another army surgeon, Dr. George M. Sternberg, collected fossils in the area over a number of years, but later became involved in the field of bacteriology, earning the distinction of becoming the first US bacteriologist. Perhaps his greatest contribution to the field of paleontology was introducing his younger brother, Charles, to the joy of fossil collecting. Charles H. Sternberg went on to become one of the most celebrated names in paleontology. He first started out collecting for Cope, but soon after, Cope had become more interested in collecting further west in his continued rivalry with Marsh. Sternberg chose to continue collecting in the Chalk on his own. Over the next near century, Charles and his three sons collected specimens from the Chalk, as well as various other places, and today their specimens fill museums around the world. It is hard to find a mosasaur from the Chalk that does not have something to do with a Sternberg.

The "Sternberg spirit" for collecting mosasaurs and other fossils from the Chalk lives on today in a different sort of way. While two of Charles' children went their own way, looking for fossils in various places outside of Kansas, the oldest, George, continued his father's work in the Chalk. George befriended a young Marion Bonner, who in his own right made many famous fossil discoveries, including a nearly complete *Platecarpus* mosasaur with large amounts of preserved soft tissue that even now, forty years after its discovery, continues to help shape our understanding of mosasaurs. One of his sons, Chuck, still lives out in Kansas running a small shop and taking people out on fossil hunts in the Chalk.

To this day, there is no place on earth that has yielded so many individual and well preserved specimens of mosasaurs as the Smokey Hill Chalk. They appear rather suddenly at the end of the Age of Dinosaurs and quickly become the dominant predators of the Late Cretaceous seas, reaching sizes far beyond that of their dinosaur counterparts on land. Mosasaurs are not dinosaurs and are in no way related to ichthyosaurs and plesiosaurs; they are thought to be closely related to varanid lizards such as the Komodo dragon, though some scientists think they are more closely related to snakes (Caldwell, 1999), but there is still much debate about this. To better understand mosasaurs, especially those found in the chalk, one should understand the nature of the chalk itself and so we will begin there.

Since the Jurassic, massive tectonic forces had been tearing the super continent of Pangaea apart. As a result, by the Cretaceous, the lack of polar ice caps and the formation of undersea mountain chains along welts pushed sea levels to some of the highest points ever seen. As the breakup of Pangaea continued, it pushed North America to the northwest, causing it to collide with the now destroyed Farallon Plate. This collision and subsequent subduction of the Farallon Plate under North America caused the formation not only of the Rocky Mountains, but also of a foreland basin in the middle of the continent. As a result of the basin's formation, the high eustatic sea levels allowed the creation of a vast epicontinental seaway that split North America in two. The eastern half was known as Appalachia and the western, Laramidia.

In an ironic twist, Kansas retains a near complete geologic record of the sea's history. If you drive west on I-70, you'll literally be driving through about 30 million years of this seaway's history (geologically speaking), beginning with the sea's first transgressions about 100 million years ago (the Comanche Sandstone) and continuing to about 71 million years ago as the seaway finally began to close (the Pierre Shale). The Smokey Hill Chalk itself was laid down between 88 and 82 million

years ago (late Coniacian to the early Campanian). By this time the sea was at its widest and its deepest, but even then it was relatively shallow (no more the 600 feet in depth). The sea was relatively warm, and being as shallow as it was, allowed for an abundance of not only animal life, but also of microscopic, brown-green algae called *Chrysophyceae*. The remains of these creatures, along with the microscopic coprolites from the organisms that fed on them (Hattin, 1982), produced a near constant rain of debris to the sea floor, forming a thick and soft, limey-mud that covered the sea's bottom. When an animal died and sank to the bottom, it would quickly be covered in this organic debris and sink into the soft sediment. This process led not only to an abundance of remains, but also spectacular fossilized specimens of the various life forms that inhabited the sea, including Rudistid clams, crinoids, squid, complete sharks, various bony fish, turtles, plesiosaurs, *Pteranodon* spp., several species of toothed birds, some dinosaur remains and, of course, mosasaurs.



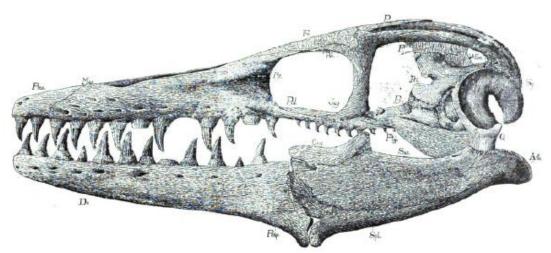
Map of the Western Interior Sea during the deposition of the Chalk. (By Dr. Ron Blakey, NAU Geology)

While remains of mosasaurs in the Chalk are relatively common and a number of genera are known, three genera stand out in terms of abundance. The rest are rather rare and are represented by incomplete or single specimens.

Platecarpus is by far the most common genus found throughout the Chalk. In fact, a study done by Russell of specimens collected by Marsh that are housed in the Smithsonian and Yale Peabody museum collections found that sixty two percent of mosasaurs found in the Chalk belongs to *Platecarpus* (Russell, 1967). As with so many fossils, when it comes to classifying an extinct animal on the species level, there often is much confusion and no less so with this genus. Thanks to a recent publication by Takuya Konishi and Michael Caldwell (2007), the field of named species has been narrowed down to two. *Platecarpus planifrons* is now considered the most abundant species in the

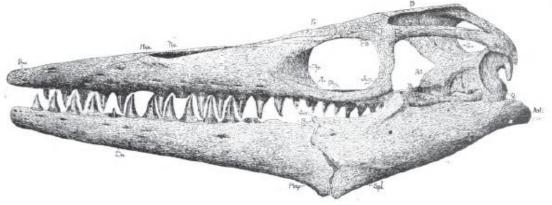
lower Chalk and *P. tympaniticus* in the upper. *P. coryphaeus* and *P. intericus* are now considered junior synonyms of *P. tympaniticus* (Konishi & Caldwell, 2010).

Overall, *Platecarpus* is a medium sized genus reaching lengths of about 24 feet. The tail is long and down-turned, with large, stiff paddles, and a skull unique among mosasaurs. The skull is rather short and contains fewer teeth than any other genus. The teeth tend to be rather thin and extend all the way to the end of the premaxilla.



Skull of *Platecarpus [tympaniticus] coryphaeus*. Note that the teeth extend to the very end of the premaxilla. Williston 1898.

The second most abundant genera in the Chalk are *Tylosaurus*. At present, three species are known from the Chalk: *T. nepeaolicus* and *T. kansasensis* in the lower 1/3 of the formation, and *T. proriger* in the other 2/3. *T. proriger* is by far is the largest in size of the three species, as well as the largest of any mosasaur found in the chalk. Reaching lengths of over forty feet, its teeth are far more conical and robust than in *Platecarpus* and the teeth do not reach to the end of the premaxilla as in *Platecarpus*, but instead the premaxilla ends in a bony knob. Over the years some scientists have believed that this knob was used against other Tylosaurs or as a ram in attacking prey, though current thought suggests otherwise.



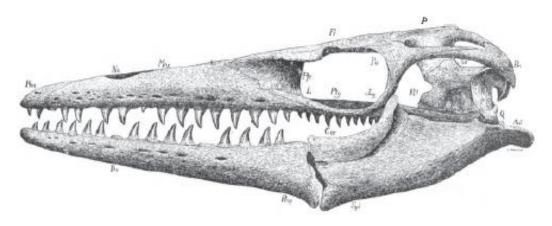
Skull of *Tylosaurus proriger*. Note that the teeth in the upper jaw do not reach to the end of the premaxilla; instead a boney knob has formed. Williston, 1898.

As an interesting side note, a *Tylosaurus proriger* specimen was found in 1911 by a group led by C.D. Bunker. It was found in the Pierre shale of Kansas just above the contact with the Smoky Hill Chalk (Everhart, 2005). With a skull of about six feet long and a body length of about forty five feet from nose to tail, it is one of the largest mosasaurs ever found.



The massive 6 foot long skull of a *Tylosaurus proriger*. This specimen is better known as the "Bunker Mosasaur". University of Kansas.

The third, *Clidastes*, is the smallest and, ironically, also the rarest of these three main genera in the Smokey Hill Chalk. Reaching only about 12 to 15 feet in length, it has a slim build and is possibly the most primitive of the mosasaur genera of the western interior sea (Everhart, 2005). Interestingly, it is by far the most common genus in the Selma Chalk of Alabama and Mississippi, which was deposited in a near shore environment, suggesting that *Clidastes* preferred living closer to shore (Russell, 1970). Near the top of the Smokey Hill Chalk *Clidastes* is more frequently found, and it's more abundant presence there suggests that the sea was narrowing, bringing Kansas closer to the shoreline.



Skull of Clidastes [propython] velox. Williston, 1898.

By the time of the Chalk's deposition, mosasaurs were the dominant predators in the western interior sea. Fully aquatic, mosasaurs had first appeared during the Turonian age, right after the Cenomanian-Turonian age extinction event. Whatever the cause was of this event, ichthyosaurs did not survive it, and pliosaurs soon followed, leaving an ecological niche and it has long been proposed that mosasaurs were the organisms that filled that niche (Russell, 1993). However, there remained plenty of competition for top predator of the western interior sea even with the demise of these two groups of reptiles and the arrival of mosasaurs.

Large sharks, such as *Cretoxyrhina mantelli*, which reached up to 22 feet in length, were abundant, along with other large fish such as Xiphactinus, which reached lengths of 18 feet, and these predators presented plenty of competition for the newcomers to the sea. Fossil evidence from the Chalk overwhelmingly supports this. It is not uncommon to find bones of mosasaurs that have been clearly acid etched, suggesting these bones were swallowed and then regurgitated by large sharks (Everhart, 1999). In fact, in the five years I spent collecting in the Chalk, I do not recall seeing one mosasaur specimen that was not unaffected by sharks. One specimen I found last summer (2010) not only had numerous marks on it from shark scavenging, but also had a tooth lodged in the side of a large *Platecarpus*' caudal vertebra's centrum. It is hard to say whether this evidence suggests scavenging only or active predation by sharks. Many examples, such as the specimen I found last summer, almost certainly are a result from scavenging, since the tooth belonged to the genus Squalicorax, a shark species which was much smaller than the mosasaur on which it was feeding. However, small genera, such as *Clidastes*, or young mosasaurs would have been easy prey for a large shark like Cretoxyrhina, and though while not as commonly found as Squalicorax teeth, there are from time to time Cretoxyrhina teeth associated with mosasaur remains (Everhart, 1999). Nevertheless, despite these threats. Mosasaurs continued to thrive, and by the end of the Chalk's deposition in the early Campanian, Cretoxyrhina became extinct (Everhart, 2005), perhaps due to being out competed by mosasaurs.

Large mosasaurs almost certainly preyed on sharks, and young sharks would have made an especially easy meal. It was also around the time of *Cretoxyrhina's* extinction that new mosasaur species where coming onto the scene and were reaching sizes not seen before, and while these sharks occasionally had been prey for mosasaurs in the past, this new wave of evolving mosasaurs might have out competed *Cretoxyrhina* and helped cause its extinction, but we will never know for sure.



A mark made on the left dentary of a *Platecarpus* skull by a *Squalicorax* during scavenging (scribe pointing to mark). Personal collection.

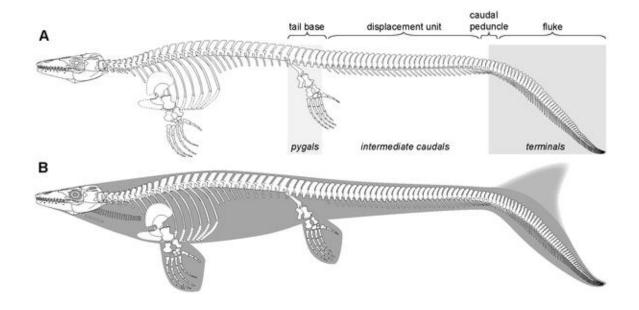
Besides sharks, mosasaurs of the western interior had a wide variety of prey, though the choice of prey most likely varied with the species and size of mosasaur. *Platecarpus*, whose teeth were much less robust than those of *Tylosaurus*, most likely fed on soft bodied and quick moving prey such as squid, belemnites, fish, and perhaps ammonites as well. *Clidastes*, having a small and narrow body, most likely had a similar diet. As for the *Tylosaurus*, fossilized stomach content has shown that it had a widely varying diet and would most likely have eaten anything it could swallow. One specimen of a *Tylosaurus proriger*'s stomach content (SDSMT 10439) that is on display at the South Dakota School of Mines and Technology contains several shark teeth, the remains of a large fish, Hesperornis bones (a large toothed sea bird that stood five feet in height), and part of a *Clidastes* (Martin & Bjork, 1987). Another Tylosaur specimen found by Charles Sternburg in 1918 contained the remains of a young polycotylid plesiosaur, and a turtle was found in a *Hainosaurus* specimen from Belgium (Dollo, 1887).



Gut contents of a *Tylosaurus proriger* (SDSMT 10439) that contain remains of a large fish, shark, *Hesperornis* and *Clidastes*. Museum of Geology.

It was more than size, however, that made them efficient predators at the top of the food chain. Mosasaurs were highly specialized hunters and well adapted for life in the water. Their tails were long and muscular, with tall neural spines and long chevrons that made the tail wide and flat. In a description of a *Tylosaurus proriger*, Osborn (1899) took note that the tail made a sharp downward bend, observing that the centra of the vertebrae where slightly longer above than below this curve. Further studies have shown this feature to be present not only in other Tylosaurs but also in *Platecarpus, Clidastes* and *Halisaurus*. Schumacher and Varner (1996) also showed that the

transverse processes become reduced in the caudal vertebrae and the neural spines are taller below this bend. Features like these are similar to anatomical aspects seen in ichthyosaurs, suggesting, that like ichthyosaurs, mosasaurs had a lobe or fin as well. A recent study conducted by Lindgren, Caldwell, Konishi, and Chiappe (2010) on the exceptional *Platecarpus* specimen found by Marion Bonner (LACM 128219, which is not only articulated but also has large amounts of soft tissue preservation) backed up this idea of a tail fluke. This deepening of the tail would not only have helped in forward momentum, but also would have provided a slight downward thrust to help with buoyancy problems. Mosasaurs are believed to most likely have moved in an undulating motion (such as a snake's) to propel themselves through the water. This swimming method was not as efficient as an ichthyosaur's, and therefore, they most likely could not have traveled at very high rates of speed for long distances (Massare, 1987). However, this method did allow them to make short bursts of high speed. Because of this, mosasaurs most likely were "ambush predators", surprising and outrunning their prey. It is thought this method of hunting allowed them to conserve energy as opposed to the method of the more streamlined ichthyosaur.



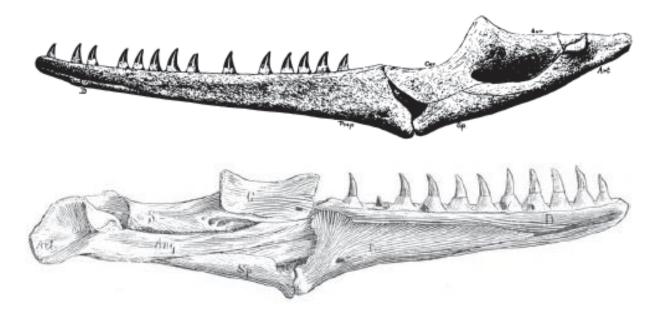
Skeletal reconstruction and inferred body outline based on the *Platecarpus* specimen LACM 128319. (Lindgren, J., Caldwell, M.W., Konishi, T., Chiappe, L.M. PLoS ONE)

While mosasaurs used an undulating motion to propel themselves through the ocean, this movement would have been mainly present in the tail. Anyone who has had a pet iguana (as I have) and has given it a bath or let it swim in a pool would have seen not only a similar movement but would be surprised at how well this tree living reptile can swim using this movement. In mosasaurs, this type of movement was due to the anatomy of the vertebrae (Everhart, 2005). If a person takes a close look at a mosasaur vertebra they'd notice that the cotyle is concave and the condyle is convex. This design would set each vertebra securely into the next and would not allow any cushioning to be present between vertebrae, allowing little flexibility in the vertebral column. This meant that while in motion, the animal's head and body would have been fairly stiff, with the tail undulating back and forth. The paddles were almost certainly not used so much for propelling the animal as in steering the animal (Russell, 1967). When not needed, the paddles would have stayed next to the animal's body.

Life in the water meant that the animal's weight could be supported by the surrounding water, and so the shoulder and hip girdle in mosasaurs shrunk and detached from the ribs and vertebral column. Mosasaurs never developed the extreme hyperphalangic paddles like plesiosaurs and ichthyosaurs. Rather, the proximal bones of the limbs shrunk and the feet evolved into wide paddles made of five digits loosely webbed together. This allowed their flippers to be much more flexible as compared to those of plesiosaurs and ichthyosaurs. While they were superb for life in a marine environment, it these adaptations also meant that the limbs could not be used in catching and subduing potential prey. In addition, due to the virtual weightlessness of the environment, prey could easily elude its captors, and after a kill was made the carcass could easily float away, allowing it to be stolen by a competitor. As with many other tetrapods whose limbs cannot be used in helping the animal feed, the head of the animal has to make up for the drawback. To solve these problems mosasaurs evolved unique ways of feeding, unlike those of either plesiosaurs or ichthyosaurs. Everhart, in his presentation on mosasaur evolution, gives an excellent description of this interesting feeding adaptation:

Mosasaurs...retained a relatively large skull that was 10-14% of their total body length. In addition, the skull in the earlier genera (Tylosaurus, Platecarpus and Clidastes) was highly kinetic, an adaptation seen in modern snakes that made the skull of these animals flexible enough to swallow much larger prey. Other feeding adaptations in mosasaurs included: a mobile quadrate that provided additional fore and aft movement to the lower jaw; an intermandibular hinge that allowed the lower jaws to bow outward as the prey was pulled into the mouth; pterygoid teeth that kept the prey from escaping as the lower jaw disengaged and moved forward; and a symphysial hinge between the tips of the lower jaws that allowed some degree of independent movement. Cope was one of the first to describe the feeding mechanism in mosasaurs: "They were furnished, like snakes, with four rows of formidable teeth on the roof of the mouth. Though these were not designed for mastication, and, without paws for grasping, could have been little used for cutting, as weapons for seizing their prey they were very formidable. And here we have to consider a peculiarity of these creatures, in which they are unique among animals. Swallowing their prey entire like snakes, they were without that wonderful expandability of throat due in the latter to an arrangement of levers supporting the lower jaw. Instead of this each half of that jaw was articulated or jointed at a point nearly midway between the ear and the chin. This was of the ball-and-socket type, and enabled the jaw to make an angle outward, and so widen by much the space enclosed between it and its fellow. The arrangement maybe easily imitated by directing the arms forward, with the elbows turned outward and the hands placed near together. The ends of these bones were in the Pythonomorpha as independent as in the serpents, being only bound by flexible ligaments. By turning the elbows outward and bending them, the space between the arms becomes diamond-shaped and represents exactly the expansion seen in these reptiles, to permit the passage of a large fish or other body." (Everhart, 2005b)

Teeth in mosasaurs tended to be slightly recurved and cone shaped, yet did not come to a sharp point or have serrations like dinosaur teeth, but rather were more like that of modern crocodiles. Like both crocodiles and dinosaurs, these teeth were regularly replaced over time (Caldwell, Bundy and Lamoureux, 2003). Later genera of mosasaurs, such as *Globidens* and *Lieodon* (which came on the scene long after the chalk was deposited) did have some specialization in their teeth, but this was not the norm.



Top: Left mandible, outer side of *Clidastes*. Bottom: Left mandible of *Platecarpus*, inner side. Williston. 1898.

For many years it was thought that mosasaurs would return to shore and lay eggs on a beach, not unlike that of present day sea turtles, and with no evidence to the contrary, the idea of sea turtle-like nesting remained a popular idea among scientists. Interestingly enough, rare fossils of ichthyosaurs (such as those found at Holzmaden, Germany) had long been known, and these fossils showed ichthyosaurs giving birth at the time they died, proving that at least these reptiles were viviparous. (It is also worth taking note that modern day members of the order Squamata are the only known living reptiles that give live birth. This same order includes mosasaurs.)

The idea of live birth in mosasaurs remained controversial for many years until, in 1996, a *Plioplatecarpus* was found in South Dakota that finally settled the controversy (Bell, Sheldon, Lamb and Martin, 1996). In the abdominal region, several fossilized fetuses were preserved, finally demonstrating that mosasaurs gave live birth. This evidence is further supported by the fact that mosasaurs were so well adapted to life in the ocean it would have been physically impossible for them to return to land to nest. Any that did would most likely be just as helpless as a beached whale of today.

Fossilized remains of young mosasaurs in the Chalk are not uncommon, which suggests that not

only did mosasaurs give birth to live young, but that they would have given birth in the open ocean. Everhart (2005a) points out that any remains found in the Chalk would have been deposited in the open ocean almost 200 miles from the nearest land. So while there is no evidence that mosasaurs cared for their young, it would seem odd if at least some parental care was not given due to the fact that so many predators, such as *Cretoxyrhina*, *Xiphactinus*, and even other mosasaurs, were around. Everhart, in support of parental care, states:

... While modern monitor lizards do not care for their young, the female American alligator is known to move newly hatched babies from their nest to the water, and to protect them to some extent from predators. Unlike alligators and monitor lizards, mosasaurs were not egg-layers, and they were well adapted in many other ways for their life in the ocean. Like most other animals in the wild, the mortality rate among young mosasaurs must have been high. However, from the number of adult specimens that have been found and their success in spreading around the world, it appears that many of them survived and successfully reproduced. While it is possible that the poorly circulated Western Interior Sea had masses of floating seaweed that young animals could hide in, there is no fossil evidence to support this idea. The presence of many fast-swimming predators, such as the ichthyodectid fish Xiphactinus audax and short-necked polycotylids like *Polycotylus* and Dolichorhynchops, seems to argue for large area of unobstructed, open water. One variety of primitive swordfish (Protosphyraena perniciosa) had long pectoral fins that extended two to three feet outward on either side of the body, hardly a good design for efficient hunting in a kelp forest. (Everhart, 2005a)

In 1967, Dale Russell published his study *Systematics and Morphology of American Mosasaurs*, which is considered by many to be the finest work ever done on this group of reptiles. In it he states, "The Niobrara Formation of western Kansas has yielded more mosasaurs of more different kinds and generally in a better state of preservation than any other formation in the world." (Russell, 1967). Since collecting in the chalk began roughly 140 years ago, many fantastic specimens have been found, collected and preserved. Except for a few notations, there has been little reference on the stratigraphic occurrence of these animals in the formation. However, little blame can be put on the collectors themselves since there has only been a detailed stratigraphic column of the Chalk for the past 28 years.

The first real attempt at mosasaur biostratigraphy was made by Samuel W. Williston in 1897. Originally known as only the Niobrara beds, W.N. Logan noticed that the formation consisted of a lower limestone member and an upper chalk member (Williston, 1897). Based on the fossil remains found in the chalk member, Logan referred to this section as the "Pteranodon beds". Williston took Logan's division a step further by dividing the "Pteranodon beds" into the upper *Hesperornis* beds and lower *Rudistes* beds on the basis of differences in color (Hattin, 1982).

A year later, Williston went on to do the first serious study of mosasaurs in the Chalk and made some interesting observations on mosasaur biostratigraphy. *Clidastes*, he reported, did not occur in the *Rudistes* beds (Williston, 1897), and *Platecarpus*, he felt, was "Known nowhere outside of Kansas and Colorado, and [was] here restricted exclusively to the Niobrara." He also noted that *Tylosaurus* "… so far as was known, beg[an] near the lower part of the Niobrara and terminate[d] at its close or in the beginning of the fort Pierre." (Williston, 1898b).

Further progress on the chalk stratigraphy was made by Moore and Hays (1917) who made the Niobrara a formation, and designated the lower limestone member that Logan noted into the Fort Hays Limestone member and the upper Niobrara Chalk into the Smokey Hill Chalk member. But detailed boundary markers in the Chalk itself were still lacking, making any work on precise placement of specimens in the Chalk difficult. Finally, in 1982, a huge breakthrough was made when Donald E. Hattin noticed bentonite layers that could be traced throughout the Chalk member, along with other geological features. Using these, he made a comprehensive stratigraphic column which he divided with twenty three lithologic marker units (Hattin, 1982). Having a column available, detailed placement of mosasaur specimens and other fossil species in the Chalk was now possible.

Dale Russell tried to make further progress in terms of mosasaur biostratigraphy in his afore mentioned publication. In it he proposed that *Clidastes liodontus*, *Platecarpus coryphaeus* and *Tylosaurus nepaeolicus* were found in the lower half of the Chalk, and *Tylosaurus proriger*, *Platecarpus ictericus* and *Clidastes propython* in the upper half. Stewart, in his work from 1988, was skeptical of Russell's biostratigraphic conclusions based on several exceptions of which he was aware. In a 1970 publication focusing on the Selma Chalk of Alabama, Russell made note that *Clidastes* was far more abundant here as compared to the Smokey Hill Chalk. Noting that *Clidastes* becomes far more abundant in the upper Chalk of Kansas, Russell proposed that the upper Chalk was deposited in a more near shore environment and that the sea's shoreline came closer to western Kansas (Everhart, 2005a, Russell, 1967).

Schumacher, in 1993, and Sheldon, in 1996, made further studies using material from the Yale Peabody Museum and the Sternburg Museum collections. These studies, along with new fossil discoveries since their publications, have greatly enhanced mosasaur biostratigraphy. In 2001, Michael Everhart released the latest proposed mosasaur biostratigraphy of the Niobrara Chalk. Since then, there have been several changes in mosasaur taxonomy, so while his publication retains the old names, I will use the current names in this description (see Table 1).

The oldest remains of *Clidastes liodontus* come from the late Coniacian of the lower Chalk, just below marker unit four. This species seems to continue in the Chalk to the top of the formation. *C. propython* appears in the middle of the Chalk, which is mid-Santonian in age, and, as with *C. liodontus*, continues through to the top of the formation. (There are possible remains of this genus in the Fairport Chalk, which is Turonian in age, but the assignment of this genus is still uncertain.) This genus disappears sometime early in the Campanian.

Tylosaurus nepaeolicus and *T. kansasensis* are both found in the lower Chalk of the late Coniacian, and die out before marker unit 6 of the early Santonian. *T. proriger* appears in the early Santonian and continues through the top of the formation. Remains are also known from the later Pierre shale and other Campanian age formations, and even possibly from the Maastrichtian age. Whether *T. Proriger* evolved from or replaced the two earlier Tylosaur species is not known, but it is the only species present after its earliest appearance in the geologic record.

Platecarpus planifrons seems to be the most common species of *Platecarpus* in the lower Chalk, disappearing in the upper part of the Chalk. *P. tympaniticus* first appears at the bottom of the Smokey Hill Chalk, and after the mid-Santonian, becomes the most common species in the Smokey Hill through the top of the formation, after which it is replaced by *Plioplatecarpus* in the Pierre shale.

Mosasaurs as a whole appeared rather suddenly in the geologic record and go on, in a relatively short period of time (geologically speaking), to become the dominant predators of the world's oceans. Mosasaurs themselves probably evolved from aigialosaurs, small land dwelling lizards that lived near the shoreline during the late Jurassic and early Cretaceous. It is very possible that the early mosasaur ancestors lived in a way very similar to that of marine iguanas of the Galapagos, living near the shoreline and venturing into the oceans only to acquire food. In recent years, the discoveries of *Dallasaurus* and *Russellosaurus* in Texas by amateurs have, both, greatly helped in our understanding of the origins of the mosasaurs. *Dallasaurus*, for example, still retains plesiopedal features (terrestrial limbs), but it also has many features found in later mosasaurs.

We start seeing the first evidence of fully aquatic mosasaurs as early as the Turonian age. As to why these reptiles took to the sea is still up for debate, however, as mentioned earlier, the recent extinction of the ichthyosaurs by the start of the Turonian and the disappearance of pliosaurs by the mid-Turonian opened the way for the emergence of a new kind of aquatic reptile. Bakker suggests plesiosaurs replaced the niche left by the ichthyosaurs, while mosasaurs filled the gap left by the marine crocodilians which became extinct during the Coniacian (Bakker, 1993). Russell, on the other hand, believes that it was the mosasaurs that filled many of the niches left by ichthyosaurs (Russell, 1993). Regardless, in a very short period of time, mosasaurs were already well on their way to adapting to life in the sea. In fact, two sets of vertebrae and a jaw element which have much in common with *Clidastes*, and another skull element that came from a *Platecarpus*-like mosasaur, were described by Martin and Stewart (1977). These fossils, which come from the middle Fairport Chalk of Kansas, are mid-Turonian in age, just slightly younger than the *Dallasaurus* specimens, which are early mid-Turonian. These fossils from the Fairport Chalk seem to indicate that by this time the two main monophyletic groups had split from one another. One group would lead to the subfamilies Russellosaurina and Halisauromorpha, and the other, Mosasaurinae (see Table 2).

Everhart describes mosasaur evolutionary history "... as occurring in three distinct waves, each of which radiate[s] outward from their point of origin." (Everhart, 2005b). By the time of the mid-Coniacian, we see this first "wave" of mosasaur diversification. The most primitive and smallest of this first wave is *Clidastes* (Mosasaurinae), reaching lengths of only 3-4 meters. The larger *Platecarpus* (Russellosaurina) reaches lengths of about 4-6 meters, and *Tylosaurus* (also a Russelosaurine) is 7-8 meters in length and by far the largest mosasaur of this period. By this time mosasaurs are fully aquatic and top predators in the food chain. It is about this time that the Chalk's deposition begins and continues throughout the rest of the Coniacian, Santonian, and early Campanian. We already see in these genera a trend for becoming larger, which will continue to the end of the Cretaceous.

By the early Campanian, the Chalk's deposition comes to an end and gives way to the formation of the Pierre shale. By this time *Tylosaurus* reaches 9-10 meters, *Platecarpus* is 7-8 meters and *Clidastes*, 4-5 meters in length. It is also around this time that a new, second "wave" of mosasaurs emerges. *Platecarpus* disappears and is either replaced by or evolves into *Plioplatecarpus*. *Clidastes* becomes extinct, but new and diverse genera of the subfamily Mosasaurinae, which includes *Mosasaurus*, *Prognathodon*, and *Globidens*, takes its place. Some Mosasaurinae, like *Prognathodon* and *Globidens*, evolve heavy, robust skulls and teeth able to tackle hard shelled prey. *Tylosaurus* continues through at least part of the Campanian, and possibly into the Maastrichtian, and its huge close cousin, *Hainosaurus*, makes its premier.

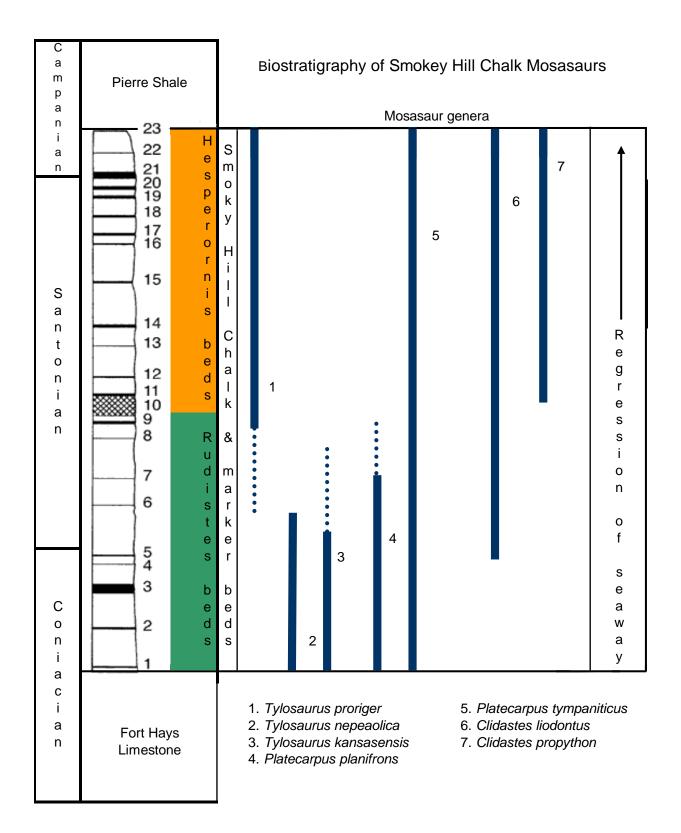


Table 1. By Michael T. Payne, (Everhart, 2001. Russell, 1967. Schumacher,1993 and Sheldon, 1996.)

			Time of Chalks deposition	deposition		
99.6 mya 93.5	89.3		Upper Cretaceous 85.8 83.5	ceous	70.6	K-Pg boundary
Cenomanian	Turonian	Coniacian	Santonian		Campanian	Maastrichtian
	Dallasaurus	sp.		Clidastes spp.	9	
Mosasaurinae			_		Globidens spp.	
				_	Prognathodon spp.	
						Mosasaurus sdd.
Mosasaliridae						Plotosaurus spo.
	Halisauromorpha	morpha	_		Halisaurus spo.	
				Ectenosaurus spp.		
		Platecarpus spp				
					Plioplatecarpus spp.	
	Russellosaurina	saurina		H		c
			ŀ		L	,
Haasiasaurus so.	Russellosaun	s sp.		J	Hainosaurus soo.	



By the Maastrichtian, a third and final "wave" of mosasaurs make its way around the world. Specialized mosasaurs like *Plotosaurus* evolve an ichthyosaurian appearance, while *Goronyosaurus* develops an almost crocodile-like form (Lingham-Soliar, 1999). Genera such as *Globidens* and *Prognathodon* still abound, as do older forms like *Mosasaurus* and *Hainosaurus*. There is even evidence that mosasaurs begin to invade fresh water habitats by the time the Cretaceous comes to a close (Holmes, Caldwell & Cumba, 1999). Many mosasaurs reach giant proportions. *Mosasaurs hoffmanni* reaches lengths of up to 16 meters. *Hainosaurus* grows to 17 meters, while *Prognathodon* approaches 12 meters and *Plioplatecarpus*, only 7. By the close of the Cretaceous, mosasaurs reach their peak of diversity and size, yet despite this evolutionary success, they disappear at the K-Pg boundary along with the dinosaurs and many other organisms.

Why they died out along with so many other organisms is up for debate. Ironically, around the same time that the mosasaurs died out, the western interior sea finally disappeared. Since the end of the Chalk's deposition, the slow but steady uplift of the Rocky Mountains that helped form the seaway also had abetted its destruction. Along with the lowering of eustatic sea levels, this uplift caused the central part of the continent to rise far above the sea level, precipitating the sea's retreat to the southeast and securing its fate. In its wake, the receding sea left behind spectacular fossils of its animal residents, none more so than the mosasaurs. I'm sure that in the future many more spectacular finds will help us to understand them and other secrets still contained in the Chalk. Without a doubt, they'll continue to cause awe and enhance the imagination of many generations to come, and perhaps, for the local residents of Kansas, remind them that there is no place like home.

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Giant Cretaceous Pterosaurs in the Air and on the Ground John A. Catalani

Introduction to Pterosaurs

For me, the evolution of flight has always been one of the most interesting and contradictory events in the evolution of life on Earth. Granted that flight is an excellent way to avoid predators, unless they also have the ability to fly, but the process of flight is very energy costly. Flight has been invented four times (five if you consider the Wright Brothers) in Earth's history and all but one, insects, have involved vertebrates--pterosaurs, birds (or avian dinosaurs), and bats. Although I had read several books on pterosaurs, it was two articles and an intriguing life restoration that appeared in the on-line journal *PLoS ONE* that inspired me to delve into the world of the super-giant pterosaurs.

Pterosaurs were the first vertebrate to achieve powered flight. They arose in the Triassic and survived until the Cretaceous-Paleogene (K-Pg) boundary extinction event. The wings of pterosaurs were somewhat similar to those of modern bats in that they were made of membranes of skin, albeit supported differently--bats support the membrane with elongated second through fifth digits whereas pterosaurs used an extremely elongated fourth digit.

The two suborders of pterosaurs are the Rhamphorhynchoidea and the Pterodactyloidea. Rhamphorhynchoids were the first to evolve sometime in the Late Triassic Period with the pterodactyloids appearing in the Middle Jurassic, the two lineages overlapped during the Late Jurassic and Early Cretaceous. Exact ancestry is unknown but pterosaurs probably evolved from a Middle Triassic thecodont such as *Scleromochlus* or *Marasuchus* (=*Lagosuchus*) both possibly bipedal and arboreal. Although pterosaurs are not generally thought of when talking about arboreal habitats, a small pterosaur was recently discovered possessing curved phalanges strongly suggestive of an arboreal lifestyle. Certainly there could have been other arboreal pterosaurs but their fossil record is biased toward lakeshore and marine coastal environments.

The two suborders can be compared by way of general morphologic features. The rhamphorhynchoids were generally small in size but with long tails some with rudder-like membranes at the distal end and were equipped with large numbers of teeth. Pterodactyloids, on the other hand, were larger with small tails and fewer teeth trending toward toothlessness through time (although some species were equipped with large numbers of long, thin teeth that were used to strain organisms from the water).

The real fascination with pterosaurs is their performance both in the air and on the ground. For the smaller pterosaurs with short and broad wings, powered flight (active flapping) was similar to birds since both have a coracoid bone that connects the shoulder girdle to the sternum. The sternum of pterosaurs had a keel for the attachment of flight muscles. Larger pterosaurs with long, narrow wings were better adapted for soaring and gliding with limited flapping flight. Pterosaurs were equipped with three types of flight membranes: the main wings that were attached to the lower leg bones, membranes that were located along the front of both arms, and a membrane that was positioned between the legs. For rhamphorhynchoids, this last type of membrane consisted of one relatively large flap of skin that connected both hindlimbs down to the toes. Pterodactyloids, on the other hand, were equipped with two smaller membranes positioned on the inside of each hindlimb freeing up each side to move independently making them much more maneuverable on the ground than rhamphorhynchoids. The wing membranes themselves were reinforced with fibrous rods probably made of collagen, referred to as aktinofibrils, that were closely spaced and rigid in the outer part but more widely spaced and flexible on inner part. Superbly preserved pterosaur fossils from the Solnhofen limestones (Upper Jurassic rocks in which Archaeopteryx is found) of Germany clearly show these fibrous rods in the wing impressions. The presence of these rods makes sense since there is no other internal support for the wing, such as the additional digits of bats, to localize and minimize tearing of the wing membrane associated with an injury and to maintain the tension of the wing membrane itself during flight. These fibers were more flexible nearer the body so that the wings could fold easier when the animal was on the ground. Additionally, muscles in the wings helped in maintaining membrane tension and allowed the animal to adjust the wing shape for better pitch, roll, and vaw control in the air. Pterosaurs were also equipped with weight-saving hollow bones that were often filled with air as part of a pneumatic system that was part of the animal's respiration system as in modern-day birds. In some pterosaurs this pneumatization affected only the vertebrae whereas in others it involved virtually the entire skeleton. Studies have shown that, based on the amount of body weight placed on the wings, the ability to glide during flight and landings, and the low stall speed, pterosaurs were very skillful fliers with some probably able to perform in the air more proficiently than modern bats or birds. It has even been suggested that small pterosaurs may have been able to hover in the air like present-day kestrels.

The skin of pterosaurs has provided researchers with some surprises. For the most part, the skin is fairly smooth with some fine texturing consisting of lines and grooves. Scales are absent on the skin except for the soles of the feet and probably the "palms" of the hands, which makes sense since this is obviously where pterosaurs contacted the ground when walking. But the most interesting and amazing structure discovered when investigating the skin is the presence of hair-like fibers made of keratin that covers the skin, except for the wings and jaws, to varying degrees of thickness. Unlike mammal hair, pterosaur hair was hollow, not solid, and grew from the outer skin, not from follicles. The question of pterosaur hair was rendered moot by the discovery of specimens of the rhamphorhynchoid *Sordes pilosus* ("hairy devil") from Upper Jurassic rocks of Kazakhstan that displayed large amounts of dense hair. Interestingly, pterosaur hair has been recognized for over 100 years and has been found on numerous specimens found world-wide. The purpose of hair on pterosaurs include display during mating, camouflage, insulation either by the density of the hair or by trapping air, or a combination. It is interesting to speculate that, if one purpose of the hair was insulation and given the active and energy-demanding life-style of any flying vertebrate, pterosaurs were probably endothermic or at the very least homeothermic.

Another interesting feature of pterosaurs was the amazing diversity of bony nasal and cranial crests. These crests were present on both subgroups of pterosaurs but attained their maximum diversity and size with the Cretaceous pterodactyloids. The crests were various shapes that were either simply covered by a membrane of skin or were actually extended and made even larger by rod-reinforced flaps of skin. Speculations on the functions of these crests have run the gamut from rudders to sails to jaw counter-balancing structures to water guides employed during fishing. There are several problems with each of these speculations but the major problem is that there appears to be as many functions as there are differently shaped crests. However, with further study, it was found that these large crests are not present on all members of a particular species or genera; some have

much smaller crests. Therefore, the most parsimonious answer is that these large crests were analogues of horn and frill arrangements of ceratopsians and tail feathers of today's peacocks--male features used for sexual display and species recognition, both important during mating season. The jaws and teeth also displayed a remarkable diversity indicating that pterosaurs employed a variety of feeding strategies. Speculated feeding techniques include catching insects on the fly (short, peg-like teeth), skimming surface waters for fish (long teeth that meshed, or teeth restricted to the front of the jaws), filter feeding either from the shore or by wading (long, bristle-like feeding apparatus), and crushing crabs and molluscs (jaws equipped with bony knobs).

Interestingly, it has been posited that at least small pterosaurs were able to swim. Now before you chuckle at the thought of an animal with a membranous wing swimming, let me relate a story about my early (1970s) days at the high school. I once had a student, both in class and in my Science Club, that studied bats. He was, at his young age, considered something of a wunderkind when it came to bats. During one Christmas, sorry, Holiday break, some members of the Science Club joined us in data gathering at a central Illinois abandoned mine that bats used for hibernation. In gathering data, one of the students and I would take the bats gently off the wall (using gloves so we would not get our skin oils on the bats' fur), determine the species, sex them, and, after placing them in paper bags, determine their mass using a very sensitive scale. Normally we could complete the procedure and return the bat to the same spot on the wall with minimal disturbance. However, we must have taken too much time with one bat because he was fully awake when I attempted to take him out of the bag and he jumped onto the ground and then further jumped into one of the numerous pools of water that dotted the floor of the mine. We were frantic that the bat would drown but, much to our amazement, the little guy just swam toward the other side of the pool (sounded a bit like a motorboat), climbed out, and flew away. Needless to say, I learned something that day about the tenaciousness of animals. As evidence for this proposed swimming ability, pterosaur tracks have been found with impressions of webbing between the large toes.

The real keys to successful flight are, as with airplanes, the takeoffs and landings. Given their slow stall speeds and ability to alter their wing configuration, pterosaurs, particularly pterodactyloids, must have been able to land gently by touching the ground with their hind feet and simultaneously folding their wings and falling forward on their front "hands" or digits to assume a quadrupedal stance with their bodies supported by well-muscled arms. Except for the giants, most pterosaurs, especially rhamphorhynchoids, were also able to land on vertical cliffs or in trees. The ability and methods used by pterosaurs to launch into flight has been argued since they were first discovered. It has been speculated that many pterosaurs simply dropped from cliffs or trees allowing gravity to provide the initial acceleration needed to begin powered flight. Others have proposed that small pterosaurs were able to run like birds to gain lift speed or simply jump into the air and began flapping as bats do today.

When it came to walking on level ground, it appears that most, if not all, pterosaurs employed quadrupedal (four-footed) locomotion, although rhamphorhynchoids appear to have preferred high perches. Pterodactyloids were much more adept at ground walking because, as mentioned above, the lack of a rhamphorhynchoid-like membrane connecting both legs permitted their legs a greater range of motion. Fossil trackways assumed to have been made by pterosaurs confirm this conclusion. Bird-like, bipedal walking has also been suggested but differences in the structure of the pelvis, leg, and foot between birds and pterosaurs, as well as the problem of wing positioning and centers of gravity, cast doubts on this hypothesis, except possibly during running takeoffs.



Fig. 1. Size comparisons of a giant azhdarchid pterosaur, a giraffe, and a not-quite six-foot paleontologist. (Drawn by Mark Witton.)

The Giant Pterosaurs

In the Late Cretaceous, only three pterosaur families persisted: the Nyctosauridae, typified by *Nyctosaurus* with a 2-3 meter wingspan; the Pteranodontidae, represented by *Pteranodon*, the most well-known pterosaur, with a 6-7 meter wingspan; and the Azhdarchidae, exemplified by the supergiant *Quetzalcoatlus*, its most famous member, with an incredible 10-12 meter wingspan and nearly as tall as a giraffe when walking on the ground (see Fig. 1). A comparison of the morphology of the two most well-known giants points to differences in lifestyles. *Pteranodon* was equipped with relatively long, narrow wings and a small body as well as a shorter neck. These features, as well as fossils that have been found in marine sediments deposited hundreds of miles from land, indicate that *Pteranodon* was a skilled flier able to dynamically soar for extended periods of time traveling long distances and covering large amounts of area in search of food. (Although not as well known, the same can probably be said for the smaller *Nyctosaurus.) Quetzalcoatlus*, on the other hand, had relatively shorter and broader wings due to a proportionally shorter wing finger, a larger body, and elongate cervical vertebrae resulting in a long, inflexible neck. Azhdarchid remains are mostly found in continental and lucustrine sediments and this, along with their immense size, has sparked debate over both their flight characteristics (takeoff and method of flight) and their feeding strategies.

Azhdarchids were the last and most derived pterosaurs to evolve and attained virtually worldwide distribution. The oldest specimens have been found in Lower Cretaceous rocks of Brazil and China--widely separated enough to cloud their origins. Since their hindlimbs and forelimbs were of about equal length and were positioned under the body, it appears that azhdarchids were accomplished quadrupedal walkers. They walked on the padded soles of their feet and the ends of their arms balanced by the three small "fingers" located where the fourth digit diverges and becomes elongated to support the main wing membrane. As typically found with pterosaurs, their bones were hollow, yet very strong, some of which were penetrated by pneumatic foramina acting as openings for air sacs. As described above, this pneumatic system not only provided the animal with flowthrough ventilation to aid in respiration but also lightened the skeleton such that even the largest azhdarchids probably weighed only around 200 kg, although, as one might imagine, mass estimates are tentative at best. It has been suggested that such large animals had limited ability when it came to flapping flight and that the placement of the center of gravity level with the wings is indicative of a dominant soaring and gliding lifestyle. However, evidence of strong bones and massive flight muscles suggests that they may have been a bit more proficient at flapping flight than previously assumed.

When *Quetzalcoatlus* fossils were first discovered in 1975 and its immense size was recognized, researchers were hard-pressed to come up with possible feeding strategies for these animals. In the first *PLoS ONE* article, Mark Witton and Darren Naish (2008) evaluated food gathering methods that had been proposed for azhdarchids. These methods included vulture-like carrion feeding (the original suggestion), probing soft sediment for invertebrates, high-speed aerial predation, and various fishing methods including skimming, snatching, and wading. The authors rejected these strategies as primary feeding techniques for various reasons that included lack of adaptations for a specific method, lack of neck flexibility, shape of the jaws, immense size, and relatively small feet. They do, however list several of these methods as possible supplementary feeding strategies including carrion feeding and wading. The authors suggested that, since azhdarchids were adept at quadrupedal walking, their preferred feeding strategy was as "terrestrial

opportunists, finding much of their food via terrestrial, ground-level foraging" (p. 12). Azhdarchid adaptations for this lifestyle included unusually long hind legs (for pterosaurs) that positioned the body nearly horizontally, small feet with padded soles, long necks that increased feeding range, stiff necks that supported the skull comfortably, and skulls attached perpendicularly to the neck that placed the jaws near ground level. It would have required very little movement of the forelimbs and/or the neck to place the beak at ground/feeding level. Habitats in which food could have been acquired ranged from dry lands to plains to woodlands to lake shores and stream banks. Food items would have included invertebrates, fish, and small terrestrial vertebrates including juvenile dinosaurs (see Fig. 2).

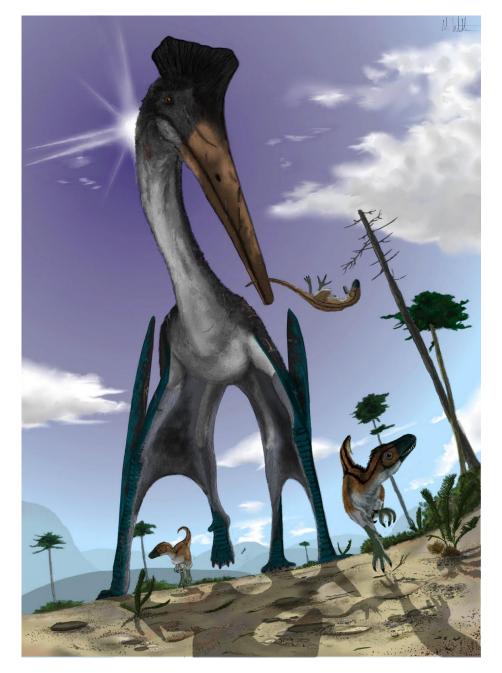


Fig. 2. Terrestrial feeding strategy of a quadrupedal azhdarchid. (Drawn by Mark Witton.)

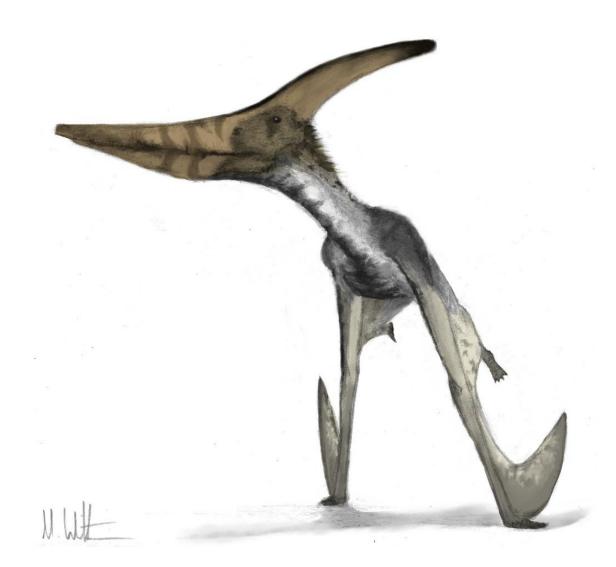


Fig. 3. *Pteranodon* in the process of launching into the air from a stationary, quadrupedal stance similar to the takeoff strategy employed by azhdarchids. (Drawn by Mark Witton.)

The other difficulty pertaining to azhdarchids was attempting to determine how, assuming they could actually fly, such large animals would have launched themselves off the ground and into the air with enough velocity to begin powered flight. In the second article, Mark Witton and Michael Habib (2010) evaluated speculations that the giant azhdarchids were flightless. Based on comparisons to modern-day birds, it had been suggested that, since a bird of similar weight would have to be flightless, these giants would have also been flightless. Some researchers further suggested that if an individual azhdarchid weighed over 70 kilograms takeoff would have been mechanically impossible. The authors concluded, however, that azhdarchids possessed strong enough bones, even though they were hollow, and sufficient muscle mass to easily takeoff and maintain flight, albeit not necessarily as adept at sustained flight as *Pteranodon*. In attempting to establish a possible means of takeoff, it had been assumed that such a large animal would have had to face into a headwind with wings extended, possibly while also running downhill, in order to achieve liftoff. However, azhdarchid skeletal morphology and center of gravity would have made any

such bipedal movement difficult at best. Also, restricting an animal to such a set of requirements for takeoff certainly limits its options when, say, predators are in full attack mode--a bit unrealistic in my opinion. The authors indicated, as did Habib in a previous paper (2008), that "there is good evidence that pterosaurs launched from a standing, quadrupedal start" (p. 12). The sequence of events employed by the animal to carry out such a takeoff (and I would have paid to see this) would have been to initially push off with its hindlimbs, "leap-frog" over the forelimbs, and at the same time thrust upwards using the powerful forelimbs while extending the wings to begin powered flight, an amazingly quick process not dependant on external conditions (see Fig. 3). In fact, the authors speculated that it was the development of the quadrapedal launch that "may have facilitated pterosaurs to become much larger than any avian fliers" (p. 12).

Witton and Habib evaluated published comparisons between pterosaurs and birds and concluded, as many of us have when *Nautilus* is used exclusively as an analogue for ammonoids, that many of the authors of these previous studies "have relied too heavily on this analogy" (p. 2) and that "pterosaur anatomy is completely unique, and any study of its function that ignores this individuality is likely to be flawed" (p. 15). This reinforces the need for discretion and restraint when using present-day animals as analogues to guide speculations on the physiology and lifestyles of extinct animals.

Acknowledgements

I would like to thank Paula Mikkelsen and PRI for permission to include this paper, a modified version of which appears in the Spring 2011 issue of *American Paleontologist* magazine, in this year's EXPO Edition. I would also like to thank Mark Witton for permission to include his wonderful paleo-art of these fantastic animals in this paper.

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Fifteen Years of Observations of an Archaeologist in the Hell Creek

Steven Nicklas

My Ph.D. (1988) is from the Institute of Archaeology, University of London and is in Old World Archaeology. From 1974 to 1995 I was involved in academic archaeological projects in the Middle East, Europe and in North America; in all, over 80 field projects, both surveys and excavations. I am currently an Assistant Professor of Anthropology and Archaeology at Gainesville State College in Oakwood, Georgia.

As a result of a lifelong interest in vertebrate paleontology I started Paleo Prospectors in 1995. Since then I have spent over 30 months in the field and have been involved in supervising fossil collecting trips on private land in the Hell Creek in which over 1,000 individual collectors have participated. All scientifically important specimens have been donated to academic institutions, or sold at cost to those institutions, while all other specimens have been retained by the participants. To date we have donated over 40 major fossil specimens to museums and other institutions.

At first glance the fields of archaeology and vertebrate paleontology seem to be almost identical. This perception is reflected in the general public's continuing confusion about the two disciplines. Thanks to Hollywood, their viewpoint seems to be: if you're "a bone digger" you're an archaeologist. It doesn't matter if it's a dinosaur bone, a Neanderthal bone or a bone from a medieval European burial. A surprising number of academicians and government bureaucrats are also confused. The 1906 Antiquities Act, which was written to protect archaeological sites and artifacts, is the primary law used today by the government to "protect" fossil resources on public land. Although the law, as written, deals with cultural material (artifacts and archaeological sites only), it is used by the federal government to control access to fossils on federal lands. Adding to the confusion is the fact that in some cases both archaeologists and paleontologists do work on the same site. This is especially true on early man sites in the Old World and Paleo Indian sites in the New. In the final analysis it's not about how you dig but what you dig that defines the discipline.

In this presentation, I will compare and contrast methodology in the fields of archaeology and vertebrate paleontology; I will focus on the following areas of comparison: survey work (prospecting in paleontology), subsurface testing, excavation, specimen stabilization, preparation and analysis.

Survey

The field survey is the primary form of site identification in both archaeology and paleontology. In almost all cases the survey involves the visual inspection of the surface of the ground, where visibility allows. Typically in archaeology, surface artifacts are used to define the surface extent of the site, they are individually mapped only if the spatial relationship of the artifacts has not been substantially disturbed over time. An example of a surface scatter that would not be mapped would be artifacts in a plowed field. This is the case because the most important information recovered in

the field is the spatial relationship between artifacts in the ground. It is from this data that most of the conclusions about the site and the artifacts are made. When the archaeologist is faced with limited visibility, shovel cuts are utilized at regular intervals across the study area. Soil recovered from this process is then screened through ¹/₄ inch mesh to determine if artifacts are present in the immediate area of the test.

Generally speaking, areas of human habitation in the past are relatively flat and easy to traverse and surveys are easy to carry out. This is not the case in paleontology – especially in the Hell Creek. Prospecting (the paleontological equivalent of survey) in the Hell Creek Formation involves the pedestrian inspection of visible exposure. Fortunately, surface visibility in the Hell Creek is seldom a problem; unfortunately a lot of it is vertical. Subsurface testing is highly impractical due to the hardness of the matrix and seldom necessary due to the abundance of good exposure.

The spatial relationship of fossils in paleontology comes into play when the specimen is semi or fully articulated or associated with other fossils that are. This type of situation is rare in the Hell Creek, and rarer still on the surface, but when it happens all individual bones are mapped. Articulation is rare because of the depositional history of the formation and the heavy erosion that occurs in the region today.

One type of controlled surface collection that is unique to paleontology and paleo anthropology is the 100% surface survey. This involves a number of crew members getting on their hands and knees, side by side, and the collection of all fossils in the target area. This operation usually occurs when an important fossil is discovered on the surface in an area of high erosion.

The goal of the survey in both archaeology and paleontology is to locate and define the site (in archaeology) or the fossil locality (in paleontology). Once located and defined it's time for phase two: subsurface test.

Subsurface Testing

In general, the extensive use of subsurface testing is far more common and necessary in archaeology than in paleontology. In the Hell Creek, excavation usually occurs only during the removal of a specific specimen or bone and so the area of excavation is relatively small, and as a result the need for subsurface testing is greatly reduced. When subsurface testing is utilized in vertebrate paleontology it is usually in the form of a small test unit and almost always is done in conjunction with the actual excavation.

Subsurface testing in archaeology is far more important, and this is especially the case in prehistoric archaeology. The goal of the testing is to establish the depth of the cultural material and the overall extent of the site. This is usually accomplished by randomly establishing a number of test excavation units across the surface area of the site and excavating down to sterile subsoil. If archaeological features are encountered, the area of the test unit is typically increased to expose the entire feature.

Excavation

Excavation in archaeology is only undertaken if a site is in danger of being destroyed or damaged or to answer specific research questions. This is the case because archaeological sites are usually located in areas of high deposition, mostly in flood plains, and the longer they are left alone the deeper buried they become and the safer they are. In paleontology, because fossils are almost always found in areas of high erosion, the opposite is the case. If a fossil is visible and not collected it erodes to nothing within a year or two. So in this sense every paleontological excavation is a salvage excavation saving the specimen from certain destruction.

In archaeology excavation methods can vary from site to site, especially from prehistoric to historic sites. The primary difference is the presence or absence of permanent architectural elements at the site in question. In every case, however, recording the site's stratigraphy and the spatial relationship of artifacts and features in the ground is of the upmost importance. Here is the primary difference between excavation in vertebrate paleontology and archaeology. In most cases paleontological digs are exercises in extraction not recording. Only with articulated or semi articulated specimens is mapping utilized, and section drawings (the visual recording of the site's stratigraphy) is almost never done. One important element of archaeological field recording that should be more frequently utilized in paleontological work is the frequent recording of elevations. In archaeology this is done on daily diagrams of the excavation area called top plans.

In the field it's the archaeologist who excels at recording data, while it's the paleontologist who excels at specimen extraction. The concept of the field jacket, as simple as it is, is not utilized on archaeological sites and many features such as burials and storage pits are destroyed during the course of excavation after of course all elevations are recorded and the mapping finished. Plaster jackets utilized for the protection and extraction of archaeological features is extremely rare; I've seen it done a few times in the United Kingdom and in the former Soviet Union.

Specimen stabilization, preparation and analysis

Out of necessity paleontological techniques of specimen stabilization are rather sophisticated. The extremely delicate nature of most vertebrate fossils has resulted in the almost universal use of reversible chemical stabilizers. This is a reflection of the fact that for the paleontologist the important work starts after the fossil is out of the ground. It is therefore necessary to ensure the stability of the specimen from the field to the lab and beyond. For the paleontologist the main focus of his or her research is the analysis of the fossils and the inherent information within them.

In many cases in archaeology, more emphasis is placed on recording the excavation process than on the artifacts recovered. This all goes back the importance of recording the spatial relationship of artifacts in the ground. Unfortunately, this sometimes results in artifacts being inadvertently damaged after excavation, or worse being consigned to a paper bag and then being lost forever in a university basement. This is not to say that artifact analysis is not an important part of archaeological research because it is; but lab work in archaeology is almost .always secondary to the excavation process. On occasion artifacts require stabilization and restoration; typically these steps occur after the artifacts have been cleaned but before they are analyzed. Generally speaking, artifact analysis is done to support or supplement the field report. Some artifacts have intrinsically more information than others, coins, colonial pipe stems, and some types of lithics and pottery for example. These artifacts are frequently the subject of research, not because of their archaeological context but because of the intrinsic information they hold.

In the US all academically excavated archaeological artifacts are labeled with a unique number which identifies the state, county and site at which artifact was recovered. The number will sometimes list the excavation unit and level as well. This is so that in theory, the artifact could be replaced exactly where it had been found. The site numbering system is maintained by the State Archaeologist in every state. Unfortunately, there is no similar system in place in the US for paleontological localities. I discovered recently that the South Dakota Archaeological Resource Center in Rapid City, SD maintains a numbered list of paleontological sites in South Dakota that have been located during cultural resource surveys for the county, state and federal governments in the state of South Dakota. The amazing thing was that no one at the Geological Museum at the School of Mines, which monitor paleontological research in the state, who knew anything about the existence of the listing or the numbering system.

Conclusions

In summary, both disciplines of archaeology and paleontology are very similar in many respects. They are separated by degrees of emphasis, with archaeology more concerned with accurate record keeping and paleontology more concerned with fossil extraction. Both have areas of technical expertise that could greatly benefit the other. The lucky ones are those who work on the Early Man sites In Europe, with both archaeologists and paleontologists; they have the best of both worlds.

A Dinosaur Tail Rob Sula

When people ask me what I did over the summer, my answer for well over a decade has been the same: "I was digging dinosaurs!" I am the Senior Field Supervisor for Paleo Prospectors, a company that takes paleontology enthusiasts on tour of late Cretaceous fossil sites in Montana, Wyoming, Nebraska and North and South Dakota. I then incorporate what I've learned in the field into the paleontology classes that I teach at the College of DuPage in Glen Ellyn, Illinois.

As amazing and relatively rare as dinosaur bones are, if you go to the right places and know how to look for them, the fossils are abundant. Our team focuses primarily on the Hell Creek formation, which ranges from 65.5 to 67.2 million years from top to bottom. The Hell Creek formation is significant because it is one of the best geologic representations of the Cretaceous-Tertiary (K-T) boundary. In other words, it's perhaps the best place in the world to see the final days of that remarkable group of animals known as dinosaurs.

Dinosaurs are by no means the only group of animals found in the Hell Creek. A diverse fauna of at least 61 taxa of vertebrates that include fish, turtles, crocodilians, lizards, amphibians, pterosaurs, birds and mammals represent the formation. That being said, the headliners of this act are, of course, the dinosaurs. And not just any dinosaurs mind you—the Hell Creek hosts some of the world's most well-known dinosaurs including Triceratops, Edmontosaurus, Ankylosaurus, Pachycephalosaurus, and perhaps the most famous of all the dinosaurs, Tyrannosaurus rex.

Triceratops and Edmontosaurus are by far the most common dinosaur remains found in the Hell Creek. This makes sense as 66 million years ago there were herds of these animals that may have numbered in the thousands. Furthermore, these were both large and sturdy animals, in life probably weighing in the range of 4 to 12 tons. Therefore, the bones of these dinosaurs were robust enough to survive the ravages of time and erosion. As common as the fossils from these two dinosaurs are, their complete skeletons are rare. When we find one, the bones are often spread over large areas or stacked on top of one another in a complicated mess. These finds are described as associated. That is, the bones are from the same animal, but they are not in life position.

True articulation (the animal's bones laying neatly together as they were in life) is very rare in the Hell Creek. This is due to the turbulent nature of the environment that these animals lived in. 66 million years ago eastern Montana and the western extremes of the Dakotas were a series of river deltas flowing down eastward from the Rockies and feeding into the Western Interior Seaway that effectively bisected North America. Think of southern Mississippi today: lush, dynamic, and crisscrossed by river systems.

These rivers not only attracted the dinosaurs (providing them with fresh water and lush vegetation) but their ensuing floods and storm surges buried the animals rapidly enough to give them a chance to eventually become fossils. Unlike the gentle silting of lake bed deposits, which can often preserve articulated specimens, the more violent deposition of flood plains like the Hell Creek tend to scatter skeletons about. As a result, what you typically find there are what appear to be isolated bones. The bones may in reality be part of associated skeletons, but the massive proportions and unpredictable patterns of these sites often make excavations impractical.

That's why our team was so excited when we found a perfectly articulated hadrosaur tail in 1999. With the exception of a few associated aspects of the pelvis, the tail was all that was left of the animal. There was not enough of the animal preserved to positively identify it to a species. Based on the length of the tail (23 feet), we project the overall body length of this hadrosaur to be over 40 feet. Based on that immense size, there was some speculation that this specimen is an Anatotitan ("large duck"). Some dispute the validity of this species believing all Anatotitans to be large examples of Edmontosaurus. This specimen may indeed be an exceptionally large Edmontosaurus but without anterior elements of the skeleton, we cannot be certain.

Every excavation is different and each one always presents its own unique engineering challenges. This hadrosaur tail was no exception. For starters, the tail was protruding out of a cliff facing over 100 feet to the ground. Secondly, the matrix that entombed the fossil was a sandstone that was harder than concrete. And finally the tail went directly into the cliff. It would have been very convenient if the tail had been at ground level, oriented parallel to a nice, soft clay or mudstone butte and (as long as we're fantasizing) next to a road. Naturally, we had no such luck. We essentially had to dig a 25-foot long tunnel directly into an extremely dense cliff in order to excavate this specimen. That all being said, we weren't complaining.

Any kind of articulation is a cause for celebration in the Hell Creek, and the bone quality of this specimen was exceptional. As I worked I remember having a fleeting thought: *With bone quality this nice, I wonder if we'll find preserved skin on this tail?* With that thought in mind, we were very careful to remove and plaster-jacket the surrounding matrix along with the bones of the tail.

One of my paleontological mantras is to never do preparation in the field. The purpose of an excavation is to collect data, document the site and safely remove and transport the specimen to the lab. Once delivered, the fossil can then be safely prepared in a controlled environment. As events unfolded, this turned out to be a good policy.

The excavation was challenging but satisfying. Once we plaster-jacketed the bones and surrounding matrix, we used ropes to raise them up to the top of the cliff. This was no small task considering the fact that some of these jackets weighed hundreds of pounds. Once safely to the top, we plastered 2x4s to the jackets and carried them out stretcher style over almost a mile of rough terrain to the jeeps.

Once the excavation was completed, my job was done and I made my way back to Chicagoland. A few weeks later I received a very odd message on my answering machine: "SKIN! THERE'S SKIN ALL OVER THIS TAIL!" It was my partner, the owner of Paleo Prospectors, Steve Nicklas. He had been preparing the tail in his lab in Georgia. What Steve had discovered was profound. I got in my car and began to drive south.

Soft tissue preservation like skin is the rarest of the rare in dinosaur paleontology. Of the few existing examples, most specimens of dinosaur skin are relatively small. Here was a 23-foot long tail and over 70% of it was covered in skin! At the time of its discovery, from the standpoint of square footage, this was the third largest amount of skin ever found on a dinosaur. Another thing worth mentioning is that most specimens of preserved dinosaur skin are "skin impressions." That is, a trace fossil formed when a dinosaur pressed its skin into some matrix (usually sand) and left a molded

negative fossil copy of the skin (think of footprints.) The skin on our fossil is not an impression. The skin itself was mineralized and preserved which can clearly be seen in cross-section.

The skin itself superficially looks like hexagonal scales ranging in size from 1/8 inch to almost 1/2 inch in diameter. These "scales" are more accurately epidermal tubercles not dramatically different from our own skin when looked at under magnification. These tubercles provided the dinosaur armor-like strength as well as a reasonable amount of flexibility.

The quality of the preservation on this fossil is remarkable. Different locations on the tail have different kinds of tubercles. Some are thick and almost pebble-like while others are delicate and reminiscent of snake skin. There is even what appears to be keloidal scar tissue from and a serious injury that the hadrosaur had suffered and survived.

Preparation of the skin was a long, arduous process. The skin layer was so delicate that typical preparation methods such as pneumatic air scribes and even air abrasion would have blown right through it. Instead, once we got close to the skin layer, we had to remove the sandstone with scalpels and nylon brushes often one grain at a time.

I'm often asked how dinosaur skin can survive 66 million years. It's a legitimate question. Indeed, mineralization of even sturdy anatomical features like bones and teeth are somewhat miraculous; the idea that something as fragile as skin can be preserved seems impossible. But there it is, mineralized skin along with ossified tendons and bone.

The circumstances by which such soft tissue preservation can occur are extraordinary. First, as with an articulated specimen, there must be little or no scavenging prior to burial. The animal needs to be essentially intact when it is buried. Secondly, once it is buried, the environment must either be very arid or one that lacks enough oxygen to support decomposing organisms. Examples of such an environment would include a desert, the bed of a swamp, or the bottom of an ocean. None of these conditions matches what we believe Hell Creek looked like 66 million years ago. Considering the Hell Creek's river delta environment, the following is one theory on how this animal was preserved in such a pristine state.

The western extreme of late Cretaceous South Dakota was experiencing a significant drought. Whether it was due to this drought or to some other unknown reason, our hadrosaur died in a driedup riverbed. The animals that would typically scavenge its carcass had migrated to find water or had also succumbed to the drought. In any case, our deceased dinosaur lay in an undisturbed state baking in the sun. The drought created a micro-arid climate in which microorganisms could not thrive. This resulted in only partial decomposition of our hadrosaur. Aspects of its body that were moisture-rich like eyes, muscle and internal organs decayed, while bone, tendon and even skin remained mostly undisturbed. As the animal desiccated, it lost volume and appeared to deflate. More importantly, the skin and connective tissues hardened. Now fully desiccated, the hadrosaur had a minimum of microbial activity within it and could be accurately described as mummified.

Then something in the environment dramatically changed. The hadrosaur was very rapidly covered in sand. Whether the drought ended abruptly and the hadrosaur was buried in a flash flood or the carcass was buried by some other means is unclear. What is certain is that this dried and hardened hadrosaur was buried rapidly in a low oxygen environment resulting in almost no further

decomposition. Over the next several million years this unlikely combination of events resulted in the mineralization of not only the dinosaur's bones but also its connective tissue and skin.

Paleontologists are always looking for more information. This amazing fossil can teach us things about hadrosaurs that bones alone could never do. We can actually see how the ossified tendons supported the weight of the tail confirming that hadrosaurs did indeed carry their tails off the ground. We do not have to speculate about what hadrosaur skin looks like and as a result we have a much better idea what the living animal looked like. Specimens like this can even shed some light on that most mysterious aspect of paleontology... the behavior of extinct animals. Is the scar a healed wound from a large carnivore bite? If so, what does this say about Tyrannosaurus rex being a scavenger?

Some people ask me why I go digging for dinosaurs for two months every summer. I tell them that it's a rescue mission. If we had discovered that hadrosaur a few decades or perhaps only a few years earlier, we may have found more of the animal's body. As things turned out, the majority of the hadrosaur's body (which was most likely also covered by skin) weathered out of the cliff facing, crashed down to the bottom of the valley and eventually eroded into dust.

I wonder what we'll rescue next summer.



Picture 1. The excavation of the tail. The pickax gouges above the fossil will attest to the density of the sandstone.



Picture 2. Painstakingly removing the matrix, one grain of sand at a time!



Picture 3. Close-up of the skin.



Picture 4. A 3-1/2 foot section of the prepared tail clearly showing the preserved tendons and skin.



Picture 5. View of the skin "draped" over the vertebrae and neural processes.

The Nightmare Before The Cenozoic What did the dinosaurs look like and what happened to their ecosystem? By Scott McKenzie Geology Department Mercyhurst College

It happened in the night, the eternal night of space. It was somewhere between the orbits of Mars and Jupiter, in the realm of the asteroid belt, where trillions of rocks from specks to sub planets orbit the sun. Usually the asteroids keep their meek and silent course through the heavens, but occasionally they are hit by comets or collide with one another. When that happens, pieces are flung into new trajectories. Sometimes those new paths lead to collisions with Earth. In this instance, the belt collision happened 160 million years ago. So how did something that happened 160 million years ago in space affect life on Earth 95 million years later?

To begin with, the world of the dinosaurs was unlike our own. The climate was warm enough to allow dinosaurs and amphibians to live on Alaska's North Slope and in Antarctica. The composition of Earth's atmosphere was much higher in CO2 than the 0.03% we have today. Plants thrived and animal life grew gigantic. It was our planet but it was a different world, a world ruled by birds.

When settlers began to find dinosaur footprints in the Connecticut River Valley, the tracks were thought to be those of Noah's raven. When the dinosaurs were first scientifically described by Sir Richard Owen in 1842, he wrote they were reptiles but remarked, "notice the bird-like characteristics of the skeleton"...prophetic words.

Today we recognize that all of the dinosaurs were birds or were closely related, but we labor under the illusion that we understand what they were like. To fully embrace the concept, we have to re-imagine them and their world.

The first step is to realize that scientists estimate we have found only 3 to 5 percent of the kinds of dinosaurs that lived. Imagine a jigsaw puzzle with thousands of pieces missing; how can we understand the picture? Well, we really can't. We have just a vague idea of them and their ecosystem.

The dinosaurs that we have found are frequently pictured in books, online and in movies as near naked grey beasts. The fossils are telling us differently. Finds at lagerstätte deposits in China are spilling the beans. The dinosaurs were feathered, and the feathers were colorful! Studies of the feathers show at least some dinosaurs were covered with iridescent feathers, some had stripes or spots. The inescapable conclusion is that they were as colorful as and much more diverse than modern birds.

We should also think about dinosaurs having rooster-like combs on their heads and maybe waddles hanging from their necks. Male turkeys have "snoots" - a colorful long pendulum of flesh hanging from their nasal region. Turkeys are theropod dinosaurs, so there is reason to think some

other dinosaurs were as well decorated. Feathers could also change the shape of dinosaurs - think barn owl. A barn owl's skull is rather small but add the feathers to the flesh and it has a large head with feather sculpting to funnel sound signals to its hearing organs; could we imagine T. rex with a similar arraignment? Could some of the Theropods have been barn owl like?

One interesting idea was recently posed by Brian Gula, Environmental Educator at the Tom Ridge Environmental Center at Presque Isle State Park. He noted that many eagles, owls and some other modern birds have "fixed vision" meaning their eyes do not move much if at all; the whole head turns. This may be because some bird eyes are so large that they cannot move or in the case of owls, the eyes are not round in cross section. Did dinosaurs share fixed vision with these modern birds? Is there any way to really tell?

The Ceratopsians are also due for a major make-over. Chinese fossils now show early Triceratops relatives with large plumes on their tails. The frills over their necks may have been for purposes we cannot yet imagine. The idea that they were for protection from the likes of T. rex is probably all wrong. The frills are often very thin bone that a big predator could chomp right through with little trouble and the frills were covered with living tissue in life. We know this because the fossil frills show unmistakable grooves from blood vessels on inside and outside surfaces.

One thing is clear; dinosaurs were birds or were close relatives and had bird-like behaviors and appearance. I suppose we have to wrap our minds around the great long-neck Sauropods being bird-like. Of course many (most?) of the dinosaurs were small. Fossils of chickadee sized animals are harder to find and prepare than apatosaur size bones and many small dinos may never emerge in our museums. The big idea here is not just what the dinosaurs looked like but how their ecosystem got permanently deleted at the end of the Cretaceous.

Many theories of how the dinosaurs vanished are still kicking around. There are well over a hundred published reasons on what ended the Mesozoic. Some of the more colorful reasons include them becoming ill with some genera-hopping plague. The plague idea fails when we consider the variety of life forms that were affected: plants, one cell planktonic forams, rudist clams, flying reptiles, marine reptiles and ammonites to name a few. It would have been a gifted pathogen to do all that and in so short a time. Disease organisms also tend to leave a few of their hosts alive to serve as food for the future.

The Fartosphere. Yes you read that right, it has been suggested that the dinosaurs were gassy, especially the big sauropods. Some authors say that they were so flatulent that standing behind one would be like standing in a wind tunnel. Their barrel-shaped bodies acted like fermenting tanks to process low energy vegetation; this would produce lots of gas. The argument postulates huge amounts of methane acting on the atmosphere like CO2 on steroids. The Mesozoic was host to a higher CO2 atmosphere than today and the dinosaurs might have contributed to another of the many "global warming" events.

Reptile dysfunction. Published theory advocates the extinction event was triggered by size induced loss of reproductive function...they became too big to successfully reproduce. Interesting

theory, but remember the dinos were gigantic for tens of millions of years and reproduced just fine. The big picture is again: any explanation of what happened to the dinosaurs must also account for the other diverse plants and animals that were affected by the end Cretaceous event. By the way, birds are classified as reptiles now days.

Verne shot. The newest theory is called the "Verne shot" named after the great sci-fi writer (who would have loved this). The Verne shot involves a massive build up of gas under continental cratons, and when the pressure reaches critical strength, it blows mountain-sized blocks of the Earth's crust into low sub orbit. The chunks fall causing crater-form structures and triggering massive chaos. Strange as this seems, there is some evidence that Verne shots may be possible. Circular target-like features may have been resolved by geologists on the underside of several cratons. Massive outpourings of lava are also associated with Verne shots. In fact, catastrophic volcanism is associated with several extinction events. Much more research needs to be done but it is an interesting idea.

We do have one line of evidence that seems to be correct. The dinosaurs' world was shot. The culprit may have been one or more members of the Baptistina family. No, not some ancient crime family, but even more dramatic: a family of rogue asteroids. As mentioned earlier, a collision in space around 160 million years ago may have doomed the dinos before most of them even evolved. The breakup of that asteroid is also linked by computer modeling to the formation of the crater Tycho on the moon. Chemical evidence is equivocal, but a case can be made here.

We do have overwhelming evidence of not one but several impacts near the Cretaceous/Tertiary boundary. The most familiar is the 100+ Km. crater on the Yucatan peninsula in Mexico. The crater is named Chicxulub and in the ancient Mayan language, it means "the tail of the devil". The crater is deeply buried by later sedimentation. Witnessing the flight of an asteroid or comet of this size in the atmosphere would have instantly incinerated any animal life close enough to witness it.

The dynamics of crater formation indicate that mile high tsunamis would have resulted from the impact(s). The crater would not produce a mushroom cloud; instead pillar clouds would form a tunnel through the atmosphere powerful enough to suck up rock, ocean and atmosphere from ground zero and hurl them into space. Later, a wall of flame with hurricane winds would rush over the landscape. Roast and boast. The sun was blocked by soot and dust for months, temperatures plummeted world-wide, freezing the toasted landscape. The end of the dinosaur's ecosystem was a nightmare beyond our understanding. It resulted in a changing of the guard in ecosystems. Small primitive life burrowed into the ground or hid deep under water or waited as seeds. They survived. Larger exposed life perished. The asteroid (or comet) pressed the Earth's reset button.

The nearest outcrops of rocks from the time of the crater's formation are today in Belize. In the 1990's members of the scientific community and the Planetary Society visited the exposures in quarries on and around Albion Island, Belize. Massive sedimentary formations show features of colossal catastrophic impact. The quarries that expose the key strata are operated to produce road and construction aggregate. Sampling the rocks by visitors is strangely not permitted. On one Planetary Society expedition, the participants stayed at a place called Pook's Hill Jungle Lodge. One

evening several members went to a lookout point to watch the sun set. While there, some of them noticed round rocks lying about. Some had oddly polished surfaces and strange dents on them. These rocks were later named "Pook's Pebbles".

The pebbles have now been carefully examined and are carbonate rocks from Chicxulub. These rocks were shot out of the crater during the impact and went into a suborbital flight with some actually going into space. When the billions of Pook's pebbles reentered earth's atmosphere, they were red hot. Their polish came from passing through a dense dust cloud and the dents were from hits by other Pook's pebbles. Some broke, twisted and re-joined during flight.

Another impact specific rock type at the quarry is the carbonate spherule. They formed like hailstones from dust and some accreted into the size of a beach ball or SUV. They also abound at the Albion Island quarry. Greenish rock called smectite is also found there. Smectite probably formed through the decomposition of impact glass made from the heat of the impact. Micro diamonds are reported to be an ingredient of the famous K/T boundary layer. They should be looked for in sediments from other extinction horizons.

Although one scientist still disputes the age of the crater, most now accept it as the best answer to the dinosaur ecosystem's demise. There are other craters that may have formed at the same time or very near that time. Today the dinosaurs are still with us in the form of birds. The asteroid/comet threat is also still with us. If we found an object in space tomorrow that was to hit us in a year, we have no real way to stop it. In this respect, we are in the same basket as the dinosaurs once were.

The race is not to the swift, nor the battle to the strong, ...but time and chance happeneth to them all. - Ecclesiastes 9:11

Some sources I consulted that you may find interesting are:

Paul & Jutta Dudley, www.rasny.org/belize/belize.html

Dinosaur Heresies, by Bob Bakker, 1986, Morrow

Everything is going to kill everybody, by Robert Brockway, 2010, Three Rivers Press

BBC-News, Astronomy site on Baptistina, 2007

Prolog from the movie Armageddon

If you want to see if birds today are as fierce as the dinosaurs check out YouTube **"Eagle hunts wolf in Mongolia"**. Version by Marcelnad (thought provoking).