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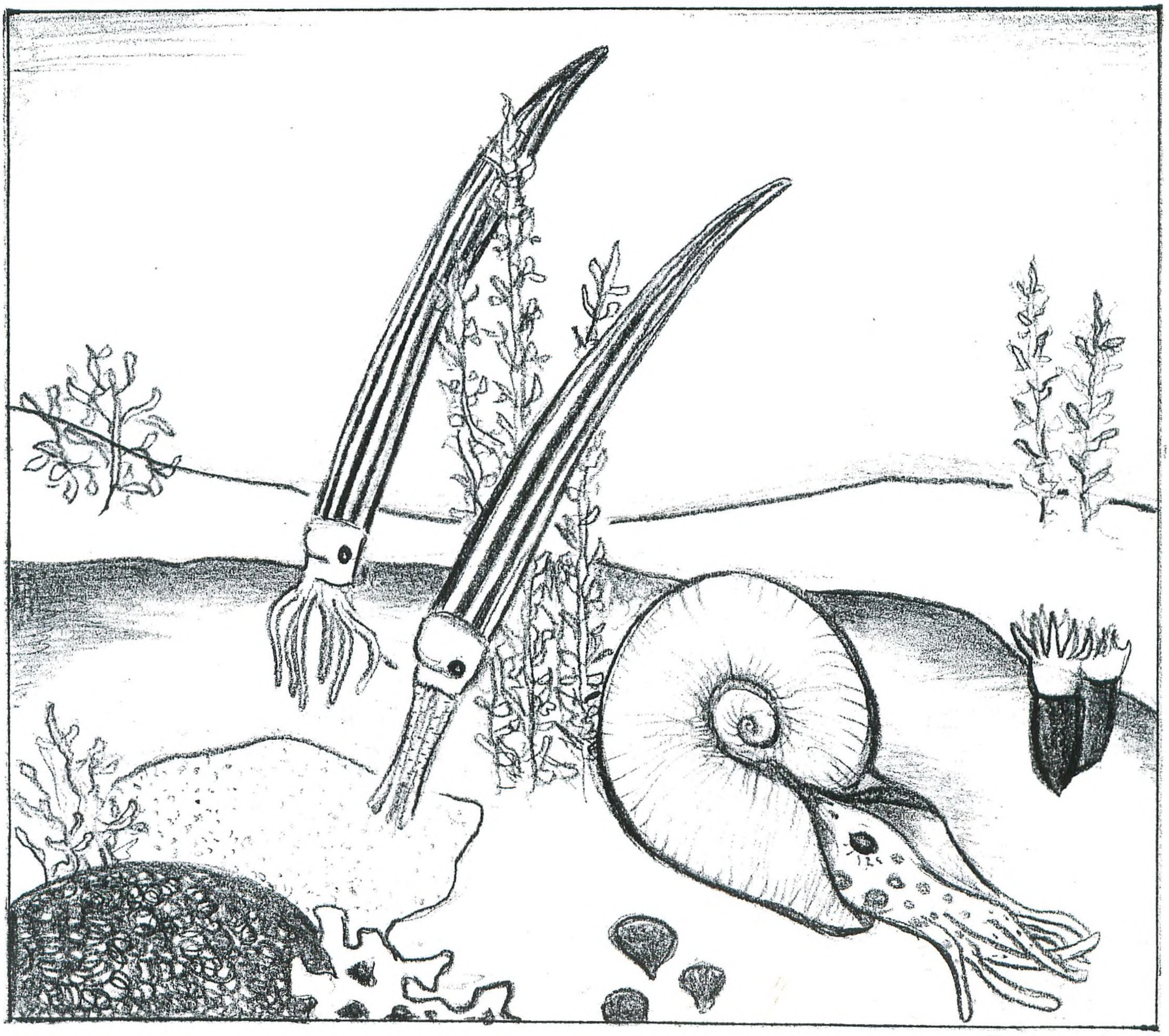
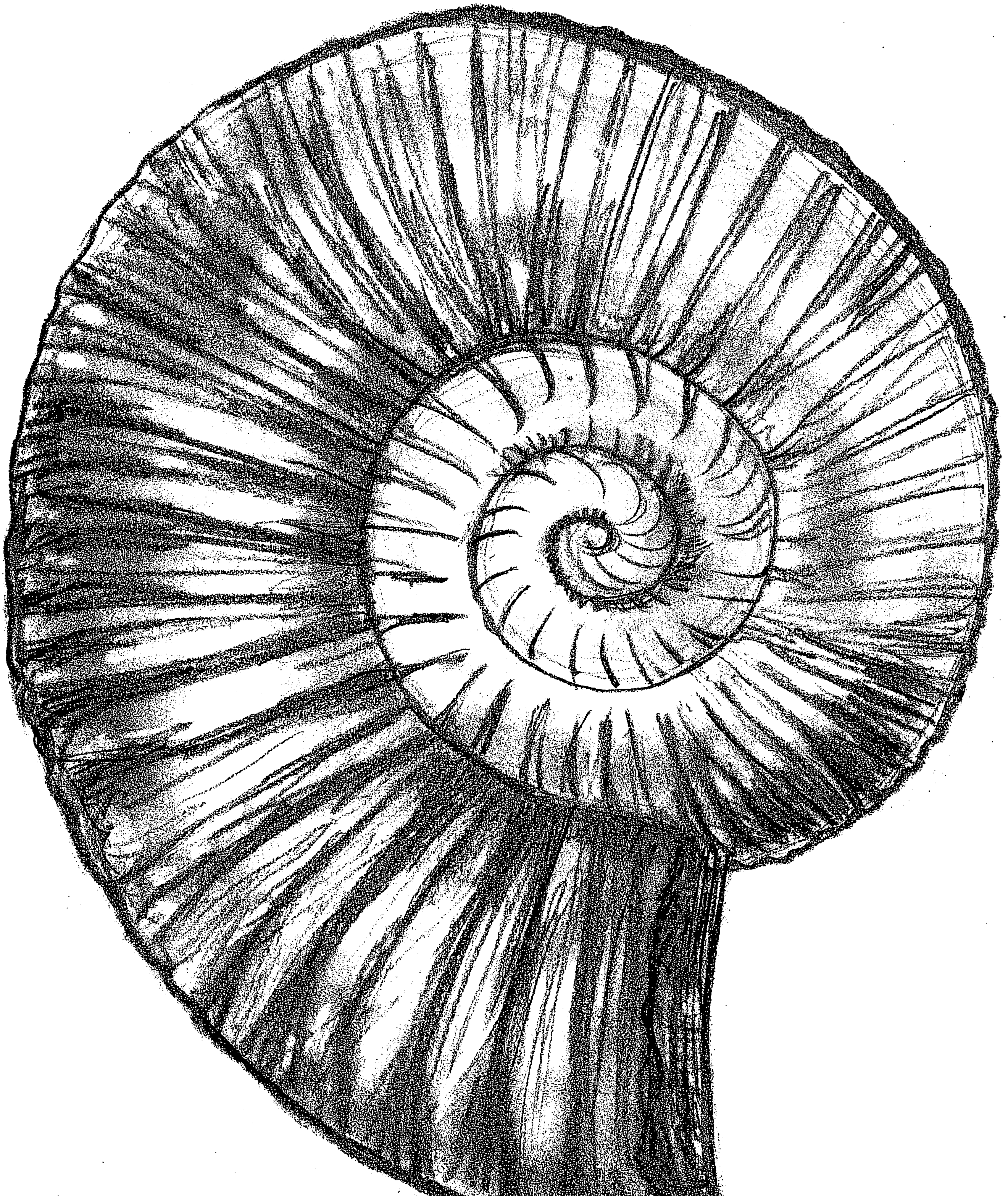


S. Heinzl 03

A LOVE OF FOSSILS BRINGS US TOGETHER



AMMONITES

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M.A.P.S. DIGEST

EXPO XXV EDITION

MID-AMERICAN PALEONTOLOGY SOCIETY

A LOVE OF FOSSILS BRINGS US TOGETHER

WESTERN ILLINOIS UNIVERSITY
UNION BALLROOM
MACOMB, ILLINOIS

MARCH - 2003

The **Mid-American Paleontology Society** was formed to promote popular interest in the subject of paleontology, to encourage the proper collecting, study, preparation and display of fossil material; and to assist other individuals, groups and institutions interested in the various aspects of paleontology. It is a non-profit society incorporated under the laws of the State of Iowa.

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COVER

Serena Heinzl graciously provided the art for the front, inside front, and back cover for this years Digest. And when I could not find a suitable drawing of a St. Ammon Stone for my introduction, she drew one for me. Serena is the daughter of Lez Heinzl and is seventeen. Serena also provided the drawings for her father's article.

The front cover depicts two nautiloid cephalopods feeding on the seafloor and an ammonite browsing beside them. The back cover depicts what they would look like as fossils. The inside front cover was her first draft for the back cover, and I thought it was too good to lay aside. It is a fossil ammonite.

Thank you Serena and I hope we see more of your work in the future!

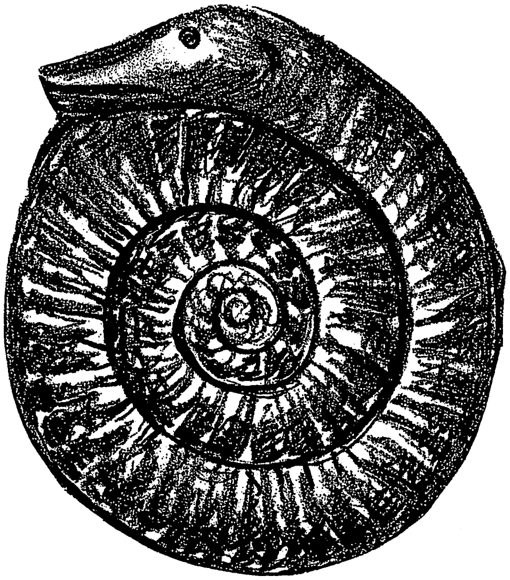
ACKNOWLEDGEMENTS

Some time in January, I wrote my introduction to this year's EXPO issue. At that time I had three articles in hand, a total of twenty-one pages. As I wrote the introduction, filled with little teasers, I wished that I had articles that provided in depth discussions on these topics. And by golly at this writing, I do.

I wish to extend special thanks to Sharon Sonnleitner and members of the MAPS board of Directors who beat the bushes to gain articles for this EXPO Digest. It goes without saying that I very much appreciate all the authors who have contributed articles to this Digest. I have not had a chance to fully read all of what has been submitted. I like humor - Steven Jorgensen! And James Preslicka, I am standing there with you amid that Devonian Sea in Iowa. And last but not least the must read article is Fossil Hunting on the Yorkshire Coast by Barbara Ermler. I hope the printer can reproduce her pictures, but I got to read her article with color pictures and the sea coast of Black Nab and Saltwick Nab - I could just step into the picture and sit a while - No way - I would be racing the tide to collect ammonites!

The subject for MAPS EXPO XXV is **AMMONITES**. Ammonites belong to the phylum Mollusca, class Cephalopoda, and subclass Ammonoidea. The ammonites are group of marine invertebrates [no fresh water examples are know to exist - either fossil or living].

The word ammonite comes from the Greek word for ramshorn, [ammon]. There are many folktales, which portray ammonites as petrified snakes. In Whales St. Keyne turned snakes to stone. At Whitby in Yorkshire St. Hilda drove the snakes off a cliff, thus cutting off their heads. In both of these cases fossil ammonites in the area are said to be the remains of these sakes turned to stone. Local shops sell ammonites with snakeheads carved on the last whorl as souvenirs. These are sometimes referred to as St. Ammon Stones, however ammonites in general have also been referred to as St. Ammon Stones.



Art by *Serena Heinzl*

Cephalopods first appeared in the fossil record in the Late Cambrian. The first forms were straight, elongated conical shells, which evolved into the semi-coiled forms [*Lituites* sp.] in the Ordovician. These in turn may have evolved into the coiled forms of the ammonites and natutiloids. The first ammonites appeared in the Early Devonian, rapidly diversified, and reached their zenith in the Jurassic and Cretaceous and became extinct at the end of the Mesozoic.

Ammonites were predatory creatures with tentacles and the ability to swim very rapidly. If their soft organs were like the living *Nautilus*, argonauts, squids and octopi, the ammonites possessed well- developed sensory organs and defense mechanisms. They would have had remarkable eyes, tentacles with suckers, the ability to change color and an ink sac for covering their escape. We do know that their mouth contained a beak, capable of tearing their prey apart.

The ammonites evolved rapidly and lived over vast geographic areas. Ocean currents transported larval stages to the far corners of the earth. The cosmopolitan habitat and rapid evolution of the ammonites made them perfect fossils for differentiating rock units. A fossil that can be used in this manner is refereed to as an "index fossil". In the Paleozoic, twenty-four ammonites are used for index fossils. There are twenty-nine ammonite zones in the Triassic and sixty-plus zones in the Jurassic.

Present day cephalopods spend much of their time on the sea floor, but there is very little hard evidence that fossil cephalopods spent considerable time exploring the sea floor. A few impressions of nautiloid cones with associated tentacle impressions are known to exist and a few scrape-trails of ammonite tests with possible tentacle impressions are in debate. Ammonites probably spent most of their time swimming. The present day *Nautilus* propels itself along by "jet propulsion" using a muscular tube called a hyponome. The *Nautilus* has broad shallow indentation called a hyponomic sinus that allows the hyponome to flex. This allows the Nautilus to change direction rapidly. The growth lines on many fossil ammonites indicate that they had a hyponomic sinus, thus it is reasonable to believe that they were proficient and active swimmers.

Vertical movement, going up and down was probably accomplished by either taking in seawater or using internal fluids to descend and producing gas to fill the cameral chambers [displacing the fluids or seawater] for ascension. There has been considerable discussion and speculation over the purpose of the complex sutures and shell ornamentation of ammonite shells and their role in supporting and or withstanding pressure of the ocean depths. W. J. Arknell [1956] purported that complex sutures reflected deepwater forms, while simple sutures indicated shallow water habitats. Gayle Scott, working with Cretaceous ammonites from Texas [1940] thought that coarsely ribbed types inhabited the infranertic zone [20-100 fathoms]. The smooth ovate forms inhabited the epibathyal zone [80-100 fathoms] and the smooth obese forms inhabited the deep water or the infrabathyal zone.

The sexes are separate in modern cephalopods. Sometimes the sexes are represented by morphological differences. Male and female fossil ammonites have been mistakenly described as separate species. Modern cephalopods mate, the eggs are laid, and the male dies shortly thereafter, and the female generally does not live to see her eggs hatch. Life expectancy in shell-less cephalopods is from six to twenty-four months. The *Nautilus* may live seven or eight years. The first five years are used to reach sexual maturity.

In order to efficiently describe a species of ammonite the ontogeny or life cycle of the ammonite must be studied. There may be striking changes in the shape of the shell. For example, as an ammonite reaches sexual maturity, there may be changes in coiling, or the living chamber may increase or decrease in size.

The modern *Nautilus* is a carnivore and to some degree an opportunistic scavenger, feeding on small crustaceans and fish. Small ammonites and those with restrictive apertures may have fed on plankton. Anna M. Bidder [1962] produced a report on the function of various tentacles in the living *Nautilus*, assigning three phases - "alert", "search" and "feeding" functions and studied the multiple uses of these specialized tentacles in the everyday life of the *Nautilus*.

The *Nautilus* is a nautiloidal cephalopod not an ammonite. However, it is a close living relative to the ammonites and shares many of the biological, structural, and environmental aspects of ammonites. It is reasonable to use the *Nautilus* as a living laboratory to study the life habits of its extinct cousin the ammonite.

The ammonites were fast agile swimmers, capable of quickly changing directions, in the horizontal plane, changing depths, and possessing superior sensory organs. Living relatives are predaceous carnivores. And yet, they swam backwards. Thus providing a convenient source of protein. Beginning in the Devonian, fishes and sharks must have found the ammonite a tasty treat. Direct fossil evidence of such attacks are rare because, because these attacks would have resulted in the destruction of the shell. However, a few survived the attack and somehow survived the ravages of time and were preserved as fossils.

Unlike the natutiloids, which in many cases, the fossils need to be cut open [particularly the orthocones] to study the internal details. Ammonite classification is based on three primary external features: sutures, ornamentation on the conch and shape of the conch.

The suture with its lobes and saddles are extremely important to identification. Sutures did undergo change as the ammonite matured, and for that reasonably adult specimens are used for identification purposes.

Ornamentation of the shell is visible only if the shell material is present. There may be fine or coarse lines [lirae]. Some lines run transverse, others longitudinal and there are combinations, creating a cross-hated pattern. Nodes and or ribs may be present.

Conch shape includes the size and shape of the umbilicus, whorl width and height and overall diameter.

An old trick used by paleontologists to study the suture lines of ammonites is to lay a piece of cellophane [off a pack of smokes] on one side of the ammonite and using a worn [sharp - would pierce the cellophane] pencil, trace the suture lines. Now you have a representative of the suture lines that may be compared to line drawings in reference books. Modern day plastic film will do nicely. Did I just give away my age?

I have touched upon a few interesting aspects of ammonite life. Now it is time to enjoy the articles submitted by those who love ammonites. I hope you enjoy them as much as I have.

Predation and Pathologies in the Late Cretaceous Ammonite Family *Scaphitidae*

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Abstract-Ammonites were extremely abundant and efficient marine predators. They fed on crustaceans, pelecypods, gastropods, echinoids, plankton, other cephalopods, and possibly fish. Although ammonites were voracious feeders, they lacked the size to be at the top of the food chain, and were attacked and eaten by larger reptiles, fish, and other cephalopods. The Late Cretaceous marine deposits of South Dakota have vast numbers of ammonites that exhibit both healed and unhealed wounds resulting from predation. Ammonites from the Family Scaphitidae perhaps display a higher percentage of healed and unhealed injuries than any other ammonite form within the Western Interior. Scaphites and other ammonites are found abundantly in the heartland of North America, with some horizons preserving millions of shells of predominantly mature macroconchs and microconchs of various species. Such mass mortality concentrations implies that many species of Ammonoidea probably died soon after spawning as do many species of extant squid and octopus.

Introduction

The Late Cretaceous ammonite Family Scaphitidae (or scaphites), has been recognized as an extremely important diagnostic ammonite form within some biozones of the Western Interior of North America. Their abundance within these zones gives us great insight into the lives and deaths of these fascinating creatures. The evidence they left behind, consisting mostly of their shells, shows us the similarities between ammonites and modern cephalopods. With extensive collection of the ammonites and the other animals they are preserved with, careful and exhaustive preparation, and research of these comprehensive collections, we can better understand these long-extinct creatures.

The Family Scaphitidae, Gill (1871), existed worldwide from the uppermost Early Cretaceous (Albian) through the end of the Late Cretaceous (Maastrichtian). For most of their existence, there were generally only a couple species of scaphites that coexisted with the many other cephalopod species in the same area at the same time. But by the end of the Cretaceous, the cephalopod fauna of the Fox Hills Seaway was dominated by the scaphite form, with only a few other types of cephalopods present.

Most members of the Scaphitidae lived near the bottom of the water column in shallow waters (50-300 feet) according to isotope studies performed on their aragonitic shell (personal communication with Neil Landman 2000). It was because of their position in the bottom of the water column that they occupied nearly the same environment as extant octopods. It may be partially inferred from this, that their life may have been similar to that of extant octopods.

Background

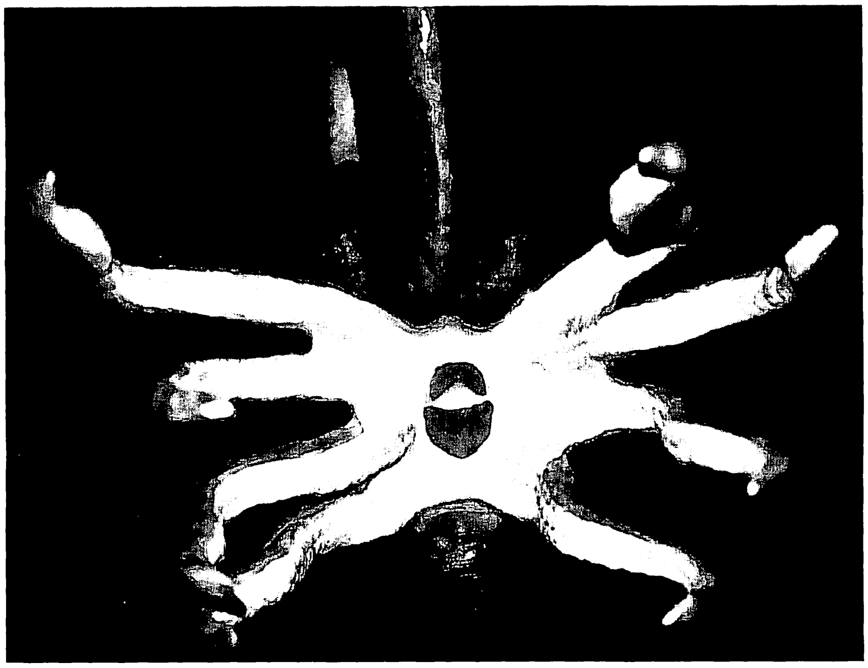
Predation among modern cephalopods is common. From the moment the female lays eggs and those eggs hatch, grow, mature, reproduce, die, and are buried; cephalopods are under attack from a wide variety of predators. In order to gain some insight into their life habits, we must assume that the fossil cephalopods lived and died in a fashion similar to their living relatives. Observations to the evidence left behind in their preserved conchs indicate some of these relationships.

The Scaphitidae was an important and abundant Late Cretaceous heteromorph ammonite family, and the *Hoploscaphites* and *Jeletzkytes* of the Campanian and Maastrichtian of the Western Interior probably originated in Greenland (Landman et al. 1996). Scaphites are characterized by a tightly coiled phragmocone on a J-shaped body chamber. Scaphites were generally small with diameters or shell height rarely exceeding 15 cm. They were compressed, involute to evolute, with a smooth to very ornate ribbed and noded exterior. There are extremely abundant in the Turonian through the Late Maastrichtian of North America and Europe and are found throughout the world, but primarily in the northern hemisphere.

Since the 1970's, the author and his colleagues at the Black Hills Institute of Geological Research have been fortunate to have participated in the collection of tens of thousands of specimens of Late Cretaceous scaphites from the Turonian through the Maastrichtian rocks of the Western Interior. We have collected from ammonite mass mortality layers, occasional ammonite bearing rocks, and countless miles of nearly barren, almost unfossiliferous marine shales and sands. The following observations are based on the study of these enormous collections, the collections of friends and colleagues, paleontological publications, and the research regarding recent and fossil cephalopods.

Anatomy

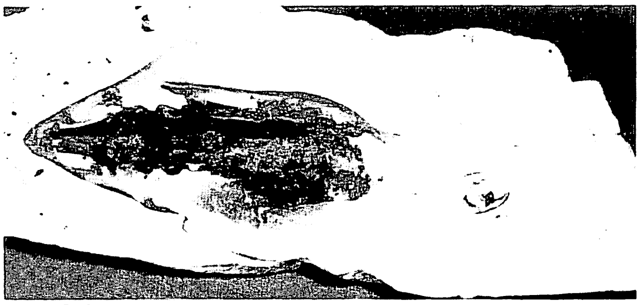
The Ammonoidea is an extinct order of cephalopods that lived from the Late Silurian Period until the end of the Cretaceous Period, a time span of approximately 335 million years. Ammonites are similar to the living *Nautilus* by having an external shell (consisting of a body chamber and phragmocone) that housed their body and provided buoyancy for their mass. Their body mass was probably very similar in appearance to that of other living cephalopods (not *Nautilus*), probably consisting of eight arms, possibly two tentacles, a hyponome (funnel), large head, large eyes, large brain, a pair of large beaks or jaws (***Figure 1***), the mantle, and assorted internal organs.



Sculpture & Photo: Neal L. Larson

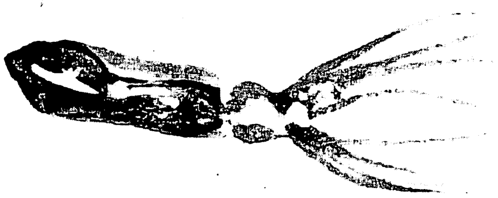
Figure 1

The remains of both fossil squids (***Figures 2*** and ***3*** – *Tusoteuthis sp.;* Santonian, Late Cretaceous; Hakel, Lebanon) and an octopus have been found with their arms, portions of their bodies, and perhaps their internal organs preserved (Engeser, 1988), but the soft parts of ammonites and nautiloids strangely have never been found. This fact alone would make it difficult to correlate between living coleoids and fossil ammonites if it were not for so much other fossil evidence.



Neal L. Larson

Figure 2



Neal L. Larson

Figure 3

Like modern coleoids, the male is generally much smaller than the female (***Figure 4*** – *Discoscaphites conradi*). Like that of extant coleoids, the size of the ammonite eggs is generally one mm or smaller; and like the present day squids and octopus, the ammonites were quite prolific; each female often would lay hundreds to thousands of eggs during spawning. *Nautilus*, on the other hand, has a very large size for its eggs (approximately 3/4 inch x 1/4 inch), and lays only a few eggs (less than 10) a year (Ward, 1987). It also appears that most ammonites, like extant coleoids, grew rapidly and probably matured within a year or two before reproducing and dying (Bucher et al., 1996). A *Nautilus* matures much slower, and lives upwards to perhaps 17 or more years (Ward, 1988).

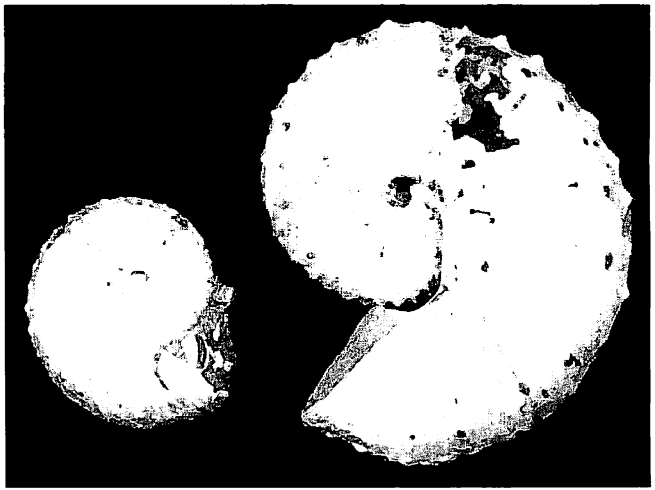

Ed Gerken

Figure 4

Ammonites have been characterized by many to have been a slow swimming, sluggish creature, capable of only scavenging or eating plankton and vegetable matter. But by studying the extant cephalopods, nothing could be further from the truth. The placement and type of the muscle scars on ammonites are more similar to squid than *Nautilus*, and the body chamber ratio size is generally much greater than in *Nautilus*. This would suggest that ammonites were possibly between squids and *Nautilus* in their swimming ability as well.

Although ammonites and *Nautilus* are similar in appearance to each other, many families of ammonites, like the scaphites, have a proportionately larger body chamber than *Nautilus*. Because the body mass of the *Nautilus* fills most of its body chamber volume, this leaves little capacity for the intake of water to expel through their hyponome during propulsion. An excited *Nautilus*, with its shell drag and limited mantle intake and propulsion, is generally a slow swimmer, but has been known at times to swim faster than a man (Ward, 1988). Scaphites, with a body chamber at least proportionately twice as large as in *Nautilus*, must have had the potential to be more rapid then Nautilus, though not nearly as fast as some squids or extant octopuses. Scaphites, like other ammonites, were also restricted to an immobile shell that restricted the amount of fluids in and out of the mantle and hyponome, and thus their speed would have been restricted as well. The drag on their shell would have been reduced because of ribs and tubercles, but not enough to make them fast. Still, they would have been able to compete for food in the oceans and be much higher up on the food chain than any other invertebrates except squid and octopus.

The Shell

The often well preserved, aragonitic shell was the home for the ammonite. The entire shell of ammonites, like *Nautilus*, is composed of alternating layers of aragonite and conchiolin (Larson, P. 1989). Especially in the Mesozoic, the ammonites' shell was characteristically quite thin, when compared to *Nautilus* or other molluscs. This thinner shell was much lighter in weight, and because of the complex underlying septa, it was very strong and able to withstand crushing from extreme water pressure. The shell was created by a large soft organ called the mantle, which laid directly underneath the shell of the entire body chamber. The shell of the ammonite, like *Nautilus*, is made up of two basic parts, the phragmocone and the body chamber. ***Figure 5*** (N. Larson et al., 1997) and ***Figure 6*** (P. Larson, 1989) show the basic external and internal features of the scaphite shell.

The ammonite's phragmocone, the initial portion of the shell, consisted of a series of chambers that were separated by septal walls and connected by a siphuncle ***Figure 5***. The phragmocone served as the buoyancy chambers for the ammonite. Ammonites kept the chambers filled with gas and fluid to maintain near neutral buoyancy in the ocean water so they would neither sink nor float. The septal walls were created by the rear portion of the mantle. As the ammonite grew, it needed more buoyancy for its increasing weight. The ammonite would pull its mantle forward, from the last septa, and create a new septa a slight distance ahead of the last. This new chamber was filled with fluid that the ammonite would pump out through its siphuncle by osmosis. Only the right amount of fluids would be removed from each chamber to keep the animal near neutrally buoyant and in the upright position.

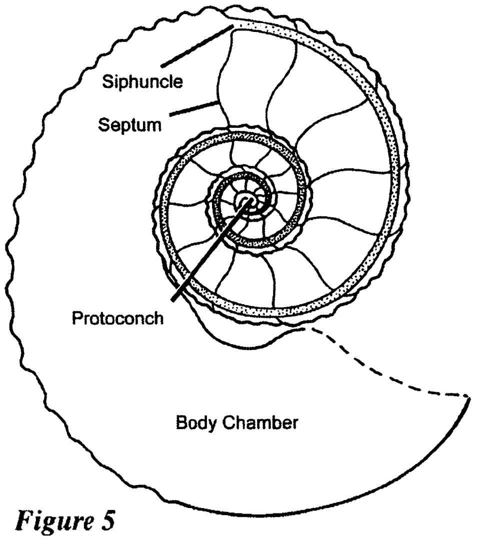
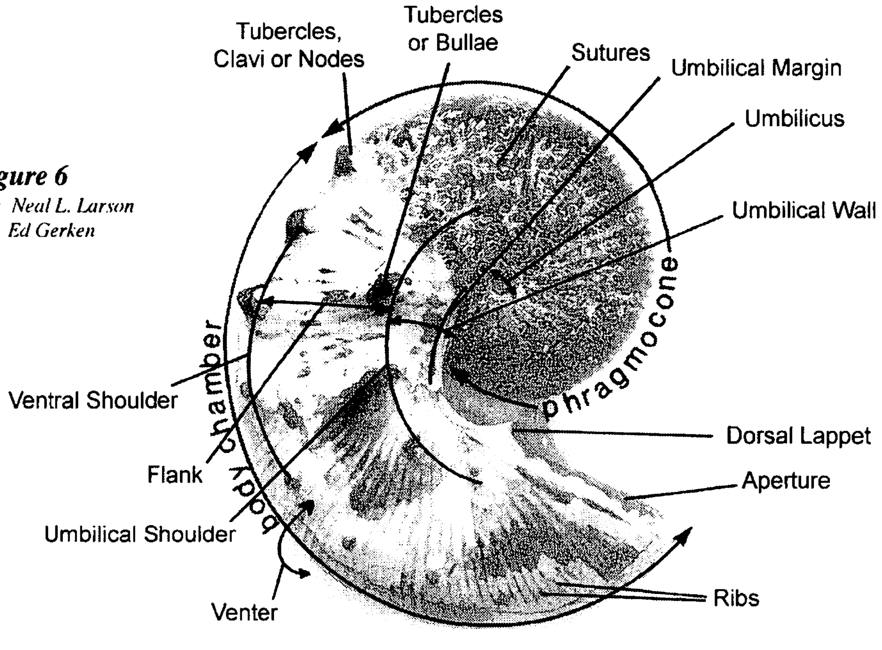


Figure 5
Dorothy Sigler Norton

Figure 6
Illustration: Neal L. Larson
Photo: Ed Gerken



The body chamber was the last portion of the ammonite's shell, and housed the mantle, organs, and the entire body if need be. The body chamber was created by the lip of the mantle as the animal grew. Ribs, and tubercles were added, depending on the species and sex of the animal. The body chamber made up the largest portion of the shell, and in some forms would only grow more after maturity if the animal was injured. In most extant molluscs, only the lip of the mantle excretes the calcite or aragonite necessary to manufacture the shell (Vermeij, 1993). This was not the case with the ammonites nor is it the case with the extant *Nautilus*. Ammonites would use all parts of their mantle to repair their shell in any damaged portion of its body chamber if the damage or injury was not fatal. Any damage to the phragmocone could not be repaired. If the early chambers of the phragmocone were damaged, the animal could possibly seal them off, pump more fluids out of the other chambers of their phragmocone (to regain near neutral buoyancy), and than grow larger to compensate for the loss of the shell.

Muscle Scars

Crick (1898) was the first paleontologist to recognize the dorsal muscle attachment scars preserved in some fossil ammonites. It wasn't until Jones (1961) described an unpaired ventral scar in the Cretaceous *Diplomoceras*, that any further descriptive work was done on ammonite muscle scars. Since that time several paleontologists, including Landman and Bandel (1985) and Doguzhaeva and Mutvei (1991 & 1992), have recognized and described these scars in dozens of ammonite genera. Some ammonites also had muscle scars on other parts of their body chamber. These consist of a pair of lateral lobes, a sinus line, and an unpaired mid dorsal scar in the internal sutural lobe. Muscle scars are not often seen on ammonite body chambers, perhaps because of preservation or, as in recent *Nautilus* shells, the muscle attachments are not distinct enough to be seen unless the specimen has quit growing and those attachments have been in the same place for a long time,. From all of the research to date, it seems that nearly all ammonites possessed at least a pair of dorsal attachment scars and an unpaired ventral attachment scar. It has also been postulated that the complex septal walls of ammonites may in fact reflect the shape of the back portion of the mantle, and that the ammonite used the septal walls as another way to anchor itself in the shell (Henderson, 1984, and Lewy, 2002), thus making the septal walls also muscle attachments.

Muscle scars indicate where the soft body of the ammonite attached itself to the interior of the shell. By comparing the muscle attachment scars in ammonites with the muscle scars in *Nautilus* and the retractor muscles in coleoids, we get a glimpse into the the ammonite's working body. When the muscles of the mantle were contracted, and the body was withdrawn into the shell, water would be expelled through the hyponome propelling the ammonite through the water (Kennedy and Cobban, 1976). By studying the cephalic (head) retractor muscles at the paired dorsal attachment scars, the hyponome (funnel) retractor muscle at the unpaired ventral attachment scar, and the ratio of the size of the body chamber, we may be able to estimate the speed and swimming ability of the ammonite.

In Scaphitidae, both dorsal and ventral muscle attachment scars have been found in both *Hoploscaphites* (Landman and Waage, 1993), and in *Jeletzkytes* and *Discoscaphites* (this paper). A ventrolateral muscle scar, similar to those found in *Aconeceras* (Doguzhaeva and Mutvei, 1991), is located on the rear portion of the body chamber of *Discoscaphites conradi* macroconch near the phragmocone (***Figure** 7*). There is a septal or transverse line very evident on *Jeletzkytes spedeni* microconch, directly below the suture pattern (***Figure** 8*), an umbilical muscle scar above the umbilicus on a *Jeletzkytes spedeni* macroconch (***Figure** 9*), and the ventrolateral muscle scar in the shape of a teardrop on the venter of a *Discoscaphites conradi* microconch (***Figure 10***).

The position of these muscle attachment points in scaphites is important, because some of them (ventral and cephalic) are in the same location on the shell where most of the predation holes, both repaired and unrepaired, are also found. Ammonites bitten in this location would never see their attacker coming, and after the shell was broken in this place, the ammonite could be filleted from its shell (pulled through the hole) and than eaten without putting up a fight. The evidence among the scaphites from the Western Interior seems to indicate that this is the most common form of shell damage.

Neal L. Larson

Figure 7

Ed Gerken

Figure 8

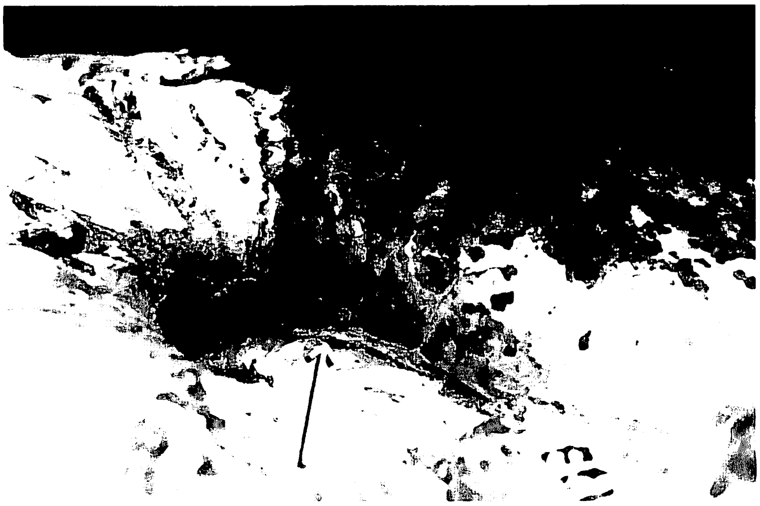


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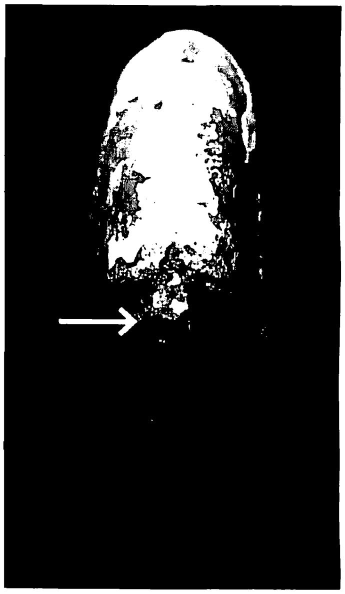
Figure 9

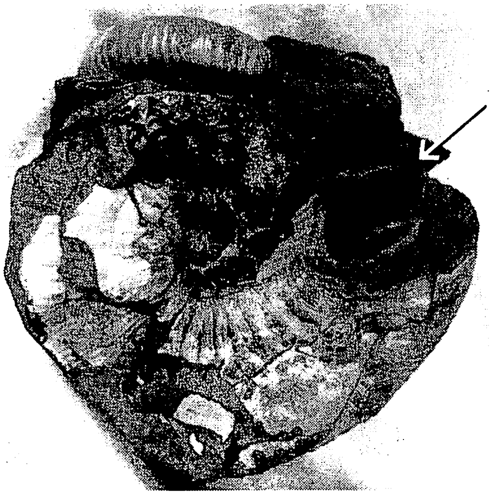


Ed Gerken

Figure 10

Jaws and Radula

Jaws in recent and fossil cephalopods are well documented. The jaws of ammonites are quite large with respect to their size (***Figures 11*** and ***12***). For many years paleontologists (Moore, 1957, and Closs, 1960) believed that the jaws or aptychi were the operculum of the ammonite; that is, a covering of the aperture embedded in the hood as in *Nautilus*, or maybe even a covering for the nidamental gland in female cephalopods. It was not until Lehmann (1972, 1981a, and other publications), proved that these large 'bivalved' shaped objects were analogous with the jaws in living cephalopods that anyone considered that they were therefore ammonite jaws. The jaws in ammonites would have been used, as in modern cephalopods, to break the prey or food into tiny pieces and to help defend themselves.



Neal L. Larson

Figure 11

Neal L. Larson

Figure 12

Unfortunately, in order to satisfy the number of geologists and paleontologists who believed that these aptychi were too large in proportion to the body chamber size to be jaws, Lehmann (1981a) proposed that the jaws may have served a dual purpose of jaws and an operculum. Many paleontologists have jumped on this unusual idea. How and why would the ammonites develop or even need an operculum? No other extant cephalopod has one, nor a need for one. Their arms, beak, and teeth were formidable enough weapons to protect themselves, and sealing themselves up in a shell for protection would most likely only bring them death. And how would it be possible for the ammonite to force its arms and body behind its jaws and then seal its aperture with its jaws? The concept of this idea seems to be biologically unfeasible.

Not all genera or families of ammonites have been found with their jaws in place, or even associated, so to assume that all ammonites were voracious feeders, like the squid or octopus, would perhaps be premature at this time. The jaws of scaphites are well known and some were illustrated by Landman and Waage (1993), and also by Kennedy and Cobban (1976). The jaws or beaks of the scaphites consist of a large two-part lower jaw, and a small two-part upper jaw made up of calcite and conchiolin. They may be described as resembling upside down parrots' beaks and more than likely, they were also extremely strong and powerful. Nearly all that is preserved and found from the jaws of scaphites is the chitinous layer, the outer calcite layer that makes the jaws strong and sharp is most likely dissolved away during diagenesis.

Only jaws from some fossil cephalopods are known, yet the species of recent cephalopods can be determined by differences in the jaw shape and ornamentation (Clarke and Maddock, 1986). It should be possible, since the shape and ornamentation of the jaws in different ammonites are so varied, to determine and distinguish the genus and the species of ammonites by their jaws alone, using the same criteria that is used to determine the species in extant cephalopod jaws.

Located directly behind and inside the jaws of the ammonite are the radula or teeth of the cephalopod. Cephalopod radula are generally quite small, (although some ammonite radula are larger in proportion to their size than in any extant cephalopod) and most of the work of breaking up the prey and chewing, prior to digestion, has to be done by the jaws. The function of the radula is to tear, scratch, and grind up the food, like a rasp, as it passes over them on its way to the stomach (Cooke, 1959). The teeth in mollusks are not like ours, but are similar to tiny shark teeth set in parallel rows and situated on one side of an elongated tongue (Cooke, 1959). Ammonite radula have been observed in only a few specimens. The publications by Landman and Waage (1993) , Lehmann (1971, 1981a & 1981b), Doguzhaeva and Mutvei (1992), and Kennedy, et al. (2002) contain illustrations of nearly all the ammonite radula that have been described to date.

Diet

The diet of ammonites must have been dependent upon their need for certain nutritious minerals. Ward (1987, 1988) observed living *Nautilus* scavenging dead fish and crustaceans that had been placed in traps to lure the *Nautilus*. It is not known if extant *Nautilus* catch living prey, as this has not yet been observed in nature. Hanlon and Messenger (1996) reported on the almost insatiable diet of living squid, cuttlefish, and octopus. These highly mobile cephalopods will feed on or eat anything that they can get their 'hands' on including fish, crustaceans, echinoids, and mollusks inclusive of other cephalopods. Norman (2000), noted that all extant cephalopods are carnivores, without exception. Why should the extinct forms be any different?

The chambered *Nautilus* requires a high calcium intake to build and repair its aragonitic shell. Although other cephalopods no longer have an external shell, they have retained the need and desire for food rich in calcium. The Ammonoidea would have also needed this enriched calcium food to build their shells. Even though most molluscs take the calcium that they need from the water (Vermeij, 1993), the ammonites also had another source in the food that they ate. It is believed that most ammonites lived only a year or two before they died. If their complicated, sometimes large shell was to be created in such a short time it probably would need a substantial amount of shelled animals to satisfy its dietary needs.

Ammonites are thought to have eaten a wide variety of foods. Lehmann (1981b) analyzed the crop content of the ammonite *Arnioceras* and attributed its diet to ostracods and foraminifera. Jager and Fraaye (1997) inspected the stomach contents of a *Harpoceras* and determined that it fed on small decapod crustaceans. Microscopic investigation of a *Rhaeboceras* (BHI-4818) a scaphite from Montana, revealed the presence of fragments of a ground-up crustacean, in what appears to be coprolites located behind the jaws and radula in either its stomach, or caecum. This would be consistent with the diet of many extant cephalopods. Specimens of small pea shaped coprolites associated in and with the ammonites *Aconeceras* and *Deshayesites* from Volga area of Russia (also in the BHI collection), show the abundance of fine, ground up molluscan shell material indicating a diet of molluscs for these species of ammonites.

Like extant cephalopods, ammonites probably also fed on each other, with the larger species feeding on the smaller ones. Lehmann (1981b) studied the stomach contents of a Jurassic *Hildoceras* from Germany and found that it contained the lower jaws of smaller ammonites. O'Dor (1983) related that smaller males of living cephalopods may often fall victim to the larger females either before or after sex. Perhaps this is why, in ammonites, the smaller microconchs (males) were often ornamented with larger spines than the macroconchs (females).

Hanlon and Messenger (1996) have documented cannibalism in every known species of living coleoids except *Sepioteuthis sepoidea,* where all ages of this species coexist peacefully. As with many forms of ammonites, the Scaphitidae were probably cannibalistic to some degree. The more abundant the scaphite remains, the higher the percentage of pathologies seem to be. It is also rare to find juvenile scaphites preserved with mature adult scaphites, suggesting that they did not live together perhaps because of fear of cannibalism from the larger individuals (***Figure 13***).

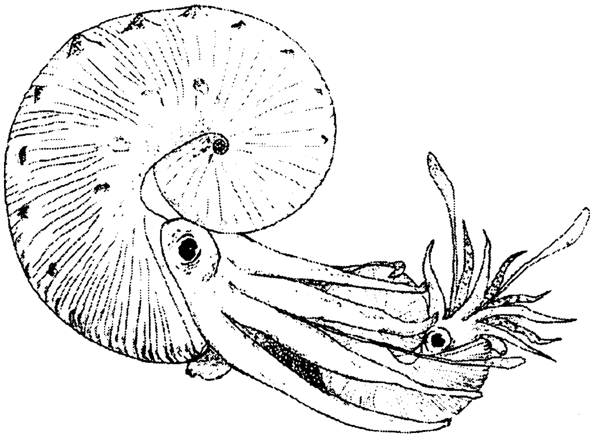


Figure 13
Neal L. Larson

Lehmann (1981b) believed that ammonites were the vacuum cleaners or the "health police" of the oceans' depths doing the job some modern gastropods do today. The evidence, however, not only suggests, but manifests that most ammonites were predators and carnivores just like their living relatives, and would eat whatever they could catch or scavenge. Their diet consisted of plankton, echinoids, crustaceans, molluscs including (other ammonites), fish, and anything else that they could catch and devour.

Predation

Evidence shows that predation was prevalent within the family Ammonoidea. Modern-day cephalopods are among the most important sources of food for larger vertebrates in the sea, and ammonites must have served that same purpose. Cousteau and Diole (1973) write about fish that consume squid. Hanlon and Messenger (1996) describe how modern cephalopods fall victim to the larger cephalopods and vertebrates. Ward (1988) describes his frustration when a trigger fish eats a *Nautilus* that he is returning to the sea, and there is further documentation regarding the predation of *Nautilus* in Saunders and Landman (1987).

Many paleontologists have noted predation in ammonites and have attributed this damage to a variety of predators. Roll (1935) attributed shell damage in some Jurassic ammonites to predatory decapods, as did Thiermann (1964) in a Cretaceous perisphinctid. Lehmann (1981b) believed that reptiles, fish, crabs, and other cephalopods fed on ammonites. Reeside and Cobban (1960) speculated that the fragmentary mollusk shells (gastropods, pelecypods, and ammonites) found as the nucleus of many concretions, may be the fecal accumulation from large carnivores such as fish, reptiles, or even cephalopods.

Perhaps the most dramatic paper presented on ammonite predation was by Kauffman and Kesling (1960) in which they described a *Placenticeras* that had been bitten several times by a mosasaur, a large, predatory, marine reptile. Since that paper there have been dozens to hundreds of claims of *Placenticeras* with mosasaur bites. Most of these claims have been discredited, many of these holes actually attributed to the borings of a predatory or parasitic limpet (a gastropod), by Kase et al. (1998). However, there is another *Placenticeras* (Larson, 1997 & 1999) that shows a definite tooth pattern identical to that of a mosasaur bite, with no evidence of limpet borings to the shell or any sign of limpets in the rock that contained the ammonite. Using the evidence presented by Kase et al. (1998), it seems that this must, in fact, be the result of a mosasaur bite. It seems logical to assume that large reptiles were capable of eating ammonites just as sea turtles and marine mammals feed on cephalopods today and that the ammonite shells could exhibit the evidence of such attacks. Given the placement and support structure of the underlying septa, it is also reasonable to assume that nearly round holes would be made in the shell, if the ammonite was bitten by a toothed animal in its phragmocone.

There is more evidence of predation and scavenging of the ammonites shells than has been previously recognized. The Scaphitidae seem to have three major locations on their shell that are commonly damaged or missing: large chunks of shell broken away from the body chamber near the junction with the phragmocone; small to somewhat large holes punctured in the side or flank of the scaphite; and pieces broken off the apertures. There are also the fragments of body chambers, pieces of phragmocones, and nearly whole phragmocones with portions of the body chamber still attached, found in such abundance that they probably represent the parts of scaphites that were not consumed by their predators. There is no other explanation that could reasonably be given.

Healed Pathologies and Shell Resorption

Healed injuries in ammonites are an extremely fascinating subject. Some ammonite genera from certain localities seem to have a high percentage of abnormalities, while other ammonite genera from the same horizon but different localities may have a relatively low to nonexistent percentage of shell abnormalities. Most pathologies seem to be related to injuries, but there are also abnormalities in shell growth and structure that could be attributed to parasites, the environment, or perhaps even genetics. Most injuries are often related to predation, but they could also be a scarring of the shell as a result of mating or friendly fighting (see frontal assault).

Hengsbach's "Ammonoid Pathology" paper (1996) presented 29 different 'Forma' types of ammonite pathologies and their supposed causes. His classification, used extensively in Europe, proves confusing, and does not relate the simple diagnosis to the injuries themselves. Helmut

Keupp, of the University of Berlin, Germany has published the most papers on ammonite pathologies, but they are all unfortunately all in German. To my knowledge, Larson P. (1984), Landman and Waage (1986), Bond and Saunders (1989), Larson N. (1998), and Klinger and Kennedy (2001) comprise the majority of the published papers dealing directly with North American ammonite pathologies. It is because of the extensive scaphite collections made by the institutions where Landman, Waage (deceased), and the Larsons work, that the abnormalities in Scaphitidae can be so well documented.

Shell repair in mollusks is quite common. The remarkable mantle, which creates and excretes the aragonitic shell on the ammonite as the animal grows, is also able to repair holes inflicted anywhere on the body chamber, as long as the animal survives. In many cases, it seems as if the animal had resorbed some of its shell, while it is repairing the damaged area. Potential resorption of the shell may be observed in all of the figured 'healed' specimens. If the shell did not partially resorb some of the broken and damaged shell, there would be a definite line between the original and the rebuilt shell, this would also result in a weakened area around the new shell. Thus shell resorption in ammonites must be possible to some extent, otherwise determination of the precise shape and location of the injury would be easier to see. Shell resorption, in modern molluscs, is very rarely noted and is only discussed with forms of extant spiny molluscs that must resorb some of their shell when growing over a particularly rough textured part (Vermeij, 1993).

Landman and Waage (1986), and Larson, P. (1984), discovered that between ten and forty percent of the scaphites from the Late Cretaceous Fox Hills Formation exhibited some form of healed abnormalities. This is comparable to a study by Bond and Saunders (1989) on Mississippian ammonites from Arkansas, that showed a similar percentage of injured and healed ammonites. This high percentage of repaired shells might be inconsistent with most ammonite studies from Europe, but it may be consistent with a large population of intelligent creatures living and feeding close together. Ammonites would be highly susceptible to attack from outside sources and would have had a dense enough population that they would have to fight for food and for the affections of a mate. Hanlon and Messenger (1996) relate how living cephalopods, although living together in large shoals (schools), are rapacious when it comes to eating and reproducing.

Landman and Waage (1986) classified and diagnosed the most common forms of injuries in scaphites. This paper will attempt to give examples of scaphites that survived the types of predation previously listed. It will also avoid using the "forma" names for the types of injuries, and will give them a name more reflective to the place of the predation, in an effort to make it less confusing.

Back Breaking Predation

In scaphites, the most common form of shell breakage is represented by a missing portion of shell along the ventral edge near the junction of the phragmocone and the body chamber in the specimens of *Hoploscaphites* and *Discoscaphites* from the Fox Hills Formation (***Figure 14***). Lehmann (1981b) figured an *Eleganticeras* from Germany that exhibits this same type of predation, and Landman and Waage (1993) show some *Hoploscaphites* and *Discoscaphites* with similar shell damage. The author recently examined a lot of 57 scaphites from the Fox Hills Formation, in South Dakota. In that particular lot there were 17 scaphites that exhibited this type of shell damage on the back of the conch.

Ed Gerken

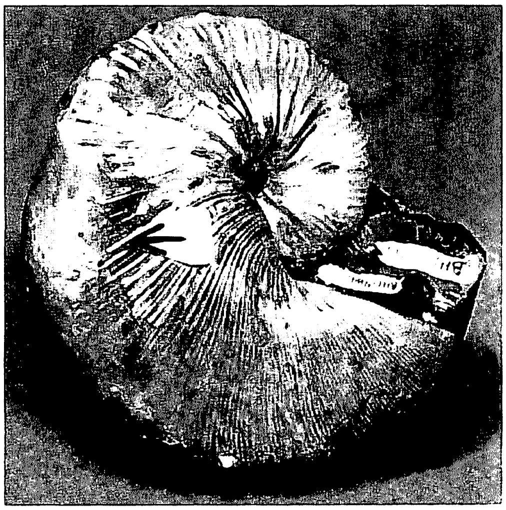
Figure 14

It does not seem to be a coincidence that so many of these ammonites would show such similar abuse. The rear portion of the body chamber would be a 'blind spot' the animal could not see, and this is also the area of the shell where the retractor muscles attach. This blind spot would be away from the jaws and arms of the formidable ammonite. A scaphite bitten in this area could easily be pulled out of the shell without putting up a fight. Biting into the scaphite near its retractor muscles (see ***Figure 9***) would have made it all too easy to filet the ammonite once the shell was broken. A swimming ammonite would have to be attacked from above and behind, not by a ground crawling decapod, but by a swift, cunning, powerfully biting cephalopod or fish. When the jaws of a larger *Jeletzkytes spedeni* are set beside the break in the shell of a *Discoscaphites conradi* (***Figure 15***), it is amazing how similar the size and shape of the jaws are to the break. The jaws of the scaphite were powerful and large enough to have attacked, killed, and eaten a smaller ammonite. It is assumed that it did.

Ed Gerken

Figure 15

Figures 16 and ***17*** show ammonites that survived the 'back breaking' attack (described earlier under predation) in two different manners. *Hoploscaphites nicolletii* (***Figure 16***), suffered an extreme loss of shell that had to be rebuilt. The injury to the mantle was deep, and the ammonite was unable to rebuild its lost ribs or tubercles.



Ed Gerken

Figure 16

Ed Gerken

Figure 17

Jeletzkytes spedeni (***Figure 17***) suffered a large bite to the bottom of the hook of the body chamber. Even though a large section of the mantle may have been lost, the ammonite was able to patch and repair its shell, leaving a deep scar on the back, or venter, of the shell. Because of a large proportion of damage to the mantle, a large portion of the shell around the aperture was never rebuilt.

This *Discoscaphites gulosus* (***Figure 18***) displays a large rupture and then a shell rebuilding to the mantle. The animal was bitten near the ventral muscle scar, but managed to escape. The ruptured mantle was able to excrete a shell over most of the exposed wound. It appears that the bite marks never healed, but rather remained somewhat open until the animal's death. The shell around the wound is smooth and blends in with the uninjured shell, suggesting that some shell resorption took place. This specimen also exhibits the aperture which is broken or bitten away, indicating that the scaphite suffered a second fatal attack.

The *Jeletzkytes nebrascensis* microconch (***Figure 19***), shows a rip or tear with a subsequent rupture in the same general area as the tear. It is probable that this animal was perhaps ripped open by the teeth of the fish and then managed to escape and repair its shell.

Ed Gerken

Figure 18

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Figure 19

Body Piercing Predation

The second most common break to the shell of the scaphite is a peculiar puncture in the middle of the flank as seen in the *Hoploscaphites* and *Discoscaphites* of the Fox Hills Formation (***Figure 20***). From that same lot of 57 scaphites, six scaphites had these bizarre hole in their sides. Radwanski (1996) was convinced that similar holes in the flanks of some *Hoploscaphites* from Nasilow, Poland were caused by large crabs. Although Radwanski recovered parts of large unidentified crabs from above the zone of *Hoploscaphites*, he failed to note if any large decapod parts were recovered from the same horizon as the ammonites (it is believed there were not). It would seem reasonable to assume that predatory decapods would have broken the shell up into much smaller pieces, and probably completely destroyed the body chamber in an attempt to remove the meaty cephalopod parts located inside of the shell.

Ed Gerken

Figure 20

The holes punctured into the body chambers of the shell are initially perplexing. The damage is often only on one side, although sometimes the hole will go all the way through. When the hole is punctured all of the way through the shell, there is a large hole on one side, and a small hole on the other side. It is probable that this type of injury is indicative of a tooth or teeth of a vertebrate, and it seems unlikely that an invertebrate could have caused this type of injury. The holes caused to the shell are similar to the shape of the holes noted by Kesling and Kauffman (1963) and also illustrated by Larson (1999), that were determined to be from a large reptile. It is not too far fetched to assume that many of these holes could also be from fish. Fish often follow the shoals of extant squids and get into a feeding frenzy on them while the squids spawn (Norman, 2000).

It is uncommon to find ammonites that survived the 'body piercing' attacks, but the *Jeletzkytes spedeni* (***Figure 21***), and the *Hoploscaphites nicolletii* (***Figure 22***), display a blister on the mid flank that could indicate a pierce at an earlier time. The *Jeletzkytes spedeni* (***Figure 21***) also shows some distortion on the venter of the ammonite, implying that this specimen was perhaps bitten by a larger vertebrate, possibly a fish, and escaped for a time. The broken aperture suggests that this ammonite did not survive a second head on attack.

Ed Gerken **Figure 21**

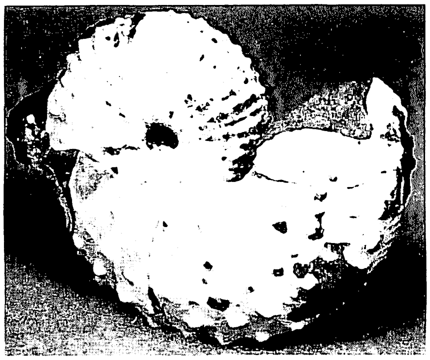
Neal A. Larson **Figure 22**

Frontal Assault Predation

The third type of shell damage noted is breakage or damage to the aperture as seen in the *Discoscaphites gulosus* macroconch (***Figure 23***). From the above mentioned lot of 57 ammonites, there were two scaphite specimens that featured this type of affliction. Ward (1988) related how male *Nautilus* will fight and bite on each other's aperture. This apparent type of damage could be directly caused by a head to head confrontation of the scaphite with either another ammonite or perhaps a fish. Damage in a frontal assault can be minute, with only small pieces of the aperture missing, or there can be a large amount of damage with much of the aperture and some of the phragmocone gone. The *Hoploscaphites nicolletii* in ***Figure 24*** shows massive damage to the phragmocone, near the aperture, caused by a frontal attack by a larger animal.

Ed Gerken **Figure 23**

Neal A. Larson **Figure 24**



Ed Gerken **Figure 25**

This *Discoscaphites gulosus* (***Figure 25***), demonstrates a deep healed bite to the front of the ammonite in the aperture region. The broad 'V' wound indicates biting by either a fish or another scaphite. This ammonite also suffered a second fatal bite to its 'blind spot', perhaps as a result of being handicapped and slowed down from an earlier attack that it had already healed from.

A surprisingly large numbers of scaphites show shell repair that is reflected as a long scar or as a groove on the flank or the venter of the body chamber such as on the *Jeletzkytes spedeni* (***Figure 26***). These scars are probably the result of an apertural injury, inflicted deep into the mantle, that occurred long before the scaphite reached maturity. Because the mantle was so badly damaged in this specimen, all of the shell that the ammonite created following the injury is shown as extreme disfigurement on the venter.

Ed Gerken **Figure 26**

Multiple Bites

The remainder of the 57 scaphite specimens, from the before mentioned lot, contained nine scaphites with holes and breaks in various places in the body chamber and the phragmocone, and 24 mostly complete or nearly complete shells. ***Figure 27*** shows a *Jeletzkytes nodosus* (not from that lot) that exhibits several bites to its phragmocone and a healed injury on its body chamber. Any ammonite with severe damage to its phragmocone would have become waterlogged and died because it would be unable to repair its phragmocone, and would have sunk to the bottom of the ocean.

The *Jeletzkytes spedeni* in ***Figure 28*** shows multiple injuries to its shell. The bubble on the phragmocone is the result of a rupture, probably from a bite, that happened when the animal was much younger and that portion of the shell was still a part of its body chamber. The rupture was probably located near the dorsal retractor muscle attachment site at the time of the injury. It also shows some major repair about midway on the body chamber, maybe from about the same time as the previous injury when this place may have been near the animal's aperture.

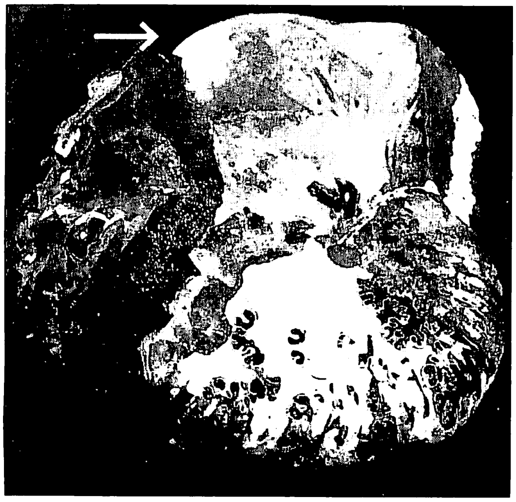
A *Hoploscaphites nicolletii* (***Figure 29***) showing multiple injuries, but at different times in the animal's life. The first injury is shown as a swelling or blister on the body chamber, and the second by a large gaping hole directly beside it. Another ammonite, *Jeletzkytes nebrascensis* (***Figure 30***) also shows two different injuries; one that was not fatal and left a scar in middle of the flank from a deep injury to the mantle, and another fatal back biting hole. Perhaps ammonites that had managed to survive one attack were slower, or somewhat crippled, and thus more susceptible to further attacks.

Neal L. Larson

Figure 27

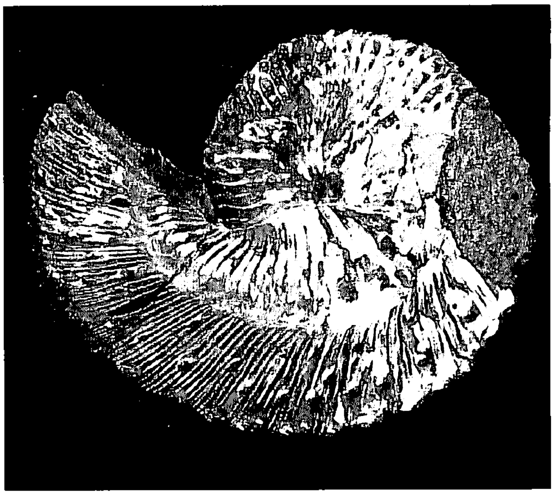
Neal A. Larson

Figure 28



Neal A. Larson

Figure 29



Neal A. Larson

Figure 30

Crushing

Several ammonites have a characteristically crushed look to them. While most crushed ammonites suffered this fate upon or after death, some others were not quite so lucky. ***Figure 32*** shows a *Jeletzkytes nodosus* that has its shell broken up and partially displaced, possibly from a predator. Some scaphites exhibit bent or distorted venters, such as the *Hoploscaphites comprimus* microconch (***Figure 31***). Specimens like this may, in fact, have been bitten by turtles or perhaps some other toothless animal, and managed to escape.

Ed Gerken ***Figure 31***

Neal A. Larson ***Figure 32***

Neal L. Larson ***Figure 33***

A *Hoploscaphites comprimus* (***Figure 33***) shows the remarkable ability to heal from a crushing injury. Note how the ribs of the shell are at different angles to each other, and the smooth shell in between some of the rib sections. This ammonite was apparently crushed, as an adult, and as its injuries were repaired, it resorbed some of its shell hiding the obvious shell damage. Scaphites depicted as having 'Mortons Syndrome' (Landman and Waage, 1986), with distorted and bent venters, are possibly scaphites that survived being crushed by a turtle or some other animal.

The remaining types of scaphite breakage and fragments show almost no regularity. This type of behavior would be consistent with a fish or a reptile going for as much as it can get, as fast as it can. This voracious eating would consume vast quantities of ammonites, though probably not the entire shell. Such table manners would explain the abundant fragments of ammonites, like portions of body chambers or only phragmocones, that are so often found in the fossil record.

Miscellaneous

Numerous other types of pathologies are present in scaphites and other ammonites and many of these were probably not life threatening. The apparent loss of a portion of a phragmocone could have resulted in a rapid growth spurt to try and maintain neutral buoyancy, this would have been reflected in a wider spacing of the septa. Closely spaced septa, in an adult ammonite, mean sexual maturity and an end to growth. Many specimens of ammonites, especially some individuals within the very aberrant genera (*Didymoceras*, *Baculites*, etc.), often show a growth spurt after apparent maturity. This rapid growth could be the result of damage to, or a partial loss of, the phragmocone.

The unusual circumstances concerning dwarfism and giantism are common within the Family Scaphitidae, but seem to be the result of environment and genetics instead of injury. Deformities caused by parasites and other symbionts are unusual and very rare in the Scaphitidae, although they are common in some other Families of ammonites. Other deformities to scaphites that may be a result of their environment are very rare, and are not reported in this paper.

There are dozens of references regarding healed and unhealed pathologies in other types of ammonites. Many of these publications date back to 1824, but only a few of them are written in English. Perhaps the greatest investigator and researcher of pathological ammonites is Helmut Keupp, his papers and books document more pathologies, of almost every kind, than from any other author. The bibliographies in Hengsbach (1996) and in Keupp (2000) are recommended to the reader for further reading and to find more references regarding ammonite pathologies.

Mass Mortality Layers

Scientists worldwide use mass mortality horizons of ammonites as biostratigraphic guides. Because ammonites were extremely abundant, they changed rapidly to adapt to environmental demands, and they are relatively easy to identify and distinguish, they make a perfect fossil for this use. Some species of ammonites from the Western Interior are so widespread that they are found in Europe, Asia, and South America. Ammonites serve as perfect index fossils to correlate formations and ages across continents and oceans.

The occurrence of these extensive horizons most often containing only one species of ammonites has perplexed geologists for generations. Some geologists and paleontologists have suggested that these deaths could be the result of mass suffocation caused by periodic up-welling of anoxic bottom water, storm generated toxic clouds from the deep anaerobic zone (Maeda and Seilacher,1996), volcanic activity, red tide, change in water salinity, or variations in water temperature (Kennedy and Cobban, 1976).

The obvious answer, however, may lie with natural events that occur annually with modern squids. Squid and octopus are animals whose motto is to live fast and die young. Most squids, cuttlefish, and octopods live only an average of one to two years. Even the giant *Architeuthis* may live only as long as five years (Gauldie et al., 1994). The reason that these animals die so young, and often "en mass", is due to death after the natural act of spawning, similar to the mass deaths of salmon and many other marine organisms. Many species of extant cephalopods get together every year at certain times and at certain places to lay and fertilize their millions of eggs, and then die. Only a few individuals seem to manage to avoid their bodies' natural response to breed and die. Each year along the coast of California and other locations worldwide, miles and miles of coastline are covered with the millions of dead carcasses of squids that died after spawning (Norman, 2000).

Perhaps these unexplained mass mortality layers of ammonites, that provide us with different ammonite zones, were merely mass spawning deaths. The occurrence of such large horizons or zones of individual species and often primarily macroconchs (female) of *Baculites*, *Didymoceras*, and *Hoploscaphites* etc. from the Western Interior, and other similar ammonite mass mortality layers from around the world would then be understandable. They are simply the remains of marine cephalopods that lived, bred, reproduced, and then died, in enormous numbers after spawning. ***Figure 34*** shows an assemblage of macroconchs (*Hoploscaphites nicolletii*) in a portion of a concretion from the *Hoploscaphites nicolletii* Range Zone, Fox Hills Formation, north central South Dakota. This death assemblage is so extensive that Waage (1968) calculated that this individual *Hoploscaphites nicolletii* zone contained the remains of about 20 million of these specimens in only a 20 square mile area. This accumulation of macroconchs suggests that like their extant relatives, these ammonites probably got together by the millions, spawned, and died soon after that.

Ed Gerken

Figure 34

Conclusions

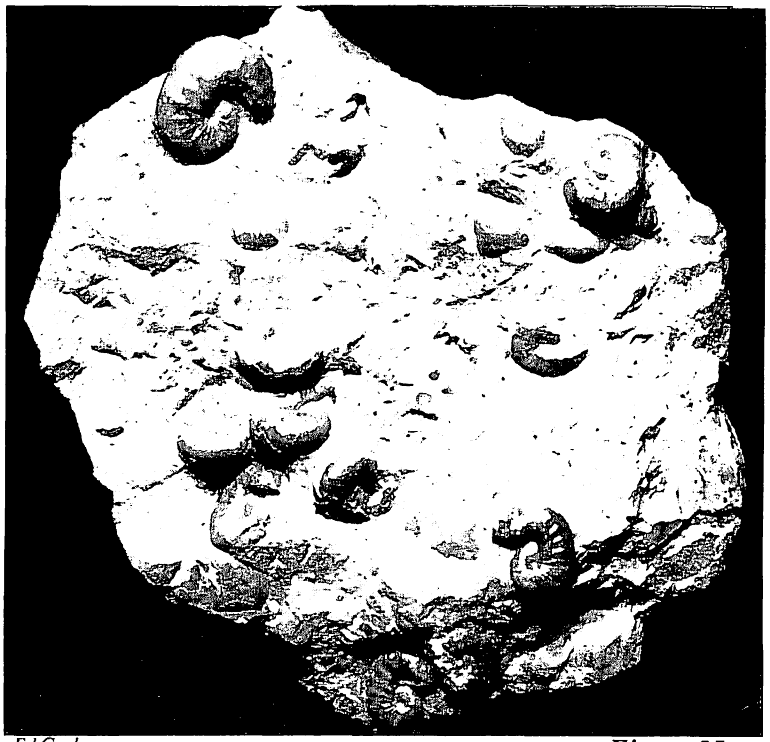
Ammonites were predatory cephalopods that filled many different ecological niches in the ancient seas. While some ammonites were probably swift and somewhat able to compete with fish and squids for food, others may have been much slower, relying on plankton or scavenging for food. The Scaphitidae were probably much faster than *Nautilus*. With a larger body chamber to phragmocone ratio, they had more capacity for intake and ejection of water during propulsion and should have been able to have bursts of speed somewhere between *Nautilus* and extant squids.

Ammonites, like modern cephalopods, must have required a high calcium diet. To satisfy this need, they fed on crabs, lobsters, echinoids, mollusks, and possibly fish. Ammonites were also a major food source for larger cephalopods and vertebrates, and their carcasses fed the scavengers that lived on the ocean bottoms. Some researchers have thought that crabs and lobsters preyed upon ammonites, but only rarely do decapods prey on living cephalopods, and it is doubtful that a quick, mobile, living ammonite would have often been the prey of these bottom dwelling, clawed crustaceans.

As more collectors realize how to distinguish the jaws, radula, and muscle attachments of the ammonites, we will better understand these animals and their relationships to the modern cephalopods. Perhaps some day, we will be able to distinguish the individual species of ammonites by differences in their jaws, in the same manner that some modern cephalopod biologists can identify the extant species. We may be able to calculate the ammonite's propulsion speed by their muscle scars, their placement on the body chamber, and the size of the body chamber with relationship to the rest of the shell.

Scaphites had an amazing recuperative proficiency, reflected in the almost elastic capabilities of the mantle. In one scaphite horizon, nearly 40% of their preserved shells show some signs of healed pathologies. Most pathologies seem to have been caused by injuries related to predation, fighting, or mating. The absence of obvious breaks or cracks in the shell suggest that the ammonite could partially resorb some of the shell around the injury while it was rebuilding its shell, thus hiding the sharp edges of the broken shell and creating a smooth transition from the undamaged shell to the rebuilt shell.

Extensive Range Zones of different ammonite species have been identified throughout the Paleozoic and Mesozoic marine rocks of the world. These large horizons of dead ammonites represent the mass spawning deaths from the different species of ammonites, which would be consistent with the mass spawning deaths of many species of squids in the oceans of the world today.



Ed Gerken

Figure 35

Mass mortality of *Scaphites whifieldi*
Turner Sandy Member, Carlile Shale; Turonian, Late Cretaceous; South Dakota

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I thank Dr. W. A. (Bill) Cobban, and Dr. Neil H. Landman for their editorial comments, and the knowledge they have shared as they answered my sometimes foolish and often many questions about ammonites. I also thank Peter L. Larson, Steven D. Jorgensen, Robert A. Farrar, Peter Harries, and Marion K. Zenker for their critical and editorial reviews. I thank the dozens of ammonite collectors from my area who have been so kind as to save the pathological specimens for research. All of the specimens photographed in this manuscript are in the Black Hills Institute of Geological Research's permanent research collection and will be reposited in the Black Hills Museum of Natural History.

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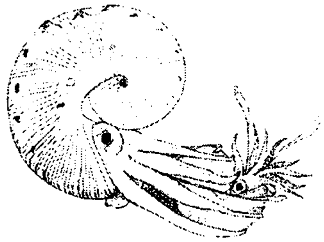


Ammonoids - The Front-Running Time Setters

by

Brian F. Glenister

Department of Geoscience, University of Iowa

Ammonoids are an extinct group of shelled organisms related to abundant living Cephalopoda such as the Pearly *Nautilus*, squid and octopus. They appeared 410 million years (m.y.) before the present, near the base of the Devonian interval of geological time, and diversified as one of the most abundant groups of shelled fossils for the following 350 m.y.

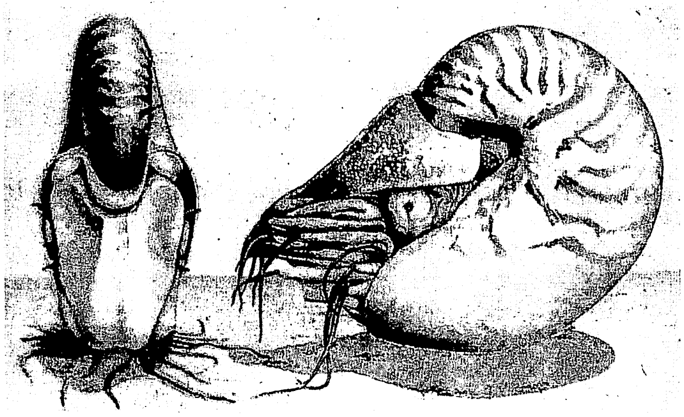


Figure 1. Drawing of Pearly *Nautilus*.

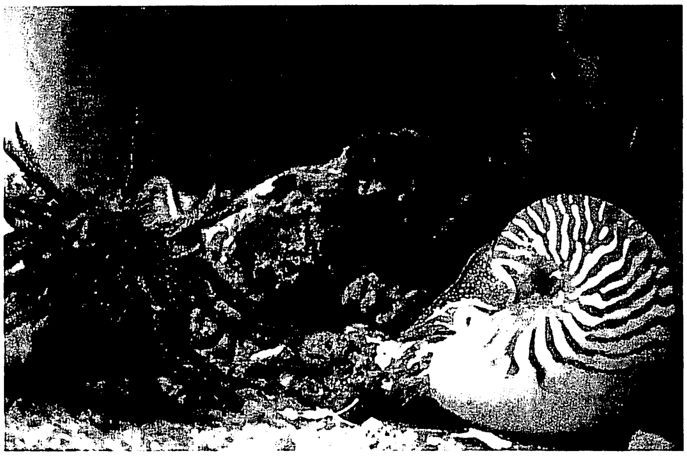


Figure 2. Live *Nautilus* in laboratory tank (Indonesia, 1964).

The group came near to extinction 250 m.y. ago, coincident with the demise of many other organisms across the Permian/Triassic time boundary, but later diversified again before final extinction across the Cretaceous/Tertiary boundary at 65 m.y.

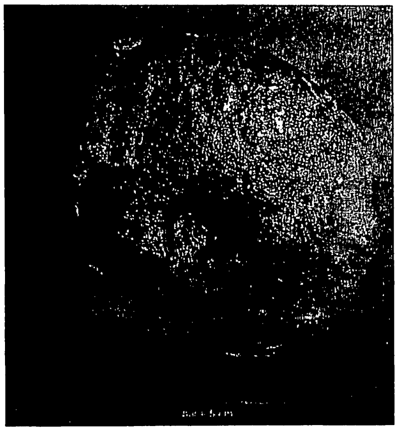


Figure 3. Permian ammonoid, *Cyclolobus oldhami*, Salt Range, Pakistan

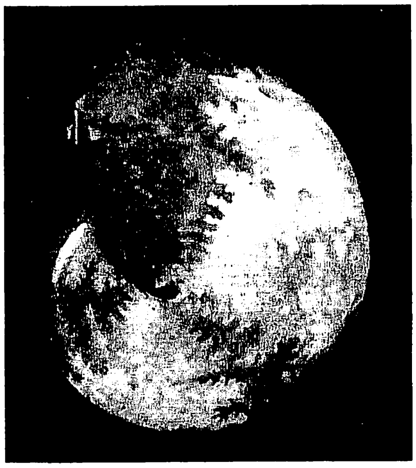


Figure 4. Triassic ammonite, *Arcestes* sp., Tyrol, Austria

Like modern *Nautilus*, ammonoids were free-swimming organisms that maintained balance and neutral buoyancy by adjusting the percentage of gas and liquids in connected chambers constructed successively at the base of the body chamber by transverse shell partitions known as septa. The line of contact of each septum on the inside of the shell is termed the suture line. During individual growth (ontogeny), as well as evolution through time, the septa became progressively more crenulate to provide increasingly complex suture lines. These sutural patterns allow us to recognize the stage of evolution, and hence the geological age of the parent sediment (see Examples 1, 2). An important additional attribute is that ammonoid shells commonly became buoyant after death and the decay of the soft tissue, so that they were transported by ocean currents into environments beyond their original habitats. This enhances the potential for paleontologists to use them for biostratigraphic correlation.

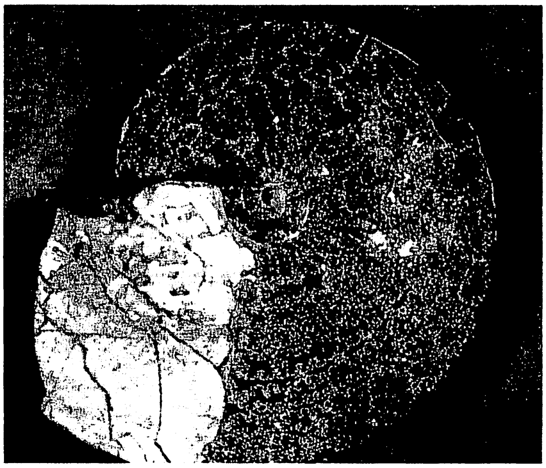


Figure 5. Cretaceous ammonite, *Placenticeras intercalare*, Pierre Shale, South Dakota

In summary, ammonoids were a rapidly evolving, diverse and abundant group of organisms that provide us with an almost uniquely precise basis for recognition of geologic age of sediments throughout much of geologic time.

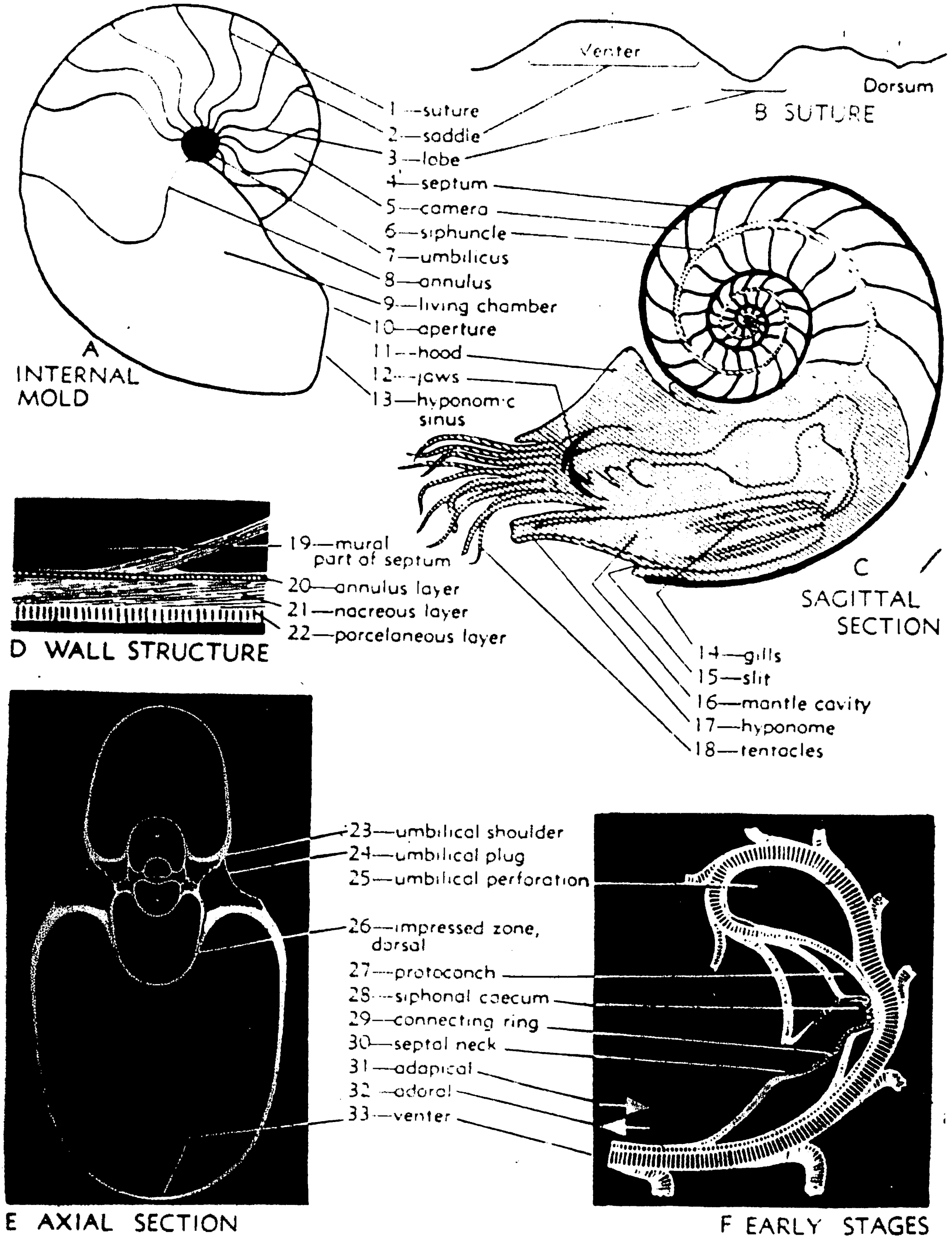
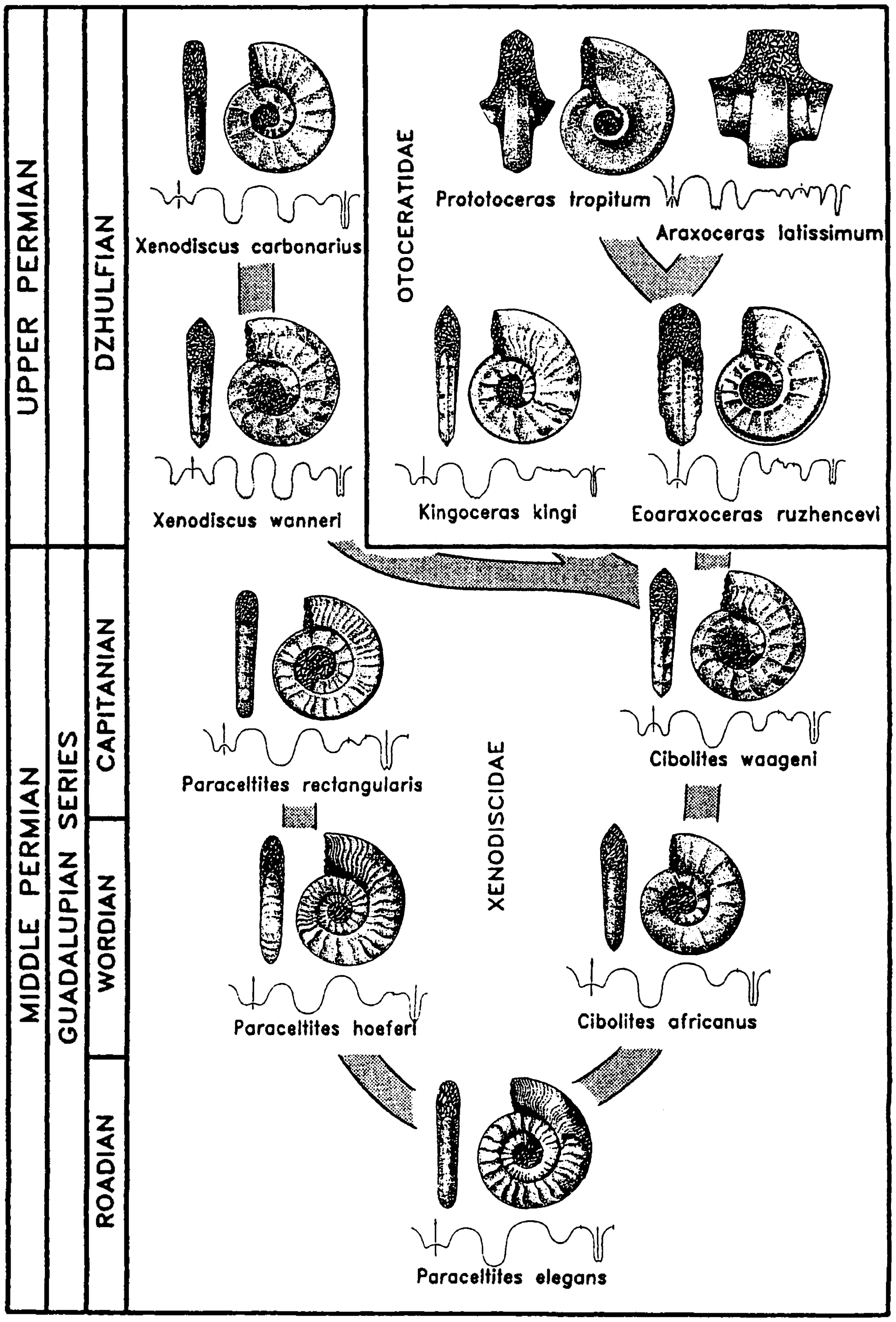
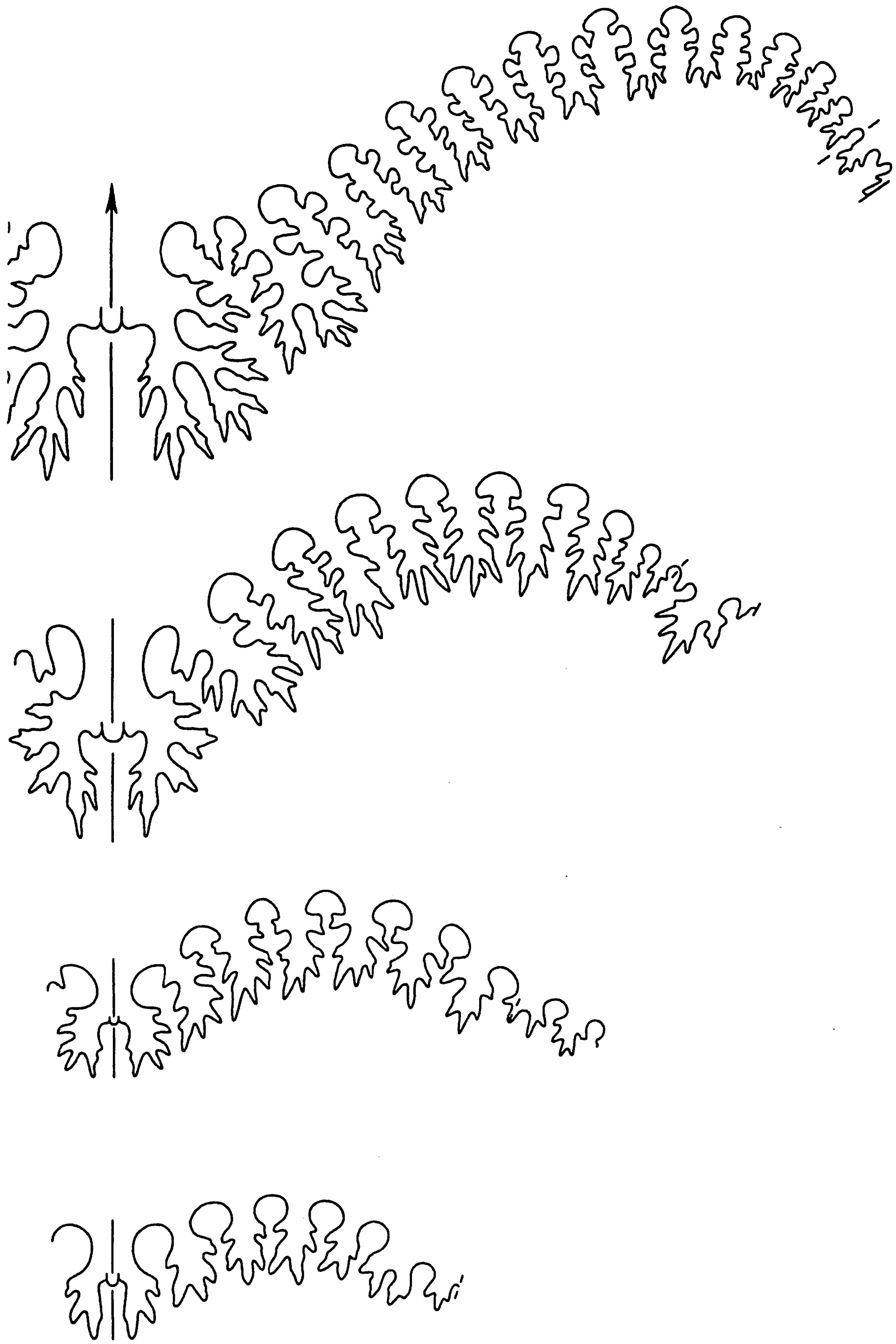


Figure 6. Morphology of a cephalopod.



Example 1. Evolution of a superfamily of ammonoids (Otoceratoidea) through 50 m.y., from the Middle Permian through Early Triassic. Note the progressive changes in sutural pattern, including increase in number of lobes and change from smooth to digitate lobe bases. Whorl cross-sections and coiling also undergo significant change. (Smithsonian Contributions to the Earth Sciences no. 32, 2000, co-authored Glenister and former advisee, colleague Professor Claude Spinosa).



Example 2. External sutures of an ammonoid family (Cyclolobidae) through 25 m.y., from basal Middle Permian (base) through Upper Permian (top). Note progressive increase in number of lobes and degree of digitation, reflecting changes in septal geometry (Treatise on Invertebrate Paleontology Revision Volume manuscript, co-authored by Glenister and Chinese colleague Zhou Zuren).

Multi-Episodal Extinction and Ecological Differentiation of Permian Ammonoids

by Zuren Zhou (1), Brian F. Glenister (2), William M. Furnish (2) and Claude Spinosa (3)

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(a newsletter of the Subcommission on Permian Stratigraphy)

Introduction

Biotic changes across the Permo-Triassic boundary have been noted for over one and one-half centuries, and constitute the basis of delimitation of the Paleozoic and Mesozoic eras. However, several recent papers have suggested that a comparable mass extinction characterizes the end of the terminal Middle Permian Capitanian Stage [Guadalupian (or Maokouan) Series]. This "double mass extinction" has been reputed to apply to ammonoid distributions, with generic extinction rates of 94.6% and 95.2% attributed respectively to the end-Guadalupian (Maokouan) and end-Permian (Changhsingian Stage) of South China (Yang Fengqing, 1991). Data we have compiled for the forthcoming Paleozoic Ammonoid Revision volume of the Treatise on Invertebrate Paleontology (Glenister et al., manuscript) confirm the mass extinction across the Erathem boundary. However, when taxonomic revisions are provided in relation to world-wide occurrences and the refined chronostratigraphic standards, the end-Capitanian extinction is recognized as comparable in intensity to those of the other Permian *stage* boundaries, and unlike the end-Paleozoic mass extinction. The purpose of the present report is to document the summary distribution data upon which these interpretations are based. A full analysis will be provided in a forthcoming publication.

Data Quality

Taxonomy. – Evaluation of the biologic validity of the ammonoid taxonomy that we have developed cannot be pursued adequately until publication of the Paleozoic Ammonoid Treatise revision. However, it is appropriate to note that the authors are active specialists from China and North America who have benefited from generous advice and assistance of other ammonoid specialists, particularly those from Russia, Europe and Canada. With this collaboration, the taxonomy should be of higher quality than in previous presentations, many of which were non-specialist generalizations from the literature.

Chronostratigraphy. – Members of the Subcommission on Permian Stratigraphy (SPS) have been aggressively involved for two decades in selection and additional study of the most promising sequences, world-wide, for standardization of the subdivisions of Permian time. Recent contributions in *Permophiles*, including results of formal votes of SPS Titular Members, suggest that international consensus (Fig. 1) is close to achievement. Without unnecessary digression into detailed review, two of many recent examples of inadequacy of stratigraphic control for extinction documentation can be cited: 1) use of the entire Maokouan (Guadalupian: Roadian, Wordian and Capitanian stages) interval (Yang Fengqing, 1991), and 2) adoption of the Tatarian as reference for the whole of the post-Guadalupian Lopingian Series (Stanley and Yang, 1994), comprising Wuchiapingian and Changhsingian stages.

Although the standard chronostratigraphic subdivisions that we are employing appear to be the most realistically useful choice, some limitations remain. Firstly, the duration of individual standard subdivisions of Permian time are still uncertain: only a few reliable radiometric ages ("tie points") are available for the entire System (upper and lower boundaries, plus one or two internal boundaries), and other ages are based on stratigraphic inference (Ross et al., 1994).

Consequently, duration of stages will inevitably be somewhat unequal. Additionally, the entire post-Artinskian pre-Roadian interval (Fig. 1) is considered herein as Artinskian sensu lato, based on inadequacy of the Kungurian stratotype and the general similarity of Kungurian ammonoids to those of the Artinskian sensu stricto.

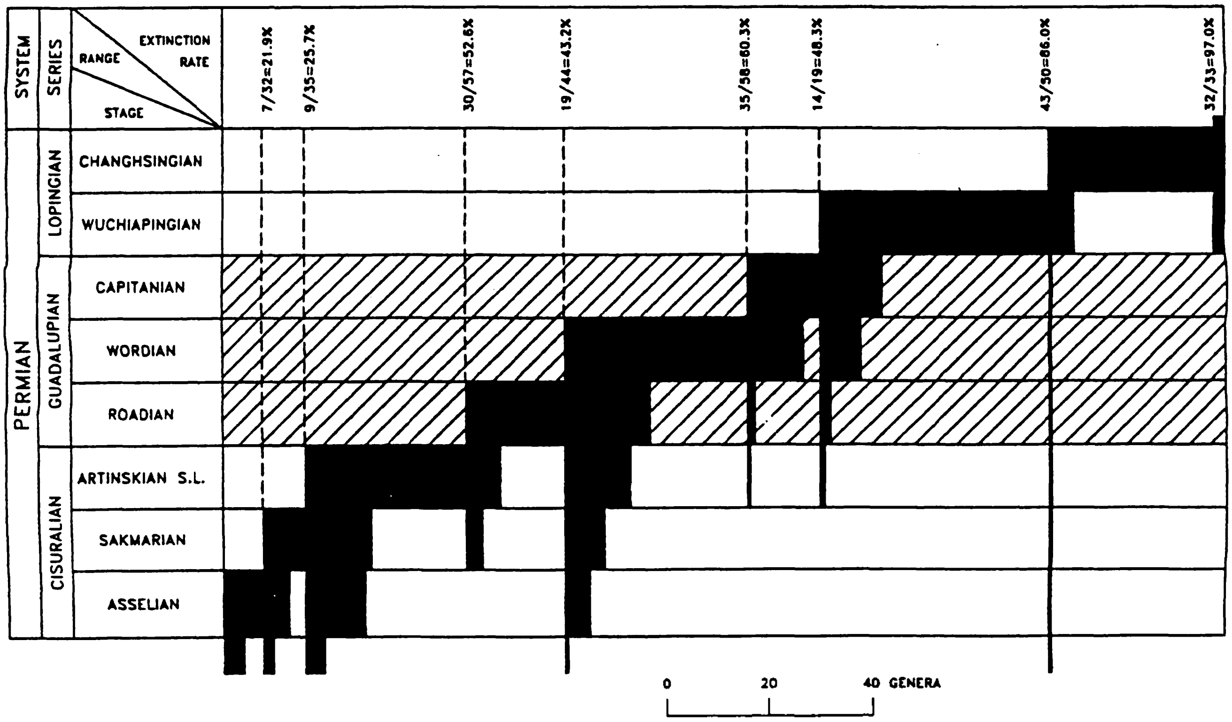

Figure 1. Geochronologic ranges and extinction rates for genera of Permian ammonoids.

Geographic Coverage. – Mass extinctions such as that at the Erathem boundary are by definition global in extent. In compiling our ammonoid distributions (Tbl. 1), we have utilized all available lines of biostratigraphic as well as non-biologic evidence to afford precise world-wide chronostratigraphic correlation of different ecologic provinces. Reliance on a singe area, such as South China (Yang Fengqing, 1991) invites misinterpretation of regional extinction as equivalent to the mass extinction phenomenon that characterizes the end of the Permian.

Multi-Episodal Permian Ammonoid Extinctions

Taxonomy and chronostragraphic distribution of the 190 genera of Permian ammonoids recognized in the Treatise revision are represented in Table 1. Generic originations and extinctions are summarized (Fig. 1), at the stage level, for the 8 primary subdivisions of the Permian System. Since world-wide ranges cannot generally be refined within stage boundaries, all originations and extinctions are represented as occurring at these

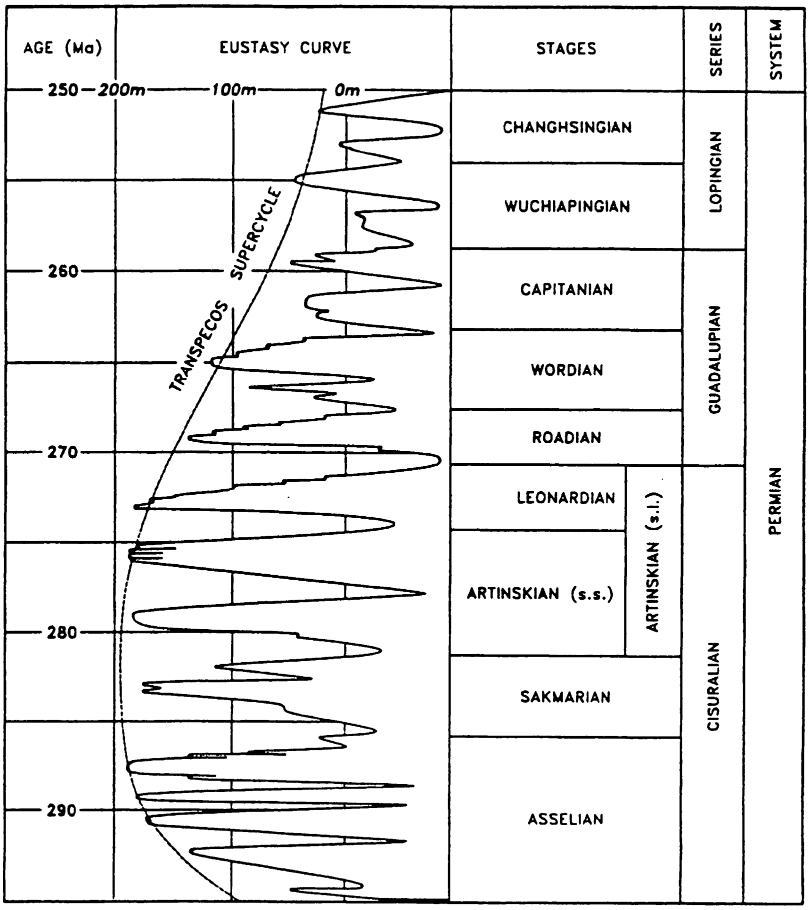

Figure 2. Eustacy curves related to international standard subdivisions of the Permian System. Overall regression that characterizes the upper part of the Transpecos Supercycle broadened restricted seas and resulted in increase in the number of short-ranging endemic ammonoid genera (modified after Ross and Ross, 1994).

boundaries; consequently, the stepped occurrence pattern to some extent represents stage boundaries rather than strictly isochronous changes in distribution. Black blocks portray the ranges of genera, and the width of each is in direct proportion to the number of genera represented. Genera that became extinct in each stage are grouped into two categories. Those with relatively short ranges (no greater than one stage) are arranged on the right side of the stage-level distribution plots, whereas those with ranges of two or more stages are plotted on the left. Numbers of genera that became extinct in each stage, divided by total numbers present are expressed at the top as percentage extinction rates. The following basic characteristics of Permian ammonoid extinctions can then be recognized:

1) Extinctions were probably episodic, although this appearance of periodicity is enhanced by the practical necessity of recording ranges at stage level. However, note that Permian stage boundaries correspond approximately to major lowstands of sea level (Fig. 2); this eustatic cyclicity inevitably contributed in turn to originations and extinctions.

2) Rates of extinction increased spectacularly throughout the Permian.

3) There is no global peak at the end of the Capitanian in either the absolute number of genera becoming extinct or the generic level extinction rate. In fact, rates are higher in the preceding Wordian (60%), and markedly so in the succeeding Wuchiapingian Stage (86%). No "double mass extinction" is recognizable.

4) It has been contended elsewhere (Zhou, 1986) that short-ranging genera of Permian ammonoids tend to be characterized by bizarre and diverse morphologies and occurred in ephemeral epicontinental "Restricted-Seas", whereas long-ranging genera generally displayed standardized morphology and favored "Open-Sea" environments. Increase in the number of short-ranging genera (Fig. 1; see Roadian/Wordian boundary) coincides with the regressive (low sea) terminal phase of the Transpecos Supercycle (Ross and Ross, 1994; see Fig. 2 herein).

5) Episodes of Permian ammonoid extinction appear to coincide with regressions of the third-order eustatic cycles, whereas Carboniferous/Permian boundary originations and Permian/Triassic extinctions relate in a general way to the second order Transpecos Supercycle (Fig. 1, 2).

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Table 1. Geochronologic ranges of Permian ammonoid genera.

	PERMIAN								SYSTEM
	CISURALIAN			GUADALUPIAN			LOPINGIAN		SERIES
	ASSELIAN	SAKMARIAN	ARTINSKIAN S.L.	ROADIAN	WORDIAN	CAPITANIAN	WUCHIAPINGIAN	CHANGHSINGIAN	STAGE / GENUS
—	—								*Emilites*
—	—								*Glaphyrites*
—	—								*Neoglaphyrites*
—	—								*Aristoceras*
—	—								*Mescalites*
	—								*Protopopanoceras*
	—								*Shikhanites*
—	—	—							*Boesites*
—	—	—							*Daixites*
—	—	—							*Prothalassoceras*
	—	—							*Andrianovia*
	—	—							*Svetlanoceras*
	—	—							*Juresanites*
	—	—							*Tabantalites*
		—							*Propopanoceras*
		—							*Synuraloceras*
—	—	—	—						*Somoholites*
—	—	—	—						*Artinskia*
—	—	—	—						*Metapronorites*
—	—	—	—						*Neopronorites*
—	—	—	—						*Cardiella*
	—	—	—						*Akmilleria*
	—	—	—						*Paragastrioceras*
—	—	—	—						*Almites*
—	—	—	—						*Kargalites*
	—	—	—						*Sakmarites*
	—	—	—						*Properrinites*
		—	—						*Uraloceras*
			—						*Miklukhoceras*
			—						*Metaperrinites*
			—						*Darvasiceras*
			—						*Artioceras*
			—						*Neouddenites*
			—						*Pseudohalorites*
			—						*Zhonglupuceras*
			—						*Lianyuanoceras*
			—						*Epijuresanites*
			—						*Tumaroceras*
			—						*Gaetanoceras*
			—						*Eothinites*
			—						*Suakites*
			—						*Pamiritella*
			—						*Neoshumardites*
			—						*Veruzhites*
			—						*Pseudoemilites*
			—						*Artioceratoides*
		—	—	—					*Stenolobulites*
		—	—	—					*Synartinskia*
		—	—	—					*Eohyattoceras*
		—	—	—					*Sverdrupites*

PERMIAN								SYSTEM
CISURALIAN			GUADALUPIAN			LOPINGIAN		SERIES
ASSELIAN	SAKMARIAN	ARTINSKIAN S.L.	ROADIAN	WORDIAN	CAPITANIAN	WUCHIAPINGIAN	CHANGHSINGIAN	STAGE / GENUS
		—	—					*Perrinites*
		—	—					*Popanoceras*
		—	—					*Bransonoceras*
		—	—					*Pseudoschistoceras*
			—					*Aulagastrioceras*
			—					*Texoceras*
			—					*Chekiangoceras*
			—					*Daubichites*
			—					*Spirolegoceras*
			—					*Tongluceras*
			—					*Glassoceras*
			—					*Peritrochia*
			—					*Aulacaganides*
			—					*Yinoceras*
			—					*Guiyangoceras*
—	—	—	—	—				*Agathiceras*
—	—	—	—	—				*Martoceras*
—	—	—	—	—				*Daraelites*
—	—	—	—	—				*Crimites*
—	—	—	—	—				*Sicanites*
—	—	—	—	—				*Prostacheoceras*
	—	—	—	—				*Thalassoceras*
	—	—	—	—				*Medlicottia*
	—	—	—	—				*Metalegoceras*
		—	—	—				*Aricoceras*
		—	—	—				*Propinacoceras*
		—	—	—				*Parapronorites*
		—	—	—				*Clinolobus*
		—	—	—				*Bamyaniceras*
			—	—				*Demarezites*
			—	—				*Paratongluceras*
			—	—				*Liuzhouceras*
			—	—				*Pseudovidrioceras*
				—				*Kurdiceras*
				—				*Newellites*
				—				*Sosioceras*
				—				*Tauroceras*
				—				*Adrianites*
				—				*Doryceras*
				—				*Neoaricoceras*
				—				*Palermites*
				—				*Pseudagathiceras*
				—				*Sizilites*
				—				*Sosiocrimites*
				—				*Hoffmannia*
				—				*Aristoceratoides*
				—				*Epithalassoceras*
				—				*Epiglyphioceras*
				—				*Jilingites*
				—				*Lanceoloboceras*

PERMIAN								SYSTEM
CISURALIAN			GUADALUPIAN			LOPINGIAN		SERIES
ASSELIAN	SAKMARIAN	ARTINSKIAN S.L.	ROADIAN	WORDIAN	CAPITANIAN	WUCHIAPINGIAN	CHANGHSINGIAN	STAGE / GENUS
		—	—	—	—			*Neocrimites*
			—	—	—			*Shengoceras*
				—	—			*Waagenoceras*
				—	—			*Mexicoceras*
				—	—			*Shouchangoceras*
				—	—			*Elephantoceras*
				—	—			*Erinoceras*
				—	—			*Sangzhites*
				—	—			*Paramexicoceras*
				—	—			*Shangraoceras*
				—	—			*Mongoloceras*
				—	—			*Nielsenoceras*
					—			*Xenaspis*
					—			*Angrenoceras*
		—	—	—	—	—		*Hyattoceras*
		—	—	—	—	—		*Eumedlicottia*
			—	—	—	—		*Paraceltites*
				—	—	—		*Roadoceras*
				—	—	—		*Neogeoceras*
				—	—	—		*Strigogoniatites*
				—	—	—		*Epadrianites*
				—	—	—		*Cibolites*
				—	—	—		*Altudoceras*
					—	—		*Kingoceras*
					—	—		*Syrdenites*
					—	—		*Timorites*
					—	—		*Difuntites*
						—		*Sundaites*
						—		*Doulingoceras*
						—		*Paedopronorites*
						—		*Epitauroceras*
						—		*Nodosageceras*
						—		*Rotaraxoceras*
						—		*Discotoceras*
						—		*Urartoceras*
						—		*Pseudotoceras*
						—		*Vescotoceras*
						—		*Dzhulfoceras*
						—		*Vedioceras*
						—		*Avushoceras*
						—		*Planodiscoceras*
						—		*Leptogyroceras*
						—		*Fengchengoceras*
						—		*Lenticoceltites*
						—		*Anderssonoceras*

PERMIAN								SYSTEM
CISURALIAN			GUADALUPIAN			LOPINGIAN		SERIES
ASSELIAN	SAKMARIAN	ARTINSKIAN S.L.	ROADIAN	WORDIAN	CAPITANIAN	WUCHIAPINGIAN	CHANGHSINGIAN	STAGE / GENUS
						—		*Xiangulingites*
						—		*Pericarinoceras*
						—		*Pachyrotoceras*
						—		*Araxoceras*
						—		*Prototoceras*
						—		*Periptychoceras*
						—		*Anfuceras*
						—		*Eoaraxoceras*
						—		*Konglingites*
						—		*Jinjiangoceras*
						—		*Kiangsiceras*
						—		*Sanyangites*
—	—	—	—	—	—	—	—	*Neoaganides*
						—	—	*Stacheoceras*
						—	—	*Pseudogastrioceras*
						—	—	*Huananoceras*
						—	—	*Xenodiscus*
						—	—	*Cyclolobus*
							—	*Changhsingoceras*
							—	*Dzhulfites*
							—	*Shevyrevites*
							—	*Abichites*
							—	*Iranites*
							—	*Phisonites*
							—	*Paratirolites*
							—	*Rongjiangoceras*
							—	*Liuchengoceras*
							—	*Tapashanites*
							—	*Sinoceltites*
							—	*Pseudostephanites*
							—	*Mingyuexiaceras*
							—	*Pseudotirolites*
							—	*Chaotianoceras*
							—	*Schizoloboceras*
							—	*Dushanoceras*
							—	*Pachydiscoceras*
							—	*Trigonogastrites*
							—	*Pernodoceras*
							—	*Longmenshanoceras*
							—	*Qinjiangoceras*
							—	*Rotodiscoceras*
							—	*Pentagonoceras*
							—	*Pleuronodoceras*
							—	*Qinglongites*
						—	—	*Episageceras*

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BACULITES:
Calamari On A Stick

What?!?

Yes. Baculites were essentially an octopus that had its mantle surrounded by a nacreous shell. Lewy (2002) makes a strong case that extant octopods are essentially nude ammonoids. Just imagine eight tentacles sticking out of a very long waffle cone next time you are in the ice cream shop!

The genus *Baculites* derives its name from the Latin "baculum" (staff) and "ites" (stone). Therefore, a Baculite is a "stone staff". The Family Baculitidae contains a total of nine recognized genera, one of which is the very common, and cosmopolitan, genera *Baculites.* Klinger and Kennedy (2001) list approximately 180 described species from worldwide localities. There are certainly many known species that have yet to be described, as well as many species that have yet to be discovered.

Baculites first appeared during the Turonian stage of the Late Cretaceous approximately 93 M.A. and they disappeared at the end of the Cretaceous. In the Western Interior of North America, the Baculite lineage consisted of approximately 45 species, each of which lasted for an average of 0.5 M.A.

The relatively short life span for each Baculite species makes them ideal as biostratigraphic index fossils, particularly in the Pierre Shale and equivalent-age strata throughout the Western Interior. Beginning in the Lower Campanian (approximately 82 M.A.), and extending up in to the Lower Maastrichtian (approximately 69 M.A.), a remarkable series of 18 endemic Baculite species are used as index fossils. The only biostratigraphic zones in the Upper Campanian that are not based on Baculites are the zones of the very distinctive ammonites *Didymoceras* (four species) and *Exiteloceras* (one species). All of these ammonite taxa are illustrated in Larson, et. al. (1997).

The largest Baculite species had adults that may have been well over five feet long. However, absolutely complete adult specimens are unknown. Whatever their ultimate adult size, all Baculites started out as a tiny coiled shell (ammonitella) approximately one millimeter in diameter at the time of hatching. After growing to about 1.5 coils, the shell of the Baculites became straight, or very nearly so. A few species do have very slightly curved shells. Buoyancy forces may have created a compressional force on the dorsum (top) of the shell and a tensional force on the venter (bottom) of the shell, and, thereby, possibly inducing a differential growth rate between the top and the bottom of the shell.

The viscera of the animal occupied the body chamber of the shell. As the body grew, the shell was lengthened as the mantle tissue secreted new shell on to the edge of the shell at the aperture. As the animal grew larger it became heavier (increased mass). The animal compensated for the added mass of the body and the shell by creating its own buoyancy compensation device.

The Baculites, and all other ammonites, periodically partitioned off the back of the body chamber to form a series of chambers. Each new chamber was initially filled with cameral fluid but the fluid was slowly drained from the chamber via osmosis through the siphuncle, a thin tube of living tissue that extends from the back of the body chamber all the way back to the first chamber in the ammonitella. The buoyancy of the evacuated chambers (they actually had a slight negative pressure) offset the mass of the animal and shell and allowed the entire system to be in equilibrium at neutral buoyancy. Unless the animal used its jet propulsion, the animal would virtually stay immobile.

The partitioning walls between each chamber of the phragmocone (the chambered portion of the shell vacated as the animal moved forward in the body chamber) are called septa. The intricately fluted edge of the septa can be seen when the nacreous shell is removed from the phragmocone. The suture lines formed where the septa contacted the inside of the shell. Contrary to popular urban legend, the suture pattern is not an absolute diagnostic feature for a species as it is common for related species to have very similar suture patterns.

A much more reliable method of identifying Baculite species is with the external shell morphology (ornamentation). The shape of the cross-section of the shell and the location and frequency of the ribbing are more diagnostic. Depending on the species, the shell cross-section many be round, oval, triangular or anything in between. Some species have not ribs whereas others can have ribs on the dorsum, the flank, and or the venter.

Just remember the ice cream cone.

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Biographical Profile

Steve is a Professional Geologist in Wyoming and Nebraska, a Professional Engineer (Civil) in Nebraska, a Certified Professional Geologist through the American Institute of Professional Geologists, and a member of the Geological Society of America. He is the current president of the Nebraska Geological Society and was the first president of the Western Interior Paleontological Society (WIPS) in 1985.

AMMONITES

By Stan Balducci

These extinct marine animals were cephalopods and are thus related to squids, octopus, cuttlefish, and the chambered nautilus. Ammonites were able to swim, thanks to the unique construction of their shell, which was divided into a series of air chambers. Fossils of ammonites are found all over the world.

As different species of ammonites lived during different time periods, scientists use these animals to determine the relative age of the rocks in which their fossils are found. Because ammonites lived exclusively in marine environments, their presence also indicates the location of ancient seas.

There were about 7,500 species of ammonites that lived during the later Paleozoic and Mesozoic eras. Ammonites were so numerous during the Cretaceous period that they are referred to as the "fish" of the Cretaceous oceans. Ammonites varied in size from one to two inches in diameter to about six feet in diameter.

Ammonoids (the order to which ammonites belong) differ from nautiloids, another marine animal that lived during the same time, most conspicuously in the nature of the sutures (the junction of continuous parts), which in ammonoids are folded into complex patterns. Ammonoids also differ from nautiloids in having siphuncles (a narrow tube passing through the septa) that are near the outer margin of the whorls (the circular arrangement of the parts) and septal necks (dividing membranes) and that are directed forward. Some ammonoids have a ridge along the center, called a keel.

In early ammonoids (Devonian period), the sutures were of a fairly simple form and lack accessory crenulations (i.e., a rounded projection), but by Permian times, some genera (i.e., types of ammonoids) were showing more complex sutures of a kind that reached their full flowering in the Mesozoic period, when ammonoid genera with extremely complex sutures were the norm. The suture is very important in taxonomy (i.e., division into ordered groups or categories); particular kinds of sutures characterize distinct ammonoid families and are very useful in identification.

The layered shell structure of ammonites gave the thin shell part of its strength to withstand crushing under extreme pressure. The septa created chambers in the phragmocone (or divided part of a shell) that enabled these cephalopods to maintain neutral buoyancy. Arrangement of the buoyant hard shell and soft tissues enabled the ammonite shell and visceral mass to maintain a particular orientation in the water.

It is a well-known fact among paleontologists that in certain periods in geological history some groups of ammonites evolved shells of highly aberrant form. Such shells are known as *heteromorphs* (dissimilar in shape or structure). Some appeared during the late Triassic, some in the Jurassic, and there was a more extensive development of heteromorphs during the later Cretaceous period. Though there were heteromorphs at the end of ammonite history, the majority of the ammonites in the Cretaceous period were normally coiled.

All ammonites began life as an embryonic shell stage called an *ammonitella*, which had a diameter of about one millimeter. These tiny animals were then able to disperse throughout the ancient ocean, along with other plankton, simply by movement of the water currents until they became large enough to colonize an area of the sea.

Ammonoids reached their greatest abundance and variety in waters of about 120 to 600 feet deep, but various kinds needed different ocean bottoms or the conditions that went with them, such as temperature or type of bottom. Sandy limestones and shales contain ornate shells of several types, as well as the narrow ones found in deposits of shallower waters.

The typical ammonoid shell was beautifully engineered for withstanding the pressure of seawater at the depths at which the animals lived but was poorly engineered for escaping or discouraging predators. Ammonites were preyed upon by a number of animals, both invertebrates and vertebrates, including large crabs and fish. Marine reptiles, mososaurs, are a classic example of ammonite predators. One ammonite specimen of *Placenticeras*, for example, from the Cretaceous period of South Dakota, was severely bitten 16 times by a mososaur as determined by the sets of tooth marks on the shell.

Ammonites may have fed on carrion and vegetable matter, and it seems the majority may have lived on or near the bottom. Diets for several ammonites are specifically known. Stomach contents show that one type of ammonite, *Arnioceras*, preferred forams *(i.e., single-celled animals)* and ostracods (animals with a small, bivalved, calcareous carapace of vastly diversified morphology). *Hildoceras*, a type of ammonite, was a predator of other ammonites, while yet others ate sea lilies.

Jaws of many ammonites indicate that they were not primarily predators, for the jaws were not designed for cutting. The shovel-like lower jaws of many may have been used to stir up ocean bottom sediments and benthonic *(i.e., bottom-dwelling)* organisms, which were then consumed. Also, some forms may have been planktonic and ingested microplankton.

Ammonoids and nautiloids are commonly found in the same sedimentary strata, and so they probably lived at similar depths in the ocean. The walls and septa of ammonoid shells are much thinner, however, than those of nautiloid shells of similar diameter. Thus it appears that the complexity of the ammonoid shells made them as strong as nautiloid shells even though they were lighter.

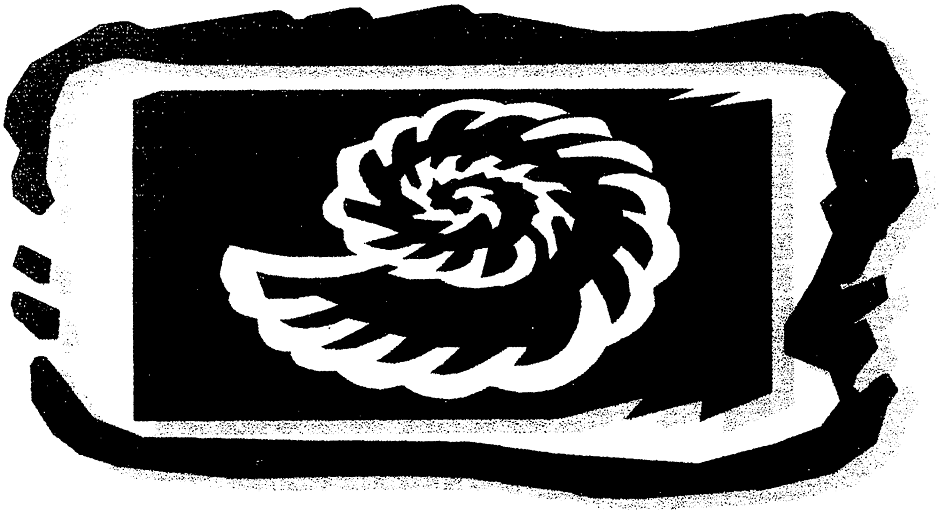
The following six orders have been distinguished in the Subclass *Ammonoidea*:

- Order *Anarcestida* (lower Devonian-upper Devonian); example, Anarcestes.
- Order *Clymeniida* (upper Devonian); example, Cymenia.
- Order *Goniatitida* (middle Devonian-upper Permian); example: Tornoceras.
- Order *Prolecanitida* (lower Carboniferous-upper Permian); example: Prolecanites.
- Order *Ceratitida* (upper Permian-upper Triassic); example: Ceratites.
- Order *Ammonititida* (lower Triassic-upper Cretaceous); example: Lytoceras.

It has been estimated that the average lifetime of ammonite species was between one and two million years (the time that the ammonite species lived before extinction). Scattered among these short-lived taxa (i.e., a group of organisms of any rank), however, are a few genera that were far more durable; some genera survived for as long as 100 million years. Toward the end of the Cretaceous period, the reduction in ammonite diversity was almost entirely due to the extinction of short-lived taxa.

In the upper Cretaceous, the ammonites went into a slow decline over a long period of time, and towards their final end they had become restricted to certain parts of the world only. The number of genera became fewer, and finally no new characters appeared.

At the end of the Cretaceous period, 90 percent of all plankton species went extinct. Juvenile ammonites hatched from small eggs probably spent their first weeks of life as members of the plankton. The ammonites may thus have been caught up in the collapse of the plankton ecosystems, either as hatchlings or as adults feeding lower down on the food chain than the nautiloids. Thus ended the approximate 330 million reign of the ammonites.



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AMMONOID RELATIONSHIPS

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INTRODUCTION

Cephalopods are the most specialized and highly organized of the mollusks and, "in terms of speed, intelligence, and sensory ability, they represent the acme of invertebrate evolution" (Ward, 1988, p. 16). Among the cephalopods, nautiloids and ammonoids are unique in that they possessed an external shell (the extant nautiloids *Nautilus* and *Allonautilus*, of course, still do). Other cephalopods (belemnites, squids, cuttlefish, and *Spirula*) employ an internal shell for rigidity and/or to aid with buoyancy control while still others (octopods) have no shell at all.

Since the vast majority of ammonoids possessed coiled shells, it is logical that *Nautilus* (for the sake of brevity, my use of *Nautilus* is meant to include *Allonautilus*) should serve as an analogue for ammonoid physiology and life habits. But is this analogy valid? Recent evidence points to a possible closer relationship between ammonoids and the coleoids (present-day non-*Nautilus* cephalopods). In this paper, I will present evidence and speculation that addresses this controversy.

CLASSIFICATION

A detailed classification of cephalopods is not needed here but an overview of the three subclasses would be beneficial. The first subclass to evolve, and thus the ancestor to all subsequent cephalopods, is the Nautiloidea--the nautiloids. This group was, by far, the most morphologically diverse of all the cephalopod subclasses. Shell forms included straight, curved, flattened, coiled, some that shed juvenile shells to decrease weight, and even one true heteromorph. *Nautilus* and *Allonautilus* are the only representatives of this subclass that exist today (but make no mistake--the nautiloids did survive the various extinction events that saw the elimination of many "more successful" organisms).

The next subclass to evolve was the Ammonoidea--the ammonoids. Shell types included not only coiled, the most common, but also less symmetrical forms, the so-called heteromorphs. This subclass included three distinct groups based essentially on the type and complexity of their sutures. These groups include the goniatites with relatively simple sutures, the intermediate ceratites, and the true ammonites with very complex sutures. This entire subclass lasted until the end of the Cretaceous when they, like their contemporaries the dinosaurs, went extinct.

The final subclass, and the one which contains the vast majority of extant cephalopods, is the Coleoidea--the coleoids. This group contains the extinct belemnites as well as squids, cuttlefish, octopods, and several other less well known types. As mentioned above, the shell for these cephalopods is either internal or absent.

MORPHOLOGY

At this time it might be prudent to describe the basic morphology of the cephalopod shell as it applies to nautiloids and ammonoids so that comparisons between the two groups can be facilitated. Similarities and differences in the structures of the two groups will be noted.

The conch itself is divided into two main parts, the anterior living (body) chamber (where the animal resided) and the phragmocone. The opening of the body chamber is called the aperture and it allowed the animal access to its environment. The hyponomic sinus is an indentation in the aperture of nautiloids (absent on most ammonoid shells) where the hyponome (used for locomotion and respiration) was located. In a coiled shell, each complete coil is termed a whorl.

The phragmocone contains most of the structures which are used for classification and identification. The phragmocone is divided into many chambers called camerae by a series of concave partitions (chamber walls) called septa. Each camera represents part of a former living chamber that the animal closed off by the secretion of a septum as it grew larger and extended its shell. Septa may be concave forward as in nautiloids or convex forward as in many ammonoids. On steinkerns (fossilized remains of the inner portion of conchs without the outer shell covering), the edge of the septa where they would have attached to the inside of the shell form transverse markings called sutures which can be straight or display various lobes (bends away from the aperture) or saddles (bends toward the aperture). Ammonoid, particularly ammonite, sutures often trace extremely complex patterns in which further crenulations or frills modify both the lobes and the saddles.

The siphuncle, a tubular structure that runs the length of the conch piercing each chamber wall, is the most important ectocochliate structure. It is primarily the development of this structure in primitive monoplacophorans, rather than merely the ability to secrete septa and form chambers, that is believed to have given rise to the cephalopods (Holland, 1987). The siphuncle of *Nautilus*, positioned near the center of the conch, removes (by salinity-induced osmosis) cameral fluid from the chambers thereby reducing the weight/volume ratio so that neutral buoyancy (actually very slight negative buoyancy which is more energy efficient than positive buoyancy) can be maintained as the animal grows. Although the siphuncle undoubtedly served the same main function in extinct nautiloids and ammonoids, many fossil nautiloid siphuncles are much larger and contain structures and deposits that have no analogies in *Nautilus*. Speculated functions of these nautiloid siphuncles range from reproduction to the secretion of cameral and siphuncular deposits. Location of the siphuncle in fossil nautiloids is variable but the simple siphuncle of most ammonoids (and all coiled ammonites) was positioned on the outside of the whorl.

Other structures associated with siphuncles include septal necks, extensions of the septa where the siphuncle pierces the septa, and connecting rings, cylindrical or ring-shaped sheaths that extend between and connect two successive septal necks. The necks in nautiloids (and in *Nautilus*) always point away from the aperture (retrosiphonate) while the necks of most ammonoids, particularly true ammonites, point toward the aperture (prosiphonate). Interestingly, the necks of belemnites, extinct coleoids, also point toward the aperture. For nautiloids, the various combinations of curvatures of the necks and shapes of the rings are, along with types of siphuncular and cameral deposits, used extensively in identification and classification. Since the position, size, and shape of ammonoid siphuncles have such little variation, they are of limited taxonomic value.

Ammonoids often contain calcareous or chitinous plates, called aptychi, that are considered by some to have been opercula--structures that served the same function as the protective hood of *Nautilus*. Others interpret them as ammonoid jaw elements (Morton, 1981; Frye and Feldmann, 1991). Several specimens of a Silurian orthoconic nautiloid have been found with articulated aptychi-like plates preserved at the aperture (Stridsberg, 1984). Because the areas of the aptychi and of the apertures are very similar, Stridsberg (1984) has interpreted them to be true opercula. This operculum is presumed to have remained outside the conch resting on the dorsum, similar to the hood of *Nautilus*, and would have covered the aperture thus protecting the withdrawn animal. However, if interpreted as opercula, ammonoid aptychi were apparently drawn into the body chamber at the bottom of the aperture. Lehmann and Kulicki (1990) have postulated that aptychi served both functions--opercula and jaw elements.

Situated behind the jaws in cephalopods is the radula--a rasping structure used to break-up and transport food to the crop. The radula consists of rows of teeth: 13 teeth in each row for *Nautilus* and 7 to 9 teeth in each row for coleoids. Fossil ammonoid radulas contain 9 teeth in each row, more like coleoids than *Nautilus*.

Shell shapes in nautiloids were extremely diverse pointing to a variety of life modes. Shapes varied from straight (orthoconic) to curved (cyrtoconic) to coiled. Coiled shells can take several distinct forms. Loosely coiled conchs in which the whorls are not in contact are called gyrocones. Planispirally coiled conchs, in which the whorls are in contact, range from evolute in which the inner whorls are exposed to involute in which the inner whorls are poorly exposed or hidden by the outer whorl. In addition, certain forms evolved in which shell morphology changed, sometimes radically, during ontogeny. These types, which increased in abundance during the Cretaceous, are grouped under the general term heteromorphs. Heteromorphs included "straight-shelled" forms in which the juvenile conch was coiled (*Baculites*), gastropod shaped conchs (*Turrilites*), those in which the body chamber curved back towards the phragmocone (*Scaphites*), shells essentially folded in half (*Solenoceras*), and those which grew more-or-less randomly (*Nipponites*).

One of the most, if not *the* most, obvious difference between nautiloids and ammonoids is the morphology of the sutures. Nautiloid sutures are often more-or-less straight with only the occasional lobe or saddle while ammonoid, particularly ammonite, sutures display crenulations that reflect a high degree of fluting and folding of the septa. Why such an elaborate design? The most common explanation offered is that the fluted septa strengthened the inherently weak design (flat-sided and highly compressed) of the planispiral ammonoid shell so that it would be able to resist the crushing force of hydrostatic pressure at the *Nautilus*-type depths ammonoids were assumed to have reached. Nautiloids, with their simple sutures and gently curved septa, relied on the slow growth of a thick shell to resist water pressure. All evidence points to a faster growth rate in ammonoids which resulted in a much thinner shell and even thinner septa. The elaborate fluting of the septa provided, like cardboard corrugations, added strength thus buttressing the thin shell against hydrostatic pressure. However, a recent study by Daniel et al. (1997) suggests that any deviation from a simple hemispherical septal design results in higher septal stress not lower as had been assumed. Thus, ammonoids with the most complex sutures (most fluted septa) would have been restricted to shallow-water habitats. More recently, a study by Hassan et al. (2002) refutes this conclusion and supports the original speculation that fluted septa increased resistance to such water pressures. Interestingly, ammonoids could have designed a very resistant shell by inverting the nautiloid hemispherical septum (which they did) *and* keeping the septum a simple hemisphere (which they did not).

If in fact such complex septa resulted in less pressure resistance, why evolve such complexity in the first place? Although many interpretations have been postulated, the one that is, in my opinion, the most logical involves fluid removal and buoyancy control. The larger surface area provided by the fluted septa may have not only helped to increase the rate of fluid removal after decoupling but also facilitated the supposed refilling of some chambers relatively quickly to assist in both diurnal vertical migrations and buoyancy regulation to compensate for a damaged shell. The folds in the septa may also have allowed ammonoids to retain liquid in some chambers to act as ballast in stabilizing the shell.

Soft-part morphology is, understandably, virtually unknown. Evidence consists of muscle-attachment scars, traces of tentacular impressions, and comparisons to modern forms. An obvious difference in soft-body structures is the number of arms/tentacles. Phylogenetic relationships suggest that members of the nautiloid order Orthocerida and the ammonoids were equipped with 10 coleoid-like arms (Jacobs and Landman, 1993). (Actually all coleoids have eight arms. Squids and cuttlefish are additionally equipped with two food-gathering tentacles often much longer than the arms.) This seems reasonable since both ammonoids and coleoids are presumed to have risen from the Orthocerida by way of the Bactritida. These same inferences suggest, however, that members of the nautiloid order Oncocerida may have had numerous *Nautilus*-type tentacles, which also seems reasonable since it is assumed that the Nautilida (the order which contains *Nautilus*) arose from the Oncocerida.

Using gross morphology, early paleontologists erected genera (called form-genera) that for nautiloids, since they display very little intraspecific variation except for slight sexual dimorphism, have mostly withstood the test of time and are still considered valid. Ammonoids, on the other hand, exhibit tremendous intraspecific variation in morphology, at times as great or greater than variation between different species. Dagys and Weitschat (1993) documented the variation in *Czekanowskites rieberi* from the Middle Triassic of Siberia. Approximately 700 specimens, mostly adults, were found in a single concretion, possibly representing a mass death due to post-spawning mortality similar to many present-day coleoids. Shell types ranged from flat, smooth, compressed forms through weakly ornamented intermediates (the most abundant form) to strongly ornamented depressed types. In addition, a complete range of transitional forms are present so that it is possible to show continuous morphological gradation between the two extreme shell types. All shell types, however, exhibit the same ceratitic suture line with little variation. Such intraspecific variation brings into question both the supposed connection between conch morphology and mode-of-life (shell shape may have had little adaptive significance) and the validity of ammonoid taxonomy with speciation based solely on morphological differences.

ONTOGENY AND GROWTH

Ontogeny of extinct nautiloids and ammonoids is based on sparse fossil evidence and on studies of *Nautilus* (Ward, 1987, 1988). Female nautiloids probably laid only a few (about 12 for *Nautilus*) large eggs per year but could breed for several years. Hatchlings were relatively large (25 mm in *Nautilus*) with several camerae (7 in *Nautilus*) already formed. Landman et al. (1983) described a Cretaceous nautiloid (*Eutrephoceras*) with a hatchling size of about 9 mm and four embryonic septa which seems to suggest one evolutionary trend of nautiloids--increase in egg and hatchling size through time.

Ammonoids, on the other hand, probably produced a large number of small (.5 to 1.6 mm) eggs with the post-hatching juveniles spending some time in the plankton (Ward, 1983; Landman, 1984). Shigeta (1993) calculated the density of Cretaceous post-hatching larvae and found them to be positively buoyant and not able to reach neutral buoyancy until a diameter of 2.0 to 2.5 mm was attained. Thus the reproduction of ammonoids, in contrast to the nautiloids, may have involved migration and congregations of large number of individuals followed by post-mating mass mortality similar to many coleoids today (Jacobs and Landman, 1993). Fossil evidence for this speculated behavior includes preserved embryonic ammonite shells (averaging 1 mm in diameter) from the Cretaceous of Montana (Landman, 1984) and monospecific deposits of ammonoids such as the *Czekanowskites rieberi* occurrence described above (Dagys and Weitschat 1993).

Septa formation and fluid removal by salt-induced osmosis was probably similar in nautiloids and ammonoids. In the case of *Nautilus*, cameral fluid is removed through the siphuncle (connecting rings are permeable to liquids and gases) until the fluid in the chamber falls below the level of the siphuncle, a process called decoupling. Decoupling in *Nautilus* aids in fluid removal at greater depths since the fluid is not in contact with the siphuncle and not subject to reverse osmosis caused by increased hydrostatic pressure (Ward, 1983, 1987). The fluid is replaced by gas which enters the chambers by diffusion from the siphuncular tissues. As the animal grows, the processes of septum secretion, chamber formation, and fluid removal occur continuously until maturity is reached. Fluid removal after decoupling is accomplished by the pellicle (a membrane lining the inside of each chamber) that acts as a wick and draws cameral fluid to the siphuncle. *Nautilus* can adjust the rate of fluid removal and evidence indicates that some fluid can be *slowly* returned to the chambers to compensate for a weight reduction due to shell damage (Ward, 1987, 1988). Ammonoids used organic sheets that subdivided the chambers into fluid-retaining compartments to remove fluid after decoupling at a much faster rate, apparently, than *Nautilus*. Therefore, as mentioned above, ammonoids *may* have been capable of vertical movements facilitated by the quick removal or addition of fluid to the chambers. *Nautilus* is not capable of such rapid emptying and refilling. Because of the position of the siphuncle (outside of whorls), decoupling in ammonoids (especially ammonites) could not take place in the chambers nearest the body chamber. Thus, fluid removal and buoyancy control would be much less efficient at greater water depths than for *Nautilus*. Additionally, as also mentioned above, some have speculated that the corrugations of fluted septa provided increased surface area to aid in fluid removal after decoupling.

The nautiloids most likely had growth characteristics very different not only from other invertebrates but also from other cephalopods. It seems probable that most nautiloids grew slowly, secreted thick shells, and reached a mature size (coincident with reaching sexual maturity) after which growth ceased. An adult *Nautilus* conch may contain 30-36 chambers which represents 10-20 years or more of growth. Ammonoids, however, secreted much thinner shells which may have contributed to their supposed shorter life span, again similar to present-day coleoids.

SEXUAL DIMORPHISM

In a study by Saunders and Spinosa (1978), it was determined that *Nautilus* males have wider shells and broader apertures (to provide the extra room needed to accommodate the spadix) than females. They also determined that dimorphism is a function of sexual maturity since juveniles display no significant differences.

To determine sexual dimorphism in fossil nautiloids, large numbers of specimens are needed so that a significant population can be sampled. This has been accomplished for only a few species and has shown only slight differences in conch morphology. It has even been proposed that some populations in which two similar forms have been designated as separate species may, in fact, simply be sexual variants of the same species. This is further complicated by the fact that two similar forms may indeed be separate species. Male/female determination, therefore, is very tentative.

Sexual dimorphism in ammonoids is often much more pronounced. The enormous difference in size between males and females has often resulted in separate *generic* names being assigned to the two forms of the same species. The males (called microconchs) can be as much as five times smaller in size with the living chambers of adult females (called macroconchs) as much as 125 times larger in volume (Lehmann, 1981). A similar situation occurs in the present-day octopod *Argonauta*, the so-called paper nautilus, in which the female can be 20 times larger than the male (the shell, by the way, is an egg brood chamber secreted by females). Evidence used to determine ammonoid sexual dimorphs includes preliminary identification of egg sacs in macroconch body chambers and presumed single species population studies (Lehmann, 1981). Numbers of individuals of males and females are often not equal possibly due to the two sexes living in different locations and congregating only during mating as in some present-day coleoids. Differences between adult forms include ornamentation (although there is usually no difference in juvenile ornamentation), shape of the aperture (males often have lateral projections called lappets), and crowding of the septa at maturity which affects the last two or three septa in male shells but the final five to ten septa in the shells of females (Lehmann, 1981). Interestingly, male lappets, once assumed to have been grasping structures used during mating, are now interpreted as being analogous to the male peacock's tail--sexual display (Monks and Palmer, 2002).

LIFE MODES

Orientation of the cephalopod conch, particularly orthocones, was one of the first life-style factors to be investigated. Some early cephalopod workers assumed that, if the numerous chambers contained only gas, a vertical orientation with the aperture pointing down was inevitable. This debate was finally resolved upon sectioning specimens and examining the interiors of the camerae (see Flower, 1955). Chambers located near the posterior end of many medium to large straight-shelled forms were found to contain a series of structures called cameral deposits that were concentrated on the venter. These mineral deposits were organic secretions which counterbalanced the mass of the living animal, thus counteracting the buoyant effect of gas in the phragmocone, so that the conch could assume a "comfortable" horizontal orientation. As the animal grew and increased in size, the mass of the cameral deposits (mineral ballast) also increased so that the centers of buoyancy and mass would remain coincident near the middle of the conch and a horizontal orientation could be maintained. Ventrally concentrated deposits would also have increased the stability of the shell by lowering the center of mass and preventing "roll-over".

Coiled forms with short body chambers did not contain or require cameral (or other) deposits since their gas chambers were positioned above the living chamber thus placing the center of buoyancy directly above the center of mass. This would have given them an advantage over orthocones in that neutral buoyancy and stability could be maintained without the necessity of secreting heavy mineral deposits (ammonoids, regardless of shape, did not utilize mineral deposits).

The aperture of *Nautilus* points forward and slightly upward due to the relatively short body chamber which concentrates the living animal at the bottom of the shell. Ammonoid body chambers, however, displayed a wide size range, some occupying as much as one complete whorl. Long body-chambered ammonoids most likely lived with their aperture pointed upwards at a high angle. With such an orientation, feeding off the seafloor would have been impossible and it is speculated they may have been passively floating filter feeders. Of course, since it is impossible to determine the size of the living animal, only a portion of the body chamber may have been occupied (similar to gastropods) thus affecting the position of the aperture as well as allowing the animal to retreat deep into the living chamber when threatened.

Although present-day cephalopods are exclusively marine predators/scavengers, the enormous number of fossil cephalopod species, as well as the wide range of shell morphologies, points to a variety of life-styles ranging from active predator to planktonic filter feeders. There are about 650 extant species of cephalopods (including *Nautilus* and *Allonautilus*) but over 10,000 fossil species are recognized. Holland (1987) suggests that the feeding habits of the nautiloids ranged from planktonic filter feeders to free-swimming nektonic predators to benthic grazers. Evidence exists for active nautiloid predation on brachiopods and trilobites in the form of damaged specimens consistent with presumed nautiloid feeding apparatuses.

For ectocochliates, an evaluation of swimming ability is the key in any attempt to theorize about modes-of-life. The swimming ability of neutrally buoyant fossil nautiloids, particularly coiled forms, is assumed to have been not much different than that of *Nautilus* (some orthocones may have had squid-like quickness when moving backwards). The presence of a deep hyponomic sinus in many species seems to indicate that these individuals were equipped with movable hyponomes which allowed not only propulsion either forward or backward but also vertical navigation in the water column similar to present-day *Nautilus*. Coiled forms would have had greater maneuverability as a result of both the positioning of the center of buoyancy directly above the center of mass and the absence of heavy mineral deposits.

Not all nautiloids were able to maneuver in the water column, however. Those with closely spaced septa (small chambers), highly depressed shells (low volume to surface area ratios), very large siphuncles (heavy deposits), and extremely large orthoconic phragmocones (large mass and heavy deposits) were most likely severely limited in maneuverability or even confined to the substrate.

Recently, the presumed swimming ability of ammonoids has been questioned. Swimming efficiency in ectocochliates is mostly a function of stability. Stability in a chambered shell is achieved when the centers of buoyancy and mass are widely separated so that the majority of the force from the ventrally located hyponome jet is transferred into horizontal motion and only a small amount is transferred into rocking motion (Ward, 1980, 1983; Jacobs, 1992). Separation of these two centers is greatest in shells with short body chambers such as *Nautilus* (Ward, 1980). Some ammonites with large body chambers (a shell is least stable with a body chamber equal to one whorl) had these centers closer together and would have tended to rotate as horizontal forces were applied (Ward, 1980). In addition, fossil evidence shows that nautiloid and ammonoid retractor muscles, which are used in mantle-powered swimming (jet-propulsion), were different in size and location. Nautiloids had muscles that were stronger and positioned differently depending on shell shape whereas ammonoids had weaker muscles located in essentially the same position regardless of shell shape (Mutvei and Reyment, 1973). Thus, the horizontal swimming ability of ammonoids is viewed as having been inefficient and limited. Most ammonoids were probably better adapted to vertical movements, perhaps following the diurnal migration of plankton (Mutvei and Reyment, 1973; Ward, 1986). Jacobs and Landman (1993) disagree maintaining that more streamlined, evolute shell forms with longer body chambers had the aperture positioned higher up on the shell which, when combined with a non-ventral hyponome, would allow any horizontal force applied to act more through the center of mass thus limiting rotation. Also, they indicate the possibility of body extension in these ammonoids which would have had the effect of reorienting the aperture at will and reducing hydrodynamic drag.

The above discussion primarily concerns the "normal" planispiral ammonoids (mainly ammonites). What about heteromorph ammonites? Heteromorphs with "U"-shaped body chambers are inherently more stable with widely separated centers of mass and buoyancy, although much less streamlined, than planispirals (Ward 1979, 1983; Klinger, 1980). If some of the chambers were left partially flooded with cameral fluid, a negative buoyancy would have been imparted to the shell thus confining the animal to the substrate and an existence as a benthic crawler similar to bottom-dwelling gastropods (Ward, 1979, 1983; Klinger, 1980). It seems more probable, however, that the chambers of "U"-shaped heteromorphs were mostly empty so that the shell would have been positively buoyant with the body chamber suspended below the phragmocone and that these forms lived as nektoplanktonic filter feeders (Ward, 1979, 1983; Klinger, 1980; Okamoto, 1988). Orthoconic heteromorphs, such as *Baculites*, were apparently oriented vertically although a horizontal orientation is possible if cameral fluid remained in, or was reintroduced into, the chambers. Once again, depending on buoyancy, a benthic crawler or nektoplanktonic filter feeder mode-of-life is presumed (Klinger, 1980).

EVOLUTIONARY HISTORY

Solutions to the problem of regulating an inherently positively buoyant shell have dominated the evolutionary trends of nautiloids. Five separate solutions (or combinations) were used to solve the buoyancy problem (modified from Crick, 1988):

(1) crowding of the septa thereby decreasing chamber and gas volumes,
(2) retention and/or re-introduction of fluid as ballast,
(3) secretion of ventrally concentrated mineral ballast in the camerae and/or siphuncle,
(4) coiling of the shell, and
(5) truncation (shedding) of juvenile longicones.

Ammonoids also show evolutionary trends, possibly in response to the increased numbers of shell-crushing predators that evolved during the Mesozoic marine revolution, in which the following morphologies increased in diversity through time, particularly during the Cretaceous (modified from Ward, 1983):

(1) streamlined planispiral shells,
(2) heavily ornamented shells of all types,
(3) complex sutures (septal fluting), and
(4) heteromorphs.

Although it was a major evolutionary trend, Boyajian and Lutz (1992) have shown that, somewhat surprisingly, increased suture complexity does not correlate with differential survival, taxonomic longevity, or increased stratigraphic range.

The evolutionary history of nautiloids and ammonoids show similar patterns of first increase and then decrease in diversity leading to taxonomic bottlenecks. The timing of the extinctions are, however, not always synchronous between the two groups. One pattern that is similar concerns the survivors of a bottleneck or crisis. In every case the few surviving genera "were simple forms, generally with smooth shells" (Teichert, 1988b, p. 72).

As mentioned above, nautiloids evolved first and are the ancestors to all subsequent cephalopods. The earliest true cephalopod so far discovered is *Plectronoceras* from the Late Franconian (Late Cambrian) of China. The virtually explosive increase in the number of cephalopod species in the Late Cambrian represents a late phase of the initial metazoan radiation in which new innovations (in this case a septate shell with a siphuncle from which fluid could be removed) gave animals a competitive edge. At the end of this diversification, and about 2.5 million years before the end of the Cambrian, the first of three major bottlenecks in the history of the nautiloids occurred. It appears that only two genera survived this bottleneck and diversified into all post-Cambrian cephalopods (Teichert, 1988a).

The greatest nautiloid diversity, with over 300 genera, occurred during the Ordovician when nine new orders appeared. These orders evolved from the Ellesmerocerida--the only nautiloid order to cross the Cambrian/Ordovician boundary.

During the Late Silurian or, more probably, the Early Devonian, two orders appeared which would dominate the rest of cephalopod evolution: the Nautilida which evolved planispirally coiled shells and became the dominant post-Devonian nautiloid order (*Nautilus* and *Allonautilus* are members of this order) and the Bactritida which was the ancestor group to both the ammonoids and the coleoids (Jacobs and Landman, 1993).

Ammonoids appeared suddenly near the end of the Early Devonian and diversified slowly for the first 20 million years of their history. The first ammonoid crisis occurred at the end of the Middle Devonian and resulted in only two genera crossing into the Upper Devonian.

For about seven million years, ammonoids once again diversified only to experience a second crisis at end of the Frasnian Stage when only 3-4 genera survived into the Famennian, the final stage of the Upper Devonian. This pattern repeated again during the Famennian with only two genera surviving into the Lower Carboniferous (Mississippian).

The Permian saw a gradual decrease in nautiloid diversity. At the end of the Permian what appears to be a major extinction is really just a continuation of the decreased diversity experienced during most of that period (Teichert, 1988a). The diversity of ammonoids also decreased during the Permian, although a bit more dramatically than the nautiloids--only a handful of genera survived the Permian-Triassic boundary.

During the Triassic the Nautilida continued to diversify until the end of the Norian Stage, about 5-6 million years before the end of the Triassic, when the nautiloids experienced their second major bottleneck. Apparently, only one genus, *Cenoceras* of the Nautilida, the last surviving nautiloid order, persisted into the Jurassic where it immediately began to diversify (Teichert, 1988a). During the Triassic, the diversity of ammonoids virtually exploded. This diversity continued until near the end of the Triassic when ammonoid numbers decreased so drastically that not one identifiable Triassic genus passed into the Jurassic. Thus, the exact relationship between Triassic ammonites and those in the Jurassic remains uncertain (Teichert, 1988b).

The remainder of the Mesozoic saw a continued, gradual diversification of the Nautilida with only a moderate reduction at the end of the Cretaceous. "As with the Permian-Triassic boundary, the Cretaceous-Tertiary boundary was no hurdle in the evolution of the nautiloids" (Teichert, 1988a, p. 13). True ammonites, however, diversified explosively during the Jurassic and into the Cretaceous displaying the evolutionary trends mentioned above. The ammonites continued to the end of the Cretaceous but started to decrease in diversity perhaps as much as 30 million years before the end of the period. Ward (1983) maintains that this decrease in diversity was due to the extinction of short-lived taxa and the survival of long-lived taxa, mostly heteromorphs and planispirals. At the end of the Cretaceous, the ammonites suffered their final crisis from which they did not recover.

The third major bottleneck in nautiloid evolution occurred in the late Tertiary, following a steady decline during the Cenozoic, resulting in only *Nautilus* and *Allonautilus* surviving to the present. Some would have us believe that they are living fossils doomed to extinction. However, it is just possible that, as with the first two bottlenecks, a subsequent radiation event may result in still another diversification (Teichert, 1988a). Since each identified species is genetically variable, "it appears that living nautiloids may be actively speciating" (Holland, 1987, p. 13).

As mentioned above, the nautiloids passed through the Cretaceous-Tertiary boundary with only a modest decline; the ammonites, however, became extinct. Why? Several explanations based on the differences in morphology, ontogeny, and life habits between nautiloids and ammonites have been proposed.

One explanation centers around shell design. Nautiloids relied on the slow process of calcification to strengthen the shell and septa in order to resist water pressure. This added a great deal of weight to the animal. Ammonites, on the other hand, apparently grew at a faster rate by reducing the amount of calcium carbonate secreted to form the shell and septa. The resulting shell was well designed for fast growth but poorly designed to resist or avoid the many shell-crushing predators that appeared during the Mesozoic marine revolution, particularly during the Late Cretaceous (Ward, 1983, 1992).

A second explanation points to the great number of ecologically specialized species of ammonites present in the Cretaceous that would have been susceptible to large or even small scale environmental changes. More complex or specialized organisms are always subject to higher rates of speciation and extinction (Landman et al., 1983; Boyajian and Lutz, 1992). By contrast, the few nautiloid species not only exploited a wide range of habitats but also fed opportunistically and were thus more likely to survive environmental change (Holland, 1987).

A third explanation seems to account for both the rapid dispersal of ammonite species and their subsequent extinction. It involves the difference in reproductive strategies between ammonites and nautiloids. As stated previously, most nautiloids, at least from the Mesozoic onward, produced few but large eggs that hatched into physiologically advanced juveniles which would have immediately adopted the deep-water adult mode-of-life near the area of hatching, not an efficient method of dispersal. Ammonite reproduction, on the other hand, involved the production of extremely numerous and extremely small eggs that hatched into positively buoyant juveniles. These hatchlings would have spent time feeding in the plankton (as do the hatchlings of many present-day coleoids) which accounts for their rapid world-wide dispersal. Unfortunately, this also made them susceptible to the terminal Cretaceous event which resulted in the collapse of the planktonic ecosystem (Holland, 1987; Gallagher, 1991; Ward, 1983, 1992). Whatever caused this collapse, the ammonite progeny were decimated which, when coupled with the possibility of adults living only one year, spelled the end of the entire group.

Recently, evidence has been presented that indicates some ammonites may have had longer *Nautilus*-type life spans (Monks and Palmer, 2002). Certainly this is possible--not all present-day coleoids live only one year. The following question, however, immediately comes to mind: If ammonites had adult life-styles and life spans similar to nautiloids, why didn't they also survive the Cretaceous extinction? Even if the juveniles were wiped out, some adults should have survived. Since both groups were in decline, the only possible answer is that these longer-lived species lived in shallow water habitats (nautiloids lived much deeper) and so, along with the planktonic juveniles, succumbed to the Cretaceous extinction event. There is, unfortunately, a problem with this scenario. Normally, species that live in warm, shallow-water environments grow rapidly and have shorter life spans while those living in deeper, colder habitats, like *Nautilus*, grow much more slowly but live longer. Clearly, we have not heard the last of this debate.

CONCLUSION

The history of ectocochliates displays a series of, sometimes rapid, diversifications and subsequent crises or bottlenecks or extinctions. Several times, both nautiloids and ammonoids were on the brink of total extinction only to have one or two genera survive and radiate once again. Thus, it is natural to compare ammonoids to nautiloids and particularly to *Nautilus* and *Allonautilus*--the last cephalopods with external shells. Certainly this is reasonable when discussing shell dynamics such as stability, maneuverability, and methods to resist hydrostatic pressure. However, when discussing physiology, soft anatomy, and behavior it appears that present-day coleoids are a more appropriate analogy. Based on all of the evidence as currently interpreted, tentative phylogenetic relationships have been established (Fig. 1.). This situation illustrates the caution one must exercise when comparing any extinct group of animals to extant ones. However, any hope that we might entertain of understanding the behavior, physiology, and ontogeny of extinct organisms will only be realized through cautious comparisons with similar present-day forms and thoughtful speculation based on the fossil evidence.

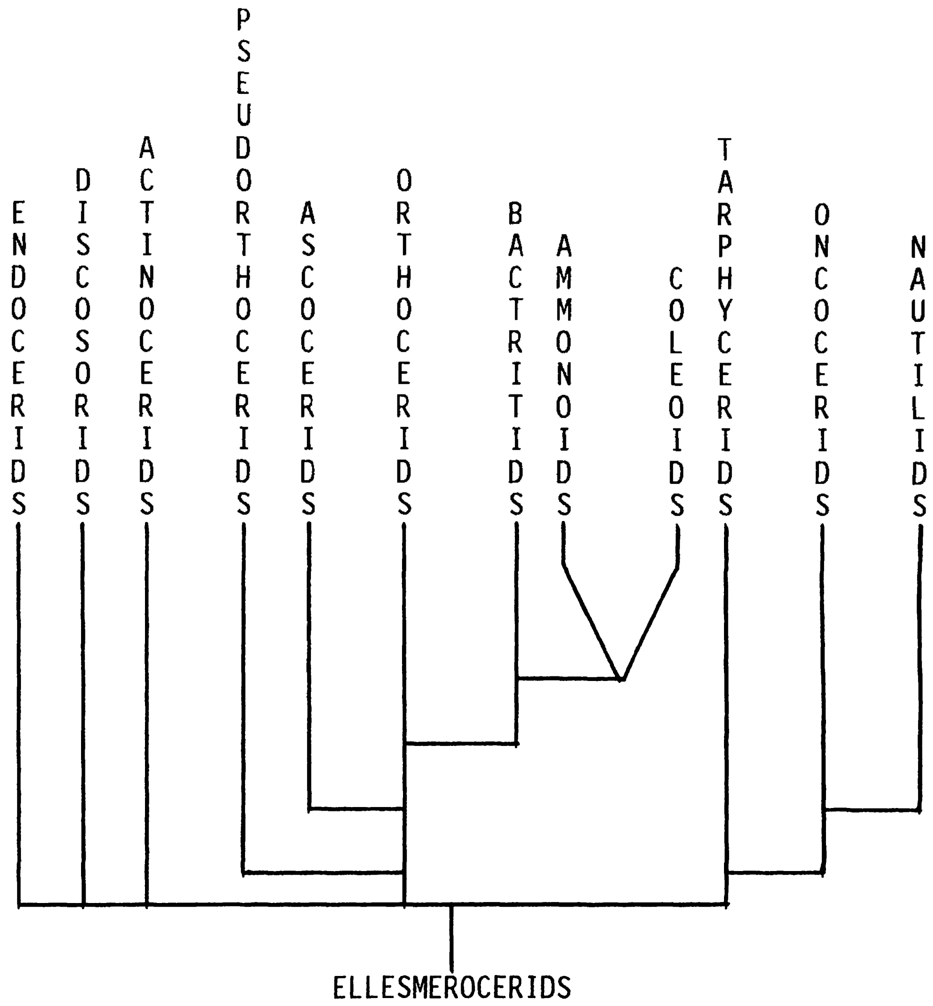

Fig. 1. Phylogenetic relationships of post-Cambrian cephalopods. Only two groups, coleoids and nautilids, are extant. Highly modified after Jacobs and Landman (1993) and Wade (1988).

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CYRTOCONIC NAUTILOIDS IN THE UPPER PENNSYLVANIAN OF NORTH TEXAS

John D. McLeod
Mark G. McKinzie
Curtis Faulkner

Cyrtocones are a group of extinct nautiloid cephalopods characterized by curved shells that achieve less than one revolution of coiling. They may be either elongate (longicone) or short and stubby (brevicones) Based on shell morphology, they are primitive and polytaxic – they were among the first known nautiloids of the Lower Ordovician, and they occur numerous times throughout the Paleozoic fossil record.

Our interest in cyrtocones stems from an ongoing 10-year study of key fossil assemblages in Pennsylvanian strata of North Texas (McKinzie and McLeod, 2003) where numerous cytrocones were recovered from two formations. It is part of a vast collection of fossil material recovered over the last 10 years, and is part of ongoing investigation by the authors. In identifying these forms, we realized their afffinities are very controversial. This paper documents their occurrence, describes their morphologic characteristics, and relates them to published references of similar material.

Age and Stratigraphy

Outcrops in North Texas range through three of the five recognized Pennsylvanian Stages (in ascending order): Desmoinesian, Missourian and Virgilian. Our specimens represent two small disparate intervals in two of the Stages: 1) the Missourian Lake Bridgeport Shale, and 2) the lower Virgilian Finis Shale.

Lake Bridgeport Shale

The Lake Bridgeport Shale Member of the Wolf Mountain Shale Formation outcrops in a small arc around the south and east side of Lake Bridgeport in Wise County, Texas (Fig.1). The unit has been considered to be of Middle Missourian (Upper Pennsylvanian) age (Plummer and Scott, 1937). Boardman et al. (1997) assigned it to their M6 ammonoid zone, and correlated it to the Dewey Formation of Northeast Oklahoma and the Kansas Shelf.

The Lake Bridgeport Shale outcrop belt exposes at least 65 feet of shale with interbedded sandstone that directly underlies the Rock Hill Limestone (Figure 1). The unit was deposited on the eastern shelf of the slowly subsiding Ft. Worth basin. It received clastic sediment from rivers draining from the current-day eastward direction off the now-buried southern extension of the Ouachita Mountains (Erxleben, 1973). The shale contains numerous concretions that sometimes formed around fossil nuclei. A diverse marine invertebrate assemblage is present in the concretions and shale, and rare plant material (mostly *Calamites*) occurs in the interbedded sandstone and concretions.

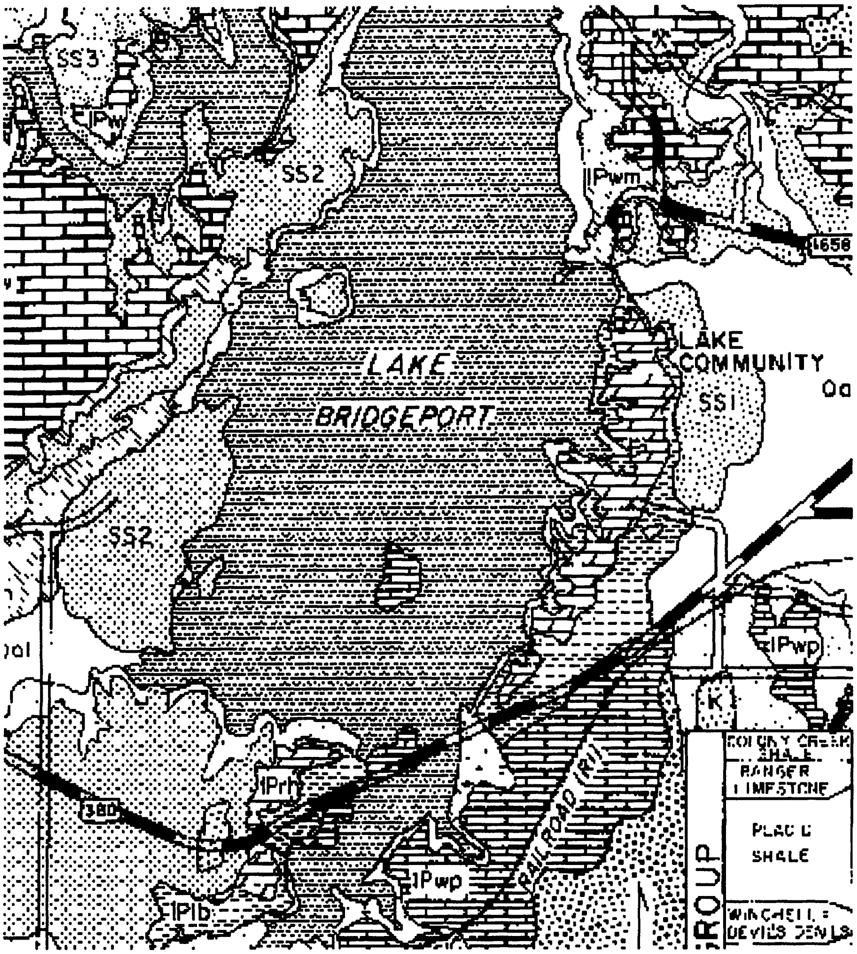

Figure. 1. Geologic map of Lake Bridgeport, Wise Co., Texas. Unit Iplb contains the cyrtoconic cephalopod fauna described here (after Erxleben, 1973). Unit IPrh is the overlying Rock Hill Limestone, and IPwp is the underlying Willow Point Limestone.

Bridgeport brevicones were part of a diverse cephalopod assemblage that contains many large, well-preserved forms.

Paleontology

Phylum Mollsuca
Class Cephalopoda
Subclass Nautiloidea
Order Oncocerida

? Poterioceras M'Coy 1844 Variety 1

Characteristics: The shell is a compressed or subcircular, exogastric, breviconic cyrtocone with a convex ventral asigmoid dorsal profile. The body chamber is inflated dorsally, then contracted adorally. The peristome is circular or faintly ellipsoidal in outline, without a hyponomic sinus. The siphuncle is empty, ventral and marginal in early stages, and only slightly on ventral side of center at maturity. The septal necks are cyrtochoanitic, at least in some species and more strongly curved dorsally than ventrally.

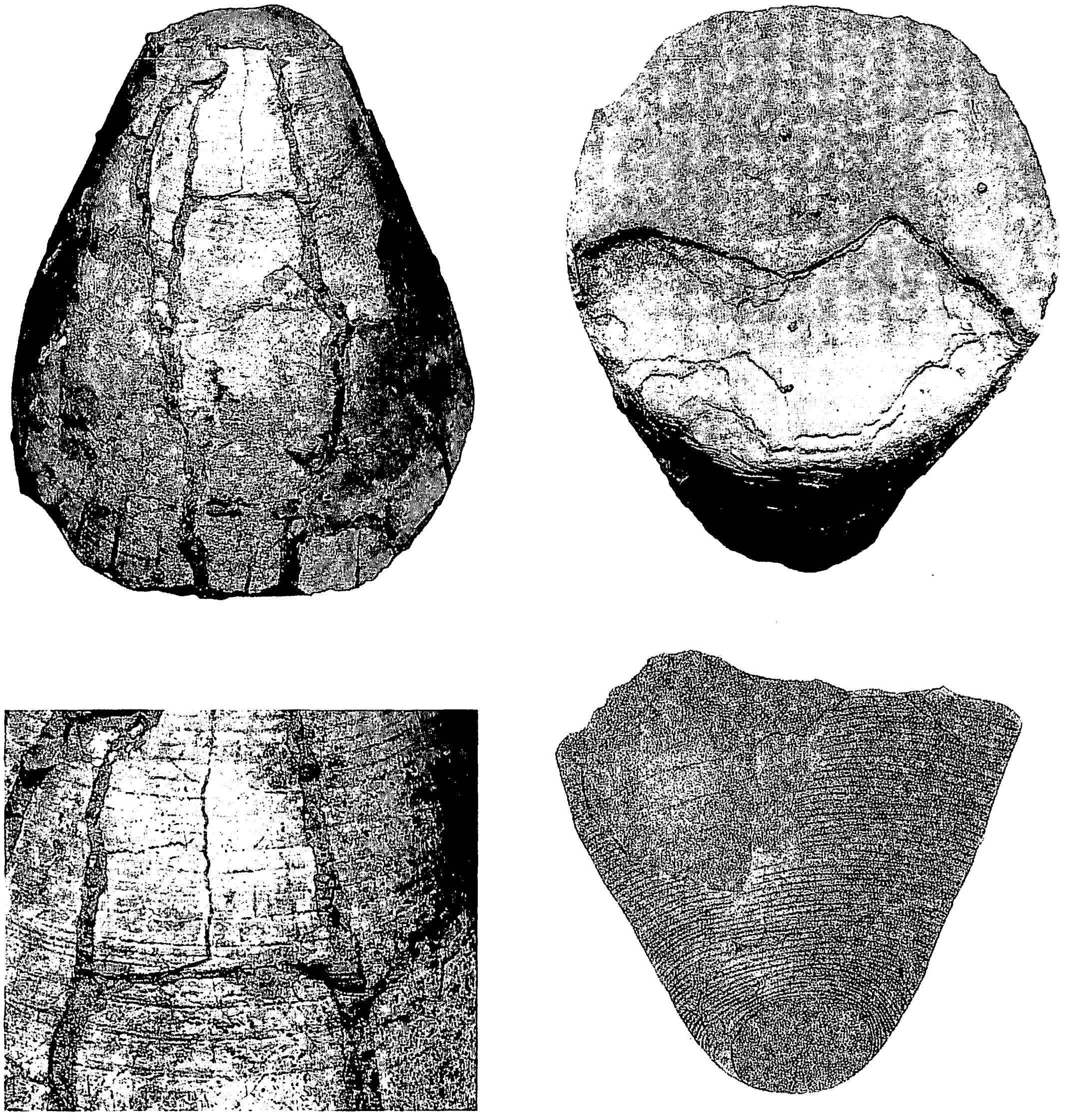

Figure 2. ?*Poterioceras* sp Variety 1, **Above,** ventral view of a near-circular section, x 1.2; **below left,** enlargement of shell banding x 2.2 ; **below right** ?*Cyrtoceras. dislatum* , described by Meek and Worthen (1860) from the Pennsylvanian Coal Measures of Illinois, x 1. Note the round section.

Comments: Rare - 7 specimens from east shore of Lake Bridgeport. This form is characterized by a nearly round section and resembles forms first described as ?*Cyrtoceras dislatum* or *Cyrtoceras curtum* (Meek and Worthen, 1860). Furnish, Glenister and Hansman (1962) illustrated a specimen as *Brachycycloceras curtum* from Lake Bridgeport. The latter authors considered it to be a "deciduous" nautiloid, i.e., one that truncated its shell as it grew. Gordon (1964) referred similar forms from the Mississippian of Arkansas to *Mariceras*. Sturgeon et al. (1997) recently reassigned it to *Poterioceras* and cited the work of Windle (1972), who refuted its deciduous characteristics and affinities with *Brachycycloceras*. The siphuncle and sutures are not visible on these specimens, and the living chamber is unknown. The shell is slightly curved in profile, and growth lirae are present on all specimens. A complete specimen of *Poterioceras* would be expected to show a flaring body chamber.

Finis Shale

The Finis Shale Member of the Graham Formation is the basal unit of the Cisco Group and was deposited at the base of the Virgilian Stage. Cisco Group deposition, much like the preceding Canyon Group, was controlled by the complex interplay of delta progradation, basin subsidence, shelf stability and terrigenous clastic input from the surrounding mountainous coastline to the east. This occurred in conjunction with eustatic sea-level fluctuations attributed to major glaciation events in the southern mega-continent of Gondwana.

The Finis Shale at the Lost Creek Reservoir spillway (just northeast of Jacksboro) in Jack County, Texas (Figure 3) is quite uniform in lithology and reaches 9.5 meters thickness. The lower half consists of a dark gray to almost black, carbonaceous, heavily bioturbated mudstone (Lobza et al, 1994). Siderite nodules and burrows are common. It is highly fossiliferous with a benthic fauna containing conularids, rugose corals, brachiopods, gastropods and less common pelecypods. The pelagic fauna consists of ammonoids and nautiloids plus various genera of marine sharks. In addition, an assortment of terrestrial plant debris consisting of fossil seed pods and wood fragments are present.

The upper half is just as fossiliferous and contains numerous, thin, discontinuous sandstone lenses. Overall, the cephalopods (including the cyrtocones) become larger as you move up-section toward the Jacksboro Limestone. The upper few meters beneath the Jacksboro Limestone become progressively lighter gray, sandier and extremely fossiliferous with the top containing an abundance of the fusilinid *Tricites*.

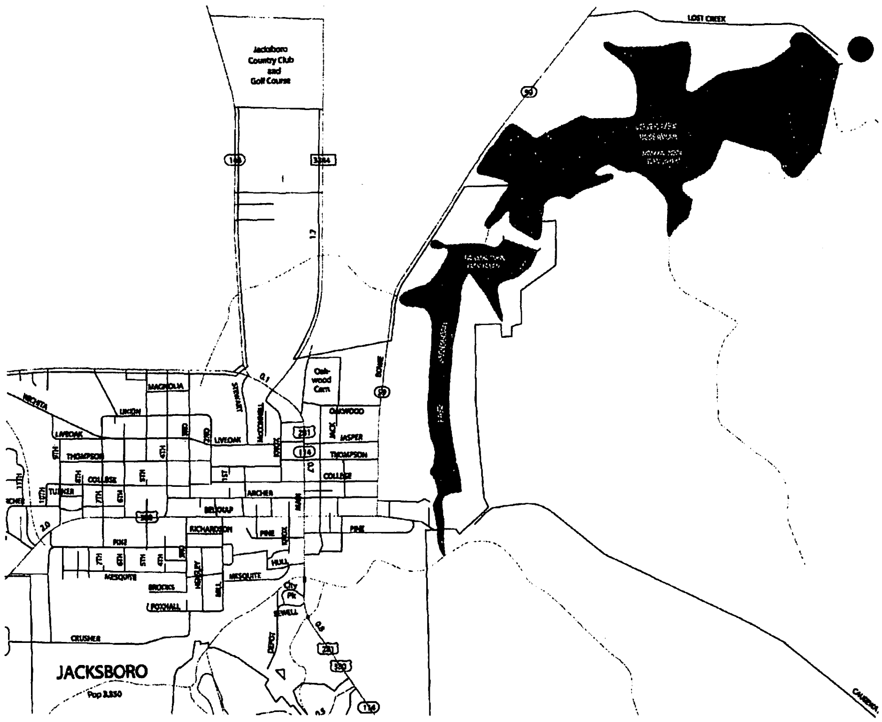

Figure 3. Locality map for the Finis Shale Member of the Graham fomation, Lost Creek Spillway, Jacksboro Reservoir, Jack County, Texas. Black dot denotes locality.

Paleontology

Phylum Mollsuca
Class Cephalopoda
Subclass Nautiloidea
Order Oncocerida

***? Poteriocera*s**M'Coy 1844 Variety 2

Characteristics: Same as previously described for the genus.

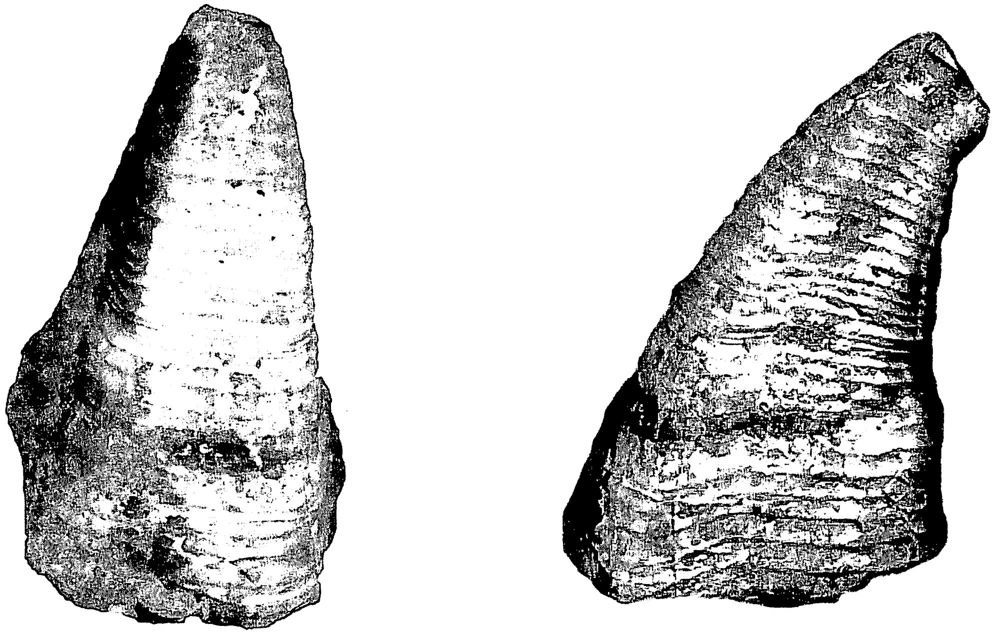

Figure 4 ?*Poterioceras* Variety 2, front-oblique and side profile, showing rugosity and trapezoidal shell. X 2.5.

Comments: Very rare - known from a single well preserved phragmocone fragment and a few smaller fragments. It is subtrapezoidal in section and covered by a rugose shell. This form was previously assigned to *Brachycycloceras curtum* by Furnish, Glenister and Hansman, 1962 and was reassigned to *Poterioceras* by Sturgeon et al. (1997), who expanded the definition of the genus to include cyrtocones with circular, subelliptical or trapezoidal sections.

?*Poterioceras*M'Coy 1844 Variety 3

Characteristics: Obliquely-slanted cap-shaped shell with a smooth, rounded nose-like protoconch, two deeply scalloped flanks, and moderately-spaced sutures. The siphuncle and living chamber are unknown.

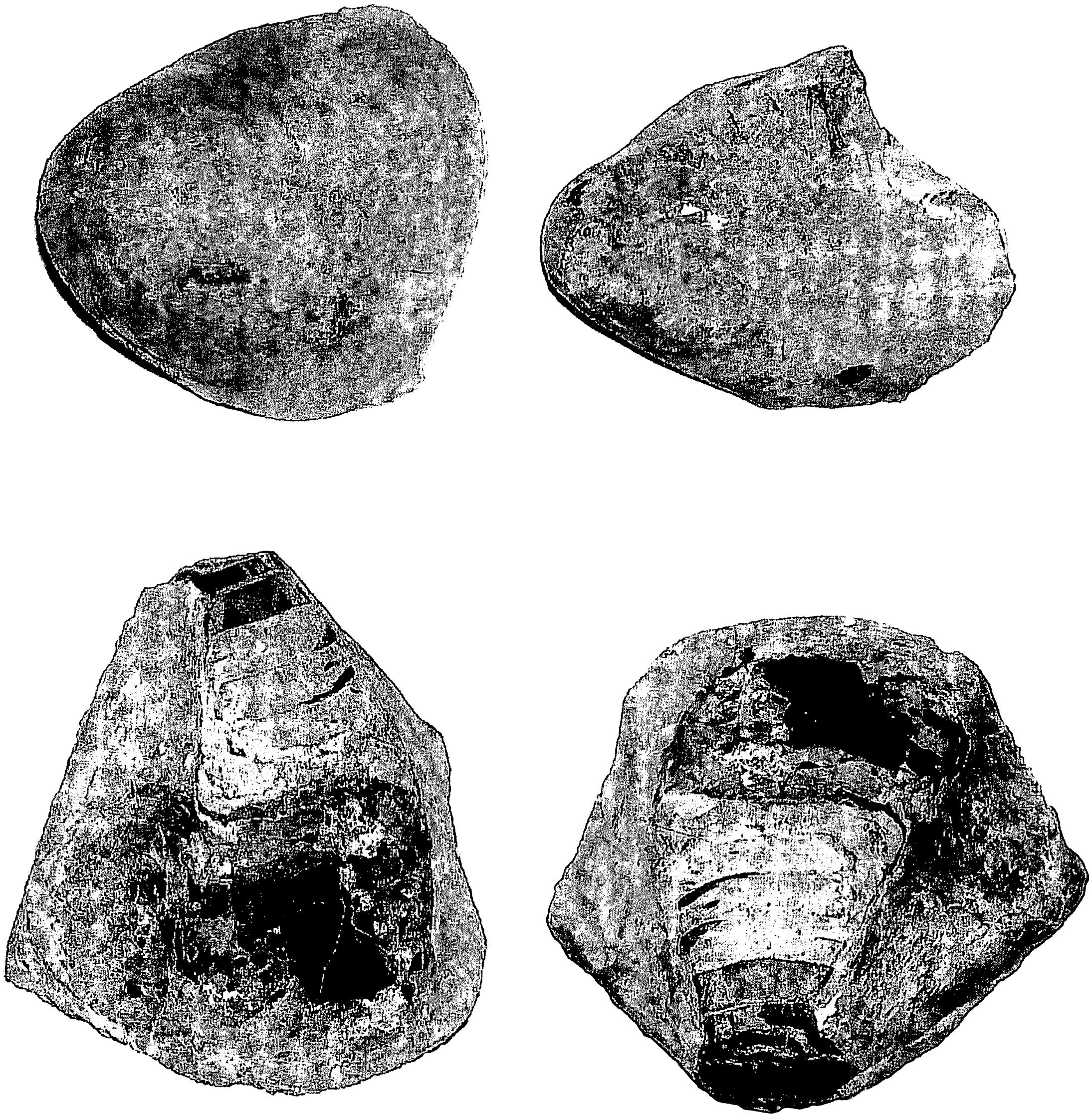

Figure 5 Above, two specimens of ?*Poterioceras* Variety 3 that show the rounded protoconch, x 1.5; **below**, two views of a single specimen that show an eroded, round-section protoconch, sutures and deeply scalloped flanks x 1.5

Comments: This enigmatic form is known from several fragments, and as far as we know, it is unique to the Finis Shale. It is possibly assignable to *Poterioceras*, although it will require further investigation. Gordon (1962) described some smoothly scalloped brevicones from the Late Mississippian of Arkansas as "*Mariceras* sp. A and B"

About the Authors

John McLeod is a geologist with the Illinois State Geological Survey in Champaign, IL. Mark McKinzie is a geologist with Remington Oil and Gas Corp. in Dallas, Texas. Curtis Faulkner is a geologist with Geoscience Data Management in Dallas, Texas. This paper is excerpted from information contained in the book *Pennsylvanian Fossils of North Texas* published 2003 by the Dallas Paleontological Society.

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A Few Pennsylvanian Age Cephalopods of the Pittsburgh Area

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During the Late Pennsylvanian Period (approximately 290 million years ago), the Pittsburgh area of Western Pennsylvania was a vast delta and swamp area that was repeatedly invaded by warm shallow seas. These shallow seas would lay down marine sediments for a few hundred thousand years and then the sea would recede to west only to return hundreds of thousands years later. During these marine transgressions, a wide variety of mollusks (including cephalopods), flourished in the shallow seas at the edge of the deltas and swamps. A few of the cephalopods that can be found in the Pittsburgh area are shown in this brief article. Most of these fossil cephalopods are specimens that I collected from 1969 to 1977, however similar fossils can still be found today in various outcrops of the region.

Two notable rock formation beds, the Ames Member and the Brush Creek Member of the Glenshaw Formation, are marine layers in which fossil mollusks (including cephalopods) are very abundant. Additional beds in the Glenshaw in which cephalopods and other mollusks might be found include the Woods Run and Pine Creek limestone and shale. Typically, the thin marine beds of the region consist of lower shale, a middle limestone, and an upper shale. These layers represent the gradual marine sea invasion (lower shale) and gradual sea retreat (upper shale). In addition, very thin coal seams are often associated with these beds, indicating a swamp environment.

The Ames Formation has typical thin marine strata of the region in there is a lower shale, limestone, and upper shale. A wide variety of well-preserved mollusks, including gastropods, bivalves, and cephalopods are very common in the lower shale of the Ames Member. The straight-shell nautiloid, *Pseudorthoceras* sp., is probably the most common cephalopod in this stratum and even small complete specimens are occasionally found. Although usually found in fragments, the coiled cephalopod, *Tainoceras monilifer*, is also quite common. Careful splitting of the lower shale will sometimes yield complete specimens. For those collectors interested in other marine invertebrates, brachiopods, corals, and crinoids are very abundant in the limestone and upper shale of the Ames Member.

In contrast to the Ames Member, cephalopods and other mollusks are common in the upper shale and limestone of the

Brush Creek Member. This dark-gray(almost black) shale is very fossiliferous and the wide variety of gastropods, bivalves and cephalopods are extremely well-preserved, many with some the original shell material unaltered. Among the more common cephalopods found again, the straight-shell nautiloid, *Pseudorthoceras* sp. One of the more common coiled-shell cephalopod species in the Brush Creek is *Metacoceras cornutum*. There are several other coiled-shell cephalopods found in this stratum, but are more rare. Sometimes, the fossils in the shale are found in association with concretions or in the concretion itself.

The Woods Run Member is very similar to the Brush Creek with regard to the very dark gray limestone and shale layer. Although the stratum is generally much thinner, the cephalopod and other mollusk species found in this layer are mostly the same as in the Brush Creek Member.

Although I have not actively collected fossil mollusks in the Pittsburgh area for several years, new rock exposures and hilly nature of the region leads me to the conclusion that cephalopods and other marine fossils can be readily found with some research and exploration. The key is to be able to recognize the thin marine strata among the other formations of the area.

Acknowledgements:

I would like to especially thank my daughter, Serena, for her artistic illustrations of my fossil specimens.

I would also like to express my sincere appreciation to the following people who have either provided information to me in the past concerning Pittsburgh area geology, fossil identification, collecting, and locality information: Alan Saltsman, Harold B Rollins, and John Harper, as well as the Carnegie Museum Staff. The fossil displays and dioramas at the Carnegie Museum of Natural History provide outstanding paleontology information to the serious collector. I would also like to express my gratitude to the authors of the following references:

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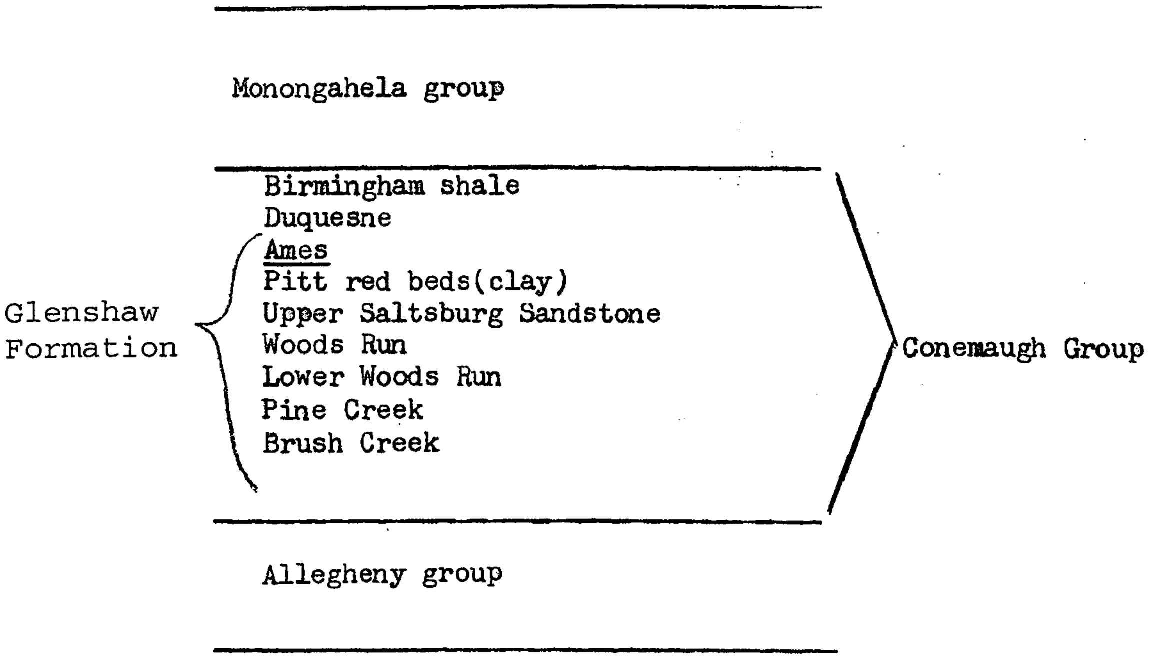
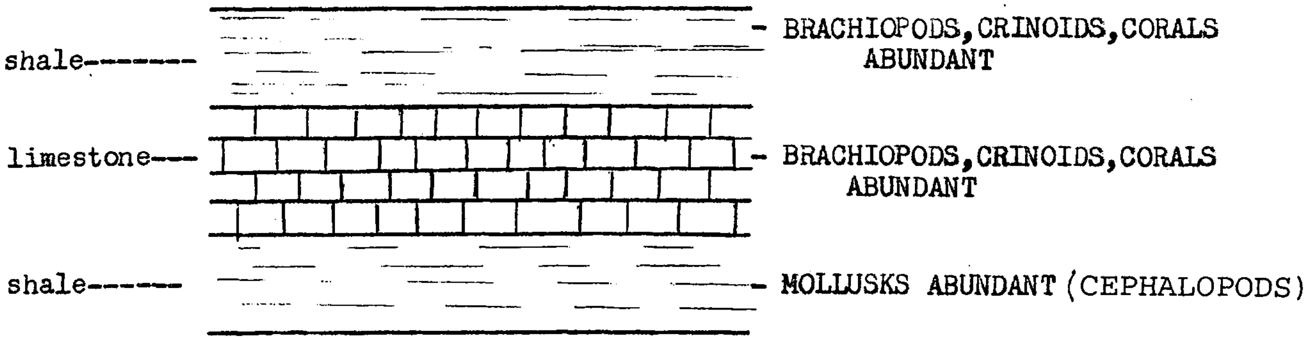
THE PITTSBUGH SERIES OF THE PENNSYLVANIAN PERIOD
(290 million years ago)



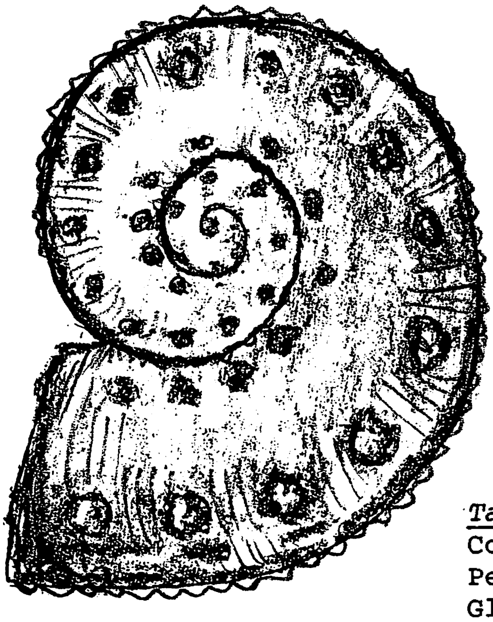
THE AMES LIMESTONE AND SHALE MEMBER



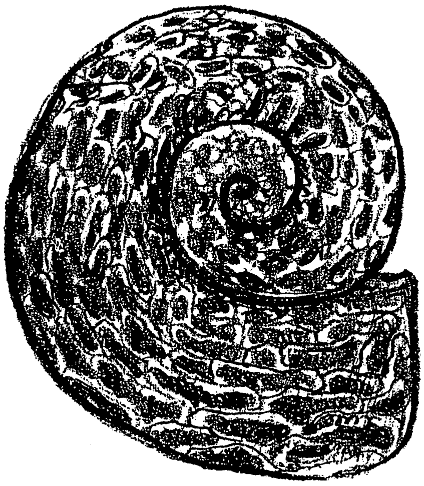
FORMATION DESCRIPTION

upper shale-	greenish-gray color	2 feet thick
limestone	greyish-tan color	3-4 feet thick
lower shale	grey color	3-4 feet thick

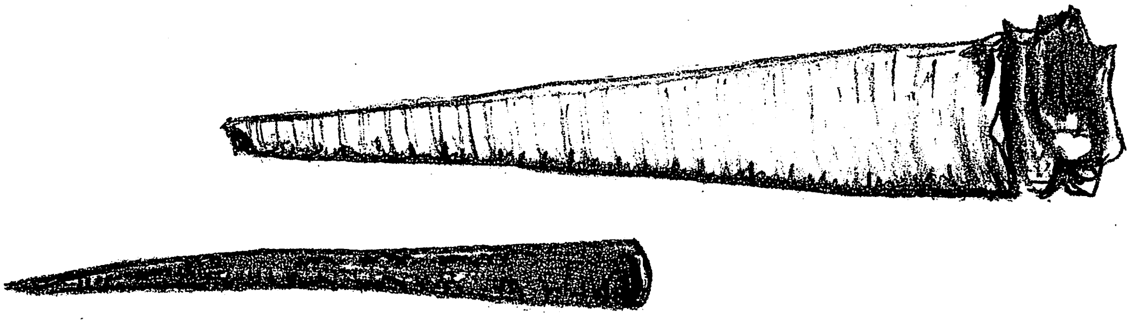
Pseudorthoceras sp. x1
Cephalopod- Nautiloid
Pennsylvanian Age
Glenshaw Formation
Ames Lower-Shale Member
Allegheny Co., Pennsylvania



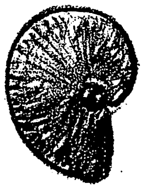
Tainoceras monilifer x1
Coiled Cephalopod
Pennsylvanian Age
Glenshaw Formation
Ames Lower-Shale Member
Delmont, Pennsylvania



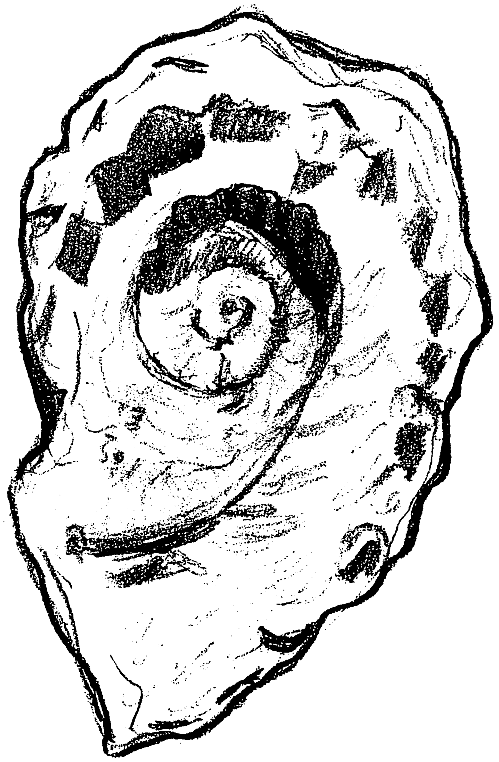
Goniatite-Sutured Ammonoid x1
(undetermined species)
Pennsylvanian Age
Glenshaw Formation
Ames Limestone
Monroeville, Pennsylvania
(Found by Alan Saltsman)



Pseudorthoceras sp. x1
Cephalopod- Nautiloid
Pennsylvanian Age
Glenshaw Formation
Brush Creek Shale
Murrysville, Pennsylvania



Pennoceras seamani x2
Coiled Cephalopod
Pennsylvanian Age
Glenshaw Formation
Brush Creek Shale
Murrysville, Pennsylvania



Metacoceras cornutum x1
Coiled Cephalopod
Pennsylvanian Age
Glenshaw Formation
Woods Run Limestone
Allegheny Co.,Pennsylvania

S. Heinzl 03

Devonian Ammonoids in Iowa

Forward by James E. Preslicka, Iowa City, Iowa

The following article is part of an independent study that was done under the guidance of Professors Brian F. Glenister and Gilbert Klapper (Professors Emeritus at the University of Iowa). The original study was to summarize in detail the fauna from the Lime Creek Formation: Price Creek Amana Beds, in particular the ammonoids, echinoids, and conodonts. Since the focus of the *MAPS Digest* this year is ammonites, that is the only section I have submitted for publication here. We hope to submit the study to the *Journal of Paleontology* in the (hopefully) not too distant future.

In general, ammonoids make excellent guide fossils and are very useful in biostratigraphy. They began their long history in the Devonian, and remained an important part of marine ecosystems until their demise at the end of the Cretaceous. In the Iowa Devonian, ammonoids are not common, so any find of well preserved material is potentially very important. Ammonoids occur in three places in the Iowa Devonian stratigraphic column. The oldest are from the lower Little Cedar Formation (Middle Devonian - Givetian), which are very rare. The focus of the present paper is the ammonoids from the lateral equivalents of the Cerro Gordo Member of the Lime Creek Formation (Upper Devonian - Frasnian). In addition a fauna of clymenid ammonoids occurs in the English River Siltstone (Uppermost Devonian - Famennian).

Ammonoids (*Manticoceras*) have been reported from the well known collecting sites in the type area of the Lime Creek Formation (North Central Iowa near Rockford) for well over a century. However, as stated later in our article, specimens are quite scarce, and poorly preserved to boot. Those familiar with the Rockford area know how large the exposures of strata are. The thickness of the Lime Creek near Rockford approaches 60 meters. In my personal experience, my friends and I have spent many hours searching the Lime Creek Formation inch by inch, oftentimes crawling on hands and knees, which can be quite trying on a hot afternoon. Amongst the countless specimens of fossils there, and the hundreds or more collected by us, we have found but one fragment of *Manticoceras*, consisting of only two chambers of the phragmocone. That's it - two chambers!

That is why the Price Creek site is so important. This small site consisting of three cutbank exposures, with a maximum thickness of roughly three meters, has yielded abundant and well preserved cephalopods, among other things. Since it is a creek bed exposure, new specimens are constantly weathering out, especially in wet years. Frequently, a complete *Manticoceras* can be found within the first five minutes of a trip there. The most found on a single trip was one dozen! The number of specimens found at the time our study was written was 109. Additional finds in subsequent years have pushed the number collected from the site closer to 150. This is more than five times the number of ammonoids known from the Lime Creek Type area. These discoveries will allow us to more accurately describe the species, *M. regulare*, that is endemic to Iowa.

The Amana Beds sit roughly halfway between the relatively shallow water shelf area to the north around Rockford and the deep-water anoxic shales of the Sweetland Creek Formation to the southeast. I like to think of the Amana Beds as the "Graf" of the Iowa Devonian. The Upper Ordovician Maquoketa Formation exposed in the Graf, Iowa area reveals two cephalopod coquina layers. Apparently countless numbers of orthocerid cephalopods congregated in the sea above what is now the Graf area, which lay on the edge of the shelf, between shallow water carbonates to the north and west, and deep basinal shales to the south and east. Certainly the Amana Beds do not have such coquinas, but they do contain numerous cephalopods of all shell forms and various sizes. When I close my eyes, while standing in the creek bed, the sound of the gurgling water makes it very easy to picture numerous schools of cephalopods in a myriad of shapes and sizes flitting to and fro above the muddy bottom of the Devonian sea over what is now south central Iowa.

Upper Devonian (Frasnian) Ammonoids from the Amana Beds at Price Creek, Iowa

by Brian F. Glenister, Douglas W. Hanson, and James E. Preslicka

Abstract: New exposures of the Upper Devonian (Frasnian) Amana Beds near Main Amana (Iowa County, southeastern Iowa) have yielded abundant and diverse biotas, notably the two ammonoid genera *Manticoceras* and *Sphaeromanticoceras* and the cidarid echinoid *Nortonechinus* in association with brachiopods and datable conodonts. The present study provides stratigraphic detail plus descriptions of previously known ammonoid species (*Manticoceras regulare* and *Sphaeromanticoceras rhynchostomum*).

INTRODUCTION

The Price Creek site was discovered in 1993 by former University of Iowa student Jayson Full, who collected several specimens of *Manticoceras* and provided the general location of the outcrop. Subsequent work has determined that the exposure runs for approximately 1.5 kilometers (from the NE 1/4, SW 1/4, SW1/4, Sec. 9, T81N, R9W, Middle Amana, Iowa, Quadrangle, to the SE 1/4, SE 1/4, NE 1/4, Sec. 16, T81N, R9W, Middle Amana, Iowa, Quadrangle) at a general elevation of 730-740 feet. The previously known outcrop of the Amana Beds occurs along Iowa Highway 220 (N 1/2, Sec. 29, T81N, R9W, Middle Amana, Iowa, Quadrangle) at the same general elevation. The beds also appear to be continuous underneath the ridge that separates the two main exposures, as scattered outcrops of blue/gray shale occur along an unnamed stream (SE 1/4, SE 1/4, Sec. 21, T81N, R9W, Middle Amana, Iowa, Quadrangle) at elevations ranging from 740-750 feet.

Both localities of the Amana Beds have yielded specimens of *Manticoceras*, which in Iowa is restricted to the Lime Creek Formation and equivalents. The Lime Creek can be traced in the subsurface along a belt from Hancock County in north-central Iowa to Des Moines County in the southeast corner of the state, and varies in thickness from 50 to 61 meters. It unconformably overlies various formations of the Cedar Valley Group (Baker, Glenister, and Levorson, 1986, p. 7).

The Lime Creek Formation consists of three members that crop out mainly in Hancock, Cerro Gordo, and Floyd Counties:

Juniper Hill Member: This is the lowest member of the formation and is composed of blue/gray shale ranging in thickness from 23 to 30 meters. Ammonoids are not known from this member, and other macrofossils are generally rare (Baker, Glenister, and Levorson, 1986, p. 7), but become more common in the upper part near the contact with the Cerro Gordo Member. These macrofossils include small brachiopods and bryozoans. In contrast, microfossils are common, and the equivalents of Montagne Noire Frasnian Conodont Zone 11, (This and all subsequent references to the zonation are in Klapper, 1989) have been recognized throughout most of this member (Day, 1990) based on the occurrence of *Palmatolepis semichatovae*. The Juniper Hill rests unconformably on different formations of the Cedar Valley Group, and is conformable underneath the Cerro Gordo Member.

Cerro Gordo Member: This member consists of a sequence of interbedded shales and argillaceous dolomitic limestones with a maximum thickness of 14 meters. Macrofossils are abundant and include corals, bryozoans, brachiopods, gastropods, bivalves, echinoids, cephalopods, and crinoids (Baker, Glenister, and Levorson, 1986, p. 7).

The Cerro Gordo yielded the type specimen and two partially articulated topotypes of the cidarid echinoid *Nortonechinus primus* Fenton and Fenton (1923), in addition to disarticulated plates and spines. This member also produced the type specimen of *Manticoceras regulare* Fenton and Fenton (1924) which is thought to be restricted to the Cerro Gordo and equivalents (Baker, Glenister, and Levorson, 1986, p. 7). Until the present study, *M. regulare* was the only ammonoid known from the Cerro Gordo. The presence of *M. regulare* and *Sphaeromanticoceras rhynchostomum* Clarke (1899) [specimens from the present study] indicates correlation of the Cerro Gordo with the *Neomanticoceras* Zone (Becker et al., 1993, p.308) in the Canning Basin of Australia and with the *Sphaeromanticoceras rhynchostomum* Zone (#22 of House and Kirchgasser, 1993) of the Angola Shale of New York.

Microfossils are common, and Montagne Noire Zone 11 has been recognized in the lower part of the member (Day, 1990), again based on the occurrence of *Palmatolepis semichatovae*. Day did not recover any specimens of *Palmatolepis foliacea*, one of the characteristic species of Zone 12 (Johnson and Klapper, 1992); however, Anderson (1966) illustrated one specimen of the species from the middle part of the Cerro Gordo. *P. foliacea* is common in the correlative Sweetland Creek Shale in the southeastern part of Iowa near Muscatine, so the near absence of it around the Rockford area is probably due to facies differences between the two locations (G. Klapper, 1995, personal communication).

The Cerro Gordo conformably underlies the Owen Member.

Owen Member: The Owen is a 15 meter thickness of interbedded dolomite and limestone. It is highly fossiliferous, including gastropods, stromatoporoids, brachiopods, echinoids, and cephalopods. Ammonoids from the Owen include *Sphaeromanticoceras lindneri* Glenister (1958) and *S. rhynchostomum*? Clarke (1899). The presence of *S. lindneri* suggests that the Owen lies within Montagne Noire Zone 13, since the *S. lindneri* Zone in the Canning Basin of Western Australia is contained within Zone 13 (Becker et al., 1993). The *S. lindneri* zone is correlative with the *S. rickardi* Zone in the Hanover Shale of New York (Becker et al., 1993). However, *S. rhychostomum* is not known to range into the *S. rickardi* Zone (House and Kirchgasser, 1993). Further work is needed, as the precise stratigraphic position of the ammonoid specimens within the Owen is not known.

Conodont correlation has been hampered by the fact that the Owen is in the *Polygnathus* biofacies so that diagnostic species of the Frasnian zonation have not been found.

The Owen unconformably rests beneath the Upper Devonian (Famennian) Sheffield Formation (Baker, Glenister, and Levorson, 1986, p. 7).

The Amana Beds at the Highway 220 roadcut near Middle Amana were previously attributed to the Independence Shale (Müller and Müller, 1957), but that designation should properly be restricted to sinkhole fillings of Frasnian shale occurring at various levels within the Cedar Valley Group (Middle and Lower Upper Devonian, Givetian through Lower Frasnian; see Cooper, 1967, for review of the problem of the Independence Shale). The Amana Beds, which unequivocally lie above the Cedar Valley Group, should not be termed as Independence Shale.

Precise correlation of the Amana Beds at Price Creek is facilitated by the number of important guide fossils the exposure has yielded. Conodont work by Gilbert Klapper indicates correlation with Montagne Noire Zone 12 and with part of the type section of the Sweetland Creek Shale (Johnson and Klapper, 1992) based on the occurrence of *Palmatolepis foliacea*. The site also correlates with the middle Cerro Gordo Member of the Lime Creek Formation based on the occurrence of *P. foliacea* there as illustrated by Anderson (1966).

Numerous specimens of *Manticoceras* have been recovered from the Amana Beds, including representatives of *M. regulare*, which is known elsewhere only from the Cerro Gordo Member. In addition, several specimens referable to *Sphaeromanticoceras rhynchostomum* have been found in the Amana Beds at Price Creek indicating direct correlation with the *S. rhynchostomum* Zone (#22 of House and Kirchgasser, 1993) of the Angola Shale of New York.

Brachiopod and conodont work done by Jed Day (Illinois State University) has also determined that the Price Creek section correlates with Montagne Noire Zone 12, and additional work by Day is currently in progress.

Additional evidence of age relationships at Price Creek is the occurrence of *Nortonechinus stainbrooki*, known previously only from outcrops of the Independence Shale. The echinoid is closely related to *N. primus*, which in Iowa is found only in the Cerro Gordo Member around the Lime Creek type area near Rockford.

Precise correlation of the Price Creek site with the Iowa Highway 220 location of the Amana Beds is somewhat hampered by the fact that the latter is a roadcut exposure that is almost completely covered. Müller and Müller (1957) divided the Iowa Highway 220 outcrop into 13 separate units, but these evidently did not extend the entire length of the exposure (W.M. Furnish, 1994, personal communication). *Palmatolepis foliacea* and *Ancyrognathus triangularis* were listed as occurring in units 1 through 8 at the roadcut exposure. Since these two conodonts also occur at the Price Creek locality, it appears that the lower part of the roadcut section (as defined by Müller and Müller) may be correlative (Fig. 1).

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class CEPHALOPODA Leach, 1817
Order ANARCESTIDA Miller and Furnish, 1954
Suborder GEPHUROCERTINA Frech, 1897
Superfamily GEPHUROCERATACEAE Frech, 1897
Family GEPHUROCERATIDAE Frech, 1897
Genus MANTICOCERAS Hyatt, 1884

Type Species.-- *Goniatites simulator* Hall (1879)

Diagnosis.-- See Baker, Glenister, and Levorson, 1986.

Sutural formula: $(V_2V_1V_2)U{:}ID$

Occurrence.-- Lower Upper Devonian (Frasnian) of North America (U.S.: Iowa, Missouri, Michigan, Indiana, New York, West Virginia, Utah, Arizona, New Mexico, Nevada; Canada: Alberta and Northwest Territories), Western Europe, Russia (Urals including Timan and Rudnyy Altay), North Africa (Algeria, Morocco), China, and Western Australia (Canning Basin) (Baker, Glenister, and Levorson, 1986, p. 9).

Discussion.-- Over 60 species were once referred to the genus *Manticoceras*, which achieved worldwide distribution during the Upper Devonian Frasnian Stage, but became extinct by the end of that interval. No species of the genus, or of the family, extend into the Famennian (Becker et al., 1993, fig.7.4). Recent research has resulted in the removal of several taxa from *Manticoceras*, which is currently regarded as somewhat of a "carpetbag" genus (Becker et al., 1993).

Species recognition in *Manticoceras* is especially difficult, since many of the taxa are based on poorly preserved material, were originally inadequately described, or are identified by large or small specimens only (Baker, Glenister, and Levorson, 1986, p. 10). This problem can be illustrated by the difficulties with the classification of the type species of two genera (*Manticoceras* and *Gephyroceras*) in the family Gephuroceratidae, *Goniatites simulator* (Hall, 1879) and *Goniatites sinuosus* (Hall, 1879). The types were later interpreted as representatives of the same species. *Gephyroceras* actually had page priority, but was suppressed in favor of *Manticoceras*, since the type specimen of *Gephyroceras* was actually based on an earlier ontogenetic stage of *Manticoceras*, in addition to the fact that *Manticoceras* was widely recognized and used worldwide (Glenister, 1958; Bogoslovskiy, 1968). It is also possible that some species may represent sexual dimorphs. Recognition of dimorphism requires examination of large collections of well preserved adult specimens that have retained mature modifications (Davis, Furnish, and Glenister, 1969). In the Iowa Devonian, ammonoids are rare, and few if any retain mature modifications. The Price Creek site has yielded what is believed to be the most abundant ammonoid fauna known from the state, producing 109 specimens to date, but of these only two (SUI 62376 and 62447) appear to show any mature modifications. Even with future collecting, it is doubtful that enough specimens can be recovered from the site to provide a sufficient basis for a study of dimorphism in *M. regulare*.

Many authors (Bogoslovskiy 1968, Schmidt 1921, Miller and Furnish 1954, Glenister 1958, and Clausen 1969) have speculated on the taxonomic importance of growth lines, ritzsteifung, and runzelschicht.

It appears that there is wide intra-specific variation in these features and that species in different genera commonly show comparable form (Baker, Glenister, and Levorson, 1986, p. 9). Therefore, it is difficult to differentiate between genera based on these factors, as some authors have attempted to do. Unfortunately, only one of the specimens acquired in the present study (impression SUI 62449) has any of these features preserved (partial faint impressions of the growth lines), so we are unable to provide a description of these characters as they may have appeared in *M. regulare*.

MANTICOCERAS REGULARE Fenton and Fenton, 1924

Manticoceras regulare FENTON and FENTON, 1924, p 196-197, Pl. 39, figs. 1-3. MILLER, 1938a, p. 97-99; Pl. 21, fig 1; Pl. 22 figs. 1-6. CLAUSEN, 1969, p. 119, 127. Baker, Glenister, and Levorson, 1986, p. 11-12, fig 2;3, 6B-E, G, H; table 1.

Diagnosis.-- A species of *Manticoceras* characterized by combination of proportionally narrow conch (W/D 0.26 average), a large umbilicus (U/D 0.31 average), and a suture with broad ventral prongs and broad, nearly symmetrical lateral saddle.

Description.-- Until discovery of the Price Creek site in 1993, knowledge of *M. regulare* was based on only 28 poorly preserved molds from the Lime Creek Formation, Independence Shale, and the Amana Beds (Highway 220 exposure). The type specimen, from the Rockford, Iowa area, reaches a diameter of 110 mm, but is so extensively weathered that it provides no other reliable measurements (Baker, Glenister, and Levorson, 1986, p. 11).

Until 1986, it was thought that *M. regulare* might not even be a valid species, and was possibly conspecific with *M. intumescens* from Europe or perhaps with *M. sinuosum* from New York (Bogoslovskiy, 1969, p. 124). Baker, Glenister, and Levorson (1986) redefined the species, based on some new discoveries and a reexamination of specimens already collected. Only four specimens besides the holotype were reasonably complete, and not coincidentally, all of them are from the Iowa Highway 220 roadcut exposure of the Amana Beds.

As a general rule, fossils from the Amana sites tend to be larger (except in the case of the gastropods), and in a better state of preservation than those from the Lime Creek Formation around Rockford. Specimens of *M. regulare* from the type area of the Lime Creek tend to be in the same condition as the holotype, that is broken, warped, and/or abraded. Since its discovery in 1993, the Price Creek site has produced more complete (albeit immature) specimens of *M. regulare* than are known from the Lime Creek type area after well over 100 years of collecting. Of the 109 ammonoid specimens produced from the Price Creek site, 85 are interpreted herein as *M. regulare*.

Only 26 of the 85 examples are partial whorl fragments, and 26 of the remaining specimens have a diameter greater than the 110 mm diameter of the holotype. Available material now suggests that the holotype and the topotypes previously collected do not represent mature individuals, and that the actual adult size of *M. regulare* was much larger, approaching 170mm in diameter. Only two specimens (SUI 62376 and SUI 62447) appear to show any mature modifications (definite crowding of the last few septa).

Several previously collected incomplete specimens of *M. regulare* in the University of Iowa Repository (SUI 9631, 727, 726, 54225, 54224, 50161, and 50162) were reexamined and appear to be too large to have come from specimens 110mm or less in diameter.

Since none of the smaller complete individuals retain any definite mature modifications, it does not appear that the larger specimens represent a sexual dimorph, but show the fully mature size of *M. regulare*.

Characteristically, specimens of the genus *Manticoceras* have a body chamber occupying the last 1/2 volution. However, the body chamber of the specimens acquired in the present study (when preserved) reaches only approximately 1/3 of a volution. If *M. regulare* achieved the 1/2 volution body chamber typical of the genus, its actual mature diameter would have approached 200mm.

Measurements of conch diameter, whorl height, whorl width, and width of the umbilicus were taken and compiled for study and comparison with other specimens (Fig. 2). In addition, the preservation was good enough that sutural measurements could be taken from 37 specimens, allowing for the first known quantification of several sutural characteristics for *M. regulare.*

The following specimens represent previously collected examples from the Repository of the University of Iowa which were included in the list for comparative purposes:
M. regulare: SUI 728, 50158, 50159, 50160, 50162
Sphaeromanticoceras rhynchostomum?: SUI 50157

The breakdown of characteristics for *M. regulare* is as follows:

Measurement:	Average:	Range:
H/D:	0.42 (37 specimens)	0.32 (SUI 62342) to 0.56 (SUI 62387)
W/D:	0.25 (34 specimens)	0.13 (SUI 62328) to 0.37 (SUI 50160)
U/D:	0.30 (36 specimens)	0.23 (SUI 62335) to 0.39 (SUI 62378)
W/Vw:	1.40 (26 specimens)	0.72 (SUI 62337) to 2.45 (SUI 62343)
W/sw:	0.56 (30 specimens)	0.35 (SUI 62359) to 0.93 (SUI 62332)

Occurrence.-- *Manticoceras regulare* is known only from the Cerro Gordo Member of the Lime Creek Formation, the "Independence Shale", and the Amana Beds. Associated faunas in the Amana Beds at Price Creek suggest it occurs within the *Sphaeromanticoceras rhynchostomum* Zone (House and Kirchgasser, 1993) in New York, the *Neomanticoceras* Zone (Becker et. al., 1993) in Western Australia, and within Montagne Noire Zone 12. However, if *M. regulare* occurs throughout the Cerro Gordo Member as stated by Baker, Glenister, and Levorson (1986), it would then range down into the upper part of Montagne Noire Zone 11.

Repository.-- The holotype (USNM 78964, Fenton and Fenton, 1924, p. 196-197; Pl. 39, figs. 1-3) is housed in the United States National Museum, Washington. All specimens from the present study (SUI #62326-62399), plus the topotypes from the 1986 work (SUI 724-727, 9631, 50158-50164) and a plaster cast of the holotype (SUI 728) are reposited at the University of Iowa.

Comparisons: *M. regulare* has been regarded as closely related to the following species: *M. intumescens* Beyrich (1837), *M. sinuosum* Hall (1843), *M. cordiforme* Miller (1936), *M. guppyi* Glenister (1958), *Sphaeromanticoceras rhynchostomum* Clarke (1899), and *S. lindneri* Glenister (1958), and but can now be differentiated from them, using information from the new finds at Price Creek.

The most distinctive features of *M. regulare* are the large size of its conch (probably 170mm but possibly approaching 200mm), and its very large umbilicus (U/D average 0.3), and the fact that its body chamber occupies roughly 1/3 of a volution. The large conch serves to distinguish it from *M. intumescens* and *M. sinuosum*, as well as *M. guppyi* (maximum diameter 135mm).

Only *Manticoceras cordiforme*, *Sphaeromanticoceras lindneri*, and *S. rhynchostomum* are known to have conchs in the size range of 170mm or greater. *Manticoceras regulare* can be distinguished from those three based on its relatively large umbilicus. The *S. rhynchostomum* specimens from the present study have a U/D ratio of 0.14, whereas *M. cordiforme* has a ratio of about 0.17, and *S. lindneri* has a ratio of about 0.22 U/D. *M. regulare* can also be separated from *S. lindneri* based on the ratio of width to diameter, which in *S. lindneri* is about .42, while *M. regulare* has a W/D ratio of .25.

Eleven other specimens from the Amana Beds at Price Creek are referred with question to the genus *Manticoceras*. Two juvenile ammonoids (SUI #62380, 62398B) were recovered from the site, but their small size (and pyrite coating on one of the specimens) makes definite specific assignment questionable. In addition, no sequence of ontogeny has been described for *M. regulare.* Seven molds were made where the stream flow had washed away the ammonoid, leaving only its impression behind. The molds apparently represent *M. regulare*, based on comparison of conch diameter, height, and width of the umbilicus. Also, a small fragment (SUI 62363A) from Unit#2 was recovered and resembles known *M. regulare* specimens. Due to the lack of sutures, classification of these molds cannot be certain. Lastly, two other impressions have been recovered, (SUI 62449 and 62462) one of which (SUI 62449) appears to retain faint partial impressions of the growth lines. Both specimens evidently represent *M. regulare*, but again, with no sutures preserved, specific affiliation cannot be determined with certainty.

***Sphaeromanticoceras rhynchostmum* (Clarke 1899)**

The remaining 13 specimens collected for the present study appear to be referable to *S. rhynchostomum*, marking the first known occurrence of that species in the Amana Beds. Most of them are not particularly well preserved, but taxonomic assignment seems to be reliably based on numerical comparison of various conch parameters. The specimens are characterized by a rapidly increasing conch height and width (when not compressed), a relatively small umbilicus, and widely spaced sutural elements.

ACKNOWLEDGMENTS

Mr. Clarence Volz and the rest of the Volz family allowed us continuous access to the site; without their understanding and cooperation this study would not have been possible. Gilbert Klapper volunteered much of his time to help with the identifications of the Price Creek Conodonts. Julia Golden, Curator of Paleontology at the University of Iowa was instrumental in providing access to the specimens and information contained within the repository at the University of Iowa. W.M. Furnish, Brian Witzke, and David Work helped in identifications of some specimens and in discussions on past work done on the Frasnian of Iowa. Jed Day (Illinois State University) identified most of the brachiopod specimens acquired in the present study. Charles Newsom provided use of his digital camera and some of his fossils for the pictures taken for this article.

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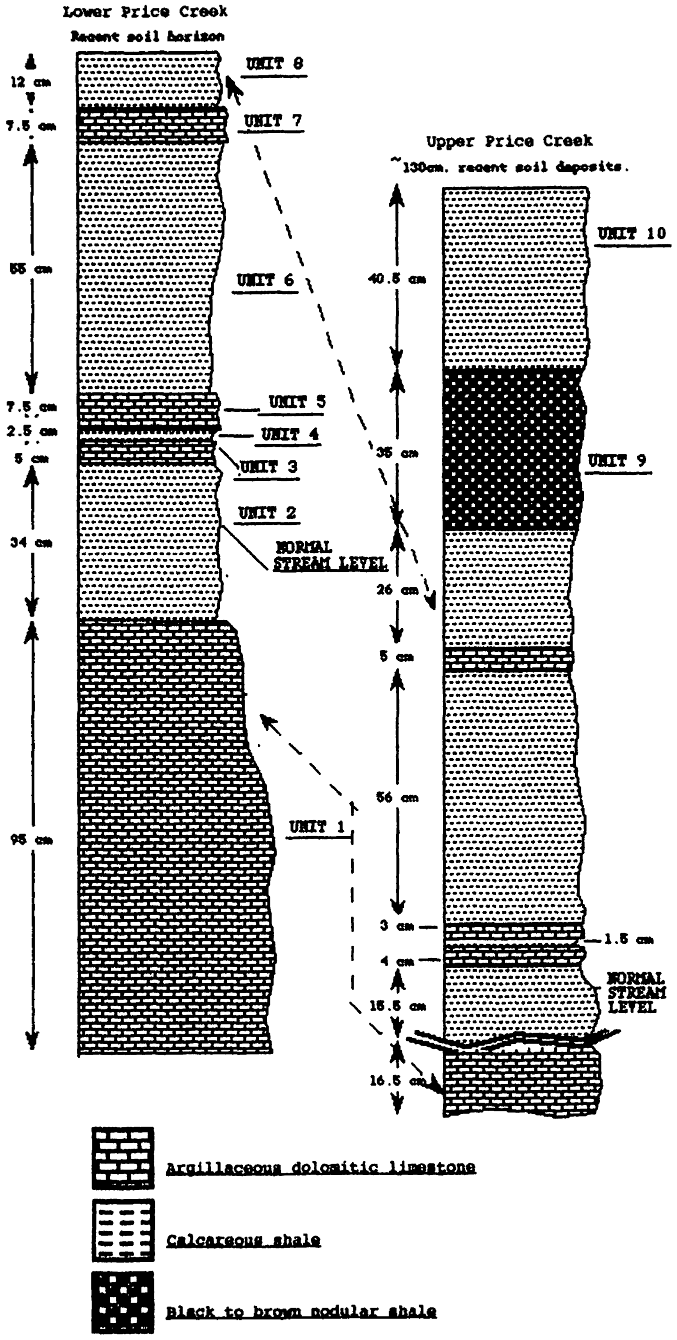
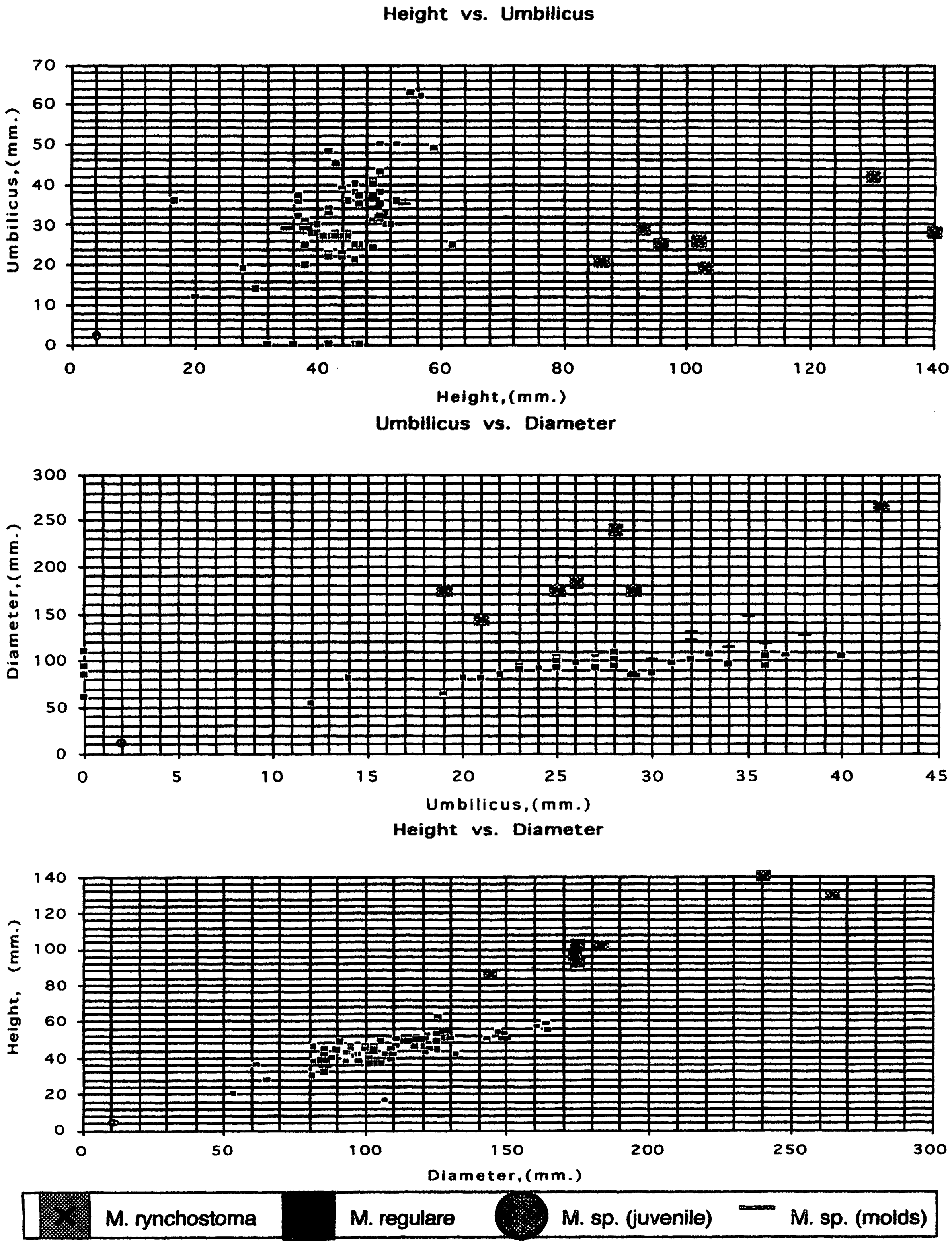


Figure 1. Amana Beds, Price Creek section. Ammonoids have been found in-situ in units 1-6. In addition, ammonid aptychii occur in the nodular shales of unit 9.


Height vs. Umbilicus

Umbilicus vs. Diameter

Height vs. Diameter

Figure 2. Measurements of *Manticoceras regulare* and *Sphaeromanticoceras rhynchostomum* clearly indicate the difference between the species.

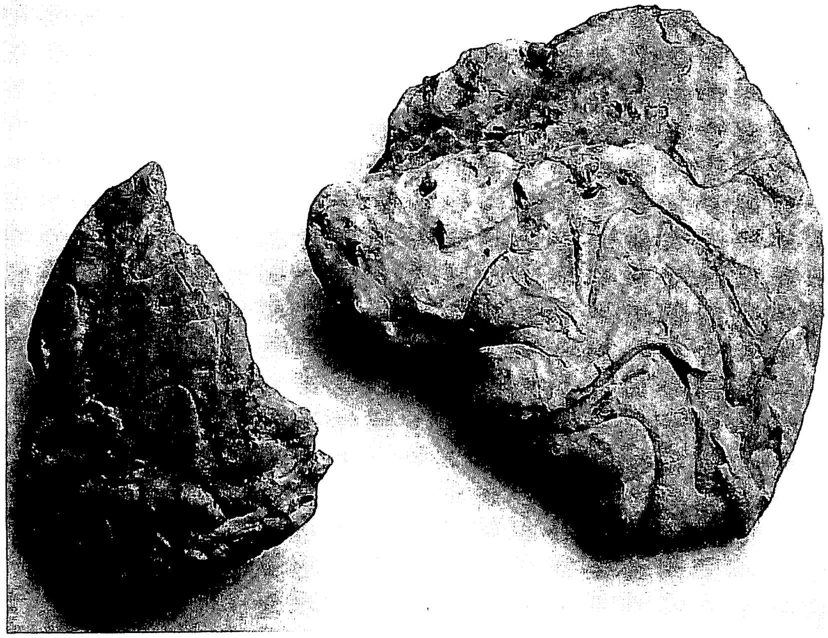


Figure 5. *Sphaeromanticoceras rhynchostomum* (2 fragments), maximum whorl height: left specimen – 65 mm, right specimen – 80 mm.

Figure 6. *Manticoceras regulare*, from unit 2, actual maximum diameter 60 mm.

Figure 3. *Manticoceras regulare*, actual maximum diameter 110 mm.

Figure 4. *Manticoceras regulare*, actual maximum diameter 125 mm.

A TRIASSIC JOURNEY THROUGH NEVADA

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El Cajon, California 92091

Our story begins about 245 million years ago. That region of the world we call the Arctic was a relatively warm sea covering parts of regions we now call Greenland, Spitsbergen, Russian Siberia and Arctic Canada with an arm extending from British Columbia to Southeastern California. Towards the end of the Permian there was wide spread extinction of many ammonoid families. During the Triassic, the seas began to swarm with many new life forms. The ammonoids began to flourish again with great diversity, sharing the seas with ichthyosaurs, counterparts of todays whales and dolphins. It is in these marine deposits, now uplifted to about 5000 feet in elevation that we will visit.

The first Triassic exploration of Western North America began under the leadership of J.D. Whitney of the Geological Survey of California. The state politicians were more interested in gold discovery than geology and Whitney had great difficulty in funding the survey. W.M. Gabb was the paleontologist with the survey who described ammonoids from the Humboldt and East Ranges in what is now present day Nevada. Shortly thereafter, Clarence King led the 40th Parallel Survey by the Federal Government, finding new Triassic localities in Nevada. F.B. Meek and C.A. White's description of the cephalopods and geologic findings were published in this project. Many of the collecting localities became known as a result of mining activities in the 1800s.

We begin our present day trip in Lone Pine, California. Highway 395 winds north thru the Owens Valley with the Sierras on the west side and the Inyo Mountains on the east. From Lone Pine we can see Mt. Whitney, the highest mountain in the contiguous United States. As we are about to leave Lone Pine, we drive east towards the former town of Owenyo and then up the old McAboy trail leading to Saline Valley. Our first stop on the right side of the trail is the Neopopanoceras beds, the highest stage of the Lower Triassic. This locality and most of the then known Triassic deposits of the Western United States were visited and described by J.P. Smith of Stanford University in the early 1900 s.

The ammonoids are found in a dark grey limestone bed about a yard thick and 150 yards long. Most of Smith's generic assignments have been modified. The Haugi Zone in the Northern Humboldt Range, which includes fauna of this locality, is currently under study by Bucher, Guex and Taylor. About a mile up the trail on the right side, there is an older Meekoceras bed in a light grey limestone. The preservation is poor here. Most of the ammonoids are distorted and look like they have been stretched. Smith described over 20 ammonoids from this locality. Nearly all of these specimens except Inyoites oweni, can be found in excellent condition at other Nevada and Idaho localities. For this reason, I still revisit this locality in hope of finding more Inyoites. It is a coincidence that at a site we will discuss later, my friend Jim Jenks has found 6 Inyoites stokesi and in 20 years of collecting at this site, I have never found one!

After a short drive back to Lone Pine and Highway 395, we drive towards Bishop, California. At Bishop, we take Highway 6 and head towards Montgomery Pass Casino in Nevada. For those persons who have never been to Nevada, the casinos almost always have fine inexpensive food, large clean rest rooms and very modestly priced rooms. From the casino it is less than an hours drive to the New York Canyon area near Luning. At Luning, we stop at the Longbranch saloon and talk to the owner, Dick Hegg. Hegg spent part of World War II at the nearby munitions depot at Hawthorne and fell in love with the area around Luning. He tells many stories about paleontologists from Austria, France, Switzerland and geology students from the United States who have studied the Triassic and Jurassic in New York Canyon. One of the most well known European workers was Jean Guex of Switzerland. Siemon Muller did extensive geologic mapping and collecting in this region in the 1930s.

From the Longbranch we drive about 4 miles east on a dry lake bed and walk about 1½ miles up the main branch of New York Canyon. One can see most of the colors of the rainbow on the walls of the canyon and step on chunks of colorful copper ore as we hike towards one of the collecting localities in the canyon. It is a phenomenon here that has attracted so much world wide interest. This is one of the few known localities in the world where the Upper Triassic and Lower Jurassic are both exposed and fossiliferous. The Gabbs Formation (Triassic) is overlain by the Lower Jurassic Sunrise Formation. In this vicinity, the most common Upper Triassic ammonoids we find are of the genera Arcestes, Cochloceras and Rhabdoceras.

They are usually found in a hard dark grey mudstone along with ichthyosaur parts.

From Luning, we take Highway 361 north to Gabbs and then east to Berlin Ichthyosaur State Park. Several nearly complete ichthyosaurs have been uncovered here and a building has been constructed over one specimen for public viewing. Here, the most important Upper Triassic exposure is the Luning Formation which is exposed in Union Canyon. The descriptions of the ammonoids and the stratigraphy of the Union District Shoshone Mountains is contained in U.S.G.S. Professional Paper 322 by Norman Silberling. Silberling has spent much of his life working on mapping, stratigraphy and Triassic paleontology in Nevada. He has also given encouragement and guidance to many graduate students and other workers. He has been most generous and helpful to the amateur collectors.

From the park, we drive on dirt roads for about 50 miles north to Highway 50 and then to a gold mine in the Desatoya Mountains. Don and Kathy Jung have operated the New Pass Mines for over 30 years. It is a beautiful experience to collect ammonoids at an elevation of 7800 feet in a pine forest, then have a shower, enjoy dinner with the Jungs and have a room with a fifty mile panorama. There are exposures of both Middle and Upper Triassic ammonoids here. F.N. Johnston described the Upper Triassic ammonoids in the September 1941 Journal of Paleontology. Some of the less common Anisian stage genera I have found here are *Balatonites*, *Cuccoceras* and a new genus *Augustaceras* described by Bucher (1988).

From the New Pass Mines, we drive west on Highway 50 to Fallon, then north on Highway 95 to Lovelock, north on Interstate 80 a few miles to Oreana, then a short drive east to the Humboldt Mountains and Fossil Hill. This is one of the most important and interesting Middle Triassic sites in North America. J.P.Smith made several trips here in the early 1900s, collecting thousands of ammonoids mostly in float. In his 1914 monograph, he described 110 Upper Anisian species from this vicinity. In the following years, many collections were made here. Some of them ended up in Europe at the British Museum of Natural History where Spath also studied and refigured some of the material (1934,1951). During the 1950s and 1960s, Silberling and others mapped the entire Humboldt Range. At this time it would be appropriate to introduce Tim Tozer of the Canadian Geologic Survey. Tozer has spent a great part of his lifetime working on all phases of the geology and paleontology of the Triassic. He has traveled to most parts of the world, discussed stratigraphy with all of the important workers and most importantly organized the efforts of previous workers and present day stratigraphers to develop a time scale for the Triassic. His book *The Trias and its Ammonoids: The Evolution of a Time Scale* is a monumental land mark as it has a wealth of information for the professional and the amateur written with the style of a master mystery writer that makes it impossible for the reader to lay the book down until he has read it from cover to cover.

During the 1960 s Tozer and Silberling were coordinating their efforts and ideas. Silberling was busy making painstaking stratigraphically controlled population samples from bedrock collections on the south side of Fossil Hill and at a nearby site on Saurian Hill. With new information, larger population samples and observation of intraspecific variation, Silberling began work on reorganizing most of the work done on the ammonoid fauna of the West Humboldt Mountains. Soon, he was joined in the work by Kathryn Nicols, a post-doctoral fellow at U.S.G.S. and later to become his wife. In this work, U.S.G.S. Professional Paper 1207, Smith's 110 Upper Anisian ammonoid species had been reduced to 37. The *Rotelliformis*, *Meeki* and *Occidentalis* zones at Fossil Hill became a world wide biostratigraphic standard of reference for the Upper Anisian. Many of the ammonoids found here are quite cosmopolitan. The author has a Siberian collection in which *Gymnotoceras rotelliformis* (Meek) is represented. These Middle Triassic rocks belong to the Fossil Hill Member of the Prida Formation of the Star Peak Group.

To collect here, one must be prepared for almost any weather scenario. I have collected in the snow, rain, wind and oppressive heat. Years ago, during wet cycles one might endure rain for several days and see lots of cattle. For the last five years, much of Nevada has been in a severe drought and now one sees mostly flocks of sheep in this area. The sheepherders are usually from Spain or Peru and always welcome company in the late afternoon for a bowl of stew. Two years ago, I brought three Japanese paleontologists, Hisao Ando, Haruyoshi Maeda and Kazushige Tanabe to this locality. The first afternoon was a beautiful warm one. By the next morning, the temperature had dropped to 40°Fahrenheit, and my friends were very cold and uncomfortable. Last year, my friend Wolfgang Weitschat (Hamburg University) wanted to compare the Spitsbergen fauna with the Nevada counterparts. The first thing we did before leaving for Nevada was the purchase of a warm coat and sleeping bag for Wolfgang.

One cannot anticipate every event. On my next trip here, I punctured a tire, struggled with a frozen lock nut and then found that I also had a loose steering box. I survived these inconveniencies, but tore the cartilege in my knee climbing the hill. On the way down, I made a rare encounter with a large rattle snake that didn't want to move off the trail. Remembering my grandson had asked me to get him a rattle snake skin, I combined a rest for my knee with the skinning of the snake.

From Lovelock, we drive for about 250 miles east on Interstate 80, then turn north on Highway 233 for 25 miles to Montello, and then drive 18 miles on a gravel road to the Gamble Ranch. On this ranch of over 75,000 acres, one can step back in time and see cattle drives with real cowboys. Until two years ago, Jim Fretwell had been the ranch foreman for 25 years, always giving everyone a warm welcome and a helping hand if needed. In the 1950s during a survey of the regional stratigraphy of Northwestern Nevada, Grant Steele (Gulf Oil Company) made a collection of Lower Triassic ammonoids on the ranch about a mile northeast of Crittenden Springs. Bernhard Kummel (Harvard University) described the ammonoids in the July 1962 Journal of Paleontology. The preservation of the Meekoceras fauna at this locality is considered to be the finest in North America. This site has been visited over the past 30 years by most of the Triassic specialists and many amateur collectors. The deposition of these beds continue to be a subject of much differing interpretation. Some of the beds lie in a manner corresponding to similar beds in Idaho, whereas some are completely overturned. Jim Jenks, a metallurgical engineer from Salt Lake City, Utah has been collecting and studying the area for 25 years. His favorite tool is a steel bar about six foot long. He usually moves more boulders in an hour than the usual collector does in a day of hard work.

Here, one finds the oldest ammonoids in the world with "colour" patterns. About five years ago, I sent Royal Mapes (Ohio University) some specimens which later resulted in the paper The Oldest Ammonoid "Colour" Patterns by Mapes and Sneck published in Palaeontology, 1987. More intense collecting and study was done in June, 1988 under the umbrella of a National Geographic Society Research Project directed by Royal Mapes. Wolfgang Weitschat has collected the genera, Arctoceras, Paranannites and Xenoceltites from Spitsbergen which are also represented here.

For the serious student, complete listings and descriptions of the ammonoids found in the above mentioned localities can be found in the references. For the collector, there are many other Triassic collecting localities in California, Idaho and Nevada. However, as in most other places, material is getting scarce and one must move a lot of rock and hike a lot to be successful.

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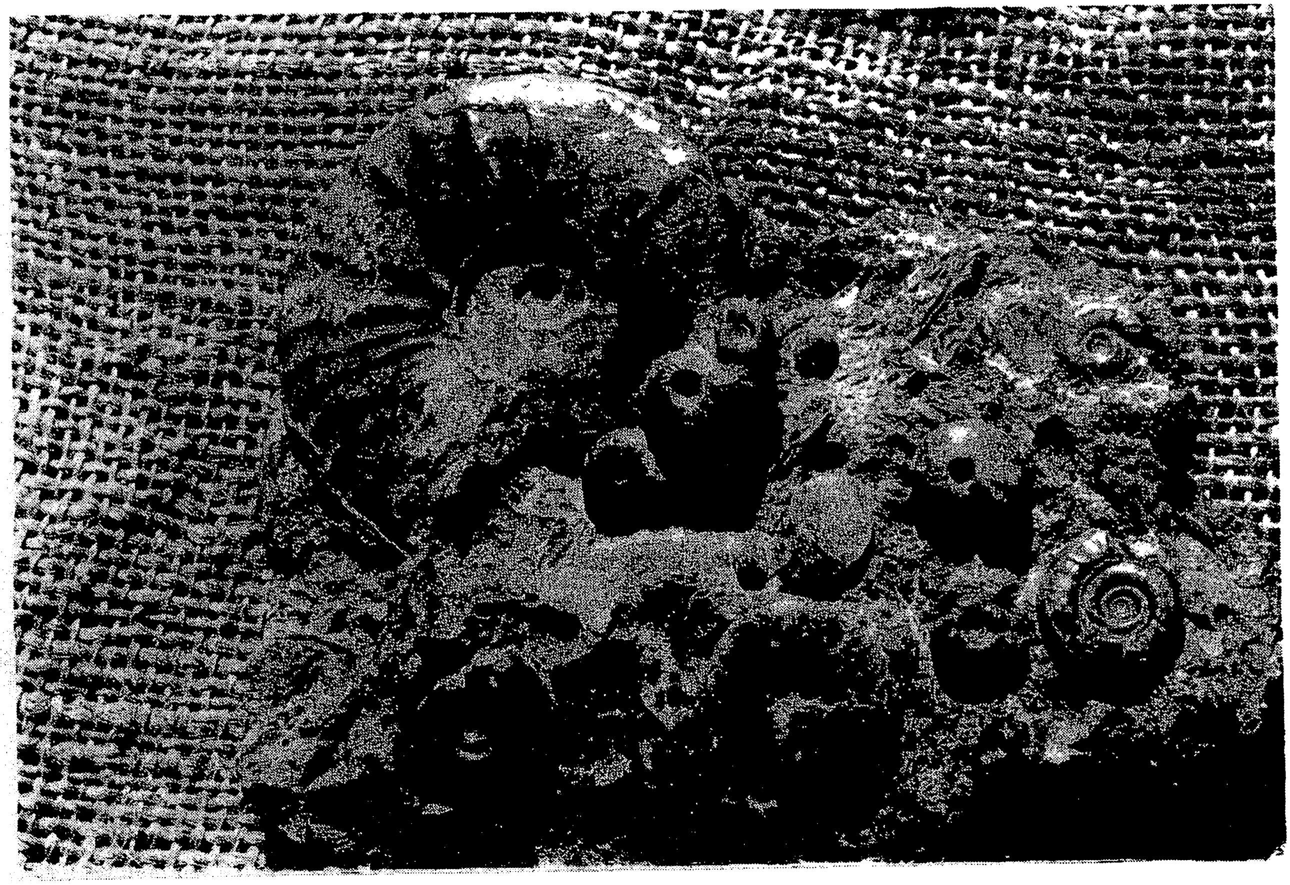

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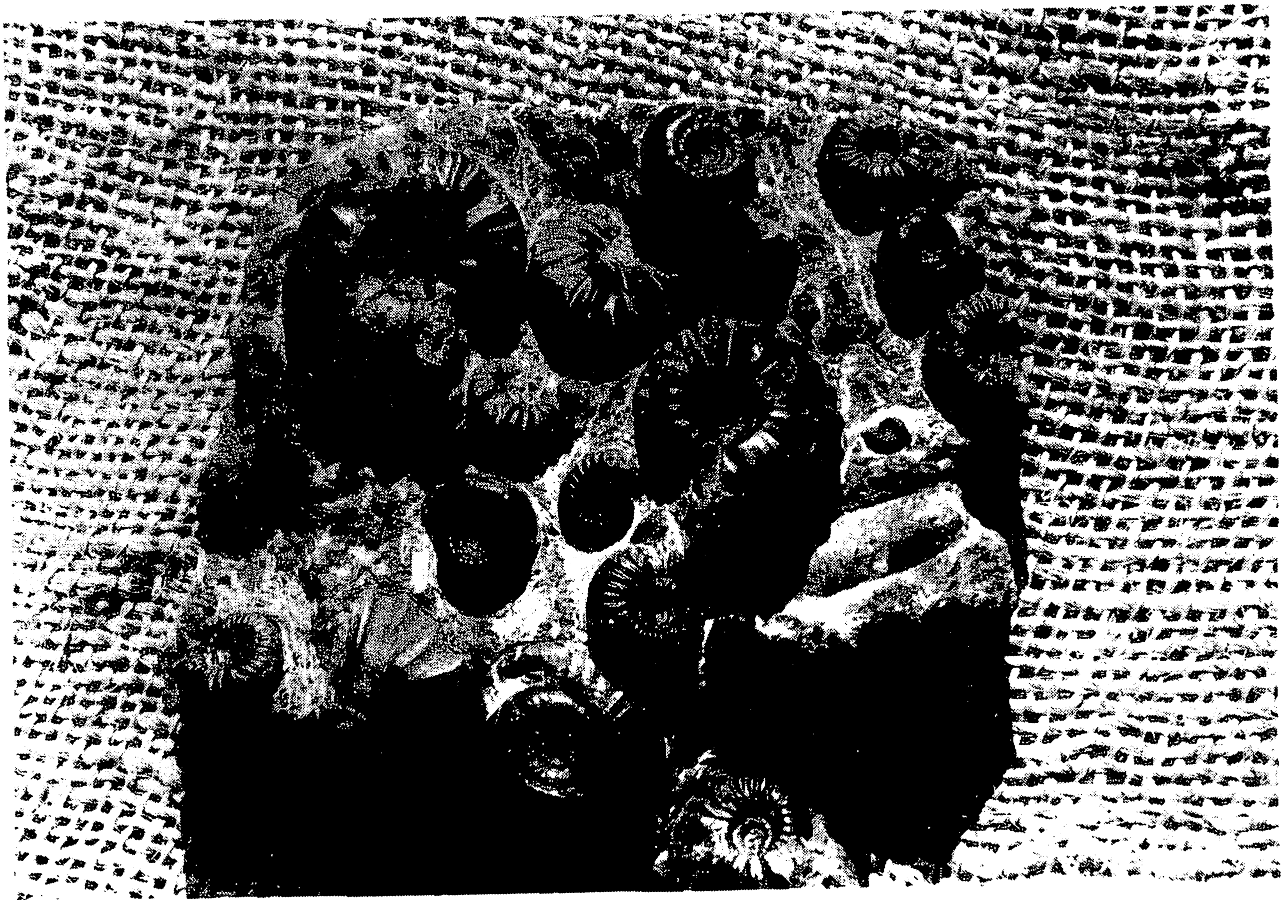

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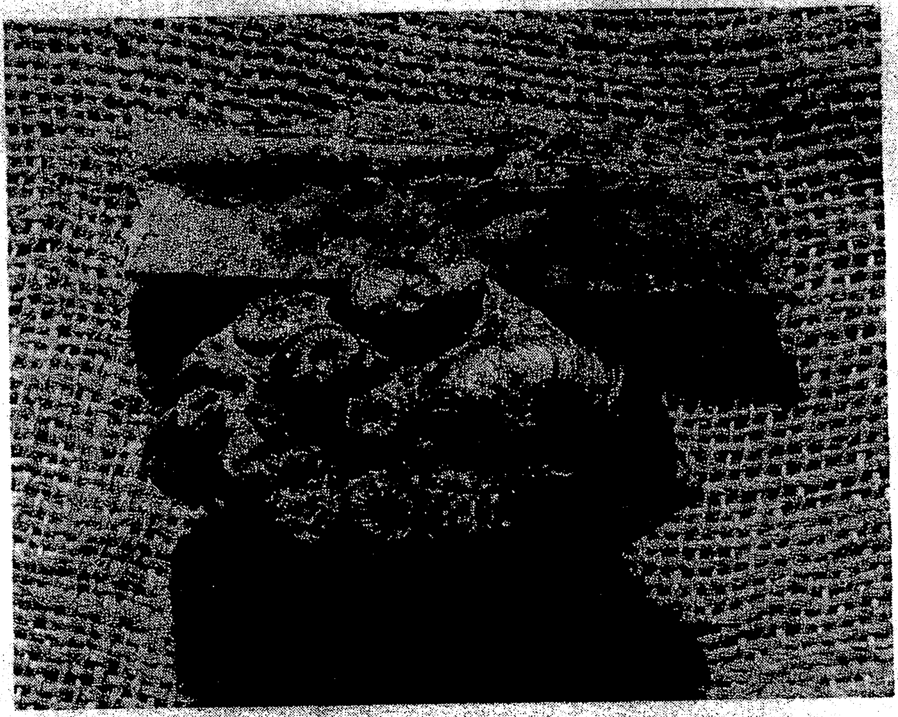

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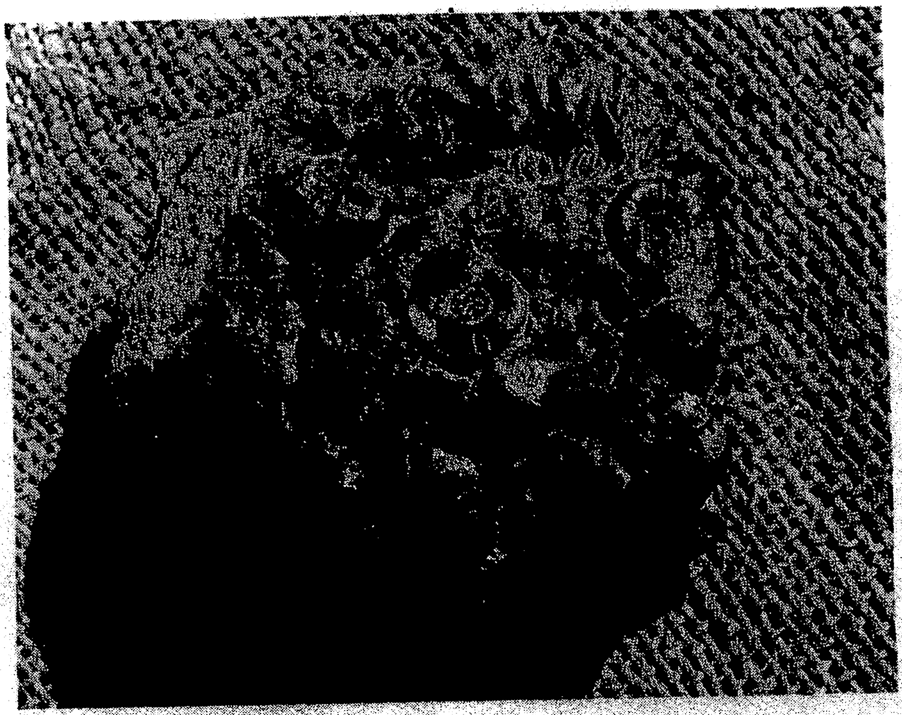

A	Lower Triassic slab, Crittenden Springs, Nevada Smithian stage
B	Middle Triassic slab, Fossil Hill near Lovelock Upper Anisian stage, Meeki zone
C	Middle Triassic slab, New Pass Mines Upper Anisian stage, Rotelliformis zone
D	Lower Triassic slab, Union Wash, California Spathian stage, Haugi zone

All figures one half natural size

A	Arctoceras tuberculatum Dieneroceras knechti Dieneroceras spathi Juvenites septentrionalis Meekoceras gracilitatus Owenites koeneni Paranannites aspenensis
B	Frechites nevadanus Parafrechites meeki Tropigastrites louderbacki
D	Karangatites multicameratus Neopopanoceras haugi "Acrochordiceras" cf. "A" inyoense
C	Proarcestes gabbi Gymnotoceras rotelliformis Paraceratites clarkei Atractites sp.

TEXAS CRETACEOUS AMMONITES

by

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Introduction

Cretaceous exposures (Figure 1) cover about twenty-eight percent of Texas extending from Texarkana in the northeast corner southwest on a broad curve almost to El Paso in the west. The Lower Cretaceous outcrops are further inland and cover an area almost three times larger than that of the Upper Cretaceous. This Period, 135 through 65 million years ago (MYA), is not fully represented in Texas outcrops. The oldest Cretaceous beds of this Period in Texas are in the Torcer Formation of Valanginian Age (131 MYA - 126 MYA) and are exposed only in the Malone Mountains of West Texas in southern Hudspeth County. Figure 2 shows selected Cretaceous stratigraphic units in Texas along with comparable European stages.

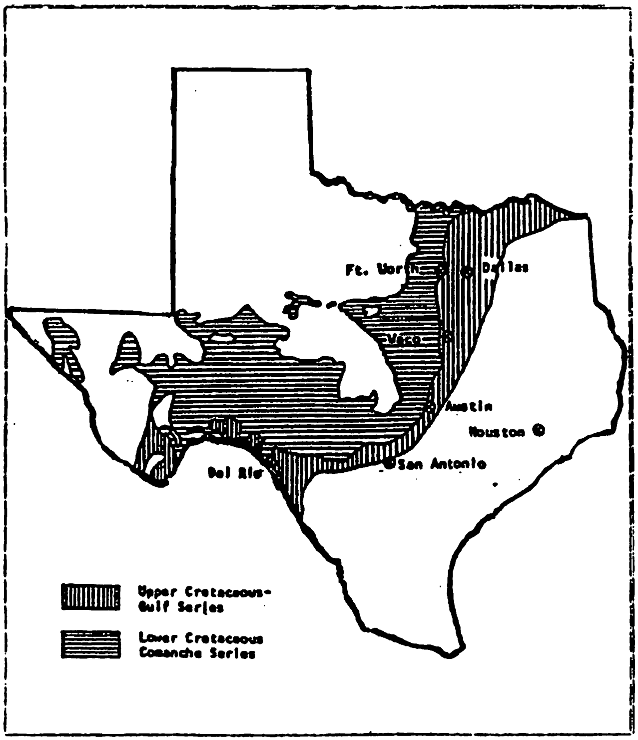


Figure 1.
Cretaceous Exposures in Texas

At various times during the Cretaceous Period in Texas the land was inundated by marine seas. Warm seas provided a variety of conditions: shallow and deep water, tidal flats, extensive reef formations, turbulent currents, and quiet pools. Conditions were very similar to those found today offshore of southern Florida. A gamut of marine vertebrate and invertebrate fauna developed. A group of now-extinct rudistid clams formed large reef complexes in the warm, clear, shallow waters. Coral reefs were created also. Oyster banks were widespread in near-shore bay and lagoon marine environments. Mud flats in low-lying coastal areas allowed the preservation of dinosaur tracks. These ancient Texas environments formed during the Cretaceous Period allowed the creation of one of the most intensely fossiliferous areas found anywhere in the world.

Texas provided excellent living environments for a wide variety of ammonites during a portion of the Cretaceous Period between 115 and 65 MYA. Many areas of Texas were inundated by marine seas and became part of the inland seaway connecting the Gulf of Mexico with the Arctic Ocean. Large numbers of ammonites inhabited these Texas waters at the beginning of the

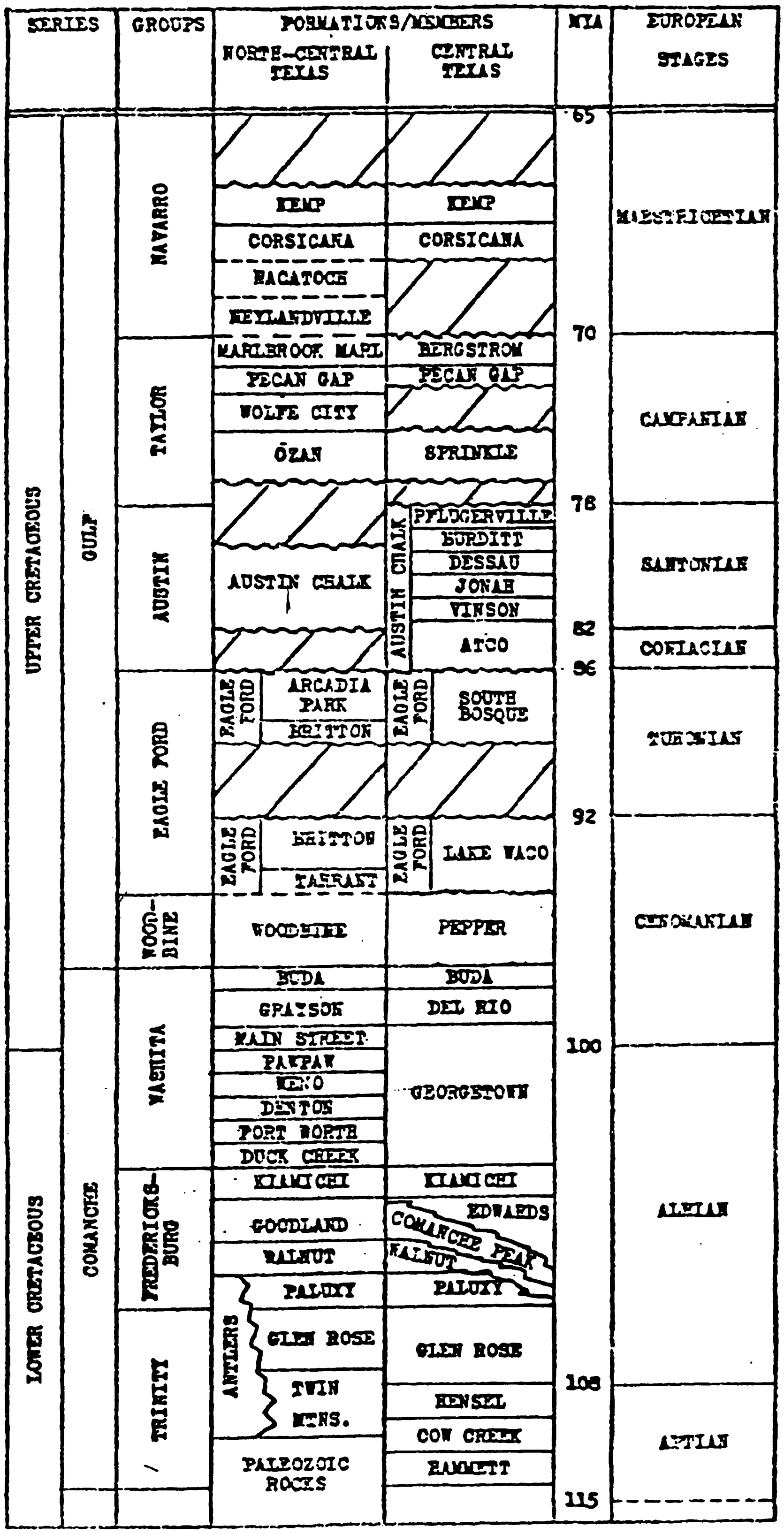


Figure 2. Correlation of Cretaceous stratigraphic units in Austin - Waco - Dallas - Fort Worth areas.

Cretaceous Period. However, near the end of the Period the number and variety of ammonites had greatly declined, and they ceased to exist by the end of the Mesozoic Era.

The abbreviations UK (Upper Cretaceous, Gulfian Series) and LK (Lower Cretaceous, Comanchean Series) have been used extensively in this work. The UK contains the Navarro, Taylor, Austin, Eagle Ford and Woodbine Groups. The LK contains the Washita, Fredericksburg and Trinity Groups.

Ammonites are divided into two general catagories: cosmopolitan and endemic. The cosmopolitan were spread worldwide by the oceans and seas while the endemic were restricted to local areas. At the time, Pangaea had recently separated thus providing shorter open-water journeys than would be necessary today for the cosmopolitan type to spread far and wide. As the Zuni Sea of the Cretaceous Period transgressed and regressed over the North American Craton, many cosmopolitan ammonites were deposited in the sediments. These fossils are identical to those found in the four corners of the world today. It is thought that endemic species evolved by being isolated from the open oceans by the growth of large reefs. Texas seas, as well as others, provided these special conditions. The endemic type comprises about thirty percent of the total ammonite population.

Amateur paleontologists favor ammonites due to their relative rarity, unique ornamentation, and intricate, coiling shapes. Today ammonite research is an active area when, seemingly, work on other mollusks is on the decline. Because of ammonites' short life span and rapid evolution, scientists use them as markers in stratigraphic research to aid in correlating sediments throughout the world. Generally, two areas can be said to be of the same age if the same cosmopolitan ammonite is found in each area.

Published professional literature lists about two hundred ammonite genera and six hundred fifty species in the Texas Cretaceous Period. Many of these ammonites have been described and identified in the last few years, and it is thought that many more are yet to be named. We plan to summarize this material in a future publication. Some of the highlights and descriptions of some common ammonites are presented in this article.

Ammonite Classification

The classification of ammonites has undergone constant review and change since the 1800's. C.W. Wright authored the Cretaceous ammonite classification system revision in the 1957 Treatise of Invertebrate Paleontology. This revision was based largely on the forty years' work of L.F. Spath. Twenty years after the 1957 Treatise publication, Wright wrote that, "-- over three hundred new Cretaceous genera have been published along with many proposed revisions to the classification system." Again, in 1981, Wright revised the Cretaceous classification system in The Ammonoidea, edited by M.R. House and J.R. Senior. Wright concludes that after forty-five years' study on ammonites his new system is "--always liable to be overturned by new discoveries or by a better explanation of known material." Figure 3 compares the order of Cretaceous ammonite Superfamilies found in the 1957 Treatise to the order in the 1981 Ammonoidea classification.

Classification

Treatise	Ammonoidea
Phylloceratacea	Phylloceratidae
Lytoceratacea	Lytoceratacea
(Tetragonitidae)*	Tetragonitacea
Ancyloceratacea	Haploceratacea
Turrilitacea	Perisphinctacea
Scaphitacea	Desmoceratacea
Haploceratacea	Hoplitacea
Perisphinctacea	Acanthoceratacea
Desmoceratacea	Ancyloceratacea
Hoplitacea	Douvilleiceratacea
Acanthoceratacea	Deshayesitacea
	Turrilitacea
	Scaphitacea

Figure 3. Comparison of Cretaceous Ammonite Classification Order
*Family Tetragonitidae changed to Superfamily Tetragonitaceae in Ammonoidea

Differences are found in the heteromorphic families, Turrilitaceae and Scaphitaceae. In 1957 these two Superfamilies were considered to be "old" stock or phylogerontic (as seen in Adkins, 1928). However, in 1981, Turrilitaceae and Scaphitaceae were moved to a later position. Also, the 1957 Hoplitaceae was subdivided into three 1981 Superfamilies: Hoplitaceae, Douvilleiceratacea and Deshayesitaceae.

Morphology

Each fossil phylum and class has unique descriptive terms, and in order to study and identify fossils, the terms should be learned and used properly. Figure 4 illustrates and names common ammonite features.

1. BODY CHAMBER. The body chamber is the last portion of the shell occupied by the living animal.
2. APERTURE. The aperture is the exit of the body chamber and is directed forward (adoral).
3. SEPTA. The posterior shell compartments or septa, successively vacated as the animal built and moved into a new body chamber, were partially filled with fluid and used to regulate hydrostatic pressure or water depth.
4. SIPHUNCLE. A siphuncle or tube connects the septa to allow fluids and gases to fill or empty the chambers enabling the ammonite to ascend or descend.
5. PROTOCONCH. The center of the ammonite spiral is the protoconch and is the first chamber occupied by the juvenile.
6. PHRAGMOCONE. The septa form the phragmocone. The body chamber and protoconch are not included.
7. WHORL. Each shell volution is termed a whorl. The outer portion of the whorl is designated ventral and the inner portion is dorsal.

8. FLANK. The side portion of a whorl is the flank.
9. UMBILICUS. The concave surface on either side enclosed by the last whorl is called the umbilicus.
10. KEEL. A keel is a ridge running along the ventral edge of some ammonites.
11. SUTURE PATTERN. Sutures form a line of contact between the septa and the inside of the shell and can be seen only on some steinkerns or specimens with part of the shell missing. Comparison of suture patterns is essential in separating look-alike ammonites.
12. LAPPET. A lappet is a projection from the aperture which may be a male ammonite feature.

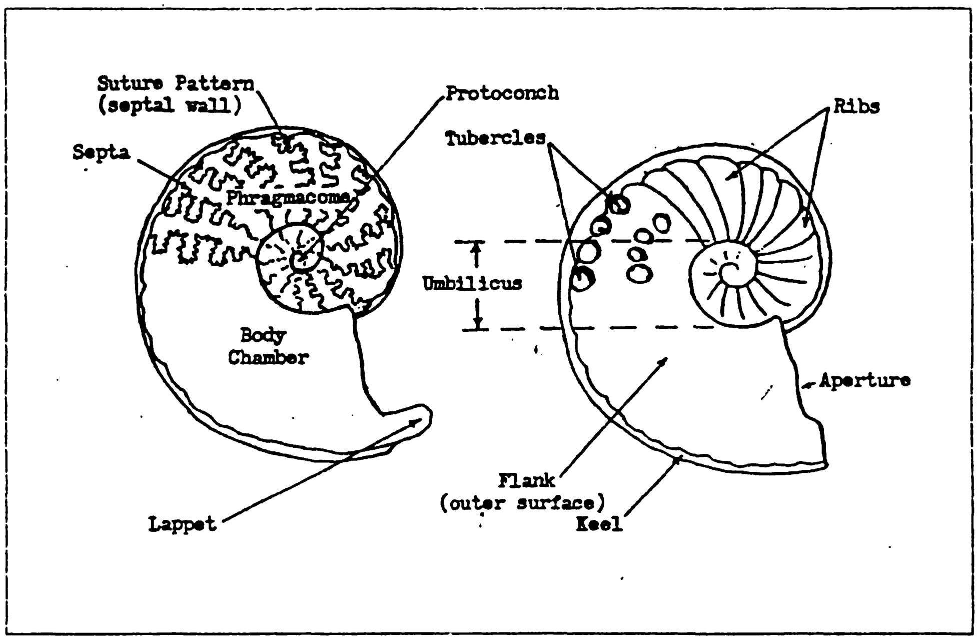


Figure 4. Common Ammonite Features

Shells of ammonites were variously ornamented. Perhaps ornamentation served as a defensive mechanism, camouflage or as a wall-strengthening function. Ornamentation consists of ribs and tubercles which occur in many types, sizes and patterns. Tubercles might appear on the ribs or might appear to be separate from them, and spines grew on some species. Color patterns are thought to have been present on the shell.

Ammonites are further defined by the shell shape. Involute types have overlapping whorls which enclose the previous whorl. Evolute types do not have overlapping whorls. However, there are many stages to be found between involute and evolute. Ammonites that have only partial or no coiling may be found and are called heteromorphs. General types of ammonite shells are given in Figure 5, cross sections of whorl outlines are in Figure 6, and direction of rib slant is shown in Figure 7.

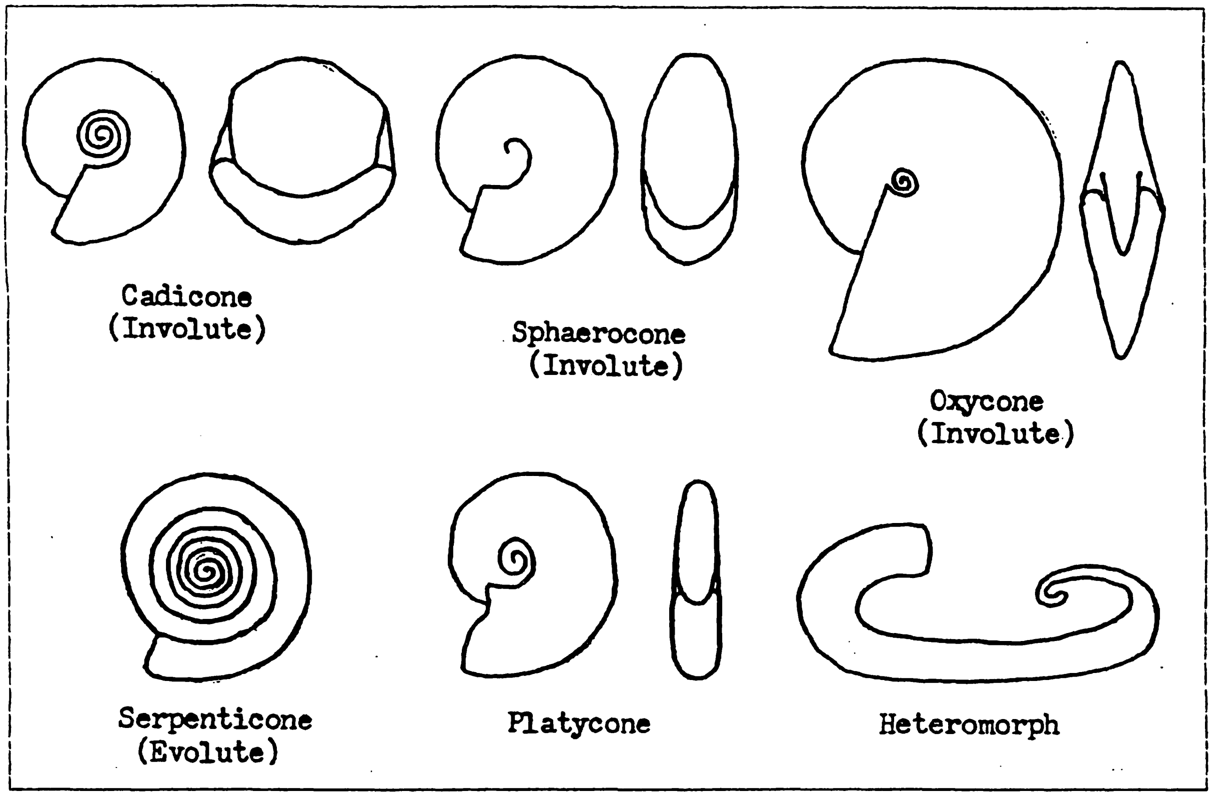


Figure 5. Types of Ammonite Shells (redrawn from Lehman)

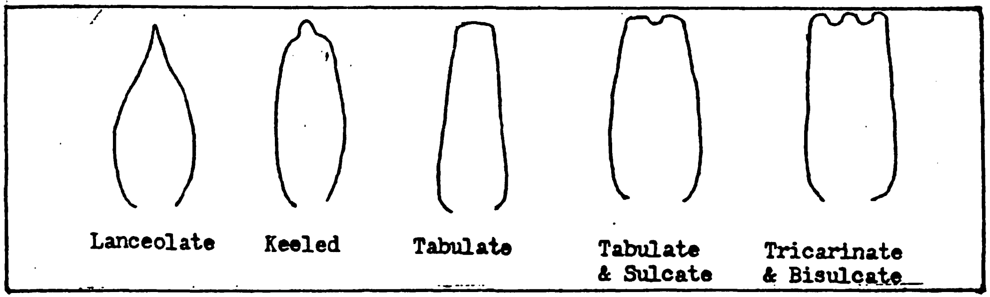


Figure 6. Types of Whorl Outlines

Ammonite Size is relative and subject to interpretation. For this publication the following sizes are used: Micromorph = up to one inch (25 mm), Small = one to three inches (25-75 mm), Medium = three to eight inches (75-200 mm), Large = eight inches to three feet (200-900 mm), and Giant = over three feet (over 900 mm). Careful measurement of the ammonite specimen provides good hard information for identification. Figure 8 illustrates locations for measurements.

Ammonite Identification Problems

Paleontologists have devised many methods to sort out and cope with the diversity of identification problems. W.S. Adkins, in the 1920's, felt unique shell

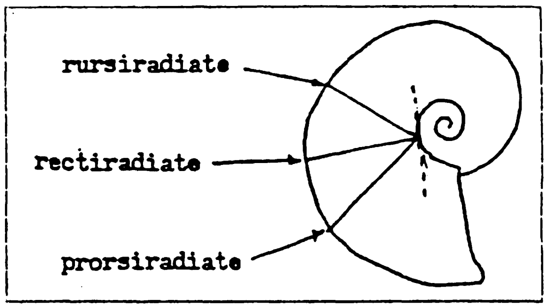


Figure 7. Types of Rib Angles

features helped catagorize the ammonites, and G. Scott, in 1940, used general shell structure. Lately, several authors rely heavily on suture patterns for separation of genera. The main difficulties are: <u>Ornamentation</u> can, and often does, change with the specimen's age. Thus, the outer whorl of a mature ammonite can be different from that of a specimen of a juvenile of the same species. <u>Suture Pattern</u> can change as the ammonite ages. Therefore, the pattern on an inner whorl probably is different than that on an outer whorl. <u>Sexual Dimorphism</u> creates different sizes, and there is controversy as to which sex is "macro" and which is "micro". The general belief is that the female (macroconch) is larger than the male (microconch). Many "identified" species actually may be a different sex of the same species. <u>Short Life Span</u> and <u>Rapid Evolution</u> caused many variations. The rapid evolution often allowed the re-development of features found on earlier genera. Thus, in many cases, a young species may have features of an older one. <u>Steinkerns</u> (internal molds) are the most commonly found ammonite fossil. Thus, their state of preservation is of extreme importance in identification. The living chamber is rarely found with the main ammonite shell. Steinkerns have the advantage of revealing the sutura pattern and internal ornamentation. External ornamentation is generally unknown.

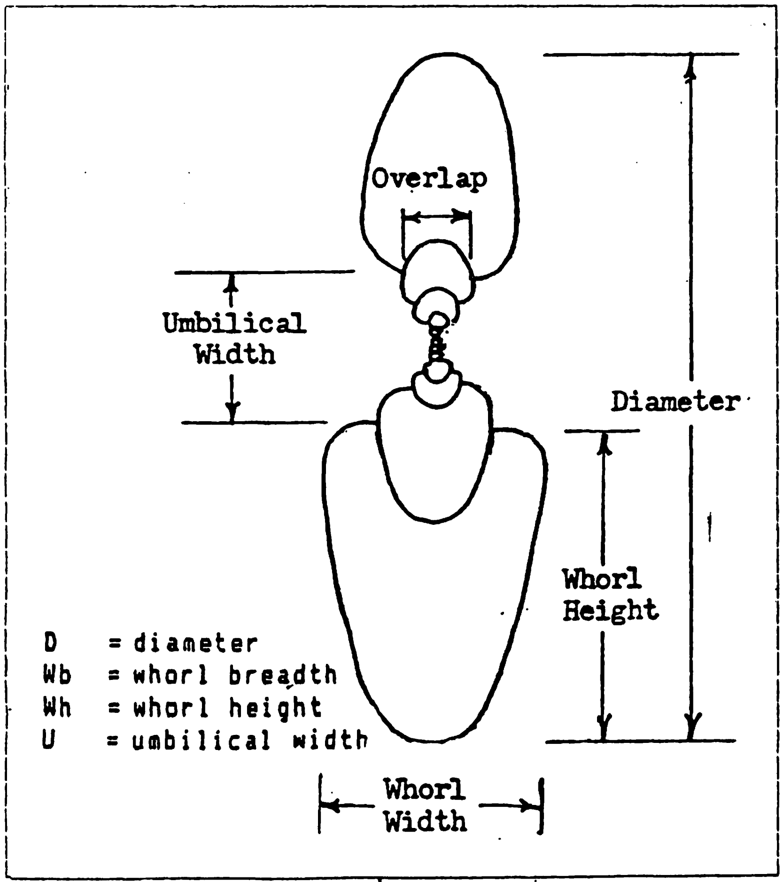


Figure 8. Locations for Measurements

All of the identification methods developed by paleontologists have value. Usually, identification is achieved through using a combination of all techniques.

<u>Steps To Identification</u>

Collect and record precise data from the best specimens available for

Figure 9

AMMONITE MEASUREMENT DATA

Sample

Genus/Species Prionocyclus hyatti

Location Found Dallas County

Group/Formation Eagle Ford Group   Arcadia Park Frm.

Ammonite Shape evolute - robust

Whorl Shape depressed

Rib Pattern Coarse, distinct

Ornamentation shoulder tubercles; nodate, siphonal keel

Specimen Number	1	2	3
Diameter (D), mm	33.8		
Umbilical Dia. (U), mm	13.4		
Whorl Height (Wh), mm	11.3		
Whorl Breadth (Wb), mm	15.8		
Wb/Wh Ratio	1.40		

Suture Drawing

identification. It is preferred to have more than one specimen to compare. Reliable, accurate identifications require exact location and detailed geological information (including group and formation). Careful observation of the whorl shape, rib pattern and other ornamentation should be made. Basic measurements, including umbilical diameter, whorl height and breadth, and whorl ratio are necessary. Sketch the suture pattern if visible. Figure 9 is a typical ammonite measurement form.

After the basic data have been obtained, the following Identification Key can be used to help identify the specimen to the genera level. The Key presents steps to narrow the search by identifying features as being present or absent. The first step divides ammonites into either conventional, flat, coiled ammonites or heteromorph ammonites. Conventional ammonites are divided into keeled and non-keeled types. Heteromorphs are divided into those in one plane or those in more than one plane. At this time this Key does not include all genera found in Texas.

Artificial Key To Texas Cretaceous Ammonite Genera
(Revised Adkins, 1928, Key)

- I. Discoidal coiling (shell almost a planospiral coil).
  - A. No Keel
    - 1. Venter convexly rounded in adult.
      - a. Ribs cross venter.
        - (1) Large (*Eopachydiscus*)
        - (2) Medium (*Douvilleiceras*, *Kazanskyella*, *Tarrantoceras*)
        - (3) Small (*Moremanoceras*, *Quitmanites*, *Stoliczkaia* [*Mantelliceras*, *Dufrenoyia* - ribs may be interrupted on venter])
      - b. Ribs do not cross venter.
        - (1) Mid-line of venter smooth.
          - (a) Micromorph complex suture.
            - [1] Oval whorl form (*Kossmatella*)
            - [2] Square to trapezoidal whorl form (*Tetragonites*)
          - (b) Micromorph simplified suture.
            - [1] Ribs and tubercles are absent. (*Flickia*)
          - (c) Macromorph. (*Pachydiscus*)
        - (2) Form compressed, venter is truncated or excavated.
          - (a) Venter excavated, bounded by nodes. (*Metoicoceras*)
          - (b) Venter narrow, involute, not bounded by nodes. (*Placenticeras*)
        - (3) Form not compressed. (*Mammites*, *Pseudaspidoceras*)
        - (4) Mid-line of venter is tuberculate.
          - (a) Mid-tubercle is prominent. (*Acanthoceras*, *Budaiceras*, *Conlinoceras*)
          - (b) Mid-tubercle is reduced or absent in adult. (*Eucalycoceras*)
    - 2. Venter is narrow.
      - a. Giant species.
        - (1) Ribs do not cross venter in some species. (*Parapuzosia*)
      - b. Medium species.
        - (1) Saddles are generally undivided. (*Engonoceras*, *Knemiceras*. *Metengonoceras*, *Protengonoceras*)
        - (2) Saddles are divided. (*Sphenodiscus*, *Coilopoceras*)
  - B. Keel present.
    - 1. Keel is nodose or serrate.
      - a. Nodose keel. (*Prionocycloceras*)
      - b. Coarsely serrate keel. (*Barroisiceras*)
      - c. Medium-sized serrations on keel, ribs are fine and numerous. (*Collignoniceras*)
    - 2. Keel is uninterrupted.
      - a. Whorl is taller than wide and thin from side to side.
        - (1) Numerous curved ribs and no tubercles. (*Oxytropidoceras*)

(3) Branching flat ribs on its early whorls. (*Manuaniceras*)

(4) Ribs with steep forward slopes with flank and shoulder tubercles, but no umbilical tubercles. (*Venezoliceras*)

b. Whorl is taller than wide, but not thin side to side.

(1) Three plus rows of tubercles.

(a) Three or more rows of tubercles. (*Mortoniceras*, *Texanites*)

(b) Multiple rows of tubercles. (*Craginites*)

(2) One or two rows of tubercles.

(a) Two ventral-shoulder tubercles and no mid-flank tubercles. (*Mortoniceras* (*Drakeoceras*))

(b) Ribs and tubercles normally absent. (*Dipoloceras*)

(c) Ribs are many and obscure. (*Prohysteroceras*)

c. Whorl is quadrate with three rows of tubercles, keel not depressed. (*Pervinquieria*)

II. Heteromorphs, partially uncoiled or coiling not discoidal.

A. Coiled or bent in one plane.

1. Shaft is simple and straight (early minute coil rarely preserved). (*Baculites*, *Sciponoceras*, *Lechites*)

2. Several subparallel shafts with early helical coiling. (*Hamites*, *Metaptychoceras*)

3. Open plane, spiral usually followed by shaft or hook.

a. Two almost parallel shafts, tubercles connected across venter by rib. (*Idiohamites*)

b. Irregular coil, ribs thin, tubercles joined across venter by rib. (*Allocrioceras*)

c. Fragments only, two rows of ventrolateral and one row of ventral tubercles. (*Phlycticrioceras*)

4. Evolute or involute shell followed by a shaft or hook. (*Scaphites*, *Yezoites*, *Worthoceras*)

B. Coil or inflections *not* in one plane.

1. Coil is a loose spire followed by shaft and hook. (*Anisoceras*)

2. Coil is a tight, turrilitic spire at some stage.

a. Four rows of equal-sized tubercles, middle row separated by spiral groove, tending to uncoil at the body chamber.

(1) Apical angle starts at tight coil. (*Mariella* (*Plesioturrilites*))

(2) Apical angle starts with a straight shaft. (*Mariella* (*Wintonia*))

b. Two to four equal-sized tubercles with ribs in a tight coil. Variable apical angle. (*Turrilites*)

c. Two or three tubercles per rib, very dense ribs. (*Ostlingoceras* (*Ostlingoceras*))

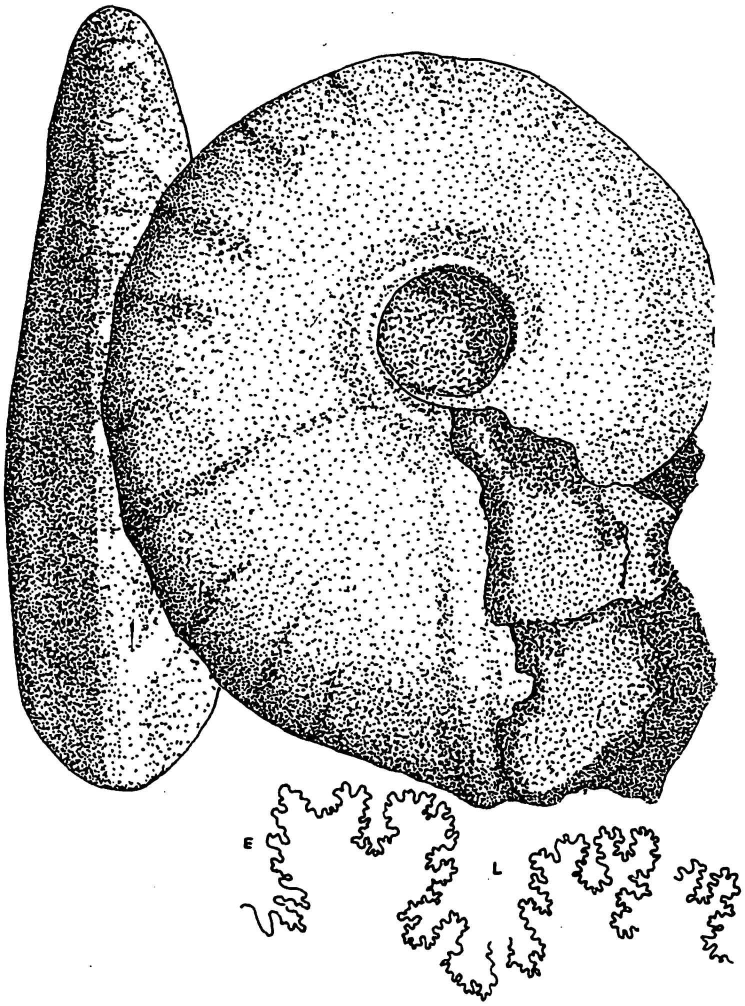
d. Middle row of tubercles are fewer and larger, ribs almost absent. (*Hypoturrilites*)

3. Coiling is irregular and tubercles are subordinate to dense ribs. (*Bostrychoceras*, *Nostoceras*)

Eopachydiscus marcianus (Shumard, 1854)

LK Washita (Duck Creek, Georgetown), Fredericksburg (Edwards) - Albian
Superfamily Hoplitaceae

1854 Ammonites marcianus Shumard*
1860 Ammonites brazoensis Shumard
1904 Pachydiscus laevicaniculatus Roemer manuscript; Lasswitz
1955 Eopachydiscus laevicaniculatus (Lasswitz, ex Roemner manuscript); Wright
1955 Eopachydiscus brazoensis (Shumard); Wright
1957 Eopachydiscus marcianus (Shumard); Wright



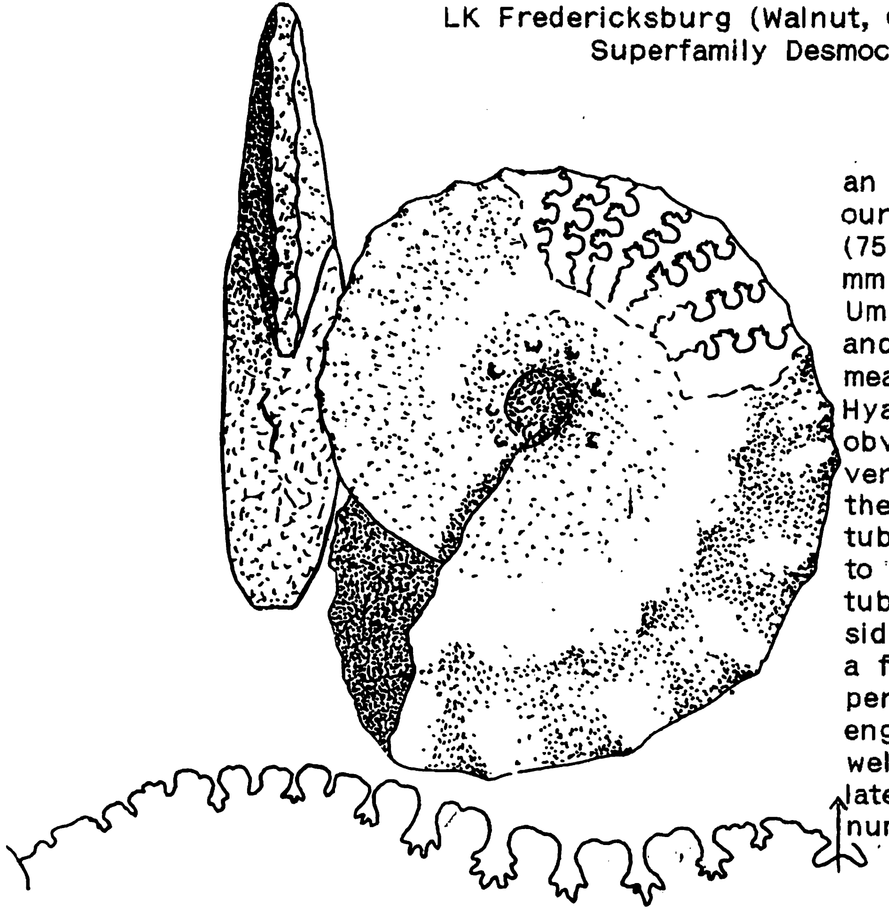
x 0.7

E. marcianus is so numerous in some localities near Lake Texoma, it has been used as flower bed edging and gate posts. Medium to large- sized, it is moderately involute and compressed with a high oval whorl. The diameters of juvenile specimens range from 2 to 6 inches (50 to 150 mm), and 14 inches (355 mm) is common for adults. Cragin measured one specimen at 2 feet (610 mm) in diameter with a whorl height of 8 inches (200 mm) and a whorl width of 6 inches (150 mm). The ribs are gently undulating and cross the rounded venter, swinging forward in the crossing. These ribs may be elevated in the young, but may fade to obscurity in some adults. Whorls are few in number. The suture pattern is a major identification feature, and it is composed of a trifid lateral lobe and numerous auxilaries, all of which, are minutely frilled.

*Note: This synonymy is intentionally abbreviated. The species actually went through a Pachydiscus stage for both Ammonites marcianus and A. brazoensis in the early 1890's and through a Desmoceras stage for all three species in the mid-1920's.

Engonoceras gibbosum Hyatt, 1903

LK Fredericksburg (Walnut, Goodland) - Albian
Superfamily Desmocerataceae



x 1

E. gibbosum is medium-sized with an oxycone shape. Measurements of our steinkern are: diameter: 3 inches (75 mm), whorl height: 1.75 inches (44 mm), whorl width: 0.8 inches (20 mm). Umbilicus width is 0.3 inches (8 mm), and the Wb/Wh ratio is 0.47. (These measurements compare favorably with Hyatt's specimens.) Tubercles are obvious on the lateral edge of the venter and umbilicus, but are faint on the flank. The number of flank tubercles does not seem to be related to either umbilical or ventral tubercles. The later alternate on each side producing a zigzagging outline to a flat, narrow venter. Ribs are not perceptible. A major feature is the engonocerid suture pattern which is well-separated. Each side has ten lateral lobes and eleven saddles, a number of which are bifid or notched.

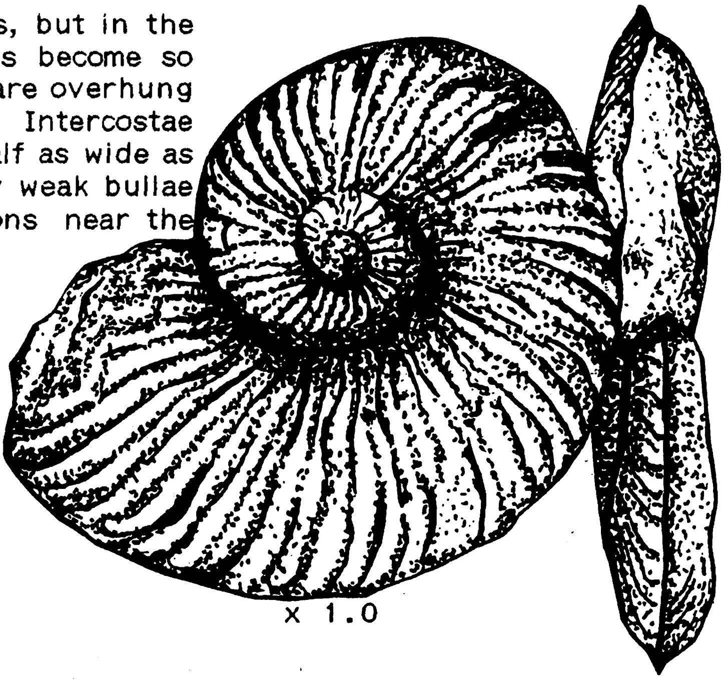
Suture pattern enlarged.

Manuaniceras supani (Lasswitz, 1904)

LK Fredericksburg (Walnut, Goodland, Comanche Peak, Kiamichi) - Albian
Superfamily Acanthocerataceae

1904	Sonneratia supani Lasswitz
1920	Schloenbachia acutocarinata (Shumard); Adkins and Winton
1927	Oxytropidoceras n.sp. (aff. supani Lasswitz); Adkins
1938	?Oxytropidoceras sp. ind. Riedel
1956	Oxytropidoceras carbonarium (Gabb); Benavides
1966	Manuaniceras supani (Lasswitz); Young

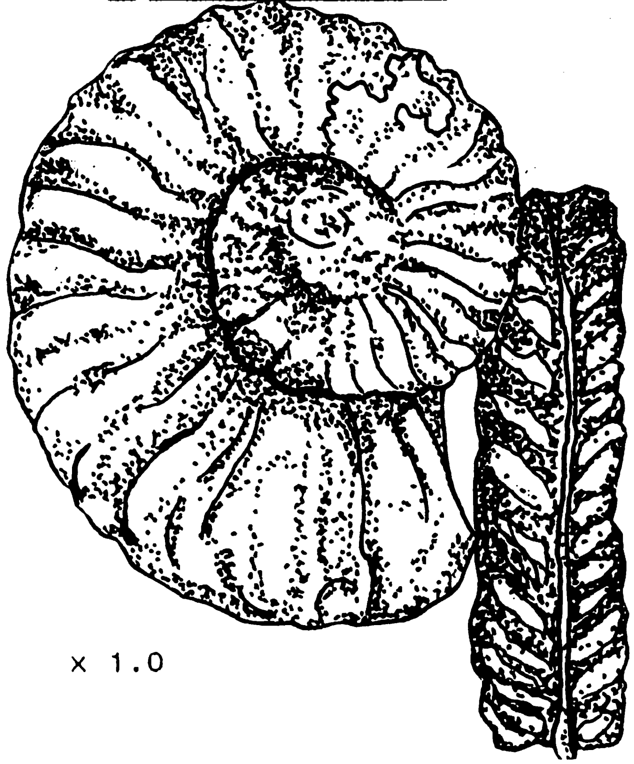
M. supani is one of the most widely spread ammonites of the Fredericksburg Division. It ranges from Williamson County on the south to the Red River on the north and westward beyond Ft. Stockton, even into Chihuahua, Mexico. M. supani is medium-sized, obtaining diameters up to 8 inches (200 mm), and has a slightly expanding umbilicus with an elongate oval whorl section. The height-width ratio of the whorls decreases at the greatest diameter. Ribbing is dense, and the young have flattened ribs, but in the mature specimens the ribs become so high that the intercostae are overhung by the walls of the ribs. Intercostae are normally about one-half as wide as costae. Elongate and very weak bullae might appear at bifurcations near the umbilicus.


x 1.0

Dipoloceras fredericksburgense Scott, 1928
UK Fredericksburg (Upper Goodland) - Albian
Superfamily Acanthocerataceae

1928 Dipoloceras fredericksburgense Scott
1951 Dipoloceras (Diplasioceras) fredericksburgense Scott; Collignon
1966 Dipoloceras fredericksburgense Scott; Young

D. fredericksburgense has been found in the Upper Goodland Limestone in Tarrant County. The holotype measures 3.25 inches (83 mm). The venter has a longitudinal groove with a thin prominent keel which is a striking feature of this species. The coiling is nearly flat, almost slender, and the umbilicus is wide and deep. The whorl section is quadrate. The ribs are irregular and flexuous, either single or dividing near the venter. Occasionaly, the ribs flare, thicken, and turn forward. Sometimes the ribs thicken at the ventrolateral edges then gradually fade away beside the sulcate area. Umbilical tubercles, common on the African form, are absent on Texas fossils.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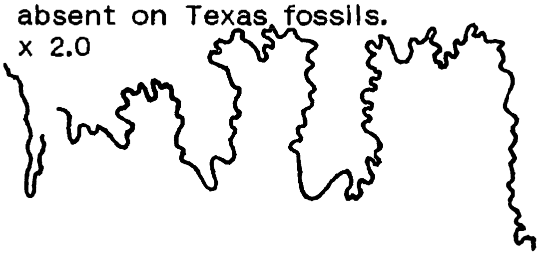
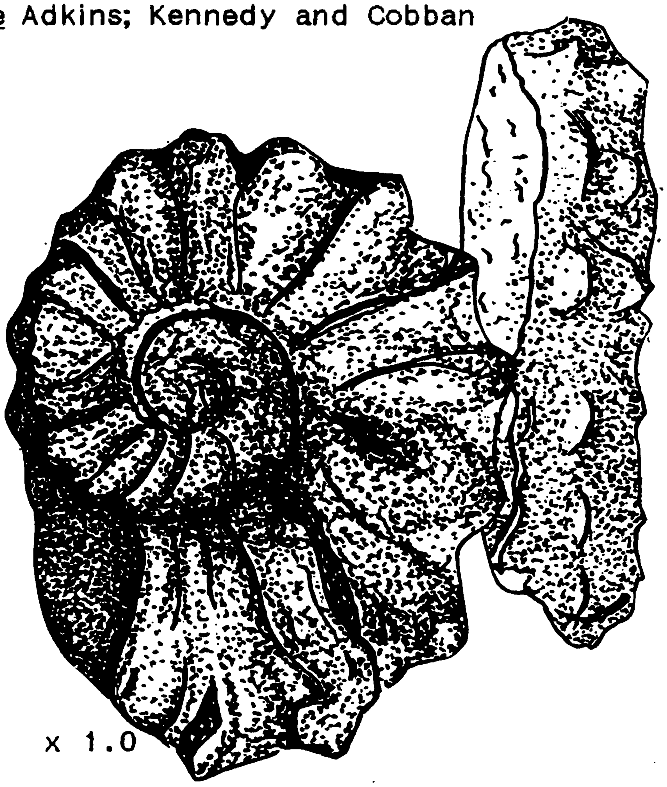


Acanthoceras bellense Adkins, 1928

UK Eagle Ford (Tarrant) - Cenomanian
Superfamily Acanthocerataceae

1928 Acanthoceras bellense Adkins
1942 Acanthoceras aff. rhotomagense (Defrance); Moreman
1942 Acanthoceras aff. hunteri Kossmat; Moreman
1942 Acanthoceras validum Moreman
1942 Acanthoceras aff. sherborni Spath; Moreman
1942 Acanthoceras stephensoni Adkins; Moreman
1942 Acanthoceras aff. cunningtoni (Sharpe); Moreman
1942 Acanthoceras aff. cunningtoni var. cornutum Kossmsat; Moreman
1942 Acanthoceras pepperense Moreman
1959 Acanthoceras n. sp. aff. A. turneri White, Adkins; Matsumoto
1990 Acanthoceras bellense Adkins; Kennedy and Cobban



x 1.0

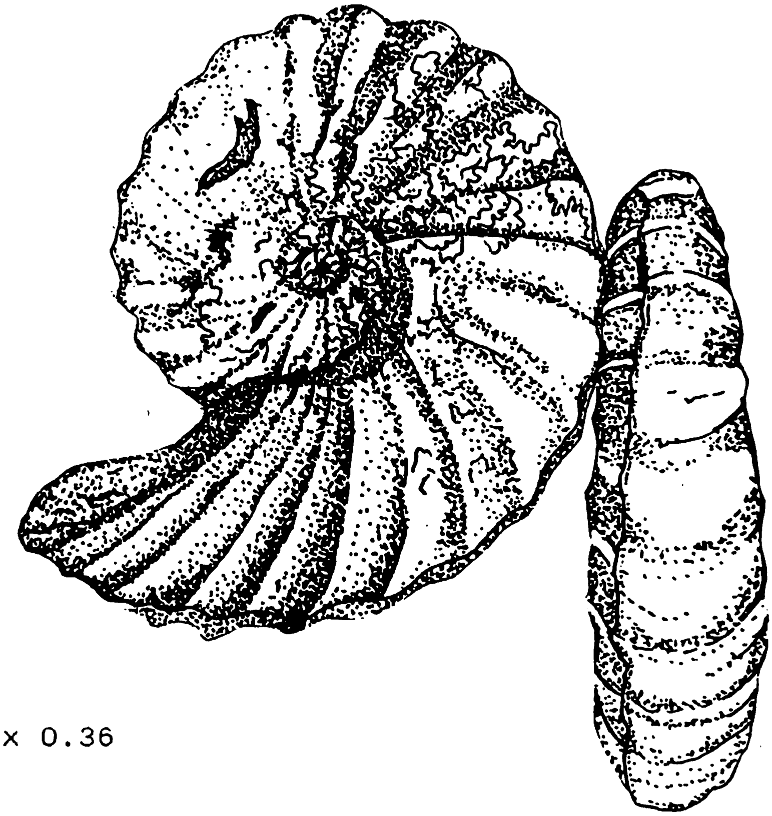
A. bellense is small to medium-sized with fairly evolute coiling. The holotype measures 3.5 inches (87.5 mm), and an average of the specimens studied by Kennedy and Cobban is 3.5 inches (87.5 mm). It has a moderately deep and wide umbilicus with rounded walls taking about thirty per cent of the specimen's diameter. The whorls are massive and slowly expanding. The venter is flattened with broadly rounded ventrolateral shoulders. The intercostal whorl section is depressed trapezoidally with the greatest breadth just outside the umbilical shoulder. The primary ribs are bullate alternating with shorter or non-bullate primary at the smallest diameter. In middle growth, ornamentation is highly variable with most specimens having 17-20 primary ribs per whorl. Bullae give rise to straight, broad prorsiradiate ribs (weak to strong) which terminate in inner ventrolateral tubercles that are initially clavate but become conical and horn-like as the specimen's size increases.

Metoicoceras geslinianum (d'Orbigny, 1850)

UK Eagle Ford (Britton) - Turonian
Superfamily Acanthocerataceae

1841 Ammonites catillus d'Orbigny
1850 Ammonites geslinianus d'Orbigny

1927 Metoicoceras irwini Moreman
1942 Metoicoceras ornatum Moreman
1942 Barroisiceras trinodosum Moreman
1942 Barroisiceras brittonense Moreman
1981 Metoicoceras geslinianum (d'Orbigny); Wright and Kennedy



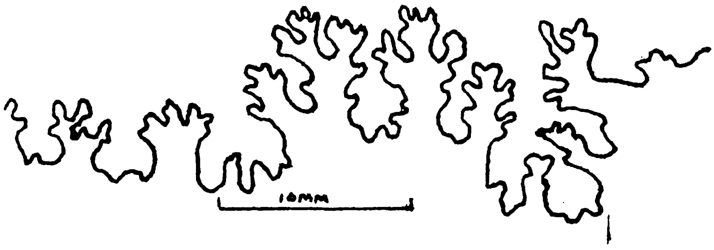
x 0.36

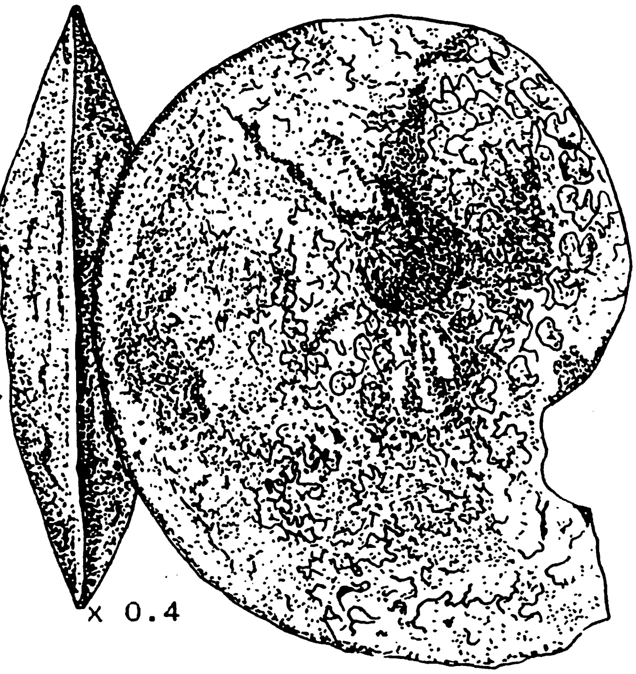
M. geslinianum is strongly dimorphic with the microconch ranging in size from 5.3 inches (135 mm) to 8.3 inches (210 mm) in diameter. It is evolute, stoutly whorled, coarsely ribbed and tuberculate. Commonly, there are eight to ten strong umbilical bullae per whorl in the middle growth stages. The ribs are strong, straight, prorsiradiate in pairs with additional short intercalatories for about 20 ribs per whorl. The macroconchs are adult when the diameter is between 7.7 inches (195 mm) and 9.6 inches (245 mm). Coiling is more involute than in the microconch, the whorl section is higher and more compressed, and the tubercles are lost on the body chamber. The macroconch umbilicus is smaller with many more ribs, numbering twenty-eight to thirty-two in most cases.

Coilopoceras springeri Hyatt, 1903
UK Navarro (Escondido) - Maestrichian
Superfamily Acanthoceratacea

1903 Coilopoceras springeri Hyatt
1931 Coilopoceras eaglefordense Adkins
1931 Coilopoceras chispaense Adkins
1931 Coilopoceras sp. aff. C. springeri Hyatt; Adkins
1978 Glebsoceras chispaense (Adkins); Young and Powell
1978 Coilopoceras eaglefordense Adkins; Young and Powell
1980 Coilopoceras springeri Hyatt; Cobban and Hook

C. springeri represents both the smooth and ribbed forms of the genus. Specimens with diameters ranging from seven inches (175 mm) to fourteen inches (355 mm) have been described by Kennedy. In the middle and late growth stages it is compressed, involute, smooth or feebly ribbed with a sharp venter. It can be stouter, more evolute and those with ribs can have about twelve ribs per whorl. No ventrolateral tubercles are found. The venter in very early whorls is well-rounded but changes to lanceolate later. There is no keel. Occasionally, if the ribbing is pronounced, umbilical bullae are present.

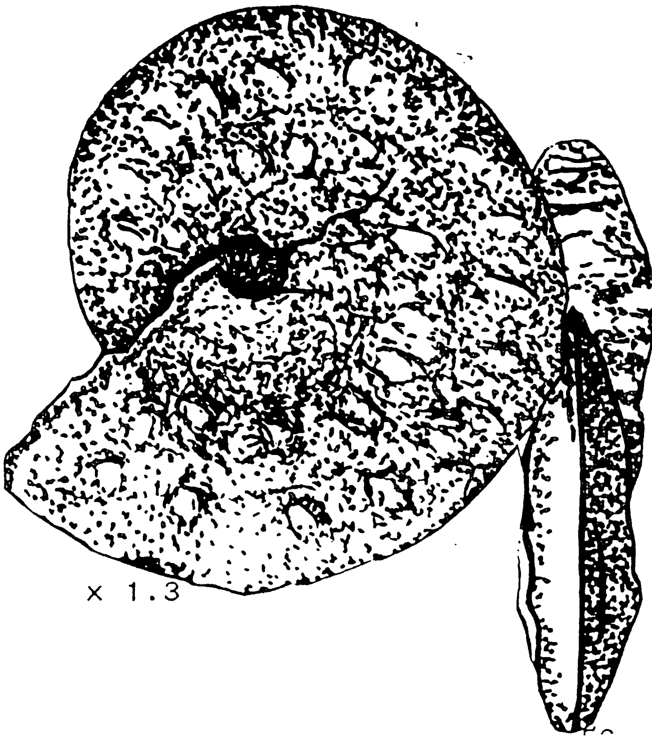




Sphenodiscus pleurisepta (Conrad, 1857)
UK Navarro (Escondido) - Maestrichian
Superfamily Acanthocerataceae

1857 Ammonites pleurisepta Conrad
1873 Ammonites pedernalis Binckhorst
1898 Sphenodiscus pleurisepta (Conrad); Bohm

S. pleurisepta is found in Texas near Laredo and near Eagle Pass in Webb and Maverick Counties from the Eagle Pass Beds of the Upper Cretaceous. This medium-sized species [Hyatt describes a range from 4.5 inches (114 mm) to 7.5 inches (190 mm)] has a narrow and abrupt umbilical zone. It is involute and has a solid keel. The acute venter becomes blunted on the last part of the exposed volution. The outer part of the whorl is convex while the surface between the inner line and the umbilical shoulder is definitely concave. There can be fold-like, short costae between tubercles, and they may have a bifurcated look when well-developed. Two distinct rows of lateral tubercles (nodes), transversly elongated and radiating about 0.3 inches (8 mm) apart, are a feature of the species.

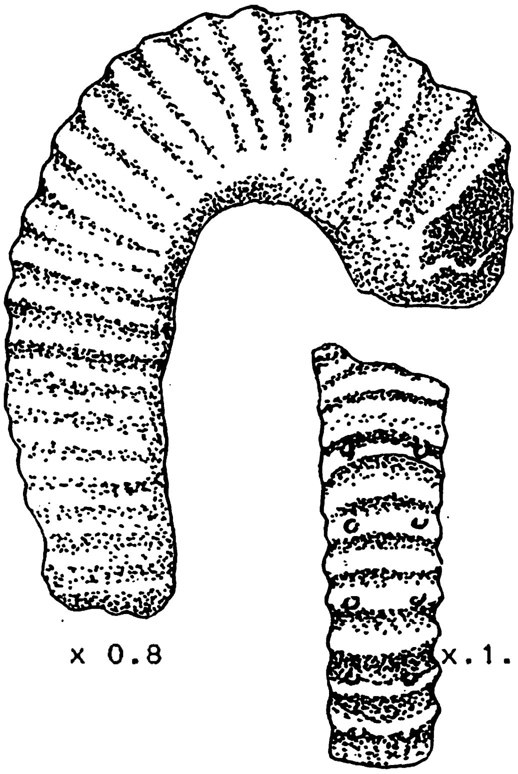


Idiohamites fremonti (Marcou, 1858)

LK Washita (Duck Creek), Fredericksburg (Kiamichi and Del Carmen) - Albian
Superfamily Turrilitaceae

1858 *Hamites fremonti* Marcou
1928 *Exiteloceras fremonti* (Marcou); Adkins
1933 *Idiohamites fremonti* (Marcou); Adkins
1965 *Idiohamites comanchensis* (Adkins and Winton); Clark

I. fremonti is usually found as straight or hooked, candy-cane fragments 2 inches (50 mm) to 4.7 inches (120 mm) long. The circular to oval whorl section has a diameter of about 0.8 inches (20 mm). Ribs are ventrally prominent and become obscure over the dorsal border. The ribs can be perpendicular or slightly oblique. A tubercle is found on the ventral margin of every second to fourth rib. Occasionally, tubercles are found below the mid-lateral position. It is a rarity to find these fossils with either shell or suture pattern. Mud casts frequent Texas collections.



x 0.8

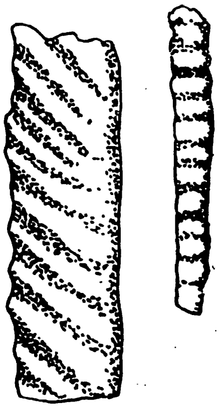
x.1.2

Sciponoceras gracile (Shumard, 1860)

UK Eagle Ford (Britton) - Upper Cenomanian
Superfamily Turrilitaceae

1860 *Baculites gracile* Shumard
1951 *Sciponoceras gracile* (Shumard); Cobban

The protoconch and initial whorl of *S. gracile* are rarely found. The remainder is a slender, straight ammonite that enlarges gradually toward the aperture. The cross section is circular to oval. The diameter of the shaft is about 0.28 to 0.35 inches (7 to 9 mm). Occasional large adults [shaft diameter about 1.6 inches (40 mm)] are thought to be macroconchs. Ornamentation consists of prorsiradiate, ventral ribs and regularly spaced constrictions which are 1.0 to 1.5 diameters apart and have 5 to 7 ribs in between. The ribs become stronger near the dorsally facing aperture. The suture has a bifid, lateral lobe and a small



x 1.0

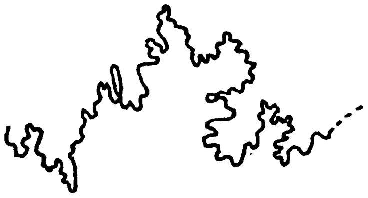
trifid, antisiphonal lobe. Saddles and E, L and U lobes are rectangular in shape. The S. gracile zone is an important coordinating zone for the Upper Cenomanian from Texas through to Montana and in Western Europe. The type species is from Grayson County, Texas.

Mariella (Wintonia) brazoensis brazoensis (Roemer, 1849)

LK Washita (Main Street, Grayson, Del Rio, Georgetown) - Albian
Superfamily Turrilitaceae

1849 Turrilites brazoensis Roemer
1853 Paraturrilites (Plesioturrilites) brazoensis (Roemer); Breistroffer
1957 Mariella (P.) brazoensis (Roemer); Arkell, Kummell and Wright
1965 Mariella (P.) brazoensis brazoensis (Roemer); Clark
1978 Mariella (Wintonia) brazoensis brazoensis (Roemer); Klinger and Kennedy

These medium to large conical shells can reach one foot (305 mm) in length with a diameter of eight inches (200 mm). The body chamber uncoils, but is rarely found in place. The whorls coil tightly with an overlap that obscures one row of tubercles. Two sets (four rows) of tubercles are found on each whorl, and the two sets are separated by a spiral band. The tubercles are lengthened and aligned obliquely on the whorl flank. Occasionally, the tubercles are joined by a slight elevation. The suture pattern is rarely preserved.

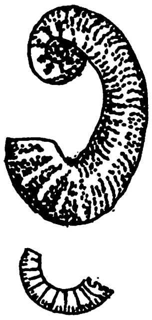


x 0.8

x 0.9

Otoscaphites subevolutus (Bose, 1928)
LK Washita (Grayson, Del Rio) - Cenomanian
Superfamily Scaphitaceae

1928 *Scaphites subevolutus* Bose
1978 *Eoscaphites subevolutus* (Bose); Young and Powell
1979 *Otoscaphites subevolutus* (Bose); Young*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x 2.0

O. subevolutus is a micromorph fossil and is discoidal. The specimens are often preserved as iron pyrite. The hook and shaft is almost always found broken and separated from the coiled shell. The initial whorls are evolute and the umbilicus may occasionally be perforate. The discoidal part of the shell is followed by a curved shaft and a semi-circular hook. The aperture is not well described. Ornamentation reports vary. Clearly, the early whorls are nearly smooth and later whorls develop ribs which become intercalated by about four, thin, rather obscure ribs. This intercalation continues over the shaft and hook. Young states that the measurements are about 0.4 inch (10 mm) each for the evolute shell, the shaft and the hook. Measurements are most often made of the coiled part. Six specimens by Bose averaged 0.35 inch (9 mm) diameter, 0.16 inch (4 mm) width of last whorl, 0.16 inch (4 mm) height of last whorl, and 0.12 inch (3 mm) diameter of umbilicus.

*Note: In 1979, Young renamed the genus to *Otoscaphites*, but was unsatisfied with the designation. Kennedy, in 1988, when dealing with slightly younger Texas fossils in the Eagle Ford Group, stated *Yezoites* equals *Otoscaphites* and the earlier *Yezoites* prevails. Kennedy did not review the *subevolutus* species.

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FOSSIL HUNTING ON THE YORKSHIRE COAST:
AMMONITES, BELEMNITES... AND MORE

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In the summer of 2000 I joined a tour out of the Philadelphia Academy of Natural Sciences to hunt fossils along the Yorkshire coast of England. Our leader from the American side was Dr. William Gallagher of the New Jersey State Museum, and our leader from the British side was a retired stone mason and geologist by the name of Ken Brooks. In 1999 I traveled with this same team to hunt Cretaceous fossils on the Isle of Wight. This time we would be hunting in the Upper Lias shales of the Lower Jurassic.

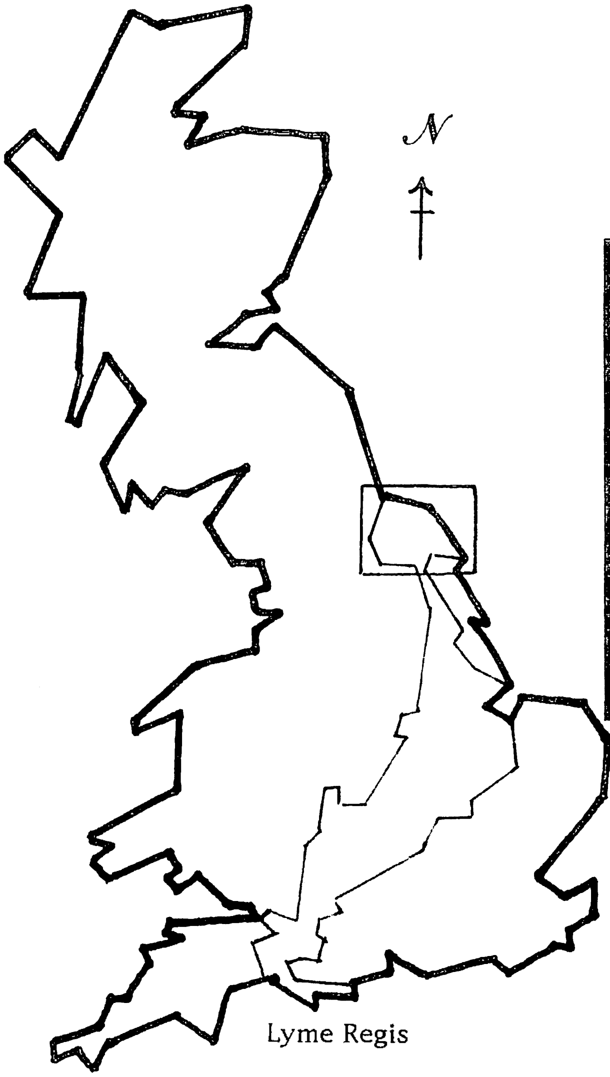
My research produced the following description, written in 1817:
"...these shores are not only dangerous to mariners in stormy weather, but cause many fatal accidents to others who frequent them. The most singular accident that ever happened on the coast, occurred about 15 years ago, under the high cliffs a little to the west of Staiths. While two girls of the name Grundy, belonging to Staiths, were sitting on the *scar*, or rocky beach, with their backs to the cliff, a splinter, which by striking against a ledge had acquired a rotary motion, fell from the cliff, and hitting one of the girls on the hinder part of the neck, severed her head from her body in a moment, and the head rolled to a considerable distance along the scar."

This gave me pause... but not enough to keep me home! On July Fourth we flew out of Philadelphia to Manchester, England. There we boarded a private bus and drove through the Yorkshire countryside to the seaside fishing village of Whitby (Fig. 1) at the mouth of the river Esk. We lodged above the town at beautiful Larpool Hall, a 1796 mansion, most recent in a string of buildings on this site since the 12th century!

Figure 1 - Whitby, looking down the River Esk toward the sea

A series of fishing villages like Whitby lines the north Yorkshire coast, designated the Heritage Coast. (Fig. 2) A trail running along its entire length is known as the Cleveland Way. The main outcrop of Jurassic rocks in England runs in a strip right across the country from this coast in the northwest down to the southwest. (Fig. 3) There it comes out in the cliffs around Lyme Regis, where Mary Anning found the original ichthyosaur when she was only twelve!

We spent the weekend exploring. Whitby is dominated by the clifftop ruins of Whitby Abbey, approached by a flight of 199 stone steps. The present ruins date from 13th - 14th century reconstructions of a Benedictine abbey (Fig. 4) founded after the Norman conquest in 1066, but the abbess St. Hilda founded her monastery on this site in 657. *Hildoceras bifrons* (Fig. 5) now bears the saint's name. Legend says that St. Hilda drove out the town's snakes, decapitating and throwing them over the cliffs. This explains, of course, the curled, headless "snakes" of stone found below the cliffs - ammonites! The legend was made real for the people of the Middle Ages by having snake heads fashioned on specimens of *Dactylioceras commune*. (Fig. 6) These "snake stones" are on the town's arms, and are still carved in Whitby today.



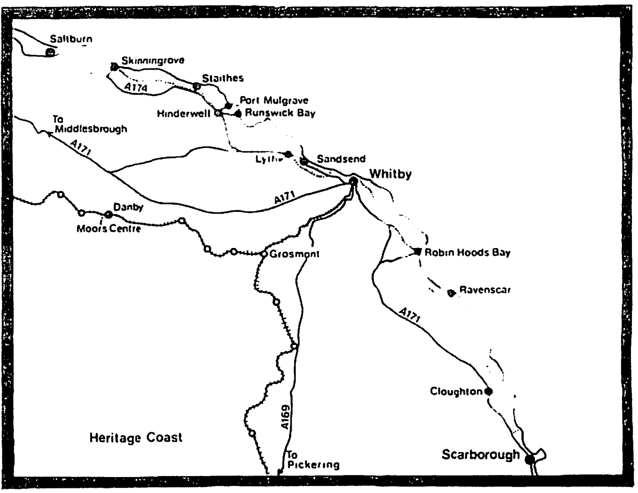


Figure 2 (left) - Map showing main Jurassic rock outcrops in England [adapted from Winchester]

Figure 3 (above) - Map showing the series of villages along the Heritage Coast [from *Heritage Coast Fossils*]

Figure 4 - Ruins of Whitby Abbey

Figure 5 - *Hildoceras bifrons*
3" across

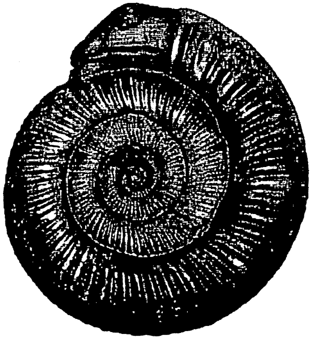


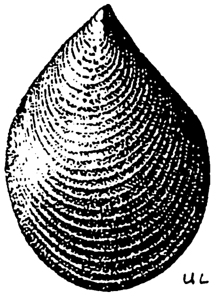
Figure 6 - "snake stone" carved from *Dactylioceras commune*
2 1/4" across

Back at the bottom of those 199 steps are many small 18th century houses. Nineteenth century jet workers lived here, working in small rooms or huts on the cliffs, and the town's most prestigious jet shop is here. Jet is prized for jewelry, as it takes a high polish and can be cut and etched. It was once thought to be a form of carbon or fossilized sap. It is now accepted as fossil wood from the *Araucaria* , or monkey-puzzle tree. It is found in the bituminous shales of the Upper Lias Formation, which happens to dip below sea level right around Whitby. Miners had to be able to identify the jet rock without an extensive knowledge of geology. Ammonites were particularly useful here because each stratum is characterized by one particular species. (An 1836 paper by young British geologist Louis Hunton, on the limited vertical range of ammonite fossils in the Yorkshire Lias, defined *zone fossils* and laid the groundwork for the science of biostratigraphy!) The ammonite in the jet rock is *Harpoceras exeratum.* On the day I finally dug my huge specimen out of the shale, someone nearby found a huge branch of jet!

A walk through the oldest section of Whitby takes you down many narrow, winding streets, including Church Street, the oldest street in the town, and Grape Lane, which contains the house of Captain James Cook. In the 19th century, there would have been many jet shops here, and today many shops still offer jet and jet jewelry for sale. The only fossil shop we ever saw was also here. I asked about getting a "snake stone" carved, but ultimately it would have cost more than buying one over the Internet--so I waited and did so when I got home. Most of us bought several fossils at the shop. We also visited the famous Whitby Museum, a combination of Victorian kitsch and superb fossil specimens. All sizes and species of ammonite were there and the museum's pride - their icthyosaurs and plesiosaurs. And at our first night's briefing we heard that an amateur had just found another icthyosaur in the Whitby area!

Sunday night's briefing described the alum shales in which we would be collecting. (These shales are also known as the Whitby Mudstone, and the Jet Rock is one of its rock units.) Alum has been mined in Yorkshire for over 300 years, and there are over 20 quarries on the moors, with beds over 100 feet thick. Alum was once used as a fixer for dye in cloth, and since the Middle Ages, those knowing the secret of how to make it controlled vast wealth and wielded political influence. At some point the secret got out, and between 1600 and 1870 the alum works along the Yorkshire coast were going fast and furious, with many towns springing up exclusively for the alum trade. The cliffs were ripped apart and thrown down on the beach. This tearing up of the earth uncovered the "monsters" which we know as alligators, icthyosaurs and plesiosaurs, and Whitby lost as often as it gained in the mad competition among the emerging natural history museums for who would get these specimens!

Monday morning we were more than eager to get down to serious fossiling. We started out one mile south of Whitby at Saltwick Bay or Saltwick Nab. (The word "nab" means "stack," and refers to a rock formation that rises from the sea at high tide, and to which you can walk at low tide.) The descent was steep. We soon learned that this is the only kind of descent on the entire coast. The tide was still high, but there was enough room to sit right up against the cliffs and hammer into blocks of matrix. Here we found a few small belemnites, numerous little *Nuculana*, or nut clams, and the ubiquitous bivalve *Inoceramus dubius,* but nothing really fabulous. What we wanted were ammonites!



Inoceramus

As the tide began to recede, we started slowly making our way south along the beach toward Black Nab. This involved rather strenuous clambering over rocks beneath rather ominous looking sections of cliff, all the while lugging backpacks heavy with tools and rock. We were warned to watch our heads, and were even wearing hard hats! We stopped once for lunch and again to pull some belemnites out of blocks of gray matrix. (Fig. 7) Still no ammonites! Moving on, we hit rocks slippery with seaweed, and at one point I dropped my camera into the water! Finally we stumbled, hot, tired, sweaty and overburdened, out onto the flats at Black Nab. (Fig. 8) What should we see but families, in shorts, sun dresses and sandals, strolling along the beach! A little girl named Eve showed me her bucket already full of *Dactylioceras* in concretions. She insisted I take a few because she "already had lots at home!" I finally had an ammonite, but little of my dignity!

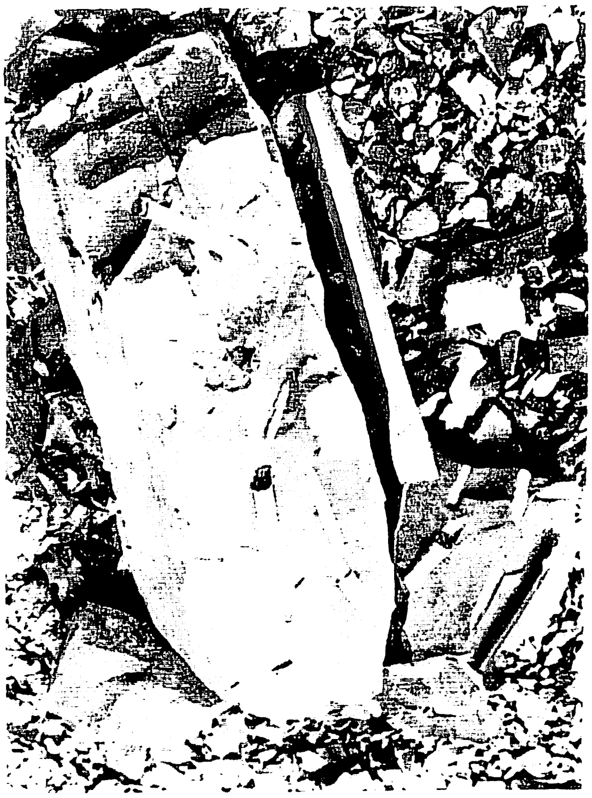


Figure 7 - Belemnites in matrix

Figure 8 - Black Nab, tide going out

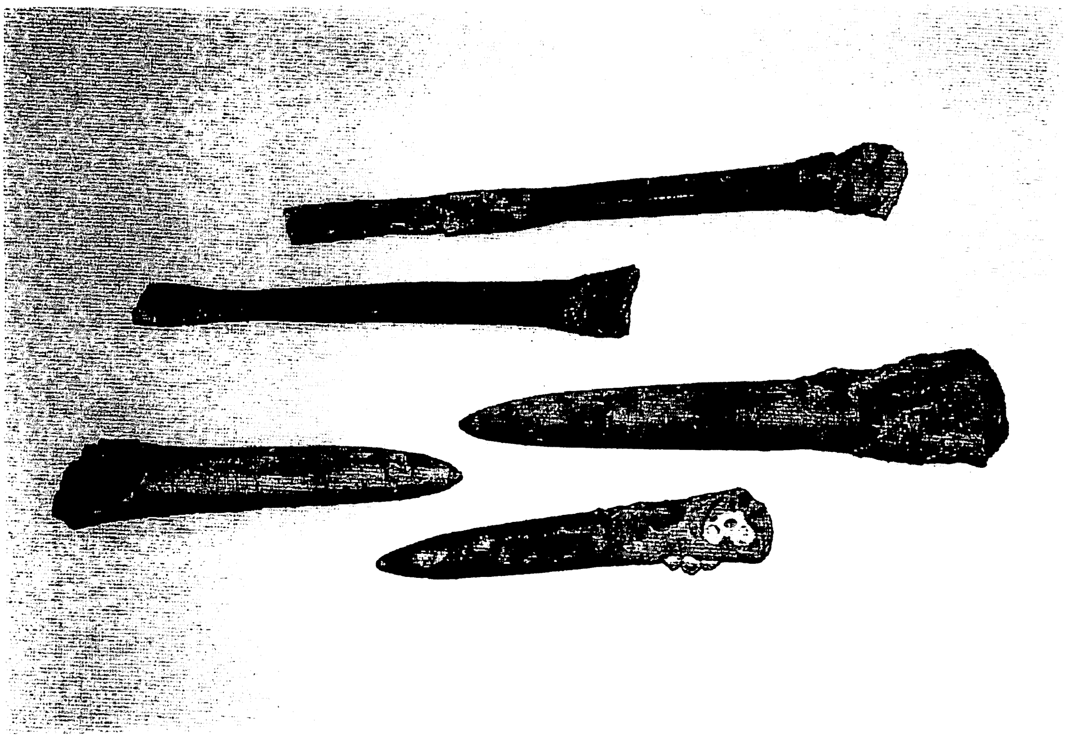


Figure 9 - *Cuspiteuthis tubularis* (above) longer specimen 5"
Acrocoelites (below) longest specimen 4 1/2"

When the sea receded, we got our first look at the vast layers of shale which lie just beneath the water. Everywhere there were flattened ammonites - *Dactylioceras* and *Harpoceras* of all sizes. Many were golden from the pyrite in them and would have made Midas proud, but they were exceedingly hard to dig out whole. Belemnites (Fig. 9) abounded, both the robust *Acrocoelites* and the more fragile *Cuspiteuthis tubularis.* These belemnites could be had, but not without breaking them. (*Cuspiteuthis* has a particularly long, thin anterior end, doubling its length, which I did not even try to save.) We soon agreed to call "perfect" any specimen with only <u>one</u> break. After dinner that night, several of us gathered with my Elmers glue and repaired and wrappped our belemnite specimens.

Tuesday we set out for Robin Hood's Bay, a legendary haven for smugglers and the best exposure of the oldest Jurassic rocks, known as the Redcar Mudstone. The walk through town was steeply downhill, and we arrived on the beach at fairly high tide - two conditions that plagued us the entire trip. The tide was too high to get around the bend to the beach where we were headed, so we relaxed our pace and began beach combing. I found my first small pieces of jet, and a friend found a gorgeous clam and two great *Gryphaea*, or "Devil's toenails." We also found crinoids and two kinds of coral.

As soon as the water was low enough, we inched around the perilous point on a narrow ledge hugging the slippery cliffside and emerged onto the beach which was our destination. Once again, we ran into happy sunbathers and swimmers who had come down by a more direct route! Dr. Gallagher split open a rock and found several nice ammonites, but the rest of us were not so lucky!

Wednesday is traditionally for rest and sightseeing, but several of us were feeling a little low on fossils at this point and were determined to return to the cliffs on our own. We set out on the Cleveland Way, along the cliffs behind the abbey, back to Saltwick Nab. The stairway down was still steep, and getting over the slippery shale down to the flats was treacherous, but once down we were in Lias heaven! And the tide was out! Belemnites and flattened ammonites were everywhere. I finally found a large *Harpoceras* (Fig. 11) I couldn't live without and settled down to prise it out. (Fig. 12) By the time the tide was returning, I was close...and a friend delivered the last few hammer blows. I was filthy, but happy. The only problem now was getting back to Larpool Hall. My pack was so heavy I needed aid just to lift it onto my back. Then I had to crawl back up the shale (slippery), up the steps (steep), along the path around the abbey (long), down the 199 steps, through the town (where we stopped in a pub for a short one), then last, but worst, back up the mile-long incline to the Hall!

Figure 10 - *Harpceras exeratum* in matrix 4 1/2" across

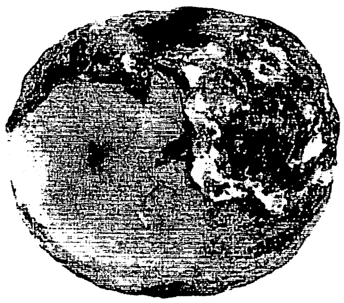
Figure 11 - The author, extracting a *Harpoceras* at Saltwick Nab

On Thursday we headed north to Runswick Bay. On an exposed shale platform by a cliff wall, we dug out more belemnites, then moved on to a beach littered with huge boulders and rubble. Everyone was really tired today, so for awhile we just sat and ate and talked and sunned ourselves and dug poorly-preserved nut clams and ammonite parts out of the rubble. Finally, Ken led us back to a scree slope we had passed earlier. As we rounded the cliff wall where we had dug the belemnites, we heard a loud *Whoomph*! Looking back, we saw the dust rising from a cliff slump, right where we had just been. I couldn't help but think of the unfortunate Grundy girl who had lost her head near here almost 200 years ago!

On the scree slope we were looked for round, rough-looking nodules and were shown how to strike them just so with a hammer. If we were lucky, they contained ammonites. If we were really lucky, the ammonites would not be broken by the hammer blows! Most of us let the more-experienced Ken do the hammering. These *Dactylioceras* in nodules (Fig. 12) are perhaps the most well-known fossils from the Yorkshire coast.

Figure 12 - *Dactylioceras commune* in opened nodule

Friday, our last day, we spent the morning on a relaxed stroll down the beach just below Sandsend, now a little resort village like all the others, but which started at the height of the alum industry. My biggest triumph here was finding a large, envy-producing piece of jet. We saw a young seal pup at the water's edge, and in the town we had a run-in with a comical troop of geese which come every day to be fed at a local restaurant. In the afternoon we ventured out for a walk on the moors - a truly romantic end to our Yorkshire adventure!



closed nodule

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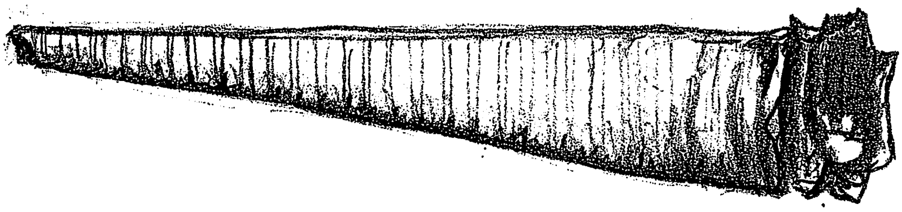
M.A.P.S. EXPO XXV



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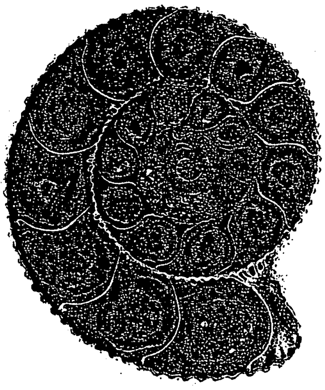

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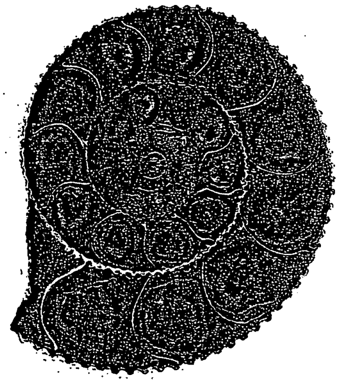

AMMONITES