

## Chapter 7

# Predation on Cephalopods

## A General Overview with a Case Study From the Upper Carboniferous of Texas

ROYAL H. MAPES and DAVID T. CHAFFIN

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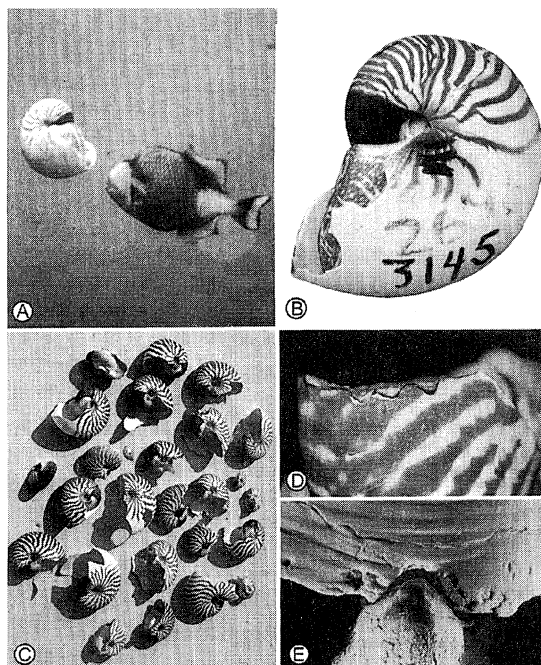
### 1. Introduction

Predation occurs throughout nature. Predators feed in order to survive long enough to reproduce. Likewise, prey animals attempt to avoid being eaten long enough to reproduce. Avoidance of predation is much more important to the prey because a failed attempt at predation only necessitates that the predator searches elsewhere for a meal.

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ROYAL H. MAPES and DAVID T. CHAFFIN • Department of Geological Sciences, Ohio University, Athens, Ohio 45701.

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**FIGURE 1.** Damage created by lethal and sublethal predation on present-day *Nautilus*. (A) Triggerfish (*Balistoides* sp.) attacking *N. belauensis* in Palau after the animal had been released in shallow water; according to Saunders *et al.* (1987), the attack ultimately proved to be lethal despite the rescue of the specimen while the animal was still alive. (B) Damage to *N. pompilius* inflicted by a grouper (*Epinephelus* sp.) after release in shallow water in Manus, Papua New Guinea. The attack produced large jagged, scalloped-shaped breaks at the aperture. L.E. Davis, who collected the damaged shell, witnessed the attack. (C) Collection of damaged *N. macromphalus* collected from a beach on Lefou, Loyalty Islands, by R. A. Davis in 1975. One of these specimens is better illustrated in Fig. 3. Most of this damage probably represents lethal predator damage. (D) Sublethal damage to the aperture of young *N. belauensis*, Palau, in the form of V-shaped embayments. (E) Mandible of *Nautilus* sp. and a V-shaped break in the aperture of *N. belauensis* that fits the shape of the mandible. (Photographs A, B, and D, courtesy of W. B. Saunders, for additional information see Saunders *et al.*, 1987, photograph C courtesy of R. A. Davis, and photograph E courtesy of Desmond Collins.)

Successful predation certainly means the prey's demise. Cephalopods can be both predator and prey. Studies of predation on present-day and fossil cephalopods (exclusive of the Coleoidea, which are not considered in this report) are relatively few.

Present-day *Nautilus* is the only living externally shelled cephalopod, and, therefore, virtually all observations on fossil cephalopods eventually come back to a comparison with this living model. Actual photography of a lethal attack involving present-day *Nautilus* is limited to a single event involving a teleost fish (Saunders *et al.*, 1987) (Fig. 1 A, B).

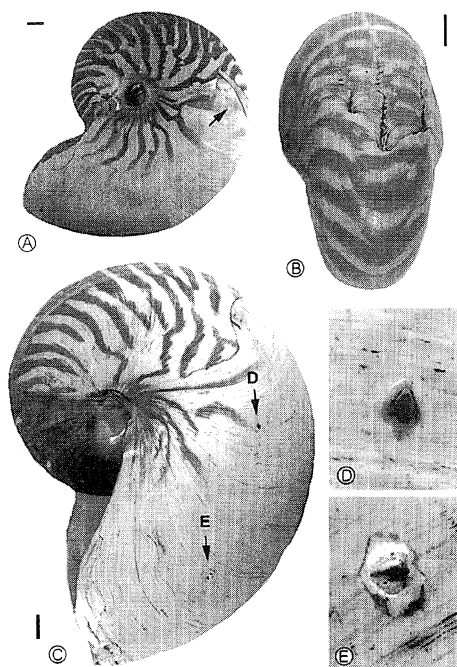
Other reports of lethal and sublethal damage include direct (but not photographed) observations and indirect evidence, such as the stomach contents of predators and the presence of bore holes in *Nautilus* shells that are presumably produced by octopus attacks (Tucker and Mapes, 1978a; and see Saunders *et al.*, 1987, for other reports) (Fig.

2 C, D, E). In addition to these lethal and sublethal examples, *Nautilus* inflicts damage on its own kind. Haven (1972) reported new V-shaped shell damage that occurred in a group of newly caught and caged *Nautilus* specimens and speculated that these breaks were bite marks from conspecific fighting and, possibly, attempted cannibalism. Shell damage in the form of these V-shaped bite marks on live-trapped specimens is common in *Nautilus* shells (Haven, 1972; Arnold, 1985; and Saunders *et al.*, 1987) (Fig. 1 D, E).

Additional studies on predation of *Nautilus* are necessary to develop a better understanding of predator-prey relationships. With better understanding of cephalopod predator-prey relationships and variations in shell damage, these organisms will provide a valuable tool for enhanced taphonomic understanding of cephalopod shell accumulations, paleoecological reconstructions, and evolutionary studies of fossil cephalopods through the Phanerozoic.

## 2. Background

Externally shelled cephalopod predation can be considered from three perspectives. One is the information that we have observed and determined about present-day *Nautilus*; another is specific studies of specific fossil cephalopod collections and the



**FIGURE 2.** (A) *Nautilus* sp. (OUZC 4067) with massive repaired break at arrow (scale bar = 1 cm). (B) Juvenile specimen of *Nautilus pompilius* (OUZC 4068) showing three black-streaked repaired areas on venter that altered shell coloration (scale bar = 1 cm), (C, D, E) *Nautilus* sp.(OUZC 4069) with massive repaired break at posterior end of body chamber (scale bar = 1 cm). Specimen has two octopus borings shown in D, E.

third, which is considered at the end of this chapter, is an overview of the fossil cephalopod record and how it relates to predator evolution.

With both the present-day observations and the record of events preserved on the shells of ancient cephalopods, it is possible to estimate and, in some cases, determine with a high degree of probability whether the shell damage was lethal (in which case, no repairs to shell damage occurred) or sublethal (damage where repair of the shell indicates the animal survived the attack). Shell damage (both lethal and sublethal) can be caused by agencies other than predators, and taphonomic factors may cause post-mortem damage. Indeed, separation of predatory activity from other causes of shell damage is one of the most difficult aspects of investigation of predation in cephalopods. An attempt to distinguish presumed predation events from other causes of shell damage is considered in the case study provided in this overview of cephalopod predation.

In the Finis Shale case study discussed in this report, complete specimens of coiled nautiloids and ammonoids are unusually rare; most specimens were damaged prior to or sometime after burial. Specimen incompleteness may have been caused by storm breakage, shell collapse by lithostatic pressure, crushing and/or dissolution while buried, mechanical damage by weathering and erosion after being exposed, collision with hard substrates while the animal was alive, scavenging, or collision of the empty shell on a hard substrate as it was transported after death, bioturbation of empty shells on the seafloor, or predation. By exploring taphonomic pathways, most of the causes of conch damage on the Finis Shale coiled nautiloids and ammonoids can be partly or completely determined. When the taphonomic causes of damage are eliminated, then it is probable that the damage observed on an ammonoid or a coiled nautiloid is the product of predators.

### 2.1. Sublethal and Lethal Shell Damage and Abnormalities in Present-day *Nautilus*

Sublethal damage to the soft tissues of present-day *Nautilus* without altering shell growth has been observed and documented on live-trapped specimens (R. A. Davis and W. B. Saunders, pers. comm., 2001). Damage is usually confined to the exposed tentacles and hood, and leaves no record of the event on the shell of the animal. However, if damage to the mantle occurs and the animal survives the attack (Figs. 1 C, D, 2 A, B, C), then shell growth and/or repair at the damaged area will usually reflect this traumatic event.

Most shells of present-day *Nautilus* show signs of repaired shell damage (e.g., Willey, 1903; Arnold, 1985; Bond and Saunders, 1989), suggesting that individuals of this genus are subject to frequent sublethal attacks that damage the mantle tissue. Sometimes the identity of the predator can be determined by the resultant marks on the shell. Tucker and Mapes (1978a) recorded a boring frequency of 28.7% on a purchased set of presumably drift shells of *Nautilus pompilius* from an unknown location in the Philippines (Fig. 2 C, D, E). They concluded that these borings were caused by predatory octopus attacks. Later, Saunders *et al.* (1987, 1991) and Arnold (1985), in live-trapping expeditions in the Indopacific, reported the following bore hole frequencies produced by octopus predation on several different species of *Nautilus*: *N. pompilius* – the ALPHA HELIX expedition in the Philippines had four bored specimens out of 353 live-caught individuals (1.1%); *N. pompilius* – Papua New Guinea had five bored individuals out of 270 live-caught specimens (1.9%); and *N. belauensis* – Palau had 211 bored specimens out of 2720 live-caught specimens (7.5%); Tanabe *et al.* (1988)

reported that in Fiji only one of 41 specimens (0.4%) was bored. Thus, it appears that octopi are capable of sometimes killing *Nautilus* by boring small holes and injecting venom that subdues the prey prior to ingestion. The high percentage of bored shells in the Tucker and Mapes (1978a) study suggests that collections of drift shells may be selectively enhanced in numbers by octopus predation. However, additional study of collections of *Nautilus* drift shells needs to be accomplished before a definitive statement can be made concerning the overall influence of predators on shell damage, geographic distribution, and beach accumulations.

Fish are considered to be major predators of *Nautilus*. Saunders *et al.* (1987), in their study of *Nautilus* predation, provided the only photographically documented example of fish predation on a living *Nautilus* (Fig. 1 A). In their description of the event, the fish forced the *Nautilus* against a reef and systematically slashed at the aperture and hood of the *Nautilus* and spit out pieces of shell. This attack resulted in scallop-shaped breaks in the apertural edge of the body chamber of the shell (Fig. 1 B). In one case the *Nautilus* was rescued before the fish could eat its prey; however, they reported that the released animal probably died as a result of this attack. Additional evidence of lethal fish predation was provided by Willey (1903), Lehmann (1976), Ward (1984), and others, who indicated that fish, including "conger eels" and "sea perch," prey on *Nautilus*. Some sharks also are known to eat *Nautilus*; both Ward (1984) and Tanabe *et al.* (1988) reported recovering *Nautilus* mandibles in the stomachs of cat sharks. In a surprising situation, Ward (1998) observed that sea turtles in an aquarium attacked and ate *Nautilus* placed in the same turtle holding tank. Indeed, the turtles were observed to crush the shell in a way that was "like hitting a porcelain plate with a hammer" (Ward, 1998, p. 138), and then the body of the *Nautilus* was eaten with what appeared to be remarkable ease and familiarity.

Sublethal damage in present-day *Nautilus* is relatively common (Fig. 2 A, B, C). Virtually every shell we have examined has repaired damage, ranging from the interruption of a few growth lines to massive removal of large parts of the body chamber. Frequently, in association with the larger shell breaks, there is a secretion of black material at the injury site that is presumably the same as the black layer deposited on the dorsum of the body chamber (Fig. 2 B). When critical parts of the mantle are damaged in predator attacks, shell abnormalities frequently result in *Nautilus* (Arnold, 1985). These abnormal shells have unusual features such as blister pearls, loss of color banding, asymmetry of the section of repaired shell, unusual growth lines, changes from normal umbilical growth, and changes in the rate of coiling.

Under some conditions, *Nautilus* exhibits conspecific shell-damaging behavior (Haven, 1972; Arnold, 1985; Saunders *et al.*, 1989). Such behavior has been observed when numerous *Nautilus* specimens were caged together in a restricted space. Some of these caged specimens that had complete shells, when placed in the cage, developed V-shaped gaps in the apertural margin of their shells that match the shape and size of the mandibles of the other caged *Nautilus* specimens (Fig. 1 D). Because all other large predators were excluded from the cage, other *Nautilus* individuals must have caused the damage. It is not clear whether this V-shaped damage is a byproduct of mating behavior or whether *Nautilus* was exhibiting cannibalistic tendencies. However, it is clear that, if aggressive *Nautilus* individuals had sufficient time to continue the attacks, these sublethal events in the cage would have become lethal events. Indeed, *Nautilus* is known to use scavenging as its major feeding strategy (Tshudy *et al.* 1989); however, this animal can be an opportunistic predator under certain circumstances. Thus, in a

crowded situation in a confining cage, some *Nautilus* individuals are likely to act as opportunistic predators. The differentiation between sublethal *versus* lethal attacks in these artificial situations probably rests on the time span the animals are caged and the availability of supplied food. The fact that these V-shaped divots in the shells of live-trapped specimens are often repaired suggests that sublethal encounters with conspecifics occur with some regularity in natural circumstances.

## 2.2. Sublethal Shell Damage and Abnormal Shells in Fossil Cephalopods

Shell abnormalities represent one of the largest sources of data on sublethal damage in fossil cephalopods (for examples, see Hengsbach, 1996, and Kröger, 2000, with their extensive bibliographies on this subject). Many of these abnormalities are attributed to parasitic infestations, diseases, or repairs after the body and shell of the cephalopod were attacked and damaged by external forces such as predators. Abnormal shell development also can be produced by artificial environmental conditions, as is exhibited in *Nautilus* shell growth in aquariums (Martin *et al.*, 1978; Arnold, 1985). This latter condition has not yet been documented in the fossil record; however, such shells may exist and must be differentiated from shells malformed as a result of sublethal damage inflicted by predators.

Shapes of breaks in fossil cephalopod shells are often ascribed to different kinds of predators based on present-day observations of the damage produced by predators on other molluscs (mainly gastropods and pelecypods). As previously stated, only one case (Saunders *et al.*, 1987) of shell damage by any specific predator has been documented for present-day *Nautilus*. Thus, the style of damage produced by most types of potential predators on *Nautilus* is inferred, and not available for direct comparison. For example, the repaired crescentic breakage in fossil cephalopods is usually interpreted as damage inflicted by fish or arthropod, including crab, attacks (for examples, see Thiermann, 1964; Roll, 1935; Lehmann, 1976; Keupp and Ilg, 1992). We suspect that, in most fossil cases, shell damage has been attributed correctly. However, some caution should be used in making conclusions about predator-inflicted damage, since studies on present-day *Nautilus* have not been performed, and we do not really know the types of damage that can be produced by different forms of offensive armament (e.g., teeth that are used to cut, as compared to teeth that are used to puncture).

Sublethal damage presumably caused by predation in early and middle Paleozoic cephalopods has not been studied in detail. Abnormalities in shells are known (for example, the orthoconic nautiloid in Barrande, 1869, pl. 299); however, these abnormal shells are simply mentioned or are illustrated with no extensive analysis of the lethal or sublethal damage. In fact, we are aware of no comprehensive studies of predators and of sublethal or lethal damage on any populations of any group of fossil nautiloids; all of the major studies using large sample sizes have concentrated on the Ammonoidea.

The only extensive study of sublethal damage in the Paleozoic is by Bond and Saunders (1989) on an Upper Mississippian ammonoid assemblage from the Imo Formation of Arkansas. Their data set included more than 2000 specimens. They concluded that the Mississippian ammonoids were preyed upon less frequently than is present-day *Nautilus*, with 15% of the ammonoid shells recording sublethal damage, compared to 57% of the *Nautilus* specimens from Palau showing similar repaired injuries. V-shaped breakage and repair on many of the ammonoids described by Bond and Saunders (1989) are consistent with the jaw structure of upper Paleozoic

cephalopods (e.g., Tanabe and Mapes, 1995; Doguzhaeva *et al.*, 1998), suggesting that conspecific attacks or attempted cannibalism probably took place.

Relatively few studies of sublethal damage in Mesozoic ammonoids have been published. There are no studies known to us that deal with sublethal damage in Triassic ammonoids. Jurassic ammonoids have received moderate study (see Keupp, 2000; Kröger, 2000 for numerous citations), and in the Upper Cretaceous only the scaphitid heteromorphs have been examined (Landman and Waage, 1986). Abnormal specimens are known to us from all these time periods. However, in the literature on abnormal specimens, reports typically focus on the deformity with little information on the cause of the abnormality, which could be the result of predation damage, or damage caused by parasitic infestations and disease.

Significant sublethal damage to Jurassic ammonoids that was probably in part related to predation was described by Geczy (1965), Guex (1967), Bayer (1970), and Morton (1983). Geczy (1965) reported that ammonoid collections from Hungary contained a variety of abnormal shells including damaged shells that had been repaired. Guex (1967) reported that 2% of the 2000 ammonoid specimens from Aveyron, France, had repaired shell breaks, including 20 of 800 specimens (2.0%) from the *bifrons* zone. Bayer (1970), in his study of Middle Jurassic ammonoids from Germany, noted different proportions of repaired scars in different families (Graphoceratinae with a frequency of 0.3%; Sonniniidae with a frequency of 1.0%; Stephanocerataceae with a frequency of 9.7%, excluding the Sphaeroceratinae which had a frequency of 1.4%). He explained these differences in damage repair frequencies by suggesting that each ammonoid group probably had a different life mode. Morton (1983) analyzed the occurrence of a single ammonoid genus from the Isle of Skye in Scotland. He reported a repair frequency of 0.7%. He attributed the abnormalities as being due to either parasites or disease, but recognized that sublethal predation could also have caused such damage.

In a study of Upper Cretaceous scaphitid ammonites, Landman and Waage (1986) concluded that approximately 10% of the 2000 specimens they analyzed showed repaired external damage. Also, after completion of the Cretaceous study and surveying the limited data available in the literature, they concluded that there was no general increase or decrease in predation from the Mississippian through the Cretaceous. Despite the fact that there was no detectable relationship between predation repair frequencies and morphologic changes among ammonoids, they did discern a gradual increase in the relative numbers of coarsely ornamented ammonoids compared to weakly ornamented ammonoids. They declined to attribute this ornamental change through time to predation as an all-embracing mechanism because they thought that some of the injuries were not caused by predators, and because the correlation between sublethal and lethal injuries could be poor.

Additional studies on sublethal damage in fossil cephalopods are highly desirable. Indeed, this area of paleobiology seems ripe for study, with well-preserved cephalopod faunas lying untouched in fossil repositories around the world. Such studies would, for example, allow the additional testing of Vermeij's (1987) escalation hypothesis on the evolutionary changes in cephalopod shell structure and ornament in the fossil record.

### 2.3. Lethal Damage in Fossil Cephalopods

Few studies involve shell damage produced at the time the cephalopod was killed and eaten by a predator. Arguably, the most famous report of lethal cephalopod

predation was written by Kauffman and Kesling (1960), who analyzed the circular and semicircular perforations in the shell of a Cretaceous *Placenticer* ammonoid. They suggested that the holes were bite marks from a mosasaur that bit the ammonite sixteen times. Later, Kauffman (1990) expanded the shell perforation model by examining the overall extent of reptilian predation on ammonites during the Cretaceous. Ward and Hollingsworth (1990) reported a Jurassic ammonoid, *Kosmoceras*, that had a shell perforated by an attack by a marine reptile.

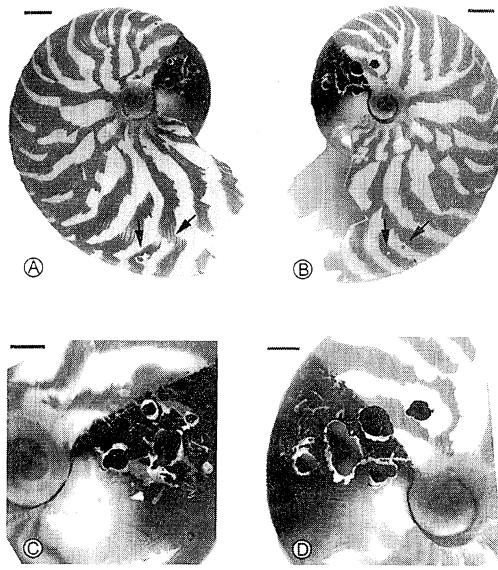
The 1960 analysis by Kauffman and Kesling was recently challenged by Kase *et al.* (1998) and Seilacher (1998), who considered the alleged bite marks to be limpet home-scars produced by limpet rasping of the ammonoid shell (Kase *et al.*, 1994), followed by lithostatic crushing of the home scar site, producing circular and semicircular holes. To support their limpet home-scar hypothesis, Kase *et al.* (1998) constructed a mechanical mosasaur jaw apparatus designed to produce circular holes in present-day *Nautilus* shells like those observed on the *Placenticer*. Their experiment failed to produce circular and semicircular holes in the *Nautilus* shells tested. Based on this experiment, they concluded that all the circular and semicircular holes in *Placenticer* were caused by the collapse of limpet home-scars. Ward (1998) independently attempted to produce circular perforations in present-day *Nautilus* shells like those seen on *Placenticer* shells using a mechanical device approximating a mosasaur jaw. He also failed to create circular holes like those seen on the Cretaceous fossils. He concluded that the ammonites bitten by mosasaurs had their shells crushed prior to consumption.

We suggest, as have Davis *et al.* (1999), that the mechanical mosasaur model experiments of Kase *et al.* (1998) and Ward (1998) used to attempt to produce circular holes in present-day *Nautilus* shells are flawed. Arguments against the all-inclusive conclusion of Kase *et al.* (1998) have not yet been developed in detail; however, we are aware of several points that should be considered before their conclusions are accepted. In 1975 R. A. Davis (pers. comm., 2001) collected 25 freshly drifted *Nautilus* shells on the shoreline at Lifou Island, Loyalty Island Group, in the Pacific Ocean (Fig. 3A - D). All of the specimens were massively damaged (Fig. 1C). Some of the damage is in the form of circular holes (Fig. 3A, B) in the phragmocones and the body chambers of the shells. It is arguable that these circular holes, which are symmetrically placed on both sides of the phragmocone and the body chamber in Fig. 3, were caused by predators, but other taphonomic factors, such as empty shells impacting hard substrates by wave activity, must be considered.

However, based on the specimens collected by Davis, there can be no question that circular holes can be made naturally, and it appears that these circular and oval holes were made in these *Nautilus* shells by methods other than boring, rasping, or the collapse of limpet home sites during burial and compaction of the sediment. Additional arguments against the creation of all the holes in *Placenticer* shells by limpet home-scar crushing are as follows: (1) Mutvei (1967) suggested that *Nautilus* has a different shell structure than ammonoids, which could in part explain why mechanical mosasaurs failed to produce circular holes in *Nautilus*. Ammonoids typically have much thinner shells (although some *Placenticer* shells are much thicker than that of *Nautilus*), which are constructed with numerous organic membranes between the nacre sheets as compared to the relatively few organic membranes between the aragonite nacre sheets in the shell of *Nautilus*. (2) We are aware of more than 100 *Placenticer* shells with circular and semicircular holes in the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada (R. A. Davis, pers. comm., 2001); most of the external



shells of these ammonoids are buried in the concretion matrix, and none of the exposed shell surfaces has limpets attached to the ammonoid shells. In fact, only three ammonite specimens with encrusting limpet colonies are known to us. The disparity between the numbers of holed limpet-bearing ammonoid specimens and specimens with limpets and limpet home-scars that are not crushed inward has not yet been adequately addressed. (3) Hewitt and Westermann (1990) contended that the complex ammonitic septa promote a strong, flexible shell, and this condition explains why the conchs of ammonites could buckle rather than be fragmented under point loads such as those produced by mosasaur teeth. This observation suggests that septal-supported phragmocones should show holes, whereas the body chambers should fragment. This theoretical observation has not yet been fitted into the controversy. Additionally, they rejected implication of a shallow-water life mode for desmoceratacean ammonites suggested by the limpet home scar scenario (Westermann and Hewitt, 1995). (4) The assumption that ammonites were like *Nautilus* with the chambers of the phragmocone being empty of fluid may not be warranted. If the chambers being put under a point stress (such as by mosasaur teeth) were fluid filled, then it is probable that a circular hole could be created. (5) Mapes and Hansen (1984), Hansen and Mapes (1990), Mapes *et al.*



**FIGURE 3.** *Nautilus macromphalus* (OUZC 4070) collected by R. A. Davis on a beach at Lefou Island, Loyalty Islands. (A, C) Right and left views, respectively, of the specimen showing small diameter circular holes in body chamber at arrows and larger holes on phragmocone in the black layer (scale bar = 1 cm). (B, D) Magnified right and left views, respectively, of holes on phragmocone (scale bar = 5mm). This symmetrical damage was probably caused by a predator with puncture-type teeth. The presence of these circular and oval holes demonstrates that this kind of damage can occur in modern *Nautilus*, contrary to the conclusions of Kase *et al.*, 1998, and Ward, 1998.

(1995), and the case study (herein) report circular holes in both coiled nautiloids and ammonoids of Pennsylvanian age. There is no evidence that limpets or any similar rasping organisms that created circular home sites had evolved by Pennsylvanian time. Thus, they could not have produced the structures necessary to create circular or oval holes in the manner suggested by Kase *et al.* (1998). The fact that circular holes exist in these Pennsylvanian specimens indicates that there are probably several ways to create circular holes in cephalopod shells.

In the Pennsylvanian case study provided herein, circular and semicircular holes are reported in both coiled nautiloids and ammonoids. Hence an alternative explanation for these features other than the innovative limpet model must be developed. Some of the holes in the case study are similar to the holes described by Mapes and Hansen (1984), who matched the dentition of the Carboniferous shark *Symmorium reniforme* (Zangerl, 1981) to perforations observed on a fragmented Pennsylvanian age coiled nautiloid body chamber. Later, Hansen and Mapes (1990) described and illustrated an orthoconic nautiloid with perforations similar in shape to the teeth of the shark *Petalodontus ohioensis* (Zangerl, 1981). Mapes *et al.* (1995) studied predation on the ammonoid *Gonioloboceras goniolobum* (Sayre, 1930) from numerous Pennsylvanian localities in Texas, Oklahoma, Kansas, and Missouri. The study included specimens from the same stratigraphic level as the case study provided in this report. They concluded that *Gonioloboceras* shows direct as well as indirect signs of predation from various chondrichthyan predators, including circular and semicircular holes produced by *Symmorium reniforme*.

The controversy regarding the cause of circular and semicircular holes in cephalopod shells is not over. Additional studies on the damage produced by present-day predators on *Nautilus*, as well as examination of cephalopod specimens from throughout the Phanerozoic fossil record, must be done before a conclusive assessment of the kind of damage and the predators (different kinds of fish, crabs, and other cephalopods) that produced the damage can be separated from other kinds of taphonomically produced shell damage such as limpet home site scars and diagenetic crushing.

Evidence of possible lethal cephalopod predation on other cephalopods is the presence of cephalopod mandibles in the crop or stomach area of other cephalopods. In a speculative case, Zangerl *et al.* (1969), Quinn (1977), and later Dalton and Mapes (1999) and Mapes and Dalton (in press) analyzed the occurrence of large numbers of goniatite ammonoids in carbonate concretion halos around the conchs of large (up to 2 to 3 meters in diameter) actinoceratid nautiloids from a Mississippian shale in Arkansas. All of these researchers concluded that the ammonoids were part of the stomach contents of the nautiloid and that the nautiloid had ingested the ammonoids and then died. Several other workers have observed a similar condition in Mesozoic ammonoids (see summary by Nixon, 1988). All of these cases have only two possible explanations: (1) that one cephalopod attacked and ate another cephalopod, and (2) that a cephalopod scavenged the carcass of a dead cephalopod.

Reeside and Cobban (1960) suggested cephalopods were the prey of predators in the Cretaceous when they speculated that masses of whole and fragmentary shells (often preserved as the nuclei of concretions) were the fecal accumulation of a large unidentified carnivore. Such accumulations of cephalopod debris, including cephalopod mandibles, have been recovered within Carboniferous coprolites preserved as nuclei in phosphate concretions in black shales (Mapes, 1987). Mehl (1978a) reported Late

Jurassic ammonoid aptychi in coprolites and clusters of equal-sized ammonoid shell fragments in the Early Jurassic (Mehl, 1978*b*). This latter case was attributed to teuthoid predators. Westermann (1996) suggested that these teuthoid predators probably were responsible for most of the peristomal mantle injuries in Jurassic and Cretaceous ammonoids, and that when the ammonoids survived attack, the result was an abnormally shaped shell.

### **3. Case Study: Lethal Predation on Upper Carboniferous Coiled Nautiloids and Ammonoids**

#### **3.1. Background: Stratigraphic and Paleoenvironmental Considerations**

A diverse collection of cephalopods from the Finis Shale Member of the Graham Formation (Pennsylvanian; lower Virgilian) has been recovered from 13 localities within 80 kilometers of Jacksboro, Young County, Texas (see Chaffin, 2000, for details). The cephalopod fauna encompasses at least twenty-nine genera, which include orthoconic, cyrtconic, and coiled nautiloids, ammonoids (Miller and Downs, 1950; Boardman *et al.*, 1994), coleoids (Doguzhaeva *et al.*, 1999) and bactritoids (Mapes, 1979). This case study of the coiled nautiloids and ammonoids attempts to determine differences between taphonomic damage and damage caused by lethal predation. After taphonomic damage is eliminated as an explanation, comparisons are made to determine whether shell shape, shell size, and ornamentation influenced predation, and whether there are differences in predation frequency between ammonoids and coiled nautiloids.

The Graham Formation in the Jacksboro, Texas, region is primarily shale with some sandstone and limestone. The formation includes several transgressive-regressive sequences called cyclothems that have received extensive study in north-central Texas by Cleaves (1973), Heckel (1977, 1978, 1980), Boardman *et al.* (1984), Boston (1988) and others. The cephalopods were recovered from part of the Finis Shale Member of the Graham Formation.

In the fossil-bearing interval, there are several different invertebrate communities that could have yielded the study specimens, and, because each community has a different set and number of predators and prey, it was important to identify the specific community and paleoenvironmental conditions that produced the study specimens. Based on community successions identified by Boardman *et al.* (1984), the Finis Shale interval that yielded all of the cephalopods for this study is identified as the "Mature Molluscan Community." This community is characterized by having a fully marine, oxygenated water column from the surface to the water-sediment interface. Ammonoids and other cephalopods, gastropods, pelecypods, rostroconchs, and polyplacophores (Boardman *et al.*, 1984; Hoare and Mapes, 1985; Hoare *et al.*, in press) dominate the Mature Molluscan Community of the Finis Shale. In addition to the molluscs, there are a variety of other fossils, including but not limited to brachiopods, sponges, bryozoans, corals, conulariids, ostracodes, foraminifers, and conodonts (see Boardman *et al.*, 1984) and shark and other fish debris. Thus, the Mature Molluscan Community in the Finis Shale contains a diverse marine fauna that is typical of an oxygenated middle-to-outer-shelf marine environment. Discussions of the Mature Molluscan Community and stratigraphically adjacent communities are found in Boardman *et al.* (1984) and Kammer *et al.* (1986).

The Mature Molluscan Community was probably deposited tens of kilometers from the shoreline (based on basin reconstructions and because the sedimentation rates are modest to low, suggesting an offshore setting relatively far from the active deltas at the shoreline). The water depth, combined with turbidity, was sufficient to deter phylloid algal development that does appear higher in the stratigraphic succession. The rarity of storms is evidenced in part by the lack of reworking of concretions that show a heavier epifaunal growth on one side of the shell. This feature indicates that shell debris was exposed on the bottom prior to burial and was not frequently disturbed by storm events and excessive bioturbation.

Most of the cephalopod specimens collected from the oxic part of the Finis Shale are preserved by infilling the shell with a mud-based carbonate concretion. The quality of the recovered specimens ranges from moderately good to poor, with most specimens retaining some external shell that preserves growth lines. Both the ammonoids and the coiled nautiloids are generally recovered without the body chamber. In most cases, mud apparently entered the empty phragmocones. The early transformation of the mud into concretion material protected the conch from later lithostatic crushing. Where concretionary mud did not fill the phragmocone (i.e., cameral spaces that were probably partly gas filled) and/or the body chamber, later lithostatic pressure crushed the shell, leaving remnants of shell fragments adhering to that part of the three-dimensional conch preserved as a concretion.

### 3.2. Methodology and Generic Identities of the Case Study Specimens

Coiled nautiloids ( $n = 692$ ) and ammonoids ( $n = 193$ ) from 13 localities were analyzed for this study. Only specimens from the regressive phase of the Finis Cyclothem that fit the preservational and depositional criteria defined for the Mature Molluscan Community by Boardman *et al.* (1984) were utilized (Figs. 4, 5).

Figured specimens are cataloged with OUZC (Ohio University Zoological Collection) repository numbers. Specimens were measured for height (H), width (W), and diameter (D). Values for incomplete shells were estimated. The specimens were inventoried for presence or absence of the body chamber, encrusting organisms, circular and semicircular holes, irregular holes filled with shell debris, and both lethal and sublethal damage exhibited by missing and repaired shell breakage, respectively. Conch damage was interpreted as potentially lethal if no repair occurred in the damaged area. In the case of sublethal damage, specimens were examined for repaired damage using the criteria developed by Bond and Saunders (1989), which they ranked as minor, moderate, massive, deep-acute, mantle damage, or perforation, depending on the nature and severity of the injury.

The study specimens were identified to the generic level. Because of the great variance in abundance between different genera there is a statistical problem of normalizing the genera so that specimens identified to the generic level can be treated as "populations" that can be evaluated equally. Reasons for the inconsistency in abundance may result from better adaptation by some genera to the paleoecologic conditions, collection bias, or differences in reproduction rates. The problem of normalizing the populations was resolved by using a Z-test for independent proportions. This test is designed for comparisons of large samples for equality of two independent proportions. The test effectively equalizes the numbers, allowing for an equal contribution to the analysis with a 95% confidence interval.

Most of the coiled nautiloids and ammonoids used in the study were recovered loose on the surface of the outcrops. However, some specimens were recovered *in situ*, and these specimens confirm that incomplete shells recovered loose on the surface are not incomplete because of exposure to present-day weathering and erosion. Thus the relative completeness of specimens at the time of burial can be estimated easily by the freshness of any breakage on the specimens recovered from the surface of the shale exposures.

The following coiled nautiloid genera occur in the Mature Molluscan Community paleoenvironment and were utilized in this study: *Domatoceras*, *Ehippioceras*, *Liroceras*, *?Liroceras*, *Metacoceras*, *Neobistrialites*, *Peripetoceras*, *?Peripetoceras*, and *Tainoceras* (see Fig. 4 for some examples). Other genera, such as *Titanoceras* and *Solenocheilus*, were also present in the collection. However, due to their low abundance ( $n = 2$  and  $n = 5$ , respectively) and fragmentary preservation, these latter two taxa were not included in the study. In some cases, the precise generic identity of certain morphologically grouped sets of coiled nautiloids is uncertain because a detailed systematic investigation for the coiled nautiloids for the Finis Shale has not yet been undertaken. This study focuses on the kinds and causes of damage in a population of cephalopods with the goal to establish a rationale to distinguish predatory from non-predatory damage. After that goal was attained, then different aspects of shell diameter, ornamentation, and width (wide and narrow conch forms) were evaluated to see whether these parameters had an impact on the predation frequencies of the different coiled nautiloid genera. In order to provide insight into the features that are significant in the studied taxa, a brief descriptive generic-level overview is provided in the Appendix.

Although 12 ammonoid genera are known from the Finis Shale, only *Gonioloboceras*, *Glaphyrtes*, *Schistoceras*, and *Neodimorphoceras* are present in the collection in sufficient numbers from the Mature Molluscan Community to use in this predation study. These four taxa are described briefly in the Appendix; each has a body chamber that is about one complete revolution.

### 3.3. Predation Versus Taphonomy of the Finis Cephalopods

The events that will damage or break the shell of a cephalopod can be separated into two distinct phases: (1) events that happen during the lifetime of the animal, including the predatory attack that causes the demise of the animal; and (2) post-mortem events, including those that occur after the dead cephalopod is consumed; this latter phase is called taphonomy.

Taphonomy, generally defined as the forces that acted upon an organism between its death and subsequent discovery, plays an important role in preservation (Canfield and Raiswell, 1991; Maeda and Seilacher, 1996). The taphonomic factors that may interact with a deceased organism include events that happen prior to burial, during burial, and prior to collection, including exhumation and weathering. Prior to burial, shell damage may be caused by the following: (1) breakage due to impact during transportation or reworking, (2) dismemberment by scavengers, (3) mistaken predation on an already dead and empty shell, and (4) utilization of the shell by another organism for shelter. After burial, shells may be broken or destroyed by dissolution, crushing or distortion by compaction, and bioturbation. When shells are exhumed by erosion, they are exposed to the vicissitudes of chemical and mechanical weathering, which will produce shell dissolution and breakage. These phenomena adversely affect the condition of

specimens, and, alone or in combination, can complicate the identification of fossils and obscure the damage produced by a predation event.



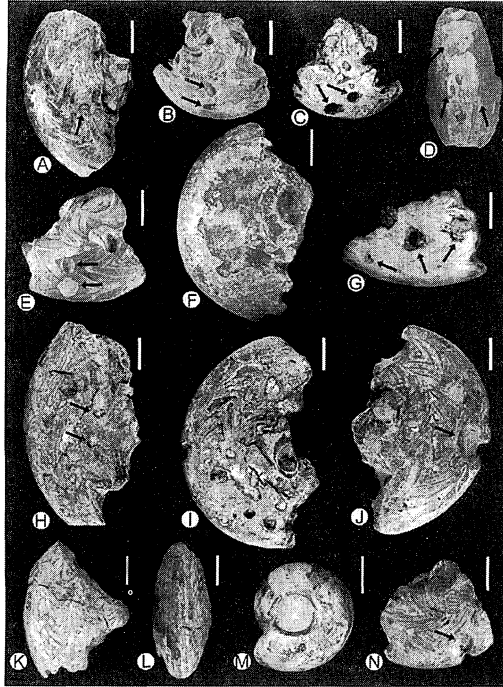
**FIGURE 4.** Coiled nautiloids from the Finis Shale. For locality information see Chaffin (2000). (Bar scale = 1 cm). (A) *Tainoceras* (OUZC 3774; locality TXV-41 ) showing circular holes along left lateral side of phragmocone. Based on the size and linear orientation of the holes, these perforations were probably caused by the shark, *Symmorium reniforme*, which co-occurs with these cephalopods in the Finis Shale. (B) *Liroceras* (OUZC 3778; locality TXV-56) showing removal of a massive “U” shaped portion of both the phragmocone and body chamber along the venter. The missing ventral section is interpreted to have been removed by an arthropod. (C) *Domatoceras* (OUZC 3780; locality TXV-200) showing a “U” shaped portion of the phragmocone and body chamber along the venter that was probably removed by an arthropod. (D) *Tainoceras* (OUZC 3775; locality TXV-34) showing circular holes along the left lateral side. These perforations are of approximately the same size, suggesting that an unidentified shark or other large fish may have been the predator. (E) *Metacoceras* (OUZC 3776) taken from the Iola Formation of Oklahoma (Upper Carboniferous) illustrating that the “U” shaped conch damage is not limited to the Finis Shale. (F) *Tainoceras* (OUZC 3779; locality TXV-200) showing a large perforation accompanied by two smaller punctures on the right lateral side. Based on the size of the punctures and their relative orientation, we suggest that *Symmorium reniforme* bit the *Tainoceras* at an angle allowing the maximum penetration of the main cusp and two of the lateral denticles. (G) *Domatoceras* (OUZC 3787; locality TXV-56) with four perforations reasonably aligned along the left lateral side of venter that were probably caused by a predator. (H) *Neobistrialites* (OUZC 3777; locality TXV-34) showing a perforation along the apical end of the venter. This single perforation suggests predation by a fish. (I) *Domatoceras* (OUZC 3784; locality TXV-56) with repaired damage along right lateral side, indicating that the injuries were sublethal. The sublethal injuries appear to cross several growth lines and are interpreted as “moderate.” However, the body chamber is absent, suggesting that lethal predation took place at a later time.

Taphonomic processes often obscure or destroy the evidence of predation, but sometimes these processes enhance the evidence of predation. When concretionary mud fills the empty body chamber and/or phragmocone of a cephalopod, it produces a smooth mold of the internal surface of the shell on the surface of the concretion steinkern. In the case of puncture-type predation, the conch is pierced by the predator's tooth. This hole leaves a void that prevents the formation of a smooth mold on the surface of the steinkern. Conchs with larger irregular pieces of missing shell also possess voids that will not allow the formation of smooth molds. Sometimes the mud that filled the conch body chambers and/or phragmocones became cemented by mineral components that created a solid concretion. This early diagenetic process fortified that portion of the infilled conch and protected it from diagenetic crushing. Based on the Finis specimens, the coiled nautiloid conch phragmocones only rarely became filled with mud, and ultimately, concretions, because the chambers were intact and were probably partially or completely filled with gas. During compaction these gases could not protect the shell from collapse. Thus, in the Finis Shale, there are few complete coiled nautiloid specimens with both body chambers and phragmocones intact. The most common preservational condition of the Finis coiled nautiloids is an incomplete concretion-filled body chamber. The inner whorls of these nautiloid specimens are preserved as fragmented, crushed shell that adheres to the dorsum of the body chamber. These specimens presumably had complete phragmocones, but, because the phragmocones were not concretion-filled during compaction, this part of the conch has been crushed by lithostatic pressure. However, if the chambers in the phragmocone were filled with water, then there is a tendency to preserve these chamber spaces with a crystallized mineral infilling, and these fillings, as described by Maeda and Seilacher (1996), preserved the three-dimensional shape of the conch. In the ammonoids, the body chamber (which was rarely present) or the damaged phragmocone often filled at least partly with sediment that formed a concretionary infilling and with crystallized mineral infillings that preserved the shell from the crushing effects of lithostatic pressure. Where diagenetic crushing occurred, pieces of the shell are usually crushed inward in irregular patterns.

One of the more obvious challenges in isolating damage produced by predators during lethal attacks is determining whether the processes involved with transportation created the shell damage. To evaluate this factor, the distribution of the cephalopod shells within the Mature Molluscan Community must be considered.

Cephalopod specimens are distributed randomly through the Finis Shale (Mapes *et al.*, 1996) suggesting that, at the time of death, the negatively buoyant specimens sank to the bottom and were not transported any appreciable distance. We suggest that many more specimens potentially lived and died in the Finis area, but most shells were positively buoyant at the time of death because of the loss of shell material and the removal of body tissues. These shells drifted away and are no longer part of the fossil record in the Jacksboro region. Thus, shell damage on the recovered specimens could be due to predation, or it could be the result of diagenesis or post-mortem trauma.

Post-mortem scavenging could have produced the same effect. Scavengers may have damaged the conch of moribund nautiloids to obtain any remaining soft tissue within the conch. The degree to which this activity damaged the conch of the dead animal is uncertain; however, larger predators/scavengers were more likely to have been involved with the removal of the tissue of the dead animal and less involved with the



**FIGURE 5.** Selected ammonoids from the Finis Shale with damage produced by lethal predator attacks. All ammonoids except M were recovered without their body chamber. For locality information see Chaffin (2000). (Bar scale = 1 cm). (A) *Gonioloboceras* (OUZC 3791; locality TXV-34) with a circular perforation along the right lateral side of the phragmocone. Based on the circular puncture (arrow) and the missing body chamber, this specimen is interpreted to have been attacked by an unknown predator with puncture-type teeth. (B, C) Lateral views of *Gonioloboceras* (OUZC 3796; locality TXV-41) phragmocone with multiple circular perforations (arrows) on either side. Based on the size and orientation of the punctures, we suggest that these holes were produced by a symmoriid shark, perhaps *Symmorium reniforme*. (D) Ventral view of *Neodimorphoceras* (OUZC 3818; locality TXV-99) showing U-shaped removal of the shell material along the venter on the phragmocone (arrows). This specimen is missing the body chamber, suggesting that it may have been attacked by a fish or possibly an arthropod. (E) Lateral view of a partial phragmocone of *Gonioloboceras* (OUZC 3795; locality TXV-34). This specimen has two circular perforations on the side of the phragmocone (arrows), and the specimen is missing the body chamber. The orientation of the holes suggests that the specimen was killed by a symmoriid shark. (F) Lateral view of a *Schistoceras* phragmocone (OUZC 3802; locality TXV-200). This specimen lacks perforations but is missing the body chamber and about half of the phragmocone. The lack of perforations suggests that shell crushing was involved. (G) Lateral view of a *Gonioloboceras* phragmocone (OUZC 3793; locality TXV-34). The three perforations occur in a line, suggesting that they were caused by a large fish with puncture-type teeth (arrows). (H) Lateral view of a *Gonioloboceras* phragmocone (OUZC 3794; locality TXV-42). Note the alignment of the two perforations (arrows). The combination of the linear holes and the missing body chamber suggests that this specimen was attacked by a predator with puncture-type teeth. (I) Lateral view of a *Gonioloboceras* phragmocone (OUZC 3798; locality TXV-42). The numerous holes on the conch are interpreted to be caused by dissolution rather than predation. However, the body chamber is missing, suggesting this specimen was attacked by a predator with a crushing-type dentition. (J) Lateral view of a *Gonioloboceras* phragmocone (OUZC 3792; locality TXV-56). This specimen has a semicircular hole located along the venter (see arrow). It is not known whether the hole is related to predation; however, the missing body chamber suggests that predation was the cause. (K,



shelly material that has no nutritive value. Smaller scavengers/predators were probably attracted to smaller tissue volumes, and even the siphuncular cord may have been of interest to the smaller scavengers. Moreover, such small scavengers may not have had the ability to do major shell damage.

Missing body chambers are probably an indirect indicator that lethal predation occurred. Likewise, missing sections of shell along the venter, either on the phragmocone or on the body chamber, suggest that damage was a product of lethal predation (Figures 4, 5). Other evidence of possible predation imprinted on coiled nautiloid and ammonoid conchs may include the following features: (1) Indentations or holes from teeth, which may occur in a straight line with counter marks on the counter side of the shell being reasonably aligned; however, marine predators, such as sharks and other fish, often lose teeth, leaving gaps in such lines. Also, small cephalopod genera and immature specimens may show only one or two tooth marks in the case of larger predators with larger mouths and widely spaced teeth. (2) Perforations caused by teeth may show consistency in shape, size, and spacing on the conch, while post-depositional compaction perforations are irregular in size and position. (3) Theoretically, shell material broken due to puncturing by predators could be driven inside the cameral chamber (Buckowski and Bond, 1989), and internal structures such as septa should show damage consistent with surface damage produced by long conical puncturing teeth (Mapes *et al.*, 1995).

The marine system during regression was within storm wave base because the maximum flooding surface located near the base of the Finis Shale was removed during the regressive phase by a storm (Rothwell *et al.*, 1996). The oxygenated nature of the marine shale above the storm bed suggests some low current energy sources were active in the environment. However, storms and other high-energy events could not have been the main factor in producing the broken cephalopod conchs. If storms played a role in the preservation of the cephalopods, they would be size-sorted and transported into clusters or lenses, and these concentrations would occur as part of lag deposits with preferential orientations to the conchs and other shell debris. The coiled nautiloids and other cephalopods appear to be randomly distributed throughout the exposed shale sections at all the collected localities. Minor accumulations of the shells of invertebrates (brachiopods, bivalves, gastropods, etc.) occur as discrete lensoidal concretions or as pods in the shale that may represent storm or current concentrations; however, the amount of energy was relatively low because larger shells are not part of these concretions. It is also possible that some of these shell concentrations were produced by organisms and would therefore be considered trace fossils. This conclusion is supported by the presence of shell-packed burrow linings throughout the Mature Molluscan Community interval.

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L) Phragmocone of *Neodimorphoceras*, lateral and ventral views, respectively (OUZC 3801; locality TXV-56). There are no perforations present on the conch. However, the specimen retains about one-third of the phragmocone and is missing the body chamber, suggesting that it was attacked by a predator with a crushing-type dentition. (M) Lateral view of a *Glaphyrites* (OUZC 3800; locality TXV-56). There are no holes present on the conch, and this *Glaphyrites* retains the body chamber. There is no evidence that this specimen was killed by a predator. (N) Lateral view of a *Gonioloboceras* (OUZC 3797; locality TXV-54) phragmocone. The specimen has a circular perforation located on the umbilical shoulder and a missing body chamber, suggesting that it may have been attacked by a predator with puncture type teeth (arrow).

It is possible, though unlikely, that conchs were damaged by impact with other organisms having robust skeletons (e.g., rugose corals) that co-existed on the mud bottom that later formed the Finis Shale. However, organisms such as rugose corals are not abundant, and it is doubtful that the energy level was consistently high enough during regression to cause the observed shell damage on the coiled nautiloids and other cephalopods. Additionally, both the geographic and vertical stratigraphic distribution of the coiled nautiloids and other cephalopods is random. The breakage patterns and the areas of shell loss observed on the conchs are often repetitive, suggesting there may be common causes for the damage. Collisions with hard substrates probably would cause random breakage patterns on the coiled nautiloid conchs and on the body chambers of the ammonoid specimens. We have observed that the other invertebrate faunal elements (bivalves, gastropods, brachiopods, etc.) are not as damaged as are the cephalopods. All of these observations argue against high energy levels causing the damage observed on the cephalopod specimens.

It is conceivable that the shells of cephalopods living in shallow water where wave motion is pronounced and floating nekroplanktic cephalopod specimens concentrated by wave and current patterns on the surface could have collided with one another during storm events. This type of damage has not been analyzed on present-day *Nautilus* nor have studies been done under such conditions. Our presumption is that this kind of damage would be rare, and the collision of shelled cephalopods would cause random breakage patterns that would be confined mostly to the outer whorl and to the body chamber. Also, we think it unlikely that cephalopods would have collided with one another often enough to account for the damage we have observed in the cephalopod data set; one would expect such broken conchs to be accompanied by lag deposits and other signs of a storm event showing that high-energy wave activity had occurred. We cannot totally reject the scenario that shell damage was caused by collision with other hard substrates; however, if the collision of conchs did occur on rare occasions, it is unlikely that it would have produced damage like the circular perforations seen on present-day *Nautilus* (Fig. 3) and the fossil coiled nautiloids and ammonoids described herein (Figs. 4, 5).

There is no evidence that the Finis Shale was subaerially exposed, which eliminates terrestrial weathering and erosional influences as sources of conch damage during the Finis cycle. Immediately after the Finis cycle, and for an unknown number of subsequent subaerial exposures, erosional damage probably did occur. However, it would seem that more recent weathering and erosion has had a greater impact. The specimens recovered *in situ* and as loose specimens on the surface from some localities (see especially locality TXV-200 in the locality register of Chaffin, 2000) have only been uncovered in the past seven years as opposed to the other localities, which may have been exposed for decades. Therefore, freshly exposed outcrop specimens can be compared directly with those from localities that have sustained long-term weathering and erosion. The conch damage produced by subaerial exposure is entirely different from the types of damage produced by diagenetic and taphonomic processes or biologic events. Thus, newly broken surfaces produced by present-day weathering are quite different in appearance from the ancient broken surfaces in terms of color and texture. Many of the TXV-200 specimens have not been oxidized from the original gray to the weathered brown color, and therefore freshly exposed shells retain their gray color that was developed during fossilization. Thus, subaerial exposure cannot be used to explain all the damage to coiled nautiloids and other cephalopods in the Finis Shale. Subaerial

exposure damage is characterized by fresher breaks caused by the various mechanical and chemical processes associated with recent weathering and erosion that have acted upon the specimens since the time they were uncovered.

Presumably the Mature Molluscan Community ecosystem of the Finis Shale was typical in that it contained a variety of both predators and prey. Based on observations of present-day *Nautilus*, coiled nautiloids and ammonoids of the Late Pennsylvanian were probably opportunistic predators and scavengers. They also served as a food resource for larger fish and other larger cephalopods. Thus, it seems a reasonable assumption that the Finis coiled nautiloids and ammonoids were attacked and eaten by predators in their natural habitat.

Coiled nautiloid conchs missing the body chamber are frequently recovered, suggesting that the damage was caused by predation. In cephalopods, the body chamber houses the soft tissue of the animal, which would serve as nourishment for the predator. The phragmocones are also often damaged, possibly as a result of previous attempts by the predator to subjugate the coiled nautiloids. Predators could produce multiple punctures on the conchs of the coiled nautiloids that would flood with water, thereby causing them to become negatively buoyant and sink (Chamberlain *et al.*, 1981). We suggest that cephalopods were preyed upon throughout the geographic extent and time span of the Mature Molluscan Community, and that some prey sank within a reasonable distance of where they died. This process would account for the random distribution of conchs in the stratigraphic sequence.

Any remaining soft parts in otherwise empty shells resting on the ocean floor were likely to have been consumed by scavengers. Scavengers may have removed parts of the shell in order to extract the tissue. Burrowing organisms also may have damaged the shells as they moved through the mud. Both scavenging and bioturbation could have damaged the shells, affecting their preservation quality but not their stratigraphically random distribution. Recovered conchs often show damage, which, in many of the coiled nautiloid cases ( $n = 328$ ), we have concluded was caused by predation. In some cases the conchs show the "puncture type" predation style. The least controversial lines of evidence probably are the circular and subcircular holes in the conch. Some of these specimens show larger holes often accompanied by one or two smaller perforations. The main holes are as large as 11 mm in diameter, and we suggest that they were produced by a predator with a dagger-like tooth cusp with smaller cusps on either side. The large holes and smaller lateral perforations support the conclusion that these features were probably caused by a shark, most likely *Symmorium reniforme* (Figures 4A, D; 5B, C, E, G, H, I, J), which is the only known Pennsylvanian age predator to have an offensive armament of this size and morphology (Mapes and Hansen, 1984). In other cases, there is just one perforation in the shell, suggesting that either the penetration was not deep enough for the lateral cusps to contact the shell or that a different predator, such as another type of shark or other large fish, produced the damage. When singular holes are observed, they are in the phragmocone, and the body chamber is missing. Also the phragmocones are typically only partly complete, suggesting that there may have been additional punctures that produced the conch damage.

While shell perforations are interpreted as the best available evidence of predation, they are not the most common form of shell damage in the ammonoid collection, because only 30% of the total specimens exhibit this kind of damage. The possible size difference between predator and prey may account for the lack of multiple punctures on the ammonoid conchs, and it is logical that a predator with a sufficient size advantage

and crushing dentition could have completely shattered an ammonoid conch without leaving tooth holes. In all cases, a comparison of the morphology of the holes in the Finis Shale cephalopod data set with modern hole producers has been made. The holes in the fossil cephalopods are circular to subcircular and have slightly crushed, untapered edges. Borings produced by octopi have small irregular slit-like holes (Fig. 2 C, D, E), and those produced by gastropods (described elsewhere in this volume), are smooth, circular, and evenly tapered. There is no evidence that either octopi or gastropods produced the punctures in the Finis Shale cephalopod shells.

Carnivorous organisms such as sharks and other fish lived in the Finis ecosystem, including the Mature Molluscan Community. Coiled nautiloids and ammonoids were likely prey for sharks or other fish that were the dominant predators in the ecosystem at that time. Predation would explain the random distribution of conchs in the stratigraphic section, as well as the recurrent absence of the body chambers that contained the majority of the animals' tissue, the missing parts of phragmocones, and the circular holes in phragmocones. Thus, the damage to the conchs is probably the result of predators attacking and eating the ammonoids. The partially fragmented conchs probably were damaged by predators that were much larger than the ammonoids. Conchs containing multiple punctures, as well as missing pieces of phragmocone or body chamber, usually would have filled with water and lost their positive buoyancy, causing them to sink (Chamberlain *et al.*, 1981). After the predation event, scavengers and burrowing organisms presumably consumed any remaining soft tissue within the otherwise empty shells resting on the ocean floor. Scavengers may have affected the appearance of the ammonoid conchs; however, the presence of encrusting organisms concentrated mostly on one side of the shell suggests that, after the scavengers were finished, the conchs were generally left undisturbed on the seafloor prior to burial. While encrusting organisms and micro-boring organisms also may have affected the preservation of the conchs, it is unlikely that any of this damage was sufficient to alter the overall appearance of the conch significantly.

Other specimens in the analyzed cephalopod collection have damage expressed in the form of small segments or chips of shell that appear to have been removed piecemeal from the venter of the body chambers of coiled nautiloids and ammonoids (Figures 4B, C, E; 5D). Damage of this type has been observed on present-day mollusks, and was caused by crabs and other arthropods (Vermeij, 1987). Although no arthropods with massive crushing claws have been recovered from the Finis Shale, decapods of the genus *Palaeopalaemon*, from the Late Devonian (Schram *et al.*, 1978), possessed the requisite armament for producing the chipping effect. Additionally, phyllocarid arthropods have strong crushing jaws that were capable of producing the shell damage observed on the cephalopods, and these arthropods are known to have been present in the Finis seas. As a result, such arthropods cannot be ruled out as possible predators or scavengers on coiled nautiloids and ammonoids (a more complete treatment of arthropods as predators and scavengers is provided by Babcock, Ch. 3, this volume). Possibly the peeled ammonoid and nautiloid phragmocones represent mistaken predation by a decapod or by an animal creating a "home place" to avoid predation (Walker and Yamada, 1993) (Fig. 5 D). Another possibility for this kind of damage is that other coiled nautiloids or ammonoids, seeking cryptic locations for egg-laying, peeled the moribund conchs themselves and laid their eggs in the vacant shells. While possible, we do not think this scenario is likely.

A significant, and as yet unappreciated, possible evidence of cephalopod predation is the presence of massive damage to, or complete removal of, the body chamber. Because the body chamber contains the nutritive tissue, this part of the conch will most concern the predator. In the Finis Shale collection of cephalopods, the body chamber is seldom found attached to the conch, indicating that it must have been removed. Only 12% of the ammonoids in the Mature Molluscan Community were recovered with the body chamber attached to the conch. It seems to us that it is unlikely that this amount of body chamber removal on so many specimens could have been caused by diagenesis, mechanical weathering, or post-mortem breakage; thus, we suggest that it was caused by predators attacking and eating the cephalopods.

Both coiled nautiloids and ammonoid conchs were recovered from the Mature Molluscan Community that are missing massive portions of phragmocone or body chamber along the venter. This type of damage, which we refer to as "peeling," may have been caused by arthropods attacking or savaging the living or newly dead, respectively, nautiloids and ammonoids when they were on the seafloor (see Babcock, Ch. 3, in this volume, for an extended discussion of arthropod predation and scavenging). Historically arthropods (particularly crabs) have been known to attack cephalopods as well as other ectocochleates (Thiermann, 1964; Roll, 1935; Lehman, 1976; Keupp and Ilg, 1992). Also, Walker and Yamada (1993) reported instances of Recent arthropods mistakenly attacking empty molluscan shells. This kind of post-mortem damage may explain why some ammonoid and coiled nautiloid phragmocones, which contain virtually no tissue except for the siphuncle cord, have been "peeled."

#### 3.4. Analysis of the Coiled Nautiloids

The recovered specimens show the following percentages of potentially lethal predation: *Domatoceras* 54%, *Ephippioceras* 83%, *Liroceras* 33%, *Metacoceras* 39% *Neobistrialites* 33%, *Peripetoceras* 47% and *Tainoceras* 72% (examples of the damage are illustrated in Fig. 4). Genera were recovered in varying abundances, with one genus accounting for more than a third of the total number of recovered specimens (*Liroceras*,  $n = 297/692$ ), whereas other genera recovered, such as *Ephippioceras* and *Neobistrialites*, account for fewer than 10 specimens.

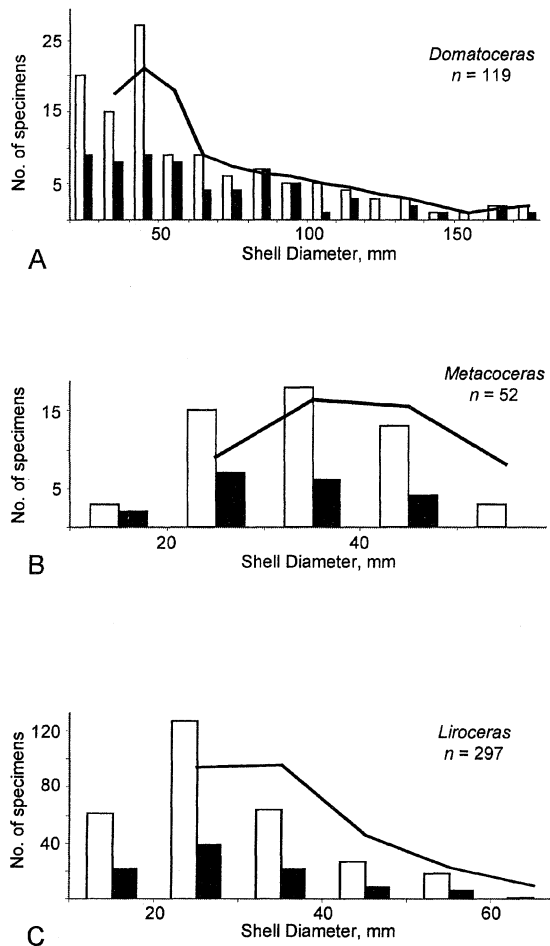
While *Domatoceras* has the largest apparent conch diameter of the genera analyzed (excluding *Titanoceras*), it seldom reached full maturity. The smaller conchs are recovered much more commonly, and show high frequencies of predation (Fig. 6A). The predation frequencies remained constant as the animals grew from post-hatchling to mature specimens, whereas the total numbers of specimens decreased through ontogeny. Although infrequent, larger specimens are always fragmented, which we interpret as due to predation. This suggests that *Domatoceras* was heavily preyed upon throughout ontogeny, and that the decrease in recovered mature specimens is due to attrition rather than collecting bias.

The size-frequency distribution of *Metacoceras* forms a bell-shaped curve both for total numbers of specimens and preyed-upon specimens (Fig. 6B). This suggests that *Metacoceras* could have had different predators at different sizes. Although there appear to be more instances of predation at smaller diameters, one must consider the possibility that fewer specimens survived into maturity to be attacked.

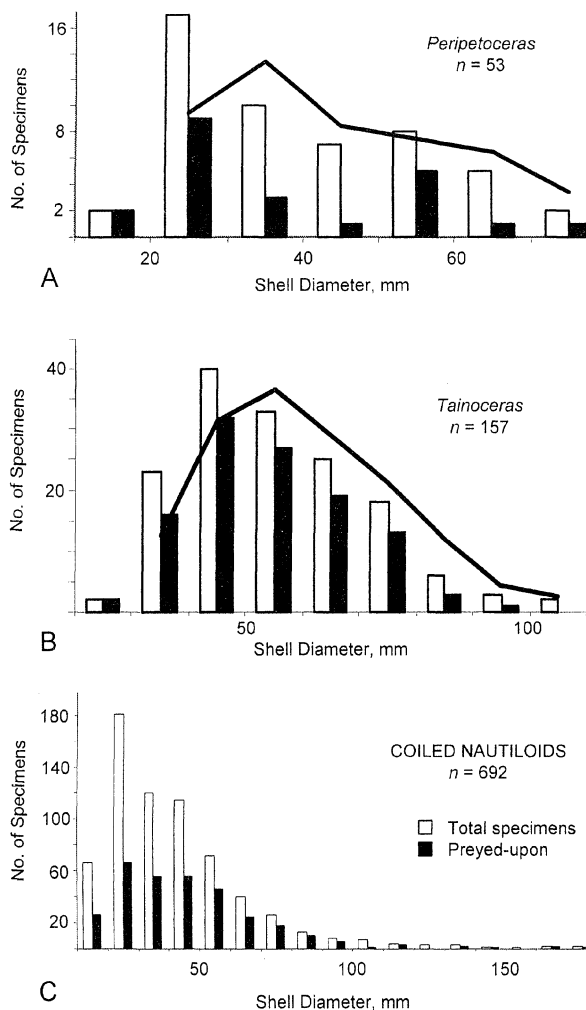
The size-frequency distribution of *Liroceras* forms a bell-shaped curve for total numbers as well as those specimens that were preyed upon (Fig. 6C). The *Liroceras*

distribution is skewed to the smaller diameter specimens. We suggest that this distribution is due in part to the presence of two species with small diameters. However, *Liroceras* specimens were heavily preyed upon at smaller diameters, and fewer specimens survived into maturity to be preyed upon.

The size-frequency distribution of *Peripetoceras* seems to form a bimodal distribution in both total numbers of specimens and in terms of numbers of preyed-upon specimens (Fig. 7A). This distribution suggests that the sample represents two distinct taxa. Alternatively, because part of the distribution is represented by only two specimens, this part of the distribution may represent collecting bias.



**FIGURE 6.** Histogram showing the presumed maximum growth based on conch diameter (in gray) at the time of death of *Domatoceras* (A), *Metacoceras* (B), and *Liroceras* (C), as well as predation frequencies (in black). An estimated 1/3 volution has been added to the diameter when appropriate to better evaluate the conch's maturity at death.



**FIGURE 7.** Relative abundances of *Peripetoceras* and *Tainoceras* and the overall diameter and predation distribution for all the coiled nautiloid genera. (A) The *Peripetoceras* distribution has a trend that gradually declines as specimens attain larger diameters. Maximum predation is in the 25 mm diameter size class. Based on slight morphological differences, two species may be present. (B) The *Tainoceras* distribution is skewed with mean shell diameter between 40 and 50 mm. Predation is most frequent in this size range. (C) A composite histogram of all the coiled nautiloid specimens for the five genera analyzed for predation from the 10 localities in the Finis Shale. The distribution shows that, while smaller diameter specimens are relatively intensely attacked, they are not attacked as intensely as the larger diameter specimens. Note that *Liroceras* and *Peripetoceras* are smaller diameter at maturity and that *Domatoceras* and *Tainoceras* make up the entire right side of the distribution at >100 mm diameters. These differing maturity sizes shift the overall shape of the distribution but they do not detract from the fact that intense predation occurs in all the taxa.

Although recovered conchs of *Tainoceras* have a size range of 20-110 mm, the size-frequency distribution of preyed-upon specimens is slightly skewed toward the smaller to mid-size specimens (Fig. 7B). One interpretation of this distribution is that there were fewer predators of larger-diameter specimens. Another interpretation is that few specimens of *Tainoceras* lived to reach maturity. This second interpretation is supported by the overall decrease in numbers of recovered specimens with diameters between 80 and 110 mm.

As stated earlier, it was necessary to equalize the genera statistically in order to compare them in terms of predation preference. The statistical analysis determined that, in some cases, genera were preferentially selected. *Tainoceras* appears to have been preferentially selected over all other genera, with the exception of *Ephippioceras*. *Liroceras* was not preferentially selected. *Domatoceras* was preferentially selected over *Liroceras*, but equally selected with all of the other genera with the exception of *Tainoceras*. *Peripetoceras*, *Metacoceras*, and *Neobistrialites* were not preferentially selected. *Ephippioceras* was preferentially selected over *Liroceras*, *Peripetoceras*, and *Metacoceras*. However, the findings on *Ephippioceras* are suspect due to the paucity of specimens.

Based on the fact that both *Domatoceras* and *Tainoceras* have the largest diameters of the genera analyzed and have the highest proportions of predation, there appears to be a relationship between conch diameter and predation. Thus, larger-diameter conchs appear to have attracted predators more readily than smaller specimens.

Ornamentation does not appear to affect predation greatly. The larger coiled nautiloids, such as *Domatoceras*, have a smooth conch, whereas the largest diameter conchs with ribs and nodes belong to *Tainoceras*. These two conch forms (smooth versus nodose) both have frequencies of predation greater than 50%; however, the statistical analysis shows that *Tainoceras* was more frequently selected than *Domatoceras*. When coiled nautiloids with smaller diameter conchs at maturity with nodes (*Metacoceras*) and smooth surfaces (*Liroceras*) are compared, the frequencies of predation are similar at 39% and 33%, respectively; these taxa were also much less likely to have been attacked than were the larger-diameter genera.

Genera with relatively wide body chambers were not preferred over those with relatively slim body chambers. Since the size of the body chamber is directly related to the amount of tissue (= the amount of food value), predators should prey selectively upon the volumetrically larger tissue source if possible. Thus, it would seem that a wide body chamber with proportionately more tissue than a narrow body chamber should be preyed upon more frequently. *Domatoceras* has a relatively narrow body chamber, whereas *Liroceras*, *Peripetoceras*, and *Neobistrialites* have relatively wide body chambers. *Domatoceras* exhibits a 54% predation frequency, whereas the taxa having wide body chambers have frequencies of 33%, 47%, and 33%, respectively. In other words, contrary to expectations, the narrow form has a higher predation frequency than the wider forms. The reason for this is not clear, but may relate to other biological factors such as swimming ability, camouflage, or even the possibility that the wider taxa did not taste as good.

In addition to body chamber width and ornamentation, there are other characteristics that could have affected predation. Both *Tainoceras* and *Domatoceras* have a large diameter-to-width ratio; this may have resulted in a smaller hyponome relative to some of the wider genera such as *Liroceras* and *Peripetoceras*. Present-day *Nautilus* ejects water through the hyponome to move rapidly. Fossil genera that possessed a large

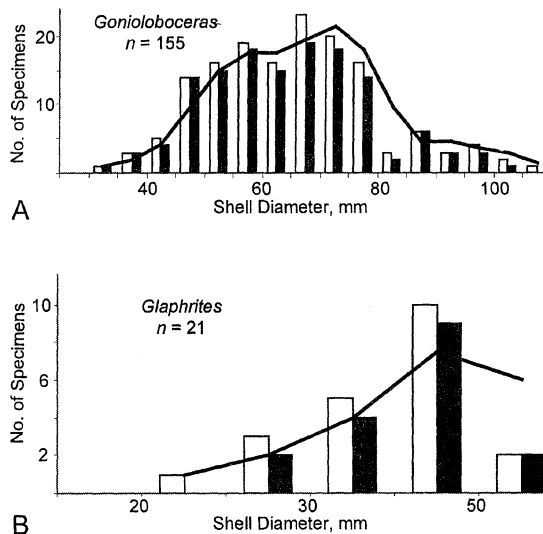


hyponome might have had a mobility advantage in avoiding predators. In addition, certain genera may have been better camouflaged, and this may have contributed to successful avoidance of predators.

### 3.5. Analysis of the Ammonoids

Of the recovered ammonoid shells ( $n = 206$ ), 88% are broken. Predation is the most likely cause of this breakage when taphonomic or other post-mortem phenomena can be ruled out. In most cases ( $n = 169/206$ ), the ammonoid conchs were recovered without body chambers, and many specimens are also missing large segments of the phragmocone (Fig. 5). Because the body chambers of these ammonoids are a complete whorl, the loss of the body chamber significantly reduces the overall volume of the conch.

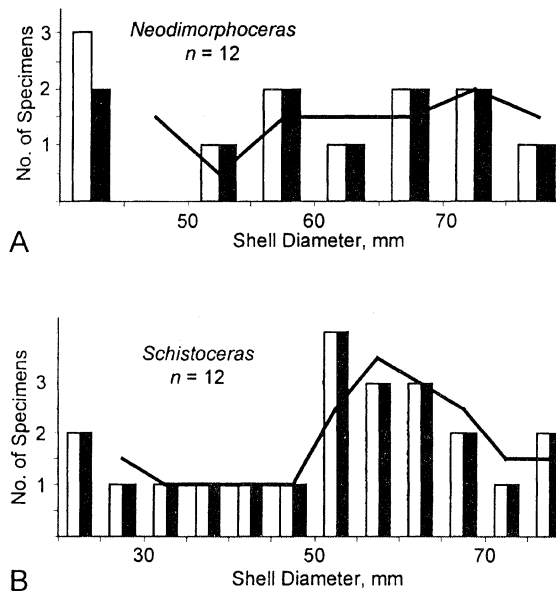
*Gonioloboceras* dominates ( $n = 155$ ) the ammonoid fauna. Every specimen in the collection is missing its body chamber, which is about one revolution in length. Pieces of the body chamber of this ammonoid are frequently recovered on the outcrop; however, since such pieces cannot always be identified with absolute certainty, they usually are not collected. When the diameters of the specimens are plotted, their size-frequency distribution approximates a bell-shaped curve for total numbers and those damaged by predators (Fig. 8 A). Predation levels are consistently high for all size classes, suggesting that the lack of larger-diameter specimens may be due to attrition, with high numbers of juvenile specimens being killed.



**FIGURE 8.** Histograms of *Gonioloboceras* (A) and *Glaphyrites* (B) populations from Finis Shale localities near Jacksboro, Jack County, Texas, showing the calculated growth (gray) at the time of death as well as predation frequency (black) at each size level. Note that there are no specimens below the 20 mm range, suggesting that post-hatching and early juvenile specimens lived in a different biofacies, and that when a certain level of growth was attained, the animal migrated into the Mature Molluscan Community.

*Glaphyrtes* ( $n = 21$ ) is the next most abundant ammonoid. Most specimens fall in the 35–40 mm diameter size range. Predation frequencies are consistently high, suggesting that all size classes are equally preyed upon (Fig. 8B). This overall high rate of predation may explain the lack of larger diameter specimens. Of the four ammonoid genera used in this study, this is the only genus with some shells that do not exhibit some form of damage. Some specimens retain the complete body chamber, and, other than some slight crushing around the aperture, there is no appreciable damage to the conch. This does not mean that these undamaged conchs were not killed by predators; rather, it means only that there is not any evidence of a predator attack that damaged the shell.

Specimens of *Neodimorphoceras* and *Schistoceras* constitute a relatively small part of the ammonoid collection ( $n = 12$  and  $n = 18$ , respectively). Both taxa have been subjected to intense predation; virtually all the specimens are missing the body chambers, and most are missing parts of the phragmocone. All of the specimens are more than 20 mm in diameter with no early juveniles being recovered, and there seems to be no evidence of any size selectivity by predators (Fig. 9A, B).



**FIGURE 9.** Histogram and trend line of *Neodimorphoceras* and *Schistoceras* from Finis Shale localities near Jacksboro, Jack County, Texas, showing the size (gray) at the time of death as well as predation mortality (black) at each size level. Note that there are no specimens <20 mm diameter, suggesting that post-hatching and early juvenile specimens are absent because of different biofacies preferences, as with *Gonioloboceras* and *Glaphyrtes*. (A) *Neodimorphoceras* exhibited nearly equal predation frequencies throughout all size ranges. The irregular distribution is due to the number of specimens rather than a lack of predation. The lack of specimens may be due to a collecting bias; however, more probably this genus was not competitive in this environment. *Neodimorphoceras* shows nearly 100% predation, suggesting that there were predators for all sizes of animals. (B) *Schistoceras* reveals no appreciable pattern, probably due to sample size. As with *Neodimorphoceras*, the predation level of 100% suggests these prey are selected without regard to size.

Overall, the Finis Shale ammonoids appear to have been preyed upon heavily, with 88% of the specimens exhibiting one or more kinds of damage that was probably caused by predatory attacks. The specimens were preyed upon with the following frequencies: *Gonioloboceras*, 87% ( $n = 155$ ), *Glaphyrites*, 80% ( $n = 21$ ), *Neodimorphoceras*, 100% ( $n = 12$ ), and *Schistoceras*, 100% ( $n = 18$ ). Results of the Z-test for independent proportions concluded that *Glaphyrites*, *Gonioloboceras*, *Schistoceras*, and *Neodimorphoceras* all had equal frequencies of predation despite the differences in percentages of preyed-upon specimens.

In all of the ammonoid collections from the Mature Molluscan Community from the localities that provided the research material for this study, there are no specimens that have diameters of 20 mm or smaller. Indeed, the smaller-diameter specimens are usually recovered from the underlying dark gray shale that is interpreted as having been deposited in a dysaerobic environment (see Boardman *et al.*, 1984 for an extended discussion); some localities have yielded large numbers (thousands to tens of thousands of ammonitella and early juvenile steinkerns up to about 20 mm in diameter) (see Tanabe *et al.*, 1994, for an exceptional case). This size distribution is not an artifact of collecting; rather it is more likely a reflection of a paleobiological condition, in which the smaller growth stages of most ammonoid genera in the Finis Shale preferred a habitat or biofacies that was lower in dissolved oxygen and relatively predator poor, compared to the habitat preferred by adults. Thus, the earliest growth stages are more or less confined to the dysoxic Juvenile Molluscan Community in the Finis Shale (see Boardman *et al.*, 1984 for details). Thus, when growth approached a diameter of about 20 mm (this diameter is somewhat variable, depending on the taxon being considered), the ammonoids appear to have migrated into the Mature Molluscan Community where they became prey for a host of different predators.

### 3.6. Lethal Damage: Comparisons Between the Ammonoids and Coiled Nautiloids

A much larger proportion of ammonoids were preyed upon (88%) than the coiled nautiloids (47%). This suggests that ammonoids were preferentially selected as prey over coiled nautiloids. *Gonioloboceras*, *Neodimorphoceras*, and *Schistoceras* show preferential predation over all the coiled nautiloids, with the exception of *Ephippioceras*. *Glaphyrites* shows preferential predation over all of the coiled nautiloids, with the exception of *Ephippioceras* and *Tainoceras*.

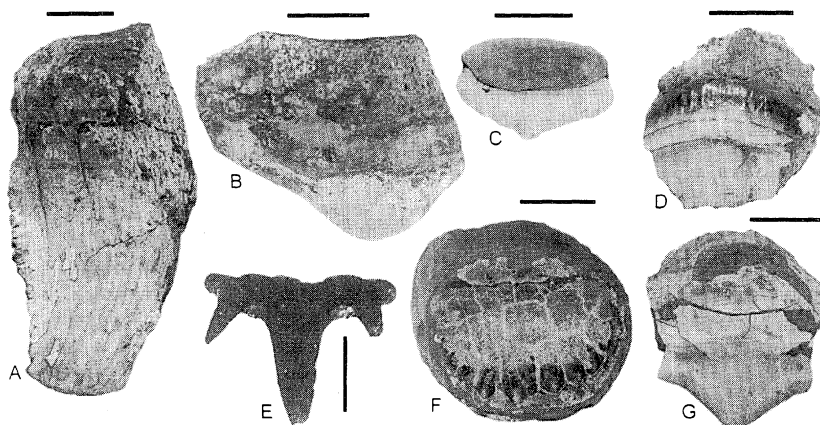
Reasons for the difference in predation frequencies between ammonoid and coiled nautiloid genera may be due to collecting bias, in that there are more coiled nautiloids in the collection ( $n = 692$ ) than ammonoids ( $n = 193$ ). However, 193 specimens should be adequate as an indicator of predation selectivity given the Z-test for independent proportions, which is designed to make comparisons between samples of different sizes. Based on percentage differences, the predation frequencies for both ammonoids and coiled nautiloids are substantial, and we consider this a real phenomenon. We speculate that these differences in predation frequencies between Ammonoidea and Nautiloidea may be due to life mode, habitat, mobility, and other biological factors.

### 3.7. A Hypothetical Predation Scenario

There are several kinds of predation scenarios that can be developed from this analysis. The Carboniferous predators that must be considered are sharks and other fish,

arthropods (especially the phyllocarids), and other cephalopods. The fish had a wide variety of dental armament in the Carboniferous, including crushing plates, piercing teeth and cutting teeth (Fig. 10). Predatory effects on the conchs of coiled nautiloids and ammonoids include loss of body chamber and punctures in gas chambers that result in a buoyancy control problem.

It would seem likely that there were different fish predators that employed slightly different methods of subjugation. Based on the analysis by Mapes and Hansen (1984), we conclude that predators may have tried to surprise nautiloids by attacking from the rear. Sharks and other fish with conical teeth may have attempted to bite into the phragmocone to grasp the nautiloids and possibly to reduce the prey's ability to escape due to a loss of buoyancy control. They could then either shake the conch until the shell was fragmented and the animal was dislodged or continue to bite the conch to expose the tissue. Continued biting could cause the conch to fragment, exposing the tissue of the animal without the shell fragments that are of no nutritional value.



**FIGURE 10.** Shark teeth recovered from the Finis Shale and other Upper Carboniferous units from Ohio, Oklahoma, and Texas. The teeth were used for a variety of purposes but are generally classified as cutting, puncturing, crushing, or a combination thereof. Though the sizes of the teeth vary, all recovered teeth would have caused significant shell damage to any of the cephalopods analyzed from the Finis Shale. (Bar scales = 1 cm). (A) *Edestus* sp. The tooth is missing the crown. Note the size of this tooth relative to the other teeth as well as the serrated edge (left side). This tooth was used for cutting, but, given the size, could have easily crushed small cephalopods. (B) *Ordus* sp. The tooth is missing the right portion of the crown and root. Note the blunt rounded surface of the tooth. This tooth was used for crushing. It seems likely that this kind of dentition could have decimated the shell of almost all Finis cephalopods. (C) Petalodontid tooth with root. This tooth has a serrated edge and was likely used for cutting. It is also relatively wide and flat, which might have made it effective for crushing as well. (D) Petalodontid tooth and root that is missing the bottom of the crown. This tooth was likely used for cutting. (E) *Symmorium reniforme* tooth. Note the large main cusp and the smaller lateral denticles. This tooth was primarily used for puncturing and grasping prey. The symmoriid sharks were probably one of the more formidable predators of cephalopods during the Late Carboniferous. (F) Petalodont? tooth in a concretion. Judging by the serrations, this tooth was probably used for cutting and crushing. (G) Petalodont tooth with portions of the root intact. This tooth was interpreted to have been used for cutting as well as crushing, given the size, width, and edge.

Sharks and other fish also may have attempted to target the body chamber to access the animal. Predators in this scenario were likely to have attacked from behind and beneath the coiled nautiloid. The teeth would have acted as scissors, effectively cutting the body chamber from the phragmocone. In some cases, the body chamber may have been crushed to free the tissue.

In the case of a coiled nautiloid or ammonoid with a punctured conch or a missing body chamber, the conch probably would have risen toward the surface while the broached chambers filled with water. The weight of the extra water could ultimately cause the conch to become negatively buoyant and sink to the seafloor. Chamberlain *et al.* (1981) explained the ascent/pressure relationships of cephalopod conchs in detail. It is unknown how many conchs retained enough post-mortem buoyancy to float to the water surface, and eventually float away from the site of the attack. We suggest that the specimens utilized in this study represent the specimens that were negatively buoyant at the time of death, and that the collection used in the case study represents only a fraction of the animals that inhabited the Finis Sea in the Jacksboro, Texas, region.

The arthropod predators include a wide range of possibilities during Carboniferous time (see Babcock, Ch. 3, in this volume). Likely candidates include trilobites, crustaceans (e.g. phyllocarids and decapods) and eurypterids. The remains of the latter have not been observed in the Finis Shale. Most of these arthropods are inferred to be nektonic, and they probably procured their food resources by predation and scavenging. Thus, an ambush scenario would be as follows: some of these arthropods probably hid among the mud and broken shells on the bottom of the sea. When the cephalopod searched the seafloor for its food, an arthropod attacked, overcame the cephalopod, and then, with jaws or pincers, opened the cephalopod shell like a “can of sardines” (Fig. 4B, C, E). A more likely scenario is that the arthropod was an opportunistic predator, attacking and eating wounded or dying cephalopods, and the best-case scenario is probably that the arthropods scavenged moribund specimens on the bottom for soft tissue. All of these scenarios could be used to explain the damage seen in Fig. 4B, C, and E.

Cephalopods may have preyed upon other cephalopods. Many cephalopods in the Carboniferous and at later times possessed mandibles that would have been capable of removing pieces of shell (and flesh) from other cephalopods. Using present-day *Nautilus* as a model, we conclude that ancient cephalopods may have preyed on juvenile and post-hatchling specimens, as *Nautilus* generally eats small organisms (Nixon, 1988) or the shells or bodies of larger organisms in small-capacity bites. Furthermore, it is doubtful whether coiled nautiloids had the ability to prey upon other cephalopods when those prey animals had grown sufficiently large to be immune from such opportunistic predators. We suspect that there is a somewhat greater probability that hatchlings and young juveniles of cephalopods were prey for larger cephalopods.

### 3.8. Summary and Conclusions Drawn from the Upper Carboniferous Case Study

Predation is inferred to be largely responsible for the fragmentary condition of the recovered conchs. As at present, ancient marine organisms rarely died a natural death. Thus, it can be reasonably assumed that both ammonoids and coiled nautiloids were attacked and eaten. This could have caused the conchs either to sink to the substrate or to float to the air/water interface. In the Finis Sea, only the negatively buoyant specimens formed the collections used in the case study. The sedimentation rate was

sufficiently rapid to cover the empty, negatively buoyant specimens gradually, allowing time for some encrusting organisms to colonize some of the conchs, yet quickly enough to ensure preservation. After the specimens were buried, the sections of the phragmocone not filled by mud-based concretion material or mineral deposits were crushed by compaction.

A lethal predation frequency of 47% (coiled nautiloids and ammonoids, combined) may seem high compared to the findings of Mapes *et al.* (1995), who reported a lethal predation frequency of less than 2% for the specimens of the ammonoid *Gonioloboceras* they studied. However, if Mapes *et al.* (1995) had considered the loss of the body chamber as a sign of predation, their conclusion as to the percent of preyed-upon specimens would have changed dramatically. In the collection of specimens they analyzed, every specimen having a diameter of over 35 mm ( $n = 954$ ) from every locality they analyzed is missing the body chamber, and this would give a predation frequency of 100%. However, we suggest that our numbers in this case study are quite conservative, as many specimens were not included due to poor preservation and excessive fragmentation. These poorly preserved specimens and excessively fragmented conchs probably represent the remains of preyed-upon specimens.

When the results of this case study are compared to the frequencies of sublethal damage and/or abnormal shell growth reported in other studies, there is a remarkable difference in the frequencies reported. For example, Bond and Saunders (1989) reported, in their Carboniferous goniatite ammonoid study, a range from 9 to 38% for different taxa. For different Jurassic ammonoid taxa, Guex (1967) reported a frequency of 2 to 2.5%, Morton (1983) a frequency of 8.1%, and Bayer (1970) a range of 1.4 to 9.7%. Landman and Waage (1986) reported a range of 10% to 40% for Cretaceous scaphitid ammonites. By comparison, the test case has 88% as its lowest frequency in the ammonoids, with all other genera at or near 100%. In the coiled nautiloids the frequency of predation ranges widely in the seven genera, from 33% to 83%, which is remarkably different than the predation frequencies of 88% to 100% seen in the ammonoids.

Based on our study, we suggest that the levels of lethal predation cannot be evaluated accurately by an analysis of sublethal repairs. Also, ammonoids appear to have an overall higher level of predation than coiled nautiloids. As Bond and Saunders (1989) observed, present-day *Nautilus* exhibits a sublethal repair frequency of over 50%, and most specimens that we have observed have more than one repaired area on the shell. Thus, this present-day analogue may not provide an accurate model for the ancient cephalopod record.

#### 4. Studies of Predation and Cephalopods Through Time

Overviews of the relationship between predation and morphologic adaptation of cephalopods in the Phanerozoic are limited to three major summary reports. In 1981, Ward quantified the ornament of ammonoids from the Paleozoic to the Upper Cretaceous and determined that ornament roughness increased through time. He hypothesized that this increase in ammonoid ornamentation served as a protective (defensive) function against the increased numbers of durophagous predators such as brachyuran crabs, lobsters, teleost fish, and rays during the mid-Mesozoic radiation. Ward recognized that the ornament on the ammonoids probably served additional functions, and he provided a list of these alternative functions. Later, Ward (1996)

utilized this information to help explain the evolutionary patterns of the ammonites prior to their extinction at the Cretaceous-Tertiary boundary.

Ward (1981), in an insightful analysis, noted that shell changes could be a response to the sublethal damage created by the cephalopod prey on the predator in its efforts to escape. In our opinion, this explanation has considerable merit as it can be used to explain the occurrence of some of the sublethal damage observed in many of the juvenile shells of fossil cephalopods and present-day *Nautilus* specimens that have very thin apertural margins and that could be damaged easily during any kind of major struggle with an uncooperative victim.

Signor and Brett (1984) examined the mid-Paleozoic record of durophagous predators (specifically fish, arthropods, and cephalopods) and applied this information to the morphological changes that could be detected in several invertebrate groups, including the coiled nautiloids (specifically the tarphycerids and barrandeocerids for the pre-Devonian and the nautilids for the post-Silurian). Using sculpture classes similar to those used by Ward (1981), they noted that these sculptural features probably had multiple functions. They concluded that nautiloids did respond to the origin of durophagous predators by a gradual increase in the degree of ornamentation robustness. Their overall conclusion, based on all the invertebrate groups that they analyzed, was that the origin of durophagous predators had a profound effect on the mid-Paleozoic invertebrate biota.

Vermeij (1987) proposed that evolution is in part driven by escalation of evolutionary innovation with enhancement of predator abilities followed by increased efficiency in prey defenses. In this context, he noted that externally shelled cephalopods were much more common in the Paleozoic and Mesozoic with, according to Saunders (1981), only one family (the Nautilidae) surviving to the present. From this fact, Vermeij (1987, p. 271) inferred "...that passive shell armor has not proven successful for cephalopods in the long run." While one may agree with this conclusion, given the current diversity of externally shelled versus internally shelled cephalopods, we disagree with the implication that externally shelled cephalopods were doomed to extinction because of the inherent limitations of an external shell. We see the externally shelled cephalopods as having been successful for more than 400 million years. In addition to achieving considerable diversity over a long time span, they survived four major extinctions. The fact that externally shelled cephalopods are still with us today suggests to us that they are still successful in the race against extinction.

Vermeij (1987) explored two different facets of cephalopod paleobiology to support his escalation hypothesis: (1) the problems of rapid locomotion with the obvious corollary of predator avoidance, and (2) the effect of pressure on the gas-filled chambers with depth. His analysis of cephalopod evolution and body plan limitations and the development of predators in the Phanerozoic seems to make sense, given some of the morphological changes in cephalopods that can be tracked through the fossil record. However, some caution should be exercised before Vermeij's (1987) hypothesis is accepted. We have little evidence that the externally shelled fossil cephalopods were predators in the strict sense as Vermeij (1987) assumed. Present-day *Nautilus* can only be considered an opportunistic predator and, in fact, seems to prefer scavenging as its major method of food gathering (Tshudy *et al.*, 1989). Also, as Vermeij (1987, p. 289) indicated, additional studies of the details of cephalopod history are needed. Analysis of architectural shell features in relation to paleoecological conditions and the life mode of different cephalopod taxa at a number of different times in the Phanerozoic should be

integrated into the escalation hypothesis framework. Also, studies of both sublethal and lethal damage on cephalopods need to be undertaken to determine the effects of predation on cephalopod evolution.

## 5. Conclusions and Future Studies

Vermeij (1987) invoked predation as a driving mechanism of evolution. His challenge to cephalopod workers is to evaluate the fossil record of this molluscan class to see whether there was an evolutionary response in the Cephalopoda to the diversification of predators in the Phanerozoic. Only his work (Vermeij, 1987), the work on some mid-Paleozoic nautiloids by Signor and Brett (1984), and the ammonoid study of Ward (1981) directly address the issue of predator/prey responses in cephalopod evolution. Reasons as to why more studies have not been done may be due in part to the unresolved taphonomic problems in quantifying the degree and cause of damage in cephalopod shells. The quantification problem was resolved in part by studies like those of Bond and Saunders (1989), Kröger (2000), and Landman and Waage (1986), who evaluated sublethal damage and repairs that created abnormal shells in ammonoid populations. The other problem has been the assignment of a causal agent to the damage seen on cephalopod shells. Few studies have separated shell damage due to non-biological agencies (e.g. lithostatic crushing, partial dissolution, shell breakage from impact on hard substrates, breakage due to burrowers, etc.) from different kinds of damage caused by predator attacks (shells altered by piercing, cutting, crushing, etc.). This difficulty has been compounded by the lack of data on damage caused by predators on present-day *Nautilus*. Thus, we recommend that actualistic taphonomic studies be performed on *Nautilus* to gain a reasonable idea of the kinds of damage created on *Nautilus* shells by different kinds of predators with different kinds of offensive armament. Probably equally important is whether the damage is randomly inflicted on the shell or is mostly directed to specific places on the conch. When this kind of information becomes available, it can be applied using taxonomic uniformitarianism to the fossil record of coiled nautiloids and ammonoids to compare the effect of evolution in predators to lethal and sublethal damage in the Cephalopoda.

Evidence of predation on coiled nautiloids, orthoconic nautiloids, and coleoids has not received the same level of attention as evidence on ammonoids. Coiled nautiloids can be treated in the same ways as ammonoids; however, because the sample sizes for nautiloids are usually smaller, it is more difficult to obtain good data sets for this group of cephalopods. Coleoids will continue to be difficult to evaluate because most damage to coleoids involves the flesh-covered exterior; predatory traces on the internal shell may not be present. Orthoconic nautiloids, because of their tendency to break into multiple segments, create difficulties in counting the actual numbers of injured individuals in a collection. The number of orthoconic nautiloid segments in a collection will not necessarily equal the number of individuals, and this will create a degree of unreliability in the conclusions that are drawn from any predation study.

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## Appendix

The following is a brief description of the coiled nautiloid and ammonoid genera utilized in the case study. The coiled nautiloids are as follows:

*Tainoceras* has a relatively large diameter (up to 130 mm) at maturity. The conch at the late juvenile and mature state is subrectangular in cross section, with a slightly impressed dorsum. *Tainoceras* has an evolute, perforate umbilicus and is heavily ornamented with nodes on the umbilical shoulders, ventro-lateral margins, and on the venter (Miller *et al.*, 1933).

*Liroceras* has a relatively small diameter (up to 39 mm) conch with the width typically greater than the height. The umbilicus makes up approximately 9% of the total conch diameter. The innermost whorl of the conch is covered with coarse longitudinal lirae around the umbilical region (Tucker and Mapes, 1978b). Conchs that contain more than two and one-half volutions are considered mature; the shell is smooth.

Specimens that have similar proportions to mature *Liroceras* but with diameters exceeding 50 mm were grouped under the name *?Liroceras*. *?Liroceras* is relatively wide, although less so than *Liroceras*. *?Liroceras* also lacks longitudinal lirae in the earliest volution on the umbilical region.

*Domatoceras* has the greatest conch diameter of the genera being evaluated and possesses a relatively narrow, smooth conch. Specimens of *Domatoceras* are evolute, with a deep ventral lobe, and square venter and umbilical shoulders (Tucker and Mapes, 1978b). Two species of *Domatoceras* exist within the collection. The differences are based on external features such as conch width *versus* diameter and ornamentation on the ventrolateral shoulders.

*Peripetoceras* has a wide body chamber and a relatively small (< 40 mm) conch diameter. The shell has a reniform to rounded subtrapezoidal cross section at maturity. The suture has shallow ventral and lateral lobes and a moderately deep dorsal lobe. The umbilicus makes up approximately 14% of the total conch diameter, and, at maturity, has flanges that partly cover the umbilical opening (Tucker and Mapes, 1978b).

Specimens with proportions similar to *Peripetoceras* but larger than 40 mm in diameter were assigned to *?Peripetoceras*. These specimens lack the flanges that cover the umbilicus in *Peripetoceras*. *?Peripetoceras* also has a smaller height-width ratio than *Peripetoceras*.

The overall shape of *Metacoceras* is hexagonal in cross section. The umbilical shoulders range in shape from subangular to broadly rounded. Ventrolateral nodes are prominent, and the venter is smooth. *Metacoceras* is somewhat similar in appearance to *Tainoceras*; however, it does not have the ventral nodes, and it never attains the conch

diameters seen in *Tainoceras*. It has been suggested that the two genera are closely related (Miller *et al.*, 1933).

*Ephippioceras* has an involute conch, which expands rapidly and consists of about three whorls. *Ephippioceras* possesses a small umbilicus that makes up approximately 10% of the conch diameter. *Ephippioceras* is also characterized by having a suture with a U-shaped ventral saddle (Tucker and Mapes, 1978b).

The conch of *Neobistrialites* is slightly involute, with a convex venter and a flattened dorsum. The umbilicus is roughly 30 percent of the total conch diameter. The internal mold has nodes on the umbilical shoulders, and a conchal furrow is present (Tucker and Mapes, 1978b).

The following is a general overview of some of the morphological features that separate the ammonoid taxa used in the case study at the generic level; additional morphological descriptive details can be found in Miller and Downs (1950).

*Glaphyrites* has a subglobular to globular conch with a moderate-sized umbilicus. The conch is moderately evolute, with a goniatitic 8-lobed suture. *Eoasianites* can have a similar conch and suture, with the major difference being that *Eoasianites* has conspicuous umbilical ribs during the early juvenile growth stages. It is possible that some of the specimens identified as *Glaphyrites* in this study will prove to be *Eoasianites* when all the specimens are evaluated as part of a future systematic redescription of this ammonoid fauna.

*Gonioboceras* has a discoidal conch and a small umbilicus that is not closed at late juvenile and mature growth stages. The whorls are compressed and somewhat convex laterally while strongly impressed dorsally. The medial portion of the venter is slightly flattened at maturity. *Gonioboceras* sutures have eight lobes and saddles, with all but the first saddle being rounded.

*Neodimorphoceras* possesses a discoidal conch with a small umbilicus at maturity. The venter is characterized by a prominent groove. Growth lines form ventral and lateral sinuses and dorsolateral and prominent ventrolateral salients. The suture is similar to that of *Gonioboceras* except that *Neodimorphoceras* develops an adventitious lobe in the first lateral saddle.

*Schistoceras* possesses a rounded conch with a moderate to large umbilicus and reticulated ornament. Nodes adorn the umbilical shoulders in early ontogeny. Sutures are goniatitic, with prongs of the ventral and lateral lobes being flared and lanceolate. A critical diagnostic feature for this genus is the small umbilical lobe element on the suture that forms early in ontogeny and migrates to an umbilical shoulder position.

## References

- Arnold, J. M., 1985, Shell growth, trauma, and repair as an indicator of life history for *Nautilus*, *Veliger* 27:386-396.
- Barrande, J., 1869, Système silurien du centre de la Bohême, Première Partie: Recherches paléontologiques, v. 2, Class des Mollusques, Ordre des Céphalopodes, part I, 712 pp.
- Bayer, U., 1970, Anomalien bei Ammonititen des Aaleniums und ihre Beziehung zur Lebensweise. *N. Jahrb. Geol. Paläont., Abh.* 135:19-41.
- Boardman, D. R. II, Mapes, R. H., Yancey, T. E., and Malinky, J. M., 1984, A New Model for the Depth-Related Allogenic Community Succession within North American Pennsylvanian Cyclothem and Implications on the Black Shale Problem, in: *Limestones of the Mid-Continent* (N. J. Hyne, ed.), Tulsa Geological Society Special Publication No.2, pp.141-182.
- Boardman, D. R., II, Work, D. M., Mapes, R. H., and Barrick, J. E., 1994, Biostratigraphy of Middle and Late Pennsylvanian (Desmoinesian-Virgilian) ammonoids, *Kansas Geol. Surv. Bull.* 232:1-48.

- Bond, P. N., and Saunders, W. B., 1989, Sublethal injury and shell repair in upper Mississippian ammonoids, *Paleobiology* **15**:414-428.
- Boston, W., 1988, The surficial geology, paleontology, and paleoecology of the Finis Shale (Pennsylvanian, Lower Virgilian) in Jack County, Texas. Unpublished M.S. thesis, Ohio University.
- Buckowski, F., and Bond, P., 1989, A predator attacks *Sphenodiscus*, *Delaware Valley Paleont. Soc.*, **IV**:69-74.
- Canfield, D. E., and Raiswell, R., 1991, Pyrite formation and fossil preservation, in: *Taphonomy: Releasing the Data Locked in the Fossil Record* (P. A. Allison and D. E. G. Briggs, eds.), Plenum Press, New York, pp. 338-382.
- Chamberlain, J. A., Ward, P. D., and Weaver, S., 1981, Post-mortem ascent of *Nautilus* shells: implications for cephalopod paleobiogeography, *Paleobiology* **7**:494-509.
- Chaffin, D. T., 2000, Predation of Pennsylvanian cephalopods from the Finis Shale, Texas. Unpublished M. S. Thesis, Ohio University.
- Cleaves, A. W., II, 1973, Depositional systems of Upper Strawn Group of north-central Texas, in: *Pennsylvanian Depositional Systems in North-central Texas: A Guide for Interpreting Terrigenous Clastic Facies in a Cratonic Basin* (F. L. Brown, A. W. Cleaves II, and A. W. Erxleben, eds.), pp. 31-42.
- Dalton, R. B., and Mapes, R. H. 1999, Scavenging or predation: Mississippian ammonoid accumulations in carbonate concretion halos around *Rayonoceras* (Actinocerida) body chambers from Arkansas, *V International Symposium, Cephalopods – Present and Past*, Vienna, Abst. Vol., p. 30.
- Davis, R. A., Mapes, R. H., and Klofak, S. M., 1999, Epizoa on externally shelled cephalopods, in: *Fossil Cephalopods: Recent Advances in Their Study* (Yu. A. Rozanov, and A. A. Shevryev, eds.), Russian Acad. Sci. Paleontol. Inst., Moscow, pp. 32-51.
- Doguzhaeva, L. A., Mapes, R. H., and Mutvei, H., 1998, Breaks and radulae of early Carboniferous goniatites, *Lethaia* **30**:305-313.
- Doguzhaeva, L. A., Mapes, R. H., and Mutvei, H., 1999 (1998), A late Carboniferous spirulid coleoid from the southern Mid-Continent (USA), in: *Advancing Research on Living and Fossil Cephalopods* (F. Oloriz and F. J. Rodriguez-Tovar, eds.), Plenum Press, New York, pp. 47-52.
- Geczy, B., 1965, Pathologische jurassische Ammoniten aus dem Bakony-Gebirge, *Annales Univ. Scientiarum Budapestensis, sectio Geol.* **9**:31-37.
- Guex, J., 1967, Contribution à l'étude des blessures chez les ammonites, *Bull. Laboratoires de Géol. Minér., Géophys. et du Musée Géol. de l'Univ. de Lausanne* **165**:1-16.
- Hengsbach, R., 1996, Ammonoid pathology, in: *Ammonoid Paleobiology* (N. H. Landman, K. Tanabe, and R. A. Davis, eds.), Plenum, New York/London, pp.581-605.
- Hansen, M. C., and Mapes, R. H., 1990, A predator-prey relationship between sharks and cephalopods in the late Paleozoic, in: *Evolutionary Paleobiology of Behavior and Coevolution* (by A. Boucot), Elsevier, Amsterdam, Netherlands, pp.189-192.
- Haven, N., 1972, The ecology and behavior of *Nautilus pompilius* in the Philippines, *Veliger* **15**:75-81.
- Heckel, P. H., 1977, Origin of phosphatic black shale facies in Pennsylvanian cyclothems of Mid-Continent North America, *Am. Assoc. Petrol. Geol. Bull.* **61**:1045-1068.
- Heckel, P. H., 1978, Field guide to Upper Pennsylvanian cyclothem limestone facies in eastern Kansas, *Kansas Geological Survey Guidebook Series 2*, pp. 1-69, 76-79.
- Heckel, P. H., 1980, Paleogeography of eustatic model for deposition of Mid-Continent Upper Pennsylvanian cyclothems, in: *Paleozoic Paleogeography of West-central United States, West-Central U.S. Paleogeography Symposium 1* (T. D. Fouch and E. R. Magathan, eds.), Rocky Mt. Section SEPM, pp. 197-215.
- Hewitt, R. A., and Westermann, E. G., 1990, Mosasaur tooth marks on the ammonite *Placenticeras* from the Upper Cretaceous of Alberta, Canada, *Earth Sci.* **27**:469-472.
- Hoare R. D., and Mapes, R. H., 1985, A new species of Pennsylvanian Polyplacophora (Mollusca) from Texas, *J. Paleontol.* **59**:1324-1326.
- Hoare, R. D., Mapes, R. H., and Yancey, T. E., in press, Structure, taxonomy and epifauna of Pennsylvanian rostroconchs (Mollusca), *J Paleontol.*
- Kammer, T., Brett, C., Boardman D. R. II, and Mapes, R. H., 1986, Ecologic stability of the dysaerobic biofacies during the late Paleozoic, *Lethaia* **19**:109-121.
- Kase, T., Shigeta, Y., and Futakami, M., 1994, Limpet home depressions in Cretaceous ammonites, *Lethaia* **27**:49-58.
- Kase, T., Johnson, P. A., Seilacher, A., and Boyce, J. B., 1998, Alleged mosasaur bite marks on Late Cretaceous ammonites are limpet (patellogastropod) home scars, *Geology* **26**:947-950.
- Kauffman, E. G. and Kesling R., 1960, An Upper Cretaceous ammonite bitten by a mosasaur, *Univ. Michigan Contrib. Mus. Paleont.* **15**:193-248.

- Kauffman, E. G., 1990, Mosasaur predation on ammonites during the Cretaceous – an evolutionary history, in: *Evolutionary Paleobiology of Behavior and Coevolution* (by A. Boucot), Elsevier, Amsterdam, Netherlands, pp.184-199.
- Keupp, H., 2000, Ammoniten, *Thorbecke Band 6*, Herausgegeben von Wighart v. Koenigswald, 165 pp.
- Keupp, H., and Ilg, A., 1992, Palaopathologische Interpretation der Ammoniten Fauna des Ober-Calloviun von Viller sur Mer/Normandie, *Berliner Geowiss. Abh.*, Reihe E, 3:171-189.
- Kröger, B., 2000, Schalenverletzungen an jurassischen Ammoniten – ihre paläobiologisch und paläoökologische Aussagefähigkeit, *Berliner Geowiss. Abh.* Reihe E, Band 33, 97 pp.
- Landman, N. H., and Waage, K. M., 1986, Shell abnormalities in scaphitid ammonites, *Lethaia* 19:211-224.
- Lehmann, U., 1976 (trans. 1981), *The Ammonites: Their Life and Their World*, Cambridge University Press, Cambridge, 246 pp.
- Maeda, H., and Seilacher, A., 1996, Ammonoid taphonomy, in: *Ammonoid Paleobiology* (N. H. Landman, K. Tanabe and R. A. Davis, eds.), Plenum, New York, pp. 543-578.
- Mapes, R. H., 1979, Carboniferous and Permian Bacitroidea (Cephalopoda) in North America, *Univ. Kansas Paleontol. Inst.*, Art. 64, 75 pp.
- Mapes, R. H., 1987, Upper Paleozoic cephalopod mandibles: frequency of occurrence, modes of preservation and paleoecological implications, *J. Paleontol.* 61:521-538.
- Mapes, R. H., and Dalton, R. B., in press, Scavenging or predation: Mississippian ammonoid accumulations in carbonate concretion halos around *Rayonoceras* (Actinocerida) body chambers from Arkansas, *V International Symposium. Cephalopods – Present and Past*.
- Mapes, R. H., and Hansen, M. C., 1984, Pennsylvanian shark-cephalopod predation: a case study, *Lethaia* 17:175-182.
- Mapes, G., Rothwell, G. W., and Mapes, R. H., 1996, Intriguing ovulate fructifications from Upper Pennsylvanian dysoxic marine shale (Finis Shale) in mid-continent North America, *Am. J. Botany* 74:1205-1210.
- Mapes, R. H., Sims, M. S., and Boardman, D. R., II, 1995, Predation on the Pennsylvanian ammonoid *Gonioloboceras* and its implications for allochthonous vs. autochthonous accumulations of goniatites and other ammonoids, *J. Paleontol.* 69:441-446.
- Martin, A., Catala-Stucki, I., and Ward, P., 1978, The growth rate and reproductive behavior of *Nautilus macromphalus*, *N. Jahrb. Geol. Paläont. Abh.* 156:207-225.
- Mehl, J., 1978a, Ein Koprolith mit Ammoniten-Aptychin aus dem Solnhofer Plattenkalk, *Jber. Wetterau. Ges. Naturkunde* 129-130:85-89.
- Mehl, J., 1978b, Anhäufungen scherbenartiger Fragmente von Ammonitenschalen im süddeutschen Lias und Malm und ihre Deutung als Frassreste, *Ber. Naturforsch. Ges. Freib. Breisgau* 68:75-93.
- Miller, A. K., Condra, G. E., and Dunbar, C. O., 1933, The nautiloid cephalopods of the Pennsylvanian system in the Midcontinent region, Nebraska Geol. Surv. Second Ser. 9, 240 pp.
- Miller, A. K., and Downs, H. R., 1950, Ammonoids of the Pennsylvanian Finis Shale of Texas, *J. Paleontol.* 24:185-218.
- Morton, N., 1983, Pathologically deformed *Graphoceras* (Ammonitina) from the Jurassic of Skye, Scotland, *Palaentology* 26:443-453.
- Mutvei, H., 1967, On the microscopic shell structure in some Jurassic ammonoids, *N. Jahrb. Geol. Paläont.* 129:157-166.
- Nixon, M., 1988, The feeding mechanisms and diets of cephalopods-living and fossil, in: *Cephalopods Present and Past*, Second International Cephalopod Symposium (J. Wiedmann and J. Kullman, eds.), E. Schweizerbart'sche Verlagbuchhandlung (Nägele u. Obermiller), Stuttgart, pp. 641-652.
- Quinn, J. H., 1977, Sedimentary processes in *Rayonoceras* burial, *Fieldiana Geol.* 33:511-519.
- Reeside, J. B., Jr., and Cobban, W. A., 1960, Studies of the Mowry Shale (Cretaceous) and contemporary formations in the United States and Canada, U.S. Geol. Survey Professional Paper 355, 126 pp.
- Roll, A., 1935, Über Frassspuren an Ammonitenschalen, *Zbl. Miner. Geol. Paläont. Abt. B* 1935:120-124.
- Rothwell, G. W., Mapes, G., and Mapes, R. H., 1996, Anatomically preserved voynovskyaean seed plants in Upper Pennsylvanian (Stephanian) marine shales of North America, *J. Paleontol.* 70:1067-1079.
- Saunders, W. B., 1981, The species of living *Nautilus* and their distribution, *Veliger* 24:8-17.
- Saunders, W. B., Spinoso, C., and Davis, L. E., 1987, Predation on *Nautilus*, in: *Nautilus* (W. B. Saunders and N. H. Landman, eds.), Plenum, New York, pp. 201-212.
- Saunders, W. B., Bond, P. N., Hastie, L. C., and Itano, D., 1989, On the distribution of *Nautilus pompilius* in the Samoas, Fiji and Tonga, *Nautilus* 103:99-104.
- Saunders, W. B., Knight, R. L., and Bond, P. N., 1991, Octopus predation on *Nautilus*: evidence from Papua, New Guinea, *Bull. Mar. Sci.* 49:280-287.
- Sayre, A. N., 1930, The fauna of the Drum Limestone of Kansas and western Missouri, *Univ. Kansas Bull.* 17:73-160.

- Schram, F. R., Feldmann, R. M., and Copeland, M. J., 1978, The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans, *J. Paleontol.* **52**:1375-1387.
- Seilacher, A., 1998, Mosasaurs, limpets or diagenesis: how *Platoniceras* shells got punctured, *Geowissenschaftliche Reihe* **1**:93-102.
- Signor, P. W., and Brett, C. E., 1984, The mid-Paleozoic precursor to the Mesozoic marine revolution, *Paleobiology* **10**:229-245.
- Tanabe, K., and Mapes, R. H., 1995, Jaws and radula of the Carboniferous ammonoid *Cravenoceras*, *J. Paleont.* **69**:703-707.
- Tanabe, K., Shinomiya, A., and Fukuda, Y., 1988, 4. Notes on shell breakage in *Nautilus pompilius* from Fiji, in: *Marine Ecological Study on the Habitat of Nautilus pompilius in Fiji (The Second Operation)*, (S. Hayasaka, ed.), *Kagoshima Univ. Res. Center S. Pac. (KUSP), Occasional Papers* **15**:52-55.
- Tanabe, K., Landman, N. H., Mapes, R. H., and Faulkner, C. J., 1994, Analysis of a Carboniferous embryonic ammonoid assemblage – implications for ammonoid embryology, *Lethaia* **6**:215-224.
- Thiermann, A., 1964, Über verheilte Verletzungen an zwei kretazischen Ammonitengehäusen, *Fortschr. Geol. Rheinld. Westf.* **7**:27-30.
- Tshudy, D. M., Feldmann, R. M., and Ward, P. D., 1989, Cephalopods: biasing agents in the preservation of lobsters, *J. Paleontol.* **63**:621-626.
- Tucker, J. K., and Mapes, R. H., 1978a, Possible predation on *Nautilus pompilius*, *Veliger* **21**:95-98.
- Tucker, J. K., and Mapes, R. H., 1978b, Coiled nautiloids of the Wolf Mountain Shale (Pennsylvanian) of North Central Texas, *J. Paleontol.* **52**:596-603.
- Vermeij, G., 1987, Evolution and escalation: An ecological history of life, Princeton University Press, 527 pp.
- Walker, S. E., and Yamada, S. B., 1993, Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells, *Palaentology* **36**:735-741.
- Ward, D. J. and Hollingsworth, N. T. J., 1990, The first record of a bitten ammonite from the Middle Oxford Clay (Callovian, Middle Jurassic) of Bletchley, Buckinghamshire, *Mesozoic Res.* **2**:153-161.
- Ward, P. D., 1981, Shell sculpture as a defensive adaptation in ammonoids, *Paleobiology* **7**:96-100.
- Ward, P. D., 1984, Is *Nautilus* a living fossil?, in: *Living Fossils* (N. Eldredge and S. Stanley, eds.), Academic Press, London, pp. 247-56.
- Ward, P. D., 1996, Ammonoid extinction, in: *Ammonoid Paleobiology* (N. H. Landman, K. Tanabe, and R. A. Davis, eds.), Plenum, New York, pp. 815-824.
- Ward, P. D., 1998, Time machine: scientific explorations in deep time, Copernicus, Springer-Verlag, New York, 241 pp.
- Westermann, G. E. G., 1996, Ammonoid life and habitat, in: *Ammonoid Paleobiology* (N. H. Landman, K. Tanabe, and R. A. Davis, eds.), Plenum, New York, pp. 607-707.
- Westermann, G. E. G., and Hewitt, R. A., 1995, Do limpet pits indicate that desmoceratacean ammonites lived mainly in surface waters?, *Lethaia* **28**:24.
- Willey, A., 1903, Contribution to the natural history of the pearly Nautilus: Zoological Results based on material from new Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897, University Press, Cambridge, England, Part 6, pp. 691-830.
- Zangerl, R., 1981, Chondrichthyes I, Paleozoic Elasmobranchii, in: *Handbook of Paleichthyology* 3A (H. P. Schultze, ed.), Gustav Fisher Verlag, Stuttgart, New York, pp. 1-155.
- Zangerl, R., Woodland, B. G., Richardson, Jr., E.S., and Zachry, Jr., D.L., 1969, Early diagenetic phenomena in the Fayetteville black shale (Mississippian) of Arkansas, *Sed. Geol.* **3**:87-119.