General trends in predation and parasitism upon inoceramids

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ABSTRACT:

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Inoceramid bivalves have a prolific evolutionary history spanning much of the Mesozoic, but they dramatically declined 1.5 Myr prior to the Cretaceous-Tertiary boundary. Only the enigmatic genus *Tenuipteria* survived until the terminal Cretaceous event. A variety of hypotheses have attempted to explain this disappearance. This study investigates the role that predation and parasitism may have played in the inoceramids' demise. Inoceramids show a range of predatory and parasitic features recorded in their shells ranging from extremely rare bore holes to the parasite-induced *Hohlkehle*. The stratigraphic record of these features suggests that they were virtually absent in inoceramids prior to the Late Turonian and became increasingly abundant through the remainder of the Cretaceous. These results suggest that predation and parasitism may have played a role in the inoceramid extinction, but more rigorous, quantitative data are required to test this hypothesis further.

Probably the commonest death for many animals is to be eaten by something else.

C. S. Elton (1927)

INTRODUCTION

The inoceramid bivalves arose in the Permian and by the Cretaceous were dominant constituents of level-bottom communities in a wide variety of shelfal settings. Although they are well-known inhabitants of oxygen-depleted, marine facies, they also thrived in a wide range of well-oxygenated environments, including shallow-water settings (*e.g.* KAUFFMAN & HARRIES 1996). Hence, the group and even some species appear to have had very broad ecological tolerances that are also mirrored in their broad geographic distribution. Despite their abundance and diversity, all inoceramids, except for species of *Tenuipteria*, disappeared 1.5 Myr prior to the Cretace-

ous-Tertiary boundary (KAUFFMAN 1988). The marked demise of such an important group has led to the formulation of a wide range of hypotheses to explain this phenomenon. To date, most of these explanations have hinged on global change brought on by cooling, alteration of oceanic circulation, or general environmental degradation (*e.g.* KAUFFMAN 1984; 1988; KAUFFMAN & *al.* 1992; MACLEOD 1994; FISCHER & BOTTJER 1995; MACLEOD & HUBER 1996). This overview aims to investigate initial data in support of a further hypothesis in this debate: the role of predation and parasitism.

EVIDENCE OF PREDATION AND PARASITISM IN INOCERAMIDS

Evidence for parasitism on bivalve shells generally comprises a variety of pits, scars and addi-

tional calcitic secretions which modify the shell morphology. Predation signatures on molluscs are typically confined to those predators that either bore through or bite and crush the shell. Because inoceramids are very rarely bored by predators, most evidence for predation intensity derives from sublethal (rehealed) injuries. The study of these features as a proxy for predation intensity is less than ideal (VERMEIJ 1982); it is difficult to directly relate predatory failure to predatory success. Despite the limitations, it is the best indicator available. Common predatory and parasitic features found on inoceramid valves are described briefly below.

Boreholes

The line of evidence most commonly used to evaluate the role of predation in the fossil record of invertebrates is the presence of boreholes. In most cases they are produced by gastropod predators, especially naticids and muricids (SOHL 1969). Unlike predatory processes that result in fragmentation, where unequivocal causes are difficult to determine, boreholes can be readily interpreted. Because the borer leaves its signature in the morphology of the borehole, this predator-prey system has the advantage of identifying not only the obvious prey, but the predator as well. Typically, completed boreholes are interpreted to represent a successful predatory attack, in which the prey was successfully subjugated, killed, and consumed. Bored shells also have the advantage of generally being preserved as reliably as pristine ones (but see ROY & al. 1994); therefore, population dynamics and estimates of such aspects as predator efficiency can be reconstructed. The geologic record is replete with evidence of boring in a wide variety of groups and by a spectrum of predators. To date, only a single horizon in the Lower Maastrichtian is known to contain inoceramids bored by gastropod predators (SCHOPF & HARRIES, in prep.)

Shell breakage and repair

Unfortunately it is difficult, if not impossible, to determine whether most fragmentation in inoceramids was due to the action of predators or whether it simply reflects shell breakage due to wave and current activity prior to burial, post-

burial compaction, or simply the differential degradation of the organic matrix that held the prismatic layer together. Although consistent breakage patterns have been documented in some predator-prey relationships (e.g. CADEE 1968), this has not been seen from most available inoceramid data. HATTIN (1975) has suggested that Ptychodus was an extremely efficient processor of inoceramids. He hypothesized that their predation and excretion of bivalve material was responsible for the common inoceramid-prism-rich calcarenites in mid-Cretaceous Western Interior sequences. However from the numerous specimens investigated from this interval (strata spanning the Cenomanian-Turonian boundary), only a single occurrence of sublethal injuries has been documented (see Pl. 1, Fig. 1; WALASZCZYK 1992). Unless these predators were almost 100% efficient, which seems extremely unlikely (see discussion in VERMEIJ 1982), there should be evidence of failed prey subjugation. Additionally, SAGEMAN (1996) in his study of Western Interior calcarenites, suggested that they formed "through winnowing by storm events during relative sea-level fall and condensation due to starvation during subseqent rise" (p. 891). Hence, the primary control appears to be relative sea-level position and not a function of predatory efficiency.

Inasmuch as predators are rarely completely efficient and effective attackers of their prey, one of the ways in which shell attacks can be estimated is through the relative abundance of repaired shells. Because bivalves precipitate calcium carbonate throughout their lives, earlier ontogenetic events are preserved in their shells. Therefore, previous attacks on the shell that produced sublethal injuries have the potential to be recorded, especially those events that resulted in injuries to the mantle. Numerous inoceramid specimens show evidence of injury to the mantle and shell (Pl. 1, Fig. 4; Pl. 2, Fig. 2b). These features have a variety of morphologies, but they generally consist of mantle damage which then is reflected by aberrant growth following the attack. Some of these attacks can be quite localized (Pl. 1, Figs 1-2), while in other cases the attack may be more severe and substantially affect the shell morphology (Pl. 1, Figs 3-4 and Pl. 2, Fig. 2b). In certain instances, the predator may leave a fairly distinctive bite (e.g. KAUFFMAN 1972), but in the majority of cases it is difficult to precisely determine the predator.

Fecal pellets and regurgitated masses

Another common mode of predation on marine invertebrates, especially among fish, is to swallow bivalves and other benthic organisms. In a study of stomach volumes of modern hogfish, RANDALL & WARMKE (1967) determined that 42.6% of the stomach contents were bivalves. Clearly, certain fish can play a significant predatory role on bivalves, although extrapolating the results of these modern studies directly to the fossil record is tenuous. Rays also have the ability to ingest large quantities of bivalves (GRAY & al. 1997). Unfortunately, stomach contents of predators are rarely preserved in the fossil record. Instead, paleontologists must rely on preserved fecal pellets (coprolites) or regurgitation of shell masses to reconstruct predation patterns of the past. One of the main stumbling blocks to this approach is the difficulty in determining which predator produced the various defecated or disgorged masses present in the fossil record. Shell masses composed of inoceramid remains are relatively common, but their origin is questionable.

SPEDEN (1971) has documented several types of shell masses from the Albian-Cenomanian? Clarence Series in New Zealand very similar to Pennsylvanian shell masses attributed to fish predation (ZANGERL & RICHARDSON 1963) The most likely candidates to have produced these fecal or regurgitated masses are fish, sharks, rays, or marine reptiles, such as mosasaurs. Given the common co-occurrences of inoceramids and *Ptychodus* teeth (KAUFFMAN 1972, COLLOM 1991), these durophagous sharks would seem to be the leading candidate for many Cretaceous localities. However, the absence of *Ptychodus* teeth from New Zealand sequences (CRAMPTON, pers. comm., 1998) suggests that fish may be more important in that region.

"Bubbly" nacre

Features which may be indicative of the mantle responding to parasites potentially living between the shell interior and the mantle are the presence of "bubbles" on the internal shell surface. They can differ substantially in shape and size ranging from very small features confined to the nacreous layer (Pl. 2, Fig. 1) to larger features which probably influenced the external, prismatic layer as well. These shell features, some-times referred to as "mud blisters" (HOFSTETTER 1965), form when the mantle is irritated and additional nacre is precipitated over the irritant. In its most extreme form, this results in pearl formation, but in most cases it simply results in the secretion of additional nacreous layers.

Parasitic tracks

One of the most evident types of parasitic scars left on modern bivalves is the presence of polydorid worm borings. *Polydora* produces a distinctive U-shaped boring, but because the boring occurs following shell precipitation, it does not disrupt the mantle and later shell formation. However, where the parasite resides between the shell and the mantle, dramatic changes in shell precipitation can occur. Some inoceramid parasites clearly disrupted the mantle's ability to precipitate calcium carbonate, while in other cases, such as the formation of a *Hohlkehle* (discussed below), the inferred parasite was covered by nacre. In the former case, the shell contains pronounced, but often very localized, deformities (*see* IVANNIKOV 1979).

"Hohlkehle"

One of the common features found in Santonian through Maastrichtian inoceramids, and which may be present in Coniacian and potentially even in Jurassic inoceramids (MORRIS 1995), is a pronounced internal rib or *Hohlkehle*, that initiates behind the beak and is oriented towards the posterior margin (Pl. 1, Fig. 5 and Pl. 2, Fig. 2a). The *Hohlkehle* has been the source of considerable debate. WHITFIELD (1880) used this feature as the critical character in identifying the subgenus (or genus of some authors) *Endocostea*. Some recent workers have followed WHITFIELD's convention and used the internal rib as the diagnostic character (MACLEOD 1994, MORRIS 1995). TOOTS (1964), following ROEMER's (1852) and HEINZ's (1928) positions, suggested that the *Hohlkehle* was the result of a specialized parasite feeding on material expelled by the exhalent current. He based his conclusion on five lines of evidence summarized here: 1) the ridge commences at variable distances from the beak; 2) the ridge abruptly terminates in some specimens; 3) the nacre in specimens with

a *Hohlkehle* is thicker – a common response to the presence of parasites; 4) the ridge is a hollow cavity; and 5) the surface of the hollow is ornamented in a manner suggesting the encasement of an organism or at least living tissue. SEITZ (1966; 1967) has a thorough discussion of the problem as well as a plethora of morphologic, stratigraphic, and facies distribution data of this feature. SEITZ (1967) also noted that including all the inoceramid morphotypes with a *Hohlkehle* within a single genus was problematic. The *Hohlkehle* is present in a very broad spectrum of inoceramids (*e.g.* including *Platyceramus, Cladoceramus, Cordiceramus, Selenoceramus,* and *Endocostea* species; SEITZ 1967) that, in the absence of the feature, would be grouped as separate genera. A final line of observation that suggests the feature is a response to parasites is that rare specimens have the *Hohlkehle* only on one valve, whereas the other shows no evidence of it. Hence, if the inoceramid were disarticulated, some workers would place the two valves from a single specimen into separate genera. This paper follows SEITZ's (1967, p. 37) conclusion that the *Hohlkehle* has no taxonomic value.

A modern analog to this type of parasitism occurs in modern freshwater mussels. COKER & *al.* (1921) have documented a feature that is similar in terms of the consistency in position and the well-developed scar produced on the affected shells (see their plate XII). Because of its regularity and its spatial repetition regardless of substrate, they attribute the feature to an unknown parasite rather than due to mechanical injury. Although the shell scar produced is not identical to the *Hohlkehle*, it nevertheless suggests that parasites can preferentially inhabit a given location on a shell.

STRATIGRAPHIC TRENDS

To determine the efficacy, efficiency, intensity, and the temporal distribution of predation and parasitic types on the inoceramids, it is critical to investigate the stratigraphic as well as geographic patterns. The data summarized below are (*see* Text-fig.1), for the most part, solely qualitative and represent culling material from the literature as well as from unpublished data from the Western Interior of North America – in the future, based on new collections and a re-examination of existing collections emphasizing evidence for predation and parasitism, the trends depicted here may be substantially altered.

The earliest incidence of predation on inoceramids was documented by SPEDEN (1971) from the Albian (?Cenomanian) of New Zealand. He has attributed a series of "inoceramid patches" – small-scale, inoceramid-prism-rich masses – contained in horizons within a siltstone sequence to the predatory activities of fish and marine reptiles (SPEDEN 1971). Based on comparison to similar masses depicted from the Pennsylvanian by ZANGERL & RICHARDSON (1963), he interpreted these inoceramid concentrations as either regurgitated masses or fecal pellets. Although this may represent a mode of predation throughout the inoceramids stratigraphic range, to this point, it has only been documented from this single interval. It is possible that these inoceramid masses have not been preserved (the fecal masses may have become disaggregated and redistributed by current activity), been overlooked or their importance simply not recognized in other sequences. If they were as common through other portions of
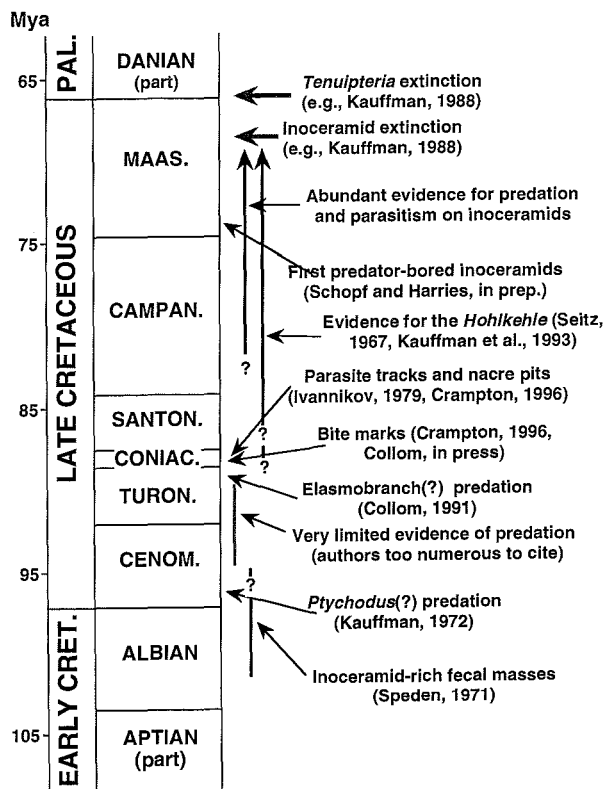

Fig. 1. Overview of the evidence of predation and parasitism from the Albian through the Maastrichtian

the Cretaceous as in the surfaces investigated by SPEDEN (1971), it is likely they would have been identified.

KAUFFMAN (1972) has documented *Ptychodus* bite marks on the type of *Inoceramus tenuis* MANTELL. This inoceramid ranged from the Early to Middle Cenomanian. Because the bites are limited to the large left valve and the attack only included a single bite, he concluded that the inoceramid was probably dead prior to the predation attempt. He also concluded that predation by ptychodids and other swimming vertebrates, such as rays, skates, and mosasaurs, must have played a major role in the ecology and differential preservation of inoceramids. However, direct evidence in support of this hypothesis is lacking. Indirect evidence, such as fragmentation of inoceramids in deeper-water settings, selective crushing, and common *Ptychodus* teeth in association with inoceramids, may support the contention, but the rarity of documented shell injuries throughout the majority of inoceramid history makes the claim doubtful.

The inoceramids of the Upper Cenomanian and Lower Turonian have been more extensively studied than any other portion of the group's range (authors too numerous to cite). From the >21,000 inoceramid specimens that have been investigated from a variety of different depositional settings through this interval in the Western Interior (ELDER 1987, HARRIES 1993), not a single convincing case of predation or parasitism has been documented in this region. In addition, a survey of various publications from this interval have revealed only a single case of sublethal injury (*see* Pl. 3, Fig. 1 *in* WALASZCZYK 1992). The rarity of predation evidence also places in question HATTIN's (1975) hypothesis of ptychodid harvesting of inoceramids as the source for Upper Cenomanian – Lower Turonian inoceramid-rich calcarenites. It seems highly unlikely that ptychodids had a predator efficiency of 100%; i.e., they ingested all the inoceramids they attacked and none were able to survive and continue growth. VERMEIJ (1982) has documented numerous examples were the predatory efficiency is less than 10%, and only a few cases where efficiencies were greater than 90%. For the latter, most of these involved the victimization of an especially vulnerable size class and not the entire population.

Following the virtual lack of evidence through the Cenomanian-Turonian boundary

interval, predation intensity by vertebrates increased in the Late Turonian. COLLOM (1991), in his detailed study of Upper Turonian and Lower Coniacian strata (*Inoceramus perplexus* biozone) within the Western Interior Basin, noted an increased abundance of *Ptychodus* teeth as well as inferred predation scars on approximately 40% of Late Turonian inoceramids within the informal "Quetzalcoatal Bed" of the Carlile Formation (COLLOM, *pers. comm.* 1998). However, cremnoceramids in the overlying Fort Hays Member of the Niobrara Formation contain relatively fewer sublethal injuries (COLLOM 1991). CRAMPTON (1996, *see* Pl. 1, Fig. 4) has depicted a Late Coniacian specimen of *Inoceramus pacificus* WOODS that shows where a large portion of the ventroposterior margin was removed, probably bitten, as seen in the distinct deformation of the ornamentation approximately 8 cm along the growth axis as well as the abrupt truncation and change in the orientation of the ornamentation. The specimen survived this attack and resumed shell precipitation, but the effects of the sublethal attack persisted throughout the remainder of ontogeny.

The first documented evidence of inferred parasitism in the inoceramids occurs in the Late Coniacian. IVANNIKOV (1979, his Pl. 20, Fig. 2) has documented a species of *Inoceramus margaritae* IVANNIKOV with two pronounced furrows. These features were probably the result of a parasite, most likely a worm (TRÖGER, per*s. comm.* 1996), which locally disrupted the mantle. Although the inoceramid continued to live after the parasite infestation, it clearly had a marked effect upon shell precipitation. CRAMPTON (1996, Pl. 19B) has relatively evenly spaced pits in a specimen of *Cremnoceramus bicorrugatus bicorrugatus* MARWICK; these features may represent another type of parasite.

Further evidence of potential parasitism comes from SEITZ (1967). He has documented the presence of the *Hohlkehle* from the Lower Santonian through the Lower Campanian in northwest Germany. His data depict a trend of increasing presence of the feature through the Santonian. In the Lower Santonian, 11% of his specimens had a *Hohlkehle*, whereas by the Lower Campanian the value had increased to 56%.

In the Upper Campanian through the lowest Upper Maastrichtian portions of the Pierre Shale in the Western Interior Basin, evidence of inoceramid predation and parasitism becomes more

abundant. It should be stressed that the majority of the predation and parasitic events documented prior to this interval tend to be quite temporally and geographically localized. Although the levels of both have not been quantified (OZANNE, *in progress*), from a qualitative perspective there is a marked increase in the presence and frequency of recorded predatory and parasitic behavior on inoceramids. In contrast to the earlier portions of the Cretaceous where at least sublethal attacks are relatively rare and stratigraphically isolated (see discussion above), in this interval evidence is common and essentially continuous. Another important difference is that rather than being limited to generally a single type of predation or parasitic style as seen in stratigraphic horizons earlier in the Cretaceous, many fossil assemblages show a number of different types of attack and infestation. The most common feature during this interval is the *Hohlkehle*, but evidence of sublethal attacks by predators and "bubbly" nacre are also common. Finally, the only known bored inoceramid specimen comes from the lowest Maastrichtian (*Baculites eliasi* Zone) within this interval (SCHOPF & HARRIES, *in prep.*).

DISCUSSION

The qualitative data presented here suggests that the marine environment was becoming increasingly hostile for the inoceramids through most of the Late Cretaceous, and this trend accelerated during the Campanian and Maastricthian. Prior to the latest Turonian, evidence for predation on and parasitism in inoceramids is rare to absent. In the case of predation, this may reflect very high predatory efficiencies, but the fact that most predators are substantially less than 100% efficient (VERMEIJ 1987) makes this interpretation tenuous. If predators were a significant factor in cropping inoceramid populations, there should be some indication of unsuccessful attacks. For the majority of the inoceramids' stratigraphic range, this evidence is, for the most part, strikingly rare. Moreover, for parasitism, tracks and traces of parasitic activity should also be preserved, but prior to the Coniacian there is no documented case in the inoceramids.

The implications of these predation and parasitism trends can be tied to a number of critical factors in inoceramid and benthic ecosystem evolution operating at a variety of evolutionary and ecologic scales. One of the important biotic trends during the Phanerozoic is the Mesozoic marine revolution documented by VERMEIJ (1977). This biotic revolution is characterized by the development of anti-predatory aptations, such as pronounced external ornamentation and modified apertures in gastropods, in response to the Late Mesozoic evolution of shell-crushing predators. Because the inoceramids dominated the epifaunal habitat during the Mesozoic, they were likely to be affected by the evolution and diversification of the groups that were disrupting this environment. Although sharks and rays are potential inoceramid predators, they became durophagous in the Jurassic and in the Cretaceous respectively (*see* Table 1 *in* VERMEIJ 1977). If inoceramids comprised a substantial portion of their diet, the evidence for their predatory attacks should appear earlier and be more prevalent in the fossil record. However there are two groups who attained durophagy during the Late Cretaceous corresponding to the interval where evidence for inoceramid predation increases: the Stomatopoda and the Brachyura, both crustaceans (VERMEIJ 1977). In support of this contention, BISHOP (*e.g.* 1973; 1982; 1985) has documented the appearance of several species and genera during the Lower Maastrichtian.

One of the ecologic characteristics that is becoming increasingly documented from the modern is the ecologic and environmental havoc invading or introduced taxa can wreak upon ecosystems (*e.g.* ELTON 1958). From a geologic perspective, a newly evolved predator could potentially cause similar types of ecologic disruption, especially if the biogeographic range of the descendant taxon exceeds that of its ancestor. Therefore, the rise of stomapods and brachyuran crabs and the associated change in potential predation efficiency upon the inoceramids may represent an example of this process.

The primary anti-predatory mechanisms available to epifaunal bivalves are avoidance and escape (VERMEIJ 1983). Avoidance is generally accomplished by adapting to or living in environments where predators are inhibited. For the inoceramids, escape from predators would seem relatively unlikely. Some forms contain byssal slits, suggesting attachment to the substrate, and their general morphology, from weakly impressed adductor muscle scars to, in certain cases, their sheer size, makes even short-term swimming unlikely. Throughout most of their history,

they thrived in black-shale environments (KAUFF-MAN & SAGEMAN 1990) where potential predators appear to have been relatively rare. Inhabiting regions where predators are excluded or rare can be a decisive factor in determining the habitats available to a species. Experiments on extant *Mytilus edulis* show that if they were protected from predators, such as starfish, they could thrive in environments where under normal conditions they would be excluded by predation pressure (WAR-REN 1936). If the inoceramid predators moved into environments that they previously were unable to inhabit (or if they developed durapha-gous ability within those environments), inocera-mids would have been fairly defenseless prey. The strength of their prismato-nacreous shell may have afforded them some protection, but the evidence of increased predation suggests that its effectiveness in warding off predators may have been waning.

Another factor is that predation and parasitism on prey or host organisms play important roles in regulating the abundance of taxa and community structure (*e.g.* DODD & STANTON 1981). From the study of modern ecosystems it is known that a distinctive relationship exists between predators and their prey. The cropping pressures exerted by predators regulates the abundance of prey which in turn controls the predator population. In the vast majority of cases, the balance between predators and their prey ensures the prey's, and hence the predator's, survival. However, if a predator is not dependent on a primary prey source, there is the possibility that overcropping and potentially extinction could occur. Parasites can also make their hosts more vulnerable, hence the inferred increase in parasitism, which occurred simultaneously with increased predation, potentially had profound effects upon inoceramid populations.

Despite the dominance of the inoceramids during the Cretaceous, they (except for taxa within the enigmatic genus *Tenuipteria*) disappeared approximately 1.5 Myr prior to the Cretaceous-Tertiary (K-T) boundary (KAUFFMAN 1988). Several hypotheses have been presented to explain the Late Maastrichtian disappearance of the inoceramids: 1) the first step in the K-T mass extinction (KAUFFMAN 1988); 2) the disappearance of abundant low-oxygen habitats during the latest Cretaceous (FISCHER & BOTTJER 1995, KAUFFMAN & al. 1992); and 3) a change in Late Cretaceous oceanic circulation (BARRERA 1994; 1997; MACLEOD & HUBER 1996). These hypothesized

mechanisms are potentially interrelated and clearly could have produced major environmental and ecological disruptions. The question remains, however, whether these would have been sufficient to cause extinction of the inoceramids. Given the length of their evolutionary history (from the Permian to the Late Cretaceous), the inoceramids experienced many of the same environmental changes invoked by the extinction mechanisms outlined above. Certainly, the changing oceanic and atmospheric conditions in the Late Cretaceous may have influenced the inoceramids, especially if they were forced to live in environments favored by predators as black-shale habitats became restricted. These events compounded by the radiation of durophagous crustaceans may have played an important role in the inoceramids' demise.

Even if the predation itself were not responsible for the ultimate extinction of the various inoceramid clades which disappeared in the Late Maastrichtian, it may have reduced population sizes, changed community structure, and altered geographic distribution to the point where smaller-scale perturbations, that under normal circumstances would have simply led to reduced population sizes, could become the proximate causes of extinction. SIMBERLOFF (1986) has outlined a range of different small-scale perturbations which could lead to extinction of species limited to small populations and geographic ranges. If the inoceramids were being cropped by increased predation, weakened by increased parasitism, affected by changing oceanographic parameters including the loss of their favored habitat, the cumulative effects may have been more than the group, with the exception of *Tenuipteria*, could withstand.

Further potential evidence in support of predation as a factor in Late Cretaceous biotic dynamics is seen in ammonite data. In their study of abnormalities in Late Cretaceous scaphitid ammonites from the Western Interior Basin, LAND-MAN & WAAGE (1986) investigated a range of injuries found in this group. One of their goals was to evaluate the level of predation intensity in scaphitid ammonites approaching the Cretaceous-Tertiary boundary. Their analysis covered a variety of ammonite biozones from the Turonian through the Maastrichtian, although it was focussed on evidence from the Fox Hills Formation. They showed that throughout in strata below the Fox Hills Formation, sublethal injuries occurred

in approximately 10% of the individuals found (values varied from a minimum of 4.0% in *Scaphites leei* III macroconchs to a maximum of 11.1% in *Scaphites hippocrepis* I microconchs). In the lower Trail City Member of the Fox Hills Formation, the incidence of injury is 10.4%; a value virtually identical to the earlier values. In the overlying Timber Lake Member, the incidence rises to 30%. LANDMAN & WAAGE (1986) interpreted these data as a function of several potential factors, including: 1) a facies change; 2) an overall decrease in prey abundance resulting in increased predation pressure on those present; and 3) the ability of these scaphitids to survive injury. These data could also be interpreted as evidence that predation on ammonites was also becoming increasingly intense approaching the end of the Cretaceous. Although the predators feeding on ammonites and inoceramids were probably different, this scaphitid data suggests that the overall predation pressure upon the marine biota was increasing.

CONCLUSIONS

Despite an extensive evolutionary history, the vast majority of inoceramids disappeared 1.5 Mya prior to the K-T boundary. This pre-K-T disappearance is striking because the inoceramids were dominant elements of the Cretaceous benthic communities and were adapted to a remarkably.wide range of habitats. The hypotheses presented to explain their apparently premature demise do not seem convincing in that the group had survived similar environmental, climatic, and paleoceanographic changes earlier in their history. However, there is a marked difference in the Late Cretaceous: inoceramids became much more prone to predatory attacks and parasitic infestations. Therefore, an escalation among predators, most likely from brachyuran crabs, combined with an increase in parasites may have sufficiently stressed the inoceramids to the point where they could no longer survive environmental perturbations which they had weathered previously. The observations discussed here, however, must be considered preliminary. More quantitative data with stratigraphic and biogeographic breadth required to determine the actual intensity of predation and parasitism and to thoroughly document the temporal and spatial trends in their distribution and style.

REFERENCES

BARRERA, E.S.M. 1994. Global environmental changes preceding the Cretaceous-Tertiary boundary: early-late Maastrichtian transition. *Geology*, **22**, 877-880.

BARRERA, E.S.M., SAVIN, E.T. & JONES, C.E. 1997. Evidence for thermohaline-circulation reversals controlled by sea-level change in the latest Cretaceous. *Geology*, **25**, 715-718.

BISHOP, G.A. 1973. *Homolopsis dawsonensis*; a new crab (Crustacea, Decapoda) from the Pierre Shale (upper Cretaceous, Maastrichtian) of Cedar Creek Anticline, eastern Montana. *Journal of Paleontology*, **47**, 19-20.

— 1982. *Homolopsis mendryki*; a new fossil crab (Crustacea, Decapoda) from the Late Cretaceous Dakoticancer assemblage, Pierre Shale (Maastrichtian) of South Dakota. *Journal of Paleontology*, **56**, 221-225.

— 1985. A new crab, *Eomunidopsis cobbani* n. sp. (Crustacea, Decapoda), from the Pierre Shale (early Maastrichtian) of Colorado. *Journal of Paleontology*, **59**, 601-604.

CADÉE, G.C. 1968. Molluscan Biocoenoses and Thanatocoenoses in the Ria de Arosa, Galicia, Spain. Leiden, E. J. Brill, 121 p.

COKER, R.E., SHIRA, A.E., CLARK, H.W. & HOWARD, A.D. 1921. Natural history and propagation of fresh-water mussels. *Bulletin of the United States Bureau of Fisheries*, **37**, 77-181.

COLLOM, C.J. 1991. High-resolution stratigraphic and paleoenvironmental analysis of the Turonian-Coniacian stage boundary interval (Late Cretaceous) in the lower Fort Hays Limestone Member, Niobrara Formation, Colorado and New Mexico. *Unpublised Master's Thesis thesis, Brigham Young University.*

CRAMPTON, J.S. 1996. Inoceramid Bivalves from the Late Cretaceous of New Zealand. Institute of Geological & Nuclear Sciences Limited, *Monograph*, **14**, 1-188. Lower Hutt.

DODD, J.R. & STANTON, R.J. 1981. Paleoecology, Concepts and Applications, 1-559. *John Wiley and Sons*; New York.

ELDER, W.P. 1987. The Cenomanian-Turonian (Cretaceous) stage boundary extinctions in the Western Interior of the United States. *Unpublished PhD dissertation thesis, University of Colorado*; Boulder, CO.

ELTON, C.S. 1958. The Ecology of Invasions by Animals and Plants, 1-181. *Chapman and Hall*; New York.

FISCHER, A.G. & BOTTJER, D.K. 1995. Oxygen-depleted waters: A lost biotope and its role in ammonite and bivalve evolution. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, **195**, 133-146. Stuttgart.

GRAY, A.E., MULLIGAN, T.J. & HANNAH, R.W. 1997. Food habits, occurrence, and population structure of the bat ray, Myliobatis californica, in Humboldt Bay, California. *Environmental Biology of Fishes*, **49**, 227-238.

HARRIES, P.J. 1993. Patterns of repopulation following the Cenomanian-Turonian (Upper Cretaceous) mass extinction. *Unpublished PhD dissertation thesis, University of Colorado*; Boulder.

HATTIN, D.E. 1975. Stratigraphy and depositional environment of Greenhorn Limestone (Upper Cretaceous) of Kansas. *Kansas Geological Survey Bulletin*, **209**, 1-128.

HEINZ, R. 1928. Ueber die bisher wenig beachtete Skulptur der Inoceramen-Schale und ihre stratigrapische Bedeutung (Inoceramen IV*). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **10**, 5-39. Hamburg.

HOFSTETTER, R.P. 1965. The Texas Oyster Fishery. *Texas Parks and Wildlife Department Bulletin*, **40**, 1-39. Austin, TX,

IVANNIKOV, A.V. 1979. Inoceramids of the Upper Cretaceous deposits of the southwest Eastern European Platform, 1-104. *Naukova Dumka*; Kiev. [*In Russian*]

KAUFFMAN, E.G. 1972. Ptychodus predation upon a Cretaceous *Inoceramus. Palaeontology*, **15**, 439-444. London.

— 1984, The fabric of Cretaceous marine extinctions. *In*: W.A. BERGGREN & J.A. VAN COUVERING (*Eds*), Catastrophes in Earth History, 151-246. *Princeton University Press*; Princeton, NJ.

— 1988, The dynamics of marine stepwise mass extinction. Paleontology and evolution: Extinction events; 2nd International Conference on Global Bioevents, 57-71.

KAUFFMAN, E.G. & HARRIES, P.J. 1996. The importance of crisis progenitors in recovery from mass extinction. *In*: M. B. HART (*Ed.*), Biotic Recovery from Mass Extinction Events. *Special Publication, Geological Society of London*, 15-39. London.

KAUFFMAN, E.G. & SAGEMAN, B.B. 1990. Biological sensing of benthic environments in dark shales and related oxygen-restricted facies. *In*: R.N. GINSBERG & BEAUDOIN, B. (*Eds*), Cretaceous Resources, Events, and Rhythms: Background and Plans for Research. ASI Series C, Mathematical and Physical Sciences, NATO, 121-138.

KAUFFMAN, E.G., VILLAMIL, T., HARRIES, P.J., MEYER, C.A. & SAGEMAN, B.B. 1992. The flat-clam controversy: Where did they come from? Where did they go?. *Fifth North American Paleontological Convention*, 157.

LANDMAN, N.H. & WAAGE, K.M. 1986. Shell abnormalities in scaphitid ammonites. *Lethaia*, **19**, 211-224. Oslo.

MACLEOD, K.G.1994. Extinction of inoceramid bivalves in Maastrichtian strata of the Bay of Biscay region France and Spain. *Journal of Paleontology*, **68**, 1048-1066.

MACLEOD, K.G. & Huber, B. T. 1996. Reorganization of deep ocean circulation accompanying a Late Cretaceous extinction event. *Nature*, **380**, 422-425.

MORRIS, N.J. 1995. Maastrichtian Inoceramidae from the United Arab Emirates-Oman border region. *Bulletin Natural History Museum, Geology Series*, **51**, 257-265. London.

RANDALL, J.E. & WARMKE, G.L. 1967. The food habits of the hogfish (*Lachnolaimus maximus*), a labrid fish from the western Atlantic. *Caribbean Journal of Science*, **7**, 141-144.

ROEMER, F. 1852. Die Kreidebildungen von Texas und ihre organischen Einschluesse, 1-100. *Adolph Marcus*; Bonn.

ROY, K., MILLER, D.J. & LABARBERA, M. 1994. Taphonomic bias in analyses of drilling predation; effects of gastropod drill holes on bivalve shell strength. *Palaios*, **9**, 413-421.

SAGEMAN, B.B. 1996. Lowstand tempestites: Depositional model for Cretaceous skeletal limestones, Western Interior basin. *Geology*, **24**, 888-892.

SEITZ, O. 1966. Die Hohlkehle bei Inoceramen des Santon und Unter-Campan, ein Pseudo-Skulptur-Element: *Geologisches Jahrbuch,* **84**, 189-192. Hannover.

— 1967. Die Inoceramen des Santon under Unter-Campan von Nordwestdeutschland III. Teil : Taxonomic und Stratigraphie der Untergattungen *Endocostea, Haenleinia, Platyceramus, Cladoceramus, Selenoceramus* und *Cordiceramus* mit besonderer Berücksichtigung des Parasitismus bie diesen Untergattungen. *Beihefte zum Geologischen Jahrbuch*, **75**, 1-171. Hannover.

SIMBERLOFF, D. 1986. The proximate causes of extinction. *In*: D.M. RAUP & JABLONSKI, D. (*Eds*), Patterns and Processes in the History of Life, 259-276. *Springer Verlag*; Berlin.

SOHL, N.F. 1969. The fossil record of shell boring by snails. *American Zoologist*, **9**, 725-734.

SPEDEN, I.G. 1971. Predation on New Zealand Cretaceous species of *Inoceramus* (Bivalvia). *New Zealand Journal of Geology and Geophysics*, **14**, 56-60.

TOOTS, H. 1964. Reinterpretation of *Endocostea* WHITFIELD. *Journal of Paleontology*, **38**, 85-86.

VERMEIJ, G.J. 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology*, **3**, 245-258.

— 1982. Unsuccessful predation and evolution. *American Naturalist*, **120**, 701-720.

— 1983. Traces and trends of predation, with special reference to bivalved animals. *Palaeontology*, **26**, 455-465. London.

WALASZCZYK, I. 1992. Turonian through Santonian deposits of the Central Polish Uplands; their facies development, inoceramid paleontology and stratigraphy. *Acta Geologica Polonica*, **42**, 1-122. Warszawa.

WARREN, A.E. 1936. An ecological study of the sea mussel (*Mytilus edulis* LINN.). *Journal of Biological Board of Canada*, **2**, 89-94.

WHITFIELD, R.P. 1880. Paleontology of the Black Hills of Dakota. *In*: H. NEWTON & JENNEY, W.P. (*Eds*), Report of the Geology and Resources of the Black Hills of Dakota, United State Geographical and Geological Survey, Rocky Mountain Region, 329-468. Washington.

ZANGERL, R. & RICHARDSON, Jr. E.S. 1963. The paleoecological history of two Pennsylvanian black shales. *Fieldiana, Geology Memoir*, **4**, 1-352.

PLATES 1 – 2

PLATE 1

1 – *Mytiloides labiatus* (SCHLOTHEIM), Lower Turonian, left valve; arrow shows localized, healed attack (*from* WALASZCZYK 1992); × 1

2 – *Cremnoceramus crassus* (PETRASCHECK), Middle Coniacian, left valve; arrow shows healed attack (University of Colorado Museum [UCM] 1722); × 0.5

3 – *Inoceramus* n. sp.?, left valve; arrow shows substantail shell deformation from a sublethal attack (United States Geological Survey [USGS] D1983); × 1

4 – *Inoceramus pacficus* WOODS, Upper Coniacian, left valve; note the dramatic change in direction of ornamentation following the severe attack (see arrows) (*from* CRAMPTON 1996); × 0.5

5 – *"Endocostea" typica* WHITFIELD, Upper Campanian, articulated specimen, with pronounced *Hohlkehle* (see arrows); there is also an area of shell deformation near the anterioventral margin (additional arrows); × 1
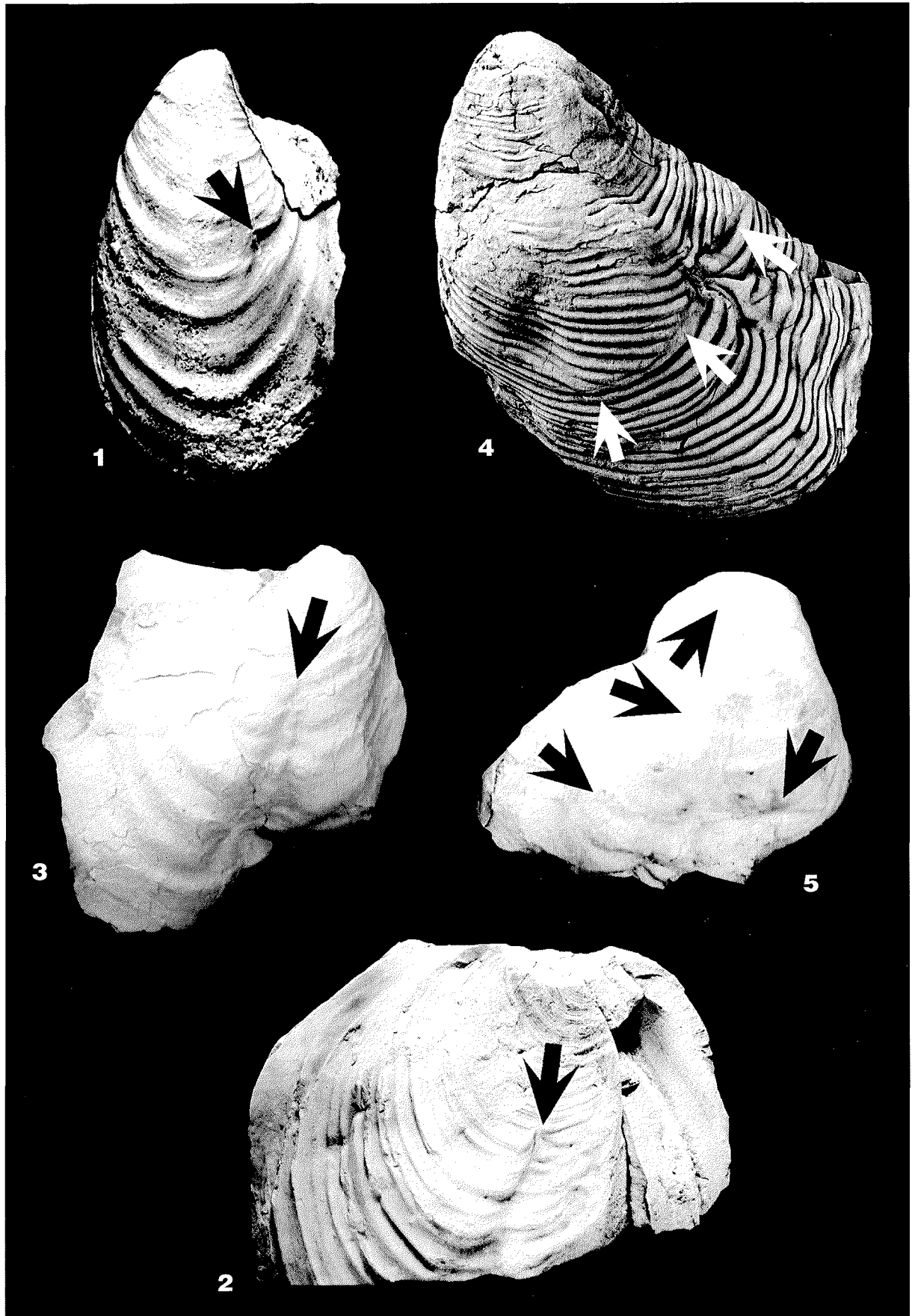
All specimens whitened with ammonium chloride

PLATE 2

1 – Fragment of *Inoceramus proximus* TUOMEY, Upper Campanian; arrows denote "bubbles" formed on the nacreous layer; × 1

2a-2b – *Cataceramus balticus?*(BOEHM), left valve; specimen has a *Hohlkehle* as well as significant shell deformation following geniculation (see arrows)(USGS D3137); × 1

All specimens whitened with ammonium chloride