



**Scavenging or Predation? –
Mississippian Ammonoid Accumulations
in Carbonate Concretion Halos
Around *Rayonnoceras* (Actinoceratoidea – Nautiloidea) Body Chambers
from Arkansas**

ROYAL H. MAPES & RODNEY B. DALTON*)

3 Text-Figures, 1 Table and 4 Plates

*USA
Arkansas
Carboniferous
Mississippian
Cephalopods
Ammonoidea
Nautiloidea
Predation*

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**Aasfresser oder Beutegreifer? –
Gehäuftes Vorkommen von Ammoniten in karbonatischen Konkretionshalos
rings um die kollabierten Wohnkammern von *Rayonnoceras* (Actinoceratoidea – Nautiloidea)
im Mississippium von Arkansas**

Zusammenfassung

ZANGERL et al. (1968) und QUINN (1977) haben das gehäufte Vorkommen von Ammoniten in karbonatischen Konkretionshalos rings um die kollabierten Wohnkammern des actinoceratiden Nautiloiden *Rayonnoceras* im Mississippium (Fayetteville-Formation – Chesterium) von N Arkansas beschrieben. Beide nahmen an, dass die Massenvorkommen Mageninhalte von *Rayonnoceras* seien. Die andere Hypothese ist, dass die Ammoniten während ihrer auf Aas gerichteten Nahrungsaufnahme durch Sauerstoffmangel oder durch die Konzentration giftiger Gase bei der bakteriellen Zersetzung der Leichen von *Rayonnoceras* oder durch beides zugrunde gegangen sind. Zur Untersuchung, welche die zutreffende Hypothese sei, wurden fünf konkretionäre Halos in 2 bis 4 cm dicke Scheiben geschnitten. Von allen einigermaßen kompletten Ammonitenquerschnitten (742 Stück) wurden die Maximaldurchmesser und der Einbettungswinkel gemessen sowie das Vorhandensein der Wohnkammer registriert. Um später hinzugekommene auszuschließen, wurden verdrückte Ammoniten von der Oberfläche der Konkretionen nicht berücksichtigt. Die Ergebnisse wurden mit Daten ähnlicher ammonitenreicher Karbonatkonkretionen aus der unteren Trias von Kanada und dem mittleren Karbon von England und Irland verglichen.

*) Authors' addresses: ROYAL H. MAPES, Department of Geological Sciences, Ohio University, Athens, OH 45701, U.S.A; e-mail: mapes@ohio.edu.
RODNEY B. DALTON: Department of Geological Sciences, Ohio University, Athens, OH 45701, U.S.A; e-mail: geogod@hotmail.com.

Die sichtbaren Ammonitendurchmesser variieren beträchtlich (min. 1,0 mm, max. 34,0 mm), Durchschnittswert ist 11,3 mm. Bei den meisten Stücken fehlt die Wohnkammer ganz oder teilweise, die Ammonitellen fehlen fast zur Gänze. Nur drei Gattungen aus den Konkretionen wurden bestimmt, während GORDON (1965) 25 Gattungen in seinem Überblick über die Cephalopoden der Fayetteville-Formation auflistet. Wir betrachten daher die Diversität der Cephalopoden in den Halos als gering. Die meisten Ammoniten sind mehr oder weniger zufällig orientiert. Bei den Vergleichsstücken sind die Ammoniten bei niedriger oder mäßiger Diversität meist schichtparallel eingebettet. Bei diesen Konkretionen ist ein Großteil der Wohnkammern erhalten. Die Verteilung der Durchmesser ergibt eine annehmbare Überlebenskurve.

Gestützt auf die Zahl der Individuen mit fehlender Wohnkammer, die signifikante Abweichung von einer akzeptablen Überlebenskurve, die eingeschränkte Diversität und die eher zufällige Orientierung zur Schichtebene, schließen wir, dass die Ammoniten um eine vorhandene Wohnkammer die letzte Mahlzeit eines *Rayonnoceras* gewesen sind. Daher sind unsere Ammonitenakkumulationen die einzige Dokumentation, dass Nautiloiden sich von Ammonoideen ernährt haben.

Abstract

ZANGERL et al. (1968) and QUINN (1977) described the occurrence of large numbers of ammonoids in carbonate concretion halos surrounding collapsed body chambers of specimens of the actinoceratid nautiloid *Rayonnoceras* in the Mississippian (Fayetteville Formation – Chesterian) of Northern Arkansas. Both ZANGERL et al. and QUINN speculated that these accumulations are the stomach contents of the *Rayonnoceras*. An alternate hypothesis is that the ammonoids died while scavenging because of the lack of oxygen, the concentration of poisonous gases produced by bacterial decomposition of the *Rayonnoceras* carcass or both. To test which hypothesis is more viable five concretion halos were cut into 2 to 4 cm thick slabs. All reasonably complete ammonoid specimens (n = 742) visible on the slabs were measured for their maximum apparent diameter, the presence or absence of the body chamber, and the angular relationship of the conch to the bedding. Crushed ammonoids on the concretion surface were eliminated from the data because they could have been introduced at a later time. These data were compared to similar data from ammonoid-rich carbonate concretions from the Lower Triassic of Canada and the Middle Carboniferous of England and Ireland.

Apparent diameters of the ammonoids vary greatly (min. 1.0 mm to a max. of 34.0 mm) in the *Rayonnoceras* concretion halos. Mean apparent diameter is 11.3 mm. Most of the specimens are missing part or all of their body chambers, and ammonitellas are almost completely absent. Only three genera have been identified in the concretion halos, whereas, GORDON (1965) lists 25 genera in his overview of the cephalopods that have been recovered from the Fayetteville Formation. Thus, we consider the cephalopod diversity in the concretion halos to be low. Most of the ammonoids appear to be randomly oriented to the bedding. In the comparative concretions, the medial planes of the ammonoids are mostly aligned parallel to the bedding and have low to moderate diversity. In those concretions the ammonoids retain most of their body chambers with the apparent diameter distribution conforming to reasonable survivorship curves.

Based on the number of specimens with missing body chambers, the significant deviation from a reasonable survivorship curve, the limited diversity, and the random conch orientation to bedding, we conclude that the ammonoids around a given body chamber are the last meal of the *Rayonnoceras*. Thus, these ammonoid accumulations represent the only documented occurrence that nautiloids preyed on ammonoids.

1. Introduction

The black shale of the Fayetteville Formation in northern Arkansas and northeastern Oklahoma is known for its relatively diverse cephalopod fauna (GORDON, 1965; HOROWITZ, 1977; SAUNDERS et al., 1977; MAPES, 1979; MANGER et al., 1999B; and other reports cited therein). Cephalopods occur as crushed individuals on bedding planes and as three-dimensional specimens in both the black shale and in the carbonate and phosphate concretions. Because some bedding planes are so ammonoid covered, with most specimens belonging to only a few taxa, MANGER et al. (1999B) speculated these occurrences could be the product of mass mortality associated with reproduction. Exceptionally large specimens have been interpreted to be pathologic giants (MANGER et al., 1999A). In some intervals, relatively large actinoceratid nautiloids are common; the largest recovered to date is nearly 3 meters in length (MANGER et al., 1999A). Sometimes, massive carbonate concretions, weighing up to 50 kilograms, have formed around the body chambers of these large orthoconic nautiloids. Within these concretions, there are sometimes large numbers of ammonoids. The early taphonomic history of these ammonoid accumulations is the subject of this research.

2. Previous Reports and Discussion

In 1969, ZANGERL and his associates described the emplacement of body chambers and phragmocones of the orthoconic actinoceratid nautiloid *Rayonnoceras* in the Fayetteville Shale as occurring commonly at both high and low angles to the bedding. Individual animals reached relatively large sizes, with segments of phragmocone over

one-half meter in length being relatively common at some localities. In addition to bedding plane relationships, they noted that around some of the *Rayonnoceras* body chambers there were massive carbonate concretions containing numerous ammonoids, and, in one case, a sponge (NITECKI & RIGBY, 1966). Microfossils and structures interpreted as arm hooks and a beak belonging to the *Rayonnoceras* were also reported as being in the concretions. Later, in 1977, QUINN redescribed this kind of *Rayonnoceras* occurrence and illustrated new specimens of *Rayonnoceras*, diagramming the relationship of the nautiloid body chamber to the bedding. In QUINN's reanalysis, thixotropic mud flows and rates of burial and compaction were considered. He also suggested a mechanism for the observed ammonoid accumulations. This proposed mechanism involved the sudden release of decomposition gases produced by the bacterial decay of the soft tissue in the body chamber of the nautiloid. The ammonoids were ejected into the surrounding sediment from the dead *Rayonnoceras* body chamber and there was subsequent rapid formation of the carbonate concretion. Based on his analysis, QUINN considered the ammonoids to have been a staple food resource for the *Rayonnoceras*.

Several aspects of these two reports require comment. QUINN (1977) in his reanalysis and presentation of newly recovered specimens makes no mention of sponges and does not acknowledge the report in 1966 by NITECKI & RIGBY. Indeed, it is the report by NITECKI & RIGBY that first suggested the possibility the goniatites and the sponges were, in fact, the last meal of the *Rayonnoceras*. In their report, they also mention that sponge spicules

“... are scattered throughout the chert matrix ...” (1966, p. 1373.).

Later (ibid., p. 1376) they said the

“... matrix surrounding the spicules is composed of silt and clay-sized particles and some sand ...”

This report of sand, silt, and chert is puzzling; we have not seen these associated with several hundred *Rayonnoceras* specimens collected in the past 30 years in the Fayetteville Formation. Indeed, the Fayetteville Shale that encases the *Rayonnoceras* conchs is a black shale that does sometimes contain pyritized sponge spicules, but not silt, sand, or chert.

It is apparent that QUINN (1977) did not see sponges or sponge spicules within the specimens he described. Also, in his discourse on the clays, burial rates, and sedimentation, there is no mention of chert, sand, or silt. In the five specimens we have sectioned, no chert, silt, or sand has been observed. Thus, the occurrences of the sponges described by NITECKI & RIGBY in 1966 may represent a unique occurrence; in any case, none were encountered by either QUINN or us.

The possibility exists that a silicified specimen of *Rayonnoceras* from the underlying Moorefield Shale was recovered and analyzed by ZANGERL and his colleagues. The Moorefield Shale, with silicified *Rayonnoceras*, is exposed in a fault block on Trace Creek near Leslie, Arkansas. Numerous silicified specimens occur in the Pleistocene and Recent gravel deposits that fill parts of the stream bed where the Fayetteville Shale with its calcified/pyritized *Rayonnoceras* is exposed. This creek is immediately adjacent to the Cove Creek locality

where ZANGERL and his colleagues collected some of their material.

The same also holds true for the arm hooks and beak of *Rayonnoceras* reported by ZANGERL et al. (1969, p. 111). QUINN did not report any similar structures in the material he analyzed, and we have not observed any arm hooks or beaks in the halo concretions we have sectioned and examined.

3. Focus of This Study

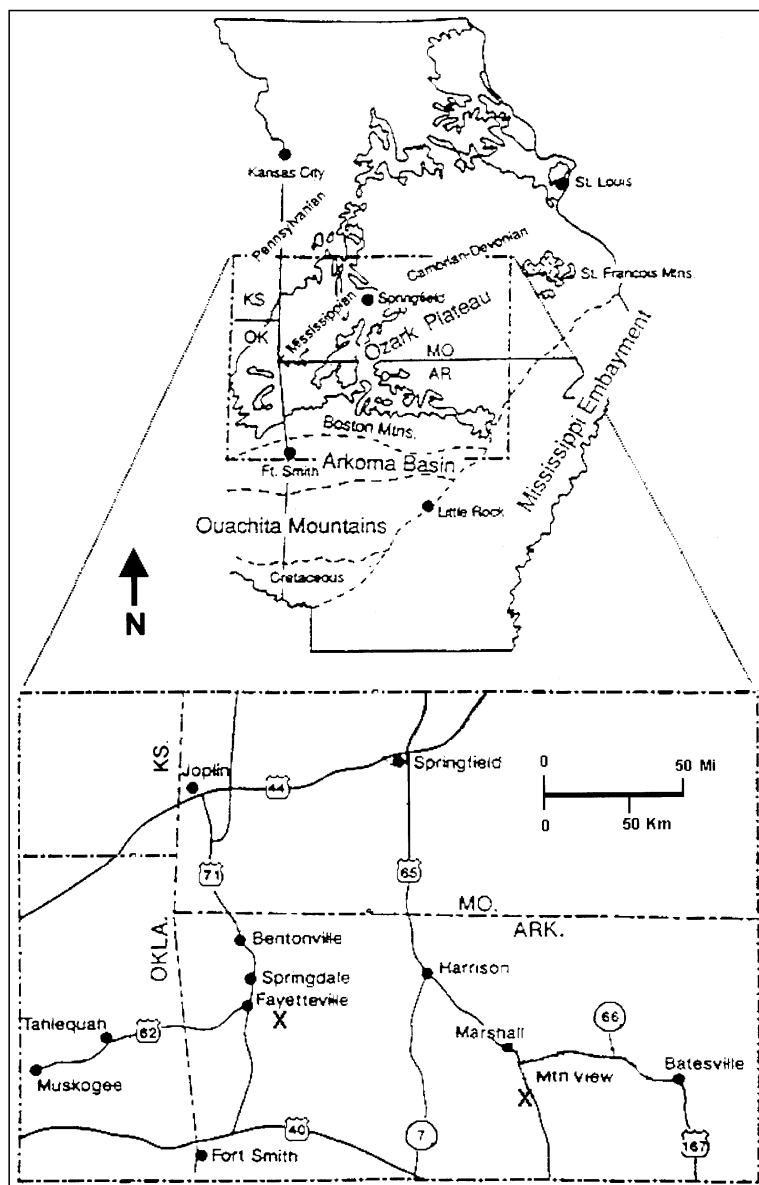
NITECKI & RIGBY (1966), ZANGERL et al. (1969), and QUINN (1977) have concluded that the ammonoids in the concretionary masses around the body chambers of *Rayonnoceras* specimens are the last meals of the nautiloids. An alternative possibility that was not considered in depth by those researchers is that the ammonoids could be a gradual accumulation of scavengers that were killed by poisonous gases, lack of oxygen or both. Aerobic bacterial decomposition of a decaying *Rayonnoceras* carcass in what was already a strongly dysoxic environment would locally reduce even further the already low oxygen levels at the water-sediment interface in the vicinity of the dead animal. Anaerobic bacteria consuming the carcass might have also increased on the local sea floor the levels of methane, hydrogen sulfide, and other poison gases.

To test to see which hypothesis is more likely to be correct, five halo concretions recovered from *Rayonnoceras* body chambers were compared to other cephalopod-bearing concretions that were recovered from low oxygen shale environments but which do not include actinoceratid nautiloids as part of their recovered cephalopod faunas.

4. Localities

4.1. Fayetteville Formation Concretions

Five carbonate halo concretions were recovered from two locations in the Fayetteville Formation (Text-Fig. 1). Three were collected from the bed of White River at Durham, Washington County, Arkansas (see MAPES [1979], locality M-26, p. 7–8 for more details), and two were recovered in the bed of Trace Creek near Leslie, Searcy County, Arkansas (see MAPES [1979], locality M-21, p. 7 for more details). At both locations, the concretions, with their associated *Rayonnoceras*, were excavated from the black shale about 2 to 3 meters above the base of the formation. In this shale interval, some



Text-Fig. 1. Locality map showing the general geographic locations (marked with an X) that yielded the Fayetteville Formation halo concretions in northwest (near the community of Fayetteville) and north central (near the community of Marshall) Arkansas, USA.

bedding planes are covered with pteriomorph pelecypods and crushed ammonoids. Both localities also have yielded a variety of ammonoids (GORDON, 1964), coleoid rostra including *Hematites barbara* FLOWER & GORDON 1959 (see DOGUZHAeva, MAPES & MUTVEI in this volume), shark debris (LUND & MAPES, 1984), plant petrifications (G. MAPES, 1980; G. MAPES & ROTHWELL, 1985), orthoconic and coiled nautiloids, several kinds of bactritoids (MAPES, 1979), agglutinated Foraminifera, sponge spicules, and microgastropods (NUTZEL & MAPES, in Press). Some researchers (see WIGNALL [1993]; SAGEMAN et al. [1991], and WIGNALL & SIMMS [1990] for an extended discussion) now are convinced that these pteriomorph pelecypods were probably part of the plankton, perhaps having been attached to floating debris. They are convinced that they did not live on the bottom, as suggested by NITECKI & RIGBY (1966) and ZANGERL et al. (1969). However, the agglutinated Foraminifera and the sponges recovered as spicule root tufts in the shale were apparently tolerant of the relatively hostile bottom conditions because they are the only common benthic organisms in the fauna. The small size of the gastropods indicates that they were probably at the end of their larval stage when they settled to the bottom where they died, and this abrupt termination of growth supports an interpretation of hostile environmental conditions at the water/sediment interface (NUTZEL & MAPES, in Press). All other animals appear to have been able to swim or at least maintain a position in the upper part of the water column, where the oxygen level was adequate for both small and large organisms.

4.2. Comparative Concretions from Other Places and Ages

Comparative material was selected from cephalopod-bearing concretions stored at the Ohio University Invertebrate Fossil Repository. No attempt was made to compare the halo concretions with all the varieties of concretions that occur with or without cephalopods. Indeed ZANGERL et al. (1969) recorded eight kinds of concretions from the Fayetteville Formation outcrops he and his co-investigators visited. Considering the number of environmental scenarios possible for concretion formation, it seems most reasonable to compare the *Rayonnoceras* halo concretions only to carbonate concretions from shales deposited in a low oxygen environment and containing large numbers of cephalopods to establish primary differences and similarities.

Concretions from three localities were chosen for comparison. These localities are as follows:

○ Starwood Oakamoor, England

Concretions from the *Reticuloceras gracile* Marine Band were recovered loose in the stream bed and in situ. The location is at grid reference SK 0614 4605 and is approximately 580 meters N40/1W from Star Inn (MORRIS, 1969). The pink to dull red concretions consist of ferruginous dolomite. In addition to ammonoids, other cephalopods include coiled and orthoconic nautiloids and bactritoids. Other fauna in the concretions are conodonts, ostracodes, Foraminifera, fish debris, and spat of pelecypods and gastropods. Fossil plants also are well represented as petrifications (SCOTT et al., 1997).

○ The "Pothole Locality" in north-west County Clare, Ireland

It was described by HODSON (1954, locality 72) as an accumulation of loose bullion in the bed of Glenarwin

River about 250 meters upstream from "the Pothole". At this locality, the concretions contain specimens of a variety of different ammonoid taxa, and there is stratigraphic mixing of different marine bands. Because of mixing and the lack of in situ material, relatively little work has been done on this particular site.

○ Toad Formation, Canada

The Lower Triassic concretions were collected as loose specimens from black shale at an exposure on the Tetsa River between mileposts 375 and 377 on the Alaskan Highway, British Columbia, Canada. TOZER (1994, 299–300) listed this locality as GSC loc. 10732 (Lower Anisian, Caurus Zone). In addition to the ammonoid fauna, the concretions contain orthoconic nautiloids, coleoids, conodonts, and fish debris.

5. Methodology

The *Rayonnoceras* concretions used in this study were initially prepared by removing the excess shale from around the carbonate concretions, leaving only the concretions and the *Rayonnoceras* body chambers. These specimens were then cut more-or-less perpendicular to bedding into 2 to 4 centimeter slabs using a standard diamond saw. All of the slabs were ground with 200, 400, and 600 carborundum grit. Individual slabs were etched for about 15 seconds with a 5 % hydrochloric acid solution to bring specimens into relief. To avoid measuring the same ammonoid specimen twice, individual slabs were labeled so that only one surface of each cut was used for the study.

Slab faces were traced onto graph paper so as to be able to measure the size of each face in square centimeters. Using a standard dissecting microscope, each reasonably complete ammonoid was recorded for maximum apparent diameter, the presence or absence of the body chamber, and the angular relationship of the conch to the bedding. Some ammonoids were only partly exposed when the concretions were cut, and these specimens were excluded from the study since accurate measurements could not be taken. Crushed ammonoids on the concretion surface may have been introduced at a later time, so such specimens were also not included in the data. Some isolated cephalopod shell pieces of ammonoids and *Rayonnoceras* were present in the concretions, however, no sponges or cephalopod organs such as mandibles, opercula, and radulae were observed on the etched slab surfaces or in formic acid residues. All measurements less than one millimeter were recorded as one millimeter. Graphic results were derived using Microsoft Excel.

6. Comparison of Data Sets

The following parameters are provided in Table 1 for the four concretion occurrences: number of ammonoids measured, surface area, and maximum apparent ammonoid diameter. The following calculations were made from these data and other observations and are included in Table 1: number of specimens per cm², mean apparent diameter, and percent of ammonoids with body chambers. All ammonitellas were considered to have complete body chambers because no fragmentary specimens were observed.

In general, the concretions from each locality have the following characteristics:

Table 1.

Measurements and calculations of ammonoid density, size range, mean apparent diameter, and the percent of specimens that retain at least part of the body chamber, from four localities in the United States, England, Ireland, and Canada.

	Number of Ammon.	Amount of Surface Area Analyzed in cm ²	Ammonoid Size Range in mm	Calculated Number of Specimens per cm ²	Mean Apparent Diameter in mm	Percent of Ammonoids With Some Body Chamber
<i>Rayonnoceras</i> Halo Concretions, Arkansas	736	3541	1-34	0.21	11.2	30.8%
Starwood Oakamoor Concretions, England	352	37	1-21	9.51	2.2	98.9%
"The Pothole" Concretions, Ireland	841	80	1-15	10.51	1.8	100%
Toad Formation Concretions, Canada	227	192	1-28	1.18	3.6	83.7%

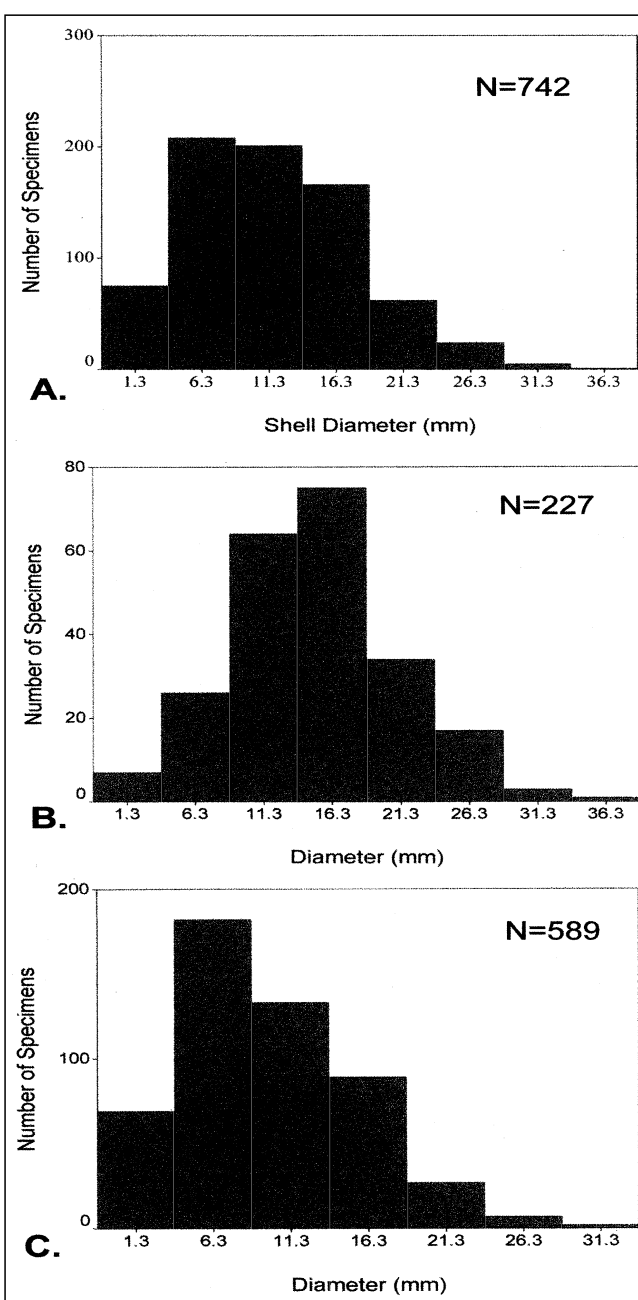
The *Rayonnoceras* halo concretions

are preserved as dark gray to nearly black calcite (Plates 1, 2, and 3.1). The white, calcite-filled ammonoid phragmocones tend to stand out in sharp relief on the dark concretion matrix; crushed and partly crushed body chambers filled with concretion matrix tend to be less obvious, especially on smaller diameter specimens. The ammonoids in these concretions using the taxonomy of SAUNDERS & WORK (1999) belong to the following genera: *Richardsonites fayettevillae* (GORDON, 1965), *Tumulites varians* MCCAULEY, QUINN & FURNISH, 1964 and *Paracravenoceras ozarkense* GORDON, 1965. These and other ammonoid genera, as well as a variety of orthocerid and coiled nautiloids and other cephalopod genera, occur commonly in the shale surrounding the *Rayonnoceras* halo concretions (see GORDON [1965] for a nearly complete list and description of these Fayetteville cephalopod taxa). However, the other cephalopod taxa have not been observed in any of our slabbed or broken *Rayonnoceras* halo concretions. The three ammonoid genera appear to be randomly mixed together in all of the *Rayonnoceras* halo concretions; however, without breaking the individual specimens free of the concretion, a complete and accurate taxon identification and the ratio of the generic proportions cannot be obtained. Also, these ammonoids are mixed in terms of apparent diameter, with no particular size selection occurring in any one of the *Rayonnoceras* halo concretions. Almost all of the ammonoid conchs in the *Rayonnoceras* halo concretions occur at apparently random angles to the bedding in the shale (See Plates 1, 2 and 3/1).

Text-Fig. 2.

Histograms of the Fayetteville Formation halo concretions.

- A) Comparison of the number of specimens measured (n = 742) with the apparent diameter of the specimens. The distribution observed is more-or-less bell shaped, and this distribution is very different from that observed in the English, Irish, and Canadian concretions seen in Figure 3.
- B,C) Comparison of the apparent diameters of the specimens with the number of specimens interpreted to have partial body chambers (n = 227) and the number of specimens interpreted to be missing their body chambers (n = 515), respectively. Based on the similarity of all the histogram distributions of the Fayetteville Formation halo concretions and the assumption that ZANGERL et al. (1968) and QUINN (1977) are correct, the conclusion can be drawn that the presence or absence of the body chamber on an ammonoid cannot be used exclusively as the evidence of predatory event by another cephalopod.

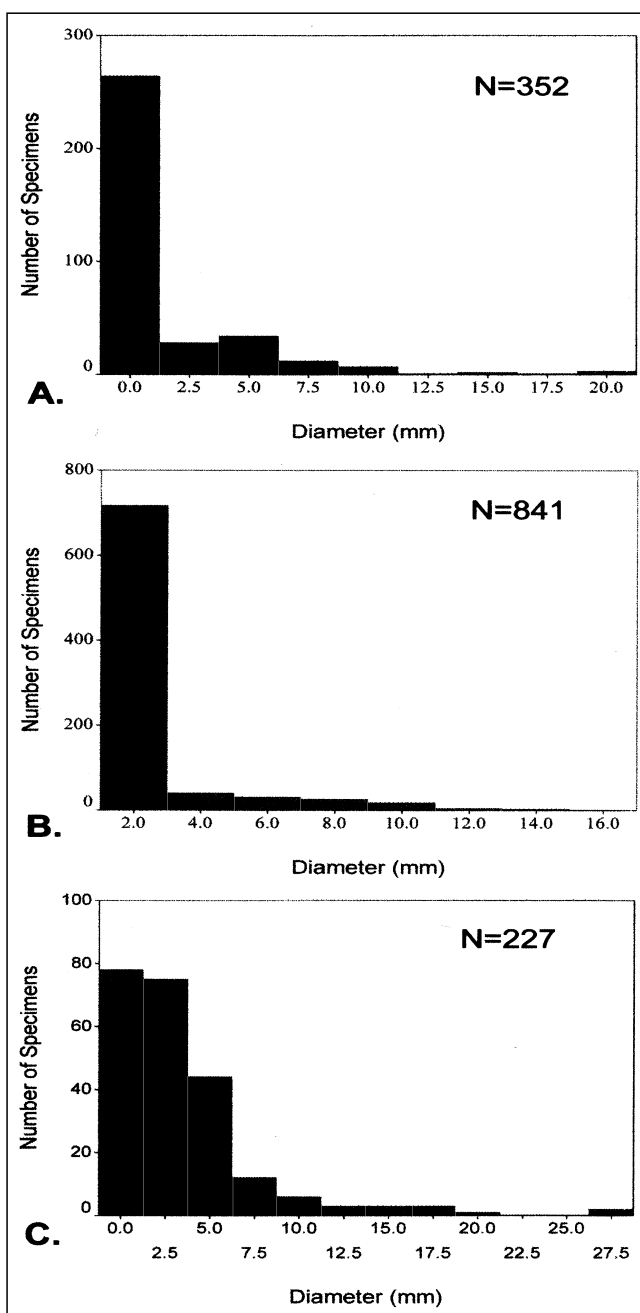


A comparison of the histogram of apparent ammonoid diameter of all the ammonoids (Text-Fig. 2C) and mean ammonoid apparent diameter of 11.3 mm (Table 1), indicate that there are relatively few ammonitellas and early post ammonitella specimens in the five concretions. Indeed, the overall impression is that the ammonoid fauna in the halo concretions is dominated by late juvenile and relatively mature specimens. Fragments of both ammonoid and *Rayonnoceras* external shell and septa are present in the concretions; the *Rayonnoceras* external shell and septal fragments are distinguishable from the ammonoid external shell fragments by their greater thickness, lack of ornament, presence of septal necks, and less pronounced curvature.

There are 742 measured ammonoid specimens in the Fayetteville data set (Table 1). The total slab surface area of the concretions analyzed was 3541 cm². The mean number of specimens per square centimeter is 0.21. For the Fayetteville data set, the measured apparent diameters of the ammonoids range from one millimeter to 34 millimeters, with the mean being 11.3 millimeters. Most apparent diameters range between 6 mm to 19 mm. Only 30.8 % of the specimens retained observable body chamber. When the apparent diameters of specimens that retain some part of their body chamber are compared to the apparent diameters of specimens with no discernable body chamber (Text-Figs. 2A and B), the overall distributions are similar. Both of these histograms resemble, with no major difference, the histogram comparing the apparent diameters with the total number of specimens (Text-Fig. 2C).

The ferruginous dolomite concretions from Starwood Oakmoor, England

appear as pink to reddish brown carbonate masses, with the larger diameter three-dimensional ammonoid phragmocones in the center of the concretions being filled with white to cream colored calcite. Where lesser amounts of calcite were present during concretion formation, the ammonoids and other organic debris are compressed into dark brown bands which are especially apparent at the top and bottom of the concretions (Pl. 3.2). The matrix that surrounds the phragmocones and fills the body chambers of the three-dimensional ammonoids in the concretions is medium to pinkish brown, and it is distinctly lighter in color than the more compressed matrix around the edges of the concretion. The cephalopod fauna includes both ammonoids and some undescribed bactritoids, with gastropod and pelecypod spat being relatively common. The ammonoid fauna appears to be of low diversity and there are high numbers of specimens; the only ammonoid that can be readily identified is *Reticuloceras gracile* BISAT. The more juvenile (15 mm and smaller diameters) ammonoids and ammonitella specimens cannot be identified at this time. Within the single piece of concretion analyzed for this study and in other concretions from this same horizon there is crushed and degraded fossil plant material and some pieces of plant debris that are well-preserved as permineralizations (SCOTT et al., 1997). Shell debris is common in the concretions. Where the concretions are carbonate rich, only minor evidence of crushing of the ammonoid shells by compaction can be observed. The ammonoids in the carbonate parts of the concretions tend to retain at least part if not most of their body chambers (98.9 %), and in the matrix that fills these body chambers, many ammonitellas are present. Overall, ammonitellas and early postembryonic



Text-Fig. 3. Histograms of the ammonoid bearing concretions from A. England, B. Ireland, and C. Canada, respectively.

All three of the histograms are type 3 survivorship curves that show the demise of a large number of small specimens (ammonitella and early post ammonitella specimens) followed by a relatively rapid decrease in the number of specimens with larger apparent diameters.

ammonitella shells dominate the concretions, with a mean diameter of 2.2 mm (Table 1 and Text-Fig. 3A). Larger diameter specimens are more obvious on the slabs, but these larger specimens constitute only a small fraction of the overall ammonoid population preserved in the concretions. As can be seen in Pl. 3.2, the plane of symmetry of most of the larger diameter ammonoids is parallel or nearly parallel to bedding.

The England data set (Table 1) has 352 measured specimens, and the surface area of the slabbed piece of concretion used for this study is 37 cm². The average number of specimens per square centimeter is 9.51. The England data set has ammonoids ranging in size from 1 to 21 mm. A histogram of apparent diameter 3 compared to the num-

bers of specimens produced a type 3 survivorship curve with nearly all of the specimens being less than 3 millimeters in apparent diameter.

The concretions from "The Pothole" in Ireland

are dark gray to black with the phragmocones of the ammonoids filled with white to light green calcite (Pl. 4.1). Overall, this ammonoid fauna is relatively low in diversity with three taxa being known from this marine horizon. These taxa are *Reticuloceras compressum* BISAT & HODSON, *Homoceratoides magistorus* (HODSON) and *Vallites henkei* (SCHMIDT). At some levels in some of the concretions the ammonoids form a packstone of shells that are so dense that we were forced to select a concretion with slightly more sediment so that the individual specimens could be clearly observed. Ammonitellas and post-ammonitella shells dominate the concretions. Larger diameter specimens are common but make up only a small percentage of the overall ammonoid fauna. As can be seen in Pl. 4.1, most of the larger diameter ammonoids are parallel or nearly parallel to the bedding surface. Many of the ammonoids exhibit some degree of distortion due to compaction crushing prior to concretion formation. As with the material from Starwood Oakamoor, the body chamber matrix material is a lighter shade of gray than that of the background concretion matrix. Both ammonoids and bacrtritoids with pelecypod and gastropod spat constitute the invertebrate fauna. Ammonoid shell debris is common in the concretions.

There are 841 measured ammonoids in the Ireland data set (Table 1), and the analyzed piece of concretion had a measured surface area of 80 cm². The mean number of specimens per square centimeter is 10.51. The Ireland data set has specimens ranging in apparent diameter from 1 to 15 mm with a mean diameter of 1.8 millimeters. It appears that all (100 %) of the measured specimens retain some part of the body chamber. A histogram of the apparent diameter versus the number of specimens reveals a type 3 survivorship curve and that almost all of the specimens are between 1 and 3 millimeters in apparent diameter (Text-Fig. 3B).

The concretions from the Toad Formation in British Columbia, Canada

of Triassic age are dark gray with the phragmocones of the ammonoids being filled with white crystalline calcite (Pl. 4.2). The matrix of the concretion is filled with unidentified shell debris. Ammonoids tend to be somewhat crushed in this concretion, especially the body chambers; conch distortion appears to have been produced by compaction before concretion formation took place. The ammonoid fauna is moderate in diversity and there is a relatively large number of specimens in the piece of concretion used in this study. TOZER (1994) reports the following taxa are present: *Stenopopanoceras normale* (MCLEARN), *Columbisculites maclearni* TOZER, *Grambergia tetsaensis* (MCLEARN), *Paracrochordiceras americanum* MCLEARN, *Stenophyllites kindlei* (MCLEARN), and *Ussurites muskwa* MCLEARN. Both ammonitellas and post ammonitella shells are common in these concretions, with moderately large specimens (greater than 50 mm in diameter) commonly recovered (Text-Fig. 5c). As can be seen in Pl. 4.2, most of the larger diameter specimens were deposited parallel or nearly parallel to the bedding.

There were 227 specimens measured in the western Canada data set (Table 1), and the analyzed concretion surface area is 192 cm². The mean number of specimens

per square centimeter is 1.18. For the western Canada data set, the ammonoids range in apparent diameter from 1 to 28 mm, with the mean diameter being 3.6 mm. Most (83.7 %) of the measured ammonoids have at least some part of the body chamber preserved. A histogram of the total number of specimens versus the apparent diameter produces a type 3 survivorship curve, with most specimens being less than 8 millimeters in apparent diameter (Text-Fig. 3C).

7. Conclusions and Significance

When distributions of the apparent conch diameters for the four different localities are compared, three of the distributions are somewhat similar in distribution and the fourth is considerably different. In the concretions associated with the *Rayonnoceras*, the apparent diameter data of the goniatites approximates a generalized bell-shaped curve, with the mean size of 11.3 mm occurring approximately near the middle between the end points of the curve (Text-Fig. 2C). The ammonoids in the concretions from England, Ireland, and Canada have similar apparent mean diameter size ranges of 2.2 mm, 1.8 mm, and 3.6 mm respectively (see Table 1). These average values are significantly smaller than the average apparent diameter of 11.2 mm for the ammonoids in the *Rayonnoceras* halo concretions. When apparent diameter is plotted against the number of specimens for the English Starwood Oakamoor, Irish "Pot Hole", and Canadian Toad Formation concretions, normal survivorship curves similar to that described by RAUP & STANLEY (1978) are present.

The mean diameter measurements for these four localities were tested using an Analysis of Variance table. The null hypothesis was that all four means were equal to each other. The alternate hypothesis was that at least one of them was significantly different. The significance level for the area of rejection was set at 5 %. After running the table, the critical F value was 2.61, and the calculated F value for the means was 686.46, well outside the 95 % acceptable range of 0 to 2.61. This gives us no reason not to believe that the alternate hypothesis is correct.

We then tested the Fayetteville mean diameters against those of the other three localities individually using a t-Test: Paired Two Sample for Means. The null hypothesis for all three tests was that the two means in each test were statistically equal. The alternate hypothesis is that they are not. Again, a 5 % significance level was chosen as the area of rejection. The t critical for all three tests was 1.65, and the t statistical values were 26.50, 38.65, and 18.29, for the England, Ireland, and Canada localities, respectively. All of these values are deep inside the area of rejection, giving us no reason to not believe that there was one means different in each of the tests. Our overall belief that the Fayetteville mean diameter is significantly different than the other localities is supported by these tests.

The orientation of the ammonoids in relation to the bedding in the *Rayonnoceras* halo concretions appears to be essentially random. In the concretions from the other localities, it appears that most of the ammonoids were deposited with the plane of symmetry being parallel or nearly parallel to the bedding. The explanation for the randomness in the ammonoid orientations in the *Rayonnoceras* halo concretions is that the conchs of the ammonoids were randomly spilled out of the *Rayonnoceras* body chambers into the sediment by decomposition gases from soft tissue decay after burial but before severe mud compaction oc-

curred. Concretion formation apparently occurred rapidly, because most of the ammonoids are only partly crushed by compaction.

There is a very low concentration of ammonoids per square centimeter in the *Rayonnoceras* concretions (0.21 specimens/cm²); whereas, in the English, Irish, and Canadian concretions (9.51 specimens/cm², 10.5 specimens/cm², and 1.18 specimens/cm², respectively) the ammonoid concentrations are 5 to 50 times as densely packed within the concretion matrix. Thus, the low density of ammonoids in the *Rayonnoceras* concretions seems unusual. This unusual condition is a product of the relatively low numbers of ammonitellas and early post-hatched ammonitella conchs in the *Rayonnoceras* concretions. In the English, Irish, and Canadian concretions there are high numbers of similar sized ammonitella and early post juvenile sized ammonoids (compare Text-Fig. 2C with Text-Figs. 3A–C). This difference might be explained by the hypothesis that the relatively large *Rayonnoceras* probably did not and could not effectively prey on the ammonitellas and early post-hatched ammonitellas because the tiny ammonoids were too individually small for these large predatory animals. Additionally, it is possible that the ammonitella hatching areas and the habitat of the early post-hatched ammonitellas were different from the habitat where the larger *Rayonnoceras* lived. If so, then the smaller ammonoids would not have been available as a food source. Thus, there are several possible reasons why there are so few small ammonoids in the *Rayonnoceras* halo concretions.

In summary, we are convinced that these data provide strong circumstantial evidence that the ammonoids associated with the *Rayonnoceras* halo concretions are the stomach contents of the *Rayonnoceras*, and that, before a given individual of *Rayonnoceras* died, it ate a large number of ammonoids. After death, the *Rayonnoceras* shell, with the soft tissues in the body chamber, settled to the muddy sea floor.

As the body of the *Rayonnoceras* decayed, the stomach contents were ejected out of the body chamber by decomposition gases being suddenly released into the surrounding mud where rapid concretion development took place.

Our conclusion confirms and reinforces those of ZANGERL et al. (1969) and QUINN (1977), and, therefore, the ammonoid scavenging hypothesis can be rejected as an explanation for the accumulation of the ammonoids around the body chambers of *Rayonnoceras*. The significance of this conclusion is that these ammonoids are the only known specimens that exhibit the damage produced by another cephalopod as an act of predation.

Additional studies of the ammonoid conchs in the *Rayonnoceras* halo concretions are warranted. These ammonoid conchs will provide base line information on the destruction of ammonoid shells within the *Rayonnoceras* stomach, and the degree of ammonoid shell completeness and breakage will give valuable paleobiologic information on recognition criteria of cephalopod predation damage produced by other cephalopods.

Plate 1

- Figs. 1,2: General relationship of an inclined *Rayonnoceras solidiformae* phragmocone and body chamber to the concretionary mass. The body chamber is surrounded by an ammonoid-bearing halo concretion shown before (Fig. 1) and after (Fig. 2) cutting by a diamond saw. The horizontal of the page approximates the orientation of the bedding plane. Reproduced from QUINN (1977). Scale bar: about 20.0 cm.
- Fig. 3: Segment of a typical slab of a cut Fayetteville Formation halo concretion from Arkansas showing the relatively thick *Rayonnoceras* shell and septa fragments and the randomly distributed ammonoids within the concretion. Scale bar: 3.0 cm.

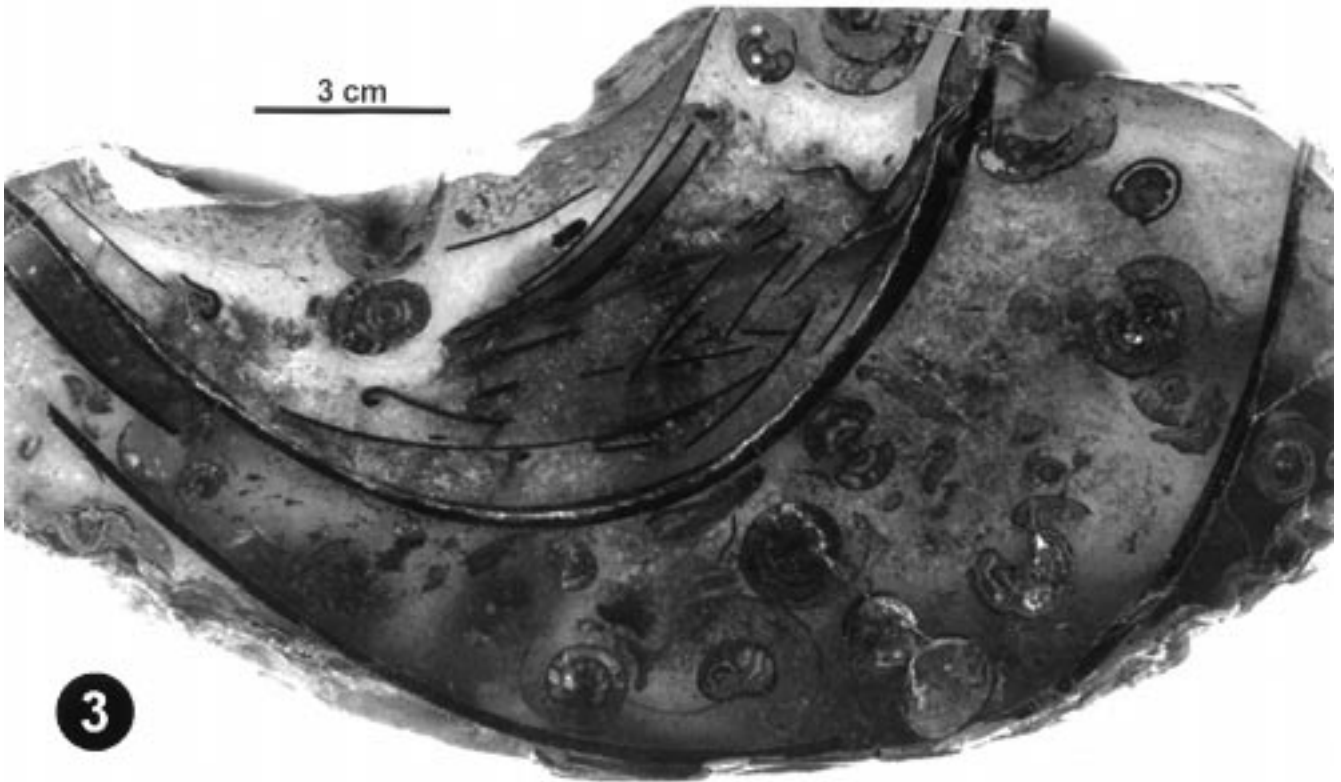
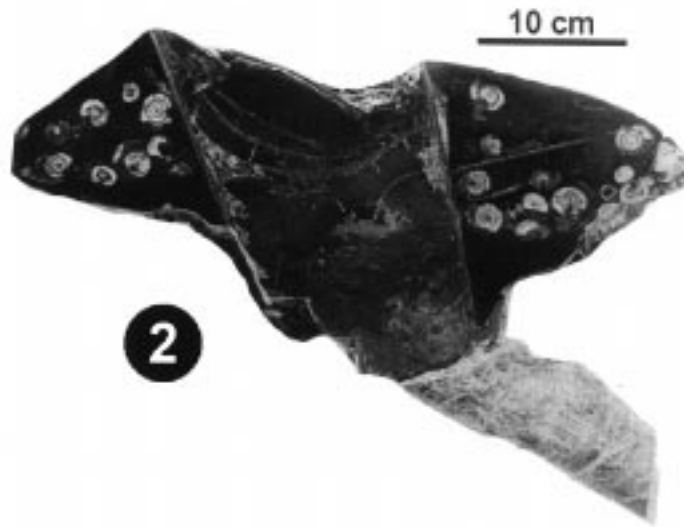
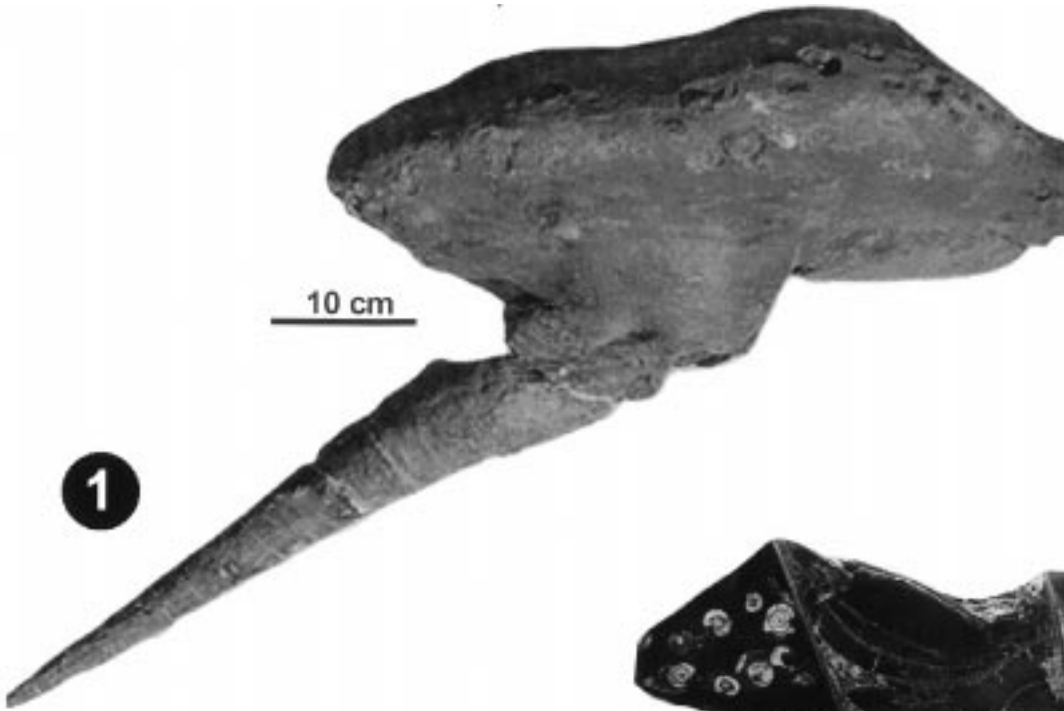


Plate 2

- Fig. 1: A portion of a *Rayonnoceras* halo concretion showing the numerous crushed ammonoids on the concretion surface. Because these surficial ammonoids could have been introduced at a later time, they were not included in the data set.
- Fig. 2: Enlargement of the slab seen in Fig. 3 of Pl. 1 showing several sectioned and unidentified ammonoids with incomplete body chambers. Note the cyrtchoanitic septal necks on some of the septal fragments from the *Rayonnoceras* and the partial ammonoid phragmocone in the lower left corner.
- Fig. 3: General view of a slab of a *Rayonnoceras* halo concretion showing the random orientation of the ammonoids within the concretionary mass. The slabs in Figs. 2 and 3 have been etched for 15 seconds in a five percent hydrochloric acid, rinsed in water and dried, and covered with acetone and an acetate peel.

Scale bar in all Figures: 1.0 cm.

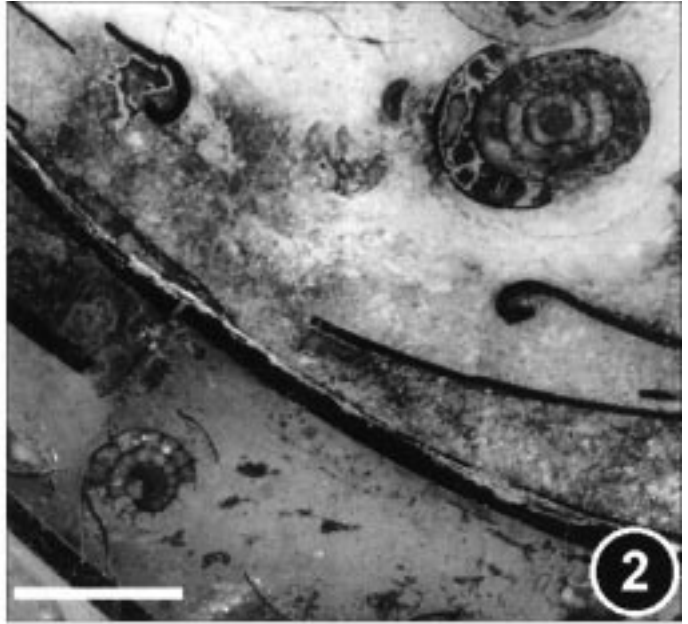
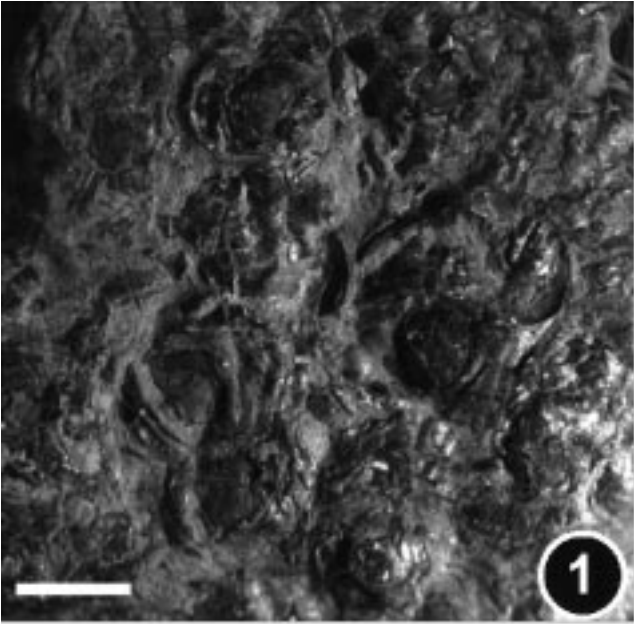


Plate 3

Fig. 1: General view of an acetate peel covering a slab of a *Rayonnoceras* halo concretion with the ammonoids being less well preserved in this concretion than in those illustrated on Plates 1 and 2.

This degree of preservation and the random orientation of the ammonoids is typical of those seen in most of the slabs.

Fig. 2: Acetate peel of a slab of an ammonoid-bearing concretion from Starwood Oakamoor, England.

Although somewhat distorted by compaction, the general orientation of the bedding can be determined, and, despite the undulations of the bedding, the plane of symmetry of the majority of the ammonoids is more-or-less parallel to the bedding. The small, white, circular dots most easily observed in the matrix rich areas of the concretion are ammonitellas and early growth stage post ammonitella shells with conch diameters of 0.5 to 2.0 mm being most common.

Scale bar in both Figures: 1.0 cm.

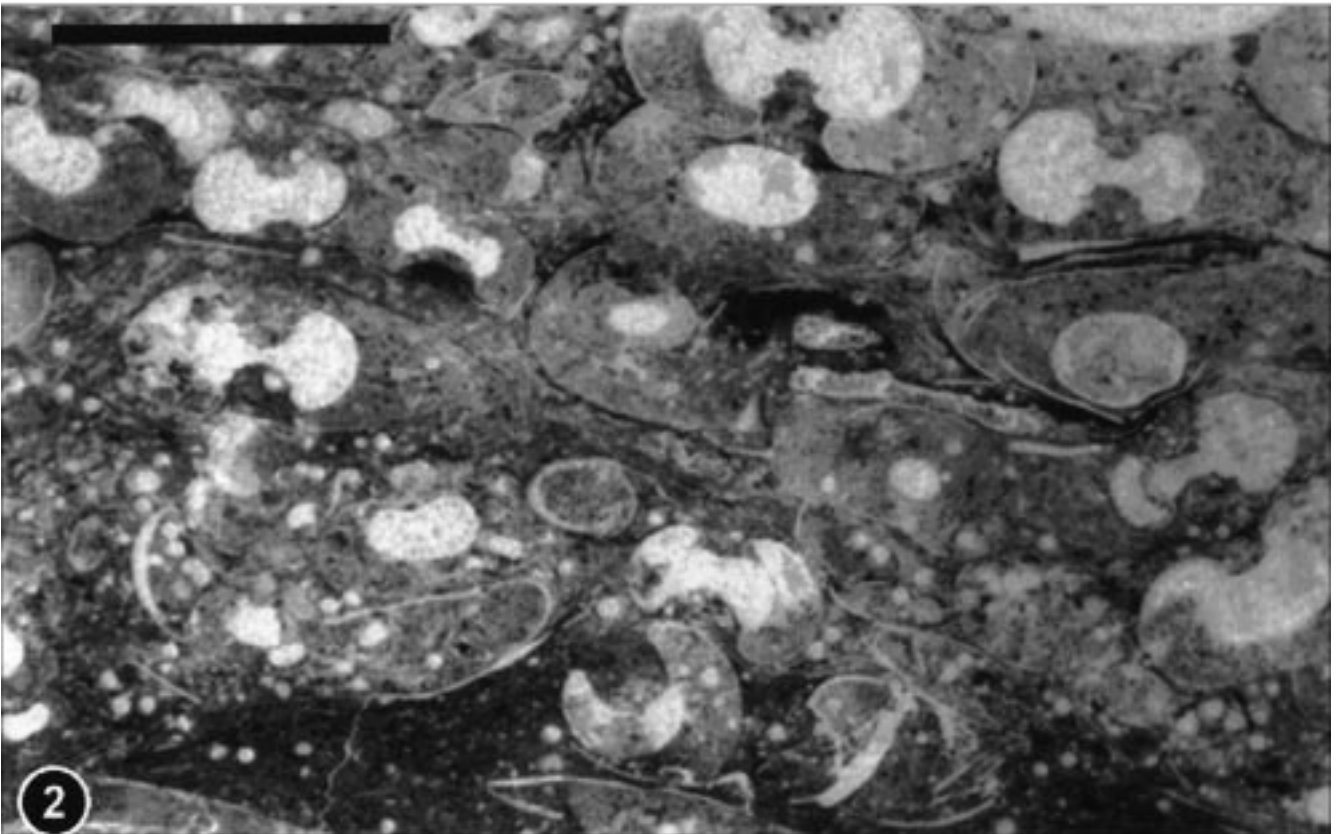
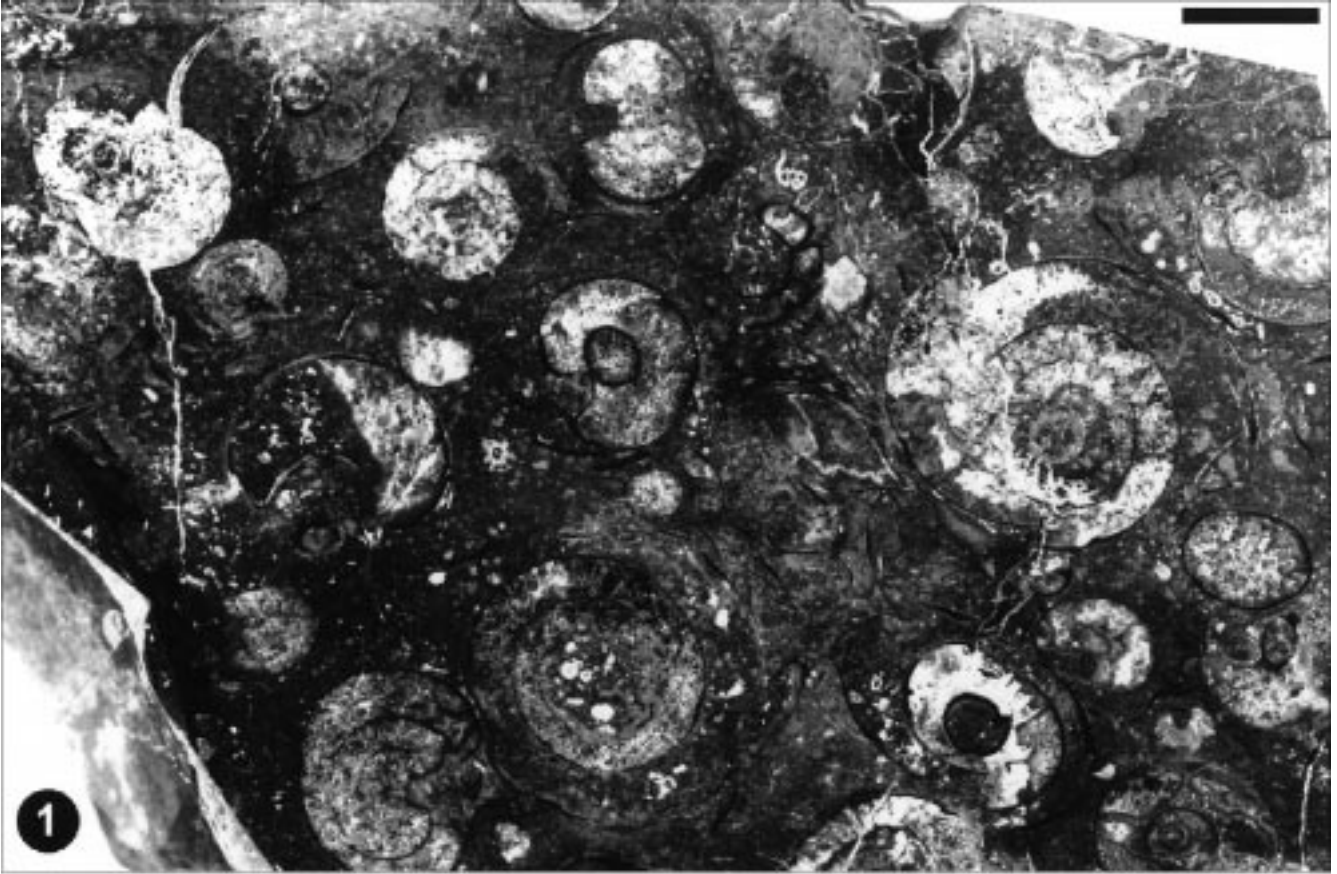
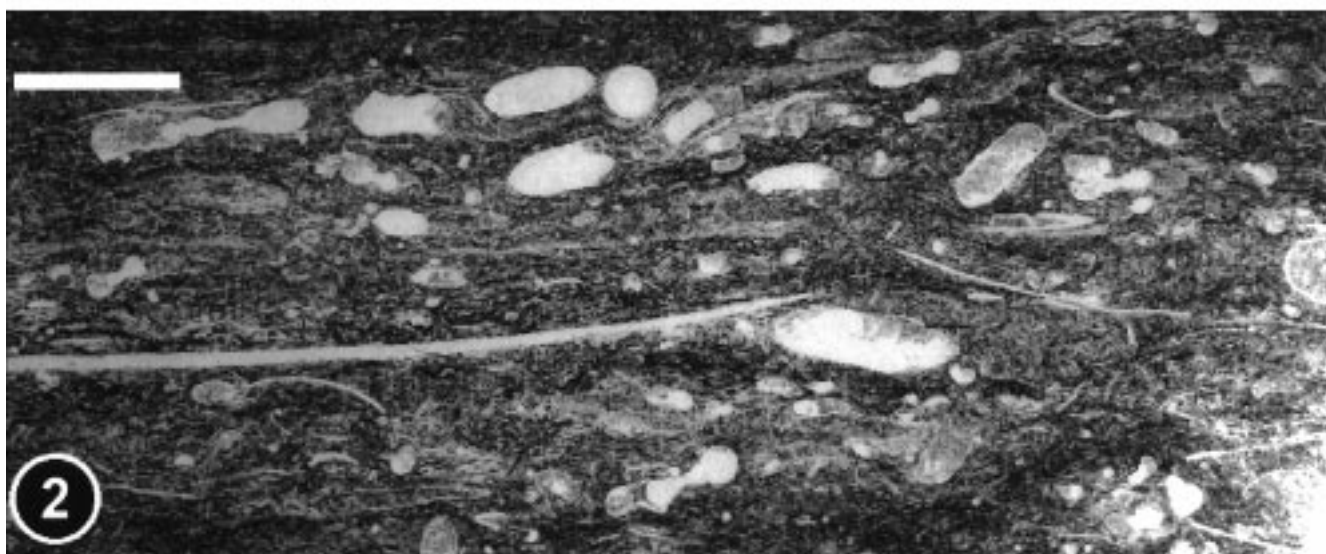
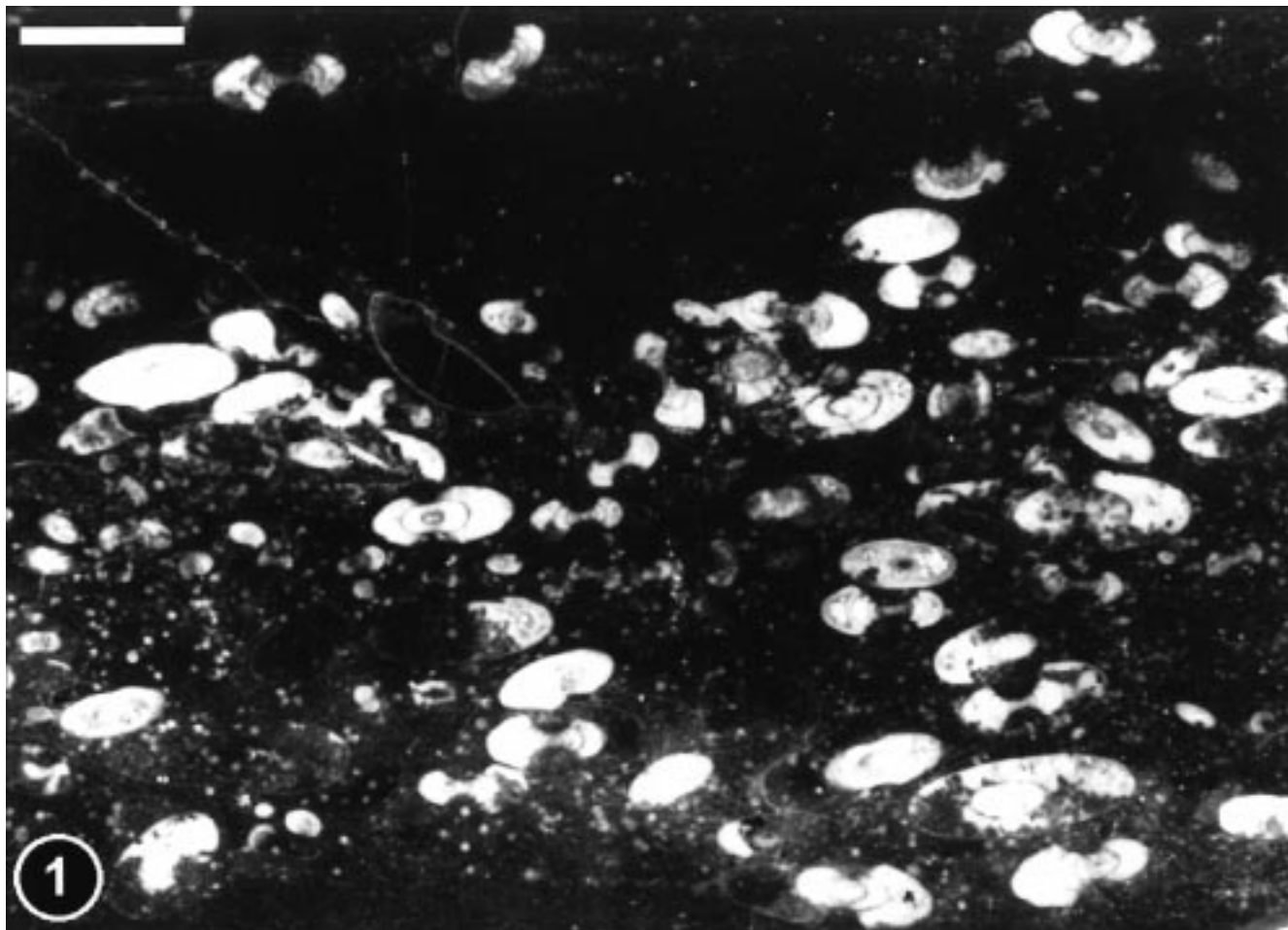


Plate 4

- Fig. 1: Acetate peel of a slab of an ammonoid-bearing concretion from "The Pothole" in Ireland.
The bedding is only slightly distorted with the plane of symmetry of most of the ammonoids being more-or-less parallel to the bedding. The small, white, circular dots, with diameters of 0.5 to 2.0 mm, are ammonitellas and early growth stage post ammonitella shells.
- Fig. 2: Acetate peel of a slab of an ammonoid-bearing concretion from the Toad Formation in Canada.
The bedding is relatively undistorted, and the plane of symmetry of most of the ammonoids is more-or-less parallel to the bedding. Ammonitellas and post ammonitella conchs are present; however, the general preservation is relatively poor when it is compared to the preservation in the English and Irish concretions.

Scale bar in both Figures: 1.0 cm.



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