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GASTRIC CONTENTS OF AN ICHTHYOSAUR FROM THE SUNDANCE FORMATION (JURASSIC) OF CENTRAL WYOMING

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ABSTRACT

An ichthyosaur specimen, presumably of *Ophthalmosaurus natans*, was discovered with gastric material preserved between the ribs of the skeleton. The specimen is from the Redwater Shale Member of the Sundance Formation, Natrona County, Wyoming. The specimen is comprised of numerous vertebrae and ribs, a partially articulated forelimb, and other unidentified bones within a calcite concretion. A portion of the gastric mass is visible between the ribs within one concretion block. The friable, low density mass appears to be located in the central or posterior torso, with a smaller amount of material more anteriorly located. The gastric material consists of badly fragmented coleoid cephalopod hooklets, loosely cemented by calcite crystals. The stomach contents are comparable to those reported from ichthyosaurs from the Lower Jurassic of England and Germany, although the mode of preservation is not.

INTRODUCTION

An ichthyosaur specimen (UW34653) excavated recently from the lower Redwater Shale in northwestern Natrona County, Wyoming, includes digested remains of its prey items within the body cavity. The specimen has not yet been prepared, but is probably referable to *Ophthalmosaurus natans*, the only currently recognized species from the Jurassic of North America (Motani and McGowan, 2003). The specimen was found in the Redwall area of northwestern Natrona County, WY (University of Wyoming location VP-2002-02), and was excavated in July 2002.

Preserved stomach contents of ichthyosaurs were first reported over 150 years ago (Pollard, 1968). Most of the specimens described in the literature are from the Lower Jurassic of southern England and southern Germany (Pollard, 1968; Keller, 1976; Böttcher, 1989; Bürgin, 2000), although ichthyosaurs with preserved stomach contents are also known from the Middle Triassic of Switzerland (Reiber, 1970). Here we report the first specimen of an ichthyosaur with stomach contents from the Upper Jurassic of North America. As with most of the other finds, the gastric material is comprised of cephalopod hooklets.

RECORD OF STOMACH CONTENTS

Pollard (1968) reviewed the occurrences of preserved stomach contents in ichthyosaurs when reporting on a new specimen, the anterior portion of an *Ichthyosaurus* skeleton from the Lower Jurassic of Lyme Regis, England. The gastric mass of this specimen is roughly oval in shape and rests against the pectoral girdle (Pollard, 1968). Numerous ribs are pressed into the mass. The ichthyosaur specimen itself is not well articulated, yet the gastric mass is fairly compact, not scattered. Pollard (1968) indicated that stomach contents from Lyme Regis ichthyosaurs are much more common than the literature would suggest, citing three specimens in the Oxford University Museum and six at the Natural History Museum, London, that preserve gastric material. In all cases, this material is comprised of densely packed cephalopod hooklets, similar to the specimen that he described (Pollard, 1968). However, two other Oxford University Museum specimens were described by Buckland (1836, cited in Pollard, 1968) that included mainly fish material, identifiable as *Pholidophorus*, in a clay matrix. One of these specimens also had a few cephalopod hooklets in the matrix as well.

Keller (1976) described gastric and intestinal material from 28 ichthyosaur specimens, representing several species of *Stenopterygius* from the Lower Jurassic Posidonienschiefer of Holzmaden, Germany. This material was composed primarily of cephalopod hooklets, but small amounts of fish remains and wood fragments were also found. In some specimens the stomach contents were in a well-defined, compact mass of hooklets, but other specimens had gastric material scattered in small, widely spaced clumps throughout the rib cage. Accumulations of hooklets near the hindlimb were interpreted as intestinal contents (Keller, 1976). More recently, Böttcher (1989) reported stomach contents in a skeleton of the large (over 8 meters long) lower Jurassic ichthyosaur *Leptopterygius burgundiae* from the Posidonienschiefer of Ohmden, Germany. The gastric mass was comprised mainly of cephalopod hooklets (Belemnitida and Belemnoteuthida). The hooklets occurred in a compact, oval mass approximately 30 by 20 centimeters. In addition, up to 200 small (10 millimeters or less) ichthyosaurian vertebrae were scattered between the ribs, mainly anterior to the mass of hooklets. The vertebrae were interpreted as remains of juvenile *Stenopterygius* preyed upon by the much larger *Leptopterygius.* Bürgin (2000) described yet another Holzmaden specimen, a 2 meter long *Stenopterygius quadriscissus*, with the remains of an actinopterygian fish between its ribs. The 30 centimeter long fish was fairly complete with an articulated vertebral column, both pectoral fins, and many dermal skull elements. The fish was facing backwards inside of the ribcage, just ventral to the vertebral column (Bürgin, 2000). Stomach contents comprised of cephalopod hooklets are also know from ichthyosaurs of the Middle Triassic Grenzbitumenzone of Monte San Giorgio, Switzerland (Rieber, 1970). Thus it appears from the literature that coleiod cephalopods made up the diet of many ichthyosaur species.

STRATIGRAPHY

The Redwater Shale is the uppermost member of the Sundance Formation (Imlay, 1982). It is unconformably overlain by the Windy Hill Sandstone, the basal marine unit of the Morrison Formation. Below the Redwater Shale is the Pine Butte Member, a white, cross-bedded sandstone (Specht and Brenner, 1979). The Redwater Shale has been biostratigraphically dated from ammonites to the Late Callovian – Middle Oxfordian (Imlay, 1982).

In the Redwall area, the Redwater Shale consists of dark gray to greenish-gray shales, thin-bedded green, gray, or tan sandstones, and thin to medium bedded limestones. Within the Redwater Shale in this area are two fairly distinct limestone beds, referred to as the upper and lower *Camptonectes* beds. The beds vary in thickness, and usually include layers of coquina or fossil hash comprised of pieces of the large clam *Camptonectes*. The upper bed is thicker and better exposed than the lower one in this area. The lower bed often includes small oysters (*Gryphea*) and other invertebrates along with *Camptonectes*. In the Redwall area, a tan, thin-bedded, crossbedded sandstone occurs between the two *Camptonectes* beds. Specht and Brenner (1979) pointed out that the bioclastic limestones within the Redwater Shale are the result of storm deposits and are discontinuous throughout northeastern Wyoming. In the Redwall area, however, the two *Camptonectes* beds seem to be good stratigraphic markers across distances of several kilometers.

The specimen UW34653 was found approximately 2.5 meters below the lower *Camptonectes* bed, which was less than 20 centimeters thick at this location. The *Camptonectes* bed was at the top of a small ridge, so its upper portion may have eroded. The ichthyosaur specimen was located several centimeters below a thin limestone bed.

The specimen is encased in a light gray limestone concretion. Much of the concretion was exposed at the surface when discovered and was fractured into several blocks. Some bones had weathered out of the anterior end, and weathered ribs covered the top surface of much of the concretion. The concretion varies in thickness from a few centimeters to 25 centimeters. Some unconcreted ribs were found in the surrounding dark gray shale. Although some of the shales in the Redwater Member have abundant glauconite, none was noticeable at this site.

DESCRIPTION OF SPECIMEN

The ichthyosaur specimen (UW34653) consist of a string of at least ten articulated vertebrae and at least as many disarticulated ones, along with many disarticulated ribs. A partial limb was also preserved, comprised of an articulated humerus, radius, and ulna, as well as several disarticulated, scattered and weathered

metacarpals and phalanges. The specimen is not fully prepared, so it is difficult to ascertain what other bones are preserved. No cranial material was found.

Two pockets of presumably gastric material were found within the specimen. The larger mass of material is approximately 1 meter posterior to the humerus. This mass extended into the soil below the concretion but the top, anterior portion is clearly visible in cross-section, in between the ribs within the limestone concretion designated 'Block 8' in the field (Figure 1). A second, much smaller mass is more anteriorly located, below a concretion block designated 'Block C' in the field. This block is thought to contain part of the shoulder girdle as it was anterior to the articulated forelimb and was the thickest part of the concretion. The gastric material is at the bottom of the concretion block. Both masses are comprised of badly fragmented cephalopod hooklets.

The posterior (Block 8) mass is the most extensive, and the description which follows applies to that material unless otherwise noted. Although concreted around the edges, the black gastric mass is poorly cemented and friable, with a granular texture. It is difficult to see any specific shapes in the central, densest part of the mass. The mass disaggregates readily in water, so it is not possible to obtain a good measurement of the density. It is much less dense than the surrounding concretion. Disaggregation produces a fine silt of calcite and hooklet fragments. Whole hooklets cannot be extracted by disaggregation. The outer edges of the mass are lighter in color and well cemented (Figures 2, 3). Hooklets located in the outer areas are more dispersed and a few whole specimens can be seen among the fragments (Figure 4). These are similar to Pollard's (1968) Type C and Type D hooklets.

CONCRETIONS IN THE REDWATER SHALE

The association with a concretion makes the preservation of these stomach contents quite different than previously reported finds. Concretions are common throughout the Redwater Shale, and layers of reworked and bioeroded concretions have been documented (Andersson, 1979). In the Redwall area, dark red ironstone concretions as well as gray calcitic concretions occur. Both kinds of concretions sometimes encase ichthyosaur bones. Concreted partial skeletons of other ichthyosaurs have been recovered from the same area as the specimen of interest. Only one of these (UW24802) was found below the lower *Camptonectes* bed. Four other specimens (UW19686, UW24216, UW15936, and UW15937) were found between the two *Camptonectes* beds, but at different stratigraphic levels. UW15936 was within 200 meters of this site. Three of the aforementioned specimens are almost entirely encased in

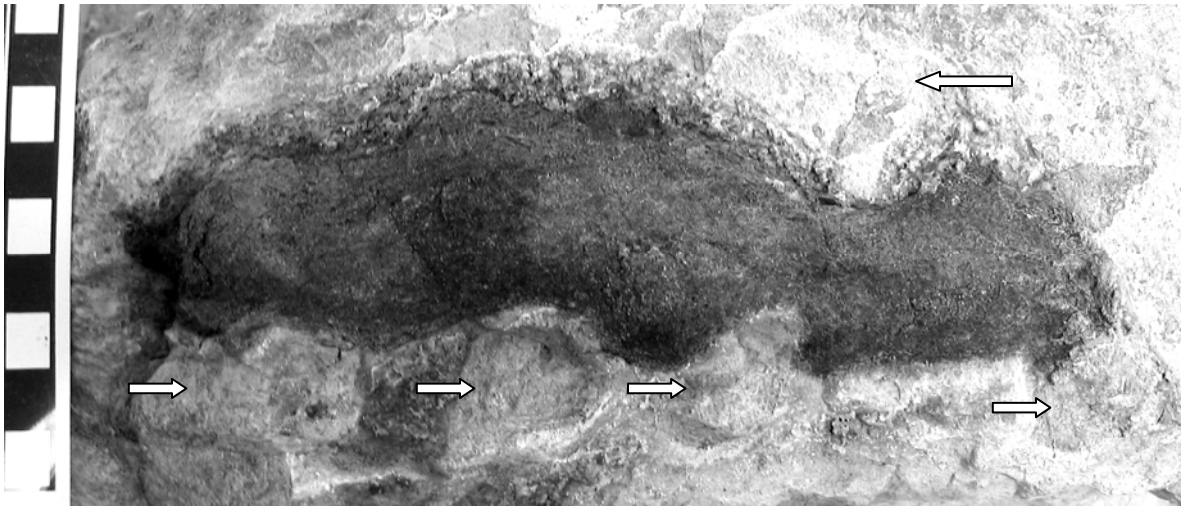


FIGURE 1. Cross-section of concretion block containing gastric mass (Field designation Block 8). It rests on four ribs. Another rib is pressed into it on the top right. Note that the upper edge of the mass is gray rather than black. This region is better cemented and the hooklets are more dispersed and better preserved. Arrows indicate position of ribs. Upper rip is pushed into mass. Scale bar in centimeters.

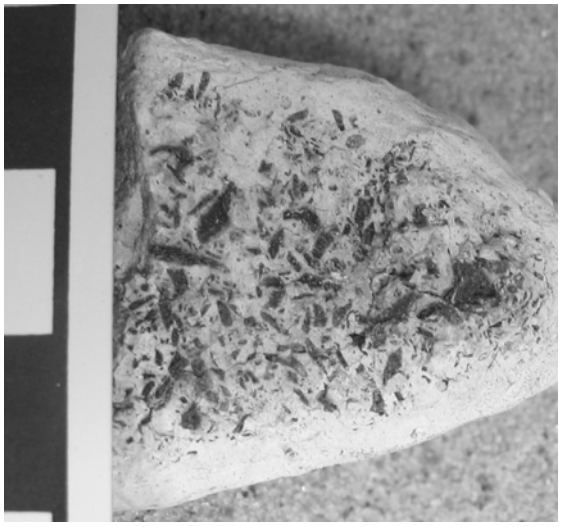


FIGURE 2. Scattered hooklets in the concretion near the main mass. Note a nearly complete, curved hooklet in upper left. Scale in centimeters.

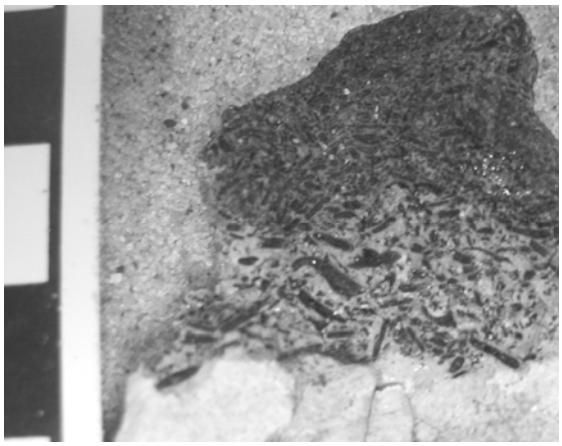
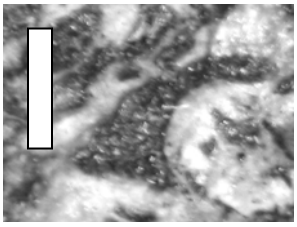


FIGURE 3. A piece of concretion from the anterior block (Block C) showing the gradational contact between the dense black gastric mass (top) and the concretion. Along the edge of the mass, the hooklets are more dispersed and better cemented. Scale in centimeters.

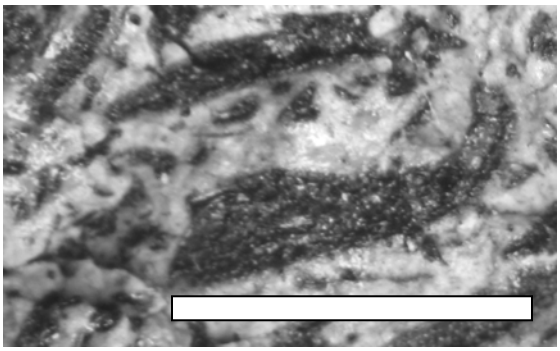
concretions. Portions of one other is partially concreted. Only UW34653, however, includedsstomach contents even though the mode of preservation seems to be similar to the others.

Compositional Analyses

We compared the concretion surrounding UW34653 to concretions associated with three other ichthyosaur specimens from the Redwall area (UW 24216, UW 15936, and UW 15937 to



A



B

FIGURE 4. Microscopic view of two types of hooklets found in the outer, well cemented region of the gastric mass of UW 34653. A. A sharply curved hooklet similar to Pollard's (1968) Type D. Scale bar is 2 millimeters B. Larger hooklet similar to Pollard's (1968) Type C. Scale bar is 5 millimeters.

ascertain whether some peculiarity of the concretion allowed the preservation of the hooklets.

The percent of insoluble material in the concretion was determined for each concretion. One sample from each concretion was collected by chipping off small pieces, trying to avoid the weathered surface. The sample was weighed, and then crushed by hand and placed in 10-15% HCl for several days, until the calcite was completely dissolved. The undissolved material was dried and weighed.

We also examined the mineralogy of the concretions using X-ray diffraction. A sample from an unweathered portion of each concretion was ground to a fine powder using a mortar and pestle and packed into a well slide for mounting in the diffractometer. Diffraction patterns were produced with a Philips X-Pert Pro diffractometer. We also analyzed a sample of the shale surrounding UW34653. The peaks in the diffraction graphs enabled us to identify the dominant minerals. A calcite/quartz ratio was estimated as the relative heights of the major

diffraction peak for each mineral (height of calcite peak/height of quartz peak).

Comparison of Concretions

The concretions vary from dark gray to light gray, probably reflecting the organic content of the concretion. Interestingly, the UW34653 concretion was a light gray color, not the darkest of the four. Thus it does not appear to contain an usually high amount of organic material compared to the other concretions.

The UW34653 concretion is fossiliferous. Shells of the clam *Astarte* and other fossil fragments are visible on both the upper and lower surface of the concretion. Andersson (1979) reported limestone cobbles that had been bored and encrusted by pelycopods. This is not the situation with this concretion as there are fossils within the concretion as well. Furthermore, the concreted block was part of an articulated specimen and not an isolated cobble that could have been rolled around by the currents so that organisms could encrust both sides. Instead, the carcass could have acted as a baffle to trap some coarser material that may have been carried in by a storm. There was no evidence of a coarse layer in the surrounding shale. UW34653 is not unique, however, in being encased in a fossiliferous concretion. Although many specimens are encased in an unfossiliferous, fine grained micrite, the concretion associated with UW15936 is also fossiliferous.

No major differences among the concretions are evident from the compositional analyses. Although some variation exists in the percent of insoluble material among the concretions, the value for UW34653 is similar to the values for the others (Table 1).

TABLE 1. Insoluble residue data for concretions associated with or encasing partial skeletons of ichthyosaurs from the Redwater Shale. The first specimen listed is the one with stomach/intestinal contents.

Ichthyosaur Specimen	Sample weight (g)	Insoluble residue (g)	Percent Insoluble
UW 34653	27.3	12.3	45
UW 24216	27.8	13.0	47
UW 15937	31.0	15.3	49
UW 15936	39.7	14.1	36

X-ray diffraction analyses showed that the mineralogy of the UW34653 concretion is similar to that of the surrounding shale, except for a much higher amount of calcite (Figure 5). Thus the concretion was probably a diagenetically early cementation of the muds that comprise the shale. The mineralogical composition of the four concretions is similar. The most prominent peaks are calcite and quartz, the dominant minerals in the concretion. Comparison of the diffraction patterns of the four concretions (Figure 6) shows that although the same mineralogy is present, the ratio of calcite to quartz does vary among the concretions (Table 2). Two samples of the UW34653 concretion shows the highest proportion of calcite relative to quartz, but a third sample is within the range of the other concretions. Interestingly, UW15937 was the most weathered of the four specimens and had the lowest calcite/quartz ratio. Only parts of UW15937 were concreted, and even then, bones were not completely encased. This suggests that the ratio is probably a function of both the primary composition of the concretion and the amount of modern weathering. The higher ratios for UW34653, however, suggest that perhaps that concretion formed more quickly than the others such that less of the terrigenous "background" sediments were incorporated into the concretion.

TABLE 2. Calcite/Quartz ratio for concretions associated with ichthyosaur remains. Block 8 encased some of the gastric mass.

Specimen	C/Q	
UW 34653	9.0	Block 6
	6.0	Block D
	1.8	Block 8
UW 24216	2.5	
UW 15937	1.7	
UW 15936	3.8	

DISCUSSION

Stomach contents of ichthyosaurs are known from the lower Jurassic of Europe, with most reported specimens coming from the Posidonienschiefer of southern Germany. The Posidonienschiefer is a black, bituminous shale that is known for its extraordinary preservation of skin and fin outlines of ichthyosaurs, and to a lesser extent plesiosaurs (Hauff and Hauff, 1981). The lack of benthic invertebrates and the high organic content have suggested an anoxic sea floor that would have inhibited scavenging and decay (Etter and Tang, 2002). However, a

soupy substrate has been proposed as an alternate explanation for the lack of benthic invertebrates (Martill, 1993). A carcass sinking into a soft, muddy substrate would achieve the rapid burial that is considered a necessary condition for preservation of soft tissue (Brett and Baird, 1986). Martill (1993) mentions ichthyosaurs whose rostra lie at a steep angle to the bedding but whose torsos lie along bedding. This suggests that that the carcass hit the seafloor head first, with the head sinking into a soft substrate. He further reported that belemnite guards are commonly oriented at a high angle to bedding, as if they dropped from above into a soft substrate (Martill, 1993).

A soupy substrate may be the situation in the Redwater Shale. One ichthyosaur specimen, UW24216, was preserved with its skull at almost a right angle to the bedding, whereas the articulated postcranial skeleton was lying along the bedding plane. The Redwater Shale probably had a slow sedimentation rate. Some of the ribs of UW24216 show borings that suggesting an exposure long enough for the soft tissue to decay (Massare et al., 1999). Furthermore, small concretions from the Redwater Shale often have encrusting oysters. A soupy substrate may explain how stomach contents could be preserved by rapid burial, even in an environment that had a slow sedimentation rate. An alternative explanation, however, is that the skeleton may have served as a baffle, collecting shell pieces and coarser sediments that may have been moved by storms. This episodic sedimentation could have partially buried the specimen. If rapid formation of the concretion followed, the gastric material could have been isolated from the affects of currents and

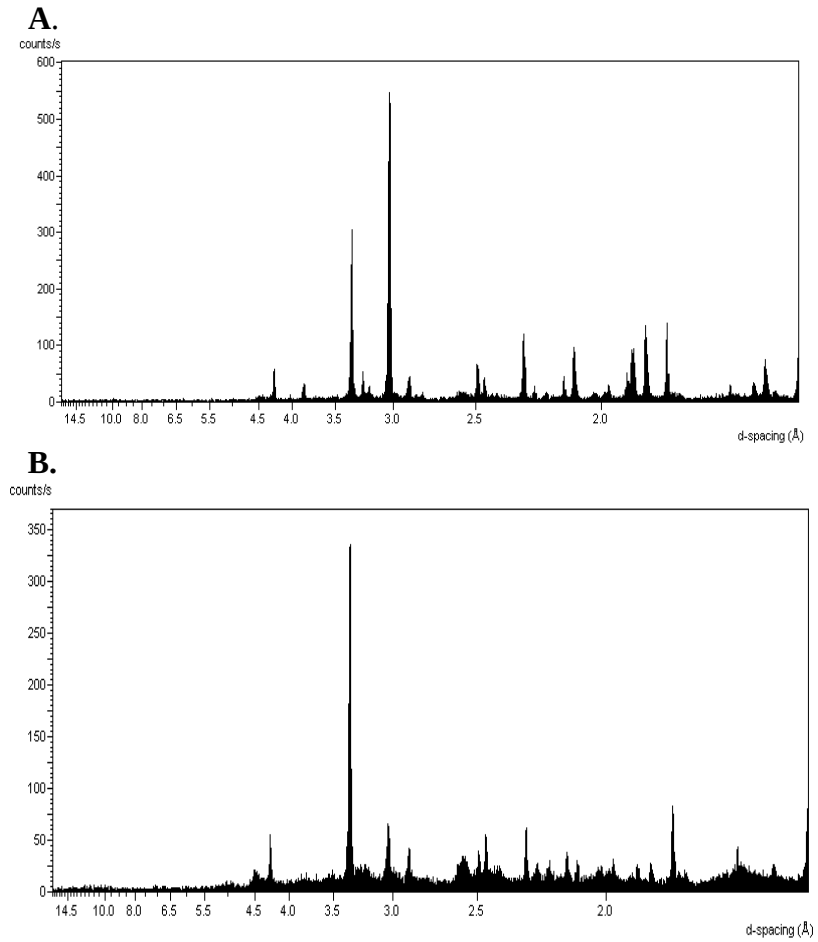


FIGURE 5. X-ray diffraction pattern of the concretion (A) and surrounding shale (B) associated with UW34653. The x-axis is d-spacing. A. The highest peak is the main calcite peak. The highest peak to its left is the main quartz peak. Sample was taken from block 8, the block that included the partially digested remains. B. The highest peak is the main quartz peak. The main calcite peak is to its right.

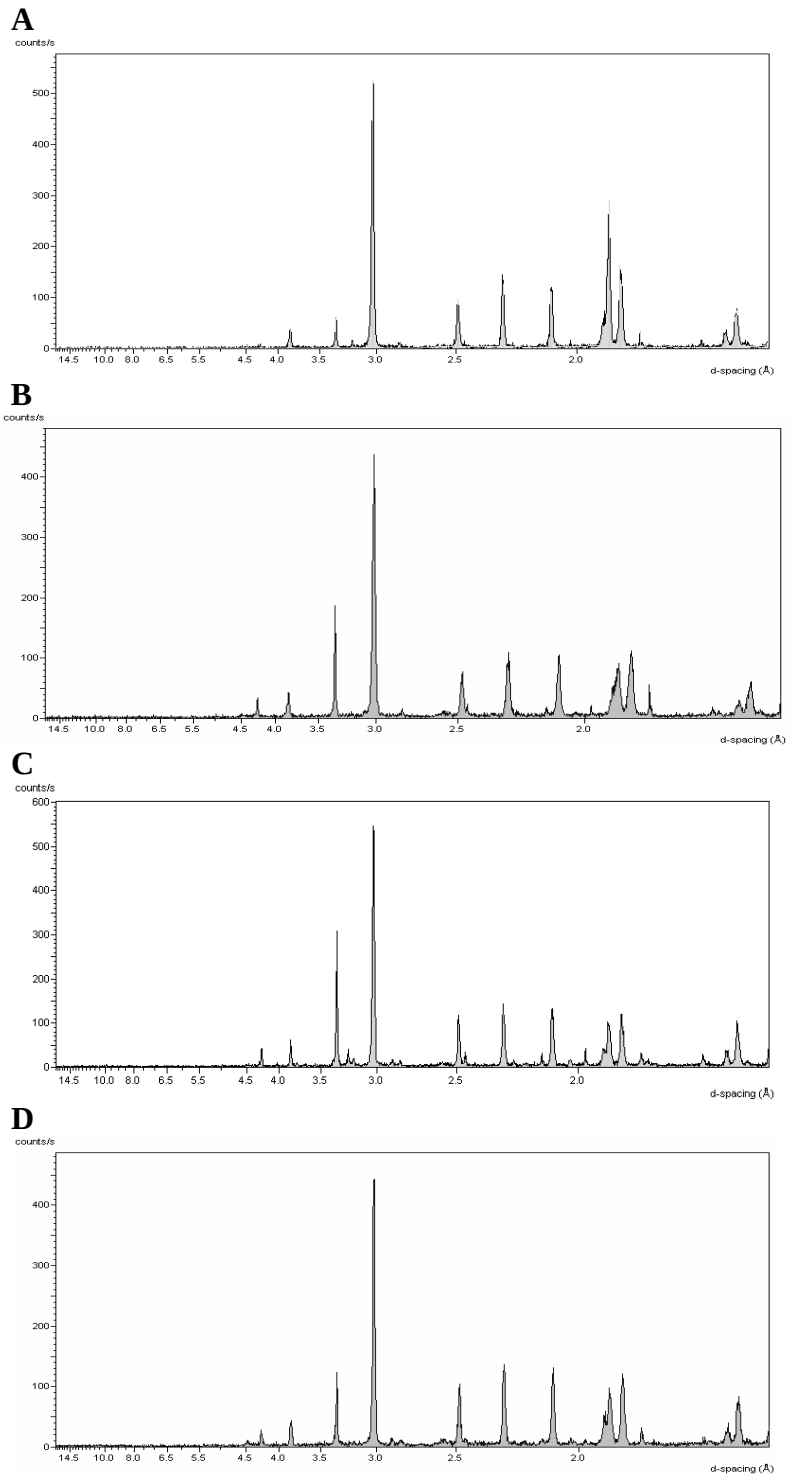


FIGURE 6. Comparison of the x-ray diffraction patterns of the four concretions. Note the similarity in all of the diffraction peaks. A. UW 34653, Block 6. Note that the difference in relative size of the main calcite and quartz peaks compared to Fig 5A. The two highest peaks are calcite. B. UW 24216 C. UW 15937 D. UW 15936. The same peaks are present, indicating a similar mineralogy. The highest peak in all four patterns is the main calcite peak. The peak to its left is the main quartz peak. Note that the relative size varies.

organisms that would have dispersed it.

The stomach contents of UW 34653 show some differences compared to those previously reported for other ichthyosaurs. The mode of preservation is unusual in that the gastric material is preserved in limestone, not in organic-rich shales. The main mass seems to be more posteriorly located than in other reports, but as the specimen is still under preparation, this assessment is preliminary. Finally, the hooklets in the gastric mass are very fragmented, especially in the central portion of the mass, with relatively few intact hooklets. Nonetheless, it is similar to previous reports in that it indicates that this species fed on coleoid cephalopods.

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