

LATE EOCENE SHARK COPROLITES FROM THE YAZOO CLAY IN NORTHEASTERN LOUISIANA

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Abstract—Systematic, long-term surface collecting of two sites in the marine sediments of the upper Eocene Yazoo Clay (34.3 Ma) in Caldwell Parish, Louisiana, has resulted in the procurement of nearly 1200 shark coprolites. A sample ($n = 374$ or approximately 30% of total) of the 1196 collected coprolites is described in detail based on length, width, weight, density, coloration, external features, internal features (when possible), and morphology. Two primary morphological types, spiral and scroll, were recognized. Approximately 98.01% of the coprolites were classified as either spiral (556 specimens) or scroll (617 specimens) based on external and internal morphological features. X-ray analysis showed the coprolites to be composed of moderately crystalline fluorapatite [$\text{Ca}_5(\text{PO}_4)_3\text{F}$] with no compositional differences between the types. An annotated review of the literature dealing specifically with chondrichthyan coprolites was prepared. Prior studies at the sites produced extensive collections of shark teeth (> 2500) and provided statistical abundance data on the shark taxa. The shark tooth data, which provided occurrence and abundance, coupled with modern information on shark size, anatomy, and excretory characteristics allowed for a more specific identification of the shark coprolites as to possible source animals. The most likely source animals for the spiral coprolites were the lamniform *Isurus praecursor* and the carcharhiniform *Abdounia enniskilleni*, while the scroll coprolites were most likely produced by the carcharhiniform *Carcharhinus gibbesi* with the exception of several large specimens, which may be related to *Galeocerdo alabamensis*. Some of the coprolites had inclusions such as fish bones and scales that provided evidence of the dietary habits of the sharks. The extensive and longitudinal nature of this project has resulted in one of the most complete and exhaustive studies of late Eocene shark coprolites from the Gulf Coast.

INTRODUCTION

Coprolites, with the origin of their name stemming from the Greek *kopros*, meaning dung or excrement, and *litos*, which signifies stone or rock, are found in a variety of paleontological environments including marine and terrestrial. By formal definition, coprolites are the fossilized excrement of vertebrates such as fishes, reptiles and mammals and are larger than the fecal pellets of invertebrates (Bates and Jackson, 1984). Coprolites are generally accepted as fossilized excretion rather than fossilized material in the intestine (Williams, 1972; Pollard, 1990). K. Chin, one of the leading researchers on coprolites, also refers to coprolites as fossil feces, fossil dung, and fossil droppings (Chin, 1994). Coprolites have a fairly large range of size from approximately 5 mm to over 35 cm (Häntzschel et al., 1968).

Chin (1997) noted that, despite the ephemeral nature of animal feces, lithified coprolites of vertebrates have been found on every continent and as far back as the Silurian. Coprolites are quite rare compared to the immense quantity of excretion by organisms because they tend to decay rapidly. However, coprolites of vertebrates are preserved in the fossil record, and some, especially carnivorous vertebrate coprolites, are quite distinctive in their morphology. Häntzschel et al. (1968) suggested that the source animals for coprolites over 5 mm and composed of fluorapatite were most likely carnivorous vertebrates. Other researchers have used a similar minimum size measurement of 4 mm (Schafer, 1972; Savrda and Bottjer, 1993).

Vertebrate coprolites from terrestrial settings, including freshwater environments, are better known and have been investigated in greater detail (Amstutz, 1958; Häntzschel et al., 1968; Chin, 1994, 1997, 2002; Hunt et al., 2007). Unfortunately, it is a different situation with vertebrate coprolites from the marine environment, which have not been studied to the extent of their terrestrial and freshwater counterparts. This is especially true of marine shark coprolites. Whereas coprolites attributed to Paleozoic freshwater sharks have been fairly well reported and studied (see the Literature Review in this paper), the investigation of marine

shark coprolites has received much less attention. Kent (1994) noted that shark coprolites are not particularly rare, but they are frequently overlooked because of their nondescript nature.

It is somewhat ironic that comprehensive studies of marine shark coprolites are uncommon since they are known from many formations, especially in the Cretaceous, Paleogene, and Neogene of the Gulf Coast. The distinctive morphology of shark coprolites, which forms as the fecal material passes through the intestinal valve (often called the spiral valve), assists in the recognition of these characteristic trace fossils. Many studies mention the occurrence of shark coprolites in the Gulf Coast, but few of them provide any detailed information on them.

The principal objective of this research was to collect, describe, and analyze late Eocene shark coprolites from the Yazoo Clay in Caldwell Parish, Louisiana. A secondary objective was to provide an intensive review of the literature dealing specifically with any aspect of chondrichthyan coprolites. The presence of coprolites was known because of previous studies in the area, especially Stringer (1977), Breard (1978), Breard and Stringer (1995), King (2002), and Stringer and King (2010). The goal was to provide a more detailed and in-depth examination of shark coprolites and to see what information could be gleaned from these trace fossils.

Bulk sampling would have been an ideal method of collecting, but this method proved to be very ineffective in the procurement of shark coprolites in this formation. Therefore, a systematic, long-term surface collecting technique was adopted and performed basically over the same area several times per year (usually about five times per year) for an extended period (more than 30 years). Two localities in the Copenhagen area of southeastern Caldwell Parish in northeastern Louisiana were chosen for this research based on several factors. First, the two localities consisted of fossiliferous marine sediment from the Yazoo Clay and were stratigraphically equivalent. Second, both of the localities were fairly large in areal extent, which was needed for systematic, long-term collecting. Third, the two localities and the surrounding region had yielded abundant vertebrate remains since the 1830's (Harlan, 1834) as well as in

more recent studies (Domning, 1969; Hall, 1976; Stringer, 1977, 1979; Breard, 1978; Breard and Stringer, 1995; King, 2002; Cappetta and Stringer, 2002; Nolf and Stringer, 2003; Fierstine and Stringer, 2007).

Collecting at the two localities yielded 1196 specimens of shark coprolites, which were classified mainly as one of three types: spiral, scroll, and indeterminate. Classification of the shark coprolites was based primarily on external features, although internal features, inclusions, and chemical composition were also considered. Two of the coprolite types are numerous (the scroll and spiral types comprised 98.01% of the total), while the other type was present in small numbers. A random sample of 374 shark coprolites (approximately 30% of the total) was chosen for detailed description based on eight categories (length, width, weight, density, coloration, external and internal features, and morphological type). The significances of the differences between the length, width, weight, and density of the spiral and scroll coprolites were tested by developing directional hypotheses, which were evaluated with a simple t-test.

Randomly selected spiral and scroll shark coprolites from the two localities ($n = 10$) were analyzed on a Philips model PW1840 x-ray diffractometer with a copper target x-ray anode. The diffraction pattern of the coprolites was compared to the x-ray diffractions of calcite, aragonite, fluorapatite crystal, modern deer bone, and ancient deer bone from an archeological site. The x-ray diffraction patterns obtained from the coprolites matched the pattern of the fluorapatite crystal very closely, and the composition was determined to be moderately crystalline fluorapatite $[\text{Ca}_5(\text{PO}_4)_3\text{F}]$.

THE INTESTINAL VALVE OF THE CHONDRICHTHYES

Although the primary objective of this research was to collect, describe, and analyze chondrichthyan coprolites from the late Eocene Yazoo Clay in Caldwell Parish, Louisiana, fundamental aspects of the shark's excretory system as it relates to the formation of coprolites are addressed. The development of shark coprolites with their diagnostic morphology is directly linked to the modification of the shark's digestive tract to increase the absorption of nutrients since elasmobranchs have a relatively short intestine, especially compared to other vertebrates (see photograph in Holmgren and Nilsson, 1999, fig. 6-3, p. 148). This alteration takes the form of an intestinal valve, often referred to as a spiral valve, in the lower portion of the intestine (Bertin, 1958; Williams, 1972; Holmgren and Nilsson, 1999). Orr (1971), in his classic book on vertebrate biology, noted that the intestine of elasmobranchs is divided into a small and large portion. The small portion of the intestine is characterized by the presence of a spiral valve, which greatly increases the absorptive surface. The spiral valve consists of mucosa and submucosa along the intestine. The number of the turns of the spiral valve appears to be highly variable with as few as two or three or as many as 50 according to Bertin (1958). Castro (1983), in his *The Sharks of North American Waters*, noted that the intestinal valve usually resembled a carpenter's auger enclosed in a tube, but it could also be constructed in a scroll-like fashion. It is important to note that although the intestinal valve is often called the spiral valve, the arrangement can also be scroll-like in nature.

Although there is some disagreement among zoologists, there appear to be three basic forms of intestinal valves in sharks (including rays and skates), often termed spiral, ring, and scroll. Holmgren and Nilsson (1999, p. 149) illustrated four basic types, but the only difference in their type B and C is whether the funnels point backward or forward. It should also be noted that these figures of spiral valves were taken from Bertin (1958), who actually took them from another source published in the late 1800's (Parker, 1885). The spiral valve represents the "classic" shark intestinal partition, resembling a wood auger in shape, and is found in families such as cow sharks (family Hexanchidae), spiny dogfishes (family Squalidae), and catsharks (family Scyliorhinidae). A second intestinal valve is the ring valve, which resembles a series of tightly packed lamellae (plates), and is found in all extant lamnoids (such as the mackerel sharks). The spiral and ring valves are similar in structure and are often

grouped together since the resulting coprolite has a spiral pattern (Fig. 1A-C). A third type of intestinal valve is the scroll valve, which resembles a loose roll of paper in shape, and is found in some, but not all, of the carcharhiniforms (Fig. 1D).

As noted previously in this paper, all chondrichthyes, such as sharks, rays, and skates, possess a valvular intestine (often referred to as a spiral valve). These specialized structures in the chondrichthyans have been scientifically studied for almost 200 years (Buckland, 1829). Parker (1885) reported that Sir Richard Owen recognized two basic types of intestinal valves and referred to them as longitudinal and transverse valves. The longitudinal valve was described as a scroll-like and found in some of the carcharhiniforms (i.e., a scroll-type intestinal valve). The transverse valve was compared to the wood auger encased in a hollow tube (i.e., a spiral-type intestinal valve). Parker (1885) studied the spiral-type intestinal valve extensively and classified them into four categories because of variability he found in modern genera such as *Raja*. He also noted structural differences in the spiral valve of the clearnose skate (*Raja eglanteria*) and suggested several more transitional categories in addition to the four basic types. The validity of all these categories is not known. Fee (1925) also studied the spiral-type intestinal valve in-depth and even reported on its phylogeny. Romer (1966) addressed the valvular intestines of the chondrichthyans. Regarding the valvular intestine in non-fish organisms, Romer clearly stated that "no living tetrapod has the slightest trace of this organ."

One of the most intensive and detailed studies of the intestinal valves of chondrichthyans and their relationship to coprolites was that of Williams (1972). Williams conducted an exhaustive study of heteropolar spiral coprolite specimens from the Lower Permian Wymore Shale in Kansas. His study included the investigation of spiral valves (intestinal valves) of modern sharks as well as the study of hundreds of thin sections of the fossil heteropolar spiral coprolites. The microscopic thin section studies indicated the presence of well-preserved mucosal

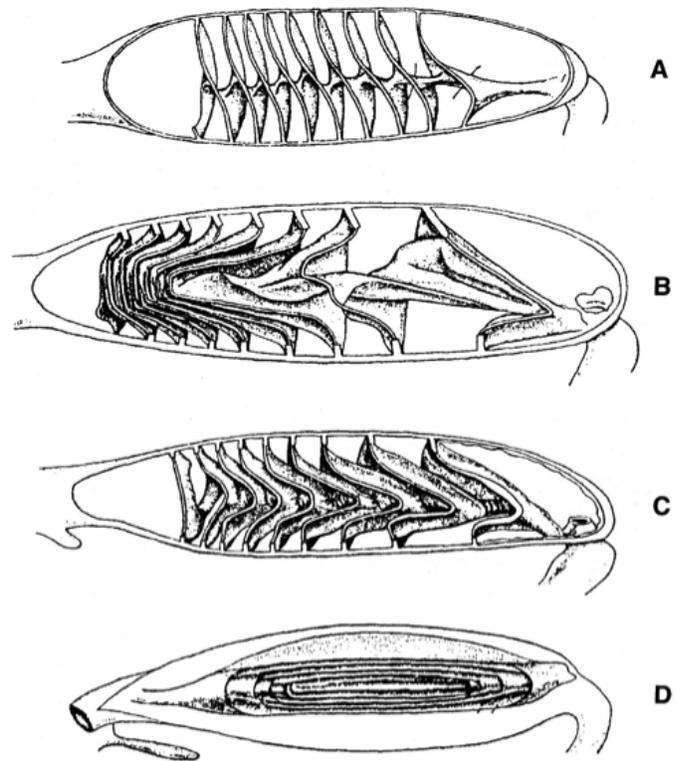


FIGURE 1. Line drawings of the spiral valves of elasmobranch intestines (originally from Parker, 1885; reproduced in Bertin, 1958, as well as in Holmgren and Nilsson, 1999). A-C would produce a spiral coprolite. D would produce a scroll coprolite.

folds, and he concluded that the heteropolar spiral coprolites from the Lower Permian of Kansas were not excreted material but represented fossilized intestinal or spiral valves. He agreed with Fritsch that the term enterospirae should be employed to describe these structures.

Subsequent to Williams (1972), McAllister (1985) conducted another major study on the relationship of spiral coprolites and valvular intestines. It appears that much of the work of McAllister was an outgrowth of his research for his Masters thesis in 1984 at the University of Kansas. McAllister performed extensive investigations of the spiral valve of the extant shark *Scyliorhinus canicula*. McAllister believed that what was described as enterospirae (fossilized valvular intestines) by previous investigators such as Fritsch (1895), Neumayer (1904), Williams (1972), Stewart (1978), and Duffin (1979) were actually fecal ribbons that coiled spirally within the colon. McAllister contended that these spiraled fecal masses could be expelled from the chondrichthyan without distortion.

In the late 20th century, several researchers published papers related to the intestinal valves of chondrichthyans that have application to the study of shark coprolites. Wetherbee and Gruber (1993), in an extensive and detailed study of absorption efficiency of lemon sharks, noted the importance of the spiral valve for increasing surface area versus the tubular intestine common in teleosts. This research as well as others such as Wetherbee et al. (1987), Holmgren (1989), Wetherbee and Gruber (1990), and Holmgren and Nilsson (1999) provided information pertinent to coprolitic studies of sharks. It was noted in studies that the chemical composition of shark feces collected from different sharks at different time intervals within the experiments did not vary significantly. This appears to indicate that the digestive process of the sharks is quite consistent as far as the resulting chemical composition of the feces. Another applicable observation is that the composition of feces exposed from one minute to 60 minutes to saltwater did not show significant decrease in the concentration of the marker or the energy values. This seems to indicate that the saltwater is not significantly leaching or affecting the composition of the feces during that time interval.

There were other notable observations in the above-mentioned references such as the low rate of consumption by the sharks, the extended food retention time, gut motility, and the slow rate of growth. The research indicated that voiding could begin within 16-17 hours after ingestion, but the complete emptying of the shark's digestive tract could take up to 82 hours (over 3 days), and there are indications that food can be stored for extended periods. This long interval of voiding can also have an effect on shark coprolites. As pointed out by Chin (1994), feces may be partitioned into smaller units and can also be mechanically broken and separated after excretion. Therefore, the entire fecal material may not be recovered as a fossil because of the fragmentary nature of the feces. Northwood (2005) aptly noted that fecal material prone to fragmentation may be over-represented in the fossil record and that segmentation may bias quantitative studies of morphological forms and inclusions. Recent films and pictures, both in the wild and at aquariums, have documented shark excretions (much to the delight of many people on the Internet). Many sharks typically have a bolus of waste material, but there may also be a liquid portion that is typically a dirty light brown in color.

Fecal habits of the coral catshark *Atelomyxerus marmoratus*, which is in the Family Scyliorhinidae (Carcharhiniformes), have been observed by curators and keepers at the Mississippi Museum of Natural Science aquarium (John Hardy, personal commun., 2011). The coral catshark typically excretes once about every two days. The fecal material has a spiral shape with a diameter of about 5 mm and a length of approximately 5-7 cm. The captive coral catsharks are not very large (only about 30 cm), but they produce fecal material of substantial length. It would appear that the fecal material would most likely break during fossilization. This supposition seems to be supported by the spiral coprolites from the study area. Many, and probably a majority, of the spiral coprolites with similar diameters, approximately 5 mm, are frequently broken

on both ends. Furthermore, the spiral coprolites are typically only about 2 to 3 cm in length. This seems to be a strong indication that the coprolites are either fragmenting before preservation or possibly post-depositional. In either scenario, the coprolites are not indicative of their original length.

Romer and Parsons (1986) stated that in addition to the sharks (including the rays and skates) very primitive fish such as the lungfish also possess a spiral valve and that the spiral valve, which is considered a primitive character, is subsequently lost in teleost fish and tetrapods. Chin (1994) noted that a few teleosts retain a vestige of the spiral valve. Fossil evidence indicates that the spiral valve of the sharks evolved quite early. There are several older publications that contain illustrations of unusually well preserved Middle Paleozoic sharks such as *Cladoselache* with external and internal impressions in shale that clearly show the spiral valve (Claypole and Wright, 1893; Dean, 1893; Fritsch, 1895; Woodward, 1917). Zangerl and Richardson (1963) also mentioned a spiral fecal mass in a Pennsylvanian shark, but they did not describe or figure the specimen.

LOCALITY DATA

The focus of this study is the shark coprolites collected from the late Eocene sediments, primarily the Yazoo Clay, located south of the town of Columbia along the Ouachita River in Caldwell Parish in the central part of northeastern Louisiana (see Cappetta and Stringer, 2002, for map). More specifically, it concentrates on the area between the old community of Copenhagen and the Ouachita River, about 9.7 km southeast of Columbia and east of State Highway 849 (Columbia 1/24 000 quadrangle, x = 591.900 m, y = 3544.100 m). The study area consists of two localities, which were chosen because they were stratigraphically equivalent, extensive, and yielded abundant vertebrate materials in previous studies. The prairies and exposures along the Ouachita River in Caldwell Parish have been scientifically studied since approximately 1829 and were the sites for the initial discovery of the late Eocene whale *Basilosaurus cetoides* (Harlan, 1834; Huner, 1939; Stringer and King, 2010).

Locality I, the more extensive of the two localities, is approximately 1.0 km wide and 1.75 km long. Locality I is roughly rectangular in shape and oriented northeast to southwest. The elevation of Locality I varies from 33 m above sea level to 60 m above sea level. Upland prairie areas associated with rolling hills are characteristic of the locale. The yellowish-gray Yazoo Clay exposures and the lack of trees are also prominent characteristics. The vegetation consists mainly of various types of grasses, small herbaceous plants, several types of wildflowers, and red cedars in the prairie. The vegetation is much more diverse along the drainages (intermittent creeks) with abundant and large numbers of hardwood trees, vines, and shrubs. The vegetation in the Copenhagen area is the most diverse in Louisiana and rivals the diversity of areas such as the Appalachians according to the Nature Conservancy.

Locality II is very similar to Locality I in many ways. Locality II is approximately 0.5 km wide and 0.75 km in length. The elevation of Locality II is from 36 m above sea level to 53 m above sea level. Locality II, like Locality I, is characterized by yellowish-gray Yazoo Clay exposures and a paucity of trees in the prairie areas. Extensively weathered, rolling hills with numerous gullies are present. The vegetation is similar to that at Locality I. Fairly dense vegetation with large numbers of diverse hardwoods, shrubs, and vines also characterizes the drainage areas as it does at Locality I.

STRATIGRAPHY

Exposed sediments in both localities consist primarily of the upper Eocene Yazoo Clay. This formation and the Moodys Branch Formation comprise the Jackson Group in Louisiana. In some parts of Louisiana the Yazoo Clay is divided into members, which are, in ascending order, the Tullos, Union Church, and Verda. The uppermost part of the

Verda is designated as the Danville Landing Beds, which consist of interbedded, fossiliferous marine clays and sands (Huner, 1939). The aforementioned members of the Yazoo Clay are recognized mainly in Louisiana and are not mapped in adjacent states. Other subdivisions of the Yazoo Clay are used in Mississippi and Alabama (Dockery, 1996). The coprolites were collected from the Tullos Member of the Yazoo Clay at both localities. The age of the Yazoo Clay in Louisiana is considered to be Priabonian, except for the lowermost and uppermost strata. Radiometric dating (K/Ar) of the Yazoo Clay has shown it to be approximately 34.3 million years old (Obradovich and Dockery, 1996). The stratigraphic relationships of the Yazoo Clay are shown in Figure 2.

METHODOLOGY

The methodology portion of this study was broken into four fundamental phases: 1) collection of the coprolites from the Tullos Member of the Yazoo Clay; 2) cleaning and cataloging of the coprolites; 3) classification of the coprolites as to morphological type and a detailed description of a sample representing approximately 30% of the total coprolites; and 4) x-ray analysis of selected coprolite specimens. These phases are described in the following section.

Collection Phase

The ideal procedure for collecting coprolite specimens from the study area would have been to collect bulk samples from the two localities of Yazoo Clay. However, bulk sampling had not proved effective for obtaining coprolites (Stringer, 1977). Another previous study collected over 500 kg of material from Locality I, which was screen-washed with tap water (Nolf and Stringer, 2003). Unfortunately, this technique yielded only three shark coprolites. This is directly related to the scarce and sporadic occurrence of the coprolites. The coprolites are not concentrated in any specific layers but are randomly distributed throughout the section. Therefore, a systematic, long-term surface collecting technique has been shown to be the most productive type of procedure when collecting shark coprolites in this area. The surface collecting traced a designated route each time and concentrated on ravines, gullies, and several drainages at the two localities. The timing of the surface collecting often corresponded to periods of rain, which often exposed coprolites on the surface of the Yazoo Clay. Field collection was accomplished using very basic field tools such as topographic maps, a 10x doublet magnifying hand lens, and sample bags. A Global Positioning System was utilized in locating sites previously reported in the literature.

Cleaning and Cataloging Phase

Age	Stage	Group	Formation	Member/Bed	Lithology
L		J		Danville Landing Beds	Interbedded sands, clays, w/ fossiliferous concretions (32 m)
A	P	A	Y		
T	R	C	A		Lignitic clays, silty sands, lenticular
E	I	K	Z	Verda Member	marine sandstone, and clays (64 to 72 m)
	A	S	O		
E	B	O	O	Union Church Member	Sandy silts, calcareous concretions (4.8 m)
O	O	N			
C	N		C		
E	I	G	L		
N	A	R	A		
E	N	O	Y	Tullos Member	Deep blue-gray clay (weathers tan), minor marl and limy clay beds, abundant fossils (24 to 56 m)
		U			
		P			
	BARTONIAN				

FIGURE 2. Stratigraphic column of the Jackson Group (upper Eocene), Ouachita River section, Louisiana (from Nolf and Stringer, 2003).

The fairly dense and indurated nature of the late Eocene shark coprolites facilitated their cleaning. Most of the coprolites could be cleaned with tap water. A soft brush was utilized on some specimens to remove the clay with only a few specimens requiring placement in an ultrasonic cleaner to eliminate more consolidated material. For those specimens requiring ultrasonic cleaning, no chemicals were used in the process. The cleaned coprolites were allowed to air dry for several days before proceeding with cataloging. Coprolites were assigned identification numbers, counted, and cataloged.

Detailed Description Phase and Classification of Coprolites

Chin (2002) noted that as a general rule, damage of fossil specimens should be studiously avoided if possible. Therefore in this study, shark coprolites were classified mainly as spiral, scroll, or indeterminate based primarily on external morphological features. This procedure minimized damage and destruction of specimens. It should be noted that all of the shark coprolites appear to be composed of fluorapatite, which is very useful in the identification of the coprolites. In some instances, internal features were available on broken specimens and assisted in classification. In both spiral and scroll shark coprolites that are complete or reasonably complete, the length is much greater than the width.

There are prominent external characteristics or features utilized to differentiate between spiral and scroll coprolites. Spiral coprolites tended to have moderately distinct to well-defined twisting patterns on their external surfaces. The twisting patterns were characteristically oriented approximately from side to side or across the width of the coprolite (Fig. 3, left and right). The number of whorls varied with the length of the spiral coprolites. On shorter spiral coprolites, there may be as few as two or three whorls, but on the longer specimens, the number of whorls often exceeds five. The width of many of the Yazoo Clay spiral coprolites tended to be quite uniform for the entire length of the specimen. This is unusual since the width of many coprolites identified as spiral from the Cretaceous in Texas, New Jersey, and England tended to be quite variable, and the spiral coprolites were almost tear-drop in shape (Buckland, 1829; Case, 1967; Case, 1973; Case, 1982; Welton and Farish, 1993; McKinzie et al., 2001). Spiral coprolites from the study area, which were broken or weathered, seldom showed discernable internal structures.

The major external features of the scroll coprolites were the moderately to deeply incised, very distinctive folds and grooves (Fig. 4, left and right). These folds and grooves were primarily oriented from end to end (longitudinally or the length direction of the coprolite). The width of the scroll coprolites tended to be slightly more variable, especially toward the center (Fig. 4, right). Internal features of scroll coprolites such as folds were common and quite distinct in broken specimens. The ends of the scroll coprolites often showed distinct whorls (Fig. 5, left and right).

The key differences in the spiral and scroll coprolites are the twisting versus fold and groove features and the orientation of these structures (width versus length). Specimens meeting the criteria as selachian but not having identifiable features of spiral or scroll coprolites were identified as indeterminate. The indeterminate specimens were quite variable in shape such as oval or oblong, were often nodular in appearance, and were often more flattened (Fig. 6). It is possible that some of the indeterminate specimens were scroll coprolites that had been flattened to the extent that the characteristic folds and grooves could not be detected. Some of the amorphous types could also represent cololites rather than extruded fecal material (coprolites).

Enterospirae or the fossilized intestinal contents have also been reported in the literature by several authors such as Fritsch (1895), Williams (1972), Stewart (1978), and Pollard (1990). Enterospirae and coprolites have many similarities since coprolites are excreted feces while the enterospirae represents intestinal contents that have not been excreted. It can be difficult to distinguish between the two since both show

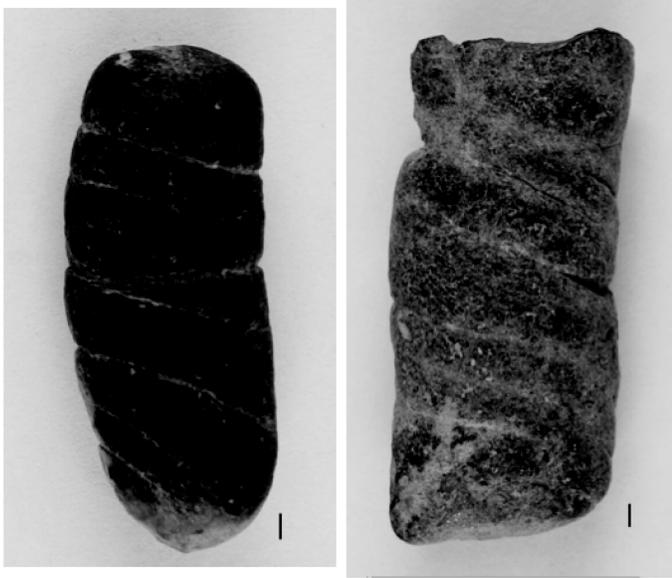


FIGURE 3. **Left**, Specimen of a spiral coprolite from the late Eocene Yazoo Clay. Scale bar = 1 mm. **Right**, Specimen of a spiral coprolite from the late Eocene Yazoo Clay. Scale bar = 1 mm. Note the well-defined twisting patterns that are oriented mainly across the width of the coprolite.



FIGURE 4. **Left**, Specimen of a scroll coprolite from the late Eocene Yazoo Clay (light coloration is due to slight weathering of the fluorapatite). Scale bar = 5 mm. **Right**, Specimen of a scroll coprolite from the late Eocene Yazoo Clay. Scale bar = 5 mm. Note the deep groove or fold patterns that are oriented primarily longitudinally along the length of the coprolites.

the features of the spiral valve.

A random sample consisting of 374 specimens, approximately 30% of the total 1196 coprolites, was chosen for detailed descriptions. Eight categories (maximum length, maximum width, weight, density, coloration, external features, internal features, and morphological type) were utilized to describe each coprolite specimen. Each coprolite specimen was measured for the maximum length and width in millimeters using a set of scientific calipers. The weight in grams of each specimen was obtained by using an Acculab VI-350 Electronic Scale, which is precise to 0.01 g.

Density was obtained by using a displacement method. Each coprolite specimen was placed in a 100 ml-graduated cylinder. The volume (amount of displacement in ml) was divided into the mass, and the density was determined in cubic centimeters (density = mass / volume). The coprolites that were too small to displace the water column significantly to gain an accurate reading for density were weighed together and averaged. These small coprolites (weighing less than 2.0 g) were analyzed as a group (usually five specimens depending on size), and an average was determined. The densities determined by this averaging method are designated with the symbol (A) in Table 1.

The color of each coprolite was determined by comparison with the Munsell Rock-Color Chart (Geological Society of America, 1991). Color was determined for external appearance only, unless otherwise noted in the tables. If the color was determined for the interior, then it is denoted by the abbreviation (int). Any significant or distinguishable external or internal features such as twists and grooves were noted. In describing features, the abbreviation "ex" was used for excellent, and "wx" was used to designate a weathered specimen.

The final aspect in this phase of the study was to attempt to relate the shark coprolites to possible source animals in the Yazoo Clay. Generally, classification of coprolites more specific than the class is not possible because of the difficulty of relating them to a specific animal (Hunt et al., 1994). Northwood (2005) applied several parameters to identifying coprolites such as the shape, surface marks, size, inclusions, composition (chemical makeup), depositional context, and morphological features of the taxa to which coprolites are attributed with co-occurring skeletal remains. Chin (2002) had recommended similar procedures when she stated that the size, composition, contents (inclusions), and stratigraphic placement of the coprolites could constrain the number of perpetrators. This study addressed the suggested parameters of Chin and Northwood. Fortunately, prior studies such as Breard and Stringer (1995) at the two localities produced representative collections of shark teeth (> 2500 specimens) and provided important data on the occurrence and the abundance of the 14 identified shark taxa. This supplied essential information on the co-occurring sharks represented by skeletal remains and enabled an analysis of possible source animals. The study of the teeth of the Yazoo Clay sharks provided occurrence and abundance data that, when coupled with information on modern shark size, anatomy, and excretory characteristics, allowed the shark coprolites to be more accurately related to the possible source animal.

X-ray Analysis Phase

A Philips model PW1840 x-ray diffractometer with a copper target x-ray anode was utilized to determine the mineralogical composition of the randomly selected coprolites. The x-ray diffraction was accomplished by the grinding of selected coprolite specimens to a size of less than 230 mesh and preparing powder pack mounts for scanning. The tube current was set at 40Kv and 35 angstroms. The negative aspect of the x-ray analysis was the grinding and destruction of all or part of the coprolite specimen in order to prepare the powder mount. This is a major reason the x-ray analysis was limited to ten specimens.

In addition to the x-ray diffraction scans of the coprolites, x-ray analysis was conducted and scans were obtained for the minerals calcite, aragonite, and crystalline apatite as well as for modern deer bone and ancient deer bone (from an archeological site). Calcite and aragonite were

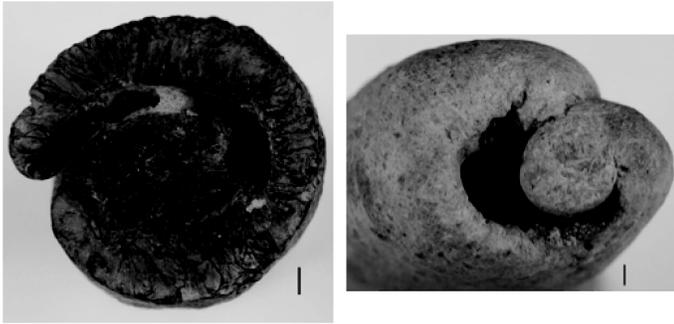


FIGURE 5. **Left**, Cross-sectional view of a broken scroll coprolite showing the spiral configuration. Scale bar = 1 mm. **Right**, End view of a scroll coprolite illustrating the whorl produced by the scroll valvular intestine. Scale bar = 1 mm.

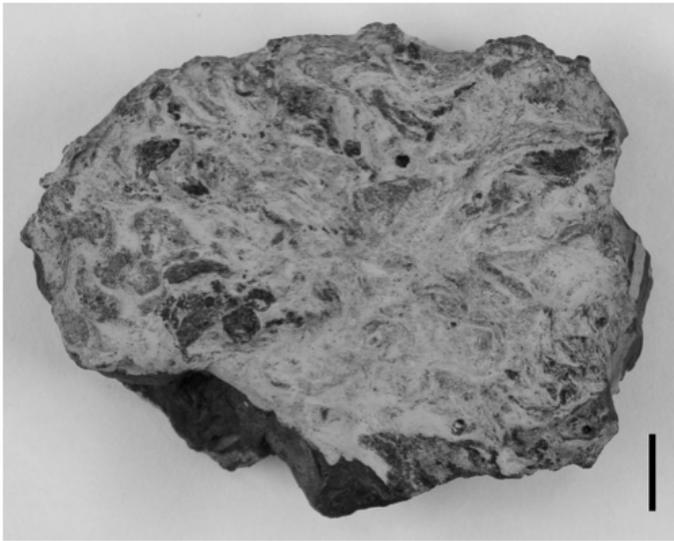


FIGURE 6. Specimen of an indeterminate (amorphous) coprolite from the late Eocene Yazoo Clay. Scale bar = 5 mm.

examined as possible components in the shark coprolites. Bone (modern and ancient from an archeological site) and apatite scans were obtained to provide comparisons of the degree of crystallization in the coprolites.

X-ray analysis of coprolites is important for several reasons. Chin (2002) noted that carnivore coprolites are usually easily differentiated from herbivore coprolites because they are typically phosphatic and often contain skeletal inclusions. Many other researchers such as Dietrich (1951), Edwards (1973), Hallgren (1987), and Northwood (2005) have pointed out that the presence of a high proportion of phosphate has been used as evidence that coprolites were produced by a carnivore. Hollocher et al. (2005) investigated the chemistry, mineralogy, and mineralization of Triassic coprolites from Argentina and noted that the presence of bone fragments and crystalline apatite was a confirmation of carnivore source animal. X-ray analysis supplies evidence for the composition of the coprolite and can indicate if the source animal was a carnivore, such as a shark. X-ray analysis of the coprolite and the surrounding matrix can also provide evidence that the coprolite is not being affected by the chemical composition of the matrix. In other words, the composition of the coprolite is related to the diet of the source animal and not the composition of the surrounding sediment.

Hallgren (1987) conducted extensive infrared spectroscopic analysis of fossil coprolites that provides relevant data to this study of late Eocene shark coprolites. Hallgren noted that carnivores frequently ingest the bones of their prey and that bone is 85% water, fat, and other organics. The remaining 10-15% of the bone is inorganic calcium, phos-

phate, or carbonate. This inorganic material has chemical and physical properties that are very similar to the mineral apatite. In many carnivorous animals, the digested mass is dewatered, formed into semi-solid feces, and excreted. Bacteria and other organisms usually attack the remaining organic matter. The only material left is phosphate and calcium carbonate. Hallgren also found that chemically intact carbonates and apatite in a coprolite are preserved and that the mineral apatite in a coprolite is convincing evidence of a bone-eating animal. His research also indicated that the composition of carnivore coprolites was extremely similar in chemical composition regardless of age and locality. Experimentation with modern feces in freshwater and saltwater by Johnson and Varricchio (2007) also showed that there was substantial preservation bias for bone-bearing feces.

LITERATURE REVIEW

The primary purpose of this literature review is to investigate references specific to coprolites produced by chondrichthyans, not to review coprolites in general. As noted in the introduction, research on shark coprolites from the marine environment is quite restricted and inadequate. Therefore, the resulting reports and literature are sparse, and when information on shark coprolites is present in many publications, it is typically very brief. This is evident in several of the following reviews. It should also be noted that publications that described chondrichthyan coprolites but attributed them to some other source animal are also included. In the review of literature related to chondrichthyan coprolites, the term “fish” often had different meanings. The term “fish” is frequently used to describe all gill-bearing, aquatic lower vertebrates and includes agnathans, ostracoderms, placoderms, chondrichthyans, acanthodians, and actinopterygians. However in some publications (especially older ones), fish was used only for actinopterygians or bony fishes. It was often necessary to verify the parameters of the term to ensure that it included chondrichthyans.

Gideon Mantell, famous for his early dinosaur discoveries in England, discussed and illustrated Cretaceous spiral coprolites (which were probably shark in origin) in an 1822 publication. However, he did not correctly recognize them as excretion and identified them as “aments or cones of unknown vegetables.” William Buckland (1829) was probably the first scientist to actually recognize coprolites as fecal material and to use the term “coprolite.” Buckland read two papers to the Geological Society of London in 1829. In the second letter, he remarked, “the faeces of terrestrial and aquatic carnivorous animals have been preserved; and proposes to include them all under the generic name of Coprolite” (Folk, 1965; Pemberton and Frey, 1991). He was also probably the first person to relate certain coprolites to sharks. In his studies of the coprolites from the Lias at Lyme Regis in England, Buckland noted that the most abundant type was spiral in shape and resembled the intestines of sharks and rays. Most of the line drawings of Buckland’s coprolites, such as the ones on plate 28, clearly illustrated spiral coprolites, but at least one (fig. 8) appeared to be a scroll type (Fig. 7). Buckland’s illustrations have been reproduced in many subsequent studies on coprolites, such as Hantzschel et al. (1968), Stewart (1978), Chin (1994), and King (2002).

Buckland made casts of modern elasmobranch intestines using cement (Buckland, 1829, pl. 31, figs. 19, 20, 21, 22), but for some reason, he attributed most of the coprolites to ichthyosaurs (Buckland, 1841). This is particularly perplexing since the casts of the shark and skate intestines were so similar to the coprolites, especially the cast of the skate intestine (fig. 22), which appears almost identical to the heteropolar coprolites. It is also interesting to note that Buckland included information from Agassiz (1838) in his 1841 publication. Regarding the Early Jurassic coprolites from the Lyme Regis in England, Agassiz remarked that the specimens were “either the petrified intestines of fishes or the contents of their intestines.” Agassiz referred to them as cololites. Mantell is also included in Buckland (1841) where he reassigned his “aments or cones of unknown vegetables” (spiral coprolites) to sharks. Mantell

TABLE 1. Results of the detailed description of the shark coprolites in the randomly selected sample.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-1	48.65	15.5	12.19	2.44	10YR 4/2 Dark yellowish brown	Deep scroll marks	Wx	Scroll
C-2	42.3	20.15	12.16	3.04	5Y 4/1 Olive gray	Deep scroll marks	Wx	Scroll
C-3	19.8	11.4	3.01	3.01	5YR 5/2 Pale brown	Distinct folds	Wx	Scroll
C-4	16.1	7.80	1.67	1.48(A)	10YR 6/2 Pale yellowish orange	Ex. twist marks	N/A	Spiral
C-5	12.2	9.60	1.44	1.48(A)	10YR 8/2 Very pale brown	Ex. twist marks	Wx	Spiral
C-6	11.2	8.50	1.33	1.48(A)	10YR 4/2 Dark ye lowish brown	Wx	Wx	Spiral
C-7	20.75	13.35	4.60	2.50	N2 Grayish black (int) 5YR 3/2 Grayish brown	N/A Ex. folds	Glassy Wx	Scroll
						folds		
						folds		
C-11	10.8	6.50	2.35	2.30	10YR 6/2 Pale yellowish brown	Wx	N/A	Spiral
C-12	19.3	6.05	1.25	2.54(A)	10YR 8/2 Very pale brown	Very wx	N/A	Spiral
C-13	12.0	6.00	0.65	2.54(A)	5Y 2/1 Olive black	Very wx	Wx	Scroll
C-14	11.9	5.65	0.64	2.54(A)	10YR 4/2 Dark yellowish brown (int) N2 Grayish black	N/A Very wx	Glassy N/A	Spiral
C-15	25.0	8.50	2.93	1.47	5Y 2/1 Olive black	Ex. twist marks	Wx	Spiral
C-15	23.65	9.25	2.89	1.45	5YR 3/2 Grayish brown	Ex. twist marks	Wx	Spiral
C-17	19.7	7.50	2.22	2.22	5YR 3/2 Dusky brown	Ex. twist marks	Wx	Spiral
C-18	35.3	8.50	4.44	2.22	5YR 2/2 Dusky brown	Ex. twist marks	Wx	Spiral
C-19	26.0	13.20	2.53	1.27	10YR 4/2 Dark ye lowish brown	Distinct folds	Ex. Folds	Scroll
C-20	33.5	7.70	3.81	1.91	5YR 5/2 Pale brown	Ex. twist marks	Wx	Spiral
C-21	61.8	17.1	22.51	2.5	10YR 8/2 Very pale orange 10YR 4/2 Dark yellowish brown (int)	Ex. folds N/A	Ex. Folds Glassy	Scroll
C-22	28.0	8.00	2.90	1.45	N1 Black	Pitted marks	N/A	Spiral
C-23	28.1	16.0	2.03	2.02	N4 Medium dark gray	Wx	N/A	Indeterminate
C-24	28.9	7.10	2.76	2.76	5YR 3/2 Grayish brown	Ex. twist marks	N/A	Spiral
C-25	36.7	8.40	2.9	2.9	10YR 8/2 Very pale orange	Deep twist marks	N/A	Spiral
C-26	18.25	8.80	2.23	2.33	5B 5/1 Medium bluish gray	Deep twist marks	Wx	Spiral
C-27	23.7	9.20	2.89	2.89	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
C-28	21.8	7.00	1.97	1.97	10YR 8/2 Very pale orange	Deep twist marks	N/A	Spiral
C-29	16.5	10.65	1.76	1.76	N2 Grayish black	Wx	Wx	Scroll
C-30	30	29.2	5.61	2.81	10YR 8/2 Very pale orange	Wx	Good folds	Scroll
C-31	20	7.90	1.98	1.98	10YR 2/2 Dusky yellowish brown	Wx	N/A	Spiral
C-32	21.25	8.40	2.15	2.15	10YR 6/2 Pale yellowish brown 5YR 3/2 Grayish brown (int)	Wx N/A	Good folds Glassy	Spiral

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-33	30.1	12.15	4.17	2.09	10YR 5/4 Medium yellowish brown	W/x	N/A	Seroll
C-34	18.5	14.0	2.24	2.24	5Y 8/1 Yellowish gray	W/x	W/x	Seroll
C-35	24.45	7.7	1.36	1.36	5YR 4/1 Brownish gray	W/x	W/x	Seroll
C-36	19.1	12.8	4.32	2.88	5Y 8/1 Yellowish gray	W/x	W/x	Seroll
					5YR 3/2 Grayish brown (int)	N/A	Glassy	
C-37	23.5	10.0	2.28	2.28	5B 5/1 Medium bluish gray	W/x	N/A	Seroll
C-37	23.5	10.0	2.28	2.28	5B 5/1 Medium bluish gray	W/x	N/A	Seroll
C-38	23.4	7.80	1.67	1.67	10YR 4/2 Dars yellowish brown	W/x	N/A	Seroll
C-39	18.5	8.10	1.80	1.80	10YR 4/2 Dars yellowish brown	W/x	N/A	Seroll
C-40	24.4	10.00	3.63	2.42	10YR 8/2 Very pale orange	W/x	W/x	Seroll
C-41	24.35	7.55	2.31	2.31	5Y 8/4 Grayish yellow	W/x	N/A	Seroll
C-42	30.2	9.80	3.31	1.66	10YR 6/2 Pale yellowish brown	Deep grooves	Good folds	Seroll
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-43	35.3	9.1	3.54	1.77	10YR 6/2 Pale yellowish brown	Folds	W/x	Seroll
C-44	24.4	9.4	3.7	1.85	5Y 8/1 Yellowish gray	Groove twists	W/x	Spinal
C-45	35	11.9	4.23	2.16	5YR 3/2 Grayish brown	Excellent folds	W/x	Seroll
C-46	30.2	12	4.02	2.01	10YR 8/2 Very pale orange	Deep grooves	Et Folds	Seroll
C-47	33.8	8.2	3.32	1.66	10YR 6/2 Pale yellowish brown	Valve impression	N/A	Seroll
C-48	21	8.3	3.14	2.09	10YR 6/2 Pale yellowish brown	Ex. twist marks	W/x	Spinal
C-49	45.3	11.3	7.02	2.34	5YR 2/1 Brownish black	Smooth	Et Folds	Seroll
C-50	50.8	15	15.45	3.09	10YR 6/2 Pale yellowish brown	Excellent Folds	Double folds	Seroll
C-51	56.9	15.3	20.12	2.24	10YR 8/2 Very pale orange	Excellent Folds	W/x	Seroll
C-52	7.40	4.45	0.17	2.79(A)	5B 7/1 Light bluish gray	W/x	W/x	Spinal
C-53	10.8	4.50	0.35	2.79(A)	N6 Medium light gray	W/x	W/x	Seroll
C-54	7.35	8.10	0.58	2.79(A)	10YR 8/2 Very pale orange	W/x	N/A	Spinal
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-55	17.6	7.60	0.60	2.79(A)	5Y 8/1 Yellowish gray	W/x	W/x	Seroll
C-56	10.65	6.10	0.76	2.79(A)	N2 Grayish black	W/x	W/x	Spinal
C-57	26.1	7.50	3.03	2.79(A)	10YR 6/2 Pale yellowish brown	Deep twist marks	N/A	Spinal
C-58	12.5	4.10	0.35	2.25(A)	N9 White	W/x	N/A	Indeterminate
					5YR 6/1 Light brownish gray (int)	N/A	Glassy	
C-59	22.15	9.60	1.64	2.25(A)	5YR 6/1 Light brownish gray	Good folds	W/x	Seroll
C-60	13.7	7.00	1.09	2.25(A)	5YR 6/1 Light brownish gray	W/x	W/x	Spinal
C-61	16.3	8.70	1.57	2.25(A)	5YR 6/1 Light brownish gray	W/x	W/x	Spinal
C-62	22.8	6.50	1.51	2.25(A)	5YR 5/2 Pale brown	Good twist marks	N/A	Spinal
C-63	20.0	6.80	2.04	2.27(A)	5YR 2/1 Brownish black	W/x	N/A	Spinal

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-64	23.4	7	2.03	2.27(A)	10YR 4/2 Dark yellowish brown	Wx	Wx	Spiral
C-65	30.7	6.6	1.37	2.27(A)	10YR 4/2 Dark yellowish brown	Wx	N/A	Scroll
C-66	19.05	7.15	1.33	2.27(A)	10YR 6/2 Pale yellowish brown	Very wx	Wx	Spiral
C-67	18.5	7.4	1.33	2.09(A)	10YR 8/2 Very pale orange	Good twist marks	N/A	Spiral
C-68	21.2	8	1.3	2.09(A)	N3 Dark gray	Wx	N/A	Spiral
C-69	10.7	8.6	0.49	2.09(A)	10YR 8/2 Very pale orange	Wx	Wx	Scroll
C-70	15.5	8.1	1.03	2.09(A)	10YR 2/2 Dusky yellowish brown	Wx	N/A	Scroll
C-71	18.8	7.9	1.09	2.09(A)	10YR 4/2 Dark yellowish brown	Good folds	N/A	Scroll
C-72	13.8	5	0.47	2.09(A)	10YR 4/2 Dark yellowish brown	Very wx	N/A	Spiral
C-73	6.9	7.8	0.39	1.94(A)	5E 7/1 Light bluish gray	Very wx	Wx	Scroll
C-74	14.2	4.5	0.43	1.94(A)	10YR 6/2 Pale yellowish brown	Wx	N/A	Spiral
C-75	12.3	6.6	0.65	1.94(A)	10YR 2/2 Dusky yellowish brown	Wx	N/A	Spiral
C-76	13.3	5.8	0.69	1.94(A)	10YR 4/2 Dark yellowish brown	Wx	N/A	Spiral
C-77	10.4	6.4	0.34	1.94(A)	5Y 8/4 Grayish yellow	Very wx	N/A	Indeterminate
C-78	10.4	4	0.35	1.94(A)	5B 9/1 Bluish white	Wx	N/A	Spiral
C-79	42.2	12.9	6.02	3.01	10YR 4/2 Dark yellowish brown	Excellent folds	N/A	Scroll
C-80	37.9	8.2	4.01	2.67	5YR 4/1 Brownish gray	Good twist marks	N/A	Spiral
C-81	29.8	8.1	2.72	2.31(A)	5YR 3/2 Grayish brown	Wx	N/A	Spiral
C-82	15.6	8.1	1.85	2.31(A)	5YR 3/2 Grayish brown	Wx	Wx	Spiral
C-83	18	7.3	1.22	2.31(A)	5YR 3/2 Grayish brown	Wx	N/A	Spiral
C-84	29.6	7.6	3.02	3.02	10YR 4/2 Dark yellowish brown	Good twist marks	N/A	Scroll
C-85	25.7	9.6	3.15	3.16	N4 Medium dark gray	Excellent folds	Good folds	Scroll
C-86	25.1	7.3	1.77	2.07(A)	5YR 3/2 Grayish brown	Wx	N/A	Spiral
C-87	22.8	7.3	1.75	2.07(A)	5YR 3/2 Grayish brown	Wx	Wx	Spiral
C-88	18.4	7.2	1.44	2.07(A)	5YR 5/2 Pale brown	Wx	Wx	Spiral
C-89	25	5.6	1.24	2.07(A)	5YR 5/2 Pale brown	Wx	N/A	Spiral
C-90	15.1	8.1	1.05	2.61(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
					5B 6/2 Pale blue (int)	N/A	Glossy	
C-91	15	8	1.3	2.61(A)	10YR 7/4 Grayish orange	Wx	Wx	Spiral
C-92	15.3	6.6	0.97	2.61(A)	5YR 2/2 Dusky brown	Wx	N/A	Spiral
C-93	14.8	7.3	1.05	2.61(A)	5YR 2/2 Dusky brown	Wx	Wx	Spiral
C-94	19.6	6.3	0.82	2.61(A)	5YR 2/2 Dusky brown	Wx	Wx	Spiral
C-95	15.4	7	1.02	2.54(A)	5B 5/2 Grayish blue	Wx	Wx	Spiral
C-96	14.8	5.8	0.63	2.54(A)	5YR 6/1 Light brownish gray	Wx	N/A	Spiral
C-97	14	4.8	0.43	2.54(A)	N2 Grayish black	Wx	N/A	Spiral
C-98	10.7	4.8	0.19	2.54(A)	5YR 3/4 Moderate brown	Very wx	N/A	Scroll

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External/unless noted)	External Features	Internal Features	Morphological Type
C-99	6.7	4.5	0.22	2.54(A)	10YR 8/2 Very pale orange	Wx	Good folds	Spiral
C-100	43.8	22.2	20.64	2.58	5Y 8/4 Grayish yellow	Wx	Layered	Scroll
C-101	22.3	24.3	7.61	2.54	10YR 8/2 Very pale orange	Very wx	Good folds	Scroll
C-102	56.1	22.5	28.09	2.55	5Y 8/1 Yellowish gray	Ex. condition	Excellent folds	Scroll
C-103	38.5	15.1	7.42	2.47	5Y 8/1 Yellowish gray	Excellent folds	Good folds	Scroll
C-104	42.8	14.3	10.35	2.07	10YR 7/4 Grayish orange	Ex. impression	Good folds	Scroll
					10YR 5/4 Med. yellowish brown (int)	N/A	Glassy	
C-105	52.9	14.9	5.44	2.72	5Y 8/1 Yellowish gray	Wx	Good folds	Scroll
C-106	28.8	14	6.85	2.28	10YR 6/2 Pale yellowish brown	Wx	Excellent folds	Scroll
					5YR 3/2 Grayish brown (int)	N/A	Glassy	
C-107	25.4	12.8	3.24	3.24	5YR 3/2 Grayish brown	Wx	Wx	Scroll
C-108	31.1	14	4.84	2.42	5YR 2/2 Dusky brown	Wx	Wx	Scroll
C-109	28.4	11.9	3.4	2.14(A)	5YR 5/2 Pale brown	Good folds	N/A	Scroll
C-110	21.3	9.9	2.16	2.14(A)	5PB 5/2 Grayish blue	Wx	N/A	Scroll
C-111	26.1	8.4	2.06	2.14(A)	10YR 4/2 Darks yellowish brown	Good folds	N/A	Scroll
C-112	26.8	16.1	7.84	2.61	5Y 8/1 Yellowish gray	Wx	Good folds	Scroll
					5YR 5/2 Pale brown (int)	N/A	Glassy	
C-113	21.4	8	1.69	2.46(A)	5Y 8/1 Yellowish gray	Wx	Excellent folds	Spiral
					N1 Black (int)	N/A	Glassy	
C-114	21.7	7.2	1.7	2.46(A)	N2 Grayish black	Ex. impressions	Wx	Spiral
					10YR 7/4 Grayish orange (int)	N/A	Glassy	
C-115	22.3	9.3	1.48	2.46(A)	5Y 8/1 Yellowish gray	Wx	Good folds	Scroll
C-116	17.2	11.7	2.41	2.46(A)	5Y 8/1 Yellowish gray	Wx	Distinct folds	Scroll
					5YR 4/1 Brownish gray (int)	N/A	Glassy	
C-117	25.1	7.3	2.11	2.46(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
C-118	7.5	7	0.46	2.46(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
					N1 Black (int)	N/A	Glassy	
C-119	18	5.7	0.99	2.09(A)	10YR 6/2 Pale yellowish brown	Wx	N/A	Spiral
C-120	12.5	3.5	0.27	2.09(A)	5Y 8/1 Yellowish gray	Wx	Wx	Spiral
C-121	11.6	6.7	0.71	2.09(A)	N1 Black	Very wx	Wx	Spiral
C-122	13.1	7.5	1.13	2.09(A)	10YR 7/4 Grayish orange	Excellent twists	N/A	Spiral
C-123	9.7	6.3	0.4	2.09(A)	10YR 8/2 Very pale orange	Wx	Wx	Spiral
C-124	16.6	5.3	0.68	2.09(A)	10YR 6/2 Pale yellowish brown	Wx	Wx	Spiral
C-125	16.6	6.3	0.89	1.64(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
C-126	10.4	6.1	0.52	1.64(A)	5B 5/1 Medium bluish gray	Wx	N/A	Spiral
C-127	17	3.5	0.37	1.64(A)	10YR 8/2 Very pale orange	Wx	N/A	Indeterminate

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell/Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-128	15.7	6.1	0.94	1.64(A)	N9 White	W/x	N/A	Spiral
C-129	17.8	5.1	0.59	1.64(A)	10YR 8/2 Very pale orange	W/x	W/x	Scroll
C-130	17.6	4.1	0.55	2.18(A)	N7 Light gray	W/x	N/A	Spiral
C-131	15.5	4.7	0.49	2.18(A)	N7 Light gray	W/x	N/A	Indeterminate
C-132	13.1	4.7	0.37	2.18(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-133	13.9	6.3	0.53	2.18(A)	5B 5/1 Medium bluish gray	W/x	N/A	Scroll
C-134	12.3	3.8	0.24	2.18(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-135	11.6	4.9	0.32	1.37(A)	N9 White	W/x	W/x	Spiral
C-136	12.6	1.2	0.39	1.37(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-137	18.2	3.65	0.39	1.37(A)	10YR 8/2 Very pale orange	W/x	N/A	Scroll
C-138	10.7	5	0.44	1.37(A)	10YR 8/2 Very pale orange	W/x	N/A	Spiral
C-139	15.9	5.5	0.43	1.37(A)	10YR 7/2 Grayish orange	Very w/x	N/A	Scroll
C-140	2.3	5.5	0.75	1.37(A)	10YR 8/6 Pale yellowish orange	W/x	N/A	Scroll
C-141	15.1	6.2	0.54	2.05(A)	5PB 5/2 Grayish blue	W/x	N/A	Scroll
C-142	11.9	4.8	0.45	2.05(A)	5PB 5/2 Grayish blue	W/x	N/A	Scroll
C-143	13.9	5	0.39	2.05(A)	5Y 8/1 Yellowish gray	W/x	N/A	Indeterminate
C-144	14.8	4.8	0.43	2.05(A)	5Y 8/1 Yellowish gray	W/x	W/x	Indeterminate
C-145	10.6	4.2	0.21	2.05(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-146	17.1	6.4	0.45	1.71(A)	10YR 6/2 Pale yellowish brown	Very w/x	N/A	Scroll
C-147	11.4	4.9	0.4	1.71(A)	N7 Light gray	W/x	N/A	Spiral
C-148	15.7	4	0.39	1.71(A)	5Y 2.8/1 Light bluish gray	W/x	N/A	Scroll
C-149	12.5	3.8	0.25	1.71(A)	5Y 3.8/1 Light bluish gray	W/x	N/A	Spiral
C-150	9.7	4	0.22	1.71(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-151	7.4	4.3	0.22	1.07(A)	10YR 8/2 Very pale orange	W/x	N/A	Spiral
C-152	14.7	3.5	0.22	1.07(A)	10YR 8/2 Very pale orange	W/x	N/A	Spiral
C-153	14.1	4.45	0.25	1.07(A)	5Y 8/1 Yellowish gray	W/x	N/A	Scroll
C-154	14.4	3.5	0.21	1.07(A)	N8 Very light gray	W/x	N/A	Spiral
C-155	10.3	3.2	0.15	1.07(A)	N8 Very light gray	W/x	N/A	Spiral
C-156	8.5	3.5	0.15	0.97(A)	5Y 3.8/1 Light bluish gray	W/x	N/A	Spiral
C-157	10.5	3.5	0.2	0.97(A)	5Y 3.8/1 Light bluish gray	W/x	N/A	Spiral
C-158	11.6	2.9	0.15	0.97(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-159	7.3	4	0.17	0.97(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-160	11	2.7	0.07	0.97(A)	5Y 3.8/1 Light bluish gray	W/x	N/A	Spiral
C-161	13.4	2.9	0.12	0.97(A)	5Y 3.8/1 Light bluish gray	W/x	N/A	Spiral
C-162	10.8	2.8	0.07	0.97(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spiral
C-163	8.2	2.1	0.03	0.97(A)	5Y 6/1 Light brownish gray	W/x	N/A	Scroll

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-164	21.1	14.2	3.8	1.9	10YR 6/2 Pale yellowish brown	Distinct folcs	N/A	Scroll
C-165	22.8	15.5	3.01	2.06	5B 5/1 Medium bluish gray	Distinct folcs	N/A	Scroll
C-166	13.3	10	1.23	1.55(A)	10YR 8/2 Very pale orange	W/x	Very nice folds	Scroll
					5YR 7/2 Grayish brown (int)	N/A	Glassy	
C-167	13.1	8.7	1.16	1.65(A)	5B 6/2 Pale blue	W/x	N/A	Scroll
C-168	11.5	9.4	0.91	1.65(A)	10YR 8/2 Very pale orange	W/x	N/A	Spinal
					10YR 5/4 Med. yellow brown (int)	N/A	Glassy	
C-169	20.2	6.9	0.88	2.49(A)	5PB 5/2 Grayish blue	Very wx	N/A	Scroll
C-170	14.4	8.1	0.62	2.49(A)	5YR 3/2 Grayish brown	Very wx	W/x	Scroll
C-171	12.5	9.7	1.6	2.49(A)	5PB 5/2 Grayish blue	W/x	W/x	Scroll
C-172	17.5	8.5	1.78	2.49(A)	5Y 8/1 Yellowish gray	W/x	W/x	Scroll
C-173	13.9	10.7	1.19	1.93(A)	10YR 6/2 Pale yellowish brown	W/x	W/x	Scroll
C-174	14.8	8.5	0.84	1.93(A)	10YR 8/2 Very pale orange	W/x	W/x	Scroll
C-175	13.6	9	1.11	1.93(A)	5B 5/1 Medium bluish gray	W/x	W/x	Scroll
C-176	21.3	7.7	1.69	1.93(A)	5B 7/1 Light bluish gray	Very wx	N/A	Spinal
C-177	34.2	7.4	1.6	1.55(A)	5Y 8/1 Yellowish gray	W/x	N/A	Scroll
C-178	12	7.5	0.65	1.55(A)	5Y 8/1 Yellowish gray	Excellent folds	N/A	Scroll
C-179	15.1	9	1.5	1.55(A)	5Y 8/1 Yellowish gray	Very wx	W/x	Spinal
C-180	18.1	9.4	1.28	1.55(A)	10YR 6/2 Pale yellowish brown	Very wx	N/A	Scroll
C-181	20.5	7.8	1.22	1.55(A)	10YR 6/2 Pale yellowish brown	Very wx	N/A	Indeterminate
C-182	18.3	7.1	0.93	1.95(A)	N4 Medium dark gray	Very wx	N/A	Indeterminate
C-183	15.1	7.3	0.92	1.95(A)	5Y 8/1 Yellowish gray	W/x	N/A	Scroll
C-184	10.4	7.5	0.68	1.95(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spinal
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-185	10	5.8	0.57	1.95(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spinal
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-186	16.7	7.5	0.93	1.95(A)	5Y 8/1 Yellowish gray	W/x	N/A	Spinal
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-187	19.6	8	1.82	1.95(A)	5B 5/1 Medium bluish gray	Excellent twists	N/A	Spinal
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-188	18.5	8.3	1.25	2.52(A)	5B 5/1 Medium bluish gray	Very wx	N/A	Spinal
C-189	17.7	6.1	0.72	2.52(A)	5Y 8/1 Yellowish gray	W/x	N/A	Scroll
C-190	15.7	9.8	0.97	2.52(A)	5Y 8/1 Yellowish gray	W/x	N/A	Scroll
C-191	19	6.8	1.42	2.52(A)	10YR 8/2 Very pale orange	W/x	N/A	Spinal
C-192	13.5	7.5	0.68	2.52(A)	5B 6/2 Pale blue	W/x	N/A	Scroll
C-193	15.5	6.3	0.9	2.25(A)	10YR 4/2 Dark yellowish brown	W/x	N/A	Spinal

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-194	9.2	6.7	0.51	2.25(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
C-195	20.3	5.9	0.84	2.25(A)	5B 7/1 Light bluish gray	Distinct folds	N/A	Scroll
C-196	18.5	7.2	1.05	2.25(A)	5B 7/1 Light bluish gray	Wx	N/A	Indeterminate
C-197	17	6.5	0.64	2.25(A)	5B 7/1 Light bluish gray	Wx	N/A	Scroll
C-198	15.3	6	0.55	2.25(A)	5B 5/1 Medium bluish gray	Wx	N/A	Scroll
C-199	6.8	8.8	0.53	2.13(A)	5Y 8/1 Yellowish gray (ext)	Wx	N/A	Spiral
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-200	15	7.8	0.87	2.13(A)	5Y 8/1 Yellowish gray	Nice folds	N/A	Scroll
C-201	11.4	5.2	0.29	2.13(A)	5Y 8/1 Yellowish gray	Very wx	N/A	Indeterminate
C-202	16.4	9	0.99	2.13(A)	5Y 8/1 Yellowish gray	Good impression	Wx	Scroll
C-203	16.4	6	0.63	2.13(A)	N3 Very light gray	Flattened and wx	N/A	Spiral
C-204	14.45	5.4	0.44	2.13(A)	5Y 8/1 Yellowish gray	Very wx	N/A	Spiral
C-205	8.9	6.8	0.5	2.13(A)	5Y 8/1 Yellowish gray (ext)	Wx	Glassy	Spiral
					10YR 4/2 Dark yellowish brown (int)			
						N/A	Glassy	
C-206	12.2	6.4	0.49	1.55(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
C-207	7.4	4.7	0.2	1.55(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
C-208	13.4	6.5	0.54	1.55(A)	5Y 8/1 Yellowish gray	Wx	N/A	Scroll
C-209	13.5	6.1	0.47	1.55(A)	5Y 8/1 Yellowish gray	Wx	Good folds	Scroll
C-210	13.6	6.9	0.75	1.55(A)	N9 White	Wx	N/A	Spiral
					5YR 4/1 Brownish gray (int)	N/A	Glassy	
C-211	9	4.3	0.23	1.55(A)	N1 Black	Wx	N/A	Indeterminate
C-212	8	6.2	0.42	1.55(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
					5YR 5/2 Pale brown (int)	N/A	Glassy	
C-213	8.6	6.1	0.33	2.02(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-214	8.35	5.1	0.22	2.02(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-215	17.75	6.1	0.46	2.02(A)	5Y 8/1 Yellowish gray	Wx	N/A	Scroll
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-216	7.9	5.9	0.4	2.02(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-217	8.5	5.9	0.2	2.02(A)	5Y 8/1 Yellowish gray	Wx	N/A	Scroll
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-218	8.3	4.6	0.28	2.02(A)	5Y 8/1 Yellowish gray	Wx	N/A	Spiral
					5YR 2/1 Brownish black (int)	N/A	Glassy	

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-219	9	2.9	0.13	2.02(A)	5E 7/1 Light bluish gray	W/x	N/A	Spiral
C-220	43	15.3	11.89	2.38	10YR 6/2 Pale yellowish brown	Good folds	N/A	Scroll
C-221	46.8	21.6	25.05	2.51	5PB 5/2 Grayish blue	Excellent folds	N/A	Scroll
C-222	40.8	22	18.4	3.07	10YR 6/2 Pale yellowish brown	Excellent folds	Excellent folds	Scroll
C-223	35.2	25.1	13.25	2.65	10YR 8/2 Very pale orange	Good folds	Excellent folds	Scroll
C-224	28.8	17.9	8.51	2.13	10YR 6/2 Pale yellowish brown	Good folds	Excellent folds	Scroll
C-225	31.5	17.4	7.5	2.5	10YR 8/2 Very pale orange	W/x	Excellent folds	Scroll
C-226	37.4	17.7	10.2	2.55	10YR 8/2 Very pale orange	W/x	Excellent folds	Scroll
C-227	40.85	23	17.12	2.85	10Y 8/2 Pale greenish yellow	Excellent folds	Excellent folds	Scroll
C-228	27.85	19.4	16.15	2.88	5E 7/1 Light bluish gray	W/x	N/A	Scroll
C-229	34.6	19.3	9.85	2.46	5Y 8/1 Yellowish gray	W/x	Excellent folds	Scroll
C-230	30.9	12.4	4.63	2.32	5Y 8/1 Yellowish gray	Distinct folds	Excellent folds	Scroll
C-231	38.5	13.5	4.64	2.32	5Y 8/1 Yellowish gray	Distinct folds	Excellent folds	Scroll
C-232	33.4	15.4	5.16	2.58	5B 5/1 Medium bluish gray	Distinct folds	Excellent folds	Scroll
C-233	32.4	15.1	6.48	2.16	5B 3/1 Medium bluish gray	Distinct folds	W/x	Scroll
C-234	29	17.5	8.27	2.07	5Y 8/1 Yellowish gray	W/x	W/x	Scroll
C-235	38.7	17.2	5.59	2.8	5Y 8/1 Yellowish gray	Good folds	W/x	Scroll
C-236	36.6	16.1	9.4	3.13	5B 5/1 Medium bluish gray	Good folds	Good folds	Scroll
C-237	33.4	16.5	7.68	2.56	5B 7/1 Light bluish gray	W/x	W/x	Scroll
C-238	27.3	16.8	6.29	3.15	5B 7/1 Light bluish gray	W/x	N/A	Scroll
C-239	31.7	19.5	7.4	2.47	5YR 4/1 Brownish gray	W/x	Good folds	Scroll
C-240	32.8	15.1	5.17	2.59	5B 7/1 Light bluish gray	W/x	Good folds	Scroll
C-241	29.5	10	1.34	1.34	5B 7/1 Light bluish gray	W/x	W/x	Scroll
C-242	48.1	26.4	19.39	3.23	10YR 6/2 Pale yellowish brown	Deformation	N/A	Scroll
C-243	32.5	18.4	5.41	2.71	10YR 6/2 Pale yellowish brown	Deformation	N/A	Scroll
C-244	36	24.4	13.94	2.79	10YR 6/2 Pale yellowish brown	Deformation	Ganoid scale	Scroll
C-245	19.2	15.85	3.91	1.96	5Y 8/1 Yellowish gray	W/x	N/A	Scroll
C-246	22.9	25.2	3.39	2.26	5Y 8/1 Yellowish gray	Deformed	N/A	Scroll
C-247	41.9	16.8	7.54	2.51	10YR 6/6 Dark yellowish orange	W/x	N/A	Scroll
C-248	22.4	21.4	4.81	2.41	5Y 8/1 Yellowish gray	Flattened	W/x	Scroll
C-249	33.7	14.5	4.76	2.38	5Y 8/4 Grayish yellow	W/x	W/x	Scroll
C-250	38.5	19.7	7.85	2.62	5YR 5/2 Pale brown	Very w/x	W/x	Scroll
C-251	28.9	20.6	8.55	2.85	5B 5/1 Medium bluish gray	Partial w/x	N/A	Scroll
C-252	20.7	10.9	2.69	1.79	10YR 8/2 Very pale orange	W/x	Good folds	Scroll
					5YR 2/2 Dusky brown (int)	N/A	Glassy	
C-253	29.2	5.7	3.06	3.06	10YR 8/2 Very pale orange	W/x	N/A	Spiral

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-254	47	17.1	8.19	2.05	5YR 2/2 Dusky brown (int) 5B 7/1 Light bluish gray 5YR 2/2 Dusky brown (int)	N/A Very wt N/A	Glassy N/A Glassy	Spiral
C-255	25.35	17.2	4.94	2.47	10YR 8/2 Very pale orange	Wx	Wx	Scroll
C-256	23.4	12.5	2.69	2.69	5B 5/1 Medium bluish gray	Wx	Wx	Scroll
C-257	30.5	16.85	4.51	2.26	5B 5/1 Medium bluish gray	Wx	Wx	Scroll
C-258	18.5	11	1.43	1.43	10YR 8/2 Very pale orange	Wx	Wx	Scroll
C-259	22.3	12.3	2.83	2.83	5B 5/1 Medium bluish gray	Wx	N/A	Scroll
C-260	28.5	10.7	3.79	2.53	5B 5/1 Medium bluish gray	Wx	N/A	Scroll
C-261	22.3	10.2	1.57	1.57	5B 5/1 Medium bluish gray	Wx	N/A	Scroll
C-262	27.6	12.6	5.88	1.94	10YR 8/2 Very pale orange	Wx	N/A	Scroll
C-263	14.8	7.8	1.61	2.84(A)	10YR 8/2 Very pale orange 10YR 4/2 Dark yellow brown (int)	Wx N/A	Good folds Glassy	Scroll
C-264	17.35	17.1	1.89	2.84(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
C-265	21.4	11.6	2.18	2.84(A)	10YR 8/2 Very pale orange 10YR 4/2 Dark yellow brown (int)	Wx N/A	Good folds Glassy	Scroll
C-266	18	9.5	1.33	2.20(A)	5B 5/1 Medium bluish gray	Wx	Wx	Scroll
C-267	13.8	8.8	1.29	2.20(A)	10YR 8/2 Very pale orange	Wx	Wx	Scroll
C-268	17.1	9	1.78	2.20(A)	5B 5/1 Medium bluish gray	Wx	Wx	Scroll
C-269	21.85	9.2	1.93	2.72(A)	5B 6/2 Pale blue	Very wt	N/A	Spiral
C-270	14.8	8.1	1.47	2.72(A)	5YR 4/1 Brownish gray	Faint twist marks	N/A	Spiral
C-271	15.2	7.1	1.06	2.72(A)	5Y 8/1 Yellowish gray	Very wt	N/A	Spiral
C-272	22.3	7.8	0.98	2.72(A)	5B 6/2 Pale blue	Very wt	N/A	Spiral
C-273	40.2	13.5	8.66	2.89	10YR 8/2 Very pale orange	Good folds	Wx	Scroll
C-274	12.8	17.3	3.21	1.61	10YR 6/2 Pale yellowish brown	Wx	Distinct folds	Scroll
C-275	23.5	12.4	3.4	1.7	5B 5/1 Medium bluish gray	Very wt	Wx	Scroll
C-276	26.4	9	2.25	2.81(A)	10YR 8/6 Pale yellowish orange	Excellent folds	Excellent folds	Scroll
C-277	31.2	10.3	2.43	2.81(A)	5B 9/1 Bluish white	Good folds	N/A	Scroll
C-278	26.4	11.8	2.21	2.81(A)	10YR 6/6 Dark yellowish orange	Very wt	Wx	Scroll
C-279	14.4	12.8	1.54	2.81(A)	5B 7/1 Light bluish gray	Very wt	Wx	Scroll
C-280	24.4	11.7	4.19	2.1	N6 Medium light gray	Nice folds	Wx	Scroll
C-281	30.5	8.5	2.54	2.54	10YR 8/2 Very pale orange	Wx	N/A	Scroll
C-282	33.8	18.1	10.52	2.58	N6 Medium light gray	Wx	Distinct folds	Scroll
C-283	26.6	13.9	3.37	1.69	N6 Medium light gray	Wx	N/A	Scroll
C-284	23.1	11.8	1.45	2.31(A)	10YR 6/6 Dark yellowish orange	Very wt	N/A	Indeterminate
C-285	15.6	7.6	1.45	2.31(A)	5Y 2/1 Olive black	Smooth	N/A	Spiral

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
					N1 Black (int)	N/A	Glassy	
C-286	22.8	8.2	1.72	2.31(A)	5B 5/1 Medium bluish gray	W/x	N/A	Scroll
C-287	28.4	13.8	3.62	1.81	5Y 8/1 Yellowish gray	Good folds	Good folds	Scroll
C-288	27.1	14.2	4.07	2.04	5Y 8/1 Yellowish gray	W/x	Excellent folds	Scroll
C-289	25.6	14	4.86	2.43	5B 5/1 Medium bluish gray	W/x	Excellent folds	Scroll
C-290	24	11.3	3.25	1.73	N6 Medium light gray	W/x	N/A	Scroll
C-291	44	14.2	7.45	2.48	N6 Medium light gray	Excellent folds	Excellent folds	Scroll
C-292	29.5	12.6	2.95	1.97	5Y 8/1 Yellowish gray	Good folds	W/x	Scroll
C-293	17.5	8	1.67	2.25(A)	5B 9/1 Bluish white	W/x	N/A	Scroll
C-294	7.5	9.8	0.53	2.25(A)	5Y 6/1 Light olive gray	W/x	N/A	Scroll
					10YR 4/2 Dark yellow brown (int)	N/A	Glassy	
C-295	26.8	12.8	2.97	1.98	5Y 8/4 Grayish yellow	W/x	N/A	Scroll
C-296	29.3	14	5.34	2.67	5B 3/1 Medium bluish gray	W/x	N/A	Scroll
C-297	10	8.9	1.17	2.82(A)	N9 White (ext)	W/x	N/A	Spiral
					5YE 2/2 Dusky brown (int)	N/A	Glassy	
C-298	18.3	12	2.69	2.82(A)	10YR 6/2 Pale yellowish brown	W/x	Good folds	Scroll
C-299	18.1	11.35	1.77	2.82(A)	10YR 6/2 Pale yellowish brown	Excellent folds	Excellent folds	Scroll
C-300	13	11.6	1.07	1.75(A)	5PB 3/2 Dusky blue	W/x	W/x	Scroll
C-301	10.1	9.0	0.89	1.75(A)	5B 9/1 Bluish white	W/x	W/x	Scroll
C-302	12.05	9.7	0.67	1.75(A)	5B 9/1 Bluish white	W/x	W/x	Scroll
C-303	6.35	9.9	0.49	3.01(A)	5YR 2/2 Dusky brown	W/x	W/x	Scroll
C-304	14.2	15	2.83	3.01(A)	5B 5/1 Medium bluish gray	Very w/x	W/x	Scroll
C-305	11.8	7.2	0.53	3.01(A)	5B 5/1 Medium bluish gray	W/x	W/x	Scroll
C-306	11.2	9.5	1.27	3.01(A)	5B 9/1 Bluish white	W/x	N/A	Spiral
					5YR 2/2 Dusky brown (int)	N/A	Glassy	
C-307	9.1	8.5	0.84	3.01(A)	5B 5/1 Medium bluish gray	W/x	W/x	Spiral
					5YE 2/2 Dusky brown (int)		Glassy	
C-308	33.4	15.3	6.27	3.14	5B 5/1 Medium bluish gray	Good folds	N/A	Scroll
					5YE 2/2 Dusky brown (int)		Glassy	
C-309	32.3	12.1	3.85	1.93	5YR 2/2 Dusky brown (int)	W/x	N/A	Scroll
					10YR 4/2 Dark yellow brown (int)	N/A	Glassy	
C-310	27.4	12.5	3.94	1.97	5B 9/1 Bluish white	Excellent folds	N/A	Scroll
					5YE 2/2 Dusky brown (int)		Glassy	
C-311	34.2	18.2	7.09	2.55	10YR 8/2 Very pale orange	W/x	Good folds	Scroll
					5YR 3/2 Grayish brown (int)	N/A	Dull glassy	
C-312	24	9.9	2.94	1.96	5B 9/1 Bluish white	W/x	N/A	Spiral

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-313	13.2	16.1	1.75	1.75	5YR 3/2 Grayish brown (int) 10YR 8/2 Very pale orange 5YR 3/2 Grayish brown (int)	N/A Wx N/A	Dull glassy N/A Dull glassy	Scroll
C-314	23	9.2	3.04	1.52	5Y 8/1 Yellowish gray 5YR 2/1 Brownish black (int)	Wx N/A	N/A Very glassy	Spiral
C-315	20.1	7.1	1.53	2.14(A)	5B 9/1 Bluish white	Wx	N/A	Spiral
C-316	32.6	6.2	1.79	2.14(A)	5B 9/1 Bluish white	Wx	N/A	Spiral
C-317	20.8	6.5	1.03	2.14(A)	5B 5/1 Medium bluish gray	Wx	N/A	Spiral
C-318	26.8	10.6	3.25	1.63	5YR 3/2 Grayish brown	Wx	N/A	Spiral
C-319	21.9	7.1	1.25	2.26(A)	5B 9/1 Bluish white	Wx	N/A	Spiral
C-320	23.2	6.6	1.44	2.26(A)	5YR 3/2 Grayish brown (int) 5Y 8/1 Yellowish gray	N/A Wx	Glassy N/A	Spiral
C-321	22.4	7.6	1.85	2.26(A)	5YR 3/2 Grayish brown (int)	N/A	Glassy	Spiral
C-322	25.6	7.8	1.52	2.16(A)	5B 7/1 Light bluish gray	Wx	N/A	Spiral
C-323	26.75	8.1	2.49	2.16(A)	5B 5/1 Medium bluish gray	Wx	N/A	Spiral
C-324	24.3	9.3	2.43	2.16(A)	5B 9/1 Bluish white	Wx	N/A	Spiral
C-325	31	7.5	2.15	1.90(A)	5B 9/1 Bluish white	Good twist marks Wx	N/A	Spiral
C-326	23	6.85	1.45	1.90(A)	5B 5/1 Medium bluish gray	Wx	N/A	Spiral
C-327	20.55	7.95	1.43	1.90(A)	5B 5/1 Medium bluish gray	Wx	Cycloid scale	Spiral
C-328	16.25	5.6	0.63	1.90(A)	5B 5/1 Medium bluish gray	Wx	N/A	Spiral
C-329	21.1	4.4	0.71	2.51(A)	10YR 8/2 Very pale orange	Very wx	N/A	Spiral
C-330	20.6	8.6	1.63	2.51(A)	10YR 8/6 Pale yellowish orange	Very wx	Wx	Spiral
C-331	16	8	1.15	2.51(A)	5B 5/1 Medium bluish gray	Wx	N/A	Spiral
C-332	17.4	8.1	1.47	2.51(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
C-333	22.3	5.5	1.13	2.74(A)	10YR 8/2 Very pale orange	Wx	N/A	Spiral
C-334	18.6	7.8	1.45	2.74(A)	10YR 6/2 Pale yellowish brown	Very wx	N/A	Spiral
C-335	22.05	6.5	1.07	2.74(A)	5B 7/1 Light bluish gray	Wx	N/A	Spiral
C-336	20.2	3.8	0.31	2.74(A)	5B 8/2 Very pale blue	Wx	N/A	Spiral
C-337	29.5	12.3	6.33	2.11	10YR 6/2 Pale yellowish brown	Excellent folds	N/A	Scroll
C-338	23	12.7	4.07	2.04	10YR 4/2 Dark yellowish brown	Wx	Wx	Scroll
C-339	25.6	8.45	2.23	1.93(A)	10YR 8/2 Very pale orange	Wx	Good folds	Scroll
C-340	23.4	8.45	1.5	1.93(A)	5YR 5/2 Pale brown	Ex. impressions	N/A	Scroll
C-341	27.8	11.1	2.43	1.93(A)	5B 3/1 Medium bluish gray	Wx	Good folds	Scroll
C-342	17.8	9.4	1.56	1.93(A)	10YR 4/2 Dark yellow brown (int) 5B 3/1 Medium bluish gray	N/A Wx	Glassy Wx	Scroll

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-343	44.3	13.9	10.55	2.64	5B 5/1 Medium bluish gray	Excellent folds	Good folds	Scroll
C-344	30.5	9.6	3.87	1.79	5B 9/1 Bluish white 10YR 2/2 Dusky yellow brown (int)	Wx N/A	N/A Glassy	Spiral
C-345	23.7	9.1	3.1	2.07	5B 7/1 Light bluish gray	Ex. twist marks	N/A	Spiral
C-346	26.9	9.4	3.15	2.1	5YR 4/1 Brownish gray	Ex. folds	N/A	Scroll
C-347	46.1	13.3	9.31	2.33	5B 5/1 Medium bluish gray	Wx	Good folds	Scroll
C-348	56.9	19.6	21.18	2.65	10YR 4/2 Dark yellowish brown	Good folds	Excellent folds	Scroll
C-349	54.4	17.1	15.12	2.52	10YR 4/2 Dark yellowish orange	Good folds	Excellent folds	Scroll
C-350	70.5	17	25.02	2.5	10YR 8/2 Very pale orange	Excellent folds	N/A	Scroll
C-351	61	20.3	28.86	2.41	10YR 8/2 Very pale orange	Good folds	Excellent folds	Scroll
C-352	23.1	8.05	2.08	1.39	10YR 6/2 Pale yellowish brown	Excellent twists	Wx	Spiral
C-353	12.3	7.85	0.68	2.30(A)	5YR 2/1 Brownish black	Wx	N/A	Spiral
					5YR 2/2 Dusky brown (int)	N/A	Glassy	
C-354	11.8	7.00	0.6	2.30(A)	10YR 3/4 Moderate yellow brown	Wx	Wx	Spiral
C-355	16.5	6	1.10	2.30(A)	5Y 7/2 Yellowish gray	Wx	Wx	Spiral
C-356	16.45	7.4	1.51	2.30(A)	10YR 4/2 Dark yellowish brown	N/A	Wx	Spiral
C-357	11.35	5.3	0.71	2.30(A)	10YR 5/4 Moderate yellow brown	Wx	N/A	Spiral
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-358	12.3	5.1	0.82	2.12(A)	10YR 5/4 Moderate yellow brown	Wx	N/A	Spiral
C-359	15.05	5.8	0.82	2.12(A)	10YR 6/2 Pale yellowish brown	Good twist marks	N/A	Spiral
C-360	21.4	17.25	1.94	2.12(A)	10YR 8/2 Very pale orange	Impressive	Fold striations	Scroll
C-361	23.5	10	2.58	2.12(A)	5YR 3/2 Grayish brown	Grooves/folds	N/A	Scroll
C-362	7.75	4.85	0.20	2.12(A)	10YR 2/2 Dusky yellowish brown	Small folds	N/A	Scroll
C-363	31.4	18.1	12.65	2.53	5YR 2/1 Brownish black	Deep folds	N/A	Scroll
C-364	12.7	6.85	0.96	2.44(A)	5YR 2/1 Brownish black	Deep grooves	N/A	Spiral
C-365	20.3	5.9	1.16	2.44(A)	5YR 2/2 Dusky brown	Distinct folds	Distinct folds	Scroll
					5YR 2/2 Dusky brown (int)	N/A	Glassy	
C-366	18	8.3	2.04	2.44(A)	10YR 2/2 Dusky yellowish brown	Mottled	N/A	Spiral
C-367	20.1	8	2.73	2.44(A)	10YR 7/4 Grayish orange	Ex. spiral twists	N/A	Spiral
C-368	9.2	4.8	0.44	2.14(A)	10YR 4/2 Dark yellowish brown	Wx	N/A	Spiral
					N1 Black (int)	N/A	Glassy	
C-369	10.3	11.35	0.61	2.14(A)	5YR 2/1 Brownish black	Wx	N/A	Indeterminate
					5YR 2/1 Brownish black (int)	N/A	Glassy	
C-370	22.4	5.7	0.74	2.14(A)	10YR 7/4 Grayish orange	Very wx	Wx	Spiral
C-371	7.3	4.6	0.25	2.14(A)	N1 Black	Wx	N/A	Spiral
C-372	23.3	7.6	1.93	2.14(A)	5PB 5/2 Grayish blue	Wx	N/A	Spiral

TABLE 1. Continued.

Specimen Number	Max. Length (mm)	Max. Width (mm)	Weight (grams)	Density (g/cc)	Coloration (Munsell Color Chart) (External unless noted)	External Features	Internal Features	Morphological Type
C-373	11.9	4.2	0.50	2.14(A)	5PB 5.2 Grayish blue (int)	N/A	N/A	Spiral
C-374	11.6	7.2	0.86	2.14(A)	NE Medium dark gray 5Y 2/1 Olive black	Wx Wx	Glossy N/A	Spiral Spiral

Explanation of tables:

1. The table columns consist of the maximum length, maximum width, weight, density, coloration, external features, internal features and morphological type for each of the 374 randomly selected coprolites. Table rows represent the descriptive data of the individual coprolites. The sample represents approximately 30% of the total coprolites in the study.
2. Under the column labeled as "Density," the symbol (A) denotes that the specimen's density was an average. For further details, please see "Classification of coprolites and detailed description phase" in the "Methodology" section of this paper.
3. Under the column labeled as "Coloration," color is based on the predominant color of the coprolite specimen compared to the Munsell Rock-Color Chart (GSA, 1991). The color is for the external view of the coprolite unless noted by (int), which indicates the color is for the internal view.
4. Under the columns "External Features" and "Internal Features," the following abbreviations are used:
 - a. "Ex" = excellent; referring to a feature in unusually good condition.
 - b. "Wx" = weathered; referring to a specimen that has been weathered or eroded, and features have been adversely affected.

stated, "may have been derived from fishes of the Shark family (*Ptychodus*) whose large palatal teeth . . . abound in the same localities of the chalk formation with them, at Steyning and Hamsey, England."

One of the earliest accounts of coprolites, if not the earliest, in the United States that may be related to sharks is that of Dekay (1830). Dekay collected a spiral-shaped coprolite from an unspecified locality in the Cretaceous of New Jersey (pl. 3, fig. 6). Williams, in his 1972 publication, believed that the specimen was probably from the Navesink Formation. Dekay actually reported the find to Buckland in England via a letter. When Buckland replied, the two letters were combined and published in the *Philosophical Magazine* in 1830. Lea (1843) presented different coprolites to the American Philosophical Society in an attempt to generate interest in them. Some of them were spiral in nature and may have been spiral shark coprolites.

Permian coprolites assigned to a "scavenger fish or amphibian" were described by Germar in 1840 (p. 30-32). The coprolites were glossy black, spindle-shaped, and quite large (10 to 20 cm long and 2-3 cm wide). In his lengthy discourse on geology and organic remains, Mantell (1844) once again addressed shark and fish coprolites. He described coprolites with convolutions and noted the microscopic impression of mucous or lining of the intestines on the specimens (p. 650-656). He also reported the presence of minute bones and scales of fishes in the coprolites. He stated that this provided evidence of the carnivorous habits of the fish that produced the coprolites.

Two Cretaceous coprolites identified as belonging to fish were reported by Dixon (1850). The coprolites were described as elongate with spiral convolutions (fig. 33). The same year, Wyman (1850) reported that spiral coprolites of enormous size had been known for a long time in the Miocene of Virginia. He also noted that rolled cylindrical bodies of rather amorphous structures were very suggestive of fossil fish excrement that were occasionally found at several localities in the Eocene of Maryland and Virginia. Wyman was also quoted in the classic work of Clark and Martin (1901) on the Eocene deposits of Maryland. However, there are no illustrations or further discussion on the coprolites.

Two short articles in a Russian bulletin dealing with probable shark coprolites were published by Kiprijanoff (1852, 1854). The first article was on Cretaceous coprolites from the Ural and Kursk provinces in Russia. In the article, several of the specimens appear to be heteropolar and amphipolar coprolites from sharks. A second article by Kiprijanoff (1854) suggested that the coprolites were saurian in nature. However, Häntzschel et al. (1968) attributed the coprolites to sharks (probably either *Otodus* or *Ptychodus*). Fraas (1891), in his study of ichthyosaurs, proposed that the coprolites attributed to these marine reptiles were actually produced by sharks. He noted that the coprolites were rare in the sediments where the ichthyosaurs were most abundant. He pointed out that most of the coprolites, especially the spiral or twisted forms, were probably produced by selachians (p. 34). He commented that spiral coprolites were common in the German Muschelkalk, which ranged in age from Anisian to Ladinian.

In a study of the Paleogene and Cretaceous formations of Kansas, Mudge (1876) noted the fairly common occurrence of vertebrate coprolites ("frequently found"), commented on their inclusions ("small fish appear to be the most common food"), and attributed them to fish and reptiles (p. 217). Mudge's comments are believed to be one of the earliest documentations of coprolites from the Smoky Hills Chalk in the Cretaceous of Kansas (Everhart, 2007). Many of the coprolites to which Mudge referred are believed to have been chondrichthyan in origin. A few years later in an extensive study of the Pranhita Godavari Valley in India, King (1881) made reference to abundant coprolites, which are believed to have included shark. King was describing the Maleri Formation when he stated, "The commonest remains are coprolites which lie about the field in large numbers, of all sizes and shapes . . ." King's report would lead to further studies on the coprolites of the Maleri Formation by other researchers.

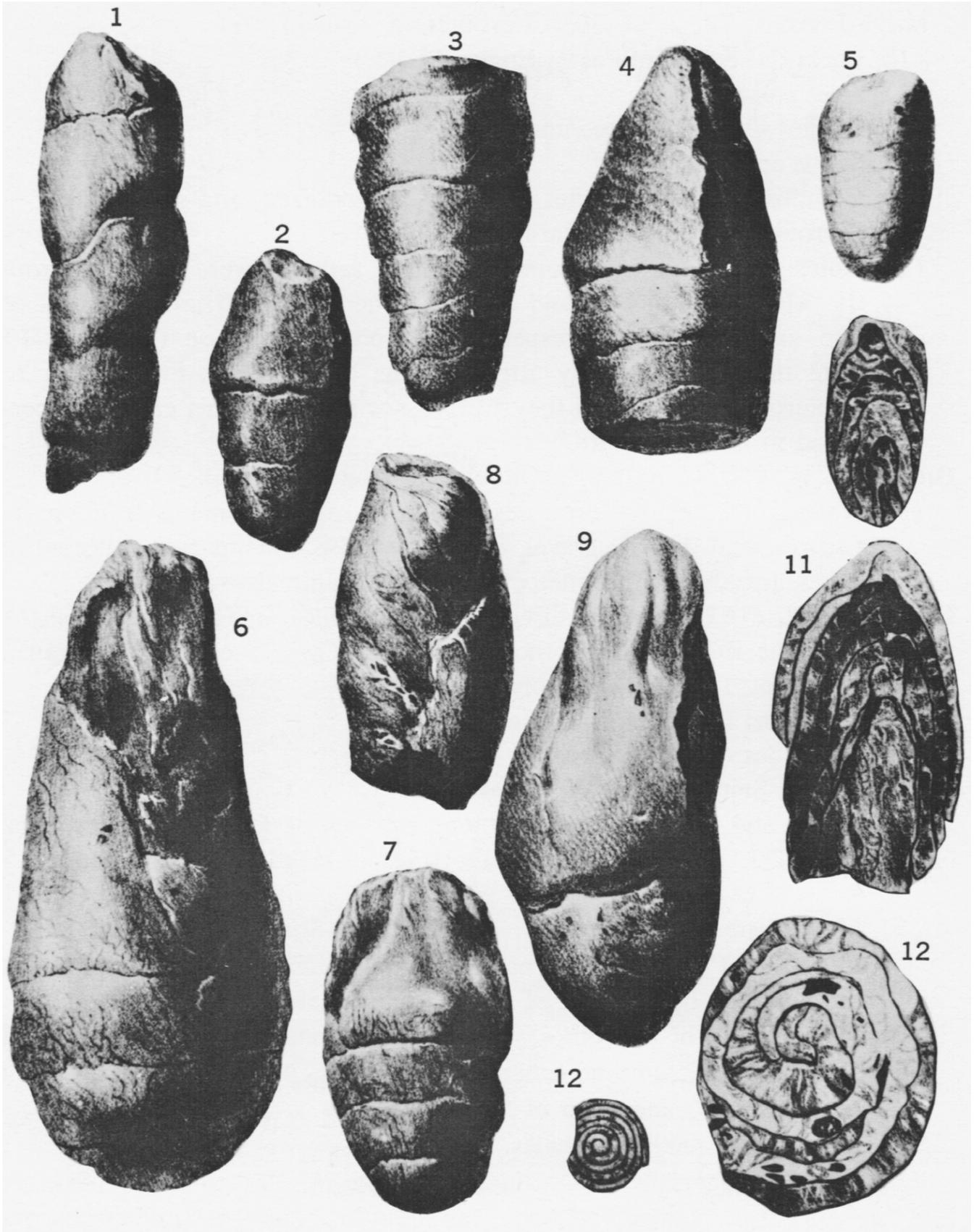


FIGURE 7. Coprolites and sections of coprolites from the Lias at Lyme Regis, England (from Buckland, 1829, plate 28). No scale was given on the original plate.

A new cladodont shark, *Cladoselache newberryi*, was reported from the Waverly Formation in Ohio by Dean (1893). He remarked that a well-preserved coprolite was observed in the visceral region of the shark. He contended that the coprolite furnished a cast of the intestinal wall and provided definite evidence as to the presence of a spiral valve in sharks (p. 117). Although the figure of the coprolite is not very good, it appears to have six spirals. The coprolite was also noted as being quite small in comparison to the rest of the shark.

Fritsch (1895, 1907, 1910) contributed three papers that are related to shark coprolites. In his 1895 paper, he proposed that spiral coprolites were not excreted fecal material. Fritsch had some amazingly well-preserved specimens of freshwater sharks such as *Xenacanthus* from the Lower Permian of the Czech Republic. In these specimens, the spiral valve was preserved in its natural position and was identical to many of the fossils that had been identified as coprolites. Therefore, he contended that many of the spiral coprolites were not "excrement of fishes" but the spiral-valved intestine filled with fecal matter (natural casts of the spiral valves). Since the spiral coprolites were not excreted material, he introduced the term enterospira for the fossilized spiral intestinal valve with its contained fecal material. Williams (1972) believed that Fritsch was the first paleontologist to suggest that spiral coprolites represented fossilized spiral valves of sharks. Williams also noted that the term enterospira could be applied for fecal material fossilized in the spiral intestinal valve. Fritsch published another paper in 1910 on Late Cretaceous coprolites from Czechoslovakia. Two coprolites were shown in figures 4 and 5. Coprolite A was 7 cm long and had about 20 lobate folds, while coprolite B was only 2.5 cm long with 3 to 5 turns. Fritsch believed that the source animals for the coprolites were sharks.

Etheridge (1904) reported on coprolites from the Cretaceous of South Australia. He figured them on plate 14 of his publication, and numbers 1-3 seem to be heteropolar shark coprolites. However, the other specimens do not appear to be coprolites. Also in 1904, Hoernes reviewed the literature on coprolites, including chondrichthyans, prior to the 1900's. He proposed that if the fossil represents fecal material in the spiral-valved intestine, then use the term enterolites. He had observed this preservation in fossil selachians. Hoernes also proposed that the term coprolites should be used strictly for fossil feces.

Woodward (1917) contended that the well-known, spirally coiled coprolites of the Lyme Regis in England were produced by sharks such as *Hybodus* and *Acrodus* rather than by ichthyosaurs to which they had been attributed. As evidence of the relationship of the spiral valve to sharks, Woodward included a picture of the ventral view of the shark *Cladoselache clarki* (Upper Devonian of Ohio) that showed the intestine with a spiral fecal mass in the pelvic region. Fraas (1894) had also indicated that he believed sharks, rather than ichthyosaurs, produced the spiral coprolites. Woodward (1917) is considered one of the first publications with definitive links between spiral coprolites and sharks (Gilmore, 1992).

There were several coprolite studies beginning in the early 20th century that were related to sharks although it was not evident at the time of their publication. Neumayer (1904) published his well-known paper on the spiral coprolites from the Permian of Texas, and he coined the terms heteropolar and amphipolar, which were to become quite popular in later coprolite studies. Heteropolar had a fairly large number of closely spaced spiral turns on one end of the coprolite. Amphipolar had a much smaller number of widely spaced spiral turns that extended the entire length of the coprolite. Neumayer followed the lead of Fritsch (1895, 1907) and also suggested that the spiral coprolites were fossilized fecal material in the spiral intestinal valves and had not been excreted.

Stauffer and Schroyer (1920), Case (1922), and Price (1927) published studies that were concerned primarily with spiral coprolites from the Pennsylvanian, Permian, and Triassic. Several of these studies included large numbers of coprolite specimens including spiral coprolites. For example, Price (1927) studied over 1000 coprolite specimens from

the Upper Pennsylvanian of West Virginia. He reported that heteropolar and amphipolar coprolites were present in the large collection of specimens. Price stated that the heteropolar spiral coprolites were not as numerous and contended that they were produced by sharks.

A few years after the study of Price (1927), Johnson (1934) provided information on a large number of similar specimens from a coprolite horizon in the Pennsylvanian of Colorado. Johnson recounted collecting several thousand coprolites from black shales at several localities in Chaffee and Park counties. He reported several different types of coprolites, and 14 were figured (p. 478). He stated that most were flattened, and many showed a definite spiral coil structure. He differentiated between spiral coprolites that had three to five coils and those with a larger number of closely-spaced coils. Johnson believed that sharks produced the spiral coprolites with the large number of closely spaced coils.

Abel (1935) described Cretaceous coprolites from England and Germany and assigned their origin to shark or fish. The description of the specimens was part of a chapter that included coprolites of other vertebrates and invertebrates. Abel discussed the spiral valves present in the elasmobranchs and its relationship to coprolites. Augusta (1938), in a brief article, also reported Cretaceous coprolites from the Kladno area of the Czech Republic. He noted a meter-thick layer that was composed of over 80% fish coprolites. The coprolites measured up to four cm in length, and their composition was reported as collophanite, which is a cryptocrystalline variety of apatite.

Triassic spiral coprolites from the Maleri Formation of India were studied by Matley (1939a, b). The abundance of spiral coprolites in this formation had been addressed previously by King (1881). Matley described 17 spiral coprolites in detail and noted that most of his specimens were from 5.0 to 5.5 cm in length except for one, which was 7.4 cm long. Matley reported that Hughes had collected 16 of the coprolites in 1876 with one other specimen added to the collection at a later date. The Matley study influenced a subsequent study by Jain (1983). Sharks were mentioned as the source animal, but the studies indicated it was quite inconclusive.

Wetmore (1943) briefly described the occurrence of bird feather impressions in a coprolite found near Parker's Creek (cited as the north end of Scientist's Cliffs) in the Miocene deposits in the cliffs along Chesapeake Bay in Maryland (p. 441). The coprolite was described as roughly rounded, but it was broken (noted as a fragment of a coprolite). The size was approximately 6.0 cm with one side flattened and both ends broken. Wetmore believed the coprolite to have come from some type of large fish or crocodile. Unfortunately, there were no illustrations or pictures of the coprolite. However, the coprolite is presently being re-examined and studied by Karen Chin, Curator of Paleontology at the University of Colorado Museum; Stephen Godfrey, Curator of Paleontology at the Calvert Marine Museum; and Carl Mehling, Division of Paleontology at the American Museum of Natural History (S. Godfrey, personal commun., July, 2011).

In 1947, Rusconi published a brief paper on Triassic and Permian coprolites from the Mendoza area in Argentina. The emphasis was on reptilian coprolites, but there were also spiral coprolites present (figs. 1-4). In a more extensive paper on the same area, Rusconi (1949) illustrated spiral forms (figs. 2-4) as well as small, cylindrical forms (fig. 5). The Triassic sample contained a larger number of coprolites and was dominated by the spiral forms. As noted by Hunt et al. (2007), the spiral coprolites appear to be dominantly heteropolar (the first two coprolites in the first row of fig. 4 of Rusconi, 1949) although a few may be amphipolar (the bottom left coprolite in fig. 2 of Rusconi, 1949). The source animals of these coprolites appear to be chondrichthyan.

In a brief paper in 1951, Dietrich noted that since calcium phosphate was the main component of bone, then the compound is expected to be associated with coprolites of carnivorous vertebrates, which would include sharks. Langston (1953), in a study of Permian amphibians, mentioned that spiral coprolites were common in the shales of Welles Quarry (Permian, El Cobre Canyon Formation) in north-central New

Mexico. These coprolites, which were probably chondrichthyan in origin, were extensively studied by Hunt et al. (2005). A thorough review of the literature on coprolites, including chondrichthyan coprolites, was published by Amstutz (1958), and is often cited. A decade later, Amstutz was a co-author of another definitive study on coprolites (an annotated bibliography) that discussed sharks (Häntzschel et al., 1968).

Studies such as Moran and Romer (1952), Romer (1958), and Vaughn (1963) included information, although often brief, on spiral coprolites. For example, Romer (1958) described the vertebrates from the Permian redbeds in Texas, and he reported on the occurrence of spiral coprolites in the redbeds. The spiral coprolites in many of these studies were attributed to a wide variety of organisms (such as amphibians), but it appears now that many of them were produced by chondrichthyans such as the freshwater shark *Pleuracanthus*. Matthews (1962) alluded to the external markings of shark coprolites such as grooves and spirals. He noted that these external features gave evidence of unusual characteristics of the alimentary tract of the animal making them. He figured a coprolite on p. 27, but it was not of a chondrichthyan.

Extensive coverage of shark coprolites was included in the extensive paleoecological study of two Pennsylvanian black shales in Indiana by Zangerl and Richardson in 1963. Coprolites were covered on numerous pages, illustrated in several figures (29, 32, 35, 36), and pictured in several plates (46-50). The two authors recognized three basic coprolite forms, but the spiral coprolites were probably the most significant. The spiral coprolites were almost always found preserved in three dimensions with no substantial flattening, which is quite rare since the surrounding rock was shale. Inclusions in the coprolites included various types of teeth, scales, spine fragments, and bone pieces. Most of the inclusions were from primitive fish and sharks. The source animal for the spiral coprolites was believed to be a shark (no specific genera were mentioned). A few years later, Case (1967) pictured two coprolite specimens from the Cretaceous Navesink Formation of New Jersey. Case assigned the specimens to bony fish, but they appear to be shark coprolites (also noted by Williams, 1972).

Häntzschel et al. (1968) completed one of the most comprehensive reviews of coprolites. They gathered more than 376 bibliographic notes of coprolites from invertebrates and vertebrates. This study included discussion of shark coprolites as well as numerous illustrations and has become one of the most quoted references on coprolites in the literature. Häntzschel et al. (1968) proposed that there was no advantage in restricting the term coprolite to larger excrements such as that of chondrichthyans, reptiles, and mammals (p. 1-3). He used the term small coprolites or fecal pellets and noted that these fossils were generally less than 5 mm in length and diameter. This is unusual since El-Baz in the same year (1968) stated that there were strong criteria that supported restricting the use of coprolites to fossilized fecal remains of vertebrates, including selachians, and that these remains were normally between 1 mm and 20 cm (p. 526). El-Baz suggested that invertebrate fecal remains (usually smaller than 1 mm) should be fecal pellets, and when fossilized, fossil fecal pellets. He also noted that it was feasible to classify coprolites according to shape, size, color, and composition.

Olson (1971), in his extensive coverage of the paleozoology of vertebrates, briefly discussed coprolites on pages 134-135. He noted that some feature of the source animal may be stamped on the coprolite and used the spiral valve in the intestines of sharks as an example. He also pointed out that coprolite origins could possibly be determined by processes of association and elimination based on the vertebrate fauna. One of the most influential studies on spiral shark coprolites was published a year later in 1972 by Michael Williams at the University of Kansas (The Origin of "Spiral" Coprolites). He analyzed 38 more or less complete spiral coprolite specimens (heteropolar in the sense of Neumayer, 1904) as well as numerous fragments from the Lower Permian from Kansas (plate 1, p. 11). In addition, he studied coprolites from several other locations and prepared 200 thin sections from 19 spiral coprolites. He also prepared and analyzed histological slides of the spiral

valve in the common dogfish. Williams concluded that the Permian spiral coprolites from Kansas were fossilized spiral valves or enterospirae rather than coprolites that had been excreted. He attributed the enterospirae to pleuracanth sharks, but he noted that many of the spiral coprolites previously described in other works could be true coprolites. Although Williams' study concentrated on Permian heteropolar spiral enterospirae attributed to pleuracanth sharks, the influence of his research had far-reaching effects on many subsequent coprolite papers.

Case (1973) figured three spiral shark coprolites from the Cretaceous of New Jersey (figs. 256 and 257). The caption with the figures noted that shark coprolites are distinctive in that they have a twisting pattern caused by the spiral valve and that the pattern corresponds directly to the action of the fecal material as it passes through the spiral valve. The statement is partially true, but not all coprolites have spiral twists as some have folds. Case (1975, p. 8, pl. 1, fig. 14) illustrated five shark coprolites from the Eocene Twiggs Clay in central Georgia. The photographs are quite good as is the preservation of the coprolites. The caption reads, "Shark coprolites (fecal pellets)." The shark coprolite specimens are significant to this study because they are similar in age to the Yazoo Clay, which is also Eocene. The long, slender coprolite on the far left appears to be a spiral coprolite. The other four coprolites are scroll coprolites. Ochev (1974) published a brief paper on Triassic vertebrate coprolites from Guryev area in the Ukraine in the Paleontological Journal, the principal Russian periodical in paleontology. He compared the coprolites to those described by Case (1922) from the Triassic of Texas. Included in this brief paper are small, heteropolar coprolites with three to four coils forming less than one-half of the length (fig. 1a, p. 254). These coprolites were later identified as *Heteropolacopros* by Hunt et al. (1998) and attributed to a xenacanth shark or possibly a lungfish.

Broughton et al. (1978) reported the occurrence of tens of thousands of coprolites of vertebrate origin from the Whitemud Formation (Late Cretaceous) exposures in south-central Saskatchewan, Canada. It is very intriguing that many of the coprolites are described as spiral or helicoidal. The possibility of activity among the larger elasmobranchs was mentioned for the origin of the coprolites. However, there are many factors that would discount chondrichthyans as the source animal. First and most importantly, the shape and structures of the coprolites certainly do not appear to be that of sharks, as numerous pictures of the coprolites, and their morphology do not match spiral shark coprolites (p. 447, pl. 43). There is also the issue of preservation of the coprolites, which was noted as well preserved by the authors, but the coprolites have gone through several stages of replacement. The original fecal matter was first replaced by siderite and pyrite. Then, several limonitic minerals replaced this composition. The Whitemud Formation is also considered non-marine in origin. The authors reconsidered the source animals and decided that chondrosteans (sturgeons) or holosteans (bowfins) may account for the coprolites of the Whitemud rather than elasmobranchs. Ash (1978) presented a brief study of spiral coprolites from the Upper Triassic Chinle Group in western New Mexico. The coprolites were believed to have been deposited in a Late Triassic lake. There is the possibility that some of the coprolites were related to freshwater sharks (actually demonstrated in later studies of the Chinle). However, Ash stated that several different and unspecified groups and sizes of organisms probably produced the spiral coprolites.

Stewart (1978) described enterospirae of sharks from the Upper Cretaceous Niobrara Formation of western Kansas and figured them (p. 11, fig. 4). He utilized gross morphology and the microscopic study of thin sections to identify the coprolites as having the same nature as the enterospirae of Williams (1972). Stewart recognized five categories of enterospirae and tentatively assigned them to a small, undescribed selachian. He noted that articulated vertebrate remains were present in the formation. Stewart also stated that teleosts and reptiles are not known to have spiral intestinal valves. Duffin (1979), in a brief review of coprolites and coprolite specimens from the Rhaetic bone-beds of England and

South Wales, also confirmed the lack of spiral-valved intestines in marine reptiles.

Numerous specimens of vertebrate coprolites were reported from the Upper Triassic Maleri Formation in central India by Sohn and Chatterjee (1979). They reported vertebrate coprolite specimens of varying shapes including spheroid, ovoid, ellipsoidal, and spirally coiled. The authors associated the coprolites with fish, amphibians, and reptiles in the formation. Freshwater ostracodes were fortuitously found in the coprolites and were released from the coprolitic matrix by the use of formic acid. The ostracodes were utilized to interpret paleoenvironmental conditions in central India during the Late Triassic. Case, in his *Pictorial Guide to Fossils* (1982), illustrated a well-preserved specimen of a spiral shark coprolite from the Cretaceous of New Jersey (fig. 24-111, p. 258), but as is often the case, there is little discussion to accompany the picture.

Following the study of the Upper Triassic Maleri Formation in India by Sohn and Chatterjee (1979), Jain (1983) conducted a study on the same formation, but he limited his study only to the spirally coiled and cylindrical coprolites. Jain noted that only the Maleri Formation had spirally-coiled coprolites related to fish when compared to other Mesozoic localities in India. The freshwater shark *Xenacanthus* was reported from the Maleri Formation at the site. Jain used heteropolar (type A) and amphipolar (type B) morphological types for his identification of the coprolites (p. 815, fig. 2). He emphasized that amphipolar was characterized by a relatively small number of widely-spaced spiral turns extending the length of the specimen. He also thought that many of the flattened cylindrical coprolites were related to types A and B. His study consisted of 43 specimens (21 identified as amphipolar and 9 as heteropolar). His study included thin sections and the identification of inclusions such as fish scales. Jain noted that the internal features (transverse sections) of all of the specimens were alike and that there was no internal difference in the heteropolar and amphipolar types. Jain suggested that a scroll valve had formed the coprolites and had reconstructions of the possible configuration of the scroll valvular intestine. It should be noted that the late Eocene scroll-type coprolites identified in this study are dramatically different structurally from the Triassic “scroll” coprolites of Jain (1983).

Lauginiger and Hartstein (1983) reported on the fossil sharks, skates, and rays from the Chesapeake and Delaware Canal area in Delaware. Their research covered five Upper Cretaceous formations, and they reported recovering shark coprolites from all of the formations. They illustrated a 3.8 cm shark coprolite (p. 10, fig. 3) and had excellent photographs of two well-preserved shark coprolites (p. 61, pl. 4), which were 5.1 cm and 3.0 cm, respectively. Although not noted, the coprolites all appear to be spiral types and are similar in size to the coprolites from the study area.

Two important studies that involved chondrichthyan coprolites were conducted by McAllister (1984, 1985). McAllister investigated the valvular intestines in various types of fossil and extant fishes for his Masters thesis in 1984 at the University of Kansas. He noted that fossils with strong evidence of valvular intestines were placoderms and chondrichthyans. These investigations led him to reassess the formation of spiral coprolites that had been presented by previous researchers such as Fritsch (1895), Neumayer (1904), Williams (1972), Stewart (1978), and Duffin (1979). In his 1985 research, McAllister performed extensive investigations of the spiral valve of the extant shark *Scyliorhinus canicula* and noted that fecal ribbons coiled spirally within the colon of this elasmobranch. McAllister contended that these spiraled fecal masses could be expelled from the shark without distortion. Thus, using the modern shark as an analog, he presented an explanation of the origin of spiral coprolites in the Lower Permian Wymore Shale. McAllister proposed that previously described enterospirae (fossilized valvular intestines) by the above-mentioned researchers were actually expelled spiral fecal masses. He presented his reasoning and evidence for this proposal on pages 7-10. This led McAllister to publish his often-quoted and

controversial paper entitled “Reevaluation of the Formation of Spiral Coprolites” in the University of Kansas Paleontological Contributions in 1985. McAllister (1988) continued his studies when he reported on vertebrate coprolite material from the Upper Pennsylvanian of Kansas, which included heteropolar spiral coprolites (most likely from sharks). The study was based on a small sample (“less than 30 specimens”). One of the objectives of the study was to demonstrate the value of coprolites that was not normally available from body fossils.

Fenton and Fenton (1989) briefly mentioned coprolites (“dung stones”) in their general book and illustrated a terrestrial mammal coprolite (p. 4). They noted that the grooves in coprolites created by the spiral valve in the shark’s intestine make the origin obvious. Coprolites and enterospirae (fossilized intestinal contents) related to sharks are compared in Pollard (1990). The two fossilized trace fossils have many similarities since coprolites are excreted feces while the enterospirae represents fecal contents in the intestinal valve that have not been excreted. It can be difficult to distinguish between the two since both show the features of the intestinal or spiral valve. However, the authors believe that separation of true coprolites (excreted material and a trace fossil) and enterospirae (non-excreted material and actually a body fossil) is possible, especially with well-preserved specimens. Stewart (1990) discussed spiral coprolites attributed to sharks in his paper on the vertebrate stratigraphy of the Niobrara Formation (Cretaceous) in the Niobrara Chalk Excursion Guidebook (p. 19-30).

Probably the oldest vertebrate coprolites reported are those by Gilmore (1992) from the Silurian of Ireland. In his graduate research, Gilmore studied 160 coprolites as well as fragments and deduced the source animal as most likely agnathans. Unfortunately, many of the coprolites were completely flattened and argillaceous in composition. Although the coprolites were attributed to agnathans, the study had important implications for shark coprolites. Gilmore identified the coprolites as scroll-like in nature produced by a longitudinal valve and provided an extensive discussion on the scroll valve development (text-fig. 3, p. 322). He reiterated what Fee (1925) had proposed – that the scroll valve developed first and that the transverse or spiral valve developed from secondary modification. He also stated that the scroll valve that presently exists among some chondrichthyans (Compagno, 1988) might have subsequently re-arisen from a transverse valve.

However, it should be noted that there is disagreement with the assertions of Fee and Gilmore. For example, the scroll shark coprolites common in the Paleogene and Neogene appear to be structurally, compositionally, and fundamentally quite different from the agnathan “scroll” coprolites of Gilmore. Furthermore, biologists have long noted the simplicity of the cyclostome digestive system. Little (1932), in his study of vertebrate structure, stated that cyclostomes have a straight intestinal tube that is not divided into anatomical regions. This is verified by recent studies by Khanna and Yadav (2005) in their *Biology of Cyclostomes*, which refers to cyclostomes as fish without a differentiated stomach. Wischnitzer and Wischnitzer (2006) discussed that the evolutionary pattern starting with the cyclostomes indicated that the digestive tract has become increasingly complex and includes progressively more components (fig. 10-7, p. 95). It has also been noted that the valvular-like intestine of the modern lamprey is reduced and quite different from that of gnathostomes (Hardisty, 1979; Fänge and Grobre, 1979). Youson (1981) was convinced that the gnathostome valvular intestine is not homologous with the structure present in the intestine of the lamprey. The authors of this paper do not believe that the “scroll-like” valvular intestine possessed by the agnathans is analogous to those found in advanced chondrichthyans such as the carcharhiniforms. The authors contend that the “scroll-like” valvular intestine of the agnathans only superficially resembled the scroll valve of the chondrichthyans and was a completely different structure than the one present in the gnathostomes, the sister group of the agnathans.

Hoch (1991) identified nodules from the Cretaceous (Turonian) of Greenland as coprolites of a durophagous shark. The coprolites, which

had fragments of *Inoceramus* shells in them, were attributed to the shell-crushing shark *Ptychodus*. However, the shape and features of the coprolites are not similar to other known Cretaceous shark coprolites. Late Pennsylvanian coprolites from central New Mexico that included heteropolar forms were studied by Hunt (1992). He reported 12 coprolites and 9 possible coprolites recovered by splitting shale (fig. 1, p. 222). All of the specimens displayed a high degree of flattening and were visible mainly in cross section because of the matrix. He attributed all of the coprolites except those with conchostracan inclusions to fish. The source animal for the heteropolar forms were noted as fish with a spiral valve such as sharks, dipnoans, or primitive bony fish and suggested a tentative assignment to xenacanth sharks. Hunt also proposed the term bromalite to apply to anally or orally derived ejecta and in-situ intestinal matter and would include coprolites (restricted to matter extruded from anus), cololites (enterospira would be a type), and regurgitalites. Hunt specified that coprolites could be recognized by some or all of 13 characteristics (p. 223).

Manning and Dockery (1992) illustrated a partial shark coprolite from the Frankstown vertebrate fossil locality (Upper Cretaceous) in Prentiss County, Mississippi (fig. 1, p. 30). The coprolite appears to be a spiral type based on the twist marks extending across the width of the specimen. The authors noted that coprolites are originally bullet-shaped but often become flattened in fossilization. The authors also stated that shark coprolites are preserved because they are largely composed of ground-up bone. The vertebrates from this same assemblage were analyzed in much greater detail by Manning (2006), but no additional information on the shark coprolites was presented. Stringer (1992), in his study of teleostean otoliths from a Mississippi River mudlump island, mentioned the importance of the excreta of piscivorous animals, such as sharks, in depositing otoliths in the sediment. He also mentioned the occurrence of otoliths in shark coprolites. Everhart and Everhart (1992) described elongate ovoid fossil structures from the Smoky Hill Chalk Member of the Niobrara Chalk (Cretaceous) in western Kansas and proposed their use as stratigraphic markers. The structures were characterized by oyster concentrations. He suggested that the structures and their contained oyster shell fragments (70 specimens) might represent durophagous shark coprolites similar to those described by Hoch (1991) from the Cretaceous of Greenland. The possible coprolites are also pictured on his website Oceans of Kansas Paleontology (www.oceansofkansas.com).

In their exhaustive study of the fossil sharks and rays from the Cretaceous of Texas, Welton and Farish (1993) cover coprolites in their chapter on ichnology (p. 35). They figure what they label as "possible shark coprolites" from the Eagle Ford Group in Dallas County, Texas. One of the two pictures appears to be a fairly well preserved spiral shark coprolite (twist marks are discernable across the width of the coprolite). The other picture is quite spectacular with numerous fish bones including a vertebra. Unfortunately, the coprolite appears to be badly weathered and eroded, and it is not possible to identify any diagnostic features.

Another significant paper published in 1993 that was related to shark coprolites was Savrda and Bottjer (1993). They reported on the trace fossil assemblages, which included coprolites, in the fine-grained strata of the Cretaceous Western Interior of the United States. In their research, they contended that fecal matter smaller than 4 mm was predominately related to planktonic and benthic invertebrates. This agrees with Schafer's definitive work in 1972 on the ecology of the North Sea in which he emphasized that the abundant, but small, oval segmented fecal pellets of various invertebrates had the greatest lithological significance but little paleontological value. Fecal material that was greater than 4 mm was most likely coprolites and could be attributed to vertebrate organisms, including chondrichthyans, especially where remains of macrovertebrates were present in the sediments.

A 1994 study by Storrs addressed Late Triassic shark coprolites from the Rhaetian in England. Storrs (1994) noted that probable shark coprolites, cololites (colon contents), or enterospirae (intestinal spiral

valve contents) are known from most of the Rhaetian exposures. According to Storrs, these fossils were easily identified by their spiral appearance corresponding to the soft anatomy of the selachian alimentary track, specifically the spiral valve found in the small intestine (p. 228). He pointed out that the coprolites from the Westbury Formation frequently contained the remains of ingested fishes often in concentric or spiral orientation.

Both spiral and scroll shark coprolites are discussed and illustrated in Kent (1994). There are line drawings showing the differences in coprolites produced by a spiral intestinal valve and a scroll intestinal valve (p. 11). Kent also noted that more primitive forms such as the lamniforms have a spiral valve while more advanced forms (many of the carcharhiniforms) have a scroll valve.

Morphologically complex, spiral coprolites from the Upper Cretaceous Dinosaur Park Formation were the focus of an important study by Coy in 1995. Approximately 300 well-preserved coprolite fragments were surface collected from two closely associated localities in southeastern Alberta, Canada. Thirteen essentially complete specimens were found, but the vast majority of the specimens were broken and fragmentary. Coy (1995) reported two variants of the ovoid-to-cone-shaped coprolites. One had a pronounced external spiral, which was widely spaced and continuous for the entire length. The other was a coprolitic mass where the external spiral is vague or not preserved. Finally, he also recognized cigar-shaped coprolites, which were smaller with no preserved external spiral (the three coprolite types are shown in fig. 3, p. 1193). Scales and vertebrae were common inclusions in the coprolites. Coy deduced that the source animal was a large vertebrate predator with a spirally valved intestine, capable of ingesting prey up to 30 cm (based on size of scale inclusions). Based on vertebrate remains at the two sites and the previously mentioned parameters, the shark *Hybodus* was determined to be the most likely source of the spiral coprolites. Coy believed that the most likely explanations for the morphological diversity were ontogenetic changes in a single taxon of shark (juvenile, subadult, and adult of *Hybodus*) and variations in diet and digestive processes.

McAllister (1996) described coprolitic and cololitic remains from the Devonian Escuminac Formation of Miguasha, Quebec, Canada (p. 328-378). The Devonian fish fauna included agnathans, anapsids, placoderms, acanthodians, and very rare actinopterygians. Although chondrichthyan remains were not found, McAllister addressed the difficulty of identifying coprolitic remains and the problem of finding modern analogs for comparison. This difficulty applies also to primitive freshwater sharks as well other as elasmobranchs. Also in 1996, Finsley provided photographs of Early Permian, Late Cretaceous, and Paleocene shark coprolites. The three Permian coprolites are identified as belonging to *Orthacanthus* or *Xenacanthus* based on their occurrence with the teeth of this species in Texas (photo 413, plate 95). The three coprolites ranged from 3.7 cm to 7.9 cm in length and appear to be heteropolar although this was not noted by the author. The author noted that the coprolites were rather common in the areas where the *Orthacanthus* teeth are found. There are also photographs of a Cretaceous 9.5 cm coprolite and a Paleocene 3.5 cm coprolite, both from east Texas (photo 414, plate 95). Both of the coprolites are labeled as spiral coprolites from fish. However, the large Cretaceous specimen, which is broken, does not appear to be a typical spiral coprolite. The smaller Paleocene specimen does seem to be a spiral coprolite, but the coiling is similar to the enterospira type.

Abundant coprolites (4,400 specimens) from the Early Triassic Arcadia Formation of Australia were initially studied by Northwood (1997). In spite of the very large number of specimens, only about 10% were unbroken, and these specimens were analyzed most intensively. She reported three different morphotypes (spiral, longitudinally striated, and indeterminate). Most of the coprolites did not have inclusions, but in those that did, fish scales were most common. Chemical analysis indicated that all of the coprolites were composed mainly of fluorapatite and were considered to represent carnivores. Northwood stated that

clearly fish that retained a spiral valve produced the spiral coprolites. Further studies by Northwood on this formation were later published in *Palaeontology* in 2005.

Shimada (1997a) reported a shark-tooth bearing coprolite from the Upper Cretaceous Carlile Shale from Kansas. The coprolite had an ellipsoidal shape and was phosphatic in composition. The coprolite had a *Ptychodus* tooth visible on the outer surface. The coprolite was only partially preserved, and it was not known if the originator was a shark or not. Shimada noted that it could represent an animal not yet known from the fauna. Shimada (1997b) also discussed coprolitic tooth sets in describing the preservation of tooth sets in the fossil record of sharks. Coprolitic tooth sets were shark teeth that were enclosed in a coprolite and were considered as a subtype of a semi-associated tooth set. The study focused primarily on the contained inclusions (i.e., shark teeth) rather than the coprolite.

Chin (1997) presented information applicable to shark coprolites when she surveyed over 60 localities that had lithified coprolites. She noted that coprolite specimens are preserved primarily in fine-grained mudstones or siltstones (64%), sandstones (18%), and limestones or chalks (13%) in the marine environment. Her survey indicated that coprolite preservation indicates a bias for low-energy aquatic systems subject to episodes of rapid sedimentation and a sensitivity to exposure and transport. These parameters would certainly apply to chondrichthyan coprolites. In 1998, Beddard produced a field guide designed primarily for students to identify remains from the world-famous phosphate deposits near Aurora, North Carolina. Six coprolites were figured in the field guide (p. 14-15). The coprolite on page 14 appears to be shark (scroll type), and several of the ones figured on page 15 may also be shark (spiral types).

The significance of vertebrate coprolites for taxonomy, stratigraphy, and facies interpretation for the Upper Triassic Chinle in the western United States was addressed by Hunt, Lucas, and Lockley in 1998. Hunt et al. (1998) noted seven localities/areas in Wyoming, Arizona, New Mexico (three sites), and Texas (two sites) that yielded important concentrations of coprolites in the Chinle Group. The ichnotaxon *Heteropolacopros texaniensis* was described as heteropolar (in the sense of Neumayer, 1904), usually less than 4 cm in length, and 3-4 coils forming less than 50% of the length (fig. 2C-L, p. 229). The form represented half of the coprolites in the Chinle Group red beds. The ichnotaxon was believed to have been produced by a xenacanth shark or dipnoan.

A year later, Swift and Duffin (1999) reported that coprolites were common in the bone beds of the Upper Triassic Westbury Formation of the Penarth Group in England. Storrs (1994) had also presented data on the coprolites in the Westbury Formation. Swift and Duffin recognized four broad morphological types of coprolites in their study. They noted that large coprolites (up to 8 cm) with well-defined amphipolar morphology were most likely related to sharks, possibly myriacanthid holocephalans. They also reported equally large heteropolar coprolites and related them also to sharks (fig. 32A). These coprolites contained abundant inclusions, most commonly fish scales.

McKinzie et al. (2001) figured what they labeled as a typical shark coprolite from the Cretaceous sediments of the North Sulphur River in northeast Texas (p. 60) and an excellent color photograph of another shark coprolite (fig. 10, pl. 17). Although not noted, both of the specimens are spiral coprolites. The authors contend that shark coprolites are more common in the fossil record because the excreted material is encased in a thin membrane that reduces the tendency of fecal matter to be softened or dissolved by the seawater. In 1991, Everhart posted pictures of three shark coprolites under the category "Coprolites and Fossilized Gut Contents" on his web site "Oceans of Kansas Paleontology." The three specimens were from the Niobrara Chalk (Cretaceous) of Kansas. Although the specimens were labeled as spiral shark coprolites and certainly appeared to be produced by a shark valvular intestine, the deeply incised, longitudinal groove on the center specimen indicated a scroll shark coprolite. Walker and Ward (2002) have a color photograph

of a coprolite that they identified as probably from an extinct shark (p. 10). The authors noted the difficulty in relating coprolites to the animal that produces them. The coprolite, which appeared to be only half complete, has distinctive twist marks that are oriented across the width of the specimen and is most likely a spiral coprolite. Another study of vertebrate fossils (Kocsis, 2002) provided a picture of a Miocene shark coprolite (p. 2) from the well-known deposits in Aurora, North Carolina. The author pointed out a bone fragment imbedded in the fecal material. Although the coprolite appears to be worn, it seems to be a scroll coprolite (note: there is a typographical error, and coprolite is misspelled in the caption).

Chin, one of the leading and most prolific researchers on coprolites, published a paper on the analysis of coprolites produced by carnivorous vertebrates in 2002. Of course, carnivorous vertebrates would certainly include sharks. Chin discussed the difficulty of relating coprolites to specific producers. However, she emphasized that coprolite contents, composition, size, and stratigraphic placement are important aspects of constraining the number of likely perpetrators. She pointed out that carnivore coprolites, such as sharks, are usually easily differentiated from herbivore coprolites because they are typically phosphatic (apatite) in composition and often contain inclusions that are indicative of the diet. Another study of that year that involved chondrichthyan coprolites was Hoganson and Murphy (2002), who investigated the stratigraphy and vertebrate fossil record of the marine Breien Member of the famous Hell Creek Formation (Maastrichtian) in North Dakota. The most abundant vertebrate fossils in the Breien assemblage were the chondrichthyans with 13 species. They noted finding coprolites, which they believed were fish or shark. Unfortunately, there are no illustrations or data on the coprolites.

Shark coprolites, primarily Cretaceous, were mentioned in a very interesting study entitled "Coprolite Mining in England" by Ford and O'Connor in 2002. Ford and O'Connor (2002, fig. 1, p. 1780) figure several phosphate coprolite nodules, but there were no descriptions of the coprolites except noting possible source animals. Phosphatic nodules including shark coprolites were mined in England beginning in the 1820's as a source of fertilizer. The authors calculated that possibly 2 million tons of phosphate were mined in England. Of course, coprolites were part of the phosphate being mined. The authors posed the rhetorical question, "how many fossil specimens were lost to science by being ground up for fertilizer?"

In a brief report, Harbour and Dorfman (2004) described shark coprolites from central New Jersey. The shark coprolites were collected from the Late Cretaceous and the early Miocene. They noted that shark teeth were more common in the deposits and coprolites were much harder to locate. They attributed the Cretaceous coprolites (fig. 1, p. 29) to mainly lamniform sharks (a "pellet shaped feces") while they ascribed the Miocene coprolites (fig. 2, p. 30) to carcharhiniforms (scroll feces). The shark coprolites were reported as abundant in some of the fossil-producing zones and as often containing inclusions, especially of bone.

A large number of Triassic coprolites from two localities in Australia were analyzed by Northwood in 2005. This study is significant for several reasons including the large number of specimens (2,703 from one locality and 1,566 from the other) and the comprehensive nature of the research. Northwood stressed that coprolites should be "studied in conjunction with vertebrate fossil assemblages." She discussed terminology used in coprolite studies on page 51 and compared coprolites, cololites, and enterospirae. Vertebrate animals were considered as the source of all of the coprolites based on the fluorapatite composition and the size (greater than 5 mm in length). Although the number of coprolites in the study was extremely large, Northwood reported that only 8% of the coprolites were intact. The fragmentary nature of the coprolites was thought to have been related to the weathering processes of the matrix sediment. Northwood classified the coprolites into one of three categories: spiral, striated, and indeterminate (pictures of the three types are shown in text-fig. 2, p. 53). She remarked that it was "generally accepted

that spiral coprolites were produced by fish with spiral valves” and noted several major coprolitic studies attributing heteropolar, spiral coprolites to sharks. She identified her spiral-type coprolites as heteropolar in shape, and she believed that they represented “fully extruded or true coprolites” from sharks. One of the other types of coprolites had parallel striations, and a third had no features (indeterminate). She described inclusions such as scales, teeth, tooth plates, and bones from the coprolites. Over one-half of the unbroken specimens had inclusions on the external surfaces.

Another study related to shark coprolites published in 2005 was by Hunt, Lucas, and Spielmann. Early Permian vertebrate coprolites from the El Cobre Canyon Formation were described from three quarries in north-central New Mexico by Hunt et al. (2005). Two of the ichnotaxa represented derived fish, possibly chondrichthyan or dipnoan (figs. 2-3, p. 41). The shark *Xenacanthus* had been reported from one of the quarries. They also noted that the ichnotaxa from this study occurred in the collection that Neumayer (1904) described from Texas.

Shimada et al. (2006) described an extensive chondrichthyan and actinopterygian fauna from the Upper Cretaceous Greenhorn Limestone in Colorado. In this description, there was a coprolite that contained a partial fish scale (fig. 16, p. 32). The coprolite was phosphatic in composition and was slightly over 1 cm in total length. The coprolite was believed to be vertebrate in origin, but it is not known if it was chondrichthyan. In the same year, Shimada (2006) published once again on the marine vertebrates from the Blue Shale Member of the Carlile Shale in Kansas. A coprolite that contained a *Ptychodus* tooth, which was previously reported in 1997, was re-described. Although the origin was attributed to a vertebrate animal, it is not known if it represented a shark.

Hunt et al. (2007) conducted a thorough review of vertebrate coprolites of the Triassic, which included chondrichthyans. It was asserted, “coprolites are the least studied and most under-sampled vertebrate trace fossils.” In this study, Hunt et al. erected several new ichnotaxa from the Mesozoic and stressed the biostratigraphic and paleoecologic value of coprolites. They noted the abundance of vertebrate coprolites in the Permian-Triassic redbeds around the world (fig. 1, p. 89) and discussed differences in heteropolar and amphipolar morphological types (p. 90). They also provided a list of all Triassic coprolite specimens in the Geosciences Collection of the New Mexico Museum of Natural History and Science in Albuquerque, New Mexico (p. 98-107), which is purported to be the largest collection available.

Phillips and Stringer (2007) reported on the rare occurrence of matched pairs of teleostean otoliths from two possible coprolites in the Glendon Limestone (Oligocene, Rupelian) in central Mississippi. The two coprolites were exposed in indurated strata (limestone) in a quarry, and the typical shape of shark coprolites was not discernable. In addition to the otoliths, numerous teleostean bones and spines were also recovered in the coprolitic material. Other criteria were employed to investigate possible originators of the suspected coprolites. Several parameters pointed to a larger predator such as shark. At least seven taxa of sharks are known from the Glendon Limestone at the site, but statistical information on the abundance of the sharks was not available.

Also in 2007, Everhart reported finding remains of a pycnodont fish from a coprolite from the Niobrara Chalk (lower Santonian) in Kansas. The 3.0 cm coprolite was slightly eroded and no discernible features were present (fig. 1, p. 36). Everhart stated that it was not a spiral coprolite and presented no information on the producer. However, he did note that 18 other coprolites including a spiral coprolite were also collected in close proximity to the pycnodont-bearing coprolite, but these were not figured. The spiral coprolite could represent a chondrichthyan. Everhart reported that vertebrate coprolites were common at various stratigraphic levels in the Smoky Hill Chalk and that about 10% contained visible inclusions (mainly bone).

In 2008, two studies were published that utilized shark teeth and shark coprolites for isotopic analysis to determine paleoecological parameters. One study by Ounis et al. (2008) used the oxygen isotopic

composition of shark coprolites as a proxy for climatic evolution during the deposition of the Paleogene phosphorite sediments in Tunisia. The shark coprolites were used since they are composed of marine biogenic apatite. These same authors also published in Palaeogeography, Palaeoclimatology, and Palaeoecology on the rare earth elements and stable isotope geochemistry of the phosphorite deposits in the Gafsa Basin in Tunisia based on shark coprolites (Ounis et al., 2008).

Condensed sections of Eocene phosphatic conglomerates in Mali, northwestern Africa were the focus of study by Tapanila et al. (2008). It was found that the clasts of the phosphatic conglomerates were composed primarily of bones and coprolites. Coprolites and possible coprolites were determined to compose almost 75% of the conglomerate clasts. Tapanila et al. (2008) reported five distinct varieties of coprolites including three different spiral forms that he attributed to three separate fish taxa. It was also noted that bony and cartilaginous fish dominated the vertebrate assemblage with only a minor reptilian presence.

A 2009 study of Mansby included detailed analyses of shark coprolites from the Kristianstad Basin in southern Sweden. Analysis included external morphology, microscopic surface examination, thin sections, scanning electron microscope examination, and acid dissolution. Mansby differentiated between the heteropolar spiraled and the amphipolar spiraled types of coprolites (fig. 1, p. 5). The Upper Cretaceous sediments (Campanian) produced various vertebrate remains including numerous shark taxa in addition to the coprolites. Mansby chose only five coprolites for detailed analysis. The total number of coprolite specimens in the study was unclear, and only five were classified and analyzed. He recognized three different groups of ichnotaxa. He attributed one specimen with a heteropolar mode of spiraling to a macrophagous lamniform shark (fig. 6, p. 12). He also tentatively assigned one non-spiraled coprolite, which contained an invertebrate inclusion, to a bottom-dwelling durophagous shark.

Duffin (2009) presented a review of coprolite research with an emphasis on the early studies. Duffin noted the particular interest of Buckland in spiral coprolites and described how Buckland sectioned and polished spiral coprolites. He also pictured spiral coprolites of Buckland (figs. 15-16, p. 107) and related how he compared them to chondrichthyans. Duffin also reviewed the work of many researchers who addressed shark coprolites such as Fritsch (1895), Neumayer (1904), Williams (1972), and McAllister (1985). Godfrey and Smith (2010) reported on two coprolites from the famous Miocene Calvert Cliffs in Maryland that had impressions of shark teeth preserved in them. These are believed to be the first coprolites known with preserved teeth marks. It is not known if the coprolites are chondrichthyan in origin or not. Godfrey noted that no spiral markings were present, but he did not eliminate the possibility of a chondrichthyan origin. A chemical analysis of the Calvert Cliffs’ coprolites indicated a composition to be expected with a carnivorous vertebrate such as a shark or crocodile. The coprolites may also represent a portion of preserved intestinal valves (enterospirae) rather than excreted material. Godfrey noted that coprolites (including shark) are not common at Calvert Cliffs. However, he also commented that in situ and float specimens are occasionally found along the beaches below the cliffs.

Danian (Lower Paleocene) coprolites from the Faxe Quarry, which is located in the southeastern part of Zealand, Denmark, were investigated by Milàn in 2010. Milàn utilized 49 coprolites, which were all believed to be vertebrate in origin based on their size (greater than 5 mm in length) and composition. Unfortunately, Milàn reported that most of the coprolites were eroded and fragmentary and that only 11 specimens were deemed sufficiently well preserved to be identified and studied in detail. Milàn recognized three general morphotypes, and one of these was a heteropolar, spiral coprolite. The heteropolar spiral coprolites were not very large, ranging from 1.4 cm to 2.3 cm in total length (fig. 3, p. 216). The coprolites (two complete and two broken) seem to be highly weathered and eroded. The external surface appears to be rough and highly irregular, but spirals are visible although not well preserved.

One broken specimen shows internal spirals expected with this type of coprolite. The heteropolar spiral coprolite morphotype was attributed to sharks as the source animal by Milàn (2010).

Shark coprolites were discussed and pictured in a general book on vertebrate morphology, pathology, and cultural modifications by Sinibaldi (2010). He stated that shark coprolites (fossilized feces) are occasionally found, especially from unconsolidated sediments from the Tertiary Period. However, he also noted that coprolites might be common in many localities. He also pointed out that the majority of coprolites are from carnivores because the high content of bone material in the diet allows their fecal material to survive a sufficient amount of time for fossilization. He pictured two specimens that were labeled as shark coprolites from the Miocene of Beaufort County, South Carolina (fig. 3.66, p. 113). The shark coprolites were found in a deposit with hundreds of *Carcharocles megalodon* teeth. One of the coprolites is quite large at 14 cm in length. Although somewhat distorted in shape, the coprolites appear to be spiral in nature. This would be consistent with *Carcharocles megalodon*, which was a lamniform with a spiral valve.

Scheetz et al. (2010) mentioned the occurrence of hybodontid shark coprolites from a horizon near the base of the Yellow Cat Member of the Cedar Mountain Formation (Early Cretaceous, Aptian) of eastern Utah. However, there is no further discussion of the coprolites as the emphasis of the study was dinosaur remains. Mehling (2010) reviewed two coprolites from Maryland that contained feather inclusions. Based on the coprolite size, morphology, and provenience, he asserted that whales were the possible producers although fish or crocodiles had been previously proposed as the source animals. It is important to note that Mehling characterized coprolites as a sort of biomatrix that can preserve fossil remains that would have little chance of preservation otherwise.

Preliminary analysis of the coprolites from the Arlington Archosaur Site in Tarrant County, Texas has been completed by King et al. (in press). The site is located in the Lewisville Member of the Woodbine Formation, which is Cretaceous (Cenomanian). They have reported 140+ coprolites and have recognized three morphotypes. Two of the morphotypes have been attributed to Cretaceous sharks.

Several studies have specifically addressed the late Eocene shark coprolites from the Yazoo Clay in varying degrees. One of the first studies to collect and identify shark coprolites from these localities was Stringer (1977). He collected and briefly described approximately 20 coprolites from the Copenhagen area. He also performed x-ray analysis on a single coprolite specimen, which was reported as calcium fluoride phosphate. There was no mention on the degree of crystallization of the calcium fluoride phosphate. This is the composition most frequently reported by Häntzschel et al. (1968). However, the thrust of Stringer's study was teleostean otoliths.

Breard (1978) noted collecting over 100 shark coprolites from the Copenhagen area in his study of the macrofaunal ecology, climate, and biogeography of the Jackson Group in Louisiana and Mississippi. He does not make any attempt at classifying the shark coprolites. Breard and Stringer (1995) noted the occurrence of 179 coprolites from the Yazoo Clay from the Copenhagen area, but they do not address them any further. King (2002) made the first attempt at a more comprehensive study of the late Eocene shark coprolites from the area. King's study consisted of 400 coprolites that included shark, possible bony fish, and indeterminate coprolites and incorporated the coprolites previously collected by Stringer and Breard. It should be noted that the present study has nearly 1200 coprolites attributed specifically to sharks. Stringer and King (2011) mentioned the study of shark coprolites in the Copenhagen vicinity. Finally, King and Stringer (2011) reported on additional late Eocene coprolites from several localities at Copenhagen.

RESULTS AND DISCUSSION

The systematic, long-term collecting at the two localities resulted in the procurement of 1,196 late Eocene shark coprolites from the Yazoo Clay. The detailed description of this sample consists of the length

(maximum), width (maximum), weight, density, coloration, external features, internal features, and morphological type conducted on 374 randomly selected coprolites, and is presented in Table 1. In addition to the detailed description for each of the coprolites in the sample presented in Table 1, a summary and discussion of each of the eight categories are provided below.

Length

The average length of the spiral coprolites was 17.3 mm, which was much less than the average length of the scroll types. The range in the length of the spiral coprolites was 6.7 mm to 47.0 mm with a standard deviation of 7.1 mm. However, it should be noted that many of the spiral coprolites appear to be broken at one or both ends. As discussed earlier, this may be the result of the fragmentation of the spiral coprolites either prior to complete fossilization or after fossilization. The width of the spiral coprolites (see discussion below) would make them more susceptible to breakage and fragmentation. Therefore, the average length of the spiral coprolites may be misleading as to the original length of the specimens.

The average length of the scroll coprolites was 25.9 mm. The range in the length of the scroll coprolites was 6.35 to 70.5 mm with a standard deviation of length of 11.9, which is more variable than the spirals. The range in the length of the scroll coprolites was 64.15 mm, which was much greater than the range of the length of the spirals (40.3 mm). Frequency analysis of the length of the scroll types revealed significant skew toward the longer lengths.

Width

Just as the average length of the spiral coprolites is much less than the scroll coprolites, the average width of the spirals also appears to be significantly less than the average width of the scrolls. Based on the analyzed specimens in the sample, the spiral coprolites have a range in width from 1.2 to 17.1 mm with a standard deviation of 2.1 mm. The average width of the spirals is 6.8 mm. In comparison, the width of the scroll coprolites ranged from 2.1 to 29.2 mm with a standard deviation of 5.0 mm. The standard deviation of the width of the scrolls was over twice that of the spirals. The average width of the scroll coprolites was 12.1 mm.

Weight

The spiral coprolites averaged 1.3 g in weight with a range from 0.07 to 8.19 g. Frequency analysis shows that the most commonly occurring categories are from 0 to 2 g for the spiral types. The average weight of the scroll coprolites was 4.8 g with a range from 0.03 to 28.86 g. Frequency analysis of the scrolls indicates a large number of specimens in the lower weight categories (0-8 g). Since the scroll coprolites were much longer and wider than the spiral coprolites, then it is not surprising that the average weight was much greater.

Density

The spiral coprolites have an average density of 2.10 g/cc with a range from 0.97 to 3.24 g/cc. The average density of the scroll coprolites is 2.14 g/cc with a range from 0.97 to 3.06 g/cc. The standard deviation shows very little variability in the density of the scroll and spiral types. The extremely similar densities are a very strong indication that the chemical compositions and crystalline structures of the spiral and scroll coprolites are very close, if not identical.

External and Internal Features

As noted earlier, the spiral coprolites showed a moderately distinct to well-defined twisting pattern unless affected by significant weathering. The twisting pattern of the spirals was oriented approximately from side to side rather than from end to end. The width of the spirals tended to be fairly similar for the length of the specimen although some

variation was observed. Many of the spirals showed very little deviation in width from one end to another. However as discussed earlier, this lack of variation may be related to the possible fragmentation of the spiral coprolites. The spiral coprolites rarely showed discernable internal structures based on broken specimens.

The major external features of the scroll coprolites were the moderately to deeply incised, distinctive folds and grooves. These folds and grooves were consistently oriented from end to end or in a longitudinal direction. The width of the scroll coprolites tended to be slightly more variable, especially near the center. Internally, distinctive and obvious folding features could be seen in many of the scroll types.

A number of the coprolites contained several different types of inclusions that provided evidence of the dietary habits of the sharks. One of the problems encountered in examining the coprolites for preserved remains is that the color of the fluorapatite of the coprolites and the skeletal remains of the fish are very similar and often the same. This is not unexpected since the coprolites and many of the fish remains are composed of biogenic fluorapatite. Locating and recognizing inclusions in the spiral coprolites was generally more difficult and was believed to be related to the coloration of the spirals.

In spite of the problem of coloration in some of the coprolites, inclusions were located both externally and internally. Several coprolites that had been broken or weathered contained fairly well preserved fish remains such as a ganoid fish scale, a cycloid fish scale, fish spines, fish vertebrae, and indeterminate fish bones. The indeterminate fish bones were the most common inclusions in the spiral and scroll coprolites. Identification of the inclusions would be a daunting task considering the diversity of the Yazoo Clay vertebrate assemblage, which exceeds 80 in number. In addition to the 14 sharks, there are 5 rays, 56 actinopterygians (44 based on otoliths and 12 based on skeletal remains), 3 reptiles, 1 bird, and 2 mammals (Breard and Stringer, 1995; Nolf and Stringer, 2003).

Inclusions were more commonly found in the scroll coprolites and tended to be more numerous than in the spiral coprolites. The reason for inclusions being more common in the scroll coprolites is not clear, but may include the greater size (length and width) and the different coloration of the scrolls. However, there may be other factors that have yet to be determined.

One scroll-type coprolite had several, exceptionally well-preserved fish remains on the surface because the outer surface had been eroded. This coprolite was 81 mm in length with some slight side-to-side flattening. It was a light brown and beige in color, and the fish remains were black or dark brown (Fig. 8, left). The contrasting colors made the fish remains more obvious. On one side of the coprolite, there were at least nine inclusions of fish. One of these was a 5.2 mm long fish spine, which had an articulation on the proximal end (Fig. 8, right). Located near the fish spine were two fish vertebrae (one relatively complete and one partial). The complete fish vertebra was 2.34 mm in length, and the partial was 3.01 mm in length. On the other side of the coprolite, there were at least eight recognizable fish remains. Some of the inclusions are preserved amazingly well. For example, a 5.27 mm fish bone was located, and the diameter of the thin fish bone was only .45 mm.

It is possible that additional skeletal remains could be identified if the external surface of the shark coprolites were systematically and microscopically studied, experimenting with various lighting angles and intensities. Future plans include investigating this possibility. The study of the interior of the coprolites presents a greater challenge, as sectioning of the coprolite is highly destructive and has the potential to also destroy possible remains.

Coloration

The colors of the spiral and scroll coprolites were based on a Munsell color chart. The most common colors of the spirals were pale yellowish brown (10YR 6/2), yellowish gray (5Y 8/1), grayish brown (5YR 3/2), light bluish gray (5B 7/1), and medium bluish gray (5B 5/1). The predominant colors of the scroll coprolites were dark yellowish

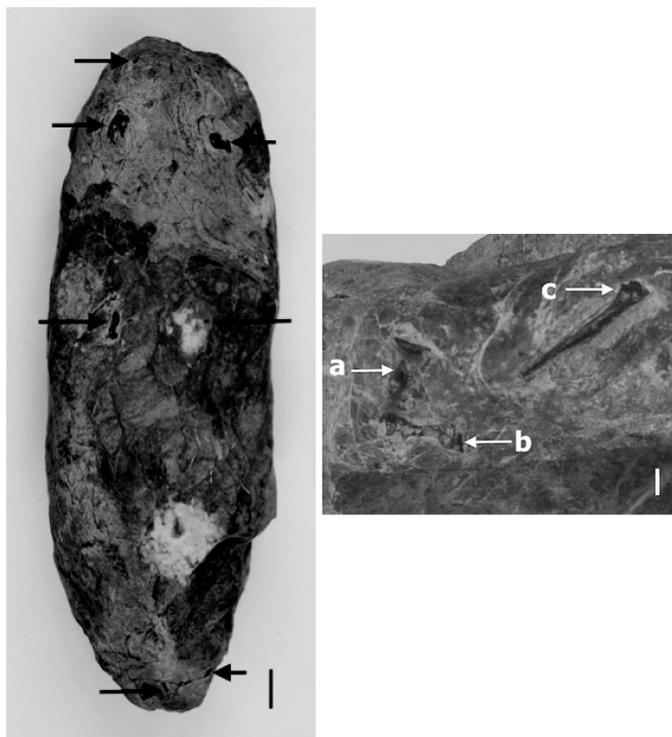


FIGURE 8. **Left**, Specimen of a scroll coprolite with prominent inclusions. Arrows point to various inclusions, primarily fish bones. Scale bar = 5 mm. **Right**, Detailed view of same specimen showing fish vertebrae (a and b) and fish spine (c). Scale bar = 1 mm.

brown (10 YR 4/2), very pale orange (10 YR 8/2), and grayish brown (5YR 3/2).

Morphology

The vast majority of 1196 coprolites (1173) were classified as either spiral or scroll (98.01%). The 556 spirals comprised 46.49% of the total number of coprolites, while the 617 scrolls comprised 51.59% of the total. The 23 indeterminate coprolites accounted for only 1.92% of total coprolites.

It is possible, and quite likely, that a small number of the spiral specimens from the late Eocene Yazoo Clay may represent enterospirae. However, the number of possible enterospirae is extremely minor (< 1% of the total specimens) in comparison to the number of specimens thought to be extruded. The possible enterospirae may be related to skates or rays, but further research will be needed before this can be confirmed. The specimens that may represent enterospirae are dramatically different from the other spiral specimens. The possible enterospirae are small spiral coprolites (around 2 cm) with numerous, extremely well-defined spiral structures that are almost perpendicular to the longitudinal axis (Fig. 9, left and right). The shape is classic heteropolar, as defined by Fritsch (1895), Neumayer (1904), and Williams (1972). Likewise, some of the indeterminate specimens may represent cololites, but again, the number is believed to be very small and will require additional investigation.

Significance of Results

In order to determine if the differences in the averages between the length, width, weight, and density of the spiral and scroll coprolites were statistically significant, directional hypotheses were developed. These directional hypotheses were then evaluated with simple t-tests. The t-test assesses whether the means of two groups are statistically different from each other. The following hypotheses regarding the spiral and scroll coprolites were considered:

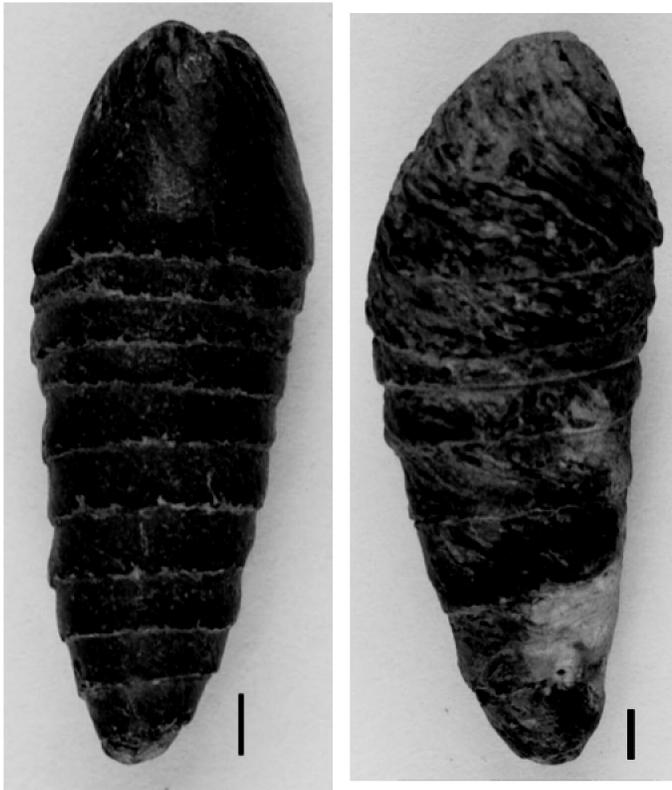


FIGURE 9. **Left**, Specimen of a possible enterospira (note heteropolar shape) from the late Eocene Yazoo Clay. Scale bar = 1 mm. **Right**, Specimen of a possible enterospira from the late Eocene Yazoo Clay. Scale bar = 1 mm.

Hypothesis #1: The mean length of the scroll coprolites is greater than the mean length of the spiral coprolites.

Hypothesis #2: The mean width of the scroll coprolites is greater than the mean width of the spiral coprolites.

Hypothesis #3: The mean weight of the scroll coprolites is greater than the mean weight of the spiral coprolites.

Hypothesis #4: The mean density of the scroll coprolites is greater than the mean density of the spiral coprolites.

The results of the t-tests are given below (at a 0.05 level of significance):

Hypothesis 1 P value = 2.590
Critical t value (one-tail) = 1.649
Df = 319

Hypothesis 2 P value = 6.566
Critical t value (one-tail) = 1.651
Df = 267

Hypothesis 3 P value = 2.881
Critical t value (one-tail) = 1.652
Df = 210

Hypothesis 4 P value = 0.000485
Critical t value (one-tail) = 1.649
Df = 345

The results indicated that the mean length, width, and weight of the scroll coprolites were significantly different (i.e., greater) than the mean length, width, and weight of the spiral coprolites. However, the t-test pointed to no significant difference in the densities of the two major morphological types of coprolites.

Results of X-ray Diffraction

Five randomly chosen spiral and five randomly chosen scroll coprolites were analyzed by powder x-ray diffraction analysis. The external appearances of the specimens selected for x-ray analysis were quite similar and did not indicate any extensive weathering or diagenetic changes. The preservation of the specimens was comparable and should not have introduced any type of bias. All of the analyses of the ten shark coprolites indicated that the composition was moderately crystalline fluorapatite [$\text{Ca}_5(\text{PO}_4)_3\text{F}$]. Since the coprolites were composed of moderately crystalline apatite, they are comparable to the composition of vertebrate bones and teeth. Although the coprolites are not well ordered as crystals of apatite, they do display moderate crystallinity. They are far more crystalline than bone material from archaeological sites, which tended to be poorly crystalline. No other major minerals were detected in the coprolites by the x-ray analysis.

The x-ray diffraction patterns obtained from the coprolites were compared to an apatite (fluorapatite) crystal. The fluorapatite peak assignments to hkl values were obtained from the Mineral Powder Diffraction File (card 15-876). The fluorapatite pattern displays well-defined, sharp peaks characteristic of a well-ordered crystal lattice (Fig. 10). The coprolite diffraction scans showed one major peak, three moderate peaks, and two minor peaks. The diffraction pattern of the coprolite is composed of moderately broad diffraction peaks that are almost identical to the location of the peaks of the crystalline fluorapatite (Fig. 11). The disparity in the crystallinity of the coprolites and the mineral apatite causes the difference in the shape (sharpness) and width of the diffraction bands. The apatite has very narrow, sharp peaks consistent with a high degree of crystallization while the coprolite sample has broader and less intense peaks that are consistent with moderately crystallinity. However, it is clearly evident that the coprolites are composed of fluorapatite. The composition of the ten analyzed spiral and scroll coprolites was very consistent with little variation and indicated the same chemical makeup for all specimens as shown in Figure 12.

As noted by Hallgren (1987), the mineral apatite in a coprolite is convincing evidence of a bone-eating animal. Since all of the analyzed coprolites were determined to be calcium fluoride phosphate (fluorapatite), this is a strong indication that carnivores produced the late Eocene coprolites from the study area. It should be noted that although all of the specimens were not subjected to x-ray analysis, it is believed that they all have the same composition. This supposition is based on the premise that the specimens have almost identical densities, the same luster (un-weathered), very similar colors, comparable hardness, and the same general appearance. The fluorapatite composition of the late Eocene coprolites also agrees with many other studies for the composition of carnivorous vertebrate coprolites (Dietrich, 1951; Hantzschel et al., 1968; Edwards, 1973; Hallgren, 1987; Northwood, 2005).

The fluorapatite composition of the coprolites from the study area also differs substantially from the surrounding matrix. All of the coprolites in this study were collected in the Tullos Member of the Yazoo Clay. Pitalo et al. (2004) performed 240 x-ray diffraction analyses on the Yazoo Clay and found the average composition to be 28% smectite (probably montmorillonite), 24% kaolinite, 22% quartz, 15% calcite, 8% illite, 2% feldspar, and 1% gypsum. Thus, the composition of the Yazoo Clay is significantly different from the composition of the shark coprolites, which were crystalline fluorapatite [$\text{Ca}_5(\text{PO}_4)_3\text{F}$]. This is another indicator of coprolites with carnivorous diets.

SOURCE ANIMALS FOR THE SHARK COPROLITES

As duly noted by Chin (1994), coprolite analysis is encumbered by two major problems when compare to fresh feces: information loss and anonymity. She attributed these difficulties to the high variability in feces of organisms and to diagenesis. Most previous studies of marine shark coprolites, which are quite limited, have found it almost impossible to associate a coprolite with specific sharks that may have pro-

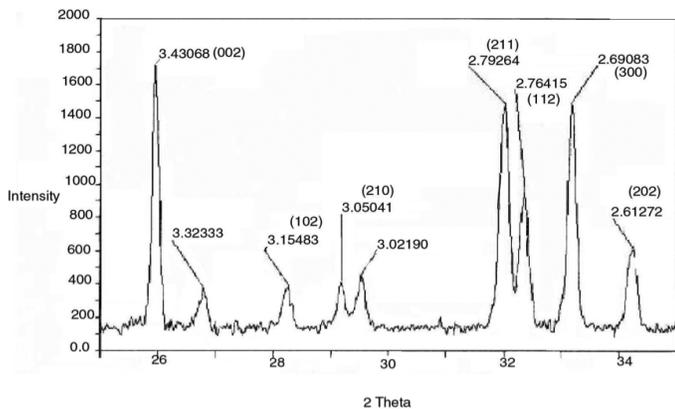


FIGURE 10. X-ray diffraction pattern with “d” and “hkl” values of analyzed specimen of crystalline fluorapatite.

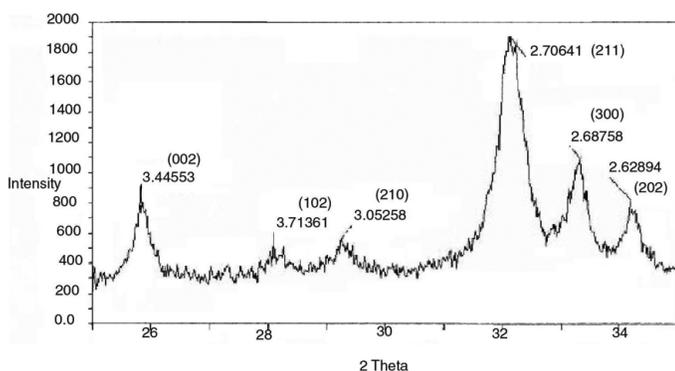


FIGURE 11. X-ray diffraction pattern with “d” and “hkl” values of a late Eocene coprolite from the study area.

duced it. In fact, the connotation “shark coprolite” is often the level of identification of marine shark coprolites in many studies. Fortunately, earlier studies at the two localities produced extensive collections of shark teeth (> 2500) and provided statistics on the relative abundance of the identified shark taxa.

The identified shark taxa from the two localities represented the following four orders: Heterodontiformes, Orectolobiformes, Lamniformes, and Carcharhiniformes (Nelson, 2006). The Heterodontiformes and Orectolobiformes were each represented by only one taxon in the Yazoo Clay at Copenhagen. These include the Port Jackson shark (*Heterodontus pineti*) and the nurse shark (*Nebrius obliquus*). Furthermore, these two taxa made very minor contributions to the total number of shark teeth (< 1%). Therefore, these sharks and their orders were removed from consideration. Based on the abundance of teeth, the major orders for consideration as the source animals of the coprolites were the orders Lamniformes and the Carcharhiniformes. All of the representative sharks in the order Lamniformes produce spiral coprolites. The lamniforms include the modern mackerel sharks such as the white (*Carcharodon*), mako (*Isurus*), and porbeagle (*Lamna*), sand tiger sharks, and thresher sharks (Castro, 1983; Nelson, 2006). The sharks in the order Carcharhiniformes have some representatives that produce spiral coprolites, while others produce scroll types. The Order Carcharhiniformes (ground sharks) include the present-day cat sharks, houndsharks, hammerhead sharks, bull sharks, lemon sharks, tiger sharks, and snaggletooth sharks (Compagno, 1988, 1999). The shark tooth data, which supplied occurrence and abundance of the shark taxa, combined with modern data on shark size, anatomy, and excretory characteristics, allowed for a more precise identification of the shark coprolites as to the possible originators. The abundance of lamniform and carcharhiniform sharks based on shark teeth that were identified at the two localities is

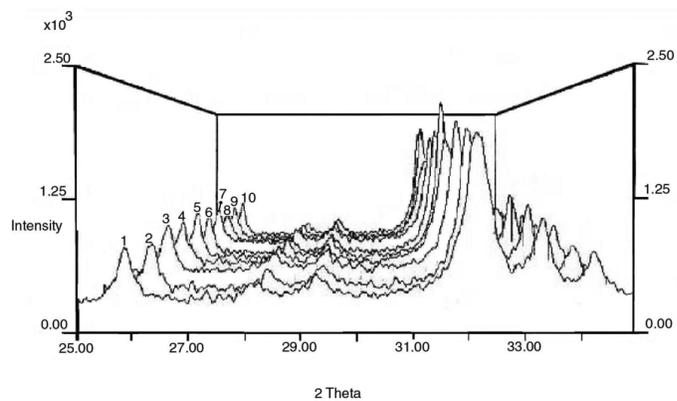


FIGURE 12. X-ray diffraction patterns of all ten of the late Eocene coprolites from the study area. The diffraction patterns for each coprolite specimen are shown in a staggered arrangement beginning with the first coprolite (XR1) in the front and the last coprolite (XR10) in the rear of the figure.

shown in Figure 13, and along with other parameters, allowed for the constraint of possible coprolite producers. It should be noted that the taxonomy of fossil shark teeth continues to be highly debated with tremendous differences among the researchers.

While it is not possible to identify the exact shark species that may have produced a certain coprolite, there is the potential to determine the most likely candidates for the producer of the spiral and scroll coprolites at the two localities. The most likely sharks to produce the largest number of spiral coprolites in the study area were the lamniform *Isurus praecursor* and the carcharhiniform *Abdounia enniskilleni*. The largest number of the scroll coprolites in the study area was most likely produced by the carcharhiniform *Carcharhinus gibbesi* with the exception of several large coprolite specimens, which may be attributed to *Galeocerdo alabamensis*. *Galeocerdo alabamensis* probably represented the largest shark with a scroll valve in the study area. An extant representative similar to this taxon, the tiger shark (*Galeocerdo cuveri*), has been reliably reported as large as 7.4 m in length (McEachran and Fejhelm, 1998).

CONCLUSIONS

Conclusions derived from this research regarding the late Eocene shark coprolites from the Yazoo Clay of Caldwell Parish, Louisiana are as follows:

1. Systematic, long-term surface collecting proved to be an effective technique for the procurement of shark coprolites from the Yazoo Clay at the two localities.
2. Over a 30-year period, 1196 shark coprolites were obtained from the two localities utilizing systematic, surface-collecting techniques.
3. A sample (n = 374) of the 1196 collected coprolites was described in detail using the following characteristics: length, width, weight, density, coloration, external features, internal features (when possible), and morphology.
4. Classification of all of the collected coprolites revealed two primary morphological types: spiral and scroll. Approximately 98.01% of the coprolites were identified as either spiral (556 specimens) or scroll (617 specimens) based on external and internal morphological features.
5. The average length of the spiral coprolites was 17.3 mm, which was significantly less than the scroll types, which averaged 25.9 mm in length. However, the lengths of the spiral coprolites were probably affected by fragmentation.
6. The spiral coprolites averaged 6.8 mm in width and had a range from 1.2 to 17.1 mm. This was significantly less than the average width of the scroll coprolites, which was 12.1 mm with a range from 2.1 to 29.2 mm.
7. The spiral coprolites averaged 1.3 g in weight, while the average

Order/Family	Genus/species	Number of Teeth	Spiral Valve	Scroll Valve
Lamniformes				
Alopiidae	<i>Alopias latidens</i>	14	X	
Odontaspidae	<i>Carcharias hopei</i>	58	X	
Lamnae	<i>Carcharocles sokolovi</i>	20	X	
	<i>Isurus praecursor</i>	438	X	
	<i>Lamna lerichei</i>	48	X	
Carcharhiniformes				
Scyliorhinidae	<i>Abdounia enniskilleni</i>	109	X	
Hemigaleidae	<i>Hemipristis curvatus</i>	53	X	
Carcharhinidae	<i>Galeocerdo alabamensis</i>	131		X
	<i>Rhizoprionodon sp.</i>	1		X
	<i>Carcharhinus gibbesi</i>	1,737		X

FIGURE 13. Lamniform and carcharhiniform sharks known from the two localities in the study area based on shark teeth. Number of specimens and the type of valvular intestine are also indicated.

weight of the scroll coprolites was 4.8 g. This difference was not unexpected given the significant differences in length and width. The differences in weight between the spirals and scrolls were determined to be significant.

8. The spiral coprolites had an average density of 2.10 g/cc, and the average density of the scroll coprolites was 2.14 g/cc. The standard deviation shows very little variability in the density of the scroll and spiral types, which is not unexpected since the chemical composition appears to be identical according to the x-ray analysis. The density differences in the two major morphological types were determined not to be statistically significant.

9. The spiral coprolites, unless affected by weathering, had moderately distinct to well-defined twisting patterns, which were oriented primarily from side to side or across the width. The width of the spirals tended to be fairly similar for the length of the specimen although some variation occurs. Spiral coprolites rarely showed discernable internal structures.

10. Key external features of the scroll coprolites were the moderately incised to deeply incised, distinctive folds and grooves. The folds and grooves were oriented longitudinally and commonly extended the entire or a majority of the length of the coprolites. The width of the individual scroll coprolites tended to be more variable. The variability in width was most common near the center of the scroll coprolites. Prominent and distinctive folding structures could be seen internally on many of the scroll specimens.

11. Some of the coprolites supplied evidence of the dietary habits of the sharks. The similarity of the coloration of the fluorapatite of the coprolites and the skeletal remains of the fish is problematic. In spite of this, fish remains in the coprolites included a ganoid fish scale, a cycloid fish scale, fish spines, fish vertebrae, and numerous fish bones. Indeterminate fish bones were the most common inclusions in both spiral and scroll coprolites. More inclusions were found in the scroll coprolites, but the reason for this is not clear and may include the greater size (length and

width) and the different coloration of the scrolls as well as other factors.

12. Five randomly chosen spiral and five randomly chosen scroll coprolites were analyzed by powder x-ray analysis, and the analyses indicated that the composition of all of the shark coprolites was moderately crystalline fluorapatite [$\text{Ca}_5(\text{PO}_4)_3\text{F}$]. There were no discernible differences in the composition of the spiral and scroll coprolites.

13. Previous studies at the two localities produced extensive collections of shark teeth (> 2500) and provided data on the abundance of the identified shark taxa. The major orders for consideration as contributors of coprolites were the Lamniformes and the Carcharhiniformes. The lamniforms produce spiral coprolites exclusively, but some of the carcharhiniforms produce spiral coprolites, while others produce scroll types. The shark tooth data combined with modern data on shark anatomy and excretory characteristics allowed for a more precise identification of the shark coprolites as to the possible originators.

14. Although it was not possible to ascertain the exact shark species that produced specific coprolites, it was possible to constrain the possible candidates and identify the most likely source animals of the spiral and scroll coprolites.

15. The most likely sharks to produce the largest number of the spiral coprolites in the study area were the lamniform *Isurus praecursor* and the carcharhiniform *Abdounia enniskilleni*. The largest number of the scroll coprolites in the study area was probably produced by the carcharhiniform *Carcharhinus gibbesi* with the exception of several large specimens, which may be attributed to *Galeocerdo alabamensis*.

16. The longitudinal nature of this project (> 30 years) and the number of shark coprolites collected and analyzed have resulted in one of the most detailed, exhaustive studies of late Eocene shark coprolites in the Gulf Coast.

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Disaggregated sloth dung in the collection of the National Museum of Natural History, Washington, D.C.