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THE ORIGIN OF "SPIRAL COPROLITES"

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ABSTRACT

Heteropolar spiral coprolites from Central Kansas are described and several morphological features not noted by previous workers are illustrated. Microscopic study of thin sections reveals the presence of numerous well-preserved mucosal folds including the tunica propria, confirming Fritsch's suggestion that coprolites of this sort are fossilized intestines (Fritsch, 1907). Accordingly, Fritsch's term *enterospira* has been used to designate these specimens.

Comparison of the *enterospirae* with the spiral valves of modern sharks shows that they most clearly resemble that of the genus *Scyllium*, and suggests that a possible explanation for the fossilization of the valve may be its complex morphology which causes the very slow passage of food and a subsequent tendency for it to be full at the time of the animal's death.

A brief analysis of the faunal assemblage suggests the intestines may be attributed to pleuracanth sharks and gives an indication of certain aspects of the food chain.

INTRODUCTION

In the fall of 1968, Mr. Frank Wind, then a graduate student in the Geology Department at the University of Kansas, found a specimen in the Lower Permian Wymore Shale near Manhattan, Kansas, which I subsequently identified as a spiral coprolite. Two collecting trips to the area in the spring of 1969 yielded 30 more or less complete specimens as well as numerous fragments. The abundance of spiral coprolites preserved at this locality, and their excellent state of preservation, provides an opportunity for an investigation into their origin.

The specimens discussed in this study were obtained from the lower 3 meters of the Wymore Shale member of the Lower Permian (Wolfcampian) Matfield Shale. These rocks are exposed on the western side of a roadcut 1.7 km south of the junction of Kansas Highways 177 and 113 in the NE¼, NW¼, Sec. 35, T.9S., R.7E., Riley County, Kansas. At this locality, the Wymore Shale is approximately 4 m thick and

consists of varicolored shales resting on top of a prominent cherty limestone bed, the Schroyer Limestone. In the area in which the specimens are found, the lowermost 40 cm of the shale are fine grained and thinly laminated, ranging in color from gray-black to light green and containing several layers of land plant remains. This unit is followed by 60 cm of green blocky shale while the remaining portion consists of alternating layers of blocky red and green shale containing small calcareous nodules (Fig. 1).

The spatial distribution of coprolites at this locality appears to be restricted to a lens of gray-green shale, thickest at its center and thinning both to the north and south. The original specimen was collected from a light green plant-bearing layer about 15 cm from the bottom of the formation. Further collecting has shown coprolites to be present as high as 2 m above the base, but they appear to be concentrated in the lowermost meter. Horizontally, they are limited to a

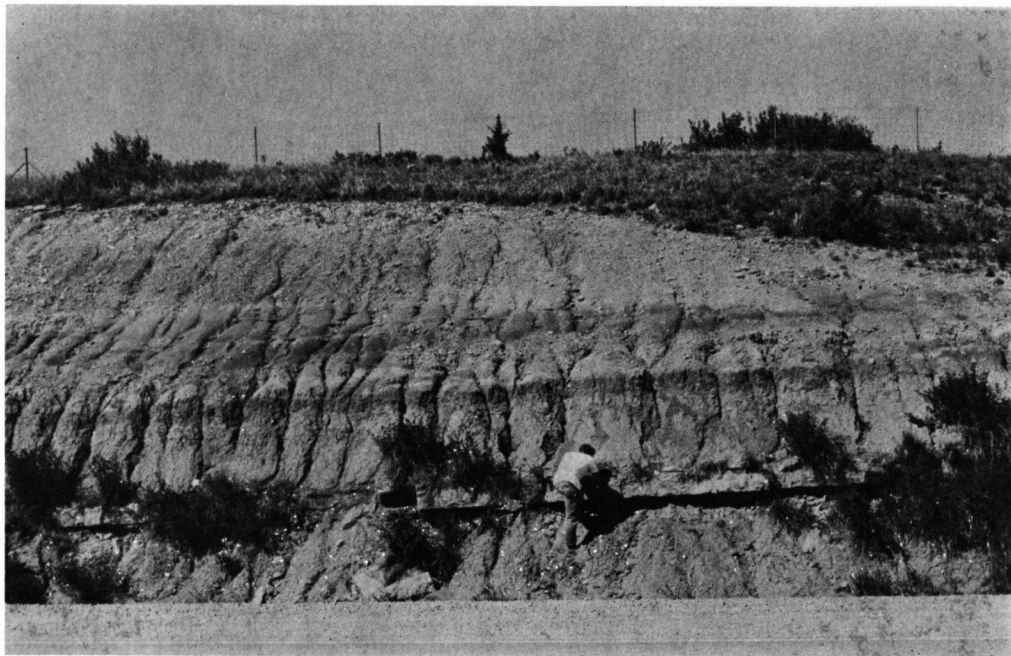


FIG. 1. Roadcut exposure of Wymore Shale from which the specimens were collected. The ledge-forming unit at the collector's waist is the Schroyer Limestone. The lens producing the specimens is delimited above by the first prominent color band and thins both to the left and right.

stretch beginning about 60 m south of the northern end of the cut and extending southward for about 15 m.

Approximately 100 kg of matrix were taken from the outcrop and some 50 kg of this were washed and picked for microfossils. In addition to spiral coprolites, smaller non-spiraled forms and fragments of both types were found. The residue contained carbonized plant fragments, limonite molds of plants (primarily *Pecopteris*), high-spired gastropods, gastropod opercula, ostracodes, small phosphatic worm? tubes, and arthropod (crustacean?) limb fragments.

Vertebrates are represented by the sharks *Xenacanthus* and *Helodus*, calcified cartilage, edestid dermal denticles, the lungfish *Monongahela* and another larger lungfish, possibly *Sagenodus*, fragmental lungfish scales, several small microsauro jaws (*Cardiocephalus?*), palaeoniscoid scales and teeth, and palatal elements of an undetermined form.

Sulfides are represented in the residues only by a few small euhedral crystals of pyrite while limonite flakes are exceedingly abundant. The great majority of these flakes are coatings on plant

debris, although a few of the microsauro jaws, pleuracanth teeth, and palaeoniscoid scales as well as several coprolites also show such coatings. The occurrence of limonite as flakes and coatings rather than three-dimensional particles, its presence on relatively non-degradable material such as scales and teeth rather than the coprolitic material, and the lack of concentration near those coprolites observed *in situ* suggest that the limonite was deposited epigenetically and is not altered pyrite precipitated during the decomposition of the faunal remains (see Zangerl, 1971).

Although a few quartz grains were found, very little detrital material above clay size is present in the residue. The faunal and floral elements and the lack of large detrital particles suggest an extremely quiet freshwater environment of deposition such as a marsh or swamp. There seems to be no evidence of anaerobic bottom conditions of the type found by Zangerl and Richardson (1963) in the Mecca and Logan Quarry Shales of Indiana. The total absence of articulated vertebrate remains in a quiet water, low energy environment of deposition conceivably may be due to the action of scavengers.

PREVIOUS INVESTIGATIONS

Coprolites were first described by Lister in 1678 although he was evidently uncertain as to their affinities (El-Baz, 1968) while Gideon Mantell (1822) was apparently the first to suggest an animal origin for them. Numerous specimens had been collected from the English Chalk but had been generally interpreted as aments or cones of the larch. As other naturalists of the day had begun to suspect they might be the remains of animals, Mantell and his brother made a collection of some 50 specimens and studied them in an attempt to solve the problem (Fig. 2).

Mantell's own comments notwithstanding, this is a remarkable series of observations. Elsewhere (1822, p. 158) under a discussion of fossil plants of the Chalk, he summed up his views of these fossils as follows:

"The constituent substance of the fossils, is precisely of the same nature as the vertebrae and other bones of cartilagenous fishes that occur in the Chalk; this resemblance is so striking, that it is with considerable hesitation I have noticed them in this place, being fully of the opinion, that they may hereafter prove to be parts of fishes."

It was William Buckland (1829) who coined the term "coprolite" and it was he who first recognized their true nature as fecal material. In his study of specimens from Lyme Regis in England, Buckland noticed that the most common type were spiraled in nature and resembled the intestinal passage of sharks and rays. Although Buckland made Roman cement casts of the intestines of sharks (Fig. 3), he attributed the bulk of the coprolites to ichthyosaurs. "The certainty of the origin I am now assigning to these coprolites, is established by their frequent presence in the abdominal region of the numerous small skeletons of Ichthyosauri, which together with many large skeletons of Ichthyosauri and Plesiosauri have been found in the cliffs at Lyme. . . ." In a later paper Buckland (1841) specifically referred the spiral forms to ichthyosaurs, suggesting that they possessed a spiral valve similar to that of modern sharks. Abel (1935) cites Gaudry, von Ammon, and Neumayer as having made similar mistakes due to the same line of reasoning. Gaudry attributed such coprolites to a labyrinthodont, *Actinodon*, and suggested it had a spiral valve. He was followed by von Ammon and Neumayer, both of whom assigned spiral coprolites to stegocephalians. It was Eberhard Fraas who pointed out that spiral coprolites are abundant in the German Muschelkalk and Keuper although ichthyosaurs and plesiosaurs are rare and that the coprolites are rare at Bad Boll and Holzmaden, well known for their ichthyosaur and plesiosaur skeletons (Abel, 1935).

In 1917, Smith Woodward aptly reviewed this information and pointed out that the spiral

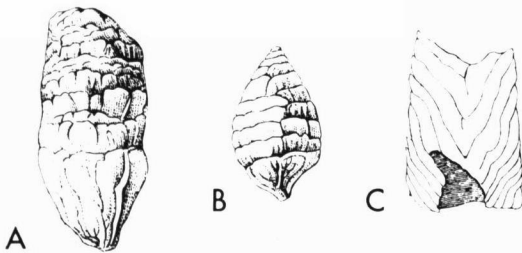


FIG. 2. Spiral coprolites from the Cretaceous Chalk of England similar to those studied by Mantell.—A, B. Two representative examples.—C. A longitudinal section of a spiral coprolite showing the imbricated layers (size not given, apparently nat. size) (modified from Buckland, 1841).

Mantell said he was unable to offer anything new on the subject but mentioned the following points:

1. The constituent substance of coprolites is precisely of the same nature as that of the vertebrae and other bones found in the Chalk Formation.
2. Some specimens have scales of fishes attached to them.
3. They differ from cones in that the imbricated layers do not proceed from a common axis (i.e., they are not in a cone-in-cone arrangement), but form one continuously wound spiral coil.
4. Some specimens show a hollow cavity on one end which is usually filled with marl (the matrix).

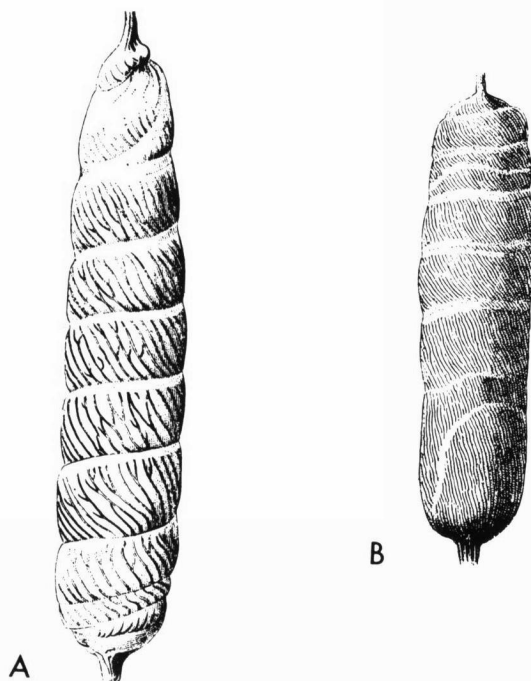


FIG. 3. Intestines of the two most common English species of dogfish injected with Roman cement. The vascular structure is still apparent in the desiccated membrane (A is 0.67 nat. size, size of B not given (modified from Buckland, 1841).

forms had never been found in any of the skeletons considered. Furthermore, wherever spiral coprolites were found, the remains of sharks, especially *Acrodus* and *Hybodus*, were also present. He then referred spiral coprolites to sharks, where they would be “normal” rather than to reptiles or amphibians where they would not be, and included as rather impressive proof a figure of the Devonian shark *Cladoselache clarki* from the Cleveland Shale of Ohio showing a spiral fecal mass in the pelvic region (Fig. 4). He was apparently unaware of the work of several previous investigators who had published similar figures. In 1893, Bashford Dean had described *Cladoselache newberryi* from the Waverly Formation of Ohio, which shows a spiral coprolite preserved in the region of the pelvic fins. He stated (1893, p. 117) that it “is especially interesting since it furnishes a cast of the intestinal wall and gives direct evidence as to the presence of a spiral valve.” Another specimen of *Cladoselache* containing a spiral valve had been illustrated by Claypole and

Wright (1893) although these authors do not discuss its significance. Four specimens of pleuracanth sharks, belonging to *Pleuracanthus parallelus* and *P. carinatus*, and two specimens of *Xenacanthus decheni*, were figured by Fritsch (1895) who interpreted both these and isolated spiral coprolites as fossilized intestines. More recently, another example was mentioned, but neither described nor figured, in Zangerl and Richardson’s monumental work (1963, p. 142) *The Paleocological History of Two Pennsylvanian Black Shales*: “In a mutilated shark specimen (PF2207) irregularly formed intestinal content is followed in the pelvic area by a spiral fecal mass.”

In several of the examples mentioned by Woodward (1917), Claypole and Wright (1893), and Fritsch (1895, pl. 98), it seems obvious that the spiral fecal mass represents the fossilized spiral valve itself (Fig. 5). However, in both the specimen figured by Dean (1893) and that mentioned by Zangerl and Richardson (1963) the coprolite is in the region of the pelvic fins and in those figured by Fritsch (1895, pl. 92, fig. 2 and pl. 97) the coprolite is actually displaced from the body. Although there may be a tendency to interpret the latter specimens as coprolites *sensu stricto*, it may well be that the intestine has merely slipped out of place after the death of the shark. That this situation frequently occurs after the deaths of modern sharks is seen in the following remarks to laboratory students in Hyman’s comparative anatomy text: “Beyond the duodenum the intestine widens considerably, and its surface is marked by parallel rings. These rings are the lines of attachment of a spiral fold, the *spiral valve* which occupies the interior of the intestine. (A portion of the intestine often protrudes through the anus and should be pulled back into the coelom by grasping the portion in the cavity and exerting a gentle pull.)” (Hyman, 1942, p. 256).

Although Buckland was obviously wrong in assigning spiral coprolites to ichthyosaurs, he made several noteworthy contributions to the study including the suggestion that the linear surface markings on the specimens are related to folds in the intestine, and identifying the “fir cones” of the Chalk as coprolites.

The first occurrence of coprolites in North America was reported in a letter from DeKay to Buckland. This letter together with Buckland’s reply was published in the *Philosophical Maga-*

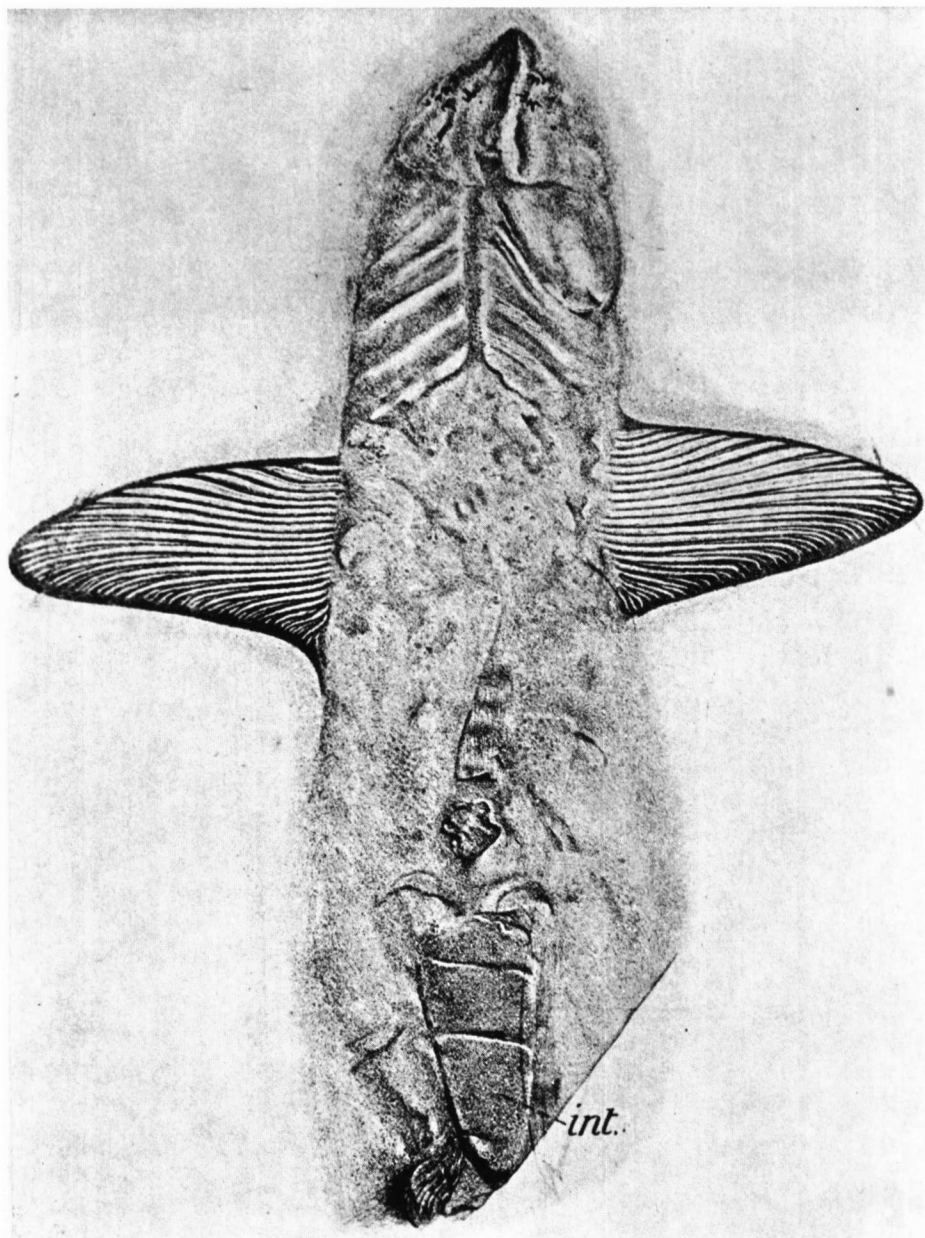


FIG. 4. Ventral view of a shark (*Cladoselache clarki*) from the Upper Devonian of Berea, Ohio, showing the intestine (*int.*) with a spiral valve, filled with partially digested food, $\times 0.17$ (British Museum, No. P.9271; from Woodward, 1917).

zine in May of 1830. It is interesting to note that the coprolite concerned is one of the spiral type. Concerning the specimen, Dekay wrote: "My imagination may possibly be too vivid, but in the confused irregularly impressed lines on the surface of my coprolite, I feel sure that I detect the

marks left by the membranous coats of the smaller intestine."

Although the locality is not specified, the specimen was collected from the Cretaceous of New Jersey. In a popular account of fossils, Case (1967) has figured two specimens from the Cre-

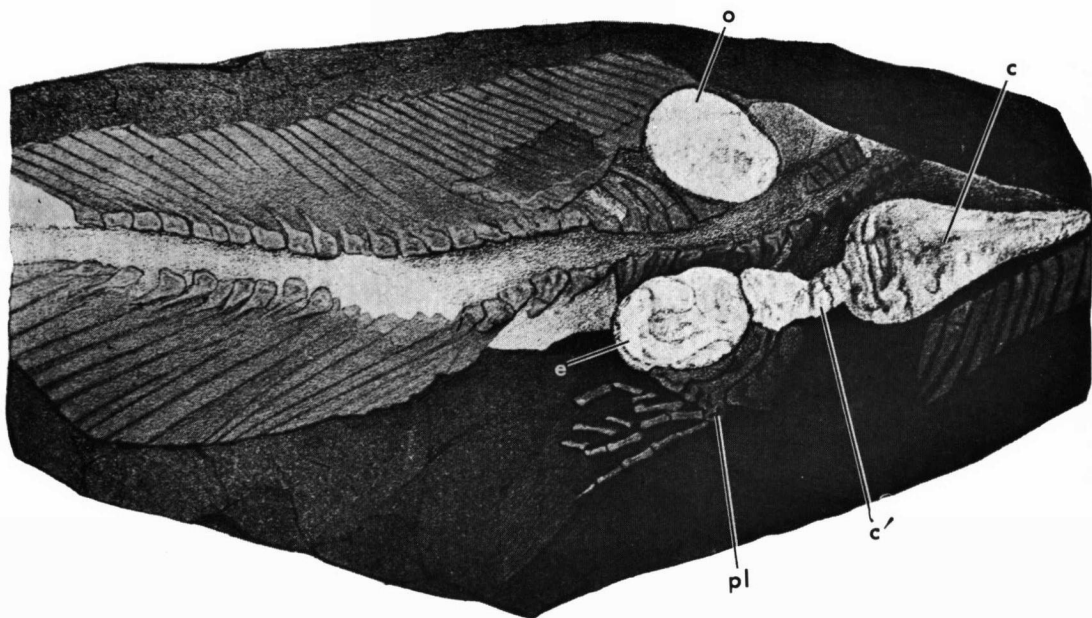


FIG. 5. Hind portion of a complete specimen of *Xenacanthus decheni* Goldfuss, with the spiral valve in its natural position, from Lower Permian Rothen Plattenkalk from Ruppertsdorf bei Braunau, Bohemia, Czechoslovakia. Length of slab equals 19.5 cm (from Fritsch, 1895). [Explanation: *c*, spiral valve; *c'*, apparently a cast of the cloaca; *o*, supposed "egg"; *e*, suggestion of an embryo; *pl*, basal elements of one of the pelvic fins.]

taceous Navesink Formation of New Jersey, very probably the same formation which yielded DeKay's specimen. It should be noted here that Case's assignment of these forms to either *Amia* or *Enchodus* is highly doubtful, especially in view of the fact that abundant shark and ray remains as well as those of chimaeras are present in the formation. To be sure *Amia* has a spiral valve, but the complexity of the coiling in the coprolites makes it much more likely that they belong to one of the other forms cited.

In 1843, Lea exhibited several specimens of foreign coprolites to members of the American Philosophical Society in order to promote interest in their study. He commented on the spiral nature of some of them and suggested that they had been produced by passage through a spiral valve (Lea, 1843).

Two types of spiral coprolites were recognized by Neumayer (1904) in his paper on the Permian spiral coprolites from Texas. Type A, which he called heteropolar, is characterized by a relatively large but variable number of closely spaced spiral turns concentrated on one end of the coprolite (Fig. 6, *A,B*), and type B, which he called amphipolar, characterized by a relatively small number

of widely spaced spiral turns extending the length of the specimen (Fig. 6, *C,D*). As has been previously mentioned, he followed the lead of Gaudry and attributed these coprolites to stegcephalians. More specifically, he assigned the larger heteropolar type to the rhachitome *Eryops* and the smaller amphipolar type to the nectridean *Diplocaulus*.

A number of spiral coprolites were figured in a description of the fauna of the Dunkard Series of Ohio (Stauffer and Schroyer, 1920). The specimens were broken into two groups, essentially those of Neumayer, and the smaller forms were assigned to fishes. Concerning the larger or heteropolar forms, these authors state the following (p. 147): "Dr. Williston says they are evidently from amphibians and cannot be distinguished from those that occur abundantly in the Permian of Texas."

Besides the Texas Permian, at least two other areas have produced copious quantities of spiral coprolites. Price (1927) reported on a collection of over 1,000 specimens from the Upper Pennsylvanian of West Virginia, and Johnson (1934) on several thousand from Chaffee and Park Counties, Colorado, of about the same age. Although both

heteropolar and amphipolar types occur in both areas, the latter are very much in the majority. Price suggested that the amphipolar type has been produced by the action of a simple spiral valve such as that which was probably present in the palaeoniscoids, while the heteropolar form has been produced by sharks which have a complex spiral valve. An analysis of associated teeth and scales shows that palaeoniscoid remains are much more abundant than shark remains, lending support to this interpretation.

Two spiral coprolites from the Triassic of West Texas were figured by Case (1922) and attributed by him to dipnoans although this assignment was not supported by evidence.

Two further studies (Moran and Romer, 1952; Vaughn, 1963) mention spiral coprolites but do not discuss them in detail.

It appears that spiral coprolites have had a rather varied taxonomic history. Following the previously mentioned description of *Cladoselache newberryi* by Bashford Dean, two authors, E. D. Cope and Arthur Hollick, noted the similarity of the coprolite preserved in the shark skeleton to other fossils. The following comment by Hollick was published by Dean (1893):

"One part of Dr. Dean's investigations throws an unexpected light upon a matter in which I am much interested, and in regard to which there has always been a great diversity of opinion.

"I refer to certain peculiar screw-like fossils which have been described from time to time, both in this country and abroad, under the names *Spiraxis*, *Spirangium*, *Palaeoxyris*, *Paleobromelia*, *Fayolia* etc. It may perhaps be remembered that Dr. Newberry described two species from the Chemung Sandstone, under the names *Spiraxis major* and *Spiraxis randalli*, in the Annals of the Academy (vol. III 1885, 217-220, Pl. XVIII). His descriptions and figures and the type specimens upon which they are founded are here for comparison, and we can hardly doubt that they are identical with the coprolite figured by Dr. Dean from the intestine of the shark.

"These fossils have been referred by different investigators to *Xyris*, *Bromelia*, *Chara*, stems of algae, etc. Dr. Newberry did not venture any positive opinion as to their affinities, but mentioned incidentally their possible reference to algae or sponges. . . .

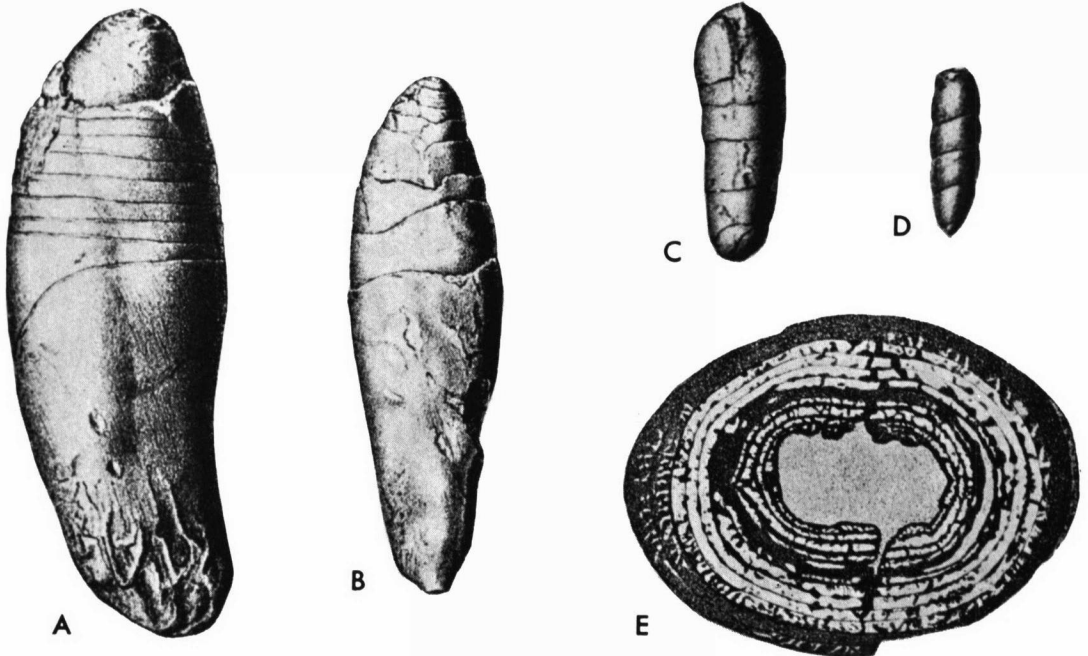


FIG. 6. Spiral coprolites from the Permian of Texas.—A, B. Heteropolar spiral coprolites.—C, D. Amphipolar spiral coprolites.—E. Cross section of a heteropolar spiral coprolite showing alternating layers of light and dark materials. (A-D, $\times 1.5$, size of E not given, approx. $\times 5$ (modified from Neumayer, 1904).

“Of course we cannot say that all the fossils mentioned may be referred to the same source, but in regard to the specimens from the Chemung there can hardly be any doubt, and as all or nearly all others are likewise from rocks representing geologic horizons in which sharks were plentiful, we may at least assume the probability of a similar origin for all.”

Several years later Cope (1895) made similar comments on the same subject. The affinities of the genera mentioned by Hollick have been discussed at length by various authors. The current opinion is that most of these forms are the egg cases of elasmobranchs (Crookall, 1932). While most of the forms discussed are obviously not coprolites, it should be noted that those specimens described by Newberry (1885) as *Spiraxis* and later referred by Crookall to *Fayolia* (see especially Crookall, 1930, pl. 4, fig. 6) bear an uncanny resemblance to a natural cast of a spiral valve.

Numerous authors have mentioned the general morphologic similarity of spiral coprolites to certain land snails. Fritsch (1907, p. 15) stated that spiral coprolites actually have been described as land snails in America. He was apparently referring to Dawson (1855, p. 160-163) who described an apparent spiral coprolite from the Upper Carboniferous Joggins Formation as a land snail.

Another case of mistaken identity is reported in a semipopular account of the Mazon Creek Fauna (Langford, 1963). Several specimens of spiral coprolites are figured, two of which according to Langford, were apparently mistaken for insect larvae by Scudder.

The majority of authors writing on spiral coprolites have considered them to be coprolites in the strict sense (i.e., excreta) and have usually attributed them to forms having a spiral valve. In addition, there is usually a vague suggestion that the fecal matter coils up in some fashion after leaving the spiral valve. Perhaps the best explanation of this sort is that offered by Buckland (1841):

“These cone-shaped bodies are made up of a flat and continuous plate of digested bone, coiled round itself whilst it was yet in a plastic state. The form is nearly that which would be assumed by a piece of ribband, forced continuously forward into a cylindrical tube, through

a long aperture in its side. In this case, the ribband moving onwards, would form a succession of involuted cones, coiling one round the other, and after a certain number of turns within the cylinder, (the apex moving continuously downwards) these cones would emerge from the end of the tube in a form resembling that of the coprolites. In the same manner, a lamina of coprolitic matter would be coiled up spirally into a series of successive cones, in the act of passing from a small spiral vessel into the adjacent large intestine.”

In discussing spiral coprolites from the Mecca and Logan quarries of Indiana, Zangerl and Richardson (1963) suggested that the plasticity of the fecal matter may be an important factor in the formation of spiral coprolites:

“Some coprolites show fairly but not perfectly regular spiral structure internally; in others the spiral arrangement is incomplete, and in some it may be very irregular and barely recognizable; furthermore there are many fecal masses without spiral structure, although we may (to judge from the size) confidently assume that they were shed by sharks. In addition to these, there are fecal masses that formed splatters and were obviously poorly consolidated. These observations tend to suggest that the development of a spiral fecal mass is related to the consistency of the fecal matter in the lower portion of the intestine.

“A rubber cast of the lumen of the spiral intestine of a modern shark shows that the fecal mass has the shape of a spiral ribbon. Upon extrusion into the rectum, given proper plasticity, it would probably roll itself into a more or less perfect coil. Deviation in either direction from the plasticity optimum would probably result in imperfect coiling or in lack of spiral structure.”

Anton Fritsch (1895) was apparently the first to suggest that isolated spiral coprolites were fossilized spiral valves and not simply coiled fecal material. In a later paper, Fritsch (1907) discussed his specimens in greater detail and although he was explicit in interpreting these fossils as spiral valves, he did not discuss his reasons for doing so. He did, however, state that one seldom finds these structures within the body cavity but pressed out and lying beside the skeleton. Pre-

sumably, this relationship occurred with sufficient regularity to convince him that they were all intestines. As these fossils are not to be regarded as excreta, Fritsch proposed the term "enterospira" for fossilized spiral valved intestines. Agassiz (in Buckland, 1841) had earlier suggested the term "cololite" for petrified fish intestines. However, as Fritsch's term is more specific, and in deference to Fritsch's contributions, it is recommended that the term enterospira be applied where appropriate.

This interpretation of spiral coprolites as fossilized spiral valves was also suggested by Neumayer (1904) in his paper on the Permian specimens from Texas. Although his opinions as to the affinities of these specimens have largely been disregarded, Neumayer's discussion is quite interesting. His conclusions are based primarily on the morphology of the heteropolar type and may be summarized as follows:

1. Numerous closely spaced spiral turns are visible on one end of the coprolite.
2. In cross section, the coprolites are seen to appear as a tight spiralling coil of alternating light and dark bands (Fig. 6,E). The dark bands are fecal ground mass and have abundant inclusions of bone. The light bands represent the replaced intestinal flap.
3. Where the outer layers have spalled off, the individual whorls are seen to dip in toward the center forming a nest of cones.
4. The last spiral turn trails off in much the same manner as the last turn of the valve in the modern lungfish *Neoceratodus*.

Neumayer argues that if the coprolites are excreta, the spiral turns should be present throughout the length of the pellet or should be obliterated throughout the length of it.

FECAL MATERIAL OF MODERN FISHES

In a fairly comprehensive survey of the literature on recent sharks I was unable to find anything on the shape of modern shark fecal pellets, or indeed, to confirm that fecal pellets *per se* exist.

In a further attempt to obtain information on this subject, I wrote Dr. Perry W. Gilbert of the Mote Marine Laboratory in Sarasota, Florida. Dr. Gilbert (states the following written communication):

"As far as I know, the material egested from the cloaca of a shark is either in a liquid or loosely viscous form. We have never found pellets of any type in our shark pools at the Lerner Marine Laboratory on Bimini or at the Mote Marine Laboratory in Sarasota."

The above is, of course, negative evidence and cannot be used to support the idea that the fossil specimens concerned are spiral valves. The physiology and eating habits of these sharks may have been substantially changed in transferring them from their marine environment to a tank. In addition, these modern sharks are wholly unrelated to the Permian pleuracanth sharks in the faunas with which most of the spiral coprolites are associated.

On the other hand, it should be noted that spiral fecal pellets do exist in modern fishes. Bashford Dean (1903) has figured spiral fecal pellets produced by the African lungfish *Protopterus*

annectans (Fig. 7). In addition, a long-nosed gar, *Lepisosteus osseus*, kept as a pet in the Museum of Natural History at the University of Kansas periodically produces spiral fecal pellets of a similar type.

It should be noted that the pellets produced by both the lungfish and the gar are the amphipolar type of Neumayer and not the more complex heteropolar type on which he based his interpretations.

It seems quite reasonable to assume, then, that the amphipolar forms are truly coprolites and may well have been derived from palaeoniscoids as suggested by Price (1927).

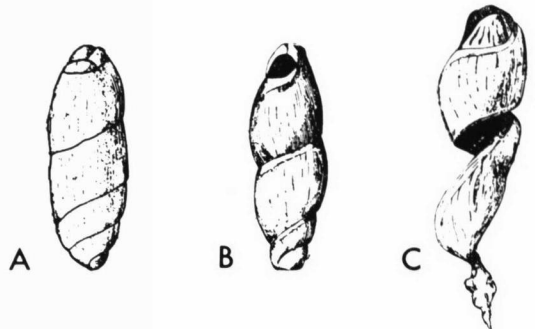


FIG. 7. Fecal material of the modern lungfish *Protopterus annectans*.—A. At the time of deposition.—B. After remaining in water several hours.—C. After twenty-four hours (A-C, approx. $\times 1.5$) (from Dean, 1903).

DESCRIPTION OF THE KANSAS SPECIMENS AND COMPARISON WITH MODERN SPIRAL VALVES

GROSS MORPHOLOGY OF MODERN SPIRAL VALVES

Owen recognized two types of spiral valves which he called longitudinal and transverse valves (Parker, 1885). The longitudinal valve consists of a flap of skin attached in a sinuous line running longitudinally along the intestine and having a width approximately two-thirds its length. The flap is therefore rolled upon itself in a scroll-like fashion. This type of valve is present in the hammerhead shark and in certain members of the Carchariidae (Fee, 1925). Denison (1941) has also shown it to have been present in the Devonian antiarch *Bothriolepis*.

The transverse valve is the more typical form and may be visualized by thinking of a wood auger encased in a hollow tube, producing a hollow, spirally coiled canal for the passage of food. This analogy is essentially correct if one envisions the origin of the spiral flap as taking place on, and growing from, the outer wall. Parker (1885) classified this type of valve into four categories based on the width of the flap:

1. Type A is one in which the width of the flap is less than half the inside diameter of the intestine. This leaves a hollow central canal in the valve through which material may move freely.
2. Type B refers to a valve in which the width of the flap is equal to half the intestinal diameter. In this type, the free ends fuse together to form a central core or columella. This valve type is that described as resembling a wood auger encased in a hollow tube.
3. Type C is a valve type in which the width of the valve exceeds the semidiameter, causing the shape of an individual turn of the valve to be thrown into a cone with its apex pointing posteriorly.
4. Type D is the same as above except that the apex points anteriorly.

In his study of the spiral valve in the genus *Raja*, Parker noted the extreme variability of the structure. He found that the following structures vary within the genus:

1. Length of the attached or outer edge in

EXPLANATION OF PLATES

(KU=University of Kansas, Museum of Natural History)

PLATE 1

Heteropolar "spiral coprolites" from the Lower Permian Wymore Shale near Manhattan, Kansas (Fig. 1-8); sections of whole specimens showing clay infilling (*c*) in posterior end. (Fig. 9-10). (All figures are $\times 1.67$)

FIGURE

- 1.—Large specimen showing numerous palaeoniscoid scales on the surface of the first whorl (KU 17851).
- 2.—Large specimen showing the tendency of individual whorls to spall off. Note that each successive whorl dips gently under the preceding one (KU 17852).
- 3.—Large broken specimen showing numerous palaeoniscoid scales in the interior. Prominent folds related to mucosal folds are well shown (KU 17853).
- 4.—Broken specimen showing prominent folds and the peculiar thin raised lip on the free edge of each successive whorl (KU 17854).
- 5.—Complete specimen in which successive whorls, though present, are indistinct (KU 17855).
- 6.—Specimen with prominent raised lip and numerous, inclined folds (KU 17856).

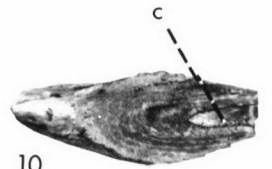
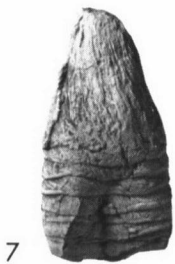
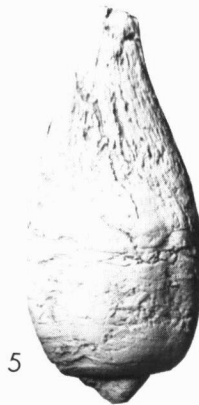
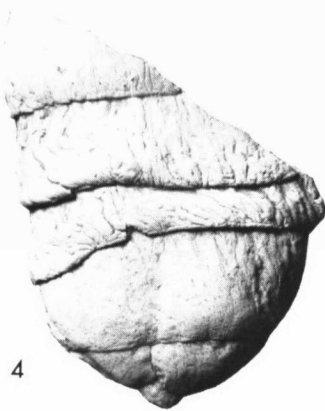
- 7.—Small specimen with prominent raised lip and individual folds. The posterior end has collapsed, a feature seen in many specimens (KU 17857).
- 8.—Small, somewhat atypical specimen (KU 17858).
- 9.—Cross section near the posterior end (KU 17859).
- 10.—Longitudinal section (not quite median). The darkened, rounded area behind the clay infilling is a hollow cavity which was never filled with matrix (KU 17860).

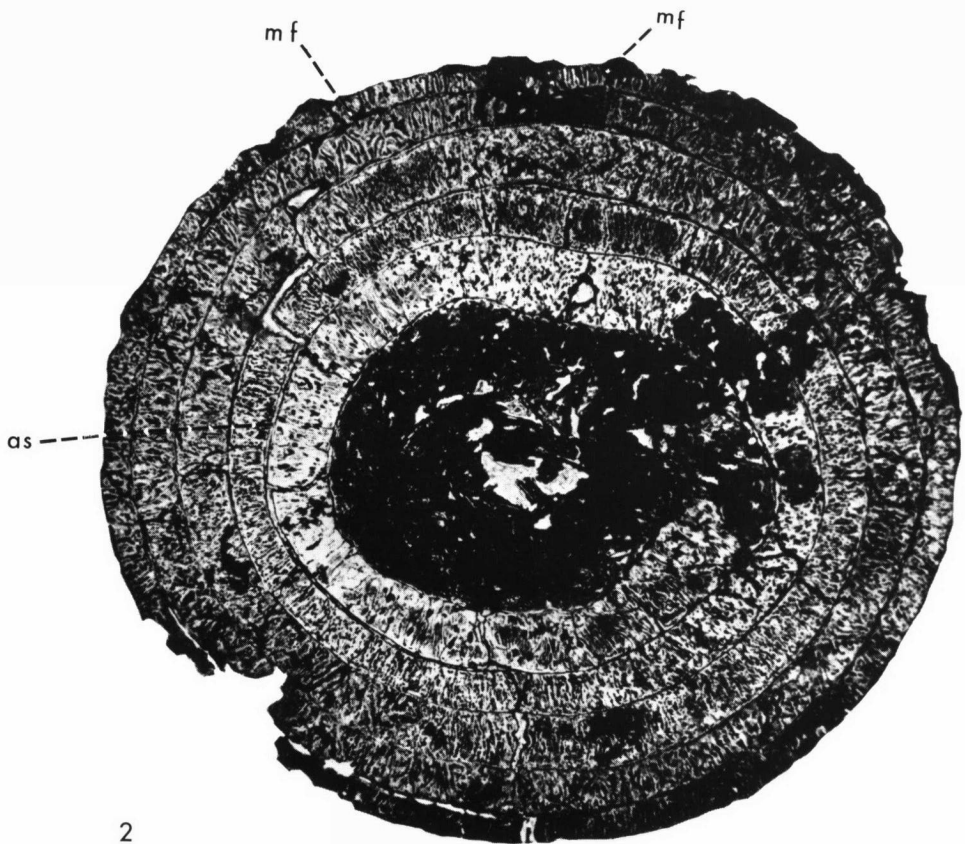
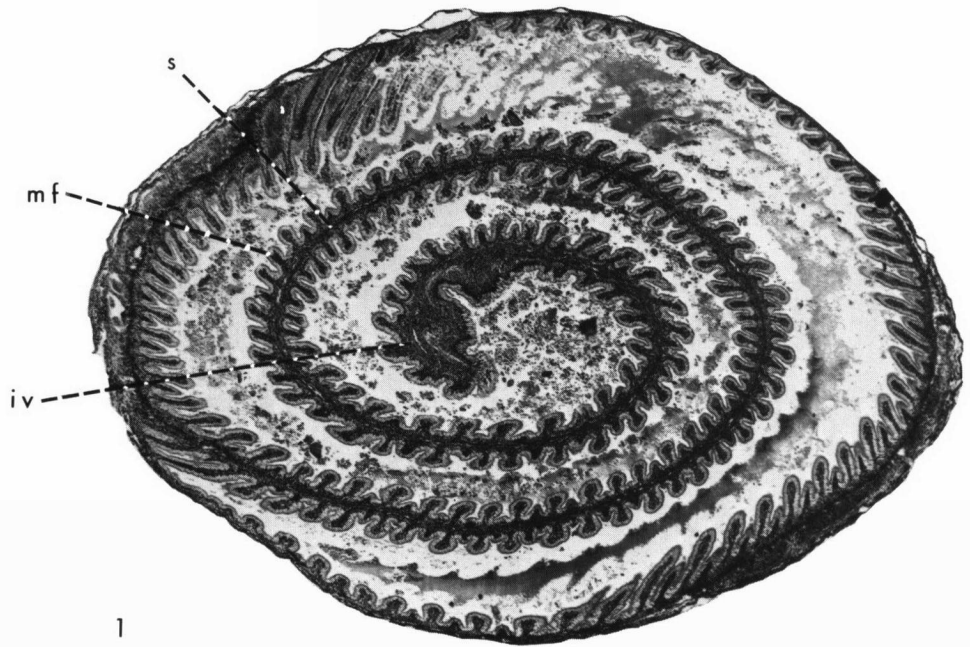
PLATE 2

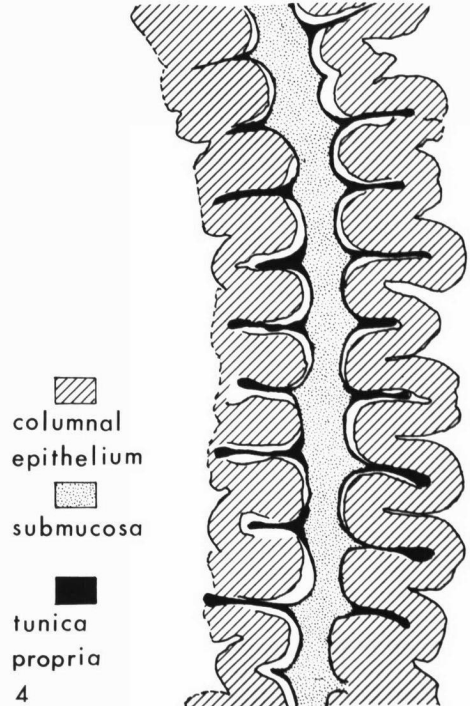
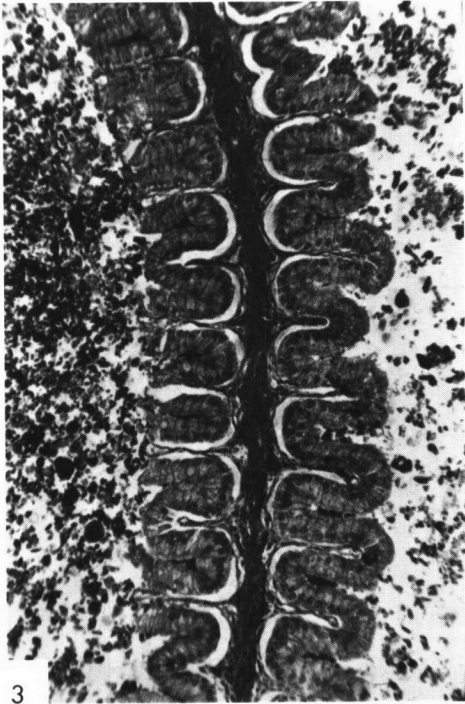
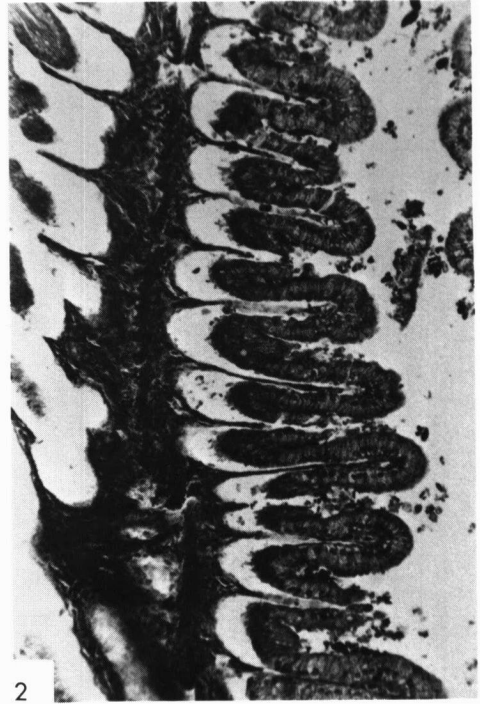
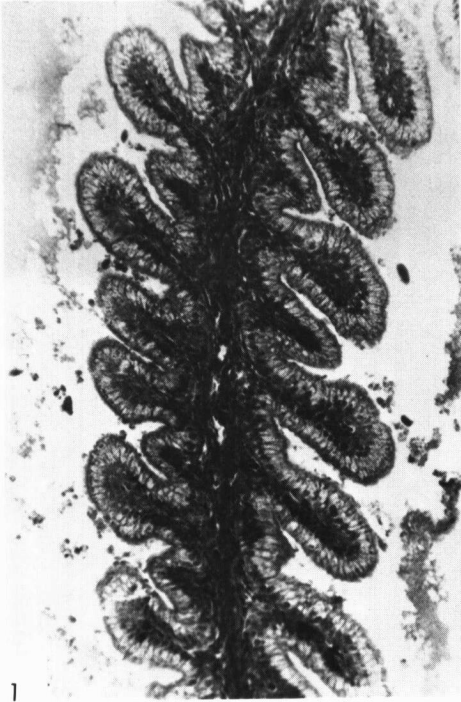
Cross sections of the spiral valve in *Squalus acanthias* and a Texas Permian "spiral coprolite."

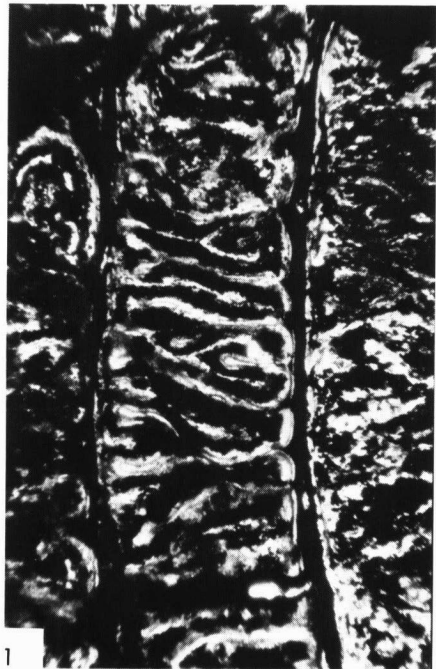
FIGURE

- 1.—Cross section of the spiral valve in the modern dogfish, *Squalus acanthias*, stained with Mallory Triple stain, $\times 21.7$ (KU 17861 Sec. 1). [Explanation: *iv*, intra-intestinal vein; *mf*, mucosal folds; *s*, submucosa.]
- 2.—Cross section through a heteropolar "spiral coprolite" from the Lower Permian, Wichita Falls, Texas, $\times 6.8$





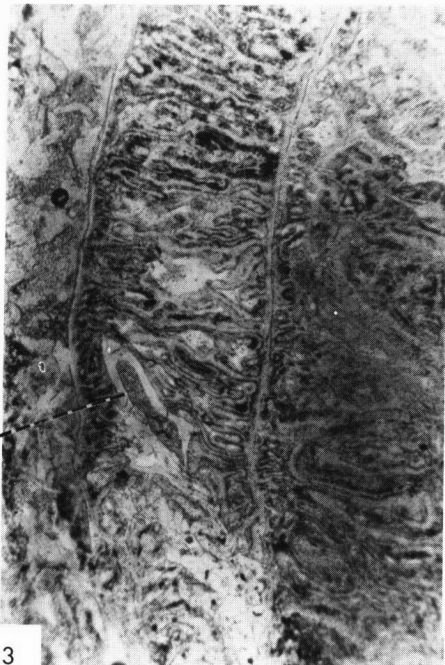




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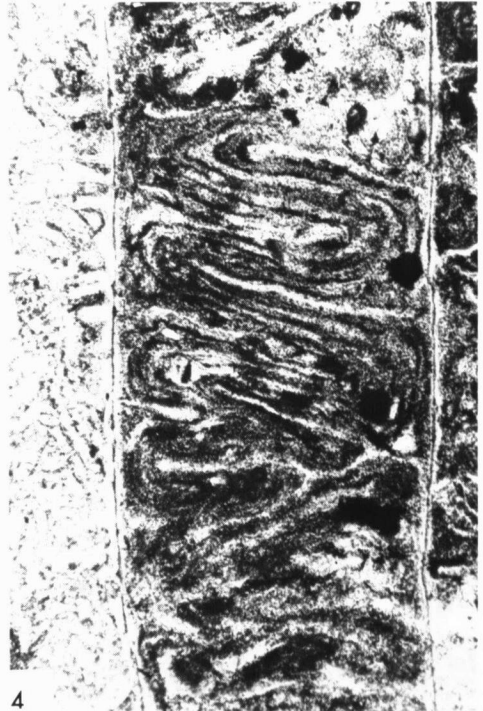
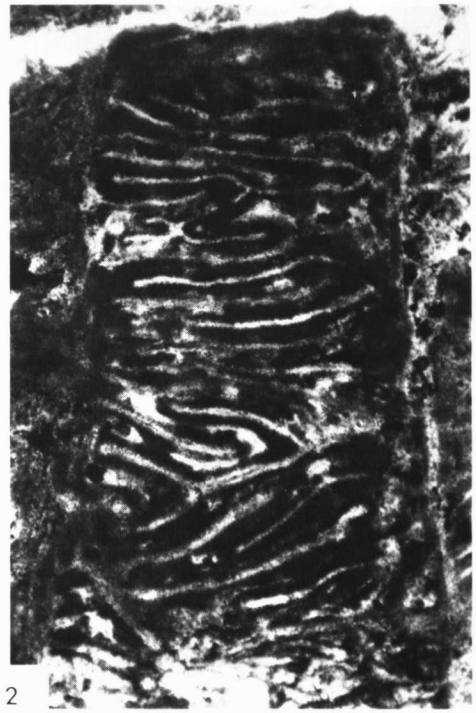
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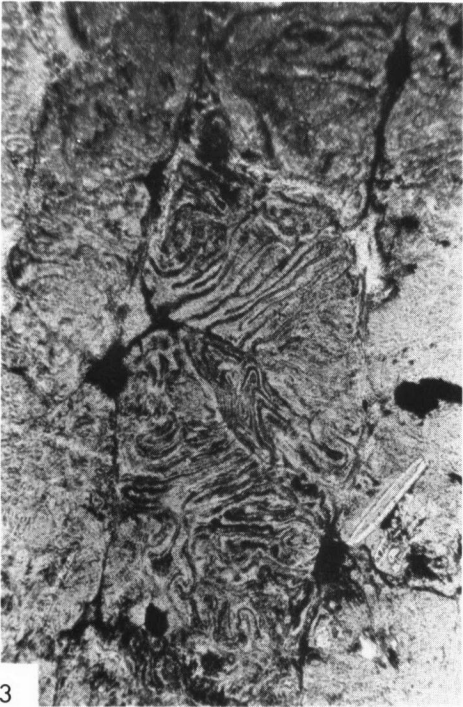
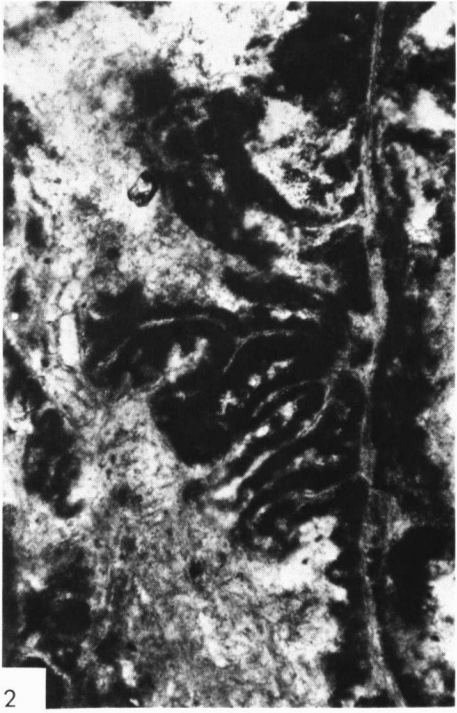


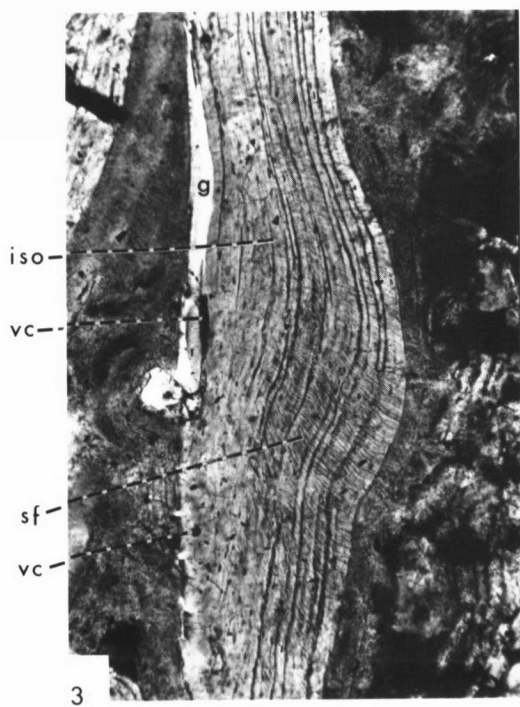
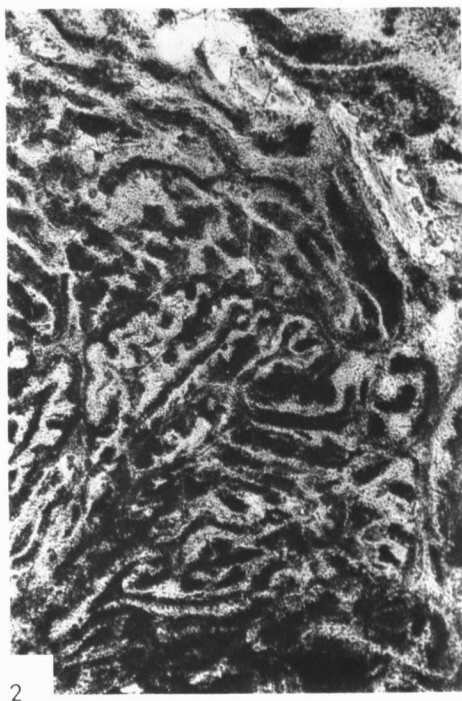
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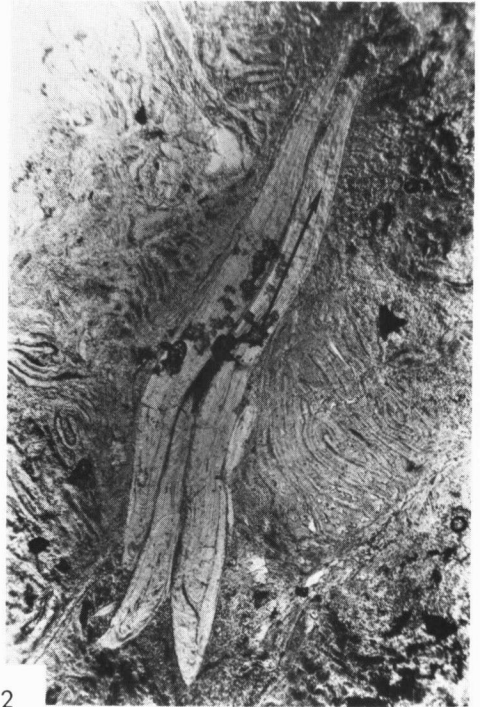
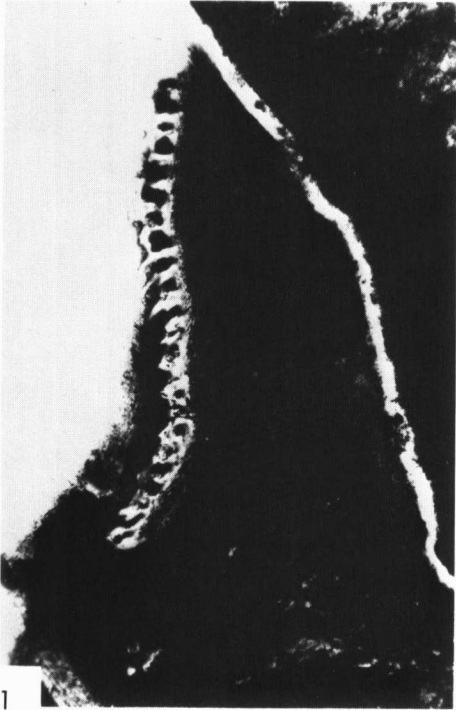


4









(KU 17862 Sec. 8). [Explanation: *as*, area of the submucosa; *mf*, mucosal folds.]

PLATE 3

Histologic details of the spiral valve in *Squalus acanthias* (stained with Mallory Triple stain). (All figures are $\times 106$.)

FIGURE

- 1.—Portion of one individual whorl of the spiral valve in *Squalus acanthias* showing mucosal folds and the various tissues in their normal relationship (KU 17861 Sec. 2).
- 2.—Portion of the spiral valve in another section (KU 17861 Sec. 3) in which the tunica propria has separated from the columnal epithelium.
- 3.—Histologic section of another area (KU 17861 Sec. 3) similar to the above.
- 4.—Semidiagrammatic representation of the relationship of the tissues seen in fig. 3.

PLATE 4

Histologic details of fossil specimens.

FIGURE

- 1.—Photomicrograph of well-preserved area in a heteropolar "spiral coprolite" from the Lower Permian, Wichita Falls, Texas (KU 17862 Sec. 6). The section shows portions of two successive turns of the valve and related mucosal folds, $\times 37.5$. Several may be seen to bifurcate.
- 2.—Enlargement of a portion of fig. 1. Note the double layering of the mucosal folds, the fact that the tissue is continuous from one fold to the next, and the shape of the hematite infilling in the area of the submucosa (*as*), $\times 106$.
- 3.—Photomicrograph of an area comparable to fig. 1, seen in a Manhattan, Kansas, specimen (KU 17863 Sec. 1). Portions of two successive turns of the valve are seen. Mucosal folds are preserved on both sides of the right or inner whorl, while only the inner folds are preserved on the left or outer whorl. Note the large bone fragment (*b*) passing through in the process of digestion, $\times 45$.
- 4.—Enlarged view of fig. 3. Mucosal folds (*mf*) are seen to bend around the bone fragment as it moves through in the digestive process. Relative movement is from bottom to top, $\times 106$.

PLATE 5

Diversity in mucosal folds.

FIGURE

- 1.—Complex branching folds seen in a specimen from the Lower Permian Putnam Fm. near Bellvue, Clay Co., Texas (KU 17864 Sec. 10), $\times 117$.
- 2.—Thin bifurcating folds in a Manhattan, Kansas, specimen (KU 17863 Sec. 5), $\times 106$.
- 3.—High thin folds from two successive whorls which apparently interdigitate (KU 17863 Sec. 1), Manhattan, Kansas, $\times 106$.

- 4.—Complex "concentric" folds with a fingerprint-like appearance (KU 17865 Sec. 4), Manhattan, Kansas, $\times 117$.

PLATE 6

Complex mucosal folding in Manhattan, Kansas, specimens.

FIGURE

- 1.—Two complex arborescent folds analogous to the valve of Kirkring in the mammalian intestine (KU 17866 Sec. 10), $\times 45$.
- 2.—Enlarged view of the upper folded structure seen in fig. 1, $\times 106$.
- 3.—Complexly folded structure (KU 17867 Sec. 2), $\times 45$.
- 4.—Enlargement of same, $\times 117$.

PLATE 7

Complex folding with glandular appearance and bony inclusions. All specimens from the Manhattan, Kansas, locality.

FIGURE

- 1.—Complex folded structure seen in a Manhattan, Kansas, example (KU 17867 Sec. 4). The structure is difficult to interpret but has a distinct glandular appearance (see fig. 2), $\times 37.5$.
- 2.—Enlargement of the complex fold seen in fig. 1, $\times 117$. The glandular appearance is striking.
- 3.—Histologic details of an included palaeoniscoid scale (KU 17868 Sec. 2), Manhattan, Kansas, $\times 106$. [Explanation: *g*, ganoin; *iso*, isopidine (laminated compact bone); *sf*, Sharpey's fibers; *vc*, vascular canal.]
- 4.—Histologic details of an unidentified scale (haplolepid palaeoniscoid?) (KU 17863 Sec. 7), Manhattan, Kansas, $\times 106$. [Explanation: *dt*, dentine tubules; *vc*, vascular canal.]

PLATE 8

Bony inclusions and fecal groundmass. (All specimens from the Manhattan, Kansas, locality.)

FIGURE

- 1.—Lungfish scale at the extreme outer limit of the first lamina. The white space to the right of the scale is a void left by rotting of the submucosa (KU 17863 Sec. 10), $\times 106$.
- 2.—Stack of 3 palaeoniscoid scales passing through the valve in the process of digestion. Mucosal folds below (to the right) of the scales are being pushed aside. Relative movement is in the direction of the arrow (KU 17863 Sec. 2), $\times 45$.
- 3.—Bone fragment moving through the valve. Relative movement is in the direction of the arrow. The mucosal fold at the extreme right tip of the bone bends around the fragment while those above it have been pushed aside (KU 17863 Sec. 8), $\times 117$.
- 4.—Fecal ground mass in the center of the anterior end of KU 17863 Sec. 12. Note the bone fragment and total absence of folds, $\times 45$.

relation to the width of the intestine, upon which depends a) number of turns, and b) position of the posterior end of the valve.

2. Course and length of the inner or free edge, upon which depends a) direction of successive turns of the valve (i.e., anterior or posterior), b) surface area of the valve, c) width of the valve flap, and d) resistance offered to the passage of food.
3. Character of the mucous membrane, especially development and position of villi and longitudinal ridges.

Indeed, the only features he found constant were the position of the anterior edge of the valve and the course of the outer or attached edge.

All four types of valve, A, B, C, and D were found in the genus *Raja* as well as several transitional types. These marked variations in the valve were found to be independent of species or sex and wholly independent of the age of the animal. Parker dissected three rays not over three inches long and found all the variability exhibited in adults of the genus.

The spiral valves of two genera, *Raja* and *Scyllium*, are shown in Figure 8, A, B. Both valves consist of a series of cones with their apices directed anteriorly. In this example of *Raja*, the cones are not present posteriorly; instead, there is a central canal due to the narrowing of the valve flap in this region. In *Scyllium* the cones are steeply imbricated. A cast of this valve would show a series of elongate cones with the posterior-most ones dipping beneath those more anterior, while a cross section in the midregion or posterior region would appear as a spiral. With the exception of the first turn of the valve, the attached edge is essentially perpendicular to the long axis of the intestine and successive turns are more closely spaced in the posterior region than in the anterior. The drawing of the valve in *Raja* shows numerous, well-developed ridges of mucosa running along the valve flap and on the inside of the outer sheath. They are inclined at about 60 degrees to the long axis of the intestine and are essentially parallel to the path taken by food material in the process of digestion.

GROSS MORPHOLOGY OF KANSAS SPIRAL COPROLITES

Representative examples of the Wymore Shale

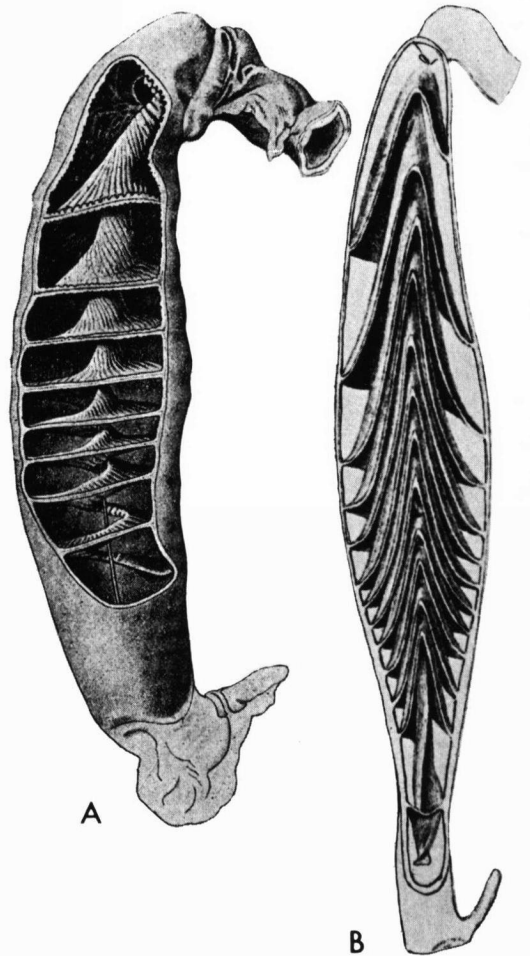


Fig. 8.—A. Valvular intestine of the ray *Raja*. Note longitudinal folds on the valve flap, nat. size (from Daniel, 1934, after Paul Mayer).—B. Spiral valve in the modern shark *Scyllium*, $\times 0.5$ (from Parker, 1885).

specimens are shown in Plate 1, figures 1-10. Among 38 more or less complete specimens, the length varied from 13 to 64 mm, with a mean of 27 mm, and the width varied from 6 to 30 mm, with a mean of 13 mm. This apparent 2:1 length to width ratio is somewhat misleading due to crushing of the specimens. Comparison of uncrushed examples from the Permian of Texas suggests that the true length to width ratio is probably 2.5:1.

It will be seen that all the specimens are of Neumayer's heteropolar type. The steeply imbricated whorls from a succession of "cones" bearing

a strong resemblance to the spiral valve of *Scyllium*. The pointed, uncoiled end apparently represents the first whorl of the valve while the broad, coiled end represents the posterior portion. As in the valve of *Scyllium*, posterior cones dip beneath more anterior ones.

The orientation of each of the whorls (i.e., the posterior edge of the ribbon) is essentially perpendicular to the long axis of the specimen. This fact suggests that simple coiling of fecal matter as suggested by Buckland is unlikely since fecal matter being coiled in the rectum would essentially be "fed" from above, causing successive whorls to be inclined rather than perpendicular to the long axis. This is, however, precisely the orientation of the outer or fixed edge of the valve.

A number of the specimens (see for example Pl. 1, fig. 7) have collapsed on the posterior end. Longitudinal sections often reveal a conical cavity with its base at the posterior end and its apex nearly halfway up the specimen. The cavity is invariably filled with matrix material, proving it was open at the time the enclosing sediments were deposited (Pl. 1, fig. 9, 10). This configuration is fully consistent with the morphology of the spiral valve and argues strongly against any interpretation of these specimens as fecal matter. If they were fecal pellets, the material would not only have to be coiled in such a manner as to leave a hollow conical cavity in the posterior end, but must have remained so after passing through a sphincter muscle in the anus.

Also present on many of the specimens (Pl. 1, fig. 4, 6, 7) are a series of subparallel folds inclined at an angle of about 60 degrees to the long axis. They are obviously related to the mucosal lining of the intestine, a fact recognized by DeKay as early as 1830. They are usually interpreted as sculpturing produced by the passage of fecal material over the mucosal folds but may also represent casts of mucosal folds on the outer sheath of the intestine.

One additional feature noted on a number of specimens is the presence of a thin, raised lip on the free edge of each whorl (Pl. 1, fig. 4, 6, 7). As shown by dissection of modern sharks, spiraling branches of both the anterior mesenteric artery and the anterior mesenteric vein occur at the junction of the fixed edge of the spiral valve and the outer intestinal sheath. The vein, the larger of the two, is more anterior and is located

in precisely the position of the peculiar raised lip. Unfortunately this structure has not been observed in thin section and it has not been possible to establish its origin with certainty although it should be noted that the modern lungfish fecal pellets (Fig. 7) show a similar structure. In the latter case the structure is probably due to casting of a small pocket at the junction of the spiral valve and the outer intestinal wall. A similar phenomenon may well be the cause of the raised lip seen in the fossil specimens.

CROSS SECTION OF A MODERN SPIRAL VALVE

As very little has been written on the detailed histology of the spiral valve in sharks, a number of histologic slides of the valve in an embryo of the common dogfish, *Squalus acanthias*, were made. Plate 2, figure 1, shows a section through the midregion of the valve. The overall structure is a prominent spiral fold of mucosa and submucosa which arises from the outer wall of the intestine and spirals toward the center of the lumen. Arising from this spiral flap are numerous smaller folds, the mucosal folds, consisting of an outer layer of columnar epithelial cells and a very thin central investment of tunica propria. The tunica propria, a thin connective tissue containing granule cells, leukocytes, basophilic mast cells, and eosinophils, is best seen where portions of the epithelium have torn away (Pl. 3, fig. 2). Note that it is continuous from one fold to the next. The apparent double layering of the mucosal folds seen in Plate 2, figure 1, is due to the darker staining epithelial cell nuclei at the base of those cells.

CROSS SECTION OF A SPIRAL COPROLITE

Plate 2, figure 2, shows a cross section of a specimen from the Permian of Texas. The general spiral nature of the section and the presence of numerous high, thin folds bears a striking resemblance to the histologic section seen above.

THIN SECTION STUDIES

A series of 200 thin sections made from 19 spiral coprolites reveals a remarkably complex series of folds originating from the area separating successive whorls (Pl. 4-7). The most reasonable

explanation for this structure seems to be that the area between successive whorls is actually the valve flap of the spiral valve, and that the numerous prominent folds are the folds of mucosa lining it. In general, the folds are much higher and thinner than those seen in the *Squalus* embryo. Many of the folds (Pl. 4, fig. 1; Pl. 5, fig. 2) are seen to bifurcate, a situation which does not occur in *Squalus sucklii* (Fee, 1925) or in my thin sections of *Squalus acanthias*. Such complex folds are present however, in the salmon *Oncorhynchus* (Greene, 1912) and in the shark *Scyllium* (Fig. 9).

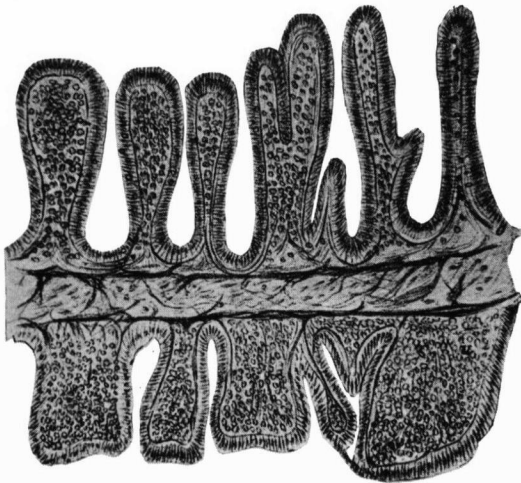


FIG. 9. A portion of the spiral valve in *Scyllium canicula*, $\times 85$ (from Edinger, 1877).

Specific details of the histology are often difficult to interpret due to differential preservation. The color of the folds varies from specimen to specimen, from anterior to posterior in the same specimen, and in some instances, from place to place in the same section.

It seems obvious that the mucosa including the tunica propria has been preserved. Plate 4, figures 1 and 2, show two photomicrographs of what is probably the best preserved and most comprehensible area I have seen in the entire series of thin sections.

High, thin, bifurcating mucosal folds are readily apparent and are seen to be double layered as in modern forms. The thin, gray line present in the folds marks the separation of the columnar epithelium and the central tunica propria. It is continuous from fold to fold and may either be the outer surface of the tunica propria or a mani-

festation of darker staining cell nuclei as seen in modern histologic slides.

As mentioned earlier, the tunica propria consists of a relatively fibrous connective tissue. The submucosa, however, is composed of a loose connective tissue characterized by a semifluid, somewhat gelatinous matrix of protein, mucopolysaccharide, and water, which is supported by a loose meshwork of collagenous fibers and, to a considerably lesser extent, reticular and elastic fibers (Patt and Patt, 1969).

In the thin section shown on Plate 4, figure 2, the position of the submucosa is occupied by a dark, black substance which seems to be hematite. Close examination of this region in many sections makes it apparent that the loose submucosa was only rarely preserved. In some instances it either has been replaced by another mineral or the void left by its decomposition was filled (compare the shape of the hematite filling to the shape of the submucosa in Pl. 3, fig. 3, 4). However, in others it appears that no infilling at all has occurred, a fact which explains the tendency for individual whorls to spall off in thin laminae (Pl. 1, fig. 2).

Preservation in general, and of the submucosa in particular, seems to have been more complete in the Kansas specimens than in those seen from the Texas redbeds. The latter almost invariably show evidence of mineral infilling (Fig. 10, 2) while the former seem to have preserved submucosa or a void with little or no such infilling (Fig. 10, 1). In addition, the mucosal folds seem to be more complex in the Kansas specimens than in those from the Texas Permian although specimens from both areas exhibit an astonishing diversity (Pl. 4-7). While some folds are relatively simple in structure and easy to understand, others are considerably more complex. Folds from adjacent whorls may interdigitate (Pl. 5, fig. 3), the mucosa may form what appears to be a series of concentric folds (Pl. 5, fig. 4), branch in an arborescent fashion analogous to the valve of Kirkring in the mammalian intestine (Pl. 6), or form complex structures with a distinct glandular appearance (Pl. 7, fig. 1, 2).

INCLUSIONS

Virtually all of the Kansas specimens show traces of bony material, primarily palaeoniscoid and lungfish scales. They are present both on the

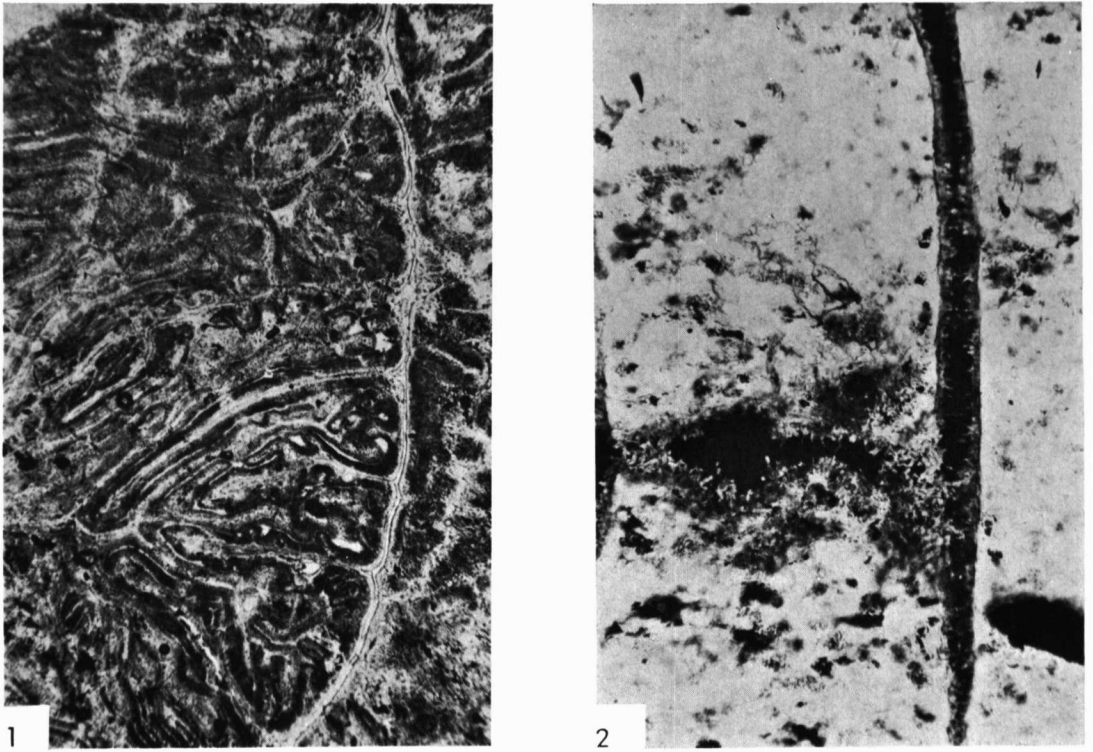


FIG. 10. Evidence of loss of submucosa in two specimens.—1. Complex mucosal folds in a Manhattan, Kansas, specimen. The thin white line at the base of the folds is a void left by rotting of the submucosa. This apparently explains the tendency of individual laminae to spall off in thin shells (KU 17863 Sec. 6), $\times 117$.—2. Area of exceedingly poor preservation in which the submucosa has decomposed leaving a void which was later filled in, first by a group of lath-shaped crystals (gypsum?) and later by hematite. Mucosal folds are lacking in this view but are seen elsewhere in the thin section (KU 17864 Sec. 13), Lower Permian Putnam Fm. near Bellvue, Clay Co., Texas, $\times 106$.

surface and in the interior as is seen where portions of individual whorls have spalled off (Pl. 1, fig. 1, 3). As might be expected, numerous inclusions are also seen in thin sections. The histologic detail of these inclusions is often quite well preserved (Pl. 7, fig. 3, 4).

These bone fragments are, of course, undigested food material in the process of passing through the valve and are discussed later in conjunction with the food chain. In many places they are seen to have pushed mucosal folds aside in the

course of their movement (Pl. 4, fig. 4; Pl. 8, fig. 2, 3). Another feature commonly seen in thin section is the failure of bony fragments to penetrate from one whorl to another. Many bone fragments are seen to abut against the base of an individual whorl but in 200 thin sections only two were seen to penetrate from one whorl to the next. In both of these instances, the bone fragments were very large in comparison to the diameter of the valve at that point and may well have punctured the flap during postmortem compression.

PRESERVATION

A detailed study of the morphology of the Kansas specimens shows that they are preserved intestines closely resembling those of the modern shark, *Scyllium*. The question naturally arises as

to how such delicate structures were preserved. One seemingly necessary factor is that, at the time of the death of the animal, the intestine be full of undigested or partially digested food matter. In

studying the valve of *Scyllium*, Parker (1885) made the following comment:

“There are twelve turns to the valve, all but the last of which are strongly deflected forwards, producing a structure which must offer an immense amount of resistance to the passage of the intestinal contents, and, of course, making a decidedly greater proportional increase of surface than in any of the cases recorded for the ray. The difficulty of cleaning out the intestine afforded a good criterion of the forms of these points; the finely divided contents stuck so tightly between the successive ‘cones’, that a stream of water was often quite insufficient to dislodge them. In fact chyle (if one may apply the term to what rather resembled fine mud) completely filled up the whole available space in the intestine, so that, although the animal was preserved entire in spirits, the gut and its valve were in as good a condition for examination as if the former had been carefully emptied and distended with spirit while still fresh.”

Whatever condition causes the intestine to be packed in such a manner, whether unusual eating habits, or some quirk of physiology, any animal dying with its intestine so filled would stand an excellent chance of having it fossilized.

When viewed with a petrographic microscope these intestines appear to consist almost entirely of calcium phosphate. A mass spectographic analysis showed major amounts of P and Ca and minor amounts of Si, Al, Mg, Mn, Pb, and Cu. These findings are in accordance with those of several authors (Dana, 1845; Bradley, 1946).

In an analysis of fossil mammal and reptile coprolites from the Eocene Bridger Formation, Bradley (1946) compared their composition to an analysis of modern dog feces and found the P_2O_5 content to be as high in the dog feces as in the

coprolites. The analysis yielded the following results:

<i>Modern Dog Feces</i>	<i>Percentage</i>
ignition loss	23.7
P_2O_5	31.5
CaO	40.3
sand	1.1
indet.	3.4
	100.0

Comparing the dry weight P_2O_5 content of herbivores and omnivores, Bradley obtained the following results:

<i>Animal</i>	<i>Dry Weight P_2O_5 (%)</i>
hog	0.66
steer	1.49
human	4.55

These data led Bradley to the following conclusions:

“It seems to be general that the mineralizing substance of coprolites is largely tricalcium phosphate. The analysis of carnivore feces given above perhaps suggests that only such fecal matter as is exceptionally rich in calcium phosphate becomes fossilized. This might account for the absence of coprolites that were unmistakably derived from herbivores.”

It seems quite likely that these intestines were packed with what was essentially an apatite paste in which undissolved bones and scales were floating. Due to its intimate association with the mucosal folds and the adjacent fibrous connective tissue, this paste solidified very early after the death of the animal and caused the preservation of these structures. The submucosa which was not in contact with the paste and which is not as dense and fibrous has, in most cases, rotted, leaving a void which was filled by secondary mineralization in some cases and left open in others.

DESIGNATION OF THE SPECIMENS

On the basis of morphological details, it seems readily apparent that the heteropolar specimens examined are fossilized spiral valves and not coprolites in the strict sense. Due to a general lack of understanding of the nature of these fossils, it is

felt that adoption of Fritsch's (1907) term *enterospira* may help to distinguish their true nature. Accordingly, this term is used in subsequent discussions.

TABLE 1. *Inclusions in Coprolitic Matter.**

	Palaeoniscoid	Lungfish	Arthropod limb	Nothing	Indet.	Other
Complete Enterolites	23/50	12/50	1/50	8/50	8/50	1 <i>Helodus</i> tooth plus calcified cartilage
Broken Enterolites	14/41	7/41	0/41	9/41	13/41	—
Structureless Coprolitic Material	11/23	1/23	10/23	1/23	1/23	1 Placoid scale 1 Palatal element (microsaur?) 1 Pleuracanth tooth

*Ratios of inclusions (food material) in various types of coprolitic material. The denominator denotes the total number of each type examined. The numerators add to a sum larger than the denominator since several specimens contained more than one type of inclusion.

ANALYSIS AND APPLICATION

As the Kansas enterospirae occur in rocks which do not contain articulated vertebrate remains, no association between the enterospirae and any of the other faunal elements is recognizable. Hence, it is impossible to refer them to a proper taxon with certainty. Those elements of the fauna known to have possessed a spiral valve are the sharks *Xenacanthus* and *Helodus*, the lungfishes *Monongahela* and *Sagenodus?*, and conceivably the palaeoniscoids. The spiral valve of palaeoniscoids was probably of the simple type seen in the modern gar, *Lepisosteus*. In addition palaeoniscoid scales as well as lungfish scales are abundant in the enterospirae, making it obvious that the "owner" preyed on these forms.

Xenacanthus is by far the most abundant of the two selachians and possessed a tearing type dentition while the crushing teeth of *Helodus* are much rarer. Furthermore, teeth of *Xenacanthus* are present at most of the Pennsylvanian and Permian localities where enterospirae are found (Stauffer and Schroyer, 1920; Price, 1927; Moran and Romer, 1952; Romer, 1958). *Xenacanthus*,

then, must be regarded as the most likely taxon with which to associate the Kansas enterospirae. However, this is in no way meant to imply that the many different forms referred to by various authors as spiral coprolites are pleuracanth enterospirae. As mentioned earlier, many of the forms described are probably true spiral coprolites.

Specimens from the Cretaceous Chalk of England are almost certainly not related to pleuracanth and may or may not represent enterospirae. This is almost certainly true for specimens found in many other localities and geologic horizons. Thin section studies and analyses of the related faunal assemblages are needed to interpret accurately specimens from each of these areas.

Bony inclusions in the Kansas specimens are tabulated in Table 1.

If it is accepted that the enterospirae present in the fauna are the intestines of pleuracanth, several interesting conclusions may be drawn from the data presented in this table.

Pleuracanth sharks were apparently the dominant predators in the fauna, subsisting primarily

on palaeoniscoids, with lungfish as a secondary source of food. As might be expected, broken enterospirae show essentially the same ratio of food materials as do complete ones.

With one exception, all of the arthropod limb fragments found in the specimens were present in structureless coprolitic material.

Of the 23 structureless fragments examined, only one showed both arthropod limbs and palaeoniscoid scales. It is tempting to attribute those fragments containing arthropod limbs to the lungfish although they may conceivably belong to microsaurs. The remaining structureless fragments may belong to microsaurs or, more likely, represent either very small fragments of enterospirae or excreta of pleuracanthus.

While these latter interpretations are based on small samples and are, of course, highly speculative, it seems obvious that the arthropods were ingested at a lower trophic level than that of the pleuracanthus.

Further studies on enterospirae from other localities and geologic horizons are needed to determine the variability of histologic details in these unique fossils. Faunal analyses from each of many localities are also needed to assign accurately the enterospirae to the proper taxon. Such studies will enable at least partial reconstruction of the food chain and may conceivably lead to an evolutionary understanding of the spiral valve in the taxon represented.

ACKNOWLEDGMENTS

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