REEVALUATION OF THE FORMATION
OF SPIRAL COPROLITES[1]

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Abstract—The type D valvular intestine of the extant elasmobranch *Scyliorhinus canicula* produces fecal ribbons that coil spirally within the colon. Spiral fecal masses are expelled from the body without distortion. These masses are similar in morphology and internal structure to heteropolar coprolites from the Wymore Shale of Permian age in Kansas, which were previously described as enterospirae (fossilized valvular intestines).

FOSSILIZED FECES are called coprolites. Amstutz (1958) reviewed the literature defining coprolites and provided criteria for their identification. One type of coprolite, a spirally coiled form, first gained attention in the early 19th century. Mantell (1822) concluded that it was of animal origin and was not a fir cone as originally thought. His conclusion was based on the composition of the fossil, inclusions, and the testimony of a Mr. Konig of the British Museum. Konig noted a peculiar smell, unlike any in the plant kingdom, when hydrochloric acid was applied to the fossil. Spiral coprolites were first recognized as fossilized feces by Buckland (1829). Fritsch (1895) and Neumayer (1904) concluded that spiral coprolites are fossilized

valvular intestines, for which Fritsch (1907) proposed the term enterospirae. Williams (1972) described in detail spiral coprolites from the Permian of Kansas and agreed that they are enterospirae. Subsequently, Stewart (1978), Duffin (1979), and Jain (1984) also described spiral coprolites with enterospiric morphology. Spiral coprolite studies have been reviewed by Hoernes (1904), Williams (1972), and Duffin (1979).

Localities.—Spiral coprolites from Kansas, which have been described as enterospirae, are from either the Lower Permian Wymore Shale in the NE1/4, NW1/4 sec. 35, T. 9 S., R. 7 E. of Riley County (Williams, 1972) or the Upper Cretaceous Niobrara Formation in the NE1/4 sec. 12, T. 8 S., R. 22 W. of Graham County and the E1/2 sec. 27, T. 14 S., R. 26 W. of Gove

County (Stewart, 1978).

Terminology.— Spiral coprolites that have previously been described as enterospirae all have the appearance of a ribbon coiled spirally around a central axis. The coils are at a slight outward angle, with the innermost coils protruding farther than the outer coils (Fig. 1). Neumayer (1904) described the morphology of some coprolites as heteropolar, a condition in which the coils are concentrated on one end of the coprolite. This differs from amphipolar, in which the coils are evenly spaced from one end to the other and the last coil is rarely elongated.
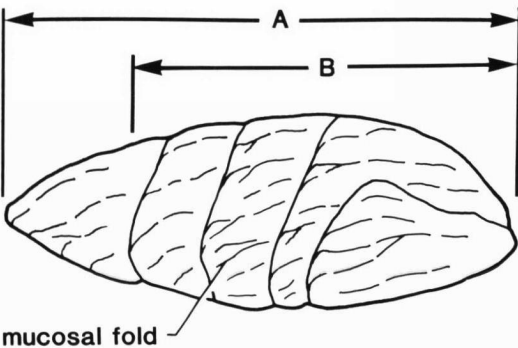

Fig. 1. Diagram of a spiral coprolite illustrating measurements of total length (a) and coil length (b), spiral count is four.

Cololite is a term proposed by Agassiz (in Buckland, 1837) for fecal matter preserved in the intestine. I here use the term coprolite for fossil feces that have been expelled from the body, cololite for internal fossil or recent fecal matter and enterospirae for preserved valvular intestines. Additionally the terms fecal matter will be used for internal feces and fecal mass for external feces.

Generally I follow the terminology of Daniel (1934) for the gross anatomy of the intestinal tract (Fig. 2). The stomach empties into the duodenum through the pyloric sphincter. The bursa entiana, a chamber between the pyloric sphincter and duodenum, occurs in some species. The bile and pancreatic ducts consistently empty into the duodenum. The duodenum may have a valve-free portion in some species. A valvular intestine is directly posterior to the duodenum in most kinds of primitive fishes. This part of the gut is typified by the presence of a spiral fold. The colon

begins where the spiral fold ends. The rectum begins and continues posteriorly from where the duct of the rectal gland opens into the intestine.

Valvular intestines assume many shapes. Those with true spiral and scroll valve form were termed transverse and longitudinal, respectively, by Richard Owen (Fee, 1925). Embryologically, a scroll valve develops as a flap in the sagittal plane descending from the intestinal wall. The flap widens into a plate and expands across the lumen to the opposite side where it rolls up like a scroll. The spiral form differs in having the fold twisted along its axis from posterior to anterior (Daniel, 1934). Parker (1885) distinguished the scroll valve *(valvula voluta)* from the spiral valve *(valvula spiralis)* and defined four types of the latter based on width of the infolding tissue and the direction in which cones of the valve point. In the type A, or ring spiral valve the radius of the mucosal fold is less than the radius of the lumen. In type B
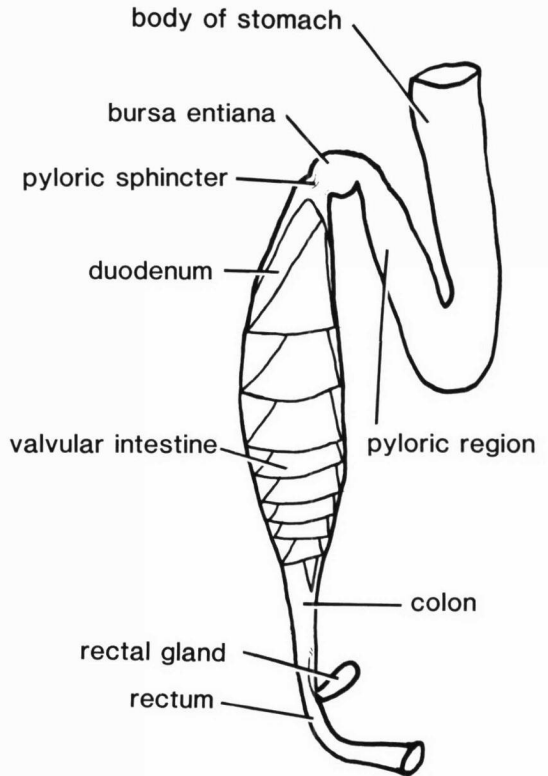

Fig. 2. Terminology for a type D valvular intestine.

the radius of the infolding mucosa equals the radius of the lumen. Types C and D have infolding mucosa with a radius greater than the radius of the lumen and the mucosa forming spiraling cones. In type C the apices of the cones are directed posteriorly except for the first, and in type D the apices of the cones are directed anteriorly. Type D is the most common type of spiral valve within fishes.
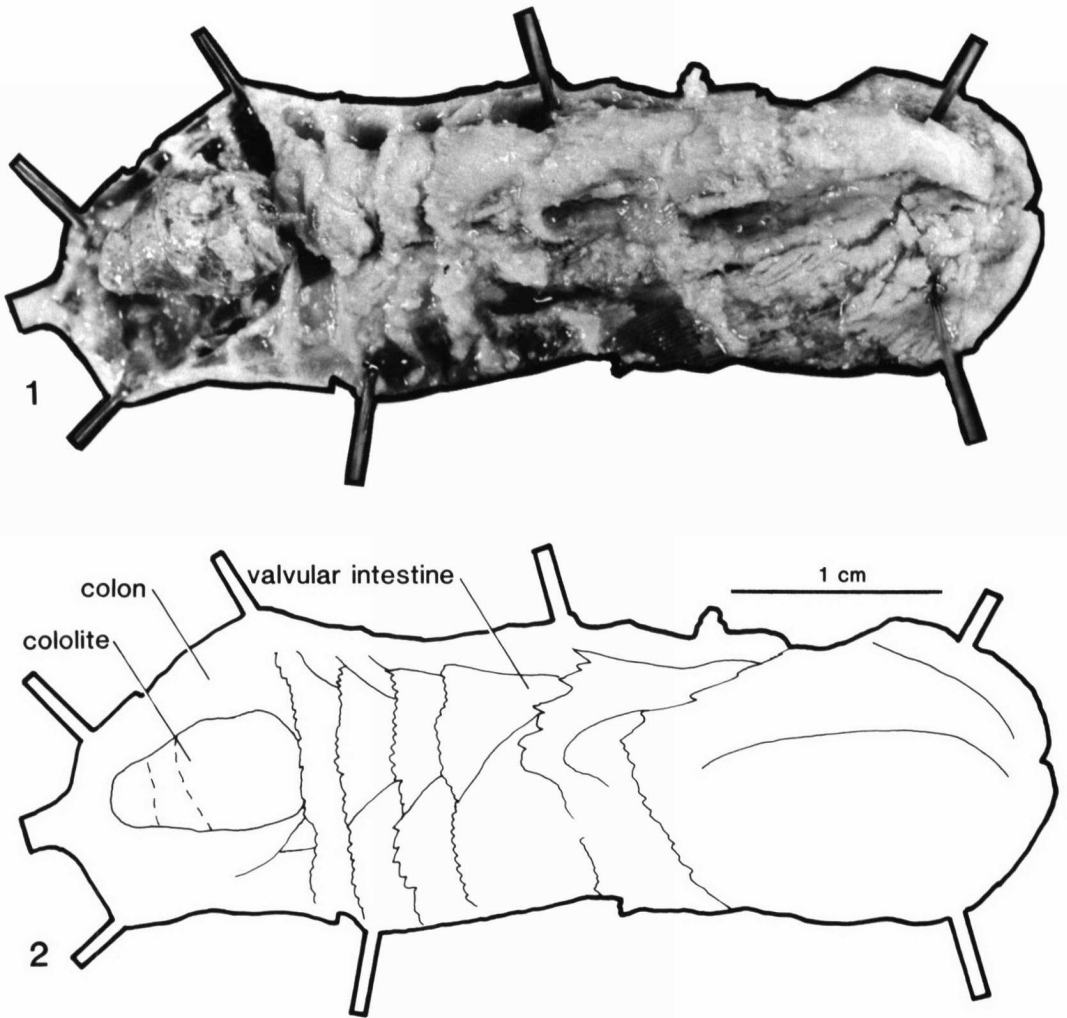
Fig. 3. *Scyliorhinus canicula*, MCZ lot 57053.——— *1.* Dissected intestine with fully formed, spiral cololite in colon.——— *2.* Explanatory drawing of *1.*

SPIRALLY COILED COLOLITES

I agree with Williams (1972) that spiral fossils of the Wymore Shale were formed inside the body; however, Williams interpreted them to be fossilized valvular intestines, whereas I interpret them to have been spirally formed in the colon and subsequently expelled as a fecal mass.

The origin of these fossils is reviewed due to the discovery of a modern analogue produced by the shark *Scyliorhinus canicula.* I learned from M. E. Williams of reports from Stewart Springer via Perry Gilbert of hardened fecal matter in the intestines of *S. canicula.* Williams thought this species might clarify the mode of formation of the spiral fossils of the Wymore Shale and suggested that I check some specimens.

Fourteen specimens of *S. canicula* (selected from MCZ lot 57053) have hardened fecal matter in their intestinal tracts. The fecal matter in some specimens is strikingly similar in gross morphology and cross section to fossils from the Wymore Shale. Hardened spiral feces are in the colon of four of the MCZ specimens (Fig. 3). Each fecal axis is parallel to the intestine. Two other specimens have hardened fecal matter in the posterior portion of the valvular intestine and in the colon. During laboratory extraction, the fecal matter commonly breaks into many fragments. In one specimen (Fig. 4,*1-4*), fecal matter is present in the rectum. In another specimen, fecal matter in the colon and the valvular intestine is continuous. These three kinds of hardened intestinal contents are fully formed spiral fecal masses (Fig. 3), incipient spiral fecal masses (Fig. 4,*5*), and a spiral fecal mass in the process of expulsion (Fig. 4,*1-4*), respectively.

Buckland (1837:152) envisioned the process of spiral cololite formation as follows:

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 riband, forced continually forward into a cylindrical tube, through a long aperture in its side. In this case, the riband 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 continually 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. Coprolites thus formed fell into soft mud, whilst it was accumulating at the bottom of the sea, and together with this mud, (which has subsequently been indurated into shale and stone,) they have undergone so complete a process of petrifaction, that in hardness, and beauty of the polish of which they are susceptible they rival the qualities of ornamental marble.

Zangerl and Richardson (1963:144) described the same method for the formation of the spiral coprolites from Pennsylvanian black shales of Indiana:

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 a lack of spiral structure.

I agree with these descriptions of spiral cololite formation. A plastic ribbon of fecal matter continuously coiling through the valvular intestine into the rectum would form a spiral cololite. The fecal matter can form a cohesive ribbon. While searching for parasites in elasmobranchs, Daniel Brooks (verbal communication) pulled out such fecal ribbons. I consider the second set of movements described by Cannon (1908:327) for *Squalus* to be the prime locomotor of the fecal ribbon.

A movement starting posteriorly and passing forward, which consisted in a local shifting of the wall towards the left, *i.e.,* clock-wise with reference to the axis of the valve viewed from behind. As shown by small holes cut in the wall, the shifting of the wall towards the left was accompanied by a shifting of the inner folds towards the right.

As the ribbon enters the empty colon it is curled by the restraining intestinal wall. If the wall of the colon is tightly contracted, the lumen will be narrow and the initial coil of the ribbon will be tight. If the lumen is wide, the initial coil may be loose and a conical cavity may be present in the finished fecal mass. Further progress of the fecal ribbon into the colon will produce more coils and push the initial coils posteriorly a short distance. After forming, the spirally coiled fecal matter is transported through the rectum and ejected from the body. Dean (1903) as well as Anne Kemp, William Bemis, and Barbara Conant (verbal communications) have observed spiral fecal masses in their aquaria. Spirally coiled feces enclosed in mucous coats have been observed by Conant
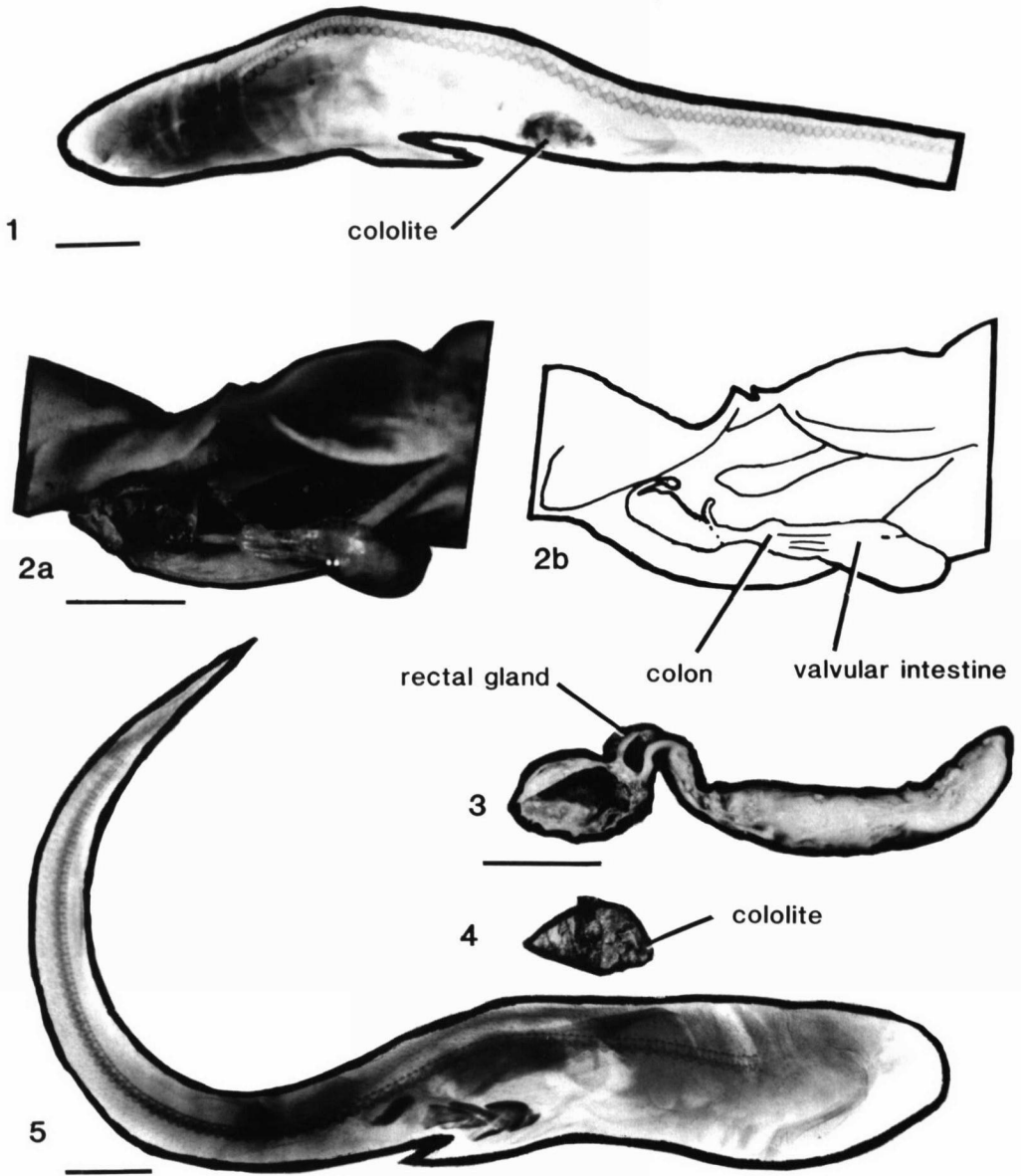
Fig. 4. *Scyliorhinus canicula,* MCZ lot 57053.———*1.* Radiograph of cololite in rectum.———*2.* Enlargement *(2a)* and explanatory drawing *(2b)* of part of specimen in *1,* valvular intestine draped over body wall.———*3.* Valvular intestine and rectum from specimen in *1.*———*4,5.* Radiograph showing incipient cololite in colon, anterior coils within the valvular intestine, and triangular artifact at left jaw joint. Scale equals 1 cm.

being expelled from lungfish. The fecal mass of the recent dipnoan *Protopterus* figured by Dean (1903) has amphipolar morphology whereas all the spiral cololites of the recent *Scyliorhinus* are heteropolar. The valvular intestines of *Scyliorhinus* and *Protopterus* are both type D.

Based on the similarity of the intestines I expect the two kinds of fecal masses to be formed in a similar manner and to be gradational in morphology. The variation in fecal morphology may be more dependent on diet and consistency of fecal material than on the variation of the

type D valvular intestine. Attribution to animal group strictly from coprolite morphology is not possible.

Fecal matter in the colon and rectum lacks striations, which would be indicative of significant friction between the fecal matter and colon while coiling, or between the spirally coiled fecal matter and the rectum while in the process of expulsion. The fecal matter needs to be pliable in order to coil in the colon but it also needs to be firm enough to prevent distortion and striations from peristaltic waves in the rectum and from the sphincter muscle at the anus. Possibly a mucous coat protected the fecal matter. Also, it is possible that the spiral fecal matter hardened in the colon. Cololites in the posterior of the valvular intestine and colon of *Scyliorhinus* are almost as hard as the fossil coprolites from the Wymore Shale. Hardening of cololites in *Scyliorhinus* may be partly an effect of alcohol preservation, but hardening may occur normally in the intestine of the living fish. In one specimen remains of fish scales and head bones were observed in the stomach. In the duodenum and the anterior half of the valvular intestine a soft, finely ground chyme of undigested fish bones was present. In the posterior half of the intestine and the colon the fecal ribbon was hard. These observations indicate progressive hardening of the contents of the digestive tract.

In cross section, the hardened fecal ribbon and the spiral fecal matter both have microstructure perpendicular to the flow of the rib-

bon. The microstructure apparently results from folding of the fecal ribbon as it moves posteriorly, just as a throw rug folds when pushed from one end (Fig. 5). Folding in observed sections of both fossil and recent fecal matter is rarely continuous or clear. In some specimens the ribbon may not have been flexible enough to deform without breaking under stress in the intestine. Excessive stress would cause the ribbon to fracture at points of maximum bending and become layered. More complex folding may occur when a previously folded ribbon overrides folds to the posterior. The formation of spiral cololites within the colon was rejected by Williams, who thought that fecal matter entered the colon from an anterior rather than from a lateral direction (the direction fecal matter moves in the valvular intestine). Posterior movement would cause coils to be parallel to the long axis of the intestine. Lateral movement would produce perpendicular coils. Although this is a reasonable assumption, the fecal ribbon in the modern analogue does retain its cohesiveness and coiling direction during passage from the valvular intestine into the colon.

DISCUSSION

Basically, Williams (1972) presented six lines of evidence for concluding that the Wymore Shale fossils are enterospirae. Following is a review of that evidence with a comparison to the cololite interpretation. The first five items
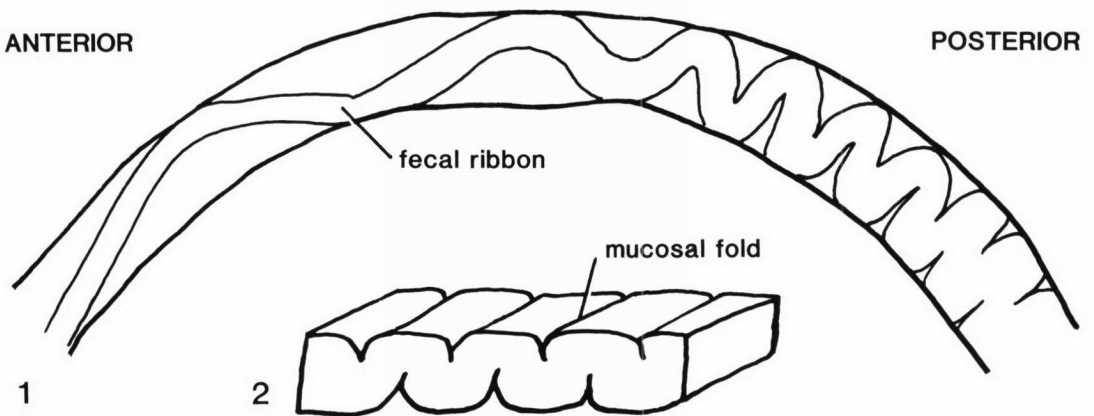

Fig. 5. Origin of microstructure of spiral feces.———*1.* Idealized folding of fecal ribbon through the valvular intestine.———*2.* Mucosal folds of enterospirae, interpreted here as cross section and surface of the folded fecal ribbon.

involve similarities in gross morphology.

1) The fossils resemble a type D valvular intestine, with posterior cones dipping beneath anterior ones. Both the Wymore Shale fossils and the cololites in *S. canicula* have this shape.

2) Orientation of the whorls to the long axis of the specimens is nearly perpendicular. This morphology would be consistent with a fossilized intestine. It is also similar to the cololites in *S. canicula.*

3) Some spiral fossils of the Wymore Shale have a conical cavity. The base of the cavity is at the posterior end of the fossil and the apex extends anteriorly. These cavities may be filled with matrix. Williams considered this to be evidence against a cololite origin. He did not consider that fecal matter could coil into this configuration, pass through the remainder of the intestinal tract, and subsequently receive matrix infilling. Nevertheless, the cololites in *S. canicula* coil in the rectum and are hard enough to pass through the remainder of the intestinal tract without distortion. After excretion the cololites could be filled with matrix.

4) Subparallel folds at approximately 60 degrees to the long axis were interpreted as casts of mucosal folds on the lining of the intestine. These subparallel striations are present all the way to the middle of the specimens. They are on both sides of the whorl and are at similar angles outside and inside the specimens. In cross section, the cololites of *S. canicula* show these surficial "mucosal folds" being continuous with valleys between the more prominent folds of the deformed ribbon. The inferred process of spiral cololite formation takes into account this morphology, whereas casts of mucosal folds should be counterparts and not steinkerns of the folds.

5) Williams (1972) noted that the raised lip on the edge of the whorl of some fossils had been suggested to have some relation to the annular veins that circumscribe the intestine. Actually, the course of the annular veins of *Squalus* is semicircular with offset ends. Williams also suggested that the lip could be formed by embayments along the junction of the outer intestinal wall and the valvular intestine. He also noted a lip on the spiral fecal mass of *Protopterus* and interpreted this as a cast of a small pocket at the junction of the valvular intestine and the outer intestinal wall. I concur that the embayment process is possible. Alter-

natively, it is possible that the lip is caused by an underlapping of the fecal ribbon as it moves around the valvular intestine. In either case, the presence of a lip neither supports nor denies either interpretation.

6) Cross sections of modern spiral valves are similar to spiral fossils of the Wymore Shale. Williams considered the folds seen in cross sections of the fossils to be preserved mucosal folds of the mucosal lining. The line between the whorls was considered to represent the space formerly occupied by the rotted valve flap of the valvular intestine. Although there are resemblances, there are also many difficulties with this interpretation. The folds seen in many slides are continuous and fill the entire distance between whorls (Fig. 6). No animal with a spiral valve has folds on one side of the valve flap and not the other (compare Williams, 1972: pl. 2). Furthermore, there is no differentiation between the lumen and the space once occupied by the submucosa. Complex folds are an additional complication, being on the same level as the simple continuous folds. They are not present below mucosal folds where glandular material of such complexity would be present. In sections of elasmobranchs that I have made or read of there is nothing similar to this complex folding.

In my observations, the variability of the mucosal folds in enterospirae is extreme; however, the expected variability in size and shape of mucosal folds should be consistent from anterior to posterior. Serial sections of fossil specimens show no pattern in the variation. In sections of valvular intestines of modern elasmobranchs, the most obvious variation is a reduction in size from the anterior to the posterior end. The size relationships of the fossil folds are different from that expected for a spiral valve. The fossils show no obvious gradations. In histological sections from living species, the spiral flap of the valvular intestine is approximately as thick as half the mucosal fold height. Small specimens tend to be below this ratio. The fossils show little or no available space for the rotted valve flap.

Sections through hardened fecal masses of *S. canicula* reveal microscopic structure similar to that of fossil sections (Fig. 7). Interpretation of the Wymore Shale spiral fossils as coprolites, produced as described before, circumvents the inconsistencies between modern intestinal
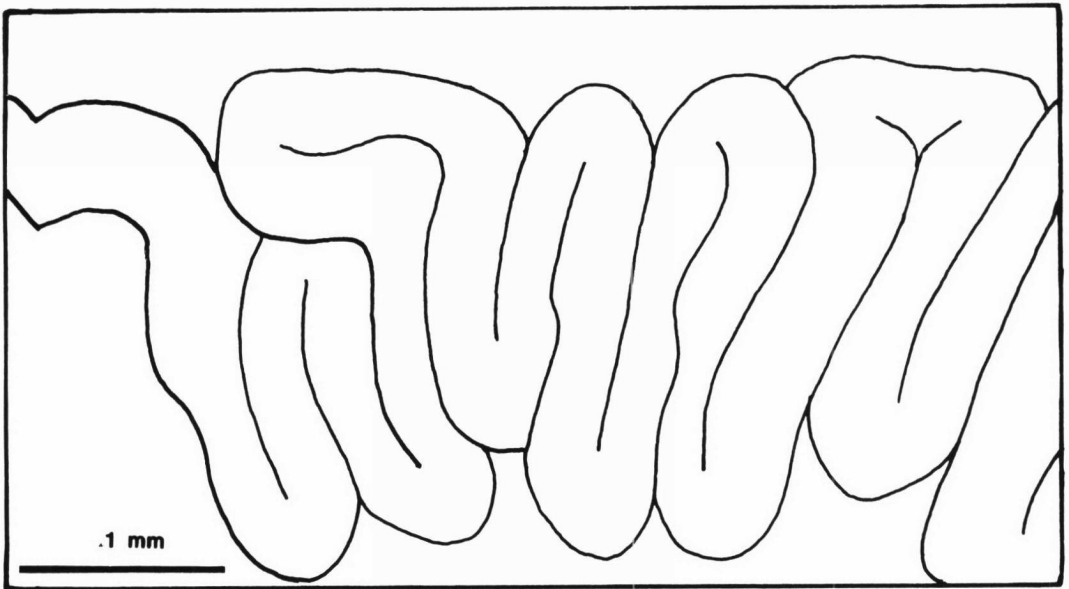
structures and enterospirae.

Other evidence against an enterospiric interpretation includes the lack of an intestinal lumen in the spiral fossils. Spiral intestines of all animals I have examined or read about have a large lumen for the passage of fecal matter. There is no lumen in the fossil specimens, all available space being filled by mucosal folds.
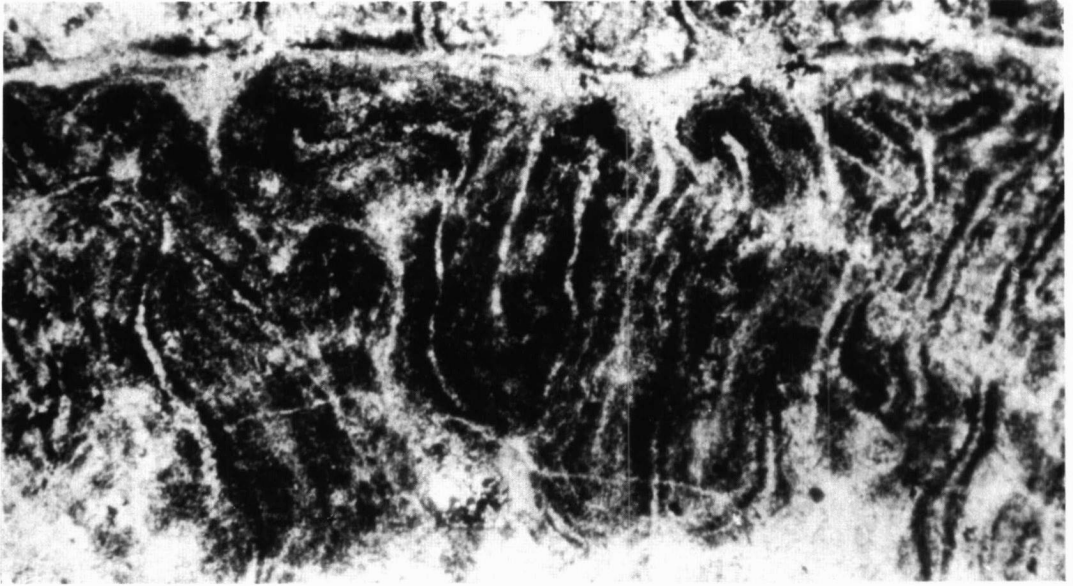
Fig. 6. Spiral coprolite from the Permian of Kansas, MNH-KUVP 17872 section 1.———*1*. Photomicrograph of microscopic folding.———*2*. Explanatory drawing of *1*.
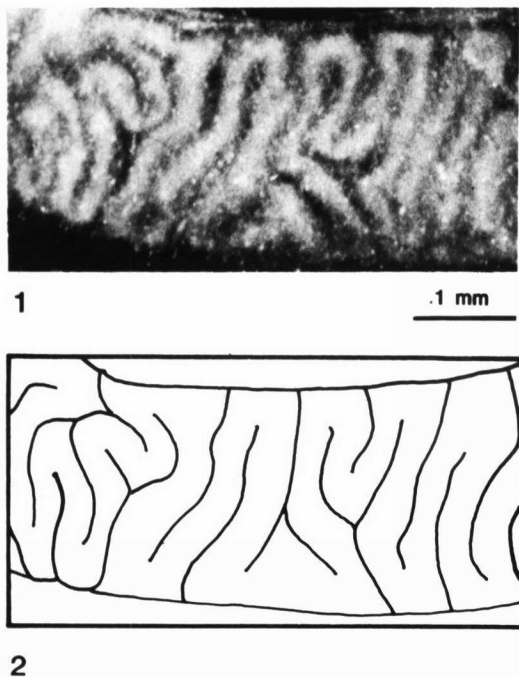
1 .1 mm

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Fig. 7. Section of a hardened spiral cololite from *Scyliorhinus canicula*, MCZ lot 57053.———*1*. Photomicrograph of microscopic folding.———*2*. Explanatory drawing of *1*.

When interpreting the convolutions as mucosal folds there cannot be constriction or shrinkage allowed to compensate for the lack of the intestinal lumen due to the hypothesized preservation process. Normally, tissue that is unpreserved will start to autolyze immediately. Williams (1972) considered preservation of enterospirae to be due to the packing of undigested or partly digested matter around the mucosal folds. This chyme would somehow prevent self-digestion and preserve the mucosal folds. Williams (1972:16) stated:

> 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.

With the solidified paste in the intestine enveloped around the mucosal folds, there can be no displacement or shrinkage of the spiral flap before it rotted. The solidified paste would retain the normal spacing of the whorls in relation to each other.

The final line of evidence for a coprolitic origin for the Wymore Shale fossils is based on the extreme ranges of their size and spiral number. Fifty specimens were measured to obtain the ratio of the coiled length (distance of a straight line, parallel to the axis, from the anterior of the specimen to the last external coil) to the total length, and the coil count (see Fig. 1). The ratio between coiled length and total length would provide an index for the heteropolar and amphipolar condition. The total length of the specimens ranges from 0.84 to 6.61 cm, with an average of 2.42 cm. The ratio ranges from .18 to .79, with an average of .48. The number of coils ranges from 3 to 12, with an average of 7.

If the spiral fossils are interpreted as enterospirae, they should have variations similar to original valvular intestines. For comparison only enterospirae having an unbroken subparallel trailing edge on the anterior whorl are considered. Such morphology would be consistent with an unbroken fossilized intestine.

The amount of variability to be expected in spiral valves is largely based on Parker's (1885) study of *Raja*. Williams (1972), Zidek (1980), and Duffin (1979) all mentioned the variability Parker described, and overall imply that it is significant. Parker found the spiral valve of *Raja* to be constant in position of the anterior end of the valve (where and how the anterior end attached to the wall of the intestine) and the course the outer edge of the spiral describes on the intestine wall.

Parker (1885) identified three categories of variable features. The first is length of the attached edge of the valve versus the width of the intestine. The number of turns and the position where the posterior end of the valve stops are dependent on this. The second category is the course and length of the inner edge of the valve, on which depends the direction of the turns, the width of the valve, the total surface area, and the resistance given to the contents. The third category is the character of the mucose membrane. In essence, variability depends on the number of turns, the width of the spirals and if they are directed anteriorly, and the character of the mucose membrane.

I do not believe all possible interpretations of Parker's study have been considered. Parker (1885) analyzed variability in available specimens in the genus *Raja*, not a single species;
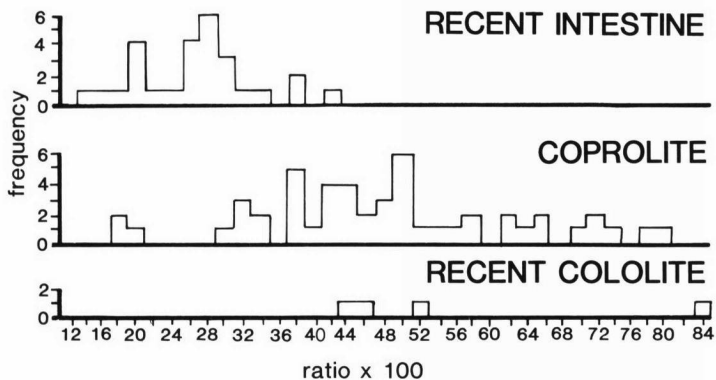
Fig. 8. Ratios of coil length and total length for intestines of *Squalus sucklii*, coprolites from the Wymore Shale, and cololites of *Scyliorhinus canicula*.

hence, variability will be far greater than if only one species were analyzed. It seems Parker wanted to present the total diversity possible, not that typical of the majority of specimens. Another point to consider is that the diversity may not be so great as is implied. Parker considered the type A ring valve to be more or less hypothetical in *Raja*. When present it is only in the posterior portion of the valve. He described type B from only two dried specimens. Drying may have caused more distortion than just the displacement of the columella from the central axis, which Parker noted.

Fee (1925:177) advised moderation in considering the variability described by Parker. He noted that the apparent disparity ''between the different valves was further lessened by the work of Paul Mayer (1897) when he showed that many of the specific differences in the spiral valves were either artifacts or functional conditions standing in the closest relation to digestion. On inflation by food the valve of *Raja* becomes so tightened that the anterior part no longer forms a cone with its apex pointing toward the pylorus.''

Fee (1925) also noted differences in shape and arrangement of the valve in relation to the amount of fecal matter, and contrary to Parker, in relation to the age of the fish. Finally, Parker's method of preparing material was to wash out the contents, distend the spiral intestine, and then harden the intestine in chromic acid. Considering Fee's comments, this method would surely cause some distortion.

I chose *Squalus sucklii* for comparison with the fossil specimens because it is easily obtained, has a type D spiral, and does not appear to be as specialized as *Raja* in body and food

habits. Twenty-seven specimens were dissected and their valvular intestines measured. They included 7 embryos (defined here as being inside the parent) with yolk sacs, 8 embryos that had absorbed their yolk sacs, and 12 adults. The length of intestines ranges from 2.0 to 19.0 cm, with an average of 8.7 cm. The coil number ranges from 13 to 15, with an average of 14. The ratio between coiled length and total length ranges from 0.13 to 0.41, with an average of 0.26. Within the valvular intestines the amounts of variation in coil counts and ratio values are consistent between the three stages of development. The size variation is approximately nine-fold in both the enterospirae and modern valvular intestines; however, the ratio value of the enterospirae is more than twice the ratio value of the valvular intestine. The coil count variation of the enterospirae is also comparatively large, being three times that of the valvular intestine (Figs. 8, 9).

Coil counts in five available cololites of *S. canicula* range from 1 to 9 and ratio values range from 0.44 to 0.83. The 39 percent range of variation in ratio values for recent cololites is greater than the 26 percent range for recent valvular intestines but less than the 61 percent variation in fossil specimens. Considering the small size of the recent cololite sample, it is my opinion that variation in the Wymore Shale spiral fossils is more reasonable if the fossils are interpreted as cololite-coprolites rather than enterospirae. The ratio values of 0.18 to 0.79 for the fossils, if they are considered coprolites, would indicate a gradation from extreme heteropolar to amphipolar type by the earlier definition of Neumayer (1904).

SUMMARY

A modern analogue, *Scyliorhinus canicula,* is used to explain the origin of spiral fossils in the Wymore Shale as coprolites. It is demonstrated that a fecal ribbon can spiral through a type D valvular intestine and spirally coil in the colon. The spiral fecal material hardens and is voided in this condition. The physiological cause of the hardening is unknown. The morphology and internal structure of modern feces are very similar to those of the coprolites. Similarities of spiral valves and heteropolar coprolites, which have been used as evidence of an enterospiric origin of the fossils, do not eliminate a cololitic-coprolitic origin. The evidence best supports a cololitic-coprolitic origin.

Living vertebrates with valvular intestines include agnathans, chondrichthyans, actinopterygians, dipnoans, and actinistians. Fossils exhibiting evidence of preserved valvular intestines include placoderms, chondrichthyans, possibly acanthodians, and actinopterygians (McAllister, 1984). The most common intestine is type D, which here is considered to represent the primitive condition. Producers of spiral coprolites similar to the Wymore Shale specimens cannot be easily identified because the intestinal morphology needed for production is common to all major groups of fishes. Association of fossils in the Wymore Shale suggests xenacanths as possible producers of the spiral coprolites.
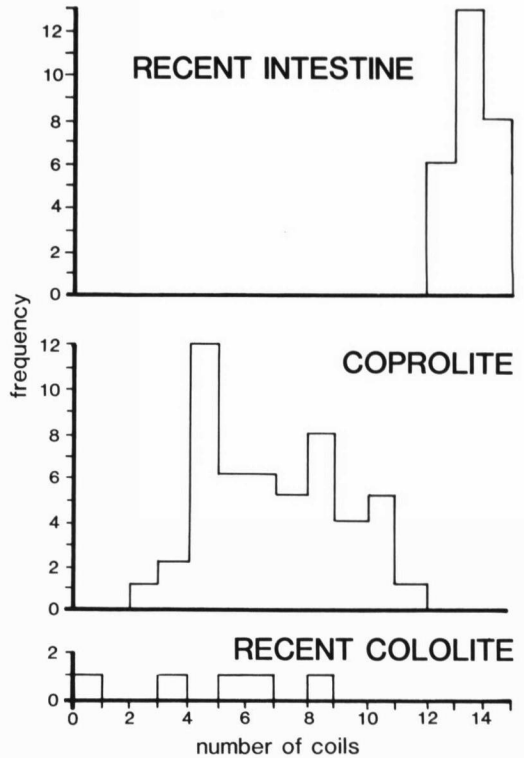

Fig. 9. Coil numbers for intestines of *Squalus sucklii,* coprolites from the Wymore Shale, and cololites from *Scyliorhinus canicula.*

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