

THE VALVULAR INTESTINE IN FISHES AND A REASSESSMENT OF
THE FORMATION OF SPIRAL COPROLITES

by

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Abstract

Living vertebrates with valvular intestines include agnathans, chondrichthyans, actinopterygians, dipnoans, and the actinistians. Fossils which have valvular intestines preserved, are included in the placoderms, chondrichthyans, possibly the acanthodians, and the actinopterygians. The most common intestine is Type D, found in all groups (except the agnathans), and is considered as the primitive condition. The actinopterygians progressively reduce the valvular intestine until it is lost.

The Type D valvular intestine in Scyliorhinus canicula is demonstrated to produce spirally coiled fecal masses. The fecal masses are similar in morphology to heteropolar coprolites, previously described as "enterospirae" (fossilized valvular intestines). The "enterospirae" are reinterpreted as true coprolites.

Introduction

At the time when this research was beginning, the goal was conceived to be an intensive description, reconstruction, and possibly a better indication of the producer of the spirally coiled coprolites from the Permian of Kansas. At that time they were considered to be "enterospirae" or fossilized valvular intestines. Gradually the original ideas were dropped and the research on valvular intestines took on a dual nature. One line of research led to a review of the fishes, fossil and recent, which possessed valvular intestines; while another line led to a reconsideration of the nature and mode of formation of spiral coprolites. The two lines of research are not totally independent because the production of the spiral coprolites is dependent on the presence of a valvular intestine. Despite some unification, I will present the material in two sections. This, I hope, will increase the clarity and understanding of the research.

Terminology

The digestive canal of fishes can be divided into two regions. The "Kopfdarm" includes the buccal cavity and the pharynx while the "Rumpfdarm" includes the fore-gut (esophagus, stomach), mid-gut (intestine), and hind-gut (rectum). Barrington (1957) while summarizing much of the general information concerning the digestive system of fishes considers further subdivisions of the system to be misleading by suggesting differentiation not characteristic of lower vertebrates. Although in some fishes there is less differentiation than in higher vertebrates, there is still a need for terminology that describes additional areas of more differentiated fishes. The problem to which Barrington could be alluding is the use of terms common to fishes and humans that are functional or structural equivalents but are not necessarily homologous. A second problem in the terminology is the use of different terms by different authors for the same structure. An example of this is the name used for the duodenum. Some authors refer to the duodenum as the bursa entiana. Parker (1885) is only one author of many who considers the two names interchangeable. In order to avoid such confusion I will specify the terminology for each structure I will refer to. Generally the terminology of Daniel (1934) is

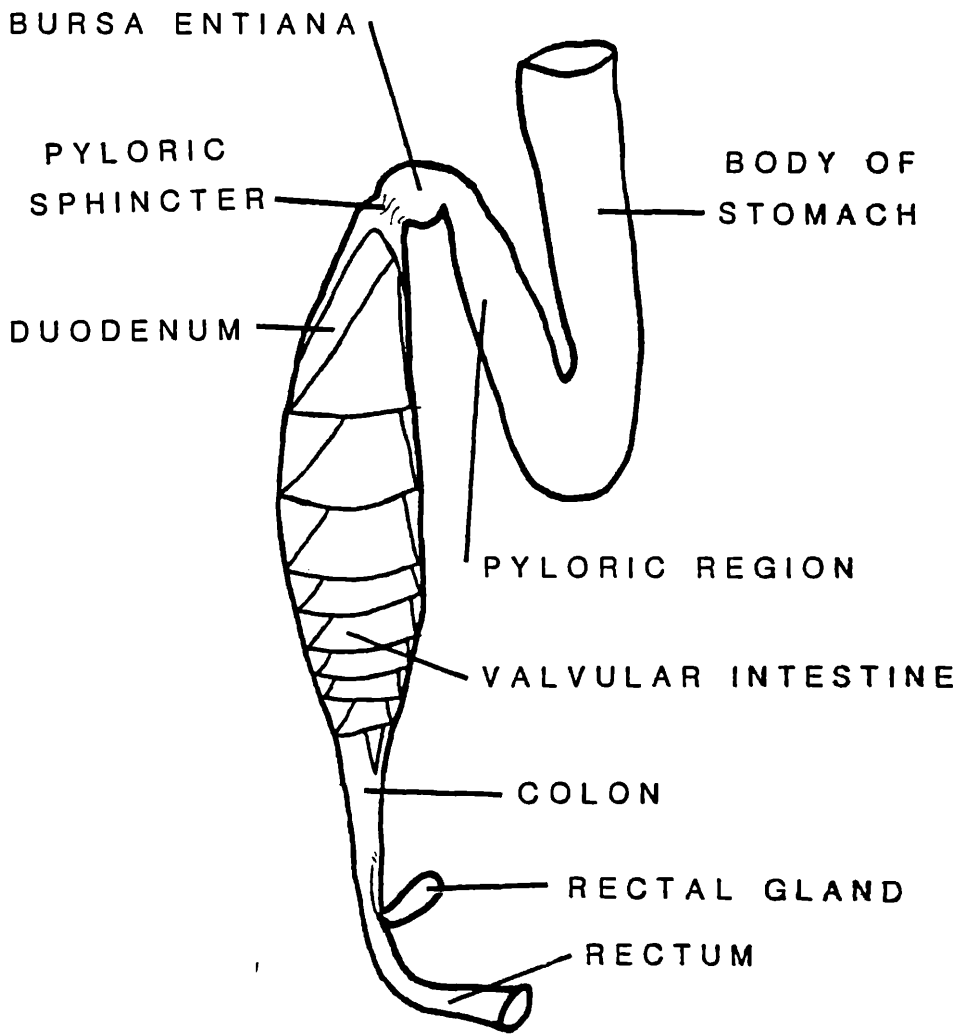


FIG. 1

used. He differentiated the structures both on a gross anatomical and histological basis.

The first terms to be defined begin at the stomach (Fig. 1). The shark stomach is usually divided into two parts. One part is a large sac referred to as the body (the cardiac region, or the proximal or descending limb), the other part is the pyloric region (the distal or ascending limb), which is typically more cylindrical. The pyloric region is separated from the intestine by the pyloric sphincter. Barrington (1957, page 155) writes that the nomenclature of the cardiac and pyloric regions is derived from mammalian anatomy and the regions may better be referred to as the corpus or body and pyloric region, respectively. In some elasmobranchs the pylorus empties into a chamber called the bursa entiana. This is still part of the fore-gut being anterior to the pyloric sphincter.

The stomach empties into the duodenum with a pyloric sphincter separating them. Although the duodenum may or may not have a valvular-free portion, the bile duct and pancreatic duct both empty into it consistently. The valvular intestine is directly posterior to the duodenum in most kinds of fishes. This segment of the gut is typified by the presence of a spiral fold. At the point where the spiral fold ends the colon begins. The colon can be compared in function

to the large intestine. At the point where the duct from the rectal gland opens into the intestine the rectum begins and extends posteriorly.

The valvular intestine assumes many shapes (Fig. 2). The first dichotomy separates valvular intestines into the true spiral valve form and the scroll valve form. Owen termed these the transverse and longitudinal types, respectively (Fee, 1925). The scroll valve, found in the living elasmobranch families Carcharinidae and the Sphyrnidae, seems to be the most misunderstood type. Embryologically all valvular intestines begin their formation similarly with the development of a longitudinal infolding of the mucosa. In a scroll valve the longitudinal valve widens into a plate and expands longitudinally across the lumen to the opposite side where it rolls into a "scroll". The spiral form differs in that the longitudinal fold twists along its axis from the posterior to the anterior (Daniel, 1934). Figure 3 illustrates the scroll valve. One point to note concerning the scroll valve is that the incurrent fecal material does not flow directly into the scroll; it is theoretically possible for the food to continue along the side of the intestinal wall and exit the valve without entering the scrolled portion. Material which does enter the scroll eventually encounters a dead end and must retrace its path to some extent to leave the

scroll and then exit the intestine. Although the scroll valve is often compared to a rolled piece of paper this is a misleading analogy in that the anterior edge of the outer whorl is bound to the intestinal wall by a peculiar twisting so that unrolling the valve causes torsion along the anterior free edge posteriorly to the mid-point.

White (1937) divided valvular intestines into three types. Type III has a scroll valve as described above, Types II and I have transverse valves. Type II is the ring spiral valve. The infolding mucosa, perpendicular to the intestinal wall, becomes a continuous spiral that does not reach the center of the lumen: the result resembles a narrow spiral staircase in a wide well. Type I includes spiral valves in which the infolding mucosa meets itself in the center of the lumen and forms a columella. the columella resembles a central pillar which the spiraling intestine pivots around.

Parker (1885) separated the scroll valve (*valvula voluta*) from the spiral valve (*valvula spiralis*) and divided the latter into four types. Type II of White is the same as Type A of Parker. White's Type I includes Types B, C, and D of Parker. Parker split these types based on the width of the infolding tissue and the direction the spiraling cones of the valve point. If the radius of the infolding mucosa equals the radius of

the lumen, it is Type B. Types C and D occur when the infolding mucosa has a radius greater than the radius of the lumen and the mucosa forms 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. Parker's terminology will be used as it is most specific and is widely cited by others.

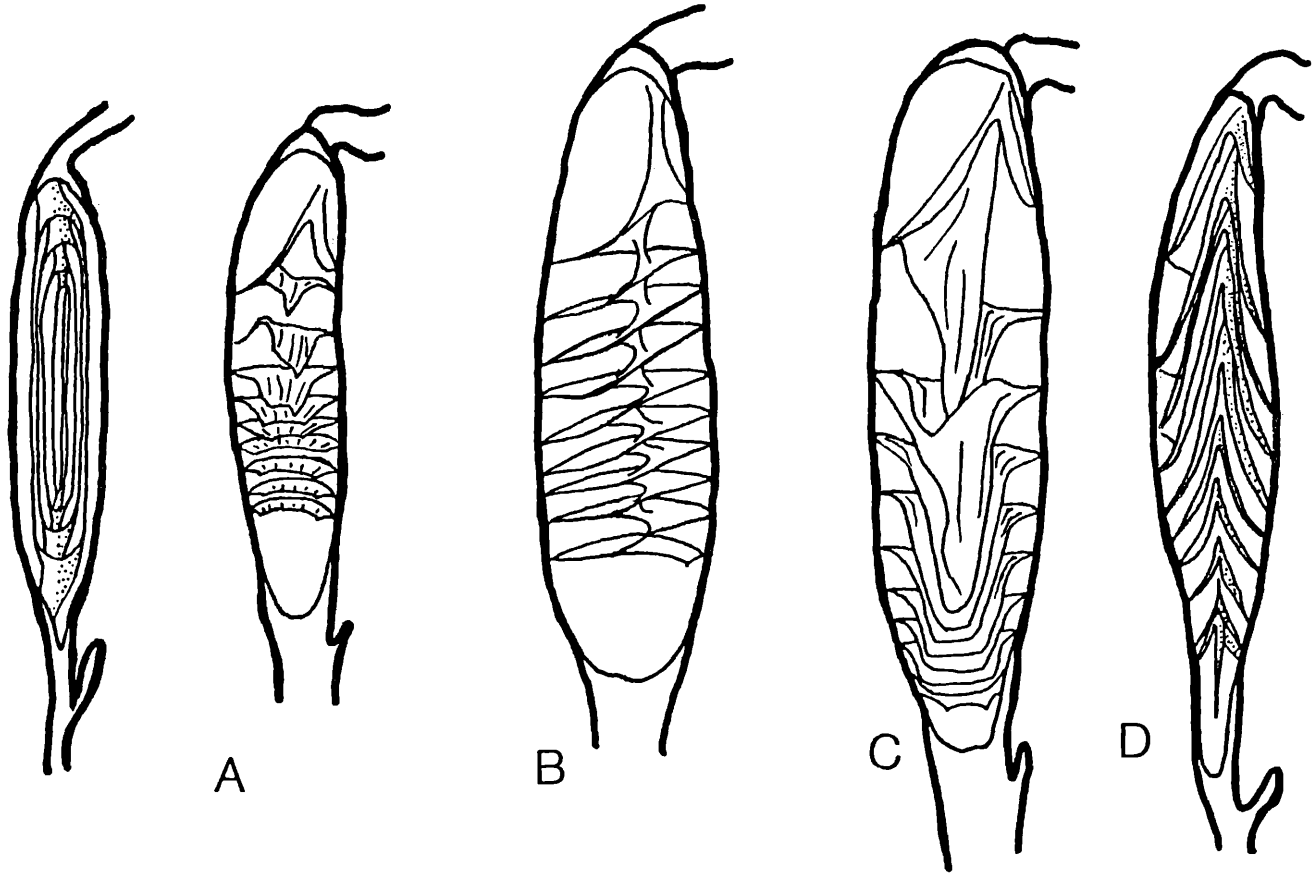
Distribution of Valvular Intestine in Extant Fishes

Among extant vertebrates valvular intestines are known in agnathans, holocephalians, elasmobranchs, dipnoans, crossopterygians, and some actinopterygians.

Agnatha

The Agnatha contain two living groups. The Myxiniiformes (hagfish) do not possess a spiral valve in their intestines while the other group, the Petromyzontiformes (lampreys), do possess a spiral valve. Their spiral valve (sometimes termed a typhlosole) is a large elongate fold that travels in a very slight spiral course the length of the intestine. Kluge et al. (1977) figure the intestine of Petromyzon marinus and Entosphenus tridentata.

Romer (1966) warns that although the lampreys and hagfish are obviously lower in their body organization



A

B

C

D

SCROLL VALVE

SPIRAL VALVE

FIG. 2

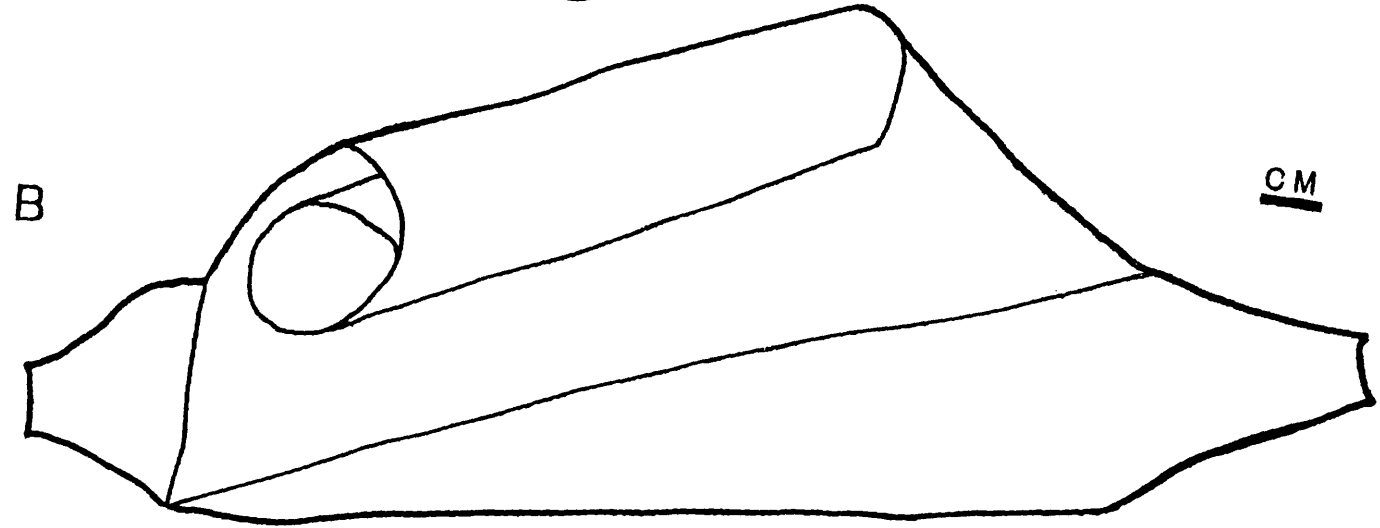
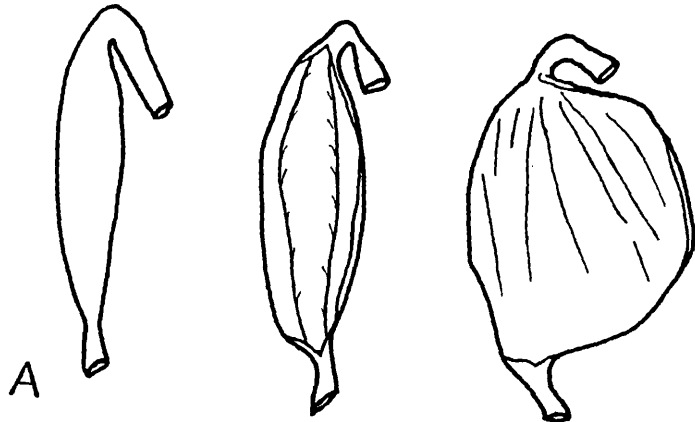


FIG 3

than other living vertebrates, they do not necessarily portray the primitive condition of vertebrates. While they are modern representatives of the oldest vertebrate group their parasitic lifestyle is specialized and degenerative and does not necessarily conserve ancestral characteristics.

Chondrichthyes

The living elasmobranchs, subclass Elasmobranchii, are typically the first animals considered when valvular intestines are mentioned. They contain all the types of intestines including the scroll type. Based on the diversity the literature portrays, it is my opinion that the most common type of valvular intestine present in the elasmobranchs is type D of Parker, the anteriorly pointing cone in cone type.

The other subclass of the Chondrichthyes is the subclass Holocephali. The holocephalians of which I am aware have the type D spiral valve [a specimen of Chimaera collei (Museum of Comparative Zoology 39718), Callorhynchus (Romer, 1971, fig. 256c), and Chimaera monstrosa (Pernkopf and Lehner, 1937, fig. 332)].

In the literature there are many articles that figure or describe only one or two valvular intestines. One source easily overlooked is the literature primarily concerned with parasites. Gudger (1950) documents the early research on valvular intestines, and reproduces

some of the earliest valvular intestine illustrations of sharks and actinopterygians. Two other articles that contain tables describing many different valvular intestines are White (1937), and Osipov (1972).

Osteichthyes...Actinopterygii

Many primitive living actinopterygians retain a spiral valve in the posterior portion of their intestines. The spiral valve is reduced compared to that of nonactinopterygian fishes.

The most primitive grade of Actinopterygii, the "chondrosteans", contains the living families Polypteridae, Acipenseridae, and Polyodontidae. Representatives of these families have a reduced type D spiral valve in their intestines.

The neopterygian actinopterygians include the primitive living families Lepisosteidae and the Amiidae. These families retain a reduced type D spiral valve.

Jacobshagen (1911, pg. 585) lists the spiral counts of some of the primitive actinopterygians. The spiral counts of the "chondrosteans" range from eight to five and that of primitive neopterygians range from five to two. All these animals have the spiral restricted to the posterior portion of the intestine. This is possibly a reflection of the torsion of the spiral which begins posteriorly and advances anteriorly during the

embryologic development.

There is much confusion in the literature about the presence of a valvular intestine in the Teleostei. Migdalski and Fichter (1976, pg. 109) note that Chirocentrus is the only herring with a spiral valve present, and that it is a feature Chirocentrus shares with elasmobranchs and a few other bony fishes. However Budker (1971, pg. 60) claims the Chirocentrus spiral valve is not a true spiral valve (i.e., not homologous to lower fishes) but that Osmerus and Gymnarchus do retain a true vestigial one.

I suspect the confusion is mostly caused by the difficulty of finding and reading old non-english journals. In the last century the odd intestines of some teleosteans were noted but not worked on extensively. Wiedersheim (1897, pg. 259) held this opinion, "Traces of a spiral valve can be recognized amongst the Teleostei (Chirocentrus and possibly certain Salmonidae).". Jacobshagen later provided a conflicting opinion in Korovina 1976, pg. 619: "The spiral valve has been described as an exceptional formation in some adult Teleosts (Chirocentrus, Gymnarchus). However, Jacobshagen (1915, 1937) considered that in bony fishes the circular, non-spiral folds, formed only partly from the mucous coat (situated in the very center of the gut) are erroneously taken to be a spiral valve, while in

lower fishes, the mucous coat is completely incorporated into the spiral valve, together with the compact layer of specialized collagen (stratum compactum).".

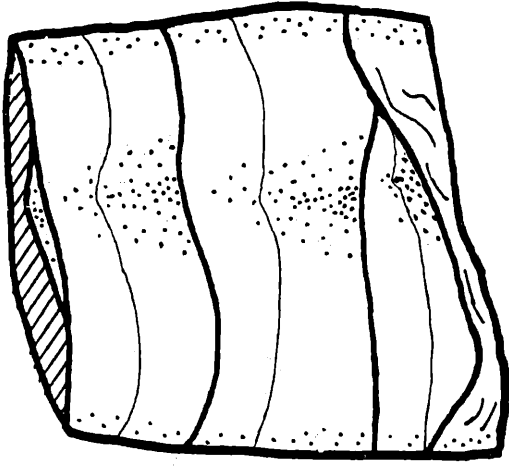
Authors aware of Jacobshagen's work would perpetuate the idea that the Teleostei do not have a spiral valve homologous with that of other actinopterygians.

Using Jacobshagen's criteria defining a spiral valve, Korovina and Reshetnikov (1982) concluded that the salmonid Prosopium cylindraceum did indeed possess a spiral valve with spirally arranged folds composed of the mucous membrane including the compact layer and sometimes the underlying muscular layer. Korovina (1976) believes Jacobshagen may have observed histological sections that did not display the involvement of the deeper layers in the spiral valve. Histological sections of the same animal can provide different degrees of visibility and completeness of the layers involved.

Figures of the whole spiral valve are scant. Korovina and Reshetnikov (1982, pg. 86, fig. 3) have one picture showing approximately forty compact spirals, of the ring type, in the salmonid Prosopium cylindraceum. Burgot et al. (1975, pg. 40, fig. 2) figure part of the bisected spiral valve of Salmo gairdneri. It has at least fifteen ring spirals. Goodrich (1909, fig. 77,

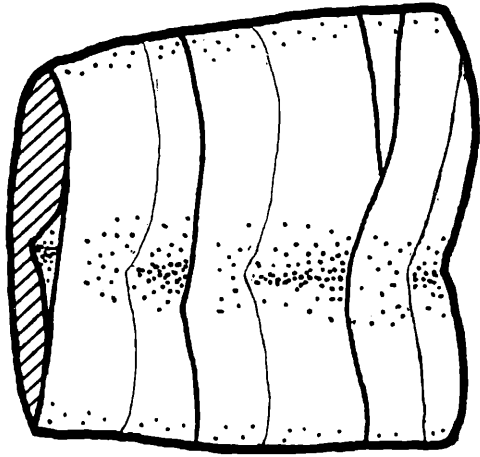
pg. 116) figures the spiral intestine of Chirocentrus dorab, the wolf herring with thirty-six spirals apparent.

While checking the gross morphology of small inverted sections of intestinal tract taken from Salmo gairdneri (KU 10169), Chirocentrus dorab (KU 10518), and Prosopium cylindraceum (KU 15417), I found annular rings present but they are not spirally arranged. Annular rings are transverse infoldings not continuous with one another. The most complex sections belong to P. cylindraceum (Fig. 4). In some places the rings form "spirals" while in other places they do not. Under close examination some rings end underneath the adjoining ring but are not continuous, providing only the illusion of a spiral. The other two sections from the specimens listed above had no spiraling rings at all. In the Russian literature the cross-section of the intestines has been misinterpreted. For example Korovina (1976) interprets a series of cross-sections as demonstrating the spiral nature of a valve (Fig. 5a,b,c). It may better be interpreted as a series through an asymmetrical ring. In cross-section the annular rings are attached to the intestinal wall anteriorly and extend posteriorly into the lumen with no posterior connection or spiral. A true spiral valve (Type D) cross-section has only one connection to the



B

CM



A

FIG. 4

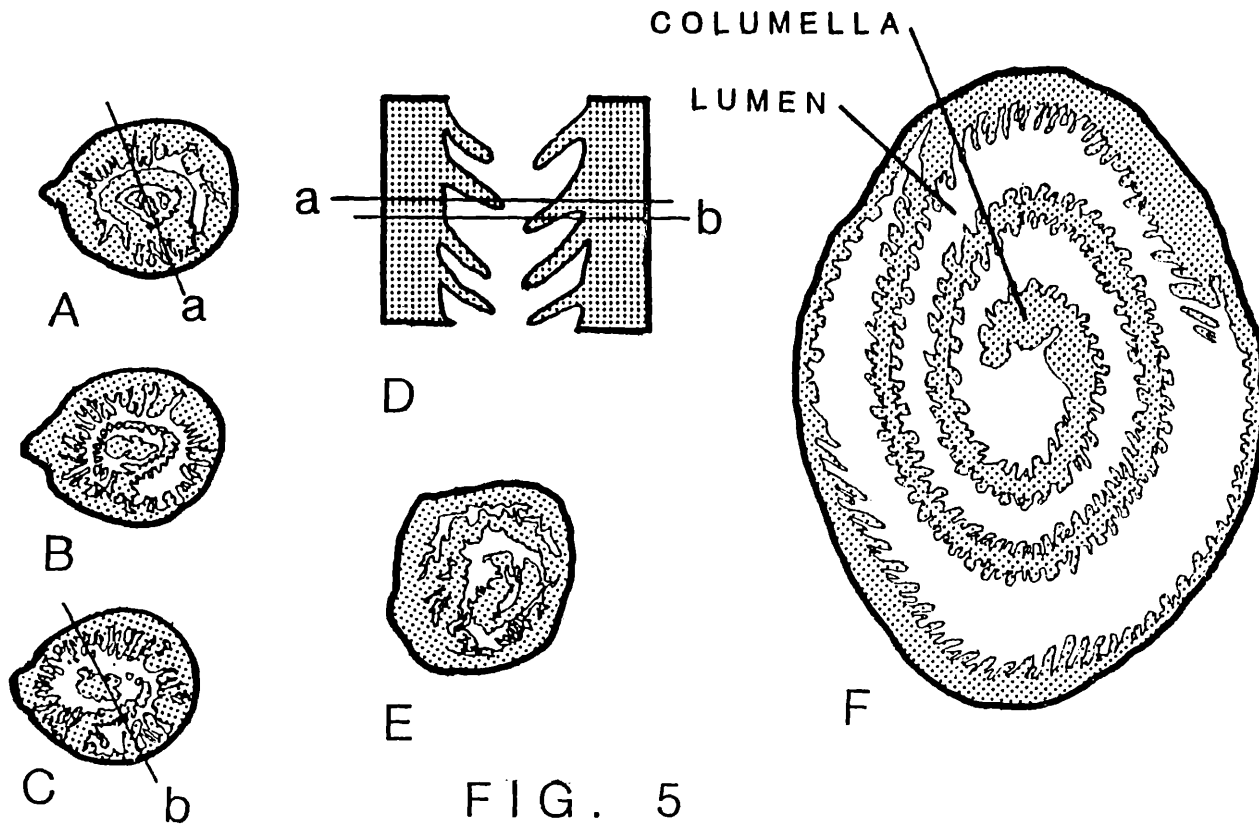


FIG. 5

intestinal wall and ends in the center of the lumen in a columella (Fig. 5f). The ring sections initially form a complete circle which begins and ends on the intestinal wall. This is a case where the connection of the ring is cut by the cross-section on one side but is anterior to the cut on the other side. In the following sections of the series the more anterior side of the ring is gradually lost leaving a crescent of tissue from the more posterior side (Fig. 5d). These observations again raise the question of whether the intestinal rings in the Teleostei are homologous or convergent to the spiral valve found in other fishes.

I consider annular rings to be convergent. Ring folding is not as complex as a Type D spiral valve and is more likely to be a converging morphology. For example, Günther, as reprinted in Cramer and Swain (1963), illustrates the vas deferens of Chlamydoselache anguinea which displays annular rings. If annular rings can arise in the vas deferens then it is possible they could also independently arise in the intestine. A second point is that the non-spiraled, numerous rings present in some Teleostei do not seem a likely derivative of the progressively^e reduced Type D of the more primitive actinopterygians.

Osteichthyes...Dipnoi

The intestine of the dipnoan Protopterus annectens

is figured in Wiedersheim (1897, fig. 209, pg. 260) and Owen (1841 plate 25). The intestine of Neoceratodus fosteri is figured in Garman (1913, plate 28, fig. 6) and in Jain (1983, fig. 5, pg. 823) but in the latter is anteriorly-posteriorly reversed. Kerr (1910), figures many stages in the development of Lepidosiren. They are all of Parker's Type D spiral valve.

Osteichthyes...Actinistia

Latimeria chalumnae is the representative of the Coelacanthii in which the soft anatomy is well documented. Millot et al. (1978, pg. 21) state:

"L'intestin spiral de Latimeria se rattache au type de <<valvule spirale>>, appartenant presque exclusivement aux squales de la famille des Carcharinides, qu'on appelle le <<type en cylindres ou en rouleaux>>."

However, the intestine has a Type D spiral valve, not a scroll valve (Fig. 6). The spiral cones are extremely elongate, nearly parallel, and the inner cones attach more anteriorly than the outer cones. This condition is initially confusing and can cause misinterpretations, but the food bolus would still travel in a one-way spiral and be ejected from the intestine through the central core of the innermost cone as is typical of a true spiral valve. Other criteria that the intestine is not of the scroll type include: the bases of the spiraling cones do connect to the intestinal wall; and

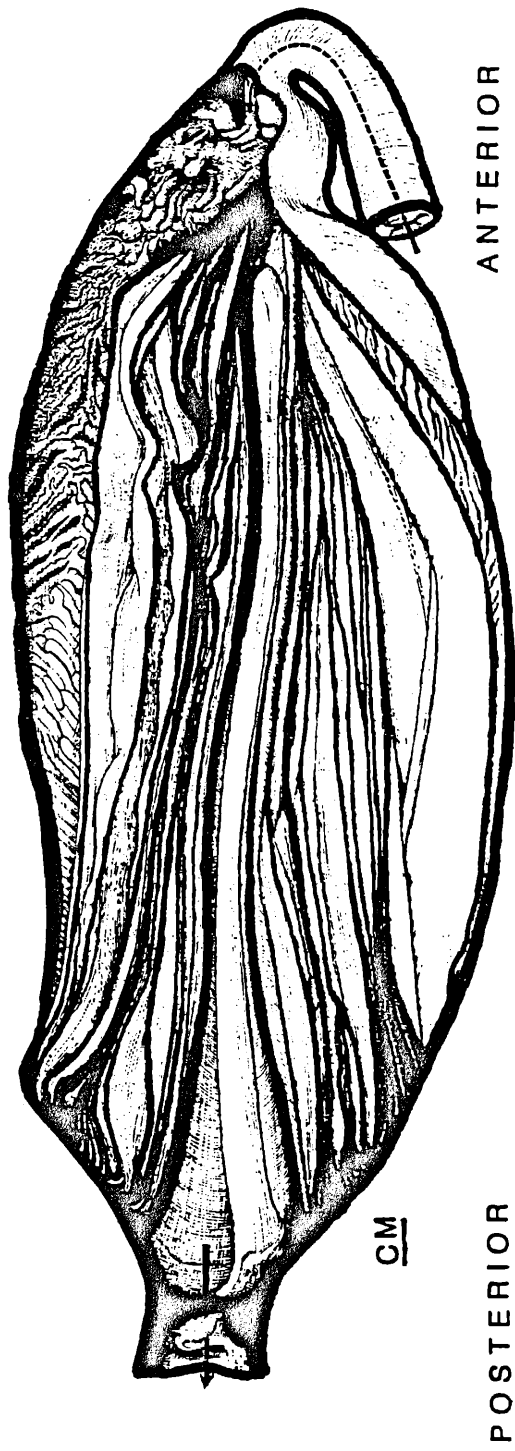


FIG. 6

the number of spirals present (14) is far more than expected in a scroll valve.

Distribution of Valvular Intestines in Extinct
Fishes

Placoderms, elasmobranchs, holocephalians, acanthodians, and actinopterygians all have fossil members which exhibit some form of preserved valvular intestine.

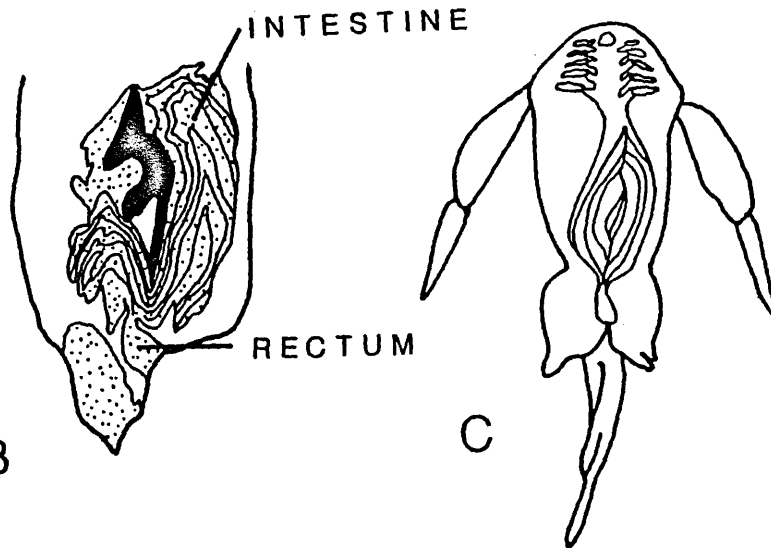
Placoderms

The valvular intestine of Bothriolepis canadensis, a placoderm, was first recognized by Denison (1941). It had been originally identified as gills by Patten (1912). The valvular intestine is made apparent by concentric layers of fine silt that were ingested, and remained within the intestinal cavity at the time of the animal's death. Denison considers the intestine to be of the scroll type. There may be cause to reconsider the morphology of the digestive tract but unfortunately the location of the specimens Denison figured is unknown, so that any reconsideration has to be based only on his text figures.

Figures 4 and 5 of Denison (1941) and figure 251 of Patten (1912) portray the intestine in anterior-posterior asymmetry (Fig. 7). Figure 5 is most



A



INTESTINE

RECTUM

B

C

FIG. 7

subject to interpretation because this section is more medially centered in the frontal plane. This conclusion is based on the rectal connection in figure 5 which is not present in other figures.

Evidence for these figures being of a true spiral valve, Type D of Parker, are as follows: the rectal connection in figure 5 seems to connect to the inner whorls; the section on the right in figure 4 shows the outer whorls ending blindly posteriorly as a cone would end, asymmetrically; the cone-like structures of figures 5 and 251 appear asymmetrical; and the number of whorls is just over the number expected. The number of whorls present in the sections ranges from a possible low of five to a possible high of eight. Denison writes that the Bothriolepis specimens show six or seven complete whorls. The criteria to distinguish spiral from scroll valves earlier discussed would lead to the conclusion that Bothriolepis had a Type D spiral valve.

Denison's reconstruction of the soft anatomy of Bothriolepis (1941, fig. 10) has discrepancies when compared to modern scroll valves (Fig. 7c). The scroll in the reconstruction has a columella connecting the whorls. As figured the complete scroll could not be unwrapped without tearing the connection between the nested whorls. In modern scroll valves this is not the case.

Of course conclusions drawn only from selected sections of a few figures could be misleading. Proper examination of a full series of sections, in well-preserved specimens, would eliminate any problems of perspective which off-centered sections could present.

Chondrichthyans

Sacco (1886) describes a specimen which he interprets as a cast of an elasmobranch intestine. It is an isolated fossil and is not absolutely certain to be either elasmobranch or an intestinal cast.

The best evidence for the presence of a valvular intestine in a fossil would be to find the actual valvular intestine, or a cast of it, in its natural position within the body of that fossil. There are such fossils in the elasmobranchs and holocephalians. Williams (1972) refers to specimens described by Woodward (1917), Claypole and Wright (1893), and Fritsch (1895) and refigured specimens from the latter two. These are specimens with casts of the spiral valve preserved in their natural position. Both the Woodward specimen of Cladoselache clarki, and Claypole and Wright's cladodont specimen are preserved in ventral view with the posterior of the intestine cast in fecal material. Two specimens that display very similar fecal

masses in similar positions provide great credence to the idea that the fecal masses are in a natural situation and not a chance association of one fossil preserved on top of another.

In an example of remarkable preservation Zangerl and Case (1976, fig. 36) describe a specimen of Cobelodus aculeatus that contains within the body 26 bands representing the spiral intestine. They speculate that there are more spirals than the 26 observed. They further note the presence of helminth egg casts in the rectal area of another specimen.

Zangerl and Case (1973) have also described a holocephalian with the spiral valve preserved. In describing two specimens of Iniopteryx rushloui, Zangerl and Case (1973, pg. 10) say "These structures are almost beyond doubt the casts of the inner surfaces of the spiral intestine, burst open following bloating, and the beige mass is gastric and/or intestinal content that oozed out of the digestive tube into the peritoneal cavity during the earliest stages of post-mortem bacterial degradation."

Zangerl (1981) in the Handbook of Paleoichthyology, summarizes the known soft anatomy of fossil elasmobranchs.

Acanthodians

Fossil evidence for the presence of valvular intestines in the acanthodians is poor. Zidek (1980) considers spiral coprolites found in the Heath Formation of Montana to be true coprolites and tentatively to have been produced by Acanthodes lundi. His conclusion is based on evidence of natural associations. One specimen figured (Carnegie Museum 25598, fig. 1c, pg. 52) has a coprolite associated with its tail region. This specimen has a second coprolite near its head but it is not well preserved and does not possess any discernable exterior structure so Zidek does not consider it associated (pers. comm.). Other coprolites of the same external morphology as the one near the tail are found associated with other Acanthodes specimens but not with the patches of paleoniscoid scales (which are the only other specimens found in these particular layers). Zidek considers the paleoniscoids as the only other possible producer of these coprolites. In my opinion the spiral coprolites found in the Heath Formation could only be produced by a Type D valvular intestine. Justification for this opinion will be discussed later in this text.

To assume acanthodians produced spiral coprolites based on association is risky. There are many associations made by earlier workers that are now considered unfounded, but were reasonable when the

association was made. Woodward (1917) provides examples of associations of coprolites with amphibians and reptiles that are not considered tenable now. The cases he cites are situations where the coprolites and skeletal remains are within the same strata but not with the coprolite contained in the skeletal fossil. Although the acanthodian case is more subtle, the evidence is inconclusive.

Zidek (1980) also directs readers to two other possible coprolites. These two specimens are from the Upper Carboniferous of Czechoslovakia and are described and figured by Fritsch as Coprolithes acanthodi. Based on the association described and the imbricating cones present in cross-section, Zidek considers them to be acanthodian enterospirae. The figures in Fritsch (1907, plate 11 and plate 12) are all very good except for the Coprolithes acanthodi specimens. However plate 11 figure 8 may show the coprolite enclosed inside the acanthodian body scales.

Based on the evidence presented by Zidek and Fritsch the presence of a spiral valve in the acanthodians is tentatively assumed.

Actinopterygians

Evidence for fossil actinopterygian spiral valves is poor. The most recent speculation is by Zidek (1980, pg. 73), who compared the external morphology of spiral

coprolites found in association with palaeoniscoid specimens to the "enterospirae" Williams (1972) described. "To my knowledge none of the heteropolar coprolites associated with palaeoniscoid specimens have been sectioned but their morphology and their position with respect to the body of the fish leave little doubt that they are fossilized intestines. It thus appears that in at least some palaeoniscoids the spiral valve was a structure as complex as that in elasmobranchs."

The specimens cited by Zidek in Fritsch (1907) are isolated coprolites Fritsch assigned to palaeoniscoids. The specimen cited by Zidek in Stamberg (1976) is a palaeoniscid, Paramblypterus rohani (Fig. 8). Next to it is a spiral coprolite which is one-third the length of the fish. The size of the "coprolite" appears too large for the specimen. The coprolite would still seem too large if the interpretation of the coprolite as an enterospira is true. Of most importance, scales of the specimen look undisturbed. It would seem impossible for an enterospira to move out of the dead body without disrupting the scaled integument. The size of the enterospirae would preclude an everting of the intestine through the anus. Heyler (1969) figures the same specimen and disagrees that it is a natural association. These specimens are not compelling evidence for the presence of a palaeoniscid valvular intestine.

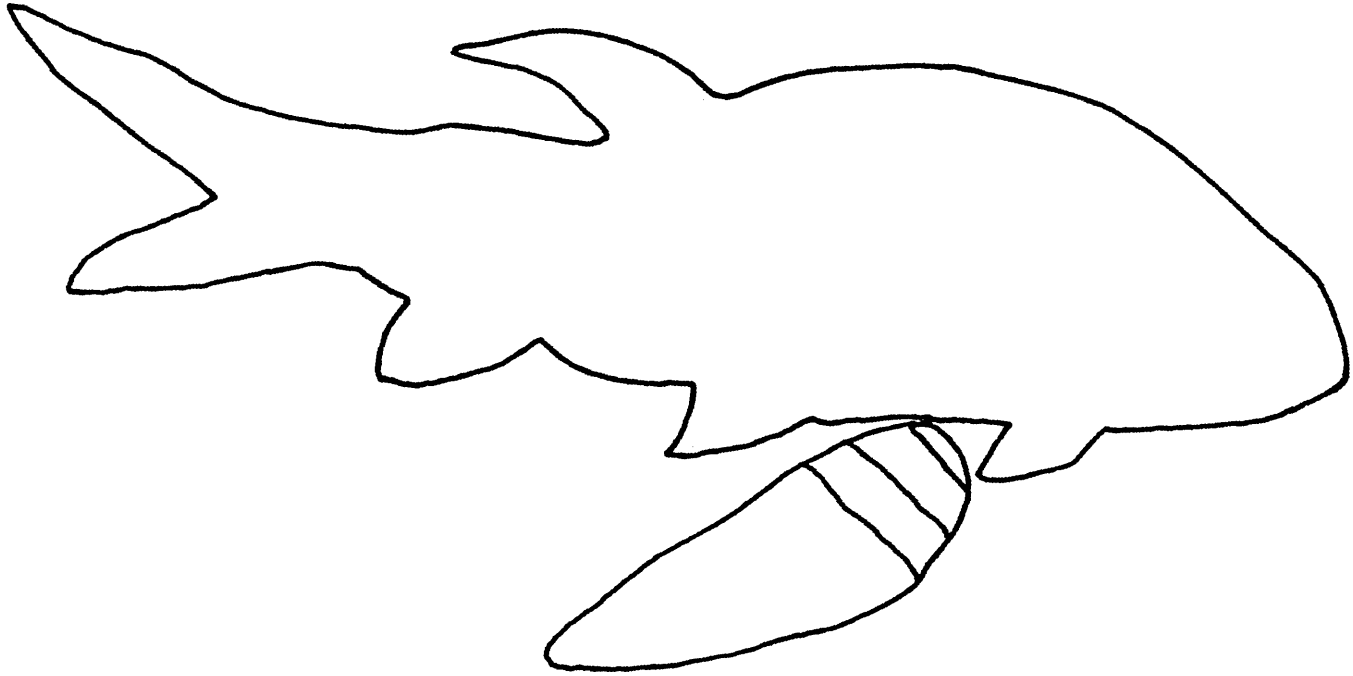


FIG. 8

In an article describing rope shaped coprolites, Edwards (1976) compares the specimens he describes to Lumbricaria. In that text he perpetuates the hypothesis that Lumbricaria, a trace fossil genus that looks like madly coiled rope, represents fossilized fish intestines. Buckland (1837) relates the history the genus had up until that time. Apparently from its initial description by Graf Münster through the time of Buckland it was considered as petrified intestines, or their contents, of fish. Edwards (1976, pg. 115) states:

"Agassiz long ago suggested that Lumbricaria represented fossilized fish intestines (Buckland, 1869), a suggestion which Müller (1969) has satisfactorily supported." However, Müller (1969) concluded that Lumbricaria are long excretory strips of a free-swimming animal, possibly a fish, but not an intestine.

Broughton et al. (1977, 1978) describe coprolites from the Cretaceous of Canada and attribute them to sturgeons (Acipenser). They consider some of the spirally and helicoidally shaped fecal masses to be fossilized intestinal tracts. This is disputable because the spiral coprolite they figure (1978, plate 4, fig. 5) as an enterospira possesses the cross-section of an extruded round band of fecal material and most importantly, the internal folds are present as at least four series of concentric bands arranged in an offset

row. These bands are not spirally arranged as a cross-section would be, or imbricating as in a frontal or sagittal section. I suspect these authors perceived the spiral intestine literally as a spirally wound tube, and not as a tube with a spiral structure infolding from the inner layers of the tube. The organic material of the coprolites they describe have been replaced by pyrite, siderite, and hydrous iron oxides. They note the banding this has caused on most of their specimens. The specimens they describe as gut infillings should probably be reinterpreted as true coprolites with normal mineral banding.

There is possible evidence of fossil actinopterygian spiral valves. In a paper describing the digestive tract of fossil fishes, Neumayer (1919) provides examples of actinopterygians with fecal material forming casts of the digestive tract. The specimens illustrated are whole fish fossils with masses interpreted as gut contents within the boundaries of the fish. Inspection of the figures leads me to believe some of the "spiral valve" casts are in reality chains of food boli. I characterize the food boli chains to be rounded fecal masses of randomly mixed sizes. I would expect casts of the spiral valves to be more angular, of uniform descending size in anterior-posterior direction, tending to be located near the anal fin, and

the visible spiral to be at a reasonable angle (so that the grooves if continued around would connect to the next visible groove of the spiral).

Of the specimens illustrated, Caturus (family Caturidae) and Leptolepis (family Leptolepidae) have casts of the spiral valve present. In my opinion three of the four figures of Caturus are examples of food boli chains, the fourth is a cast of a spiral valve based on the criteria previously given. Possible spiral valve casts are present in specimens of Eurycormus (family Caturidae), Clupea (family Clupeidae), Spaniodon (a possible elopiform), and Thrissops (a possible ichthyodectid)

One specimen illustrated by Neumayer, Asthenocormus, was first studied by Vetter (1881) and interpreted as containing a spiral valve. This structure is considered to be a calcified air bladder by Eastman (1914). Bridge and Haddon (1893) illustrate the internal septa of Siluriform air bladders. The ridges on the fossil structure could be interpreted as transverse septa which partition the air bladder into chambers. The lack of coprolitic material in the interior, the small diameter of the tube, and the tapering of the structure past the anal fin are all compelling reasons provided by Eastman against an intestinal interpretation.

Lastly, Gillette (1972) describes assumed elopids with filled coelomic cavities. A comparison is made to a specimen of Thrissopater intestinalis (= Pachyrhizodus minimus) which seems to have preserved in the body a structure near the anal region, reminiscent of a spiral valve.

Summary

Living vertebrates with valvular intestines include agnathans, chondrichthyans, actinopterygians, dipnoans, and the actinistians. Fossils which have valvular intestines preserved include the placoderms, chondrichthyans, possibly the acanthodians, and the actinopterygians (Fig. 9). The most common intestine is Type D, found in all groups, and here is considered as the primitive condition. The actinopterygians progressively reduce the spiral valve until the teleosts no longer possess one (Fig. 10). Some members of the teleosts have intestinal involutions (annular rings) that I consider independent of valvular intestines. The tetrapods show no indication of possessing a valvular intestine.

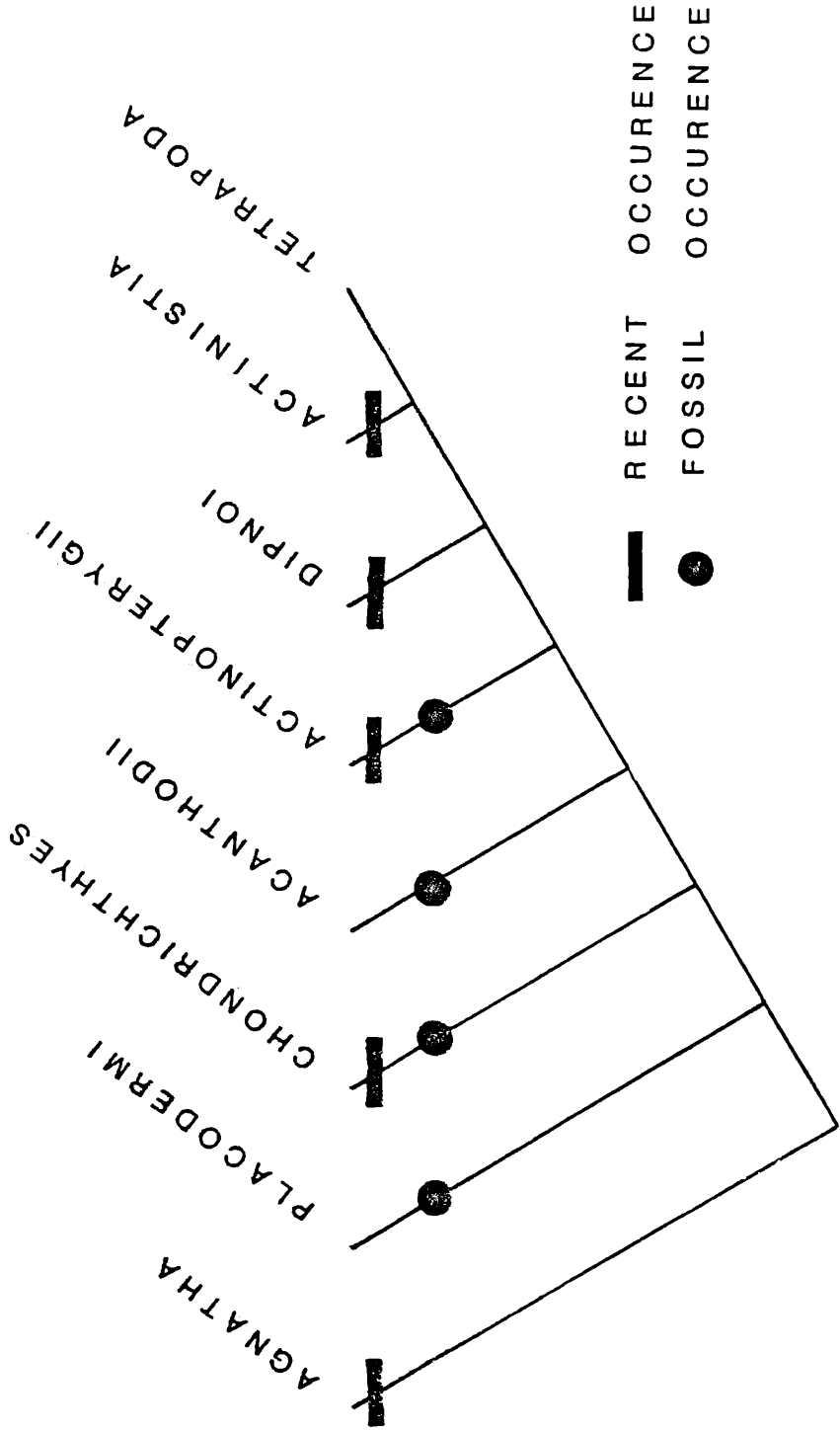


FIG. 9

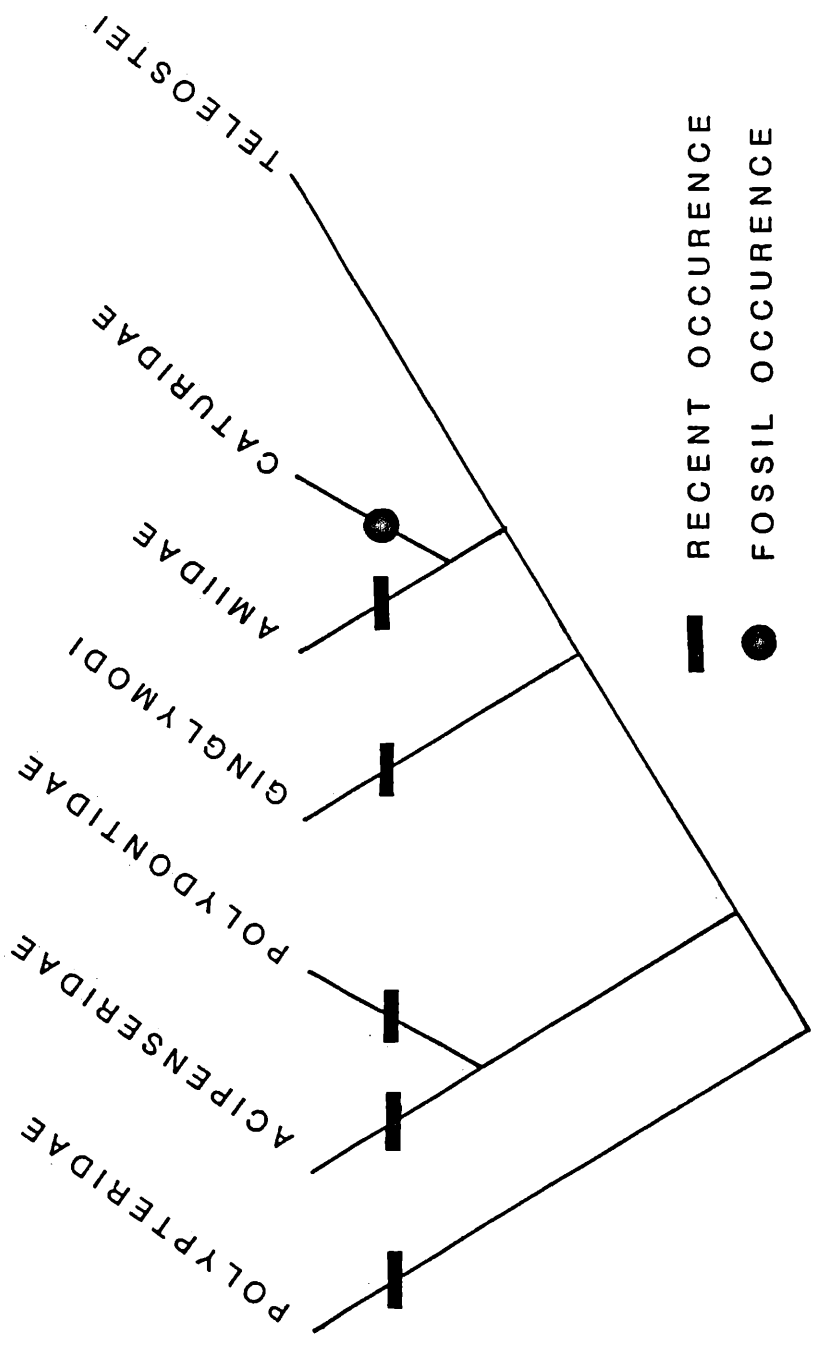


FIG. 10

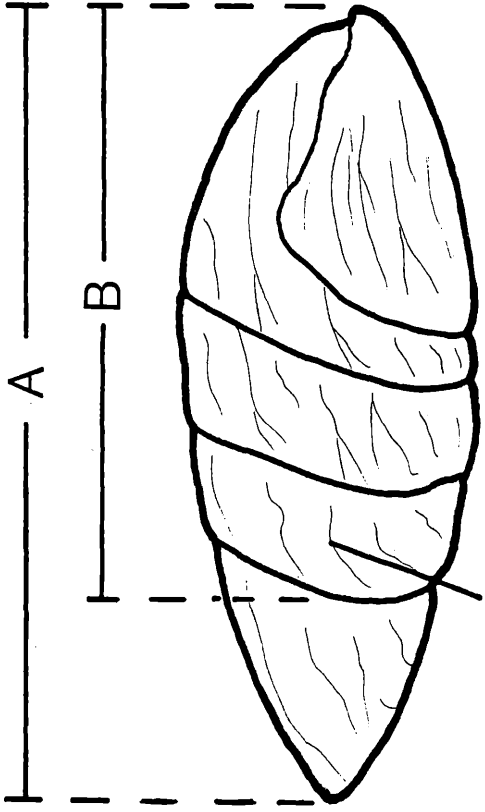
The fossilized excrements of animals are called coprolites. Amstutz (1959) reviews the literature defining coprolites and provides criteria for their determination. One type of coprolites is the spirally coiled ones which first gained attention in the early 19th century. Mantell (1822) concluded they were of animal origin and were not cones from fir trees as first thought. His conclusion was based on the composition of the fossil, inclusions, and the testimony of Mr. Konig of the British Museum (who noted a peculiar smell, unlike any in the plant kingdom, when hydrochloric acid was applied to the fossils). Spiral coprolites were first recognized as fossil fecal waste eight years later by Buckland (1829). Fritsch (1895) and Neumayer (1904) concluded that spiral coprolites were fossilized valvular intestines for which Fritsch (1907) proposed the term "enterospirae". Williams (1972) described in great detail "spiral coprolites" from the Permian of Kansas and agreed that they were enterospirae. Since 1972 three papers describing spiral coprolites with enterospiric morphology have appeared. These are Stewart (1978), Duffin (1979), Jain (1984). The reader is referred to reviews of greater scope in Hoernes (1904), Williams (1972), and Duffin (1979), for further

details on spiral coprolite history.

Spiral coprolites from Kansas described as enterospirae are from the Lower Permian Wymore Shale (NE 1/4, NW 1/4, sec. 35, T.9 S., R. 7 E., Riley County, Williams, 1972), and the Upper Cretaceous Niobrara Formation (NE 1/4, sec. 12, T.8 S., R.22 W., Graham Co.; and E 1/2, sec. 27, T.14 S., R.26 W., Gove Co, Stewart, 1972).

Spiral coprolites which are described as enterospirae all have the appearance of a ribbon spirally coiled around a central axis. The coils are at a slight outward angle, with the innermost coils protruding farther than the outer coils (Fig. 11). The morphology of the coprolites was described by Neumayer (1904) as heteropolar. The heteropolar condition is defined by Neumayer as a coprolite with the coils concentrated toward one end, the other end (at least 1/3) being free of coils. This contrasts with amphipolar spiral coprolites in which the coils are evenly spaced from one end to the other, the last coil rarely elongated.

Cololite is a name proposed by Agassiz in Buckland (1837) given to fecal material which is preserved in the intestine. I will use the term coprolite for fossil feces that are expelled from the body, cololite for internal fossil feces (and in a broader sense for recent



“MUCOSAL FOLD”

FIG. 11

coiled feces in the body), and enterospirae for spiral coprolites in the sense of being interpreted as preserved valvular intestines.

Spirally Coiled Coprolites

Both Williams (1972) and I hypothesize that the Wymore Shale spiral coprolites were formed inside the body. However Williams hypothesized them to be enterospirae while I hypothesize them to be formed in the colon and subsequently expelled.

I feel a re-evaluation of the Wymore Shale spiral coprolites, with reference to a cololite formation, may be productive due to the presence of a modern analog (Scyliorhinus canicula). Stewart Springer suggested to Williams that study of this species could prove valuable but Williams was not able to obtain material so Williams suggested that I look at S. canicula.

Fourteen specimens of Scyliorhinus canicula (selected from Museum of Comparative Zoology lot #57053) have hardened fecal masses in their intestinal tracts. The fecal masses are strikingly similar in gross morphology and cross-section to the fossil specimens. They are present as hardened spiral feces in the colon of four of the specimens. Their long axes are parallel to the long axes of the intestines (Fig. 12). Two other

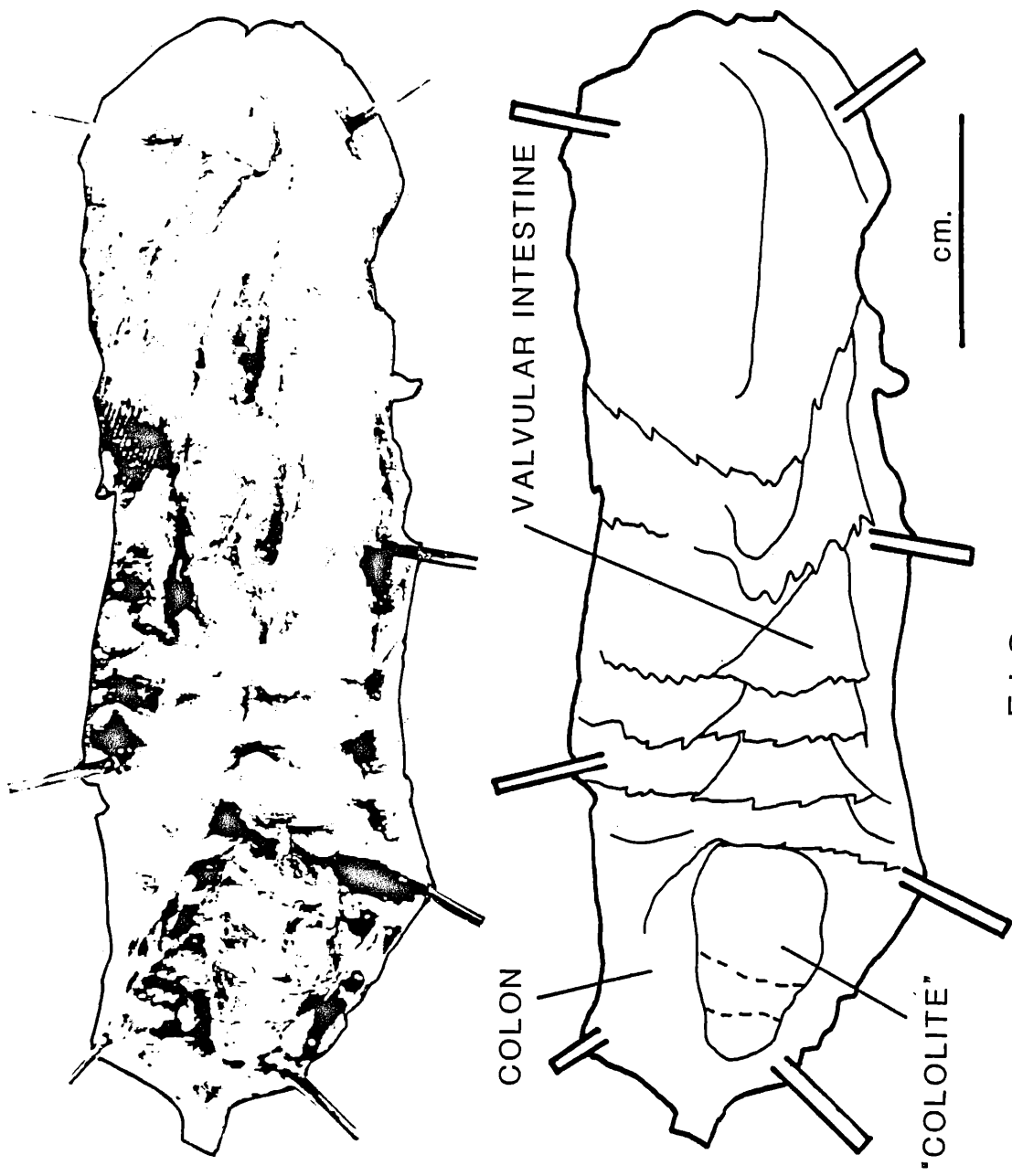


FIG. 12

specimens have hardened fecal material in the lower portion of their valvular intestines and in their colons (Fig. 13). During extraction the fecal material breaks into many fragments. However in the specimen figured the feces in the colon were continuous with the feces in the valvular intestine. In another specimen the fecal material is present in the rectum (Fig. 14). I consider these three kinds of hardened intestinal contents to be fully formed spiral fecal masses, incipient spiral fecal masses and a spiral fecal mass in the process of expulsion, respectively.

Buckland (1837, p. 152) had already 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, Pl. 15, Figs. 3, 5, 7, 10, 11, 12, 13, 14. In the same manner, a lamina of coprolitic matter would

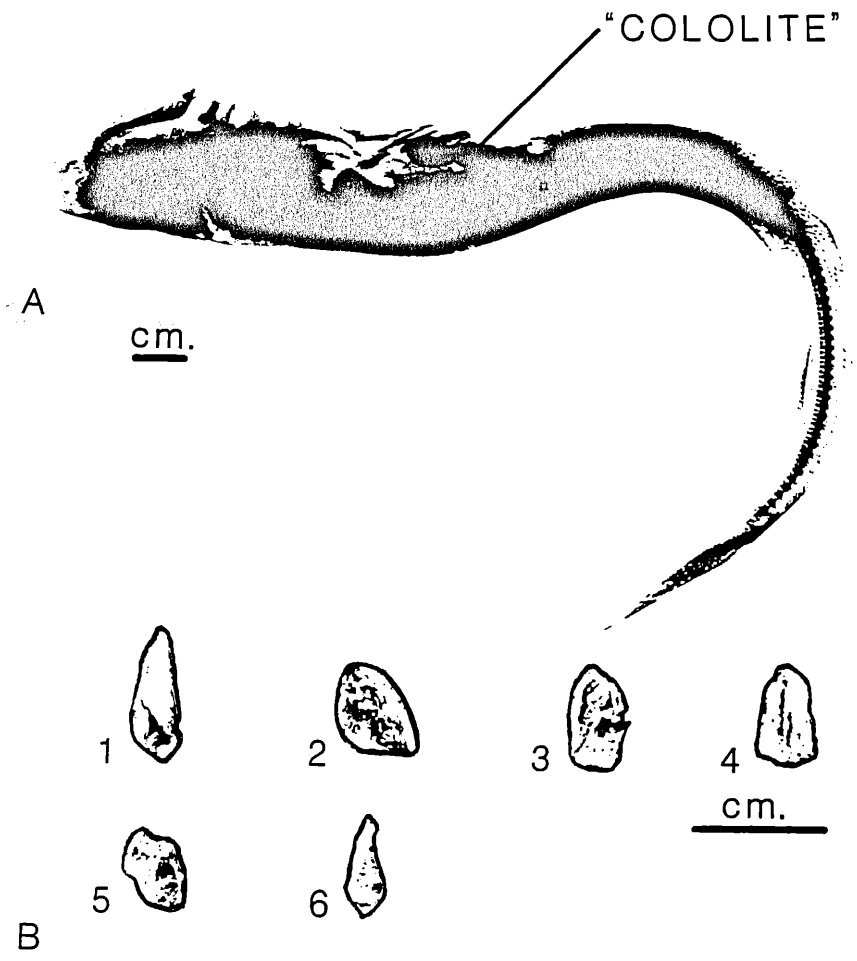


FIG. 13

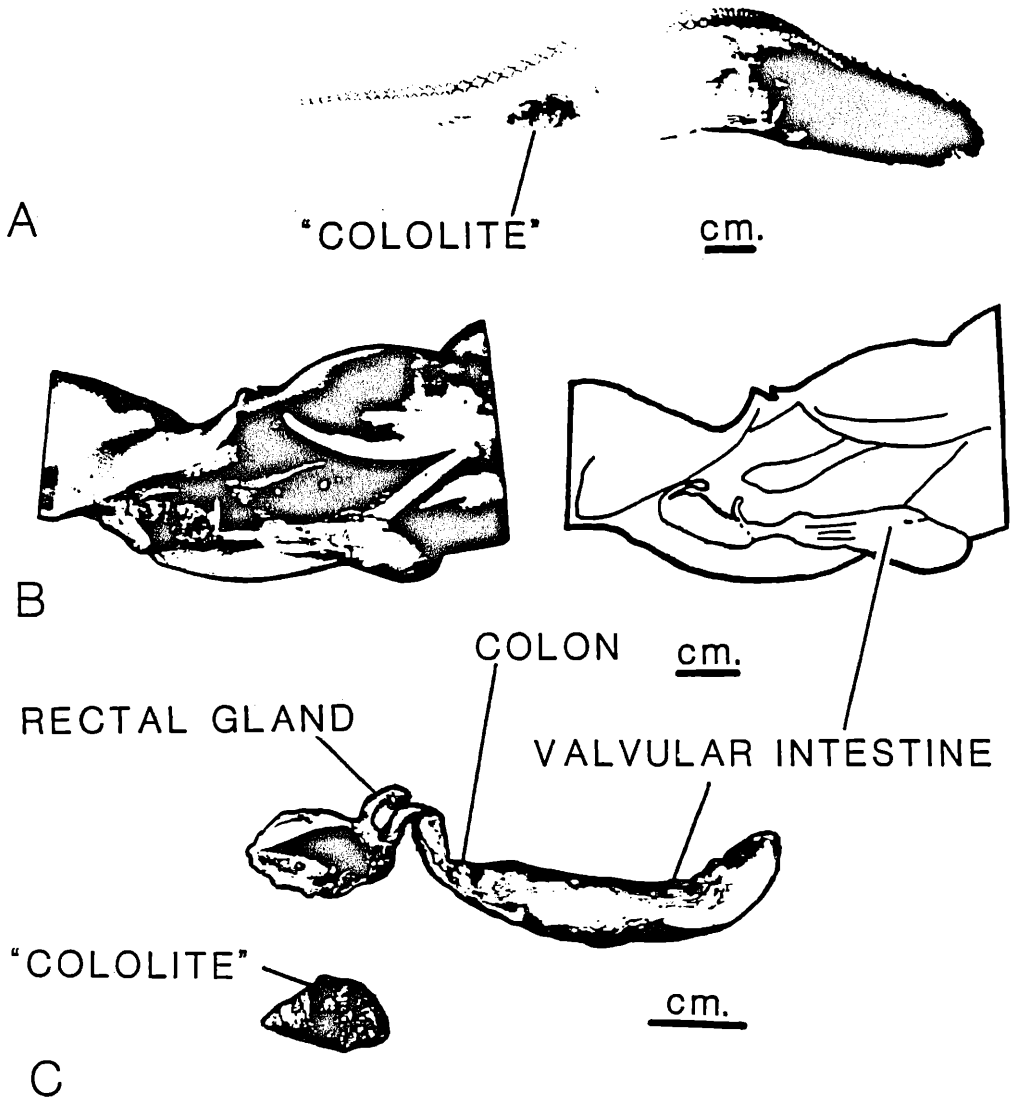


FIG. 14

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 petrification, that in hardness, and beauty of the polish of which they are susceptible they rival the qualities of ornamental marble."

I accept the process of spiral coprolite formation as described by Buckland (1837). Zangerl and Richardson (1963, p. 144) describe the same method for the formation of the spiral coprolites found in the Pennsylvanian Black Shales of Indiana. "A rubber cast of the lumen of the spiral intestine of a modern shark (fig. 30) 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." They however did not know of a modern analog at that time, and were probably hesitant to apply their hypothesis as far as they may have wanted.

A plastic ribbon of fecal material continuously

coiling through the valvular intestine into the rectum would form a spiral fecal mass. The feces can be found as a cohesive ribbon. While looking for parasites in elasmobranchs D. Brooks has pulled out such fecal ribbons (pers. comm.). I consider the second set of movements described by Cannon (1903 p.327) for squalus to be the prime locomotors 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 walls. If the intestinal 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 will be more loose and a conical cavity will be present in the finished fecal mass (Fig. 13B, 1). Further progress of the fecal ribbon into the colon will produce more coils and push the initial coils posteriorly a short distance. After the spiral fecal mass is formed it is transported through the rectum and ejected from the body as an entire unit. Lungfish researchers have seen spiral fecal pellets in their

aquaria: Dean (1903), A. Kemp, W. Bemis, B. Conant (pers. comm.). Conant has seen the spirally coiled feces expelled from the fish as an entire unit enclosed in a mucous coat. The dipnoan fecal mass that Dean figures (from Protopterus) has the amphipolar morphology while the recent fecal masses from Scyliorhinus are heteropolar. The valvular intestines of Scyliorhinus and Protopterus are both Type D and are generally similar. I consider the two kinds of fecal masses to be formed by similar processes and possibly to be gradational, because of variation discussed at the end of the text. If this is true, determination of the animal group which forms a specific kind of coprolite would not be possible without more information.

The fecal masses in the colon and rectum do not show any striations indicating friction between the feces and colon while coiling, or between the spiral fecal mass and the rectum while in the process of expulsion. The feces need to be pliable in order to coil in the colon but they also need to be firm enough to prevent distortion and scraping from peristaltic waves in the rectum or from the sphincter muscle at the anus. Possibly a mucous coat protected the feces. More likely the spiral feces hardened in the colon. The recent spiral feces are as hard as the fossil coprolites from the Wymore Shale. Hardening of the recent feces

may be partly due to the effects of alcohol preservation, but hardening may normally occur to a lesser degree in the intestine of the living fish. In one specimen the 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 chyme was present (possibly the finely ground mass of undigested fish bones). In the posterior half of the intestine and the colon the fecal ribbon was hard. The mechanism for hardening of the feces may possibly be linked to water absorption which normally occurs in this region of the gut.

The hardened fecal ribbon and the spiral fecal mass both have in cross-section, microstructure perpendicular to the flow of the ribbon. The microstructure is difficult to explain. I consider it to be the fecal ribbon which ideally would fold upon itself as it is moved posteriorly, similar to a throw rug folding if pushed from one end (Fig. 15). Folding in the observed sections is rarely continuous or clear. The ribbon is not at optimum plasticity to deform to the degree that it is typically subjected to in the intestine. The excessive stress causes the ribbon to fracture at the points of maximum bending and become layered. More complex folding can occur when a previously folded ribbon over-rides the folds posterior to them (Fig.

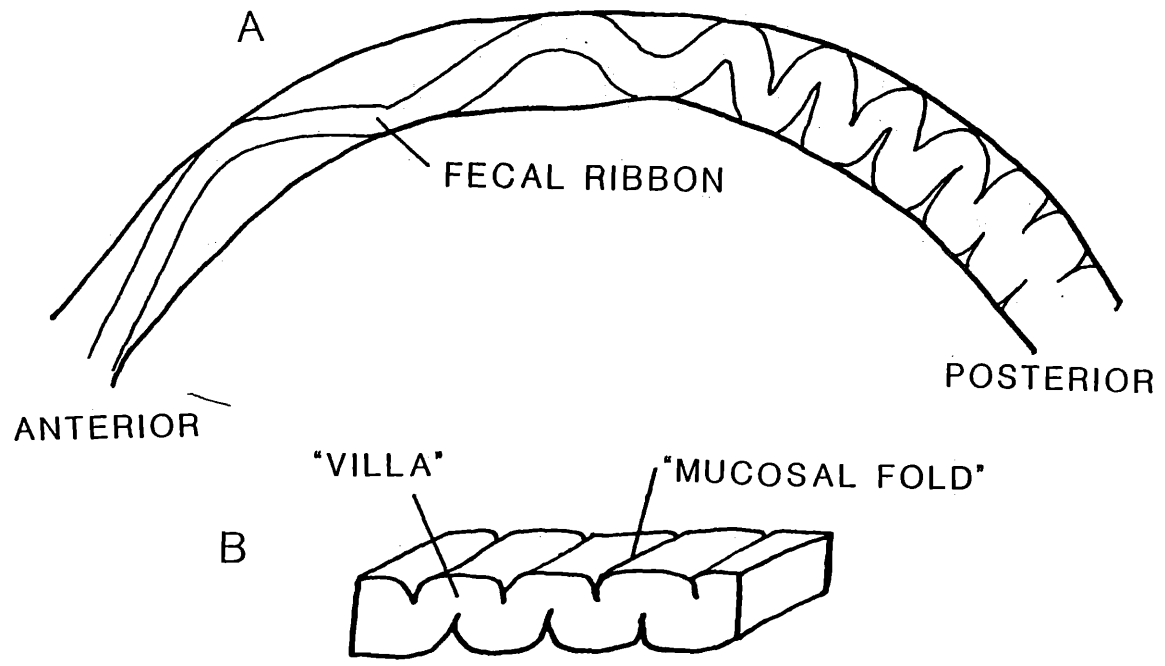


FIG. 15

16B).

The formation of spiral coprolites within the colon was rejected by Williams. He felt the fecal material entering the colon would have to enter from an anterior direction rather than from a lateral direction (the direction the fecal material is moving in the valvular intestine). This would cause the coils to be parallel rather than perpendicular to the long axis of the intestine. Although this is a reasonable speculation, the modern analog indicates that the fecal ribbon does retain its cohesiveness and coiling direction from the valvular intestine into the colon.

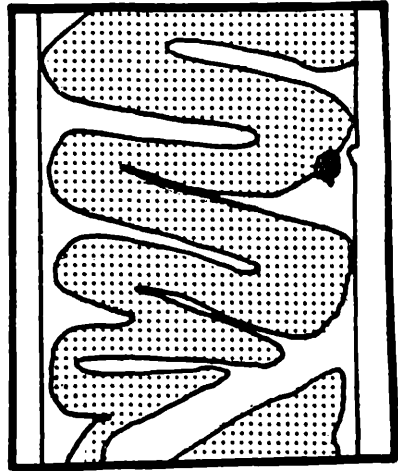
Basically Williams (1972) had six lines of evidence for concluding the Wymore coprolites to be enterospirae. The following is a review of his reasons with a comparison of the cololite interpretation. The first five reasons Williams gave are similarities in gross morphology.

His first evidence is the resemblance to a Type D spiral valve, with posterior cones dipping beneath anterior ones. Both the Wymore Shale coprolites and the modern analog have this shape.

His second reason is the nearly perpendicular orientation of the whorls to the long axis of the specimens. This morphology would be consistent with a fossilized intestine. It is also similar to the modern



A



B

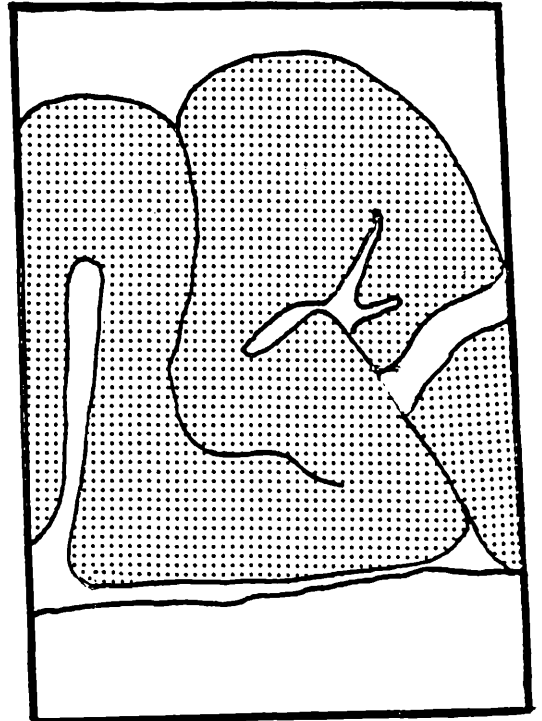


FIG. 16

coiled fecal masses.

Third, some of the Wymore Shale specimens have a conical cavity. The base of the cavity is at the posterior end of the fossil and the apex extends anteriorly. These cavities can be found filled with matrix. Williams considered this as evidence against a cololite origin. He did not consider that fecal material could coil into this configuration, pass through the rest of the intestinal tract, and subsequently get matrix infillings. However the fecal material of S. canicula can coil in the rectum and is hard enough to travel through the rest of the intestinal tract without distortion. The coprolite could then be filled with matrix.

Fourth, subparallel folds found at approximately 60 degrees to the long axis are interpreted as casts of mucosal folds on the outer wall of the intestine. However 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. Large mucosal folds are not typical of elasmobranch intestines. When they do occur, for example in Chimaera, they are localized on the outer anterior intestinal wall. The outer wall of the intestine would not leave mucosal folds on the inner whorls. There would be present only pitting left by the

villae. The modern fecal ribbons show these "mucosal folds" being the valleys between the more prominent folds of the deformed ribbon.

Fifth, Williams (1972) noted that the raised lip on the edge of the whorl of some fossil specimens has been suggested to have some relation to the annular veins which circumscribe the intestine. However the annular veins are really two semicircles with offset ends in Squalus. Also suggested by Williams was that the lip could be formed by embayments along the junction of the outer intestinal wall and the valvular intestine. Williams also noted a lip on the spiral fecal pellets of Protopterus. This he thought to be a cast of a small pocket at the junction of the valvular intestine and the outer intestinal wall. I think the embayment process is possible. Alternately it is possible that the lip is caused by an underlapping of the fecal ribbon as it moves around the valvular intestine. In any case, the existence of a lip neither supports nor denies either hypothesis.

The sixth line of evidence Williams employs is the similarity of the cross-sections of modern spiral valves and the fossils. He considers the folds seen in the fossil cross-section to be the preserved villae of the mucosal lining. The line between the whorls is

considered to be the space in which the rotted valve flap of the valvular intestine once was present. While there are resemblances, there are also many difficulties with this interpretation. The mucosal folds in many slides can be seen to fill the entire distance between whorls with a single continuous fold (Fig. 16A). No animal with a spiral valve has folds present on one side of the valve flap and not the other. Complex folding (Fig. 16B) is another problem. They occur on the same level that the "mucosal folds" occur. They are not present below mucosal folds where glandular material would appear. In sections of elasmobranchs which I have made and sections I have seen in the literature there is nothing similar to this complex folding present. Sections of intestinal tissue usually cut through the villae at odd angles leaving islands of tissue in the lumen. The "villae" of the fossil coprolites do not section as true villae would, but as a structure that extends into the section for a much greater length than villae would.

The variability of the "villae" in the enterospirae is extreme. However while some variability would be expected in intestinal villae size and shape, it should be a consistent variation from anterior to posterior. Observations of serial sections of fossil specimens show no pattern in the variation. In modern elasmobranch

sections, the most obvious variation seen is a gradation in size from large at the anterior to small at the posterior end of the valvular intestines. The size relationships of the fossil folds are different than would be expected for a spiral valve. The fossils do not show any obvious gradations. In the histological sections of living species which I have examined, the spiral flap of the valvular intestine is approximately as thick as one-half the villae height. Small specimens tend to be below this ratio. The fossils show very little or no available space for the rotted valve flap to occur. Interpretation of the Wymore Shale coprolites as true coprolites, produced as described earlier, circumvents all these problems.

Other evidence against an enterospiric interpretation includes the lack of an intestinal lumen in the fossils. Spiral intestines of all animals I have examined and seen in the literature all have a large lumen for the fecal material to travel through. There is no lumen present in the fossil specimens, all available space is filled by the "villae". When interpreting the folds as "villae" there cannot be constriction or shrinkage allowed to compensate for the lack of the intestinal lumen. Normally tissue that is unpreserved will start to autolyze immediately. Williams considers preservation of enterospirae to be

due to the packing of undigested or partly digested matter around the villae. This chyme would somehow prevent self-digestion and preserve the villae.

Williams (1972, p. 16) stated it in this manner:

"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 villae, 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 is based on the extreme range of sizes and spiral numbers in the Wymore Shale coprolites. Fifty coprolites were measured for total length, the ratio of the coiled length (the distance a straight line, parallel to the axis, would be that goes from the anterior of the coprolite to the last external coil) to total length was calculated, and the coil count

determined (Fig. 11). The ratio between coiled length and total length would provide an index to the heteropolar and amphipolar condition. The total length of the fossil specimens ranges from 6.61 cm. to .84 cm., with an average of 2.416 cm.. The ratio ranges from .79 to .18, with an average of .476. The number of coils ranges from 12 to 3, with an average of 7.4.

If the coprolites are interpreted as enterospirae then they should have similar variations to the original valvular intestines. A comparison could be made with recent valvular intestines to see if the fossil "intestines" vary as little or as much .

Recent thoughts on the amount of variability to be expected in spiral valves are largely based on Parker's (1885) study of the genus Raja. Williams (1972), Zidek (1980), and Duffin (1979) all mention the variability Parker described and overall imply that it is significant.

Parker found the Raja spiral valve to be constant in the 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.

The variable features are considered to be:

-length of attached edge of the valve versus the width of the intestine, on which depends the number

of turns and the position where the posterior end of the valve stops.

-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 food.

-the character of the mucose membrane.

In essence the variability is the number of turns, the width of the spirals and if they are directed anteriorly, and the character of the mucose membrane.

Although I do not contend that there is no variability, I do not believe all possible interpretations have been considered. Parker (1885) considered the variability in the available specimens in the genus Raja, not a single species hence variability may be far larger than if only one species was considered. It is also my impression that Parker wanted to present to his audience the total diversity possible, not what is typical of the majority of specimens. Another point to consider is that the diversity may not be as large as is implied. Parker considers Type A (the ring valve) to be more or less hypothetical in Raja. When it occurs it is found only in the posterior portion of the valve. He describes Type B from only two specimens, both of which were dried out. This may have caused more distortion than just the displacement of the

columella from the central axis which Parker noted.

Fee (1925, p. 117) expounds moderation in considering Parker's variation, "The apparent disparagement 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." In addition to evidence by Mayer, Fee also noted differences in shape and arrangement of the valve in relation to the amount of fecal material present and contrary to Parker in relation to the age of the fish. Finally Parker's method of preparing the study material was to wash out the contents, distend the spiral intestine and then harden the intestine in chromic acid. This I am sure would cause some distortion in light of Fee's comments.

I do not think Parker's variability is reasonable as a comparison for modern studies not only due to the problems and comments just mentioned, but especially because more than one species is included in his paper. If compared to fossils it would be as if comparing one unknown to another.

For comparison with the fossil specimens I chose

Squalus sucklii. It is easily obtained, has a Type D spiral, and does not appear too specialized (compared to the specialized body and food habits of Raja).

Twenty-seven specimens were dissected and their valvular intestines measured. They included seven embryos (defined here as being inside the parent) with yolk sacs, eight embryos which had absorbed their yolk sacs, and twelve adults. The intestine lengths range from 19.0 cm. to 2.0 cm., with an average of 8.73 cm.. The coil number ranges from 15 to 13, with an average of 14. The ratio between coiled length and total length ranges from .417 to .163, with an average of .262. The Type D valvular intestine is consistent in all sizes and coil number variation is not related to size. Both the coprolites and the modern intestines have a comparable magnitude of size variation (approximately ten-fold) but the variation in the coprolites is over two times the ratio values, and four and one-half times the coil count average compared to the modern intestines (Figs. 17, 18).

The few (five) fecal masses available for comparison have great variation in their coil count (from 1 coil in the "incipient coprolite" to 9 in one fully formed) and the ratio values (from .45 to .83). The range of variation in the ratio values for the recent fecal masses (38%) is greater than the range for the recent valvular intestines (25%) but less than the

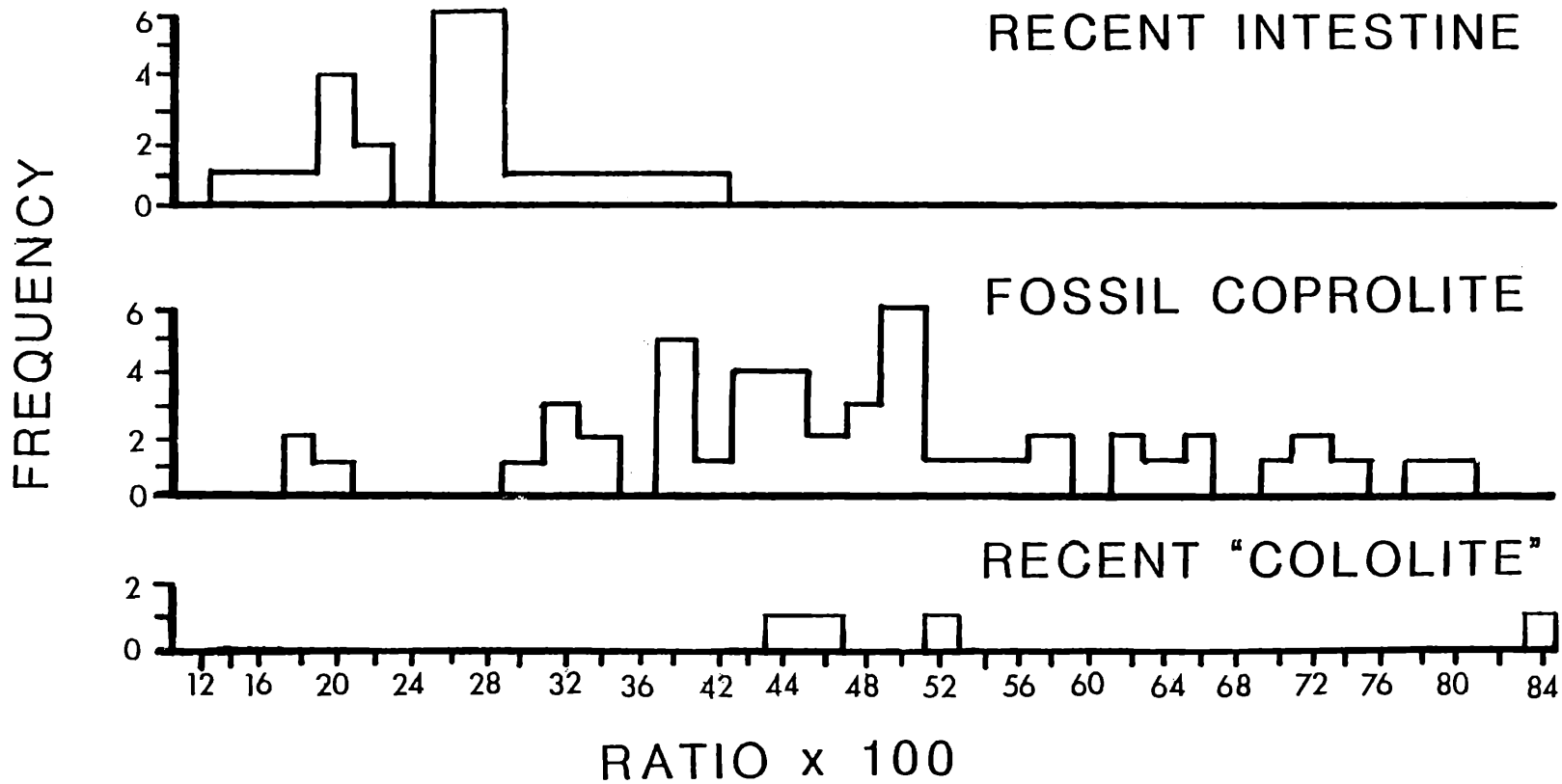


FIG. 17

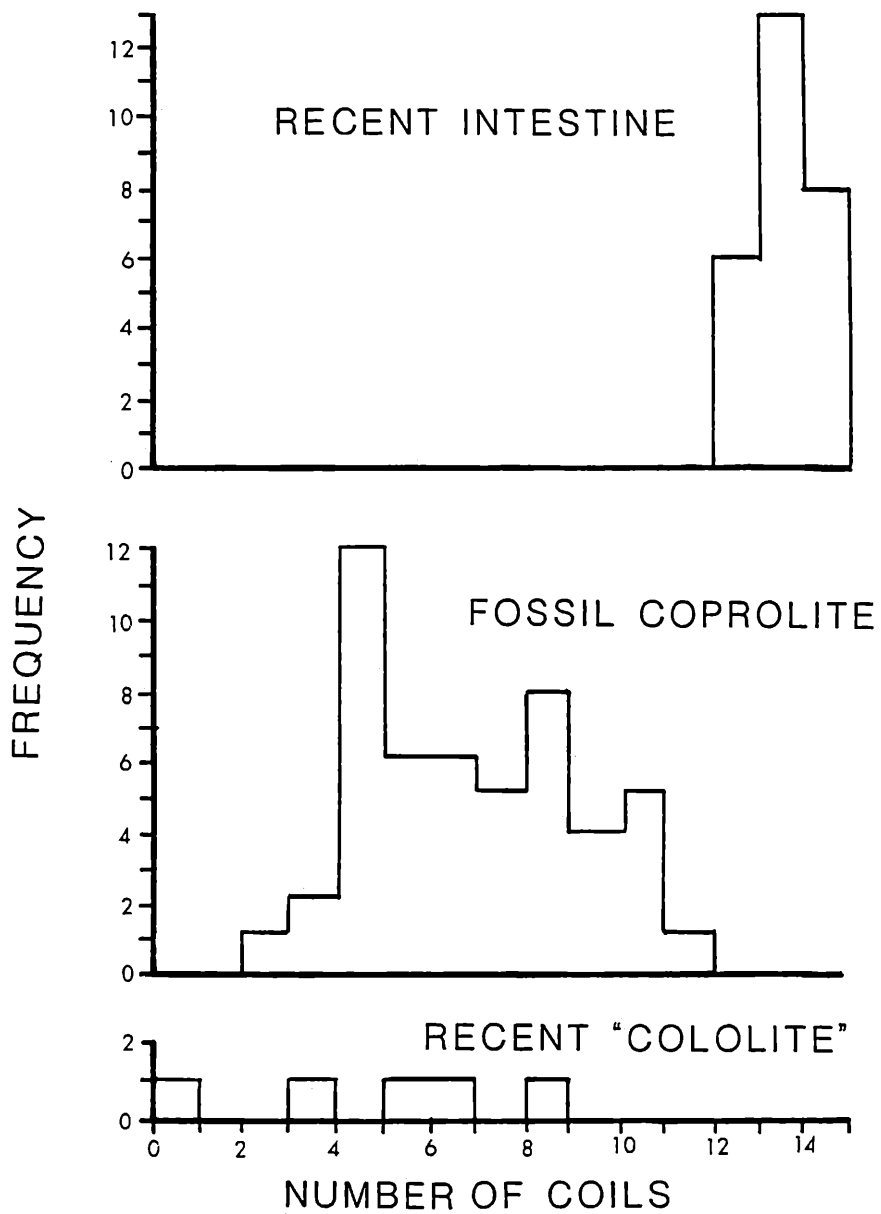


FIG. 18

variation in the fossil coprolites (61%). With the small sample size of the recent fecal masses taken into consideration, it is my opinion that the variation present in the Wymore Shale coprolites is more reasonable if interpreted as fossil fecal masses rather than enterospirae. Interestingly, considered as coprolites, the ratio values (.79 to .18) would indicate a gradation from extreme heteropolar to amphipolar type by the earlier definition.

Summary

A modern analog (Scyliorhinus canicula) is used to explain the origin of the Wymore Shale spiral coprolites. It is demonstrated that a fecal ribbon spirals through a Type D valvular intestine and spirally coils in the colon. The spiral fecal mass hardens and is expelled in this condition from the body. The gross morphology and the internal structures of the modern fecal masses are very similar to the fossil coprolites. The six major lines of evidence (basically similarities of spiral valves and the "enterospirae" in gross morphology and "histology") Williams (1972) uses to advocate the enterospiric origin of the fossils does not eliminate a cololite-coprolitic origin and in some instances would be better explained by a cololite-coprolitic origin.

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