

COPROLITES: A BRIEF REVIEW WITH REFERENCE TO SPECIMENS FROM THE
RHAETIC BONE-BEDS OF ENGLAND AND SOUTH WALES.

by

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Summary

The morphological nature and the various interpretations of the provenances of spiral coprolites are reviewed. The suite of faecal structures found within the Rhaetic bone-beds is described, and four morphological coprolitic types recognized. These four types are assigned to selachian + palaeoniscid chondrosteian, dipnoan, and indeterminate producers. Ichthyosaur coprolites remain to be identified from the ichnofauna. The problem of distinguishing between faecal structures and phosphatic nodules is briefly discussed. It is concluded that the spiral coprolites from the British Rhaetic are true enterospirae (fossilised small intestines).

Introduction

'Coprolite' is a term proposed by Buckland (1829) for structures interpreted as fossil faeces. The first description of coprolites appears to be that of Lister in 1678 (Hantzchel, *et al.*, 1968; Williams 1972), but Mantell (1822) was the first to suggest their animal origin. The problem of spirally coiled coprolites has been a topic of active discussion in recent years. This subject is briefly reviewed here, with particular consideration of the groups of fossil vertebrates to which spiral coprolites have been assigned as a result either of association or articulation. The more unlikely explanations of the provenance of these enigmatic fossils are considered, followed by a review of the evidence in support of the idea that spiral coprolites represent fossilised intestines. The coprolites of the British Rhaetic bone-beds are then described and discussed in relation to previous theories of coprolite origins.

Spiral coprolites - history of research

The morphology of spiral coprolites was the particular study of Neumayer (1904) who worked on a suite of specimens from the Permian of west Texas. Neumayer recognised two types, and introduced some descriptive terms which remain in current use in the literature. 'Heteropolar' designates spindle-like forms with relatively closely spaced turns concentrated toward the least pointed end of the specimen, which Neumayer called anterior. 'Amphipolar' forms possess relatively blunt ends, and the more widely spaced spiral turns are more regularly spaced along the entire or greater part of the length of the specimens.

Spiral coprolites have been assigned to a number of vertebrate groups.

1. Selachians

In an early account, Buckland (1829) assigned coprolites found in the Liassic strata of the Lyme Regis succession to the large marine ichthyosaurs on the premise that remains of this reptile and the examined coprolites are most common at coincident stratigraphical horizons. Buckland (1841) later noted the occurrence of a spirally coiled coprolite within the body cavity of an ichthyosaur from these beds. Woodward (1917) remarked that this coprolite is flattened and not conclusively shown to be present in 'life position'. Woodward also noted that the hybodont sharks *Acrodus* and *Hybodus* are common within this Liassic succession. He considered that sharks were the most likely candidates for the production

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pp.191-204, Plates 21 and 22.

of the spiral coprolites since all extant forms possess a spiral valve in their digestive tract. As further evidence in support of his conclusions, Woodward noted that similar spiral coprolites have been located in the body cavity of the Devonian ctenacanth *Cladoseleache* (cf. also Dean 1893; Claypole & Wright 1893; Fritsch 1895). A similar conclusion was reached by Fraas (1891) who noted that although spiral coprolites are common in the German Muschelkalk and Keuper, ichthyosaurs are rare. Similarly, sites at which ichthyosaurs are common, such as Bad Boll and Holzmaden, yield only rare spiral coprolites.

In a classic work on the palaeoecology of a series of Pennsylvanian shales exposed in Parke County, Indiana, Zangerl & Richardson (1963) describe several types of faecal debris. These occur in association with a vertebrate fauna comprising at least a dozen elasmobranch genera, including *Petrodus* and *Listracanthus*, an acanthodian and several other indeterminate placoderms, and a crossopterygian. In addition to spiral coprolites with few inclusions, these authors also describe irregular, compact faecal structures showing shrinkage and degassing channels (the latter having developed during anaerobic decomposition, cf. also Zangerl 1971, p.1208). The recognition of separate food boli, differing in colour, density and inclusion composition, leads to the conclusion that the mass was located for some time in the gut or rectum of the host, with successive additions to the faecal bulk. Trains or splatters of coprolitic groundmass are also described. All three of the faecal structures mentioned above are assigned to the selachian component of the fauna on the basis of size relationships. Zangerl & Richardson (1963) also recognise oral ejecta (mildly disoriented and disarticulated complete prey specimens strewn with brownish ?coprolitic material) and gastric residues (vertebrate material intermingled with seemingly coprolitic groundmass, preserved as loosely strewn or pelletal masses).

G.R. Case (1967) figures spiral coprolites from the New Jersey Cretaceous, assigning them to the actinopterygians *Amia* or *Enchodus*, while Williams (1972, p.6) considers that the selachian components of the fauna are more likely candidates.

2. Palaeoniscid chondrosteans

Vetter (1881) and Eastman (1914) consider that spiral coprolites may also have been produced by palaeoniscids. As evidence in support of this, they cite the occurrence of a 'coprolite' within the body cavity of *Asthenocormus titanus* from the Bavarian Lithographic Stone. This species is now considered to be a pachycormid holostean (Lehman 1966, p.155), and the spiral structure interpreted as an air bladder.

Johnson (1934) reports spirally coiled coprolites from the upper part of the Weber Formation (Pennsylvanian), as exposed in Park and Chaffee Counties, Colorado. Measuring 0.64 cm to 1.64 cm in length, the coprolites are restricted to the black shales of the succession. The spiral coprolites are flattened, probably due to compaction, and contain scales, teeth, bone and shell fragments enclosed in a fine groundmass. Johnson considers these coprolites to be virtually identical to those ascribed to *Palaeoniscus* by Price (1927).

3. Dipnoans

Matley (1939a) described coprolites first recorded by Oldham (1859) from the Maleri Formation of the Indian Upper Trias. These coprolites vary in length from an average of about 5 cm to a maximum length of 8 cm. They are of broadly oval cross-section and possess a smooth, polished, brown ferruginous coating. The smoothness possibly represents a mucous surface, and the colouration may be due to the nature of the enclosing matrix. The coprolites consist of a thin lamina of mineralised material wrapped spirally around itself in a closed coil of several overlapping turns, tapering toward the terminal end. The lamina varies in thickness from 1 mm to 3 mm. These coprolites lack visible inclusions of vertebrate remains. The groundmass is a 'fine grained paste'. From a chemical analysis of one of the coprolites, Matley concluded that the producers were vegetable or soft invertebrate feeders. The latter suggestion might seem more in accordance with the recorded calcium oxide percentage in these specimens.

Matley (1939b) also described spiral coprolites showing dessication cracks, from the Cretaceous of Pijdura. Since none of the Maleri Formation coprolites exhibit any indication of sub-aerial exposure, Matley considered that the producer was probably aquatic. The vertebrate fauna of beds of the Maleri Formation comprises several species of amphibian and reptile, in addition to the dipnoan *Ceratodus*. Of these forms, only the dipnoan is likely to have possessed a spiral valve in its intestinal tract. Matley concluded that the spiral coprolites of the Maleri Formation are confidently attributable to *Ceratodus*.

E.C. Case (1922 p.84) later assigned spiral coprolites from the Triassic of west Texas to dipnoans. These coprolites are 3.5 cm in length, and belong to the heteropolar type of Neumayer (1904).

Ochev (1974, p.253) described a series of coprolites collected from the basal Upper Triassic rocks on the north eastern shore of Lake Inder (Kazakhstan, U.S.S.R.). The beds also contain labyrinthodont, dicynodont, thecodont and theriodont remains. The coprolites described by Ochev were placed into three morphological groups which correspond almost exactly with the three types categorised from the Texas Trias by Case (1922). The spiral coprolites (heteropolar) forming one of the Russian groups contain inclusions of bone fragments, probably fish, and measure up to 3 cm in length. Ochev notes that dipnoans are found in Russian Platform deposits of similar age and implies that the coprolites which he describes may have been produced by such candidates. Realising that previous authors have considered labyrinthodonts as producers of spiral coprolites, he defers making a firm statement as to the nature of the producer in this instance.

4. Other groups

As mentioned above, certain authors have considered amphibians as likely producers of spiral coprolites. Neumayer (1904) concludes that the coprolites belonging to his larger heteropolar type were produced either by a juvenile *Eryops*, or by a smaller stegocephalian. He concludes that the amphipolar forms were produced by *Diplocaulus*, a nectridean. In reaching these conclusions he followed the lead of Gaudry (1887) and Ammon (1889) who also ascribed spirally coiled coprolites to labyrinthodont sources.

Rusconi (1949) refers certain spiral coprolites from the Middle Triassic deposits of Mendoza, Argentina, to a reptilian source. The coprolites often contain inclusions of ganoid scales, possibly referable to *Pholidophorus dentatus* Rusconi. The scales are often partially destroyed, and display some alignment to the spiral folds. On the basis that dermal scutes, which he ascribes to the large aetosaur *Typhothorax punctatus*, are found in the same deposits, Rusconi concludes that the coprolites must have been produced by this fish eating reptile. From this assumption, he continues his extremely suspect process of logic to conclude that *Typhothorax* was aquatic. In a revision of the aetosaurs of Elgin, N.E. Scotland, Walker (1962, p.194) makes no mention of this Argentinian material, and reaches the conclusion that, as far as the Elgin specimens are concerned, *Typhothorax* was thoroughly terrestrial, possibly adapted for digging. Thus, the Mendoza coprolites are much more likely to have been produced by other, as yet undetermined elements of the vertebrate fauna from these beds.

A certain dichotomy of opinion has arisen concerning the precise relationships of spiral coprolites. Many authors have preferred to interpret them as fully extruded faecal structures, and hence coprolites *sensu stricto*. Others consider that they may represent the intestine, fossilised in its entirety. Williams (1972) reviews this dispute, offering new evidence based on a suite of spiral coprolites from the Lower Permian Wymore Shale, near Manhattan, Kansas. The review given by Williams is supplemented here.

In concluding that the spiral fossils found at Lyme Regis were faecal in origin, Buckland (1829) closely compared their structure with that of modern shark and ray intestinal passages. The spiral valves present in the digestive tracts of modern fish were recognised as belonging to two morphological types by Owen (Parker 1885); the longitudinal valve, comprising a flap of tissue running longitudinally along the intestine in a sinuous line (as, for example, in the Hammerhead shark, certain members of the Carchariidae, and also in *Bothriolepis* - Denison, 1941); the transverse valve, a highly variable feature comprising a screw-like flap of tissue descending the length of the intestinal case (Parker 1885).

Both Matley (1939a) and Price (1927) note that in addition to sharks, the lower actinopterygians and Dipnoi are the only extant groups to exhibit a spiral valve in the intestinal tract. The spiral valve is unknown in modern amphibians and reptiles.

Although Buckland was almost certainly wrong in concluding that spiral coprolites from the Lower Lias were produced by ichthyosaurs, his descriptions of the specimens are meticulous and highly accurate. He chose to attempt some explanation for many features ignored by other and later workers. Buckland states that the mucous membrane to the small intestine of the host transferred "a series of vascular impressions and corrugations" to the surface of the coprolite (Buckland 1829, p.195). He concludes that the faecal material was extruded and fully retained its spiral configuration inherited by passage through the small intestine. This explanation was accepted by Lea (1843) and many subsequent workers.

Dean (1893, p.117) states that the coprolite found within the body cavity of *Cladoselache newberryi* "furnishes a cast of the intestinal wall and gives direct evidence as to the presence of a spiral valve". Fritsch (1895) later interpreted coprolites found in the body cavities of four pleuracanth sharks as fossil small intestines, and extended this conclusion to include isolated bodies of spiral morphology. He later (Fritsch 1907) suggested the term 'enterospirae' for these forms.

At one point in his discussion, Neumayer (1904) compares the heteropolar coprolites to the intestinal structures of *Ceratodus*, suggesting that, since the spiral turns are consistently concentrated toward one end of the structure, they may represent fossilised intestines. He further suggests, though, that the faeces were deposited prior to fossilisation, and that the processes of diagenesis imparted the spiral banding.

Zangerl & Richardson (1963, p.142, and see also Williams 1972, p.4) mention the presence of a spiral coprolite in the pelvic region of a mutilated shark specimen from the Pennsylvanian of Indiana. They continue by considering that the isolated coprolites in the fauna were produced by sharks, on the basis of their size. Zangerl and Richardson conclude that the diversity of ejection types found within the sequence which they studied reflect the diversity of microenvironments to be found in the small intestine. They notice that some of the spiral coprolites from Indiana possess well defined spiral structure (although not perfect), and some demonstrate incomplete spiral structure, while some specimens lack internal spiral structure entirely. They consider that faecal material of considerable plasticity would retain a spiral form when extruded into the rectum. Deviation from the plasticity optimum would result in either imperfect coiling, or total lack of spiral structure.

As mentioned above, many authors have referred to the intestinal tracts of modern fish in considering the origin of spiral coprolites. Buckland (1829) made Roman Cement casts of shark intestines, and Zangerl & Richardson (1963) made rubber casts. Williams (1972, p.9) searched the literature for information on modern shark faecal pellets, but was able to discover only that laboratory sharks eject liquid or loosely viscous faeces. My own enquiries of the London Zoo achieved the same results - shark faeces have never been observed (Vevers, pers. comm.).

Dean (1903) has figured spiral coprolites produced by *Protopterus*, the African lungfish, and Williams (1972, p.9) notes that the long nosed gar (*Lepisosteus osseus*) produces similar faecal pellets. Both of these examples of modern faecal structure belong to the amphipolar type.

Histological evidence

The specimens studied by Williams (1972) from the Permian of Kansas are all heteropolar. The specimens show whorl orientation comparable to that of a spiral valve. Some specimens show collapse structures at the posterior end, with a cavity formed inside the faecal mass itself, a configuration consistent with the morphology of a spiral valve. Williams also recognises mucosal folds on the exterior of the specimens. His most impressive evidence, however, lies in the thin sections which he prepared. Bifurcating mucosal folds arise from whorl interfaces

in remarkable similarity of histological form to that of the spiral valve in recent elasmobranchs. Thus, Williams concludes that heteropolar coprolites are true 'enterospirae', and should be regarded as fossilised spiral valves. He concludes by assigning the specimens which he studied to pleuracanth selachians.

Broughton, Simpson & Whitaker (1977; 1978) describe a series of spirally coiled faecal structures from the Upper Cretaceous Whitemud Formation of Saskatchewan, Canada. Referring to previous work they consider that the perforations on certain of the specimens which they describe represent gas escape phenomena (cf. also Jepsen 1963; Zangerl, Woodland & Richardson 1969). Possible mucosal fold structures are present in certain of the specimens which they describe, in spite of their total replacement by limonite. This evidence favoured interpretation of the faecal structures as fossil intestines. Broughton *et al.* conclude (1978) that certain of the specimens represent fully extruded faecal masses since plant debris adheres to their surface. This suggests their deposition in an aqueous medium. The range of coprolitic form is accounted for by these authors with regard to variation in plasticity of the faecal material involved.

Further evidence in favour of interpretation that at least certain of the faecal structures preserved by the fossil record are fossil intestines is provided by Stewart (1978). He studied heteropolar spiral faecal bodies from the Niobrara Formation (Upper Cretaceous) of west Kansas. The presence of well defined mucosal folds in these specimens led Stewart to conclude that the faecal debris represent true 'enterospirae'. From an analysis of the contemporary fauna, he suggests that they form the record of a previously undetected selachian in the Formation.

Coprolite diversity from single horizons

It is regrettable that the study of spiral coprolites has tended to eclipse the consideration of the range of their diversity in single faunas. This is partly due to the difficulty in distinguishing phosphatic nodules of coprolitic origin from purely diagenetic phosphorites. Most of the better documented coprolite assemblages come from deposits of the lower Mesozoic, particularly the Trias (see Häntzschel *et al.* 1968, and Neumayer 1904, Case 1922, Ochev 1974 considered above). A recent study considering a wide spectrum of faecal remains of Upper Triassic age has recently been published by Ash (1978). These coprolites, obtained from the Ciniza Lake Beds of the Chinle Formation of New Mexico, are divisible into two morphological groups; smooth coprolites, cylindrical to cigar-shaped, with occasional longitudinal and transverse striae, transverse ridges and spiral grooves; rough, flattened coprolites, of round to oval outline. The spiral coprolites appear to be amphipolar for the most part, with occasionally well preserved heteropolar forms. The internal spiral structure is invariably obliterated, although separate food boli are occasionally recognisable. Ash does not consider the problem of coprolitic versus enterospiral origin for the spiral forms, but appears instead to consider them all as fully extruded features. He speculates that the flatter specimens may have been fairly viscous and deposited from some height in the water column, while the more regular forms could have been defaecated closer to the sediment surface, in accordance with the previous suggestions of Waldman and Hopkins (1970). An interesting feature of the coprolites forming this association is the wealth of inclusions which they hold. These vary from bone and wood fragments, through spores to conchostracans (branchiopod Crustacea). In studying the lipid components of the coprolites, Weber and Lawler (1978) conclude that the specimens represent a digested concentrate of organic hydrocarbons, supporting the view that these specimens are faecal structures rather than being of inorganic origin.

Vertebrate remains found in association with the coprolites are rare in the Ciniza Lake Beds, but comprise amphibian and fish remains. It is likely that the spiral coprolites were produced by an as yet undetermined member of the fauna (Ash 1978, p.70). Considering the environment of deposition and the nature of many of the coprolitic inclusions, it may well transpire that the producer of the spiral faecal bodies was a dipnoan.

Faecal structures from the British Rhaetic

'Coprolites' are very common within the various bone-bed lithologies of the British Rhaetic. As a direct result of the sorting influence of the prevailing currents, a reduced ratio of 'coprolites' to other vertebrate remains is often present in well sorted, sandy bone-beds of Barnstone (Nottinghamshire) and Chilcompton (Somerset). The faecal structures of the various bone-beds of Rhaetic age often show a concentric structure and are divisible into four broad morphological types:

Type 1:

This group comprises large, brown, often tapered, ?amphipolar coprolites measuring up to 80 mm in length. Undigested fish remains are visible in the coprolitic ground mass, and are arranged concentrically in cross section. Coprolites in this group possess well defined spiral structure (plate 21, figs.1-5; plate 22, figs.8-9). The material examined includes material presently held in the National Museum of Wales (specimens G 2066 to G 2068 inclusive and Jackson Collection 22. 345.G1 - all specimens are from Lavernock Point) and the Bristol City Museum (cb. 4891, cb. 3916).

In thin section (plate 22, figs.8,9), the spiral structure remains obvious. The included vertebrate remains are often arranged either tangential or radial to the spiral coils, and may show some imbrication. Distinct food boli are discernible (plate 22, fig.9) as areas of differing colour and density in the section. The spiral structure is not perfect; the spiral turns are complete, but not perfectly concentric. This may be due to collapse of the structure during diagenesis, although it should be noted that no degassing channels are obvious in the thin sections taken. The collapse may well have been accentuated in its effects by compaction pressures from overlying sediments. There is no evidence for the presence of mucosal structures in the thin sections examined.

Type 2:

This group comprises light brown to black, elongate faecal structures with well defined spiral structure. The spiral coiling is amphipolar in most cases, but appears to be heteropolar in a few specimens (Bristol City Museum specimen cb. 4898). In these latter forms, the specimen is often incomplete, making their spiral configuration difficult to determine accurately. Faecal structures belonging to this group lack included vertebrate remains, and measure up to 3 cm in length (plate 21, figs.6-11). Examples of this coprolitic type include Bristol City Museum (henceforward abbreviated as BCM) specimens cb. 4898 and 4900. Type 2 coprolites tend to fracture easily, so hindering the cutting of thin sections.

Type 3:

Coprolites of type 3 are capsule shaped, lacking undigested vertebrate remains, and measuring up to 3 cm in length. The coprolites of this group do not show spiral coiling. Material includes BCM cb. 4897 (cf. also plate 22, fig.2,7). In thin section (plate 22, fig.7) the coprolites are seemingly structureless. The ground mass is fine-grained and there is some disseminated pyrite present. In the case of the specimen sectioned, a phosphatised skin is present around the whole specimen. This phosphatic coat is 0.5 mm thick, and is a product of diagenesis.

Type 4:

Flattened, shiny black coprolites measuring up to 3 cm across, often with included scales and teeth breaking the surface are allocated to type 4. The shiny black appearance of the specimens is due to phosphatisation (plate 22, fig.6). Material includes that figured in plate 21, fig.12; plate 22, figs.1,3 and 6, and also BCM cb. 4896 and P.23353 in the British Museum (Natural History). There is no trace of spiral structure in the coprolites of this group.

As yet, it is impossible to assess the relative abundances of these coprolite groups. Such a project would require the development of a vast amount of bone-bed material. It is noticeable, however, that the coprolites of groups (3) and (4) are by far the most common.

Discussion

Affinities of the Rhaetic coprolites

With reference to the literature survey above, and the anatomy of extant forms, it is likely that the hybodont and euselachiform sharks, the palaeoniscids, and the dipnoan represented in the Rhaetic bone-beds all possessed a spiral valve in their intestinal tracts. The spiral coprolites comprising types 1 and 2 are thus attributable to certain of these forms.

The sharks and palaeoniscids were well-suited to a predatory mode of life, and as such, probably gave rise to the coprolite of type 1. These coprolites contain undigested fish remains. In addition, coprolites possibly referable to this group may contain crustacean remains (Duffin, 1978).

The coprolites of type 2 lack undigested fish remains. *Ceratodus*, the dipnoan, with its crushing tooth plates, would appear to be the most suitable candidate to have produced coprolites in this group.

Ichthyosaur coprolites

Coprolites have been assigned to ichthyosaurs by Buckland, 1829; Prout, 1829; and Firtion 1938. Pollard (1968) studied the gastric contents of ichthyosaurs, and concluded that a diversification of feeding habits may have been present in Lower Jurassic ichthyosaurs. The coprolites described by Buckland (1829) would have been produced by fish eaters, whilst those ichthyosaur skeletons preserving a gastric mass packed with dibranchiate cephalopod hooklets, were invertebrate feeders. In a more thorough study of ichthyosaur stomach contents, Keller (1976) finds little evidence in favour of a fish diet for Lower Jurassic specimens from Germany. The possibility remains that these ichthyosaurs ate both fish and cephalopods, the cephalopod hooklets being retained in the stomach, instead of being defaecated with undigested fish remains. In either case, the prey is nektonic and the ichthyosaur an active predator.

Rhaetic ichthyosaurs were presumably also of nektonic feeding habits. Belemnites are not represented in the British Rhaetic, having their first appearance in the basal Jurassic beds, (Roger 1952, p.708). The invertebrate remains of the British Rhaetic, with the exception of ostracods, are all benthonic. It is unlikely that an ichthyosaur would prey on benthos. More feasible is that the Rhaetic ichthyosaurs were fish eaters.

It remains for ichthyosaur coprolites to be identified from the Rhaetic trace fossil assemblages, if present at all.

The problem of phosphatic nodules

The separation of coprolites from phosphatic nodules is exceedingly difficult. Little is known about the geology of these nodules, although the nature of phosphorites has begun to come under scrutiny in recent years (Antia 1979). Phosphatic nodules are suggested as being common in association with diastems, glauconite, areas of non-deposition of terrigenous material, and vertebrates, especially coprolites (Pettijohn, 1957). All of these conditions are present, or have been suggested as being present, in the Rhaetic bone-beds, so that it is quite probable that phosphatic nodules occur within it. Phosphatic nodules are reported to contain various organic remains, both vertebrate and invertebrate.

The coprolite types 3 and 4 are the most likely to be confused with, to include, or to comprise phosphatic nodules, since they lack a well defined spiral or other such characteristic internal organisation. The coprolites of type 4 are common and consistent in their structure, with inclusions of vertebrate remains breaking the surface. Certain other small, black, polished forms, apparently lacking significant amounts of inclusions of vertebrate material, probably represent phosphatic nodules. These forms are easily confused with the coprolites of types 3 and 4.

Specimen H38, in the Buckland Collection of Oxford University Museum, greatly resembles the coprolites of type 4. This specimen, from the bone-bed at the base of the Rhaetic succession of Aust Cliff, has its smooth surface broken by the presence of small lumps. A broken surface shows the inclusion of many structures not present in the coprolites of type 4. These structures include almost complete valves of bivalve molluscs, and small pieces of glauconite. Glauconite grains would not be expected in a coprolite, and the bivalves would be considerably triturated, if present at all. It is concluded that this specimen is indicative of one type of structure displayed by phosphatic nodules in the Rhaetic bone-beds, although it is not necessarily typical.

It is also interesting to note here that certain coprolites belonging to type 4 show unusual projections from the main body of the specimen. These projections are usually of flat aspect, although a few specimens do show thinner developments (plate 21, fig.12). The flattened projections on certain specimens often are present along the greater length of the structures, and may on occasion completely circle the specimen. Specimens of this nature may represent phosphate precipitation around a suitable nucleus, with preferential lateral growth along the sediment/water interface, or along bedding laminations.

Gindy (1978) made a recent study of the alpha radioactivity of constituent phosphate particles in Maestrichtian pelletal phosphorites from Egypt. He found considerable range of values of alpha radioactivity; the constituent particles in order of increasing radioactivity are 1, chert and quartz lithoclasts and cements; 2, vertebrate fragments; 3, colourless and clear colophonite pellets; and 4, pellets of assumed faecal origin. Both carbonaceous matter and calcium phosphate are concentrate collectors of uranium from solution. Gindy further notes that certain of the vertebrate fragments and possible faecal pellets showed the development of superficial films of increased radioactivity. He states that the following is a likely explanation of these results (Gindy 1978, p.544); "A film of mucilaginous cement deposited on the outer surface of some particles, a common feature of faecal matter, could have avidly collected any available uranium from sea water as well as from later intergranular solutions. This could have started during the early diagenesis of the pelletal phosphate and continued epigenetically for a long time afterwards."

It has so far not been possible to examine phosphate particles from the Rhaetic bone-beds for alpha radioactivity, so the distinction between phosphatic remains of faecal and inorganic origin remains obscure at the present time.

The problem of the origin of coprolites

The histological evidence offered by Williams (1972) and Stewart (1978) is overwhelming proof that at least some 'coprolites' are fossilised intestines. This histological evidence is so far true only for heteropolar forms. Spiral coprolites from the Rhaetic bone-beds are all amphipolar, and none shows evidence of the preservation of mucosal folds on the whorl interfaces in thin section.

The small intestine, when filled with food material, is the soft organ of the body most likely to be preserved in the fossil record. It is protected from external destructive processes for some time, depending upon the precise mode and site of death, while the processes of carcass decay are going on. The Kansas 'enterospirae' show consistent preservation of spiral valve histology. If the Rhaetic coprolites described above are indeed fossil spiral valve contents, then the lack of preserved mucosal remains must be due to the microenvironment in the centre of the coprolite at the time of burial, and during diagenesis. It may be that the spiral valves in the Kansas deposits were rapidly enclosed by sediment. Further decay of the walls of the spiral valves in the Rhaetic specimens may have been a feature of long exposure on the sea bed in reducing conditions.

The whorl orientation and surface features are certainly more explicable if the Rhaetic coprolites are spiral valve contents. It is unlikely that spiral structure would be retained by the contents of the intestines after squeezing through the sphincter at the base of the small intestine, and extrusion into the rectum. This is well illustrated by the rarity of spiral faecal bodies recorded from extant organisms which are known to possess a spiral valve in their digestive tract, and the difficulty faced in trying to produce fully extruded spiral faecal structures experimentally.

Thus, it is concluded here that the most likely explanation for the origin of the Rhaetic spiral coprolites described above, is that they are spiral valve contents, and should be regarded as true 'enterospirae'. It remains possible that certain specimens showing spiral configuration may represent fully extruded faecal material of optimum plasticity for subsequent shape retention.

The question remains as to whether these conclusions can be extended to include all coprolites as enterospirae. It is possible that all of the coprolites from the Rhaetic bone-beds are small intestine contents. Many specimens, especially certain of those belonging to type 3, are probably not, since they show evidence of total extrusion, such as a small twist at the posterior end, and occasional impact features. Thus, the remainder of the coprolites from the Rhaetic bone-beds quite probably includes coprolites *sensu stricto*, and small intestines. The lack of definitive structure in these forms obscures their precise origins.

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Explanation for Plate 21

Coprolite types 1, 2, 4

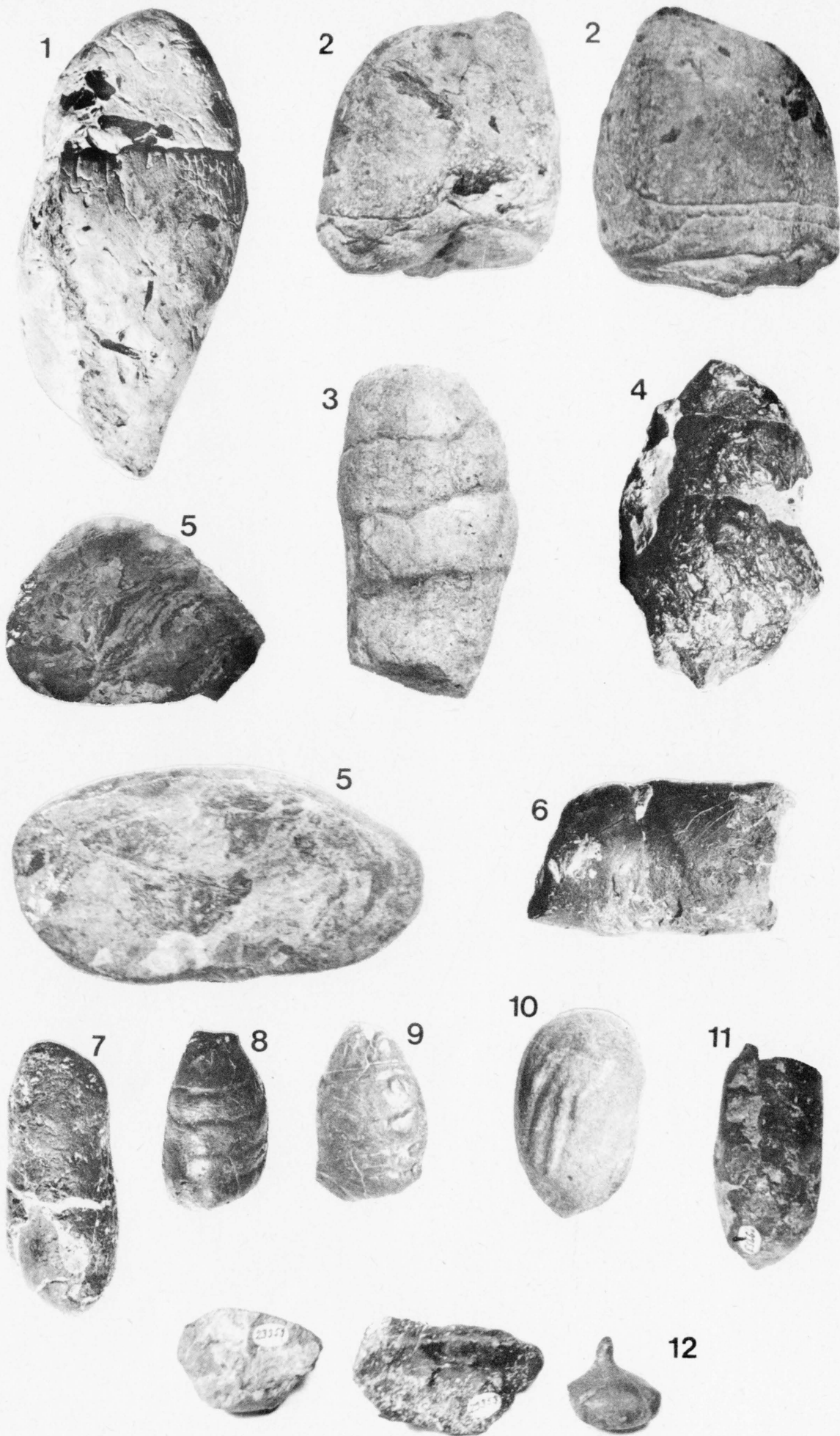
- Fig. 1 Type 1 spiral coprolite, x 1. BCM 4891. Aust. Cliff, Avon.
- Fig. 2 (a & b) Type 1 spiral coprolite, x 1. G2066 Nat. Mus. Wales,
Lavernock Point.
- Fig. 3 Type 1 spiral coprolite, x 1. G2067 Nat. Mus. Wales,
Lavernock.
- Fig. 4 Type 1 spiral coprolite, x 1. BCM Cb.4893. Aust.
- Fig. 5 (a & b) Type 1 spiral coprolite, sliced, x 1. G2068 Nat. Mus.
Wales, Lavernock.
- Fig. 6 Type 2 spiral coprolite, x 1. BCM Cb.4892. Aust.
- Fig. 7 Type 2 spiral coprolite, x 1. BCM Cb.4900. Aust.
- Fig. 8 Type 2 spiral coprolite, x 1. BCM Cb.4898. Aust.
- Fig. 9 Type 2 spiral coprolite, x 1. BCM Aust.
- Fig. 10 Type 2 spiral coprolite, x 1. BCM Cb.4900. Aust.
- Fig. 11 Type 2 spiral coprolite, x 1. BMNH P.23353. Aust.
- Fig. 12 Type 4 coprolites, x 1. BMNH P.23353. Aust.

(BCM = Bristol City Museum, BMNH = British Museum (Natural History),
Nat. Mus. Wales = National Museum of Wales, Cardiff).

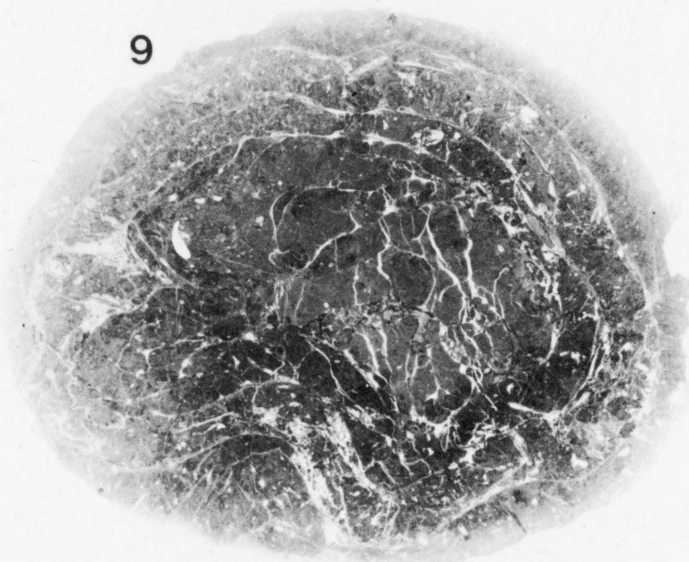
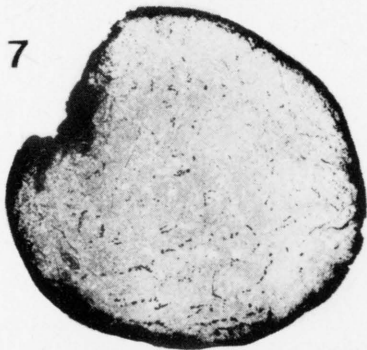
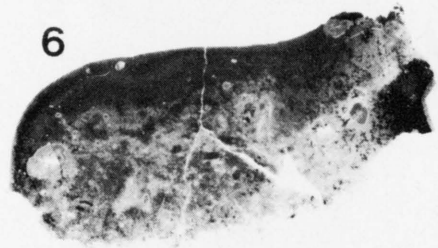
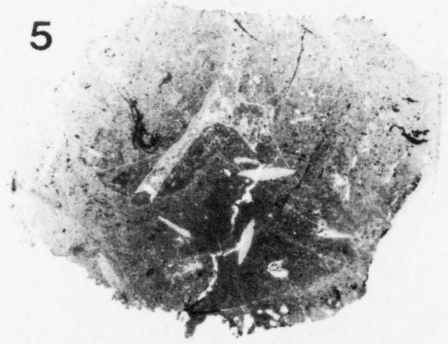
Explanation for Plate 22

Coprolite types 1, 2, 3 and 4

- Fig. 1 Type 4 coprolites, x 1. BMNH P.23353. Aust.
- Fig. 2 Type 3 coprolites, x 1. BMNH P.23353. Aust.
- Fig. 3 Type 4 coprolites, x 1. BCM Cb.4899. Aust.
- Fig. 4 Assorted coprolites from Holwell fissure, Moore Collection,
Bath Museum, x 1.
- Fig. 5 Type 2 spiral coprolite in thin section (x 4). BCM Cb.4895. Aust.
- Fig. 6 Type 4 coprolite in thin section (x 4). BCM Cb.4891. Aust.
- Fig. 7 Type 3 coprolite in thin section (x 4). BCM Cb.4894. Aust.
- Fig. 8 Type 1 spiral coprolite in thin section (x 2½). Nat. Mus.
Wales, Lavernock. Longitudinal section.
- Fig. 9 Type 1 spiral coprolite in thin section (x 2). Nat. Mus.
Wales, Lavernock. Transverse section.



Duffin-Coprolites



Duffin-Coprolites