

# SPIRALLY COILED 'COPROLITES' FROM THE UPPER TRIASSIC MALERI FORMATION, INDIA

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**ABSTRACT.** A new collection of coprolites exhibiting spiral markings from the upper Triassic Maleri Formation in the Pranhita-Godavari valley of southern India is critically examined. An attempt is made to relate their internal structure to the Maleri faunal elements. *Ceratodus* is a conspicuous member of the Maleri fauna. Some anatomical features such as the morphology of the spiral valve and faeces and the relationship between dental plates and body size in living *Neoceratodus forsteri* have been examined. The internal structure of the coprolites reveals the presence of a scroll valve which is quite dissimilar to the spiral valve of *Neoceratodus*. Critical assessment of the coprolites, based on external morphology and thin sections, does not support their determination as 'fossilized excrement', 'fossilized intestinal contents', or 'enterospirae' of *Ceratodus*. The evidence to relate the coprolites to other faunal members is equivocal. It is suggested that the 'coprolites' may belong to an as yet undetermined member of Maleri fauna.

THE study of coprolites has provided valuable information about certain aspects of the biology of the animals which have been associated with them (e.g. Zangerl and Richardson 1963; Williams 1972; Stewart 1978; Broughton *et al.* 1978; Sohn and Chatterjee 1979; Zidek 1980). The coprolites may indicate the nature of the large intestine, the food habits of the animal, and, indirectly, the environment in which it lived. There have been a number of interpretations of the precise nature of coprolites. They have been interpreted as 'fossilized vertebrate excrements', 'fossilized intestinal contents', or 'fossilized intestine or enterospirae' (see Williams 1972, for full references), produced, for example, by larger fishes preying upon smaller individuals of their own species (Zidak 1980) or by an otherwise unknown member of a fauna (Ash 1978). Some coprolites have also been identified as egg cases of elasmobranch fishes (Crookall 1930), land snails (Fritsch 1907), or even insect larvae (Langford 1963).

Coprolites from the upper Triassic Maleri Formation have been known since the nineteenth century (Oldham 1859) and a preliminary description was published eighty years later (Matley 1939a). A collection of 'rounded, oval or ellipsoidal' coprolites from the Maleri Formation has recently been examined by Sohn and Chatterjee (1979). They reached conclusions about the palaeoposition of India mainly on the basis of contained diagnostic freshwater ostracods. The present study is restricted to the cylindrical and spirally coiled coprolites and concerned largely with their biological nature; as such it may be regarded as complementary to that of Sohn and Chatterjee.

Three main aspects relating to the coprolites are considered: (1) their precise morphology, including that revealed in thin section; (2) the biological characteristics of the Maleri fauna, especially in relation to mode of life, food habits, and structural peculiarities of feeding and digestive apparatuses; and (3) the structure of the intestine (including spiral valve), faeces, and the ratio of dental plates to body size in *N. forsteri*, the extant Australian lungfish (chosen for comparison because *Ceratodus* is a conspicuous member of the Maleri fauna). Information on coprolites and associated faunas elsewhere was also considered. There is equivocal evidence to associate the coprolites with members of the Maleri fauna but they may not be their preserved faeces, gut contents, or enterospirae (see Zangerl and Richardson 1963).

## MESOZOIC COPROLITE OCCURRENCES IN INDIA

Although coprolite occurrences have been sporadically mentioned along with fossil remains from various parts of the Indian peninsula, most are known from the Wardha and Pranhita-Godavari valleys. The following summary (and text-fig. 1) indicates the nature and occurrence of the material:

*Wardha valley.* Upper Cretaceous sediments near Pisdura; 600 specimens collected from which 350 were examined (Matley 1939*b*); ovoid, ribbed and subcylindrical in shape; associated with sauropod dinosaurs (titanosaurs) and chelonians.

*Pranhita-Godavari valley.* 1. Lower Jurassic Kota Formation near Pochampalli (Jain *et al.* 1975); numerous specimens (not yet described); rounded, oval, or ellipsoidal with desiccation marks; associated with sauropod dinosaurs.

2. Upper Triassic Maleri Formation near Maleri; numerous specimens; spheroid, ovoid, ellipsoidal (with desiccation marks), and spirally coiled; associated with fish, amphibian, and reptile remains (Oldham 1859; King 1881; Matley 1939*a*; Sohn and Chatterjee 1979).

3. Late lower or early middle Triassic Yerrapalli Formation, near Yerrapalli; few specimens; spheroid or ovoid, with desiccation marks; different in shape and size from Maleri coprolites (Chatterjee 1967); associated with labyrinthodont (capitosaur), dicynodonts, erythrosuchid, and therapsids (Jain *et al.* 1964).

### Terminology

The coprolites at Maleri vary in shape and size. They can be grouped broadly as non-spiral and spiral. The non-spiral coprolites may be rounded, ovoid, or ellipsoidal and are comparable to coprolites from other localities in India. The spirally coiled coprolites are, however, restricted in their distribution. Two types of spiral coprolites were recognized by Neumayer (1904) in the Permian of Texas. These categories were adopted by Williams (1972) in an exhaustive work on the origin of spiral coprolites. Spiral coprolites may be *heteropolar* (type A) 'characterised by a relatively large but variable number of closely spaced spiral turns concentrated on one end of the coprolite', or *amphipolar* (type B) 'characterised by a relatively small number of widely spaced spiral turns extending the length of specimen'. This terminology is adopted here since most of the coprolites under study fit the above definitions. However, a few coprolites which do not show clear spiral markings have been included because spiral features are seen in damaged portions of them. It is likely that coprolites with a flattened cylindrical shape are related in some manner to either type A or B. This third category termed here as *cylindrical* includes oblong-cylindrical, flattened cylindrical, and spindle-shaped coprolites.



TEXT-FIG. 1. Main localities and gross morphological features of Mesozoic coprolites in central India.

*Material*

All coprolite specimens used in the present study have been obtained from a locality close to Maleri (see Roychowdhury 1965, for locality map). A few poorly preserved specimens were also collected from a site near Angrezpalli, close to Maleri. *Ceratodus* teeth are common in both localities.

The nature of the occurrence of coprolites in the Maleri was noted by King (1881, pp. 121-122): 'The commonest remains are coprolites which lie about the field in large numbers, of all sizes and shapes, from the short cylindrical form with tapering ends and spiral foldings up to large flat rudely discoidal coils.' Subsequently, Aiyengar (1937, p. 104) remarked that 'Coprolites are abundant about a mile W.S.W. of Maleri. They are generally greenish yellow in colour varying in size from that of a walnut to a coconut. In shape some are flat and cake like, some cylindrical, spiral, reniform or botryoidal. In cross-section they present a central core surrounded by layers of iron-impregnated material.' Matley (1939a) made a detailed study of sixteen specimens collected by Hughes in 1876, plus one added at a later date.

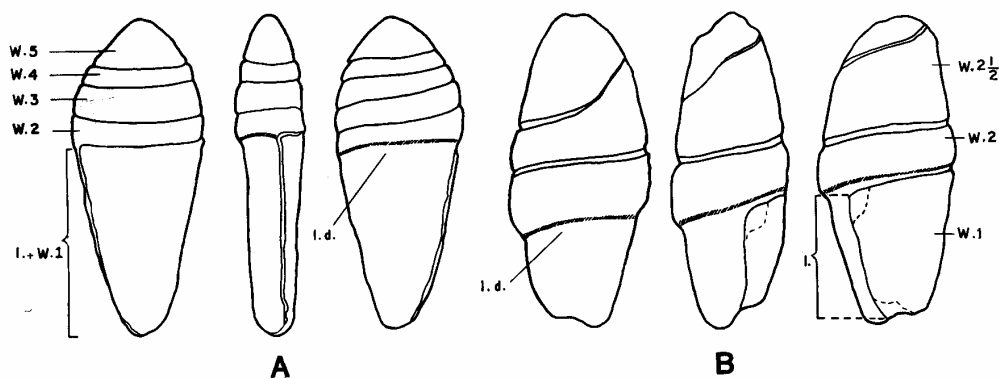
Sohn and Chatterjee (1979) have recently studied a collection of twelve coprolites from a site near Achalapur (within the Maleri Formation), a few kilometres from Maleri. The coprolites are fairly large, heavy, rounded, oval, or ellipsoidal, averaging  $70 \times 50$  to  $100 \times 80$  mm. This site has not yet yielded spirally coiled coprolites but is otherwise well known for Maleri vertebrates. All the specimens of the labyrinthodont amphibian *Metoposaurus maleriensis* described by Roychowdhury (1965, p. 12), were obtained from a locality north-west of Achalapur. Subholostean fish were also found near Achalapur in 1958 (Jain *et al.* 1964; Jain 1980).

The registration number of all specimens mentioned in the text, including thin sections, refer to the Palaeontological Collections, Indian Statistical Institute (I.S.I.), Calcutta.

## DESCRIPTION OF THE COPROLITES

*Gross morphology.* The collection includes forty-three specimens; twenty-five collected prior to 1978 and the remaining eighteen during the 1979-80 field season. Of these twenty-one are amphipolar, nine heteropolar, and the remaining oblong-cylindrical, flattened-cylindrical, or spindle shaped. A number of specimens of cylindrical coprolites are illustrated in Pl. 81, figs. 1-7, 10. Some are cylindrical with rounded ends (Pl. 81, figs. 2, 3), one resembles a flattened pebble (Pl. 81, fig. 10), and some show faint spiral markings (Pl. 81, figs. 4-7). Embedded ganoid fish scales have been observed in some coprolites (Pl. 81, fig. 3). The length of these coprolites varies between 27 and 40 mm with a maximum diameter of 10 to 32 mm, and minimum diameter 0.9 to 27 mm.

The *amphipolar* type of coprolite (text-fig. 2B) is robust in appearance and oval to circular in cross-section. The lip extends to less than half the length. The number of complete coils in the whorl varies between two and four and a half and a distinct lip depression (l.d.) is present. In P. 56 (Pl. 81, figs. 8-9) the whorl is displaced in the middle. The coil has a thickness of 32 mm. P. 78 is the largest coprolite in the collection measuring  $79 \times 30 \times 27$  mm. It exhibits the usual features of such coprolites, except displacement of the lip. Two other



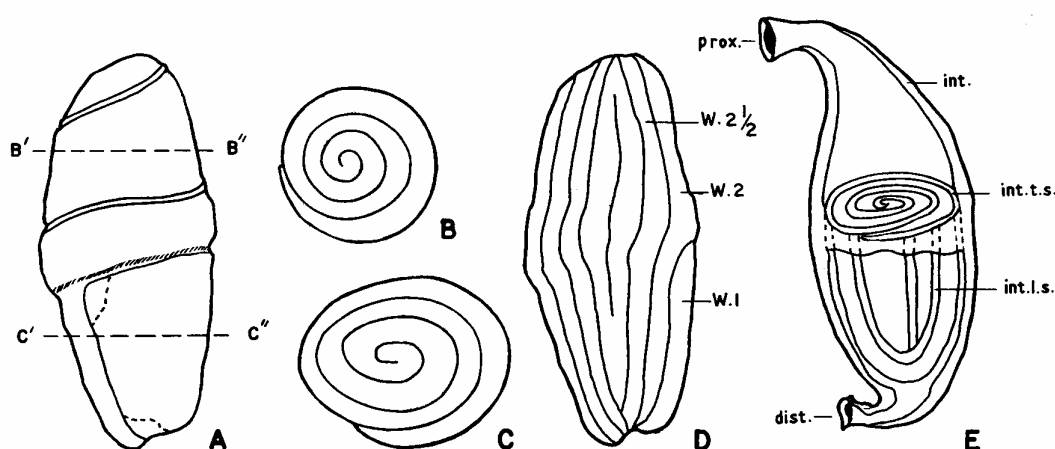
TEXT-FIG. 2. Gross morphology of spiral coprolites from the Maleri Formation, India. A, heteropolar coprolite (based on ISI P. 49), and B, amphipolar coprolite (based on ISI P. 51) in obverse, lateral, and reverse views. l., lip of the whorl; l.d., lip depression; w. 1-w. 5, whorls, 1-5 of the coil.

coprolites, P. 82 and P. 90, are embedded in oval sheaths (cf. Matley 1939*a*, fig. 7) but are partly exposed to exhibit amphipolar features. The dimensions of these coprolites range as follows: total length 34–79 mm, maximum diameter 18–40 mm, minimum diameter 13–30 mm, and maximum width of the lip 20–23 mm.

The *heteropolar* type of coprolite (text-fig. 2A) is shaped like a snail shell. The whorl starts with a wide 'lip' extending to more than half of the total length of the specimen and is then thrown into several narrow coils ending in a smooth conical termination. Most specimens exhibit lateral compaction. P. 80 is the smallest heteropolar coprolite (45 × 17 × 14 mm) and P. 91 the largest (66 × 28 × 22 mm) but it is highly encrusted, which obviously exaggerates the dimensions. The heteropolar coprolites exhibit two and a half to five complete whorls which are sometimes obscured by abrasion. There is a distinct lip depression (l.d.) which is evident on the surface opposite to the lip area. The dimensions of these coprolites range as follows: total length 45–66 mm, maximum diameter 17–28 mm, minimum diameter 14–26 mm, and maximum width of the lip 26–42 mm. The thickness of the lip varies from 2.5 to 3.5 mm at the lip region.

*Thin section studies.* A cylindrical coprolite (P. 57) abraded and damaged at one end, was polished and found to have three whorls in cross-section, each approximately 1.7 mm thick.

One amphipolar coprolite (P. 75) was prepared as a polished transverse section. This revealed three complete and close-set whorls varying from 1.4 to 1.6 mm in thickness. A series of longitudinal sections of another



TEXT-FIG. 3. The anatomical interpretation of an amphipolar coprolite from the Maleri Formation, India. A, gross morphology. B and C, transverse sections (semi-diagrammatic, based on present studies and Matley 1939*a*) in the region B'-B'' and C'-C'' of A. D, longitudinal section (simplified from Matley 1939*a*). E, reconstruction of intestine with scroll valve in transverse and longitudinal section. int., intestine; int. t.s., intestine in transverse section; int. l.s., intestine in longitudinal section; prox., proximal end; dist., distal end; w. 1-w. 2½, whorls of the coil.

#### EXPLANATION OF PLATE 81

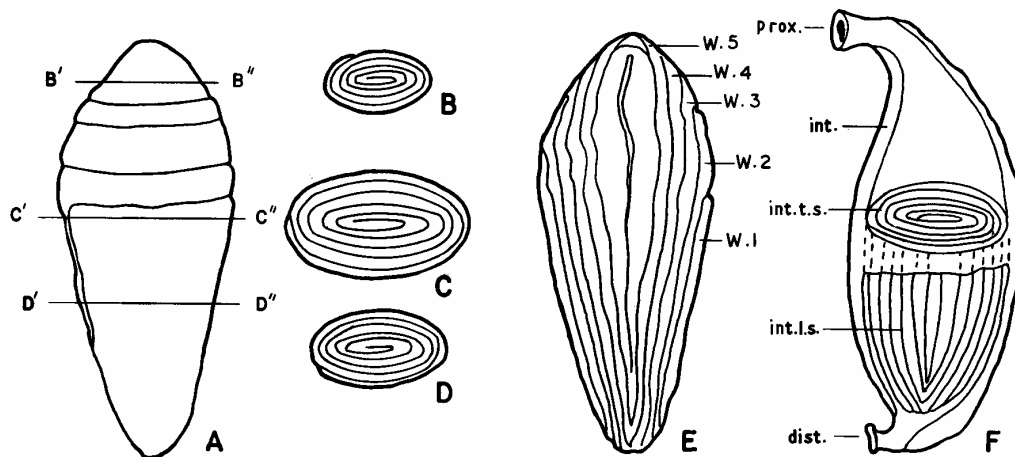
Figs. 1-18. Cylindrical and amphipolar coprolites from Maleri Formation, India. 1-3, cylindrical coprolites: 1, ISI P. 52, × 1.2; 2, ISI P. 53, × 1.5; 3, ISI P. 54, ganoid scales indicated by arrow, × 1.1. 4, 5, oblong coprolite with spiral markings: 4, obverse; 5, reverse, ISI P. 50, × 0.9. 6, 7, oval-elongated coprolite with spiral marking: 6, obverse; 7, reverse, ISI P. 61, × 1.1. 8, 9, amphipolar coprolite with displaced coil in the middle: 8, obverse; 9, reverse, ISI P. 56, × 0.8. 10, cylindrical-flattened coprolite with faint spiral markings, ISI P. 71, × 1. 11, 12, amphipolar coprolite (also shown in text-fig. 2A and 3A) with well-marked coils and lip: 11, obverse; 12, reverse, ISI P. 49, × 0.9. 13, 14, amphipolar coprolite, damaged at both ends: 13, obverse; 14, reverse ISI P. 68, × 0.64. 15, 16, amphipolar coprolite, somewhat damaged: 15, obverse; 16, reverse, ISI P. 69, × 0.9. 17, 18, amphipolar coprolite from Matley (1939), GSI collection: 17, longitudinal section, × 2; 18, transverse section, × 1.



JAIN, Triassic 'coprolites'

amphipolar coprolite (P. 77) revealed the presence of calcium phosphate granules and fish scales in between parallel folds. Longitudinal and transverse sections of amphipolar coprolites, reproduced here (Pl. 81, figs. 17-18) from Matley (1939*a*), bear a close resemblance to the specimens studied here. These reveal the presence of two and a half to three whorls of scroll and show that the faecal mater was compacted. The scroll valve in the intestine as evidenced by amphipolar coprolites from Maleri is reconstructed in text-fig. 3.

One heteropolar coprolite (P. 70) was sectioned longitudinally (Pl. 82, figs. 7, 8). The whorls run along the whole length of the coprolite and do not exhibit any valves or spirals in between. The specimen is seen to have a coil of five whorls before sectioning (Pl. 82, figs. 3 and 4). The outer two have been peeled off and the remaining three are visible in the section. The thickness of the whorls varies from the outer which are approximately 2 mm to the inner which are 1.0 to 1.5 mm thick. Another heteropolar coprolite (P. 76) was cut into a series of eight transverse sections. These have revealed the presence of a single coil in the intestine thrown into five whorls. The whorls are compact and close set and are filled with mineral, mostly calcium phosphate. The scroll valve as evidenced by heteropolar coprolites is reconstructed in text-fig. 4.



TEXT-FIG. 4. The anatomical interpretation of a heteropolar coprolite from the Maleri Formation, India. A, gross morphology. B, C, and D, transverse sections (semi-diagrammatic, based on thin section studies) in the region B'-B'', C'-C'', and D'-D'' of A. E, longitudinal section (restored and simplified). F, reconstruction of intestine with scroll valve in transverse and longitudinal section. dist., distal end; int., intestine; int. t.s., intestine in transverse section; int. l.s., intestine in longitudinal section; prox., proximal end; w. 1-w. 5, whorls of the coil.

#### EXPLANATION OF PLATE 82

##### Heteropolar coprolites from Maleri Formation, India.

Figs. 1-6. Some selected heteropolar coprolites. 1, 2, obverse and reverse of ISI P. 59,  $\times 0.7$ . 3, 4, obverse and reverse of ISI P. 70,  $\times 0.8$ . 5, 6, obverse and reverse of ISI P. 58,  $\times 0.7$ .

Figs. 7, 8. Longitudinal section (bisected halves) of ISI P. 70,  $\times 1.6$ ; the sections represent only the inner core as two layers have been peeled off during section cutting (see text for details).

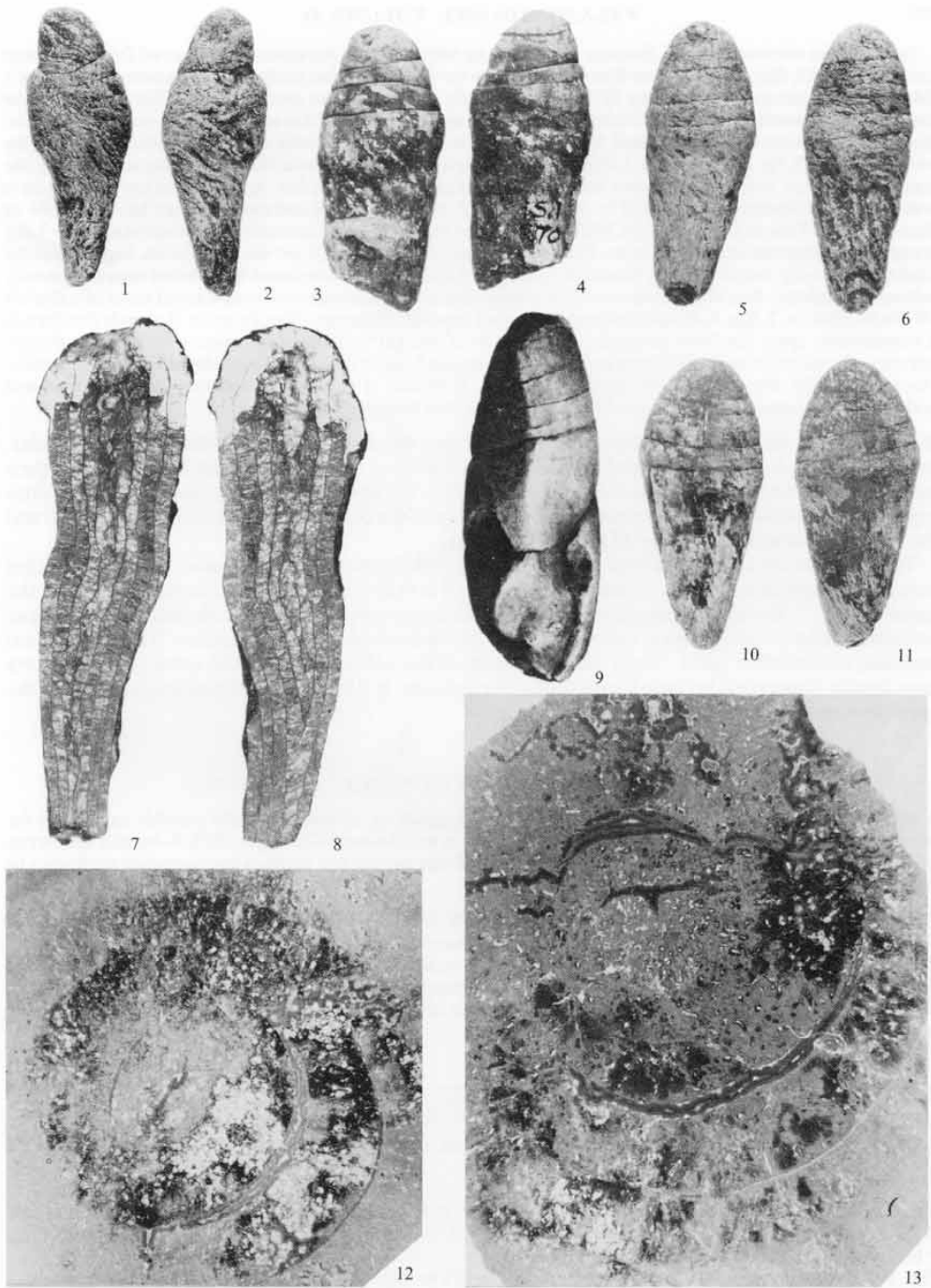
Fig. 9. A heteropolar coprolite from Matley (1939*a*) GSI collection, K. 42/419,  $\times 1.2$ , showing five spirals.

Fig. 10, 11. Obverse (10) and reverse (11) of an undamaged coprolite, ISI P. 51,  $\times 0.8$ ; also shown in text-figs. 2B and 4A.

Figs. 12, 13. Transverse sections of ISI P. 76, showing the disposition of whorls of the coil and mucosal folds.

12, showing compact contents of lumen of the intestine with mucosal folds (serial section no. 3),  $\times 4.3$ .

13, showing mucosal folds, restricted to the lining of the inner whorls of the coil (serial section no. 7),  $\times 5.5$ .



JAIN, Triassic 'coprolites'

In some thin sections of P. 76, features which may be interpreted as impressions of mucosal folds have been preserved (Pl. 82, figs. 12, 13). These thin sections show features somewhat similar to the transverse section of a fish intestine (illustrated by Williams 1972, pl. 3, figs. 3, 4). However, there are three main differences. First, the impressions of mucosal folds in the Maleri coprolites are seen only in a few thin sections and in very limited areas, generally in the inner coils of the whorl. Secondly, the mucosal folds are double in the inner coils but single in the outer ones (Pl. 82, fig. 12; Pl. 83, figs. 1, 2) and occupy only a fraction of the total thickness of the coil. Thirdly, the mucosal folds are very gently thrown into shallow corrugations (Pl. 83, figs. 3, 4) and do not seem to have complex folded features as indicated by Williams (1972, pls. 4-7). These corrugations may be continuous or discontinuous. Thin section studies by Williams show that the thickness of each coil of the whorl is almost wholly occupied by arborescent mucosal folds. The Maleri coprolite thin sections, on the other hand, suggest that the thickness is largely contributed by intestinal inclusions which have been replaced by different minerals (mostly calcium phosphate). It is interesting to make a comparison of a transverse section of a spiral valve of a dogfish (Williams 1972, pl. 2, figs. 1, 2) and a heteropolar 'spiral coprolite' from the lower Permian. It reveals that there is a considerable space for food materials in the lumen of the gut between two adjacent folds in the dogfish intestine. On the other hand, Williams has identified complex folds in the same area in the heteropolar coprolite. His photographs are undoubtedly most convincing. However, it may be argued that the folds represent sculpturing produced by the passage of faecal materials over mucosal folds.

*Remarks.* Two important conclusions may be drawn from this study: (1) although heteropolar, amphipolar, and some cylindrical Maleri coprolites have different external morphologies their internal features are more or less alike, differing only in the number of whorls; and (2) the coprolites suggest a scroll valve type of intestine in which one flap of the coil is attached to the intestinal wall and the remaining whorl is rolled up like a scroll of paper.

These results are at variance with the conclusions of Williams (1972, p. 13) who has suggested that heteropolar coprolites have a 'configuration (which) is fully consistent with the morphology of the spiral valve . . .'. It may be mentioned that it is not always possible to interpret the internal features as being related to a scroll or spiral valve exclusively on the basis of transverse sections. The longitudinal sections, on the other hand, reveal the true nature of the valve. Williams and other recent workers have largely illustrated their work with transverse sections. It is likely that longitudinal sections of the specimens may reveal their true nature.

#### THE MALERI FAUNA

A review of the Maleri fauna is attempted below to designate or narrow down the possible candidates for possession of an intestine with a scroll valve. The fauna is well known (Chatterjee 1978; Sohn and Chatterjee 1979; Jain 1980). Fishes, amphibians, and reptiles are well represented and bivalves and ostracods are known to occur.

*Fishes.* A few species of a lungfish, *Ceratodus* (Miall 1878; Jain 1968; Shah and Satsangi 1969; Chatterjee and Roychowdhury 1974) and one species of a freshwater elasmobranch, *Xenacanthus* (Jain 1980) are known from the Maleri formation. In addition, there is evidence of a small subholostean fish (Jain *et al.* 1964). *Ceratodus* is comparable to the extant *N. forsteri* of Queensland (described in detail below), in having comb-like ridged mandibular and palatal dental plates in addition to a pair of small vomerine teeth. The Maleri *Ceratodus* may range from 1 to 2 m in length.

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#### EXPLANATION OF PLATE 83

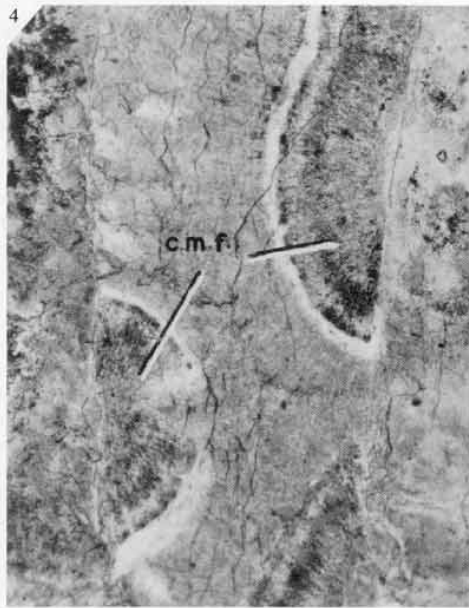
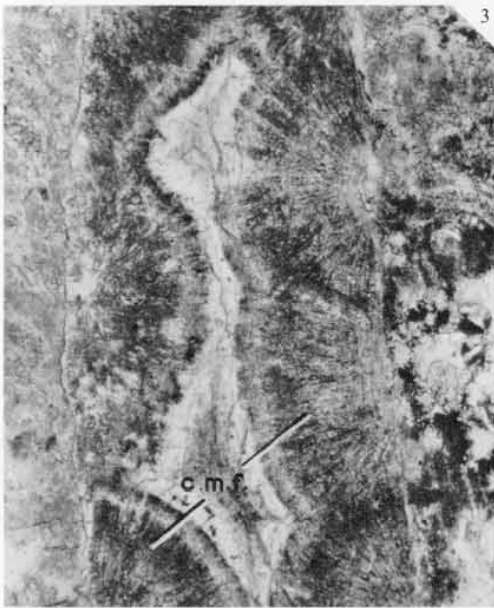
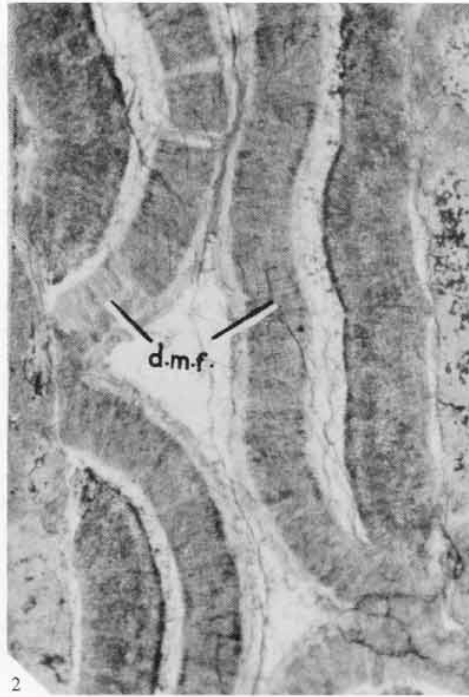
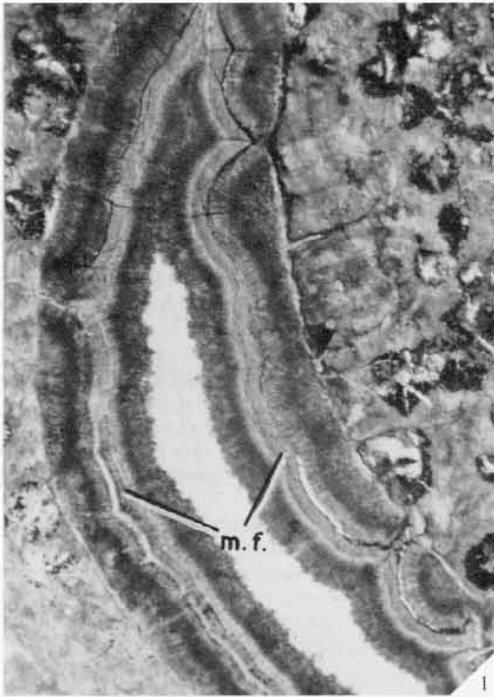
Thin sections of Maleri Coprolites.

Fig. 1. A portion of thin section (TS serial no. 4) of ISI P. 76 to show mucosal fold (m.f.) and the lumen,  $\times 105$ .

Fig. 2. A portion of thin section (TS serial no. 3) of ISI P. 76 to show closely spaced double mucosal folds (d.m.f.) (enlargement from Pl. 82, fig. 12),  $\times 105$ .

Figs. 3, 4. Photomicrographs of a portion of thin section (TS serial no. 5) of ISI P. 76 to show corrugated mucosal folds (c.m.f.) as 3, continuous and 4, discontinuous bands,  $\times 105$ .





JAIN, Triassic 'coprolites'

The Xenacanth is estimated to be about 1.2 m long, predaceous, and a swift swimmer. A spiral valve is present in the intestine of *X. decheni* (lower Permian of Bohemia, Czechoslovakia) which is one of the species in which the body is preserved. The subholostean was a 'small fish since the preserved head is no more than 25 mm' (Jain 1980). It probably fed by nibbling on aquatic vegetation, and fell an easy prey to piscivorous phytosaurs.

**Amphibians.** A metoposaurid amphibian, *Metoposaurus maleriensis*, has been described by Roychowdhury (1965). The large labyrinthodonts were probably sluggish creatures generally inhabiting bottom waters and feeding upon unwary prey. The teeth are indicative of carnivorous habit. Spiral coprolites have not been found associated with the Maleri metoposaurid.

**Reptiles.** The most common member is a rhynchosaur, *Paradapedon huxleyi* (Chatterjee 1974), which grows up to 1.4 m and was *not* adapted to an aquatic mode of life. It fed on vegetable foods such as rhizomes and seeds or mussels as available (Chatterjee 1980a). A phytosaur, *Parasuchus hislopi*, attaining a length of up to 2.7 m, is also known (Chatterjee 1978). The animal lived for the most part in water but made occasional excursions on land particularly during egg laying. Among other reptiles is an eosuchian, *Malerisaurus robinsonae* (Chatterjee 1980b), a cynodont, *Exaeretodon statisticae* (Chatterjee 1982), an aetosaur, similar to *Typhorax*, a thecodontosaur, and a coelurid. With the exception of the eosuchian, these were all land animals. Chatterjee (1980b, p. 187) argued that *M. robinsonae* may have found it advantageous to escape into tree branches from potential predators and its food may have consisted of insects and snails. The Maleri cynodont was a herbivore with specialized post-canine 'molariform' teeth (Chatterjee 1982, p. 203).

An attempt has been made recently (Jain 1980) to relate the more important members of the Maleri fauna to a possible food chain and ecology. Sohn and Chatterjee (1979) have already speculated about the producer of the rounded, oval, or ellipsoidal coprolites. They have suggested that (1) these are possibly droppings on the ground because a few specimens show surface cracks and (2) their large size suggests that they came from a large animal, e.g. a rhynchosaur. These large reptiles were abundant. They could have produced them as faecal excrement, but it is also possible that any other land animal from the Maleri fauna may have also produced them.

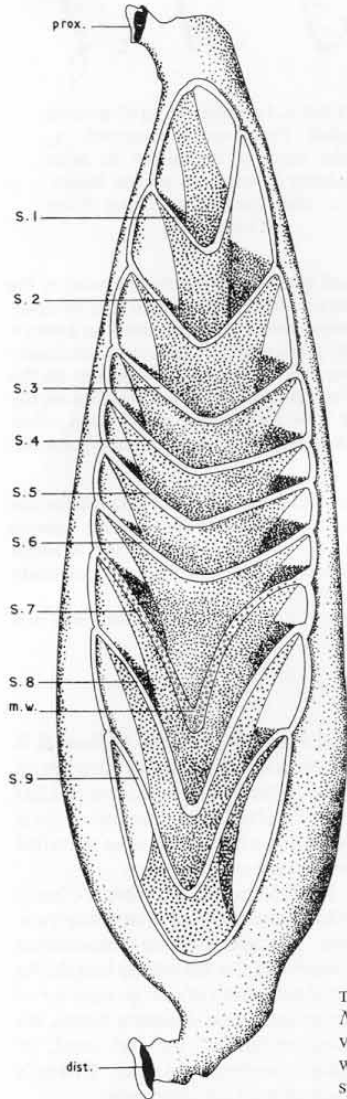
#### SPIRAL VALVE, FAECES, AND THE RELATIONSHIP OF DENTAL PLATE TO BODY LENGTH IN *NEOCERATODUS FORSTERI*

**Spiral valve.** The precise structure of the spiral valve of *N. forsteri* has not been figured in any current literature, though Jollie (1972) figures the gut of *Protopterus* showing the spiral valve and distinct stomach. Through the courtesy of Dr. Anne Warren, I obtained a specimen of the intestine of *N. forsteri* (text-fig. 5) removed from a fish 102 cm long.

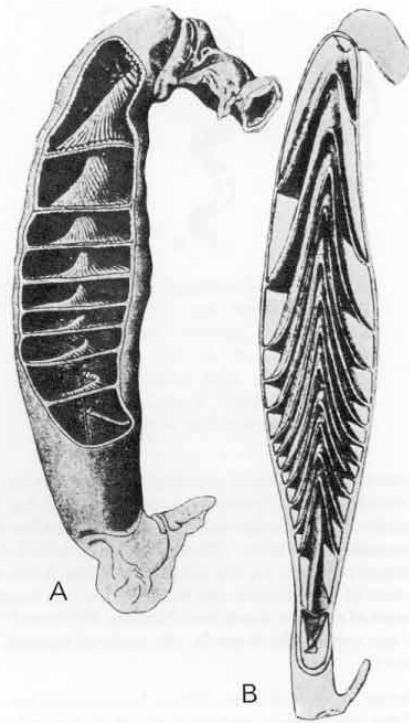
The spiral valve is present throughout the length of the sac-like intestine which is about 27 cm long and 9 cm at its maximum diameter in the lower one-third. The valve is of the shape of a carpenter's auger or a staircase with nine loose spirals of variable dimensions. The rectum opens into a small cloaca. The nine spirals increase in depth posteriorly. The seventh, eighth, and ninth folds are very deep and may be as much as three to four times larger than the anterior ones. The seventh fold is highly muscular (text-fig. 5).

The presence of a spiral valve in the intestine, as a device to increase the surface area for absorption, is known in many early vertebrates. It is present in cyclostomes and in all bony fishes except teleosts. A great deal of diversity is exhibited by the spiral valve of modern sharks. In *Raja* and *Scyllium* (text-fig. 6A, B) the spiral valve consists of a series of cones with their apices directed anteriorly but the configuration and depth of cones varies considerably between the two. A spiral valve is present in all the three-surviving dipnoans, though it is probably more primitive in *Neoceratodus* than in *Lepidosiren* and *Protopterus*. The folds of spiral in *Neoceratodus* are disposed as if a number of funnels of varying sizes were placed one on the top of another in series. In *Protopterus* the funnels face in the opposite direction in a fashion similar to a typical shark, *Callorhynchus* or *Acipenser*, as illustrated by Romer (1966). The disposition of intestinal folds in *Neoceratodus* is somewhat similar to those figured in Greenwood (1963) for a ray (*Raja* sp.). In a minority of sharks (e.g. *Scoliodon* sp.) the base of the valve twists but little and hence is relatively short; the valve fold, however, is highly developed and rolled up into a great scroll running the length of the intestine. This is referred to as a scroll valve, as distinct from spiral valve, but has the same function of increasing the area of absorption.

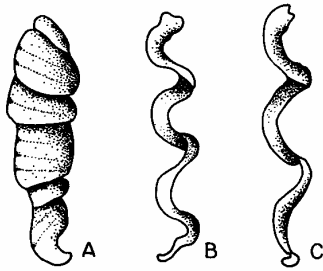
**Faeces.** Information on *N. forsteri* faecal matter has been provided by Dr. Anne Kemp who writes (pers. comm., 25 September 1979): 'In my experience the faeces of adult lungfish are loosely spiral but they usually fall apart. Juveniles produce much closer spirals.' Her photographs showing faecal pellets after ejection and following



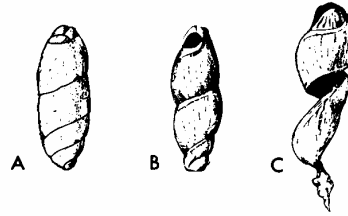
TEXT-FIG. 5. A dissected intestine (semi-diagrammatic) of *Neoceratodus forsteri*, showing morphology of the spiral valve ( $\times \frac{1}{2}$ ). dist., distal end of intestine; m. w., muscular wall of the seventh valve; prox., proximal; s. 1 to s. 9, spiral valve whorls.



TEXT-FIG. 6. Valvular intestine of two sharks to show basic patterns. A, *Raja* (from Daniel 1934, after Paul Meyer); B, *Scyllium* (from Parker 1885).



TEXT-FIG. 7. Drawings of faecal material (actual size 3–5 cm) of *Neoceratodus forsteri*, based on photographs. A, at the time of deposition; B, after remaining in water for several hours, and C, after twenty-four hours.



TEXT-FIG. 8. Faecal material of modern lungfish *Protopterus annectans*. A, at the time of deposition B, after remaining in water for several hours, and C, after twenty-four hours (from Dean 1903).

several hours in water provided the basis for text-fig. 7. Dean (1903) figured spiral faecal pellets produced by the African lungfish *Protopterus annectans* (text-fig. 8). The faecal pellet is thrown initially into at least four compact spirals which become somewhat loosened after remaining in water for several hours. After twenty-four hours it becomes like a spiral ribbon. It may be noted that the faecal pellets of *N. forsteri* and *P. annectans* are closely similar in shape. In the former the pellet is less compact than in the latter. No information is available on the faeces of *Lepidosiren*, the South American lungfish. There is an almost virtual absence of information on the shape of modern shark faecal pellets. Williams (1972, p. 9) quotes from Dr. P. W. Gilbert who never found pellets of any type in shark pools, 'the material egested from the cloaca of a shark is either in a liquid or loosely viscous form'.

*Dental plate-body size relation.* No information seems to have been recorded on the relationship between the size of the dental plate and the body of *N. forsteri*. In view of the close resemblance of dental plates in the Triassic *Ceratodus* and *N. forsteri* this proportion could be utilized to estimate the size of extinct species. A single measurable specimen of *N. forsteri* 800 mm long in the collections of the Museum of Natural History, University of Kansas has a dental plate 30 mm long. Thus the dental plate/body length ratio is 3:80.

On the basis of range of teeth size the Maleri *Ceratodus* is estimated to have been 1–2 m long, but it is emphasized that dental plate size changes dramatically throughout growth.

## DISCUSSION

A variety of vertebrates and invertebrates comprise the rich faunal assemblage in the Maleri. It is unlikely that any invertebrate could have produced the coprolites in question. Among the vertebrates the Maleri tetrapods are either aquatic, semi-aquatic, or land animals. In the foregoing account it has been suggested that none of them is likely to have had a spiral or scroll valve in the intestine. This is further supported by the general remark of Romer (1966, p. 356) who, while discussing spiralled features in the intestine, said that 'no living tetrapod has the slightest trace of this organ'.

There is no definite evidence of a scroll or a spiral valve in any fossil tetrapod. However, Charig (1979, p. 30) has illustrated an enormous coprolite (29 cm long) with a distinct whorl of seven spirals, as 'possibly' from a dinosaur. The locality and age are not given. The spirals have a maximum diameter in the middle of the specimen and the spiral structure is continued for the whole length. As such it can be called an amphipolar coprolite. In our own experience of collection of a large number of coprolites from a lower Jurassic locality in India, along with numerous sauropod dinosaur bones, we have never come across such spiral coprolites. All the coprolites are either rounded, oval, or ellipsoidal, usually with desiccation marks, similar to recent drying cow-dung. As such, Charig's specimen, though intriguing, must await confirmation of its association with the dinosaurs.

The records of coprolites with spiral markings reveals that they may occur at localities which have not yielded an animal with a spiral valve. Coprolites studied by Broughton *et al.* (1978) from the late Cretaceous Whitemud Formation of Western Canada exhibit coiling, folding, and contraction marks but are not spirally coiled and are quite distinct from the Maleri coprolites. The following examples, however, are worth noting:

1. Middle Triassic of Mendoza, Argentina (Rusconi 1949): spiral coprolites associated with *Tyothorax*, an aetosaur.
2. Lower Lias of Lyme Regis, Britain (Buckland 1829; Pollard 1968): spiral coprolites associated with ichthyosaurs.
3. Upper Triassic rocks on the north-eastern shore of Lake Inder, U.S.S.R. (Ochev 1974): spiral coprolites associated with labyrinthodonts, dicynodonts, thecodonts, and theriodonts.

In addition amphibians, e.g. *Eryops* and *Diplocaulus*, have been considered the producers of heteropolar and amphipolar coprolites (Neumayer 1904).

In view of the fact that a spiral intestine has never been found in any living tetrapod it is unlikely that the tetrapods listed above produced the associated coprolites. It is, however, possible that new faunal elements, including fishes in which a spiral valve is widespread, will be discovered with the above occurrences in the future.

TABLE 1. The Maleri Fish

DIPNOI:		
<i>Ceratodus</i>	<i>C. hislopianus</i>	Described by Oldham (1859); commented on by Miall (1878); suggested size of the fish 1 to 2 m (Jain 1980).
	<i>C. hunterianus</i>	
	<i>C. virapa</i>	
	<i>C. nageswari</i>	Described by Shah and Satsangi (1969); smaller in size than above species.
ELASMOBRANCHII:		
<i>Xenacanthus</i>	<i>X. indicus</i>	Presence of Xenacanth suggested by Jain <i>et al.</i> (1964); described by Jain (1980); suggested size 1.2 m.
SUBHOLOSTEI:		
Unnamed genus and species		Presence mentioned by Jain <i>et al.</i> (1964); discussed by Jain (1980); size of head 25 mm, suggested size of fish 6-8 cm.

The possibility that the Maleri fishes (Table 1) produced the spiral coprolites raises three questions: 1. How widespread is the occurrence of a spiral valve in fishes? 2. Do fishes having a spiral (or scroll) valve pass faeces with spiral markings? 3. Are there any examples of fossil fish in which spiral structures have been found inside the body or close to it?

Romer (1966, pp. 355-356) provided an answer to question 1: 'This (spiral intestine) is characteristically developed in elasmobranchs in which it is typically a large cigar shaped body, extending nearly straight anteroposteriorly and occupying most of the length of the abdomen.' For the remaining fishes Romer has this to say: 'The spiral intestine is present in chimeras and to some degree in cyclostomes, and fossils even demonstrate its presence in the ancient class of Placoderms. Further, it was present in the early bony fishes, for living lungfishes and all lower actinopterygians retain a spiral valve, and even a few teleosts have a vestige of this structure.'

The available information on question 2 is somewhat contradictory. Although a spiral valve is known to be present in a number of extant shark species, faecal pellets of the same are unknown. Definite evidence of the presence of spiral features in the faecal material of extant fishes is available only in the dipnoans *P. annectens* (Dean 1903) and *N. forsteri* (present study), and in the holosteans *Amia* and *Lepisosteus* (Williams 1972). These fishes have a definite spiral valve in the intestine.

Regarding question 3, there are at least four good examples of inclusions with spiral markings within the preserved body of fish. Dean (1903) figured and described a specimen of *Cladoselache newberryi* in which a cast of the intestinal wall gives a direct evidence of the presence of a spiral valve. Zangerl and Richardson (1963) mentioned the presence of a spiral coprolite in the pelvic region of a mutilated shark specimen from the Pennsylvanian of Indiana. Zidek (1980) found a spiral coprolite in the tail region of *Acanthodes* from the Mississippian of Montana. Fritsch (1907) figured a shark, *Xenacanthus decheni* (lower Permian, Czechoslovakia), in which the spiral valve of the intestine occurs in its natural position, and also found a number of isolated bodies, having similar features, besides the skeleton of the same fish.

The spiral coprolites do not exhibit desiccation marks, in contrast to the rounded, oval, or ellipsoidal forms, suggesting that they have been deposited in an aquatic environment. As noted by Duffin (1979, p. 199): 'It is unlikely that the spiral structure would be retained by the contents of the intestine after squeezing through the sphincter at the base of the small intestine and extrusion into the rectum.' The faeces of *Neoceratodus* and *Protopterus* are extruded in the form of spiralled ribbons which tend to change into loose spirals after exposure. It is difficult to visualize the preservation and fossilization of such bodies into compact coprolites.

A second possibility is that these coprolites are actually 'enterospirae' (see Fritsch 1907, Williams 1972). Williams has recognized detailed anatomical features of the intestinal wall in thin sections of spiral coprolites from the Permian and Cretaceous of Kansas. By contrast, spiral coprolites from the Rhaetic bone-beds never show evidence of the preservation of mucosal folds on the whorl interfaces in thin section (Duffin 1979). Similarly the anatomical features illustrated by Williams have not been observed in Maleri coprolites, though the presence of mucosal folds has been observed in some thin sections. The mucosal folds either perished before fossilization or were never present. Thus the Maleri coprolites cannot be designated 'enterospirae' *sensu stricto*.

A third possibility (suggested by Stewart 1978, p. 13 for spiral coprolites from the upper Cretaceous Niobrara Formation) is that they represent 'fossilized intestinal contents'. In this connection it may be significant that in *Scyllium* the spiralled intestine is filled with finely divided gut contents (Williams 1972), resembling mud, which sticks so tightly between successive cones of the spiral that it is difficult to remove it with a stream of water. Any intestine so filled would stand an excellent chance of being fossilized. Since sections of the Maleri coprolites reveal finely compacted contents, extraneous elements like fish scales being rare, these could be interpreted as 'fossilized intestinal contents'. If the coprolites are fossilized intestinal contents, their possible association with the Maleri *Ceratodus* merits consideration. Several species are represented which were variable in body length as indicated by the size of the dental plates. Over 60% of the dental plates in the collections from Maleri (over 250 specimens) at I.S.I are around 40 mm long and they range from 15 to 60 mm. This suggests large fish, averaging over 1.0 m but reaching up to 1.6 m, based on the comparison with *N. forsteri*. The spiral coprolites in the present collection range from 50–65 mm, except one specimen which is about 80 mm long. Matley (1939a) recorded a size range of 50–55 mm. Only one specimen in his collection was 74 mm. Thus 50–65 mm may be considered the normal size range of Maleri coprolites. The spiral intestine of *N. forsteri* studied measured 27 cm, from a fish 102 cm long, indicating a ratio of 1:3.7. Dissection and measurement of a large number of fish would provide more accurate figures but this is not important for the present discussion. If the Maleri *Ceratodus* was similar to *N. forsteri* (their dental plates show close similarity), then they might show somewhat similar proportions between body length and the length of intestine or 'fossilized intestinal contents'. However, the Maleri coprolites have a size range which is far too small to fit the robust Maleri *Ceratodus*, even allowing for possible shrinkage of intestine. It may be argued that the entire length of the intestine may not be represented by the coprolites and that it may not have been complete at the time of fossilization. The compactness of the intestine, however, favours entire preservation. Moreover, collections made for nearly a century indicate a limited size range. The spiral valve of *N. forsteri* does not resemble the features evidenced by thin sections of Maleri coprolites either.

If the comparison between *N. forsteri* and *Ceratodus* is valid neither the size nor the internal

features of the Maleri coprolites provide a convincing evidence of their association with *Ceratodus*. If the Maleri coprolites cannot be associated with *Ceratodus* with any degree of confidence, what of the remaining fish? There is evidence of a spiral valve in the intestine of *X. decheni* (Williams 1972). Teeth of *Xenacanthus* are present in most of the Pennsylvanian and Permian localities where spiral coprolites have been found (Price 1927, Moran and Romer 1952, Romer 1958, Williams 1972). Although it therefore appears logical to associate the xenacanth with the spiral coprolites, three important factors suggest otherwise. These are: (1) frequency of occurrence, (2) anatomical features, and (3) size discrepancy. *X. indicus*, so far, is known from only two blocks of calcified skull cartilages, possibly representing two specimens. This is inconsistent with the abundance of spiral coprolites. It is possible, however, that isolated xenacanth teeth occur frequently in Maleri clays but have been missed because of their microscopic size. A similar situation has been mentioned by Stewart (1978, p. 14) in dealing with Kansas Permian xenacanth remains. Xenacanth fish have a spiral valve in the intestine whereas coprolites suggest a scroll valve. *X. indicus* is estimated to be about 1.2 m long. The spiral coprolites from Maleri appear to be too small to represent 'fossilized intestinal contents' of this robust xenacanth, though no data are available on relative size. Thus the evidence to associate the xenacanth fish with spiral coprolites is inconclusive.

Since some palaeoniscoids (e.g. *Palaeoniscus*) and the extant holosteans have a spiral valve in the intestine, the possibility that the subholostean was the producer of the spiral coprolites appears to be quite strong. However, the Maleri subholostean is as yet undescribed and in any case its estimated size is almost the same as most of the coprolites. Thus the possibility of their association cannot be seriously considered.

The interpretation of the Maleri coprolites is still far from satisfactory and a number of tantalizing problems remain. Ash (1978) suggested that the upper Triassic (Chinle) spiral coprolites were probably produced by several different unspecified groups and sizes of animals. There is equivocal evidence that the Maleri spiral coprolites are either preserved intestines (enterospirae), intestinal contents, or faeces of known Maleri fauna. It is also possible, however, that they were produced by some unknown faunal element or represent the body of an as yet undetermined faunal element in the Maleri beds.

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