

Taphonomy and palaeobiology of early Middle Triassic coprolites from the Luoping biota, southwest China: Implications for reconstruction of fossil food webs



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ABSTRACT

Abundant, exceptionally preserved coprolites are documented from the Luoping biota (Anisian, Middle Triassic) of Yunnan Province, southwest China. These coprolites can be categorized into four morphological types: A) bead to ribbon-shaped, B) short to long cylindrical-shaped, C) flattened, disk-like, and D) segmented faeces. Detailed multi-disciplinary studies reveal that coprolite type A was likely produced by invertebrate animals, while coprolite types B to D could be faeces generated by carnivorous fishes or marine reptiles, perhaps from different taxonomic groups. When compared with coprolites reported from the Lower Triassic, the Luoping forms indicate more complicated predation-prey food web networks. These evidences, combined with body fossil discoveries from Luoping, suggest the emergence of complex trophic ecosystems in the Anisian, marking the full biotic recovery following the Permian–Triassic Mass Extinction.

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1. Introduction

The Permian–Triassic Mass Extinction (PTME) resulted in not only the largest biodiversity crisis in Earth history, but also catastrophic devastation to the contemporaneous global ecosystems (Erwin, 2006; Benton et al., 2013). Subsequent biotic recovery was also protracted, so that it was not until the early Middle Triassic that the complete ecosystem structure recovered fully (Knoll et al., 2007; Chen and Benton, 2012; Benton et al., 2013). Such an early fully recovered, complex ecosystem is well represented by the exceptionally preserved biota from the early Middle Triassic strata of Luoping in Yunnan Province, southwest China (Hu et al., 2011; Chen and Benton, 2012; Benton et al., 2013; Liu et al., 2014; Zhang et al., 2014). It has been proposed that a complex food web was rebuilt and operated in such a fully recovered shallow marine ecosystem, with a hypothesized model based on fossil

evidence and a comparison of the Luoping biota with modern marine taxa (Hu et al., 2011; Chen and Benton, 2012).

Apart from abundant body fossils of at least seven major clades – marine reptiles, fishes, echinoderms, crustaceans, molluscs, branchiopods, and plants (Hu et al., 2011) – the Luoping biota also records abundant trace fossils, including burrows, nesting traces, various trackways, and coprolites (Hu et al., 2011; Luo et al., 2013; Zhang et al., 2014). Most of these trace fossils are exceptionally preserved (Zhang et al., 2014). Of these, coprolites are very common, but remain understudied in terms of taphonomy, palaeobiology, and identity of the producers, although they have been briefly reported in earlier publications (Hu et al., 2011; Luo et al., 2013).

Coprolites, together with fossilized gut contents (consumulites), form two important sources of information for interpreting the dietary habits and trophic levels of ancient animals in ecological communities (Richter and Wedmann, 2005; Eriksson et al., 2011; Hunt and Lucas, 2012a; Khosla et al., 2015). Besides, as an important palaeobiological source for reconstructing animal diet and behaviour, coprolites record direct evidence of ancient predator–prey relationships among animals, thus serving as excellent materials for reconstructing trophic structures and energy flow models of past ecosystems (Hunt et al., 1994; Chin and Gill, 1996; Eriksson and Terfelt, 2007; Eriksson et al., 2011; Hunt and Lucas, 2012a; Matsukawa et al., 2006, 2014). Combining multiple lines

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of evidence from the morphology, elemental geochemistry and inclusions of coprolites, the faeces-producing animals and depositional environments of the faeces can then be recognized with some confidence (Northwood, 2005; Bajdek et al., 2014; Zatoń et al., 2015). When occurring in association with body fossils, taphonomic features of coprolites can provide additional insights into the processes acting on the

preservation of body fossils, which otherwise might not be available from the body fossils.

Recently, several studies have been made on some Early Triassic coprolites (Northwood, 2005; Nakajima and Izumi, 2014; Brachaniec et al., 2015; Hao et al., 2015), highlighting the significance of coprolite studies in probing into fossilized food chains of marine ecosystems

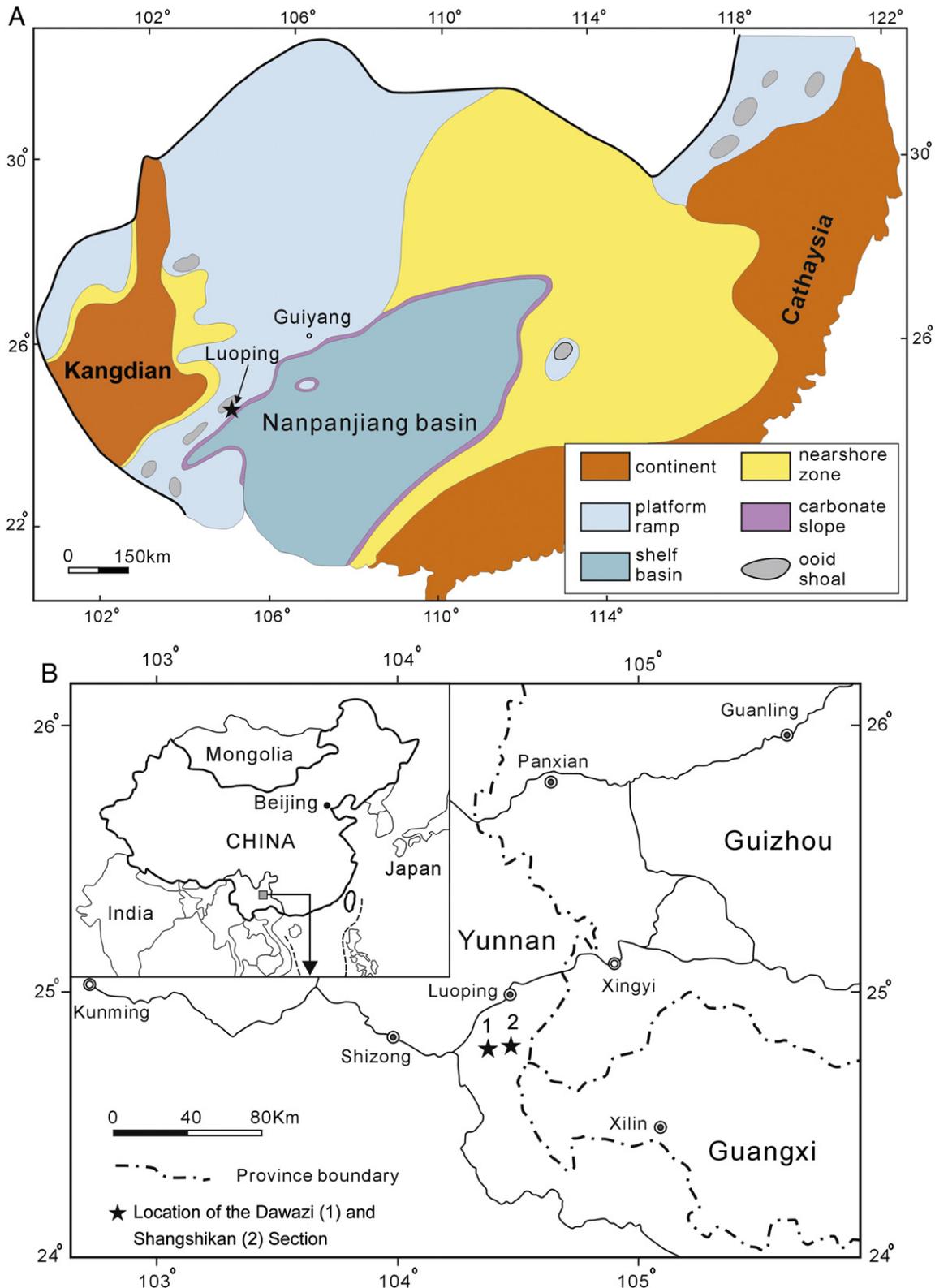


Fig. 1. A, Middle Triassic palaeogeographic map of South China showing the palaeogeographic setting of the Luoping area during that time [base map was modified from Feng et al. (1997)]. B, Location of the Shangshikan and Daozi sections of Luoping County, eastern Yunnan Province, southwest China.

during the recovery process following the PTME. However, detailed information on the diet types, predatory activities, and feeding strategies from these Early Triassic coprolites still remain unknown. A comparison of these Early Triassic examples with Middle Triassic coprolites is non-existent, hindering our understanding of the transition of the marine ecosystem through this time interval.

In this study, we present a systematic study of early Middle Triassic coprolites preserved with the Luoping biota (Middle Triassic, Yunnan, southwest China). Morphology, elemental analysis, and food inclusions within different coprolite samples are first described in detail in order to understand their origins. Complexity and functionality of this early Middle Triassic ecosystem is reconstructed based on food webs derived from the Luoping body fossils and coprolites.

2. Geological and stratigraphic settings

The coprolites described below were collected mainly from the Dawazi and Shangshikan excavation quarries of the Luoping biota, which are located 2 km northeast and 1 km south of Dawazi Village, respectively, 20 km southeast of Luoping County town, eastern Yunnan Province, southwest China (Fig. 1B). During the early Middle Triassic, the Luoping area, together with the Yunnan–Guizhou Provinces border areas, was situated at the southwestern margins of the Yangtze Platform, and separated from the deep marine Nanpanjiang Basin by a shoal complex (Feng et al., 1997; Enos et al., 2006; Fig. 1A). Within the vast Yangtze Platform interior region, several spatially and temporally separated intraplatform basins or depressions with exceptional fossil

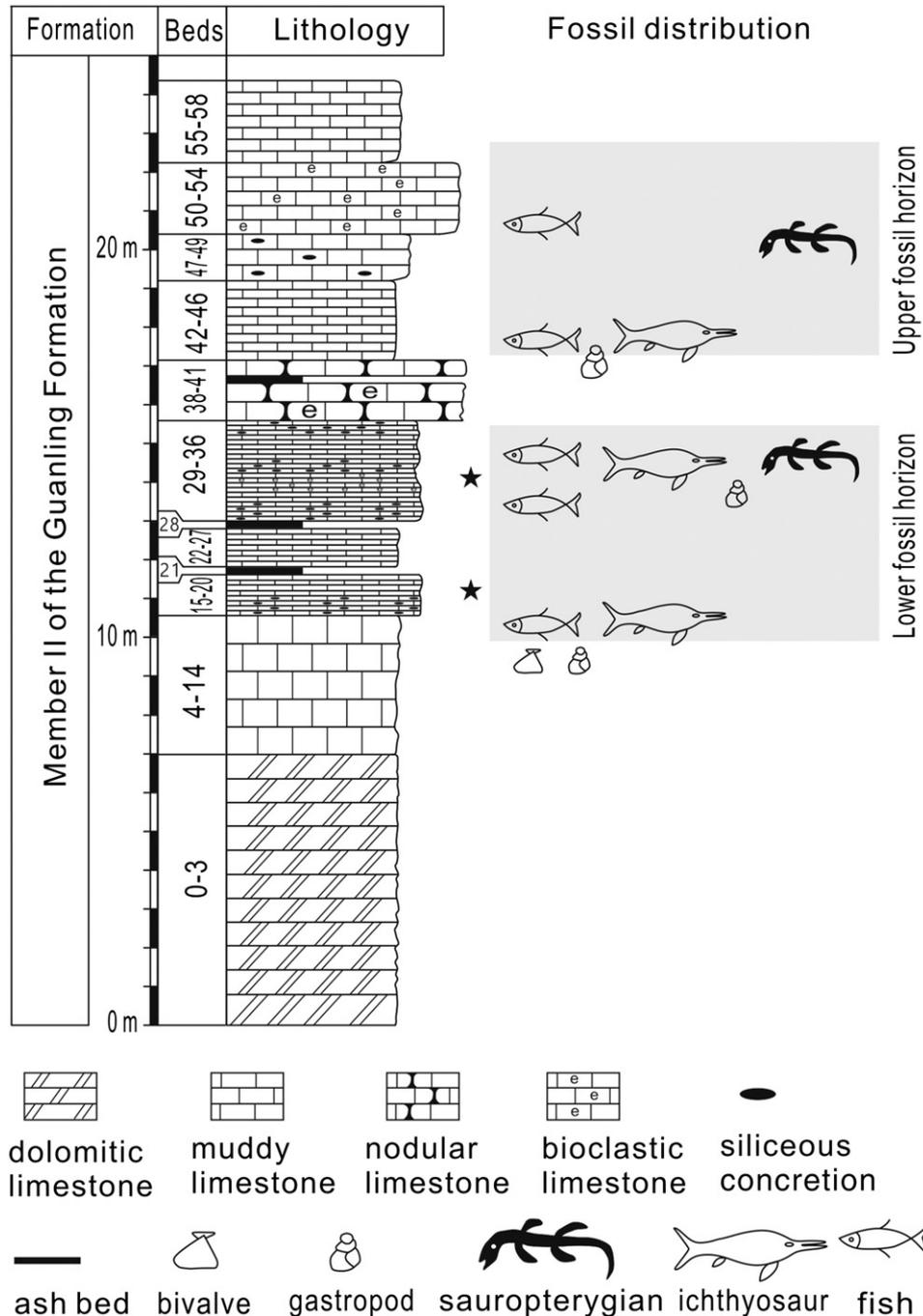


Fig. 2. Middle Triassic succession exposed in the Shangshikan section showing fossil horizons of the Luoping biota, eastern Yunnan Province (after Bai et al., 2011). Stars denote the horizons of coprolites.

preservation, namely the Panxian, Luoping, Xingyi, and Guanling locations and their biotas, have been recognized from the middle-late Anisian, late Ladinian, and Carnian intervals, respectively (Wang et al., 2009; Benton et al., 2013). In Luoping, abundant marine reptile faunas were preserved in a basinal setting represented by the upper part of Member II of the Guanling Formation (Hu et al., 2011). The highly fossiliferous, dark-coloured micrite of the upper part of Member II can be traced over an area of some 200 km² (Benton et al., 2013). However, Member I and the lower-middle parts of Member II of the Guanling Formation record similar successions over the entire Yangtze Platform interior region in the Yunnan-Guizhou border areas (Enos et al., 2006).

Therein, Member I of the Guanling Formation is dominated by siliciclastic sediments of subtidal to intertidal settings (Hu et al., 1996), while Member II by micrite, bioclastic limestone, oncoidal limestone, and dolomite in the lower and middle parts, and by black muddy limestone, cherty limestone, and grey dolomite in the upper part (Fig. 2). In both the Shangshikan and Dawazi sections, the Luoping biota came from two main horizons. The lower fossil horizon records abundant fishes, marine reptiles, shrimps, crinoids, plant fossils, and other invertebrates, while the upper fossil horizon yields numerous marine reptiles along with rare shrimps (Bai et al., 2011; Wu et al., 2009, 2011; Wen et al., 2012, 2013; Benton et al., 2013; Liu et al., 2014). Coprolites were collected mainly from the lower fossil horizon (Fig. 2). Member II of the Guanling Formation at Luoping has yielded conodonts of the *Nicoraella kockeli* conodont zone, constraining the Luoping biota to a Pelsonian (Middle Anisian) age (Zhang et al., 2008, 2009; Huang et al., 2009, 2011).

3. Materials and methods

A total of 60 coprolite samples have been collected from Member II of the Guanling Formation in excavation quarries of the Luoping biota and their equivalent horizons in the same area. In addition, some well-preserved coprolite specimens stored at the Chengdu Center of the China Geological Survey have also been examined. Coprolites used for detailed morphological and geochemical studies are all complete samples, unless otherwise stated (e.g. specimens presented in Fig. 6). All coprolite samples were firstly examined and photographed at macro-scale to note their general shape, size, morphology, and large inclusions, using a Leica M205A binocular microscope. Selected samples were further imaged at micro-scale to record possible food remains/undigested fragments and inclusions under a SU8010 Scanning Electron microscope (SEM) equipped with an energy-dispersive X-ray spectroscopy (EDS) detector. Freshly broken coprolite samples as well as broken bone skeletal remains of fishes were also polished and carbon coated for

EDS analyses to compare their elemental compositions. Selected samples representing different morphotypes were also thin-sectioned to observe food remains and inclusions under a petrological microscope. All the experiments were conducted at the State Key Laboratory of Biogeology and Environmental Geology and the State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences (Wuhan). Information relating to sample collection numbers and institutes where they stored is provided in Supplementary Table 1.

4. Characteristics of the Luoping coprolites

4.1. Morphological features

Due to the flattened nature and various morphologies exhibited by the Luoping coprolites, it is difficult to assign the new materials to any known coprolite ichnotaxa from the Mesozoic (e.g. Hunt et al., 2007; Laojumpon et al., 2012). An informal, descriptive classification scheme based on similar morphologies was preferred here to categorize the Luoping coprolites into different morphotypes. Integration of general size and shape, inclusions, and segmentation allows further classification of morphotypes among the coprolites examined. Morphotypes A and B are subdivided into two and three sub-morphotypes, respectively according to their auxiliary morphological differences. Detailed information on the general morphology, size range, food inclusions, and number of specimens from each morphotype is summarized in Table 1. Selected specimens are illustrated here (Figs. 3–6).

4.1.1. Morphotype A

These are beaded or smooth-margined, ribbon-shaped coprolites (Fig. 3A–F). The ribbon shape is sinusoidal to slightly curved, and has a roughly identical diameter along the length of each specimen. The materials within the ribbon-shaped faeces are distinct, and they are further divided into two sub-morphotypes in terms of auxiliary morphological feature and colour differences from the surrounding rocks. Sub-morphotype A1 is dark-coloured and varies from 450 µm to 1.2 mm in diameter, with a maximum length of up to 33 mm (Fig. 3A). The materials within the sub-morphotype A1 faeces are homogenous, but form pinch-and-swell structures, giving the coprolite a bead-like morphology (Fig. 3A–C). Sub-morphotype A2 is light-coloured, with a consistent diameter of 650 µm within individual ribbon-like scats. Partly broken surfaces show that two-layered structures are pronounced, with a darker inner part surrounded by a light-grey outer part on each outer margin (Fig. 3D, F). When it is well-preserved, the ribbon-like scat showed a wide middle ridge separated and two narrow lateral ridges (Fig. 3E).

Table 1

Summary of coprolite morphotypes identified from Luoping, with their general morphology, size range and food inclusion information included.

Morphotype	Morphology	Size range (length/mm)	Number of specimens	Food inclusions
A Sub-morphotype A1	 Beaded-shaped	4–29	1	Organic matter?
Sub-morphotype A2	 Elongated with constant diameter	3–10	11	Not observed
B Sub-morphotype B1	 Cylindrical, elongated with rounded segments	7.5–60	8	Fragmented bones, fish scale
Sub-morphotype B2	 Short cylindrical with irregular boundaries and rough surfaces	10–52	14	Abundant fish scales, rare bone, and indetermined fragments
Sub-morphotype B3	 Cylindrical with rounded ends and smooth surfaces	10–64	4	Fish teeth, bone fragments
C Morphotype C	 Flattened, disk-like	13–39	5	Bone and fish scales
D Morphotype D	 Short, segmented	9–20	17	Fragmented bone, indetermined fragments

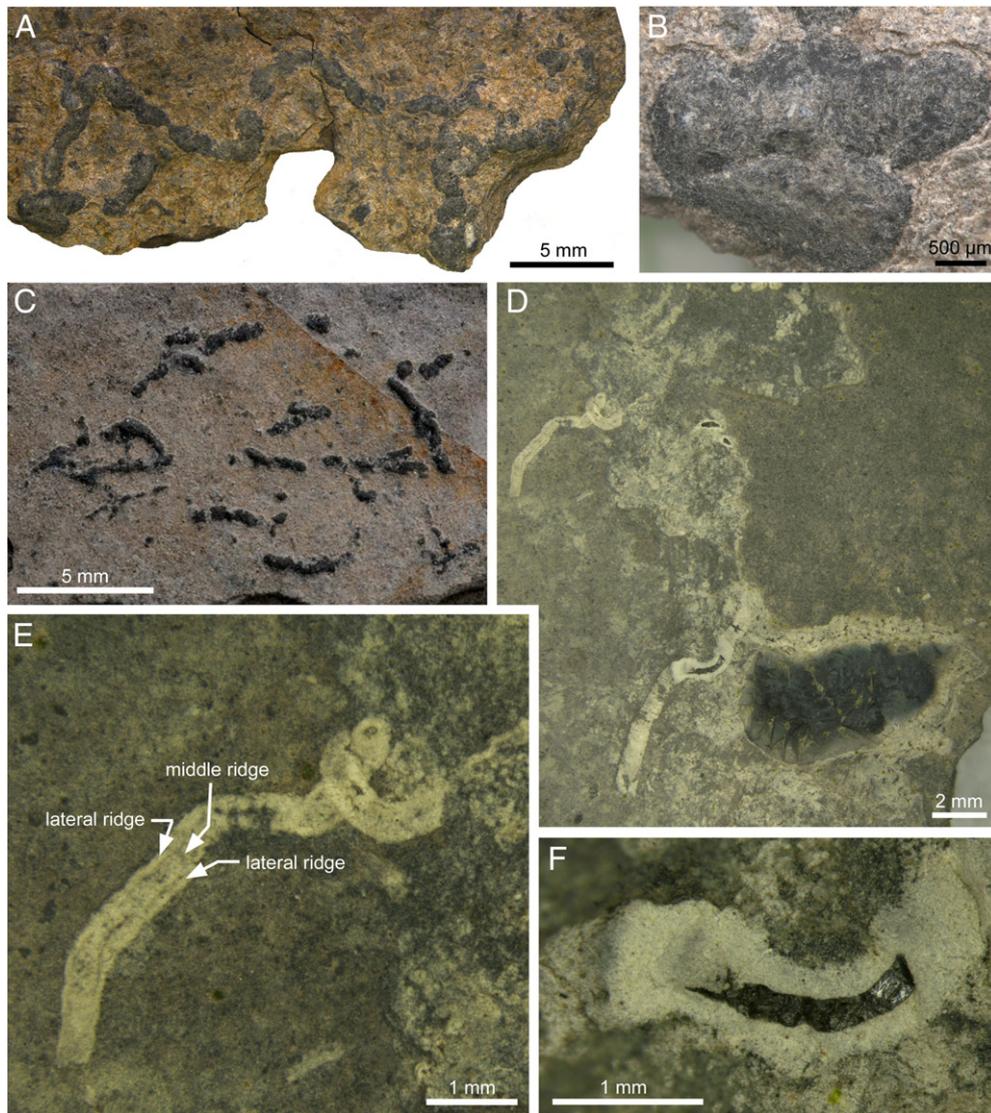


Fig. 3. Selected examples of Morphotype A coprolites from the Middle Triassic of Luoping, Yunnan, SW China. A, Sub-morphotype A1 showing the ribbon-shaped faeces winding sinuously on muddy limestone matrix (No.LPC019). Note that the bead-like morphology is distinct on some parts of ribbons. B, Close-up of the lower left part of A showing the rough surfaces. C, Short ribbon-like coprolite of Sub-morphotype A1 (No.LPC020). D, Light coloured coprolite of Sub-morphotype A2 (LPC014). Note the identical diameter of the ribbon. E, Close-up of upper left area in C showing overlapping morphology. F, Close-up of Sub-morphotype A2 coprolite showing the two-layered structure.

Overlapping structures are observed within Sub-morphotype A2 coprolites (Fig. 3E). The ends of both types of coprolite are indeterminate.

4.1.2. Morphotype B

This type of coprolite is characterized by full-relief, short to long shaped cylindrical rods. Grey to dark coloured rods are straight to slightly curved, and have lengths ranging from 12 to 28 mm and diameters of 2.5–7.0 mm. Three sub-morphotypes were further categorized. Morphotype B1 is short cylindrical rod with rounded segments, with isopolar, rounded ends (Fig. 4A, E, G). Morphotype B2 is represented by short rods having very irregular boundaries and rough surfaces (Fig. B–D). Most of them usually have one larger rounded end and a smaller tapering end (Fig. 4B, D). Morphotype B3 is characterized by regular cylindrical rod with rounded ends and smooth surfaces (Fig. 4H–I). For most of the scats, the outer surfaces are rather rough, with only a few showing smooth morphologies (Fig. 4A, H–I). Boundaries between scats and host rocks are conspicuous, although specimens from morphotype B2 were separated from their source rocks by distinct irregular boundaries (Fig. 4B–D). The most remarkable feature of

Morphotype B coprolites is the presence of abundant food inclusions, which include numerous complete to incomplete fish scales of various shapes and sizes, shattered pectoral fins, bone fragments, teeth, and some indeterminate fragments (Figs. 4A–E, 8A–I). The detailed features of these inclusions are described below.

4.1.3. Morphotype C

These are flattened, disk-like coprolites (Fig. 5A–B). These ellipsoidal disks are rather large and have a maximum length up to 37 mm and width up to 15 mm. The boundary between the dark-coloured coprolite and the light-coloured matrix is also very pronounced. Food inclusions within Morphotype C coprolites are also abundant, including fish scales and fragmented bones (see Fig. 10A–B).

4.1.4. Morphotype D (segmented faeces)

These are segmented faeces of varied sizes. Dark-coloured segments are rod- to pellet-shaped in outline and vary from 7 to 20 mm in length and from 3 to 9 mm in diameter. Scats usually have a rounded end and an indented end (Fig. 6A–E). The outer surfaces are usually fractured,

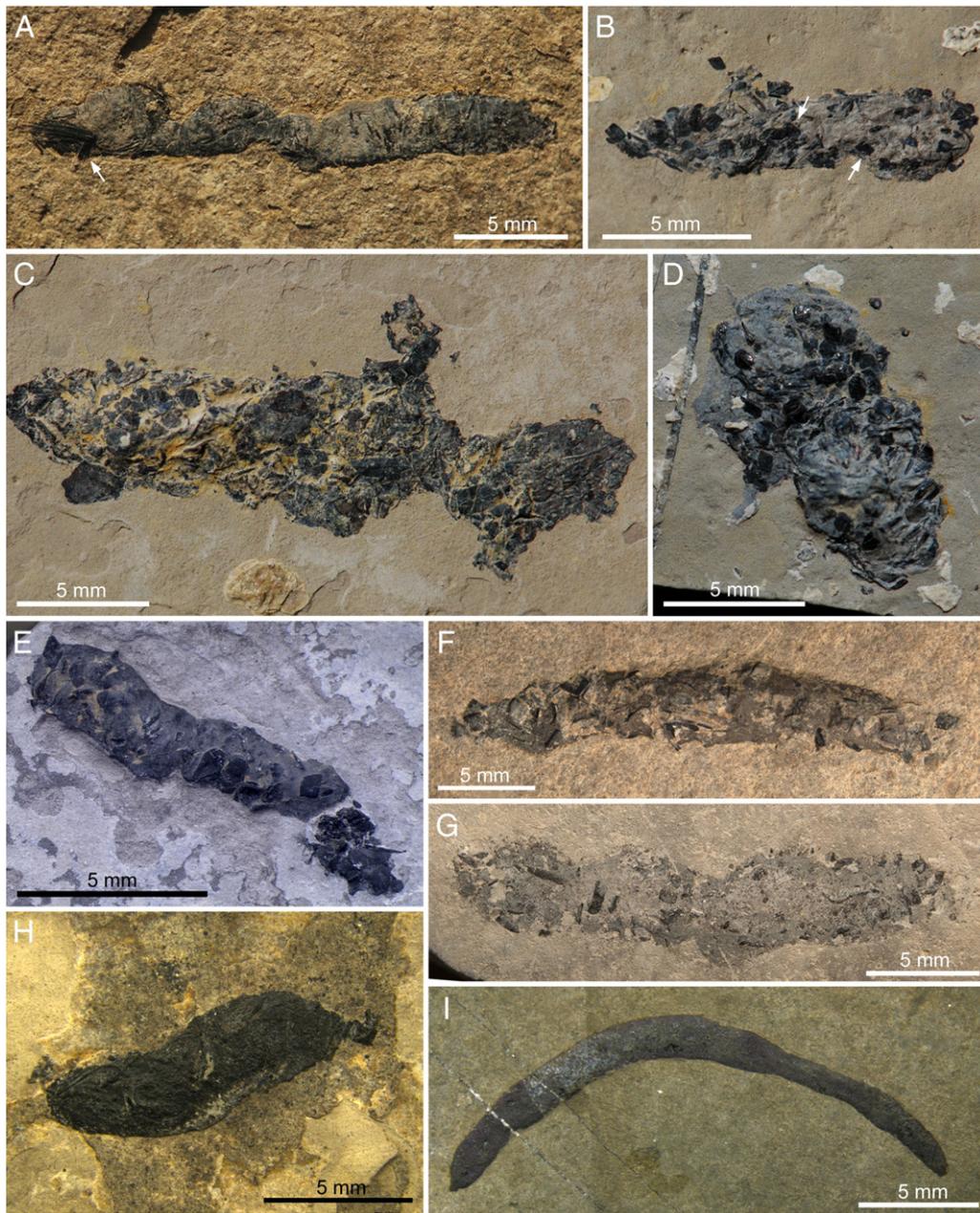


Fig. 4. Selected examples of Morphotype B coprolites from the Middle Triassic of Luoping, Yunnan, SW China. A, E and G belong to sub-morphotype B1; B–D belong to sub-morphotype B2 while H–I are examples of sub-morphotype B3. A, Long cylindrical coprolite with similarly rounded ends (LPC026). Note the pectoral fin preserved as an inclusion (arrow). B, Short, anispolar coprolite with abundant fish scales within coprolite matrix (LPC027). C, Long, isopolar coprolite with quite irregular boundary (LPC028). Note abundant food inclusions occurring in coprolite matrix. D, Short, isopolar coprolite with abundant fish scales in matrix (LPI61602). E, Cylindrical-shaped coprolite with one larger, rounded end and a smaller, tapering end (LPI61753). F, Cylindrical coprolite with uneven outer surface. Note that abundant food inclusions are pronounced in Specimen (LPI61628). G, Cylindrical coprolite exhibiting a pinch-and-swell morphology (LPI61635). H, Dark anispolar coprolite with a smooth boundary. I, Long, cylindrical coprolite with smooth surface (LPC010).

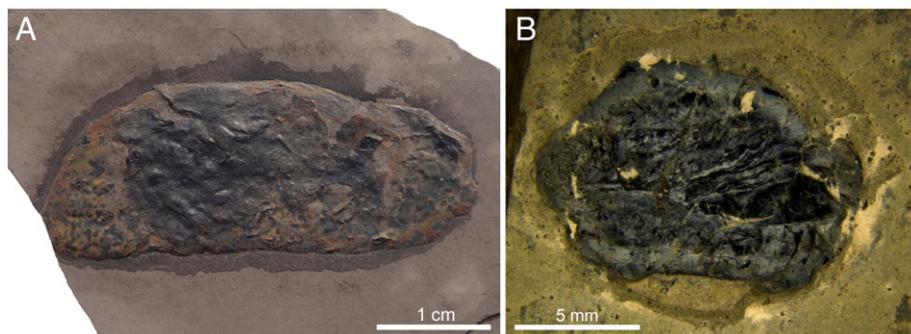


Fig. 5. Representative samples of Morphotype C coprolites from the Middle Triassic of Luoping, Yunnan, SW China. A, Discoid-shaped coprolite with a flattened morphology (LPC017) and abundant, coarse-grained food remnants within coprolite matrix. B, Another smaller discoidal coprolite preserved in muddy limestone (LPC016).

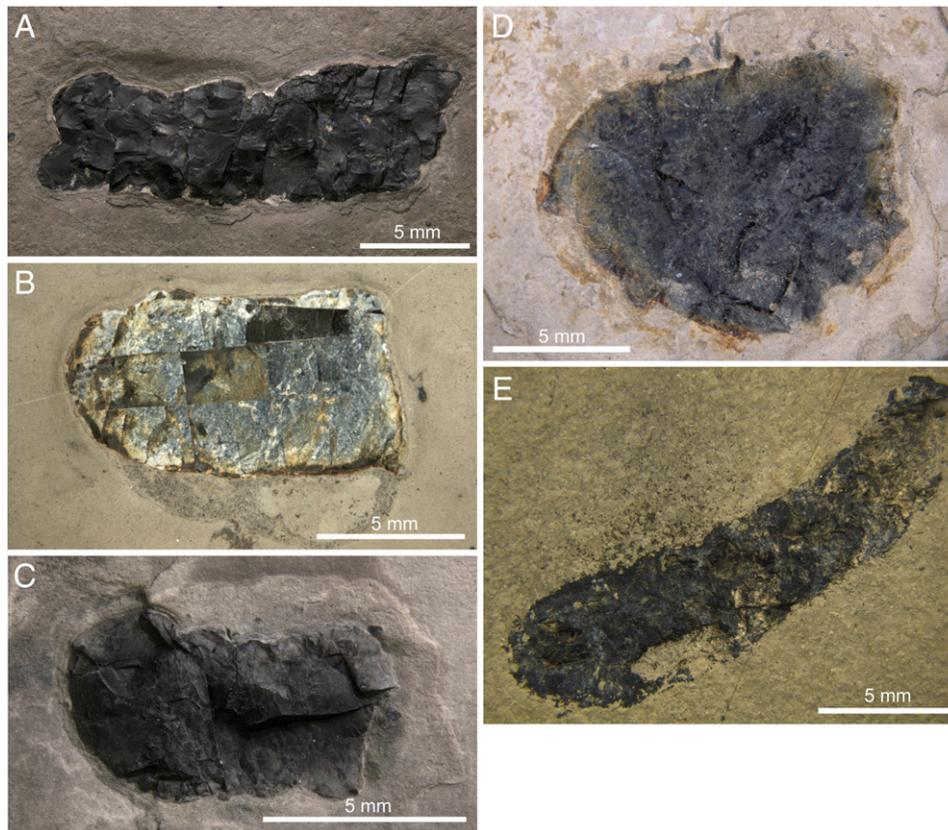


Fig. 6. Selected examples of Morphotype D coprolites from the Middle Triassic of Luoping, Yunnan, SW China. A, Segmented coprolite with a bilobate end (left) and an indented end (right), LPC012. B–C, Segmented scats with a rounded left end and indented right end (C, LPC029). Note the homogenous texture and cleavage within each specimen. D, Dark coloured segments with rounded end on the left (LPC020). E, Rod-like segments with indented end on top right (LPC004).

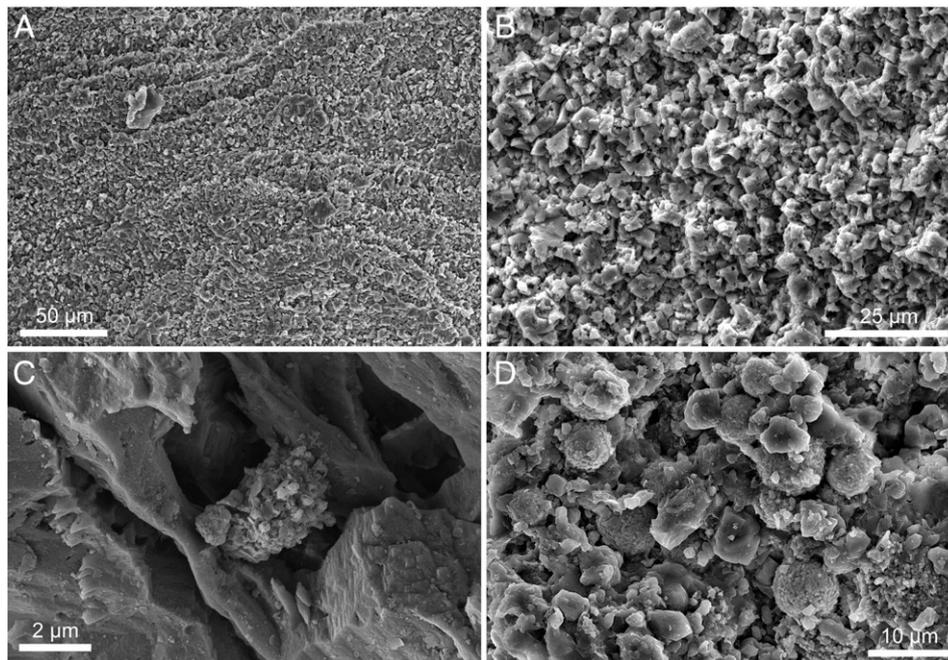


Fig. 7. SEM images showing the internal structure of Morphotype A coprolite and putative organic matter remnant, from the Middle Triassic of Luoping, Yunnan, SW China. A, Close-up of internal structure of coprolite shown in Fig. 3A (LPC019). Note the laminar structures composed of homogeneous calcium carbonate. B, Internal structure of Morphotype A coprolite shown in in Fig. 3D (LPC014). The homogeneously mineralized texture is composed of calcium carbonate. C, putative organic carbon particles found in Morphotype A coprolite shown in Fig. 3C. D, Copious pyrite framboids preserved in surrounding rock matrix of specimen LPC019 (Fig. 3A).

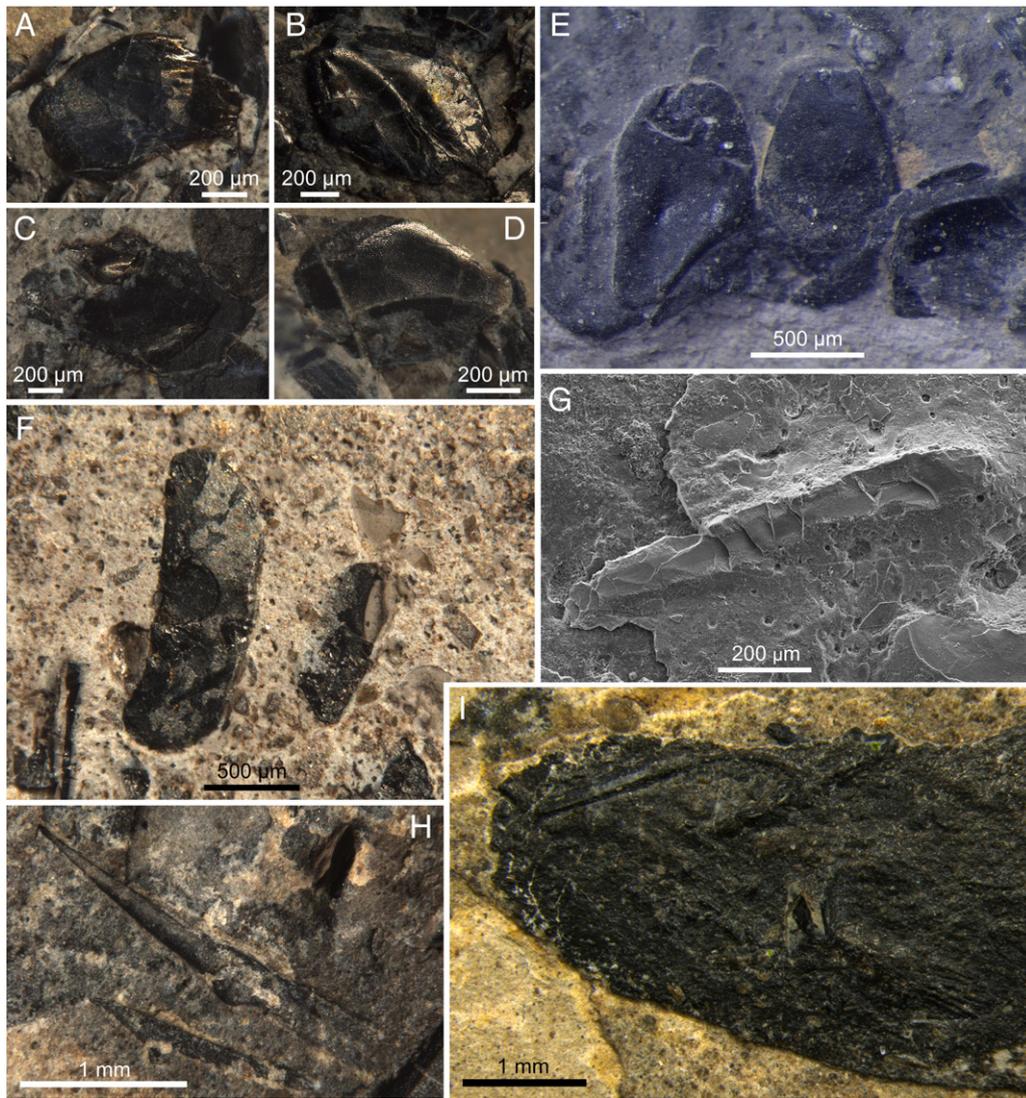


Fig. 8. Various food remains within Morphotype B coprolites, from the Middle Triassic of Luoping, Yunnan, SW China. A–D, Fish scales of various shapes (LPI61602). E, Fish scales from LPI61753 (Fig. 4E). F, Bone fragments within coprolite matrix of sample LPI61635 (Fig. 4F). G, SEM images showing another bone fragment within LPI61635. H, Close-up of indeterminate bone fragment from Fig. 4F (LPI61628). I, Close-up of bone fragment (upper left) and possible pectoral fin (lower right) within coprolite matrix of Fig. 4H (LPC001).

making the outer surface very irregular. The boundaries between segmented scats and the matrix are distinctly smooth (Fig. 6B, D–E) to sinuous (Fig. 6A, C). Inclusions are very rarely observed under the binocular microscope, with only a few tiny fragments of unknown origin found in Specimen SSK051 (Fig. 6B).

4.2. Inclusions

The abundance, morphological type, and completeness of food remains are different among the various coprolite morphotypes. Further, the type and abundance of food inclusions may be different even in coprolites of the same morphotype, which situation is quite similar to those revealed by the Late Triassic coprolite from Poland (Zatoń et al., 2015). Morphotype A coprolites record very few food remains (Fig. 7A–C). SEM imaging shows that the matrix of the coprolite is a homogeneously well-mineralized entity. A few coccoidal spheroids were observed in the pore areas between minerals. The host rocks (muddy limestones) of Morphotype 1 coprolites yield abundant pyrite framboids (Fig. 7D).

By contrast, food inclusions are abundant in the matrix of Morphotype B coprolites, including complete to slightly damaged fish

scales (Fig. 8A–E), bone materials, broken pectoral fins (Fig. 8I), and teeth (Figs. 4I, 9A–C). These food remnants were variously preserved among various specimens. For example, some specimens have only fish scales as the most abundant inclusions (Fig. 4B, D); others possess some bone materials but no identified fish scales within the coprolite matrix (Figs. 4H, 8I). In addition, some specimens bearing both fish scale and bone materials co-occur together (Fig. 4E–G). The most remarkable specimen is LPC010 (Fig. 4I), in which abundant teeth are densely arranged within the coprolite. The complete morphology of teeth is also preserved, showing the tooth root and cusp above it (Fig. 9A–C). These two parts are highlighted further by their contrasting elemental compositions under EDS analysis, with the cusp containing a high concentration of Ca and F, while the tooth root is composed of C, S, P, and Ca (Fig. 9D–E). No other food remains were found in association with the teeth in specimen LPC010 (Fig. 4I).

Food remains were also observed in Morphotype C coprolites, although they are less commonly or well preserved when compared with most of the Morphotype B samples. Food remains include large bone materials and fish scales (Fig. 10A–B). It is difficult to find any food inclusions in the Morphotype D coprolites with the aid of a binocular microscope. However, some fragmented bone materials

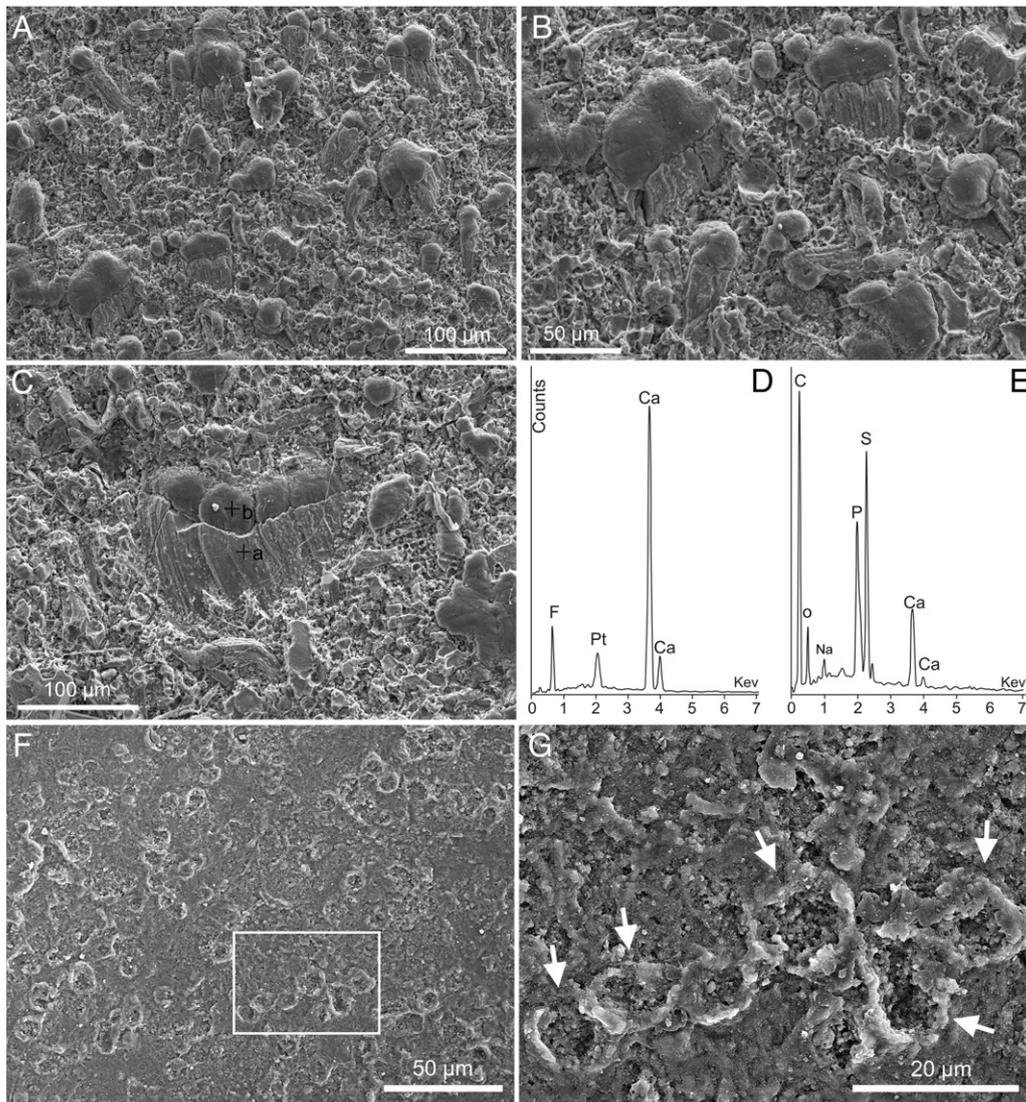


Fig. 9. SEM images showing well preserved teeth within a Morphotype B coprolite (No. LPC010; Fig. 4I), and abundant coccoidal structures. A, Teeth of various sizes densely occurring within coprolite matrix. B, Close-up of lower left areas in A showing details of the teeth. C, Large tooth within coprolite matrix. D and E are EDS results showing the different element composition of the tooth cusp and root (labelled, respectively 'a' and 'b' in C). F, densely packed coccoidal spheres with consistent diameters. G, Close-up of boxed area in F showing the details of spheres (white arrows). Note the spheres have thin-rimmed wall structures with hollowed center and they attached to one another.

were also recognized in thin sections of Morphotype D coprolites (Fig. 10C–F).

4.3. Elemental compositions

Selected samples of the four coprolite morphotypes were examined for the elemental composition of both the coprolite matrix and the host rocks (Fig. 11). The coprolite matrices of Morphotypes B to D show similar elemental compositions to each other, all of which are composed of Ca, P, C and O, suggesting a mineral form of calcium phosphate (Fig. 11). The Morphotype A coprolite has an elemental composition pointing to a mineral form of calcium carbonate. Coprolite-bearing rocks (sediment matrices) of these four morphotypes demonstrate more or less similar distribution patterns of their elemental compositions. EDS results indicate that all host rocks contain comparable elements, Ca, Si, O, C, and Mg, Al, K, suggesting that they are a mixture of Mg-bearing calcite and aluminosilicates. Food inclusions of the coprolite Morphotypes B to D are also composed of calcium phosphate, except for abundant teeth within specimen LPC010 (Fig. 9A–E).

5. Discussion

5.1. Coprolite producers

These four types of coprolites might represent consumers of different trophic levels, ranging from invertebrate to vertebrates in view of their shape, size, elemental composition, and the presence/absence of inclusions.

When compared with Morphotype D, Morphotypes A–C coprolites could be preserved in situ and they show no evidence of segmentation or breakage. Combined with their unique food inclusions, information on their size and shape therefore is very useful in reconstructing potential producers (Northwood 2005). The morphological characteristics of coprolites produced by different groups of animals in aquatic habitats have been examined frequently (Kraeuter and Haven, 1970; McAllister, 1985; Schmitz and Binda, 1991; Lamboy et al., 1994; Northwood, 2005; Milàn et al., 2012a; Eriksson et al., 2011; Chen et al., 2014; Kietzmann and Palma 2014). For example, faeces produced by marine invertebrates were relatively small, with a maximum length commonly <5 mm (Kraeuter and Haven, 1970; Arakawa, 1971;

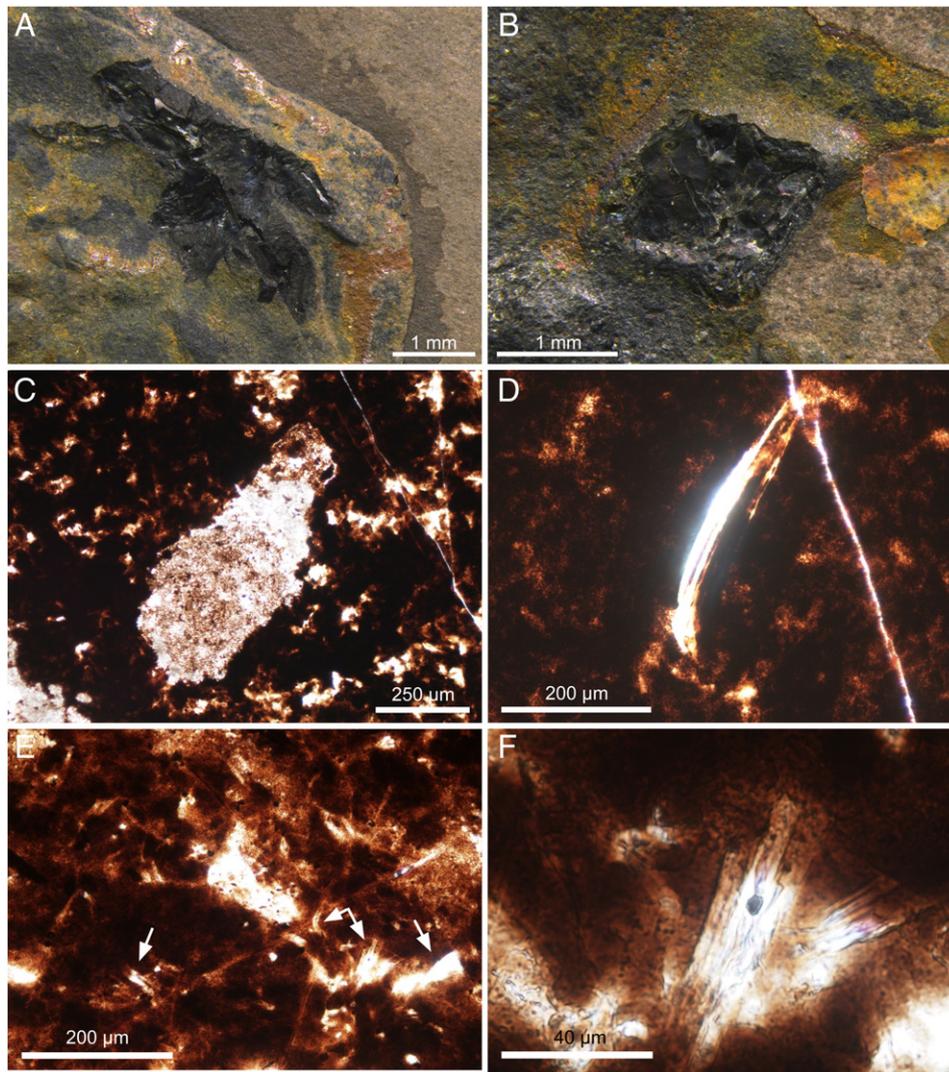


Fig. 10. Photomicrographs showing the food inclusions within Morphotypes C–D coprolites. A, Fragmented bone within coprolite matrix (No. LPC017; Fig. 5A). B, Fish scale (No. LPC017; Fig. 5A). C, Indeterminate food remains. D, Bone/fish tooth? within coprolite matrix (No. LPC004; Fig. 6E). E, fragmented bone materials (arrowed, No. LPC004); F, Close-up of lower right showing the details of bone fragments. Note the typical fibrous texture of bones.

Northwood, 2005; Chen et al., 2014; Kietzmann and Palma, 2014). Coprolites produced by various taxa of vertebrate animals usually possess varied outlines. Fish scats usually exhibit a spiral morphology at one end (heteropolar) or extending to both ends (amphipolar, Schmitz and Binda, 1991; Eriksson et al., 2011) produced by the spiral intestinal valve within some fishes. Shark faeces show heteropolar, spiral morphologies due to their complex valves, while bony fish faeces are usually amphipolarly spiral (McAllister, 1985; Diedrich and Felker, 2012; Dentzien-Dias et al., 2013). In comparison, turtle coprolites are cylindrical, tapering masses (Souto, 2008).

5.1.1. Morphotype A coprolite producer

Morphotype A coprolites are interpreted as the product of deposit-feeding invertebrates. Evidence for this is their general bead- to ribbon-like morphology and the rarity of inclusions (Krauter and Haven, 1970; Arakawa, 1971). In particular, when they are well-preserved, a mid-ridge and two lateral ridges are seen on the sub-morphotype A2 specimens. This feature, together with their universally small diameter (~0.5 mm), resembles the scat produced by isopods (Krauter and Haven, 1970). Morphotype A1 is also unlikely to be produced by a crustacean because scats excreted by the latter are

characterized by pellet to regular rod-shaped morphology with longitudinal canals (Becker and Chamberlain, 2006). The homogeneously mineralized texture of the coprolite matrix suggests that the faeces-producing animals might have fed on organic matter in sediment, defecating only homogeneously organic-poor masses as faeces. In addition, the elemental compositions show that the coprolite matrix of Morphotype A is calcium carbonate, which is also an important component of the host rocks, except for aluminosilicates. Such elemental compositions support the inference that some invertebrate deposit feeders produced these faeces. In addition, abundant tiny pyrite framboids detected from the host rocks of morphotype A coprolites also indicate a possible anoxic environment, which not only may be beneficial to the exceptional preservation of coprolites but also was conducive for sulfate reductive bacteria or other unknown microbes to proliferate (Rickard, 2012; Wacey et al., 2015). The latter could be excellent food resources for consumption of deposit feeding animals that produced morphotype 1 coprolites.

5.1.2. Morphotype B coprolite producer

The presence of abundant food remnants characterizes Morphotype B coprolites (Figs. 4, 8A–I, 9A–C). The existence of abundant, variously

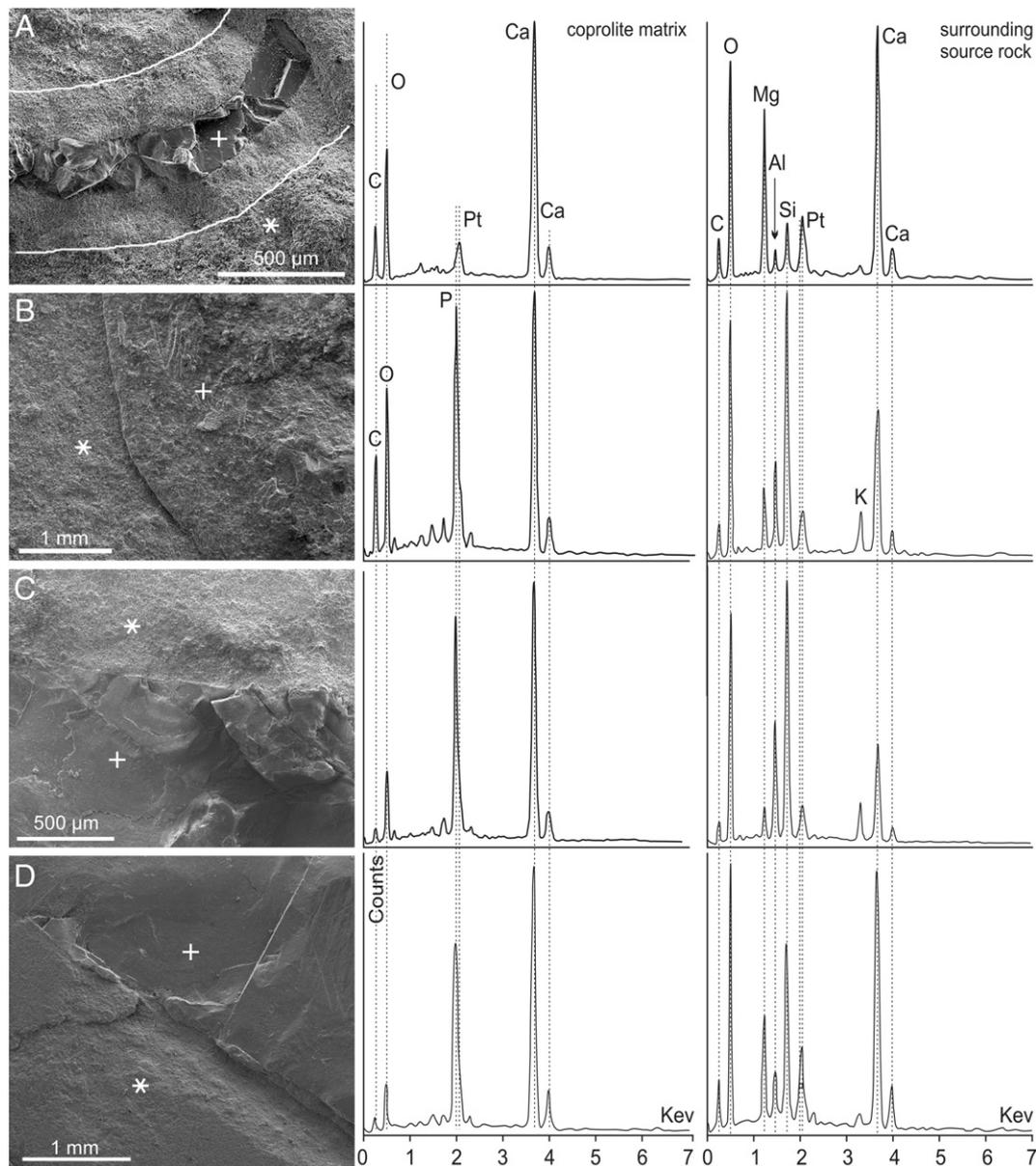


Fig. 11. SEM images showing the boundaries between the coprolite and the surrounding matrix for the four coprolite morphotypes, with relative EDS results presented on the right side. Note images A to D represent coprolite morphotypes A–D, respectively. The white cross in each SEM image represents the spot chosen from the coprolite and the white star represents the spot chosen from the rock matrix for EDS analysis. The dashed line denotes the peak location of each element. The peak of Pt is from the sample coating before SEM imaging. Note the mild deviation between P and Pt.

shaped fish scales and some fragmented bone materials suggests that Morphotype B coprolites were likely generated by carnivorous predators, either predatory marine fishes or reptiles. In general, bone material is usually more difficult to digest than fish scales (Northwood, 2005). Abundant fish scales in some Morphotype B coprolites suggest probably a short retention time of food within the intestine. Alternatively, Eriksson et al., (2011) argued that coprolites bearing abundant fish scales and rare bone materials might also be produced by scavengers. However, indented boundary features were found in some fish scales (Fig. 8A–D), suggesting that *Sangiorgioichthys* might have produced this type of coprolites. *Sangiorgioichthys* is one of the most common fish taxa among the Luoping Biota (Benton et al., 2013), and is characterized by its small size and strong, sharp teeth, suggestive of a small carnivorous predator. It should be noted that fish scats, particularly those produced by all agnathans, placoderms, dipnoans, actinistians, and chondrichthyans, are characterized by spirals (McAllister, 1987).

This is because all these taxa have valvular intestines, giving rise to the spiral-shaped faeces. While most of the fossil fish taxa of the Luoping biota belong to teleosts (e.g. Actinopterygian, Sarcopterygian), which do not exhibit such valvular intestines (McAllister, 1987). Thus, it is not uncommon that fish coprolites in Luoping do not preserve spiral-shaped morphology.

In addition, differing from most coprolites that only contain fish scales and bone fragments, but lack fish or reptile teeth, one Morphotype B (sub-morphotype B2) coprolite specimen is also of particular interest, and characterized by abundant tooth materials densely scattered in the scat without other food remains (Fig. 9A–C). Since animal teeth are the most difficult to be digested among all food inclusions (i.e. fish scales and bones; Northwood, 2005), the tooth-bearing scats therefore were likely produced by some rather large carnivorous fish/reptile that prey on small carnivorous fishes (i.e. saurichthyids). Such carnivorous fish/reptiles could also have developed an advanced

digestive system capable of absorbing and dissolving bone materials, but leaving only the teeth of the prey in the intestine. They were therefore likely positioned at the top level of the trophic pyramid.

In contrast, other specimens of Morphotype B coprolites containing fish scales or bones, but lacking teeth, are interpreted as products of some predators that may have preyed on herbivorous fishes. These faeces-producing predators therefore probably had a slightly lower trophic level than the producers of the tooth-bearing coprolites.

Accordingly, the producers of Morphotype B coprolites should have been predators of various trophic levels that preyed on herbivorous fishes, small carnivorous fishes, and even large carnivorous fishes. Given the advanced digestive system, some coprolite producers are inferred to have been top predators (large carnivorous fish/reptiles) of the marine ecosystem. If taking the various morphological features of sub-morphotype B1 to B3 into consideration, Morphotype B coprolites might represent a more diverse assemblage of predators.

5.1.3. Morphotypes C and D coprolite producers

Morphotype C coprolites are relatively larger than other types (e.g. Morphotype B) of coprolites (Fig. 5A). Fragmented fish bones and scales were also found within such discoidal faeces. These coprolites were probably produced by some larger carnivorous fishes or reptiles as the total mass of faeces produced in a single defecation event is greater among animal of larger size (Eriksson et al., 2011). For the larger flattened coprolite (e.g. Fig. 5A), its ovoid shape and angular bones contained within might suggest the producer was an ichthyosaur, as similar flattened ovoid coprolites that were likely produced by an ichthyosaur have also been reported from the Lower Liassic of Lyme Regis in UK (Hunt et al., 2012b).

Morphotype D coprolites are preserved as segmented scats. Fragmented bones were also observed in these faeces in thin section (Fig. 10C–F). Thulborn, (1991) interpreted the segmentation as originating from the squeezing of faecal pellets within the animal's intestine. If so, the segmented scats described here may represent part of a large faecal mass. The segmentation pattern may also reflect the particular digestive and defecation style of animals. Morphotype D coprolites therefore were likely produced by some possible piscivores, as suggested by Thulborn, (1991). These faeces-producers were also likely high-trophic predators in the food web.

5.2. Taphonomy and palaeoecology of the Luoping coprolites

In general, both rapid burial and subsequent rapid lithification are crucial for the exceptional preservation of coprolites (Eriksson et al., 2011). These two factors must be invoked to explain the excellent preservation of the Luoping coprolites. Previously, the proliferation of microbial mats had been considered to play a crucial role in the preservation of the exceptionally preserved invertebrate and vertebrate animals of the Luoping biota (Hu et al., 2011; Luo et al., 2013). After an animal's death, microbial mats or their biofilms may have enveloped the carcass and prevented further decay and scavenging, and disarticulation by physical turbulence (Luo et al., 2013). Such a process might also have aided the exceptional preservation and rapid lithification of coprolites and their food remains. The differing mineralization modes seen in Morphotypes A and B to D might reflect different diets of the faeces-making animals, because otherwise the coprolites were all being lithified in presumably the same physical seabed and burial conditions. As discussed above, coprolite Morphotypes B to D could have been produced by carnivorous fishes/reptiles, and their scats were preserved as calcium phosphate. Bones and flesh can provide substantial sources of phosphorus and calcium for their enrichment in these elements (Hollocher et al., 2010). After burial, the phosphorus is released into sedimentary pore waters by microbial decay of organic matter. Under such circumstances, phosphorus is incorporated into the coprolite through direct precipitation or by replacement of carbonate with apatite (Jarvis, 1980; Berndmeyer et al., 2012; Hiatt et al., 2015). Moreover,

phosphatic coprolites, characteristic of fossilized faeces of carnivorous predators, may also be phosphatized during early diagenesis due to microbes residing within the faeces. Evidence supporting this is the occurrence of abundant coccoidal structures (Fig. 9F–D) in several coprolite samples of Morphotypes B and D. These hollowed spheres have consistent diameters, and are characterized by walled structures, which are similar to coccoidal structures observed from phosphatized coprolites of the Late Triassic and Paleocene, respectively (Cosmidis et al., 2013; Zatoń et al., 2015). The latter two were interpreted as fossilized bacteria inducing the early precipitation and mineralization of phosphatized coprolites.

5.3. New evidence for food web network of the Luoping biota

Palaeoecological information on body fossil communities is crucial in reconstructing how marine ecosystems restored themselves following the PTME (Chen and Benton, 2012). Increasing evidence also shows that coprolites can provide significant information on the diet, predator-prey interactions, and food webs among various animals, and thus can serve as an important tool for probing the functions and structures of deep time ecosystems.

Coprolites are commonly present in the Lower Triassic fossil record worldwide (Northwood, 2005; Nakajima and Izumi, 2014; Brachaniec et al., 2015; Hao et al., 2015). Northwood, (2005) described two coprolite assemblages from the Lower Triassic terrestrial successions of Queensland, and found that some coprolites could have been produced by basal archosauromorphs and fishes.

Increasing numbers of coprolites have been reported from marine strata, and they provide substantial information on diet and predatory behaviours among arthropods, and carnivorous fishes and reptiles (Nakajima and Izumi, 2014; Brachaniec et al., 2015; Hao et al., 2015). Coprolites from the *Myophoria* Beds of the Lower Triassic (Olenekian) of Poland represent the earliest record of animal scats after the PTME (Brachaniec et al., 2015). These Polish coprolites were categorized into four types, which were believed to have been produced by nothosaurids, durophagous sauropterygian reptiles, and actinopterygian fishes. The authors further suggested that the Mesozoic Marine Revolution might have commenced in the late Early Triassic (Brachaniec et al., 2015), although no evidence shows the revolutionary escalation between predators and preys (the focus of Mesozoic Marine Revolution, sensu Vermeij, 1977). Similarly, the late Olenekian coprolites from the Lower Triassic Osawa Formation (upper Spathian) of Japan were also interpreted as the products of carnivorous fishes and marine reptiles (Nakajima and Izumi, 2014). Spathian (late Olenekian) coprolite materials have also been reported from the Nanlinghu Formation (Spathian) in Chaohu, South China, and the food inclusions of the coprolite matrix include conodont skeletons (Hao et al., 2015). Similar conodont skeleton inclusions have also been found in coprolites from a Late Devonian pelagic environment, and these coprolites were interpreted as products of carnivorous fishes (Zatoń and Rakociński, 2014). All information deriving from coprolites indicates that predatory animals of higher trophic levels might have been very active in a wide marine realm during the late Early Triassic, although body fossils of these predators are rarely preserved.

Of the newly obtained coprolites from the Luoping biota, Morphotypes B to D were likely produced by carnivorous fishes and reptiles. These carnivores were probably predators at various trophic levels in the food web. Some predators may have preyed on either herbivorous fishes or other carnivorous fishes (i.e., *Sangiorgioichthys* or saurichthyids; Figs. 8A–D, 9A–C). These predators therefore can be categorized as secondary and tertiary consumers (definition of Davenport and Bax, 2002) of a complete ecosystem, which is consistent with the presence of gigantic apex predators in the Luoping biota (Liu et al., 2014). In addition, marine reptiles of major clades discovered include ichthyosaurs, protosaurs, and archosauromorphs, with their species numbers comparable to those of marine reptiles from the younger

Panxian, Xingyi, and Guanling Biotas (Benton et al., 2013), suggesting a regaining of complex ecosystems in Luoping (Liu et al., 2014). The relatively rare occurrence of fossil marine reptiles in Luoping might reflect their correspondingly higher trophic level in the food web pyramid. Accordingly, the producers of the Luoping coprolites include herbivorous fishes (or other deposit feeding animals), carnivorous fishes, and large carnivorous fishes/reptiles preying on carnivorous fishes, all of which are components of a complicated, high trophic level food web.

Interestingly, other invertebrate fragments, such as bivalves, gastropods, and crinoids that are commonly found in Olenekian coprolites of Poland (Brachanec et al., 2015) are absent among the food remnants within the coprolite matrix in Luoping specimens. This is probably because vertebrates, especially fishes, had diversified greatly in Luoping during the early Middle Triassic, and they provided sufficient food resources for carnivores of various taxonomic groups. Such a diversification of fishes is strengthened by the extremely abundant body fossils documented from Luoping (Wu et al., 2009, 2011; Wen et al., 2012, 2013; Benton et al., 2013; Xu et al., 2014). In addition, some carnivorous animals seem to have developed a very strong digestive system, enabling them to dissolve bone materials and only leave teeth of those prey animals as inclusions in their scats (Figs. 6I, 9A–C). Moreover, some fishes consume faeces produced by high-trophic-level predators. For instance, extant dolphins may produce cloud-like scats that are consumed by other fishes in modern-day oceans (e.g. Sazima et al., 2003). Their coprolites therefore are unlikely to be preserved as fossilized faeces. Alternatively, it is also probable that the absence of coprolites from top predators (i.e. *Nothosaurus zhangii*) at Luoping is simply because of their non-preservation.

In comparison, most of the Early Triassic coprolite-producers could be secondary consumers in the ecosystem in view of food remains as inclusions (Brachanec et al., 2015; Nakajima and Izumi, 2014). Although some fragmented skeletons preserved in the Olenekian coprolites of Poland were suspected to have been derived from nothosaurids, direct evidence supporting such an inference is absent (Brachanec et al., 2015). Given most food inclusions are invertebrate skeletal fragments and a few vertebrate bones of uncertain origin, these Polish coprolites therefore were likely produced by some carnivorous reptiles and durophagous reptiles/fishes that were secondary consumers. The same is also true for the coprolites recorded in the late Spathian Osawa Formation, Japan and the Spathian Nanlinghu Formation, South China. They represent one type of coprolites that contain very few fragmented skeletons in inclusions (Nakajima and Izumi, 2014; Hao et al., 2015). These Spathian coprolites therefore could be the products of secondary consumers that preyed on the microbe-feeding primary consumers.

Accordingly, both Japanese and South Chinese Spathian coprolite materials are very rare, and their inclusions contain one type of food remains, representing one type of predator-prey relationship. These Spathian coprolites were likely produced by secondary consumers. The Polish Olenekian coprolites contain relatively abundant skeletal fragments including some vertebrate bones, and thus represent more diverse prey in the food chains, which is also reinforced by the presence of multi-trophic ecosystem indicated by coeval marine vertebrates (Scheyer et al., 2014). The food remains of the Polish coprolites, however, are dominated by invertebrate shell fragments with minor constituents of vertebrate bones of uncertain origin. These prey therefore embrace relatively lower trophic levels than the Luoping coprolites. Both coprolite information and body fossil characteristics indicate that the Luoping coprolite-producers may have been more diverse and have larger body sizes and higher trophic levels than the Polish coprolite-makers. It is noteworthy that, for a better documentation and comparison of all these Triassic coprolite studies, the different taphonomic factors should also be considered.

To sum up, clearly, the producers of the Luoping coprolites were more diverse than the Early Triassic coprolite-makers. They embrace much more diverse predatory behaviours than these Early Triassic

coprolite-makers, and thus constructed a more complicated food web. Moreover, the increase of food web complexity enabled different predators to obtain enough food resources, thus shortening the retention time of food in animal's intestines and easing the preservation of food skeletons, suggesting different efficiency in digestive systems among various carnivores. The same phenomena are also observed in Late Triassic (Laojumpon et al., 2012) and Late Cretaceous coprolites (Milàn et al., 2012b). The Luoping coprolites and their food remains therefore strengthen the previous view that high-trophic-level, complex ecosystems were not constructed until the early Middle Triassic, as indicated by the Luoping biota (Hu et al., 2011; Chen and Benton, 2012; Liu et al., 2014).

6. Conclusions

Abundant coprolites are documented from the Luoping biota (Anisian, Middle, Triassic, Yunnan, southwest China). They are categorized into four morphotypes. Food inclusions, and elemental compositions of coprolites and the host rocks were also examined. The combination of all information indicates that Morphotype A coprolites could have been produced by invertebrates, whereas coprolites of Morphotypes B to D were likely generated by carnivorous fishes and reptiles. When compared with Early Triassic examples, the Luoping coprolites indicate much more diverse producers. Diversified predator-prey interactions revealed from the Luoping coprolites strengthen the suggestion that a complete trophic pyramid had been established when the Luoping biota proliferated in the early Middle Triassic.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.06.001>.

References

- Arakawa, K.Y., 1971. Studies on the faecal pellets of marine invertebrates (excluding molluscs) I. Publ. Seto Mar. Biol. Lab. 20, 231–241.
- Bai, J.K., Yin, F.G., Zhang, Q.Y., 2011. Microfacies and enrichment pattern of fossils in the fossiliferous beds of Luoping biota, Yunnan Province. Geol. China 38, 393–402 (in Chinese with English abstract).
- Bajdek, P., Owoc, K., Niedzwiedzki, G., 2014. Putative dicynodont coprolites from the upper Triassic of Poland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 411, 1–17.
- Becker, M.A., Chamberlain, J.C., 2006. Anomuran microcoprolites from the lowermost Navesink formation (Maastrichtian), Monmouth County, New Jersey. Ichnos 13, 1–9.
- Benton, M., Zhang, Q.Y., Hu, S.X., Chen, Z.Q., Wen, W., Liu, J., Huang, J.Y., Zhou, C.Y., Xie, T., Tong, J.N., Choo, B., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. Earth-Sci. Rev. 125, 199–243.
- Berndmeyer, C., Birgel, D., Brunner, B., Wehrmann, L.M., Jöns, N., Bach, W., Arning, E.T., Föllmi, K.B., Peckmann, J., 2012. The influence of bacterial activity on phosphorite formation in the Miocene Monterey Formation, California. Palaeogeogr. Palaeoclimatol. Palaeoecol. 317–318, 171–181.

- Brachanic, T., Niedzwiedzki, R., Surmik, D., Krzykowski, T., Szopa, K., Gorzelak, P., Salamon, M.A., 2015. Coprolites of marine vertebrate predators from the Lower Triassic of southern Poland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 435, 118–126.
- Chen, Z.Q., Benton, M.J., 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nat. Geosci.* 5, 375–383.
- Chen, C., Pratt, B.R., Zhang, X.G., 2014. Phosphatized coprolites from the middle Cambrian (stage 5) Duyun fauna of China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 410, 104–112.
- Chin, K., Gill, B.D., 1996. Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *PALAIOS* 11, 280–285.
- Cosmidis, J., Benzerara, K., Gheerbrant, E., Estève, I., Bouya, B., Amaghzar, M., 2013. Nanometer-scale characterization of exceptionally preserved bacterial fossils in Paleocene phosphorites from Ouled Abdoun (Morocco). *Geobiology* 11, 139–153.
- Davenport, S.R., Bax, N.J., 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. *Can. J. Fish. Aquat. Sci.* 59, 514–530.
- Dentzien-Dias Jr., P.C., de Figueiredo, A.E.Q., Pacheco, A.C.L., Horn, B.L.D., Schultz, C.L., 2013. Tapeworm eggs in a 270 million-year-old shark coprolite. *PLoS One* 8, e55007.
- Diedrich, C.G., Felker, H., 2012. Middle Eocene shark coprolites from shallow marine and deltaic coasts of the pre-north sea basin in central Europe. In: Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A. (Eds.), *Vertebrate Coprolites*. New Mexico Museum of Natural History and Science, Bulletin Vol. 57, pp. 311–318.
- Enos, P., Lehmann, D.J., Wei, J.Y., Yu, Y.Y., Xiao, J.F., Chaikin, D.H., Minzoni, M., Berry, A.K., Montgomery, P., 2006. Triassic evolution of the Yangtze platform in Guizhou Province, People's Republic of China. *Geol. Soc. Am. Spec. Pap.* 417, 1–105.
- Eriksson, M.E., Terfelt, F., 2007. Anomalous faeces and ancient faeces in the latest Middle Cambrian of Sweden. *Lethaia* 40, 69–84.
- Eriksson, M.E., Lindgren, J., Chin, K., Mansby, U., 2011. Coprolite morphotypes from the Upper Cretaceous of Sweden: novel views on an ancient ecosystem and implications for coprolite taphonomy. *Lethaia* 44, 455–468.
- Erwin, D.H., 2006. *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago*. Princeton University Press, Princeton, pp. 1–296.
- Feng, Z.Z., Bao, Z.D., Li, S.W., 1997. Lithofacies Paleogeography of Middle and Lower Triassic of South China. Petroleum Industry Press, Beijing, pp. 1–222 (in Chinese with English abstract).
- Hao, T.Q., Ji, C., Sun, Z.Y., Jiang, D.Y., Andrea, T., 2015. The Early Triassic conodonts in coprolites from Chaohu, Anhui. *J. Stratigr.* 39, 188–196 (in Chinese with English abstract).
- Hiatt, E.E., Pufahl, P.K., Edwards, C.T., 2015. Sedimentary phosphate and associated fossil bacteria in a Paleoproterozoic tidal flat in the 1.85 Ga Michigan formation, Michigan, USA. *Sediment. Geol.* 319, 24–39.
- Hollocher, K.T., Hollocher, T.C., Rigby, J.K., 2010. A phosphatic coprolite lacking diagenetic permineralization from the upper Cretaceous Hell Creek formation, Northeastern Montana: importance of dietary calcium phosphate in preservation. *PALAIOS* 2010, 132–140.
- Hu, S.L., Li, Y.J., Dai, M., Pu, Z.P., 1996. The laser mass-spectrometer ^{40}Ar – ^{39}Ar age of green pisolites of Guizhou Province. *Acta Petrol. Sin.* 12, 409–415 (in Chinese).
- Hu, S.X., Zhang, Q.Y., Chen, Z.Q., Zhou, C.Y., Lv, T., Xie, T., Wen, W., Huang, J.Y., Benton, M.J., 2011. The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proc. R. Soc. B* 278, 2274–2283.
- Huang, J.Y., Zhang, K.X., Zhang, Q.Y., Lv, T., Zhou, C.Y., Bai, J.K., 2009. Conodont stratigraphy and sedimentary environment of the Middle Triassic at Dawazi section of Luoping County, Yunnan Province, South China. *Acta Microbiol. Sin.* 26, 211–224 (in Chinese with English abstract).
- Huang, J.Y., Zhang, K.X., Zhang, Q.Y., Lv, T., Zhou, C.Y., Hu, S.X., 2011. Advance research of conodont fauna from Shangshikan and Daozi section in Luoping area, Yunnan Province. *Geol. Sci. Tech. Info.* 30, 1–17 (in Chinese).
- Hunt, A.P., Lucas, S.G., 2012a. Classification of vertebrate coprolites and related trace fossils. In: Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A. (Eds.), *Vertebrate Coprolites*. New Mexico Museum of Natural History and Science, Bulletin Vol. 57, pp. 137–146.
- Hunt, A.P., Chin, K., Lockley, M., 1994. The palaeobiology of vertebrate coprolites. In: Donovan, S. (Ed.), *The Palaeobiology of Trace Fossils*. John Wiley, London, pp. 221–240.
- Hunt, A.P., Lucas, S.G., Spielmann, J.A., Lerner, A.J., 2007. A review of vertebrate coprolites of the Triassic with description of new Mesozoic ichnotaxa. In: Lucas, S.G., Spielmann, J.A. (Eds.), *The Global Triassic*. New Mexico Museum of Natural History and Science, Bulletin Vol. 41, pp. 88–107.
- Hunt, A., Lucas, S.G., Spielmann, J.A., 2012b. New coprolite ichnotaxa from the Buckland collection at the Oxford University Museum of Natural History. In: Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A. (Eds.), *Vertebrate Coprolites*. New Mexico Museum of Natural History and Science, Bulletin Vol. 57, pp. 115–124.
- Jarvis, I., 1980. Geochemistry of phosphatic chalks and hardgrounds from the Santonian to early Campanian (Cretaceous) of northern France. *J. Geol. Soc. Lon* 137, 705–721.
- Khosla, A., Chin, K., Alimohammadin, H., Dutta, D., 2015. Ostracods, plant tissues, and other inclusions in coprolites from the Late Cretaceous Lameta Formation at Pisdura, India: taphonomic and palaeoecological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 418, 90–100.
- Kietzmann, D.A., Palma, R.M., 2014. Early Cretaceous crustacean microcoprolites from Siera de la Cara Cura, Neuquén Basin, Argentina: taphonomy, environmental distribution, and stratigraphic correlation. *Cretac. Res.* 49, 214–228.
- Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S.B., Fischer, W.W., 2007. Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* 256, 295–313.
- Krauter, J., Haven, D.S., 1970. Fecal pellets of common invertebrates of Lower York River and Lower Chesapeake Bay, Virginia. *Chesap. Sci.* 11, 159–173.
- Lamboy, M., Rao, V.P., Ahmed, E., Azzouzi, N., 1994. Nanostructure and significance of fish coprolites in phosphorites. *Mar. Geol.* 120, 373–383.
- Laojumpon, C., Matkhammee, T., Wathanapitaksakul, A., Suteethorn, V., Suteethorn, S., Lauprasert, K., Srisuk, P., Loeuff, J., 2012. Preliminary report on coprolites from the Late Triassic of Thailand. In: Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A. (Eds.), *Vertebrate Coprolites*. New Mexico Museum of Natural History and Science, Bulletin Vol. 57, pp. 207–213.
- Liu, J., Hu, S.X., Rieppel, O., Jiang, D.Y., Benton, M.J., Kelley, N.P., Aitchison, J.C., Zhou, C.Y., Wen, W., Huang, J.Y., Xie, T., Lv, T., 2014. A gigantic nothosaur (Reptilia: Sauropterygia) from the Middle Triassic of SW China and its implication for the Triassic biotic recovery. *Sci. Rep.* 4, e7142.
- Luo, M., Chen, Z.Q., Hu, S.X., Zhang, Q.Y., Benton, M.J., Zhou, C.Y., Wen, W., Huang, J.Y., 2013. Carbonate reticulated ridge structures from the lower Middle Triassic of the Luoping area, Yunnan, southwestern China: geobiological features and implications for exceptional preservation of the Luoping biota. *PALAIOS* 28, 541–551.
- Matsukawa, M., Saiki, K., Ito, M., Obata, I., Nichols, D.J., Lockley, M.G., Kukihiro, R., Shibata, K., 2006. Early Cretaceous terrestrial ecosystems in East Asia based on food-web and energy-flow models. *Cretac. Res.* 27, 285–307.
- Matsukawa, M., Shibata, K., Sato, K., Xu, X., Lockley, M.G., 2014. The Early Cretaceous terrestrial ecosystems of the Jehol biota based on food-web and energy-flow models. *Biol. J. Linn. Soc.* 113, 836–853.
- McAllister, J.A., 1985. Reevaluation of the formation of spiral coprolites. *University of Kansas. Paleontol. Contrib.* 144, 1–12.
- McAllister, J.A., 1987. Phylogenetic distribution and morphological reassessment of the intestines of fossil and modern fishes. *Zoologische Jahrbücher Abteilung für Anatomie und Ontogenie der Tiere* 115, 281–294.
- Milán, J., Rasmussen, B., Bonde, N., 2012a. Coprolites with prey remains and traces from coprophagous organisms from the Lower Cretaceous (Late Berriasian) Jydegaard Formation of Bornholm, Denmark. In: Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A. (Eds.), *Vertebrate Coprolites*. New Mexico Museum of Natural History and Science, Bulletin Vol. 57, pp. 235–240.
- Milán, J., Clemmensen, L.B., Adolfsen, J.S., Estrup, E.J., 2012b. A preliminary report on coprolites from the Late Triassic part of the Kap Stewart Formation, Jameson Land, East Greenland. In: Hunt, A.P., Milan, J., Lucas, S.G., Spielmann, J.A. (Eds.), *Vertebrate Coprolites*. New Mexico Museum of Natural History and Science, Bulletin Vol. 57, pp. 203–206.
- Nakajima, Y., Izumi, K., 2014. Coprolites from the upper Osawa Formation (upper Spathian), northeastern Japan: evidence for predation in a marine ecosystem 5 Myr after the end-Permian mass extinction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 414, 225–232.
- Northwood, C., 2005. Early Triassic coprolites from Australia and their palaeobiological significance. *Paleontol.* 48, 49–68.
- Richter, G., Wedmann, S., 2005. Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 223, 147–161.
- Rickard, D., 2012. *Sulfidic Sediments and Sedimentary Rocks*. Elsevier, Amsterdam 816 p.
- Sazima, I., Sazima, C., Silva-Jr, J.M., 2003. The cetacean offal connection: feces and vomits of spinner dolphins as a food source for reef fishes. *Bull. Mar. Sci.* 72, 151–160.
- Scheyer, T.M., Romano, C., Jenks, J., Bucher, H., 2014. Early Triassic marine biotic recovery: the predators' perspective. *PLoS One* 9, e88987.
- Schmitz, M., Binda, P.L., 1991. Coprolites from the Maastrichtian Whitemud Formation of southern Saskatchewan: morphological classification and interpretation on diagenesis. *Paleontol.* 2, 65, 199–211.
- Souto, P.R.F., 2008. *Coprolitos do Brasil—Principais ocorrências e estudo*. Publitz, Rio de Janeiro, pp. 1–93.
- Thulborn, A.T., 1991. Morphology, preservation and palaeobiological significance of dinosaur coprolites. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 83, 341–366.
- Vermeij, G.J., 1977. The Mesozoic marine evolution: evidence from snails, predators and grazers. *Paleobiology* 3, 245–258.
- Wacey, D., Kilburn, A.R., Saunders, M., Cliff, J.B., Kong, C., Liu, A.G., Matthews, J.J., Brasier, M.D., 2015. Uncovering framboidal pyrite biogenicity using nano-scale CNorg mapping. *Geology* 43, 27–30.
- Wang, X.F., Chen, X.H., Cheng, L., Wang, C.S., Bachmann, G.H., Sander, M., Hagdorn, H., 2009. Sedimentary and palaeoecological environments of the Guanling and related biotas. *Acta Palaeontol. Sin.* 48, 509–526 (in Chinese with English abstract).
- Wen, W., Zhang, Q.Y., Hu, S.X., Zhou, C.Y., Xie, T., Huang, J.Y., Chen, Z.Q., Benton, M.J., 2012. A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China. *Acta Palaeontol. Pol.* 57, 149–160.
- Wen, W., Zhang, Q.Y., Hu, S.X., Benton, M.J., Zhou, C.Y., Xie, T., Huang, J.Y., Chen, Z.Q., 2013. Coelacanth from the Middle Triassic Luoping biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontol. Pol.* 58, 175–193.
- Wu, F.X., Sun, Y.L., Hao, W.C., Jiang, D.Y., Xu, G.H., Sun, Z.Y., Tintori, A., 2009. New species of *Saurichthys* (Actinopterygii: Saurichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. *Acta Geol. Sin.* 83, 440–450.
- Wu, F.X., Sun, Y.L., Xu, G.H., Hao, W.C., Jiang, D.Y., Sun, Z.Y., 2011. New saurichthyid actinopterygian fishes from the Anisian (Middle Triassic) of Southwest China. *Acta Palaeontol. Pol.* 56, 581–614.
- Xu, G.H., Shen, C.C., Zhao, L.J., 2014. *Pteronisculus nielseni* sp. nov., a new stem-actinopteran fish from the Middle Triassic of Luoping, Yunnan Province, China. *Vertebrate Palaeontol.* 52, 364–380.
- Zatoń, M., Rakociński, M., 2014. Coprolite evidence for carnivorous predation in a Late Devonian pelagic environment of southern Laurussia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 394, 1–11.
- Zatoń, M., Niedzwiedzki, G., Marynowski, L., Benzerara, K., Pott, C., Cosmidis, J., Krzykowski, T., Filipiak, P., 2015. Coprolites of Late Triassic carnivorous vertebrates from Poland: an integrative approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 430, 21–46.

- Zhang, Q.Y., Zhou, C.Y., Lu, T., Xie, T., Lou, X.Y., Liu, W., Sun, Y.Y., Wang, X.S., 2008. Discovery and significance of the Middle Triassic Anisian biota. *Geol. Rev.* 54, 523–527 (in Chinese with English abstract).
- Zhang, Q.Y., Zhou, C.Y., Lu, T., Xie, T., Lou, X.Y., Liu, W., Sun, Y.Y., Huang, J.Y., Zhao, L.S., 2009. A conodont-based Middle Triassic age assignment for the Luoping biota of Yunnan, China. *Sci. China Ser. D Earth Sci.* 52, 1673–1678.
- Zhang, Q.Y., Wen, W., Hu, S.X., Benton, M.J., Zhou, C.Y., Xie, T., Lü, T., Huang, J.Y., Choo, B., Chen, Z.Q., Liu, J., Zhang, Q.C., 2014. Nothosaur foraging tracks from the Middle Triassic of southwestern China. *Nat. Commun.* 5, 3973e. <http://dx.doi.org/10.1038/ncomms4973>.