Coprolites from the Late Triassic Kap Stewart Formation, Jameson Land, East Greenland: morphology, classification and prey inclusions

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Abstract: A large collection of vertebrate coprolites from black lacustrine shales in the Late Triassic (Rhaetian–Sinemurian) Kap Stewart Formation, East Greenland is examined with regard to internal and external morphology, prey inclusions, and possible relationships to the contemporary vertebrate fauna. A number of the coprolites were mineralogically examined by X-ray diffraction (XRD), showing the primary mineral composition to be apatite, clay minerals, carbonates and, occasionally, quartz in the form of secondary mineral grains. The coprolite assemblage shows multiple sizes and morphotypes of coprolites, and different types of prey inclusions, demonstrating that the coprolite assemblage originates from a variety of different producers.

Supplementary material: A description of the size, shape, structure, texture, contents and preservation of the 328 specimens is available at https://doi.org/10.6084/m9.figshare.c.2134335

Coprolites are important palaeoenvironmental indicators because they record the feeding activities of extinct animals (Hunt *et al.* 2012*a*). Their preservation is often dependent on factors similar to those that favour the preservation of skeletal remains, but sometimes they can also be preserved where no bone material is present. Coprolites are trace fossils that cannot usually be tied to a producer on the species, or even the genera, level and they do not have any application in cladistics. Because of this, vertebrate coprolites are rarely systematically collected in the field, and only few scientists devote their time to describing and interpreting this type of fossil (Hunt *et al.* 2012*c*). Nonetheless, coprolites represent animal behaviour preserved in rock and can potentially open windows into past ecologies that body fossils cannot. The shape and contents of a coprolite are dependent on the intestines and feeding habits of its producer, and can provide evidence of links in the food chain. Details of the local palaeoenvironment may be evident from coprolites when, for instance, sand grains or twigs have become stuck to the surface prior to hardening and fossilization. In the same way, trapped gas vesicles, desiccation cracks and traces of coprophagic organisms can indicate that a coprolite was subaerially exposed for some time prior to fossilization (Northwood 2005; Milàn *et al.* 2012*b*). Vertebrate coprolites may also preserve small material as pollen and seeds, fragile bones or even soft tissue that is rarely preserved elsewhere (Hunt *et al.* 2012*a*).

In the summer of 2012, members of the Geocenter Møns Klint Dinosaur Expedition searched for Late Triassic vertebrate fossils and ichnofossils at

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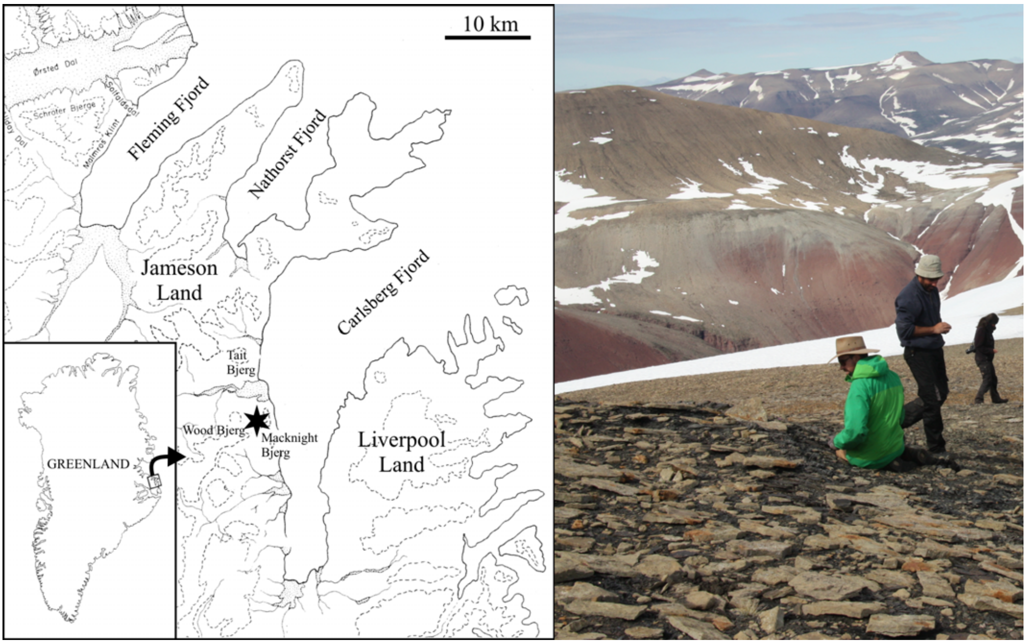

Fig. 1. Map of Greenland. The coprolite-bearing shale unit (marked with a star) is located at 71° 24.800′ N, 22° 34.417′ W at approximately 572 m elevation, near Wood Bjerg, at Carlsberg Fjord, Jameson Land, East Greenland. The black lacustrine shales are partly covered by loose slabs of delta-front sandstones (modified from Milàn *et al.* 2012*a*).

localities in Jameson Land (Clemmensen *et al.* 2015; Klein *et al.* 2015), west of Carlsberg Fjord in East Greenland. A locality at Wood Bjerg (Fig. 1) yielded more than 300 well-preserved coprolites, found as loose material weathered out of a lacustrine shale outcrop from the Kap Stewart Formation. The coprolites showed several different morphologies, of which a few were briefly described by Milàn *et al.* (2012*a*). The aim of this study is to document this diverse coprolite assemblage with regard to external and internal morphology, classification, and prey inclusions, and to compare it with the known Late Triassic vertebrate fauna from the area.

Geological setting

The Kap Stewart Formation forms the lowermost unit in the Late Triassic–Jurassic Jameson Land Group, which is distributed across the whole of Jameson Land (Surlyk *et al.* 1973). The Rhaetian–Hettangian–Sinemurian Kap Stewart Formation overlies the Carnian–Norian–early Rhaetian Fleming Fjord Formation of the Scoresby Land Group (Fig. 2; Clemmensen 1980; Clemmensen *et al.* 1998) and is overlain by the Pliensbachian–Toarcian Neill Klinter Formation (Surlyk *et al.* 1973). Surlyk (2003) has elevated the Jameson Land Group to Supergroup level and the Kap Stewart Formation to Group level, and he subdivided this new Kap Stewart Group into the Innakajik Formation, the Primulaelv Formation and the Rhætelv Formation according to their lithological characteristics and depositional environment. Here, the Kap Stewart succession will continue to be treated as a formation in accordance with all other sources to avoid confusion.

The coprolites gathered in this study were all found at a locality on the east side of Wood Bjerg, Jameson Land, East Greenland (Fig. 1). Here, lacustrine mudstones (‘paper shales’) from the basal part of the Kap Stewart Formation are exposed in a mountain slope. The coprolites were collected from an approximately 10 m-thick mudstone unit located some 30 m above the base of the formation (Figs 1, 2).

The Kap Stewart Formation was first dated by Harris (1937) based on macroplant fossils gathered from sediments exposed in the southern part of Jameson Land. Later, palynological analysis based on plant microfossils was applied to obtain more precise dating. Samples were taken from cliffs along the western shore of Hurry Inlet, which hold a rich palaeoflora. This East Greenland flora is similar to that of contemporaneous sediments in NW Europe (Pedersen & Lund 1979). It can be divided into two zones, where the lower zone is from the Rhaetian and the upper zone is from the Hettangian

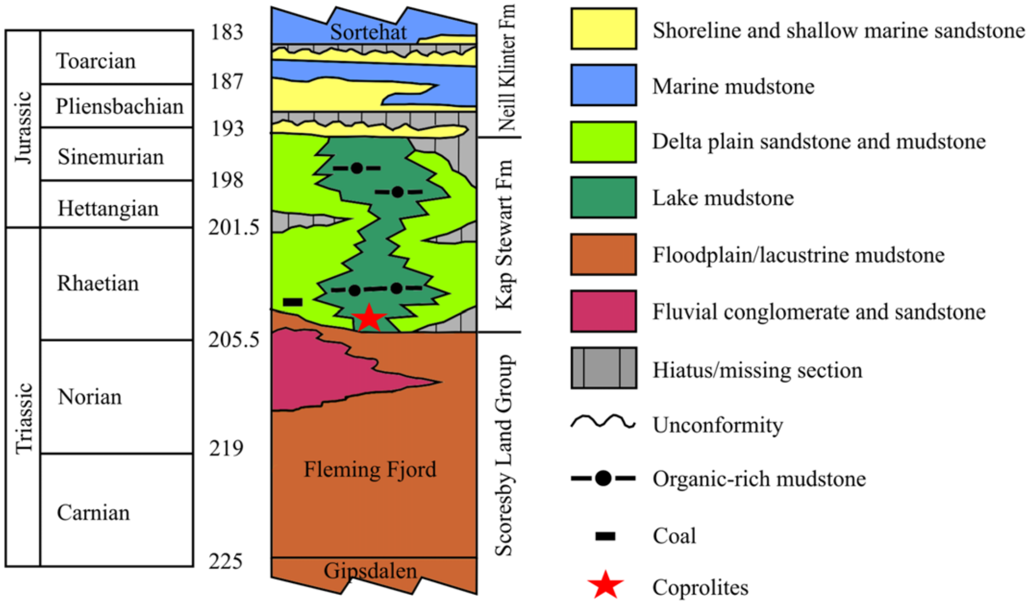

Fig. 2. The Late Triassic–Early Jurassic stratigraphy and depositional environment of Jameson Land Basin, East Greenland. Modified from Clemmensen *et al.* (1998) and Nøttvedt *et al.* (2008). Fleming Fjord and Gipsdalen denote formations, while Sortehat is a member. Here, we treat the Kap Stewart and Neill Klinter sediments as formations, as defined by Surlyk *et al.* (1973). The age of the Rhaetian is based on Wotzlaw *et al.* (2014).

(Pedersen & Lund 1979). The coprolite-bearing unit lies close to the base of the formation and the coprolites are attributed to the Rhaetian. Clemmensen *et al.* (1998) placed the Norian–Rhaetian boundary at about 208.5 Ma in the Fleming Fjord Formation at approximately 100 m below the base of the Kap Stewart Formation. New evidence from high-precision U–Pb chronology places the lower boundary of the Rhaetian at 205.5 Ma, and estimates the total duration of this stage to be slightly longer than 4 myr (Wotzlaw *et al.* 2014). Following Wotzlaw *et al.* (2014), the Norian–Rhaetian boundary in East Greenland should be moved upwards by about 3 myr and may, in fact, lie close to the lithological boundary between the Fleming Fjord Formation and the Kap Stewart Formation.

The Kap Stewart Formation comprises alternating sandstones and mudstones of terrestrial origin. The characteristics of the formation vary across the basin (Dam & Surlyk, 1993). In the NE part of the basin, which includes the studied site, the formation is composed of intercalated open-lacustrine mudstones (black shales), and wave- and storm-dominated delta-front sandstones. The sediments are interpreted as the deposits of a perennial lake with large delta systems on its shores and alluvial systems beyond. The lake was extensive and may, in periods, have covered more than 12 000 km^2 (Dam & Surlyk, 1992, 1993). It was situated in the southern end of the East Greenland rift basin, which formed as Pangaea started to split apart to later form the Atlantic Ocean (Nøttvedt *et al.* 2008). Lake margins appear to have been controlled by major fault systems to the north, east and west, while the nature of the southern border is less well known (Nøttvedt *et al.* 2008). The Kap Stewart lake sediments overlie lake deposits of the Late Triassic Fleming Fjord Formation (Clemmensen *et al.* 1998, 2015). The Kap Stewart lake formed in a temperate and relatively humid climate, and constituted a climatic end member in the Late Triassic–Early Jurassic lake succession in East Greenland, which developed during a climatic shift from arid to humid (Clemmensen *et al.* 1998, 2015). This climatic change was apparently a result of the northwards drift of the basin area (Dam & Surlyk 1992, 1993; Clemmensen *et al.* 1998; Kent & Tauxe 2005). The Jameson Land basin lay at a palaeolatitude of approximately 41° N around 209 Ma in the latest Norian (Kent & Clemmensen 1996; Kent & Tauxe 2005) and during the latest Triassic, the basin area drifted northwards at about 0.6° Ma^{-1} (Kent & Tauxe 2005).

The Kap Stewart lake experienced large cyclical changes in water depth, as seen from the repeated shifts between deep-water mudstones and shallow-water sandstones (Dam & Surlyk 1992). These high-frequency variations in lake level are likely to be records of a Milankovitch-type climatic control on lake sedimentation (Dam & Surlyk 1992). The high-frequency cycles are grouped into low-frequency cycles that can possibly be linked to contemporaneous sea-level changes (Dam & Surlyk 1992).

The vertebrate body fossil record of the Kap Stewart Formation is virtually undescribed: however, a number of specimens collected together with the coprolites include bone fragments, vertebrae, scutes, and teeth and skull parts of large temnospondyls (possibly capitosaurs, considering the large size and tusk-like teeth), one small hollow longbone, presumably from a pterosaur or theropod, a putative phytosaur scute, and some yet unidentified teeth (Milàn *et al.* 2012*a*). These, however, require further preparation and will be the topic of further publications on the locality. A single hybodontid shark fin spine has been reported from the Late Triassic part of the Kap Stewart Formation (Bendix-Almgreen 1976).

Coprolite terminology

The scientific term for fossilized faeces is 'coprolite', which was initially coined by Reverend William Buckland (1829) to describe fossils from Lyme Regis, England. Later studies have shown that not all coprolites are, in fact, excreted fossilized faeces, but, instead, represent faecal masses that fossilized within the body cavities of its producers, either in the stomach or intestines, or masses that have been regurgitated (Fig. 3). Regurgitated masses are termed 'regurgatilite', whereas fossilized stomach contents are termed 'gastrolite' – not to be confused with gastroliths, which are stomach stones (geo-gastroliths: Wings 2007). Fossilized intestine contents are termed 'enterospira' or 'intestinelite'. To encompass all these types, the term 'bromalite' has been erected to cover all fossils of ingested food masses, the specific spatial origin of which cannot be established with certainty (Hunt & Lucas 2012*a*).

Various shapes of coprolites exist, but the spiral is, without a doubt, the most common form and the one most extensively described. The first studies made by Buckland in the nineteenth century concerned themselves primarily with spirally coiled coprolites. Later, Neumeyer (1904) divided spiral coprolites into two main categories: 'amphipolar' spiral are evenly coiled coprolites, whereas 'heteropolar' spiral have coils that are concentrated towards one end. Heteropolar are the most common spiral coprolites throughout the fossil record (Hunt & Lucas 2012*b*). The heteropolar coprolites can be further divided into 'microspiral' and 'macrospiral', depending on how much of the total length is dominated by coils (Hunt *et al.* 2007).

When Buckland (1829) introduced the term coprolite, he did not discern between different kinds of fossilized faecal remains. Scientists have subsequently erected various categories for the subdivision of faecal fossils, but there has been little consistency in the use between authors. Hunt & Lucas (2012*a*) proposed an ordered classification for stable terminology, reviewed the various shapes and structures described for coprolites and recent faeces, and defined a series of faecal morphotypes with matching ichnotaxa and possible producers. For non-spiral coprolites, the terms 'isopolar' and 'anisopolar' describe shapes with similar and dissimilar ends, respectively. Anisopolar coprolites generally have one broad end that was extruded first and one pinched end that was extruded last (Thulborn 1991).

Material and methods

Coprolites

The following was collected from the surface of a black shale outcrop in the Kap Stewart Formation at Wood Bjerg, Jameson Land, East Greenland:

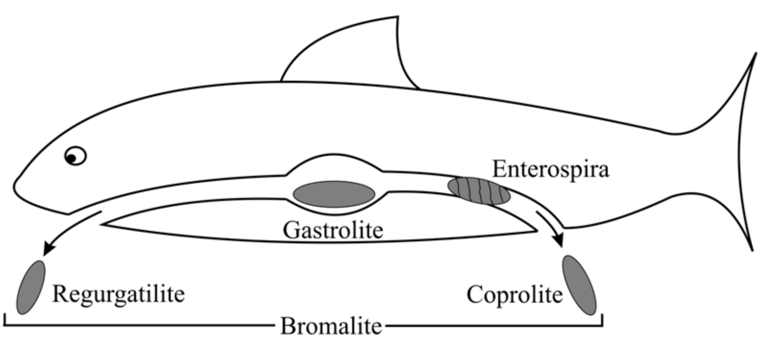

Fig. 3. The term coprolite refers to fossil faeces expelled from the producer prior to fossilization. Fossilized intestine contents are termed enterospira. Fossilized stomach contents are termed gastrolite, and regurgitated material is termed regurgatilite. These terms are collectively known as bromalites. Modified from Hunt & Lucas (2012*a*).

- a total of 323 coprolites;
- an unknown number of minor coprolite fragments;
- 10 small sedimentary concretions;
- six pieces of fossil bone;
- four fossilized invertebrate burrows;
- three sedimentary blocks that contain *in situ* coprolites.

Care was given to collecting as many sizes as possible, but small specimens might have been overlooked, or not recognized, thus creating a sampling bias favouring specimens of larger size.

Eleven coprolites from the collected material (MGUH30357–MGUH30367) were briefly described in an initial report by Milàn *et al.* (2012*a*). Our description follows the recommendations by Hunt & Lucas (2012*b*). All specimens for this study are described under their field numbers where H is for coprolites, N is non-coprolites and SED is for sediments. All specimens are stored in the collection of the Natural History Museum of Denmark. Of the 328 examined and named specimens, 290 specimens that had naturally occurring breaks were polished in cross-section to examine their internal structure. Thirty-eight specimens remained unpolished to preserve their complete shape. All examined specimens were described in terms of size, shape, structure, texture, contents and preservation. Each character was restricted to the smallest number of possible variants in order to enable comparison between specimens and to help recognize trends.

The features described from the coprolites were examined pair-wise through scatter diagrams, column diagrams and pie charts in order to identify correlations and define morphotypes. The four specimens identified as burrows (N1–N4) are excluded from all analyses.

Measurements

All specimens were measured in three planes: length, widest diameter and flattened diameter. The widest diameter was used as a representative of coprolite size. Diameters were taken perpendicular to the extrusion direction, while length follows the inferred extrusion direction. Coprolites are considered flattened when the two measured diameters deviate by at least 2 mm. Normally, volume is the most reliable measure of size in coprolites (Chin 2002), but this is meaningless in extensively weathered samples.

Shape

All coprolites of the present sample can be described as intermediates between ‘cylindrical’, ‘round’ and ‘bulbous’ (Fig. 4). ‘Bulbous’ is a ‘catch-all’ category for coprolites with unidentifiable shapes. Many fragmented specimens are only represented by a round slice: these are all included in the category ‘cylindrical’.

Structure

The examined coprolites are described as belonging to one of the following structures: (1) few to many irregularly wrapped layers; (2) one continued spirally coiled layer; and (3) structureless mass (Fig. 5). Strong surface weathering did obscure the structure in some of the specimens.

Texture

The texture of the coprolites is described using three main types. ‘Massive’ refers to coprolites with a massive, fine-grained texture without colour variation. ‘Swirly’ refers to coprolites with a fine-grained texture containing abundant swirls and twirled patterns of dark and light material (Fig. 6). ‘Nodular’ coprolites are composed of small pellets (Fig. 7).

When a specimen displays more than one texture, it is noted which texture is dominant. For example, specimen H026 is noted as ‘massive’, which means it only consists of massive material. Specimen H192 (Fig. 7d, e), however, has a ‘swirly-nodular’ texture, meaning that the specimen is dominated by a swirly texture, but some nodules or pellets are present.

Contents

For all described specimens, it is noted whether or not any fossilized prey remains are present. If fossil fragments are present, the amount is estimated and the largest fragment is measured. In order to minimize the damage due to cross-sectioning, each coprolite was polished on a previously broken surface. As few specimens are sectioned in a plane perfectly perpendicular to the extrusion direction, it is not possible to compare their contents of fragments directly. As an alternative, the amount of fragments is described by assigning each specimen to one of four categories. These are: ‘0’ for fragment-free specimens; ‘1’ for specimens containing only a few fragments; ‘2’ for specimens containing some fragments; and ‘3’ for specimens containing numerous fragments.

Mineral grains

The contents of mineral grains on the surface and in the interior of coprolites are examined. On the surface, some mineral grains can be recognized as

Fig. 4. The external shapes used to classify the coprolites from the Kap Stewart Formation: (**a**) cylindrical coprolite with constant diameter (MGUH30357); (**b**) cylindrical with pinched ends (H069); (**c**) bulbous coprolite (H246); (**d**) & (**e**) round coprolite (H075 and H077); (**f**) round-bulbous (H078); (**g**) round-cylindrical (H081); (**h**) cylindrical-bulbous (H070); and (**i**) cylindrical-bulbous (H201).

adhesive material that was attached to the specimen prior to fossilization. In the interior, some mineral grains can be recognized as mineral infills in pore spaces, or possible gastroliths (Wings 2012). Some mineral growths occurred in voids from gas bubbles or material that had decayed prior to fossilization. Minerals that appear to have grown inside or on the surface of the coprolite some time after initial burial are noted. Adhesive material is difficult to recognize when minerals have grown in the coprolites.

Preservation

The preservation of each specimen was noted, including the number of ends preserved, the colour of the surface, and the interior and the thickness of the alternation rims. The alternation rims are divided into dark and light rims. A dark rim is the result of chemical alteration that took place during diagenesis. A light rim is the result of recent weathering processes that attacked the surface of the coprolite as it lay exposed on the rock face.

X-ray diffraction (XRD)

The mineralogical contents of the material were examined by XRD analysis at the Department of Geoscience and Natural Resource Management, University of Copenhagen, using a Bruker D8 Advance X-ray Diffractometer. Analysis was carried out on both powdered and intact specimens of

Fig. 5. External and internal structures used to classify the coprolites: (**a**) structureless coprolite (H089); (**b**) polished cross-section of (H089), showing a structureless interior; (**c**) & (**d**) irregularly wrapped coprolite (H037 and H205); (**e**) polished section of H205 showing a weak internal wrapping; (**f**) irregularly wrapped coprolite (H202); (**g**) longitudinal section through spiral coprolite (H007); and (**h**) & (**i**) spiral coprolites (MGUH30365 and MGUH30367).

Fig. 6. Examples of the internal textures used to describe the coprolites: (**a**) massive texture in a structureless coprolite (H269); (**b**) massive texture with a grainy appearance (irregularly wrapped coprolite) (H065); (**c**) swirly-massive texture (spiral coprolite) (H006); (**d**) swirly texture (spiral coprolite) (H017); and (**e**) massive-nodular texture with fossil fragments (irregularly wrapped coprolite) (H043).

different morphologies. The powdered samples were taken from: H026, an irregularly wrapped coprolite with fragments; H096, a structureless coprolite; and H228, a coprolite consisting of pellets. Specimen H199, a pellet-like coprolite still embedded in sediment, was sampled twice so both the coprolite (H199-C) and the surrounding sediment (H199-S) was studied for control. N4 was a suspected fossilized burrow. Care was taken to avoid weathered surface layers during sampling.

In order to determine the composition of some of the prey inclusions in the coprolites, diffraction analysis was attempted on polished surfaces of intact specimens. For this purpose, four coprolites (H029, H045, H075 and H313) containing prey inclusions were examined. Each specimen was mounted in the X-ray diffractometer so that the prey inclusions in question lay as close to the central measuring area (of about 1 cm^2) as possible. Care was taken to mount the specimens so that the measured area was horizontal and level with the edge of the sample holder. Normal procedure is to rotate a sample during measuring, but here a manual program was run to keep the specimens stationary. Minerals are only identified to group level as the various mineral structures within each group can be very similar, and precise identification is very difficult without a supporting chemical analysis. Typical representatives of each mineral group were used in the interpretation of XRD data. For example, muscovite was used as representative for the micas.

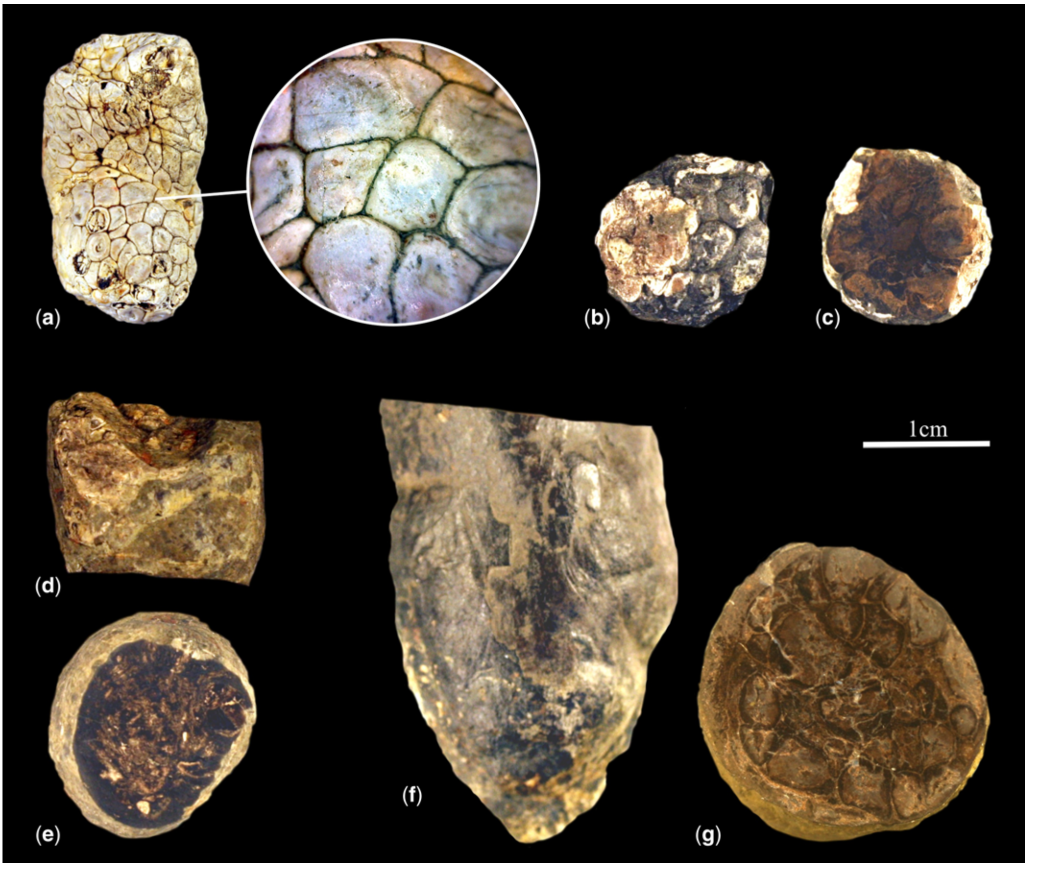

Fig. 7. (**a**) Nodular coprolite with an enlarged section of surface (H187); (**b**) nodular coprolite (H178); (**c**) a polished section of H178 showing a completely nodular interior; (**d**) swirly-nodular (H192); (**e**) a polished section of H192 showing a few large nodules covered in a thick wrap of swirly texture; (**f**) specimen mistakenly classified as entirely nodular (see text for details) (H202); and (**g**) a polished section of H202 showing numerous large nodules with a thin wrap of massive texture.

Results

Coprolite size

The measured diameters of the coprolites are between 7.5 and 48 mm, with the most common diameter being 19 mm. Ninety-five per cent of the coprolites have diameters of between 12 and 30 mm (both values included), and 75% between 16 and 26 mm (Fig. 8). The four burrows that were found in the material had diameters of 19–20 mm, which is why they were at first misinterpreted as coprolites.

Shape

Of the examined specimens, 321 were sufficiently well preserved to be sorted by external shape and could be placed into the following shape categories: bulbous ($n = 12$); cylindrical ($n = 264$); cylindrical-bulbous ($n = 34$); round ($n = 4$); round-bulbous ($n = 4$); and round-cylindrical ($n = 3$) (see Fig. 4).

Structure

Three distinctive structures are recognized in the studied material: irregularly wrapped ($n = 179$); structureless ($n = 124$); and spiral/coiled ($n = 19$) (see Fig. 5).

Texture

The following 10 groups are used to describe the internal textures found in the material: massive ($n = 107$); massive-nodular ($n = 44$); massive-swirly ($n = 31$); nodular ($n = 39$); nodular-massive ($n = 15$); nodular-swirly ($n = 14$); swirly ($n = 10$); swirly-massive ($n = 13$); swirly-nodular ($n = 24$); and unknown ($n = 27$) (see Figs 6 & 7).

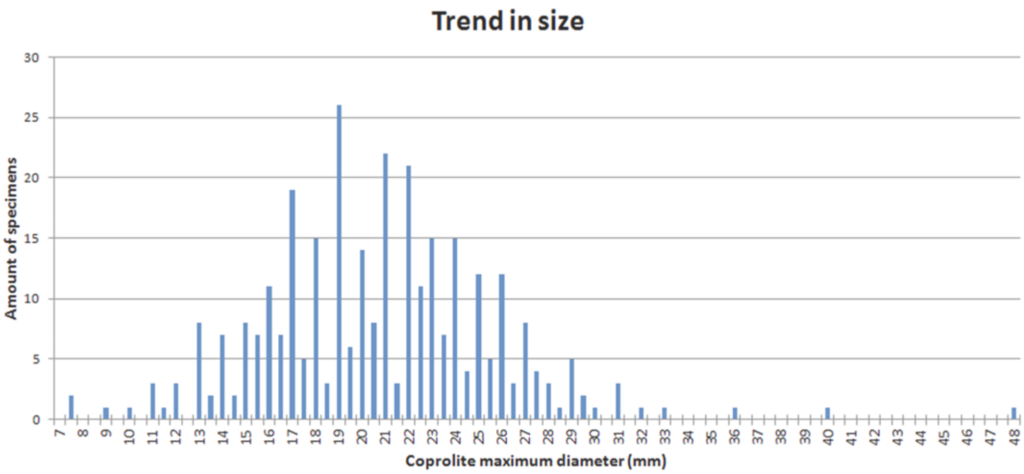

Fig. 8. Diagram showing the distribution of coprolites across all measured diameters.

Fossil prey remains

Prey remains are found in various sizes within each coprolite, but the largest fragment present defines a maximum size that is used to characterize the specimen. Fragments are found in 236 specimens, and measure between 0.1 and 10 mm (Figs 9 & 10).

Nodules

Nodules are found in 163 specimens, and measure between 0.1 and 6 mm (Fig. 7). When studied in cross-section, nodules and pellets can be hard to distinguish, and they are treated as closely related entities in the analyses.

Mineral grains

Authigenic mineral grains are found in 242 specimens, and measure between 0.1 and 4 mm. The 37 specimens that were not polished and had unknown interiors were excluded from this analyses.

Bent specimens

Twenty specimens had a slightly bent shape. The specimens are all cylindrical, and have diameters of between 13 and 24.5 mm, and the bend occur in coprolites of all structures. Four specimens also bear contraction marks (two of these also have pinched ends). Most coprolite textures are represented – the exceptions are massive-swirly and swirly-massive.

Flattened specimens

There were 135 specimens with a flattened shape, with short diameters of between 8 and 33 mm. Most of the specimens are cylindrical, but bulbous, cylindrical-bulbous and round-bulbous shapes are also represented. All coprolite textures are represented: however, the nodular-massive coprolites appear to have been more prone to flattening – 13 out of 15 nodular-massive specimens are flattened.

Pinched specimens

Twelve specimens have pinched ends. They are of cylindrical, cylindrical-bulbous and round-cylindrical shape, with diameters of between 13 and 22 mm. Eight specimens bear contraction marks (two of these are also bent). Spiral/coiled coprolites are not represented. Textures present: massive; massive-swirly; nodular-massive; and nodular-swirly. Half of the pinched specimens have unknown textures.

Specimens with contraction marks

Twenty-one specimens bear contraction marks. They are cylindrical and cylindrical-bulbous, with diameters of between 11 and 22.5 mm. Four specimens are bent and eight specimens have pinched ends (two of these are also bent). Spiral/coiled coprolites are not represented. Textures present: massive; massive-nodular; massive-swirly; and nodular-swirly. Seven of the specimens have unknown texture.

Correlations between coprolite size, shape, structure and texture

Coprolite size and shape

There is no clear correlation between coprolite diameter and shape. The four round specimens have

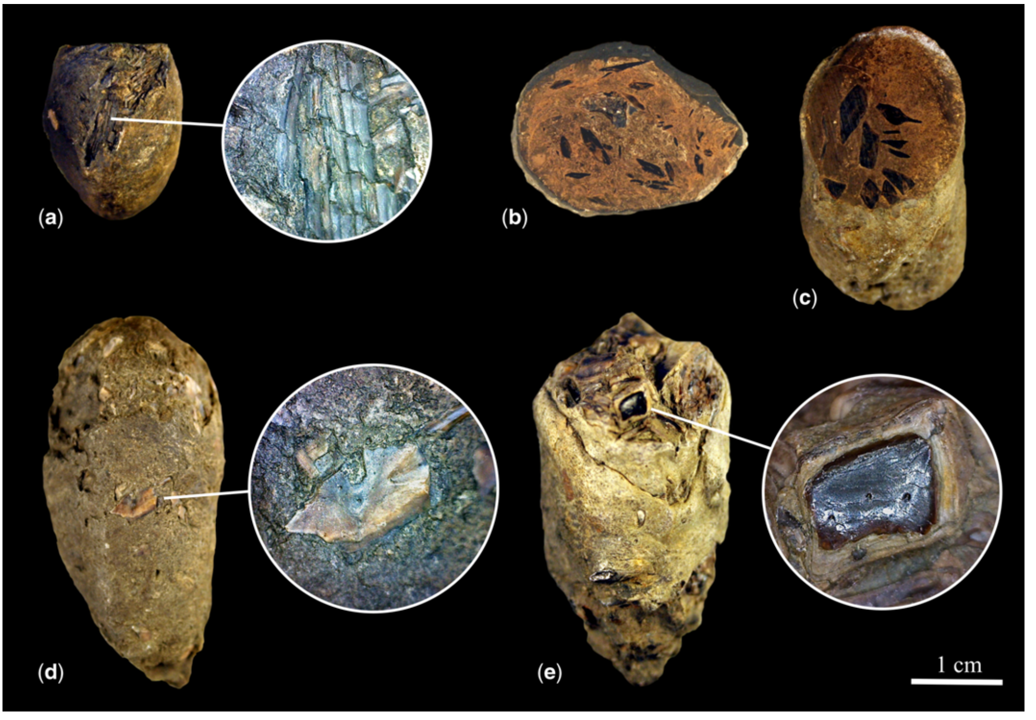

Fig. 9. Inclusions of prey remains encountered in the coprolites: (**a**) round coprolite with rows of unknown tile-like scales (H075) – each scale is about 1 mm long; (**b**) irregularly wrapped coprolite bearing slim lenticular fragments of up to 5 mm (H254); (**c**) irregularly wrapped coprolite bearing thick angular fragments of up to7 mm (H029); (**d**) spiral coprolite bearing a flat rectangular scale with a triangular extrusion (H009) – the scale is about 4 mm long; and (**e**) irregularly wrapped coprolite bearing thick rectangular scales with residues of black coating (H200) – the scales are up to 10 mm.

diameters of between 15 and 20 mm, and the three round-cylindrical specimens have diameters of between 16.5 and 20 mm.

Shape and structure

Cylindrical coprolites are the most common in all of the three structures (irregularly wrapped, structureless and spiral/coiled). Round specimens are not found among the spiral/coiled coprolites. Round coprolites are dominated by structureless specimens, and round-bulbous coprolites only contain structureless specimens. In the other coprolite shapes (bulbous, cylindrical, cylindrical-bulbous and round-cylindrical), irregularly wrapped specimens are the most common. However, except for cylindrical coprolites, each shape is represented by relatively few specimens and their correlations are uncertain.

Structure and texture

The strongest correlation between structure and texture of the coprolites is found in spiral/coiled specimens that consist of massive and swirly textures, and do not contain any nodular textures. Contrarily, irregularly wrapped specimens are independent of coprolite texture as they contain all textures. Structureless specimens appear to be largely independent of texture as well, but do not contain any swirly-massive specimens. Irregularly wrapped and structureless coprolites are dominated by the three primary massive textures. The two structures contain similar amounts of nodular specimens (Fig. 11).

Correlations between content of fragments and coprolite features

Structure

There is a generally normal distribution of fragment sizes within the three structures. Also, fragment-free coprolites are common within all three structures, indicating that the structure of coprolites and their contents of fragments are not correlated. The

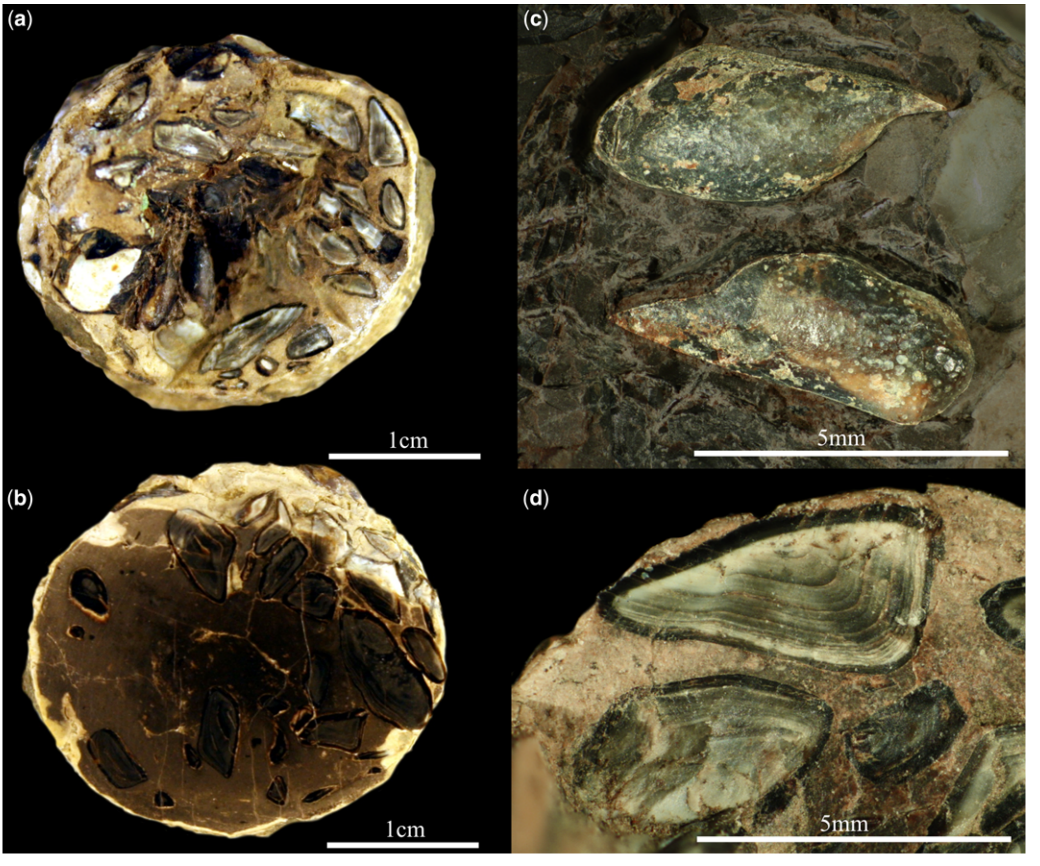

Fig. 10. Otolith-like inclusions in coprolite: (**a**) a specimen containing abundant 2–7 mm inclusions (H313); (**b**) a polished section through the specimen; (**c**) two inclusions that are partially prepared free of the coprolite matrix, showing a rounded external surface; and (**d**) a polished section through a large inclusion showing a layered internal composition. Photographs (c) & (d) by Werner Schwarzhans.

distribution of fragment categories is similar between structures. Spiral/coiled specimens are so few compared to the other structures that the apparent higher amount of category 3 specimens (numerous fragments) is uncertain.

Texture

Nodular coprolites rarely contain fragments and when they do these are less than 2.5 mm long. The other coprolite textures are difficult to define with respect to the contents of fragments. They appear to be parts of a spectrum with massive coprolites at one end, containing a large variety of fragment sizes, and swirly coprolites at the other end, containing few fragment sizes. Nodular-massive and nodular-swirly coprolites contain slightly more nodule-free specimens than the other textures, but far less than the entirely nodular coprolites (Fig. 12).

Correlations between contents of nodules and coprolite traits

Structure

Spiral/coiled coprolites do not contain nodules, except for a few single scattered nodules. For the irregularly wrapped and structureless coprolites, the specimens containing nodules are weakly normally distributed according to nodule size. Since nodule-free specimens are widespread, this indicates that the presence of nodules is dependent on structure, but the size of nodules is not.

Texture

Nodules are present in all textures, but their size is dependent on the coprolite texture. Nodular and massive-nodular specimens not only contain the

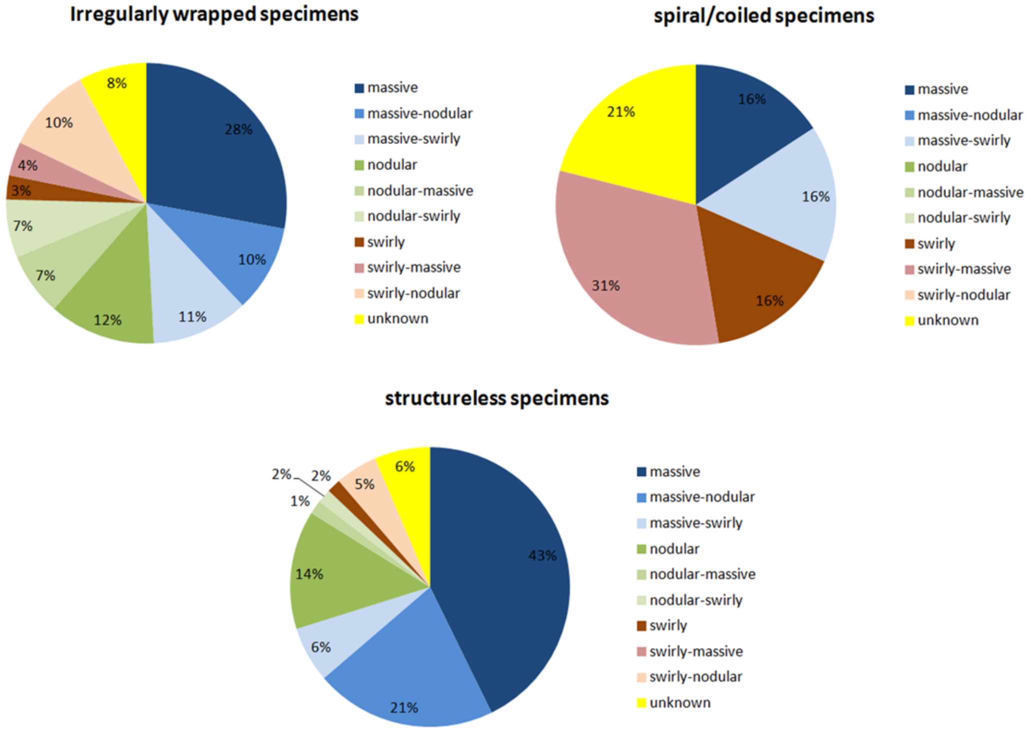

Fig. 11. Pie charts demonstrating the distribution of the various textures within the three structures 'irregularly wrapped', 'structureless' and 'spiral'.

largest nodules but also the widest range of sizes. The shortest range of nodule sizes (except for coprolites of unknown texture) is seen in swirly and swirly-massive coprolites, with only three possible sizes found in a few specimens.

Correlations between contents of mineral grains and coprolite traits

Coprolite size

There is a slight tendency for increasing mineral grain size with increasing coprolite size.

Structure

The content of mineral grains is partly dependent on coprolite structure, since irregularly wrapped and structureless coprolites can contain larger grains than spiral/coiled coprolites. Spiral/coiled specimens always contain mineral grains, but these are never larger than 1 mm.

Fossil fragments

There is no certain correlation between the contents of fossilized prey fragments and the contents of mineral grains, but there may be a tendency for mineral grain size to increase along with fragment size.

Nodules

Mineral grain size is dependent on nodule size, as the largest possible grain size decreases with increasing nodule size.

Correlations between preservational state and coprolite traits

Coprolite size

Small coprolites tend to be preserved with intact ends more often than large coprolites, and the dark alteration rims are slightly thicker in the large-diameter coprolites. There is no correlation between light rim thickness and coprolite diameter.

Fragment category

The number of preserved ends is largely independent of the fragment category, but coprolites containing numerous fragments are more often found with both ends preserved. The thickness of the

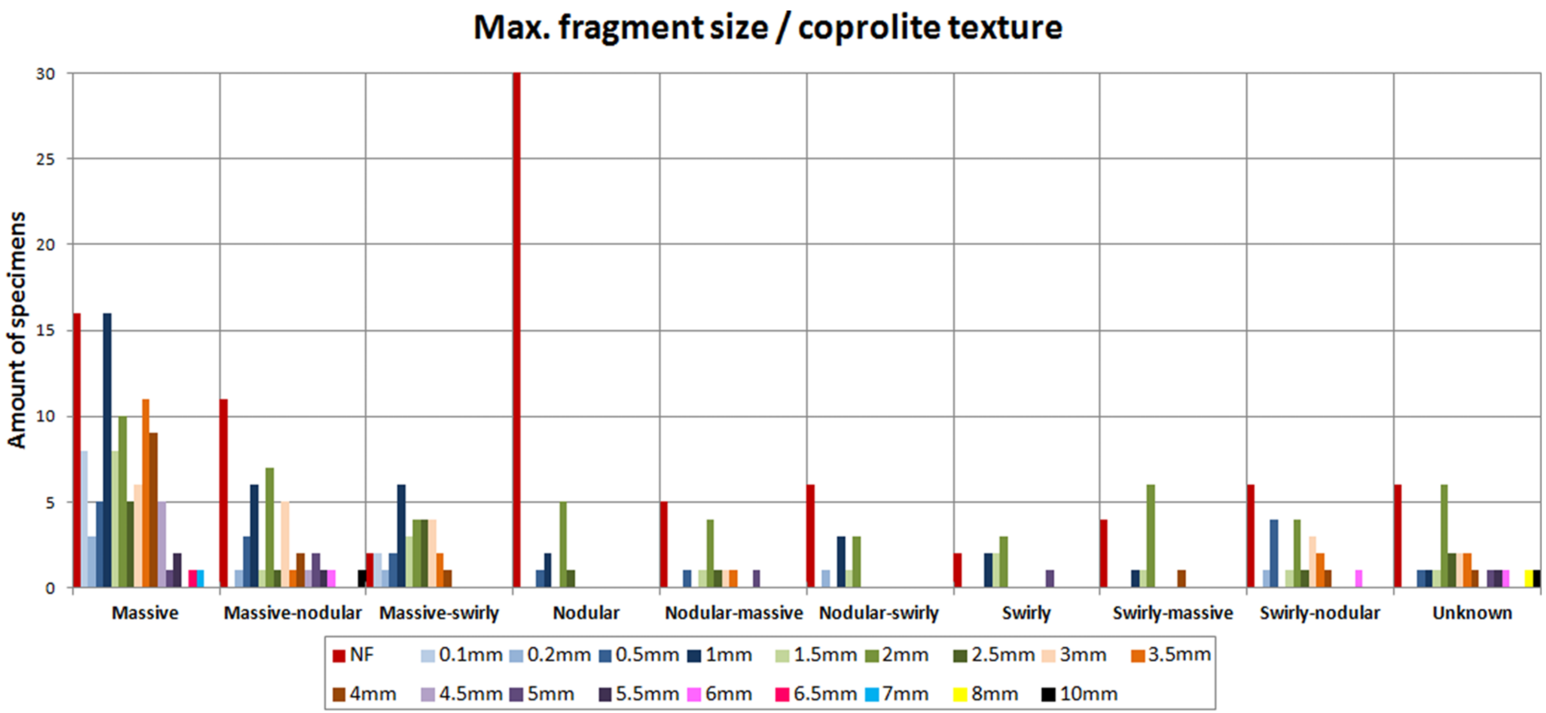

Fig. 12. Diagram of the content of fragment sizes within each coprolite texture. Each column represents the amount of specimens containing fragments of a certain size. NF refers to specimens with no fragments. Note the disproportionate amount of fragment-free specimens among coprolites with a nodular texture.

dark alteration rims is somewhat dependent on the fragment category, as category 3 coprolites appear to contain more specimens with rims. There is generally no correlation between fragment category and light rim thickness.

Mineral grains

There is a tendency for both dark and light rims to decrease in thickness with increasing mineral grain size.

Fossil fragments in coprolites

Fragmentary remains of prey are visible in 236 of the examined coprolite specimens. Most of these remains are too small or fragmental to be identified, but some specimens contain fragments of considerable size, up to 10 mm in length, which appear quite well preserved. There are at least four main types of prey remains that can be recognized either in cross-sections or on the weathered surfaces of the coprolites.

In cross-section:

- Slim to lenticular bodies that are often curved and sometimes have wavy outlines. These shapes can be tiny or large and have lengths of up to 10 mm.

On coprolite surfaces:

- Flat rectangular scales with a triangular point on one of the short sides and a matching indentation on the opposite short side. The scales have lengths of up to about 4.5 mm (Fig. 9d).
- Tiny scales of about 1 mm that link together in rows that are up to about 6 mm long. These are only unambiguously identified on the surface of H075. The individual pieces are flat and shaped like two rectangles that are displaced along a central groove. The groove of each scale connects with the one on the scale in front, so the pieces link together like tiles (Fig. 9a).
- Thick bodies that are triangular to quadratic and appear to be concentrically built. These are also recognizable in cross-sections. In H313, there are various types of these thick bodies, some are almost cylindrical and can be up to 8 mm long (Fig. 10).

The slim lenticular bodies seen in cross-sections and the thick rectangular bodies are possibly related and, rather than separate types, they represent the endpoints in a spectrum of shapes. There are some fragments that have residues of a black coating preserved on their surfaces. In specimen H200 (Fig. 9e), the fragments bear a thick and smooth coating, while some other specimens have fragments with an ornamented coating. In these fragments, the coating preserves short, narrow and tightly spaced grooves that run from the edge and towards the central ridge, and have a slightly comb-like appearance. The shapes of the fragments are often obscured owing to poor exposure or weathering, but the ornamented fragments can be at least 4 mm long.

Associated fossil material

Together with the coprolitic material, a few isolated fossil fragments were also collected: six pieces of dermal armour assigned to large temnospondyl amphibians; imprints of unknown bivalves; and unidentified fragments of reptilian bones and teeth. A single shark tooth was sufficiently well preserved to be assigned to *Rhomphaiodon minor* (Cuny & Risnes 2005; Hansen 2014).

Possible burrows

During the description and sorting of the material, four cylindrical specimens (N1–N4) were found to be different from the rest of the material and we suspect that they, in fact, represent fossilized burrows. They are preserved as short, flattened and very similar pieces, with obliquely broken ends and a peculiar creased surface. The creases lie at an angle of 60–70° to the longitudinal axis. There are also thin and tightly spaced longitudinal lines that run across the creases – a feature not seen in any other specimens. Polished sections revealed grainy and structureless interiors that support a sedimentary origin. The four suspected burrows have maximal diameters of 19–20 mm, and all have a flattened diameter of 16 mm. The high degree of similarity indicates a similar origin, and N2, N3 and N4 are possibly all fragments of one large burrow.

Results of XRD

Specimens H026, H096, H228 and H199-C all contain apatite (in the form of fluorapatite), clay minerals (in the form of clinochlore) and carbonates (in the form of magnesiumcalcite). H096 and H199-C also contain quartz. Specimens H199-S (sediment adjacent to the coprolite) and N4 (a suspected burrow) do not contain apatite or carbonates: instead, these specimens contain quartz, feldspars (in the form of microcline and albite), clay minerals (in the form of clinochlore) and micas (in the form of muscovite). Furthermore, N4 contains lepidocrocite and pyrite.

Fluorapatite is used as representative of the apatites, and its diffraction pattern is nearly indistinguishable from that of hydroxyapatite. Apatites are important minerals in vertebrate bone, teeth and scales, and are often preserved in fossilized bones and in coprolites of carnivorous origin. Carbonates in a coprolitic sample can often be related to ingested shell material (Kemp 1984; Wings 2004). Quartz is a very common mineral in many depositional settings, and can be present in coprolites as sand grains from ingested sediment (Wings 2007), as an adhesive material or as a secondary mineral that has in-filled pore spaces. In specimens H096 and H199-C, the quartz is possibly from in-filled pore spaces, as these were described from both. The identification of clinochlore shows that there are clay minerals of the chlorite group or the smectite group present in the samples. Their occurrence is not surprising given the strong weathering of the material. Feldspars and micas are common minerals, but they are easily weathered; in sedimentary rocks, they are mostly found in sands that have not been transported far from the source area prior to deposition (Nesse 2000). The similar composition of the sediment sample (H199-S) and the suspected burrow (N4) proves that N4 together with the three similar specimens (N1–N3) are, in fact, fossilized burrows and not coprolites.

The mineralogy of fossil inclusions was studied in specimens H313, H075, H045 and H029. X-ray diffraction analysis was made on polished sections for H313, H045 and H029, and the only mineral found was apatite. Specimen H075 was intact and it was attempted to take measurements directly from the original rounded coprolite surface: however, this attempt was unsuccessful.

Discussion

Coprolite assemblage

The smallest specimen in the material measures 7.5 mm in diameter and 8 mm in length. It is common for vertebrate coprolites to be smaller than this and the scarcity of small coprolites in the present material could be a result of sampling bias. However, there are other possibilities. Very small coprolites could have been rare or absent from the site owing to recent destruction by the extensive weathering or they may even have been absent originally if the palaeoenvironment or diagenesis did not support the preservation of these specimens. It is unlikely that there were no small faeces present in the original environment, but these may have been made by invertebrates rather than vertebrates. If the contents of digested bone and scale material were critical for preservation in the Kap Stewart Formation, the faeces of herbivores, insectivores and detritus feeders (mostly invertebrates) would probably not be preserved. The present coprolites from the Kap Stewart Formation are interpreted as coming from vertebrates mainly because of their large sizes.

Round to subround coprolites

Shape is not an effective way to distinguish the coprolites in the present material, and only a few can be classified clearly by their shape. The specimens H074, H075, H077, H078 and H080 are round and round-bulbous, and have smooth surfaces. These round to subround specimens have maximum diameters restricted to 15–20 mm and their interiors are structureless. They all appear to be of massive texture and contain fossil fragments of at least 0.5 mm. Specimen H081 possibly belongs in this category, although it might rather be a rounded end of a larger cylindrical specimen, showing that it is especially difficult to classify the shape of incomplete coprolites.

Spiral and coiled coprolites

Specimens of spiral to coiled structure are markedly different from other coprolites. In the present material, they can be as small as 7.5 mm in diameter, but they are also the largest coprolites (48 mm in diameter). The spiral/coiled coprolites consist of massive and swirly textures, but never nodular textures (see Fig. 11). If nodules are present, it is only as single and scattered nodules, not as well-defined pellets. Spiral/coiled specimens can contain all sizes of fossil fragments and may have a higher tendency than other types for containing numerous fragments. They always contain mineral grains, but these are never larger than 1 mm. The ends, when preserved, are never pinched but can be pointy. Nineteen specimens are included in the spiral/coiled type: H001–H013, H017, H249, H310 and MGUH30365–MGUH30367. H017 is possibly an irregularly wrapped specimen that consists of extra thin wraps. The spiral/coiled specimens are quite different from each other and some sorting is possible (Table 1).

Spiral coprolites originate from fish and other animals with a type of digestive tract that contains a spiral valve (Hunt *et al.* 2012*a*). In the Kap Stewart Formation, there are various potential producers as both sharks and actinopterygians have been identified in this project, just as coelacanths and lungfish were identified earlier from the underlying formation (Jenkins *et al.* 1994). It is not possible to determine with certainty which animals produced which coprolites, but it is plausible that large spiral coprolites were produced by sharks, while the smaller ones were partially also produced by a variety of bony fish (Hunt *et al.* 2012*a*).

Irregularly wrapped and structureless coprolites

Irregularly wrapped specimens and structureless specimens are likely to represent two separate

Table 1. *Description of 18 spiral/coiled coprolites of the Kap Stewart Formation*

Specimen	Diameter (mm)	Description (preserved number of coils in parentheses)
H001 H002 H003 H310	17.5 17 13.5 20	H001 (*c.* 1.5 coils), H002 (*c.* two coils) and H003 (*c.* two coils) are similar in diameter (13.5–17.5 mm) and are all flattened (8.5–12 mm in short diameter). They have uneven surfaces and each consists of a simple coiled layer. They all contain some or numerous fossil fragments. H310 is slightly larger (20 mm in diameter and 18 mm in flattened diameter) but bear the same characteristics
H006	14	H006 (*c.* three coils) is preserved as a posterior spire (=initial end) with unevenly overlapping layers that give it a resemblance to a pinecone. Coprolites somewhat similar to this were depicted by Buckland (1829, pl. 31, fig. 10) and by Williams (1972, pl. 1, fig. 8), where they are merely identified as heteropolar. The best match may be to the ichnotaxa group 4 of Laojumpon *et al.* (2012, fig. 7a, b). These are Late Triassic spiral coprolites from Thailand that were found in sediments deposited in brackish water. At the Thailand locality, a *Hybodus* tooth, bony fish scales and temnospondyl vertebrae were also found. This faunal composition is similar to that of the Fleming Fjord Formation of Jameson Land (Jenkins *et al.* 1994)
H010 H011	15 7.5	H010 (*c.* four–five coils) and H011 (*c.* three coils, although very uncertain) are poorly preserved, but both appear to consist of a tightly wound coil that runs the length of the coprolite
MGUH30365	48	MGUH30365 (>four coils) is the largest coprolite in the entire material. The coil is about 5 mm wide at the surface and thins towards the centre. The coprolite is very damaged, but bears affinities to the ichnotaxa *Strabelocoprus pollardi* of Hunt *et al.* (2012*b*, fig. 4a–d) and *Saurocopros bucklandi* of Hunt *et al.* (2007, fig. 4).
MGUH30366 MGUH30367	28 28	MGUH30366 and MGUH30367 (one–two coils preserved in each) are very loosely coiled. They could, perhaps, be similar to ichnotaxon *Heteropolacopros texaniensis* (Hunt *et al.*, 2005, fig. 2)
H004 H005 H007 H013 H249	24 23.5 25.5 20 25	H004 (<three coils), H005 (>two coils), H007 (>four coils), H013 (unknown coils) and H249 (unknown coils) have diameters of between 23.5 and 25.5 mm. They are cylindrical, with an apparently simple coiled layer. H007 was cut in half in the longitudinal plane and a more complex structure was revealed. The coprolite consists of at least four coils: however, as they are somewhat folded and displaced, they can be difficult to distinguish. The two outer layers do not run the entire length of the coprolite and the specimen appears heteropolar
H008	36	H008 may have been much larger originally as only the posterior spire is preserved. The coprolite is weathered and quite indeterminable
H009	17.5	H009 consists of a simple coil that runs the length of the specimen. The number of coils is uncertain. It has a smooth surface and is shaped like a slightly bent insect pupa. It might be of scroll type (Hunt & Lucas 2012*b*)
H012	16	H012 is very damaged and indeterminable

The specimens are grouped and compared to the literature when possible.

types of coprolites. However, the two types are not distinguishable in features other than their structure. Both are dominated by the three primary massive textures and the entirely nodular texture, although structureless coprolites do not contain all textures (swirly-massive is absent). All fragment sizes are found in specimens of the two structures, and specimens without prey remains are also common in both. The most common shape is cylindrical, and neither the presence of contraction marks nor pinched ends support a distinction between the two types. Furthermore, the structureless appearance of some coprolites may only be due to poor preservation.

Specimens with contraction marks are restricted to diameters of between 11 and 22.5 mm. This spectrum coincides with the most common diameters in the material in general and does not support the establishment of a separate type. The same argument is valid for bent, flattened and pinched specimens. The number of specimens with a recognizable pinched end is not likely to represent an original trend in the material, as most ends are damaged.

Nodular coprolites

Within the irregularly wrapped and structureless coprolites, a sub-type containing nodular textures can be defined (136 specimens). Entirely nodular coprolites (39 specimens) are usually very distinct, as they consist of rounded pellets of up to 6 mm and often have bulbous shapes. These specimens rarely contain fragments (more than 75% of the entirely nodular specimens are fragment-free) and, when they do, the fragments are never larger than 2.5 mm (see Fig. 12). Despite the rarity of fossil fragments in nodular specimens, there is no evidence for a herbivorous origin. X-ray diffraction analyses proved that two completely nodular specimens without fragments (H199 and H228) had mineralogical compositions similar to those found in carnivorous coprolites (e.g. see Edwards 1973). The largest nodules are found in nodular and massive-nodular specimens, which also contain the widest range of nodule sizes. Even though specimens of entirely nodular texture are quite distinct from other coprolites, they cannot be considered an isolated type. For example, H192 consists of a core of nodular texture covered in wraps of swirly texture, but it has a smooth surface that barely reveals the nodular contents. Another specimen, H202, has mistakenly been treated as an entirely nodular coprolite in the analyses though it consists of a nodular core with a thin enveloping wrap of massive material (Figs 5f & 7f, g). Occasionally, pellets are also found as single scattered bodies floating in a coprolite matrix of different texture. It is plausible that the taxon that produced the conspicuous pellet-rich faecal masses also produced faeces of more common textures. Nodular coprolites are part of a spectrum of faecal textures produced by a versatile producer. Composition of diet probably had a significant influence on the resulting faecal texture, especially as nodular coprolites rarely preserve fossil fragments. The pellets are rounded on the surface of the coprolites, but angular where they are stacked tight up against neighbouring pellets, implying that they were soft at production (Fig. 7). Nodular specimens are often preserved as quite small fragments and their structure is often difficult to determine because the pellets obscure this character. It is therefore possible that all nodular specimens are, in fact, of irregularly wrapped structure.

Identification of fossil fragments in coprolites

The coprolites from the Kap Stewart Formation contain fossil fragments of various shapes. The XRD analysis showed that the fragments consist of apatite – a group of minerals commonly found in vertebrate bones, teeth and scales. No attempts were made to free the fragments using acid because acid that is effective against the phosphatic coprolite matrix is likely to also attack the fragments. One coprolite (H313) was mechanically prepared by Werner Schwarzhans and two of the contained fragments were partly uncovered (Fig. 10). The studied fragments included in the Kap Stewart coprolites are difficult to identify, but it is assumed they originate from various Triassic fishes.

The thin rectangular scales that are seen, for instance, in specimen H009 (Fig. 9d) resemble scales depicted by Mutter (2004). These scales (Mutter 2004, fig. 3) have a quadratic to rectangular shape, with one large triangular projection on one side and a minor projection displaced of this on the opposite side. Each scale also has shallow depressions on the surface that fit the projections. When the fish was alive, the scales were arranged in a ‘peg-and-socket’ articulation along its flanks. Mutter (2004) ascribed these scales to *Crenilepis sandbergeri* in the Family Colobodontidae (Order Perleidiformes) that is known from Triassic localities on an almost worldwide scale.

It is difficult to determine the true shapes of the scales bearing a thick black coating, but at least two types are present: thick, quadratic scales with a smooth surface (e.g. H200: Fig. 9e); and rectangular scales with a grooved surface. Mutter (2004, fig. 4) depicts a variety of ganoid ornamentation in Colobodontid scales that resembles that of the grooved type from the Kap Stewart Formation coprolites. The scales, depicted by Mutter (2004), all bear parallel ridges that run across the surface in straight or slightly wavy lines. However, in the present material, these patterns might not be original features but could have formed during erosion of the surfaces, as in *Lepidotes maximus* scales depicted by Jain (1984, fig. 6). *Lepidotes* is a genus belonging in the Family Semionotidae, a group of neopterygian fish that were present throughout most of the Mesozoic. They are very common in western Gondwana, but are found almost worldwide in both marine and freshwater strata (Gallo & Brito 2004). The group is not thoroughly resolved, but the genera *Semionotus* and *Lepidotes* share the same type of simple, convex scales with moderate to well-developed, posteriorly directed spines (McCure 1986). Gallo & Brito (2004) depict thick Semionotid scales from Brazil that are covered by smooth black ganoin layers. The scales attributed to '*Lepidotes*' *oliveirai* (Gallo & Brito 2004, fig. 6) are remarkably similar to scales in the Kap Stewart Formation coprolites. They are quadratic to rectangular, have a concentric built-up, and one corner is sometimes stretched into a spike. Scales of '*Lepidotes*' *dixseptiensis* (Gallo & Brito 2004, fig. 10) are more oblong, with a slightly rhombohedral outline similar to fragments seen, for example, in H029 (Fig. 9c). Rectangular scales with parallel furrows on part of the surface are also present in *Lepidotes* (Gallo & Brito 2004, fig. 4).

The scales found in specimen H075 are smaller compared to the others described above (Fig. 9a). The identification of these scales is difficult, but it is plausible that they originate from a fish of smaller size than the other scales represent. As there are many sizes of fossil vertebrate fragments present in the coprolites of the Kap Stewart Formation, it is plausible that a wide range of fish sizes served as diet for the coprolite producers. The large fossil objects in specimen H313 (Fig. 10) are unusual because they are subtriangular in cross-section, and it was initially hypothesized that they could represent otoliths. However, the XRD analysis revealed the objects to have an apatitic composition. This refutes the otolith interpretation, as otoliths are aragonitic in composition (Campana 1999).

Shark tooth

Based on morphology and age, the tooth described from the Kap Stewart Formation is ascribed to the neoselachian shark *Rhomphaiodon minor* (Cuny & Risnes 2005; Hansen 2014). However, this challenges our present knowledge about either the habitat of this taxon or the depositional environment of the Kap Stewart Formation. In fact, teeth of this type are found in several Rhaetic deposits across NW Europe, but they always appear to be associated with marine environments (e.g. Storrs 1994). In contrast, the Kap Stewart Formation has been interpreted as exclusively lacustrine by multiple authors (e.g. Dam & Surlyk 1992; Clemmensen *et al.* 1998). The northern part of the depositional environment of Jameson Land was, however, initially interpreted as containing marine influences (Clemmensen 1976).

Conclusions

A total of 324 coprolites collected from a black lacustrine shale unit of the Late Triassic (Rhaetian) Kap Stewart Formation at Wood Bjerg, Jameson Land, East Greenland were examined with regard to external and internal morphology, and prey inclusions.

The coprolites from the Kap Stewart Formation are divided into the following types:

- Round to subround coprolites: specimens of this type have maximum diameters restricted to 15–20 mm. They are structureless and of massive texture. They contain fossil fragments of at least 0.5 mm.
- Spiral/coiled coprolites: specimens of spiral or coiled structure have cylindrical to bulbous shapes. They can be as small as 7.5 mm and as large as 48 mm in diameter. The spiral/coiled coprolites consist of massive and swirly textures. Nodules are only present as single, scattered nodules. Spiral/coiled specimens contain numerous fossil fragments of various sizes. They always contain mineral grains but these are never larger than 1 mm. The spiral/coiled coprolites can be subdivided based on size and type of coiling. Coprotaxa that are possibly represented are *Strabelocoprus pollardi*, *Saurocopros bucklandi* and *Heteropolacopros texaniensis*.
- Irregularly wrapped and structureless coprolites: many specimens are cylindrical to bulbous and consist of either wrapped or structureless material. Because of the high level of weathering, the two structures cannot be clearly separated.
- Nodular coprolites: within the irregularly wrapped coprolites, a subtype containing nodular texture is found. These coprolites present a spectrum of textures containing few to many nodules. In the end member that consists entirely of nodules, the nodules are large and shaped like pellets. These specimens rarely contain fossil fragments. The nodular textures have not previously been described in coprolites.

Fossil food remains within coprolites are identified as scales from actinopterygian fish – possibly related to Semionotids or Perleidiforms cf. Colobodontidae. A single shark tooth found alongside the coprolites was identified as belonging to cf. *Rhomphaiodon minor*, this is the first record of *R. minor* from the Late Triassic of East Greenland.

The diversity of sizes, shapes, and external and internal structures in the studied material demonstrates a coprolite assemblage originating from multiple faecal sources, where many are evidently carnivores.

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